Investigations on Cetacea
Edited by G. PILLERI
Vol. XXV, 1994, pp. 235—256

ECOLOGY OF THE COASTAL BOTTLENOSE DOLPHIN *TURSIOPS TRUNCATUS* IN THE GULF OF GUAYAQUIL, ECUADOR

FERNANDO FÉLIX

Fundación Ecuatoriana para el Estudio de Mamíferos Marinos
P.O. Box 09-01-6637. Guayaquil, Ecuador

ABSTRACT

Between February 1990 and January 1992, 110 boat surveys were carried out in the inner estuary of the Gulf of Guayaquil, Ecuador (2°45′S, 79°55′W) to study the ecology of the coastal bottlenose dolphin *Tursiops truncatus.* A total of 849 hours were spent at sea, including 207 with the animals. Photographing naturally marked dolphins resulted in the recognition of 432 different individuals. A statistically significant seasonal variation was found both in group size ($P<0.01$) and dolphin abundancy ($P<0.05$). Dolphins formed larger groups and were more abundant during the dry and cool season (from June—November) which is likely food related. Dolphins concentrated their activities within small areas, rather than being evenly spread throughout their whole home range, especially in the mouths of large channels. No relationship was found between dolphin movements and tide direction. Average swimming speed was 4 km/h. The population in the study area was estimated to be 637 dolphins (95% confidence interval = 541 − 733). Newborn calves were registered all year round without a clear seasonal tendency. Additional information about feeding, reproduction and behaviour is provided.

INTRODUCTION

The bottlenose dolphin *Tursiops truncatus* is probably the best known cetacean of the world. Its distribution is cosmopolitan, avoiding only the very high latitudes (LEATHERWOOD and REEVES, 1983). Throughout much of its distribution area two varieties have been recordered; a coastal and an oceanic type (WALKER, 1981; PERRIN, 1984; HERSH and DUFFIELD, 1990; KENNEY, 1990; MEAD and POTTER, 1990; VAN WAEREBEEK et al., 1990). One of the least studied coastal populations occurs along the west coast of South America, from Colombia as far as 34°S in Chile (AGUAYO, 1975). In the past few years VAN WAEREBEEK *et al.* (1990) obtained new information about the distribution and natural history of these dolphins during their study of the exploitation of small cetaceans off the coasts of Perú and Chile. Recent observations of coastal bottlenose dolphins have been carried out also in Perú by ECHEGARAY *et al.* (1992).

In Ecuador, the presence of bottlenose dolphins in coastal waters is poorly known and limited to casual observations (HAASE, 1990; LYRHOLM[1] *et al.,* 1992). In

1. LYRHOLM, T., KERR, I., GALLEY, L. & PAYNE. R. (1992). Report of the "Expedicion Siben" Ecuador 1988/89. Whale Conservation Institute. 37 p.

1989 I started the first observations on bottlenose dolphins — locally known as "bufeos" — doing regular surveys in the estuarine zone of the river Guayas in the Gulf of Guayaquil (southwest coast of Ecuador) where bottlenose dolphins can be seen all the year round, even in the inner channels (FÉLIX, 1990). Although their presence is known ancestrally by the local people, no attempts have been made before to study these animals.

In this paper I give the results of a two-year study. It is an attempt to describe the influence of several environmental factors, such as water temperature, salinity and tidal cycle on the abundance, distribution and movement of the dolphins. Also, information on behaviour, reproduction, and feeding habits are presented. The results are compared with similar studies carried out elsewhere.

STUDY AREA

The Gulf of Guayaquil covers approximately 12,000 km² and is the largest estuary on the Pacific coast of South America. Situated 3° south of the equator, the entrance extends 204 Km north-south along the 81°W meridian and continues inland for 130 Km (Fig. 1). The Gulf is naturally divided into an outer estuary that starts near the western side of Puná Island (80°15'W) and ends along 81°W longitude, and an inner estuary that extends northeast from Puná Island for another 74 Km before narrowing into the main course of the Guayas river, the main contributor of freshwater runoff into the estuary (STEVENSON, 1981). The Guayas river also transports a lot of sediment, causing deposits of sand and mud on the river outlet, forming many sandbanks which are exposed at low tide.

Another channel, west and parallel to the Guayas river (the Estero Salado) extends up to the city of Guayaquil. Between the Estero Salado and Guayas river are several narrow channels and islands, wholly or partially covered with mangrove. Puná Island is the biggest of the all islands in the Gulf. On its north and west sides it has rocky shores with narrow beaches; the east and south sides consists mainly of mangrove like all the other islands.

In the Gulf two well-defined seasons occur: a warm and rainy season (January—May), with more than 95% of the annual precipitation; and a cooler and dry season (June—November) with 2% or less of the annual precipitation (Data from the Servicio Nacional de Metereología e Hidrología, period 1950—1970, according to STEVENSON, 1981). The water surface temperature changes from 21.5°C in the dry season to 25°C in the warm season in the outer estuary, and from 25°C to 28°C in the inner estuary (STEVENSON, 1981).

The semidiurnal tides, with a high tidal range 2.6—3.5 m (Tide tables from the Instituto Oceanográfico de la Armada Ecuatoriana INOCAR), play an important role in the water circulation of the Gulf. The depth in the inner estuary, where present research was carried out, is on the average less than 10 m (INOCAR, Navigation chart I.O.A. 107).

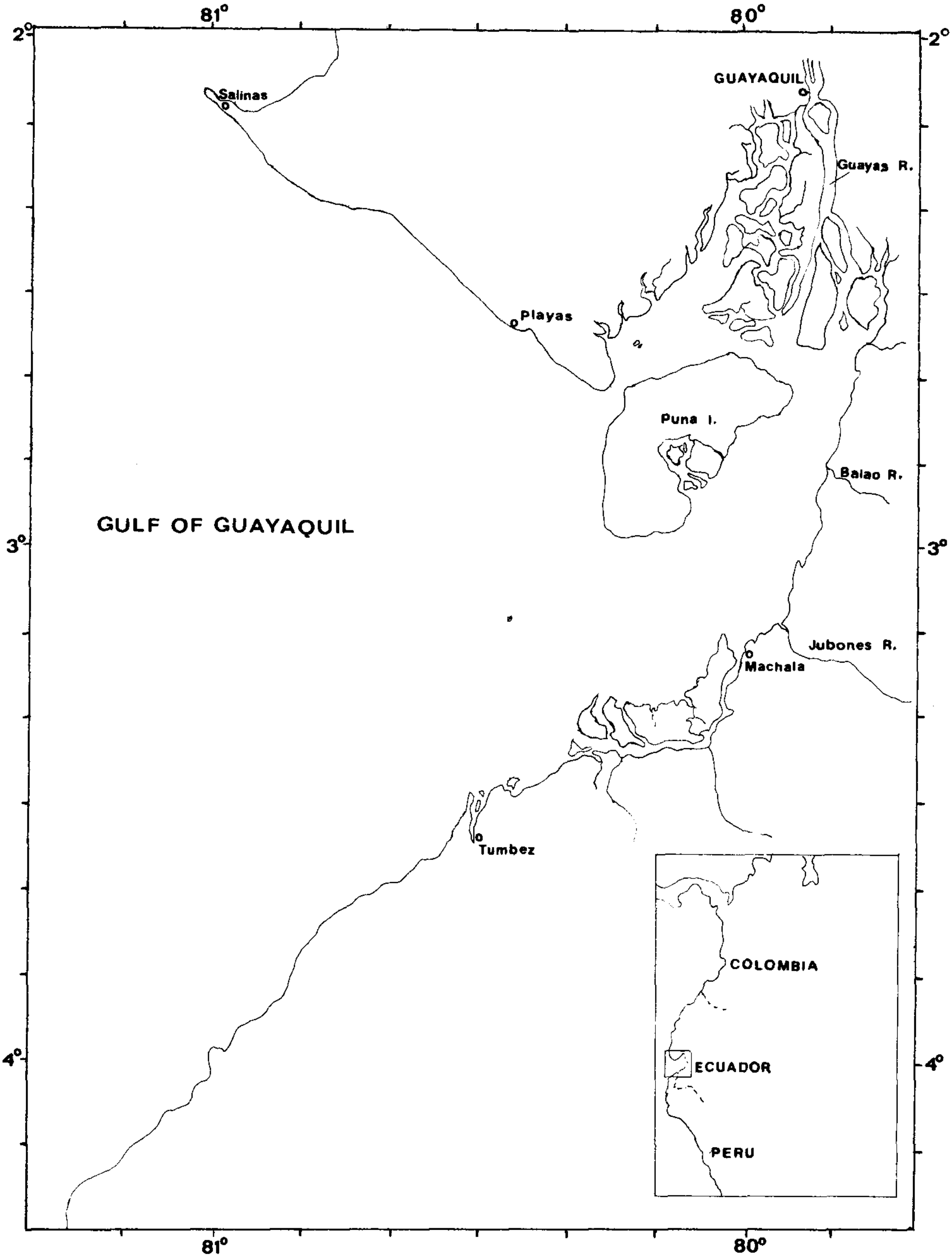

Figure 1 — The Gulf of Guayaquil.

