Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **50**, p. 97–108, May 1998
Biology and Management of Coregonid Fishes – 1996

Comparison of normal and dwarf populations of lake whitefish *(Coregonus clupeaformis)* with reference to hydroelectric reservoirs in northern Quebec

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with 6 figures and 1 table

Abstract: The effect of impoundment on the dynamics of sympatric dwarf and normal lake whitefish was studied by comparing biological characteristics of both forms in Caniapiscau Reservoir (Northern Quebec), in a natural lake from the same region, Sérigny Lake, and in an allopatric normal whitefish population (Hazeur Lake). The length distribution of mature specimens was bimodal in Caniapiscau Reservoir and Sérigny Lake, but unimodal in Hazeur Lake. Compared to normal specimens, dwarf whitefish mature at an earlier age (2–3 y vs 6–7 y) and show significantly smaller mean back-calculated total lengths starting at age 2. Chironomid and trichopteran pupae and/or planktonic crustaceans (mostly cladocerans) were the main food items of dwarf individuals from Caniapiscau Reservoir and Sérigny Lake, and of normal individuals < 250 mm from the 3 waterbodies. Varius items of vegetation (reservoir) and benthic taxa (natural lakes) were dominant in the diet or normal individuals > 250 mm. Before flooding, normal whitefish outnumbered dwarfs by a factor of 6 in natural lakes impounded to create Caniapiscau Reservoir. In 1991, 9 years following impoundment, dwarf individuals were slightly more abundant in the catches, due to an increase in their catches-per-unit-of-effort and a simultaneous decrease of normal individuals. After 1991, the relative abundance of both forms gradually returned to pre-impoundment values. The length structure of mature lake whitefish in 4 northern Quebec regions suggests that the occurrence of the dwarf form is related to the absence or scarcity of cisco *(Coregonus artedi)*.

Introduction

The sympatric occurrence of normal and dwarf lake whitefish *(Coregonus clupeaformis)* is relatively common in natural lakes and reservoirs in northern Quebec (GENDRON 1988, FORTIN & GENDRON 1990, DOYON 1995a) and on the south shore of the St-Lawrence River (CHOUINARD et al. 1996), but relatively rare elsewhere in North America (see BODALY et al. 1991). Earlier studies on this phenomenon focused mainly on differentiating the two forms using genetic, morphological, and population dynamics characteristics (FENDERSON 1964, FORTIN & GENDRON 1990, BODALY et al. 1991, VUORINEN et al. 1993, and others). The origin of this differentiation has been discussed at length in several of these studies. One question which has drawn little attention concerns the factors responsible for the variations in relative abundance of the two forms in lakes and reservoirs. BRUCE (1984) hypothesized that dwarf lake whitefish in Smallwood Reservoir may have been favored by increased zooplankton production which generally occurs in the first years after flooding. However, no study has yet tested this hypothesis by examining the impact of reservoir impoundment on the temporal evolution of population dynamics of dwarf and normal lake whitefish.

The objectives of this study were to compare the 1993 population characteristics of dwarf and normal lake whitefish in Caniapiscau Reservoir (Caniapiscau Reservoir; northern Quebec; Fig. 1) and in nearby reference natural lakes, and to describe changes in the relative abundance of the two forms following the impoundment of Caniapiscau Reservoir in 1982.

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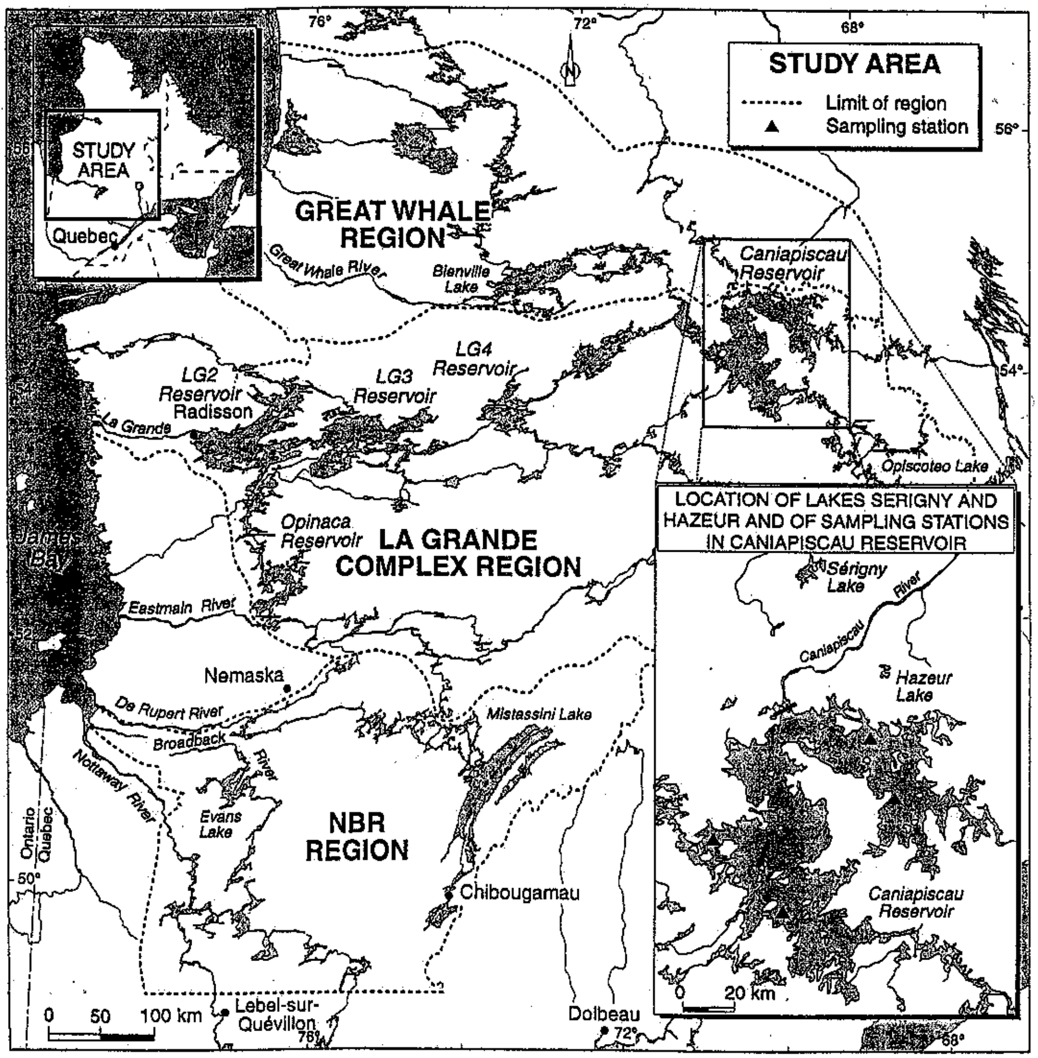


