

Brain Behav Evol 1989;34:5-12

Embryology, Ethology and Ecology of Ontogenetic Critical Periods in Fish

Howard I. Browman

Department of Systematics and Ecology, University of Kansas, Lawrence, Kans., USA

Key Words. Neurobiology · Fisheries · Aquaculture · Sensitive periods · Morphogenesis · Morphometrics
Epigenesis · Foraging behavior

Abstract. Overviews of critical period concepts, as they appear at several biological levels, are presented. In embryology, critical periods generally refer to restricted periods in development during which undifferentiated groups of cells can be induced to differentiate. In neurobiology, critical periods are those during which neural circuits are particularly plastic and subject to molding by cellular processes and by experience.

The ethological critical period concept advances the idea that an individual's behavioral characteristics can be more strongly influenced by a given event (some stimulus) at one stage of development than at others. For example, this is the period during which young birds imprint upon their parent(s) and learn their species' songs, or during which young salmon imprint to the odor of their home streams.

The fisheries science critical period, an ecological concept, refers to a restricted time in the early life history of fish during which there is massive mortality. For many fish, this event is generally considered the primary factor controlling the size of the adult population. The cause of variable mortality between years is thought to be a result of differential food availability and predation during a critical stage in early fish larval development.

At each biological level of the critical period, spatial and temporal overlap between the developing organism and specific environmental input is essential. It is likely that critical periods in embryology, neurobiology and ethology are causally interrelated in a hierarchical manner and that they can be manifested as ecological critical periods. For example, if the abundance of food for fish larvae is low for the duration of a sensitive period in neural development, the appropriate neural network underlying foraging behaviors may not develop optimally even if food abundance subsequently increases. These fish will die, producing, in this case by definition, an ecological critical period.

Introduction

There is often a lack of communication between scientists working on essentially the same research questions at different levels of analysis. This seems particularly true of fisheries science: fisheries biologists investigating population level problems commonly overlook useful information produced by ichthyologists working at other levels, and vice versa. It seems clear that fish biologists working on embryol-

ogy, neurobiology, ethology or ecology would benefit greatly from insights that can be developed through an interdisciplinary awareness and approach. The purpose of this essay is to illustrate and emphasize this point. To do this effectively, I have chosen to discuss a concept with which readers in all of these sub-disciplines will be familiar, yet which holds a different meaning in each. This concept is that of a critical period.

In embryology, the concept is usually referred to as

a critical or sensitive period and it is framed at the cellular level. In ethology, the concept is associated with the terms critical moments, sensitive phases and imprinting, and in ecology there is a concept known as the critical period hypothesis. Common to all of these concepts is the requirement for spatial and temporal overlap between appropriate genetic and/or environmental input and the developing organism.

In the text that follows, overviews of the critical period concepts at each of these biological levels are presented and it is suggested that they are interrelated in a hierarchical manner. That is, critical periods in an organism's embryological development underlie behavioral critical periods, which may in turn be manifested as ecological critical periods. The possible extent of the interrelations among these processes is explored, as is their relevance to fisheries science, aquaculture and early life history studies in general.

Embryological Concept

Sensitive periods (here considered synonymous with the term critical period) were first identified in experimental embryology: chemical induction of undifferentiated groups of cells occurs only during a restricted stage in their ontogeny. Further, in tissue transplant experiments, undifferentiated cells only assume the characteristics of host location cells if transplanted during this sensitive period [1]. Sensitive periods have subsequently been described, across the phylogenetic series, in a growing number of morphogenetic studies of the brain and peripheral nervous system [2-4].

Neural development, like development generally, is genetically determined and is also influenced by all interactions among gene products, cells, tissues, organs and the environment that result in the formation of an organism (i.e. epigenetic factors [5, 6]). Several other relevant principles of neural development [7] are: (1) Developing nerve cells influence the proliferation and specialization of their neighbors but become less susceptible to such extragenetic influences as development proceeds. (2) As vertebrate neurons mature, they acquire obligatory trophic dependences [8]. Retrograde and anterograde interactions between one nerve cell and its target indicate that neurons affect the properties of their targets and that targets affect the properties of the nerve cells that innervate them [9]. This kind of interdependence is presumably a

means of ensuring that every nerve cell in the adult has a useful function, and it is also a means by which epigenetic factors can affect neural networks. (3) More neurons initially innervate targets than can be trophically supported. As a result, nerve cell terminals compete with one another for trophic support; some survive, while others withdraw and atrophy. This process has been referred to as neuroecology.

