

Nesting habitat of *Arapaima gigas* (Schinz) in Amazonian floodplains

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Most nests of *Arapaima gigas* in floodplains of the Amazon were built at the margins of the forests surrounding temporary or permanent lakes and their connecting channels. They were found under forested levees in locations that were shallow and sandy. From 2000 to 2005, the adult population increased six-fold but nest density increased only two-fold.

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It is important to understand the spawning habitat of fishes because it may provide a focal point of home range, facilitate mating, and increase the survival of eggs and larvae (Potts, 1984). Moreover, fishes are susceptible to overexploitation if they are fished while spawning (Reynolds *et al.*, 2002). However, the spawning habitat of floodplain fishes has been poorly studied, and both floodplains and their fishes are highly threatened worldwide (Tockner & Stanford, 2002; Allan *et al.*, 2005). Knowledge on the spawning habitat of floodplain fishes potentially could be applied readily in conservation schemes, thus providing critical protection to fish populations. This study surveyed the nests of giant pirarucu *Arapaima gigas* (Schinz) in a floodplain of the Amazon River, Brazil.

There is limited information on the nesting habitat of giant pirarucu. Fontanele (1948) concluded that the nests are ‘cooking-pan’ like holes in the substrata, which the fish dig with their mouths. The nests measure *c.* 500 mm in diameter, and occur in shallow areas (*c.* 1 m in depth) away from floating vegetation (Fontanele, 1948). Based on a survey of 11 nests, Queiroz (2000) concluded that the nests were built in lakes, occur at average densities of 2.1 nests km⁻¹ along margins and banks, and have diameters ranging from 190 to 670 mm. Mean depth of the nests was 120 mm (Queiroz, 2000).

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The reproductive behaviour of the giant pirarucu makes them vulnerable to fishing, as the males, while caring for their young, are easy targets for harpoon-specialist fishers. This vulnerability is exacerbated by their physiological need to come to the surface of the water to breathe air every 5–15 min (Castello, 2004). Moreover, the giant pirarucu grow up to 3 m in total length (L_T) and 200 kg in mass (Queiroz, 2000). The giant pirarucu thus have constituted one of the most historically important fisheries of the Amazon (Veríssimo, 1895). Government-run management regulations for the giant pirarucu in Brazil have included a minimum landing size, a closed season during the spawning period (December to May), and even a moratorium in the State of Amazonas (Castello, 2007). But these regulations have been largely ineffective because of poor enforcement and widespread illegal fishing (McGrath *et al.*, 1993; Viana *et al.*, 2004). Consequently, the giant pirarucu are now overexploited in many regions (Queiroz & Sardinha, 1999) and have been extirpated near urban centres (Goulding, 1980). The giant pirarucu is being conserved by local fishers through community-based initiatives (McGrath *et al.*, 1993; Castello, 2007). Several fishers protect lakes from fishing or establish closed seasons for the giant pirarucu, but these conservation strategies remain poorly studied.

A summary of the existing information on the main reproductive and migratory activities of the giant pirarucu during an annual flood cycle suggests most giant pirarucu inhabit lakes but can be found also in rivers and connecting channels during low water levels, roughly from September to January every year (Castello, *in press*; pers. obs.). At that time, the adults form pairs. Both sexes of adult giant pirarucu collaborate to build their nest in the margins and banks of lakes, temporary lakes and connecting channels during rising water levels (Queiroz, 2000). They take from 3 to 5 days to build their nests, spawn immediately after the nests are ready, and the young hatch from 3 to 5 days after the adults spawn (Fontanele, 1948). After the larvae hatch, most females leave (*pers. obs.*), and some may reproduce again in the same season (Queiroz, 2000). The males protect the young by staying close to them, usually no farther than 1 m away. The males protect and guide the young by swimming slowly through the food-rich environments of flooded forest during the following weeks. The male giant pirarucu care for their young for *c.* 3 months (Castello, *in press*). As water levels decline, the adult giant pirarucu separate from their young, and they all migrate to communicating channels and lakes.

This study was done at the Mamirauá Sustainable Development Reserve, State of Amazonas, Brazil, located at the confluence of the Solimões and Japurá Rivers (*c.* 3° S; 65° W). The area is formed by várzea, a type of floodplain that flanks the sediment-rich white water rivers of the Amazon; it is a complex mosaic of seasonally inundated rain forests, lakes and winding channels (Ayres, 1995; Junk, 1997; Castello, *in press*). Water levels fluctuate *c.* 12 m annually (Ayres, 1995), flooding the entire ecosystem during high water levels, and leaving most of it dry during low water levels.

