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THE ROLE OF LIGHT AND ENDOCRINE FACTORS IN THE DEVELOPMENT OF BIMODALITY OF GROWTH IN THE JUVENILE ATLANTIC SALMON (SALMO SALAR L.)

CESAR A. VILLARREAL G.

Ph.D. DECEMBER 1983

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THE ROLE OF LIGHT AND ENDOCRINE FACTORS IN THE DEVELOPMENT OF BIMODALITY OF GROWTH IN THE JUVENILE ATLANTIC SALMON (*SALMO SALAR* L.).

A thesis submitted for the degree of

Doctor of Philosophy at the

University of Stirling

by

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6/84

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To my lifelong companion

Mayra Villarreal

The work presented in this thesis is the result of my own investigations and has neither been accepted nor is being submitted for any other degree.

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14. Dec. 1983

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The role of light and endocrine factors in the development of bimodality of growth in the juvenile Atlantic salmon (*Salmo salar* L.)

ABSTRACT

The timing of the development of bimodality in the frequency distribution of length and weight within sibling populations of juvenile Atlantic salmon was independent of change in day-length or photoperiod. However, photoperiod affected the proportion of fishes in the upper modal group, from none under short photoperiod to higher proportions under constant light.

The photoperiod exerted its effects on the development of bimodality in two ways, through its proportional effects (length of daylight *per se*) and by its differential effects (rate of change in day-length). It is postulated that the rate of change in day-length exerted its effect during a period of sensitiveness to light, called the "critical photosensitive period" (CPP).

Temperature had an unimportant role in development of bimodality relative to light since fish grew well in constant light when the temperature was declining, but poorly under short constant photoperiod at a time when the water temperature was increasing.

The biochemical and morphometric assessment of cellular growth (nucleic acid content and muscle fibre diameter measurements) showed

that fish growth was due to both cell enlargement (hypertrophy) and proliferation (hyperplasia). The preponderance of one process over the other depended on developmental stage and season.

The lowest muscular DNA content and highest RNA-DNA ratio was reached at the end of July, independent of the photoperiod or family, indicating therefore that cellular processes of growth (e.g. cell enlargement and protein precursor accumulation) were photoperiod independent and under endogenous seasonal regulation.

The lowest water content and highest dry weight values were reached by late summer for all photoperiodic treatments indicating their endogenous character.

Specific growth rate was correlated significantly with RNA-DNA ratio before midsummer and with the natural logarithm of RNA concentration after that. RNA concentration then, as an index of growth, was more affected by cell size during spring than during summer. It is concluded that RNA concentration alone was an appropriate index of growth when it was not affected by cell size.

Fishes of the upper modal group synthesised more protein and lipids than those of the lower group, since the former showed consistent and significantly higher dry and wet weights, total RNA and RNA concentrations, total DNA, DW-DNA ratios and RNA-DNA ratios.

The female salmon allocated more resources to gonadal growth than the males did as assessed by histological measurements. Among males upper

modal group fishes showed more advanced testicular development than did the lower modal ones. These results were at variance with the hypothesis that the development of bimodality was due to differential allocation of resources to somatic and gonadal growth.

Gonadal growth was highly independent of the gonadotropes, since they did not show any parallel cytological changes with the gonads.

The Somatotropes (GH cells) and thyrotropes (TSH cells) were involved in fish growth regulation, because they showed consistent and in some cases significant increases in cell and nucleus diameters and cell numbers during the somatic growth season.

The prolactin cells (LTH cells) were larger in female and in small fish. No interaction was found between the two factors (sex and size). This result suggested that the two fish groups were under osmotic stress.

It was concluded that photoperiod exerted its effects on fish body growth through the hypothalamo-hypophysial axis, since good correlations were found between morphometric estimates of pituitary cell activity and somatic growth and development.

The role of light and endocrine factors in the development of bimodality of growth in the juvenile Atlantic salmon (*Salmo salar* L.)

Acknowledgements

Abstract

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Introduction

1.1 Bimodality of growth in Atlantic salmon

It has been demonstrated that juvenile sibling populations of Atlantic salmon (Salmo salar L.) reared under artificial conditions develop bimodal distributions of length and weight (Simpson and Thorpe, 1976; Thorpe, 1977). A similar phenomenon has been reported in Canadian experiments and is also apparent in a Norwegian experimental report (Bailey et al., 1980; Saunders et al., 1982; Knutsson and Grav, 1976).

It has been assumed that this length frequency distribution represents the outcome of a physiological "decision" under genetic control (Simpson and Thorpe, 1976; Thorpe and Morgan, 1978; Thorpe et al., 1980). This genetic "decision" is probably mediated through variations of growth rate and sensitivity to endocrinological stimulation. Simpson and Thorpe (1976) suggested that during late summer of the first year of juvenile growth, metabolic rate dropped in response to falling water temperature but, in part, was compensated by a photoperiod-induced increase in the secretion in TSH, followed by a concomitant increase in thyroxine plasma level. The physiological prerequisite was that a certain threshold level of circulatory hormone should have been exceeded, and that such a response threshold be determined genetically at the target and secretory sites (Thorpe et al., 1980). It must be expected , therefore, that the synthesis and release of hormone by the pituitary of Atlantic salmon should be different for the lower and upper modal groups, and at the same time the target organs of growth, bones and muscle, likewise, will respond differently. Further

more, fishes with lower thresholds of response to thyroxine will continue to grow and those with higher thresholds will diminish their rate of growth. The overall result of this differential response to thyroxine level will be expressed during winter as a differential pattern of growth for each modal group (Thorpe and Morgan, 1978).

In 1980, Thorpe et al., confirmed the assumption that critical variables such as critical minimal length at which the "decision" takes place, and the timing of it, differ between families; all in agreement with the notion of genetical control of timing of separation of the two modes (Thorpe and Morgan, 1978). However, they pointed out that length frequency distribution is not a sensitive enough method to reveal the beginning of change in growth processes leading to separation of potential one year from potential two year smolts. On the other hand, the promising labelled glycine method for indicating changes in anabolic activity between the two modal groups before they become separable on lengths grounds, was unable to show up any difference. Nevertheless, they further suggested that similar experiments must be carried out on a range of families, and over a range of weeks until the precise moment of change in metabolic activity could be detected.

Thorpe (1977) reported that both sexes showed similar patterns of length frequency distribution, including precociously mature males, and concluded that sexual differences and maturation do not account for the bimodal pattern of growth in juvenile Atlantic salmon. Although, recently Bailey et al. (1980) pointed out that the lower size mode had more males, and the upper size mode contained more females. The same authors observed that precocious males were observed most frequently in

the upper tail of the lower mode and to lesser extent, in the lower tail of the upper mode. This observation suggests that a mimimum size must be reached before maturation can occur, and the "decision" to mature must be made early in the growing season in order to allow precocious mature males to participate during spawning. Because sexual maturation implies diversion of resources from somatic growth to gonadal development, a reduced growth rate must be expected for maturing males compared to that of immature fishes. Elson (1957) indicated that a critical minimum length must be reached in autumn before the "decision" to smoltify the following spring can occur. Simpson and Thorpe (1976) concluded that lower modal group fish developed into 2-year old smolts (S2), and upper modal group into 1-year old smolts (S1); later Thorpe et al. (1980) showed upper mode fish reached the critical size for the "decision" to smoltify early in summer. Because Bailey et al. (1980) found mature males in both size modes, they concluded that the size threshold for precocious maturation is lower than that for early smolting, and the "decision" to mature as a parr or smolt early, must be independent. These results suggest a primary role for sexual maturation, and only an incidental one for smoltification, in the development of bimodality in the frequency distribution of length and weight in juvenile Atlantic salmon. Therefore, it seems likely that the lower modal length group should represent both those fishes whose initial growth was most rapid, and in which maturation has been triggered and somatic growth retarded as a consequence of gonadal development, and those whose initial growth was slowest. In the fastest growing population the degree of "precocity" should be greatest, evident soonest, and the size separation of the modal group most pronounced; conversely in the slowest growing group these developments should appear more slowly and the divergence of the population should be least (Thorpe et al., 1980).

1.2 Photoperiodism and temperature as regulating factors of fish growth

It has been postulated that photoperiodism (day-length) is the main environmental factor in controlling the neuroendocrine activity and the rate of metabolism of fishes, both of which in turn alter their rate of growth (Saunders and Henderson, 1970; Hoar, 1965, 1976; Lundqvist, 1980, 1983).

Photoperiodism has been defined as the control of the annual cycle in animals and plants by the use of the annual cycle of day-length, allowing the restriction of part of the life cycle to the optimal time of the year (Farner, 1965; Follett, 1982; Saunders, 1982). Photoperiodic control of annual cycles means, at the same time, that one physiological process is linked with time measurement (Bünning, 1960, 1963). The organisms have an endogenous time scale against which they compare, throughout the year, any physiological activity with the annual change of day length. The time scale system of comparison is known as "critical day length" (critical photoperiod). According to this, if a particular process is switched on at some precise day-length, the more a light period exceeds this critical day length the faster the process occurs; conversely, if it is switched off, the more the day-length decreases below the critical photoperiod the faster it wanes.

Organisms may respond to absolute day or night lengths of naturally changing photoperiods or to sequences of short-to-long or long-to-short day length at different stages of their development (Saunders, 1982).

Animals and plants alternatively, may also measure the rate of change of

day-length by the so-called circannual rhythm clock, that shares many of the formal properties of the circadian rhythms, clock like temperature-compensation; free-running in constant light or in unchanging 24 h light-dark cycle; and periods close to a year, commonly between 40 to 50 weeks. Circannual rhythms in insects, birds and fishes seem to be synchronised by seasonal changes in photoperiod (Saunders, 1982; Lundqvist, 1983). Photoperiodic behaviour is the result of transduction of light signals through peripheral detectors (retinae, pineal, mid-brain surface) to the Nucleus lateralis tuberis of the hypothalamous, from which neuro-endocrine transmissions via the pituitary induce physiological responses to light change (Ball, 1981; Follett, 1982).

In many fishes it has been possible to demonstrate the influence exerted by the photoperiod on different physiological processes, for example: growth (Gross et al., 1965; Saunders and Henderson, 1970; Clarke et al. 1978, 1981; Lundqvist, 1980, 1983), reproductive hormonal level (Breton and Billard, 1977; Bormage et al., 1982), reproductive cycles (Baggerman, 1972, 1980; Billard and Breton, 1978; Borg, 1982; Borg and van Veen, 1982); locomotor activity (Richardson and McCleave; 1974; Eriksson, 1975; Müller, 1978; Kavaliers and Ross, 1981), smoltification (Saunders and Henderson, 1970; Zaugg and Wagner, 1973; Wagner, 1974; Knutsson and Grav, 1976; Clarke et al., 1981), and sexual maturation (Eriksson and Lundqvist, 1980; Lundqvist, 1983). These cyclic physiological processes may be under the control of an endogenous circannual clock. A few studies have given detailed information of the nature of this clock, or the way by which external factors exert an effect on it. Sundaraj et al. (1978), for example, reported that the catfish

(Heteropneustes fossilis) kept in constant light (LL) or darkness (DD) at 25°C for 34 months showed an ovarian rhythm comparable to that seen in fish collected from nature (nL), but out of phase with it. They further suggested that environmental factors brought circannual reproductive cycles into phase, so that reproduction could occur at the proper time of the year. The most complete study of circannual rhythmicity and its environmental control has been made by Lundqvist (1983), in juvenile Atlantic salmon. He reported that in this species not less than ten different biological processes occur cyclically with an approximate period of a year. Some of them, (growth and smolting) run free when subject to constant photoperiod of 12 h light, 12 h dark (12L:12D) with an endogenous period of 40 weeks (Eriksson and Lundqvist, 1982; Lundqvist, 1983). Similar but less detailed results have been reported in other salmonids. Brown (1945) in her classic study of growth in brown trout (Salmo trutta) under constant conditions, proposed the involvement of a strong endogenous factor in the regulation of physiological activities. In the same way, rainbow trout (Salmo gairdneri) subject to a constant light-dark regime of 12L:12D for a year spawn at approximately the same time as those subject to normal seasonal day-length cycle (nL) (Whitehead, et al., 1978). Finally, steelhead trout (S.gairdneri) reared under complete darkness (DD) showed an endogenous rhythm in smoltification, and in gill Na^{+}-K^{+}- ATPase activity (Wagner, 1971, 1974; Zaugg and Wagner, 1973).

The circannual rhythm is assumed to be modified by the rate of change in day-length during the year. In accordance with this Müller (1978) has reported that the seasonal and diel pattern of fish activity at high latitude (60° 42' N) shows wide amplitude change with the maximal amplitude

of light-dark change at these latitudes. The smoltification of steelhead trout, reared under advanced or accelerated annual photoperiod was more rapid than in those reared under natural photoperiod; by contrast under delayed or decelerated annual photoperiod smolting was delayed when compared with a control group (Wagner, 1974). In rainbow trout ovulation occurred between July and August, when subject to a decreasing photoperiodic regime from December to August, comparable to that of the controls which ovulated in winter (Breton et al., 1983). In the same species, accelerated annual photoperiod shortened the time at which the highest levels of calcium and phosphorus protein were attained when compared with the control fish (nL) (Bromage et al., 1982). In yearling S.salar parr, increase in the rate of decreasing day-length during autumn advanced the time of ripening when compared with those subject to normal photoperiod (Eriksson and Lundqvist, 1980). Underyearling coho salmon (Oncorhynchus kisutch) increased its growth significantly when subjected to increased photoperiod (Wedermeyer et al., 1980, Clarke et al., 1981 During the same stage coho and sockeye (O.nerka) under decreasing photoperiod (12 to 8 h) showed rapid growth and smolting inhibition (Clarke et al., 1978).

From the results so far described, it may be concluded that photoperiod is capable of entraining the circadian and circannual rhythms in salmonids. The entraining agent or "Zeitgeber" acts upon these biological rhythms either by its proportional effect (actual day-length) or by its differential effect (rate of change of day-length) (Aschoff, 1960; Eriksson and Lundqvist, 1980).

The temperature is the second environmental factor that seems to be quite

important in the control of biorhythms. In general, endogenous rhythms are insensitive to temperature, and it is said they show temperature compensation. Although, there must exist some sensitivity to it, because the phase of circadian rhythms in many animals can be set by temperature (temperature transient) (Bünning, 1960). Müller (1978) has pointed out that temperature determines the amount of activity but not the phase position of annual locomotor activity of brown trout (Salmo trutta), char (Salvelinus alpinus) and brook trout (S.fontinalis). Similar results have been reported by Wagner (1974) for the smoltification of steelhead trout (Salmo gairdneri). Temperature in general modifies smoltification, and sexual maturation in juvenile salmonids, through growth (Wagner, 1971, 1974; Clarke et al., 1978). Finally higher temperature accelerates the gonadal recrudescence of the three-spined stickleback (Gasterosteus aculeatus) (Baggerman, 1980).

On the other hand the sexual cycle of the longjaw goby (Gillichthys mirabilis) is primarily regulated by seasonal temperature variation, rather than by photoperiod. Ovarian maturation of Cyprinodon rubrofluviatilis, and spermatogonial proliferation of Fundulus heteroclitus were more affected by temperature regime than by photoperiod (for review see de Vlaming, 1974). Interaction of both photoperiod and temperature in the regulation of biological rhythms has been reported repeatedly in fishes (see de Vlaming, 1974; Wagner, 1974; Clarke et al., 1978, 1981; Baggerman, 1980), though in all the cases photoperiod is the leading factor as an entraining agent. This is not surprising as changing photoperiod conveys more reliable seasonal information than does environmental temperature, which is a much more noisy variable.

1.3 The link between environmental clues and internal development

The information on day-length variation and other exogenous factors (e.g. twilight) throughout the year is detected by retinal and extra-retinal organs (e.g. pineal organ). The information is then conveyed directly or indirectly, to the hypothalamus, which acts as a final common path in the neuroendocrine interaction (Scharrer, 1965; Hoar, 1965, 1976; Poston, 1978). The hypothalamus is a highly compartmentalised structure, in which each of its divisions (nuclei or areas) is specialised in the control of one or few pituitary cells. The environmental information arriving to the hypothalamic centre is redirected towards the pituitary or hypophysis; therefore the hypothalamus acts as some sort of transducer, that transforms the information coming in from the reception centre in the form of nerve impulses, into chemical signals, the so-called neurohypothalamic hormones or hypothalamic factors (Reichlin et al., 1976). In fishes the different hypothalamic centres seem to synthesise different hypothalamic factors, that stimulate (releasing factors) or inhibit (inhibiting factors) the synthesis and release of hormones by the adenohypophysis. The release of hypothalamic factors is said to be direct when the innervation ends on the adenohypophyseal cell, or area, or indirect when the factors are released throughout the capillary plexus (Peter, 1973; Ball, 1981). A direct neuronal connection between the hypothalamus and the hypophysial cell exists in the vast majority of Teleosts (Follénious, 1965; Zambrano, 1970, 1972; Peter, 1973; Ekengren et al., 1978; Ball, 1981), but in salmonids and in the eel, the link is established through the capillary plexus of the rostral neurohypophysis (indirect connection) (Sharrer, 1965; Fridberg and Ekengren, 1977; Ball, 1981).

It is proposed here, that photoperiod acts as a synchroniser of a genetic endogenous rhythm, timing the moment of "decision" of the growth pattern of Atlantic salmon in artificial and natural conditions. This synchroniser action is exerted through the hypothalamo-hypophysial axis which will increase the synthesis and secretion of growth (GH), thyrotophic (TSH) and prolactin (LTH) hormones, in that part of the population more sensitive to variation of day-length.

Bimodality in growth of juvenile Atlantic salmon may be the result of a differential allocation of resources to the diverse components of the body by the two modal groups; or the expression of an altogether different pattern of growth by each mode; or finally by some mixture of both phenomena. It seems likely the cycles of synthesis and releasing of hormones by the adenohypophysis should account for the divergent types of development in juvenile Salmo salar.

The most important cells of the adenohypophysis involved in the regulation of growth and development in fishes are the somatotropes, thyrotropes gonadotropes and lactotropes.

The role of somatotropes (α cells, GH cell) in fish growth have been recorded for several species (Ball and Baker, 1969; Holmes and Ball, 1974; Donaldson et al., 1979; Jalabert et al., 1982). For example, somatotropes increase in number and size in yearling Atlantic salmon kept under long photoperiods during smoltification (Olivereau, 1954a, b; Komourdjian et al., 1976). A similar result has been obtained in Pacific salmon (Oncorhynchus) during sea growth (Olivereau and Ridgeway, 1962). Castration of sockeye salmon (O.nerka), which resulted

in acceleration of growth, is accompanied by hyperplasia and hypertrophy of somatotropes (McBride and Van Oberbeene, 1969; Nagahama, 1973). Letherland (1970) found that the threespine stickleback (G. aculeatus) α - cells exhibited the highest diameter during the period of maximum growth. It can be said then, that growth in fishes is stimulated by growth hormone produced by the somatotropes of the pars distalis.

The secretion of thyrotrophin by the thyrotropes (δ cell, TSH cell) is important for maintaining the physiological status of thyroid glands. The thyroid hormone (thyroxine, in turn, has growth promoting effects in fishes, though a high degree of inconsistency in this respect has been reported (Sage, 1967; Donaldson, et al, 1979; Jalabert, 1982). Nevertheless, Leatherland (1970) communicated that G. aculeatus presented the maximal thyrotrophic activity during the period of maximal growth, though he pointed out that this activity might be related with preparation for migration. Poecilia reticulata treated with thyroxine increased in weight, but the treatment had no effect on the staining properties of TSH cell or GH cell (Sage, 1967). Similar results have been obtained in rainbow trout (Barrington et al, 1961), coho salmon (Higgs et al, 1976) and Atlantic salmon (Piggins, 1962).

TSH cells are present in small numbers in trout and Atlantic salmon parr; however in migrating salmon smolts, which have highly active thyroids, and about to migrate to sea thyrotropes are numerous and very active (Ball and Baker, 1969). In the same way Oncorhynchus masou and O. keta had a marked increase of TSH cell activity during parr-smolt transformation, suggesting some relationship with osmoregulation in seawater and/or migratory behaviour of these fishes (Nagahama, 1973).

The synergistic action of growth and thyroid hormone in promoting fish growth seems to be well established (Graw and Stetson, 1979); and both hormones may play a role in their mutual regulation. In conformity with this it seems that thyroxine exerts a negative feedback action upon somatotropes, because decreasing of thyroid hormone by thiourea treatment produced an increase of GH cells (Sage, 1976). Higgs et al. (1976) reported similar results for underyearling coho salmon (O.kisutch) (see Jalabert et al., 1982 for review). In hypophysectomised Fundulus heterochitus ovine GH and TSH act synergistically producing serum thyroxine levels which are nearly twice the sum of levels produced by each administered separately (Graw and Stetson, 1979). In Poecilia reticulata GH interacted with thyroxine and produced a growth effect (Sage, 1967). The same results were obtained in killifish (Fundulus grandis) by Pickford (1957).

The other adenohypophyseal hormone that has been involved in the regulation of fish growth is prolactin (LTH). In one study with underyearling sockeye salmon (O.nerka) it was found that growth hormone or prolactin alone stimulated growth in weight and length at 17.5°C and 12 h photoperiod. Additional growth enhancement was not noted when growth hormone and prolactin were administered together (Clarke, 1976; Donaldson et al., 1979). By contrast, an autotransplant experiment with hypophysectomised Black bullhead (Ictalurus melas), suggested that native prolactin in this species has little endogenous promoting effect (Kayes, 1977). Chronic treatment of hypophysectomised killfish (F.grandis) and Poecilia, with ovine prolactin never enhanced growth (Donaldson, et al., 1979). Lastly, Graw and Stetson (1979) have proposed

that thyroidal activity in F.heteroclitus is modulated by two developmental hormones, prolactin (inhibitory) and growth hormone (stimulatory). Apart from the roles described hitherto, the most important function of prolactin is in favouring adaptation to freshwater, by promoting retention of electrolytes (e.g. Chloride and Sodium) (Olivereau, 1968; Ball, 1969; Sage and Bern, 1971; Schreibman, et al., 1973; Nagahama, 1973; and Ensor, 1978). Therefore it is not surprising to find that Peocilia prolactin cell (ηcell or LTH cell) are always more active in freshwater than in dilute or full strength seawater; similar effects were obtained for F.heteroclitus (Olivereau, 1968; Ball and Baker, 1969). Consistent with these findings, Atlantic salmon smolts exhibit a reduced cell height (15 - 20 μ) of LTH cell when kept for 14 days in seawater (Olivereau, 1968). The rostral par distalis (RPD) of steelhead trout (S.gairdneri), which is the area of localisation of LTH cells, is smaller in trout raised in seawater for 21 months, than in fishes collected on the spawning grounds in the Columbia river (Olivereau, 1968). Leatherland (1970a) reported that the cell index (average of two principal axes) of LTH cell of G.aculeatus was significantly larger for fish maintained in freshwater, when compared with fish collected in seawater. Before entering the river, LTH cells of coho salmon (O.kisutch) acclimatised to seawater, appeared much less active, than in those acclimatised to freshwater for periods from 3 days up to 18 months (Nagahama et al., 1977).

1.4 Muscle as a principal growth tissue in fishes

Fish growth may be defined as an increase of fish flesh accomplished

through protein synthesis (Bulow, 1970). This definition reflects the fact that the main target organs of growth hormone and other anabolic hormones are bones and muscle. It is then possible to gain insights into the intimate patterns of fish growth by studying the biochemical and morphological changes of muscle fibres. In accordance with this line of reasoning a great deal of information has been accumulated during the last twenty years or so, about the chemistry and physiology of muscle fibres (Love, 1970, 1980; Bone, 1978; Johnston, 1981, 1982).

1.4.1 Variations in nucleic acids and water content as an estimate of muscle growth

From the different chemical components of muscle fibre, special attention has been directed to the study of nucleic acids, as a way of measuring the growth due to cellular enlargement or multiplication; and because RNA is regarded as a necessary precursor of protein synthesis, therefore the rate of protein synthesis is some function of RNA concentration in growing fishes. Love (1958b) for example, showed that concentration of muscular DNA decreases when the North Sea cod (*Gadus callarias*)(sic.) increases in length, this same variation holding for other species. In *S.gairdneri* the RNA and DNA concentrations decrease when the weight increases from 20 to 3,400 gms (Luquet, 1970; Luquet and Durand, 1970). Mustafa (1977a), comparing the DNA content of white and dark muscle in three species of fishes (*Catla catla*, *Labeo rohita* and *L.bata*), reported that growth is accompanied by a decrease of DNA in both types of

muscle. Similar results were obtained in the Black bullhead (Ictalurus melas) (Kayes, 1979).

The effects of different exogenous factors on muscular concentration of DNA have also been studied. The nutritional status of the fish seems to be of fundamental importance. During starvation DNA content increases whereas RNA decreases in winter flounder (Pseudopleuronectes americanus) larvae, and in Black bullhead (Kayes, 1978; Buckley, 1980). Brook trout (Salvelinus fontinalis) fed with restricted rations have higher levels of DNA compared with fish fed at high rations (Wilder and Stanley, 1983). DNA muscle concentration of lata fish (Ophicephalus punctatus) and Seratherodon mossambica (Medda and Ray, 1979; Matty et al., 1982) is not affected by thyroxine content or its analogues. Sexual maturation, on the other hand, is accompanied by an increase in the concentration of white muscle DNA in the catfish (Clarias batrachus). These results are easier to understand if we consider that DNA concentration is a measure of the number of cells per unit weight of tissue. Since 1949 it has been known that the amount of DNA is constant per nucleus of somatic cell (Vendrely and Vedrely, 1950; Davidson and Leslie, 1950; Enesco and Leblond, 1962). Therefore, the increase of DNA during maturation, starvation or at feed-restricted ration, is due to a heavy depletion of cellular components (e.g. proteins, fat and carbohydrates) without change in the amount of DNA per nucleus (Mustafa, 1977, Love, 1980). It must be expected then that hormonal treatment, which does not produce nuclear proliferation, will not change the overall DNA concentration. In the same way, tissue growth not produced by cellular multiplication (hyperplasia) but by cellular enlargement

(hypertrophy) will likely result in a decrease of DNA concentration.

On the other hand, the RNA concentration in muscle varies more widely when fishes are subject to diverse treatments. The effects reported so far, suggest that RNA content reflects variation in the synthesis or degradation of muscle protein.

The RNA concentration of a wide variety of organisms has been related to growth rate (Sutcliffe, 1970); however Dagg and Littlepage (1972) concluded that the RNA concentration and growth rate relationship lacked sufficient specificity to predict growth rate. Nevertheless Bulow in 1970, demonstrated that RNA-DNA ratio can be used as an indicator of recent growth rate (see also Bulow 1971). Later, Haines (1973) reported that RNA-DNA ratio was a reliable indicator of long-term growth in populations of fishes; since then, several reports have sustained similar claims (Bulow et al., 1978; Kayes, 1978; Kearn and Atchinson, 1979; Haines, 1980; Thorpe et al., 1982; Wilder and Stanley, 1983). The RNA-DNA ratio is regarded as a more accurate index of growth than RNA concentration alone, because the former is not affected by cell number or size in the tissue sample (Haines, 1973). However, Kayes (1979) suggested that RNA concentration in skeletal muscle provided a more precise measure of growth rate in the bullhead than RNA-DNA ratio does.

Variations in RNA content and RNA-DNA ratio, in general express changes in protein synthesis. During growth, increase in RNA concentration of muscle is follwed by an increase in protein synthesis (Mustafa and Jafri, 1977; Medda and Ray, 1979; Buckley, 1980; Matty et al., 1982;

Lone and Matty, 1982a, b) or its decrease during starvation (Buckley, 1982; Medda and Ray, 1979). This variation in RNA and protein synthesis seems to be under the control of external and internal factors. Among the most important internal factors are hormones (Medda and Ray, 1979; Kayes, 1979; Lone and Matty, 1982a, b) and sexual maturation (Mustafa, 1977); whereas the external factors include contamination (Kearns and Atchinson, 1979; Wilder and Stanley, 1983); and seasonality (Bulow et al., 1981). Another important chemical component of muscle which permits assessment of the condition of the fish is water. Water content shows an inverse relationship with lipid and protein content of muscle (Love, 1970). This relationship has been observed in juvenile Atlantic salmon in natural conditions (Gardiner and Geddes, 1980) and in the laboratory (Talbot unpubl.) and in brown trout under artificial conditions (Elliott, 1976).

1.4.2 Variation of muscle fibres during somatic growth

A great deal of effort has been put into the study of the morphological changes of muscle fibres during fish growth. Throughout this process the size of the fish increases but the relative role played by cell multiplication and enlargement is usually unknown, especially in those cases in which growth is defined solely as weight increase. The latter statement is important, because weight may increase without somatic growth, especially when it is due to body fat accumulation (Enesco and Leblond, 1962) or the increase of gonadal weight during sexual maturation (Saunders et al., 1982).

The study of the changes of muscle fibre diameter and their relationships with size allow an independent assessment of the relative contribution of hyperplasia and hypertrophy during fish growth. Both types of growth pattern seem to occur in fishes; in this respect the model of fish growth differs from that of mammals in which, as a rule, the number of fibres becomes fixed about the time of birth, therefore any further growth is due to hypertrophy (Kryvi and Eide, 1977; Willemse and Van den Berg, 1978; Johnston, 1982). Nevertheless, a great many species - specific differences, as well as those due to stage of development and fibre type, may occur in fishes.

For example:

a) developmental differences: in rainbow trout of 5 - 20 cm in length, white muscle grows mainly by recruitment of new fibres; between 20 - 50 cm in length, this growth occurs by hypertrophy as well (Weatherley 1980a, b), as it also does in young eels (Anguilla anguilla) (Willemse and Van den Berg, 1978):

b) species - specific differences: in herring (Clupea harengus) and the shark (Etmopterus spinax), mosaic muscle grows by hypertrophy alone (Walker et al., 1972; Kryvi and Eide, 1977) in contrast to the eel and trout (cf (a) above):

c) fibre-type differences: by contrast the red muscle of E. spinax grows mainly by hyperplasia (Kryvi and Eide, 1977), whereas that of young eels grow by hypertrophy alone (Willemse and Van den Berg, 1978):

d) fibre-type and developmental differences: at sexual maturation, red muscle in eels increases more in volume than does their white muscle (Pankhurst, 1982).

Different factors may affect muscle fibre growth patterns. The diet, for example, can modify fibre number in the mosaic muscle of rainbow trout. In this species feeding ad lib. produces higher growth rate at 12° than 16°C, and at 12°C much higher growth rate than fish fed 3 - 4% of dry body weight of trout pellets per day. At equivalent body size the fastest growing trout were found to have significantly smaller fibre diameter consistent with an increase of fibre number (Weatherley et al., 1979; Weatherley and Gill, 1982). Stimulation of growth by increased ration, or by growth hormone treatment enhanced the fibre recruitment of white muscle, rather than increased the fibre diameter (Weatherley et al., 1980 a, b).

1.5 Somatic and gonadal growth as antagonistic strategies in allocation of resources

If bimodality in length and weight distribution of juvenile S.salar is considered to be the outcome of differential allocation of resources by the two modal groups, the tissues most likely to share those resources are muscle and gonads, for two reasons. Firstly, because the proportion of precocious males present in the lower modal group tends to be higher than in the upper modal group; for females it occurs the other way round. Secondly, because the formation of reproductive tissue implies the diversion of costly foodstuffs away from conversion to muscle tissue resulting in an overall reduction

of growth; conversely high rates of growth mean lesser gonadal development. It must be added here that the more the fish eats the faster it grows and the higher the fraction of assimilated food spent on gonadal production (Thorpe, 1975; Ursin, 1979).

Thorpe et al. (1983), in accordance with the above statement, have proposed that the lower modal length group includes those fishes whose initial growth was most rapid, and in which maturation has been triggered and somatic growth retarded as a consequence of gonadal development. In a manner consistent with this, Bailey et al. (1980) found high proportions of mature male parr among the lower modal length group in November of the first year, and a few individuals matured in the upper modal group at the same time. Thorpe and Morgan (1980) reported the occurrence of such mature parr only in the lower modal group, and then only at the end of their second summer.

This thesis describes the results of a series of studies on the physiology of development of bimodality in the frequency distributions of length and weight in populations of sibling 0+ Atlantic salmon. The main objective was to determine the timing and conditions under which divergence into distinct modal groups occurred ascertained through short term measurements of growth by RNA-DNA ratio and RNA content. This is of particular importance because studies of length frequency distribution alone only reveal the occurrence of the event weeks or months after it has taken place. Another important aim was to define the role of external factors such as photoperiod and temperature, and endogenous factors like pituitary activity and gonadal growth affecting

the development of bimodality. Special attention has been given to morphological changes of skeletal muscle as an independent means of checking the interpretation of the nucleic acid data. Where appropriate, data were also collected on x-ray measurement of food consumption, gonadosomatic index, water content, and these results are discussed in relation to growth pattern changes.

2 Materials and Methods

2.1 Animal handling and rearing

2.1.1 Experiment I - Normal photoperiod and constant light

During late October and early November 1980, mature adult salmon were caught by electrofishing from the River Almond, Perthshire, Scotland. In November, 9200 eggs were stripped from a female salmon of 85.0 cm in fork length and aged 2.2+ (2 year smolt; 2+ year at sea). The milt was obtained from a male of 69.0 cm fork length and aged 2.2+. Fertilised eggs were incubated in standard baskets (Thorpe, 1981) at the Almondbank hatchery, and when the alevins hatching from them reached an embryo:alevin dry weight ratio of approximately 80% (Marr, 1966) they were transferred for first feeding into four 2 m diameter radial-flow fibreglass tanks (Minaur, 1973; Thorpe and Wankowski, 1979; Thorpe, 1981). On the 22nd June 1981, 1600 fry were transferred in batches of 400 to four 1 m diameter radial-flow tanks. Two of these tanks were housed in wood-framed compartments covered with black polythene sheets, and completely lightproof; the other two tanks were uncovered (Plate 1). The covered tanks were exposed to constant light (LL); the uncovered tanks were exposed to natural photoperiod (nLD) (Fig. 1). In order to test if any increase in growth is due to light treatment directly or to prolonged availability of food, because of the increased light period, fishes of both covered and uncovered tanks were subjected to two regimes of feeding frequency: in one case, a constant amount of food was delivered at 10-min intervals (T rate) whereas for the other it was at 5-min intervals (2T rate) throughout the 24 hours. The fork length of all fishes in each tank was measured at roughly monthly

Plate 1 Photograph of the covered experimental rearing tank.

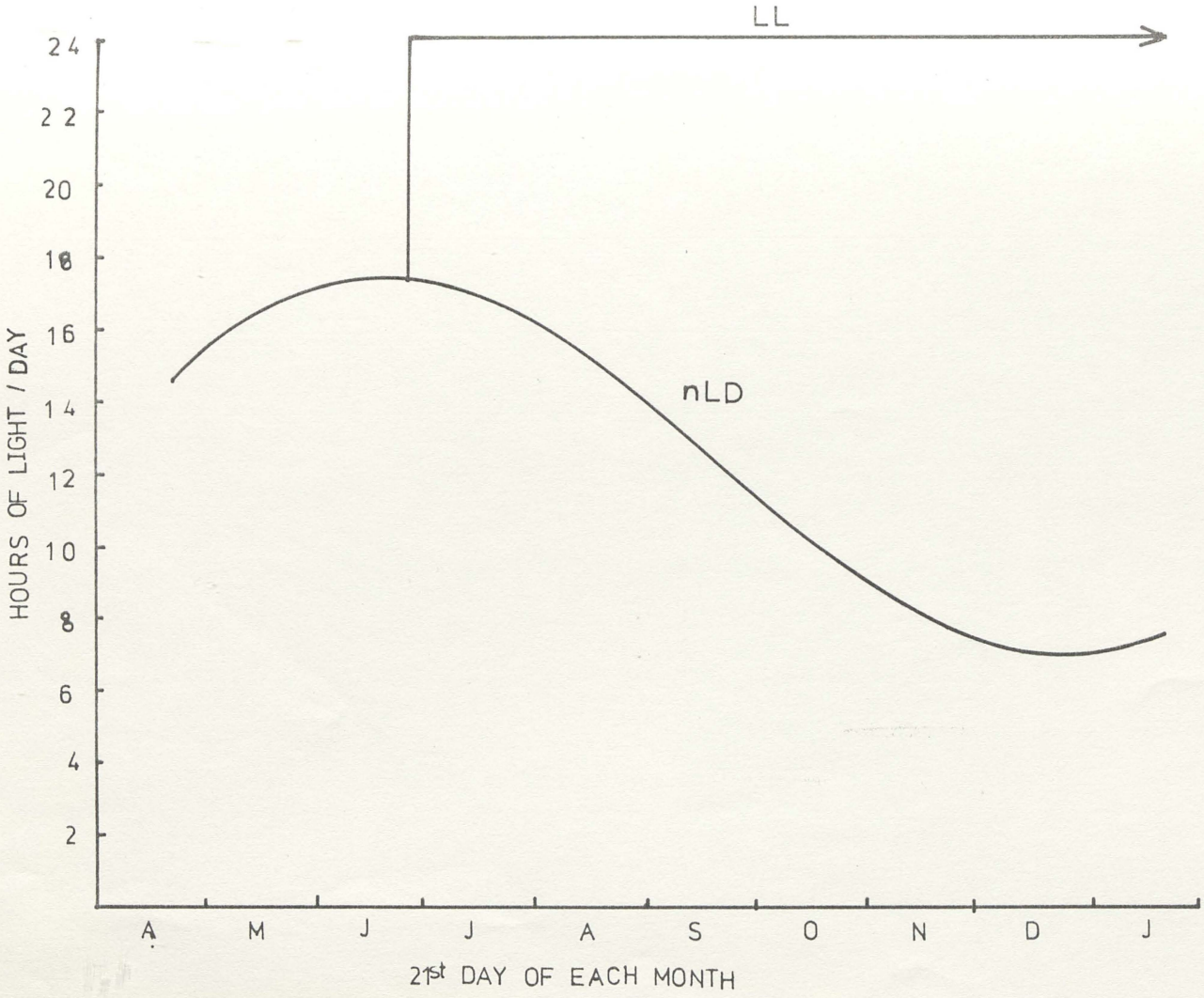

LL
24
22
20
18
16
14
12
10
8
6
4
2
HOURS OF LIGHT / DAY
nLD
A
M
J
J
A
S
O
N
D
J
21st DAY OF EACH MONTH

Figure 1 Photoperiod cycles used in Experiment I. nLD, natural photoperiod. LL, constant light.



intervals, beginning on the 22nd August 1981 up to the 4th February 1982, when all fishes were sacrificed, sexed, and their gonado-somatic index determined.

2.1.2 Experiment II - Effect of different rates of photoperiod change on growth

In November 1981, 11200 eggs from an 83.5 cm fork-length salmon, aged 2.2+, were fertilised by the milt of a 69.0 cm fork-length (2.2+) salmon male. Alevins from this pairing were transferred at first feeding to 2 m radial flow tanks until the end of June 1982. On the 25th June 1982, 2880 fry were transferred in batches of 480 to six 1 m radial flow tanks; five of which were housed in black polythene compartments and the remaining tank was uncovered. All tanks were subjected to a feed regime of T-rate interval, for 24 h. Three of the covered tanks were exposed to three different rates of photoperiodic changes (differential changes), the other two were subjected to two constant photoperiod regimes (proportional change). Fork length of all fishes in each tank was measured at monthly intervals from July 1982 up to March 1983 when the experiment finished.

2.2 Photoperiodic regimes and automatic control

Rearing tanks were covered to control the day-length, at which fishes were exposed. An entrance to the compartment was made by two over-lapping black polythene sheets to prevent exposure to natural day-light.

Illumination was provided by a 122 cm 40 w "Osram" white fluorescent tube. Distance from the light source to the water surface was 137 cm. The intensity of light falling on the covered tanks was measured with a Photometer (Model 40 x United Detector Technology Inc. Sta. Monica, Calif. U.S.A.), and reached a value of 58 lux at the water surface. In Experiment I the covered tanks were exposed to constant photoperiod (LL) (Figure 1). The uncovered tanks of Experiments I and II were under Natural photoperiod (nLD) which meant no artificially controlled change of day-length. No special light control was required for the constant light experiment, nor for natural photoperiod.

During Experiment II the five covered tanks were exposed to the following photoperiodic change regimes (Figure 3):

a - L3D. Annual cycle of natural photoperiod change completed in 3 months;

b - L4D. Annual cycle completed in 4 months;

c - L6D. Annual cycle completed in 6 months;

d - 8LD. Day-length was kept constant at 8 h light, 16 h dark (8L:16D) during the whole experiment;

e - LL. Constant light, exactly the same as in Experiment I.

Figure 2. Young specimens of Atlantic salmon to show where parts were removed for microscopical and biochemical analysis.

1. Head preserved for pituitary cell measurements.
2. Body trunk preserved for the microscopic study of muscle fibre and gonads.
3. Body segment preserved for biochemical analysis.

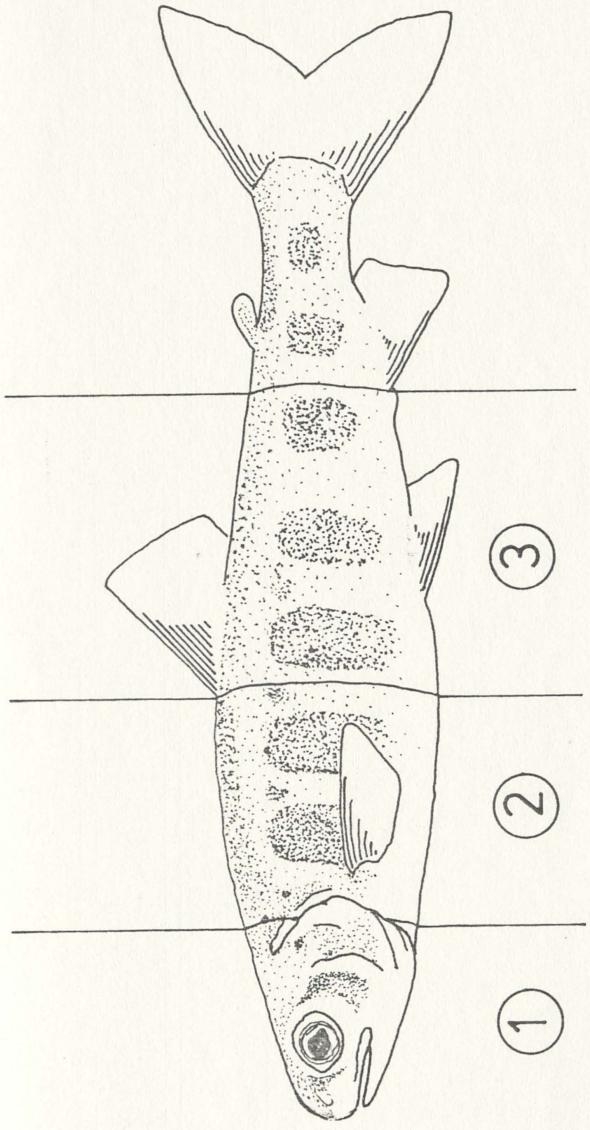
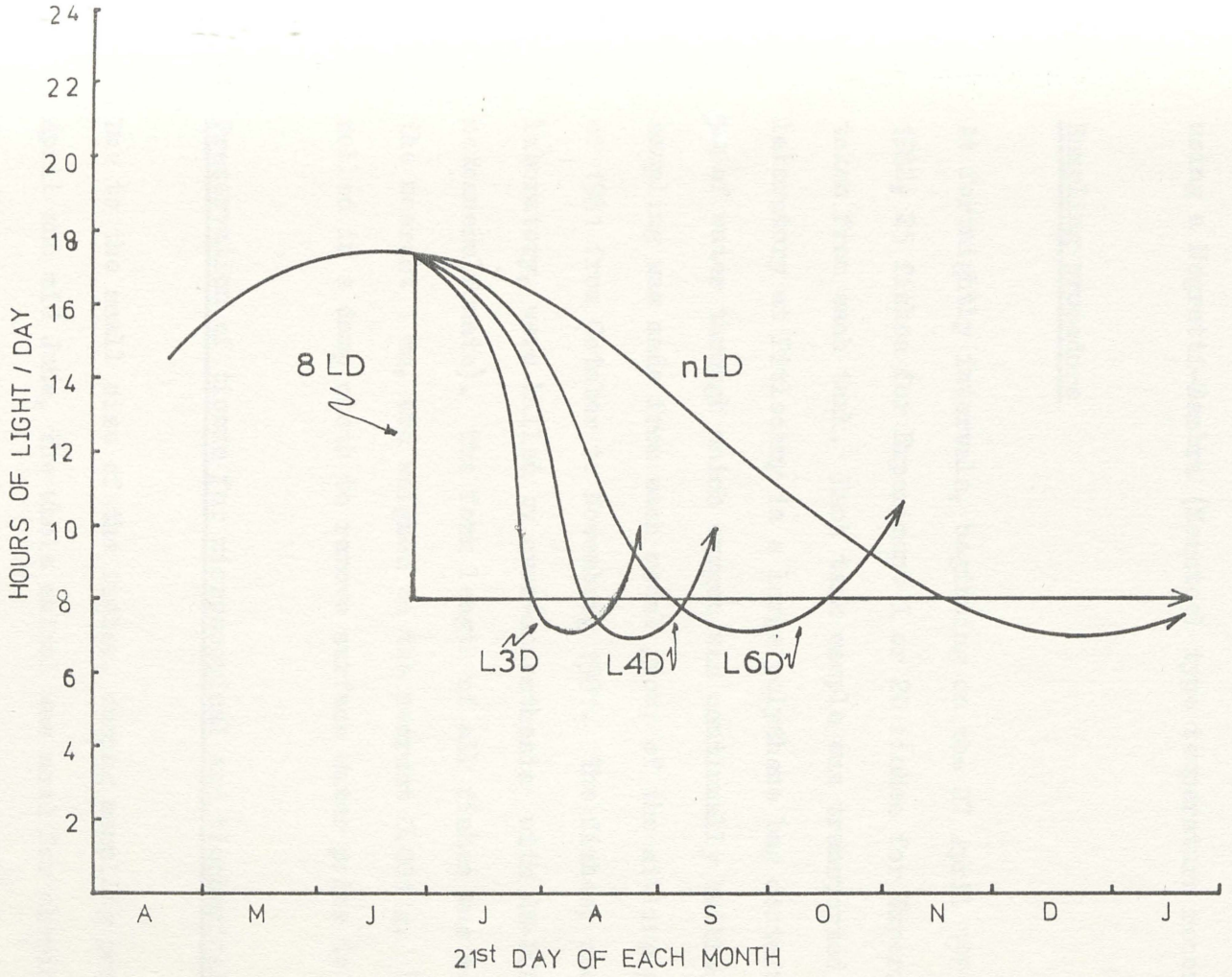

3
2
1

Figure 3 Photoperiod cycles used in Experiment II. nLD, natural photoperiod; 8LD autumn photoperiod; L3D, 3 month cycle; L4D, 4 month cycle; L6D, 6 month cycle.


24
22
20
18
16
14
12
10
8
6
4
2
HOURS OF LIGHT / DAY
8 LD
nLD
L3D
L4D
L6D
A
M
J
J
A
S
O
N
D
J
21st DAY OF EACH MONTH

Day-length change was controlled by mechanical timer (Sangamo Weston Solar Clock, U.K.), adjusted automatically for natural seasonal advancement in astronomical day-length for this latitude (56° 20' North). No morning or evening twilight period was provided. The daily maximum and minimum water temperature in the hatchery were chart-recorded continually during the whole year 1981, 1982 (Figure 4) using a Negretti-Zambra (Mersteel type temperature recorder).

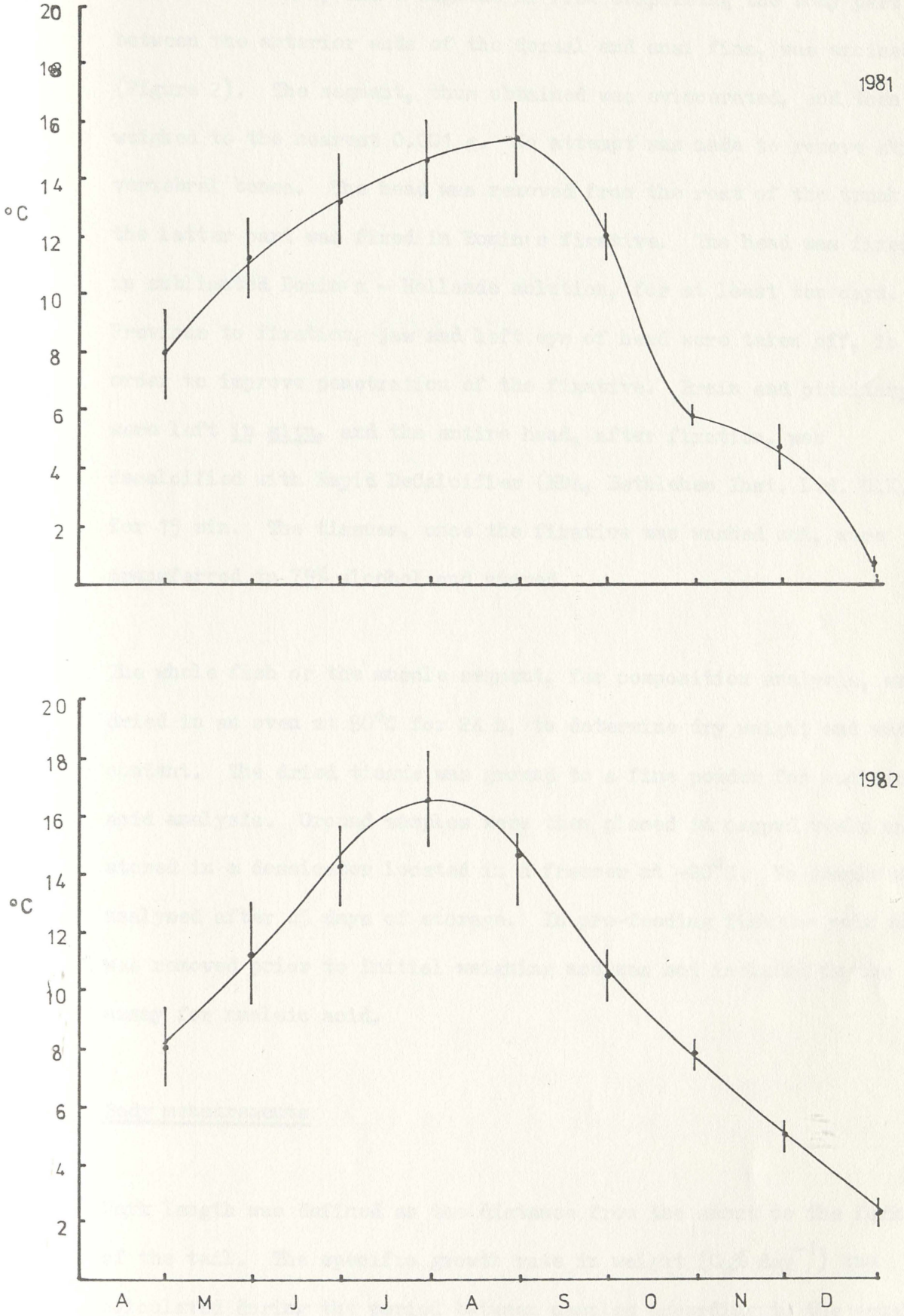
2.3 Sampling procedure

At fortnightly intervals, beginning on the 27 April 1981 and 7 May 1982, 25 fishes for Experiment I or 20 fishes for Experiment II, were taken from each tank. Each tank sample was transported to the laboratory at Pitlochry in a large polythene bag containing approximately 5-1 of water through which oxygen was continually bubbled. Similar sampling was made from each modal group of the sibling population of 1981 from October to November, 1981. The fishes, once in the laboratory, were killed by over-anaesthesia with MS-222 (tricaine methanesulfonate). The fork length of all fishes was measured to the nearest 1 mm, and weighed to the nearest 0.001 g. Each fish was rolled in a damp cloth to remove surface water prior to weighing.

