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SHORT COMMUNICATION

Mid-distance movements of common bottlenose dolphins in the coastal waters of Greece

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Abstract While bottlenose dolphins in Mediterranean waters often display a high degree of site fidelity, movements across distant areas can occur. Such movements have important implications in terms of population viability, particularly in basins with low bottlenose dolphin densities. We report movements of nine individuals photo-identified up to 265 km apart in western Greece. Four showed a certain degree of site fidelity to one area across several years, but were also found elsewhere, with two individuals moving between two areas. This study provides further evidence that animals appearing to be "resident" within a given area can temporarily leave and range widely.

Keywords Common bottlenose dolphin · *Tursiops truncatus* · Ecology · Movements · Mediterranean Sea

Introduction

Insight into the movement patterns of common bottlenose dolphins *Tursiops truncatus* (hereafter "bottlenose dolphins") and other cetacean species can be successfully derived from individual photo-identification (Wells et al. 1990). Based on information obtained through photo-identification methods, bottlenose dolphins in Mediterranean coastal waters are sometimes considered "resident" in a given location, their range often being described and interpreted from the perspective of the study area covered by the researchers. In the region, researchers investigating bottlenose dolphin movements and site fidelity normally operate within relatively small study areas (Bearzi et al. 2008b) and they return to a given port every day. When recognizable animals are not seen for a period of time, researchers rarely know how far and wide the animals have ranged. Lack of recorded occurrence of individual dolphins in a given month or year may relate to a number of reasons, including insufficient survey effort, behavior by individual animals (e.g., boat avoidance) or movements away from the study area.

Insufficient information on long-distance movements tends to result in higher emphasis on site fidelity, and less emphasis on roaming or use of alternative core habitats. Dispersion and roaming, however, are biologically important and serve a number of key functions (Lack 1954; Wynne-Edwards 1962; Hansson 1991; Stenseth and Lidicker 1992). Animals may disperse when their food supplies (or other resources) diminish below a critical level (Lidicker 1962; Grant 1978). Conflict over resources such as food, shelter or mates can result in dispersal, mammalian females usually competing for food and males competing for females (Dobson 1982; Moore and Ali 1984). Individuals of one sex (typically males in mammals; Greenwood 1980) may disperse to mate with unrelated conspecifics, therefore reducing the likelihood of inbreeding (Dobson 1982; Dobson and Jones 1985). Of the factors resulting in dispersal, resource shortage and conflict over resources will usually act in a density-dependent way, while inbreeding avoidance should lead to density-independent dispersal (Hansson 1991). For instance, bottlenose dolphins off the Azores Archipelago (Portugal) make extensive movements of almost 300 km and have large home ranges, which represent a response to the low density and patchy distribution of their prey (Silva et al. 2008). Wide-ranging behavior and lack of territoriality in the

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Azores also provide, and possibly increase, opportunities for interbreeding, thus enhancing genetic differentiation and reducing the likelihood of inbreeding (Silva et al. 2008).

Results

To complement existing information in the scientific literature, we report the movements of nine bottlenose dolphins in the coastal waters of western Greece, individually photo-identified based on long-term natural marks on their dorsal fins (Würsig and Würsig 1977; Würsig and Jefferson 1990; Fig. 1).

Approximately 100 bottlenose dolphins were identified and repeatedly observed in the Inner Ionian Sea Archipelago within an area of 1000 km^2, where photo-identification effort began in 1993 (Bearzi et al. 2005; Tethys Research Institute, unpublished data). Approximately 150 individuals were identified and repeatedly observed in the Amvrakikos Gulf, a semiclosed basin of 400 km^2 where photo-identification started in 2001 (Bearzi et al. 2008a; Tethys Research Institute, unpublished data). A total of 31 individuals were identified within an area of 1400 km^2 situated in the central part of the Gulf of Corinth, where photo-identification started in 2009 (Bearzi et al. 2010; Tethys Research Institute, unpublished data; Fig. 2).

