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THE CETACEAN OFFAL CONNECTION: FECES AND VOMITS OF SPINNER DOLPHINS AS A FOOD SOURCE FOR REEF FISHES

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ABSTRACT

At Fernando de Noronha Archipelago, southwest Atlantic, reef fishes associated with spinner dolphins (*Stenella longirostris*) were recorded when the cetaceans congregated in a shallow inlet. In the reef waters the dolphins engaged in several behaviors such as resting, aerial displays and other social interactions, as well as eliminative behaviors such as defecating and vomiting. Twelve fish species in seven families were recorded feeding on dolphin offal. The black durgon (*Melichthys niger*) was the most ubiquitous waste-eater, and its group size was positively and significantly correlated with dolphin group size. The durgons recognized the postures a dolphin adopts prior to defecating or vomiting, and began to converge to an individual shortly before it actually voided. Offal was quickly fed upon, and the fishes concentrated in the area occupied by the dolphins until the latter left the shallows. Since all the recorded offal-feeding species feed on plankton or drifting algae, feeding on cetacean droppings may be regarded as a switch from foraging on drifting organisms to foraging on drifting offal, a predictable food source in the inlet. Further instances of this cetacean-fish association are predicted to occur at sites where these mammals congregate over reefs with clear water and plankton-eating fishes.

Feeding associations between fishes and mammals are uncommon, and include mammalian examples as diverse as hippopotamuses and monkeys (Hediger, 1953; Sabino and Sazima, 1999). Associations between fishes and cetaceans are more common than those with other mammal types due to the habitat these aquatic associates share. Associations of fishes with dolphins include formation of mixed schools for protection from predators and for feeding advantages (Würsig et al., 1994; Scott and Cattanach, 1998), as well as use of these mammals for ride (Fertl and Landry, 1999) and exploitation of their feces as food (Lodi and Fiori, 1987; Lodi, 1998).

Feeding on feces, or coprophagy, is a habitual foraging behavior for several fish species in the Pacific, fish feces being regarded as a diverse and rich food source (Bailey and Robertson, 1982; Robertson, 1982). The use of feces of the spinner dolphin (*Stenella longirostris*) as food is recorded for three reef fish species in southwest Atlantic (Lodi and Fiori, 1987; Lodi, 1998). Herein we advance the brief reports of the aforementioned authors, centering our study on the foraging behavior of the fishes. As the dolphin waste may be regarded as a particulate and predictable food resource, we hypothesized that the fish species feeding on offal are plankton-eaters, and that their numbers correlate with dolphin numbers. Besides general observations on the associations between reef fishes and spinner dolphins, we focused our study on three main questions: (1) Which reef fish species use dolphin offal as food and what are their general feeding habits? (2) Is the fish group size correlated with the dolphin group size? (3) Do the fishes approach this food source only when offal is already voided or do they recognize that a dolphin is about to void?

METHODS

The study was conducted at the archipelago of Fernando de Noronha (03°50′S, 32°25′W), about 345 km off the northeastern coast of Brazil (see Maida and Ferreira, 1997; Carleton and Olson 1999, for map and description). The observation sessions were conducted at the Baía dos Golfinhos or Enseada do Carreiro de Pedra, a 15–25 m deep inlet used by spinner dolphins for resting and social interactions (Lodi and Fiori, 1987; Silva-Jr., 1996). The inlet bottom is a mixture of open sandy areas dotted with patchy reef formations similar to those found in another spinner dolphin resting place, Kealakekua Bay in Hawaii (Norris and Dohl, 1980; Wells and Norris, 1994).

