Foraging Behaviour of Brazilian Riverine and Coastal Fishers: How Much is Explained by the Optimal Foraging Theory?

Priscila F.M. Lopes[a,b] #, Mariana Clauzet[a,c], Natalia Hanazaki[a,d], Milena Ramires[a], Renato A.M. Silvano[a,e] and Alpina Begossi[a,f]

[a]Fisheries and Food Institute (FIFO), Campinas, SP, Brazil

[b]Depto. de Botânica, Ecologia e Zoologia, CB, UFRN, Natal, RN, Brazil

[c]Pós Graduação em Desenvolvimento e Sociedade, UNICAMP, Campinas, SP, Brazil

[d]Depto. de Ecologia e Zoologia, CCB, UFSC, Florianópolis, SC, Brazil

[e]Depto. de Ecologia, UFRGS, Porto Alegre, RS, Brazil

[f]CAPESCA (LEPAC, PREAC) and CMU (UNICAMP), Campinas, SP, Brazil

#**Corresponding author. E-mail:** priscila@cb.ufrn.br

Abstract

Optimal Foraging Theory (OFT) is here applied to analyse the foraging behaviour of Brazilian artisanal fishers of the Atlantic coast (Itacuruçá and São Paulo Bagre villages) and of the inland Amazonian region (Jarauá and Ebenezer villages). Two OFT predictions are tested. Hypotheis1: A fisher who travels to more distant sites should return with more fish, and Hypothesis 2: The further a fisher goes, the longer s/he should stay fishing in a patch. OFT did not explain fishers' behaviour (non-significant regressions for coastal villages) or explain it in specific seasons (low water season for one Amazonian village: H1 r^2=24.1; H2 r^2=37.2) and in specific habitats (e.g., lakes and backwaters in Jarauá village, Lakes: H1 r^2=13.5; H2 r^2=24.0; Backwaters: H1 r^2=34.4; H2 r^2=46.5). The findings can indicate areas or seasons that are under higher fishing pressure, when fishers try to get the best out of a situation without any concern about resource conservation. By knowing the variables that influence fishers' decision-making processes, management initiatives may be more fine-tuned to the local reality and are thus more likely to succeed.

Keywords: Amazon, Atlantic forest, Brazilian fisheries, fisheries management, human optimal foraging

INTRODUCTION

Originating in microeconomic theory (Rapport & Turner 1977), optimal models were first applied to understand animal foraging behaviour (Stephens & Krebs 1986). Their potential to explain human foraging behaviour through simple, operational

and realistic approaches was soon realised (Winterhalder 1981). Such models offer plausible explanations for a variety of questions that goes from human settlement pattern to the size and composition of social groupings (Winterhalder & Smith 1981), and have been useful in estimating foraging behaviour in archaeological studies (Bettinger 1991). The basic assumption of optimality theories states that the foragers' decisions aim at the maximisation of their fitness (Stephens & Krebs 1986). However, measuring fitness in humans is usually a hard and even unfeasible task due to practical and ethical reasons. One of the alternatives is to choose a short-term energy-return currency, assumed to have direct implications in fitness, as fitness is supposed to be positively related to the rate of energy intake acquired while foraging (Winterhalder

1981). Successful examples using such indirect measures can be found in archaeological studies (Bettinger 1991; Burger *et al.* 2005; Lupo & Schmitt 2005) as well as in studies among contemporary indigenous groups (Winterhalder & Smith 1981; Smith & Winterhalder 1992; Bird & Bliege Bird 1997).

The first optimal foraging space-use model—the patch choice model—was developed by MacArthur and Pianka (1966) and explores the selection of foraging areas in a heterogeneous environment. Charnov (1976) developed another model that dealt with the selection of a foraging pathway, the marginal value theorem, predicting when a forager should leave a patch. This model assumes that the foraging activity in a patch reduces the food availability in its immediate vicinity. An optimal forager should leave a patch when the marginal intake rate in that patch drops to the average rate of intake in the overall habitat (Charnov 1976). Orians and Pearson (1979) developed yet another model—the central place model—which can be understood as a variation of the marginal value theorem, where the forager has a central place (a house, a village, etc.) to return to after foraging. Doing so, an optimal forager should maximise the rate of energy delivered to the central place, including the expenses involved in the round trip to the foraging ground. This model has been widely applied to human foragers, as they usually have fixed settlements (central places) where they return after a foraging day (Glover 2009).

Optimal foraging models, such as central place foraging, show potential to go beyond the understanding of the evolution of human behaviour. They offer an alternative to study local resource management by demonstrating whether foragers forego short-term benefits for long-term ones through sustainable harvests (Alvard 1993; Hames 1987). A constant maximisation strategy, as assumed by optimal foraging, implies that foragers would not refrain from overexploiting their resources, if needed. Nevertheless, it is demonstrated that, depending on the biological characteristics of the species (e.g., annual maximum sustainable yield, intrinsic rate of increase), foragers can behave according to predictions of the optimal foraging theory and still exploit their local resources in a sustainable way (Alvard 1998). Sustainability in this case is not a synonym for conservation, the latter being a side effect.

Aswani (1998) was one of the first persons to apply the foraging theory to understand marine resource management strategies. Studying fishers from the Solomon Islands, he showed that it is possible to integrate optimisation model studies to provide practical management suggestions for the sustainability of long-term fisheries. In Brazil, optimal foraging studies have also been applied to investigate fishers' behaviour in freshwater and marine environments (Begossi 1992; Begossi & Richerson 1992; Begossi *et al*. 2005).

