

Long-Term Assessment of Spatio-Temporal Association Patterns of Dusky Dolphins (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand

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Abstract

The challenges of monitoring fully aquatic and long-living mammals have limited research on cetaceans that spans several decades to only a few populations. We report the first long-term assessment of association and residency patterns of dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand. Dorsal fin images, spanning 30 years of data collection, were used for photo-identification and social structure analyses. A total of 4,022 uniquely marked individuals were identified. Most (80%) were sighted only one time. The population of dusky dolphins off Kaikoura appears to be open, with the possibility of immigration and emigration. Dusky dolphins showed preferences for assembly into either large or small groups, which appear to drive association patterns. They did not demonstrate significant preferred or avoided associations with each other, and had overall weak association patterns. Individuals reside in the Kaikoura area for approximately eight years, and also have temporally stable associations lasting approximately eight years. Dusky dolphins fit the model of a fission-fusion society, and their association patterns may reflect unique local ecological conditions and foraging opportunities.

Key Words: cetacean, fission-fusion, residency, longitudinal study, photo-identification, social structure

Introduction

Much research on free-swimming populations of whales, dolphins, and porpoises applies cross-sectional and opportunistic approaches because the aquatic environment, offshore movements, large habitat ranges, and deep diving patterns of many species of cetaceans present challenges to long-term observations and data acquisition. However, as cetaceans are long-lived species with K-selected life history strategies, some spatio-temporally stable and coastal populations can be conducive to long-term (exceeding 10 y), systematic, and continuous assessments of individuals in the wild (Mann et al., 2000; Mann & Karniski, 2017). For example, there have been ongoing studies of populations of common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida (USA) since 1970 (Wells, 2014), killer whales (*Orcinus orca*) in the northeast Pacific since 1973 (Ellis et al., 2011), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, since 1982 (Connor & Krützen, 2015), and Atlantic spotted dolphins (*Stenella frontalis*) and common bottlenose dolphins in the Bahamas since 1985 (Elliser & Herzog, 2016). Such long-term studies of free-swimming cetacean populations can yield important insights into ecophysiology, social systems, population and community ecology, and conservation, thereby increasing the understanding of how natural variation affects fitness and providing some of the most complete and detailed information on cetacean societies (reviewed in Mann &

Karniski, 2017). Photo-identification is the most commonly employed technique through which unique naturally occurring markings are used to distinguish individuals (Würsig & Würsig, 1977; Katona et al., 1979; Würsig & Jefferson, 1990). Photo-identification remains a reliable and non-invasive tool to assess the associations, residency, abundance, movements, and life history of cetacean species and populations over long durations (e.g., Sprogis et al., 2016; McDonald et al., 2017; reviewed in Mann, 2000).

Dusky dolphins (*Lagenorhynchus obscurus*) are a relatively small delphinid (170 to 180 cm body length) and have weak sexual size dimorphism, with males marginally larger than females (Cipriano, 1992). Dusky dolphins are estimated to have life expectancies of 25 to 30 years, although they have been reported to live up to 36 years (Cipriano, 1992). They are long-lived, slow growing, and slow to reproduce. They are a coastal and mesopelagic (“semi-pelagic”) species that is widely but discontinuously distributed in the southern hemisphere. Populations occur off both coasts of South America, southwest South Africa, most of New Zealand, and occasionally off southern Australia and some sub-Antarctic islands (Gaskin, 1968; Van Waerebeek et al., 1995). Populations are typically found in waters less than 2 km deep (Jefferson et al., 1993). However, seasonal changes in distribution suggest prey abundance is the main predictor, rather than water depths or temperature (Cipriano & Webber, 2010).

Photo-identification research on dusky dolphins began to flourish in 1973 when Würsig & Würsig (1980) first explored the daily behavioral patterns of a population in Golfo San José, Argentina. In 1984, photo-identification research was later paired with descriptions of anatomy from *post-mortem* specimens to assess the life history traits of dusky dolphins off Kaikoura, New Zealand (42° 25' 23" S, 173° 42' 00" E; Cipriano, 1992). Research on the Kaikoura population of dusky dolphins has been ongoing, spanning over 34 years, reflecting the efforts of Würsig and his former graduate students. While much is known about the behavior, human interactions, and foraging, mating, and calf-rearing patterns of dusky dolphins off Kaikoura (Würsig & Würsig, 2010), an understanding of long-term association and spatio-temporal patterns can yield insights on societal structure and future conservation needs.

