



Occurrence of false killer whales (*Pseudorca crassidens*) and their association with common bottlenose dolphins (*Tursiops truncatus*) off northeastern New Zealand

JOCHEN R. ZAESCHMAR,¹ Coastal-Marine Research Group, Institute of Natural and Mathematical Sciences, Massey University, Private Bag 102904, North Shore, Auckland 0745, New Zealand; INGRID N. VISSER, Orca Research Trust, PO Box 402043, Tutukaka 0153, New Zealand; DAGMAR FERTL, Ziphius EcoServices, 8112 Springmoss Drive, Plano, Texas 75025, U.S.A.; SARAH L. DWYER and ANNA M. MEISSNER, Coastal-Marine Research Group, Institute of Natural and Mathematical Sciences, Massey University, Private Bag 102904, North Shore, Auckland 0745, New Zealand; JOANNE HALLIDAY, 6 Kennedy Street, Opua 0200, Bay of Islands, New Zealand; JO BERGHAN, 4 Access Road, Kerikeri 0230, Bay of Islands, New Zealand; DAVID DONNELLY, Australian Marine Ecology, 82 Parsons Street, Kensington, Victoria 3031, Australia; KAREN A. STOCKIN, Coastal-Marine Research Group, Institute of Natural and Mathematical Sciences, Massey University, Private Bag 102904, North Shore, Auckland 0745, New Zealand.

ABSTRACT

On a global scale, false killer whales (*Pseudorca crassidens*) remain one of the lesser-known delphinids. The occurrence, site fidelity, association patterns, and presence/absence of foraging in waters off northeastern New Zealand are examined from records collected between 1995 and 2012. The species was rarely encountered; however, of the 61 distinctive, photo-identified individuals, 88.5% were resighted, with resightings up to 7 yr after initial identification, and movements as far as 650 km documented. Group sizes ranged from 20 to *ca.* 150. Results indicate that all individuals are linked in a single social network. Most observations were recorded in shallow (<100 m) nearshore waters. Occurrence in these continental shelf waters is likely seasonal, coinciding with the shoreward flooding of a warm current. During 91.5% of encounters, close interspecific associations with common bottlenose dolphins (*Tursiops truncatus*) were observed. Photo-identification reveals repeat inter- and intraspecific associations among individuals with 34.2% of common bottlenose dolphins resighted together with false killer whales over 1,832 d. While foraging was observed during 39.5% of mixed-species encounters, results suggest that social and antipredatory factors may also play a role in the formation of these mixed-species groups.

Key words: false killer whale, *Pseudorca crassidens*, bottlenose dolphin, *Tursiops truncatus*, mixed-species groups, interspecific associations, photo-identification, foraging, seasonality, New Zealand.

¹Corresponding author (e-mail: jzaeschmar@hotmail.com).

Very little is known of free-ranging false killer whales (*Pseudorca crassidens*) (Baird *et al.* 2008). Despite a worldwide distribution in tropical and warm temperate waters, this species is encountered infrequently in most locales where they occur (Odell and McClune 1999). Occurrence in most areas is primarily inferred from stranding records (Stacey *et al.* 1994), including for New Zealand (*e.g.*, Hector 1872, New Zealand Marine Mammal Stranding Database²). While mostly oceanic in distribution, false killer whales are known to venture close to shore at oceanic islands (Acevedo-Gutiérrez *et al.* 1997, Garrigue and Greaves 2001, Gannier 2002) and are observed occasionally in shallow continental shelf waters (Palmer *et al.* 2009). High site fidelity has been documented in some areas (Baird *et al.* 2008). Although cases of long-distance travel (Tomilin 1957, Leatherwood *et al.* 1989) and seasonal occurrence (Kasuya 1985) are reported, it is not clear if, or to what extent, populations of the species migrate.

Described as gregarious, false killer whales typically travel in groups of 20–100 animals (Baird 2008). Long-term associations between individuals have been recorded off Hawaii (Baird *et al.* 2008) and Costa Rica (Acevedo-Gutiérrez *et al.* 1997), with stable social clusters that differ in home range identified within the Hawaiian insular population (Baird *et al.* 2012). However, little is known about the species' overall social structure from other regions. There have been a number of mass and single strandings of false killer whales in New Zealand. Based on the number of stranded individuals, false killer whales rank second only to pilot whales (*Globicephala* spp.) within New Zealand waters (New Zealand Marine Mammal Stranding Database). Despite this prominent stranding history, few data or specimens have been collected from these events and data collected from free-ranging individuals are limited and primarily anecdotal (Gaskin 1972, Cawthorn 1981). The species is currently listed as *Not Threatened* within New Zealand waters, although confidence in the assessment is low due to poor data availability (Baker *et al.* 2010).

False killer whales have also been observed in nonaggressive associations with several other cetacean species (*e.g.*, Leatherwood *et al.* 1989), in particular with the common bottlenose dolphin (*Tursiops truncatus*) (*e.g.*, Best and Reeb 2010, Visser *et al.* 2010, Zaeschmar *et al.* 2013). While increased foraging success and predator detection and/or avoidance are suggested as possible factors in the formation of these mixed-species groups (Zaeschmar *et al.* 2013), the exact nature and extent of such interactions remain unclear.

The present study documents the occurrence and association patterns of false killer whales in the waters off northeastern New Zealand, taking into account seasonality, group size, and composition. Hypotheses for seasonality and population size and structure are provided. *Ad libitum* behavioral observations, focusing on the presence or absence of foraging are also discussed to further elucidate false killer whale use of the study area. Additionally, the study describes false killer whale interactions with common bottlenose dolphins, and provides hypotheses as to the nature and extent of such associations.

MATERIALS AND METHODS

All sightings were collected in five locations along an approximate 650 km stretch of the northeastern coast of New Zealand, between February 1995 and March 2012.

²New Zealand Marine Mammal Stranding Database, Museum of New Zealand Te Papa Tongarewa, % Department of Conservation, PO Box 10420 Wellington, New Zealand.