Movements of nine individual dolphins observed across study areas are shown in Fig. 2, based on global positioning system (GPS) positions combined with individual photo-identification data confirming presence of the relevant animals within groups of variable size and composition, with none of the animals being consistently sighted together. Movements were recorded during 193 continuous boat follows averaging 94 min [standard deviation (SD) 0.47 min, range 10–289 min]. Convoluted courses (Fig. 2)

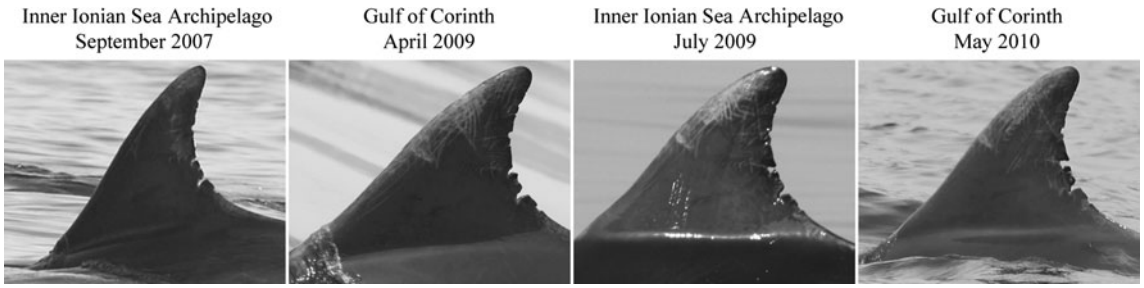

Fig. 1 Dorsal fin profile of bottlenose dolphin designated as T4 in Fig. 3, photo-identified in the Inner Ionian Sea Archipelago and in the Gulf of Corinth

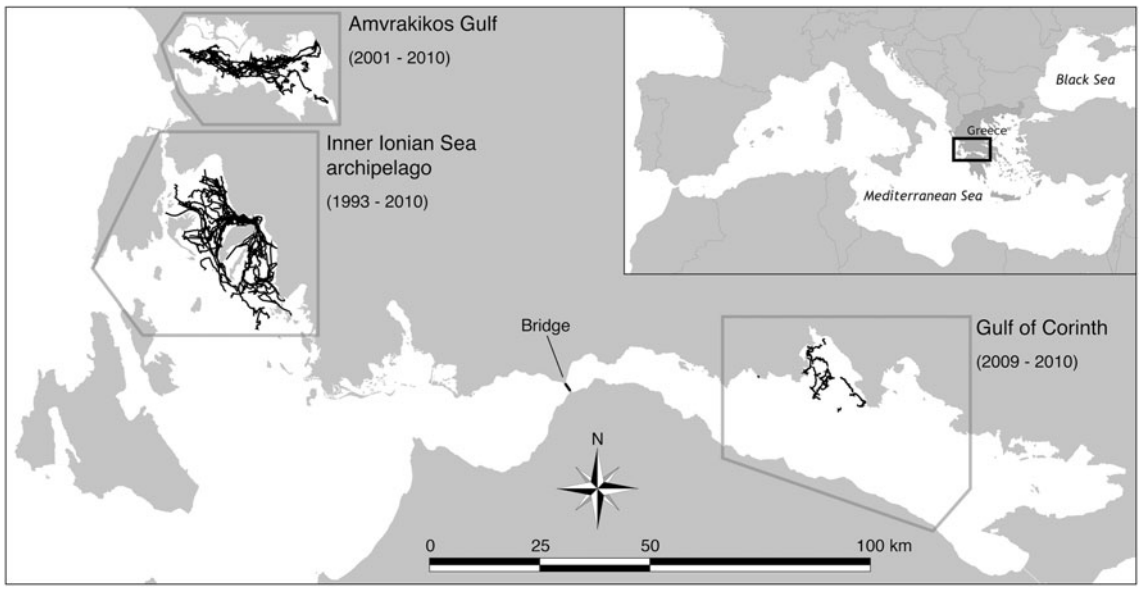

Fig. 2 Location of the three study areas in Greece (delimited by *grey lines*). *Black lines* indicate movements by nine bottlenose dolphins (T1–T9 in Fig. 3). Time intervals indicate years of photo-identification effort. Movements from the Inner Ionian Sea Archipelago to the Gulf of Corinth (and back) imply transit through the 1.9-km-wide Rion–Antirion Strait below a four-pylon bridge (the Charilaos Trikoupis Bridge; http://www.gefyra.gr)