With these principles in mind, critical periods in development can be described as representing the time during which tissue differentiation, axonal guidance to target cells, or neurons competing to innervate target cells, are particularly susceptible to genetic and epigenetic influences. It is during critical periods, and perhaps at no other time, that certain genes are activated or deactivated.

Because neural activity influences the competitive interactions between nerve cells vying for target cell trophic support, experience, in the sense of postnatal neural activity, will necessarily affect the end result [10-13]. The seminal examples of this principle have been generated from studies of the visual system, primarily at the level of the visual cortex in cats and monkeys [14].

Susceptibility to the effects of eye closure in kittens begins about the 4th week of life, remains high for several weeks, and finally disappears about 3 months of age [15]. During the period of maximum susceptibility, monocular closure for as little as 3-4 days produces an obvious decline in the number of cortical neurons subsequently activated by that eye: these kittens are functionally blind in the deprived eye. Raising kittens through the sensitive period in a visual environment consisting exclusively of vertical bars results in important changes in cortical connectivity. When tested in the adult animal, an abnormally high percentage of neurons in the primary visual cortex are responsive to vertical stimuli, but few or none are sensitive to horizontal stimuli.

Although clearly manipulative and unnatural, these experiments illustrate that an individual must be exposed to patterned visual input during the critical period or pattern recognition circuits will not develop. Nonetheless, under more natural conditions, it seems that the purpose of the critical period is to allow the outside world to influence cortical connectivity; 'This mechanism may be adaptive, the feature-detecting apparatus of the visual system being optimally matched to the animal's visual environment' [16; also see ref. 17, 18].

Critical periods for deprivation effects occur in other sensory systems, including the neural induction of taste buds in rats [19], the interaction between visual and auditory experience and sound localization maps in the optic tectum of barn owls [20, 21] and visual pattern recognition in flies [22]. Differential activity between the identical paired claws and closer muscles of juvenile lobsters can determine which of the pair will differentiate into the crusher and which the cutter; the side with greater activity becomes the crusher [23]. Further, asymmetries in firing patterns between the motoneurons of mature crusher and cutter claws are affected by bilateral differences in the reflexive activity of the undifferentiated claws during development [24].

Similar processes seem to govern the development of tectal projections in fish [25, 26]. Dark rearing in the cichlid *Sarotherodon mossambicus* affects the laminar structure of the optic tectum: the optic layer is significantly reduced and the structure of synapses altered [27]. Significant reductions in the number of synapses per unit area, and in the length of synaptic contact zones, are observed in the optic tectum of rainbow trout deprived of light during the main period of synaptogenesis [28, 29]. Enucleation in the cichlid *Haplochromis burtoni* results in an enlarged ipsilateral projection to the optic tectum from the intact eye [30]. Further, such alterations in the fish's visual centers are manifested as changes in visual acuity: light-deprived young rainbow trout (*Salmo gairdneri*) and *Sarotherodon* exhibit significantly reduced visual acuity (minimum separable angle) [31, 32]. It should be noted that studies of this nature do not always result in such pronounced changes [33, 34].

Primary sex determination in Atlantic silverside (*Menidia menidia*) is irreversibly influenced by water temperature during larval development [35]. The interaction between genetic and environmental influences on sex determination in this species varies with latitude and is adaptive [36], illustrating how determination of an adult trait during a restricted period in development can have a fundamental impact upon a species' ecology.

All of these concepts and examples address embryological questions aimed at explaining developmental plasticity and the interaction of genetic and epigenetic information in determining neurological and morphological pattern (phenotype). Central to all is spatial and temporal overlap between the developing organism and environmental conditions. Clearly, the

amount and quality of input to which the developing organism is exposed can affect the phenotype expressed and susceptibility to these effects is greater during one or more critical periods in development. In the next section, the ethological analogues of these concepts, as well as evidence illustrating how neurobiological critical periods underlie behavioral critical periods, will be presented.