The study area is influenced by the shoreward progression of the warm, southeastward flowing East Auckland Current (EAUC) during December and its subsequent departure around May (Zeldis *et al.* 2004). The EAUC carries warm subtropical water (Sutton and Roemmich 2001) as well as associated marine fauna (Francis *et al.* 1999) into the study area. Sea surface temperature (SST) reaches 23°C during the austral summer and falls to 15°C in winter (Chiswell 1994). Records of false killer whales were primarily collected in waters off, or adjacent to, the Bay of Islands (BOI), (approximate position 35°S, 174°E), between February 1995 and March 2012. The area is characterized by a number of features; approximately 150 islands and islets with numerous bays and estuaries, and the Cape Brett peninsula, which intersects the warm EAUC, providing a large catchment area for nutrients (Baker and Madon 2007). Water depth between the islands and the mainland is generally <20 m while on the seaward side, water depth ranges from 50 to 120 m. The edge of the continental shelf is *ca.* 50 km to the northeast of Cape Brett.

Additional records of false killer whales were collated from the following four areas:

- (1) The Three Kings Islands (TKI) 2008, (approximate position 34°09'S, 172°08'E). Located 55 km northwest of New Zealand's North Island, situated near the continental shelf break, the area is characterized by submarine canyons and seamounts, with water depths generally ranging from 100 to >1,600 m.
- (2) The Poor Knights Islands (PKI) 2010, 2012, (approximate position 35°28'S, 174°44'E). Located 19 km off the New Zealand's northeastern coast, these small islands (271 ha) are volcanic remnants that rise steeply from the otherwise flat ocean floor. Water depth in the area ranges from *ca.* 80 to >150 m.
- (3) The Hauraki Gulf (HG) 2011, (approximate position 36°10'–37°10'S, 174°40'–175°30'E) is a shallow (<60 m), semi-enclosed body of temperate water. The seabed in the area is predominantly flat.
- (4) The Bay of Plenty (BOP) 2012, (approximate position 36°30'–38°10'S, 175°40'–178°00'E) is a large open embayment with a generally flat seabed, containing a small number of islands. The shoreward flow of the EAUC ceases around East Cape, the southern limit of BOP, with the current turning away from the coast (Stanton *et al.* 1997). Water depth in the area ranges from 50 to >200 m.

The majority of records (53.2%) were collected from the *Tutunui*, an 11 m fiberglass catamaran powered by twin 350 hp jet engines, with a cruising speed of approximately 30 km/h and an observer's eye height of 3 m above sea level. *Tutunui* is a commercial whale watching vessel staffed by experienced marine mammal observers that operates year round in BOI, although trips are more frequent between October and May. Additional records were collected from tour boats (*ca.* 11–22 m with 3–5 m observer eye height and travel speed of 15–35 km/h) and research vessels (*ca.* 5–6 m, observer eye height 2–3 m and survey speed of *ca.* 20 km/h) operating in the five study locations. Tour vessels encountered false killer whales opportunistically during wildlife/marine tours throughout the study area, while the research vessels encountered false killer whales during dedicated cetacean surveys. All vessels followed a similar, asystematic survey methodology which was dictated by factors such as prevailing weather conditions. Depth was determined by plotting the GPS coordinates of the sighting locations on the relevant bathymetric chart while distance from shore was measured by plotting sighting locations in ESRI ArcGIS version 9.3. Sea surface temperature (SST) was determined using onboard thermometers.

Ad libitum behavioral observations (Altmann 1974), focusing only on the presence or absence of foraging behaviors were recorded in transcript, audio log (dictaphone), or video form. Following Acevedo-Gutiérrez *et al.* (1997), foraging was defined by frequent, asynchronous dives with subgroups dispersing over larger areas, as well as by the presence of fish near the surface or sea birds feeding on fish remains near the whales. Prey species were confirmed by photographic record. As most of the observation platforms did not operate in the respective locations on a year round basis, seasonal occurrence was assessed from the records of *Tutumui*, which ran continuous trips up to twice daily in BOI between 1995 and 2007. Following Wiseman *et al.* (2011), a monthly index of false killer whale encounters was determined using a trip encounter rate (TER), which was calculated from the number of trips on which whales were encountered in proportion to the total number of trips undertaken that month. Results for each month from different years were pooled and calculated as an average sighting rate per 100 trips. To avoid pseudo-replication, only one sighting record per day was included in the analysis. A social network diagram of false killer whales photo-identified in the study area was produced using the program Netdraw 2.123.³ A spring embedded layout was chosen, placing more connected nodes at the center of the network while those with fewer connections were placed around the periphery. To test for the significance of encounter duration and presence/absence of foraging on group size estimates, a General Linear Model (GLM) with a negative binomial model approach was applied. All analyses were completed in R using the “Stats” (R Core Development Team⁴) and “Mass” (Venables and Ripley 2002) packages.

Following Baird *et al.* (2008) it was assumed that all false killer whales occurring in the area at any one time were part of the same group. This definition is supported by the infrequency of false killer whale encounters in the study area and the fact that false killer whales may at times disperse >20 km and still be moving in the same direction and engaged in the same behavior (Baird *et al.* 2008). Consequently, no spatial parameters were placed on group definitions. Given the frequency of association between false killer whales and bottlenose dolphins, for the purpose of this study, the term mixed-species group refers to associations between these two species only. Following Shane (1990), a mixed-species group was defined as any number of individuals of one species observed in apparent association with the other species and generally moving in the same direction and engaged in similar behavior (Fig. 1).

As the majority of observations described herein were of large, dispersed groups containing more than one cetacean species and recorded by several observers, group size estimates may be biased upwards. To address this possible bias, estimates were treated as pertaining to maximum group size, and in cases where minimum, best, and maximum group size estimates were available, the maximum estimate was used.

Two forms (coastal and oceanic) of the common bottlenose dolphin frequent New Zealand waters (Baker *et al.* 2010). The oceanic form is readily distinguishable based on gross morphology (Visser *et al.* 2010); they are comparatively more robust and typically exhibit wounds and scars, presumed to be inflicted by the cookie cutter shark (*Isistius* spp.) (Dwyer and Visser 2011). In contrast, the New Zealand coastal form does not usually exhibit cookie cutter shark scarring (Visser *et al.* 2010). The

³Borgatti, S. P., 2002. NetDraw software for network visualization. Analytic Technologies, Lexington, KY. Available at <http://analytictech.com/Netdraw>.

⁴R Core Development Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.



Figure 1. A mixed-species group of false killer whales and common bottlenose dolphins. Bay of Islands, New Zealand, January 2007. Photo: David Hall.

form of common bottlenose dolphin observed in association with false killer whales was determined from photographs and/or video footage of the respective encounters.