Feeding associations between fishes and dolphins were observed directly, photographed, and videotaped during snorkeling over 18 days from May to October 2001. Snorkeling and passive diving are little disturbing methods particularly suited for study of marine mammals and open-water fishes (Silva-Jr., 1996; pers. observ.). Dolphins and fishes were given 1–3 min to habituate to divers before starting observation sessions of 35–70 min. Records concentrated in the morning, the best period for recording the association of fishes with defecating dolphins, as these mammals feed at night (Silva-Jr., 1996; Lodi, 1998). During observational sessions, 'focal animal' and 'all occurrences' samplings were used in 1006 min of direct observation in which all occurrences of specified actions (e.g., defecation, vomiting, offal ingestion) over a period were recorded (Altmann, 1974; Lehner 1979). We focused on waste-feeding events, i.e., the ingestion of offal by a given fish species on a defecate or vomit void by an individual dolphin. Each offal-feeding event was scored only once irrespective of the number of fish individuals feeding on a particular defecate or vomit. A defecate or vomit would score for two or three fish species simultaneously if this specific void was consumed by a mixed group. On the other hand, a fish species recorded feeding on offal in only one observation session would score more than once depending on the number of dolphin defecates or vomits the fish fed on this specific session. Size of fishes was estimated visually and later checked against specimens of similar size range caught at the study site or nearby.

The group size of black durgons associated with spinner dolphin groups was assessed through an adjusted version of the stationary sampling method of Bohnsack and Bannerot (1986), repeated regularly along transects of 200–400 m. Since the dolphin groups traveled back and forth through the inlet, the transects were traced across the inlet to intercept their path at least once or twice, thus allowing for records in the presence versus absence of the dolphins, as well as records with variable dolphin numbers. Two observers swam side by side at a regular pace for two min, then stopped and one of them counted and recorded all black durgon individuals sighted during a single 360° rotation within an imaginary cylinder of 10–12 m radius, while the other did the same for the dolphins. The observers swam/stopped/recorded repeatedly for a period of 30–50 min, thus making at least 5 samples per transect, in a total of 62 samples throughout the study. The relationship between the black durgon group size and the spinner dolphin group size was examined with use of Pearson's correlation (Zar, 1996). Records were limited to days when at least 250 dolphins were present within the inlet, a number judged minimal for this type of data recording (JMS-Jr., pers. observ.). Daily dolphin numbers were assessed through direct counts of surfacing individuals as they entered the inlet along the morning, sighted from a belvedere at the Baía dos Golfinhos (Silva-Jr., 1996).

Five specimens of the black durgon, *Melichthys niger*, the most ubiquitous fish recorded in association with dolphins, were examined for gut contents (due to the protected status of the study site we refrained from taking a larger sample). Feeding habits of the fish species recorded in association with dolphins were observed directly in the field or drawn from literature (Randall, 1967; Hobson, 1974). Four specimens of *M. niger* from the study site are deposited as vouchers in the Museu de História Natural, Universidade Estadual de Campinas (ZUEC 5349-1, 5350-3). Voucher photographs and video-records (tape # 8) of defecating spinner dolphins, and black durgons feeding on offal are on file in the ZUEC record collection. Usage of the name *Sotalia guianensis* for the marine tucuxi follows Monteiro-Filho et al. (2002).

RESULTS

Spinner dolphin (*Stenella longirostris*) groups congregated at the study site over the morning and early afternoon, the first individuals entering the inlet at about 0600–0700 h and the last ones leaving at about 1300–1600 h. Daily dolphin numbers in the inlet ranged 18–2046 throughout the study period (mean = 575.99; SD ± 449.83; n = 138), most groups including adults of both sexes and juveniles. In the inlet the dolphins engaged in several behaviors such as resting, aerial displays and other social interactions, including parental care and copulation, as well as eliminative behaviors such as vomiting and defecating a rich particulate and/or amorphous matter (Fig. 1), whitish to pinkish, often in an oily matrix. Vomits contained squid beaks along with partly digested material. Shortly before defecating, the spinner dolphin habitually arched its body and contorted itself backwards (however, smaller amounts of feces may be voided with no such posture). A similar contortion, but directed forwards and preceded by 1–4 openings of the mouth, was made shortly before vomiting. Ratio of defecates to vomits varied from 3:1 to 20:1 throughout the study.

