Behaviour and movements of bottlenose dolphins, *Tursiops truncatus*, in the entrance to Ensenada De La Paz, Mexico

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Behaviour and movements of bottlenose dolphins, *Tursiops truncatus*, were studied in the entrance to Ensenada de La Paz, a coastal lagoon, from May to September 1987. Dolphins were tracked from land by theodolite. Dolphins used the entrance to Ensenada de La Paz as a feeding area. The relative number of dolphin feeding instances was higher in June and July than in other months of the study (feeding instances/ non-feeding instances: 1.6 in June and July, 0.7 in other months). The number of non-migratory feeding seabirds was highest in June (feeding seabirds/hr: 25 in June, 11 in other months), indicating an increase in the abundance of fishes at this time. Although dolphins and seabirds fed independently of each other, both fed more often in the same region of the study area. The regular occurrence of dolphins and feeding birds might have been related to availability of prey in this mangrove-based estuary. Behaviour and movement of dolphins were related to tidal current, suggesting a response to likely short-term movements of prey.

Introduction

In estuaries, fishes tend to move with tidal current (Day *et al.* 1989); various studies have also reported that behaviour and movements of bottlenose dolphins, *Tursiops truncatus*, are related to tides (review by Shane *et al.* 1986). Although the relationship between dolphin behaviour and tidal current appears to be important in estuaries due to the influence of the latter on prey movements, no study has been conducted in a coastal lagoon with only one connection to the open sea, where this relationship can be readily studied.

Behaviour and movements of bottlenose dolphins have been studied in several regions of the world: for example, South Africa (Saayman *et al.* 1973), Florida (Irvine *et al.* 1981; Shane 1990a), Argentina (Würsig 1978; Würsig and Würsig 1979), Texas (Shane 1977, 1980; Gruber 1981), northern Gulf of California (Ballance 1990), and southern California (Hansen

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1990). Various studies conducted in estuarine systems show that these habitats are regularly used by dolphins as feeding areas (review by Shane *et al.* 1986). These studies also suggest that dolphin behaviour and movements are related to tides, time of day, depth, and other variables. Nonetheless, the significance of these relationships is unclear because relating the same variable to various parameters reduces the level of significance of each test (Zar 1984). Also, statistical tests from earlier studies assumed independent observations; this assumption is incorrect when measuring behavioural change (Bishop *et al.* 1975). A more useful approach is to analyse data with the concept of conditional probabilities (Bakeman and Gottman 1986).

The regular presence of bottlenose dolphins in the entrance to Ensenada de La Paz, and adjacent waters, has been well known for a long time (Michel 1986); however, no study had been conducted before in this area. Since the entrance to Ensenada de La Paz is the only connection between Ensenada de La Paz, a coastal lagoon, and the open sea, the relationship between dolphin behaviour and tidal current can be readily studied. The objective of this study was to relate behavioural states (from now on referred as behaviours) and movements of bottlenose dolphins in the entrance to Ensenada de La Paz to tidal current using conditional probability analysis techniques.

