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False killer whales (*Pseudorca crassidens* Cetacea: Delphinidae) along the Pacific coast of Central America and Mexico: Long-term movements, association patterns and assessment of fishery interactions

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ABSTRACT

Introduction: Worldwide, false killer whales (*Pseudorca crassidens*) are infrequently encountered, yet long-term studies have shown strong site fidelity as well as long-term associations among individuals in several locations. Detailed studies of this species have primarily been conducted around tropical oceanic islands or in the subtropical southern hemisphere.

Objectives: We assess movements and association patterns among false killer whales along the Pacific coasts of the USA, Mexico, Guatemala, Nicaragua, Costa Rica including Isla del Coco, and Panama, representing one of the longest-running (albeit non-continuous) studies of this species. We also examine photos for evidence of interactions with fisheries, a known source of mortality to false killer whales.

Methods: From Central America, we selected 212 individuals (50 encounter groups) out of 244 individuals (56 encounters) for inclusion in analyses based on photo quality and distinctiveness. Photos were collected on dedicated surveys from 1991-1994 and dedicated and opportunistic surveys from 1998-2022. Other than the effort off the oceanic Isla del Coco (1993-1994), surveys were undertaken in continental shelf waters. Additionally, we selected by photo quality and distinctiveness 124 (33 encounter groups) out of 189 individuals from southern California and Mexico for inclusion in these analyses. Association patterns were analyzed in SOCPROG and movements were analyzed in R.

Results: Of the 328 total individuals, 158 (48.2 %) were encountered more than once, and 114 (34.8 %) were re-sighted after a year or more. The longest individual sighting history spanned 26.2 years with six re-sightings over that period between southern Costa Rica and Panama. Association and movement analyses revealed that individuals identified off southern Costa Rica and Panama linked into a single social network, with extensive movements between the two countries. Three individuals encountered off northern Costa Rica were re-sighted off northern Nicaragua, and individuals encountered off Nicaragua were encountered off Guatemala and central mainland Mexico. Nine matches were found among false killer whales between central mainland Mexico and Central America. There were no matches between the mainland coastal waters and the 33 individuals encountered around Isla del Coco. Dorsal fin disfigurements consistent with interactions with line fisheries ranged from 0 to 21 % for individuals within social clusters identified by community division.

Conclusions: The infrequency of sightings combined with a high re-sighting rate of individuals and groups from the same area, suggests multiple small populations with large home ranges that include coastal waters. Small populations are sensitive to environmental changes, and as the human population grows, so do the demands on fisheries and ecotourism, which could directly impact the different populations. Additional effort in offshore areas is needed to determine the population status of false killer whales in pelagic waters, how often false killer whales using coastal waters move into pelagic waters, and the relationship between whales in the two habitats.

Key words: small cetacean; photo-identification; fisheries; dorsal fin disfigurement; social network; social organization.

RESUMEN

Falsas orcas (*Pseudorca crassidens* Cetacea: Delphinidae) de la costa del Pacífico de Centroamérica y México: movimientos, patrones de asociación y evaluación de interacciones pesqueras

Introducción: Alrededor del mundo, las falsas orcas (*Pseudorca crassidens*) son encontradas con poca frecuencia, aunque estudios a largo plazo han demostrado una fuerte fidelidad al sitio, así como asociaciones a largo plazo entre individuos. Estudios detallados de esta especie se han realizado principalmente alrededor de islas oceánicas tropicales o en la región subtropical del hemisferio sur.

Objetivo: Se evaluaron los movimientos y patrones de asociaciones a largo plazo entre falsas orcas, a lo largo de las costas del Pacífico de E. U., México, Guatemala, Nicaragua, Costa Rica (incluyendo a la Isla del Coco) y Panamá, lo que representa uno de los más extensos (aunque no continuos) estudios de esta especie. Además, se analizaron las fotos de aletas dorsales en busca de evidencia de interacciones con la pesca, una fuente de mortalidad conocida para las falsas orcas.

Métodos: Seleccionamos a 212 (50 encuentro grupos) de 244 individuos (56 encuentros) de Centroamérica para incluirlos en los análisis basados en la calidad y el carácter distintivo de las fotografías. Utilizamos fotos recopiladas en muestreos dedicados de 1991 a 1994 y encuentros dedicados y oportunistas de 1998 a 2022. Aparte del esfuerzo alrededor de la isla oceánica, Isla del Coco (1993-1994), se realizaron estudios en aguas de la plataforma continental. Además, seleccionamos basados en la calidad y el carácter distintivo de las fotografías 124 (33 encuentro grupos) de 189 individuos del sur de California y México para incluirlos en los análisis. Patrones de asociaciones fueron analizados en SOCPROG y los movimientos fueron analizados con el programa R.

Resultados: Del total de 328 individuos encontrados en Centroamérica, 158 (48.2 %) fueron observados más de una vez y 114 (34.8 %) se volvieron a avistar después de un año o más. El historial de avistamientos individuales más largo abarcó 26.2 años con seis re-avistamientos durante ese período entre el sur de Costa Rica y Panamá. Los análisis de asociación revelaron que todos los individuos identificados en el sur de Costa Rica y Panamá, se vincularon a una sola red social, con amplios movimientos entre los dos países. Tres individuos encontrados frente al norte de Costa Rica fueron avistados frente al norte de Nicaragua, y los individuos encontrados frente a Nicaragua fueron encontrados frente a la región central continental de México. Hubo traslape de nueve individuos entre México y Centroamérica. No hubo traslape entre los individuos avistados en el continente y los 33 individuos identificados alrededor de la Isla del Coco. Las desfiguraciones de la aleta dorsal, consistentes con interacciones con artes de pesca que usan líneas variaron de 0 a 21 % para los individuos dentro de los grupos identificados por división de la comunidad.

Conclusiones: La poca frecuencia de avistamientos combinada con muchos re-avistamientos de individuos y grupos en la misma área, sugiere que las falsas orcas representan muchas poblaciones pequeñas con áreas de distribución grandes que incluyen aguas costeras. Las poblaciones pequeñas son sensibles a los cambios ambientales y, a medida que crece la población humana, también lo hacen las demandas sobre la pesca y el ecoturismo, lo que podría afectar directamente a estas poblaciones. Se necesitan más estudios en las áreas alejadas de la costa para determinar el estado de conservación de las falsas orcas en regiones pelágicas, la frecuencia con la que las falsas orcas que usan aguas costeras se trasladan a aguas pelágicas y la relación entre ellas en los dos hábitats.