Twelve reef fish species in seven families were recorded feeding on the spinner dolphin offal (Table 1), the most ubiquitous of them being the black durgon (*Melichthys niger*). The black durgons apparently recognized the postures dolphins adopt prior to defecating and vomiting, as they promptly converged at individuals about to void. Thus, at the time of actual voiding variably sized groups of black durgons were close to the dolphin, some of them already feeding on its offal (Fig. 1). The durgons were particularly prone to follow dolphins about to vomit, probably due to richer nutrient contents of vomits compared to that of feces. As the offal sank, the mid-water hovering durgons individually picked off the drifting particulate and/or amorphous matter, foraging in a similar way they feed on planktonic organisms (i.e., with visually oriented strikes at individual prey or particle, see Hobson, 1974, 1991). Up to 80–100 durgon individuals congregated to feed on a particularly plentiful defecation (Fig. 2). The sinking offal was foraged on for 3-37 sec (mean = 10.5; SD ± 7.2; n = 42), this variation related mostly to the amount and type of offal and the number of feeding fish.

Several durgon individuals flanked and followed the dolphins for up to 2–3 m, especially when the latter were cruising at low speed or resting. This following probably was related to the prospect of feces voiding, including those instances when offal was available in smaller amount and voided with no characteristic postures. Competition for offal is likely one cause for such following, since as soon as the first black durgon began to feed on the voided particles, all individuals within sight readily converged to the spot (Fig. 1).

There was a tendency to find the durgon groups along with the dolphin groups within the inlet, even if the fish were unable to follow a dolphin's swimming pace. The durgon groups began to converge and move as to intercept the cetaceans before these latter were actually within sight (apparently the fish were able to perceive the cetaceans by their moving or signaling, or learned the paths of the dolphins during the roaming of the latter within the inlet). The durgon groups size was positively and significantly correlated with dolphin groups size ($r = 0.73$; $P < 0.0001$; $n = 62$). As the dolphin groups moved to leave the inlet at early afternoon, the black durgon groups began to move closer to the shore. When spinner dolphins were absent from the inlet the black durgons concentrated along the shore and fed both on plankton and benthic organisms (this was particularly evident

