Presence, Behavior, and Resighting Pattern of Transient Bottlenose Dolphins (*Tursiops truncatus*) in the Humboldt Current System off North-Central Chile

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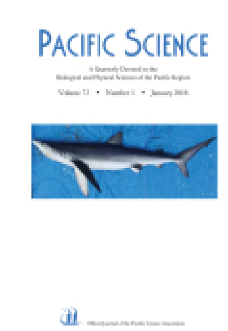

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Presence, Behavior, and Resighting Pattern of Transient Bottlenose Dolphins (*Tursiops truncatus*) in the Humboldt Current System off North-Central Chile[1]

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Abstract: Biotic and abiotic factors determine presence and habitat use pattern of individuals within a population. In this study, presence, behavior, and resighting patterns of transient bottlenose dolphins (*Tursiops truncatus*) were evaluated in relation to upwelling and downwelling events in a marine reserve in North-Central Chile, between 2005 and 2009. The study period was divided into four phases according to wind direction and intensity: upwelling-favorable (UF), transition I (TI), convergence (Cv) or downwelling, and transition II (TII). Results show that transient bottlenose dolphins are an open population with low resighting rates. Highest occurrence and a largest number of transient dolphins were identified during 2009, probably due to an increase in prey availability. The most frequent behavior observed was traveling, followed by feeding and socializing. Traveling was mainly recorded in individuals seen only once and in years with low productivity. In contrast, feeding was observed in individuals seen two or more times, was similar among phases, and was more frequent in more-productive years. Social behavior was associated with the highest resighting rates. This study documents how transient bottlenose dolphins use the area based on their resighting patterns and suggests that periods of upwelling and downwelling modulate behavior displayed by these dolphins within the area.

Keywords: *Tursiops truncatus*, upwelling, downwelling, year, phase, photo-identification

Presence, abundance, and habitat use of marine species are influenced by different biotic and abiotic factors, such as temperature and salinity (Parsons 1998), abundance and distribution of resources (Stevick et al. 2006), and competition and predation (Papastamatiou et al. 2006), among others. The spatial and/or temporal variation of these factors, as well as the possible interactions among them, generally determine habitat use by animals, and in turn their presence, residency, behavior, and group size patterns (Wilson et al. 1997, Heithaus and Dill 2002). Because of habitat heterogeneity, variability in behavior and habitat use is to be expected in different areas.

For some cetacean species, habitat characteristics have been found to strongly influence differences in site fidelity (e.g., Ballance 1992, Rossi-Santos et al. 2007). In the bottlenose dolphin, *Tursiops truncatus* (Montagu), three residence patterns (i.e., temporal variations in

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presence in a given area) have been described (Wilson et al. 1997, Connor et al. 2000, Zolman 2002). Year-round residents maintain a small home range and live within the same area for many years, or even their entire life. These individuals display daily feeding, reproductive activities, and relatively short distance movements within the area (Connor et al. 2000, Gubbins 2002). This type of residency is generally observed when resources are predictable in both space and time (Gowans et al. 2007). Seasonal residents are individuals that use a specific area for a couple of months or an entire season during consecutive years (Zolman 2002). This pattern is usually associated with spatiotemporal variation in prey availability (Mead and Potter 1990, Barco et al. 1999, Toth et al. 2011) and/or the presence of predators (Heithaus 2001, Heithaus and Dill 2002). Transient or nomadic residents are animals that show minor or no site fidelity (Defran et al. 1999, Zolman 2002). These animals are generally observed in areas where resources are sparsely and unpredictably distributed (Gowans et al. 2007). The latter group has larger home ranges in comparison to those of year-round resident groups, and the schools are likely to include a greater number of individuals and possess foraging and anti-predator strategies as consequence of their extensive home ranges (Ballance 1992, Defran and Weller 1999, Gowans et al. 2007). However, presence and behavior of transient groups can be expected to change within areas with high productivity.

In North-Central Chile, the Marine Reserve of Chañaral and Choros-Damas Islands (MRC-CD), within the Humboldt Current System, is a dynamic and productive coastal environment due to the presence of an important wind-driven coastal upwelling center (Montecino, Strub, et al. 2006; Thiel et al. 2007). This upwelling center is characterized by high levels of primary production and is driven by prevailing southwest winds particularly during late spring and summer (Montecino, Strub, et al. 2006). In contrast, there is downwelling, or upwelling relaxes during winter due to convergent winds coming from the north, and productivity is lower than in summer (Montecino, Strub, et al. 2006). Also, Montecino, Paredes, et al. (2006) defined two transitional phases, one in autumn and the other during early spring, based on the sea-surface temperature.

The MRC-CD hosts a high diversity of marine animals, including marine birds and mammals (Luna-Jorquera et al. 2003, Pérez et al. 2006, Sepúlveda et al. 2009). Among these species, a year-round resident group of bottlenose dolphins has been reported since 1981 (González et al. 1989), with a total of 45 individuals sighted in subgroups of between two and 40 individuals (Gibbons 1992, Thomas 2005). In addition, the occurrence of larger groups of more than 100 individuals has been recorded in this area. These larger groups have been classified as *pelagic* by Hanshing (2001), *nonresident* by Thomas (2005), and *transient* by Santos-Carvallo et al. (2015). To the best of our knowledge, no further studies have focused on habitat use and resighting patterns of transient groups in this productive but seasonally variable area.

