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Four natural cyprinid hybrids recorded from Lake Vansjø, SE Norway[1]

PER PETHON

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An examination of a sub-sample of 356 cyprinid specimens collected in Lake Vansjø, SE Norway in June, Aug. and Oct. 1978 revealed 187 specimens of *Abramis brama* (L.) and 94 specimens of *Blicca bjoerkna* (L.) together with four natural cyprinid hybrids, i.e. *Abramis brama* (L.) x *Blicca bjoerkna* (L.) (n = 67), *Rutilus rutilus* (L.) x *Abramis brama* (L.) (n = 3), *Rutilus rutilus* (L.) x *Blicca bjoerkna* (L.) (n = 1), and *Blicca bjoerkna* (L.) x *Scardinius erythrophthalmus* (L.) (n = 4). The identification of the *Abramis* x *Blicca* hybrid required a five character complex, i.e. rays in anal fin, lateral line scales, pharyngeal teeth, operculum shape, and age/growth pattern, while the other hybrids agreed with previous descriptions. All four hybrids show intermediacy of their parentals, but the range of variation in the *Abramis* x *Blicca* hybrid characters indicates involvement of more than just the F_1 generation and thus suggests hybrid fertility. It is concluded that the cause of hybridization is due to overlap in spawning time in mutually shared spawning areas.

Per Pethon, Zoologisk Museum, Sarsgt. 1, N-Oslo 5, Norway.

INTRODUCTION

Cyprinid hybridization is quite commonly reported in Europe (Spillmann 1961, Berg 1964, Gasowska 1968, Wheeler 1969), and recently several cyprinid hybrids have been recorded and their discriminating features described from the British Isles (Brassington & Ferguson 1976, Wheeler 1976, 1978, Child & Solomon 1977, Wheeler & Easton 1978). In Norway, however, the only cyprinid hybrid recorded has been that between bream *(Abramis brama)* and roach *(Rutilus rutilus)* (Halvorsen 1966, Pethon 1978).

During investigations in Lake Vansjø, SE Norway (Brabrand 1979) difficulties arose in the determination of several cyprinids, especially concerning bream and silver bream *(Blicca bjoerkna)*. A closer examination revealed natural hybrids among four of the cyprinid species present in this lake, roach, bream, silver bream, and rudd *(Scardinius erythrophthalmus)*. The hybrids are briefly described below with particular emphasis on the hybrid between bream and silver bream.

MATERIAL AND METHODS

The material consists of 356 specimens selected from a larger material because of identification problems. It was collected from eight localities in Lake Vansjø (Fig. 1) with gillnets and beach seine on 13—15 June (n = 76), 22—23 August (n = 101), and 10—11 October (n = 179) 1978. The original samples also included a larger num-

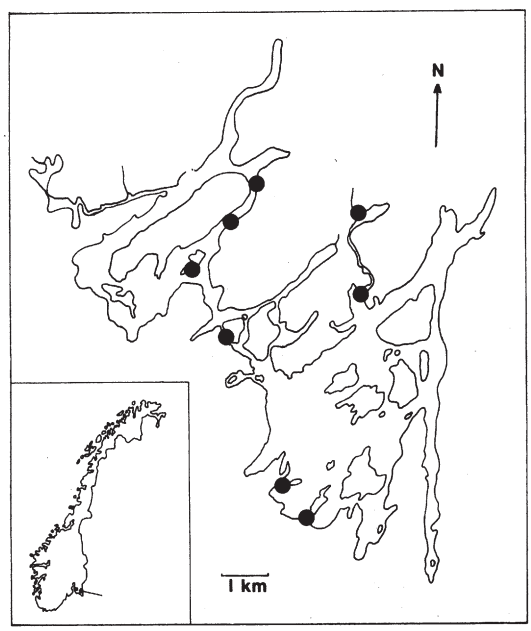

Fig. 1. Map of Lake Vansjø. Sampling localities yielding cyprinid hybrids shown by black dots.