The social structure of dusky dolphins off Kaikoura may be driven by the unique ecological habitat provided by the Kaikoura Canyon. The Kaikoura Canyon is one of the most productive canyons worldwide. Located near the subtropical convergence where Antarctic and tropical waters mix, the Kaikoura Canyon is up

to 1,200 m deep and reaches within 500 m of shore (Boyd et al., 1999; Würsig et al., 2007). The predictable spatio-temporal resources attract diverse trophic levels, including mesopelagic prey and marine mammals, close to shore in high abundance (Lewis, 1998). The local population of dusky dolphins forage nocturnally and off-shore on mesopelagic prey, including lanternfish (Family Myctophidae) and squid (*Nototodarous* sp. and *Todaroides* sp.; Cipriano, 1992; Benoit-Bird et al., 2004). Foraging dives are coordinated to coincide with the diel migration of the deep scattering layer toward the surface (Benoit-Bird et al., 2004, 2009). Dusky dolphins then move closer to shore during the day where they rest and socialize (Würsig et al., 1997, 2007).

Approximately 2,000 dusky dolphins are present off Kaikoura at any given time from an estimated population size of 12,000 dusky dolphins in New Zealand waters (Markowitz, 2004). Group sizes are highly variable, ranging from two to over 1,000 dolphins (Würsig et al., 1997). Inshore groups tend to be smaller than offshore groups (all groups within 50 km of shore), potentially functioning to reduce predation risk (Markowitz, 2004) as has been found in other mesopelagic cetacean species (Gygax, 2002). The dusky dolphins off Kaikoura are highly gregarious animals with fission-fusion societies, where individuals regularly break apart from and join other groups (Würsig et al., 1997; Markowitz, 2004). However, dusky dolphin populations in other regions of New Zealand may exhibit stronger association patterns. For example, approximately 300 km north of Kaikoura, dusky dolphins in Admiralty Bay have been observed foraging together during the daytime in smaller and more stable groups during the austral winter (Markowitz, 2004; Pearson, 2009; Vaughn et al., 2010; Pearson et al., 2017). Individuals have been resighted between Kaikoura and Admiralty Bay (Markowitz, 2004). The social structure and behavioral ecology of dusky dolphins off Kaikoura are hypothesized to resemble those of other small delphinid species and populations that forage nocturnally on mesopelagic prey associated with the deep scattering layer such as spinner dolphins (*Stenella longirostris longirostris*) off the main Hawaiian Islands (Norris & Dohl, 1980; Würsig et al., 1994). Herein, we contribute to the literature on delphinid societies by reporting the first long-term (30 years) assessment of social dynamics in the dusky dolphin.

Our objective was to use long-term photo-identification data to assess the association and residency patterns of the population of dusky dolphins off Kaikoura. Specifically, we explored (1) resighting rates, (2) gregariousness, (3) preferences/avoidances and the strength of associations, (4) spatial stability, and (5) temporal stability of associations.

Methods

Photographs of dusky dolphin dorsal fins were collected opportunistically during boat-based surveys by several researchers affiliated with the Marine Mammal Behavioral Ecology Group at Texas A&M University and Texas A&M University at Galveston from 1984 to 2014 (Table 1). Most field research occurred during the austral summer months (November to March). Dusky dolphins were photographed in the Kaikoura region, which ranged from 10 km north of the Kaikoura Peninsula to 10 km south of the Haumari Bluffs, and up to 50 km of shore. Due to large group sizes, changing weather conditions, time-restricted observations of groups because of voluntary codes of conduct, and variable researcher objectives, oftentimes less than half the members of a group were photographed.

Film photography was used to capture dorsal fin images prior to 2002. Camera models included Nikon 6006, Nikon F100, Nikon 8008, and Nikon F4. All film slides were digitized using a Powerslide 5000 converter (Pacific Image Electronics Co., Ltd, Torrance, CA, USA) paired with the program *CyberView X5* (16 bit resolution, up to 5,000 dots per inch). Digital photography was used from 2002 onward. A variety of camera models and lenses were used, including Nikon D1H, Nikon D200, Nikon D7000, and Canon 40D dSLR cameras with lenses ranging up to 400 mm.