Fig. 1. Map of the study area showing major sampling regions and Caniapiscau Reservoir, Sérigny and Hazeur Lakes. **NBR:** Nottaway-Broadback-Rupert.

Materials and methods

Filling of Caniapiscau Reservoir, which is the largest reservoir in "La Grande Complex" (Fig. 1; 4275 km^2), occurred between October 1981 and September 1984. Sérigny Lake (Sérigny Lake; Fig. 1) and Hazeur Lake (Hazeur Lake, Fig. 1) have areas of 47, 5 km^2 and 5,7 km^2, respectively. The three bodies of water are acid (pH 5,9–6,4), weakly conductive (9–13 µS), and relatively clear (Secchi disk readings: 2–4 m). Surveys show the two natural lakes to be dominated by lake whitefish, longnose sucker (*Catostomus catostomus*), and lake trout (*Salvelinus namaycush*) (Doyon et al. 1995a). The same species dominated catches in lakes impounded to create Caniapiscau Reservoir. However, northern pike (*Esox lucius*) relative abundance increased after filling of Caniapiscau Reservoir, peaked in 1987, and decreased to pre-impoundment levels thereafter. The relative abundance of lake trout has been decreasing in Caniapiscau Reservoir since 1981 (DesLandes et al. 1995).

Biological characteristics of sympatric normal and dwarf lake whitefish were compared in Caniapiscau Reservoir and Sérigny Lake, and in the normal population from Hazeur Lake. Specimens were sampled during the 1993 campaign of the James Bay Phase I Environmental Monitoring Network. From 1981 to 1993, 4 stations in Caniapiscau Reservoir, 1 in Sérigny Lake, and 1 in Hazeur Lake were sampled 4 times between June 30 and September 21, with 2 pairs of nets set for 24 h (1 experimental gill net, 6 pannels, stretched meshes varying from 25 to 102 mm, and a uniform 76 mm or 102 mm stretched mesh net; all nets were 45,7 m long x 2,4 m high). In 1995, sampling was conducted at the 4 stations in July and August only, with 4 pairs of nets.

Specimens were measured (total length, ±0,5 mm), weighed (Large specimens: ±10 g; small specimens: ±0,1 g), and dissected to determine sexual maturity, collect stomach contents, and otoliths. Individuals showing NIKOLSKY (1963) maturity stage III before September 1, or a higher maturity stage for any month, were considered mature. Otoliths were used for age determination and back-calculation of total lengths at annulus formation.

Diet was quantified from the volume of the various prey taxa in the stomach contents. Volumes were measured to the nearest 0,1 ml by liquid displacement (70 % ethanol) in graduated cylinders. Organisms were generally identified to the genus level, but data were pooled to higher categories for presentation. The mean diet (% volume) was computed from the individual percentage composition of the stomach contents of all dwarf individuals from a given site. For normal individuals, mean diet was computed for three size-classes (< 250 mm; 250–350 mm; > 350 mm).

Changes in relative abundance of dwarf and normal lake whitefish following the impoundment of Caniapiscau Reservoir were determined from the length composition and catches-per-unit-of-effort (CPUE; number of specimens per net-day) of mature specimens in experimental catches conducted in 1980 and 1981 (pre-impoundment), 1982 (first year of filling), 1991, 1993, and 1995 (9, 11, and 13 years after impoundment).

The possibility of sympatric occurrence of dwarf lake whitefish and cisco *(Coregonus artedi)* was verified by comparing the length composition of mature whitefish between regions in northern Quebec where the cisco is abundant and others where it is rare or absent.