[1]Contribution No. 158 from the Zoological Museum, University of Oslo.

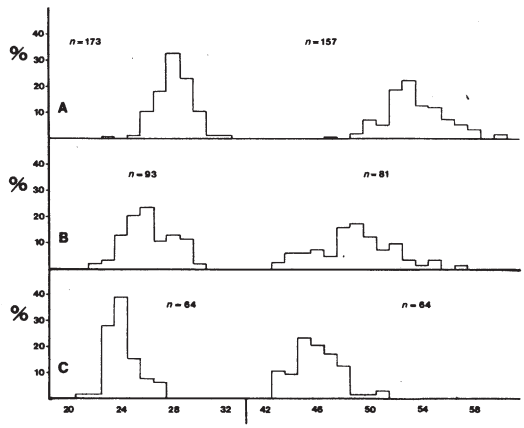

Fig. 2. Frequency distribution (%) of number of rays in anal fin (left side) and scales along lateral line (right side) in bream (A), the hybrid bream x silver bream (B), and silver bream (C).

ber of roach and bleak *(Alburnus alburnus)* together with some rudd. Lake Vansjø is 35.8 km² and situated 25 m a.s.l. in the south-eastern part of Norway. It has two main basins, the larger and deeper Storefjord basin with a maximum depth of c. 40 m and the smaller and shallower Vannemfjord basin with a maximum depth of c. 16 m. The lake is eutrophic and has been increasingly influenced by urban pollution. The phytoplankton bloom is most pronounced in the Vannemfjord basin, where temporary anoxia may occur in the deepest parts in late winter.

Morphometric characters of the fish were recorded according to Lagler et al. (1962), and age and growth determined by opercula according to Hansen (1980). The pharyngeal teeth were removed and rinsed in boiling water before examination. On smaller specimens fin rays were counted from X-rays. An artificial index (R_1/R_2) of opercula shape was utilized in the examination of *Abramis* and *Blicca* specimens. R_1 is the distance of the dorsal edge of the operculum from the joint socket to the posterior corner and R_2 the distance from the joint socket to the posterior ventral corner.

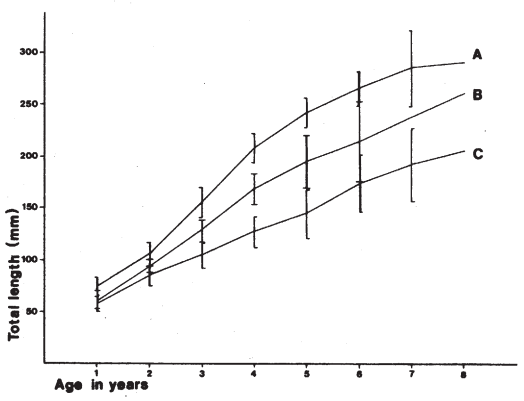

Fig. 3. Back-calculated growth of bream (A), the hybrid bream x silver bream (B), and silver bream (C) drawn to the eighth year. Vertical bars give 95% conf. limits (n > 5).

RESULTS

Bream x silver bream

The main identification problem within the present material concerned the bream, the silver bream and their hybrid. Apparently normal bream and silver bream both showed deviation from their normal character distribution. For the identification of the hybrid a five character complex was required, viz. number of rays in anal fin, number of scales along the lateral line, the pharyngeal teeth formulae, the shape of the operculum, and the age/growth pattern. According to an evaluation based on this character complex 187 specimens were identified as bream, 94 specimens as silver bream, and 67 specimens as their hybrid.

