THE IMPLICATION OF NEUTOENDOCRINE MECHANISMS IN THE REGULATION OF POPULATION CHARACTER OR ON A MORE CHRISTIAN VIEW OF THE BLACK BOX

By

Carl J. George

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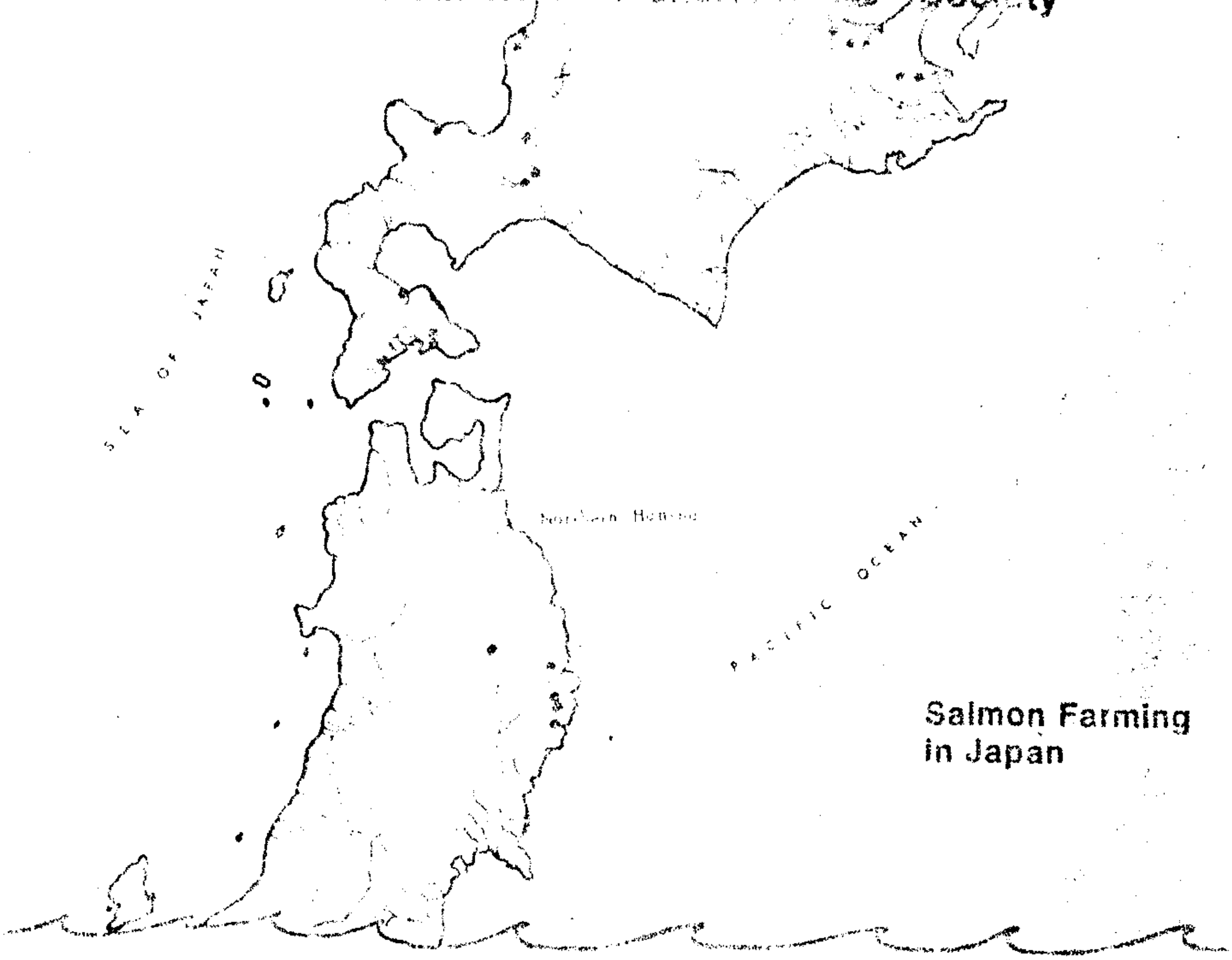

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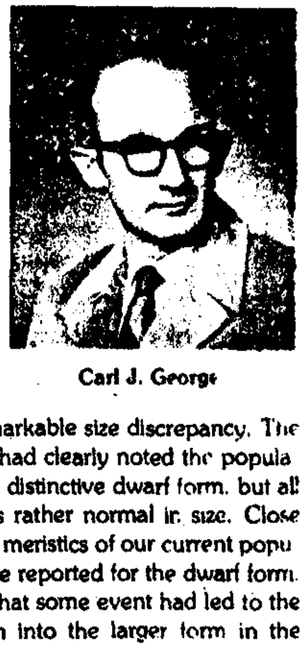

