

**Interspecific competition, predation, and the
coexistence of three closely related neotropical
armoured catfishes (Siluriformes-Callichthyidae)**

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**Interspecific competition, predation, and the
coexistence of three closely related neotropical
armoured catfishes (Siluriformes-Callichthyidae)**

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Proefschrift

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PhD Thesis. Department of Experimental Animal Morphology and Cell Biology, Wageningen Agricultural University (WAU), P.O. Box 338, 6700 AH Wageningen, The Netherlands. The research described in this thesis was performed in Suriname (South America) at the Anton de Kom University of Suriname, P.O. Box 9212, Paramaribo, Suriname. It was supported by the Stichting Bevordering Nederlands Wetenschappelijk Visonderzoek and by Wageningen Agricultural University within the framework of the cooperation between Wageningen Agricultural University and Anton de Kom University of Suriname.

Stellingen

1. Gezien het belang dat door zowel visserij biologen als ecologen aan predatie wordt toegedacht verdient het kwantificeren van directe en indirecte effecten van predatie op vissen en hun larven onmiddellijke aandacht.
Dit proefschrift.
2. Hoewel meer dan een derde deel van het maag volume in volwassen *Hoplosternum* en *Callichthys* wordt ingenomen door detritus (zoals gedefinieerd door Bowen) speelt het detritus als zodanig een ondergeschikte rol als voedsel van de pantsermeervallen.
Bowen, S.H. (1983). Detritivory in neotropical fish communities. *Environmental Biology of Fishes* 9, 137-144.
Singh, T.B. (1978). *The Biology of the Cascadura Hoplosternum littorale Hancock 1834 with Reference to its Reproductive Biology*. Ph.D. thesis University of the West Indies, Trinidad.
Dit proefschrift.
3. Op grond van verschillen in de voortplantingsstrategie tussen enerzijds *Hoplosternum littorale* en anderzijds *H. thoracatum* en *Callichthys callichthys* is onderzoek naar de oorzaken van de mortaliteit onder eitjes, larven en juveniele pantsermeervallen in stilstaand water van zwampen en in stromend water van krekten in het regenbos gewenst.
Dit proefschrift.
4. Naast onderzoek naar het feitelijk voorkomen van competitie en predatie, waarbij in veldexperimenten veranderingen in de aantallen van organismen worden gemeten, zonder echter met zekerheid de oorzaak van de waargenomen aantalsveranderingen te kunnen vaststellen, is vooral proces-analytisch onderzoek naar de wijze waarop predatie en competitie plaatsvinden nodig om inzicht te verkrijgen in het belang van beide processen in complexe levensgemeenschappen.
Tilman, D. (1987). The importance of the mechanisms of interspecific competition. *American Naturalist* 129, 769-774.
5. Het feit dat een belangrijke groep vissen in de tropen een min of meer amfibisch bestaan leidt illustreert dat, rekening houdend met de grote diversiteit aan vis soorten in de tropen, zowel het spreekwoord 'Als een vis in het water' als het gelijknamige boek waarin de beschrijving van leven en functioneren van vissen in hoofdzaak wordt gebaseerd op het 'standaard' vis type zoals dat wordt aangetroffen in de gematigde streken, aanvulling behoeven.
Osse, J.W.M., Zijlstra, J. & Emden, H.M. van (1983). *Als een Vis in het Water*. Wageningen, PUDOC.
6. Aangezien de organismen die leven in de floodplains en zwampen zowel aangepast moeten zijn aan een terrestrische levenswijze (in de droge tijd) als aan een aquatisch leven in de regentijd kan de ecologie van de floodplains en zwampen noch uitsluitend vanuit de invalshoek van de aquatische ecologie (limnologie) noch uitsluitend vanuit de terrestrische ecologie optimaal worden bestudeerd.
Junk, W.J. (1980). Die Bedeutung der Wasserstandschwankungen für die Ökologie von Überschwemmungsgebieten, dargestellt an der Varzea des mittleren Amazonas. *Amazoniana* 7, 19-29.
Junk, W.J. (1984). Ecology of the varzea, floodplain of Amazonian white-water rivers. In *The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River* (Sioli, H., ed.), pp. 215-243. Dordrecht, Dr W. Junk Publishers.

7. Gegeven het potentieel gebrek aan nutriënten in de humide tropen als gevolg van de in hoge mate gesloten nutriënten kringloop in het tropisch regenbos en problemen met een nutriënten overschot uit mest in gematigde streken verdient het aanbeveling de export van eiwitrijke produkten vanuit de humide tropen te beperken tot hoogwaardige (luxe) produkten.
8. Gezien het mondiale belang van de tropische biodiversiteit en de biodiversiteitscrisis in deze gebieden verdient het aanbeveling tropische landen met een laag nationaal inkomen een aanzienlijk financieel belang te verschaffen in het beheer van en onderzoek aan hun biologische hulpbronnen en tevens de dialoog tussen de landen in de tropen en de rijke landen in de gematigde gebieden in deze te intensiveren.
Wilson, E.O. (ed.) (1988). *Biodiversity*. Washington D.C., National Academy Press.
9. Emissie- en milieukwaliteitsnormen zoals vastgesteld voor de gematigde gebieden kunnen niet zonder meer, zonder nader onderzoek, worden gehanteerd in de tropen.
10. Om te komen tot een effectieve bestrijding van luchtvervuiling is naast onderzoek naar de bronnen van de vervuiling met name fundamenteel onderzoek naar het gedrag (reactie evenwicht, invloed pH) van de milieugevaarlijke stoffen in het reactie medium lucht noodzakelijk.
11. De mindere smaak en kwaliteit van onder kunstlicht en 'optimale' bemesting in kassen geteelde tropische groenten en fruit vergeleken met de eigenschappen van dezelfde soorten afkomstig uit de tropen moet waarschijnlijk worden gezocht in verschillen in het licht regime, de bodem en mogelijk de aan/afwezigheid van natuurlijke vijanden.
12. Hoewel het experimenteren met de bereiding van de kwikwi vis (*Hoplosternum littorale*) moet worden toegejuicht, verdient de onlangs ontwikkelde methode om deze pantsermeervallen van hun pantser van beenplaten te ontdoen alvorens de vis op te dienen geen navolging. Weliswaar dient deze bereidingswijze het gemak van de consument, maar het genoegen en eigen karakter van het eten van de kwikwi, dat in hoge mate wordt bepaald door de pantsermeerval in alle glorie in zijn pantser te mogen aanschouwen en vervolgens eigenhandig de dubbele rij beenplaten van de vis af te schuiven, wordt ernstig geschaad terwijl mogelijk ook de smaak negatief wordt beïnvloed.

Stellingen behorende bij het proefschrift "Interspecific competition, predation, and the coexistence of three closely related neotropical armoured catfishes (Siluriformes-Callichthyidae)", Jan H.A. Mol. Wageningen, 15 September 1995.

"Those who eat the cascadura will, the native legend says,
Wheresoever they may wander, end in Trinidad their days."

From *History of the West Indies* by Allister Macmillan

(cascadura or soké kwikwi is *Hoplosternum littorale*)

aan mijn ouders

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Voorwoord

Het verschijnen van dit proefschrift, de afsluiting van mijn opleiding tot wetenschappelijk onderzoeker, biedt mij een welkome gelegenheid mijn dankbaarheid te uiten jegens allen, die mij in staat hebben gesteld het hier gepresenteerde onderzoek te verrichten. In de eerste plaats wil ik mijn ouders bedanken, die een universitaire studie mogelijk hebben gemaakt en mij steeds hebben gestimuleerd in mijn belangstelling voor de natuur en wetenschap.

De eerste kennismaking met Suriname vond plaats in 1983 en werd mogelijk gemaakt door Dr. Jan Lindeman (Rijks Universiteit Utrecht) die zich bereid verklaarde een doctoraal onderzoek aan de onkruid vegetaties van Suriname te begeleiden. Met goede vriend en studiegenoot Frank van der Lugt werd het onderzoek vlot aangepakt terwijl Jozef Joghi mij land en bevolking leerde kennen en mij behoedde voor de ergste misstappen.

Onder leiding van Dr. Eddy Lammens en Dr. Henk de Nie van het toenmalige Limnologisch Instituut heb ik vervolgens in het Tjeukemeer laboratorium (Fr.), wederom samen met Frank van der Lugt, de interactie tussen aal en brasem middels aquarium experimenten bestudeerd. Ik heb veel mogen leren van de wijze waarop Koos Vijverberg leiding gaf aan het onderzoek van het Tjeukemeer laboratorium en een uitstekende werksfeer wist te creëren.

Nadat ik in 1987 in dienst kwam bij de Anton de Kom Universiteit van Suriname kreeg ik de gelegenheid om binnen het kader van het project Visteelt van de Werkgroep Agrarisch Onderzoek ecologisch onderzoek aan tropische zoetwatervissen op te starten. Ellen Naarendorp gaf mij de taak, als voorbereiding op de eigenlijke visteelt experimenten, de ecologie van de drie kwikwi soorten in Suriname te onderzoeken.

Met veel hulp van Paul Ouboter, curator van de Nationale Zoölogische Collectie van Suriname, werd een aanvang met het onderzoek gemaakt en werd de probleemstelling nader uitgewerkt. Door deel te nemen aan expedities van de Zoölogische Collectie leerde ik ook de uitgestrekte oerwouden en de visfauna van het binnenland van Suriname goed kennen. Paul, ik dank je voor de uitstekende samenwerking en het stimulerend commentaar dat je steeds hebt geleverd op mijn werk. Het veldwerk in de zwampen van de kustvlakte zou niet mogelijk zijn geweest zonder medewerking van de heren Stolk (Weg Naar Zee) en Bissumbhar (Lelydorp). Bij de laboratorium experimenten en verwerking van de gegevens heb ik veel ondersteuning gekregen van het personeel van het Centrum voor Landbouwkundig Onderzoek in Suriname (CELOS) en haar directeur Ro Sweeb. Stanly Ramanand, Jolanda Bernstein, Ricky Stutgard, Sharma Kisoen-Misier, Lily Samson en Joyce Ramlal (CELOS) hebben mij uitstekend geassisteerd bij de verschillende werkzaamheden.

Toen in de loop van het onderzoek de economische situatie in Suriname verslechterde heeft ondersteuning vanuit Nederland door familie, vrienden en de vakgroep Experimentele Dier Morfologie en Cel Biologie (EDC) van de Landbouw Universiteit Wageningen het mij mogelijk gemaakt verder te werken. Mijn broer Tuur Mol voorzag mij steeds tijdig van aangevraagde literatuur, Professor Jan Osse (EDC) hielp mij aan een computer en Jozef Joghi heeft veel kleine en grote obstakels weten te verwijderen.

Professor Osse en zijn medewerkers van de vakgroep Experimentele Dier Morfologie en Cel Biologie hebben mij voortreffelijk opgevangen en ondersteund tijdens het jaar dat ik met sabbatical leave in Nederland verbleef t.b.v. de afronding van dit proefschrift. De vruchtbare gesprekken met Leo, Mees, Nand en overige collega's van de vakgroep en de wekelijkse werkbesprekingen heb ik zeer gewaardeerd.

Jan Osse, veel heb ik van je mogen leren, zowel tijdens de korte maar intensieve werkbezoeken in Nederland waarbij je structuur in het onderzoek hebt gebracht, als in het

laatste jaar van de afronding van het proefschrift. Je enthousiasme en grote kennis van de biologie van vissen maakten de kritische bespreking van de diverse hoofdstukken van het proefschrift voor mij leerrijk, spannend en iets om steeds weer met genoegen naar uit te zien. Onze discussies hebben in belangrijke mate bijgedragen tot verheldering en verscherping van de inhoud van de manuscripten. De gesprekken met Dr. Lowe-McConnell bij je thuis hebben mij zeer gestimuleerd. Jan, het is mij een eer en een genoegen dat je voor dit proefschrift mijn promotor bent.

Tenslotte rest mij een hartelijk woord van dank aan jou Evelien. Het moet niet altijd even gemakkelijk zijn geweest als ik vaak lijfelijk afwezig was of in gedachten teruggetrokken. Weet dat de ondersteuning die ik van je kreeg en de vrijheid die je me gaf om te werken het tot stand komen van dit proefschrift zeer hebben verlicht.

Chapter 1

General introduction

INTRODUCTION TO THE SCIENTIFIC PROBLEM AND STUDY OBJECTIVES

Tropical ecosystems are renowned for their high biodiversity (World Conservation Monitoring Centre, 1992) with many closely related species living together. Since Hutchinson (1959) posed his celebrated riddle: "Why are there so many animals?", factors potentially affecting species diversity have been important subject of study and discussion in ecology (Hairston *et al.*, 1960; Pianka, 1966; Connell, 1975; Menge & Sutherland, 1987). Factors thought to influence biodiversity are evolutionary/ecological time (Pianka, 1966; Gould, 1981), spatial heterogeneity (MacArthur, 1965), climate and climatic stability (Klopfer, 1959; Brown, 1981; Currie, 1991), productivity (Connell & Orias, 1964), disturbance (Connell, 1978), competition (Dobzhansky, 1950; Birch, 1957) and predation (Paine, 1966; Roughgarden & Feldman, 1975). Given the limits of the physical environment two different biological processes are probably responsible for most of the organization of equilibrial communities: competition and predation.

Competition has been a central focus in ecology for the last forty years. Many ecologists believed that competitive exclusion of allied species was one of the most important factors in structuring communities (Cody & Diamond, 1975; Schoener, 1983; May & Seger, 1986). What, it was asked, may be the limit to (morphological) similarity among coexisting competitors and how much niche overlap is consistent with coexistence (Hutchinson, 1959; MacArthur & Levins, 1967)?

At the same time, critics of the view that competition plays a leading role in structuring communities argued that periodic extreme conditions, predation and the dynamics of small populations may keep populations below a density where competition could be strong (Andrewartha & Birch, 1954; Den Boer, 1968; Connell, 1975, 1978; Wiens, 1977). For example, Strong (1984) shows that in phytophagous insects predators and low quality food keep population densities at a level at which even intraspecific competition hardly occurs.

In order to demonstrate the 'importance' of interspecific competition in nature, ecologists designed field experiments in which the abundance of one or more hypothetically competing species is manipulated (for problems with the interpretation of these field experiments see Bender *et al.*, 1984; Tilman, 1987). Schoener (1983) and Connell (1983) independently summarized the results of more than 150 field experiments. Although there are differences between their reviews, both found evidence for interspecific competition in more than 80% of the experiments. However, unlike Schoener, Connell found the strength of competition to be variable in more than half of the studies, waxing and waning in response to environmental changes. Periodic extreme environmental conditions are probably more characteristic of temperate regions than of the tropics and in this respect it is important that only 9% of the 164 studies cited by Schoener was conducted in the tropics (only 5 studies concerned the tropical rainforest).

In a review of field experiments on predation, Sih *et al.* (1985) found in more than 90% out of 139 papers significant effects of predation on prey populations or species diversity. However, again only 9% of the studies were conducted in the tropics. Sih *et al.*

(1985) also found in 40% of the studies unexpected and presumably indirect predator-mediated effects. Recently, there has been a growing awareness that indirect effects of predation may play an important role in ecosystems (Holt, 1977; Lawlor, 1979; Kerfoot & Sih, 1987). The 'keystone-predator' effect describes the situation in which a predator has an indirect, beneficial effect on a suite of inferior competitors by depressing the abundance of a superior competitor (Paine, 1966). A less prominent indirect interaction is the 'three-trophic-level' effect where a top consumer benefits prey two trophic links lower in the food chain because it reduces the abundance of an intermediate consumer (Abrams, 1984). A third and entirely different kind of indirect effect results if the mere presence of a predator alters the behaviour of prey and its distribution in time or space (Sih, 1980; Power, 1984). Here the predator acts more like a catalyst, altering interactions without necessarily directly influencing prey population densities.

The tropical rainforest is probably one of the most stable environments in the world. In the shaded forest understory below the closed canopy of trees, temperature and humidity are almost constant (Schulz, 1960), but in the creeks, rivers and swamps important fluctuations in the water level (and flow velocity) occur. Extreme environmental conditions limiting population densities are often hard to imagine. Species diversity is extremely high, resulting in a low (but constant) density of populations and complex biological interactions. Although the number of predatory species may be high, outbreaks of insect pests common to temperate forests do not occur in tropical rainforests. In multi-species communities with low population densities of the member species, complex interactions such as diffuse competition (MacArthur, 1972) and the collective predation pressure from several different predator species may be important. Indirect effects (Lawlor, 1979), accounting for the difference between the direct process of pairwise interspecific interaction and the total effect that one species has on another in a multi-species community, are probably also important. These thoughts have influenced the way in which the primary problem of this thesis was attacked. More studies on competition and predation in the tropical rainforest are necessary to evaluate the importance of both processes in structuring communities.

Alpha diversity of tropical freshwater fishes is extremely high (Lowe-McConnell, 1987), as exemplified by the cichlid fauna of the Great African lakes (Fryer & Iles, 1972) and the neotropical characins (Gery, 1978; Goulding *et al.*, 1988). In this thesis a case study will be presented concerning three medium-sized armoured catfishes of the family Callichthyidae: *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys*. The Callichthyidae is a large family of approximately 125 small- or medium-sized armoured catfishes restricted in their distribution to neotropical freshwater bodies (Burgess, 1989). The three largest species of the family, *H. littorale*, *H. thoracatum* and *C. callichthys*, occur sympatric in Suriname (South America). These three catfishes are adapted to oxygen depleted tropical standing waters by their intestinal respiration (air breathing) and the construction of floating foam nests (Carter & Beadle, 1931; Chapter 4). They are quite similar in size and body form (Chapter 7). The three species are among the most abundant bottom-dwelling fishes of neotropical swamps and potentially strong competitors. The impact of competition and predation on their communities was evaluated by 1) mapping their geographical distribution, 2) determining the overlap in their diet, 3) investigating reproductive seasonality, reproductive capacity and nest (micro)habitat differentiation, and 4) determining the potential impact of predation. Both field studies and laboratory experiments were performed in order to optimize the problem solving power of the present research.

SIDE LINES OF GENERAL INTEREST

Freshwater fish is still the most important source of animal protein to the rural population of South America (Junk, 1984). In Suriname, a decrease in the supply of swamp fish during the last decades to one quarter of the pre-1970 landings (Ouboter & Mol, 1994) and the appearance of small-sized specimens on the markets indicate over-exploitation of local stocks. Although protected by law in their main reproductive season (Rondeel, 1965), the three armoured catfishes probably also suffer from over-fishing and the destruction of their habitat. The results of the present study will be an important tool in formulating a plan of sustainable management of the stocks and natural habitat of the armoured catfishes.

Since the introduction in 1955 of the African Tilapia *Oreochromis mossambicus* by the Fisheries Department of Suriname (Lijding, 1958) the local public interest in aquaculture has grown exponentially. The first aquaculture trials with an indigenous species started in 1974 when the Ministry of Agriculture adopted a pilot project with the popular armoured catfish *Hoplosternum littorale* (locally known as soké kwikwi). This project was ultimately transferred to the Anton de Kom University of Suriname. Several local companies invested heavily in developing the culture of this popular food fish, among them Comfish N.V. and Surland N.V. (Lovatelli & Loria, 1993). Farmers cultivate the soké kwikwi in small, earthen family ponds. Both groups of entrepreneurs will profit from the data on the ecology of *H. littorale* resulting from the present study. Knowledge of the ecology of the two armoured catfishes that occur in the interior of the country, *H. thoracatum* and *C. callichthys*, may stimulate the culture of these species in an area which is in many ways neglected by the government. More important, such knowledge is essential in the protection of their specific habitats.

In view of the recent international interest in the high biodiversity of tropical rainforests (Earth summit at Rio de Janeiro; United Nations, 1993), the study of the ecology of rainforest species and of ecological interactions is urgently needed in order to allow us to manage these important forests in a sustainable way.

THE STUDY AREA

The study has been conducted in Suriname, northern South America. Suriname is situated between 2 and 6° N, and has consequently a genuine tropical climate (Af according to the classification of Köppen; Köppen, 1900). The mean daily temperature is about 27° C with an annual variation of only 2° C. Annual rainfall averages 2200 mm, and is distinctly seasonal. Two wet and two dry periods are distinguished. The short rainy season occurs from December to January and is followed by the short dry season from February to March. The long rainy season occurs from April through late July and is followed by the long dry season from August to November (Snow, 1976).

Suriname can be divided into three zones: in the north the flat coastal plain covered with extensive swamps and swamp forests (21,000 km²), to the south of it the savanna belt characterized by savannas and savanna forests (8,500 km²), and the hilly interior on the Precambrium Guiana Shield covered with tropical rainforest (126,000 km²). The coastal plain is divided into the young coastal plain with holocene sediments and, to the south of it, the old coastal plain with pleistocene sediments (Lindeman, 1953; Noordam, 1993).

The two study sites at Weg Naar Zee and Lelydorp are situated in the coastal plain,

approximately 2 and 23 km south of the Atlantic coast, respectively. The Weg Naar Zee site in the young coastal plain consists of a narrow, old sandy beach bordered by extensive herbaceous swamps dominated by *Typha angustifolia* (Chapter 5; Teunissen, 1993). The swamps are shallow not reaching water depths of 100 cm in the rainy season. The Lelydorp site is part of a narrow east-west running swamp/swamp forest located in the old coastal plain. The heart of the swamp consists of dense stands of *Eleocharis interstincta*, but locally swamp forest occurs with among others *Pterocarpus officinalis*, *Triplaris surinamensis* and *Virola surinamensis* (Chapter 5; Teunissen, 1993). At both study sites, open water with floating aquatics occurs at the outer edge of the swamp. More information on the swamps and swamp forests of Suriname is compiled by Ouboter (1993).

RESULTS

DISTRIBUTION IN SURINAME AND SOUTH AMERICA

Co-occurrence is the first requirement for competition. In Suriname, both *H. thoracatum* and *C. callichthys* occur all over the country (Chapter 2). They are abundant in swamps and swamp forests of the coastal plain, but also conspicuous members of the fish fauna of 'clear water' creeks (terminology of Sioli, 1950) in the rainforests of the interior (e.g. Ouboter & Mol, 1993). In 'black water' creeks of the savanna belt, situated between the coastal plain and the interior, *H. thoracatum* seems more abundant. *Hoplosternum littorale* is restricted in its distribution to coastal plain swamps. In salinity tolerance experiments with the three species 1-week-old larvae of *H. littorale* did not survive in electrolyte-poor water (e.g. rain water). The clear water of the rainforest creeks of the interior is usually compared to slightly contaminated distilled water (Sioli, 1950, 1984; Leentvaar, 1975), and its conductivity is not much higher than that of rain water. Larvae of both *H. thoracatum* and *C. callichthys* survived and developed further in rain water. Both species were collected in clear water creeks.

The pattern of distribution of *H. littorale* in Suriname may serve as a model for the distribution of this species on the South American continent. *Hoplosternum littorale* was not collected in clear water creeks draining the weathered soils of the Precambrium Guyana and Brazilian Shields. Again, only *H. thoracatum* and *C. callichthys* were found in these creeks. In waters with higher electrolyte concentrations, such as 'white water' streams loaded with sediments originating in the young Andes mountains, savanna pools in the dry Venezuelan Llanos and coastal swamps, all three species are usually present.

When two species are sympatric in an area, additional investigation is necessary to establish whether they actually occur together in the same habitat (i.e. syntopy). In most coastal plain swamps in Suriname at least two species occur together and it is not unusual to collect all three species at the same locality. Intensive sampling by chemofishing with rotenone during the Lake Brokopondo Biology Research project in 1964-1970 revealed that in rainforest creeks of the interior often two species, *C. callichthys* and *H. thoracatum*, are present. Consequently, interspecific competition among the three catfishes is possible and plausible to occur.

DIET OVERLAP

Analysis of the stomach contents of three different developmental stages of the three species (larvae, juveniles and adults) revealed no significant interspecific differences in diet composition (Chapter 3). Horn's index of overlap was not significantly different from 1 (meaning complete overlap). However, ontogenetic differences among the diets of larvae, juveniles and adults were significant for all three species. Adults showed minor qualitative differences in their diet between dry season and rainy season.

The larvae of *H. littorale*, *H. thoracatum* and *C. callichthys* fed almost exclusively on Rotifera and micro-crustacea (mainly Cladocera and Copepoda). Stomach contents of juveniles were more diverse and included micro-crustacea, insect larvae, aquatic insects and some detritus. Adults ingested large quantities of detritus which probably reflected the inability of large fish to separate effectively benthic invertebrates from substrate. Chironomid larvae were found in large numbers in the stomachs. Although Oligochaeta were not often detected in the stomachs due to their fast digestion (Kennedy, 1969), setae were typically present in large quantities, suggesting that these worms were also important in the diet. Several morphological features of the alimentary tract make it improbable that the callichthyids are able to assimilate detrital nonprotein amino acids (terminology of Bowen, 1980). A large part of the intestine has a respiratory function (Carter & Beadle, 1931; Huebner & Chee, 1978) and the anterior digestive portion is relatively short.

The diet of *H. littorale* was investigated in Trinidad (Singh, 1978) and in Venezuela (Winemiller, 1987). Information on the stomach contents of *C. callichthys* is available for a population in a small rainforest creek near Manaus (Knöppel, 1970). The data of these researchers support the results of the present study. The similarity in the diet of the three species and their bottom-dwelling habit provide the basis for grouping the three armoured catfishes into one ecological guild (defined as a group of species exploiting a common resource base in a similar fashion; Root, 1967). Competitive interactions are expected to be potentially strong among the members of a guild (Root, 1967; but see Simberloff & Dayan, 1991).

REPRODUCTIVE SEASONALITY AND NEST HABITAT DIFFERENTIATION

Male *H. littorale*, *H. thoracatum* and *C. callichthys* construct and guard floating foam nests in flooded swamps (Chapter 4). The conspicuous nests make it possible to study the temporal pattern of breeding, the spatial distribution of the nests and the nest-site microhabitat differentiation among the three species. Adult *H. littorale* remain reproductively active during the breeding season (Pascal *et al.*, 1994) and this probably also holds for *C. callichthys* and *H. thoracatum*. It follows that habitat use in the breeding season largely coincides with the use of nest habitat. In addition, Singh (1978) and Winemiller (1987) provided evidence that at least in *H. littorale* the rainy season is not only the spawning season, but also the main feeding period.

Daily surveys in two coastal plain swamps during a three year period revealed a similar, bimodal breeding season in the three species (Chapter 5). The construction of the nests was correlated with the annual distribution of rainfall. The (un)reliability of the rainfall in the first (short) rainy season following the main dry period of Augustus-November may

account for differences in the seasonal pattern of reproduction in Suriname and the (unimodal) breeding season of *H. littorale* in French Guiana (Hostache *et al.*, 1993).

Significant differences in nest macrohabitat selection were found among the three callichthyids (Chapter 5). Nests of *H. littorale* were built in herbaceous swamps (and in rice fields), while *H. thoracatum* and *C. callichthys* constructed their nests in swamp forest. The two forest nesting species differed in the microhabitat at the nest site. Nests of *C. callichthys* were observed in extremely shallow water and in holes of tree roots and earth. Nest densities in the selected macrohabitat were low for *H. littorale* and *C. callichthys*, but some clumping of nests of *H. thoracatum* was observed. Nest-site differentiation among the three catfishes is probably one of the main factors which prevents competitive exclusion of one of them.

Although the habit of constructing a floating bubble nest probably evolved as an adaptation to the oxygen depleted environment of tropical standing waters (Carter & Beadle, 1930, 1931; Chapter 4), some of the characteristics of the nests and nest sites of both *H. thoracatum* and *C. callichthys* may have evolved as a response to the unpredictability of the stream habitat with respect to fluctuations in water velocity and water level (Chapters 4, 5). Both species occur in rainforest creeks of the interior, where *H. littorale* is absent (Chapter 2). In the swamps changes in water level are slow and more predictable while strong water currents do not occur.

TIME OF ACTIVITY

The third important component of the niche, the time of activity, was not investigated in detail in the armoured catfishes. The diel cycle of food intake, locomotor activity and air breathing of *H. littorale* was studied by Boujard *et al.* (1990). They found *H. littorale* most active during the night. Lowe-McConnell (1991) observed *C. callichthys* foraging at night on the bottom of a small creek. Personal observations in aquariums and experience with angling also revealed that all three species were active at night and in the early morning and late afternoon during the twilight hours. For all three species the breeding period was the same as well (Chapter 5). This suggested that competition was probably not alleviated by segregation in time of activity.

The results of Chapters 3 and 5 support the 'compression hypothesis' of MacArthur & Wilson (1967) which implicates habitat segregation, and not differences in diet or time of activity, as the major means of coexistence among competing species on an ecological time-scale.

THE POTENTIAL IMPACT OF PREDATION

Most predation on the three callichthyids probably takes place in the period between hatching of the eggs and the development of the bony armour by the juveniles, 2-3 months after hatching. In order to estimate the potential predation pressure in this vulnerable period, eggs, 1-week-old larvae, and 3-, 5- and 7-week-old juveniles of *H. thoracatum* were exposed to 24 different predators (both vertebrates and invertebrates) known to occur in the swamps (Chapter 6). Predation rates (prey predator⁻¹ h⁻¹) on the five developmental stages of *H. thoracatum* were recorded in the laboratory under light, twilight and dark conditions.

Although the experiments were performed with *H. thoracatum* there is, at present, no good reason to expect important differences in predation rates among the three armoured catfishes. The density of the predator species in the swamps was estimated by sampling a 5x5 m² plot with the piscicide Rotenone (which also effects invertebrate predators). The combination of the laboratory predation rates and data on predator densities in the field allowed the determination of the potential predation pressure on the different developmental stages of armoured catfishes in the swamp.

The contribution of a particular predator species to the potential predation pressure on catfishes was determined to a large extent by the density of the predator in the swamp. Seemingly innocuous predators with low or moderate laboratory predation rates may be extremely important in the swamp due to their abundance. Small-sized fishes and aquatic invertebrates are probably major predators of early developmental stages of armoured catfish.

The predation pressure on eggs is potentially high, but the aggressive nest guarding behaviour of the male (Chapter 4) and concealment of the nests (Chapter 5) probably protect the eggs of the three species effectively from most aquatic predators. However, larvae of armoured catfishes are not guarded by the male and the potential impact of the 24 predators on larvae was large. Even if only 2.5% of the potential predation will be realized due to other prey available, the high mortality of early developmental stages of *H. thoracatum* (and *C. callichthys* and *H. littorale*) in the swamp can be easily explained as the effect of predation. Potential predation pressure and the number of predators that were able to prey on *H. thoracatum* juveniles sharply declined with increasing age (size) of the juvenile catfish.

The heavy armour of bony plates and the stout pectoral spines protect older juveniles and adult callichthyids from most potential predators. Predation pressure on adults is probably highest in the dry season when the swamps dry up and the water retreats in canals and small pools (Lowe-McConnell, 1964). In these restricted dry season water bodies the fish are packed in high densities together with potential predators. A survey of the literature and field observations suggests that otters, birds, caimans, water snakes and adult piscivores like *Hoplias malabaricus* and *H. macrophthalmus* may prey on adult callichthyids.

The high potential predation pressure on larvae of armoured catfish and the low density of juvenile catfish at the end of the rainy season (compared to the yearly production of larvae; Chapter 6) suggest that predation is important in structuring the community of armoured catfishes. In armoured catfishes, ontogenetic changes in defense mechanisms result in a situation in which both predation and competition exert control at different times in the life cycle (Werner, 1986; Menge & Sutherland, 1987). Predators may kill most of the larvae and juveniles, leaving only a few individuals to escape and reach adulthood. If the number of escapes exceeds the number of adult deaths, the populations eventually become sufficiently dense to compete. In this situation nest-habitat segregation may prevent competitive exclusion of one of the catfishes.

MORPHOLOGY, BODY COMPOSITION AND SPECIFIC GRAVITY

Although *C. callichthys*, *H. littorale* and *H. thoracatum* are quite similar in appearance, morphometric analysis revealed significant interspecific differences in their morphology (Chapter 7). Morphological differentiation was most pronounced between

shallow-bodied *C. callichthys* on the one hand and both *Hoplosternum* species on the other hand. Morphological differences between *H. littorale* and *H. thoracatum* were small. The three callichthyids showed only minor interspecific differences with respect to the chemical composition of their body (e.g. water, protein, fat and mineral content). All three species showed distinct seasonality in their water and fat content.

The heavy body armour and reduced swimbladder accounted for the unusually high specific gravity of the three callichthyids. The high density of these armoured catfishes helps to keep them in position on the bottom in running water. In the oxygen-depleted water of tropical swamps the three catfishes use their thin-walled intestinal tract as an accessory respiratory organ. In these standing waters the gas-filled intestine may also function as a hydrostatic organ in reducing the density of the armoured catfish and thereby the costs of surfacing.

IMPLICATIONS FOR ARMOURED CATFISH FISHERIES AND CULTURE

The three armoured catfishes are considered a delicacy with high commercial values in some countries in northern South America. The most popular of the three species, *H. littorale*, is exported to West Indian immigrant communities in Europe and North America. Well developed fisheries on armoured catfish are known from Brazil, Suriname, Trinidad and Venezuela (Chapter 8). In Suriname, landings of armoured catfish in the period 1970-1993 showed a significant decrease to about a quarter of the pre-1970 figures (Ouboter & Mol, 1994). Mol & Van der Lugt (in press) argue that the decline in the landings of armoured catfish is probably not related to the introduction of the exotic *Tilapia Oreochromis mossambicus* in 1955 (Lijding, 1958). Possible threats to the armoured catfish stocks are agricultural pesticides, the destruction of catfish habitats and overfishing (Chapter 8). I recommend the conservation of coastal plain swamps and swamp forests and some amendments to the Surinamese fish protection legislation (Rondeel, 1965) based on ecological research. More research is needed to determine the toxicity of pesticides to early developmental stages of armoured catfishes and the effects of habitat modifications.

Recent developments in the culture of armoured catfish are described by Luquet *et al.* (1989) (French Guiana) and Lovatelli & Loria (1993) (Guyana, Suriname and Trinidad). Important investigations into the culture of *H. littorale* were conducted by French scientists of the Institut National de la Recherche Agronomique (INRA) in French Guiana (e.g. Luquet *et al.*, 1989; Pascal *et al.*, 1994; Moreau *et al.*, 1992). Some promising possibilities are the culture of fingerlings for stocking fishing canals, family ponds and natural waterbodies, a polyculture with large Amazonian food fishes (e.g. *Colossoma* spp), and the culture of juvenile *H. thoracatum* for the ornamental fish trade (Chapter 8). Data on the growth of *H. littorale* at various stocking densities and feeding regimes are badly needed in order to evaluate the aquaculture potential of armoured catfishes.

CONCLUSIONS

- 1) The three armoured catfishes, *C. callichthys*, *H. littorale* and *H. thoracatum*, are important potential competitors (habitat, size, food preference, dentition, etc.)
- 2) Although larvae of the three species differ in tolerance of water with low electrolyte concentrations they occur syntopically in coastal swamps.
- 3) Stomach content analysis revealed very high diet overlap. Interspecific competition is not restricted by food preferences.
- 4) The three species are active at night and at twilight. All three catfishes showed a similar bimodal breeding season. Segregation by time of activity was not observed.
- 5) In the rainy season the armoured catfishes built characteristic floating bubble nests in flooded swamps. Differences in the nest habitat of the three species may alleviate interspecific competition when food is most abundant, and, in the long run, prevent competitive exclusion.
- 6) The collective predation pressure from multiple predators in the swamp on eggs, larvae and juveniles of armoured catfishes is potentially very high. The high mortality of early developmental stages of the armoured catfishes in the swamp could easily be explained as the effect of predation. When the swamps dry up at the end of the rainy season, stranding of juvenile catfishes may further contribute to the high mortality of the three species. Population densities of juvenile armoured catfishes at the end of the reproductive season are low.
- 7) Ontogenetic changes in defense mechanisms of armoured catfishes result in a situation in which both predation and competition exert control at different times in the life cycle. Predators probably kill most of the larvae and juveniles, leaving only a few individuals to escape and reach adulthood. If the number of escapes would exceed the number of adult deaths, the populations may eventually become sufficiently dense to compete. In this situation nest-habitat segregation may prevent competitive exclusion of one of the catfishes.

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Chapter 2

Effects of salinity on distribution, growth and survival of three neotropical armoured catfishes (Siluriformes - Callichthyidae)

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Abstract

Three species of closely related armoured catfishes, *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys*, are widely distributed throughout (sub)tropical South America, but a detailed inspection of collection localities in both Suriname and the South American continent reveals a clear pattern. *Hoplosternum littorale* is not found in rainforest creeks and clear-water rivers draining the Precambrium Guiana and Brazilian Shields. Here, waters are extremely poor in dissolved minerals. In salinity tolerance experiments, 1-week-old larvae of *H. littorale* were found to be incapable of surviving in rainwater that is also very poor in electrolytes. Probably for the same reason, *H. littorale* is not collected in black-water rivers like the Rio Negro. Within the Amazon river-system *H. littorale* is found in sediment-laden white-water rivers originating in the Andes. Larvae of *H. thoracatum* and *C. callichthys* are able to survive and develop further in rainwater and consequently have a less restricted distribution than *H. littorale*. Both species are found in clear water and black water. All three species tolerate salinities up to 2000 mg Cl l⁻¹, and show a marked decrease in growth at low salinities.

Key words: *Hoplosternum littorale*; *Hoplosternum thoracatum*; *Callichthys callichthys*; distribution; salinity tolerance; Amazon; Suriname.

INTRODUCTION

The number of species within a community resulting from diversification in a variety of ecological niches (alpha diversity) is typically very high in many tropical freshwater fish communities (Lowe-McConnell, 1987). In neotropical waterbodies up to 70 species are often found together (Eigenmann, 1912; Marlier, 1967; Ouboter & Mol, 1993). When species living together are closely related and morphologically similar, it is often not clear how they share resources, and are able to coexist.

In Suriname three armoured catfishes of the family Callichthyidae (subfamily Callichthyinae; Hoedeman, 1952), *Hoplosternum littorale* (Hancock, 1828), *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840), and *Callichthys callichthys* L., 1758 are very

common in swamps of the coastal plain. The three species are adapted to stagnant, oxygen-depleted waters of tropical swamps. All three species build floating bubble-nests (Mol, 1993).

Hoplosternum littorale, *H. thoracatum*, and *C. callichthys* are widely distributed throughout (sub)tropical South America (Müller & Weimer, 1976; Burgess, 1989). On a large scale they are sympatric. However, it is not clear to what extent the three species really occur together (i.e. are syntopic). This paper describes their general distribution in some detail, both in Suriname and South America. It also explores how salinity affects growth and survival of the three species, which might explain some aspects of their biogeography (as suggested by Müller & Weimer, 1976). As the three callichthyids are specially adapted to tropical standing waters, poor in dissolved oxygen and often very acidic, the abiotic factors oxygen, pH and temperature are probably of minor importance with respect to the distribution of these fish within their (sub)tropical range.

MATERIALS AND METHODS

STUDY AREA

Suriname is situated in the neotropics between 2 and 6° N, and has consequently a genuine tropical climate (Af according to the classification of Köppen). The mean daily temperature is about 27° C with an annual variation of only 2° C. The mean daily temperature range is 9° C in Paramaribo. Annual rainfall averages 2200 mm, and is distinctly seasonal.

The country can be divided into three zones: in the north the flat coastal plain (21,000 km²), to the south of it the savanna belt (8500 km²), and the hilly interior (126,000 km²) on the Precambrium Guiana Shield (Fig. 2.1). The coastal plain is divided into the young coastal plain with holocene sediments and, to the south of it, the old coastal plain with pleistocene sediments.

The young coastal plain is covered with swamps, swamp forests and mangrove forests. The tidal influence in the dry season, and dilution with electrolyte-poor rainwater in the rainy season are responsible for large fluctuations in salinity in standing waters (Table 2.1). In the old coastal plain post-depositional weathering of soils and diminishing tidal influence create a predominantly freshwater environment in the swamps and swamp forests (Table 2.1).

The savanna belt is characterized by savannas and savanna forests on often very poor, podzolic soils. The creeks draining this area are stained black by dissolved humic substances. They may be classified as black waters (terminology of Sioli, 1950).

The interior covers three-quarters of the country and is almost completely covered with tropical rainforest. Stagnant waters are rare. Creeks and rivers draining the Guiana Shield principally carry clear water (terminology of Sioli, 1950), poor in dissolved minerals, and saturated with dissolved oxygen (Table 2.1).

DISTRIBUTION

Data on the large scale distribution of *H. littorale*, *H. thoracatum*, and *C. callichthys* were obtained from fish collections in Europe, the U.S.A. and South America: British

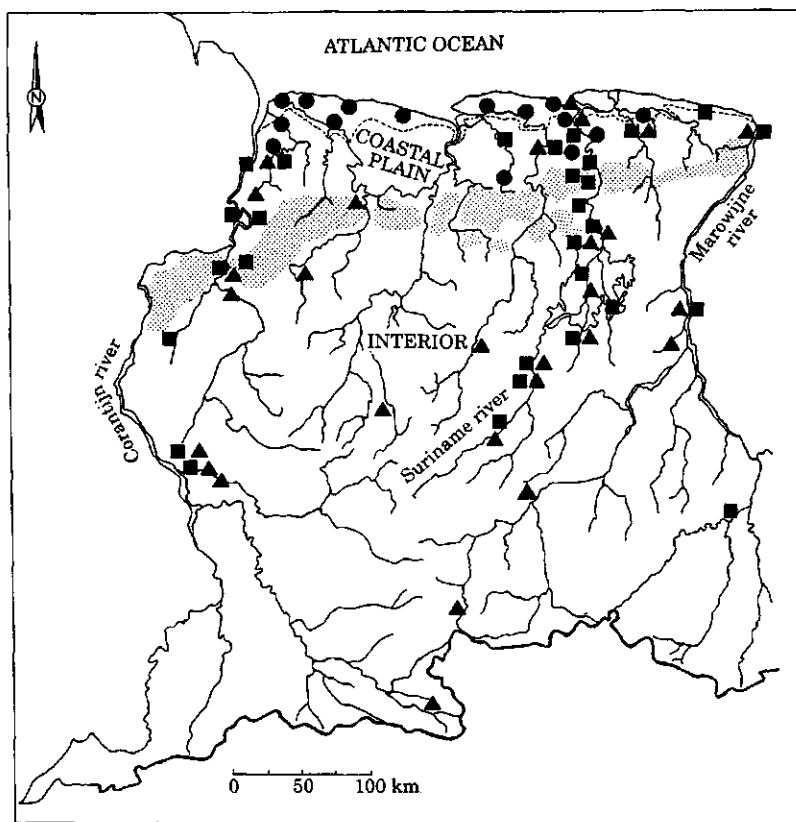


Fig. 2.1. Distribution of *Hoplosternum littorale* (●), *Hoplosternum thoracatum* (■) and *Callichthys callichthys* (▲) in Suriname. Collection localities along the Suriname river refer to the situation before the man-made Brokopondo lake was constructed. The 1000 mg Cl l⁻¹ limit for fresh water is drawn after Pons (unpublished). ▨▨▨, savanna belt; ---, 1000 mg Cl l⁻¹.

Museum of Natural History (BMNH), London; Musée National d'Histoire Naturelle (MNHN), Paris; Institute of Zoological Taxonomy (ZMA), Amsterdam; National Museum of Natural History (RMNH), Leiden; Naturhistorisches Museum Wien (NMW), Vienna; American Museum of Natural History (AMNH), New York; United States National Museum, Smithsonian Institute (USNM), Washington; Museum of Zoology, University of Michigan (UMMZ), Ann Arbor; Museum of Comparative Zoology (MCZ), Cambridge; Museum of the University of Stanford (US), Palo Alto; Academy of Natural Sciences of Philadelphia (ANSP), Philadelphia; California Academy of Sciences (CAS), San Francisco; National Museum of Natural History (NMNH), Washington; Museu de Zoologia, University of Sao Paulo (MZUSP), Sao Paulo; Instituto Nacional de Pesquisas da Amazonia (INPA), Manaus; Museu de Ciências, University of Rio Grande do Sul (MCP), Porto Alegre; and the National Zoological Collection, University of Suriname (NZCS), Paramaribo.

Data on the distribution in Suriname of *H. littorale*, *H. thoracatum* and *C. callichthys* were obtained from the fish collections at Amsterdam (ZMA), Leiden (RMNH) and Paramaribo (NZCS), and specimens collected by the author in 1987-1993.

SALINITY TOLERANCE

Naturally spawned eggs of *H. littorale*, *H. thoracatum*, and *C. callichthys* were collected from floating bubble-nests in an *Eleocharis* dominated freshwater swamp at Lelydorp, 20 km south of Paramaribo (Suriname). The nests of the three species were built within 500 m of each other in the same swamp. The swamp-water was acidic (pH 4.20-5.75) and had a low salinity (21.5 mg Cl l⁻¹), and low conductivity (65-165 μ S cm⁻¹). Eggs collected three days after oviposition hatch immediately after contact with swamp-water (Mol, 1993). The newborn larvae were transported in oxygen inflated polyethylene bags to the laboratory.

Water analyses of natural waterbodies in Suriname, tap water and rainwater (Table 2.1), and water in experimental tanks (Table 2.2) followed standard methods (APHA-AWWA, 1976). Water temperature was not controlled during the experiments and varied between 24.1° C and 27.8° C. To inhibit the accumulation of metabolites and growth of micro-organisms two-thirds of the water in each tank was changed twice daily before feeding. Salinity (expressed as mg Cl l⁻¹), conductivity, pH, dissolved oxygen, and temperature were measured in the tanks at weekly intervals.

Salinity tolerances of 7-day-old larvae were tested in rectangular tanks with a capacity of 12-liter under continuous light conditions. Since the eggs of the three callichthyids are deposited in a floating bubble-nest above the water surface (Mol, 1993), the newborn larvae are the first and probably most sensitive developmental stage to come into contact with the aquatic environment. Larvae were fed laboratory reared *Artemia* nauplii twice daily at 06.00 and 18.00 h. For each test series, groups of 50 larvae were placed in the experimental tanks containing tap water (Table 2.2). After a 1-week adjustment period one-third of the water was siphoned off from each tank and replaced with a NaCl solution of sufficient concentration to raise the tank salinity to the desired level. The test solutions of 1 mg Cl l⁻¹ (rainwater) and 275 mg Cl l⁻¹ (tap water) were not enriched with NaCl.

The fish were observed for 7 days. Progressive mortality on a probit scale was plotted against the logarithm of time to death as described by Otto (1970). The median survival time, i.e. the time required for 50% of the test fish to die, was obtained from the line fitted by the eye to the probit plot. The fish that survived the tolerance experiments were followed for an additional 3-week period in order to record growth at different salinities. During this period no further mortality occurred.

A natural day length was maintained for the growth studies. Weights and lengths were recorded at weekly intervals before feeding for 10 freshly killed specimens of each species. Total length and standard length (± 0.5 mm) were measured. The fish were then blotted on damp filter paper and weighed on an analytical balance (± 0.0001 g).

Table 2.1. Selected physico-chemical data (mean \pm S.E.) of rain water, tap water and natural waterbodies in Suriname. Number of observations in parentheses.

	Young coastal plain		Old coastal plain		Savanna belt (black water)	Interior (clear water)	Rain water	Tap water*
	Rainy season	Dry season						
pH	5.9 ± 0.17 (25)	7.2 ± 0.23 (17)	5.1 ± 0.21 (10)	4.8 ± 0.26 (17)	5.8 ± 0.07 (64)	6.3 ± 0.23 (11)	6.7 ± 0.01 (59)	
EC (μ S cm ⁻¹)	673 ± 125.1 (25)	1755 ± 635.1 (17)	76.5 ± 13.38 (10)	42.6 ± 3.18 (16)	30.5 ± 2.34 (62)	19.8 ± 3.07 (11)	1193 ± 6.0 (1)	
Cl (mg l ⁻¹)	163 ± 39.7 (25)	1163 ± 592.4 (17)	15.4 ± 1.45 (10)	10.0 ± 1.42 (12)	6.6 ± 1.24 (10)	0.7 ± 0.09 (11)	265 ± 4.5 (59)	
hardness (mg l ⁻¹ CaCO ₃)	125 ± 17.9 (24)	134 ± 26.0 (13)	11.0 ± 2.91 (6)	6.8 ± 1.54 (5)	10.7 ± 2.19 (6)	4.4 ± 0.31 (11)	266 (1)	
Ca (mg l ⁻¹)	2.7 ± 0.37 (25)	21.5 ± 5.74 (17)	0.6 ± 0.20 (3)	1.3 ± 0.47 (3)	3.6 ± 0.95 (2)	1.2 ± 0.05 (11)	27.6 (1)	
Mg (mg l ⁻¹)	16.4 ± 2.62 (25)	78.1 ± 36.9 (17)	0.8 ± 0.09 (3)	1.0 ± 0.10 (3)	- (2)	0.2 ± 0.02 (11)	48.1 (1)	
Fe (mg l ⁻¹)	- (25)	0.3 ± 0.10 (16)	0.9 ± 0.35 (5)	0.2 ± 0.06 (7)	0.4 ± 0.11 (6)	0.3 ± 0.22 (11)	0.1 ± 0.01 (59)	
O ₂ (mg l ⁻¹)	2.0 ± 0.59 (23)	1.4 ± 0.41 (17)	1.9 ± 0.69 (7)	2.6 ± 0.58 (6)	5.1 ± 0.44 (13)	- (1)	2.8 (1)	
BOD (mg l ⁻¹)	3.3 ± 0.24 (25)	4.3 ± 0.51 (13)	3.7 ± 0.75 (7)	2.9 ± 0.41 (4)	2.9 ± 0.84 (6)	- (1)	- (1)	
PO ₄ (mg l ⁻¹)	0.2 ± 0.02 (25)	0.7 ± 0.24 (16)	0.1 ± 0.03 (7)	0.1 ± 0.01 (7)	0.1 ± 0.02 (8)	0.1 ± 0.04 (11)	0.0 (1)	
NO ₃ (mg l ⁻¹)	0.1 ± 0.04 (25)	0.3 ± 0.22 (14)	0.1 ± 0.04 (7)	0.4 ± 0.23 (7)	0.3 ± 0.07 (8)	0.6 ± 0.35 (10)	0.0 (1)	
HCO ₃ (mg l ⁻¹)	74.1 ± 10.18 (25)	140 ± 22.4 (17)	7.3 ± 1.0 (6)	7.3 ± 1.52 (6)	15.7 ± 1.90 (6)	4.4 ± 1.07 (11)	80.7 ± 1.87 (59)	
SO ₄ (mg l ⁻¹)	73.3 ± 10.35 (25)	137 ± 79.8 (17)	24.6 ± 0.65 (3)	0.9 ± 0.03 (2)	0.0 ± 0.00 (2)	1.5 ± 0.22 (11)	122 (1)	

* Harris Inc. & IMACO (unpublished). BOD, Biological Oxygen Demand; EC, electric conductivity

Table 2.2. Survival of *Hoplosternum littorale*, *H. thoracatum* and *Callichthys callichthys* for groups of 50 1-week-old larvae exposed to various salinities.

Salinity (mg l ⁻¹ Cl)	Test conditions (mean ± S.E.)				Total mortality (%)	Median survival time (min)
	Salinity (mg l ⁻¹ Cl)	Electric conductivity (μS cm ⁻¹)	pH	Dissolved oxygen * (mg l ⁻¹)		
<i>Hoplosternum littorale</i> (standard length 7.8 mm)						
1	4.7	8	6.02	-	100	2,000
275	273±2.3	1,203±10.4	6.43±0.015	2.3±0.67	0	-
500	522±6.0	1,978±9.0	6.49±0.031	2.0±0.58	0	-
1,000	1,024±9.1	3,458±29.3	6.55±0.047	2.2±0.43	0	-
2,000	1,973±22.3	6,332±65.9	6.59±0.058	2.3±0.34	2	-
4,000	3,939±39.0	11,795±107.4	6.62±0.057	2.2±0.34	4	-
8,000	7,739	22,200±100	6.77±0.020	-	100	150
16,000	15,499	42,500±1500	6.74±0.045	-	100	30
<i>Hoplosternum thoracatum</i> (standard length 8.4 mm)						
1	7.1	37	6.09±0.170	2.4±0.93	0	-
275	277±0.6	1,193±2.5	6.47±0.068	2.3±1.13	0	-
500	522±4.7	1,962±4.7	6.53±0.087	2.5±1.56	0	-
1,000	1,026±7.4	3,440±5.8	6.58±0.062	1.9±1.20	4	-
2,000	1,976±29.9	6,317±17.6	6.61±0.062	2.3±1.18	0	-
4,000	3,910±23.9	11,700±75.5	6.62±0.070	2.7±1.01	46	2,600
8,000	7,988	22,400	6.74	5.0	100	160
16,000	15,414	40,600	6.70	4.6	100	15
<i>Callichthys callichthys</i> (standard length 7.2 mm)						
1	5.1	15	6.10±0.153	3.2±0.80	0	-
275	270±0.0	1,196±5.2	6.42±0.038	2.4±0.30	8	-
500	523±12.0	1,992±19.2	6.53±0.065	2.4±0.50	14	-
1,000	1,030±7.5	3,510±20.0	6.54±0.049	2.1±0.65	0	-
2,000	1,970±35.5	6,313±39.3	6.54±0.052	1.9±0.55	0	-
4,000	3,918±1.5	11,607±276.6	6.59±0.072	3.0±0.05	24	-
8,000	7,618	21,500±500	6.72±0.045	-	100	200
16,000	15,052	40,500±100	6.66±0.020	-	100	25

* water temperature 24.1-27.8° C

RESULTS

DISTRIBUTION IN SURINAME

The distribution between the coastal plain, the savanna belt and the interior was significantly different from random for all three species (X^2 ; $p < 0.0001$) (Table 2.3, Fig. 2.1). *Hoplosternum littorale* occurs in the coastal plain, and is completely absent from the interior and the savanna belt. Within the coastal plain area it is especially abundant in the northern part, the young coastal plain. Most localities are located north of the 1000 mg Cl l⁻¹ limit for fresh water (Fig. 2.1). Floating bubble-nests were observed in brackish water bodies (e.g. Bigi Pan; salinity 1975 mg Cl l⁻¹). Local fishermen concentrate their efforts to catch this popular food fish in the swamps of the young coastal plain.

Hoplosternum thoracatum and *C. callichthys* occur all over the country, but *C. callichthys* seems somewhat less abundant than *H. thoracatum* in the black-water creeks draining the savanna belt. Ninety-five percent of the 288 specimens of *C. callichthys* from the savanna belt were collected by Vari (unpublished) at one locality on a single day. In the coastal plain *H. thoracatum* and *C. callichthys* sometimes live together with *H. littorale* in

Table 2.3. Number and percentage of specimens of *Hoplosternum littorale*, *H. thoracatum* and *Callichthys callichthys* collected in the coastal plain, the savanna belt and the interior of Suriname.

	<i>H. littorale</i>		<i>H. thoracatum</i>		<i>C. callichthys</i>	
	n	%	n	%	n	%
Coastal plain	119	99	197	24	130	22
Savanna belt	1	1	151	18	288	49
Interior	0	0	476	58	164	28
Total	120	100	824	100	582	99

the same swamp (e.g. the swamp at Lelydorp). However, *H. thoracatum* and *C. callichthys* built their floating bubble-nest with dicotyledonous leaves (Mol, 1993), and are probably restricted in their distribution to swamp forests (Mol, in preparation). *Hoplosternum littorale* is able to construct its nest of filamentous materials (e.g. grass) and also inhabits grass and *Typha* swamps (Mol, 1993). In the interior *H. thoracatum* and *C. callichthys* were collected in clear-water creeks sampled by chemofishing (Mees, unpublished; Nijssen, unpublished; Richter & Nijssen, 1980; Vari, unpublished). From the unpublished data of Mees and Vari it can be concluded that the two species occur syntopically in many of the creeks. Within the Amazon river system *H. thoracatum* and *C. callichthys* also seem to live in the same creeks (Rapp Py-Daniel, pers. comm.).