MATERIAL AND METHODS

From February 1990 until January 1992 (24 months) weekly surveys were carried out through the inner estuary of the Gulf of Guayaquil in a 4.8 m fiberglass boat with a 75 HP outboard motor at 35—40 km/hr. The surveys started in Guayaquil and ended at the site called Río Hondo on Puná Island, covering a distance of about 85 km. The reverse trip was made one or two days later. The main route went along the Guayas river coast and the east side of Puná Island, but several alternate routes were taken as well (Fig. 2). However, the surveying effort in the different zones of the estuary was not uniform; the further away a site from the main route, the less frequent were the surveys carried out at those places. The Estero Salado was surveyed twice, from Guayaquil to Posorja and three more times from the river Guayas crossing the interior channels between the Escalante Island and Chupadores Island. On the northeast side of the estuary, the Mondragón channel was surveyed 15 times; in five cases the survey extended as far as Balao river and then crossed toward Puná Island (see Fig. 2). A total of 110 surveys were conducted, accounting for 849 hours spent at sea, of which 207.3 hours were spent with the animals. Dolphins were sighted in 88 trips (80%). The surveys were carried out between 8:00 and 15:00 hours.

Every dolphin seen during a sighting was considered to form part of a group when it was moving more or less in the same direction as other dolphins, or when it was obvious that it maintained in contact with these, even when it occupied a wide area. Observation time varied between 5 minutes and 3 hours, depending on the number of individuals, their activity and the environmental conditions. When a group of dolphins was spotted, they were approached in a discrete way to avoid frightening them. Group size and composition was determined and behavioral descriptions were made. When it was not possible to determine the exact number of animals in a group, this was estimated within a range, and the mean of this range used for statistical analysis.

Information about the position and swimming direction of the dolphins, related to the height and direction of the tide, was used to investigate their pattern of movement. The heading of the dolphins with respect to the tide was classified into 4 categories: with, against, milling or unknown. It was considered that the dolphins were milling when they stayed in the same area during the entire observation period, or when they moved perpendicular to the tidal current. Heading was classified as unknown when the observation period was too short to be sure of their direction.

Usually the sea surface temperature was measured during a sighting, except between November 1990 and March 1991. The oceanographic conditions showed little variation throughout the year, although during the dry season from August to October there was more wind up to 4 on the Beaufort Scale, causing some swell in the more open water.

A 35 mm camera with a zoom lens 70—200 mm and color film ISO 100 were used to take pictures of dorsal fins or any other natural mark to allow the identification of individual dolphins (see WÜRSIG and WÜRSIG 1977). More than 4000 photos were taken during the study, allowing for the identification of 432 different dolphins.

Naturally marked dolphins were used to estimate the size of the population. For

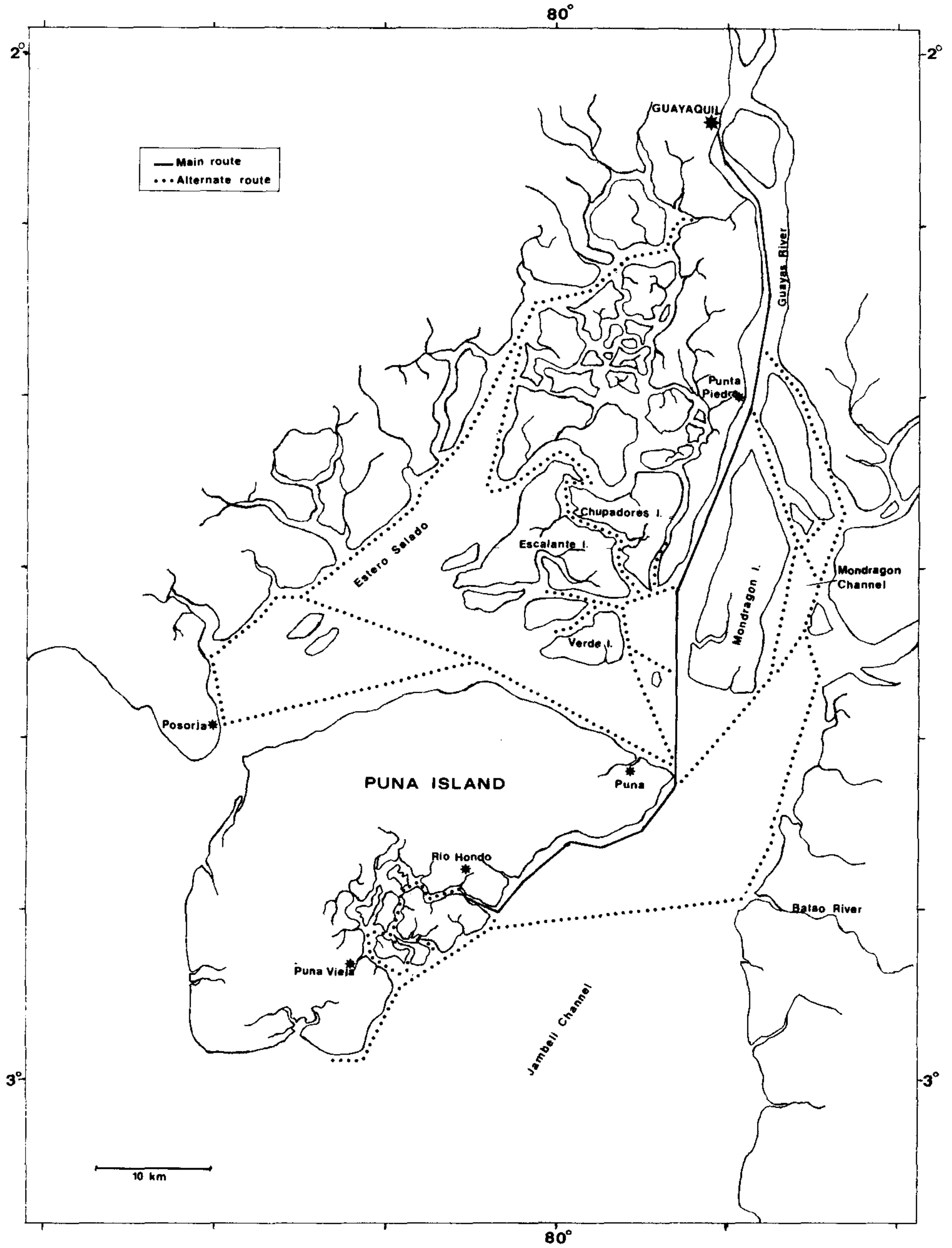

Figure 2 — Survey routes for the inner estuary of the Gulf of Guayaquil. The main route is indicated by a continuous line, while the dotted line shows the alternate routes.

this purpose the Petersen estimator modified by Bailey was employed (SEBER, 1982, p. 61),

$$N = n_1(n_2 + 1)/m_2 + 1$$

where N is the estimate of abundance; n_1 is the number of different individuals seen in 1990; n_2 is the number of different individuals seen in 1991; and m_2 is the number of individuals seen in both 1990 and 1991. This estimator has been used to estimate other whale populations and it is appropiate for studies using photographs of naturally marked whales, where sampling is with replacement (HAMMOND, 1986).

The speed of the dolphins was estimated by measuring the time taken by the animals to move between two points, using well-known geographical landmarks, and afterwards calculating the distance on a map. The speed was measured on three different occasions along 7—15 km of coastline.

Information about feeding behaviour comes from direct field observations when the animals were seen chasing or tossing up fish. Marine birds were also generally observed at this stage. Stomach contents were analyzed from three specimens from Puná Island. All these animals belonged to the coastal variety according to skull measurements given by VAN WAEREBEEK *et al.* (1990). Data obtained during informal interviews with fishermen gave additional information about feeding behaviour, dolphin site preferences and interactions with man.

Young calves were classified in two age categories. Very small sized animals, recognizable by their dark colour and the habit of raising the head out of the water whilst breathing, were classified as "neonates". Their age was estimated as less than 2 weeks. Animals older than 2 weeks, but younger than 3 months, were classified as "calves". A more subjective approach, based on personal experience was used to place a calf in this category ("calves"), comparing its size to that of the mother. Animals estimated to be older than three months were no recorded as calves in order to avoid more subjetive bias.

