Stress, environment and reproduction in teleost fish

Roland Billard, Christian Bry, Christian Gillet

Roland Billard, Christian Bry, Christian Gillet. Stress, environment and reproduction in teleost fish. Stress and fish, Academic Press, 1981, 0-12-554550-9. hal-01600274

9. Stress, Environment and Reproduction in Teleost Fish

R. BILLARD, C. BRY and C. GILLET

Laboratoire de Physiologie des Poissons, I.N.R.A.,
78350 Jouy-en-Josas, France

Abstract. The effects of acute or chronic stress on reproduction and hormone levels are well documented in higher vertebrates. On the contrary, little information is available on fish. It is known that some aspects of fish reproduction are changed by various modifications to the environment and that some of these changes may occur under conditions of stress. Reproduction can be stimulated or inhibited by environmental factors such as temperature, photoperiod, food availability and water quality, by overcrowding and social interaction and by other stresses such as handling, captivity and confinement. Under these conditions, several steps of the reproductive cycle can be blocked: gametogenesis (initiation, completion, quantity of eggs [fecundity] and quality of gametes); oocyte maturation and ovulation; spermiation; spawning behaviour.

There are only a few data in fish showing interactions between gonadotrope and corticotrope systems and the effect of environmental factors on the endocrinology of reproduction.

I INTRODUCTION

The fish's environment is a complex system with varying water quality (physical and chemical composition), current velocity, abundance and type of aquatic vegetation, light intensity and periodicity, temperature, food availability and social interaction. In the case of cultivated or managed species, man's influence is of major importance when fish are extensively or intensively reared in captivity for breeding, stocking or human consumption. Under these conditions the fish are submitted to confinement, handling, grading and drug treatment. Man may also have an indirect effect on fish *via* changes made in the natural environment and through pollution. Most of the environmental factors fluctuate throughout the year in both temperate and tropical zones, and fish are adapted in various ways to these changes. Some fish are even adapted for survival in an apparently hostile environment, tolerating sub-zero temperatures and high pressure in the ocean as well as dry conditions. Fish respond to these environmental changes in many ways by modifying their hormone or neuro-hormone secretion, metabolism and behaviour (for a review see Chavin, 1973).

A stress response may be defined as the series of rather non-specific reactions of an organism to any of the exacting demands made on it (for further discussion of this concept see Pickering, 1981, this volume). This phenomenon involves both physiological and behavioural reactions which may help the fish adapt to a new situation. A stress maintained over a long period may exceed the adjustment capabilities of the animal, severely disturbing growth and reproduction. Neuro-endocrine activation, among other reactions, has been shown to occur under adverse conditions in various fish species, leading to the secretion of corticosteroids and catecholamines (see Mazeaud *et al.*, 1977; Strange *et al.*, 1977). The interrenal gland however may also be activated in natural, non-stressful situations, especially in the female fish at ovulation and spawning time. Thus, the same endocrine system (pituitary–interrenal axis) may be activated by factors inhibiting reproduction and by others triggering final maturation. Moreover, the nature of the response to external elements depends upon internal factors and endogenous rhythms, and also varies according to the species and between individuals of the same species. For example, Mitton and Koehn (1976) noted individual differences in the response of *Fundulus heteroclitus* to temperature. Similarly, Sawara and Egami (1977) demonstrated differences in the gonadal response of *Oryzias latipes* collected from different localities to photoperiod changes and Weibe (1968) showed that the environmental factors which stimulate gametogenesis in *Cymatogaster aggregata* are not the same for males and females. The response of fish to changes in the environment also varies with respect to the degree of domestication of the species.

The present paper deals with the effects of environmental factors, including situations which can be considered stressful, on the reproductive function in teleost fish.

II FACTORS INTERFERING WITH REPRODUCTION

(a) Temperature, Thermoperiod and Photoperiod

Temperature level and changes in temperature and photoperiod during the year are the main physical environmental factors in the control of fish reproduction in the temperate zones. The importance of these factors varies with the species and the stage of the reproductive cycle.

The water temperature directly affects fish physiology, mode of reproduction, growth rate and population dynamics and structure. Hokanson (1977) classified temperate zone fish as stenotherms, mesotherms and eurytherms, according to their thermal requirements (Table I—for a further discussion of temperature relationships in fish the reader is referred to Elliott, 1981, this volume). An optimal temperature level is necessary for reproduction. In cyprinids, gametogenesis is sensitive to both low and high temperatures (Gillet *et al.*, 1977a, b); low temperatures are required to initiate gametogenesis (Ahsan, 1966; de Vlaming, 1974; Gillet *et al.*, 1977a, b), whilst high temperatures stimulate gonadotropin (maturational hormone) secretion and temporarily inhibit gametogenesis (Gillet *et al.*, 1977b; Gillet and Billard, 1977; Gillet *et al.*, 1978). Warm-water fish such as the guppy, *Poecilia reticulata*, show optimal spermatogenesis at 25°C (Billard, 1968), coinciding with the thermal preference (Billard, 1968; Johansen and Cross, 1980). In rainbow trout, *Salmo gairdneri*, gametogenesis occurs at either 8 or 18°C (Billard and Breton, 1977), but the fish do not ovulate and the early stages of embryonic development are perturbed at 18°C (K. Goriczko, personal communication; Kazakov, 1971). Salmonid gamete physiology is also affected by temperature; the fertilization rate decreases slightly when artificial insemination is carried out near 0°C (Billard, 1980).

During the year, the temperature varies simultaneously with the photoperiod, and the effects of these two variables can only be distinguished by experimentation. The extensive data in the literature on this subject have been thoroughly reviewed by de Vlaming (1974), Htun-Han (1977) and Peter and Crim (1979). A typical example of a strong photoperiodic influence on reproduction is that of salmonid gametogenesis (spermatogenesis and vitellogenesis) which occurs normally under decreasing photoperiod but which can be advanced if the decreasing photoperiod is artificially advanced (Breton and Billard, 1977) or if the annual photoperiod is contracted into a 6-month period (Whitehead *et al.*, 1978). However, other external or internal factors must also be involved because there are several indications that gametogenesis occurs normally when trout are kept under constant light or constant dark from hatching (Pyle, 1969; Bieniarz, 1973). The photoperiodic effect is more subtle in other teleost fish; the increasing daylength in late winter facilitates gonad growth in goldfish, *Carassius auratus* (Gillet *et al.*, 1978), and tench, *Tinca tinca* (Quillier, 1981), and induces nycthemeral fluctuations in plasma gonadotropin (Hontela and Peter, 1978; Gillet *et al.*, 1980). A slight photoperiodic effect is evident in *Couesius plumbeus* when kept at low temperatures (Ahsan,

TABLE I Classification of some Temperate Climate Freshwater Fish According to Water Temperature Requirements: Effects of Temperature and Photoperiod on Gametogenesis and Spawning.

Classification	Ultimate upper incipient lethal temperature	Physiological optimum	Gametogenesis			Spawning		Examples
			Season	Temp.	Photop.	Season	Temp.	
Temperate stenotherm	<26°C	<20°C	Summer	<20°C	↘	Autumn to spring	5–15°C	Salmonids
Temperate mesotherm	28–34°C	20–28°C	Summer to winter	<12°C	↘	Spring	2–23°C	Percids Pike
Temperate eurytherm	>34°C	>28°C	Summer and spring	>10–12°C	↗	Spring and summer	>15–18°C	Cyprinids

1966). Long days are necessary for gonad growth in the stickleback, *Gasterosteus aculeatus*, (Baggerman, 1969) whose photostimulatory sensitivity shows a daily rhythm with an optimum 14 to 16 h after the onset of the light period (Baggerman, 1972).

In conclusion, changes in temperature and light are the obvious cues for temperate zone fish. Circannual changes in photoperiod act mainly on long-term processes like gametogenesis, while temperature fluctuation influences the short-term processes such as spermiation, oocyte maturation, ovulation and oviposition. Light and temperature may interact in goldfish where ovulation is synchronized with circadian changes in light (Stacey *et al.*, 1979a, b).

(b) Water Quality

The physico-chemical properties of the water, represented by such factors as current velocity, dissolved oxygen content, pH and salinity are prime factors in the survival of aquatic animals and may be critical for reproduction. For example, the water current velocity has been shown to influence the spawning activities of *Tilapia nilotica* (Maruyama and Nagashima, 1978).

(i) *Acidic waters.* The effect of acidic water on fish physiology is now well documented (see review by Fromm, 1980). Low pH decreases fecundity and egg fertility in fathead minnows, *Pimphales promelas* (Mount, 1973), flagfish, *Jordanella floridae* (Ruby *et al.*, 1977; Craig and Baski, 1977) and brook trout, *Salvelinus fontinalis* (Menendez, 1976). The final part of the reproductive cycle is also disturbed. For example, Beamish (1976) noted that female fish did not release their ova in acidic waters and low pH is reported to adversely affect successful fertilization (Billard, 1980), embryogenesis (Daye and Garside, 1980) and hatching (Johansson *et al.*, 1973; Mount, 1973; Peterson *et al.*, 1980). In acid water, *Catostomus commersoni* shows a reduced feeding response and weight loss which may interfere with reproduction (Beamish, 1972).

(ii) *Dissolved oxygen content.* Little information is available concerning the direct effect of reduced water oxygen levels on reproduction. A low level of dissolved oxygen depresses the growth of the gonad in goldfish (Gillet *et al.*, 1981) and an oxygen concentration of less than 1 mg l^{-1} prevents spawning in the fathead minnow (Brungs, 1971). Similarly, 2–4 mg l^{-1} dissolved oxygen prevents spawning in the black crappie, *Pomoxis nigromaculatus* (Siefert and Herman, 1977; Carlson and Herman, 1978).

