

A Gillnet Fishery Considered as an Experiment in Artificial Selection

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Temporal patterns of change in growth, condition, and mean age of samples of lake whitefish (*Coregonus clupeaformis*) taken from Lesser Slave Lake, Alberta, during 1941-75 are described. Growth rate and condition have declined, while mean age has increased. Gillnet fisheries are highly selective of large, heavy, fast-growing individuals, and we suggest that culling of this sort will provoke an evolutionary response in the stock, which may be reflected in patterns of change in growth and age. This hypothesis and others are discussed, and the general importance of artificial selection in lake fisheries is briefly considered. The possible implications for fishery management are outlined.

Key words: artificial selection, evolution, growth rate, gillnet, *Coregonus clupeaformis*.

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Nous décrivons les changements qui se sont produits avec le temps dans la croissance, l'état d'embonpoint et l'âge moyen d'échantillons de grands corégones, *Coregonus clupeaformis*, prélevés dans le Petit lac des Esclaves, Alberta, durant 1941-75. Le rythme de croissance et l'état d'embonpoint ont diminué, alors que l'âge moyen a augmenté. Les pêches au filet maillant sont hautement sélectives en faveur d'individus grands, lourds et à croissance rapide, et nous croyons qu'une sélection de cette nature déclenchera une réponse évolutionnaire dans le stock, qui pourrait se refléter dans des changements dans la croissance et l'âge. Nous analysons cette hypothèse ainsi que d'autres, et discutons brièvement de l'importance de la sélection artificielle dans les pêches lacustres. Nous esquissons les implications possibles pour la gestion des pêches.

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WHEN the rate of mortality in a population of fish is increased by exploitation, competition for food may be reduced, causing an increase in individual growth rates. At the same time, the removal of the older (and larger) fish increases the representation of younger animals in the population, leading to a decrease in mean age. This effect of exploitation on mean age and growth rate has often been observed in populations of whitefish, and indeed Healey (1975) has used it as a criterion of the ability of a fish stock to withstand further exploitation.

We have analyzed data from experimental and commercial catches of lake whitefish (*Coregonus clupeaformis*) from Lesser Slave Lake, central Alberta, between 1941 and 1975 and have found that in several respects they do not conform to the scheme outlined above. In this paper we

describe the relevant features of the data, and offer an explanation of them in terms of an evolutionary response to the selective effects of exploitation by a gillnet fishery.

Materials and Methods

Lesser Slave Lake is a mesotrophic lake about 1200 km² in extent that has been fished commercially since the turn of the century. Lake trout (*Salvelinus namaycush*) was fished out by the 1920s and is now extinct; the other commercial species, walleye (*Stizostedion vitreum vitreum*), cisco, or tullibee (*Coregonus artedii*), and lake whitefish, have all shown progressive declines in abundance (Alberta Fish and Wildlife unpublished data). In 1965 the whitefish fishery collapsed and was closed until 1972; in 1971 the cisco fishery collapsed and is still closed.

Most of the samples discussed here are from the commercial catch, but some were obtained from test nets set from 1965 onwards. Only catches from the 5 and 5½-in. meshes have been used in the present analysis. From the records for each sample, we have the weight and length of all individuals in the sample; we have restricted the analysis to males to avoid any complications caused by the sampling of gravid

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females, but the data for females have been analyzed and are in no way substantially different. Ages were determined as described by Bell et al. (1977). From these data we have calculated the secular changes in length and weight at given age, in mean age, and in condition. The condition factor, k , is computed as $10^3 W/L^3$, where W is wet weight in grams and L is fork length in millimetres; it is thus a measure of the fatness of the fish.