Carl J. George

During the summers of 1973 and 1974 I was privileged to work as a member of the International Biological Program team studying the Lake George, New York, ecosystem. My task was the characterization of the several fish species represented in the lake. In the course of our studies a few hundred ciscoes, *Coregonus artedii*, were collected and, curiously, some 85% of these were females. Review of the literature for the ciscoes of Lake George also revealed a remarkable size discrepancy. The earlier reports (e.g., Koelz 1931) had clearly noted the populations of Lake George ciscoes as a distinctive dwarf form, but all of our data affirmed our form as rather normal in size. Close inspection of the proportions and meristics of our current populations matched up well with those reported for the dwarf form, and thus we were led to believe that some event had led to the transformation of the small form into the larger form in the intervening years. The intervening period was also notable as one of extreme cisco abundance apparently terminated by a massive and extensive die-off during December of 1952 and January of 1953. Local memory and various state files attested thoroughly to this fact. The dead fish were examined by several specialists without any conclusive results other than the suggestion that the die-off may have been a consequence of post-spawning exhaustion.

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This complex of observations including sexual disproportionality, increased size at maturity, and reduced numbers following a period of extreme abundance of dwarfed individuals led to the consideration of the literature on other coregonine populations.

The case history of the bloater, *Coregonus hoyi*, in Lake Michigan is one of the best documented (Brown 1970). Gillnet samples taken in 1928–1932 included 13,089 fish, of which 92% were females. In 1954–1955, more large samples made with both trawl and gill nets yielded 79% females. Female predominance continued to rise in the early sixties to 87% and then in 1963 reached 95%, and continued in the mid-ninety percentiles through to the end of the study in 1969. Female predominance was evident in age groups II and III but did not increase for older age groups. Average total lengths increased in a consistent manner from 174 mm in 1954 to 249 mm in 1969. Average ages for males ranged from a low of 3.0 in 1954 to a high of 5.4 in 1968. Average ages for females ranged from a low of 3.3, also in 1954, to a high of 6.0 in 1969. Average age for the males was typically greater except for 1919, 1928, 1954, and 1969. A progressive reduction of representation of the younger age groups—i.e., I–III—in the course of the study, a reduction of numbers of fish taken in standard 10-minute trawl tows, and the reports of commercial fishermen suggested a general decline of the population from high densities experienced in the 1954–1961 period. Condition indices are not reported. Sampling was diverse in type, place, and time, and overcomes the criticism that sexual disproportionality might be a consequence of sampling method. An especially key element of this study was the female predominance among the youngest age groups sampled; i.e., a differential mortality rate for the sexes is not explicit. It is reasonable, of course, to offer that the males died when very young, but it is also possible to suggest as Brown does that earlier events resulted in a modification of the primary sex ratio. This is one of the few places in the literature (see also Svärdson 1965) where this idea is presented.

Population changes of the cisco in Birch Lake, Michigan, constitute another unexplained phenomenon (Clady 1967). Birch Lake is spring fed, is 295 acres in extent, and has a maximum depth of 95 feet. For many years it had supported a fall sport gillnet fishery for the cisco monitored by the Michigan Department of Conservation. In 1939, 20,750 ciscoes were taken at the rate of 4.51 fish per net per hour. Because of the simultaneous capture of many recently stocked rainbow trout, *Salmo gairdneri*, the fishery was closed until 1944, when 18,137 ciscoes were taken at the rate of 6.28 per net per hour. Thereafter, the fishery began a decline, culminating in a total catch of only 37 fish in 1950 at a rate of 0.17 ciscoes per net per hour. Concurrently, the sex ratios and growth characteristics of the population changed. In 1939, 1943, and 1944, males predominated in the fishery. In 1945, 84% of the catch were female, and female predominance increased continually through 1949 when 99% of the examined sample (N = 154) were female. Thereafter, sample sizes were smaller and thus less reliable. Commencing in 1954 the sex ratio was observed again to be equal or dominated by males. For example, samples of 44 fish taken in 1955 were 27% female and in 1962 samples of 63 fish were 35% female.