Standard photo-identification methods (Würsig and Jefferson 1990, Baird *et al.* 2008) were applied to identify individuals (Table 1). A *capture* was defined as one or more useable images of an individual taken on an independent day. Primary identification features included notches on or adjacent to the dorsal fin and permanent distinguishing features such as dorsal fin disfigurement. Secondary features included scars as well as fresh subdermal wounds such as those presumed to be the result of cookie cutter shark bites. Only primary features were used to confirm matches, with secondary features used only as an aid to identification. Individuals, as well as images, were graded according to the likelihood of successful recapture and matching. The quality of each image was assessed by its focus, contrast and the angle of the fin relative to the frame and graded on a scale of 1 to 4 with 1 being *excellent*, 2 being *good*, 3 being *fair*, and 4 being *poor* (Table 1). The distinctiveness of each dorsal fin was graded on a scale of 1 to 4 with 1 being *very distinctive*, 2 being *distinctive*, 3 being *slightly distinctive*, and 4 being *not distinctive* (Table 1). Only *distinctive* and *very distinctive* individuals and images of *good* or *excellent* quality were included in the analysis. Each new image was carefully examined and all matches were confirmed by at least two experienced matchers. Successful photo-identifications were entered into the New Zealand False Killer Whale Identification Catalogue (NZFKWC; JRZ, unpublished data⁵), and New Zealand Oceanic Bottlenose Dolphin Identification Catalogue (NZOBDC; JRZ, unpublished data), respectively.

RESULTS

Forty-seven sightings of false killer whales were recorded between 1995 and 2012. The majority of observations (33 of 47; 70.2%) were made in BOI (2005, 2007, 2009, and 2010, with no false killer whales encountered in 2006, 2008, 2011, or 2012), with additional records from TKI (2008) (10.6%, $n = 5$), BOP (2009, 2012) (10.6%, $n = 5$), HG (2011) (4.2%, $n = 2$) and PKI (2010, 2011) (4.2%, $n = 2$). The majority

⁵Both catalogs are curated by the senior author.

Table 1. Grading system and assessment criteria applied for determining image quality and dorsal fin distinctiveness used for photo-identification. The quality of each image was assessed by its focus, contrast and angle of the fin relative to the frame. Only images of *good* or *excellent* quality of *distinctive* and *very distinctive* individuals were included in the analysis.

Image quality grading	Assessment criteria
1 (<i>excellent</i>)	All quality criteria are met: sharp focus with clear contrast and taken at an angle that allowed a clear profile of the dorsal fin's leading edge.
2 (<i>good</i>)	One of the quality criteria was compromised but the information content remained intact, allowing for the identification of <i>distinctive</i> and <i>very distinctive</i> individuals.
3 (<i>fair</i>)	Two or more quality criteria were compromised allowing only for identification of <i>very distinctive</i> individuals.
4 (<i>poor</i>)	One or more quality criteria were compromised to the point that successful identification of the individual was not possible.

Dorsal fin distinctiveness	Assessment criteria
1 (<i>very distinctive</i>)	Multiple notches including large notches and could be identified from photos of all quality categories except <i>poor</i> .
2 (<i>distinctive</i>)	Multiple notches and could be identified from <i>fair</i> , <i>good</i> and <i>excellent</i> photographs.
3 (<i>slightly distinctive</i>)	Few notches and could only be identified from <i>good</i> or <i>excellent</i> photographs.
4 (<i>not distinctive</i>)	Clean fins (<i>i.e.</i> , no notches or other permanent distinguishing features) or showed notches that could only be seen in <i>excellent</i> images within an encounter but unlikely between encounters.

of sightings comprised of mixed-species groups (91.5%, $n = 43$). Encounter duration ranged from 10 min to 3 h 45 min ($n = 47$, $\bar{x} = 68.9$, $SD = 49.2$). False killer whales were rarely encountered. Records collected aboard *Tutunui* in BOI show 29 sightings during 6,108 trips on 4,082 discrete days between 1995 and 2007, resulting in an overall TER of 0.47 encounters per 100 trips. Sightings only occurred during the austral summer (December–February) (TER = 0.37, $n = 8$) and autumn (March–May) (TER = 1.33, $n = 21$) with TER highest in March (TER = 2.04, $n = 12$) and April (TER = 1.98, $n = 10$) (Fig. 2). False killer whales were encountered in SST ranging between 18°C and 23°C ($n = 47$, $\bar{x} = 20.5$ °C, $SD = 1.3$) (Fig. 2). Bottom depth for the sightings ranged from 25 to 350 m ($n = 47$, $\bar{x} = 105.3$ m, $SD = 86.7$) with 63.8% of encounters (30 of 47) occurring in waters <100 m deep. Distance from shore ranged from 0.2 to 67.4 km ($n = 47$, $\bar{x} = 9.2$, $SD = 14.8$).

Mixed-species group sizes ranged from 28 to *ca.* 400 ($n = 43$, $\bar{x} = 120.4$, $SD = 64.6$). Within those mixed-species groups ($n = 43$), species-specific group size estimates were made during 76.6% of encounters (36 of 47), with group size for false killer whales ranging from 20 to 150 individuals ($\bar{x} = 46.7$, $SD = 28.5$). Group size estimates for false killer whales observed in single-species groups ranged from 20 to 50 individuals ($n = 4$, $\bar{x} = 35$, $SD = 12.9$).

Between 2005 and 2012, *good* or *excellent* images of false killer whale dorsal fins were obtained during 15 encounters (BOI = 7; BOP = 3; TKI = 2; HG = 2; PKI = 1).

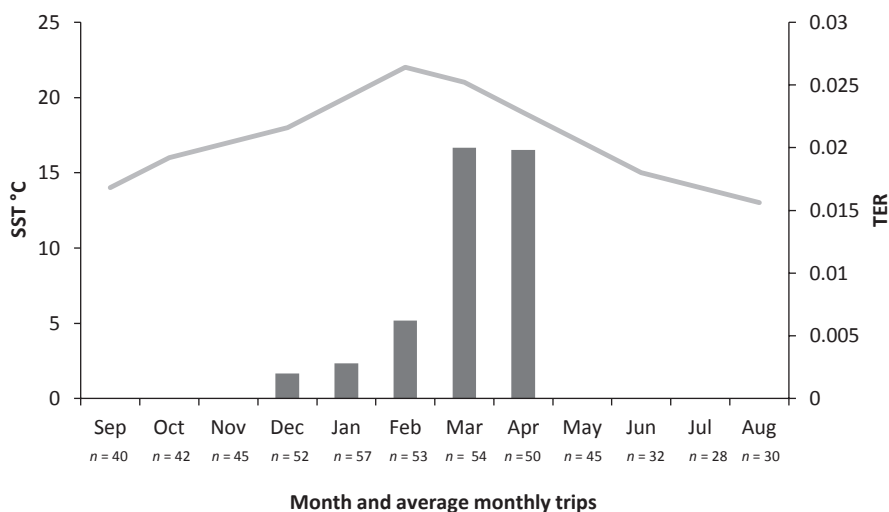


Figure 2. Mean monthly sea surface temperature (SST) and trip encounter rate (TER) of false killer whales in the Bay of Islands, January 1995–June 2007.

