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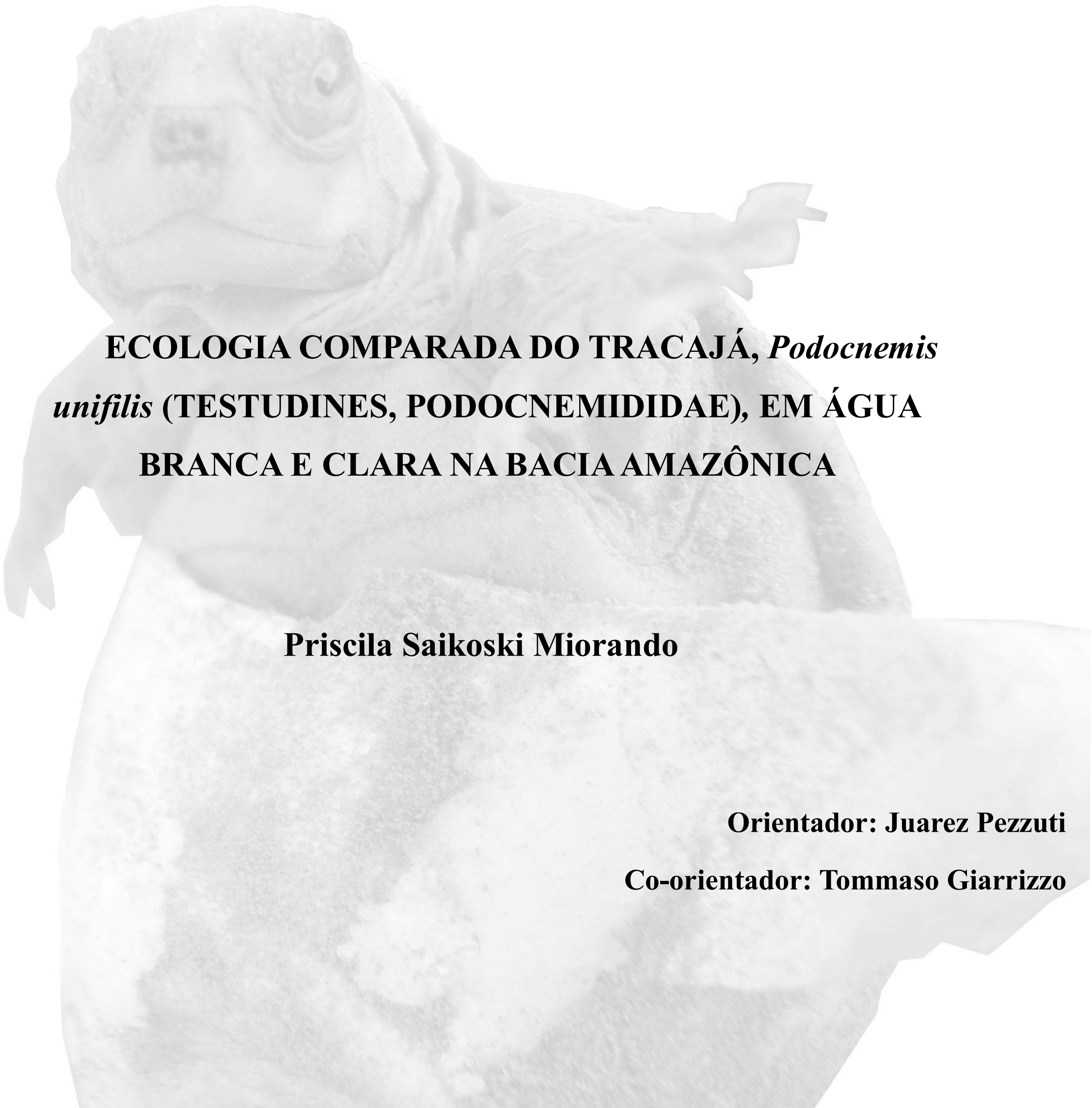

ECOLOGIA COMPARADA DO TRACAJÁ, *Podocnemis unifilis* (TESTUDINES, PODOCNEMIDIDAE), EM ÁGUA BRANCA E CLARA NA BACIA AMAZÔNICA

Priscila Saikoski Miorando

Orientador: Juarez Pezzuti
Co-orientador: Tommaso Giarrizzo

BELÉM

2016

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PRISCILA SAIKOSKI MIORANDO

Ecologia comparada do tracajá, *Podocnemis unifilis,* em água branca e clara na bacia Amazônica (TESTUDINES, PODOCNEMIDIDAE)

Tese apresentada ao Programa de Pós-Graduação em Ecologia Aquática e Pesca da Universidade Federal do Pará como requesito para obtenção do título de Doutora em Ecologia Aquática e Pesca.

Orientador: **Dr. Juarez Carlos Brito Pezzuti**
Co-orientador: **Dr. Tommaso Giarrizzo**

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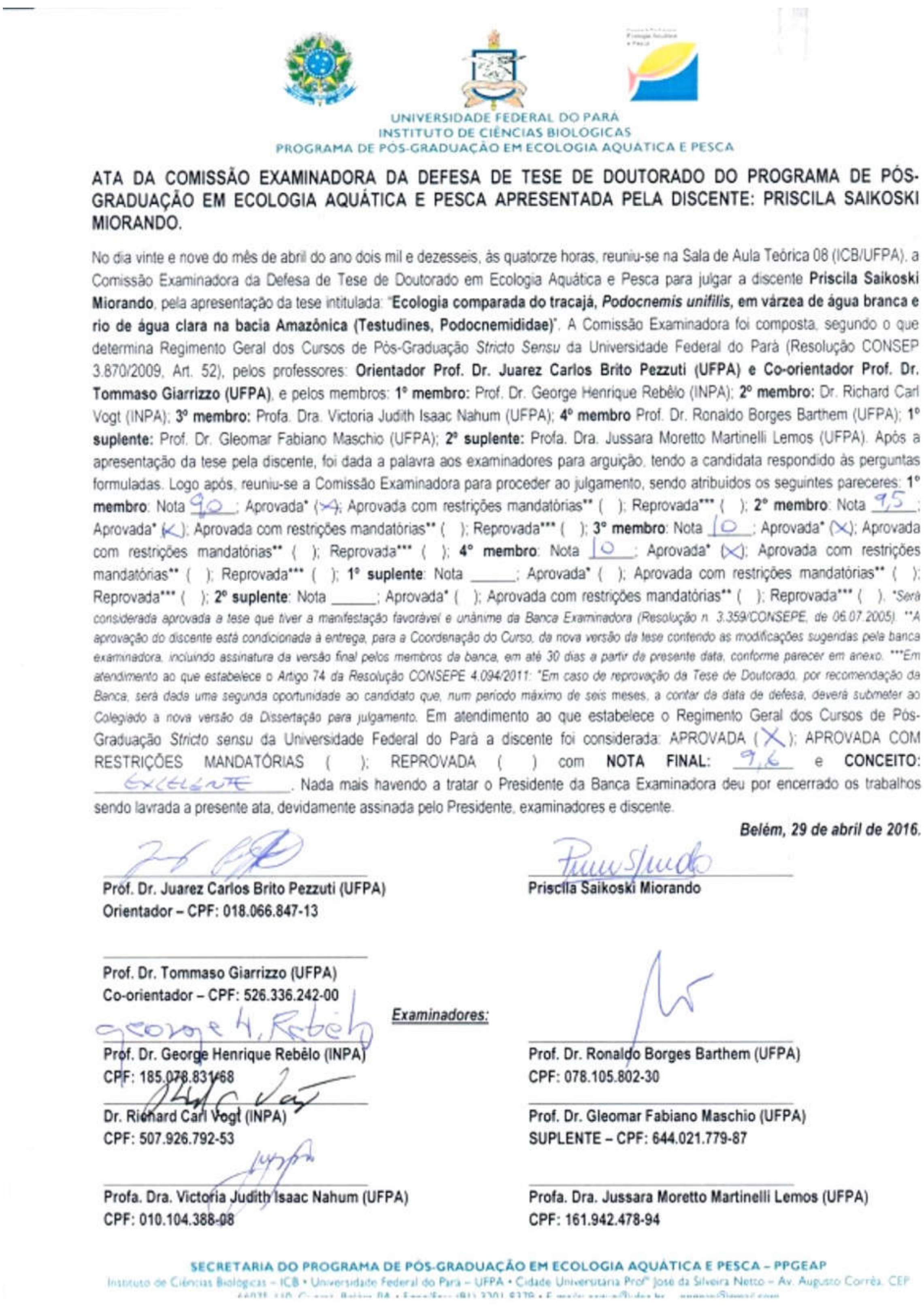

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ATA DA COMISSÃO EXAMINADORA DA DEFESA DE TESE DE DOUTORADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA AQUÁTICA E PESCA APRESENTADA PELA DISCENTE: PRISCILA SAIKOSKI MIORANDO.

No dia vinte e nove do mês de abril do ano dois mil e dezesseis, às quatorze horas, reuniu-se na Sala de Aula Teórica 08 (ICB/UFPA), a Comissão Examinadora da Defesa de Tese de Doutorado em Ecologia Aquática e Pesca para julgar a discente **Priscila Saikoski Miorando**, pela apresentação da tese intitulada: "**Ecologia comparada do tracajá, *Podocnemis unifilis*, em várzea de água branca e rio de água clara na bacia Amazônica (Testudines, Podocnemididae)**". A Comissão Examinadora foi composta, segundo o que determina Regimento Geral dos Cursos de Pós-Graduação *Stricto Sensu* da Universidade Federal do Pará (Resolução CONSEP 3.870/2009, Art. 52), pelos professores: **Orientador Prof. Dr. Juarez Carlos Brito Pezzuti (UFPA) e Co-orientador Prof. Dr. Tommaso Giarrizzo (UFPA)**, e pelos membros: **1º membro:** Prof. Dr. George Henrique Rebêlo (INPA); **2º membro:** Dr. Richard Carl Vogt (INPA); **3º membro:** Profa. Dra. Victoria Judith Isaac Nahum (UFPA); **4º membro** Prof. Dr. Ronaldo Borges Barthem (UFPA); **1º suplente:** Prof. Dr. Gleomar Fabiano Maschio (UFPA); **2º suplente:** Profa. Dra. Jussara Moretto Martinelli Lemos (UFPA). Após a apresentação da tese pela discente, foi dada a palavra aos examinadores para arguição, tendo a candidata respondido às perguntas formuladas. Logo após, reuniu-se a Comissão Examinadora para proceder ao julgamento, sendo atribuídos os seguintes pareceres: **1º membro**: Nota 9,0; Aprovada* (X); Aprovada com restrições mandatórias** ( ); Reprovada*** ( ); **2º membro**: Nota 9,5; Aprovada* (X); Aprovada com restrições mandatórias** ( ); Reprovada*** ( ); **3º membro**: Nota 10; Aprovada* (X); Aprovada com restrições mandatórias** ( ); Reprovada*** ( ); **4º membro**: Nota 10; Aprovada* (X); Aprovada com restrições mandatórias** ( ); Reprovada*** ( ); **1º suplente**: Nota ______; Aprovada* ( ); Aprovada com restrições mandatórias** ( ); Reprovada*** ( ); **2º suplente**: Nota ______; Aprovada* ( ); Aprovada com restrições mandatórias** ( ); Reprovada*** ( ). **Será considerada aprovada a tese que tiver a manifestação favorável e unânime da Banca Examinadora (Resolução n. 3.359/CONSEPE, de 06.07.2005). **A aprovação do discente está condicionada à entrega, para a Coordenação do Curso, da nova versão da tese contendo as modificações sugeridas pela banca examinadora, incluindo assinatura da versão final pelos membros da banca, em até 30 dias a partir da presente data, conforme parecer em anexo. ***Em atendimento ao que estabelece o Artigo 74 da Resolução CONSEPE 4.094/2011: "Em caso de reprovação da Tese de Doutorado, por recomendação da Banca, será dada uma segunda oportunidade ao candidato que, num período máximo de seis meses, a contar da data de defesa, deverá submeter ao Colegiado a nova versão da Dissertação para julgamento.* Em atendimento ao que estabelece o Regimento Geral dos Cursos de Pós-Graduação *Stricto sensu* da Universidade Federal do Pará a discente foi considerada: APROVADA (X); APROVADA COM RESTRIÇÕES MANDATÓRIAS ( ); REPROVADA ( ) com **NOTA FINAL:** 9,6 e **CONCEITO:** EXCELENTE. Nada mais havendo a tratar o Presidente da Banca Examinadora deu por encerrado os trabalhos sendo lavrada a presente ata, devidamente assinada pelo Presidente, examinadores e discente.

Belém, 29 de abril de 2016.

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SECRETARIA DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA AQUÁTICA E PESCA – PPGEAP
Instituto de Ciências Biológicas – ICB • Universidade Federal do Pará – UFPA • Cidade Universitária Profº José da Silveira Netto – Av. Augusto Corrêa, CEP

DEDICATÓRIA

Ao Caio Miorando,

e a todas as crianças, por um futuro

mais amigo da natureza

AGRADECIMENTOS

Esta tese é resultado de uma história iniciada em 2007, quando cheguei a Belém, e que foi possível e gratificante graças a muitas pessoas. **Agradeço a todos!**

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RESUMO

A Amazônia abrange uma diversidade de ambientes aquáticos para os quais as adaptações da fauna ainda são pouco conhecidas. Os quelônios do gênero *Podocnemis* são de grande importância ecológica como elo de ligação entre produtores primários e consumidores de topo de cadeia, e constituem recurso historicamente utilizado na alimentação de povos ribeirinhos. Este estudo teve como objetivo geral comparar aspectos da biologia de *Podocnemis unifilis* entre dois ecossistemas aquáticos distintos da bacia Amazônica: o rio Iriri, rio típico de água clara, e a várzea do baixo Amazonas, de água branca. As populações foram descritas quanto a estrutura de tamanho, razão sexual e proporção de imaturos no contexto socioambiental específico a cada área. Entre as populações, foram comparados: ecologia trófica, tamanho de maturidade sexual, tamanho dos adultos, morfologia da carapaça, e investimento reprodutivo. A população do rio Iriri foi dominada por machos adultos, da qual resultou uma razão sexual de 9,15♂:1♀. Os imaturos representaram 23,6% das capturas. Na várzea, a população foi dominada por fêmeas adultas por 0,51♂:1♀; e a proporção de imaturos foi similar, de 23,9% dos indivíduos capturados. O estudo comparado da ecologia trófica a partir da análise de isótopos estáveis de ^{13}C e ^{15}N mostrou maior amplitude de nicho na várzea do baixo Amazonas, refletindo uma utilização de maior diversidade de fontes autotróficas nesta área. A maturidade foi observada nos machos a partir de 184 mm no rio Iriri e de 177 mm na várzea. Entre as fêmeas, os tamanhos mínimos reprodutivos foram de 318 mm e 301 mm na várzea e no rio Iriri, respectivamente. A morfologia da carapaça diferiu entre os sexos e populações, sendo relativamente mais alta na várzea e mais baixa e larga no rio Iriri. Entre os sexos, as fêmeas tem casco relativamente mais alto e com plastrão mais longo do que machos. Não houve diferença significativa de comprimento de carapaça dos machos adultos entre as populações, mas elas diferiram quanto ao peso. As fêmeas da várzea foram maiores e mais pesadas na várzea do que no rio Iriri. Os ninhos na várzea tiveram, em média, maior número de ovos e biomassa total que no rio Iriri. Contudo, os ovos foram maiores e mais pesados no rio Iriri. Os resultados foram discutidos no contexto da hipótese de condição trófica. O padrão de variação observado nas fêmeas, revelou plasticidade em traços da história de vida que afetam a dinâmica das populações. A ocorrência de variação natural entre populações deve ser levada em consideração na elaboração e avaliação de planos de conservação e uso sustentável para a espécie ao longo de sua distribuição geográfica.

Palavras-Chave: Plasticidade fenotípica; ecologia alimentar; isótopos estáveis; maturidade sexual; reprodução

ABSTRACT

The Amazon covers a variety of aquatic environments for which adaptations of the aquatic fauna are still little known. Turtles of the genus *Podocnemis* are link between primary producers and top consumers in food webs, besides being historically used for food by riverine people. The main objective of this study was to compare biological traits of *P. unifilis* between two distinct aquatic ecosystems in the Amazon basin: the clear water Iriri River, and the white water floodplain at lower Amazon River. Populations were compared regarding trophic ecology, size at maturity, adult size, shell morphology, and reproductive output. Also, populations were described regarding size structure, sex ratio and proportion of immature, which were discussed in the social-environmental context specific to each area. Population of the Iriri river was dominated by adult males, which resulted in a sex ratio of 9,15♂: 1♀. Immature represented 23.6% of captures. In the lower Amazon, population was dominated by adult females by 0,51♂: 1♀; and proportion of immatures was similar, 23.9% of individuals captured. Comparative study of trophic ecology from the analysis of stable isotopes 13C and 15N showed a higher niche breadth in the lower Amazon, reflecting the use of greater diversity of primary producers in this area. Size at sexual maturity of males was 184 mm in the Iriri River, and 177 mm in the lower Amazon. Among females, minimum reproductive sizes were 318 mm and 301 mm in the lower Amazon floodplain and Iriri River, respectively. Shell morphology differed among sexes and populations, being relatively higher, with a more doomed-shape in the lower Amazon. Between sexes, females had a higher carapace and longer plastron than males. Adult males size did not differ between populations, but mean weight was significantly superior in the lower Amazon. Females were significantly larger and heavier in the lower Amazon than in the Iriri River. Clutch size and total clutch mass were higher in the lower Amazon; egg size and mass, however, were greater in the Iriri River. Results were discussed according the better trophic condition hypothesis, that expect individuals with higher growth rates and sizes under better trophic conditions. Population variations observed in this study, mainly on females, revealed plasticity of life-history traits that affect population dynamics. Occurrence of natural variation among populations should be taken into account in the design and evaluation of conservation and sustainable use programs for the species throughout its geographical distribution.

Keywords: phenotypic plasticity; feeding ecology; stable isotopes; sexual maturity; reproduction

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SUMÁRIO

APRESENTAÇÃO DA TESE

Esta tese, intitulada "**Ecologia comparada do tracajá, *Podocnemis unifilis* (Testudines, Podocnemididae), em água branca e clara na bacia Amazônica",** é composta por quatro capítulos, sendo o primeiro introdutório conforme previsto no regimento interno do Programa de Pós-Graduação em Ecologia Aquática e Pesca (PPGEAP). Os demais capítulos correspondem a artigos científicos redigidos na língua inglesa que tiveram como objetivo descrever a estrutura das populações nos distintos contextos socioambientais (Capítulos 2 e 3), e compreender a plasticidade de *P. unifilis* quanto a ecologia trófica e aos parâmetros de tamanho de maturidade sexual, tamanho corpóreo dos adultos, morfologia da carapaça e investimento reprodutivo entre uma população de várzea de água branca e uma de rio de água clara na Amazônia.

O Capítulo 2 descreveu a população de *P. unifilis* no rio Iriri em seu trecho interno a Estação Ecológica Terra do Meio (ESECTM). Foram descritas a distribuição de tamanho em comprimento de carapaça, a razão sexual e a proporção de imaturos capturados. Adicionalmente, foram estabelecidas relações morfométricas que permitem as estimativas de estrutura de tamanho e biomassa a partir de uma única medida morfológica de animais vivos ou de partes remanescentes pós-consumo (como carapaça, plastrão e cabeça). O capítulo foi publicado em 2015 como artigo científico no periódico Anais da Academia Brasileira de Ciências (Qualis B2) sob o título "**Population structure and allometry of *Podocnemis unifilis* (Testudines, Podocnemididae) in a protected area upstream Belo Monte dam in Xingu River, Brazil**".

O Capítulo 3 descreveu a população de *P. unifilis* na várzea do Baixo Amazonas, em uma comunidade ribeirinha que cumpre com um Acordo de Pesca e protege uma área de Reserva com praia de desova em seu território desde 1990. Foram apresentados os resultados de variação da estrutura de tamanho e razão sexual dos indivíduos capturados com diferentes métodos; e a variação populacional entre anos utilizando o método de captura mais adequado para o monitoramento da população adulta. O capítulo está formatado para submissão ao periódico Oryx (Qualis B1) sob o título **"Population of the vulnerable yellow-spotted river turtle, *Podocnemis unifilis*, under community-based management in the lower Amazon floodplain, Brazil"**.

O capítulo 4 analisou a plasticidade trófica e dos parâmetros de tamanho de maturidade sexual, tamanho corpóreo adulto, morfologia da carapaça e investimento reprodutivo entre as duas populações descritas nos capítulos anteriores. O capítulo está formatado para submissão ao periódico Hydrobiologia (A2) sob o título "**Trophic plasticity and life-history traits variation of the river turtle *Podocnemis unifilis* between water types in the Amazon basin (Testudines, Podocnemididae)**".

CAPÍTULO 1

CAPÍTULO INTEGRADOR

1.1 INTRODUÇÃO GERAL

Pressões seletivas distintas ao longo do gradiente ambiental na área de distribuição de uma espécie são capazes de provocar plasticidade de traços morfológicos, fisiológicos, comportamentais e outros entre organismos de populações distintas. É improvável considerar que um único fenótipo apresente alto *fitness*[1] sob condições ambientais com pressões seletivas distintas (VIA et al., 1995). A plasticidade fenotípica constitui, assim, um mecanismo capaz de aumentar o *fitness* dos organismos e de gerar novidades evolutivas em ambientes distintos, permitindo maior persistência das populações, distribuições geográficas mais amplas e redução da vulnerabilidade a extinção frente a alterações ambientais (AGRAWAL, 2001; WHITMAN; AGRAWAL, 2009).

A importância da variação morfológica nos processos evolutivos que geram a biodiversidade desperta o interesse científico desde os tempos de Darwin. A plasticidade fenotípica levanta inúmeras questões fascinantes para a compreensão da evolução, da relação genótipo-ambiente e do desenvolvimento dos organismos (STEARNS, 1989; VIA et al., 1995). Além destas, em tempos de crescente degradação ambiental, é urgente compreender também seus impactos ecológicos, que podem ser observados em escala populacional, de comunidade ou mesmo do funcionamento dos ecossistemas (MINER et al., 2005). Em nível populacional, o estudo da plasticidade entre habitats e regiões geográficas distintas permite compreender as adaptações de uma espécie sob condições ambientais distintas e suas implicações sobre a dinâmica das populações (MINER et al., 2005).