Results

All year-classes show an initial increase in mean weight between about 1941 and 1945, this increase being most marked in the older fish. Thereafter, despite some fluctuation, all classes show a progressive decline. This decline was steeper in older fish, so that at present there is much less difference between young and old fish than there was 30 yr ago; fish of given age now weigh less than half of what they did in the mid-1940s (Fig. 1). Fork length has changed over the years in a way similar to weight (Fig. 2). In contrast with weight, however, the decline in length did not begin until about 1958 and has been such that mean length at given age is now approximately the same as in the early 1940s. As with weight, there is at present much less difference between young and old fish than there was formerly. Condition has declined dramatically in all age-groups since 1941; the curve is steepest during the 1950s and is now apparently almost asymptotic (Fig. 3). This decline is not an artifact of month of capture, which does not vary systematically from year to year and which could only produce changes of much small magnitude in any case. Again, although condition is related to mean length, it varies within a given year by only about 0.25 units of k over the extreme length

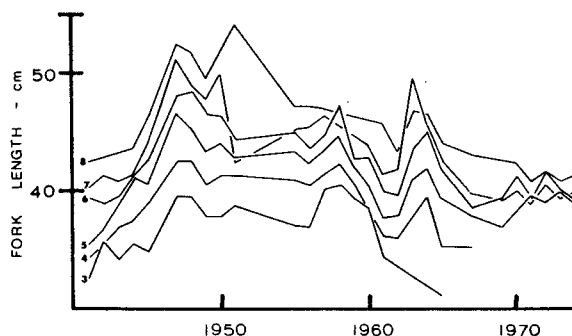


FIG. 2. Changes in length at given age in samples of lake whitefish from Lesser Slave Lake, 1940-75.

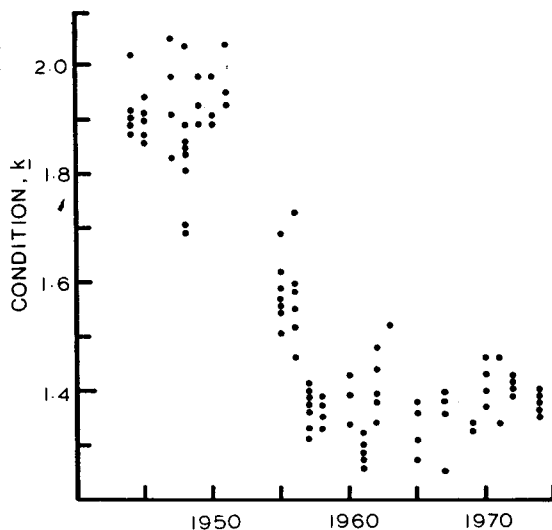


FIG. 3. Change in condition ($k = 10^3 W/L^3$) of male lake whitefish from Lesser Slave Lake, 1940-75.

range of 34-54 cm; moreover, condition declines with increasing length, while the opposite relationship would be required to contribute to the situation shown in Fig. 3.

Finally, under continued exploitation catches have shown an overall increase in mean age, although with temporary periods of decrease in the early 1940s and the mid-1950s (Fig. 4). It is evident that this progression from a mean age of 4-5 yr to one of 7-8 yr is not a simple consequence of the precession of strong year-classes, although of course these do occur and may be traced through the data (Table 1).

Selective Netting Hypothesis

Gill nets select a narrow range of fish from the fish stock, with regard to overall size and body proportions (see extensive review in Hamley 1975), yet the possibility of an evolutionary

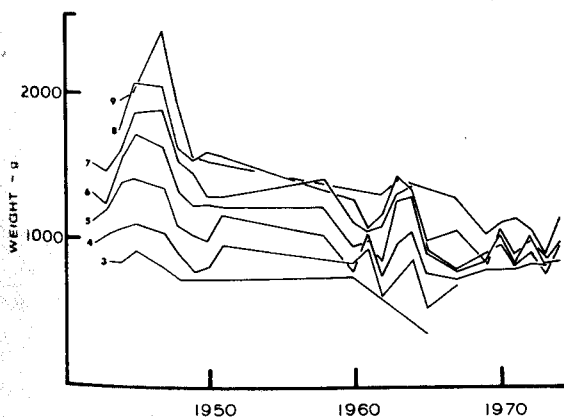


FIG. 1. Changes in weight at given age in samples of lake whitefish (*Coregonus clupeaformis*) from Lesser Slave Lake, 1940-75.