(iii) *Salinity.* In some euryhaline species, several stages of the reproductive process are inhibited in fresh water. For instance in Israel, *Mugil cephalus* kept in fresh water do not reproduce; ovarian development is inhibited when the females are kept in freshwater ponds and ovulation is inhibited in Lake Kinneret (Abraham and Blanc, 1966; Blanc and Abraham, 1968; Eckstein, 1975). However, Stequert (1972) stated that *Mugil labrosus* spawns normally in fresh water in the Arcachon Basin in France although he also indicated that confinement of female sea bass, *Dicentrarchus labrax*, in fresh water inhibits oocyte maturation and ovulation. Nevertheless, it seems that complete spermatogenesis and spermiation may occur in male sea bass in salinities as low as 1–2‰ (Roblin, 1980).

(iv) *Pollution.* The effects of numerous pollutants are detrimental to gametogenesis and reproduction. Global studies show that fish fecundity is reduced in a polluted environment (Zalewski, 1979). Sometimes, the depressed reproduction observed in polluted water cannot be related to any particular factor, which suggests a possible synergism of the various sources of pollution (Dean and Bailey, 1979).

Pollutants such as selenium (Cumbie and Van Horn, 1979), copper (Benoit, 1975), mercury (Kihlstrom *et al.*, 1971), waste-oil (Hedtke and Puglisi, 1980) and the pesticides PCB (Nebeker *et al.*, 1974; Bengtsson, 1980), parathion (Billard and de Kinkelin, 1970) and DDT (Macek, 1968a; Saxena and Garg, 1978) may alter or inhibit various steps in fish reproduction. In addition, pesticides accumulated in the ovaries can be harmful during embryogenesis and reduce hatching and fry survival (Burdick *et al.*, 1964, 1972). Brook trout fed a sublethal concentration of DDT are more sensitive to stress, and the mortality of DDT-exposed fish is caused by interactions with various factors, including the physiological state associated with spawning (Macek, 1968b).

(c) Food Availability

Availability of food is also an important factor affecting reproduction. A lack of food usually leads to decreased fecundity in the plaice, *Pleuronectes platessa* (Bagenal, 1966), salmonids (Scott, 1962; Bagenal, 1969), the roach, *Rutilus rutilus* (Kuznetzov and Khalitov, 1978) and in the guppy (Dahlgren, 1979). Starved females tend to produce fewer eggs but the egg size remains the same. However, the decreased egg diameter in severely starved brown trout, *Salmo trutta* L., fed dry pellets at a rate of 0·4% body wt day^{-1} is accompanied by a reduction of absolute fecundity but an increased relative fecundity (Fig. 1). The problem of food availability, linked to the size of the territory, may be different for males and females (Ebersole, 1980). A decrease in fecundity was also attributed to a copepod infestation in rainbow trout (Gall *et al.*, 1972).

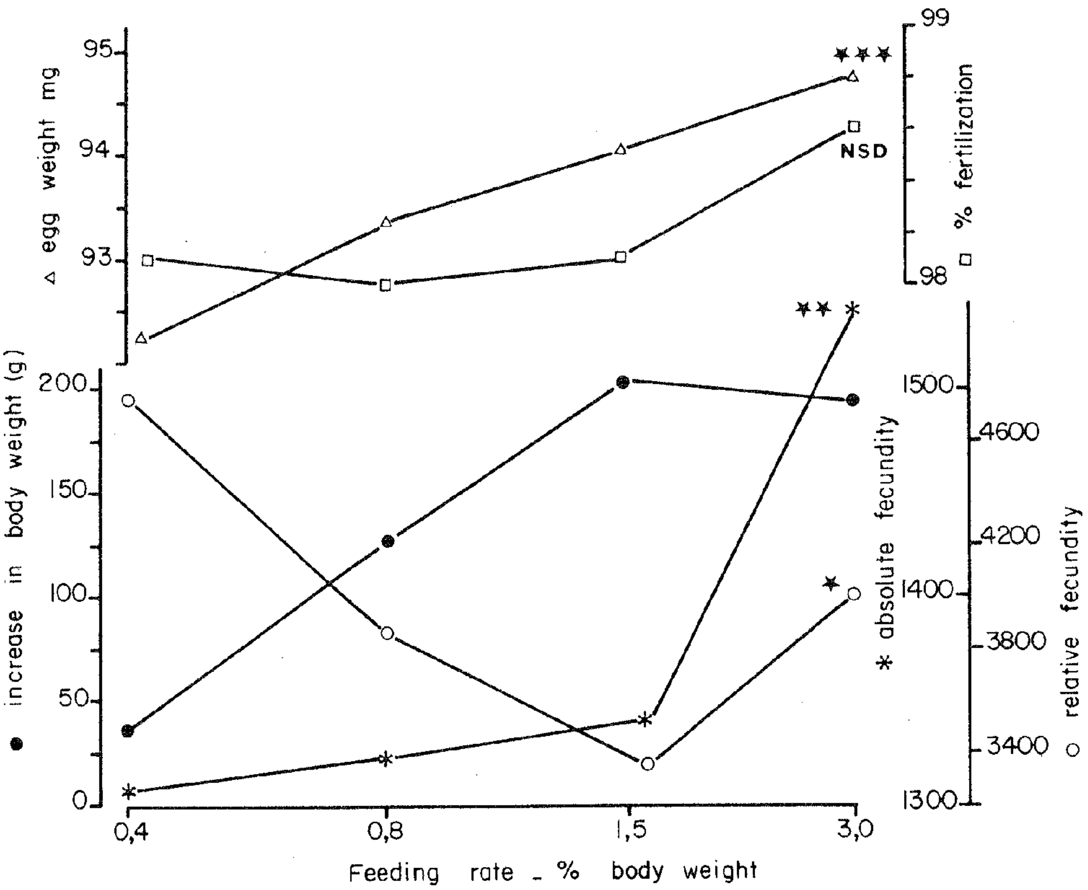

Fig. 1 Effect of feeding rate on absolute (total number of eggs stripped per female) and relative (number of eggs kg^{-1} body wt) fecundity, egg weight and egg fertility of the brown trout. Body weight increase corresponds to the feeding period from March to September (Billard and de Fremont, 1980. Comparison by analysis of variance: one star $p < 0{\cdot}05$, two stars $p < 0{\cdot}01$, three stars $p < 0{\cdot}001$.

(d) Social Environment

Social pressure caused by overcrowding may interfere with fecundity and the final step of reproduction independently of food availability. In poecilids, the follicles show atresia and vitellogenesis is inhibited by high population densities (Ball, 1960) and a decreased fecundity has been reported in pike which is possibly related to high population density (Kipling and Frost, 1969). Social pressure may be direct (aggression) or indirect (pheromonal mediation). There is increasing evidence of pheromonal intervention in fish. Inhibiting or crowding factors reduce fecundity in guppies (Rose, 1959) and inhibit spawning in goldfish (Swingle, 1953; Greene, 1964; Whiteside and Richan, 1969), the zebrafish *Brachydanio rerio* (Yu and Perlmutter, 1970) and largemouth bass, *Micropterus salmoides* (Chew, 1972). These crowding factors (sometimes metabolites) reduce growth and cardiac activity, induce embryonic mortality and shorten the life-span. Pfuderer *et al.* (1974) attempted to extract the crowding factors;

some biological activity was found in the pthalate esters associated with neutral lipids. It appears then that overcrowding affects reproduction *via* food availability, visual interactions and also pheromone release. Overcrowding may be deterimental to spawning activities, especially if there are too many females for the number of spawning sites. In some species, adult males fight vigorously if stocked too densely.

Pheromones are also positively involved in reproductive migrations (review by Solomon, 1977; Saglio, 1979a) and spawning. Sex pheromones are implicated in the attraction between males and females during spawning in salmonids (Newcombe and Hartman, 1973, Emanuel and Dodson, 1979) and in other species (for review see Saglio, 1979b). In the female zebrafish, *Brachydanio rerio*, a pheromone released by the male stimulates ovulation and counteracts the repressive effect of the metabolites produced by the fish (Chen and Martinich, 1975). In the same species, a sex pheromone attracting conspecifics repels a closely related species, *B. albolineatus* (Bloom and Perlmutter, 1978).

(e) Stress Associated with Fish Cultivation

Man is a generator of numerous stresses especially when fish are bred in captivity. The fish are often confined and are captured by net, electricity or even poison! They undergo transport, transfer, handling and drug treatment and are subjected to changes in water quality and flow rate. This may result in physical injury and various endocrine and metabolic responses.

We have little detailed information on the effect of such procedures on reproduction in fish. According to a study by Vincent (1960), domesticated brook trout, hatchery-bred for 90 years, were less sensitive, in terms of mortality, to the concentration of accumulated water metabolites and to high temperature but had less stamina than wild trout. Domestication resulted in better growth in hatchery conditions but higher mortality in small streams. Therefore, experimental results depend on the history of the fish population studied.