O tamanho corpóreo é uma característica central na ecologia dos organismos, influenciando parâmetros da dinâmica das populações, tais como a sobrevivência (vulnerabilidade a predação) e a fecundidade (STEARNS, 1992). Em quelônios, animais caracterizados por uma carapaça rígida que não expande para a acomodação dos ovários em expansão, o tamanho corpóreo tem importante efeito na quantidade e tamanho dos ovos e filhotes produzidos pelas fêmeas em diversos taxons (CONGDON et al., 1983; VALENZUELA, 2001; BONACH et al., 2006; LITZGUS; MOUSSEAU, 2006; RYAN; LINDEMAN, 2007; ROLLINSON; BROOKS, 2008). O tamanho corpóreo atingido pelos adultos é relacionado ao tamanho de maturidade sexual, com o sexo de menor porte atingindo a maturidade mais cedo e com menor tamanho do que o sexo de maior porte (BERRY; SHINE, 1980; GIBBONS; LOVICH, 1990). Espécies de água doce com hábito mais nadador ativo seguem um padrão com fêmeas maiores que os machos; enquanto machos maiores ou ausência de dimorfismo

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[1] *Fitness* é definido como o valor adaptativo de um fenótipo, medido pelo sucesso reprodutivo que permite a perpetuação do seu pool gênico na população.

sexual de tamanho são mais observadas nas espécies de hábito semiaquático ou mais caminhadoras de fundo ("*bottom-walking*") (MOLL; MOLL, 2004). É sugerido que o dimorfismo com machos maiores evoluiu nas espécies onde interações competitivas na disputa por fêmeas ocorram com maior frequência; enquanto o dimorfismo com fêmeas maiores seja selecionado por aumentar a quantidade ou tamanho dos ovos (*Fecundity Advantage Hypothesis*) (BERRY; SHINE, 1980). O tamanho de maturidade sexual, portanto, é uma característica comumente plástica entre os sexos (BERRY; SHINE, 1980), e que também pode variar entre populações (TINKLE, 1961; GIBBONS et al., 1981).

Qualquer fator ambiental - biótico ou abiótico - pode promover plasticidade de uma ou mais características dos organismos (FORSMAN, 2014). Em quelônios de água doce, são documentadas variações populacionais de forma em função do tipo de ambiente, com a carapaça mais achatada (hidrodinâmica) em ambientes lóticos, e mais alta e ovalada em ambientes lênticos (LUBKE; WILSON, 2007; RIVERA, 2008; STAYTON, 2011). O tamanho corpóreo e investimento reprodutivo, contudo, são os traços cujas variações foram mais pesquisadas, especialmente ao longo do gradiente latitudinal na América do Norte. Em espécies das Famílias Kinosternidae e Emydidae, populações do norte apresentam fêmeas maiores que produzem ninhadas maiores, porém com ovos menores que as populações do sul (TINKLE, 1961; IVERSON; SMITH, 1993; LITZGUS; MOUSSEAU, 2006). Estas, por outro lado, desfrutam de um período reprodutivo mais longo, o que permite às fêmeas aumentarem o número de ninhadas produzidas por ano (GIBBONS, 1982; LITZGUS; MOUSSEAU, 2003). Os autores sugeriram que tal padrão reflita adaptações a maior taxa de mortalidade nos extremos de temperatura e ao período reprodutivo mais curto aos quais estão submetidas as populações do norte.

Em outras escalas geográficas, a plasticidade de tamanho e demais traços a ele associados foi sugerida em função de condições locais de produtividade (IVERSON; SMITH, 1993; LEFEBVRE et al., 2011) e pressão antrópica (CLOSE; SEIGEL, 1997). A diferença de produtividade foi sugerida para explicar variações geográficas em espécies das Famílias Emydidae nos Estados Unidos, *Graptemys ouachitensis* (Moll, 1976), *Emydoidea blandingii* (GRAHAM; DOYLE, 1977), *Actinemys marmorata* (BURY et al., 2010); e Chelidae na Austrália, *Emydura macquarii macquarii* (JUDGE, 2001). Nestes, os locais considerados mais produtivos proporcionaram maior crescimento dos juvenis ou de ambos, adultos e juvenis, o que acarretou em variação populacional do tamanho dos adultos em todas as espécies acima citadas, com exceção de *G. ouachitensis* (MOLL, 1976).

A Amazônia abrange uma diversidade de ambientes aquáticos para os quais as adaptações da fauna ainda são pouco conhecidas. O clima na região é quente e úmido, com a sazonalidade marcada pelo regime de chuvas com um período chuvoso e um seco que se alternam ao longo do ano (SIOLI, 1984; ALVARES et al., 2014). Os corpos aquáticos variam fundamentalmente entre as sub-bacias em função do tipo de água que apresentam: branca, clara ou preta (SIOLI, 1984). Os diferentes tipos da água refletem variações de geomorfologia, características físico-químicas e vegetação associada às nascentes e à área de drenagem dos distintos rios amazônicos. Os rios de águas claras têm origem em antigos maciços cristalinos que sofrem baixa erosão, conferindo à água alta transparência, especialmente na estação seca. As águas claras têm pH variado entre neutro e pouco ácido, e a baixa quantidade de sedimentos e nutrientes resulta em sistemas com menor produtividade do que os de água branca (SIOLI, 1984). O baixo nível de nutrientes na água é considerado o fator limitante para o desenvolvimento da maioria das macrófitas flutuantes nestes ambientes (JUNK et al., 2011). As águas brancas têm origem Andina ou pré-Andina, apresentam pH próximo a neutro (6,6 – 7,0) e carregam grande quantidade de sedimento e nutrientes essenciais como nitrogênio e fósforo para as várzeas, o que acarreta em baixa transparência e, apesar disso, na maior produtividade primária dentre os ambientes aquáticos amazônicos (SIOLI, 1984; JUNK et al., 2011).

A maior quantidade de nitrogênio, fósforo e partículas em suspensão favorece a produtividade de fitoplâncton e a ocorrência de vastos bancos de macrófitas flutuantes na água branca (JUNK; PIEDADE, 1997), base da cadeia trófica que sustenta a comunidade de peixes e outros vertebrados aquáticos. Para os quelônios do gênero *Podocnemis*, cujos principais alimentos são de origem vegetal (RUEDA-ALMONACID et al., 2007), as diferenças de produtividade primária entre os distintos tipos de água da Amazônia supostamente influenciam a disponibilidade e qualidade dos alimentos e, consequentemente, a taxa de crescimento, tamanho de maturidade sexual, tamanho corpóreo dos adultos e, por fim, a produção de ovos pelas fêmeas devido a alometria reprodutiva existente (VALENZUELA, 2001; BONACH et al., 2006; PIGNATI; PEZZUTI, 2012). Assim, estudos comparativos da ecologia trófica da espécie podem revelar como as populações utilizam as distintas fontes vegetais disponíveis, e ajudar a compreender as relações tróficas dos quelônios nos distintos ambientes amazônicos.

Os quelônios *Podocnemis* spp. constituem historicamente uma importante fonte de alimento para o sustento dos povos ribeirinhos (BATES, 1892). Após a colonização europeia, o forte aumento da pressão com a demanda mercantil levou *P. expansa* a drásticos declínios populacionais, e provocou o redirecionamento da pressão sobre *P. unifilis* (MITTERMEIER, 1978; SMITH, 1979). Ambas continuam a ser amplamente exploradas em suas áreas de ocorrência (KEMENES; PEZZUTI, 2007; PEZZUTI et al., 2010; PANTOJA-LIMA et al., 2014). Além da exploração direta, os quelônios estão crescentemente ameaçados pela alteração e destruição de habitat devido a construção de grandes barragens hidrelétricas nos rios amazônicos (FEARNSIDE, 2016), que ameaçam as áreas de alimentação, reprodução e nos padrões de deslocamento e rotas migratórias (MOLL; MOLL, 2004).

O tracajá, *Podocnemis unifilis*

Podocnemis unifilis é uma espécie de ampla distribuição geográfica nas bacias dos rios Orinoco, Solimões-Amazonas e Tocantins-Araguaia, habitando do alto ao baixo curso dos rios de águas brancas, claras e pretas e suas planícies alagadas. É caracterizada pela presença de apenas uma barbela sob o maxilar (o que dá o nome da espécie *unifilis*), mas esse caractere pode variar e são encontrados indivíduos com o padrão do gênero com duas barbelas (RUEDA-ALMONACID et al., 2007). Apresenta manchas amarelas na cabeça, que são mantidas nos machos, mas perdidas nas fêmeas durante seu desenvolvimento (Figura 1). Espécie de tamanho médio para o gênero, caracterizada por dimorfismo sexual de tamanho com os machos alcançando até 33,5 cm de comprimento de carapaça e as fêmeas até 50 cm (PRITCHARD; TREBBAU, 1984; RUEDA-ALMONACID et al., 2007). A espécie é classificada na IUCN como "Vulnerável", necessitando atualização (IUCN, 2011)

Informações sobre aspectos reprodutivos são abundantes para a espécie (FACHÍN-TERÁN; VON MÜLHEN, 2003; HALLER; RODRIGUES, 2005; PANTOJA-LIMA et al., 2009; FERREIRA-JR; CASTRO, 2010; PIGNATI et al., 2013a; 2013b). VANZOLINI (2003), em uma análise comparativa entre populações, constatou diferenças geográficas no tamanho médio das ninhadas e no volume dos ovos em *P. unifilis* e *P. expansa*. No mesmo ano, FACHÍN-TERÁN; VON MÜLHEN (2003) apresentaram uma discussão sobre a variação geográfica do número médio de ovos por ninho indicando que os maiores valores foram observados em áreas de várzea de água branca, e sugeriram que a alta produtividade das águas provenientes dos Andes possa ter um efeito positivo sobre o investimento reprodutivo de *P. unfiilis.*

A quantidade e tamanho dos ovos produzidos são influenciados pelo tamanho da fêmea em *Podocnemis* (PIGNATI; PEZZUTI, 2012). A variação geográfica dos dados reprodutivos apresentados em VANZOLINI (2003) provém, muito possivelmente, de uma variação geográfica de tamanho das fêmeas entre estas áreas, para as quais havia poucos dados disponíveis (VANZOLINI, 2003). Variação de tamanho pode ser percebida entre populações com fêmeas relativamente maiores descritas na Amazônia peruana e colombiana (PRITCHARD; TREBBAU, 1984), no rio Guaporé (FACHÍN-TERÁN; VOGT, 2004), e várzea do baixo Amazonas (Capítulo 2 nesta tese); e fêmeas menores nos *llanos* venezuelanos e colombianos (PRITCHARD; TREBBAU, 1984; THORBJARNARSON et al., 1993), e nos rios Xingu (ALCÂNTARA et al., 2013), Iriri (MIORANDO et al., 2015), e Tocantins no reservatório da UHE de Tucuruí (FÉLIX-SILVA, 2009). O tamanho de maturidade, especialmente de machos, não é conhecido para a espécie; sendo as populações descritas a partir de medidas arbitrárias (FACHÍN-TERÁN e VOGT, 2004; CHACÍN, 2010) ou sem considerar o tamanho de maturidade (FÉLIX-SILVA, 2009; ALCÂNTARA et al., 2013).

A dieta da espécie é primariamente herbívora com hábito oportunista, sendo comum a ingestão de material de origem animal (FACHÍN-TERÁN et al., 1995; BALENSIEFER; VOGT, 2006). Os estudos contrastam quanto à existência de variação entre os sexos, observada por FACHÍN-TERÁN et al. (1995) no rio Guaporé, mas não por BALENSIEFER; VOGT (2006) na várzea da Reserva de Desenvolvimento Sustentável Mamirauá. Diferenças de dieta em função da disponibilidade de alimento em cada ecossistema amazônico não foram descritas. Sendo oportunista, a variação na disponibilidade de alimento entre os distintos ecossistemas amazônicos provavelmente influencia na dieta da espécie entre populações dentro de sua distribuição geográfica. A área de vida de *P. unifilis* é relativamente restrita (BOCK et al., 1998; LEÃO, 2015) comparada às demais espécies do gênero (FACHÍN-TERÁN et al., 2006; CARNEIRO et al., 2015), o que reforça a possibilidade de populações próximas serem unidades demográficas independentes que demandam programas de manejo específicos, sendo necessário cautela para generalizações a partir de dados coletados em apenas uma localidade. Compreender as variações populacionais de *P. unifilis* relacionadas à diversidade de ambientes aquáticos na Amazônia é um importante passo rumo ao estabelecimento de estratégias de conservação e uso sustentável que atendam às características específicas de cada uma e proporcionem a permanência do maior número de populações ao longo da área de ocorrência da espécie.

Figura 1. *Podocnemis unifilis* (A) juvenil, (B) macho adulto, e (C) fêmea adulta.

1.1.1 Objetivo geral

Investigar variações populacionais de ecologia trófica, maturidade sexual, tamanho corpóreo, morfologia e biologia reprodutiva de *Podocnemis unifilis* em função da variação ambiental entre dois dos ecossistemas aquáticos amazônicos: a várzea do baixo rio Amazonas, sistema típico de águas brancas; e o rio Iriri, rio de correnteza típico de águas claras. Foram testadas as hipóteses de que i) a população residente na várzea aproveita maior disponibilidade de alimento, o que acarreta em adultos maiores, atingindo a maturidade sexual com maior tamanho, e fêmeas produzindo ninhadas maiores (em biomassa) neste ambiente do que no rio Iriri; ii) as populações apresentam variação morfológica como adaptação às distintas pressões bióticas e abióticas a que os indivíduos estão submetidos em cada ecossistema.

1.1.2 Objetivos específicos

- Descrever a estrutura de tamanho e razão sexual da população de *P. unfilis* na Estação Ecológica Terra do Meio, Unidade de Conservação de Proteção Integral que abrange um sistema típico de água clara na bacia amazônica; e, estabelecer relações morfométricas e de peso-comprimento que permitam estimativas da estrutura de tamanho e biomassa de animais consumidos a partir de medidas obtidas de partes do corpo encontradas pós-consumo (Capítulo 2);
- Descrever a estrutura de tamanho e razão sexual da população de *P. unfilis* sob condição de manejo comunitário em lago no baixo Amazonas, sistema típico de várzea de água branca na bacia amazônica, e estabelecer relações morfométricas e de peso-comprimento específicas para esta população que simplifiquem a coleta de dados para monitoramento participativo da população manejada e de animais consumidos na comunidade (Capítulo 3);
- Elucidar a ecologia trófica (amplitude de nicho) de *P. unifilis* de forma comparativa entre as populações através da análise de isótopos estáveis de Carbono e Nitrogênio (Capítulo 4);
- Estabelecer o tamanho de maturidade sexual de machos e fêmeas das duas populações (Capítulo 4);
- Testar diferenças na distribuição de tamanho de machos e fêmeas entre as populações (Capítulo 4);
- Testar por diferenças na morfologia da carapaça entre os sexos e populações (Capítulo 4);
- Testar diferenças de investimento reprodutivo entre as populações a partir do número de ovos por ninho, tamanho e massa dos ovos, e massa total das ninhadas (Capítulo 4).

1.2 ÁREA DE ESTUDO

O estudo foi realizado em duas áreas com ecossistemas distintos na bacia amazônica: o rio Iriri, sistema típico de água clara; e a várzea do baixo rio Amazonas, sistema de água branca. Especificamente, foram amostrados o trecho do rio Iriri no interior da Estação Ecológica Terra do Meio – ESECTM, e o território da comunidade Água Preta na várzea de Santarém; ambos no Estado do Pará (Figura 2). Os ambientes aquáticos de ambas as áreas variam em função do regime sazonal de chuvas, dinâmica de pulso de inundação descrita para toda a bacia Amazônica (JUNK et al., 1989)

O Rio Iriri tem suas nascentes na serra do Cachimbo e percorre cerca de 900 km até desaguar na margem esquerda do rio Xingu, no Estado do Pará. A ESECTM se localiza em uma área de clima tropical de monção, com temperatura média anual acima dos 26ºC (ALVARES et al., 2013). O período de chuvas ocorre de dezembro a maio, com média de 350 mm mensais; enquanto o período seco ocorre de junho a novembro, com média de 30 mm mensais. O nível do rio Iriri pode variar entre quatro e oito metros entre a seca e a cheia. Durante a cheia, a floresta de igapó das margens e vegetação das ilhas ficam inundadas (Figura 3A) disponibilizando alimento para a fauna aquática. Na seca, emergem inúmeras ilhas de tamanhos variados no leito do rio, cobertas predominantemente por vegetação herbácea, arbustiva e arbórea de pequeno porte, enquanto as margens são cobertas por floresta ombrófila aluvial (Figura 3B-C) (MMA-ICMBio, 2015).

Na região do baixo Amazonas, a várzea alcança 40 km de largura e é caracterizada por terrenos aluviais planos e baixos, não ultrapassando 20 metros de altitude, incluindo muitas ilhas extensas com lagos interiores (Figura 4A). O clima é do tipo tropical de monção, quente e úmido, com temperatura média anual acima de 26ºC e pluviosidade anual entre 1,900 e 2,200 mm. O regime de chuvas varia entre 60 mm mensais na estação seca (junho-dezembro), e até 300 mm mensais na estação chuvosa (janeiro-maio) (ALVARES et al., 2014). O nível das águas sofre uma flutuação de aproximadamente seis metros entre as estações cheia e seca nesta região. As áreas de terras mais altas são cobertas por florestas de galeria, enquanto nas terras baixas predominam as gramíneas flutuantes (MCGRATH et al., 1993; JUNK et al., 2011). Durante a cheia, tudo exceto as restingas mais altas se encontra submerso (Figura 4B); enquanto na seca, apenas os canais e lagos mais profundos não ficam reduzidos a poças de lama isoladas (MCGRATH et al., 1993) (Figura 4C).

A gestão territorial e o contexto social são muito distintos entre as áreas, mas ambas apresentam práticas de conservação que, teoricamente, favorecem a manutenção das populações de *Podocnemis unifilis* nas áreas. O rio Iriri se localiza em um território conhecido como Terra do Meio, área que compreende o maior maciço de Áreas Protegidas (Terras Indígenas e Unidades de

Conservação) no Estado do Pará. A ESECTM é uma Unidade de Conservação (UC) de Proteção Integral criada em 17 de fevereiro de 2005 abrangendo uma área de 3.372.111 ha nos municípios de Altamira e São Félix do Xingu. A população ribeirinha residente ao longo dos aproximadamente 200 km do rio Iriri na ESECTM se distribui em 15 núcleos familiares remanescentes das atividades nos seringais e mineração que ocorreram na região antes da criação da UC. Esta ainda enfrenta problemas fundiários e ambientais relacionados a presença de fazendas, grilagem e invasões para assentamento (MMA-ICMBio, 2015).

A região do baixo Amazonas, por sua vez, é ocupada por comunidades ribeirinhas que tem a pesca como principal atividade econômica, consorciada com agricultura e pecuária de pequena escala durante a estação seca (MCGRATH et al., 1993). A região teve importante participação no processo de institucionalização do atual sistema de co-manejo de pesca baseado nos Acordos de Pesca, amplamente adotados na Amazônia (MCGRATH et al*.,* 1993; CASTRO; MCGRATH, 2003). Atualmente, o baixo Amazonas apresenta um contexto fundiário peculiar na várzea amazônica. A região foi contemplada com a criação dos Projetos de Assentamento Agroextrativistas (PAE) no âmbito da Reforma Agrária promovida pelo INCRA em 2006 (MCGRATH et al., 2008). Esta categoria de assentamento "*destina-se à exploração de áreas dotadas de riquezas extrativas, por meio de atividades economicamente viáveis, socialmente justas e ecologicamente sustentáveis"* (INCRA 2010). O regime de concessão e usufruto das terras é coletivo, passado para as comunidades mediante um Plano de Utilização (PU) que contemplou os Acordos de Pesca previamente estabelecidos em cada região e formalmente proibiu o uso, mesmo para consumo, das demais espécies da fauna. No entanto, sem atividade de fiscalização por parte dos órgãos competentes, a exploração dos recursos fica, na prática, a critério de regras informais particulares a cada comunidade.

A comunidade Água Preta situa-se no PAE Aritapera e abriga cerca de 60 famílias. O manejo da pesca é controlado pelas regras do Acordo de Pesca preexistente (IN 11, de 14/10/2004; Anexo I). Além das regras de pesca, em 1991, uma área de Reserva (como eles a denominam) de aproximadamente 8 km^2 foi estabelecida por decisão comunitária com o objetivo de proteger uma área de desova de quelônios e canais com partes mais profundas onde peixes e quelônios se concentram durante a seca (PIGNATI et al., 2013). Dentro da Reserva, a pesca, coleta de ovos e demais atividades produtivas são proibidas. Fora dos limites da Reserva, a comunidade informalmente permite a coleta de tartarugas e ovos para consumo. Em ambas as áreas de estudo, o consumo de quelônios existe, mas as ações de conservação iniciadas há cerca de 25 anos na várzea e há 10 anos na EETM proporcionaram populações abundantes.

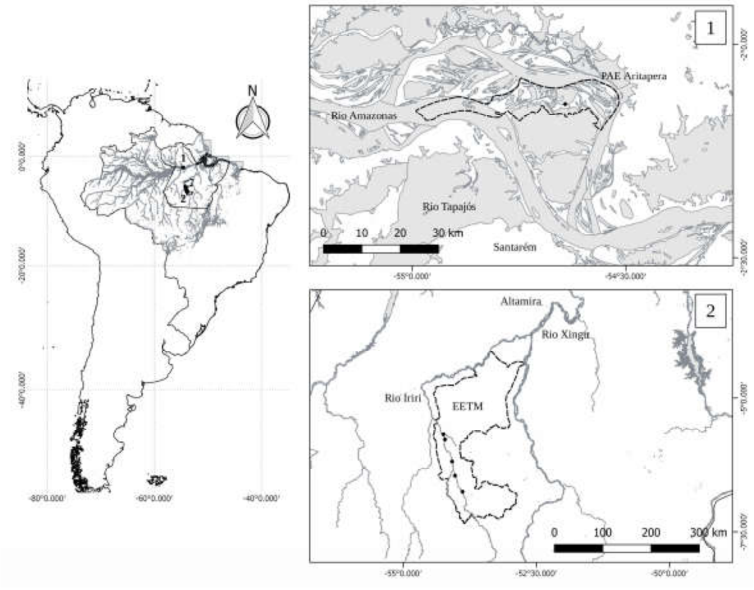

Figura 2. Áreas de estudo: (1) comunidade Água Preta (●) no Projeto de Assentamento Agroextrativista (PAE) Aritapera, várzea de Santarém, baixo rio Amazonas; e (2) pontos de coleta (●) no rio Iriri na Estação Ecológica Terra do Meio (EETM).

Figura 3. Rio Iriri, Altamira - PA. (A) cheia - maio de 2013; (B) vista aérea em agosto de 2012; (C) ambientes de pedrais, corredeiras e praias típicos da seca.

Figura 4. Várzea do baixo Amazonas, Santarém - PA. (A) vista aérea em janeiro de 2015; *localização da área de desova protegida pela comunidade Água Preta; (B) floresta alagada na cheia; (C) praia de substrato fino em canal de ligação entre lagos na seca.

1.3 DESENHO AMOSTRAL

1.3.1 Captura e biometria

A coleta de dados para descrever a estrutura populacional foi realizada de forma diferenciada entre as áreas de estudo. No rio Iriri, foram realizadas campanhas para captura na seca de 2012 (agosto e outubro) e estações cheia (maio) e seca de 2013 (agosto e outubro). Na várzea do baixo Amazonas, atividade de captura foi realizada na seca de 2009 (novembro e dezembro), e seca de 2014 (novembro). A captura foi realizada utilizando técnicas locais de captura eficientes nos ambientes específicos a cada área de estudo.