The nesting habitat of the giant pirarucu was determined through surveys of four habitats of the várzea in years 2000, 2001 and 2005 (Table I). It was assumed that only these habitats provide conditions suitable for nesting giant pirarucu, following knowledge of local fishers and a previous study (Queiroz, 2000). In 4 years of fieldwork, only one nest was observed in habitats that were

TABLE I. The Amazonian habitats surveyed. Note that the chavascal vegetation is not considered to be a forest *per se* (Ayres, 1995), but here will be referred to as such for practical reasons

	Habitat type	Description
Surveyed habitats	Rio	The main river channel. The rio is wide (up to 3 km), deep (up to 50 m), and swift flowing (Junk, 1997); the Japura River was sampled.
	Paraná	Channels transporting river waters and crossing sections of várzea. Both ends connect to the rio (Junk, 1997).
	Lago	Lakes of various sizes and shapes (Junk, 1997). Lagos hold water throughout the flood cycle.
	Ressaca	Temporary lakes that are shallow with a large and open mouth. Most ressacas dry up during the dry season (local classification).
Surrounding forests	Chavascal	Low swampy, scrub forest. Flooding depth between 6 and 7 m (Ayres, 1995).
	Restinga Baixa	Silt-heightened riverbanks and bars on which grow tall forest; flooding depth between 3 and 6 m (Ayres, 1995).
	Restinga Alta	Like the restinga baixa, but riverbanks and bars are higher and the forests are taller, older and more diverse; flooding depth between 1 and 2.5 m (Ayres, 1995).

not surveyed in this study (pers. obs.). The surveyed habitats varied greatly in size and form (Table I), so survey work was designed to distribute per-habitat effort homogeneously. One long stretch of rio, one of paraná, five lagos and five ressacas were surveyed. A total of 43.8 km of várzea were surveyed every year: 15.9 km of ressaca, 10.2 km of lago, 8.5 km of paraná and 9.1 km of rio habitats. These locations were measured using a geographical position system, and were walked by two local expert fishers and the author in years 2000 and 2001 and by the same fishers alone in 2005. The surveys were done late in the low water season (November and December each year), when the nests that were built the previous year were exposed to dry conditions and could be recognized easily. The surveys were done along the interface of the selected 'aquatic' habitats and the surrounding 'terrestrial' forests. Thus, the surveys covered the areas delimited by the aquatic-terrestrial interface on the 'aquatic' side, and by the reach of the vision of the fishers inside the forest on the 'terrestrial' side. Here, these areas are referred to by their habitat names (Table I).

The following data were collected for every nest found: (i) diameter of the hole, measured at the top along the direction of the greatest length, (ii) depth of the hole, measured at the centre, (iii) diameter of the round area of clean substratum surrounding the hole (*i.e.* free of fallen tree-leaves and small branches), (iv) description of surrounding vegetation, following Ayres (1995;

see Table I), (v) depth relative to the maximum flooding level the previous year, as indicated by marks on nearby trees and (vi) soil type (*i.e.* clay or sand). Data on diameter and depth of the hole were used to calculate the volume of the nests, assuming the nests had the shape of cylinders. Possible interannual differences in the data were analysed using Kruskal–Wallis tests. The nesting habitat of the giant pirarucu was determined by first calculating density measurement of nests in each habitat (*i.e.* ‘x’ nests km⁻¹ of ‘y’ habitat) and then comparing the density of nests among the surveyed habitats.

The abundance of nests was compared to population censuses of giant pirarucu for the same years. The abundance of giant pirarucu was considered for an area that covered and was larger than the area comprising the nest surveys. Comparing the abundance of nests and giant pirarucu in the exact same areas was not feasible, because the giant pirarucu migrate between the lakes and connecting channels immediately before building their nests (Castello, *in press*), probably searching for nesting habitat. The abundance of spawners was obtained by annual census conducted by local fishers using the method described by Castello (2004). This method allowed expert local fishers to estimate the number of giant pirarucu accurately through counts made at the moment of aerial breathing. Castello (2004) estimated that the counts varied *c.* ±10% of the true value. The counts differentiate two length classes: juveniles (0–1.5 m) and adults (>1.5 m; the Brazilian minimum size of capture). The fishers censused the population of giant pirarucu in a large area comprised of *c.* 80 water bodies during low water levels (*c.* September and November) when the giant pirarucu are concentrated in lakes and channels (Arantes *et al.*, 2006; Castello, 2007). The L_T class criteria used in the counts of adult giant pirarucu (>1.5 m, following management regulations) is approximately consistent with