Palabras clave: pequeños cetáceos; foto-identificación; pesca; desfiguración de la aleta dorsal; red social; organización social.

Nomenclature: SMT1: Supplementary material Table 1; SMF1: Supplementary material Figure 1.

INTRODUCTION

False killer whales, *Pseudorca crassidens* (Owen, 1846) primarily inhabit pelagic tropical and warm temperate waters worldwide, with the highest density in the tropics (Ferguson & Barlow, 2003). There are a few well-documented populations that are island-associated or encountered in nearshore waters (Baird et al., 2008; Palmer et al., 2017; Zaeschmar, 2014). Although this species is highly surface-active and tends to travel in large groups (20–100 individuals), false killer whale encounters are infrequent even in areas where they are resident year-round (e.g., Hawai'i; Baird, 2016) or present seasonally (e.g., New Zealand; Zaeschmar, 2014). In the eastern tropical Pacific (ETP), extensive large and small vessel surveys conducted in the Exclusive Economic Zone of Costa Rica from 1979 to 2001 documented only nine encounters of false killer whales (May-Collado et al., 2005) and sightings were relatively few and sparsely distributed throughout the ETP (Martínez-Fernández et al., 2011; Quintana-Rizzo & Gerrodette, 2009; Quintana-Rizzo, 2012; Wade & Gerrodette, 1993). Based

on extensive survey work of the eastern Pacific Ocean from 1985–2005, no false killer whales were encountered north of Mexico (Hamilton et al., 2009), although there have been occasional documented encounters off California and even farther north into British Columbia (Baird et al., 1989; Norris & Prescott, 1961).

The first photographic identification (photo-ID) study of this species was conducted from 1991–1995 by Acevedo-Gutiérrez et al. (1997) in the coastal waters of Golfo Dulce, southern Costa Rica, and off Isla del Coco, an island approximately 500 km southwest of Costa Rica. Acevedo-Gutiérrez et al. (1997) found that individuals were re-sighted over two years in Golfo Dulce and three years off Isla del Coco, and stable associations between some individuals were evident. Based in the same area of southern Costa Rica (not including Isla del Coco) but using a separate photo-ID catalog and dataset, Sánchez Roblado et al. (2020) estimated that 92 false killer whales used this area. Although these earlier studies were spatially limited, they indicated that there is a small population encountered occasionally off southern Costa Rica, with no documented

interchange with Isla del Coco (Fig. 1). An entirely separate photo-ID study identified 14 individuals but documented no re-sightings in Guatemala (Quintana-Rizzo, 2012).

The question of how far these individuals are ranging along Mexico, Central America, and into offshore waters is unclear. Genetic and photo-ID studies in the eastern Hawaiian Islands show a distinct insular/island-associated population of false killer whales with high site fidelity (Baird et al., 2008, Baird et al., 2012), and a genetically differentiated broadly ranging offshore population (Anderson et al., 2020; Chivers et al., 2007; Fader et al., 2021; Martien et al., 2014). Home ranges for groups and individuals from the main Hawaiian Islands' insular population tend to be extensive, but predictable (Baird et al., 2012), while individuals from the pelagic population appear to be much wider ranging (Anderson et al., 2020; Fader et al., 2021). The maximum travel distance for a satellite tagged insular main Hawaiian Islands false killer whale was 421 km (Baird et al., 2010), while it was 2 263 km for an individual from the pelagic population (E. Oleson personal communication, 27

July, 2022). Although far less is known about populations elsewhere, Palmer et al. (2017) reported that the maximum travel distance from a satellite-tagged false killer whale in the Arafura and Timor Seas off Australia was about 880 km from 104 days of tag transmission. Off New Zealand, Zaeschmar (2014) reported a maximum travel distance of 647 km based on photo-ID. From photo recapture studies in the Hawaiian Islands, the greatest span of years for an individual was 33 years (S. Mahaffy 6 May, 2022, personal communication).

The ongoing studies on false killer whales in the Hawaiian Islands have shown that there are three discrete yet partially overlapping populations (Chivers et al., 2007, Chivers et al. 2010; Baird et al., 2008, Baird et al., 2010, Baird et al., 2013; Martien et al., 2014). Individuals within a population maintain strong bonds over decades, hunt cooperatively, and share prey with hunting partners (Baird, 2016; Martien et al., 2019). Martien et al. (2019) found that both male and female main Hawaiian Islands insular false killer whales remain in their natal social groups throughout their lives and that between 34 to 64 % of matings occurred in the same

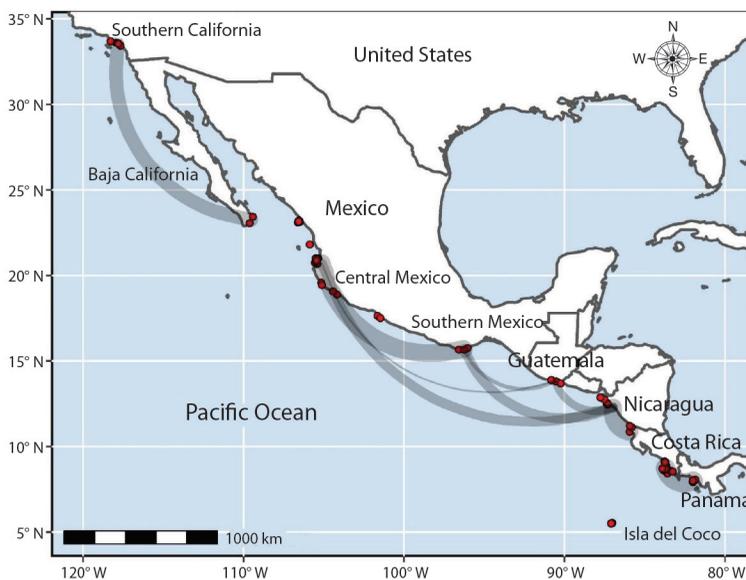


Fig. 1. Map of sighting locations (red circles) of false killer whales (*Pseudorca crassidens*) with acceptable quality photographs. Line width between sightings reflects the number of re-sightings of individuals between areas. Map created using R Statistical Software (R Core Team, 2021).

social group. This differs from other highly social species that may practice natal dispersal or exogamy to avoid inbreeding. As with other top predators, false killer whale population numbers are fairly low, they are slow to mature, have low birth rates, and females remain active in their family groups past their reproductive years (Baird, 2018a). False killer whales are active during the day and night and have been observed feeding on various species of fish including neritic, demersal, bathydemersal, reef, and pelagic game fish (Baird, 2016; Herzog & Ellis, 2016) and an analysis of stomach contents of stranded animals has shown that oceanic and neritic-oceanic squids make up a large part of their diet as well (Alonso et al., 1999). False killer whales' cooperative and adaptable hunting styles as well as their propensity to share prey within their group and occasionally with divers and boaters (Baird, 2018b) tend to put this species in conflict with small and large fishing boat operators where human and false killer whale fishing areas overlap.

