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Feeding Ecology of the Amazonian Manatee (*Trichechus inunguis*) in the Mamirauá and Amanã Sustainable Development Reserves, Brazil

Michelle G. Guterres-Pazin,[1] Miriam Marmontel,[2] Fernando C. W. Rosas,[1] Victor F. V. Pazin,[3] and Eduardo M. Venticinque[4]

[1]*Instituto Nacional de Pesquisas da Amazônia (INPA), Laboratório de Mamíferos Aquáticos, Caixa Postal 478, Manaus, AM, 69011-970, Brasil*
E-mail (MGG-P): pxbois@gmail.com
[2]*Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Estrada do Bexiga, 2584, Fonte Boa, Tefé, AM, 69470-000, Brasil*
[3]*Área de Proteção Ambiental da Baleia Franca (APABF/ICMBIO), Avenida Santa Catarina, 1465, Imbituba, SC, 88780-000, Brasil*
[4]*Universidade Federal do Rio Grande do Norte (UFRN), Centro de Biociências, Departamento de Ecologia. Campus Universitário, Lagoa Nova, Natal, RN, 59072-970, Brasil*

Abstract

The Amazonian manatee (*Trichechus inunguis*) is an exclusively herbivorous freshwater mammal. Between 1994 and 2008, 230 fecal and 16 stomach content samples from wild Amazonian manatees were obtained. The material was collected during both dry and wet seasons in the sustainable development reserves of Mamirauá (MSDR) and Amanã (ASDR) from floodplain and *terra firme* and *igapó* (not subject to long-term flooding) habitats, respectively. Species constituting the diet of the Amazonian manatee were identified through a comparative analysis with a reference collection of epidermis from 69 plant species of potential consumption by the species. Forty-nine plant species were identified in the species' diet. In the MSDR, 32 plant species were found—18 during the dry season and 28 during the wet season. In the ASDR, 48 species were identified of which 40 occurred in both periods. A total of 30 new species were added to the Amazonian manatee diet known to date. The species that were found most frequently in the material were *Hymenachne amplexicaulis*, *Oryza grandiglumis*, *Paspalum repens*, *Azolla caroliniana*, and *Limnobium spongia*. Poaceae was the family with the greatest frequency of occurrence (91.5%). Plant species most consumed present emergent or floating habits. There was a difference in the composition of plant species found in manatee feces between the dry and wet seasons ($p = 0.0002$) but not between floodplain and *igapó*. Results show that the Amazonian manatee feeds on a great variety of plant species during the wet and dry season alike, and both in floodplain and *igapó* environments. Therefore, food availability alone does not represent a determining factor to explain the seasonal migration of the species.

Key Words: aquatic plants, central Amazon, diet, floodplain, *igapó*, seasonality, Sirenia

Introduction

The Amazonian manatee (*Trichechus inunguis*) is the smallest extant member of the order Sirenia and the only one to live in freshwater. It may reach 275 cm total length and weigh up to 420 kg (Amaral et al., 2010). The species occurs from the headwaters of the Amazon basin, in Colombia, Peru, and Ecuador, to the Atlantic Ocean (Best, 1984). In Brazil, it occurs in the main rivers of the Amazon (Domning, 1981) but may be rare in the upper reaches of the Tocantins, Xingu, and Tapajós Rivers (Bertram & Bertram, 1973; Domning, 1981). The factors related to its distribution include the flood pulse, presence of calm waters, and availability of aquatic plants (Best, 1984).

The water bodies in the Amazon undergo dramatic changes due to the flood pulse, which affects their physico-chemical conditions throughout the year (Junk et al., 1989). Such changes influence the presence of aquatic macrophyte species, especially those of short life cycle and high nutritional demand (Junk & Piedade, 1997), since their occurrence and development are intricately associated with the availability of nutrients in water systems (Junk & Piedade, 1993). Areas with nutrient-rich waters are favorable to most floating aquatic macrophytes, whereas acidic and nutrient-poor waters limit their occurrence (Junk & Piedade, 1993; Piedade et al., 2000). Following seasonal variations in the hydrological cycle in the Amazon, manatees undertake seasonal migrations, moving from floodplain areas that are rich in aquatic macrophytes where they remain during the flood to deep holes in *terra-firme* lakes or main river channels during the dry season when food availability decreases (Best, 1981, 1982, 1983, 1984; Calvimontes, 2009; Arraut et al., 2010).

The manatee is an exclusively herbivorous (Best, 1981, 1982) and non-ruminant (Lemire, 1968; Moir, 1968; Marsh et al., 1977) aquatic mammal, presenting post-gastric fermentation, similar to the horse's digestive process (Burn, 1985). Apparently opportunistic, the species consumes a wide variety of aquatic and semi-aquatic plant species, generally grasses such as *Paspalum repens* and *Echinochloa polystachya* (Best, 1981, 1984; Montgomery et al., 1981; Colares & Colares, 2002; Guterres et al., 2008). The manatee consumes the equivalent of approximately 8% of its body weight in food daily (Best, 1984). It is important to the maintenance of aquatic ecosystems in that it functions as a natural fertilizer to the waters, which become enriched by its nitrogen-rich feces and urine. Therefore, it contributes to the nutrient cycle of aquatic ecosystems, favoring the development of phyto- and zooplankton, besides the growth of macrophytes, further promoting the primary production and development of associated fauna in the habitats where it occurs (Best, 1982, 1984).

A variety of aquatic plants from families Araceae, Convolvulaceae, Cyperaceae, Fabaceae, Lentibulariaceae, Nymphaeaceae, Onagraceae, Poaceae, Pontederiaceae, Salviniaceae, and Urticaceae are listed as Amazonian manatee food in the wild, including non-identified species of algae (Ferreira, 1903; Pereira, 1944; Marmol, 1976; Best, 1981, 1983, 1984; Montgomery et al., 1981; Timm et al., 1986; Colares et al., 1987). Nevertheless, most studies on feeding habits of the Amazonian manatee have been conducted with captive animals (Best, 1982; Gallivan & Best, 1986; Rodriguez-Chacón, 2001). Only Colares & Colares (2002) analyzed some stomach contents of wild manatees from lakes near Manaus and the Amanã Lake. Guterres et al. (2008), based on the traditional knowledge of local inhabitants of the Mamirauá and Amanã Sustainable Development Reserves (MSDR and ASDR), identified plants potentially consumed by the Amazonian manatee in the wild.