Ethological Concept

Among the important conclusions of ethological studies is the idea that an individual's behavioral characteristics can be more strongly influenced by a given event at one stage of development than at other stages [37–40]. A corollary of these findings is that during critical periods animals are particularly sensitive to deprivation or abnormal experience, something that may be of significance in aquacultural rearing of fish and invertebrates [33].

Imprinting, the process or set of processes by which various kinds of social preferences can be influenced by experience, must occur during a brief temporal window – a critical period. For example, the masculinizing influences of androgens in rodents and monkeys are only found at certain stages of development; socialization of monkeys must occur during early life or be forever abnormal, and handling of infant rats only influences their behavior as adults if it occurs while they are still being reared by the mother [17]. In chicks, imprinting is associated with an increase in excitatory amino-acid-binding sites in the brain; this could increase the effectiveness of synaptic transmission in the brain areas implicated in imprinting and thereby represent a neural basis for this process [41].

Bird song in some species must be learned during a limited time in the first season. In male song sparrows (*Melospiza melodia* and *georgiana*), song learning begins at 22 days of age and is heavily concentrated in the following 40-day period; 79% of song learning is completed by 50 days, and 90% by 90 days of age. Imitations of songs acquired early in this sensitive period are more complete than those of songs acquired later [42, 43]. Similar results have been obtained in other species [44].

In Salmonids, olfactory imprinting to homestream odor occurs during a restricted phase of development, when juveniles (parr) undergo marked transitions in

morphology, physiology and behavior (smoltification) just prior to their seaward migration [45-47]. Further, rainbow trout exposed to thyroid-stimulating hormone (TSH) before smoltification learn faster and retain the information longer than control fish; postsmoltification fish exposed to TSH do not exhibit this effect [45]. These authors conclude that '... imprinting in salmon requires an alteration in neural substrate and that this alteration requires an increase in the concentration, and perhaps in the binding of thyroid hormones in the brain at a critical period of development ...' [45, p. 99].

In common silversides (*M. menidia*), early experiential contact with conspecifics appears to be an essential element influencing the later establishment of normal schooling behavior. Silversides reared in isolation exhibit a pattern of schooling, and a 'lateral turning' behavior, that is not exhibited by fish reared with conspecifics [48]. In the cichlid fish *H. burtoni*, mate choice and recognition of conspecifics is also affected by early experience [49] and in toads (*Bufo americanus*) there is a sensitive period in early development during which tadpoles familiarize themselves with other individuals [50].

All of these concepts and examples address ethological questions and are aimed at explaining the effects of experience during a restricted temporal window on behavioral expressions later in the life history. Again, all are based upon spatial and temporal overlap between the developing organism and the environmental conditions around it. In several cases it has been clearly established that changes in an animal's neurological and morphological make-up, which are themselves influenced by critical periods, underlie critical periods in behavioral development. In the next section, a critical period framed at the ecological level will be described and, in the section following that, the assertion that neurobiological and behavioral critical periods can be manifested at higher levels will be explored.

Ecological Concept

For many fish stocks, annual fluctuations in egg production or adult biomass remain within an order of magnitude but year class size (the number of fish in the population of a given age, a cohort) fluctuates over several orders of magnitude without obvious relationship to adult population size [51]. This has led

ecologists to ask why there is such a poor relationship between the size of the spawning population and the number of young fish derived from it (recruits) [52, 53]. It is now generally agreed that the precipitous decline in survivorship observed in the early life history of many fish controls the size of adult populations. This mortality is considered to result mainly from starvation and predation [53-55].

Hjort [56] made two important generalizations about the question of variance in the size of adult populations. The first is that year class size is determined early in the life history prior to recruitment to the fishery and the second, that year class size is not a simple function of egg production. Hjort hypothesized that the timing between spawning and phytoplankton blooms, both of which are variable, was at the heart of the variance problem: the cause of differential mortality between years is a result of differential food availability (young stages of zooplankton) at a critical stage in early fish larval development. This has come to be known as the critical period hypothesis.

Elaborations and formalizations of this hypothesis include Cushing's match/mismatch theory [57] and Sinclair's recently proposed member/vagrant hypothesis [53]. The match/mismatch theory proposes that the degree of overlap between a fish population's fixed time of spawning and the annually variable timing of phytoplankton and zooplankton blooms determines year class size. Sinclair's [53] hypothesis expands upon Cushing's with the assertion that the size of a population's distributional area (which is characterized by specific oceanographic features), determines its absolute abundance. In this hypothesis, temporal variability in abundance is a function of intergenerational losses of individuals, through vagrancy (emigration) and mortality, from the species' distributional area(s).