The aim of this study was to evaluate the presence, resighting, and behavior patterns of transient bottlenose dolphins in the MRC-CD. Because these parameters have been associated with biotic and abiotic factors, the dynamic and productive coastal environment was expected to influence bottlenose dolphins in this area. Based on this, we hypothesized that: (1) higher occurrence, more frequent feeding behavior, and a higher resighting rate in transient dolphins would be related to periods of upwelling-favorable winds (Aravena et al. 2014, Rahn et al. 2015); (2) more frequent travel behavior, lower occurrence, and lower resighting rate in these groups would be related to convergent winds or downwelling conditions (Montecino, Strub, et al. 2006; Aravena et al. 2014); and (3) a medial situation of occurrence and resighting rate would be related to transitional periods between upwelling and downwelling conditions.

MATERIALS AND METHODS

Study Area and Data Collection

The study was conducted between January 2005 and September 2009 in the MRC-CD:

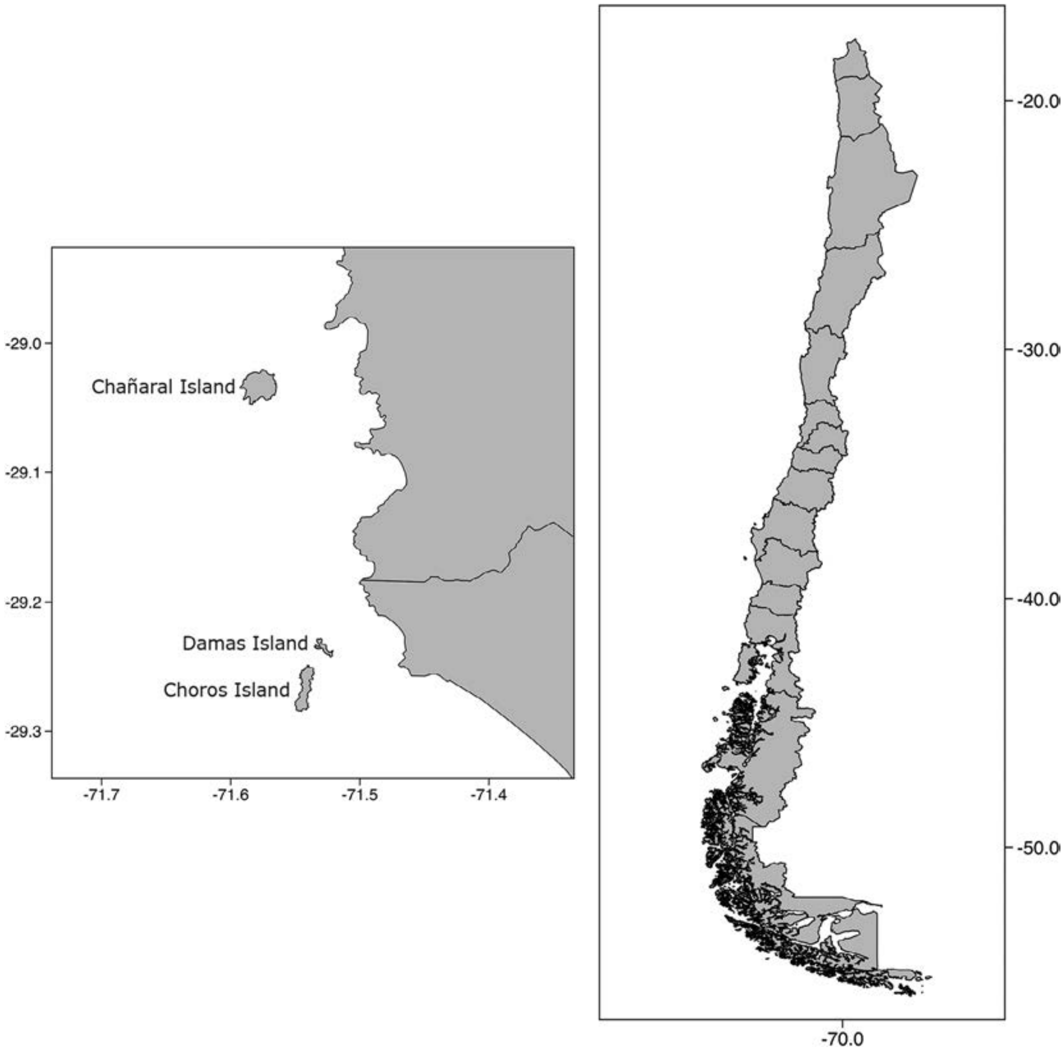

FIGURE 1. Map showing the study area (*left*) and Chile (*right*).

Chañaral Island (29.03° S, 71.57° W), Choros Island (29.26° S, 71.54° W), and Damas Island (29.23° S, 71.52° W) (Figure 1). A total of 83 boat-based surveys was conducted, using a 7 m local fishing vessel equipped with a 40-horsepower outboard motor. Surveys were carried out during daylight hours from 0800 hours to 1600 hours in Beaufort sea states of 3 or less.

During each survey, a visual examination of the area was undertaken by at least three experienced observers with the naked eye and binoculars. In the presence of dolphins, the boat approached them at a constant speed with caution, remaining parallel to the group without disturbing them, following the protocol of Würsig and Jefferson (1990). A "group" was defined as two or more dolphins in association, within 100 m of each other, moving in the same direction and engaging in the same behavior (Shane 1990, Hastie et al. 2003). A "sighting" corresponded to each time an individual or group was observed (Karczmarski et al. 2000).

For each sighting, time, position, group size, and group behavior were recorded. Group size and composition was determined by counting the minimum, maximum, and mean number of adults and calves (Karczmarski et al. 2000).