Methods

Ensenada de La Paz is a mangrove-based coastal lagoon located at the southeast end of La Paz Bay near the southeast tip of the Baja California Peninsula, México (Fig. 1). My study area was at the entrance to Ensenada de La Paz; it was divided into three distinct regions: the Channel, the Mouth, and Punta Prieta (Fig. 1). The study area is shallow, mostly less than 5 m deep, with a dredged ship channel running in a north-south direction. The east side of the study area has been developed for tourism; as a result, the mangrove communities there have been destroyed (Mendoza *et al.* 1984). The physical and biological environment of the study area was described by Gómez *et al.* (1984),
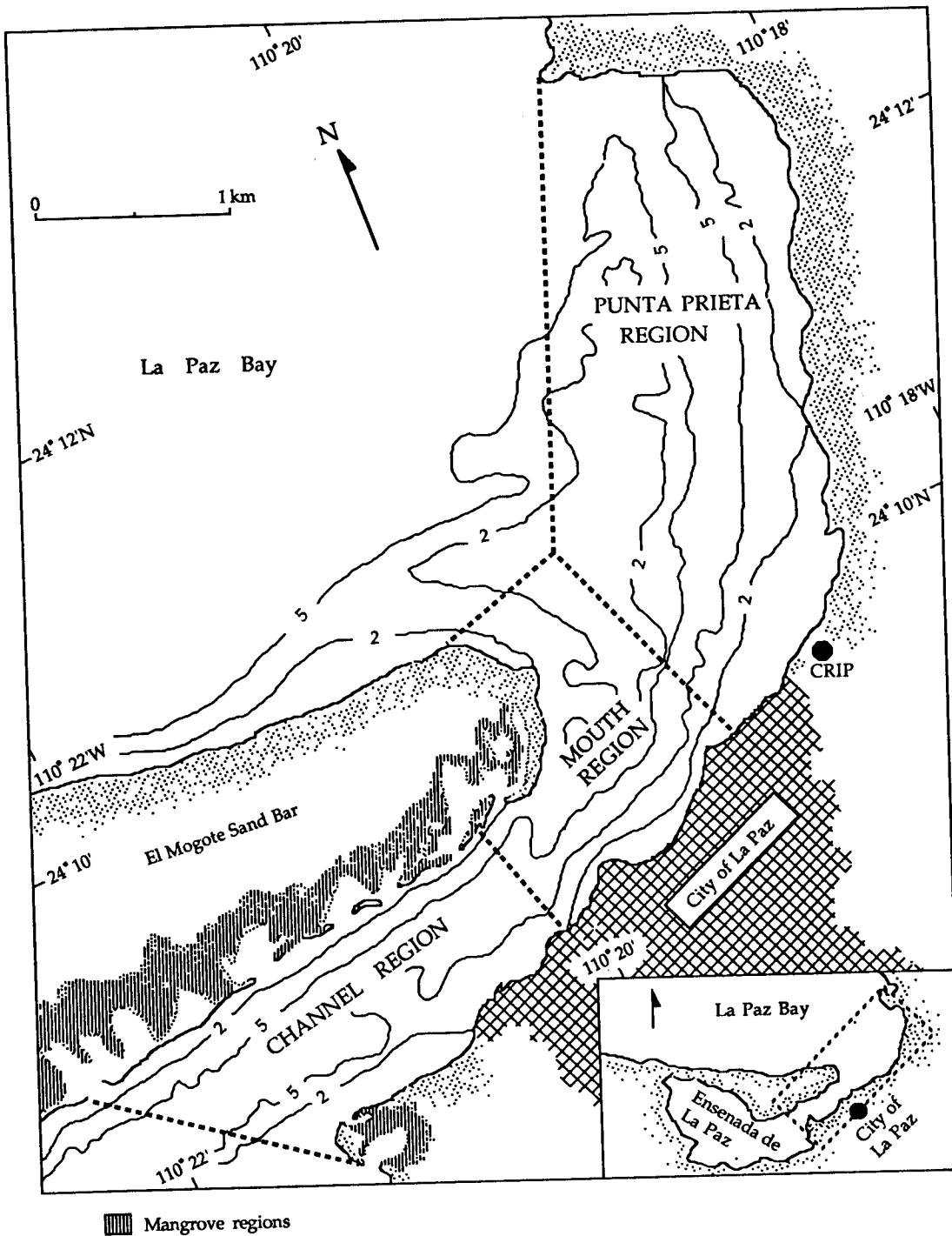
Figure 1. Location and bathymetry (in metres) of the study area, the entrance to Ensenada de La Paz. Dashed lines indicate boundaries between the three regions.

González and Mendoza (1984), and Mendoza *et al.* (1984).

The study was conducted from May through September 1987. I searched for dolphins from a point 15 m above mean low water at the Centro Regional de Investigaciones Pesqueras (CRIP) (Fig. 1). When dolphins were sighted, I continuously observed them with 7 × 50 binoculars using focal group sampling (Martin and Bateson 1986). The following behavioural events were continuously recorded (Martin and Bateson 1986) every 7 min with a sampling duration of 10 min to define behaviours: surfacing patterns, group geometric shape, orientation, and relative proximity of individuals (Acevedo 1989; Shane 1990a). I recorded the position of the centre of the group with a surveyor's theodolite (20 s of arc precision, 30-power monocular) every 10 min. Groups were defined as individuals swimming in a coordinated manner within 100 m of each other and exhibiting the same behaviour. Environmental data, boat traffic, and seabird feeding activity were also recorded.

Theodolite bearings of bottlenose dolphins were plotted on a bathymetric map to define dolphin movements. Plots were used as a measure of relative velocities between regions. I used location and number of feeding seabirds as independent indicators of distribution and abundance of prey. When no dolphins were sighted, seabird feeding bouts were continuously recorded every 10 min with a sampling duration of 15 min; when dolphins were sighted, seabird feeding bouts were continuously recorded every 12 min with a sampling duration of 5 min.

I analyzed the two-event sequence of bottlenose dolphin behaviours using transition probabilities (Bakeman and Gottman 1986). I used conditional probabilities (Bakeman and Gottman 1986) to analyze dolphin behaviour and movements in relation to tidal current. Other statistical analyses were based on Cochran (1984) and Zar (1984).

Results

I observed 71 dolphin groups on 54 times for 106 hours. Dolphins were observed an average of 2.4 h per sighting (s = 1.9, n = 54). Median group size (Med = 12, Range = 2–25, n = 71) was largest in June (May = 8, June = 17, July = 15, August = 12, September = 10: $H_4 = 10.06$, p < 0.05; SNK test p < 0.05 due to June; n = 71). Group sizes most frequently observed ranged from 10 to 25 individuals (n = 45).