DISTRIBUTION IN SOUTH AMERICA

Hoplosternum littorale is collected in the coastal areas of the Guianas, Venezuela and on Trinidad (Fig. 2.2(a)). In Venezuela it is found in the savanna-like Llanos. *Hoplosternum littorale* also occurs in the white-water rivers draining the Andes, among them the Amazon and its upper reaches, and the swamps of Bolivia and Paraguay. Its southern limit is in the Brazilian state of Rio Grande do Sul and at Buenos Aires in Argentina. *Hoplosternum littorale* is not found in rainforest creeks and clear-water rivers draining the ancient Guiana and Brazilian Shields, respectively north and south of the Amazon (Fig. 2.2(a)).

Hoplosternum thoracatum is distributed over tropical South America (Fig. 2.2(b)). It is present in most of the Guianas and Venezuela, in the Venezuelan Llanos, and in Bolivia and northern Paraguay. Its occurrence on Trinidad needs confirmation (Boeseman, 1960). *Hoplosternum thoracatum* is probably the only callichthyid present west of the Andes (Müller & Weimer, 1976); it is found in rainforest creeks in Panama. It also occurs in white-water rivers draining the Andes, clear-water rivers draining the Guiana and Brazilian Shields, in black-water rivers in the Guianas (Ouboter & Mol, 1993), and the Rio Negro (Goulding et al., 1988). *Hoplosternum thoracatum* is absent from the subtropical parts of the continent (e.g. Rio Grande do Sul).

Callichthys callichthys is widely distributed over South America (Fig. 2.2(c)). The general pattern of distribution resembles that of *H. thoracatum* with a range somewhat extended to the south. *Callichthys callichthys* is abundantly present along the coast of Brazil.

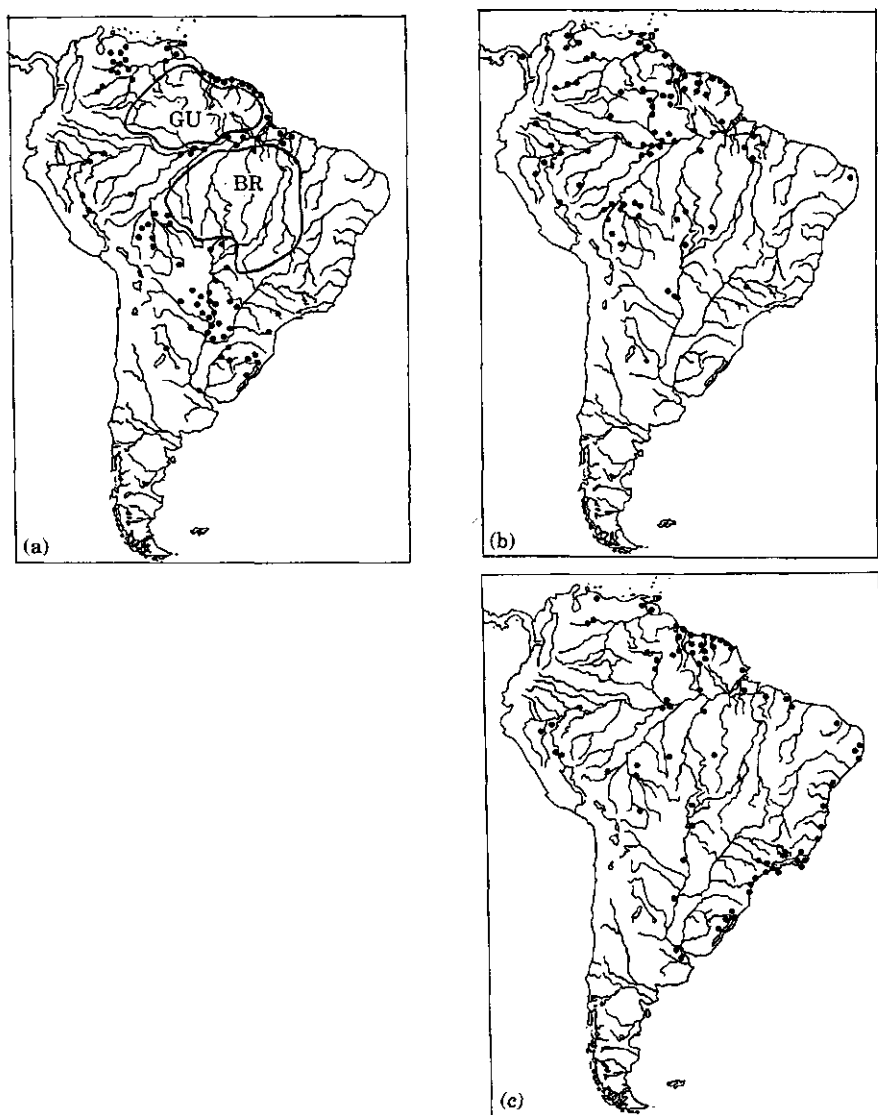


Fig. 2.2. Distribution of *Hoplosternum littorale* (a), *Hoplosternum thoracatum* (b) and *Callichthys callichthys* (c) in South America. *Hoplosternum littorale* is not collected in rainforest creeks and rivers draining the Precambrium Guiana Shield (Gu), and Brazilian Shield (Br).

SALINITY TOLERANCE

Distinct adaptive capacities of 1-week-old larvae of *H. littorale*, *H. thoracatum* and *C. callichthys* to salinity were observed. All three species were incapable of surviving salinities of 8000 and 16,000 mg Cl l⁻¹ (Table 2.2). The upper incipient lethal salinity, the

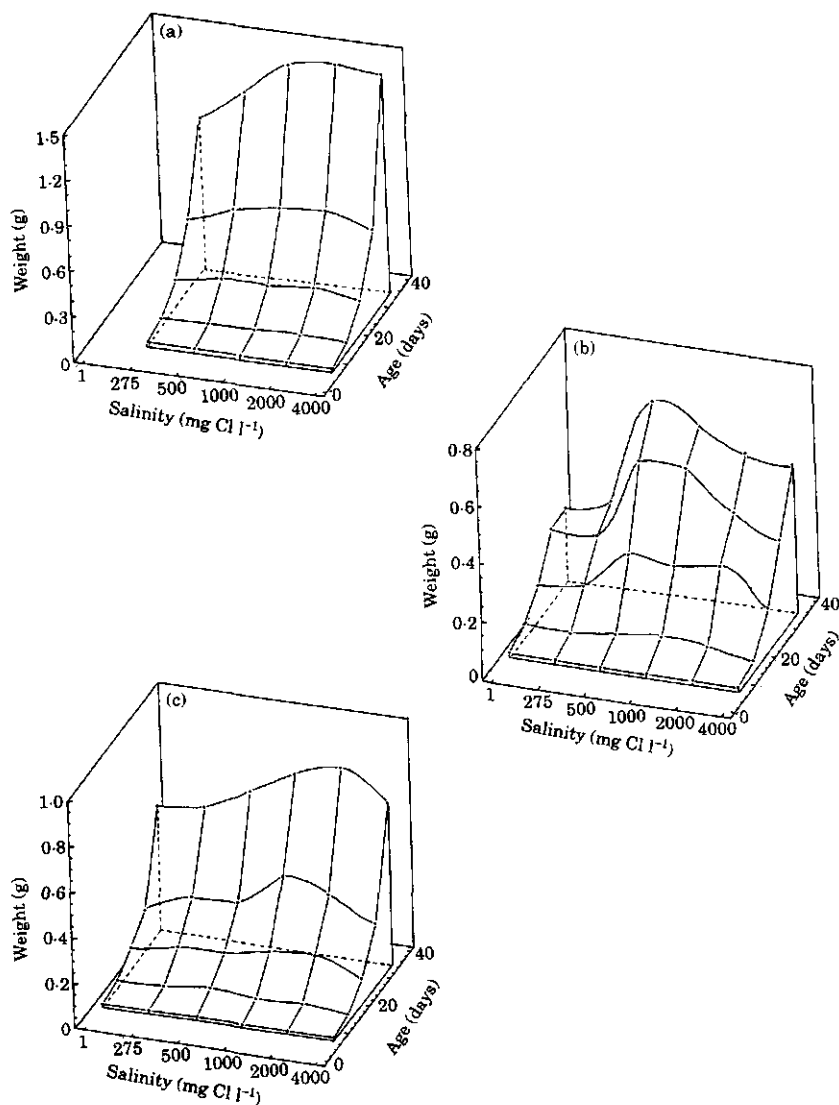


Fig. 2.3. Mean weights for independent groups of 10 larvae/juveniles of *Hoplosternum littorale* (a), *Hoplosternum thoracatum* (b) and *Callichthys callichthys* (c) maintained at various salinities. The curves are fitted by eye.

concentration at which 50% of the test population would be expected to survive the effects of salinity for an indefinite period, is for *H. littorale* between 4000 and 8000 mg Cl l⁻¹. Survival of *H. thoracatum* and *C. callichthys* at 4000 mg Cl l⁻¹ was, respectively, 48 and 24%. The upper incipient lethal salinity of both *C. callichthys* and *H. thoracatum* is between

2000 and 4000 mg Cl l⁻¹. Taking into account the 100% mortality of larvae of *H. littorale* exposed to rainwater (1 mg Cl l⁻¹; Table 2.2), it is of great interest that this species was not collected in creeks and rivers draining the interior of Suriname and the Amazonian Guiana and Brazilian Shields (Figs. 2.1, 2.2(a)). The water of these streams was described by Sioli (1975) as 'slightly contaminated distilled water', extremely poor in dissolved ions and with low salinity (also see Table 2.1). All 50 larvae of both *H. thoracatum* and *C. callichthys* survived in rainwater (Table 2.2).

Because fresh weights of the larvae of the three species at the start of the experiment were approximately equal (age 7 days; Appendix 2.1) and the growth curves did not fit a simple linear regression of the logarithm of fresh weight on age, growth was analyzed with a two-way ANOVA of the fresh weight of the fish at the end of the experiment (age 35 days). The ANOVA revealed differences in growth between the three species ($p < 0.0001$), and between the salinities tested ($p < 0.0001$). A small interaction between the two main effects was present ($p = 0.0205$). Growth of *H. littorale* was inhibited at salinities below 1000 mg Cl l⁻¹ (Fig. 2.3(a)). A distinct ridge occurred in the response distribution of *H. thoracatum*: growth was optimal at 500 mg Cl l⁻¹ (Fig. 2.3(b)). *Callichthys callichthys* shows maximization of growth at salinities of 1000-2000 mg Cl l⁻¹ (Fig. 2.3(c)). All three species show a decrease in instantaneous growth rate (Ricker, 1979) at the lower salinities (Fig. 2.4).

DISCUSSION

In discussing the South American fish fauna, Gery (1969) recognized eight faunistic regions. *Hoplosternum littorale*, *H. thoracatum*, and *C. callichthys* were collected in the Orinoco-Venezuelan region, the Paranean region, the Amazonian-Guianan region, and the East-Brazilian region (Fig. 2.2). Lüling (1971) collected *C. callichthys* in Peruvian headwater streams (Andean region). *Hoplosternum thoracatum* occurs in the isolated Magdalena river-basin (Magdalenean region), where it is sometimes referred to as *H. magdalenae* (Burgess, 1989), and west of the Andes in Panama (Trans-Andean region).

Müller & Weimer (1976) suggested that tolerance of high salinities might explain the presence of *H. thoracatum* west of the Andes mountains. Most of the primary freshwater fishes of South America were probably not able to cross the Panamanian-Columbian interocean barrier that existed until the late Pliocene (Myers, 1949, 1966). Larvae of *H. thoracatum* survived and grew up in brackish water with salinities up to 2000 mg Cl l⁻¹ (Table 2.2; Fig. 2.3). However, *H. littorale* and *C. callichthys* also were found to be tolerant of salinities up to 2000 mg Cl l⁻¹, and it seems therefore that salinity tolerance alone cannot explain the distribution of *H. thoracatum* in Panama.

When the distribution of *H. littorale*, *H. thoracatum*, and *C. callichthys* is studied in detail a clear pattern is revealed. *Hoplosternum littorale* is in Suriname limited in its distribution to waters rich in dissolved minerals, characteristic of the coastal plain (Fig. 2.1; Table 2.1). Growth of *H. littorale* is optimal at salinities between 1000 and 4000 mg Cl l⁻¹ (Fig. 2.3) and most of the collection localities in Suriname are north of the 1000 mg Cl l⁻¹ limit (Fig. 2.1). *Hoplosternum littorale* is not found in the rainforest creeks of the interior and black-water creeks of the savanna belt. These waters are extremely poor in dissolved minerals (Table 2.1), and salinity tolerance experiments showed larvae of *H. littorale* incapable of surviving in electrolyte-poor rainwater (Table 2.2).

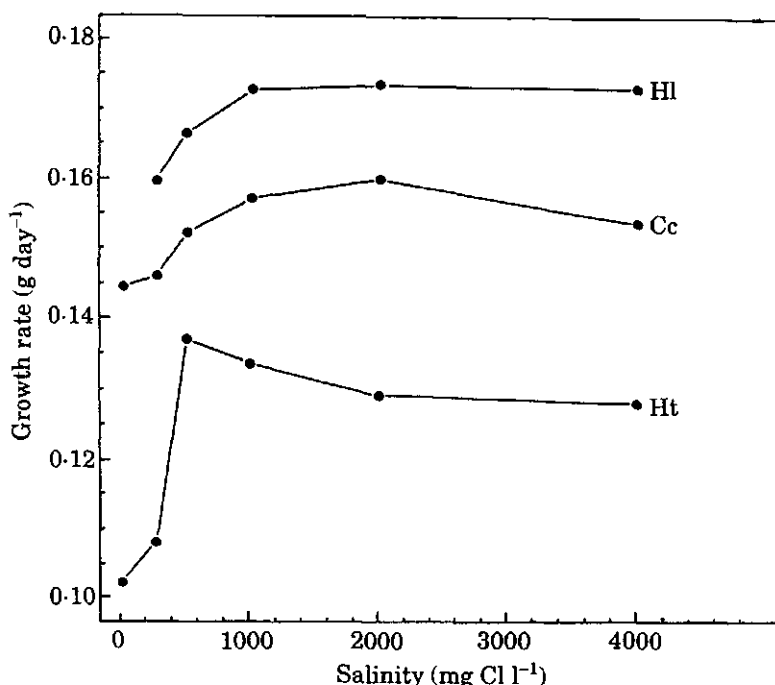


Fig. 2.4. Mean instantaneous growth rates in weight for groups of 10 juveniles of *Hoplosternum littorale* (Hl), *Hoplosternum thoracatum* (Ht) and *Callichthys callichthys* (Cc) at various salinities.

In Guyana and French Guiana *H. littorale* is also restricted to the coastal region (Eigenmann, 1912; Puyo, 1949). In Venezuela *H. littorale* occurs in large numbers in the Llanos, some distance from the coast (Mago, 1970; Machado-Allison & Zaret, 1984). Here, annual rainfall is distinctly lower than in Guyana, Suriname and French Guiana (Snow, 1976). Evaporation-crystallization processes and rock-weathering in the geologically young Andes mountains may account for relative high amounts of dissolved minerals in inland waters (Gibbs, 1967, 1970). Evaporation-crystallization processes probably also explain the high conductivity of swamp water in the Paraguayan Chaco where *H. littorale* is very common (Carter & Beadle, 1930, 1931). Within the Amazon river-system *H. littorale* is restricted to white-water rivers (also noticed by Porto & Feldberg, 1992). Erosion processes in the Andes account for the relative large amounts of dissolved minerals in white-water rivers (Sioli, 1950; Gibbs, 1967). Headwater rivers draining the Andes, e.g. the Ucayali, have conductivities of approximately $150 \mu\text{S cm}^{-1}$ (Schmidt, 1972), comparable with a salinity of 30 mg Cl l^{-1} .

Hoplosternum thoracatum and *C. callichthys* are less restricted in their distribution than *H. littorale*. In Suriname they occur over most of the country (Fig. 2.1). Although

optimal growth of *H. thoracatum* and *C. callichthys* is realized at, respectively, 500 and 2000 mg Cl l⁻¹ (Fig. 2.3), larvae of both species survive and grow up in rainwater (Table 2.2; Fig. 2.3). Within the Amazon river-system both species occur in the three major water types distinguished by Sioli (1950, 1975): white water, clear water, and black water.

The restricted distribution and 100% mortality of *H. littorale* in extremely electrolyte-poor water mark this species within the Amazon river-system as a good indicator of white waters. Gery (1984) pointed out that many Amazonian fishes, once believed to be indicators of a certain type of water, merely proved to be endemic to some restricted localities and, after introduction, easily acclimated to other types of water. With *H. littorale*, however, the restriction to white waters is within a wide neotropical distribution. Also experimental evidence from salt tolerance tests, illustrating its incapability of surviving in electrolyte-poor rainwater, must be taken into account.

Geisler & Schneider (1976) showed that differences in mineral composition of the vertebral column of two species of discus fish (*Symphysodon*) reflected the chemistry of the water from which they were sampled (white water and clear water). Considering the structure of the bony armour of the Callichthyidae (Bhatti, 1938), the question was raised whether a characteristic chemical composition of the armour of *H. littorale* restricted this species to waters rich in dissolved minerals. I could not detect a significant difference in the ash content of the body armour and skeleton of the three species sampled in the coastal plain (ANOVA, $p=0.0453$, $n=47$; Mol, in preparation). On the other hand the short time to death of the 50 larvae of *H. littorale* in rainwater points to a physiological mechanism, possibly in osmoregulatory capacity, preventing *H. littorale* from surviving in electrolyte-poor water.

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APPENDIX 2.1

Length and weight of *H. littorale*, *H. thoracatum* and *C. callichthys* at various salinities during a 4-week period. Mean \pm S.E. (n=10).

Salinity (mg l ⁻¹ Cl)	Age (days)	Total length (mm)	Standard length (mm)	Weight (mg)
<i>Hoplosternum littorale</i>				
275	7	10.0 \pm 0.16	7.8 \pm 0.11	11 \pm 0.5
	14	15.7 \pm 0.26	11.6 \pm 0.23	45 \pm 2.4
	21	25.3 \pm 0.50	18.5 \pm 0.39	163 \pm 9.8
	28	35.0 \pm 0.48	25.7 \pm 0.43	444 \pm 23.8
	35	43.2 \pm 0.74	31.9 \pm 0.56	986 \pm 53.2
500	14	16.5 \pm 0.22	12.2 \pm 0.20	52 \pm 2.1
	21	27.6 \pm 0.46	20.0 \pm 0.42	214 \pm 10.4
	28	37.3 \pm 0.82	27.3 \pm 0.60	555 \pm 47.0
	35	46.2 \pm 0.68	34.2 \pm 0.50	1190 \pm 51.6
	14	17.0 \pm 0.27	12.5 \pm 0.19	58 \pm 2.6
1000	21	27.9 \pm 0.24	20.3 \pm 0.19	209 \pm 5.6
	28	38.0 \pm 0.71	27.6 \pm 0.52	603 \pm 37.9
	35	47.7 \pm 0.55	35.1 \pm 0.35	1418 \pm 51.7
	14	17.4 \pm 0.19	12.8 \pm 0.17	60 \pm 2.0
	21	28.8 \pm 0.32	21.1 \pm 0.19	242 \pm 7.6
2000	28	38.1 \pm 0.55	27.8 \pm 0.40	623 \pm 29.1
	35	48.9 \pm 0.59	36.3 \pm 0.46	1453 \pm 62.2
	14	16.0 \pm 0.31	11.8 \pm 0.21	51 \pm 2.6
	21	26.0 \pm 0.89	19.2 \pm 0.52	202 \pm 11.7
	28	35.7 \pm 0.68	26.1 \pm 0.46	543 \pm 30.4
4000	35	46.6 \pm 0.70	34.8 \pm 0.58	1431 \pm 76.8

APPENDIX 2.1 Continued

Salinity (mg l ⁻¹ Cl)	Age (days)	Total length (mm)	Standard length (mm)	Weight (mg)
<i>Hoplosternum thoracatum</i>				
1	7	10.5 ± 0.20	8.4 ± 0.14	14 ± 0.6
	14	15.5 ± 0.38	11.6 ± 0.28	46 ± 3.2
	21	18.9 ± 0.65	14.5 ± 0.49	115 ± 12.5
	28	24.6 ± 0.63	18.5 ± 0.42	238 ± 16.5
	35	25.4 ± 1.59	19.3 ± 1.22	246 ± 47.0
275	14	15.0 ± 0.39	11.4 ± 0.29	40 ± 3.1
	21	20.6 ± 0.39	15.8 ± 0.28	132 ± 6.4
	28	25.1 ± 0.98	19.0 ± 0.77	239 ± 27.9
	35	27.4 ± 1.13	20.8 ± 0.86	294 ± 35.1
	14	17.2 ± 0.32	13.1 ± 0.24	62 ± 3.0
500	21	25.6 ± 0.72	19.6 ± 0.60	267 ± 25.6
	28	33.1 ± 0.80	25.4 ± 0.65	522 ± 39.2
	35	36.5 ± 0.72	28.0 ± 0.55	659 ± 42.7
	14	18.6 ± 0.30	14.2 ± 0.24	75 ± 3.9
	21	25.1 ± 0.58	19.2 ± 0.47	251 ± 17.2
1000	28	33.3 ± 1.09	25.7 ± 0.86	526 ± 49.3
	35	35.1 ± 0.94	27.1 ± 0.77	600 ± 51.7
	14	17.2 ± 0.36	13.2 ± 0.28	61 ± 3.8
	21	25.5 ± 0.41	19.6 ± 0.33	269 ± 13.3
	28	29.6 ± 0.55	22.6 ± 0.46	394 ± 23.1
2000	35	33.7 ± 0.72	26.1 ± 0.60	525 ± 30.6
	14	14.3 ± 0.26	11.0 ± 0.21	40 ± 2.7
	21	20.8 ± 1.00*	15.9 ± 0.84*	157 ± 19.6*
	28	27.5 ± 0.40*	20.9 ± 0.32*	325 ± 15.2*
	35	32.2 ± 2.15*	25.1 ± 1.63*	516 ± 105.1*
<i>Callichthys callichthys</i>				
1	7	9.5 ± 0.20	7.2 ± 0.13	9 ± 0.6
	14	13.2 ± 0.41	10.3 ± 0.28	29 ± 2.5
	21	19.6 ± 0.47	15.4 ± 0.37	84 ± 5.5
	28	24.8 ± 1.49	19.2 ± 1.14	167 ± 25.3
	35	33.7 ± 0.86	26.2 ± 0.67	535 ± 42.9
275	14	15.1 ± 0.50	11.3 ± 0.39	33 ± 3.5
	21	22.3 ± 0.81	17.0 ± 0.66	116 ± 14.0
	28	28.8 ± 1.23	22.4 ± 0.96	251 ± 33.9
	35	36.4 ± 0.78	28.2 ± 0.66	560 ± 41.1
	14	17.3 ± 0.99	13.1 ± 0.78	54 ± 9.1
500	21	23.0 ± 0.99	17.7 ± 0.75	122 ± 15.3
	28	29.2 ± 1.20	22.4 ± 1.01	264 ± 31.0
	35	38.0 ± 1.03	29.5 ± 0.88	664 ± 62.4
	14	16.7 ± 0.53	12.5 ± 0.44	40 ± 3.8
	21	25.1 ± 0.80	19.3 ± 0.64	161 ± 16.4
1000	28	34.1 ± 0.96	26.7 ± 0.75	406 ± 36.1
	35	39.1 ± 1.17	30.5 ± 1.01	766 ± 69.6
	14	17.2 ± 0.52	12.9 ± 0.40	48 ± 4.3
	21	25.8 ± 0.46	19.9 ± 0.39	174 ± 10.7
	28	31.5 ± 1.19	24.3 ± 1.00	358 ± 45.5
2000	35	40.0 ± 1.30	31.4 ± 1.08	826 ± 90.0
	14	14.2 ± 1.11	10.6 ± 0.82	30 ± 5.7
	21	21.2 ± 1.42	16.3 ± 1.11	105 ± 17.0
	28	28.6 ± 1.72	22.0 ± 1.43	257 ± 53.7
	35	37.6 ± 5.06**	29.7 ± 4.04**	699 ± 238.3**

* n=5

** n=3

Chapter 3

Ontogenetic diet shifts and diet overlap among three closely related neotropical armoured catfishes

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Abstract

Analysis of stomach contents of larvae, juveniles and adults of three closely related armoured catfishes in coastal plain swamps of Suriname, South America, revealed major ontogenetic diet shifts. Larvae of *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys* showed a restricted diet of rotifers and microcrustacea. Diets of juveniles and adults were more diverse, but large volumes of microcrustacea, aquatic insect larvae and detritus were always present. In all three species diet overlap was especially low between larvae and adults. The proportion of detritus in the stomach was positively related to fish size, which probably reflected the inability of larger size classes to separate effectively benthic invertebrate prey from bottom substrata, and not a specialization towards detritivory. Adults showed only minor seasonality in diet composition, and no effect of season on diet breadth. Interspecific diet overlap among larvae, juveniles and adults did not differ significantly from 1 (complete overlap). Lack of food partitioning was probably related to a similar morphology of the three catfishes. Intraspecific between-size-class diet overlap was considerably lower than interspecific within-size-class overlap. I suggest that large interspecific diet overlap occurred because food was not limiting the populations of these catfish and nest habitats of the three species differed.

Key words: *Hoplosternum littorale*; *Hoplosternum thoracatum*; *Callichthys callichthys*; resource partitioning; diet breadth; seasonality; Suriname.

INTRODUCTION

Alpha diversity, the number of species that occur together in a particular biotope, is characteristically very high in many tropical freshwater fish communities (Lowe-McConnell, 1987). Two central questions in neotropical fish ecology are: what factors determine how many different species are able to coexist in the same community, and how do they divide or share the available resources?

In a recent review of resource partitioning in fish communities, Ross (1986) observed greatest separation of species along the diet axis (57%), followed by habitat (32%) and time of activity (11%). As Goulding (1980) pointed out, investigation of the use of food is probably the best starting point for understanding how fish communities function. Studies on

neotropical freshwater fish have shown marked seasonality in diet composition and feeding level (Lowe-McConnell, 1964; Zaret & Rand, 1971; Goulding, 1980), ontogenetic diet shifts (Angermeier & Karr, 1983; Winemiller, 1989), size-related fat storage potential (Goulding, 1980; Junk, 1985) and (lack of) resource partitioning (Knöppel, 1970; Zaret & Rand, 1971; Goulding, 1980; Angermeier & Karr, 1983; Winemiller, 1989).

Conclusions on the importance of food resource partitioning derived from the studies mentioned above are radically different. Knöppel (1970) was unable to detect significant differences in the diet composition of fishes in Amazonian rainforest streams. Zaret & Rand (1971) found low diet overlap in the dry season among fishes of a rainforest stream in Panama. Angermeier & Karr (1983), also working with Panamanian stream fish in the dry season, found large diet overlap within feeding guilds. Goulding (1980) reported important feeding specializations in large floodplain fishes in the wet season, although resource partitioning was much less distinguishable between closely related species. In the Venezuelan Llanos, Winemiller (1989) found low dietary overlap among piscivores throughout the year.

According to the 'competitive exclusion principle' two species occupying identical ecological niches cannot coexist indefinitely in the same place, one will ultimately exclude the other (Giller, 1984). Consequently it is the coexistence of closely related and morphologically similar species that is the most difficult to explain. Most studies on food partitioning among neotropical freshwater fishes explore patterns of food exploitation among a relatively large number of species that are more often than not only distantly related with each other, and also morphologically very distinct. Yet, if food partitioning is important in preventing competitive exclusion, differences in food utilization must exist not only at the generic level, but also, and more important, between closely related and morphologically similar species.

The present study examines diet composition and diet overlap among three closely related and morphologically similar armoured catfishes of the subfamily Callichthyinae (Hoedeman, 1952; Burgess, 1989), *Hoplosternum littorale* (Hancock, 1828), *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840), and *Callichthys callichthys* L., 1758. All three species are widely distributed throughout (sub)tropical South America, and often occur together in the same waterbody (i.e. they are syntopic) (Mol, 1994). In Suriname, they are among the most common bottom dwelling fish of coastal plain swamps (Ouboter & Mol, 1993). Floating bubble nests of the callichthyids appear in the newly flooded swamps at the onset of the rainy season (Mol, 1993a). Reproduction continues with few interruptions until swamp water levels drop and the fish move back to their dry season habitat of pools, canals and creeks. The following questions are essential to this study: (1) Do these closely related catfishes partition available food resources? (2) Do seasonal trends of resource availability affect diet composition and diet overlap among the three species? (3) What is the relationship between ontogeny and food resource partitioning?

MATERIAL AND METHODS

STUDY SITE

In the period December 1989 - December 1992, *H. littorale*, *H. thoracatum*, and *C. callichthys* were collected in swamps and swamp forests in the coastal plain of Suriname (situated between 5 and 6° Northern Latitude). Most fish (89%, n=681) were collected at

two localities; a *Typha* dominated swamp at Weg Naar Zee, 5 km north of the capital Paramaribo; and a mixed swamp and swamp forest area at Lelydorp, 20 km south of Paramaribo. The coastal plain experiences extensive sheet flooding during the two rainy seasons each year (December-January and April-July; Snow, 1976). In the main dry season of August-November the water retreats into small pools, canals and creeks. The chemistry of the coastal plain water bodies changes considerably during the seasonal cycle, mainly as a result of dilution by electrolyte-poor rainwater, and the influence of penetrating sea water in the dry season (Mol, 1993b). Fish and aquatic invertebrates also react to the regular flooding of the swamps (Mol, 1993a,b). As rainfall in December-January was relatively heavy during the period of investigations and the swamps remained flooded in February and March, the annual cycle was divided in a rainy season or high water period from 15 December to 15 August, and a dry season or low water period from 15 August to 15 December.

SAMPLING

In the rainy season, larvae (terminology of Balon, 1985), juveniles and adults were collected in the swamps. In the dry season adults and a few juveniles were collected in pools, canals and creeks. Because I was not successful in catching larvae at the breeding grounds, I collected eggs on the point of hatching from floating bubble nests (Mol, 1993a) and reared the newborn free embryo's (yolksac larvae) for four days at the exact location of the nest in enclosures of mosquito mesh (1.0 x 0.5 x 0.5 m; 1.7 mm unstretched mesh). The mesh size of the enclosures was larger than the width of the mouth gape of the larvae (0.73 ± 0.04 mm, mean \pm SE, $n=60$; age 4 days). One or two days after hatching the yolksac was consumed, and at approximately 7 mm total length the larvae started feeding on exogenous food. The stomach fullness of the larvae (Appendices 3.1-3.3) did not indicate a negative effect of the enclosures on the feeding activity of the fish. Larvae of *H. littorale* were identified by the nest from which they were taken (Mol, 1993a); larvae of *H. thoracatum* and *C. callichthys* were identified by their pigmentation pattern (Mol, in prep) after rearing a few fish of each nest for 10 days in the laboratory with *Artemia* nauplii. Juveniles were collected by seines at the spawning grounds at various intervals during the rainy season. They were identified by their pigmentation pattern and morphological characteristics. Adults were collected by gill net in the rainy season and by seine or cast net in the dry season. Larvae and juveniles were preserved in 4% formalin. Adults were preserved in 10% formalin or frozen at -15° C.

PREPARATION AND ANALYSIS OF STOMACH CONTENTS

All specimens were measured for standard length to the nearest 0.1 mm; fresh weight was determined to the nearest 0.1 mg for larvae and juveniles, and to the nearest 0.1 g for adults. The width of the mouth gape was measured to the nearest 0.1 mm as the maximum horizontal distance across the inner side of the open mouth. Unpublished data from a laboratory culture (data obtainable from the author) were also used to determine the relationship between the standard length and the width of the mouth gape. In order to establish morphological similarity between the three callichthyids 25 adult specimens of each species were examined following methods developed by Keast (1966) and Nijssen (1970).

The alimentary canal of the larvae and juveniles was removed and opened under a dissecting microscope. Stomach fullness was estimated as 0, 5, 25, 50, 75 or 100% of a fully extended stomach. The stomach contents of each individual were spread out on a 5x5 cm glass slide and examined systematically under a light microscope (100x and 400x). Food items were identified, counted, and their volume was estimated as a percentage of total stomach contents by determining the amount of surface of the glass slide covered for each item. Estimated volume percentages were adjusted for stomach fullness in all further calculations (Hyslop, 1980). Frequency of occurrence was based on presence or absence of food items and expressed as a percentage of all stomachs examined, including empty stomachs. Calculations of the mean number of food items also included empty stomachs.

Adult specimens often showed large visceral fat deposits in the coelomic cavity. The fat deposits were removed and weighed to the nearest 0.1 g. The length of the intestine was measured to the nearest 1 mm. The contents of the stomach were spread out on a petri disc and examined under a dissecting microscope following procedures described above for larvae and juveniles. Samples of the stomach contents of each fish were examined under a light microscope for presence of small food items and setae of Oligochaeta.

Initially 46 categories of food items were recognized, but for analyses of diet breadth and diet overlap, food items were grouped into 16 categories: algae, Testacea (diffugiids), Rotifera, Nematoda and Oligochaeta, microcrustacea (Cladocera, Copepoda, Ostracoda and Conchostraca), aquatic larvae and nymphs of insects, aquatic adult insects, Gastropoda, terrestrial Arthropoda (including insects), fish scales, invertebrate cysts, seeds/spores, detritus, chitinous remains, vegetative plant matter, and a miscellaneous group. Detritus was defined as dead organic matter that has been altered in some way that renders it unlike its original form (Bowen, 1983).

For analysis of ontogenetic diet shifts, dissected specimens were grouped into 10 mm intervals. The average volumetric proportion of the major food items, Rotifera, microcrustacea, aquatic insects (including larvae and nymphs) and detritus, was determined for each interval.

DIET BREADTH AND DIET OVERLAP

Only specimens caught at Lelydorp in the 1991/92 breeding season were used for the determination of diet breadth and diet overlap ($n=374$, Table 3.2). Estimated percentage volumes adjusted for stomach fullness were used in the calculations. Diet breadth was calculated by Levins' measure (Krebs, 1989). Levins' standardized measure was also used because the number of resource categories in the diet differed among developmental stages.

$$B = 1 / (\sum p_i^2) \quad \text{and} \quad B_A = (B - 1) / (n - 1)$$

where B = Levins' measure of niche breadth

p_i = proportional contribution of resource i to the total diet ($\sum p_i = 1.0$)

B_A = Levins' standardized niche breadth

n = number of possible resource categories

Diet overlap was calculated by Horn's information index (Krebs, 1989). Horn's index was chosen because it is commonly used, the bias for number of resource categories, sample size and resource unevenness is relatively low compared to other indices (Smith & Zaret, 1982), and the index can be statistically evaluated by Chi-square (Zaret & Smith, 1984). Horn's index (R_0) varies from 0, when diets are completely distinct (containing no food categories in common), to 1 when diets are identical with respect to proportional food category composition.

$$R_0 = [\sum (p_{ij} + p_{ik}) \cdot \log (p_{ij} + p_{ik}) - \sum p_{ij} \cdot \log p_{ij} - \sum p_{ik} \cdot \log p_{ik}] / 2 \cdot \log 2$$

where R_0 = Horn's index of overlap for species j and k
 p_{ij} = proportional contribution of resource i to the
total resources utilized by species j
 p_{ik} = proportional contribution of resource i to the
total resources utilized by species k .

Statistical evaluation by Chi-square of the null-hypothesis of complete overlap follows Zaret & Smith (1984):

$$X^2_R = 4 \cdot n \cdot (\ln 2) \cdot (1 - R_0) \quad \text{with } r-1 \text{ degrees of freedom}$$

where X^2_R = Chi-square statistic
 n = $2 \cdot N_j \cdot N_k / (N_j + N_k)$
 N_j = sample size species j
 N_k = sample size species k
 R_0 = Horn's index of diet overlap for species j and k
 r = number of food items used by both species

Principal Component Analysis based on volume percentages of food items grouped into 16 categories was used to summarize the results. Computation was done using STATGRAPHICS produced by Statistical Graphics Corporation.

RESULTS

Although adult *H. littorale*, *H. thoracatum* and *C. callichthys* look very similar, small but significant differences in body form, width of the mouth gape, length of the barbels, eye diameter, and form of the caudal fin were found (Table 3.1).

ONTOGENETIC DIET SHIFTS

Dominant food items in the diet of *H. littorale*, *H. thoracatum* and *C. callichthys* were rotifers, microcrustacea, aquatic insects and detritus (Appendices 3.1, 3.2 and 3.3 respectively). All three species experienced ontogenetic shifts in the consumption of these four major food items (Fig. 3.1).

Table 3.1. Morphological data for adults of three armoured catfishes, *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys* in the coastal plain of Suriname (mean \pm SE; n=25). Ratio's were tested for normality; one-way ANOVA was used to test for differences between the three species.

	<i>H. littorale</i>	<i>H. thoracatum</i>	<i>C. callichthys</i>	ANOVA	
				F	p
Total Length TL (mm)	165.8 \pm 3.5	157.0 \pm 1.6	164.3 \pm 3.6	NS	0.0358
Standard Length SL (mm)	128.4 \pm 3.0	125.4 \pm 1.3	133.8 \pm 2.7	NS	0.0573
Fresh weight (g)	89.9 \pm 6.7	78.7 \pm 3.5	77.1 \pm 4.6	NS	0.1641
Mouth width / SL	9.7 \pm 0.2	9.5 \pm 0.2	10.3 \pm 0.2	5.5	0.0061
Eye diameter / SL	4.8 \pm 0.1	4.1 \pm 0.1	2.7 \pm 0.1	113.5	<0.0001
Head length / SL	28.3 \pm 0.2	25.9 \pm 0.2	22.3 \pm 0.0	122.9	<0.0001
Body width / SL	26.9 \pm 0.5	27.0 \pm 0.4	26.4 \pm 0.4	NS	0.6423
Body depth / SL	31.7 \pm 0.3	29.5 \pm 0.4	21.5 \pm 0.3	282.7	<0.0001
Body depth / Body width	1.19 \pm 0.02	1.09 \pm 0.01	0.82 \pm 0.01	161.6	<0.0001
Intestine length / SL	1.36 \pm 0.04*	1.02 \pm 0.04**	1.56 \pm 0.04*	37.2	<0.0001
Length barbel upper lip / SL	29.4 \pm 0.6	28.9 \pm 0.7	23.3 \pm 0.7	27.2	<0.0001
Length barbel lower lip / SL	46.3 \pm 1.9	49.7 \pm 1.0	32.0 \pm 0.8	49.6	<0.0001
Number of lateral scutes	23 ventral row	23	26		
	25 dorsal row	25	28		
Mouth position	terminal	terminal	terminal		
Form of caudal fin	forked	rectangular	rounded		
Form of body	fusiform, laterally compressed	fusiform, laterally compressed	fusiform, dorsoventrally compressed		

* n=18; ** n=14

Four days after hatching and approximately two days after they start feeding, the diet of the larvae of *H. littorale*, *H. thoracatum* and *C. callichthys* was dominated by Rotifera (e.g. *Lecane*, *Monostyla*, *Platys*, *Cephalodella*) and microcrustacea (mainly Cladocera). Algae, difflugiids (e.g. *Arcella*, *Difflugia*, *Centropyxis*) and Oligochaeta were present in small quantities (Appendices 3.1-3.3). Larvae of *C. callichthys* seemed to be able to handle slightly larger food items like small chironomid larvae and Oligochaeta (Appendix 3.3).

During the first three weeks after hatching larvae of the three callichthyids show considerable changes in form of the head, body and fins (Mol, in prep). Approximately two weeks after hatching, at a standard length of 8-9 mm, positive allometric growth of the mouth gape changed into isometric growth (Fig. 3.1). Transformation to a juvenile fish was completed in the third week. Juveniles shifted to a mixed diet comprised primarily of aquatic insects (mainly chironomid larvae) and microcrustacea, with Rotifera still important to the smallest size classes, and detritus to the larger size classes (Fig. 3.1).

At a standard length of 70-75 mm (*H. thoracatum*), 80-85 mm (*H. littorale*) and 85-90 mm (*C. callichthys*), the fully developed armour of bony plates and mature gonads revealed that juveniles had reached maturity. The diet of adult fish was dominated by aquatic insects and detritus (Fig. 3.1). Chironomid larvae were found in large numbers in the stomach of all three species. Oligochaeta were not often detected probably due to their fast digestion (Kennedy, 1969), but setae were typically often present in the stomachs (compare frequency of occurrence of setae with that of Oligochaeta in Appendices 3.1-3.3). Oligochaeta are quite abundant in coastal plain zoobenthos samples (Mol, 1993b). Two specimens of *C. callichthys* had consumed a small characoid fish. The width of the mouth gape of *C. callichthys* is larger than that of both *Hoplosternum* species (Table 3.1; Fig. 3.1).

The relative intestine length (intestinal ratio), defined as the length of the intestine divided by the standard length of the fish, is relatively short in adult *H. littorale*, *H. thoracatum* and *C. callichthys* (1.0-1.6; Table 3.1) compared to that of known detritivores like *Labeo*, *Oreochromis mossambicus* and *Prochilodus* (Bowen, 1983). A muscular grinding stomach, pyloric caeca and extensive mucosal folding of the intestine wall characteristic of *Prochilodus* (Bowen, 1983) are absent in the callichthyids. The intestine is often filled with air.

Diet breadth in larvae of *H. littorale*, *H. thoracatum* and *C. callichthys* was low (Table 3.2). Levins' standardized index is well below 0.1, and only two or three food items out of 16 categories were consumed frequently (Table 3.2). Diet breadth in juveniles (0.096-0.287) showed no large differences with that in adults in the rainy season (0.165-0.354) (Table 3.2). Although Levins' index for juveniles and adults indicates a varied diet for the population as a whole, individual fish often feed on only a few food items. With 44% of the juvenile fish only one or two food items made up 90 volume percent of the diet. In both rainy and dry seasons 68% of the adult fish had one or two food items making up 90% of their diet.

SEASONALITY IN DIET COMPOSITION

In the dry season mainly adults were collected. Most specimens showed large visceral fat deposits in the coelomic cavity during the first months of the dry season (Table 3.3). These fat stores made up approximately 1% of the body weight in the dry season and 0.3%

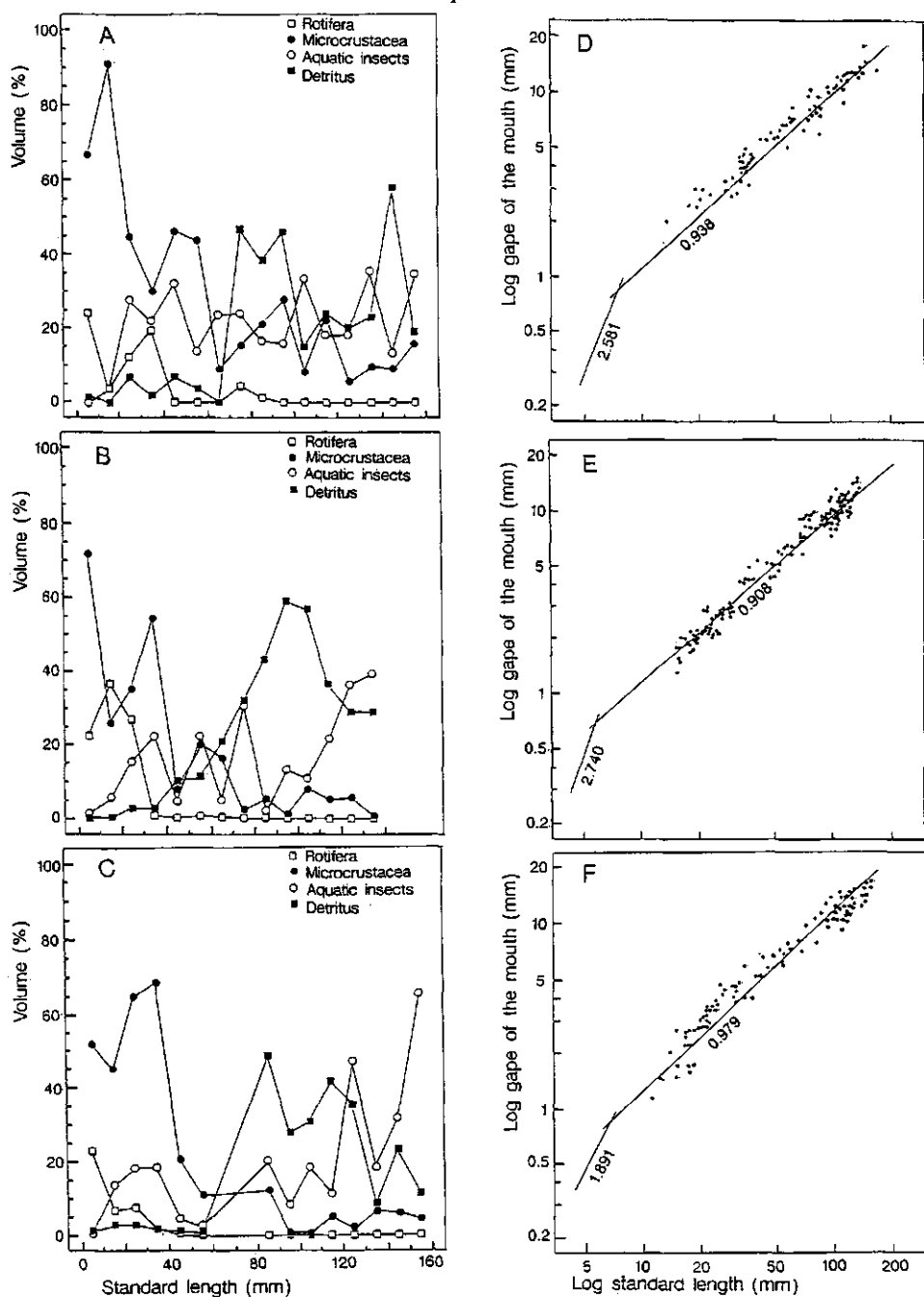


Fig. 3.1. Average volume percentages of Rotifera, microcrustacea, aquatic insects (including larvae) and detritus in the stomach of *H. littorale* (A), *H. thoracatum* (B) and *C. callichthys* (C) grouped by length interval. Growth of the mouth gape with respect to body length of *H. littorale* (D), *H. thoracatum* (E) and *C. callichthys* (F) based on tank culture data (solid lines) and field data (dots).

Table 3.2. Dietary diversity (diet breadth) as expressed by Levins' index (B), Levins' standardized index (B_A) and the number of frequently consumed food items (volume >5%) for larvae, juveniles and adults of *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys* at Lelydorp, Suriname (1991/92).

	n	B	95% confidence interval for B	B_A	number of food items with volume >5%
Larvae					
<i>H. littorale</i>	52	1.81	± 0.452	0.054	2
<i>H. thoracatum</i>	50	1.57	± 0.367	0.038	2
<i>C. callichthys</i>	78	2.21	± 0.544	0.081	3
Juveniles					
<i>H. littorale</i>	29	3.05	± 1.428	0.137	5
<i>H. thoracatum</i>	25	5.31	± 2.208	0.287	6
<i>C. callichthys</i>	41	2.44	± 0.887	0.096	4
Adults, rainy season					
<i>H. littorale</i>	11	3.47	± 2.003	0.165	4
<i>H. thoracatum</i>	14	4.33	± 8.260	0.222	4
<i>C. callichthys</i>	15	6.31	± 3.422	0.354	6
Adults, dry season					
<i>H. littorale</i>	18	3.74	± 2.079	0.183	4
<i>H. thoracatum</i>	27	4.08	± 1.977	0.205	6
<i>C. callichthys</i>	14	3.94	± 1.904	0.196	4

in the rainy season, the difference being significant (Mann-Whitney test; *H. littorale*, $p=0.026$; *H. thoracatum*, $p<0.001$; *C. callichthys*, $p<0.001$).

Adults showed no significant seasonal differences in the proportion of empty stomachs and in mean stomach fullness (Appendices 3.1-3.3). Dietary diversity was also little affected by season (Table 3.2). When the consumption of major food items was compared between seasons, only minor differences were found. *Hoplosternum thoracatum* consumed more microcrustacea (t-test, $p=0.051$) and less Rotifera (t-test, $p=0.051$) in the rainy season. However, Rotifera were not important in the diet of adult *H. thoracatum* (Appendix 3.2). Differences in consumption of aquatic insects, aquatic insect larvae, and detritus were not significant. In the rainy season Gastropoda were of some importance in the diet of *H. littorale* and, to a lesser extent, *C. callichthys* (Appendices 3.1, 3.3). Fish scales were found in dry season stomachs of *H. littorale*, *C. callichthys*, and both juveniles and adults of *H. thoracatum* (Appendices 3.1-3.3). Juveniles of *H. thoracatum* and *H. littorale* fed on unicellular algae (mainly Euglenophyta) in the dry season. On 20 October 1992 six juvenile *H. thoracatum* were collected in a dry season mud pool with fully extended stomachs filled with the euglenids *Phacus*, *Trachelomonas*, *Lepocinclis*, and *Euglena*.

INTRA- AND INTERSPECIFIC DIET OVERLAP

Average diet overlap among *H. littorale*, *H. thoracatum* and *C. callichthys* was high for larvae (0.964), juveniles (0.770) and adults, both in the rainy season (0.857) and dry season (0.715) (Table 3.4). Most of the pairwise interspecific diet overlaps within one developmental stage were not significantly different from 1 (Table 3.4), which means that these diets showed complete overlap. Interspecific diet overlap within one developmental

Table 3.3. Visceral fat deposits of *H. littorale*, *H. thoracatum* and *C. callichthys* in the dry season and rainy season expressed as percentage of body weight (mean \pm SE). Number of observations in parentheses.

Species	Body weight (g)	Fat deposits (%)
Dry season		
<i>H. littorale</i>	79.9 \pm 5.3 (39)	1.15 \pm 0.26 (39)
<i>H. thoracatum</i>	54.3 \pm 3.0 (48)	1.19 \pm 0.14 (48)
<i>C. callichthys</i>	62.3 \pm 6.2 (35)	1.11 \pm 0.18 (35)
Rainy season		
<i>H. littorale</i>	83.8 \pm 8.4 (15)	0.27 \pm 0.06 (15)
<i>H. thoracatum</i>	59.0 \pm 2.3 (74)	0.19 \pm 0.03 (74)
<i>C. callichthys</i>	75.7 \pm 4.0 (42)	0.45 \pm 0.28 (42)

stage was larger than intraspecific overlap between two developmental stages. Diet overlap was relatively low between larvae and adults (0.349-0.575, Table 3.4).

Overlap between the diets of the adults of a species in the rainy and dry season averaged 0.707. They were not significantly different from 1 (Table 3.4).

Principal Component Analysis was used to summarize the results of the diet analyses (Fig. 3.2). Diets of larvae, juveniles and adults of *H. littorale*, *H. thoracatum* and *C. callichthys* were grouped into clusters which reflected primarily the three developmental stages of the callichthyids, and not the species themselves. Clusters were most clearly differentiated by proportional consumption of Rotifera, microcrustacea, insect larvae and detritus (Fig. 3.2). The rainy season diet of adult *H. littorale* was not assigned to a cluster due to the large Gastropoda component (Appendix 3.1).

DISCUSSION

DIET COMPOSITION

Larvae of *H. littorale*, *H. thoracatum* and *C. callichthys*, fed almost exclusively on microcrustacea and rotifers. Although he did not provide quantitative data, Machado-Allison (1986) stated that in the Venezuelan Llanos three-day old larvae of *H. littorale* consumed mainly zooplankton. Zooplanktivorous feeding in larvae of temperate freshwater fish (Keast, 1980; Hartmann, 1983; Mark *et al.*, 1987) and marine fish (Hunter, 1980) is well documented.

Associated with the transformation of the larvae into juveniles, *H. littorale*, *H. thoracatum* and *C. callichthys* started feeding on a more diverse diet of microcrustacea, aquatic insects, Oligochaeta, Nematoda and detritus. The growth of the mouth gape seems to be of special importance, improving prey catch success (Drost, 1987) and allowing feeding on larger, alternative food items (Hartmann, 1983; Osse, 1990). Dietary change with age appears to be the rule in fishes where growth is indeterminate (Helfman, 1978; Werner & Gilliam, 1984), and is also reported for neotropical freshwater fish (Angermeier & Karr, 1983; Winemiller, 1989).

The diet of juvenile *H. littorale* in the coastal plain of Suriname corresponds well with quantitative data on stomach contents of juvenile *H. littorale* in the Venezuelan Llanos (Winemiller, 1987). In the Surinamese swamps, diets of juvenile *C. callichthys* and

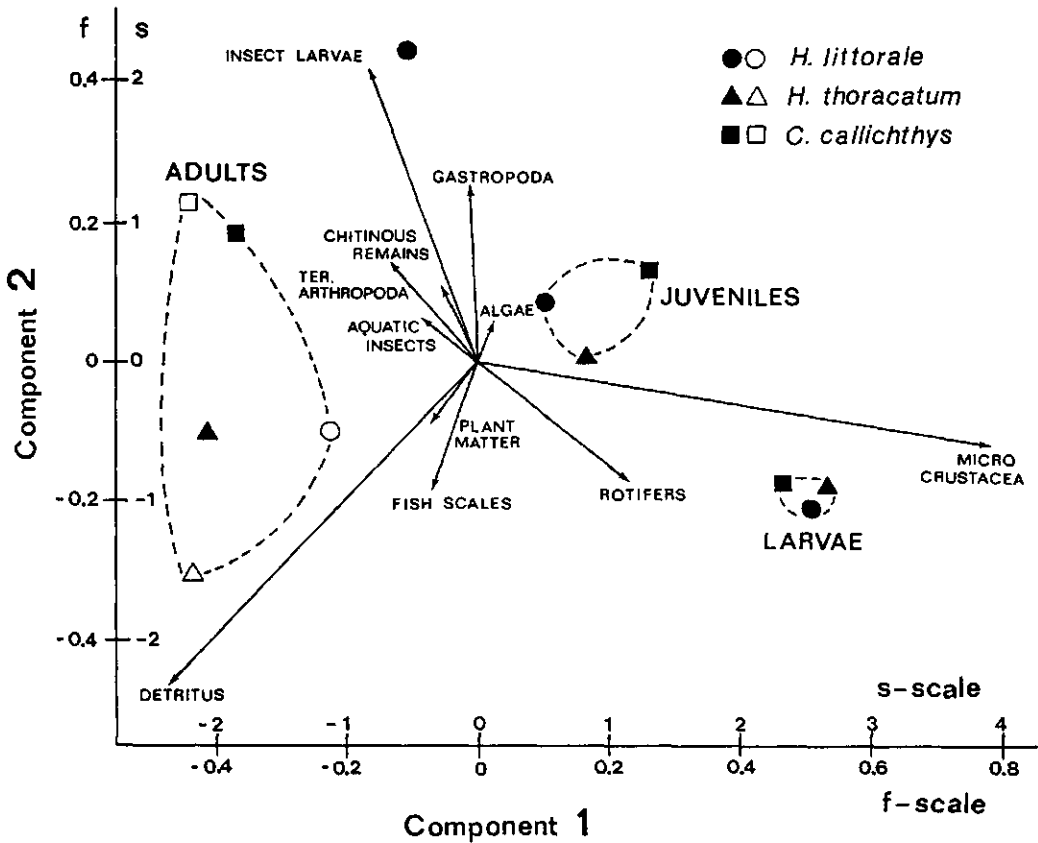


Fig. 3.2. Principle Component Analysis ordination diagram of the stomach contents of larvae, juveniles and adults of *H. littorale*, *H. thoracatum* and *C. callichthys* in covariance biplot scaling (Jongman *et al.*, 1987) with the food items represented by arrows. Closed symbols represent diets in the rainy season and open symbols represent diets of adults in the dry season. The *f* scale applies to food items, the *s* scale to species and their developmental stages. Food items not represented in the diagram lie close to the origin (0,0). The first component axis accounts for 83.4% of the variance and the second axis explains 5.7%. Dashed lines show the grouping of stomach contents derived from Average Linking Cluster Analysis of the same data.