A notable feature of the female predominance is that it emerged in age group II in 1944 for the first time: 61% of the fish were female. In the following year, 1945, 85% of age group II fish were females. A differential male mortality can be detected by following the several year classes, but it is not explicitly clear that the predominance of females in age group II for 1944 through 1950 was the result of a differential male mortality. There is also the observation that average ages for males and females as observed each year were not notably different except for 1955 and after.

Size changed greatly concurrently with the emergence of female predominance. In 1943 the average total length for age group IV was 12.1 inches. In 1955 this had increased to 17.4 inches, and to 18.8 inches in 1962. At the same time the average age appears to have increased. Before 1959 fishes of age group V were common and age groups VI and VII were uncommon but present. During 1954 and after, fishes older than age group IV were not present in the samples. In contrast, the average age of males trended upward until 1950 to about 5.5 years and then commenced a decline to 2.8 in 1955. Females similarly showed an average increase in age up to 1955 when the average age was 5.4. In 1956, however, this value had fallen to 3.2. A key event thus emerges as the appearance of the 1954 and 1955 year classes as in the fishery. These were especially large fish. For example, age group I fish taken in 1956 averaged 12.1 inches in total length, which was the average attained by age group III and IV fish of 1943.

One more remarkable observation is possible and this is that the average total length of prominent age groups III, IV, and V had increased from 1943 through 1947, a time when the population was high and presumably highly competitive.

One of the most circumspect and authoritative articles ever written on the cisco is Hile's (1936) report on the populations of four lakes in the northwestern highlands of Wisconsin. The lakes studied were selected because of their representative and unfished character. Nearly 4,000 specimens were collected by gill net during the summer months of 1928, 1930, 1931, and 1932. Three lakes—Trout Lake (1,051 hectares, South basin), Muskellunge Lake (157 hectares), and Silver Lake (167 hectares)—yielded small forms rarely exceeding 200 mm in standard length. Clear Lake (373 hectares), in contrast, produced forms commonly greater than 300 mm standard length. Weight gain (Δw) per unit of weight (w) was also notably different. For age group III values, this index, 100 $\Delta w/w$, for Trout Lake, Muskellunge Lake, and Silver Lake were 19.4, 10.9, and 22.0, respectively. In contrast, those for Clear Lake ciscoes were 56.6 for males and 77.7 for females. The theoretical condition factors increased with standard length for fish in Clear and Silver Lakes but declined with length for those in Trout and Muskellunge Lakes with a crossover point of about 155 mm. Trout Lake demonstrated the emergence of strong female predominance in older age groups: the female:male ratio exceeded 11:1 for age groups V and VI. Muskellunge and Silver Lakes also showed female predominance increasing with age but to a lesser degree. Clear Lake, in contrast, showed male predominance to a modest degree for age groups I through V. Populations showing heavy female predominance illustrated earlier sexual maturation. The ciscoes of the predominantly female population of Trout Lake matured at the end of July. Muskellunge Lake ciscoes with the next highest female predominance matured in late August. The third-ranked Silver Lake population ripened in early September and the male-dominated group of Clear Lake matured in late September or early October. On the basis of catch per unit of effort the densities of the populations decreased in the same order with Clear Lake having the lowest value. Longevity was nearly similar: "The Muskellunge Lake cisco has definitely the shortest average life span. The Trout Lake cisco falls second and the Silver Lake cisco third, while the average life span of the Clear Lake cisco is quite long" (page 267).

An unusual aspect of the length-frequency data for the Muskellunge Lake specimens was the bimodality observed for length detected for several year classes as back-calculated at the end of the first and second years of life. Predation on adult ciscoes in Trout Lake was implied by concurrent catches of both lake trout and burbot. Egg and fry predation was also suggested for Muskellunge Lake by the presence of very large numbers of yellow perch among the net samples. Whitefish were also netted in Trout Lake. No large predators and very few yellow perch were taken with the Clear and Silver Lake samples suggesting little population constraint from these quarters. Parasites were common in all but the Clear Lake specimens. Only 2 out of 60 fish from Clear Lake were infested while 80% or more of the ciscoes from the other three lakes bore cestodes or Acanthocephala.

The productivity of the four lakes seemed quite contrary to expectation. "The investigators who collaborated in planning and initiating the studies of which the present one is a part harbored no delusions to the effect that the relationship between the growth of fishes and the environment is in any sense simple. It was nevertheless surprising to find early in the investigation of the growth of the cisco that the growth rates of the populations did not fall at all in the order of estimated productive capacities of the lakes in which they occurred, but rather that the reverse was true" (page 253).

