Aquatic Mammals 2017, *43*(2), 177-184, DOI 10.1578/AM.43.2.2017.177

Short Note

Mixed-Species Associations of Marine Mammals in the Southern California Bight, with Emphasis on Risso's Dolphins (*Grampus griseus*)

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Mixed-species associations are temporary associations of individuals of two or more animal species involved in similar activities (Stensland et al., 2003). Among marine mammals, mixed-species associations are relatively uncommon and appear to vary by such factors as region, season, prey availability, and behavioral state (Stensland et al., 2003; Bearzi, 2005a; Smultea et al., 2014). While mixed-species associations occasionally are reported for marine mammals in portions of the Southern California Bight (SCB) (e.g., Santa Catalina Island, Shane, 1994; Santa Monica Bay, Bearzi, 2005b), little attention has been given to understanding the broader extent and context of these interactions within the larger SCB. Over a 6-y period, we conducted line-transect aerial surveys throughout much of the SCB and became interested in the mixed-species associations we observed. Herein, we examine the relative frequency of species and behaviors found in marine mammal mixed-species associations, and describe those involving Risso's dolphins (*Grampus griseus*) since it was the most common species among mixed-species associations. We review and compare our observations with other data on mixed-species associations of marine mammals from California waters.

Between 2008 and 2013, we flew 18 aerial surveys (n = 97 d) totaling 87,735 km of flight effort. Observations occurred primarily from a high-wing, twin-engine Partenavia aircraft (P68 or Observer; 89% or 86 d, 76,224 km), with the remaining effort conducted from a fixed-wing Aero Commander aircraft (9 d, 10,976 km) or a Bell 206 helicopter (2 d, 535 km; Smultea & Bacon, 2012, 2013; Smultea, 2016). Nine surveys were in warm-water months (May through October), and nine surveys were in cold-water months (November through April) (Carretta et al., 2000). Our SCB study area (12,563 km^2) extended west from the mainland California coast to approximately 200 km offshore and encompassed waters surrounding San Clemente Island (SCI), including the San Nicolas and Santa Catalina basins (Figure 1). Systematic transect lines perpendicular to bathymetric contours/the coastline (oriented west-southwest to east-northeast) were flown at an altitude of 305 m and a speed of 185 km/h following standard line-transect protocol (Buckland et al., 2001, 2015) (Figure 1). Two trained observers scanned for marine mammals from bubble windows, one on each side of the plane, and a third person recorded data on a laptop using custom software, including *Mysticetus Observation System*™ (www.mysticetus.com). More flight time occurred east of SCI due to more flight restrictions related to higher levels of U.S. Navy training activities to the west and the larger relative size of the Santa Catalina Basin.

A *group* was defined as > 50% of individuals engaged in the same, polarized behavioral state up to 100 body lengths (BL) apart within visual range of observers (after Norris & Schilt, 1988; Baird & Dill, 1996; Lusseau & Newman, 2004; Smultea, 2016). Within observed groups, individuals were typically within 10 to 20 BL of each other but occasionally up to 50 to 100 adult BL apart among baleen whales and Risso's dolphins (Smultea & Bacon, 2012; Smultea, 2016). Following an ethogram (as defined in Smultea & Bacon, 2012), we