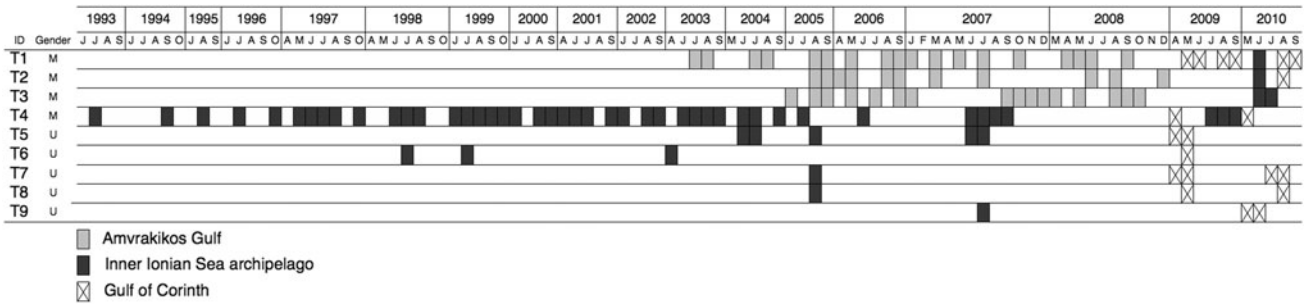

Fig. 3 Resighting patterns of nine bottlenose dolphins photo-identified in the Amvrakikos Gulf, Inner Ionian Sea Archipelago, and Gulf of Corinth. Individuals T1, T2, and T3 were males (*M*) based on photographs of their genital area. T4 was most likely a male based on absence of associations with a calf throughout the whole study period. All other individuals were of unknown gender (*U*)

suggest that the animals did not simply transit through the areas, but made movements indicative of food search or foraging (Bearzi et al. 1999; Bailey and Thompson 2006), as confirmed by observations of diving behavior. Extent of movement between areas, calculated as the minimum linear distance connecting the two most distant points where each of the nine dolphins was photo-identified, excluding land, ranged between 128 and 265 km (mean 187 km, SD 45.7 km, $n = 9$).

Eight of the dolphins photo-identified in the Inner Ionian Sea Archipelago between 1993 and 2010 were also encountered in 2009 and 2010 in the upper central Gulf of Corinth, largely within the Bay of Itea (Fig. 2), since a study in this area began in April 2009 resulting in the photo-identification of 31 individuals.

The individual designated T1 in Fig. 3 was consistently observed in the Amvrakikos Gulf. From 2009, T1 appeared in the Gulf of Corinth, then in the Inner Ionian Sea Archipelago, and then again in the Gulf of Corinth. Individuals T2 and T3 made a similar transition from the Amvrakikos Gulf to the Inner Ionian Sea Archipelago, T2 being also subsequently observed in the Gulf of Corinth. All three individuals were identified as males based on photos depicting their genital area and dorsal fin.

Individual T4—most likely a male based on lack of observed associations with calves across 17 years, encompassing 46 months—was the second most "resident" animal observed in the Inner Ionian Sea Archipelago, where he was encountered for 15 consecutive years, from July 1993 to September 2007, across a total of 43 months (Fig. 3). T4 was observed in the Gulf of Corinth in April 2009, he returned to the Inner Ionian Sea Archipelago between July and September 2009, and was resighted in the Gulf of Corinth in May 2010. From June 2006 this dolphin had what appeared to be a portion of trammel net stuck into his blowhole and protruding for about 20–30 cm. A fragment of net about twice as long, suggesting progressive extrusion, was still present in April 2009, but had disappeared by July 2009. This incident, which apparently had a favorable outcome, did not prevent wide-ranging movements.