Behaviour

I defined five behaviours (described in Acevedo 1989): 1) moving in a defined direction (TR), 2) back and forth movement in a small area (100–300 m long) (PA), 3) moving in a defined direction with sudden and transitory changes of orientation (FT), 4) diving in a small area (approximately 100 m radius) with surface activity (SF), and 5) diving in a small area (about 100 m radius) with no surface activity (NS). I interpret each behaviour as travelling (TR), passive state (PA), feeding while travelling (FT), feeding with surface activity (SF), and feeding without surface activity (NS).

Feeding behaviours were defined based on: 1) fish observed within 100 m of dolphins, 2) fish leaping out of water in front of dolphins, 3) sudden and momentaneous changes of orientation by dolphins indicating prey capture, 4) seabirds trying to feed next to a surfacing dolphin, and 5) relative percentage of time in which seabirds fed within 100 m of dolphins. The first four characteristics were only observed during FT, SF, and NS. The percentage of time in which seabirds fed within 100 m of the dolphins were 42.2% for SF, 22.8% for NS, 14.4% for FT, and 9.1% for TR; seabirds never fed within 100 m of dolphins in PA. Both TR and PA were considered non-feeding behaviours. FT, SF, and NS were considered feeding behaviours.

Feeding behaviours had higher mean duration (NS = 43.0, SF = 32.0, FT = 25.9, PA = 26.7, TR = 23.3 min: $ANOVA_{4,207} = 5.62$, p < 0.001; SNK test, p < 0.05 due to NS; n = 212) and occurred less frequently (NS = 33, SF = 38, FT = 58, PA = 42, TR = 93 instances: $G_4 = 26.19$, p < 0.001, n = 264; without TR and FT: $G_2 = 1.07$, p > 0.05, n = 113) than non-feeding behaviours. The number of feeding behaviours increased with respect to the number of non-feeding ones in June and July (May = 22/17, June = 23/36, July = 16/27, Aug = 46/36, Sept = 28/13 non-feeding/feeding behaviours: $G_4 = 13.08$, p > 0.01, n = 264; without June and July: $G_2 = 1.81$, p > 0.05, n = 162). Based on their sequence, behaviours were classified in three groups: 1) TR and PA, 2) FT and SF, and 3) NS. The first two groups include behaviours that preceded each other more than any other behaviour. NS was a behaviour that preceded both TR and FT, but at a lower frequency than PA and SF respectively (Fig. 2).

Relation to tidal current

The direction of movement of the dolphins was always parallel to the coast. Three directions of movement were observed: north (outwards), south (inwards), and undefined (back and forth). Dolphins moved more frequently against the current during ebb and flood. They also moved back and forth in the study area during flood (Fig. 3). Dolphin behaviour varied with tidal current. TR and PA occurred most frequently during flood and slack, FT and SF occurred least frequently during flood, and NS occurred most frequently during flood and ebb (Fig. 4).
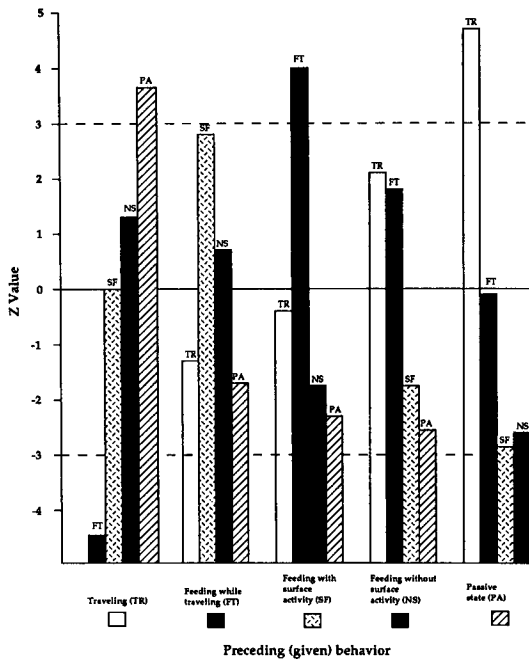
Figure 2. Two-event sequence between dolphin behaviours. For Z values larger than zero, the behaviour followed the preceding behaviour with a frequency higher than expected. For Z values smaller than zero, the behaviour followed the preceding behaviour with a frequency lower than expected. Dashed lines indicate critical values of Z ($p < 0.05$).

Figure 3. Direction of movement of dolphins in relation to tidal current. Same indications as Figure 2.

The behavioural sequence and the movements of dolphins in relation to tidal current are summarized in a transition diagram. During flood, the most common movement was due north or undefined, and the most common behaviours were TR, PA, and NS. During slack and ebb, the most common movement was due south, and the most common behaviours were FT and SF (Fig. 5).