The variation in distribution of number of rays in anal fin and lateral line scales is shown in Fig. 2. Although there is considerable overlap in these two characters between the hybrid and its parentals, the intermediacy of the hybrid is significantly demonstrated for both characters ($P < 0.001$, t-test). Parental intermediacy is also demonstrated by the back-calculated growth of the hybrid (Fig. 3), while the age distribution shows that hybrids were produced in all eight successive years from which material is present (Fig. 4). The examination of opercula also revealed a hybrid difference in the zone formation pattern and the opercula shape. In bream the winter zones were broadly spaced and opercula more rectangular in shape than in silver bream where the winter zones were closer, the posterior ventral corner being markedly obtuse-angled, and the posterior dorsal corner acute-angled. As might be expected from the back-calculated growth, the hybrid was intermediate in zone formation, and also in operculum shape (Fig. 5). The average artificial index R_1/R_2 which expresses the observed differences in shape, was for bream 1.087 (SD = 0.040), for silver bream 1.228 (SD = 0.055), and for the hybrid 1.174 (SD = 0.062), and shows significant

Table 1. Observed distribution (numbers) of pharyngeal teeth phenotypes for bream, bream x silver bream, and silver bream. L-R = left side — right side of the pharyngeal teeth pair.

Pharyngeal teeth formules L-R/L-R	BREAM n = 174	HYBRID n = 92	SILVER BREAM n = 66
3-5/5-3	1 / 2		
4-4	1		
4-5/5-4	6 / 7		
5-5	154	10	
6-6	1		
4.0-1.5		1	
5.0-1.5/5.1-0.5	1 / 1	4 / 6	
5.0-2.5		2	1
2.1-1.4		1	
4.1-1.4			1
4.1-1.5/5.1-1.4		2 / 2	1 / 0
4.1-2.5/5.2-1.4		0 / 1	1 / 0
4.2-2.4		1	
4.2-1.5/5.1-2.4		3 / 0	0 / 1
4.2-2.5/5.2-2.4		0 / 1	1 / 1
4.3-3.5			1
5.1-1.5		37	1
5.1-2.5/5.2-1.5		5 / 5	8 / 5
5.2-2.5		8	43
5.3-2.5		1	
6.1-1.5		1	
6.2-2.5			1
7.1-2.9		1	
Nos. of phenotypes	9	19	13

parental intermediacy for the hybrid ($P < 0.001$, t-test). This suggests that the shape of opercula is one of the useful characters in identification of the bream x silver bream hybrid in Lake Vansjø.

The Lake Vansjø hybrid and its parental species shows a considerable variation in pharyngeal teeth formulae, and 9 different phenotypes were found in bream, 13 in silver bream, and 19 in the hybrid (Tab. 1). With the exception of two specimens, however, the variations of pharyngeal teeth dentition in bream were restricted to the single row pattern, while all silver bream variations were within the double row pattern. In the hybrid the main formula was 5.1—1.5 (39%), and although most variation was within the double row pattern, 10 specimens exhibited the single-row pattern 5—5.

The gonadal cycle of the hybrid agrees with that of the parental species, and they mature at an age of 2—3 years. Mature hybrids from June were spent, indicating spawning.

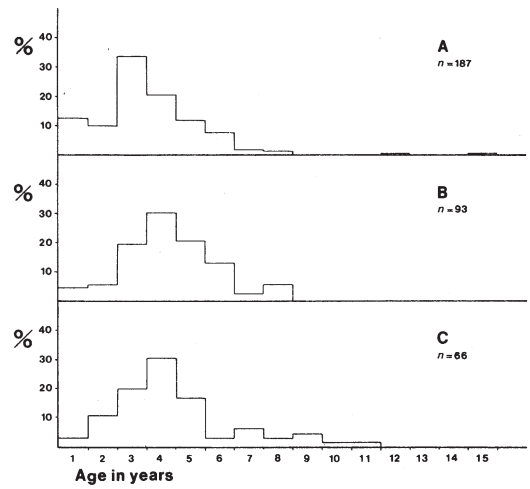

Fig. 4. Age distribution of bream (A), the hybrid bream x silver bream (B), and silver bream (C) in the material present.