Some effects of handling on reproduction have been reported and most are deleterious. A typical example was given by de Montalambert *et al.* (1978) who showed inhibition of the ovarian response to exogenous gonadotropin and follicular atresia after handling and captivity in pike, *Esox lucius* (Fig. 2). Horseman *et al.* (1976) and Meier and Horseman (1977) observed that various species of vertebrates, when handled daily at the same time of day, showed marked changes in gonad weight. In *Tilapia aurea*, noise or mechanical stimulation, when given 16 h after lights-on, induced a *rise* in testis weight. The case of *Mugil cephalus* (Abraham and Blanc, 1966) is interesting: oogenesis does not occur in freshwater ponds probably due to

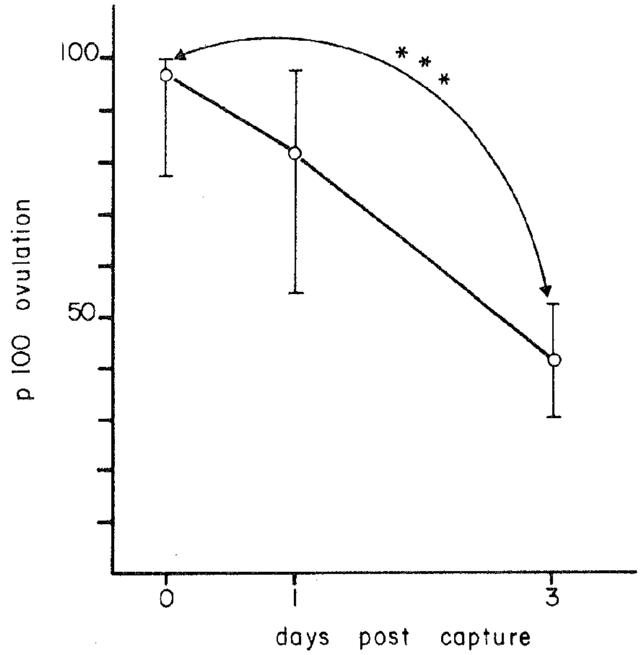

Fig. 2 Effect of time between capture (day 0) and hypophysation with a salmon pituitary extract on ovulation rate in female pike. After capture the fish were transported for 6 h, then kept in captivity until ovulation (vertical bars show confidence limits at the 95% level of probability). Number of fish: 8 (day 0), 7 (day 1), 8 (day 3). *** $p < 0{\cdot}001$. (From de Montalembert *et al.*, 1978).

confinement but it is completed in lakes; if fish are kept in fresh water, they do not ovulate. Oogenesis and ovulation occur in sea water, except when fish are kept in ponds, again underlining the deleterious effect of confinement. Scott (1979) mentioned that the transfer of female minnows, *Phoxinus phoxinus*, from the natural environment to an aquarium tank resulted in massive atresia of vitellogenic oocytes within a few days. A decrease of ova fertilizability has been reported after ovulated females (Marriott, 1973) or embryos (Godfrey, 1957; Marriott, 1973) were given an electric shock. However, fecundity was not modified after immature rainbow trout were exposed to a direct pulsating current (Maxfield *et al.*, 1971).

(f) Synergism and Interaction between Factors

Some of the factors mentioned above were tested independently. Recent studies have tried to show the interaction of several factors affecting fish in the wild and influencing reproduction. An example of such an interaction was reported by Scott (1979) who repeated Bullough's experiments (1939, 1942) in the minnow showing that final vitellogenesis could be stimulated by increasing the photoperiod in late spring. Scott (1979) observed that the GSI increased under a rising photoperiod only when the rearing temperature was high. The GSI rose to 10% and 10% of the oocytes were yolk-laden; these values are higher in nature (12–14% and 20%, respectively). A similar elevation was obtained after a sudden increase in daylength from 8 to 15 h within one week in February–March. Ecological observation showed that when the temperature is less than 8°C in nature, the minnow stays in relative darkness under stones during the daytime. Above that temperature, it swims in open water and is, consequently, exposed to a relatively long photoperiod. In nature, therefore, temperature-sensitive behavioural changes may lead to a sudden exposure to the photoperiod thereby generating the maximum vitellogenic yield; this could not be obtained in a conventional laboratory experiment because the environmental changes imposed are not based on the ecology of fish in nature. Other examples showing the interactive effects of environmental factors have been reported by Stacey *et al.* (1979b), experimenting on ovulation and oviposition in goldfish. It was first observed that a warm shock induced ovulation which was synchronized with the photoperiod. Females kept under a regime of 16 h light : 8 h dark ovulated in the latter half of the dark phase, regardless of the time of day at which they were warmed to 20°C (Stacey *et al.*, 1979a). It was then shown that ovulation was influenced by both water temperature and vegetation (Table II). The additive effect of two stimuli, one visual and the other chemical, has been demonstrated in the angelfish, *Pterophyllum scalare* (Chien, 1973).

TABLE II The Influence of some Environmental Conditions on Ovulation of the Goldfish kept under a Photoperiod of 12 h Light : 12 h Dark. The Initial Temperature for all Groups was 12°C (from Stacey *et al.*, 1979a).

Group	Temperature °C	Flowing water	Standing water	Aquatic vegetation	Male courtship	No. of females Total	No. of females Ovulated
1	12	−	+	+	+	9	0
2	22	−	+	+	+	10	10
3	21	+	−	+	+	7	7
4	21	+	−	−	−	10	3
5	21	+	−	+	−	9	9
6	21	+	−	−	+	8	1

III MECHANISMS OF ACTION

We have shown that various environmental factors influence reproduction in fish, some of which are stimulatory and others, especially those due to man, are inhibitory. Whether these effects are mediated *via* the General

Adaptation Syndrome (Selye, 1946) is still open to debate. In fish as in other vertebrates, a drastic environmental change or aggression is followed by an elevation of the levels of plasma corticosteroids and catecholamines, a primary stress response. These hormones also appear to be normal components of the natural reproductive endocrine pattern in fish, so that hormonal fluctuations due to aggression may interfere with reproduction. More generally, responses to environmental changes involve the whole endocrine system which has been considered as a chemical link between the organism and its environment (Hoar, 1965).

It is now known that handling, loading, transport, confinement and temperature change result in an elevation of circulating corticosteroids in various salmonids (Strange *et al.*, 1977; Strange and Schreck, 1978; Barton *et al.*, 1980; Specker and Schreck, 1980) and in goldfish (Spieler, 1974; Fryer, 1975). Similarly, cortisol increases were observed after fish were exposed to copper, but not after they were exposed to cadmium (Schreck and Lorz, 1978) or chromium (Hill and Fromm, 1968). Social aggression between eels, *Anguilla anguilla*, under conditions of captivity and confinement also results in a rise of cortisol in the subordinate fish (Peters *et al.*, 1980). For a full review of the role of the pituitary–interrenal axis in the stress responses of fish, the reader is referred to Donaldson (1981, this volume). Changes in catecholamines are not so well documented, but available information has been reviewed by Mazeaud *et al.* (1977) and Mazeaud and Mazeaud (1981, this volume).

Other hormones are involved in the response after handling or physical injury. For instance, in goldfish a short-term prolactin decrease was seen 9 to 17 min after capture (Spieler and Meier, 1976). Furthermore, Brown *et al.* (1978) demonstrated that physical injury such as removal of blood or saline injection causes a temporary elevation of plasma thyroxine (T4) in rainbow trout. Several hormones (corticosteroids or cortisol, prolactin, thyroid hormone) have been shown to have diel and annual rhythms in fish (for review see Spieler, 1979). This is interesting because the temporal hormonal synergism probably helps the fish to seasonally integrate into the changing environment.

The action of seasonal environmental factors on reproduction is mediated through specific endocrine changes, and the endocrine mechanisms controlling reproduction are roughly similar in fish and higher vertebrates. Gonadotropin-releasing hormone (Gn-RH) stimulates the secretion of gonadotropic hormone (GTH). GTH stimulates spermatogenesis and oogenesis and induces the gonads to produce sex steroids which, in turn, exert a negative feedback on the hypothalamo–pituitary axis.

Corticosteroids, often identified in plasma or ovaries, appear as normal components of the reproductive endocrine pattern. In adult fish, many authors have shown seasonal variations in blood corticosteroid levels in several species. The metabolic clearance rate, volume of distribution and calculated rate of cortisol and cortisone secretion have been studied. In several salmonid species, corticosteroids rise during sexual maturation (sometimes associated with spawning migration) (Schmidt and Idler, 1962; Donaldson and Fagerlund, 1968, 1970; Fagerlund and Donaldson, 1970) and a hyperplasia of the interrenal gland coincides with ovarian development (Robertson and Wexler, 1960). Fuller *et al.* (1976) also observed high levels of cortisol in mature, female *Coregonus lavaretus* caught on the spawning grounds, but not in those outside the spawning grounds. Similarly, Pickering and Christie (1981) demonstrated a rise in the plasma cortisol levels of the mature, female brown trout at a time coincident with the onset of ovulation in the population. By comparison, no such elevation was found in immature fish kept under identical conditions. In goldfish, Peter *et al.* (1978) identified plasma cortisol and showed that maturing females (in full vitellogenesis) had a higher level with wider fluctuations than fully mature females (at the end of vitellogenesis). However, Cook *et al.* (1980) discovered a sharp peak of cortisol just before the ovulatory GTH surge. Ovulation was induced experimentally in ayu, *Plecoglossus altivelis*, after the injection of very high doses of cortisol (Hirose and Ishida, 1974). Similarly, the injection of 11-deoxycortisol to female guppies induced parturition (Kujala, 1978). The possibility that ovarian corticosteroid peaks might affect ovulation in teleosts has been discussed by Colombo *et al.* (1973).