H. thoracatum resembled that of *H. littorale*. Knöppel (1970) found mainly larvae of Ephemeroptera and Trichoptera in the stomach of juvenile *C. callichthys* from Amazonian rainforest streams. This different diet probably reflects differences in habitat between the shaded rainforest stream (studied by Knöppel, 1970) with very low autochthonous production, and an open floodplain swamp or savanna with more nutrient-rich water and autochthonous production (Lowe-McConnell, 1987). In Suriname, larvae of Ephemeroptera and Trichoptera are characteristic of small rainforest streams in the interior (Leentvaar, 1975).

Adult *H. littorale*, *H. thoracatum* and *C. callichthys* showed a diet comprised mainly of benthic invertebrates (primarily chironomids) and detritus, although microcrustacea were also taken. In Venezuela, Winemiller (1987) also found large volumes of chironomid larvae

Table 3.4. Comparison of diets of larvae, juveniles and adults of *Hoplosternum littorale* (Hl), *Hoplosternum thoracatum* (Ht) and *Callichthys callichthys* (Cc) at Lelydorp (1991/92) using Horn's index of diet overlap. Values marked with an asterisk did not differ significantly from 1 (complete overlap) (Chi-square $X^2_{df=0.05}$).

	Larvae	Juveniles	Adults
	Ht Cc	Hl Ht Cc	rainy season dry season
	Hl Ht Cc	Hl Ht Cc	Hl Ht Cc
Larvae			
H. littorale	0.976*	0.964*	
H. thoracatum	0.952*	0.833	
C. callichthys		0.596 0.591 0.838	0.575* 0.444 0.302
		0.697 0.551 0.838	0.577* 0.437 0.280
		0.733 0.590 0.871*	0.592* 0.460 0.349
Juveniles			
H. littorale		0.791*	0.850* 0.774* 0.764*
H. thoracatum		0.681	0.866* 0.582* 0.528
C. callichthys			0.830* 0.713* 0.573
Adults, rainy season			
H. littorale			0.895* 0.819*
H. thoracatum			0.857* 0.771*
C. callichthys			0.777* 0.633* 0.494
			0.798* 0.720* 0.557*
Adults, dry season			
H. littorale			0.806* 0.662*
H. thoracatum			0.676* 0.633*
C. callichthys			0.717* 0.557*

and detritus in the stomach of adult *H. littorale*. In contrast, detritus (82 volume %) and microcrustacea were the most important food items in adult *H. littorale* in Trinidad (Singh, 1978). The two isolated findings of piscivory in *C. callichthys* in Suriname are probably no coincidence as this species was found to feed occasionally on fish in Amazonian rainforest streams as well (Knöppel, 1970).

The intestine of adult callichthyids (Table 3.1) is short compared to that of detritivores (Bowen, 1983). Knöppel (1970) even found an intestinal ratio of 0.8 in young adults of *C. callichthys*. The anterior digestive portion of the alimentary tract of *Hoplosternum* is relatively short compared to other teleosts (Huebner & Chee, 1978), and the transparent wall of the larger posterior part is structurally adapted to a respiratory function (Carter & Beadle, 1931; Huebner & Chee, 1978). The same conclusion probably holds for *C. callichthys*. The short intestine and absence of a grinding stomach, pyloric caeca and extensive mucosal folding, indicate that these fish probably are not able to assimilate detrital nonprotein amino acids (as demonstrated in *O. mossambicus* by Bowen (1980, 1981)). The composition of the detritus in the stomach of the three callichthyids differed from detritus found in *O. mossambicus*. Callichthyid detritus consisted of partial decomposed but easily recognizable plant matter originating from both trees and macrophytes, mixed with small quantities of animal remains. Inorganic mud was never observed in the stomach and sand not frequent (Appendices 3.1-3.3). Detritus in the stomach was very similar to detritus in the posterior part of the intestine, indicating that little digestion had occurred. Detritus in the stomach of *O. mossambicus* consists of a complex aggregate of very fine, flocculant organic matter of uncertain origin, and substantial amounts of inorganic mud (unpublished observations, $n=23$; also see Bowen, 1981, 1983). I think it probable that the three callichthyids accidentally ingested large amounts of detritus when they foraged on benthic invertebrates. On the other hand the callichthyids may actively forage on detritus, and utilize the associated microflora of fungi and bacteria as suggested by Singh (1978).

SEASONALITY AND DIET

Seasonal fluctuation of the water level was probably the single most important factor affecting the life of fishes in the coastal plain of Suriname. Zooplankton densities in the flooded swamps (rainy season) were higher than in dry season pools, canals and creeks (Mol, 1993b). Competition theory predicts less dietary overlap between similar species during the lean season when resources are scarce (Schoener, 1982).

Goulding (1980) pointed out that large fish react in a different way to the reduced food availability in the dry season than small species. Large fishes, having a greater volume per surface area, are able to store sufficient fat reserves during the high water period to survive their 'physiological winter' (dry season) (Goulding, 1980; Junk, 1985). A large proportion of empty stomachs and low stomach fullness reveal that large fish almost cease to feed in the dry season. It is during the high water season that they most clearly show their feeding adaptations and partition food resources (Goulding, 1980). Small species, limited by their size in fat storage potential, do not cease to feed in the dry season. Intense competition of large numbers of fish for shrinking food supplies may force these species to specialize in the dry season as was found by Zaret & Rand (1971).

Medium-sized *H. littorale*, *H. thoracatum* and *C. callichthys* did show large fat stores in the first months of the dry season (Table 3.3). This was reported for *H. littorale* in Trinidad (Singh, 1978) and Venezuela (Winemiller, 1987). On the other hand mean stomach fullness and the number of empty stomachs in the dry season indicated that adults callichthyids did not cease to feed when confined to low-water habitats (Appendices 3.1-3.3). Diet breadth was also little affected by season (Table 3.2). I could detect only minor differences in the diet between seasons, e.g. the presence of fish scales in dry season stomachs. Overcrowding in a shrinking aquatic habitat and deterioration of the water quality cause the death of many fish in the dry season. The callichthyids are hardy fish adapted to low oxygen levels by their air-breathing habit (Carter & Beadle, 1931) and to desiccation by their armour of bony plates. In the dry season they probably feed partly on the accumulating remains of dead fish. It is not likely they are true scale-eating fish (Sazima, 1983) because they are morphologically not well equipped for fast attacks on living fish and lack specialized teeth (Table 3.1; Burgess, 1989).

A possible explanation for the lack of seasonality in the diet of these bottom-dwelling catfishes is that their major food source, benthic invertebrates, is less affected by season than other food items like zooplankton and allochthonous food (Bonetto, 1975; Mol, 1993b).

DIET OVERLAP

Interspecific diet overlap among *H. littorale*, *H. thoracatum* and *C. callichthys* was typically high (approximately 0.8; Table 3.4). In fact, most pairwise overlaps among larvae, juveniles and adults did not differ significantly from 1.

In temperate lakes interspecific diet overlap values are typically low (<0.3), except for congeneric species, were values may be moderate (Keast, 1978), and larvae/juveniles which often show highly similar diets (Mark *et al.*, 1987; but see Keast, 1980).

Within a tropical river system, Lowe-McConnell (1987) showed high dietary overlap correlated with shaded Amazonian headwater streams, where fishes are mostly polyphagous, and important feeding specializations and low overlap with a greater diversity of niches provided by the floodplain habitat downstream. In Panamanian rainforest streams, Angermeier & Karr (1983) found large diet overlaps (>0.9) within feeding guilds. However, only 6 food categories were distinguished by these authors. In another study of Panamanian stream-fish, Zaret & Rand (1971) report low diet overlap in the dry season and moderately high overlap (>0.6) in the rainy season. Although diet overlap was not calculated by Knöppel (1970) and Saul (1975), stomach contents analyses indicated that most fishes in small Amazonian streams ate whatever was available. In floodplains of the Venezuelan Llanos, Winemiller (1989) found low dietary overlaps (<0.3) among 9 piscivores. However, Winemiller's calculations were based on 118 food categories, making bias of his values probably high (Smith & Zaret, 1982). Furthermore, if search images of fishes are rather roughcasted (Hartmann, 1983), the question whether the 118 food categories distinguished by Winemiller are really relevant to the fishes he studied, must also be considered. Goulding (1980) reported important feeding specializations (low dietary similarity) in large Amazonian floodplain fishes.

Thus, compared with other studies on food partitioning in neotropical freshwater fish, interspecific diet overlap among *H. littorale*, *H. thoracatum* and *C. callichthys* was high. The high overlap is most probably due to a similar morphology of these catfishes (Table 3.1).

Food overlap values of a comparable high magnitude (>0.9) were found among juveniles and adults of two morphologically similar *Astyanax* species in Brazil (Arcifa *et al.*, 1991). Goulding (1980) also found little food resource partitioning between large, congeneric floodplain species.

Intraspecific diet overlap in the callichthyids was distinctly lower than interspecific overlap, stressing the importance of the effects of indeterminate growth on fish interactions (Helfman, 1978; Keast, 1978; Werner & Gilliam, 1984). Keast (1978) argued that some fish species simultaneously occupy several niches. Size (age) classes may function as 'ecological species' by showing the same differences in morphology and resource use as exists between biological species (Polis, 1984).

Given this large diet overlap among three callichthyids, what prevents competitive exclusion from occurring? First, it is not clear to what extent food availability is really limiting. High predation pressure and stranding at the end of the rainy season probably result in high mortalities (Lowe-McConnell, 1987), and population densities may not reach levels at which competition becomes important (Connell, 1975; Roughgarden & Feldman, 1975). In the wet season (reproductive season) densities of zooplankton, the most important food item of larvae and juveniles, are relatively high (Mol, 1993b) while dispersal of the fishes is extensive. Second, the three catfishes might separate out on time of activity or habitat use. Segregation in time of activity on a daily or a yearly basis does not seem probable. *Hoplosternum littorale* is active at dusk and in the night (Boujard *et al.*, 1990) and the same diel pattern of activity probably holds for *H. thoracatum* and *C. callichthys* (pers. observations in tanks and experience with angling). Reproduction is strongly correlated with seasonality in rainfall in all three species. Onset and duration of the spawning season do not differ much (Mol, in prep), and larvae and juveniles grow up in the same period of the year.

Habitat differentiation among the three callichthyids seems not important as all spent most of their time in the same bottom habitat. However, I have observed that in the rainy season nest (micro)habitats of the three species differ with respect to vegetation type and waterdepth (Mol, in prep). Whereas the reproductive season lasts as long as the swamps are flooded and individual fish remain reproductively active during this period (Pascal *et al.*, 1994), the three species (reproducing adults, larvae and possibly juveniles) are separated spatially when population sizes are largest and most of the feeding takes place. Werner (1977) pointed out that where considerable intraspecific size (age) class segregation of food resources exists, habitat separation of closely related species is far more effective than food separation in preventing species overlap. After comparing primary and secondary production in a temperate and a tropical lake, Burgis & Dunn (1978) concluded that the size of fish populations in a tropical lake might well be limited by lack of suitable nursery and breeding areas or predation on juveniles and not by food shortage. Habitat segregation among congeneric tropical freshwater fishes with similar feeding habits is reported for two *Astyanax* species in Brazil (Arcifa *et al.*, 1991) and three *Barbus* species in Sri Lanka (De Silva & Kortmulder, 1977).

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APPENDIX 3.1. Composition of the diet of *Hoplosternum littorale* in the coastal plain of Suriname. Frequency of occurrence (%), mean numerical composition and mean volume (%) of stomach contents of larvae, juveniles and adults in the rainy and dry season.

Food items	Larvae			Juveniles			Adults					
							Rainy season			Dry season		
	Freq	Num	Vol	Freq	Num	Vol	Freq	Num	Vol	Freq	Num	Vol
Filamentous algae	11.5	0.19	0.10	30.8	4.75	0.50	19.0	20.71	0.07	7.8	4.61	0.43
Chlorophyta	55.8	1.62	1.98	50.0	9.50	1.98	-	-	-	2.0	0.59	0.00
Bacillariophyceae	3.8	0.06	0.02	26.9	17.96	1.16	-	-	-	11.8	158.80	0.17
Euglenophyta	-	-	-	19.2	2.54	0.23	9.5	11.90	0.00	2.0	98.00	0.38
Rhizopoda (Testacea)	44.2	0.98	1.19	48.1	11.40	1.29	-	-	-	7.8	3.90	0.17
Rotifera	94.2	10.15	21.16	67.3	43.40	8.02	4.8	4.76	0.00	13.7	25.10	0.47
Nematoda	9.6	0.10	0.78	44.2	4.27	2.30	47.6	5.33	0.81	35.3	3.50	2.67
Oligochaeta	9.6	0.12	1.75	23.1	0.88	1.42	14.3	0.14	0.14	17.6	0.80	0.96
Oligochaeta, seta	13.5	-	-	59.6	-	-	38.1	-	-	41.2	-	-
Hydracarina	-	-	-	7.7	0.12	0.06	9.5	0.48	0.27	2.0	0.04	0.00
Cladocera	96.2	13.33	68.89	84.6	252.30	33.59	57.1	980.40	22.04	37.2	769.70	12.59
Copepoda	15.4	0.47	2.26	75.0	13.01	5.72	42.8	7.76	0.77	37.2	156.20	6.36
Ostracoda	-	-	-	11.5	38.81	2.06	47.6	75.95	7.74	19.6	40.60	4.73
Palaeomonetes carteri	-	-	-	-	-	-	4.8	0.14	0.02	2.0	0.02	0.64
Diptera larvae	-	-	-	78.8	10.33	11.96	71.4	15.33	19.70	45.1	30.60	13.57
Coleoptera larvae	-	-	-	30.8	0.52	2.88	28.6	1.38	5.38	9.8	0.50	1.29
Odonata nymphs	-	-	-	5.8	0.08	0.11	4.8	0.05	0.23	3.9	0.20	0.38
Aquatic adult Coleoptera	-	-	-	-	-	-	9.5	0.10	0.09	29.4	0.70	2.36
Hemiptera	-	-	-	-	-	-	14.3	0.14	0.59	5.9	0.10	0.11
Gastropoda	-	-	-	7.7	0.27	0.05	47.6	11.28	16.02	13.7	0.40	0.82
Terrestrial Arthropoda	-	-	-	23.1	0.29	0.92	19.0	0.19	1.36	21.6	0.40	1.24
Fish scales	-	-	-	19.2	0.62	0.36	4.8	0.10	0.00	27.4	3.00	3.02
Invertebrate cysts	1.9	0.04	0.05	36.5	9.15	3.21	4.8	0.05	0.09	7.8	0.60	0.00
Seeds/spores	1.9	0.02	0.03	13.5	0.98	0.20	33.3	0.57	0.63	29.4	4.40	1.90
Detritus	1.9	-	1.75	42.3	-	11.54	71.4	-	15.54	54.9	-	35.03
Chitinous remains	-	-	-	32.7	-	-	52.4	-	5.88	45.1	-	3.58
Vegetative plant matter	-	-	-	-	-	-	42.8	-	2.26	39.2	-	4.22
Sand	-	-	-	17.3	-	4.46	23.8	-	0.11	21.6	-	2.53
Other items	-	-	-	3.8	0.82	0.56	-	-	-	2.0	0.24	0.36
TOTAL	27.08	99.96		422.00	99.99		1136.76	99.74		1303.00	99.98	
No. of stomachs examined	52			52			21			51		
No. of empty stomachs	0			3			4			21		
Mean stomach fullness (%)	77			70			53			46		
Standard length range (mm)	5.6 - 7.0			13.5 - 81.4			86 - 152			86 - 158		

APPENDIX 3.2. Composition of the diet of *Hoplosternum thoracatum* in the coastal plain of Suriname. Frequency of occurrence (%), mean numerical composition and mean volume (%) of stomach contents of larvae, juveniles and adults in the rainy and dry season.

Food items	Larvae			Juveniles			Adults					
							Rainy season			Dry season		
	Freq	Num	Vol	Freq	Num	Vol	Freq	Num	Vol	Freq	Num	Vol
Filamentous algae	6.0	0.06	0.05	50.0	6.02	1.23	1.2	1.16	0.04	1.6	0.08	0.00
Chlorophyta	36.0	0.50	0.45	73.1	29.10	4.23	-	-	-	-	-	-
Bagillariophyceae	32.0	0.64	0.07	62.8	7.50	0.78	9.3	4.13	0.04	15.6	119.10	0.08
Euglenophyta	2.0	0.02	0.00	14.1	0.33	8.94	3.5	59.77	0.26	1.6	3.91	0.04
Rhizopoda (Testacea)	82.0	3.20	2.33	71.8	30.78	5.02	-	-	-	6.2	3.30	0.13
Rotifera	98.0	12.80	17.40	80.8	100.80	16.38	2.3	1.45	0.02	14.1	126.90	0.23
Nematoda	-	-	-	47.4	1.27	1.36	20.9	0.88	0.29	31.2	2.60	2.53
Oligochaeta	6.0	0.06	0.79	26.9	0.54	1.30	12.8	1.21	0.58	15.6	0.90	0.91
Oligochaeta, seta	20.0	-	-	59.0	-	-	47.7	-	-	35.9	-	-
Hydracarina	-	-	-	5.1	0.05	0.18	4.7	0.07	0.00	4.7	0.04	0.00
Cladocera	100.0	15.88	69.20	71.8	85.15	22.79	23.2	614.90	9.03	20.3	3.40	0.47
Copepoda	46.0	2.18	5.13	73.1	184.55	7.87	12.8	12.19	0.71	20.3	26.80	1.74
Ostracoda	28.0	0.42	3.44	7.7	0.27	0.24	17.4	5.94	1.02	15.6	2.90	0.33
Palaemonetes carteri	-	-	-	1.3	0.01	0.12	4.7	0.06	0.12	3.1	0.30	2.28
Diptera larvae	2.0	0.02	0.55	57.7	3.69	8.77	47.7	14.08	14.26	46.9	6.20	6.33
Coleoptera larvae	-	-	-	25.6	0.37	1.69	23.2	1.28	5.27	14.1	0.30	2.17
Odonata nymphs	-	-	-	-	-	-	4.7	0.05	0.10	4.7	0.10	2.31
Aquatic adult Coleoptera	-	-	-	-	-	-	7.0	0.10	0.87	17.2	0.30	4.86
Hemiptera	-	-	-	-	-	-	4.7	0.05	0.12	1.6	0.02	0.19
Gastropoda	-	-	-	1.3	0.01	0.12	11.6	0.17	0.22	7.8	0.40	0.13
Terrestrial Arthropoda	-	-	-	15.4	0.28	1.95	12.8	0.29	2.18	4.7	0.10	0.96
Fish scales	-	-	-	7.7	1.51	2.69	10.5	0.66	0.45	43.8	9.90	17.31
Invertebrate cysts	4.0	0.32	0.22	14.1	1.81	0.35	1.2	0.17	0.02	-	-	-
Seeds/spores	2.0	0.02	0.04	12.8	3.08	6.49	17.4	4.23	1.84	29.7	6.00	3.44
Detritus	-	-	-	47.4	-	5.99	73.2	-	48.46	73.4	-	39.08
Chitinous remains	-	-	-	30.8	-	1.28	54.6	-	6.68	53.1	-	6.75
Vegetative plant matter	-	-	-	-	-	-	39.5	-	6.15	37.5	-	6.28
Sand	-	-	-	-	-	-	7.0	-	1.13	9.4	-	0.51
Other items	-	-	-	3.8	0.68	0.23	4.6	0.36	0.12	3.1	-	0.56
TOTAL	36.12	99.67		457.80	100.00		723.20	99.98		313.55	99.62	
No. of stomachs examined	50			78			86			64		
No. of empty stomachs (%)	0			0			23			19		
Mean stomach fullness (%)	73			77			57			62		
Standard length range (mm)	6.2 - 7.4			15.2 - 69.3			85 - 136			70 - 150		

APPENDIX 3.3. Composition of the diet of *Callitichys callitichys* in the coastal plain of Suriname. Frequency of occurrence (%), mean numerical composition and mean volume (%) of stomach contents of larvae, juveniles and adults in the rainy and dry season.

Food items	Larvae			Juveniles						Adults					
	Freq	Num	Vol	Freq	Num	Vol	Freq	Num	Vol	Freq	Num	Vol	Freq	Num	Vol
Filamentous algae	1.3	0.02	0.02	17.9	0.73	0.21	-	-	-	-	-	-	-	-	-
Chlorophyta	12.8	0.20	0.56	22.4	0.79	0.12	-	-	-	-	-	-	-	-	-
Bacillariophyceae	6.4	0.06	0.01	61.2	5.70	0.46	4.2	15.62	0.04	2.9	14.70	0.08	-	-	-
Euglenophyta	-	-	-	4.5	0.10	0.03	-	-	-	-	-	-	-	-	-
Rhizopoda (Testacea)	82.0	2.54	3.81	68.6	20.51	1.71	-	-	-	-	-	-	-	-	-
Rotifera	88.5	7.01	19.38	73.1	66.06	5.32	2.1	10.42	0.04	-	-	-	-	-	-
Nematoda	5.1	0.05	0.66	31.3	0.52	0.31	12.5	0.46	0.23	20.6	0.60	0.47	-	-	-
Oligochaeta	17.9	0.19	7.17	34.3	3.73	8.28	8.3	0.33	0.68	2.9	0.10	0.17	-	-	-
Oligochaeta, seta	35.9	-	-	73.1	-	-	27.1	-	-	14.7	-	-	-	-	-
Hydracarina	3.8	0.04	0.41	3.0	0.03	0.02	8.3	0.08	0.04	5.9	0.10	0.00	-	-	-
Cladocera	80.8	4.95	57.10	76.1	511.10	55.43	31.2	304.40	8.52	2.9	22.00	5.15	-	-	-
Copepoda	23.1	0.83	6.64	65.7	10.67	1.94	25.0	77.69	1.56	-	-	-	-	-	-
Ostracoda	-	-	-	13.4	0.24	0.32	18.8	2.00	0.38	-	-	-	-	-	-
Palaemonetes carteri	-	-	-	1.5	0.01	1.92	-	-	-	5.9	0.10	0.52	-	-	-
Diptera larvae	2.6	0.02	1.12	68.6	5.92	12.09	35.4	4.56	4.62	17.6	1.60	2.75	-	-	-
Coleoptera larvae	-	-	-	38.8	0.86	5.05	35.4	2.75	12.95	11.8	0.40	2.45	-	-	-
Odonata nymphs	-	-	-	1.5	0.07	0.46	4.2	0.06	0.43	8.8	0.90	11.59	-	-	-
Aquatic adult Coleoptera	-	-	-	-	-	-	43.8	1.64	6.47	29.4	1.20	13.07	-	-	-
Hemiptera	-	-	-	-	-	-	10.4	0.12	0.34	5.9	0.10	0.62	-	-	-
Gastropoda	-	-	-	4.5	0.09	0.30	16.7	0.35	3.58	2.9	0.03	0.00	-	-	-
Terrestrial Arthropoda	-	-	-	10.4	0.18	1.80	27.1	1.00	5.12	23.5	0.70	10.77	-	-	-
Fish scales	-	-	-	3.0	0.18	0.05	-	-	-	8.8	1.40	2.58	-	-	-
Invertebrate cysts	2.6	0.42	0.59	6.0	0.15	0.01	8.3	1.60	0.43	2.9	0.20	0.00	-	-	-
Seeds/spores	1.3	0.01	0.01	17.9	0.85	1.15	10.4	0.46	0.23	8.8	0.40	0.13	-	-	-
Detritus	7.7	-	1.36	25.4	-	2.68	58.3	-	29.04	38.2	-	27.53	-	-	-
Chitinous remains	-	-	-	6.0	-	0.33	45.8	-	12.74	29.4	-	18.46	-	-	-
Vegetative plant matter	-	-	-	-	-	-	29.2	-	4.96	11.8	-	1.84	-	-	-
Sand	-	-	-	-	-	-	4.2	-	0.16	14.7	-	0.11	-	-	-
Other items	3.8	0.01	0.39	3.0	0.01	0.01	10.4	3.66	5.39	2.9	3.63	1.70	-	-	-
TOTAL	16.35	99.23			628.50	100.00		427.20	99.95		48.16	99.99			
No. of stomachs examined	78				67			48			34				
No. of empty stomachs	4				12			16			16				
Mean stomach fullness (%)	52				74			48			34				
Standard length range (mm)	5.6 - 8.4				11.1 - 86.2			101 - 161			92 - 160				

Chapter 4

Structure and function of floating bubble nests of three armoured catfishes (Callichthyidae) in relation to the aquatic environment

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Abstract

For five years, the floating bubble nests of three armoured catfishes, *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys*, were studied at two localities in the coastal plain of Suriname. The structure of the nests is described in some detail mainly from cross-sections through frozen nests. Multiple spawnings and nest guarding of the males are described. Based on the structure of the nest, field experiments and laboratory tests, the function of the foam nest is discussed in relation to the habitat of the fish. The nests of *H. littorale*, *H. thoracatum* and *C. callichthys* differ in many striking features. The geographical distribution of the three species is also distinct, *H. littorale* being limited to the swamps of the coastal plain. *Hoplosternum thoracatum* and *C. callichthys* also inhabit the lotic environment of small forest creeks in the interior. An attempt is made to relate differences in the reproductive strategy of the three species to the environment in which they live.

1. Introduction

Armoured catfishes of the family Callichthyidae are represented in Suriname by 17 small-sized fishes of the well-known genus *Corydoras* (Nijssen 1970) and three larger food fishes of the genera *Hoplosternum* and *Callichthys* (Hoedeman 1952). The latter three species, *Hoplosternum littorale* (Hancock, 1828), *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840) and *Callichthys callichthys* (Linnaeus, 1758), are the most preferred and expensive food fishes of Suriname. They are the only fish species in the country protected by law in their main reproductive season (Rondeel 1965). Still, overfishing, human-induced habitat modifications and the introduction of the exotic Tilapia *Oreochromis mossambicus* present serious threats to the survival of these popular fishes. Especially *H. littorale* is in danger of local extinction, its distribution being confined to the more densely populated coastal plain (Mol in prep). In 1987 the University of Suriname started a research programme on the three larger callichthyids with the ultimate aim of producing the fishes on a large scale, thus

removing some of the pressure that now rests on the natural stocks (Mol in press). *Hoplosternum littorale* also attracted considerable regional attention as a food fish with aquacultural potential (Lowe-McConnell 1984; Luquet *et al.* 1989).

Hoplosternum littorale, *Hoplosternum thoracatum* and *Callichthys callichthys*, together with two Amazonian species of the genus *Dianema*, make up the subfamily Callichthyinae (Gosline 1940; Hoedeman 1952; Burgess 1989). Contrary to the species belonging to the second callichthyid subfamily Corydoradinae, the Callichthyinae are aphrophilic nest-guarding fishes (Balon 1975). The aphrophilic reproductive guild is characterized by the building and guarding of floating bubble nests. Carter & Beadle (1931) consider the structure of the nests of *H. littorale* of importance in providing an oxygen-rich environment for the developing eggs and early larvae, but alternative advantages of the foam-nesting habit have also been suggested (Balon 1975). As Carter & Beadle (1931) point out, *Hoplosternum* and *Callichthys* often live in tropical standing waters deprived of oxygen. Their description of the swamps of the Paraguayan Chaco (Carter & Beadle 1930) closely corresponds with the water conditions of the standing waters of the Surinamese coastal plain (see Mol 1993). Another well established adaptation of *Hoplosternum* and *Callichthys* to the oxygen-depleted aquatic environment is their (obligatory?) air-breathing habit and intestinal respiration (Carter & Beadle 1931; Gee & Graham 1978; Huebner & Chee 1978; Kramer *et al.* 1978).

Floating bubble nests of *H. littorale* are associated with the annual flooding of shallow swamps (Carter & Beadle 1931; Singh 1978; Machado-Allison & Zaret 1984). Detailed descriptions of the nests of *H. littorale* are provided by Carter & Beadle (1931) and Machado-Allison & Zaret (1984). The nests of *H. thoracatum* and *C. callichthys* are only known from observations in aquariums (see Breder & Rosen 1966). Contrary to *H. littorale*, which in Suriname is collected only in coastal plain standing waters, *H. thoracatum* and *C. callichthys* also inhabit the lotic environment of small creeks in the interior of Suriname (Mol in prep). The aquatic habitat of these headwater streams, which drain the very poor soils of the Precambrium Guyana Shield, is very different from the coastal plain swamps and swamp forests. Leentvaar (1975), following the terminology of Sioli (1950), characterizes these creeks as clear water with very low concentrations of dissolved nutrients and minerals (e.c.), and often saturated with oxygen (also see Haripersad & Ouboter 1993).

The nests of *H. littorale* were studied during a five-year period (1987-92) in a *Typha* dominated swamp at Weg Naar Zee, only 2 km south of the Atlantic Ocean, and in an *Eleocharis* dominated swamp at Lelydorp, 20 km south of Paramaribo. The nests of *H. thoracatum* and *C. callichthys* were studied in 1990 and 1991 in the Lelydorp swamp. Confirmation of the nest building species by rearing the newly hatched larvae for one week was often necessary in order to distinguish nests of *H. thoracatum* from nests of *C. callichthys*. Fecundity of the three species was determined by counting ripening eggs present in the ovaries, preserved with Gilson's fluid (Bagenal & Braum 1978). This study aims at linking the differences in structure of the nests of the three species with differences in their environment.



Fig. 4.1. Nest of *Hoplosternum littorale* in a *Typha* dominated swamp at Weg Naar Zee, young coastal plain, Suriname. The guarding male is caught with the scoop net.

2. The Nests

2.1. The Nests of *Hoplosternum littorale*

2.1.1. Nest Construction, Oviposition and Incubation of the Eggs.

Floating bubble nests of *Hoplosternum littorale* (Sur. sokè or hé-edé kwikwi) are built by the male in shallow, herbaceous swamps during the rainy season (Fig. 4.1). Nests are also abundant in flooded rice fields. In standing waters of the coastal plain of Suriname the first nests are usually observed in late December or January when the water level in the swamps reaches about 25 cm (Mol in prep). The reproductive season lasts until July/August and is considerably longer than reported for Venezuela (Machado-Allison & Zaret 1984) and Trinidad (Singh 1978) but shorter than reported for ponds in French Guiana (Hostache *et al.* 1990). The length of the reproductive season changes with increasing rainfall from Venezuela towards French Guiana (Snow 1976). Within the main reproductive period, nesting of *H. littorale* in the Surinamese coastal plain was concentrated in the two rainy seasons: December-February and April-August (Mol in prep).

Table 4.1. Selected data (mean \pm S.E.) on the floating bubble nests of three callichthyid catfish *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys*. Number of observations in parentheses.

	Nests of <i>H. littorale</i>	Nests of <i>H. thoracatum</i>	Nests of <i>C. callichthys</i>
Nest construction material	grass	dicotyledonous leaves	dicotyledonous leaves
Number of leaves in a nest	-	5.2 \pm 0.21 (225)	2.8 \pm 0.21 (77)
Dry weight nest material (g)	33.1 \pm 3.1 (48)	4.5 \pm 0.5 (20)	1.5 \pm 0.2 (16)
Nest surface area (cm ²)	706 \pm 20 (109)	413 \pm 35 (20)	181 \pm 30 (16)
Nest height (cm)	6.0 \pm 0.4 (109)	0.5-1.0	0.5-1.0
Number of eggs	23,339 \pm 4,473 (11)	3,467 \pm 342* (20)	2,953 \pm 762* (16)
Fresh weight egg mass (g)	73.02 \pm 12.89 (11)	11.82 \pm 1.05 (18)	11.03 \pm 2.66 (16)
Dry weight egg mass (g)	13.05 \pm 2.40 (11)	2.13 \pm 0.21 (18)	2.29 \pm 0.57 (16)
Volume egg mass (ml)	73.74 \pm 13.23 (11)	11.24 \pm 1.00 (18)	10.29 \pm 2.52 (16)
Egg developmental stages in nest	1	1-3	1-3
Egg hatching time (days)	3.3 \pm 0.1 (59)	2-3	2-3
Life span of nest (days)	3.9 \pm 0.1 (89)	5.7 \pm 0.2 (190)	4.6 \pm 0.3 (56)
Standard length guarding male (cm)	15.9 \pm 0.2 (76)	11.0 \pm 0.3 (6)	14.3 \pm 0.5 (5)
Attack distance guarding male (m)	0.57 \pm 0.07 (71)	0	0

* average number of eggs/nest present at one point in time

Although the actual construction of the nest of *H. littorale* was not observed, daily surveys in the swamps early in the morning suggest that nest-building is concentrated in the late evening or during the night. Completed nests without eggs were often observed between 7.00 and 09.00 hours at localities in the swamp where in the afternoon of the day before no nest was present. Gautier *et al.* (1988) describe in detail the construction of the nest of *H. littorale* in tanks, but they do not mention the time of nest-building activities. Luquet *et al.* (1989) state that nest-building of *H. littorale* in fish ponds of French Guiana occurs during the night.

In the swamps of Suriname, oviposition is usually between 10.00 and 14.00 hours on the first day after nest construction and is indicated by more or less violent movements of the nest. I have observed the process of oviposition three times and have indirect confirmation of oviposition between 10.00 and 14.00 hours for another four nests. Local fishermen are well acquainted with the timing of oviposition and catch both male and females by positioning a bottomless basket over the nest as soon as they notice the nest shaking. All females spawn in the nest simultaneously, so the eggs in the nest are always of the same age and developmental stage (Table 4.1).

The eggs hatch on an average three days after oviposition, the exact time of development depending on nest temperature during incubation (Hostache *et al.* in press).

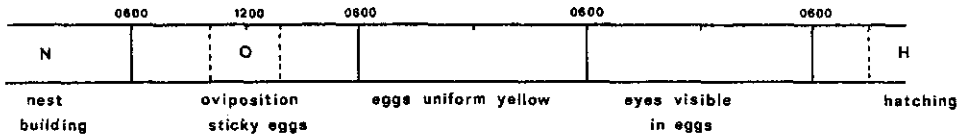


Fig. 4.2. Time schedule of nest construction, oviposition and hatching for *Hoplosternum littorale* in the swamps of northern Suriname.

Although small variations in incubation time occur in the swamps, probably due to weather conditions and microclimate in the immediate surroundings of the nest, the overall hatching time is fairly constant (Table 4.1; Fig. 4.2). It is not clear whether the nest of *H. littorale* deteriorates and flattens on the water surface shortly before hatching or immediately after hatching. The newborn larvae stay for one or two days among the floating nest materials before they move to the bottom of the swamp and start living on exogenous food (Singh, 1978; Machado-Allison 1986; Mol in press).

2.1.2. Nest Structure.

Fig. 4.3A shows a well developed nest of *Hoplosternum littorale* floating on the surface of a grass swamp in the coastal plain of Suriname. The internal structure of the nest is revealed by a cross-section through a frozen nest illustrated diagrammatically in Fig. 4.3B. The nest consists of a dome of dead or dying plant material, particularly grasses (e.g. *Hymenachne amplexicaulis*), *Typha angustifolia*, *Thalia geniculata*, *Hydrocotyle umbellata*, *Nymphoides indica*, *Nymphaea spec* and floating aquatics like *Pistia*, *Salvinia*, *Azolla* and Lemnaceae. Rarely are nests built of leaves of dicotyledonous trees. The thickness of the plant cover is 2 to 3 cm. The inner layer of about 1 cm consists of tightly packed grass and other plant material, contrary to the outer surface of the nest, where the plant material is more loosely interwoven. The dry weight (70° C, 48 hours) of the plant material averages 33.1 ± 3.1 g (Table 4.1). The fresh weight of the plant material is more difficult to measure in a uniform manner since part of the nest material is always soaked with swamp water, but a rough estimate is 240 ± 22 g (mean \pm SE). Nests of *H. littorale* average 30.0 ± 5.0 cm in diameter and are 6.0 ± 0.4 cm in height above the water surface (Table 4.1). Large nests may measure up to 42 cm in diameter and 10 cm in height. The eggs are glued together and to the underside of the dome of plant material. Below the eggs and covering the whole of the underside of the nest is a mass of foam. The eggs are not in contact with the oxygen-depleted swamp water.

The description of the nests of *H. littorale* in the coastal plain of Suriname closely corresponds with the drawings of Carter & Beadle (1931) for nests in the Paraguayan Chaco and with the description of Machado-Allison & Zaret (1984) for nests in the Venezuelan Llanos.

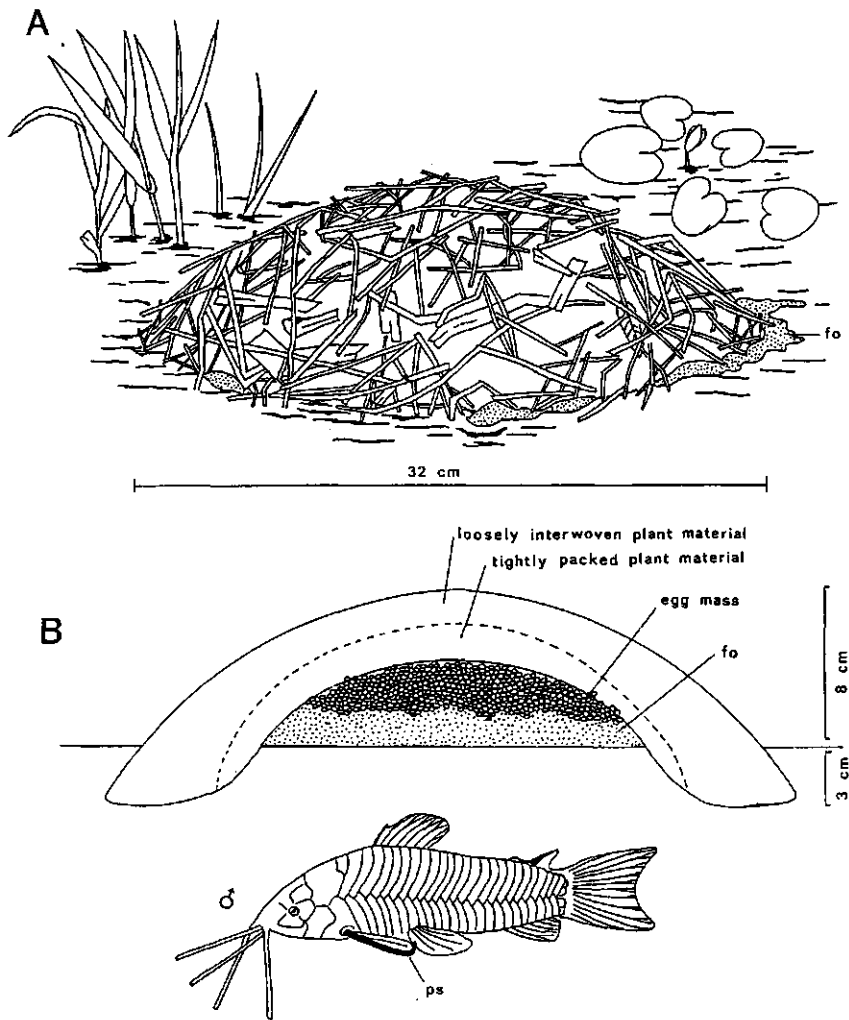


Fig. 4.3. The floating bubble nest of *Hoplosternum littorale*. A. The huge and complex construction of dead and dying grass leaves floats on the surface of the swamp. The foam (fo) which keeps the nest in shape can be seen at its edge. B. Cross-section of a frozen nest illustrating in the center of the nest the mass of sticky eggs glued to the underside of the plant cover, out of the oxygen-depleted swamp water and embedded in the foam. Also shown is the guarding male, in the breeding season easily distinguished from the female by the large, modified, ski-like pectoral spine (ps).

2.1.3. Nest Fauna.

The huge and complex construction making up the nest of *Hoplosternum littorale* provides a habitat for a rich and diverse fauna of aquatic, semi-aquatic and even terrestrial animals (Table 4.2). In 48 nests examined an average of 764 individuals nest⁻¹ or 11,012 ind m⁻² nest surface were counted. This number is still low compared to the 26,665 ind m⁻²

recorded for the root zone of the floating vegetation in the coastal plain of Suriname (Table 4.2; see also Mol 1993). However, the composition of the fauna of these nests was quite different from that of the root zone of the floating vegetation. Relatively well represented in the nests were Gastropoda, aquatic Coleoptera, Collembola, Isopoda, terrestrial Arthropoda and especially Formicidae. In 12.5% of the nests examined, ant colonies, including larvae, had been established. A negative effect of the presence of the ant colonies on the development of the eggs of *H. littorale* could not be detected. The ants may even provide some protection for the nests against egg predators like snakes or birds. In two nests a juvenile of the swamp eel *Synbranchus marmoratus* was detected. Examination of the stomach contents of these two specimens did not reveal the presence of eggs of *H. littorale*.

2.1.4. Number of Eggs, Spawnings per Nest and Parental Care.

The mean number of eggs counted in eleven nests of *Hoplosternum littorale* in the coastal plain of Suriname is 23,340 (Table 4.1). Minimum and maximum numbers recorded are respectively 3888 and 51,981 eggs nest⁻¹. Machado-Allison & Zaret (1984) report an average of 17,100 eggs nest⁻¹ and a range of 5600-55,300 eggs nest⁻¹ for nests of *H. littorale* in the Venezuelan Llanos. Singh (1978), working in the swamps of Trinidad and Guyana, recorded only 10,200 (2000-22,800) eggs nest⁻¹. In swamps and fish ponds in French Guiana, Luquet *et al.* (1989) report an average of 14,700 eggs nest⁻¹ and a minimum and maximum of respectively 3100 and 51,500 eggs nest⁻¹.

Data on the fecundity of *H. littorale* in Suriname are summarized in Table 4.3. An average of 5509 ripe eggs (diameter >1 mm) are present in females ready to spawn. Machado-Allison & Zaret (1984) counted an average of 4500 mature eggs per female and Luquet *et al.* (1989) report separate spawnings in aquariums of 600 to 10,000 eggs for 100 g females. Table 4.3 also shows immature eggs (<1 mm) present in most of the ovaries. Their number is on average 922 ± 213 . Machado-Allison & Zaret (1984) conclude that the females spawn only once in the breeding season, but Luquet *et al.* (1989) report multiple, successive spawnings for females in tanks and in fish ponds. In the prolonged reproductive season in Suriname females probably spawn at least in both the short and the long rainy season (Mol in prep).

Following Machado-Allison & Zaret (1984) the number of females that contributed to the egg mass in a particular nest of *H. littorale* may be estimated by dividing the number of eggs/nest by the mean number of mature eggs/female. Estimates of the mean and maximum number of spawnings per nest are four and nine, respectively, so most nests receive their eggs from more than one female. This corresponds well with reports of local fishermen catching many specimen of *H. littorale* during oviposition at one nest. The fairly constant life-span of the nests of *H. littorale* (three to four days) and the observation that the eggs in the nests are always of the same developmental stage, indicate that multiple spawnings are all performed at the same time.

Fig. 4.4A shows that there is a positive correlation between the size of the nest of *H. littorale* and the number of eggs contained in the nest.

Adult males of *H. littorale* are of larger average size than the females. In the reproductive season they are easily distinguished from the females by their elongate and modified pectoral spines (Fig. 4.3B) and fat deposits at the base of the pectoral fin (Winemiller 1987).

Table 4.2. Comparison of the fauna of floating bubble nests of *Hoplosternum littorale* (ind nest⁻¹ and ind m⁻²) with the fauna in the root zone of the floating vegetation (ind m⁻²) in the coastal plain of Suriname.

Taxon	Nests of <i>H. littorale</i> mean \pm S.E. (n=48) ind nest ⁻¹	Nests of <i>H. littorale</i> mean \pm S.E. (n=48) ind m ⁻²	Floating vegetation mean \pm S.E. (n=25) ind m ⁻²
Oligochaeta, Naididae	186 \pm 50	2679 \pm 727	6000 \pm 1658
Hirudinea	0.6 \pm 0.2	8 \pm 3	40 \pm 27
Nematoda	150 \pm 66	2159 \pm 952	1376 \pm 657
Gastropoda	48 \pm 26	692 \pm 374	67 \pm 24
Diptera larvae	78 \pm 21	1127 \pm 304	5536 \pm 1173
Coleoptera larvae	8.5 \pm 2.5	123 \pm 36	167 \pm 36
Odonata larvae	0.7 \pm 0.2	10 \pm 3	151 \pm 56
Ephemeroptera & Trichoptera larvae	0.2 \pm 0.1	3 \pm 1	31 \pm 16
aquatic Coleoptera	13 \pm 2.6	191 \pm 37	33 \pm 10
Hemiptera	2.7 \pm 0.7	39 \pm 10	196 \pm 60
Ostracoda	153 \pm 109	2209 \pm 1,568	2394 \pm 1044
Copepoda	19 \pm 9.1	279 \pm 131	6070 \pm 1672
Cladocera	5.7 \pm 1.9	82 \pm 28	3906 \pm 1140
Conchostraca	0.7 \pm 0.3	10 \pm 4	468 \pm 338
Hydracarina	7.6 \pm 1.4	109 \pm 20	72 \pm 14
Hydra spec.	3.5 \pm 1.6	50 \pm 22	128 \pm 72
Collembola	4.5 \pm 1.9	65 \pm 27	8 \pm 3
terrestrial Arthropoda	2.6 \pm 0.6	38 \pm 9	21 \pm 14
Formicidae	79 \pm 44	1135 \pm 634	-
Isopoda	0.3 \pm 0.1	4 \pm 1	-

The male defends the nest site, and vigorously attacks every moving object in the direct surroundings of the nest (Winemiller 1987). Gautier *et al.* (1988) describe the aggressive behaviour of the male towards the female after oviposition in tanks. This aggressive guarding behaviour makes it possible in 74.5% of the nests containing eggs to catch the male with a 50 cm diameter scoop-net by gently beating the water surface above the net with a small stick. The large nests are usually built and guarded by large males (Fig. 4.4B). However, when defence is measured by the maximum distance from the nest where an attack on the stick can still be provoked, smaller males are more aggressive (Fig. 4.4C). The territory established by the male is defined as the defended area around the nest: a circle with an average radius of 57 cm (Table 4.1). The minimum distance recorded between two nests of *H. littorale* in rice fields is 3 m. In swamps the nests are generally built more than 10 m from each other.

Mark-recapture experiments with nest-guarding males of *H. littorale* in the swamps have so far not been very successful, possibly due to the crude marking method of clipping parts of the pectoral fin. At one nest site, however, a marked male was replaced by a second one that took over the nest site and nest material within a week after the hatching of the eggs. This second male constructed, after hatching of his first batch of eggs, a second nest at the same nest site, using the same nest material, thus demonstrating that males can build and guard more than one nest in a season. This experiment also shows that nests constructed at one nest site are not necessarily built by the same male.

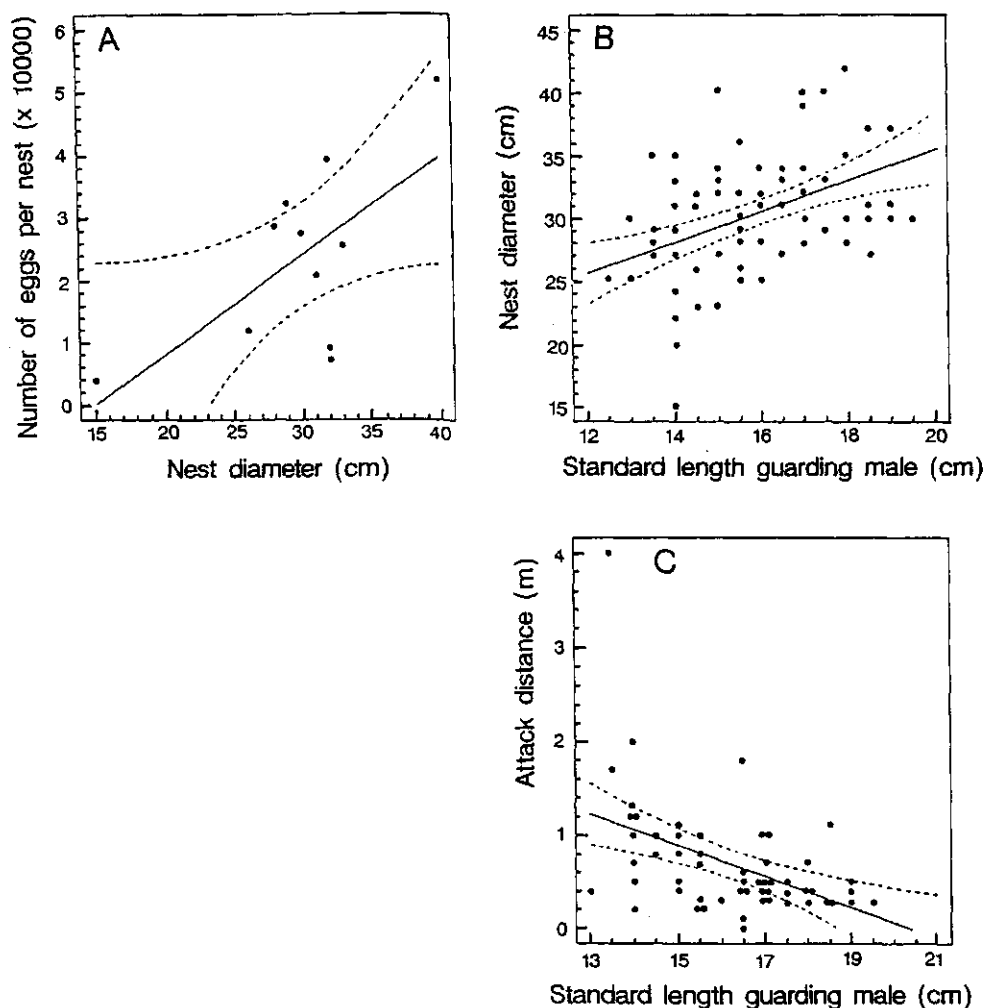


Fig. 4.4. A. Relationship between nest diameter of floating bubble nests of *Hoplosternum littorale* and the number of eggs nest⁻¹. The linear regression equation (\pm 95% confidence limits) is: $Y = -23,600 + 1574 X$; $r=0.64$ ($p=0.0327$).

B. Relationship between the size of nest-guarding males of *Hoplosternum littorale* and the diameter of the floating bubble nest. The linear regression equation (\pm 95% confidence limits) is: $Y = 10.8 + 1.23 X$; $r=0.45$ ($p=0.00006$).

C. Relationship between the size of nest-guarding males of *Hoplosternum littorale* and the distance from the center of the nest at which the male attacks a small stick gently beating the water surface. The linear regression equation (\pm 95% confidence limits) is: $Y = 3.37 - 0.16 X$; $r=-0.45$ ($p=0.00052$).

Table 4.3. Fecundity of three callichthyid catfish *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys* (mean \pm S.E.).

Weight class (g)	Frequency	Weight (g)	Standard length (cm)	Gonad weight (g)	Number of ripe eggs (≥ 1 mm)	Number of immature eggs (< 1 mm)
<i>H. littorale</i>						
30.0 - 60.0	4	52.5 \pm 3.69	10.9 \pm 0.2	5.49 \pm 1.44	2898 \pm 663	894 \pm 273
60.0 - 90.0	5	81.5 \pm 2.32	12.6 \pm 0.3	4.70 \pm 1.34	3598 \pm 956	431 \pm 235
90.0 - 120.0	7	99.5 \pm 3.06	13.7 \pm 0.2	10.05 \pm 1.21	6914 \pm 772	1141 \pm 467
120.0 - 150.0	2	133.1 \pm 7.05	15.0 \pm 0.2	19.60 \pm 6.00	10,596 \pm 5944	1432 \pm 561
	18	87.8 \pm 5.99	12.9 \pm 0.3	8.76 \pm 1.47	5509 \pm 868	922 \pm 213
<i>H. thoracatum</i>						
0.0 - 16.0	1	12.2	6.8	2.02	926	515
16.0 - 32.0	3	29.9 \pm 0.70	9.2 \pm 0.2	2.67 \pm 0.48	1667 \pm 847	527 \pm 331
32.0 - 48.0	11	43.1 \pm 1.04	10.5 \pm 0.2	5.00 \pm 0.28	2944 \pm 296	1246 \pm 415
48.0 - 64.0	6	53.3 \pm 1.80	11.2 \pm 0.3	5.68 \pm 1.18	2857 \pm 678	2011 \pm 616
64.0 - 80.0	1	68.6	12.0	3.20	1007	2350
	22	43.8 \pm 2.53	10.4 \pm 0.2	4.65 \pm 1.72	2566 \pm 284	1374 \pm 285
<i>C. callichthys</i>						
23.0 - 33.0	1	25.2	9.5	1.30	426	237
33.0 - 43.0	4	38.6 \pm 1.85	10.8 \pm 0.3	2.05 \pm 0.29	1636 \pm 294	3231 \pm 2336
43.0 - 53.0	6	49.8 \pm 0.73	12.3 \pm 0.1	4.00 \pm 0.53	1330 \pm 148	3429 \pm 528
53.0 - 63.0	4	57.5 \pm 1.93	12.7 \pm 0.1	4.93 \pm 1.16	2230 \pm 549	3504 \pm 1289
63.0 - 73.0	1	63.5	12.9	5.90	1708	2194
	16	48.2 \pm 2.57	11.9 \pm 0.3	3.61 \pm 0.46	1599 \pm 191	3122 \pm 659

2.2. The Nests of *Hoplosternum thoracatum*

2.2.1. Nest Construction, Oviposition and Incubation of the Eggs.

Nests of *Hoplosternum thoracatum* (Sur. catharina kwikwi) are built by the male in shallow swamps or swamp forests during the rainy season (Fig. 4.5). The nests are always located in the direct environment of a dicotyledonous tree or shrub (Fig. 4.6A). Nests were observed in the same periods as those of *H. littorale* (December - August), but *H. thoracatum* started nesting one or two weeks earlier than *H. littorale* (Mol in prep).

Actual construction of the nest of *H. thoracatum* by the male was not observed in the swamps, but detailed descriptions of observations in aquariums are reported (Schubert 1948; Zukal 1981; Burgess 1989). The nests do not have the complex structure of nests of *H. littorale* and nest building probably does not take much time. I suspect that nest building takes place shortly before oviposition because nests without eggs were rarely observed in the swamps.

I have confirmation of the time of oviposition for only four nests. In three nests oviposition was between 9.30-12.00 hours and in one nest eggs were deposited between 11.00 and 18.00 hours. It is quite possible, however, that oviposition is concentrated in the night or early morning because many nests with sticky eggs were observed between 7.00 and 8.00 hours.

Oviposition in nests of *H. thoracatum* is not limited to a single spawning session. Multiple successive spawnings are indicated by the many observations of the presence of eggs of more than one developmental stage in one nest at one point in time and by the large variation in the life-span of the nests (2-21 days). Nests with eggs of only one developmental stage have a life-span of two or three days and this seems to be a reasonable estimate of the incubation time of the eggs in the swamps. Only 17% of the 239 nests observed in the swamps did not acquire more than one spawning.