TABLE 1. Age composition (expressed as percent of catch) of commercial catches of lake whitefish (*Coregonus clupeaformis*), Lesser Slave Lake, Alberta, 1941-74.

	Year	n	Age (yr)										
			2	3	4	5	6	7	8	9	10	11	12
Oct.	1941	109	3.7	2.8	9.2	27.5	24.8	17.4	12.8	0.9	0.9	—	—
Oct.	1942	48	—	2.1	6.3	33.3	50.0	8.3	—	—	—	—	—
Feb./June	1943	161	—	14.9	32.9	27.3	18.0	5.0	1.2	0.6	—	—	—
Sept.	1944	485	—	10.5	41.9	22.1	8.0	7.0	7.8	1.6	1.0	—	—
Oct.	1945	500	—	0.4	20.8	37.2	24.2	12.0	4.4	0.4	0.6	—	—
Oct./Nov.	1947	601	0.2	23.1	59.1	8.2	3.8	2.3	1.5	1.2	0.3	0.3	—
Sept./Oct.	1948	499	—	0.8	52.7	24.2	8.6	2.8	4.0	3.2	2.2	1.2	0.2
Aug./Sept.	1949	498	—	—	5.8	70.5	18.7	1.2	1.6	1.0	1.0	—	0.2
Aug.	1950	500	—	—	9.0	69.6	16.4	2.6	1.0	0.6	0.6	0.2	—
Aug./Sept.	1951	500	—	—	1.6	23.4	49.8	23.2	1.8	0.2	—	—	—
	1952	500	—	—	—	11.0	40.0	36.0	12.0	0.4	0.6	—	—
	1953	500	—	—	1.4	2.8	28.1	47.9	17.1	2.6	—	—	—
	1954	500	—	0.4	2.4	5.0	14.0	30.2	32.2	11.4	4.0	—	—
	1955	300	—	5.5	29.0	13.4	13.5	21.7	13.0	3.8	—	—	—
	1956	300	—	6.8	47.8	25.4	7.4	4.1	5.3	2.0	0.3	0.9	—
	1957	300	—	0.4	51.2	27.5	12.7	1.6	1.4	3.2	1.0	—	—
Sept./Oct.	1958	295	—	1.4	35.9	42.7	12.2	4.7	0.3	0.7	0.3	1.0	0.7
Sept./Oct.	1960	245	—	1.2	3.3	18.0	51.8	21.2	2.9	0.8	0.4	0.4	—
Sept./Oct.	1961	198	—	0.5	20.7	15.7	32.3	19.2	10.1	1.5	—	—	—
June	1962	201	—	—	5.5	21.9	18.4	23.4	22.9	7.0	1.0	—	—
July	1963	585	—	—	5.8	18.8	28.2	31.1	15.8	—	—	—	—
July	1964	69	—	—	8.7	8.7	13.0	23.2	15.9	23.2	4.4	2.9	—
Nov.	1965	17	—	—	5.9	29.4	41.2	5.9	17.6	—	—	—	—
	1967	33	—	3.0	6.1	24.2	30.3	12.1	6.1	6.1	9.1	—	3.0
	1969	46	—	—	2.2	8.7	39.1	34.8	4.3	6.5	—	—	4.3
Sept.	1970	82	—	—	1.2	1.2	12.2	31.7	29.3	15.9	7.3	1.2	—
Sept.	1971	50	—	—	—	4.0	16.0	32.0	20.0	24.0	4.0	—	—
	1972	65	—	—	—	4.6	13.8	12.3	38.5	20.0	9.2	1.5	—
June	1973	62	—	—	—	3.2	24.2	32.3	17.7	19.4	1.6	1.6	—
Oct.	1974	417	—	—	—	1.9	13.7	27.8	44.4	7.2	4.8	0.2	—
Aug.	1975	189	—	—	—	13.2	19.5	32.2	13.2	2.0	0.5	—	—