The resighting patterns of five other dolphins, photo-identified in the Inner Ionian Sea Archipelago between 1998 and 2010 and also encountered in the Gulf of Corinth, are shown in Fig. 3. Overall, eight (25.8%) of the 31 bottlenose dolphins photo-identified in the Gulf of Corinth in 2009 and 2010 were also seen in the Inner Ionian Sea Archipelago, and two in the Amvrakikos Gulf.

Discussion

All the animals of known gender in this study were males, and one was most likely a male. This preliminary evidence is consistent with the hypothesis that males are more wide-ranging than females, and they may therefore be the primary vectors of genetic exchange (Wells et al. 1987; Bearzi et al. 1997).

While the information presented in this study relied on individual photo-identification, bottlenose dolphin movement patterns can also be investigated using remote tracking methods such as radio and satellite telemetry (Tanaka 1987; Mate et al. 1995; Corkeron and Martin 2004; Klatsky et al. 2007). Such methods, however, are often quite invasive and have never been successfully applied to bottlenose dolphins in the Mediterranean Sea. Below, we provide a short overview of the available information on movements by bottlenose dolphins worldwide, based on evidence from both individual photo-identification and remote tracking.

Bottlenose dolphins living in sheltered coastal environments (e.g., embayments) usually display a high degree of site fidelity to local areas and may belong to relatively small communities or populations (Wells et al. 1987; Bearzi et al. 2008b), whereas animals inhabiting less protected waters (e.g., open coasts) tend to exhibit more extensive ranging patterns and appear to be part of larger

populations. For instance, bottlenose dolphins off southern California show no evidence of site fidelity, and many range widely along portions of coast up to approximately 500 km, normally within 1 km of the shoreline (Defran and Weller 1999; Defran et al. 1999). Dolphins living at high latitudes, in cold water at the extremes of the species' range, may migrate seasonally. At the northern limit of their range in the northeastern Atlantic, bottlenose dolphins have a seasonal residency pattern, spending the winter in the waters of southern Cornwall and moving north during spring and summer. Individual dolphins use the area intermittently across a linear range of coast of 650 km, making repeated long-distance journeys (the longest covered 1076 km and took 20 days; Wood 1998). Long-distance movements, possibly common though not always observed by researchers, may also occur as a consequence of regime shifts and may be influenced by temperature changes and oceanographic phenomena such as El Niño (Hansen and Defran 1990; Mead and Potter 1990; Wells et al. 1990).

Mate et al. (1995) used a satellite transmitter to track the movements of a bottlenose dolphin in Tampa Bay, Florida. The dolphin traveled at least 581 km during 25 days, the longest distance traveled in a day being 50 km. Dolphins in Sarasota Bay, Florida traveled less than 30 km/day (Irvine et al. 1981). An animal satellite-tracked off Japan traveled about 600 km in 18 days along the Kuroshio Current (Tanaka 1987). Two bottlenose dolphins, *Tursiops* sp., satellite-tracked off eastern Australia for 30 and 143 days, covered ranges of up to 778 km^2, with a core area of 86 km^2 (Corkeron and Martin 2004). Several bottlenose dolphins photo-identified off Argentina made a 600 km round trip (Würsig 1978), and eight bottlenose dolphins photo-identified off southeastern Brazil showed movements of up to 100 km (Lodi et al. 2008). The most extensive movements reported so far come from two bottlenose dolphins satellite-tracked following their stranding in Florida: one covered 2050 km in 43 days, the other 4200 km in 47 days, swimming through waters 5000 m deep (Wells et al. 1999).