Sundararaj and Goswami (1977) suggested that 11-deoxycortisol might be one of the steroids mediating GTH action on oocyte maturation and ovulation in the Indian catfish, *Heteropneustes fossilis*. Jalabert (1976) demonstrated that corticosteroids potentiate GTH action on oocyte maturation (Fig. 3) and hypothesized that some fish, cyprinids for example, show an elevation of plasma corticosteroids associated with the true ovulatory surge (see also Breton *et al.*, 1972; Stacey *et al.*, 1979b). This rise may be indirectly responsible for ovulation by lowering the oocyte sensitivity threshold to GTH or by displacing the plasma equilibrium between protein-bound and free 17α-hydroxy-20β-dihydroprogesterone.

Other mediators such as catecholamines, which are involved in the primary stress response, also seem to play a natural role in the process of ovulation; Jalabert (1976) noted that epinephrine induces ovulation of matured oocytes *in vitro*.

There are a few data showing that adverse environmental conditions or aggression may interfere with reproduction via a decrease of plasma GTH. For instance, Gillet *et al.* (1980) observed a decline in both plasma and pituitary GTH in goldfish kept under conditions of starvation (Fig. 4). However, starvation probably inhibited all synthesis of gonadotropic

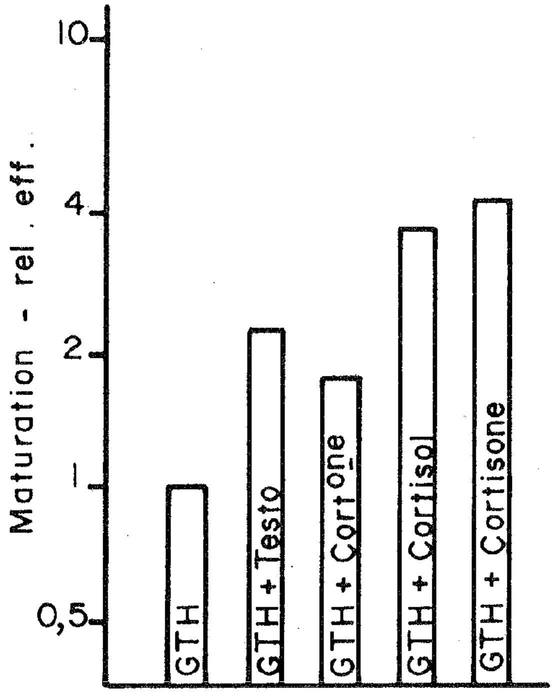

Fig. 3 Corticosteroid amplification of gonadotropin effect on *in vitro* oocyte maturation of rainbow trout follicles (redrawn from Jalabert, 1975).

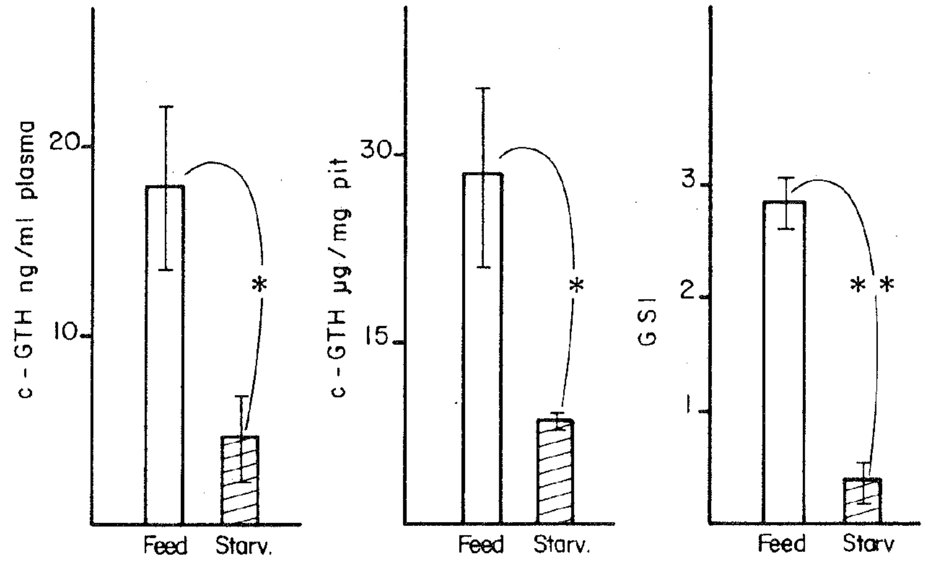

Fig. 4. Effect of starvation on plasma and pituitary gonadotropin (c-GTH) and gonadosomatic index (GSI) in male goldfish kept for 3 months under 16 h light: 8 h dark photoperiod at 30°C. Blood was sampled at 8 a.m. at the onset of the light period. Vertical bars indicate ±SEM, number of fish are 6 (feed) and 5 (starv.) (from Gillet *et al.*, 1981). $^{*}p < 0.05$, $^{**}p < 0.01$.

hormone, due to a lack of adequate material, rather than inhibited the secretion of the hormone. Similarly, a decrease of plasma GTH and GSI was observed in male goldfish kept at 30°C under hypoxic conditions (1·5 and 3 mg l^{-1} O_2 (Fig. 5)). During a study involving catheterization of the dorsal aorta in rainbow trout (Bry and Zohar, 1980; Zohar, 1980), one fish failed to

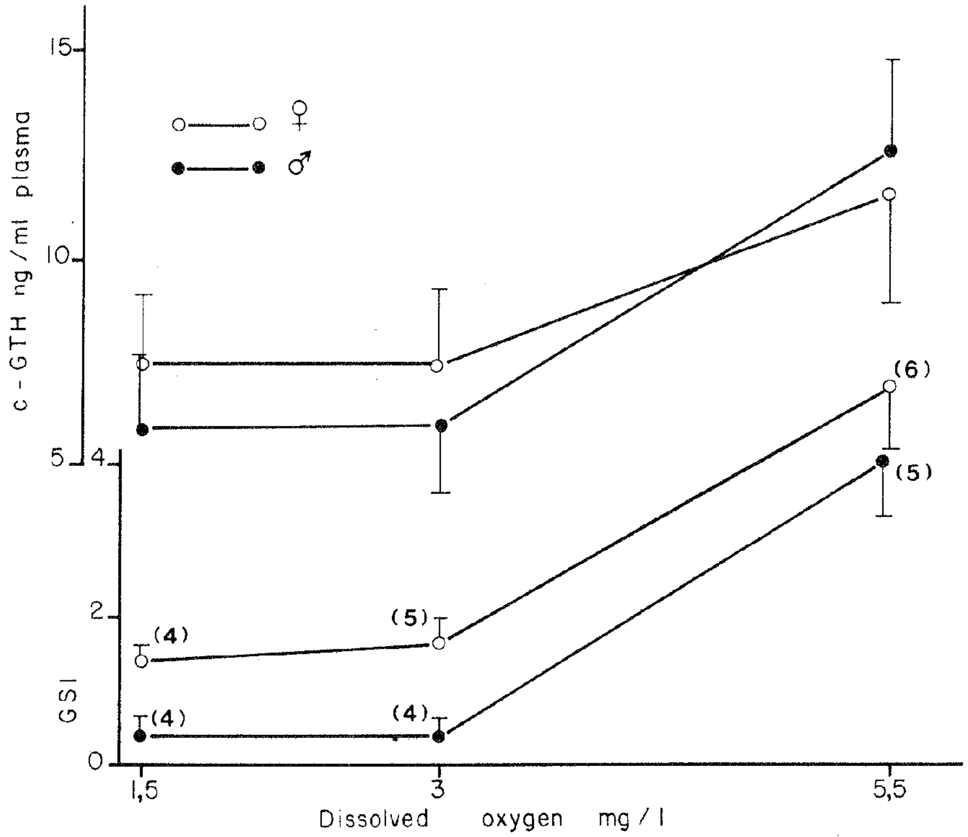

Fig. 5 Influence of dissolved oxygen in the rearing water on GSI and c-GTH in goldfish after 3 months of rearing. Vertical lines indicate ±SEM, the number of fish are shown in brackets (from Gillet *et al.*, 1981).

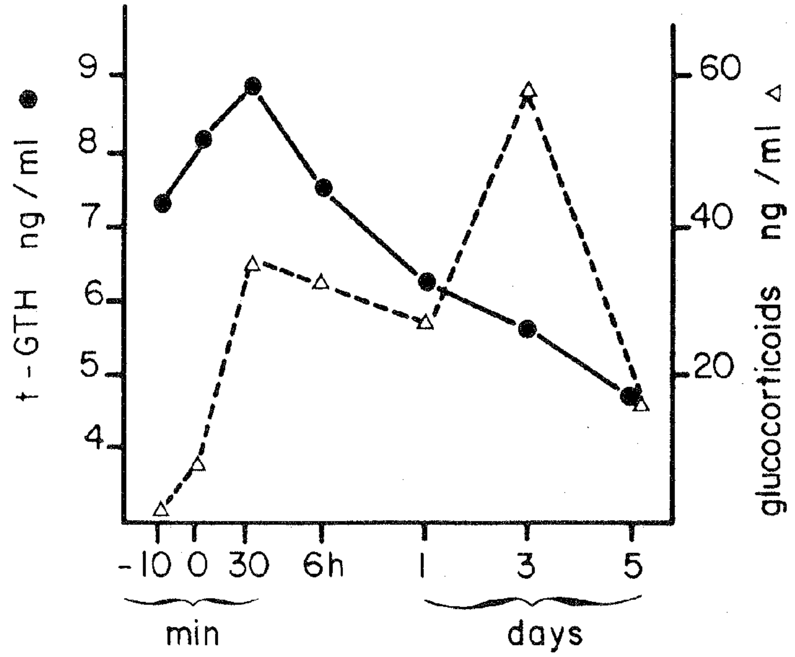

Fig. 6 Changes in glucocorticoids and gonadotropin (t-GTH) in a catheterized rainbow trout for 5 days after cannulation of the dorsal aorta. Time 0 indicates the end of surgery (cannula implantation). The example given is a female ill-adjusting to catheterization and not resuming feeding after the operation (from Bry and Zohar, 1980; Zohar, 1980).

acclimate to the experimental conditions and did not resume feeding. It is interesting that this severely stressed fish (as evidenced by a prolonged elevation of plasma glucocorticoids) also showed a marked decline in plasma gonadotropin after the operation (Fig. 6). On the other hand, when rainbow trout were netted and left struggling out of the water for 3 min, no significant change in plasma gonadotropin was observed after 10 min, 30 min or 24 h (Fig. 7; C. Bry unpublished data).