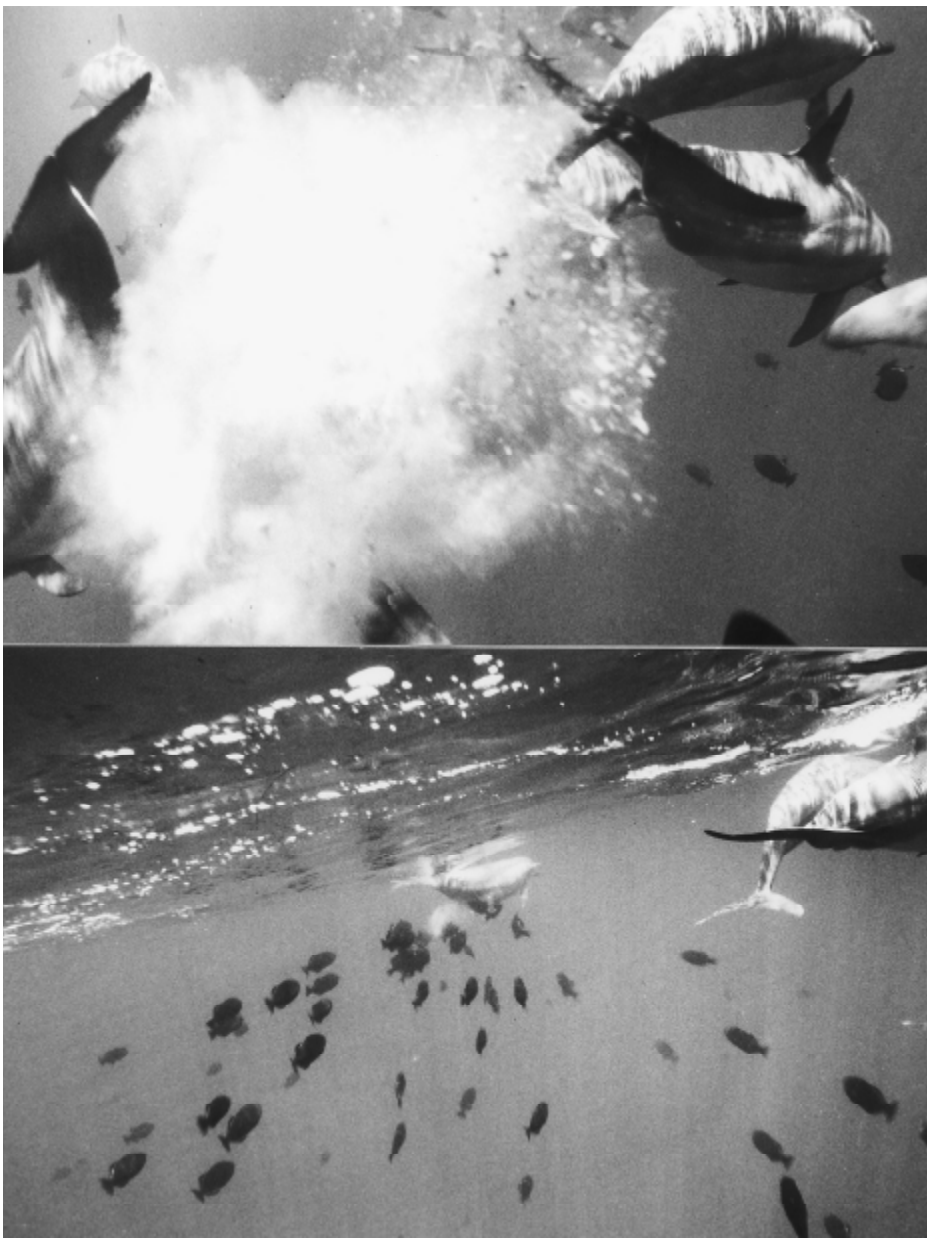

Figure 1. Black durgons (*Melichthys niger*) capitalize on spinner dolphin (*Stenella longirostris*) offal at Fernando de Noronha Archipelago, off northeast Brazil: a cloud of feces voided by one dolphin shows the type and amount of the food source thus available (above), and the fish readily converging to a defecating dolphin (below).

when the dolphins were absent for two or more consecutive days). Gut contents of black durgons (n = 5) yielded unidentified amorphous and particulate material, as well as zooplankton (mostly crustaceans and tunicates) and algae fragments.

All the other fish species here recorded foraging on dolphin offal represented about 22 % of total records (Table 1). The fish species recorded feeding on offal were present in

Table 1. Reef fish species recorded feeding on spinner dolphin offal at Fernando de Noronha Archipelago, off northeast Brazil (1006 min of direct observation over 18 days). n = number of feeding events (see methods); group size and total length (cm) = estimates for the recorded individuals (remora numbers refer to fish attached to a single dolphin); trophic categories based on field observations and literature records (Randall, 1967; Hobson, 1974); arrangement of families follows Nelson (1994).

Species	n	Group size	Total length	Trophic category
Exocoetidae				
Hemirhamphus brasiliensis	3	10	25	omnivore, planktivore
Carangidae				
Carangoides bartholomaei	6	1–2	25–40	carnivore, planktivore
Carangoides crysos	13	1–2	30–35	carnivore, planktivore
Caranx latus	3	1	40	carnivore, planktivore
Decapterus macarellus	2	30	20	planktivore
Echeneidae				
Remora australis	2	1–3	10–40	carnivore, planktivore (?)
Kyphosidae				
Kyphosus sectatrix	26	5–100	50–60	herbivore
Pomacentridae				
Abudefduf saxatilis	22	30–80	12–15	planktivore, omnivore
Chromis multilineata	3	15–40	10–12	planktivore
Acanthuridae				
Acanthurus coeruleus	2	2–3	25	herbivore
Balistidae				
Canthidermis sufflamen	7	2–3	50–60	planktivore
Melichthys niger	312	4–350	30–40	planktivore, omnivore

the inlet throughout the study period except for the scad *Decapterus macarellus*, which is seasonal at Fernando de Noronha and occurs there from August to October (J.M.S-Jr., pers.observ.).