No rio Iriri, foram utilizadas as técnicas de captura “puçá” ou “landau” e “pulo” nas estações seca e cheia. Ambos os métodos são ativos com perseguição dos animais após sua visualização na superfície da água. O pulo consiste, literalmente, em pular da embarcação e perseguir o animal para sua captura na água (Figura 5A), procedimento realizado durante o dia preferencialmente nos horários mais quentes. O puçá de mão consiste em uma pequena rede em uma armação circular de metal que é utilizada para captura dos animais observados na superfície (Figura 5B). Esta técnica é principalmente utilizada à noite, combinado a um holofote que permite a visualização dos animais e provoca ofuscamento temporário nos mesmos, o que facilita a captura.

Na várzea de Santarém, foram utilizadas técnicas típicas de pesca – redes malhadeiras e tarrafa – e uma técnica local de alto rendimento que era utilizada para captura comercial de quelônios, o puçá. Este consiste em uma rede em forma de funil, sem pesos, que é amarrada em uma armação de madeira e arrastado na lateral de uma embarcação com motor de centro (Figura 6A) ou entre duas canoas com motor regional do tipo rabeta (Figura 6B). O método pode ser aplicado tanto de dia quanto à noite. A armação de madeira é móvel, permitindo que a rede seja posicionada com a abertura na superfície da água, via pela qual os animais podem ser retirados (Figura 6C). Em comum, as técnicas ativas do rio Iriri e do puçá na várzea utilizam a visualização dos animais na superfície da água como ponto de partida para a captura e o conhecimento de que o barulho de motor na água provoca que mais animais subam para a superfície.

Os animais capturados tiveram o sexo identificado por características sexuais secundárias como o tamanho da cauda e coloração cefálica (PRITCHARD; TREBBAU, 1984), foram marcados individualmente por cortes nos escudos marginais, e mensurados quanto a: comprimento curvilíneo da carapaça; comprimento reto da carapaça, largura da carapaça, altura da carapaça, comprimento máximo do plastrão, largura da cabeça e peso. As populações foram descritas quanto à distribuição de tamanho em classes de 20 mm, razão sexual e proporção de imaturos em função dos tamanhos de maturidade determinados neste estudo conforme tópico a seguir. As medidas morfométricas retilíneas foram analisados por método multivariado de ordenação (Análise Canônica de Coordenadas Principais - CAP) para verificação de existência de variação na morfologia da carapaça entre os sexos e áreas de estudo. Os dados de tamanho e peso foram comparadas entre populações por Análise de Variância Permutacional Univariada. Análises de dados específicas a cada população estão descritas nos respectivos capítulos.

Figura 5. Métodos de captura de *P. unifilis* no rio Iriri, Estação Ecológica Terra do Meio. (A) Pulo em outubro de 2012; (B) puçá de mão em agosto de 2013

Figura 6. Método de captura de *P. unifilis* na várzea do baixo Amazonas, comunidade Água Preta: puçá utilizado (A) na lateral de embarcação com motor de centro; (B) entre duas canoas com motor rabeta; e (C) puçá posicionado para retirada dos animais capturados.

1.3.2 Estudo da ecologia trófica por análise de isótopos estáveis de Carbono e Nitrogênio

Os isótopos estáveis são traçadores naturais representados por átomos enriquecidos com nêutrons que se estabilizam com níveis de valência diferentes, produzidos como consequência de processos metabólicos e fenômenos energéticos naturais. Estes elementos possuem um peso atômico maior que seu semelhante não estável, apresentando maior tempo de permanência nos tecidos. O uso de isótopos estáveis como traçadores biológicos é baseado na premissa de que as razões isotópicas são conservativas e que a combinação de distintas fontes determina o fluxo de nutrientes entre os organismos produtores, consumidores e decompositores (PETERSON; FRY, 1987). Assim, inferências sobre o nicho trófico de um organismo a partir da relação entre o isótopo mais pesado e o mais leve (notação δ) de $\delta^{13}C$ e $\delta^{15}N$ são possíveis porque a composição isotópica nos tecidos corporais dos consumidores é derivada do conjunto de itens de sua dieta (PETERSON; FRY, 1987).

Medidas de $\delta^{15}N$ são indicadoras do nível trófico de um organismo, pois há um aumento progressivo de ^{15}N com o aumento do nível trófico devido à retenção deste isótopo no corpo dos animais durante a excreção, o que gera valores de $\delta^{15}N$ nos tecidos animais geralmente enriquecidos de 3 a 5‰ quando comparados às suas fontes de alimento (PETERSON; FRY, 1987; VANDER-ZANDEN; RASMUSSEN, 1999). A assinatura do $\delta^{13}C$, por sua vez, permite distinguir as fontes de alimento assimiladas por um consumidor mais precisamente do que $\delta^{15}N$, pois seu valor sofre menor mudança, entre 0.5 e 2‰, conforme o ^{13}C percorre a cadeia trófica (CAUT et al*.,* 2009). A diferenciação das fontes autotróficas pode ser realizada devido ao posicionamento natural das plantas em diferentes categorias isotópicas como resultado da variação de fracionamento entre as vias fotossintéticas (LOPES; BENEDITO-CECÍLIO, 2002). Em quelônios do gênero *Podocnemis,* a técnica já foi utilizada para verificar diferença de dieta entre as espécies *P. unifilis* e *P. expansa* no baixo rio Araguaia (LARA et al., 2012), e este estudo é o primeiro a utilizar a técnica para verificar variação populacional.

Amostras de pele foram retiradas da extremidade das patas posteriores de 44 animais no rio Iriri (20M:24F), e de 65 no baixo Amazonas (36M:29F) durante as estações de seca e cheia. O comprimento retilíneo de carapaça médio (dp; mín-máx) dos machos foi de 227.27 mm (dp = 39.1; 93.5 – 275) no rio Iriri, e de 218.19 mm (dp = 42.63; 106 – 290) no baixo Amazonas. As fêmeas amostradas no rio Iriri mediram, em média, 266.26 mm (dp = 59.44; 112.2 – 375), e no baixo Amazonas, em média, 281.79 mm (dp = 88.16; 111 – 434). Após a retirada, as amostras foram congeladas para transporte ao laboratório de Biologia Pesqueira e Manejo dos Recursos Aquáticos/UFPA. Neste, o processamento das amostras consistiu em i) limpeza mecânica com auxílio de escova em água destilada; ii) extração de lipídios em um sistema de três banhos, com 24hs de duração cada, em mistura 2:1 de clorofórmio:metanol, finalizado com lavagem em água destilada; iii) secagem em estufa a 50°.C por 24 horas; iv) fragmentação em pequenos pedaços com auxílio de bisturi; e v) pesagem de uma subamostra de 0.9 mg para encapsulamento em cápsulas (*tin cap*) de estanho. Estas foram dispostas em bandejas próprias identificadas, e enviadas ao Centro de Isótopos Estáveis da Universidade do Novo México, onde foram analisadas em um Analisador Elementar Costech ECS 4010 acoplado a um espectrômetro de massa ThermoFisher Scientific Delta V Advantage via interface CONFLO IV. Os valores da assinatura dos isótopos estáveis são expressas pela notação delta (δ), definida como o desvio em partes por mil (‰) de uma amostra em relação a uma referência padrão, conforme a fórmula geral para um isótopo R, onde o δ se refere a razão do isótopo pesado em relação ao leve: $\delta R = [(R_{amostra}/R_{referência}) - 1]*1000$. Os padrões internacionalmente considerados são Vienna Peedee Belemnite limestone (V-PDB) para carbono e N2 atmosférico para nitrogênio.

Os dados de $\delta^{13}C$ e $\delta^{15}N$ foram comparados entre populações através de uma Análise de Variância Permutacional Univariada. As assinaturas isotópicas foram representadas em um espaço *bi-plot* de $\delta^{13}C$ no eixo *X* e $\delta^{15}N$ no eixo *Y*, a partir do qual as métricas de nicho foram calculadas. As amplitudes de nicho das populações foram calculadas pela área das elipses corrigidas para amostras pequenas (standard ellipse areas -SEAc). A sobreposição entre elipses foi calculada como indicativo da sobreposição de nicho isotópico entre as populações. As análises foram realizadas através do pacote Elipses Baysianas de Isótopos Estáveis (Stable Isotope Bayesian Ellipses – SIBER) (JACKSON et al., 2011) do programa R (R CORE TEAM, 2014).

1.3.3 Determinação do tamanho de maturidade sexual

A maturidade sexual foi determinada a partir de análise anatômica e histológica de gônadas de fêmeas e machos coletados conforme autorização do Comitê de Ética da Universidade Federal do Pará (CEPAE – Parecer 211-14). Adicionalmente, animais que se destinavam ao consumo dos moradores no rio Iriri tiveram suas gônadas doadas para esta pesquisa. Foram analisadas gônadas de 38 fêmeas e 32 machos nas campanhas de seca de 2012 e cheia e seca de 2013 no rio Iriri; e de 10 fêmeas e 11 machos na seca de 2014 na várzea do baixo Amazonas. A maturidade foi determinada nos machos pela presença de espermatozoides livres nos túbulos seminíferos ou ductos extratesticulares (Figura 7A-B). Testículos imaturos apresentam túbulos seminíferos visivelmente menores e sem lúmen aparente. Nas fêmeas, a maturidade foi indicada pelo aspecto frouxo dos ovários, com presença de ovócitos grandes (>15 mm), ovos calcificados ou *corpora albicans* nos ovários (Figura 7D-E). A imaturidade é percebida pelo aspecto compacto dos ovários contendo apenas ovócitos com poucos milímetros (<5 mm) (Figura 7E). Para cada área e sexo, foram estabelecidos o tamanho mínimo de maturidade e o tamanho a partir do qual todos os indivíduos estavam sexualmente maduros (L_{100}).

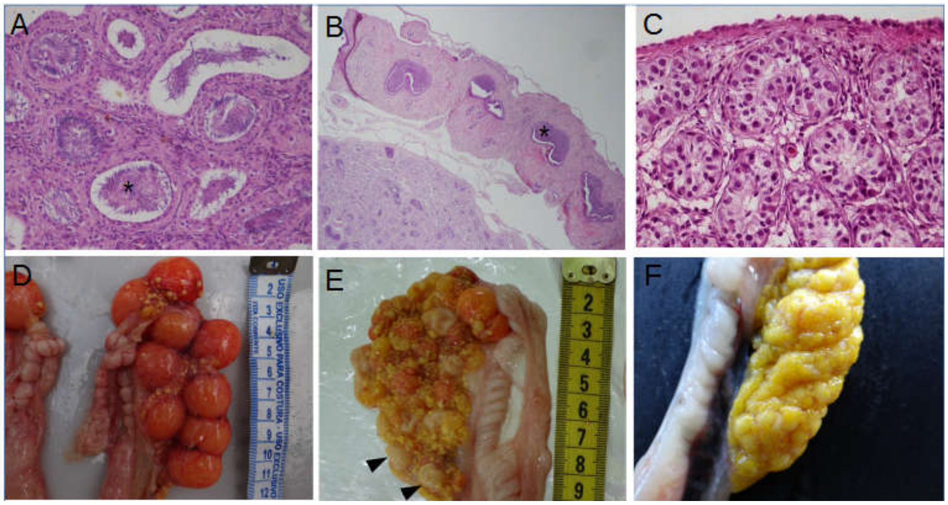

Figura 7. Maturidade sexual de *P. unifilis* indicada nos machos pela presença de espermatozoides (*) nos (A) túbulos seminíferos, e (B) ductos extratesticulares; (C) aspecto de testículo imaturo; e nas fêmeas pela presença de (D) ovócitos grandes (> 15mm); e (E) *corpora albicans* (cabeça de seta); (F) aspecto de ovário imaturo.

1.3.4 Biologia reprodutiva

A coleta de dados reprodutivos acontece por meio de visitas às áreas de desova nas primeiras horas da manhã, quando os ninhos recentes podem ser mais facilmente identificados (PEZZUTI; VOGT, 1999). Informações de número de ovos por ninho, e medidas de comprimento, largura e peso de uma amostra de 10 ovos por ninhos foram coletadas durante a estação reprodutiva de 2013 no rio Iriri (agosto-outubro), e de 2014 na várzea do baixo Amazonas (setembro-dezembro). Os dados foram comparados entre as populações por Análise de Variância Permutacional Univariada.

1.4 Síntese dos Resultados

1.4.1 Ecologia trófica

A análise de isótopos estáveis revelou que as populações não diferiram quanto à assinatura de δ^{15}N (t = -1.8257; p = 0.0707), mas foram significativamente distintas quanto a δ^{13}C (*Pseudo-F* =

67.505; $p < 0.001$). Os valores médios ± dp de $\delta^{15}N$ foram 9.3 ± 0.8‰ (7.4 – 10.9; N = 44) no rio Iriri e 9.0 ± 1.1‰ (6.5 – 11.5; N = 65) na várzea do baixo Amazonas. Quanto ao $\delta^{13}C$, os indivíduos da várzea foram mais enriquecidos, com média de -24.9 ± 1.3‰, e tiveram maior amplitude, entre -25.5 e -21.2 (N = 65), do que os indivíduos do rio Iriri, cujo valor médio foi de -26.6 ± 0.6‰, e amplitude entre -27.9 e -24.1 (N = 44). A maior amplitude de $\delta^{13}C$ reflete maior amplitude de fontes autotróficas consumidas na região de várzea do baixo Amazonas. A área total (métrica isotópica TA) abrangida pelo polígono convexo dos pontos individuais no espaço bi-plot foi de 20.3 ‰^{2} para a várzea do baixo Amazonas, e de 8.3 ‰^{2} para o rio Iriri (Figura 2A no Cap. 4, pg. 88). A amplitude de nicho trófico isotópico, representada pela área das elipses SEAc, foi significativamente maior na várzea, 4.4 ‰^{2}, do que no Iriri, de 1.5 ‰^{2} (Figura 2B no Cap. 4, pg. 88).

1.4.2 Tamanho de maturidade sexual

Os machos apresentaram espermatozoides nos testículos a partir de 184 mm de comprimento de carapaça no rio Iriri e 177 mm na várzea, sendo que gônadas de indivíduos entre 93,5 e 180 mm não foram analisadas no rio Iriri. A partir dos tamanhos acima citados, todos os indivíduos analisados eram maduros. Assim, o tamanho mínimo de maturidade coincidiu com o L_{100} para os machos em ambas as áreas de estudo. Esta coincidência do tamanho mínimo com L_{100} não foi observado para as fêmeas. No rio Iriri, o tamanho mínimo de maturidade foi 301 mm e o L_{100} foi 310 mm; enquanto no baixo Amazonas, o mínimo foi de 318 mm e L_{100} foi de 333 mm.

1.4.3 Estrutura populacional e relações morfométricas

Um total de 2.565 e 1.028 indivíduos foram capturados na várzea do baixo Amazonas e no rio Iriri, respectivamente. A partir dos tamanhos mínimos de maturidade específicos para cada área, as populações capturadas tiveram proporção muito similar de imaturos, 23,6% e 23,9% no rio Iriri e várzea do baixo Amazonas, respectivamente. A população capturada no rio Iriri foi dominada por machos adultos, enquanto na várzea predominaram as fêmeas adultas. A razão sexual, portanto, diferiu entre desviada para machos no rio Iriri por 9,15:1, e desviada para fêmeas por 0,51:1 na várzea.

A comparação de tamanho (comprimento de carapaça) e peso dos adultos entre as áreas mostrou fêmeas maiores e mais pesadas na várzea, com média de 365,29 mm (dp = 25,76) e peso médio de 5.950 g (dp = 1.280), do que no rio Iriri, onde as médias foram de 333,30 mm (dp = 22,21), e 4.030 g (dp = 820). Os machos da várzea foram, em média, mais pesados (1.560 g; dp = 510) do que os do rio Iriri (1.380 g; dp = 350); mas não foram maiores em comprimento de carapaça, com média de 234,61 mm (dp = 24,72) na várzea, e 234,29 mm (dp = 23,23) no rio Iriri (Tabela 1 no Cap. 4, pg. 90).

As relações de peso-comprimento (valor do parâmetro *b*) específicas a cada sexo mostraram que machos e fêmeas acumulam mais peso por unidade de crescimento em comprimento de carapaça na várzea do que no rio Iriri (Tabela 2 no Cap. 4, pg. 90). A Análise Canônica de Coordenadas Principais indicou a formação de quatro grupos distintos, separando sexos e populações quanto à morfologia da carapaça e largura da cabeça (Figura 3 no Cap. 4, pg. 91). As fêmeas de ambas as áreas apresentaram plastrão proporcionalmente mais comprido e carapaça mais alta que os machos. Entre as áreas, os indivíduos do rio Iriri (machos e fêmeas) apresentaram carapaça proporcionalmente mais larga, enquanto na várzea a carapaça foi proporcionalmente mais alta.

1.4.4 Biologia reprodutiva

Foram analisados 49 ninhos no Iriri e 52 na várzea, entre os quais houve diferença significativa no número e tamanho dos ovos (Tabela 4 no Cap. 4, pg. 92). Os ninhos da várzea apresentaram, em média, maior quantidade de ovos (29,4 ± 6,34; 13-44) do que os ninhos do rio Iriri (17,55 ± 3,82; 11-27), com a diferença sendo estatisticamente significativa ($p < 0,001$). Os ovos, contudo, foram significativamente ($p < 0.001$) maiores em comprimento e largura, e mais pesados no rio Iriri (26,94 ± 3,24 g; 16-35) do que na várzea (22,73 ± 3,36 g; 14,8-31,7). Apesar dos ovos menores, os ninhos da várzea tiveram maior massa total estimada (677,94 ± 208,67 g; 291,85-1.009,72) do que os do rio Iriri (475,85 ± 124,69 g; 199,1-747,9).

1.5 CONCLUSÕES GERAIS

- A população de *Podocnemis unifilis* na Estação Ecológica Terra do Meio foi fortemente dominada por machos adultos, indicativo de pressão histórica sobre as fêmeas ou de algum fator ambiental não analisado neste estudo, que favoreça o número de machos na população.
- A população de *P. unifilis* da comunidade Água Preta na várzea do baixo Amazonas foi

dominada por fêmeas adultas, capturadas em grande quantidade dentro do território da comunidade utilizando técnica local no período da seca, indício da população não estar sobre-explorada sob o sistema de manejo em andamento na Água Preta.

- A amplitude dos valores de $\delta^{13}C$ e a área da elipse foram maiores na população da várzea do baixo Amazonas, indicando maior amplitude de nicho trófico explorado por *P. unifilis* nesta área do que no rio Iriri.
- O tamanho de maturidade sexual dos machos foi similar entre as áreas de estudo; enquanto o das fêmeas diferiu entre as populações, com o tamanho mínimo de maturidade na várzea sendo superior ao L_{100} observado no rio Iriri.
- O tamanho dos machos adultos não diferiu entre as populações, mas os indivíduos do baixo Amazonas foram mais pesados do que os do Iriri.
- As fêmeas da várzea do baixo Amazonas foram maiores em comprimento de carapaça e mais pesadas do que as do rio Iriri.
- A espécie apresentou plasticidade na forma da carapaça entre os sexos e áreas de estudo, sendo as fêmeas de ambas as áreas relativamente mais altas e com plastrão mais comprido; enquanto as populações divergiram em função da carapaça proporcionalmente mais larga no rio Iriri e mais alta, em formato de cúpula, no baixo Amazonas. A diferença entre populações foi interpretada em função diferença de correnteza entre a paisagem plana de várzea dominada por lagos no baixo Amazonas, e o rio Iriri íngreme e com presença de corredeiras.
- Os ninhos da várzea apresentaram maior quantidade de ovos e massa total que os ninhos do rio Iriri; enquanto os ovos foram maiores (largura e comprimento) e mais pesados no rio Iriri.
- O padrão de variação populacional observado nas fêmeas seguiu o esperado pela hipótese inicial de maior produtividade na várzea, enquanto os machos não apresentaram diferença de maturidade sexual e tamanho entre as áreas, mas tiveram diferença de peso, provavelmente em função da variação na forma da carapaça.

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Capítulo 2

POPULATION STRUCTURE AND ALLOMETRY OF *Podocnemis unifilis* (TESTUDINES, PODOCNEMIDIDAE) IN A PROTECTED RIVER UPSTREAM BELO MONTE DAM AT XINGU RIVER, BRAZIL

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Population structure and allometry of *Podocnemis unifilis* (Testudines, Podocnemididae) in a protected area upstream Belo Monte dam in Xingu River, Brazil

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ABSTRACT

Amazon river turtles are increasingly threatened by habitat loss and alteration due to the Brazilian energy policy based on construction of hydroelectric dams, meanwhile, population studies remain scarce. We described the population structure, and established body allometric relationships of *Podocnemis unifilis* in the Terra do Meio Ecological Station in the Iriri River, tributary of the Xingu River upstream from the Belo Monte dam under construction. Turtles were captured by hand net and diving in 2012 and 2013 dry seasons, and 2013 rainy season. A total of 728 males, 296 females and four juveniles were captured. Adult sex ratio was male-biased by 9.15♂:1♀. Females were significantly larger than males. Mean straight carapace length was 268.9 ± 46.7 mm (165 – 403) for females; and 232.7 ± 24.8 mm (167 – 303) for males. The sexes were morphologically distinct in function of a proportionally larger plastron, and higher carapace, on females. Allometric relationships between straight carapace length and other morphometric traits were strong for males (*R2 range* = 0.87 - 0.96*)* and females (*R2 range* = 0.79 - 0.98*)*. Exploitation of *P. unifilis* in biomass extirpated from the Middle Xingu River may be estimated from body parts found post-consumption by the presented regressions.

Key words: Amazon, clear water river, length-weight relationship, sex ratio, tracajá.

INTRODUCTION

River turtles have been consumed by indigenous people as a food source since pre-colonial times in the Amazon region (Bates 1863, Johns 1987). The intense commercial consumption after European colonization has led *Podocnemis* populations to a drastic decline, especially the largest Amazon turtle *Podocnemis expansa* (Schweigger, 1812), which has increased the pressure on the smaller species *Podocnemis unifilis* Troschel, 1848 (Mittermeier 1975, Smith 1979, Johns 1987). Since then, *P. unifilis* continues to be widely consumed and traded in the Amazon region (Rebêlo and Lugli 1996, Fachín-Terán et al. 2004, Pezzuti et al. 2010). Nowadays, besides intense poaching, turtle populations have been increasingly threatened by the establishment of multiple hydroelectric dam complexes in the Amazon rivers (Ferreira et al. 2013). Hydroelectric dam complexes are amongst the main causes of habitat loss and destruction of aquatic ecosystems, and are a priority for Brazilian government policies for the Amazon region. The river impoundment by dams turns natural lotic habitats into lentic ones, a habitat alteration that may affect turtle populations in many ways. Riverine habitat is flooded (Ferreira et al. 2013) and it affects the availability of nesting, nursery, and feeding areas, and may also interfere on movement patterns of migratory species and fragment river turtle populations (Moll and Moll 2004, Tucker et al. 2012). Alteration of temperature in nesting areas may influence the population structure of species whose sex is determined by the incubation temperature, such as *P. unifilis* (Souza and Vogt 1994). The Belo Monte dam hydroelectric complex is planned to be the third largest hydroelectric power station in the world regarding installed capacity and the largest entirely Brazilian one. It is more complex than only one dam in the main river since it includes a water diversion from the main channel to feed an artificial reservoir which will include another dam (ANEEL 2010). Therefore, downstream of the first dam, the river channel will keep the dry season water level all year round and will no longer be seasonally flooded as per the natural flood pulse of the Amazon rivers (Junk et al. 1989). It may severely affect the water temperature and the vegetation of the fluvial islands which are adapted to the flooding pulse. For river turtles, it implies a drastic reduction of feeding areas and alteration of nesting sites environments. Besides the environmental effects, the establishment of large constructions usually attract more people, which increases demand on natural resources.