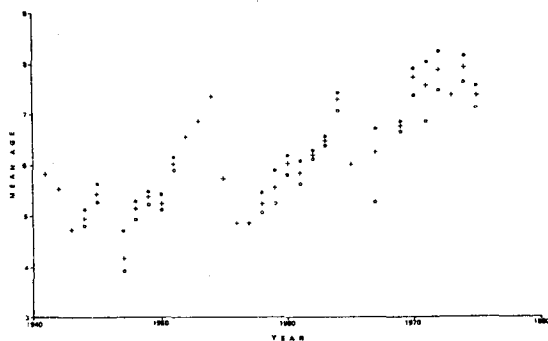


FIG. 4. Mean age of samples of lake whitefish from Lesser Slave Lake, 1940-75. ○, Males; ● females; and +, total catch.

response by culled populations has seldom been seriously considered (but see Miller 1957; Calaprice 1969; Schaffer and Elson 1975). In the following sections we raise and discuss this possibility.

The 5½-in. gill nets used in Lesser Slave Lake will selectively cull large fish with relatively large girth, i.e. high condition, which will be the fastest growing fish of a given age. Recent test-gang samples provide evidence for the contemporary selectivity of the gear used. Figure 5 is a scatter diagram of log weight and condition of male lake whitefish from a single large test-gang sample. The envelopes contain all individuals caught in a mesh of specified size. The selectivity of the 5-5½-in. gear for high weight and condition is readily apparent. Further, we have compared 5½-in. gillnet catches with trawl catches, which provide a more random sample of the available fish with respect to size and shape. In all cases, the fish in the gillnet samples have higher mean condition than those in the trawl samples (Table 2); the two-tailed probability of obtaining this result if there were really no difference between the two sampling techniques is about 10⁻⁵. In 14 of a total of 16 comparisons of the coefficient of variation of condition between the gillnet and

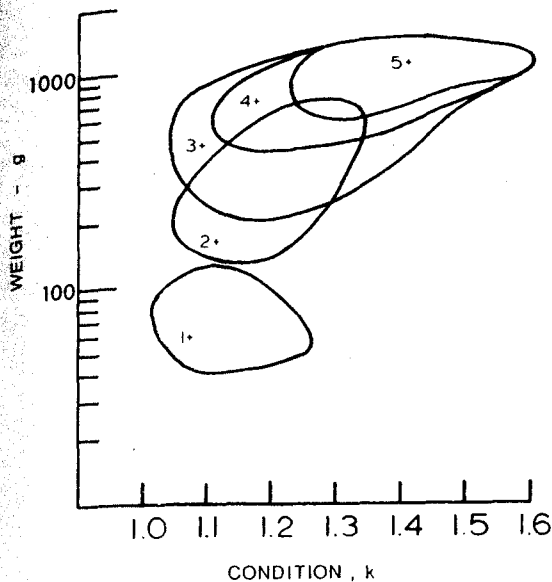


FIG. 5. Scatter diagram of weight and condition, k , of a test-net sample of male lake whitefish, August 1975. Envelopes contain all individuals caught in mesh of indicated size.

TABLE 2. Mean condition of male whitefish in various samples taken in 1974 from Lesser Slave Lake.

	Age (yr)							
	2	3	4	5	6	7	8	9
Trawl								
1	1.21	1.20	1.22	1.24	1.33			
2		1.18	1.23	1.28	1.30	1.29	1.31	
Gill net								
1				1.39	1.38	1.39	1.36	
2					1.34	1.41	1.38	
3				1.41	1.38	1.32	1.35	1.26

trawl samples, the gillnet samples were less variable (Table 3); here, the one-tailed prediction (that the gillnet catches should be less variable) is significant beyond the 1% level. We can therefore conclude that the mortality caused by 5½-in. gill nets acts to reduce mean condition and phenotypic variation of condition.

