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ORIGIN AND DISTRIBUTION OF THE BELGIAN JOURNAL OF ZOOLOGY

par

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The Royal Zoological Society of Belgium and its Belgian Journal of Zoology are continuing a long scientific tradition devoted to the promotion of zoology and to the publication of research in zoology. This tradition goes back to the 19th century and more precisely to 1863, when the « Société malacologique de Belgique » was founded in Brussels. This Society, whose history has been recently analysed by A.V. Dhondt (1989), had for main objectives to « propagate the taste of the malacological studies (...) and to contribute to the advancement of Science ». « Malacology » must be understood in its old meaning as the scientific study of all invertebrate animals except the Arthropods. To this end, among other activities, the Society started in 1865 to publish the « Annales de la Société malacologique de Belgique » and settled exchange agreements with foreign research workers and institutions. Ten years after its foundation the Society was already sending its « Annales » to foreign libraries in as many as 15 countries and 50 cities, mostly in Europe, but also in the United States of America and in Latin America. In exchange, it received publications which constituted the bulk of its own library.

In the early 20th century, the Society widened its field of interests to include the whole animal kingdom. The Society and the « Annales » changed name twice : in 1903 the title of the Journal becomes « Annales de la Société royale malacologique et zoologique de Belgique » and in 1923 « Annales de la Société royale zoologique de Belgique ». The growth policy however remained unchanged. The « Annales » were sold or exchanged in an increasing number of countries and cities, thereby contributing to the national and international diffusion of zoological studies emanating from most Belgian Universities and Research Centers.

With the internationalization of its editorial board in 1989 and the choice of a new title (« Belgian Journal of Zoology ») in 1990, the Journal has entered a new era. On this occasion it seems worthwhile to take stock of its current distribution in the world.

Table 1 and Figs 1-3 summarize the data concerning the distribution of the journal throughout the world. They only include information about the cities where the journal can be consulted in the library of Universities, Museums, and other institutions.

Table 1 lists these cities by continent (North America, Latin America, Europe, Africa, Asia and Oceania), and by country. It also gives information about the types of institutions and refers to the maps (Figs 1-3).

Fig. 1 shows the general distribution of the countries of the world where the Journal can be found. Fig. 2 is a more detailed map for the U.S.A. and Fig. 3 for the European countries.

Table 1

World distribution of the Belgian Journal of Zoology (see text)

Column (1) continent or region
(2) country (state for the U.S.A.)
(3) cities
(4) institution (A, academy - C, city library, F, faculty or school - I, institute - M, museum - S, society - U, university - X, other research institution)
(5) n° of the fig (map)
(6) reference number on the map

(1)	(2)	(3)	(4)	(5)	(6)
A.	*North America*				
	Bermudas (U.K.)	St George	X	1	A1
	Canada	Halifax	U	1	A2
		Nanaimo	X		
		Ottawa	M,X		
		St Andrews	X		
		Toronto	U		
		Vancouver	X		
	U.S.A. :				
	California	Berkeley	U	2	A3
		La Jolla	U		
		Los Angeles	U		
		San Diego M			
		San Francisco	A		
	Columbia (D. of)	Washington	X	2	A4
	Connecticut	New Haven	U	2	A5
		Storrs	U		
	Florida	Gainesville	U	2	A6
		Tallahassee	U		
	Georgia	Athens	U		A7
	Hawaii	Honolulu	U		
	Indiana	Bloomington	U	2	A8
		Indianapolis	A		

	Kansas	Lawrence	U	2	A9
	Louisiana	Baton rouge	U	2	A10
	Massachusetts	Amherst	U	2	A11
		Cambridge	U		
		Woods Hole	X		
	Maryland	Beltsville	X	2	A12
	Michigan	Ann Arbor	U	2	A13
		Detroit	U		
	Minnesota	Minneapolis	U	2	A14
	Missouri	Kansas City	A	2	A15
	New Jersey	Princeton	U	2	A16
	New York	Buffalo	M	2	A17
		Ithaca	U		
		New York	M		
		Rochester	A		
		Stony Brook	U		
	North Carolina	Chapel Hill	U	2	A18
		Raleigh	U	2	
	Oklahoma	Stillwater	U	2	A19
	Pennsylvania	Philadelphia	A,S,X	2	A20
		Univ. Park	U		
	Utah	Salt Lake City	U	2	A21
	Washington	Seattle	U	2	A22
	Wisconsin	Madison	A	2	A23
		Milwaukee	M		
	Wyoming	Laramie	U	2	A24
B.	*Latin America*				
	Argentina	Buenos Aires	M,S	1	B1
		Cordoba	A		
		La Plata	F		
		Mendoza	M		
	Brazil	Butanta	U	1	B2
		Recife	X		
		Rio de Janeiro	M		
		Sao Paulo	U		
	Chile	Concepcion	S,X	1	B3
		Iquique	X		
		Santiago	M		
		Valparaiso	X		
	Ecuador	Quito	U	B4	
	Mexico	Mexico	A,F,U	1	B5
	Nicaragua	Leon	M	1	B6
	Uruguay	Montevideo	M	1	B7
	Venezuela	Caracas	F	1	B8
		Maracaibo	U		
C.	*Europe*				
	Austria	Graz	U	3	C1
		Wien	M,S,X		
	Belgium	Antwerpen	S	3	C2
		Bruxelles/Brussel	A,M,S,U,X		

	Gembloux	F,S		
	Gent	S,U		
	Hasselt	X		
	Landen	S		
	Liège	S,U		
	Meise	S		
	Namur	S		
	Rekem	X		
	Sint Niklaas	S		
	Tervuren	M		
Bulgaria	Sofia	U	3	C3
Czechoslovakia	Brno	A	3	C4
	Praha	S		
Denmark	Kopenhavn	U	3	C5
Finland	Helsinki	S	3	C6
France	Angers	S	C7	
	Banyuls	U		
	Besançon	U		
	Caen	U		
	Cherbourg	S		
	Dijon	U		
	Draguignan	S		
	Grenoble	F		
	Le Havre	S,M		
	Lyon	S		
	Marseille	M,X		
	Metz	A		
	Nancy	C		
	Orléans	X		
	Paris	A,M,S,X		
	Rennes	S,U		
	Roscoff	X		
	Saint Brieuc	S		
	Talence	U		
	Toulouse	U		
	Villeneuve d'Ascq	U		
Germany (E)	Berlin	U	3	C8
	Dresden	M		
	Eberswalde	A		
	Halle	A		
Germany (W)	Bonn	S		C9
	Düsseldorf	U		
	Frankfurt/Main	S		
	Giessen	S		
	Hamburg	U,X		
	Köln	U		
	Mainz	M		
	Marburg/Lahn	U		
	München	C		
Greece	Kifissia	M		C10

Hungary	Budapest	M		C11
	Veszprem	M		
Irlande	Baile Atha Cliath (Dublin)	A		C12
Italy	Bologna	A,U		C13
	Brescia	A,M		
	Catania	A,U		
	Firenze	U		
	Genova	M		
	Messina	S		
	Milano	M		
	Modena	U		
	Napoli	S,U,X		
	Pisa	U		
	Roma	A		
	Siena	A		
	Torino	A,M		
	Trento	M		
	Venezia	I		
	Verona	M		
Luxemburg (G.D.)	Luxembourg	I,S	3	C14
Monaco	Monaco	M	3	C15
Netherlands (The)	Amsterdam	A,M,U	3	C16
	Den Haag	X		
	Leiden	M		
	Maastricht	M,S		
	Texel	I		
	Utrecht	U		
Norway	Bergen	U	3	C17
	Oslo	M,U		
	Stavanger	M		
	Trondheim	X		
Poland	Biolowieza	A	3	C18
	Krakow	A		
	Lominaki	A		
	Warszawa	A,I		
	Wbun	U		
	Wroclaw	X		
Portugal	Coimbra	U	3	C19
	Lisboa	F,X		
	S.Mamede de I.	X		
	Porto	U		
Rumania	Bucuresti	X	3	C20
	Nucet	X		
Spain	Almeria	A	3	C21
	Barcelona	M,S,U		
	Madrid	A		
Sweden	Göteborg	U	3	C22
	Lund	U		
	Stockholm	U		

		Uppsala	U		
	Switzerland	Aarau	S	3	C23
		Bern	U		
		Genève	M,U		
		Gland	S		
		Lausanne	S		
		Neuchatel	C		
		Sankt Gallen	C		
		Zurich	S,X		
	Turkey	Ankara	S,X	3	C24
	United Kingdom	Belfast	U	3	C25
		Boston	X		
		Cambridge	S		
		Cullercoats	X		
		Edinburgh	U		
		Liverpool	U		
		London	M,S,X		
		Lowestoft	X		
		Newcastle	S		
		Norwich	X		
		Plymouth	S		
		Croydon	S		
	USSR	Leningrad	A	3	C26
		Moskva	A,X		
	Yugo-Slavia	Ljubliana	A,U	3	C27
		Skopje	U		
D.	*Africa*				
	Algeria	El Djezaïr (Alger)	U	1	D1
	Cameroons	Yaounde	U	1	D2
	Egypt	Djiza (Gizeh)	U	1	D3
	Morocco	Rabat	S	1	D4
	Namibia	Windhoek	X	1	D5
	South Africa	Cape Town	M	1	D6
		Pietermaritzburg	M		
		Pretoria	M		
	Tunisia	Salambo	X	1	D7
	Zaïre	Kisangani	U	1	D8
E.	*Asia*				
	China	Pekin	A	1	E1
	Japan	Fukuoka	U	1	E2
		Kanazawa	U		
		Niigata	U		
		Okayama	U		
		Osaka	U		
		Sapporo	U		
		Sendai	U		
		Shizuoka	U		
		Tokyo	M,U,X		
F.	*Oceania*				
	Australia	Adelaide	S	1	F1

		Brisbane	M,U		
		Hobart	M		
		Melbourne	M,S		
		Sydney	M		
		Wagga Wagga	S		
	New Zealand	Auckland	I,M	1	F2
		Christchurch	M		
		Wellington	M		

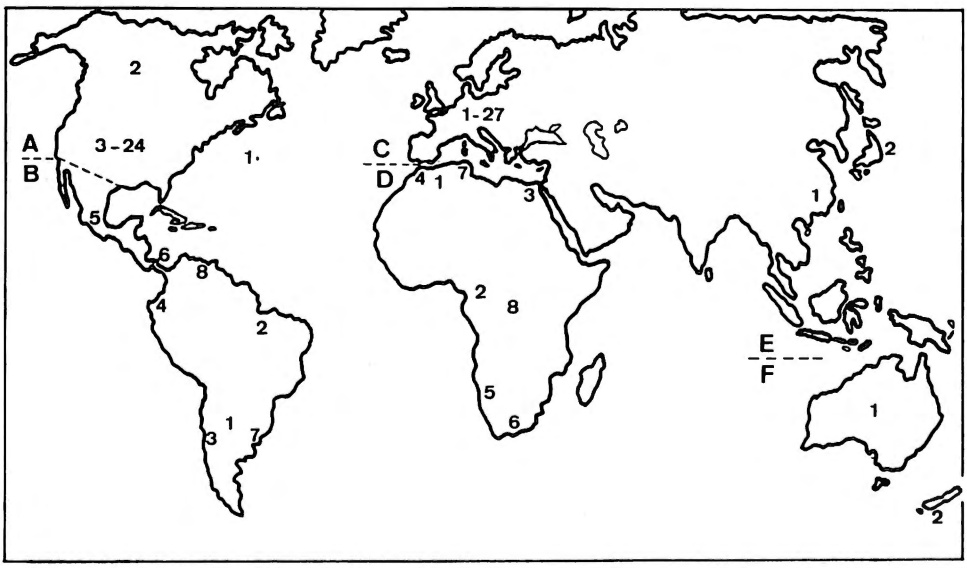

Fig. 1. — Distribution of the Belgian Journal of Zoology (see text) in 6 major regions of the world (A, North America - B, Latin America - C, Europe - D, Africa - E, Asia - F, Oceania). In each region, a country is referred by the same number as in table 1.

These data show that the Belgian Journal of Zoology is currently accessible, in all the continents, in 50 countries and 223 cities. As for the types of institutions where the Journal is received, they can be ranked as follows : Universities and Faculties (37 %), Museums (17 %), Societies and City libraries (16 %), Research institutions (15 %) and Academies and Institutes (14 %). 125 years after the publishing of its first volume, the Journal has achieved, under four successive names, a large distribution and has proved to be a good tool for the worldwide diffusion of research in zoology.

The Journal still remains to be introduced in a number of countries. The maps in Figs 1-3 help us to identify them, and will most certainly be useful in the coming years for appreciating the new progress of the diffusion of the « Belgian Journal of Zoology ».

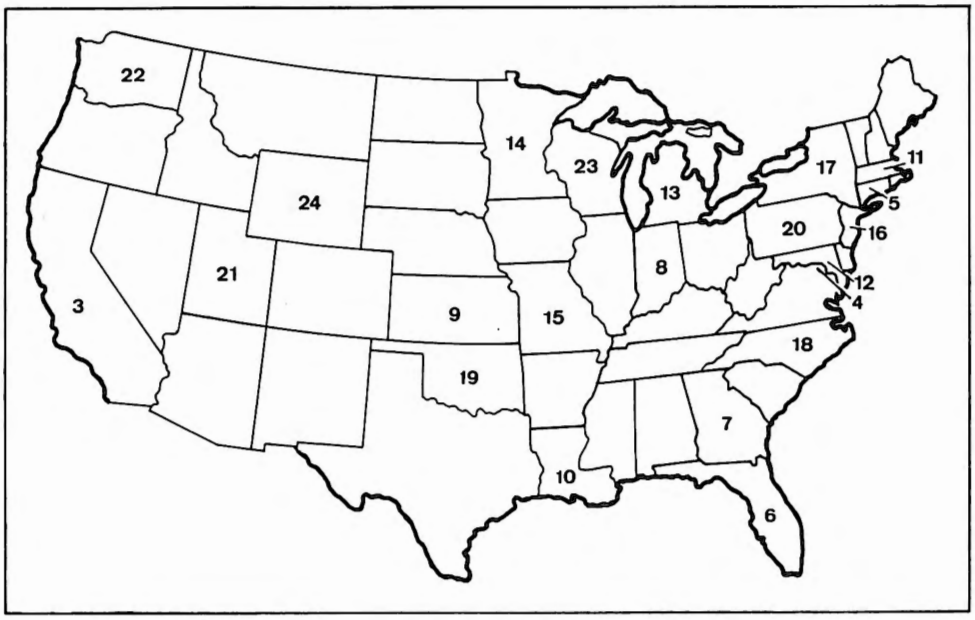

Fig. 2. — Distribution of the Belgian Journal of Zoology in the U.S.A. (see text). A State is referred by the same number as in table 1 (A).

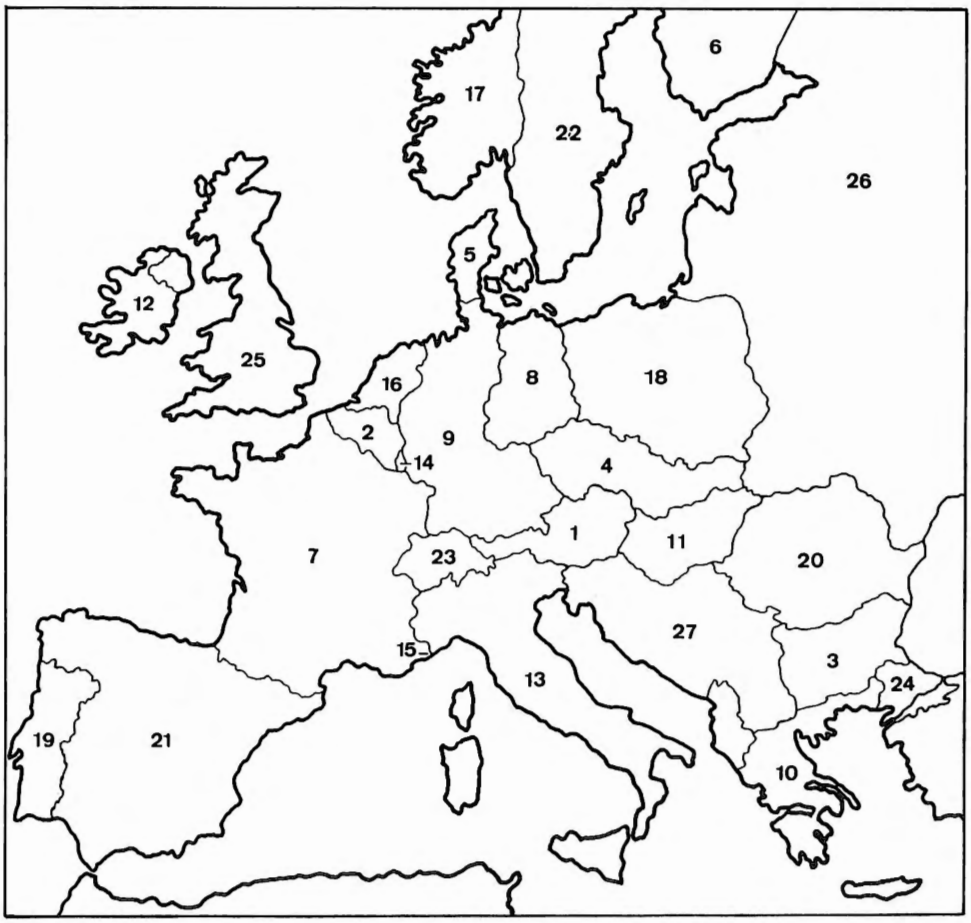

Fig. 3 Distribution of the Belgian Journal of Zoology in Europe (see text). A country is referred by the same number as in table 1 (C).

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DHONDT, A.V. (1989) — La Société malacologique de Belgique 1863-1902. *Annls Soc. r. zool. Belg.*, 119(2), 139-153.

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ÉTUDE DU COMPORTEMENT PRÉCOPULATEUR D'*ARION DISTINCTUS* MABILLE, 1868

par

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RÉSUMÉ

Le comportement précopulateur d'*Arion distinctus* est caractérisé par une phase dite de poursuite au cours de laquelle, un individu poursuit un autre *Arion* tout en broutant le globule muqueux accumulé au niveau de la glande caudale du poursuivi. Dans ce travail, 51 phases de poursuite ont pu être observées. Au cours de ces phases, les *Arion* peuvent être indifféremment poursuivant ou poursuivi. Les poursuites n'ont pu être observées que chez les individus sexuellement matures et en quête d'un partenaire sexuel. Il n'a jamais été possible d'observer une copulation qui n'ait été précédée d'au moins une phase de poursuite. De même, tous les *Arion* qui ont participé à une phase de poursuite, ont copulé au moins une fois au cours de nos expériences. A l'inverse, les individus qui n'ont participé à aucune phase de poursuite n'ont jamais copulé. Il existe une corrélation très étroite entre ces deux comportements ($r = 0,95$; $P < 0,001$) et ce phénomène de poursuite pourrait bien être considéré comme un indicateur facilement perceptible de la maturité sexuelle des deux partenaires. Comme ces phases de poursuite ont débuté après que le poursuivant ait rejoint le poursuivi en suivant la piste de celui-ci (2 cas sur 51) ou plus fréquemment en se dirigeant directement vers le globule muqueux (49 cas sur 51), il est possible que ce globule renferme une substance attractante qui renseigne les *Arion* sur l'état de maturité sexuelle du porteur.

Mots clés : Comportement — Copulation — Arion — Piste muqueuse.

The precopulatory behaviour of *Arion distinctus* Mabille, 1868

SUMMARY

The precopulatory behaviour of *Arion distinctus* has been studied and some outstanding points may be noted. Copulation is always preceded by a particular pursuit during which two mature slugs crawl together, the follower eating the caudal-gland mucus of the other one. From one pursuit to another, *Arion* may be indifferently follower or followed. These pursuits

can only be observed with animals which are sexually mature and searching for a partner to copulate. Copulations never occur without a preliminary pursuit and slugs which have participated in the pursuit, copulated at least once during our experiments. On the contrary, those which never copulate never pursue.

The correlation between these two types of behaviour is very strong ($r = 0.95$; $P < 0.001$) and the pursuit might be considered an easily perceptible sign of sexual maturity.

The pursuit begins when the follower comes in close contact with the other one after trail following (2 cases in 51 pursuits) or turning towards the caudal-gland mucus (49 on 51). This suggests that the caudal mucus contains a substance which may serve as a recognition mark between animals which are sexually mature.

Key words : behaviour — copulation — slugs — mucus trail.

INTRODUCTION

La majorité des Mollusques Gastéropodes sont dioïques. Néanmoins, les Opisthobranches et les Pulmonés sont hermaphrodites. Chez les Pulmonés, il existe une alternance de sexe, les individus fonctionnant d'abord comme mâles ensuite comme femelles. Les hermaphrodites présentent une fécondation réciproque avec échange de spermatophores, ceux-ci étant caractéristiques de l'espèce de par leur forme (RUNHAM and HUNTER, 1970). En règle générale, la copulation proprement dite est précédée par des séquences de comportement qui peuvent être fort complexes. Chez les Arionidae, les préliminaires à l'accouplement sont simples et semblent se limiter, en règle générale, à une poursuite avec léchage, éventuellement mutuel, du globule muqueux (ADAMS, 1910 ; GERHARDT, 1935, 1940 ; QUICK, 1946 ; WEBB, 1950). Chez *Deroceras reticulatum* (MÜLLER, 1774) (Agriolimacidae), NEWELL (1966) et plus récemment WAREING (1986) ont observé que la copulation est précédée par un suivi de piste. Un specimen qui croise par hasard la piste de son futur partenaire sexuel, la suit jusqu'à la rencontre précédant l'accouplement. Chez *Limax maximus* LINNAEUS, 1758 (Limacidae) (ADAMS, 1898 ; GERHARDT, 1933 ; CHACE, 1952), la copulation a lieu sur une branche d'arbre ou au sommet d'un mur. Pendant 30 à 90 minutes, les individus se suivent en formant un cercle fermé, tout en se caressant avec leurs tentacules. Par la suite, les individus se suspendant grâce à un cordon muqueux, les sacs péniaux sont évaginés et le transfert du sperme a lieu. D'autres espèces ont un comportement encore plus spectaculaire. Ainsi, BINDER (1976) a montré chez *Gymnarion coronatus* BINDER, 1976 (Urocyclidae) que la première manifestation d'un comportement sexuel est une phase de poursuite rapide du partenaire avec léchage de la trace muqueuse laissée à même le substrat. Lorsque le poursuivant a rejoint le poursuivi, il lèche le globule muqueux se trouvant au niveau d'une glande située à l'extrémité postérieure de l'animal (glande caudale). Par la suite, une nouvelle phase de poursuite intervient jusqu'au moment où les deux specimens se trouvent face à face. Dès cet instant, débute une phase de « duel », interrompue par de courtes phases de poursuite et qui aboutit finalement à la copulation proprement dite. Chez une autre espèce, *Gymnarion sowerbyanus* (PFEIFFER, 1848), BINDER (1976) observe également une longue phase de poursuite au cours de laquelle le poursuivant ingère le mucus sortant du pore caudal du poursuivi.

Ces divers exemples soulignent l'importance de la « trace » dans le comportement précopulateur et laissent sous-entendre que l'on trouve dans le mucus de piste une substance, de nature actuellement inconnue, qui renseigne le poursuivant sur l'état de maturité sexuelle du poursuivi et donc, sur sa capacité à copuler (TOWNSEND, 1974).

Les Arionidae, tout comme les Urocyclidae, possèdent également une glande caudale, située à la partie postérieure dorsale du pied et qui supporte une accumulation de mucus appelée globule muqueux. L'origine et la fonction de ce globule ont été longtemps discutées (SAINT SIMON, 1852 ; ANDRÉ, 1898 ; BARR, 1928 ; ADAM, 1933 ; VAN MOL *et al.*, 1970 ; RICHTER, 1980 ; SHERIDAN et DEVOS, 1983), mais plusieurs auteurs s'accordent à penser que le globule des Arionidae renferme lui aussi une substance, agissant comme attractant, qui favoriserait la rencontre des individus en période de copulation ou servirait de signal de maturité sexuelle (BARR, 1928 ; ADAM, 1933 ; RICHTER, 1980). Selon ces auteurs, il existerait une relation entre la reproduction et le globule muqueux. Toutefois, l'existence de ce lien n'a jamais pu être prouvée expérimentalement.

MATÉRIEL ET MÉTHODES

Specimens expérimentaux

Pour ce travail, nous avons utilisé uniquement des *Arion distinctus* MABILLE, 1868 adultes d'une taille comprise entre 2,3 et 4 cm de long. Tous les animaux ont été récoltés dans le Hainaut. Les spécimens expérimentaux n'ont pu être identifiés que sur base de critères morphologiques externes : absence de couleur rouge ou violette au niveau de la tête et des tentacules, bande latérale droite du manteau s'étendant plus bas que le pneumostome (DAVIES, 1977, 1979 ; DE WILDE, 1983). Compte tenu de la confusion possible avec *A. hortensis* DE FÉRUSSAC, 1819, seuls les individus typiques ont été pris en considération. Parmi eux, quelques spécimens ont été sacrifiés et disséqués. La morphologie de leur tractus génital, conforme à la description donnée par DE WILDE (1983), a confirmé notre identification basée sur les caractères externes.

Dès leur récolte, les limaces sont placées isolément dans des boîtes de Pétri en plastic munies d'un système d'aération (diamètre 14 cm, hauteur 2 cm) dont le fond est recouvert d'un papier filtre humidifié à l'eau distillée et réhumidifié chaque jour. Les boîtes sont gardées à la température du laboratoire soit environ 20° C et subissent un rythme nycthéméral normal. L'alimentation est constituée de morceaux de pomme de terre ou de carotte délivrés *ad libitum*. Les specimens sont gardés en boîtes de Pétri de un jour à un mois avant l'expérimentation. Toutes les expériences se sont déroulées au cours des mois de novembre et décembre 1986.

Dispositif expérimental

Notre dispositif expérimental est constitué d'une caméra T.V., d'un magnétoscope et d'un ordinateur. Les prises de vues sont réalisées à l'aide d'une caméra T.V. Bosch de type low-level (pour faible intensité lumineuse), munie d'un objectif Schneider-Kreuznach Variogon 1:2/18-90. Le système d'enregistrement est basé sur l'utilisation d'un magnétoscope JVC portable modèle MR 2650 EG. Les images sont enregistrées sur cassette Maxell epitaxial vidéocassettes E-180 VHS. Un ordinateur Apple-II Europlus connecté à un disk drive et à un interface commande au magnétoscope d'entrer en phase d'enregistrement ou de se mettre en pause. Le système de contrôle est constitué d'un moniteur Bosch à écran vert.

Avec un tel dispositif expérimental, l'accélération maximale des processus comportementaux est réalisée en utilisant des prises de vues les plus courtes possible séparées par des pauses les plus longues possible. Les séquences de prises de vues ont duré de deux secondes minimum a quatre secondes maximum, ce qui correspond au temps nécessaire pour apprécier avec certitude l'activité des limaces. La durée des pauses entre deux séquences d'enregistrement, dépend de la vitesse maximale du specimen étudié, elle a été de 60 secondes dans le cadre de cette étude. En effet, il est important de noter que cet intervalle de temps doit être inférieur au temps que mettrait la limace, se déplaçant à sa vitesse maximale, pour parcourir une distance égale à celle de son corps en extension. Cette condition est indispensable pour que les « images de limaces » soient toujours partiellement superposées lors de la projection et que rien ne soit perdu du chemin effectivement parcouru par chaque specimen. Cela évite aussi toute erreur d'identification lorsque les individus se séparent après s'être éventuellement agglutinés.

Déroulement de l'expérience

Les expérimentations ont lieu en boîtes de Pétri (diamètre : 14 cm ; hauteur : 2 cm) dont le fond est recouvert d'un papier filtre humide et contenant un cube de nourriture identique à celle donnée habituellement (pommes de terre et/ou carottes). L'expérience a lieu à la température du laboratoire et dans l'obscurité quasi totale. Seuls les écrans du moniteur de contrôle et de l'ordinateur interviennent comme source lumineuse. Une horloge placée à côté de la boîte de Pétri, de manière à ce qu'elle apparaisse sur les images, permet de déterminer rapidement les temps consacrés aux différentes activités observées.

Chaque expérience dure approximativement une nuit (en moyenne 14 heures) et fait intervenir quatre *Arion distinctus*.

L'examen des bandes vidéo, qui peut se faire immédiatement, permet de déterminer sans délai la nature des diverses activités qui se sont déroulées durant la nuit (déplacement, nutrition, repos, copulation). Il permet aussi d'établir la séquence des diverses activités ainsi que la durée de chacune d'entre elles. En plaçant une feuille transparente sur l'écran du moniteur on peut également relever sans difficulté le tracé précis des différentes pistes.