In our study, using examples of artisanal fishers from the Brazilian Amazonian region and southeastern Atlantic coast, we addressed the central place foraging model by examining two of its main predictions (hypotheses): a) fishers should stay longer when foraging in more distant spots, and b) by doing so, they should catch more fish in those spots. By considering different case studies and using OFT as a tool, we wanted to better understand which factors (gear, seasonality, types of habitat exploited, etc.) are relevant to define the behavioural strategy adopted by fishers in different places. The results also have management implications: If fishers are predominantly 'catch maximisers', such behaviour must be carefully considered when developing management strategies, as they will invest in short-term benefits, trying to get the best out of a situation, which can mean exploiting fish stocks to the limits, regardless of the resource's abundance.

MATERIAL AND METHODS

Study Sites

Four sites—two on the Atlantic coast (Itacuruçá island and São Paulo Bagre) and two in the inland Amazonian region (Jarauá and Ebenezer)—were studied, as they represent small villages where fishing is the main subsistence and economic activity (Figure 1).

The research in Itacuruçá island, Rio de Janeiro State, was conducted at fish-landing points at Itacuruçá beach (22º55'92"S and 43º54'83"W) and in Gamboa (22º55'90"S and 43º53'73"W), from September 1989 to February 1990. During this period, there were 26 families living there, all dependent on fisheries to some degree. Local fishing is mostly practised by men, although children and women do fish for subsistence at times. Besides fishing, the people also work as maids or housekeepers for tourists. Local fishers generally use gillnets and encircling nets to catch mainly whitemouth croaker *(Micropogonias furnieri,* Sciaenidae), rays and catfish (Ariidae), besides shrimp (Penaeidae) (Begossi, 1992, 1995). São Paulo Bagre is a fishing community located in the estuary of Iguape-Ilha Comprida (24°57'51"S and 47°53'13W"). Shrimp fishing (*Litopenaeus schmitti*, Penaeidae) is the main activity, carried out by an artisanal fishing method using the 'gerival', a small mesh-sized gillnet attached to a pole and trawled on the bottom of the estuary by a fisher in a paddled canoe (Hanazaki *et al.* 2007). The São Paulo Bagre community comprises 17 families, who base their economy on fisheries, shrimp collection to be sold as bait, subsistence agriculture and tourism-related activities, such as working as boat captains for tourists. Plants and timber are rarely extracted (Hanazaki *et al.* 2007). Here, fishing is mostly by men.

Jarauá (02º51'849 S, 64º55'750 W, Amazonas State) is a fishing village located at the confluence of the Japurá and Jarauá rivers, in the Mamirauá Sustainable Development Reserve, home to 35 families in 1994 (Queiroz 1999), but this figure has probably changed significantly in the last decade. The Mamirauá Sustainable Development Reserve has been under management since 1990 with special focus on two important commercial fishes—*tambaqui* (*Colossoma macropomum*, Serrasalmidae) and *pirarucu* (*Arapaima gigas*, Osteoglossidae) (Queiroz & Crampton 1999; MacCord *et al*. 2007; Castello *et al*. 2009; Silvano *et al*. 2009). Their co-management programme involves rotation of fishing pressure among lakes, monitoring (counting) of *pirarucu* by local fishers
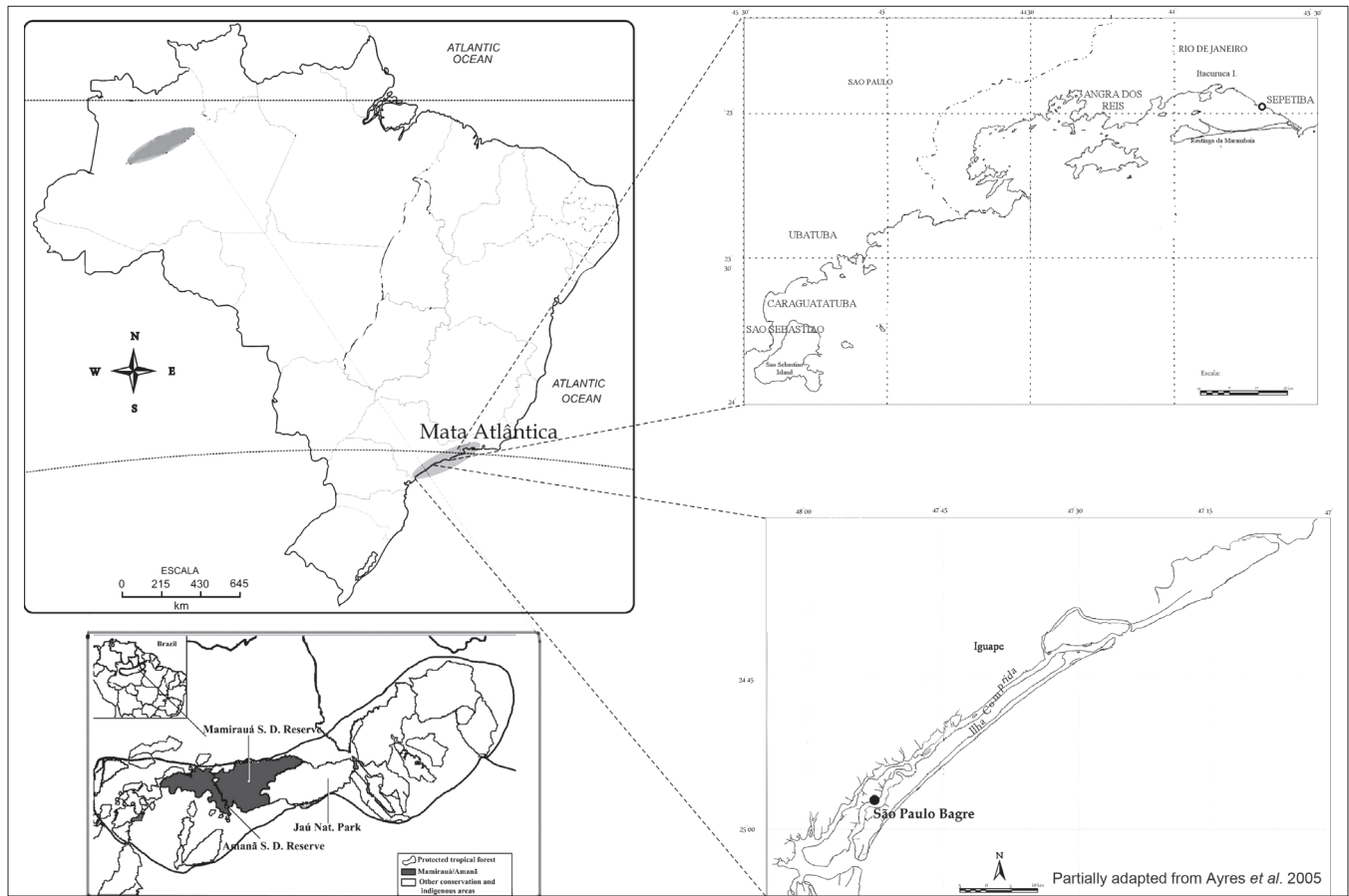
Figure 1
Map showing the study villages