Among the habitual planktivores, the sergeant major (*Abudefduf saxatilis*) and the brown chromis (*Chromis multilineata*) often foraged in mixed groups with the black durgons, and fed on the particulate offal in a way similar to that described for the latter species (visually oriented picking). However, the brown chromis fed on the offal rarely as its groups did not venture far from the shallow, 2–6 m depth reef sites not often used by the dolphins (the few instances we recorded this damselfish feeding on offal were all near reef pinnacles). The mackerel scad (*D. macarellus*) and the ocean triggerfish (*Canthidermis sufflamen*) did not mix with the durgons, the latter traveling mostly alone.

The less habitual planktivores such as the blue runner (*Carangoides crysos*) and the yellow jack (*Carangoides bartholomaei*) roamed over the inlet and from time to time joined the reef fish groups to forage on offal. These two jacks and the horse-eyed jack (*Caranx latus*) made passes through the offal cloud, and either visually selected and engulfed particles or, less often, fed on offal through ram-filtering (see Anderson and Wassersug, 1990, for a review of suspension-feeding in vertebrates).

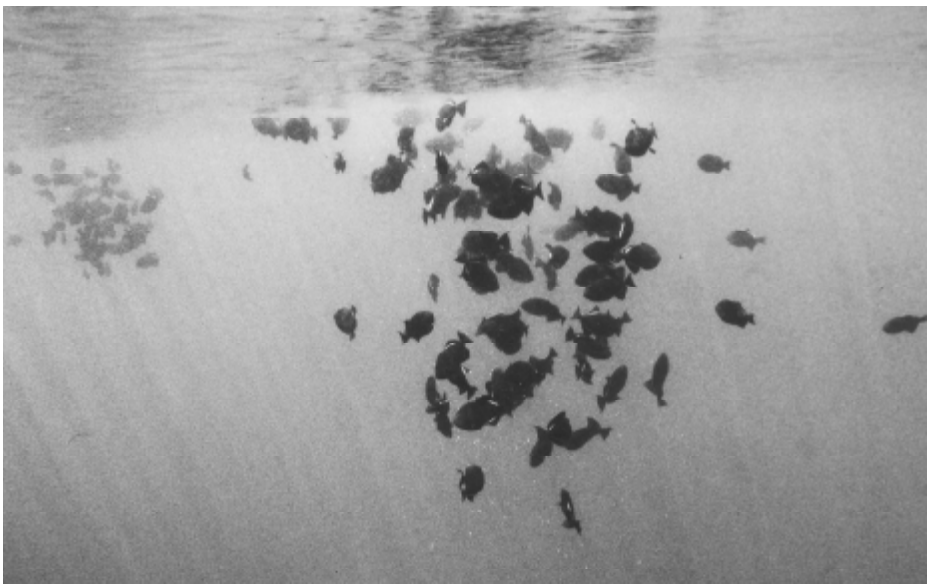

Figure 2. Two large groups of black durgons feeding upon defecates of spinner dolphins at Fernando de Noronha Archipelago.