Identification of Productivity Phases

The presence of different phases of productivity in the MRC-CD was evaluated using wind direction and intensity. Local wind information for the entire study period was obtained from a coastal meteorological station located in Coquimbo Bay (30.0° S, 71.4° W) at 122 m above sea level. These data also characterize the Coquimbo Bay upwelling system, where the study area is located (Bravo et al. 2016). Wind data were separated into north-south (along-shore) and east-west (across-shore) wind components. Only the along-shore wind component was considered in this study, because it directly triggers upwelling events (Figueroa and Moffat 2000). Positive values correspond to north winds (downwelling), and negative values correspond to south winds (upwelling). Four phases were defined for the study area: (1) upwelling-favorable (UF), from October to February, with a predominance of southerly winds (negative values) of 0.9 msec^{-1} and 0.6 msec^{-1} and corresponding to higher primary productivity than the rest of the phase; (2) transition I (TI), from March to April, with southerly winds (negative values) of intensities of 0.2 msec^{-1}, corresponding to a transition from higher to lower primary productivity; (3) convergence (Cv) or downwelling, from May to July, with northerly winds (positive values) of 0.5 msec^{-1} and 0.1 msec^{-1}, corresponding to lower primary productivity than upwelling phase, and (4) transition II (TII), from August to September, with southerly winds (negative values) of 0.4 msec^{-1} and 0.5 msec^{-1}, corresponding to a transition from lower to higher primary productivity (Figure 2) (modified from Montecino, Paredes, et al. 2006).

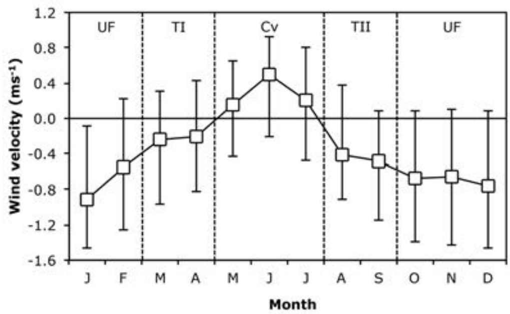

Figure 2. Monthly distribution of wind velocity (msec^{-1}) by phase in Coquimbo Bay from 2005 through 2009. Upwelling-favorable (UF), transition I (TI), convergence (Cv), and transition II (TII). Boxes indicate median values and whiskers indicate 25th and 75th percentiles.

Occurrence Patterns

To evaluate the occurrence of transient dolphins in the study area, two time-scale analyses (annual and per phase) were conducted. The annual occurrence index (AOI) is the total number of transient dolphin sightings per year in relation to the annual effort (2005–2009). Similarly, the phase occurrence index (POI) considers the total number of transient dolphin sightings per phase (UF, TI, Cv, and TII) in relation to phase effort.

Resighting Patterns

The identification of individuals was done using photo-identification. This technique relies on matching the distinctive dorsal fin features using natural markings such as nicks and notches on both the trailing and leading edges of the dolphin fin (Würsig and Jefferson 1990). Each dolphin group was photographed by at least two researchers with experience in photo-identification using digital cameras (Canon EOS 5D and 40D) and autofocus 70–200 mm and 100–400 mm zoom lenses. The photographs were taken randomly and perpendicular to the body axis, as was suggested by Würsig and Jefferson (1990).

In the laboratory, photographs were first assessed for quality (focus, clarity, contrast, angle, visible portion of fin, and percentage of picture filled by the fin) using imaging software (Adobe Photoshop CS2), and the best-quality photographs were selected for analysis. Second, only individuals that had distinguishable features on the dorsal fin were considered. Third, photographs of each encounter previously selected were visually compared over all encounters to perform the matching process. The visual process was carried out by two experienced researchers, using imaging software [Windows Photo Gallery and Adobe Photoshop Lightroom (version 2.7)]. The matching process determines whether dolphins from an encounter are already considered in the existing catalog or are new additions (Würsig and Jefferson 1990). In this way the photo-identification catalog of transient bottlenose dolphins in the MRC-CD was constructed. The number of identified individuals was standardized according to the annual and phases effort.

A discovery curve was constructed based on the identification and resightings of individuals. The transient bottlenose dolphin population within MRC-CD was considered closed if the same individuals were always found in the area, or open if new individuals were found entering and leaving the area (Bearzi et al. 1997, Toth et al. 2011).

Resighting patterns were quantified by a residence index (RI) (ranging from 1 to 100), using the following equation (modified from Lusseau 2005):

$$RI = \frac{S}{M} \times 100$$

where RI = residence index, S = total number of months in which a particular individual was observed, and M = total number of monthly surveys. Multiple sightings of a dolphin within the same month were considered as a single sighting.

In addition, a resighting rate (RR) was calculated to show the proportion of identified individuals resighted in the MRC-CD on an annual basis [Annual Resighting Rate (ARR)] and on a phase basis [Phase Resighting Rate (PRR)]. ARR or PRR were quantified using the following equation (modified from Wedekin et al. 2010):

$$RR = \frac{rd}{di}$$

where RR = resighting rate (annual, ARR; phase, PRR), rd = number of resighted dolphins during a particular year [annual (rda) or phase (rdp)], di = number of dolphins identified in that year [annual (dia) or phase (dip)]. The number of resighted individuals was standardized according to the annual and phase effort [ARR (or PRR) / annual (or phase) effort].