2.3.1 Preservation of tissue for microscopical and biochemical purposes

Due to the small size of the fishes, during sampling period between April and mid June, the whole animal was used for chemical analysis; from then onwards only muscle composition analysis was performed. After the end of June, after measurements were made, dorsal and pelvic

Figure 4 The monthly mean water temperature ($\pm$ SD) of the River Almond over the study period.


1981
1982
°C
20
18
16
14
12
10
8
6
4
2
A
M
J
J
A
S
O
N
D

fins were cut off, and a segment of fish comprising the body part between the anterior ends of the dorsal and anal fins, was excised (Figure 2). The segment, thus obtained was eviscerated, and then weighed to the nearest 0.001 g. No attempt was made to remove skin or vertebral bones. The head was removed from the rest of the trunk and the latter part was fixed in Bouin's fixative. The head was fixed in sublimated Bouin's - Hollande solution, for at least ten days. Previous to fixation, jaw and left eye of head were taken off, in order to improve penetration of the fixative. Brain and pituitary were left in situ, and the entire head, after fixation, was decalcified with Rapid DeCalcifier (RDA, Bethlehem Inst. Ltd. U.K.) for 15 min. The tissues, once the fixative was washed out, were transferred to 75% alcohol and stored.

The whole fish or the muscle segment, for composition analysis, was dried in an oven at 80°C for 24 h, to determine dry weight and water content. The dried tissue was ground to a fine powder for nucleic acid analysis. Ground samples were then placed in capped vials and stored in a dessicator located in a freezer at -20°C. No sample was analysed after 45 days of storage. In pre-feeding fish the yolk sac was removed prior to initial weighing and was not included in the assay for nucleic acid.

2.3.2 Body measurements

Fork length was defined as the distance from the snout to the fork of the tail. The specific growth rate in weight (G_W% day^{-1}) was calculated during the period between samples according to the equation:

$$G_w = \frac{(\log_e W_2 - \log_e W_1)}{t} \times 100$$

where W_1 and W_2 are the sample mean weights at the start and end of a period between samples, and t is the number of days in the period (Brown 1945a, b).

The gonadosomatic index was determined from the expression:

$$GSI = \frac{\text{wet weight gonads}}{\text{total wet weight}} \times 100$$

The condition factor of each sample was calculated as follows:

$$K = \frac{100\ W}{L^3}$$

where W is the weight in g and L is the length in cm.

2.4 Biochemical Analysis

Nucleic acids were extracted according to the method of Schneider (1957), modified by Bulow (1970) and Bulow et al. (1981).

30 mg samples of dry powder were weighed and suspended in 6 ml of cold 10% trichloroacetic acid (TCA), in order to remove interfering substances (e.g. reducing carbohydrates, free nucleotides, etc.). The suspension was then centrifuged for 15 min. to 4,000 RPM (Centrifuge MSE, England), and the resulting supernatant discarded. The procedure was repeated once more, and the pellet thus obtained was made of tissue proteins, nucleic acid and lipids. The nucleic acids were then extracted in two 4 ml aliquots of 5% TCA at 90°C

for 30 min, and the combined extracts were made up to 10 ml final volume. No attempt was made for defatting the dry sample. The final supernatant fluid contained the mix of nucleic acids.

The RNA content was determined by the reaction between orcinol and ribosa (Lusena, 1951; Munro and Fleck, 1966). Orcinol reagent (1% w/v orcinol + 0.5% w/v of $FeCl_3$ dissolved in 12N HCl) was mixed with the extract at 1:1 proportion and incubated at 90°C for 30 min. The DNA was determined by the diphenylamine (DPA) reaction modified by Burton (1956) (see Munro and Fleck, 1966 for recent review).

One volume of sample was added to two volumes of DPA reagent (1 g of DPA dissolved in 100 ml of glacial acetic acid and 2.75 ml of concentrated H_2SO_4) followed by incubation at 35°C for 20 hr. Standard solutions were prepared from yeast RNA (Sigma), and herring sperm DNA (Type III, Sigma), according to Bulow's (1970) procedure, and standard curves relating optical density to micrograms of RNA and DNA, were made, to estimate nucleic acid concentration.

The concentration of nucleic acid in the extract, and in standards were measured using a Pye Unicam SP spectrophotometer.

RNA and DNA contents were expressed in µg/100 mg of dry tissue, the amounts of nucleic acid in mg, and the dry weight in mg.

2.5 Reagents

All reagents were purchased from BDH Chemical Ltd.and Sigma, and were analytical standard. The dyes described in the staining procedure, if not otherwise stated, were procured from Gurr Ltd. (BDH Chemical Ltd., U.K.).

2.6 Histological techniques

2.6.1 Processing

The fixed tissues, brains and trunks were dehydrated in an ethyl alcohol series, cleared in Xylene, and embedded in paraffin wax (Melting Point 50°C), all through an automatic tissue processing machine (Shandon Duplex Tissue Processor, Shandon Suth. Product Ltd., U.K.).

Blocks were sectioned at 7 or 10 μ and subsequently stained. For muscle diameter measurements, fish were sectioned at the point adjacent and anterior to the dorsal fin (Figure 2).

2.6.2 Staining Procedure

2.6.2.1 Muscle and gonadal tissue

The trunk sections used for measuring muscle fibre diameter were 10 μ thick and cut at right angles to the main axis; for gonadal studies sections were 7 μ thick. Sections consequently obtained were stained with Mayer's Haematoxylin and contrastained with eosin.

2.6.2.2 Pituitary

Longitudinal sections of pituitary were made at 7 µ and mounted serially. The sections so obtained were placed in Lugol's - iodine for 10 min, and subsequently in sodium thio-sulphate (5%) for 10 min, to remove the mercuric chloride precipitate from the fixation (Drury and Wallington, 1967). The sections were then stained with performic acid-alcian blue, periodic-acid - Schiff, Orange G, and acid fuchsin (PFAB - PAS - OG - AF, Jafri, 1979); Herlant's Alizarin blue tetrachrome (Aliz BT, Herlant, 1960); periodic acid - Schiff with Orange G (PAS - OG, Drury and Wallington, 1967). The best result with the Aliz BT staining was obtained with a French version of Herlant's Erythrosin - B (Erythrosine 239, Serlabo, Paris).

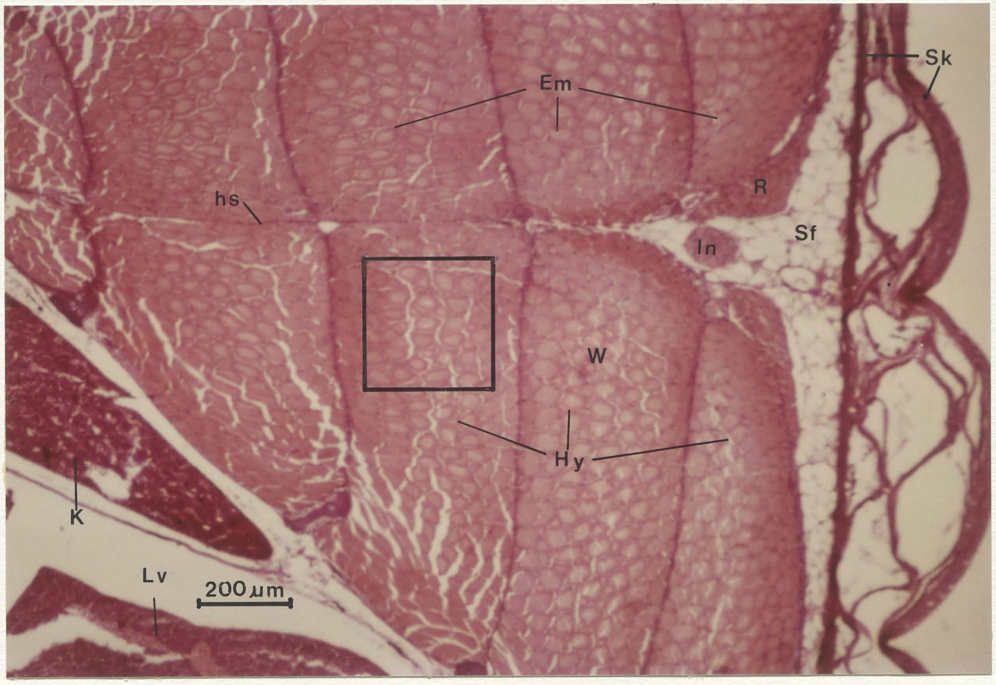
2.6.3 Histological measurements and observations

All histological measurements were made using an eyepice graticule in an Olympus BH - 2 (Olympus Optical Co., Tokyo) binocular microscope.

2.6.3.1 Diameter of muscle fibre

The procedure to measure fibre diameter was modified from Weatherley et al. (1979; 1980a). It consisted of locating microscopically the representative area, which corresponded to the 3rd hypaxial myotome counting from the skin, near to horizontal septum. (Plate 2). This area was photographed at a magnification of 1250 X and the photograph printed at an enlargement of 7 X. A square grid of 10 x 10 cm, was superimposed,

Plate 2 Transverse section showing the area from which muscle fibres were sampled. Em, epaxial myotome; Hy, hypaxial myotome, hs, horizontal septum; k, kidney; Lv, liver; ln, lateral nerve; R, red muscle; Sk, skin; sf, subcutaneous fat; W, white muscle. (Mayer's haematoxylin and eosin. X50).


Em
Sk
hs
R
Sf
In
W
Hy
K
Lv
200 µm

sampling all fibres within, with the exception of all those outside or touching the lower and right side of it. (Plate 2). Images of included fibres were cut out with a designer knife (Letraset Ltd.) and weighed individually. Areas of images were calculated from the known weight per unit of area of photographic paper and equivalent area diameters (Dea) were calculated from the magnification and enlargement records. Dea is the diameter of a circle having the same area of myofibre (MA). The former, may be calculated assuming the area described by the myofibre corresponds to the area of a perfect circle, using the formula:

$$Dea = 2\sqrt{\frac{MA}{\pi}}$$ (Clancy and Herlihy, 1979)

2.6.3.2 Gonadal tissue

In ovaries, the mean diameter of oocytes (sum of two measurements taken at right angles and divided by two) was taken from 25 cells, whose nuclei were included in the section, which has been shown to be representative of the true oocyte diameter. (Foucher and Beamish, 1980; Robb, 1982). Measurements of nucleus and nucleous mean diameter, and number of cells per cyst were noted. Other characteristics such as, intensity of cytoplasm staining, cellular stage of development (e.g. chromatin nucleolus stage, early peri-nucleolus stage etc.); and the number and localisation of nucleuli, were recorded as well. The intensity of cytoplasm staining was recorded subjectively as, weak, (+). moderate (++) and intense (+++).

In the female gonad cell, the presence and the time of appearance of the yolk nucleus of the Balbiani's vitelline body was recorded. The

yolk nucleus was defined, for the present purpose, as a well-limited aggregation or bodies of basophilic sustances, usually preserved by classic techniques of cytology (Guraya, 1979).

For testes, measurements were made of mean diameters of 25 spermatogonia cells, nuclei and nucleoli. Intensity of cytoplasm staining and number of spermatogonia per cyst were similarly recorded.

2.6.3.3 Pituitary cells

The cell diameter, nucleus diameter and cell density of 25 cells per pituitary were measured for thyrotropes (TSH cell), gonadotropes (GTH cell), somatotropes (GH cell) and lactotropes (LTH cell) according to the method of Leatherland (Leathland, 1970a; Schreibman et al., 1973).

Cell and nucleus diameter were defined as the averages of two principal cell or nucleus axes, and described by the expression:

$$\text{Diameter} = \frac{\text{maximum cell or nucleus length plus maximum cell or nucleus width}}{2}$$

Cell density means the number of cells per unit area, obtained by counting the number of cell nuclei within a standard ocular grid and converted to number of cell nuclei/μ^2. The cell density of LTH cells was recorded in ten different regions of lobular area of the rostral pars distalis of the adenohypophysis (RPD). The same number of measurements was made for estimating the cell density of GH cells in the

proximal pars distalis of the adenohypophysis (PPD).

The mitotic activity of the different cell types was also recorded.

2.7 Statistical methods

The probabilities of the reality of differences in the results of simple pair comparisons were evaluated by Student's t-test. Differences between groups subjected to diverse treatments were compared by one-way analysis of variance (ANOVA); and a posteriori comparison among the means was performed by a Student - Newman - Keuls test (SNK test). In cases in which the data showed high levels of heterogeneity appropriate transformation was applied. In the case of percentages, angular transformations ($F(x) = \mathrm{Sin}^{-1}\sqrt{x}$) were used to stabilise all data. When homogeneity was not achieved after transformation, the non-parametric Kruskal - Wallis test was used, followed by a non-parametric simultaneous test procedure (STP) for a posteriori tests (Siegel, 1956; Sokal and Rohlf, 1964).

Regression analysis was applied to some results and the corresponding tests of significance of regression coefficients were performed. Analysis of covariance (ANCOVA) was applied to certain data, as described under results.

The frequency distributions of fish length were analysed by Cassie's (1954) method, using arithmetic probability paper to separate the component modal groups.

3 Results

3.1 Feeding regime

The two feeding frequency regimes (T rate and 2T rate) to which juvenile Atlantic salmon were subjected during Experiment I (1981) did not exert any differential effects on their growth, nor on the pattern of development of bimodality in the length frequency distributions (Fig.5, Table 21). For that reason, in the results presented here, data from the two feeding rates for each photoperiod are pooled together.

3.2 Effect of light on the development of bimodality

The fish populations of 1981 (Experiment I) and 1982 (Experiment II) showed symmetrical unimodal length frequency distributions until the end of August. From October of both years the different photoperiodic populations, especially that subject to natural photoperiod (nLD) showed a skewed distribution with an extended upper tail, which became more pronounced from then onwards (Fig.6a; 7a and 8). The fishes in the tanks subject to constant light (LL), showed an increase in the number in the upper tail of the frequency distributions (Fig.6b and 7b). On the contrary, for the autumn photoperiod fish group (8LD) the upper tail was shorter and the number of small size fish increased (Fig.7c). The accelerated rate of change of day length did not seem to exert any important effect on the length frequency distribution (Fig.8).

Figure 5 Length frequency distribution of a sibling population of juvenile salmon under natural (nLD) and constant (LL) photoperiod, each of them subjected to two different feeding regimes (T-rate and 2T-rate).

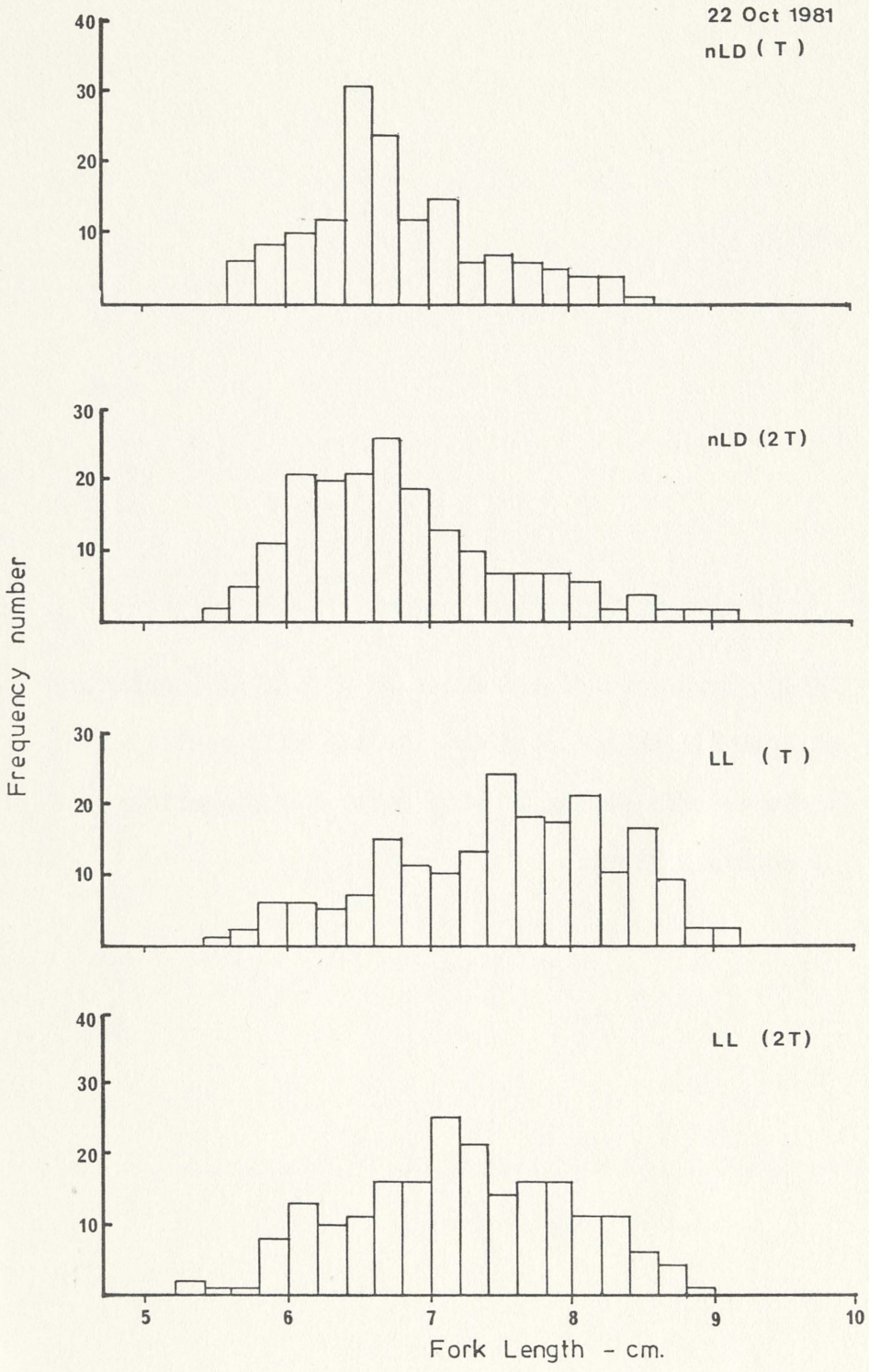

22 Oct 1981
nLD (T)
nLD (2 T)
LL (T)
LL (2T)
Frequency number
Fork Length - cm.
40
30
20
10
5
6
7
8
9
10

Figure 6 Length frequency distribution of a sibling population of juvenile salmon subjected to two different photoperiodic regimes. nLD, natural photoperiod; LL constant light.

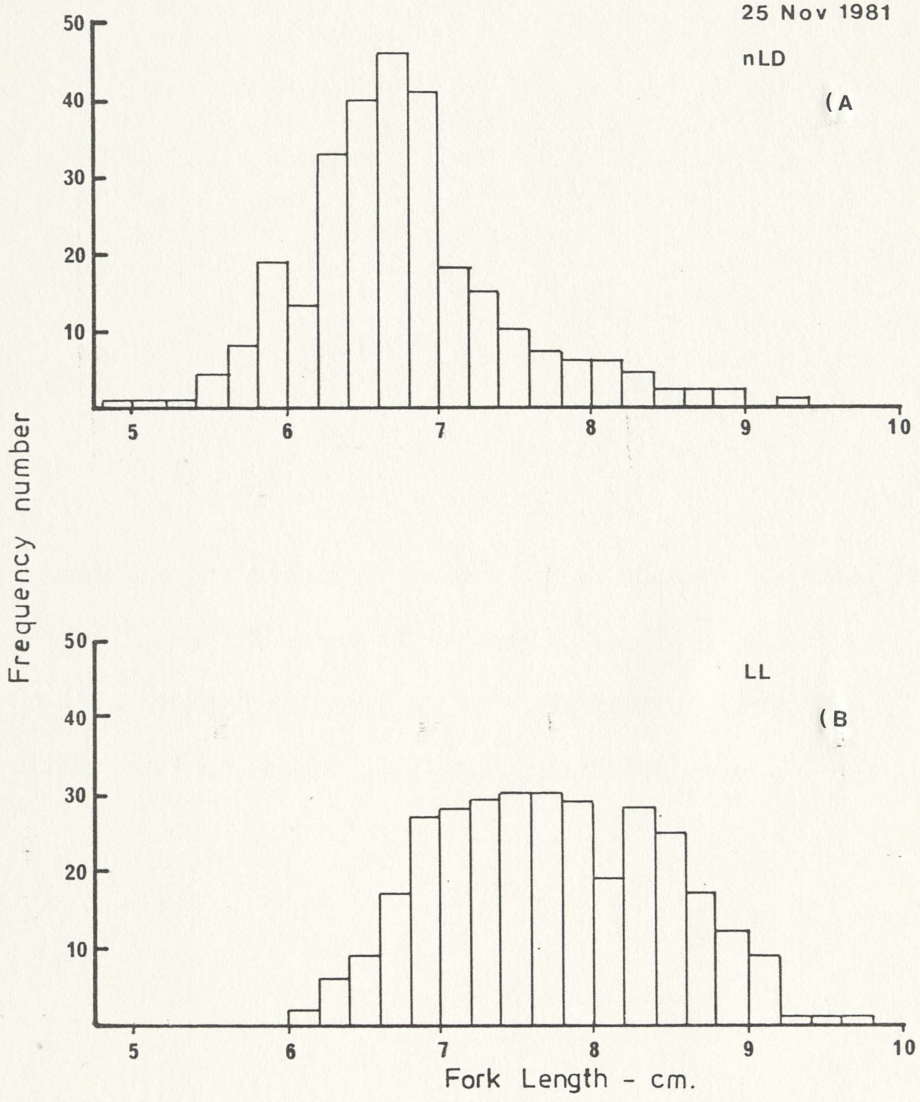

25 Nov 1981
nLD
(A
LL
(B
Frequency number
Fork Length - cm.
50
40
30
20
10
5
6
7
8
9
10

Figure 7 Length frequency distribution of sibling populations of juvenile salmon subjected to three different photoperiodic regimes. A - nLD, natural photoperiod; B - LL, constant light; C - 8LD, autumn photoperiod.

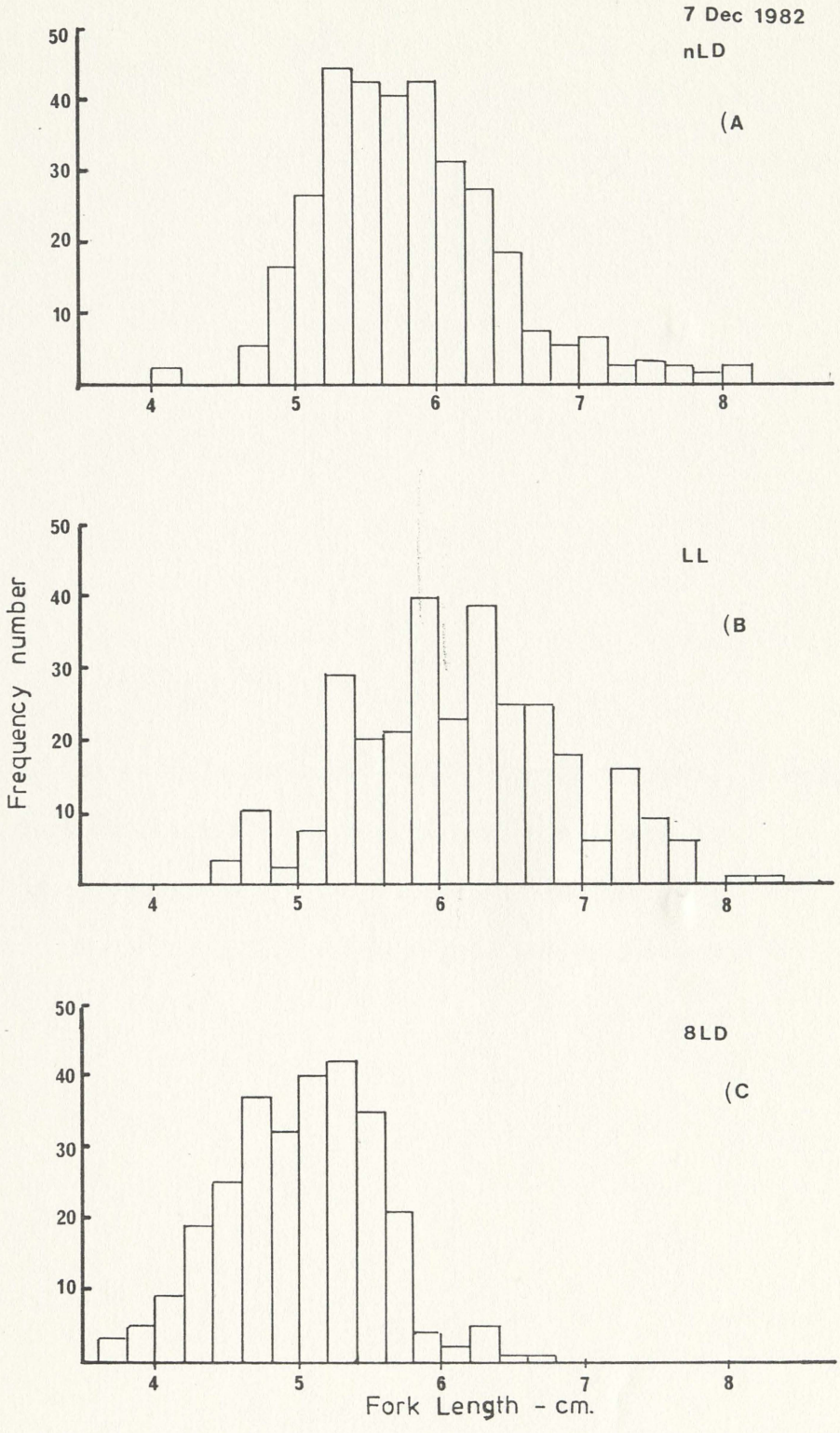
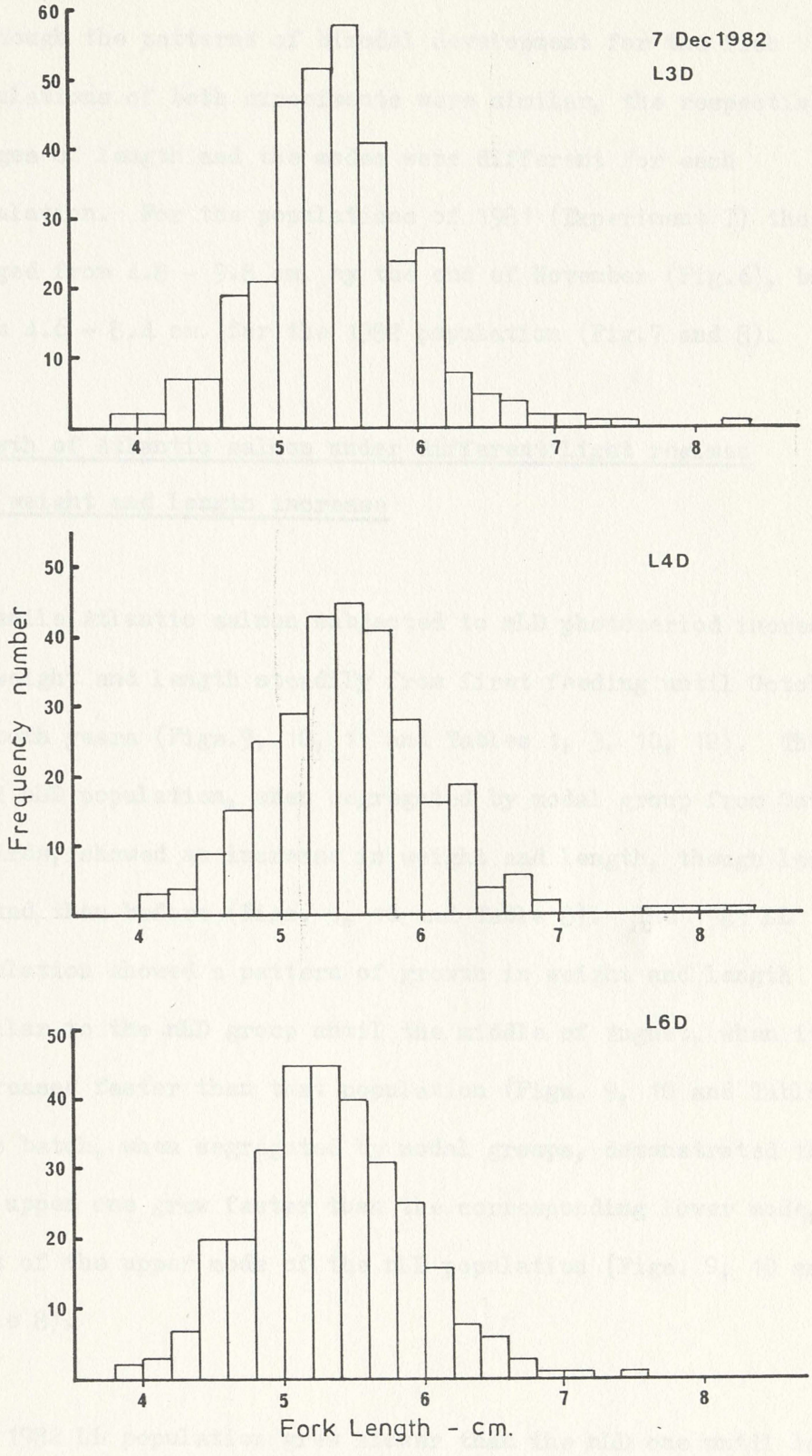

7 Dec 1982
nLD
(A
LL
(B
8LD
(C
Frequency number
50
40
30
20
10
4
5
6
7
8
Fork Length - cm.

Figure 8 Length frequency distribution of sibling populations of juvenile salmon subjected to three different photoperiodic regimes. L3D - 3 month cycle; L4D, 4 month cycle; L6D, 6 month cycle.


7 Dec 1982
L3D
L4D
L6D
Frequency number
Fork Length - cm.
60
50
40
30
20
10
4
5
6
7
8

Although the patterns of bimodal development for the fish populations of both experiments were similar, the respective ranges of length and the modes were different for each population. For the populations of 1981 (Experiment I) the length ranged from 4.8 - 9.8 cm. by the end of November (Fig.6), but from 4.6 - 8.4 cm. for the 1982 population (Fig.7 and 8).

3.3 Growth of Atlantic salmon under different light regimes

3.3.1 Wet weight and length increase

Juvenile Atlantic salmon subjected to nLD photoperiod increased in weight and length steadily from first feeding until October in both years (Figs.9, 10, 11 and Tables 1, 3, 10, 12). The 1981 nLD population, when segregated by modal group from October onwards, showed an increase in weight and length, though less marked than before (Figs. 9, 10 and Table 8). The 1981 LL population showed a pattern of growth in weight and length similar to the nLD group until the middle of August, when it increased faster than that population (Figs. 9, 10 and Table 3). This batch, when segregated by modal groups, demonstrated that the upper one grew faster than the corresponding lower mode, or that of the upper mode of the nLD population (Figs. 9, 10 and Table 8).

The 1982 LL population grew slower than the nLD one until late August, and then faster through September (Figs. 11, 13 and Table 12). All other photoperiodic regimes of that year showed poor growth compared with nLD group (Figs. 11 - 13 and Table 8).

Figure 9 Change in mean length ($\pm$ 2SE), of two sibling populations of juvenile salmon, subjected to natural photoperiod (nLD) and constant light (LL). Experiment I (1981). um, upper mode; lm, lower mode; ff, first feeding day; ms, midsummer day.

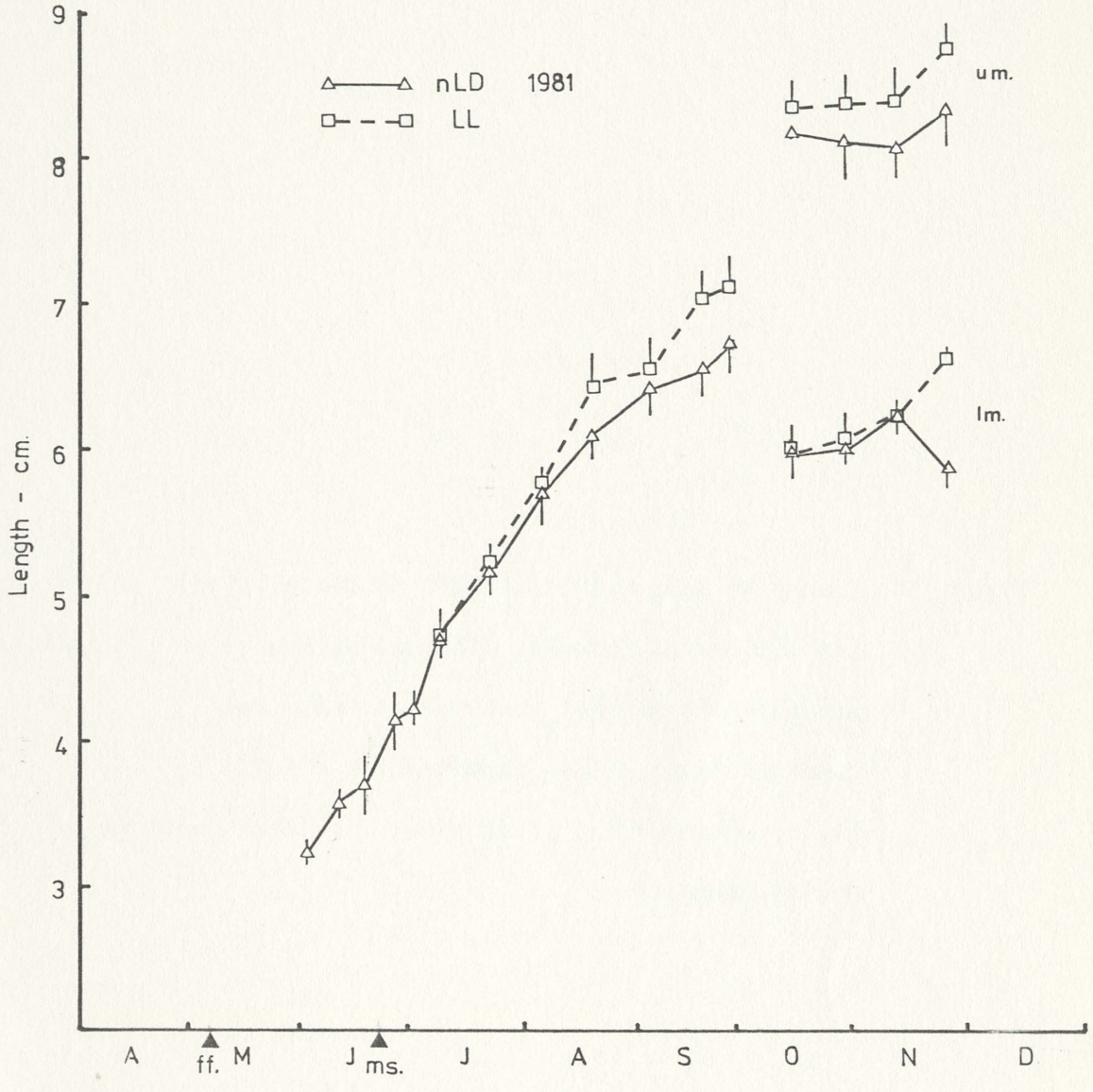

nLD 1981
LL
um.
lm.
Length - cm.
9
8
7
6
5
4
3
A
ff.
M
J
ms.
J
A
S
O
N
D

Figure 10 Change in mean weight ($\pm$ 2SE) of two sibling populations of juvenile Atlantic salmon subjected to natural photoperiod (nLD) and constant light (LL). Experiment I (1981). um, upper mode; lm, lower mode; ff, first feeding; ms, midsummer day.

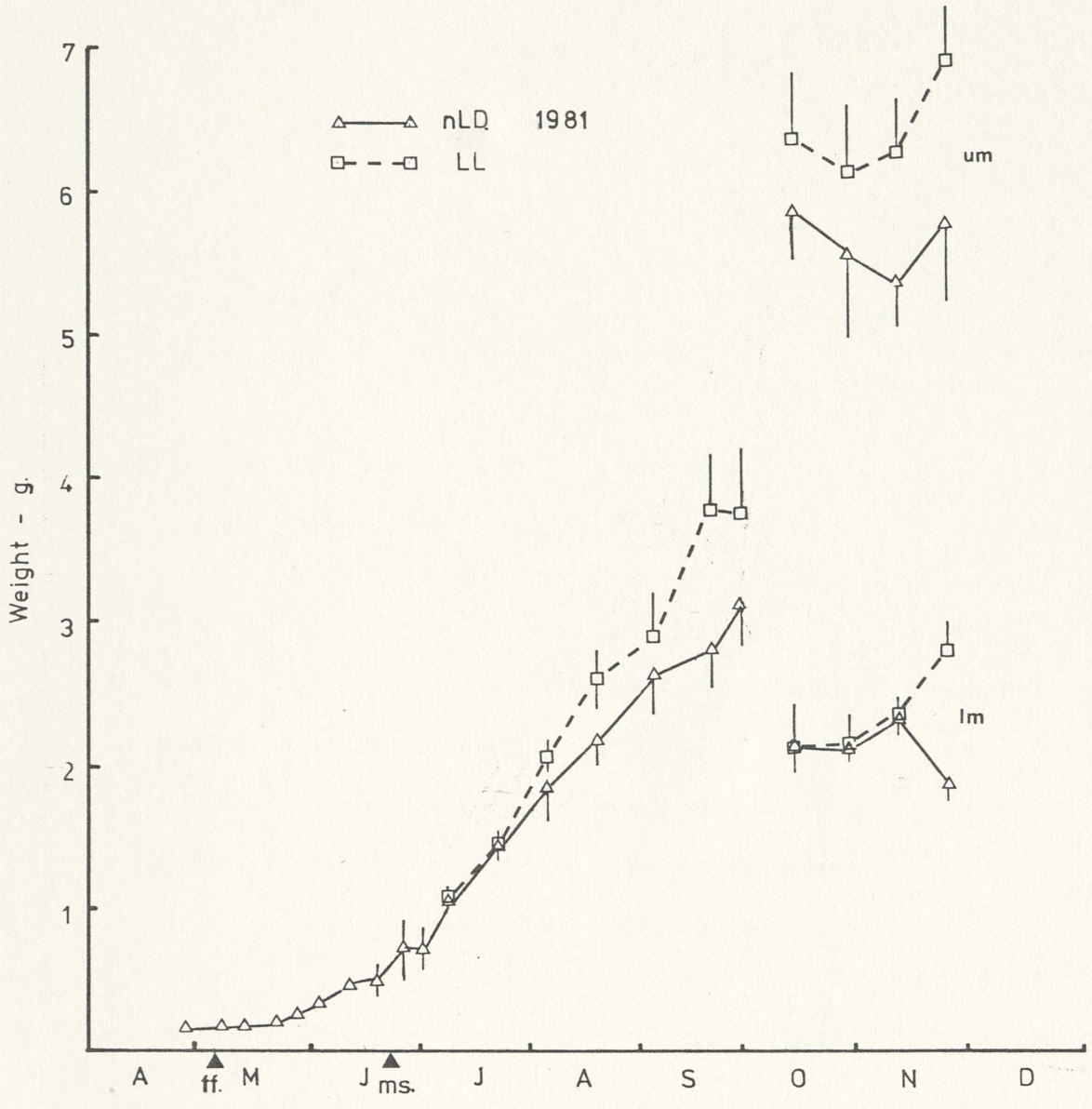

nLD 1981
LL
um
lm
Weight - g.
7
6
5
4
3
2
1
A
ff.
M
J
ms.
J
A
S
O
N
D

Figure 11 Change in mean length and weight (± 2SE) of two sibling populations of juvenile Atlantic salmon, subjected to natural photoperiod (nLD) and autumn photoperiod (8LD). Experiment II (1982). ff, first feeding; ms, midsummer day.

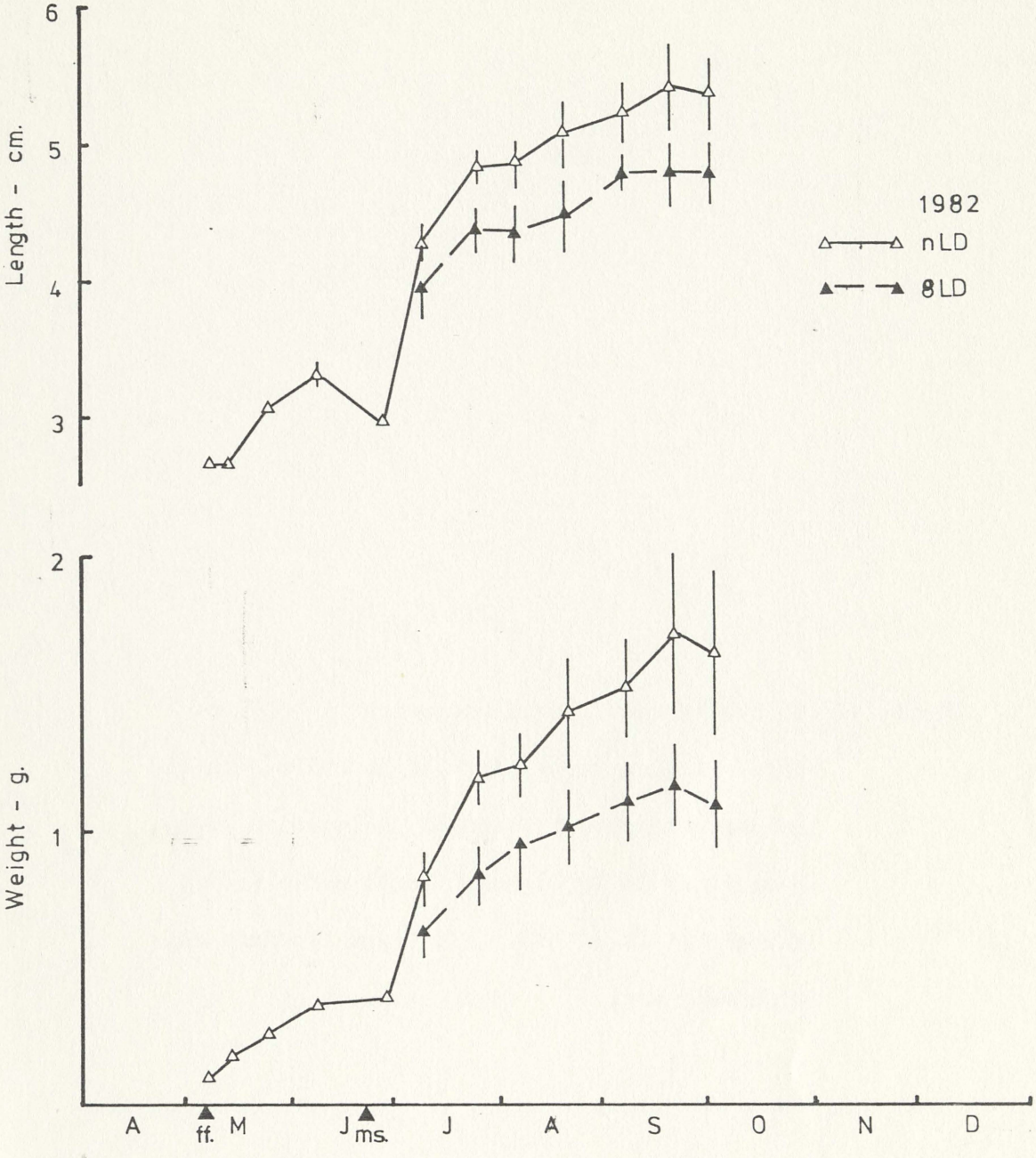

Length - cm.
6
5
4
3
1982
nLD
8LD
Weight - g.
2
1
A
ff.
M
J
ms.
J
A
S
O
N
D

Figure 12 Change in mean length and weight (± 2SE) of three sibling populations of juvenile Atlantic salmon subjected to natural photoperiod (nLD), 3 month cycle (L3D) and 6 month cycle (L6D). Experiment II (1982). ff, first feeding; ms, midsummer day.

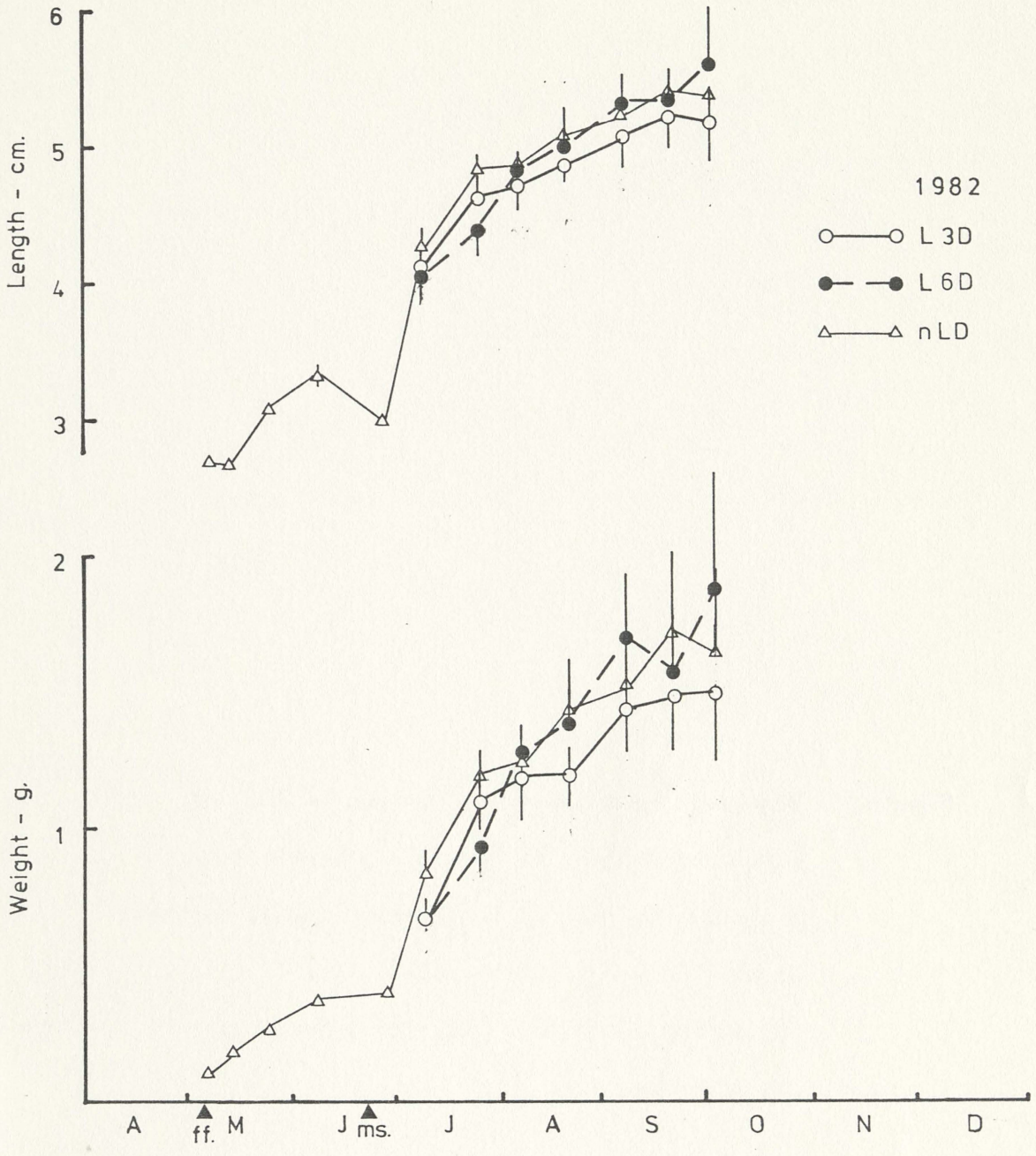
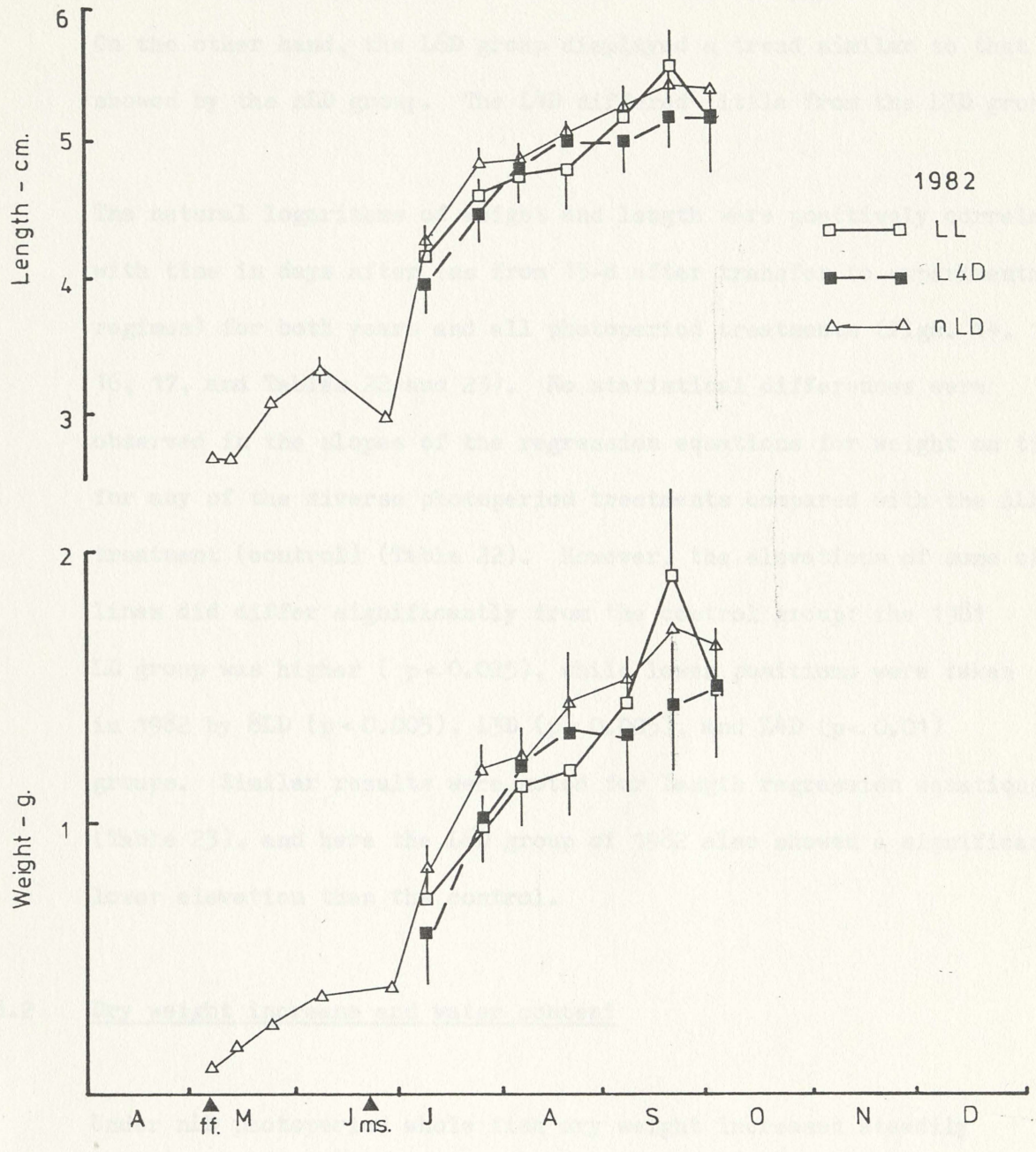

Length - cm.
6
5
4
3
1982
L 3D
L 6D
nLD
Weight - g.
2
1
A
ff.
M
J
ms.
J
A
S
O
N
D

Figure 13 Change in mean length and weight (± 2SE) of three populations of juvenile Atlantic salmon subjected to natural photoperiod (nLD), constant light (LL) and 4 month cycle (L4D). Experiment II (1982). ff, first feeding; ms, midsummer day.