A total of 79 individuals were identified, 22.8% of which ($n = 18$) were considered *slightly distinctive* resulting in 61 *distinctive* or *very distinctive* individuals included in the analysis. Using only *good* and *excellent* quality photographs, 226 identifications of these 61 individuals were made ($\bar{x} = 3.7$, $SD = 2.1$). The number of individuals identified in each encounter ranged from 1 to 41 whales ($n = 15$, $\bar{x} = 14.7$, $SD = 11.1$), while the mean group size for encounters with identified individuals was 49 ($SD = 31.6$). Fifty-four individuals (88.5%) were resighted, with 70.5% ($n = 43$) encountered on three or more occasions and two individuals observed on eight occasions. Additionally, 85.2% ($n = 52$) were observed in more than one year and 62.2% ($n = 38$) were encountered in more than one of the five sighting locations within the study area. The longest time-frame between initial identification of an individual and its most recent resighting (disregarding sightings in between) was 2,551 d (approximately 7 yr, $n = 2$). The shortest time frame between any two resightings of an individual was 5 d ($n = 4$). Distances between sighting locations ranged from <1 km (BOI, $n = 29$, 1074 d) to ca. 650 km (TKI–BOP, $n = 8$, 284 d). Overall, the proportion of new identifications decreased as the rate of resightings increased (Fig. 3). While every encounter after the initial observation included previously cataloged individuals, previously unidentified individuals were only captured during 53.3% of encounters ($n = 8$). The highest number of resightings between any two encounters was 29 individuals (January 2007 and December 2009, both BOI). All individuals photo-identified were linked by association in one large social network albeit separated into two social clusters (Fig. 4). Fresh subdermal wounds and scars presumed to be inflicted by cookie cutter sharks were observed on individuals during all encounters.

During 91.5% ($n = 43$) of encounters, false killer whales were observed in association with bottlenose dolphins with *good* or *excellent* quality photo-identification images obtained from nine encounters. The two species were considered mixed-species groups as individuals of both species were interspersed or in close association and generally acted as one homogenous group (Fig. 1). Based on the presence of cookie cutter shark scars on individuals, reported during all 43 encounters and

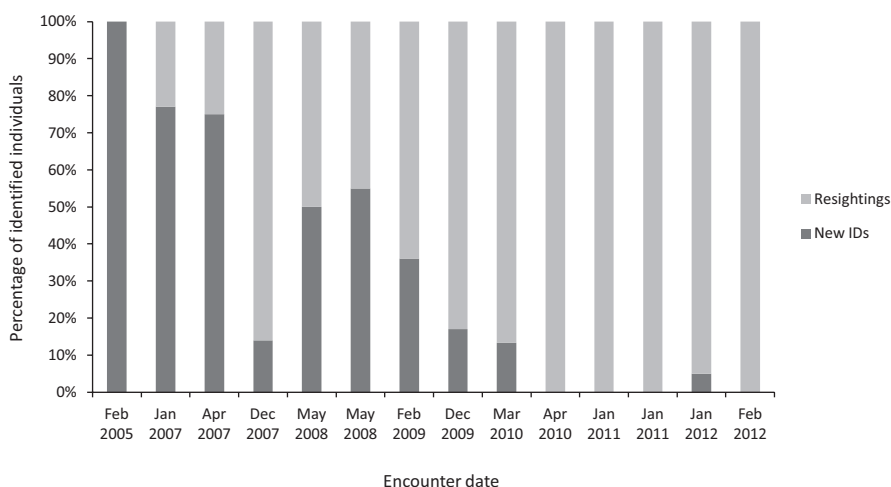


Figure 3. Percentages of newly (New IDs) and previously (Resightings) photo-identified false killer whales per encounter. Recorded off northeastern New Zealand between 2005 and 2012.

photographed during 15 encounters, bottlenose dolphins identified in association with false killer whales were presumed to be of the oceanic form. Group size for bottlenose dolphins were estimated during 36 encounters and ranged from 5 to *ca.* 250 individuals ($n = 36$, $\bar{x} = 62.8$, $SD = 42.8$). Using the same parameters as for false killer whales, 163 individuals were photo-identified, 8.6% ($n = 14$) of which were classified as *slightly distinctive* and not included in the analysis, resulting in 217 identifications of 149 *distinctive* or *very distinctive* individuals ($\bar{x} = 1.45$). Of these, 34.2% ($n = 51$) were resighted, with 10.1% ($n = 15$) observed on three or more occasions and two individuals (1.3%) on four occasions. Additionally, 28.2% ($n = 42$) were encountered in more than one year and 18.1% ($n = 27$) were observed in more than one of the five sighting locations within the study area. The longest time between first identification of an individual and its most recent resighting was 1,832 d (*ca.* 5 yr) documented for two individuals. Distances between sighting locations ranged from <1 km (BOI, $n = 14$, 1,074 d) to *ca.* 650 km (TKI–BOP, $n = 1,284$ d). The number of dolphins identified in each encounter ranged from 1 to 54 individuals ($n = 149$, $\bar{x} = 24.1$, $SD = 16.5$). Every encounter included previously photo-identified individuals. The highest number of resightings between any two encounters was 13 individuals. At least 34.2% of bottlenose dolphins ($n = 51$) had repeat associations with false killer whales involving 41 individuals (67.2%). Of these, 10.1% of bottlenose dolphins ($n = 15$) and 59% of false killer whales ($n = 36$) were re-encountered together on three or more occasions and during more than one year, with 8% of dolphins ($n = 12$) and 45.9% of whales ($n = 28$) observed together on three or more occasions as well as in different years and locations. Spatial separation/dispersion of individuals varied, ranging from all individuals being in close proximity (total area <1 km²) to wide distribution of individuals and subgroups within the whole mixed-species group (total area estimated at >5 km²). During all encounters, the two species were generally behaving as a single group, swimming within a body length of the other species (Fig. 1). However, clear segregation into conspecific subgroups within the primary group was also observed.