Roach x bream

Three specimens were present in the material, of which some data are given in Tab. 2. The specimens agree with those from Lake Øyeren (Pethon 1978), and were intermediate between the parental species. The gonads were normally developed.

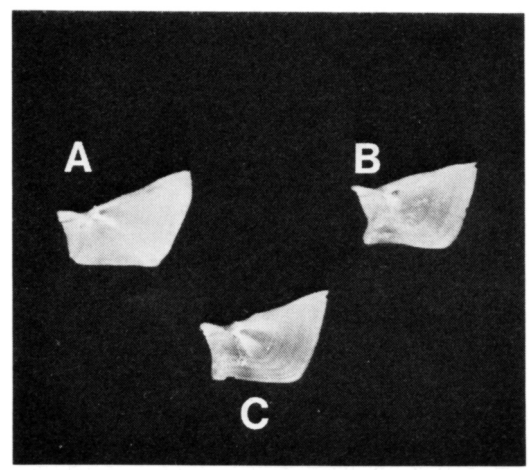

Fig. 5. Operculum of silver bream (A), bream (B) and the hybrid bream x silver bream (C). Note the difference in general shape.

Table 2. Specimen data of three cyprinid hybrids from Lake Vansjø 1978.
A = rays in anal fin, P.t. = pharyngeal teeth formula, T = total length, S = standard length, + = teeth pectinated.

Hybrid	Month	Sex	Gonads	Length (mm)	Age	A	Lin.lat.	P.t.
Roach x bream	June	♂	Immature	189 (T)	5	III 13	50	5-5
—«—	Aug.	♀	Immature	175 (T)	3+	III 16	49	5-5
—«—	Oct.	♂	Developing	180 (S)	4+	III 17	50	5-5
Roach x silv.bream	Aug.	♀	Developing	258 (T)	9+	III 16	47	5-5
Rudd x silv.bream	June	♀	Spent	245 (T)	5+	III 16	43	5.3-3.5+
—«—	Oct.	♂	Developing	122 (S)	5+	III 16	46	5.2-3.6+
—«—	Oct.	♀	Developing	122 (S)	5+	III 14	41	5.2-1.4+
—«—	Oct.	♂	Developing	139 (S)	6+	III 15	43	5.3-3.5+

Roach x silver bream

One female with developing gonads was present in the material (Tab. 2). The meristic characters A = III 16, D = III 10, Lin.lat. = 47, and the pharyngeal teeth formula 5—5 with smooth teeth fit both the hybrid of roach x bream, and of roach x silver bream (Spillmann 1961, Berg 1964, Wheeler 1969). Compared to roach x bream hybrids from Lake Øyeren in the collections of the Zoological Museum, Oslo however, this specimen differed in regard to its larger eye size (i.e. eye far larger than snout), and the shape of the operculum (i.e. corresponding to that of silver bream).

Rudd x silver bream

Four specimens of this hybrid were present in the material (Tab. 2). They agreed with previous descriptions (Berg 1964, Wheeler 1969), i.e. silvery body with red coloured anal, pectoral and pelvic fins, oblique mouth position, large eyes (i.e. about 1/3 of head length), pectinated pharyngeal teeth in two rows, and number of rays in anal fin (i.e. III 12—17). The gonads were normally developed, and the female specimen taken 14 June was spent, suggesting hybrid spawning.

DISCUSSION

Most reports of cyprinid hybrids concern only few specimens, and reports of high numbers of hybrids such as that reported by Kennedy & Fitzmaurice (1973), Wheeler (1976) and Pethon (1978) are rare in the literature. The few recorded specimens of the hybrids of roach x bream, roach x silver bream, and rudd x silver bream in Lake Vansjø may suggest that these hybrids are an accidental situation in this lake. Observations of roach x bream hybrids, and rudd x silver bream hybrids are commonly reported from Europe, while roach x silver bream hybrids are considered rare (Wheeler 1969). In Norway only the roach x bream hybrid is previously known (Halvorsen 1966, Pethon 1978). According to the present material the hybrid between bream and silver bream, on the other hand, is fairly abundant in Lake Vansjø, and hybridization an annual event. This hybrid is reported as uncommon in Europe, and is not known to occur in the British Isles (Wheeler 1969, Wheeler & Easton 1978).