Habitat use
I observed bottlenose dolphins an average of 4 days per week ($x = 4.1$, $s = 1.8$, $n = 20$). Their frequency of occurrence was not related to spring and neap tides (spring $= 4.1$, neap $= 3.9$ days/week: $t = -0.25$, $p > 0.05$, $n = 20$), nor to tidal change (tidal change $= 42$, no tidal change $= 39$ days; $G_1 = 0.222$, $p > 0.05$, $n = 81$ days). Their weekly frequency of occurrence was not different among months (May $= 3.7$, June $= 2.4$, July $= 3.7$, Aug $= 5.6$, Sept $= 5.4$ days/week: ANOVA$_{4,15} = 2.90$, $p > 0.05$, $n = 20$).

In the entrance to Ensenada de La Paz, bottlenose dolphins spent most of their time in the mouth region (Channel $= 19.3$, Mouth $= 83.0$, Prieta $= 11.4$ hours: $G_2 = 76.74$, $p < 0.001$, $n = 113.72$; without mouth: $G_1 = 2.09$, $p > 0.05$, $n = 30.71$). They travelled along
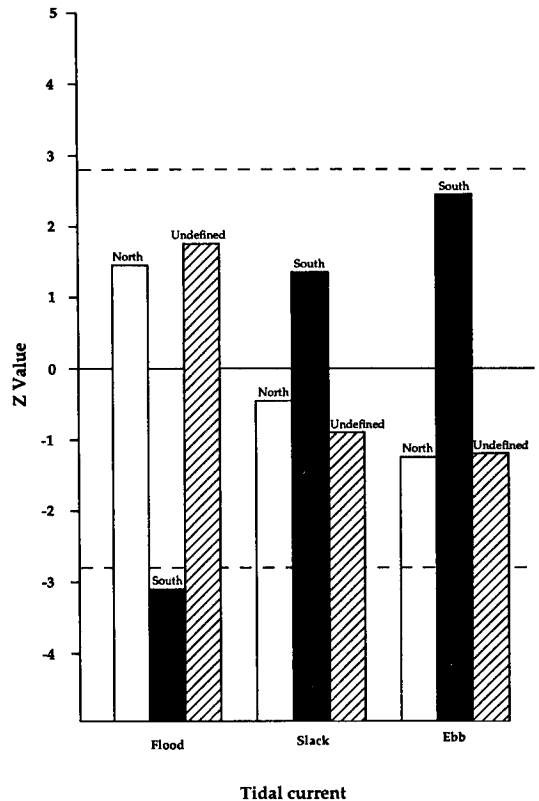
well-defined routes to feed in three locations, each in a different region of the study area (Fig. 6). The feeding location in the mouth region was used most frequently (Channel $= 8$, Mouth $= 35$, Prieta $= 15$ feeding instances: $G_2 = 19.84$, $p < 0.001$, $n = 58$; without Mouth: $G_1 = 2.16$, $p > 0.05$, $n = 23$) and the speed of travel was lowest there (Channel $= 3.2$, Mouth $= 2.3$, Prieta $= 4.5$ km/h: ANOVA$_{2,97} = 16.00$, $p < 0.001$; SNK test, $p < 0.05$ due to all regions; $n = 100$).

Seabirds
The feeding seabirds that I observed were mainly brown pelican (*Pelecanus occidentalis*: 48.1% of feeding seabirds recorded), magnificent frigate bird (*Fregata magnificens*: 29.9%), brown (*Sula leucogaster*: 9.1%) and blue-footed (*S. neuboxii*: 4.6%) boobies, Heerman's (*Larus heermanii*: 3.3%) and yellow-footed (*Larus livens*: 1.5%) gulls, and least tern (*Sterna antillarum*: 3.2%). At all times the number of seabirds feeding within 100 m of dolphins was less than 15% of number of seabirds feeding more than 100 m from the dolphins.
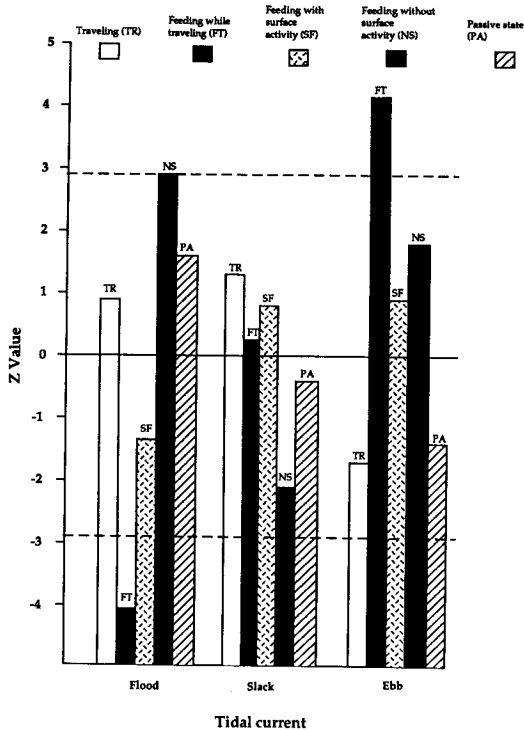
Figure 4. Behaviour of dolphins in relation to tidal current. Same indications as Figure 2.
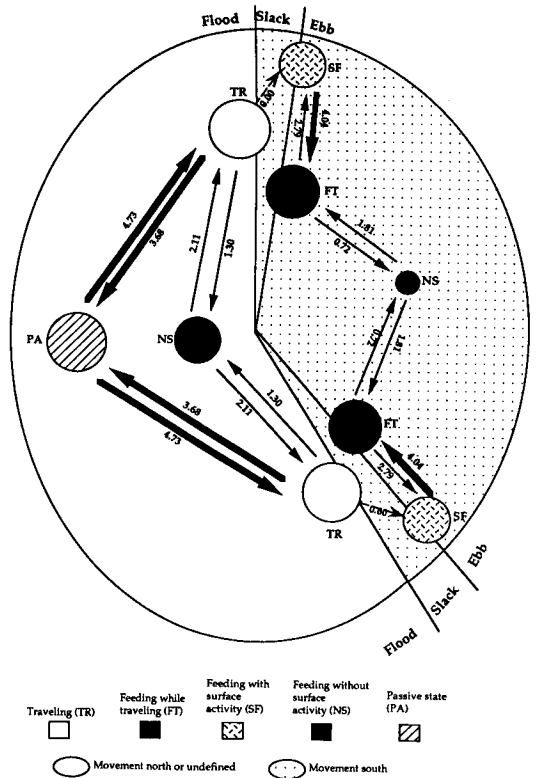