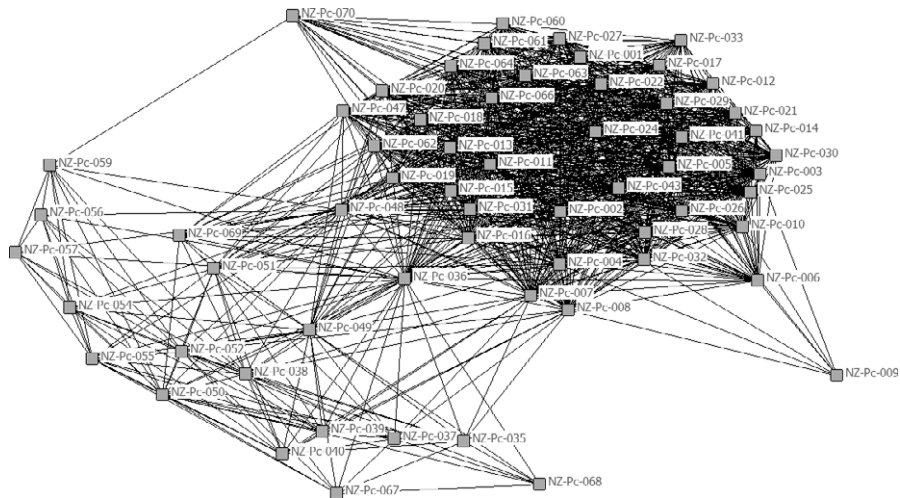


Figure 4. Social network diagram of 61 *distinctive* or *very distinctive* false killer whales photo-identified off northeastern New Zealand during 15 encounters between 2005 and 2012 using a spring embedded layout. Individual false killer whales with their corresponding catalog number are represented by nodes. Only individuals with *good* or *excellent* quality photos are included.

Note: Clustering suggests the existence of two social clusters.

Foraging was observed during 42.6% of all encounters ($n = 20$) and during three of the four single-species observations of false killer whales. Within the mixed-species observations ($n = 43$), foraging by at least one of the two species was observed during 39.5% ($n = 17$) of encounters. Mixed-species groups involved in foraging were generally larger ($n = 17$, $\bar{x} = 135.8$, $SD = 92.9$) than those groups where foraging was not observed ($n = 26$, $\bar{x} = 112.5$, $SD = 57.1$). However, encounters where foraging was observed were generally longer ($n = 20$, $\bar{x} = 82.5$, $SD = 55.4$) than those where it was not detected ($n = 27$, $\bar{x} = 58.9$, $SD = 42.3$). A negative binomial regression found no evidence that encounter duration ($P = 0.994$) and foraging behavior ($P = 0.420$) had any significant effect on group size estimates (Table 2). Evaluation of residuals found the assumption for homogeneous variance and normal distribution of residuals to be met and the P -value was considered reliable. Kahawai (*Arripis trutta*) was confirmed as a prey species for false killer whales and bottlenose dolphins on six occasions (BOI $n = 3$, HG $n = 2$, BOP $n = 1$). False killer whales were observed feeding on hapuku (*Polyprion oxygeneios*) during one mixed-species encounter (TKI).

DISCUSSION

Here we provide the first investigation of false killer whale occurrence in New Zealand waters. To our knowledge, only three other photo-identification studies have been conducted on the species worldwide: a dedicated, species-specific study currently examining distribution, social structure, home ranges, and genetic differentiation off Hawaii (Baird *et al.* 2010), a study resulting from cetacean surveys off Gabon and Côte d'Ivoire (Weir *et al.* 2013), and a previous study off Costa Rica (Acevedo-

Table 2. Negative binomial regression investigating potential predictors of false killer whale group size estimates. Model: $NB_{\text{Group Size Estimate}} = \alpha + \beta_{\text{Encounter Duration}} + \beta_{\text{Foraging Behavior}} + \varepsilon$.

Parameter	Estimate	Standard error	Z-value	Pr(> z)
Intercept	4.782000	0.135800	35.212	<0.001
Encounter duration	-0.000012	0.001593	-0.007	0.994
Foraging behavior	0.113030	0.161600	0.806	0.420
Null deviance: 45.216 on 42 degrees of freedom				
Residual deviance: 44.496 on 40 degrees of freedom				

Gutiérrez *et al.* 1997), which examined false killer whale occurrence as part of a broader three year study on dolphin ecology.

Despite their reported pelagic distribution (Wade and Gerrodette 1993, Baird 2008), false killer whales are known to approach close to shore at oceanic islands (Baird *et al.* 2010), with forays into shallow continental shelf waters also reported (Acevedo-Gutiérrez *et al.* 1997, Palmer *et al.* 2009, Zaeschmar *et al.* 2013). However, the latter are thought to be uncommon (Baird *et al.* 2008). Our data reveal repeat occurrence by individuals well within the continental shelf and in waters of less than 100 m in bottom depth. However, the extremely low encounter rate in the study area indicates that the species' distribution in New Zealand waters is likely also centered further offshore. The observed scars, presumed to be the result of cookie cutter shark bites, may provide further indication of false killer whale distribution in the area. Cookie cutter sharks typically occur in deep, tropical and temperate waters (Jones 1971, Jahn and Haedrich 1988) and their bite marks have been used as indicators to differentiate between cetacean populations (Dwyer and Visser 2011). The cookie cutter scars observed on both false killer whales and bottlenose dolphins suggest a potential distribution centered in warmer pelagic waters, which is consistent with the distribution generally reported for false killer whales (Baird 2008). Consequently, false killer whales encountered in the study area are likely to frequent deep oceanic waters as well as the shallow continental shelf region in which most of our observations were made.

While seasonality could only be assessed from records in BOI, all encounters from the different locations within the study area fall within the same period (December–May), further supporting the suggestion that occurrence in nearshore waters is seasonal. Changes in seasonal occurrence have been reported from Japanese waters (Kasuya 1971) and movements of false killer whales have been linked with warm water masses and migrations of prey (Tomilin 1957, Kasuya 1971, Leatherwood *et al.* 1989). Similarly, false killer whale occurrence in the study area coincides with the seasonal flow of the EAUC, a warm current that begins its shoreward progression towards northeastern New Zealand in December and completes its annual cycle by May (Zeldis *et al.* 2004). SST within the EAUC is approximately 2°C warmer than on the continental shelf (Sharples 1997) (Fig. 2). This current is associated with the arrival of warm water species such as various *Thunnus* and *Istiophoridae* species (Francis *et al.* 1999), the latter two being known prey items for false killer whales (Baird 2008). Our findings support the hypothesis that the seasonal occurrence of false killer whales in the study area may be the result of the species following the shoreward flow of the EAUC presumably in pursuit of prey, as has also been suggested for other regions (Tomilin 1957, Kasuya 1971, Leatherwood *et al.* 1989).