Length - cm.
6
5
4
3
1982
LL
L 4D
n LD
Weight - g.
2
1
A
ff.
M
J
ms.
J
A
S
O
N
D

The worst growth performance was that of the 8LD population. On the other hand, the L6D group displayed a trend similar to that showed by the nLD group. The L4D differed little from the L3D group.

The natural logarithms of weight and length were positively correlated with time in days after (as from 15-d after transfer to experimental regimes) for both years and all photoperiod treatments (Figs. 14, 15, 16, 17, and Tables 22 and 23). No statistical differences were observed in the slopes of the regression equations for weight on time, for any of the diverse photoperiod treatments compared with the nLD treatment (control) (Table 22). However, the elevations of some of the lines did differ significantly from the control group: the 1981 LL group was higher ($p < 0.025$), while lower positions were taken in 1982 by 8LD ($p < 0.005$), L3D ($p < 0.005$), and L4D ($p < 0.01$) groups. Similar results were noted for length regression equations (Table 23), and here the L6D group of 1982 also showed a significantly lower elevation than the control.

3.3.2 Dry weight increase and water content

Under nLD photoperiod whole fish dry weight increased steadily between the 5th April and the 1st July 1981 (Table 1; Fig. 18), and similarly between 7th May and 29th June 1982 (Table 10).

The skeletal muscle also increased steadily in dry weight, between July and September of both years (Fig. 18 and Tables 4, 14). Under LL photoperiod in 1982 skeletal muscle dry weight

Figure 14 Semilogarithmic plot of the mean length and weight of juvenile Atlantic salmon, subjected to natural photoperiod (nLD) and constant light (LL). Experiment I (1981).

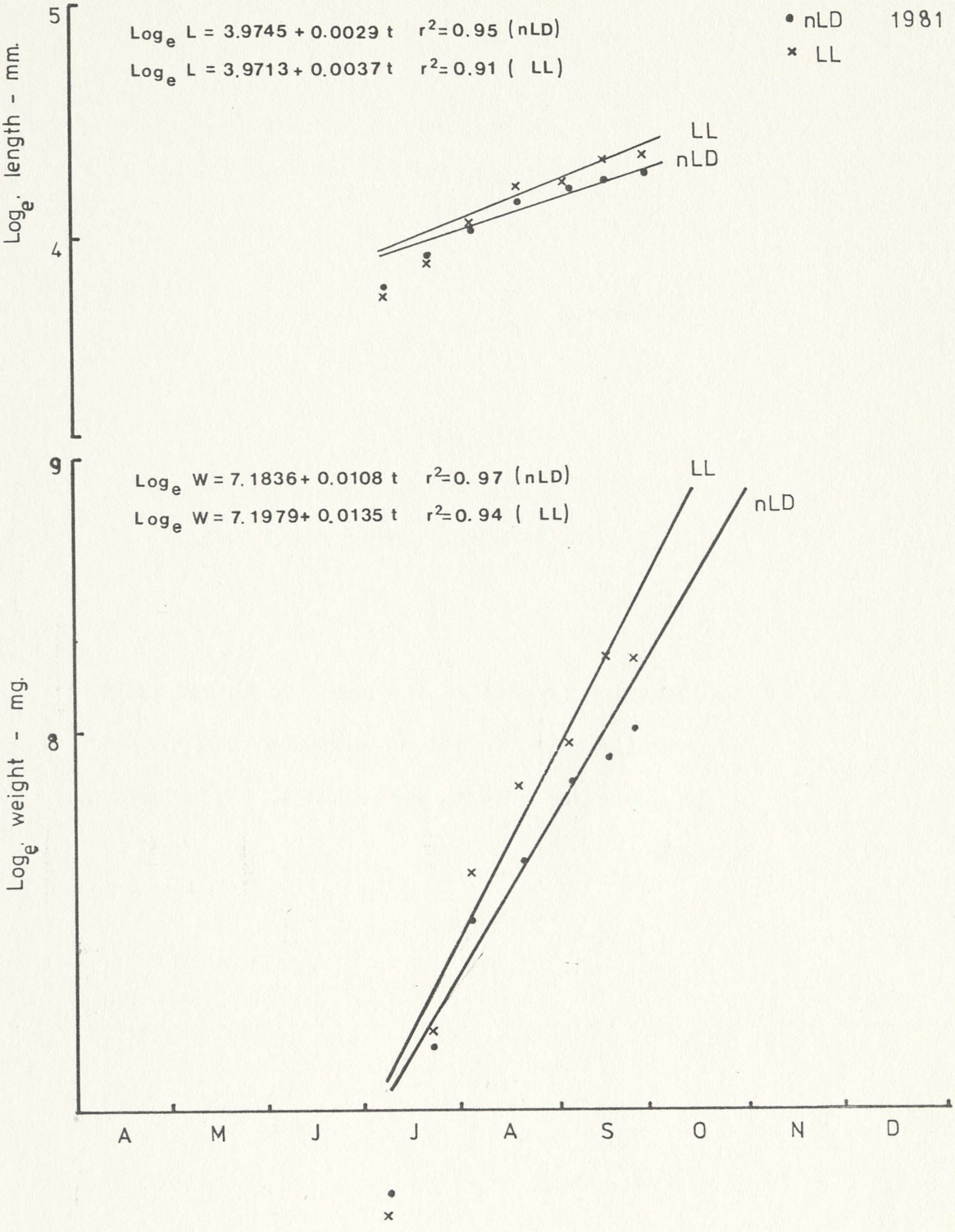

Log$_e$ L = 3.9745 + 0.0029 t r^2=0.95 (nLD)
Log$_e$ L = 3.9713 + 0.0037 t r^2=0.91 (LL)
• nLD 1981
× LL
Log$_e$ length - mm.
5
4
LL
nLD
Log$_e$ W = 7.1836 + 0.0108 t r^2=0.97 (nLD)
Log$_e$ W = 7.1979 + 0.0135 t r^2=0.94 (LL)
Log$_e$ weight - mg.
9
8
LL
nLD
A
M
J
J
A
S
O
N
D

Figure 15 Semilogarithmic plot of the mean length and weight of juvenile Atlantic salmon subjected to constant light (LL); and 4 month cycle (L4D). Experiment II (1982).

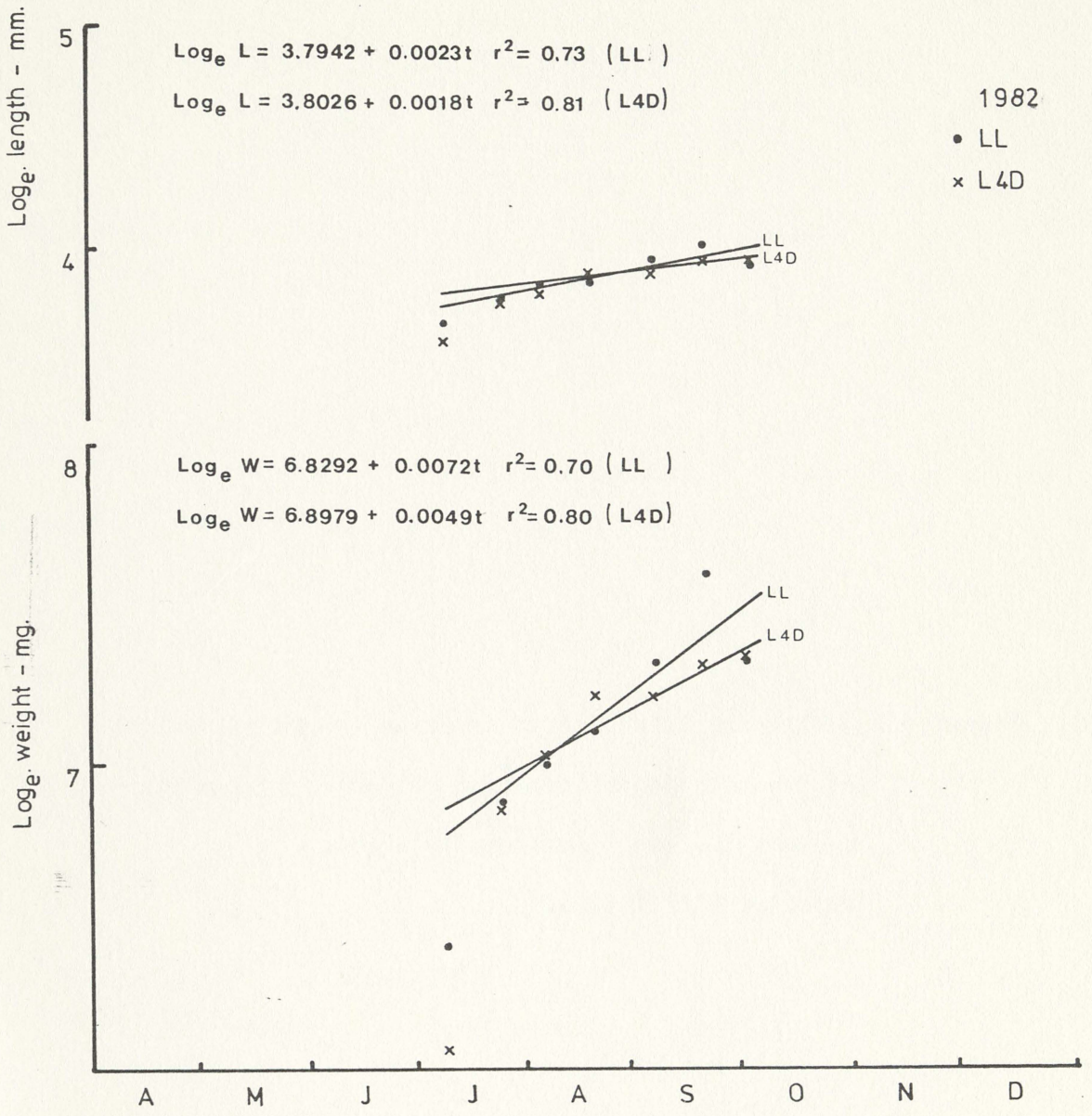

Log$_e$ length - mm.
5
4
Log$_e$ L = 3.7942 + 0.0023t r^2= 0.73 (LL)
Log$_e$ L = 3.8026 + 0.0018t r^2= 0.81 (L4D)
1982
• LL
× L4D
LL
L4D
Log$_e$ weight - mg.
8
7
Log$_e$ W= 6.8292 + 0.0072t r^2= 0.70 (LL)
Log$_e$ W= 6.8979 + 0.0049t r^2= 0.80 (L4D)
LL
L4D
A
M
J
J
A
S
O
N
D

Figure 16 Semilogarithmic plot of the mean length and weight of juvenile Atlantic salmon subjected to 3 month cycle (L3D) and 6 month cycle (L6D). Experiment II (1982).

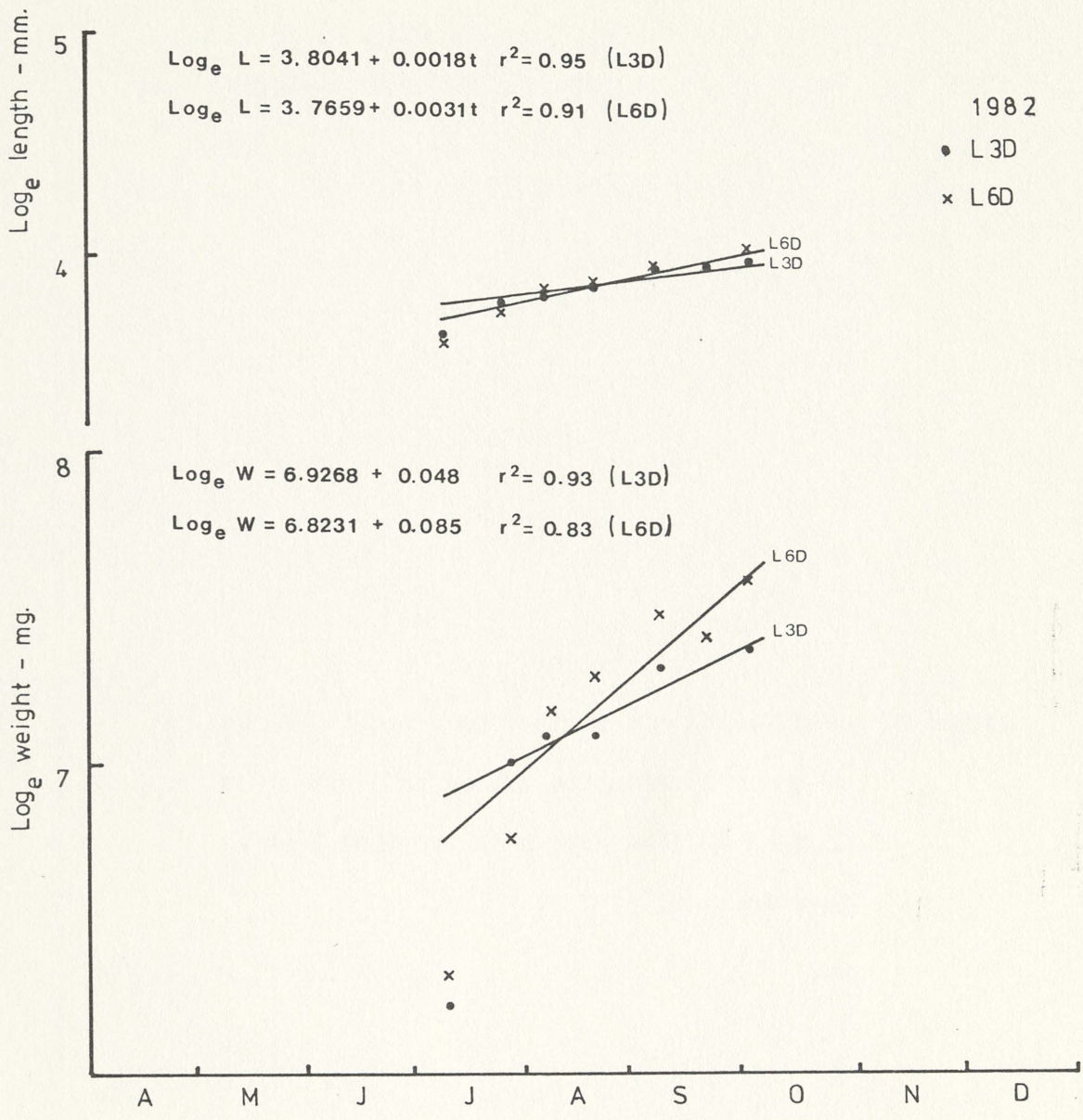
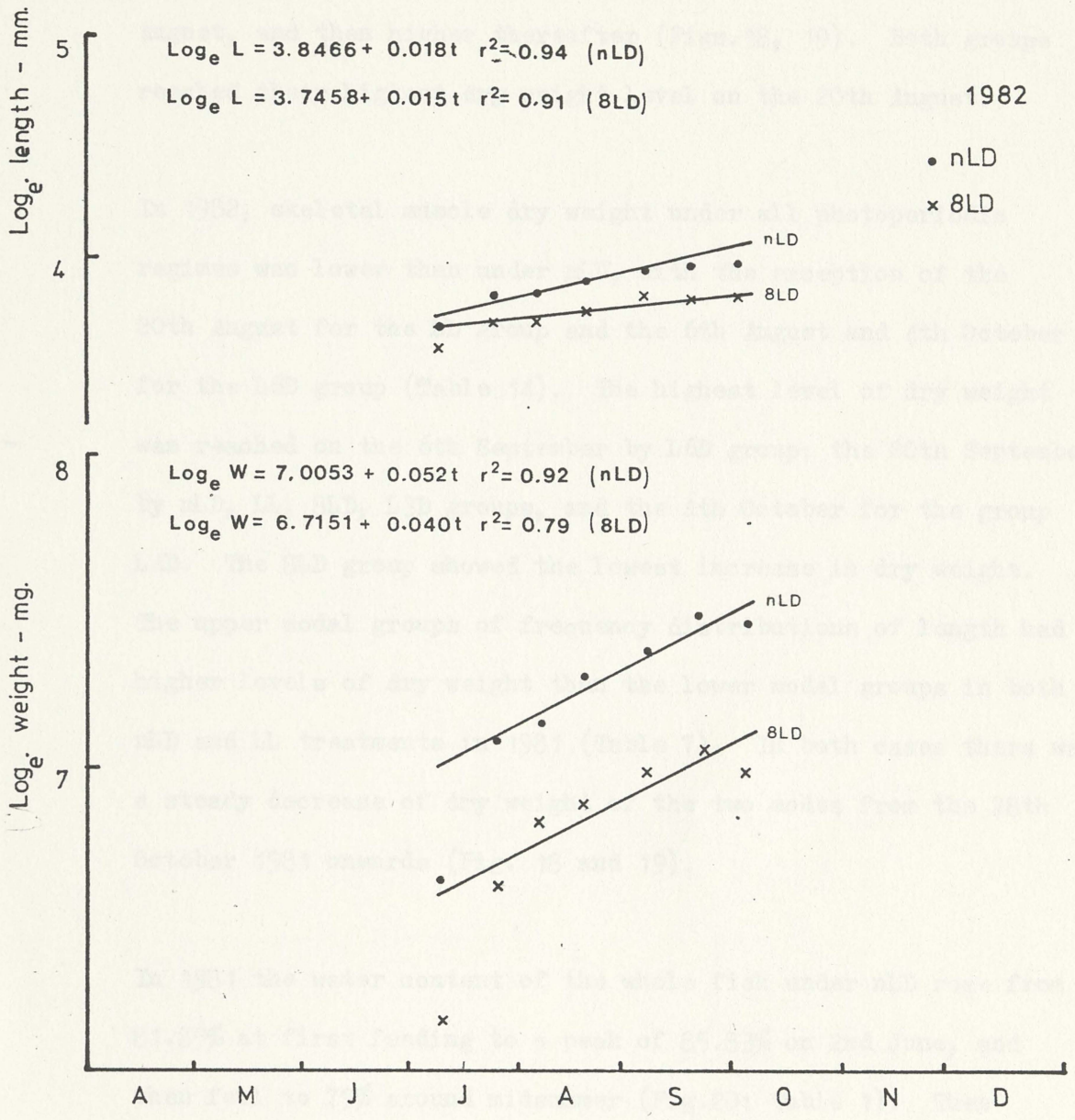

Log$_e$ length - mm.
5
4
Log$_e$ L = 3.8041 + 0.0018t r^2= 0.95 (L3D)
Log$_e$ L = 3.7659+ 0.0031t r^2= 0.91 (L6D)
1982
• L3D
× L6D
L6D
L3D
Log$_e$ weight - mg.
8
7
Log$_e$ W = 6.9268 + 0.048 r^2= 0.93 (L3D)
Log$_e$ W = 6.8231 + 0.085 r^2= 0.83 (L6D)
L6D
L3D
A
M
J
J
A
S
O
N
D

Figure 17 Semilogarithmic plot of mean length and weight of juvenile Atlantic salmon subjected to natural light (nLD) and autumn photoperiod (8LD). Experiment II (1982).


Log$_e$ length - mm.
5
4
Log$_e$ L = 3.8466 + 0.018t r^2= 0.94 (nLD)
Log$_e$ L = 3.7458 + 0.015t r^2= 0.91 (8LD)
1982
• nLD
× 8LD
nLD
8LD
Log$_e$ weight - mg.
8
7
Log$_e$ W = 7.0053 + 0.052t r^2= 0.92 (nLD)
Log$_e$ W = 6.7151 + 0.040t r^2= 0.79 (8LD)
nLD
8LD
A
M
J
J
A
S
O
N
D

was similar but lower than that of the nLD group until the 5th August, and then higher thereafter (Figs.18, 19). Both groups reached their highest dry weight level on the 20th August.

In 1982, skeletal muscle dry weight under all photoperiodic regimes was lower than under nLD, with the exception of the 20th August for the LL group and the 6th August and 4th October for the L6D group (Table 14). The highest level of dry weight was reached on the 6th September by L6D group; the 20th September by nLD, LL, 8LD, L3D groups, and the 4th October for the group L4D. The 8LD group showed the lowest increase in dry weight. The upper modal groups of frequency distributions of length had higher levels of dry weight than the lower modal groups in both nLD and LL treatments in 1981 (Table 7). In both cases there was a steady decrease of dry weight of the two modes from the 28th October 1981 onwards (Fig. 18 and 19).

In 1981 the water content of the whole fish under nLD rose from 81.85% at first feeding to a peak of 85.83% on 2nd June, and then fell to 79% around midsummer (Fig.20; Table 1). Then skeletal muscle fluctuated at about 76% water content from July to September in nLD, and decreased steadily from 79% to 76% in LL. On July 8th the water content of muscle under nLD was significantly lower than under LL ($p < 0.001$).

Under both photoperiod treatments the upper modal group had a consistently lower water content than the lower modal group, ranging from 75.32 - 76.80%, and 75.75 - 78.38% respectively (Figs 20 and Table 7).

Figure 18 Changes in the mean dry weight (± 2SE) of the whole body and muscle of young salmon under natural photoperiod (nLD). Experiment I (1981). ff, first feeding; ms, midsummer day.

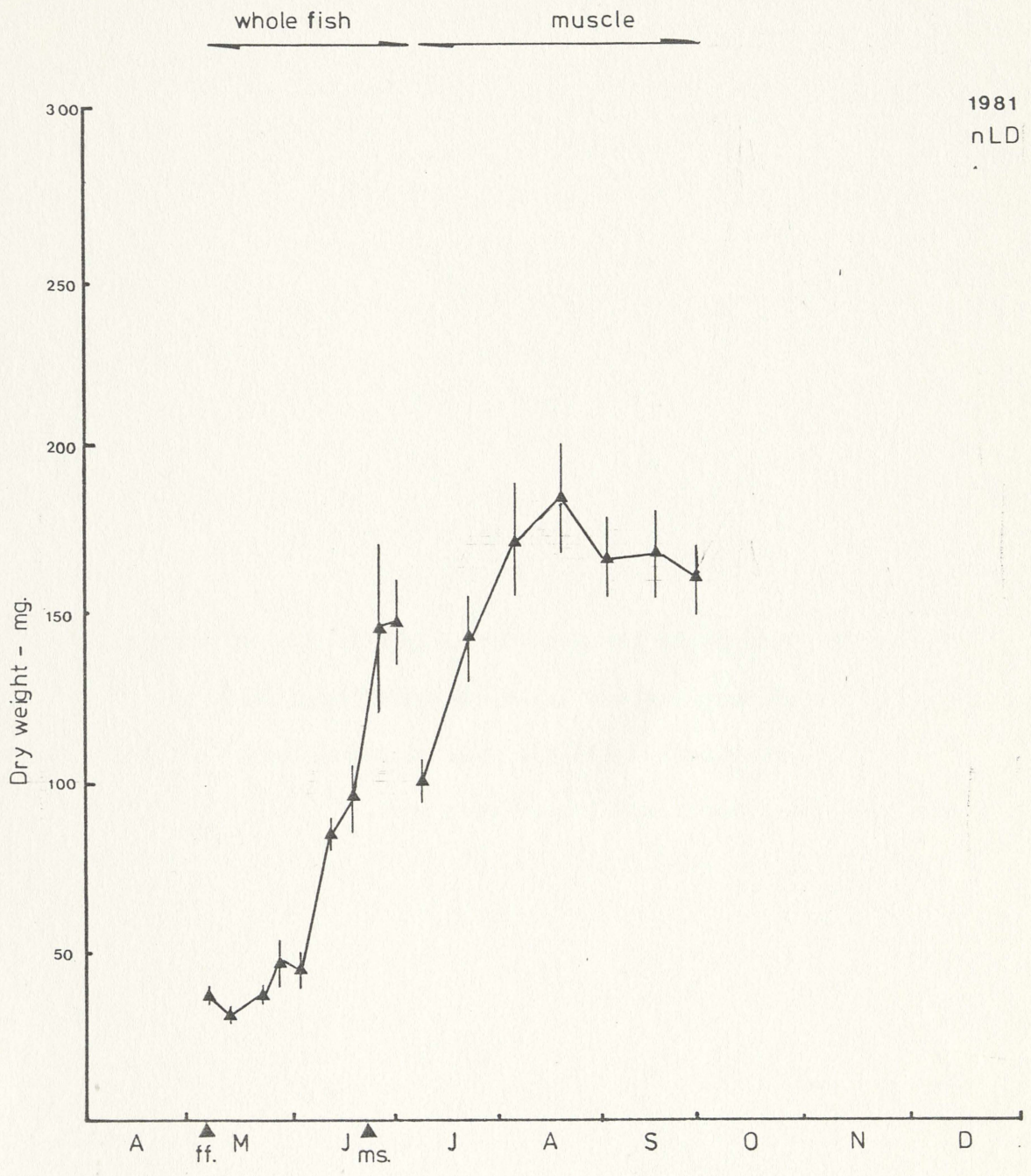

whole fish
muscle
1981
nLD
300
250
200
150
100
50
Dry weight - mg.
A
ff.
M
J
ms.
J
A
S
O
N
D

Figure 19 Changes in the mean dry weight (± 2SE) of muscle of young salmon under constant light (LL). Experiment I (1981). ms, midsummer day.

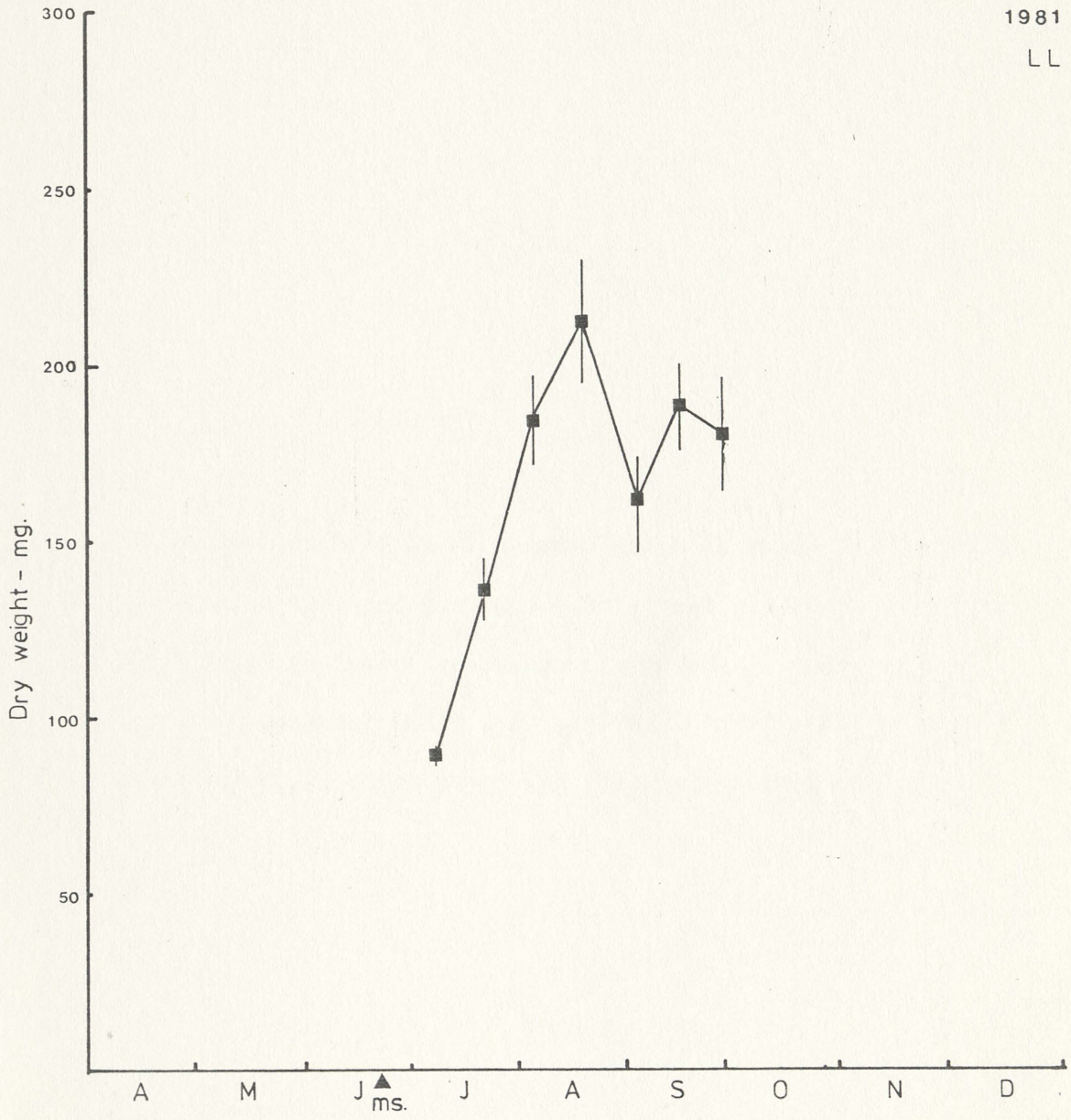
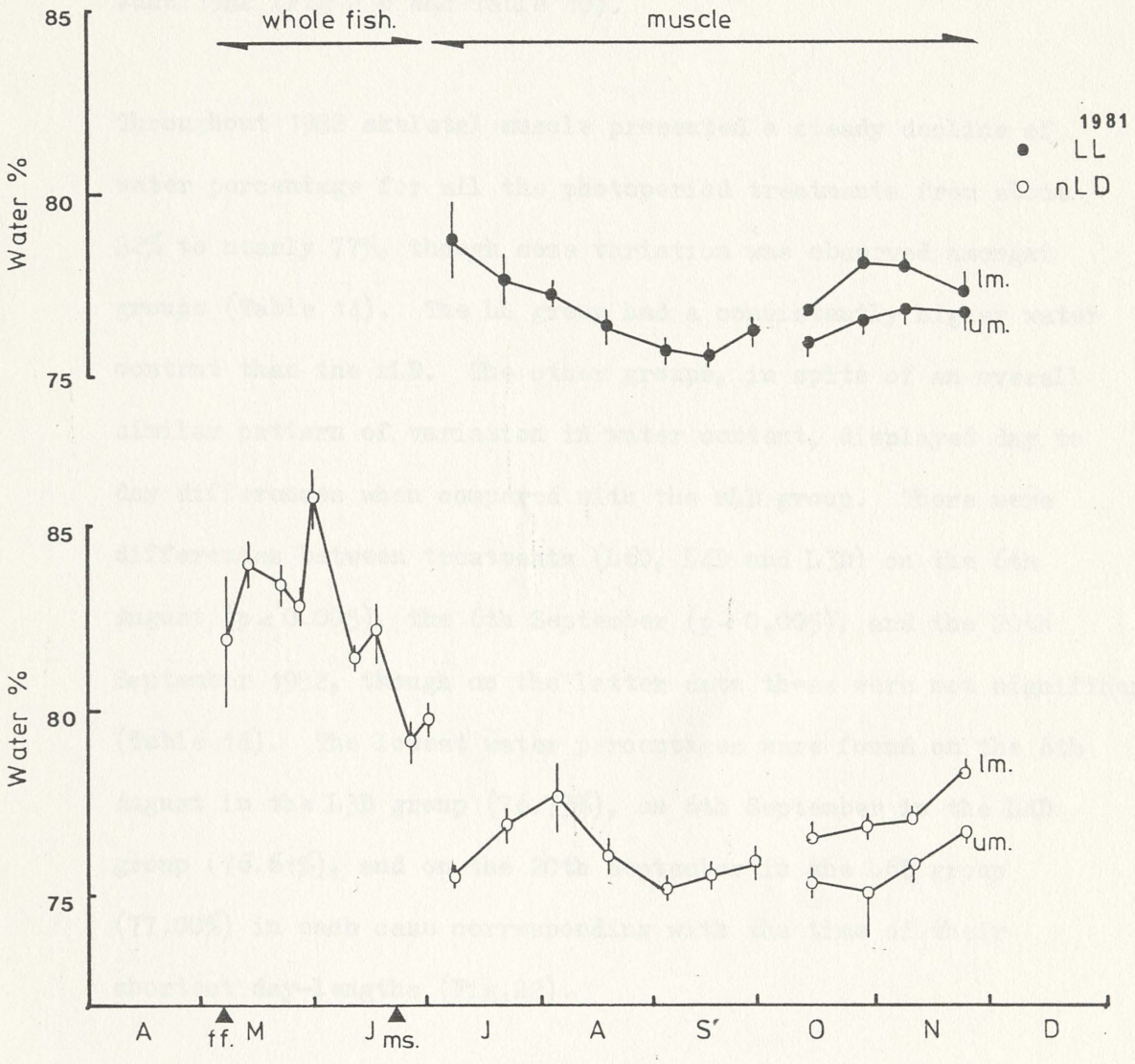

1981
L L
300
250
200
150
100
50
Dry weight - mg.
A
M
J
ms.
J
A
S
O
N
D

Figure 20 Changes in water content ($\pm$ 2SE) of the whole body and muscle of juvenile salmon subjected to natural photoperiod (nLD) and constant light (LL). Experiment I (1981). ff, first feeding; ms, midsummer day; um, upper mode; lm, lower mode.


whole fish.
muscle
1981
LL
nLD
Water %
85
80
75
lm.
um.
A
ff.
M
J
ms.
J
A
S
O
N
D

In 1982 whole fish under nLD showed a steady decline of water content from 83.83% at first feeding to 82.36% at the end of June 1982 (Fig 21c and Table 10).

Throughout 1982 skeletal muscle presented a steady decline of water percentage for all the photoperiod treatments from about 82% to nearly 77%, though some variation was observed amongst groups (Table 14). The LL group had a consistently higher water content than the nLD. The other groups, in spite of an overall similar pattern of variation in water content, displayed day to day differences when compared with the nLD group. There were differences between treatments (L6D, L4D and L3D) on the 6th August ($p < 0.005$), the 6th September ($p < 0.005$), and the 20th September 1982, though on the latter date these were not significant (Table 14). The lowest water percentages were found on the 6th August in the L3D group (76.73%), on 6th September in the L4D group (76.61%), and on the 20th September in the L6D group (77.00%) in each case corresponding with the time of their shortest day-lengths (Fig.22).

3.3.3 Condition factor

The condition factor (K) of fishes during Experiment I increased from a value of 0.95 to 1.14 over the period between first feeding (6th May) and 17th June, then fluctuating about 1.04 during the rest of the experiment under the two photoperiodic treatments (Tables 1 and 3). When fish were segregated by modal group, K values in the upper ones for both photoperiodic treatments were higher than in the lower modes (Table 8).

Figure 21 Changes in water content (± 2SE) of whole body and muscle of juvenile salmon subjected to A. constant light (LL); B. autumn photoperiod, (8LD); C. natural photoperiod (nLD). Experiment II (1982). ff, first feeding; ms, midsummer.

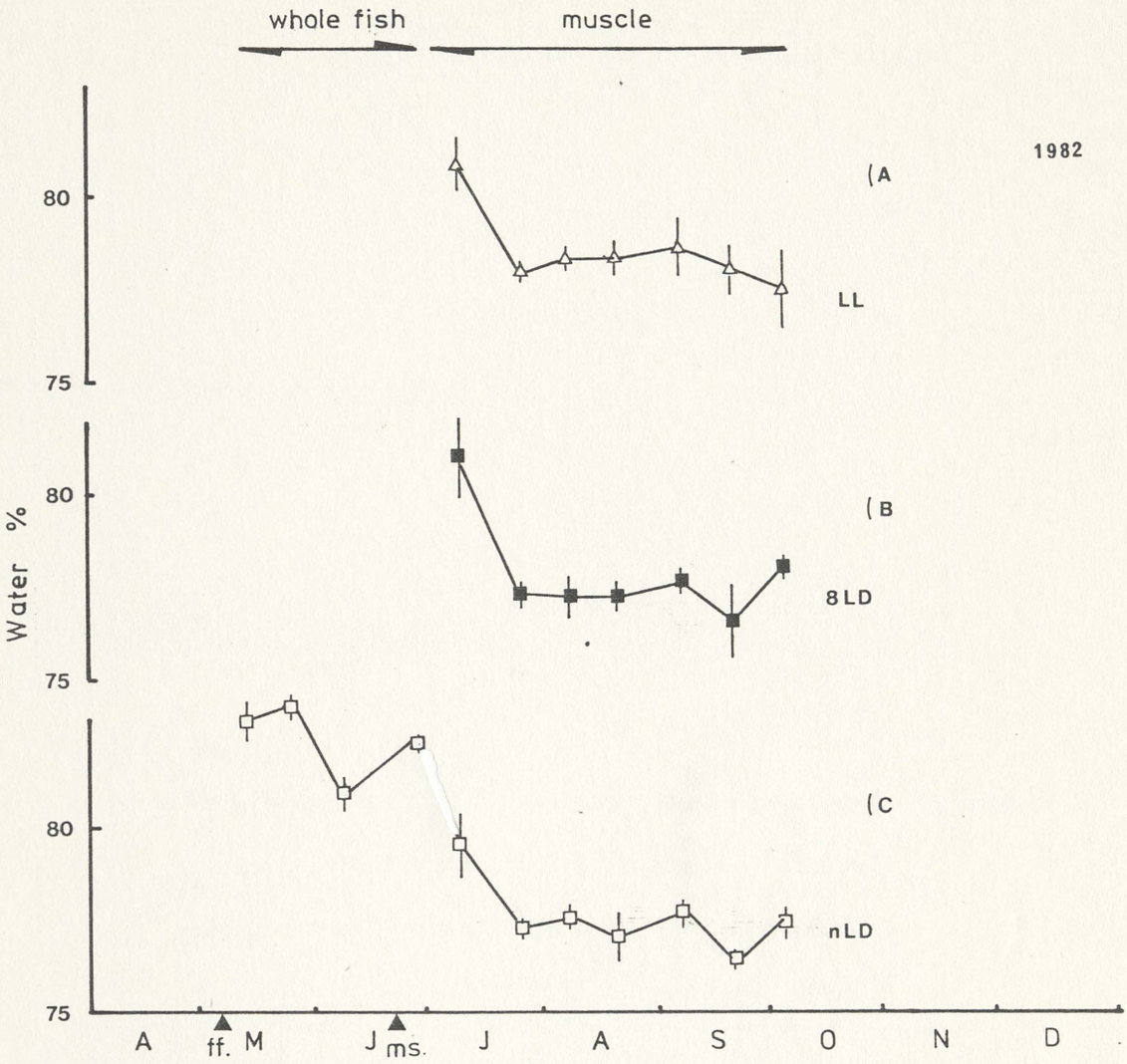
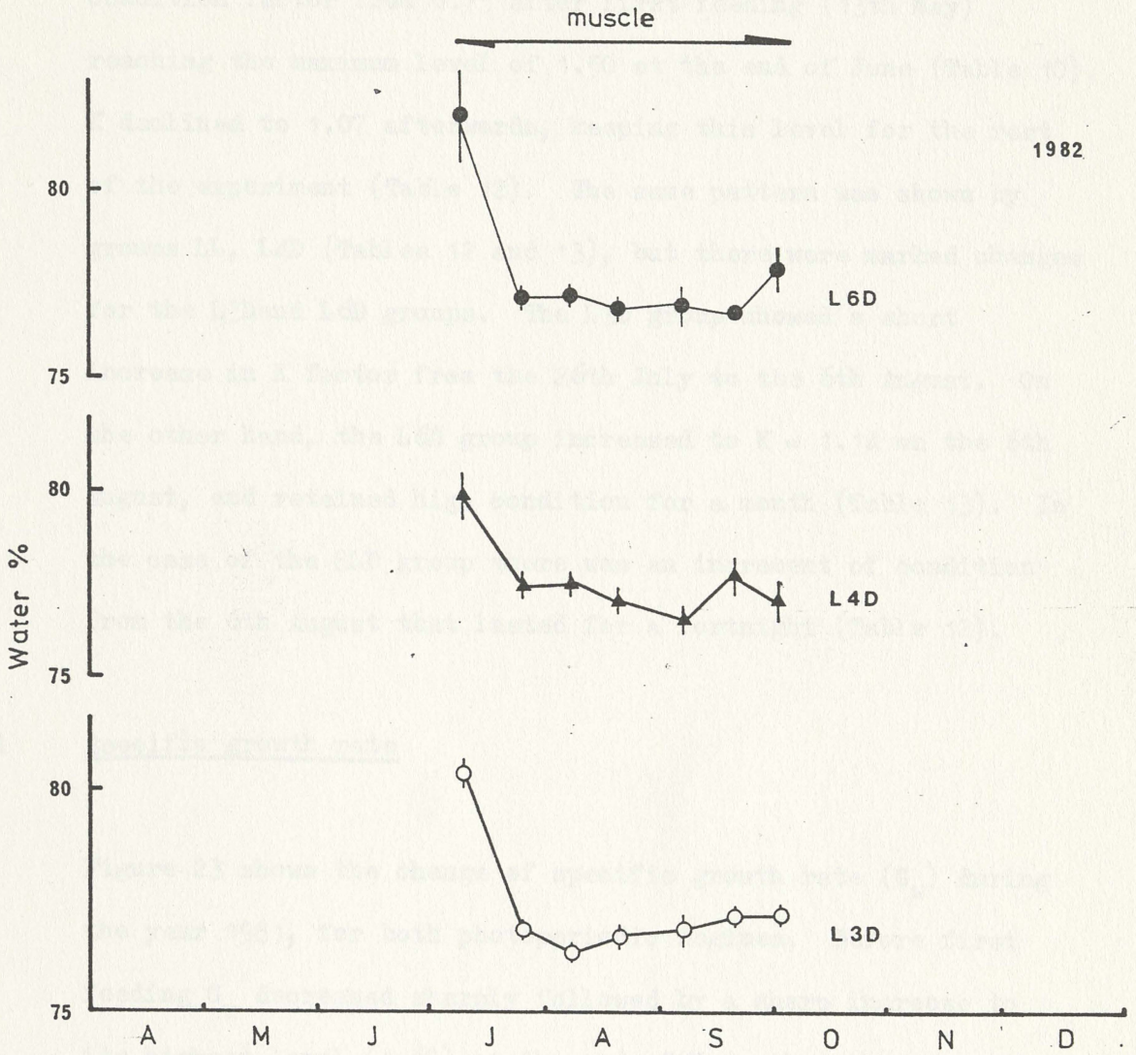

whole fish
muscle
1982
(A
LL
(B
8LD
(C
nLD
Water %
80
75
80
75
80
75
A
ff.
M
J
ms.
J
A
S
O
N
D

Figure 22 Changes in water content (± 2SE) of muscle of juvenile salmon subjected to; 6 month cycle (L6D), 4 month cycle (L4D), and 3 month cycle (L3D). Experiment II (1982).


muscle
1982
L 6D
L 4D
L 3D
Water %
80
75
80
75
80
75
A
M
J
J
A
S
O
N
D

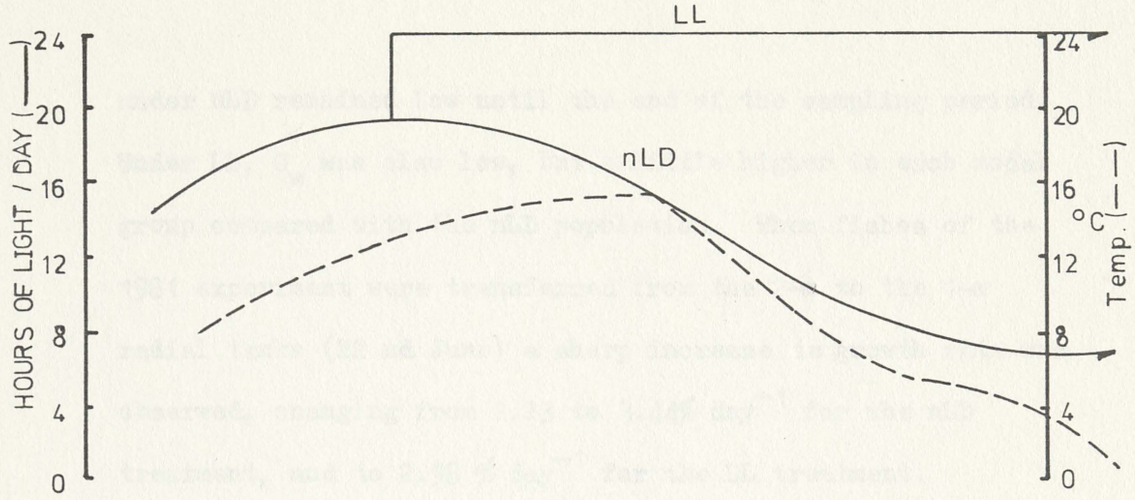
Throughout Experiment II, the nLD group showed an increase of condition factor from 0.75 after first feeding (13th May) reaching the maximum level of 1.50 at the end of June (Table 10). K declined to 1.07 afterwards, keeping this level for the rest of the experiment (Table 12). The same pattern was shown by groups LL, L4D (Tables 12 and 13), but there were marked changes for the L3Dand L6D groups. The L3D group showed a short increase in K factor from the 26th July to the 6th August. On the other hand, the L6D group increased to K = 1.14 on the 6th August, and retained high condition for a month (Table 13). In the case of the 8LD group there was an increment of condition from the 6th August that lasted for a fortnight (Table 12).

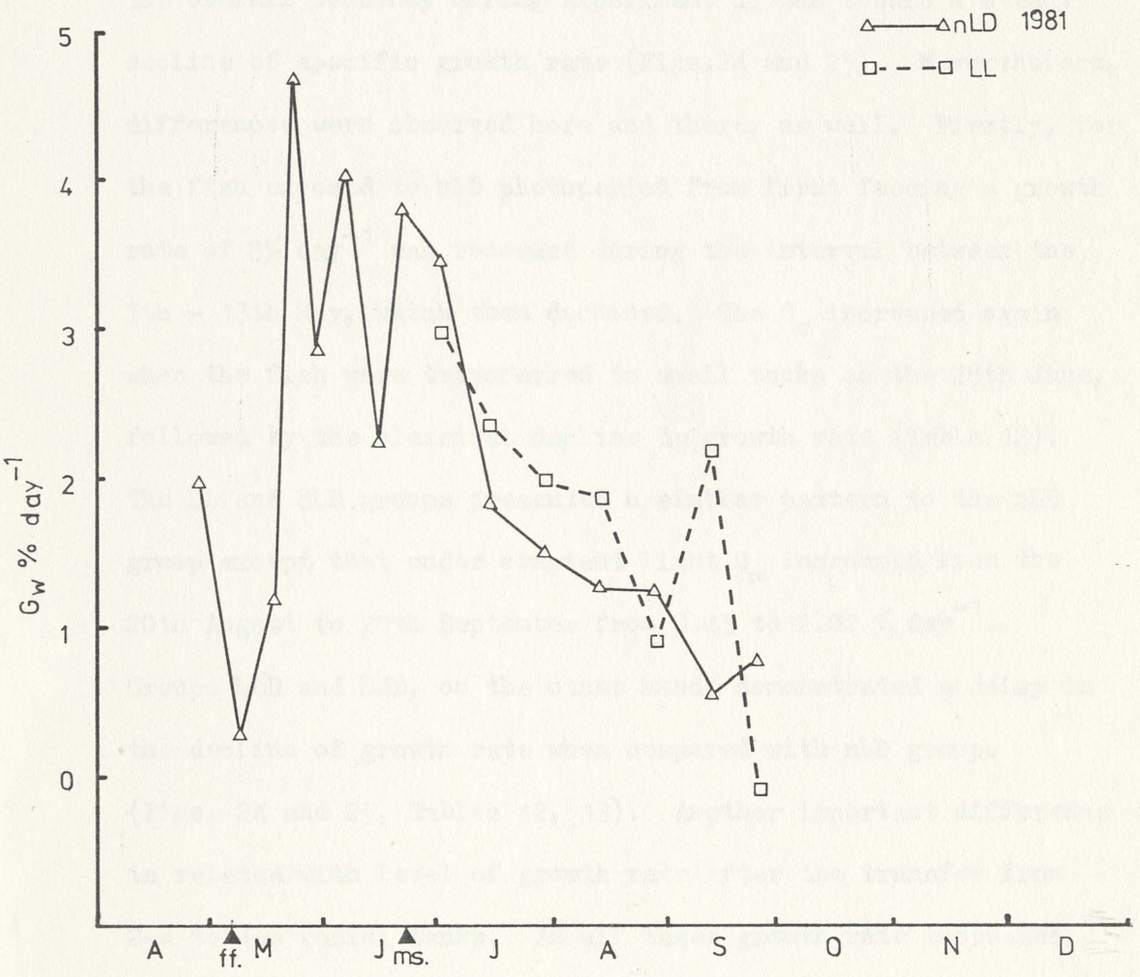
3.3.4 Specific growth rate

Figure 23 shows the change of specific growth rate (G_w) during the year 1981, for both photoperiodic regimes. Before first feeding G_w decreased sharply followed by a sharp increase to its highest level (4.68) at the end of May; then there was a sustained decline. The lowest level of G_w for nLD treatment was reached in the middle of September, and at the end of the same month for the LL treatment (Table 3). The latter, at the same time showed a lesser marked decline of specific growth rate when compared with the nLD treatment, with the obvious exception at the beginning of September when G_w for the LL group was lower than that for the nLD group. (Fig.23). Table 8 shows the growth behaviour of juvenile Atlantic salmon when segregated by modal groups. From the middle of October G_w for both modal groups

Figure 23 A. Experimental conditions: photoperiod (—); temperature (---).

B. Changes in specific growth rate (G_w) of two sibling populations of juvenile salmon subjected to natural photoperiod (nLD), and constant light (LL). Experiment I (1981). ff, first feeding; ms, midsummer day.


LL
nLD
HOURS OF LIGHT / DAY (——)
Temp. (— —)
°C
0
4
8
12
16
20
24


nLD 1981
LL
G_w % day^{-1}
0
1
2
3
4
5
A
ff.
M
J
ms.
J
A
S
O
N
D

under nLD remained low until the end of the sampling period. Under LL, G_w was also low, but a little higher in each modal group compared with the nLD population. When fishes of the 1981 experiment were transferred from the 2-m to the 1-m radial tanks (22 nd June) a sharp increase in growth rate was observed, changing from 2.23 to 3.44% day^{-1} for the nLD treatment, and to 2.98 % day^{-1} for the LL treatment.