TABLE II. Summary of observations on the nests of giant pirarucu (see Table I) measurements

Year	Habitat	Nests (<i>n</i>)	Density nests (km ⁻¹)	Volume of hole (l) Median ± IQR	Diameter of clean area (mm) Mean ± s.d.	Depth relative to last flood (m) Mean ± s.d.
2000	Lago	16	1.57	62.2 ± 23.6	1380 ± 410	5.11 ± 0.81
	Ressaca	35	2.20	56.5 ± 54.9	2060 ± 920	6.12 ± 1.10
	Parana	14	1.65	51.8 ± 32.7	1890 ± 410	5.44 ± 1.00
	Rio	0	0.00	—	—	—
	Total	65	1.48	56.5 ± 39.5	1840 ± 780	5.72 ± 1.10
2001	Lago	35	3.43	41.4 ± 61.5	1710 ± 510	5.82 ± 0.87
	Ressaca	36	2.26	31.5 ± 28.8	1550 ± 340	6.80 ± 0.59
	Parana	12	1.41	29.4 ± 13.6	2160 ± 490	6.60 ± 0.97
	Rio	3	0.33	90.7 ± 18.2	4000 ± 1000	6.17 ± 0.58
	Total	86	1.96	35.6 ± 41.4	2290 ± 630	6.32 ± 0.89
2005	Lago	31	3.04	32.7 ± 25.3	2770 ± 630	3.21 ± 0.18
	Ressaca	89	5.60	26.6 ± 32.4	3130 ± 770	3.68 ± 0.85
	Parana	29	3.41	2.8 ± 3.2	2930 ± 830	3.95 ± 0.72
	Rio	1	0.11	2.5	4000	3.30
	Total	150	3.42	24.4 ± 31.6	3043.8 ± 776.2	3.65 ± 0.77

the L_T at which female giant pirarucu become sexually mature in the study area (1.7 m; Queiroz, 2000). Thus, it was assumed that the counts of giant pirarucu were directly and positively correlated to the number of spawning-size pirarucu.

A total of 301 nests of giant pirarucu were found in the 3 years surveyed. The nests were holes in the ground with shapes like 'cooking pans', as described by Fontanele (1948). The nests had a mean \pm s.d. diameter of 570 ± 180 mm and depth of 160 ± 40 mm, and a median \pm IQR calculated volume of 38.9 ± 29.4 . The clean circular areas surrounding the holes, which are assumed to have been made by the spawners, had a mean \pm s.d. diameter of 1790 ± 530 mm. The habitat surrounding the nests was relatively homogeneous. Most nests were built in sand (95%), under restinga baixa forests (87%; see Table I), and at mean \pm s.d. maximum depth of 5.11 ± 0.77 m (Table II). Depth of water over the nest at the time of spawning was *c.* 1–1.5 m (pers. obs.). The volume and clean circular areas of the nests varied among the years (Kruskal–Wallis, $n_{2000} = 72$, $n_{2001} = 93$, $n_{2005} = 150$, $P < 0.01$). As the years advanced, the nests became smaller with respect to volume, and larger with respect to the clean circular areas (Table II). Their median volume in 2000 was about twice that in 2005 (Table II). Their depths differed between years also (Table II; Kruskal–Wallis, $n_{2000} = 72$, $n_{2001} = 93$, $n_{2005} = 150$, $P < 0.001$), probably due to annual differences in flood cycles.

The nests of giant pirarucu were most abundant in ressaca habitats in 2000 and 2005 (Table II), and also when the data were averaged for the 3 years (3.25 nests km^{-1} in ressaca, compared to 2.68, 2.15 and 0.14 nests km^{-1} in lago, parana and rio, respectively). In 2000 and 2005, the nests were equally abundant in lago and parana habitats, but in 2001 they were more abundant in lago than in parana habitats (Table II). The nests of giant pirarucu were not equally abundant in all surveyed locations of lago and ressaca habitats. Their abundance varied little in three ressaca locations (from 0 to 4.2 nests km^{-1}), but in two of them their abundance increased markedly from 2000 to 2005. In lago habitats, from 2000 to 2005 the abundance of nests decreased in two locations, and increased markedly in one location, the Lago Samaumeirinha.