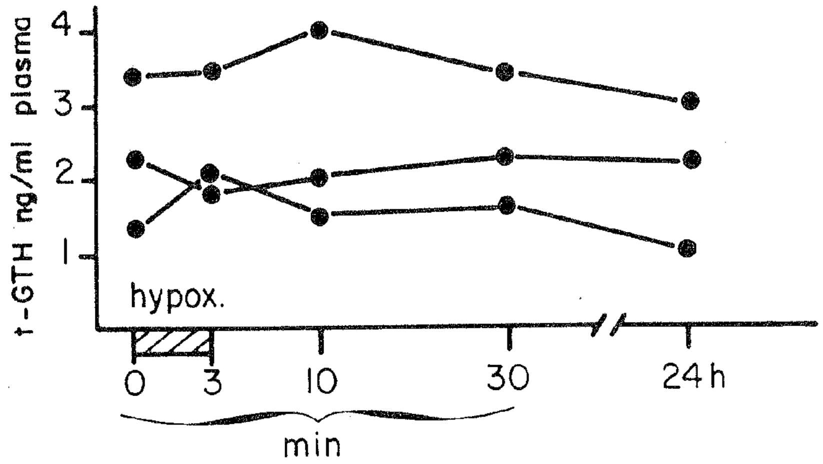

Fig. 7 Plasma gonadotropin (t-GTH) profiles in three catheterized and unanaesthetized rainbow trout after they had struggled for 3 min out of water (hypoxia).

The effects of deleterious changes in the environment on the other main area of reproductive endocrinology, that of oestrogen and androgen metabolism by the gonads, has received very little attention. Androgen metabolism is reported to be modified in brook trout exposed to sublethal levels of cadmium (Sangalang and Freeman, 1974; see also the abstract by Freeman *et al.*, 1981, this volume) but the whole relationship between environmental stress and sex steroid metabolism is a field in which much more research is needed.

IV CONCLUSIONS

The various steps of reproduction depend largely on environmental changes and involve many factors (Fig. 8). Circannual changes influence long-term processes such as gametogenesis. On the contrary, short-term phenomena such as ovulation may be more dependant upon sudden changes in the environment (fluctuation of temperature, rain, salinity, water quality). Fish species which release small eggs with a short incubation period normally ovulate in the spring after these sudden variations, which coincide with the climatic changes initiating or increasing food production in the water. These

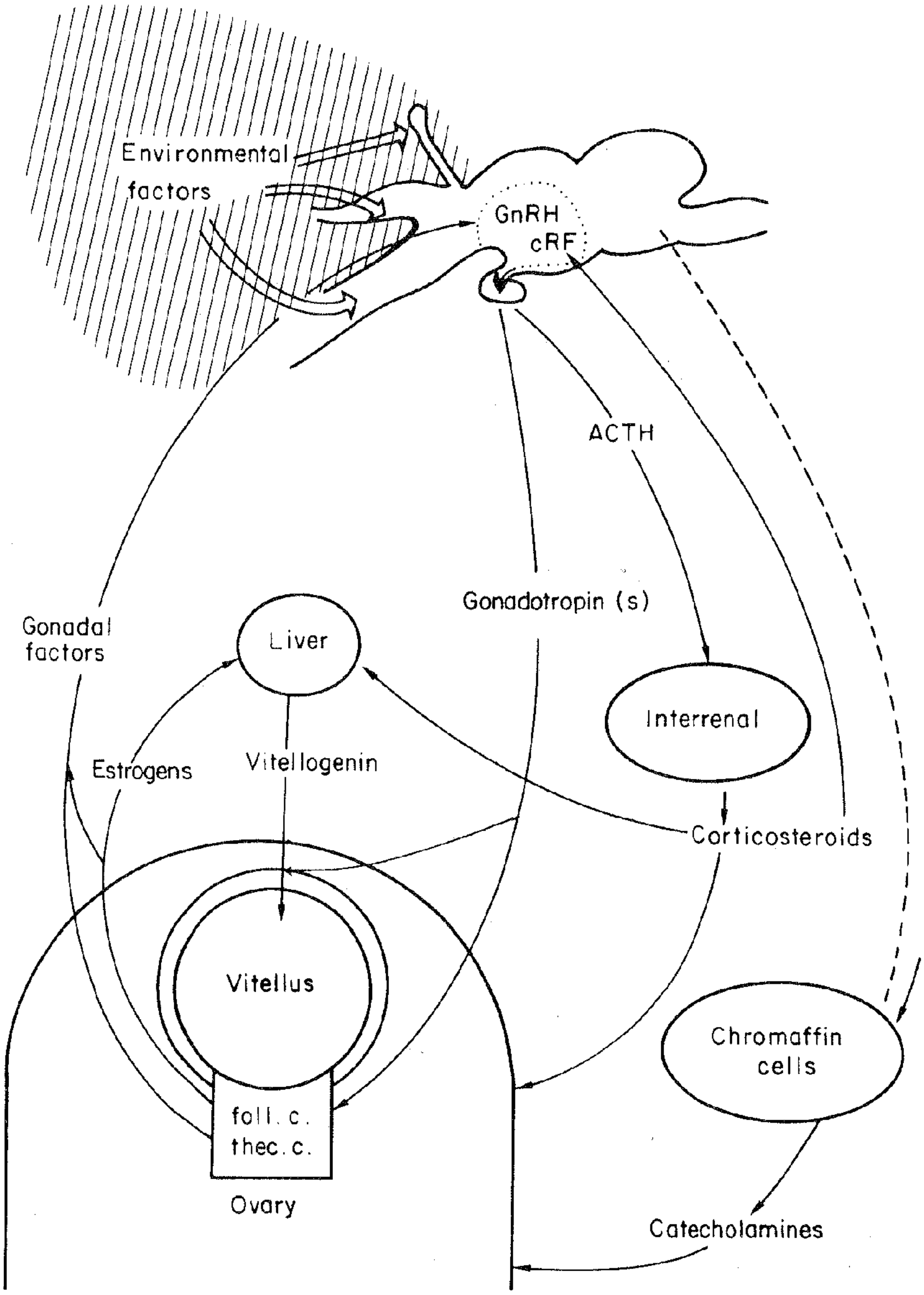

Fig. 8. Some endocrine interrelations between reproduction, corticosteroids and catecholamines in the female teleost fish.

environmental cues are responsible for egg-laying and synchronize hatching with food availability.

Some of these modifications may cause an increase in circulating cortisol levels. The hypothesis that environmental stress may incite the final step of gametogenesis, i.e. oocyte maturation and ovulation, has been put forward by Jalabert (1976). The situation in males may be different; spermiation usually starts earlier than ovulation and no GTH surge occurs when spermiation is initiated. On the other hand, Mazeaud *et al.* (1977) observed sex-dependent differences in plasma corticosteroids in salmonids; female corticosteroid levels were higher than male levels; when the fish were left struggling, these levels rose markedly in males but not in females which already had high levels.

The stressful environment created by man when handling and breeding fish in captivity in overcrowded ponds seems to be overcome by domestication. After several generations, it is possible that some cultivated fish species become adapted (by selection) to their new environment. This should be emphasized now when man is trying to rear wild species intensively. Research is needed to minimize the consequences of stressful conditions on survival, growth and reproduction and to define optimal rearing conditions. Furthermore, the rearing conditions must be adapted to the various physiological rhythms of the fish (see Spieler, 1977).

Environmental factors may stimulate or inhibit reproduction in fish and a given factor may be either inhibitory or stimulatory, depending on the time of the year or day or the stage of sexual development. The where, when and why of these phenomena need further study.

ACKNOWLEDGEMENTS

Thanks are due to Ms Alice Daifuku for editing the manuscript in English.

REFERENCES

Abraham, M. and Blanc, N. (1966). Oogenesis in five species of grey mullets (Teleostei, Mugilidae) from natural and landlocked habitats. *Israel J. Zool.* **15**, 155–172.

Ahsan, S. N. (1966). Effects of temperature and light on the cyclical change in the spermatogenetic activity of the lake chub *Couesius plumbeus* (Agassiz). *Can. J. Zool.* **44**, 161–171.

Bagenal, T. B. (1966). The ecological and geographical aspects of the fecundity of the plaice. *J. mar. biol. Ass. U.K.* **46**, 161–186.

Bagenal, T. B. (1969). The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *J. Fish Biol.* **1**, 167–182.

Baggerman, B. (1969). Influence of photoperiod and temperature on the timing of breeding season in the stickleback, *Gasterosteus aculeatus*. *Gen. comp. Endocr.* **13**, 491.