The overall tendency during Experiment II was toward a steady decline of specific growth rate (Figs.24 and 25). Nevertheless, differences were observed here and there, as well. Firstly, for the fish exposed to nLD photoperiod from first feeding a growth rate of 8% day^{-1} was recorded during the interval between the 7th - 13th May, which then declined. The G_w increased again when the fish were transferred to small tanks on the 25th June, followed by the classical decline in growth rate (Table 12). The LL and 8LD groups presented a similar pattern to the nLD group except that under constant light G_w increased from the 20th August to 20th September from 0.43 to 2.02 % day^{-1}. Groups L6D and L4D, on the other hand, demonstrated a delay in the decline of growth rate when compared with nLD group. (Figs. 24 and 25, Tables 12, 13). Another important difference is related with level of growth rate after the transfer from 2-m to 1-m radial tanks. In all cases growth rate increased after the change, was highest for the nLD tank, and was about 5% day^{-1} for the rest excepting tank L4D where it was 3.89%.

Figure 24 Changes in specific growth rate (G_w) of three sibling populations of juvenile salmon reared under: natural photoperiod (nLD), constant light (LL) and autumn photoperiod (8LD). Experiment II (1982). ff, first feeding; ms, midsummer day.

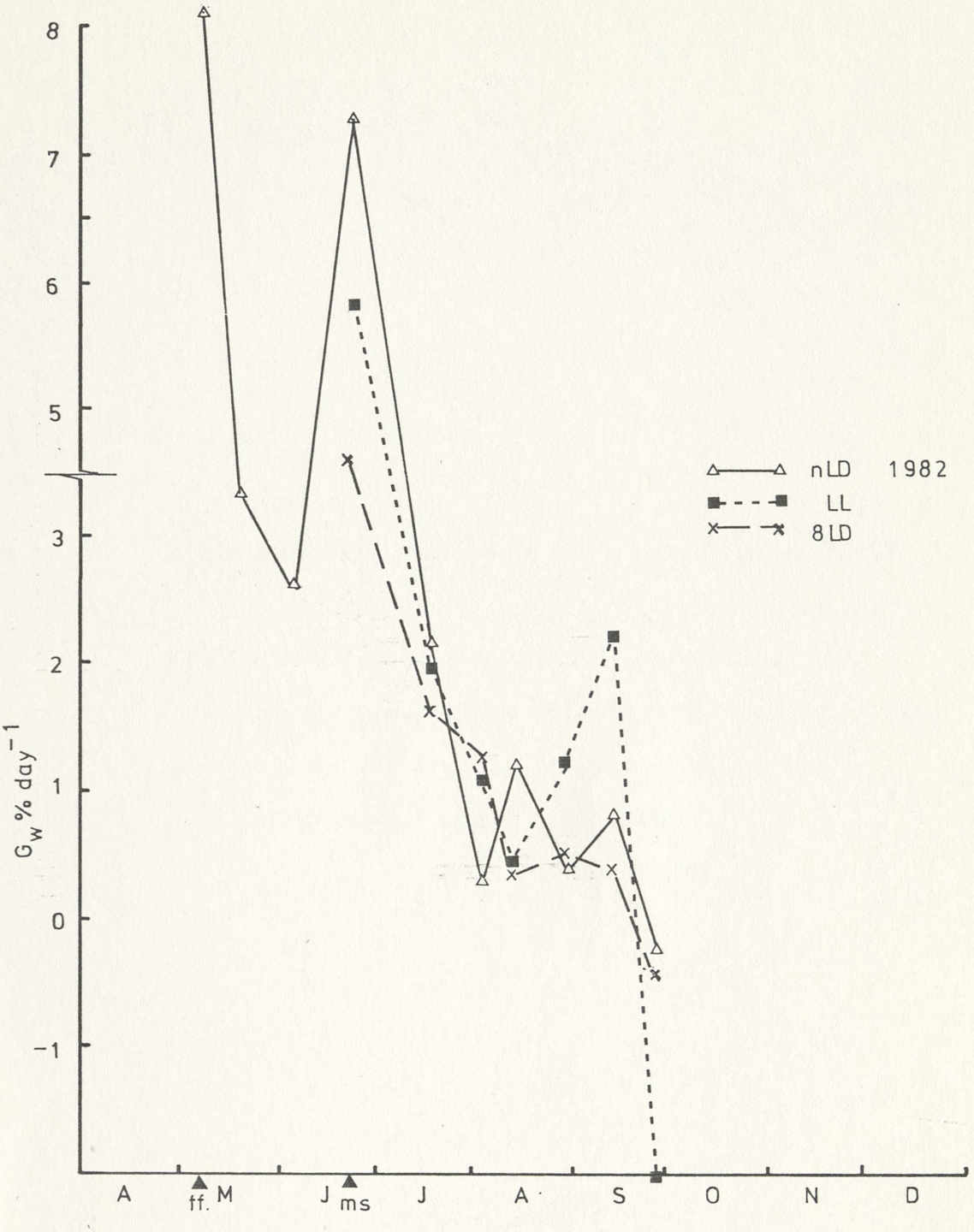
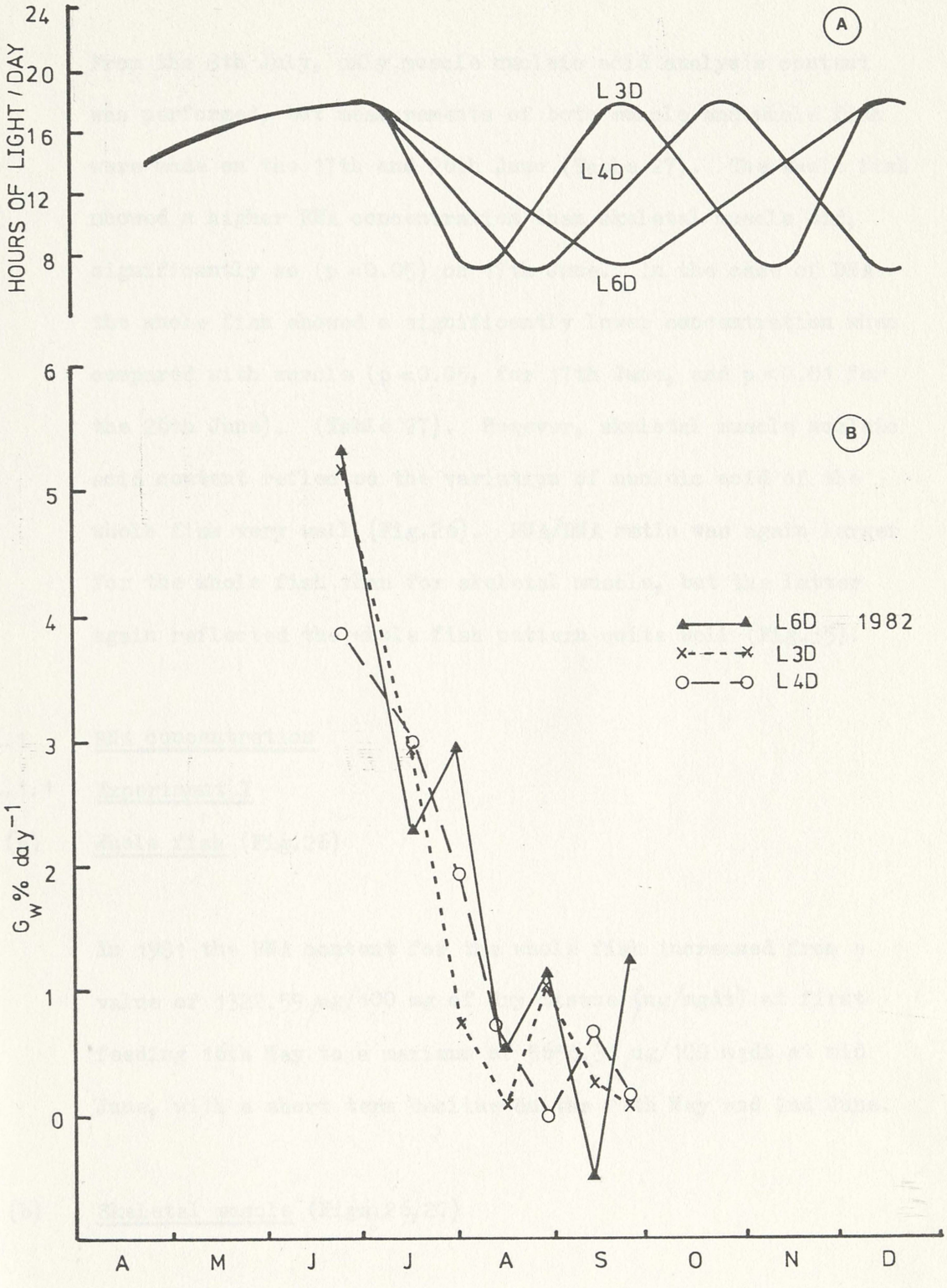

8
7
6
5
3
2
1
0
−1
G_w % day^{-1}
nLD 1982
LL
8LD
A
ff.
M
J
ms
J
A
S
O
N
D

Figure 25 A. Experimental conditions (photoperiod);

B. Changes in specific growth rate (G_w) of three sibling populations of juvenile salmon reared under: 6 month cycle (L6D); 3 month cycle (L3D), 4 month cycle (L4D). Experiment II (1982).


A
HOURS OF LIGHT / DAY
24
20
16
12
8
L 3D
L 4D
L 6D
B
G_w % day^{-1}
6
5
4
3
2
1
0
L6D 1982
L 3D
L 4D
A
M
J
J
A
S
O
N
D

3.4 Nucleic acid content

From the 8th July, only muscle nucleic acid analysis content was performed, but measurements of both muscle and whole fish were made on the 17th and 26th June (Table 27). The whole fish showed a higher RNA concentration than skeletal muscle did, significantly so ($p < 0.05$) on 17th June. In the case of DNA the whole fish showed a significantly lower concentration when compared with muscle ($p < 0.05$, for 17th June, and $p < 0.01$ for the 26th June). (Table 27). However, skeletal muscle nucleic acid content reflected the variation of nucleic acid of the whole fish very well (Fig.26). RNA/DNA ratio was again larger for the whole fish than for skeletal muscle, but the latter again reflected the whole fish pattern quite well (Fig.35).

3.4.1 RNA concentration

3.4.1.1 Experiment I

(a) Whole fish (Fig.26)

In 1981 the RNA content for the whole fish increased from a value of 1322.59 µg/100 mg of dry tissue (µg/mgdt) at first feeding 16th May to a maximum of 5656.31 µg/100 mgdt at mid June, with a short term decline on the 27th May and 2nd June.

(b) Skeletal muscle (Figs.26,27)

The muscular RNA content of the nLD group decreased steadily all through the summer growth season (Table 5)

Figure 26 Changes in the mean concentration ($\pm$ 2SE) of DNA and RNA of whole body and muscle of juvenile salmon reared under natural photoperiod (nLD). Experiment I (1981). ff, first feeding; ms, midsummer; um, upper mode; lm, lower mode.

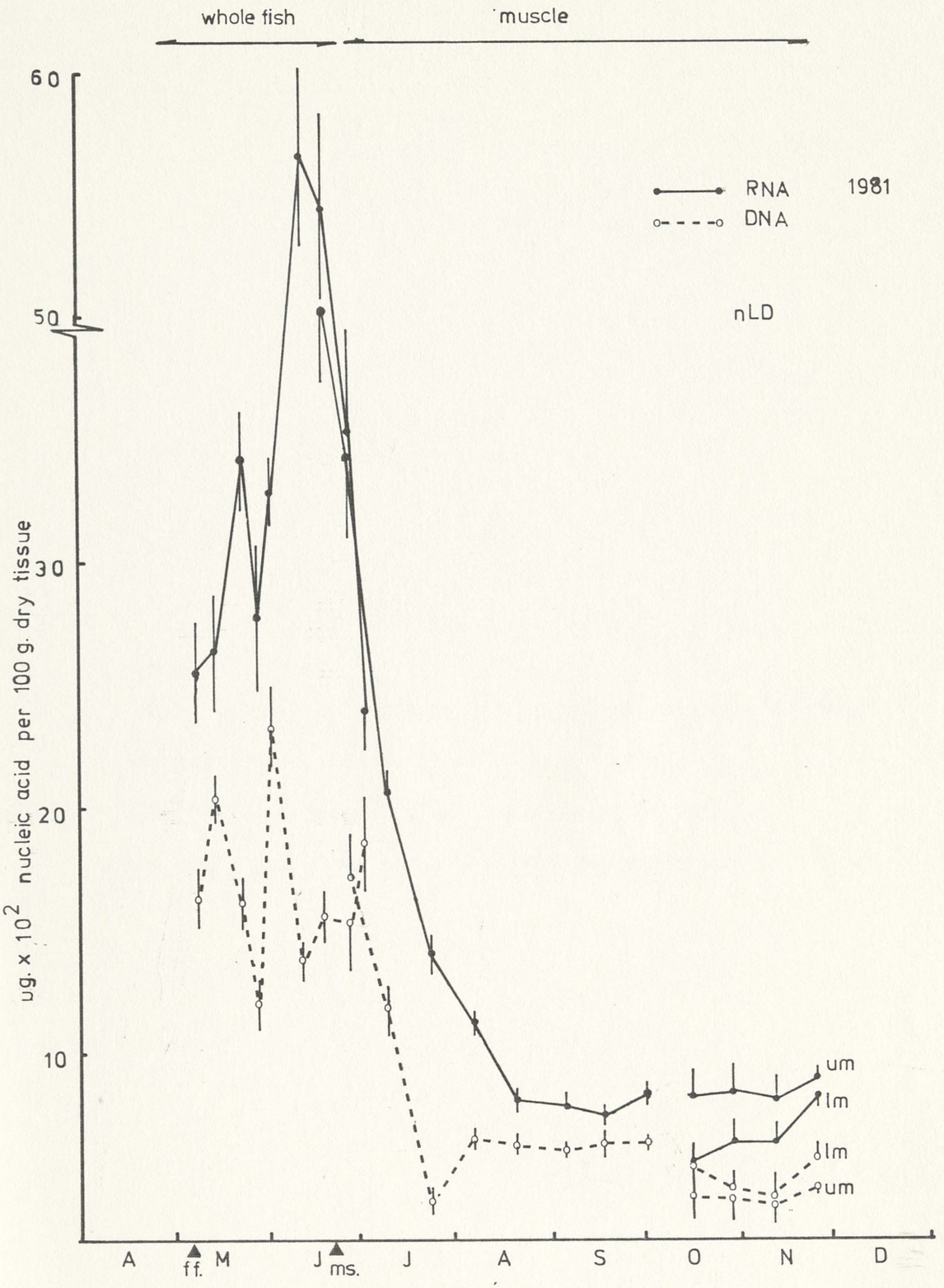
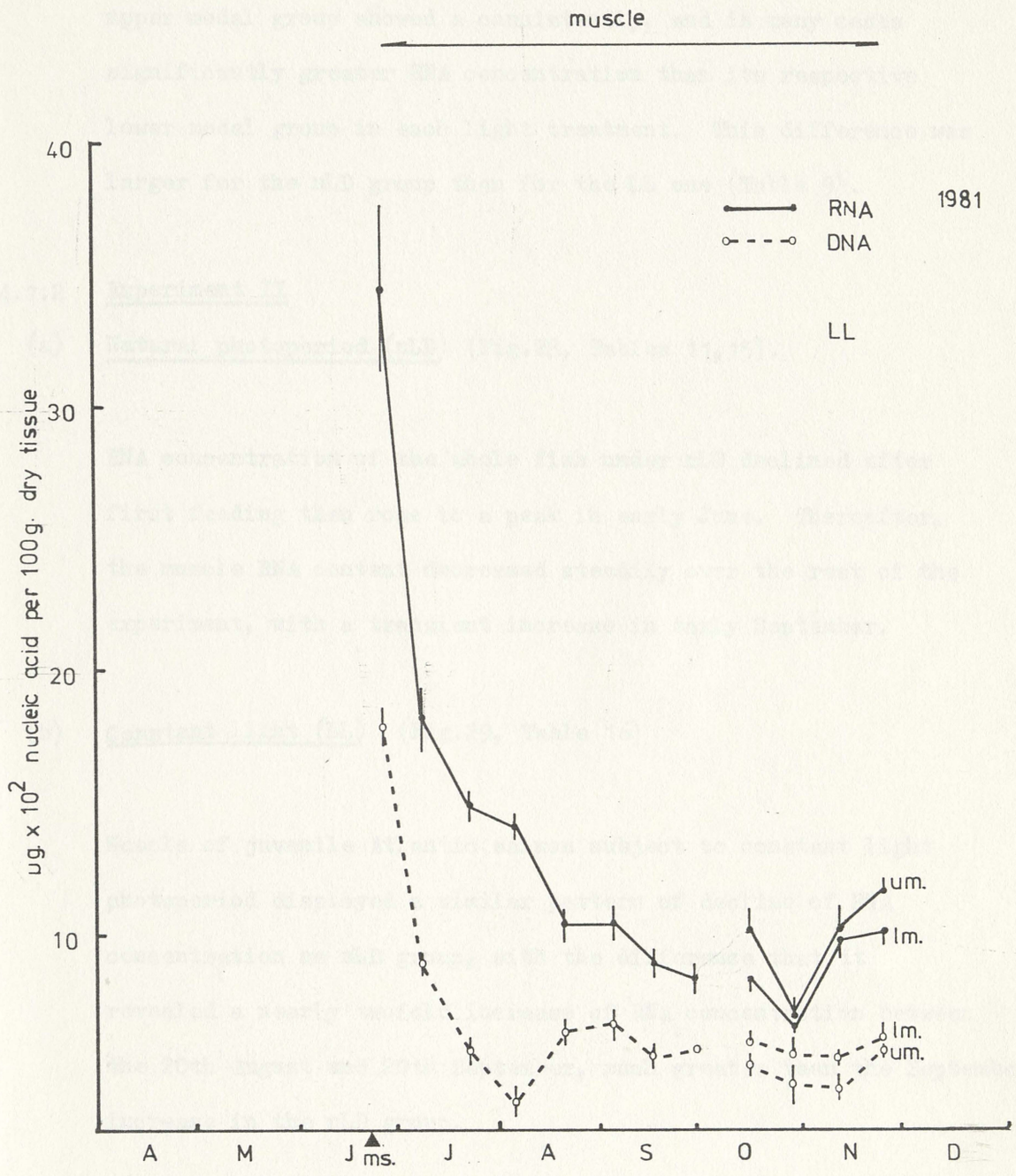

whole fish
muscle
60
50
30
20
10
RNA
DNA
1981
nLD
ug. x 10² nucleic acid per 100 g. dry tissue
um
lm
lm
um
A
ff.
M
J
ms.
J
A
S
O
N
D

Figure 27 Changes in the mean concentration (± 2SE) of DNA and RNA in the muscle of juvenile salmon reared under constant light (LL). Experiment I (1981). ms, midsummer day; um, upper mode; lm, lower mode.


muscle
40
30
20
10
RNA
DNA
1981
LL
um.
lm.
lm.
um.
A
M
J
ms.
J
A
S
O
N
D
µg. x 10² nucleic acid per 100g. dry tissue

The same is true for the LL group, though the decline was less sharp than for nLD, especially during the interval between the 5th August to 30th September (Table 6). After separation the upper modal group showed a consistently, and in many cases significantly greater RNA concentration than its respective lower modal group in each light treatment. This difference was larger for the nLD group than for the LL one (Table 9).

3.4.1.2 Experiment II

(a) Natural photoperiod (nLD) (Fig.28, Tables 11,15).

RNA concentration of the whole fish under nLD declined after first feeding then rose to a peak in early June. Thereafter, the muscle RNA content decreased steadily over the rest of the experiment, with a transient increase in early September.

(b) Constant light (LL) (Fig.29, Table 16)

Muscle of juvenile Atlantic salmon subject to constant light photoperiod displayed a similar pattern of decline of RNA concentration as nLD group, with the difference that it revealed a nearly twofold increase of RNA concentration between the 20th August and 20th September, much greater than the September increase in the nLD group.

(c) Autumn photoperiod (8LD) (Fig.30, Table 17)

The muscle RNA content of the 8LD fish group exhibited a sustained

Figure 28 Changes in the mean concentration ($\pm$ 2SE) of DNA and RNA of whole body and muscle of juvenile salmon reared under natural photoperiod (nLD). Experiment II (1982). ff, first feeding; ms, midsummer day.

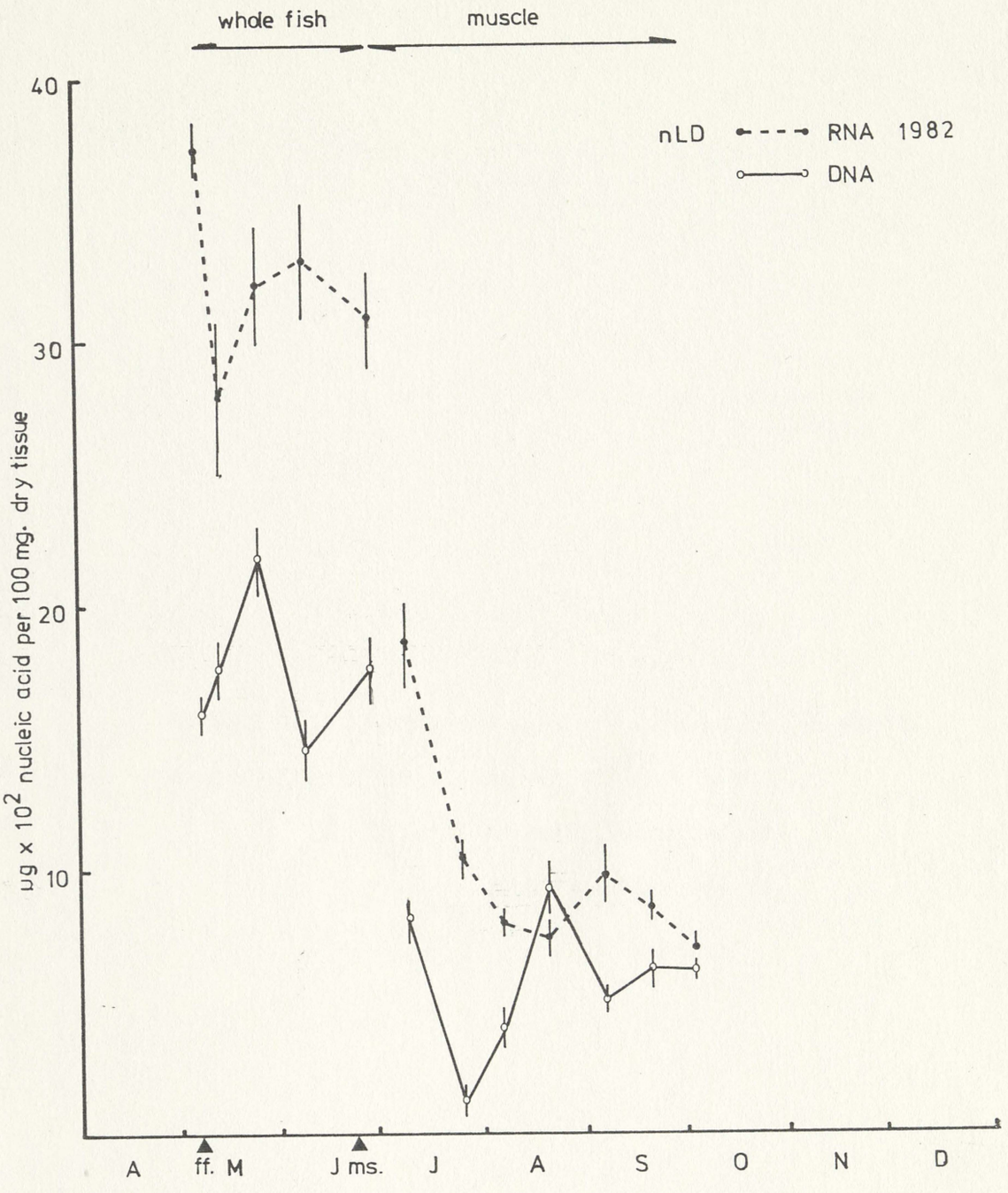

whole fish
muscle
nLD
RNA 1982
DNA
40
30
20
10
µg x 10² nucleic acid per 100 mg. dry tissue
A
ff. M
J ms.
J
A
S
O
N
D

Figure 29 Changes in the mean concentration (± 2SE) of DNA and RNA in the muscle of juvenile salmon reared under constant light (LL). Experiment II (1982).

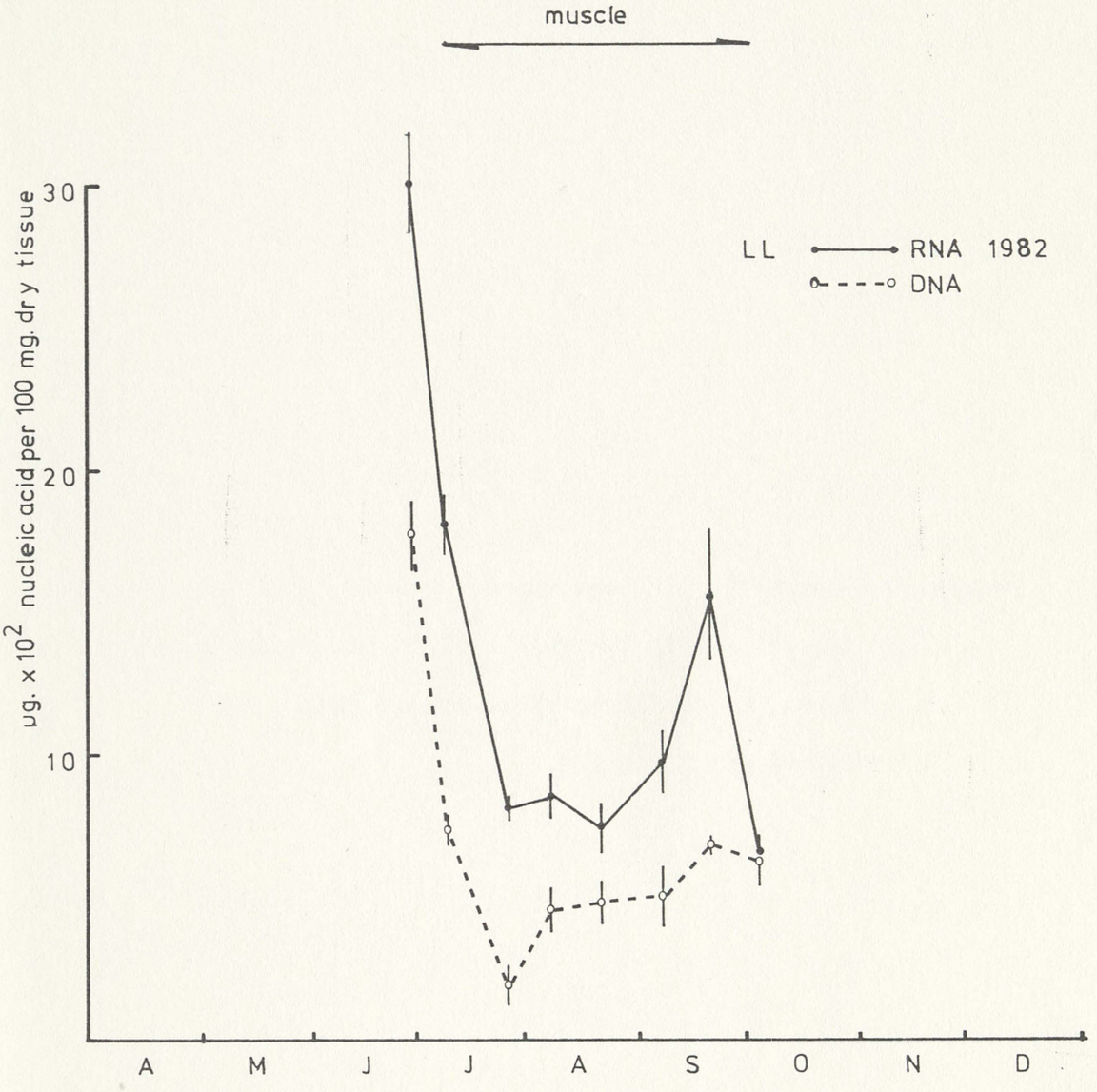
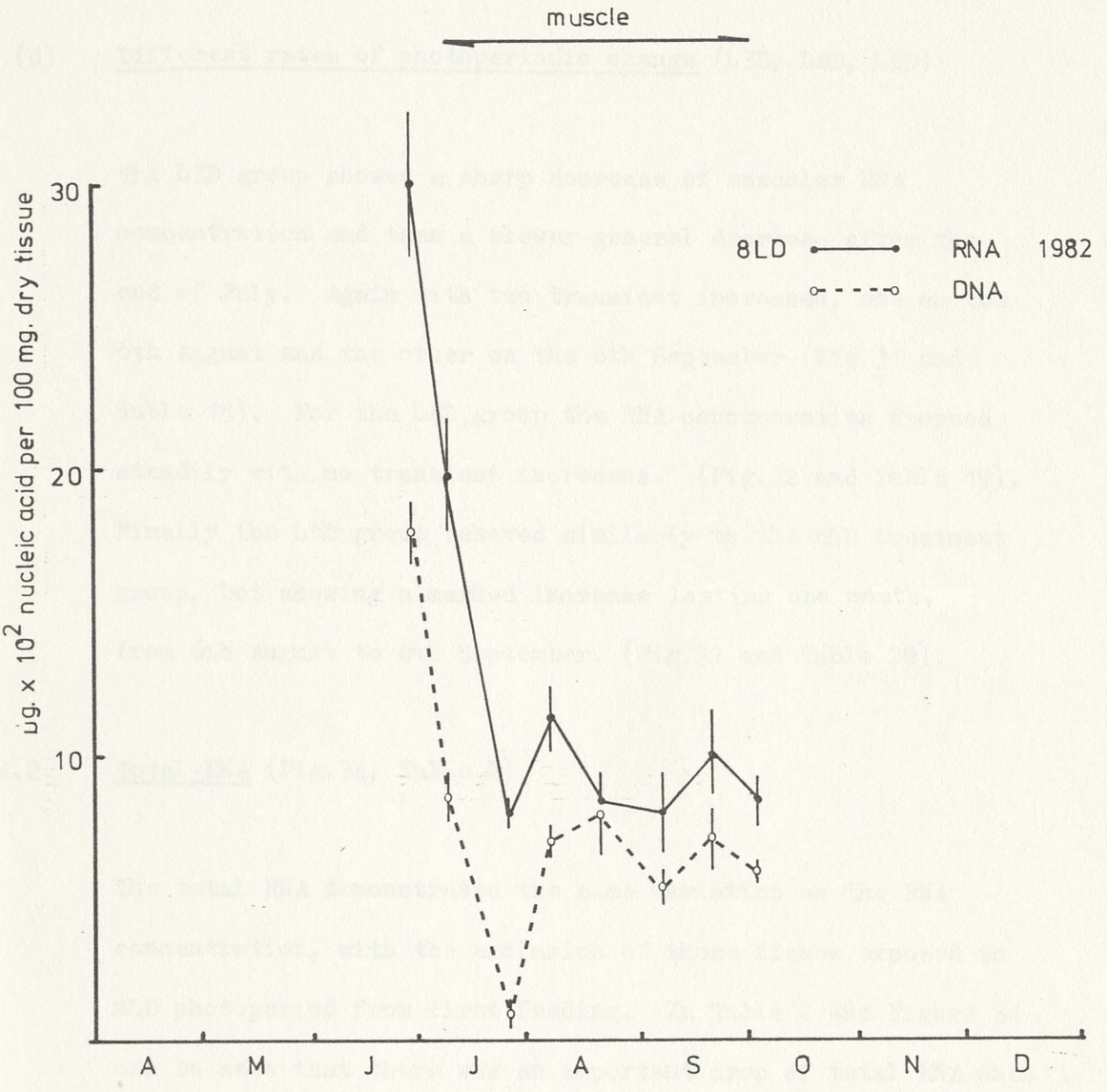

muscle
LL
RNA 1982
DNA
µg. x 10² nucleic acid per 100 mg. dry tissue
30
20
10
A
M
J
J
A
S
O
N
D

Figure 30 Changes in the mean concentration ($\pm$ 2SE) of DNA and RNA in the muscle of juvenile salmon reared under autumn photoperiod (8LD). Experiment II (1982).


muscle
8LD
RNA
DNA
1982
µg. x 10² nucleic acid per 100 mg. dry tissue
30
20
10
A
M
J
J
A
S
O
N
D

decay, similar to the nLD group, with two transient increases, one on the 6th August, and the other on the 20th September.

(d) Different rates of photoperiodic change (L3D, L4D, L6D)

The L3D group showed a sharp decrease of muscular RNA concentration and then a slower general decrease after the end of July. Again with two transient increases, one on the 6th August and the other on the 6th September (Fig 31 and Table 18). For the L4D group the RNA concentration dropped steadily with no transient increases. (Fig.32 and Table 19). Finally the L6D group behaved similarly to the nLD treatment group, but showing a marked increase lasting one month, from 6th August to 6th September. (Fig.32 and Table 20).

3.4.2 Total RNA (Fig.34, Table 2)

The total RNA demonstrated the same variation as the RNA concentration, with the exclusion of those fishes exposed to nLD photoperiod from first feeding. In Table 2 and Figure 34 can be seen that there was an important drop of total RNA when fish changed from yolk as a source of nutrients to exogenous food. From the 13th May the total RNA started to increase in the same fashion as RNA concentration. In all the other cases total RNA changed in a similar way to RNA concentration.

Figure 31 Changes in the mean concentration (± 2SE) of DNA and RNA in the muscle of juvenile salmon reared under 3 month cycle (L3D).
Experiment II(1982).

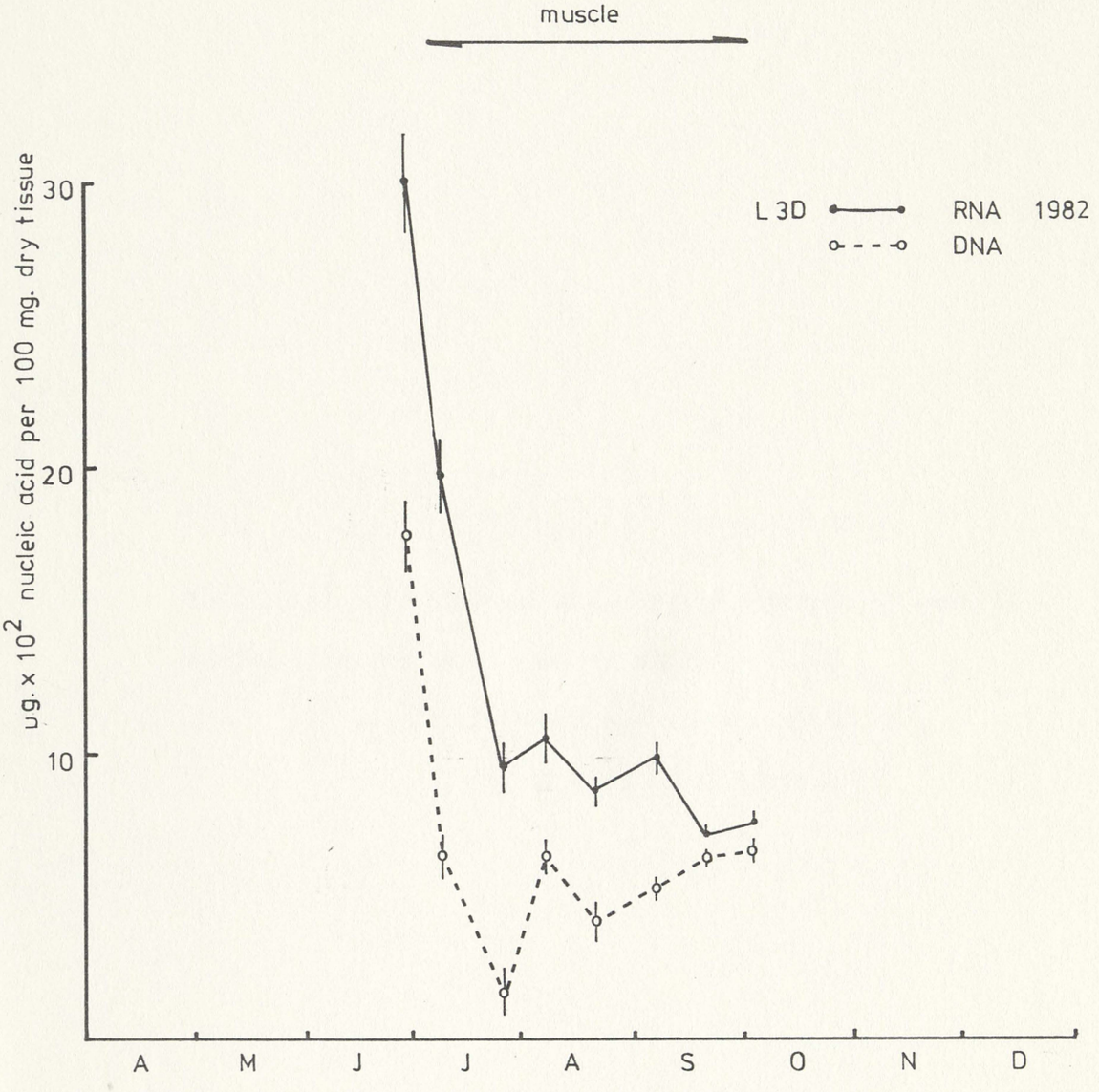

muscle
L 3D
RNA 1982
DNA
ug. x 10² nucleic acid per 100 mg. dry tissue
30
20
10
A
M
J
J
A
S
O
N
D

Figure 32 Changes in the mean concentration (± 2SE) of DNA and RNA in the muscle of juvenile salmon reared under 4 month cycle (L4D). Experiment II (1982).

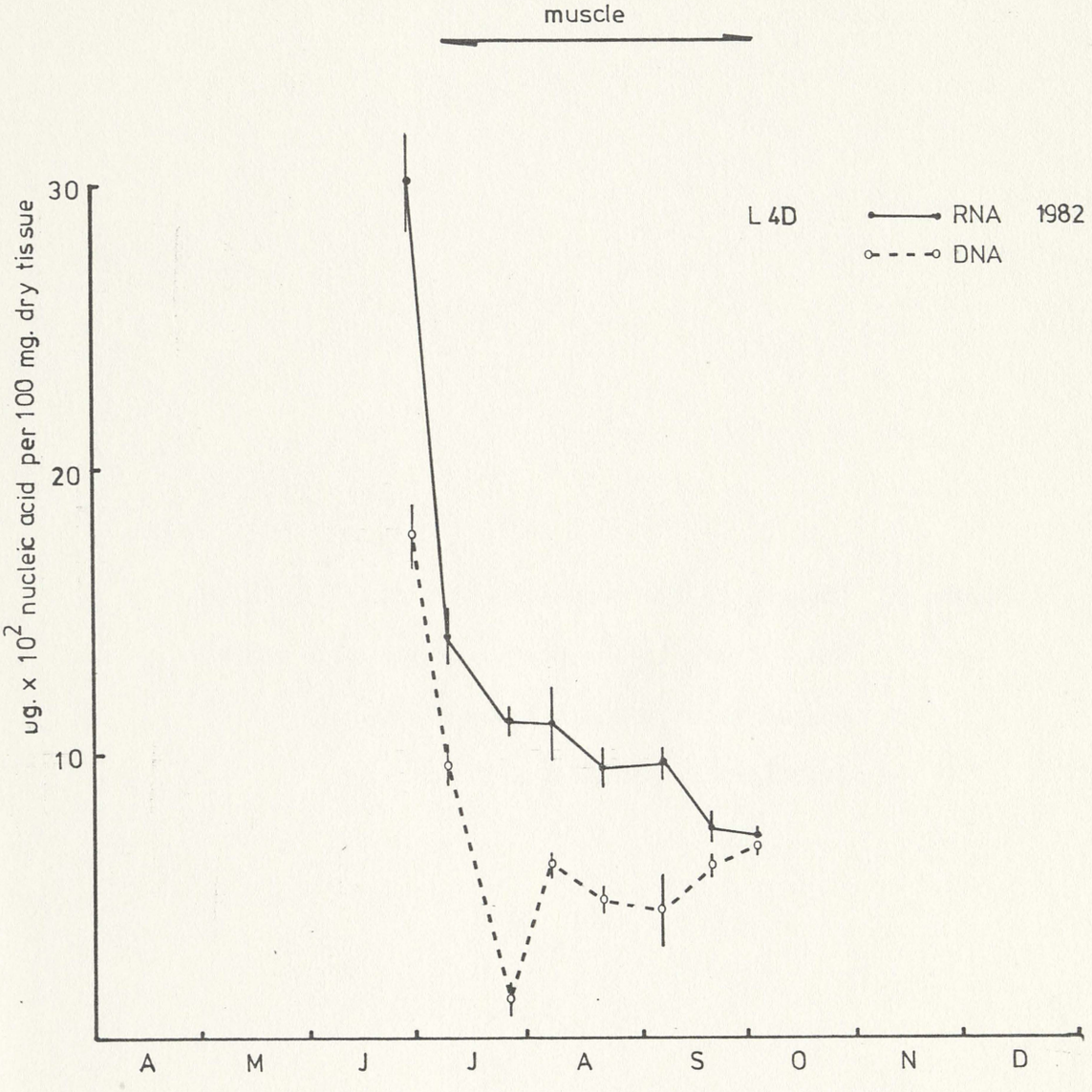

muscle
L 4D
RNA 1982
DNA
ug. x 10^2 nucleic acid per 100 mg. dry tissue
30
20
10
A
M
J
J
A
S
O
N
D

Figure 33 Changes in the mean concentration (± 2SE) of DNA and RNA in the muscle of juvenile salmon reared under 6 month cycle (L6D). Experiment II (1982).

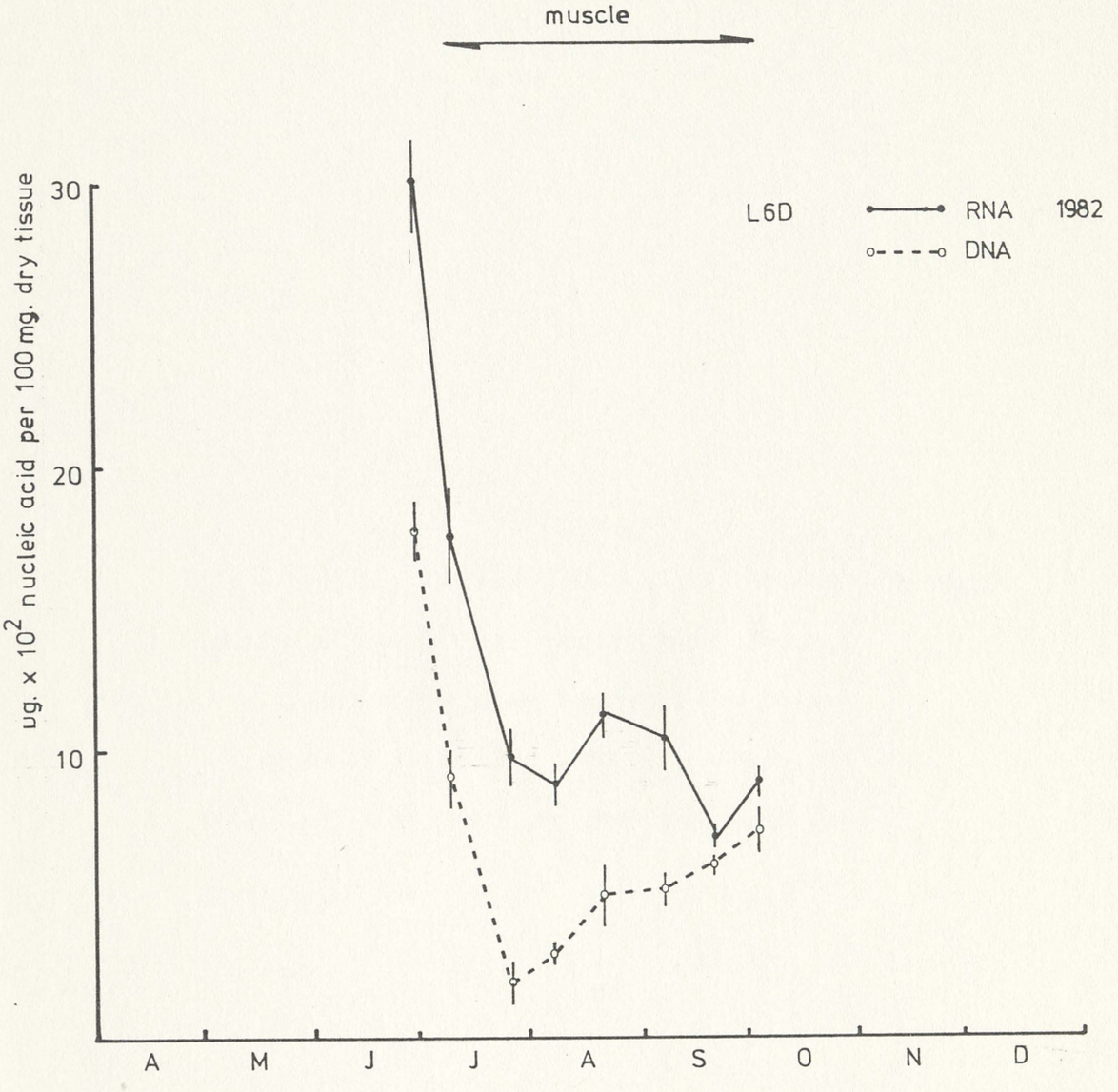
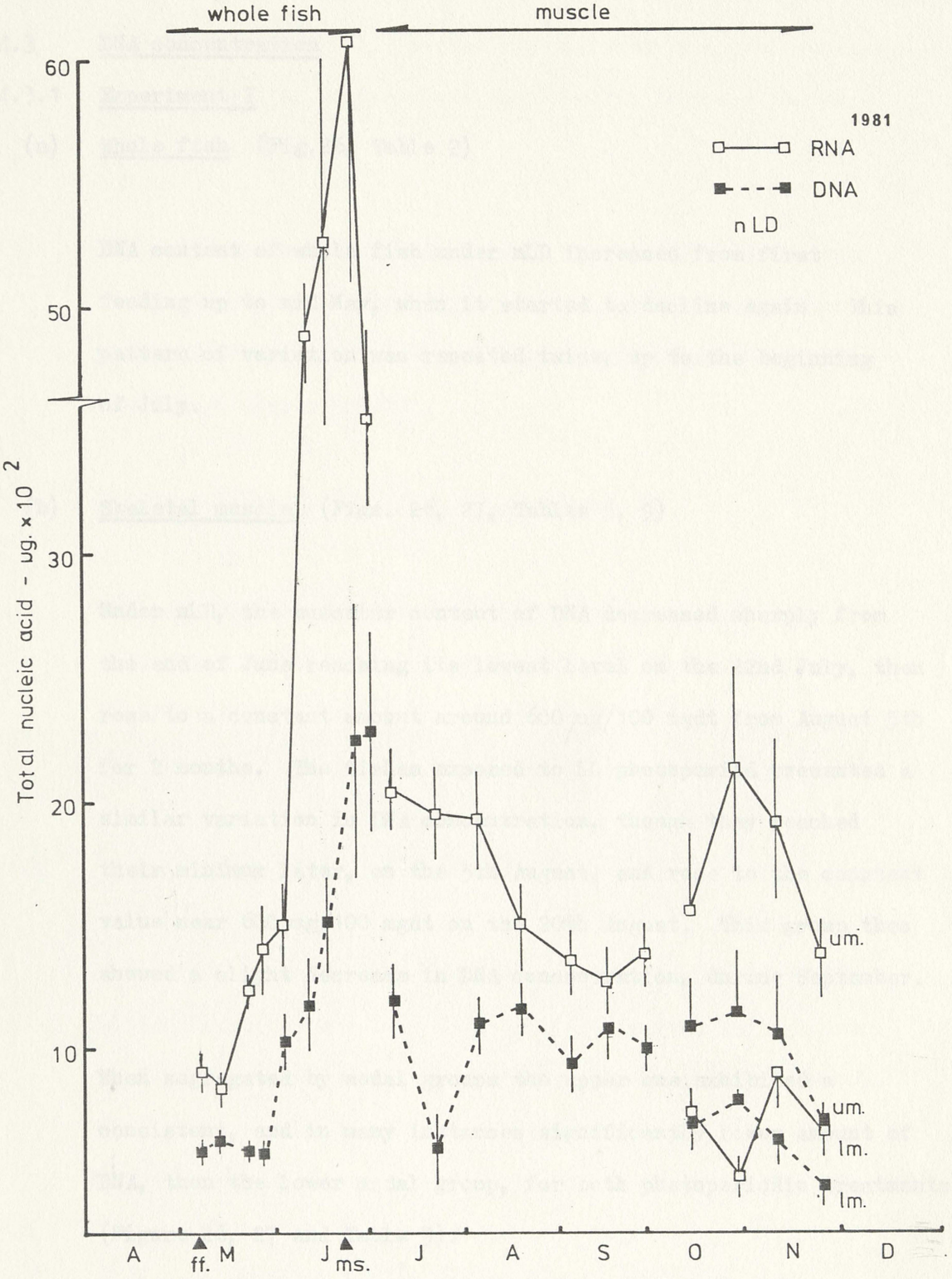

muscle
L6D
RNA
DNA
1982
ug. x 10^2 nucleic acid per 100 mg. dry tissue
30
20
10
A
M
J
J
A
S
O
N
D

Figure 34 Changes in the mean total DNA and RNA ($\pm$ 2SE) in whole body and muscle of juvenile salmon reared under natural photoperiod (nLD). Experiment I (1981). ff, first feeding; ms, midsummer day; um, upper mode; lm, lower mode.


whole fish
muscle
1981
RNA
DNA
n LD
60
50
30
20
10
Total nucleic acid - ug. x 10 2
um.
um.
lm.
lm.
A
ff.
M
J
ms.
J
A
S
O
N
D

3.4.3 DNA concentration

3.4.3.1 Experiment I

(a) Whole fish (Fig.26, Table 2)

DNA content of whole fish under nLD increased from first feeding up to mid May, when it started to decline again. This pattern of variation was repeated twice, up to the beginning of July.

(b) Skeletal muscle (Figs. 26, 27, Tables 5, 9)

Under nLD, the muscular content of DNA decreased sharply from the end of June reaching its lowest level on the 22nd July, then rose to a constant amount around 600 µg/100 mgdt from August 5th for 2 months. The fishes exposed to LL photoperiod presented a similar variation in DNA concentration, though they reached their minimum later, on the 5th August, and rose to the constant value near 600 µg/100 mgdt on the 20th August. This group then showed a slight decrease in DNA concentration, during September.

When segregated by modal groups the upper one exhibited a consistent, and in many instances significantly lower amount of DNA, then the lower modal group, for both photoperiodic treatments (Figure 26, 27 and Table 9).

3.4.3.2 Experiment II

(a) Natural photoperiod (nLD) (Fig.28, Table 15)

The whole fish presented a considerable increment in DNA

concentration after first feeding, followed by a pronounced decrease, rising again before the transfer from 2-m to 1-m radial tanks.

The skeletal muscle showed a steady decrease of DNA content to a minimum on the 26th July, peaking again in late August before reaching a constant level of about 620 µg/100 mgdt by the end of the experiment.

(b) Constant light (LL). (Fig.29, Table 16)

Skeletal muscle of fishes exposed to constant light displayed a decrease in DNA content, which attained its lowest level on the 26th July. From then on it increased very slowly, towards the constant level of the nLD group at the end of experiment.