The information presented here deals with two annual periods, one for 1990, covering February 1990 to January 1991, and the other for 1991, covering February 1991 to January 1992. "Seasonal variation" is used to mean the statistically significant difference of any feature during the two 6 months periods: December—May (the warm rainy season) and June—November (cool dry season).

RESULTS

Distribution and seasonality

Dolphin groups were encountered along the entire main route, but a consistently higher number of sightings in certain locations clearly indicated those as favorable sites. Fig. 3 shows all the sites where dolphins have been observed. In general dolphins preferred the entrances of the bigger channels, e.g. between the Verde, Escalante and

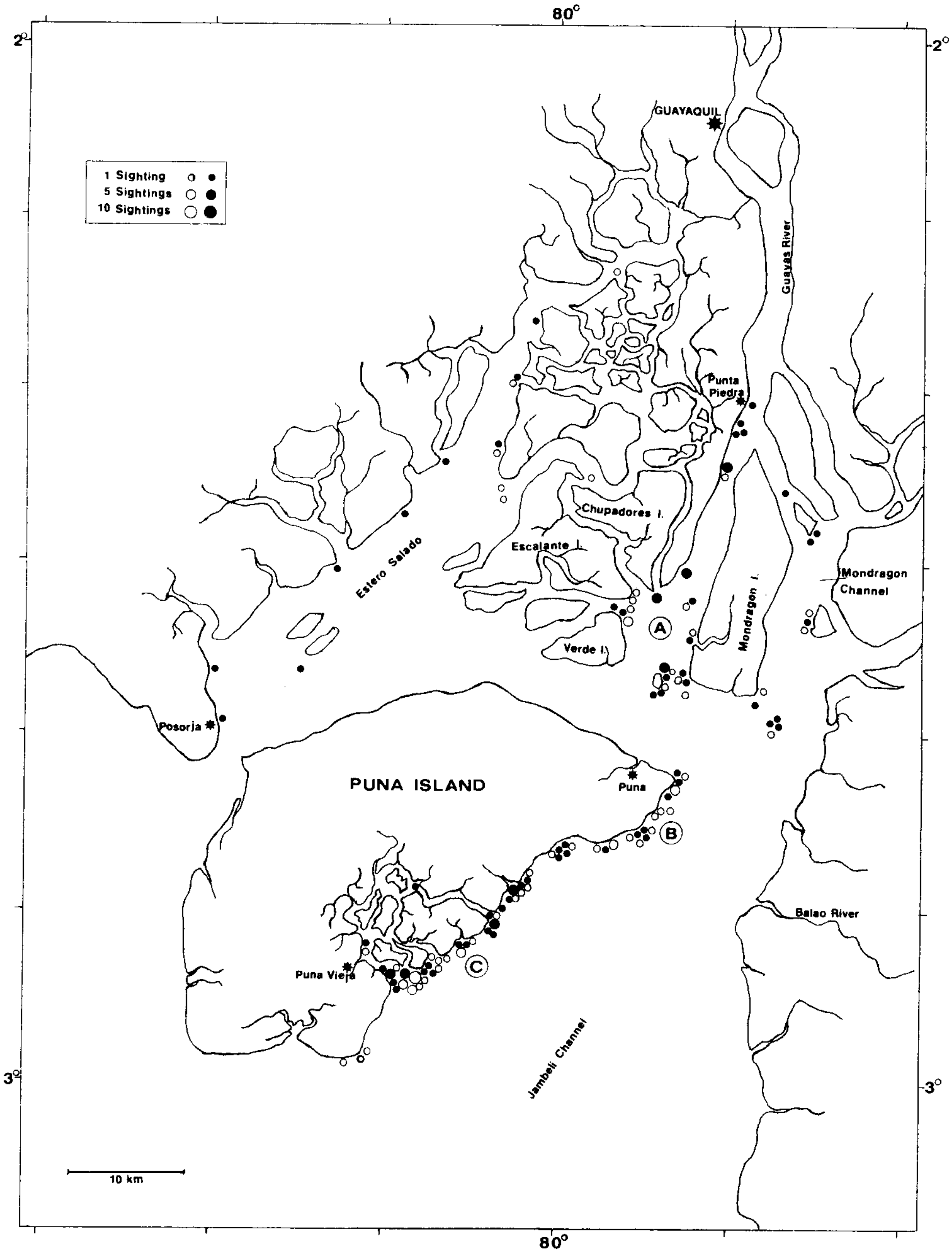

Figure 3 — Sightings of bottlenose dolphins in the inner estuary of the Gulf of Guayaquil. Open circles indicate sightings made from December to May and full circles show sightings between June and November, for both years (1990 and 1991).

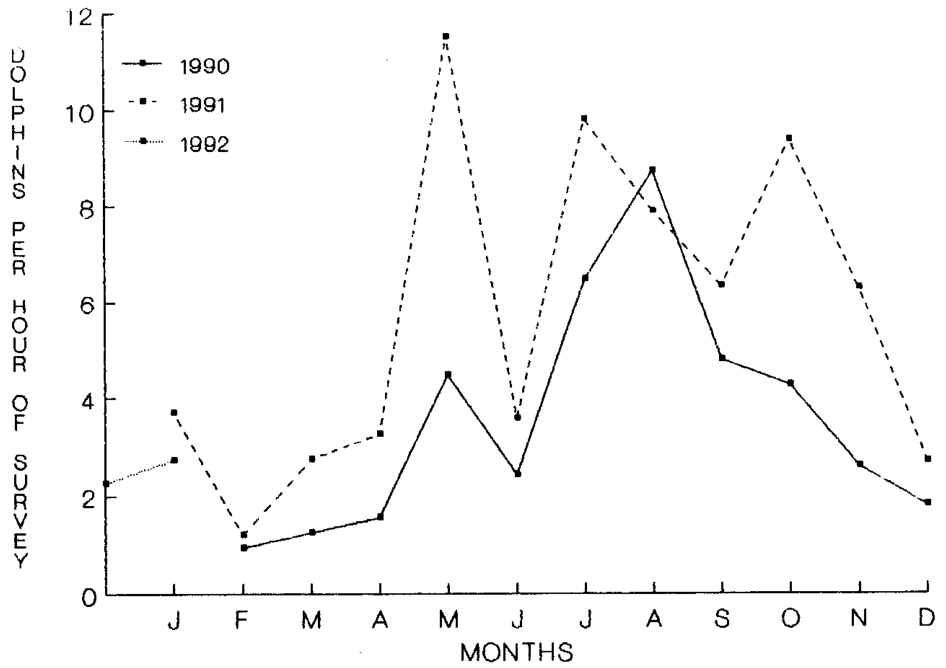

Figure 4 — Abundance of bottlenose dolphins in the inner estuary. One hour of survey was considered as a unit of effort.

Chupadores islands (in the Guayas river outlet) and in the mouth of Río Hondo and Puná Vieja channels, at the southeast end of Puná Island. The presence of the dolphins in those sites was most often related to feeding activities.

The northern distribution limit in the Guayas river seems to be at Punta Piedra, 20 Km south of Guayaquil. To the south, dolphins occur further south than the limit of the study area, at the southern end of Puná Island. Dolphins were seen further up in the Estero Salado than in the Guayas river, with records as close as 4 Km south of the Guayaquil sea harbour. This suggests that the distribution of the dolphins could be influenced by salinity, because the Estero Salado is separated from the main freshwater run-off by a land tongue (Fig. 3), so that its salinity is greater than that of Guayas river. Although the Estero Salado and the channels between the interior islands of the Gulf were surveyed with less frequency, dolphins were always sighted, which indicates a permanent use of these channels.

In the Mondragón channel (east side of the estuary) dolphins were observed throughout the zone (Fig. 3). However, further south along the continental coast as far as the Balao river, no dolphins were seen. Neither were dolphins seen in the middle of the Jambelí channel on surveys across it from Balao river to Puná Island, suggesting that this zone is used less frequently.