Behavioral Sampling and Analysis

Behavioral observations of transient bottlenose dolphins were conducted using the group scan sampling methodology (Mann 1999) to include the greatest proportion of individuals within the group (Altmann 1974) and to avoid bias due to conspicuous individuals and/or behaviors (Mann 1999). This method assumes that all individuals within that group showed the same behavior (Mann 1999). The behavior of dolphins was classified into four categories based on specific observed behavioral events (Shane et al. 1986): feeding, resting, socializing, and traveling (Table 1). The behaviors were ordered according to their observed frequency during the sighting. In this way, the most frequent behavior was recorded first and the least frequent at the end.

The frequency of the behavior observed during the entire study period was compared using a standardized measure of the frequency of each predominant behavior with the following proportion:

$$SFB = \frac{\Sigma fc}{\Sigma ER} \times 100$$

where SFB is the standardized frequency of a behavior, Σfc is the sum of frequencies of a particular behavior in a defined period, and ΣER is the sum of total behaviors displayed during the same period. $SFBa$ and $SFBp$ refer to the frequency of displayed behaviors among years and phases, respectively. A similar

TABLE 1

Behavior Classification of Bottlenose Dolphin Groups in the MRC-CD According to Shane et al. (1986)

Behavior	Definition
Traveling	Dolphins involved in persistent directional movement usually faster than the idle speed of the observing boat. Group spacing varies and individuals swim with short, relatively constant dive intervals.
Feeding	Dolphins involved in efforts to capture and consume prey as shown by chasing fish on the surface, coordinated deep diving with loud exhalations (but not chuffing), and rapid circle swimming in one location (but not chasing another dolphin). There was usually no contact among individuals (as often observed when socializing). Prey were sometimes observed in dolphins' mouths and frequently observed during the foraging bout.
Resting	Dolphins engaged in a low level of activity, with slow movements as a tight group (i.e., less than one body length between individuals) and were occasionally stationary. Resting lacked the active components of the other behaviors described.
Socializing	It is composed of several high-energy activities. Dolphins observed leaping, chasing, and engaged in body contact with each other. Involved aspects of play and mating with other dolphins.

analysis was performed grouping individuals with the same RI. Thus, for each RI a SFB_{RI} was calculated. These last analyses were performed for the three most frequently recorded behaviors.

Statistical Analyses

Group sizes were presented as medians (25% and 75%, interquartile range) because the data were highly variable and sample sizes were relatively small. Kruskal-Wallis nonparametric tests were used to compare survey effort across phases and years, and to compare occurrence patterns across years (AOI) and phases (POI), because the data departed from normality (Zar 1999). The Mann-Whitney *U* test was performed to compare differences between years and phases when variances were not homogeneous. Contingency tables (2 × 2) were created to test whether the main behavioral categories varied among years, phases, and/or RI, and to test differences in the number of identified individuals per hour among years and phases. All the analyses were performed in Statistica 7.0 (StatSoft Inc. 2004) at the significance level $\alpha = .05$.

RESULTS

Survey effort lasted from 2 to 7 hr survey^{-1} (mean = 4.2 hr) and was similar across years ($H = 1.68$; df = 4, 83; $P = .79$), and phases ($H = 6.82$; df = 3, 83; $P = .08$). The total survey effort was 353 hr; 28 hr were spent with transient bottlenose dolphins.

Occurrence Patterns

Transient bottlenose dolphins were recorded in 28 of the 83 surveys (33.7%). The AOI showed significant differences among years ($H = 13.34$; df = 4, 83; $P = .01$), with higher occurrence of transient bottlenose dolphins during 2009 (Table 2). Otherwise, no differences were found in the POI per phase ($H = 0.14$; df = 3, 83; $P = .99$) (Table 3).

Resighting Patterns

In 22 of the 28 surveys transient bottlenose dolphins were photo-identified. After the matching process, 581 distinct individuals were identified. Of these, 465 (80%) were sighted only once (RI = 2.5), 91 (15.7%) were sighted twice (RI = 5.0), and 25 (4.3%) were sighted three or four times (RI = 7.5–10). The discovery curve increased continuously and did not reach an asymptote (Figure 3). Most distinct individuals per hour occurred during 2009, and the fewest were recorded in 2005 (Figure 4*A*). In terms of phase, most distinct individuals were recorded during UF and TI phases and the fewest during the Cv phase (Figure 4*B*).

TABLE 2

Annual Occurrence Index (AOI) of Transient Bottlenose Dolphins (*Tursiops truncatus*) in the MRC-CD from 2005 to 2009

		2005		2006		2007		2008	
Year	AOI	*U*	*P*	*U*	*P*	*U*	*P*	*U*	*P*
2005	0.06	—	—						
2006	0.06	214.0	.86	—	—				
2007	0.10	121.5	.35	100.0	.25	—	—		
2008	0.11	164.0	.25	136.0	.18	115.5	.96	—	—
2009	0.22	52.5	**<.01**	41.5	**<.01**	39.0	**<.05**	55.0	**<.05**

Note: Results of Mann-Whitney tests are shown; significant differences are presented in **bold**.

TABLE 3

Phase Occurrence Index (POI) of Transient Bottlenose Dolphins (*Tursiops truncatus*) in the MRC-CD from 2005 to 2009

		UF		TI		Cv	
Phase[a]	POI	*U*	*P*	*U*	*P*	*U*	*P*
UF	0.11	—	—				
TI	0.08	375.0	.73	—	—		
Cv	0.12	227.0	.94	116.5	.78	—	—
TII	0.09	228.0	.95	90.0	.87	75.5	.81

Note: Results of Mann-Whitney tests are shown.
[a] Upwelling-favorable (UF), transition I (TI), convergence (Cv), and transition II (TII).