Histologie

A la fin des expériences, les specimens sont fixés au Bouin aqueux pendant 24 à 48 heures puis déshydratés à l'alcool et inclus à la paraffine. Les blocs sont débités en coupes d'une épaisseur de 10 microns. La coloration utilisée est le Bleu Alcian non oxydé — Acide périodique — Schiff (B.A.N.O-P.A.S.).

RÉSULTATS

Description du comportement précopulateur (Fig. 1)

Nous avons réalisé 11 expérimentations avec 18 *Arion distinctus* différents. Certains d'entre eux n'ont été expérimentés qu'une seule fois, d'autres l'ont été à plusieurs reprises.

Une première analyse des bandes vidéo a permis de classer les résultats en trois catégories :

1. expériences avec phase de poursuite et copulation ;
2. expériences avec uniquement une ou plusieurs phases de poursuite ;
3. expériences sans phase de poursuite et sans copulation.

1. *Expériences avec phase de poursuite et copulation.*

Pour l'ensemble de nos expériences, nous n'avons pu observer de « suivi de piste » qu'à deux reprises. Dans le premier cas (expérience du 4 décembre) (Fig. 1a), le specimen 2 a rejoint la piste laissée par le spécimen 1 et l'a suivie sur une courte distance. Il l'a quittée peu après pour se diriger directement vers le specimen 1. Dans le deuxième cas (expérience du 10 décembre) (Fig. 1b), le specimen 2 a croisé la piste du specimen 1 et l'a suivie jusqu'à ce que son extrémité antérieure entre en contact avec l'extrémité postérieure du specimen 1.

Dans la majorité des cas cependant, le poursuivant s'est dirigé directement vers la glande caudale du futur poursuivi (Fig. 1c). Ce dernier pouvant être soit en déplacement soit au repos. Il n'y a donc pas eu de « suivi de piste » préalable. Dès qu'il y a contact entre les deux specimens débute ce que nous appelons la « phase de poursuite » (Fig. 1d). Au cours de cette phase, les deux specimens se déplacent conjointement. Le specimen poursuivant broutant le globule muqueux accumulé au niveau de la glande caudale du specimen poursuivi. Après la phase de poursuite dont la durée peut être fort variable, les deux specimens peuvent se placer tête-bêche et se brouter mutuellement le globule muqueux (Fig. 1e). Selon les cas, ils restent dans cette position sans bouger ou en tournant dans le sens des aiguilles d'une montre. A la suite de cette phase, les specimens se séparent (Fig. 1f) et se déplacent pendant un certain temps. Cette séparation peut être définitive mais une nouvelle phase de poursuite peut intervenir entre ces deux individus (Fig. 1g). Notons que le specimen poursuivant lors de la première phase de poursuite peut être indifférem-

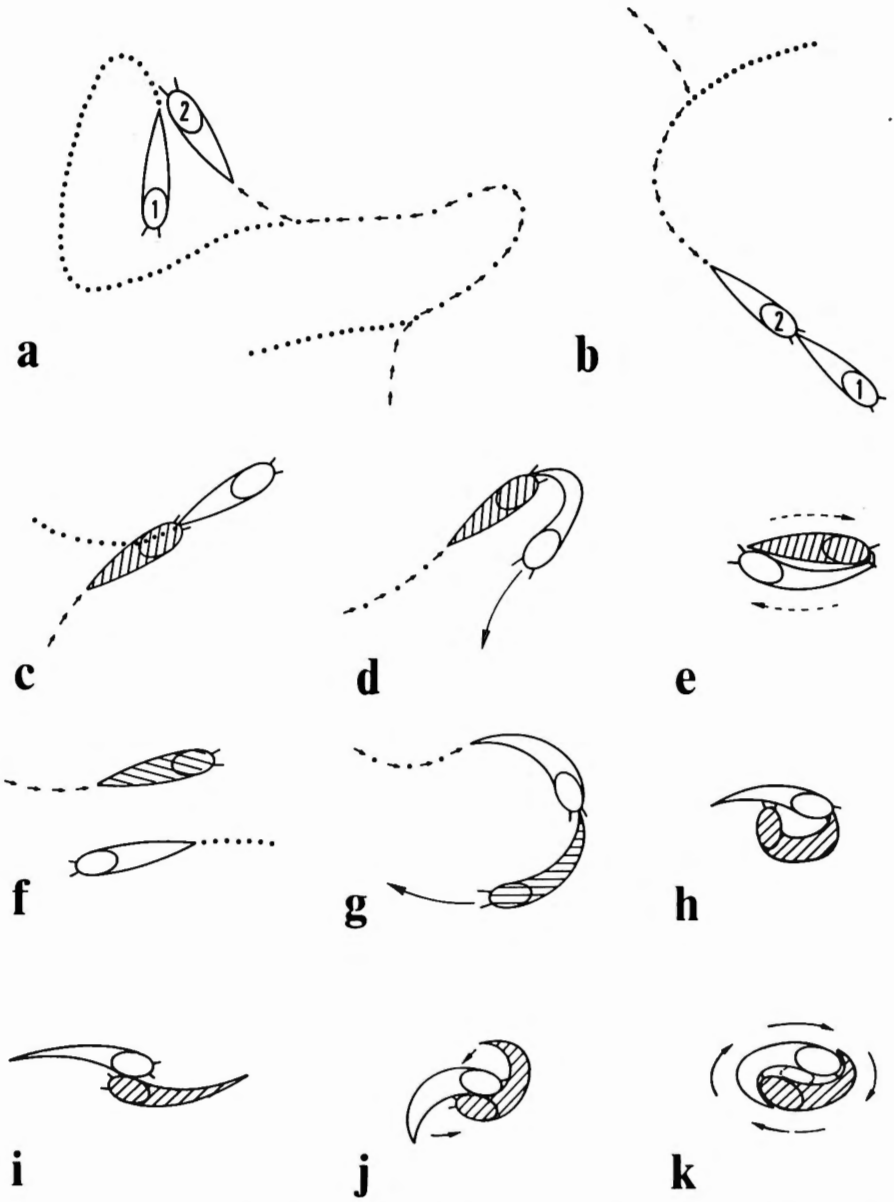

Fig. 1. — Représentation schématique du comportement précopulateur.
a, b : suivi de piste ; c, d, g : poursuite ; e : position tête-bêche au cours de laquelle les *Arion* se broutent mutuellement le globule muqueux ; f : séparation ; h, i, j : positionnement préalable à la copulation ; k : copulation. Les phases c, d, h, i et j précèdent obligatoirement la copulation ; les phases a, b, f et g sont occasionnelles.

ment poursuivant ou poursuivi lors de la seconde. Pour terminer le specimen poursuivi positionne sa partie antérieure au niveau de la partie postérieure du bouclier du poursuivant (Fig. 1h). Par la suite, les deux specimens font coïncider leurs orifices génitaux (Fig. 1i). A partir de ce stade, le poursuivant ne broute plus le globule muqueux. Les parties postérieures des deux specimens sont ramenées vers le côté gauche du bouclier de chacun (Fig. 1j). Finalement, les deux individus adoptent la position typique caractérisant la copulation (Fig. 1k) telle que décrite dans la littérature (QUICK, 1946). Au cours de cette phase, on observe presque toujours la rotation des deux specimens dans le sens des aiguilles d'une montre.

Il faut remarquer que l'on n'observe pas toujours la phase durant laquelle les specimens se broutent mutuellement le globule muqueux. De même, la première phase de poursuite peut aboutir directement à la copulation.

Expérience du 24 novembre

Quatre *Arion distinctus* isolés depuis un mois (A, B, C, D).

On observe dans ce cas de nombreuses phases de poursuite intéressant les 4 specimens expérimentaux. Rappelons que lors de ces phases, le specimen poursuivant broute le gobule muqueux se trouvant au niveau de la glande caudale du poursuivi. En ce qui concerne le specimen A, la première phase de poursuite commence 96 minutes après le début de l'expérience. Lors de cette phase, le specimen A est poursuivi par le specimen D. Par la suite, on observe 5 phases de copulation entrecoupées par des phases de poursuite relativement courtes. Lors de ces phases de poursuite, le specimen A est soit poursuivant, soit poursuivi. Ces copulations ont duré respectivement 28, 4, 44, 26 et 18 minutes. Après une interruption correspondant aux autres activités (nutrition, déplacement, repos), une nouvelle phase de poursuite intervient. Lors de celle-ci, le specimen A poursuit le specimen B et cette phase aboutit à une copulation de 36 minutes. Après une brève interruption, on assiste à une nouvelle phase de poursuite qui aboutit à une copulation, de 72 minutes cette fois, entre ces deux specimens. En ce qui concerne le specimen C, on observe dans un premier temps des phases de poursuite (dans lesquelles le specimen C est toujours poursuivant) entrecoupées par 3 phases de copulation avec le specimen D (12, 22 et 30 minutes). Les phases caractérisant le comportement précopulateur sont interrompues, puis, le specimen C poursuit à nouveau le specimen D. Cette dernière phase aboutit à une copulation beaucoup plus longue (70 minutes). Notons que lors de cette expérience, les phases caractérisant le comportement précopulateur des quatre specimens s'arrêtent presque en même temps.

Expérience du 27 novembre

Quatre *Arion distinctus* déjà utilisés les 24 et 25 novembre (A, B, C, D).

Lors de cette expérience, on observe pour le specimen B une première phase de poursuite au cours de laquelle il est poursuivi par le specimen D. Par la suite, ces

deux specimens copulent pendant 24 minutes. Trois phases de poursuite suivront, au cours desquelles le specimen B sera successivement poursuivi, poursuivant et à nouveau poursuivi. Après une interruption, le specimen B sera poursuivi par le specimen D. Cette phase aboutit à une seconde copulation plus longue que la première (54 minutes). Notons que les specimens A et C ne copulent pas au cours de cette expérience. Le specimen A n'est impliqué dans aucune phase de poursuite et le specimen C n'est poursuivi qu'à une seule reprise par le specimen D.

Expérience du 04 décembre

Quatre *Arion distinctus* maintenus un jour en captivité (I, J, K, L).

Dans ce cas, les quatre specimens (I, J, K, L) se poursuivent et copulent. Après avoir suivi la piste du specimen J sur une courte distance (Fig. 1a) le specimen I quitte la piste, se dirige directement vers le specimen J et entame avec lui une phase de poursuite. Après une interruption (autres activités), le specimen I est poursuivi par le specimen J et finalement ils adoptent très brièvement (2 minutes) la position typique caractérisant la copulation. Directement après cette phase, le specimen I poursuit le specimen K. et finalement copule avec lui. La copulation dure cette fois 138 minutes. Après une longue interruption dans les activités précopulatrices, le specimen I poursuit le specimen K. Cette phase est suivie à nouveau d'une interruption. Par la suite, on observe une phase de poursuite (I poursuivant L) à laquelle succède une copulation de 50 minutes entre ces deux specimens. Une nouvelle phase de poursuite intervient (I poursuivi par L), suivie par une copulation de 40 minutes. Enfin, après une dernière interruption, le specimen L poursuit le specimen I et ils copulent pour la troisième fois (72 minutes). Pendant l'interruption entre les deux phases de poursuite intéressant les specimens I et J, le specimen J poursuit à deux reprises le specimen K. Par la suite, le specimen J sera poursuivi par le specimen K et ces deux specimens finiront par copuler pendant 106 minutes. Après les phases déjà décrites pour le specimen K, celui-ci sera poursuivi par le specimen I.

Expérience du 09 décembre

Deux *Arion distinctus* maintenus un jour en captivité (M et N) et deux *Arion distinctus* utilisés les 24, 25, 27 et 28 novembre (A et B).

Dans cette expérience, tous les specimens se poursuivent et copulent (A, B, M, N). Pendant que les specimens M et B se poursuivent et finalement copulent durant 142 minutes, le specimen A poursuit à deux reprises le specimen N. La troisième phase de poursuite (A poursuivi) aboutit à une copulation de 32 minutes. Après une interruption (autres activités), le specimen A est poursuivi par le specimen N et ils copulent pour la deuxième fois (86 minutes). On observe ensuite quatre nouvelles interruptions de durée variable. A chacune d'entre elles succède une phase de poursuite aboutissant à la copulation (10, 10, 34 et 96 minutes).

Expérience du 15 décembre

Deux *Arion distinctus* utilisés les 24, 25, 27, 28 novembre ainsi que les 9 et 10 décembre (A, B) et deux *Arions distinctus* utilisés les 9 et 10 décembre (M, N).

Lors de cette expérience, les specimens A et N n'ont pas copulé. Les phases de poursuite et de copulation ont à nouveau été observées chez les specimens B et M. Dans ce cas, la première phase de poursuite débute une heure après le début de l'expérience. Dans un premier temps, le specimen M est poursuivi par le specimen B pendant 6 minutes. Par la suite, les deux specimens copulent (34 minutes), se poursuivent et copulent à nouveau (30 minutes).

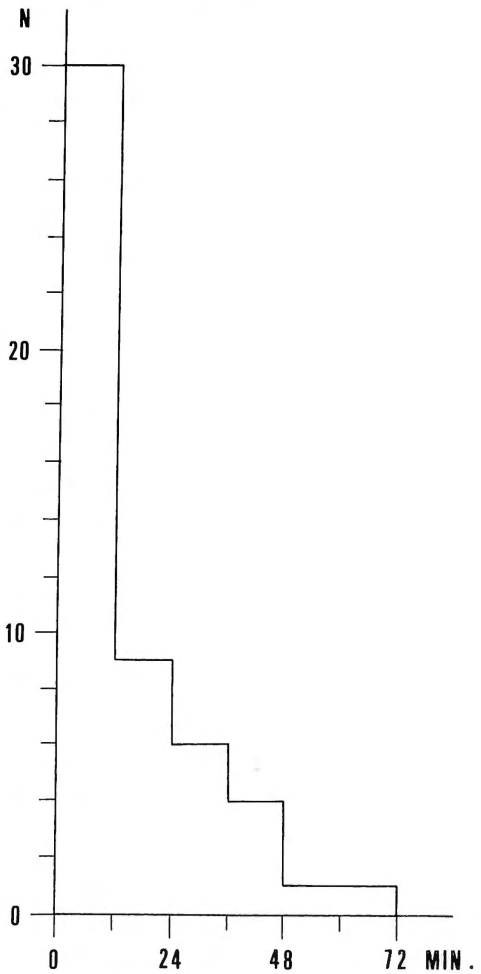

Fig. 2. — Durées (en minutes) des phases de poursuite (histogramme).

2. *Expériences avec une ou plusieurs phases de poursuite.*

Lors de ces expériences (25 novembre : A, B, C, D ; 28 novembre : A, B, C, D ; 10 décembre : A, B, M, N) nous avons observé uniquement des phases de poursuite sans phase de copulation.

Tous les specimens avaient déjà été utilisés. Ils avaient tous copulé le 24 novembre, le 27 novembre ou le 09 décembre. Signalons que c'est lors de l'expérience du 10 décembre que le specimen A a suivi la piste du specimen N (Fig. 1b).

3. *Expériences sans phases de poursuite et sans copulation.*

Lors de ces expériences (2 décembre : E, F, G, H ; 8 décembre : I, J, K, L ; 11 décembre : O, P, Q, R), nous n'avons observé aucune phase de poursuite et aucune copulation. Les specimens ont présenté leurs diverses activités telles qu'elles se déroulent en temps normal, à savoir : le repos, le déplacement et la nutrition. Pour l'expérience du 2 décembre et du 11 décembre, les specimens utilisés avaient été capturés un jour avant leur expérimentation. En ce qui concerne l'expérience du 8 décembre, les quatre specimens avaient déjà été utilisés le 4 de ce mois et avaient tous copulé.

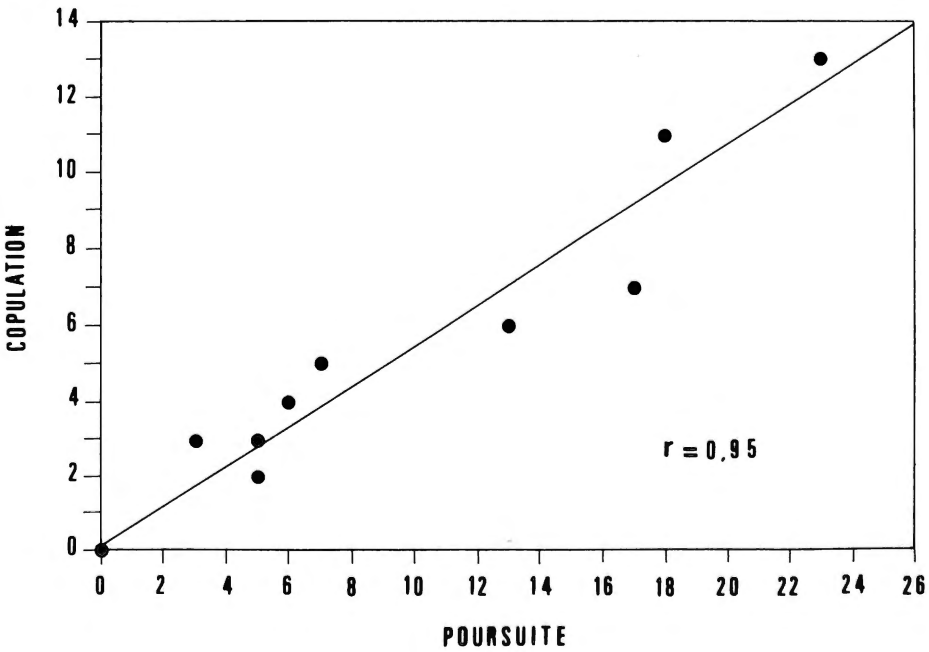

Fig. 3. — Relation entre le nombre de copulations et de poursuites observées pour chaque individu. Les *Arion* qui n'ont pas copulé (8 spécimens) n'ont participé à aucune poursuite.

En résumé, 28 copulations ont pu être observées au cours de ces 11 expériences. Parfois extrêmement brèves (2 minutes), ces copulations peuvent aussi se prolonger pendant plus de 2 heures (142 minutes). En moyenne, elles durent 47 minutes ($\sigma = 37$). Les phases de poursuite sont au contraire extrêmement brèves (Fig. 2). Sur un total de 51 poursuites, 22 d'entre elles ont duré moins de 6 minutes, la plus longue a duré une heure. D'une phase de poursuite à l'autre, les individus peuvent être indifféremment poursuivants ou poursuivis. Certains individus se poursuivent et copulent une seule fois au cours d'une nuit, d'autres au contraire se poursuivent et copulent à maintes reprises. Il semble exister une corrélation très étroite entre ces deux activités ($r = 0{,}95$; $P < 0.001$) (Fig. 3).

Analyse histologique.

Tous les animaux expérimentés ont été soumis à un examen histologique. Au cours de cette analyse, nous avons examiné successivement : le développement de l'ovotestis ainsi que son contenu (spermatozoïdes différenciés et oocytes), le canal hermaphrodite (pour y constater l'éventuelle présence de spermatozoïdes), la glande à albumen, le degré de développement du spermoviducte ainsi que le contenu de la bourse copulatrice.

Nous n'avons jamais observé ni spermatophore ni spermatozoïde dans la bourse copulatrice, mais, l'ovotestis était toujours développé et contenait des spermatozoïdes matures ainsi que des oocytes. Le canal hermaphrodite était très distendu par les spermatozoïdes. La glande à albumen et le spermoviducte étaient également bien développés. Tous les specimens utilisés, y compris ceux qui n'ont pas copulé au cours de nos expériences, présentaient par conséquent les caractéristiques d'individus sexuellement matures.

DISCUSSION

C'est en 1966, que NEWELL a mis au point un système expérimental destiné à l'étude d'un Pulmoné Stylommatophore, *Deroceras reticulatum*. Ce dispositif lui a permis de préciser le comportement précopulateur chez cette espèce. NEWELL a pu montrer qu'un specimen prêt à copuler peut croiser plusieurs pistes par hasard pour ne s'intéresser finalement qu'à la piste de son futur partenaire sexuel qu'il suivra jusqu'à la rencontre précédant l'accouplement. BINDER (1976) signale chez *Gymnarion coronatus* que la première manifestation d'une activité sexuelle est l'apparition d'un individu se déplaçant rapidement, organe frontal déployé, en suivant la trace d'un congénère et en léchant la traînée de mucus déposée sur le substrat. Enfin, COOK (1985) montre qu'*Euglandina rosea* (FÉRUSSAC, 1821) est capable également de suivre la piste de son futur partenaire avant la copulation proprement dite.

L'ensemble de ces observations suggère la présence au niveau de la piste muqueuse d'une substance attractante favorisant le rapprochement des individus en période de reproduction. Il est toutefois indéniable qu'en dehors de cette période, les individus de certaines espèces sont sensibles à la piste laissée sur le substrat par

des congénères ou par eux-mêmes. Cela a été démontré chez diverses espèces de Gastéropodes (FUNKE, 1968 ; WELLS and BUCKLEY, 1972 ; TOWNSEND, 1974 ; COOK, 1977, 1980, 1985 ; CHASE and BOULANGER, 1978 ; CHASE *et al.*, 1978, 1980 ; CHASE and CROLL, 1981 ; TROTT and DIMOCK, 1978 ; MC FARLANE, 1980 ; USHADEVI and KRISHNAMOORTHY, 1980 ; BRETZ and DIMOCK, 1983). Aussi, il est raisonnable d'admettre qu'une substance attractante ne pourra être considérée comme « attractant sexuel » que dans la mesure où elle n'attire que les individus sexuellement mûrs et en quête d'un partenaire. Cette substance attractante, présente dans la piste, servirait à renseigner les autres limaces sur l'état de maturité sexuelle du specimen.

Dans ce travail, nous avons pu montrer qu'*Arion distinctus* a un comportement précopulateur caractérisé par une phase de poursuite au cours de laquelle le poursuivant broute le globule muqueux du poursuivi. Ce comportement de poursuite semble être un préliminaire indispensable à la copulation puisqu'il n'a jamais été possible d'observer des individus en copulation qui ne s'étaient pas poursuivis préalablement. D'autre part, s'il nous a parfois été possible de relever des phases de poursuite sans phase de copulation, il s'agissait toujours d'individus qui s'étaient déjà accouplés au cours d'expériences précédentes. Il existe une corrélation très étroite entre ces deux comportements ($P < 0{,}001$) et l'observation de ce phénomène de poursuite pourrait bien être considérée comme un indicateur facilement perceptible de la maturité sexuelle du poursuivant aussi bien que du poursuivi.

Les copulations que nous avons pu observer, sont d'une durée extrêmement variable. Elles se sont échelonnées de 2 à 142 minutes. Les copulations de 2, 4 et 10 minutes ne sont probablement que de simples tentatives puisque ce délai est trop court pour permettre l'échange de spermatophores. Nos résultats sont néanmoins en opposition avec le travail de DAVIES (1977). En effet, cet auteur signale qu'il faut de 20 à 30 minutes pour qu'il y ait échange de spermatophores chez *A. distinctus,* mais que cet intervalle est de 80 à 105 minutes et parfois plus pour *A. hortensis.* Rappelons cependant que tous les individus (sans exception) qui ont copulé au cours de nos expériences, ont copulé indifféremment pendant des temps supérieurs à 80 minutes, inférieurs à 30 minutes ou encore intermédiaires, que ce soit ou non avec le même partenaire, au cours de la même nuit ou lors de nuits différentes. Nous pouvons donc exclure une hétérogénéité spécifique éventuelle de notre matériel expérimental. Contrairement à DAVIES (*op. cit.*), les données que nous rapportons ont été obtenues en laboratoire à l'aide d'une caméra vidéo ; il est par conséquent possible que l'absence totale d'éléments perturbateurs (y compris la présence éventuelle d'un observateur) entraîne parfois un allongement de phénomènes normalement plus courts en milieu naturel.

Les phases de poursuite ont toujours débuté après que le poursuivant se soit dirigé directement vers le globule muqueux du poursuivi ou après qu'il ait suivi la piste de ce dernier sur une certaine distance. Par conséquent, nos expériences laissent sous-entendre qu'il y a dans le mucus d'*Arion distinctus* présence d'un attractant sexuel. Chez cette espèce, le « suivi de piste » est cependant assez rare, et si nos expériences montrent que le poursuivant est capable non seulement de suivre une piste mais aussi d'en percevoir le sens, elles montrent aussi que dans la majorité des cas, les *Arion* se dirigent directement vers le globule muqueux. Chez *Arion distinc-*

tus, l'attractant sexuel serait donc non seulement présent au niveau de la piste mais encore et surtout au niveau du globule muqueux comme l'avaient déjà supposé BARR (1928) et ADAM (1933).

L'origine et la fonction de ce globule ont été longtemps discutées. Selon SAINT SIMON (1852) et ANDRÉ (1898), le globule muqueux serait sécrété uniquement par la glande caudale. Pour BARR (1928), il proviendrait d'une part de la glande caudale et d'autre part des glandes intertégumentaires dorsales et de la frange pédieuse. Plus récemment, VAN MOL *et al.* (1970) ont pu mettre en évidence l'origine du globule muqueux en saupoudrant de talc un *Arion rufus*. Cette expérience a montré clairement que le mucus synthétisé par la glande pédieuse migre vers l'arrière au cours du déplacement. Il glisse le long de la frange pédieuse et vient s'accumuler finalement au niveau de la glande caudale. La formation du globule muqueux sera d'autant plus rapide que l'animal effectue de grands déplacements. A partir d'un certain moment, le globule devenu trop important restera collé au substrat. Le globule a plusieurs origines mais c'est probablement le mucus de la glande pédieuse qui en constitue la plus grande partie. Par conséquent, la ou les substances attractantes se trouvant initialement dans le mucus de piste se retrouveront également au niveau de la glande caudale et on peut supposer que le plus grand pouvoir attractant du globule est lié tout simplement à la présence, à son niveau, d'une plus grande quantité d'attractant.

Il est raisonnable de supposer que la présence dans la piste d'une substance attractante favorise le rapprochement d'individus fort éloignés les uns des autres. Par contre, dès qu'ils seraient suffisamment proches, le plus grand pouvoir attractant du globule muqueux permettrait au poursuivant de « prendre un raccourci » et de se diriger directement vers son partenaire potentiel, sans plus devoir se préoccuper de la piste. La rareté des « suivis de piste » observés au cours de nos expériences, pourrait toutefois être liée à nos conditions expérimentales et l'étroitesse de l'arène a peut-être favorisé plus particulièrement le deuxième comportement au détriment du premier. L'utilisation d'une arène de plus grandes dimensions devrait confirmer ou infirmer cette hypothèse. Il serait aussi très intéressant de pouvoir tester la spécificité de cette substance sur d'autres espèces d'*Arion* faisant ou non partie du même complexe. Dans l'affirmative, cet attractant serait dès lors considéré comme une véritable phéromone. Elle pourrait peut-être jouer un rôle en tant que facteur de ségrégation entre les différentes espèces, comme l'avait déjà suggéré DAVIES (1977) à propos des différences touchant la structure des organes génitaux ou la durée des copulations.

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RÉGIME ALIMENTAIRE DES *HAPLOCHROMIS* (TELEOSTEI : CICHLIDAE) DU LAC KIVU EN AFRIQUE

I. RELATIONS TROPHIQUES INTERSPÉCIFIQUES

par

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RÉSUMÉ

La présente étude a porté sur l'analyse des contenus stomacaux de 456 échantillons d'*Haplochromis* représentant 10 espèces d'*Haplochromis* endémiques du lac Kivu. Il ressort de ces analyses que ces *Haplochromis* ne présentent pas de fortes interactions compétitives. Elles occupent dans le lac des niches écologiques nettement distinctes, excluant les regroupements de prédations sur des proies fondamentales de leur régimes spécifiques.

Les rares pressions compétitives observées concernent des proies d'importance secondaire pour l'une ou l'autre espèce lors de l'exploitation partielle en commun d'une proie relativement abondante.

L'absence de compétition alimentaire chez les *Haplochromis* serait la conséquence de la radiation adaptative du régime des espèces adaptées à rechercher un type donné de nourriture. Elle pourrait aussi être la conséquence des adaptations liées à une compétition ancestrale.

Mots clés : Compétition interspécifique, relations trophiques, *Haplochromis*, Cichlidae, lac Kivu.

Food and feeding habits of *Haplochromis* (Teleostei : Cichlidae) from lake Kivu in Africa

I. Interspecific trophic relations

SUMMARY

The present study deals with the analysis of stomach contents of 456 *Haplochromis* belonging to 10 distinct species endemic to lake Kivu. It is shown that there is no marked food competition between *Haplochromis* species.

Each species occupies in the lake an ecological niche sufficiently distinct from others and competition for important preys is avoided. The exceptional cases in which competition for food was observed, concern some prey of minor importance suggesting a partial overlap of some *Haplochromis* species to prey on abundant prey items.