The observations of predation on kahawai, a schooling coastal species endemic to areas within temperate Australasian waters (Paulin 1993), has previously been

described in the study area (Zaeschar *et al.* 2013), but have so far not been documented from other regions. Additionally, individual false killer whales observed to be feeding on coastal fish species were also observed to be feeding on hapuku in off-shore waters. Predation on hapuku, a large demersal fish, inhabiting deep waters off the continental slope (Beentjes and Francis 1999), is more consistent with the feeding ecology reported for false killer whales from other regions (Odell and McClune 1999). These findings further support the suggestion that this population frequents both in- and offshore waters in New Zealand. The larger group sizes recorded during foraging observations may be the result of groups contracting when abundant prey is encountered. Indeed, satellite tagging in Hawaiian waters revealed that groups may disperse over more than 20 km (Baird *et al.* 2010).

All individuals photo-identified in the study area so far, are linked in a single social network and results suggest the existence of two social clusters within this social network, similar to the clustered social structure identified within the Hawaiian insular false killer whale population (Baird *et al.* 2012). However, given the likelihood that not all individuals were photo-identified in some of the encounters, the apparent clustering may result from incomplete capture of all individuals present in the groups observed. While the exact extent of this network remains unknown, it is certainly larger than the 79 identified individuals since nondistinctive individuals were present during all encounters, with maximum group size estimates during some encounters estimated to be as high as 150 individuals. These group size estimates are in sharp contrast to the actual number of individuals identified in each encounter. Possible explanations are that only certain individuals allow close enough approaches to observation vessels for successful capture or that group size estimates are biased upwards. Observer bias has to be considered when estimating the size of large mixed-species groups distributed over several square kilometers. The fact that group size estimates of false killer whales in single-species groups were considerably lower than those in mixed-species groups supports the likelihood of upward observer bias. However, false killer whale social networks can include hundreds of individuals, as is evidenced by mass stranding events, both in New Zealand (Baker 1981) and elsewhere (Ferreira 2008), suggesting that networks of this size also occur in New Zealand waters. It is worth noting that the rate of new identifications generally decreased over the course of the encounters described herein and that during some encounters no “new” individuals were identified at all. While false killer whales may initially appear to be infrequent visitors within New Zealand waters, photo-identification data presented here suggest recurrent use of the study area by a number of individuals and a level of site fidelity higher than generally assumed. Known individuals exhibited evidence of long-term associations, in many cases lasting years and spanning hundreds of kilometers. These findings are consistent with photo-identification from Hawaii (Baird *et al.* 2008) and Costa Rica (Acevedo-Gutiérrez *et al.* 1997). This, together with the high resighting rate over more than 7 yr, suggests a relatively small number of individuals with a reasonably high degree of site fidelity, albeit with a strong seasonal component, occurring in the study area. Further data are needed to ascertain if these individuals constitute a low-numbered, closed local population or form part of a larger, wide ranging metapopulation. Genetic sampling of the species in Hawaiian waters shows that individuals with high site fidelity form part of a closed population with a limited home range (Chivers *et al.* 2007, Baird *et al.* 2012).

The extremely high frequency of associations with bottlenose dolphins in the study area, including repeat associations between individual false killer whales and bottlenose dolphins spanning more than 5 yr and up to 650 km, suggests that such

associations are not random. False killer whales are known to associate with other delphinids and have been observed in close, nonaggressive association with a number of cetacean species (e.g., Leatherwood *et al.* 1989, Baird *et al.* 2008), in particular the bottlenose dolphin (Mizue and Yoshida, 1961, Tsutsumi *et al.* 1961, Zhou *et al.* 1982, Leatherwood *et al.* 1989, Scott and Chivers 1990, Flores *et al.* 2003, Anderson 2005, Maze-Foley and Mullin 2006, Baird *et al.* 2008, Best and Reeb 2010, Zaeschmar *et al.* 2013). However, although bottlenose dolphin and false killer whale associations are reported previously in the literature and are considered relatively common (Reeves *et al.* 2002), very few studies have so far attempted to elucidate the possible extent and function of these associations (Zaeschmar *et al.* 2013). Associations (of any duration) between cetaceans are often linked to prey occurrence (Bearzi 2005). Indeed, apparent cooperation by false killer whales and bottlenose dolphins during foraging on large schools of prey has previously been reported within the study area (Zaeschmar *et al.* 2013) and has also been observed on several occasions during the present study. However, based on these observations alone, parasitism by one of the two species cannot be excluded. As foraging observations increased with encounter duration, it is likely that joint foraging is more prevalent than is currently being observed. However, the fact that foraging was not seen during many of the mixed-species encounters also suggests that additional factors may influence these associations. Standard group benefits such as increased predator detection and avoidance (Norris and Schilt 1988, Stensland *et al.* 2003, Kiszka *et al.* 2011) likely also apply. Indeed, predation by killer whales (*Orcinus orca*), for both false killer whales and bottlenose dolphins, is a *bona fide* risk in New Zealand waters (Visser 1999, Visser *et al.* 2010). Additionally, social factors may play a role and have been suggested as the driving factor behind some mixed-species associations (Bearzi 1997, Baraff and Asmutis-Silvia 1998). While results provide basis for the hypothesis that increased foraging success may be a contributing factor in the apparent stable nature of these associations, more data are required to ascertain the exact nature and function of their formation.

We have illustrated that false killer whales observed in coastal waters of northeastern New Zealand show long-term site fidelity to the region despite a strong seasonal peak in occurrence. All individuals indentified so far are linked by association in one single social network, with repeat associations between individuals documented. Individuals were encountered in shallow coastal as well as deeper offshore waters, with occurrence close to shore possibly linked to the seasonal shoreward flooding of a warm ocean current. While further data are required to elucidate questions regarding population size and home range, a small local and possibly closed population cannot be ruled out. It is also evident that false killer whale associations with bottlenose dolphins are far from random in these waters. Our findings highlight the importance of long-term data collection and strongly support the need for dedicated research to be conducted on the species in New Zealand waters. Given these findings, a reassessment of the current conservation status in New Zealand may also be prudent.