and participation of fishers and other community members in decision-making processes, including the enforcement of the rules. Because of its successful local management process, the Mamirauá Reserve was recommended for the international fishing certification awarded to products that come from well-managed and sustainable fisheries by the Marine Stewardship Council (Wilson *et al.* 2001). This is true of Mamirauá as a whole, and Jarauá specifically, where formal co-management has been successfully carried out in the last 20 years, resulting in a significant increase in some fish populations (e.g., *pirarucu, tambaqui*), as well as in socio-economic improvements to fishers (higher income), despite an increase in the number of fishers entering the fishery (Castello *et al.* 2009; Silvano *et al.* 2009). Ebenezer (02º34'222 S, 64º58'676 W, Amazonas State) is located on the margin of the Coraci river, in the Amanã Sustainable Development Reserve, created in 1998 (Viana *et al.* 2004). *Tambaqui* and *pirarucu* are also important commercial fishes in Ebenezer, but the different geographic and social features here result in a greater dependence on migratory fishes, such as many catfish species (MacCord *et al.* 2007). Both Jarauá and Ebenezer villages practise slash-and-burn agriculture, mostly focused on cassava to produce cassava flour. Although fishing is the main economic activity, fishers and their families can be involved in, and get

paid to, work in the Reserve projects, such as forest, caiman, turtle or bird management. In both communities, children and women fish mostly for subsistence, although wives sometimes help their husbands on longer fishing trips.

The Habitat Types

The habitats regularly exploited by Jarauá and Ebenezer fishers are:
• River: The main river channel, which is larger and deeper than other habitats and with a faster water flow. Fishers usually exploit the river to catch large migratory fishes, such as catfish (Pimelodidae).
• Flooded forest: Also locally called 'várzeas', this ecosystem is created during the high water season, when water from the main river and lakes flood the adjoining forest, forming an important environment for fish feeding and nursery grounds.
• Lakes: These floodplain lakes are usually seasonally connected to the main river and to one another during the high water season, when they form lake systems. Some of the largest lakes in the Mamirauá Reserve were created by a channel that was separated from the main river due to sedimentation.

- Connecting canals: Locally called 'paranás', these channels link the floodplain lakes to the river or link together several floodplain lakes during the high water season. These channels usually increase considerably in size during the floods, but become much shallower or even dry out during the low water season.
- Backwaters: These are lakes that are permanently connected to the main river (or its tributaries) by an open-ended mouth. These backwaters are thus more accessible. Water characteristics and fish assemblages may experience less seasonal change than lakes, which are not linked to the river during the low water season.

More details about aquatic habitats and fishing communities of Mamirauá can be found in other surveys (Crampton 1999; Henderson & Robertson 1999; Silvano *et al*. 2009).

Procedures

Data from fishing trips were assessed at landing points, gathered directly from fishers. A total of 113 fishing trips were sampled monthly (six consecutive months) in the spring and summer of 1989-90 at Itacuruçá island. Monthly appraisals of fishing trips and catches were collected in 1999-2000 in Sao Paulo Bagre for 10 consecutive months, totalling 204 fishing trips. In the Amazonian communities, fish landings were assessed during the high water (17 consecutive days in June) and low water (15 consecutive days in October) seasons, as logistics made monthly evaluation difficult. This resulted in 268 fishing trips in Jarauá and 204 in Ebenezer.

Fishers were asked about the distance (in minutes) travelled to the fishing spot for each trip, the time spent fishing, fishing gear used and fish composition. Fish caught were weighed by the researchers and identified to the nearest possible taxonomic level. More detailed data about these four fishing villages are available in other surveys (Begossi 2006a; Hanazaki *et al*. 2007; MacCord *et al*. 2007). Simple linear regressions were used to analyse the data after normalisation through natural logarithm when needed. It is assumed, based on interviews, that in most of the fishing trips fishers visit only one fishing spot. We performed two separate regressions to answer the questions below:

1. Do fishers catch more fish when they forage in distant patches? Dependent variable (y): amount of fish caught (kg) X independent variable (x): travel time (min).