According to Hubbs (1955) it is an almost universally valid rule that natural interspecific hybrids are intermediate between their parental species. This is in accordance with previous descriptions of European cyprinid hybrids (Gasowska 1968, Wheeler 1969, Pethon 1978) and with that found for the four Lake Vansjø cyprinid hybrids.

Although introgressive hybridization among some fish species is known, sterility is a frequent feature of natural interspecific hybrids (Hubbs 1955). In the roach x bream hybrid gonads mature and the fish participate in spawning, but nevertheless sterility has been suggested (Pepin et al. 1970, Child & Solomon 1977, Pethon 1978). However, Wheeler (1969) states that fertile offspring of roach x bream, and roach x rudd are common, and may in isolated waters give rise to introgressed populations. Recent investigations concerning the roach x rudd hybrid support this statement on the basis of morphometric analysis (Wheeler 1976). The discriminant characters gi-

ven for the Lake Vansjø hybrid between bream and silver bream in general confirm the parental intermediacy, but their considerable variation range and overlap with parental characters may be due to more generations than solely F_1. Since the main pharyngeal teeth formula for *Abramis* is 5—5, and for *Blicca* 5.2.—2.5, the expected hybrid formula should be 5.1—1.5 for the F_1 generation. Thus the particularly large number of pharyngeal teeth phenotypes observed both in hybrid and silver bream may indicate a backcrossing of F_1 hybrids with the silver bream. Some parentals also show deviations from the usual range of rays in anal fin and lateral line scales (Spillmann 1961, Berg 1964, Wheeler 1969), which may be interpreted as a remote introgression. Although the results presented seem to indicate fertility of this hybrid, only biochemical investigations like those of Brassington & Ferguson (1976) and Child & Solomon (1977) would really prove this indication.

In natural fish populations spatial niche distributions rarely overlap due to environmental adjustments and competition between coexisting species, thus preventing species introgression. According to Hubbs (1955), however, the incidence of hybridization is increased if natural spawning areas are very limited, forcing spawning fish into close proximity. A similar situation also may arise when a small number of one species coexist with a large number of another related species, especially if the scarce species has been introduced. This latter situation is, according to Wheeler (1976), the main cause for the frequent cyprinid hybridization in the British Isles in addition to man-made environmental changes reducing spawning areas.

All fish species in Lake Vansjø are of natural origin, the earliest immigration taking place about 4500—4000 years B.P. according to the shoreline displacement curves given by Sørensen (1978) and Henningsmoen (1979). Man-made environmental impact on the lake limiting spawning areas is minor, although increasing eutrophication due to urban pollutants has occurred. Therefore, environmental changes with respect to limitation of spawning areas, or introduction of species cannot account for the observed cyprinid hybridization.

The littoral areas with submerged vegetation are the main spawning habitat for roach, bream, silver bream and rudd in Lake Vansjø, but only to a lesser extent for bleak which largely spawns on stony littoral areas. The spawning of roach takes place from late May to early June, of bream and silver bream in June, and of rudd in late June, while the long intermittent spawning periods of bleak are from early June to early July. Thus the spawning period for roach overlaps with that of bream and silver bream but scarcely with that of rudd, while bream and silver bream overlap with rudd. Bleak spawning occurs over the same period as all the other four cyprinids, but bleak share the spawning areas of the others only to some extent. The spawning sequence, therefore, explains the observed frequent hybridization between bream and silver bream, and the less frequent hybridization between the other species. Hybrids between roach and rudd, which elsewhere seem to be common, are unlikely to occur in Lake Vansjø due to differentiation in spawning time, as is also hybridization between bleak and the other cyprinids due to differences in spawning areas.

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