Photographs were subjected to rigorous screening and were deemed of suitable quality for further analyses if distinguishing features could be consistently recognized and appeared to be stable over time (Urian et al., 2015). An estimated 52% of dusky dolphins off Kaikoura have distinctive markings on their dorsal fins (Kügler & Orbach, 2014). Suitable photographs were in sharp focus, not backlit, with good contrast and within a few degrees of perpendicular to the dorsal fin. Additionally, photographs were only included if they were not obscured and there were

no splashes. Photographs were then cropped to accentuate the dorsal fin and renamed to reflect the date, group encounter number, and sex of the dolphin (if known). Sex was confirmed by observation of the genital slit of the dolphin, observations of the extruded penis, or by body positioning during copulation (Orbach et al., 2015). Additionally, sexually mature animals consistently observed with a calf within one body width distance throughout the encounter were classified as mothers (females). A single best image of each individual throughout the encounter was selected for inclusion in the analyses by one researcher (DNO).

Photographs were manually traced into *Finscan 1.5.4* (Hillman et al., 2003), a semi-automated, computer-assisted, individual recognition system for marine animals. *Finscan 1.5.4* computes a quantitative description of the dorsal fin edge and compares it to a database of edges obtained from previously processed images (Hillman et al., 2003). Each dorsal fin was matched within its own catalog and across all other catalogs by a minimum of two researchers (Table 1). Suggested possible matches were cross-validated by a third and occasionally a fourth researcher.

Analysis

We tested whether individual, sexually mature dusky dolphins show nonrandom association and spatio-temporal patterns using *SOCPROG 2.7*, a MATLAB-based social structure analytical program (Whitehead, 2009). Sexually mature adults were distinguished from sexually immature subadults and calves based on body lengths (Cipriano, 1992). Within *SOCPROG 2.7*, the sampling period was set as date, and the group variable was set as encounter. Groups were defined as dolphins within 10 m of another group member (Smolker et al., 1992). Five separate research questions were addressed for the dusky dolphin population off Kaikoura:

Table 1. Dusky dolphin (*Lagenorhynchus obscurus*) photo-identification catalogs of dorsal fin images collected off Kaikoura, New Zealand, between 1984 and 2014

Researcher (Catalogue)	Years	# of usable photographs	# of distinct individuals
Frank Cipriano	1984-1988	260	224
Suzanne Yin	1995-1999 2001	128	122
Amy Beier-Engelhaupt	2002	788	709
Jody Weir	2004-2006 2009	944	744
Sierra Deutsch/Mridula Srinivasan	2006-2007	846	606
Dara Orbach	2011-2014	2,454	2,244

1. *Resighting Rate* – Discovery curves were generated to determine the rate that previously unknown individuals entered the dataset and what proportion of the population has been identified (Whitehead, 2009). Discovery curves were generated for individuals by sampling period and by identifications to determine if the population of dusky dolphins off Kaikoura was open (i.e., not geographically isolated and able to gain or lose members over time due to immigration and emigration in addition to birth and death) or closed (i.e., not able to exchange members with different populations and only able to gain or lose members due to birth and death; Whitehead, 2008). The discovery curves also yielded information on sampling effort patterns.
2. *Gregariousness* – We tested if dolphins had tendencies to form associations in general, and if some individuals were found in consistently larger or smaller groups compared to others (Whitehead et al., 2005). Data were restricted to instances where each individual was resighted five or more times (Numsamp > 4; Whitehead, 2008). A standard half-weight association index was applied, which determines the proportion of time any two individuals spend together. This association index is appropriate in cases where < 50% of individuals in a group were photographed (Karczmarski et al., 2005). Permutation tests were used to test the null hypothesis that all individuals in the population had the same level of gregariousness (Whitehead, 2009). Specifically, the ‘permute groups within samples’ function was used to test empirical patterns of association against a randomly generated dataset (Whitehead et al., 2005; Whitehead, 2009). To confirm that the empirical data differed from random data and to determine the number of permutations required to obtain a stable *p* value, increasingly larger numbers of permutations and repetitions were applied (Bejder et al., 1998). The sum of association index values (by individual) was also calculated to provide a measure of the average group size as a proxy for gregariousness (Whitehead, 2009).
3. *Preferences/Avoidances and the Strength of Associations* – We tested the hypothesis that dusky dolphins had individual preferred or avoided associations rather than preferences for being in large or small groups (e.g., an artifact of optimal group size). In contrast to the gregariousness test that assessed if dolphins tended to form associations, the preferred/avoided associations test assessed the degree of companionship at the individual level. Data were restricted to instances where dusky dolphins were resighted five or more times (Numsamp > 4). Associations were analyzed using the half-weight index. Permutation tests were used to test the null hypothesis that there were no preferred or avoided companions across sampling periods given the number of associations each individual had in each sampling period (Whitehead, 2008). Specifically, the ‘permute associations within samples’ function was used to test empirical patterns of association against a randomly generated dataset (Whitehead et al., 2005; Whitehead, 2009). Increasingly larger numbers of permutations and repetitions were applied (Bejder et al., 1998). Preferred/avoided association patterns were not divided into short- and long-term trends because of inconsistent researcher sampling efforts. Association indices were calculated to determine the proportion of time two individuals were seen together (Whitehead, 2008). Association indices range from 0 to 1 and explain the probability that a dolphin seen today with another individual will never be observed together again (0, when “today” is excluded from the analysis) through to will always be observed together (1) at a later time. The general null hypothesis is that individuals associate with the same probability with all other individuals given their availability. The mean association index (average proportion of two dolphins associating together) and mean maximum association index (average proportion that two dolphins associate with their closest associate) were calculated (Whitehead, 2008).
4. *Spatial Stability* – The lagged identification rate was calculated to assess spatial stability (average residency) over time and to determine if dusky dolphins depart from Kaikoura at a standardized rate. The lagged identification rate addresses the probability that a dolphin identified today will be resighted again at some later time lag (Whitehead, 2007). The lagged identification rate was calculated using the movement analysis function in *SOCPROG 2.7* for the whole study area. The time axis (x-axis) was log-transformed because the data spanned several decades. A boot-strapping approach was applied with 100 repetitions to explore confidence intervals (Whitehead, 2008). Four exponential decay models that tested assumptions about open and closed populations were fitted to the empirical data (Whitehead, 2007). The

best fitting model was selected based on the lowest quasi-Akaike information criterion (qAIC) value (Whitehead, 2007). The exponent value of the exponential decay model indicates the rate of decline. To calculate the approximate duration that any given dolphin remained in the Kaikoura area, the inverse of the exponent value of the best fitting model was divided by 365 d (per year).

5. *Temporal Stability of Associations* – The temporal stability of pair bonds was measured using lagged association rates, which assess the probability that two individuals associating together at a given time will still be resighted together at various subsequent time lags (Whitehead, 1995). The data were standardized, and the time axis was log-transformed. A jackknifing method was applied, with a moving average set to over 40,000 to estimate the precision of the lagged association rate (Efron & Stein, 1981). The null association rate (the expected rate if there were no preferred associations among pairs given the number of associations of each individual in each sampling period) was compared to the lagged association rate (Whitehead, 1995, 2009). Four exponential decay models were fit to the data to test how paired associations could change over time depending on preferred companions and casual acquaintances (Whitehead, 2007). The best fitting model was selected based on the lowest qAIC value (Whitehead, 2007). The exponent value of the exponential decay models indicated the rate of decline. To calculate the approximate time frame in which half the dolphins in the population were still observed in

stable dyadic associations, the inverse of the exponent value of the best fitting model was divided by 365 d (per year).

Results

A total of 5,420 images were deemed suitable for inclusion in the photo-identification analyses across a 30-year time span (1984 to 2014). Of these, 4,022 uniquely marked individuals were identified, 627 of which matched across researcher catalogs. Most individuals were sighted only one time (80% of dolphins), but one dolphin was resighted 15 times (Supplemental Table 1; the supplemental tables are available in the “Supplemental Material” section on the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). Seventy individuals were resighted five times or more and were included in the analyses of gregariousness, preferred or avoided associations, and strength of associations. A total of 750 dolphins were resighted on multiple days, of which 537 individuals were resighted in different years.

Resighting Rate

The population of dusky dolphins off Kaikoura appears to be open based on both the discovery curve (Figure 1a) and the cumulative number of identifications curve (Figure 1b). The slope of the cumulative number of identifications curve also indicates that not all individuals in the population were photo-identified. The discovery curve indicates variable sampling effort over 30 year, with peaks in the graph corresponding with researcher field seasons.

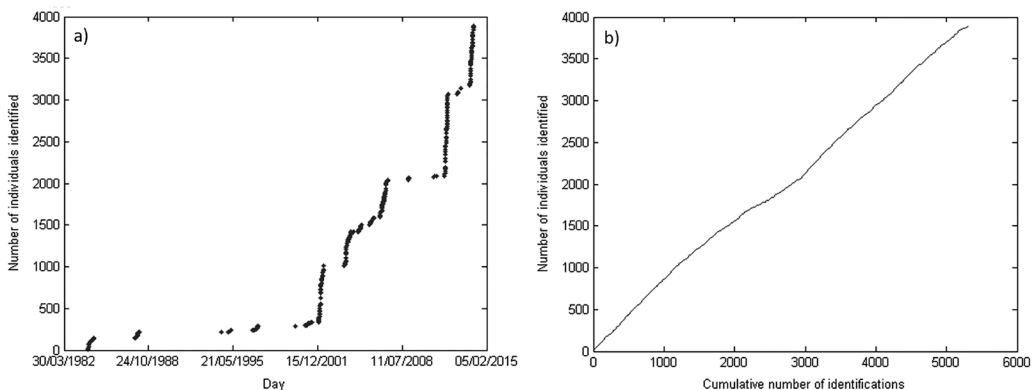


Figure 1. (A) Discovery curve and (B) cumulative number of identifications curve for dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand. The slopes of both curves indicate an open population where not all individuals have been sampled.

Gregariousness

Among individual dusky dolphins, some showed significant preferences for small groups and some for large groups (Test statistic: Standard Deviation [SD], Real = 2.00, Mean = 1.93, $p = 0.02$), with substantial variability in preferences for group size (Figure 2a). A total of 10,000 permutations

were run at 10,000 trials per permutation. The mean sum of association index values per individual was 3.62 (SD \pm 1.92; Figure 2a) and is a conservative estimate of group size as not all individuals in a group were photo-identified or resighted five or more times.

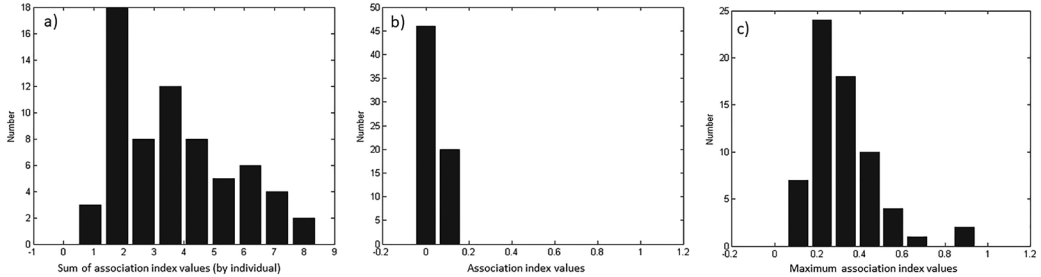


Figure 2. Association indices of dusky dolphins resighted off Kaikoura > 4 times: (A) Distribution of group size (sum of association index values), (B) distribution of association index values, and (C) distribution of maximum association index values

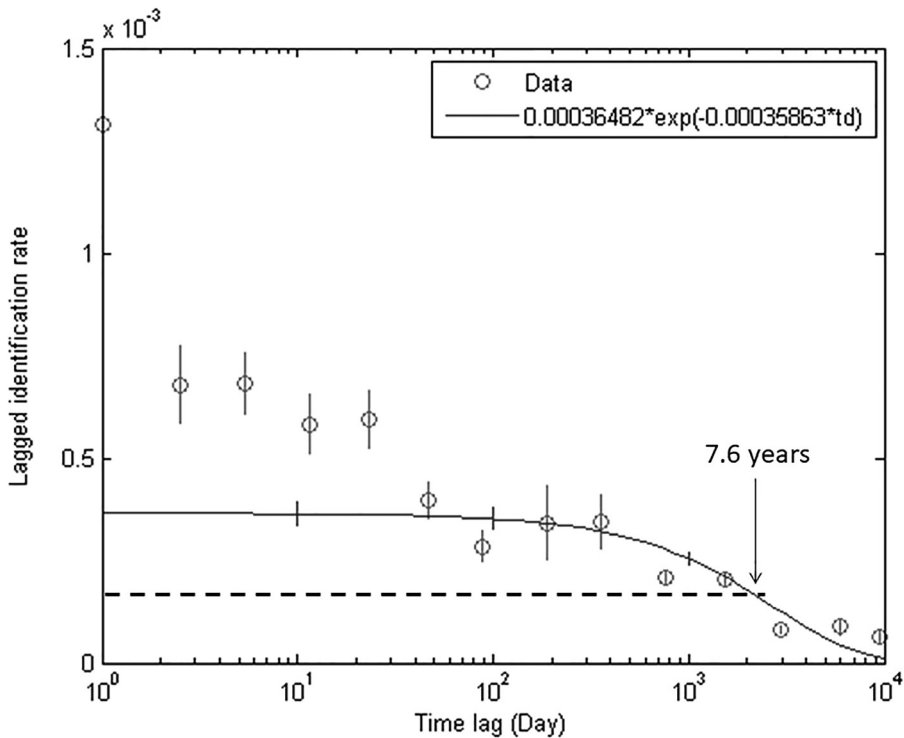


Figure 3. Lagged identification rate (LIR): The circular data points depict the LIR. The solid line is the best fitting LIR decay model; and the hashed line (midpoint of the best fitting LIR at time 0) intersects the best fitting LIR at the time lag when approximately half the dusky dolphins remained in the Kaikoura area. The inverse of the exponent value was divided by 365 d to calculate this duration.

Preferences/Avoidances and Strength of Associations

Individual dusky dolphins did not exhibit preferred or avoided associations with specific individuals (Test statistic: Coefficient of Variation, Real = 2.20, Mean = 2.19, $p = 0.42$). A total of 10,000 permutations were run at 10,000 trials per permutation. The mean association index was 0.04 (SD ± 0.03 ; Figure 2b). The mean maximum association index was 0.32 (SD ± 0.15 ; Figure 2c).

Spatial Stability

In general, dusky dolphins remained in the Kaikoura area for ~ 7.6 y. The decay model that best fit the lagged identification rate data included emigration and mortality variables ($\chi^2 = 1,372.141$, $df = 249$, $p < 0.001$; Figure 3; Supplemental Table 2), expressed as

$$r(T) = 0.00036482 * \exp(-0.00035863 * td)$$

where $r(T)$ is the lagged identification rate at a lag of T time units, and td is the time lag. Dolphins do

not appear to use Kaikoura as a temporary stopping place while travelling to other regions as there was no sharp drop-off in the fitted lagged identification rate curve in the first 100 d of residency.

Temporal Stability of Associations

Although they did not demonstrate significant preferred or avoided associations, dusky dolphins were estimated to remain together in the Kaikoura region for 8.2 years. The lagged association rate remained higher than the null model, indicating that pairs of dolphins remained stable over long periods. The decay model that best fit the lagged association rate data for dusky dolphins off Kaikoura included casual acquaintance variables ($\chi^2 = 1,044.710$, $df = 79$, $p < 0.001$; Figure 4; Supplemental Table 3), expressed as

$$g(T) = 0.0025003 * \exp(-0.00033331 * td)$$

where $g(T)$ is the lagged association rate at a lag of T time units, and td is the time lag. The standard error bars were wide, suggesting poor precision in

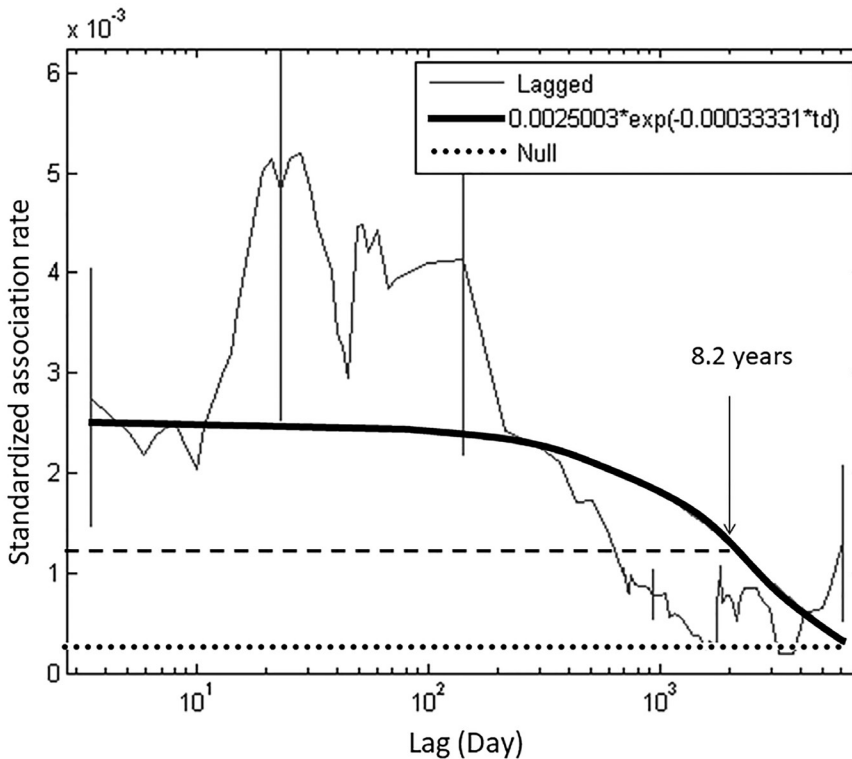


Figure 4. Lagged association rate (LAR): The spiking empirical data depict the LAR. A jackknife approach indicates where the data are accurate (small vertical spikes) and deficient (large vertical spikes). The thick solid line is the best fitting LAR decay model; the dotted line is the null model; and the hashed line (midpoint of the best fitting LAR at time 0) intersects the best fitting LAR at the time lag when approximately half the dusky dolphins were still observed in stable dyadic associations in the Kaikoura area. The inverse of the exponent value was divided by 365 d to calculate this duration.

the lagged association rate model of dusky dolphin associations. As the best fitting model curve remained stable over the first several years, paired associations appear to be long-lasting.

Discussion

Dusky dolphins off Kaikoura appear to belong to an open population, with substantial immigration and emigration of individuals. Few dusky dolphins were resighted within this large population. In closed populations of other cetacean species in New Zealand waters, discovery curves level off when all individuals are identified (e.g., Hector's dolphins [*Cephalorhynchus hectori*], Bejder & Dawson, 2001; bottlenose dolphins, Williams et al., 1993). As discovery curves for dusky dolphins did not level off, the catalog does not include all individuals in the Kaikoura population. Accordingly, previous estimates of approximately 2,000 dusky dolphins present off Kaikoura at any given time from a larger overall population of 12,000 individuals may be conservative (Markowitz, 2004).

Dusky dolphins demonstrated substantial variability in their preferences for small or large groups. Such variability in grouping patterns is the hallmark of fission-fusion dynamics (Aureli et al., 2008) and may be attributed to the benefits and costs of grouping such as predator protection (Norris & Dohl, 1980), mating opportunities (Orbach et al., 2014), sexual harassment (Scott et al., 2005), and scramble competition (Gowans et al., 2008). As most individuals were not of known sex, it was not possible to determine if variability in group size preference reflected sexual segregation. For example, dusky dolphin mating groups off Kaikoura typically consist of four males chasing one female (Orbach et al., 2014), and nursery groups are often comprised of seven mother-calf pairs (Weir, 2007).

Dusky dolphins did not exhibit preferred or avoided associations. Additionally, they exhibited a low mean association index value. These findings suggest overall weak association patterns. Our mean association index value (0.04) was slightly higher than that noted for dusky dolphins off Kaikoura during the 1997 to 2003 time period by Markowitz (2004; mean association index value for individuals resighted more than once = 0.03), although we used more stringent inclusion criteria. Overall, our results support the hypothesis that dusky dolphins off Kaikoura are highly gregarious and have a fission-fusion society, with pod membership changing over a timeframe of hours to days (Würsig et al., 2007).

Dusky dolphins off Kaikoura and Admiralty Bay, New Zealand, exhibit patterns of social

bonding that have similar mean association index values (Kaikoura = 0.04 ± 0.03 ; Admiralty Bay = 0.03 ± 0.01) and temporal stability (both > 5 y; Pearson et al., 2017). These similarities are striking given the ecological differences between Kaikoura and Admiralty Bay. Kaikoura is characterized by a deep open water habitat with variable predation pressure, largely from killer whales (Srinivasan & Markowitz, 2010), and relatively predictable prey availability (Benoit-Bird et al., 2004). In contrast, Admiralty Bay is characterized by a shallow protected habitat with low predation pressure and patchy prey availability that drives coordinated foraging strategies (Würsig & Pearson, 2014). The overall bonding patterns of dusky dolphins may be impervious to ecological differences (Pearson et al., 2017). However, a notable difference in social bonding between the two locations is the presence of preferred/avoided associates in Admiralty Bay, possibly related to coordinated foraging and a smaller population of dolphins (Pearson et al., 2017). Off Kaikoura, there is an absence of preferred/avoided associates and a larger population size, with a corresponding lower probability of two dolphins encountering each other. Dusky dolphins off Kaikoura showed a preference for either large or small groups off Kaikoura; whereas in Admiralty Bay, group size is more labile, and fission-fusion dynamics are more pronounced (e.g., individuals join and split from groups on average every 5 min; Pearson, 2009). Genetic evidence indicates that the Admiralty Bay population of dusky dolphins is largely comprised of males during the austral winter (Harlin et al., 2003), potentially indicating some spatio-temporal sexual segregation between Kaikoura and Admiralty Bay that could contribute to variation in social affinities between the two locations.

Although dusky dolphins resided off Kaikoura for approximately 8 years (with likely exceptions) and did not appear to use Kaikoura for short-term residency while migrating to other areas, individuals may use the Kaikoura region seasonally. Seasonal patterns were not assessed in the present study because most research efforts were constrained to austral summer months. However, dusky dolphins observed off Kaikoura during austral summer months have been observed in several areas of New Zealand during other seasons (Würsig et al., 1997, 2007; Markowitz, 2004). Similarly, dusky dolphins from other regions of New Zealand's South Island may reside in the Kaikoura area during austral winter months when larger groups form (Würsig et al., 1997). While a decline in residency was not observed within the first 3 mo, additional research effort off Kaikoura in the

austral winter and shoulder months could yield insights on seasonal patterns of abundance. Dusky dolphins tend to form larger groups offshore during the winter compared to summer, likely due to seasonal changes in predation risk and prey availability. These factors appear to be important determinants of residency and habitat use (Würsig et al., 1997). Similarly, Hawaiian spinner dolphins off the main Hawaiian archipelago exhibit daily inshore–offshore movement patterns and forage nocturnally on prey associated with the deep scattering layer, although they do not appear to exhibit seasonal variation in movement patterns (Norris & Dohl, 1980; Norris et al., 1994).

As the best fitting lagged association rate model varied from the null hypothesis, enduring dyadic associations could reflect preferences/avoidances of certain individuals or patterns of gregariousness. However, no evidence of preferred/avoided companions was found, while significant patterns were evident in gregariousness. Accordingly, we suggest that dusky dolphins remained together because of preferences for group sizes. However, we caution that photo-identification images of most individuals in large pods (often consisting of several hundred individuals) were not captured or of suitable quality for inclusion in our analyses and that data were restricted to individuals resighted five or more times, which could alter interpretations of preferred group sizes.

This longitudinal study has afforded the unique opportunity to assess long-term spatio-temporal patterns of association in a semi-pelagic delphinid, providing an important comparison to other long-term studies of coastal delphinids. This study helps shape our understandings of fission-fusion dynamics and how ecological factors can influence site fidelity and use among cetaceans. As dusky dolphins experience substantial anthropogenic interactions off Kaikoura (e.g., Lundquist et al., 2012), longitudinal research can inform sustainable mitigation practices (Mann & Karniski, 2017). Our results demonstrate that dusky dolphins off Kaikoura are part of an open population that exhibits an overall pattern of weak associations, juxtaposed against some spatio-temporal stability. We caution that our results primarily reflect behavior observed during austral summer and that different patterns could occur at other times of the year. Our finding that individuals tend to prefer either large or small groups warrants further study. Future investigation into the association patterns of specific group types off Kaikoura (e.g., mating or nursery groups) will provide further insight into the function of social bonding among dusky dolphins.

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