These observations, especially the inverse relationship of his criteria of productivity and growth characteristics of the cisco—i.e., the "partial independence of the factors that determine growth rate and the factors that determine condition"—led Hile to propose the possible role of a space factor quite apart from specific food supply. He also noted the earlier work of Willer (1924) and Jarvi (1920) on the European *Coregonus albula*, which arrived at a similar conclusion.

One of the most confusing and perverse situations is that of the sympatric occurrence of large and small forms of what may be presumed to be the same species or closely related subspecies. The lake whitefish, *Coregonus clupeaformis*, appearing in some 76 lakes of northwestern Maine, illustrates the phenomenon exasperatingly well (Fenderson 1964, 1976). In Cliff Lake, for example, fish may be taken together that sort out bimodally in terms of size and age with mature individuals occurring within each mode. One sample revealed numerous fish 6–7 inches long that were mature along with other fish constituting a group showing 100% maturity at 15 inches and more length. The smaller mature fish were predominantly members of age Group I and IV, while the larger mature fish were predominantly VI and older.

Some lakes in this Maine group have only dwarf, short-lived, early-maturing forms, while others have only normal, long-lived, and late-maturing forms. Transplants of dwarfed populations to unoccupied lakes such as Haymock Lake resulted, in some cases, in normal-sized progeny. The same observation has been made for several coregonids in Scandinavian Lakes (Svärdson 1965).

Morphology revealed differences from population to population in terms of gill-raker, fin-ray, and scale numbers, proportionality of the orbit and caudal peduncle, and other aspects, but the differences were not consistently linked to dwarfage of normal populations. This is to say that the meristic features of a dwarf form in one lake may be represented in the normal form in another lake. Dwarfs did, however, commonly show more gill-rakers when sympatric with a normal form. It is also possible to challenge the utility of orbital diameter proportionalities because of the commonly observed phenomenon of continued eye lens growth, as in stunted centrarchid populations. Similarly, caudal peduncle proportionality tends to change with the hierarchical positions of a fish in a social situation.

Erythrocyte antigens were compared for the dwarf and normal forms and found to show differences that may be genetic in origin. Separate spawning runs were observed, further indicating at least a partial genetic barrier. Such a set of observations has led Fenderson to propose ". . . this variation may be due in part to varying degrees of convergence of two whitefish forms that once diverged from a common progenitor" (page 77).

Sympatric dwarfed and normal-sized populations of the whitefish are also known for Lake Opeongo, Ontario (Kennedy 1943), and as was the case for the Maine lakes the two forms do not appear to occupy different depths or sectors of the lake. Lateral line scale number and gill-raker number were found to differ only slightly.

Additional descriptions of irregularities in coregonine populations (and other taxa as well) could be presented almost ad infinitum (e.g., Kendall 1926; Greene 1930; Dence 1948; Svärdson 1965; Beamish and Tsuyuki 1971) but these at hand serve to illustrate the point that as in Lake George several population characteristics tend to vary in an apparently regular way. Specifically, under some conditions (e.g., low density), fish grow quickly to a certain size, mature, grow slowly thereafter, and live for a relatively short time. Under other conditions (e.g., high density), within the same region and in some cases within the same lake, the initial growth is slow, maturation occurs later at a relatively large size, and the fish are long-lived. Coupled to these two life styles are variations in the ratio of the sexes, which may emerge in either young or older age groups. In this regard there is a tendency for populations of large, slow-growing forms to show female predominance and, conversely, small, fast-growing forms to show greater equality of the sexes or perhaps even male predominance in younger age groups.

There is still another tendency for larger, slower-growing forms to show relatively small parasite burdens, but this is much more conjectural. Finally, the growth characteristics as described are not easily related to the trophic structure or productivity of the supporting lake.

It is also worth noting that the often-cited Lee's phenomenon may simply be a consequence of a population simultaneously having members of both growth types.

THEORY

The regulation of population character remains one of the key concerns of the fisheries biologist. The density of the population and growth rates are two of the more pivotal parameters. The most successful model proposed is essentially a fish sandwich with the subject fish population purportedly constrained between an overlayer of predators, parasites, and microbes and an underlayer of forage forms. In other terms it is a pair of predator-prey systems with the focal fish species being the common linking variable. Models of this form have been refined in exquisite detail (e.g. May 1976) and have proven moderately useful in the prediction of outcomes. But often as not, the individuals of the key species are considered to be 'black boxes' with a relatively stable life program that works itself out under the essentially controlling variables of predation and food. The black box is given relatively little credit for the regulation of population character itself. Density-dependent variables are indeed mentioned, but these are again commonly considered as black box phenomena involving interactions between forms with a limited repertoire of responses. An example of this is the explanation for slowed growth rate under conditions of high population density. The most common explanation is that the reduced growth rate is due to the simple paucity of food for each fish rather than some shift of neuroendocrine (or other) mechanisms within each fish activated by the high population density.