Figure 5. Summary: behavioural sequence and movements of bottlenose dolphins in relation to tidal current. Size of each ellipse division indicates the relative amount of time in which dolphins were observed in each tidal current. Size of each circle indicates number of occurrences of each behaviour. For both movements and behaviours, only occurrences with a probability higher than, or equal to, expected are depicted in the diagram. The start of each line indicates preceding behaviour; the arrow points towards the following behaviour. Numbers indicate Z values. Bold lines indicate significant (p < 0.05) two-event sequences between behaviours.

Based on the number of seabirds feeding per effort hour I identified four different feeding areas (Cochran quotient comparisons, p < 0.05 due to all regions; n = 524.4 effort hours, 7402 feeding seabirds; Fig. 7). The highest number of seabird feeding instances was recorded in the Mouth region; the lowest number was observed in the Channel region (Channel = 18, Mouth = 105, Prieta = 46 feeding instances: G_2 = 71.25, p < 0.001, n = 169; without Mouth: G_1 = 12.67, p < 0.001, n = 64). The number of seabird feeding instances, adjusted for effort hours, was highest in June and lowest in May (May = 26, June = 68, July = 27, Aug = 24, Sept = 24 feeding instances; G_4 = 14.81, p > 0.005, n = 169; without June: G_3 = 0.37, p > 0.05, n = 101). The number of seabirds feeding, adjusted for effort hours, was highest in June (May = 0.83, June = 4.54, July = 1.42, Aug = 0.36, Sept = 1.00 × 10³ feeding seabirds: G_4 = 5452.18, p < 0.001 due to all months, n = 7402).