Baggerman, B. (1972). Photoperiodic responses in the stickleback and their control by a daily rhythm of photosensitivity. *Gen. comp. Endocr. Suppl.* **3**, 466–476.

Ball, J. N. (1960). Reproduction in female bony fish. *Symp. zool. Soc., Lond.* **1**, 105–135.

Barton, B. A., Peter, R. E. and Paulencu, C. R. (1980). Plasma cortisol levels of fingerling rainbow trout (*Salmo gairdneri*) at rest, and subjected to handling, confinement, transport, and stocking. *Can. J. Fish. Aquat. Sci.* **37**, 805–811.

Beamish, R. J. (1972). Lethal pH for the white sucker *Catostomus commersoni* (Lacépède). *Trans. Am. Fish. Soc.* **2**, 355–358.

Beamish, R. J. (1976). Acidification of lakes in Canada by acid precipitation and resulting effects on fishes. *Wat. Air Soil Pollut.* **6**, 501–514.

Bengtsson, B. E. (1980). Long-term effects of PCB (clophen A 50) on growth, reproduction and swimming performance in the minnow, *Phoxinus phoxinus. Wat. Res.* **14**, 681–687.

Benoit, D. A. (1975). Chronic effects of copper on survival, growth, and reproduction of the bluegill (*Lepomis macrochirus*). *Trans. Am. Fish. Soc.* **104**, 353–358.

Bieniarz, K. (1973). Effect of light and darkness on incubation of eggs, length, weight and sexual maturity of sea trout (*Salmo trutta* L.) brown trout (*Salmo trutta fario* L.) and rainbow trout (*Salmo irideus* Gibbons). *Aquaculture* **2**, 299–315.

Billard, R. (1968). Influence de la température sur la durée et l'efficacité de la spermatogénèse du guppy *Poecilia reticulata. C.r. hebd. Séanc. Acad. Sci., Paris* **266**, 2287–2290.

Billard, R. (1980). Reproduction and artificial insemination in teleost fish. *9th Int. Congr. anim. Reprod., Madrid* Vol. II, 327–337.

Billard, R. and Breton, B. (1977). Sensibilité à la température des différentes étapes de la reproduction chez la truite arc-en-ciel. *Cah. Lab. Montereau* **5**, 5–24.

Billard, R. and de Kinkelin, P. (1970). Stérilisation des testicules de guppies par des doses non léthales de parathion. *Annls Hydrobiol.* **1**, 91–99.

Billard, R. and de Fremont, M. (1980). Taux d'alimentation pendant le gametogenese et performance de reproduction chez la truite fario. *Bull. Franc. Pisc.* **279**, 49–56.

Blanc, N. and Abraham, M. (1968). Evaluation du pouvoir gonadotrope dans l'hypophyse de *Cyprinus carpio* et *Mugil cephalus. C.r. hebd. Séanc. Acad. Sci., Paris* **267**, 958–961.

Bloom, H. D. and Perlmutter, A. (1978). Possible pheromone mediated reproductive isolation in two species of cyprinid fishes of the genus *Brachydanio. J. Fish Biol.* **13**, 47–50.

Breton, B. and Billard, R. (1977). Effects of photoperiod and temperature on plasma gonadotropin and spermatogenesis in the rainbow trout *Salmo gairdneri* Richardson. *Annls Biol. anim. Biochim. Biophys.* **17**, 331–340.

Breton, B., Billard, R., Jalabert, B. and Kann, G. (1972). Dosage radioimmunologique des gonadotropines plasmatiques chez *Carassius auratus* au cours du nycthémère et pendant l'ovulation. *Gen. comp. Endocr.* **18**, 463–468.

Brown, S., Fedoruk, K. and Eales, J. G. (1978). Physical injury due to injection or blood removal causes transitory elevations of plasma thyroxine in rainbow trout, *Salmo gairdneri. Can. J. Zool.* **56**, 1998–2003.

Brungs, W. A. (1971). Chronic effects of low dissolved oxygen concentrations on the fathead minnow (*Pimephales promelas*). *J. Fish. Res. Bd Can.* **20**, 1119–1123.

Bry, C. and Zohar, Y. (1980). Dorsal aorta catheterization in rainbow trout (*Salmo gairdneri*): glucocorticoid levels, hematological data and resumption of feeding during five days after surgery. *Reprod. Nutr. Develop.* **20**, 1825–1834.

Bullough, W. S. (1939). A study of the reproduction cycle of the minnow in relation to the environment. *Proc. zool. Soc., Lond.* **109A**, 79–102.

Bullough, W. S. (1942). Gametogenesis and some endocrine factors affecting it in the adult minnow (*Phoxinus laevis* L.). *J. Endocr.* **3**, 211–219.

Burdick, G. E., Harris, E. J., Dean, H. J., Walker, T. M., Skea, J. and Colby, D. (1964). The accumulation of DDT in lake trout and the effect on reproduction. *Trans. Am. Fish. Soc.* **93**, 127–136.

Burdick, G. E., Dean, H. J., Harris, E. J., Skea, J., Karcher, R. and Frisa, C. (1972). Effect of rate and duration of feeding DDT on the reproduction of salmonid fishes reared and held under controlled conditions. *N.Y. Fish Game J.* **19**, 99–115.

Carlson, A. R. and Herman, L. J. (1978). Effect of long-term reduction and diel fluctuation in dissolved oxygen on spawning of black crappie, *Pomoxis nigromaculatus*. *Trans. Am. Fish. Soc.* **107**, 742–746.

Chavin, W. (1973). *Responses of Fish to Environmental Changes*. Springfield, Illinois: C. Thomas.

Chen, L. C. and Martinich, R. L. (1975). Pheromonal stimulation and metabolite inhibition of ovulation in the zebrafish, *Brachydanio rerio*. *Fishery Bull. Fish Wildl. Serv. U.S.* **73**, 889–894.

Chew, R. L. (1972). The failure of largemouth bass, *Micropterus salmoides floridanus* (Le Sueur), to spawn in eutrophic, over-crowded environments. *Proc. a. Conf. South. Ass. Game Fish Commn.* **26**, 1–28.

Chien, A. K. (1973). Reproductive behaviour of the angelfish *Pterophyllum scalare* (Pisces: Cichilidae) II. Influence of male stimuli upon the spawning rate of females. *Anim. Behav.* **21**, 457–463.

Colombo, L., Bern, H. A., Pieprzyk, J. and Johnson, D. W. (1973). Biosynthesis of 11-deoxycorticosteroids by teleost ovaries and discussion of their possible role in oocyte maturation and ovulation. *Gen. comp. Endocr.* **21**, 168–178.

Cook, A. F., Peter, R. E. and Stacey, N. E. (1980). Periovulatory changes in serum cortisol levels in the goldfish, *Carassius auratus*. *Gen. comp. Endocr.* **40**, 507–510.

Craig, G. R. and Baksi, W. F. (1977). The effects of depressed pH on flagfish reproduction, growth and survival. *Wat. Res.* **11**, 621–626.

Cumbie, P. M. and Van Horn, S. L. (1979). Selenium accumulation associated with fish mortality and reproductive failure. *Proc. a. Conf. S. East. Assoc. Fish Wildl. Agencies* **32**, 612–624.

Dahlgren, B. T. (1979). The effects of population density on fecundity and fertility in the guppy, *Poecilia reticulata* (Peters). *J. Fish Biol.* **15**, 71–91.

Daye, P. G. and Garside, E. T. (1980). Structural alterations in embryos and alevins of the Atlantic salmon, *Salmo salar* L., induced by continuous or short-term exposure to acidic levels of pH. *Can. J. Zool.* **58**, 27–43.

Dean, J. and Bailey, H. (1979). Reproductive repression of largemouth bass in a heated reservoir. *Proc. a. Conf. S. East. Assoc. Fish Wildl. Agencies* **31**, 463–470.

de Vlaming, V. L. (1974). Environmental and endocrine control of teleost reproduction. In *Control of Sex in Fishes* (C. B. Schreck, ed.), Blacksburg, Virginia: Virginia Polytechnic and State University.

Donaldson, E. M. (1981). The pituitary–interrenal axis as an indicator of stress in fish. In *Stress and Fish* (A. D. Pickering, ed.), pp. 11–47. London and New York: Academic Press.

Donaldson, E. M. and Fagerlund, U. H. M. (1968). Changes in the cortisol dynamics of sockeye salmon (*Oncorhynchus nerka*) resulting from sexual maturation. *Gen. comp. Endocr.* **11**, 552–561.

Donaldson, E. M. and Fagerlund, U. H. M. (1970). Effect of sexual maturation and gonadectomy at sexual maturity on cortisol secretion rate in sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd Can.* **27**, 2287–2296.

Ebersole, J. P. (1980). Food density and territory size: an alternative model and a test on the reef fish *Eupomacentrus leucostictus*. *Am. Nat.* **115**, 492–508.

Eckstein, B. (1975). Possible reasons for the infertility of grey mullets confined to fresh water. *Aquaculture* **5**, 9–17.

Elliott, J. M. (1981). Some aspects of thermal stress on freshwater teleosts. In *Stress and Fish* (A. D. Pickering, ed.), pp. 209–245. London and New York: Academic Press.

Emanuel, M. E. and Dodson, J. J. (1979). Modification of the rheotropic behavior of male rainbow trout (*Salmo gairdneri*) by ovarian fluid. *J. Fish. Res. Bd Can.* **36**, 63–68.