The Yellow-spotted Amazon River Turtle, *P. unifilis,* is a medium to large Podocnemididae species with sexual size dimorphism; male's carapace length reach up to 33.5 cm and female's carapace up to 46.5 cm (Pritchard and Trebbau 1984). It is widely distributed in the Amazon and Orinoco river basins and it is categorized as "vulnerable" by IUCN (2011), however, the Tortoise and Freshwater turtle Specialist Group (TFTSG/IUCN) has recently drafted the species as "endangered" (Van Dijk et al. 2012). Reproduction was intensely studied throughout the Amazonia (Foote 1978, Thorbjarnarson et al. 1993, Escalona and Fa 1998, Ferreira-Júnior and Castro 2006, Pignati et al. 2013), whilst some essential ecological information lacks for most populations. The size of maturity, home range, comparative analysis of population structure in distinct environments and human pressure conditions are examples of important information that is still lacking. Studies on population ecology of *P. unifilis* are scarce and short in temporal and spatial scales (Fachín-Terán and Vogt 2004, Alcântara et al. 2013, D. Félix-Silva, unpublished data). Male and female biased populations were found. Immature individuals were always captured in small quantities and there was no consensus about the expected structure in a natural population (Vogt 2008). Therefore, there is still need for basic data collection in order to attain a complete understanding of *P. unifilis* populations' demography.

Population parameters such as size structure, sex ratio and proportion of immature, reflect the life history tracts that allowed the permanence of populations in time (Cole 1954). Monitoring such parameters is a core tool used in applied sciences of fisheries biology and wildlife management (Caughley and Sinclair 1994, Cadima 2003, Froese 2004). Population parameters of freshwater turtle species have been comparatively analyzed at temporal and spatial scales to study the effects of particular environmental conditions, habitat alteration and human pressure on the environment (Marchand and Litviatis 2004, Steen and Gibbs 2004, Dodd and Dreslik 2007). Allometric relationship is another tool used in applied sciences to monitor and evaluate the status of wild populations. The most common is the length-weight relationship (LWR), used to convert lengths into biomass, to determine fish stock status, to compare fish growth amongst areas, and also as a complement to species-specific reproduction and feeding studies (Froese 2006). Allometric relationships are useful when the collection of complete morphological data is too difficult or too expensive, such as when you have only parts of consumed animals as carapace, plastron, and head (in the case of turtles). It may also be used in participative monitoring and management programs on which a single simple morphological measurement could be gathered by trained local people.

The present paper describes the population structure and establishes the length-weight relationship and other allometric relationships of interest for a *Podocnemis unifilis* population living in a 3.3 million ha protected area, located about 450 km upstream from the future reservoir of the Belo Monte dam. The data presented may be used as a reference of a *P. unifilis* natural population in a typical clear water river in the Amazon basin, an ecosystem increasingly threatened by habitat alteration.

MATERIALS AND METHODS

STUDY AREA

The study was conducted inside the Terra do Meio Ecological Station (TMES), one of the most restrictive Protected Areas under the Brazilian environmental legislation (National System of Protected Areas – SNUC - law 9,985). TMES comprises 3,373,133.89 ha, covered mostly by pristine tropical forest and drained by Iriri River and its smaller tributaries. The Iriri River is 1,300 km long from its headwaters in the state of Mato Grosso to its mouth on the left margin of the Xingu River, about 80 km upstream Altamira city. Despite the exploitation of turtles along the Xingu Basin, human pressure on turtle population inside the TMES is low as a result of its location (far away from urban centers), and to its low human density – about 17 families live sparsely along more than 300 km of the Iriri River inside the TMES. Furthermore, upstream and downstream territories are Indigenous Lands approved by law. Turtle captures were carried out between coordinates -6°54' 6.79" S, -53° 49' 29.74" W and -5° 25' 8.11" S, -54° 24' 22.93" W (Fig. 1).

The Xingu River and its tributaries constitute a typical clear water ecosystem in the Amazon Basin. Clear water ecosystems are characterized by transparent nutrient-poor water that rapidly flow over a rocky bed. Aquatic fauna is highly adapted to that condition and to the seasonal flood pulse characteristic of Amazonian rivers (Junk et al. 1989, Goulding 1980). During the high water season the marginal forest is flooded and provides food source for the aquatic fauna, whilst in the lowwater season deep pools and extensive shallows remain in the river bed, and islands, sand bank and rocky rapids emerge. These ecosystems are currently threatened by gold mining activities and the construction of the Belo Monte dam (Ferreira et al. 2013).

SAMPLING METHODS

Data on the population structure of *P. unifilis* were obtained by capturing the turtles using a hand net (locally called *landuá* or *puçá*) and by diving and chasing. The hand net consists of a wooden shaft attached to a metal ring with a bag-shape net with a 10 cm mesh attached. Both methods include active search along the river bed, pursuit and capture of animals previously viewed due to the high transparency of the Iriri River. Active search to see the turtles at surface is done by navigating on an aluminum boat with outboard motor (15 – 30 hp) along the river bed. Pursuit consists on navigating in circles around the observed turtles with one person in the bow. The person either dives to chase the turtle underwater, or traps the turtles using the hand net. Diving must be undertaken at daylight, whilst the hand net is used with a spotlight at night. Both methods can be applied where the outboard motor is able to operate. Both methods are based on previous observations of the behavior of *P. unifilis*, that comes to surface due to the noise of the motor in the water, especially when the motorboat navigates in circles in the places turtles gather. These capture techniques are amongst the traditional methods used by local dwellers of Xingu and Iriri River to catch turtles for subsistence and commercialization (J.C.B. Pezzuti, unpublished data). The hand net was previously applied to sample *P. unifilis* in the Xingu River by Alcântara et al. (2013). In the present study, hand net was used by researchers and local people, whilst diving was performed only by the local dwellers that collaborated in the study. Both methods were applied during 20 to 25 consecutive days in all sample trips: August and October (low water season) in 2012; May (high water season), August and October (low water season) 2013.

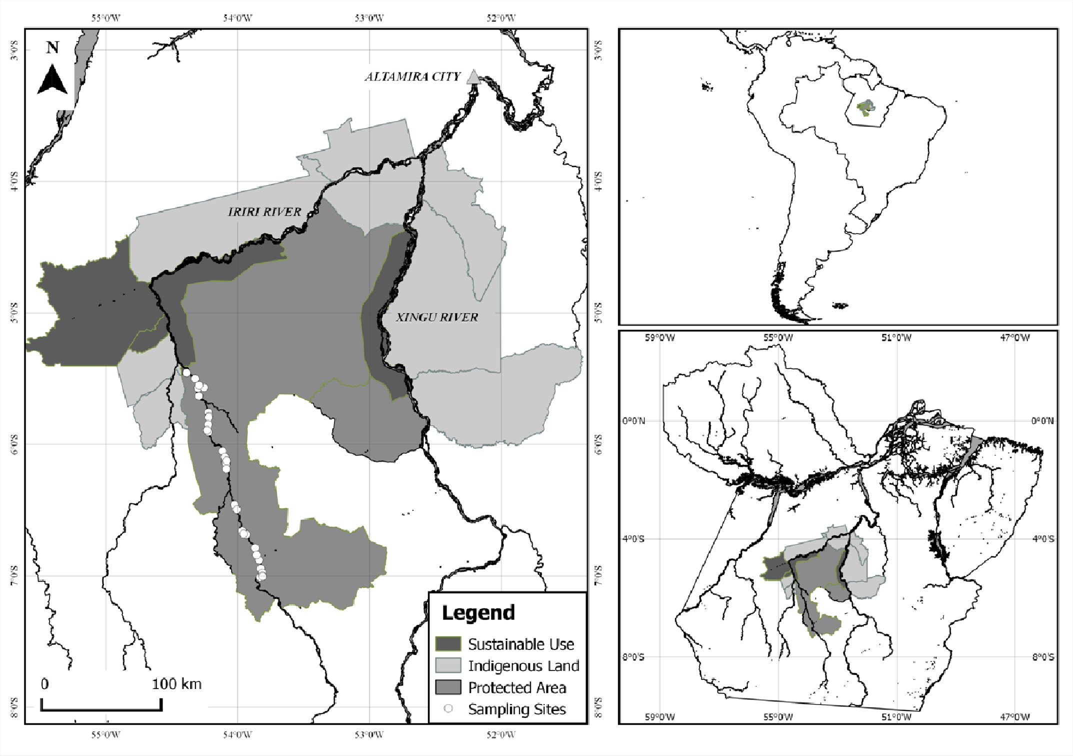

Figure 1. Study area, Terra do Meio Ecological Station, Pará, Brazil. Circles indicate sampling sites along the Iriri River from August 2012 to October 2013.

Captured turtles were weighed on Pesola® spring scales (±10.0 to ±100.0 g) and measured on maximum sizes (mm): straight carapace length (SCL), carapace height (CH), carapace width (CW), plastron length (PL), and head width (HW), with calipers Haglöf® (±1 mm) or Mitutoyo® (±0.1 mm). Curved carapace length (CCL) was obtained using a plastic metric tape with millimetric scale. Captured animals were marked with holes drilled in the marginal shields following a coding system that allowed for individual recognition. Sex was identified according to the secondary sexual characteristics of head color, pre-cloacae distance and length and thickness of the tail (Pritchard and Trebbau 1984). Males are smaller and maintain on their heads the yellow spots typical of hatchlings, and present a thicker and longer tail. Individuals on which secondary sexual characteristics were not evident were considered juveniles. Males were considered sexually mature (adult) with SCL ≥ 18 cm; and females with SCL ≥ 30 cm. Sexual maturity sizes refer to the minimum sizes at wich males and females were observed in the study area. Sexual maturity was elucidated from morphological and histological analysis of 32 males' and 38 females' gonads from the same area (P.S. Miorando, unpublished data). Males and females smaller than the size of sexual maturity were considered sub-adult (sexually immature).

All procedures with animals were carried out according to the international practices and care under the control of the internal ethical committee of the Universidade Federal do Pará (Process 211-14).

DATA ANALYSIS

Data on size distribution (SCL and weight) of males and females were described by mean, minimum and maximum standard deviation. Size (SCL) and weight were compared between the sexes and methods by the non parametric Mann-Whitney *U*-test, after verification that the data were not normally distributed. The sex ratio was compared between methods of capture by Pearson Chi-square test (Zar 2010). Measurements of SCL, CW, CH, PL and HW of individuals captured in 2013, in which complete biometrics were taken, were used to perform a Principal Components Analysis (PCA) to verify morphological variation between the sexes (sex as a fixed factor, 2 levels). Values of measurements were standardized by the maximum (SCL) to avoid size effect. Morphological difference based on a resemblance matrix (Euclidean distance) amongst individuals was statistically tested by Permutation Multivariate Analysis of Variance (PERMANOVA) to an α-of-significance = 0.05 (Clarke 1993). PCA and PERMANOVA were performed on PRIMER® v.6 (Clarke and Gorley 2006). Allometric relationships were performed on morphometric data measured from individuals captured in August 2012 and 2013. Allometric relationships CCL-SCL, PL-SCL and HW-SCL were estimated by simple linear regression model. LWR was estimated by the equation $W = aLb$ (W: weight; L: length) (Froese 2006). length and weight values were log-transformed to linearize the equation to a simple linear model, $\ln(W) = \ln(a) + b*\ln(L)$ (Froese 2006). Parameter b of regressions was compared between sexes by the Welch-T test (Zar 2010).

RESULTS

A total of 1,028 individuals of *P. unifilis* were captured: 728 males, 296 females and four immature individuals without the secondary sexual characteristics (SCL range = 51.6 - 117 mm). Captures occurred mostly (89%) in August, during the low water season (Table I). Hand net captured 839 individuals; whilst 191 were caught by diving (five captures were occasional by locals). Methods did not differ either in the sex ratio (Pearson chi-square = 2.411, df = 1, P = 0.120) nor in the SCL of captured turtles (U = 75318.3, N = 1022, P = 0.353). Therefore, data from individuals captured with hand net and diving were pooled to express the population structure. Population was dominated by adult males, which accounted for 68.7% of all individuals captured (Fig. 2). Considering only sexually mature individuals, sex ratio was strongly male-biased by 9.15♂:1♀ (705 males, 77 females); and it was still male-biased by 2.45:1 when all sexed individuals were accounted for. Sexually immature individuals accounted for only 2.7% of males, and for 73.8% of females.

Females were larger (U = 154994, N = 1016, P < 0.0001) and heavier (U = 161440, N = 1009, P < 0.0001) than males. Males measured on average SCL 232.7 ± 24.8 mm (167–303 mm, N = 724) and weighed 1357 ± 363 g (450–2450 g, N = 721). Size structure was normally distributed with higher proportion in the classes between 220 and 260 mm SCL. Females mean SCL and weight were 268.9 ± 46.7 mm (165–403 mm, N = 292) and 2329 ± 1184 g (540–6900 g; N = 288), respectively. Despite the significant difference, the most frequent size classes for females were similar to those for males, from 220 to 280 cm SCL (Fig. 2). There was significant difference between males' and females' morphology (PERMANOVA, pseudo-F = 320.09, P = 0.001), explained mainly by a longer plastron, and higher carapace in females (Fig. 3). PCA explained in two axes, 90.6% of morphological variation between males and females (PC1 = 65.6% and PC2 = 25%). Variation was mainly driven by PC1, based on PL (eigenvector coefficient = 0.939) and CH (eigenvector coefficient = 0.343). PC2 was based on CW (eigenvector coefficient = 0.982) and on CH (eigenvector coefficient = 0.141), and had minor contribution to explain morphological variation between sexes, since males and females showed similar distribution along this axis (Fig. 3). HW had the least contribution to compose both axes.

Allometric regressions were all statistically significant to P= 0.0001, and SCL was better estimated by CCL and PL (Table II). Amongst females, regressions made considering all individuals (adults and sub-adults) resulted in higher coefficients of determination and narrower confidence limits. In contrast, regressions performed for adult females had lower sample sizes and more variability, which led to a wider confidence interval (Table II). Adult females had higher values of *b* parameter than adult males (Wt = 26.043, df = 56, P = 0.0001), and than sub-adult females (Wt = 8.935, df = 60, P = 0.0001); and sub-adult females also had higher *b* parameter than adult males (Wt = 78.381, df = 235, P = 0.0001) (Table II).

TABLE I

Captures of *Podocnemis unifilis* in the Terra do Meio Ecological Station, Pará, Brazil, carried out in 2012 and 2013.

	2012		2013			
	August	**October**	**May**	**August**	**October**	**N individuals**
Males	433	32	11	222	30	728
Females	182	8	7	83	16	296
Juveniles	1	0	3	0	0	4
SUM	616	40	21	305	46	**1028**

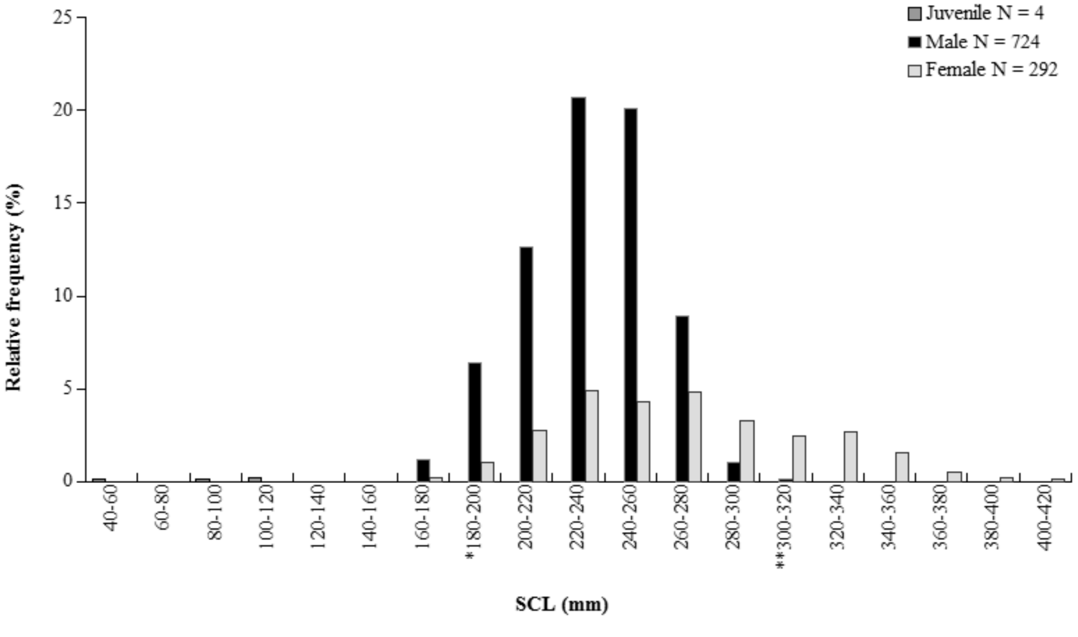

Figure 2. Population structure (SCL, straight carapace length) of *Podocnemis unifilis* captured in Terra do Meio Ecological Station, Iriri River, 2012-2013. Size of sexual maturity for *males and ** females.

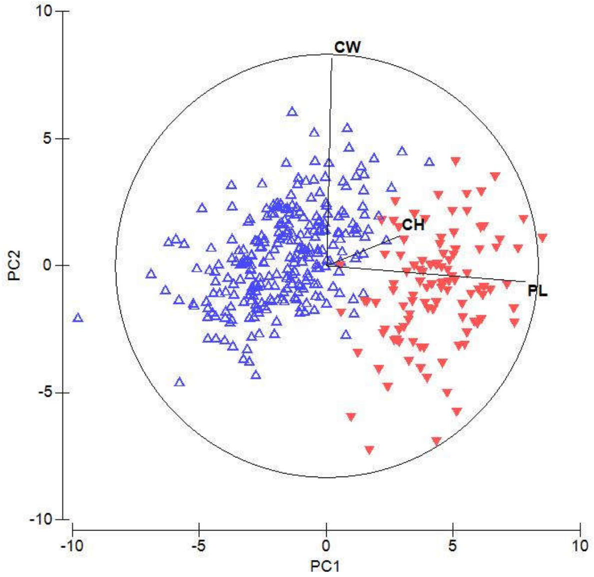

Figure 3. Principal Component Analysis (PCA) of morphometric measures of *Podocnemis unifilis* males (blue) and females (red) from Ecological Station of Terra do Meio, PA, 2013. PL = plastron length; CH = carapace height; CW = carapace width.

TABLE II

Allometric regressions of *P. unifilis* from Terra do Meio Ecological Station on August 2012 and August 2013. LWR: length-weight relationship. Parameters of simple linear regression (Y = *a* + *bX) are given. N: sample size; CI: confidence interval; R^2: coefficient of determination (all relationships significant at $P < 0.0001$). SCL straight carapace length (mm); W: weight (g); CCL: curved carapace length (mm); PL: plastron length (mm); HW: head width (mm).**

LWR (ln(W) = ln(*a*) + *bln(SCL))**								
		X		Y				
Group	N	min	max	min	max	*a*	*b* (95% CI)	R^2
Female; all	245	179	403	680	6900	-8.37	2.87 (2.81-2.93)	0.974
Female; subadult	186	179	299	680	3100	-7.71	2.75 (2.65-2.85)	0.942
Female; adult	59	300	430	2800	6900	-8.60	2.91 (2.63-3.19)	0.883
Male; adult	598	180	303	630	2450	-6.11	2.44 (2.38-2.50)	0.900

				SCL = *a* + *bCCL**				
Female; all	245	195	434	179	430	-5.61	0.94 (0.92-0.95)	0.986
Female; subadult	186	195	340	179	299	-8.73	0.95 (0.92-0.97)	0.964
Female; adult	59	322	434	300	430	16.09	0.87 (0.82-0.93)	0.938
Male; adult	598	200	320	180	303	-13.12	0.96 (0.95-0.98)	0.956
				SCL = *a* + *bPL**				
Female; all	245	158	354	179	430	2.78	1.12 (1.10-1.14)	0.985
Female; subadult	186	158	274	179	299	9.65	1.08 (1.05-1.12)	0.964
Female; adult	59	261	354	300	430	6.87	1.11 (1.02-1.19)	0.924
Male; adult	598	150	242	180	303	-9.92	1.25 (1.23-1.28)	0.952
				SCL = *a* + *bHW**				
Female; all	245	30.5	58.1	179	430	-56.72	8.09 (7.85-8.32)	0.949
Female; subadult	186	30.5	47.1	179	299	-58.74	8.12 (7.73-8.51)	0.901
Female; adult	59	41.4	58.1	300	430	67.84	5.53 (4.78-6.29)	0.790
Male; adult	598	28.4	45.4	180	303	-13.09	6.88 (6.67-7.09)	0.870

DISCUSSION

Seasonal variation of capture rates has been widely described for *Podocnemis* spp. (Fachin-Terán and Vogt 2004, Fachín-Terán et al. 2003, Bernhard and Vogt 2012, Alcântara et al. 2013). During the high water season, the aquatic fauna is sparsely distributed over the extensive floodplain, but when the water recedes, turtles and aquatic fauna in general are forced to concentrate in the remaining habitats (Goulding 1980, Junk et al. 1989). In the present study, 89% of captures occurred in the low water season, when turtles were captured mainly in the deeper pools along the river bed. It is important to note that the difference in the number of captures between August, 2012 and 2013 was a result of variation in capture effort and do not reflect a population decline in the study area. The number of captures diminished in October because lower areas became flooded and offered new shallow areas (<50 cm) for turtles, where neither the hand net nor diving were efficient.