Given the conservation status of the Amazonian manatee, classified as Vulnerable (VU) on the *2012 IUCN Red List* and listed in *CITES Appendix I* as threatened with extinction, and the gaps in knowledge of its feeding habits and ecology, the objectives of this study were (1) to identify the plant species that constitute the diet of wild manatees in MSDR and ASDR; (2) to compare the results obtained through analysis of feces and stomach contents with information provided by local inhabitants; and (3) to compare the species' diet composition between dry and wet periods, and between floodplain (MSDR) and *igapó* (ASDR).

Methods

The study was conducted in the Mamirauá and Amanã Sustainable Development Reserves (MSDR and ASDR, respectively) (Figure 1). MSDR is located in the mid-Solimões River and covers an area of approximately 1,124,000 ha (03° 01' 10.2" S; 064° 53' 43.9" W). It is mostly floodplain (*varzea*), with so-called "white" (murky) water. ASDR is located between the Japurá and Negro Rivers (02° 42' 25.6" S; 064° 37' 06.5" W), comprising an area of approximately 2,313,000 ha. This area contains a mosaic of habitats, most of them *terra firme*, bathed by black waters (*igapó*).

Fecal and Stomach Content Samples

A total of 246 samples were collected—26 from MSDR and 220 from ASDR, between 1994 and 2008. Of those, 230 were fecal samples found floating close to aquatic plant mats on margins of beaches or small elevations. The remaining 16 samples were stomach contents from manatees hunted or accidentally killed in the study area. The material collected was preserved in 70% alcohol solution.

Analysis of the Samples

For the identification of the plant material consumed by the Amazonian manatee, the method of Hurst & Beck (1988) was adapted and modified to simplify the analysis. Fecal and stomach content samples were homogenized in 70% alcohol. From each sample, 10 1-ml subsamples were taken and filtered in sieves of 35 and 120 mesh. This material was again subsampled, and a drop was placed on a microscope slide and topped with a 22 × 22 mm cover slip for microscopic analysis. This procedure was repeated 5 times for each fecal and stomach content sample. Plants were identified by examining the epidermis based on epidermal cells, stomata, and metabolites (Guterres et al., 2008). Fecal samples found outside of the water, on beaches or land, hampered homogenization and identification of anatomic structures of plants. To improve visualization in those cases, samples were macerated, and a subsample was obtained from the extraction of 20 1-ml subsamples. Previous to this study, an epidermal reference collection of 69 plant species potentially consumed by the Amazonian manatee, based on local traditional knowledge (see Guterres et al., 2008), was compiled. Plants identified in the present sampling scheme were then compared with the reference collection. All plant fragments found during analyses were identified to species level, except *Calathea* sp. Some species mentioned in literature as manatee food had undergone taxonomic revision at the family, genus, or species level. The genus *Cecropia* was formerly classified

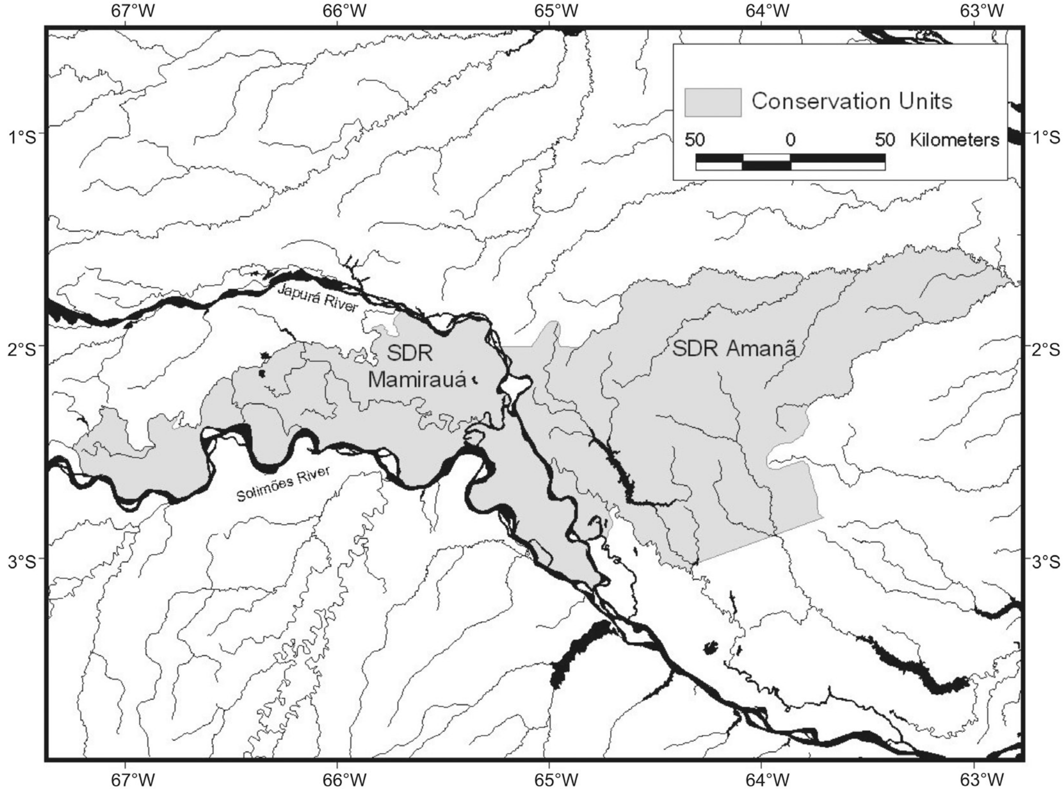

Figure 1. Location of Mamirauá (MSDR) and Amanã (ASDR) Sustainable Development Reserves, Amazonas, Brazil

in the family Moraceaebutis now placed in Urticaceae. The species *Reussia rotundifolia* (Pontederiaceae) is now classified as *Pontederia rotundifolia*, and the species *Salvinia minor* (Salviniaceae) is now named *Salvinia minima*. It is important, therefore, to consider this when comparing older papers, which used the old nomenclature, with the present work, which uses the revised nomenclature, to avoid possible confusion and erroneous interpretation.

Plant species were also grouped by their life habits as emergent, free-floating, fixed floating, amphibious, riverine trees, and free submersed, according to Guterres et al. (2008).