Among the herbivores occasionally feeding on plankton, the Bermuda chub (*Kyphosus sectatrix*) picked off the feces in much the same way it caught drifting algae pieces, as also did the blue tangs (*Acanthurus coeruleus*) recorded among a mixed group of black durgons and sergeant majors. When larger groups (20–60 ind) of chubs approached the dolphins to feed on offal, black durgons generally retreated. In the feeding record of the surface-dwelling ballyhoo (*Hemirhamphus brasiliensis*), the fish fed on offal available in the 5–10 cm layer below the surface, and thus seemed limited to feces voided by surfacing dolphins only. We recorded no a single instance of a fish feeding on the feces of conspecifics or any other fish species.

The whalesucker (*Remora australis*) made very short forays to forage on offal, detaching itself from its dolphin host to pick off a larger particle and quickly returning to its host. Feeding on offal by the whalesucker was recorded only while the dolphin group moved slowly and when a dolphin defecated or vomited immediately in front of the whalesucker's host.

Discussion

Fish feces were demonstrated as a rich food source for herbivorous, detritivorous, and carnivorous reef fishes in the Pacific (Bailey and Robertson, 1982; Robertson, 1982; Hobson, 1991). Feces from carnivorous fishes probably are nutrient-richer than those from herbivorous species and are sought by coprophagous fishes accordingly (Robertson, 1982). As spinner dolphins feed on squids, fishes, and shrimps (Würsig et al., 1994; Silva-Jr., 1996), their feces and vomits may be regarded as a nutritive and energy rich food source, possibly less dilute and richer than those of carnivorous fishes due to the particularities of water absorption by cetaceans (Eckert and Randall, 1988). Feeding on

fish feces is a habitual behavior among several Indo-Pacific reef fish species (Robertson, 1982; Hobson, 1991; Randall, in press), but we recorded no a single instance of fish feces-eating at our study site. In another oceanic island in SW Atlantic, Trindade Island off southeastern Brazil, feces produced by two herbivorous species, the scarid *Sparisoma amplum* (mentioned as *S. viride*) and the kyphosid *Kyphosus* sp., are eaten by the black durgon (Lodi, 1998). We think that the absence (or rarity) of fish feces consumption by the reef fishes we noted at Fernando de Noronha may be related to the plentiful and presumably less dilute and more nutritive dolphin feces released in the inlet.

All the reef fishes recorded feeding on spinner dolphin offal at Fernando de Noronha feed on plankton or drifting algae to some extent. The zooplankton and algae fragments recovered from the gut contents of the black durgons are consistent with previous findings at other sites, and species of *Chromis* and *Abudefduf* are well known reef planktivores, as is the case of the open-water dwelling *C. sufflamen* and *D. macarellus* (Randall, 1967; Hobson, 1974, 1991). Several carangid species, including *C. crysos*, were recently recorded foraging on plankton either by ram-feeding or picking off individual plankters (Sazima, 1998, C.S. and I.S. pers. observ.). Species of *Hemirhamphus* and *Kyphosus* feed habitually on drifting algae fragments (Randall, 1967; Carvalho-Filho, 1999), whereas species of *Acanthurus* feeds in this way occasionally (Sazima and Sazima, 2001; I.S. pers. observ.). Thus, feeding on cetacean droppings by the aforementioned fishes may be regarded as a simple switch from foraging on drifting plankton or algae fragments to foraging on a novel and predictable plankton-like drifting food. However, even if regarded as an opportunistic feeding switch, offal-foraging apparently became habitual for black durgons in the Baía dos Golfinhos, as the spinner dolphin occupation of the inlet is about 90% of the days throughout the year (Silva-Jr., 1996). The significantly positive correlation here recorded between black durgon numbers and dolphin numbers is indicative of the importance of cetacean offal as a food source for these reef fish.

The 'predictive' behavior recorded herein for black durgons, converging to dolphin individuals before these actually voided, is similar to that recorded for some coprophagous Pacific reef fishes (Robertson, 1982). The tendency of some fish species to behave in a characteristic manner shortly before and during defecation enable the coprophagous fishes to predict the appearance of this food source and facilitate feeding on the sinking feces (Robertson, 1982). At Fernando de Noronha the foraging movements performed by the first black durgon to reach the feces readily attracted nearby individuals, and thus to perceive and learn the pre-eliminative behavior of spinner dolphins is advantageous to lessen intraspecific competition for this resource.