The commonly observed suppression of growth in dense populations in highly productive lakes is explained using the concept of competition. One of the better statements in this regard appears in Ralph Hile's already cited paper.

> If it is assumed that the various stocks do not differ greatly in their hereditary capacities for growth and that environmental conditions are in general comparable, then it may be expected that the amount of growth in the various populations will depend in large measure upon the availability of food. The determining factor is then the amount of food available to each individual fish. If the poorest growth occurs in the lake that produces the greatest amount of food, it may be assumed that here in all probability the number of feeding individuals is so great and the competition for food so strong that these individuals cannot secure a sufficient amount of food to maintain their normal rate of growth. On the other hand, if a relatively rapid growth occurs in a lake with a scanty basic supply of food it may be assumed that the feeding population in that lake is so small that in spite of the scarcity of food the individuals are still able to secure sufficient nourishment to maintain rapid growth (page 254).

Another aspect of our existing predator-prey models is that they must remain superficial and highly simplified in order to be manageable. This means that they provoke little curiosity regarding the more profound processes such as growth regulation. Certainly one of the most important parameters in fishery biology is the production of a certain weight of fish per unit area per unit of time. In most predator-prey models one must assume a fixed annual pattern of growth rates; thus, change in biomass becomes a function of predation and other forms of mortality.

natality, migration, forage, production, and population density. Thoughts about the physiological regulation of the growth process, such as that due to the activity of the hypothalamus, pituitary gland, and the secretion of growth hormones thyrotropin and gonadotropin, must be set aside.

A further consequence of our current dedication to predator-prey models in fisheries management is the delegation to curiosity status of a number of often observed phenomena, e.g., varying sex ratios, growth rates, longevity, and ages of maturation for the two sexes, Lee's phenomenon, and dwarfing, including the existence of sympatric dwarfed and normal-sized populations. The reduction of growth rate (but not of condition index) in the presence of an apparently rich food base, and remarkable variation in fecundity and fertility are probably the more conspicuous "irregularities" that most fisheries biologists commonly observe but rarely can explain.

So where do we go from here? Obviously, we must look for ideas that can serve to enhance or refute our prevailing concepts about how population characteristics are regulated. Note that I have consistently used the term "characteristics" rather than "size" in an effort to keep the challenge in better perspective. An appealing alternative approach involves the theory of stress physiology, in great part the work of Hans Selye, who has been developing the topic in the medical literature since the early 1930's. His 1956 account is especially readable. In brief, Selye suggests that environmental adversities such as high or low temperature, low oxygen concentration, paucity of food, and intensity of encounter including social interaction, regardless of their diverse character, induce an identical physiological state of adaptive character called "stress" with the various stigmata or observable changes comprising the "General Adaptation Syndrome" or G. A. S. Note that the physiological state is called "stress," the environmental factors being termed "stressors." The G. A. S. is initiated with the impingement of stimuli on the various sensory organs, which then, more or less directly, reach the hypothalamus of the brain, which in turn stimulates the production of adrenocorticotropic hormone, or ACTH, by the anterior lobe of the pituitary. This ACTH then moves via the blood stream to the adrenal cortex, where it triggers the release of adrenocorticosteroids. Of these, cortisol and corticosterone are the most prominent. These "glucocorticoids" act to shift body chemistry toward the production of glucose, the primary metabolic energy resource, apparently in preparation for the energy-demanding adaptive activity of the threatened organism. This process called "gluconeogenesis" activates those enzymes essential to the conversion of *both* fats and proteins to glucose. As a consequence the synthesis of these same materials is curtailed and otherwise greatly altered. The ramifications of this are diverse, ranging from the reduced production of antibody to the reduced synthesis of the main muscle proteins, actin and myosin.