Several solitary bottlenose dolphins have been known to range widely, although others have remained within relatively small areas over extended periods (Wilke et al. 2005). The solitary dolphin nicknamed Dolphy traveled approximately 400 km along the Spanish and French Mediterranean coast (Lockyer and Müller 2003).

Long-term residency among bottlenose dolphins often involves repeated occurrence in a given area over many years. For instance, bottlenose dolphin communities along Florida's west coast have maintained stable home ranges since 1970 (Wells 2003). The home range of coastal bottlenose dolphin communities may encompass areas of around 100–150 km^2 (Maze and Würsig 1999; Wells and Scott 1999). This pattern, however, does not always imply permanent or year-round residency. For example, bottlenose dolphins in the Moray Firth, Scotland, were seen year-round but there were seasonal fluctuations in the number of individuals, numbers being lower in winter and spring but higher in summer and autumn. One individual was sighted at locations 190 km apart within a 5-day period (Wilson et al. 1997).

A recent study conducted in the waters around Ireland provides comprehensive evidence of wide-scale, long-distance movements of bottlenose dolphins in European waters (O'Brien et al. 2010). Resightings of 23 individuals were recorded across three seasons between 2005 and 2009, at distances ranging from 130 to 650 km. The study suggests that bottlenose dolphins in Irish coastal waters move around the entire Irish coast and are highly mobile and transient, although individuals photo-identified in the Shannon Estuary—home to Ireland's only known resident group of bottlenose dolphins—have not been recorded elsewhere (O'Brien et al. 2010).

In Mediterranean waters, some bottlenose dolphin communities have shown high levels of long-term site fidelity, e.g., around the island of Lošinj, Croatia (Bearzi et al. 1997, 1999) and in the semiclosed Amvrakikos Gulf, Greece (Bearzi et al. 2008a). Genetic or other evidence of coastal and offshore "ecotypes", as found in other areas (Duffield et al. 1983; Van Waerebeek et al. 1990; Mead and Potter 1995), has not been reported in the Mediterranean Sea (Natoli et al. 2005). Bottlenose dolphin groups are occasionally sighted in offshore waters deeper than 2000 m, and movements into and across pelagic waters may occur (Bearzi et al. 2008b). Published information on movements by bottlenose dolphins in the Mediterranean Sea, however, is scant. An individual photo-identified off northern Corsica was resighted after 50 days in the Hyères Archipelago, southeastern continental France, 228 km away from the original location (Dhermain et al. 1999). Mid-range movements were also observed among bottlenose dolphins photo-identified off the northwestern coast of Italy, between Genoa and Viareggio, with five individuals resighted 100–130 km apart (Gnone et al. 2006). So far, the longest movement reported in the region is that of the solitary dolphin mentioned previously (400 km; Lockyer and Müller 2003).

The present study further documents that, while bottlenose dolphins in coastal Mediterranean waters may display a high degree of site fidelity, they can also move extensively across geographical areas. Even animals appearing to be resident within a given area can temporarily leave "home" and range over large portions of sea. Such movements may have important implications in terms of population viability, particularly in areas with low bottlenose dolphin densities as in the coastal waters of western

Greece (Bearzi et al. 2005, 2008b). This information must be taken into account in the design of conservation actions (Berger 2004; Hoyt 2005) demanded by local and regional legislation (Bearzi et al. 2008b). Research effort resulting in extensive photo-identification catalogues can increase understanding of bottlenose dolphin movement patterns in the region and inform management action.

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References

Bailey H, Thompson P (2006) Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. J Anim Ecol 75:456–465

Bearzi G, Notarbartolo di Sciara G, Politi E (1997) Social ecology of bottlenose dolphins in the Kvarneric (northern Adriatic Sea). Mar Mammal Sci 13:650–668

Bearzi G, Politi E, Notarbartolo di Sciara G (1999) Diurnal behavior of free-ranging bottlenose dolphins in the Kvarneric (northern Adriatic Sea). Mar Mammal Sci 15:1065–1097