Comparison of the Diet Composition

According to the seasonal variation of water level in the MSDR and ASDR and in Arraut (2008), *flood* was defined as the period between December and June, and *drought* the period between July and November. The ANOSIM (ANalysis Of SIMilarities) (Clarke, 1993) was used to compare and determine differences between plants found in the manatee diet in the MSDR and ASDR, and during drought and flood. This analysis was performed using *PAST 1.18* software (Hammer & Harper, 2003). ANOSIM is a hypothesis test for differences between groups of samples, which uses permutation and randomization methods in similarity matrices. Probabilities were calculated with 10,000 permutations, and the *R* statistic was calculated to compare distances between groups with distances within groups.

A Bray-Curtis similarity index of 11 plant species of most frequent occurrence in the manatee diet was generated. The Bonferroni correction for multiple tests of significance was also used. The similarity of percentages (SIMPER) indicates which species are most responsible for the dissimilarities between areas and periods (most discriminant species) (Clarke, 1993). This analysis simply splits the similarity between groups to calculate each species' contribution to the value of the Bray-Curtis index. It was used to help in the interpretation of results obtained in the similarity analysis (ANOSIM).

Results

Among the 246 feces and stomach content samples analyzed, 49 plant species consumed by the Amazonian manatee were found (Table 1).

The five most common species were *Hymenachne amplexicaulis* (58.5%), *Oryza grandiglumis* (44.7%), *Paspalum repens* (43.1%),

Table 1. Plant species identified in feces and stomach contents of Amazonian manatees in the Mamirauá (MSDR) and Amanã (ASDR) Sustainable Development Reserves; plant habit: emergent (E), riverine tree (RT), amphibious (A), floating (F), free floating (FF), floating fixed (FFi), riverine herbaceous (RH), submersed (S), and free submersed (FS). Species cited as manatee food in the literature (C) and via traditional knowledge (TK).

Family	Species (habit)	Common name[a]	Occurrence (%)	Site
Amaranthaceae	*Alternanthera hassleriana* (E)	Batatarana d'água	0.4	ASDR, TK
Annonaceae	*Oxandra riedeliana* (RT)	Envira preta	0.4	ASDR, TK
Apocynaceae	*Rhabdadenia macrostoma* (A)	Cipó	0.8	ASDR, TK
Araceae	*Pistia stratiotes* (FF)	Mureru branquinho	11.4	MSDR, ASDR, C, TK
Azollaceae	*Azolla caroliniana* (FF)	Chibé de peixe-boi	42.3	MSDR, ASDR, TK
	Azolla microphylla (FF)	Chibé de peixe-boi	23.2	MSDR, ASDR, TK
Convolvulaceae	*Ipomoea aquatica* (A)	Batatarana	3.3	MSDR, ASDR, C, TK
	Ipomoea squamosa (A)	Batatarana	7.7	MSDR, ASDR, TK
Cyperaceae	*Cyperus cubensis* (A)	Piri	2.4	ASDR, C, TK
	Cyperus sphacelatus (E)	Piri	2.0	MSDR, ASDR, TK
	Eleocharis variegata (A)	Piri	2.0	MSDR, ASDR, TK
	Scleria torreyana (A)	Tiririca	0.8	MSDR, ASDR, TK
Euphorbiaceae	*Mabea nitida spruce* (RT)	Seringai	5.7	ASDR, TK
Fabaceae	*Aeschynomene sensitiva* (A)	Tintarana	1.2	ASDR, TK
	Campsiandra cf. angustifolia (RT)	Acapurana	0.4	ASDR
	Cymbosema roseum (A)	Cipó	1.6	MSDR, ASDR, TK
	Macrolobium acaciifolium (RT)	Arapari	0.4	ASDR
	Phaseolus cf. pilosus (A)	Feijãorana	10.6	MSDR, ASDR, C, TK
Hydrocharitaceae	*Limnobium spongia* (FF)	Mureru	34.6	MSDR, ASDR, TK
Lentibulariaceae	*Utricularia breviscapa* (FL)	Lodo	2.0	MSDR, ASDR, TK
	Utricularia foliosa (S/ FF)	Lodo	15.5	MSDR, ASDR, C, TK
	Utricularia subulata (FL)	Lodo	11.8	MSDR, ASDR, TK
Limnocharitaceae	*Limnocharis flava* (E)	Mureru orelha de burro	1.2	MSDR, ASDR, TK
Marantaceae	*Calathea* sp. (RH/A)	Arumã	1.6	MSDR, TK
Onagraceae	*Ludwigia helminthorrhiza* (FF)	Mureru	1.2	ASDR, C, TK
	Ludwigia leptocarpa (A)	Tintarana	3.3	ASDR, TK
Parkeriaceae	*Ceratopteris pteridoides* (FF)	Mureru	23.6	MSDR, ASDR, TK
Phyllanthaceae	*Phyllanthus fluitans* (FF)	Mureru	28.9	MSDR, ASDR, TK
Poaceae	*Brachiaria purpurascens* (E)	Braquiara	6.1	MSDR, ASDR, TK
	Echinochloa polystachya (E)	Canarana	22.4	MSDR, ASDR, C, TK
	Hymenachne amplexicaulis (E)	Rabo de raposa	58.5	MSDR, ASDR, C, TK
	Leersia hexandra (E/A)	Capim navalha	28.9	MSDR, ASDR, C, TK
	Luziola spruceana (FFi/ FF)	Uamã	13.0	MSDR, ASDR, C, TK
	Oryza grandiglumis (E)	Arrozrana	44.7	MSDR, ASDR, C, TK
	Panicum dichotomiflorum (E)	Capim	5.3	ASDR, TK
	Paspalum fasciculatum (E/A)	Murim	0.4	MSDR, C, TK
	Paspalum multicaule (E/A)	Pacuã	0.8	MSDR, ASDR, TK
	Paspalum orbiculatum (A)	Graminha de peixe-boi	0.8	MSDR, ASDR, TK
	Paspalum repens (FFi)	Memeca	43.1	MSDR, ASDR, C, TK
Polygonaceae	*Polygonum spectabile* (E/F)	Quintarana	1.2	ASDR, TK
	Symmeria paniculata (AR)	Carauaçu	0.8	ASDR, TK
Pontederiaceae	*Eichhornia crassipes* (FF)	Mureru	3.3	MSDR, ASDR, C, TK
	Pontederia rotundifolia (FFi)	Mureru de orelha	5.3	MSDR, ASDR, C, TK
Rubiaceae	*Duroia genipoides* (RT)	Genipapinho do igapó	0.4	ASDR, TK
	Genipa spruceana (RT)	Genipapo	1.6	MSDR, ASDR, TK
	Oldenlandia herbacea (E)	Grama	2.0	MSDR, ASDR, TK
Salviniaceae	*Salvinia minima* (FF)	Mureru	20.7	MSDR, ASDR, C, TK
Sapotaceae	*Elaeoluma glabrescens* (RT)	Caramuri	3.7	ASDR, TK
Urticaceae	*Cecropia cf. latifolia* (RT)	Embaúba	4.5	MSDR, ASDR, C, TK