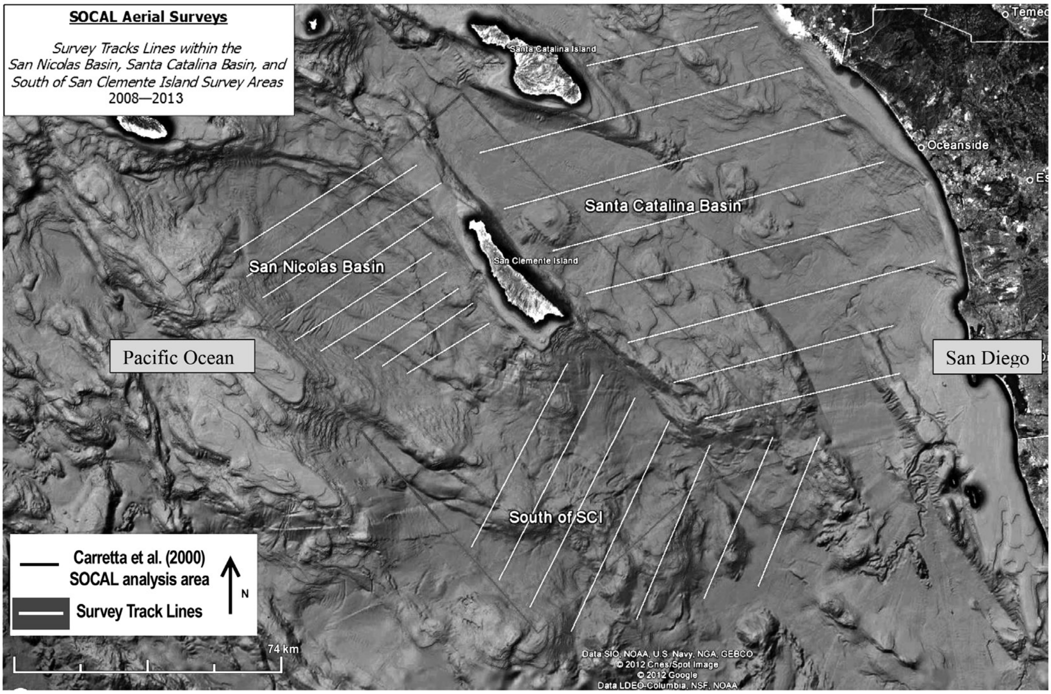

Figure 1. Survey area from 2008 to 2013 within our Southern California Bight (SCB) study area

used point and *ad libitum* sampling (Altmann, 1974; Mann, 2000) to record the first-observed behavioral state, travel heading (magnetic orientation), and minimum and maximum (i.e., individual spacing) group cohesion distance in estimated adult BL (see Smultea & Bacon, 2012; Smultea, 2016). In addition, we occasionally conducted extended (> 10 min) focal follows focused on threatened/endangered species, deep-diving odontocetes, and unusual sightings and behaviors by breaking off survey lines and circling the sighting (> 400 m) beyond Snell's sound cone (Urick, 1972) at a target altitude of 457 m and radial distance of 0.5 to 1 km to avoid potential disturbance of cetaceans (Richardson et al., 1995; Smultea & Bacon, 2012). During focal follows, the aforementioned behavioral data were collected once per minute, individual whale behavioral events were collected using all-occurrence sampling (Altmann, 1974), and a video camera (Sony HDR-XR55OV or Sony HDR-PJ79OV) was used to record behavior through an open porthole window. A digital camera (Nikon D800 or Canon EOS 7D with 100 to 400 mm lens) was used as needed to confirm species, group composition, and behavior.

Analyses were stratified and examined by species, first-observed group size, and behavioral state, as well as mean change in heading and mean maximum cohesion distance between nearest neighbors within a group during focal follows. For mixed-species associations involving focal follows of Risso's dolphins, standard multiple linear regression modeling was used to examine relationships between response variables (e.g., group size, mean change in heading, and mean maximum cohesion distance) and the explanatory variable of presence or absence of other marine mammal species in a mixed-species association. Data processing and analyses were conducted using *R* and *MATLAB* software programs.

Overall, only 2% (n = 50) of the total 2,708 sightings of marine mammals fit Stensland et al.'s (2003) definition of mixed-species associations (Figure 2 & Supplemental Table S1; the supplemental materials for this article are available on the *Aquatic Mammals* website: www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Mixed-species associations most often (90%) involved two but occasionally as many as three different marine mammal species (n = 45 and 5 of 50, respectively) (Table 1 & Supplemental Table S1). In total, mixed-species associations involved 13 cetacean species (five mysticetes and seven odontocetes) and one pinniped (Table 1). The Risso's dolphin was the most common species observed in mixed-species