Due to their occasional habit of picking at drifting algae, the parrotfish *Sparisoma axillare* (I.S. pers. observ.) and other scarids may be potential dolphin waste-eaters, the more so as several parrotfishes are already recorded as coprophages in the Pacific (Robertson, 1982). The plankton-eating Noronha wrasse *Thalassoma noronhanum* (Francini-Filho et al., 2000) may be another potential coprophage when the cetaceans pass close to the reef, as these fish rarely venture far from the substrate. This labrid species was recorded feeding on fish feces at several sites in Fernando de Noronha (H.M. Overmeer, pers. comm.; I.S. pers. observ.), but no labrids are recorded feeding on fish feces in the Pacific (Robertson, 1982).

Feeding on dolphin offal by the whalesucker *R. australis* was recorded rarely, although its occurrence is probably much commoner, perhaps even a habitual foraging mode. Its attachment to a dolphin would allow easy access to this food source, the more so as

spinner dolphins commonly dashed their feces over individuals at their rear within the group. This defecating behavior differs from that reported for the bottlenose dolphin, *Tursiops truncatus*, which seldom dashes its feces over other individuals (Shinohara et al., 1999). Scarcity of offal feeding records by the whalesucker may be explained by its feeding earlier than the other recorded fishes (due to its living on the very offal source) and its observation being hindered by the attachment itself (within an offal cloud its very short foraging forays would be scarcely perceptible). At least one species of remora is known to filter plankton by ram-feeding (Clarke and Nelson, 1997), and another possible way for the whalesucker to feed on offal is simply to open its mouth to filter, with no need to detach from its host. Our suggestion that feeding on dolphin offal may be habitual for *R. australis* is strengthened by the finding of an unidentified "...white, granular, mushy substance..." as the only stomach contents of seven specimens examined by Radford and Klawe (1965). This description fits the overall aspect of spinner dolphin feces we recorded. The whalesuckers studied by Radford and Klawe (1965) were attached to the common dolphin (*Delphinus delphis*).

Robertson (1982) aptly pointed out that coral reefs offer a combination of conditions that facilitate coprophagic interactions among vertebrates. We predict that further instances of cetacean offal-feeding fishes may be recorded at sites where these marine mammals habitually congregate for resting and other activities, provided that the water is clear and plankton-eating reef fishes are found nearby. One such site may be Kealakekua Bay in Hawaii, where large groups of spinner dolphins congregate over most of the year (Norris and Dohl, 1980; Wells and Norris, 1994). We suggest that additional sites where cetacean offal may be feed upon by reef fishes in SW Atlantic include St. Paul's Rocks, off NE Brazil, where bottlenose dolphins (*Tursiops truncatus*) are regularly found close to the island (Caon and Ott, 2000) and the Enseada dos Currais, an inlet at Anhatomirim in S Brazil favored by marine tucuxis (*Sotalia guianensis*) for feeding, resting, and social activities (Flores, 1999). The black durgon is very common at St. Paul's Rocks even in open water (Lubbock and Edwards, 1981), whereas the sergeant major (*Abudefduf saxatilis*) is a common planktivore at Anhatomirim and other reef sites in S Brazil (I.S. pers. observ.). Another possible site where reef fishes may feed on cetacean offal is Abrolhos Archipelago, off E Brazil, where humpback whales (*Megaptera novaeangliae*) congregate over shallow reef sites during the calving season (Engel, 1996). Even if the adult feed and/or defecate little or not at all at these calving grounds, the suckling calves probably defecate a nutrient-rich material. These and other similar situations merit a closer investigation to verify whether the cetacean-fish association presented here is restricted to Fernando de Noronha Archipelago (a condition which we repute as highly unlikely) or is a more widespread, although generally unrecorded phenomenon.

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