There has been a decline in the coefficient of variation of condition with time (Fig. 6, which has $r = 0.447$, $P << 0.01$). This decline is shown by all age-groups and so cannot be an artifact of the increasing mean age of the samples. Reduction of the variance of condition is of course much steeper than the reduction of the coefficient of variation because of the trend towards lower mean values of condition in time. We have also found that mean condition declines with age within a cohort and that the rate of change in

TABLE 3. Coefficient of variation of condition of male whitefish in various samples taken in 1974 from Lesser Slave Lake.

	Age (yr)							
	2	3	4	5	6	7	8	9
Trawl								
1	4.60	5.60	6.19	4.34	8.29			
2		7.40	6.02	8.12	7.83	8.55	8.31	
Gill net								
1				5.53	3.43	6.53	4.85	
2					7.55	6.67	4.62	
3				3.34	8.15	7.49	3.69	2.56

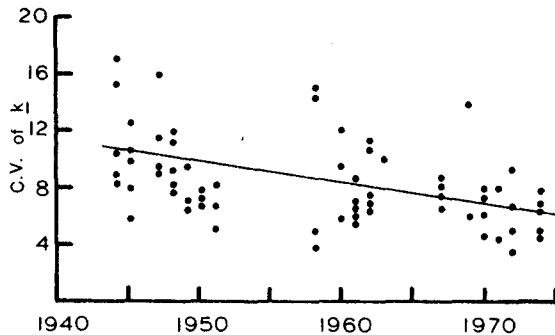


FIG. 6. Change in coefficient of variation of condition (C.V. of k) with time of male lake whitefish.

condition with age within a cohort diminishes in time.

Evidence that growth rate and characters related to the growth rate are to some degree inherited comes from response-to-selection experiments and from the direct estimation of heritability by inbreeding techniques. The recent literature includes work by Lewis (1944); Alm (1949); Donaldson and Olson (1957); Moav et al. (1964, 1974); Moav and Wohlfarth (1968); Calaprice (1969, 1970, 1974, 1976); Gall (1969); Donaldson (1970); Ryman (1970, 1971); Aulstad et al. (1972); Lindroth (1972); Kincaid (1972); Ricker (1972); Millenbach (1972); Naevdal et al. (1975); Gjedrem (1975, 1976); and Gunnes and Gjedrem (1976). In general, it is clear that growth rates will usually respond fairly quickly to selection, and we feel that the statement by Gjedrem (1976) that "the few estimates [of heritability] for growth-rate are moderately large ($h^2 = 0.1-0.2$)" is, if anything, conservative.

Fishing mortality, although not as great as in many other lakes, constitutes a significant proportion of the total mortality of the catchable fish stock at Lesser Slave Lake (see Bell et al. 1977). Moreover, this mortality is distinctly nonrandom with respect to condition and overall size, and therefore also with respect to age and growth