(c) Autumn photoperiod (8LD) (Fig.30, Table 17)

Under 8LD, as under nLD, DNA concentration decreased to its minimum value on the 26th July, rising again in early August to fluctuate about a steady concentration near 600 µg/100 mgdt. This group showed the lowest recorded DNA level, at 97.69 µg/100 mgdt.

(d) Different rates of photoperiodic change (L3D, L4D, L6D).

Consistently, the musculature of the three fish groups subject to different rates of change, showed declines in DNA content to

minima on the 26th July (Figs.31, 32, 33). Then the L3D and L4D groups increased to a steady approximate concentration of 570 µg/100 mgdt (Table 18 and 19). The L6D group showed a steady rise from the minimum reaching 740 µg/100 mgdt at the end (Table 20).

3.4.4 Total DNA (Figs. 26, 34)

The muscular total DNA content of fishes under nLD photoperiod, followed the same pattern as DNA concentration, with the important exception that when fishes were separated in modal groups, the upper modal group showed the higher total amount of DNA.

Another different characteristic of the pattern of change in total DNA amount, is noticeable in the case of the whole fish, which kept a constant amount of it for almost a month when it started to increase, reaching its highest value at midsummer day.

In all the other treatment groups of the 1982 experiment the DNA totals behaved similarly to their respective DNA concentrations.

3.4.5 RNA-DNA ratios

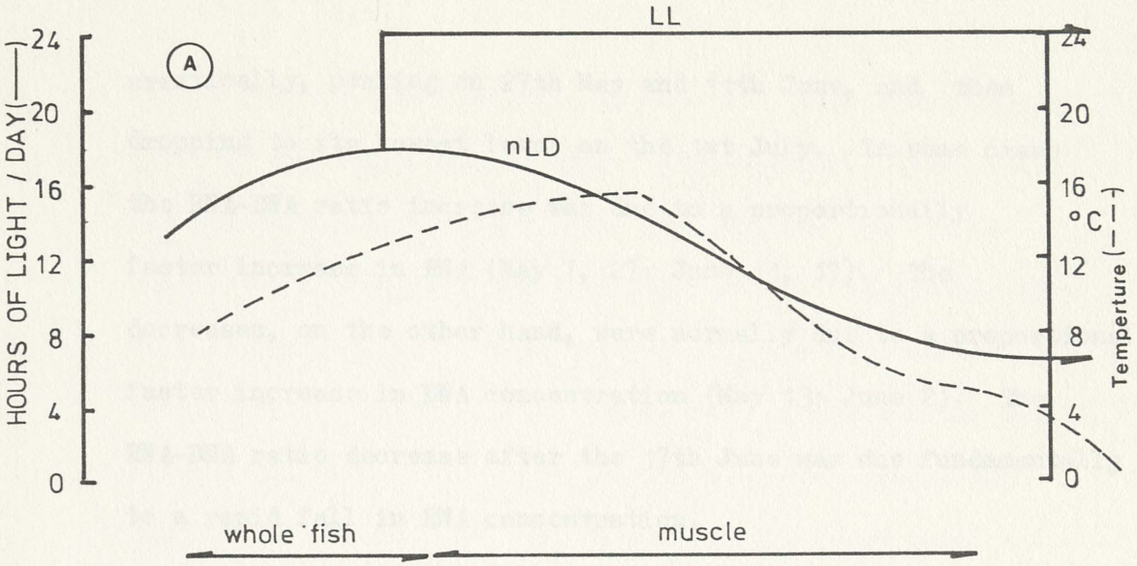
3.4.5.1 Experiment I

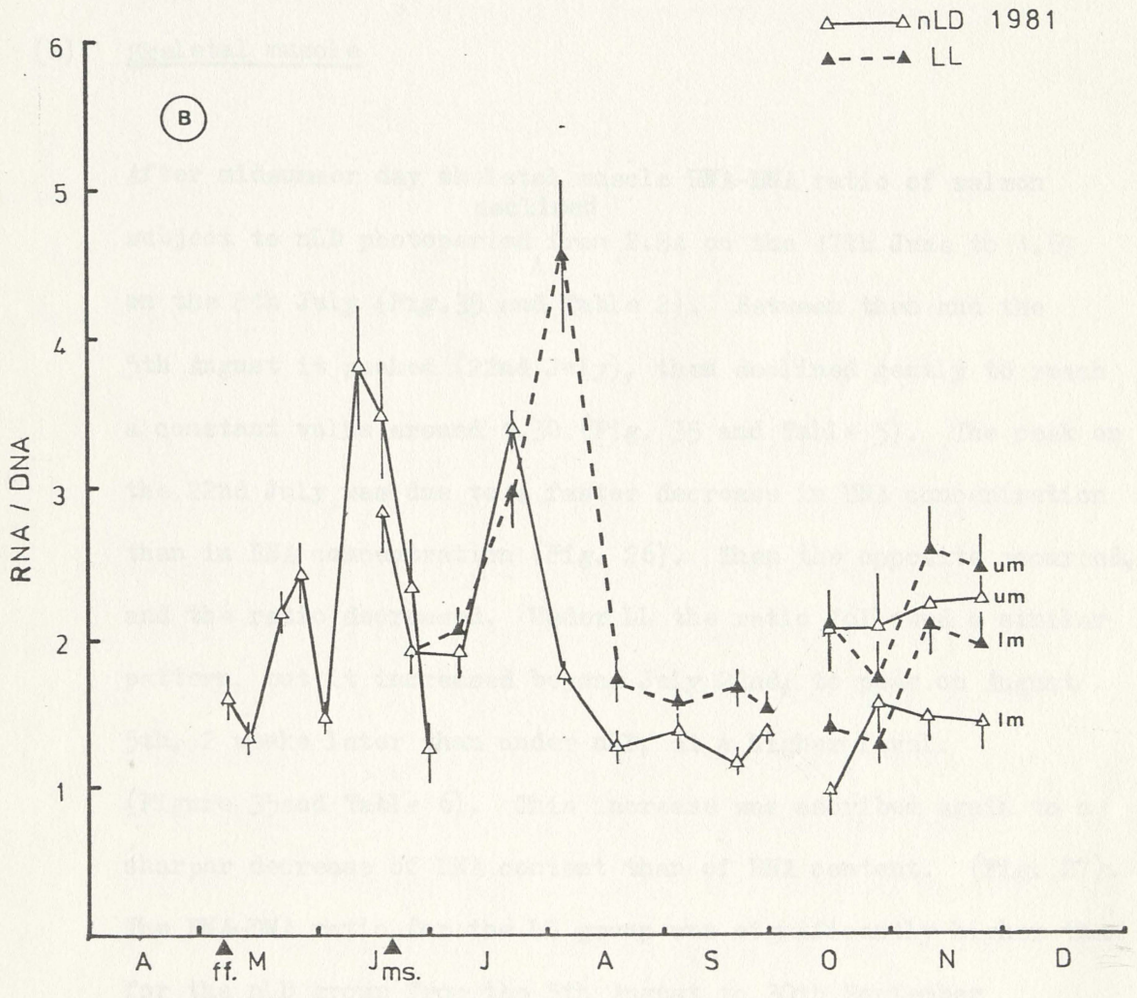
(a) Whole fish (Figs. 26, 35)

After first feeding the RNA-DNA ratio of nLD fish increased

Figure 35 A. Experimental conditions: photoperiod (—), temperature (---).

B. Changes in the mean RNA-DNA ratio ($\pm$ 2SE) in the whole body and muscle of juvenile salmon reared under natural photoperiod (nLD) and constant light (LL). Experiment I (1981). ff, first feeding; ms, midsummer day; um, upper mode; lm, lower mode.


A
LL
nLD
HOURS OF LIGHT / DAY(——)
24
20
16
12
8
4
0
°C
Temperture (— — —)
whole fish
muscle


nLD 1981
LL
B
RNA / DNA
6
5
4
3
2
1
um
um
lm
lm
A
M
J
J
A
S
O
N
D
ff.
ms.

erratically, peaking on 27th May and 11th June, and then dropping to its lowest level on the 1st July. In some cases the RNA-DNA ratio increase was due to a proportionally faster increase in RNA (May 7, 27; June 11, 17). The decreases, on the other hand, were normally due to a proportionally faster increase in DNA concentration (May 13; June 2). The RNA-DNA ratio decrease after the 17th June was due fundamentally to a rapid fall in RNA concentration.

(b) Skeletal muscle

After midsummer day skeletal muscle RNA-DNA ratio of salmon subject to nLD photoperiod declined from 2.84 on the 17th June to 1.69 on the 8th July (Fig.35 and Table 2). Between then and the 5th August it peaked (22nd July), then declined gently to reach a constant value around 1.30 (Fig. 35 and Table 5). The peak on the 22nd July was due to a faster decrease in DNA concentration than in RNA concentration (Fig. 26). Then the opposite occurred, and the ratio decreased. Under LL the ratio followed a similar pattern, but it increased beyond July 22nd, to peak on August 5th, 2 weeks later than under nLD, at a higher level. (Figure 35and Table 6). This increase was ascribed again to a sharper decrease of DNA content than of RNA content. (Fig. 27). The RNA-DNA ratio for the LL group was significantly higher than for the nLD group from the 5th August to 30th September (Tables 5, 6). On the 22nd July the RNA-DNA ratio of nLD group was significantly higher ($p<0.05$) than the LL one. The significantly greater RNA-DNA ratio values for the upper modal

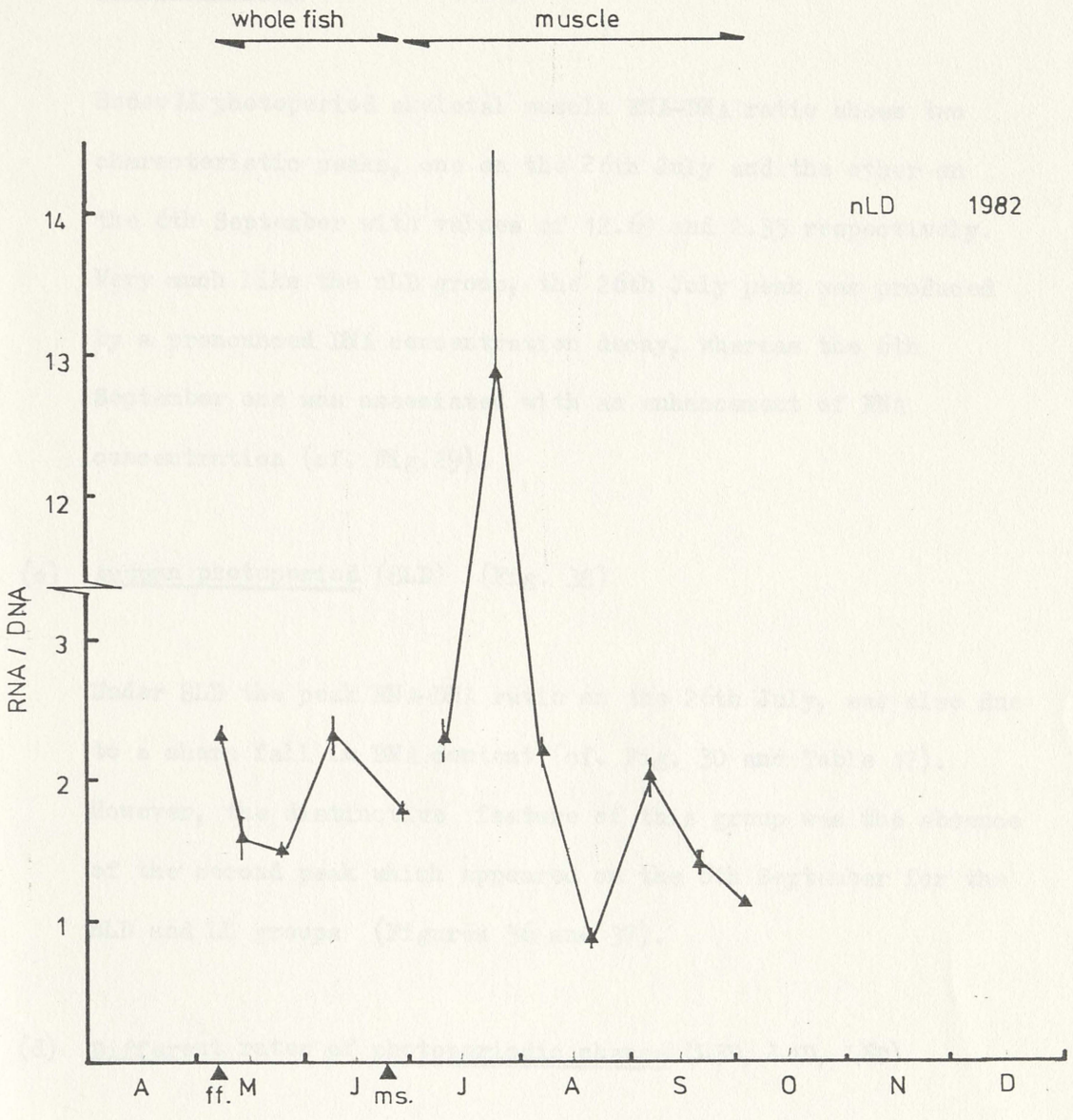
groups for both photoperiodic treatments, is also noteworthy (Fig. 35 and Table 9). On almost all cases the higher ratio was due to a significantly lower DNA content, but with a contribution also from a higher RNA content. Nevertheless it must be stressed that there were also differences due to treatment: for example, nLD treated fish showed a wider gap between the mean ratio values of the two modal groups when contrasted with LL fish, and in general the lower modal group of LL fish had a higher ratio than lower modal group nLD fish (Fig. 35).

3.4.5.2 Experiment II

(a) Natural photoperiod (nLD) (Fig.36)

The RNA-DNA ratio for whole fish fell initially, then oscillated about a value of about 1.8. As in 1981 the ratio changes are affected more by changes of RNA than of DNA (Table 11). On the contrary RNA-DNA ratio decreases are related to increments of DNA content. As in 1981, midsummer day was followed by an increase in the ratio for muscle by the 26th July, to a value almost four fold higher than the equivalent for 1981 (cf. Figure 35). The ratio then declined rapidly to a minimum by 20th August. Another transient, but less pronounced increment of ratio appeared on the 6th September, ending with a value near unity at the end of the experiment. The huge RNA-DNA ratio of 26th July was caused by a proportionally faster decrease in DNA concentration in comparison to RNA concentration. (Figure 28).

Figure 36 Changes in the mean RNA-DNA ratio in the whole body and muscle of juvenile salmon reared under natural photoperiod (nLD). Experiment II (1982). ff, first feeding; ms, midsummer day.


whole fish
muscle
nLD 1982
RNA / DNA
14
13
12
3
2
1
A
ff.
M
J
ms.
J
A
S
O
N
D

(b) Constant light (LL) (Fig.37)

Under LL photoperiod skeletal muscle RNA-DNA ratio shows two characteristic peaks, one on the 26th July and the other on the 6th September with values of 12.69 and 2.35 respectively. Very much like the nLD group, the 26th July peak was produced by a pronounced DNA concentration decay, whereas the 6th September one was associated with an enhancement of RNA concentration (cf. Fig.29).

(c) Autumn photoperiod (8LD) (Fig. 38)

Under 8LD the peak RNA-DNA ratio on the 26th July, was also due to a sharp fall in DNA content (cf. Fig. 30 and Table 17). However, the distinctive feature of this group was the absence of the second peak which appeared on the 6th September for the nLD and LL groups (Figures 36 and 37).

(d) Different rates of photoperiodic change (L3D, L4D, L6D)

Similarities as well as disparities were found in the RNA-DNA ratio variation of these three groups. Firstly, all of them peaked on the 26th July (Figs. 39, 40, 41) and secondly the cause of the enlargement was a sharp DNA content decay (Figs. 31 - 33). This peak was highest in the L4D group and lowest in the L3D group (Tables 18 - 20). The conspicuous differences were in the second peak: it was absent in L6D, early (August 20th) in L3D, and higher than in any other treatment in L4D.

Figure 37 Changes in the mean RNA-DNA ratio ($\pm$ 2SE) in muscle of juvenile salmon reared under constant light (LL). Experiment II (1982).

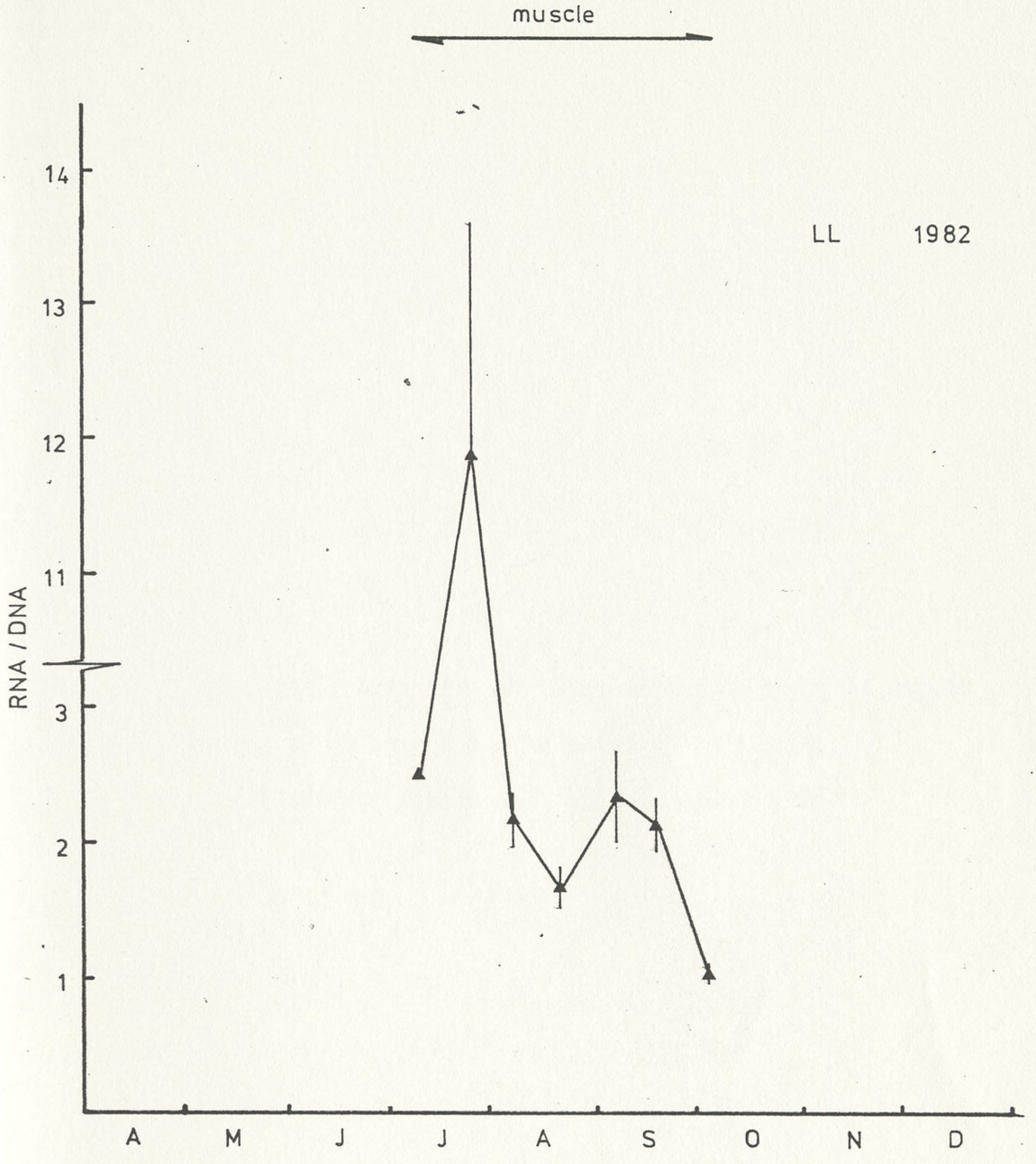

muscle
LL 1982
RNA / DNA
14
13
12
11
3
2
1
A
M
J
J
A
S
O
N
D

Figure 38 Changes in the mean RNA-DNA ratio (± 2SE) in muscle of juvenile salmon reared under autumn photoperiod (8LD). Experiment II (1982).

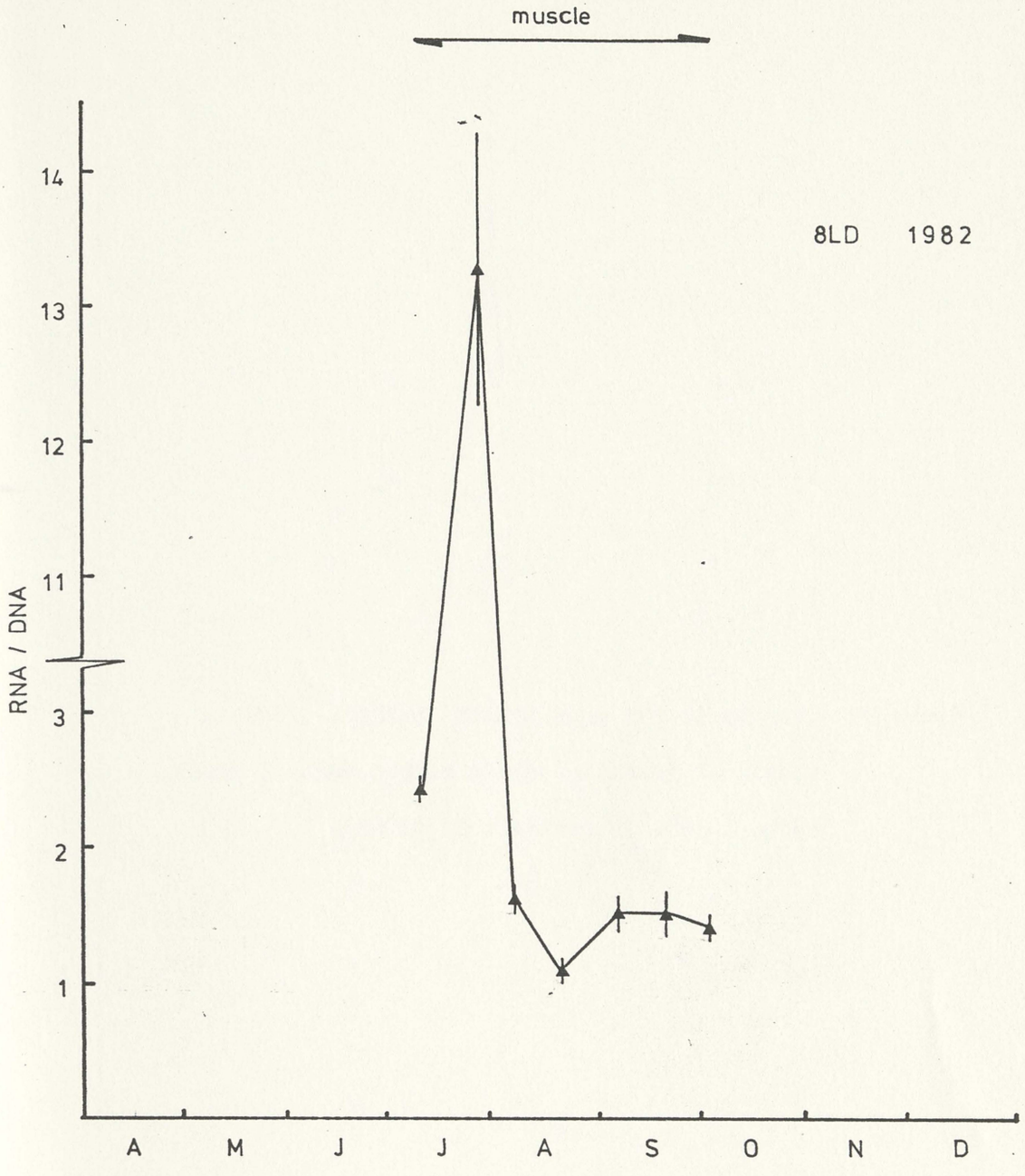

muscle
8LD 1982
RNA / DNA
14
13
12
11
3
2
1
A
M
J
J
A
S
O
N
D

Figure 39 Changes in the mean RNA-DNA ratio ($\pm$ 2SE) in muscle of juvenile salmon reared under 3 month cycle (L3D). Experiment II (1982).

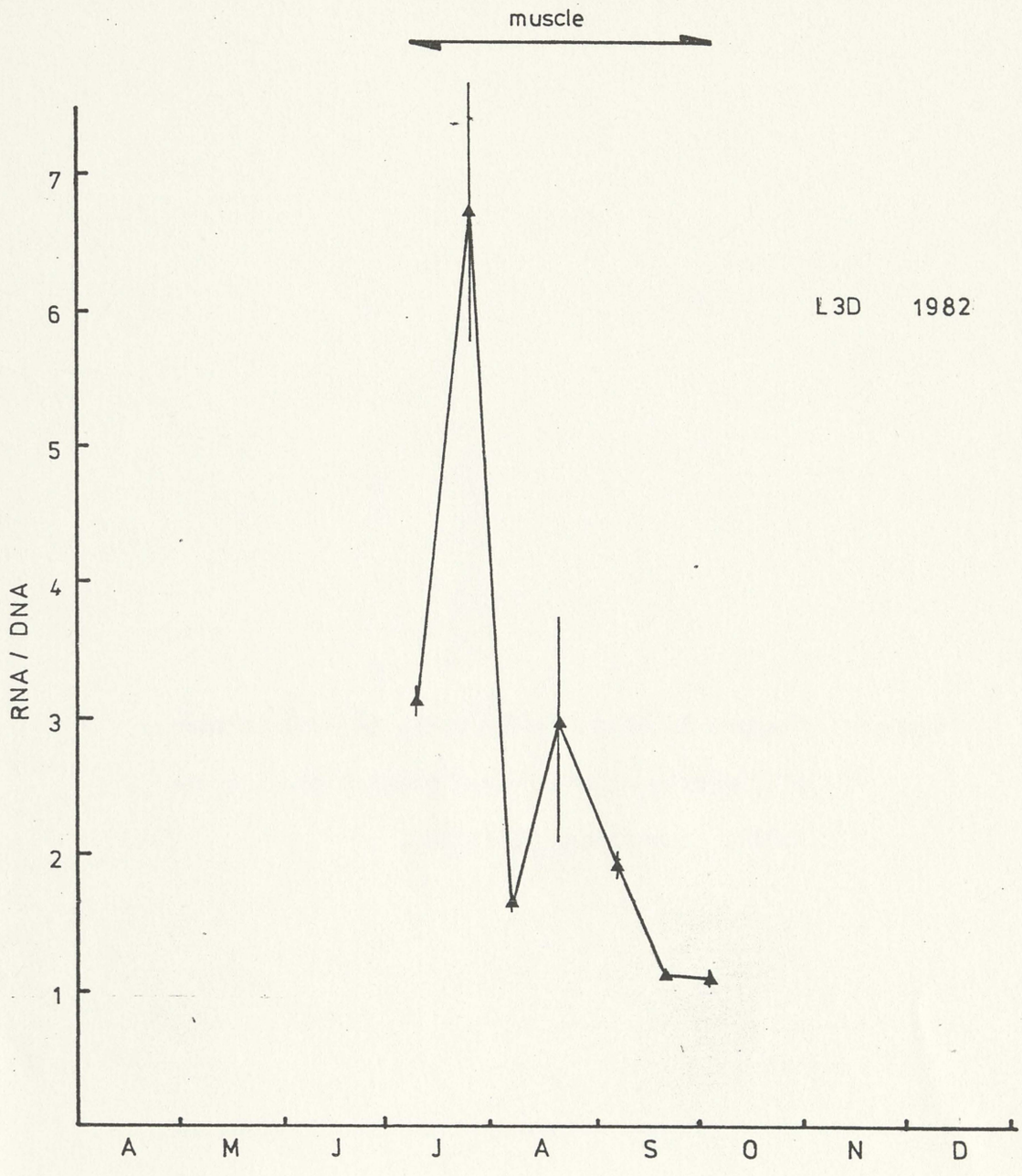

muscle
RNA / DNA
7
6
5
4
3
2
1
A
M
J
J
A
S
O
N
D
L3D 1982

Figure 40 Changes in mean RNA-DNA ratio (± 2SE) in muscle of juvenile salmon reared under 4 month cycle (L4D). Experiment II (1982).

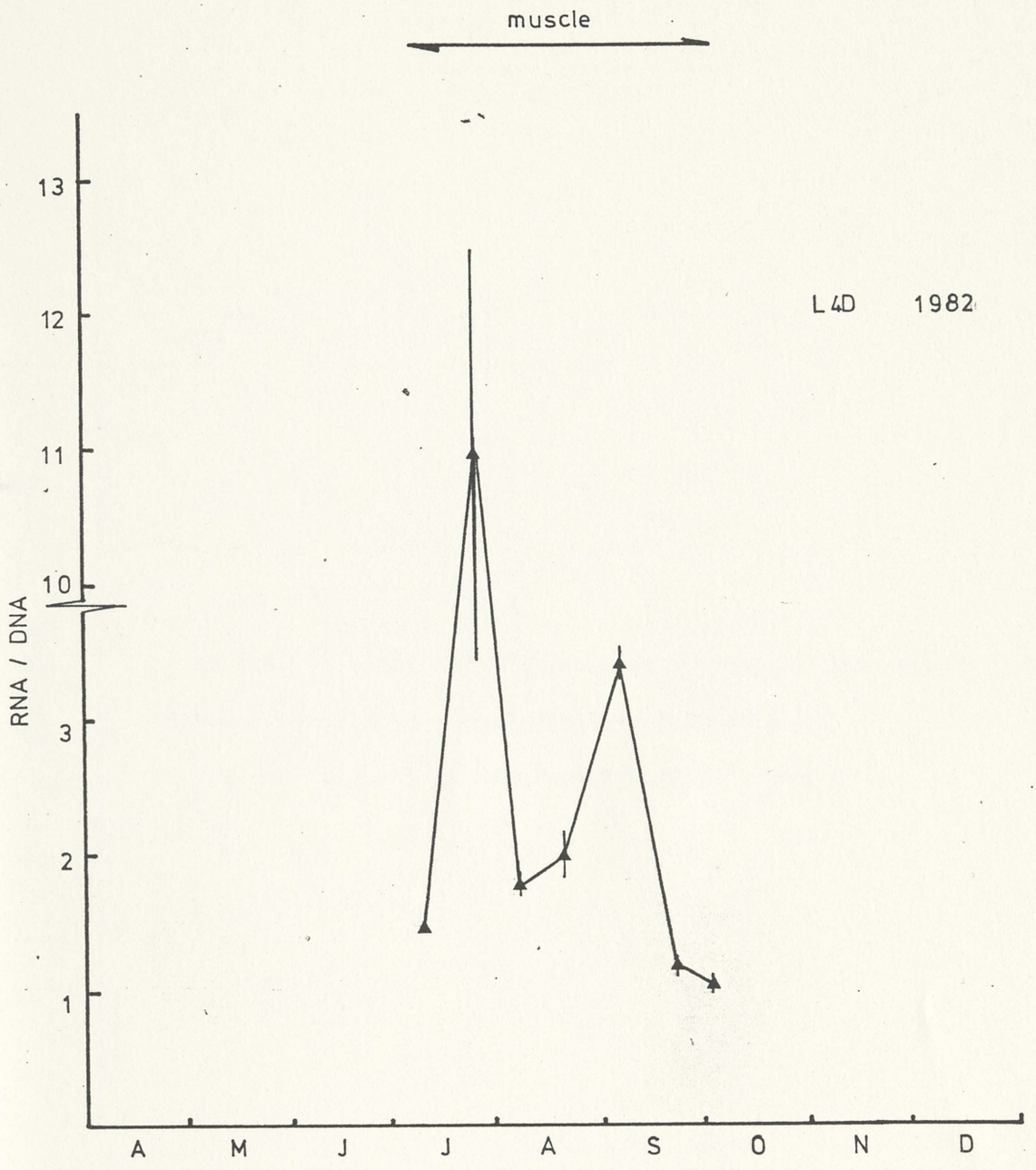
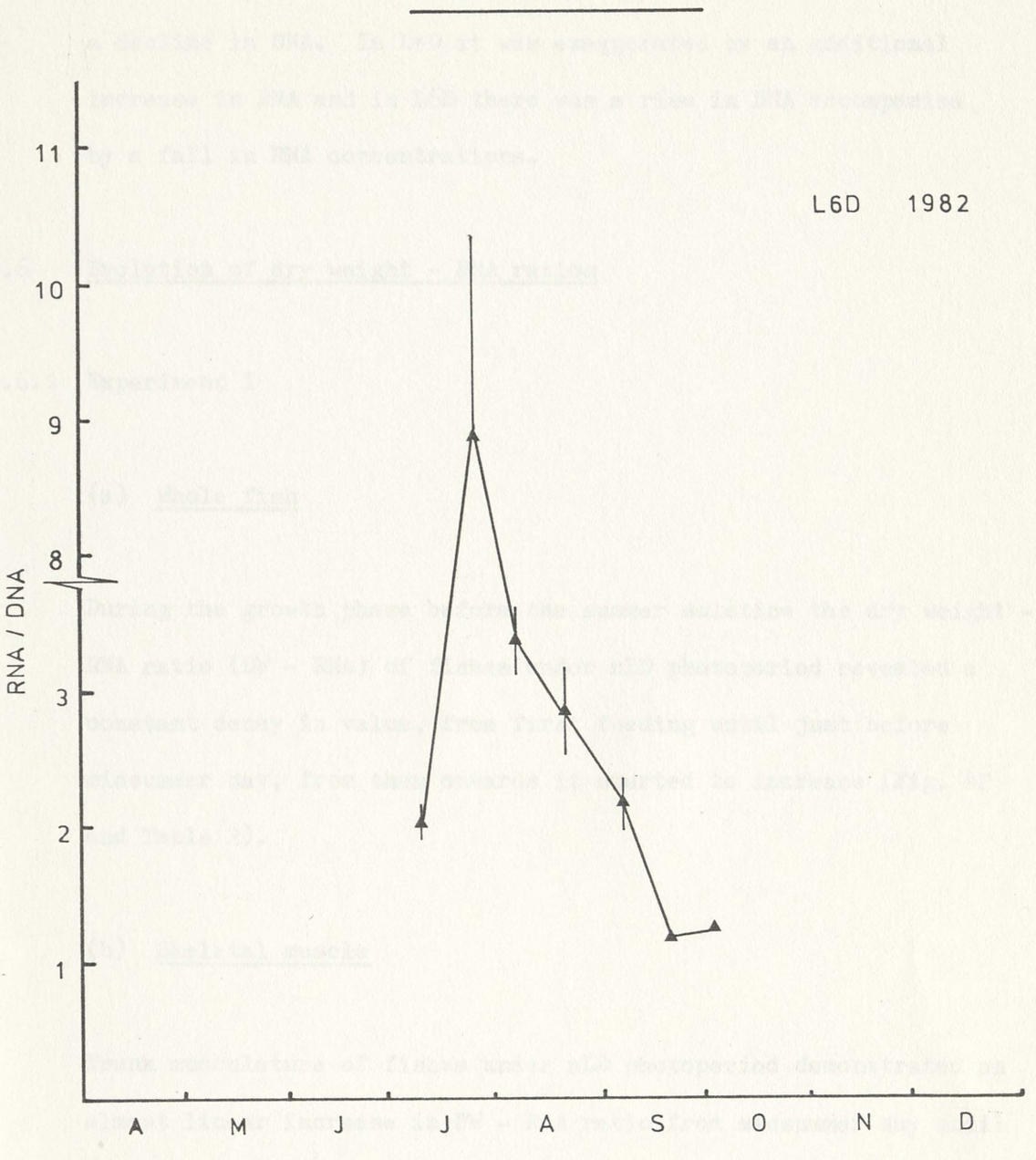

muscle
L4D 1982
RNA / DNA
13
12
11
10
3
2
1
A
M
J
J
A
S
O
N
D

Figure 41 Changes in the mean RNA-DNA ratio ($\pm$ 2SE) in muscle of juvenile salmon reared under 6 month cycle (L6D). Experiment II (1982).


muscle
L6D 1982
RNA / DNA
11
10
9
8
3
2
1
A
M
J
J
A
S
O
N
D

(Figs. 39 - 41). In L3D it was again attributable chiefly to a decline in DNA. In L4D it was exaggerated by an additional increase in RNA and in L6D there was a rise in DNA accompanied by a fall in RNA concentrations.

3.4.6 Evolution of dry weight - RNA ratios

3.4.6.1 Experiment I

(a) Whole fish

During the growth phase before the summer solstice the dry weight - RNA ratio (DW - RNA) of fishes under nLD photoperiod revealed a constant decay in value, from first feeding until just before midsummer day, from then onwards it started to increase (Fig. 42 and Table 2).

(b) Skeletal muscle

Trunk musculature of fishes under nLD photoperiod demonstrated an almost linear increase in DW - RNA ratio from midsummer day until 30th September (Fig. 42 and Table 5). On the other hand, though the LL group presented a similar trend, the ratio value was lower than that for the nLD group (Fig. 43 and Table 6). When both photoperiodic treatment were segregated by modal groups a huge difference was found amidst the two modes. (Figures 42 and 43), but was less pronounced in the LL group than in the nLD group. Nevertheless, the

Figure 42 Changes in mean dry weight - DNA and dry weight - RNA ratios (± 2SE) in whole body and muscle of juvenile salmon reared under natural photoperiod (nLD). Experiment I (1981). ff, first feeding; ms, midsummer day; um, upper mode; lm, lower mode.

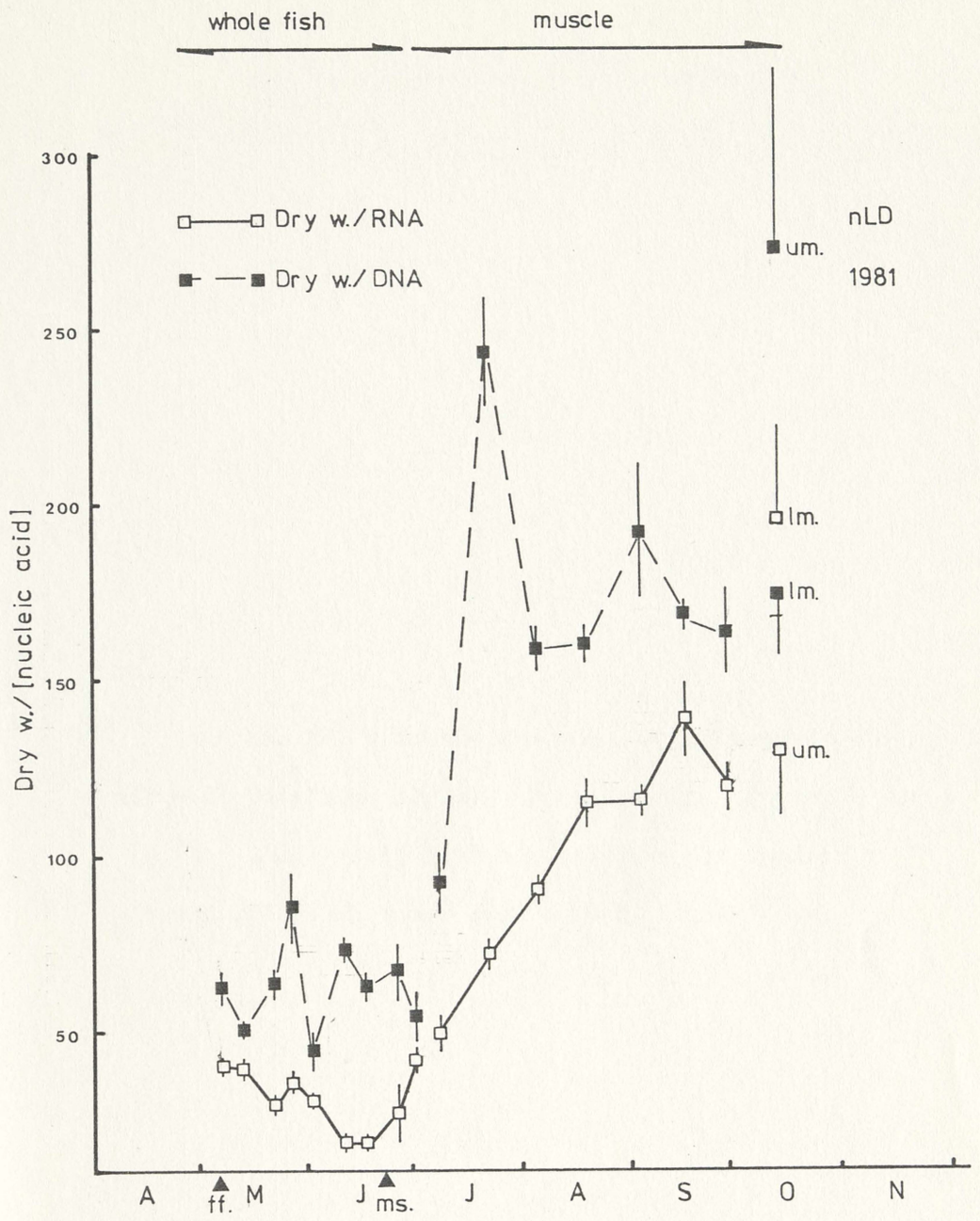
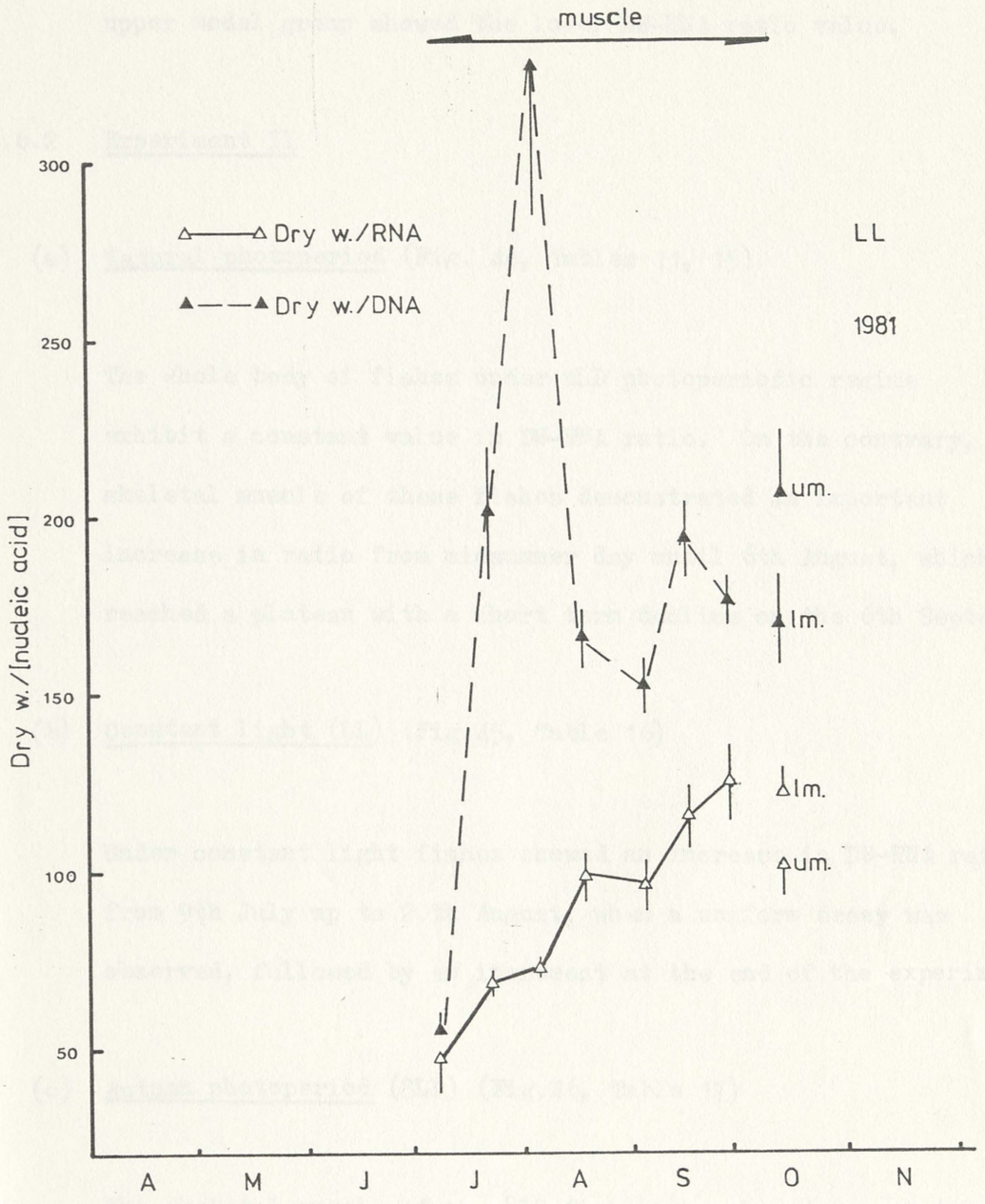

whole fish
muscle
Dry w./RNA
Dry w./DNA
nLD
1981
um.
lm.
lm.
um.
Dry w./[nucleic acid]
300
250
200
150
100
50
A
ff.
M
J
ms.
J
A
S
O
N

Figure 43 Changes in the mean dry weight - DNA and dry weight - RNA ratios (± 2SE) in muscle of juvenile salmon reared under constant light (LL). Experiment I (1981). um, upper mode; lm, lower mode.


muscle
300
250
200
150
100
50
Dry w./[nucleic acid]
Dry w./RNA
Dry w./DNA
LL
1981
um.
lm.
lm.
um.
A
M
J
J
A
S
O
N

upper modal group showed the lower DW-RNA ratio value.

3.4.6.2 Experiment II

(a) Natural photoperiod (Fig. 44, Tables 11, 15)

The whole body of fishes under nLD photoperiodic regime exhibit a constant value in DW-RNA ratio. On the contrary, skeletal muscle of these fishes demonstrated an important increase in ratio from midsummer day until 6th August, which reached a plateau with a short term decline on the 6th September.

(b) Constant light (LL) (Fig.45, Table 16)

Under constant light fishes showed an increase in DW-RNA ratio from 9th July up to 20th August, when a uniform decay was observed, followed by an increment at the end of the experiment.

(c) Autumn photoperiod (8LD) (Fig.46, Table 17)

The skeletal muscle of the 8LD fish group showed a very irregular increase in DW-RNA ratio from the summer solstice to the 6th August when a plateau, showing short term decline, was reached.

(d) Different rate of photoperiodic change (L3D, L4D, L6D).

The body muscle of fishes exposed to L3D and L4D photoperiod

Figure 44 Changes in mean dry weight - DNA and dry weight - RNA ratios (± 2SE) in the whole body and muscle of juvenile salmon reared under natural photoperiod (nLD). Experiment II (1982). ff, first feeding; ms, midsummer day.

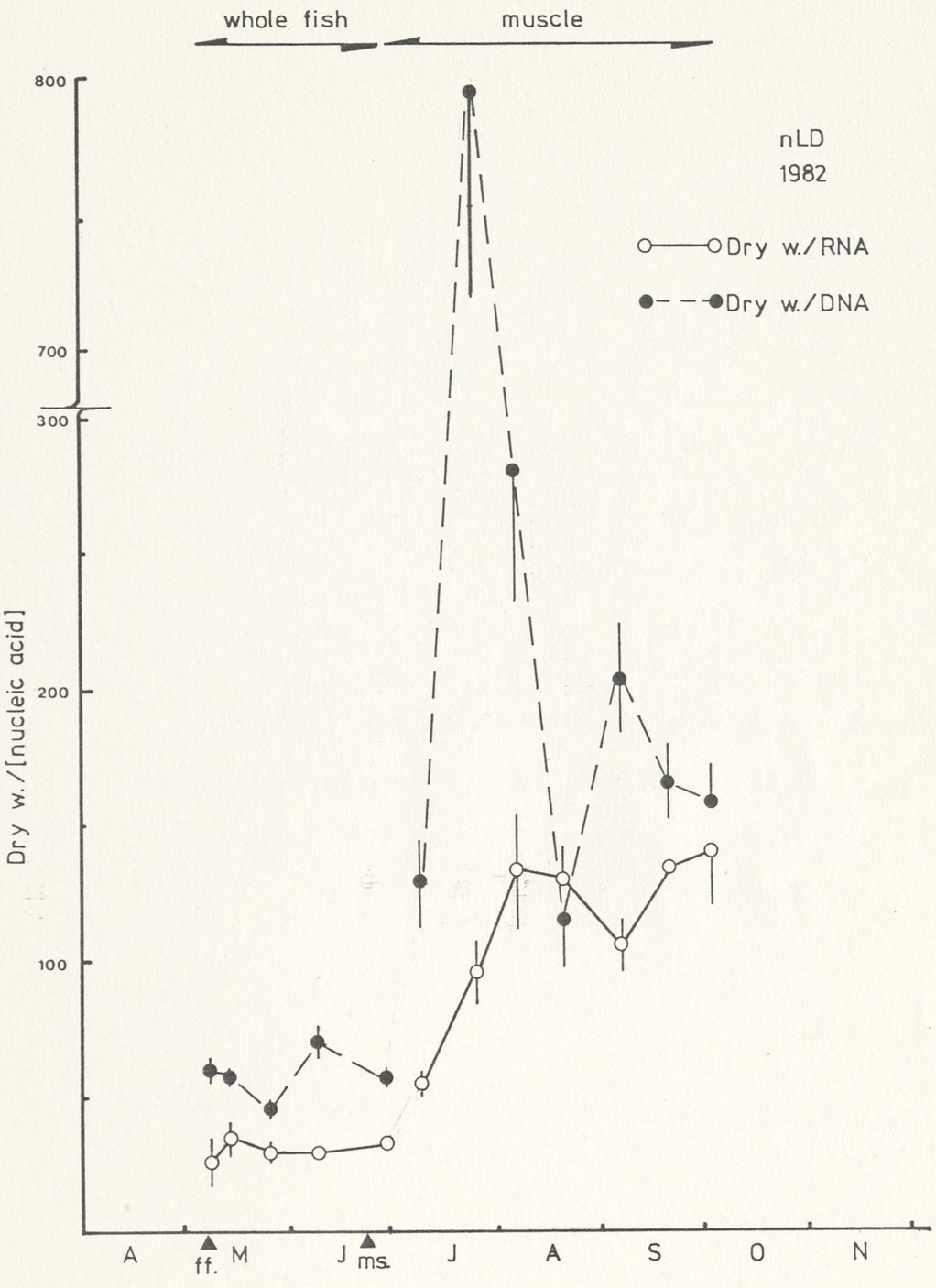

whole fish
muscle
nLD
1982
Dry w./RNA
Dry w./DNA
Dry w./[nucleic acid]
800
700
300
200
100
A
ff.
M
J
ms.
J
A
S
O
N

Figure 45 Changes in the mean dry weight - DNA and dry weight - RNA ratio ($\pm$ 2SE) in muscle of juvenile salmon reared under constant light (LL). Experiment II (1982).