2.2.2. Nest Structure.

An illustration of a nest of *Hoplosternum thoracatum*, situated at the base of a swamp tree, is presented in Fig. 4.6A. The nests consist of 1-19 dicotyledonous leaves floating on top of a thin layer of foam on the water surface. The structure of the nest is revealed in Fig. 4.6B, representing a diagrammatic illustration of a cross-section through a frozen nest. The leaves of most nests originate from dicotyledonous trees. In the coastal plain of Suriname these are e.g. *Pterocarpus officinalis*, *Syzygium cumini*, *Triplaris surinamensis* and *Vochysia tetraphylla*. Rarely is a nest built under floating leaves of *Nymphaea* spec. The average thickness of the leaves is 0.5 ± 0.06 mm (mean \pm SE).

The eggs are glued firmly to the underside of the leaves of the nest. They are deposited almost in a mono-layer, embedded in foam and not in contact with the oxygen-depleted swamp water. Table 4.1 summarizes some selected data on the nests of *H. thoracatum*.

2.2.3. Number of Eggs, Spawnings per Nest and Parental Care.

The reproductive strategy of *Hoplosternum thoracatum* makes it difficult to arrive at a reliable estimate of the total number of eggs deposited in one nest. The male, distinguished from the female by the coracoids meeting ventrally (Fig. 4.6B), maintains the floating bubble nest for quite a long time. The mean life-span of a nest is 5.7 ± 0.2 days (Table 4.1), but nests of up to 12 days old are not uncommon. One nest even lasted for 21 days. During this period females spawn in the nest and one or more batches of eggs are always present. A nest without eggs is rarely observed.

The average number of eggs counted in a nest of *H. thoracatum* at one point in time is 3467 ± 342 (Table 4.1). Minimum and maximum numbers are respectively 1159 and 7715 eggs nest⁻¹. In 60% of the 20 nests examined, eggs of more than one developmental stage were present, indicating batches of successive spawnings. A nest which reveals at one point in time both recently deposited sticky eggs and eggs about to hatch, must have a life-span of at least five or six days. This happens to be the average life-span of the nests of *H. thoracatum* in the swamp (Table 4.1) and it means that the average number of eggs present in a nest at one point of time is probably representative for the average total number of eggs deposited in the nest. A conservative estimate of the maximum number of eggs nest⁻¹ for the nest which lasted 21 days is $3467 +$ the eggs of 5 spawnings. The mean fecundity of *H. thoracatum* is 1374 eggs female⁻¹ (Table 4.3) and thus an estimate of the maximum number of eggs nest⁻¹ must be 10,337 eggs nest⁻¹. The estimated mean and maximum number of spawnings per nest are respectively two and seven spawnings nest⁻¹. In general it is very difficult to compare these data for nests of *H. thoracatum* in the swamps with data on nest building in aquariums because of spatial and social limitations (number of available females) in captivity.

Fig. 4.7 shows that the number of eggs present in a nest at one point in time correlates with the total leaf surface available for oviposition. As the eggs are deposited almost in a mono-layer (Fig. 4.6B) and on average 91% of the available leaf surface is covered with eggs, this is not very surprising.



Fig. 4.5. Nest of *Hoplosternum thoracatum* in a swamp at Lelydorp, old coastal plain, Suriname.

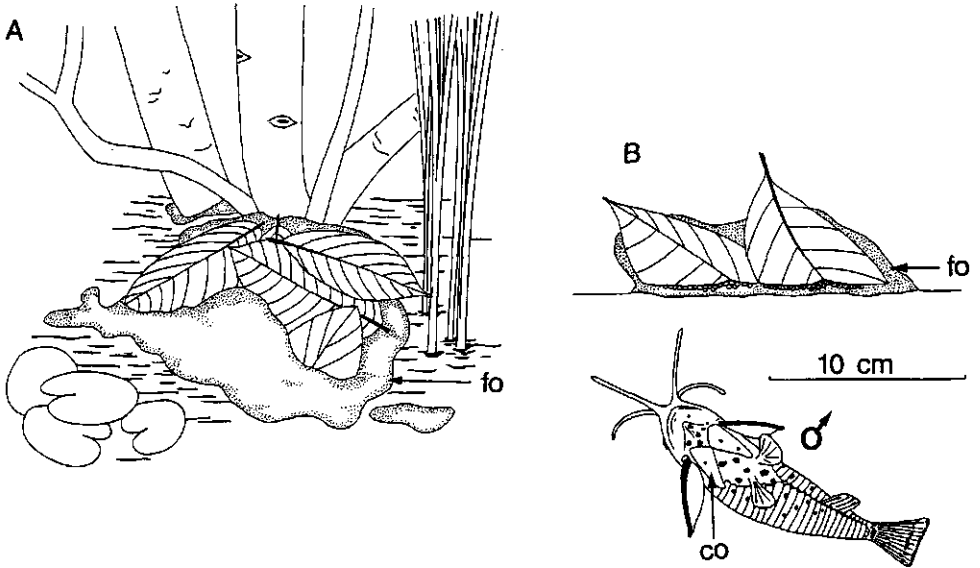


Fig. 4.6. The floating bubble nest of *Hoplosternum thoracatum*. A. The nest consisting of up to nineteen dicotyledonous leaves floating on top of a thin layer of foam (fo) on the water surface is built at the foot of a swamp tree. B. A cross-section of a frozen nest reveals the mono-layer of eggs glued to the underside of the leaves embedded in foam and not in touch with the oxygen-poor swamp water. Also note the two different developmental stages of the eggs in the nest. The guarding male, distinguished from the female by the ventrally meeting coracoids (co), is shown on its way to the surface to supply new foam to the nest.

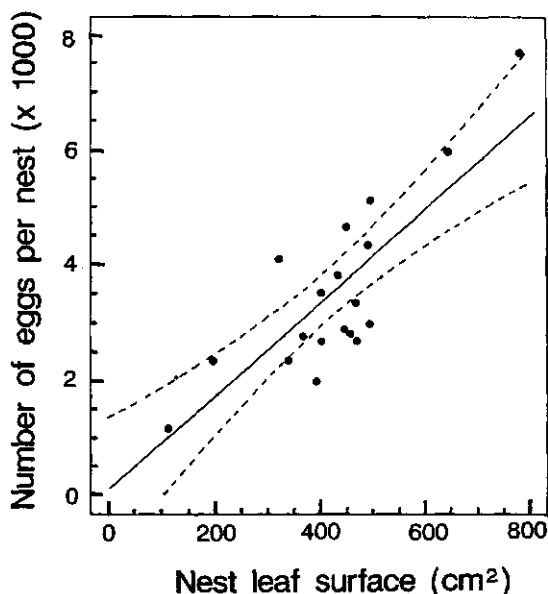


Fig. 4.7. Relationship between total leaf surface of floating bubble nests of *Hoplosternum thoracatum* and the number of eggs nest⁻¹. The linear regression equation (\pm 95% confidence limits) is: $Y = 99.4 + 8.2 X$; $r=0.83$ ($p=0.00001$).

The nest-guarding male of *H. thoracatum* is not very aggressive. Compared to *H. littorale* only 9 males out of 209 nests tested (4%) displayed attack behavior. Males of *H. thoracatum* probably do not establish a territory of the size realized by *H. littorale* because nests in the swamps are often built within 50 cm of each other. Fig. 4.6B shows the guarding male on its way to the nest in order to supplement the nest with fresh foam.

2.3. The Nests of *Callichthys callichthys*

2.3.1. Nest Construction, Oviposition and Incubation of the Eggs.

The nests of *Callichthys callichthys* (Sur. platkop or plata-edé kwikwi) are built by the male near the very edge of shallow swamps and swamp forests. Most nests of *C. callichthys* are located in very shallow water, in cavities of earth and tree roots (Fig. 4.8). Taking into account the size of *C. callichthys* (Table 4.1) it is hard to believe one's eyes when a nest of this species is detected in a shallow and small cavity of tree roots (Fig. 4.8A and 4.8C) or in an isolated pool just 30 cm in diameter and only accessible through a narrow underwater corridor (Fig. 4.8B). In fact, characteristics of the nest site microhabitat are the most reliable field marks in distinguishing the nests of *C. callichthys* from those of *H. thoracatum* (Mol in prep). Confirmation of the nest-building species was obtained for 31 of the 85 nests of *C. callichthys* observed, mostly by rearing the newborn larvae in the laboratory. Nests were observed from mid-December to August when the swamps were flooded (Mol in prep).

Construction of the nests of *C. callichthys* by the male was not observed in the swamps, but observations of nest building and spawning in aquariums are reported by Breder & Rosen (1966). The structure of the nest is very simple and nest building is probably completed in a short period preceding oviposition.

Twice oviposition of *C. callichthys* was actually observed in the swamps of Lelydorp, both times between 8.15 and 8.45 hours in the morning. In two nests oviposition was between 18.00 and 7.00 hours and once oviposition was recorded between 8.30 and 10.00 hours. Oviposition is not strictly limited to a single spawning session as was observed for *H. littorale*. Multiple successive spawnings are indicated by the variation in life-span of the nests (2-17 days), but most nests examined displayed eggs of only one developmental stage. It seems that in nests of *C. callichthys* spawning only takes place after a preceding batch of eggs has hatched. The incubation time of the eggs is probably between two and three days (Table 4.1), which means that 30% of the 85 nests observed in the swamps acquired more than one spawning.

2.3.2. Nest Structure.

Fig. 4.8A shows a nest of *Callichthys callichthys* floating on the water surface and partly hidden in a cavity of tree roots. The structure of the nest, as revealed by cross-sections through a frozen nest, is very similar to the structure of nests of *H. thoracatum* (Fig. 4.6B). The only major difference I could detect is the irregular clustering of eggs at the underside of the leaves of nests of *C. callichthys* in contrast with the almost perfect mono-layer of eggs in nests of *H. thoracatum* (Fig. 4.9). The slipshod deposition of eggs in nests of *C. callichthys* is probably a consequence of the lack of freedom of movement for the spawning female(s) at the nest site (see Fig. 4.8B, 4.8C and 4.8D) and the lack of available leaf surface in the nest. The average number of eggs cm⁻² of leaf surface is 9.8 ± 0.75 (mean \pm SE) for nests of *H. thoracatum* and 22.5 ± 6.06 for nests of *C. callichthys*, the difference being significant (t-test, $p < 0.05$). Selected characteristics of the nests of *C. callichthys* are summarized in Table 4.1.

2.3.3. Number of Eggs, Spawnings per Nest and Parental care.

The average number of eggs present at one point in time in the nests of *Callichthys callichthys* is 2953 ± 762 (Table 4.1). Minimum and maximum numbers recorded are 237 and 8474 eggs nest⁻¹, respectively. Data on the fecundity of *C. callichthys* are summarized in Table 4.3. The average number of ripe eggs per female is 1599 ± 191 .

As already noted for nests of *H. thoracatum*, these figures are not representative for the total number of eggs spawned in a nest. Contrary to nests of *H. thoracatum*, the 16 nests of *C. callichthys* examined in the laboratory only contained eggs of one developmental stage. Surveys in the swamp confirmed that nests with eggs of more than one developmental stage are very rare, although a few of such nests were observed. Nests without eggs are also uncommon and it seems that following hatching of a batch of eggs, the nests are either abandoned or obtain a new spawning shortly afterwards. With knowledge of the mean hatching time of the eggs in the swamp and the mean life-span of the nests, it is possible to calculate the total number of eggs spawned in one nest from the number of eggs present at one point in time as 5433 eggs nest⁻¹. An estimate of the maximum number of eggs per nest

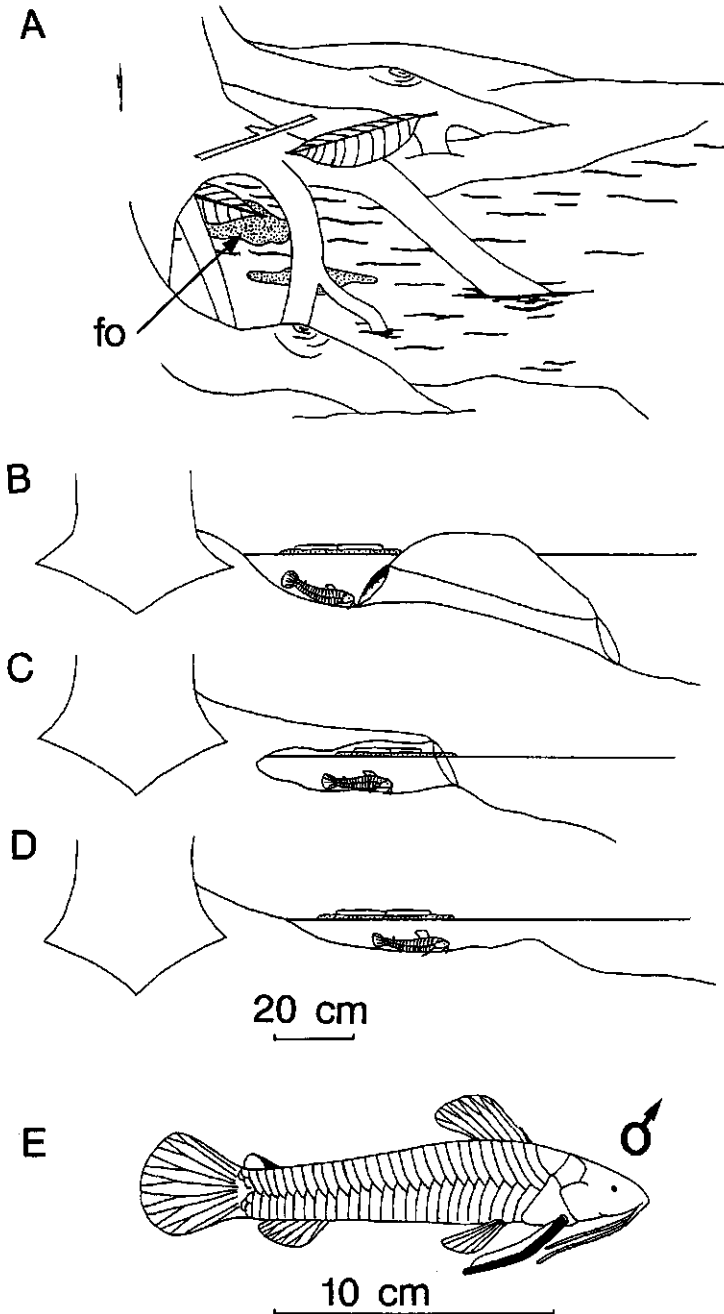


Fig. 4.8. The floating bubble nest of *Callichthys callichthys*. A. The very simple nest consists of a few dicotyledonous leaves floating on top of a thin layer of foam (fo) on the water surface. The nest is often constructed in very shallow water near the edge of the swamp and in cavities of tree roots. B, C, D. Some examples of habitats where nests of *C. callichthys* were found. E. Guarding male.



Fig. 4.9. Irregular clustering of eggs at the underside of a leaf from a nest of *Callichthys callichthys* (right) and eggs deposited in a mono-layer in a nest of *Hoplosternum thoracatum* (left).

obtained from the nest with a life-span of 17 days is 20,080. Mean and maximum number of spawnings per nest are three and twelve, respectively.

With nests of *C. callichthys* a significant linear relationship between the number of eggs that are present in the nest at one point in time and the leaf surface of the nest was not present (ANOVA, $p=0.26$) and this is not very surprising taking into account the irregular deposition of the eggs in these nests.

The male of *C. callichthys* guards the nest after finishing its construction. In the swamps guarding males displayed the attack response with only 7% of the nests examined.

3. Function of the Foam Nest

3.1. Foam Nests of Insects, Frogs and Fishes

The construction of a foam nest is reported for insects (Richards & Davies 1977), frogs (Duellman & Treub 1986) and fishes (Balon 1975). Table 4.4 summarizes the data on foam nest construction in the animal kingdom.

Insect foam nests produced by the female during oviposition (oothecae) are attached to twigs, bark, walls and other objects by mantids or buried in the ground by grasshoppers (Richards & Davies 1977). The frothy excretion of the female is viscid and very rapidly hardens to the consistency of a spongy substance. A second type of foam nest is produced by the nymphs of the families Cercopidae and Aphrophoridae. The nymphs of these 'cuckoo

Table 4.4. Construction of foam nests in the animal kingdom. In parentheses the number of species that built foam nests.

Classis Ordo Familia Genus	Producer of foam	Parental care after construction of foam nest	Geographical distribution	References
INSECTA				
Dictyoptera				
Empusidae	♀	-	Old world	Richards & Davies 1977
Mantidae	♀	-	Cosmopolitan	Richards & Davies 1977
Orthoptera				
Acrididae	♀	-	Cosmopolitan	Richards & Davies 1977
Pygomorphidae	♀	-	Old world	Richards & Davies 1977
Homoptera				
Aphrophoridae	nymph	-	Cosmopolitan	Richards & Davies 1977
Cercopidae	nymph	-	Cosmopolitan	Richards & Davies 1977
OSTEICHTHYES				
Siluriformes				Breder & Rosen 1966
Callichthyidae (5)	♂	♂	S. America	Burgess 1989
Callichthys (1)	♂	♂	S. America	Breder & Rosen 1966
Dianema (2)	♂	♂	S. America	Petrovicky 1979
Hoplosternum (2)	♂	♂	S. America	Carter & Beadle 1931
Cypriniformes				
Characidae (1)				
Hepsetus odoe	♂+♀	♂+♀	Africa	Merron et al. 1990
Synbranchiiformes				
Synbranchidae (1)				
Monopterus (Fluta)	?	♀(?)	S. Asia	Vogt 1970
Perciformes				
Belontiidae (23)			S. Asia	Richter 1979
Belontia (2)	♂	♂+♀	S. Asia	Richter 1979
Macropodus (2)	♂	♂ (+♀)	S. Asia	Breder & Rosen 1966
Pseudosphromenus (2)	♂	♂	S. Asia	Richter 1979
Malpulutta (1)	♂	♂	S. Asia	Richter 1979
Betta (6)	♂	♂	S. Asia	Breder & Rosen 1966
Trichopsis (3)	♂	♂	S. Asia	Breder & Rosen 1966
Trichogaster (4)	♂	♂	S. Asia	Breder & Rosen 1966
Colisa (3)	♂	♂	S. Asia	Breder & Rosen 1966
Anabantidae (4)				
Ctenopoma (4)	♂	♂	Africa	Richter 1979
Nandidae (1)				
Polycentropsis (1)	♂	♂	Africa	Scherpe 1981
AMPHIBIA, ANURA				
Leptodactylidae	♂		S. America	Duellman & Treub 1986
Adenomera	♂	-	S. America	Heyer 1969
Edalorhina	♂	?	S. America	
Leptodactylus	♂	?	S. America	
Lithodytes	♂	?	S. America	
Physalaemus	♂	?	S. America	
Pleurodema	♂	?	S. America	
Myobatrachidae	♀		Australia	Martin 1970
Adelotus	♀	♂	Australia	
Heleioporus	♀	?	Australia	
Kyarranus	♀	-	Australia	
Lechriodus	♀	?	Australia	
Limnodynastes	♀	?	Australia	
Megistolotis	♀	?	Australia	
Philoria	♀	?	Australia	
Rhacophoridae				Duellman & Treub 1986
Chirixalus	?	?	Africa/Asia	
Chirromantis	♂+♀	♀	Africa	
Philautus	?	?	Asia	
Polypedates	?	?	Asia	
Rhacophorus	?	?	Asia	
Hyperoliidae				Duellman & Treub 1986
Opisthothyax	?	?	Africa	

spit' insects envelop themselves in froth on plants (Richards & Davies 1977). Richards & Davies (1977) suggest that the foam may protect eggs and nymphs from predation by birds or lizards and from desiccation in the sun. The nests did not offer protection against parasitic Hymenoptera.

Within the Anura, Duellman & Treub (1986) distinguish five modes of reproduction which include the construction of a foam nest. Nests are constructed on the water surface of permanent water bodies, in small temporal pools next to a stream, in burrows next to ponds or streams (aquatic tadpoles), in burrows with tadpoles completing their development in the nest and in trees with hatching tadpoles dropping into the water. The overall evolutionary trend within these five modes of reproduction toward terrestriality, associated with avoidance of aquatic predation on eggs and larvae, is beautifully demonstrated in the families of Leptodactylidae (Heyer 1969) and Myobatrachidae (Martin 1970). Gorzula (1977) stresses the thermal properties of the foam in preventing extreme temperatures during development. A third function of the foam might be protection of eggs and larvae from desiccation (Heyer 1969). Duellman & Treub (1986) mention experimental evidence of growth-inhibiting properties of the foam. Heyer (1969) describes the viscosity of leptodactylid foam as having the consistency of beaten egg-white with some hardening of the outer layer.

Balon (1975) defines the aphrophilic reproductive guild of fishes and reports the building of foam nests for the African pike *Hepsetus odoe*, the callichthyids *Hoplosternum* and *Callichthys* and a number of anabantoid species. To this list may be added the nandid *Polycentropsis abbreviata* (Scherpe 1981), the synbranchiid *Monopterus alba* (Vogt 1970) and two species of the callichthyid genus *Dianema* (Petrovicky 1979). A number of functions of the foam nest have been proposed (Breder & Rosen 1966; Machado-Allison & Zaret 1984; Hostache *et al.* in press):

1. oxygen reservoir for eggs and newborn larvae
2. protection against predation (fishes and aquatic insects)
3. thermal properties in relation with incubation of the eggs
4. regulation of microbial growth
5. concealment of previous spawns to courting females
6. protection of eggs from sunlight (desiccation)
7. depot for deposition of the eggs
8. anchor of eggs amid plants.

Protection of eggs from desiccation by the foam (6) is mentioned for insects, anurans and fishes. This function of the foam seems very important for aquatic organisms depositing their eggs out of the water. Most nests do function as a depot for deposition of eggs (7). It is possible that properties of the foam, e.g. its stickiness, help in keeping the eggs together (Heyer 1969). The floating bubble nest of fishes may anchor the eggs amid plants (8). However, the eggs of foam-nesting anabantoids and callichthyids have a higher density than water (Richter 1979; Burgess 1989), making drift of eggs unlikely. In absence of the foam, these eggs would sink to the bottom.

3.2. Oxygen Supply to the Developing Eggs

Bagenal & Braum (1978) consider oxygen, temperature and waterflow ecological features of fundamental importance for the development and survival of fish eggs. There is a close relationship among these three parameters. In mountain streams with a strong water

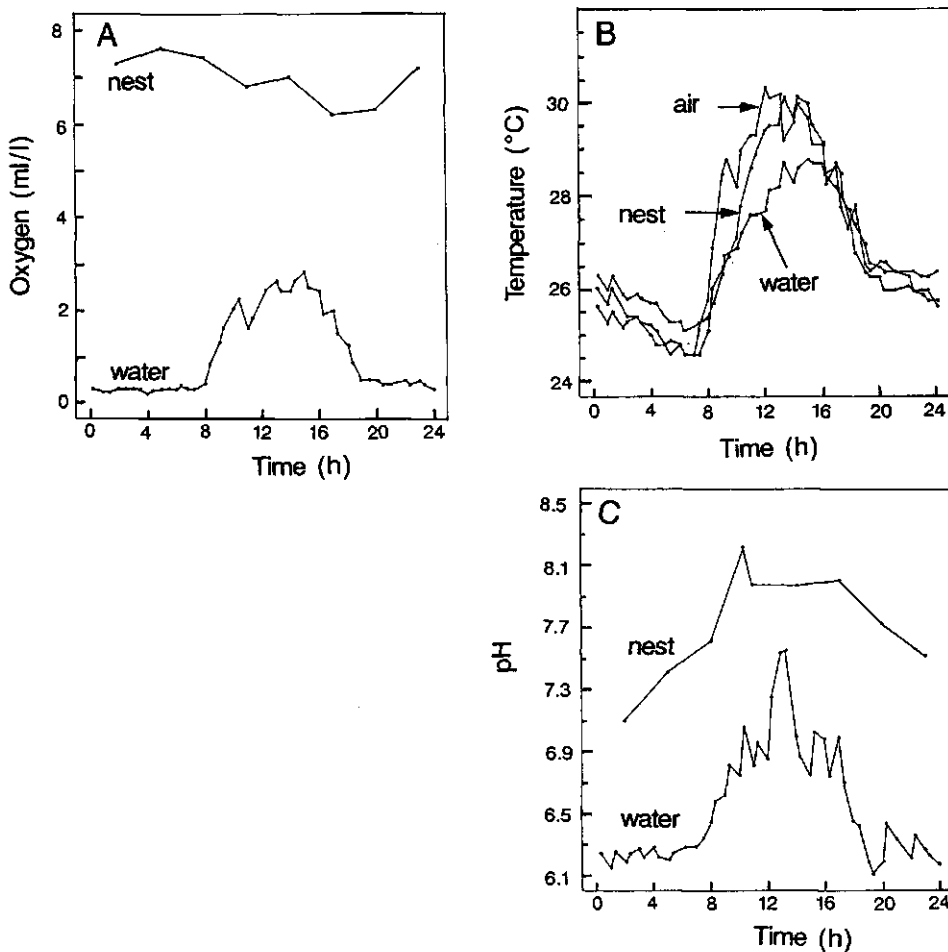


Fig. 4.10. Diurnal fluctuations of oxygen (A), temperature (B) and pH (C) during incubation of eggs of *Hoplosternum littorale*. Recordings are 5 cm under the water surface, in the foam next to the incubating eggs and 50 cm above the water surface in the shade (temperature only) on a warm and cloudless day without rain (27th January 1990).

current, oxygen is continuously supplied to developing eggs (e.g. of salmonids). If waterflow is not present, fishes can create a current over their eggs by fanning their fins (e.g. cichlids). However, if high temperatures and decaying organic materials cause oxygen to be absent, as in tropical standing waters, developing eggs are in trouble. Carter & Beadle (1931) point out that the structure of the nest of *Hoplosternum littorale* may assist in the supply of oxygen to the developing eggs and larvae in an aquatic environment without dissolved oxygen.

Cross sections through frozen nests of *H. littorale* (Fig. 4.3B), *H. thoracatum* (Fig. 4.6B) and *C. callichthys* reveal the eggs embedded in foam above the water surface. Fig. 4.10 illustrates the results of measurements of oxygen (Ag/Pt electrode), temperature and pH

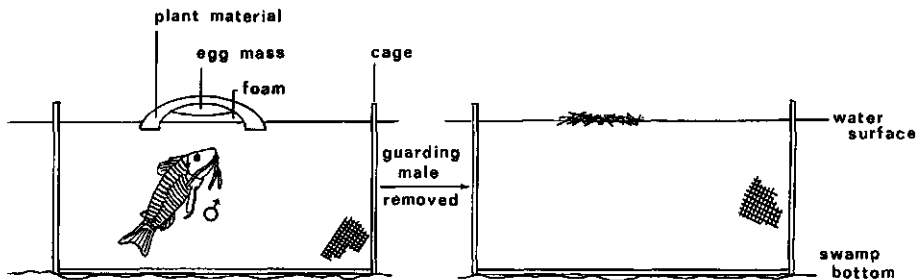


Fig. 4.11. Experiment demonstrating the effect of removing the nest-guarding male on the development of the eggs of *Hoplosternum littorale*. A cage of mosquito mesh (1.0 x 0.5 x 0.5 m) prevents disturbance from intruders. One day after removing the guarding male the nest, out of shape, flattens on the water surface. The eggs deteriorate after contact with the oxygen-depleted swampwater.

during a 24 hour period in the foam of a nest of *H. littorale*, in the swamp water next to the nest and in the air above the nest. In close agreement with measurements by Carter & Beadle (1930) in the Paraguayan Chaco, Fig. 4.10A shows the little oxygen present in the water during the day (photosynthesis) absent at night. The foam in this period is 86% oxygen-saturated and a significant difference in oxygen content between day and night was not present (t-test, $p=0.53$). Analyses of the foam at the Academic Hospital of Paramaribo confirm the measurements in the field (partial pressure of O_2 is 179.9 mm Hg cm^{-2} at 37°C, pH is 7.82). Observations during this experiment revealed the guarding male regularly supplying fresh foam to the nest.

In a second experiment the removal of the guarding male from the nest resulted in the immediate deterioration of both the nest and its eggs (Fig. 4.11). Hostache *et al.* (in press) demonstrate hatching of eggs of *H. littorale* in conical incubators with a continuous flow of oxygen-saturated water. The deterioration of the eggs after contact with swamp water is probably caused by oxygen deficiency (see Fig. 4.10A).

The male produces foam rich in oxygen, which keeps the nest in shape and the eggs out of the oxygen-depleted swamp water. The question remains whether the foam just lifts the eggs out of the swamp water in the oxygen-rich air or if it has a more direct function in the oxygen supply to the eggs. In nests of *H. thoracatum* atmospheric oxygen must diffuse through a 0.5 mm thick leaf with closed stomata in order to reach the eggs. In rainy weather oxygen must cross a 1 cm thick layer of water-soaked plant material in nests of *H. littorale* on its way to the egg mass. On the other hand, callichthyids are well-known for their aerial respiration (Carter & Beadle 1931; Johansen 1970; Gee & Graham 1978) and they are probably able to produce foam rich in oxygen by gulping air at the surface.

In order to detect a possible function of direct oxygen supply to the eggs through the foam, a nest of *H. littorale* was sealed from atmospheric oxygen by positioning a plastic basin upside down over the nest at 07.00 hours on the first day after oviposition (Fig. 4.12).

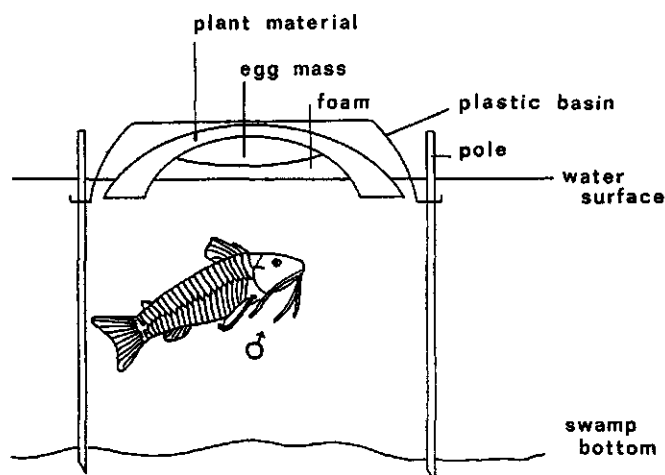


Fig. 4.12. Experiment with nest of *Hoplosternum littorale* sealed from atmospheric oxygen by means of a plastic basin positioned upside down above the nest. The eggs hatch as usual on the third day after oviposition, demonstrating that oxygen in the foam produced by the guarding male, is provided to the developing eggs (see text).

Development of the eggs proceeded normally during the 48 hours the eggs were excluded from atmospheric oxygen. Experiments of Braum (1978) demonstrate that oxygen consumption of fish eggs increases as development proceeds. Following Braum (1978) it is estimated that the eggs of *H. littorale* use 80% of the oxygen needed for their development in the last 48 hours before hatching. Using a Q_{O_2} of $1.5 \mu\text{g O}_2 \text{ mg dry-weight}^{-1} \text{ hour}^{-1}$ (Blaxter 1969), the total oxygen consumption of the egg mass with a mean dry weight of 13.05 g (Table 4.1) during the experiment is calculated as 1.13 liter of oxygen. A second estimate based on an average oxygen consumption during development of $100 \mu\text{l egg}^{-1}$ (Blaxter 1969) results in a total oxygen consumption of the egg mass of 1.87 liter of oxygen. If the foam does not take part in the oxygen supply to the eggs, at least the conservative estimate of 1.13 liter O_2 must be supplied by the air enclosed between the nest and the basin. The amount of oxygen present in the air enclosed in the basin is between 0.637-0.768 liter, depending on the percentage of water vapor in the air and the amount of air present in the outer layer of the nest. The experiment demonstrates that the oxygen available in the air enclosed by the basin was not sufficient for the development of the eggs and that additional oxygen must have been provided, presumably by the regular supply of fresh foam by the guarding male. The oxygen consumed by the nest fauna (Table 4.2) and by the micro-organisms in the decaying nest material is not taken into account.

It seems that the primary function of the foam nest of fishes is associated with the supply of oxygen to the eggs. A close relation exists between the foam nesting habit and the habitat of the fishes that build these nests. The African pike *Hepsetus odoe* is known from

swamps and slow flowing rivers (Merron *et al.* 1990). The five callichthyinids are also able to survive oxygen-depleted standing waters (Carter & Beadle 1931; Burgess 1989). Of the 25 foam nest building anabantoids for which a description of the habitat is available (Richter 1979), 84% lives in standing or slow flowing water with dense aquatic vegetation. A good description of a habitat of foam nest building anabantoids (where *Monopterus alba* (Synbranchidae) was collected as well) is provided by Furtado & Mori (1982). In addition, callichthyinids, anabantoids and synbranchyids are adapted to an oxygen-depleted aquatic environment by supplementary respiratory organs (Carter & Beadle 1931; Johansen 1970).

3.3. Protection Against Predators

Avoidance of aquatic predation by small fishes and aquatic insects is considered the primary driving force behind the evolutionary trend towards terrestrial reproduction in frogs (Duellman & Treub 1986). Heyer (1969) and Martin (1970) discuss the trend toward terrestriality and the function of the foam nest in the families Leptodactylidae and Myobatrachidae with respect to protection against aquatic predators.

Balon (1975) states that two factors play a leading role during embryonic development of fish eggs: predation and the availability of oxygen. In many families of freshwater fishes the construction and defence of a nest is quite common (Breder & Rosen 1966). All species belonging to the aphrophilic reproductive guild of Balon (1975) continue parental care after construction of the foam nest and oviposition (Table 4.4). This additional parental care always includes the maintenance and defence of the nest and sometimes removal of eggs infected with micro-organisms and defence of newborn larvae (Vogt 1970; Richter 1979; Scherpe 1981; Burgess 1989; Merron *et al.* 1990).

All nests of fish guarded by one or both parents probably offer some protection against predation, but the structure of the floating foam nest does not necessarily improve this protective function. The rich fauna of the nests of *H. littorale* collected in the swamp (Table 4.2) indicates that at least small potential predators are not effectively expelled from the nest. Nymphs of Odonata (Hostache *et al.* 1990), Hemiptera (pers. obs.) and possibly Coleoptera larvae predate on larvae of *H. littorale*. Two nests even yielded a juvenile of the swamp eel *Synbranchus marmoratus* also known to predate on larvae of *H. littorale* (Singh 1978). Moreover, the floating foam nest places terrestrial predators like egrets and snakes in a favourable position to prey upon the eggs.

Foam nests of leptodactylid frogs were sometimes observed floating on the swamp near nests of *H. thoracatum*, *C. callichthys* and *H. littorale*. However, the stickiness and consistency of the foam of the leptodactylid nests probably offers excellent protection against both aquatic and terrestrial predation (Heyer 1969).

3.4. Thermal Properties of the Foam Nest

Hostache *et al.* (in press) used conical incubators and oxygen saturated water to determine the relation between incubation temperature and hatching time of eggs of *Hoplosternum littorale*. The minimum hatching time of 36.4 hours was associated with an incubation temperature of 33.6° C, but incubation temperatures above 35° C already proved

lethal to the developing eggs. Eggs and larvae survived without problems at incubation temperatures as low as 24° C, the lowest temperature tested, and this is not surprising if the geographical distribution of the species is considered (south to Buenos Aires in northern Argentina (Burgess 1989; Mol in prep)).

Fig. 4.10B shows temperatures measured during a 24 hour period in the nest of *H. littorale*, in the swamp water around the nest and the air above the nest. The diurnal fluctuation of the temperature in the air is, to some degree, damped in the nest. Compared to the air temperatures, nest temperatures are low in daytime and high at night. The results differ in some respects from measurements by Hostache *et al.* (in press) in and around nests of *H. littorale* in fish ponds in French Guiana. In these ponds, emptied of aquatic vegetation, very high nest temperatures are recorded in daytime resulting in diurnal fluctuations up to 11° C (Hostache *et al.* in press). The average hatching time of 51 hours recorded in the ponds is also relatively short compared with the approximately 72 hours incubation in the swamps of Suriname (Fig. 4.2). However, it is my impression that the nests of *H. littorale* in the fish ponds of Socoumou, French Guiana, are not of the same size and nest materials as the nest in the Surinamese swamps (pers. obs.). I think it probable that in the swamps the aquatic vegetation surrounding the nest and the large quantities of nest materials used in the construction of the nest (see Table 4.1) account for the damping of extreme temperatures as shown in Fig. 4.10B.

Hostache *et al.* (in press) propose a brooding effect of the structure of the nests of *H. littorale* based on the high nest temperatures measured in the ponds. However, if it is lethal to the eggs if they are exposed for length to temperatures above 35° C, prevention of such extreme temperatures, not rare in the swamps, seems to me of more importance. Gorzula (1977) demonstrated a cooling effect of the foam of nests of leptodactylid frogs and stressed the function of the foam in the damping of extreme temperatures in the environment of foam nests exposed to intense sunlight. In addition to cooling the nest in daytime, the foam may also keep the nest temperature from falling very low at night, speeding up the development of the eggs. The nests of *H. thoracatum* and *C. callichthys* are often built in the shade of a dicotyledonous tree and probably do not experience the extreme temperatures of the open grass swamp.

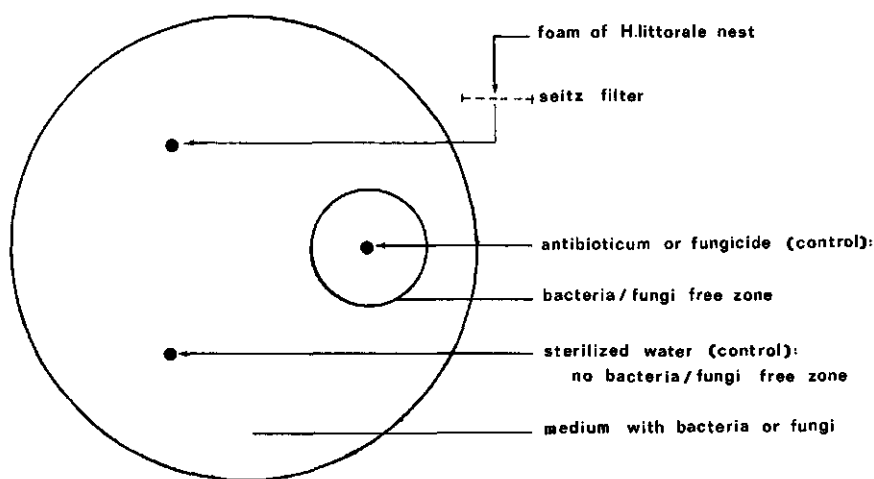
3.5. Properties of the Foam in Relation to Microbial Growth

Balon (1975) suggests that the foam produced by fish of the aphrophilic reproductive guild may attract micro-organisms on which the larvae can feed. Braum (1978) discusses the detrimental effect of fungi and bacteria on fish eggs. Duellman & Treub (1986) mention experimental evidence of growth-inhibiting properties of foam of frogs' nests.

The observation that eggs of *H. littorale* deteriorate after the male was removed from the nest (Fig. 4.11) did raise the question whether an attack by micro-organisms, made possible by the absence of protective foam, caused the decay of the eggs. To detect antimicrobial properties of the foam the sensitivity of nine species of bacteria and two species of fungi (Table 4.5) to foam of nests of *H. littorale* sterilized with a Seitz filter was tested with a modified agar-diffusion method (Fig. 4.13). As shown in Table 4.5 the experiments failed to detect any anti-microbial action of the foam.

Table 4.5. Results of agar-diffusion sensitivity tests of sterilized foam of nests of *Hoplosternum littorale*.

Test micro-organism	Culture conditions			Sensitive to foam of <i>H. littorale</i>
	Substrate	Temperature (°C)	pH	
Laboratory stock-culture bacteria				
<i>Escherichia coli</i>	BBL-Mueller/Hinton	37	7.0	no
<i>Proteus spec.</i>	BBL-Mueller/Hinton	37	7.0	no
<i>Haemophilus influenzae</i>	Chocolate agar	37	7.0	no
<i>Staphylococcus spec.</i>	Trypticase soy agar	37	7.0	no
<i>Streptococcus pyogenes</i>	Trypticase soy agar	37	7.0	no
Bacteria isolated from swampwater				
<i>Pseudomonas spec.</i>		35	7.0	no
species A (gram negative rod)		35	7.0	no
species B (gram negative rod)		35	7.0	no
species C (gram negative rod)		35	7.0	no
Fungi				
<i>Aspergillus niger</i>	PDA	30	5.6	no
<i>Penicillium spec.</i>	PDA	30	5.6	no

Fig. 4.13. Agar-diffusion sensitivity test for antimicrobial action of foam of floating bubble nests of the callichthyid catfish *Hoplosternum littorale*. The test is considered positive if a bacteria/fungi free zone is detected around the pit with foam.

It is possible that the foam attracts micro-organisms in the way the decaying nest material certainly does, but I do not think that the newly hatched larvae feed on this microflora. The larvae start feeding two days after hatching when their yolk sac is consumed (Machado-Allison 1986; Mol in press), but at this point in time they have already moved to the bottom of the swamp. One day after hatching of the eggs of *H. littorale* the larvae are rarely seen at the nest site and foam is never present.

3.6. Concealment of Previous Spawns

Machado-Allison & Zaret (1984) point out that the structure of the foam nest of *H. littorale* allows the male to conceal the presence of previously deposited eggs from courting females. While it is certainly possible that the foam hides the eggs in a nest from the view of courting females, this property of the foam is probably irrelevant to multiple spawnings of *H. littorale* which all take place at the same time. *Hoplosternum thoracatum*, and to a lesser extent *C. callichthys*, do spawn at successive intervals in one nest as is revealed by the presence at one point in time of eggs of more than one developmental stage. Consequently, concealment of previous spawns by the foam might have some importance to the guarding male of these species.

4. The Nests of *Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys* Compared

The foam nests of the three related armoured catfishes of the subfamily Callichthyinae discussed in this text share many important characteristics, but also differ in a number of striking features.

All three species deposit their eggs in foam nests out of the oxygen-poor water under a cover of plant materials. Multiple spawns are deposited in the nests. The nests are constructed and guarded by the male, the most common form of parental care in bony fishes (Blumer 1979; Baylis 1981). For all three species nesting starts with the flooding of the swamps and reproductive activities continue until the swamps dry up (Mol in prep). The eggs are more or less of the same size, and hatching times are probably quite similar (Table 4.1).

The main difference is between the nests of *Hoplosternum littorale* on the one hand and those of *Hoplosternum thoracatum* and *Callichthys callichthys* on the other hand. The nest of *H. littorale* is constructed from larger quantities of plant material than the nests of *H. thoracatum* and *C. callichthys* (ANOVA, $p < 0.0001$). The latter two species use dicotyledonous leaves as construction material, while *H. littorale* prefers grass, *Typha*, twigs and other filamentous materials. In selecting a suitable nest site *H. littorale* is not dependent on the presence of dicotyledonous trees. *Hoplosternum thoracatum* and *C. callichthys* rarely build their nests in open herbaceous swamps (but a few nests under leaves of a water-lily were observed). The number of eggs deposited in nests of *H. littorale* is larger than the numbers of eggs per nest recorded for *H. thoracatum* and *C. callichthys* (ANOVA, $p < 0.0001$). It is also striking that in nests of *H. littorale* all eggs are spawned at the same time, resulting in a relatively shorter life-span of the nest than recorded for nests of *H. thoracatum* and *C. callichthys*.

Nests of *H. thoracatum* and *C. callichthys* differ in the microhabitat at the nest site. Although the number of eggs per nest is very similar for both species, nests of *C. callichthys* are smaller with respect to the material used in the construction of the nest. T-tests show dry weight of nest material ($p < 0.0001$), the number of leaves per nest ($p < 0.0001$) and leaf surface area ($p < 0.0001$) to be significantly different. Overlap of successive spawnings, measured as the percentage of nests with eggs of more than one developmental stage, is characteristic of nests of *H. thoracatum* (60%) but is almost absent in nests of *C. callichthys*.

The foam nests of the three callichthyid catfishes represent an adaptation to oxygen-depleted water. In Suriname, deoxygenation is generally associated with standing waters of the coastal plain (see Mol 1993). The distribution of *H. littorale* is limited to this type of water (Mol in prep). *Hoplosternum thoracatum* and *C. callichthys* inhabit coastal plain standing waters too, but are restricted to habitats where trees are present, e.g. swamp forests.

Although the foam nesting habit probably evolved in oxygen-poor tropical standing waters, *H. thoracatum* and *C. callichthys* are also well represented in the fish fauna of rainforest creeks in the interior of Suriname (Mol in prep). The rugged landscape of the interior is characterized by steep slopes and rocky or stony soils. Surface runoff after heavy local rains creates an unpredictable and violent increase of water velocity in these headwater streams (Gray and Wigham 1970; Noordam 1993). Small streams often rise suddenly overnight but cease to flow shortly after the rains and are then reduced to interconnected pools. Swift currents may easily sweep away the floating bubble nests of *H. thoracatum* and *C. callichthys*. However, even in these headwater streams quiet backwaters and obstacles that block the current provide some lentic habitats. *Callichthys callichthys* probably avoids nesting in turbulent water by building its nests near the shore in very shallow water where drag reduces velocities (Gray and Wigham 1970) or in relatively calm water in cavities of tree roots. *Callichthys callichthys* is even collected in brooks in the Peruvian Andes (Lowe-McConnell 1987).

In the extreme biotope of headwater creeks it must be of adaptive advantage to produce several batches of eggs where the first may be endangered by unpredictable fluctuations in water velocity during peak flow events (Horn & Rubenstein 1984). Both *H. thoracatum* and *C. callichthys* reduce the risk of losing large quantities of eggs by building flexible nests and spreading successive spawnings in time. If a nest of *H. thoracatum* or *C. callichthys* is swept away by the current, the loss is not as serious as might have been if the strategy of simultaneous spawning of *H. littorale* was adopted. As long as conditions are favourable the nests of *H. thoracatum* and *C. callichthys* are prolonged in time.

In the extensive swamps of the flat coastal plain swift water currents and sudden changes in water level are out of question (see Amatali 1993). Seasonal flooding is generally non-catastrophic and under these more stable conditions an aggressive defence of a large reproductive investment becomes profitable. The elaborate nests of *H. littorale* and the establishment of a well-defended territory are probably associated with the predictability of the aquatic environment in the coastal plain.

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Chapter 5

Reproductive seasonality and nest-site differentiation in three closely related armoured catfishes (Siluriformes: Callichthyidae)

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Mol, J.H., in press. Reproductive seasonality and nest-site differentiation in three closely related armoured catfishes (Siluriformes: Callichthyidae). Accepted by *Environmental Biology of Fishes*.

Abstract

Three sympatric, closely related armoured catfishes showed a similar, bimodal breeding season in coastal plain swamps in Suriname (South America). The bimodal pattern of reproduction in *Callichthys callichthys*, *Hoplosternum littorale* and *Hoplosternum thoracatum* was correlated to the annual distribution of rainfall. Floating bubble nests were constructed throughout the period of swamp inundation (rainy season). Close inspection of the timing of reproduction of *H. littorale* in northern South America revealed the relationship between reproduction and rainfall, but also unexpected differences in the length of the breeding season. Strong interspecific competition among the three species was probably avoided through differentiation of nest sites with respect to water depth, distance to the nearest tree, distance to the edge of the swamp, and cover above the nest. Nests of *H. littorale* were built in herbaceous swamps, while *C. callichthys* and *H. thoracatum* build their nests in swamp-forest. Nests of *C. callichthys* were observed in extremely shallow water or in holes. Few nests of the three species were observed in canals. Over large parts of their geographical range *C. callichthys* and *H. thoracatum* are found in small rainforest streams. Several aspects of the reproductive ecology and behaviour of both species are probably related to the unpredictability of the stream habitat.

Key words: *Hoplosternum littorale*; *Hoplosternum thoracatum*; *Callichthys callichthys*; breeding season; interspecific competition; habitat selection; resource partitioning; Suriname.

INTRODUCTION

The manner in which closely related species utilize resources has been of great interest to ecologists, especially to those studying the high biodiversity in the tropics. Little quantitative information about this process is available for tropical freshwater fishes (Ross 1986), as most studies explore patterns in resource partitioning among a relative large number of species that are often only distantly related to each other (e.g. Lowe-McConnell 1964, Zaret & Rand 1971, Angermeier & Karr 1983, Moyle & Senanayake 1984, Winemiller 1989, Boujard

1992). Recent work on resource partitioning among closely related tropical freshwater fishes includes studies on African and Central American lake cichlids (e.g. McKaye 1977, Hoogerhoud *et al.* 1983, Marsh & Ribbink 1985), *Barbus* species in Sri Lanka (Schut *et al.* 1984, De Silva *et al.* 1985) and two *Astyanax* characins in Brazil (Arcifa *et al.* 1991).

In Suriname (South America), three armoured catfishes, *Callichthys callichthys* Linnaeus, 1758, *Hoplosternum littorale* (Hancock, 1828) and *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840), are among the most abundant bottom-dwelling fishes in coastal plain freshwater swamps. These closely related and morphologically quite similar catfishes (Gosline 1940, Hoedeman 1952, Burgess 1989) occur together in large parts of tropical South America (Mol 1994). A previous study of the feeding ecology of the three species has demonstrated high interspecific diet overlap among larvae, juveniles and adults (Mol in press). There is, however, little information on the temporal and spatial habitat use of these armoured catfishes.

In the rainy season male *C. callichthys*, *H. littorale* and *H. thoracatum* construct and guard floating bubble nests in flooded swamps (Vipan 1886, Mol 1993a). The conspicuous nests rather uniquely allow the study of the temporal pattern of breeding, the spatial distribution of the nests, and the microhabitat at the nest site. In ponds, male *H. littorale* may construct up to 14 nests during a 6-month breeding season (Pascal *et al.* 1994). Female *Hoplosternum* and *C. callichthys* are known as small-brood spawners (Lowe-McConnell 1987, Mol 1993a). Thus, individual fish appear to stay reproductively active during the rainy season and in that period habitat use will largely coincide with the use of nest habitat. In addition, Singh (1978) and Winemiller (1987) found that in *H. littorale* the rainy season is not only the spawning season, but also the main feeding period.

The main problem is how these three catfishes with very similar diets avoid strong interspecific competition during their breeding season. Here, I investigate whether the three species partition resources due to differences in timing or location of reproduction.

MATERIALS AND METHODS

THE SWAMP HABITAT AT THE STUDY SITES

The distribution of *C. callichthys*, *H. littorale* and *H. thoracatum* in Suriname (Mol 1994) compelled me to study the reproductive ecology of the three species at two sites. Although all three species occur at both study sites, *H. littorale* is present in large numbers at Weg Naar Zee, 2 km south of the Atlantic coast (5°50'N, 55°10'W), while *C. callichthys* and *H. thoracatum* are more abundant in the Lelydorp swamp, 23 km south of the Atlantic coast (5°40'N, 55°10'W). Suriname is at the heart of the American humid tropics: the mean annual temperature is high at sea level ($\geq 25^{\circ}\text{C}$), the diurnal temperature range ($22.4\text{--}30.2^{\circ}\text{C}$) is 4 times greater than the annual range ($24.8\text{--}26.8^{\circ}\text{C}$), and the annual range of both temperature (2°C) and day length (1 hour) is minimal (Snow 1976). Rainfall is the basis for the specification of seasons. Two wet and two dry periods are distinguished in the coastal plain. The short rainy season of December-January is followed by the short dry season in February-March. The main (long) rainy season from April to July is followed by the long dry season in August-November (Snow 1976).

The Weg Naar Zee study site in the young coastal plain consists of an old sandy

beach ridge bordered by extensive herbaceous swamps on Holocene clay soils. The swamps are shallow not reaching water depths of 100 cm in the rainy season. Diurnal fluctuations in water temperature on 27.1.1990 ranged from 25.1° C (7:00 h) to 28.8° C (16:00 h). Minimum and maximum water temperatures at 7:00-8:00 h in the period December 1989 - July 1990 were 24.2° C and 27.8° C, respectively (n=84). The swamp vegetation is dominated by dense stands of *Typha angustifolia* with locally clumps of *Cyperus giganteus*, *Thalia geniculata* and *Montrichardia arborescens*. At the outer edge of the swamp, in shallow water alongside the old beach ridge, *Typha* stands give way to more open water with floating aquatics like *Salvinia*, *Pistia* and *Azolla*, waterlilies (*Nymphaea*, *Nymphoides*) and the grass *Hymenachne amplexicaulis*. The soil of this part of the swamp completely dries up in the long dry season. Trees do not occur in the swamp. In the dry season the swamp water retreats in canals that are also penetrated by brackish water from mangrove forests.

The Lelydorp site (Fig. 5.1) is part of a narrow, east-west running swamp located in the old coastal plain. To the south the swamp is bordered by a complex of sandy ridges. The heart of the swamp consists of dense stands of *Eleocharis interstincta*, but locally swamp-forest occurs and includes trees such as *Pterocarpus officinalis*, *Triplaris surinamensis* and *Virola surinamensis*. Grasses and floating aquatics may grow in the shallower parts of the swamp bordering the ridges. In the dry season the swamp water retreats to canals. A tidal influence could not be detected.

Daily rainfall recordings were obtained from meteorological stations less than 1.5 km from both sites. Water level measurements were taken daily at a fixed location in the swamp. In the main dry season water level measurements were taken twice a month; gaps in the data were filled by extrapolation. Physico-chemical data of coastal plain standing waters are presented by Mol (1993b).

NESTS AND REPRODUCTIVE BIOLOGY

Adult males of *C. callichthys* (90-170 mm standard length), *H. littorale* (85-195 mm SL) and *H. thoracatum* (70-150 mm SL) construct and guard a floating bubble-nest (Mol 1993a). Nests of *H. littorale* are large and dome-shaped measuring up to 42 cm in diameter and 10 cm in height above the water surface. The elaborate construction consists of filamentous materials (e.g. grass, *Typha* leaves, roots of floating aquatics). Most nests of *H. littorale* were observed at Weg Naar Zee (Table 5.1). Multiple females spawn their eggs at the same time in a single nest resulting in males guarding multiple clutches (Mol 1993a). In the 3-4 days between oviposition and hatching of the embryos the nest does not acquire additional clutches (Mol 1993a). Shortly before or after hatching of the embryos the nest disintegrates and one day later nest and embryos are left by the male. The breeding of isolated couples in cages demonstrated that male *H. littorale* may construct up to 14 nests during a 6-month breeding season and females may spawn 14 times in the same period (Pascal *et al.* 1994). The longevity of *H. littorale* is at least three years and both males and females become reproductively active in their first year (Singh 1978).