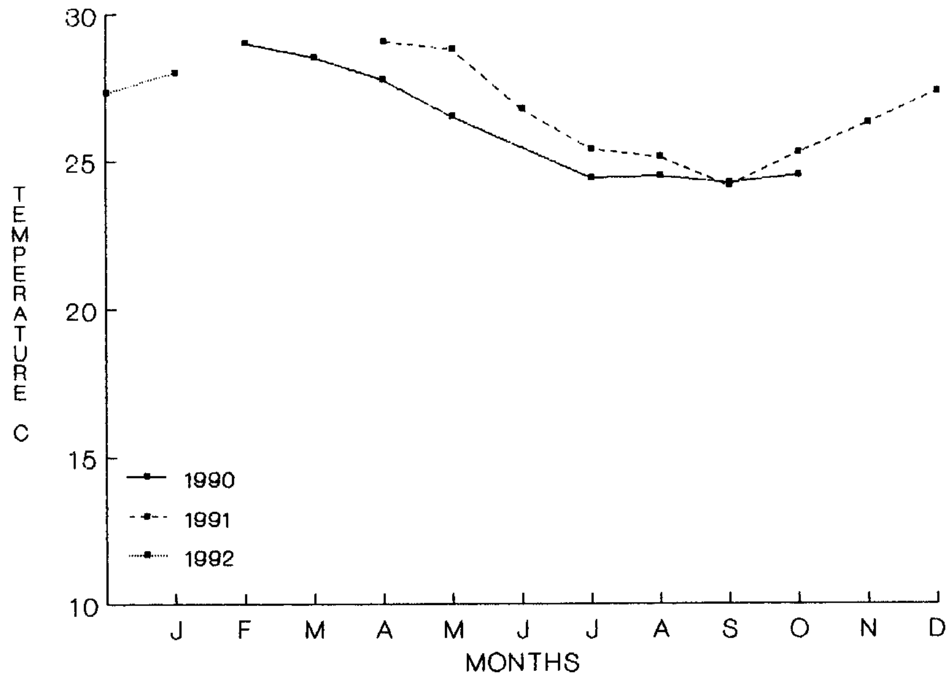

Figure 5 — Water surface temperature of the inner estuary of the Gulf of Guayaquil during the study period. Dots in the lines are the averages each month.

There was a significant seasonal difference in the distribution of the dolphins around the outlet of the Guayas river. Fig. 3 shows the sightings made in both seasons (December—May and June—November). The number of sightings in the river mouth (A) showed a statistically significant decrease during the rainy season ($X^2 = 6.77$, $P < .001$). In contrast to this, to the northeast and east of Puná Island (B and C) where the salinity is more stable year round, no significant difference was found in the number of sightings between seasons ($X^2 = 2.64$, $P > 0.1$; and $X^2 = 0.13$, $P > 0.25$ respectly). This shows that the dolphins leave the Guayas river outlet (A) during the rainy season.

The relative abundance of dolphins in the study area also showed a significant seasonal difference (ANOVA, $F_{1,23} = 7.1$, $P < 0.05$), with more dolphins present during drier months than during rainy months. Fig. 4 presents the number of dolphins sighted per survey hour per month. The number of dolphins seen was greater during the dry season in both years, increasing from May onwards (end of the warm season), when the sea water temperature drops (see Fig. 5). Dolphin numbers declined in November (end of the dry season), when the water temperature goes up again. June showed similar values to dry months in both years, although it is not clear why this occured.

Group movements

Groups of dolphins typically moved slowly, usually keeping within 100 m of the shore. When dolphins were seen in more open and deeper water, generally the groups were dispersed and engaged in periods of collective feeding. The time when groups were present in a determined area was variable and directly related to foraging periods, because they moved on to other areas when they had finished feeding.

The tide was changing the appearance of the area continuously, uncovering mud flats, narrowing the channels and creating strong currents, but there were no signs that this influenced the dolphins' movements. Table 1 shows how the groups moved in relation to the direction of the tide. Although there was a higher number of groups moving against than with the current, the difference was not statistically significant ($X^2 = 2.23$, $P > 0.1$). Most observations (79 cases) fitted into the milling category, 60% of these correlated with feeding activities. There was no significant difference between the total number of sightings during flood or ebb tides ($X^2 = 2.38$, $P > 0.1$), neither in the number of times that dolphins moved with ($X^2 = 3.77$, $P > .05$) or against the flood or ebb tides ($X^2 = 0.04$, $P > 0.25$). According to these results, dolphin movements are independent of the tides.

The transit speed of the dolphins showed a small variation in the three cases which were calculated. The average was approximately 4 km/hr. Short and fast movements were related to feeding periods or to intense social activity, and not with transit.

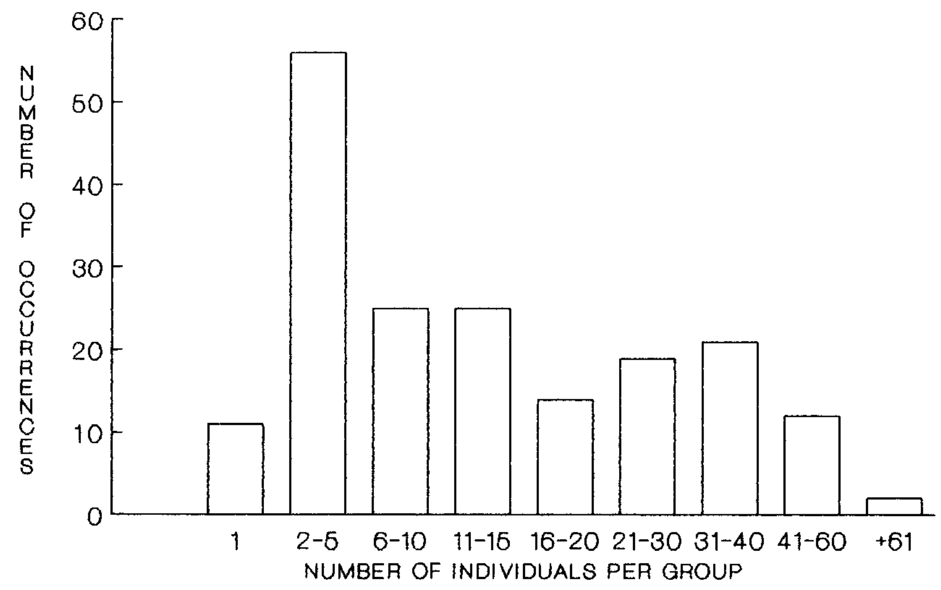

Figure 6 — Frecuency distribution of group size of the coastal bottlenose dolphins in the Gulf of Guayaquil in 1990—1991.

Group size

Fig. 6 shows the frequency distribution of the size of groups in both years. Although small groups with 2—5 animals prevailed, groups of 20 to 40 animals were not uncommon. A few times dolphins formed groups of more than 60 individuals. To see single dolphins was as unusual as groups of 40 to 60 animals. The mean group size was 16.2 animals (s.d. = 15.7, n = 185). A statistically significant seasonal difference in the group size was found (ANOVA, $F_{1,184} = 7.75$, $P < 0.01$). Groups were larger in the dry and cool season (mean 19.3, s.d. = 16.5, n = 98) than in the rainy and warm season (mean 12.9, s.d. = 14.05, n = 87). This is obvious also from Fig. 7, which shows the monthly mean group size during the study period.

Population size

The data used to estimate the size of the population are shown in Table 2. The population in the study area (715 km² of the inner estuary) was estimated to be 637 dolphins (95% confidence interval = 541—733). The results of both years show differ-

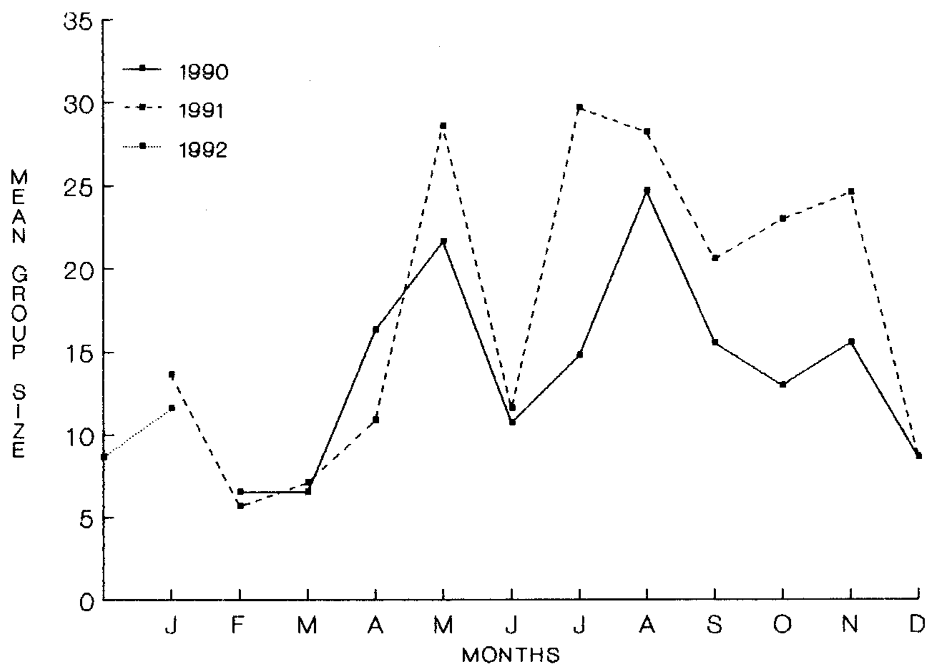

Figure 7 — Monthly mean group size in the coastal bottlenose dolphin of the Gulf of Guayaquil in 1990—1991.

ences in numbers of dolphins sighted and re-sighted; values being greater in 1991. In that year the survey effort was greater on the east side of the estuary, resulting in a larger number of dolphins identified from this zone that were not photographed previously. From the 217 identified individuals in 1990, 110 (51 %) were observed also in 1991, suggesting that a large proportion of dolphin population are resident in the study area.