2. Do fishers stay longer in more distant patches? Supposing there is no resource depletion and that the resource is evenly distributed in the environment, fishers will have to stay longer in the patch (fishing spot) to catch more fish. Dependent variable (y): time fishing (min) X independent variable (x): travel time (min).

If Regression 1 is significant but not Regression 2, there can be some evidence of resource depletion or unequal resource distribution, which was not foreseen before the samplings, as the projects developed at each of the studied sites have different goals.

Finally, as fishers in the Amazonian region use a diversified set of aquatic habitats (river canals, lakes and backwaters) and seasonality is clearly defined by the level of water (six months of flooded forest), it is likely that such factors can affect the predictive power of the models used. To test this, data about Amazonian fisheries were also analysed separately by environment exploited and season. This is not expected to be a problem on the coast, where seasons are less defined and both the villages exploit just one kind of environment each (São Paulo Bagre: estuary; Itacuruçá : open ocean).

RESULTS

Applying the Models to Field Data

Table 1 summarises the main features of each fishing village and the average values for the variables used in the regressions. The fishing communities showed differences not only between the two main environments (Amazonian region and the Atlantic coast), but also between fishing communities in the same environment, as within the Amazonian region (Table 1). For example, the time fishers spent fishing is much longer in the Amazonian region (average=534 min) than on the coast (average=243 min), while the travel time varied according to the village, regardless of the environment. On the other hand, in a coastal village whose main resource is shrimp (São Paulo Bagre), fishers do not fish for too long (average=148 min) and fish close to home (average travel time=29 min), while still assuring the highest returns in weight of catch (Table 1).

The first hypothesis proposed in this study and one of the core questions in the central place foraging model states

Table 1

Summary of the main features of each community and average values for the variables used in the main regression analyses

Community	Sample size	Fishing methods	Main fishing resources	Time fishing (min) (±SD)	Travel time (min) (±SD)	Catch (kg) (±SD)
Itacuruçá island	113	Gillnet, entangling net and encircling nets	Coastal fishes[a]	338.5 (± 234.8)	117.2 (± 112.1)	31.4 (± 58.7)
São Paulo Bagre	204	'Gerival'[c]	Shrimp[b]	147.5 (± 124.9)	29.11 (± 31.77)	94.5 (± 189.8)
Jarauá	268	Hook and line and gillnet	Tambaqui and pirarucu	517.6 (± 225.1)	143.0 (± 92.3)	71.9 (± 132.5)
Ebenezer	204	Hook and line and gillnet	Tambaqui, pirarucu, and migratory species	550.3 (± 278.8)	76.4 (± 73.0)	29.0 (± 34.9)

[a]Mostly whitemouth croaker (*Micropogonias furnieri*, Sciaenidae), catfishes (Ariidae) and ray, [b]*Litopenaeus schmitti*, Penaeidae, [c]small mesh-sized gillnet attached to a pole and trawled on the bottom of the estuary by a fisher in a paddled canoe

that a forager who travels further must bring back home a higher energetic return than when foraging closer to the central place. This assumption is reasonably confirmed by most of the linear regressions (Table 2, $r^2_{SPBagre}$=22%, $r^2_{Itacuruçá}$=19%, $r^2_{Ebenezer}$=12%; $P<0.001$). The only exception is one of the Amazonian region villages, Jarauá ($P>0.05$). The other Amazonian region village, Ebenezer, had a significant regression coefficient, but it showed that only 12% of the return in kilograms of fish caught was explained by the distance travelled by the fishers (Table 2).

If the result demonstrated above was the consequence of an optimal strategy by fishers, then it is expected that the fishers stayed longer in the more distant patches in order to catch more fish. However, this is not consistently observed among the villages. One of the coastal villages (São Paulo Bagre) had a significant but very low regression coefficient (*Travel time* barely influenced *Time fishing*; r^2=9%), while the other coastal village (Itacuruçá island) did not show a significant result ($P>0.05$), despite the significant results in the first regression based on the central place foraging model (Table 3). The Amazonian region villages were even more surprising: Jarauá, which was not significant in the first regression, now presented a very high regression coefficient (r^2=43%). If a Jarauá fisher goes to a place further away, he stays longer there. But in Ebenezer, the other village, the distance of a fishing spot did not affect the time spent there by a fisher ($P>0.05$) (Table 3).

Foraging Models and the Specificities of Each Situation

The first questions that might arise in observing the results in Tables 2 and 3 will be about the variables that influenced the fishers' decision on how far to go fishing. What are they optimising: Total catch (quantity) or a selective catch of a given fish species? Which variables are relevant: Gear used, fish target, season or habitat? In the case studies presented, fishers from only one village, the coastal São Paulo Bagre, used one single kind of gear to catch shrimp, while the others used a mix (Table 1). The same two regressions performed with the whole data set are shown for Itacuruçá island, but now separated by gear (Table 4). Confirming what was observed earlier, the results show that increasing the distance of the fishing spot from the central place increased the amount of fish caught, especially using a particular kind of gear, such as the encircling net ("rede de aperto") (r^2=43%; $P>0.001$), but this does not imply that fishers will stay longer in more distant patches (Table 4).