The strongly male-biased sex ratio observed in the present study (9.15♂:1♀) was similar to the sex ratio of 9.8♂:1♀ observed for adult *P. unifilis* in the Guaporé River, despite different methods of capture were used (Fachín-Terán and Vogt 2004). Our study and Fachín-Terán and Vogt (2004) are the only studies on *P. unifilis* that considered adult individuals alone to calculate the sex ratio, as was indicated by Bury (1979) and Lovich and Gibbons (1990). The absence of data about the size at maturity is one of main barriers to describe the correct sex ratio of populations of *Podocnemis* spp. Alcântara et al. (2013) observed a sex ratio of 1.89♂:1♀ capturing *P. unifilis* using hand net in the area of the future reservoir of Belo Monte dam in the Xingu River. A balanced sex ratio of 1.12♂:1♀ was observed for *P. unifilis* only in the Tucuruí dam reservoir using gill nets and traps (D. Félix-Silva, unpublished data). However, those sex ratios were calculated based on all sexed individuals, and not on adults alone. A male-biased sex ratio was observed for *P. sextuberculata* (1.94♂:1♀) captured by trammel nets at Mamirauá Reserve in the middle Solimões River (Fachín-Terán et al. 2003). In contrast, female-biased sex ratio was observed for *P. erythrocephala* (0.49♂:1♀) captured by trammel nets and diving in the Negro River, state of Amazonas (Bernhard and Vogt 2012). A sex ratio different than 1:1 in turtle populations should not be expected when sample sizes are not smaller than 100 (Gibbons 1970, Bury 1979). However, in spite of a greater sample size, numerous studies have reported biased sex ratios. Differential mortality, distinct behavior, temperature of incubation, different age/size at maturity, sampling methods and microhabitats sampled, are the most mentioned factors to explain a skewed sex ratio (Ream and Ream 1966, Gibbons 1990, Lovich and Gibbons 1990, Steen et al. 2006). The male-biased sex ratio commonly reported for *Podocnemis* spp. populations is usually attributable to disproportionate mortality of females (Ramo 1982, Fachín-Terán and Vogt 2004). It is well known that Amazonian dwellers traditionally prefer to consume and trade large females, mainly during the nesting season (Bates 1863, Smith 1979, Pezzuti et al. 2010). Nesting females are also more prone to predation by jaguars and caiman in pristine areas of the Amazon region (Salera Jr et al. 2009). In the United States, differential mortality of females on roads during nesting migration caused a skewed sex ratio towards males on freshwater turtle populations (e.g. Steen et al. 2006). The male-biased sex ratio of *P. unifilis* in the Guaporé River was also attributed to the lower incubation temperatures and to higher human predation of nests in open, warmer areas, which would produce primarily females (Fachín-Terán and Vogt 2004). Temperature of incubation may be a natural cause to skewed primary sex ratio in species in which sex determination is temperature dependent, as the *Podocnemis* spp. (Souza and Vogt 1994). Differences in age or size at maturity may also unbalance the sex ratio towards the sex that matures first (Lovich and Gibbons 1990), and mistakes on determination of sexual maturity can also lead to an incorrect biased sex ratio and to an incorrect proportion of juveniles when describing a population (Gibbons 1970). Moreover, the influence of methods of capture on sex ratio and size frequency distribution should not be overlooked in studies on turtle population structure (Ream and Ream 1966, Gibbons 1970, Lovich and Gibbons 1990). For amazonian species, this aspect was better discussed in Bernhard and Vogt (2012), who showed that diving and trammel nets, including variation of the mesh size, had significant effects on the sex ratio and the proportion of juveniles of *P. erythrocephala* captured in the Negro River.

In the present study, the size of sexual maturity of *P. unifilis* was elucidated as part of a wider project (P.S. Miorando, unpublished data). Histological analyses provided us security about the sizes of sexual maturity for males and females, and thus the sex ratio is unlikely to be biased due to mistakes in maturity determination. We consider that differential mortality is a possible cause to explain the strongly skewed sex ratio. Although the Terra do Meio Ecological Station is currently one of the most restrictive Protected Areas under Brazilian legislation, human settlements were denser before the creation of the protected area about 10 years ago and the pressure on turtle populations was probably much greater than present times. In addition to human pressure, nesting females are naturally predated by jaguar (*Panthera onca*) (pers. obs.).

There are natural factors that should not be overlooked in the discussion of the population structure observed in the present study. Lower incubation temperature in the Iriri region and the earlier maturity of males are natural factors that are likely to influence the higher proportion of adult males in the population. The first hypothesis should be tested by estimation of the threshold temperature for specific areas in the Amazon basin, as this parameter is probably subject to geographic variation along the large distribution of *P. unifilis*. The second hypothesis is based on the pattern observed in freshwater species that the age and size of maturity determines the sexual dimorphism, with the smaller sex maturing earlier and at a smaller size than the larger sex (Moll and Moll 2004). Differential maturity may be the most important influence on sex ratio in the absence of other factors that result either in differential mortality or skewed primary sex ratio (Gibbons 1990, Lovich and Gibbons 1990). The sex that matures earlier with smaller size will outnumber the sex that matures with larger size (Lovich and Gibbons 1990). Since in *Podocnemis* species there is sexual size dimorphism with males reaching smaller size and also maturing at smaller sizes than females

(Rueda-Almonacid et al. 2007), it is expected that mature males outnumber mature females in *Podocnemis* populations. In the present study, we consider that the strongly male-biased sex ratio observed to *P. unifilis* may be due to a combination of three possible factors: higher pressure on larger females by humans and jaguars, a primary sex ratio that may be male-biased due to the temperature regime in the study area, and the natural trend due to differential maturity size.

We could also consider the possibility that adult females were in shallow areas near nesting beaches and thus sub-sampled by the capture method, as Fachín-Terán et al. (2003) stated for *P. sextuberculata* in the Mamirauá Reserve. However, it is unlikely because no adult female was observed neither breathing on water surface nor wandering underwater in shallow areas near beach shores during the whole sampling period. On the other hand, small juveniles were occasionally found amongst rocks at shallow sites that were not sampled in this study. It was clear, by the low number of unsexed juveniles, that the methods did not work well to capture them, and it is explained by the fact that they use microhabitats that could not be sampled by the adopted methods of capture. Small juveniles are commonly sub-sampled in turtle populations due to their distinct behavior and habitat use (Bury 1979); and low proportion of smaller individuals (<150 mm) can be observed in all studies of population structure mentioned in this discussion. A proportional capture of the actual percent of juveniles in the population consists in a major challenge to demographic studies of *Podocnemis* spp. populations.

Comparisons of morphometric measures confirmed the sexual size dimorphism of the species (Pritchard and Trebbau 1984) for this population. Besides the size difference, PCA and PERMANOVA analysis showed morphological differences between the sexes mainly due to a larger plastron and higher carapace on females. A complete analysis on morphological differences between the sexes is scarce in the literature for Podocnemidids. Bernhard and Vogt (2012) compared morphometric measures, one by one, between sexes for *P. erythrocephala,* and found that females had significantly longer plastron and higher carapace, the same morphological characteristic most relevant to the *P. unifilis* sexual differences found in the present study. Males captured in the Iriri River reached similar maximum size (≈ 300 mm) as recorded in the Xingu River (Alcântara et al. 2013), Guaporé River and Mamirauá Reserve (Fachín- Terán and Vogt 2004). Females from Iriri reached similar maximum size (≈ 400 mm) as those recorded in the Xingu River (Alcântara et al. 2013), but were smaller than females from Guaporé River and Mamirauá Reserve, where females reached ≈ 460 mm (Fachín-Terán and Vogt 2004). This is the first study to establish allometric regressions of body measures, especially the LWR, to amazon turtle species. Regressions were performed separately for males and females to account for morphological differences between sexes.

The *b* parameter of LWR was higher for adult females, intermediary for subadult females, and lower for adult males, which indicate that females accumulate more biomass per unit of SCL growth than males. It was expected that regressions for adult females had a higher value of *b* parameter, a lower value of coefficient of determination and a wider confidence limits as a result of natural variation among individuals that contained shell eggs in oviducts and individuals that had already nested. We may consider that the weight of an individual varies along the year, and thus the presented LWR is more precise to estimate the weight of turtle sin the low water season. Morphometric measures of bony structures do not suffer seasonal variation, and thus they can be applied year round with the same precision. Regressions of curved carapace length, plastron length and head width related to straight carapace length may be applied to estimate the size structure, and LWR the biomass of consumed individuals in the region of Middle Xingu River. Morphological variation among populations is likely to occur, and so the regressions here presented should be cautiously applied to other areas of the geographical distribution of *P. unifilis*.

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RESUMO

Os quelônios dos rios amazônicos estão crescentemente ameaçados pela perda e alteração do habitat em função da política energética brasileira baseada na construção de barragens hidroelétricas, enquanto estudos populacionais continuam escassos. Nós descrevemos a estrutura da população e estabelecemos relações alométricas corpóreas de *Podocnemis unifilis* na Estação Ecológica Terra do Meio no Rio Iriri, tributário do rio Xingu a montante da contrução da barragem de Belo Monte. Os quelônios foram capturados por puçá de mão e mergulho nas estações seca de 2012 e 2013 e na estação cheia de 2013. Foi capturado o total de 728 machos, 296 fêmeas e quatro juvenis. A razão sexual dos adultos foi desviada para os machos por 9.15♂:1♀. As fêmeas foram significativamente maiores que os machos. O comprimento retilíneo médio da carapaça foi de 268.9 ± 46.7 mm (165 – 403) para as fêmeas, e de 232.7 ± 24.8 mm (167 – 303) para os machos. Os sexos foram morfologicamente distintos em função do plastrão e altura da carapaça proporcionalmente maiores nas fêmeas. As relações alométricas entre o comprimento reto da carapaça e as demais características morfométricas foram fortes para machos (*R2 range* = 0.87 – 0.96) e fêmeas (*R2 range* = 0.79 – 0.98). A exploração de *P. unifilis* em biomassa retirada do médio Rio Xingu pode ser estimada a partir de partes do corpo encontradas pósconsumo através das regressões apresentadas.

Palavras-chave: Amazônia, rio de água clara, relação peso-comprimento, razão sexual, tracajá.

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Capítulo 3

POPULATION OF THE YELLOW-SPOTTED RIVER TURTLE *Podocnemis unifilis* UNDER COMMUNITY-BASED MANAGEMENT IN THE LOWER AMAZON FLOODPLAIN

Manuscrito elaborado para submissão ao periódico Oryx (Qualis B1).

Population of the yellow-spotted river turtle *Podocnemis unifilis* under community-based management in the lower Amazon floodplain, Brazil

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Abstract

Podocnemis unifilis is one of the most consumed turtle species throughout the Amazon basin. We analyzed a *P. unifilis* population from a varzea lake system where one community that have been spending efforts to protect turtles since 1990. Turtles were captured during August-December in 2009 by gill net, cast net and a surface trawl net (local technique), and October-December in 2014 only by surface trawl net. Besides, locals brought turtles occasionally captured in routine fisheries. A total of 2,565 turtles were marked: 1,773 females, 721 males and 71 in which sex could not be determined. 67.3% of females and 90.4% of males were adults (reproductive individuals). Immatures accounted for 23.89% of captured population. Mean carapace length was 337 mm (sd=58.96) for females and 226.8 mm (sd=34.87) for males. Size distribution from captures by cast net was different from those captured by gill net and trawl net. Difference was due the higher proportion of smaller turtles captured in shallow habitats by cast net. Mean CPUE using trawl net was lower in 2009 (1.89 N/min; sd=1.71) than in 2014 (4.47 N/min; sd=3.41), despite more individuals were captured in 2009 (1,835) than in 2014 (502). Allometric relationships were presented to allow estimates of the population structure and biomass from a single measure of live animals or post-mortem body parts. Trawl net was a very effective method to capture and evaluate adult population, the potential manegeable stock. Community-based initiatives should be technically supported to be an effective alternative in order to promote conservation of as many turtle populations as possible.

Keywords: Amazon turtle, population monitoring, conservation, wildlife management

Introduction

The sustainable use of wildlife is a challenging goal for Conservation Biology and Wildlife Management (Primack, 2012). It is especially important in developing countries where traditional communities persist in a lifestyle strongly dependent on natural resources (Davies, 2002; Robinson & Bennett, 2013). In the Amazon, the greatest rain forest and largest fluvial system in the world, aquatic fauna is an important food source to indigenous populations since immemorial times (Roosevelt, 2000).

River turtles are present in virtually any description of naturalists along the Amazon before and after colonization (Bates, 1892; Smith, 1981; Roosevelt, 2000). After nearly three centuries of over-exploitation during colonization, the impact of harvesting of eggs and nesting females was obvious in the XX century by the drastic declines of the largest species *Podocnemis expansa,* and redirection of harvesting towards the smaller-sized *Podocnemis unifilis* (Mittermeier, 1978; Smith, 1979; Johns, 1987). All *Podocnemis* species are currently listed in the IUCN red list and CITES (Turtle Taxonomy Working Group - TTWG, 2012). *Podocnemis unifilis* is classified as "vulnerable", but it needs updating (IUCN, 2011) and has been drafted to be considered "Endangered" by the TTWG (2012).

Since the end of the 1970s, Brazilian government, Academia and NGOs have spent efforts to recover declining populations, mainly *P. expansa,* and ensure the rational use of the other species as food source (Cantarelli et al., 2014). Among the six *Podocnemis* species, *P. unifilis* is considered the best model for management experiments due to its particular biological characteristics that allow the persistence of viable populations along its range (Vogt et al., 2015). These include wide geographic distribution (Pritchard & Trebbau, 1984), relatively restricted home range (Bock et al., 1998), opportunistic diet (Fachín-Terán et al., 1995; Balensiefer & Vogt, 2005), and solitary and generalist nesting habit (Mittermeier, 1978; Rueda-Almonacid et al., 2007). Besides, being traditionally exploited throughout its range, it is a good model to assess the effects of distinct management strategies (Caputo et al., 2005).

Understanding the effects of distinct levels of harvesting and conservation strategies on wildlife populations is crucial for conservation and conservation-related management (Lande et al., 1997). Distinct management systems have distinct effects on target populations, and they need to be evaluated. Regarding the Amazon river turtles, few studies have described harvesting models, and discussed how it possibly affected the populations. Where no management initiatives are carried on, general trend is the abundance of *P. unifilis* being negatively related to proximity to human settlements (Conway-Gómez, 2007; Alcântara et al., 2013). By the other hand, positive effects on *Podocnemis* spp. populations were detected from a participatory conservation program in the Mamirauá Sustainable Development Reserve (Camillo et al., 2012) and a community-based management initiative in the lower Amazon (Miorando et al., 2013). Besides, a successful management of *P. unifilis* eggs was experienced among traditional people in the Ecuadorian Amazon (Caputo et al., 2005).

The importance of river turtles as a food source is a main reason to riverine people protect turtle populations in the Amazon (Caputo 2005, Camillo et al., 2012; Pignati et al., 2013). In this sense, community-based management programs are a promising strategy to reach turtle conservation coupled with the traditional riverine way of life in a sustainable way. To reach that, monitoring target populations is an essential part in management programs to sustainable use natural resources.

Temporal and spatial variations of abundance and population parameters, such as adult size distribution, sex ratio, and proportion of immature are usefull indexes to diagnose over-exploitation, selective pressure, and scanty recruitment (Fryxell et al., 2014). Identifying effective methods to sample a target population is a starting point to establish a protocol for monitoring, since parameters of turtle populations are influenced by the capture methods used (Ream & Ream, 1966; Vogt, 2011). Particularly when considering participative or self-sustained monitoring, it is also necessary to consider costs and logistical demands compatible with local conditions. Community-based monitoring programs need to be as simple and inexpensive as possible to allow the communities to maintain it with little external support, or even self-sustained In this sense, simple tools such as morphometric and allometric relationships can be used to simplify data collection of turtle populations in the same way they are used in Fisheries Biology (Hilborn & Walters, 2001).

This study analyzed the population structure of *P. unifilis* captured using three distinct methods/gears during dry season in the lower Amazon floodplain, in a community where *in situ* turtle nesting sites protection coupled with fisheries management occur since 1990 (Miorando et al., 2013; Pignati et al., 2013). Our goals were to i) compare size distribution and sex ratio of *P. unifilis* captured among three distinct techniques used in aquatic bodies available in the dry season; ii) test for temporal variation of a 5-years time gap on size distribution and sex ratio of turtles captured by trawl net; and iii) establish body allometric relationships to simplify data gathering by locals in a participatory monitoring program.

Methods

Study area

Sampling was carried out in the Água Preta community at Santarém floodplain (Figure 1), Lower Amazon. Água Preta was chosen because of its community-based management of *Podocnemis* spp. since 1991; and due to the interest of local dwellers to undertake sustainable management and supportive scientific research on reproduction and population parameters of turtles in their territory.

The lower Amazon floodplain is characterized by low and flat alluvial lands, with higher grounds covered by gallery forests, and lowlands dominated by natural grasses; while free-floating, floating-leaved, and emergent plants are abundant in the water (McGrath et al., 1993; Junk et al., 2011). Climate is tropical monsoon, typically rainy and warm, with annual mean temperature above 26^{o} C, and annual rainfall between 1,900 and 2,200 mm. (Alvares et al., 2013). Rainfall seasonality causes a river level fluctuation of about seven meters between dry (June-December) and flood

(January-May) seasons, a natural dynamics described as the flood pulse concept (Junk et al., 1989). During flooded season, all but the highest levees are underwater, while in the low-water season, all but the deepest water bodies may be reduced to muddy pools (McGrath et al., 1993).

The lower Amazon region is known for the origin and evolution of a spreading co-management fishery system based on Fishing Agreement (McGrath et al., 1993; McGrath et al., 2008). In 2006, INCRA (portuguese acronym to State Colonization and Agrarian Reform Institute) implemented a new settlement and land tenure policy in the lower Amazon, the Agro-Extractive Settlement Project (PAE) where local populations depend on both extractive and productive activities (McGrath et al., 2008). A Plan of Use (PU) encompasses rules to guide natural resource exploitation and other economic activities in each PAE.

Água Preta is located in the PAE Aritapera, and comprises about 60 families that live mainly around the Água Preta lake margins and the adjacent channels, Igarapé do Lago and Água Preta Channel. Fisheries management is controlled by rules established in previous Fishing Agreement (Normative Instruction 11 from 10/14/2004), which includes a year-round prohibition of gill net in the Água Preta lake, and a seasonal prohibition of gill nets in other lakes and channels, always during the dry season when fishes are concentrated in the remaining water bodies. Besides fishing rules, in 1991 a Reserve Area was established by communitarian decision to protect a turtle nesting concentration site, *Tabuleiro* da Água Preta, aiming to maintain its stock for local consumption (Pignati et al., 2013). Inside the Reserve, which includes channels where fish and aquatic fauna concentrate and reproduce during dry season, neither fishing nor harvesting are allowed (Figure 2). Outside the Reserve, the community informally permits harvesting of turtles and their eggs for consumption. Illegal trade is avoided and local robbers and invaders are sometimes caught by local dwellers, IBAMA or SEMMA (Municipal Environmental Secretary of Santarém city) are called, and rarely transgressors are legally punished.

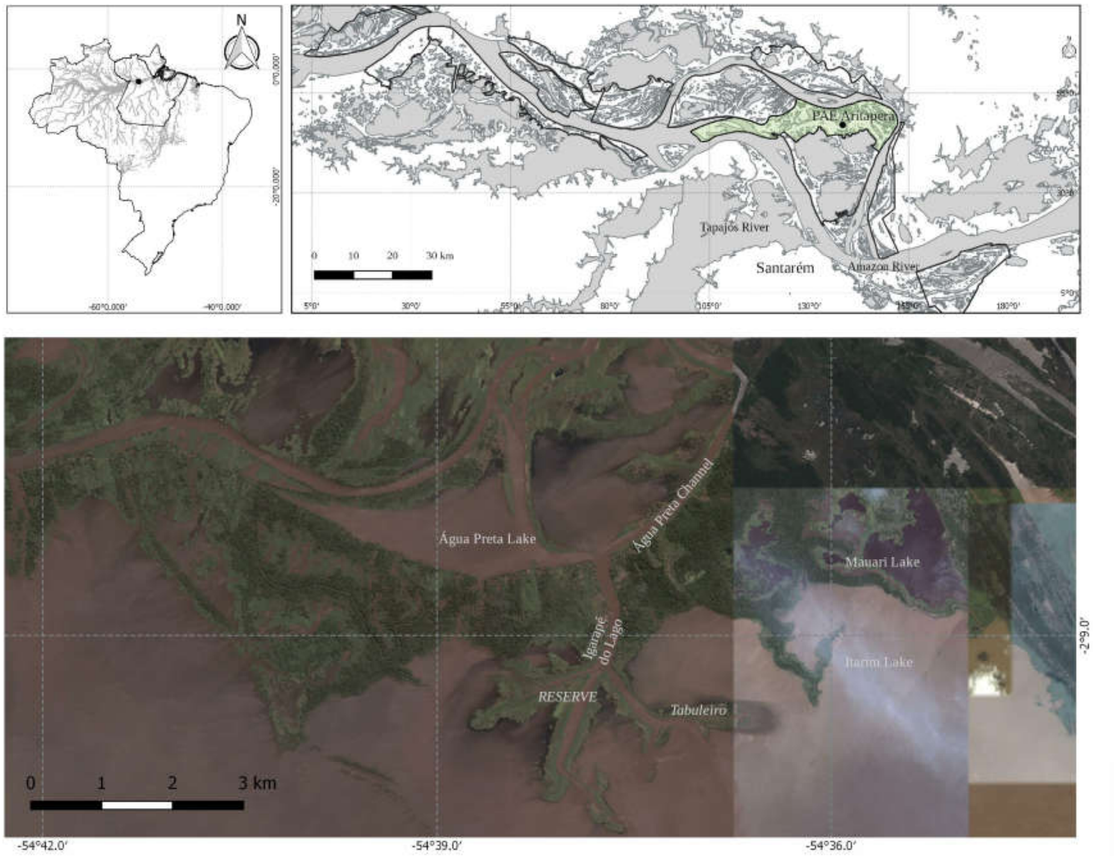

Fig. 1 Community Água Preta located inside the Agroextractive Project (PAE) Aritapera in the Lower Amazon floodplain, Santarém city.

Sampling methods

Community area was sampled in 2009 and 2014 with distinct designs. In 2009, we sampled the remaining aquatic bodies during the receding and dry season, when catchability is greater (Alcântara et al., 2013; Bernhard & Vogt, 2012; Fachín-Terán et al., 2003). Three methods - gill net, cast net and trawl net – were used to sample the distinct aquatic bodies available from August to December (Table 1). Surface trawl net consists on a funnel-shaped net with its mouth tied to a wooden frame that is vertically trawled in the superficial water. The technique is an active method with persecution, created in the lower Amazon to catch *P. sextuberculata* along its migratory routes with commercial purposes (Pezzuti et al., 2010).

From August to October in 2009, gill nets with mesh size from 12 to 30 cm between opposite knots were used to sample *Podocnemis* spp. in interior lakes, channels and near nesting areas (submerged by that time). Six standardized samplings were carried out, each sample unit consisting on three arrangements of five gill nets each, in the water for 24 hours (Miorando et al., 2013). Annually in October, the use of gill nets became forbidden (fishing agreement in the PU) and then gill nets were not used to sample turtles October ahead. In November and December, cast net was used by local dwellers to sample turtle population at muddy pools, shallow lakes and margins of the *Água Preta* lake. Nine samplings were made with the help of one or two fisherman (1-2) and a variable number of throws (31-134) considering the size of the waterbody sampled (Table 1). At same time, deeper (>1.5 m) portions of channels and lakes were sampled by trawl net.

Trawl net was used in *boiadores*, deep pools where turtles are seen concentrated in the water surface. *Boiadores* were sampled in the Igarapé do Lago channels, located in the proximal border of the Reserve, Água Preta Lake (gill nets not allowed), and once at Água Preta Channel. In 2014, only *boiadores* in the Igarapé do Lago were sampled as a local decision in order to maximize capture with minimal effort (higher yields). Samplings were executed by a team composed by one or two researchers and by 10 to 20 local dwellers. Finally, in addition to the experimental capture samples, at both years we received collaboration from local fishermen that brought us turtles occasionally captured in their routine fisheries.