[a]Plant common names, according to local inhabitants

Azolla caroliniana (42.3%), and *Limnobium spongia* (34.5%). The Family Poaceae was the most represented, constituting 91.5% of the sample, followed by Azollaceae (56.9%), Hydrocharitaceae (34.5%), and Phyllanthaceae (28.9%) (Figure 2).

The plant species of emergent habit occurred in 89.4% of the analyzed samples. Free-floating (80%) and fixed floating (46.7%) plants followed in order of consumption. Plant species of amphibious habit represented the 4th most important group in manatee diet, representing 30.5% of the total. Riverine trees (15%) and free submersed plants (14.2%) came in 5th place. Plants with more than one type of habit—free-floating or fixed (13%), emergent or amphibious (13%), submersed or free-floating (11.8%), and emergent or floating (1.2%)—were poorly represented in the manatee diet. The number of plant species per sample found in the MSDR and ASDR varied between one and 10, with an average of five per sample.

In the MSDR, 32 plant species were identified as items of the manatee diet. Eighteen of those (found in eight samples) occurred during the drought and 28 (found in 18 samples) during the flood; 14 occurred in both periods. Forty-eight species were found in the ASDR. Forty species were found either during the flood or during the drought period; 30 of those occurred in both periods. The number of samples analyzed was 151 for the flood and 69 for the drought.

In the analysis of plant species composition of manatee feces and stomach contents, there was a difference between the drought and flood periods ($R = 0.092$; $p = 0.0002$) but not between floodplain (MSDR) and *igapó* (ASDR) ($R = 0.032$; $p = 0.210$). The comparison of plant species between groups formed by the combination of locations (MSDR and ASDR) and periods (drought and flood) showed significant differences ($R = 0.096$; $p = 0.002$). *A posteriori* comparisons showed a difference in the consumption of plant species between drought and flood in ASDR ($R = 0.105$; $p < 0.001$) and between flood in MSDR and flood in ASDR ($R = 0.255$; $p = 0.008$).

The contribution of each species to the significant differences, in *a posteriori* comparisons found between these two groups, was analyzed through the percentage of similarity and is shown in Tables 2 and 3.

The average dissimilarity between the periods of drought and flood in ASDR was 67.24% (Table 2). *Oryza grandiglumis*, *Hymenachne amplexicaulis*, *Paspalum repens*, and *Echinochloa polystachya* were more present in feces found during the drought than during the flood; the main species consumed during the drought were *Azolla caroliniana*, *Limnobium spongia*, and *Phyllanthus fluitans*. The average dissimilarity in the composition of plants consumed by manatees in the dry period in MSDR and during the flood period in ASDR was 73.8%

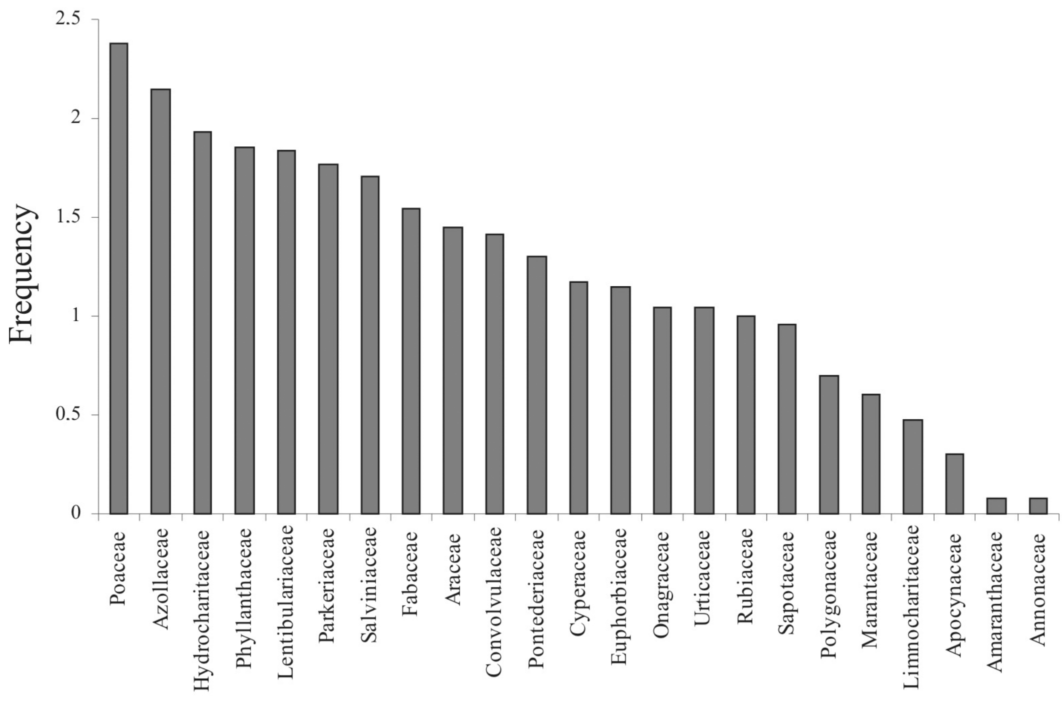

Figure 2. Frequency of occurrence of plant families found in 246 fecal and stomach content samples of Amazonian manatees (data transformed in $\log_{10}$)

Figure 3. Amazonian manatee among aquatic plants during the wet season in the MSDR

Table 2. Plant species consumed by the Amazonian manatee and its relative contribution to the Bray-Curtis dissimilarity index in the ASDR between drought (D) and flood (F) periods; values calculated by the SIMPER method.