Globally, false killer whales and other dolphin species are known to take the bait and catch off hook and line fisheries, and in the Hawai'i-based deep-set longline fishery, false killer whales are the cetacean species most frequently recorded as hooked as bycatch (Bradford et al., 2014; Forney & Kobayashi, 2005). One study of depredation in the Hawai'i-based deep-set longline fishery with 21 % observer coverage reported that ~6 % of hauls from 2004-2018 experienced odontocete depredation, most of it thought to be from false killer whales (Fader et al., 2021). The Inter-American Tropical Tuna Commission [IATTC] manages large longline vessels (>24 m) in the area from 50° N to 50° S from the coast of the Americas to the 150° W meridian of the eastern Pacific Ocean, with 1 123 longline vessels currently authorized to fish in this area (IATTC, 2022). Importantly, from the perspective of documenting fishery interactions, vessels less than 24 m are not managed by the IATTC and are not required to carry observers (IATTC, 2011). The Organization of the Fisheries and

Aquaculture Sector of the Central America Isthmus [OSPESCA] reports more than 5 000 vessels in the coastal and Pacific longline fleet (OSPESCA, 2012). The IATTC has repeatedly recommended at least 20 % observer coverage on longline vessels in this area, yet coverage has remained at only 5% (IATTC, 2019), and since April 2020, due to the COVID pandemic, the requirement of any observer coverage may be waived upon request (National Oceanic and Atmospheric Administration [NOAA], 2022). Thus, indirect methods of assessing whether individual false killer whales have survived fishery interactions may be the only way to determine the magnitude of such interactions on groups or populations.

In the case of false killer whales, when an individual ingests a hook or is hooked in the mouth and is able to break free from the line, scars around the mouthline and dorsal fin are often the only external evidence that an animal has been hooked and survived (Baird & Gorgone, 2005; Baird et al., 2014, Baird et al., 2017). In the absence of observer coverage, Baird et al. (2014) conducted a photo review of dorsal fin disfigurements and scarring of individual false killer whales encountered in Hawaiian waters. They found that 7.5 % of the individuals from the main Hawaiian Islands population bore scars consistent with fisheries interactions and had higher rates of fishery-related injuries than the offshore or northwestern Hawaiian Islands populations (Baird et al., 2014).

The purpose of the current study was to examine the movements of false killer whales along the Pacific coast of North and Central America, ranging from southern California to Panama. We combined the results of independent photo-ID efforts from six different countries, providing an assessment of association patterns and site fidelity, as well as examining individuals for evidence of prior fishery interactions. We hope that our findings will add to the current body of knowledge on false killer whales, as well as inspire future collaborative research with this species in these regions.



MATERIALS AND METHODS

Study area: The ETP is characterized by a strong shallow thermocline, relatively high sea surface temperatures and strong winds (Heileman, 2008). The southern part of Mexico and northern part of Central America form one side of the eastern Pacific warm pool, which constitutes an open-ocean biogeographic province with a distinct biological community (Fiedler & Talley 2006). The study area is part of a marine mega-ecosystem characterized by gulfs, bays, coastal lagoons, and extensive intertidal areas and barriers (Gocke et al., 2001; Lizano & Alfaro, 2004). It includes part of the Costa Rica Dome (CRD), an open-ocean upwelling region caused by a seasonally changing combination of interconnected features including the Intertropical Convergence Zone, coastal jets and eddies, and geostrophic balance at the eastern extreme of the 10° N thermocline ridge (Mora-Escalante et al., 2020). The CRD supports a higher density of marine fauna including cetaceans than other parts of the Central American marine ecosystem (Fiedler & Talley, 2006; Lavín et al., 2006), and likely influences the high productivity of the Pacific Central American coast (Heileman, 2008). For the purpose of examining movements, the study area was broken down into a number of regions reflecting discrete study sites: southern California, southern Baja California, the central and southern Mexican mainland coasts, Guatemala, Nicaragua, northern and southern Costa Rica, Panama and Isla del Coco.

Data collection: Research efforts varied by year, season and among regions (Table 1; Fig. 1). False killer whale photos were collected from 1991-1992 on directed surveys for cetaceans along southern Costa Rica and 1993-1994 off Isla del Coco (Acevedo-Gutiérrez et al., 1997). From 1998 to 2009 false killer whale encounters were documented during directed humpback whale surveys conducted during the dry season (December-March) along the Pacific coast of southern Costa Rica and northern Nicaragua (Table 1) by Cascadia

Research Collective (CRC) as well as independent researchers. Other efforts included systematic cetacean surveys conducted in Guatemala year-round 2008-2009 and between December-April from 2018 onward, and Costa Rica 2005-2006. In the majority of cases, effort was conducted from “pangas” or tour boats with an outboard motor, and were restricted to returning to the launch location at the end of the survey day. Photos and encounter details from 2010 to 2022 were collected and shared with CRC from directed surveys and whale and dolphin watch operations working along Nicaragua, Costa Rica, and Panama expressly for this project. The majority of CRC surveys were nonsystematic and attempted to cover a large coastal area with the primary objective of discovering humpback whales. Non-humpback whale cetacean encounters were approached for sighting position, species identification, group size estimation, and photo documentation depending on species and time of day. Sighting positions were based on an onboard GPS (directed surveys), an estimated position based on the photographers’ description, or a “general” position based on where the vessel launched and returned. During false killer whale encounters from directed surveys, efforts were made to photograph all individuals from a group, regardless of age class, or distinctiveness. As with the Central America collection, the southern California-Mexico photo-ID catalog and sighting data were collected by both directed research efforts and opportunistic sightings from ecotourism businesses. Mexico data were collected from 2004, 2007 to 2008, and 2011 to 2020 (Lazcano-Pacheco et al., 2023). Survey effort and collection methods are described by Ortega-Ortiz et al. (2014).