The annual resighting rate (ARR) varied among years, reaching a maximum value during 2007 (Figure 4*A*), when more than 50% of the individuals identified in that year were resighted. The lowest ARR values were recorded during 2008 (Figure 4*A*). The resighting rate also varied among phases (PRR), reaching the highest values during TII and the lowest values during UF and Cv (Figure 4*B*).

Group Size and Behavioral Patterns

Group sizes were estimated during 29 of the 33 sightings. Group sizes were highly variable, ranging from five to about 1,000 individuals, with a median (md) of 70 (25% = 12; 75% = 120). Highest median values were obtained during TI (md = 110) and UF (md = 70) phases, and lowest values were recorded during Cv (md = 30.5) and TII (md = 20) phases.

Dolphin group behavior varied significantly during the study period, with traveling occurring significantly more frequently than other behaviors (Table 4). No significant differences were found between the frequencies of feeding, resting, and socializing. An interannual comparison of the three most frequent behaviors shows that the highest frequency of traveling was recorded during 2005 (Figure 5*A*), and feeding behavior was most frequently recorded in 2008 and 2009 and not observed in 2005 (Figure 5*B*). Finally, social behavior was observed during all years but was significantly higher in 2007 (Figure 5*C*). However, when comparing behaviors among phases, traveling had higher frequency during the Cv and TII phases (Figure 6*A*); whereas feeding was similar during all four phases (Figure 6*B*). Social behavior was recorded only during UF and TI phases (Figure 6*C*). Finally, the analysis of individual behavior with respect to RI (SFB_{RI}) showed that the largest proportion of traveling behavior was displayed by the animals seen only once (RI = 2.5), and the largest proportion of feeding behavior was found in animals sighted two or more times (Table 5). No variation in RI was found in social behavior (Table 5).

DISCUSSION

The number of identified transient bottlenose dolphins observed in the study area increased continuously during the entire study period,

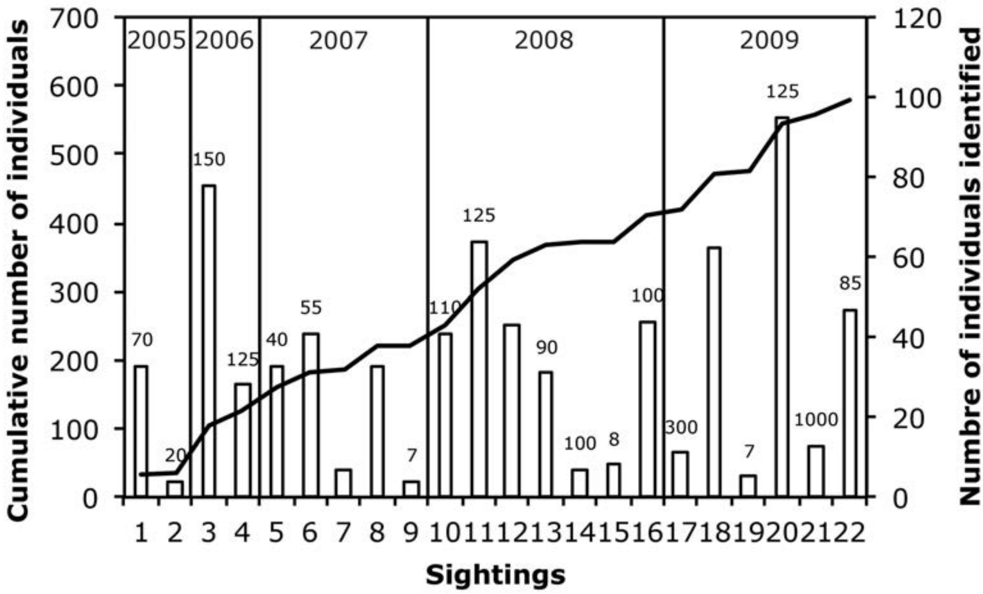

Figure 3. Cumulative discovery curve (line) and number of identified individuals per sighting (white bars) of transient bottlenose dolphins (*Tursiops truncatus*) in the MRC-CD from 2005 to 2009. Numbers on top of the bars indicate the estimated group size for each sighting.

suggesting an open population, due to a regular influx of new animals to the study area (Parra et al. 2006, Reisinger and Karczmarski 2010). The large number of identified individuals, the continuous increase of new identified animals, and the large proportion of them seen only once suggest that the animals seen in MRC-CD form part of a much larger population, as reported by Reisinger and Karczmarski (2010) for Indo-Pacific bottlenose dolphins off the South African coast.

Eighty percent of transient bottlenose dolphins were observed only once, and the most frequent behavior recorded for these individuals was traveling, suggesting that the study area is used mainly as a transit zone. These results were similar to those found by Barco (1995) off the coast of Virginia and Toth et al. (2011) off the New Jersey coast, in the United States. Both studies reported a similar increasing pattern in the rate of discovery of new individuals, and it was suggested that dolphins were possibly using the area as a corridor. By contrast, in our study individuals that were seen two or more times were using the study area not only as an area for traveling but mainly for feeding and social activities. This association between behaviors and resighting rates suggests that the residence index of transient bottlenose dolphins in the MRC-CD is in accordance with different habitat uses.