It may be concluded that absence of marked food competition among *Haplochromis* species, is a consequence of adaptative radiation which has resulted in a distinct feeding habit of the different species or the consequence of fixed adaptations probably due to passed competition.

Key words : Interspecific competition, trophic relations, *Haplochromis,* Cichlidae, lake Kivu.

INTRODUCTION

Les espèces du genre *Haplochromis* constituent l'un des groupes piscicoles les plus importants du lac Kivu. Bien que de nombreuses publications et autres ouvrages généraux aient été consacrés à leur systématique (COENEN *et al.,* 1984 ; SNOEKS, 1986 ; SNOEKS *et al.,* 1987), avec parfois quelques indications fragmentaires sur leurs régimes alimentaires (VERBEKE, 1957 ; MAHY, 1979), leurs relations alimentaires restent cependant très peu étudiées.

L'étude du régime alimentaire par analyse des contenus stomacaux permet de résoudre avant tout la question des ressources alimentaires de manière qualitative et quantitative, de comprendre si en milieu naturel, les différentes espèces d'un même groupe ont un régime individualisé ou non et de comparer les relations alimentaires existant entre les espèces étudiées. Ceci implique les notions de niche écologique, de spécialisation alimentaire ainsi que des compétitions interspécifiques qui en découlent. Tel est le but de la présente étude.

MATÉRIEL ET MÉTHODES DE TRAVAIL

Récolte des échantillons

Les poissons ont été capturés au lac Kivu à l'aide des filets maillants de 10, 12, 15, 20 et 25 mm de mailles posés entre 0 et 70 m de profondeur. 456 poissons de

longueur standard (LS) située entre 47 et 196 mm, représentant 10 espèces ont été analysés. Ce matériel provient de deux lots de capture. Le premier lot a été recolté au cours de la période d'août à octobre 1981 par la mission Murakoze I, tandis que le second lot a été pêché entre la période du 10 février au 15 mai 1987.

Afin d'arrêter le processus de digestion après capture, les poissons ont reçu immédiatement dans la cavité viscérale une injection de formaldehyde 10 % et ont été fixés soit dans l'alcool 75 %, soit dans du formol 4 % pour les analyses ultérieures.

Méthodes d'analyses de contenus stomacaux.

Les méthodes d'étude du régime alimentaire par analyse de contenus stomacaux ont déjà fait l'objet de multiples publications (HYNES, 1950 ; WINDEL, 1968 ; BERG, 1979 ; HYSLOP, 1980).

Nous avons adopté la méthode des « points » de HYNES (1950) qui est une combinaison des méthodes à la fois numériques et volumétriques ou pondérales. Elle consiste à attribuer à chaque proie dénombrée un certain nombre de points en fonction de son abondance et de sa taille. Le nombre total des points obtenus pour chaque item alimentaire est exprimé en pour-cents par rapport à l'ensemble des points obtenus pour toutes les proies.

Traitements statistiques des données.

Les données chiffrées ont été traitées par les analyses de corrélations canoniques (CANCORR) ainsi que par les analyses canoniques discriminatoires (CANDISC) utilisant le système SAS (5^{e} édition, 1985).

20 variables alimentaires et 10 variables espèces ont été retenues pour les analyses et seuls les estomacs représentant au moins 15 % du volume total de réplétion ($V_{Esto} \geq 15$) ont été utilisés pour les tests de similarités et dissimilarités. Au cours de nos analyses, nous avons considéré les premières corrélations qui décrivent la plus grande partie de la variabilité totale, soit 84 %. Elles recouvrent respectivement 41 %, 28 % et 15 % ($p < 0.0001$) et correspondent aux variables canoniques V_{C1}, V_{C2} et V_C des tableaux 1 et 2.

Pour visualiser les résultats et différencier les groupes alimentaires, nous avons projeté sur les axes des variables canoniques « proies », les scores des observations individuelles de chaque espèce de même que les corrélations de variables « espèces » avec ces variables canoniques « proies » (Fig. 1).

Sur la figure 2, nous avons fait la projection des corrélations de variables « espèces » et « proies » avec les variables canoniques « proies » sur les axes des variables canoniques « proies » (Fig. 2). Ces « biplots » permettent de visualiser les relations entre « espèces » et « proies ».

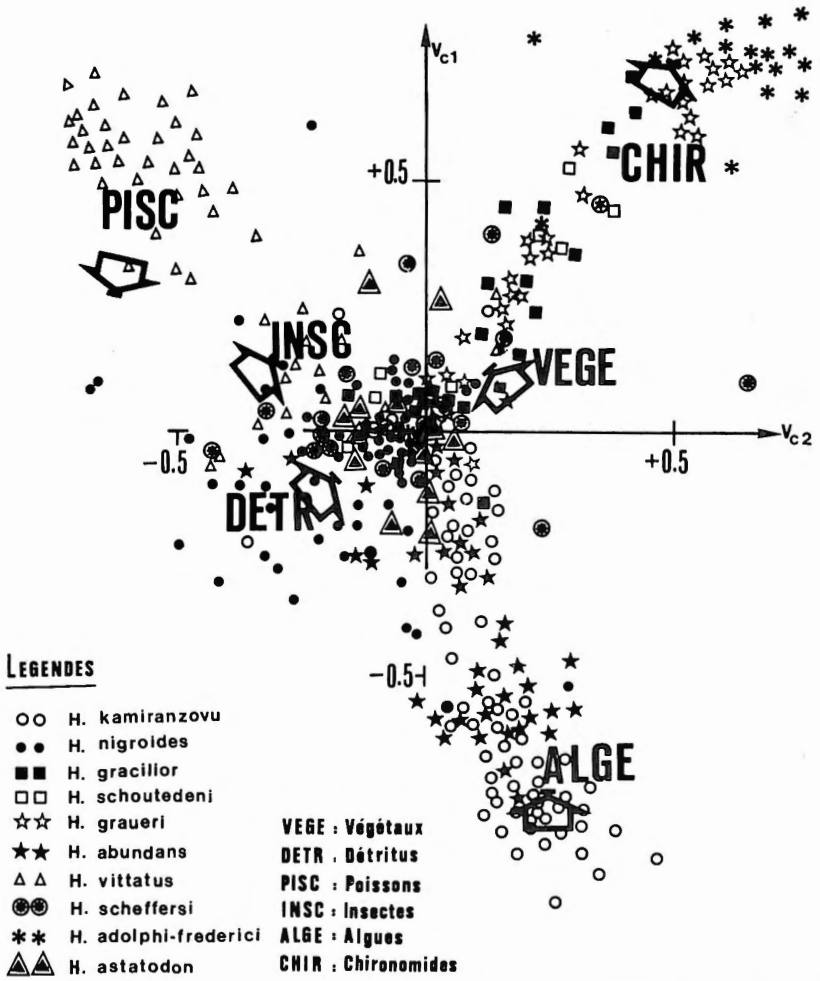

Fig. 1. — Représentation schématique des scores individuels des 10 espèces d'*Haplochromis* et valeurs de corrélations des variables « proies » avec leurs propres variables canoniques sur les axes des variables canoniques « proies ». Les flèches indiquent les positions exactes des variables canoniques « proies » (V_{C1}, V_{C2}).

Les relations alimentaires entre espèces ont été illustrées par représentation graphique dans un espace euclidien multidimensionnel des valeurs des 3 premiers axes canoniques CAN_1, CAN_2 et CAN_3, tandis que les probabilités ont été établies par les valeurs du F-test des Distances de Mahalanobis ($p > D_{mah}$) (Fig. 3, tableau 4).

TABLEAU 1

Corrélations canoniques entre les variables « proies » et leurs variables canoniques ($Pr.P_{Can}$)

Catégories des proies	$Pr.P_{Can}$		
	V_{C1}	V_{C2}	V_{C3}
Poissons (PISC)	0,23	−0,79	−0,37
Restes animaux (ANIM)	0,01	−0,12	0,22
Matières organiques (DETR)	−0,15	−0,20	0.31
Bacillariophycées (DIAT)	−0,13	0,04	0,09
Larves de chironomides (CHIR)	0,74	0,50	−0,30
Cladocères (CLAD)	−0,05	−0,02	0,39
Copépodes (COPE)	−0,19	0,02	0,20
Rotifères (ROTI)	−0,01	−0,02	0,19
Algues (ALGE)	−0,75	0,19	−0,51
Diptères (DIPT)	0,05	−0,02	0,35
Restes d'insectes (INSC)	0,15	−0,30	−0,12
Débris végétaux (VEGE)	0,13	0,12	0,06
Plécoptères (PLEC)	−0,02	−0,05	0,13
Ephéméroptères (EPHE)	−0,03	−0,05	0,16
Hyménoptères (HYMN)	0,05	0,01	0,17
Ostracodes (OSTR)	0,06	0,06	0,24
Sédiments (SEDI)	−0,02	0,14	−0,10
Nématodes (NEMA)	−0,12	0,03	0,11
Acanthocéphales (ACAN)	0,02	0,02	0,12
Acariens (ACAR)	0,04	−0,03	0,03

TABLEAU 2

Corrélations canoniques entre les variables « espèces » et les variables canoniques « proies » ($Esp.P_{Can}$)

Catégories des proies	$Esp.P_{Can}$		
	V_{C1}	V_{C2}	V_{C3}
H. « abundans » (ABUN)	−0,34	0,07	−0,13
H. adolphifrederici (ADOL)	0,41	0,28	0,24
H. astatodon (ASTA)	0,01	<0,01	0,04
H. gracilior (GRAC)	0,15	0,06	0,19
H. graueri (GRAU)	0,33	0,24	−0,08
H. kamiranzovu (KAMI)	−0,47	0,13	−0,28
H. murakoze (MURA)	—	—	—
H. nigroides (NIGR)	−0,07	−0,17	0,31
H. scheffersi (SCHE)	0,07	−0,01	0,28
H. schoutedeni (SCHO)	0,11	0,07	0,05
H. vittatus (VITT)	0,24	−0,63	−0,26

RÉSULTATS ET DISCUSSION

Caractérisation des groupes alimentaires.

Le tableau 3 donne les moyennes arithmétiques (MÆ) calculées pour 20 catégories de proies importantes inventoriées dans les contenus stomacaux de 456 échantillons d'*Haplochromis* ainsi que les volumes moyens de proies par espèce. Leurs corrélations canoniques sont consignées dans les tableaux 1 et 2.

En observant ces valeurs, on peut reconnaître à priori 4 groupes alimentaires importants composés d'algues (MÆ ± SD = 16,63 ± 27,42), de débris organiques (MÆ = 10,66 ± 16,51), de larves de chironomides (MÆ = 9,53 ± 20,85) et de poissons (MÆ = 4,27 ± 18,35). Ces groupes sont suivis des items alimentaires qui bien qu'ayant des moyennes arithmétiques relativement élevées, montrent des corrélations avec leurs variables canoniques très faibles, proches de la valeur 0 (tableau 1). Ce sont les copépodes (MAE = 4,68 ± 9,95), les Cladocères (MAE = 3,04 ± 7,46), les diptères (MAE = 1,78 ± 7.48)... Ils constituent le cinquième groupe alimentaire, celui des omnivores.

TABLEAU 3

Proportions moyennes des proies inventoriées dans les estomacs de tous les individus analysés (MÆgI ± SD) comparées à celles des catégories de proies par espèce.
Les valeurs de MÆ≤0.1 ne sont pas reprises sur ce tableau.

Espèces étudiées Nombre d'individus (N)		Volume moyen des proies (MÆ≥0.1) par espèce analysée									
		ABUN (66)	GRAU (62)	GRAC (34)	SCHO (9)	KAMI (62)	NIGR (95)	ADOL (19)	SCHE (53)	ASTA (10)	VITT (27)
Proies	MÆgI ± SD										
ALGE	16,63 ± 27,42	33,64				54,01	9,20	1,87	5,29	5,60	
DETR	10,66 ± 16,51	14,74	1,41		7,33	4,13	17,04	2,71		33,19	8,96
CHIR	9,53 ± 20,84		34,77	14,18	24,83		13,72	61,08	6,98		
COPE	4,68 ± 9,95		3,20	3,63	3,42	6,59	8,63		3,66		
PISC	4,28 ± 18,35						4,03				49,04
CLAD	3,04 ± 7,46			6,48	4,26	3,36	5,73		4,06		
ANIM	2,93 ± 11,49			3,49			4,93		6,00		3,70
DIPT	1,78 ± 7,48			4,94			2,67		4,81		
SEDI	1,74 ± 6,66	4,64							1,93	5,83	
DIAT.	1,63 ± 5,60	4,72					1,17			2,26	
INSC	1,36 ± 9,91										11,11
PONT	1,22 ± 7,63						1,69				
VEGE	0,84 ± 2,95								1,14	4,53	
EPHE	0,57 ± 4,54						1,85				
OSTR	0,18 ± 0,72								0,63		

Les légendes sont identiques à celles des tableaux 1 et 2.

TABLEAU 4

*Matrices réciproques des valeurs des distances de Mahalanobis (matrice inférieure) et de coefficients des corrélations simples (matrice supérieure) entre les paires de 10 espèces d'*Haplochromis *pour 20 variables alimentaires.*

Espèces	ABUN	SCHO	ADOL	GRAU	KAMI	GRAC	NIGR	SCHE	ASTA	VITT
ABUN	—	−0,07	−0,10	−0,14	−0,08	−0,13	−0,24	−0,17	−0,07	−0,12
PAUC	2,98 **		−0,03	−0,05	−0,06	−0,04	−0,08	−0,06	−0,02	−0,04
ADOL	4,96	3,30		−0,07	−0,09	−0,07	−0,12	−0,08	−0,03	−0,06
GRAU	3,28	1,44	2,37		−0,13	−0,09	−0,17	−0,12	−0,05	−0,08
KAMI	1,62	3,51	5,30	3,72		−0,13	−0,23	−0,16	−0,07	−0,11
GRAC	2,86	1,80	4,05	2,17	3,38		−0,16	−0,11	−0,05	−0,08
NIGR	2,02	2,28	4,66	2,84	2,57	2,13		−0,21	−0,09	−0,15
SCHE	2,38	1,88	4,34	2,47	2,96	1,89	1,46		−0,06	−0,10
ASTA	2,58 **	2,97	4,45	3,33 **	3,66 **	3,21 **	2,49 **	2,69 **		−0,04
VITT	4,75	4,56	5,70	4,72	5,16	4,48	4,05	4,28	4,72	—

** = P > 0,05 (interactions compétitives positives). Les autres valeurs sont hautement positives ($p \leq 0{,}001$).

Relations alimentaires interspécifiques.

Les différentes analyses de corrélations effectuées entre les paires de 10 espèces d'*Haplochromis* spp. pour 20 catégories de proies, ainsi que les analyses canoniques discriminatoires (CANDISC) exprimées en termes de distances de Mahalanobis (D_{mah}) reprises au tableau 4, permettent d'aboutir aux constatations suivantes :

1) les corrélations canoniques (CANCORR) entre espèces et proies distinguent nettement les groupes alimentaires c'est-à-dire les piscivores, les carnassiers entomophages, les détritiphages, les microphytophages et les omnivores.
2) les corrélations simples s'établissant entre les espèces sont en général faibles et négatives, et par conséquent les régimes alimentaires des différentes espèces sont distincts et diversifiés.
3) les analyses canoniques discriminatoires multivariées (CANDISC) montrent des valeurs de distances de Mahalanobis hautement significatives.
4) les chevauchements alimentaires entre certaines espèces ne concernent que quelques rares items alimentaires d'importance secondaire consommés par l'une ou l'autre espèce.

On observe que les régimes d'*H. schoutedeni* et *H. « abundans »* se recoupent ($D_{mah} = 2,98$, $p = 0,99$) pour certaines proies, bien que la première espèce soit entomophage à tendance omnivore, tandis que la seconde est phytophage. Ce phénomène s'expliquerait vraisemblablement par la variabilité individuelle à l'intérieur même des groupes et/ou par les différences qui existent entre les divers groupes comparés.

Il serait cependant hâtif de conclure à une compétition quelconque, en raison d'une part, du faible nombre des échantillons d'*H. schoutedeni* (n = 9) utilisés pour les analyses et d'autre part, à cause de la prédation commune sur des proies secondaires aux régimes principaux, en l'occurrence les débris organiques et les microcrustacés du zooplancton et même le sédiment.

Quelques relations de compétitions alimentaires positives apparaissent également entre *Haplochromis astatodon* (n = 10), au régime détritiphage, avec les espèces *H. « abundans »* ($D_{mah} = 2,58$, $p = 0,99$), *H. graueri* ($D_{mah} = 3,33$, $p = 0,38$), *H. nigroides* ($D_{mah} = 2.49$, $p = 0,99$), *H. kamiranzovu* ($D_{mah} = 3,66$, $p = 0,67$), *H. gracilior* ($D_{mah} = 3,21$, $p = 0,37$) et avec *H. scheffersi* ($D_{mah} = 2,69$, $p = 0,96$).

Les valeurs hautement positives ($p \leq 0,001$) observées entre les espèces de régime identique, comme par exemple *H. adolphi frederici, H. graueri,* et *H. schoutedeni,* espèces au régime carnassier entomophage, s'expliquerait par l'ordre de grandeur qu'occupe chaque item dans les régimes individuels spécifiques. Les espèces se différencient nettement entre elles par leurs proies secondaires. Ces spécificités se rencontrent également chez les espèces omnivores *H. gracilior, H. nigroides* et *H. scheffersi* qui manifestent avec *H. astatodon* une compétition partielle.

Cela conduit en effet à la notion de « niche breadth » définie par CASWELL (1976) comme point de jonction de l'utilisation d'une ressource ou de ressources par deux ou plusieurs espèces, autrement dit la région d'un espace ou portion de niche

partagée par 2 ou plusieurs niches contigues. C'est un processus consistant en une « prédation équivalente », c'est-à-dire la recherche similaire par deux espèces de proies équivalentes à la fois dans leur niche écologique propre et dans un espace environnemental commun (HANSKI, 1981). C'est ainsi que l'on observe par exemple qu'*H. astatodon* partage les algues et les pellicules organiques avec *H. kamiranzovu* et *H. « abundans »*, de même qu'il partage les sediments ainsi que les diatomées, des aliments qui représentent des volumes relativement importants dans le régime d'*H. « abundans »*. Pourtant les 3 espèces appartiennent à des groupes alimentaires différents.

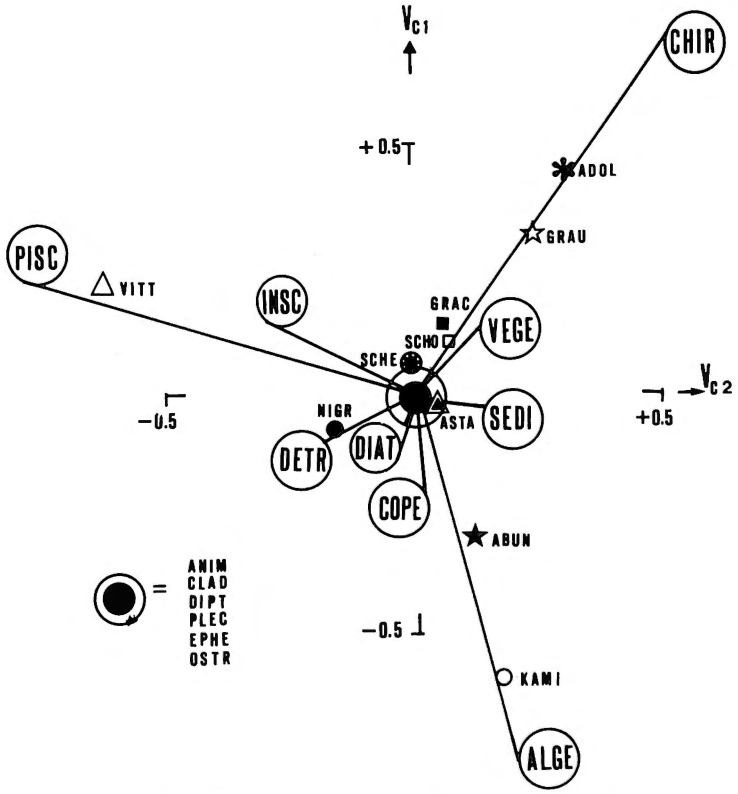

Fig. 2. — Représentation graphique des corrélations des variables « espèces » et des variables « proies » avec les variables canoniques « proies » (V_{C1}, V_{C2}).

Les espèces d'*Haplochromis* doivent donc s'être adaptées aux différents facteurs des conditions environnementales, avoir co-évolué de manière à occuper chacune une partie différente du site par « changement d'habitat » ou « habitat shift » (SCHOENER, 1974), où elles se sont retrouvées chacune le compétiteur supérieur (CONNEL, 1980).

Ainsi face à certains prédateurs comme *H. vittatus* par exemple, elles devraient tolérer la présence de celui-ci si la pression prédatrice est mineure, adapter leur physiologie, leur anatomie ou leur comportement de manière à riposter (coévolution) ou simplement occuper un environnement exempt de ce prédateur (THORP, 1986).

Toutefois, les mesures de la largeur des niches (niche breadth) au sens de COLWELL et FUTUYMA (1971) ainsi que du chevauchement des niches qui toutes deux dépendent de la distribution desindividus par rapport au niveau des ressources des catégories écologiques, devraient être indépendantes de l'abondance relative des espèces et du nombre des états de ressources considérés. Elles devraient plutôt tenir compte des degrés de distinction des états des ressources vus par les organismes concernés eux-mêmes (COLWELL et FUTUYMA, 1971).

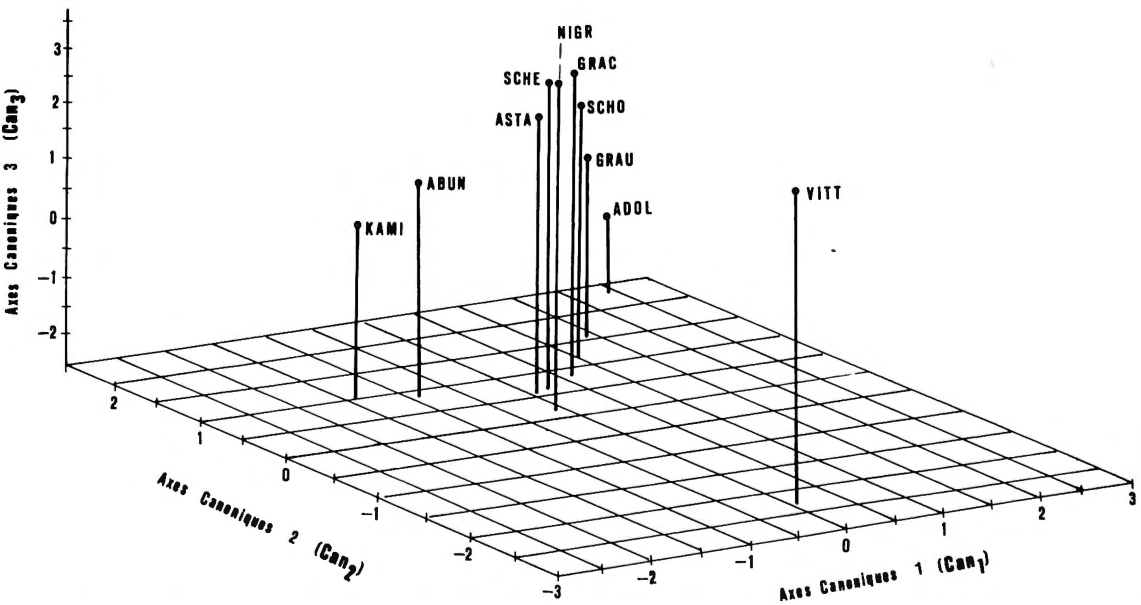

Fig. 3. — Séparation alimentaire des 10 espèces d'*Haplochromis* par la distance de Mahalanobis sur les 3 premiers axes canoniques alimentaires de 20 variables « proies ».

En définitive, bien que ni la présence, ni l'absence de chevauchement alimentaire ne soient une indication de la présence ou de l'absence d'une éventuelle compétition, nous pourrions interpréter nos résultats obtenus sur les *Haplochromis* d'après le terminologie de PIM (1980) comme étant une « compétition exploitative » modelée par deux ou plusieurs prédateurs qui partagent au moins une proie (PIMM, 1980). Elle permet en effet aux espèces en compétition partielle de coexister bien qu'elles soient l'objet des pressions multiples, faibles ou diffuses (MACARTHUR, 1972) dues à l'utilisation d'un même type d'aliment. Ce genre de ségrégation écologique pourrait aussi se produire naturellement selon différents axes comme le temps, les gradients de température (BARBAULT, 1983). Par ailleurs les valeurs positives montrant que la plupart des proies ne sont pas partagées pourraient être une indication des

adaptations résultant d'une compétition antérieure, passée ou en cours, que l'on ne saurait déterminer sur le terrain à défaut d'une réplication expérimentale en laboratoire des phénomènes naturels.

CONCLUSIONS

Les analyses présentement effectuées nous permettent d'aboutir aux constatations suivantes :

1) les *Haplochromis* se répartissent entre 5 régimes alimentaires : Carnassiers piscivores, Carnassiers entomophages, Microphytophages, Omnivores et Détritiphages ;
2) les *Haplochromis* occupent des niches écologiques distinctes. Ils exercent une prédation à des degrés différents sur des proies identiques. Ils sont un exemple de coexistence alimentaire où se chevauchent les niches écologiques sans interférences sur les individus en compétition ;
3) les relations compétitives alimentaires interspécifiques positives observées sont exercées sur des proies d'importance secondaire sans que les espèces ne soient nécessairement d'un même groupe alimentaire ;
4) deux espèces présentent des régimes relativement spécialisés : *Haplochromis vittatus* (piscivore), et *H. kamiranzovu* (microphytophage). Ceci indique une envergure ou un recouvrement de niches trophiques restreint de leurs espaces environnementaux vitaux respectifs (COLWELL et FUTUYMA, 1971).

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COMPARISON OF THE FATTY ACID PROFILE OF WILD CAUGHT FINGERLINGS AND YOLK SAC SEA BASS *(DICENTRARCHUS LABRAX)* LARVAE WITH CULTURED HEALTHY LARVAE AND LARVAE SUFFERING FROM WHIRLING DISEASE

by

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SUMMARY

Analysis of the fatty acids of total lipids of wild fingerlings (1-4 g) of sea bass (*Dicentrarchus labrax*) caught off the north coast of France shows that more than 30 % of total fatty acids consists of the two essential fatty acids eicopentaenoic (C20:5 n-3) and docosahexaenoic (C22:6 n-3) acids. One- and three-day old yolk sac larvae have even higher amounts of these two important fatty acids (about 40 %). On the other hand, laboratory-reared 60-day old larvae had much lower concentrations of C20:5 n-3 (4 % of total fatty acids) and C22:6 n-3 (5.5 % of total fatty acids). In larvae suffering from whirling or spinning disease the percentage of C20:5 n-3 was only 2.8 % and only traces of C22:6 n-3 were found. These results emphasize the importance of these fatty acids for cultured sea bass larvae.

Key-words : HUFA, Sea-Bass, Larvae.

INTRODUCTION

Highly Unsaturated Fatty Acids (HUFA's, fatty acids with at least 20 Carbons and 3 unsaturated bonds) are very important components of biological membranes. Fresh water fishes are able to synthesize them starting from lenoleic (C18:2 n-6) and lenolenic (C18:3 n-3) acid. Marine fish are incapable of de novo synthesis of HUFA's such as C20:5 n-3 and C22:6 n-3 and dietary sources of these fatty acids are therefore essential for normal growth and development (WATANABE, 1982). During the last decade many studies have demonstrated the importance of HUFA's especially C20:5 n-3 and C22:6 n-3 for the culture of marine fish larvae and shrimps

(FUJITA *et al.*, 1980 ; HALVER, 1980 ; SCHAUER *et al.*, 1980 ; WATANABE, 1982 ; LEGER and SORGELOOS, 1984 ; LEGER *et al.*, 1985 ; SUZUKI et al., 1986 ; DENDRINOS and THORPE, 1987 ; CORNEILLIE, 1989). To date the rearing of marine fish larvae still requires the use of live foods. Most intensively used are the rotifer *Brachionus plicatilis* and the crustacean *Artemia* sp... However a lot of studies showed that these organisms are very low in C20:5 n-3 and/or C22:6 n-3 (WATANABE *et al.*, 1980, 1982, 1983 ; VAN BALLAER *et al.*, 1985). Many investigators found higher survival rates and better morphologically developed larvae when the live prey were enriched with HUFA's (bio-encapsulation) just before administration to the marine fish larvae (WITT *et al.*, 1984 ; FRANICEVIC *et al.*, 1987 ; KITAJIMA, 1987 ; WALFORD and LAM, 1987).