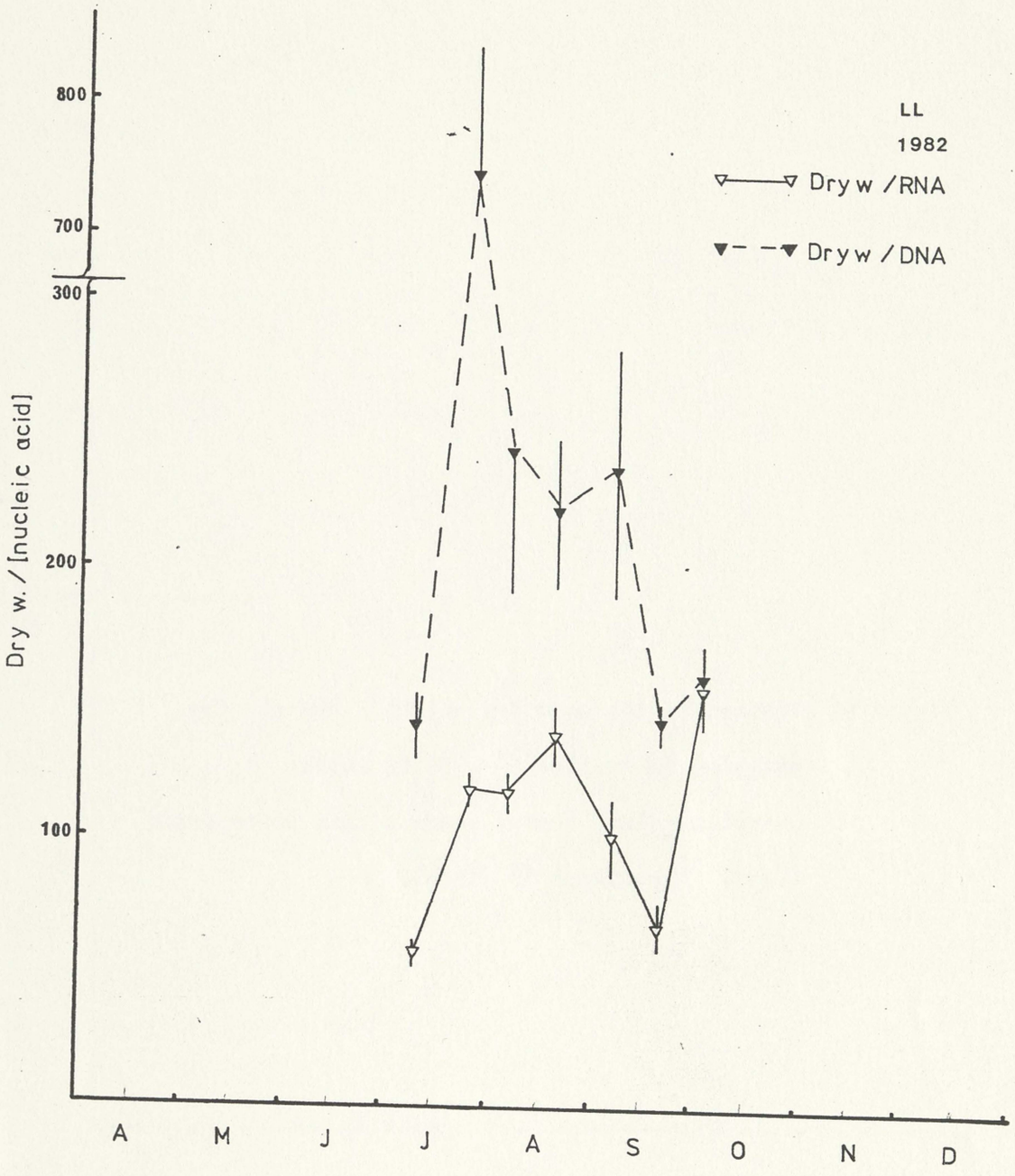
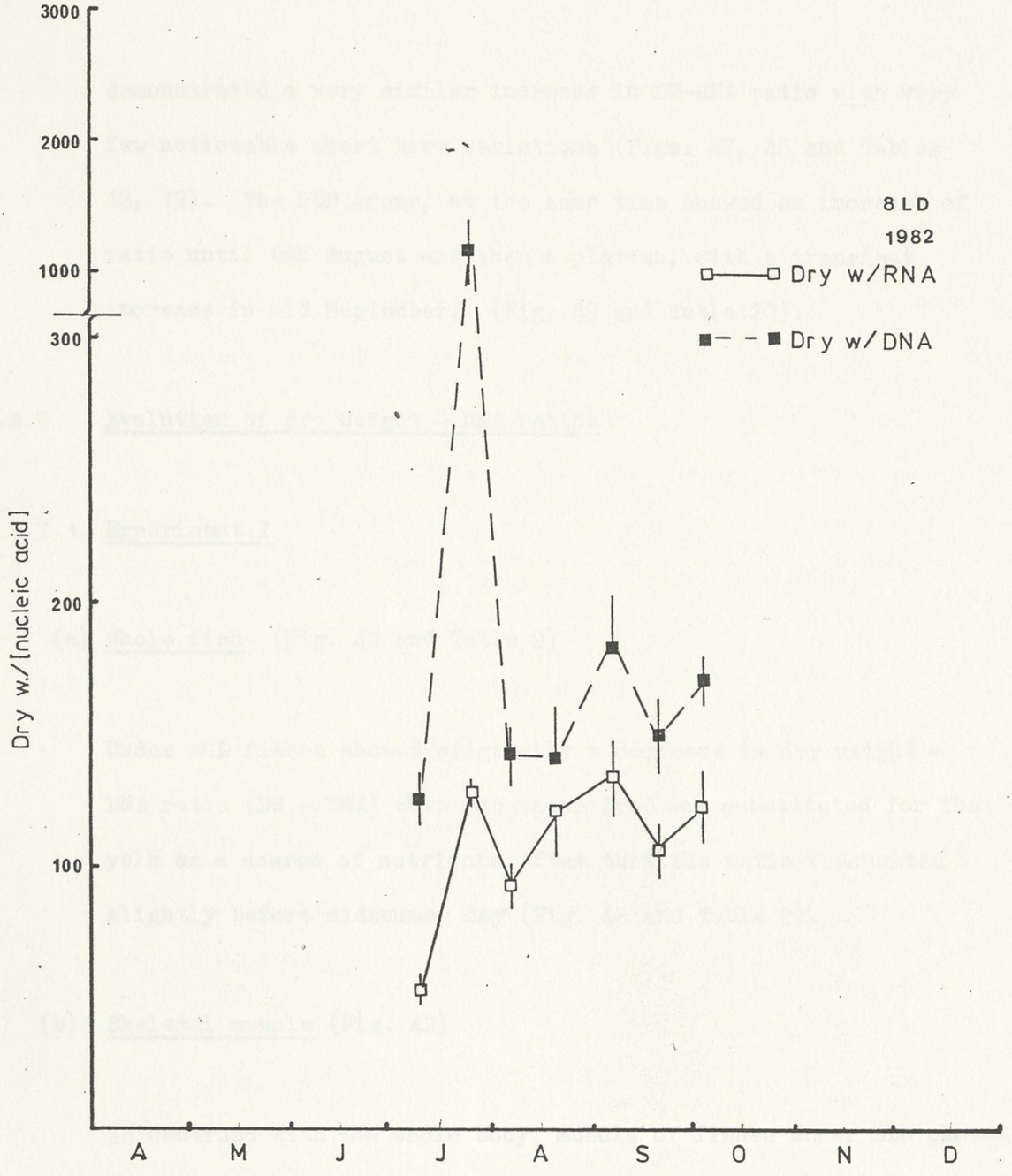

LL
1982
Dry w /RNA
Dry w /DNA
Dry w. / [nucleic acid]
800
700
300
200
100
A
M
J
J
A
S
O
N
D

Figure 46 Changes in the mean dry weight - DNA and dry weight - RNA ratios ($\pm$ 2SE) in muscle of juvenile salmon reared under autumn photoperiod (8LD). Experiment II (1982).


3000
2000
1000
300
200
100
Dry w./[nucleic acid]
8 LD
1982
Dry w/RNA
Dry w/DNA
A
M
J
J
A
S
O
N
D

demonstrated a very similar increase in DW-RNA ratio with very few noticeable short term variations (Figs. 47, 48 and Tables 18, 19). The L6D group, at the same time showed an increase of ratio until 6th August and then a plateau, with a transient increase in mid September. (Fig. 49 and Table 20).

3.4.7 Evolution of dry weight - DNA ratios

3.4.7.1 Experiment I

(a) Whole fish (Fig. 42 and Table 2)

Under nLD fishes showed originally a decrease in dry weight - DNA ratio (DW - DNA) when exogenous food was substituted for the yolk as a source of nutrients. After that the ratio fluctuated slightly before midsummer day (Fig. 42 and Table 2).

(b) Skeletal muscle (Fig. 42)

In contrast with the whole body, muscle of fishes under nLD photoperiod demonstrated an overall increase of DW - DNA ratio from the 22nd June to the 30th September, with two important short term peaks, on the 22nd July and the 4th September. The LL group demonstrated a similar enlargement of this ratio during the same period, but the two transient peaks were 15 days later in each case, on the 5th August and 16th September (Fig. 43 and Table 6).

3.4.7.2 Experiment II

(a) Natural photoperiod (Fig. 44; Tables 11 and 15)

Soon after the change from yolk to exogenous feeding fish under nLD showed a slight decrease in DW-DNA ratio followed by a fluctuating variation of ratio before the summer solstice. The trunk muscle of fishes in this treatment, presented an increase in ratio with transient peaks on the 26th July and 6th September, the first being larger than the second.

(b) Constant light (LL) (Fig.45, Table 16)

Under LL photoperiod an increase in DW-DNA ratio occurred between 9th July and the 6th September, with two transient peaks on the 26th July and the 6th September (but the latter does not differ significantly from the values for 6th August).

(c) Autumn photoperiod (8LD) (Fig. 46 and Table 17)

Fishes exposed to the short day-length showed an increase of DW-DNA ratio during the summer growth phase, with peaks on the 26th July and 6th August. The first one constituted the largest value of the all experimental treatments.

(d) Different rates of photoperiodic change (L3D, L4D, L6D) (Figs. 47 - 49: Tables 18 - 20)

All groups peaked on July 26th. L3D and L4D showed second minor

Figure 47 Changes in the mean dry weight - DNA and dry weight - RNA ratios (± 2SE) in muscle of juvenile salmon reared under 3 month cycle (L3D). Experiment II (1982).

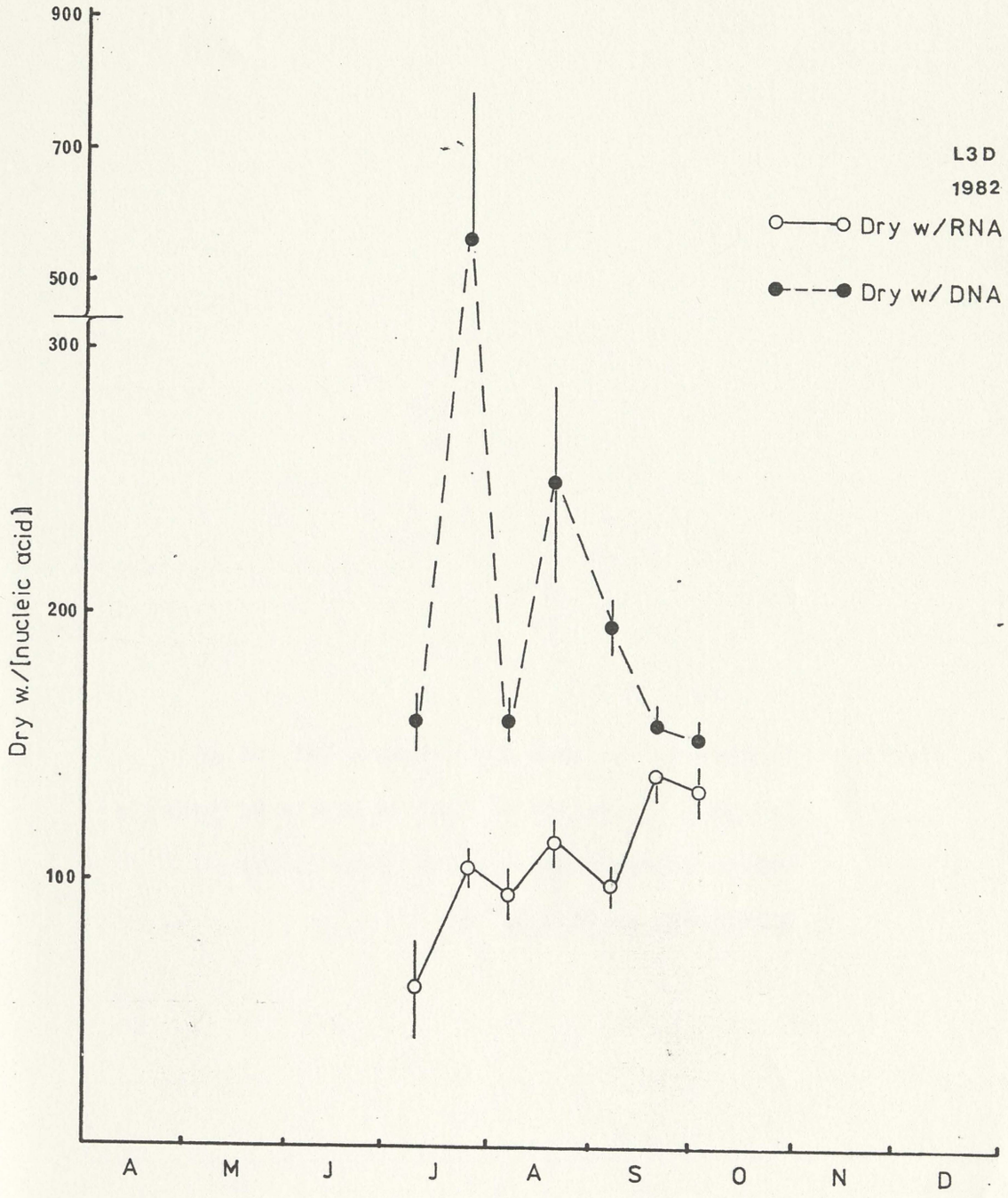

900
700
500
300
200
100
Dry w./[nucleic acid]
L3D
1982
Dry w/RNA
Dry w/DNA
A
M
J
J
A
S
O
N
D

Figure 48 Changes in the mean dry weight - DNA and dry weight - RNA ratios (± 2SE) in muscle of juvenile salmon reared under 4 month cycle (L4D). Experiment II (1982).

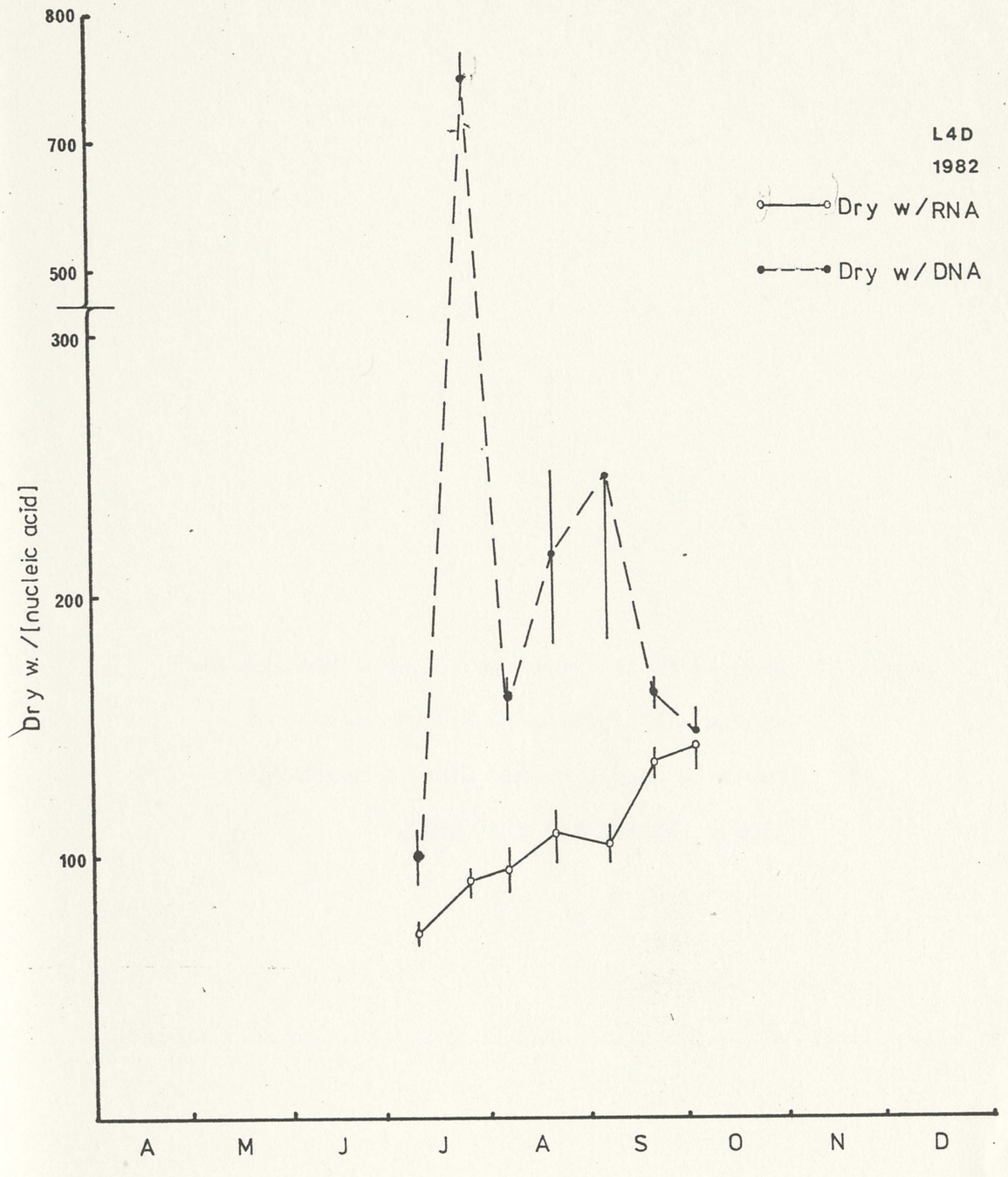
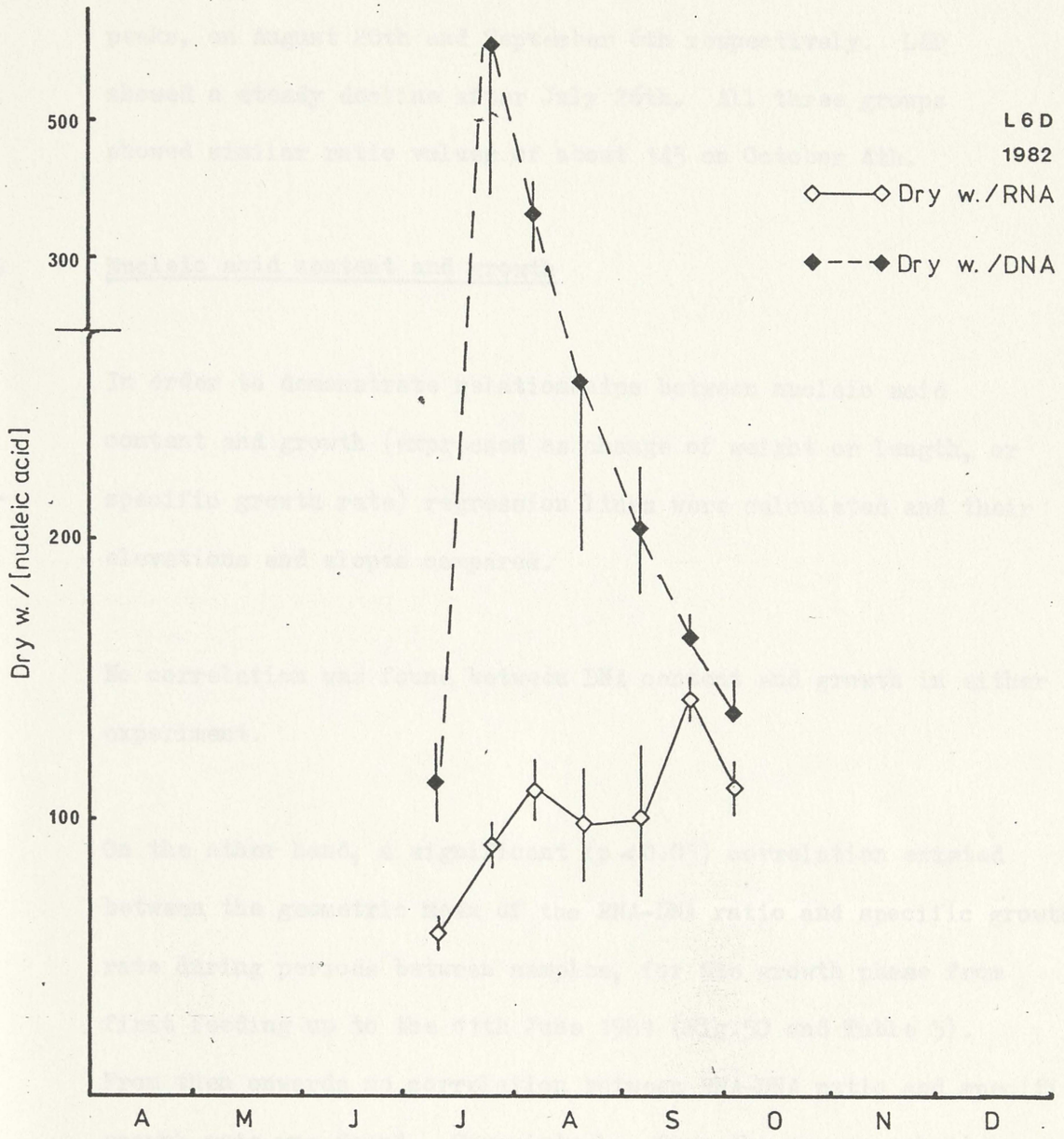

800
700
500
300
200
100
Dry w. /[nucleic acid]
L4D
1982
Dry w/RNA
Dry w/DNA
A
M
J
J
A
S
O
N
D

Figure 49 Changes in the mean dry weight - DNA and dry weight - RNA ratios (± 2SE) in muscle of juvenile salmon reared under 6 month cycle (L6D). Experiment II (1982).


L 6 D
1982
Dry w./RNA
Dry w./DNA
Dry w. / [nucleic acid]
500
300
200
100
A
M
J
J
A
S
O
N
D

peaks, on August 20th and September 6th respectively. L6D showed a steady decline after July 26th. All three groups showed similar ratio values of about 145 on October 4th.

3.5 Nucleic acid content and growth

In order to demonstrate relationships between nucleic acid content and growth (expressed as change of weight or length, or specific growth rate) regression lines were calculated and their elevations and slopes compared.

No correlation was found between DNA content and growth in either experiment.

On the other hand, a significant ($p < 0.05$) correlation existed between the geometric mean of the RNA-DNA ratio and specific growth rate during periods between samples, for the growth phase from first feeding up to the 11th June 1981 (Fig.50 and Table 5). From then onwards no correlation between RNA-DNA ratio and specific growth rate was found. Surprisingly, from the summer solstice to the 30th September 1981, a significant correlation was found between specific growth rate and the natural logarithm of the harmonic mean of RNA concentration for nLD ($p < 0.01$) and LL ($p < 0.05$) photoperiodic treatments (Table 6). An analysis of covariance (ANCOVA) showed no significant differences in the slopes, nor in the elevations of the regression lines for nLD and LL groups of Experiment I; for this reason the data have been pooled in the regression of figure 51. (Table 25).

Figure 50 Relationship between specific growth rate (G_w) and the geometric mean of RNA-DNA ratio (for the relevant period) of juvenile salmon reared under natural photoperiod.
Experiment I (1981). (April - midsummer).

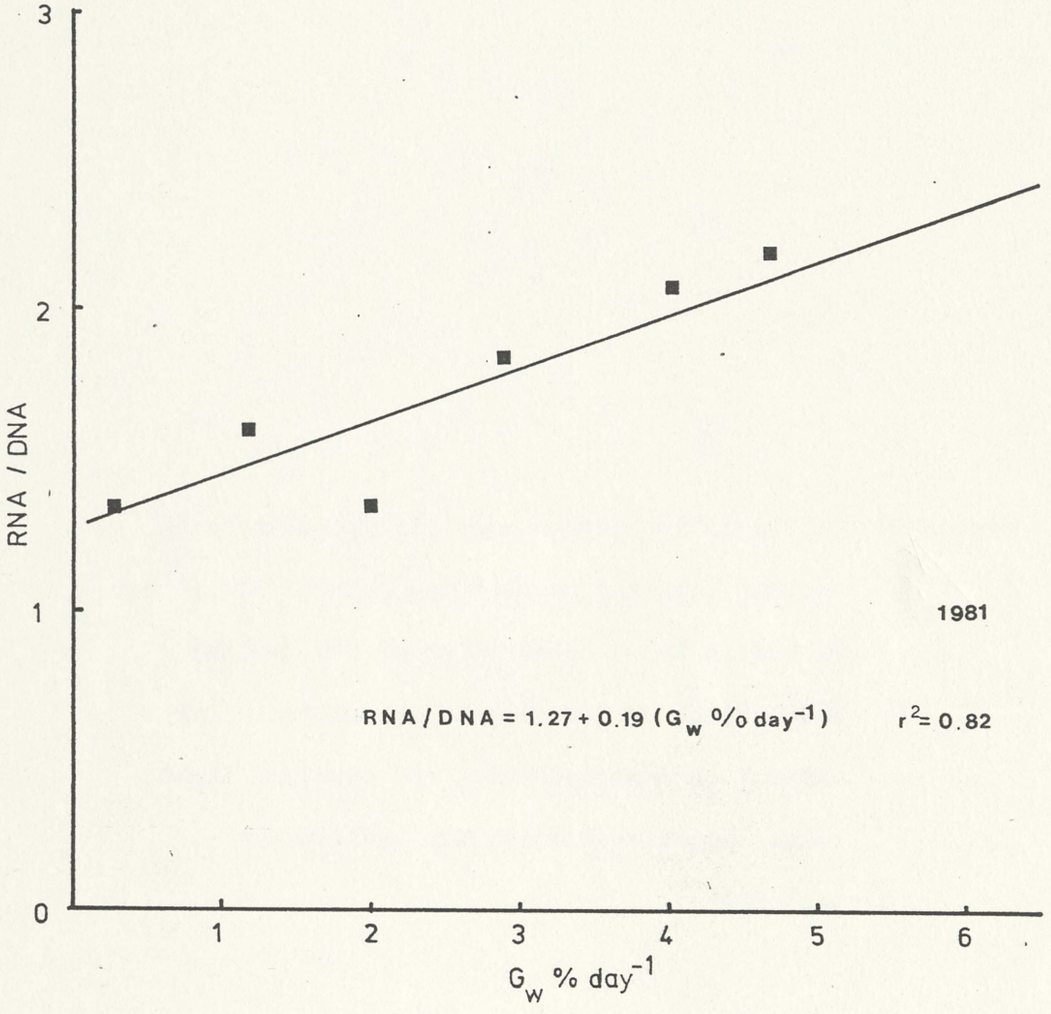
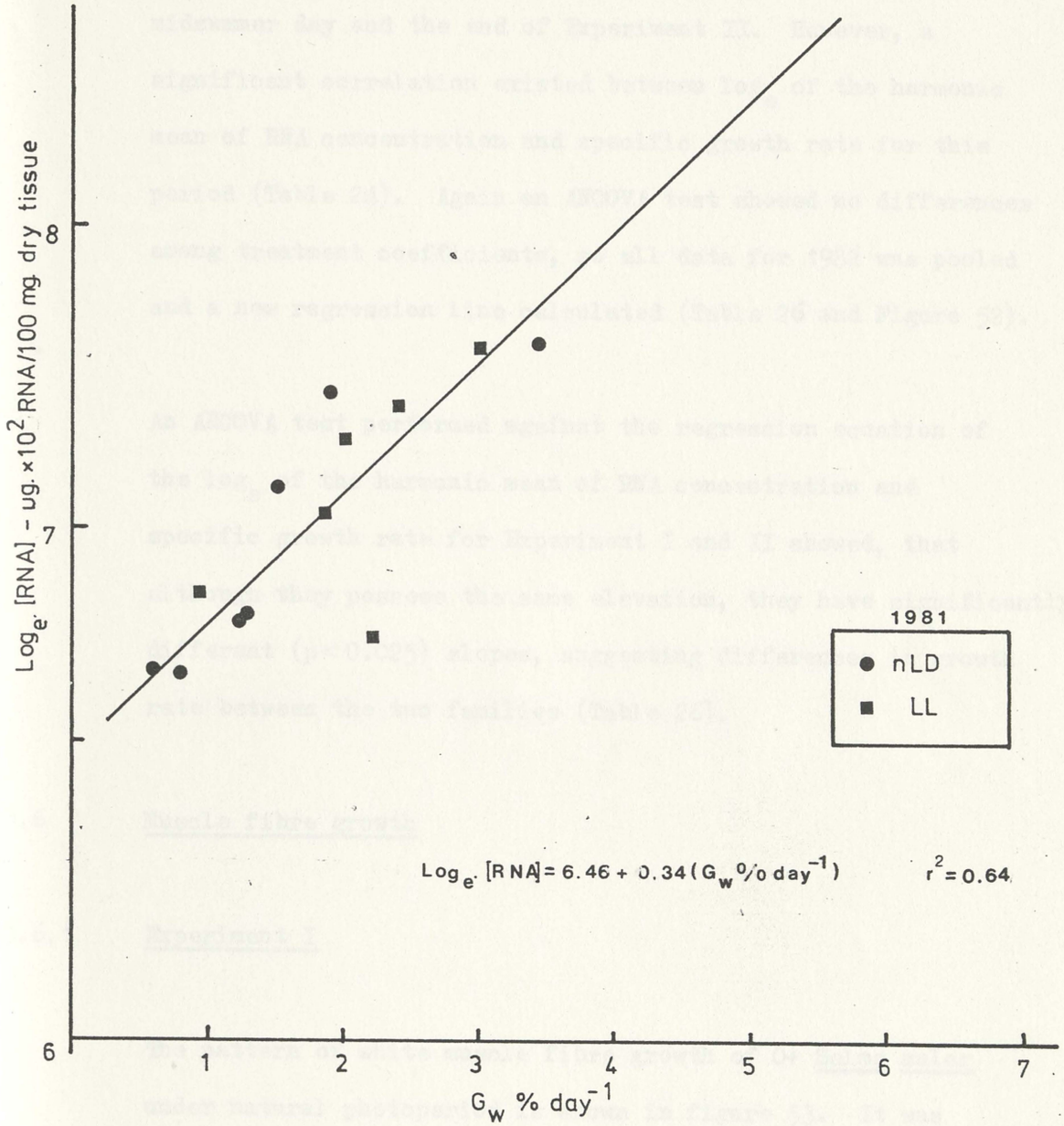

3
2
1
0
RNA / DNA
1981
RNA / DNA = 1.27 + 0.19 (G_w %/o day^{-1})
r^2= 0.82
1
2
3
4
5
6
G_w % day^{-1}

Figure 51 Relationship between specific growth rate (G_w) and the harmonic mean of the natural logarithm of muscle RNA concentration of two sibling populations of juvenile salmon reared under natural photoperiod (nLD) and constant light (LL). Experiment I (1981). (Midsummer - September).


Log$_e$. [RNA] - ug. x10^2 RNA/100 mg dry tissue
8
7
6
1
2
3
4
5
6
7
G_w % day^{-1}
1981
nLD
LL
Log$_e$. [RNA] = 6.46 + 0.34 (G_w % day^{-1})
r^2 = 0.64

Consistent with these results, no correlation was found between DNA concentration or RNA-DNA ratio and growth between midsummer day and the end of Experiment II. However, a significant correlation existed between $\log_e$ of the harmonic mean of RNA concentration and specific growth rate for this period (Table 24). Again an ANCOVA test showed no differences among treatment coefficients, so all data for 1982 was pooled and a new regression line calculated (Table 26 and Figure 52).

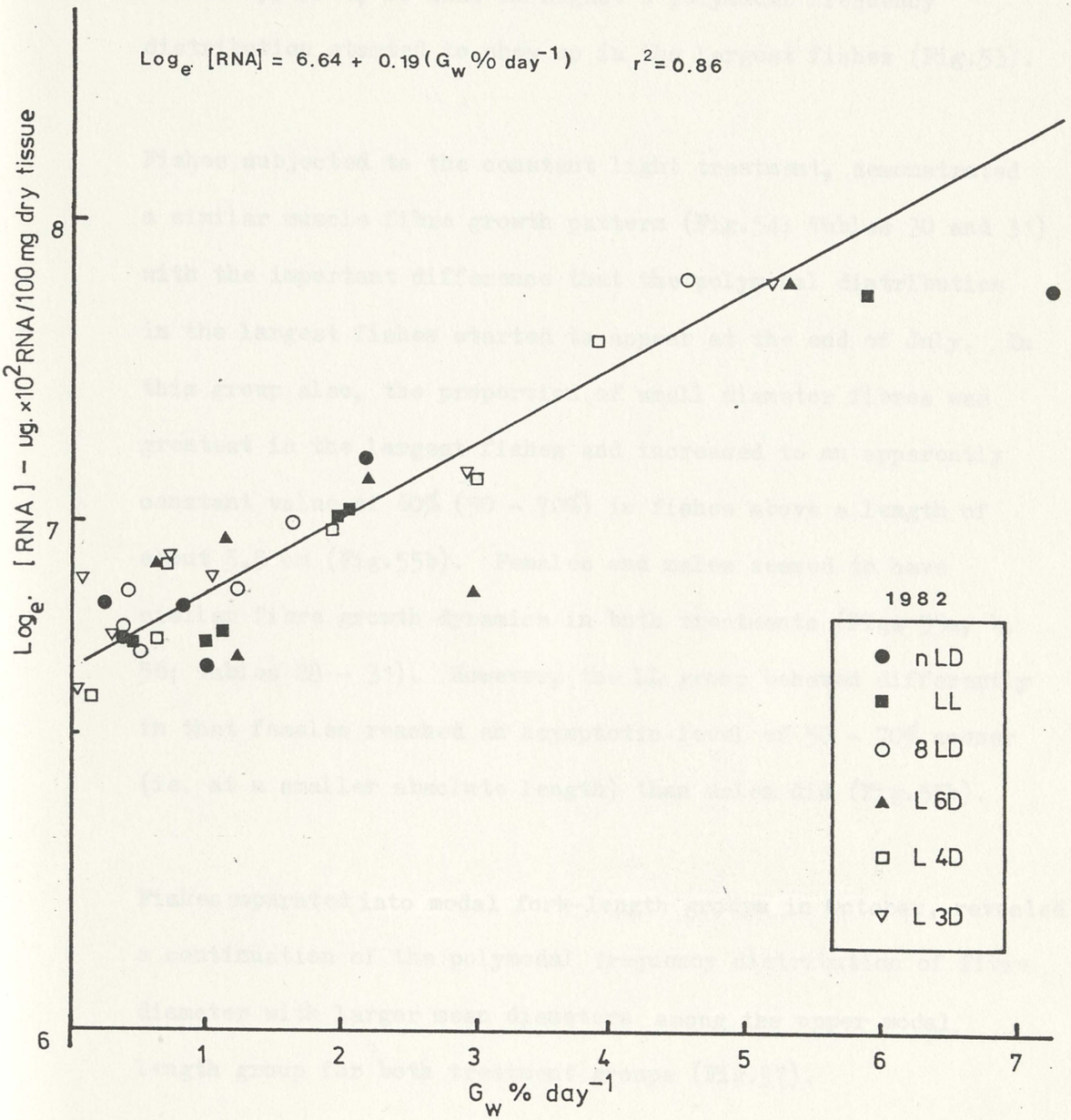
An ANCOVA test performed against the regression equation of the $\log_e$ of the harmonic mean of RNA concentration and specific growth rate for Experiment I and II showed, that although they possess the same elevation, they have significantly different ($p < 0.025$) slopes, suggesting differences in growth rate between the two families (Table 26).

3.6 Muscle fibre growth

3.6.1 Experiment I

The pattern of white muscle fibre growth of 0+ Salmo salar under natural photoperiod is shown in figure 53. It was characterised by an early development of a bimodal frequency distribution of fibre diameter, with modal values increasing with fish length (see also Tables 28 and 29). The other important feature was that the proportion of small diameter fibres was greatest in the largest fish and increased to an apparently constant value of about 60% (50 - 70) in fish at

Figure 52 Relationship between specific growth rate (G_w) and the harmonic mean of the natural logarithm of muscle RNA concentration of six sibling populations reared under different photoperiodic treatments. Experiment II (1982).


Log_e [RNA] = 6.64 + 0.19 (G_w % day^{-1}) r^2 = 0.86
Log_e [RNA] - ug. x10^2 RNA/100 mg dry tissue
8
7
6
1
2
3
4
5
6
7
G_w % day^{-1}
1982
n LD
LL
8 LD
L 6D
L 4D
L 3D

5-cm and above (Fig. 55a). As both modal values increased with fish size, from July onwards an additional recruitment of new fibres appeared, so that in August a polymodal frequency distribution started to show up in the largest fishes (Fig.53).

Fishes subjected to the constant light treatment, demonstrated a similar muscle fibre growth pattern (Fig.54; Tables 30 and 31) with the important difference that the polymodal distribution in the largest fishes started to appear at the end of July. In this group also, the proportion of small diameter fibres was greatest in the largest fishes and increased to an apparently constant value of 60% (50 - 70%) in fishes above a length of about 5.5 cm (Fig.55b). Females and males seemed to have similar fibre growth dynamics in both treatments (Figs 55a, b, 56; Tables 28 - 31). However, the LL group behaved differently in that females reached an asymptotic level of 50 - 70% sooner (ie. at a smaller absolute length) than males did (Fig.55b).

Fishes separated into modal fork-length groups in October, revealed a continuation of the polymodal frequency distribution of fibre diameter with larger mean diameters among the upper modal length group for both treatment groups (Fig.57).

3.6.2 Experiment II (Fig.58)

The nLD group showed similar muscle cell growth dynamics to those of the equivalent treatment groups of the 1981 experiment, with an initial bimodal distribution by June, followed by a

Figure 53 Changes in the white muscle fibre diameter frequency distribution of juvenile salmon reared under natural photoperiod (nLD). Experiment I (1981). L, length; W, weight; N, number of fibres

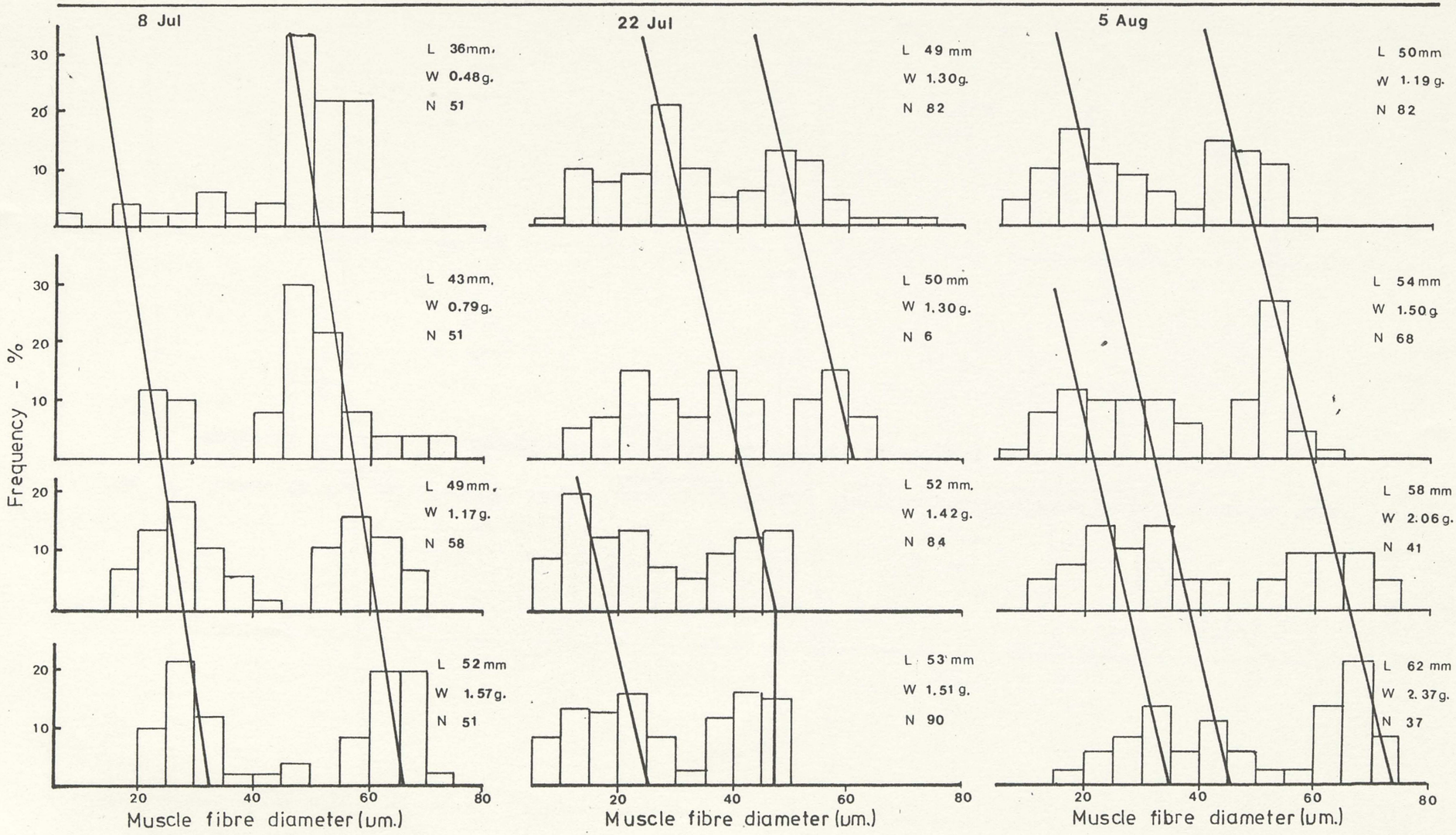

8 Jul
22 Jul
5 Aug
L 36mm.
W 0.48g.
N 51
L 49 mm
W 1.30g.
N 82
L 50mm
W 1.19g.
N 82
L 43mm.
W 0.79g.
N 51
L 50 mm
W 1.30g.
N 6
L 54mm
W 1.50g.
N 68
L 49mm.
W 1.17g.
N 58
L 52 mm.
W 1.42g.
N 84
L 58 mm
W 2.06g.
N 41
L 52mm
W 1.57g.
N 51
L 53 mm
W 1.51g.
N 90
L 62 mm
W 2.37g.
N 37
Frequency - %
Muscle fibre diameter (um.)
Muscle fibre diameter (um.)
Muscle fibre diameter (um.)

Figure 54 Change in the white muscle fibre diameter frequency distribution of juvenile salmon reared under constant light (LL). Experiment I (1981). L, length; W, weight; N, number of fibres.

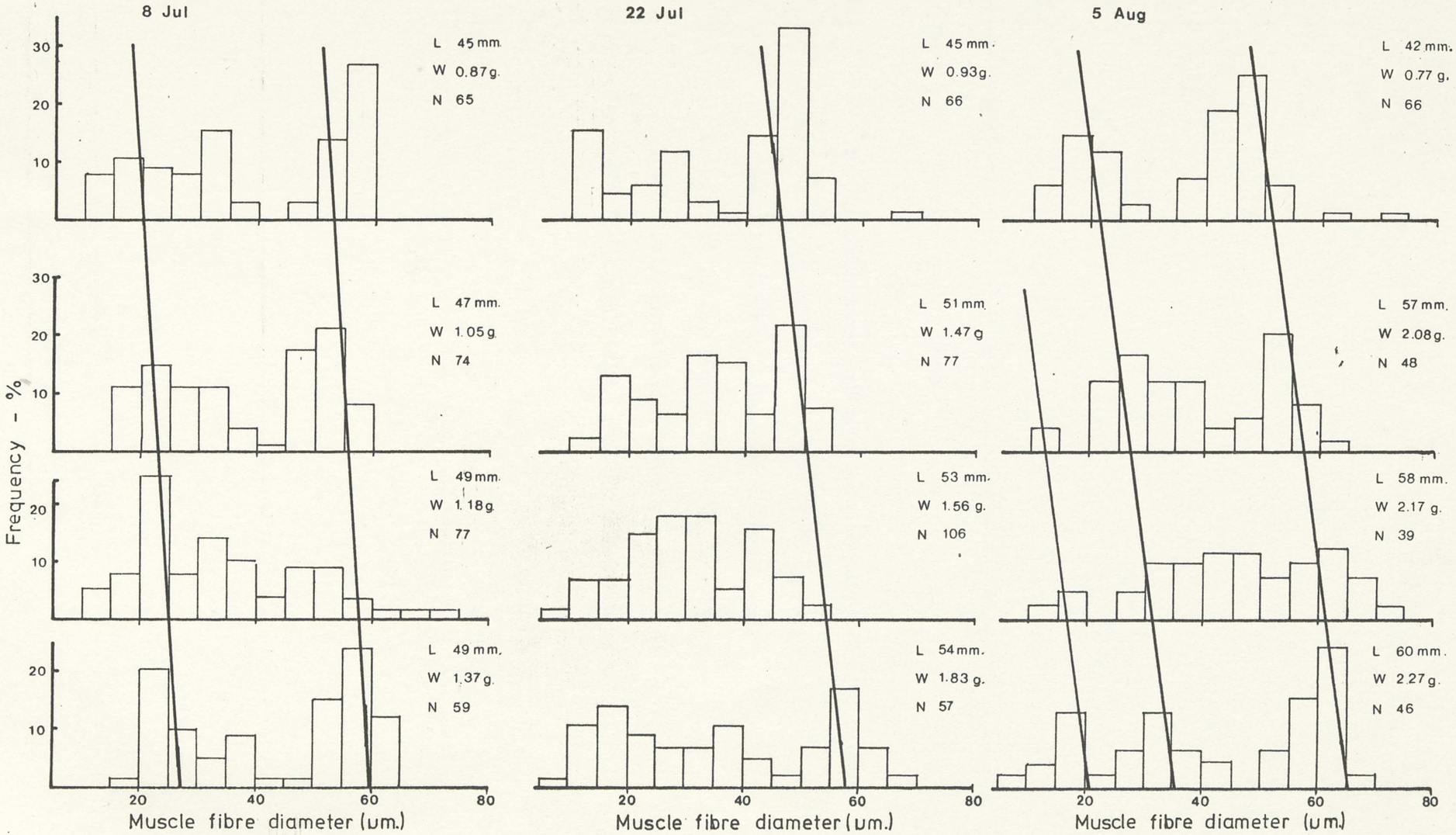
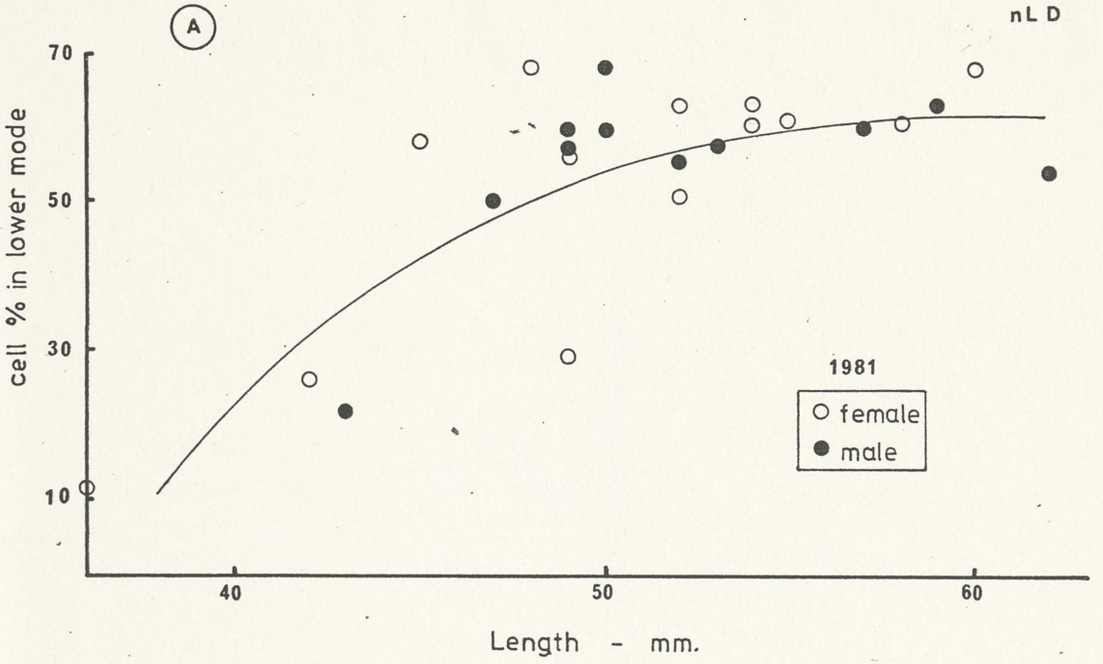

8 Jul
22 Jul
5 Aug
L 45 mm.
W 0.87 g.
N 65
L 45 mm.
W 0.93 g.
N 66
L 42 mm.
W 0.77 g.
N 66
L 47 mm.
W 1.05 g.
N 74
L 51 mm.
W 1.47 g
N 77
L 57 mm.
W 2.08 g.
N 48
L 49 mm.
W 1.18 g.
N 77
L 53 mm.
W 1.56 g.
N 106
L 58 mm.
W 2.17 g.
N 39
L 49 mm.
W 1.37 g.
N 59
L 54 mm.
W 1.83 g.
N 57
L 60 mm.
W 2.27 g.
N 46
Frequency - %
Muscle fibre diameter (µm.)
Muscle fibre diameter (µm.)
Muscle fibre diameter (µm.)

Figure 55 Relationship between the proportion (%) of fibres in the lower mode of the white muscle fibre diameter frequency distribution and length of juvenile salmon under: A. natural photoperiod (nLD); B. constant light (LL). Experiment I (1981). Lines are eye fitted.


A
nL D
70
50
30
10
cell % in lower mode
1981
female
male
40
50
60
Length - mm.

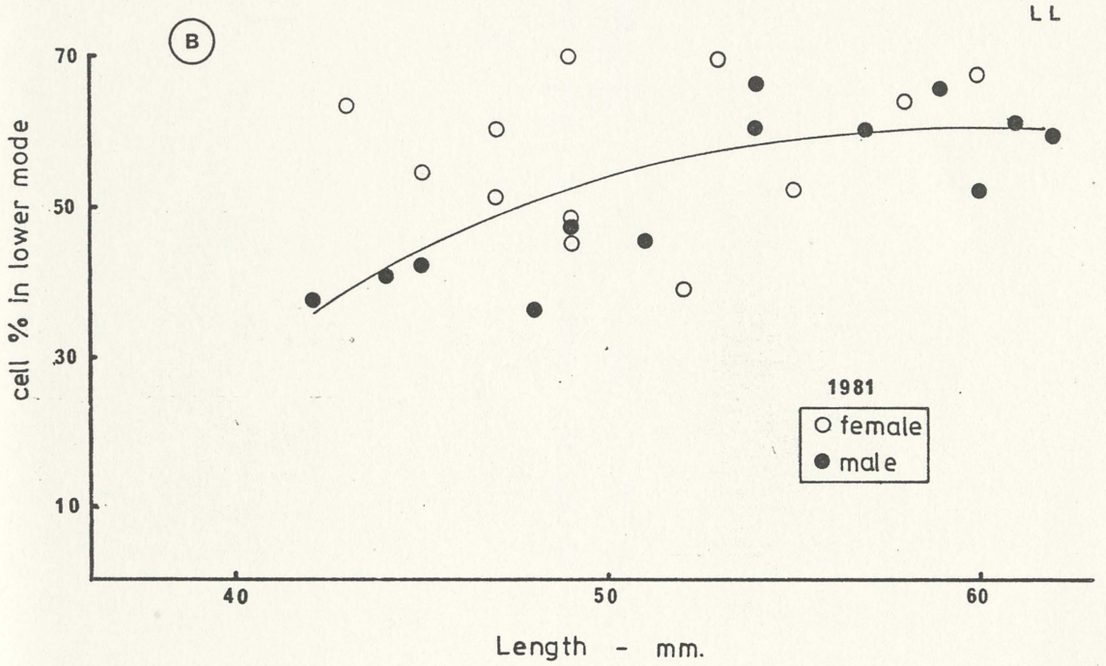

B
LL
70
50
30
10
cell % in lower mode
1981
female
male
40
50
60
Length - mm.