The density in the study area was estimated to be 0.89 dolphins/km^2. Based on this density, it is estimated that, in the whole inner estuary of the Gulf of Guayaquil (ca. 2,800 km^2) inhabit 2,492 dolphins.

Feeding

Bottlenose dolphins were seen chasing or tossing up a great variety of fish during feeding periods, including: drums *Synoscion* sp, mullets *Mugil* sp, anchovies *Anchoa* sp, catfish *Arius* sp, mojarras *Eucinostomus* sp, flat fishes and many which were unidentified. The prey size was variable; both small and big fishes were involved. The stomach contents analysis of two animals that were found dead on December 1, 1992 on Puná Island showed that they had been feeding on the same prey, the sciaenid *Synoscion* sp. In one of the stomachs were found 41 otoliths of this fish species and two small beaks of unidentified squid. In the second stomach were found 76 otoliths, 73 from *Scynoscion* sp and 3 of unidentified fish. The average length of the otoliths was 16.48 mm (s.d. = 2.69, range 10—21.5 mm). In the stomach of a third dead animal found in September 1993, 56 otoliths of the anchovia *Cetengraulis mysticetus* were found (size average 4.2 mm).

Although dolphins were observed feeding more frequently during the low tide, no significant relationship was found between feeding periods and tidal phase ($X^2 = 17.87$, d.f. = 10, $P > 0.1$). Nor was it clear whether dolphins had a preference to feed at a certain time of the day because the observations were mostly made in the morning and around noon.

Dolphins were seen foraging alone, in small groups or collectively in larger groups. The commonest observed form of feeding was by individuals chasing with speed rushes, showing the upper part of the body out of the water. In the channels and in shallow water dolphins used the shore to trap fish with rapid movements, especially at low tide when mud and sandbanks were exposed. On several occasions dolphins were seen in water only about 30 cm deep, with the upper half of the body exposed to the air, moving and maneuvering at high speed. Shore chases were made most frequently by mothers with calves and young animals, rather than by adults alone. Small groups of 2—4 individuals (mainly immatures) seemed to cooperate when they showed this behaviour. DE LA PARRA and GALVÁN (1987) have described how bottlenose dolphins trapped fish against the mangroves in a similar way in the Gulf of California. On one occasion a dolphin was observed to strand itself with more than half of its body out of the water to catch mullet that had leapt onto a mudbank, trying to escape from the dolphin. DOS SANTOS and LACERDA (1986) also reported similar behaviour in bottlenose dolphins in Portugal.

Big groups of to up 60—80 dolphins were seen feeding collectively on several occasions in more open water, but here there were no clear signs of cooperation or fish herding behaviour observed in bottlenose dolphins elsewhere (TAYLER & SAAYMAN, 1972; LEATHERWOOD, 1975; BALLANCE, 1992). A single group could occupy an area as large as 2—4 km^2. They seemed to be in no order but spread out at random. Although many dolphins were seen to leap and/or accelerate while chasing fish, these dolphins usually peaked their flukes before diving, presumably feeding on benthic organism. Usually mothers with calves dived simultaneously and probably this is a way of teaching the calf and forms part of feeding activity, as COCKCROFT & ROSS (1990) have suggested. The periods of collective feeding last 1—2 hours, after which dolphins start to form subgroups and social activities increase. Several types of leaps, fast swimming and pursuits were observed at this stage. Afterwards, the subgroups joined and moved to other areas or went their own way.

On two occasions dolphins were seen feeding behind a trawler fishing shrimps. They stayed behind the trawl net and continuously arched the body and peaked their flukes, probably to make deep dives to pick up fishes stirred up by the net. When the trawler stopped to get the net on board, the dolphins lost interest for a while, but returned to the same position behind the net as soon as the ship resumed fishing. Coastal bottlenose dolphins feeding close to trawling operations have been reported in several places (LEATHERWOOD, 1975; WELLS *et al.* 1980; DE LA PARRA & GALVÁN, 1987; CORKERON, *et al.* 1990). Dolphins were also seen feeding close to moving purse seiners fishing for small schooling fishes.

Reproduction

Calving and Mother-Calf Relationships

Newborn calves were seen all year round. Fig. 8 shows the months when calves with identified mothers were sighted for the first time. A total of 35 identified females gave birth to 36 calves during the study period. Neonates were seen in nine different months; the greatest number, three in each month, were seen in May, October and November. Most larger calves were seen in May, July and October. Although a higher number of births was recorded during the cool dry season (June—November), the ratio 'Total number of newborn calves sighted/Total number of dolphins sighted' was not significantly different between both seasons ($X^2 = 0.455$, $P > 0.25$).

One female had two calves in less than two years. In May 1990, she was observed for the first time with a calf considered to be less than 3 months old. Until the end of September of that year mother and calf were seen together six more times. But at the end of November 1990, the calf was not seen again. The estimated maximum age of the calf when seen in September was nine months, so it is not likely that the calf was weaned. More likely the calf died at sometime between September and November. On November 6, 1991, the female was seen again with a newborn calf. The gestation period in the bottlenose dolphin is about 12 months (MC BRIDE & KRITZLER, 1951; TAYLER & SAAYMAN, 1972), so this female must have became pregnant shortly after her first calf was lost.