Results

The length frequency distribution of mature lake whitefish captured in 1993 in Caniapiscau Reservoir (n=426) showed a first mode at ca. 200 mm (age range of dwarf individuals: 2–9 y; mean: 5.5 y), and a second one at ca. 480 mm (age range of normal individuals: 6–19 y; mean: 10 y) (Fig. 2). A similar distribution occurred in Sérigny Lake (n=81), where a first mode was located at 180 mm (age range of dwarfs: 3–8 y; mean: 5 y), and a second one at 520 mm (age range of normal individuals: 7–34 y; mean: 15 y). Hazeur Lake showed a single major mode (normal individuals) at ca. 490–520 mm (age range: 6–32 y; mean: 13,5 y). Dwarfs mature at ages 2 and 3, respectively, in Caniapiscau Reservoir and in Sérigny Lake and normal individuals at ages 6 (Caniapiscau Reservoir and Hazeur Lake) and 7 (Sérigny Lake).

In Caniapiscau Reservoir and Sérigny Lake, dwarfs showed mean back-calculated lengths significantly smaller ($P < 0,05$, Student-Neuman-Keuls tests; Table 1) than normal individuals at all ages tested (1–8 or 9 y) except age 1 in SR. Dwarf and normal individuals aged 3 years or less were significantly longer at a given age in Sérigny Lake than in Caniapiscau Reservoir (Table 1). No significant differences were observed between Sérigny Lake and Caniapiscau Reservoir beyond age 3. Mean back-calculated length of normal individuals were significantly smaller in Hazeur Lake than in Sérigny Lake and Caniapiscau Reservoir (Table 1).

In Caniapiscau Reservoir, the main prey items of dwarf lake whitefish were chironomid and trichopteran pupae (38,4 % volume) and planktonic crustaceans (29,7 %; mostly cladocerans;

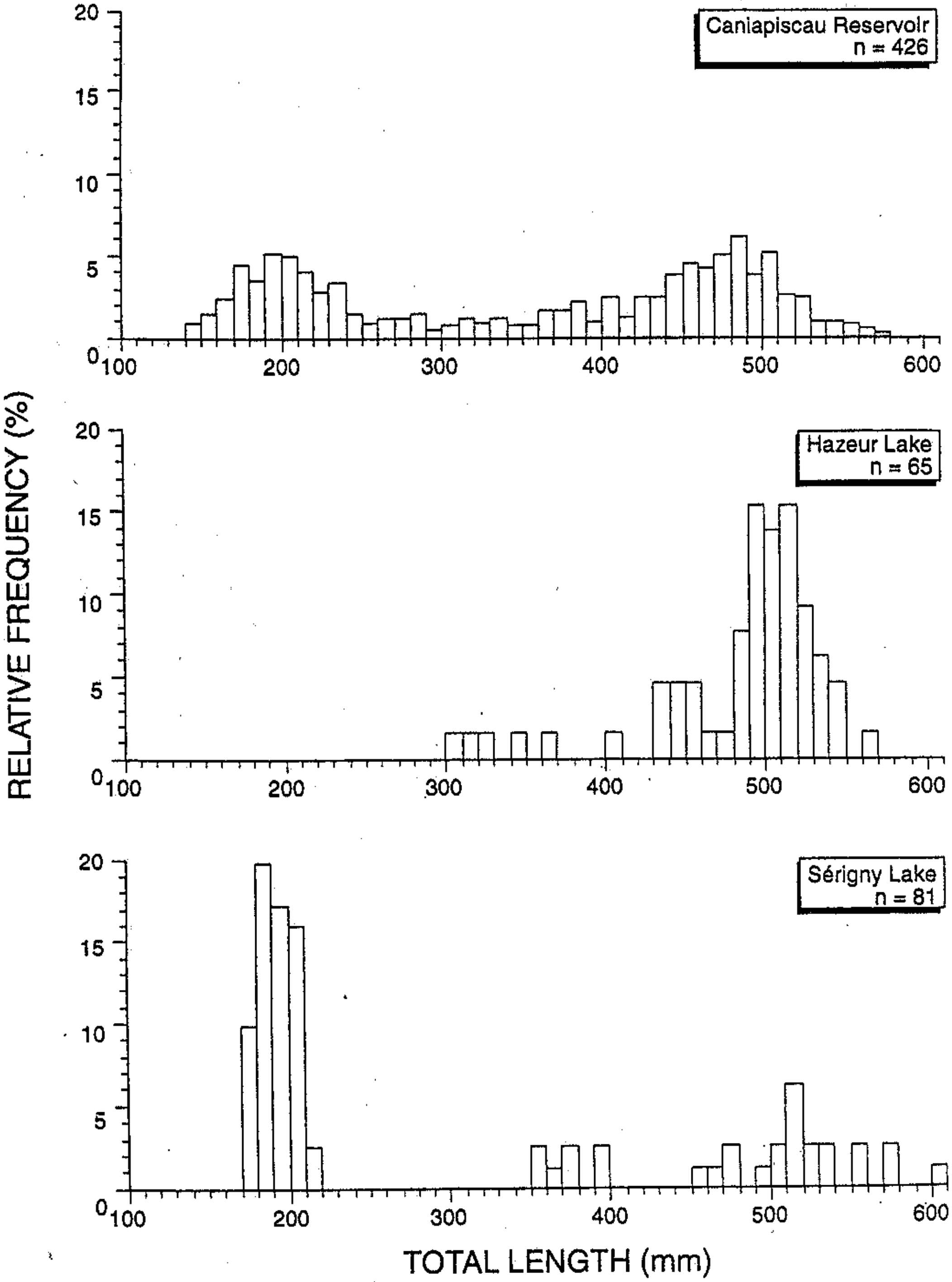


Fig. 2. Percentage composition in length of mature lake whitefish captured in Caniapiscau Reservoir, Sérigny and Hazeur Lakes in 1993.