Table 1. Marine mammal species seen in mixed-species associations during southern California marine mammal aerial survey monitoring, 2008 to 2013

Species in group	Number of groups the species seen in	Percent of mixed-species associations
Risso's dolphin (*Grampus griseus*)	23	22
California sea lion (*Zalophus californianus*)	13	12
Bottlenose dolphin (*Tursiops truncatus*)	12	11
Common dolphin sp.	12	11
Fin whale (*Balaenoptera physalus*)	9	8
Blue whale (*Balaenoptera musculus*)	8	8
Northern right whale dolphin (*Lissodelphis borealis*)	7	7
Short-beaked common dolphin (*Delphinus delphis*)	4	4
Unidentified dolphin	4	4
Pacific white-sided dolphin (*Lagenorhynchus obliquidens*)	3	3
Minke whale (*Balaenoptera acutorostrata*)	3	3
Long-beaked common dolphin (*Delphinus capensis*)	2	2
Gray whale (*Eschrichtius robustus*)	2	2
Humpback whale (*Megaptera novaeangliae*)	2	2
Sperm whale (*Physeter macrocephalus*)	1	1
Total	105*	100

*50 groups, with five groups of three species

associations ($n = 23$, 46%). Risso's dolphins associated with at least seven other marine mammal species, three of which were seen mixed with Risso's dolphins in both the cold- and warm-water seasons (the bottlenose dolphin [*Tursiops truncatus*], northern right whale dolphin [*Lissodelphis borealis*], and California sea lion [*Zalophus californianus*]) (Figures 2 & 3). Although groups of Risso's dolphins in mixed-species vs conspecific groups tended to be larger with more frequent changes in direction, these differences were not significant ($p = 0.12$ and 0.37, respectively).

Risso's dolphin mixed-species associations are relatively common based on our compilation of available records for mixed-species associations involving Risso's dolphins off California (Oregon-California state line to the U.S.-Mexico border) (Supplemental Table S2). Further, these numbers are likely underestimated because mixed-species associations are often not detailed in survey reports designed to document

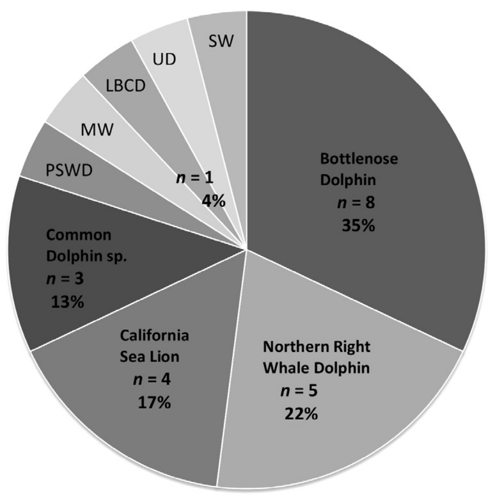

Figure 2. Risso's dolphin (*Grampus griseus*) mixed-species associations in the SCB. PWSD = Pacific white-sided dolphin, MW = minke whale, LBCD = long-beaked common dolphin, UD = unidentified dolphin, and SW = sperm whale.