Despite the awareness of the importance of C20:5 n-3 and C22:6 n-3 for the culture of sea bass larvae, no one has ever studied the fatty acid profile of wild caught juveniles, which should be indicative of optimal requirement in culture. The present study was undertaken to compare the fatty acid profiles of wildcaught and cultured fish as well as to establish whether whirling disease can be caused by fatty acid inadequacy.

MATERIALS AND METHODS

Collection and culture of sea bass larvae

Wild fingerlings (1 to 4 g, about 4-5 months old) were caught by nets at the end of April 1987 from the estuary of Ambleteuse (north France). After transporting them live to the laboratory 5 fingerlings were frozen for analysis.

Newly hatched larvae obtained from C.O.B. (Brest, France) in May 1987 were put in larval tanks of 100 litres. The larvae were cultured at Leuven under normal conditions (Corneillie *et al.*, 1989). Larvae were fed with *Brachionus plicatilis* enriched with SELCO (Artemia Systems N.V., Ghent ; day 5-13), nauplii of *Artemia* (day 10-20) ; metanauplii of *Artemia* enriched with SELCO (day 20-45), and granules 000 (Trouvit, Trouw Ghent, from day 43 on).

Five samples of 1- and 3-days old yolk sac larvae were collected and frozen for analysis ; each sample contained 150-200 larvae. At day 60, five samples of larvae each containing 3 fish were collected. Forty days old larvae suffering from whirling disease were also collected. All the samples were frozen directly in liquid nitrogen and stored in a freezer at − 70° C until analysis.

Fatty acid analysis.

Total lipids were extracted by homogenising whole fish with chloroform-methanol (2:1 V/V) (FOLCH *et al.*, 1957). Fatty acid methyl esters were prepared by transesterification using a 1 % methanolic solution of sodium methoxide. The esters were injected on to a WCOT capillary column (25 m × 0.22 mm ID fused silica, CP SII-88, stationary phase, 0.2 micron film thickness) installed in a Sigma B

Perkin Elmer gas chromatograph, using hydrogen as carrier gas, split injection and the oven temperature programmed from 140° C to 220° C at 4° C/min. Peak identification and quantification was done with a calibrated plotter-integrator Perkin Elmer 3600 data station.

RESULTS

Table 1, reveals considerable differences in the fatty acid profile of total lipids of sea bass larvae from different origins. In wild caught fingerlings the fatty acid composition shows, on average, 35 % saturated fatty acids (primarly C16:0), 17 % monoenes (C16:1 and C18:1 isomers), and almost 35 % HUFA's (mainly C20:5 n-3 (16.4 %) and C22:6 n-3 (16.3 %)). The fatty acid composition of 1- and

TABLE 1

Fatty acid composition of total lipids from larvae of sea bass from different origins (expressed as area percentage of total fatty acids)

	Wild	*Yolk Sac*		*Leuven*	
		(1 day)	(3 day)	Healthy	Whirling
C14	3.3	3.4	1.7	2.9	0.8
C16	24.4	17.1	14.3	22.2	17.1
C16 : 1w7	6.2	10.2	10.0	3.1	1.0
C16 : 1w9					
C18 : 0	7.0	4.5	2.9	6.8	7.8
C18 : 1w9	11.1	15.4	17.6	12.6	17.8
C18 : 1w7					
C18 : 2w6	(tr)	3.0	5.8	15.7	18.2
C18 : 3w3	(tr)	(tr)	(tr)	2.0	10.3
C20 : 5w3	16.4	11.0	10.2	4.0	2.8
C22 : 4w6	(tr)	(tr)	(tr)	1.7	(tr)
C22 : 4w3					
C22 : 5w3	0.3	(tr)	1.4	0.7	(tr)
C22 : 6w3	16.3	24.0	25.7	5.5	(tr)

(Wild : wild caught larvae ; Yolk sac : 1- and 3-day old yolk sac larvae ; Leuven : larvae cultured in Leuven ; Whirling : larvae suffering from whirling disease ; (tr) : traces ; values are means of 3 to 5 replicates and the difference between the replicates is less than 5 % ; Cn : XwY : Cn number of C-atoms, X number of double bonds, Y position of the first double bond starting from the methyl end.

3-days old yolk sac larvae shows on average 22 % saturated fatty acids, 26 %monoenes and 40 % HUFA's. The yolk sac larvae have very high amounts of C22:6 n-3 (60 % of total HUFA's).

Laboratory cultured larvae had nearly the same HUFA content of wild larvae ; however the percentage of C20:5 n-3 (4 %) and C22:6 n-3 (5.5 %) was rather low. These larvae had, on the other hand, high concentrations of linoleic acid (C18:2 n-6), a non-essential fatty acid for marine fishes.

Larvae suffering from whirling disease had very low concentrations of C20:5 n-3 (2.8 %) and only traces of C22:6 n-3. The proportions of linolenic acid (C18:3 n-3) at 10.3 % and linoic acid (C18:2 n-6) at 18.2 % are high when compared to the other groups.

DISCUSSION

The « probable » fatty acid requirement of sea bass larvae was assessed by analysis of the fatty acid content of yolk sac larvae and wild caught fingerlings. The fatty acid profile of the total lipids emphasise the importance of eicosapentaenoic (C20:5 n-3) and docosahexaenoic (C22:6 n-3) acids. Ten to 16 percent of total fatty acid consists of C20:5 n-3 in both groups and the percentage of C22:6 n-3 is even higher, 16 to 26 %. In 1-day old yolk sac larvae of herring (*Clupea harengus*) it is also these two HUFA's which seems to be important (6.8 and 15.6 % respectively, table 2) (TOCHER *et al.*, 1985). TOCHER and SARGENT (1984) also analysed ripe roes of different Northwest European marine fishes (cod, *Gadus merlangus*). About 70 % of the lipids were formed by the polar classes (mainly phosphatidylcholine and phosphatidylethanolamine). Analysis of the fatty acid of total phospholipids showed the importance of C20:5 n-3 (12 to 15 %) and C22:6 n-3 (28 to 31 % in all the analysed fish, 8 species). Also DENDRINOS and THORPE (1987) estimated the probable fatty acid requirement of larval Dover sole (*Solea solea*) by analysis of the fatty acid content of the yolk of sole eggs. Again C22:6 n-3 seems to be very important (21.6 %) ; however C20:5 n-3 represented only 4.6 % of total fatty acid.

As has already been mentioned FRANICEVIC *et al.* (1987) found much better survival and growth of sea bass larvae when *Artemia* metanauplii were enriched with oils containing high amounts of HUFA's. The same findings were reported for sole larvae (DENDRINOS and THORPE, 1987). WITT *et al.* (1984) also found better performance of turbot larvae (*Scophtahlmus maximus*) when they were fed with copepods, richer in HUFA content than *Artemia*. WATANABE *et al.* reported (*) poor growth and heavy mortalities of red sea bream larvae (*Pagrus major*) when they were fed rotifers containing a low percentage of n3-HUFA's. All these results confirm the importance of n3-HUFA's for marine fish larvae, not least sea bass.

(*) « International symposium on feeding and nutrition in fish », Bergen, Norway, August 23-27, 1987.

TABLE 2

Fatty acid composition of total lipids from yolk sac larvae of sea bass and herring and yolk of fertilised eggs of sole (expressed as area percentage of total fatty acids)

	Yolk sac larvae (1 day old) of		*Yolk of*
	Sea bass	Herring *	Sole #
C14	3.4	5.3	2.8
C16	17.1	21.8	19.9
C16 : 1w9	10.2	—	8.7
C16 : 1w7		6.9	—
C18 : 0	4.5	2.5	2.9
C18 : 1w9	15.4	18.9	13.1
C18 : 1w7		6.1	3.7
C18 : 2w6	3.0	1.3	1.7
C18 : 3w3	(tr)	1.4	0.9
C20 : 5w3	11.0	6.8	4.6
C22 : 4w6	(tr)	—	—
C22 : 4w3			
C22 : 5w3	(tr)	0.9	—
C22 : 6w3	24.0	15.6	21.6

((tr) : traces ; — : not detected ; — values are means of 3 to 5 replicates).

* TOCHER *et al.*, 1985

\# DENDRINOS and THORPE, 1987.

The results of the fatty acid analysis of the laboratory-reared larvae demonstrate the low percentage of these two essential fatty acids. In the healthy larvae the percentage of C20:5 n-3 and C22:6 n-3 was only 10 % of total fatty acids ; this is very low compared to the 33 % found in wild caught sea bass larvae. The low survival of the larvae found in our experiments (12 % at day 45) could be caused by this low HUFA content.

During this expirement, we lost a part of the larvae (about 25 %) due to a whirling or spinning disease. The fatty acid profile of these larvae showed the virtual absence of C22:6 n-3 and the low percentage of C20:5 n-3 (2.8 %). The percentage of linoleic and linolenic acid (18.2 and 10.3 % respectively) was high compared to that of the wild caught and yolk sac larvae. The percentage of linoleic acid was also high in healthy laboratory-reared larvae (15.7 %).

These low concentrations of the n3-HUFA's are hard to explain because the larvae were fed with live prey enriched with SELCO. The SELCO (a special diet rich

in HUFA's) is taken up by the zooplankton and stocked in the intestine (bio-encapsulation). When the fish larvae take up the zooplankton organisms, they also profit from the enrichment. A possible explanation for the low HUFA-concentration in the laboratory-cultured (whirling) larvae could be that HUFA-enriched prey were only administered once a day, because of the low density of the larvae at the end of the experiment. In addition, the live prey that were not eaten within the first hours, lost their gutcontent by normal excretion processes. By this, the effect of the enrichment disappears. Therefore it is better to feed larvae two or three times a day with freshly enriched prey. It must also be noted that larvae suffering from whirling disease had very little intestinal contents (90 % of these larvae had an empty or very poorly filled intestine). Loss of appetite could cause a dramatic decrease in the HUFA-content. Other research groups found that spinning larvae were infected with a Birna-virus (BONAMI *et al.*, 1983). In France, they also found VHS-virus in sea bass and turbot (HILL, 1986). However, there is no direct evidence to connect virus infection and whirling disease. In the present study fairly extensive virological analysis using tissue culture techniques failed to reveal any viruses in any of the larvae.

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A STUDY OF THE DOMINANCE HIERARCHY IN FOUR MBUNA-SPECIES : *MELANOCHROMIS JOHANNI, M. AURATUS, PSEUDOTROPHEUS « ORNATUS »* AND *P. LOMBARDOI* (TELEOSTEI : CICHLIDAE)

by

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SUMMARY

Social organization forms in fish groups have been very poorly studied. However, NELISSEN (1985) found that *Melanchromis auratus* (BOULENGER, 1897) establishes linear rank orders in aquarium tanks. This Mbuna cichlid (Lake Malawi) is closely related to all other species of the ten Mbuna genera (RIBBINK *et al.*, 1983) belonging to the very complex community (Mbuna is a community of a monophyletic species flock ; FRYER and ILES, 1972). After this study the question arose whether other Mbuna cichlids have the same kind of social organization. In order to find out about this a study of *M. johanni* (ECCLES, 1983), *Pseudotropheus « ornatus »* (not yet described) and *P. lombardoi* (BURGESS, 1979) was carried out. A few groups of *M. auratus* were also observed in order to make a comparison between the four species.

Individuals of the same species were kept in groups of 3 to 6 members. The colour patterns and their changes were described, the length of the individuals was measured and the agonistic acts (full display, chasing, circle fighting, mouth fighting, quivering, avoiding and fleeing) were recorded. These recordings of aggression and aggression inhibition were converted into interaction matrices for analysis.

All three species establish a linear rank order in aquaria similar to the dominance hierarchy formed in groups of *M. auratus* (see NELISSEN, 1985). In these rank orders interactions are ordered :

— the interactions depend upon the status of the animals in question.

— neighbouring animals in the hierarchy interact more frequently with each other then with other group members.

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In these linear rank order α is always the most active animal, while ω is the least aggressive animal. The ω-fish does not necessarily serve as an « aggression-sink ». The coloration of *P. « ornatus »*, *M. johanni* and *M. auratus* are status dependent and the darkness of stripes in the colour patterns changes with the aggressive motivation of the animal in all four species. The length of the individuals seems to be an important status determining factor in groups of *P. « ornatus »* and *M. johanni*. For individuals of *P. lombardoi* it is apparently more important to be yellow than to be larger for becoming dominant.

Key-words : Mbuna-cichlids, aggression, aggression-inhibition, intraspecific dominance hierarchies.

INTRODUCTION

The dominance hierarchy is a social organization form which exists in many species. WILSON (1975, p. 583) defines dominance hierarchies as follows : « The physical domination of some members of a group by other members, in relatively orderly and long lasting patterns ». Social hierarchies can only exist when individuals live in groups. In fish this subject is poorly studied. Most investigators studied pairs of fish and the factors influencing those dominance relationships (BARLOW and BALLIN, 1976 ; BARLOW and WALLACH, 1976 ; FIGLER *et al.*, 1976 ; DE BOER and HEUTS, 1973 ; ZAYAN, 1974 ; FREY and MILLER, 1972 ; BAKKER and SEVENSTER, 1983 ; MCKAY, 1971 ; KUWAMARA, 1984 ; GORLICK, 1976 ; SCHWANK, 1979 ; ERCOLINI *et al.*, 1981 ; ERICKSON, 1967 ; MILLER, 1964). Besides these investigations, dominance is often considered in relation to territoriality (MYRBERG, 1972 ; ERICKSON, 1967). The study of rank orders in groups is in most cases restricted to flocks of birds or groups of mammals considering density effects, recognition, etc. (for example : BLACK and OWEN, 1987 ; SACHSER, 1986 ; KEIPER and SAMBRAUS, 1986 ; EWBANK and MEESE, 1974 ; CHASE and ROHWER, 1987 ; CUNNINGHAM *et al.*, 1987). The investigation of the hierarchy formation and the description of the behavioural processes resulted in models to describe the dynamics in rank orders, for example the « jigsaw puzzle » approach (CHASE, 1980, 1982, 1985).

Hierarchy structures can vary from linear (an α-animal dominates all group members, a β-animal dominates all group members except α, and so on until the ω-animal which is subordinate to all group members) at one extreme, to the other extreme where one group member dominates all other group members, that are equal in rank (despotism). It is found that many rank orders in rather small groups (usually with a low number of individuals) of animals are linear (CHASE, 1980).

The establishment of a rank order always involves agonistic acts. A stable dominance hierarchy (when individuals have not changed « rank place » for several days) offers some important advantages. In such a rank order agonistic acts will be replaced in most cases by agonistic signals. In this way agonistic communication prevents injuries, and time and energy loss will be minimized (more time to get access to resources). Such communication can consist of acoustic, tactile, chemical and visual signals (SCHWARZ, 1974 ; TODD, 1971 ; BARNETT, 1977). A hierarchy can only exist when each individual knows the dominance capacity of the other group

members. Differences in capacities may be caused by genotype, age, sex, health, feeding, ... (GORLICK, 1976 ; HENDERSON and CHISZAR, 1977).

Mbuna-cichlids (Lake Malawi) form a monophyletic species-flock in which all species (ten genera ; RIBBINK *et al.*, 1983) are maternal mouth brooders (FRYER and ILES, 1972). The Mbuna live in a rocky shore habitat and feed on « Aufwuchs » (algae and micro-organisms). The flock can reach a density of seven animals or more per square meter (RIBBINK *et al.*, 1983). NELISSEN (1985, 1986) found that a representative of the Mbuna, *Melanochromis auratus* establishes a linear rank order in aquarium tanks (other experiments performed with this species : ANDRIES and NELISSEN, 1987 ; NELISSEN and ANDRIES, 1988). The questions are whether other Mbuna-species have the same kind of social organization and whether there are some kind of interspecific behavioural relationships or even interspecific rank orders. A first step in answering these questions is an intraspecific study of three Mbuna-species. Therefore we investigated groups of *M. johanni, Pseudotropheus « ornatus »* and *P. lombardoi* and compared them with *M. auratus*.

MATERIAL AND METHODS

All fish used in the experiments were imported directly from Lake Malawi and were half to full grown.

We performed observations in groups of *P. « ornatus », M. johanni* and *P. lombardoi*. Each group consisted of three to six conspecifics, picked out arbitrarily. Groups were kept together for at least five days (to obtain a stable hierarchy) before observation started. In each group each individual was identified with a random code number, independent of the later rank number. All fish could easily be recognized by the observer with the aid of the patch patterns on fins and flanks. Whenever a member of the group died or when mating occurred the observation was finished for this group (to reduce possible influences on the rank order during the observation).

All groups were placed in aquarium tanks of 1.200 l (1.5 × 1.0 × 0.8 m), 256 l (1.28 × 0.4 × 0.5 m) or 154 l (0.77 × 0.4 × 0.5 m). The temperature of the water was constantly kept at about 27 C°. The bottom of the tanks was covered with gravel or sand ; short plastic tubes and stones were placed to provide shelters. The animals were fed daily with dried flake food.

To investigate whether a linear dominance hierarchy was established we made behavioural records of the following agonistic acts (between brackets the record abbreviation is given) ; the aggressive acts : full display (A), chasing (V), circle fighting (C), quivering (T), mouth fighting (M) and the inhibition of aggression : avoiding (O) and fleeing (W).

The recordings were made with the aid of a tape recorder, for each individual separately during ten minutes. After the whole group had been observed in this way we obtained one behavioural record. For each group we made six records. All records for each group were stored and processed with the aid of a computer. The processing of the records had the following output :

Interaction matrices.

All data are recorded in interaction matrices (for example matrix 1). On top are the reactors (those individuals who receive the acts) and on the left side are the actors (those individuals who perform the acts). The group members are ranked according to their dominance status. On the right side and on the bottom the number of interactions performed and received are respectively given. The diagonal of each matrix contains zeros, as an animal does not interact with itself. The first value in each matrix cell is the observed number of acts (O). The second value is the expected number of acts (E) (for calculation of E : EVERITT, 1977), the frequency we would expect if the interactions are independent of the rank status. The third value is the relative deviation (RD), which indicates how the observed value differs from the expected value (RD = (O - E)/E). If RD is positive the individuals interact more with each other than expected, if it is negative they interact less than expected. Interaction matrices are obtained for all agonistic acts separately (A, V, C, T, M, O, W), for the aggressive acts taken together (AVCTM) and for the aggression inhibiting acts taken together (OW). Matrices for all acts taken together are also constructed, in which O and W are taken inversely (AVCTM(OW)). This means that aggression inhibiting acts will be considered as aggressive acts performed by the reactor (e.g. 1 W 3 becomes 3 (W) 1).

Likelihood Ratio Criterion.

In order to find whether the observed values differ significantly from the expected ones, the « Likelihood Ratio Criterion » (χ^2) is used (EVERITT, 1977, p. 79) :

$\chi^2 = 2\Sigma O \times \log (O/E)$ $[r - 1][c - 1]$ degrees of freedom

r = number of rows, c = number of columns.

The calculated χ^2 will be compared with the tabled χ^2 for the same degrees of freedom.

Symmetry test.

A symmetry test with the following formula (EVERITT, 1977, p. 114) :

$\chi^2 = \Sigma (Oij - Oji)^2/(Oij + Oji)$ $\frac{1}{2}r(r - 1)$ degrees of freedom.

can indicate whether the values above the diagonal differ significantly from those under the diagonal. If all group members would behave in the same way, irrespective of the dominance position, the values above the diagonal would not differ significantly from those below the diagonal, in other words the matrix would be symmetrical.

The standard length of the individuals is measured and expressed in millimeters. To find out whether body length is correlated with dominance the « Kendall rank correlation coefficient » (τ) was calculated (SIEGEL, 1956). This coefficient (between -1 and 1) gives a measure of association between two sets of ranks : a rank accor-

ding to length and a rank according to dominance status. The significance of τ is tested.

To get an insight into the action level patterns (total number of acts performed) of the groups, the total number of acts performed in six records is divided by the number of group members. This means that we calculated the mean number of acts/individual in a group. In this way we could make a comparison between groups even when they did not have the same number of group members. The differences between these mean numbers were tested for significance with a « One-Way Analyses of Variance » test.

Comparisons were made between groups of the same species (taking the number of group members in account) and between groups of different species and this for the following acts : full display (A), chasing (V), circle fighting (C), quivering (T), mouth fighting (M), avoiding (O), fleeing (W), AVCTM, OW and AVCTM(OW).

RESULTS

P. « ornatus ».

Colour patterns.

There are two major colour patterns in this species, which can be called dominant and subordinate respectively, as the pattern depends upon the rank status of the animal.

The dominant pattern is bright blue with six to eight dark blue vertical bars which become less clear near the tail of the body. On the head (between and above the eyes) two blue horizontal stripes are seen. All fins have black and light blue stripes and a light blue edge. The caudal fin always shows at least one egg spot.

The subordinate animals are light blue or grey and in most cases the dark bars on the flanks are barely visible. Beneath the upper lateral line, a dark coloured horizontal stripe can be seen. All fins are very lightly striped or transparent. Only the dorsal fin has a black edge.

The two patterns can shade off into one another rather rapidly (in a few minutes). Females as well as males (sexed by dissections) can show the dominant colour pattern. On the other hand some individuals (mostly those who have been subordinate for a long time) will always keep the subordinate pattern, regardless of their sex. Many individuals demonstrate an intermediate pattern.

Dominance hierarchy.

a) In all groups a linear dominance hierarchy was established. In this rank order a subordinate will never act aggressively towards a dominant fish when the hierarchy is stable. The dominant animal will always display the dominant colour pattern, while all others will show the subordinate patterns, regardless of the colour of the individuals before they were put together.

MATRIX 1

Example of a matrix of P. « ornatus » *for AVCTM(OW) in a group of 5 individuals (the highest RD-value of each row is underlined)*

	1	2	3	4	5	
1	0.00	56.00	61.00	55.00	32.00	204
	0.00	42.36	58.79	63.97	38.87	204.02
	0.00	0.32	0.04	−0.04	−0.18	
2	1.00	0.00	38.00	31.00	20.00	90
	2.26	0.00	31.91	34.72	21.10	89.98
	−.56	0.00	0.19	−.011	−0.05	
3	1.00	1.00	0.00	29.00	5.00	36
	0.61	10.21	0.00	15.42	9.37	36.00
	−.01	−0.19	0.00	0.88	−0.47	
4	1.00	1.00	1.00	0.00	18.00	21
	0.61	6.17	8.56	0.00	5.66	21.00
	0.65	−0.84	−0.88	0.00	2.18	
5	1.00	2.00	1.00	1.00	0.00	5
	0.12	1.25	1.74	1.89	0.00	5.00
	7.12	0.60	−0.42	−0.47	0.00	
	4.00	60.00	101.00	116.00	75.00	356.00
	4.00	59.99	101.00	116.00	75.00	356.00

note : — from top to bottom : the acting fish ranked according to their dominance position,
— from left to right : the reacting fish ranked according to their dominance position,
— first value in each matrix cell : observed frequency of acts,
— second value : the expected frequency of acts,
— third value : the relative deviation,
— at the bottom and right : column and row totals.

b) Table 1 deals with the correlation between body length and dominance ; the correlation coefficient τ and its significance (P) are given. This table shows that a lot of groups have a τ of 1 or very close to 1, in other words the length of the individual is strongly correlated with its dominance position. The low significance value of τ is due to the low numbers of group members. To find out if there is any relation between τ and the standard deviation of body length in the group (this standard deviation gives an idea of the existing length difference among the group members) the rank correlation coefficient between those two was calculated ; $\tau = 0.441$ with a significance of 0.008. This means that there is a great chance that the importance of « size » increases when length differences between group members become larger.

TABLE 1

Length in mm. of the individuals ranked according to dominance order, τ and its significance (P).

group	dominance hierarchy	τ	P
10	73 → 64 → 64 → 58	0.913	0.044
9	61 → 61 → 54 → 53	0.913	0.044
7	73 → 64 → 59 → 58 → 58	0.949	0.014
3	86 → 60 → 55 → 51 → 48	1	0.014
6	66 → 66 → 68 → 51 → 42	0.527	0.172
13	77 → 65 → 55	1	0.118
8	76 → 74 → 70 → 74 → 68	0.738	0.056
14	71 → 66 → 64	1	0.117
5	73 → 70 → 60 → 60 → 55 → 48	0.966	0.045
11	71 → 62 → 69 → 55	0.667	0.174
C	75 → 74 → 77	−0.333	0.606
F	87 → 81 → 83 → 79	0.667	0.174
B	68 → 69 → 68	0	1
A	78 → 73 → 63	1	0.117
E	76 → 75 → 66	1	0.117
12	77 → 70 → 61 → 57	1	0.041

c) Table 2 shows which animal performs most of the acts, who performs the least acts, who receives most of the acts and who receives the least of the acts. This was noted for each group and the number of times that an animal belonged to one of these four categories is given. For example in table 2, second column under P for A, α(11x) means that in 11 groups α was the most active animal.

It is clear that the α-animal is the most aggressive individual in the group. None of the other group members performs aggressive acts towards α and it is the most avoided animal. The ω-individual is the less aggressive member, the others do not avoid it. With the exception of α there is no distinction between the rest of the group members for receiving aggressive acts; this means that the ω-individual, which is the lowest in rank does not always receive most of the aggression.

d) Table 3 gives information on the symmetry, the significance between the expected and observed value of acts and the relative deviation values in matrices of AVCT(OW). The table shows that in all groups the matrices are asymmetrical and that we usually find a significant difference between observed and expected values. In most groups (in 18 out of the 23 groups) we notice that the highest RD-values for each row lie next to the diagonal (in 18 groups RD-*d* is Yes). This

TABLE 2

Performing and receiving acts in 16 groups

acts	P	*p*	R	*r*
A	α (11x)	ω (16x)	ω (11x)	α (16x)
V	α (15x)	ω (16x)	ω (7x)	α (16x)
C	/	/	/	/
T	α (12x)	/	/	α (16x)
M	—	—	—	—
O	ω (8x)	α (16x)	α (14x)	ω (16x)
W	ω (4x)	α (16x)	α (12x)	ω (16x)
AVCTM(OW)	α (15x)	ω (16x)	ω (9x)	α (16x)

P = performs most of the acts
p = performs the least acts
R = receives most of the acts
r = receives the least acts
/ = no difference between the individuals
— = the act is not performed frequently enough

indicates that most interactions occur between neightbouring animals in the rank order. The RD-values of α with the other group members (in 20 groups RD-α is Yes) decreases with the rank order of the animal in question, in other words the highest RD-α-value is with β and the lowest RD-α-value is with ω. This means that α interacts the most with β, second most with γ, and so on.

e) In Fig. 1 the mean amount of acts/individual (for AVCTM(OW)) is shown for each group together with a 95 % confidence interval, which means that there is a 95 % chance that the real mean amount of AVCTM(OW)/individual lies within that interval. The plot for 95 % confidence intervals for the factor means of AVCTM(OW) (Fig. 1) demonstrates clearly that the action levels (total amount of acts/ind. in a group) of different groups with the same size can vary enormously. A one way of variance analyses test among the groups shows that there is a significant difference ($P < 0.001$) in number of acts/individuals. However if the mean intervals are plotted according to the number of group members (Fig. 2) we notice that there is a significant difference ($P < 0.001$) in number of acts/individual among groups of 3, 4, 5 and 6 members. There seems to be a tendency for an increase of the action level with an increasing number of group members. If the intervals for factor means for each act separately is plotted, the same type of plots (the proportions of the action levels between the four types of groups are the same) appear as in Fig. 2. Only for mouth fighting [$P = 0.696$], is there no significant difference between groups consisting of 3, 4, 5 or 6 individuals. This is probably due to the

fact that the number of these acts is very low. Out of these data one can conclude that aggression in groups of *P. « ornatus »* increases with the number of group members and this is so for all considered acts.

TABLE 3

*Results of the Likelihood Ratio criterium (χ^2), the symmetry test and relative deviation position (RD-α and RD-d) in the AVCTM(OW)-matrices for the different groups (Y = yes, N = no, ex.2/3 = 2 out of the 3 RD are in the right position, namely next to the diagonal for RD-*d *or decreasing with the status of the reactor for RD-α)*

group	S-AS	χ^2	RD-α	RD-*d*	group	S-AS	χ^2	RD-α	RD-*d*
gr.Y	AS	Y	Y	N2/3	gr.10	AS	Y	N4/5	Y
gr.12	AS	Y	Y	Y	gr.15	AS	N	Y	Y
gr.2	AS	Y	Y	N3/4	gr.14	AS	Y	Y	Y
gr.B	AS	N	Y	Y	gr.1	AS	Y	N4/5	N3/5
gr.F	AS	Y	Y	Y	gr.8	AS	Y	Y	Y
gr.A	AS	Y	Y	Y	gr.3	AS	Y	Y	N3/4
gr.D	AS	N	Y	Y	gr.5	AS	Y	Y	Y
gr.E	AS	N	Y	Y	gr.7	AS	Y	Y	Y
gr.11	AS	Y	Y	Y	gr.13	AS	N	Y	Y
gr.C	AS	N	Y	Y	gr.6	AS	Y	Y	Y
gr.4	AS	Y	Y	N2/4	gr.16	AS	N	Y	Y
gr.9	AS	Y	N2/3	Y					

S-AS = symmetry or asymmetry

χ^2 = significant difference between O and E

RD-α = RD of α towards the other group member decreases with the rank order of the reactors

RD-*d* = the highest RD values of each row lie next to the diagonal

Remark : in all the experiments the α-β relationship is present, this means that in all groups α interacts the most with β.