Stress is typically short term, release of ACTH and glucocorticoids abating with the reduction or disappearance of the stressor or stressors. But in some cases the stressors may be sustained, inducing a chronic and debilitating stress condition. The prolonged catabolism of protein appears to impair kidney function. The continued reduction of protein synthesis results in reduced growth and increased vulnerability to disease including parasitization. The synthesis and release of sex steroids by the adrenal cortex also disturbs the programming of maturation and sexual activity. The production of sex hormones by the adrenal cortex may come as a surprise to some, but incubation and perfusion experiments leave no doubt that adrenocortical tissue is able to synthesize into androgens both cholesterol and C-21 steroids; i.e., those having a molecular skeleton containing 21 carbon atoms. In humans this property is demonstrated by Cushing's syndrome where excessive activity of the adrenal cortex shows not only the consequences of increased cortisol levels but also, in some cases, increased lower facial hair, temporal hair recession, deepening of the voice and clitoral hypertrophy, all manifestations of androgen activity.

The application of the concept of stress and the G. A. S. to other organisms has been championed by John J. Christian, now at the State University of New York at Binghamton, and a recent review (1975) of his is probably the best and most current extant on the subject. Christian strikes off into the relatively new, but here relevant, territory of relating stress to population density regulation. The essence of his thesis is that high population density acts as a stressor causing the train of events described above. Sexual maturation is suppressed in many members of the population, thus reducing reproductive recruitment. Disease resistance is reduced, facilitating mortality and morbidity (supportive of enhanced predation) to reduce the population. The key processes of natality and mortality are thus acted upon in a way to reduce population size. Conversely the system acts to enhance natality and to guard against mortality when population is low. Christian thus proposed in good detail an endogenous model for population character (including density) regulation shifting the function of both predators and pathogens to secondary roles. By his model, the massive infection of a population may be a manifestation of intrinsic mechanisms of the population rather than an independent cause. In the same way predators may be more effective as a consequence of endogenous processes of the population rather than as independent sources of casualties. Gary Wedemeyer (1970) describes this kind of phenomenon for fish populations.

Another aspect of the model is that certain changes once viewed as pathological and maladaptive may (indeed) be viewed as regulatory mechanisms operating at the population level.

One of the problems of Christian's population regulation model is that he does not define the circumstances under which population density is sensed. For species that live in colonies or schools this may prove to be a special problem. This matter was given particular attention by V. C. Wynne-Edwards, now emeritus professor of the University of Aberdeen, in a remarkable book entitled *Animal Dispersion in Relation to Social Behavior* (1972). In a wide-ranging analysis of certain forms of aggregative activity, he purported to recognize a phenomenon he calls epideictic (pronounced ep-i-dike-tic) behavior. Certain numbers, usually the males, of a population gather at traditional, conventional, or ceremonial locations for the purpose of mutual display of sounds, odors, colors, specific forms, and so on. The perceived intensity is related to the numbers of individuals in the population and thus a censusing mechanism is established. During these epideictic gatherings the neuroendocrine system of the organisms are especially receptive to the programming of future activity. If the numbers are large, the display activity is, in aggregate, high: hierarchical behavior is accented, reproduction is reduced, and many are caused to disperse, often into conditions of greater physiological and spatial vulnerability. If the epideictic aggregation is small, the sexual activity is allowed to emerge and be sustained by those present, fostering this reproductive vigor. Professor Wynne-Edwards asserts that such epideictic behavior must be a product of group selection. Group selection is a very controversial subject, and many have argued that because group selection is not a viable idea, epideictic behavior cannot be a reality. But as Wiens (1966) and others have suggested, epideictic behavior may be a reality regardless of how it has evolved!

We thus have a rather complex construct based on the work of Selye, Christian, and Wynne-Edwards, which suggests that populations of certain species may indeed have the means for intrinsic population control. Generally, this model has been applied to mammals, especially rodents of higher latitudes. Very little attention has been given to the application of the idea to fish populations.

It is clear that the endocrine processes of fish are quite similar to those of other vertebrates (Hoar 1969), and in fact, we may have to credit the primitive fishes with responsibility for the evolutionary emergence of the processes involved. There are differences, of course, and a prominent one is that fish do not have a distinct adrenal gland as do other vertebrates. Instead, the homologous tissues are dispersed within the anterior part of kidney, along the posterior cardinal veins. The thymus gland, on the other hand, is especially overt, being evident superficially on the side of the body under the opercular valve at the upper end of the opercular slit.