Turtle biometry and marking

Turtles were measured to maximum: curved carapace length (CCL, mm) with a metric tape (precision of 1 mm); straight carapace length (SCL, mm), carapace width (CW, mm), carapace height (CH, mm), and plastron length (PL, mm) with a Haglof® Caliper (precision 1 mm); head width (HW, mm) with caliper (precision 0.05 mm); and weighed with spring balance Pesola® scales (precision 100 or 10 g). The animals were individually marked by notches in the marginal scutes and/or tagged with numbered plastic tags. Sex was determined from secondary sexual characteristics, such as head color, and tail length and thickness (Pritchard and Trebbau, 1984). Males and females were considered adults from 177 and 318 mm of SCL, respectively, based on anatomical and histological analysis of 10 gonads of females and 11 of males (Miorando, unpublished data). Individuals smaller than those critical values were considered immature, either if the sex could be confirmed or not. Marked animals were released at same site at capture. All the procedures of capturing, marking, taking morphometry and releasing large numbers of individuals captured by trawl net relied on active participation of at least 10 local dwellers in each sampling.

Data Analysis

Population size structure was described by frequency distribution on a 20 mm of straight carapace length (SCL) size classes. Sex ratio was defined as the male:1female proportion based only on adults (Bury, 1979). Size distributions were compared among capture techniques by a two-sample Kolmogorov-Smirnov (KS) test. To compare for differences of yield between years sampled by trawl net, we used an index of relative abundance (capture per unit effort) calculated as the number of captures divided by the effective minutes of trawling (CPUE = N/min). Differences between 2009 and 2014 was tested by Mann-Whitney test, since data were not normally distributed. Sex ratio was compared between years by chi-square test (Zar, 2010).

Allometric relationships SCL-CCL, SCL-PL and SCL-HW were sex-specific estimated by simple linear regression model $Y = a + bX$. Length-Weight relationship (LWR) were estimated for each sex and life stage (immature, adult and both joint) by the equation $W = aL^b$ (W: weight; L: length). Variables were log-transformed to linearize the equation to $\log W = \log a + b\log L$ (Froese, 2006). Statistical analysis was performed in the program PAST version 3.10 (Hammer et al., 2001).

TABLE 1. Sampling effort to capture *Podocnemis unifilis* in the *Água Preta* community during 2009 and 2014.

Year	Gear	Samplings	Sites	Effort	Mean effort
2009	Gill net	N = 6	Água Preta Lake, Mauari Lake, Água Preta Channel, Igarapé do Lago/Reserve	Three arrangements of five nets each, exposed 24 hours.	Standard
	Cast net	N = 9	Muddy pools around Mauari and Itarim Lakes, and Igarapé do Lago/Reserve; Margins of Água Preta and Itarim Lakes.	Number of throws	57.6 ± 11.4 (31-134)
	Trawl net	N = 9	Igarapé do Lago/Reserve, Água Preta Lake, Água Preta Channel	Minutes trawling	117.8 ± 11.9 (70-170)
2014	Trawl net	N = 5	Igarapé do Lago/Reserve	Minutes trawling	37.6 ± 15.1 (6-95)

Results

In 2009, gill nets captured only 18 individuals (72.2% adults); trawl net captured 1,835 turtles (80.3% adults); and cast net captured 120 (6.7% adults) (Table 2). Size frequency distribution differed significantly between cast net and gill net (KS, D = 0.9417, $p < 0.000$), and cast net and trawl net (KS, D = 0.9144, $p < 0.000$); whilst no significant difference was found between trawl net and gill net (KS, D = 0.1784, $p = 0.621$) (Figure 2A-C). Sex ratio also varied among capture methods. Gill net resulted in the less skewed sex ratio (0.86:1), based only on 13 adults captured; cast net was strongly male-biased; and samplings with trawl net resulted in a sex ratio skewed towards females (Table 2).

More turtles were captured by trawl net in 2009 than in 2014 (Table 2), but mean CPUE in 2009 (1.89 N/min; sd=1.71) was significantly lower (Mann-Whitney $U = 7$; $p = 0.045$) than 2014 (4.47 N/min; sd=3.4), when less effort was spent (Table 3). Taking into account only samplings from Reserve - Igarapé do Lago, there was no significant difference of CPUE between years (Mann-Whitney $U = 7$; $p = 0.54$), despite the still lower average in 2009 (3.11 N/min; sd=2.01). Both years were female-biased, with significant difference between 2009 (0.48:1) and 2014 (0.62:1) ($Chi^2 = 4.20$; df = 1; $p = 0.04$). Size distributions of males and females were unimodal at both years. Female's mode declined one size class from 2009 to 2014, with significant difference on the size distribution between years (KS, D = 0.1232, $p < 0.005$) (Figure 2B, 2D). Despite the male's mode continued in 220-240 mm class in 2014, size distribution was also significant different between years (KS, D = 0.1481, $p < 0.011$).

During 2009 and 2014 dry season, 101 turtles were brought by local fisherman, all while using cast net (Table 2). Captures occurred mostly in the Itarim Lake, an extensive and shallow muddy lake, and it was composed by medium-sized individuals, mostly adult males (32.7%) and immature females (27.2%) (Figure 2E). Their size distribution was significantly different from trawl net (KS, D = 0.69822, $p < 0.000$), gill net (KS, D = 0.77549, $p < 0.000$), and even cast net (KS, D = 48677, $p < 0.000$) due to the higher frequency of medium-sized individuals.

Total captured population was composed by 1,773 females, 721 males, and 71 unsexed immatures. From those, only nine females and two males marked in 2009 were recaptured in 2014. Female SCL distribution was unimodal with mean on 337 mm (sd = 58.96) and highest frequency on 360-380 mm size class. Male SCL distribution was also unimodal, with mean on 226.8 mm (sd = 34.87) and highest frequency on 220-240 size class (Figure 3). By the size of sexual maturity, 1,296 females (73.1%), and 656 males (90.9%) were adults, resulting in a female-biased sex ratio of 0.51:1. Unsexed immature accounted for only 2.8% of individuals, but summed to males and females, immature represented 23.89% of captured population. Mean SCL of adult females was 365.29 mm (sd = 25.76), and mean mass was 5,950 g (sd = 1,280) (Table 4). Adult males measured, on average, 234.61 mm (sd = 24.72) SCL, and weighed 1,560 g (sd = 510) (Table 4). Allometric relationships were all significant to an alpha = 0.05 (p = 0.0001). SCL was better estimated by CCL and PL (minimum r^2 = 0.925), while head width was not a good predictor to estimate SCL of adult females (r^2 = 0.69). LWR (Table 5).

TABLE 2. Captures of *Podocnemis unifilis* at community Água Preta in the lower Amazon floodplain during 2009 and 2014 dry season. Oc. Cast: Occasional captures by local fishermen during routine fishing with Cast net. U: unsexed; M: male; F: female.

	2009						**2014**					
Gear	**Immature**			**Adult**			**Immature**			**Adult**		
	U	**M**	**F**	**M**	**F**	**M:F**	**U**	**M**	**F**	**M**	**F**	**M:F**
Gill net	0	0	5	6	7	0.86:1	-	-	-	-	-	-
Cast net	57	30	25	7	1	7:1	-	-	-	-	-	-
Trawl net	0	15	347	457	1,016	0.45:1	0	1	72	155	274	0.56:1
Oc. Cast	13	12	17	18	1	18:1	1	7	11	15	6	2.5:1
SUM	**70**	**57**	**394**	**488**	**1,025**	**-**	**1**	**8**	**83**	**170**	**280**	**-**

TABLE 3. Turtle capture samplings with trawl net in the community Água Preta in dry seasons of 2009 and 2014.

YEAR	Capture Site	Effort (min)	Captures	CPUE (N/min)
2009	Lago Água Preta	135	176	1.30
	Paraná da Água Preta	150	54	0.36
	Lago Água Preta	74	84	1.14
	Igarapé do Lago	119	683	5.74
	Lago Água Preta	170	194	1.14
	Igarapé do Lago	70	252	3.6
	Igarapé do Lago	82	146	1.78
	Igarapé do Lago	114	150	1.32
	Lago Água Preta	146	96	0.66
	SUM	**1060**	**1835**	
2014	Igarapé do Lago	28	103	3.68
	Igarapé do Lago	6	62	10.33
	Igarapé do Lago	35	112	3.2
	Igarapé do Lago	24	90	3.75
	Igarapé do Lago	95	135	1.42
	SUM	**188**	**502**	

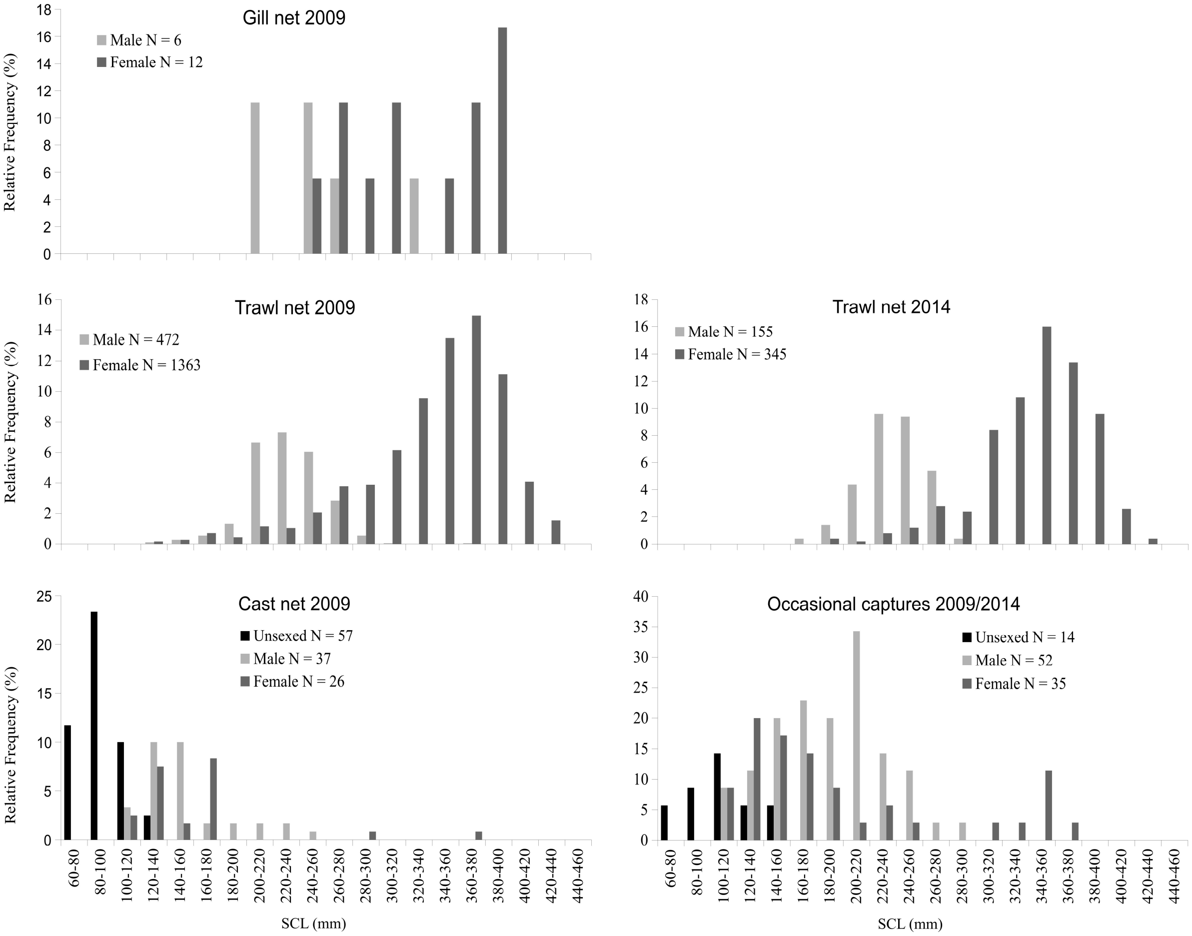

FIG. 2 Size frequency distribution of *Podocnemis unifilis* captured at community Água Preta by (A) gill net in 2009; (B) trawl net in 2009; (C) cast net in 2009; and (D) trawl net in 2014. (E) Occasional captures during routine fishing with cast net in 2009 and 2014.

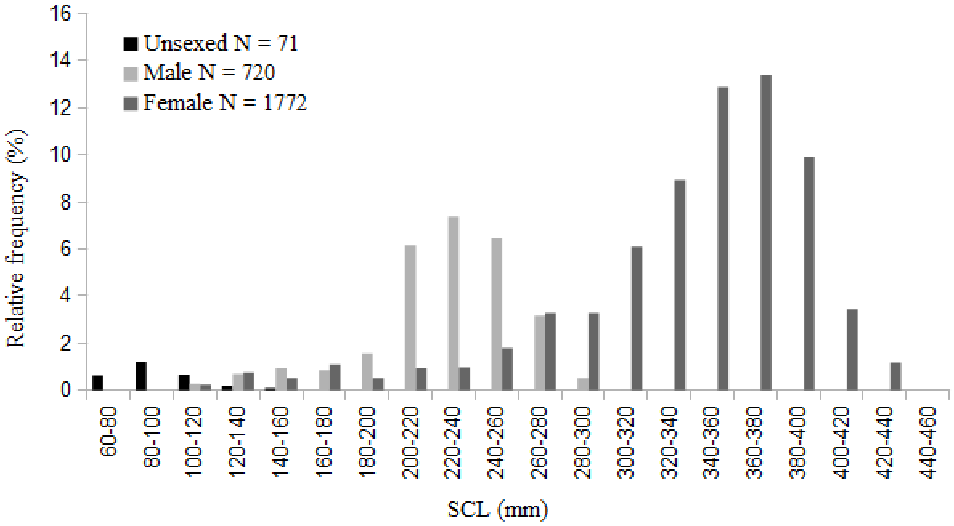

FIG. 3 Size frequency distribution of *Podocnemis unifilis* captured at community Água Preta in the lower Amazon during dry season of 2009 and 2014.

TABLE 4. Morphometric measures (mm) and weight (g) of adult *Podocnemis unifilis* captured in the Água Preta community, lower Amazon floodplain, during dry season in 2009 and 2014. CCL: curved carapace length (mm); SCL: straight carapace length (mm); PL: plastron length (mm); CW: carapace width (mm); HW: head width (mm); Weight (g).

	Adult Males (≥177 mm)		**Adult Females (≥318 mm)**	
	Mean ± SD	**Min-Max (N)**	**Mean ± SD**	**Min-Max (N)**
CCL	256.03 ± 27.27	190–385 (655)	394.89 ± 27.74	322–500 (1,293)
SCL	234.61 ± 24.72	177–361 (656)	365.29 ± 25.76	318–438 (1,296)
PL	203.09 ± 20.71	152–330 (650)	334.08 ± 23.67	286–413 (1,288)
CW	176.29 ± 16.76	136–219 (167)	260.28 ± 23.19	168–189 (270)
Height	89.31 ± 8.30	67–110 (168)	138.25 ± 10.29	117–168 (271)
HW	34.86 ± 3.65	27.75–45.25 (80)	49.20 ± 2.78	43.20–56.30 (59)
Weight	1,570 ± 520	580–5,400 (655)	5,950 ± 1,280	3,400–11,200 (1,293)

TABLE 5. Allometric regressions of *P. unifilis* from Água Preta community (lower Amazon floodplain) captured in 2009 and 2014. LWR: $W = aL^b$ from double-logarithmic transformed data (weight and length). Parameters of simple linear regression ($Y = a + b*X$) are given. N: sample size; CL: confidence limits; R^2: coefficient of determination (all relationships significant at $P < 0.0001$). Measurements (mm). CCL: curved carapace length; SCL: straight carapace length; PL: plastron length; HW: head width. W: weight (g).

					$W = a*SCL^b$			
		X		Y				
Group	N	min	max	min	max	*a*	*b* (95% CL)	R^2
Female; all	1,759	110.9	438	200	1,120	1.851E-07	2.926 (2.906-2.944)	0.99
Female; imm.	467	110.9	317	200	4,400	2.798E-07	2.848 (2.818-2.878)	0.99
Female; adult	1,292	318	438	3,400	11,200	2.414E-07	2.882 (2.825-2.938)	0.89
Male; all	712	106	361	170	5,400	4.805E-07	2.742 (2.705-2.777)	0.97
Male; adult	649	177	361	650	5,400	2.757E-07	2.843 (2.782-2.903)	0.92
					$SCL = a + b*CCL$			
Female; all	1,768	122	500	110.9	438	-0.365	0.925 (0.921-0.929)	0.99
Female; imm.	476	122	367	110.9	317	1.961	0.914 (0.907-0.922)	0.99
Female; adult	1,292	338	500	318	438	10.568	0.898 (0.883-0.912)	0.93
Male; all	717	116	385	106	361	3.758	0.901 (0.893-0.909)	0.98
Male; adult	654	190	385	177	361	6.579	0.890 (0.876-0.905)	0.97

				SCL = a + b*PL				
Female; all	1,755	100.5	413	110.9	438	4.071	1.081 (1.076-1.086)	0.99
Female; imm.	469	100.5	299.7	110.9	317	4.235	1.077 (1.069-1.086)	0.99
Female; adult	1,286	286	413	318	438	15.069	1.048 (1.031-1.066)	0.92
Male; all	713	95	330	106	361	-6.355	1.184 (1.167-1.203)	0.97
Male; adult	650	152	330	177	361	1.747	1.146 (1.114-1.176)	0.94
				SCL = a + b*HW				
Female; all	105	21.4	56.3	111	411	-77.01	8.794 (8.619-8.982)	0.98
Female; imm.	46	21.4	45.6	111	317	-64.455	8.326 (7.968-8.725)	0.98
Female; adult	59	43.2	56.3	318	411	7.7968	7.117 (6.008-8.260)	0.69
Male; all	104	20.1	45.25	106	328	-62.906	8.510 (8.135-8.909)	0.96
Male; adult	80	27.75	45.25	177	328	-34.18	7.717 (7.037-8.422)	0.9

Discussion

Sampling bias is considered one of the main causes to explain skewed sex ratio and unbalanced proportion of juveniles in turtle populations, and may not be overlooked in population studies. Intrinsic selectiveness (such as size), distinct behaviors that turn one sex more prone to capture or death, and distinct habitat use among sexes and life stages may influence the structure of the population sampled by a determined method (Ream & Ream, 1966; Lovich & Gibbons, 1990). Sex ratio and size structure were significantly different among the methods tested in this study. Gill nets were used mainly in the receding water, when it captured adult population in a 0.86M:1F proportion, the most balanced sex ratio among methods. However, total capture was only 18 *P.*

unifilis. Since gill nets captured more *P. sextuberculata* (Miorando et al., 2013), it was probably not the best time to catch *P. unifilis*, which were still under flooded macrophyte banks, according to locals. In the lowest water level phase (from October to December), small juveniles and medium-sized males and females were captured in shallow muddy pools and lakes' margins by cast net, while adults and large immature females were captured by trawl net at high quantities at *boiadores* and around it. Ontogenetic variation in habitat use is common on freshwater turtles (Lovich & Gibbons, 1990; Bodie & Semlitsch, 2000; Bury, 2003; Bernhard & Vogt, 2012), and distinct methods are necessary to access all life stages (Vogt, 2011).

CPUE was high in 2009 and 2014, with more than one individual captured per minute at all samplings with two exceptions. Highest CPUEs were obtained at Reserve border (up to 10.33 N/min), what lays about 200 meters from the nearest house of the community. Água Preta Lake and Água Preta Channel house most part of local dwellers, and both are daily used for displacement and fishing. Presence of human settlements usually implies less Amazon river turtles around (Conway-Goméz 2007; Norris et al., 2011; Alcântara et al., 2013; Conway-Goméz et al., 2014), and the more people in villages, less abundant are the turtles in the river (Bernardes et al., 2014). Direct use is in fact the main cause of local extirpation and extinction of turtle species in the world (Thorbjarnarson et al., 2000). The high numbers of captures obtained in this study (CPUE as an abundance index - Caughley & Sinclair, 1994) are not expected inside a community territory in the Amazon. Ours are the highest among data available in the literature for *P. unifilis* (Fachín-Terán et al., 2004; Félix-Silva, 2009; Alcântara et al., 2013; Miorando et al., 2015).

Besides CPUE, population parameters such as size distribution, sex ratio and recruitment are indexes of population, or stock, status (Caughley & Sinclair, 1994). Temporal variation in female size distribution from 2009 to 2014 may be a sign of a crescent pressure on large gravid females, whose price reach R$50,00 in local market and large human settlements, such as Santarém and Alenquer cities. Adult size reaching maximum values reported in the literature for males and females (Fachín-Terán & Vogt, 2004; Rueda-Almonacid et al., 2007). Long-term monitoring, but not necessary annual, is needed to confirm a population tendency on size distribution of males and females.

Female-biased populations of *P. unifilis,* with exception of the present study, were reported from data on turtle consumption and use in the Amazon (Fachín-Terán et al., 2004; Figueroa & Fachín-Terán, 2013) and Orinoco basins (Chacín, 2010). Sex ratios in populations captured with distinct methods along the Amazon basin are biased with males outnumbering females (Félix-Silva, 2009; Fachín-Terán & Vogt, 2004; Alcântara et al., 2013; Miorando et al., 2015). The cultural preference for large females and their eggs is well known since colonial times (Mittermeier, 1978; Smith, 1979; Johns, 1987), and it is frequently pointed out as a likely cause of male-biased sex ratios (Fachín-Terán et al., 2003; Fachín-Terán & Vogt, 2004; Alcântara et al., 2013). Many natural factors, however, also acts on sex ratio. Among them, Tabuleiro Água Preta location near the Ecuador Line favors solar incidence, and a consequent higher environmental and incubation temperatures. Elevated incubation temperatures promote a faster embryonic development, and favors production of females in this temperature-sex dependent (TSD) species (Bull & Vogt, 1979; Souza & Vogt, 1994; Pignati et al., 2013).

The sex ratio and size structure observed in this study likely resulted from a sampling bias, related to the large amount of turtles captured by trawl net in *boiadores* at Igarapé do Lago (N = 2,337). Towards population monitoring in a participatory system (Danielsen et al., 2009), identification of trawl net as a potential method of capture was an important step. None turtle died during or after trawl net captures, and bycatch of fish or other animals (caimans and river dolphins) that interacts with cast and gill nets did not occur with trawl net. Moreover, trawl net did not suffer damages along the sampling period, what is common when using cast, and, more intensely, gill nets. Trawl net requires lower budget, but higher human resource to help from capture to animal's biometry. Besides, the allometric relationships here established will simplify and decrease time spending in future collection of morphometric data.

Our results show that presence of human settlement may not always be linked to depleted turtle population. Água Preta showed a strategy of rational exploitation of turtles as a food resource coupled with fishing regulation, and the stablishing of a Reserve area where *in situ* nest protection occurs at Tabuleiro Água Preta. Altogether, the management system seems to attend the life stages that are more sensitive in the demography of *Podocnemis* species (Mogollones et al., 2010; Páez et al., 2015), maintaining a healthy population in this area.