Data analysis: Groups were defined as all individuals encountered on the same day within a region, and IDs obtained during that day were pooled as part of a single encounter. This is a broader definition for a group than is typically used for association analysis of odontocetes, however, as with Baird et al. (2008), we view that the choice is justified for this species

Table 1

Number of groups encountered (number of identifications) of false killer whales (*Pseudorca crassidens*) by year and region, and total number of individuals by region, restricted to identifications with fair to excellent quality photographs and slightly to very distinct dorsal fins. Group was defined as all individuals encountered on the same day in the same general area. Number of groups in which group size estimates with acceptable photos are available are also included.

Year	S. California	Baja California	Cent. Mainland Mexico	S. Mainland Mexico	Guatemala	Nicaragua	N. Costa Rica	S. Costa Rica	Panama	Isla del Coco	Total
1991								1 (10)			1 (10)
1992								1 (7)			1 (7)
1993										2 (11)	2 (11)
1994										5 (40)	5 (40)
1998								2 (5)			2 (5)
2000								1 (2)			1 (2)
2004			1 (7)								1 (7)
2005						1 (4)		4 (24)			5 (28)
2006								3 (36)			3 (36)
2007								1 (1)			1 (1)
2008			1 (5)		2 (9)	1 (7)		1 (1)			5 (22)
2009					1 (6)			6 (102)			7 (108)
2010								3 (12)			3 (12)
2011			1 (8)								1 (8)
2012			3 (17)	1 (1)				3 (4)			7 (22)
2013		2 (11)	1 (13)	2 (20)							5 (44)
2014	4 (36)										4 (36)
2015	1 (1)								2 (9)		5 (28)
2016	1 (10)					2 (13)					5 (29)
2017			1 (1)			1 (9)					2 (10)
2018			4 (7)		1 (1)				2 (20)		7 (28)
2019			1 (4)						1 (9)		3 (22)
2020			2 (13)				1 (15)				3 (28)
2021	1 (3)					2 (23)					3 (26)
2022	1 (7)										1 (7)
Sum of groups	9	2	19	3	4	7	1	26	5	7	83 (577)
Sum of groups that included group size estimates	5	2	17	3	4	7	1	24	5	7	75
Mean group size (SD)	34.5 (16.2)	42.7 (52.7)	54.5 (60.1)	17.7 (6.8)	12.5 (7.7)	13.6 (8.1)		17 (13.0)	41 (15.6)	18.1 (10.9)	28.2 (34.7)
Median (range)	32.5 (15-60)	42.7 (5-80)	35 (5-200)	20 (10-23)	14 (2-20)	10 (6-25)		13 (1-50)	25 (25-60)	14 (4-34)	18 (1-200)
Sum identifications	66	11	99	21	16	56	15	204	38	51	577
Sum individuals	37	10	77	16	16	45	15	95	31	33	375



based on the infrequency of false killer whale encounters and the small groups encountered, often traveling in the same direction and spread out over many kilometers (see e.g., Bradford et al., 2014). This choice is also justified based on the many positive re-sightings of individuals between subgroups encountered on the same day. To report the mean and median group size when only a range (min/max) of group size was available, we chose the median of the two numbers. When multiple encounters occurred on the same day of the same group of animals, we chose the largest group size number, with the assumption that smaller estimates were derived from counts of subgroups encountered. Following the photo-ID protocol described in Baird et al. (2008), a Central America catalog was constructed from photographs of individuals taken off Guatemala, Nicaragua, Costa Rica and Panama. Photos from each encounter were sorted by individual into folders, assigned temporary IDs and given separate scores for photo quality (1 – poor, 2 – fair, 3 – good, 4 – excellent) and distinctiveness (1 – indistinct, 2 – slightly distinct, 3 – distinct, 4 – very distinct). Photo quality was based on focus, angle, and proportion of the dorsal fin visible, and distinctiveness was based on the absence or presence of notches on the leading and trailing edge of the fin, and/or the dorsal fin shape. Poor quality or indistinct individuals were only compared to individuals encountered on the same day, within region, while all fair to excellent quality photos of slightly distinct to very distinct IDs were compared to all IDs in the catalog. When possible, photos of unusual scars on the body and along the mouthline were noted for each individual, and scored with the likelihood that the injury could have been associated with a fishery interaction (Baird et al., 2014, Baird et al., 2017). Once the temporary ID had been compared to the catalog, the best left and/or right dorsal fin of each individual was assigned a unique ID number, or if it was found in the historical catalog the ID was collapsed into the existing record of that individual. Every positive match found between sightings was confirmed by at least two experienced matchers.

The southern California-Mexico catalog was created with similar practices as described above with quality and distinctiveness scores for each individual. Once completed, the Central America catalog was compared with the southern California-Mexico false killer whale catalog, with two experienced matchers confirming all positive matches between catalogs. In an effort to avoid false-negative matches between these two catalogs, a second experienced matcher (SDM) compared 18 % of the IDs in the southern California-Mexico catalog that had not been found by the initial matcher (ABD) (Elliser et al., 2022), and no additional matches were found. For all catalogs, only those IDs with photo quality and distinctiveness categories of two (fair) or better were compared between catalogs – these are defined as “acceptable quality” identifications. Our decision to include “fair” quality photos and slightly-distinctive IDs was made to retain a reasonable sample size for analysis and interpretation, and while it is more permissive than many studies with larger catalogs or for less remote locations, it is not without precedent (Baird et al., 2021; Elliser et al., 2022).

Linear-geographical distances between all possible pairs of encounter locations both within regions and among all regions were calculated for all encounters where acceptable identification photos and latitude and longitude were available using R Statistical Software (R Core Team, 2021). To control for pseudo-replication, when more than one individual was identified from a particular encounter, that encounter location was only used once in the calculations. If there was more than one encounter in an area on the same day (that were pooled as a single encounter), the first location was used. Combinations of encounters were generated using the *combinations* function within the *gtools* package (Warnes et al., 2020). Straight line geographical distances were calculated using the *st_distance* function within the *sf* package (Pebesma, 2018). Distances between all encounter combinations for each individual sighted on two or more occasions were also calculated. Because of the sociality of false killer

whales, there were several instances where multiple individuals were re-sighted together more than once. Hence, when summarizing distances across individual re-sightings, we only used a single set of calculated distances between pairs of individual sightings to avoid pseudoreplication.