ACKNOWLEDGMENTS

We would like to thank Great Sights Fullers Bay of Islands for allowing access to their historic whale watch records; the crew of the *Tutunui*, in particular Tammy Johnston; Rob Hunt from Explore Images, Sue Hews from Magic Memories, and Stuart Arnold and Rosie Roess from Dolphin Seafaris for access to many photographs; Elke Reufels (Department of Conserva-

tion) for permit assistance, and Emmanuelle Martinez and Jens Currie (Pacific Whale Foundation) for statistical input. The following people supplied additional photographs: John Allan, Alex Black, Robert Bradley, Tom Brough, Sonja Clemens, Mandy Everett, Sarah Gardner, Margaret Ginnelly, Cathy Goeldner, Monica Greco, David Hall, Tommy Hatwell, Lara Kay, Lily Kozmian-Ledward, Gemma Langsdale, Karin Neumann, Daniel Panek, Taira Peters, Richard Robinson, Jean Paul Rouen, and Nathan Turner. Robin Baird, Marta Guerra, and Tom Brough provided helpful comments on earlier versions of this manuscript.

LITERATURE CITED

- Acevedo-Gutiérrez, A., B. J. Brennan, P. Rodriguez and M. Thomas. 1997. Resightings and behavior of false killer whales (*Pseudorca crassidens*) in Costa Rica. *Marine Mammal Science* 13:307–314.
- Altmann, J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49:227–267.
- Anderson, R. C. 2005. Observations of cetaceans in the Maldives, 1990–2002. *Journal of Cetacean Research and Management* 7:119–135.
- Baird, R. W. 2008. False killer whale *Pseudorca crassidens*. Pages 405–406 in W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. *Encyclopedia of marine mammals*, 2nd ed. Academic Press, San Diego, CA.
- Baird, R. W., A. M. Gorgone, D. J. McSweeney, *et al.* 2008. False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: Long-term site fidelity, inter-island movements, and association patterns. *Marine Mammal Science* 24:591–612.
- Baird, R. W., G. S. Schorr, D. L. Webster, D. J. McSweeney, M. B. Hanson and R. D. Andrews. 2010. Movements and habitat use of satellite-tagged false killer whales around the main Hawaiian Islands. *Endangered Species Research* 10:107–121.
- Baird, R. W., M. B. Hanson, G. S. Schorr, *et al.* 2012. Range and primary habitats of Hawaiian insular false killer whales: informing determination of critical habitat. *Endangered Species Research* 18:47–61.
- Baker, A. N. 1981. Strandings of cetaceans on the New Zealand coast 1862–1981. *Proceedings of the Wildlife Society New Zealand Veterinary Association* 1:1–12.
- Baker, A., and B. Madon. 2007. Bryde's whales (*Balaenoptera cf. brydei* Olsen 1913) in the Hauraki Gulf and northeastern New Zealand waters. *Science for Conservation Report* 272. Department of Conservation, Wellington, New Zealand. 23 pp.
- Baker, C. S., L. Chilvers, R. Constantine, S. Du Fresne, R. H. Mattlin, A. van Helden and R. Hitchmough. 2010. Conservation status of New Zealand marine mammals (suborders Cetacea and Pinnipedia), 2009. *New Zealand Journal of Marine and Freshwater Research* 44:101–115.
- Baraff, L. S., and R. A. Asmutis-Silvia. 1998. Long-term association of an individual long-finned pilot whale and Atlantic white-sided dolphins. *Marine Mammal Science* 14:155–161.
- Bearzi, G. A. 1997. A "remnant" common dolphin observed in association with bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *European Research on Cetaceans* 10:204.
- Bearzi, M. 2005. Dolphin sympatric ecology. *Marine Biology Research* 1:165–175.
- Beentjes, M. P., and M. P. Francis. 1999. Movement of hapuku (*Polyprion oxygeneios*) determined from tagging studies. *New Zealand Journal of Marine and Freshwater Research* 33:1–12.
- Best, P. B., and D. Reeb. 2010. A near mass stranding of cetaceans in St. Helena Bay, South Africa. *African Journal of Marine Science* 32:163–166.
- Cawthorn, M. W. 1981. New Zealand. Progress report on cetacean research, June 1979–May 1980. Report of the International Whaling Commission 31:201–203.
- 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.