The group sizes of transient dolphins were highly variable (5 to 1,000 individuals), with a greater median than previous reports (e.g., Defran and Weller 1999, Bearzi 2005, Silva et al. 2008). It has been proposed that large groups of dolphins are made up of subgroups that form temporary alliances in response to predators (Shane et al. 1986, Speakman et al. 2006, Gowans et al. 2007) or to spatiotemporal variations in resource availability (Saayman and Tayler 1973, Shirakihara et al. 2002, Gowans et al. 2007). These social strategies could be used by transient groups in the MRC-CD and could explain the high variability in group size.

The most frequent behaviors recorded in transient bottlenose dolphin groups in the MRC-CD were traveling, followed by feed-

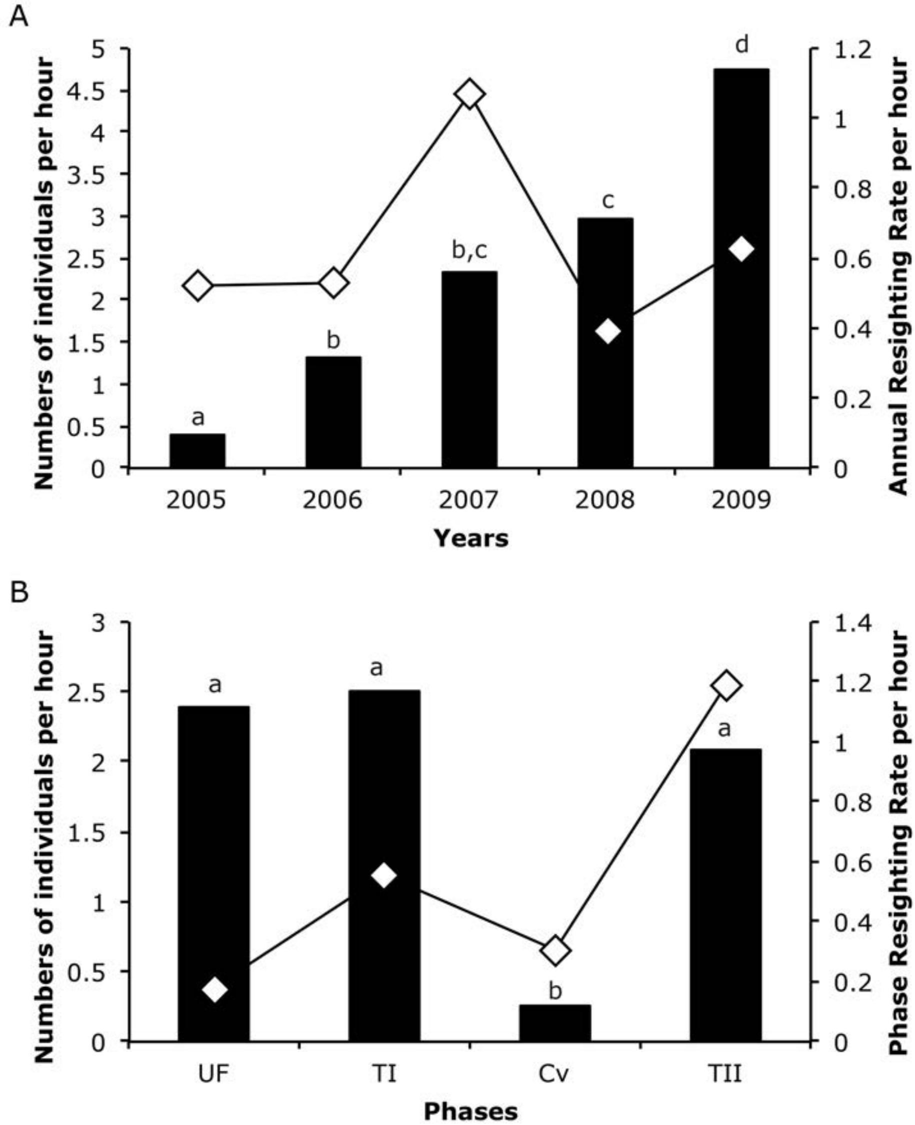

Figure 4. Total number of individuals per hour (black bars) and resighting rate per hour (line with diamonds) for (*A*) years and (*B*) phases observed in transient bottlenose dolphins (*Tursiops truncatus*) in the MRC-CD. For the total number of individuals per hour, different letters on top of the bars indicate statistically significant differences using chi-square (X^2) analysis ($\alpha = .05$).

ing and socializing, in accordance with other studies of the same species with low fidelity to one particular area (e.g., Hanson and Defran 1993, Bearzi 2005, Bearzi et al. 2009). The traveling behavior was higher in 2005, suggesting that dolphins could have invested more time traveling in search of food during that year. In fact, 2005 was characterized by minimum commercial fish landings in the port of Coquimbo, located 70 km south of the study area (Sernapesca 2005, 2006, 2007, 2008, 2009). Thus, in areas where food avail-

TABLE 4

Behavior Analysis of Transient Bottlenose Dolphins (*Tursiops truncatus*) Recorded in the MRC-CD from 2005 to 2009

		Traveling		Feeding		Resting	
Behavior	SFB[a] (%)	X^2	P	X^2	P	X^2	P
Traveling	43.9	—	—				
Feeding	22.8	5.7	**.02**	—	—		
Resting	12.3	14.1	**<.001**	2.2	.1	—	—
Socializing	21.0	12.6	**.009**	0.05	.8	1.6	.2

Note: Results of chi-square tests are shown; significant differences are presented in **bold**.