These fishery (ecological) hypotheses are aimed at explaining annual variability in the size of year classes. Central to all is spatial and temporal overlap between the developing fish and the environmental conditions (e.g. food and predator abundance) most appropriate for survival. In the next section it is asserted that, under some conditions, the effects of embryological and neurological critical periods on phenotypic and behavioral expressions may be manifested, at the ecological level, as critical periods such as that which so dramatically influences fish populations.

A Synthesis: Critical Periods Are Hierarchically Interrelated

That embryological, neurological and ethological critical periods are causally interrelated has been well established. However, the manifestations of such critical periods at the ecological level are still uncertain. Nonetheless, it seems likely that embryological, neurobiological and ethological critical periods may be manifested as ecological critical periods. How this might be so, at least for the critical period of fisheries ecology, is as follows.

Just as in the cases of bird song development, imprinting in salmon, schooling behavior in silversides or crusher claw determination in crustaceans, the developing nervous system and behavioral repertoires of fish larvae are affected by environmental input. This was suggested by Blaxter [33], who stated that 'During development, a lack of input could prevent the proper morphogenesis of the sense organs and their central connections ... and that ... there may well be sensitive periods in development where the need for input is especially vital'.

As already stipulated, for each biological level of the critical period, spatial and temporal overlap between the developing organism and specific environmental input is essential. Thus, in the match/mismatch theory or member/vagrant hypothesis, if the abundance of food for fish larvae is low for the duration of a sensitive period in neural development then, just as in the case of pattern recognition in kittens, the appropriate neural network underlying foraging behaviors may not develop optimally even if food abundance subsequently increases. Given the principles and examples set out in the preceding sections, it is clear that inappropriate or suboptimal neural networks resulting from inadequate or inappropriate input during the critical period will be manifested in an animal's behavior: in this case, a fish larva that is an inefficient or ineffective predator. A small, fragile and incompletely developed fish larva swimming about in a pelagic environment is extremely susceptible to both starvation and predation. The best way to minimize this susceptibility is to grow rapidly, something for which effective foraging behavior is required. A larva that comes through the critical period as an ineffective or inefficient predator will clearly be more susceptible to starvation and predation. This increased susceptibility is manifested as a substantial increase in mortality, an ecological critical period.

Simply stated, developing fish that are not exposed to appropriate stimuli (food) during an embryological critical period will not establish the neural network necessary for effective foraging behavior and will not be able to exploit food, even if it subsequently becomes available. The same reasoning can be applied to the development of other behaviors, including predator avoidance and orientation [46].

Most of the evidence and examples presented in the descriptions of critical periods were generated from somewhat artificial and manipulative studies. As a result, it is fair to ask whether these processes are of any real significance in the natural environment. Though the effects of epigenetic and sensitive period processes on fish in the wild may sometimes be subtle, they may still be significant, even if they result in a viable but *suboptimally* performing individual or population. These processes may also help explain the great individual variability in behavior and morphology observed in fish [58].

Further Evidence and Implications for Fisheries Biology and Aquaculture

Though the effects of epigenetic and critical period processes on wild fish may sometimes be subtle, their effects on cultivated fish are likely to be far more obvious. In this section, evidence, drawn primarily from aquacultural and experimental studies that compare wild and artificially reared individuals, is presented in support of this assertion. Some of the implications for fish husbandry and fisheries that this work suggests are also put forward.

Morphological Differences

Jewel fish (*Hemichromis bimaculatus*), raised in the laboratory under conditions of long-term (4 years) crowding (3.3 liters/fish; a common situation in hatchery-raised fish), exhibit a decreased density of dendritic spines in the optic tectum. Overall spine length and spine stem length are significantly reduced in crowded fish [59]. Additionally, short-term crowding or lack of social interaction in juvenile jewel fish arrests the formation of dendritic spines [60, 61]. Such differences in neuronal morphology, which may prevent fish from employing their full repertoire of social, escape and defensive behaviors, have profound implications for hatchery production schemes, par-

ticularly in situations where the fish are to be released into the wild.