	Average abundance			
Species	ASDR (D)	ASDR (F)	Contribution %	Cumulative %
Oryza grandiglumis	0.261	0.573	7.746	11.52
Azolla caroliniana	0.580	0.307	7.680	22.94
Hymenachne amplexicaulis	0.551	0.627	7.299	33.80
Paspalum repens	0.348	0.447	7.006	44.22
Limnobium spongia	0.435	0.253	6.681	54.15
Phyllanthus fluitans	0.362	0.267	6.061	63.17
Leersia hexandra	0.246	0.287	5.666	71.60
Ceratopteris pteridoides	0.275	0.247	5.364	79.57
Azolla microphylla	0.246	0.233	5.023	87.04
Echinochloa polystachya	0.043	0.327	4.781	94.15
Salvinia minima	0.203	0.180	3.930	100.00

Overall average dissimilarity = 67.24%

(Table 3). *Limnobium spongia*, *Oryza grandiglumis*, *Azolla caroliniana*, and *Hymenachne amplexicaulis* were the main species and contributed over 50% of the similarity (accumulated).

Discussion

The high frequency of consumption of plants from the family Poaceae observed here (91.5%) corroborates the results obtained by Colares & Colares (2002), who found Poaceae in 96% of the samples

Table 3. Plant species consumed by the Amazonian manatee and its relative contribution to the Bray-Curtis dissimilarity index between MSDR in drought (D) and ASDR in flood (F); values calculated by the SIMPER method.

	Average abundance			
Species	MSDR (D)	ASDR (F)	Contribution %	Cumulative %
Limnobium spongia	0.625	0.253	9.503	12.87
Oryza grandiglumis	0.125	0.573	9.183	25.31
Azolla caroliniana	0.625	0.307	9.164	37.72
Hymenachne amplexicaulis	0.375	0.627	9.111	50.06
Paspalum repens	0.250	0.447	7.714	60.51
Echinochloa polystachya	0.125	0.327	6.184	68.89
Leersia hexandra	0.125	0.287	5.793	76.73
Azolla microphylla	0.125	0.233	4.746	83.16
Salvinia minima	0.250	0.180	4.720	89.56
Phyllanthus fluitans	0.000	0.267	3.991	94.96
Ceratopteris pteridoides	0.000	0.247	3.720	100.00

Overall average dissimilarity = 73.83%

Figure 4. Grassy plant with signs of feeding by Amazonian manatee

examined. Similarly, Ledder (1986) observed that Poaceae also constitute an important portion of the diet of the Florida manatee (*Trichechus manatus latirostris*), stressing the importance of that family in the diet of manatees in general.

Among the five species of greatest occurrence in the manatee diet in this study (Table 1), only *Paspalum repens* was considered a frequent component by Colares & Colares (2002), and with a frequency of 17.5% only. The second most frequent species recorded by Colares & Colares (2002) was *Echinochloa polystachya* (13.8%). It is relevant that, although the frequency of occurrence of *E. polystachya* in this study (22.4%) was higher than that observed by Colares & Colares (2002), it is not among the five most frequently consumed by manatees in the areas of this study (see Table 1). These differences are likely related to the sample size analyzed by Colares & Colares (2002) or distinct characteristics of the study areas.

Plants of emergent habit presented greatest frequency in manatee diet in MSDR and ASDR, agreeing with the results of Colares & Colares (2002). On the other hand, Marmol (1976) observed a greater consumption of free-floating species (*Eichhornia crassipes*, *Pistia stratiotes*, and *Eichhornia azurea*) by Amazonian manatees in Peru. Free-floating plants were considered by Colares (1991) as the 3rd most important group, and in this study appeared as the 2nd group of plants ingested by manatees.

Domning & Hayek (1986) identified different degrees of rostral deflection in the skulls of sirenians and concluded that these represent adaptations of the different species to feeding at different levels in the water column. Their results revealed that the Amazonian manatee has the smallest degree of rostral deflection (25° to 41°) among sirenians. According to anatomical evidence, this is an adaptation of this species to feed closer to the water surface. The hypothesis that the Amazonian manatee feeds on plants at water level, associated with the characteristics of aquatic vegetation in the Amazonian environment, is possibly compatible with the greatest number of emergent and floating plants found in this study. The Florida manatee, which has a higher degree of rostral deflection (30 to 52°) (Domning & Hayek, 1986), presents a low consumption of floating plants (0.8%), with greater consumption of submerged plants (69.2%), followed by emergent and terrestrial plants (14.9%) (Ledder, 1986).

Fixed floating plants had only two representatives: *Paspalum repens* and *Pontederia rotundifolia*. Plants of amphibious habits—with both aquatic and terrestrial ecophases—were poorly represented in the sample, which concurs with Colares (1991).

Riverine trees (*Cecropia cf. latifolia*, *Elaeoluma glabrescens*, *Oxandra riedeliana*, *Symmeria paniculata*, *Genipa spruceana*, and *Duroia genipoides*), which represented the 5th group of plants ingested by manatees in this study (Table 1), are commonly found along the margins of rivers, lakes, and channels in MSDR and ASDR. During the wet season, roots and parts of the trunk (sometimes the whole plant) of these plants remain submerged. Leaves and fruit of these trees were found in analyses of manatee diet during both the flood and the drought, and were also reported by local inhabitants as potential food for the species during the wet season (Guterres et al., 2008). The genus *Cecropia* had already been mentioned by Best (1981) as a natural food for *T. inunguis*. Florida manatees also consume small amounts of leaves from riverine trees (genera *Ficus* and *Casuarina*) (1.1 and 0.02%, respectively) (Ledder, 1986).

Colares (1991) did not find any tree species in her study and attributed it to the difficulty manatees have in accessing these plants since they are rooted to the soil. Nevertheless, when the rise of the water column submerges part or even the whole of several of these trees, they become available to the manatee. Therefore, it is possible that the absence of these plants from Colares's work is related to her small sample size during the flood period (N = 10) or to some particularity of her study area. The same is true for the species *Cyperus cubensis*, which was found in six samples analyzed during the flood period in this study. Colares declares that this plant species is not part of Amazonian manatees' diet. According to Colares, during the flood, when plant availability increases, manatees become more selective in their choice of food species. Nevertheless, to make inferences about manatees' food selectivity, it is necessary to study availability and abundance of plants in areas accessed by the species in both periods—drought and flood. At this point, there is no such information, which precludes conclusive analyses on the subject.