rate Since these characters have moderately large heritabilities, the selective mortality represented by fishing is likely to permanently change the genetic composition of the stock. In other words, gillnet fisheries represent enormous experiments in artificial selection and will probably cause evolutionary change. This verbal argument suffices to establish our case, and all the phenomena described in the previous section are consistent with such a hypothesis; there have been declines in weight and length at given age, more marked in the case of weight, and a consequent decline in mean condition. Even more significantly, we have demonstrated the decline in the phenotypic variance of condition that is to be expected if selection is acting. Unfortunately, it is impossible to construct a convincing quantitative argument because of the lack of trawl data before 1974. Over the 30 yr of the study, condition has declined by about 0.6 units of k , or by very roughly 0.1 units per generation. The rate of advance under selection is defined to be the product of the applied selection differential (that is, the difference in the mean of the character studied between the population at large and the selected parents) and the heritability. Selected (gillnet) and unselected (trawl) samples differed in 1974 by about 0.11 units of k (data of Table 1), and on average about 30% of the total mortality is caused by fishing (Bell et al. 1977). For heritabilities of between 0.1 and 0.5, the rate of change in k under selection cannot be much more than 0.01 units per generation, which is consistent with our observation that the rate of change is at present very slow (Fig. 3). However, this does not shed much light on events during the critical period of the 1950s. The phenotypic variance of the population was then much greater, and we would expect the selection differential to be correspondingly greater; we would also expect heritability to be greater, because at this time the additive genetic variance of growth-related characters had not yet been depleted by selection. A very simple assumption would be that the phenotypic variance and the selection differential were directly related, in which case we should expect an initial response to selection of 0.05–0.08 units of k per generation, which is about half the change that we observe. This is pushing the data to the limit, however, and the fact that the selection differential and the heritability will have varied in time, in such a way that the direction of change can be stated but the rate of change cannot, vitiates any attempt to obtain more precise predictions. However, there is clearly no obstacle in principle to the idea that the observed changes were caused primarily by selection.

Selection will produce individuals, which by being smaller, will live longer before reaching cullable size and will therefore act to increase the rate of survival of adult fish, relative to a population that did not respond in this way. Consequently, the mean age at maturity will increase, and the age-specific fecundity will be diminished, insofar as these are determined by size rather than by age. These effects will combine to raise the mean age of the population, and at moderate fishing intensities this effect may be sufficiently powerful to reverse the expected trend towards a younger age-distribution. This is what appears to be happening in Fig. 4. This phenomenon is only to be expected in an intermediate range of fishing intensities. In a very lightly fished population, the selection differential will be too slight to provide an effective force, while in heavily exploited populations the selective effect will be overpowered by the usual demographic shift towards younger age-groups caused by density-dependent effects on individual growth.

Discussion

We have examined other interpretations of the data. Activities associated with oil exploration have greatly increased siltation in part of the lake's drainage basin (Wyldman and Poliquin 1972). Excessive siltation may reduce egg hatching success, and, since whitefish are visual feeders, may also reduce feeding success and thereby inhibit growth; growth may also be deleteriously affected by the effect of siltation on the abundance of food organisms. However, the growth-related changes described above were well underway before the period of serious oil exploration began in 1957–60 (Mudroch unpublished data). Further, it is not clear why siltation, if it depressed the growth-rate, should also produce a decline in the variance of condition. Siltation apart, there is no reason to believe that the pertinent features of the lake have changed greatly over the period in question; there has been little or no accumulation of nutrients from local farms or communities, and the water quality has been described in a recent report as "pristine."

In other lakes, increases in the mean age of fish stocks have been interpreted as being simply reflections of changes in the strengths of individual year-classes (e.g. Christie 1963; Lawler 1965). This is quite convincing for short periods of time, but for long periods of directional change in mean age it ceases to be satisfactory. However, the passage of a number of strong year-classes can be traced through the data (Table 1, Fig. 4).