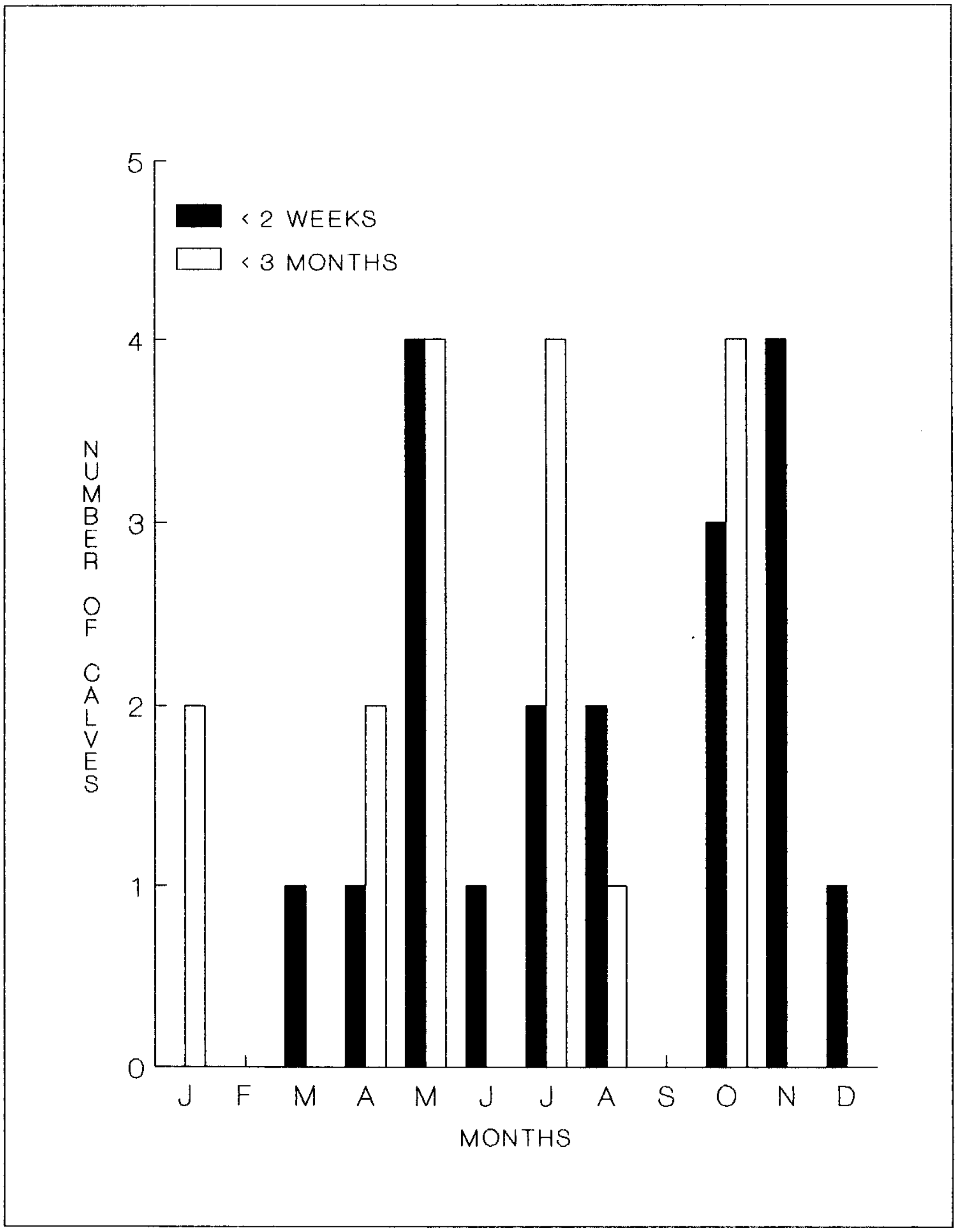

Figure 8 — Registered calves during the study period. The smallest calves (neonates) are indicated by solid columns and older calves by open columns. The given number per month indicates the first observations for calves and is not necessarily the month in which they were born.

The calves seemed to remain at least two years with their mothers. Mothers with older calves, identified at the beginning of the study and probably 1 year-old or more, were still seen together after two years. A calf seemed to become weaned after its mother gave birth to a new calf, although the case of the one female was different. She was observed with both her newborn calf and her older offspring for several months. SCOTT *et al.* (1990) reported that in the coastal bottlenose dolphins of Florida calves typically stay with their mothers 3 to 6 years, but their affective bonds are maintained longer. WÜRSIG (1978) also reported a long-term relationship in mother-calf pairs in coastal bottlenose dolphins off Argentina. Several cases from Ecuador suggest a similar long term relationship.

Birth Rate and Calf Mortality

From the 36 births recorded, 13 occurred in 1990 and 21 in 1991 (Table 3), a crude annual birth rate of 0.02 and 0.036 respectively (mean 0.028). It was based only on identified mothers to avoid counting calves more than once in later sightings.

Calf mortality was estimated at six months of age (from their estimated date of birth), when small calves had disappeared from the side of their mothers. Only 14 of the 36 calves entered into this estimation, of these nine (64%) were seen with their mothers after this period, that is, 36% mortality at six months of age (Table 3).

Mating

Mating occurred most frequently in small subgroups of 3—5 dolphins. In such tight subgroups the amount of social activity increased, the different types of behaviour including abrupt turns, rubbing and mounting over another animal, tail slaps, leaps, etc. When one dolphin, possible a female, turned away from the group, the remainder pursued it, and when they caught up with it, the activities started again. The duration of time that dolphin showed this behaviour was variable; animals could alternate chases and "playing" behaviour continuously for up to one hour or more. On several occasions some of the involved dolphins were seen to have the penis erect, indicating that they were sexually active. Most times, the dolphins involved were adult males, although sometimes subadults of unknown sex participated as well. Similar behaviour in wild bottlenose dolphins have been reported previously (SAAYMAN & TAYLER, 1972; DE LA PARRA & GALVÁN, 1987; CONNOR *et al.*, 1992).

Only on one ocasion were two dolphins observed in a belly-to-belly position, presumably mating, for a considerable length of time. Swimming at a distance of 20 m from the boat the pair suddenly stopped and the big male (a known individual), laid his head over the back of his partner for a few moments, then turned on his side and directed his ventral part toward the other dolphin. This was repeated 3 or 4 times before the other animal took up a similar side position with its belly towards the identified male. Both dolphins stayed in this position at the surface without moving for 20—30 seconds. Then they separated and a minute later the identified male approached, presumably, the same dolphin and repeated the head movement. Subsequently, a third animal joined the couple, touching the identified male and maintaining him in the middle for a few seconds and left. Then the identified male and his partner assumed the belly-to-belly position again, for about 10 seconds, and then both dolphins separated and started to swim actively. It is not certain whether the dolphins were mating, because of the turbid water only their upper parts and sides were visible, and the male's erected penis was not seen. Similar behaviour in free-ranging bottlenose dolphins was described by DOS SANTOS & LACERDA (1987) and was considered to be mating behaviour.

Suckling

When approached by a boat, even discretely, mothers with calves usually kept their distance and were more alert. So, it was difficult to observe at close range any typical mother-calf behaviour such as suckling. However, this was observed on one ocasion inside the channel of Puná Vieja within a group of 8 dolphins, including 3 calves. One calf lifted its head out of water, touching the flank of a dolphin which was presumably its mother. This dolphin reacted by ceasing to swim, turned her body towards its calf, while the latter moved its head backwards, apparently searching for the nipple to suck. In the meantime the mother remained in a position slightly inclined to the horizontal with only the head and main part of the back half out of the water. After 10 seconds this position was abandoned and they continued moving as before.

DISCUSSION

The repeated observations of a large number of known dolphins during two years suggests that at least a part of the studied population is resident, but a seasonal variation in distribution and abundance occur. Their movements in the most of the cases seem to be limited to a range, perhaps restricted to within the inner estuary. SHANE *et al.* (1986), pointed out that this type of local seasonal movements are especially typical of warm-water bottlenose dolphins and are probably related to movements of food and need for safety in reproduction. Dolphins concentrated their activities within small areas, rather than being evenly spread throughout their whole home range, especially in the mouths of large channels, sometimes in a predictable pattern. These places were often related to feeding and social activities. Coastal bottlenose dolphins seem to have a similar distribution pattern elsewhere (WELLS *et al.*, 1980; IRVINE *et al.*, 1981; DOS SANTOS & LACERDA, 1987; KNOWLES *et al.*, 1990; SHANE, 1980, 1990; BALLANCE, 1992).

Changes in salinity obviously influenced the dolphin distribution and abundance in the river Guayas outlet, where sightings were less frequent during the rainy season. Artisanal fishermen in the estuary of the Guayas river also report that during the rainy season fish are less abundant and fewer dolphins are seen. From January to May the Guayas river brings down 15 times more freshwater than during the months of the dry season (STEVENSON, 1981). This may cause changes in the number of fish species and their abundance in the area, considering that the salinity drops to almost zero. Therefore, dolphins would have to move to areas of higher salinities with more food, or with preferred species. Unfortunately, there are no statistics of artisanal fisheries for the inner estuary of the Gulf of Guayaquil, and it was not possible to make a comparison between seasons of the fish species present. It is also possible that the dolphins, by their seasonal movements, are traying to avoid damage of their skin, as is known to occur in marine odontocetes when they are placed in freshwater (GERACI *et al.,* 1986).

The seasonal variation in the abundance showed by dolphins seem also to be related to water temperature and probably to food availability as well. Although the seasonal difference in water temperature in the Gulf is small (around 4°C), it may be enough to cause changes in the composition of the dolphins' food. During the dry and cool season, purse seiners fish in the inner estuary because there is plenty of small schooling fishes, especially anchovies (*Anchoa* sp and *Cetengraulis mysticetus*). It seems that dolphins also take advantage of the abundance of these species and also prey on them, as suggested by the analysis of the dolphins' stomach contents. In other places, coastal bottlenose dolphins also prey on anchovies when they are present (WÜRSIG & WÜRSIG, 1979; VAN WAEREBEEK *et al.,* 1990). The presence of large fish schools also could explain why dolphins form larger groups during this season. Seasonal variations in the abundance of bottlenose dolphins have also been reported by WÜRSIG (1978), SHANE (1980), WELLS et al. (1980), ECHEGARAY *et al.* (1992), among others. In contrast, HANSEN (1990) reported that neither dolphin abundance nor group size followed a seasonal pattern in South Californian coastal bottlenose dolphins. In the Gulf of Guayaquil, during the warm and rainy season dolphins probably feed more individually or prey upon species which form smaller schools and possibly for this reason the dolphins form smaller groups.