Fig. 3). Comparatively, the main prey items of < 250 mm normal whitefish were planktonic crustaceans (61,7 %; cladocerans), chironomid and trichopteran pupae (26,1%), and vegetation (plant remains, 11 %; Fig. 3). The volume of planktonic crustaceans decreased with increasing

Table 1. Mean back-calculated total length (BL, mm) vs age of dwarf and normal lake whitefish from Caniapiscau Reservoir and Lakes Sérigny and Hazeur in 1993 (**n:** sample size, **s:** standard deviation; **SNK:** results of Student-Neuman-Keuls tests comparing dwarf and normal forms from the 3 lakes; different letters indicate significant differences between means (P < 0,05)).

	CANIAPISCAU RESERVOIR								SÉRIGNY LAKE								HAZEUR LAKE			
	Dwarf				Normal				Dwarf				Normal				Normal			
Age	n	BL	s	SNK	n	BL	s	SNK	n	BL	s	SNK	n	BL	s	SNK	n	BL	s	SNK
1	59	76	8,5	c	63	85	14,8	b	33	117	5,8	a	28	118	14,7	a	36	76	10,7	c
2	59	121	14,8	e	63	162	25,7	b	33	146	9,0	c	28	188	16,2	a	36	135	17,8	d
3	59	150	17,9	e	63	216	36,5	b	33	166	10,6	d	28	230	22,6	a	32	184	26,1	c
4	51	171	21,3	c	60	260	41,8	q	27	179	11,3	c	26	264	23,3	a	27	227	27,7	b
5	39	190	21,9	c	56	301	43,5	a	18	188	12,2	c	23	300	27,2	a	23	266	26,9	b
6	28	203	20,8	c	50	340	48,9	a	11	195	10,6	c	21	328	29,2	a	18	299	31,1	b
7	16	217	21,8	c	40	379	53,9	a	5	206	7,8	c	16	354	31,5	ab	15	329	33,5	b
8	7	229	25,6	b	33	408	58,6	a	1	208	–	b	13	372	36,7	a	11	352	43,4	a
9	1	261	–	b	19	443	61,0	a	–	–	–	–	9	394	49,4	a	6	367	53,1	a