Returning to the selective netting hypothesis, we shall briefly consider its generality as a significant factor in determining the qualitative response of an exploited fish stock, although it is not our intention to present a review. It is a commonplace that many exploited stocks of fish now provide smaller fish; however, little long-term data on growth and age in other whitefish populations are available in the published literature. There is suggestive but inconclusive data from two other Alberta fisheries. At Sturgeon Lake, a small lake to the west of Lesser Slave Lake, the whitefish have declined in condition and in weight at given age between 1969 and 1974 (Bishop personal communication; Table 4 and 5); this lake has supported a 6¼-in. gillnet fishery since the 1920s. However, there appears to be no information available on other changes in the lake during this period, so the data must be treated with reserve. Bidgood (1973) has described a decline in the growth rate of the Pigeon Lake, Alberta, stock between 1956 and 1970. He has attributed this trend to changes in food availability, interspecific competition for food, and increased intraspecific competition for food following a supposed proliferation of the whitefish caused by a reduction of the pike population. It is not clear from his data to what extent this situation is comparable to Lesser Slave Lake, but we may note that the Pigeon Lake stock has been subject to a fishery that has twice reduced its permitted mesh size, from 140 mm to a final 89 mm. Increased intraspecific competition can hardly be relevant to the situation at Lesser Slave Lake, where there has been no proliferation of the whitefish, rather the contrary, and where pike are still common. Nor do we find the hypothesis of interspecific competition very attractive. A recent survey of the diets of *Coregonus* and *Catostomus* in Lesser Slave Lake (Weisgerber personal communication and unpublished data; data available from Alberta Fish and Wildlife) has shown that, although the two forms feed on organisms belonging to the same or to similar families, there is very little dietary overlap at the species level; since the two forms have very different morphologies and ways of life, this result is not surprising. Finally, the most complete sequence of data on age composition is that available for the Lake Winnipeg stock, where Davidoff et al. (1973) show that mean age has decreased steadily since 1946. However, it is quite clear from Kennedy's (1954) paper that during the 9 yr prior to this there had been a consistent increase in mean age. Pending a thorough review of the literature, all that can be said is that declines in growth and condition appear to be quite common, but that the situation

TABLE 4. Average weights (grams) of commercial whitefish caught in 6¼-in nets, Sturgeon Lake, Alberta, 1969-74.

Age class	1969 n=72	1970 n=40	1971 n=38	1972 n=50	1973 n=100	1974 n=50
I	—	—	—	—	—	—
II	—	—	—	—	—	—
III	—	—	700	—	—	—
IV	—	—	1295	926	—	—
V	1565	1460	1400	1125	1078	—
VI	1831	1596	1610	1528	1204	1145
VII	2068	1940	1875	1703	1517	1234
VIII	2114	2325	1823	1800	1654	1780
IX	2498	2310	2113	1784	1803	1630
X	2661	2482	2424	1935	1980	—
XI	2779	2660	2566	2365	1957	—
XII	—	3140	2790	2445	1773	2040
XIII	—	—	—	2170	1720	—
XIV	—	—	—	—	2220	—

TABLE 5. Condition factors (*k*) of commercial whitefish caught in 6¼-in nets, Sturgeon Lake, 1969-74.

Age class	1969 n=72	1970 n=40	1971 n=38	1972 n=50	1973 n=100	1974 n=50
IV	—	—	1.53	1.39	—	—
V	1.67	1.41	1.52	1.35	1.45	—
VI	1.58	1.48	1.25	1.33	1.54	1.43
VII	1.55	1.45	1.41	1.32	1.35	1.37
VIII	1.47	1.63	1.31	1.35	1.38	1.56
IX	1.52	1.46	1.31	1.18	1.27	1.21
X	1.45	1.37	1.40	1.24	1.33	—
XI	1.47	1.38	1.39	1.29	1.35	—
XII	—	1.49	1.43	1.25	1.18	1.13
XIII	—	—	—	1.17	1.10	—
XIV	—	—	—	—	—	—
<i>k</i>	1.49	1.46	1.39	1.28	1.31	1.34

in Lesser Slave Lake may reflect an unusual set of circumstances. In the remainder of this discussion, we shall examine the effect of size-selective mortality on the fishery.

The life-history parameters of any unexploited stock of fish must be such that the population is able in the long term to maintain a rate of increase of zero. Exploitation implies a change in certain of these parameters; notably, the rate of survival of adult fish will be reduced. These changes will tend to reduce the rate of increase of the population, which, other things being equal, will become extinct. Only if other life-history parameters vary in such a way as to counterbalance the reduction of adult survival can the population persist. Only one such mechanism appears to be recognized in the current Western literature: this is the existence of certain density-dependent constraints on population growth. These might operate, for example,