Nests of *C. callichthys* and *H. thoracatum* are very similar and consist of a few dicotyledonous leaves floating on top of a thin layer of foam (Mol 1993a). The eggs are glued to the underside of the leaves. The identity of the nest building species was initially obtained by rearing a small number of young from the nests (31 nests of *C. callichthys* and

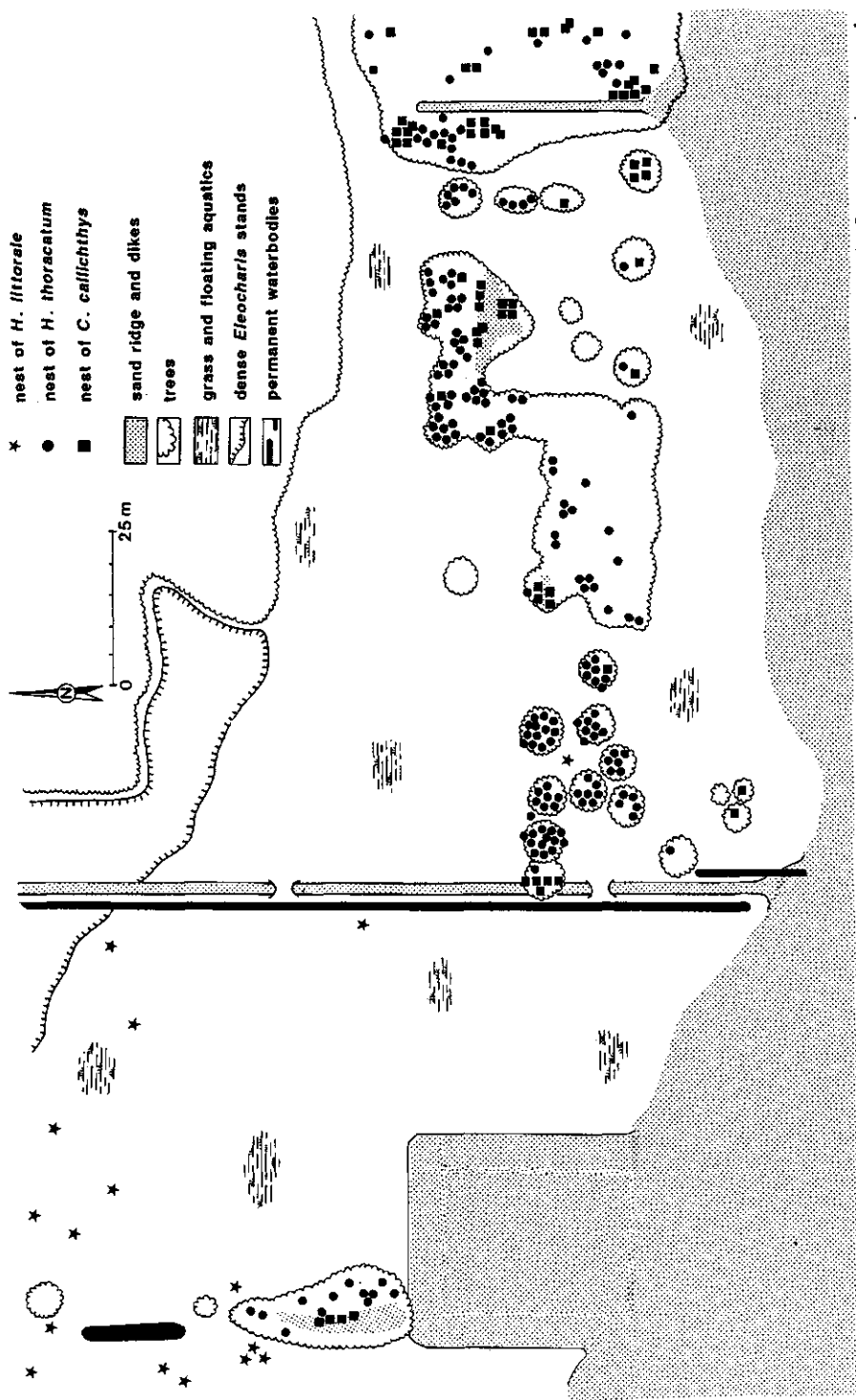


Fig. 5.1. Map of study site at Lelydorp illustrating the distribution of nest sites of *C. callichthys*, *H. thoracatum* and *H. littorale* in 1991. Note that the first two species nest under trees. A minor number of nests of *C. callichthys* (4) and *H. thoracatum* (27) in canals are not indicated on the map.

Table 5.1. Year total of rainfall (mm) and total number of nests of *C. callichthys* (Cc), *H. littorale* (Hl) and *H. thoracatum* (Ht) at Weg Naar Zee and Lelydorp.

	Weg Naar Zee				Lelydorp			
	Rainfall (mm)	Number of nests			Rainfall (mm)	Number of nests		
		Cc	Hl	Ht		Cc	Hl	Ht
Average (1965-1988)	1411.4				2319.7			
Nov 88 - Oct 89	1552.9	0*	48*	0*	-	-	-	-
Nov 89 - Oct 90	2031.6	12	136	0	2648.2	-	-	-
Nov 90 - Oct 91	1301.0	0	20	0	2052.5	70	16	225

* Period of observations 25 May - 31 October 1989

61 nests of *H. thoracatum*). Later the colour, lustre, and the way of deposition of the eggs made the identification to species of the nest possible. Most nests of *C. callichthys* and all nests of *H. thoracatum* were observed at Lelydorp (Table 5.1). In both *C. callichthys* and *H. thoracatum* oviposition occurs continuously during the days the nest is maintained by the guarding male (Mol 1993a). When the number of ripe eggs in the ovaries is compared to the number of eggs in the nest it is clear that multiple females spawn in the nests of both species (Mol 1993a). After hatching of a batch of embryos (3 days after oviposition), the nest may acquire a new clutch as egg-free leaf surface becomes available (Mol 1993a). New leaves may also be added to the nest by the male. In the laboratory females of *C. callichthys* and *H. thoracatum* mature in their first year (personal observations). In aquariums the longevity of *C. callichthys* was 9 years (Hoedeman 1960).

BREEDING SEASONALITY

Data were collected from May 1989 to October 1991 at Weg Naar Zee and from November 1990 to October 1991 at Lelydorp. In the months December-July, a daily census was performed by slowly walking in a zig-zag pattern through the swamp while recording the nests observed. In the long dry season (August-November) the swamps were surveyed twice a month. The location of the nests was fixed on a map of the study site (Fig. 5.1). Each nest was examined daily, and the developmental stages of its brood or the day the guarding male abandoned the nest without receiving a clutch were recorded. Cross-correlation coefficients between time series of the daily number of total active nests and rainfall or swamp water level were computed with different time lags using STATGRAPHICS produced by Statistical Graphics Corporation.

NEST MACROHABITAT SELECTION

Nest macrohabitat selection was analyzed using the method of Neu *et al.* (1974). The Neu method is appropriate when individual fish are not identified and habitat availability can be treated as known (Thomas & Taylor 1990). The relative numbers of nests among four major habitat types were compared to the relative availability of each habitat type in the study areas. To evaluate availability, topographic maps and aerial photographs were partitioned into

four respective habitat types: dense stands of *Typha* or *Eleocharis*, open swamp with floating aquatics and grasses, swamp-forest, and canals. The Chi-square goodness-of-fit test was used to test the null hypothesis that each habitat type was used in exact proportion to its occurrence within the study area. When a significant difference in habitat use and availability was detected, the Bonferroni Z-statistic was used to construct confidence intervals and to determine which habitat types were used more or less frequently than expected (Alldredge & Ratti 1992).

The Neu method assumes that observations are independent. Territorial behaviour for a selected habitat with limited availability, grouping behaviour or observations on the same fish would violate this assumption (Alldredge & Ratti 1992). Territoriality is not strongly developed in both *H. thoracatum* and *C. callichthys* (Mol 1993a). *Hoplosternum littorale* more often shows aggressive defence of the nest site (up to 4 m from the nest, Mol 1993a), but actual interference with conspecifics seems unlikely as nests are widely dispersed in the swamps (Table 5.5). Grouping of nesting callichthyids is probably not very important in *H. littorale* and *C. callichthys*, because nests were built at a considerable distance from the nearest occupied nest. However, in *H. thoracatum* clustering of up to five nests under the same tree was often observed in the swamp. These nests were usually well separated from each other by grass growing underneath the trees and they were presumably tended by different males. The impact of repeated observations on the same fish is probably not large in *H. littorale* as observations on nests of this species are spread over a long time period with intervening drying up of the swamps (Fig. 5.2). Most nests of *H. thoracatum* and *C. callichthys* appeared in a short time period (± 1 week) after heavy rain showers (Fig. 5.3). As the guarding male takes care of the nest during the time eggs and embryos are present (on average 4 to 5 days, Table 5.2), it follows that most nests are built by different males.

NEST MICROHABITAT DIFFERENTIATION

For comparison of the nest sites used by *C. callichthys*, *H. thoracatum* and *H. littorale* the nest site was described by seven variables potentially subject to choice: depth of water underneath the nest; distance to the outer edge of the swamp, to the trunk of the nearest tree or bush, and to the nearest occupied nest of one of the three species on the day of construction; the density of vegetation at the water surface; percentage cover above the nest; and the use of holes of earth or tree roots as nest site. Density of vegetation at the water surface and cover of overhanging vegetation and tree roots above the nest were estimated in 10% increments from <10% to >90% as percentage cover of a 1 m² quadrat with the nest at its center. Differences in separate nest-site characteristics among the three species were tested using Kruskal-Wallis tests for continuous variables and Chi-square tests for discrete variables (Sokal & Rohlf 1981). Differences among nest sites of the three species with respect to the seven variables simultaneously were evaluated using discriminant function analysis. A forward stepwise selection procedure based on Wilks's lambda criterion was used to produce an optimal set of discriminating variables (Klecka 1980). Since classification accuracy in discriminant analysis is overestimated when the same cases used to derive the function are classified, jack-knifed analysis (Hollander & Wolfe 1973) and split sample validation (Klecka 1980) were performed. The expected and observed frequencies of correctly classified results were compared using chi-square.

Table 5.2. Percentage of daily built new nests, percentage of nests that acquire eggs and develop embryos and the number of days that a nest remains active (mean \pm SE). Results of Kruskal-Wallis tests are given. Number of observations in parentheses.

	<i>C. callichthys</i>	<i>H. littorale</i>	<i>H. thoracatum</i>	H	p
Daily built new nests as percentage of total active nests (%)	23.9 \pm 4.0 (85)	35.0 \pm 2.6 (193)	20.4 \pm 3.2 (102)	15.8	0.0004
Percentage of new nests that acquire eggs (%)	87.1 \pm 4.9 (33)	52.4 \pm 4.0 (115)	91.2 \pm 3.0 (55)	39.2	<0.0001
Percentage of nests with eggs producing larvae (%)	96.4 \pm 2.2 (31)	90.9 \pm 3.11 (79)	99.5 \pm 0.5 (51)	4.0	ns
Number of days a nest is active	4.02 \pm 0.25 (82)	2.79 \pm 0.10 (220)	5.21 \pm 0.19 (225)	123.1	<0.0001
Number of days a nest that acquires eggs is active	4.25 \pm 0.27 (72)	4.00 \pm 0.08 (106)	5.44 \pm 0.19 (207)	32.5	<0.0001

Overlap in nest microhabitat use was calculated using Horn's index (Krebs 1989). Horn's index was chosen, because it is commonly used, the bias for number of resource categories, sample size and resource unevenness is relatively low compared to other indices (Smith & Zaret 1982), and the index can be statistically evaluated (Zaret & Smith 1984). Horn's index (R_0) ranges from 0 (no overlap) to 1 (complete overlap). Each variable was separated into approximately 10 categories of equal size for the calculations. A value of ≥ 0.67 was arbitrarily designated as high overlap.

RESULTS

BREEDING SEASONALITY

During the study observations were made on 82 nests of *C. callichthys*, 225 nests of *H. thoracatum* and 220 nests of *H. littorale* (Table 5.1). The method of data collection proved effective, since 80.3% of the nests were observed on the day of their construction (eggs not yet deposited or sticky and uniform-yellow in colour). Figure 5.2 shows the daily number of new nests (nests constructed per day) and total active nests (nests in use per day) of *H. littorale* at Weg Naar Zee in the period May 1989 - October 1991. Both the Kruskal-Wallis test and a one-way ANOVA with new nests or total active nests grouped by month were highly significant ($p < 0.0001$). Subsequent multiple range tests revealed that nesting occurred in the period January-June. More nests were built in 1990 than in 1991, due to a lack of rainfall and low water levels in the long rainy season of April-July 1991 (Fig. 5.2). Nesting of *C. callichthys*, *H. littorale* and *H. thoracatum* at Lelydorp (Fig. 5.3) was also restricted to the period January-June. In December a minor number of nests of *C. callichthys* and *H. thoracatum* were built in shallow depressions alongside canals before extensive flooding of the swamps occurred. Nesting of the three species was synchronous, occurring principally in the months January, March and June (Fig. 5.3).

The daily ratio of new nests to total active nests differed among the three species (Table 5.2; Fig. 5.2, 5.3). The relatively large percentage of new nests of *H. littorale*, 35% of the total active nests, reflected the high percentage of nests that did not acquire eggs, and

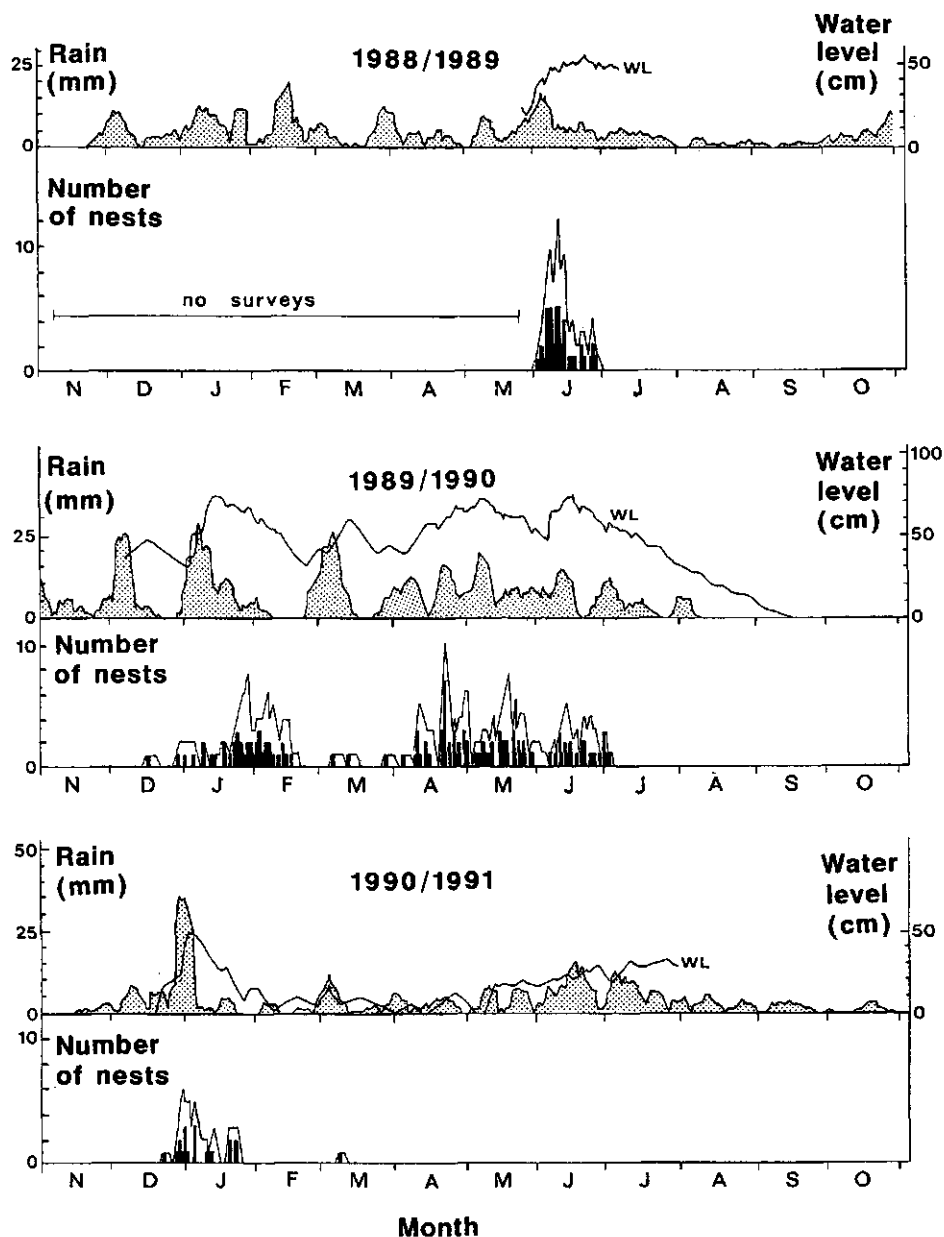


Fig. 5.2. Relationship between rainfall, swamp waterlevel (WL) and the daily variation in numbers of new (blocks) and total active (line) nests of *H. littorale* at Weg Naar Zee in 1989, 1990 and 1991. Rainfall is expressed as 7-days' moving average. Observations in 1989 started on May 25th.

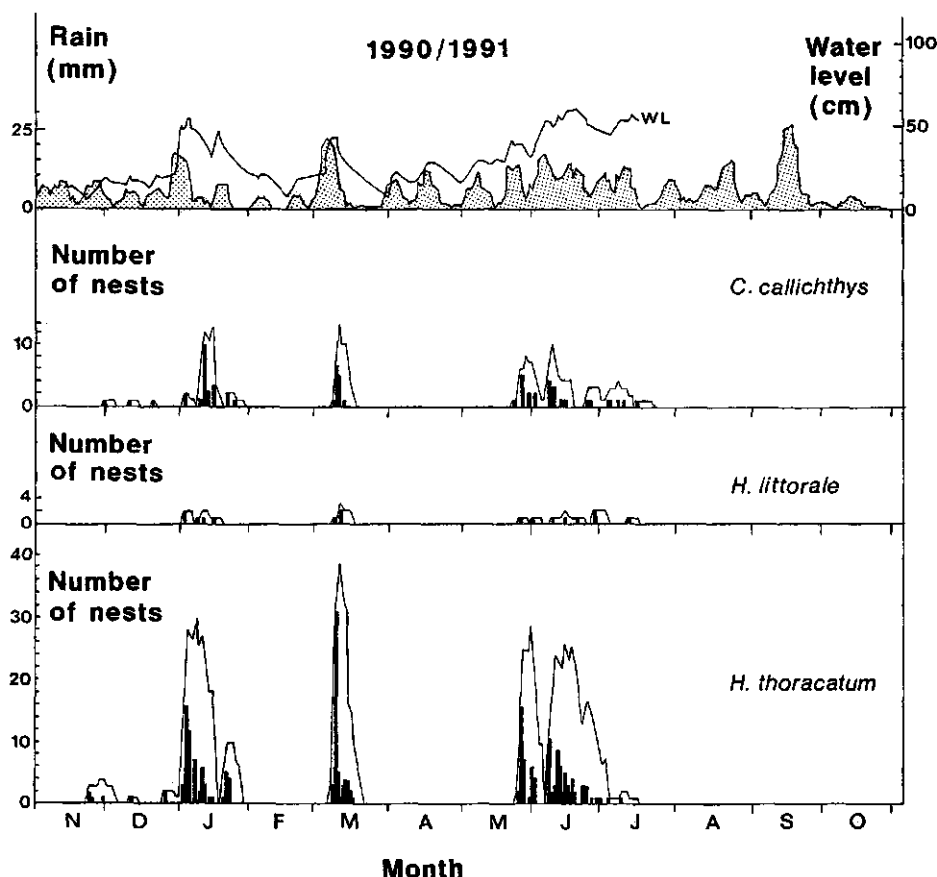


Fig. 5.3. Relationship between rainfall, swamp water level (WL) and daily variation in numbers of new (blocks) and total active (line) nests of *C. callichthys*, *H. littorale* and *H. thoracatum* in 1991 at Lelydorp. Rainfall is expressed as 7-days' moving average.

were subsequently left by the male one or two days after construction (47.6%, Table 5.2). In fish ponds in French Guiana, Pascal *et al.* (1994) also found that 48% of nests of *H. littorale* did not acquire eggs ($n=440$). Also, the average number of days that a nest with eggs remained in use is significantly larger in *H. thoracatum* and *C. callichthys* than in *H. littorale* (Table 5.2).

Table 5.3. Relation between nesting, rainfall and swamp water level. Maximum cross-correlation coefficients (r) and time lags between time series of the daily number of total active nests (7-days' moving average) of *H. littorale*, *C. callichthys* and *H. thoracatum* and swamp water level or rainfall (7-days' moving average).

Species	Study site	Period of observations	Rainfall (mm)		Swamp water level (cm)	
			r	time-lag (days)	r	time-lag (days)
<i>H. littorale</i>	WegNaarZee	May 1989-Oct 1991	0.425	-6	0.637	0
<i>C. callichthys</i>	Lelydorp	Nov 1990-Oct 1991	0.392	-3	0.543	0
<i>H. thoracatum</i>	Lelydorp	Nov 1990-Oct 1991	0.498	-4	0.589	0

Nesting of *H. littorale* at Weg Naar Zee (Fig. 5.2) closely tracked changes in swamp water level, and to a lesser extent the daily rainfall. Nesting started when the water level in the swamp reached approximately 30 cm. In the short rainy season of 1989-1990 the total number of active nests peaked approximately two weeks later than in 1990-1991. Interestingly, nests were not observed in the long rainy season of 1991. Rainfall at this time was insufficient to raise the water level to the 30 cm level. In the same period of April-July 1991 the water level in the Lelydorp swamp exceeded 30 cm and nests of *H. littorale* were observed (Fig. 5.3). At Lelydorp nesting of *H. thoracatum*, *C. callichthys* and *H. littorale* in 1990-1991 was also related to changes in water level and daily rainfall (Fig. 5.3). The timing of the start of the breeding season was similar to that of *H. littorale* at Weg Naar Zee in 1990-1991. In the midst of the short dry season (March), a second peak in nesting was observed after heavy rain showers raised the water level in the swamp. Nesting of the three species was also abundant in the long rainy season of April-July. Time-series analysis of nesting of *H. littorale* at Weg Naar Zee (1989-1991) and *H. thoracatum* and *C. callichthys* at Lelydorp revealed higher cross-correlation coefficients between the total number of active nests and swamp water level than between nesting and rainfall (Table 5.3). Nesting activities lagged 3 to 6 days behind the rainfall data.

NEST MACROHABITAT SELECTION

Figure 5.1 shows the location of nests of *H. littorale* in the Lelydorp swamp. Nests of *H. littorale* were rarely found in the dense vegetation of emergent aquatics like *Typha* and *Eleocharis* in the central region of the swamp (Table 5.4). At Lelydorp the swamp-forest was also used less than expected. Both at Weg Naar Zee and Lelydorp the open swamp habitat with floating aquatics and grasses was the most selected nest habitat. Still, nest densities observed in the open swamp habitat were low and did not exceed 0.016 nests per 100 m² swamp. The open swamp habitat is found alongside sand or shell-sand ridges towards the outer edge of the swamp (Fig. 5.1, also see Carter & Beadle 1930).

At Lelydorp, approximately 95% of the nests of *C. callichthys* and *H. thoracatum* were built under trees and in swamp-forest (Fig. 5.1, Table 5.4). Few nests of both catfishes were found in the dense stands of *Eleocharis* and in the open swamp habitat. Nesting males of *C. callichthys* and *H. thoracatum* used only 50% of the available swamp-forest habitat (Fig. 5.1). Swamp-forest areas at some distance from the edge of the swamp were not used.

Table 5.4. Nest macrohabitat selection by *H. littorale*, *H. thoracatum* and *C. callichthys* in two coastal plain swamps in Suriname. Number (n) and proportion ($p \pm 95\%$ confidence interval) of nests in 4 habitat types. *Hoplosternum littorale* prefers the open swamp habitat. *Callichthys callichthys* and *H. thoracatum* nest in swamp-forest. Chi-square tests for goodness-of-fit are significant for *H. littorale* at Weg Naar Zee ($X^2=260.5$, 2 df, $p<0.001$) and Lelydorp ($X^2=5.45$, 1 df, $p=0.019$), and for both *H. thoracatum* ($X^2=408.4$, 3 df, $p<0.001$) and *C. callichthys* ($X^2=117.9$, 3 df, $p<0.001$) at Lelydorp.

Habitat	Weg Naar Zee (157,200 m ²)			Lelydorp (19,930 m ²)				
	Surface area (%)	<i>H. littorale</i>		Surface area (%)	<i>H. littorale</i>		<i>H. thoracatum</i>	
		n	$p \pm 95\% \text{ c.i.}$		n	$p \pm 95\% \text{ c.i.}$	n	$p \pm 95\% \text{ c.i.}$
Open swamp	0.40	188	0.92 ± 0.045	0.58	14	0.88 ± 0.208	2	0.01 ± 0.016
Dense stands of <i>Typha/Eleocharis</i>	0.57	2	0.01 ± 0.017	0.05	0	0	0	
Canals/creeks	0.04	14	0.07 ± 0.043	0.03	2	0.13 ± 0.208	27	0.12 ± 0.054
Swamp-forest	0			0.34	0	0	196	0.87 ± 0.056
							65	0.93 ± 0.077

Table 5.5. Comparison of seven characteristics of nest sites used by *C. callichthys*, *H. thoracatum* and *H. littorale* (mean \pm SE). Results of Kruskal-Wallis tests and Chi-square test* are given. Number of observations in parentheses.

	<i>C. callichthys</i>	<i>H. thoracatum</i>	<i>H. littorale</i>	H/X*	p
Water depth below the nest (cm)	12.1 \pm 0.60 (81)	18.5 \pm 1.00 (220)	35.5 \pm 0.97 (213)	281.5	<0.0001
Distance of nest to edge of swamp (m)	3.6 \pm 0.83 (82)	6.8 \pm 0.44 (225)	9.2 \pm 1.06 (217)	44.1	<0.0001
Distance of nest to nearest tree (m)	0.04 \pm 0.03 (82)	0.01 \pm 0.01 (225)	9.1 \pm 0.97 (218)	340.0	<0.0001
Distance to nearest occupied nest (m)	18.0 \pm 2.02 (82)	5.7 \pm 0.65 (223)	39.6 \pm 1.12 (217)	285.9	<0.0001
Vegetation cover at the water surface (%)	12 \pm 3 (82)	45 \pm 2 (221)	34 \pm 2 (219)	77.0	<0.0001
Vegetation cover above the nest (%)	81 \pm 3 (82)	72 \pm 2 (221)	32 \pm 2 (219)	174.0	<0.0001
Percentage of nests built in holes (%)	61 \pm 5 (82)	0.4 \pm 0.4 (225)	0 (220)	292.2*	<0.0001

Maximum densities of nests of *C. callichthys* and *H. thoracatum* in the preferred part of the swamp-forest were 0.274 nests per 100 m² and 0.821 nests per 100 m², respectively. Male *C. callichthys* nested solitarily, but clumping of three or four nests of *H. thoracatum* under one tree was often observed in the swamp. Only 12 nests of *C. callichthys* and no nests of *H. thoracatum* were observed in the swamp at Weg Naar Zee (Table 5.1). In the absence of trees, *C. callichthys* constructed its nests from leaves of *Montrichardia arborescens* in the swamp at Weg Naar Zee.

NEST MICROHABITAT DIFFERENTIATION

The seven variables describing the nest site were all significantly different among *C. callichthys*, *H. thoracatum* and *H. littorale* (Table 5.5). Nests of *C. callichthys* were located in the shallowest water, with lowest vegetation cover at the water surface, nearest to the outer edge of the swamp, and often in holes of earth or tree roots. Males of *H. littorale* built their nests in the deepest water, at the largest distance from trees, the edge of the swamp and nests of conspecifics, and never in holes. Nest sites of *H. thoracatum* had intermediate values for water depth and distance to the edge of the swamp, and resembled nests of *C. callichthys* in distance to trees and cover above the nest. Only one nest of *H. thoracatum* was built in a hole.

The seven nest-site variables were only related to each other to a small extent. Within-group correlation coefficients (Klecka 1980) between the variables were all in the interval -0.262 to 0.186. Discriminant analysis with stepwise inclusion of variables did not result in exclusion of variables. The two canonical discriminant functions that could be derived from the data were both significant in their discriminating power (X^2 -test, $p < 0.00001$). Nest-site variables providing the best discrimination among groups (having the highest correlation with the two discriminant functions) included the distance to the nearest nest, the vegetation cover above the nest, the water depth and the nest site in a hole (Table

Table 5.6. Quantitative evaluation of the discriminating power of the seven nest-site variables. Pooled within-groups correlations between nest-site variables and the two canonical discriminant functions (within-groups structure coefficients of Klecka 1980).

Variable	DF 1 correlation	DF 2 correlation
Distance to nearest nest	0.70556*	0.19889
Vegetation cover above nest	-0.49270*	0.12900
Water depth under nest	0.45064*	-0.17377
Distance to nearest tree	0.32510*	-0.02493
Distance to edge of swamp	0.09837*	-0.09315
Nest site in hole	-0.23589	0.91546*
Vegetation cover at water surface	-0.03631	-0.30033*

* Within each discriminant function, the significant correlations are listed in order of decreasing magnitude.

5.6). The nest sites could be discriminated at 87.7% accuracy on the basis of the seven variables, which was significantly different from the expected classification rate due to chance alone ($X^2=674.6$, $df=1$, $p<0.00001$). The random splitting of the data set in two equal-sized subsamples did not result in a significantly lower classification percentage for the test subset when classification was based on discriminating functions derived from the other data subset. 'Jack-knife' validation also did not yield a lower classification rate.

Overlap in nest (micro)habitat use was generally moderate or low (≤ 0.67) between *H. littorale* and *C. callichthys* and between *H. littorale* and *H. thoracatum* (Table 5.7). Overlap values for *C. callichthys* and *H. thoracatum* were higher, but moderate values also occurred. Figure 5.4 summarizes the results on nest-site differentiation among *C. callichthys*, *H. thoracatum* and *H. littorale* in the Lelydorp swamp.

DISCUSSION

BREEDING SEASONALITY

The environment of a tropical swamp is characterized by markedly seasonal conditions caused primarily by fluctuations in rainfall (Carter & Beadle 1930, Welcomme 1979). Life histories of the swamp fishes are often geared to the seasonal changes in their environment (Lowe-McConnell 1987). In Suriname, reproduction of *C. callichthys*, *H. littorale* and *H. thoracatum* started with the onset of the rainy season in December-January. Peak spawning was synchronous in the three species and reflected the seasonal distribution of rainfall (Fig. 5.2, 5.3). Staggering of peak spawning times in sympatric closely related species associated with the onset of the rainy season is typical of savanna fishes (Lowe-McConnell 1964, Mago 1970) and fishes of large flood-plain river systems (Godoy 1972, Goulding 1980). In small rainforest streams species with several different seasonal breeding patterns may coexist in the same stream (Kramer 1978, De Silva *et al.* 1985).

Nesting in *C. callichthys*, *H. littorale* and *H. thoracatum* was correlated more with rising water levels in the swamps than with local rains. The lag between the daily nesting activities and rainfall probably reflected a delay in the rise of the swamp water level following rainfall. Nests of *H. littorale* were not observed in the swamp if rainfall was

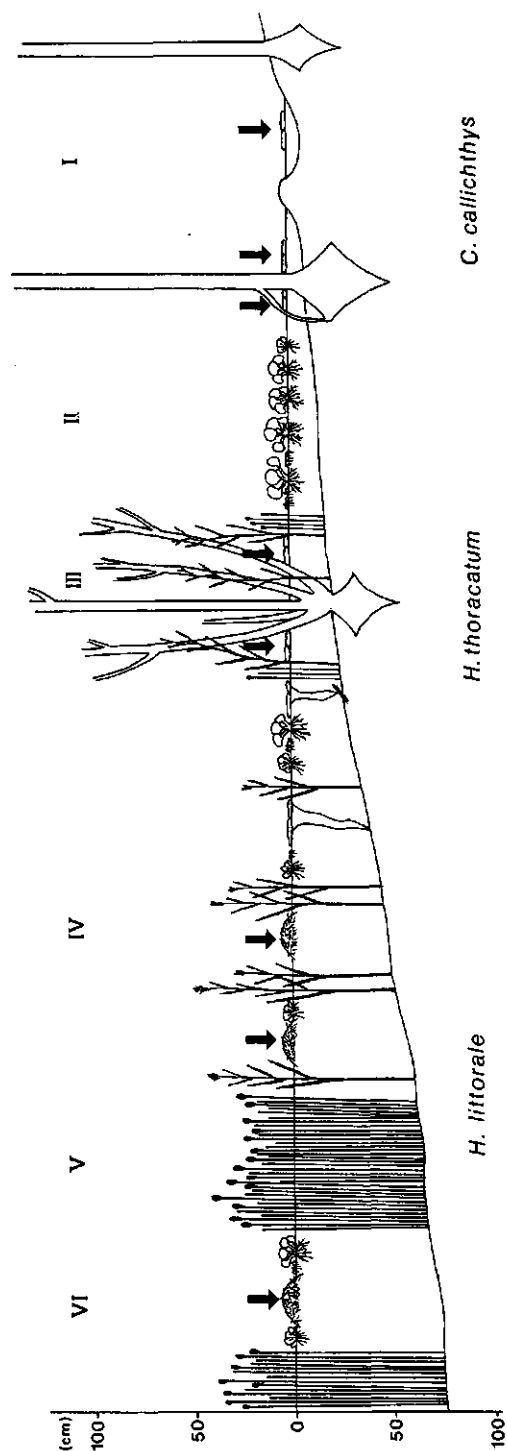


Fig. 5.4. Diagrammatic cross-section of the Lelydorp swamp in the coastal plain of Suriname showing nest-site differentiation among *C. callichthys*, *H. thoracatum* and *H. littorale*. Arrows point to the nests. I. Swamp-forest at the edge of the swamp with nests of *C. callichthys* under trees and in holes. II. Open swamp with floating aquatics in the shallow outer region of the swamp. No callichthyid nests. III. Swamp-forest or scattered trees with nests of *H. thoracatum*. IV. Open swamp with floating aquatics and slightly deeper water. Nests of *H. littorale*. V. Central region of the swamp with dense stands of *Eleocharis* and no callichthyid nests. VI. Pool in central region with nests of *H. littorale*.

Table 5.7. Nest habitat segregation among *C. callichthys*, *H. littorale* and *H. thoracatum*. Overlap values (Horn's index) for six variables characterizing the nest (micro)habitat of the three species. Values marked with an asterisk show complete overlap (see Zaret & Smith 1984) (Chi-square $X^2_{df,0.05}$). Low and moderate values (≤ 0.67) are underlined.

Nest site variable	<i>C. callichthys</i> and <i>H. littorale</i>	<i>H. thoracatum</i> and <i>H. littorale</i>	<i>C. callichthys</i> and <i>H. thoracatum</i>
Water depth below the nest	<u>0.1912</u>	<u>0.5240</u>	0.8102
Distance of nest to edge of swamp	0.8856	0.9160	0.8532
Distance of nest to nearest tree	<u>0.4196</u>	<u>0.4304</u>	0.9904*
Vegetation cover at the water surface	0.7996	0.9112	0.6768
Vegetation cover above the nest	<u>0.6207</u>	0.7099	0.8974
Percentage of nests built in a hole	<u>0.5956</u>	0.9981	<u>0.6114</u>

insufficient to raise the water level above 30 cm (Fig. 5.2). In Trinidad, Singh (1978) also noted that spawning of *H. littorale* did not occur until the water level in the swamp reached approximately 30 cm. Minor differences in the timing of first spawning were observed as *H. thoracatum* and *C. callichthys* were able to nest in very shallow water.

REGIONAL DIFFERENCES IN THE BREEDING SEASON OF *H. LITTORALE*

A comparison of the results of the present study with data on the breeding season of *H. littorale* in Trinidad (Singh 1978) and French Guiana (Hostache *et al.* 1993) shows the strong correlation between reproduction and the annual distribution of rainfall (Fig. 5.5). In Suriname, nesting of the three callichthyids reflected the semi-annual oscillation in rainfall with peak spawning in December-January and April-July. In Trinidad, the average annual rainfall is low compared to Suriname (Portig 1976) and nests of *H. littorale* were observed only in May-August (Singh 1978). A single, prominent breeding season in *H. littorale* is also found under almost identical climatological conditions in northern Venezuela (Machado-Allison & Zaret 1984, Winemiller 1987). In eastern French Guiana, annual rainfall is in excess of 3000 mm and a short dry season following the rains of December-January is difficult to detect (Snow 1976). At Kaw, French Guiana, the Gonado-Somatic-Index of female *H. littorale* peaked in December-February, but in the April-July rainy season the GSI was at its minimum and reproduction probably did not take place (Hostache *et al.* 1993).

When comparing the breeding pattern of *H. littorale* in Suriname and in French Guiana (Fig. 5.5) the question arises why *H. littorale* reproduces in the April-July rainy season in Suriname but not in French Guiana. Five hypotheses may be proposed:

(1) Predation pressure on eggs, embryos, larvae and juveniles increases with time after the initial flooding of the swamps. Mass spawning of the two most abundant piscivores in the swamps, *Hoplias malabaricus* (≤ 45 cm total length) and *Hoplerthrinus unitaeniatus* (≤ 35 cm TL), was observed after the first rains in very shallow water (10 cm) at Weg Naar Zee (24.12.1990 and 23.4.1991) and at Lelydorp (10.12.1990). The early start in breeding

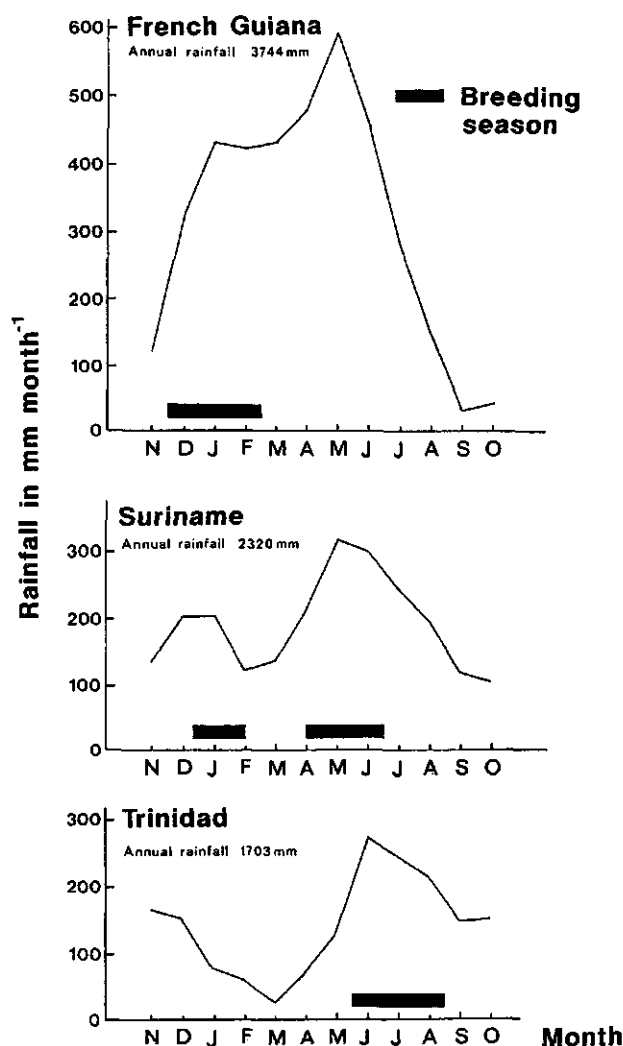


Fig. 5.5. Relationship between the mean annual distribution of rainfall and the breeding season of *H. littorale* in French Guiana (after Hostache *et al.* 1993), Suriname (present study) and Trinidad (after Singh 1978). Determination of the breeding season of *H. littorale* at Kaw, French Guiana, is based on analysis of the gonado-somatic-index (GSI) for females. Delimitation of the breeding season at Trinidad is based on both GSI measurements and nest observations. Rainfall data are provided by Snow (1976) for Cayenne, French Guiana, Portig (1976) for Trinidad and the Meteorological Service of Suriname for Lelydorp, Suriname.

gives the offspring of both piscivores a lead in growth over their future prey including young callichthyids. Stomach contents of two juvenile *H. malabaricus* (3.1 and 4.8 cm TL) consisted of a 1.5 cm SL fish (unpublished data). Reproductive synchrony in *H. littorale*, including *C. callichthys* and *H. thoracatum* (Fig. 5.3), may have an adaptive value in satiating predators (but see Ims 1990).

(2) Early reproduction results in a prolonged growing time for the offspring before they are exposed to dry-season dangers of desiccation and heavy predation in contracted water bodies. Approximately 4-6 months after hatching juvenile *H. littorale* have developed intestinal respiration, a heavy armour of bony plates and stout pectoral spines. At this age they are able to escape from drying pools by moving over land to a permanent water body (Carter & Beadle 1931, Mago 1970, Lüling 1971, personal observations). The bony armour and spines also protect the fish effectively from most aquatic predators.

(3) Food availability for larvae and juveniles decreases with time after the first flooding of the swamps. Explosive growth of microorganisms followed by an increase in the numbers of larger invertebrates is correlated with the rapid decomposition of grasses, animal dung and forest litter after the first flooding of the swamps (Lowe-McConnell 1987, Mago 1970, Welcomme 1979).

(4) Offspring of fish that reproduce early in the rainy season may outcompete offspring that hatch later in time. Larvae and juveniles of the three callichthyids have almost identical diets (Mol in press).

(5) Deterioration of the water quality in the swamp following the first inundation reduces the reproductive success of the fish. As the swamps are flooded dissolved oxygen concentrations fall swiftly as organic matter begins to decay and growth of emergent aquatics and floating vegetation protects the water surface from wind-induced disturbance (Carter & Beadle 1930). Low oxygen levels are also associated with the building up of high concentrations of H_2S in the swamp (Welcomme 1979). The toxic effects of low ambient oxygen concentrations (Blaxter 1969, Rombough 1988) and H_2S (Smith & Oseid 1973) on early developmental stages of fishes are well-known.

In Suriname, rainfall is not reliable in the short rainy season of December-January (Snow 1976). A reproductive style based on a single breeding season in this period of *H. littorale* (and *H. thoracatum* and *C. callichthys*) must include the risk of total failure of reproduction in years with deficient rainfall. A double breeding season offers the advantages of early reproduction (if the first rains do not fail) while the possibility of total failure of reproduction is reduced. In the Surinamese swamps, female *H. littorale* with ripe ovaries are present from December to July (unpublished GSI analyses) and in this period reproduction may occur if the water level is suitable. By isolating pairs of *H. littorale* in cages in fish ponds, Pascal *et al.* (1994) demonstrated up to 14 successive spawnings of a single female during a 6-month breeding period. Their results indicate that female *H. littorale* probably spawn at least twice each year in the Surinamese swamps (in both rainy seasons). In other equatorial areas with two rainy seasons fishes are also known to spawn in both floods (Lowe-McConnell 1987).

NEST MACROHABITAT SELECTION

The nests of *C. callichthys*, *H. littorale* and *H. thoracatum* were not constructed at random, but built at apparently carefully preselected sites within the fishes' habitat. The reproductive period is well marked by callichthyids shifting habitat, most fish moving from canals and dry-season pools into newly flooded swamps to breed. Such lateral movements associated with spawning are well known in neotropical swamp fishes (Mago 1970, Lowe-McConnell 1987). In the coastal plain of Suriname, *H. littorale* build its nests in open water

at the edge of herbaceous swamps (also observed in Paraguay by Carter & Beadle 1931). A habitat comparable to that of the open swamp type is created by man in rice fields. In the first weeks after inundation of the fields large numbers of nests of *H. littorale* may be observed between the young rice shoots. However, as the rice plants grow and develop into dense stands, nests of *H. littorale* disappear from the fields. In rice production areas I have often observed recently flooded fields with abundant nests of *H. littorale* and older stands without nests situated next to each other.

C. callichthys and *H. thoracatum* nested under trees in swamp-forest. Both species are absent from rice fields in Suriname (Vermeer *et al.* 1974, personal observations) and absent or rare in herbaceous swamps of the Paraguayan Chaco (Carter & Beadle 1931) and northern Venezuela (Mago 1970, Novoa 1982). Males of *C. callichthys* and *H. thoracatum* are probably unable to build their nests from filamentous materials like grass or roots, and suitable nest sites are thus confined to the direct environment of a tree or a broad-leaved shrub. All three catfishes avoided nesting in dense vegetation of emergent aquatics where zooplankton food for larvae is sparse (Carter & Beadle 1930) and adults are probably restricted in their movements. Although male *H. littorale* are able to built their nests from dicotyledonous leaves (Mol 1993a) and *C. callichthys* and *H. thoracatum* sometimes constructed a nest under a waterlily leaf or a leaf of *M. arborescens* (Mol 1993a, present study), nest (macro)habitat segregation between *H. littorale* on the one hand and *C. callichthys* and *H. thoracatum* on the other hand was almost complete.

The hydrology of the swamp probably also determines the location of the nests. In the Lelydorp swamps I did not found nests in a seemingly suitable patch of inundated forest 500 m "downstream" (west) of the study area. Although water movement was generally not detectable in the swamp, fish (among them callichthyids) were caught swimming upstream through culverts where local currents were set up at times of changing water levels, e.g. at the start of the rainy season. Dense stands of *Eleocharis* east of the study site may have prevented further movement upstream resulting in high nest densities at the study site.

In Suriname, the geographical distribution of *H. littorale* (Mol 1994) largely coincides with the occurrence of herbaceous swamps in the coastal plain (Teunissen 1993). However, the absence of *H. littorale* from the Sipaliwini savanna in the interior of Suriname (Mol 1994) and the Rupununi savanna in Guyana (Lowe-McConnell 1964) shows that it is not the open-swamp habitat that sets the limits to the distribution of *H. littorale*. Mol (1994) provided evidence that low tolerance to electrolyte-poor waters of the Guyana Shield determines the distribution of *H. littorale* in tropical South America.

NEST MICROHABITAT CHARACTERISTICS

In discussing the nest sites of *C. callichthys*, *H. littorale* and *H. thoracatum* it should be kept in mind that the nest site (and the nest) must at least offer the developing eggs some protection from predation, environmental stress (turbulence, siltation, oxygen deficit, temperature extremes, etc) and infection (Potts 1984). The structure of floating bubble nests provides the eggs with an oxygen-rich environment (Mol 1993a) and protection from siltation and dislodgement. In addition, an optimal nest site should also provide food and protection for the newly hatched embryos.

Water depth is an important nest site parameter in lake cichlids (e.g. McKaye 1977, Lowe-McConnell 1982) and centrarchids (e.g. Noltie & Keenleyside 1987). In fishes that excavate nests in the bottom, water depth choices often reflect the availability of appropriate spawning substrates. In armoured catfishes with floating bubble nests, shallow water nesting is probably in the first place associated with protection from aquatic predators. Among the three species, *H. littorale* build its nest in deepest water (Table 5.5) and also defended the nest site most vigorously against aquatic intruders (Mol 1993a). With the floating bubble nest protected by the male, a shallow water nest site is probably more important for the free embryos that are guarded by the male for only one day after hatching. Shallow water offers protection from aquatic predators (DeVries 1990) and small fish are not very susceptible to terrestrial predators (Power 1984). Shallow swamps also provide the larvae with abundant space and food (Lowe-McConnell 1987) necessary for their growth and development (Blaxter 1988).

The more sheltered the nest site the easier to provide effective protection from predators (Sargent & Gebler 1980, Potts 1984). Cover above the nest and nesting in holes conceal the floating bubble nest of armoured catfish from avian predators. In addition, hole sites are more easily defended against aquatic predators (Potts 1984). With the eggs in the floating bubble nest positioned out of the water, cover may also be important in damping extremes in nest temperature (Mol 1993a). The nests of *H. littorale* are built in herbaceous swamps without much cover from trees or shrubs, but their elaborate dome of plant material probably protects the eggs from temperature extremes (Mol 1993a).

Both *C. callichthys* and *H. thoracatum* occur over large parts of their geographical range in small rainforest streams (Mol 1994). Although the habit of building floating bubble nests probably evolved in tropical swamps with stagnant, oxygen-depleted water (Carter & Beadle 1931, Mol 1993a), Mol (1993a) suggested that several aspects of the reproductive ecology of both species may be explained as an adaptation to the lotic environment of small creeks. For example, the spreading of successive spawnings in the nest in time by *C. callichthys* and *H. thoracatum* (Mol 1993a, present study) reduces the risk of losing large quantities of eggs when a floating nest is swept away by violent currents during unpredictable peak flow events. If females spawn continuously in the nest and the number of eggs in the nest at any point in time is relatively low (compared to *H. littorale*; Mol 1993a) the development of the highly aggressive nest-guarding behaviour characteristic of male *H. littorale* may be inhibited. With the nest-guarding behaviour less developed, *C. callichthys* and *H. thoracatum* may be forced to breed in holes or shallow parts of the swamp in order to avoid nest predation. Clustering of nests of *H. thoracatum* probably offers additional protection to the nest (Dominey 1981). On the other hand, nest-site characteristics like shallow water and holes may reflect nesting in streams in a more direct way. Mol (1993a) suggested that holes provide a microhabitat with relative calm water which offers protection from physical dislodging for both the nest and newly hatched embryos during peak flow events. In shallow water drag reduces water velocities during turbulent conditions. It is of great interest to compare the nest sites and reproductive success of *C. callichthys* and *H. thoracatum* in small creeks and in swamps. Noltie & Keenleyside (1987) have found substantial differences in breeding ecology and nest-site characteristics between rock bass nesting in streams and in lakes which they ascribe to the rigours and increased variability of the stream habitat.

COMPETITION

Under natural conditions intraspecific competition for nest sites is probably not strong in *C. callichthys* and *H. littorale* as both species maintained large nearest-active-neighbour distances (Table 5.5). In flooded rice fields densities of nests of *H. littorale* may reach levels at which interference between nesting males seems possible (Mol 1993a). Nests of *H. thoracatum* were sometimes built under the same tree at close distance from each other (< 1 m). It was not possible to determine the number of males tending a group of nests associated with a single tree because the guarding males of *H. thoracatum* were not very aggressive (Mol 1993a). Social attraction (Bietz 1981) may have been more important than intraspecific competition for nest sites in this species.

Interspecific competition for nest sites among *C. callichthys*, *H. littorale* and *H. thoracatum* is probably also not important. Although temporal patterns of breeding did not differ among the three species, nest densities were rather low compared to nest densities recorded for cichlids (McKaye 1977), centrarchids (Gross & Nowell 1980) and sticklebacks (Whoriskey & FitzGerald 1987). Also nest sites were quite distinct from each other (Tables 5.5, 5.7). Interspecific competition for nest sites occurs in cichlids (McKaye 1977, 1984), centrarchids (Gross & Nowell 1980) and sticklebacks (FitzGerald 1983, FitzGerald & Whoriskey 1985). Segregation of nest microhabitat or breeding season seems common in cichlids (Lowe-McConnell 1982, 1987) and sticklebacks (FitzGerald & Wootton 1993) but not in centrarchids (Carbine 1939).

The yearly production of callichthyid larvae may be calculated by multiplying the number of nests per year (Table 5.1) by the mean number of eggs per nest (Mol 1993a). At Weg Naar Zee (1989/1990), 3174104 larvae of *H. littorale* were produced in 62363 m² open swamp. The yearly production of larvae of *C. callichthys* and *H. thoracatum* in 6731 m² swamp-forest at Lelydorp was 380310 and 780075, respectively. The present study suggests a low degree of spatial overlap in the rainy season between *H. littorale* on the one hand and both forest nesting species, *C. callichthys* and *H. thoracatum*, on the other hand. Nest sites of *C. callichthys* and *H. thoracatum* were probably sufficiently different from each other to separate larvae of both species spatially. Where high interspecific diet overlap was found among larvae, juveniles and adults of the three catfishes (Mol in press), spatial segregation in the rainy season may prevent strong interspecific competition. The results of this study support the 'compression hypothesis' of MacArthur & Wilson (1967) which implicates habitat segregation, and not differences in time of activity or diet, as the major means of coexistence between competing species.

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Chapter 6

Potential impact of predation on early developmental stages of the armoured catfish *Hoplosternum thoracatum* (Siluriformes-Callichthyidae) and an explanation of the syntopic occurrence of three closely related catfishes in a multi-predator swamp

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Abstract

1. This study investigated the role of predators in preventing competitive exclusion among three closely related armoured catfishes (*Callichthys callichthys*, *Hoplosternum littorale* and *Hoplosternum thoracatum*) that occur syntopically in multi-predator freshwater swamps of Suriname, South America.
2. The potential impact of predation on populations of armoured catfish was determined by combining laboratory predation rates on five early developmental stages of the armoured catfish *Hoplosternum thoracatum* for 24 aquatic predators with field studies of the density of the predators in the swamps.
3. The contribution of a particular predator to the total predation pressure on its prey was determined to a large extent by the density of the predator in the swamp (as determined by chemo-fishing with rotenone). Seemingly innocuous predators with low or moderate predation rates in the laboratory may be extremely important in the swamps due to their abundance. Small-sized omnivorous fishes and aquatic invertebrates are major predators of early developmental stages of armoured catfish.
4. Both qualitative and quantitative ontogenetic changes in the predation pressure on armoured catfish were observed. Predation on eggs, larvae and juveniles of *H. thoracatum* resulted from a different set of predators in each developmental stage of the prey. In all developmental stages of *H. thoracatum* the predation pressure involved several predator species and not a single, dominant predator.
5. The potential predation pressure of the 24 predators taken together and the number of predators that were able to prey on *H. thoracatum* decreased sharply with increasing age (size) of the prey.

6. Even if egg (nest) predation is prevented by the guarding male, the potential impact of the 24 predators on the populations of armoured catfish is large. Predation may easily account for the high mortality of *H. thoracatum* observed in the swamps.

7. This suggested that the high predation pressure on callichthyid catfishes may help to explain the stable coexistence of three closely related and morphologically quite similar armoured catfishes in the Surinamese swamps.

Key-words: predation intensity; invertebrate predators; fish predators; interspecific competition; *Hoplosternum thoracatum*; *Hoplosternum littorale*; *Callichthys callichthys*; Amazon; Suriname.

INTRODUCTION

Tropical ecosystems are well-known for their high biodiversity (World Conservation Monitoring Centre 1992) with many closely related species coexisting syntopically. Tropical freshwater fish communities also show stable coexistence of large numbers of closely related species (Fryer & Iles 1972; Lowe-McConnell 1987; Goulding, Carvalho & Ferreira 1988). Since Hutchinson (1959) posed his celebrated question "Why are there so many kinds of animals?", factors potentially affecting species diversity have been an important subject of study and discussion in ecology (Hairston, Smith & Slobodkin 1960; Paine 1966; Pianka 1966; Connell 1975; Menge & Sutherland 1976, 1987). Two different types of interactions between organisms are probably responsible for most of the structure of communities: competition (Dobzhansky 1950; MacArthur & Levins 1967) and predation (Paine 1966; Connell 1975).

According to the predation hypothesis, selective predation on dominant competitors can maintain a relatively high species diversity by preventing the dominant species from monopolizing the major resource. By keeping species in lower trophic levels below their carrying capacity, competition is alleviated, competitive exclusion is prevented, and additional species can invade the community (Paine 1966; Roughgarden & Feldman 1975; Holt 1977).

Despite speculation about the intensity and significance of predation in the tropics (Janzen 1970; Connell 1978), a review of field experiments on predation showed that out of 139 studies only 13 (9%) were conducted in the tropics (Sih *et al.* 1985). Virtually no experiments were performed with predators of vertebrate prey. Studies of predation on tropical fishes include the effects of the introduction of a piscivore (Zaret & Paine 1973; Witte *et al.* 1992), ontogenetic changes in predation intensity (Jackson 1961; Power 1984), the diet of predators (e.g. Prejs 1987; Winemiller 1989), behavioural and morphological adaptations in guppies (Liley & Seghers 1975), and the effect of predation on reproduction (Johannes 1978; McKaye 1984).

Fish mortality rates (Dahlberg 1979) and predation pressures on fish (Bailey & Houde 1989) are highest in early developmental stages like eggs and larvae. In marine yolksac larvae mortality due to predation may be as high as 60-80% d⁻¹ (Hewitt, Theilacker & Lo 1985). The hypothesis of Nellen (1986) on the level of fecundity of bony fish also predicts high predation rates on early developmental stages.