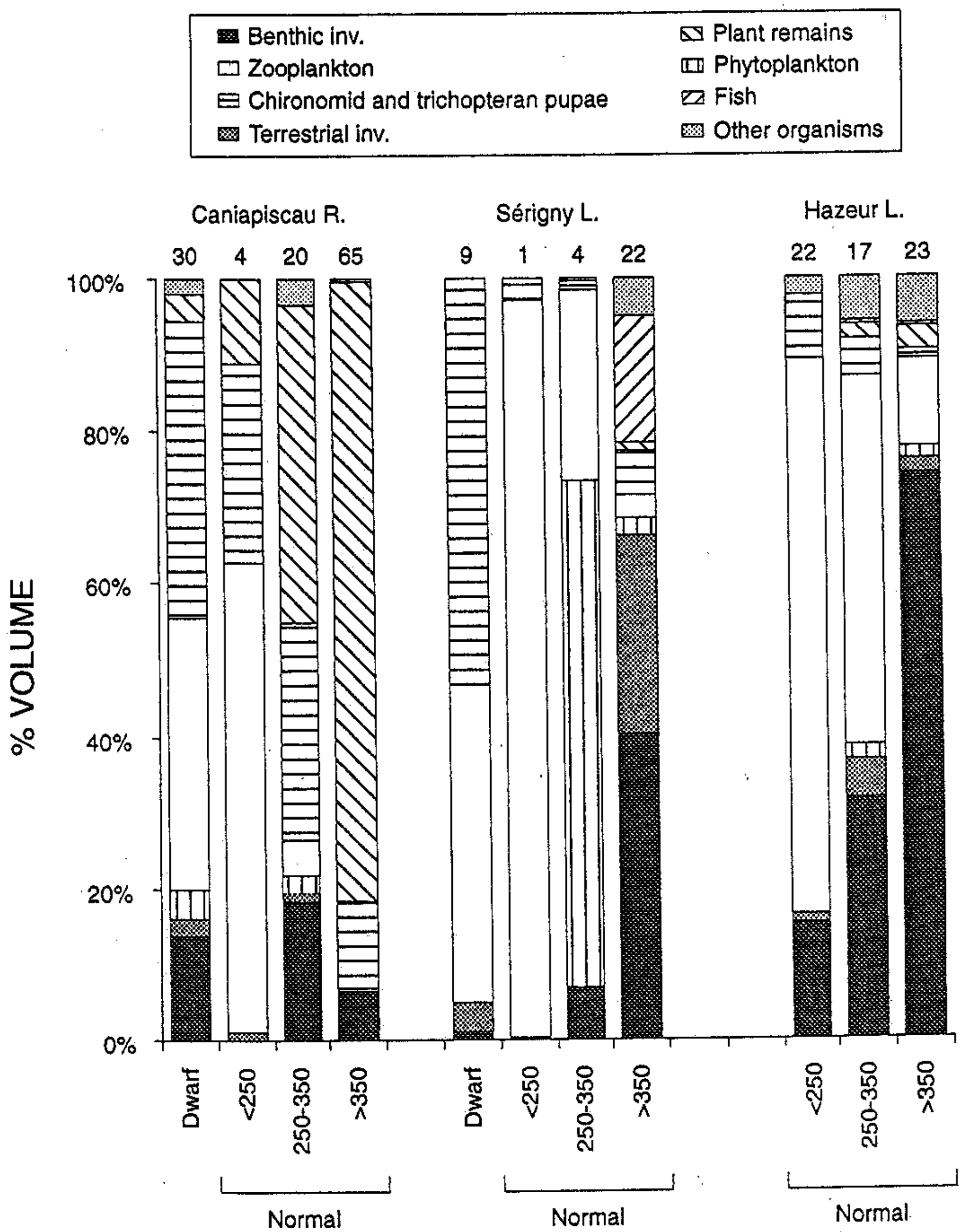


Fig. 3. Percentage composition in volume of the diet of dwarf (Dw) and three size-classes of normal whitefish (< 250 mm, 250–350 mm, > 350 mm). Sample size is given above each column.

length in the diet of normal whitefish in Caniapiscau Reservoir, while that of vegetation increased, reaching 81,5 % in > 350 mm individuals (Fig. 3). As was the case in Caniapiscau Reservoir, chironomid and trichopteran pupae (46,4 %) and planktonic crustaceans (41,7 %; cladocerans) were the major prey items of Sérigny Lake dwarf fish, while benthic taxa (40,4 %; mostly trichopterans, ephemeropterans, and bivalves), terrestrial invertebrates (26 %; mostly hymenopterans), and fish (16,4 %) were the 3 major items of the diet of > 350 mm normal individuals (Fig. 3). Planktonic crustaceans were progressively replaced by benthic taxa (mostly ephemeropterans, trichopterans, and bivalves) as the size of Hazeur Lake normal individuals increased (Fig. 3).

Before impoundment (1980–1981) and during the first year of filling (1982), the proportion of dwarf fish in the total whitefish catches varied between 9,6–12,2 % (Fig. 4 and 5), and CPUE between 0,6–1,3 specimen/net-day (Figure 5), which is 6 times lower than corresponding values for normal individuals (67,4–72,1 %; 3,6–9,3 specimens/net-day). Total CPUE in 1987 was the lowest recorded for the series. Unfortunately, the absence of data on maturity precluded the determination of the relative abundance of each form. In 1991, 9 years after impoundment, the situation was reversed, the proportion and CPUE of dwarfs having increased by a factor of ca. 3,5 from 1980–81 figures (32,7 %, 4,4 specimens/net-day; Fig. 4 and 5), and those of normal specimens having decreased by a factor of ca. 2 (29,8 % and 4,0 specimens/net-day). Dwarfs were slightly more abundant in the catches at this point. However, the proportion and CPUE of unclassified specimens reached 37,6 % and 5 specimens/net-day in 1991. The proportion and CPUE of dwarfs decreased in 1993 and 1995, as corresponding data for normal individuals increased (Fig. 4 and 5). The two groups seem to be gradually returning to pre-impoundment values.

Both the eastern part of the La Grande region, where the cisco is not present, and the Great Whale region, where the cisco is rare, show mature whitefish length distributions with a definite mode in the dwarf size-classes (Fig. 6). In the western part of the La Grande and Nottaway-Broadback-Rupert regions, where the cisco is abundant, the length structure includes almost exclusively normal individuals, although dwarf-sized mature specimens may be present.

Discussion

DESLANDES et al. (1993) were the first to mention the presence of dwarf lake whitefish in Caniapiscau Reservoir. From a practical standpoint, taking into account the presence of dwarfs and has become an important issue in the interpretation of monitoring data on growth, population dynamics, and mercury accumulation by lake whitefish in reservoirs. DOYON (1995b), DOYON et al. (1997) has shown that dwarfs accumulate mercury at a much faster rate in relation with age and size than normal individuals in Caniapiscau Reservoir and Sérigny Lake. Thus, changes in proportions of the two forms with time in a reservoir can greatly modify the interpretation of general trends in growth and mercury contamination if the two forms are not considered separately in the analyses.

From a more fundamental standpoint, the comparison of the various biological characteristics observed in this study has shown that the level of differentiation of dwarf and normal lake whitefish is quite similar in Caniapiscau Reservoir and Sérigny Lake. The fact that dwarfs mature 4 years earlier than normal individuals probably explains the major differences in growth of the two forms in Caniapiscau Reservoir and Sérigny Lake. The lower mean lengths at younger ages of both forms in Caniapiscau Reservoir vs Sérigny Lake, and higher mean lengths at older ages in Caniapiscau Reservoir vs Sérigny Lake, are probably due to increased growth rates following the impoundment of Caniapiscau Reservoir (DESLANDES et al. 1995).

A recent gene diversity analysis of microsatellite loci revealed highly significant differences in allele frequency distribution between dwarf and normal fish from Caniapiscau Reservoir and Sérigny Lake (BERNATCHEZ 1996). GENDRON (1994) has shown that sympatric dwarf and normal individuals from Caniapiscau Reservoir are also distinct morphologically. Among other characters, gill-raker count differed significantly between normal and dwarf individuals (28,6 vs 24,6 respectively). These findings are consistent with other studies of sympatric pairs of lake whitefish (BODALY et al. 1991, VUORINEN et al. 1993).