Local dwellers, their knowledge and practices, may be both a major ally and a threat to conservation or management of turtle populations (Mittermeier, 1978; Smith, 1979; Caputo et al., 2005; Miorando et al., 2013). Considering the huge extension of the Amazon in Brazil and the inability of the government (municipal, state and federal) to properly cover it, participatory monitoring and sustainable management programs should be encouraged inside and outside Conservation Units. Local (community-based) initiatives to sustainable use is pointed out as an important conservation tool in developing countries that have small budgets (Sinclair & Byrom, 2006; Danielsen et al., 2009). As more populations of *P. unifilis* are protected in a participatory system with local agents, closer we get to objectives of the Amazon turtles' conservation programs

(MMA, 2015), and to conservation of the Amazon socio and biodiversity as a unit.

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Capítulo 4

Trophic plasticity and life-history traits variation of the river turtle *Podocnemis unifilis* between water types in the Amazon basin (Testudines, Podocnemididae)

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Trophic plasticity and life-history traits variation of the river turtle *Podocnemis unifilis* between water types in the Amazon basin (Testudines, Podocnemididae)

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Abstract

Amazon basin is home to diverse aquatic environments among which plasticity of aquatic fauna is poorly known. We compared trophic ecology, and life-history traits (morphology, size at maturity, adult size and reproductive output) between two distinct ecosystems regarding water type and associated landscape: white water floodplain (WFP), and clear water river (CWR). Stable isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ showed a significant wider $\delta^{13}C$ range, and a larger niche breadth at WFP. The wider range of carbon and isotopic niche reflect a wider range of food sources explored in the WFP. Shell shape differed between areas and sexes. Females had larger plastron and higher shell at both areas, and individuals from CWR had a wider carapace, while those from WFP had a more domed-shaped carapace. Size at maturity (SM) in WFP and CWR, respectively, was 177 and 184 mm for males; 318 and 301 mm for females. Adult males did not differ in size between areas, but males from WFP were heavier than those from CWR. Adult females were significantly larger and heavier in WFP than in CWR. Mean clutch size was smaller, but eggs were heavier in CWR than in WFP. Variations are discussed under the better trophic condition hypothesis.

Keywords: morphology, size at maturity, size structure, reproductive output, trophic ecology, carbon and nitrogen stable istope analysis

Introduction

When environmental conditions vary along a species distribution, it is unlikely that a single phenotype can confer high fitness throughout the environments. Wide-distributed species, such as *Podocnemis unifilis*, are usually submitted to distinct environmental pressures that lead to plasticity among populations (Via et al., 1995). Phenotypic variation of life-history traits has important ecological impacts on population dynamics, and it should be considered in conservation and management plans to reach a sustainable use of river turtles in the Amazon.

Body size is a main trait that influences primary fitness components such as survivorship (vulnerability to predation), fecundity and reproductive success that, in turn, influence population dynamics in virtually all organisms (Stearns, 1992). In turtles, whose ecology is marked by the presence of a rigid carapace that cannot expand to accommodate enlarged ovaries, size has a strong effect on clutch size, egg mass and total clutch mass across turtle taxons (Congdon et al., 1983;

Valenzuela, 2001; Bonach et al., 2006; Litzgus & Mousseau, 2006; Ryan & Lindeman, 2007; Rollinson & Brooks, 2008). Adult body size is linked to the size at which organisms reach sexual maturity (Gibbons & Lovich, 1990; Congdon & van Loben Sels, 1993), a less studied trait that may also be plastic among sexes and populations (Tinkle, 1961; Gibbons et al., 1981).

Virtually any environmental condition, biotic or abiotic – may promote plasticity of one or more character in organisms (Forsman, 2014). In freshwater turtles, variation on body size and reproductive output are the main researched traits regarding plasticity among freshwater turtles, particularly along temperature-latitudinal gradient in North America (Tinkle, 1961; Iverson & Smith, 1993; Litzgus & Mousseau, 2003; 2006). In other geographical scales, size and size-related traits plasticity was suggested as a function of variation in productivity (food availability) (Iverson & Smith, 1993; Lefebvre et al., 2011), and selective harvesting pressure (Close & Seigel, 1997). In more productive environments, growth rates were higher and promoted larger adult body size in *Emydoidea blandingii* (Graham & Doyle, 1977), and *Actinemys marmorata* in the United States (Bury et al., 2010); and in *Emydura macquarii macquarii* from Australia (Judge, 2001). In *Graptemys ouachitensis,* Moll (1976) observed a higher growth rate in juveniles, but it was not reflected in adult body size.

Amazon, the largest fluvial system in the world, homes a high diversity of aquatic environments to which adaptations of the aquatic fauna are poorly known. Aquatic environments are basically classified regarding its water type: black, white, and clear water types reflect geomorphological and physical-chemical variations associated to the drainage areas of the distinct rivers in the Amazon basin (Sioli, 1984; Junk et al., 2011). Neutral-pH white water rivers originate in Andean and Pre-Andean region, carrying great amounts of fine-grained sediment and essential nutrients that allow high development of phytoplankton and aquatic macrophytes (Junk & Piedade, 1997). The floodplain annually flooded by white water is considered the most productive aquatic system in the Amazon (Junk et al., 2011). Clear water rivers originate at Precambrian shields, and are low to neutral-pH, poor in nutrients and sediments, resulting in higher transparency and lower productivity than white water ecosystems (Sioli, 1984; Junk et al., 2011).

Variation of primary productivity among water types in the Amazon possibly influence the availability and quality of food for *Podocnemis* spp., whose diet is opportunistic mainly composed by plants (Fachín-Terán et al., 1995; Balensiefer & Vogt, 2006). *P. unifilis* living under distinct food source availability may present differences on growth rate, age or size at sexual maturity and maximum size attained by adults. Body size, in turn, is known to influence the production of eggs by females in function of reproductive allometric relationships (Pignati & Pezzuti, 2012).

Podocnemis unifilis (Troschel 1848) is a medium-sized species with sexual size dimorphism towards females, which can reach up to 50 cm of carapace length weight up to 12 kg, while males maximum carapace length is 33.5 cm (Pritchard & Trebbau, 1984; Rueda-Almonacid et al., 2007). It inhabits lentic and lotic aquatic bodies in black, clear and white waters in the Amazon, Orinoco and Tocantins-Araguaia basins. Home range of the species is considered relatively restricted (Bock et al., 1998; Leão, 2015), smaller than those of other species of this genus (Fachín-Teran et al., 2006; Carneiro et al., 2015).

Information on reproductive biology is available to a great extant of the species range (Pritchard & Trebbau, 1984; Fachin-Terán & von Mülhen 2003; Haller & Rodrigues 2005; Pantoja-Lima et al. 2009; Ferreira-Jr & Castro, 2010; Pignati et al., 2013a; 2013b). Vanzolini (2003), in an among-population comparative analysis, detected geographical variation on clutch size and egg volume in *P. unifilis* and *P. expansa,* but with no clear pattern. At same year, Fachín-Terán & von Mülhen (2003) suggested that higher productivity of white water floodplain may explain the larger *P. unifilis* clutches found in these areas. Clutch and egg sizes are related to maternal size in *P. unifilis* (Pignati & Pezzuti, 2012), and then observed geographical variation in reproductive parameters may rely on variation of body size among those populations. However, just a few data on females' size were available and no pattern could be stated (Vanzolini, 2003). Size at maturity is not known for males or females, with minimum size of nesting females, and anecdotal information used to describe populations (Fachín-Terán & Vogt, 2004; Chacín, 2010). All *Podocnemis* spp. are currently listed in the IUCN Red List, *P. unifilis* is considered "Vulnerable", but it needs update (IUCN, 2011).

We compared trophic ecology, size at maturity, adult size, morphology, and reproductive output between two distinct areas regarding the water type and associated landscape in the Amazon: a clear water river with rapids (CWR) and a white water floodplain (WFP). We hypothesized that i) the nutrient-rich WFP provides more food sources to the herbivorous *P. unifilis* and then individuals from the lower Amazon mature at and attain larger size than individuals from the Iriri River (CWR); ii) populations shows morphological plasticity as adaptation to distinct abiotic and biotic factors under which individuals are submitted in each ecosystem; iii) related to differences in productivity, reproductive output parameters (clutch size and mass, egg mass) are higher in the WFP.

Materials and methods

Study area

The study was carried out at two typical aquatic ecosystems in the Amazon, the whitewater lower

Amazon floodplain (WFP) and the clear water Iriri River (CWR) (Fig. 1). Lower Amazon floodplain width reaches 40 km, characterized by low and flat alluvial lands, where higher grounds are covered by gallery forests, while the lowlands are dominated by natural grasses. In water, free-floating, and emergent plants prevail. Herbaceous plants predominate on mud banks along the main river channels and in lakes (Junk et al., 2011). During high water season, all but the highest levees are underwater. As the water recedes, sandbars emerge on the river channels, and the littoral lakes are exposed, providing nesting sites for a range of birds, iguanas, and turtles. During the low-water season, all but the deepest portions may be reduced to muddy pools (McGrath et al., 1993). The lower Amazon region is recognized by community-based management initiatives of fisheries in development since 1970 (McGrath et al., 1993; Castro & McGrath, 2003). Sampling was carried out at *Água Preta* community, which protect a turtle nesting beach, and have internal rules to prevent turtles being captured for illegal trade (McGrath et al., 2008; Miorando et al., 2013).

Iriri River is about 1,300 km long from its headwaters in the *Serra do Cachimbo* to its mouth on the left margin of the Xingu River at Pará State. Flooded width by the Iriri river do not excede five kilometers comprising many vegetated islands of varied sizes in the river channel. During the high water season, the marginal alluvial rain forest and islands are flooded and provides food source to aquatic fauna. However, because margins are usually steep, flooded forest availability is shorter than in the lower Amazon floodplain. In the low water season only deep pools and extensive shallows remain in the river bed, along with islands, sand banks and rocky rapids that emerge. *Podocnemis unifilis* nests in a variety of substrates, mainly sandy banks and pebbly beaches that emerge on islands and river margins. Sampling was undertaken in a 200 km section inside the Terra do Meio Ecological Station (TMES). Besides most families left the area when the Protected Area was created (2005), today about 17 families still live in the Iriri margins inside TMES, depending on natural resources from the river and the forest for their subsistence (ICMBio-MMA, 2015).

Turtle capture, marking and biometry

P. unifilis were captured by dip net and diving (description in Alcântara et al., 2013; Miorando et al., 2015) in the Iriri River during 2012 dry season (August and October), and 2013 flood (May) and dry seasons (August and October). In the lower Amazon, turtles were captured by gill net, casting net and trawl net in 2009 dry season (from August to December), by traps under logs in 2014 flood season (June) and by trawl net in 2014 dry season (November and December).

Turtles were measured to the maximum measures of straight carapace length (SCL, mm), carapace width (CW, mm), carapace height (CH, mm), and plastron length (PL, mm) using a

Haglof® Caliper (precision 1 mm); head width (HW, mm) with a Mitutoyo® caliper (precision 0.05 mm); and weighed with Pesola® scales (precision on 100 or 10 g). Turtles were individually marked by notches in the marginal scutes and/or tagged with a numbered plastic tag. Sex was determined from secondary sexual characteristics, such as head color, and tail length and thickness (Pritchard & Trebbau, 1984).

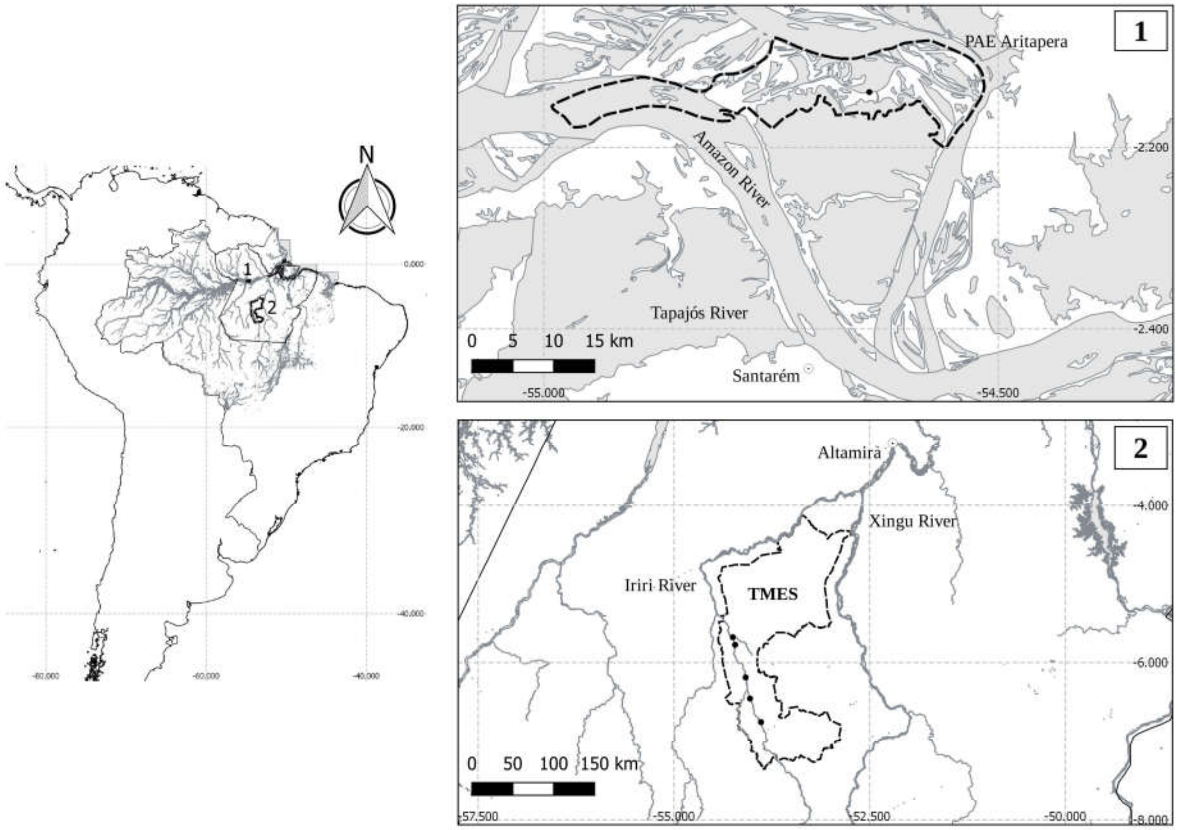

Fig. 1 Location of study areas: (1) Água Preta community (●) in the Agroextractive Project (PAE) Aritapera, Santarém, lower Amazon River floodplain; and (2) sample sites (●) in the Iriri River inside Terra do Meio Ecological Station (TMES), Pará.

Trophic ecology

Trophic ecology was elucidated by analysis of stable isotopes of ^{13}C and ^{15}N, on the assumption that isotopic signatures of a consumer is derived from the pool of its dietary itens (Peterson & Fry, 1987). Value of $\delta^{15}N$ is an index of trophic level due to the natural progressive increasing of $\delta^{15}N$ along the food web, what leads consumers' tissues $\delta^{15}N$-enriched by 3 to 5‰ compared to its food sources (Minagawa & Wada, 1984; Peterson & Fry, 1987; Vander-Zanden & Rasmussen, 1999). Value of $\delta^{13}C$, in turns, allows the identification of food sources assimilated by consumers due to distinct signatures among primary producers as a result of the distinct photosynthetic via (Smith & Epstein, 1971). Main distinction occurs among plants with C4 photosynthetic pathway (more $\delta^{13}C$-enriched) and others primary producers. Phytoplankton, in the opposite side, is the more $\delta^{13}C$-depleted primary producer (Forsberg et al., 1993; Araújo-Lima et al., 1986).

We collected skin samples of the outer edge of hind legs from 44 turtles in CWR (20M:24F), and from 65 turtles in WFP (36M:29F) during flood and dry seasons at both areas. SCL mean ± sd (range) of males was 227.27 ± 39.1 mm (93.5 – 275) in the Iriri River, and 218.19 ± 42.63 mm (106 – 290) in the lower Amazon. Sampled females from Iriri River was 266.26 ± 59.44 mm (112.2 – 375), and those from the lower Amazon was 281.79 ± 88.16 mm (111 – 434). Samples were frozen and transported to Laboratory of Fisheries Biology and Management of Aquatic Resources/UFPA. Samples were cleaned in distilled water, washed to extracted lipids (solution 2:1 of chloroform:methanol), and dried at 50º.C for 24 hours. Thereafter, samples were fragmented into small pieces with blazer, and 0.8 - 1 mg were sealed into 5x9 mm tin caps. Isotopic composition were determined using a Elementar Costech ECS 4010 elemental analyzer interfaced with a ThermoFisher Scientific Delta V Advantage mass spectrometer at the University of New Mexico Stable Isotope Facility (Albuquerque, NM, USA). Stable isotope results are expressed as δ values (parts per thousand, ‰), $\delta^{13}C$ or $\delta^{15}N = 1000 \times [(Rsample - Rstandard/Rstandard) - 1]$, where Rsample and Rstandard are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The internationally accepted standards are Vienna Peedee Belemnite limestone (V-DB) for carbon and atmospheric N_2 for nitrogen.

Analysis of gonads for sexual maturity

Reproductive tract was collected from a sample of 53 and 21 specimens from Iriri River and lower Amazon, respectively; after they had been anesthetized and humanly sacrificed (Ethics Committee for Research on Animal Experimentation of the Federal University of Pará - CEPAE / UFPA; Case 211-14). Gonads were fixed at 4% neutral formalin and transported to the Laboratory of Cellular Ultrastructure/UFPA. Fragments of testis were subjected to routine procedures to paraffin inclusion (Prophet et al., 1995) for histological analysis. From each fragment, six 5µm-thick sections were obtained by microtome Leica RM2205, stained with hematoxylin-eosin, and analyzed under light microscope NIKON Eclipse Ci coupled to a digital camera NIKON DS-Ri1. Males' sexual maturity was indicated by the presence of free spermatozoa in the lumen of seminiferous tubules or extra-testicular ducts (Gibbons, 1968; Ernst, 1971). Females' gonads were morphologically analyzed and sexual maturity determined by the loose appearance of ovaries and by the presence of at least one of the characteristics: i) enlarged oocyts (>15 mm diameter); ii) shelled eggs in the oviducts; or iii) *corpora albicans* in ovaries (Gibbons, 1968; Ernst, 1971). For each sex, we presented the minimum size at maturity and the L_{100}, size from which all individuals are mature.

Reproductive biology

Nesting sites were daily visited early in the morning to find fresh nests of *P. unifilis* during August 2013 in the Iriri River, and during October 2014 in the lower Amazon. Nests were open, eggs counted, and a sample of 10 eggs per nest were measured to maximum length (mm) and width (mm) with Mitutoyo® caliper (precision 0.1 mm); and weighed with Digital Pesola balance (precision 0.1 g). Eggs were put back into the nest together with the sand previously removed.

Data analysis

Data on $\delta^{13}C$ e $\delta^{15}N$ were compared between populations by a Univariate Permutational Analysis of Variance (Univariate PERMANOVA) (Anderson, 2001). Isotopic signatures were plotted in a bi-plot space from where niche metrics were calculated. Niche breadths were calculated by total area (TA) of convex hulls, and by the standard ellipse areas corrected for small sample sizes (SEAc). Overlap among ellipses was also calculated in order to quantify the trophic overlap between populations. Isotopic analyses were performed in R statistical program using the Stable Isotope Bayesian Ellipses (SIBER) package (Jackson et al., 2011). Isotopic data analysis was performed on PRIMER® v.6, and on R (R Core Team, 2014).

Comparative analysis on body size and weight were performed on data of adult population, based on the minimum size at maturity determined to each study area. Size (SCL) and weight data were sex-specific compared between areas by Univariate PERMANOVA. Length-weight relationship (LWR), $W = \underline{a}L^{b}$ (W: weight; L: length) (Froese, 2006), were sex-specific estimated from individuals captured only in dry season to avoid bias from natural weight variation along the year. Data was log-transformed to linearize LWR equations, and slopes were sex-specific compared between populations by an Analysis of Covariance. Morphology was analyzed from straight measures of shell (SCL, CW, CH and PL) and head (HW) of all sexed individuals. Measures were standardized by the SCL to remove size effect. A Canonical Analysis of Principal Coordinates (CAP) was performed with sex and area combined as the factor for groups, and with four axes ($m = 4$) non-arbitrary chosen

(Anderson & Willis, 2003). Total clutch mass was estimated by the product of mean egg mass (sampled N = 10) by the number of eggs in the clutch. Clutch size, total clutch mass, egg length, egg width, and egg mass values were compared between areas by Univariate PERMANOVA. Data analysis were performed on PRIMER® v.6 (Clarke & Gorley, 2006).

Results

Trophic ecology

Mean ± sd δ^{15}N were 9.3 ± 0.8‰ (7.4 – 10.9; N = 44) in the CRW and 9.0 ± 1.1‰ (6.5 – 11.5; N = 65) in the WFP, with no statistical difference between populations (t = -1.8257; P = 0.0707). Significant difference between populations was detected in δ^{13}C values (*Pseudo-F* = 67.505; $P <$ 0.001), with individuals from WFP more enriched (-24.9 ± 1.3‰) and with a wider range, from -27.5 to -21.2 (N = 65), than individuals from CWR, with -26.6 ± 0.6‰, and varying from -27.9 to -24.1 (N = 44). The wider range of δ^{13}C values at WFP reflect a higher diversity of autotrophic sources exploited by *P. unifilis* in the lower Amazon floodplain. Total area (TA) of the convex hulls formed by the points of individuals from each population was 20.3 ‰^{2} and 8.3 ‰^{2} for WFP and CWR, respectively (Fig. 2A). Isotopic niche breadth revealed by SEAc was significantly larger (P < 0.0001) at WFP (mean = 4.4 ‰^{2}) than at CWR (mean = 1.5 ‰^{2}) (Fig. 2B).

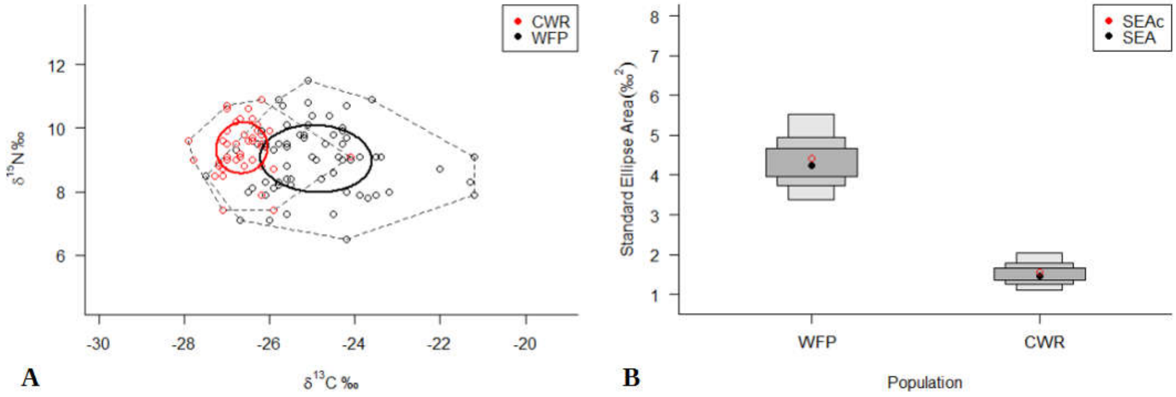

Fig. 2 (A) Isotopic niche area of *P. unifilis* from whitewater floodplain (WFP) - lower Amazon (N = 65), and from the clear water (CWR) - Iriri River (N = 44). Convex hulls (dashed line) delimited the total area (TA) of isotopic niche; and Standart Ellipses Areas corrected (SEAc) delimited by colored lines. (B) Modes, and 50%, 95% and 99% credible intervals of SEA and SEAc estimates.