Discussion

The entrance to Ensenada de La Paz appeared to be a feeding area for bottlenose dolphins, as indicated by their behaviours. Due to its low mean duration and high frequency of occurrence, I consider that TR was a short-term movement between feeding areas. I interpret PA as a behaviour in which dolphins rested or looked for prey at specific locations, almost exclusively at the mouth of the region. Würsig and Würsig (1979) defined milling as a rapid movement of dolphins involved in feeding and with frequent change of headings. Although PA and milling might seem similar, PA did not appear to be associated with feeding and was a more passive behaviour. FT was similar to individual feeding (Leatherwood 1975). The main differences between SF and NS were the absence of surface activity during the latter and the large percentage of seabirds feeding within 100 m of dolphins during the former.
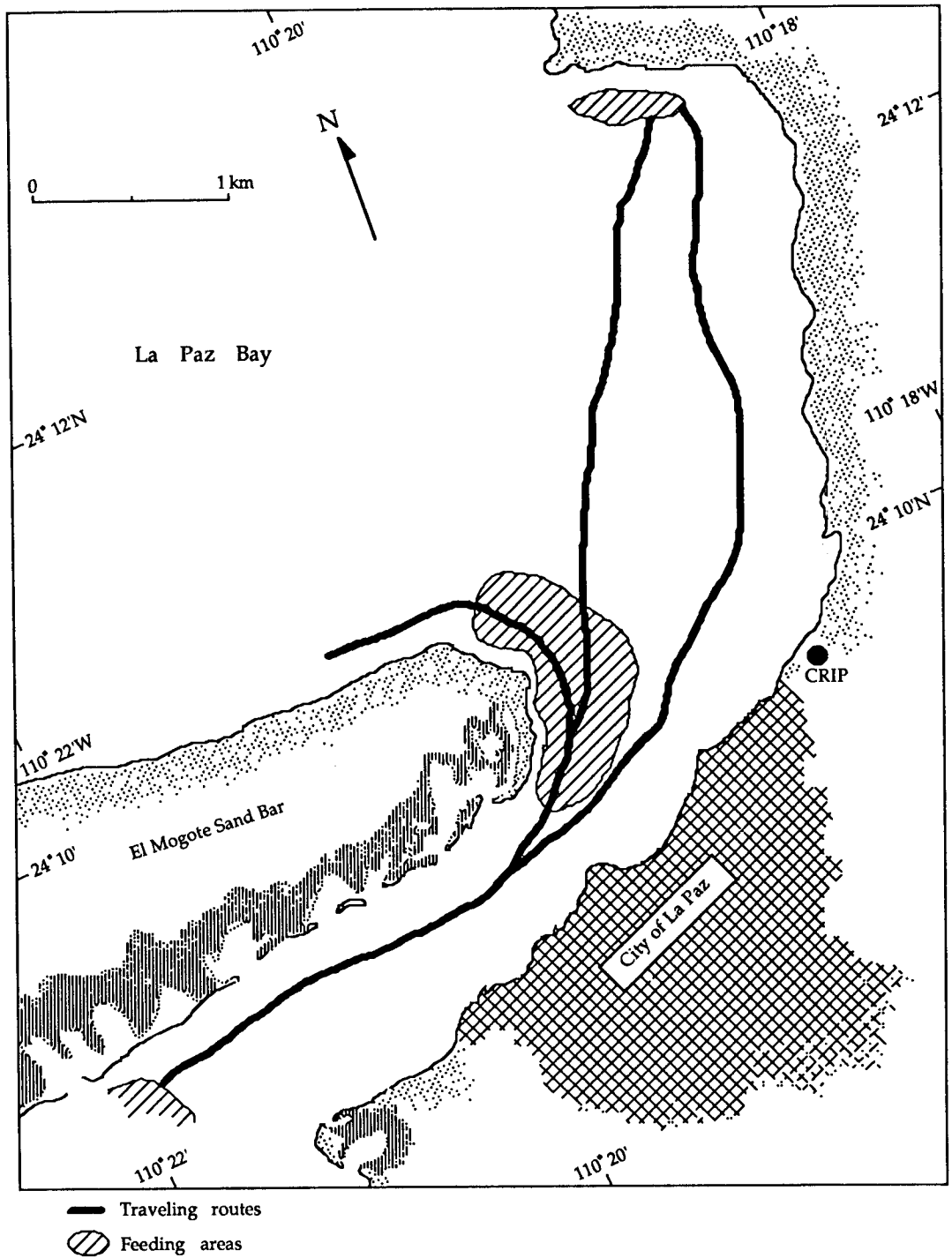
Figure 6. Feeding areas and travelling routes used by dolphins. For all travelling routes, the direction of movement is either north or south.
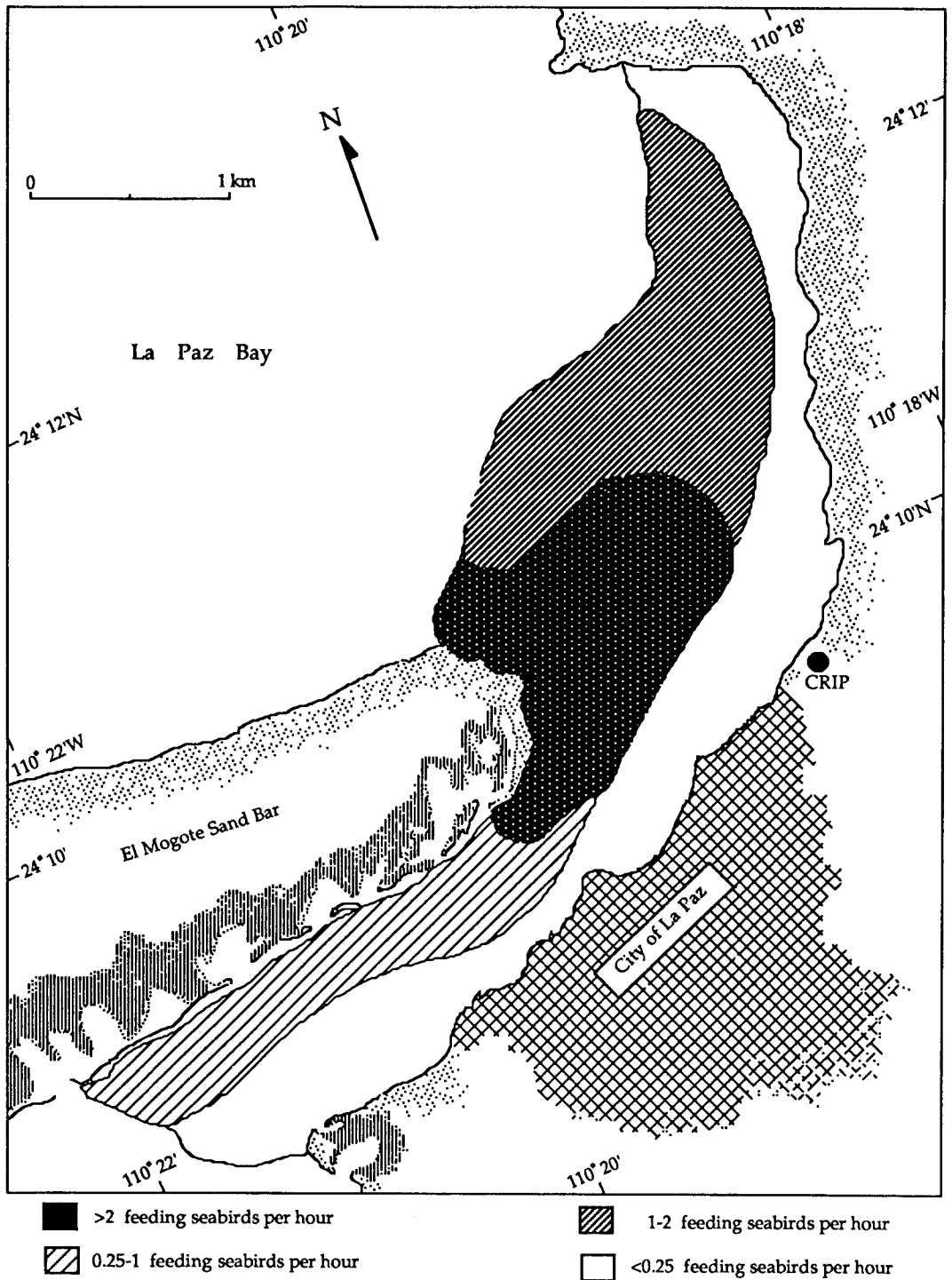
Figure 7. Regions of feeding activity of seabirds.