Hatchery-raised and wild fish also commonly differ in gross morphological features, such as jaw structure, eye diameter and lateral-line length [62-64]. Further, in the cichlid fish *Cichlasoma managuense*, phenotypic changes in morphology are attributed to retardation of normal developmental rates (heterochronies) [65]. In this study, two groups of siblings were fed different diets for 8 months after the onset of feeding and subsequently the same diet. Phenotypes that differed significantly at 8.5 months converged at 16.5 months, however, if feeding on two different diets is continued after 8.5 months the phenotypes remain distinct. It should be noted that the functional significance of these phenotypic differences was not determined in this study. Sticklebacks (*Gasterosteus aculeatus*) from two ponds, one in which zooplankton abundance was high and one in which it was low, exhibit different gape sizes and gill raker spacings which seem to be correlated with prey capture efficiency [66].

Since morphometric characters are used extensively in the identification and differentiation of closely related fish populations, morphological variability among fish populations or cohorts, resulting from exposure to different environmental conditions during ontogeny, have serious consequences for their use in fish stock identification [67-69].

Behavioral Differences

Hatchery-reared fish do not feed as effectively upon release as do their wild counterparts; it may take up to 2 months for fish reared on an artificial and inanimate diet to feed successfully on living prey. Further, there are indications that such fish may never develop as flexible and broad a range of foraging skills as do wild fish [see discussion in ref. 70]. For example, 2 months after release as parr, hatchery-reared Atlantic salmon (*Salmo salar*) consumed fewer total prey and exploited a restricted number of taxa relative to wild fish [71]. Hatchery brown trout (*Salmo trutta*) fed less, moved more and used energy-minimizing features of the substrate less than wild trout [72]. The positioning of hatchery-reared Atlantic salmon over the substrate in streams was different from that of their wild counterparts, indicating differences in substrate choice and interindividual interactions [73]. Further, fish reared in hatcheries at high density commonly exhibit pronounced agonistic behavior which persists after release into a far less crowded environment.

Summary and Concluding Remarks

It has been asserted that critical periods at different biological levels are hierarchically interrelated: even what might be considered subtle changes in an animal's neurological make-up will alter its transduction of sensory information and therefore its behavioral responses. Changes in behavior, particularly inappropriate ones - imprinting to a human, not learning your species' correct or full repertoire of songs, not developing the capacity to effectively identify and attack prey items or initiate escapes from predators - will leave an animal unfit to efficiently feed itself or defend itself from predators. At the population level, the suboptimal performance resulting from these processes may be manifested as ecological critical periods such as that described for fish.

This synthesis of information on critical periods, and the discovery that interrelationships among critical periods at different biological levels have not been adequately explored, illustrates the need for interdisciplinary and synoptic approaches to research on the early life history of fish. The insights and interdisciplinary awareness that can be generated from such an approach are both interesting and significant.

Acknowledgments

For the thoughts presented here I am indebted to a paper by John Blaxter [33] and to many hours of stimulating discussion with Brian Marcotte. I thank the following individuals for their suggestions and efforts in helping to improve the clarity of this essay: William Bell, Nancy Dahl, Michael Fine, Michael Gaines, Craig Hawryshyn, Brian Marcotte, Eric Maurer and John O'Brien.

My work on larval fish is supported by NSF grant BSR 8717454 to W. John O'Brien, and by a Natural Sciences and Engineering Research Council of Canada postgraduate scholarship and a Quebec Ministry of Higher Education and Science bursary to HIB. My participation in the Ann Arbor symposium was supported by these agencies and by a travel grant from the Kansas University Endowment Association.

References

- 1 Saxon L, Toivonen S: Primary Embryonic Induction. Englewood Cliffs, Prentice-Hall, 1962.
- 2 Scott JP: Critical Periods. Stroudsburg, Hutchinson & Ross, 1978.
- 3 Bornstein MH: Sensitive Periods in Development. Hillsdale, Erlbaum, 1987.
- 4 Rauschecker JP, Marler P: Imprinting and Cortical Plasticity:

- Comparative Aspects of Sensitive Periods. New York, Wiley, 1987.
- 5 Lovtrup S: Epigenetics: A Treatise on Theoretical Biology. London, Wiley, 1974.
 - 6 Balon EK: Reflections of epigenetic mechanisms: Hypotheses and case histories. *Dev Envir Biol Fishes* 1985;5:239-270.
 - 7 Purves D, Lichtman JW: Principles of Neural Development. Sunderland, Sinauer, 1985.
 - 8 Davies AM: The emerging generality of the neurotrophic hypothesis. *Trends Neurosci* 1988;11:243-244.
 - 9 Purves D, Snider WD, Voyvodic JT: Trophic regulation of nerve cell morphology and innervation in the autonomic nervous system. *Nature* 1988;336:123-128.
 - 10 Bateson P: Imprinting as a process of competitive exclusion; in Rauschecker JP, Marler P (eds): Imprinting and Cortical Plasticity: Comparative Aspects of Sensitive Periods. New York, Wiley, 1987, pp 151-168.
 - 11 Davies AM: Molecular and cellular aspects of patterning sensory neurone connections in the vertebrate nervous system. *Development* 1987;101:185-208.
 - 12 Edelman GM: Neural Darwinism: The Theory of Neuronal Group Selection. New York, Basic Books, 1987.
 - 13 Renner MJ, Rosenzweig MR: Enriched and Empoverished Environments: Effects on Brain and Behavior. New York, Springer, 1987.
 - 14 Wiesel T: Postnatal development of the visual cortex and the influence of the environment. *Nature* 1982;299:583-591.
 - 15 Hubel DH, Wiesel TN: The period of susceptibility to the physiological effects of unilateral eye closure in kittens. *J Physiol (Lond)* 1970;206:419-436.
 - 16 Blakemore C: Developmental factors in the formation of feature detecting neurons; in Schmitt FO, Worden FG (eds): The Neurosciences. Third Study Program. Cambridge, MIT Press, 1974, pp 105-113.
 - 17 Bateson P: How do sensitive periods arise and what are they for? *Anim Behav* 1979;27:470-486.
 - 18 Bornstein MH: Sensitive periods in development: Definition, existence, utility, and meaning; in Bornstein MH (ed): Sensitive Periods in Development. Hillsdale, Erlbaum, 1987, pp 3-17.
 - 19 Hosley MA, Hughes SE, Morton LL, et al: A sensitive period for the neural induction of taste buds. *J Neurosci* 1987;7:2075-2080.
 - 20 Knudsen EI: Early blindness results in a degraded auditory map of space in the optic tectum of the barn owl. *Proc Natl Acad Sci USA* 1988;85:6211-6214.
 - 21 Knudsen EI: Sensitive and critical periods in the development of sound localization; in Easter SS Jr, Barald KF, Carlson BM (eds): From Message to Mind: Directions in Developmental Neurobiology. Sunderland, Sinauer, 1988.
 - 22 Mimura K: Development of visual pattern discrimination in the fly depends on light experience. *Science* 1986;232:83-85.
 - 23 Govind CK, Pearce J: Differential reflex activity determines claw and closer muscle asymmetry in developing lobsters. *Science* 1986;233:354-356.
 - 24 Lnenicka GA, Blundon JA, Govind CK: Early experience influences the development of bilateral asymmetry in a lobster motoneuron. *Dev Biol* 1988;129:84-90.
 - 25 Vanegas H: Organization and physiology of the teleostean optic tectum; in Davis RE, Northcutt RG (eds): Fish Neurobiology, vol 2, Higher Brain Areas and Functions. Ann Arbor, University of Michigan Press, 1983, pp 43-90.