Fagerlund, U. H. M. and Donaldson, E. M. (1970). Dynamics of cortisone secretion in sockeye salmon (*Oncorhynchus nerka*) during sexual maturation and after gonadectomy. *J. Fish. Res. Bd Can.* **27**, 2323–2331.

Freeman, H. C., Sangalang, G. B. and Uthe, J. F. (1981). The effects of pollutants on steroid hormone metabolism in fish. (Abstract). In *Stress and Fish* (A. D. Pickering, ed.), pp. 332–333. London and New York: Academic Press.

Fromm, P. O. (1980). A review of some physiological and toxicological responses of freshwater fish to acid stress. *Env. Biol. Fish* **5**, 79–93.

Fryer, J. N. (1975). Stress and adrenocorticosteroid dynamics in the goldfish, *Carassius auratus*. *Can. J. Zool.* **53**, 1012–1020.

Fuller, J. D., Scott, D. B. C. and Fraser, R. (1976). The reproductive cycle of *Coregonus lavaretus* (L.) in Loch Lomond, Scotland, in relation to seasonal changes in plasma cortisol concentration. *J. Fish Biol.* **9**, 105–117.

Gall, G. A. E., McClendon, E. L. and Schafer, W. E. (1972). Evidence on the influence of the copepod (*Salmincola californiensis*) on the reproductive performance of a domesticated strain of rainbow trout (*Salmo gairdneri*). *Trans. Am. Fish. Soc.* **2**, 345–346.

Gillet, C. and Billard, R. (1977). Stimulation of gonadotopin secretion in goldfish by elevation of rearing temperature. *Annls Biol. anim. Biochem. Biophys.* **17**, 673–678.

Gillet, C., Billard, R. and Breton, B. (1977a). Influence de la température sur la reproduction du poisson rouge (*Carassius auratus* L.). *Cah. Lab. Montereau* **5**, 25–42.

Gillet, C., Billard, R. and Breton, B. (1977b). Effets de la température sur le taux de gonadotropine plasmatique et la spermatogénèse du poisson rouge *Carassius auratus*. *Can. J. Zool.* **55**, 242–245.

Gillet, C., Breton, B. and Billard, R. (1978). Seasonal effects of exposure to temperature and photoperiod regimes on gonad growth and plasma gonadotropin in goldfish (*Carassius auratus*). *Annls Biol. anim. Biochim. Biophys.* **18**, 1045–1049.

Gillet, C., Billard, R. and Breton, B. (1981). La reproduction du poisson rouge *Carassius auratus* élevé à 30°C. Effet de la photopériode, de l'alimentation et de l'oxygénation. *Cah. Lab. Montereau* **11**, 49–56.

Godfrey, H. (1957). Mortalities among developing trout and salmon ova following shock by direct current electrical fishing gear. *J. Fish. Res. Bd Can.* **14**, 153–164.

Greene, N. (1964). A reproduction control factor in fishes. Ph.D. Thesis, Auburn University, Auburn, Alabama, U.S.A.

Hedtke, S. F. and Puglisi, F. A. (1980). Effects of waste oil on the survival and reproduction of the American flagfish, *Jordanella floridae*. *Can. J. Fish. Aquat. Sci.* **37**, 757–764.

Hill, C. W. and Fromm, P. O. (1968). Response of the interrenal gland of rainbow trout (*Salmo gairdneri*) to stress. *Gen. comp. Endocr.* **11**, 69–77.

Hirose, K. and Ishida, R. (1974). Effects of cortisol and human chorionic gonadotrophin (HCG) on ovulation in ayu *Plecoglossus altivelis* (Temminck and Schlegel) with special reference to water and ion balance. *J. Fish Biol.* **6**, 557–564.

Hoar, W. S. (1965). The endocrine system as a chemical link between the organism and its environment. *Trans. R. Soc. Can.* **3**, 175–200.

Hokanson, K. E. F. (1977). Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *J. Fish. Res. Bd Can.* **10**, 1524–1550.

Hontela, A. and Peter, R. E. (1978). Daily cycles in serum gonadotropin levels in the goldfish: effects of photoperiod, temperature and sexual condition. *Can. J. Zool.* **56**, 2430–2442.

Horseman, N. D., Meier, H. and Culley, D. D. (1976). Daily variations in the effects of disturbance on growth, fattening and metamorphosis in the bullfrog (*Rana catesbeiana*) tadpole. *J. exp. Zool.* **198**, 353–358.

Htun-Han, M. (1977). The effects of photoperiod on reproduction in fishes: an annotated bibliography. *Library Inf. Leaflet, MAFF, Lowestoft*, **6**, 30pp.

Jalabert, B. (1975). Modulation par différents stéroides non maturants de l'efficacité de la 17-hydroxy-20-dihydroprogesterone ou d'un extrait gonadotrope sur la maturation intrafolliculaire *in vitro* des ovocytes de la truite arc-en-ciel *Salmo gairdneri*. *C.r. hebd. Séanc. Acad. Sci., Paris* (*Ser. D.*) **281**, 811–814.

Jalabert, B. (1976). *In vitro* oocyte maturation and ovulation in rainbow trout (*Salmo gairdneri*), northern pike (*Esox lucius*), and goldfish (*Carassius auratus*). *J. Fish. Res. Bd Can.* **33**, 974–988.

Johansen, P. H. and Cross, J. A. (1980). Effects of sexual maturation and sex steroid hormone treatment on the temperature preference of the guppy, *Poecilia reticulata* (Peters). *Can. J. Zool.* **58**, 586–588.

Johansson, N., Kihlstrom, J. E. and Wahlber, G. (1973). Low pH values shown to affect developing fish eggs *Brachydanio rerio* (Ham-Buch). *Ambio* **2**, 1–2.

Kazakov, R. V. (1971). Effect of alternative temperature while incubating eggs of the Atlantic salmon upon survival and growth rates of embryos and larvae (Russian–English summary). *Isv. GOS. Nauk Ichyol. Oser* **75**, 56–66.

Kihlstrom, J. E., Landery, C. and Hulth, L. (1971). Number of eggs and young produced by zebrafishes (*Brachydanio rerio*, Ham-Buch) spawning in water containing small amounts of phenylmercuric acetate. *Env. Res.* **4**, 355–359.

Kipling, C. and Frost, W. E. (1969). Variations in the fecundity of pike *Esox lucius* L. in Windermere. *J. Fish Biol.* **1**, 221–237.

Kujala, G. A. (1978). Corticosteroid and neurohypophyseal hormone control of parturition in the guppy, *Poecilia reticulata*. *Gen. comp. Endocr.* **36**, 286–296.

Kuznetsov, V. A. and Khalitov, N. Kh. (1978). Alterations in the fecundity and egg quality of the roach, *Rutilus rutilus*, in connection with different feeding conditions. *J. Ichthyol.* **18**, 63–70.

Macek, K. J. (1968a) Reproduction in brook trout (*Salvelinus fontinalis*) fed sublethal concentrations of DDT. *J. Fish. Res. Bd Can.* **25**, 1787–1796.

Macek, K. J. (1968b). Growth and resistance to stress in brook trout fed sublethal levels of DDT. *J. Fish. Res. Bd Can.* **25**, 2443–2451.

Marriott, R. A. (1973). Effects of electric shocking on fertility of mature pink salmon. *Progve Fish Cult.* **35**, 191–194.

Maruyama, T. and Nagashima, K. (1978). Effect of water current on growth and spawning activity of *Tilapia nilotica*. *Bull. Freshwat. Fish Res. Lab., Tokyo* **28**, 201–210.

Maxfield, G. H., Lander, R. H. and Liscom, K. L. (1971). Survival, growth, and fecundity of hatchery-reared rainbow trout after exposure to pulsating direct current. *Trans. Am. Fish. Soc.* **3**, 546–552.

Mazeaud, M. M. and Mazeaud, F. (1981). Adrenergic responses to stress in fish. In *Stress and Fish* (A. D. Pickering, ed.), pp. 49–75. London and New York: Academic Press.

Mazeaud, M. M., Mazeaud, F. and Donaldson, E. M. (1977). Primary and secondary effects of stress in fish: some new data with a general review. *Trans. Am. Fish. Soc.* **106**, 201–212.

Meier, A. H. and Horseman, N. D. (1977). Stimulation and depression of growth, fat storage, and gonad weight by daily stimulus in the teleost fish, *Tilapia aurea*. *Proc. a. World maricult. Soc.* **8**, 135–143.

Menendez, R. (1976). Chronic effects of reduced pH on brook trout (*Salvelinus fontinalis*). *J. Fish. Res. Bd Can.* **33**, 118–123.

Mitton, J. B. and Koehn, R. K. (1976). Morphological adaptation to thermal stress in a marine fish, *Fundulus heteroclitus*. *Biol. Bull. mar. biol. Lab., Woods Hole* **151**, 548–559.

de Montalembert, G., Bry, C. and Billard, R. (1978). Control of reproduction in northern pike. *Spec. Publs Am. Fish. Soc.* **11**, 217–225.

Mount, D. I. (1973). Chronic effect of low pH on fathead minnow survival, growth and reproduction. *Wat. Res.* **7**, 987–993.

Nebeker, A. V., Puglisi, F. A. and Defoe, D. L. (1974). Effect of polychlorinated biphenyl compounds on survival and reproduction of the fathead minnow and flagfish. *Trans. Am. Fish. Soc.* **103**, 562–568.

Newcombe, C. and Hartman, G. (1973). Some chemical signals in the spawning behaviour of rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd Can.* **30**, 995–997.