At best, the evidence for the operation in fishes of the neuroendocrine constraints proposed by Christian is fragmentary and circumstantial. It is, however, of long standing and several earlier workers (e.g., Willer 1924 as cited by Hile 1936) have proposed influences of density or space on population characteristics; several of the notable papers have already been mentioned. These instances, in my opinion, have a strong neuroendocrine overtone. Tom Thumb was small although well fed and he lived amidst normal-sized individuals. Hormonal malfunction is now a well-accepted explanation for this kind of observation. The differentiation of the sexes is also an endocrine matter and especially so in the fishes, where the administration of testosterone at the right time during the development of the individual can induce a totality of one sex or the other (Yamamoto 1964). The emergence of sexual maturity is still another, and with maturation and the deflection of metabolic resources to gonadal development it is easy to see how growth is linked to sexuality through endocrine function. Intrinsic factors must be operating.

Is there any evidence for epideictic behavior in fishes? In accord with Wynne-Edwards' thinking we should look for the congregation of male fish at certain traditionally used sites. These fish should display toward one another rather than toward the females and massively attended congregations should result in reduced reproductive efficiency in many of the attending forms. The converse must also be shown; i.e., when the epideictic display is attended by few animals, their fertility should be high. In keeping with my emphasis on the higher latitude salmonids, which are comparable to the higher-latitude rodents studied by Christian, examples should be sought for in this group. The European whitefish, *Coregonus lavaretus*, as studied by Fabricius and Lindroth (1954), probably provides the best existing set of observations on the coregonines in this regard. The observations were made in a stream aquarium, and female as well as male fish were introduced. "While swimming close to the bottom, some of the adult whitefish, males as well as females, adapted a posture resembling a lateral display. Slightly lifting the head and with the tail down they first erected their pelvic fins, and with increasing intensity of the activity they turned the pectoral fins to their foremost position, and finally they could erect their dorsal fins as well. In this way, they slowly swam about in a 'sailing manner.' Some of these 'sailing' fish could remain for several hours over a bottom of only two or three square meters . . ." (page 108). Unfortunately, most coregonine activity of this type occurs at dusk or night at colder temperatures and thus is not conducive to economical study, but there is a tantalizing fragment here that may relate to the concept of epideictic behavior. Under more normal conditions would this activity take place at a traditional site by only males?

The return of various species of trout to the sites of their spawning is now becoming better defined and we may eventually learn that this is indeed a common (although not absolutely essential) phenomenon of salmonid behavior. For example, Martin (1960) notes return to spawning grounds by the lake trout, *Salvelinus namaycush*; however, MacCrimmon (1958) emphasizes that homing is not essential to spawning for the same species. The homing of related groups such as the smelts, suckers, and minnows to spawning grounds also needs further attention. It is commonly observed, however, that males of these groups precede the females to the spawning grounds and interact prior to the arrival of the females. The fact that even a few fish are known to 'imprint' on certain indicators of their spawning grounds when very young and then act on the 'imprint' years later strongly attests to the long-term programming of organisms.

A more difficult aspect of the programming is implied by the observation that shifts in growth character and sex determination appear to occur early in the ontogeny of each fish. This seems appropriate because all the cells of an organism must share much in common in their responsiveness to endocrine stimuli. If this were not the case, we might expect the various parts of an organism to grow in a chaotic manner, the left fin perhaps growing twice as large as the right and so on. Instead, we see the various parts growing harmoniously in concert. Carrying this point to the full extent possible it seems fitting to suggest that the larva, zygote, or even sperm is programmed. This places the matter fully in the realm of sheer speculation, and (damning the inevitable torpedoes) I would like to propose a programming mechanism.

We are now aware that endocrine processes frequently exhibit negative feedback. For example, the pituitary releases gonadotropins. These act on the gonads, which produce and release sex steroids. The sex steroids act on various parts of the body to induce secondary sexual features but these steroids also act to suppress the production of gonadotropins. Thyrotropin and thyroxin act in the same way as do ACTH and the glucocorticoids. Given this somewhat heretical suggestion that the sperm or zygote with its diverse potential is programmed by the hormonal titres of the parental fish and particularly the male fish, consider two cases: If the male fish is in an intensely stressed state, as might result from the epideictic activity associated with high population density, titres of glucocorticoids and sex steroids produced by the interrenal tissue would be high. These could be released from the body to enter the newly fertilized egg to eventually suppress ACTH and gonadotropin production. It is also possible that the sperm itself may transport the hormones to the egg. Slow-growing, late-maturing, and long-lived fish would result and females would probably predominate because of the character of the sex determination process; i.e., female sex results unless testosterone is present. In the second case, if the population is small and the epideictic activity is minimal, a relatively unstressed parent fish with low levels of ACTH and thus low interrenal activity would result. Minimal suppression of ACTH and gonadotropin production in the progeny would occur and thus a stress-prone, short-lived, early-maturing fish would emerge. Under these conditions a stressful environment coupled with epideictic activity would cause an especially high male mortality, resulting in female-dominated older age groups. This situation would differ for the progeny of epideictically stressed parent fish; in this case, female predominance would be clearly evidenced by youthful age groups accentuated through modest differential male mortality in more senior cohorts. All of this becomes quite confusing, however, if sampling bias enters, and this is quite likely, as Smith (1956) has shown, especially during the spawning period when the sexes are more or less segregated. The key diagnostic difference would be the sex ratio evident in the most youthful mature cohorts.