Association analyses of photo-identified individuals were undertaken in SOCPROG 2.9 with MATLAB 9.5 (Whitehead, 2009), and social network metrics were calculated and illustrated in Netdraw 2.176 (Borgatti, 2002). To provide a quantitative measure of the frequency of co-occurrence of individuals, while controlling for effort (Whitehead, 2008), we used the half-weight index of association (HWI). Whitehead (2008) and Cairns & Schwager (1987) recommend the use of HWI in situations where it is likely that not all individuals within a sampling period are identified or when individuals of a pair are more likely to be observed separately than when together.

We used SOCPROG to assess whether the false killer whales in our study could be divided into meaningful social clusters based on levels of association between individuals using community-based modularity (Newman, 2004; Whitehead, 2009). This method divides the population into clusters in a way that maximizes associations within clusters rather than between them. A modularity value greater than 0.3 is considered to indicate the useful division of a population (Newman, 2004). We checked all cluster assignments to make sure that they made logical sense based on our knowledge of these data and the eigenvector or final bifurcation involving the individual. The eigenvector value corresponds to the certainty in the assignment of an individual in the cluster in which the individual was placed, with values near zero indicating uncertainty. We tested whether individuals showed preferential associations with companions, using the preferred/avoided association test in SOCPROG (Bejder et al., 1998; Whitehead, 2009). The null hypothesis of this test is that individuals will associate with the same probability with all other individuals in the population without individual preference.

Based on similar studies (Baird et al., 2008), we tested our data against 20 000 randomly permuted variations, so that the resultant P value was determined by the proportion of 20 000 permutations that had higher Standard Deviation (SD) values of the association indices than the SD of the association indices found in our data. For these analyses, we restricted our data to all individuals seen two or more times. We refer to groups of three or more individuals linked by association in the social network as separate components, and these components could be comprised of one or more social clusters based on the association analyses.

To evaluate possible fishery interactions, the primary catalog curator (ABD) reviewed the best left and/or right dorsal fin photo of each individual in both the Central America and southern California-Mexico catalogs for evidence of fishery interactions. Based on the presence of linear cuts, dorsal fin disfigurement (e.g., deep cut on the leading edge, missing dorsal fin, bent dorsal fin) or scarring of the area immediately in front or behind the dorsal fin (Baird et al., 2014), ABD chose photos of individuals for further evaluation. Each individual was assigned a score of one (not consistent), two (possibly consistent), or three (consistent) with a fishery interaction by ABD and two additional reviewers (SDM, RWB) with experience in reviewing dorsal fin injuries in relation to fishery interactions. The reviews were conducted independently and sent to ABD who averaged the scores for each individual whale. To assess differences in fishery interactions among areas or social clusters, we considered individuals with an average score of >2.6 as having injuries consistent with a fishery interaction (i.e., at least two reviewers would have to have scored it 3 (consistent) and the third reviewer would have to score 2 (possibly consistent)), following Baird et al. (2014).

RESULTS

Acceptable quality photos were obtained from 83 encountered groups, resulting in 577 identifications and 328 individuals (Table 1;