[a] Standard frequency behavior.

ability is poor or scarce, a search mode can be expected, where straight-line travel minimizes the time spent between patches and reduces search redundancy (Zollner and Lima 1999). The feeding behavior was higher in 2008 and 2009. Potential prey items for the bottlenose dolphin are anchovy (*Engraulis ringens*), chub mackerel (*Scomber japonicus*), Chilean jack mackerel (*Trachurus murphyi*), Pacific menhaden (*Ethmidium maculatum*), and South Pacific hake (*Merluccius gayi gayi*) (Van Waerebeek et al. 1990, Hanson and Defran 1993), and these showed highest landings in the port of Coquimbo during 2009, in comparison with the previous years (2005–2008) (Sernapesca 2005, 2006, 2007, 2008, 2009). A relationship between level of primary productivity and fisheries catches has been suggested (Beddington 1995, Pauly and Christensen 1995). Thus, maximum feeding behavior registered during 2009 could be related to an increase in food availability in the study site and in adjacent areas during that year (Wilson et al. 1997, Heithaus and Dill 2002). Similarly, during 2009 a large number of transient dolphins were identified and the highest annual occurrence index (AOI) value was recorded. A similar relationship was found across phases, where most transient individuals were identified in the UF and TI phases. This situation also suggests an increment of food availability in both phases that influences, at least in part, the presence of individuals in the study area (Wilson et al. 1997). Similar results were reported by Wilson et al. (1997), who found that the number of identified dolphins increased in summer, suggesting the arrival of new individuals during that season due to an increase in food availability.

In terms of phases, a relationship between phases of higher productivity (UF phase) and feeding behaviors was expected. On the contrary, during periods of food scarcity (CV phase), a transitory use of the habitat with more traveling behavior was expected. These predictions were partially supported. Although traveling was the most frequent behavior recorded during the CV and TII phases, feeding activities were similar all year around during all phases. Because a resident population of bottlenose dolphins is found in the study area year-round (Thomas 2005, Santos-Carvallo et al. 2015), we suppose that food availability is sufficient for dolphins and thus feeding behavior does not change across the year. It is interesting that even though dolphins were seen feeding during all phases, large groups of dolphins were registered during UF and TI phases, and only small groups of animals were seen during Cv and TII phases, suggesting that seasonal variations in food sources may influence feeding behavior and group size in transient bottlenose dolphins. Even though TI and TII are both transitional phases, these results suggest that TI would be more similar in environmental conditions to UF and thus more productive than TI, which is more similar to Cv. In this way, seasonal variations in food sources may influence feeding behavior and group size in transient bottlenose dolphins.

A different scenario occurred in 2007. During that year, the most frequent behavior displayed by transient dolphins was socializing, also with the highest value of annual resighting rate (ARR). Dolphins may prefer some habitats not only because of prey availability, but also because these habitats may allow them to carry out social interactions or avoid predators, and they feed only when the opportunity presents itself (Allen et al. 2001). In the same manner, a predominance of social behavior in the transient population was recorded during the productive phases UF