Free submersed plants constituted the 6th most consumed group of plants in this study. Colares (1991) also found a low occurrence of free submersed plants.

Aquatic plants with more than one habit were poorly represented in the manatee diet, probably due to the small number of species that make up this group. Nevertheless, when individually analyzed, these species are among the most consumed by the manatee (e.g., *Leersia hexandra* – emergent or amphibious) (see Table 1), except *Polygonum spectabile* and *Calathea* sp., which showed low occurrence in the diet.

The literature so far mentions 37 species of plants consumed by free-ranging Amazonian manatees (Veríssimo, 1895; Ferreira, 1903; Pereira, 1944; Marmol, 1976; Best, 1981, 1983; Montgomery et al., 1981; Timm et al., 1986; Colares et al., 1987; Colares, 1991). Sixteen of those were recorded through indirect information such as reports by local inhabitants; only 21 species were identified through the analyses of feces or stomach contents (Colares, 1991), in addition to unidentified species of the family Poaceae and algae. Of the 49 plant species consumed by manatees identified in this study, 19 (38%) had been described in the literature as manatee food, 15 were identified in fecal or stomach content samples (Colares, 1991), and the remaining 4 derived from indirect information. Therefore, 30 plant species found in this study had never before been cited in the literature as manatee food by either direct or indirect information.

All plant species identified here in fecal and stomach content analyses of manatee samples were cited by local inhabitants of the MSDR and ASDR reserves as manatee food. Still, 19 species mentioned by locals (see Guterres et al., 2008) were not found in feces or stomach content samples. This could be explained by a low or rare level of consumption or because they are not really part of the manatee diet. In studies with fishermen in Colombia, Herrera & Fontecha (2000) also reported as potential manatee food some of the genera found in this study (e.g., *Paspalum*, *Pistia*, *Pontederia*, *Eichhornia*, *Ficus*, and *Panicum*), which underlines the importance of traditional knowledge concerning aspects of basic biology of the species. Nevertheless, we recommend, whenever possible, the application of the scientific method to confirm the information contributed by members of local communities.

The number of plant species found in samples analyzed in this study (between one and ten, with an average of five species per sample) was similar to what Colares & Colares (2002) found for *T. inunguis*. These authors recorded one to seven plant species per sample, and an average of two to three species per sample. A study with 22 fecal and stomach content samples of West Indian manatees (*T. manatus*) revealed the presence of two to ten food items per sample, with an average of six species per sample (Borges et al., 2008). Given the long digestive tract passage time of manatees (4 to 7 d; Itavo, 1995) and considering the sample size (n = 246) analyzed here, we believe that, although manatees feed on a great variety of plants (Table 1), they likely ingest a relatively small number of plant species per feeding bout.

The greater number of plant species observed in the MSDR during the flood (N = 28) as compared to the drought (N = 18) may be related to the greater diversity of aquatic habitats allowed by a greater water volume and flooding area and, consequently, a greater diversity of aquatic plants. During the drought, with the reduction of the aquatic habitat and productivity, manatees are restricted to smaller and shallower areas such as deep holes. During this period, some plant species die or become inaccessible to the manatee. Nevertheless, the smaller number of plant species found during the drought may also be related to the small number of samples analyzed (N = 8) in comparison to the flood (N = 18). Analysis of a greater number of fecal and/or stomach content samples during the flood and the drought in the MSDR may elucidate if in fact there is a significant difference in the number of species consumed by the manatee during these periods.

In the ASDR, where larger numbers of samples were analyzed for the flood (N = 151) and drought (N = 69), there was no difference in the number of plant species consumed in both periods (N = 40). This indicates that the manatee also feeds on a variety of plants during the drought, despite the physical constraints of the environment. Nevertheless, a significant difference in species composition was found between the flood and drought periods in the ASDR. This may mean that there is a switch in species consumed over the course of the year but not necessarily a reduction in the number of species eaten. Therefore, we conclude that a similar number of manatee food species is eaten both in flood and in drought. These results contradict premises that during the dry period there is great limitation in food availability (see Best, 1981, 1982, 1983; Colares, 1991; Colares & Colares, 2002; Calvimontes, 2009) or that there is no food accessible to the manatee (Arraut, 2008).

Hard and dry spherical masses, normally containing sand, were found in the intestines of four manatees captured by fishermen during an extreme and long drought in 1980 in Amanã Lake (Lago Amanã); two other manatees that died that same year had very reduced, almost nonexistent, fat layers (Best, 1983). Best hypothesized that, during the dry period, Amazonian manatees might be obliged to consume decomposing plant material found in the bottom of water bodies, and that they might survive approximately 200 d using their fat reserves as an energy source. Nevertheless, our results, based on a large number of samples, collected over a period of 15 y, seem to indicate that, at least in the study area and based only on the number of plant species found in each sample, both during the flood and the drought, that conclusion does not hold. It is plausible that the nutritional quality of plants during the drought may be lower than that of the flood, and that a smaller volume of plants may be available, but the animals do not cease feeding, and they ingest a similar number of species during the two periods of the water cycle.

Colares & Colares (2002) found 21 plant species consumed by the Amazonian manatee during the drought and eight during the flood. The authors attributed the greater variety during the drought to the smaller availability of plant biomass during that period when manatees would tend to feed on whatever plant was available. The reduced number of species consumed during the flood would result from food selection since during that period there is a greater plant offer in the environment. Nevertheless, Colares & Colares did not take into account the difference in the number of samples analyzed during the drought (N = 40) and flood (N = 10), which may have affected the results. Manatees' alleged food selectivity, associated with plant availability in the environment, which is affected by climatic conditions each season, is a determining factor in the selection of feeding sites by the species (Best, 1981).

Analyzing the Amazonian manatee habitat, Arraut et al. (2010) concluded that the species' distribution during the flood is associated with the presence of macrophyte mats, which are selected by the manatee. During the drought, despite the lack of foods accessible in *terra-firme* lakes, manatees use those habitats as deep, low-current refuges (Arraut, 2008).