Bearzi G, Politi E, Agazzi S, Bruno S, Costa M, Bonizzoni S (2005) Occurrence and present status of coastal dolphins (*Delphinus delphis* and *Tursiops truncatus*) in the eastern Ionian Sea. Aquat Conserv 15:243–257

Bearzi G, Agazzi S, Bonizzoni S, Costa M, Azzellino A (2008a) Dolphins in a bottle: abundance, residency patterns and conservation of common bottlenose dolphins *Tursiops truncatus* in the semi-closed eutrophic Amvrakikos Gulf, Greece. Aquat Conserv 18:130–146

Bearzi G, Fortuna CM, Reeves RR (2008b) Ecology and conservation of common bottlenose dolphins *Tursiops truncatus* in the Mediterranean Sea. Mammal Rev 39:92–123

Bearzi G, Bonizzoni S, Agazzi S, Gonzalvo J, Currey RJC (2010) Striped dolphins and short-beaked common dolphins in the Gulf of Corinth, Greece: abundance estimates from dorsal fin photographs. Mar Mammal Sci (in press)

Berger J (2004) The last mile: how to sustain long-distance migration in mammals. Cons Biol 18:320–331

Corkeron PJ, Martin AR (2004) Ranging and diving behaviour of two 'offshore' bottlenose dolphins *Tursiops* sp., off eastern Australia. J Mar Biol Assoc UK 84:465–468

Defran RH, Weller DW (1999) The occurrence, distribution, and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in San Diego, California. Mar Mammal Sci 15:366–380

Defran RH, Weller DW, Kelly DL, Espinosa MA (1999) Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. Mar Mammal Sci 15:381–393

Dhermain F, Ripoll T, Bompar JM, David L, Di Meglio N (1999) First evidence of the movement of a bottlenose dolphin *Tursiops truncatus* between Corsica and Hyeres Archipelago, southeastern France. Eur Res Cetaceans 13:306–311

Dobson FS (1982) Competition for mates and predominant juvenile mate dispersal in mammals. Anim Behav 30:1183–1192

Dobson FS, Jones WT (1985) Multiple causes of dispersal. Am Nat 126:855–858

Duffield DA, Ridgway SH, Cornell LH (1983) Hematology distinguishes coastal and offshore forms of dolphins (*Tursiops*). Can J Zool 61:930–933

Gnone G, Nuti S, Bellingeri M, Pannoncini R, Bedocchi D (2006) Comportamento spaziale di *Tursiops truncatus* lungo la costa del Mar Ligure: risultati preliminari. Biol Mar Medit 13:272–273

Grant PR (1978) Dispersal in relation to carrying capacity. Proc Natl Acad Sci USA 75:2854–2858

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Hansen LJ, Defran RH (1990) A comparison of photo-identification studies of California bottlenose dolphins. In: Hammond PS, Mizroch SA, Donovan GP (eds) Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Rep Int Whal Commn, Special issue 12, Cambridge, pp 101–104

Hansson L (1991) Dispersal and connectivity in metapopulations. Biol J Linn Soc Lond 42:89–103

Hoyt E (2005) Marine protected areas for whales, dolphins and porpoises: a world handbook for cetacean habitat conservation. Earthscan, London

Irvine AB, Scott MD, Wells RS, Kaufmann JH (1981) Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. Fish Bull 79:671–688

Klatsky LJ, Wells RS, Sweeney JC (2007) Offshore bottlenose dolphins (*Tursiops truncatus*): movement and dive behavior near the Bermuda Pedestal. J Mammal 88:59–66

Lack D (1954) The natural regulation of animal numbers. Clarendon, Oxford

Lidicker WZ Jr (1962) Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. Am Nat 46:29–33

Lockyer C, Müller M (2003) Solitary, yet sociable. In: Frohoff T, Peterson B (eds) Between species: celebrating the dolphin-human bond. Sierra Club Books, San Francisco, CA, pp 138–150