I interpret these differences to be indicators of the relative water depth where prey was present.

Feeding seabirds were rarely associated to dolphins, relative to the total number of seabirds feeding in the area, suggesting that both fed independently of each other, perhaps on different food items. In La Paz, least terns fed mainly on anchovy, *Anchoa ischana*, (Palacios and Guzmán 1986) and brown pelicans on mackerel, *Scomber japonicus*, (Jiménez 1988); whereas, according to La Paz fishermen, bottlenose dolphins fed on mullet, *Mugil cephalus*, a well known prey in other regions of the world (Gunter 1942; Leatherwood and Reeves 1982; Shane 1990b). Castro-Aguirre and Salinas (1988) reported that mojarras, *Diapterus aureolus*, and mullet were abundant in the area.

Brown pelicans, the most frequently observed feeding seabird during the study, were year-round residents of the area (Jiménez 1988) and appeared to be reliable indicators of prey abundance. The apparent increase in prey abundance during June, as suggested by the increased number of feeding seabirds and seabird feeding instances, might indicate large numbers of spawning pelagic fishes such as anchovies (Engraulidae) and herring (Clupeidae). These fishes spawned in the area (Chávez 1985); they also comprised two of the main food items of brown pelicans in La Paz (Jiménez 1988). Castro-Aguirre and Salinas (1988) also noticed an increase in fish density at this time of year. Three pieces of evidence suggest that dolphins also fed on pelagic fishes at this time: 1) increase in group size, equivalent to more individuals feeding since all groups in the study area exhibited feeding behaviour, 2) higher number of feeding behaviours relative to non-feeding behaviours, and 3) increase in number of seabird instances trying to feed at the place where dolphins were surfacing. When dusky dolphins, *Lagenorhynchus obscurus*, in Argentina fed at the surface on southern anchovy, *Engraulis anchoita*, seabirds frequently fed in association with them (Würsig and Würsig 1980). Similar associations are reported for small delphinids that tend to feed on pelagic, schooling fishes (Evans 1982). Due to their behavioural flexibility and generalized food habits (Shane 1990b), it is likely that in June dolphins took advantage of an abundant resource. In Lower Tampa Bay, Florida, Weigle (1990) observed an increase in the number of dolphins from July through September, apparently related to an influx of prey.