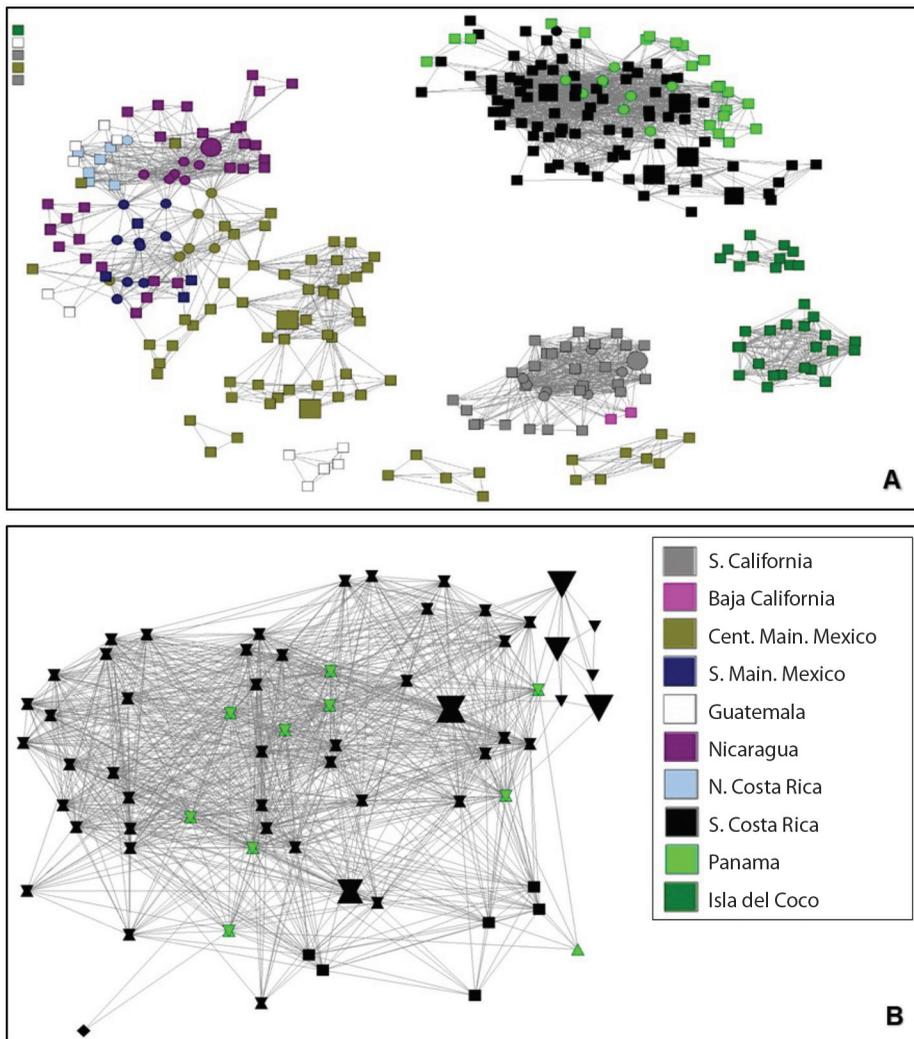


Fig. 2. Social network of false killer whales (*Pseudorca crassidens*), with individuals presented as nodes and lines between nodes indicating individuals encountered in the same area on the same day, restricted to individuals with acceptable quality and distinctiveness scores. Node color indicates the region where it was first encountered. Number of sightings by region: Southern California (n = 9); Baja California (n = 2); central mainland Mexico (n = 19); southern mainland Mexico (n = 3); Guatemala (n = 4); Nicaragua (n = 7); northern Costa Rica (n = 1); southern Costa Rica (n = 26); Panama (n = 5); Isla del Coco (n = 7). Large nodes represent individuals with injuries consistent with fishery interactions. **A.** All individuals from California to Panama and Isla del Coco (1991 to 2022), (n = 328). The greatest number of individuals linked by association (upper left - n = 119) are from mainland Mexico to northern Costa Rica. The second largest number linked by association (upper right - n = 116) represents individuals from southern Costa Rica and Panama. Node shape indicates individuals encountered in multiple regions (circle) or single region (square). **B.** False killer whales from southern Costa Rica to Panama (1991 to 2022), restricted to individuals seen 2 or more times. Node shape represents clusters: hourglass - Cluster 3; up triangle - Cluster 4; diamond - Cluster 9; square - Cluster 13; down triangle - Cluster 17 (Clusters with evidence of fishery interaction are listed in Table 4). Location first seen is indicated by color as per A. Social network metrics were calculated and illustrated in Netdraw 2.176.



were not linked to the largest component of the social network (Fig. 2A). The second largest number of individuals linked by association (242 identifications of 116 individuals over 31 encounters) was from southern Costa Rica and Panama (Fig. 2B). All individuals documented in those two areas were linked in the same component of the social network, with ten individuals encountered in both regions (Table 2). Out of the 116 southern Costa Rica and Panama individuals, 52.6 % (61) individuals have been re-sighted on more than one day, and 40.5 % (47) individuals have been re-sighted for more than one year.

No matches were found between the 33 individuals documented (from seven encounters) around Isla del Coco and individuals encountered in coastal waters, although re-sightings of individuals were reported within the region (Table 2). The majority (21 of 33, 63.6 %) of individuals from Isla del Coco were linked by association in one component of the social network, and 11 (33.3 %) were linked in another (Fig. 2A).

The average straight-line distance among re-sightings of individuals (mean = 303.3 km, SD = 505.4, median = 51.2) was far less than the average distance among encounters (mean = 1 796.7 km, SD = 1 551.2, median = 1 594.1). Greatest straight-line distances between re-sightings of individuals were between Mexico and Central America (mean = 794.5 km, SD = 626, median = 639.5), with 2 265 km being

the maximum straight-line travel distance for an individual (CRC_CA_Pc234_MX_Pc176) sighted off central mainland Mexico on 1 February 2020 and re-sighted off southern Nicaragua 6 August 2021 (Table 3, Fig. 1). Average re-sighting distances of individuals between southern Costa Rica and Panama were far less than between the other regions (mean = 79.9 km, SD = 88.5).

Social network cluster analysis and community structure: Using community division by modularity and social network analysis, we found that the 328 distinct individuals identified could be assigned into 22 clusters by association (modularity = 0.77, maximum modularity type 1 controlling for gregariousness). Tests for preferred/avoided associations among individuals were significant ($P = 0.999$), so that we could reject the null hypothesis that associations were random. Repeated associations were documented most consistently in the southern Costa Rica-Panama social network, with average and maximum mean association HWI values among individuals of 0.09 (SD = 0.04) and 0.79 (SD = 0.18), respectively (Fig. 2B). Individuals within the Costa Rica-Panama social network from Cluster 3 (average and maximum mean association HWI values 0.11 (SD = 0.03) and 0.80 (SD = 0.17)) had the longest association between individuals (CRC_CA_Pc027 and CRC_CA_Pc028) spanning 12.1 years, with five sightings of these whales

Table 3

Straight-line distances between all possible pairs of encounters where individual false killer whales (*Pseudorca crassidens*) were photo-identified, and distances among re-sightings of individuals. For the comparison of distances of re-sighted individuals, the grand mean/median values are shown.

	Mean distance (SD) (km)	Median distance (km)	Maximum distance (km)
All countries – all possible pairs	1 796.7 (1 551.2)	1 594.1	5 096.3
Re-sighted individuals	303.3 (504.4)	51.2	2 265.1
S. California & Baja California – all possible pairs	628.7 (784.0)	50.9	1 655.8
Re-sighted individuals	543.5 (745.7)	34.4	1 655.8
Cent. Mainland Mexico-N. Costa Rica – all possible pairs	1 162.5 (874.0)	1 095.0	2 710.1
Re-sighted individuals	794.5 (626.5)	639.5	2 265.1
S. Costa Rica & Panama – all possible pairs	79.8 (83.3)	48.6	246.1
Re-sighted individuals	79.8 (88.5)	42.1	238.6

encountered together. Except for the first and last encounters of CRC_CA_Pc027, in 2005 and 2019, CRC_CA_Pc027 and CRC_CA_Pc028 have been encountered together every time that one has been sighted. Long term associations have been observed in the southern California and Baja California region as well, with two individuals (IDs MX_085 and MX_90) encountered together five times between 2013-2021 (9.0 years). Additionally, individuals MX_085 and MX_166 have been encountered together five times between 2014-2022 (8.0 years).

Insufficient information on survey effort is available to quantify seasonal sighting rates. However, it is worth noting that thirty-eight (76.0 %) of Central America encounters occurred during the Boreal winter (November-March), while 90.0 % of southern California-Mexico encounters occurred during the same period. All of the southern California and one of the two Baja California encounters occurred in March, the second Baja California encounter occurred in May.