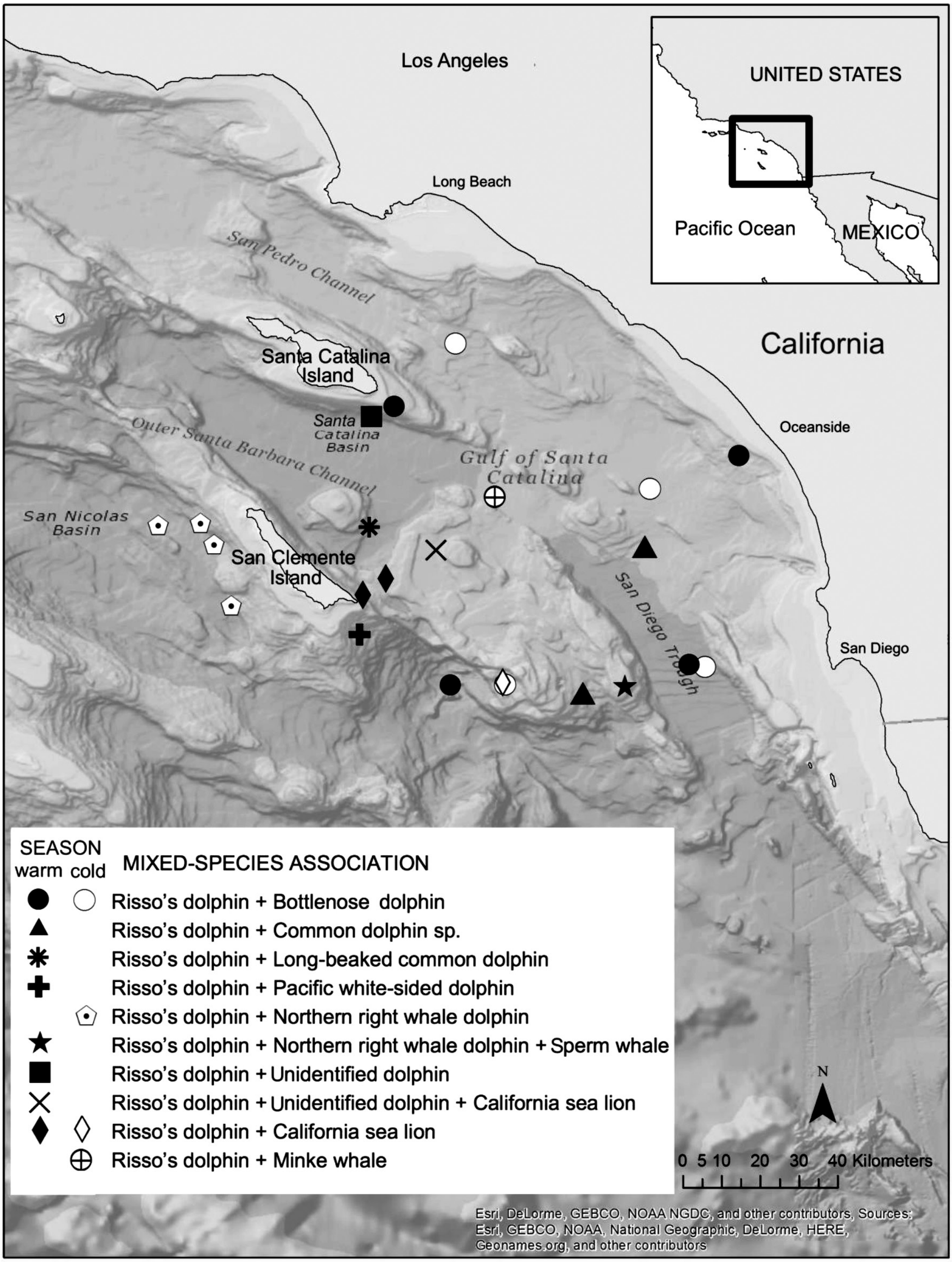

Figure 3. Locations of Risso's dolphin mixed-species sightings by warm- and cold-water periods (May-October and November-April, respectively)

distribution and abundance of marine mammals. However, reported relative proportions of Risso's dolphin groups seen in mixed-species associations in California waters vary considerably both regionally and historically.