Fig. 3 gives the proportion between the different kinds of acts performed in all the groups of *P. « ornatus »*. These acts are always the mean amount/individual performed in one behavioural record. This figure shows that avoiding (A), chasing (V) and fleeing (W) are the most frequent acts, whereas circle fighting (C) and quivering (T) are very rare. Mouth fighting (M) is almost never shown in this species. Chasing and fleeing show approximately the same frequency, because they are complementary to one another.

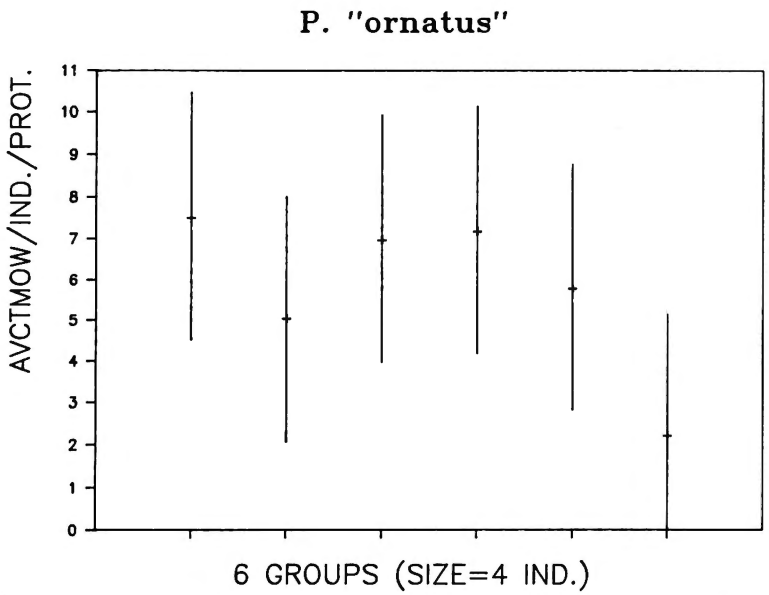

Fig. 1. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *P. « ornatus »*.

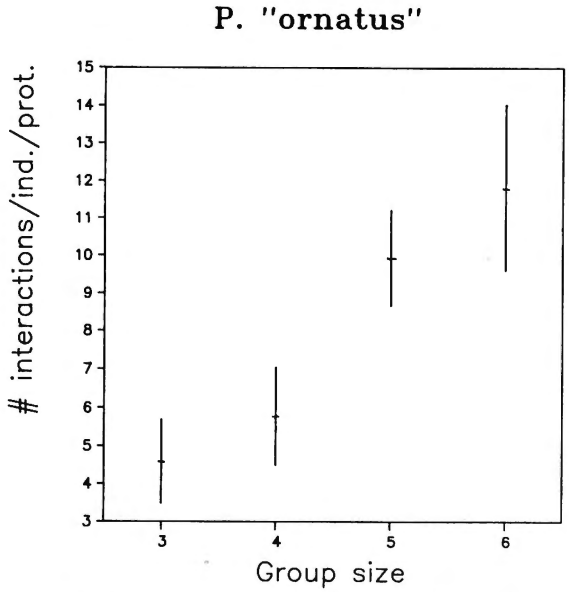

Fig. 2. — 95 % confidence intervals for the factor means for AVCTM(OW) of *P. « ornatus »* for groups of 3, 4, 5 and 6 group members.

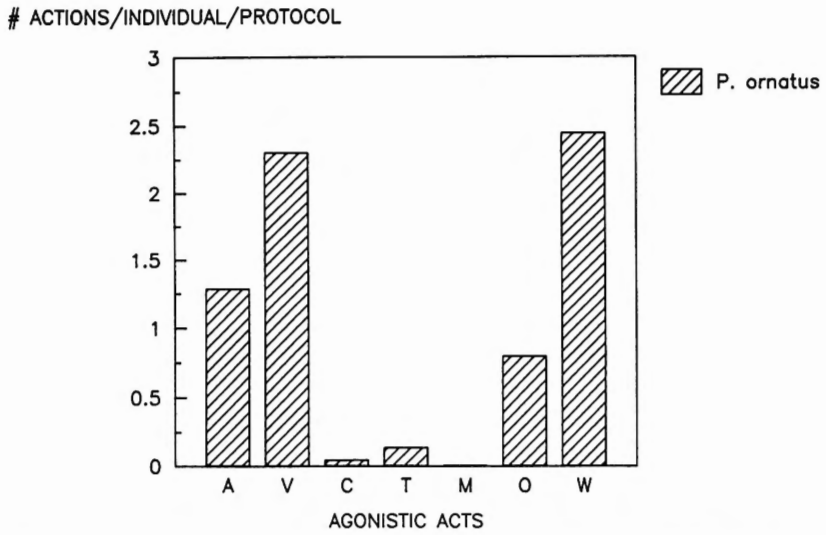

Fig. 3. — Mean amount of acts/individual in all groups of *P. « ornatus »* in one behavioural record (A = full display, V = chasing, C = circle fighting, T = quivering, M = mouthfighting, O = avoiding and W = fleeing).

P. lombardoi.

Colour patterns.

In nature *P. lombardoi* seems to live in small groups consisting of females, juveniles and non-territorial males (RIBBINK, *et al.*, 1983). In this species we notice two colour patterns : « yellow » and « blue » individuals. The first ones are yellow or orange with brown vertical bars which disappear during aggressive motivation. The fins are « bluish » transparent.

The blue animals are bright blue with dark blue vertical bars that continue in the dorsal fin. The darkness of those bars depends upon the aggression motivation of the animal. With a strong aggressive motivation the bars will become very dark.

The « yellow » animals will always be dominant when a group is put together. When only « blue » fish are put together we notice that after a long period (several weeks) the dominant animal, which was blue at first, will become yellow. An intermediate colour pattern (sandy) is seen in this period. Many individuals show this « sandy-coloured » pattern. Dissections revealed that most of the yellow individuals are males and most blue fish are females. Nevertheless, there are also females with a sandy-coloured pattern and blue males.

Dominance hierarchy.

a) In all groups a linear dominance hierarchy was established. In most groups group members never experienced aggression from an individual lower in rank. In some groups we noticed a few exceptions to this rule. When a « yellow » individual was present in the group it always became α no matter how small it was regarding to the other individuals. A group with two « yellow » individuals was very difficult to keep because of the high aggression level of these two animals. If such a group came to a stable hierarchy the two individuals became α and β, the β-animal gained the intermediate colour pattern with brown vertical bars.

MATRIX 2

Example of a matrix of P. lombardoi *for AVCTM(OW) in a group of 5 individuals (the highest RD-value of each row is underlined)*

	1	3	2	4	5	
1	0.00	13.00	84.00	77.00	87.00	261
	0.00	9.32	71.84	85.11	94.74	261.05
	0.00	0.40	0.17	−0.10	−0.08	
3	2.00	0.00	15.00	17.00	7.00	41
	0.91	0.00	11.44	13.56	15.09	41.00
	1.20	0.00	0.31	0.25	−0.54	
2	1.00	1.00	0.00	45.00	42.00	89
	2.61	4.26	0.00	38.87	43.27	88.93
	−.62	−0.77	0.00	0.16	−0.03	
4	1.00	1.00	1.00	0.00	39.00	42
	1.32	2.16	16.61	0.00	21.91	42.01
	−.24	−0.54	−0.94	0.00	0.78	
5	1.00	1.00	2.00	1.00	0.00	5
	0.17	0.27	2.09	2.47	0.00	5.00
	5.03	2.69	−0.04	−0.60	0.00	
	5.00	16.00	102.00	140.00	175.00	438.00
	5.00	16.00	101.98	140.01	175.01	438.00

(for explanation see matrix 1).

b) Table 4 (deals with the correlation between dominance position and body length ; for explanation see Table 1) shows that in many groups τ is rather low and in some groups even negative. It seems that « being yellow » is more important than « being big » to become dominant. Small yellow animals often dominate large blue

fish. This explains that the rank correlation coefficient between τ and the standard deviation (τ = 0,095, sign. = 0.587) is very low.

TABLE 4

Length in mm. of the individuals ranked according to dominance order, τ and its significance (P).

group	dominance hierarchy	τ	P
9	66 → 60 → 66 → 60	0.408	0.363
11	60 (y) → 55 (y) → 68 → 61	−0.333	0.497
5	71 (y) → 66 → 60 → 50	1	0.041
4	46 (y) → 57 → 54 → 51 → 49	0.200	0.624
6	64 (y) → 54 → 63 → 61 → 56 → 60	0.333	0.348
7	66 → 61 → 60 → 61	0.548	0.228
2	46 (y) → 49 → 48 → 45	0	1
1	57 (y) → 57 (y) → 57 → 54 → 51 → 54	0.701	0.027
3	57 (y) → 57 → 54 → 48 → 45	0.949	0.013
8	66 (y) → 72 (y) → 55 (y) → 68 → 60 → 51	0.467	0.188
10	72 (y) → 55 (y) → 68 → 60 → 61 → 51	0.467	0.188
13	72 (y) → 70 → 64	1	0.117
A	78 → 77 → 80 → 72	0.333	0.497
B	74 → 78 → 70	0.333	0.601
D	84 (y) → 81 → 82	0.333	0.601
12	58 (y) → 72 → 66	−0.333	0.601

y = a yellow animal.

c) Table 5 shows that in most groups the α-animal is the most aggressive animal, is avoided most frequently and receives no aggression. The ω-individual is the less aggressive group member and is never avoided or fled from. But ω is not always the one who receives most of the aggressive acts.

d) The symmetry, the highest RD-positions in the matrices and the results of the Likelihood Ratio Criterium tests for *P. lombardoi* are shown in table 6 (for more explanation see Table 3). The matrices for all the acts together are always asymmetrical and the Likelihood Ratio Criterium shows us that in most groups there is a significant difference between the expected and observed value. In most matrices the RD-diagonal (all highest RD-values of each row lie next to the diagonal) is complete or almost complete (only one value is missing for a total RD-

diagonal) and the interactions of α with other group members is in almost all cases status dependent.

TABLE 5

Performing and receiving acts in 16 groups (for legend table 2)

acts	P	*p*	R	*r*
A	α (14x)	ω (16x)	ω (11x)	α (16x)
V	α (16x)	ω (16x)	ω (10x)	α (16x)
C	/	/	/	/
T	α (9x)	/	/	
M	/	/	/	/
O	ω (12x)	α (16x)	α (13x)	ω (16x)
W	ω (10x)	α (16x)	α (16x)	ω (16x)
AVCTM(OW)	α (16x)	ω (16x)	ω (11x)	α (16x)

TABLE 6

Results of the Likelihood Ratio criterium (χ^2), Symmetry test and position of the Relative Deviation in the AVCTM(OW)-matrices of the groups

group	S-AS	χ^2	RD-α	RD-*d*	group	S-AS	χ^2	RD-α	RD-*d*
gr.13	AS	Y	Y	Y	gr.D	AS	N	Y	Y
gr.12	AS	N	Y	Y	gr.C	AS	Y	Y	Y
gr.A	AS	N	Y	N2/3	gr.E	AS	N	Y	Y
gr.11	AS	Y	Y	Y	gr.B	AS	N	Y	Y
gr.9	AS	Y	Y	N2/3	gr.14	AS	N	Y	Y
gr.1	AS	Y	Y	N2/5	gr.10	AS	Y	N4/5	N4/5
gr.3	AS	Y	Y	Y	gr.8	AS	Y	Y	N4/5
gr.4	AS	Y	N	N1/4	gr.6	AS	Y	Y	N2/5
gr.2	AS	Y	N2/3	Y	gr.7	AS	Y	Y	N2/3
gr.5	AS	Y	Y	N2/3	gr.15	AS	N	Y	Y
gr.16	AS	N	Y	Y					

e) Fig. 4 shows that the variation in the total number of aggression among groups of the same size is large ($P < 0.001$). A plot of the 95 % confidence levels of the intervals for factor means (Fig. 5) also shows that the level of aggression

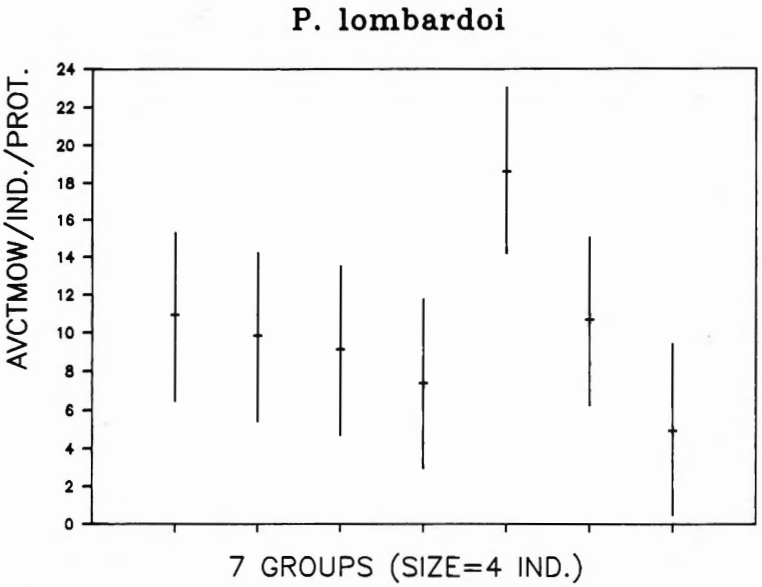

Fig. 4. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *P. lombardoi.*

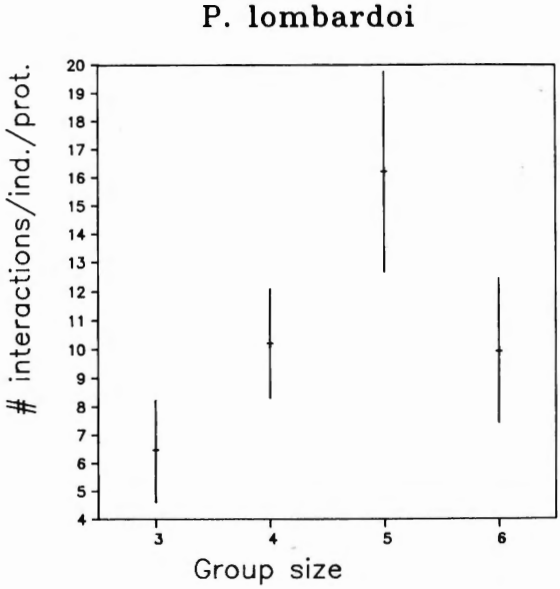

Fig. 5. — 95 % confidence intervals for the factor means for AVCTM(OW) of *P. lombardoi* for groups of 3, 4, 5 and 6 group members.

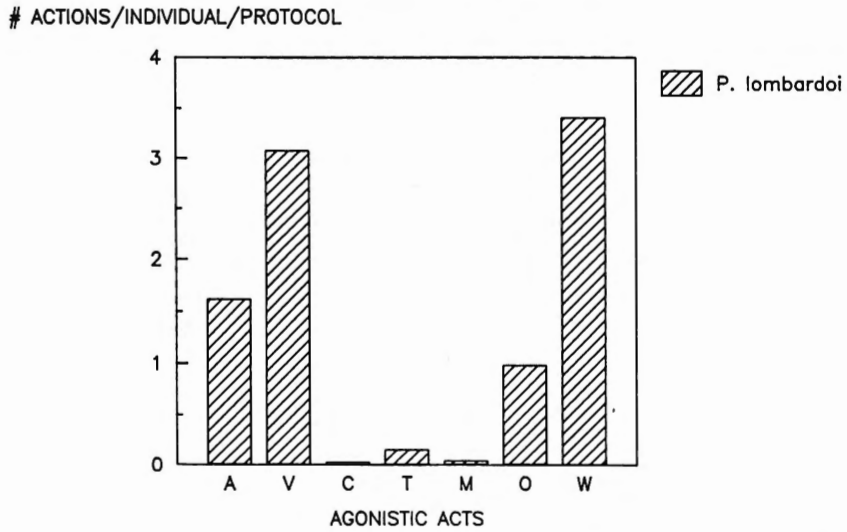

Fig. 6. — Mean amount of acts/inidividual in all groups of *P. lombardoi* in one behavioural record (expl. symbols see fig. 3).

increases with the number of individuals in a group (to 5 group members). However, in groups with 6 fish the aggression is lower. There is no significant difference between groups with 4 and 6 individuals. Plots for all the acts separately show the same kind of action levels as in Fig. 5, except for circle fighting (C), quivering (T) and mouth fighting (M), and indicate that there is no significant difference ($P = 0.076$, $P = 0.383$, $P = 0.420$ respectively), probably because these acts occur very rarely.

Fig. 6 shows that avoiding (O), chasing (V) and fleeing (W) are the most frequent acts. Circle fighting (C), quivering (T) and mouth fighting (M) are rarely shown.

M. johanni.

Colour patterns.

In litterature the two major colour patterns are often considered to be sexually determined, which is not absolutely true. The patterns depend upon the status of the animal.

Dominant animals are usually black or dark blue with two light blue horizontal stripes. In most cases the lower stripe is very vague and the other is often not continuous (the stripe consists of blocks). The head shows one light blue stripe between the eyes and one above the eyes. The dorsal fin, the caudal fin and the pelvic fins have a black and light blue edge. We always notice one or more egg spots. The caudal fin is light blue and black striped according to the fin rays.

Subordinate animals are greyish or yellow with or without brown horizontal stripes. The dorsal fin has a dark stripe, the rest of the fins are transparent (occasionally with dark spots). The change from yellow or grey to black can happen rather quickly (± 24 hours), while the change from dark to grey or yellow takes some more time.

Dominance hierarchy.

a) A linear dominance hierarchy was always established in a group of *M. johanni*. The α-individual (and sometimes also the β-animal) gains the dominant colour pattern, no matter what its colour was before the establishment of the group.

MATRIX 3

Example of a matrix of M. johanni *for AVCTM(OW) in groups of 5 individuals (the highest RD-values of each row are underlined)*

	1	2	3	4	
1	0.00	37.00	13.00	6.00	56
	0.00	22.11	15.87	18.02	56.00
	0.00	0.67	−0.18	−0.67	
2	1.00	0.00	15.00	11.00	27
	1.49	0.00	11.94	13.56	26.98
	−.33	0.00	0.26	−0.19	
3	1.00	1.00	0.00	27.00	29
	1.36	15.23	0.00	12.42	29.01
	−.27	−0.93	0.00	1.17	
4	1.00	1.00	1.00	0.00	3
	0.15	1.66	1.19	0.00	3.00
	5.73	−0.40	−0.16	0.00	
	3.00	39.00	29.00	44.00	115.00
	3.00	39.00	29.00	44.00	115.00

(for explanation see matrix 1).

b) In groups of *M. johanni* we normally find a high correlation coefficient between size and dominance (Table 7). The correlation between standard deviation and the rank correlation coefficient ($\tau = 0.272$, $P = 0.117$) indicates that even small

differences in length of the group members are important for determining dominance.

TABLE 7

Length in mm. of the individuals ranked according to dominance order

group	dominance hierarchy	τ	P
4	62 → 60 → 58 → 61 → 52 → 47	0.733	0.039
5	63 → 63 → 56 → 58 → 52 → 47	0.828	0.014
6	70 → 55 → 66	0.333	0.601
7	72 → 65 → 65 → 65 → 48	0.836	0.016
8	63 → 58 → 51	1	0.117
9	74 → 68 → 61 → 57 → 54	1	0.014
G	83 → 75 → 74 → 64 → 56	1	0.014
I	84 → 84 → 68 → 66	0.913	0.044
A	70 → 66 → 55 → 55	0.913	0.044
B	75 → 61 → 57	1	0.117
H	83 → 77 → 67	1	0.117
F	82 → 81 → 80 → 66 → 60	1	0.014
C	72 → 70 → 68 → 58	1	0.041

c) Table 8 points out that the α-individual performs most of the aggressive acts and it is the most avoided animal, whereas ω is the less aggressive animal. However, there is no difference among the individuals as far as the performance of aggression inhibition and the receiving of aggressive acts is concerned.

TABLE 8

Performing and receiving acts in 19 groups

acts	P	*p*	R	*r*
A	α (16x)	ω (19x)	ω (12x)	α (19x)
V	α (19x)	ω (19x)	/	α (19x)
C	—	—	—	—
T	α (12x)	/	/	/
M	—	—	—	—
O	/	α (19x)	α (18x)	ω (17x)
W	/	α (19x)	α (19x)	ω (19x)
AVCTM(OW)	α (19x)	ω (19x)	/	α (19x)

d) In Table 9 we see that all AVCTM(OW)-matrices are asymmetrical. The χ^2-test shows that only in half of the investigated groups there is a significant difference between expected and observed values. In most cases there is a complete or almost complete RD-diagonal (all highest RD-values of each row lie next to the diagonal) and the interactions of α with the other group members is status dependent.

TABLE 9

Results of the Likelihood Ratio criterium, the Symmetry test and the position of the Relative deviations of the AVCTM(OW)-matrices

group	S-AS	χ^2	RD-α	RD-*d*	group	S-AS	χ^2	RD-α	RD-*d*
gr.G	AS	Y	Y	Y	gr.J	AS	Y	Y	Y
gr.I	AS	N	Y	Y	gr.D	AS	Y	Y	N2/3
gr.A	AS	N	N2/3	Y	gr.K	AS	Y	N	Y
gr.C	AS	Y	N	Y	gr.H	AS	N	Y	Y
gr.B	AS	N	Y	Y	gr.E	AS	N	Y	N2/3
gr.F	AS	Y	Y	Y	gr.4	AS	Y	Y	N3/5
gr.7	AS	N	N3/4	N3/4	gr.6	AS	N	Y	Y
gr.1	AS	Y	Y	N2/3	gr.2	AS	N	N2/3	Y
gr.5	AS	Y	N	N2/5	gr.8	AS	N	Y	Y
gr.3	AS	N	Y	Y					

e) As shown in Fig. 7 one can notice that also in this species the variation in action level among groups of the same size is very substantial. There is no significant difference if groups with different number of group members are compared for all the acts together (Fig. 8 : P = 0.810) nor for all acts separately.

Chasing and fleeing are the most important acts. Circle fighting and mouth fighting almost never occur (Fig. 9).

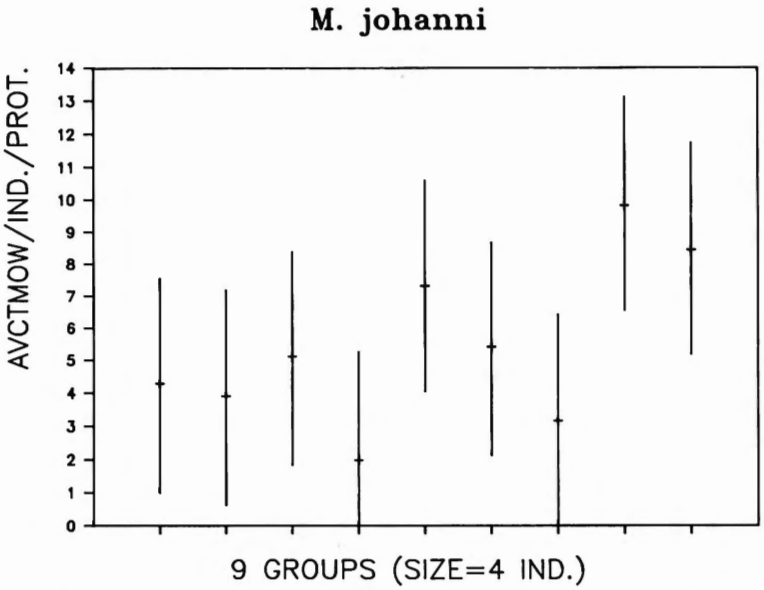

Fig. 7. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *M. johanni*.

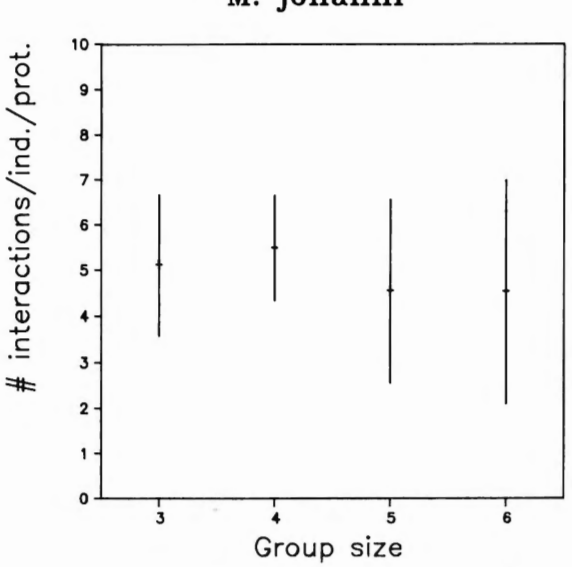

Fig. 8. — 95 % confidence intervals for the factor means for AVCTM(OW) of *M. johanni* for groups of 3, 4, 5 and 6 group members.

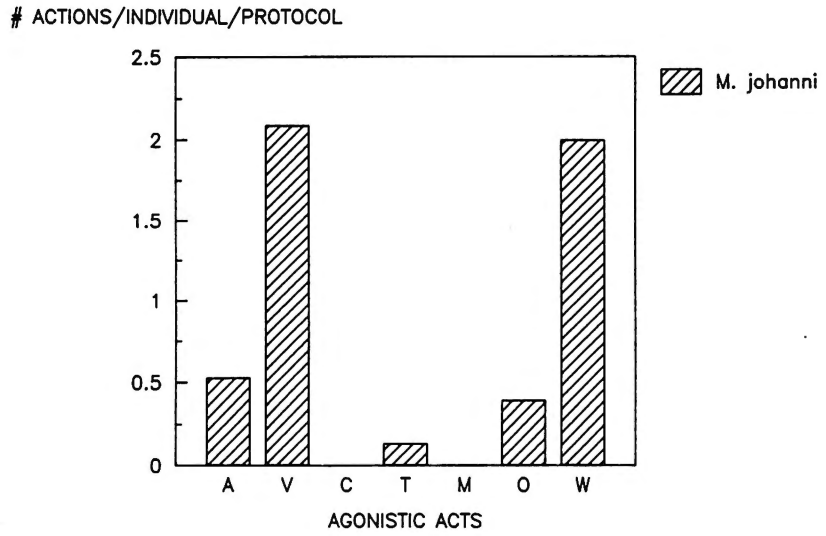

Fig. 9. — Mean amount of acts/individual in all groups of *M. johanni* in one behavioural record (expl. symbols see fig. 3).

M. auratus.

Since *M. auratus* has already been studied (Nelissen, 1985) we restrict ourselves to a brief summary of the findings in this species.

M. auratus shows two types of colour patterns : a black pattern in dominant animals and a yellow one in subordinate individuals. A linear dominance hierarchy is always established when groups of fish are kept in aquarium tanks. The α-animal is always the most active one and the ω-individual is the least aggressive one. The ω-animal receives most of the aggression. All matrices are asymmetrical and in most cases there is a significant difference between expected and observed values. The highest RD-values are found next to the diagonal. This means that in groups of *M. auratus* the interactions depend upon the rank status of the animals and that neighbouring animals interact more with each other than we would expect if there was no relationship between rank status and interactions among group members.

In order to make a comparison between the four Mbuna-species a few supplementary observations on groups of *M. auratus* were made. These observations pointed out that the aggression level of the groups is very variable (Fig. 10 ; also see Fig. 1 for explanation) and that there is a difference between groups of 3 and 4 individuals (Fig. 11 : $P = 0.033$). If we consider every act separately we notice that the only act where a significant difference is found is chasing. Unfortunately we had only groups of 3 and 4 individuals (because the supply of fish was limited) so it is not very clear if chasing would increase with the number of individuals.

Chasing and fleeing are the most frequent acts (Fig. 12). Mouth fighting almost never occurs and circle fighting and quivering are very rare.