For the Amazonian region villages, although the gear used varied consistently according to the seasons, we preferred to analyse the data by 'season' instead of by 'gear' because we believe that the gear is chosen in conformity to the local water level. Apparently, during the low water season, Amazonian fishers behaved as predicted for optimal foragers (Ebenezer r^2=25%; Jarauá r^2=24%; $P>0.01$), but this was not always the case during the high water season (Table 5).

Table 2

Simple linear regressions using 'amount of fish caught in kg (C)' as the dependent variable and 'travel time (Tt)' as the independent variable. Data were transformed in natural logarithm (Ln).

Community	Regression line	r^2 (%)	P	F	n
São Paulo Bagre	C=-0.47 +0.37 Tt	22.16	<<0.001	64.62	228
Itacuruçá island	C=-0.90 + 0.79 Tt	19.09	< 0.001	28.07	120
Jarauá	Non significant	0.05	0.29	1.13	267
Ebenezer	C = 1.5 + 0.28 Tt	12.12	< 0.001	27.9	203

Table 3

Simple linear regressions using 'time fishing (Tf)' as the dependent variable and 'travel time (Tt)' as the independent variable. Data were transformed in natural logarithm (Ln).

Community	Regression line	r^2 (%)	P	F	n
São Paulo Bagre	Tf = 3.41 + 0.29 Tt	8.80	> 0.001	21.99	228
Itacuruçá Island	Non significant	0.00	0.63	0.82	120
Jarauá	Tf = 3.1 - 0.09 Tt	42.77	> 0.001	198.2	267
Ebenezer	Non significant	0.98	0.16	1.99	203

Table 4

Simple linear regressions for Itacuruçá island, considering the three main types of gear used. 'travel time (Tt)' is used as the independent variable and 'amount of fish caught in kg (C)' or 'time fishing (Tf)' as the dependent variables. Data were transformed in natural logarithm (Ln).

Dependent variable	Gear	Regression line	r^2 (%)	P	F	n
Catch (C)	Encircling net	C=-2.54 + 0.99 Tt	43.00	> 0.001	14.48	19
	Entangling net	C=-1.66 + 0.97 Tt	25.00	> 0.001	14.67	45
	Set gillnet	C=0.18 + 0.59 Tt	11.20	> 0.01	5.92	49
Fishing time (Tf)	Encircling net	Non significant	0.05	0.75	0.10	19
	Entangling net	Non significant	3.00	0.22	1.56	45
	Set gillnet	Non significant	1.20	0.63	0.82	49

There is yet another factor to be considered in these villages—the different habitats exploited. When the two regressions were performed by habitats, the results were highly variable. The distance travelled by the fisher explained both the amount of fish caught and the time the fisher remained in a patch (as expected by the model) for some habitats only (Table 6). The only consistent result for both villages was that the model explained fishers' behaviour when fishing in lakes or in backwaters, which are similar to lakes (Table 6). It is worth noticing that for these habitats, travel time explained most of the variability in the amount of fish caught and in the time spent fishing in a patch (Table 6).

DISCUSSION

The application of optimal foraging models to understand human behaviour reached its peak in the middle of the 1980s, following important studies done among the Inuit and the Cree in Canada (Smith 1981; Winterhalder 1981) and among South American groups and Australian aborigines (O'Connell and Hawkes 1981; Hawkes & O'Connell 1982; Beckerman 1983).

After this period, a few studies were published concerning human foragers, most of these focusing on archaeological applications, including the development of new models (Metcalfe & Barlow 1992). Only by the end of the 1990s was there a resurgence of optimal foraging in anthropology and archaeology (Zeanah 2002; Lyman 2003; Lupo & Schmitt 2005), and for the first time fishers and shellfish gatherers came to be the focus of such studies (Begossi 1992; Bird & Bliege Bird 1997; Aswani 1998; de Boer *et al.* 2002; Thomas 2007). Until then, hunters and gatherers were the only ones to be considered in human ecological studies, apparently because such human groups represented the last 'real foragers'.

With these recent studies, it has become clear that the study of fishers and shellfish gatherers could also bring insights to the understanding of the evolution of human behaviour (Bird & O'Connell 2006; Nordi *et al.* 2009), of archaeological facts, such as the formation of shell assemblages (Bird & Bliege Bird 1997; Thomas 2007), and it could even help establish management measures or understand local tenure systems (Aswani 1998). These more recent applications of optimal foraging models also show that new and more elaborated

Table 5
Simple linear regressions for the Amazonian communities analysed by seasons (low and high water season). The first line corresponds to the regression 'amount of fish caught in kg (C)' as the dependent variable and 'travel time (Tt)' as the independent variable, while the second one corresponds to 'time fishing (Tf)' as the dependent variable and 'travel time (Tt)' as the independent variable. Data was transformed in natural logarithm. Only habitats with more than 15 fish landings were analysed in order to avoid biased results due to small number of observations

Fishing community	Season	Regression line	r^2 (%)	P	F	n
Ebenezer	Dry	C = 1.84 + 0.41 Tt	24.94	< 0.01	11.96	38
		Non significant	0.14	0.52	0.52	38
	Flooded	C = 2.18 + 0.17 Tt	4.85	< 0.01	8.36	166
		Tf = 5.72 + 0.14 Tt	4.38	< 0.01	7.50	166
Jarauá	Dry	C = 1.53 + 0.68 Tt	24.13	< 0.01	31.81	102
		Tf = 3.59 + 0.49 Tt	37.22	< 0.01	59.29	102
	Flooded	Non significant	2,10	0.06	3.44	166
		Tf = 4.58 + 0.35 Tt	29.97	< 0.01	70.17	166