The total abundance of nests increased from 65 to 86 to 150 in 2000, 2001 and 2005, respectively (Table II). Most of the increase occurred in the ressaca (147%), parana (107%) and lago (94%; Table II). All of the increase in abundance of nests in lago habitats occurred in Lago Samaumeirinha. From 2000 to 2005, the abundance of both nests and giant pirarucu increased (Fig. 1); the abundance of nests increased by 131% and that of adult giant pirarucu by 611% (Fig. 1).

The nests of giant pirarucu have at least three characteristics that may increase the survival rates of the young. First, the holes formed by the nests may provide the eggs with protection against predators and currents that may sweep the eggs away from the nests. This characteristic applies to many nest-building fishes (Mori, 1994; Jaroensutasinee & Jaroensutasinee, 2001; Vinyoles *et al.*, 2002; Scott *et al.*, 2005). Second, most nests (95%) were built in sand. Digging the holes in sand probably requires less effort than digging in the compacted clay that dominates in the study area. Holes made of sand may increase the survival of the young. Several fishes have been reported to

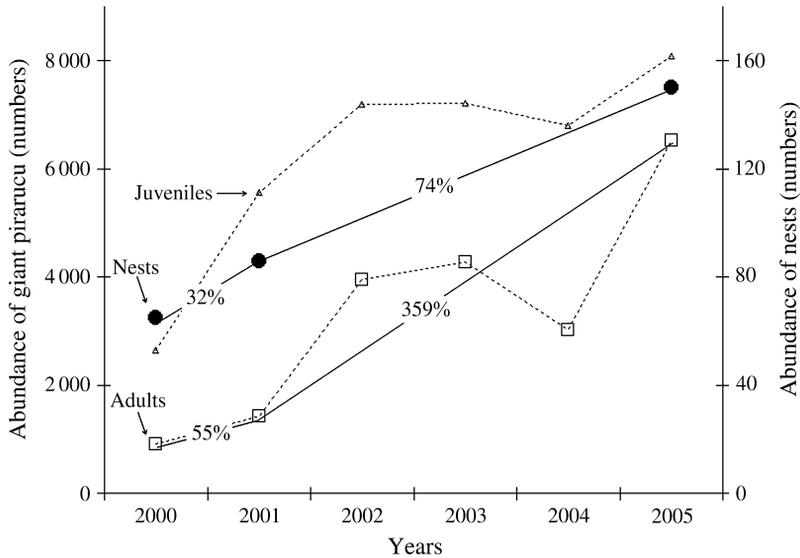


FIG. 1. Abundance of nests (●), juveniles (△) and of adult (□) giant pirarucu. The increases with time (%) are indicated for nests and adults.

select substratum type (Jaroensutasinee & Jaroensutasinee, 2001; Scott *et al.*, 2005). In salmonids, as may be the case of the giant pirarucu, a high proportion of fine materials can decrease the survival of the young (Chapman, 1988). Third, the giant pirarucu make large clean circular areas surrounding the nest holes. These clean circular areas probably assist keeping the eggs clean and free of exogenous material. They can improve visibility for the caring parent and, hence, reduce predation on the eggs. They can be related to the territorial behaviour of giant pirarucu reported by Fontanele (1948).

The spawning habitats that giant pirarucu selected most frequently were the *ressaca* followed by the *paraná* and *lago* (Table II). Both *lago* and *paraná* habitats were selected equally by the giant pirarucu. The density of nests, however, was distributed unevenly among the locations of *ressaca* surveyed, and especially so in *lago* habitats. All the increase in density of nests in *lago* habitat was due to the disproportionate increase of nests in *Lago Samaumeirinha*. This suggests that *ressaca* were selected more than *lago* habitats, and that there may be other factors influencing selection of nesting habitat. One such factor could be the depth of the channel that connects *lago* habitats to other water bodies. The channel connecting to *Lago Samaumeirinha* was 1 m shallower than all other *lago* locations surveyed. Shallow connecting channels can prevent the giant pirarucu from migrating in or out of *lago* habitats immediately before spawning when water levels are still low (Castello, in press).