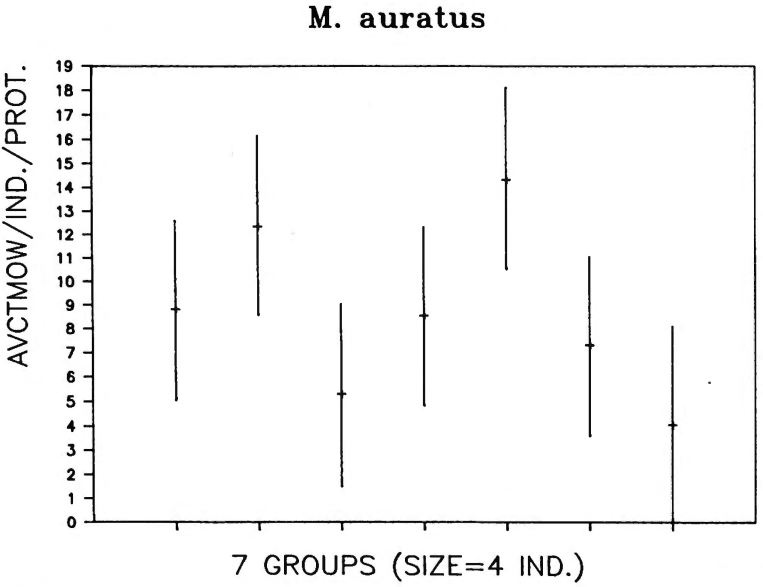

Fig. 10. — 95 % confidence intervals for the factor means for AVCTM(OW) of groups with 4 individuals of *M. auratus*.

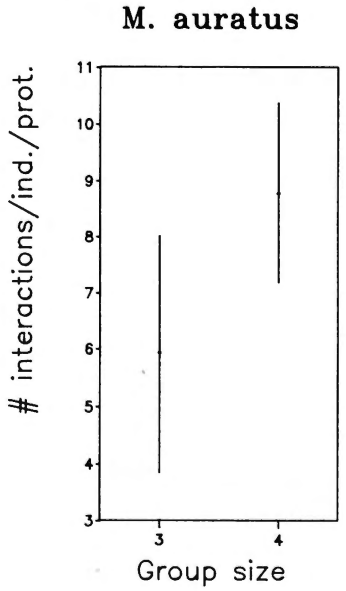

Fig. 11. — 95 % confidence intervals for the factor means for AVCTM(OW) of *M. auratus* for groups of 3 and 4 group members.

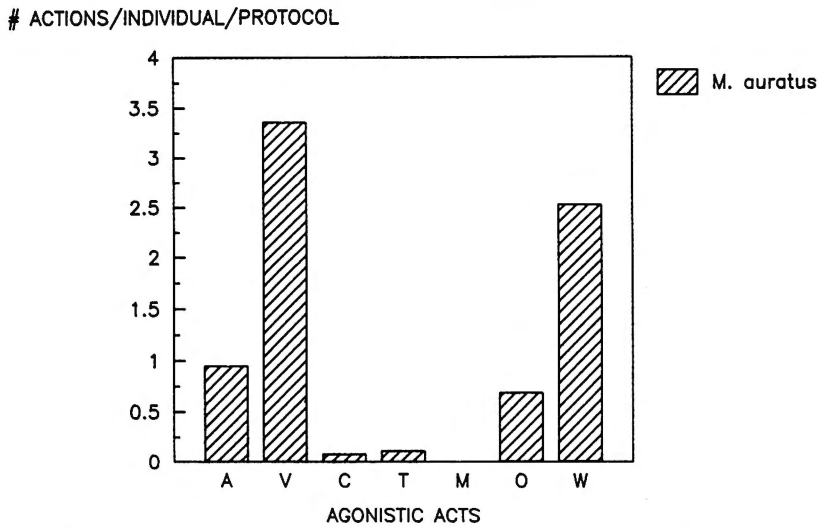

Fig. 12. — Mean amount of acts/individual in all groups of *M. auratus* in one behavioural record (expl. symbols see fig. 3).

Comparison between *P. « ornatus »*, *P. lombardoi*, *M. johanni* and *M. auratus*.

In Fig. 13 the 95 % confidence intervals for the mean amount of aggressive acts/individual are given for the four species. It shows that the four species differ significantly when the amount of aggression is considered. *M. johanni* is the least aggressive species and *P. lombardoi* is the most aggressive one. In aggression inhibition (Fig. 14) *P. lombardoi* performs much more avoiding (O) and fleeing (V), while *M. johanni* performs it the least. If all the acts are considered separately the same pattern is found as in Fig. 13 and Fig. 14, except for circle fighting (C) and quivering (T) where there is no significant difference between the four species. In Fig. 15 it is clearly demonstrated that *P. lombardoi* performs significantly more mouth fighting than the other species.

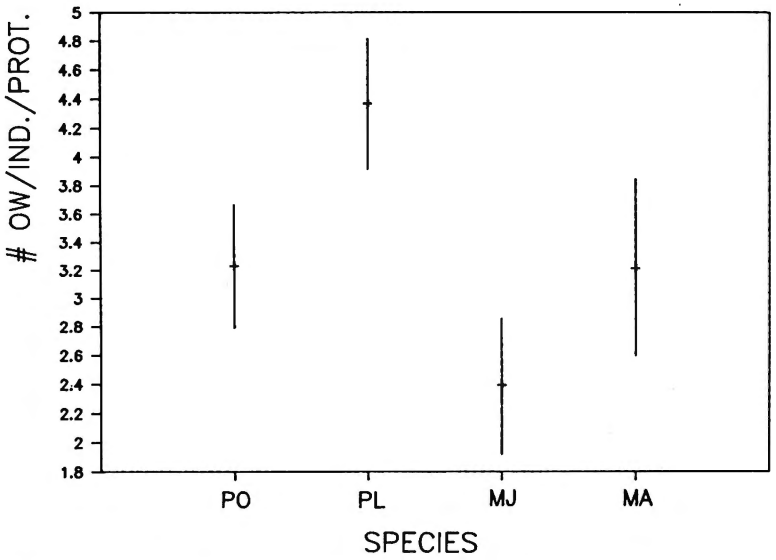

Fig. 13. — 95 % confidence intervals for the factor means of AVCTM, the aggressive acts (PO = *P. « ornatus »*, PL = *P. lombardoi*, MJ = *M. johanni*, MA = M. auratus).

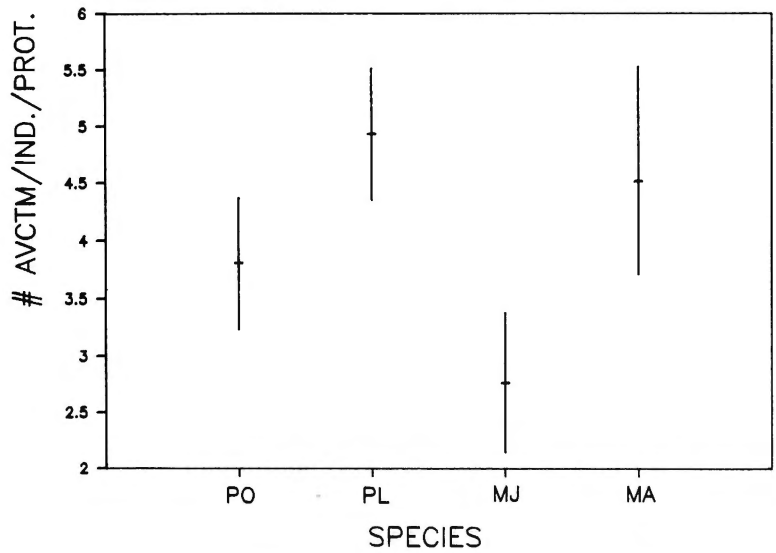

Fig. 14. — 95 % confidence intervals for the factor means of OW, the aggression inhibition.

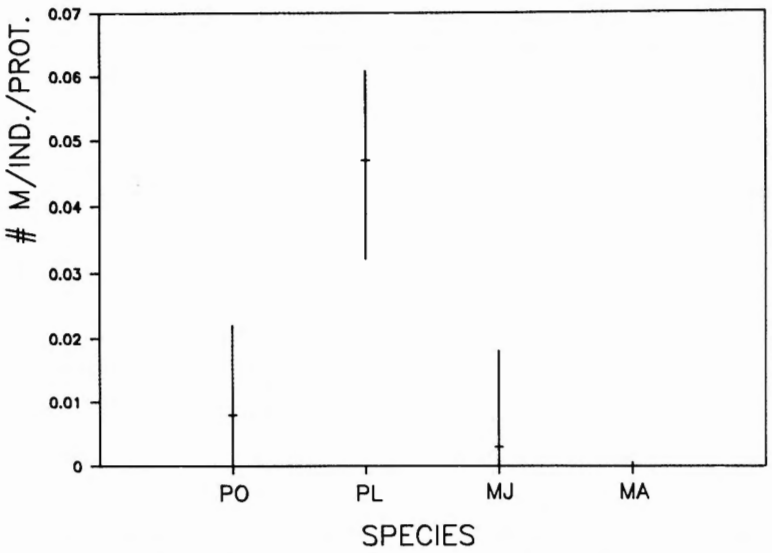

Fig. 15. — 95 % confidence intervals for the factor means of M, mouth fighting.

DISCUSSION

Because of the lack of information on the existence of dominance hierarchies in groups of fish (most experiments only involve pairs of fish and the dominance factors in such a relationship) a study was performed on three cichlid species *M. johanni, P. lombardoi* and *P. « ornatus »*. The choise of the species was based on the fact that they are very closely related to *M. auratus*. This species was investigated by NELISSEN (1985). The three species as well as *M. auratus* belong to the very closely related group of the Mbuna.

Our results show that these three species establish a linear rank order in aquarium tanks. When these hierarchies are stable a subordinate individual will never or very rarely perform an aggressive act towards a dominant animal. The very structured communication system in the dominance hierarchy of *M. auratus* found by NELISSEN (1985) also seems to apply for *M. johanni, P. lombardoi* and *P. « ornatus »*. The relations between agonistic behaviour and dominance hierarchy can be summarized as follows :

— the frequency of the aggressive acts and signals are determined by the rank number of the animals.

— neighbouring animals in the rank order interact more with each other than with the other group members.

These severe rules in a communication system minimize time and energy loss while maintaining the hierarchy. The fact that every group member takes care of

its relationship with its neighbour reduces harmful fights and acts that should confirm the rank order.

In all four species the α-individual is the most aggressive animal. This means that the α-status requires a lot of energy. So it is easy to imagine that the advantages of being α must be of some importance (PHILLIPS and SWEARS, 1979). The few observations of copulations show that only the α-animal (when it is a male) mates with the females. During the mating all other group members are chased into one area of the aquarium ; the α-individual is extremely aggressive towards them. As one occasional observation in a group of *M. johanni* has shown subordinate males seem to be able to « steal a copulation » by interfering in the mating act and spraying sperm over the eggs, before the α male is able to chase him away. Besides the advantage of reproduction the dominant animal seems to occupy the only or the best hiding place in the aquarium tank.

The ω-animal is the least aggressive fish in the group. However, this does not mean that it serves as an « aggression-sink » (WILSON, 1975, p. 290), since it does not always receive the most aggressive acts.

Circle fighting and mouth fighting are rarely seen in a stable hierarchy (if it does occur the dominant fish will always interrupt the fights). *P. lombardoi* seems to form an exception, because it performs mouth fighting more frequently than the other species. On the other hand it also performs relatively more full display and avoiding. One can assume that this rather aggressive species can still minimize time and energy loss by performing more aggression inhibition and aggressive signals. The aggression level of *M. johanni,* in aggression a very moderate species, seems to be independent of the group size (no significant difference between groups with different numbers of group members). However, in the other three species aggression increases with the number of group members. One could expect that when group size increases, a group will show the same amount of overall aggression simply spread over more individuals (which means that there would be less aggression/individual), or an increased amount of overall aggression but a constant aggression level per individual. However, non of this seems to happen : in larger groups there is not only a significant tendency towards more overall aggression, but also an increasing aggression level per individual. This tendency can not go on forever, which means that at a certain level of group size the overall aggression has to decrease again in order to make living in a group worthwhile. This level of group size where maximum aggression appears, seems to be five individuals for *P. lombardoi.* Apparently it is lying higher for *P. « ornatus ».* To get a full understanding about the impact of group size on the aggression level and possible density effects further investigation is needed.

All four species seem to have status dependent colour patterns, especially in *P. « ornatus », M. johanni* and *M. auratus.* In most cases a lot of intermediate patterns appear according to the aggression motivation (changes in darkness of the stripes and spots or changing colour) ; this was also found in *Coreoperca kawamebar* by KOHDA and WATANABE (1982). A difference with their findings is that when the Mbuna-species are placed in isolation the previous colour pattern with stripes disappears and a neutral colour pattern is seen. The blue and the yellow

colour patterns of *P. lombardoi* seem to belong to different sexes. Most blue fish are females and the yellow ones are males. On the other hand intermediate patterns often occur, in females as well as males. This means that the colour patterns in *P. lombardoi* are not strictly tied to sex. Yellow is always dominant over intermediate, which dominates blue. In contrast with the three other species individuals of *P. lombardoi* very rarely show changes in colour pattern, but the darkness of the bars is also dependent on the aggression motivation.

Size seems to play an important role in gaining a dominant position : larger fish will easily dominate smaller fish. This is especially true when size differences are increasing. *P. lombardoi* is an exception ; in this species being yellow is more important than being big, in other words small yellow fish dominate larger blue fish. BARLOW and BALLIN (1976) ; BARLOW and WALLACH (1976) and BARLOW (1983) made a similar observation in *Cichlasoma citrinellum* in which gold morphs always dominate the others, even if they are smaller. According to them this was due to the fact that gold coloration inhibits attacking by stimulating fear responses. This is also a possible explanation for *P. lombardoi* because this species performs a lot of avoiding and fleeing (much more than the other three species). However, it does not explain the fact that *M. auratus* and *M. johanni* show a yellow colour in subordinate fish. In fact *P. lombardoi* is an exception among the Mbuna, because it is the only species in which yellow dominates blue (RIBBINK *et al.*, 1983). Also in this case further investigation of data and observations are necessary for making a further hypothesis about this subject.

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MORPHOLOGICAL AND FUNCTIONAL CONSEQUENCES OF THE COEVOLUTION OF RODENTS WITH GASTRO-INTESTINAL MICROBIAL ENDOSYMBIONTS

by

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SUMMARY

In four species of muroid rodents (*Apodemus sylvaticus, Microtus arvalis, Neotoma albigula, Myospalax myospalax*) the stomach and hindgut morphology was studied as well as associations of bacteria colonizing the epithelium of the forestomach. Various adaptations of the rodent stomach and hindgut to digestion and assimilation of plant food are discussed with special emphasis on coevolution of rodents and their endosymbionts. The possibility of specificity and high functional specialization of forestomach symbiocenoses in different rodent species is demonstrated. An important role of the phenomenon of endosymbiosis in the phylogeny of herbivorous rodents is stressed.

INTRODUCTION

It is well known that animals (in particular mammals) utilize plant food only in cooperation with symbiotic microorganisms involved in digestion. The reason is that plants have two nutritional drawbacks : (1) plants contain great amounts of cellulose that mammals cannot digest and assimilate ; (2) protein content of plants is insufficient for animal nutritive requirements. If the inevitability of coevolution of plant-consuming mammals with microbial symbionts is obvious, the specific patterns of this coevolution in different lineages provide an open field for comparative studies.

In the course of mammalian evolution herbivory arose in different lineages showing a wide range of wonderful morphological variations of their stomach and hindgut. Comparative studies of the digestive system in herbivorous mammals have demonstrated different ecological and evolutionary trends. However, the role of endosymbiosis in the evolution of these varieties has been traditionally underestimated. In large herbivorous mammals, especially in ruminants, the ecological and functional aspects of their coevolution with endosymbionts are well investigated (HUNGATE, 1966 ; LANGER, 1974, 1986 ; HUME and WARNER, 1980 ;

HOFMANN, 1983). It should be noted here that ruminants totally depend on the symbiotic activity and, most interestingly, the ruminal symbiocenoses are polyfunctional in all cases : they are composed of a variety of bacteria and protozoa that are able to ferment not only cellulose but also starch, lipids, proteins and other nutrients. As to rodents, the functional and structural manifestations of the endosymbiosis are there still little understood.

MATERIAL AND METHODS

The structure of various stomach and gut patterns and modes of colonization of the corporal cornified epithelium by attached bacteria were investigated in four species of different genera of muroid rodents : the wood mouse, *Apodemus sylvaticus* (from West Ukraine, USSR), the common vole, *Microtus arvalis* (from suburbs of Moscow, USSR), the white-throated wood rat, *Neotoma albigula* (from Mexico) and the Siberian zokor, *Myospalax myospalax* (from Altai Mountains, USSR). From 5 to 10 mature specimens of each species were fixed by means of injection of 4 % neutral formaldehyde into the cavities of stomach and gut. The samples (5 mm by 5 mm) of cornified corpus ventriculi were washed in isotonic saccharose solution, fixed in neutral 4 % formaldehyde and subsequently processed for SEM (scanning electron microscopy). The samples of *N. albigula* corpus ventriculi were embedded in paraffin and sectioned at 7 mkm. Sections were stained with the Gram technique and the periodic acid-Schiff reaction combined with haematoxylin.

RESULTS AND DISCUSSION

The wood mouse is a widely distributed muroid rodent and is known to be a seed-eater. Seeds do not contain much cellulose, but their other components are digestible by means of endogenous enzymes. The stomach of the wood mouse (Fig. 1, A) may be classified (CARLETON, 1973) as bilocular-hemiglandular. The incisura angularis is not very deep, the sulcus on the greater curvature is not clearly developed and the bordering fold is not high. So the non-glandular corpus ventriculi, or the forestomach as many authors call it (*e.g.* GAERTNER and PFAFF, 1979 ; PERRIN, 1986 ; AMASAKI *et al.*, 1988) and the glandular part of the stomach are not well isolated from each other. Consequently, gastric acidity cannot be kept constant for optimal activity of symbionts and, moreover, symbionts can be easily washed out from the stomach. The symbiocenosis of the forestomach is represented by various attached bacteria (Pl. 1, A), as the food that enters the stomach of the wood mouse consists of biochemical components which can serve as a favourable substratum for the activity of proteinolytic, amylolytic and some other symbionts. But in the unisolated forestomach bacterial fermentation is not intense, so bacterial biomass is not large, and can provide the host with only a complementary source of protein.

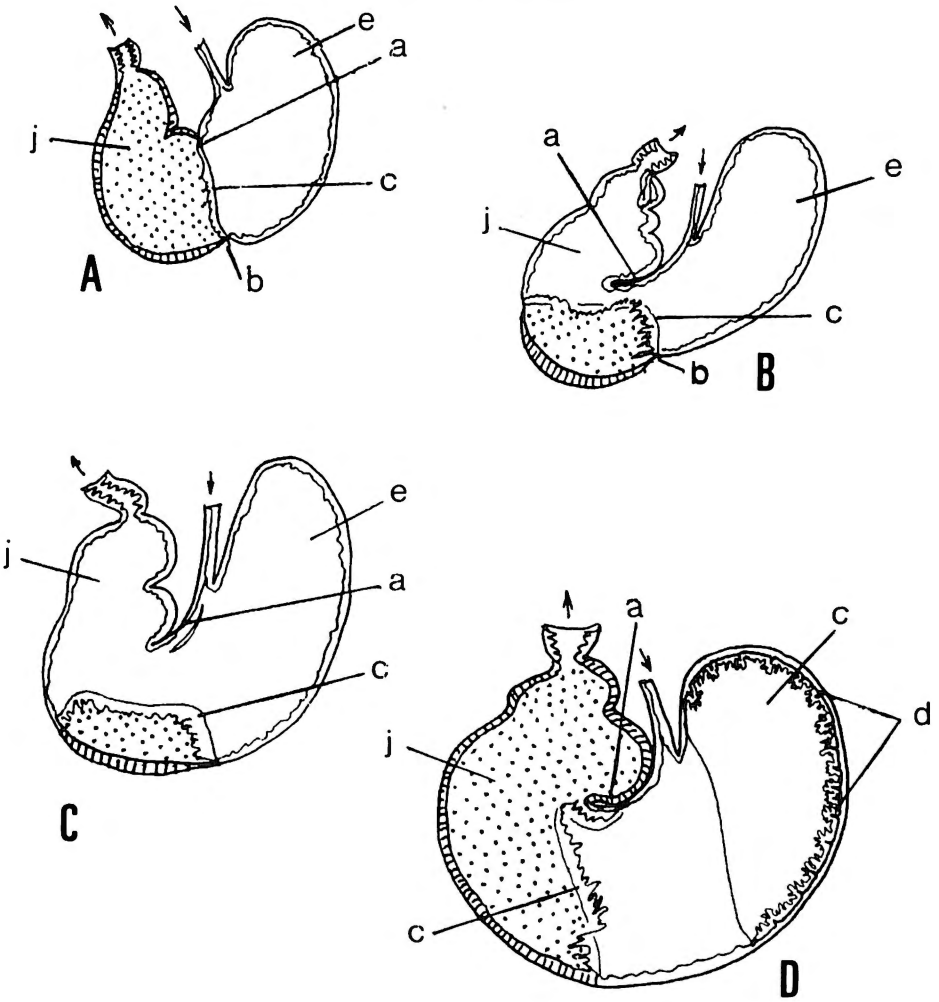
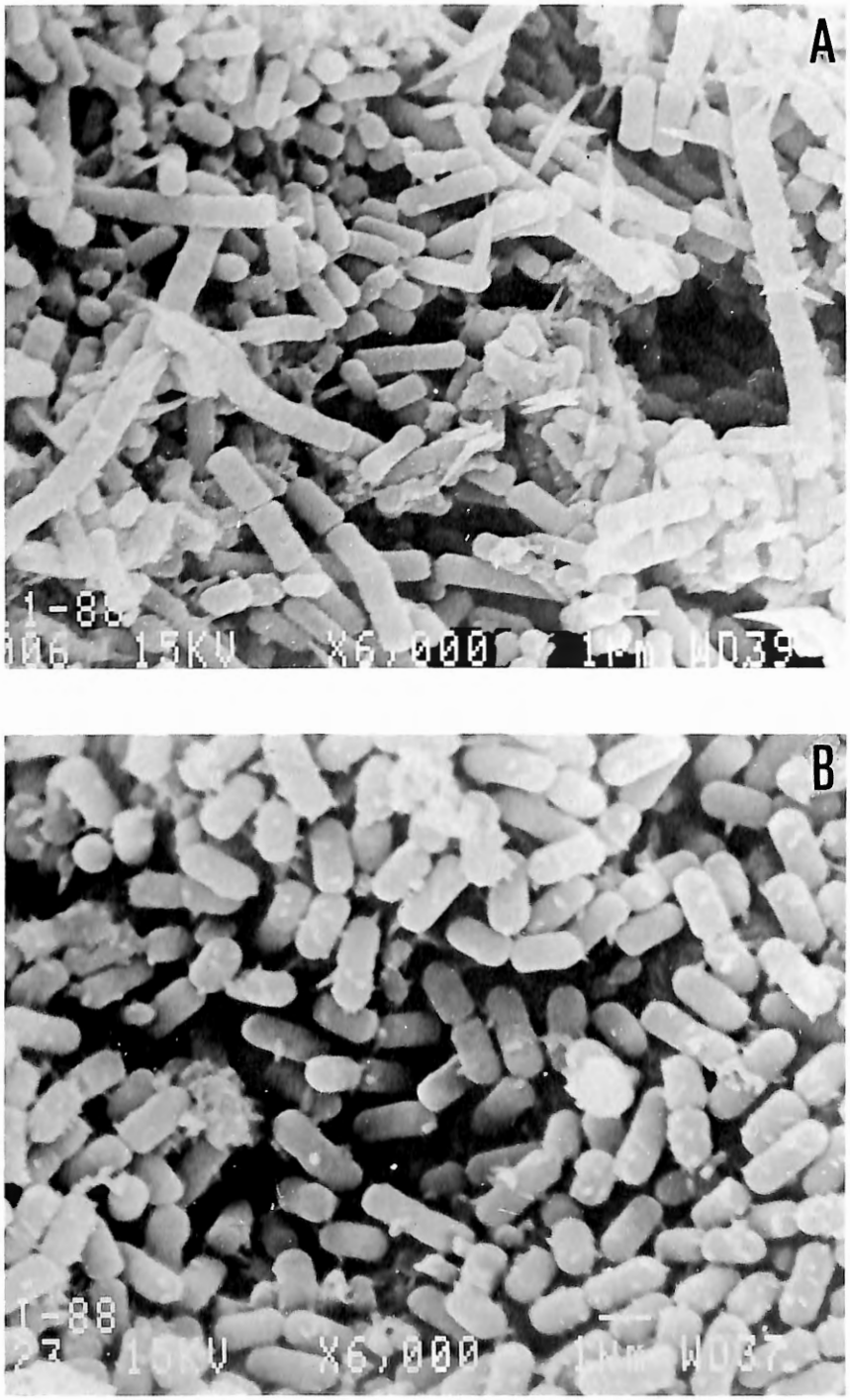


Fig. 1. — Gastric morphology of *Apodemus sylvaticus* (A), *Microtus arvalis* (B), *Neotoma albigula* (C), *Myospalax myospalax* (D) : a - incisura angularis, b - sulcus on the greater curvature, c - bordering fold, d - symbiopapillae, e - forestomach (corpus ventriculi), j - antrum.

All these facts show that endogenous and symbiont types of digestion in the wood mouse supplement each other. Indeed, the diet of this rodent contains all the components that the host needs for growth and reproduction.

In the caecum the substratum for symbionts is more uniform than the one in the stomach. Owing solely to caudal disposition of the caecum in the digestive tract caecal content is as if enriched with cellulose, since digestible nutrients have been already extracted in the stomach and small intestines. So dimensions and architec-


A
B

ture of the caecum are good indices in the first line of its role in cellulose splitting in different species.

The caecum in the wood mouse is small, the ampula coli is not clearly developed ; the colon has V-shaped form (Fig. 2, A). In the hindgut of such structure the fibrous residues of seeds probably are subjected to weak symbiotic fermentation.

The common vole consumes predominantly grasses that are rich in cellulose, and so this rodent is obliged to use bacterial symbionts intensively for utilization of these components. The common vole possesses a bilocular-discoglandular stomach that differs from that in the wood mouse in the following aspects. The zone of glandular epithelium is restricted to a small area on the greater curvature ; the incisura angularis, as well as the sulcus on the greater curvature, are appreciably deeper than in the wood mouse (Fig. 1, B). Consequently, a narrow channel connecting two chambers of the stomach is formed. The high bordering fold with a toothed ridge contributes substantially to the isolation of two chambers. The conditions described above favour a more intense bacterial fermentation of nutritional components (including cellulose) because isolation of the forestomach allows the process of fermentation to be prolongated. The composition of bacterial populations colonizing the cornified epithelium is more homogeneous than in the wood mouse (Pl. 1, B) and, hence, proves more high specialization of bacterial fermentation in the forestomach. As regards the extraction of nutrients from cellulose in the forestomach, there is evidence that some species of *Microtus* apparently are similar to ruminants. For example, *M. montebelli* produces volatile fatty acids in a ratio similar to that found in ruminants (OBARA and GOTO, 1980) ; these points to bacterial cellulose fermentation. Probably in the hervivorous *M. arvalis* similar processes take place in the forestomach.

The caecum and colon in the common vole, compared to those of the wood mouse, are more complicated (Fig. 2, B). The caecum is long and sacculated ; the double colic spiral and ampula coli are well developed. As stated above these peculiarities of the caecal morphology manifest a high degree of adaptation to digestion of cellulose.

The diet of the white-throated wood rat mainly consists of green parts of plants, like in the common vole. The stomach of this rodent is bilocular-discoglandular, but the chambers are less isolated than those in the common vole (Fig. 1, C). So both the diet and the morphology of the stomach are very similar in the common vole and the white-throated wood rat. Hence, one can expect similarities in symbiocenoses with the same functions in the stomachs of these species. Rather

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PLATE 1

Specific associations of symbionts colonizing the cornified epithelium of the forestomach. A : *Apodemus sylvaticus* ; B : *Microtus arvalis* (scanning electron micrographs).