if competition for food were reduced at some or all ages because of the reduction of population density. This would increase the rate of growth of fish beyond the age at which the effect occurred, and in this section of the population individuals of any given age would be larger than individuals of the same age in an unexploited population. To the extent that demographic schedules are dependent on size rather than on age, this will tend to increase fecundity and to decrease the age at maturity; there may also be a reduction in the mortality of very young fish. At the same time, an increase in the rate of growth will reduce the age at which individuals are recruited into the exploited section of the population, and will therefore increase the mortality experienced by at least some age-classes. Clearly, the overall effect of exploitation on the rate of increase of the population will depend on the relative magnitudes of its beneficial effect on fecundity, maturation, and early survival, and its deleterious effect on the survival of juvenile and adult fish.

This, the conventional account of the response of fish populations to exploitation, is incomplete in one important respect; it assumes that the population comprises uniform individuals whose inherited characteristics do not change with time. This is quite unlikely to be true. In a gillnet fishery, for example, only fish of greater than given dimensions are fully exposed to the risk of capture. Thus, it is inevitable that, over a certain range of age-classes, the largest individuals of given age will be selectively removed from the population. This will lead to the evolution of a slower rate of growth, that is, to smaller size at given age. Since this implies lower fecundity and delayed maturity, size-specific selection will probably reduce the rate of increase of the population and will thus diminish its ability to respond to further exploitation. Selection will, of course, always tend to maximize the rate of increase of a population; in this case, however, it is maximized relative to a population which, undergoing the same rate of exploitation, did not respond by evolving a slower rate of individual growth. But the selected population, if it were abruptly released from exploitation, would display a lower rate of increase than the original population before exploitation. Thus, density-dependent compensation and size-specific selection act in opposite senses, the former acting to increase the individual growth rate and the rate of population increase, and the latter, vice versa.

This argument requires that the schedules of maturity and fecundity be determined to some extent by age as well as by size. To prove this,

imagine the fishery to be so efficient that, once an individual should exceed a certain size, it is immediately captured. But an individual with high growth rate will mature earlier in life than a slow-growing individual, and, if fecundities at given size are equal, will usually have higher fitness because of its shorter generation period; indeed, the slow-growing individual will be at even more of a disadvantage than this argument suggests, since, maturing later in life, it will suffer more natural mortality. On the other hand, if demographic schedules are entirely age specific, then the only component of fitness affected by exploitation will be the rate of survival, and slow-growing individuals will always be the more fit. Thus, when the contribution of age, independently of size, to the schedules of fecundity and maturation exceeds some critical value, the selective removal of the larger fish of given age will favor the evolution of a slower rate of growth.

But if age makes a substantial contribution to the determination of fecundity and maturation, selection may act on the age-specific schedules as well as on the size-specific schedules; moreover, it will do so in fisheries (for example, trawl, longline, or seine fisheries) where selection for size may be negligible. For example, one possible response to the increase in mortality caused by exploitation might clearly be the evolution of a lower age at first reproduction, irrespective of the size at first reproduction. This has happened in some exploited stocks of whitefish (Healey 1975). Age-specific selection will again raise the rate of increase relative to that of an unexploited population that did not undergo selection, but it is also in principle capable of creating a rate of increase greater than that of the original unexploited population. Thus, it may act in concert with density-dependent compensation.

We conclude that present management theory may be seriously deficient in that it fails to take into account the possibility of adaptive genetic change in exploited stocks of fish. This is especially serious because the size-specific selection associated particularly with gillnet fisheries is capable of actually reducing the capacity of the population to maintain itself in the face of continued exploitation. Selection of this sort may only rarely be capable of determining the direction of change in population parameters, that is, that selection is only rarely capable of producing an effect larger than and opposed to that associated with density-dependent compensation. But even if this is so, selection would invariably enter into the dynamics of an exploited popula-

tion by influencing the rates at which population parameters change and the final extent to which they change. Until a synthetic theory appears in which ecological and evolutionary forces are recognized, it is unlikely that the behaviour of fish populations under exploitation can be fully understood.

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