From studies on the stomach contents of coastal bottlenose dolphins elsewhere it is known that they feed on a great variety of species (LEATHERWOOD, 1975; SHANE *et al.* 1986; BARROS & ODELL, 1990; COCKCROFT & ROSS, 1990; MEAD & POTTER, 1990; VAN WAEREBEEK *et al.* 1990). Bottlenose dolphins in the Gulf of Guayaquil were observed chasing and tossing up a great variety of fish, but the analysis of the stomach contents of three dead animals showed a highly specific diet. Many more samples are needed to assess the significance of this. Several authors observed a number of strategies to capture fish, including individual, collective and cooperative behaviour (LEATHERWOOD, 1975; SHANE *et al.* 1986; WÜRSIG, 1986; SHANE, 1990). Behaviour involving chasing or pursuing fish in shallow waters was also commonly observed during this study. Cooperative behaviour among dolphins was not common and restricted to trapping fish against the shore. LEATHERWOOD (1975) pointed out that the most frequently reported feeding pattern in the Gulf of Mexico is foraging behind trowlers whilst fishing. This is in contrast to what was observed in the Gulf of Guayaquil where groups of dolphins generally showed no reaction when a fishing shrimp trawler passed close to them. Also they were never seen to feed on trash fish dumped from the boats. Likewise, BALLANCE (1992) reported that on no occasion were bottlenose dolphins seen feeding behind working trawlers in the Gulf of California.

Although no significant difference was found between feeding periods and the height of the tide, dolphins preferred to feed in the channels during low tide. This was to their advantage, because at low tide the channels become narrower and the currents are strongest, carrying with them larger amounts of fish. Also, at low tide mangrove tree roots become exposed, so that fishes are denied this hiding place. When the tide rises fishes can hide again among the mangrove roots and the dolphins have less chance to catch fish. Elsewhere dolphins benefit from the low tide whilst feeding in a similar way (HOESE, 1971; WELLS *et al.,* 1980). In contrast, SAAYMAN & TAYLER (1979) reported that Indian humpback dolphin (*Sousa* sp), also a coastal dolphin species, prefers to feed during high tide. Dolphins seem to know how to minimize efforts to catch their prey, and how to take advantage of the tide, according to their prey's movements and abundance.

The tidal direction did not seem to influence the direction of transit of the dolphins. Similar results were reported by DOS SANTOS & LACERDA (1987) in Portugal. However, SHANE (1980, 1990) reported that dolphins preferred to travel against, rather than with the tidal current in southern Texas and in Florida and this was often associated with feeding periods. On the other hand, IRVINE *et al.* (1981) recorded more animals moving with the tide than against it.

The estimated travelling speed (mean 4 km/h) was lower than that reported by WÜRSIG & WÜRSIG (1979), who reported 6.1 km/h in argentine coastal bottlenose dolphins. SHANE (1990) reported 5.5 km/h in Florida bottlenose dolphins. However, my estimate may be too low because there were only three observations on speed of travel. My three observations were made on big groups containing at least 30 individuals, mainly females with calves. It is possible that small groups, or groups formed by other age classes, may travel faster. IRVINE *et al.* (1981) reported that in Florida in general the speed of the groups was between 2 and 5 km/h, but occasionally small and tight groups moved at speed exceeding 5 km/h.

Newborn calves were sighted year round, without any clear seasonality. The lower number of calves recorded between December and April was because dolphins were less abundant and not because fewer births occurred. In general, tropical dolphin species, like spotted dolphins (*Stenella attenuata*) and spinner dolphin (*S. longirostris*), present a weak pattern of reproductive seasonality with prolonged calving seasons throughout the year (PERRIN *et al.,* 1976; BARLOW, 1981). Most studies on coastal bottlenose dolphins have been carried out in temperate zones where births occur all the year round, but with a clear bimodal tendency with peaks in the spring and other in autumn (MEAD, 1975; ODELL, 1975; WÜRSIG, 1979; PIZA, 1990; SCOTT *et al.,* 1990). However, HANSEN (1990) reported only one peak in the autum in California coastal bottlenose dolphins and MEAD & POTTER (1990) also reported one peak in spring in North Carolina. In those zones the seasonality and calving peak intensity seem to depend on variable environmental factors, especially water temperature. In the Gulf of Guayaquil, the difference in water temperature between both seasons seems too small to produce any type of breeding seasonality, and the dolphins behave like other tropical cetacean species.

The estimated crude annual birth rate in this study (mean 0.028) was lower than the one reported by WELLS & SCOTT (1990) for Florida bottlenose dolphins (mean 0.055) and by WÜRSIG (1978), who recorded 5 births in a population of 53 bottlenose dolphins in the south Atlantic during a 21 months study period (0.054). The results of the present study may be lower because the population and the area surveyed are larger, resulting in a less accurate births recording. Therefore they may not represent the real reproductive capacity of the population but a minimum value.

Mortality in the first months of life was estimated to be 36 % at six months of age. A high mortality at this age has also been reported in Florida bottlenose dolphins by WELLS & SCOTT (1990), who estimated a mortality of 36.8 % in yearlings and 10.5 % in immatures of two years of age. HERSH *et al.* (1990) and FERNÁNDEZ (1991) also reported that during their studies a high proportion of the stranded animals found in Florida and Texas were yearlings, 27.3 % and 19 % respectly. None of six beached animals that were found during this study in the Gulf of Guayaquil were yearlings, but two of them were immatures of about 2 m in length. Mortality of dolphins in several cases could be caused by entanglement in gill-nets. Fishermen reported that bottlenose dolphins sometimes get caught in gill-nets set on the bottom to catch shrimp, which has also been reported by VAN WAEREBEEK *et al.* (1990). However, no attempts to quantify these interactions have yet been made.

ACKNOWLEDGMENTS

I wish to thank many people that have contributed during my study and during the preparation of this paper. Many volunteers of the Fundación Ecuatoriana para el Estudio de Mamíferos Marinos (FEMM) provided assistance in the field, special thanks to Javier Avalos. Dr. Robert Clarke, Mr. Stefan Harzen, Dr. Koen Van Waerebeek and Dr. Philip Hammond revised the manuscript and made valuable comments. Ben Haase and Daniel Palacios helped me with the translation of the Spanish version. I am also grateful to all the collegues who sent me papers and material for revision.

REFERENCES

AGUAYO, A. (1975). Progress report on small cetacean research in Chile. Journal Fisheries Research Board of Canada. 32:1123—1143.

BALLANCE, L.T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, México. Marine Mammal Science. 8(3):262—274.

BARLOW, J. (1981). Reproductive seasonality in pelagic dolphins: implication in measuring rates. Abstracts of Conference Cetacean Reproduction: Estimating Parameters for Stock Assessment and Management, La Jolla, California. November 28 – December 7, 1981. p. 14.

BARROS, N.B. & ODELL, D.K. (1990). Food habits of the bottlenose dolphins in the southeastern United States. Pp. 309—328. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

COCKCROFF, V.G., & ROSS, G.J.B. (1990). Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. Pp. 295—308. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

CONNOR, R.C., SMOLKER, R.A. & RICHARDS, A.F. (1992). Dolphin alliances and coalitions. Pp. 415—443. In: A.M. Marcourt & F.B.M. de Wall (Eds.). Coallitions in Humans and Other Animals. Oxford Science Publications.

CORKERON, P.J, BRYDEN, M.M. & HEDSTROM, K.E. (1990). Feeding bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. Pp. 329—336. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

DE LA PARRA, R. & GALVÁN, B. (1987). Observaciones del tursión costero del Pacífico en el sistema Topolobampo-Ohuira, Sinaloa, (con notas acerca del comportamiento, ritmo respiratorio e identificación individual). Memoria de la X Reunión Internacional Sobre Mamíferos Marinos. 24—27 de marzo de 1985. La Paz, México.

DOS SANTOS, M.E. & LACERDA, M. (1987). Preliminary observations of the bottlenose dolphin (*Tursiops truncatus*) in the Sado estuary (Portugal). Aquatic Mammals. 13.2:65—80.

ECHEGARAY, M., REYES, J.C. & VAN WAEREBEEK, K. (1992). Observaciones del bufeo (*Tursiops truncatus*) en el litoral de Pisco, Perú. Paper presented at: V Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur. September 28 – October 2 1992. Buenos Aires, Argentina (unpublished).

FÉLIX, F. (1990). Observaciones del delfín nariz de botella *Tursiops truncatus* en el Golfo de Guayaquil, Ecuador. Primeros resultados (Abstract). In: Resúmenes de la IV Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur. 12—15 Noviembre de 1990. Valdivia, Chile. p. 27.

FERNÁNDEZ, S. (1991). Preliminary results on age structure and life history parameters of bottlenose dolphins (*Tursiops truncatus*) stranded along the Texas coast, 1981—1990. In: Ninth Biennial Conference on the Biology of Marine Mammals. December 5—9, 1991. Chicago, U.S.A. p. 21.