The frequency of mixed-species associations involving Risso's dolphins appears to have changed in California waters since the 1950s (e.g., Jefferson et al., 2014; Smultea & Jefferson, 2014; Smultea et al., 2014) During the late 1950s and early 1960s, Fiscus & Niggol (1965) published that 30% of ten Risso's dolphin groups were in mixed-species associations from just north of Monterey south to Morro Bay, California. Dohl et al. (1983) reported that from 1980 through 1983, 20% of Risso's dolphin sightings in central and northern California waters were with another cetacean species. During the late 1980s, Kruse (1989) reported that 57% of Risso's dolphin sightings in Monterey Bay occurred in mixed-species associations. At Santa Catalina Island off San Diego, from 1983 through 1991, Shane (1994) found that bottlenose dolphins were the most frequently seen species in mixed-species associations, together with short-finned pilot whales (*Globicephala macrorhynchus*) (38%) and Risso's dolphins (9%); however, since that time, the relative abundance of Risso's dolphins has dramatically increased while pilot whales have virtually disappeared in the SCB (Shane, 1994; Jefferson et al., 2014; Smultea & Jefferson, 2014). During 1993-1994 aerial surveys in the SCB, Carretta et al. (1995) found that 36% of 24 Risso's dolphin sightings contained another species. Our 2008-2013 SCB study represents the lowest proportion of Risso's dolphin sightings involved in mixed-species associations (only 7% of 337 Risso's dolphin groups). We believe that the reason for our unusually low proportion of Risso's mixed-species associations compared with other regional and SCB studies may be related to a "dilution" effect associated with an apparent increased relative abundance of Risso's dolphins in the SCB compared to other species over the last 50 y (Pierson et al., 2004; Smultea et al., 2014).

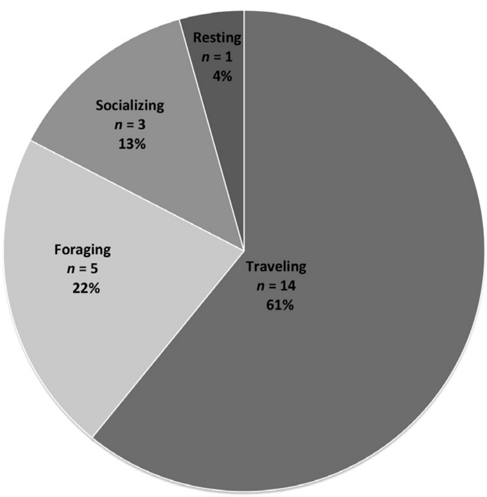

Figure 4. Risso's dolphin behavioral state in mixed-species associations in the SCB

While our study recorded behavior of Risso's dolphin mixed-species associations, none of the other 26 reviewed studies for California reported this information consistently enough to allow comparisons. Reasons for mixed-species associations of marine mammals in our southern California study commonly appear to be food-related as hypothesized in other studies worldwide (e.g., Bearzi, 2005a, 2006; Zaeschmar et al., 2013; Cords & Würsig, 2014). Foraging was observed among 22% of the total 23 Risso's dolphin mixed-species associations and 22% of all other mixed-species associations, suggesting that foraging was a driver for approximately one-quarter of mixed-species associations. In comparison, only 5% of 337 conspecific groups of Risso's dolphins and 5% of 2,708 other conspecific groups were observed foraging.

In our study, Risso's dolphins were found in mixed-species associations most frequently with bottlenose dolphins (n = 8, 35%). Shane (1995) suggested that bottlenose dolphins have a strong attraction toward Risso's dolphins, which may increase the bottlenose dolphins' ability to acquire food. During two separate focal follows, we observed that several different subgroups of northern right whale dolphins followed different single Risso's dolphins and waited at the surface while the Risso's dolphin dove. The Risso's appeared to be foraging, with individuals spread out by several hundred meters, occasionally diving steeply and abruptly in apparent chase behavior, similar to foraging behavior reported in killer whales (*Orcinus orca*) preying on salmon (Felleman et al., 1991). These data suggest that other marine mammal species may behaviorally choose to associate with Risso's dolphins for the benefit of increased foraging success.

Forming interspecific groups leads to larger group size, resulting in higher probability of food detection (Baraff & Asmutis-Silvia, 1998; Bearzi, 2005a; Acevedo-Gutiérrez, 2009). Our observed increased group sizes in Risso's dolphin mixed-species associations support the hypothesized advantages of forming larger groups, especially if different species share common prey. Larger groups may indicate elevated defensiveness, may facilitate social communication through the sensory integration hypothesis, and/or may lower predation risk through the dilution and confusion effects by decreasing an individual's probability of being attacked and making it harder for a predator to focus on one individual (Norris & Dohl, 1980; Connor, 2000; Acevedo-Gutiérrez, 2009).