Figure 56 Comparison of the white muscle fibre frequency distribution of female and male juvenile salmon subjected to natural photoperiod (nLD). Experiment I (1981).

8 Jul 1981 (nLD)

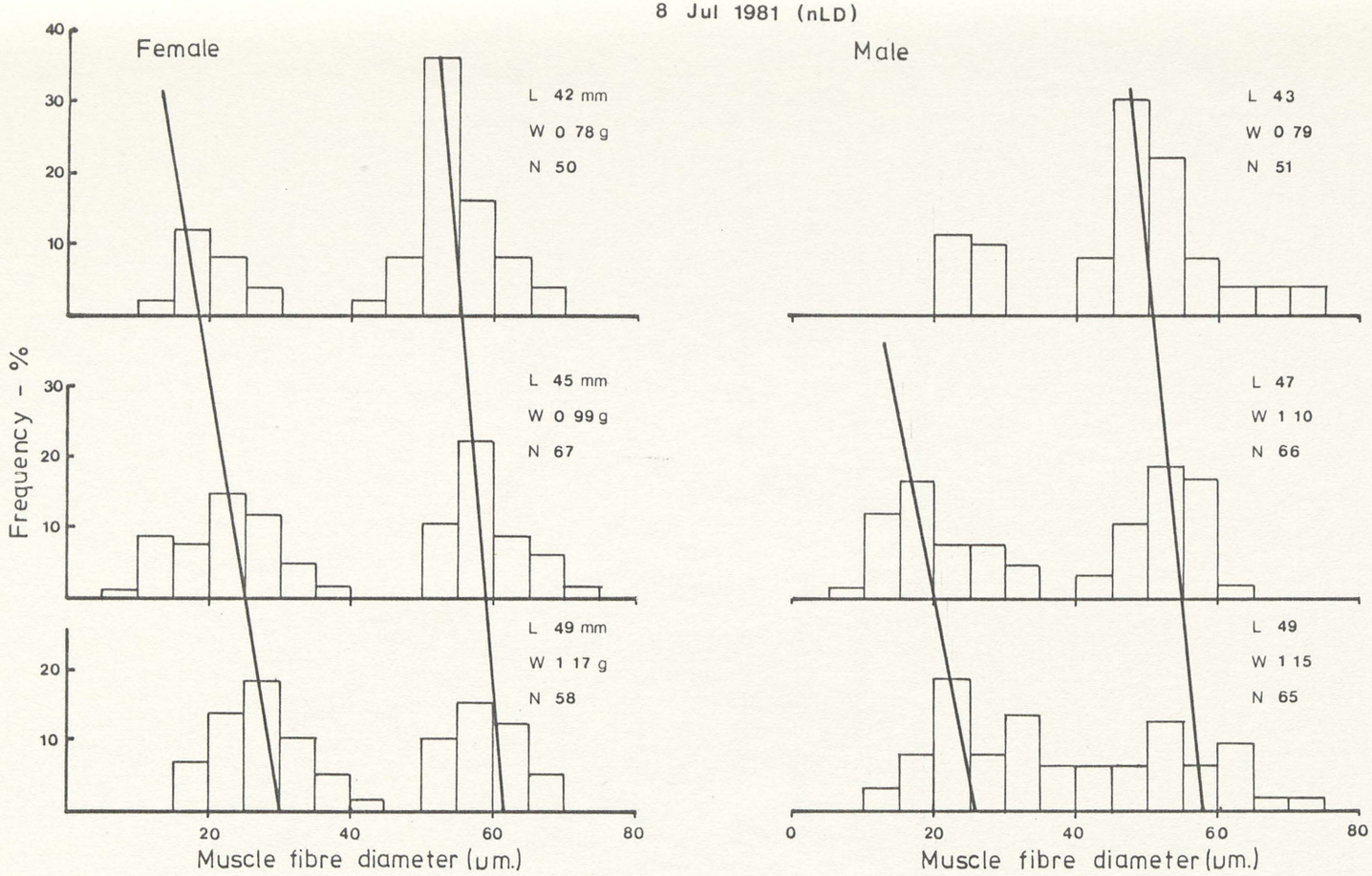


Figure 57 White muscle fibre diameter frequency distributions of fishes segregated by modal group and subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). N, number of fibres.

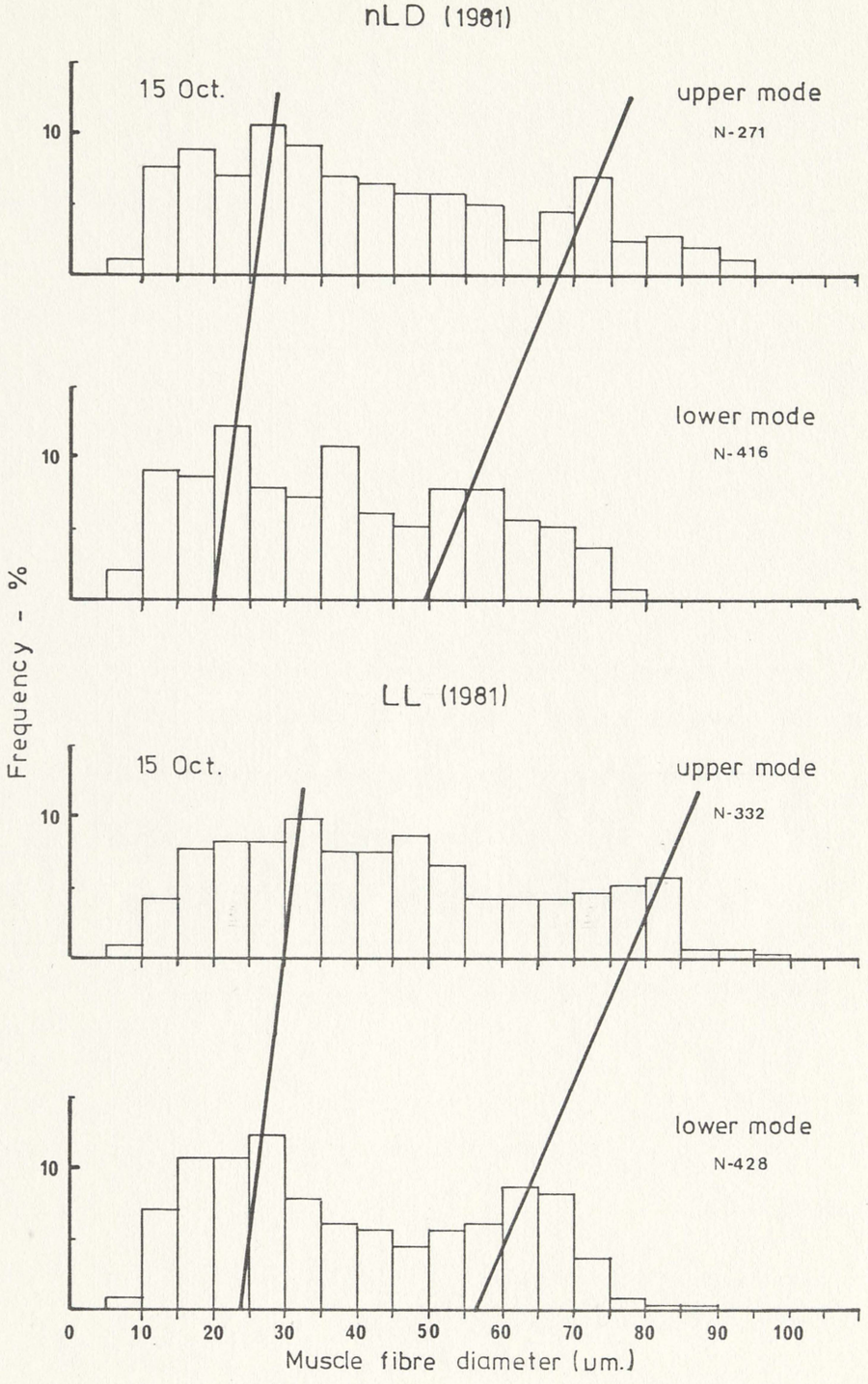
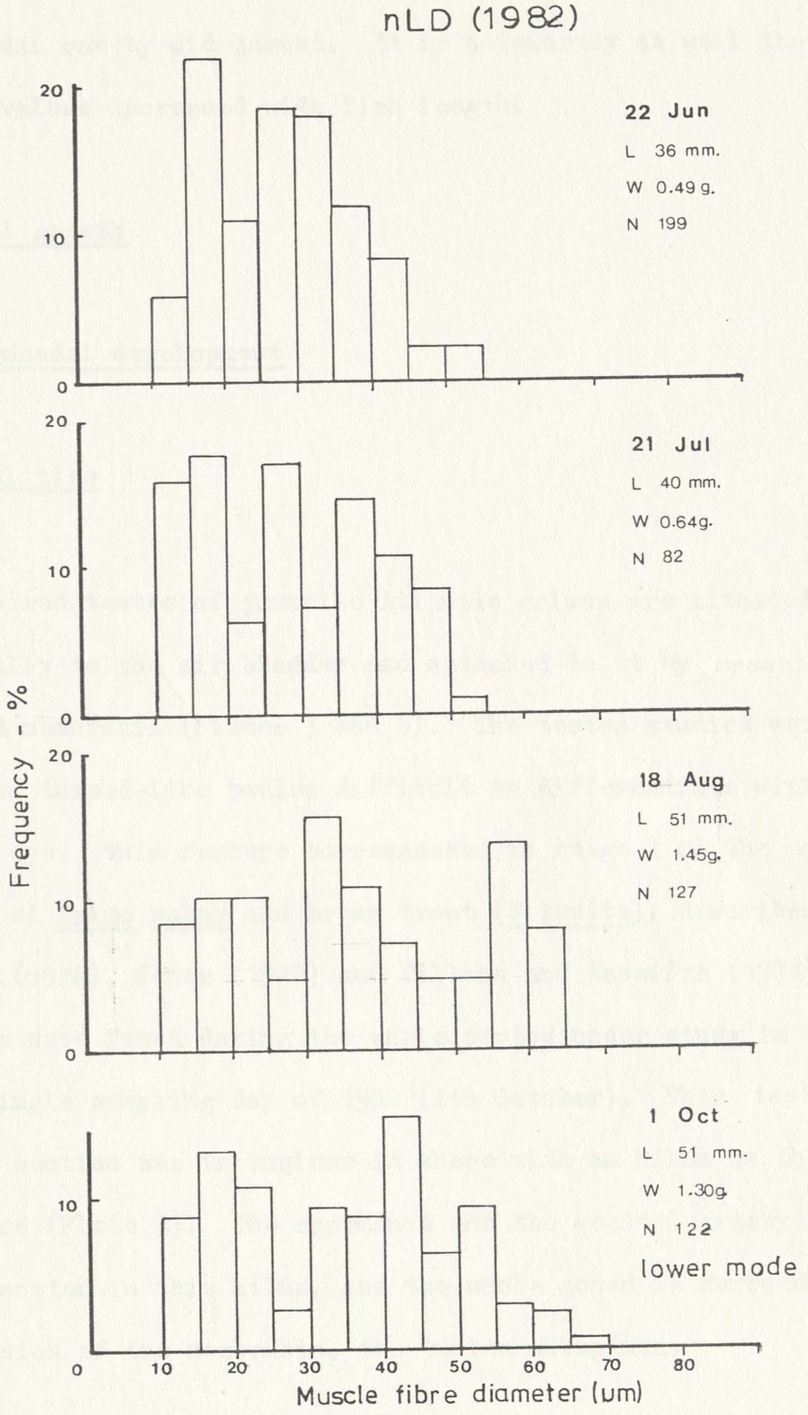

nLD (1981)
15 Oct.
upper mode
N-271
lower mode
N-416
LL (1981)
15 Oct.
upper mode
N-332
lower mode
N-428
10
Frequency - %
0 10 20 30 40 50 60 70 80 90 100
Muscle fibre diameter (µm.)

Figure 58 Changes in white muscle fibre diameter frequency distribution of juvenile salmon reared under natural light (nLD). Experiment II (1982). L, length; W, weight; N, number of fibres.


nLD (1982)
22 Jun
L 36 mm.
W 0.49 g.
N 199
21 Jul
L 40 mm.
W 0.64g.
N 82
18 Aug
L 51 mm.
W 1.45g.
N 127
1 Oct
L 51 mm.
W 1.30g.
N 122
lower mode
Frequency - %
Muscle fibre diameter (um)

polymodal one by mid August. It is noteworthy as well that the modal values increased with fish length.

3.7 Gonadal growth

3.7.1 Male gonadal development

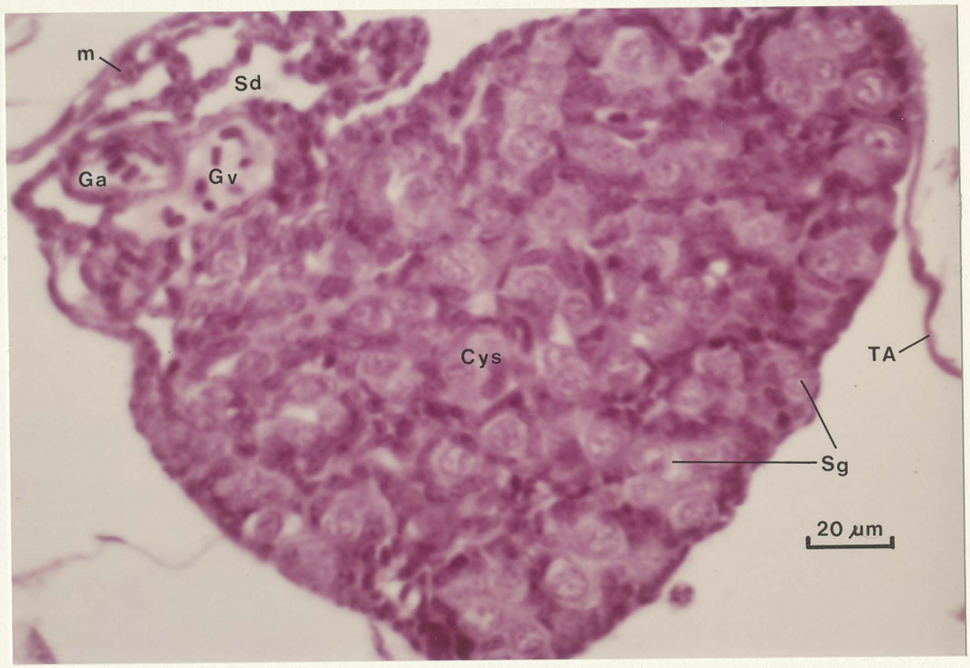
3.7.1.1 Generalities

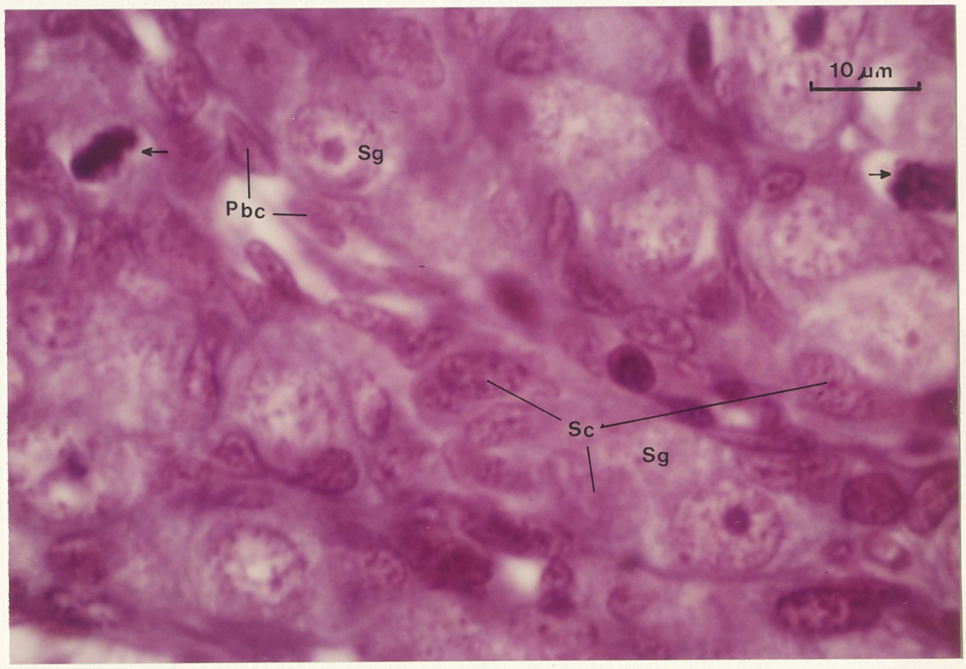
The paired testes of juvenile Atlantic salmon are situated ventro-laterally to the air bladder and attached to it by mesenteries termed mesorchia (Plates 3 and 6). The testes studied were a pair of thread-like bodies difficult to differentiate with the naked eye. This feature corresponded to stage I of the male sexual cycle of Salmo salar and brown trout (S.trutta), described by Orton et al.(1938), Jones (1940) and Billard and Escaffre (1974). Such testes were found during the whole period under study in 1981 and the single sampling day of 1982 (4th October). This testis in cross section was triangluar in shape with an hilus on the lateral surface (Plate 3). The spermduct and the genital artery and vein are located in this hilus, and the whole gonad is surrounded by an extension of the mesorchia, the tunica albuginea.

Atlantic salmon testes have been classified as of the unrestricted spermatogonial type, because their spermatogonia and their associated Sertoli cells, occur along the entire length of tubula (Frier et al 1980 and Grier 1981) (Plate 3).

Plate 3 Transverse section of immature 0+ salmon testis showing cyst (Cys) with 1 - 3 spermatogonia (Sg). Ga, genital artery, Gv, genital vein; m, mesorchium; sd, sperm duct; TA, tunica albuginea (Mayer's haematoxylin and eosin. X500).

Plate 4 Spermatogonia (Sg) cyst of male fish showing mitotic figures (arrows). Pbc, peritubular boundary cell; Sc, Sertoli-like cell. (Mayer's haematoxylin and eosin. X1250).


m
Sd
Ga
Gv
Cys
TA
Sg
20 µm


10 µm
Sg
Pbc
Sc
Sg

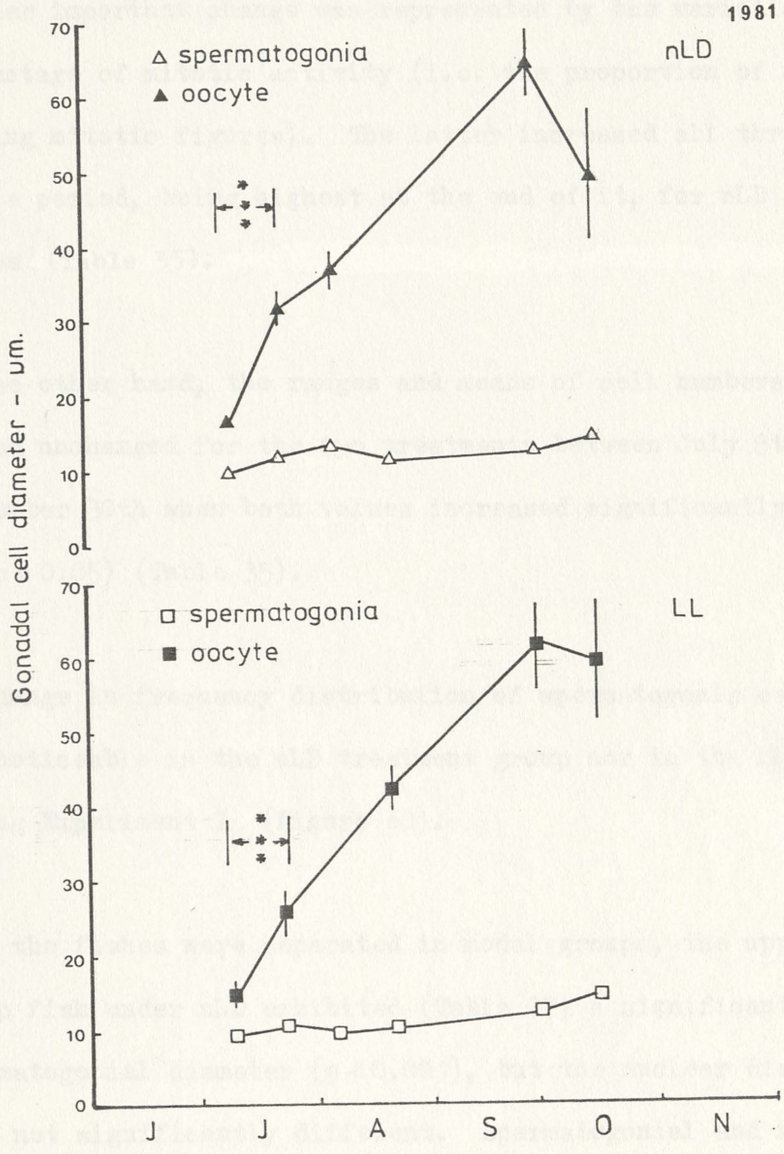
The spermatogonia or germ cells of the fishes examined were large in diameter (9.37 - 14.60 /um), spherical to oval in shape, acidophilic and weakly stainable (+). They had a moderately dense nuleus, 6.62 - 11.96 /um in diameter and a single prominent nucleolus. Mitotic divisions of the germ cells were often observed and recorded (Plate 4 and Tables 33, 34). The germ cells in the gonads were forming nests or cysts of 1 - 3 cells at the beginning of the season 1981, to 1 - 14 cells at the end (Plate 3,4,5 and Table 35). No lumina were present until proliferation of the spermatogonia. The cysts were enclosed by the peritulular boundary cell and Sertoli cells, (which, as they cannot be differentiated easily at this stage, have been recorded here as "Sertoli-like cells"). (Plate 4). No identification of intestical or Leydig cells was possible in these samples.

3.7.1.2 Developmental changes of testes

(a) Experiment I

Although no change was visible at a macroscopic level in the testis, somemodifications were evident by light microscopy during the sampling period of 1981. For example, a significant ($p < 0.005$) increase in cell diameter was determined from 8th July to 15th October, in both nLD and LL treatment fish. Nuclear diameters followed that same trend. (Fig. 59 and Tables 32, 32). The nucleus cytoplasm ratio stayed at a relatively high value of 0.70 indicating an equally fast growth of nucleus and cytoplasm, except for the LL group on October 15th, when the nuclei appeared to have grown

Figure 59 Change in mean spermatogonia and oocyte diameters ($\pm$ 2SE) of the gonads of juvenile salmon subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). *** $p < 0.001$.


1981
△ spermatogonia
▲ oocyte
nLD
□ spermatogonia
■ oocyte
LL
Gonadal cell diameter - um.
0
10
20
30
40
50
60
70
J
J
A
S
O
N

faster (Tables 33 and 34).

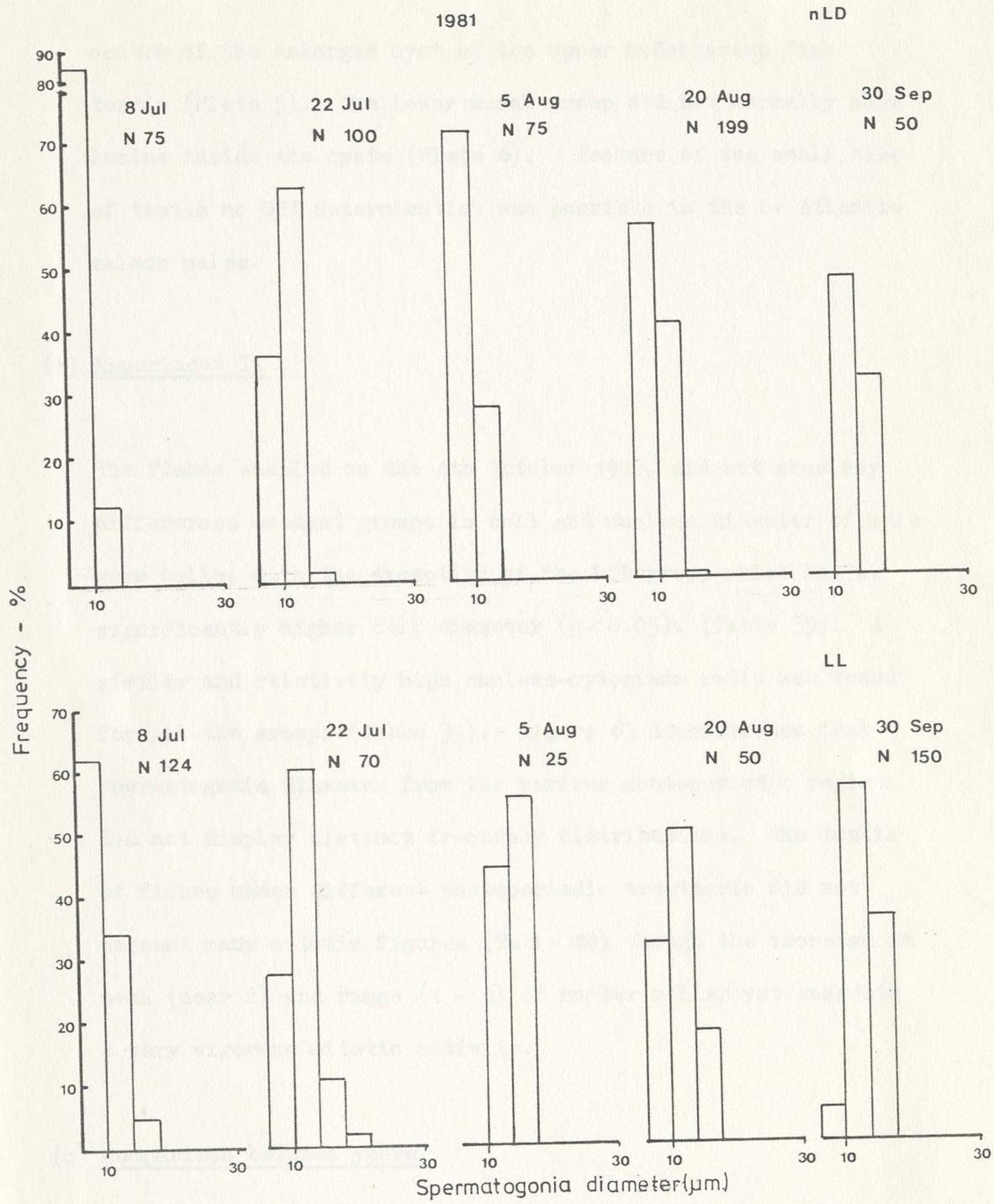
Another important change was represented by the variation in the percentage of mitotic activity (i.e. the proportion of fishes showing mitotic figures). The latter increased all throughout the sample period, being highest at the end of it, for nLD and LL groups (Table 35).

On the other hand, the ranges and means of cell numbers per cyst stayed unchanged for the two treatments between July 8th and September 30th when both values increased significantly (nLD and LL, $p < 0.05$) (Table 35).

No change in frequency distribution of spermatogonia cell diameter was noticeable in the nLD treatment group nor in the LL one, during Experiment I (Figure 60).

When the fishes were separated in modal groups, the upper modal group fish under nLD exhibited (Table 37) a significantly higher spermatogonial diameter ($p < 0.001$), but the nuclear diameters were not significantly different. Spermatogonial and nuclear diameters of the upper modal group of LL fish were not significantly different from those of the lower. Both treatment groups revealed an active proliferation of cells within the cyst, specially obvious in the upper modal group which have a significantly elevated mean no. of cells/cyst (nLD, $p < 0.01$; LL, $p < 0.05$).
Another important peculiarity was the appearance of a lumen in the

Figure 60 Spermatogonia diameter frequency distribution of juvenile salmon reared under natural photoperiod (nLD) or constant light (LL). Experiment I (1981). N, number of spermatogonia.


1981
nLD
8 Jul
N 75
22 Jul
N 100
5 Aug
N 75
20 Aug
N 199
30 Sep
N 50
LL
8 Jul
N 124
22 Jul
N 70
5 Aug
N 25
20 Aug
N 50
30 Sep
N 150
Frequency - %
Spermatogonia diameter(µm.)

centre of the enlarged cyst of the upper modal group fish testis (Plate 5). The lower modal group did not normally show lumina inside the cysts (Plate 6). Because of the small size of testis no GSI determination was possible in the 0+ Atlantic salmon males.

(b) Experiment II

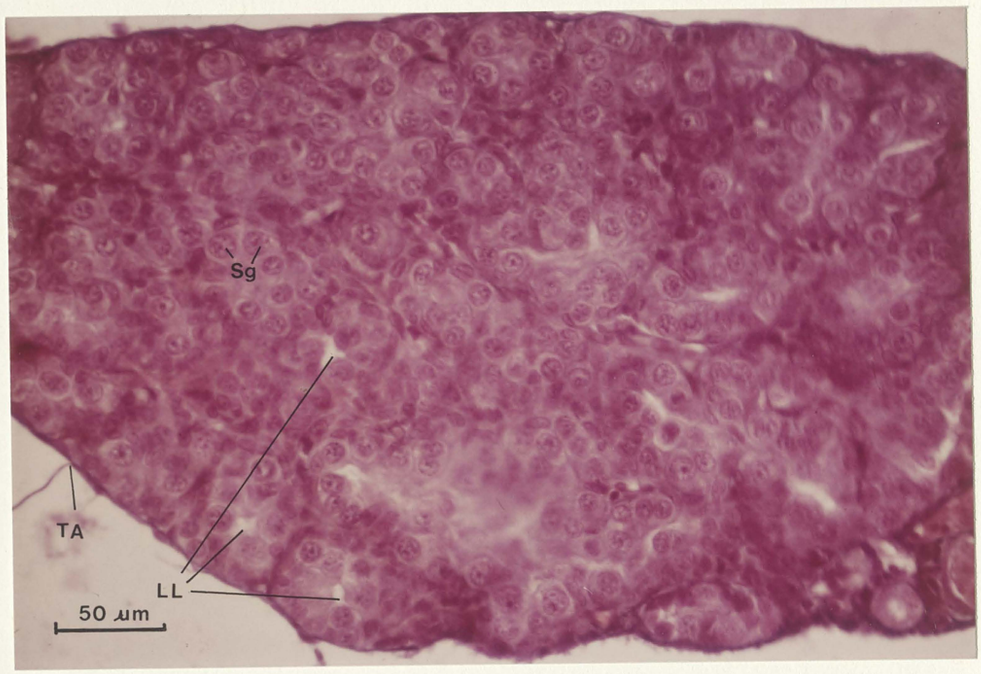
The fishes sampled on the 4th October 1982, did not show any differences amongst groups in cell and nucleus diameter of male germ cells, with the exception of the L6D group which had a significantly higher cell diameter ($p < 0.05$). (Table 39). A similar and relatively high nucleus-cytoplasm ratio was found for all the groups (Table 39). Figure 63 demonstrates that spermatogonia diameter from the various photoperiodic regimes did not display distinct frequency distributions. The testis of fishes under different photoperiodic treatments did not present many mitotic figures (Table 40) though the increase in mean (near 2) and range (1 - 6) of number cells/cyst suggests a very vigorous mitotic activity.

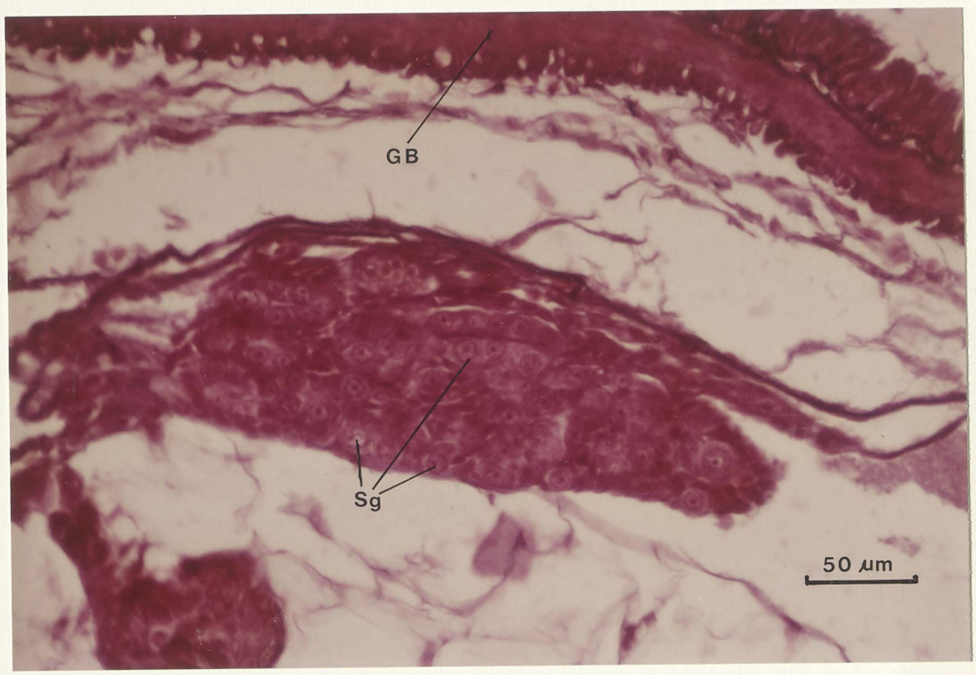
(c) Comparison between years

Cell and nucleus diameter of spermatogonia of fishes under nLD photoperiod, for the days 30th September 1981 (Experiment I), and 4th October 1982 (Experiment II) did not differ. (Table 41). Nor was there any difference in the frequency distributions of spermatogonia diameter between these days or treatments. (see Figures 60 and 63).

Plate 5 Testis of an upper modal group fish showing lumina (LL) in the centre of the enlarged spermatogonia (Sg) cysts. TA, tunica albuginea. (Mayer's haematoxylin and eosin. X250).

Plate 6 Testis of a lower modal group fish showing small spermatogonia (Sg) cyst with no lumina. GB, gas bladder. (Mayer's haematoxylin and eosin. X250).


Sg
TA
LL
50 µm


GB
Sg
50 µm

3.7.2 Female gonadal development

3.7.2.1 Generalities

The ovaries were represented, in the fishes examined by a long body located ventrally to the air bladder and attached to it by mesenteries termed mesovaria. These are continuous with the peritoneal covering of the ovarian wall or tunica albuginea. The ovaries were widest at their anterior end occupying a quarter or less of the length of the body cavity, and of a pale yellowish colour.

(b) Histological sections demonstrated that between June and October 1981 they were in the primary growth phase. This phase includes the chromatin nucleolus stage, and the early and late perinucleolar stages, but only the first two were present in female juvenile Atlantic salmon examined during this period.

(a) Chromatin nucleolus stage

The youngest oocytes are found arranged in nests or cysts embedded in follicular tissue. They had a mean diameter of 11.42 /um with a range from 8.00 - 14.00 /um. During this stage the oocyte nucleus passes through a series of changes beginning with a nucleolus connected with chromatin thread normally localised at one side of the nucleus (zygotene stage of meiosis)

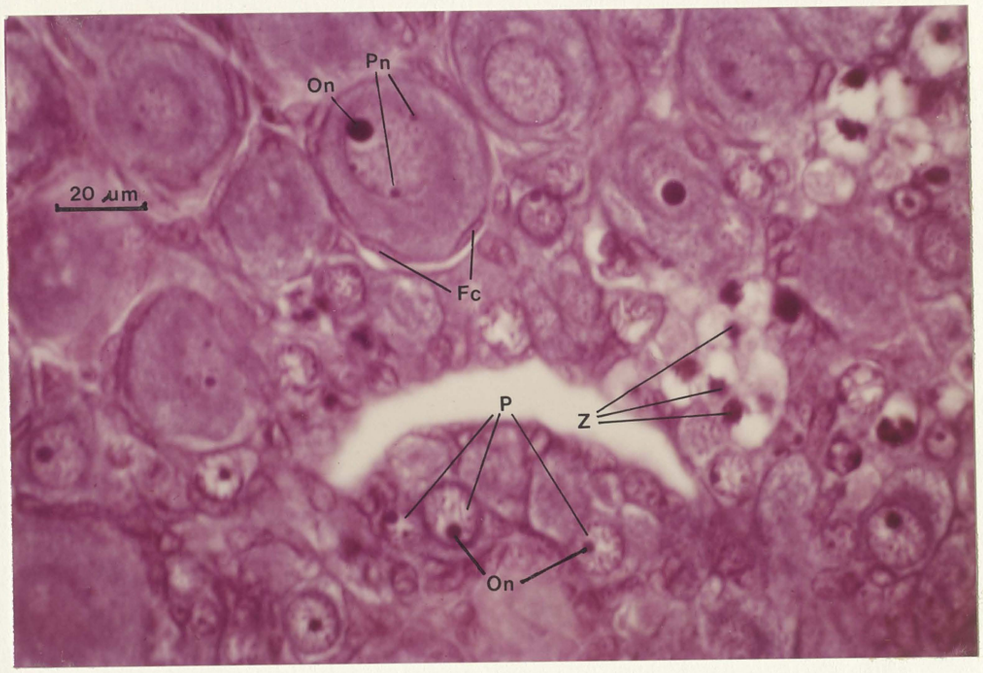
(Plate 7). As the oocytes enlarge complicated forms of the nucleolus began to appear (Plate 8). This deeply staining structure became triangular (crescent) in shape attached to the nuclear membrane by its base, and finally it became thin and disappeared from sight along with the growth of the oocyte. Subsequently the chromatin emerged ordered in a U-shape with its arms towards the nuclear membrane (pachytene stage of meiosis), and the nucleolus, took on a spherical form and increased in diameter (Plate 7). Accompanying this nuclear change the oocytes separated themselves from the cysts and became surrounded by follicule cells.

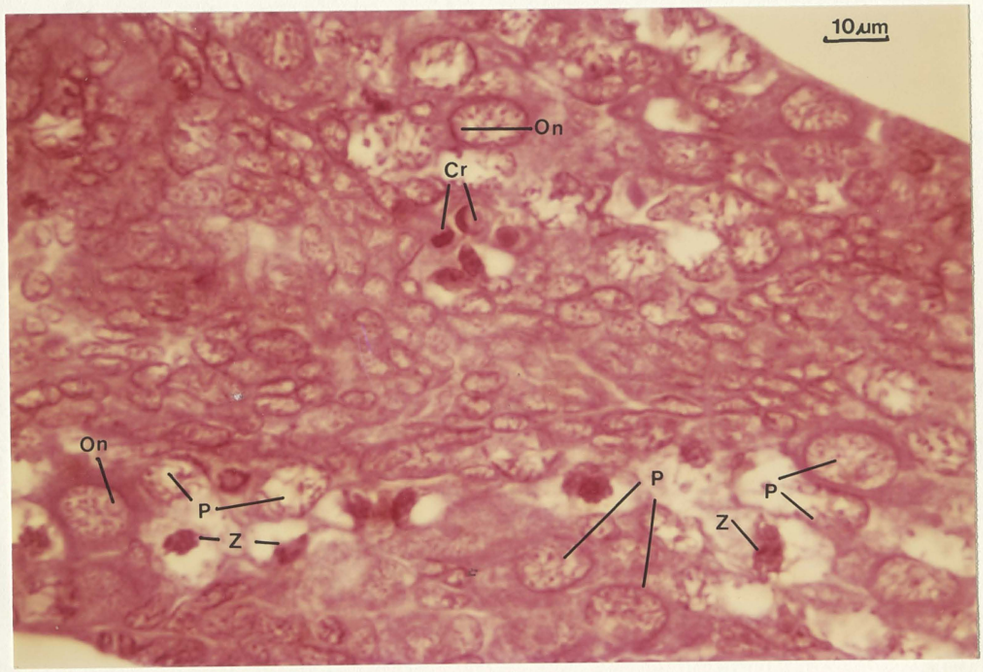
(b) Early perinucleolar stage

The most important aspects of this stage were the increase in nuclear and cytoplasmic diameters, the emergence of multiple nucleoli towards the nuclear membrane ("perinucleolar stage"), and the increment in cytoplasm haemotoxylin affinity (Plates 7 and 9). Simultaneously the chromatin became diffusely distributed all over the nuclear cavity (strepsilene stage of meiosis). During this phase the oocytes accumulated extensive aggregations of basophilic material in the perinuclear cytoplasm, the yolk nuclei (Plates 9 and 10). The oocyte diameters during this stage ranged from 14.26 - 64.47 µm (Tables 33 and 34).

Plate 7 Ovary of immature female salmon during primary growth phase, showing oocyte cysts in chromatin nucleolus stage. Fc. folicular cell; On, original nucleus; P, pachytene nucleus; Pn, provitelline nucleolus; Z, zygotene nucleus. (Mayer's haematoxylin. X500).

Plate 8 Ovary of immature female salmon during primary growth phase showing oocyte cysts in chromatin nucleolus stage. Cr, crescent nucleolus; On, original nucleolus; P, pachylene nucleus; Z, zygotene nucleus. (Mayer's haematoxylin. X600).


On
Pn
20 µm
Fc
P
Z
On


10µm
On
Cr
On
P
Z
P
Z
P

3.7.2.2 Ovarian developmental changes

(a) Experiment I

The most obvious change observed in juvenile Atlantic salmon ovaries between July and October 1981 was the significant increase ($p < 0.001$) in mean oocyte diameter; from 16.49 - 49.25 /um for the nLD group, and from 14.26 - 59.45 /um for the LL group (Figure 59 and Tables 33, 34). The frequency distributions of oocyte diameters for both photoperiodic treatments showed similar steady broadening during the same period (Figures 61 and 62). The oocyte nuclei of nLD and LL group fish also demonstrated a considerable increase of diameters, ranging from 9.16 - 31.75 /um and from 10.67 - 27.76 /um respectively.

The nucleus-cytoplasm ratio declined from a value at about 0.65 to 0.53, suggesting that the oocyte growth is mainly due to cytoplasm increase. There were no differences in this index between treatments (Tables 33 and 34).

No mitotic figures were observed in the ovaries of fishes in either of the treatment groups of Experiment I. The distinctive accumulation of basophilic material in the cytoplasm or yolk nucleus, started to emerge in the female fish by the 22nd July (Plate 9) reaching its highest expression at the end of 1981 experiment (Plate 10). Another noticeable alteration of the

Figure 61 Oocyte diameter frequency distribution of juvenile salmon reared under natural photoperiod (nLD). Experiment I (1981). N, number of oocytes.

nLD(1981)

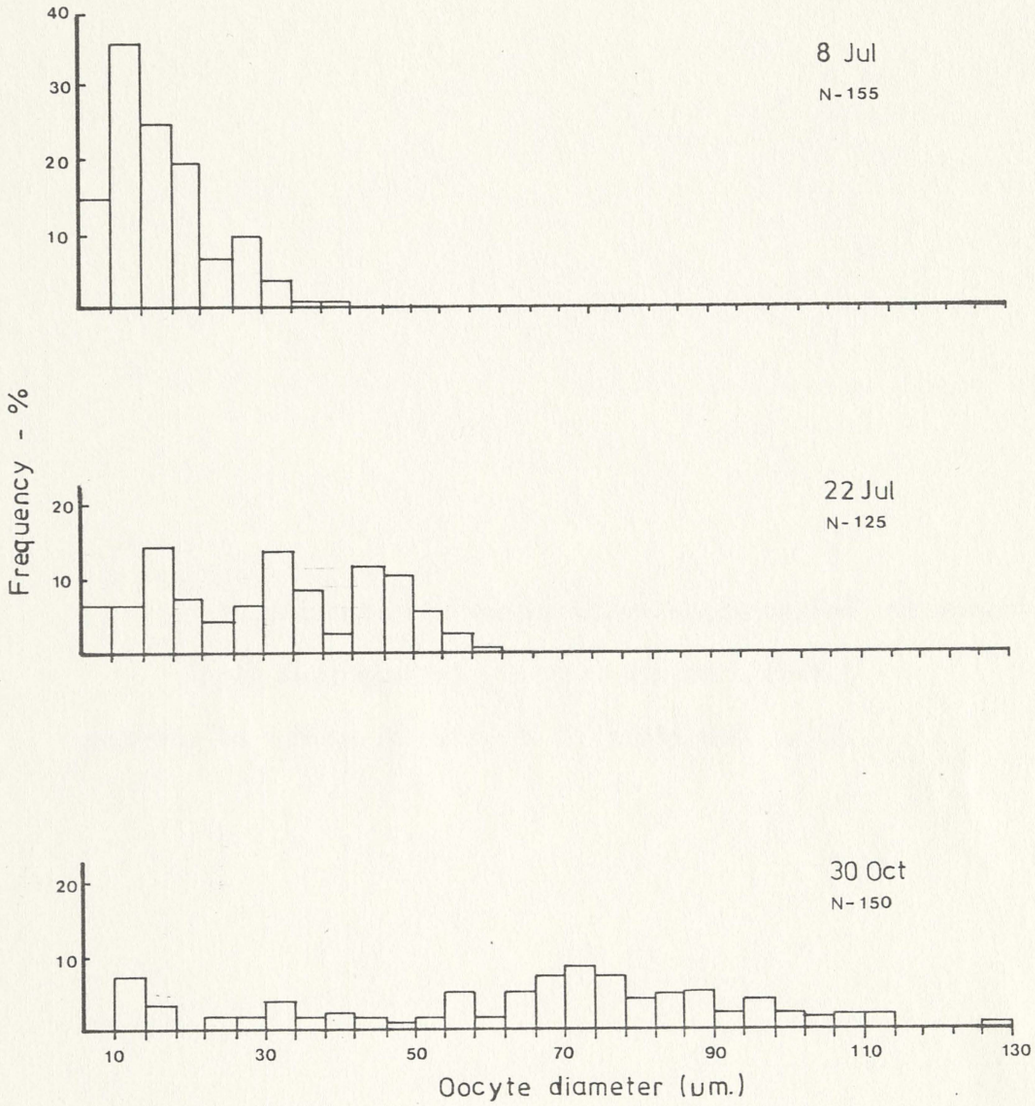

8 Jul
N-155
22 Jul
N-125
30 Oct
N-150
Frequency - %
40
30
20
10
20
10
20
10
10
30
50
70
90
110
130
Oocyte diameter (um.)

Figure 62 Oocyte diameter frequency distribution of juvenile salmon reared under constant light (LL). Experiment I (1981). N, number of oocytes.

LL (1981)

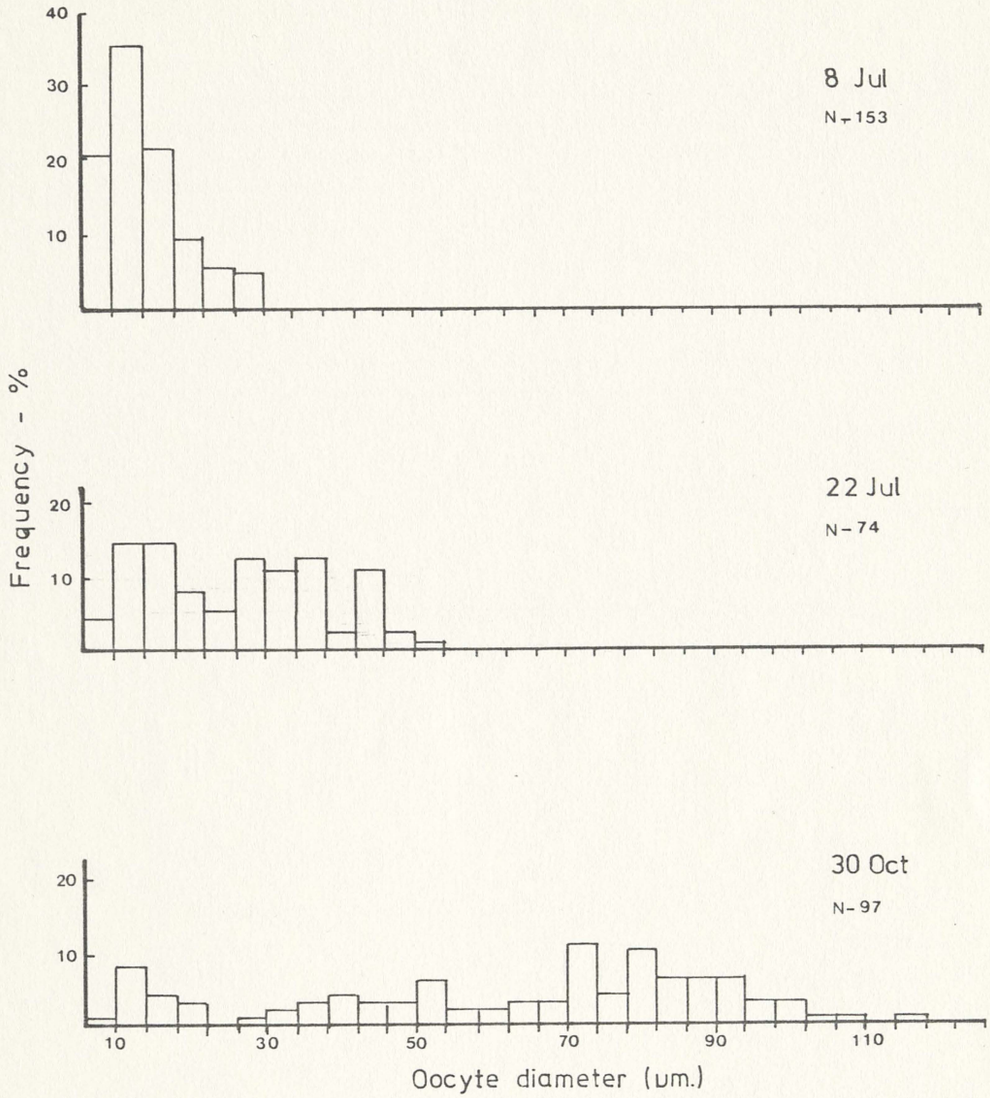

40
30
20
10
8 Jul
N=153
Frequency - %
20
10
22 Jul
N=74
20
10
30 Oct
N=97
10
30
50
70
90
110
Oocyte diameter (µm.)

Figure 63 Spermatogonia diameter frequency distribution of six sibling populations of juvenile salmon subjected to different photoperioduc regimes. Experiment II (1982). N, number of spermatogonia.