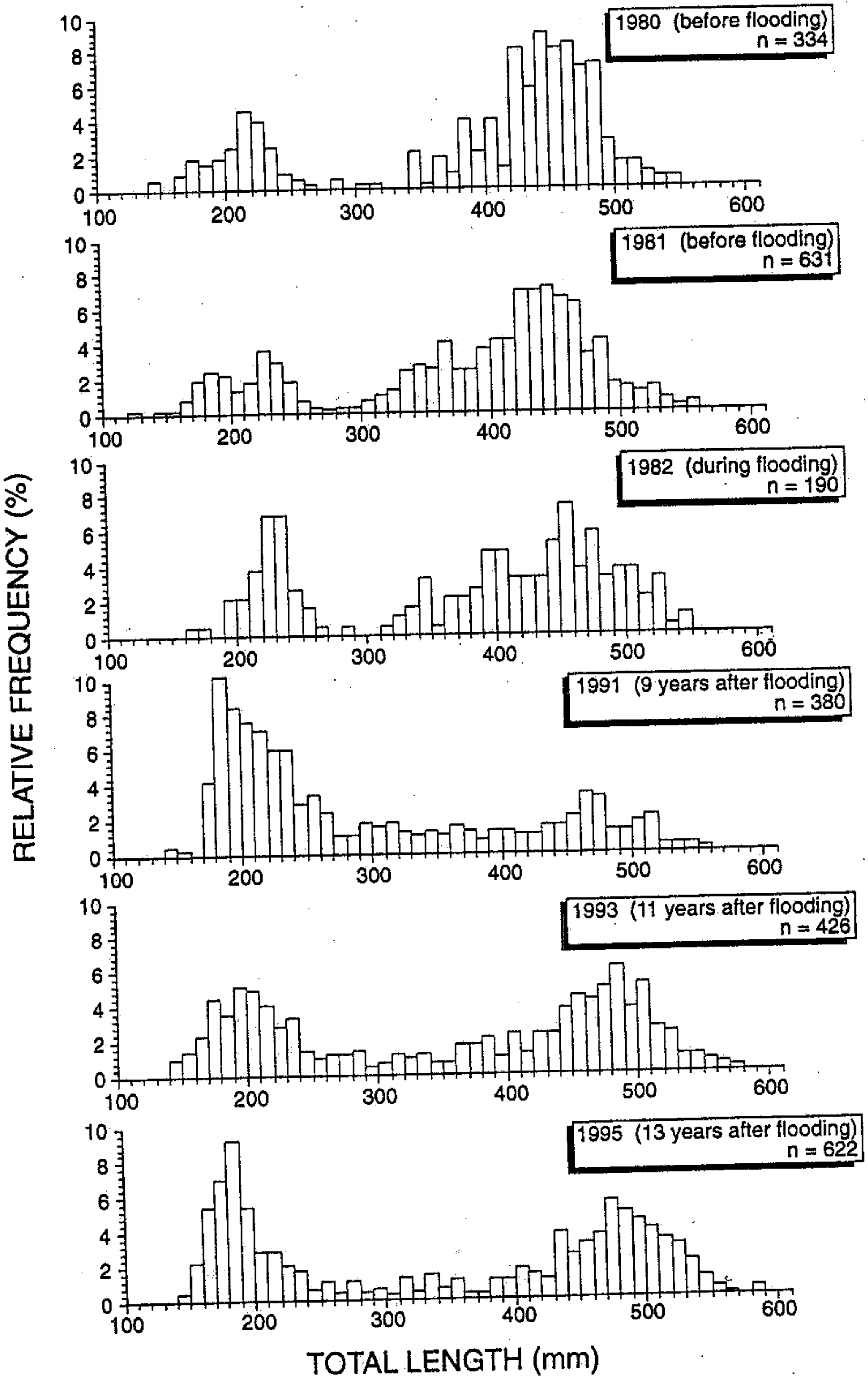


Fig. 4. Length structure of mature lake whitefish in Caniapiscau Reservoir from 1980 to 1995.