Size at maturity

Males sampled in the Iriri River ranged from 93.5 mm to 260 mm (N = 28). Only the smaller individual (SCL = 93 mm) was immature, while all others from 184 mm were adults. No gonad was sampled from males between 93.5 and 184 mm SCL. In the lower Amazon, sampled males ranged from 160 to 220 mm (N = 11). Individuals measuring up to 170 mm SCL were immature, and all individuals above 177 mm were adults. Minimum size at maturity coincided with L_{100} in males from both areas. Sampled females in the Iriri River ranged from 252 to 377 mm (N = 25). Minimum size at maturity was 301 mm SCL, and L_{100} was 310 mm. Immature were observed up to 306 mm. In the lower Amazon, sampled females ranged from 291 to 355 mm (N = 10). Minimum size at maturity was 318 mm, and L_{100} was 333 mm. Five females between 324 and 330 mm were immature.

Body size

Totals of 2,565 and 1,028 adult individuals were captured in the lower Amazon and Iriri River, respectively. Adult females from lower Amazon (N = 1,196) were significantly larger and heavier than those from Iriri River (N = 73) (Table 1). Largest female from WFP measured 438 mm and weighed 9,200 g, while the heaviest was 11,200 g with 410 mm SCL. In the CWR, the largest female measured 403 mm SCL and weighed 6,900 g. Males mean SCL was not significantly different between WFP (N = 656) and (N = 704), but males from lower Amazon were significantly heavier than those from Iriri River (Table 1). In WFP, largest male were 361 mm and 5,400 g; while in the CWR, largest male measured 303 mm with 2,300 g, and the heaviest weighed 2,450 g with a SCL of 288 mm. LWRs showed that individuals accumulated more weight per unit of growth in carapace length in the lower Amazon than in the Iriri river (Table 2). Sex-specific comparison of *b* parameter resulted in significantly higher values for males ($F = 55.781$; $P < 0.0001$) and females ($F = 4.011$; $P = 0.045$) from the lower Amazon floodplain.

Morphology

A clear separation of groups were observed in CAP, with individuals significantly grouped according its sex and area ($\delta_{21} = 0.89$, $P = 0.001$) (Fig. 3). Overall leave-one-out allocation success was 93.75% (*i.e.*, 6.25% misclassified error) (Table 3). Correlations with CAP axis scores indicated that difference between sexes was driven mainly by a longer plastron in females; while variation between areas was driven by individuals with a wider carapace in Iriri River, and a higher shell in the lower Amazon floodplain (Fig. 3).

Table 1. Morphometric data on adult males and females from Iriri River inside Terra do Meio Ecological Station (2012 and 2013), and from the lower Amazon floodplain (2009 and 2014), PA. *significant difference $p < 0.001$ on Univariate PERMANOVA. NS: non significant.

	Iriri River	Lower Amazon floodplain	*Pseudo-F*
MALES			
SCL (mm): N	704	656	
Mean±sd (mín-máx)	234.29 ± 23.23 (184-303)	234.61 ± 24.72 (177-361)	0.0679^{NS}
WEIGHT (g): N	698	654	
Mean±sd (mín-máx)	1,380 ± 350 (650-2,450)	1,560 ± 510 (650-5,400)	61.53*
FEMALES			
SCL (mm): N	73	1296	
Mean±sd (mín-máx)	333.30 ± 22.21 (301-403)	365.29 ± 25.76 (318-438)	108.04 *
WEIGHT (g): N	70	1293	
Mean±sd (mín-máx)	4,030 ± 820 (2,600-6,900)	5,950 ± 1,280 (3,400-11,200)	152.43*

Table 2. Length-weight relationship (LWR) of *P. unifilis* from Iriri River (August and October 2013 and 2013) and from lower Amazon floodplain (November – December 2009 and 2014). F: females; M: males; WFP: white water floodplain; CWR: clear water river; SCL straight carapace length; W: weight; N: sample size; CI: confidence interval; R^2: coefficient of determination (all relationships significant at $P < 0.0001$).

						LWR ($W = a*SCL^b$)		
		SCL (mm)		W (g)				
Group	N	min	max	min	max	*a*	*b* (95% CI)	R^2
F - WFP	1758	110.9	438	200	11,200	1.851E-07	2.926 (2.907-2.944)	0.99
F - CWR	245	179	403	680	6,900	2.233E-04	2.867 (2.809-2.921)	0.97
M - WFP	712	106	361	170	5,400	4.805E-07	2.742 (2.705-2.776)	0.97
M - CWR	707	167	303	450	2,450	1.9E-06	2.469 (2.402-2.537)	0.89

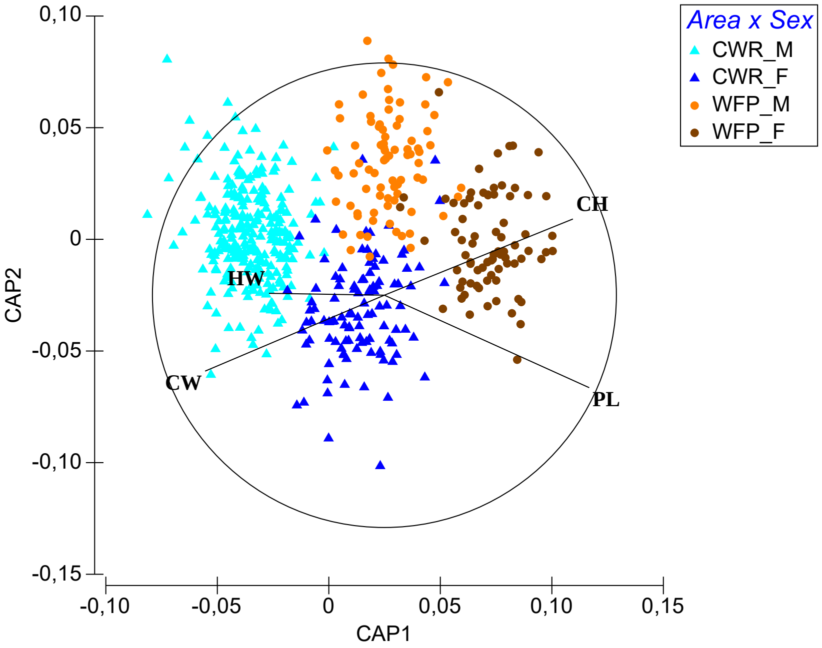

Fig. 3 Canonical Analysis of Principal Coordinates (CAP) of morphological data on *P. unifilis* males and females from Iriri River and lower Amazon floodplain. HW: head width; CW: carapace width; CH: carapace height; PL: plastron length.

Table 3. Diagnosis of Canonical Analysis of Principal Coordinates (CAP) on morphological data of *P. unifilis* males and females from Iriri River and lower Amazon floodplain.

Group	Classified as:				TOTAL	% correct	δ^2	*P*
	CWR - M	CWR - F	WFP - M	WFP - F				
CWR - M	255	7	2	0	264	96.591	0.89	0.001
CWR - F	3	95	5	3	106	89.623		
WFP - M	0	5	72	4	81	88.889		
WFP - F	0	1	3	73	77	94.805		
						Total = 93.75%		

Reproductive output

A total of 52 and 49 nests were opened at lower Amazon and Iriri, respectively. Clutch size was significantly greater in the lower Amazon, but eggs from Iriri were significantly longer, wider and heavier than those from the lower Amazon (Table 4). Estimated total clutch mass varied from 199.1 to 747.9 g (mean = 475.85; sd = 124.69) in the Iriri River, and between 291.85 and 1,099.72 g (mean = 677.94; sd = 208.67) in the lower Amazon.

Table 4. Reproductive data of *P. unifilis* nests from Iriri River inside Terra do Meio Ecological Station (2013) and from the lower Amazon floodplain (2014). sd: standard deviation; *significant difference $p < 0.001$ on Univariate PERMANOVA.

	Iriri River	**Lower Amazon floodplain**	***Pseudo-F***
Clutch size			
Mean ± sd	17.55 ± 3.82	29.40 ± 6.34	127.47*
Range (N)	11 – 27 (N = 49)	13 – 44 (N = 52)	
Egg length (mm)			
Mean ± sd	46.86 ± 2.19	43.41 ± 1.99	667.28*
Range (N)	40.9 – 53.6 (N = 490)	36.2 – 51.2 (N = 498)	
Egg width (mm)			
Mean ± sd	31.49 ± 1.61	29.75 ± 2.15	208.87*
Range (N)	25.5 – 35.8 (N = 490)	21.9 – 35.8 (N = 499)	
Egg mass (g)			
Mean ± sd	26.94 ± 3.24	22.73 ± 3.36	408.7*
Range (N)	16 – 35 (N = 490)	14.8 – 31.7 (N = 520)	
Clutch mass (g)			
Mean ± sd	475.85 ± 124.69	677.94 ± 208.67	34.38*
Range (N)	199.1 – 747.9 (N = 49)	291.85 – 1099.72 (N =52)	

Discussion

We found significant differences between populations regarding trophic niche, adult size and weight (and its relationship - LWR), shell shape and reproductive output. Stable isotope analysis clearly showed a wider trophic niche explored by *P. unifilis* in the white water floodplain than in the clear water Iriri River. Difference was driven by the wider range of $\delta^{13}C$, since populations had similar ranges regarding $\delta^{15}N$. Similarity of $\delta^{15}N$ between populations suggests they occupy the similar trophic level at both communities, since ^{15}N enrichment occurs in each step along food webs (Peterson & Fry, 1987; Vander-Zanden & Rasmussen, 1999). Both populations were $\delta^{15}N$-enriched compared to *P. unifilis* population from Araguaia River (clear water), whose mean and range was 7.59‰ (4.87 to 10.27‰) (Lara et al., 2012). Comparisons, however, need to be cautiously interpreted because they analyzed claw samples, and variation of metabolic pathways among tissues may lead to variation on isotopic signature. We agree that, as pointed out by Lara et al. (2012), stable isotope analysis suggest that *P. unifilis* may feed more on animal matter than stomach content analysis had revealed (Fachín-Terán et al., 1995; Balensiefer & Vogt, 2006). Mean value and range of $\delta^{13}C$ observed in Iriri River were similar to those reported to Araguaia River (mean = -26.2‰; -28.07‰ to -24.05‰) (Lara et al., 2012), and both were $\delta^{13}C$-depleted and whithin a narrower range when compared to lower Amazon values. $\delta^{13}C$ signature of *P. unifilis* from Iriri and Araguaia river are compatible with signatures of C3 plants that compose the flooded forest (Forsberg et al., 1993; Lara et al., 2012). Stomach content analysis of *P. unifilis* from Guaporé, middle Solimões and Iriri rivers (Fachín-Terán et al., 1995; Balensiefer & Vogt, 2006; Oliveira, unpub. data). Algae, phytoplankton, and periphyton were also recognized in stomach contents in the Iriri River (Oliveira, unpub. data) and other areas in the Amazon (Fachín-Terán et al., 1995; Balensiefer & Vogt, 2006), and their $\delta^{13}C$ signatures (Forsberg et al., 1993; Benedito-Cecílio et al., 2000) are also consistent with the range observed in turtles from Iriri River. The wider isotopic niche and the $\delta^{13}C$-enriched signatures in the lower Amazon likely reflect the known higher aquatic flora availability in the whitewater floodplain, specially due to the presence of vast banks of C4 macrophytes (*Paspalum* spp., *Echinochloa polystachya*), that are the most $\delta^{13}C$-enriched primary producer (Forsberg et al., 1993). Such macrophytes are absent in the Iriri River.

This is the first study to present comparative data on life-history traits of Amazon river turtles (*Podocnemis* spp.) under the hypothesis of better trophic condition (Wootton, 1973; Duponchelle et al., 2007). Sexes did not respond in the same way to environmental variation. For females, differences of size at maturity, and adult size and weight were consistent with the better trophic condition hypothesis, while males did not differ regarding sexual maturity and adult sizes. Only weight of adult males differed between populations. The size at maturity around 180 mm observed in this study is smaller than the estimated values of 250 mm SCL in the Guaporé River (Fachín-Terán et al., 2004), and than the geometric mean size of 279 mm CCL at Middle Orinoco (River by Chacín, 2010). Females matured 2 cm smaller size in the Iriri River than in the lower Amazon. Minimum size at maturity and L_{100} at both areas were smaller than the 350 mm SCL considered by Fachín-Terán et al. (2004), but larger than the minimum 270 mm SCL observed in the Colombian Amazon by Foote (1978).

Linked to size at maturity, females from the lower Amazon reached larger size than those from Iriri River. Populations with larger females, reaching up to 465 mm SCL and more than 10 kg, were found in the Peruvian and Colombian Amazon (Pritchard & Trebbau, 1984), Guaporé River (Fachín-Terán & Vogt, 2004), and lower Amazon floodplain (Miorando et al., in prep.); and populations with smaller females, with SCL up to 405 mm and 7 kg, were found in the Xingu River (Alcântara et al., 2013), Iriri River (Miorando et al., 2015), and Tocantins River in the Tucuruí Dam reservoir (Félix-Silva, 2009). Males size are less divergent among cited populations, but a few larger individuals were observed in Guaporé (largest with 396 mm) and lower Amazon floodplain (largest with 361 mm), and males reaching smaller sizes in Tucuruí Dam Reservoir (up to 271 mm and only 2 kg) (Félix-Silva, 2009). LWR showed that individuals accumulate more biomass per unit of growth in the whitewater floodplain than in the clear water river sampled. Individuals were weighed during dry season, when the difference of food supply between these areas is pronounced due to the availability of aquatic macrophytes in the floodplain, but not in the Iriri River bed. Under this condition, LWR may have reflected natural differences of weight due to distinct productivity between areas. Differences of LWR is also likely a result of the shell shape variation between areas.

Shell morphology plasticity, with more streamlined shape at Iriri River and a more doomed-shaped in floodplain lakes system, is likely an effect of differences in flow velocity between ecosystems (Rowe, 1997; Rivera, 2008; Selman, 2012). However, other factors such as predation may also lead to shape plasticity in turtles (Vega & Stayton, 2011). Shape variation was also observed between sexes, with females relatively higher and with a longer plastron than males, a common pattern in many turtle species (Rowe, 1997; Brophy, 2006; Selman, 2012), including the congeneric *Podocnemis erythrocephala* (Bernhard & Vogt, 2012). A higher carapace in females is likely related to the greater space required to accommodate enlarged ovaries and shelled eggs (Rowe, 1997).

Female size is well known to influence clutch and egg sizes in distinct taxa of turtles (Rowe, 1994; Valenzuela 2001; Wilkinson & Gibbons, 2005; Bonach et al., 2006; Ryan & Lindeman, 2007). As expected by the larger females in the WFP, clutch size and clutch mass were greater in this area than in CWR. Eggs, however, were larger in length and width, and heavier in CWR than in WFP. Geographical variation on clutch size and egg mass was described in Vanzolini (2003), but with no clear pattern. Based on data available in literature, clutch size is greater in white water floodplains along the Amazon basin (Foote, 1978; Soini, 1996; Fachín-Terán & von Mülhen, 2003) than in clear water rivers (Souza & Vogt, 1994; Haller & Rodrigues, 2005; Félix-Silva, 2009; Ferreira-Jr & Castro, 2010; Arraes & Tavares-Dias, 2014), Colombian llanos (Escalona e Fá, 1998), and Capanaparo River in Venezuela (Thorbjarnarson et al., 1993). Egg mass did not follow the same pattern, with the largest eggs described in the clear water Iriri River by this study, and Araguari River (Arraes & Tavares-Dias, 2014); and smaller eggs with similar mass in white water (Fachín-Terán & von Mülhen, 2003), and clear water rivers (Haller & Rodrigues, 2005; Félix-Silva, 2009). Besides the larger eggs in Iriri, it is important to highlight that estimated total clutch mass was higher in the lower Amazon than Iriri. Due to distinct reproductive strategies among populations, reproductive output should be compared by total clutch biomass, instead of only clutch size or egg mass.

The cost of reproduction is one of the basic postulates of life-history theory, and usually offspring fitness increases with increasing parental investment (Stearns, 1992). Maternal effects on reproductive output of *P. unifilis* was studied only on population from lower Amazon (Pignati & Pezzuti, 2012), and thus interpretations related to female size among the areas cited above are not possible. On the populations addressed in this study, we suggest the distinct allocation of energy on number or size of eggs may reflect adaptation to distinct ecological pressure on eggs and hatchlings. While predators fish species are more abundant in the lower Amazon, the higher transparency and lack of dense aquatic vegetation in the clear Iriri River may turn hatchlings more vulnerable to predation by fishes, birds and caimans. Moreover, the less abundant food source to hatchlings in the Iriri River may also explain a higher parental investment in egg mass in this area.

Based on the two areas sampled in this study, size and size-related traits variation was consistent with the hypothesis of better trophic condition in the white water floodplain, where *P. unifilis* explored a wider trophic (isotopic) niche than in the clear water river. Among fish species, it is well known that variation in food availability can induce phenotypic plasticity in growth rate, and age and size at maturity, being positively related to reproductive output (Hislop et al., 1978; Townshend & Wootton, 1984; Reznik & Yang, 1993). In the Amazon, *Pygocentrus nattereri* attained larger size at maturity, fecundity and condition factor (definition in Froese, 2006) in the white water Mamoré River than in the clear water Itenez River (Duponchelle et al., 2007).

Among turtle species, difference in productivity (food supply) among areas is cited as a likely cause of population variation of ecological traits (Graham & Doyle, 1977; Parmenter, 1980; Gibbons et al., 1981; Iverson & Smith, 1993; Bury et al., 2010; Lefebvre et al., 2011), however, temperature variation along latitudinal gradient is the environmental factor most addressed to explain plasticity among turtle populations (Tinkle, 1961; Gibbons, 1982; Iverson & Smith, 1993; Litzgus & Mousseau, 2003; Litzgus & Mousseau, 2006). Sex-specific variation we observed on *P. unifilis* was likely the pattern described for the turtle emydid species *Pseudemys concinna* in areas that diverged regarding food supply and temperature by Gibbons et al. (1981). At optimal environments (warmer and more productive) both sexes grew at higher rates, males matured at younger ages, but at same size as other populations; while females attained maturity with same age, but at larger size than females from less productive sites (Gibbons et al., 1981). Males respond to better trophic conditions by minimizing age at maturity, and females by maximizing size at maturity. Information on age and growth rate, however, is needed to reach a conclusive diagnosis.

We sampled two very distinct ecosystems in the Amazon basin, areas that diverge regarding geomorphology, water flow regime, water type, vegetation and flood regime. Besides the more diverse vegetation available (not species richness, but presence of aquatic macrophytes in the floodplain), flood season have a longer duration in the lower Amazon than in the steep Iriri River, what provides a longer feeding period in the flooded forest to turtles and other aquatic vertebrates. Incubation temperature influence growth rate, but we do not have data to analyze its effect between study areas. This study described plasticity of shell shape, size and size-related traits of *P. unifilis* populations under distinct ecological pressures among aquatic ecosystems in the Amazon basin. However, it is a long way to a complete understanding of *P. unifilis* responses to the diverse environmental conditions under which populations are submitted along the Amazon and Orinoco basins. Such variations should be accounted for in the elaboration and evaluation of management and conservation practices along the species range.

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ANEXO I – Instrução Normativa Nº 11, DE 14 DE OUTUBRO DE 2004, formalizando o Acordo de Pesca da microrregião do Aritapera, várzea de Santarém, Pará.

DOU de 15/10/2004
GABINETE DA MINISTRA

INSTRUÇÃO NORMATIVA Nº 11, DE 14 DE OUTUBRO DE 2004

A MINISTRA DE ESTADO DO MEIO AMBIENTE, no uso das suas atribuições legais e tendo em vista o disposto no art. 27, § 6º, inciso I da Lei no 10.683, de 28 de maio de 2003, nº art. 3º do Decreto nº 4.810, de 19 de agosto de 2003, no Decreto-Lei no 221, de 28 de fevereiro de 1967 e na Lei nº 7.679, de 23 de novembro de 1988 e na Instrução Normativa nº 29, de 31 de dezembro de 2002; considerando as decisões dos representantes das comunidades de Santa Terezina, Surubi-Açú, Ponta do Surubi-Açú, Cabeça D'Onça, Água Preta, Costa do Aritapera, Ilha de São Miguel, Carapanatuba, Mato Alto, Enseada do Aritapera, Centro do Aritapera e ainda as comunidades da região do Urucurituba: São Ciríaco, Piracãera de Cima, Piracãera de Baixo e Igarapé do Costa Fátima de Urucurituba, Arapemã e Campos de Urucurituba; e considerando o que consta do Processo no 02048.0001062/2004-50, resolve:

Art. 1º Estabelecer restrições à pesca na região do Aritapera, no município de Santarém/PA, a seguir indicadas:
I - proibir, anualmente, de 1º de novembro a 1 º de abril, a pesca com uso de malhadeira, nos lagos do Aramanaí, Mauari, Itarim e Buiuçú;
II - proibir a comercialização do acari (*Lipossarcus pardalis*) durante três anos a contar da publicação desta Instrução Normativa;
III - proibir, de 1 º de setembro a 28 de fevereiro o uso de malhadeira no lago do Maracá, lago da Enseada Grande, lago do Tomé, lago do Munguba, lago do Feliciano, laguinho e enseada de Santa Terezinha;
IV - proibir o uso de malhadeira de qualquer tipo no rio do Aritapera, da Boca do Amazoninha até a Boca do Santo André;
V - proibir o uso de malhadeiras e espinhéis nos lagos da comunidade de Ilha de São Miguel;
VI - limitar a captura de pescado a quatrocentos quilos, por barco coletor/pesqueiro, por viagem; e
VII - limitar, em até três, o número de canoas, por barco coletor/pesqueiro, para o exercício da pesca e em até cinco, o número de malhadeiras utilizadas por canoa.

Art. 2º Excluir das proibições constantes dos incisos I a V, do art. 1o desta Instrução Normativa, a pesca de caráter científico, devidamente autorizada pelo Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis-IBAMA.

Art. 3º O exercício da pesca em desacordo com o estabelecido, sujeitará os infratores às penalidades e sanções, respectivamente, previstas na Lei 9.605, de 12 de fevereiro de 1998 e Decreto no 3.179, de 21 de setembro de 1999.

Art. 4º Esta Instrução Normativa entra em vigor na data de sua publicação.

Art. 5º Fica revogada a Portaria no 41, de 15 de março de 2001, publicada no Diário Oficial da União de 16 de março de 2001, Seção 1, página 115.

MARINA SILVA