Very few organisms are the exclusive prey of only one type of predator. Fryer & Iles (1955) state that almost any fish takes eggs or larvae. Various aquatic macro-invertebrates

also prey on fish larvae (Huet 1972; Foster, Garcia & Town 1988; Bailey & Houde 1989). As the fish grow they become less susceptible to most of their (aquatic) predators, but probably more susceptible to other (terrestrial) predators (Power 1984). Although most previous studies focus on a single type of large predator (Sih *et al.* 1985), qualitative changes in predation pressure during the ontogeny of fish show the need for studies with a 'multiple-predator' perspective (Alexander 1979; Power 1984; Lima 1992; Reimchen, 1994). The multi-predator approach will be even more important in species-rich tropical communities. Large numbers of predatory species (and individuals) appear to be characteristic of South American fish communities (Lowe-McConnell 1969, 1987).

Fryer & Iles (1972: p. 237) pointed out that an abundant small predator may exert a much greater effect on the population of its prey than a rare large predator. It follows, therefore, that the density of the predators which can eat a particular prey type determines to a large extent their contribution to the predation pressure on the prey (Prejs 1987).

In coastal plain swamps of Suriname (South America) three medium-sized, closely related armoured catfishes, *Callichthys callichthys* L., 1758, *Hoplosternum littorale* (Hancock, 1828) and *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840), live together (Mol 1994) with many different types of potential predators such as aquatic macro-invertebrates (Hemiptera, Odonata, Coleoptera), fish, water snakes, caimans, birds and otters. Large interspecific diet overlap in larvae, juveniles and adults (Mol, in press a) indicates that competition among these catfishes is potentially strong, but significant differences in the nest-site (micro)habitat were also found (Mol, in press b). In the rainy season the three catfishes built floating bubble nests in flooded swamps (Mol 1993b, in press b). The nests are guarded by the male (Mol 1993b), but larvae and juveniles are probably more susceptible to predation. When the swamps dry up adults and young of the year move back to their dry season habitat of creeks, canals and small pools. When confined to these restricted waterbodies, the callichthyids are vulnerable to large aquatic and terrestrial predators (e.g. caimans and birds).

In the present study, laboratory predation rates on five early developmental stages of the armoured catfish *H. thoracatum* for 24 potential aquatic predators are combined with data on the density of the predators in the swamps as determined by chemo-fishing. The objectives are 1) to quantify, in controlled experiments, the voracity of 24 different predators preying on the eggs, larvae and juveniles of armoured catfish, 2) to determine the density of the predators in the field, 3) to estimate from these data the potential predation pressure in the swamp, and 4) to discuss the role of predation in the structuring of the catfish community referring to data on the year production of larvae of armoured catfish (Mol 1993b, in press b) and assuming that predation rates on larvae of *C. callichthys* and *H. littorale* do not differ to a large extent from predation rates on *H. thoracatum* larvae. I also discuss in qualitative terms the predation risk for armoured catfish in dry season habitats.

MATERIALS AND METHODS

STUDY SITES

Suriname is situated in the neotropics, between 2 and 6° N, and consequently has a genuine tropical climate. The annual rainfall averages 2200 mm in Paramaribo (capital), and is distinctly seasonal. In the rainy season large tracts of coastal plain swamp land are

inundated. The composition of the fish and macro-invertebrate fauna of the swamps was investigated at three localities in the coastal plain: Weg Naar Zee, Lelydorp and Prinsie. Mol (in press b) provides a description of the study sites at Weg Naar Zee and Lelydorp. In both swamps floating bubble nests of the callichthyids were observed in large numbers (Mol in press b). The swamp at Prinsie is situated 40 km south of Paramaribo and consists of dense stands of *Eleocharis* bordered by swamp forest.

PREDATOR DENSITIES IN THE SWAMP

The swamps were sampled in the main rainy season of 1994 (May-June) by cherno-fishing with rotenone (4 trials). Samples were taken in open vegetation or under trees at the edge of the swamp, the habitat where in a previous study most callichthyid nests were observed (Mol in press b). At Lelydorp and Weg Naar Zee the samples were taken at the exact location of the nest sites (see Mol in press b; Chapter 6, Fig. 6.1). In the main dry season of 1994 (August-September), canals were sampled with rotenone (3 trials). Additional sampling by seine added a few less abundant species to the catches at the three sampling localities.

Twenty-five gram of pure rotenone (Aldrich Chemical Company, Milwaukee, U.S.A.; 97% rotenone) was dissolved in 1 l acetone. A sampling area of 25 m² swamp with a water depth of ± 0.5 m or canal (dry season; water depth ± 1.5 m) was enclosed with a block net of 2 mm unstretched mesh. The net was firmly driven into the muddy bottom substrate and attached 0.3 m above the water surface in order to prevent jumping fish from escaping the sampling area. The aquatic vegetation was then removed from the enclosed area and 15 g of dissolved rotenone (97%) was evenly dispersed over the sampling area. Fish, tadpoles and macro-invertebrates started floating at the water surface approximately 30 minutes after application of the poison (rotenone concentration 1-1.5 mg l⁻¹ swamp water). The effect of the rotenone was limited to the sampling area which may have been due to the low diffusion rate of the poison into the swamp (Richter & Nijssen 1980). At the time of the rotenone sampling, healthy fish were observed approximately 2 m outside the enclosed sampling area. Dead fish and invertebrates were removed, and three hours after poisoning the sampling area was fished with a 2 mm mesh seine to check what had been missed. Few fish or aquatic macro-invertebrates were present in these seine catches. Collected specimens were preserved in 70% alcohol and later measured for total length to the nearest 0.1 mm.

Macro-invertebrates were identified with keys in Ward & Whipple (1959), Geyskes & Pain (1957), Holthuis (1959) and Nieser (1975). Cichlids were identified following Kullander & Nijssen (1989). Non-cichlid fish were identified with keys in Gery (1977), Mees (1974) and Le Bail *et al.* (1984). All specimens were deposited in the National Zoological Collection of the University of Suriname (P.O.B. 9212, Paramaribo, Suriname).

Table 6.1. Characteristics of prey used in predation trials (mean \pm S.E.): eggs, larvae and juveniles of *Hoplosternum thoracatum*. Number of observations in parentheses.

	Age (days)	Stocking density (ind/10 l)	Total length/ egg diameter (mm)	Fresh weight (mg)	Body height (mm)	Length of pectoral spine (mm)	Presence of armour of bony plates
Eggs	0	293 \pm 7.8	1.9 \pm 0.09 (14)	3.6 \pm 0.5 (14)			-
Larvae (1 week)	7	20*	10.9 \pm 0.36 (30)	9.2 \pm 1.1 (10)	1.6 \pm 0.05 (10)		-
Juveniles (3 weeks)	21	10	20.0 \pm 0.57 (10)	98.8 \pm 7.6 (10)	3.6 \pm 0.08 (10)		-
Juveniles (5 weeks)	35	5	26.7 \pm 0.73 (20)	211.9 \pm 20.3 (10)	4.9 \pm 0.17 (10)		-/+
Juveniles (7 weeks)	49	5	36.3 \pm 0.82 (10)	612.7 \pm 44.0 (10)	6.7 \pm 0.26 (10)	12.5 \pm 0.3 (10)	+

* A density of 20 larvae per litre corresponds with approximately 33,300 larvae 100m² swamp.

PREDATION EXPERIMENTS IN THE LABORATORY

Eggs, larvae, and juveniles of *H. thoracatum* were used as prey (Table 6.1; Fig. 6.1). Eggs were collected from floating bubble nests in the Lelydorp swamp. Larvae were obtained by first collecting eggs on the point of hatching and then inducing hatching by exposing the eggs to water with a temperature of approximately 35° C. Larvae were fed live *Artemia* nauplii twice daily. Larvae (age 7 days) and juveniles (21, 35 and 49 days) were reared in the laboratory in 100 l tanks following methods described in Mol (1994). Egg diameter, total length of larvae or juveniles, body height, and the length of the pectoral spine were measured to the nearest 0.5 mm. Eggs and fish were blotted out on damp filter paper and weighed on an analytical balance (\pm 0.0001 g).

Fish and macro-invertebrate predators (Table 6.2) were collected by seine at Lelydorp and transported in oxygen inflated polyethylene bags to the laboratory. The predator species were stocked separately in 12 l tanks. Their total length was measured to the nearest 0.5 mm, excluding the appendages of the abdomen of invertebrates but including the rostrum of freshwater shrimps. To inhibit the accumulation of metabolites and the growth of micro-organisms two-thirds of the water in each tank was changed daily. Most of the predators used in the experiments have previously been shown to feed on eggs, larvae or juveniles of fish (Knöppel 1970; Saul 1975; Richards & Davis 1977; Foster *et al.* 1988; Goulding *et al.* 1988; Winemiller 1989; Reimchen 1994).

Predation experiments were conducted in rectangular 12 l glass tanks, in daylight (8.00-17.00 h), at night (20.00-5.00 h) or in twilight (5.00-8.00 h and 17.00-20.00 h). Water temperature was not controlled during the experiments and varied between 24 and 28° C. Stocking densities of predators and prey are shown in Tables 6.1 and 6.2. Eggs of *H. thoracatum* were not counted but weighed on an analytical balance (\pm 0.0001 g). The number of eggs was obtained from the weight using data in Mol (1993b). Predators were starved 24 hours in the experimental tank prior to the start of a series of 4 experiments: one in daylight (9 hours), one in darkness (9 h) and two in twilight (2x3 h). Following

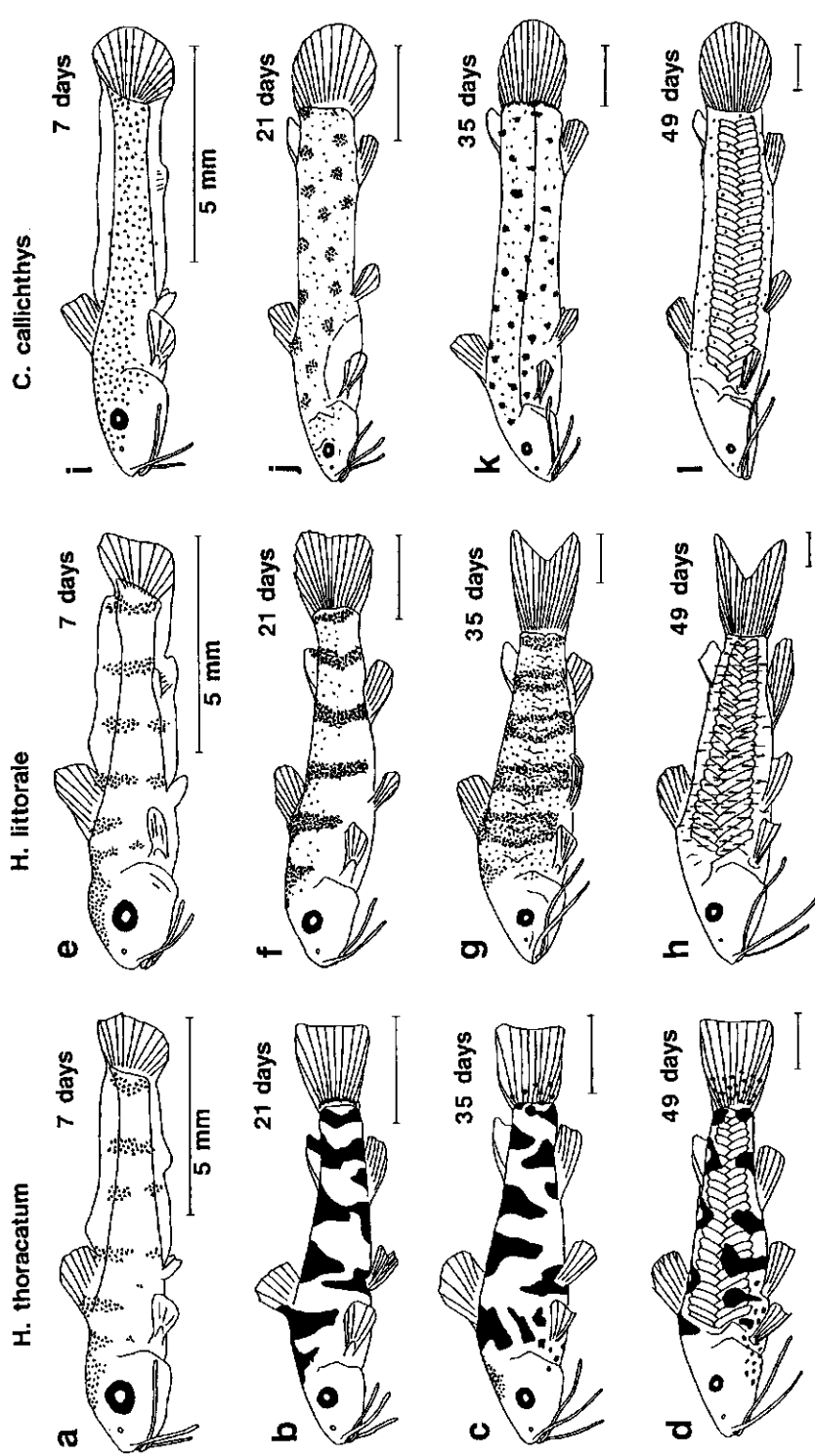


Fig. 6.1. Early developmental stages of the armored catfishes *Hoplosternum thoracatum* (a-d), *H. littorale* (e-h) and *Callichthys callichthys* (i-l): larvae (age 7 days) and juveniles (21, 35 and 49 days).

Table 6.2. Type, size, mouth gape and stocking density of predators used in laboratory predation trials.

Predator	Stocking density* (ind/10 l)	Total length range (mm)	Mouth gape (mm)
Fish			
<i>Astyanax abramoides</i>	2	42 - 46	2.9
<i>Astyanax bimaculatus</i> <6 cm	2	35 - 60	4.0
<i>Astyanax bimaculatus</i> >6 cm	1	75 - 80	4.8
<i>Hemigrammus boesemani</i>	4	32 - 44	2.9
<i>Hemigrammus unilineatus</i>	5	32 - 41	2.7
<i>Hoplias malabaricus</i>	1	75 - 80	9.5
<i>Nannostomus beckfordi</i>	5	30 - 38	1.6
<i>Pyrrhulina filamentosa</i>	5	36 - 45	2.7
<i>Callichthys callichthys</i>	1	75 - 80	7.2
<i>Hoplosternum thoracatum</i>	1	65 - 70	5.4
<i>Crenicichla saxatilis</i> <6 cm	1	35 - 40	2.8
<i>Crenicichla saxatilis</i> 6-10 cm	1	80 - 85	6.9
<i>Crenicichla saxatilis</i> >10 cm	1	110 - 115	10.9
<i>Kribia guianensis</i> <6 cm	1	51 - 59	4.2
<i>Kribia guianensis</i> >6 cm	1	110 - 115	9.1
<i>Nannacara anomala</i>	2	33 - 35	3.8
<i>Polycentrus schomburgki</i>	2	25 - 44	4.5
<i>Synbranchus marmoratus</i>	3	61 - 94	2.2
Non-fish			
<i>Pomaea dolioides</i>	2	21 - 40	
<i>Palaemonetes carteri</i> <3 cm	5	19 - 25	
<i>Palaemonetes carteri</i> >3 cm	1	40 - 45	
<i>Belostoma cf denticolle</i>	2	14 - 15	
<i>Belostoma cf harrisi</i>	1	31 - 41	
<i>Ranatra spec</i>	1	30 - 35	
Aeshnidae larvae	1	27 - 47	
Libellulidae larvae	2	12 - 18	
Dytiscidae larvae	1	34 - 56	
Hydrophilus spec	1	33 - 35	
<i>Pseudis paradoxa</i> tadpole	1	110 - 115	

* Stocking densities were chosen with regard to the habits and size of predators. To mimic natural situations some gregarious predators were stocked in small groups, e.g. *Hemigrammus*.

acclimation of the predator, prey were added to the tank in preselected numbers (Table 6.1). Consumed prey were not replaced during the experiments. At the end of each experiment, the number of prey in the tank was counted and captured prey were replaced. At the end of the 48-h period (predator starvation/acclimation time + one series of 4 experiments) the surviving prey were removed and another 48-h period started with new prey. Each 24-h series of predation trials began with a different light regime in order to compensate for the possibility that predators were satiated after the first experiments in a series. Tanks stocked at preselected prey densities (Table 6.1) but lacking predators served as control.

Following de Lafontaine & Leggett (1988) instantaneous prey mortality due to predation Z (predator⁻¹ hour⁻¹) was calculated as

$$Z = ((\ln N_i/N_p) - (\ln N_i/N_c))/(P.T)$$

where N_i is the initial number of prey stocked, N_c and N_p are the final number of prey in the control tanks and in the tanks with predators, respectively, P is the number of predators added to the tanks, and T is the duration of the experiment in hours. This equation is based

on the assumption of constant mortality (addendum) and corrects for prey depletion, as is required when prey are not replaced once eaten (Royama 1971; Rogers 1972). Predation rate I , expressed as the number of prey taken per predator per hour, was calculated as

$$I = N_p(1 - \exp(-Z))$$

PREDATION PRESSURE IN THE SWAMP

Data on the densities of the predator species and their predation rates on eggs, larvae, and juveniles of *H. thoracatum* were combined to evaluate the potential predation pressure on the early developmental stages of this callichthyid catfish in the swamps. The density of four fish predators that were not present in the rainy season rotenone samples was estimated as 0.1 ind 100m² (Table 6.6). In calculating the total predation pressure on the callichthyids it was assumed that the predatory rates of the 24 predators were additive (Wilbur & Fauth 1990; but see Soluk 1993). To evaluate the potential impact of the 24 predators on the catfish populations additional information on the reproductive ecology of armoured catfishes (Mol 1993b, in press b) was used in determining the density and yearly production of callichthyid larvae in the swamps. Because I did not find large interspecific differences in size or development among 7-day-old larvae of the three catfish species (Fig. 6.1), I assumed that laboratory predation rates on larvae of *C. callichthys* and *H. littorale* approximately equal predation rates on *H. thoracatum* larvae. However, juveniles of the three catfishes show considerable differences in their pigmentation pattern, morphology and growth rate (Fig. 6.1) and in the complex environment of the swamp interspecific differences in predation mortality of juveniles probably occur.

RESULTS

PREDATOR DENSITIES IN THE SWAMP

34 fish species were collected in the coastal plain swamps of which 22 species were present in the rotenone samples (Table 6.3). Densities of the fish species varied between 1-158 individuals 100m² swamp in the rainy season and 0.5-930.5 ind 100m² in dry season canals. Most species were present in higher numbers in the dry season, when fishes are concentrated in small pools, canals and creeks, than in the rainy season when they disperse in the swamps (Table 6.3). Total fish densities were 430 ind 100m² and 2328 ind 100m² in the rainy season and dry season, respectively. *Polycentrus schomburgki*, *Kribia guianensis* (= *Aequidens guianensis*), *Nannacara anomala*, *Rivulus urophthalmus*, *Hemigrammus unilineatus*, *Pyrrhulina filamentosa* and *Hoplias malabaricus* were the most common fishes in the swamps.

Densities of aquatic macro-invertebrates and amphibians were of the same order of magnitude as those of the fishes, except for the extremely large number of freshwater shrimps *Palaemonetes carteri* in submerged vegetation of dry season canals (Table 6.4). All collected non-fish taxa were present in the rotenone samples. With the exception of

Table 6.3. Densities (ind 100m² swamp) of fish species in coastal plain swamps (mean depth 0.5 m) of Suriname in the rainy season (n=4) and dry season (n=3). Rotenone samples. Mean \pm S.E. (x = collected in the swamps, but not present in rotenone samples). Species marked with an asterisk were used in the predator-prey experiments.

Species	Family	Total Length (mm)	Rainy season	Dry season
1 <i>Astyanax abramoides</i> *	Characidae	≤ 50	x	x
2 <i>Astyanax bimaculatus</i> *	Characidae	≤ 60	x	5 \pm 6.8
<i>Astyanax</i> bi. >6.0 cm	Characidae	60-110	x	x
3 <i>Charax gibbosus</i>	Characidae	≤ 150	x	x
4 <i>Ctenobrycon spilurus</i>	Characidae	≤ 100	x	15 \pm 21.6
6 <i>Hemigrammus rodwayi</i>	Characidae	≤ 50	x	x
5 <i>Hemigrammus boesemani</i> *	Characidae	≤ 45	2 \pm 2.0	55 \pm 43.3
7 <i>Hemigrammus unilineatus</i> *	Characidae	≤ 45	30.5 \pm 17.6	215.5 \pm 290.9
8 <i>Pristella maxillaris</i>	Characidae	≤ 50	x	10.5 \pm 9.6
9 <i>Pseudopristella simulata</i>	Characidae	≤ 30	10 \pm 4.6	114.5 \pm 150.4
10 <i>Crenuchus spilurus</i>	Crenuchidae	≤ 60	1 \pm 1.0	108.5 \pm 153.1
17 <i>Curimata cyprinoides</i>	Curimatidae	≤ 150	x	x
18 <i>Curimata spilura</i>	Curimatidae	≤ 50	x	x
19 <i>Curimatella alburna</i>	Curimatidae	≤ 60	x	x
20 <i>Curimatopsis crypticus</i>	Curimatidae	≤ 60	x	25.5 \pm 36.2
11 <i>Erythrinus erythrinus</i>	Erythrinidae	≤ 200	x	x
12 <i>Hoplias malabaricus</i> *	Erythrinidae	≤ 150	7 \pm 4.4	13 \pm 9.6
<i>Hoplias</i> ma. >150 cm	Erythrinidae	150-450	x	x
13 <i>Hoplerethrinus unitaeniatus</i>	Erythrinidae	≤ 350	x	x
14 <i>Copella arnoldi</i>	Lebiasinidae	≤ 75	2 \pm 2.0	32 \pm 45.2
15 <i>Nannostomus beckfordi</i> *	Lebiasinidae	≤ 40	1 \pm 1.0	16 \pm 22.6
16 <i>Pyrrhulina filamentosa</i> *	Lebiasinidae	≤ 55	16 \pm 14.7	23 \pm 32.5
21 <i>Parauchenipterus galeatus</i>	Auchenipterida	≤ 190	x	x
22 <i>Callichthys callichthys</i> *	Callichthyidae	≤ 205	x	x
23 <i>Hoplosternum littorale</i>	Callichthyidae	≤ 235	x	x
24 <i>Hoplosternum thoracatum</i> *	Callichthyidae	≤ 180	3 \pm 1.1	0.5 \pm 0.9
25 <i>Rhamdia quelen</i>	Pimelodidae	≤ 350	x	x
26 <i>Gymnotus carapo</i>	Gymnotidae	≤ 450	1 \pm 1.0	4 \pm 5.9
27 <i>Apistogramma steindachneri</i>	Cichlidae	≤ 70	x	14 \pm 21.6
28 <i>Crenicichla saxatilis</i> *	Cichlidae	≤ 60	1 \pm 1.0	x
<i>Crenicichla</i> sa. 6.0-10.0 cm	Cichlidae	61-100	x	4 \pm 5.9
<i>Crenicichla</i> sa. >10.0 cm	Cichlidae	101-280	x	x
29 <i>Kribia guianensis</i> *	Cichlidae	≤ 60	77 \pm 49.0	49 \pm 52.5
<i>Kribia</i> gu. >6.0 cm	Cichlidae	61-115	3 \pm 1.9	x
30 <i>Nannacara anomala</i> *	Cichlidae	≤ 60	66 \pm 34.7	930.5 \pm 1222.2
31 <i>Polycentrus schomburgki</i> *	Nandidae	≤ 75	158 \pm 59.8	639 \pm 37.3
32 <i>Rivulus urophthalmus</i>	Cyprinodontidae	≤ 58	46 \pm 8.2	17.5 \pm 19.3
33 <i>Poecilia reticulata</i>	Poeciliidae	≤ 60	x	36 \pm 43.9
34 <i>Synbranchus marmoratus</i> *	Synbranchidae	≤ 200	5 \pm 3.0	x
<i>Synbranchus</i> ma. >200 cm	Synbranchidae	200-1500	x	x

freshwater shrimps, all collected aquatic macro-invertebrates and amphibians were more abundant in the rainy season than in the dry season (Table 6.4). Conspicuous members of the swamp fauna were *P. carteri*, the freshwater snail *Pomacea dolioides*, water bugs of the genus *Belostoma*, Libellulidae naiads, Dytiscidae larvae and tadpoles (among them the giant tadpole *Pseudis paradoxa*).

Although the three armoured catfishes were only represented in the rotenone samples of the rainy season by juvenile *H. thoracatum* (<45 mm TL), nests of the other two species, *H. littorale* and *C. callichthys*, were observed in large numbers at two collection sites (Mol in press b). The Prinsie collection site was not surveyed for callichthyid nests, but adult *H. thoracatum* and *C. callichthys* were collected at Prinsie on another occasion (specimens in National Zoological Collection of the University of Suriname).

Table 6.4. Densities (ind 100m² swamp) of aquatic macro-invertebrates and amphibians in coastal plain swamps (mean depth 0.5 m) of Suriname in the rainy season (n=4) and dry season (n=3). Rotenone samples. Mean \pm S.E. (x = collected in the swamps, but not present in the rotenone samples). Taxa marked with an asterisk were used in the predator-prey experiments.

Species	Total Length (mm)	Rainy season	Dry season
Gastropoda			
1 <i>Biomphalaria glabrata</i>	≤ 25	12 \pm 12.0	2 \pm 3.0
2 <i>Pomacea glauca</i>	≤ 50	4 \pm 4.0	1 \pm 0.9
3 <i>Pomacea dolioides</i> *	≤ 65	62 \pm 34.6	37 \pm 29.1
Decapoda			
4 <i>Euryrhynchus wrzesniowskii</i>	≤ 15	6 \pm 4.8	9 \pm 7.8
5 <i>Palaemonetes carteri</i> *	≤ 30	20 \pm 8.2	13693 \pm 15847.6
<i>Palaemonetes</i> ca. >3.0 cm	31-50	5 \pm 5.0	x
Hemiptera			
6 <i>Belostoma</i> cf. <i>denticolle</i> *	≤ 15	20 \pm 12.4	1.5 \pm 1.9
7 <i>Belostoma</i> cf. <i>harrisi</i> *	≤ 45	82 \pm 53.6	5.5 \pm 4.5
8 <i>Belostoma</i> spec.	≤ 25	46 \pm 29.6	x
9 <i>Corixidae</i> spec.	≤ 15	x	7.5 \pm 10.8
10 <i>Ranatra</i> spec. *	≤ 35	5 \pm 3.0	x
Odonata			
11 Aeshnidae larvae *	≤ 50	2.5 \pm 2.4	x
12 Libellulidae larvae *	≤ 25	32 \pm 18.3	2 \pm 1.6
Coleoptera			
13 Dytiscidae larvae *	≤ 75	18 \pm 6.0	5 \pm 7.3
14 <i>Hydrophilus</i> adult *	≤ 35	4 \pm 1.6	x
Amphibia			
15 <i>Pseudis paradoxa</i> tadpole *	≤ 125	35 \pm 12.1	1 \pm 0.9
16 tadpole spec.	≤ 60	25 \pm 17.9	13 \pm 18.8
17 frog spec.	≤ 70	8 \pm 5.4	1.5 \pm 1.9

PREDATION RATES IN THE LABORATORY

1317 predation trials were conducted to determine predation rates of 14 fish predators (751 trials), 9 aquatic invertebrate predators (556 trials) and the tadpole *P. paradoxa* (10 trials) on 5 developmental stages of the armoured catfish *H. thoracatum* (Table 6.5). The average prey depletion in number of prey individuals during the experiments was $40.7 \pm 4.3\%$ (mean \pm S.E.) in trials with eggs, $34.0 \pm 1.9\%$ in trials with larvae, and $15.2 \pm 1.3\%$ (juveniles; 21 days), $8.8 \pm 0.9\%$ (35 days) and $1.4 \pm 0.4\%$ (49 days) in trials with juveniles.

Predation rates were not significantly different among light conditions for all possible predator-prey combinations, except for *Astyanax bimaculatus* (<6 cm) and *H. malabaricus* preying on larvae (Kruskal-Wallis tests, for the two species $p=0.050$ and $p=0.050$, respectively). Both species showed higher predation rates on larvae in twilight than in either daylight or darkness. Because most predators showed no significant effect of light conditions on their predation rates, I pooled the results of the predation trials in daylight, twilight and darkness for each predator-prey combination (Table 6.5).

All predators showed significantly different predation rates among prey types (developmental stages) (Kruskal-Wallis tests, $p < 0.05$ for all predator species). Predation rates decreased in the series eggs < larvae < juveniles (3-weeks < 5-weeks < 7-weeks) (Table 6.5). Within each prey type, predation rates differed significantly among predators (five Kruskal-Wallis tests, $p < 0.01$ for each of the five developmental stages of the prey).

Table 6.5. Instantaneous predation rates I (prey predator⁻¹ hour⁻¹) under laboratory conditions for 24 predator species/size-classes feeding on eggs, larvae and juveniles (3, 5 and 7 weeks) of the armoured catfish *Hoplosternum thoracatum*. Mean \pm S.E. Number of predation trials in parentheses*.

Predator	Eggs	Larvae (1-week)	3-week juveniles	5-week juveniles	7-week juveniles
Fish					
<i>A. abramoides</i>	10.16 \pm 0.00 (1)	0.534 \pm 0.271 (7)	0.000 \pm 0.000 (8)	0.000 \pm 0.000 (16)	-
<i>A. binaculatus</i>	33.53 \pm 0.00 (1)	5.406 \pm 1.022 (7)	0.687 \pm 0.202 (8)	0.076 \pm 0.024 (16)	0.004 \pm 0.004 (16)
<i>A. bi.</i> >6 cm	-	3.044 \pm 1.092 (7)	-	0.186 \pm 0.053 (16)	0.000 \pm 0.000 (16)
<i>H. boesemani</i>	6.93 \pm 0.81 (2)	0.754 \pm 0.166 (13)	0.002 \pm 0.002 (14)	0.000 \pm 0.000 (16)	-
<i>H. unilineatus</i>	15.73 \pm 0.00 (1)	0.205 \pm 0.048 (7)	0.035 \pm 0.022 (8)	0.000 \pm 0.000 (8)	-
<i>H. malabaricus</i>	121.17 \pm 21.8 (2)	9.123 \pm 1.462 (7)	1.406 \pm 0.309 (14)	0.367 \pm 0.126 (16)	0.045 \pm 0.024 (16)
<i>N. beckfordi</i>	1.55 \pm 0.67 (2)	0.089 \pm 0.042 (11)	0.000 \pm 0.000 (4)	-	-
<i>P. filamentosa</i>	-	0.407 \pm 0.138 (7)	-	-	-
<i>C. callichthys</i>	119.38 \pm 0.00 (1)	8.363 \pm 1.567 (6)	2.257 \pm 0.312 (14)	0.412 \pm 0.123 (16)	0.000 \pm 0.000 (16)
<i>H. thoracatum</i>	12.00 \pm 6.42 (2)	2.843 \pm 0.910 (13)	0.018 \pm 0.018 (14)	0.000 \pm 0.000 (8)	-
<i>C. saxatilis</i>	35.49 \pm 0.00 (1)	0.246 \pm 0.090 (7)	-	0.000 \pm 0.000 (8)	-
<i>C. sa.</i> 6-10 cm	-	5.367 \pm 1.547 (7)	-	0.317 \pm 0.090 (8)	0.000 \pm 0.000 (16)
<i>C. sa.</i> >10 cm	-	8.284 \pm 1.559 (7)	-	0.471 \pm 0.107 (8)	0.055 \pm 0.028 (16)
<i>K. guianensis</i>	12.74 \pm 3.76 (4)	6.573 \pm 0.823 (21)	0.716 \pm 0.093 (28)	0.080 \pm 0.022 (32)	0.000 \pm 0.000 (16)
<i>K. gu.</i> >6 cm	-	1.696 \pm 0.737 (7)	-	0.212 \pm 0.099 (8)	0.015 \pm 0.010 (16)
<i>N. anomala</i>	0.00 \pm 0.00 (2)	1.977 \pm 0.554 (6)	0.087 \pm 0.037 (13)	0.000 \pm 0.000 (7)	-
<i>P. schomburgki</i>	0.44 \pm 0.44 (4)	0.996 \pm 0.281 (28)	0.104 \pm 0.027 (27)	0.030 \pm 0.016 (32)	0.000 \pm 0.000 (16)
<i>S. marmoratus</i>	3.93 \pm 2.43 (4)	0.328 \pm 0.108 (15)	0.023 \pm 0.012 (14)	0.000 \pm 0.000 (16)	-
Non-fish					
<i>P. dolioides</i>	22.36 \pm 10.9 (7)	0.000 \pm 0.00 (8)	0.000 \pm 0.000 (5)	-	-
<i>P. carteri</i>	1.72 \pm 0.54 (4)	0.160 \pm 0.024 (16)	0.006 \pm 0.004 (20)	-	-
<i>P. ca.</i> >3 cm	-	0.329 \pm 0.141 (7)	0.130 \pm 0.051 (8)	0.015 \pm 0.010 (16)	0.000 \pm 0.000 (16)
<i>B. cf. denticolle</i>	-	0.146 \pm 0.064 (7)	0.058 \pm 0.013 (14)	0.013 \pm 0.011 (16)	-
<i>B. cf. harrisi</i>	1.34 \pm 1.02 (4)	0.751 \pm 0.138 (30)	0.271 \pm 0.041 (28)	0.114 \pm 0.029 (32)	0.008 \pm 0.005 (32)
<i>Ranatra</i> spec	7.37 \pm 3.57 (2)	0.322 \pm 0.065 (15)	0.037 \pm 0.021 (13)	0.000 \pm 0.000 (16)	-
<i>Aeshnidae</i> larvae	0.75 \pm 0.50 (4)	1.174 \pm 0.219 (16)	0.105 \pm 0.026 (28)	0.066 \pm 0.016 (32)	0.008 \pm 0.008 (16)
<i>Libellulidae</i> larvae	0.00 \pm 0.00 (4)	0.307 \pm 0.075 (18)	0.000 \pm 0.000 (12)	0.000 \pm 0.000 (16)	-
<i>Dytiscidae</i> larvae	8.32 \pm 3.64 (2)	0.075 \pm 0.042 (15)	0.121 \pm 0.027 (27)	0.019 \pm 0.013 (13)	0.000 \pm 0.000 (5)
<i>Hydrophilus</i>	19.28 \pm 0.00 (1)	0.087 \pm 0.080 (7)	0.000 \pm 0.000 (8)	-	-
<i>P. paradoxa</i>	0.00 \pm 0.00 (2)	0.036 \pm 0.036 (8)	-	0.000 \pm 0.000 (16)	-

* Difficulties with the collection of large quantities eggs of *H. thoracatum*, the collection of predators and their replacement following death during an experiment account for the differences in the number of predation trials per predator-prey combination.

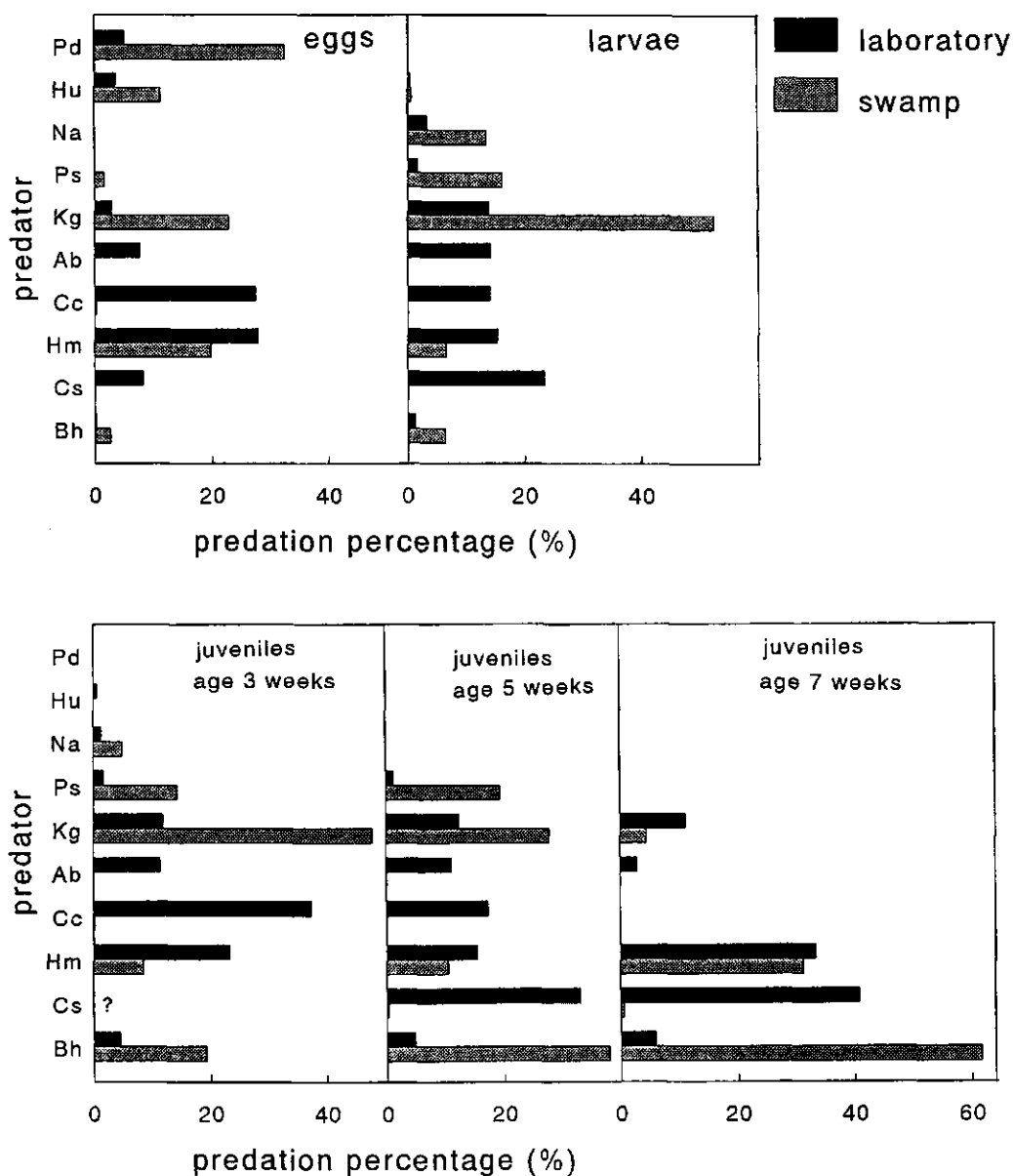


Fig. 6.2. Comparison of relative (potential) predation intensities of 10 predators of early developmental stages of the armoured catfish *Hoplosternum thoracatum* in laboratory trials and in the swamp. Predation rates are given as percentage of the total (potential) predation in the laboratory or swamp for each prey type. Pd = *Pomacea dolioides* (Gastropoda), Hu = *Hemigrammus unilineatus*, Na = *Nannacara anomala*, Ps = *Polycentrus schomburgki*, Kg = *Kribia guianensis*, Ab = *Astyanax bimaculatus*, Cc = *Callichthys callichthys*, Hm = *Hoplias malabaricus*, Cs = *Crenicichla saxatilis*, Bh = *Belostoma cf. harrisi* (Hemiptera). Predation of the pike cichlid *C. saxatilis* on 3 weeks old juveniles was not tested.

However, with the exception of 7-week-old juveniles, all prey types experienced relatively high predation mortality from several different predators.

Although most predator species readily consumed eggs of *H. thoracatum*, predation rates were especially high for the fish predators *H. malabaricus* and *C. callichthys* (Table 6.5). The laboratory predation rates for both species are almost certainly underestimated as these predators consumed all egg-prey present at the start of the trials. Egg predation rates for invertebrate predators are especially noteworthy because this type of predator may have more success in approaching the nest unnoticed by the guarding male than fish predators (Mol 1993b). With the exception of the freshwater snail *P. dolioides* all predator species took 7-day-old larvae of *H. thoracatum* (Table 6.5). Fish predators were the most voracious, followed by Aeshnidae naiads and the large water bug *Belostoma cf harrisi*. Predation rates on larvae may be underestimated to a small extent in *H. malabaricus*, *A. bimaculatus*, *C. callichthys*, *K. guianensis* and *Crenicichla saxatilis* as all these predators consumed 100% of the prey in some of their trials. *Hoplosternum thoracatum*, as a predator, showed cannibalism in preying on conspecific larvae.

For all predator species predation rates on 21-day-old juveniles of *H. thoracatum* were substantially lower than predation rates on larvae (Table 6.5). Three fish predators and four aquatic macro-invertebrates did not consume the 3-week-old juveniles. Only large specimens of the freshwater shrimp *P. carteri* (>3 cm) preyed substantially on 3-week-old juveniles. High predation rates were typical of the fish predators *H. malabaricus* and *C. callichthys*. *Astyanax bimaculatus*, *K. guianensis* and, to a lesser extent, *B. cf harrisi* (Hemiptera) showed moderate predation rates. The pike cichlid *C. saxatilis* was not tested in trials with 3-week-old juveniles.

Predation rates and the number of predator species that managed to prey on juvenile *H. thoracatum* further declined with increasing age (and size) of the prey (Table 6.5). In some fish predators only the larger individuals could handle 5-week-old juveniles. The piscivores *H. malabaricus* and *C. saxatilis* were the only effective predators of 7-week-old juveniles (3.6 cm TL, length pectoral spines 1.3 cm, armour of bony plates present; Table 6.1). *Krobia guianensis* mortally wounded some of these large juveniles but they did not consume the prey. *Belostoma cf harrisi* and Aeshnidae naiads incidentally caught and consumed a plated juvenile.

PREDATION PRESSURE IN THE SWAMP

The potential predation intensities in the swamp (Table 6.6) were obtained by multiplying the laboratory predation rates (I) by the density of the predator in the rainy season. A comparison of laboratory predation rates with estimated predation rates in the swamp (Fig. 6.2) illustrates the effect of the density of the predator on the relative importance of a particular predator to its prey in the swamp. *Callichthys callichthys*, *Crenicichla saxatilis* and, to a lesser extent, *A. bimaculatus* had high predation rates in the laboratory (with all prey developmental stages tested), but their contribution to the potential predation pressure in the swamp was negligible due to their low population density. On the other hand, the small-sized predators with moderate or low laboratory predation rates *P. schomburgki* and *B. cf harrisi* may have a considerable impact on callichthyid populations in the swamp due to their abundance.

Table 6.6. (Potential) predation rates (prey h^{-1} 100m² swamp) on five developmental stages of the armoured catfish *Hoplosternum thoracatum* in Surinamese coastal plain swamps (rainy season). The predation rates were obtained by multiplying laboratory predation rates (Table 6.5) by the density of the predators in the swamp (Tables 6.3 and 6.4).

Predator	Predator density (rainy season) (ind 100m ⁻²)	Prey (developmental stage <i>H. thoracatum</i>)				
		Eggs	1-wk larvae	3-wk jv.	5-wk jv.	7-wk jv.
Fish predators						
<i>A. abramoides</i>	0.1	1.016	0.053	0.000	0.000	
<i>A. bimaculatus</i>	0.1	3.351	0.541	0.069	0.008	0.001
<i>A. bimaculatus</i> >6 cm	0.1		0.304		0.019	0.000
<i>H. boesemani</i>	2	13.858	1.508	0.003	0.000	
<i>H. unilineatus</i>	30.5	479.418	6.255	1.109	0.000	
<i>H. malabaricus</i>	7	848.204	63.858	9.843	2.570	0.318
<i>N. beckfordi</i>	1	1.552	0.089	0.000		
<i>P. filamentosa</i>	16		6.509			
<i>C. callichthys</i>	0.1	11.938	0.836	0.226	0.041	0.000
<i>H. thoracatum</i>	3	35.999	8.529	0.052	0.000	
<i>C. saxatilis</i>	1		0.246		0.000	
<i>C. saxatilis</i> 6-10 cm	0.1	3.549	0.539		0.032	0.000
<i>C. saxatilis</i> >10 cm	0.1		0.828		0.047	0.006
<i>K. guianensis</i>	77	980.646	506.126	55.098	6.176	0.000
<i>K. guianensis</i> >6 cm	3		5.087		0.637	0.046
<i>N. anomala</i>	66	0.000	130.491	5.734	0.000	
<i>P. schomburgki</i>	158	68.912	157.284	16.435	4.752	0.000
<i>S. marmoratus</i>	5	19.630	1.639	0.116	0.000	
Non-fish predators						
<i>P. dolioides</i>	62	1386.660	0.000	0.000		
<i>P. carteri</i>	20	34.330	3.192	0.117		
<i>P. carteri</i> >3 cm	5		1.645	0.650	0.076	0.000
<i>B. cf denticolle</i>	20		2.927	1.155	0.267	
<i>B. cf harrisi</i>	82	109.842	61.562	22.247	9.317	0.628
<i>Ranatra spec</i>	5	36.834	1.609	0.184	0.000	
Aeshnidae larvae	2.5	1.876	2.935	0.264	0.166	0.019
Libellulidae larvae	32		9.827	0.000	0.000	
Dytiscidae larvae	18	149.767	1.355	2.182	0.339	0.000
<i>Hydrophilus</i> adult	4	77.115	0.348	0.000	0.000	
<i>P. paradoxa</i> tadpole	35	0.000	1.274			
Total	655.6	4264.497	977.396	115.484	24.447	1.018

With the exception of 7-week-old juveniles, all prey types may experience a high predation risk from several different predators (Table 6.6; Fig. 6.2). Potentially important predators of eggs and larvae were the freshwater snail *P. dolioides* (egg predator), and the fish predators *H. unilineatus*, *N. anomala*, *P. schomburgki* and *K. guianensis*. Predators of juvenile *H. thoracatum* were *P. schomburgki*, *K. guianensis*, *H. malabaricus* and the water bug *B. harrisi*.

Although laboratory predation rates of invertebrate predators were substantially lower than predation rates of fish predators (Fig. 6.3A) the potential impact of invertebrate predators in the swamp was still relatively large in eggs and juvenile *H. thoracatum* (Fig. 6.3B). The collective predation pressure of the 24 predators on *H. thoracatum* sharply declined with age (size) of the prey (Table 6.6; Fig. 6.4).

The importance of predation in determining callichthyid population densities may be evaluated by comparing the potential predation pressure on *H. thoracatum* as determined from the laboratory experiments (Table 6.6) with the actual mortality of *H. thoracatum* in the swamp. The question is to what extent may predation account for the mortality of *H. thoracatum* as observed in the swamp? Data on the production of armoured catfishes are

Table 6.7. Densities of callichthyid nests and larvae in the swamps at Weg Naar Zee (*H. littorale*) and Lelydorp (*H. thoracatum* and *C. callichthys*). Data from Mol (1993*, in press b**).

	<i>H. littorale</i>	<i>H. thoracatum</i>	<i>C. callichthys</i>
Locality	Weg Naar Zee	Lelydorp	Lelydorp
Total swamp area surveyed (m ²)	157,200	19,930	19,930
Preferred nesting habitat	grass swamp	swamp forest	swamp forest
Area preferred nesting habitat (m ²)	62,360	6730	6730
Number of nests per year**	136	225	70
Number of eggs per nest*	23,339	3,467	5,433
Number of larvae per year	3,174,104	780,075	380,310
Maximum nest density** (nests 100m ²)	0,016	0,821	0,274
Maximum larvae density (larvae 100m ²)	373	2846	1489

shown in Table 6.7. I assume that the guarding male effectively prevents nest (egg) predation and that all eggs that are deposited in the nests also hatch (<3% of the eggs showed deviations in colour or size). Larvae, then, are the first developmental stage of the catfish to be exposed to the predators in the swamp. The 225 nests that were built by *H. thoracatum* at Lelydorp in one year, produced 780075 eggs in the preferred nesting habitat (6730 m² swamp) (Table 6.7). At the end of the rainy season, the density of juvenile *H. thoracatum* was 3 juveniles 100m² (Table 6.3) or 202 juveniles in 6730 m² swamp. If it is assumed that the eggs are all produced at the start of the rainy season (but see Mol in press b) the mortality Z (d⁻¹) during the 180-day rainy season of January-June may be calculated using the equation of constant mortality $N_t = N_0 \exp(-Z \cdot t)$ (addendum) as 0.0459 d⁻¹. The mortality rate of *H. thoracatum* is $1 - e^{-Z}$ (Wootton, 1990) or 4.5% d⁻¹. The daily number of larvae that do not survive is highest on the first day after hatching: $0.045 \times 780075 = 35100$ larvae d⁻¹. The potential predation rate of the 24 predators in the swamp on larvae of *H. thoracatum* is 977.4 ind 100m² h⁻¹ (Table 6.6) or 1578930 larvae d⁻¹ in 6730 m² swamp. When comparing the potential predation rate on larvae of *H. thoracatum* (based on the laboratory experiments; Table 6.6) with the mortality observed in the swamp, it is clear that predation by the 24 predators may easily explain the high mortality of *H. thoracatum* (and *C. callichthys* and *H. littorale*) observed in the swamp. The difference between the potential predation rate on larvae and the actual mortality of callichthyids in the swamp may be attributed to (1) the presence of alternative prey in the swamp (Pepin 1987), (2) the presence of cover provided by the vegetation and bottom substrate in the swamp, and (3) a decrease in the mortality rate with increasing size of the fish (Wootton, 1990; Table 6.6). The effect of (1) and (2) is a decrease in the (potential) predation rate in the swamp, while (3) implies that the assumption of constant mortality during the 180-day period is not valid and that the mortality rate of larvae is higher than the mortality rate of juveniles. With respect to the effect of prey density (Tables 6.1 and 6.7) on the predation rate, it should be noted that the calculations of the density of larvae in the swamp (Table 6.7) are based on the assumption of an even distribution of the larvae and that actual densities in patches at the nest-sites may equal the laboratory density of 330 larvae m⁻² (Table 6.1) the first days after hatching. The effect of spatial patchiness of prey on predation mortality is potentially large (McGurk 1986).

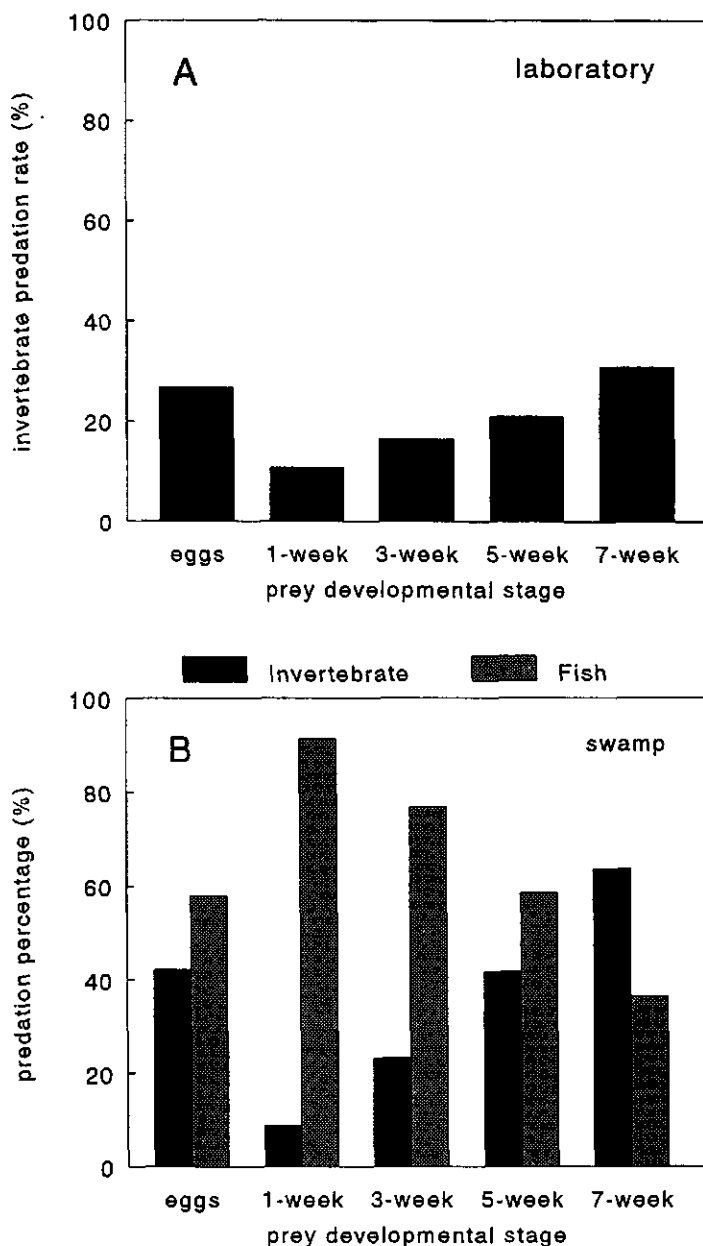


Fig. 6.3. Comparison of predation by invertebrate and fish predators on early developmental stages of the armoured catfish *Hoplosternum thoracatum*. (A) Average laboratory predation rates for invertebrate predators (≤ 9 species) expressed as the percentage of the average predation rates of fish predators (≤ 14 species). (B) Potential predation pressure of invertebrate and fish predators in the swamp expressed as the percentage of the total potential predation pressure (Table 6.6).

PREDATION ON ADULT CATFISH

Predation pressure on adult *Hoplosternum* and *Callichthys* is probably only important in contracted dry season waterbodies (pools, creeks, canals). Predators of adult callichthyids are egrets, caimans, otters, water snakes, *Hoplias malabaricus* (Table 6.8) and also human beings.

DISCUSSION

PREDATOR DENSITIES AND LABORATORY PREDATION RATES

Rotenone sampling was carried out with success in neotropical freshwater bodies by Richter & Nijssen (1980) and Rojas-Beltran (1986). The densities of invertebrate predators in the Surinamese swamps (Table 6.4) were considerably lower than densities I recorded at another occasion with different sampling techniques (Mol 1993a). The rotenone method probably underestimated the abundance of extremely small individuals (and species). The total density of the fishes in the swamp was high compared to the 180 ind 100m² caught with rotenone in a savanna creek in French Guiana (Rojas-Beltran 1986). I do not know of other studies that report densities of neotropical swamp fishes.

In the laboratory trials, all 24 predators preyed on one or more of the early developmental stages of the armoured catfish *H. thoracatum*. Predation on fish eggs, fish larvae or juvenile fish is known in most of the invertebrate predators (Huet 1972; Richards & Davis 1977; Foster *et al.* 1988; Reimchen 1994) and fish predators (Knöppel 1970; Saul 1975; Goulding *et al.* 1988; Winemiller 1989) used in the experiments. Odonata naiads (Singh 1978), the swamp eel *Synbranchus marmoratus* (Singh 1978) and *H. malabaricus* (Saul 1975; Winemiller 1989) were previously reported as predators of callichthyids. Predation on fish eggs or larvae by the freshwater snail *P. dolioides*, the shrimp *P. carteri*, the giant tadpole *P. paradoxa* and some small-sized fishes (*H. boesemani*, *H. unilineatus*, *P. filamentosa*, *N. beckfordi* and *N. anomala*) was not reported before.

Although light intensity is known to affect predator-prey interactions in the field (Hobson 1979) and in the laboratory (Cerri 1983), only two predator-prey combinations showed significant differences in predation dependent on light conditions. The small size of the experimental arenas (high prey density) and the relative large variance in the predation rates (standard errors in Table 6.5) may explain why no effect of light conditions on the predation rates was found. The laboratory predation rates of the invertebrate and fish predators preying on larvae or small juveniles of *H. thoracatum* were of the same order of magnitude as those reported in laboratory studies of marine predators preying on fish larvae (Bailey & Houde 1989).