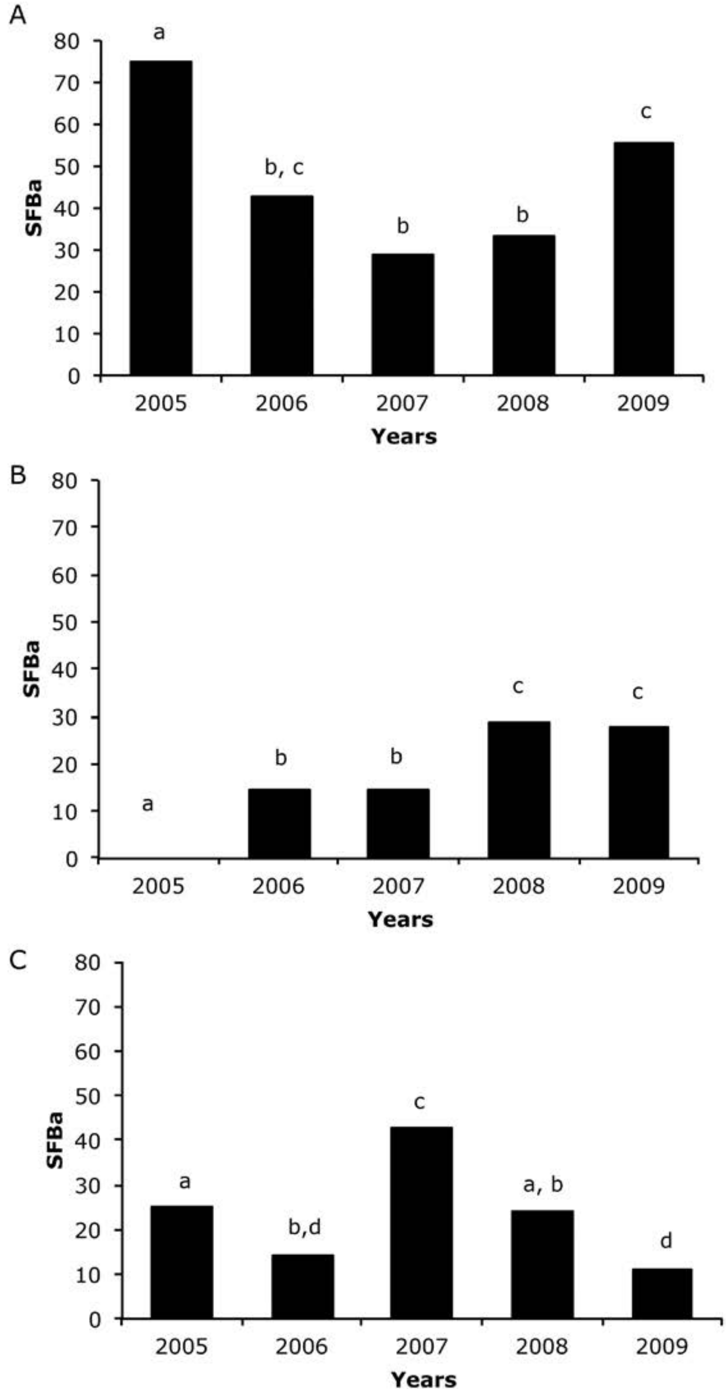

Figure 5. Standardized annual frequency of behavior (SFBa) for (*A*) traveling, (*B*) feeding, and (*C*) socializing observed in transient bottlenose dolphins (*Tursiops truncatus*) from 2005 to 2009 in MRC-CD. Different letters on top of the bars indicate statistically significant differences among years using chi-square (X^2) analysis ($\alpha = .05$).

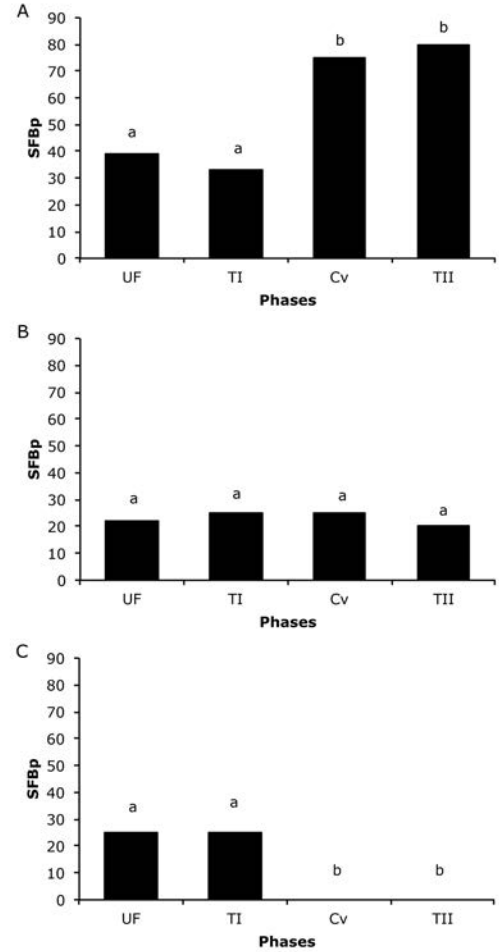

FIGURE 6. Phase standardized frequency of behavior (SFBp) for (a) traveling, (b) feeding, and (c) socializing behavior states observed in transient bottlenose dolphins *Tursiops truncatus* among phases in MRC-CD. Different letters on top of the bars indicate statistically significant differences between phases using chi-square (X^2) analysis ($\alpha = .05$).

TABLE 5

Behavior and Residence Index (RI) of Transient Bottlenose Dolphins (*Tursiops truncatus*) in the MRC-CD

			2.5		5.0	
Behavior	RI	% ind.	X^2	P	X^2	P
Traveling	2.5	68	—	—	—	—
	5.0	41	14.7	**<.001**	—	—
	≥7.5	35	21.8	**<.001**	0.8	.38
Feeding	2.5	16	—	—	—	—
	5.0	33	7.8	**.005**	—	—
	≥7.5	45	19.8	**<.001**	3.0	.08
Socializing	2.5	16	—	—	—	—
	5.0	26	3.0	.08	—	—
	≥7.5	10	0.5	.46	1.0	.31

Note: Results of chi-square tests are shown; significant differences are presented in **bold**.

and TI. It has been reported that social behaviors are generally related to reproduction (Constantine et al. 2004), which can occur year-round in this species, although births do increase during spring and summer (Urian et al. 1996, Mann et al. 2000, Currey et al. 2007). This suggests that UF and TI phases in the MRC-CD may present favorable environmental conditions, such as higher temperatures (Montecino, Strub, et al. 2006) and/or greater food availability that would promote the development of social activities linked to reproduction, care of offspring, and the reinforcement of social bonds among individuals. A similar situation was described by Hanson and Defran (1993) off San Diego, California, where the social activity of dolphins was mainly carried out during the summer months, and was attributed to seasonal changes in water temperature and prey abundance, demonstrating a seasonal adaptation of reproduction to decrease the energetic cost of thermoregulation.

In conclusion, the findings of this study reveal that resighting patterns of transient bottlenose dolphins reflect habitat use, suggesting that environmental conditions in the MRC-CD, such as food availability and upwelling-favorable winds, influence the behavior displayed by these dolphins within this area. As predicted, low occurrence of transient dolphins and traveling behaviors were more frequent during periods of food scarcity (CV and TII phases). However, the feeding behavior was not related to a period of upwelling-favorable winds and was recorded at all phases. Results from this study provide baseline data about the presence and use of the MRC-CD by bottlenose dolphins, which is relevant information considering the different activities performed in the area (resource extraction, fishery, scientific research, wildlife tourism). In addition, it is important to maintain long-term environmental and biological data collection, and long-term monitoring of the demographic parameters of these dolphins to accurately assess any future changes in prey abundance, direct anthropogenic disturbance, and/or population decline (Koper et al. 2016).

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