- Chivers, S. J., R. W. Baird, D. J. McSweeney, D. L. Webster, N. M. Hendrik and J. C. Salinas. 2007. Genetic variation and evidence for population structure in eastern North Pacific false killer whales (*Pseudorca crassidens*). *Canadian Journal of Zoology* 85:783–794.
- Dwyer, S. L., and I. N. Visser. 2011. Cookie cutter shark (*Isistius* sp.) bites on cetaceans, with particular reference to killer whales (orca) (*Orcinus orca*). *Aquatic Mammals* 37:111–138.
- Ferreira, I. M. 2008. Growth and reproduction in false killer whales (*Pseudorca crassidens* Owens [sic], 1846). M.Sc. thesis, University of Pretoria, Pretoria, South Africa. 152 pp.
- Flores, M., M.A., R. Moraga, M. José Pérez, E. Hanshing and C. Olavarria. 2003. New sightings of false killer whales *Pseudorca crassidens* (Owen, 1846) in Chile. *Revista de Biología Marina y Oceanografía* 38:83–85.
- Francis, M. P., C. J. Worthington, P. Saul and K. D. Clements. 1999. New and rare tropical and subtropical fishes from northern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 33:571–586.
- Gannier, A. 2002. Cetaceans of the Marquesas Islands (French Polynesia): Distribution and relative abundance as obtained from a small boat dedicated survey. *Aquatic Mammals* 28:198–210.
- Garrigue, C., and J. Greaves. 2001. Cetacean records for the New Caledonian area (Southwest Pacific Ocean). *Micronesica* 34:27–33.
- Gaskin, D. E. 1972. Whales dolphins and seals, with special reference to the New Zealand region. Heinemann Educational Books Ltd., London, U.K.
- Hector, J. 1872. On the whales and dolphins of the New Zealand seas. *Transactions and Proceedings of the Royal Society of New Zealand* 5:154–170.
- Jahn, A. E., and R. L. Haedrich. 1988. Notes on the pelagic squaloid shark *Isistius brasiliensis*. *Biological Oceanography* 5:297–309.
- Jones, E. C. 1971. *Isistius brasiliensis*, a squaloid shark: The probable cause of crater wounds on fishes and cetaceans. *Fishery Bulletin* 69:791–798.
- Kasuya, T. 1971. Consideration of distribution and migration of toothed whales off the Pacific coast of Japan based upon aerial sighting record. *Scientific Reports of the Whales Research Institute, Tokyo* 23:37–60.
- Kasuya, T. 1985. The fishery-dolphin conflict in the Iki Island area of Japan. Pages 253–272 in J. R. Beddington, R. J. H. Beverton and D. M. Lavigne, eds. *Marine mammals and fisheries*. George Allen & Unwin, London, U.K.
- Kiszka, J., W. F. Perrin, C. Pusineri and V. Ridoux. 2011. What drives island-associated tropical dolphins to form mixed-species associations in the southwest Indian Ocean? *Journal of Mammalogy* 92:1105–1111.
- Leatherwood, S., D. McDonald, R. W. Baird and M. D. Scott. 1989. The false killer whale, *Pseudorca crassidens* (Owen, 1846): A summary of information available through 1988. Technical Report 89-001. Oceans Unlimited, San Diego, CA. 114 pp.
- Maze-Foley, K., and K. D. Mullin. 2006. Cetaceans of the oceanic northern Gulf of Mexico: Distributions, group sizes and interspecific associations. *Journal of Cetacean Research and Management* 8:203–213.
- Mizue, K., and K. Yoshida. 1961. Studies on the little toothed whales in the West Sea area of Kyusyu—VII. About *Pseudorca crassidens* caught at Arikawa in Goto Is., Nagasaki Prefecture. *Bulletin of the Faculty of Fisheries, Nagasaki University* 11:38–52.
- Norris, K. S., and C. R. Schilt. 1988. Cooperative societies in three-dimensional space: On the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. *Ethology and Sociobiology* 9:149–179.
- Odell, D. K., and K. M. McClune. 1999. False killer whale *Pseudorca crassidens* (Owen, 1846). Pages 213–244 in S. H. Ridgway and R. Harrison, eds. *Handbook of marine mammals*. Volume 6. The second book of dolphins and porpoises. Academic Press, London, U.K.
- Palmer, C., P. Fitzgerald, A. Wood, S. Harley and A. McKenzie. 2009. False killer whales *Pseudorca crassidens*: Regular visitors to Port Essington and Darwin Harbour in the Northern Territory, Australia. *Northern Territory Naturalist* 21:49–53.

- Paulin, C. 1993. Review of the Australasian fish family Arripidae (Percomorpha), with the description of a new species. *Australian Journal of Marine and Freshwater Research* 44:459–471.
- Reeves, R. R., B. S. Stewart, P. J. Clapham, J. A. Powell and P. Folkens. 2002. *Guide to marine mammals of the world*. Chanticleer Press, Inc., New York, NY.
- Scott, M. D., and S. J. Chivers. 1990. Distribution and herd structure of bottlenose dolphins in the eastern Pacific Ocean. Pages 387–402 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- Shane, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. Pages 245–265 in S. Leatherwood and R. R. Reeves, eds. *The bottlenose dolphin*. Academic Press, San Diego, CA.
- Sharples, J. 1997. Cross-shelf intrusion of subtropical water into the coastal zone of northeastern New Zealand. *Continental Shelf Research* 17:835–857.
- Stacey, P. J., S. Leatherwood and R. W. Baird. 1994. *Pseudorca crassidens*. *Mammalian Species* 456:1–6.
- Stanton, B. R., P. J. H. Sutton and S. M. Chiswell. 1997. The East Auckland Current, 1994–95. *New Zealand Journal of Marine and Freshwater Research* 31:537–549.
- Stensland, E., A. Angerbjörn and P. Berggren. 2003. Mixed species groups in mammals. *Mammal Review* 33:205–223.
- Sutton, P., and D. Roemmich. 2001. Ocean temperature climate off north-east New Zealand. *New Zealand Journal of Marine and Freshwater Research* 35:553–565.
- Tomilin, A. G. 1957. *Mammals of the U.S.S.R. and adjacent countries*. Volume IX. Cetacea. Israel Program for Scientific Translations, Jerusalem, Israel.
- Tsutsumi, T., Z. Kamimura, and K. Mizue. 1961. Studies on the little toothed whales in the west sea area of Kyusyu—V. About the food of the little toothed whales. *Bulletin of the Faculty of Fisheries, Nagasaki University* 11:19–28.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S*, 4th ed. Springer, New York, NY.
- Visser, I. N. 1999. A summary of interactions between orca (*Orcinus orca*) and other cetaceans in New Zealand waters. *New Zealand Journal of Natural Science* 24:101–112.
- Visser, I. N., J. Zaeschmar, J. Halliday, *et al.* 2010. First record of predation on false killer whales (*Pseudorca crassidens*) by killer whales (*Orcinus orca*). *Aquatic Mammals* 36:195–204.
- Wade, P. R., and T. Gerrodette. 1993. Estimates of cetacean abundance and distribution in the Eastern Tropical Pacific. *Report of the International Whaling Commission* 43:477–493.
- Weir, C. R., T. Collins, T. Cross, A. Gill, S. Elwen, M. Unwin and R. J. Parnell. 2013. False killer whale (*Pseudorca crassidens*) in continental shelf habitat off Gabon and Côte d'Ivoire (Africa). *Marine Biodiversity Records* 6:e65.
- Wiseman, N., S. Parsons, K. A. Stockin and C. S. Baker. 2011. Seasonal occurrence and distribution of Bryde's whales in the Hauraki Gulf, New Zealand. *Marine Mammal Science* 27:E253–E267.
- Würsig, B., and T. A. Jefferson. 1990. Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission (Special Issue 12)*:43–52.
- Zaeschmar, J. R., S. L. Dwyer and K. A. Stockin. 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.
- Zeldis, J. R., R. A. Walters, M. J. N. Greig and K. Image. 2004. Circulation over the northeastern New Zealand continental slope, shelf and adjacent Hauraki Gulf, during spring and summer. *Continental Shelf Research* 24:543–561.
- Zhou, K., Q. Weijuan and L. Yuemin. 1982. *Pseudorca crassidens* (Owen) from the coastal waters of China. *Investigations on Cetacea* 13:263–269.

Received: 28 October 2012

Accepted: 13 July 2013