Lodi L, Liberali Wedekin L, Rossi-Santos MR, Marcondes MC (2008) Movements of the bottlenose dolphin (*Tursiops truncatus*) in the Rio de Janeiro State, Southeastern Brazil. Biota Neotropica 8(4). doi:10.1590/S1676-06032008000400020

Mate BR, Rossbach KA, Nieukirk SL, Wells RS, Irvine AB, Scott MD, Read AJ (1995) Satellite-monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. Mar Mammal Sci 11:452–463

Maze KS, Würsig B (1999) Bottlenose dolphins of San Luis Pass, Texas: occurrence patterns, site-fidelity, and habitat use. Aquat Mamm 25:91–103

Mead JG, Potter CW (1990) Natural history of bottlenose dolphins along the central Atlantic coast of the United States. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic, San Diego, pp 165–195

Mead JG, Potter CW (1995) Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the Atlantic coast of North America: morphologic and ecologic considerations. IBI Reports (International Marine Biological Research Institute, Kamogawa, Japan) 5:31–44

Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? Anim Behav 32:94–112

Natoli A, Birkun A, Aguilar A, Lopez A, Hoelzel AR (2005) Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). Proc R Soc B Biol Sci 272:1217–1226

O'Brien JM, Berrow SD, Ryan C, McGrath D, O'Connor I, Pesante G, Burrows G, Massett N, Klötzer V, Whooley P (2010) A note

on long-distance matches of bottlenose dolphins (*Tursiops truncatus*) around the Irish coast using photo-identification. J Cetacean Res Manage 11:69–74

Silva MA, Prieto R, Magalhães S, Seabra MI, Santos RS, Hammond PS (2008) Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. Mar Biol 156:179–192

Stenseth NC, Lidicker WZ (1992) Animal dispersal: small mammals as a model. Chapman & Hall, London

Tanaka S (1987) Satellite radio tracking of bottlenose dolphins *Tursiops truncatus*. Nippon Suisan Gakk 53:1327–1338

Van Waerebeek K, Reyes JC, Read AJ, McKinnon JS (1990) Preliminary observations of bottlenose dolphins from the Pacific coast of South America. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic, San Diego, pp 143–154

Wells RS (2003) Dolphin social complexity: lessons from long-term study and life history. In: de Waal FBM, Tyack PL (eds) Animal social complexity: intelligence culture and individualized societies. Harvard University Press, Cambridge, pp 32–56

Wells RS, Scott MD (1999) Bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). In: Ridgway SH, Harrison R (eds) Handbook of marine mammals—the second book of dolphins and porpoises, vol 6. Academic, San Diego, pp 137–182

Wells RS, Scott MD, Irvine AB (1987) The social structure of free-ranging bottlenose dolphins. In: Genoways HH (ed) Current mammalogy, vol 1. Plenum, New York, pp 247–305

Wells RS, Hansen LJ, Baldridge A, Dohl TP, Kelly DL, Defran RH (1990) Northward extension of the range of bottlenose dolphins along the California coast. In: Leatherwood S, Reeves RR (eds) The bottlenose dolphin. Academic, San Diego, pp 421–431

Wells RS, Rhinehart HL, Cunningham P, Whaley J, Baran M, Koberna C, Costa DP (1999) Long distance offshore movements of bottlenose dolphins. Mar Mammal Sci 15:1098–1114

Wilke M, Bossley M, Doak W (2005) Managing human interactions with solitary dolphins. Aquat Mamm 31(4):427–433

Wilson B, Thompson PM, Hammond PS (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. J Appl Ecol 34:1365–1374

Wood CJ (1998) Movement of bottlenose dolphins around the south-west coast of Britain. J Zool 246:155–163

Würsig B (1978) Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. Biol Bull 154:348–359

Würsig B, Jefferson TA (1990) Methods of photo-identification for small cetaceans. In: Hammond PS, Mizroch SA, Donovan GP (eds) Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Rep Int Whal Commn, Special issue 12, Cambridge, pp 43–52

Würsig B, Würsig M (1977) The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). Science 198:755–756

Wynne-Edwards VC (1962) Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh