

Programa de Pós-graduação em Diversidade Animal

Universidade Federal da Bahia

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**História natural de *Copionodon pecten*, espécie
de tricomictérico endêmica da Chapada
Diamantina, Bahia, Brasil**

Salvador

2011

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Dissertação apresentada ao Instituto de Biologia da Universidade Federal da Bahia para a obtenção do título de Mestre em Zoologia pelo Programa de Pós-graduação em Diversidade Animal.

Orientador(a): Angela Maria Zanata

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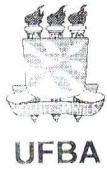
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ATA DA SESSÃO PÚBLICA DO COLEGIADO DEFESA DE DISSERTAÇÃO

Título da Dissertação: **“História natural de *Copionodon pecten*, espécie de tricomictérideo endêmico da Chapada Diamantina, Bahia, Brasil”.**

Mestrando: Camila Primitivo de Oliveira
Orientador: Dra. Angela Maria Zanata

De acordo com o regimento geral da UFBA e com o regimento interno deste programa de pós-graduação, foram iniciados os trabalhos da Comissão Examinadora, composta pelos professores **Dra. Angela Maria Zanata (presidente), Dr. Hilton Japyassú e Dr. Jansen Alfredo Sampaio Zuanon**, às 9:00 horas do dia 17 de junho de 2011.

A mestranda fez a apresentação oral da dissertação durante 45 minutos. Após o encerramento das arguições, às 11:42 horas, a Comissão Examinadora pronunciou-se pela sua APROVAÇÃO, conforme parecer em anexo.


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Salvador, 17 de junho de 2011.

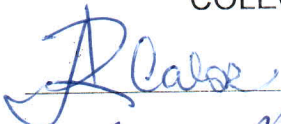
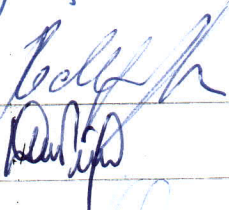
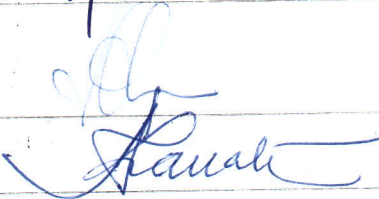
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Dedicatória

Dedico essa dissertação
aos meus pais e irmãos
que sempre me fizeram
acreditar e enxergar
o melhor lado das coisas.

Epígrafe

"Todo o futuro da nossa espécie, todo o governo das sociedades, toda a prosperidade moral e material das nações dependem da ciência, como a vida do homem depende do ar. Ora, a ciência é toda observação, toda exatidão, toda verificação experimental. Perceber os fenômenos, discernir as relações, comparar as analogias e as dessemelhanças, classificar as realidades, e induzir as leis, eis a ciência; eis, portanto, o alvo que a educação deve ter em mira. Espertar na inteligência nascente as faculdades cujo concurso se requer nesses processos de descobrir e assimilar a verdade."

Rui Barbosa

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Apresentação

Esta dissertação está dividida em Introdução Geral, seguida por um capítulo, Conclusões Gerais e Referências Bibliográficas. Na Introdução Geral, são apresentadas considerações gerais referentes ao capítulo que a sucede, seguida pelos objetivos da dissertação. O capítulo é apresentado sob forma de manuscrito e segue as normas do periódico ao qual será submetido. O item Conclusões Gerais é referente ao capítulo anterior e o item Referências Bibliográficas, ao final, contêm as citações que aparecem na Introdução Geral e manuscrito.

Introdução geral

A subfamília de interesse no presente estudo, Copionodontinae, foi descrita em 1992 por de Pinna, e talvez represente a descoberta mais intrigante na diversidade de tricomictérídeos nas décadas recentes (Bichuette *et al.*, 2008). O grupo foi originalmente descrito para a incluir os novos gêneros *Copionodon*, com as espécies *C. pecten* e *C. Orthiocarinatus*, e *Glaphyropoma* com a espécie *G. rodriguesi*. Posteriormente, foram descritas e incluídas as espécies *C. lianae* Campanario & de Pinna (2000) e *G. spinosum* Bichuette *et al.* (2008).

Copionodontinae é um grupo de especial interesse em vários aspectos. Os membros da subfamília são notavelmente primitivos morfológicamente e não possuem muitas das sinapomorfias que foram utilizadas inicialmente para definir a família Trichomycteridae (de Pinna, 1992; Bichuette *et al.*, 2008). De acordo com de Pinna & Wosiacki (2003), em contraste com a maioria dos outros tricomictérídeos, copionodontíneos (ao menos *C. pecten*) não apresentam comportamento críptico e nadam continuamente sobre o substrato. Afirmam ainda, que mesmo durante ações evasivas estes não se escondem sob rochas. Além disso, copionodontíneos são os únicos tricomictérídeos com dentes raspadores e apresentam distribuição restrita a tributários do alto rio Paraguaçu, na região da Chapada Diamantina, no Estado da Bahia.

A subfamília foi descrita originalmente como grupo irmão imediato do restante da família Trichomycteridae (de Pinna, 1992), com Trichogeninae como grupo irmão sucessivo. Posteriormente, o autor identificou sinapomorfias compartilhadas com *Trichogenes longipinnis*, espécie relictual de pequenas rios costeiros do Sudeste do Brasil (de Pinna, 1998). Atualmente, a relação de parentesco próxima entre Copionodontinae e Trichogeninae é corroborada (Bichuette *et al.*, 2008; Datovo & Bockmann, 2010), e esta última subfamília é composta de *T. longipinnis* e a espécie *T. claviger*, recentemente descrita para um riacho no Estado do Espírito Santo (de Pinna *et al.*, 2010).

De acordo com Bichuette *et al.* (2008), Copionodontinae representa um grupo monofilético, diagnosticado por várias sinapomorfias não ambíguas, incluindo dentição única, composta de dentes espatulados, não encontrados em nenhum outro grupo de Trichomycteridae. Alguns caracteres também suportam os gêneros *Copionodon* e

Glaphyropoma como unidades monofiléticas.

Estudos incluindo aspectos de história natural com enfoque em membros da ordem Siluriformes são escassos e voltados, na maioria dos casos, para peixes de ambientes cavernícolas. Estes incluem, principalmente, estudos de comportamento agonístico de *Pimelodella kronei* (Trajano, 1991), ecologia e comportamento de *Rhamdiopsis krugi* (Mendes, 1995), aspectos de ecologia e comportamento de *Taunaya* sp. (Trajano & Bockmann, 2000), habitat, dados de populações e comportamento reprodutivo de *Ancistrus cryptophthalmus* (Trajano, 2001; Secutti & Trajano, 2009) ou informações sobre aspectos da biologia de alguns outros siluriformes encontrados em trechos de publicações com enfoques não específicos em história natural (e.g., *Pimelodella spaelea* em Trajano *et al.*, (2004); *Phreatobius cisternarum* em Muriel-Cunha & de Pinna (2005); *Rhamdia enfurnada* em Bichuette & Trajano (2005); *Rhamdiopsis krugi* Bockmann & Castro (2010)). Poucos trabalhos são voltados para estudos de história natural de siluriformes não troglóbios (e.g., Sazima *et al.* (2000) para *Scoloplax empousa*; Vono & Birindelli (2007) para *Wertheimeria maculata*) ou aspectos da biologia destes (e.g., Gomiero *et al.* (2007) para *Rhamdia quelen*; Casatti *et al.* (2009) para dieta de *Aspidoras fuscoguttatus*).

Particularmente para Trichomycteridae, o conhecimento de aspectos da história da vida dos táxons também é escasso. De acordo com de Pinna (1998), apesar da diversidade e abundância dos membros da família, pouco é conhecido da biologia de tricomictérides. O autor cita alguns poucos estudos, com dados sobre preferência de habitat, hábitos alimentares, estimativa de idade e crescimento em duas espécies de *Trichomycterus* e uma de *Bullockia* (Arratia, 1983; Alvitres & Chang, 1990; Alvitres & Fiestas, 1990) e trabalhos de biologia reprodutiva de *Eremophilus mutisii* (Cala & Sarmiento, 1982; Cala, 1986), de *Trichomycterus areolatus* (Manriquez *et al.* 1988), de *T. punctatus* (Alvitres & Niquen (1990), além de dados de ecologia de *Eremophilus mutisii* (Florez & Sarmiento, 1989). De Pinna (1998), afirma ainda, que até aquela data apenas o tricomictérideo troglóbio *T. itacarambiensis* havia sido estudado quanto à ecologia de populações.

Mais de 10 anos se passaram e a situação atual do conhecimento da biologia de tricomictérides mostra poucos avanços. Nesse período, o estudo mais aprofundado sobre a história natural de uma espécie da família é o de Sazima (2004), para *Trichogenes longipinnis*, que inclui aspectos de comportamento, dieta, reprodução, habitat e variação morfológica. A este, seguem-se os estudos de história natural de *Stauroglanis gouldingi* (Zuanon & Sazima, 2004) e *Trichomycterus diabolus* (Casatti, 2003). Outras informações biológicas de tricomictérides são representadas por notas em ecologia e comportamento

incluindo descrição de novas espécies (e.g., *Ammoglanis poulex* de Pinna & Winemiller (2000); *Listrura boticario* de Pinna & Wosiacki (2002); *Ituglanis mambai* Bichuette & Trajano (2008); *Trichogenes claviger* de Pinna *et al.*, (2010)), de trecho de trabalho sobre aspectos da biologia de *Trichomycterus* sp. (Trajano *et al.*, 2009), ou informações sobre hábitos de tricomicterídeos parasitas (e.g., Spotte *et al.*, 2001; Spotte, 2002; de Pinna & Wosiacki, 2003; Zuanon & Sazima, 2004, 2005).

Estudos prévios com enfoque em hábitos alimentares, reprodutivos e interação social de membros da subfamília Copionodontinae não foram realizados. Apenas breves comentários, em estudos não especificamente de biologia do grupo, são encontradas, como é o caso de Sazima (2004), que, ao discutir aspectos da história natural de *Trichogenes longipinnis*, cita “*Copionodon* species...are active during the day as well as at night, albeit these species are less nektonic than *T. longipinnis* (de Pinna, pers. comm.)”. Na descrição de *Glaphyropoma spinosum* Bichuette *et al.* (2008), ao escreverem sobre a subfamília, afirmam “Fish tend to concentrate on quiet deep pools, though some individuals lodge in narrow rock crevices in fast flowing sectors. Habitat preferences also vary according to species.” Nesse trabalho, os autores também apresentam curta seção sobre dados ecológicos de *G. spinosum*, voltados basicamente para caracterização do habitat e dados populacionais. A autora atualmente desenvolve pesquisa de ecologia populacional e comportamento da espécie subterrânea *Glaphyropoma spinosum*. Assim, um estudo de história natural de algum integrante de Copionodontinae não foi realizado previamente.

No presente estudo, apresentamos informações inéditas sobre aspectos da biologia de *Copionodon pecten* em ambiente natural, com enfoque em comportamentos de locomoção, alimentação, reprodução e interação social e indicando diferenças de acordo com o estágio de desenvolvimento. Tais comportamentos e experimentos (reação a luz e residente *versus* intruso) foram também realizados em laboratório.

Objetivos

Objetivo geral

Descrever aspectos de história natural da espécie *Copionodon pecten* em diferentes fases do desenvolvimento, a partir de observações realizadas no rio Coisa Boa, Andaraí, Bahia e em laboratório.

Objetivos específicos

- Descrever o habitat dos indivíduos de *Copionodon pecten*;
- Descrever interações sociais, comportamento alimentar no ambiente natural e em laboratório, além do período de forrageamento da espécie;
- Descrever a distribuição espacial no habitat natural;
- Analisar e descrever a dieta;
- Analisar e descrever aspectos reprodutivos;
- Examinar reação à luz;
- Examinar se a espécie exibe reação agonística;
- Definir fases de desenvolvimento da espécie, de acordo com morfologia externa básica e padrão de colorido.

Capítulo

Esta dissertação é composta de capítulo único, com manuscrito intitulado “História natural de *Copionodon pecten*, espécie endêmica da Chapada Diamantina, nordeste do Brasil”, que será submetido para publicação no periódico científico JOURNAL OF FISH BIOLOGY. Os critérios de redação e formatação seguem as normas deste periódico, as quais se encontram disponíveis no ANEXO desta dissertação.

Natural history of *Copionodon pecten*, an endemic trichomycterid catfish from Chapada Diamantina in northeastern Brazil

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Running headline: Natural history of *Copionodon pecten*.

The natural history of *Copionodon pecten* is recorded here based on observations of specimens inhabiting Rio Coisa Boa, in the Rio Paraguaçu drainage, Chapada Diamantina. This catfish is mainly benthonic and dwells in pools beneath riffles, over rocky substrate. Period of activity, spatial distribution, foraging strategy, diet, and reaction to light show variation according ontogenetic stage, along with variation in features of external morphology. Small juveniles are diurnally active, mainly on water column of shallow borders of pools, with diet based mainly on *Spirogyra* sp. Subadults and adults of *C. pecten* are mainly nocturnally active, when spread throughout shallower areas of pools, are mainly bottom and feed mainly on a complex of periphytic algae scratched from substrate. A long digestive tract is in accordance to the mainly algivorous diet. Immature aquatic insects are also important food item throughout life of the fish. Chemical, tactile, and visual cues are used by *C. pecten* while foraging. Small individuals are preferably gregarious at night, distinct from a more diurnal gregariousness on larger individuals, usually with countercurrent polarization. The latter are apparently more numerous within the population. No distinct reproductive season was recorded for *C. pecten* on the studied period, with presence of mature individuals throughout the year and oocytes in various stages of development on ovaries, indicating multiple spawning over a long reproductive period. The species have low number of oocytes, no parental care, or external sexual dimorphism. Small juveniles of *C. pecten* are mostly indifferent or present weak reaction to light, but as the fish grows the reaction gets more evident, with tendency to be in comparatively deeper or somewhat sheltered places. *Copionodon pecten* is as a mild territorial catfish, with weak and size related dominance, mostly displayed in relation to food and shelter, and absence of complex behavioural repertoire.

Key words: Copionodontinae, biology, behaviour, reproduction, diet, Paraguaçu.

INTRODUCTION

The trichomycterid subfamily Copionodontinae is of special interest in a number of aspects. Its members are remarkably primitive morphologically and lack many of the synapomorphies that were previously used to diagnose the Trichomycteridae (de Pinna, 1992; Bichuette *et al.*, 2008). According to de Pinna & Wosiacki (2003), in contrast to most other trichomycterids, copionodontines (at least *Copionodon pecten* de Pinna) lack cryptic behaviour, swims continuously over the substrate, and do not attempt to hide under rocks. Also, copionodontines are the only trichomycterids with grasping teeth and occur exclusively in Chapada Diamantina, Bahia State, northeastern Brazil. Copionodontinae was originally described as sister group to all the rest of the family (de Pinna, 1992), and posteriorly defined as sister group of Trichogeninae (de Pinna, 1998; Bichuette *et al.*, 2008; Datovo & Bockmann, 2010), a relictual subfamily formed by two species, one (*T. longipinnis* Britski & Ortega) restricted to a few isolated coastal streams in southeast Brazil and the other (*T. claviger* de Pinna *et al.*) from one small stream in the State of Espírito Santo. Copionodontinae is composed by the genus *Copionodon*, with three species (*C. lianae* Campanario & de Pinna, *C. orthiocarinatus* de Pinna, and *C. pecten*), and *Glaphyropoma*, with two species (*G. rodriguesi* de Pinna and *G. spinosum* Bichuette *et al.*).

Published information on ecology and life history of trichomycterids is scattered and particularly about copionodontines is inexistent. On the former, most data focus on the parasitic feeding habits of the candirus of the subfamilies Vandelliinae and Stegophilinae (*e.g.*, Winemiller & Yan, 1989; de Pinna & Britski, 1991; Spotte *et al.*, 2001; Spotte, 2002; de Pinna & Wosiacki, 2003; Zuanon & Sazima, 2004, 2005). Trichomycterid species with relatively well studied aspects of life history includes only *Trichomycterus itacarambiensis* (Trajano, 1997a-b), *T. diabolus* (Casatti, 2003), *Trichogenes longipinnis* (Sazima, 2004), and *Stauroglanis gouldingi* (Zuanon & Sazima, 2004). Biology of only a few other members of the family are known by relatively short studies about biologic aspects of a few *Trichomycterus* species (Casatti, 2003; Trajano *et al.*, 2009), by short comments on habitat (*e.g.*, Nico & de Pinna, 1996; de Pinna, 1998; de Pinna & Winemiller, 2000), and ecological notes within new species description (*e.g.*, *Trichomycterus maracaya* Bockmann & Sazima, 2004; *Ituglanis mambai* Bichuette & Trajano, 2008; *Trichogenes claviger* de Pinna *et al.*, 2010).

As stated above, life history of copionodontines is not known, except for a few

short comments about general aspects of the subfamily, as declared by Sazima (2004) “*Copionodon* species...are active during the day as well as at night, albeit these species are less nektonic than *T. longipinnis* (de Pinna, pers. comm.)”, and by the comment of Bichuette *et al.* (2008) “Fish tend to concentrate on quiet deep pools, though some individuals lodge in narrow rock crevices in fast flowing sectors. Habitat preferences also vary according to species.” A short section of ecological notes is given in the recent description of *Glaphyropoma spinosum* by the latter authors.

Copionodon pecten, the species focus of this study, was described by de Pinna (1992) to Rio Mucugê, close do the municipality of Mucugê, and is usually externally diagnosed from congeners by its color pattern, the extremely elongated interopercular patch of odontodes, upper lip antero-posteriorly thickened and ventrally flattened, and upper lip folded over itself. Nowadays, the species is known to occur in various streams and small tributaries of upper Paraguaçu river. Herein the natural history of *Copionodon pecten* in Rio Coisa Boa, in the municipality of Andaraí, and also on its behaviour in laboratory is reported. The study focused mainly on aspects of the fish distribution within habitat, period of activity, foraging behaviour and diet, reproduction, and social interactions. Also, briefly features of the external morphology are described and illustrated the color pattern variation observed in different stages of development of the catfish.

STUDY SITE AND METHODS

Study site. Field work was carried out in the midcourse of the Rio Coisa Boa, a second order river (map scale 1: 100,000), tributary of Rio Paraguaçu, in Igatu district (12°53'46.5"S 41°19'5.8"W, 732 m elevation), municipality of Andaraí, central region of the state of Bahia, northeastern Brazil. The Rio Coisa Boa has its headwaters at ca 1000 m elevation on the eastern slopes of the Sincorá Range, within the Chapada Diamantina National Park. The river is perennial and torrential in the rainy season. The local climate is mesothermic, tropical semi-humid. Rains predominate in the austral summer (November–January), with a secondary maximum in March and April. During the austral winter months (May–August), rainfall decreases and a marked dry period occurs from August to October. The precipitation of the rainy season months in Andaraí usually ranges from 150-230 mm and on the dry season from 30-50 mm (HIGESA, 2000). Temperature of the environment varies from 20-30 °C on the wet season and 10-26°C on the dry. The section of the river where field observations were conducted is a lotic water environment, running over rocky bed of a complex Plateau composed of Proterozoic terrain. It is a fast-flowing stream, with riffles and variable sized pools connected by

narrow grooves around 50 cm deep and fast current water or by stretches of shallower water over rock bed. The Rio Coisa Boa runs through area dominated by “Campo Rupestre”, a herbaceous-shrub vegetation that develops on open rocky ground at elevations around 900 m. Physico-chemico water variables (pH, dissolved oxygen, conductivity, and temperature) of the studied pools were measured with a portable electrode in September 2010 and March 2011, representing the driest and wettest period of the field trips, respectively. Water velocity was measured using the floating object method. As the majority of the rivers inserted in Chapada Diamantina domain, the studied one has dark water color (fig. 1a), possibly due to the high concentration of humic substances, as fulvic acids.

Five pools, along with grooves, located just bellow small rapids were the main focus of underwater observations and sampling of the fish populations. These pools have mainly rocky bottom and less often pebbles and sand (on its shallow borders) and variable dimensions and depth, according to the particular formation of their rocky borders (figs. 4 a-c). In general, main pools studied vary from 1.2 to 8.2 m long, 0.4 to 3.3 m wide on its broader portion, 0.25 to 0.6 m deep on its centralmost portion, becoming shallower laterally, with few centimeters deep (1-2 cm) on its borders. However, broad variation of these pools dimensions occurred along the studied period, according to amount of rainfall (fig. 1 a,b). Along the study, a ‘main pool’ was chose for observations (fig. 2a), due to its permanence during the whole period of study and easier conditions for observations (a few cm to 25 cm deep X 7.9 m long X 1.23 m wide in Sept 2020). An extra pool, rounded and somewhat deeper (75 cm deep x 98.5 long and 90 cm wide), was also observed in driest field trip (fig. 2b).

Sampling and observation of fishes. Field observations and other analysis were based on six field trips, from September 2009 to March 2011, totaling 16 fieldwork days. Behaviour and abundance of *C. pecten* was recorded directly and photographed in the field during daylight and nocturnal hours, with underwater sessions by snorkeling (Sazima, 1986), as well as observations above surface while sitting on the rocky borders, totaling 68 hours of behavioural records in situ. An underwater flashlight covered with red plastic was used for night observations. Animal focal and *ad libitum* methods (Lehner, 1998) were used throughout the study. Individuals found not under shelter (*e.g.* swimming, foraging for food or feeding) were considered active, and individuals found in shelters or relatively

stationary during the whole observation period were considered inactive. Observations were focused on periods of twilight, around two-three hours after sunset, before sunrise, early morning, midday, and mid afternoon.

Chemo-sensorial ability of *C. pecten* individuals while foraging was examined by offering leaves, fruits, corn flour, biscuit, fresh meat, and ornamental fish food pellets, following Sazima (2004). Tests were performed both during day light and night hours, and no catfish group was used in two successive trials involving the same test type. Each test was replicated five times in different pools and test results were considered positive when an attraction response was perceived, irrespective of the number of catfish attracted. Population density was estimated by visual censuses, by counting the number of specimens seen in a radius of about 30 cm, in September 2010 and March 2011. The total length of catfish alive (the only external indicator of age), measured in natural environment and cited elsewhere, was estimated using a dial caliper, after training size estimative with fixed fish of the same species in the laboratory. Standard length (SL) and total length (TL) are used throughout for adults, juveniles and larvae (See 'Morphology and color pattern section'). Eye diameter is given as percentage of head length (HL).

Specimens for behavioural observations and other analyses in laboratory were captured with hand nets dragged over the rocky bottom, in all field trips. Alive individuals (13) were kept in five to eight aquariums of 37.5 l, initially filled at least partially with water from their stream habitat, provided with continuous aeration, biological filter, and bottom mounted with pebbles and pieces of rocks from field area, which could be used as shelters. The aquariums had a black ground, with light controlled on a period of 12/12 hours. A maximum of four catfish were maintained per aquarium, fed with fish ornamental pellets thrice a week on alternate days. The methodology and periods of observation were similar as that performed in field, totaling 63 hours of laboratory observation plus tests (agonistic behaviour 21 h and light reaction 16 h). Tests in laboratory were performed from August to October 2010. To study the reaction to light of *Copionodon pecten* in laboratory, the classical choice-chamber methodology was used (as that described in Trajano & Gerhard 1997, among others), based in three different light intensities, of 25-50 lux, 150-200 lux, and 1500-2000 lux. Eight adult individuals (42.5-59.4 mm TL) and five juveniles (about 20-35 mm TL) were used in the tests, distributed in three aquariums. The aquariums used were divided into clear and dark sides, aeration turned off, and rocks used for shelter removed thirty minutes before the experiment. Each test was performed for 30 minutes, with fish registered in some of the sides at intervals of 5 minutes. Experiments to evaluate

agonistic behaviour were based on pairing tests, following a resident *versus* intruder schedule, based on Trajano (1991). The tests were done with the same individuals cited above, distributed on eight aquariums. Initially, combinations used the same species, using pairs of adults and juveniles. Tests using resident specimen of *C. pecten* with an intruder of the species *C. orthiocarinatus* and also a test using the sympatric *Astyanax sp.* as intruder was performed posteriorly.

A total of 238 specimens fixed in formalin 10% and subsequently preserved in alcohol 70% were measured, dissected, and examined under stereomicroscope to check for size of the smallest reproductive individuals, size and number of mature oocytes per female (right ovary examined), breeding period, and for gut contents. In order to document the spawning period for the species, representative specimens of different periods of the year had gonads examined through a stereomicroscope. Three stages of maturity were defined (modified from Vazzoler, 1996): Immature: ovaries small, occupying less than 1/3 of abdominal cavity, filamentous, translucent, majority of oocytes small but a few larger, visible through naked eye; testes small, translucent and filamentous. Maturing: ovaries larger, occupying 1/3 to 2/3 of abdominal cavity; oocytes in variable stages of development, yellow and white, visible through naked eye; testes white, developed as a narrow ribbon; and Mature: ovaries large, occupying more than 2/3 of the abdominal cavity; mostly oocytes yellow, large, with a few small and whitish; testes white, developed as a large ribbon. Specimens for stomach content analysis were captured in different periods within 24 hours, to check for existence or not of foraging peak. Food item of the stomachs were identified to the lowest taxonomic category possible and their importance to diet was assessed by frequency of occurrence and contribution by numbers (Hyslop, 1980). To evaluate the feeding activity, the degree of fullness of each stomach was examined, following the scale: 1 (volume < 25%), 2 (25 - 50%), 3 (50 - 75%), 4 (75 - 100%), according to Kawakami & Vazzoler (1980). Insect and algae identification were done by specialists of each group.

Voucher specimens of *C. pecten* from all collection places recorded are in the Museu de Zoologia da Universidade Federal da Bahia (UFBA 5289 (5 spec., 39.7-61.9 mm SL); 5929 (6, 29.0-60.1 mm SL), 6031 (12 spec., 40.8-53.3 mm SL); 6034 (25 spec., 39.1-68.5 mm SL); 6189 (25 spec., 43.3-65.9 mm SL); 6190 (35 spec., 18.0-58.4 mm SL); 6191 (15 spec., 36.7-67.9 mm SL); 6192 (14 spec. 54.0-70.8 mm SL); 6194 (6 spec., 9.6-13.5 mm SL), 6431 (34 spec., 28.6-65.7 mm SL); 6432 (26 spec., 28.5-51.6 mm SL); 6433 (7, 15.5-16.7 mm SL); 6434 (10 spec., 16.4-30.8 mm SL); 6438 (7 spec., 12.9-19.2 mm SL);

6549 (6 spec., 19.3-48.6 mm SL); 6550 (15 spec., 21.1-61.2 mm SL); 6551 (32 spec., 20.2-56.4 mm SL).

RESULTS

Habitat. Physicochemical characteristics of water throughout the studied period were: temperature 22°-28°C, pH 6.0-7.8, conductivity 19-24 μ S/cm, flow velocity 0.11-0.66 m.s⁻¹ on pools surface. Dissolved oxygen on September 2010 was 6.6 -7.3 mg.O₂/L. No macroscopic aquatic vegetation occurs on the studied pools, except by green patches of algae complex on rocky borders or bottom. Deeper pools nearby had aquatic grass on margin.

The driest condition observed occurred in September 2010 (fig. 1b) and the wettest in March 2011 (fig. 1a). The dry period is marked by a decrease of water level around 30-35 cm, resulting in shortening of pools extension, broadening of exposed river bed and reduced connection between pools. At that time pools were connected through small stretches of shallow water over plain rocky bed or narrow grooves, usually somewhat deeper and faster-flowing water than pools. Greatest local abundance of large juveniles and adults of *Copionodon pecten* occurred in September 2010 in all pools examined. Daytime visual census on areas with high concentration of individuals yielded estimates of 100-200 subadults plus adults·m⁻², without considering food attraction tests. By night these individuals usually were spread, resulting in low number of individuals·m⁻². Counting of small juveniles and larvae, day and nighttime on driest period, yielded 3-17 individuals·m⁻². On the other hand, in March 2011, flash elevation of water level was observed, resulting in river bed completely flooded and extremely high water velocity. Consequently, all pools were submerged and unidentifiable, except by the ‘main pool’ that remained partially visible, with up to 60 cm deep (*versus* up to 25 cm deep in September 2010). Distinct from results on dry period, only a few specimens could be observed, being around 10 adults at daytime at depth of 40 cm and up to 20 small juveniles·m⁻² over a shallow horizontal rocky platform (10-15 cm deep) close to river border, or swimming along walls and bottom of a connected groove (up to 1.65 m wide and 60 cm deep). No night census was done in March 2011.

Apparently, the autochthonous aquatic fauna that coexists with *C. pecten* is relatively poor. All pools in which *C. pecten* was recorded were inhabited by only two other fish species: *Astyanax* sp., locally known as ‘piaba’ and *Hoplerythrinus unitaeniatus*,

locally known as ‘iuiú’. *Astyanax* sp. is apparently similar to the “*A. scabripinnis* species group”. However, only a few specimens (3-5) were observed at each pool, making the *Copionodon* species undoubtedly dominant at those areas. On the other hand, fish traps settled on larger pools, not observed directly on this study, resulted only on capture of *Astyanax* sp. Only two juveniles of *H. unitaeniatus* were sampled at the river stretch included in the study, but no one was seen inside the observed pools. Local dwellers informed that this species is very common in deeper pools above studied area. No other fish species is reported by the local people to occur in the river. Tadpoles of *Bockermannohyla* sp. were also observed coexisting with *C. pecten*. The invertebrate fauna is represented mainly by aquatic insects, some of which are eventually consumed by the *C. pecten*. A brief analysis of local aquatic entomofauna revealed presence of Trichoptera (Hydropsychidae, Odontoceridae, Leptoceridae, Helicopsychidae), Odonata (Zygoptera, Anisoptera), Ephemeroptera (Baetidae), Plecoptera (Perlidae), Coleoptera (Hydrophilidae), and Hemiptera (Nepidae, Gerridae).

Beyond the observed presence of *C. pecten* in the main channel of the Rio Coisa Boa, the species was also cited by local dwellers to occur on its small tributaries around the Igatu village, named Córrego do Vitorino, Córrego do Criminoso, Rio dos Pombos, Rio das Laranjeiras, Rio Tambori, and Vale do Capão de Igatu. Personal observation and analyses of the fish collection of Museu de Zoologia da Universidade de São Paulo and Museu Nacional do Rio de Janeiro revealed that *C. pecten* occurs also in various headwaters of Paraguaçu river, exclusively on Chapada Diamantina domain.

Because of its relative proximity to the touristic village of Igatu, the studied area experiences some effects of human activities. Igatu counts with around 300 inhabitants and have its domestic wastes (soap water, faeces, urine) dumped directly into the river. Also, domestic animals (*e.g.*, horses) were seen over the river bed during field expedition. However, possibly most of the environment disturbance occurred in the past, caused by the diamond rush to the region of Chapada Diamantina (Diamond Plateau), around 1900. Andaraí (including Igatu village) was part of the “Circuit of the Diamonds” and had its landscape completely revolved, with large amount of sand carried downstream and changes into the river bed. Nowadays, a few miners still work in the region.

Morphology and colour pattern. The morphological analysis of different sized specimens of *C. pecten* resulted in the definition of stages of development, based mainly on external structures with easily detectable variation. These stages are used throughout this study,

usually linked to aspects of natural history specific to certain life stage of *C. pecten*.

Larvae. Smallest individuals analyzed, 9.6-12.0 mm SL (fig. 3a). Eyes large, 23.8-25% of HL. Dorsal and ventral-fin folds developed along most of body extension. Dorsal fin fold initiates behind head and rises gradually to dorsal fin insertion, more developed posterior fin and posteriorly meets basal half of caudal-fin superior border. Ventral fin fold initiates immediately behind belly (ahead of area of future pelvic fin) and posteriorly meets basal half of caudal-fin ventral border. Dorsal and ventral fin folds on area ahead of vertical through dorsal fin with similar height, and posterior to it dorsal fold twice as wide as ventral fold. Pelvic fin not formed yet and anal-fin rays not or slightly visible and embedded in the long ventral-fin fold, at least in the two smallest specimens.

Interopercular odontodes not easily visible. Teeth conical, very small, almost hyaline and poorly visible. Overall coloration in alcohol yellowish to light brown, somewhat homogeneous. Dorsal background light brown, somewhat darker than lateral of body, dark chromatophores sparsely and almost homogeneously distributed over dorsal half of head, lateral and dorsal portions of body. A midlateral inconspicuous dark line along body.

Ventral portion of head and belly with no pigmentation. Nasal barbell darkened. Fin folds, dorsal and anal fins hyaline; pectoral with a few dark chromatophores on basal portion of first rays or sparsely distributed over first fin ray; remaining rays and membranes hyaline. Caudal fin with sparsely distributed dark chromatophores over rays, forming interrupted diffuse lines.

Juvenile 1. Specimens of 13.5-21.0 mm SL analyzed (fig. 3b). Eyes large, 20.0-25.0% of HL. Remains of dorsal fin fold anterior to dorsal fin present only in smaller specimens examined and posterior to dorsal fin fold forming the adipose fin. Ventral-fin fold restricted to caudal peduncle length and very narrow. Completely formed fins, although pelvic fin apparently too small. Interopercular patch of odontodes varying from having a discrete contour to clearly ventrally and posteriorly projected from head margin, with one series of five or six interopercular odontodes. Two series of teeth on premaxilla and two on dentary; outer series composed of larger teeth with exposed portion brown, triangular shaped, and pointed. Overall coloration in alcohol similar to the larvae pattern, but dorsal fin rays dark and adipose fin brown. Dark midlateral line more conspicuous than on larvae. Coloration in alcohol somewhat similar, although somewhat translucent (fig. 4a).

Juvenile 2. Specimens around 22.0-35.0 mm SL (fig. 3c). Eyes moderate in size, 13.7-22.7% of HL. Dorsal or ventral-fin fold absent. Patch of well developed interopercular odontodes clearly projected from head margin and with two or three series of odontodes clearly visible (usually two series). Two or three series of teeth on premaxilla and two on dentary; apparently only first series functional, with larger teeth. Exposed portion of teeth triangular, pointed and elongated, somewhat laterally expanded; teeth border somewhat roundish or slightly straight on larger specimens, mainly on lateralmost dentary ones. Overall coloration in alcohol similar to Juvenile 1, with a conspicuous dark midlateral line. First pectoral-fin ray and anal fin rays darkened. Larger specimens with lateral dark line slightly sinuous and small dark spots over head and lateral of body. Coloration in alcohol somewhat similar, although somewhat translucent (fig. 4b).

Sub-adults and adults. Specimen around 40 mm SL or larger (fig. 3d-f). Eyes small, 9.1-13.3 % of HL. Overall body and fins morphology similar to specimens of stage Juvenile 2, unless by teeth morphology, number of interopercular odontodes series, and details of colour pattern. Patch of interopercular odontodes extremely elongated, with three or more series of well developed odontodes. Two or three series of teeth on premaxilla and two on dentary; smaller specimens with one functional series of teeth on maxillas and larger with two, similar in size. Exposed portion of teeth rounded on smaller specimens, broader and straight bordered on larger. Overall coloration in alcohol somewhat variable; most specimens with dark stripe and spots and some larger specimens (larger than 70 mm SL) grayish throughout body, with no conspicuous dark marks. The former ones, in dorsal view, with two dark lines from rear of the head extending to lateral borders of dorsal-fin base; continuing or not along adipose fin base. A series of dark spots below each line, usually reaching vertical through end of dorsal fin base. From lateral view, dark midlateral line somewhat sinuous; spots below lateral line formed by concentration of dark chromatophores. Alive subadults and adults specimens usually have dark spots less conspicuous and golden reflexes on head and dorsal portions of body (fig. 6).

Spatial distribution and period of activity. Larvae and small juveniles, midsized juveniles, and larger individuals have distinct preferences of habitat and period of activity. Information below is not based on rainy days, unless when indicated.

Larvae and small juveniles (Juveniles 1): Only a few larvae (2 a 6) were observed

swimming actively during daytime and collected in very small and isolated pools (28 cm long, 12 cm wide and up to 6 cm deep, or smaller). In some cases, the tinny catfishes drifted into these pools and were not able to escape due to absence of connection to other pools. Information that follows is based mainly on small juveniles. They occupy shallow (up to 10 cm deep) and almost isolated pools, usually rocky bottomed but partially with sand or pebble, backwater of larger pools with small or no direct water current, or lateral walls of shallow grooves with sandy bottom. Just after sunrise and along daytime they are active, swimming rapidly back and forth. Daytime census revealed aggregations of up to 17 not polarized individuals on pools and 8-10 (fig. 4a) individuals swimming actively along walls of grooves. After dawn, individuals are inactive, concentrated on even shallower marginal area of pools (1-2 cm deep), carried back and forth by the smooth marginal wave's movement. At that period up to 16 individuals were observed apparently in aggregation on the border of 'main pool'. At sunrise they dispersed and were not seen anymore at those shallow portions.

Middle sized juveniles (Juveniles 2): distribution in habitat somewhat variable along 24 hours period, but usually in relatively shallow areas of pools, rocky or partially sandy bottom and mild water current. Usually observed close to bottom, horizontal submerged rocky platforms on pools (20 cm deep or shallower) or walls and bottom of grooves 20-50 cm deep. They are somewhat active night and daytime, although more intensively during the day, swimming slowly and exploring the environment continuously. During daytime, aggregations of up to 20 individuals of similar size, not polarized, were observed active at midwater, swimming back and forth in a restricted area and after dawn they scattered around in shallower marginal areas not inhabited during day. Aggregations of 11 individuals (fig. 4b) seen at 20-25 cm deep during day moved after sunset to margins of (up to 10 cm deep) and aggregated with smaller individuals (15.1-17.4 mm SL). Middle sized juveniles were rarely seen stationary in the natural environment.

Sub-adults and adults: distribution in habitat varied along 24 hours period, but during daytime they were usually aggregated on bottom (fig. 5a-c) (25-70 cm deep) and vertical walls of pools and at night spread around. Usually seem on areas with direct effect of water current and almost always on rocky bottom but observed also in pebbled bottomed pools (fig 5b). On early morning and during daytime, large number of individuals (usually 25-80 individuals·m⁻²) were observed relatively stationary in horizontal platforms of pools,

positioned in parallel to each other (with around 2 cm between them), countercurrent, posed on the substrate supported by its pectoral fins and strongly grasped to the rocky bottom through interopercular odontodes (fig. 5c). After sunset, individuals become spread throughout pools and grooves, foraging actively on shallower areas not occupied by these individuals during daytime. A few individuals can be still polarized at the beginning of night but moves away some time after. Areas occupied by individuals of stage 'Juveniles 2' during daytime, at night receives individuals of 40 cm SL or larger (usually up to 30 individuals·m⁻²). Many individuals (of different sizes, including some juveniles of stage Juvenile 2) spread throughout pool walls, usually those positioned against water entrance and covered by algae. Counting of individuals foraging at a given area, resulted in 25-30 ·m⁻² before sunrise, 45 at sunrise and 70 individuals a few hours after dark. Observations made before sunrise (around 4:30) showed pattern of distribution and activity similar to the nocturnal pattern, although in some cases, individuals already showed a tendency to concentrate in deeper areas. At sunrise individuals were usually already polarized and away from walls and foraging nocturnal areas, or concentrated along bottom of grooves. In early morning, around 6:30, areas of night foraging (walls, shallow areas of pools, and relatively shallow grooves) usually found with zero large juveniles or adult specimens. Various specimens hide under crevices and boulders of pools and grooves. When under boulders, several are seen head down, with just posteroventral portion of body visible from surface. Usually, larger individuals (apparently adults) stay closer to the water entrance, where water current is higher, with body countercurrent positioned. Gradually, large to somewhat smaller juveniles are more distantly positioned, in areas with less strong water velocity. Shallower vertical walls occupied during nighttime, have few (smaller of the group) or zero individuals during daytime. As described, individuals of this stage were seen on bottom and on midwater usually close to walls, but not near the surface. Overall larger number of individuals is seen at night. At low densities the fish swam alone and when two or more of them met during their roving they can broke away after a very brief contact or stay nearby each other. Spontaneous groupings appear to be more common on small juveniles (Juvenile 1 and 2).

In laboratory, at daytime subadults and adults tend to hide in the available shelters formed by rocks fragments, except when food was provided which they went out, fed and returned to their shelters. At night, around 30 minutes after the light was turned off, individuals were out of shelter and became more active, apparently looking for food over pebbles and pieces of rocks or stay stationary over rock bottom close to shelter,

occasionally making short incursions around. No aggregation was observed and apparently each fish had its shelter or preferred area on the aquarium. On the other hand, juveniles at daytime tended to swim near the bottom or in the water column, usually along the aquarium walls, and at night were less active, usually stationary over pebbles, without hiding.

Foraging behaviour and diet. Individuals of distinct stages of development have different period and mode of foraging. Just a few observations were done on larvae behavior and they apparently swim actively during daytime on the water column. Similarly, small juveniles (Juvenile 1) mostly forage actively at midwater during day hours, swimming back and forth at short distances and possibly picking algae on the water column. Middle sized juveniles (Juvenile 2) forage mainly daytime, although seen active also at night, mainly on lateral shallow grooves. They were seen scratching the rocky surface covered by algae and also inspecting the substrate when in pools with sand bottom.

The main foraging mode observed for large juveniles and adults was to scratch algae from rocky surface, mainly during night hours. During this tactic, individuals moves rapidly on bottom or rocky walls, with interopercular odontodes usually loosely attached to the rock and maxillary and rictal barbells in contact with the explored surface (fig. 6). They perform bites against areas covered by green algae, scraping it with clearly observable head and mouthing movements. One bite follows the other, in a continuous session. On sand bottom they can invest head against sand, sometimes with vigorous lateral body or lateral head movements or fore-body and pectoral fins as if probing and apparently searching for food on the surface. Beyond that, median sized juveniles and larger individuals were observed rubbing lateral of body against rocks, in a behaviour not clearly explainable up to date. During active foraging, periodic intervals of 30 s to 4 min in biting action were observed. Occasionally, they changed their foraging position to some rocky area nearby, but usually a given individual remained on its location as long as it was engaged in its feeding activity. All of them usually keep the body position parallel in relation to explored substrate. When in aquarium, individuals get food particles over pebbles or pieces of rocky on the bottom or swim to near surface to get it. Disturbance of the substrate, such as stirring up sand or plant debris as well as touching a rocky area, attract a few individuals, which come close, inspect and usually return to the pool's bottom. In general, they don't intercept, pursue or catch drifting particles. During daytime, when polarized against water current, they remain most of time grabbed to the substrate by

its patch of odontodes but from time to time one or another bites the adjacent substrate. Once removed from place by water current or other individual, the fish soon find another close free rocky portion to grab.

Stomach contents of 238 specimens (11.0-83.9 mm SL) was composed of Bacillariophyceae (*Actinella*, *Eunotia* spp., *Frustulia*, *Gomphonema*, *Navicula*, *Pinnularia*, *Tabellaria*), Chrysophyceae (*Mallomonas*, *Ochromonas*), Cyanophyceae (*Calothrix*, *Heteroleibleinia*, *Phormidium*, *Pseudanabaena*, *Rivularia*), and Zygnemaphyceae (*Actinotaenium*, *Cosmarium*, *Mougeotia*, *Spirogyra*, *Oedogonium*, *Xanthidium*). Also, part of the diet is composed of aquatic insects (immature of Chironomidae, Ephemeroptera, Trichoptera and less often of Diptera and Coleoptera) and unidentified arthropods' fragments. However, the percentage of each food item is variable with life stage of *C. pecten*. Stomach contents of small juveniles (Stage Juvenile 1) had 41.9 % empty stomachs and the stomachs with food were composed by 39.2 % of unidentified invertebrate fragments, 38.7 % of *Spirogyra* sp., 14.5% of Ephemeroptera, and 7.6% of Chironomidae. Stomachs contents of medium sized juveniles (Stage Juvenile 2) had 12.5% empty stomachs, 42.8% of algae complex (around 13 genera), 28.8% of *Spirogyra* sp., 23.8% of insect fragments, and 4.6% of Chironomidae; and large juveniles and adults had 43.6% of stomach empty, 71.4% of algae complex (at least 22 genera), 17.7% of *Spirogyra* sp., 6.7% of Ephemeroptera, 3.5% of Chironomidae, and 0.7% of insect fragments. When the stomach was empty, food was usually present on the intestine, irrespective of collecting time of day. The general diet of *C. pecten* is almost 100% autochthonous.

Small juveniles sampled on September 2010 (driest sampling) had predominance of *Spirogyra* sp. on 100% of the diet in various specimens, contrasting with same sized juveniles sampled on March 2011 (rainy sampling) that had almost all individuals with 100% insects on its stomach. The majority of these small juveniles with empty stomach or lower degree of stomach fullness were sampled on early morning (100% and 85.7%, respectively), contrasting with higher levels of stomach fullness on afternoon (42.9-85.7% of stomachs with degree 3 and 4). This result is in accordance to the hypothesis of diurnal feeding habit of this life stage of *C. pecten*. Within specimens with food on stomach, *Spirogyra* showed absolute dominance in September 2010 (93.2% of the stomachs contents) and insects the absolute dominance in March 2011 (100%). On the other hand, for subadults and adults higher percentage of empty stomachs or with the minimum degree of stomach fullness were observed on the afternoon (60.7-77% and 50-94.2%, respectively), and apparently lower percentage of empty stomachs or low degree of

fullness occurs at first hours of night (7.1-23.1% and 46.2-57.1%, respectively). Among those with food on the stomach, the most common condition is to have more than 50% of the specimens with lower degree of fullness, independent of the period of the day. Those usually have food on the intestine. At this stage dominance of algae complex on diet occurred on all samples (68.6-96.7% of the stomachs contents), except by samples from March 2011, with dominance of *Spirogyra* (45.1-53.1% of stomach contents) followed by algae complex (24.5-28.0%). Thus, algae complex represents more than 50% of the diet at this stage, independent of the period of the day. *Spirogyra* showed higher importance than algae complex only on March 2011, on samples from afternoon and early night.

Although lower number of individuals was dissected for the intermediated-sized individuals (Juvenile 2), a preferred period of food ingestion among samples examined was not observed. Within individuals with food at stomachs, degree of fullness was more equally distributed along degrees 1 to 3, apparently without dominance. Also, diet at this stage was variable, including algae complex, *Spirogyra* and insects, with dominance of one or the other according to period of the year (algae complex on afternoon of September 2010 and insects on afternoon and early night of March 2011). *Copionodon pecten* has digestive tract comparatively long, with stomach differentiated, sacular, and relatively small. The total length of digestive tract is variable and increases along development (Juvenile 1: 57.5-65.4% SL, mean= 60.8, n=4, varying from 0.3-0.6 times the SL; Juvenile 2: 67.9-106.1% SL; mean= 86.0%, n=11, varying from 0.7-1.0 times the SL; Subadults and adults: 116.2-172.8%SL; mean=141.9%; varying from 1.2-1.7 times the SL).

Tests performed to evaluate chemo-sensorial ability of the *C. pecten* while foraging yielded similar results in all replicates and with distinct stages of development. Positive reaction was observed to corn flour, biscuit, and ornamental fish food pellets, attracting a few to around 20 individuals. They grab small particles in the case of corn flour/biscuit or stay with head on top of food pellets/larger biscuit portions, scraping it with their teeth.

Reproduction. Maturing and mature males and females were recorded from throughout the year (January 2010 to March 2011). The smallest female with first mature oocytes measured 44.7 mm SL and the smallest mature male measured 53.2 mm SL. The largest female and male examined measured 70.8 mm SL and 68.5 mm SL, respectively. Large immature and mature females had oocytes in various developmental stages. In cases of mature females, number of oocytes per ovary ranged from 13-75, with diameter ranging from 1.5 to 3.0 mm, and a few white oocytes with diameter around 0.5 mm. In cases of

immature and/ or maturing females, number of oocytes per ovary ranged from 9-43, with oocytes at various stages of development, its diameter varying from 0.5-2.4. Larvae were found in January and September 2010, but small juveniles (up to 20.0 mm SL) were seen in all field trips. Mature individuals were also found in all field trips, representing 10.5% of the total in January 2010, 35.0% in February 2010, 42.4% in May 2010, 10.3% in September 2010, and 7.6% in March 2011. Observation of fish size on pools apparently reveals that most individuals are adult or nearly adults. Within samples dissected and with sex identified by fish dissection occurred predominance of females (37.5% female and 17.9% male). Sexual dimorphism that allows external discrimination of the sexes in *C. pecten* was not observed.

Light reaction. Observation on field, showed that *C. pecten* have moderate reaction to sudden illumination with flashlights, usually swimming slowly away from light or slightly accelerating the swimming, more rarely some individuals move towards the light. In the reaction to light experiments, juveniles and larger individuals apparently showed distinct response. In all tested light intensities, juveniles (around 20-35 mm TL) were mostly indifferent to light, *i.e.*, they did not show significant preferences, either to the dark or to the illuminated chamber. On the other hand, larger specimens (around 42.5-59.4 mm TL), rarely stayed exposed to the light chamber of the aquarium, even if in this part was settled its shelter before the beginning of the experiment. In this group, that revealed visible reaction to light, individuals usually stayed only 5 to 10 seconds on the light chamber, except by one individual that stayed longer, for about 3 minutes. No identifiable different reaction was seen for different intensities of light used.

Agonistic behaviour and resident versus intruder experiment. According to field observations, when two individuals of *C. pecten* met, apparently by chance (no spontaneous active pursuing was observed), usually the first reaction is both swim away quickly to opposite directions. They also can show the following reactions: 1) chase away one another in a quick pursuit, usually the larger one, or the smaller fish rapidly avoided the other one, without pursuing; or 2) attacks with mouth directed to head, to first half of body, mainly close do dorsal-fin base, or caudal fin area. These interactions were observed for medium sized juveniles or larger individuals, usually more commonly observed during foraging, when increased activity enhanced the chances of meeting. Nevertheless, as expected in view of the high population densities observed in the dry season, in general the

catfish seemed to be quite tolerant to the proximity of conspecifics, since no individual exhibited clear signals of stress.

On the natural environment, as for laboratory observations, the sequence of behaviour apparently varies from simple to complex, and the following components (partially adapted from Trajano, 1991) were observed for *Copionodon pecten*: “Avoidance”, displacement away from the opponent, varying from a swerve to a reversal of direction, without pursuit by the other fish; “Chasing”, represented by rapid pursuit of one fish by the other and rarely observed in the field; “Mutual chasing”, circular movement performed by the head-to-tail positioned opponents, each attempting to bite the other’s posterior region, usually involving similarly sized juveniles (medium or large sized) or between large juveniles and adults which swam head-to-tail in a circle for up to 5-6 rounds, the withdrawal of one of them ending the contest.; “Lateral and caudal attacks”, usually observed after chasing, with the opponent trying to bite the lateral region or the caudal region of the chased individual.

Under laboratory conditions, individuals show similar agonistic behaviour as for natural environment, with moderate size-related dominance mostly displayed in relation to food and shelter places. However, individuals appeared to be somewhat more aggressive and interactions with persecution generating escape or attacks had often happened. Observations showed increase of agonistic behaviour during feeding time, with competition between individuals to catch the flakes of fish food. Attacks on laboratory were registered for juveniles and adults and lasted longer than on field conditions (usually 10 seconds to one minute).

Most of the attacks were apparently closely related to territorial defense, once these began with the approach of the intruder to the resident. In aquarium with various relatively large individuals together, the defended its den against the others. While with just only one individual per aquarium, even with more than one shelter at its disposal, individuals selected only one or two shelters and used it continuously. Smaller specimens kept in aquarium usually did not used shelter continuously and showed no shelter defense as described.

Based on the resident versus intruder tests, their agonistic behaviour started from the first contact, during a period of two seconds to less than one minute, except by one pair observed which first contact occurred after seven minutes. After inserted in the aquarium, the intruder usually explored the area and when perceived by the resident, the latter got quickly out of the shelter to expulse the intruder. At first contact no direct attacks occurred

and agonistic behaviour initiates as expulsion from area of shelter, with short persecution of the intruder. The dominance was determined by the permanence or conquest of the shelter, or tendency of the subordinate fish to be constantly pursued, staying distant from the shelter or territory of the dominant. Once dominance was established the subordinate tended to swim near the surface or remained motionless at a corner, while the dominant usually returned to the shelter or moved to one shelter to the other. Thus *Copionodon pecten* is apparently territorial and the dominance consisted basically of occupation of the shelter, with new attacks occurring only if intruder approached the shelter.

Size seems to be the main factor to determine the result of a bout. In 42 pairing tests, the dominance was determined by the size of individuals, resident or intruder. The largest of two fighting individuals, was it resident or intruder, was dominant in 24 of the 30 trials with conspecific (N= 24, $\chi^2= 20.17$, $p < 0.001$), and in four of the six trials of *C. pecten* versus *C. orthiocarinatus*. The residents were dominant on 18 of the trials (N= 18, $\chi^2= 1.5$, $0.1 < p < 0.2$), not statistically significant. In tests using individuals of similar size the dominance were not defined quickly (1.5-3 minutes).

Test using the congener *C. orthiocarinatus*, not sympatric to *C. pecten* at stretch of river where observations occurred, revealed similar agonistic behaviour and dominance. As for interactions with *Astyanax* sp. (fig. 7a), in the natural environment it was observed that *C. pecten* reacted to the passage of small schools of *Astyanax* sp. leaving its place and returning after the passage. On the pairing tests, no agonistic behaviour between these species was observed. No interactions with tadpoles were observed. As for human contact, when in high concentration of individuals, they approach hands and swim over skin (fig. 7b), fleeing just when trying to capture the individuals. Agonistic behaviour recorded for *C. pecten* larvae was not evaluated herein.

Popular name. Jundiá, cari.

DISCUSSION

The results obtained for *Copionodon pecten* are herein compared, at several instances, to those for *Trichogenes longipinnis*, based on the evidence that Copionodontinae is sister group of Trichogeninae (de Pinna, 1998; Bichuette *et al.*, 2008; Datovo & Bockmann, 2010), along with the well known natural history of one member of the latter subfamily (Sazima, 2004). Whenever available, information for non-parasitic

trichomycterids was also used.

Habitat. Water current, oxygenation, transparency, bed composition, bed coloration and depth have been reported as selective environmental parameters for several species of non-parasitic trichomycterids (Arratia & Menu-Marque, 1981; Arratia, 1983). A similar influence of these parameters was also observed in the Rio Coisa Boa where *Copionodon pecten* dwells. Field and laboratory observation indicate that *C. pecten* inhabits typically well-oxygenated streams, adapted to life in rocky bottomed pools along riffles with moderate to strong water current. Fish as recorded the in small to large sized pools, variable sized grooves, and mostly in shallow depths (15-60 cm deep). Water flow preferences are linked to stage of development, with juveniles usually occupying slow-moving parts of pools and larger specimens mainly in areas with water current higher than $0.66 \text{ m}\cdot\text{s}^{-1}$. Specimens observed grabbed to the substrate on areas with water current violent enough to carry the fish outside the pool were observed mainly on rainy days.

River and pools dimensions vary considerably throughout the year, but physicochemical characteristics of the water apparently vary little. The fish are especially abundant on studied area at dry season, when individuals are concentrated on relatively shallow and at least partially isolated pools (up to $200 \text{ individuals}\cdot\text{m}^{-2}$). The lower number of individuals visualized at the rainy days may be due to floods, washing away most of the individuals and/or to a tendency to remain sheltered in deeper pools until heavy rains ceased. The population of *C. pecten* may be considered relatively large compared to data known for *Trichogenes longipinnis* that yielded up to $25 \text{ individuals}\cdot\text{m}^{-2}$. Very little is known to size of populations of other trichomycterids and data available are mainly for the cave dwelling species, with even smaller density when compared to *C. pecten* (e.g., *Trichomycterus itacarambiensis* with $0.15\text{-}0.20 \text{ individuals}\cdot\text{m}^{-2}$ in the dry season (Trajano, 1997)). Among other trichomycterids, it was recorded for *Stauroglanis gouldingi* aggregations of 3-20 individuals, visual census yielded $0.08 \text{ individuals}\cdot\text{m}^{-2}$, and capture yielded $0.4 \text{ individuals}\cdot\text{m}^{-2}$ (Zuanon & Sazima, 2004).

Such high abundance of *C. pecten*, specifically at places observed, may be related to the confinement of individuals on certain pools, higher on dry season, but the apparent high population density may be related to the efficient life strategy of the species. This involves the ability to utilize the abundant periphytic algae of the environment, which includes a series of feeding strategies and body morphology. One remarkable adaptation is

the unique spatulated-shaped teeth, along with long intestine tract, ventrally positioned mouth, and structures to attach the fish to the rocky surface (interopercular odontodes and broad paired fins).

Astyanax sp., the unique species observed co-occurring with *C. pecten* in some riffles pools, is a species similar to those included in the “*A. scabripinnis* species complex”, known by their preference to headwaters, usually steep hills streams ones. The apparently pacific co-occurrence of both species in the same pools is possibly related to the fact that they don’t compete for food, for the same position on the water column, or by the fact that although somewhat active during day, the majority of individuals of *C. pecten* in a population is mainly nocturnal, inverse to the individuals of *Astyanax* sp. The latter is mainly nektonic, diurnal, omnivorous/insectivorous, and apparently depending mainly on allocthonous income of food. Also, usually only a few specimens of *Astyanax* were observed in pools clearly dominated by *C. pecten*, and possibly, the tetra inhabits preferentially pools somewhat deeper and more heterogeneous substrate. The species *Hoplerythrinus unitaeniatus*, co-occurring with *C. pecten* (although not observed directly), is apparently the main predator faced by the species, once it is a facultative predator (Pereira et al., 2008), usually with piscivorous feeding habits.

Morphology and colour pattern. *Copionodon pecten* shows morphological differences from small juveniles to adult individuals, including decrease of eyes percentage in head length, change in dentition morphology (exposed portion of teeth conical to spatulated; one to two functional series of teeth on premaxilla and dentary), number and robustness of interopercular odontodes series, and change in color pattern (from homogeneous coloration with a straight dark line on small juveniles, lateral of body to a sinuous dark line along with dorsal dark lines and presence of dark spots over body on median to large sized individuals and almost without spots or dark line on some largest specimens). Some of these differences are possibly related to the distinct microhabitats, period of activity and diet verified for each stage of development. Larger eyes on juveniles were described for *Trichogenes claviger* (de Pinna et al., 2010) and are expected for most siluriforms. For *C. pecten*, larger eyes on small juveniles is probably related to the diurnal activity of individuals of this stage versus the mainly nocturnally active subadults and adults.

Copionodon pecten have exposed portion of teeth conical or triangle shaped at initial stage of development, feature possibly related to the diet based on planktonic algae instead of periphytic algae grasped from rock surface performed by the spatulated teeth of

medium to large sized specimens. Spatulated teeth are efficient in scrapping algae from rocky substrate. Among neotropical catfishes, particularly within trichomycterids, this tactic is not common. Algae-grazing armored catfishes (e.g., loricariids) usually have numerous elongate teeth.

Trichomycterids use their opercular and interopercular odontodes as supporting structures to move over hard substrate (Eigenmann, 1918). Interopercular odontodes are well developed in *C. pecten* as well (de Pinna, 1992), showing distinct stages of development according to fish stage of life. Thus, climbing abilities of the species varies according to fish development and its preferred habits. The broader patch, higher number and robustness of odontodes described for medium to large sized individuals are possibly related their habits, distributed mainly close to or at walls back to water entrance, usually under boulders, or along grooves with moderate to high water flow. These environments contrast to those more lentic portions of pools inhabited by juveniles. Pectoral fins, also used to stabilize the fish body, apparently are well developed throughout fish life.

Compared to other trichomycterids (e.g., *Trichomycterus bahianus*, *Trichogenes longipinnis*), *C. pecten* have stronger interopercular odontodes on a very elongated patch (patch length of 56.1% of HL on specimen of 59.1 mm SL vs. 39.5% of HL on specimens of *T. bahianus* of 61.6 mm SL), pectoral fin broader and more robust (its larger measured width of 18.4% of SL vs. 9.2% on *T. bahianus* and 15.5% on larger *T. longipinnis* measured), pelvic fin somewhat broader and more laterally positioned resulting on a broad space between its basal portions, somewhat larger eyes and shorter barbels, mouth ventrally positioned (vs. terminal or subterminal), spatulate teeth on adults (versus conical), and more elongated digestive tract. Measurement of stomach plus intestine length of medium to large sized individuals of *C. pecten* yielded 67.9-172.0% of SL vs. 59.1-85.6% in *Trichomycterus* spp., and 79.4-89.6% on two relatively large specimens of *Trichogenes* examined. The overall morphology of the digestive tract of *C. pecten* is somewhat more similar to that of *Trichogenes longipinnis* than that of *Trichomycterus* species examined.

As previously discussed, the broad odontodes patch of *C. pecten* is related to the higher water flow preferences of the species and the adherence and body stability to the almost strictly rocky substrate. The thickening of the first pectoral rays is supposed to increase the flexibility and strength of the fin, a characteristic recurrently found in rapids-dwelling fishes (Lundberg & Marsh, 1976; Zuanon & Sazima, 2004). The pectoral fins of *C. pecten* lack filamentous first ray, a feature that could be related to *C. pecten* posing propped on the substrate by its robust pectoral fins. Having large eyes and short barbells

could be related to the preferred algivorous feeding habit and the visual ability as the possible main sensory clue for food detection, although they showed good response to chemical stimuli. As cited previously, the spatulated teeth of *C. pecten*, as well as its ventral mouth and long digestive tract are related to the catfish diet.

Spatial distribution and period of activity. The observed distribution of *C. pecten* is apparently discontinuous along the Rio Coisa Boa, with tendency to be restricted to determined pools, according to its dept, water current and substrate. Moreover, differential habitat usage within these areas is correlated with the age of an individual. Thus, an ontogenetic spatial segregation was observed for *C. pecten*, with small juveniles more diurnally active and restricted to shallow and low flowing water, occupying mainly pools borders, while larger individuals preferred somewhat higher depths and fast flowing water. Although not completely similar, ontogenetic spatial segregation was previously reported for the trichomycterids *T. chiltoni* (Arratia, 1983) and *T. areolatus* (Arratia, 1983; Manriquez *et al.*, 1988) in the rivers of Chile, with juveniles preferring soft bottoms and adults restricted to gravel bottom. In contrast, adults and juveniles of *T. diabolus* occupied similar microhabitats (Casatti, 2003). *Copionodon pecten* is an active fish, but movements of individuals between distant pools were not observed. Apparently, the main factor responsible for them to move far from its ‘home pool’ is the floods of heavy rainy days.

Copionodon pecten is a bottom dwelling fish species, a trait strongly related to its feeding habits and possibly dependence of periphytic algae, at least for medium sized juveniles to large individuals. However, like *Trichogenes longipinnis*, *C. pecten* exhibits an increased midwater activity when compared to the typical bottom-dwelling trichomycterids (*e.g.*, *Stauroglanis gouldingi*, Zuanon & Sazima (2004); *Trichomycterus diabolus*, Casatti (2003)). Smaller individuals of *Copionodon pecten* hide less than larger ones and are seen on shallow areas of pools during day and night time. On the other hand, larger individuals prefer somewhat deeper and darker areas during daytime.

Gregariousness was observed in different degrees and stages of development of *C. pecten*. Small and medium sized juveniles were seen almost always grouped, both during day and night hours. Larger individuals appears to be more aggregate during daytime, the period of less activity, which could be related to individuals sharing deeper areas of pools or preference for being under shelter. The high number of individuals seen together on dry periods (*e.g.*, Sep 2010) is mainly related to the decrease of water level and restrict allowed movement of individuals between pools. Solitary individuals were rarely seen, being more

common when juveniles were trapped in isolated small pools. According to Sazima (2004), tendency to aggregate occurs in *Trichogenes longipinnis* but is apparently unrecorded for other trichomycterids. A solitary behaviour was reported for *Ituglanis mambai* by Bichuette *et al.* (2008).

Similarly to *Trichogenes longipinnis*, *C. pecten* is diurnally and nocturnally active, but apparently mainly nocturnal (at least subadults and adults), which is a habit more typical of trichomycterids. Apparently distinct from *T. longipinnis*, *C. pecten* is less nektonic and shows distinct tendency to aggregate, varying according to stage of development. The also diurnal forage of *Copionodon pecten* is unusual because most of the studied trichomycterid species are nocturnal (de Pinna, 1998). Daytime activity was also reported by Sazima (2004) as one of the most striking characteristics of *Trichogenes longipinnis* and suggested as synapomorphic of the most basal trichomycterid clade, Copionodontinae-Trichogeninae (de Pinna, 1998). However, as stated by Casatti (2003), the suggestion that species of *Trichomycterus* have twilight or nocturnal feeding activity patterns (Burgess, 1989) does not agree with all species of the genus, with diurnal foraging behaviour reported for various of its species (*e.g.*, *T. areolatus* and *T. chiltoni* Arratia (1983); *Trichomycterus* sp. (Casatti & Castro, 1998), and *T. diabolus* Casatti (2003)). As nocturnal habits represent a plesiomorphic condition among Siluriformes, probably diurnal habits arose several times during trichomycterid evolution, as previously stated by Zuanon & Sazima (2004). The continuous mode of swimming described for *T. longipinnis*, by Sazima (2004), is also regarded as a basal behaviour within Trichomycteridae (de Pinna, 1997). *Copionodon pecten*, apparently have an intermediary condition, once subadults and adults stay mainly stationary during daytime, but with short excursions nearby or are displaced by water flow or conspecifics. The juveniles also have a more continuous swimming mode than adults and its frequent exploration of water column, in addition to the bottom, may be an adaptation to increase the chances of getting planktonic food.

Foraging behaviour and diet. The diet of *C. pecten*, based mainly on algae and less commonly on autochthonous immature insects (at least for medium and large sized individuals), is distinct of the diet recorded for the two species of *Trichogenes* (Sazima, 2004; de Pinna *et al.*, 2010) and most other trichomycterids (Bockmann & Sazima, 2004; Castro & Casatti, 1997; Casatti (2003); de Pinna (1998); Zuanon & Sazima (2004); Wosiacki & de Pinna, 2008). Those are usually dependent largely upon autochthonous immature insects and allochthonous adult insects. Also, distinct from the known habits of

Trichogenes, they are mainly bottom feeding, although juveniles' exploration of the water column is an important component to diet. The feeding behaviour repertoire of *C. pecten* is not diversified, distinct from the remarkably diversified feeding behaviour described for *T. longipinnis*.

Although the same main food items were present in the diet of the juveniles and adults of *C. pecten*, different values of relative importance for each item were recorded in the studied stages of development. Most individuals belonging to stage 'Juvenile 1' fed on filamentous algae (mainly *Spirogyra* sp.) and immature aquatic insects. On the other hand, in the stomachs of larger fish was found mainly periphytic algae complex, followed by a somewhat wider variety of immature aquatic insects. A shift in food habits with size increase is well known in fish (Nikolsky, 1963). Generally, larger fish eat larger food and greater variety of organisms, whereas smaller fish feed on less diverse and smaller sized food items. The food habit of *C. pecten* seems to follow this trend. Thus, algae were the main diet component in all stages, with dominance of filamentous algae (*Spirogyra*) on juveniles and a complex of algae on larger specimens. *Copionodon pecten* may be characterized as mostly algivorous and its feeding tactic and diet are unique among trichomycterids. Among Siluriformes, diet largely based on periphytic algae is known to occur only for loricariids, astroblepids, and Chiloglanidinae (Mochokidae), while diet based on aquatic insects is largely spread throughout small members of the group. The predominance of autochthonous food items in the diets of *C. pecten*, at least regarding to the aquatic insects, was very similar to that observed for *Trichomycterus* species (Castro & Casatti, 1997; Casatti & Castro, 1998; Casatti, 2003).

Foraging behaviour varied throughout day and night, with peaks on daytime for small juveniles and at night for larger juveniles and adults. Feeding tactic is also somewhat variable along life period of *C. pecten*, with apparent higher importance of water column feeding on first stages of life, followed by a more benthonic scrapping surface mode of feeding as the fish grows. As described for *T. longipinnis* by Sazima (2004), chemical, tactile and visual cues are used by *C. pecten* while foraging, as indicated both by the observations under natural conditions and by the tests performed in the field and laboratory. Chemo-sensory detection of food apparently occurs, as the catfish were attracted to provided fish food pellets, and visual detection when individuals detected drifting particles or were attracted also by corn flour and biscuits offered. According to Sazima, using more than one sensorial ability simultaneously or consecutively is common during foraging activities for several fish groups, but visual orientation towards food,

observed by the author in *T. longipinnis* and herein for *C. pecten*, is noteworthy for species of the family Trichomycteridae, a predominantly nocturnal and/or cryptic fish group with very small eyes.

Large juveniles and adults caught on afternoon had mostly empty stomachs, whereas small juveniles had mostly full stomachs by that period of day. This result is consistent with the greater feeding activity of juveniles throughout the day and foraging by larger individuals mostly at night. The high number of empty stomachs with food restricted to the intestine in many individuals and the long digestive tract may indicate short transit time in the upper portion of the digestive tract and extended period of food absorption along intestine. Having digestive tract long, with relatively small stomach is possibly related to the mainly herbivorous diet and the longer period required for food absorption when comparing to more carnivorous fish (Kramer & Bryant, 1995). Larger individuals have intestine longer than small juveniles (116.2-172.8% versus 57.5-65.4% of the SL), what could indicate an increase on algae dependent algae as the fish grows.

Reproduction. No distinct reproductive season was recorded for *C. pecten* on the studied period, differing from the observed to *T. longipinnis*, which maturing males and females were recorded from August to December (austral late winter and early summer) (Sazima, 2004). Analysis of the gonads revealed presence of mature individuals of *C. pecten* throughout the year indicating multiple spawning over a long reproductive period. The almost absence of spent gonads in *C. pecten* (three of the 45 mature females) may be a consequence of the individuals with multiple spawning, a fact in accordance to the presence of various stages of oocytes development within ovaries of immature and maturing females. According to Winemiller & Rose (1992), small fishes with frequent reproductive bouts over a long spawning season have been classified as opportunistic strategists that are successful in disturbed habitats. The observed life-history of *C. pecten* apparently agrees with this opportunistic strategy. The presence of mature individuals throughout the year represents an additional tactic for living in a continuously fast-flowing microhabitat, where the clutches can be moved by the current (Casatti, 2003).

The minimum size of reproductive *C. pecten* females is slightly higher than the half of the maximum size recorded for the species (63.1% of the maximum female length) and, thus, somewhat higher than the condition found by Sazima (2004) for *T. longipinnis* (about 50%) and the 40-50% of the various trichomycterid species (*e.g.*, *Eremophilus mutisii*, *Trichomycterus areolatus*, *T. itacarambiensis* Florez & Sarmiento, 1989; Manriquez *et al.*,

1998; Trajano, 1997). The low oocytes numbers here obtained for *C. pecten* is somewhat similar to the condition observed in *T. longipinnis*, although with even lower number (9-75 vs. 8-186 immature and/or mature per ovary), and contrast with the high fecundity recorded for trichomycterines such as *Trichomycterus areolatus* (~1500 eggs) or *Eremophilus mutisi* (up to 53.000) (Manriquez *et al.*, 1988; Florez & Sarmiento, 1989). Adults together with juveniles were not observed and apparently the species does not have parental care, a condition apparently similar to that described for *T. areolatus* (Manriquez *et al.*, 1988). Based on the field observations and dissected specimens, the distribution of size classes is apparently skewed toward larger size/age classes. The same tendency was observed for troglobitic siluriforms (*e.g.*, *Pimelodella kronei* Trajano & Britski (1992); *Rhamdia enfunada* Bichuette & Trajano (2005)). Age distributions skewed toward larger classes is evidence of a K-selected life cycle (precocial lifestyle, *sensu* Balon 1981, 1999).

Light reaction. Small juveniles of *Copionodon pecten* are mostly indifferent or present weak reaction to light, but as the fish grows the reaction gets stronger. Weak reaction behaviour towards light is possibly related to diurnal activity; on the other hand, a strong photophobic behaviour even at low intensities is indicative of nocturnal activity (Trajano & Gerhard, 1997). The observed behaviour of *C. pecten* apparently follows this trend, once small juveniles are diurnally active while larger individuals have nocturnal peak of activity. Juveniles progressively adopting more cryptic habits as they grow were recorded for *T. longipinnis* (Bizerril & Primo, 2001; Sazima, 2004), a trend also recorded for the Loricarioidei *Nematogenys inermis* (Arratia 1983; Arratia & Huaquín, 1995) and more recently for the heptapterid *Rhamdia enfunada* (Bichuette & Trajano, 2005). However, compared to the majority of trichomycterids, *C. pecten* show reduction of the cryptobiotic habits, a tendency shared by the sister group Trichogeninae.

Agonistic behaviour and Resident versus intruder experiment. *Copionodon pecten* is herein regarded as a mild territorial catfish, with weak, size related dominance mostly displayed in relation to food and shelter. The species do not present complex behavioural repertoire and the apparently weak agonistic behaviour recorded for *C. pecten* is similar to that of *T. longipinnis* (Sazima, 2004). In general, the catfish seemed to be quite tolerant to the proximity of conspecifics, since no individual exhibited clear signals of stress as expected in view of the high population densities observed in the pools. The degree of aggressiveness is also low and variable in the few studied *Trichomycterus* species (Arratia,

1983; Trajano & Souza, 1994), and territorial behaviour seems to be restricted to certain situations such as in individuals kept isolated (Arratia & Huaquín, 1995). The observed agonistic behaviour is also similar to a few clariid, ictalurid, and heptapterid catfish species studied so far, and agrees with the general siluriform agonistic patterns in the sense of Trajano (1990). The absence of strong reaction by *C. pecten* to the presence of *Astyanax* sp. may be due to their exploration of distinct niche, once the former usually swims very close to rock surface and feeds mainly on benthonic items while the latter is more nektonic and feeds mainly on water column particles.

Conservation. *Copionodon pecten* is apparently fragile and vulnerable to environmental disturbance due to highly endemic, highly specialized diet, and K-selected life style, leading to slow population turnover. Conservation depends on the maintenance of the original characteristics of the headwaters inhabited by them, mostly the continued integrity of the riffle areas.

Comparative material examined. *Trichogenes longipinnis* MZUSP 83452 (19 spec., 14.0-74.8 mm SL); MZUSP 83454 (12 spec., 11.0-36.7 mm SL). *T. claviger* MZUSP 105732 (1 spec., 48.5 mm SL). *Trichomycterus bahianus* UFBA 4546 (33 spec., 24.1-80.5 mm SL). *Trichomycterus* sp. UFBA 6517 (13 spec., 34.7-73.3 mm SL); *Astyanax* sp. UFBA 5288 (44 spec., 38.4-88.5 mm SL); UFBA 6590 (10 spec., 65.0-83.9 mm SL); *Hoplerythrinus unitaeniatus* UFBA 6604 (2 spec., 6.8 – 9.7 mm SL).

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Legends



Fig. 1. Part of the stretch of Coisa Boa river studied. (a) flooded river channel at rainy season; (b) dry river channel at driest field trip.



Fig. 2. Habitat of *C. pecten* in Rio Coisa Boa, including pools (a,b) and groove (c) where individuals were observed.

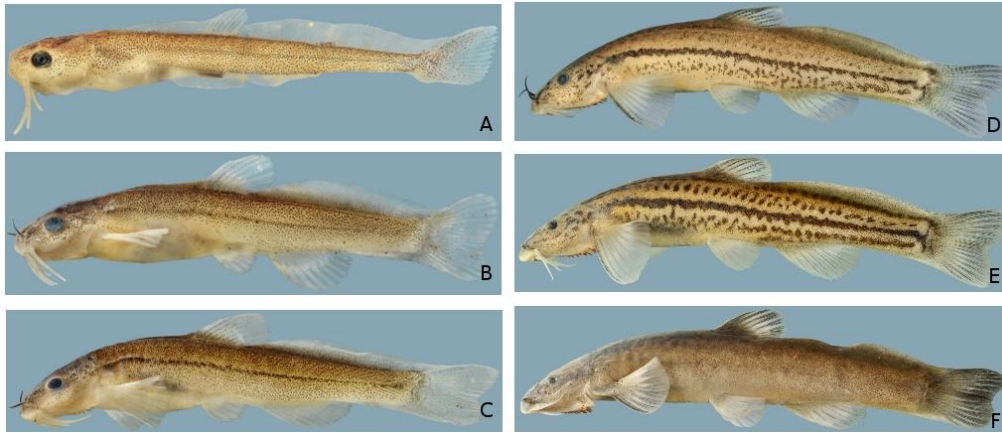


Fig. 3. Developmental stages of *C. pecten*, UFBA 6551. (a) larvae, 11.4 mm TL; (b) juvenile 1, 13.5 mm SL; (c) juvenile 2, 24.0 mm SL; (d) subadult, 39.0 mm SL; (e) adult with spotted pattern, 48.1 mm SL; (f) adult with homogeneous coloration, 58.7 mm SL.



Fig. 4. Habitat and field photographs of *C. pecten*; (a) group of small juveniles (Juvenile 1); (b) individual of Stage Juvenile 2.