Fishery interactions: Seventeen individuals were initially selected for review of injuries consistent with fisheries interactions, 12 from the Central America catalog and five from the southern California-Mexico catalog. Of these, our three reviewers agreed that nine had injuries consistent with fisheries interaction (average score > 2.6): one off southern California, two off central mainland Mexico, one individual seen off Guatemala, Nicaragua, and northern Costa Rica, and five from southern Costa Rica (see Fig. 3 for examples). A single individual

encountered off Isla del Coco bore injuries that may have been related to fisheries, but received an average score of 2.3. Individuals with fishery-related injuries were found in five of the clusters identified through community division, with the greatest percentage of individuals with fisheries-related injuries (21.4 %) found in southern Costa Rica (Cluster 17) (Table 4), and the second greatest percentage from Cluster 12 encountered off central mainland Mexico, with 7.1 % of individuals having fishery related injuries. One of the individuals from Cluster 21 (Fig. 3G) had injuries consistent with fishery interactions, although it is also possible the wound was caused by a propeller injury.

DISCUSSION

Our analyses of false killer whales individually identified from 1991 to 2022 from southern California to Panama show high levels of site fidelity, particularly off southern Costa Rica and Panama, and strong associations among individuals, with maximum HWI association values among individuals exceeding 0.50. Gero et al., (2008) and Durrell et al., (2004) note associations are considered strong when the HWI between associates was at least twice the mean index of all the dyads in the unit or cluster being considered, which was the case in Cluster 3 from southern Costa Rica and Panama. From re-sightings of individuals photographed off central mainland Mexico and Nicaragua, we documented travel distances greater than those observed from satellite-tagged pelagic false killer whales in Hawaiian waters (Anderson et

Table 4

Number and percentage of individual false killer whales (*Pseudorca crassidens*) by cluster (determined through community division) with injuries consistent with fishery interactions.

Cluster	Regions documented	Number of individuals in cluster	Number (%) with injuries consistent with fishery interactions
6	S. California & Baja California	37	1 (2.7 %)
12	Cent. Mainland Mexico	28	2 (7.1 %)
10	Cent. Mainland Mexico - N. Costa Rica	33	1 (3.0 %)
17	S. Costa Rica	14	3 (21.4 %)
3	S. Costa Rica & Panama	69	2 (2.9 %)
Total		182	9 (4.9 %)

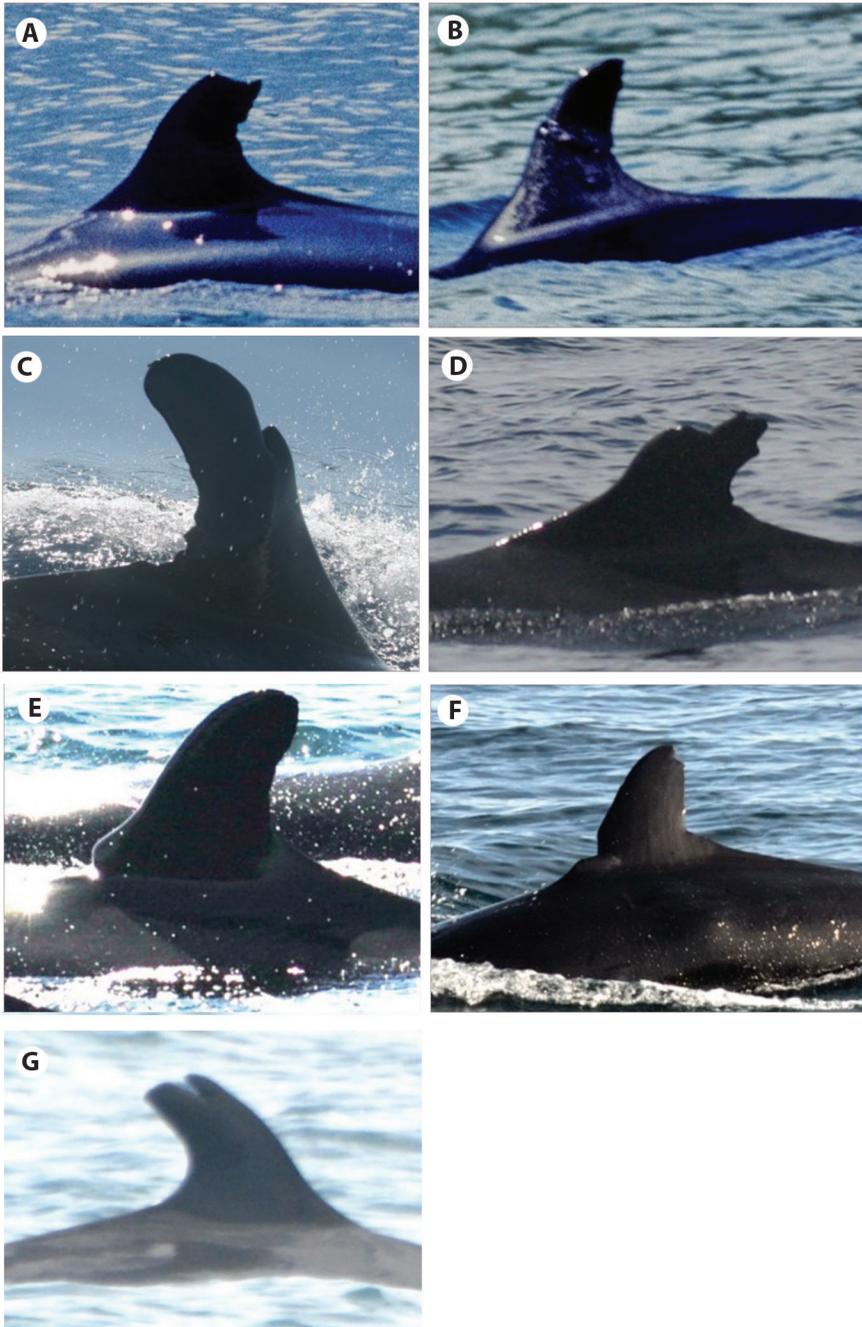


Fig. 3. Examples of scarring and injury of dorsal fins determined to be consistent with fisheries interaction (FI) from southern Costa Rica, (A) CRC_CA_Pc23, 1992, (B) CRC_CA_Pc102, 1991, (C) CRC_CA_Pc057, 2009, (D) CRC_CA_Pc032, 2006, and Central Mainland Mexico (E) MX_074, 2013, (F) MX_084, 2013. (G) CRC_CA_Pc188 from northern Costa Rica is an example of an injury that we determined to be consistent with fisheries interaction, although whether the injuries were caused by a line or propeller is unknown.

al. 2020; E. Oleson personal communication, 27 July, 2022) especially considering that we calculated straight-line distances, and did not account for non-linear movements and intervening land masses. False killer whales encountered off southern Costa Rica and Panama appear to have a much smaller range of travel, smaller even than the insular false killer whales tagged in the Hawaiian Islands (Baird et al., 2012). It is important to note, however, that there was very limited effort off the continental shelf, so we are unable to assess offshore movements. The infrequency of sightings of false killer whales on the continental shelf could be an indication that individuals documented in our study spend a considerable proportion of their time in offshore waters, that local abundance is low, or a combination of both factors. There were no matches between individuals documented off Isla del Coco in 1993 or 1994 and the mainland. While the mainland photographic sample was largely obtained from six to more than twenty years later, there were matches from the Acevedo-Gutiérrez et al. (1997) effort off mainland Costa Rica from prior to the Isla del Coco effort.