 - 26 Fritzsche B: Neuroembryology of teleosts: Patterns and processes. *Zool Wetensch Ann Sci Zool* 1986;251:73-80.
 - 27 Zeutzius I, Rahmann H: Influence of dark-rearing on the ontogenetic development of *Sarotherodon mossambicus* (Cichlidae, Teleostei): II. Effects on allometric growth relations and differentiation of the optic tectum. *Exp Biol* 1984;43:87-96.
 - 28 Jeserich G, Rahmann H: Effects of light deprivation on fine structural changes in the optic tectum of the rainbow trout (*Salmo gairdneri*, Rich.) during ontogenesis. *Dev Neurosci* 1979;2:19-24.
 - 29 Zeutzius I, Rahmann H: Quantitative ultrastructural investigations on synaptogenesis in the cerebellum and the optic tectum of light-reared and dark-reared rainbow trout (*Salmo gairdneri* Rich.). *Differentiation* 1980;17:181-186.
 - 30 Fritzsche B, Wilm C, Crapon de Caprona MD: Ipsilateral retinofugal and retinopetal projections in normal and monocular cichlid fish. *Neurosci Lett* 1987;78:259-264.
 - 31 Rahmann H, Jeserich G, Zeutzius I: Ontogeny of visual acuity of rainbow trout under normal conditions and light deprivation. *Behaviour* 1979;68:315-322.
 - 32 Zeutzius I, Rahmann H: Influence of dark-rearing on the ontogenetic development of *Sarotherodon mossambicus* (Cichlidae, Teleostei): I. Effects on body weight, body growth pattern, swimming activity and visual acuity. *Exp Biol* 1984;43:77-85.
 - 33 Blaxter JHS: Sensory deprivation and sensory input in rearing experiments. *Helgo Wiss Meeresunters* 1970;20:642-654.
 - 34 Raymond PA, Bassi CJ, Powers MK: Lighting conditions and retinal development in goldfish: Photoreceptor number and structure. *Invest Ophthalmol Vis Sci* 1988;29:27-36.
 - 35 Conover DO, Heins SW: The environmental and genetic components of sex ratio in *Menidia menidia* (Pisces: Atherinidae). *Copeia* 1987:732-743.
 - 36 Conover DO, Heins SW: Adaptive variation in environmental and genetic sex determination in a fish. *Nature* 1987;326:496-498.
 - 37 Hess EH: Imprinting: Early Experience and the Developmental Psychobiology of Attachment. New York, Van Nostrand & Reinhold, 1973.
 - 38 Horn G: Memory, Imprinting and the Brain: An Inquiry into Mechanisms. Oxford, Clarendon Press, 1985.
 - 39 Bateson PPG, Hinde RA: Developmental changes in sensitivity to experience; in Bornstein MH (ed): Sensitive Periods in Development. Hillsdale, Erlbaum, 1987, pp 19-34.
 - 40 Klopfer P: Metaphors for development: How important are experiences early in life? *Dev Psychobiol* 1988;21:671-678.
 - 41 McCabe BJ, Horn G: Learning and memory: Regional changes in N-methyl-D-aspartate receptors in the chick brain after imprinting. *Proc Natl Acad Sci USA* 1988;85:2849-2853.
 - 42 Marler P, Peters S: A sensitive period for song acquisition in the song sparrow, *Melospiza melodia*: A case of age-limited learning. *Ethology* 1987;76:89-100.
 - 43 Marler P, Peters S: Sensitive periods for song acquisition from tape recordings and live tutors in the swamp sparrow *Melospiza georgiana*. *Ethology* 1988;77:76-84.
 - 44 Slater PJB, Eales LA, Clayton NS: Song learning in zebra finches (*Taeniopygia guttata*): Progress and prospects. *Adv Study Behav* 1988;18:1-34.
 - 45 Hasler AD, Scholz AT: Olfactory Imprinting and Homing in