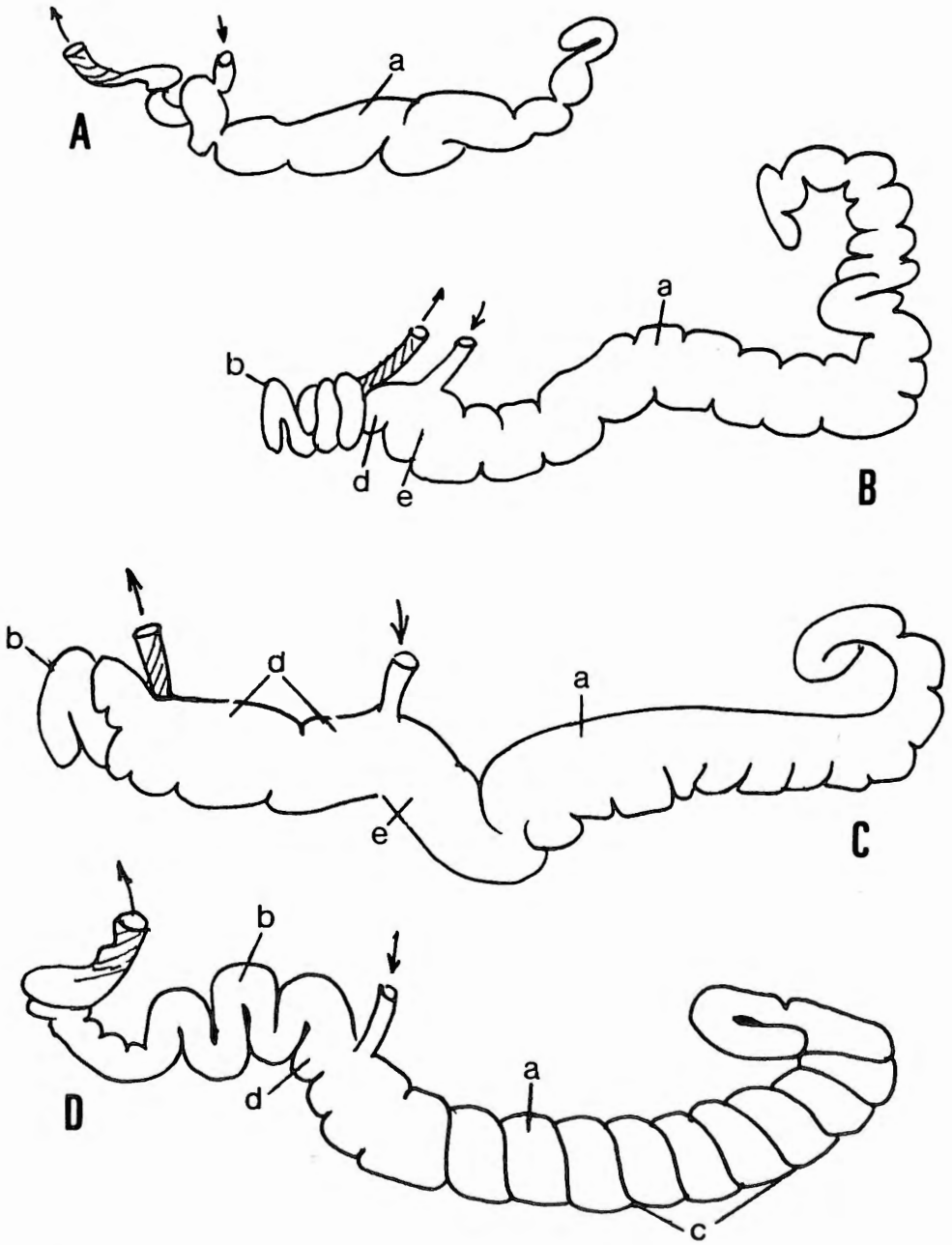


Fig. 2. — Hindgut morphology of Apodemus sylvaticus (A), *Microtus arvalis* (B), *Neotoma albigula* (C), *Myospalax myospalax* (D) : a - caecal body, b - colic spiral, c - spiral fold, d - ampulla coli, e - ampulla caecalis.

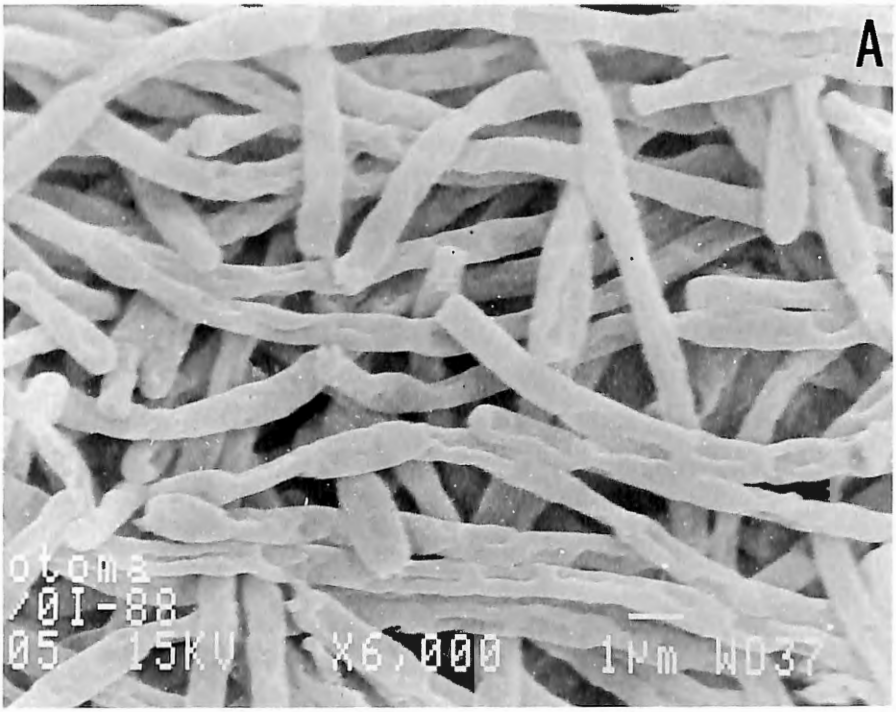
unexpectedly, together with common cocci and bacilli filiform bacteria were found colonizing the wide surface of the cornified stomach epithelium of the latter species (Pl. 2, A). Such an association of attached bacteria gives grounds to believe that the main function of symbiocenosis in the white-throated wood rat differs from its supposedly cellulosolytic function in the common vole. In these two cases the different ways of coevolution of rodents with endosymbionts are not reflected conspiciously in the morphology of the stomach but mainly manifest themselves in the different associations of attached bacteria, that probably produce different digestive enzymes.

The caecum of the white-throated wood rat is long and voluminous, has a sacculated body ; the ampulla caecalis is moderately pronounced ; the colon is V-shaped, the ampulla coli is long and wide (Fig. 2, C). According to the complicated morphology of the hindgut in this rodent it is the place of more intense fermentation of cellulose.

In the Siberian zokor, an underground rodent consuming bulbs, rhizomes and roots, as well as green parts of plants, unusual endosymbiosis was discovered. The stomach of this rodent is unilocular-hemiglandular, but the cornified epithelium of the forestomach forms papillae (Fig. 1, D). Earlier investigators used to explain these complications in the structure of the stomach as adaptations to consumption of food rich in cellulose, as it is observed in ruminants (for review see CARLETON, 1971), but recent investigations, as stated below, disproved this explanation.

Papillae in the forestomach of the Siberian zokor do not look like papillae in the rumen. In the latter papillae consist only of the host's tissues including all mucosae layers and submucosa ; their surface is covered with various attached bacteria (SOKOLOV *et al.*, 1989). To the contrary, in the Siberian zokor papillae consist of the tissues of two different organisms viz. only of cornified epithelium of the host's stomach and bacterial bodies that are embedded in these epithelial cells (Pl. 2, B). This gave me grounds to name these unusual structures « symbiopapillae » (NAUMOVA, 1981). Similar structures have been described in detail in four other species of rodents that belong to different systematic groups. These species are : *Tachyoryctes splendens,* Rhizomyidae (RAHM, 1976 ; ZINGG, 1978) ; *Mystromys albicaudatus,* Cricetidae, Cricetinae (MADDOCK and PERRIN, 1981) ; *Cricetomys gambianus,* Muridae, Cricetomyinae (PERRIN and KOKKIN, 1985) ; and *Cryptomys damarensis,* Bathyergidae (the latter species is mentioned by many authors, but it has not been investigated sufficiently).

Bacteria colonizing the stomach epithelium in the Siberian zokor belong to the gram-negative group as well as those in *Tachyoryctes.* High amylolytic activity was discovered in bacteria inhabiting forestomach papillae in *Mystromys* and *Cricetomys* (PERRIN, 1987). Supposedly, the symbiopapillae in Siberian zokor, having the same structure as in the species listed above, produce amylase or some other enzymes duplicating functions of the host's endogenous enzymes. It is explainable as a result of the phenomenon of the function transfer (KOKSHAYSKY, 1980) which implies that microbial and endogenous enzymes are interchangeable in the course of evolution. The formation in rodents' forestomachs of symbiocenoses with enzyme-systems duplicating those of the host, is biologically significant in develop-


A
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a

ment of the internal trophic chains in the course of evolution (NAUMOVA, 1981, 1989), viz. in enriching the poor plant food with microbial protein. The incorporation of bacteria into the epithelium of papillae prevents them from being washed out from a forestomach that is poorly isolated morphologically. Together with exfoliating superficial cornified epithelial cells bacterial bodies making up an appreciable biomass (see Pl. 2, A), get into the stomach cavity and are digested as the usual food.

The caecum of the Siberian zokor is voluminous and possesses a unique structure for rodents viz. the spiral fold (Fig. 2, C) that assists the circulation of the caecal content and the retention of symbionts in it. It is very likely that these symbionts produce cellulase, as the Siberian zokor consumes much cellulose with the food.

CONCLUSIONS

It is well known that different parts of a plant have a different biochemical composition. Whereas large grazing herbivorous mammals, for example ruminants, consume almost the whole plant (therefore much cellulose as well), small rodents are able to choose their food more precisely and to select the most palatable parts of plants. That is why rodents can provide a more homogeneous substratum for specific activities of their symbionts. Importantly, many rodents have retained predatory habits (LANDRY, 1970) and so complementary animal diet can compensate for the deficiency in nutritional plant protein. These two circumstances determine the differences in the ways of coevolution between hosts and endosymbionts as one can observe it in rodents and ruminants. The described examples illustrate particular traits of a coevolutionary process between muroid rodents and their endosymbionts. First of all, in the forestomach of rodents a high specialization of symbiocenoses may be formed in contrast to ruminants having only polyfunctional symbiocenoses. Secondly, because of the phenomenon of function transfer in the digestion of rodents, these animals depend less on the activity of their endosymbionts than ruminants do. Furthermore, evolutionary morphological transformations in the digestive system of rodents should be considered as adaptations not only to the particular feeding habits but also to the endosymbionts, which are the primary consumers of food entering the forestomach and simultaneously producers of valuable nutrients for the host.

PLATE 2

A : *Neotoma albigula* (scanning electron micrographs) ; B : *Myospalax myospalax*, histological section through symbiopapilla, haematoxylin and eosin, obj. 20, oc. 7, a = bacterial mass, b = cornified epithelium.

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SHORT NOTES

A SHORT NOTE ON THE OCCURRENCE OF THE GENUS *CEPHALOPS* FALLÉN (DIPTERA, PIPUNCULIDAE) IN THE U.S.S.R.

by

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SUMMARY

The occurrence of the genus *Cephalops* FALLÉN (Diptera, Pipunculidae) in the U.S.S.R. is shortly discussed, based on material from the Academy of Sciences at Leningrad and literature references. Three species are reported for the first time : *C. signatus* (BECKER), *C. subultimus* COLLIN, and *C. obtusinervis* (ZETTERSTEDT).

Key words : Pipunculidae, *Cephalops*, U.S.S.R., distribution.

INTRODUCTION

Pipunculidae are small, inconspicuous flies with a large head that is almost completely occupied by a pair of compound eyes. During the larval stage they are known as parasitoids of Auchenorrhyncha (Homoptera). The European species of the genus *Cephalops* seem to parasitize mainly on Delphacidae (WALOFF and JERVIS, 1987).

About 160 pipunculid species are known from the Palaearctic region. However, records from the U.S.S.R. of these flies are scarce. TANASIJTSHUK (1970) included three *Cephalops* species in his key for the Russian fauna : *C. furcatus* (EGGER), *C. semifumosus* (KOWARZ) and *C. vittipes* (ZETTERSTEDT). In the recently published catalogue of Palaearctic Diptera he reports four species for the country (TANASIJTSHUK, 1988), adding *C. aeneus* FALLÉN to the list. *C. aeneus* and *C. vittipes* were however already mentioned by COLLIN (1941) from the Ussuri region in the Far

Eastern territory of the U.S.S.R. KOZÁNEK (1988) reported a fifth *Cephalops* species : *C. germanicus* (ACZÉL) from the Caucasus.

Within the scope of a world revision of the genus *Cephalops* (see DE MEYER, 1989a, b) the material of this genus in the collections of the Academy of Sciences at Leningrad was revised. Although the collection of *Cephalops* material is limited (only 52 specimens), it is nevertheless a very interesting one since 8 *Cephalops* species were found, and three of them were not previously recorded from the U.S.S.R.

RECORDS

The abbreviations for the territories are identical to the ones used in the Catalogue of the Palaearctic Region : CET : Central European territory ; NET : North European territory ; SET : South European territory ; TC : Transcaucasus ; FE : Far East. Additional records from certain regions that are not represented in the collection studied, are based on KOZÁNEK (1988) and TANASIJTSHUK (1988).

Cephalops furcatus (EGGER)

NET : 1 ♀ from Leningrad region : Luga. (Also reported from CET).

Cephalops germanicus (ACZÉL)

NET : 13 ♂♂ 3 ♀♀ from Leningrad region : Lachta, Luga, N. Bronnaya, Preobrazhenskaya stat., Sablino. (Also recorded from TC : Azua).

Cephalops aeneus FALLÉN

CET : 1 ♂ from Lipetsk region : Ryazan. NET : 4 ♂♂ from Leningrad region : Kartashevka, Jukki, Yastshera ; 2 ♂♂ from A.S.S.R. : Uchta Komi. SET : 1 ♂ from Ukraine S.S.R. : Sumy. (Also reported from FE).

Cephalops vittipes (ZETTERSTEDT)

NET : 3 ♂♂ 1 ♀ from Leningrad region : Kartashevka, Luga, Rozhdestveno. (Also reported from CET and FE).

Cephalops semifumosus (KOWARZ)

CET : 1 ♂ from Moskow region : Bolshevo. NET : 5 ♂♂ 3 ♀♀ from Leningrad region : Kartashevka, Luga, Yastshera.

Cephalops signatus (BECKER)

FE : 1 ♂ from Amur river region : Zimmermanovka. New for the Russian fauna.

Cephalops subultimus COLLIN

CET : 1 ♂ 1 ♀ from Estonia S.S.R. : Koeru ; 2 ♂♂ from Bashkir S.S.R. : Bashkir reservate. NET : 2 ♂♂ 2 ♀♀ from Leningrad region : Jukki, Leningrad, Luga, Kartashevka. New for the Russian fauna.

Cephalops obtusinervis (ZETTERSTEDT)

CET : 1 ♀ from Moscow region : Lobnya. NET : 4 ♂♂ from Leningrad region : Gatchina, Luga, Sablino. New for the Russian fauna.

DISCUSSION

All 8 *Cephalops species occurring in the U.S.S.R., are widely distributed throughout the West-Palaearctic region (*DE MEYER, 1989a ; DE MEYER & BACKELJAU, in press), except for *C. signatus* which is absent from Northern Europe. In addition, *C. aeneus, C. vittipes, C. obtusinervis* and *C. furcatus* are recorded from the eastern part of the Palaearctic region, including Japan (COLLIN, 1941 ; YANO *et al.*, 1984 ; MORAKOTE, pers. comm.).

The most remarkable record is the specimen of *C. signatus* from the Far Eastern territory. This specimen is slightly different from the West-Palaearctic specimens (the legs are completely yellow, the apical part of the aedeagus is slightly longer and the cupular ends of the ejaculatory duct are somewhat different). However, these minor morphological variations do not validate a separate species status. Hence we identified the specimen as *C. signatus*.

In general, it seems that most of the Palaearctic *Cephalops* spp. have a wide distribution throughout the region although it is not yet clear whether all West-Palaearctic species also are present in the eastern part of the continent.

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ON THE FUNCTIONAL SIGNIFICANCE OF THE DORSAL PART OF THE Aω MUSCLE IN *POMATOSCHISTUS LOZANOI* (TELEOSTEI : GOBIIDAE)

by

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SUMMARY

In *Pomatoschistus* the dorsal fibres of the A_ω section of the musculus adductor mandibulae-complex insert on the tendon of the A_3 section. Three hypotheses are postulated concerning the mechanical implication of this construction during co-contraction of both muscle parts. These are tested for *P. lozanoi* by means of a mathematical statical bite model. Most likely, this adductor configuration enhances the overall bite performance whithin the spatial constraints of the gobiid head.

Key words : Biomechanics, muscle function.

INTRODUCTION

In *Pomatoschistus* the cheek muscles (musculus adductor mandibulae-complex) are very well developed (Fig. 1, A and B). Broadly, the division of these muscles follows the general percomorph pattern as discribed by WINTERBOTTOM (1974). Remarkable, however, is the insertion of the dorsal fibres of the A_ω section ($A_\omega d$) on the tendon of the A_3 portion (Fig. 1B). This paper deals with the functional relevance of such a construction.

MATERIALS AND METHODS

Pomatoschistus specimens were obtained from the Marine Section of the Institute of Zoology (Universty of Ghent). Dissections and observations were done on 10 *P. lozanoi* specimens of several length classes. One series of transverse sections (glycol-metacrylate ; 5μm) of *Pomatoschistus lozanoi* (SL 48.1 mm ;

TL 56.7 mm) was used to calculate the physiological cross sections of the muscles and the coordinates of the points in Fig. 1C. They where measured with the aid a Hewlett Packard 9826A microcomputer extended with a Summagraphics digitiser (type ID). The mathematical model was implemented on an IBM AT computer (see discussion).

RESULTS

MESTERMANN and ZANDER (1984) gave a detailed description of the cranial osteology of the *Pomatoschistus* genus. A general description was already given by REGAN (1911) and GREGORY (1933). The typically fenestrated suspensorium in this family can be related to the extensive development of the cheek muscles (DECLEYRE *et al.*, 1990).

The A_3 muscle fibres originate on the caudal rim of the fenestra (Fig. 1B). They insert as two distinct bundles on a tendinous connective tissue sheet. This sheet tapers rostrally into a tendon (A_3t ; see Fig. 1B) that passes to the medial side of the mandible at the level of the mandibulo-suspensorial articulation (called further on « the articulation *s.s.* »). A_3t inserts via the sesamoid coronomeckelium on the cartilago meckeli.

On the lateral surface of the suspensorium the A_1 section is situated dorsally from the A_3 part. They are both covered by the well developed A_2 portion of the cheek muscle which in turn is divided in a dorsal α and a ventral β part (Fig. 1A).

The A_ω section inserts on the medial surface of the mandible. Most of its fibres originate from a tendinous sheet, connected to the medial side of the suspensorium. A small portion of this muscle, the dorsalmost fibres ($A_\omega d$), however, do not attach to the tendon sheet but originate on A_3t (Fig. 1B). This description refers to *Pomatoschistus lozanoi*. The same muscle configuration has also been found in *P. minutus* and *P. norvegicus*.

The presence of a connection between the A_3 and the A_ω sections is not unique among Teleosts (see WINTERBOTTOM, 1974). For instance, a comparable configuration of A_3 and A_ω to that of *Pomatoschistus lozanoi* also exists in the carp (*Cyprinius carpio* ; SCAPALO, 1989), where all fibres of A_ω are connected to A_3t.

DISCUSSION

The contraction of A_3 will cause a moment on the lower jaw about the articulation. Contraction of $A_\omega d$, (1) can result in the lifting of A_3t (thereby increasing its angle of insertion) which will affect the moment component of the A_3 force on the lower jaw and (2) can cause an additional moment on the lower jaw (see Fig. 1C). As a functional explanation for the presence of $A_\omega d$ on A_3t three hypotheses can be proposed :

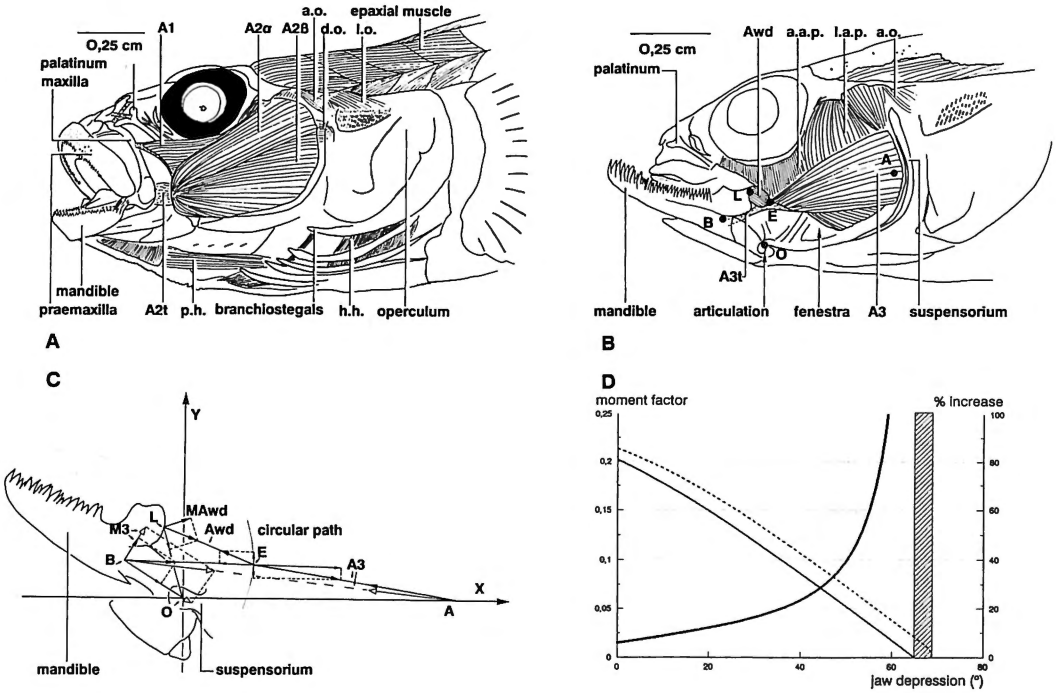

Fig. 1. — A : *Pomatoschistus lozanoi*, SL 50.55 mm ; TL 60.65 mm, dissection of the musculus adductor mandibulae-complex, skin removed. B : *Pomatoschistus lozanoi*, SL 54.2 mm ; TL 65.0 mm, dissection of the musculus adductor mandibulae-complex : A_1, $A_2\alpha$, $A_2\beta$ and upper jaw removed. C : Force diagram. The forces resulting in a moment on the lower jaw are shown. Fully black arrows are used in the case of co-contracting of A_3 and $A_\omega d$; sole contraction of A_3 is is represented by white arrow-heads. $A_\omega d$ and A_3 here refer to the line of action of these muscles ; M_3 : moment component of A_3 on the lower jaw ; $MA_\omega d$: moment component of $A_\omega d$. D : Graph of the moment factor (left Y-axis) on the lower jaw without (full line) and with the co-contraction of $A_\omega d$ (dashed line). The bold line gives the percental increase of the moment factor as the result of the co-contraction referred to the sole A3 activity (right Y-axis). The hatched zone represents the shift of DP (see text).
Abbreviations : A : caudal insertion of A_3 ; a.a.p : adductor arcus palatini ; a.o. : adductor operculi ; $A_{1,2,3}$: parts of the adductor mandibulae-complex ; A_2t : tendon of A_2 ; A_3t : tendon of A_3 ; $A_\omega d$: dorsal part of A_ω ; B rostral insertion of A_3 ; d.o. : dilatator operculi ; E : insertion of $A_\omega d$ on A_3t ; h.h. : hyohyoideus ; L : insertion of $A_\omega d$ on the coronoid process ; l.a.p. : levator arcus palatini ; l.o. : levator operculi ; M_3 : moment component of A_3 on the lower jaw ; $MA_\omega d$: moment component of $A_\omega d$; O : mandibulo-suspensorial articulation ; p.h. : protractor hyoidei.

Hypothesis 1 : From a certain degree of mouth opening onwards, A_3t will lie on the articulation. In these circumstances A_3 is no longer functional because the force exerted by the muscle passes almost through the fulcrum of the lever. The lower

jaw position in which this initially occurs is called the 'dead point' (DP). Lifting of A_3t can thus postpone the DP of A_3 to a larger angle of jaw depression.

Hypothesis 2: $A_\omega d$ can trigger the fast closure of the mouth. If the lower jaw has passed the DP, the A_3 can be active without influencing that jaw position. Hence, if A_3t could be lifted from the articulation, this would provide a trigger for the sudden release of the A_3 power. $A_\omega d$ might function as a trigger in two ways: (1) by direct elevation of A_3t and (2) indirectly by elevation of the lower jaw, which will also lift A_3t (Fig. 1C).

Hypothesis 3: For any given jaw position $A_\omega d$ contraction can lift A_3t. This can, together with the moment component of $A_\omega d$ ($MA_\omega d$ in Fig. 1C) enlarge the total moment on the lower jaw and produce a stronger bite (Fig 1C and D).

These hypotheses are tested by means of a mathematical static bite model for *Pomatoschistus lozanoi* (Fig. 1C). This calculates the moment exerted on the lower jaw by A_ω with and without the co-contraction of $A_\omega d$. All involved lengths are standardized, taking the distance OA (Fig. 1B and C) as unit length. As a simplification the muscles were considered always to contract maximally. The maximal muscle force is directly proportional to the physiological cross section (= section perpendicular to the fibre direction, see a.o. (GANS, 1982). This was used as a measure for the muscle force. The force of A_3 is arbitrary set to 1 and the ratio of the force of $A_\omega d$ to A_3 is 0.14. Consequently, the model output is given as dimensionless moment factors (Fig. 1D). In the model a fixed length for A_3t (BE in Fig. 1B and C) has been assumed. Therefore, activity of $A_\omega d$ tends to move the point E upwards along a circular path around the point B (Fig. 1C). For each position of jaw depression, there will exist only one point on this path coinciding with static force equilibrium.

The predicted shift of DP is depicted as the hatched area in Fig. 1D. It can be questioned whether an increase of only 4° adequately explains the extraordinary positioning of $A_\omega d$ muscle fibres. Moreover, measurements indicate that the angle of maximal jaw depression immediately precedes or just coincides with the hatched area in the graph (± 65°). This obviates the need for a shift in DP. Therefore hypothesis 1 is rejected. However, it must be noticed that for the maximally opened mouth the co-contracting $A_\omega d$ and A_3 exert a moment on the jaw, contrary to the sole activity of A_3 (hatched area in Fig. 1D).

$A_\omega d$ will only be able to lift the tendon, to act as the trigger for the pre-stressed A_3, for jaw positions just under the DP (hatched area in Fig. 1D). This will demand a very precise regulation of the jaw opening: if the jaw is depressed too far (beyond the hatched area) the trigger will not work. If it is not depressed far enough (before the hatched area) there will exist no pre-stressed situation. As mentioned above maximal gape might coincide with the hatched area. Thus, in these circumstances triggering will be possible. On the other hand elevation of the lower jaw (second aspect of triggering, see above) can also be done by the other sections of the musculus adductor mandibulae. Electromyography of the involved muscles may further help to falsify or to consolidate hypothesis 2.

From Fig. 1D, hypothesis 3 seems to be the most plausible one. The moment on the lower jaw is considerably enhanced for all possible opening angles of the lower jaw. For an intermediate jaw position an increase of about 20 % is calculated (see Fig. 1D). An equally forceful A_3 muscle *without the aid of* A_ωd would be more voluminous as its physiological cross section would increase to the same extent. Since the well developed $A_2\alpha$ and $A_2\beta$ sections strongly limit the expansion of A_3, the presence of the (small) A_ωd can considerably optimize the bite force.

CONCLUSION

A functional explanation for the insertion of the dorsal fibres of the A_ω section on the tendon of the A_3 portion can be found in the fact that this substantially enhances the overall biting force of the individual within the spatial constraints of the gobiid fish head.