Table 6
Simple linear regressions for the Amazonian communities analysed by habitats, having 'travel time' as the independent variable. Data was transformed in natural logarithm. Only habitats with more than 15 fish landings were analysed in order to avoid biased results due to small number of observations

Fishing community	Habitat	Dependent Variable	Regression line	r^2 (%)	P	F	n
Ebenezer	River	Fish caught (kg)	Non significant	0.06	0.19	1.67	100
		Time fishing (min)	Tf=5.41 + 0.16 Tt	5.1	0.02	5.27	100
	Flooded forest	Fish caught (kg)	C=1.43 + 0.34 Tt	22.79	> 0.001	14.45	51
		Time fishing (min)	Non significant	0.23	0.26	1.30	51
	Lake	Fish caught (kg)	C=-2.62 + 1.32 Tt	43.53	> 0.001	16.19	23
		Time fishing (min)	Tf= .55 − 0.69 Tt	49.68	> 0.001	20.73	23
	Connecting canals	Fish caught (kg)	Non significant	13.93	0.11	2.75	19
		Time fishing (min)	Non significant	0.01	0.79	0.07	19
Jarauá	Lake	Fish caught (kg)	C=7.55 − 0.87 Tt	13.51	> 0.001	27.95	181
		Time fishing (min)	Tf=4.53 + 0.35 Tt	24.00	> 0.001	56.54	181
	Connecting canals	Fish caught (kg)	Non significant	0.30	0.50	0.48	18
		Time fishing (min)	Tf=5.33 + 0.20 Tt	36.43	0.008	9.17	18
	River	Fish caught (kg)	Non significant	17.13	0.08	3.31	18
		Time fishing (min)	Tf=3.26 + 0.58 Tt	41.66	0.004	11.43	18
	Backwater	Fish caught (kg)	C=1.11 + 0.62 Tt	34.41	> 0.001	22.04	44
		Time fishing (min)	Tf=3.30 + 0.55 Tt	46.47	> 0.001	38.33	44

models are not necessarily required to understand 'current foragers', whose concerns are not only to eat and bring provisions to their families, but also to sell their foraging product (e.g., fish) to buy other goods and foodstuff (Begossi & Richerson 1992). Advocates of simple models have shown that they can be widely used in different contexts with satisfactory outcomes, although sometimes it is necessary to reformulate the hypotheses and reconsider the currencies used (e.g., calories, protein, money) (Bird & O'Connell 2006).

This is what we did in this study: We showed how a simple and well established model (central place model) can explain different fishers' behaviour in the exploitation of different resources, considering the peculiarities of each region. In our study, when we used the whole data set without considering differences in gear, habitats or seasons, we observed that the first hypothesis (s/he who travels further catches more fish) was confirmed for some villages, especially the ones on the coast. However, the second hypothesis, which should be viewed as a consequence of the first one in the original model (the further a fisher goes, the more time s/he should spend in the spot), was not confirmed for most of the villages. The results were diverse and no pattern could be established either in the Amazonian region or at the coast.

The model seems to work well when no or a minimum amount of variation is included in the foraging activity. For example, the model showed a good fit for the only situation—the coastal São Paulo Bagre—where fishers used one kind of gear (*gerival*), exploited one kind of habitat (estuary) and one kind of resource (shrimp), and where there are no pronounced seasonal differences.

In places where the first hypothesis but not the second one was confirmed (e.g., the coastal Itacuruçá), one can initially surmise that local fishers, instead of optimising, are dealing with local resource depletion; they need to go further to bring some food home, because nearby fishing spots were already depleted. Alternatively, time fishing in more distant fishing spots (or total fishing time including travel and time on the spot) may be limited by the available ice (important to avoid fish or shrimp spoilage), as observed for Amazonian fishers at the Negro river (Begossi *et al.* 2005). This would be an example of a constraint not included in the original model.

Fishing is a complex and unpredictable activity, affected by external factors such as the weather, and by individual choices, such as the use of specific gear. Fishing can be performed in different ways and with the use of an array of different methods and types of gear. Some of these require more effort and the constant presence of the fisher (e.g., diving, hook and line), while others do not (e.g., set gillnets), even allowing the performance of parallel activities (e.g., a fisher can set the nets and go back home until s/he decides to check the nets). If this is the case, it is reasonable to suppose that the gear used or the season will affect the fisher's behaviour. Such factors might represent important variables taken into account by fishers when they make their decisions about where, when and how long to stay fishing.

When we considered these factors, we did observe patterns.

Kinds of gear, for example, are an essential variable to explain the amount of fish caught in relation to the distance travelled for one of the coastal villages, Itacuruçá. For some gear, such as encircling and entangling nets, the distance travelled explained the catch, while this is not true for set gillnets. For none of these gears, however, going further implied staying longer. These results indicate a 'non-optimal' behaviour for these fishers, as it was not explained by the foraging models. Non-optimal behaviour may occur due to several reasons: For example, an open access situation where a fisher tries to get the most of a fishing spot before others arrive to exploit the same spot (Begossi 1992), or a time lag between environmental changes and the selection of optimal behaviour (adaptive lag) (Laland & Brown 2002: 142; but see Laland & Brown 2006 for a different opinion on the lag between environmental changes and human adaptation). Glover (2009) showed that even a false public announcement of good foraging places can induce non-optimal behaviour, such as human foragers staying longer in non-productive patches.