The pattern that dolphins used to arrive in the study area was unrelated to tidal current. Once in this study area, dolphins tended to behave and move in a different manner according to tidal current, as indicated by their behavioural sequence, suggesting a response to likely movements of prey. Fishes in the Ensenada de La Paz tended to move with tidal current (C. Villavicencio, pers. comm.), in a pattern which is generally true for estuaries (Day *et al.* 1989). Tidal current velocities inside the study area were close to 1.8 km/h (Gómez *et al.* 1984). Dolphins may have moved against tidal current, thus facing their prey, because it was easier to detect prey coming towards them rather than moving away. The same tendency was suggested for bottlenose dolphins in Aransas Pass, Texas (Shane 1980). In contrast, killer whales, *Orcinus orca*, in Puget Sound, Washington, moved with the tidal current to follow their prey as they moved away from them (Felleman 1986).

The mouth region was the only entrance to, and exit from, the Ensenada de La Paz for fish. Although for the most time dolphins and seabirds fed independently of each other, both preferred to feed in the mouth region, perhaps because it was easier to detect prey in this concentrating area. The mouth region was 2–5 m deep, with one shallow area less than 2 m; the latter brought fish closer to the surface and reduced their available space to escape, a situation which may have facilitated prey capture by both dolphins and seabirds. The highest densities of any species of fish were located next to mangroves (Castro-Aguirre and Salinas 1988) and mangroves were only found on the west shore of the study area (Mendoza *et al.* 1984). The preference of both dolphins and feeding seabirds for the west shore of the study area might have been related to prey distribution, in turn related to location of mangrove communities. This might also explain why dolphins travelled faster in Punta Prieta region, where mangroves were absent.

Bottlenose dolphins tended to move against tidal current in Aransas Pass, Texas (Shane 1980, 1990a), and Cavallo Pass, Texas (Gruber 1981), and with tidal current in Sarasota Bay, Florida (Irvine *et al.* 1981). In an open bay in Argentina, bottlenose dolphins tended to move to shallower waters during ebb and to deeper waters during flood (Würsig and Würsig 1979). Würsig and Würsig suggested that this movement may have been related to concentration of prey. Off southern Africa, feeding by Indo-Pacific humpbacked dolphins, *Sousa chinensis*, increased during flood tide (Saayman and Tayler 1973). Saayman and Tayler suggested that behaviour of these dolphins was largely determined by the effect of tides upon feeding activity.

Estuaries have a high primary productivity; in tropical non-sea grass estuaries most of this productivity is generated by mangroves (Day *et al.* 1989). In La Paz Bay, the highest densities of fish occurred in the entrance to Ensenada de La Paz (Castro-Aguirre and Salinas 1988). The regular occurrence of dolphins in the study area might have been related to this availability of prey. Boat surveys conducted in the south portion of La Paz Bay, although few and unevenly allocated, suggested that bottlenose dolphins are found more frequently in Ensenada de La Paz

(Acevedo 1989). Several authors also have reported a high frequency of occurrence of bottlenose dolphins in estuaries of their study areas (Ballance 1987, for Bahía Kino, México; Hansen 1990, for southern California; Scott *et al.* 1990, for Sarasota Bay, Florida). Killer whales in Washington and British Columbia (Jacobsen 1986; Heimlich-Boran 1988), and in Marion Island, south Indian Ocean (Condy *et al.* 1978), also routinely visited locations where prey is available.

Acevedo (1989) identified 28 individuals in the entrance to Ensenada de La Paz; he estimated that 60 dolphins used the study area. Michel (1986) reported group sizes as large as 67 dolphins in the south portion of La Paz Bay. The largest group size that I observed in the study area was 25 dolphins, suggesting that dolphins in the south portion of La Paz Bay split before arriving to, or congregated after departing from, the entrance to Ensenada de La Paz. A few boat observations suggest that dolphins outside the study area moved and fed near the coast of La Paz Bay. Since Ensenada de La Paz is only 75 km^2 and is the largest estuary in La Paz Bay, the apparent partition of the region by dolphins might have been related to the small size of estuarine systems available to them.

Conclusions

From May to September, bottlenose dolphins used the entrance to Ensenada de La Paz as a feeding area. Their regular occurrence in, and apparent preference for, this area appeared related to availability of prey in a highly productive ecosystem. Their behaviour and movements were related to tidal current, which were likely influenced by short-term movements of prey. The location of travel routes and feeding areas of dolphins appeared to be related to concentration sites of prey, which in turn might have been influenced by distribution of mangroves. Seabirds in the study area fed independently of bottlenose dolphins, perhaps on different prey items for most of the time; however, their occurrence, abundance and the location of their feeding areas were apparently influenced by the same prey attributes influencing bottlenose dolphin habitat use.

Due to their high productivity, estuaries are important for habitats for different organisms (Day *et al.* 1989). Mangroves generate much of the primary productivity in tropical estuaries, providing shelter for many juvenile pelagic fishes and invertebrates, which are the basis of important fisheries, and food for nearshore fishes and invertebrates (Day *et al.* 1989). This in turn attracts large fishes, seabirds, and dolphins. In La Paz, as in many other places, mangroves and estuaries are being destroyed for tourism and human development. The impact of this destruction will affect many organisms, including bottlenose dolphins and seabirds.

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