We found that the proportion of individual false killer whales with evidence of surviving prior fishery interactions for at least one cluster was higher than those found in the endangered main Hawaiian Islands insular population (Baird et al., 2014). Individuals from Cluster 17, which had the greatest percentage of fisheries interactions (21.4 %), have only been encountered off southern Costa Rica. They were encountered by Acevedo-Gutiérrez et al. (1997) in Golfo Dulce in 1991 and 1992 and the most recent sightings of any of these animals occurred off Drake Bay in 2006. In a similar study of fishery-related injuries in Hawai'i, the evaluators found significant differences in fishery interaction rates by population and cluster, with 12.8 % of individuals from Cluster 3 from the main Hawaiian island population determined to have fishery-related scarring. Baird et al. (2014) found a significant bias towards females with injuries consistent with fisheries interactions, which, the authors

note, could reduce the potential population growth rate to a greater extent than if fishery interaction was unbiased by sex. Although we identified the sex of some individuals based on close attendance of small calves, performing a comparable test with our data was beyond the scope of this study. It is important to note that false killer whales can incur severe injuries that may appear to be fishery related from sources other than fisheries interaction. For example, Ortega-Ortiz et al. (2014) describe at least one individual with injuries obtained from interactions with a billfish or sailfish.

There are a number of assumptions and biases in this study that we would like to note. Many of the encounters in this study came from community scientists or were collected opportunistically, and thus not all individuals within larger groups were necessarily photographed. Thus, there are a lot of isolated individuals or small clusters in the social network that in reality should be linked to other individuals. For example, the 2018 encounter of the only individual not linked to a cluster from Guatemala had an estimated group size of two. Therefore, we can safely assume that there is at least one and likely a number of clusters that use our larger study area that are unaccounted for in these data. Group size estimates were collected with different methodologies, and we acknowledge that false killer whale group size is difficult to assess, as individuals are generally fast moving in a spread-out group (Baird et al., 2008; Bradford et al., 2014). Sighting positions are estimated in most non-directed survey efforts, and this can impact the calculated distance between sightings, although this should not influence the large difference between encounter locations and re-sighting locations documented. Distinct individuals are more likely to be photographed and recognized over time, even with lesser quality photographs, so there are likely some missed matches within our catalog, particularly given the long duration of our study. The two individuals with the longest sighting history (CRC_CA_Pc063 seen over 26 years, and CRC_CA_Pc009 seen over 19 years) were both very distinct. Although



we are not estimating abundance here nor survival, we would like to note that our stated method of including “fair” quality photos as well as only considering recaptures with high certainty, could result in higher abundance estimates and lower re-sighting rates (Ashe & Hammond, 2022).

We recommend additional effort in offshore areas as well as satellite tagging to clarify population structure and relationship to animals in coastal areas, especially in light of the lack of connection between Central America and Isla del Coco. Additional acceptable ID photos from any region would be welcome, especially offshore waters, the Galapagos Islands, Isla del Coco, and South America. One of our authors (DMP) recalls false killer whale encounters a handful of times in the Galapagos during the warm-water season. From records collected from 1923 to 2003 there is a single record of a mass stranding of six false killer whales in the Galapagos Islands (Palacios et al., 2004). False killer whales are also encountered farther south, with an encounter noted off central Ecuador in 2003 (Baird, 2010; Castro, 2004). Photos of two individuals from the Galapagos were not included in this study due to poor quality; however, these photos are available to compare to any future identifications that we receive.

Field effort in most of the study sites was seasonally biased. However, southern California has whale and dolphin watch excursions year-round, therefore the apparent seasonal presence of false killers along southern California in March is likely not random. This consistency of presence could allow for planning a successful photo-ID and tagging effort on this group of false killer whales, which could shed light on these animals' whereabouts over time. Throughout the study area, individuals whose livelihoods depend on whale and dolphin watch tourism would benefit if these animals' patterns were better understood, and most importantly, we hope that future studies could help inform fisheries so that they could avoid encounters that are detrimental to false killer whales as well as the humans whose livelihoods depend on

the same food source. Currently, to learn more about how and why false killer whales are interacting with longline vessels, the fisheries have options of either increasing observer coverage and/or the installment of electronic monitoring systems (EMS) on fishing vessels. Due to the stated difficulty of finding observers willing to take part in the observer program, as well as the difficulties of dealing with the COVID pandemic, Costa Rica and other countries have appealed to the IATTC to provide funds for EMS (Villanueva, 2018).

In addition to recommending future survey work, we urge greater cooperation among researchers and community scientists in sharing historical catalogs/photo collections. Our data collection has been a slow process, spanning 31 years with sometimes a few photos and a general location from a tour vessel representing the only encounter for a year or a region. Additional catalogs/photo collections exist throughout this study area, which we were not able to access, and we hope that with careful planning and cooperation these data will become available in the near future. As with other odontocetes, false killer whales are viewed as sentinel species in their environment, and studies in the Hawaiian Islands have shown they have high levels of lipophilic contaminants (Kratofil et al., 2020). Greater cooperation among researchers with these data will lead to a greater understanding of how false killer whales use these waters and the depth of long-term associations with individuals and their habitat.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

Author Contribution: ABD conceptualized the manuscript, coordinated data acquisition, performed analysis, interpreted the data

results, and drafted the initial and revised versions of this manuscript. FGA, AAG, SDM, KR, EQR, JDW, DMP, DMF, CLP, CDOO, JC, and RWB contributed with data, and interpretation of the results for each study site, reviewed and approved the various drafts and final version of the manuscript. NR, AFJ and FV contributed data and reviewed the final version of the manuscript.

See supplementary material
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