Seasonality also showed to be an important variable taken into account by fishers in their foraging activity, depending on the situation. In the Amazonian region villages, we saw that in one of them (Jarauá), fishers optimised in the low water season. In this season and specifically in this village, fishers focus on the capture of *pirarucu*, a large fish that occurs in lakes and comes to the surface every 5 to 15 minutes to breathe. *Pirarucu* fisheries are regulated by a co-management agreement, occurring in a very specific period of the year and following a quota system defined yearly (Castello *et al.* 2009). During the few days when *pirarucu* fishing is allowed, fishers have to do their best to reach their quota and it is not surprising that they optimise their fishing behaviour, as predicted by the models.

Finally, the third variable we considered—the kind of habitat exploited—was also important to the degree to which foraging models can predict fisher behaviour. Again, our results indicated that fishers' optimisation as predicted by models was only reached in some habitats, namely lakes and backwaters. Both habitats have well-defined boundaries, even though both can be connected regularly or temporarily to the main channel. During the low water season, the prey (fish) has usually nowhere to go. Lakes are thus very similar to a patch as idealised in the original model proposed by Charnov (1976). Having conditions more similar to the original model can indeed assure a better fit, but, as we showed before, this is not necessarily required. Aswani (1998), studying the fishers from the Solomon Islands, also considered different habitats when analysing optimal behaviour, but in this case each major habitat category considered was a large patch. Aswani confirmed the predictions of the optimal foraging models for the studied fishers, showing that fishers spend more time in the more productive habitats (patches) and also spend more time in the fishing spots of less productive habitats in a given season (Aswani 1998).

The analyses made in this and in other studies (Aswani 1998; Thomas 2007; Glover 2009) were performed at the population level, therefore not addressing individual behavioural variation.

Nevertheless, individual variation can affect the observation of an optimal behaviour. Individuals vary in several aspects: Ability to learn, which also depends on life stage (Bird & Bliege Bird 2000); need to acquire information before they can behave optimally (Clark & Mangel 1984); and variations in proneness to take risks (Smith & Wilen 2005). Such factors are important approaches to a fine-grained analysis, and could be investigated in the future, perhaps even including the fishers' own explanation for their behaviour. Nevertheless, a population level of analysis may be the most useful one to support fishery management approaches (Aswani 1998), as it shows the behaviour of the majority of individuals that will ultimately affect the exploited resources.

Comparing Studies on Foraging Models Applied to Brazilian Fishers

Table 7 summarises the main results of published Brazilian studies on fishers' optimal foraging. In general, these studies approach at least one of the two hypotheses tested here: A fisher should catch more fish if s/he travels further or a fisher should stay longer in a spot if s/he travels further. Some of these studies also indirectly test a third hypothesis: A forager should leave the patch at the optimal time, after which the costs of searching for the prey will be higher than the potential benefits of catching additional prey. This assumption is hard to test without measuring the forager's load curve, which can be done experimentally. It is only possible to provide indirect evidence of this hypothesis if it is shown that there is a negative correlation between the time spent fishing and the amount of fish caught:

Fishers should stay for shorter time in productive patches.

The nine studies found in the literature seem to show a good fit to the model because they considered, with a few exceptions, different gear and seasons separately, but the results for the whole data set have not been presented (Table 7). Even though this is just indirect evidence, such studies seem to confirm the relevance of including pertinent variables that describe the environment (e.g., seasons or habitats) or foraging methods (e.g., types of gear) in the optimal models as a means of understanding human foraging behaviour.

Another important point interpreted from these published studies is that focusing on one prey, especially on a less mobile prey (such as shrimp), is key to a better fit of foraging models to fishers' behaviour (optimisation). Fishers can more easily access the location and density of a less mobile prey in a foraging patch. This is suggested by Begossi (1992) when explaining the optimal behaviour for Sepetiba shrimp fishers on the southeastern Brazilian coast.

CONCLUDING REMARKS: OPTIMAL FORAGING AND MANAGEMENT

The results from our survey and the comparison with other published studies show that simple optimal foraging models can be more widely and successfully applied to current foragers, if the details and particularities of each situation are taken into account, such as changes in behaviour due to seasons, climate change, foraging gear, and habitat variability. By doing so, we can be more convincing when applying foraging models to predict fishers' behaviour and thus state

Table 7

Regression lines from other published sources on Brazilian fishing communities (regression coefficient equal or higher than 10%) using 'total catch (C)' (kg or number of individuals) or 'time fishing (Tf)' as the dependent variables and 'travel time (Tt)' or 'time fishing (Tf) (total time excluding travel time)' as the independent variables. H1=a fisher who travels further should come back with more fish; H2=the further a fisher goes, the more time s/he should spend in the fishing spot; H3=a fisher should stay shorter in productive patches