The reasons that drive the Amazonian manatee to migrate are habitat and available food (Arraut, 2008). According to Arraut et al. (2010), during the flood, manatees remain in the floodplains (MSDR) where their main food is plentiful; when waters recede (dry period), the animals move to *terra-firme* lakes (ASDR) where they fast. When the water rises (flooding period), the species returns to the floodplain lakes. These conclusions regarding feeding during the flood and fasting during the drought are not supported by the results of this study. The main aquatic plant species consumed by the manatee are found in both periods (flood and drought) and habitats (floodplain and *terra firme*), and the species does not fast during the dry period. However, there occurs a variation in the relative importance of plant species in the manatee diet between periods and habitats. The nutritional value and the chemical and physical defenses of the plant species ingested by the manatees are probably important factors in diet determination between flood and drought seasons, but they were not analyzed in this study.

As stated by Best (1983), it is possible that during atypical periods, as during extraordinary and prolonged drought events in the Amazon, plants may become unavailable to the manatee, preventing it from feeding.

Seasonal water fluctuation in Amazonian habitats is among the main factors determining migrations of manatees due to the difficulty of movement and vulnerability of the species in shallow areas as concluded by Arraut et al. (2010). Even though the "food" factor may also be related to the species' migration, it seems to have a lower influence in this regard as previously mentioned. Manatee movements from floodplains to *terra-firme* lakes during the descending water period may be related, besides the physical constraints of the environment, to unavailability, reduction, or mortality of populations of some plant species that are part of its diet during the drought. The return of the species to the floodplains during the rising water period may also be explained by the low nutritional value of plants in *terra-firme* habitats as compared to plants in floodplains.

Further studies on feeding habits and nutritional needs of Amazonian manatees are necessary, however, as well as on distribution, diversity, and nutritional parameters of aquatic plants in Amazonian environments so as to better understand their roles in the migratory processes of the species.

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Literature Cited

Amaral, R. S., da Silva, V. M. F., & Rosas, F. C. W. (2010). Body weight/length relationship and mass estimation using morphometric measurements in Amazonian manatees *Trichechus inunguis* (Mammalia: Sirenia). *Marine Biodiversity Records*, *3*, 1-4.

Arraut, E. M. (2008). *Migração do peixe-boi Amazônico: Uma abordagem por sensoriamento remoto, radiotelemetria e geoprocessamento* [Migration of the Amazonian manatee: An approach using remote sensing, radio-telemetry and geoprocessing] (Ph.D. thesis). Instituto Nacional de Pesquisas Espaciais, São José dos Campos, São Paulo, Brasil.

Arraut, E. M., Marmontel, M., Mantovani, J. E., Novo, E. M. L. M., Macdonald, D. W., & Kenward, R. E. (2010). The lesser of two evils: Seasonal migrations of Amazonian manatees in the Western Amazon. *Journal of Zoology*, *280*, 247-256. http://dx.doi.org/10.1111/j.1469-7998.2009.00655.x

Bertram, C. G. L., & Bertram, C. K. R. (1973). The modern Sirenia: Their distribution and status. *Biological Journal of the Linnean Society*, *5*, 297-338. http://dx.doi.org/10.1111/j.1095-8312.1973.tb00708.x

Best, R. C. (1981). Food and feeding habits of wild and captive Sirenia. *Mammal Review*, *11*, 3-29. http://dx.doi.org/10.1111/j.1365-2907.1981.tb00243.x

Best, R. C. (1982). A salvação de uma espécie: Novas perspectivas para o peixe-boi da Amazônia [The salvation of a species: New perspectives from the Amazonian manatee]. *Revista IBM*, *14*, 1-9.

Best, R. C. (1983). Apparent dry-season fasting in Amazonian manatees (Mammalia: Sirenia). *Biotropica*, *15*, 61-64. http://dx.doi.org/10.2307/2388000

Best, R. C. (1984). The aquatic mammals and reptiles on the Amazon. In H. Sioli (Ed.), *The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin* (pp. 371-412). The Hague, The Netherlands: Dr W. Junk Publishers. http://dx.doi.org/10.1007/978-94-009-6542-3_15

Borges, J. C. G., Araújo, P. G., Anzolin, D. G., & De Miranda, G. E. C. (2008). Identificação de itens alimentares constituintes da dieta do peixe-boi marinho (*Trichechus manatus*) na região Nordeste do Brasil [Identification of food items consumed by the Antillean manatee (*Trichechus manatus*) from northeastern Brazil]. *Biotemas*, *21*, 77-81. http://dx.doi.org/10.5007/2175-7925.2008v21n2p77

Burn, D. M. (1985). *The digestive strategy and efficiency of the West Indian manatee*, Trichechus manatus (Unpublished Master of Science dissertation). University of Miami, Coral Gables, Florida.

Calvimontes, J. M. (2009). *Etnoconocimiento, uso y conservación del manatí Amazónico* Trichechus inunguis *en la Reserva de Desarrollo Sostenible Amanã, Brasil* [Traditional ecological knowledge, use and conservation of the Amazon manatee *Trichechus inunguis* in the Amanã Sustainable Development Reserve, Brazil] (Dissertação de Mestrado). Universidad Nacional Agraria la Molina, Peru.

Clarke, K. R. (1993). Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*, *18*, 117-143. http://dx.doi.org/10.1111/j.1442-9993.1993.tb00438.x

Colares, I. G. (1991). *Hábitos alimentares do peixe-boi da Amazônia (*Trichechus inunguis*, Mammalia: Sirenia)* [Feeding habits of the Amazonian manatee (*Trichechus inunguis*, Mammalia: Sirenia)] (Dissertação de Mestrado). Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brasil.

Colares, I. G., & Colares, E. P. (2002). Food plants eaten by Amazonian manatees (*Trichechus inunguis*, Mammalia: Sirenia). *Brazilian Archives of Biology and Technology*, *45*, 67-72. http://dx.doi.org/10.1590/S1516-89132002000100011

Colares, I. G., Colares, E. P., & Lima, A. C. (1987). *Variação anual de vegetais que servem de alimentação para o peixe-boi amazônico (Mammalia: Sirenia)* [Annual variation of the plants consumed by the Amazonian manatee (Mammalia: Sirenia)]. Anais da 2ª Reunião de Trabalho de Especialistas em Mamíferos Aquáticos da América do Sul, Rio de Janeiro, Brasil.