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ABSTRACTS

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Aquatic Zoology

EFFETS DE LA DENSITÉ CELLULAIRE DE *CHLORELLA VULGARIS* BEIJER SUR LA DYNAMIQUE DE PRODUCTION ET LA QUALITÉ NUTRITIONNELLE DU ROTIFÈRE *BRACHIONUS CALYCIFLORUS* PALLAS

par

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La production de proies vivantes destinées essentiellement aux premiers stades de développement des larves de poissons se limite généralement à l'utilisation d'une seule espèce, *Brachionus plicatilis* MÜLLER, un rotifère d'eaux saumâtres. GALKOVSKAYA (1963) a proposé l'utilisation du rotifère *Brachionus calyciflorus* PALLAS espèce d'eaux douces, comme source d'alimentation pour les larves en aquaculture dulcaquicole. Une maîtrise parfaite de la production de cette espèce sur certains substrats alimentaires s'impose toutefois afin de subvenir aux besoins nutritionnels des larves. Des essais de production en masse de ce rotifère sur l'algue monocellulaire *Chlorella vulgaris* ont été réalisés après détermination du niveau optimal d'alimentation des organismes durant un cycle journalier et en relation avec la densité algale dans les milieux de culture. La densité cellulaire de Chlorelles doit être voisine de 4.10^6 cell/ml afin de maintenir les rotifères à satiété. A cette densité, le rotifère atteint son taux d'ingestion maximal, soit 16.000 cell/animal.h avec un taux de filtration de 4.04 µl/animal.h. La production de cet organisme est correlée linéairement à la densité cellulaire de *C. vulgaris* et son accroissement entre 1,5 et 6.10^6 cell/ml est hautement significatif ($P < 0,001$). L'accroissement journalier maximal, soit 31,5 rotifères/ml.j est obtenu avec 6.10^6 cell/ml. Le temps de doublement de la population décroît significativement ($P < 0,05$) de 5,81 à 3,01 jours avec l'accroissement de la densité cellulaire entre 1,5 et 6.10^6 cell/ml. Sa valeur minimale, soit 2,88 jours est atteinte avec 6.10^6 cell/ml. L'augmentation du taux de croissance (de 0,12 à 0,23) entre ces deux densités est significative ($P < 0,01$). Celle de la densité de population est sensiblement régulière entre 3 et 6.10^6 cell/ml et atteint un facteur 3 en moyenne à 6.10^6 cell/ml. La densité maximale enregistrée à cette concentration cellulaire, après 13 jours de culture est de 202,5 rotifères/ml. Sur le plan nutritionnel, l'accroissement de la densité cellulaire de *C. vulgaris* entre 1,5 et 6.10^6 cell/ml s'est traduit par une amélioration de la valeur protéique des *Bra-*

chionus de 92,10 à 107,52 ng de Protéine/rotifère. La composition en acides aminés (AA) des rotifères au terme de la culture dépend de la densité initiale des chlorelles. Le rapport (AA)essentiels/(AA)non essentiels varie de 0,95 à 1,36 entre 1,5 et 6.10^6 cell/ml. Il n'y a pas de différence significative entre 3 et 6.10^6 cell/ml ($P < 0,05$). On note d'autre part une large représentation des acides gras (AG) de la famille oléique, environ 50 % des AG totaux dont l'acide oléique C18:1n-9. Le pourcentage des acides gras longs poly-insaturés (AGLPI) est sensiblement amélioré avec l'accroissement de la densité cellulaire et principalement pour les familles linoléique et linolénique. Les AGLPI essentiels, comme C18:2n-6 et C20:5n-3 représentent respectivement 8,42 et 1,95 % des AG totaux à 6.10^6 cell/ml. La production de *B. calyciflorus* peut être entravée par la prolifération du cilié *Vorticella nebulifera* et de certains flagellés Bodonidés dans les cultures, avec comme conséquence une diminution croissante des possibilités de nutrition du rotifère et une perturbation probable de son cycle de développement.

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POPULATION GENETIC AND SYSTEMATIC STUDY OF THE *VENUS GALLINA* COMPLEX IN THE RIA FORMOSA, SOUTHERN PORTUGAL (MOLLUSCA, BIVALVIA)

by

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Venus gallina s.l. is a common bivalve species which occurs along the European coasts from northern Norway to the Black Sea. Yet, despite its abundance and commercial importance, the species still presents systematic problems. Indeed, three contrasting opinions on the taxonomy of *Venus gallina s.l.* persist in the literature. The species has been considered as (1) a single, but polymorphic species with a vast and continuous distribution, (2) a complex of two distinct species whose distributions partly overlap and, finally, (3) a single species consisting of two subspecies, *viz.* the Mediterranean *V. gallina gallina* and the Atlantic *V. gallina striatula*. These (sub)species would differ in some minor conchological details too.

In order to investigate this controversy, we performed an electrophoretic analysis of *V. gallina s.l.* in the Ria Formosa, southern Portugal, where the two presumed (sub)species live microsympatrically. A total of seven enzyme systems, viz. MDH, ME, XDH, PGD, GPI, SOD and GPD, were surveyed by means of polyacrylamide gel electrophoresis in four populations (149 individuals), of which three comprised both (sub)species.

The results of this analysis show that *V. gallina s.l.* is genetically highly variable. As a matter of fact, if the three mixed populations are considered, all loci studied turn out to be polymorphic (0.95 criterion). Yet, for most loci there are very significant deviations between

the observed genotype frequencies and those expected under Hardy-Weinberg conditions. On the other hand, if in each of the mixed populations the two presumed (sub)species are treated separately, the degree of polymorphism decreases substantially, while for most loci the deviation from Hardy-Weinberg equilibria disappears and is replaced by a significant concordance. This observation suggests that the mixed populations have a heterogeneous genetic structure and hence may consist of two (or more) gene pools between which genetic exchange is reduced, if not absent. Therefore, we conclude that *V. gallina s.l.* in the Ria Formosa consists of two reproductively isolated species (*V. gallina* and *V. striatula*). This is further confirmed by an analysis of the genetic identities between the two species, as well as by both conchological and anatomical data. A much more profound account of this study will be published in a forthcoming paper.

THE EUROPEAN EEL (*ANGUILLA ANGUILLA* L.) : AN ENDANGERED SPECIES IN FLANDERS ?

by

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Major concern has arisen about the actual situation and further evolution of our European eel (*Anguilla anguilla* L.) stocks over the continent. The Working Party on Eel states (1) that the recruitment of eel to European waters has declined, (2) that evidence has been presented of the restriction of habitat available to wild eel, and (3) that there is thus a possibility that the European eel could become an endangered species requiring international cooperation to maintain or restore the stocks (1).

Estimating eel stocks is feasible on four different levels :

1. Estimating population density of migrating leptocephali in the Atlantic ocean. Figures show that since 1979 leptocephali catches have been very low (< 5 individuals per 1h trail with an Isaacs Kidd Midwater Trawl with a 6 m^2 opening). However, to ensure a standardised methodology in the different working areas, international cooperation is still needed.

2. In most rivers of western Europe glasseel catches have diminished significantly from 1980 onwards. On the river Yser (Flanders) the situation is similar : after an abrupt decline in the amounts of ascending elvers in the years 1980-81 catches remain on a very low level.

3. Total catches of yellow eel in the EC countries have been decreasing already since 1970. Evidence has been provided on the decrease of yellow eel stocks on the river Yser as a result of the extreme eutrophication of the river. Several studies have been carried out resulting in data on natural eel stocks, indicating that quite different environmental conditions may influence eel populations profoundly.

4. No reliable data are available on the migration of silver eel in Flanders.

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It is concluded that there are reasons to believe that declining eel stocks in Flanders may be linked with the general decrease in water quality and the import of several foreign eel pathogens.

Long-term monitoring and international cooperation is needed to provide reliable information on future evolution of the eel populations in order to set up adequate stock management.

PRELIMINARY EVALUATION OF THE ABC METHOD FOR THE ASSESSMENT OF DISTURBANCE IN RIVER ECOSYSTEMS, USING FISH POPULATIONS

by

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WARWICK (1986) suggested that the distribution of numbers of individuals among species should behave differently from the distribution of biomass among species when an ecosystem is influenced by disturbance. Using combined k-dominance plots for species biomass and numbers, three situations could be distinguished ; unpolluted, moderately polluted and grossly polluted. An abbreviated name for this technique is the ABC method (Abundance Biomass Comparison).

In this study, the applicability of the ABC method was evaluated for the assessment of disturbance in water courses, using fish populations. The biomass and density of the fish populations was determined by electrofishing in fifteen different watercourses. The sample points represent both undisturbed, slightly disturbed and grossly disturbed water courses. By the selection of the sample sites, a distinction was made between disturbance by pollution and physical disturbance (*e.g.*, canalization).

Field data from undisturbed sample sites (good water quality and absence of physical disturbance) support the model of WARWICK. For the disturbed water courses the model was supported as well, but it was difficult to make a distinction between physical disturbance and disturbance by pollution.

There are indications that the ABC method is applicable for the assessment of disturbance in natural fish populations in rivers. However, this method gives indications of the physical disturbance together with the disturbance caused by pollution.

It seems that the ABC method could be useful to evaluate the disturbance of fish populations in unpolluted rivers caused by physical modifications of the rivers. Further field data are required to evaluate the method.

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PRELIMINARY RESULTS CONCERNING THE CULTURE OF FRESHWATER ANOSTRACANS AND CONCHOSTRACANS (CRUSTACEA, BRANCHIOPODA) FOR APPLICATIONS IN AQUACULTURE AND AQUATIC TOXICOLOGY

by

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Freshwater anostracans and conchostracans have for a long time been considered as biological curiosities. Only in recent years, there is a growing interest to use these phyllopods as a new type of live food in aquaculture and as additional test organisms in aquatic toxicology. Especially, their common feature of producing resting eggs (cysts) with a high storage capacity, makes these animals attractive for various kinds of applications.

This study presents some quantitative reproductive characteristics of two freshwater phyllopod species cultured at 25° C and fed with micro-algae. For both species, high fecundity rates were observed. Results are here presented as averages with standard deviations. Females of the conchostracan *Caenestheriella australis* produced a clutch of 338 ± 79 cysts every 1.5 ± 0.25 days, for a total number of 39 ± 21 broods. In the fairy shrimp *Streptocephalus proboscideus,* cysts were deposited with a frequency of 1 clutch of 167 ± 16 cysts every 2.1 ± 0.9 days, for a total number of 31 ± 27 broods. Fecundity, however, was found to be affected by daily manipulations and water quality.

To assure a good water quality and a constant food concentration in the tanks, a culture system for the controlled production of fairy shrimp cysts was constructed. This system is equipped with separate recirculation units and an automatic feeding apparatus and is furthermore readily modified for the culture of the more benthic conchostracans. Deposited cysts are easily removed for further processing. The use of these cysts as starting material in ecotoxicological testing minimizes technical and financial problems inherent to continuous culturing of live stock. Cysts could also be used to inoculate large scale culture systems in aquaculture.

Because of their non-selective and continuous filter feeding habits, mainly on phytoplankton, freshwater phyllopods could help to control the accumulation of agricultural wastes and tertiary effluents from purification processes by converting organic particulate material into phyllopod biomass. This energetically acceptable culture method offers promising perspectives in the artificial propagation of several kinds of freshwater fishes.

A CULTURE SYSTEM FOR FAIRY SHRIMPS (CRUSTACEA, ANOSTRACA)

by

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In contrast with *Artemia* cysts which can be harvested in a monospecific way, fairy shrimps generally co-occur with several other species in their respective biotopes and a mixture of resting stages is found in the sediments. To obtain specific fairy shrimp resting eggs, a culture system is required and suitable culture techniques must be developed for a successful production of cysts.

A semi-automatic and small-scale culture system is developed which aims at optimizing water quality, maintaining a constant food concentration and at facilitating a regular monitoring of the organisms and the harvesting of their cysts. The design is directed towards an automation of both the algal food culture and the feeding of the organisms themselves. The fairy shrimps are reared in conical tanks, equipped with a recirculation system consisting of a sand filter. Deposited cysts are collected in a separate compartment, which is easily removed for further processing of the harvest.

Streptocephalus proboscideus, a subtropical species, was reared at an initial density of 56 animals per litre. Several physico-chemical (pH, O_2, NH_3-N, NO_2-N, NO_3-N, and PO_4) and biological (survival, growth, diseases, brood size, hatching quality) variables were monitored at regular intervals and compared to the results derived from a static/renewal system with an initial density of 30 indiv./l. and with discontinuous food supply.

In the static/renewal system, the carrying capacity is clearly exceeded. The accumulation of ammonia (max : 0.92 mg l^{-1}) and nitrite (max : 1.48 mg l^{-1}) resulted in a crash of almost the entire experimental population during the first week.

The conditioned recirculation system proved to be a reliable technique. A steady state was established and a biological overcapacity was observed, effectively handling the initial peak load, assuring low mortality rates (± 5 % per week) and a high cyst production (± 200 cysts per brood cycle) in the experimental fairy shrimp population (sex ratio 1/1), opening possibilities for several types of applications in aquaculture and aquatic toxicology. Total production yielded an average of 18,000 cysts per day and per culture unit (volume : 6 l.). Increased production yields can be expected from higher population densities, manipulation of sex ratio and diet, and from optimization of the filter unit.

THE GENUS *LIMNOCYTHERE s.s.* IN AFRICA (CRUSTACEA, OSTRACODA)

by

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Lake Galla is a fossil lake in southern Ethiopia and consists at present of four clearly separated and typologically very different basins : the most northernly situated lake Zwai, the central lakes Langano and Abijata and the southern lake Shala. Both Zwai and Langano are freshwater lakes (salinity < 1 ‰), Abijata and Shala are saline lakes (salinity = c. 17 ‰). Geological data suggest high lake levels in the early Holocene (9220 ± 190 BP) and in the mid Holocene (5610 ± 100 BP) and a smaller transgression of late Holocene age (GROVE *et al.*, 1975). Lake Awassa, also a freshwater lake, is situated south of the Galla basins and is supposedly completely isolated from the former.

The five lakes hold an interesting ostracod fauna, the most important component being a (sub)specific cluster of *Limnocythere*-taxa : *L. thomasi thomasi* in Lake Zwai, *L. borisi borisi* in Lake Abiyata, *L. borisi awassaensis* in Lake Awassa, *L. borisi shalaensis* in Lake Shala and the same *L. borisi shalaensis* and *L. thomasi langanoensis* in Lake Langano. All taxa are endemic to their basin, *L. borisi shalaensis* being the only one occurring in two lakes.

It thus appears that *Limnocythere* has experienced a very active and rapid speciation in East African lakes and it would at first glance seem acceptable to situate at least the subspeciation in the period since the last pluvial, i.e. between 5000 BP and present. There are, however, several arguments against this hypothesis, for example the presence of a subspecies of *L. borisi* in the completely isolated Lake Awassa. There are thus two possibilities :

(1) Subspeciation indeed ocurred in the past 5000 years and in that case, *L. borisi* was passively introduced in Lake Awassa.

(2) The said (sub-)speciation is of a much older date and the various taxa persisted sympatrically in the filled Galla-basin at various times.

In vitro cross-breeding experiments, combined with the fossil record of the Galla-basins, could possibly provide a solution to this dilemma.

FOOD ITEMS OF PERCH (*PERCA FLUVIATILIS* L.) IN THE MONTH OF JULY IN W.P.C. DE BLANKAART IN 1982 AND 1988

by

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Food items of different length classes of perches were studied in 1982 and 1988 in the eutrophicated storage reservoir (60 ha, max depth 5 m) of W.P.C. De Blankaart (W. Flanders, Belgium).

The main food items of perches, smaller than 205 mm, were zooplankton followed by Chironomidae. Perches with a length between 205 and 250 mm and those with a length greater than 250 mm eat a lot of Chironomidae and no fish.

The fish biomass measured in 1988 consisted of perch *Perca fluviatilis* (number (n) : 353,124 ; total weight (tw) 1,709 kg), bream *Abramis brama* (n : 5 ; tw : 22.9 kg), pike *Esox lucius* (n : 1 ; tw : 0.7 kg), pikeperch *Stizostedion lucioperca* (n : 43 ; tw : 0.5 kg), eel *Anguilla anguilla* (n : 566 ; tw : 128 kg). The total fish biomass obtained a value of 31 kg/ha, which is very low for a eutrophicated reservoir. The total fish biomass in july 1988 was calculated to be 0.21 fish/m^3 or 1.1 g/m^3.

Each year a great number of cormorants (*Phalacrocorax carbo*) were observed during several months on the reservoir. Their influence on the fish biomass could be great but has not been directly measured.

Abundance and biomass of zooplankton to feed on was great enough and not considerably influenced by the turbidity due to the presence of phytoplankton. In 1982 and 1988 the chlorophyll concentrations were respectively 19.9 mg/m^3 and < 10 mg/m^3 and the total number of Cladocera were respectively 385 and 150 organisms/l.

The density of Chironomidae reached a value of 70,000 animals/m^2 in the summer of 1986 (GODDEERIS, pers. comm.). There were no data available on the density of Chironomidae in 1982 and 1988.

The relation between length and weight in 1982 and 1988 was calculated to be respectively $\log G = -5.086 + 3.163 \log L$ ($R2 = 0.997$) and $\log G = -5.008 + 3.118 \log L$ ($R2 = 0.972$). As these relations are comparable with data cited in literature for other perch populations, we may conclude that the lack of fish in the diet does not reduce the growth of perches in the reservoir of W.P.C. De Blankaart.

USE OF AERIAL ADULT INSECTS (EPHEMEROPTERA, PLECOPTERA AND TRICHOPTERA) FOR THE ECOLOGICAL SURVEY OF THE MEUSE RIVER IN BELGIUM : PRELIMINARY RESULTS AND PROSPECTS

by

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In order to palliate the difficulties of adequately sampling benthic macroinvertebrates in as large a river as the Meuse in Belgium, the possibility of using aerial adult insects as a reflecting image of the aquatic communities was considered, with a view to manage a practical method for a long-term survey of the river. The purpose of the preliminary study presented here was to check this possibility by comparing the Ephemeroptera, Plecoptera and Trichoptera caught in three differenciated sampling sites, assuming that a method that would allow a characterization of spatial differences would also be likely to reveal temporal changes.

The three sampling sites, Dinant, Tailfer and Andenne, show a decreasing environmental quality, with a strongly marked impairment in Andenne, below Namur, and confluence with

the polluted Sambre river (4) (2). In each site, a modified light-trap (1) was placed on the steady substructure of the weir. Sampling was carried out from April to October 1987 ; the light-traps operated two hours a day, from one our before to one hour after sunset.

Thirty-four species were caught : 9 Ephemeroptera, 2 Plecoptera and 23 Trichoptera. Larvae of 26 of them had already been found in banks or other accessible places of the Meuse, some having only been identified at the genus level (2) (3). Besides 2 clearly exogeneous Trichoptera species, the other newly recorded species are typical of large rivers and are thus supposed to come from poorly accessible media of the Meuse.

Comparison of the species caught in each site revealed a clear decrease of species richness from Dinant (25 species) and Tailfer (22 species) to Andenne (12 species), also expressed by diversity indices (Shannon-Wever's index respectively 2.18, 1.34 and 0.38). Most species progressively decrease or disappear, whereas the few reputedly tolerant species as *Hydropsyche contubernalis* McLachlan and *Ecnomus tenellus* (Rambur) survive or even develop in Andenne.

These preliminary results tend to indicate a relative efficiency of the method for space and probably also time-spread comparisons. A condition for its practical use as survey method would be a strong reduction of the sampling period. Current researches aim at defining optimal periods and weather conditions for an effective sampling.

MICRORÉPARTITION DE SAUMONS JUVÉNILES INTRODUITS ET DE TRUITES *FARIO* AUTOCHTONES DANS LE SAMSON (BASSIN DE LA MEUSE)

par

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Le saumon atlantique (*Salmo salar* L.), poisson migrateur anadrome, a disparu de Belgique vers les années 1930 suite à la construction d'une série de grands barrages sur la Meuse et à l'accroissement généralisé de la pollution des milieux fluviaux vers cette période.

Dans le cadre du projet de réintroduction du saumon atlantique dans le bassin mosan, des déversements d'œufs, d'alevins et de tacons 0^+ (= saumons dans leur première année de vie) ont eu lieu en 1988 dans plusieurs affluents de la Meuse dont le Samson, rivière calcaire salmonicole de la région namuroise.

Au printemps 1989, la microrépartition des truites (*Salmo trutta trutta* m. *fario* L.) autochtones et des saumons juvéniles introduits a été relevée dans le Samson.

(1) Fontaine, J. (1982) — *Bull. Soc. linn. Lyon*, **51**, 81-89.

(2) Meurisse-Genin, M., A. Reydams-Detollenaere, Ph. Stroot and J. C. Micha (1987) — *Arch. Hydrobiol.*, **109**, 67-88.

(3) Mol, A. W. M. (1987) — *Ent. Ber.*, **47**, 60-64.

(4) Van Craenenbroeck, W. and M. Van den Bos (1983) — RIWA, Amsterdam, 146 pp.

Le secteur de pêche, d'une longueur de ± 800 m et d'une largeur moyenne de 3 à 5 m, formé d'une succession de radiers à écoulement rapide et de zones plus profondes à écoulement plus faible, est situé dans le bois de Gesves, sous couvert forestier.

La technique d'échantillonnage consistait à relever les caractéristiques du microhabitat (hauteur de la colonne d'eau, vitesse de courant à 0,6 fois la hauteur d'eau, la granulométrie du substrat et la plus petite distance par rapport à la berge) chaque fois qu'un Salmonidae appartenant à une des deux espèces avait été capturé par pêche à l'électricité. Le relevé des mesures du microhabitat se faisait généralement à l'endroit où le poisson avait été observé pour la première fois.

Les resultats obtenus plaident en faveur d'une ségrégation spatiale des deux espèces : bien que le nombre de saumons 1^+ capturés était faible ($n = 17$), la différence de microrépartition avec les truitelles de même âge ($n = 156$) a été significative pour le facteur vitesse de courant ($p < 0{,}001$, test de chi-carré) et pour la distance des poissons à la berge ($p < 0{,}01$, test de chi-carré) : les truites occupaient en majorité des microhabitats à proximité des berges et à faible vitesse de courant tandis que les tacons de saumon abondaient dans les zones à courants plus rapides, à substrat grossier (galets ou blocs) et plus éloignées des berges. En ce qui concerne la hauteur de la colonne d'eau, aucune différence interspécifique n'a été observée, mais nous avons constaté une tendance très nette des truites 2^{++} ($n = 115$) à occuper des habitats plus profonds que les truites 1^+ ($n = 160$) et les saumons 1^+ ($n = 17$).

Cependant, la preuve d'un effet de la compétition sur le choix du microhabitat des saumons juvéniles n'a pas été établie jusqu'à présent. Nous ne savons pas si la répartition des tacons de saumons, notamment en ce qui concerne la préférence pour les stations à courant rapide, est la conséquence d'une ségrégation sélective (c.à.d. que les juvéniles des deux espèces occupent d'office des niches écologiques séparées) ou d'une ségrégation interactive (où la microrépartition des tacons serait le produit d'une interaction compétitive avec les truitelles). Cette question fera l'objet de recherches expérimentales dans un avenir prochain.

GRAZING PATTERNS OF *ACARTIA TONSA* ON *CHLAMYDOMONAS* SP.

by

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Both the Coulter Counter and C^{14} method were used to measure the grazing activity of the marine calanoid copepod *Acartia tonsa* on different concentrations of a *Chlamydomonas* sp. culture.

Both methods show that the ingestion rate increases with food concentration until some critical value, at which it seems to begin to decline.

The ingestion rate measured by the C^{14} method increases at a slower rate than that measured by the Coulter Counter method.

In most cases, the ingestion and clearance rates measured by the Coulter Counter method are higher than those measured by the C^{14} method.

Ingestion rate measurements by the C^{14} method only include grazing on labelled living particles whereas ingestion rate measured by the Coulter Counter method includes all particles grazed on.

Compared with the Coulter Counter method, the C^{14} method provides a short term measurement of the grazing rate. This makes it very useful in measuring the precise rhythms of copepods grazing activity, but the C^{14} method does not give any information about size class selectivity. By using C^{14} and Coulter Counter methods together, one can obtain more complete information about the total grazing activity of copepods.

PCBs UPTAKE AND ELIMINATION KINETICS IN FRESHWATER FISH

by

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^{14}C-PCB (Aroclor 1242) was directly (in water) or/and indirectly (in food) administered to freshwater fish (*Lebisles reticulatus*). Low chronic doses were used : 0.27-2.5 ng.ml^{-1} water and 8.5-35.6 ng.g^{-1} food. The uptake and elimination parameters obtained for direct exposure of PCBs are similar to the parameters obtained for direct plus indirect exposure routes ; they differ significantly from the kinetics observed during indirect contamination and elimination experiments. The accumulation equilibrium with direct PCB exposure is rapidly reached (t 1/2 < 0.5 day). A dose-independent bioconcentration factor of ± 4700 was calculated, corresponding to the value predicted for physicochemical partitioning. The accumulation of PCBs during chronic exposure through the food is slower (t 1/2 = 3 days) ; no bioaccumulation was measured. The results indicate that physicochemical partitioning of PCBs between fish lipids and water is the most important mechanism for uptake of PCBs through the water. The elimination of PCBs after exposure through water, food or water plus food includes biologically regulated mechanisms. Part of the PCB load can even remain in the body for a very long period.

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ABSTRACT

Colloquium Malacologie le 20 mai 1989 à l'I.R.S.N.B.

RELATION ENTRE LA VITESSE, LA DURÉE DU DÉPLACEMENT ET LA MORPHOLOGIE PÉDIEUSE CHEZ QUELQUES PULMONÉS STYLOMMATOPHORES

par

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Dans le cadre de ce travail, nous avons mesuré, pour 14 espèces de limaces belges, les vitesses de déplacement. Nous avons pu comparer, pour 7 d'entre elles (*Arion rufus* (LINNAEUS, 1758), *A. distinctus* MABILLE, 1868, *Deroceras reticulatum* (MÜLLER, 1774), *Lehmannia marginata* (MÜLLER, 1774), *Limax cinereoniger* WOLF, 1803, *L. maximus* LINNAEUS, 1758, *Malacolimax tenellus* (MÜLLER, 1774)), les temps qu'elles consacrent à leurs différentes activités. Nous avons également tenté d'établir, pour ces mêmes 7 espèces, les éventuelles relations entre ces résultats et les particularités morphologiques de leur sole pédieuse.

Nous avons pu mettre en évidence que les vitesses de déplacement sont caractéristiques des différentes espèces. Il n'existe toutefois aucune relation entre ces mêmes vitesses et la taille des espèces considérées. Il nous a également été permis d'observer des différences spécifiques pour les diverses activités (déplacement, repos et nutrition). Toutefois, ce ne sont pas nécessairement les espèces les plus rapides qui se déplacent le plus. Par conséquent, la distance maximale susceptible d'être parcourue en une nuit par une espèce donnée peut dépendre autant de la vitesse du déplacement que du temps qu'elle y consacre. Notre étude histologique montre que les 7 espèces examinées possèdent les mêmes mucocytes au niveau de la sole pédieuse. Il n'y a pas de cellule glandulaire qui soit caractéristique des espèces rapides ou lentes. Seules la répartition et la densité de certains types cellulaires varient parfois d'une espèce à l'autre. En ce qui concerne la composition cellulaire de la glande pédieuse, nous avons pu observer des particularités spécifiques touchant la nature des sécrétions. Signalons, néanmoins, que les différents types de cellules décrits dans la glande pédieuse correspondraient, en réalité, à des stades physiologiques différents d'une même cellule (ADAM, 1933 ; CHETAIL et BINOT, 1967). Dans aucun cas, il n'a été possible d'obtenir une relation entre certaines particularités glandulaires de la sole et de la glande pédieuse et les « performances locomotrices » (vitesse et durée). Il est toutefois possible qu'une analyse morphométrique ou une

étude histochimique détaillée permette d'aboutir à un tel résultat. Il est cependant plus probable que les vitesses soient sous la dépendance de différences touchant la musculature, tant au niveau morphologique que physiologique (DENNY, 1981). Les 3 espèces les plus rapides, *D. reticulatum, L. cinereoniger* et *L. maximus,* ont en effet une musculature pédieuse plus développée que les autres.

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CONTENTS

J. DELIGNE : Origin and distribution of the Belgian Journal of Zoology . 117

R. SHERIDAN et E. ROLAND : Etude du comportement précopulateur d'*Arion distinctus* MABILLE, 1868 127

A. ULYEL, F. OLLEVIER, R. CEUSTERS et D. THYS VAN DEN AUDENAERDE : Régime alimentaire des *Haplochromis* (Teleostei : Cichlidae) du lac Kivu en Afrique. I. Relations trophiques interspécifiques 143

S. CORNEILLIE, C. AGIUS and F. OLLEVIER : Comparison of the fatty acid profile of wild caught fingerlings and yolk sac sea bass (*Dicentrarchus labrax*) larvae with cultured healthy larvae and larvae suffering from whirling disease 157

S. ANDRIES and M. NELISSEN : A study of the dominance hierarchy in four Mbuna-species : *Melanochromis johanni, M. auratus, Pseudotropheus « ornatus »* and *P. lombardoi* (Teleostei : Cichlidae) 165

E. NAUMOVA : Morphological and functional consequences of the coevolution of Rodents with gastro-intestinal microbial endosymbionts 195

Short Notes

M. DE MEYER and V. TANASIJTSHUK : A short note on the occurrence of the genus *Cephalops* FALLEN in the U.S.S.R. 205

D. DECLEYRE, P. AERTS and W. VERRAES : On the functional significance of the dorsal part of the Aω muscle in *Pomatoschistus lozanoi* (Teleostei : Gobiidae) 209

Abstracts

Meeting at the K.U.L. on 14 March 1990 : Aquatic Zoology 215

Colloquium Malacologie le 20 mai 1989 à l'I.R.S.N.B. 227

The **BELGIAN JOURNAL OF ZOOLOGY** is covered in **Current Contents** and in **Science Citation Index.**

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