GERACI, J.R., ST. AUBIN, D.S. & HICKS, B.D. (1986). The epidermis of odontocetes: a review from within. Part I: Anatomy and Physiology. Pp. 3—21. In: M.M. Bryden and R. Harrison (Eds.). Research in Dolphins. Oxford University Press. 400 pp.

HAASE, B. (1990). Resultados preliminares de observaciones sobre cetáceos en la costa continental suroeste del Ecuador (Abstract). In: Resúmenes de la IV Reunión de Trabajo de Especialistas en Mamífeors Acuáticos de América del Sur. 12—15 Noviembre de 1990. Valdivia, Chile.

HAMMOND, P.S. (1986). Estimating the size of naturally marked whale populations using capture-recapture techniques. Rep. int. Whal. Commn. (special issue 8). 253—281.

HANSEN, L.J. (1990). California coastal bottlenose dolphins. Pp. 403—420. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

HERSH, S.L., ODELL, D.K. & ASPER, E.D. (1990). Bottlenose dolphin mortality patterns in the Indian/Banana river system. Pp. 155—164. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

HERSH, S.L. & DUFFIELD, D.A. (1990). Distinction between northwest Atlantic offshore and coastal bottlenose dolphins based on hemoglobin profile and morphometry. Pp. 129—139. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

HOESE, H.D. (1971). Dolphin feeding out of water in a salt marsh. Journal of Mammalogy, 52(1):222—223.

IRVINE, A.B., SCOTT, MD., WELLS, R.S. & KAUFMANN, J.H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus,* near Sarasota, Florida. Fishery Bulletin: Vol. 79(4):671—688.

KENNEY, R.D. (1990). Bottlenose dolphins off the Northeastern United States. Pp. 369—386. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

KNOWLES, J., HAMMOND, P. & THOMPSON, P. (1990). Ecology of bottlenose dolphins *Tursiops truncatus* in the Moray Firth, northeast Scotland. Pp. 76—77. In: P.G.H. Evans, A. Aguilar, and C. Smeenk (Eds.). Proceedings of the Fourth Annual Conference of the European Cetacean Society. 2—4 March, 1990. Palma de Mallorca, Spain.

LEATHERWOOD, S. (1975). Some observations of feeding behavior of bottle- nosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops* cf *T. gilli*) off Southern California, Baja California, and Nayarit, Mexico. Marine Fisheries Review. Vol. 37(9):10—16.

LEATHERWOOD, S. & REEVES, R.R. (1983). Whales and Dolphins (The Sierra Club Hadbook). Sierra Club Books. San Francisco. 302 pp.

MASSAY, S. (1983). Revisión de la lista de los peces marinos del Ecuador. Boletín Científico y Técnico, Instituto Nacional de Pesca del Ecuador. Vol. 6(1). 113 pp.

McBRIDE, A. & KRITZLER, H. (1951). Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. Journal of Mammalogy. Vol. 32:251—266.

MEAD, J.G. (1975). Preliminary report on the former net fisheries for *Tusiops truncatus* in the western north Atlantic. Journal Fisheries Research Board of Canada. Vol. 32(7):1155—1162.

MEAD, J.G. & POTTER, C.W. (1990). Natural history of bottlenose dolphins along the central Atlantic coast of the United States. Pp.165—195. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

ODELL, D.K. (1975). Status and aspects of the life history of the bottlenose dolphin, *Tursiops truncatus,* in Florida. Journal Fisheries Research Board of Canada. Vol.(7):1055—1058.

PERRIN, W.F. (1984). Patterns of geographical variation in samall cetaceans. Acta Zool. Fennica 172, 137—140.

PERRIN, W.F., COE, J.M. & ZWEIFEL, J.R. (1976). Growth and reproduction of the spotted porpoise, *Stenella attenuata,* in the offshore eastern tropical Pacific. Fishery Bulletin: Vol. 74(2): 229—269.

PIZA, J. (1990). Pregnancy research in bottle-nosed dolphins *Tursiops truncatus.* Pp. 86—87. In: P.G.H. Evans, A. Aguilar, and C. Smeenk (Eds.). Proceedings of the Fourth Annual Conference of the European Cetacean Society. 2—4 March, 1990. Palma de Mallorca.Spain.

SAAYMAN, G.A. & TAYLER, C.K. (1979). The Socioecology of humpback dolphins. Pp. 165—226. In: H.E. Winn and B.L. Olla (Eds.). Behavior of Marine Animals, Vol. 3. Cetacea. Plenum Press. New York. 438 pp.

SCHEFLER, W.C. (1981). Bioestadística. Fondo Educativo Interamericano. México. 267 pp.

SCOTT, M.D. & CHIVERS, S.J. (1990). Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. Pp.387—402. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

SCOTT, M.D., WELLS, R.S. & IRVINE, A.B. (1990). A long-term study of bottlenose dolphins on the west coast of Florida. Pp.235—244. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

SEBER, G.A.F. (1982). The Estimation of Animal Abundance and Related Parameters. Griffin, London. 654 pp.

SHANE, H.S. (1980). Ocurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus,* in southern Texas. Fishery Bulletin. Vol. 78(3):593—601.

SHANE, H.S. (1990). Behavior and ecology of the bottlenose dolphin at Sanibel island, Florida. Pp. 245—265. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

SHANE, H.S., WELLS, R.S. & WÜRSIG, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: a review. Marine Mammal Science, 2(1):34—63.

STEVENSON, M.R. (1981). Variaciones estacionales en el Golfo de Guayaquil, un estuario tropical. Boletín Científico y Técnico, Instituto Nacional de Pesca del Ecuador. Vol. 4(1):5—32 + figs.

TAYLER, C.K. & SAAYMAN, G.S. (1972). The social organization and behaviour of dolphins (*Tursiops aduncus*) and baboons (*Papio ursinus*): some comparisons and assessments. Annals of the Cape Provincial Museum (Natural History). Vol. 9:11—41.

VAN WAEREBEEK, K., REYES, J.C., READ, A.J. & McKINNON, J.S. (1990). Preliminary observations of bottlenose dolphins from the Pacific coast of south America. Pp. 143—154. In: S. Leatherwood and R. Reeves (Eds.). The Bottlenose Dolphin. Academic Press. San Diego. 653 pp.

WALKER, W.A. (1981). Geographical variation in morphology and biology of bottlenose dolphin (*Tursiops*) in the eastern North Pacific. NMFS/SWFC Admin. Rep., No. LJ-81-03C. 54 pp.

WELLS, R.S., IRVINE, A.B. & SCOTT, M.D. (1980). The social ecology of inshore odontocetes. Pp.263—317. In: L.M. Herman (Ed.). Cetacean Behavior. Wiley-Interscience. New York. 463 pp.

WELLS, R.S. & SCOTT, M.D. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Rep. Int. Whal. Commn. (Special Issue 12): 407—415.

WÜRSIG, B. (1978). Ocurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an argentine bay. Biological Bulletin, Vol. 154:348—359.

WÜRSIG, B. (1986). Delphinid Foraging Strategies. Pp.347—359. In: R.J. Schusterman, J.A. Thomas and F.G. Wood (Eds.). Dolphin Cognition and Behavior: a Comparative Aproach. Lawrence Erlbaum Associates. London.

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

WÜRSIG, B. & WÜRSIG, M. (1979). Behavior and ecology of the bottlenose dolphin *Tursiops truncatus,* in the south Atlantic. Fishery Bulletin: Vol. 77(2):399—412.

Table 1 — Dolphin movements related to tidal current in the Gulf of Guayaquil.

Dolphin Heading	Tide			
	Flood		Ebb	
	n	%	n	%
With	16	16	21	26
Against	29	28	22	27
Milling	49	47	30	36
Unknown	9	9	9	11
	103		82	

Table 2 — Dolphins sighted during the study and population size estimation.

ITEM	1990	1991
A) Total sighted dolphins	1117	1738
B) Total of naturally marked dolphins	217	325
C) Total re-sighted dolphins	586	1055
D) Naturally marked dolphins sighted previously	—	110
E) Estimated population size 95% confidence limits		541—733

Table 3 — Estimated crude annual birth rate and calf survival at 6 months-age in bottlenose dolphins in the Gulf of Guayaquil.

ITEM	1990	1991	Total
A) Estimated population size	637	637	1274
B) Identified mothers with newborn calves during the study period	13	23	36
C) Birth rate (B/A)	0.020	0.036	0.028
D) Identified mothers sighted 6 months after birth of calf	10	4	14
E) Calves born to identified mothers re-sighted after 6 months	6	3	9
F) Calf survival at 6 months-age (E/D × 100)	60%	75%	64%