Lake systems will differ greatly. Lakes with high fish mortalities due to a fishery might leave a relatively small number of survivors to reach the spawning grounds. This would result in minimal epideictic display and in progeny that mature rapidly but live short lives and reach small size. Other lakes where populations are high relative to the capacity of a certain epideictic site might produce quite large, slowly maturing, long-lived forms. It would also be possible, given the presence of two or more different epideictic sites, to have two or more corresponding populations each with its own growth characteristics that appear to have little rapport with the vagaries of food supply. The sympatric occurrence of dwarf and normal forms and their plasticity on transfer to other lakes might thus be explained. There is also the possibility that this dimorphic or polymorphic situation would allow a species to harvest the resources of the lake better, the dwarfs eating small things and the normals eating the larger.

The parental programming of the offspring by endocrine means has been observed by Christian (1975) in mammals, but in this case there is the intimacy of intrauterine contact. In the case of the fish, assuming the male to be the epideictic sex, any message would have to flow via the sperm or the environment. It is possible that the intimate linkage of the interrenal tissue and the kidney is directed toward the release of steroid (or other) hormones (as the soluble conjugates of gluconic and sulfuric acids) into the environment through urinary products, as is the mode of release in other vertebrates. It is also interesting to ponder the phylogeny of the pituitary gland. It is an invagination of the epidermis of the stomodaeum. Could this feature have once been a communicative organ sensing steroid messages directed more to the watery environment than it is now? It is also appropriate to consider steroid hormones in this regard because we are now learning that they appear to function in regulating membrane permeability and the flow of genetic information from DNA to the cytoplasm.

The implications of a population dynamics model stressing endogenous regulation seem quite dramatic to me in terms of fisheries management. For one thing it would convert data on sex ratio, age at maturity, condition indices, and various other observations into increasingly useful prognostic tools. It would also place greater emphasis on ethology, endocrinology, and histology as tools of the fisheries biologist. It would also place special importance on the detection and preservation of spawning (and nearby) grounds as the traditional sites for epideictic behavior. The role of pollutants, especially organic ring compounds, which might mimic the hormonal (pheromonal) messages passing between generations, might also receive additional consideration.

Parthian shots: The evidence, at least as I interpret it, seems to restrict Christian's model to the Salmonidae and other high latitude dwelling forms. The populations of the various Centrarchidae, in contrast, where male nest-and-fry-tending prevails, do not seem to conform nicely to the model. Such forms tend to belong to warmer-water assemblages of high species diversity, where territoriality and ecosystemic controls may be important in the regulation population character. More northerly forms as best illustrated by the Salmonidae, however, participate in relatively simple trophic systems in lake areas where population isolation is common and thus where intrinsic mechanisms of population regulation may be highly adaptive.

Next, the thoughts expressed here are intended only to modify and not to displace our existing ideas on the role of genetic and extrinsic biotic mechanisms in population regulation. Genetic information seems basic to the characteristics that individuals and populations express. It is only the extent to which and how these foundations are able to produce different outcomes; that is, the potential of epigenetic systems. An unexpected result of this might be the realization that these epigenetic processes may, in time, act to change the genetic wellsprings. The sympatry of dwarf and normal-sized forms, for example, may indeed be, in part, the consequence of hormonal-behavioral processes that act to isolate and genetically differentiate segments of an originally unified population. The remarkable frequency of such sympatry implies that the often-used explanation of dual origins may indeed be overworked.

Finally, the changes in the character of populations explained through this behavioral-endocrine model may be more or less rapid and may not entrain every individual fish. Thus, the conventional averaging of the properties of individual fishes may obscure many of the clues that are present and may generate in the mind of the investigator a false sense of population stability and genetically based uniqueness. Thus result the confusion and frustration often associated with the labeling of a certain population as migratory or non-migratory, slow-growing or fast-growing, male- or female-dominated, and so forth. The individual fish must be much more talented, better socially regulated, and more under the influence of its total environment than we usually perceive.

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