ONTOGENETIC CHANGES IN PREDATION PRESSURE

Both laboratory predation rates and calculations of the potential predation pressure in the swamps show that each developmental stage of the prey *H. thoracatum* had to face more than one dangerous predator (Tables 6.5, 6.6). In a multi-predator environment, qualitative

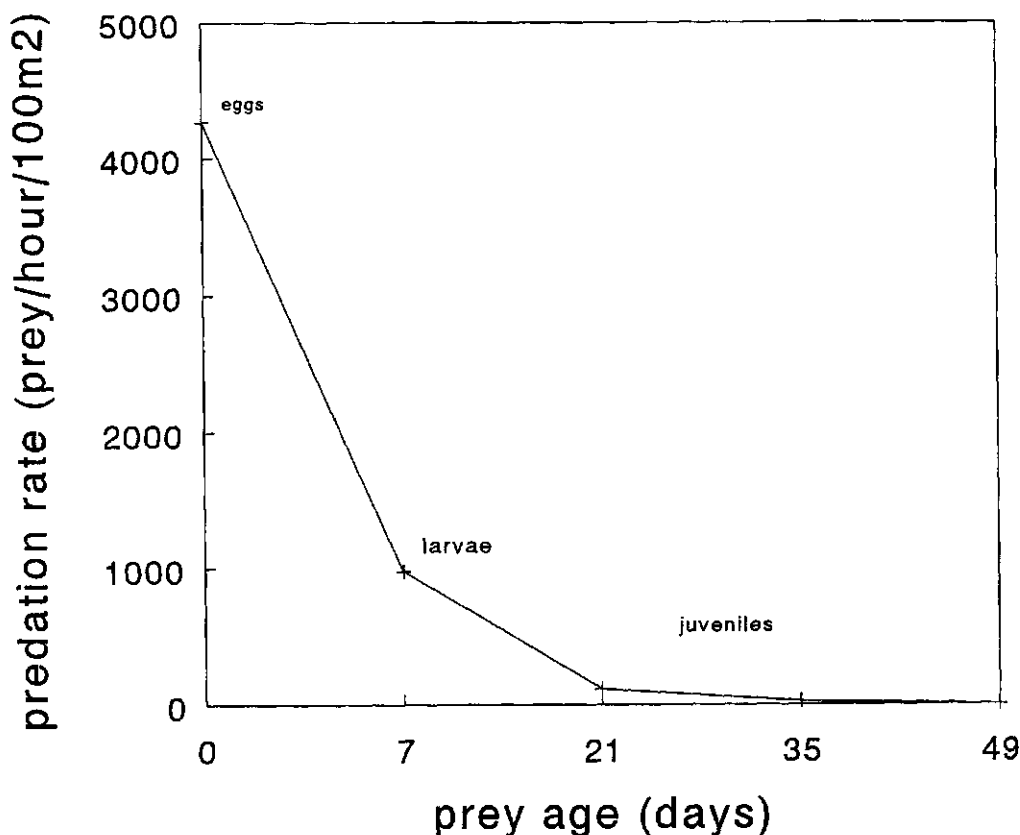


Fig. 6.4. Potential predation pressure in the swamp for five developmental stages of the catfish *Hoplosternum thoracatum*. Combined predation rates of 14 fish predators and 10 non-fish predators (see Table 6.6).

and quantitative changes in the impact of predation may occur during the ontogeny of the prey species. Power (1984) demonstrated a qualitative change in predation pressure on loricariid armoured catfishes, from aquatic predators in juveniles to terrestrial predators in adult catfishes. Sticklebacks were also exposed to different predatory regimes during their ontogeny (Reimchen 1994). In the laboratory, high predation mortality of eggs, larvae and juveniles of *H. thoracatum* resulted from a different set of predators in each developmental stage of the prey (Table 6.5; Fig. 6.2).

The vulnerability of individual prey to predators may first show a small increase with increasing prey size, but then rapidly declines as the prey outgrow their predators (Ware 1975; Zaret 1980; Greene 1986). In the Venezuelan Llanos, prey fish larger than 35 mm standard length were rarely found in the stomach of 9 piscivores among them *H. malabaricus* and *Crenicichla alta* (Prejs 1987; Winemiller 1989). The African tiger-fish *Hydrocynus vittatus*, a gape-limited predator, always swallowed prey less than 40% of its own length

Table 6.8. Predators of adult armoured catfishes *Hoplosternum* and *Callichthys* (10-25 cm TL).

Predator	TL predator (cm)	Prey species	TL prey (cm)	Reference
Fish				
<i>Hoplias malabaricus</i>	40.0	<i>H. littorale</i>	15.0	unpublished stomach contents analysis
<i>H. malabaricus</i>	41.5	<i>Hoplosternum</i> spec.	9.5	unpublished stomach contents analysis
<i>H. malabaricus</i>	30.5	<i>H. littorale</i>	9.5	Winemiller 1989
<i>H. malabaricus</i>		<i>C. callichthys</i>		Saul 1975
Water snakes				
<i>Helicops angulatus</i>	72.0	<i>H. thoracatum</i>	14.0	unpublished stomach contents analysis
<i>Eunectes gigas</i>		armoured catfish		Beebe 1946
Crocodylians				
<i>Caiman crocodilus</i>		<i>Hoplosternum</i> spec.		Schaller & Crawshaw 1982
<i>C. crocodilus</i>		<i>H. littorale</i>		Seijas & Ramos 1980
Birds				
Egrets		<i>Hoplosternum/Callichthys</i>		unpublished (personal observations)
Egrets, kingfishers		loricariid catfish		Power 1984
Otters				
<i>Pteronura brasiliensis</i>		<i>H. thoracatum</i>		Duplaix 1980
<i>Lutra enudris</i>		<i>Hoplosternum/Callichthys</i>		unpublished analysis of spraints

(Jackson 1961). In the laboratory experiments with *H. thoracatum* prey, all predators showed a decrease in their predation rates with increasing size of the prey (Table 6.5). Laboratory predation rates on the largest juveniles (36 mm TL) were extremely low. In addition, the number of predator species that managed to prey on the callichthyids declined with increasing size of the prey (Table 6.5).

Although most prey fish rapidly grow to a size where they are immune from the impact of small predators, Fryer & Iles (1972) held that an abundant small predator can exert a much greater effect on the population of its prey than can a rare large species. Predation by seemingly innocuous predators is probably especially important in size-structured prey populations. Neotropical freshwater bodies characteristically have many small characoid fishes (Gery 1977) that often occur in large numbers (Goulding *et al.* 1988). Most of these species are omnivorous (Knöppel 1970; Saul 1975; Goulding *et al.* 1988). When the density of the predators in the Surinamese swamps was taken into account, small-sized (but abundant) predators with low laboratory predation rates did contribute more to the total predation pressure on the callichthyids than the rare large 'piscivores' *H. malabaricus* and *C. saxatilis* (Fig. 6.2; Table 6.6). Although the impact of invertebrate predators on eggs and larvae of marine fishes is well-known (Bailey & Houde 1989), it is here demonstrated for the first time that aquatic invertebrates due to their abundance can also have a major impact on freshwater fish populations (Fig. 6.3). Prejs (1987) held that the abundance of predators which can eat a particular prey is probably the best measure of the predation pressure on the prey. However, in this study it is shown that a combination of the density of the predators and their predation rates on the prey is a better measure of predation pressure. With the predation rates of the 24 predators combined, predation pressures on armoured catfish sharply declined with increasing size of the prey (Fig. 6.4).

EFFECT OF PREDATION ON MORTALITY OF *HOPLOSTERNUM THORACATUM*

When comparing the yearly production of *H. thoracatum* larvae (Table 6.7) with the density of juveniles in the rotenone samples of May-June at the end of the reproductive season (Table 6.3) it is clear that mortality of *H. thoracatum* is extremely high in the pre-adult period. High mortality rates may be caused by abiotic factors (e.g. stranding, oxygen deficiency) or biotic factors (starvation and predation). There are few quantitative estimates of the mortality of fish caused by predators (Bailey & Houde 1989). Eggs and yolk sac larvae do not depend on the environment for their food supply and, in a benign abiotic environment, their mortality rate must be due to predation. Mortality rates of yolk sac larvae may be as high as 60-80% d⁻¹ (Dahlberg 1979; Hewitt *et al.* 1985; Bailey & Houde 1989). Eggs of *H. thoracatum* are deposited in a bubble nest that is guarded by the male, but predation on the unguarded larvae by 24 predators could easily explain the high mortality of *H. thoracatum* observed in the Surinamese swamps. Even if only 2.5% of the potential predation (Table 6.6) will be realized due to other prey available (Tables 6.3, 6.4) the high mortality of *H. thoracatum* in the swamps can be explained as the effect of predation. If the rich fauna in nests of *H. littorale* (Mol 1993b) and the presence of leeches in nests of *H. thoracatum* (personal observations) are taken into account, incidental predation on callichthyid eggs may also occur in the swamps.

In large enclosures (mesocosm) with abundant food supply, Oiestad (1985) demonstrated that predation was also an important cause of mortality in older, post-yolk sac larvae of marine fish. In juvenile *H. thoracatum*, predation pressure rapidly declines with age (size) (Fig. 6.4). Three-week-old juveniles still have to face numerous predators in the swamp (Table 6.6), but increased size and the development of defence mechanisms such as a bony armour and pectoral spines presumably protect older juveniles from most predators. In French Guiana, early reproduction after the first flooding of the swamps may give the offspring of *H. littorale* a lead in growth over the offspring of their predators (Mol in press b). However, in Suriname the first rains of December/January are not reliable and a reproductive strategy based on a single contracted breeding season after the first rains would imply the risk of a total failure of reproduction in years with deficient rainfall (Mol in press b). When the swamps dry up and callichthyids are trapped in contracted dry season water bodies large piscivores (e.g. *Hoplias*), caimans and birds may have a serious impact on juveniles and even on adults (Lowe-McConnell 1964, 1987). The drying up of small pools in times of retreating swamp water may also contribute further to the mortality of stranded catfish (Lowe-McConnell 1964, 1987). This was observed for juvenile *H. littorale* at Weg Naar Zee. Adults may escape desiccation or predation by birds in such dry season pools by moving over land to deeper water bodies (Mol in press b).

PREDATION AND COMPETITION AMONG ARMOURED CATFISHES

A previous study of the feeding ecology of *H. thoracatum*, *H. littorale* and *C. callichthys* (Mol in press a) has demonstrated high interspecific diet overlap among larvae, juveniles and adults of the three species. I also found significant differences in the nest (micro)habitat of the three catfishes (Mol in press b). According to the 'compression hypothesis' (MacArthur & Wilson 1967) high interspecific diet overlap and (nest) habitat

segregation may result from strong interspecific competition among the three catfishes. However, the present study suggests that the combined predation pressure of 24 aquatic predators on early developmental stages of *H. thoracatum* (and presumably also *H. littorale* and *C. callichthys*) is capable of reducing callichthyid population densities to a level at which competition may not be important.

Differences in the nest habitat and reproductive ecology among the callichthyids may be related to competition (Mol in press b) but also to the strong predation pressure on eggs and larvae. Male *H. littorale* built their nest in deepest water in herbaceous swamps and aggressively defend the nest-site against intruders (Mol in press b). The larvae hatch simultaneously, a strategy which may satiate predators present at the nest-site at the time of hatching (Ims 1990). While male *H. thoracatum* and *C. callichthys* are less aggressive at the nest-site than *H. littorale*, both species select sheltered nest-sites under trees, in very shallow water or, in *C. callichthys*, in holes of earth and tree-roots (Mol in press b). Eggs are deposited in the nest at regular intervals and the larvae hatch in batches (Mol 1993b). In both foam-nesting leptodactylid frogs (Heyer 1969) and cichlids (McKaye 1984) nest-site selection has been associated with differential predation pressure. The structure of the callichthyid bubble nest, in effectively positioning the eggs above the water surface out of reach of aquatic predators (Mol 1993b), and the clustering of nests of *H. thoracatum* (Mol in press b) may also have an anti-predator function (Dominey 1981).

Other behavioural and also morphological characteristics of the callichthyids are probably related to strong predation pressure. In view of the extremely high predation pressure on the eggs of armoured catfish (Fig. 6.4) the nest guarding behaviour of the male must be an important factor in the reproductive success of these catfish. The reason why the guarding behaviour is not extended to the larvae (in spite of their apparent vulnerability to predators in the swamps; Fig. 6.4) is probably the need for dispersal to avoid food depletion at the nest site. The armour of bony plates and stout pectoral spines offer protection from fish predators (Hoogland, Morris & Tinbergen 1957; McLean & Godin 1989; Reimchen 1994). Lowe-McConnell (1969) pointed out that catfishes with an armour of bony plates are poorly represented in African freshwaters where predation appeared to her less pronounced than in South America. In swamp vegetation, the striped colour pattern of juveniles of *H. thoracatum* and *H. littorale* (Fig. 6.1) may conceal the catfish from predators. Aquatic macro-invertebrates (Mol 1993a) and small fish predators are especially abundant in floating vegetation. Juveniles of *C. callichthys* lack these stripes, but this species breeds in holes or in very shallow water without much aquatic vegetation (Mol in press b). Kramer & Graham (1976) suggested that synchronous air breathing in *H. thoracatum* has an anti-predator function analogous to schooling, but with clustering in time rather than in space. Synchronous air breathing was also observed in *H. littorale* (personal observations; Boujard, Moreau & Luquet 1991).

In Suriname, three bottom dwelling armoured catfishes with similar diets live together in coastal plain swamps. The three catfishes are quite similar in size and morphology, and probably members of the same ecological guild (Root, 1967). Stable coexistence of strong competitors is possible if interspecific competition is alleviated. This study suggests that the predators in the swamps are capable of reducing population densities of armoured catfishes to a level at which competition is no longer important. It seems that in armoured catfishes, ontogenetic changes in defense mechanisms result in a situation in which both predation and competition exert control at different times in the life cycle (Werner 1986; Menge &

Sutherland 1987). Predators probably kill most of the larvae and juveniles, leaving only a few individuals to escape and reach adulthood. However, if the number of escapes would exceed the number of deaths in the adult size-class, the populations eventually become sufficiently dense to compete. In this situation nest habitat segregation may prevent competitive exclusion of one of the species.

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ADDENDUM

Derivation of the equation of instantaneous prey mortality due to predation Z_{pred} of de Lafontaine & Leggett (1988) from the basic equation of (constant) mortality between time $t=0$ and $t=t$ (Wootton 1990)

$$N_t = N_0 \cdot \exp(-Z \cdot t) \quad \text{basic equation of constant mortality}$$

$$\exp(-Z \cdot t) = N_t / N_0$$

in the predation experiments: $N_t = N_f$ and
 $: N_0 = N_i$ and
 $: t = T$

$$\exp(-Z \cdot T) = N_f / N_i$$

if only mortality due to predation must be calculated: $N_i = N_c$

$$\exp(-Z_{pred} \cdot T) = N_f / N_c$$

$$-Z_{pred} \cdot T = \ln(N_f / N_c)$$

$$Z_{pred} \cdot T = \ln(N_c / N_f)$$

$$= \ln((N_i / N_f) \cdot (N_c / N_i))$$

$$= \ln(N_i / N_f) - \ln(N_i / N_c)$$

$$Z_{pred} = (\ln(N_i / N_f) - \ln(N_i / N_c)) / T$$

If P predators are used in the experiment, then the predation rate Z_{pred} per predator is

$$Z_{pred} = (\ln(N_i / N_f) - \ln(N_i / N_c)) / (P \cdot T) \quad (\text{de Lafontaine \& Leggett 1988})$$

Definitions

- Z = instantaneous per capita mortality rate
- Z_{pred} = instantaneous prey mortality due to predation
- N_0 = number of prey at time $t = 0$
- N_t = number of prey at time $t = t$
- N_i = number of prey at the start of the predation experiment
- N_f = final number of prey in tank with predator
- N_c = final number of prey in control tank
- T = the duration of the predation experiment
- P = number of predators in the experiment

Chapter 7

Morphology, chemical composition and specific gravity of three armoured catfishes (Siluriformes-Callichthyidae) in relation to the aquatic environment

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Abstract

Morphometric analysis of three closely related armoured catfishes, *Callichthys callichthys*, *Hoplosternum littorale* and *Hoplosternum thoracatum* (Callichthyidae), revealed interspecific differences between shallow-bodied *C. callichthys* on the one hand and both deep-bodied *Hoplosternum* species on the other hand. Morphological differences between *H. littorale* and *H. thoracatum* were small. The most conspicuous features of the three armoured catfishes were their thick armour of bony plates, their reduced swimbladder, and the functioning of their intestinal tract as an accessory respiratory organ. The heavy armour and reduced swimbladder accounted for the unusually high specific gravity of these catfishes. The function(s) of the catfish armour are discussed in relation to the aquatic environment of the fishes. In addition to its function as a respiratory organ, the gas-filled intestinal tract also functions as a hydrostatic organ. Both functions of the callichthyid intestine are probably more important in standing waters of tropical swamps than in running water of small rainforest creeks. The chemical composition of the three armoured catfishes showed pronounced seasonality within each species, but only minor interspecific differences.

INTRODUCTION

Neotropical catfishes of the family Callichthyidae are characterized by their heavy armour of bony plates consisting of a head shield of fused bony plates and two rows of bony scutes on each side of the body (Bhatti, 1938). Superficially the Callichthyidae resemble primitive fossil fish groups like the ostracoderms and placoderms in appearance (e.g. Moy-Thomas & Miles, 1971).

Hoedeman (1952) distinguishes two subfamilies within the Callichthyidae. The subfamily Corydoradinae consists of a large number of small-sized species in the genera *Corydoras* (>110 species), *Aspidoras* (15) and *Brochis* (3) (Burgess, 1989). Most corydoradinids are collected in shaded rainforest creeks with relatively cool, running water. Five slightly larger species of the genera *Callichthys* (1), *Dianema* (2) and *Hoplosternum* (2) make up the subfamily Callichthyinae.

Callichthys callichthys L., 1758, *Hoplosternum littorale* (Hancock, 1828) and *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840) are conspicuous inhabitants of the

vast swamps of South America (Carter & Beadle, 1931). Although *C. callichthys* and *H. thoracatum* also occur in Amazonian rainforest creeks (Mol, 1994), all three species show adaptations to standing waters of tropical swamps characterized by extremely low concentrations of dissolved oxygen. Eggs of the three species are deposited in floating bubble nests out of the oxygen-depleted swamp water (Mol, 1993). Adults are capable of aerial respiration and use the intestinal tract as an accessory respiratory organ (Carter & Beadle, 1931; Huebner & Chee, 1978).

The Callichthyidae belong to the "Siluriformes abnormales" (Bridge & Haddon, 1894), a group of catfish families distinguished from other catfishes by an extremely small swimbladder. Bridge & Haddon (1894) suggested that the reduced swimbladder volume, resulting in a negative buoyancy, evolved to promote a benthic life, particularly in fast running water. The heavy armour of bony plates will also contribute further to the density of the Callichthyidae (Alexander, 1965). The great majority of callichthyid catfishes are found in the lotic environment of small streams and rainforest creeks.

Alexander (1964) further advanced the hypothesis that a reduced swimbladder volume could have evolved to compensate for the increased buoyancy resulting from gas held in the accessory respiratory organ during air-breathing in species that live in standing waters. However, Gee (1976) pointed out that several armoured catfishes with a reduced swimbladder volume showed no ability for aerial respiration (e.g. most Corydoradinae and Loricariidae) and that species with the highest capacity for air-breathing do not have the smallest swimbladder volume.

Qasim & Hasan (1961) were the first to point out that the gas contained in accessory respiratory organs will increase the buoyancy of a fish. Gee (1976) found that *H. thoracatum* breathed air in normoxic (near air-saturated) water and hypothesized that this was done in part to keep the accessory respiratory organ at the requisite volume for optimal buoyancy (assuming that O₂ was removed without equivalent replacement of CO₂; Johansen, 1970). Gee & Graham (1978) discussed the respiratory and hydrostatic functions of the intestine of *H. thoracatum* and *Brochis splendens*.

This paper analyses the external morphology, body composition and specific gravity of three closely related callichthyid catfishes, *C. callichthys*, *H. littorale* and *H. thoracatum*. We are especially interested in the role of the body armour in the ecology and physiology of the armoured catfishes. In Suriname, *H. littorale* is found in standing waters of coastal plain swamps while *C. callichthys* and *H. thoracatum* occur in both coastal plain swamps and rainforest creeks of the interior (Mol, 1994). In other parts of South America, *H. littorale* also seems to be restricted to a lentic environment (Carter & Beadle, 1931; Mol, 1994). Here, we investigate 1) how the morphology and chemical composition of the three catfishes is related to the environment in which they live, and 2) what are the differences and similarities in morphology and body composition among the three species.

MATERIALS AND METHODS

MORPHOMETRIC ANALYSIS

Adult specimens of *C. callichthys* (n=25), *H. littorale* (n=25) and *H. thoracatum* (n=25) were collected in coastal plain swamps of northern Suriname as part of a previous

study of the feeding ecology of the three catfishes (Mol, in press a). Most morphometric data were obtained following methods developed by Nijssen (1970) for catfishes of the genus *Corydoras* (Callichthyidae). The characters with their conventional abbreviations are: (1) TL, total length, from the snout to the end of the caudal fin; (2) SL, standard length, from snout to caudal end of vertebral column (hypural plate); (3) BD, maximum body depth; (4) BW, maximum body width; (5) HL, head length, from snout tip to the posterior edge of the operculum; (6) HD, head depth at the posterior edge of the operculum; (7) HW, head width at the posterior edge of the operculum; (8) WI, least width of interorbital region; (9) LBO, horizontal length of the bony orbit (eye diameter); (10) SN, snout length, from snout tip to the nearest edge of the bony orbit; (11) MW, mouth width, horizontal distance across the inner side of the open mouth; (12) UBL, length of the barbel of the upper lip; (13) LBL, length of the barbel of the lower lip; (14) DCP, least depth of the caudal peduncle; (15) WCP, least width of the caudal peduncle; (16) LDS, length of the dorsal spine; (17) LPS, length of the pectoral spine; (18) DBS, number of dorsolateral body scutes; (19) VBS, number of ventrolateral body scutes; (20) PAS, number of azygous pre-adipose scutes; (21) PFR, number of pectoral fin rays; (22) VFR, number of pelvic fin rays; (23) DFR, number of dorsal fin rays; (24) AFR, number of anal fin rays; (25) CFR, number of caudal fin rays; (26) AC, aspect ratio of the caudal fin S^2/A (S = tail height; A = surface area tail blade). All continuous characters were measured to the nearest 0.1 mm with vernier callipers. Only male fish were used in calculations of LPS because in all three species the length of the pectoral spine showed sexual dimorphism. Although in all three species the pectoral spine of males is larger than the pectoral spine of females (Winemiller, 1987; Boujard & Meunier, 1991), inspection of the gonads is often necessary to distinguish males from females. The number of vertebrae was counted using radiographs.

In most fishes body measurements covary strongly with body size, while counts of scutes and fin rays do not change during growth. Linear regression analysis was used to evaluate the relationship between continuous morphometric characters and standard length. Principal components of continuous data were computed from the covariance matrix of logarithmically transformed data. The logarithmic transformation preserves allometries, standardizes variances, and produces a scale-invariant covariance matrix (Jolicoeur, 1963). Character ratios are often used in the description of species. To investigate the behaviour of ratios with respect to body size, all possible pairs of continuous morphometric characters were used to generate 182 ratios (the ratio and its reciprocal for each character pair), and their correlations were examined across species with the standard length. Ratios of raw data were used to be consistent with taxonomic practice. Ratios were considered to be satisfactory descriptive when they were uncorrelated with standard length ($r \leq 0.10$).

BUOYANCY AND CHEMICAL ANALYSIS

Armoured catfishes from the coastal plain swamps of northern Suriname were obtained alive at the central market of Paramaribo in October-November (dry season) and May-June (rainy season). Freshly killed specimens of the three catfishes were weighted (± 0.1 g) in air and in tap water (26°C) with a 1000 g torsion balance. Care was taken for the weighing under water to have no bubbles of air inside the mouth or on the armour of the catfish. Water analyses of swamp water and tap water are provided by Mol (1994).

Table 7.1. Morphological characters of three armoured catfishes (adults), *C. callichthys*, *H. littorale* and *H. thoracatum*, from the Surinamese coastal plain (continuous characters: mean \pm SE; n=25). All continuous morphometric characters in mm, except fresh weight in g. Results of Kruskal-Wallis tests for differences among species (p) are given.

Character	<i>C. callichthys</i>	<i>H. littorale</i>	<i>H. thoracatum</i>	p
Total length	164.3 \pm 3.6	165.8 \pm 3.5	157.0 \pm 1.6	0.20
Standard length	133.8 \pm 2.7	128.4 \pm 3.0	125.4 \pm 1.3	0.12
Axial length	164.3 \pm 3.6	152.5 \pm 3.2	157.0 \pm 1.6	0.04
Body depth	28.7 \pm 0.8	40.7 \pm 1.0	37.0 \pm 0.6	<0.01
Body width	35.3 \pm 1.0	34.4 \pm 0.8	33.9 \pm 0.6	0.45
Head length	29.6 \pm 0.5	36.2 \pm 0.7	32.5 \pm 0.4	<0.01
Head depth	23.2 \pm 0.8	31.9 \pm 0.8	28.3 \pm 0.4	<0.01
Head width	35.0 \pm 0.8	33.1 \pm 0.9	32.0 \pm 0.5	0.04
Interorbital width	20.7 \pm 0.5	23.2 \pm 0.6	22.0 \pm 0.2	<0.01
Orbital diameter	3.7 \pm 0.1	6.1 \pm 0.1	5.2 \pm 0.1	<0.01
Snout length	9.8 \pm 0.3	14.6 \pm 0.4	13.6 \pm 0.3	<0.01
Mouth width	13.8 \pm 0.4	12.4 \pm 0.3	11.9 \pm 0.3	<0.01
Upper barbel length	30.9 \pm 1.1	37.5 \pm 0.9	35.9 \pm 0.8	<0.01
Lower barbel length	42.4 \pm 1.2	57.5 \pm 2.0	61.7 \pm 1.2	<0.01
Caudal peduncle depth	21.0 \pm 0.5	20.7 \pm 0.5	20.8 \pm 0.3	0.83
Caudal peduncle width	8.0 \pm 0.3	9.1 \pm 0.4	9.2 \pm 0.3	0.02
Dorsal spine length	4.5 \pm 0.2	14.3 \pm 0.3	12.2 \pm 0.3	<0.01
Pectoral spine length ♂	33.6 \pm 1.4	35.2 \pm 3.1	31.5 \pm 1.6	0.75
Pectoral spine length ♀	19.1	22.2 \pm 1.0	24.2 \pm 1.7	-
Fresh weight	77.1 \pm 4.6	89.9 \pm 6.7	78.7 \pm 3.5	0.37
Vertebrae*	26	23	23	
Dorsolateral scutes	28	25	25	
Ventrrolateral scutes	26	23	23	
Pre-adipose scutes	16	7	8	
Pectoral fin rays	I+6	I+8/9	I+7	
Pelvic fin rays	I+5	I+5	I+5	
Dorsal fin rays	I+7	I+8/9	I+8	
Anal fin rays	I+6	I+7	I+7	
Caudal fin rays	14	14	14	
Aspect ratio caudal fin	1.440	1.907	1.565	

* not included in the vertebrae count are the first vertebra, the enlarged "complex vertebra" (the fused second, third, and fourth vertebrae) and the fifth and sixth vertebrae; counting started with the first free moving (= 7th) vertebra.

Direct measurements were made of the contribution of the gas in the intestinal tract to the buoyancy of the fish. The volume of the gas in the intestinal tract was determined by obtaining the weight of the intact fish in water, opening the intestine under water and squeezing out its gas, and reweighing the fish under water. The difference in weight (g) equals the volume (ml) of gas in the intestine (Gee, 1970). The contribution to the buoyancy by the intestinal tract was determined by dividing the volume of the gas in the intestinal tract by the weight of the gas-free fish in water ($<1.0 \text{ ml g}^{-1}$ = negative buoyancy; 1.0 ml g^{-1} = neutral buoyancy). Correction for depth of capture in the measures of buoyancy was not possible, but the three catfishes occur in shallow swamps with water depths $\leq 1 \text{ m}$ (Mol, in press b) and differences in depth would have an almost negligible effect on measurements of the intestine volume. The volume of the extremely small swimbladder (Alexander, 1964; Fig. 7.2) was not determined.

For chemical analysis the fresh weight and dry weight of the fish were determined with an analytical balance ($\pm 0.1 \text{ mg}$). The water content of the fish was determined after

Table 7.2. Ratios of continuous morphometric characters and standard length of three armoured catfishes (adults), *C. callichthys*, *H. littorale* and *H. thoracatum*, from the Surinamese coastal plain (mean \pm SE; n=25). Results of Kruskal-Wallis tests for interspecific differences in the ratios are given (p). *Hoplosternum littorale* and *H. thoracatum* differed in ratios marked with an asterisk (Kolmogorov-Smirnov test, $p < 0.05$).

Character/SL	<i>C. callichthys</i>	<i>H. littorale</i>	<i>H. thoracatum</i>	p
Body depth /SL *	21.5 \pm 1.4	31.7 \pm 0.3	29.5 \pm 0.4	<0.01
Body width /SL	26.4 \pm 1.7	26.9 \pm 0.5	27.0 \pm 0.4	0.94
Head length /SL *	22.2 \pm 0.4	28.3 \pm 0.2	25.9 \pm 0.2	<0.01
Interorbital width /SL	15.6 \pm 0.4	18.0 \pm 0.2	17.5 \pm 0.1	<0.01
Orbital diameter /SL *	2.7 \pm 0.1	4.8 \pm 0.1	4.1 \pm 0.1	<0.01
Snout length /SL	7.4 \pm 0.2	11.4 \pm 0.2	10.9 \pm 0.2	<0.01
Mouth width /SL	10.3 \pm 0.2	9.7 \pm 0.2	9.5 \pm 0.2	<0.01
Upper barbel length /SL	23.3 \pm 0.7	29.4 \pm 0.6	28.9 \pm 0.7	<0.01
Lower barbel length /SL	32.0 \pm 0.8	46.3 \pm 1.9	49.7 \pm 1.0	<0.01
Caudal peduncle depth /SL	15.8 \pm 0.2	16.2 \pm 0.2	16.6 \pm 0.1	0.01
Caudal peduncle width /SL	6.0 \pm 0.2	7.1 \pm 0.2	7.3 \pm 0.2	<0.01
Dorsal spine length /SL *	3.4 \pm 0.2	11.2 \pm 0.2	9.7 \pm 0.2	<0.01
Pectoral spine length δ /SL	24.5 \pm 0.6	25.4 \pm 1.6	25.2 \pm 1.5	0.77

drying the fish for 48 h at 70° C. The dry weight of the lateral bony armour and of the axial skeleton and head bones was determined. The whole fish was then thoroughly ground with a meat grinder. The crude lipid content was determined after extraction with petroleum ether in a Soxhlet apparatus. Total nitrogen was determined using the method of Kjeldahl. The protein content was taken as being 6.25 x total nitrogen. The mineral content of the fish was determined after ashing in a muffle furnace at 600° C for 6 h.

RESULTS

SIZE AND SHAPE VARIATION

The three armoured catfishes superficially resembled each other in appearance (Fig. 7.1), but a closer look revealed significant interspecific variation in external morphology. Most continuous characters differed significantly among species (Table 7.1). Although the three catfishes differ to some extent in their maximum body size (170 mm SL in *C. callichthys*, 195 mm SL in *H. littorale* and 150 mm SL in *H. thoracatum*), 95% of the specimens we used in collecting morphometric data were between 110-150 mm SL, and standard length did not differ significantly among the three species (Table 7.1). Consequently, most ratios of continuous character/standard length were also different among species (Table 7.2). Within the given data set only 8 out of 13 continuous morphometric characters were significantly correlated with standard length (Table 7.3). PCA resulted in a low correlation between standard length and the first principal component (accounting for 50.3% of the total variance in the data; PC2 accounted for 25.3% of the variance) (Table 7.3).

Of the 182 ratios generated from the raw data, only 28 were uncorrelated with standard length ($r \leq 0.10$). When both a ratio and its reciprocal were size-free, the one with the lowest correlation coefficient was selected, giving a total of 17 ratios. Another 12 ratios of character pairs having no obvious functional relationship to one another were omitted from

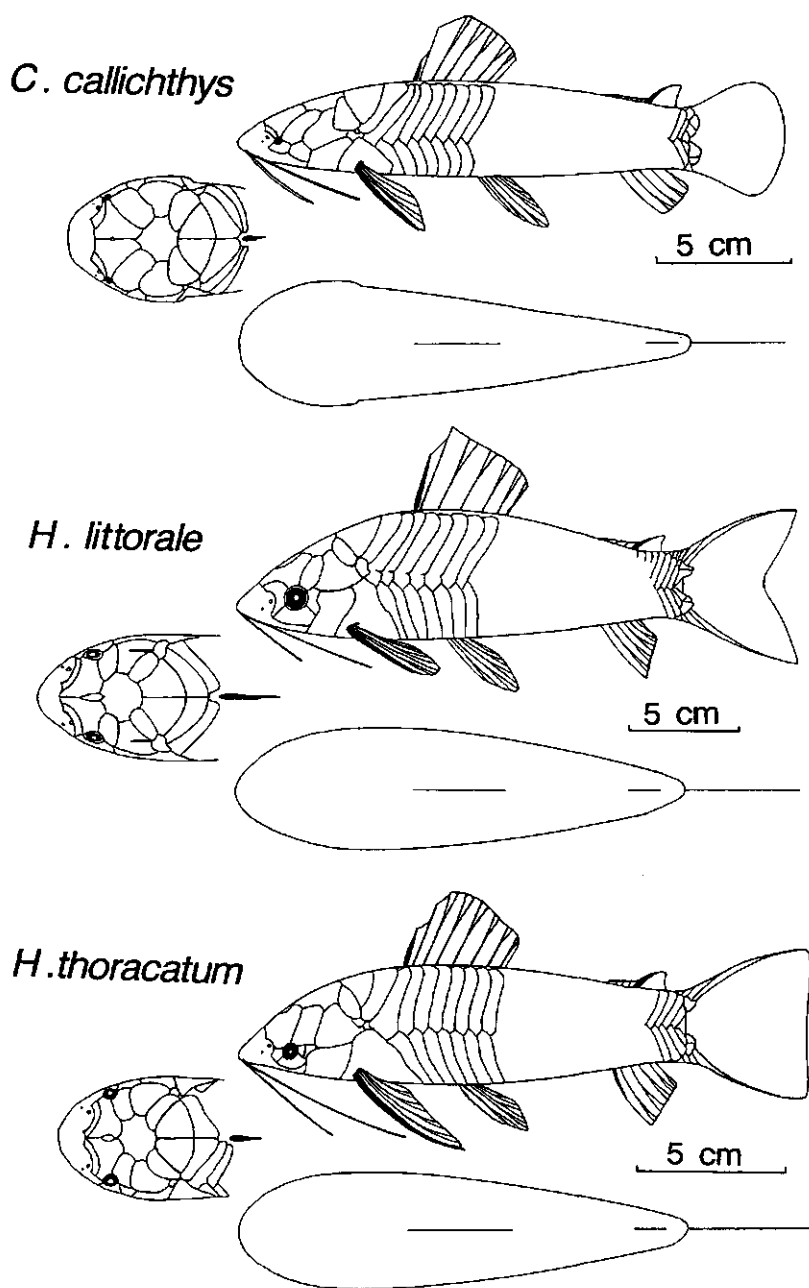


Fig. 7.1. General body morphology of three closely related South American armoured catfishes *C. callichthys*, *H. littorale* and *H. thoracatum* (Callichthyidae).

Table 7.3. Slope of linear regression (\pm SE) of morphometric characters to standard length, and correlations of the characters with standard length and the first two principal components in PCA. Slopes marked with an asterisk are not significantly different from 0 ($p > 0.05$).

Character	Slope of linear regression	Correlation with		
		Standard length	PC1	PC2
Standard length	-	-	0.027	0.927
Body depth	0.65 \pm 0.22	0.33	0.910	0.308
Body width	0.93 \pm 0.10	0.75	0.150	0.854
Head length	0.55 \pm 0.13	0.44	0.814	0.445
Snout length	0.38 \pm 0.27*	0.16	0.870	0.129
Interorbital width	0.71 \pm 0.11	0.61	0.597	0.653
Orbit diameter	0.20 \pm 0.33*	0.07	0.875	0.055
Mouth width	1.01 \pm 0.13	0.68	-0.204	0.826
Upper-barbel length	0.37 \pm 0.19*	0.23	0.744	0.233
Lower-barbel length	-0.33 \pm 0.29*	0.14	0.791	-0.129
Caudal-peduncle depth	0.89 \pm 0.06	0.86	0.226	0.898
Caudal-peduncle width	0.58 \pm 0.23	0.28	0.451	0.415
Dorsal-spine length	-1.07 \pm 0.66*	0.19	0.914	-0.243
Pectoral-spine length (δ)	1.24 \pm 0.27	0.61	-	-

the set of size-free ratios. The remaining five ratios were selected as the most reasonable descriptive variables: BD/HL, BW/SL, MW/SL, MW/BD and SN/LBO (Table 7.4). In addition, we added two ratios commonly used in descriptions of species of *Corydoras* (HL/SN and HL/LBO; Nijssen & Isbrücker, 1980) and two ratios including body depth (BD/BW and DCP/BD) to Table 7.4 (all four ratios are correlated to a small extent with standard length ($r \leq 0.15$)).

Most morphometric variation was found between *C. callichthys* on the one hand and both *Hoplosternum* species on the other hand (Figs. 7.1, 7.2; Tables 7.1, 7.2, 7.4). Compared to both *Hoplosternum* species, *C. callichthys* was relatively shallow bodied with a short head, a short snout, small eyes, short barbels, a large mouth, a short dorsal spine, a large number of vertebrae and associated lateral scutes, and a low aspect ratio of its rounded caudal fin. *Hoplosternum littorale* differed from *H. thoracatum* in its deeper body, longer head, larger eye, larger dorsal spine, and in the form and aspect ratio of its caudal fin (Table 7.2; Fig. 7.1). The BW/SL ratio did not differ among the three catfishes (Table 7.4) and is optimal for reducing drag (Hertel, 1966).

CHEMICAL ANALYSES

The three catfishes differed only to a small extent in their chemical composition (Table 7.5). The water content was relatively low in all three species when compared to other fishes (80-85%; Love, 1957), but fat content (in the dry season) and especially mineral content (8.2-11.4% fresh weight) were very high. Mineral content was highest in *H. thoracatum* (9.7-11.4% fresh weight) and lowest in *C. callichthys* (8.2-8.8% FW). The dry weight of the head shield, lateral scutes and axial skeleton accounted for 52 and 67% of the body dry weight (or 17.5 and 23.0% of the fresh weight) in *C. callichthys* (dry season) and *H. thoracatum* (rainy season) respectively.

Table 7.4. Character ratios (mean \pm SE; $n=25$) uncorrelated with standard length ($r < 0.15$) for three armoured catfishes. All ratios multiplied by 100. Results of Kruskal-Wallis tests for difference among the three species are given (p). *Hoplosternum littorale* and *H. thoracatum* differed in ratios marked with an asterisk (Kolmogorov-Smirnov test, $p < 0.05$).

Character ratio	Correlation with SL (r)	<i>C. callichthys</i>	<i>H. littorale</i>	<i>H. thoracatum</i>	p
BD/BW *	-0.14	81.7 \pm 1.39	118.7 \pm 1.74	109.4 \pm 1.33	<0.01
DCP/BD *	0.13	73.4 \pm 0.94	51.0 \pm 0.46	56.3 \pm 0.69	<0.01
BD/HL	0.10	97.1 \pm 1.80	112.4 \pm 1.04	113.8 \pm 1.44	<0.01
BW/SL	0.09	26.4 \pm 0.46	26.9 \pm 0.47	27.0 \pm 0.36	0.94
MW/SL	0.01	10.3 \pm 0.20	9.7 \pm 0.19	9.4 \pm 0.18	0.01
MW/BW	0.07	39.3 \pm 0.76	36.4 \pm 0.84	35.2 \pm 0.86	<0.01
HL/SN *	-0.11	306.1 \pm 7.43	249.1 \pm 4.20	240.5 \pm 5.24	<0.01
HL/LBO	0.12	840.5 \pm 29.6	601.0 \pm 14.7	631.2 \pm 13.6	<0.01
SN/LBO	0.07	281.4 \pm 15.1	243.4 \pm 7.8	264.4 \pm 6.9	0.09

All three species showed seasonal differences in condition, body composition and specific gravity (Table 7.5). The fishes were in better condition in the dry season than in the rainy season, the difference being significant for *C. callichthys* and *H. littorale* (Kolmogorov-Smirnov test, $p < 0.05$). The building up of large visceral fat deposits in the dry season (Mol, in press a) is reflected in the high dry-season fat content (Table 7.5). Water and mineral contents tended to be lower in the dry season than in the rainy season. Seasonal differences in water content, protein content, fat content and mineral content (ash) were significant for *C. callichthys* and *H. thoracatum* (Kolmogorov-Smirnov test, $p < 0.05$). Seasonal differences in water content, protein content and mineral content were not significant in *H. littorale* (Kolmogorov-Smirnov test, $p > 0.05$), possibly due to the too small sample size of rainy season specimens (Table 7.5). The specific gravity of the three species (with gas removed from the intestine) was significantly higher in the rainy season than in the dry season (Kolmogorov-Smirnov tests, $p < 0.05$). The low density of the catfishes in the dry season probably results from the dry season fat deposits.

BUOYANCY

Observations in aquariums indicated that all three catfishes were negatively buoyant during aerial respiration, remaining on or near the bottom most of the time. The specific gravity of freshly killed specimens was found to be 1.04-1.05 (Table 7.5). With the gas removed from the intestinal tract the specific gravity was 1.10-1.12 in *C. callichthys*, 1.09-1.12 in *H. littorale* and 1.12-1.13 in *H. thoracatum*. The volume of the gas in the intestine varied between 3.5 and 5.1 ml. The contribution of the gas in the intestine to the buoyancy of the fish varied between 0.47 and 0.64 ml g^{-1} fresh weight. The swimbladder of both *Callichthys* and *Hoplosternum* is reduced and encapsulated in bone (Fig. 7.2; Alexander, 1964). Gee (1976) demonstrated that the contribution of the swimbladder to the buoyancy of *H. thoracatum* was small (± 0.02 ml g^{-1}) compared to the contribution of the gas-filled intestine. Radiographs also show the extreme ossification of the exoskeleton of callichthyid catfishes and the gas in the intestine (Fig. 7.2).

Table 7.5. Condition, chemical composition, specific gravity and contribution to buoyancy by the intestinal tract in three armoured catfishes (adults), *C. callichthys*, *H. littorale* and *H. thoracatum*, from the Surinamese coastal plain in the dry season and rainy season. Note the small sample size of rainy season specimens of *H. littorale*.

Parameter	<i>C. callichthys</i>		<i>H. littorale</i>		<i>H. thoracatum</i>	
	Dry season (n=10)	Rainy season (n=10)	Dry season (n=10)	Rainy season (n=4)	Dry season (n=10)	Rainy season (n=10)
Standard length SL (mm)	139 ± 2	138 ± 4	126 ± 4	135 ± 12	120 ± 2	115 ± 3
Fresh weight FW (g)	85.6 ± 2.8	72.5 ± 8.2	92.9 ± 12.0	99.2 ± 30.2	65.2 ± 2.5	50.1 ± 4.3
Dry weight (g)	28.6 ± 1.3	20.2 ± 1.9	35.6 ± 4.7	35.9 ± 10.6	25.3 ± 1.0	16.1 ± 1.6
Condition factor (FW/SL ³)	3.12 ± 0.07	2.62 ± 0.08	4.08 ± 0.07	3.73 ± 0.05	3.83 ± 0.05	3.23 ± 0.09
Water (%FW)	66.5 ± 1.0	71.3 ± 0.7	61.7 ± 0.7	63.6 ± 0.6	59.8 ± 0.4	68.2 ± 0.5
Protein (Nx6.25) (%FW)	17.9 ± 0.8	17.4 ± 0.5	17.0 ± 0.4	19.1 ± 1.2	17.6 ± 0.2	15.9 ± 0.5
Fat (%FW)	7.4 ± 0.7*	2.5 ± 0.4	12.2 ± 0.6*	4.8 ± 0.9	10.9 ± 0.5*	2.4 ± 0.3
Ash (%FW)	8.2 ± 0.2	8.8 ± 0.5	9.0 ± 0.3	10.5 ± 0.4	9.7 ± 0.3	11.4 ± 0.4
Lateral bony scutes (%DW)	29.6 ± 1.2	31.0 ± 0.9	31.2 ± 0.7	28.8 ± 1.0	35.2 ± 0.5	37.1 ± 0.5
Body armour + axial skeleton (%DW)	51.9 ± 1.6	62.5 ± 1.3	55.3 ± 1.1	56.8 ± 0.6	57.3 ± 0.7	67.3 ± 1.4
Specific gravity with air in intestine	1.05 ± 0.00	1.05 ± 0.00	1.04 ± 0.00	1.06 ± 0.00	1.05 ± 0.00	1.04 ± 0.00
Without air in intestine	1.10 ± 0.00	1.12 ± 0.00	1.09 ± 0.00	1.12 ± 0.00	1.12 ± 0.00	1.13 ± 0.00
Volume intestine (ml)	3.81 ± 0.29	4.24 ± 0.63	3.50 ± 0.38	5.12 ± 1.60	4.07 ± 0.38	3.61 ± 0.32
Buoyancy intestine (ml g ⁻¹)	0.47 ± 0.03	0.55 ± 0.05	0.54 ± 0.03	0.48 ± 0.00	0.54 ± 0.03	0.64 ± 0.03

* n = 8

Table 7.6. Contribution of body components to the specific gravity and buoyancy of three armoured catfishes *Callichthys callichthys*, *Hoplosternum littorale* and *Hoplosternum thoracatum*. %FW = percentage of fresh weight. Wwater = weight (g) in fresh water per 100 g fish (negative weights imply that the component has a positive buoyancy in fresh water).

Component	Specific gravity	<i>C. callichthys</i>				<i>H. littorale</i>				<i>H. thoracatum</i>			
		Dry season		Rainy season		Dry season		Rainy season		Dry season		Rainy season	
		%FW	Wwater	%FW	Wwater	%FW	Wwater	%FW	Wwater	%FW	Wwater	%FW	Wwater
Fat	0.91 1)	7.4	-0.73	2.5	-0.25	12.2	-1.21	4.8	-0.47	10.9	-1.08	2.4	-0.24
Protein	1.33 2)	17.9	+4.89	17.4	+4.32	17.0	+4.22	19.1	+4.74	17.6	+4.37	15.9	+3.94
Body fluids	1.013 3)	66.5	+0.85	71.3	+0.91	61.7	+0.79	63.6	+0.82	59.8	+0.77	68.2	+0.88
Other components including bone	4)	8.2	+4.09	8.8	+5.73	9.0	+4.40	10.5	+5.62	9.7	+6.64	11.4	+6.92
Whole fish without gas in intestine			+9.1		+10.7		+8.2		+10.7		+10.7		+11.5
Gas in intestine		0.0	-4.3	0.0	-5.9	0.0	-4.4	0.0	-5.0	0.0	-5.9	0.0	-7.7
Whole fish with gas in intestine			+4.8		+4.8		+3.8		+5.7		+4.8		+3.8

1) Biology Data Book (1964).

2) Biology Data Book (1964). Specific gravity is taken as the reciprocal of the partial specific volume.

3) We assume that the density of the body fluids is half way between that of distilled water and sea water (Denton & Marshall, 1958).

4) Specific gravity values are given by difference. Percentage FW is given as ash percentage (Table 7.2).

Using the data from Table 7.5 it is now possible to draw up balance sheets (Denton & Marshall, 1958) showing the buoyancy properties of the three armoured catfishes (Table 7.6). The bones of the skeleton and body armour accounted for 50-60% of the weight of the fishes in water. Protein accounted for approximately 35-45% of the weight of the fishes in water. The gas in the intestines provided approximately 50% of the lift required to attain neutral buoyancy in *C. callichthys* and *H. littorale* while it supported up to 67% of the body weight of *H. thoracatum*. In the rainy season fat supported 8, 15 and 10% of the weight of *C. callichthys*, *H. littorale* and *H. thoracatum*, respectively.

DISCUSSION

The most conspicuous morphological feature of *C. callichthys*, *H. littorale* and *C. callichthys* is their heavy armour of bony plates (Bhatti, 1938). The weight of the dried armour and skeleton of the three callichthyids (20% of the body fresh weight) was high compared to the weight of the armour and skeleton of the loricariid armoured catfish *Hypostomus* (= *Plecostomus*) (13% FW; Alexander, 1965) and to the scales and skeleton of three cyprinid species (5.5, 7.1 and 8.1% FW; Alexander, 1959). The bony armour and reduced swimbladder (Bridge & Haddon, 1894; Alexander, 1964) accounted for the unusually high specific gravity of the three callichthyids (1.09-1.13 with gas removed from the intestinal tract). Most fish which lack a swimbladder have specific gravities of 1.06-1.09 (Jones & Marshall, 1953). The loricariid armoured catfish *Hypostomus* has a specific gravity of 1.10 (Alexander, 1965). The armour of the three catfishes may function in:

- (1) keeping the fish close to the bottom and in the same position in running water (Alexander, 1965). The high density of the fish due to the heavy armour (and reduced swimbladder) increases frictional forces between the fish and the bottom substrate.

- (2) offering protection against predators (reflected in the use of terms like "armour" or "shield"). The armour may also reduce the palatability of the catfish (Lowe-McConnell, 1987).

- (3) providing a storage site for minerals, especially calcium and phosphorus necessary for muscle activity (Moy-Thomas & Miles, 1971). However, it is not clear how the callichthyids obtain the minerals necessary for the formation of the armour and how they prevent leakage of Ca and P from the gills in Amazonian waters with low ion concentrations, described by Sioli (1950) as slightly contaminated distilled water. Luquet *et al.* (1991) stress the need to study the Ca and P metabolism of armoured catfishes living in water with low electric conductivity.

- (4) offering protection against desiccation when the fish move over land in order to escape from drying pools in the dry season (e.g. Carter & Beadle, 1931; L\"uling, 1971; Mago, 1970; personal observations).

- (5) offering protection against damage from collisions with rocks in rapids and in streams that may change into raging torrents in the rainy season.

C. callichthys, *H. littorale* and *H. thoracatum* are bottom dwelling catfish. They are probably occasional swimmers; the low aspect ratio of the caudal fin nor the body form show adaptations to low cost permanent swimming (Webb, 1984). *Hoplosternum littorale* has a forked caudal fin with a relatively high aspect ratio and is more often observed in the water

column than *C. callichthys* and *H. thoracatum* (personal observations in aquariums). The armour of these catfishes may impede manoeuvrability. At night the catfish wriggle along in the mud and bottom debris of swamps or shallow streams (Lowe-McConnell, 1991). In daylight the fish rest most of the time on the bottom (personal observations in aquariums). The mouth is small and toothless, and the diet of adults consists mainly of bottom invertebrates such as chironomid larvae and Oligochaeta (Mol, in press a). The mouth of *Callichthys* is slightly larger than the mouth of both *Hoplosternum* species and *C. callichthys* may occasionally consume a small fish (Mol, in press a). All three species have large pectoral spines with an elaborate locking mechanism (Hoedeman, 1960). Both the pectoral spines and the dorsal spine are probably highly effective in defence against predators (Lowe-McConnell, 1987). The dorsal spine of *C. callichthys* is considerably shorter than the dorsal spine of both *Hoplosternum* species. *Callichthys callichthys* lives in extremely shallow water where large aquatic predators are probably not abundant (Power, 1984).

The body of *C. callichthys* is very shallow compared to the body of both *Hoplosternum* species. The flattened shape of *C. callichthys* allows this fish to live in small headwater creeks and in shallow water at the very edge of the swamps. The floating bubble nests of *C. callichthys* were found in extremely shallow water and in holes at the edge of the swamp (Mol, 1993; in press b). While in shallow waterbodies, *C. callichthys* must face the risk of being captured in drying pools when the water starts to retreat at the end of the rainy season. *Callichthys callichthys* is the most amphibious species of the three armoured catfishes and it was observed moving considerable distances (>100 m) over land (Lüling, 1971; personal observations). We observe in this respect that *C. callichthys* has the lightest body armour of the three species. The large number of vertebrae of *C. callichthys* (compared to *Hoplosternum*) may assist in an eel-like movement when travelling over land.

Both *Callichthys* and *Hoplosternum* are capable of air-breathing. The transparent wall of the intestinal tract of *C. callichthys* and both *Hoplosternum* species is structurally adapted to a respiratory function (Carter & Beadle, 1931; Huebner & Chee, 1978). Although accessory respiratory organs like the callichthyid intestine probably evolved as an adaptation to the oxygen-depleted environment of tropical standing waters (Carter & Beadle, 1931), they may also function as a hydrostatic organ (Qasim & Hasan, 1961). The gas in the intestinal tract of the three callichthyids provided 50-67% of the lift needed to remain neutrally buoyant. Gee (1976) found that the intestine of *H. thoracatum* supported 70% of the weight of the fish in water and the small swimbladder only 2%. Gee & Graham (1978) provided evidence for the functioning of the intestinal tract of *H. thoracatum* as a buoyancy regulating organ.

In standing waters of tropical swamps the advantage of being denser than water is hard to see because remaining stationary on the bottom represents no problem and the fish are obliged to make periodic visits to the surface for air. In the swamps the intestinal tract of armoured catfish may have a double function: primarily as an accessory respiratory organ and secondary as a hydrostatic organ. In the relatively cool, oxygen-rich running water of rainforest creeks there is probably no need for an accessory respiratory organ. A decrease in density associated with a gas-filled intestine will force the catfish to spend more energy in maintaining its position on the bottom of the creek. In Suriname (and South America), *C. callichthys* and *H. thoracatum* are found in both rainforest creeks with running water and swamps with standing water (Mol, 1994). Gee & Graham (1978) show that *H. thoracatum*

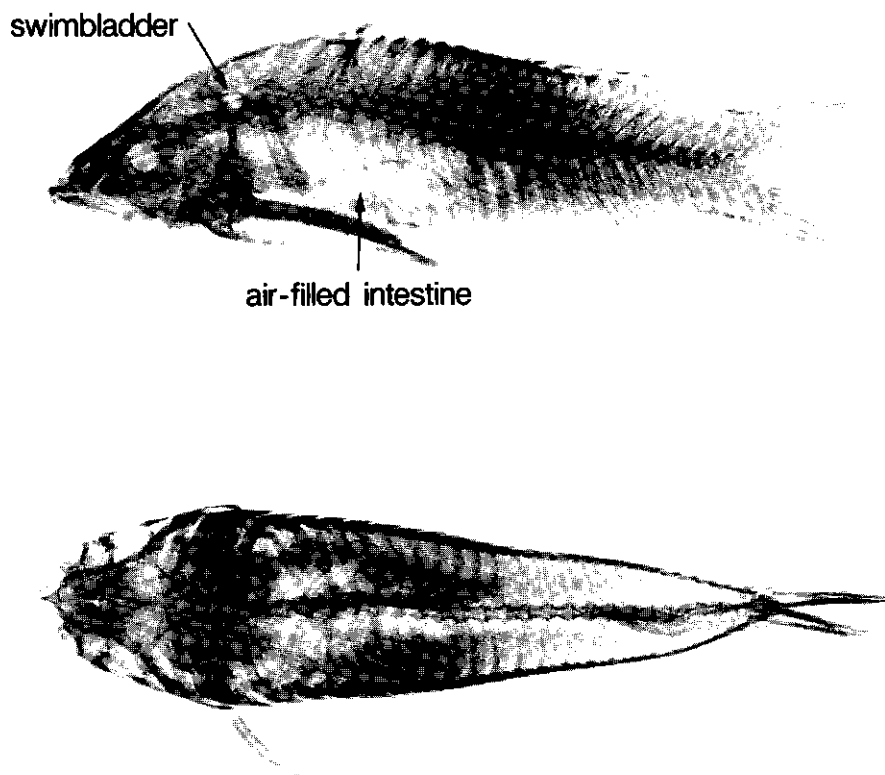


Fig. 7.2. Radiographs of an adult male *Hoplosternum littorale* (156 mm SL) showing the reduced swimbladder, the air-filled intestine, and the extensive ossification of the body armour.

is a facultative air-breather. In theory it should be possible for *H. thoracatum* to adjust its specific gravity to the velocity of the water in its environment by changing the volume of gas in its intestine. *Hoplosternum littorale* occurs mainly in swamps with standing water (Mol, 1994). In this environment the high specific gravity of armoured catfishes is probably not advantageous and with a gas-filled intestinal tract these fishes may reduce the costs of swimming. Carter & Beadle (1931) showed that *H. littorale* is in fact an obligate air-breather.