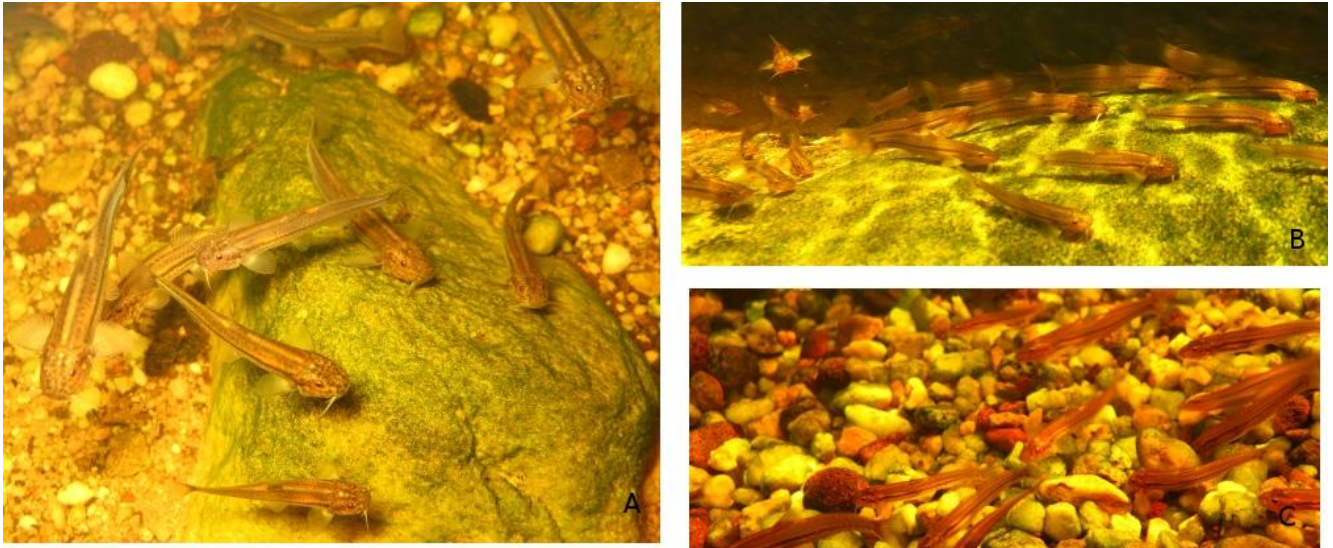


Fig. 5. Habitat and field photographs of subadults and adult individuals *C. pecten* aggregated; (a) group of individuals not polarized; (b) polarized individuals on algae rocky bottom; (c) individuals inspecting the pebbled substrate.



Fig. 6. Individual of *C. pecten* (around 45.0 mm SL) scratching the substrate.



Fig. 7. *Copionodon pecten* in its habitat. (a) showing co-occurrence with *Astyanax* sp.; (b) showing reaction to human presence.

Conclusões gerais

1. *Copionodon pecten* é uma espécie de hábito principalmente bentônico, que ocorre em cursos d'água com substrato rochoso, preferencialmente em poças e frestas, água bem oxigenada e de velocidade moderada a forte. A distribuição no ambiente varia de acordo com estágio de desenvolvimento: juvenis usualmente ocupam áreas rasas marginais substrato arenoso ou rochoso e com características de ambiente mais lântico; indivíduos maiores ocorrem principalmente em áreas comparativamente mais fundas (até 1 metro), com preferência por substrato rochoso e velocidade da água usualmente superior à 0.66 m.s^{-1} .
2. O período de atividade de *C. pecten* também mostra variação ontogenética. Pequenos juvenis são mais ativos durante o dia e, durante a noite, permanecem nas margens, ao sabor de pequenas ondas. Já os indivíduos maiores ativos principalmente à noite, quando se espalham para forrageamento, atingindo áreas mais rasas; durante o dia permanecem relativamente estacionários junto ao substrato, polarizados ou não.
3. Quanto à morfologia externa, *Copionodon pecten* mostra variação ao longo do desenvolvimento, com diminuição do tamanho do olho, mudança na forma dos dentes e número de séries de dentes funcionais, aumento no número e robustez dos odontódeos interperculares e alteração no colorido do corpo. Algumas dessas diferenças são possivelmente relacionadas aos diferentes microhabitats, período de atividade e dieta relativamente característicos de cada estágio de desenvolvimento.
4. *Copionodon pecten* possui tendência à agregação. Juvenis permanecem relativamente agregados durante dia e noite, enquanto indivíduos maiores parecem se agregar principalmente durante o dia, quando compartilham áreas mais fundas ou tocas. Aparentemente, a composição da população é direcionada para maior número de indivíduos subadultos e adultos.
5. A população de *C. pecten* pode ser considerada comparativamente grande, com observação de maior número de indivíduos na estação seca, quando estão concentrados em

poças relativamente rasas e parcialmente isoladas (até 200 indivíduos·m⁻²).

6. A tática alimentar predominante é a raspagem de algas do substrato, principalmente nos juvenis de tamanho médio e maiores. Ao forragear, apresentam resposta a estímulos químicos, táteis e visuais, de acordo com observações em ambiente natural e em laboratório.

7. A dieta de *C. pecten* é baseada, principalmente, em algas (filamentosas e não filamentosas) e menos comumente em insetos aquáticos imaturos. Juvenis menores alimentam-se principalmente de *Spirogyra* e insetos aquáticos, enquanto estômagos de indivíduos maiores mostram altas porcentagens de um complexo de algas perifíticas, seguidos por variedade maior de insetos aquáticos imaturos. *Copionodon pecten* pode ser caracterizada como espécie onívora, mas com forte tendência à algivoria, e sua tática alimentar e dieta são únicos entre tricomictérides.

8. A maioria dos juvenis de tamanho médio a adultos com estômagos vazios foram encontrados no período da tarde, enquanto juvenis tinham estômagos cheios nesse período, o que é consistente com forrageamento principalmente noturno para grandes indivíduos e diurno para pequenos.

9. *Copionodon pecten* tem trato digestivo longo, o que pode estar relacionado com amplo período para absorção do alimento no intestino, o qual é relativamente pobre em nutrientes.

10. A análise das gônadas revelou presença de indivíduos maduros ao longo de todo o período de estudo, indicando desova múltipla ao longo de amplo período reprodutivo. Assim, uma marcada estação reprodutiva não foi observada.

11. A espécie apresenta baixo número de oócitos e aparentemente não apresenta cuidado parental. Também não foi encontrado dimorfismo sexual externo.

12. *Copionodon pecten* possui reação moderada à luz, sendo que pequenos juvenis são quase indiferentes e adultos raramente ficam na câmara clara durante os experimentos. Assim, os indivíduos progressivamente adotam hábitos mais crípticos, conforme com o desenvolvimento. De modo geral, *C. pecten* mostra redução de hábitos criptobióticos,

quando comparado a outros membros da família.

13. A espécie mostra comportamento agonístico relativamente fraco. Ao se encontrarem, principalmente em período de forrageamento ou disputa por toca, podem apresentar rápida perseguição ou ataques com boca direcionada à cabeça ou lateral do corpo. A maioria dos ataques está aparentemente relacionada com defesa territorial, uma vez que estes usualmente começam com aproximação do intruso ao residente. Dominância é relacionada ao tamanho.

14. *Astyanax* sp. foi a única espécie observada co-ocorrendo com *C. pecten*, aparentemente pacificamente. *Hoplerythrinus unitaeniatus*, presente no Rio Coisa Boa, mas não observado nas poças estudadas, aparentemente é o principal predador de *C. pecten*.

15. *Copionodon pecten* é uma espécie aparentemente frágil e vulnerável à distúrbios ambientais, uma vez que é altamente endêmica, possui dieta especializada, e estratégia de vida tipo K, levando à lenta recuperação da população.

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Anexo

Author Guidelines

INSTRUCTIONS FOR AUTHORS

1. *Journal of Fish Biology* welcomes research manuscripts containing new biological insight into any aspect of fish biology. We invite papers that report results and ideas of value to fish biology that will serve a wide international readership. Hence the novelty of the content of manuscripts should have relevance beyond a particular species or place in which the work was carried out. **All material submitted must be original and unpublished, and not under consideration for publication elsewhere.** If in doubt about overlap, please give details of any related work submitted or in press when submitting your manuscript. The *Journal* uses plagiarism detection software, so in submitting your manuscript you accept that it may be screened against previously published literature.

The Fisheries Society of the British Isles (FSBI) considers that scientists should avoid research threatening the conservation status of any species of fish, which is already regarded as threatened according to the IUCN Red List of Threatened Species and the associated Red List Categories and Criteria version 3.1 (<http://www.iucnredlist.org/technical-documents/categories-and-criteria>) or which is listed as such in a Red Data Book appropriate to the geographic area concerned. In accordance with this view, papers based on such research will not be accepted, unless the work had clear conservation objectives.

2. **Submission of manuscripts.** We will consider: Regular papers (original research), Review papers, which will either be invited or agreed with an Associate Editor (see 17), Brief Communications (see 18), Letters (see 19), and Comments and Replies (see 20). Manuscripts are submitted online at <http://jfb.edmgr.com>, where a user ID and password are assigned on the first visit. Full instructions and support are available on this site. **Authors are expected to suggest potential referees**, selected internationally, for their manuscripts in the 'Suggest Reviewers' section.

3. **Preparation of manuscripts.** Authors should consult a recent issue of *Journal of Fish Biology* for details of style and presentation. **If their manuscript does not follow the**

format of the Journal, it will be returned to them unreviewed. Manuscripts must be **double-spaced throughout**, all pages must be numbered and **line numbering set to continuous**, including tables, figure legends and reference lists. **Use a font size ≥ 12 . Do not save files in PDF (portable document format) format.**

The first page must contain the following information: the title of the paper, name(s) (initials ONLY for forenames) and FULL academic address(es) of ALL author(s); if the address of any author has changed, it should be added as a footnote. Telephone number and email address for the corresponding author (**one only**) should be provided as a footnote. A concise running headline of not more than 45 characters inclusive of spaces should also be given on this page. For regular papers arrange sections in the following sequence: Title page (as a separate page), Abstract and Key Words (as a separate page), Introduction, Materials and Methods, Results, Discussion (**a combined Results and Discussion is not acceptable and Conclusions as a heading is only acceptable in Review Papers**), Acknowledgements (for individuals use initials only for forenames and no titles), References, Tables (with captions; see 6 below), Figure captions, Figures and Appendices. Within sections, subdivisions should not normally exceed two grades; decimal number classification of headings and subheadings should not be used (see recent past issues). Footnotes should not be used except in Tables. Spelling must be U.K. English, e.g. Concise Oxford English Dictionary (as distinct from American English) throughout, except in quotations and references. All Latin words (but excluding scientific words other than genus and species) should be in italics. **Do not write text in the first person.**

Do not duplicate information in tables and figures, or *vice versa* or in text and figures. Do not repeat table headings and figure legends in the text. Punctuation should be consistent and only a single space inserted between words and after punctuation. **Do not indicate positions of tables and figures in the text.** Two blank lines should be left after headings and between paragraphs. Text should be typed without end of line hyphenation, except for compound words. Lower case 'l' for '1' or 'O' for '0' should not be used.

4. **Abstract.** This must be concise and summarize **only** the significant findings of the paper (*i.e.* not the background or methods). It should be followed by a list of ≤ 6 **key words or key phrases that are not included in the title, with a maximum of 100 characters (including punctuation and spacing).**

5. **Illustrations.** Photographs should be selected only to illustrate something that cannot adequately be displayed in any other manner. Magnification should be given in actual

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Gilbert, C.R., Lea, R.N. & Williams, J.D. (2004). *Common and scientific names of fishes from the United States, Canada, and Mexico*. Committee on Names of Fishes. 6th edn. Bethesda, MD, U.S.A.: American Fisheries Society (for North American fishes; except those covered above for British fishes); Froese, R. & Pauly, D. (Eds) (2010). FishBase. World Wide Web electronic publication. www.fishbase.org; *FAO Guides for Fisheries Purposes*.

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