Environment/ State	Local/Village	Gear	Hypothesis	Regression line	r^b(%)	P	n	Catch	Source
Amazon/ Amazonas	Negro River/ Barcelos[a]	Zagaia (harpoon-type trident)	H2	$Tf=0.42 - 0.33Tt^b$	23.0	< 0.001	65	Fish (kg)	Begossi *et al.* 2005
Inland river/São Paulo	Piracicaba River/ Tanquã and Santa Maria	Gillnets	H1	$C=11.12 + 0.49 Tt$	22.0	< 0.01	30	Fish (kg)[c]	Begossi *et al.* 2005; Silvano 1997
Coast/Rio de Janeiro	Sepetiba Bay/ Gamboa	Encircling nets	H3	$C=-24.05 + 0.61 Tf$	52.0	< 0.001	23	Shrimp (number)	Begossi 1992
Coast/Rio de Janeiro	Sepetiba Bay/ Gamboa	Encircling nets	H2	$Tf=49.26 + 1.53Tt$	22.0	< 0.02	22	Shrimp (kg)	Begossi 1992
Coast/Rio de Janeiro	Sepetiba Bay/ Gamboa	Encircling nets	H3	$C=0.04 + 0.18Tf$	26.0	< 0.001	47	Fish (kg)	Begossi 1992
Coast/São Paulo	São Sebastião/ Búzios Island	Mixed gear (hook and line and gillnets)	H3	$C=-0.56 + 2.20Tf$	14.0	< 0.001	784	Fish (kg)	Begossi 1995
Coast/São Paulo	Ubatuba/Puruba	Mixed gear (hook and line and gillnets)	H3	$C=0.21+ 0.75Tf$	13.0	< 0.001	112	Fish (kg)	Begossi 1995
Coast/São Paulo	Ubatuba/Puruba	Mixed gear (hook and line and gillnets)	H2	$Tf= - 0.0008 - 0.24Tt$	32.0	< 0.001	111	Fish (kg)	Begossi 1995
Coast/São Paulo	Cananéia/São Paulo Bagre	Gerival	H1	$C=1.20 + 0.77Tt$	19.0	< 0.001	204	Shrimp (number)	Begossi *et al.* 2009

[a]Dry Season, [b]Time: day fraction. In all the remaining regressions, time was converted to minutes. [c]Only 'lambari', the main fish caught, was included in the regression. *Lambari* is the local name for four Characidae species: *Astyanax bimaculatus*, *A. schubarti*, *Moenkhausia intermedia* and *Triportheus signatus*.

whether specific foragers do or do not optimise. More than that, the fact that a forager optimises in one situation does not imply s/he will always do it. As shown here, seasonal changes may affect the perception a forager has of the pursued resource, new kinds of gear are introduced and it takes time to learn how to get the best out of them, and different environments may offer additional difficulties in their exploitation.

This has important implications for resource management, especially regarding new management approaches where resource users are an important part of the measures adopted (Warner 1997). In these approaches the way users behave are considered in the rules developed, which are sometimes proposed and discussed by the users themselves (Castello *et al.* 2009). Optimal foraging can then bring insights about when, where and why users go fishing and to what extent they are optimising their fishing returns. Management can reflect more accurately on the reality if we know the variables that influence fishers' decision-making processes (Béné & Tewfik 2001). In the case of fisheries, optimal foraging can help decide, for example, which areas or periods are under high fishing pressure (i.e., when fishers optimise regardless of the resource status, maximising their short-term harvesting rate).

Alvard (1993) was one of the first to show that groups that depend directly on natural resources may not be averse to overexploitation. Despite that, sustainable harvests can still happen and conservation would be, in this case, a side effect (Alvard 1995), depending on the size of the human group exploiting the resources, the biological characteristics of the prey, imperfect information about the environment and within-group rules to control resource exploitation, among others. In our study, regardless of the reasons that explain optimal or non-optimal behaviour, there are periods or methods that can potentially put the resource under high exploitation pressure, while others work as release phases when the fish resources could potentially recover. For example, in the Amazonian region, slash-and-burn cassava agriculture is essential for fishers' subsistence, as cassava flour represents their main source of carbohydrate. They have to share their working time between fishing and planting/harvesting, which may reduce fishing pressure (Silva & Begossi 2009). This was also the case on the Atlantic coast, but continuous regulation by the Brazilian Federal Environmental Agency hampered the slash-and-burn agriculture, which could have increased the fishing pressure. We cannot be sure if that indeed happened, but apparently coastal fishers shifted from agriculture to tourism-related activities as well (Begossi 2006b).

In general, Brazilian fishers, especially those in the Amazonian region, do not seem concerned with conservation per se, but with assuring a steady or increasing use of resources, even if they have to regulate their fishing activities to guarantee future use of resources. This pattern reinforces what the optimisation results have shown here. This is the case of the Amazonian fishing agreements, where lakes are officially closed to outsiders or have their access controlled by local artisanal fishers. In return, fishers have to regulate their own exploitation as well, which can be done by gear regulation,

quotas, seasonal access and even a mix of different measures, which are re-evaluated after a certain period (usually from three to five years) (Lopes *et al.* 2011). By regulating their exploitation fishers can achieve unintentional conservation, as observed also in the Pacific islands (Aswani 1998).

Fisheries management measures, in this case, could use the knowledge obtained from optimal foraging to establish access rules using the observed patterns of behaviour. Some of the fisheries of this study, such as Jarauá and Ebenezer, are well-managed fisheries that embody monitoring processes and adaptive co-management (MacCord *et al.* 2007; Castello *et al.* 2009). For them and based on what we found here, more specific measures could be adopted to protect the fish resources during the high water season, when fishers are already non-optimising and would probably be more willing to accept new regulations. The same idea could be applied for any other village, based on what, when and how fishers are optimising or not optimising their exploitation.

Different fish resources will support different fishing pressures and this also needs to be taken into account. If the biological information of the species exploited is associated to the fisher's behavioural information, better management strategies can be delineated and applied not only in Brazil and not only to artisanal fishers (Bergmann *et al.* 2004; Silvano & Begossi 2005). Simple models, as the one applied here, have shown to be robust enough to help understand human behaviour concerning the use of different resources and at different levels of exploitation.

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