Alternatively, mixed-species associations may be of no benefit to either species and can simply be the result of two or more species choosing a similar habitat because of a resource that may be of interest to both species (Stensland et al., 2003). For example, interspecific associations are often associated with prey aggregations (e.g., Shane et al., 1986; Acevedo, 1991; Vaughn et al., 2007) within which different species may compete for food or space. Prey distribution has a powerful effect on the benefits and costs of foraging and overall predator performance (Benoit-Bird & Au, 2003).

Our observations also support other studies suggesting that mixed-species associations may be related to interspecific social harassment (Herzing & Johnson, 1997; Stensland et al., 2003; Cords & Würsig, 2014). For example, on two occasions, we observed one species closely chasing and/or circling another for no obvious reason (e.g., no evidence of prey or foraging). This involved three fin whales pursuing a lone minke whale (*Balaenoptera acutorostrata*) for approximately 15 min, and a northern right whale dolphin circling a resting Risso's dolphin mother-calf pair at least three times. In another incident, a Risso's dolphin group member repeatedly charged the head of a sperm whale (*Physeter macrocephalus*) that reacted by opening its mouth (Smultea et al., 2014). Interspecific aggression may be a form of interspecific communication, protection, or harassment (Norris, 1967; Cotter et al., 2012). Specifically, the aggressive behavior observed between the Risso's dolphin and sperm whale may have been kleptoparasitism and/or social parasitism: Risso's dolphins may have charged the sperm whale to induce regurgitation of prey remains that the dolphins could consume without the cost of a deep dive (Smultea et al., 2014).

Mixed-species associations for marine mammals are comparatively rare and little described (Stensland et al., 2003; Bearzi, 2005a). We suggest that the proportion of Risso's dolphin mixed-species associations in the SCB varies between regions, as well as temporally and spatially, but appears particularly low based on our current study relative to past studies. Our observations support other studies suggesting that important drivers for mixed-species associations in the SCB are to increase foraging opportunities and social interaction (including harassment), and/or to decrease predation risk. Herein, we provide the most comprehensive and longitudinal examination of Risso's dolphin mixed-species associations in the SCB and compare those to 26 other studies elsewhere off California. These analyses allow for a better understanding of the potential reasons under which marine mammals form mixed-species associations in the SCB.

Acknowledgments

We thank all who assisted with fieldwork, logistics, GIS, or data analysis: K. Ampela, J. Biondi, C. Boerger, R. Braaten, J. Bredvik, S. Burgess, M. Cotter, M. Deakos, D. Engelhaupt, A. Fowler, G. L. Fulling, S. Garrett, C. Goertz, J. C. Grady, V. James, C. Johnson, C. Kyburg, K. Lomac-MacNair, M. MacKay, L. Mazzuca, R. Merizan, J. Mobley, Jr., T. Norris, M. Richie, F. Robertson, D. Steckler, Aspen Helicopters (R. Throckmorton and pilots B. Hansen, C. Bartush, A. Blasingame, N. Carillo, M. Estomo, S. Jones, C. Kluzek, D. Moody, I. Ufford, and K. Veatch), and Smultea Environmental Sciences and the Marine Mammal Research Consultants. We thank Western EcoSystems Technology (WEST), Inc. for their statistical assistance: S. Howlin, T. McDonald, C. Nations, and S. Nomani. Funding was provided by the U.S. Navy, Commander, Pacific Fleet under the U.S. Navy's Marine Species Monitoring Program, including through sub-agreements with Marine Mammal Research Consultants, Scripps Institution of Oceanography, Smultea Environmental Sciences, and HDR, Inc., under contract to Naval Facilities Engineering Command (NAVFAC). We thank L. Mazzuca and S. Hanser at NAVFAC Pacific, J. Bredvik at NAVFAC Southwest, and K. Ampela at HDR for technical support, project management, and contractual support. Data were collected under NMFS Permit Numbers 14451, 15369, and 774-1714-09.

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