The interfaces between the *ressaca*, *paraná* and *lago* habitats and the surrounding forests may provide the populations of giant pirarucu with at least three advantages over other habitats in the area. First, the giant pirarucu avoid spending as much energy as they would if they migrated to more distant habitats, such as the *rio*. The *ressaca* and *paraná* habitats tend to be close to the *lago* habitat, where most giant pirarucu are found during low water levels and

where they probably form pairs (Castello, in press). Second, the ressaca, paran and lago habitats tend to have slower currents than the rio (Castello, in press), so slow-flowing conditions may be a necessary condition for the development of the young giant pirarucu that are not found elsewhere at the time of spawning. The giant pirarucu prefer habitats with slow currents, *c.* 0.12 m s⁻¹ (Castello, in press). Many other fishes construct nests in habitats with slow-flowing currents (Mori, 1994; Jaroensutasinee & Jaroensutasinee, 2001; Vinyoles *et al.*, 2002; Armstrong *et al.*, 2003; Crampton & Hopkins, 2005; Scott *et al.*, 2005). Third, and perhaps most important, the interface between the ressaca, paran and lago and the surrounding forests may provide the young giant pirarucu with a strategic combination of low densities of predators, high availability of food and slow currents. Most nests (95%) were built in restinga baixa forests, immediately next to, and on top of, the terrains that have the greatest slopes of the area. So, conditions optimal for the survival of the young exist only when rising water levels flood the forests. When that happens, fish densities decrease (reduced predation) and food becomes more abundant (Bayley, 1988). The shallow depth observed at the time of spawning in this habitat (1–1.5 m) may be critical for the offspring to come to the surface to breathe and for the spawners to be able to breathe and protect the eggs at the same time.

The increase in abundance of nests and adult giant pirarucu from 1999 to 2005 suggests that there is a positive relation between the two (Fig. 1), with nests increasing at a lower rate than adult giant pirarucu. There are insufficient data points, however, to define the exact form of the relationship.

There are at least five implications for the management and conservation of the giant pirarucu in the vrzea floodplains. First and most important, the fish is extremely susceptible to overfishing. The giant pirarucu are vulnerable to fishing not only when they breathe and reproduce, but also where they reproduce. Their spawning grounds are used by fishers to move within and between their communities. Second, the giant pirarucu can be conserved more effectively through seasonal rather than spatial protection. Protecting only the lago habitats from fishing, as local fishers do, offers little protection for the reproduction of giant pirarucu. The fish build most of the nests in ressaca, paran and lago habitats, which are widespread through the vrzea and are easily accessible to fishers. Also, the spawners and their offspring swim away from the spawning area once the offspring have the capacity (Castello, in press). Seasonal bans (established by Brazilian regulations) protect the reproduction of the giant pirarucu when they are both most vulnerable and most valuable for future stocks. Third, the riparian forests require protection. They are the spawning grounds of the giant pirarucu, are easily accessible and thus suffer anthropogenic impacts. The riparian forests are protected by Brazilian law, but such regulations are rarely enforced by local communities. In the community in the study area, So Raimundo do Jarau, agricultural clearings are made behind the riparian forests. Fourth, the protection of the nesting habitat of giant pirarucu must be location-specific. The density of their nests varies disproportionately between and within the habitats. Finally, it is uncertain whether counts of nests of giant pirarucu are reliable indicators of the abundance of their populations (Fig. 1).

This study has shown that the riparian forests of floodplains are critical nesting habitats for the giant pirarucu. 'Nest building is very common among

floodplain fishes' (Welcomme, 1979); so many other floodplain fishes may also need to spawn in the riparian forests that are now disappearing so rapidly throughout the world. Additional studies on the spawning ecology of floodplain fishes are urgently needed to foster conservation initiatives run by local fishers and to allow for large-scale conservation planning.