- Salmon: Investigations into the Mechanisms of the Imprinting Process. Berlin, Springer, 1983.
- 46 Dodson JJ: The nature and role of learning in the orientation and migratory behavior of fishes. *Dev Envir Biol Fishes* 1988; 23:161-182.
- 47 Morin P-P, Dodson JJ, Dore FY: Cardiac responses to a natural odorant as evidence of a sensitive period for olfactory imprinting in young Atlantic salmon, *Salmo salar*. *Can J Fisher Aquat Sci* 1989;46:122-130.
- 48 Williams MM, Shaw E: Modifiability of schooling behavior in fishes: The role of early experience. *Am Mus Novitates* 1971; 2448:1-19.
- 49 Cragon de Caprona MD: The influence of early experience on preferences for optical and chemical cues produced by both sexes in the cichlid fish *Haplochromis burtoni* (*Astatotilapia burtoni*, Greenwood 1979). *Z Tierpsychol* 1982;58:329-361.
- 50 Waldman B: Ecological correlates and potential functions of kin recognition and kin association in anuran larvae. *Behav Genet*, in press.
- 51 Ricker WE: Stock and recruitment. *J Fisher Res Board Can* 1954;11:559-623.
- 52 Pitcher TJ, Hart PJB: *Fisheries Ecology*. Westport, Avi, 1983.
- 53 Sinclair M: *Marine Populations: An Essay on Population Regulation and Speciation*. Seattle, Washington Sea Grant Program and University of Washington Press, 1988.
- 54 Hunter JR: Feeding ecology and predation in marine fish larvae; in Lasker R (ed): *Marine Fish Larvae*. Seattle, University of Washington Press, 1981, pp 33-77.
- 55 Leggett WC: The dependence of fish larval survival on food and predator densities; in Skreslet S (ed): *The Role of Freshwater Outflow in Coastal Marine Ecosystems*. Berlin, Springer, 1986, pp 117-137.
- 56 Hjort J: Fluctuations in the great fisheries of northern Europe. *Rapp Proc-Verb Réunion Cons Int Explor Mer* 1914;20:1-228.
- 57 Cushing DH: *Marine Ecology and Fisheries*. London, Cambridge University Press, 1975.
- 58 Magurran AE: Individual differences in fish behavior; in Pitcher TJ (ed): *The Behaviour of Teleost Fishes*. Baltimore, The Johns Hopkins University Press, 1986, pp 338-365.
- 59 Burgess JW, Coss RG: Effects of chronic crowding stress on midbrain development: Changes in dendritic spine density and morphology in jewel fish optic tectum. *Dev Psychobiol* 1982; 15:461-470.
- 60 Burgess JW, Coss RG: Short-term juvenile crowding arrests the developmental formation of dendritic spines on tectal interneurons in jewel fish. *Dev Psychobiol* 1981;14:389-396.
- 61 Coss RG, Globus A: Social experience affects the development of dendritic spines and branches on tectal interneurons in the jewel fish. *Dev Psychobiol* 1979;12:347-358.
- 62 Matsumiya Y, Kanamaru H, Oka M, et al: Morphometric comparison between artificially released red sea bream and 0-age wild fish. *Bull Jap Soc Scient Fisher* 1984;50:1173-1178.
- 63 Witte F: Consistency and functional significance of morphological differences between wild-caught and domestic *Haplochromis squamipinnis* (Pisces, Cichlidae). *Neth J Zool* 1984;34: 596-612.
- 64 Suda Y, Shimizu M, Nose Y: Morphological differences between cultivated and wild jack mackerel *Trachurus japonicus*. *Nippon Suisan Gakk* 1987;53:59-61.
- 65 Meyer A: Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implications for speciation in cichlid fishes. *Evolution* 1987;41:1357-1369.
- 66 Ibrahim AA, Huntingford FA: Foraging efficiency in relation to within-species variation in morphology in three-spined sticklebacks, *Gasterosteus aculeatus*. *J Fish Biol* 1988;33:823-824.
- 67 Blouw DM, Saxon SD, Chadwick EMP: Temporal variation of meristic traits within an Atlantic salmon (*Salmo salar*) stock, and implications for stock identification. *Can J Fisher Aquat Sci* 1988;45:1330-1339.
- 68 Corti M, Thorpe RS, Sola L, et al: Multivariate morphometrics in aquaculture: A case study of six stocks of the common carp (*Cyprinus carpio*) from Italy. *Can J Fisher Aquat Sci* 1988;45: 1548-1554.
- 69 Lindsey CC: Factors controlling meristic variation; in Hoar WS, Randall DJ (eds): *Fish Physiology: The Physiology of Developing Fish. Viviparity and Posthatching Juveniles*. New York, Academic Press, 1988, vol 11B.
- 70 Marcotte BM, Browman HI: Foraging behavior in fishes: Perspectives on variance. *Envir Biol Fishes* 1986;16:25-33.
- 71 Sosiak AJ, Randall RG, McKenzie JA: Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. *J Fisher Res Board Can* 1979;36:1408-1412.
- 72 Bachman RA: Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Trans Am Fisher Soc* 1984;113:1-32.
- 73 Dickson TA, MacCrimmon HR: Influence of hatchery experience on growth and behavior of juvenile Atlantic salmon (*Salmo salar*) within allopatric and sympatric stream populations. *Can J Fisher Aquat Sci* 1982;39:1453-1458.

Howard I. Browman
 Department of Biology
 University of Montreal
 C.P. 6128, Succ. 'A'
 Montreal, Quebec H3C 3J7 (Canada)