Peter, R. E. and Crim, L. W. (1979). Reproductive endocrinology of fishes: Gonadal cycles and gonadotropin in teleosts. *A. Rev. Physiol.* **41**, 323–335.

Peter, R. E., Hontela, A., Cook, A. F. and Paulencu, C. R. (1978). Daily cycles in serum cortisol levels in the goldfish: effects of photoperiod, temperature, and sexual condition. *Can. J. Zool.* **56**, 2443–2448.

Peters, G., Delventhal, H. and Klinger, H. (1980). Physiological and morphological effects of social stress in the eel (*Anguilla anguilla* L.) *Arch. FischWiss.* **30**, 157–180.

Peterson, R. H., Daye, P. G. and Metcalfe, J. L. (1980). Inhibition of Atlantic salmon (*Salmo salar*) hatching at low pH. *Can. J. Fish. Aquat. Sci.* **37**, 770–774.

Pfuderer, P., Williams, P. and Francis, A. A. (1974). Partial purification of the crowding factor from *Carassius auratus* and *Cyprinus carpio*. *J. exp. Zool.* **187**, 375–382.

Pickering, A. D. (1981). Introduction. In *Stress and Fish* (A. D. Pickering, ed.), pp. 1–9. London and New York: Academic Press.

Pickering, A. D. and Christie, P. (1981). Changes in the concentrations of plasma cortisol and thyroxine during sexual maturation of the hatchery-reared brown trout, *Salmo trutta* L. *Gen. comp. Endocr.* **44**, (in press).

Pyle, E. A. (1969). The effect of constant light and darkness on the growth and sexual maturity of brook trout. *Fish. Res. Bull., NY* **31**, 13–19.

Quillier, R. (1981). Influence de photoperiodes constantes sur l'activité testiculaire de la tanche (*Tinca tinca* L.). *Bull. Franc. Pisc.* (in press).

Robertson, O. H. and Wexler, B. C. (1960). Histological changes in the organs and tissues of migrating and spawning Pacific salmon (Genus *Oncorhynchus*). *Endocrinology* **66**, 222–238.

Roblin, C. (1980). Etude comparée de la biologie du dévelopement (gonadogénèse, croissance, nutrition) du loup (*Dicentrarchus labrax*) en milieu naturel et en élevage contrôlé. *Acad. de Montpellier Thèse 3ème cycle, Univ. Sci. Techn. Languedoc.*

Rose, S. M. (1959). Population control in guppies. *Am. Midl. Nat.* **62**, 474–481.

Ruby, S. M., Aczel, J. and Craig, G. R. (1977). The effects of depressed pH on oogenesis in flagfish *Jordanella floridae*. *Wat. Res.* **11**, 757–762.

Saglio, P. (1979a). Communication chimique et migration reproductrice chez les salmonidés. *Bull. Franc. Pisc.* **275**, 72–82.

Saglio, P. (1969b). Interactions sociales chez les poissons: les pheromones. *Bull. Franc. Pisc.* **273**, 173–184.

Sangalang, G. B. and Freeman, H. C. (1974). Effects of sublethal cadmium on maturation and testosterone and 11-ketotestosterone production *in vivo* in brook trout. *Biol. Reprod.* **11**, 429–435.

Sawara, Y. and Egami, N. (1977). Note on the differences in the response of the gonad to the photoperiod among population of *Oryzias latipes* collected in different localities. *Annotnes zool. jap.* **50**, 147–150.

Saxena, P. K. and Garg, M. (1978). Effect of insecticidal pollution on ovarian recrudescence in the fresh water teleost *Channa punctatus*. *Ind. J. exp. Biol.* **16**, 689–691.

Schmidt, P. J. and Idler, D. R. (1962). Steroid hormones in the plasma of salmon at various states of maturation. *Gen. comp. Endocr.* **2**, 204–214.

Schreck, C. B. and Lorz, H. W. (1978). Stress response of coho salmon (*Oncorhynchus kisutch*) elicited by cadmium and copper and potential use of cortisol as an indicator of stress. *J. Fish. Res. Bd Can.* **35**, 1124–1129.

Scott, D. B. C. (1979). Environmental timing and the control of reproduction in teleost fish. *Symp. Zool. Soc., Lond.* **44**, 105–132.

Scott, D. P. (1962). Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd Can.* **19**, 715–730.

Selye, H. (1946). The general adaptation syndrome and the diseases of adaptation. *J. clin. Endocr.* **6**, 117–230.

Siefert, R. E. and Herman, L. J. (1977). Spawning success of the black crappie *Pomoxis nigromaculatus* at dissolved oxygen concentrations. *Trans. Am. Fish. Soc.* **106**, 376–378.

Solomon, D. J. (1977). A review of chemical communication in freshwater fish. *J. Fish Biol.* **11**, 369–376.

Specker, J. L. and Schreck, C. B. (1980). Stress responses to transportation and fitness for marine survival in coho salmon (*Oncorhynchus kisutch*) smolts. *Can. J. Fish. Aquat. Sci.* **37**, 765–769.

Spieler, R. E. (1974). Short-term serum cortisol concentrations in goldfish (*Carassius auratus*) subjected to serial sampling and restraint. *J. Fish. Res. Bd Can.* **31**, 1240–1242.

Spieler, R. E. (1977). Diel and seasonal changes in response to stimuli: a plague and a promise for mariculture. *Proc. a. World Maricult. Soc.* **8**, 865–874.

Spieler, R. E. (1979). Diel rhythms of circulating prolactin, cortisol, thyroxine, and triiodothyronine levels in fishes: a review. *Rev. Can. Biol.* **38**, 301–315.

Spieler, R. E. and Meier, H. (1976). Short-term serum prolactin concentrations in goldfish (*Carassius auratus*) subjected to serial sampling and restraint. *J. Fish. Res. Bd. Can.* **33**, 183–186.

Stacey, N. E., Cook, A. F. and Peter, R. E. (1979a). Spontaneous and gonadotropin induced ovulation in the goldfish, *Carassius auratus* L. effects of external factors. *J. Fish Biol.* **15**, 349–361.

Stacey, N. E., Cook, A. F. and Peter, R. E. (1979b). Ovulatory surge of gonadotropin in the goldfish, *Carassius auratus*. *Gen. comp. Endocr.* **37**, 246–249.

Stequert, B. (1972). Contribution a l'étude de la biologie du bar (*Dicentrarchus labrax* L.) des réservoirs à poissons de la région d'Arcachon. *Thèse 3ème cycle, Univ. Bordeaux.*

Strange, R. J. and Schreck, C. B. (1978). Anaesthetic and handling stress on survival and cortisol concentration in yearling chinook salmon (*Oncorhynchus tshawytscha*). *J. Fish. Res. Bd Can.* **35**, 345–349.

Strange, R. J., Schreck, C. B. and Golden, J. T. (1977). Corticoid stress responses to handling and temperature in salmonids. *Trans. Am. Fish. Soc.* **106**, 213–218.

Sundararaj, B. I. and Goswami, S. V. (1977). Hormonal regulation of *in vivo* and *in vitro* ovocyte maturation in the catfish, *Heteropneustes fossilis* (Bloch). *Gen. comp. Endocr.* **32**, 17–28.

Swingle, H. S. (1953). A repressive factor controlling reproduction in fishes. *Proc. Pacif. Sci. Congr.* **38**, 865–871.

Vincent, R. E. (1960). Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). *Trans. Am. Fish. Soc.* **89**, 35–52.

Whitehead, C., Bromage, N. R., Forster, J. R. M. and Matty, A. J. (1978). The effects of alterations in photoperiod on ovarian development and spawning time in the rainbow trout (*Salmo gairdneri*). *Annls Biol. anim. Biochim. Biophys.* **18**, 1035–1043.

Whiteside, B. G. and Richan, F. J. (1969). Repressive factors controlling reproduction in goldfish. *Progve Fish Cult.* **31**, 165.

Wiebe, J. P. (1968). The reproductive cycle of the viviparous seaperch, *Cymatogaster aggregatas* Gibbons. *Can. J. Zool.* **40**, 1221–1234.

Yu, M. L. and Perlmutter, A. (1970). Growth inhibiting factors in the zebrafish (*Brachydanio rerio*) and the blue gourami (*Trichogaster trichopterus*). *Growth* **34**, 153–175.

Zalewski, M. (1979). The effect of pollution on the fecundity of roach *Rutilus rutilus* L. from river of barbel region. *3rd Europ. Ichthyol. Cong. Warszawa. 18–25 Sept. 1979.*

Zohar, Y. (1980). Dorsal aorta catheterization in rainbow trout (*Salmo gairdneri*): Its validity in the study of blood gonadotropin patterns. *Reprod. Nutr. Develop.* **20**, 1811–1823.

STRESS AND FISH

Edited by

A. D. PICKERING

Freshwater Biological Association
Cumbria, England

1981

ACADEMIC PRESS

A Subsidiary of Harcourt Brace Jovanovich, Publishers

London New York Toronto Sydney San Francisco

ACADEMIC PRESS INC. (LONDON) LTD
24–28 Oval Road,
London NW1

U.S. Edition published by
ACADEMIC PRESS INC.
111 Fifth Avenue,
New York, New York 10003

British Library Cataloguing in Publication Data

Stress and fish.
1. Stress (Physiology)
2. Stress (Psychology)
I. Pickering, A. D.
597'.5041'88 QL615

ISBN 0–12–554550–9

LCCN: 81–67907

Printed in Great Britain by
J. W. Arrowsmith Ltd, Bristol