The chemical composition of the three catfishes (Table 7.5) may be compared to the water, fat, protein and ash content of 40 Amazonian species studied by Junk (1985) and to the chemical composition of *H. littorale* from fish ponds in French Guiana (Luquet *et al.*, 1991). The great majority of the species analyzed by Junk (1985) showed a pronounced seasonality in chemical composition. *Callichthys callichthys*, *H. littorale* and *H. thoracatum* were in better condition in the dry season than in the rainy season. Singh (1978) also noted a deterioration of the condition of *H. littorale* following reproduction in the rainy season. As a result of spawning the loss in weight was much higher in females than in males (Singh,

1978). The three catfishes showed seasonal differences in fat content (Table 7.5) associated with the building up of large visceral fat deposits in the first months of the dry season (Mol, in press a). The fat is apparently utilized prior to the rainy season for the building up of the gonads. Junk (1985) found seasonality in fat storage especially pronounced in migratory species. The water content of *Callichthys* and *Hoplosternum* varied inversely with fat content. Graphs of the relationship of water content to fat content ('fat-water lines') are well known in many fishes (Love, 1970; Junk, 1985). The protein content of the three armoured catfishes showed no marked seasonal change and was within the range of protein values of Amazonian fishes (17-20%; Junk, 1985). The chemical composition of *H. littorale* from the swamps of Suriname agreed well with that of *H. littorale* from fish ponds in French Guiana (Luquet *et al.*, 1991). Considering the differences in water quality between coastal plain swamps and rainforest creeks (Mol, 1994), it may be of great interest to determine the chemical composition of *C. callichthys* and *H. thoracatum* from rainforest creeks in the interior of Suriname. Geisler & Schneider (1976) showed that differences in the mineral composition of the vertebral column of two species of discus fish (*Symphysodon*) reflected the chemistry of the water from which they were sampled.

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Chapter 8

Fisheries and culture of armoured catfishes in northern South America with recommendations based on recent ecological studies

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Abstract

The fisheries and fish culture of three medium-sized armoured catfishes, *Callichthys callichthys*, *Hoplosternum littorale* and *Hoplosternum thoracatum* (Siluriformes-Callichthyidae), are of considerable importance in some countries in northern South America. In French Guiana, Guyana, Suriname and Trinidad the three catfishes are considered a delicacy with high commercial value. In Brazil and Venezuela, armoured catfishes are an important source of animal protein to poor people. In addition, both Brazil and Venezuela export minor quantities of armoured catfish to Europe, the U.S.A. and Canada. When the three species are compared, *Hoplosternum littorale* is the most valued as a food fish while *Hoplosternum thoracatum* is the most popular among ornamental fish hobbyists. A post-1970 decline in the landings of armoured catfishes in Suriname is discussed in relation to recent ecological research on the three species. I suggest some improvements to the Surinamese fish protection legislation and I also recommend the conservation of one of the major habitats of armoured catfishes: the freshwater swamps and swamp forests of the coastal plain. The state of art and perspectives of the culture of armoured catfishes are discussed in the light of recent developments in aquaculture research with *Hoplosternum littorale* in French Guiana. The culture of fingerlings of *H. littorale* for the stocking of fishing canals, family ponds and natural waterbodies, and a polyculture of *H. littorale* with large Amazonian food fishes such as *Colossoma* spp are probably the most promising options.

INTRODUCTION

For the human population of tropical South America fish is traditionally the most important source of animal protein (Junk, 1984). Neotropical freshwater fisheries are of great economic importance but often difficult to study (Junk, 1984; Lowe-McConnell, 1984; Petrere, 1989). Until recently the supply of fish was sufficient and there was no need for the development of a fish culture. Therefore, fish culture has no tradition in South America and even today people often consider it uneconomic. However, Goulding (1980), Junk (1984) and Lowe-McConnell (1984) mentioned recent declines in catches of preferred species near large centers of human population suggesting local over-exploitation of the stocks. The introduction

of exotic fish species, pollution, and habitat modifications due to deforestation, the creation of hydroelectric barrages, dams blocking wetland drainage, also present major threats to the fisheries (Petrere, 1989; Lowe-McConnell, 1994). Junk (1984) stresses the need for an immediate and strong development of Amazonian fish culture.

Three medium sized armoured catfishes of the family Callichthyidae, *Callichthys callichthys* L., 1758, *Hoplosternum littorale* (Hancock, 1828) and *Hoplosternum thoracatum* (Cuvier & Valenciennes, 1840), are regarded as a delicacy (with high attached commercial value) in some countries in northern South America: French Guyana (Luquet *et al.*, 1989), Guyana (Singh, 1978), Suriname (Rondeel, 1965) and Trinidad (Singh, 1978). As a group the three armoured catfishes are known as Tamuata in Brazil (Tuma, 1978; Smith, 1979), Atipa in French Guiana (Planquette, 1989), Hassar in Guyana (Singh, 1978), Kwikwi in Suriname (Mol, 1993), Cascadura in Trinidad (Singh, 1978) and Busco or Curito in Venezuela (Novoa, 1982). The popularity of the armoured catfishes is given expression in folklore (Selvon, 1972) and in its depiction on a stamp of Suriname. Market needs of the largest and most popular of the three species, *H. littorale*, are partly covered (or were covered in the case of Suriname) by import from Brazil and Venezuela. Small quantities of *H. littorale* are also exported from both Brazil and Venezuela to West Indian immigrant communities in Canada and England (Singh, 1978) and Surinamese immigrants in the Netherlands. In Brazil, *H. littorale* is caught in swamps of the Ilha de Marajo near Belem (Tuma, 1978), but it is not an important species in the freshwater fisheries (Smith, 1979; Goulding, 1981; Petrere, 1989) nor highly valued for its taste. Important fisheries on *H. littorale* are reported for the Venezuelan Llanos and the Orinoco delta (Novoa, 1982). *Hoplosternum littorale* is present in large numbers in dry-season water bodies of the Llanos (Mago, 1970; Winemiller, 1987). In both Brazil and Venezuela callichthyid catfishes are important in small-scale subsistence fisheries, where they provide animal protein to poor people.

In spite of the introduction in Suriname of extensive fish protection legislation directed to armoured catfishes (Rondeel, 1965), landings of these fishes dropped in the years 1970-1993 to approximately one quarter of the pre-1970 period (Ouboter & Mol, 1994). Subsequent calls for the development of a culture of armoured catfish are not only strong in Suriname, but also in French Guyana (Luquet *et al.*, 1989), Guyana (Hickling, 1961) and Trinidad (Singh, 1978). *Hoplosternum littorale* is being cultured on a small (experimental) scale in Guyana, Suriname and Trinidad (Lovatelli & Loria, 1993) while the intensive culture of *H. littorale* was investigated more thoroughly in French Guiana by scientists of the Institut National de la Recherche Agronomique (INRA) (e.g. Luquet *et al.*, 1989; Pascal *et al.*, 1994).

Since the important work of Carter & Beadle (1931) knowledge of the ecology of armoured catfishes has increased exponentially (Willmer, 1934; Singh, 1978; Machado-Allison & Zaret, 1984; Machado-Allison, 1986; Winemiller, 1987; Gautier *et al.*, 1988; Hostache *et al.*, 1993; Mol, 1993, 1994, in press b). The implications of the ecology of armoured catfish for a healthy development of the fisheries and culture of these catfish have been discussed by Singh (1978). In the light of recent ecological investigations (see above) it seems appropriate to reexamine the relation of the ecology of armoured catfish to the sustainable development of its fisheries and culture.

ARMoured CATFISH FISHERIES

MAJOR NEOTROPICAL FISHERIES ON ARMoured CATFISHES

Rapidly developing fisheries on *H. littorale* in the Orinoco delta (Venezuela) were described by Novoa (1982). Singh (1978) described the fisheries on *H. littorale* in Trinidad and in Guyana. A concise description of the Surinamese fisheries on armoured catfishes is provided by Ouboter & Mol (1994). In all fisheries, the main fishing period is the dry season (low water period).

In the Orinoco delta fishermen worked in groups of 6-8 men (Novoa, 1982). Fishing trips of 2-7 days were made with boats of ≥ 10 m length and a storage capacity of 2000-4000 kg. In the period 1979-1982 the mean total catch of the 47 boats in use was estimated at approximately 680,000 kg *H. littorale* per year (Novoa, 1982). Armoured catfish were caught with 40-80 m long nets of 2.5 cm stretched mesh. While driving the catfish into a refuge area of floating vegetation by slapping the water the fishermen slowly pull the 5-10 m high net around the refuge vegetation. The floating vegetation is then removed from the area encircled by the net, and both net and fish are pulled into the boat.

In Guyana, Suriname and Trinidad there are few full-time fishermen involved in freshwater fisheries. Most are farmers for whom the armoured catfish fishery serves as a source of extra cash in the dry period between the planting and harvesting of their crops. The main fishing gears are cast net, gill net and seine (all 2.5 cm stretched mesh). When these nets are used large areas must usually be cleared of floating vegetation. In addition gill nets must be regularly emptied as the air-breathing armoured catfish tend to die by drowning if prevented from surfacing. Fish traps made from bamboo or wire netting are used when water levels rise or fall with changing seasons and local currents are set up. A large trap used in Trinidad and Suriname is described by Singh (1978; p.37). Hook and line is used in Suriname and in Trinidad (Singh, 1978). In Suriname, angling the armoured catfishes is a national sport (Ouboter & Mol, 1994). In the dry season, high yields of armoured catfish are recorded from irrigation and drainage canals of sugar-cane fields in Guyana (Hickling, 1961) or rice fields in Suriname (personal observations). In the breeding season (rainy season) a rather destructive method of fishing *H. littorale* is practiced in Trinidad (Singh, 1978) and Suriname (Ouboter & Mol, 1994). The aggressive nest-guarding males are caught at the nest-site by beating the water while a hand net is positioned under the bubble nest. Once the male attacks the source of disturbance the net with trapped fish is lifted. The eggs are then removed from the nest and cooked. Experienced fishermen may catch both male and multiple egg-laying females (Mol, 1993) by positioning a basket over the nest when they notice the nest shaking during the act of oviposition.

RECENT DEVELOPMENTS IN SURINAMESE FISHERIES ON ARMoured CATFISH

The Surinamese fisheries on armoured catfish are carried out in extensive freshwater swamps, swamp forests and cultivated lands in the coastal plain. In the period 1955-1969 an average of $79,400 \pm 10,700$ kg year⁻¹ (mean \pm S.E.) of armoured catfish (the three species taken together) passed through the central market of Paramaribo in Suriname (Ouboter & Mol, 1994). In this period the production of armoured catfish was approximately 30% of the annual catches of swamp fish and 4% of the annual landings of fish and shrimps in Suriname

(which consist mainly of marine species; Charlier, 1993). The importance of armoured catfishes to the fisheries of Suriname may be underestimated to some extent as catches of farmers for direct consumption and catches of sport fishermen are not included in the figures mentioned above.

Concern of the Surinamese government for the potential problem of over-fishing resulted in the fish protection legislation of 1961 (Rondeel, 1965). To a large extent the legislation is directed to the protection of the national fish, the Kwikwi (mainly *H. littorale*, but both *C. callichthys* and *H. thoracatum* are included in the laws). The 1961 fish protection legislation not only establishes a 'closed season' for fishing and transporting armoured catfishes from 1 April to 15 July (main breeding season) and a minimum size of 12 cm for fishable catfish, but it also explicitly prohibits destruction, disturbance and removal of nests and eggs of armoured catfishes (Rondeel, 1965).

In spite of the excellent fish protection legislation of 1961, the supply of armoured catfish to the central market of Paramaribo dropped in the period 1970-1993 to approximately one quarter of the pre-1970 figures: $18,300 \pm 2600 \text{ kg year}^{-1}$ (mean \pm S.E.) (Ouboter & Mol, 1994; Fig. 8.1). The difference with the landings in the pre-1970 period is highly significant (Mann-Whitney-U test, $p < 0.0001$). Over the same period, landings of other swamp fish (e.g. *Hoplerethrinus unitaeniatus*) also showed a comparable negative trend (Fig. 8.1). The decreasing supplies of armoured catfishes are of great concern to the Surinamese people. Prices of armoured catfish are soaring and effectively place this extremely popular fish out of reach of the largest part of the population. In recent years attempts have been made by the Fisheries Department of the Ministry of Agriculture to improve data collection (Charlier, 1993), but the number of qualified scientists to deal with the problems is quite insufficient.

POSSIBLE THREATS TO THE ARMoured CATFISH FISHERIES

Mol & Van der Lugt (in press) pointed out that the decline in the landings of armoured catfishes does not necessarily reflect a bad condition of the stocks. An increase in the fishing activities of anglers and a growing rural population may force professional fishermen to travel long distances to unexploited fishing grounds and in this way reduce their catch per unit effort. Nowadays more people are fishing the armoured catfishes and the catch per fisherman is often too small to sell the fish at the market. However, if the decrease in the supply of armoured catfish really reflects a bad status of the stocks several factors may be responsible, viz. 1) introduced species, 2) pesticides, and 3) habitat destruction.

(1) Surinamese fishermen have accused the exotic Tilapia *Oreochromis mossambicus* (Peters, 1852) of bringing about a decrease in the catches of armoured catfish. The Tilapia was introduced to Suriname in 1955 by the Fisheries Department for aquaculture and stocking natural water bodies (Lijding, 1958). Populations of *O. mossambicus* stocked in brackish lagoons expanded rapidly (Mol & Van der Lugt, in press), but landings of the Tilapia to the central market of Paramaribo (Ouboter & Mol, 1994; Fig. 8.1) show that, until recently, the Tilapia was not fully accepted by the Surinamese people. Although the distribution in Suriname of the Tilapia and the armoured catfish *H. littorale* show almost complete overlap (Mol, 1994; Mol & Van der Lugt, in press), important differences in both diet and habitat use make a strong interaction between the two species unlikely (Mol & Van

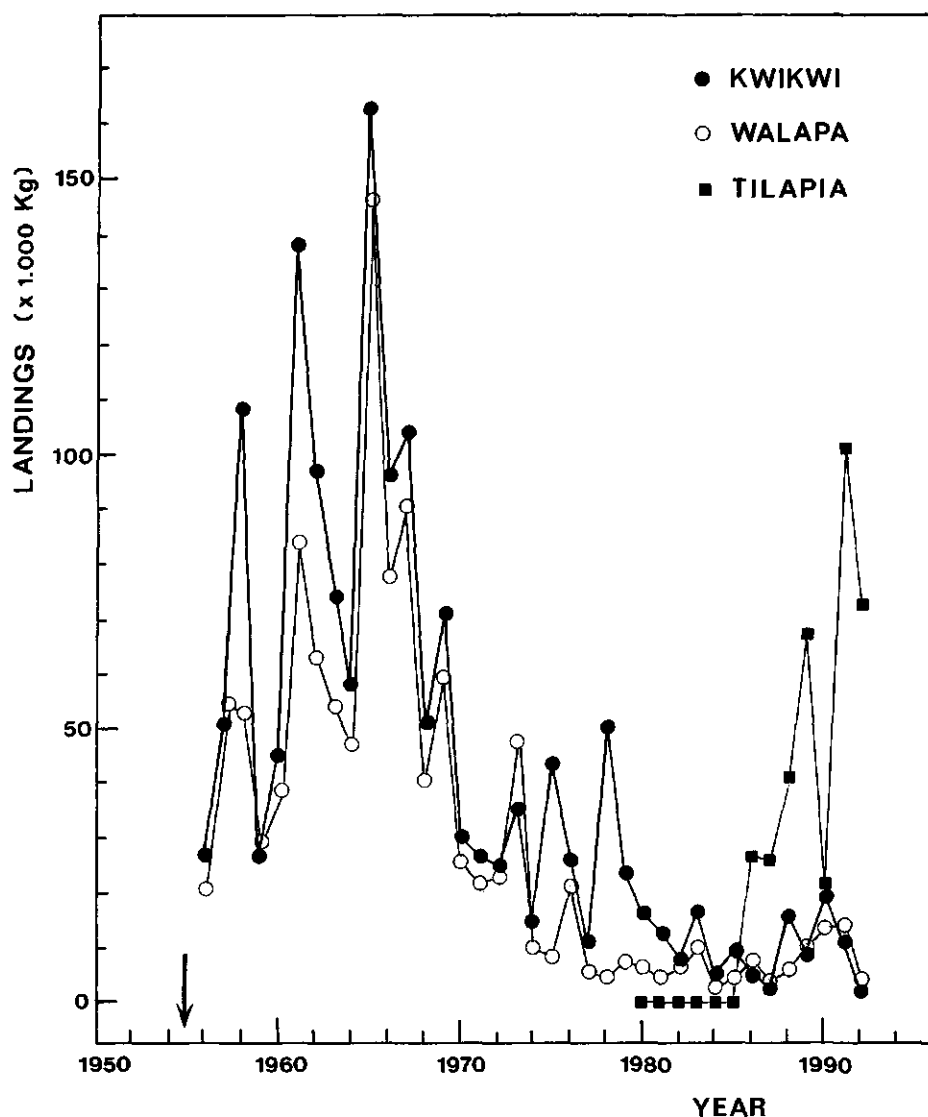


Fig. 8.1. Landings of Kwikwi (*Hoplosternum littorale*, *Hoplosternum thoracatum* and *Callichthys callichthys*), Walapa (*Hoplerthrinus unitaeniatus*) and Tilapia (*Oreochromis mossambicus*) at the central market of Paramaribo (Suriname) in the period 1956-1993. The arrow points to the year in which *O. mossambicus* was introduced to Suriname. Subsequent release of the Tilapia in natural waterbodies by the Fisheries Department started in 1956. The figure is based on unpublished data of the Fisheries Department of the Ministry of Agriculture, Animal Husbandry and Fisheries (from Ouboter & Mol, 1994).

der Lugt, in press). The suspicion of Surinamese fishermen of a predatory behaviour of Tilapia toward young armoured catfish is probably based on the misinterpretation of the mouth-breeding habit of the Tilapia.

(2) Extensive use of pesticides in agriculture will also have negative effects on the stocks of armoured catfishes. Vermeer *et al.* (1974) describe large fish kills after extensive application of NaPCP and other pesticides in rice fields in west Suriname. High levels of pentachlorophenol were found in tissues of snails, frogs, caimans, birds and fishes (among them *H. littorale*). Following spraying with Endrin, Vermeer *et al.* (1974) also found a high residue of this insecticide in dead *H. littorale*. Since the study of Vermeer *et al.* (1974) the large scale application of extremely toxic pesticides like NaPCP and Endrin is no longer customary in the rice fields. I did not observe any large kills of armoured catfish in rice fields in the period 1987-1994. However, armoured catfish are hardy fish which even construct their nests in the extremely polluted ditches of the capital Paramaribo (personal observations) and a sublethal effect of pesticides on catfish is much more difficult to detect in the field. The effect of various pollutants (insecticides) on early life stages of armoured catfish (e.g. eggs and larvae) is unknown but probably important.

(3) A serious threat to the armoured catfishes is the destruction or modification of their habitat. *Callichthys callichthys* and *H. thoracatum* occur in small creeks of the hilly interior of Suriname. The effect of the construction of the Brokopondo hydroelectric barrage in the interior of Suriname on the composition of the fish fauna 14 years later was investigated by Richter & Nijssen (1980). Out of 53 species collected in 1966-67 shortly after the construction of the dam, 30 were not collected in 1978, among them both *C. callichthys* and *H. thoracatum* (Richter & Nijssen, 1980). *Hoplosternum littorale* is restricted in its geographical distribution to waters that are relatively rich in electrolytes (Mol, 1994). This type of water is often associated with fertile soils that may sustain dense human populations, e.g. coastal plains of Suriname and Guyana and the varzea of Amazonian white-water rivers. Extensive swamps and flooded forests on these fertile soils are being turned into cultivated lands, notably rice fields. Goulding (1980) has demonstrated how many fish species heavily depend on the flooded forests for their food. Swamps and swamp forests are also important nesting habitats of armoured catfishes (Mol, in press c). The construction of dams, dikes and roads may prevent free movement of water and fishes (Welcomme, 1992). In Suriname, *H. littorale* is found almost exclusively in the young coastal plain (Mol, 1994) that is also the most densely populated area of Suriname (Stichting Planbureau Suriname & Organization of American States, 1988). Agriculture, animal husbandry and freshwater fisheries are concentrated in the coastal plain and conflicting situations between the three may arise.

CULTURE OF ARMOURED CATFISH

INTRODUCTION

Brown (1942, cited in Hickling 1961) was probably the first to note the possibility of a culture of *Hoplosternum littorale*. He suggested the production of fry of *H. littorale* in order to increase stocking rates of the flood-fallowed sugar-cane fields of Guyana.

A more scientific approach to the culture of *H. littorale* was attempted in Trinidad by Singh (1978). Although Singh (1978) presented important information on the reproduction and growth rate of *H. littorale* under field conditions, he did not have much success with the culture of larvae beyond the stage of yolk sac resorption. Mass mortality due to starvation was related to the unavailability of suitable food sources.

In Suriname, extensive culture of *H. littorale* is practiced by means of construction of fishing canals (Sur. 'visgat') in swampy areas. Armoured catfish reproduce and feed during the rainy season in extensive inundated swamps. With dropping water levels in the dry season, large numbers of *H. littorale* accumulate in the fishing canals. Owners of the canals sell the fish at local markets or they give sport fishermen the opportunity to catch them on payment of a small fee in advance. Semi-intensive culture of *H. littorale* is practiced in small family owned ponds near farms. Armoured catfish are grown in these simple, shallow ponds together with ducks and other swamp fishes.

Although callichthyids were not included in a recent review of South American freshwater fishes with aquaculture potential (Saint-Paul, 1986), *H. littorale* is considered one of the most promising aquaculture species of French Guiana due to its high commercial value in northern South America (Boujard *et al.*, 1988). Subsequent investigations into the culture of *H. littorale* by French scientists at the Hydrobiology Laboratory of the Institut National de la Recherche Agronomique (INRA) at Kourou, French Guiana, have been very successful (e.g. Luquet *et al.*, 1989; Pascal *et al.*, 1994; see below). In Suriname, there is a keen interest in the culture of armoured catfishes (Ouboter & Mol, 1994). At the 2nd Joint Conference of the University of Guyana and the University of Suriname, Mol (in press a) reported the first successful trials in raising larvae of *C. callichthys*, *H. littorale* and *H. thoracatum* fed on life *Artemia* nauplii. The effects of salinity on the growth and survival of larvae of the three armoured catfishes were studied by Mol (1994). Arguments of Junk (1984) in favor of the development of an Amazonian fish culture also apply to the culture of armoured catfishes.

AQUACULTURE OF *HOPLOSTERNUM LITTORALE* IN FRENCH GUIANA

Recently, important work on the culture of *H. littorale* was undertaken by a team of scientists of the Institut National de la Recherche Agronomique (INRA) at Kourou, French Guiana (e.g. Luquet *et al.*, 1989). Here I summarize their main results, some of which may be compared with data on *C. callichthys* and *H. thoracatum* in Mol (1993, in press c).

Spawning of *H. littorale* occurs in floating bubble nests which are built and guarded by the male (Carter & Beadle, 1931; Singh, 1978; Machado-Allison & Zaret, 1984; Gautier *et al.*, 1988; Mol, 1993). The behaviour of male and female(s) during nest building, oviposition, fertilization and care for the eggs was studied in aquariums by Gautier *et al.* (1988). The most peculiar steps are oral milt collection by the female (also see Khoda *et al.*, 1995) and the transfer of the milt to the nest before oviposition. The floating bubble nests of *H. thoracatum* and *C. callichthys* are described by Mol (1993).

Both males and females of *H. littorale* reach sexual maturity during their first year, sometimes as early as 6-7 months after hatching (Luquet *et al.*, 1989; Boujard & Meunier, 1991). Small breeding ponds of 500-1000 m² and low stocking rates (± 20 fish/pond; ratio females:males = 3:1) were used for reproduction (Luquet *et al.*, 1989; Pascal *et al.*, in press). Spawning was restricted to the rainy season (Pascal *et al.*, 1994) and did not differ from the reproductive season in swamps (Hostache *et al.*, 1993; Mol, in press c). Experiments aimed at an extension of the breeding season by artificial means were not successful (Pascal *et al.*, 1994).

Fecundity of *H. littorale* is extremely high. A single female may achieve up to 14 spawnings per breeding season (Pascal *et al.*, 1994). During oviposition females deposit approximately 5000 eggs per spawning in the nest (Machado-Allison & Zaret, 1984; Mol, 1993). The average mass of eggs spawned in one breeding season is 180 g (48,600 eggs) per 90 g female and 340 g (91,900 eggs) per 210 g female (Pascal *et al.*, 1994). Females lose 10-23% of their initial weight during the breeding season, while males lose only 4% of their weight in the same period (Pascal *et al.*, 1994). Both in ponds (Pascal *et al.*, 1994) and in swamps (Mol, in press c) only 48% of the nests of *H. littorale* are used for spawning. The remaining 52% of the nests do not acquire eggs. In ponds, 49% of the nests that acquired eggs were spawned by more than one female (Pascal *et al.*, 1994). Up to 9 females may spawn simultaneously (in *H. littorale*) or at regular intervals (in *C. callichthys* and *H. thoracatum*) in one nest (Machado-Allison & Zaret, 1984; Mol, 1993; Pascal *et al.*, 1994).

Incubation of the eggs of *H. littorale* is practiced in ponds (in the nest) or in conical incubators in the laboratory (Hostache *et al.*, 1992). When the egg 'cake' is removed from the nest early in the morning on the third day after the construction of the nest hatching rates of $\geq 85\%$ can be achieved by submersing the eggs in water of approximately 30° C (personal observations) or with other methods (Luquet *et al.*, 1989; Hostache *et al.*, 1990). In the laboratory, the minimum incubation time was 36 h at 33.6° C, while 36° C would be the upper limit allowing hatching (Hostache *et al.*, 1992). The minimum 'energy' required for hatching was 1201 degrees-hours at 31.3° C (Hostache *et al.*, 1992). In the ponds, incubation of the eggs of *H. littorale* took 47-54 h (Hostache *et al.*, 1992). In the swamp, hatching took approximately three days in all three catfish species (Mol, 1993).

Newly hatched larvae of *H. littorale* measure 6 mm Total Length and their fresh weight is approximately 2 mg. When larvae are grown in ponds survival is often very poor. In the ponds of Soucoumou (French Guiana) only 0.1-1% of the larvae stocked on the first day after hatching were recovered after one month (Luquet *et al.*, 1989). The reason(s) for such dramatic mortality are not clear although predation by aquatic invertebrates is suspected to play an important role (Luquet *et al.*, 1989; Hostache *et al.*, 1990; Mol, in prep). Much better survival of larvae and early juveniles (up to 100% in the first month) is achieved when the larvae are grown in tanks and fed with life *Artemia* nauplii (Mol, in press a, 1994). If stocking density in the ponds is low (0.2 fish m⁻²) growth rates of *H. littorale* are potentially very high. In the ponds of Soucoumou, *H. littorale* grows to 12 g in one month and 50 g at the end of the third month (Luquet *et al.*, 1989). Although it is clear that males grow faster and to a larger size than females, few quantitative data on the growth of *H. littorale* in ponds are available (Hostache *et al.*, 1990; Boujard & Meunier, 1991). Hostache *et al.* (in prep) investigated the effect of egg incubation temperature on the sex-ratio of progenies of *H. littorale* nests.

Boujard *et al.* (1990) found evidence for the synchronization of locomotor, air breathing and feeding activity by circadian alternation of light and dark. Feed demand started at dusk and increased throughout the night with a peak between 2.00 and 5.00 h. Luquet *et al.* (1989) suggested the application of a night schedule of feeding in the culture of *H. littorale*.

Luquet *et al.* (1991) investigated changes in the body composition and energy requirements of sub-adult six-month-old *H. littorale* during 50 days of starvation. Due to the presence of a heavy armour of bony plates, bony parts of *H. littorale* accounted for 55-60% of the body fresh weight (muscle tissue represented no more than 30% of body weight).

Minerals constituted 9% of the body fresh weight and approximately 25% of the body dry weight (Luquet *et al.*, 1991; Chapter 7). Calcium and phosphorus accounted for respectively 8-10% and 4-5% of the body dry weight. During the 50 days of starvation daily energy losses of *H. littorale* varied between 25 and 33 kJ kg⁻¹ d⁻¹ (Luquet *et al.*, 1991). However, the nature and the amount of catabolized substrates were not constant over the fasting period. Basal or routine metabolism of starved *H. littorale* (29 kJ kg⁻¹ d⁻¹) is in agreement with energy requirements of temperate species (Brett & Groves, 1979), but rather low compared to values of 50 kJ kg⁻¹ d⁻¹ given by these authors for tropical fish at 26° C. A study of the energy metabolism of *H. littorale* fasted for 10 days by indirect calorimetry (Moreau *et al.*, 1991) yielded an average energy expenditure of 1.58 kJ kg⁻¹ h⁻¹ (38 kJ kg⁻¹ d⁻¹). Endogenous lipids were the main energy purveyor. No difference was found in the energy metabolism of *H. littorale* between dark and light environmental conditions (Moreau *et al.*, 1991). A study of the postprandial utilization of energy substrates by *H. littorale* (Moreau *et al.*, 1992) revealed that protein was the main energy-yielding substrate during the 60 h period after feeding. A gradual increase in the use of lipids was noticed 14 h after feeding. Over a 24 h period following food intake, a 30 g fish catabolized 90 mg of proteins and 43 mg of carbohydrates (while 3.7 mg of fat was synthesized).

RECOMMENDATIONS

Although the fish protection legislation of 1961 is an important tool in the protection of armoured catfish populations (Rondeel, 1965; personal observations) the following improvements based on recent ecological research on armoured catfishes are suggested. After studying the growth of *H. littorale* in the swamps of Trinidad, Singh (1978) suggested to limit the minimum size of exploitable catfish to 13 cm Total Length (12 cm in the 1961 fish protection legislation; Rondeel, 1965). Although *C. callichthys* and *H. thoracatum* grow to a slightly smaller size than *H. littorale*, the minimum size of 13 cm TL should apply to all three species in order to avoid confusion. Based on the main breeding season of armoured catfish, the Surinamese fish protection legislation further establishes a 'closed season' for fishing armoured catfishes from 1 April to 15 July (Rondeel, 1965). Recent investigations (Mol, in press c) show that all three species have in fact two breeding seasons per year in Suriname: the small rainy season (15 December to 15 February) and the main rainy season (1 April - 15 July). Large numbers of nests of the three species were observed in both rainy seasons (Mol, in press c). The small rainy season (15 December - 15 February) following the large dry period of August to November may be extremely important for the young catfish as food is abundant and predator pressure is probably still low (Mol, in press c). I suggest that both rainy seasons are fixed as a closed season in the Surinamese fish protection legislation for all three species of armoured catfish.

The Surinamese fish protection legislation is not concerned with the protection of the habitat of the fishes. Junk (1984) pointed out that in order to assess the effects of pesticides and habitat destruction on the production of fishes comparative investigations in areas used by agriculture and in untouched areas are urgently needed. As far as I know studies of this kind have not been carried out until now. In Suriname, the densities of armoured catfishes and their nests in cultivated areas (e.g. rice fields of west Suriname) may be compared with data from Mol (in press c; in prep) for coastal plain swamps. In anticipation of the results

of these investigations I recommend the conservation of large areas of coastal plain swamps and swamp forests based on the vegetation maps of northern Suriname by Teunissen (1978).

The three armoured catfishes have some biological characteristics which make them promising for aquaculture purposes. Some major advantages are: easy spawning in confinement, control of reproduction via control of the number of floating bubble nests, high fecundity (Mol, 1993; Pascal *et al.*, 1994), good tolerance of crowding in ponds and of low oxygen levels due to accessory intestinal respiration (Carter & Beadle, 1931; Kramer *et al.*, 1978), high growth rates (Singh, 1978; Hostache *et al.*, 1990; Mol, 1994), and their hardness due to the presence of an armour of bony plates, facilitating live transportation and handling out of water. Singh (1978) mentioned the ability of *H. littorale* of utilizing detritus as a major food resource, but Mol (in press b) argues against a specialization towards detritivory in armoured catfish. Disadvantages are: small size, negative effects of high stocking density on the growth rate, and their exotic appearance making them less suitable as an export product.

When the three armoured catfishes are compared, *H. littorale* is probably most suited for aquaculture purposes because of its 'large' size and reproductive strategy (Mol, 1993). A culture of juvenile *H. thoracatum* for export as ornamental fish may also be feasible (Burgess, 1989; also see Chapter 6, Fig. 6.1). In discussing the perspectives for a culture of armoured catfish as food fish it must be kept in mind that the market for these exotic looking fishes is probably rather limited. In the near future, only small-scale export of armoured catfish to immigrant communities in Europe, the U.S.A. and Canada seems feasible. On the export markets, the catfish culture must compete with low-income subsistence fisheries of Brazil and Venezuela. When armoured catfish are to be produced for local markets, costs must be kept low due to the low purchasing-power of the people.

Intensive culture of fingerlings (2-month-old juveniles) of *H. littorale* for stocking fishing canals, irrigation/drainage canals of rice fields, family ponds or natural water bodies seems of special interest. Low tolerance of larvae of *H. littorale* to electrolyte-poor water (Mol, 1994) restricts the culture of *H. littorale* to coastal plain fresh waters. In view of the extremely high potential impact of predation on early developmental stages of armoured catfish (Chapter 6; Mol, in prep) culture in tanks probably gives the best results (Mol, 1994). Fingerlings of *H. littorale* may be sold to farmers, owners of fishing canals and rice producers or stocked in natural water bodies. In nature, predation pressure on armoured catfish probably rapidly declines with age (size) of the juveniles to approximately zero in seven-week-old fish (Chapter 6; Mol, in prep).

Data on the growth of *H. littorale* at various stocking density and feeding levels are badly needed in order to evaluate the feasibility of a culture of full-grown adult catfish in ponds. Studies on the composition of the food and the water quality of the ponds in relation to the development of the bony armour of the catfish are also needed. Most growth of *H. littorale* occurs in the first eight months after hatching (Singh, 1978; Hostache *et al.*, 1990). This would make it economically inefficient to delay harvesting beyond the 8-month period. It may be necessary to develop a food from local ingredients, not only to keep fodder costs low, but also in order to provide additional minerals for the development of the armour (Luquet *et al.*, 1991).

A third important approach to the culture of armoured catfish is to use these bottom-dwelling fishes in a polyculture with midwater species like *Colossoma* spp or cichlids (indigenous species like *Cichla* or tilapiine species). The culture of *Colossoma* spp seems especially promising (Werder & Saint-Paul, 1978; Saint-Paul, 1985, 1986).

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SUMMARY

Tropical ecosystems are renowned for their high biodiversity with many closely related species living together. Alpha diversity of tropical freshwater fishes is also extremely high, as exemplified by the cichlid fauna of the Great African lakes and the neotropical characins. Since Hutchinson in 1959 posed his often quoted question: "Why are there so many animals?", factors affecting species diversity have been important subject of study and discussion in ecology. Given the limits of the physical environment, two different biological processes are probably responsible for most of the organization of equilibrial communities: competition and predation. Critics of the view that competition and predation play a major role in structuring communities argued that several factors keep populations below a level where competition or predation could be strong. Reviews of the literature on field experiments designed to demonstrate the influence of competition and predation revealed that only 9% of the studies were conducted in the tropics.

The tropical rainforest is one of the most stable environments in the world. Temperature and humidity are almost constant, but important fluctuations in the water level of streams and swamps occur. Extreme conditions limiting population densities and leading to the extinction of populations are often hard to imagine. The high number of species will lead to complex biological interactions. More studies on competition and predation in the stable environment of the tropical rainforest are necessary to evaluate the importance of both processes in structuring communities.

A case study is presented concerning three medium-sized armoured catfishes of the family Callichthyidae: *Callichthys callichthys*, *Hoplosternum littorale* and *Hoplosternum thoracatum*. In order to evaluate the influence of competition and predation on the catfish communities, four factors were investigated in detail: 1) geographical distribution, 2) diet overlap, 3) reproductive seasonality and nest-site differentiation, and 4) predation.

In Suriname (South America), both *C. callichthys* and *H. thoracatum* occur all over the country. Both catfishes are abundant in both coastal plain swamps with standing water and rainforest creeks in the interior with running water. *Hoplosternum littorale*, on the other hand, is restricted in its distribution to coastal plain swamps. Salinity tolerance experiments demonstrated that one-week old larvae of *H. littorale* could not survive in electrolyte-poor water (e.g. rain water). The 'clear water' of rainforest creeks in the interior may be compared to slightly contaminated distilled water with very low electric conductivity. Larvae of both *C. callichthys* and *H. thoracatum* survived and developed further in rain water. The pattern of distribution in Suriname can be considered as a model of the distribution of the three catfishes in South America. In South America, *H. littorale* is not only conspicuously absent from clear water streams draining the weathered Precambrium Guyana and Brazilian Shields, but also from 'black water' streams with humic acids and also a low conductivity (e.g. the Rio Negro). Within the Amazon drainage system *H. littorale* seems restricted to 'white water' streams loaded with Andean sediments and with a higher conductivity than both clear water and black water. In Suriname, actual syntopy of the three species occurs in coastal plain swamps. In rainforest creeks of the interior *C. callichthys* and *H. thoracatum* occur syntopically. Consequently interspecific competition among the three callichthyids is possible.

Analysis of the stomach contents of larvae, juveniles and adults of the three armoured catfishes revealed no significant interspecific differences in the diet of larvae, juveniles and adults. However, ontogenetic differences in diet composition among larvae, juveniles and adults were significant for all three catfishes. Larvae of *C. callichthys*, *H. littorale* and *H. thoracatum* fed almost exclusively on Rotifera, Cladocera and Copepoda. The stomach contents of juveniles were more diverse and included micro-crustacea, insect larvae, aquatic insects and some detritus. Adults ingested large quantities of detritus which probably reflected the inability of large fish to separate effectively benthic invertebrates from substrate. Chironomid larvae were found in large numbers in the stomach of adult specimens. The short alimentary tract of the three catfishes and the structure of its wall make it improbable that these fishes are able to assimilate detrital nonprotein amino acids. The posterior part of the intestine is thin-walled and has a respiratory function. The anterior digestive portion is relatively short. Morphologically the three callichthyids are adapted to a benthic way of life and a diet of soft-bodied aquatic invertebrates. The similarity in the diet and their bottom-dwelling habit provide the basis for grouping the three armoured catfishes into one ecological guild. Competitive interactions are expected to be potentially strong among members of a guild.

Male *C. callichthys*, *H. littorale* and *H. thoracatum* construct and guard a floating bubble nest in flooded swamps. Although the habit of constructing a floating bubble nest probably evolved as an adaptation to the oxygen-depleted environment of tropical standing waters, some of the characteristics of the nests of *C. callichthys* and *H. thoracatum* may have evolved as a response to the unpredictability of the fluctuations in water level and water velocity in rainforest creeks. The conspicuous nests allow the study of the temporal pattern of breeding, the spatial distribution of the nests and the differentiation of the nest-site microhabitat among the three species. Daily surveys in coastal plain swamps revealed a similar, bimodal breeding season in the three catfishes. Nests were observed in both the short and long rainy season. The bimodal breeding pattern in Suriname is probably related to the unreliability of the rainfall in the short rainy season of December-January. In French Guiana the rains of December-January usually do not fail and an unimodal breeding season of *H. littorale* is found. Significant differences in nest macrohabitat selection were found among the three callichthyids. Nests of *H. littorale* were built in herbaceous swamps, while *C. callichthys* and *H. thoracatum* nested in swamp forest under trees. The two forest nesting species differed in the microhabitat at the nest site. Nests of *C. callichthys* were constructed in extremely shallow water and in holes of tree roots and earth. Nest densities in the selected habitat were low in *C. callichthys* and *H. littorale*, but relatively high in *H. thoracatum*. Nest-site differentiation in the rainy season (the main feeding period) may prevent competitive exclusion among the three catfishes.

The potential predation pressure on eggs, larvae and juveniles of *H. thoracatum* was estimated by combining laboratory predation rates of 24 predator species (both invertebrates and vertebrates) with the density of the predators in the swamp as determined by chemofishing with rotenone. The contribution of a particular predator species to the total predation pressure on *H. thoracatum* was determined to a large extent by the density of the predator in the swamp. Seemingly innocuous predators with low or moderate predation rates in the laboratory may be extremely important in the swamp due to their abundance. Small-sized fishes and aquatic invertebrates are probably major predators of early developmental stages of *H. thoracatum*. The potential predation pressure on eggs is high, but the aggressive

nest guarding behaviour of the male catfish and concealment of the nests probably protects the eggs effectively from most aquatic predators. Larvae are not guarded by the male and the potential impact of the 24 predators on the larvae of *H. thoracatum* is large. Although the experiments were performed with *H. thoracatum* there is no good reason to expect important differences in predation rates on larvae of the three armoured catfishes. Even if only 2.5% of the potential predation will be realized due to other prey available, the high mortality of early developmental stages of *H. thoracatum* (and *C. callichthys* and *H. littorale*) in the swamp could be easily explained as the effect of predation. Potential predation pressure and the number of predators that were able to prey on *H. thoracatum* sharply declined with increasing age (size) of the juvenile catfish. The heavy armour of bony plates and stout pectoral spines protect older juveniles and adults from most potential predators. The high potential predation pressure in the swamps and the low density of juvenile catfish at the end of the rainy season suggest that predation is important in structuring these catfish communities.

Although larvae of the three armoured catfishes *C. callichthys*, *H. littorale* and *H. thoracatum* show differences in tolerance to electrolyte-poor water, the three species occur together in coastal swamps. Interspecific diet overlap is very high, and the three catfishes show no differentiation in their breeding season and diel pattern of activity. Ontogenetic changes in the defense mechanisms of armoured catfishes result in a situation in which both predation and competition exert control at different times in the life cycle. Predators probably kill most of the larvae and juveniles, leaving only a few individuals to escape and reach adulthood. If the number of escapes would exceed the number of adult deaths, the populations eventually become sufficiently dense to compete. However, in this situation nest-habitat segregation may prevent competitive exclusion of one of the three species.

SAMENVATTING

Tropische ecosystemen zijn vermaard om hun grote diversiteit aan soorten en biologische interacties. Alpha diversiteit van tropische zoetwater vissen is ook zeer groot. Bekend zijn de rijke cichliden faunas van de grote meren van Afrika en de enorme hoeveelheid soorten en vormen binnen de karperzalmen van Zuid Amerika. Sinds Hutchinson zich in een klassieke publikatie uit 1959 afvroeg "Waarom zijn er zo veel soorten dieren?" zijn factoren die de diversiteit aan soorten bepalen een belangrijk onderwerp van onderzoek en discussie binnen de ecologie. Binnen de grenzen van het abiotisch milieu zijn het waarschijnlijk de biologische interacties competitie en predatie die grotendeels verantwoordelijk zijn voor de structuur van stabiele levensgemeenschappen. Critici van de rol van competitie en predatie in het structureren van levensgemeenschappen zijn echter van mening dat verschillende factoren de populatiedichtheid van soorten kunnen beperken tot een niveau waarop competitie en predatie niet meer belangrijk kunnen zijn. Inspectie van de literatuur over veldexperimenten m.b.t. het belang van competitie en predatie toont aan dat slechts 9% van dit soort onderzoek in de tropen werd verricht.

Het tropisch regenbos is een van de meest stabiele ecosystemen van de aarde. Temperatuur en luchtvochtigheid zijn bijna constant, maar in kreken en zwampen komen belangrijke schommelingen in de waterstand voor. Extreme omgevingscondities die de populatiedichtheid van soorten laag houden zijn vaak moeilijk voor te stellen. Het grote aantal soorten geeft aanleiding tot complexe biologische interacties. Meer onderzoek aan competitie en predatie in het tropisch regenbos is nodig om vast te kunnen stellen wat het belang is van beide processen in de organisatie van levensgemeenschappen.

In dit proefschrift wordt een case-study aan de orde gesteld betreffende drie middelgrote, nauw verwante pantsermeervallen van de familie Callichthyidae: *Callichthys callichthys*, *Hoplosternum littorale* en *Hoplosternum thoracatum*. Vier factoren werden in detail onderzocht: 1) de geografische verspreiding, 2) overlap in het dieet, 3) het voortplantingsseizoen en de nest habitat, en 4) predatie.

C. callichthys en *H. thoracatum* worden over heel Suriname aangetroffen, zowel in de zwampen van de kustvlakte met stilstaand water als in kreken van het binnenland met stromend water. De derde soort, *H. littorale*, wordt echter alleen in de zwampen van de kustvlakte aangetroffen. In zouttolerantie experimenten bleken 1-week oude larven van *H. littorale* niet te overleven in water met een zeer laag geleidend vermogen zoals regenwater. Het helder water ('clear water') van de kreken uit het binnenland van Suriname heeft eveneens een zeer lage ionenconcentratie en wordt door limnologen omschreven als bijna gedestilleerd water. Larven van *C. callichthys* en *H. thoracatum* ontwikkelen zich normaal in regenwater. Het verspreidingspatroon van *H. littorale* in Suriname kan als een model dienen voor de verspreiding van deze soort in Zuid Amerika. Binnen het drainage bekken van de Amazone rivier wordt *H. littorale* niet (en *C. callichthys* en *H. thoracatum* wel) aangetroffen in 1) helder water afkomstig van de verweerde bodems van de Precambrische Guyana en Brazilië schilden en 2) zwart water ('black water') met veel humuszuren dat vaak zijn oorsprong vindt in bodems met een podzolprofiel. *Hoplosternum littorale* wordt alleen aangetroffen in 'white water' stromen die hun kleur ontleen aan sediment uit het jonge Andes gebergte en een relatief hoog geleidend vermogen hebben. Aangezien *C. callichthys*, *H. littorale* en *H. thoracatum* in de kustvlakte van Suriname in dezelfde zwampen kunnen

worden aangetroffen (syntopie) is competitie tussen deze drie meervallen in principe mogelijk.

Analyse van de maaginhoud van de larvae, juvenielen en volwassen exemplaren van *C. callichthys*, *H. littorale* en *H. thoracatum* toont aan dat het dieet van de drie soorten niet significant verschilt. Bij alle drie de pantsermeervallen werden echter ontogenetische verschillen tussen het dieet van larvae, juveniele en volwassen vissen gevonden. Larvae van *C. callichthys*, *H. littorale* en *H. thoracatum* aten vooral raderdierpjes (Rotifera) en microcrustacea (Cladocera en Copepoda). De maaginhoud van juveniele pantsermeervallen was meer gevarieerd en bestond uit microcrustacea, insectenlarven, aquatische insecten en detritus. Volwassen vissen hadden vooral detritus en benthische invertebraten in hun maag. Het relatief korte darmkanaal en de structuur van de darmwand geven aan dat de pantsermeervallen waarschijnlijk geen detritus kunnen verteren. Het achterste deel van het darmkanaal heeft een dunne, sterk doorbloedde wand en functioneert als een ademhalingsorgaan. Het voorste deel van het darmkanaal waar de vertering van voedsel plaatsvindt is kort. Morfologisch zijn de drie soorten aangepast aan een bentisch leven en een dieet van aquatische invertebraten. De gelijkenis in dieet en levenswijze is de basis waarop de drie pantsermeervallen kunnen worden ingedeeld in een ecologisch gilde ('guild'). Het optreden van hevige interspecifieke competitie mag in het bijzonder worden verwacht daar waar het soorten betreft die tot hetzelfde gilde behoren.

Volwassen mannelijke exemplaren van *C. callichthys*, *H. littorale* en *H. thoracatum* maken in de regentijd een drijvend schuimnest in geïnundeerde zwampen en zwampbossen. Na het afzetten van de eitjes wordt het nest bewaakt door het mannetje. Hoewel de wijze van voortplanting middels een schuimnest waarschijnlijk is geëvolueerd als een aanpassing aan het zuurstofarme milieu van tropische zwampen met stilstaand water, lijken sommige eigenschappen van de nesten en voortplantingsstrategie van *C. callichthys* en *H. thoracatum* een aanpassing aan de onvoorspelbare schommelingen in stroomsnelheid en waterpeil in de kleine kreek van het binnenland. De opvallende schuimnesten van de pantsermeervallen maken het mogelijk om de tijd van nestbouw, de ruimtelijke verspreiding van de nesten en het (micro) habitat op de lokatie van de nesten te onderzoeken. De drie pantsermeervallen maken hun nesten in dezelfde tijd van het jaar, zowel in de grote als kleine regentijd. De bimodaliteit van het voortplantingsseizoen van de pantsermeervallen in Suriname kan waarschijnlijk worden toegeschreven aan de wisselvalligheid van de regenval in de kleine regentijd (December-Januari) in Suriname. In Frans Guyana blijven de regens van December-Januari zelden in gebreke en heeft *H. littorale* een enkelvoudig voortplantingsseizoen. De drie soorten bouwen hun nesten op verschillende plaatsen in de zwampen. Nesten van *H. littorale* werden aangetroffen tussen kruidachtige vegetatie, terwijl nesten van *C. callichthys* en *H. thoracatum* steeds onder bomen in zwampbos werden gevonden. De nesten van *C. callichthys* werden gebouwd aan de rand van de zwamp in zeer ondiep water (< 15 cm) en ook in hopen van boomwortels of aarde. De dichtheid van de nesten in de zwamp was laag in *C. callichthys* en *H. littorale*, maar relatief hoog in *H. thoracatum*. Door het verschil in nest habitat worden de drie pantsermeervallen ruimtelijk gescheiden in de regentijd, de tijd waarin ook het meeste voedsel in de zwampen aanwezig is. Nest habitat differentiatie kan competitieve uitsluiting ('competitive exclusion') van een van de soorten voorkomen.

Een indruk van de potentiële predatiedruk op de eitjes, larvae en juvenielen van *H. thoracatum* werd verkregen door de predatie (prooiën predator⁻¹ uur⁻¹) in het laboratorium voor 24 soorten predatoren (zowel invertebraten als vissen) te bepalen en te

vermenigvuldigen met de dichtheid van de predatoren in de zwamp (rotenon bemonstering). De bijdrage van een predator soort aan de potentiële predatiedruk in de zwamp lijkt voor een groot deel bepaald te worden door de populatiedichtheid van de predator in de zwamp. Op het eerste gezicht onschuldige predatoren met een lage predatiesnelheid ('predation rate') in het laboratorium kunnen in de zwamp van groot belang zijn door hun hoge populatiedichtheid. Kleine vissen en aquatische (macro)invertebraten lijken de belangrijkste predatoren van larvale en juveniele *H. thoracatum* te zijn. De potentiële predatiedruk op eitjes van de pantsermeervallen is zeer groot, maar het agressieve gedrag van het mannetje tijdens het bewaken van de nesten en de locatie van de nesten in de zwamp zijn waarschijnlijk effectief in de bescherming van de eitjes tegen de meeste predatoren. Larvae van de pantsermeervallen worden niet beschermd door het mannetje en de potentiële predatiedruk van de 24 predatoren op de larvae van *H. thoracatum* is groot. Hoewel de predatie experimenten met *H. thoracatum* werden verricht is er geen reden om grote verschillen in predatie op de larvae van de drie pantsermeervallen te verwachten. Zelfs als slechts 2.5% van de potentiële predatie wordt gerealiseerd a.g.v. de aanwezigheid van alternatieve prooien, kan de hoge mortaliteit van *H. thoracatum* (en *C. callichthys* en *H. littorale*) in de zwamp gemakkelijk worden verklaard door predatie. De potentiële predatiedruk en het aantal predatoren dat in staat is op pantsermeervallen te prederen nemen snel af met toenemende leeftijd (en afmetingen) van de juveniele pantsermeerval. Het zware pantser van beenplaten en de enorme borstvinstekels beschermen oudere juveniele en volwassen pantsermeervallen tegen de meeste potentiële predatoren. Het belang van predatie in het structureren van de pantsermeerval gemeenschappen kan worden afgeleid uit de grote potentiële predatiedruk op larvae in de zwampen en de lage dichtheid van juveniele pantsermeervallen aan het eind van het voortplantingsseizoen (de regentijd).

Hoewel larvae van de drie pantsermeervallen *C. callichthys*, *H. littorale* en *H. thoracatum* verschillen in tolerantie voor water met laag geleidend vermogen worden de drie soorten in zwampen van de kustvlakte samen aangetroffen. De drie meervallen verschillen niet in voedselpreferentie, voortplantingsseizoen en de tijd van de dag waarop ze actief zijn. Ontogenetische veranderingen in de verdedigingsmechanismen van de pantsermeervallen hebben tot gevolg dat predatie en competitie beide van belang zijn, echter in verschillende fasen van de levenscyclus van de pantsermeerval. Predatoren elimineren waarschijnlijk het grootste deel van de larvale en juveniele pantsermeervallen. Indien in een bepaald tijdsbestek het aantal pantsermeervallen dat de predatie overleeft groter is dan het aantal volwassen vissen dat sterft, zal de populatie dichtheid op den duur voldoende groot worden voor (interspecifieke) competitie. Nest habitat differentiatie zal echter in deze situatie competitieve uitsluiting van een van de drie soorten kunnen voorkomen.

CURRICULUM VITAE

Jan H.A. Mol werd op 24 November 1958 geboren in Oss. In 1977 behaalde hij het VWO-diploma aan het Titus Brandsma Lyceum in Oss. In hetzelfde jaar werd aan de Rijks Universiteit Utrecht gestart met de studie Biologie. In 1984 behaalde hij het doctoraal diploma Biologie met als hoofdonderwerpen lever- en nier disfunctie bij vogels (pathologie der bijzondere dieren), classificatie van de onkruid vegetaties van Suriname (systematische plantkunde) en ecologische interacties tussen aal en brasem in het Tjeukemeer (ecologische zoölogie en taxonomie). Van 1986 tot 1987 verzorgde hij biologie onderwijs op verschillende middelbare scholen in Paramaribo (Suriname). Van 1987 tot 1995 was hij als onderzoeker in dienst van de Anton de Kom Universiteit van Suriname, faculteit Technologische Wetenschappen. Tijdens deze periode werd het in dit proefschrift beschreven onderzoek aan de ecologie van drie neotropische pantsermeervallen opgestart en uitgevoerd. Van Oktober 1994 tot September 1995 was hij als gastmedewerker verbonden aan de vakgroep Experimentele Dier Morfologie en Cel Biologie van de Landbouw Universiteit Wageningen waar hij met sabbatical leave werkte aan de afronding van dit proefschrift.

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