Domning, D. P. (1981). Distribution and status of manatees *Trichechus* spp. near the mouth of the Amazon river, Brazil. *Biological Conservation*, *19*, 85-97. http://dx.doi.org/10.1016/0006-3207(81)90044-6

Domning, D. P., & Hayek, L. C. (1986). Interspecific and intraspecific morphological variation in manatees (Sirenia: *Trichechus*). *Marine Mammal Science*, *2*, 87-144. http://dx.doi.org/10.1111/j.1748-7692.1986.tb00034.x

Ferreira, A. R. (1903). Memória sobre o peixe-boi e o uso que lhe dão no estado do Grão Pará [Memories about the Amazonian manatee and its use in the Great-Pará state]. *Arquivo Museu Nacional Rio de Janeiro*, *12*, 169-174.

Gallivan, G. J., & Best, R. C. (1986). The influence of feeding and fasting on the metabolic rate and ventilation of the Amazonian manatee (*Trichechus inunguis*). *Physiological Zoology*, *59*, 552-557.

Guterres, M. G., Marmontel, M., Ayub, D. M., Singer, R. F., & Singer, R. B. (2008). *Anatomia e morfologia de plantas aquáticas da amazônia utilizadas como potencial alimento por peixe-boi Amazônico* [Anatomy and morphology of the Amazonian aquatic plants used as potential food for the Amazonian manatee] (1st ed.). Belém, Brazil: IDSM.

Hammer, O., & Harper, D. A. T. (2003). *PAST, Version 1.18*. Retrieved 20 March 2014 from http://folk.uio.no/ohammer/past.

Herrera, M. E. P., & Fontecha, E. C. (2000). *Evaluacion del estado de conservacion del manati Amazonico (*Trichechus inunguis*) e identificacion de los habitos alimenticios de la especie en la zona de influencia de Puerto Narinõ, Amazonas – Colombia* [Evaluation of the conservation status of the Amazon manatee (*Trichechus inunguis*) and identification of feeding habits of the species in the influence zone of Puerto Nariño, Amazonas, Colombia] (Tesis de Licenciatura). Universidad Pedagogica Nacional, Santafe de Bogotá, Colombia.

Hurst, L. A., & Beck, C. A. (1988). *Microhistological characteristics of selected aquatic plants of Florida, with techniques for the study of manatee food habits* (Biological Report 88[18]). Washington, DC: U.S. Fish and Wildlife Service. 145 pp.

International Union for Conservation of Nature (IUCN). (2012). *2012 IUCN red list of threatened species*. Retrieved 28 November 2012 from www.iucnredlist.org.

Itavo, R. V. (1995). *Tempo de passagem do alimento no trato digestivo do peixe-boi da Amazônia* (Trichechus inunguis) *em cativeiro* [Food passage time in the digestive tract of Amazonian manatee (*Trichechus inunguis*) in captivity] (Monografia de conclusão de curso em Ciências Biológicas). Universidade Estadual de Londrina, Paraná, Brasil.

Junk, W. J., & Piedade, M. T. F. (1993). Herbaceous plants of the Amazon floodplain near Manaus: Species diversity and adaptations to the flood pulse. *Amazoniana*, *12*, 467-484.

Junk, W. J., & Piedade, M. T. F. (1997). Plant life in the floodplain with special reference to herbaceous plants. In W. J. Junk (Ed.), *The Central Amazon floodplain: Ecological studies* (pp. 147-185). Berlin, Germany: Springer-Verlag. http://dx.doi.org/10.1007/978-3-662-03416-3_8; http://dx.doi.org/10.1007/978-3-662-03416-3

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. In D. P. Dodge (Ed.), *Proceedings of the International Large River Symposium (LARS)*. *Canadian Special Publication of Fisheries and Aquatic Sciences*, *106*, 110-127.

Ledder, D. A. (1986). *Food habits of the West Indian Manatee,* Trichechus manatus latirostris*, in south Florida* (Unpublished Master's thesis). University of Miami, Florida.

Lemire, M. (1968). Particularites de l'estomac du lamantin *Trichechus senegalensis* Link (Sireniens, Trichechidae) [Stomach particularities of the West African manatee (*Trichechus seneaglensis*) Link (Sirenia, Trichechidae]. *Mammalia*, *32*, 475-520. http://dx.doi.org/10.1515/mamm.1968.32.3.475

Marmol, B. A. E. (1976). *Informe preliminar sobre las plantas que sirven de alimento al manati de la Amazonia (*Trichechus inunguis*)* [Preliminary report about the plants eaten by the Amazonian manatee (*Trichechus inunguis*)]. Lima, Peru: Primer Congresso Nacional de Botánica.

Marsh, H., Heinsohn, G. E., & Spain, A. V. (1977). The stomach and duodenal diverticula of the dugong (*Dugong dugon*). In R. J. Harrison (Ed.), *Functional anatomy of marine mammals* (pp. 271-295). New York: Academic Press.

Moir, R. J. (1968). Ruminant digestion and evolution. In C. F. Code (Ed.), *Handbook of physiology* (pp. 2673-2694). Washington, DC: American Physiological Society.

Montgomery, G. G., Best, R. C., & Yamakoshi, M. (1981). A radio-tracking study of the Amazonian manatee *Trichechus inunguis* (Mammalia: Sirenia). *Biotropica*, *13*, 81-85. http://dx.doi.org/10.2307/2387708

Pereira, M. N. (1944). O peixe-boi da Amazônia [The Amazonian manatee]. *Boletim do Ministério da Agricultura, Divisão de Caça e Pesca*, *33*, 21-95.

Piedade, M. T. F., Junk, W. J., & Parolin, P. (2000). The flood pulse and photosynthetic response of trees in a white water floodplain (*várzea*) of Central Amazon, Brazil. *Verhand Lungen der International en Vereinigung fuer Theoretische und Angewandt e Limnologie*, *27*, 1734-1739.

Rodriguez-Chacón, Z. M. (2001). *Características alimentares e nutricionais do peixe-boi da Amazônia* Trichechus inunguis *(Mammalia, Sirenia), em condição de cativeiro* [Feeding and nutritional characteristics of the Amazonian manatee *Trichechus inunguis* (Mammalia, Sirenia) in captivity] (Tese de Doutorado). Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brasil.

Timm, R. M., Albuja, V. L., & Clauson, B. L. (1986). Ecology, distribution, harvest, and conservation of the Amazonian manatee *Trichechus inunguis* in Ecuador. *Biotropica*, *18*, 150-156. http://dx.doi.org/10.2307/2388757

Veríssimo, J. (1895). *A pesca na Amazônia* [Fishing in the Amazon]. Rio de Janeiro, Brasil: Livraria Clássica de Alves e Companhia.