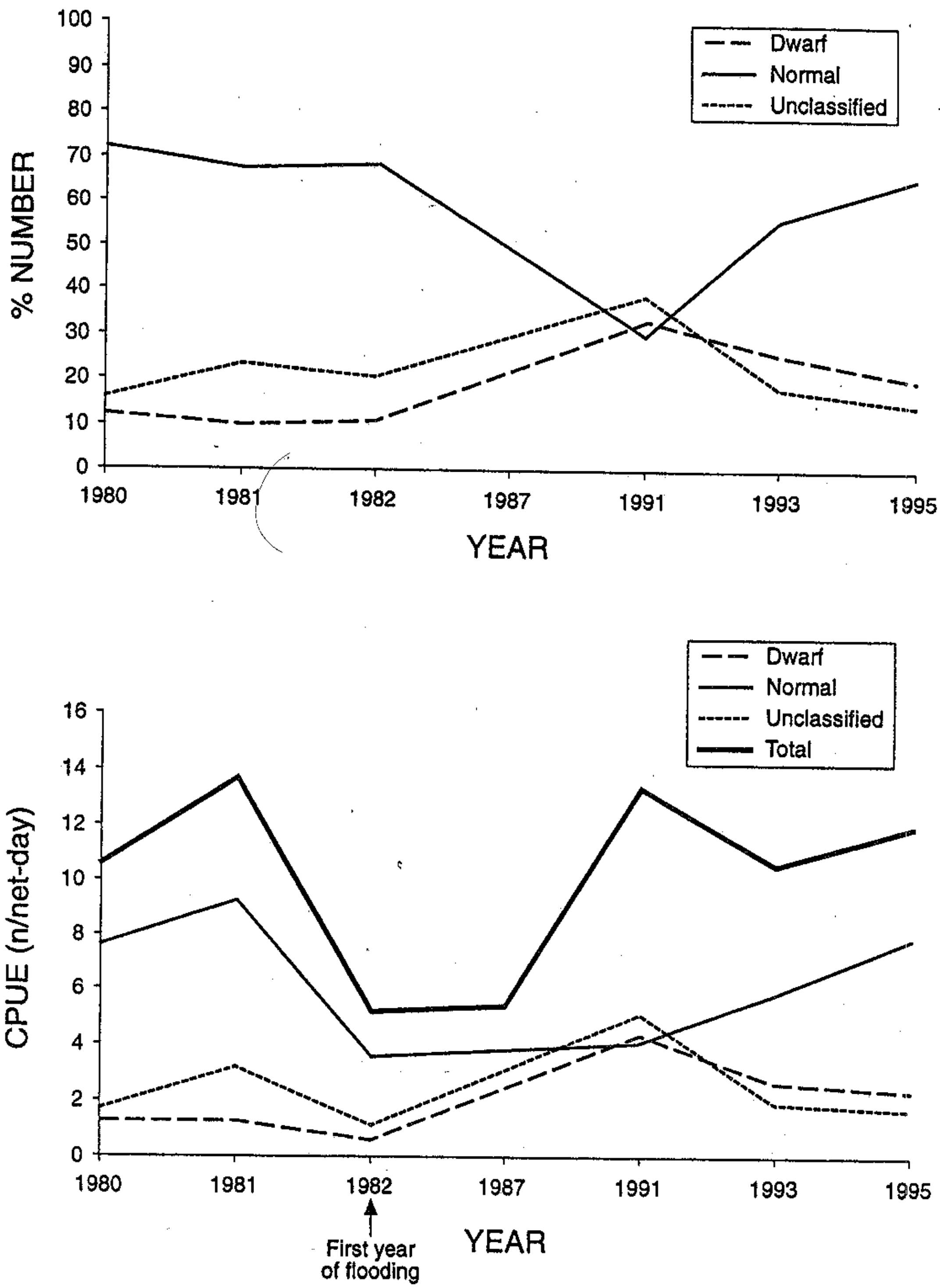


Fig. 5. Changes in percentage contribution in numbers and catches-per-unit-of-effort (CPUE) of dwarf, normal, and unclassified lake whitefish in Caniapiscau Reservoir from 1980 to 1995.

In 1993, chironomid and trichopteran pupae and/or planktonic crustaceans (mostly cladocerans) were the major items in the diet of dwarf and < 250 mm normal individuals from