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References

- Allan, J. D., Abell, R., Hogan, Z., Revenga, C., Taylor, B. T., Welcomme, R. L. & Winemiller, K. (2005). Overfishing of inland waters. *BioScience* **55**, 1041–1051.
- Arantes, C., Garcez, D. & Castello, L. (2006). Densidades de pirarucu (*Arapaima gigas*, Teleostei, Osteoglossidae) em lagos das Reservas de Desenvolvimento Sustentável Mamirauá e Amanã, Amazonas, Brasil. *Uakari* **2**, 37–43.
- Armstrong, J. D., Kempa, P. S., Kennedy, G. J. A., Ladle, M. & Milner, N. J. (2003). Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62**, 143–170.
- Ayres, J. M. (1995). *As matas de várzea do Mamirauá*. Tefé, Brazil: Conselho Nacional de Desenvolvimento Científico e Tecnológico, Sociedade Civil Mamirauá.
- Bayley, P. B. (1988). Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. *Environmental Biology of Fishes* **21**, 127–142.
- Castello, L. (2004). A method to count pirarucu: fishers, assessment and management. *North American Journal of Fisheries Management* **24**, 379–389.
- Castello, L. (2007). A socio-ecological synthesis on the conservation of the pirarucu (*Arapaima*) in floodplains of the Amazon. PhD Thesis, State University of New York, Syracuse, NY, U.S.A.
- Castello, L. (in press). Lateral migration of *Arapaima gigas* in floodplains of the Amazon. *Ecology of Freshwater Fish*. doi: 10.1111/j.1600-0633.2007.00255.x
- Chapman, D. W. (1988). Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* **117**, 1–21.
- Crampton, W. G. R. & Hopkins, C. D. (2005). Nesting and paternal care in the weakly electric fish *Gymnotus* (Gymnotiformes: Gymnotidae) with descriptions of larval and adult electric organ discharge of two species. *Copeia* **2005**, 48–60.
- Fontanele, O. (1948). Contribuição para o conhecimento da biologia do pirarucú, "*Arapaima gigas*" (Cuvier), em cativeiro (Actinopterygii, Osteoglossidae). *Revista Brasileira de Biologia* **8**, 445–459.
- Goulding, M. (1980). *The Fish and the Forest*. Los Angeles, CA: University of California Press.
- Jaroensutasinee, M. & Jaroensutasinee, K. (2001). Bubble nest habitat characteristics of wild Siamese fighting fish. *Journal of Fish Biology* **58**, 1311–1319. doi: 10.1006/jfbi.2000.1538
- Junk, W. J. (1997). *The Central Amazon Floodplain: Ecology of a Pulsing System*. Berlin: Springer Verlag.
- McGrath, D. G., Castro, F., Futemma, C., Amaral, B. D. & Calabria, J. (1993). Fisheries and evolution of resource management on the Lower Amazon floodplain. *Human Ecology* **21**, 167–195.
- Mori, S. (1994). Nest site choice by the three-spined stickleback, *Gasterosteus aculeatus* (form *leiuurus*), in spring-fed waters. *Journal of Fish Biology* **45**, 279–289.

- Potts, G. W. (1984). Parental behaviour in temperate marine teleosts with special reference to the development of nest structures. In *Fish Reproduction: Strategies and Tactics* (Potts, G. W. & Wootton, R. J., eds), pp. 223–244. Orlando, FL: Academic Press.
- Queiroz, H. L. (2000). Natural history and conservation of pirarucu, *Arapaima gigas*, at the Amazonian várzea: red giants in muddy waters. PhD Thesis, University of St Andrews, St Andrews, Scotland.
- Queiroz, H. L. & Sardinha, A. D. (1999). A preservação e o uso sustentado dos pirarucus em Mamirauá. In *Estratégias para o Manejo de Recursos Pesqueiros em Mamirauá* (Queiroz, H. L. & Crampton, W. G. R., eds), pp. 108–141. Tefé, Brazil: Conselho Nacional de Desenvolvimento Científico e Tecnológico, Sociedade Civil Mamirauá.
- Reynolds, J. D., Dulvy, N. K. & Roberts, C. M. (2002). Exploitation and other threats to fish conservation. In *Handbook of Fish Biology and Fisheries*, Vol. 2 (Hart, P. J. & Reynolds, J. D., eds), pp. 319–341. Oxford: Blackwell Publishing.
- Scott, R. S., Kosick, R., Clement, M., Noakes, D. L. G. & Beamish, F. W. H. (2005). Nest site selection and spawning by captive bred Atlantic salmon, *Salmo salar*, in a natural stream. *Environmental Biology of Fishes* **74**, 309–321.
- Tockner, K. & Stanford, J. A. (2002). Riverine flood plains: present state and future trends. *Environmental Conservation* **29**, 308–330.
- Veríssimo, J. (1895). *A Pesca no Amazônia*. Rio de Janeiro: Livraria Clássica Alves and Companhia.
- Viana, J. P., Damasceno, J. M. B., Castello, L. & Crampton, W. G. R. (2004). Economic incentives for sustainable community management of fishery resources in the Mamiraua Sustainable Development Reserve, Amazonas, Brazil. In *People in Nature: Wildlife Conservation in South and Central America* (Silvius, K., Bodmer, R. & Fragoso, J. M. V., eds), pp. 139–154. New York: Columbia University Press.
- Vinyoles, D., Côté, I. M. & de Sostoa, A. (2002). Nest orientation patterns in *Salaria fluviatilis*. *Journal of Fish Biology* **61**, 405–416. doi: 10.1006/jfbi.2002.2045
- Welcomme, R. L. (1979). *Fisheries Ecology of Floodplain Rivers*, 2nd edn. London: Longman Press.