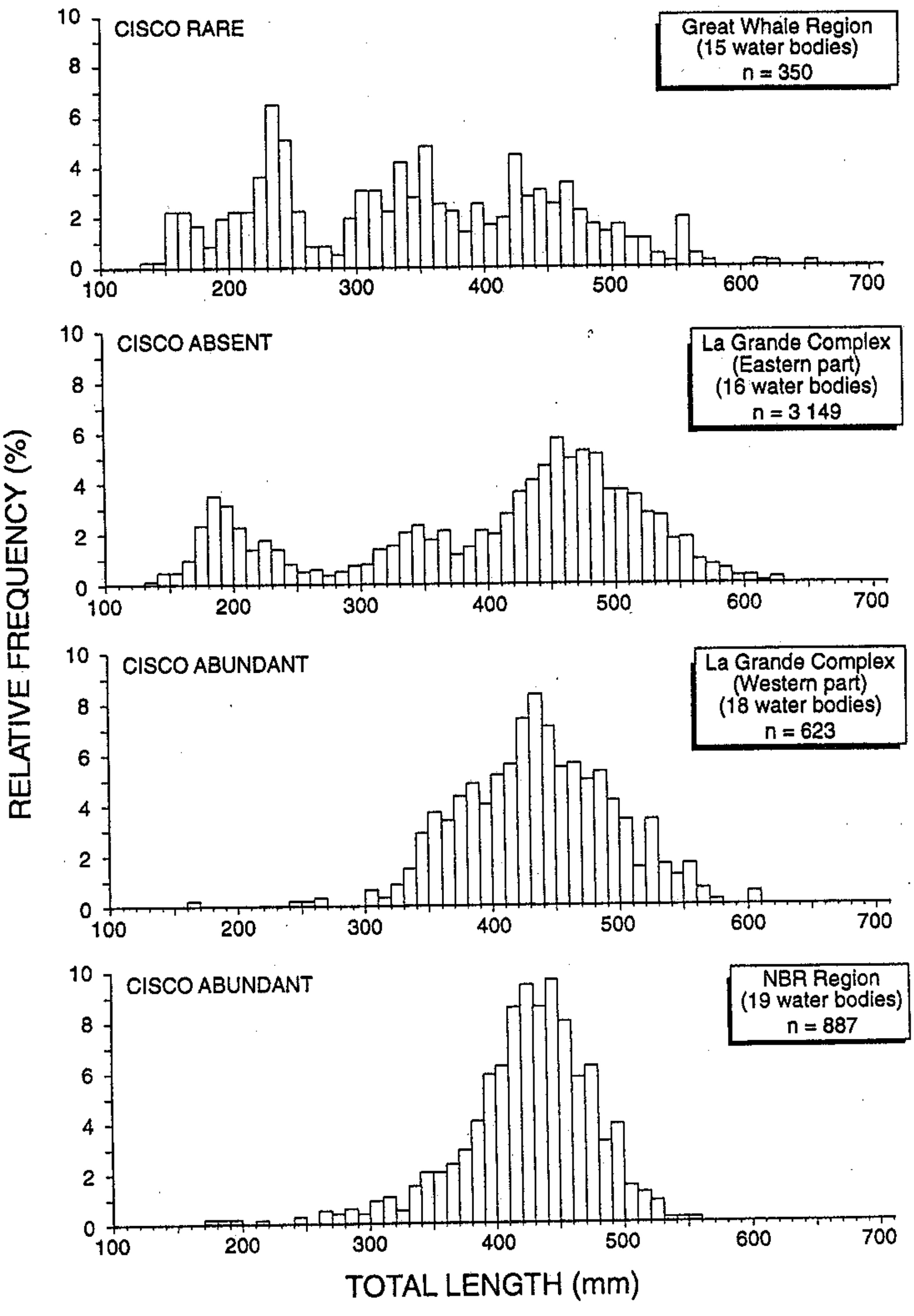
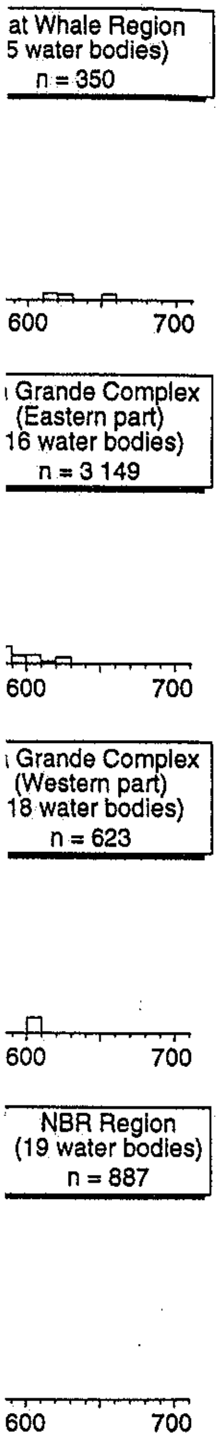


Fig. 6. Length structure of mature lake whitefish in the Great Whale region, in the eastern and western parts of the La Grande hydroelectric complex region, and in the Nottaway-Broadback-Rupert (NBR) region.



tern and western parts
)ert (NBR) region.

Caniapiscau Reservoir and Sérigny Lake, and of < 250 mm normal individuals from Hazeur Lake, suggesting that they feed in the water column. Comparatively, larger-sized normal individuals from Caniapiscau Reservoir, Sérigny Lake, and Hazeur Lake fed more on the bottom, using various benthic taxa, terrestrial invertebrates, and vegetation remains.

Trends in percentage composition and CPUE of normal and dwarf lake whitefish over time in Caniapiscau Reservoir suggest that, during the first years, dwarfs may have taken greater advantage of the general abiotic and biotic changes accompanying impoundment: nutrient enrichment brought about by the decomposition of organic matter, temporary increase in zooplankton biomass, etc.; see CHARTRAND et al. (1994), SCHETAGNE (1994), and DESLANDES et al. (1995) for the particular case of Caniapiscau Reservoir. This general interpretation, which was first suggested by BRUCE (1984), needs to be examined more critically for Caniapiscau Reservoir. Growth rates of normal whitefish increased after impoundment (DESLANDES et al. 1995), which suggests that they also benefited from the increased production.

An alternative interpretation to the increased relative abundance of dwarf individuals in 1991, while normal individuals had decreased, could be the former's earlier maturity and higher relative fecundity (GENDRON 1988, FORTIN & GENDRON 1990) and the fact that they devote a much higher proportion of their energy to gamete production than to somatic growth. On the r-K continuum, the dwarf life history strategy would be more r-selected than that of normal individuals. This could temporarily favor dwarf individuals who may increase their numbers more rapidly after the sudden expansion of available habitat which followed impoundment. The advantage of the dwarf life cycle strategy would be of short duration, since a trend towards restoration of natural conditions was evident in the later part of the series. A working hypothesis for future studies would be that differences in life history strategies, rather than in feeding habits, may lead to differential responses to the impoundment process, and explain shifts in dominance of the two forms.

The fact that in northern Quebec dwarf whitefish seem to occur only in water bodies where cisco are rare or absent, suggests a competitive superiority of the latter species over this form of whitefish. BODALY et al. (1988) have also shown that dwarf whitefish survive only in the absence of cisco. Cisco in reservoirs La Grande 2 and Estmain-Opinaca feed on planktonic crustaceans, mostly cladocerans, but also on a variety of aquatic insects, particularly chironomids, and on small fish (stickleback, among others, SAGE LTÉE 1983, DOYON et al. 1996). In the presence of cisco, dwarf lake whitefish are possibly disadvantaged by a narrower trophic niche and by the general similarity in life cycle strategy between the two taxa.

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