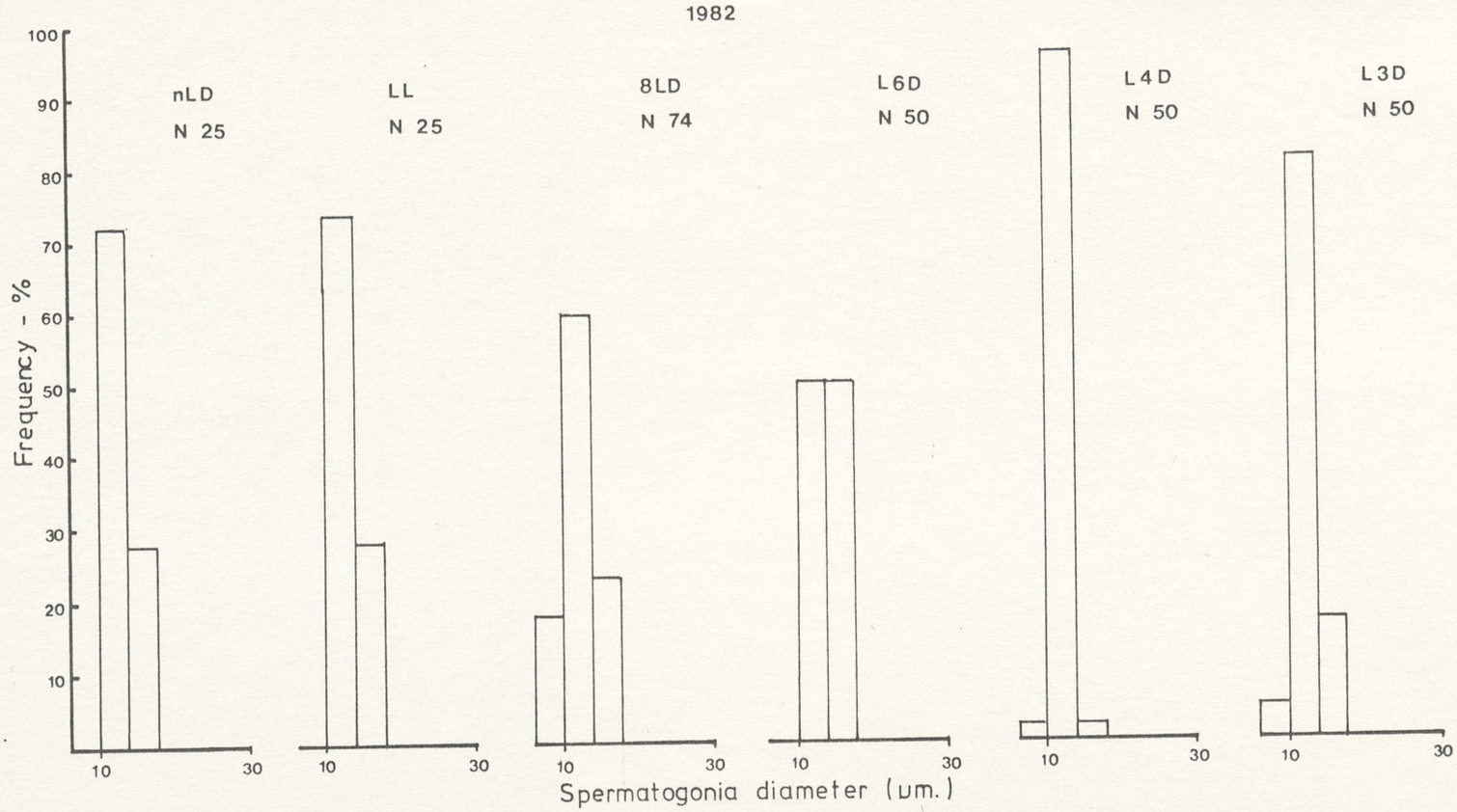
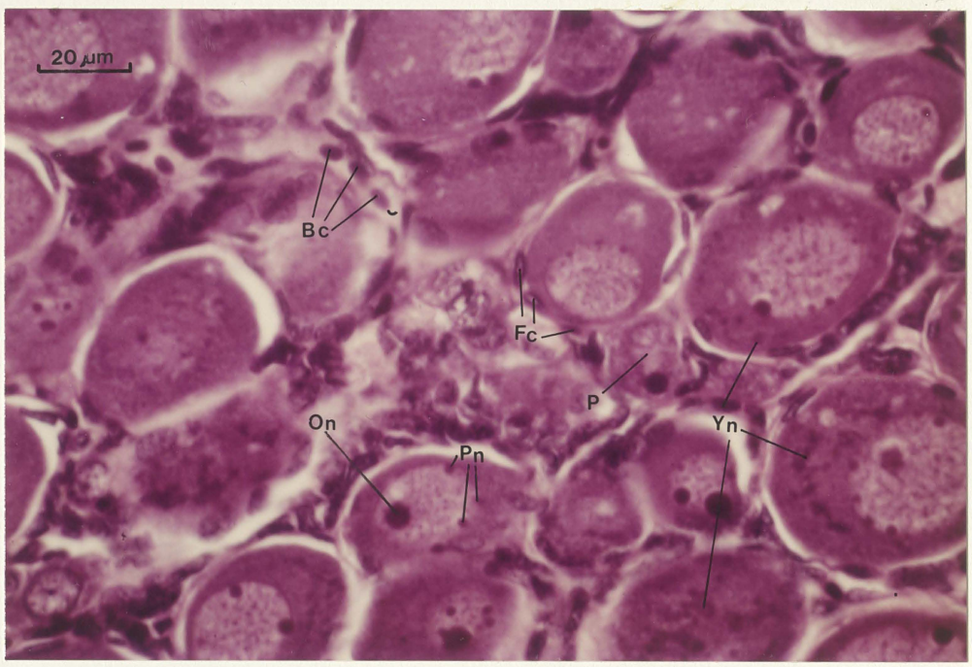
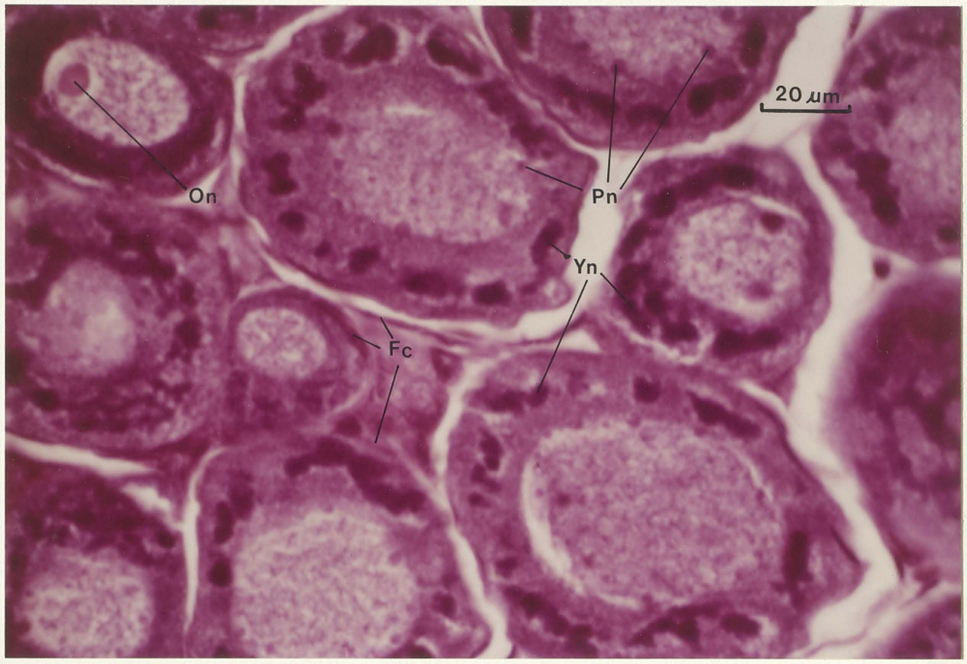

1982
nLD
N 25
LL
N 25
8LD
N 74
L6D
N 50
L4D
N 50
L3D
N 50
Frequency - %
100
90
80
70
60
50
40
30
20
10
10
30
Spermatogonia diameter (µm.)

Plate 9 Ovary of immature female salmon with oocytes in early perinucleolar stage. Bc, blood cell; Fe, follicular cell; On, original nucleolus; P, pachytene nucleus; Pn, provitelline nucleolus; Yn, yolk nucleus. (Mayer's haematoxylin and eosin. X500).

Plate 10 Ovary of immature female salmon with oocytes in early perinuleolar stage, but more advanced than in Plate 9. Fc, follicular cell; On, original nucleolus; Pn, Provitelline nucleolus; Yn, yolk nucleus. (Mayer's haematoxylin and eosin. X500).


20 µm
Bc
Fc
P
On
Pn
Yn


20 µm
On
Pn
Yn
Fc

cytoplasm was represented by an enhancement in its affinity for haematoxylin, being weak (+) or moderate (++) at the beginning of the observation period to very intense (+++) at the end. The percentage of oocytes of nLD fish showing weak or moderate haematoxylin affinity was large, with values of 65.79% and 34.21% respectively by the 8th July, and very low by the 15th October (26.26% and 4.04% respectively)(Table 32). On the other hand, the oocytes presenting intense (+++) affinity increased throughout the same period from 0 - 69.70% for the same treatment group (Table 32). Similarly the LL group showed higher weak and moderate affinity (40.63 and 57.81% respectively) at the beginning and lower at the end (15.75 and 0% respectively). In the same way, the percentage of cells showing intense affinity at the start was low (1.56%) and high (84.25%) at the end (Table 32).

The oocyte nucleus characteristically, possessed a large nucleolus (original nucleolus) with a mean diameter ranging from 3.02 - 5.06 µm, which persisted throughout the observation period (see Plates 7,9,10 and Tables 33,34) in both treatments. At the same time, the small nucleoli, located near the nuclear membrane (provitelline nucleoli), increased considerably in number, for both day-length regimes (Plates 9 and 10). For the nLD group the mean number of provitelline nucleoli per nucleus changed from 4.26 - 13.86 (ranging from 1 - 25), and from 4.30 - 16.85 (ranging from 1 - 39) for LL group (Table 36).

When the data of the sample of the 15th October for the two treatments, were segregated in modal groups, the oocyte and

nucleus diameters did not differ between these, and nor did the ranges and mean number cells/cyst. The ovaries of fishes sacrificed on the 4th February 1982 were large enough to permit calculation of a gonadosomatic index (GSI). This GSI tended to decrease as fork length increased (Fig.65), a significant negative regression described this relationship ($p < 0.001$).

The mean GSI for the nLD group was significantly larger than that of the LL group ($p < 0.001$) (Table 42). There were no differences in sex ratio between treatments nor did they differ from 1:1.

(b) Experiment II

On 4th October 1982, the oocytes showed the characteristics of the primary growth phase. The bulk of them were in the early perinucleolar stage though some were in the chromatin nucleolus stage. The different treatment groups showed a high percentage of oocytes with intense (+++) haematoxylin affinity, ranging from 80 - 91.75% (Table 38). The cell and nucleus diameters of the oocytes of the nLD group were significantly larger ($p < 0.05$) than in any of the other groups, which did not differ among themselves (Table 39). It is noteworthy, as well, that the original nucleolus, inside the nucleus has the same diameter for the various treatments. The nucleus-cytoplasm ratio, also did not differ between photoperiodic regimes, and the range and mean number cells/cyst of oocytes was equal for all treatments (Table 40). In the same way no noticeable differences existed amongst treatments in the frequency distribution of oocyte diameter (Figure 64).

Figure 64 Oocyte diameter frequency distribution of six sibling populations of juvenile salmon subjected to different photoperiodic regimes. Experiment II (1982). N, number of oocytes.

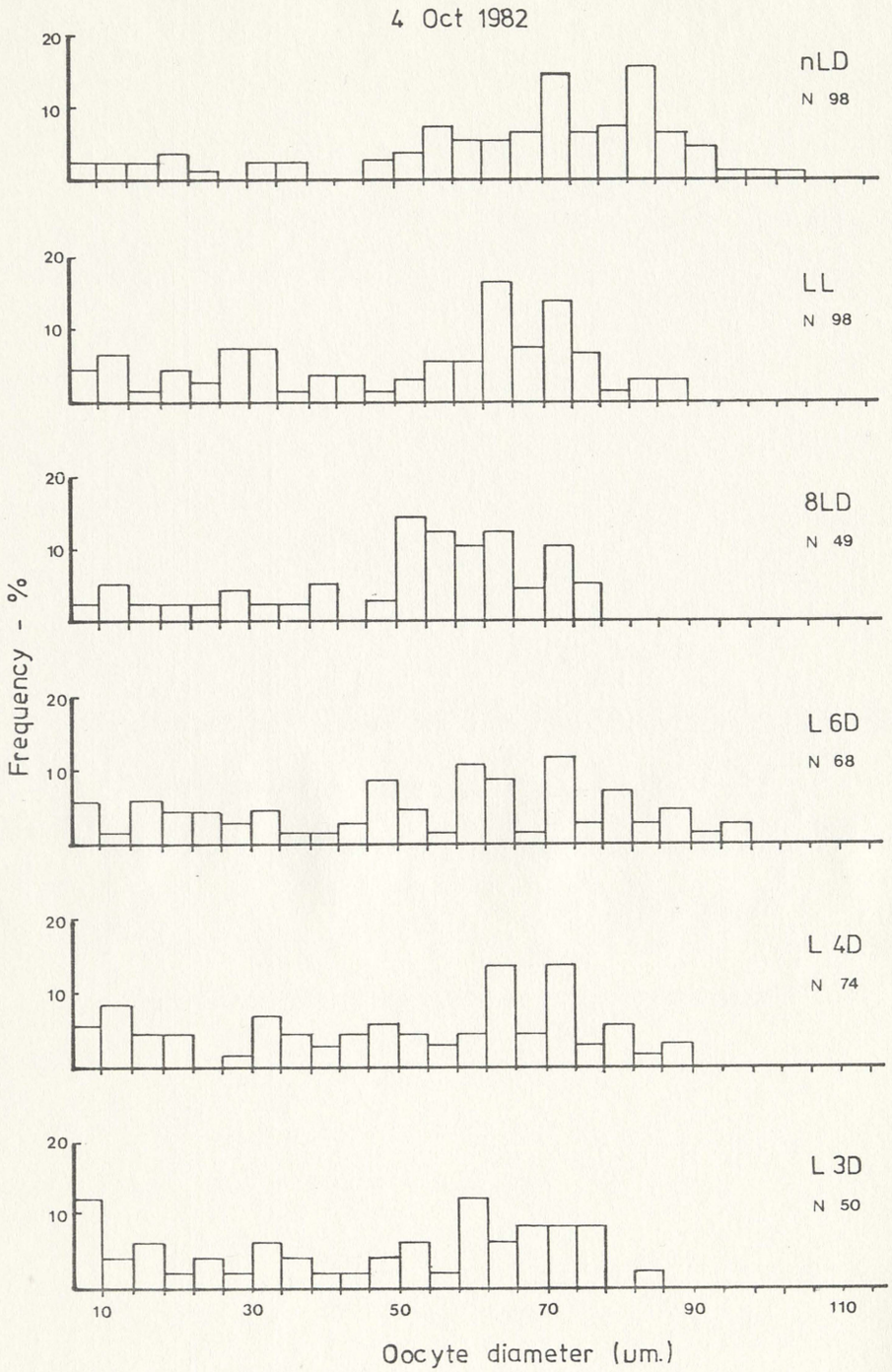
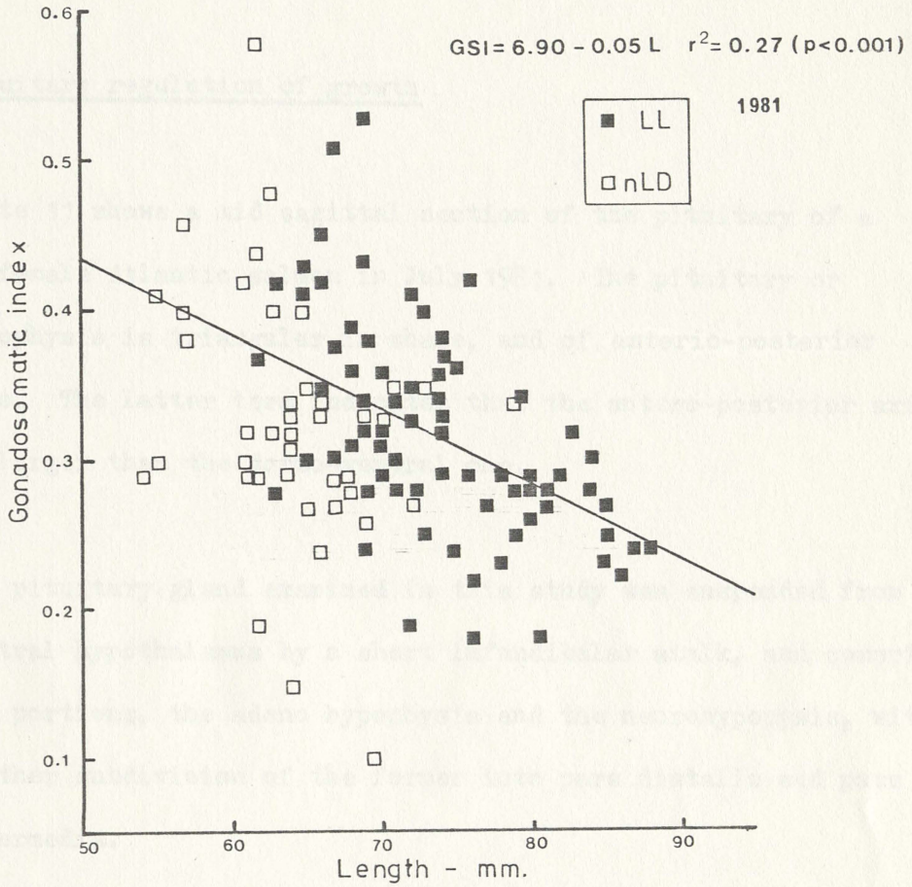

4 Oct 1982
nLD
N 98
LL
N 98
8LD
N 49
L 6D
N 68
L 4D
N 74
L 3D
N 50
Frequency - %
20
10
10
30
50
70
90
110
Oocyte diameter (um.)

Figure 65 Relationship between gonadosomatic index and the length of female juvenile salmon reared under natural photoperiod (nLD) and constant light (LL).


GSI = 6.90 - 0.05 L r² = 0.27 (p<0.001)
1981
LL
nLD
Gonadosomatic index
0.6
0.5
0.4
0.3
0.2
0.1
50
60
70
80
90
Length - mm.

Cell and nucleus diameters of oocytes of nLD fish on 30th September 1981 and 4th October 1982, did not differ either (Table 41).

3.8 Pituitary regulation of growth

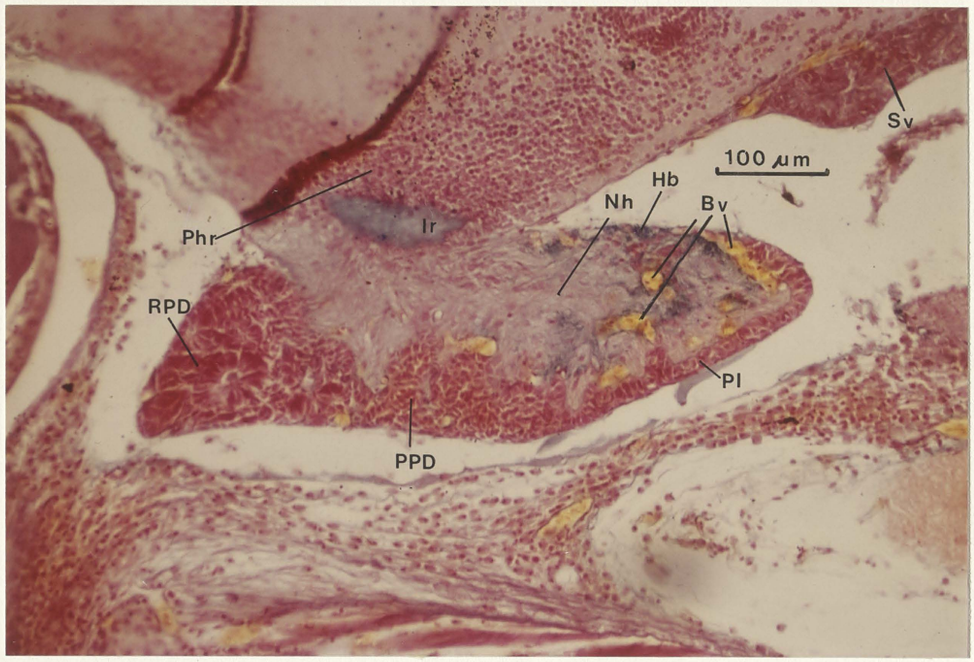
Plate 11 shows a mid sagittal section of the pituitary of a 0+ female Atlantic salmon in July 1981. The pituitary or hypophysis is triangular in shape, and of anterio-posterior type. The latter term indicates that the antero-posterior axis is larger than the dorso-ventral one.

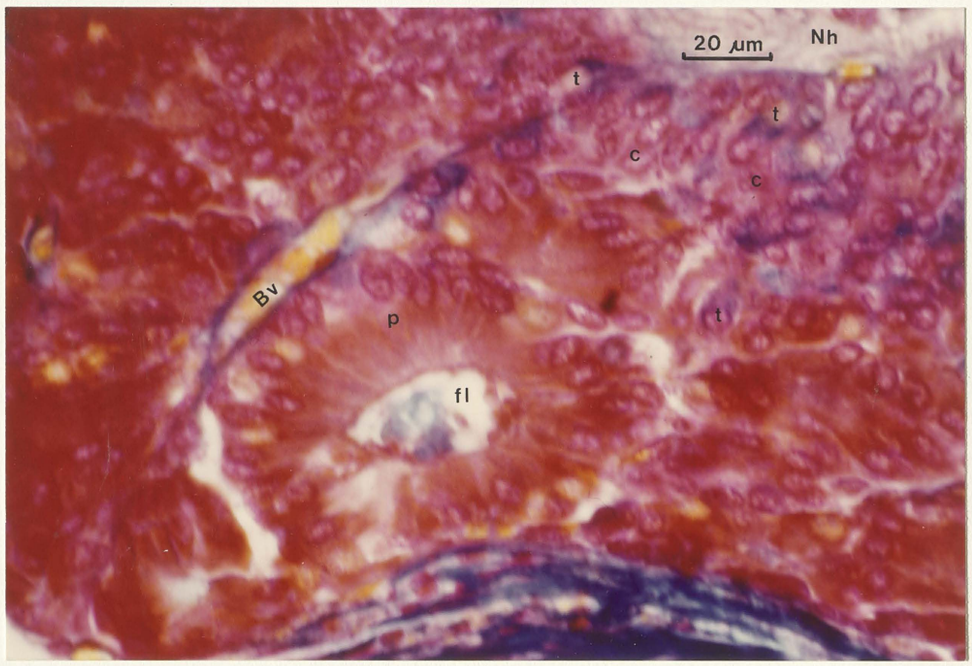
The pituitary gland examined in this study was suspended from the central hypothalamus by a short infundibular stalk, and comprised two portions, the adeno hypophysis and the neurohypopysis, with a further subdivision of the former into pars distalis and pars intermedia.

The neurohypophysis constituted the neural element of the gland and occupied the dorsal half of the posterior gland, though its branches can be found penetrating into each lobe (Plate 11 and 13). In Plate 11 it is easy to note that according to its staining properties the neurohypophysis can be divided into two regions, the anterior and posterior neural lobes. Although no definite boundary existed between the two regions, the posterior neurohypophysis possessed neurosecretory material (herring bodies) which stained heavily with Alcian blue with the Jafri's staining.

Plate 11 Sagittal section of juvenile salmon, showing its different cellular regions: rostral pars distalis (RPD), proximal pars distalis (PPD), pars intermedia (PI) and neurohypophysis (Nh). Bv, blood vessels; Hb, herring bodies; Ir, infundibular recess; Phr, periventricular hypothalamic region; Sv, succus vasculosus. (Jafri's staining, X125).

Plate 12 Sagittal section of the rostral pars distalis of the juvenile salmon pituitary showing a prolactin cell follicle. Bv, blood vessel; c, chromophobes cells; fl, follicular lumen; Nh, neurohypophysis; p, prolactin cell; t, thyrotropes (Aliz-BT, X500).


Sv
100 µm
Hb
Nh
Bv
Ir
Phr
RPD
Pl
PPD


20 µm
Nh
t
t
c
c
Bv
p
t
fl

The pars distalis of the adenohypophysis comprised two regions, the anterior or rostral pars distalis (RPD), and the posterior or proximal pars distalis (PPD) (Plate 11).

The RPD occupied the anterior portion of the gland and contained three hormone secreting cells, thyrotropes, corticotropes, and lactotropes, the latter in a typical follicular arrangement. The PPD was in the central region of the gland and contained two populations of hormone secreting cells, somatotropes and gonadotropes.

The pars intermedia occupied the ventro-posterior portion of the adenophyophysis, formed by cells arranged as a columnar monolayer which surrounded the neural lobe of the neurohypophysis (Plate 11). These cells secrete melanocyte stimulating hormone (MSH).

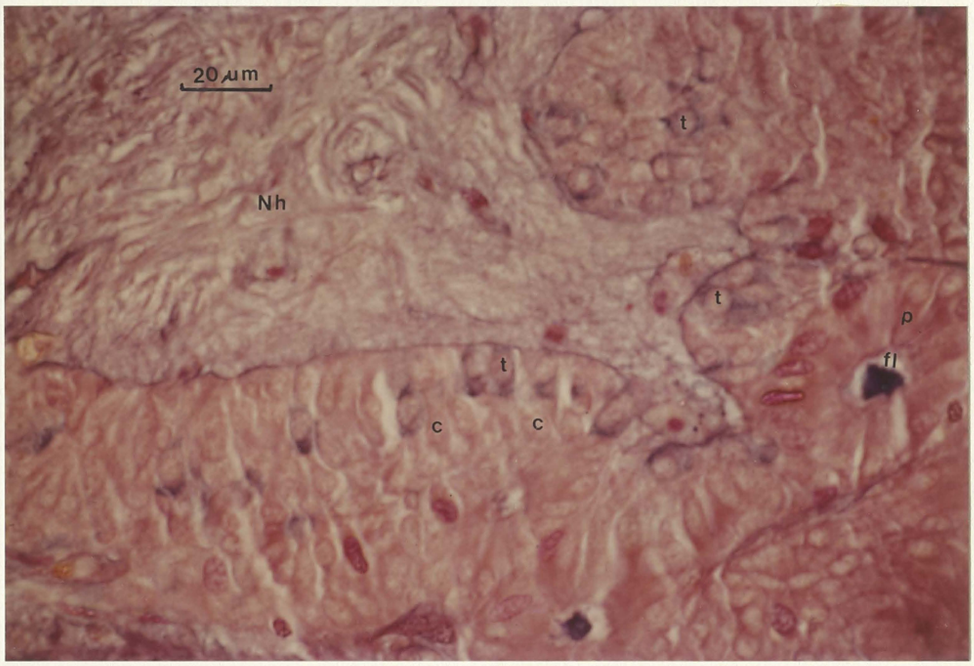
3.8.1 Pituitary cytology

(a) Lactotropes (LTH cells)

In the fishes investigated in the present study, these cells occupied the major part of the RPD (Plate 11). They were arranged with cells of columnar shape surrounding a follicular lumen. The follicular lumen usually contained a colloidal material which stained with PAS, Aniline blue, and Alcian blue (Plate 12 and 13). The LTH cell nucleus was located towards the base of the cell. Its secretory material stained red with acid fuchsin (Jafri's stain,

Plate 13 Sagittal section of the RPD and PPD of juvenile salmon pituitary. c, chromophobes cells; fl, follicular lumen; Nh, neurohypophysis; p, prolactin cell; t, thyrotropes. (Jafri's staining, X500).

Plate 14 Sagittal section of PPD of juvenile salmon pituitary, showing an accumulation of somatotropes (S). Bv, blood vessels; c, chromophobes cells; Nh, neurohypophysis; t, thyrotropes (Aliz-BT, X500).


20 µm
Nh
t
t
p
fl
t
c
c

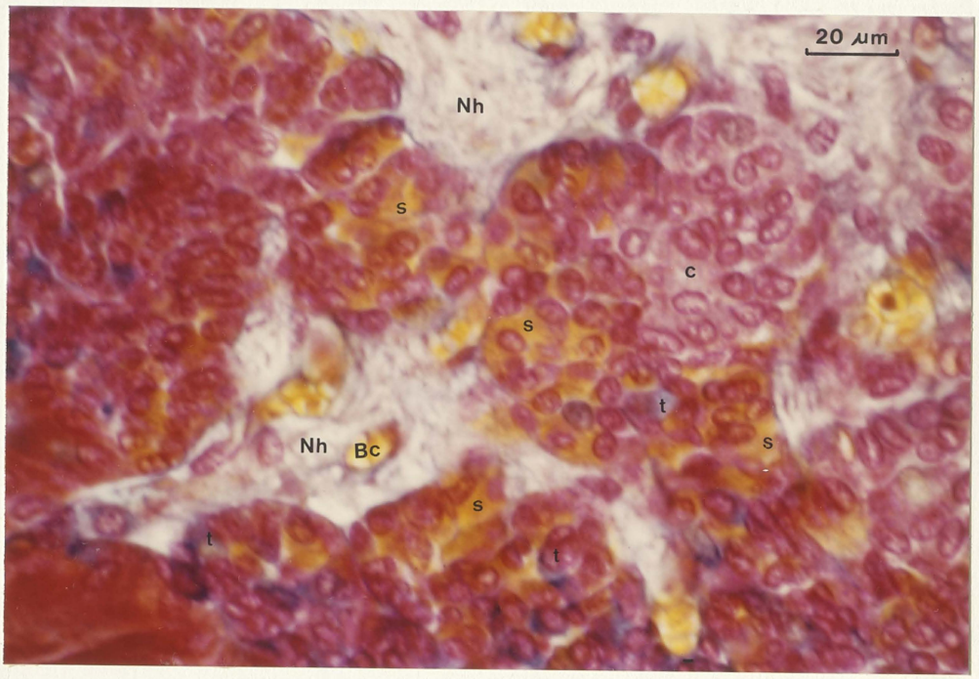

20 µm
Nh
s
c
s
t
Nh
Bc
s
s
t
t

Plate 11) and erythrosin (Aliz-BT, Plate 12), or yellow with orange G (PAS - OG stain). This cell had the largest size within the pituitary with a diameter range from 11.40 - 13.26 /um, and with a nucleus diameter from 5.96 - 6.79 /um (Tables 43 - 44).

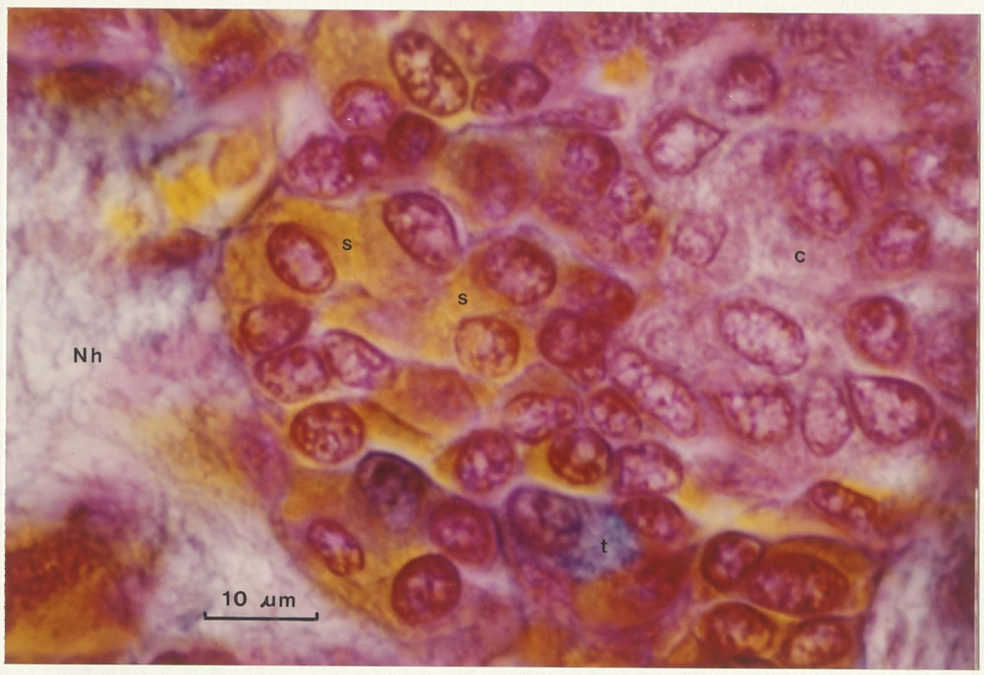
(b) Thyrotropes (TSH cells)

The thyrotropes consituted one of the two populations of basophilic (mucoid) cells found in the Atlantic salmon pituitary. Both stained similarly, but in salmonids they show a marked topographical separation. For the purpose of the present study only those basophilic cells localised at the dorsal portion of RPD were recorded as TSH cells (Ball and Baker, 1969; Holmes and Ball, 1974). These latter were small, polygonal or round in shape and although normally localised in the dorsal RPD they could be infiltrated between LTH cell follicules (Plate 12). Their inclusions stained blue with Aniline blue (Aliz-BT stain), and Alcian blue (Jafri's staining) and pink with PAS (PAS - OG stained) (Plates 12, 13 and 14). The TSH cell diameters ranged from 8.67 - 10.18 /um and the nucleus from 5.92 - 6.94 /um (Tables 43 and 44).

(c) Somatotropes (GH cells)

Somatotropes occupied the major part of PPD of the 0+ Salmo salar. They are characteristically acidophilic (serous) cells, but could be distinguished from the other acidophilic cells, because they stained selectively with Orange G, whereas the latter stained with erythosin of the Aliz-BT technique. (Plates 14 and 15). The cells

Plate 15 Enlargement from the right-centre of plate 14 showing details of somatotropes (s) and thyrotropes (t). Nh, neurohypophysis.


s
s
c
Nh
t
10 µm

were round, elongated or angular and measured from 8.30 - 9.24 /um in diameter whereas their nuclei had diameters ranging from 5.45 - 6.28 /um (Plate 14 and 15; Tables 43 and 44).

(d) Gonadotropes (GtH cells)

In O+ Atlantic salmon the gonadotropes normally lay in the PPD, generally in the ventral and lateral regions. For reasons indicated elsewhere (section 3.8.1 (b)), GtH cells were defined as all those basophilic cells localised at the ventral portion of the PPD (Plate 17). They were typically basophilic, with secretory granules that stained strongly with PAS, Aniline blue (Aliz-BT stain) and Alcian blue (Jafri's stain). They were the smallest cells of the pituitary with cell and nucleus diameters ranging from 7.57 - 8.31 /um, and from 5.45 - 6.06 /um respectively (Tables 43 and 44).

(e) Chromophobe cells (ACTH cells)

These cells stained faintly or not at all, and hence their name. However, in the Atlantic salmon pituitary, they stained purple with Aliz-BT technique (Plate 12, 14 and 15). They were arranged in 3 - 4 layer sheets at the dorsal portion of the RPD (Plate 12 and 13). Chromophobe cells were usually elongated with their long axis perpendicular to the adeno-neurohypophysial interface (Plate 13). No cytological measurements were taken from these cell types.

3.8.2 Pituitary cell changes during growth

Changes in diameter of pituitary cells and nuclei were recorded between the 8th and 22nd July 1981, when dramatic variations in nucleic acid content were observed (Figures 26,27 and 35). Additional measurements were made on the 30th September of the same year, just before the length frequency distributions became clearly bimodal. For Experiment II, measurements were made on the 4th October 1982.

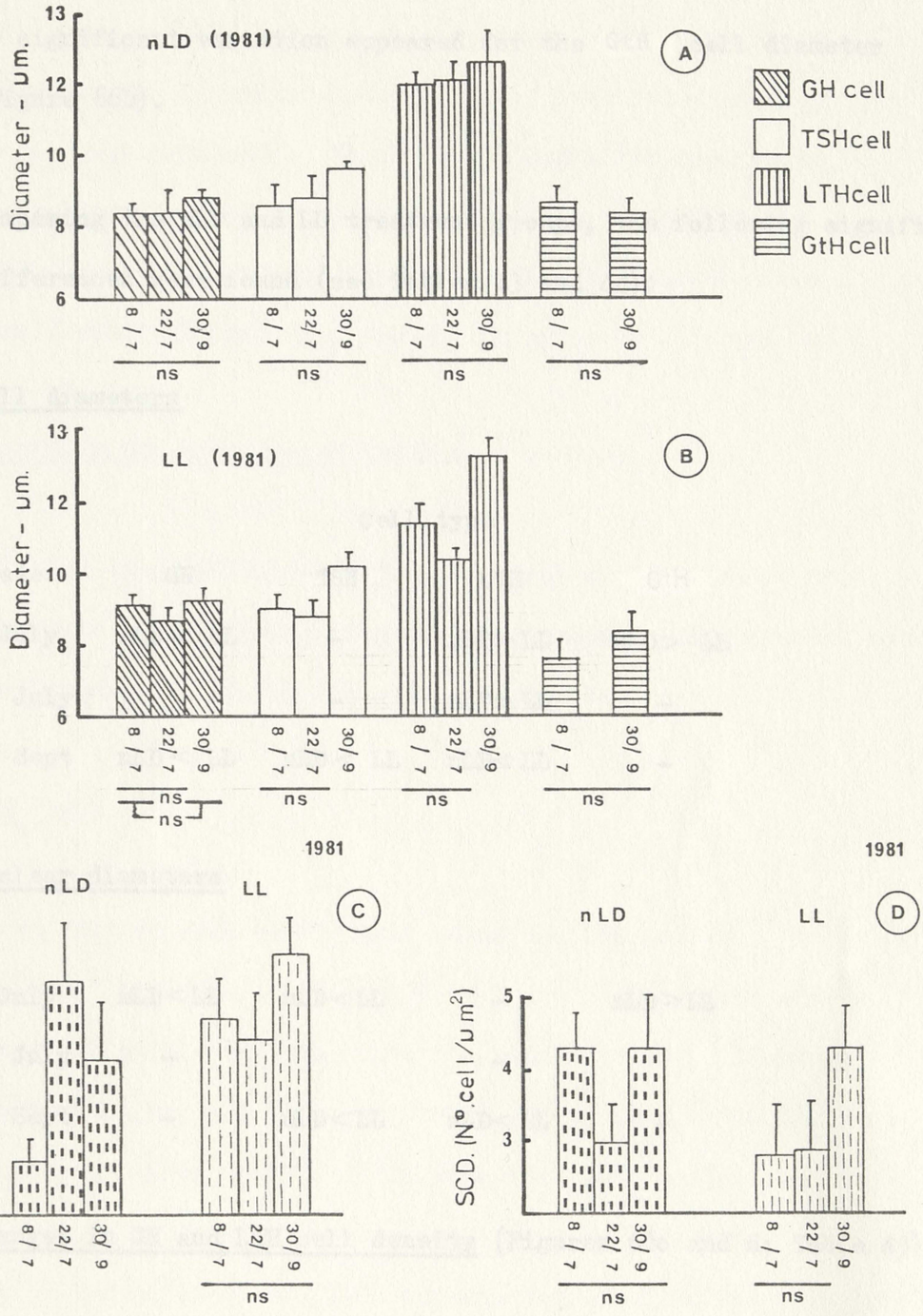
3.8.2.1 Experiment I

(a) Changes in pituitary cell and nucleus diameter

Although there was an increment in diameter for GH, TSH and LTH cells of the pituitary of nLD group fish, (Fig. 66a; Table 43) it was not significant. In the case of GtH cells, there was an insignificant decline of diameter. The same variation was observed for the nucleus diameter of pituitary cells for this group (Table 44).

On the other hand although LL fish showed no variation in cell or nucleus diameter, during the first two days of observation for GH, TSH, LTH cell, a significant ($p < 0.05$) increase in cell diameter was shown by TSH, LTH cells by the 30th September (Figure 66b and Table 43). GH cells for this fish group, presented a significantly ($p < 0.05$) lower diameter for the 22nd July when compared with the correspondent diameter for the 30th September

Figure 66 Histograms showing the changes in mean pituitary cell diameter and cell density ($\pm$ 2SE) of juvenile salmon subjected to A. natural photoperiod (nLD) B. constant light (LL). Experiment I (1981). C. PCD, prolactin cell density D. SCD somatotrope cell density. ns, not significantly different.


nLD (1981)
A
Diameter - um.
13
12
10
8
6
GH cell
TSHcell
LTHcell
GtHcell
8 / 7
22/ 7
30/ 9
ns
LL (1981)
B
1981
nLD
LL
C
PCD. (N°.cell/um²)
8
7
6
1981
nLD
LL
D
SCD. (N°.cell/um²)
5
4
3

No significant variation appeared for the GtH cell diameter (Figure 66b).

Comparing the nLD and LL treatment groups, the following aignificant differences were found (see Tables 43 and 44):

Cell diameters

	Cell type			
Date	GH	TSH	LTH	GtH
8 July	nLD < LL	-	nLD > LL	nLD > LL
22 July	-	-	nLD > LL	-
30 Sept	nLD < LL	nLD < LL	nLD < LL	-

Nuclear diameters

8 July	nLD < LL	nLD < LL	-	nLD > LL
22 July	-		-	
30 Sept	-	nLD < LL	nLD < LL	-

(b) Changes in GH and LTH cell density (Figures 66c and d; Table 45)

The nLD fishes displayed a significantly different ($p < 0.005$) number of prolactin cells per μm^2 or density (PCD) on the three sample days in 1981, being low on the 8th, high on the 22nd July, and intermediate on the 30th September. The PCD of the LL group did not show any significant differences. The nLD somatotrope

cell density (SCD) was the same throughout the period under study but the LL group showed a significant increase ($p < 0.05$) on the 30th September. The LL group had a PCD significantly higher than the nLD group on the 8th July ($p < 0.001$) and 30th September ($p < 0.01$) only. SCD for the nLD group was significantly larger than for the LL group on July 8th only.

(c) Pituitary sex differences (Tables 46 - 50)

In order to establish the role of sexual differences on the synthesis and releasing of pituitary hormones, the data collected was segregated by sex for each sampling day.

nLD fish:

There were no such differences among the LTH and GtH cells or nuclei of nLD fish. TSH and GH cell and nucleus diameters were identical until the 30th September, when the male pituitary showed a higher TSH cell ($p < 0.001$) and nucleus ($p < 0.02$), and similarly higher GH cell ($p < 0.05$), than the female.

The cell density of GH (SCD) was exactly the same for both sexes at all times. The PCD in contrast demonstrated that males increased the number of LTH cells from the 22nd July until the 30th September.

LL fish:

The LL fish presented disparities here and there between the sexes. The LTH cell diameter was significantly ($p<0.01$) larger for females on the 30th September. The males showed a significantly ($p<0.001$) lower nucleus diameter of LTH cells by the 22nd July (Tables 46 and 48). The GtH cell of females was significantly larger on the 30th September, but no differences were observed in the nuclear diameters on any of the days sampled. TSH and GH cells were significantly larger ($p<0.05$) among females on July 8th, but nuclear diameters did not differ from those of the males. There were no differences in PCD between the sexes on any date. The only difference in SCD occurred on the 22nd July, when the density was significantly ($p<0.02$) lower for males.

(d) Pituitary cytological changes and fish size

With the aim of obtaining an indication of variation in synthetic and releasing activity of the pituitary before the two groups became separated in length distribution, the data collected was separated by size range into groups that would later comprise one or the other modal group of the distribution (Table 51).

The smaller fishes under nLD showed a significantly larger TSH cell ($p<0.01$) and nucleus diameter ($p<0.05$) than the larger ones on the 8th July. On July 22nd these differences had gone, and by September 30th were reversed, significantly ($p<0.001$) in

cell diameter. For this treatment group there were no dissimilarities in cell or nucleus diameter between the two size ranges for gonadotropes, nor for lactotropes (Tables 52 and 53). LL fish presented more variation from day to day. The TSH cell and nucleus diameters were significantly ($p<0.05$) higher for the large size range on the 22nd July, but for the small size range on the 30th September ($p<0.001$) (Tables 52 and 53). The GH cells did not differ between the two size ranges, but the smaller fish had larger LTH cells than the larger fish on 22nd July and September 30th. (Tables 53 and 53).

(e) Pituitary mitotic activity

The pituitaries of fishes sampled on the 22nd July 1981 (Experiment I) were unusual in showing mitotic figures in the pars distalis of the adenohypophysis. Five out of seven of these mitotic figures were localised in the PPD, and the other two in the RPD. No special cytological region seemed to be more affected than another, because mitotic figures were found amidst follicles of prolactin cells (Plate 16), gonadotropes, thyrotropes (Plate 17), somatotropes (Plate 18), and chromophobes (Plate 19). No mitotic activity was recorded on any other sample day.

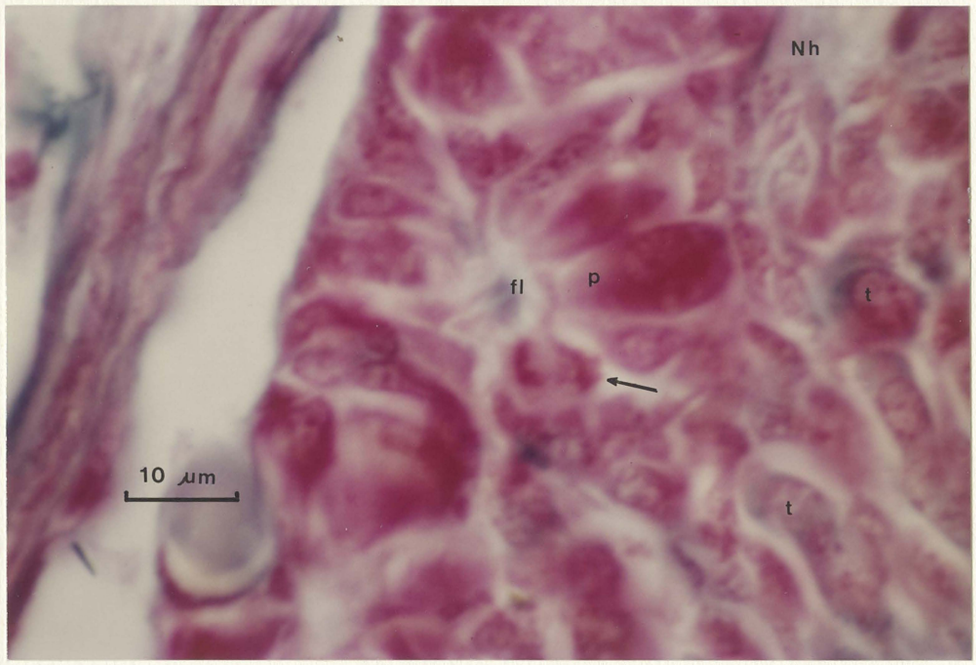
3.8.2.2 Experiment II

(a) Changes in pituitary cell and nucleus diameter

There were no differences between the mean cell diameters for TSH and GtH cell of the various photoperiodic regimes on October 4th, 1982

Plate 16 Sagittal section of the prolactin follicle, showing a prolactin cell in mitotic division (arrow). fl, follicle lumen; Nh, neurohypophysis; p, prolactin cell; t, thyrotropes (Jafri's staining, X1250).

Plate 17 Sagittal section of the PPD of the adenohypophysis showing mitotic figure (arrows) amidst thyrotropes (t) and gonadotropes (g). Nh, neurohypophysis; s, somatotropes (Jafri's staining, X1250).


Nh
fl
p
t
t
10 µm

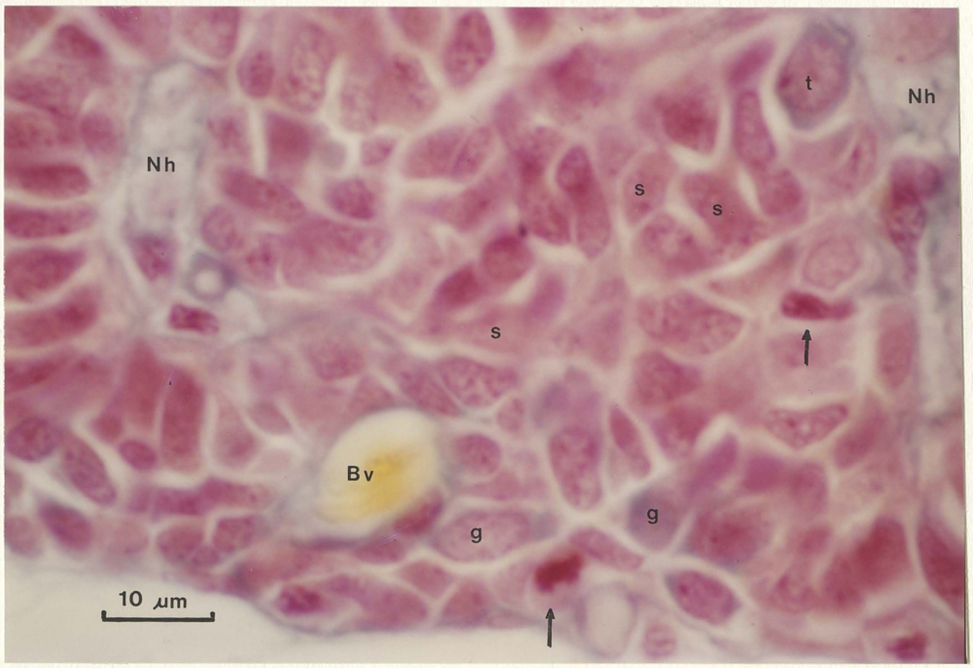
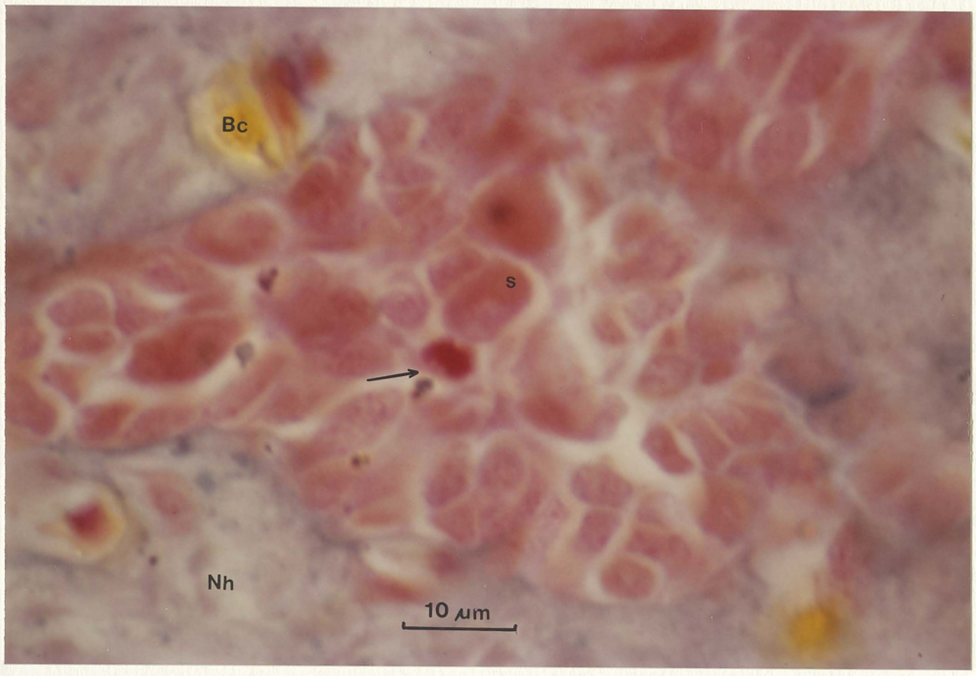
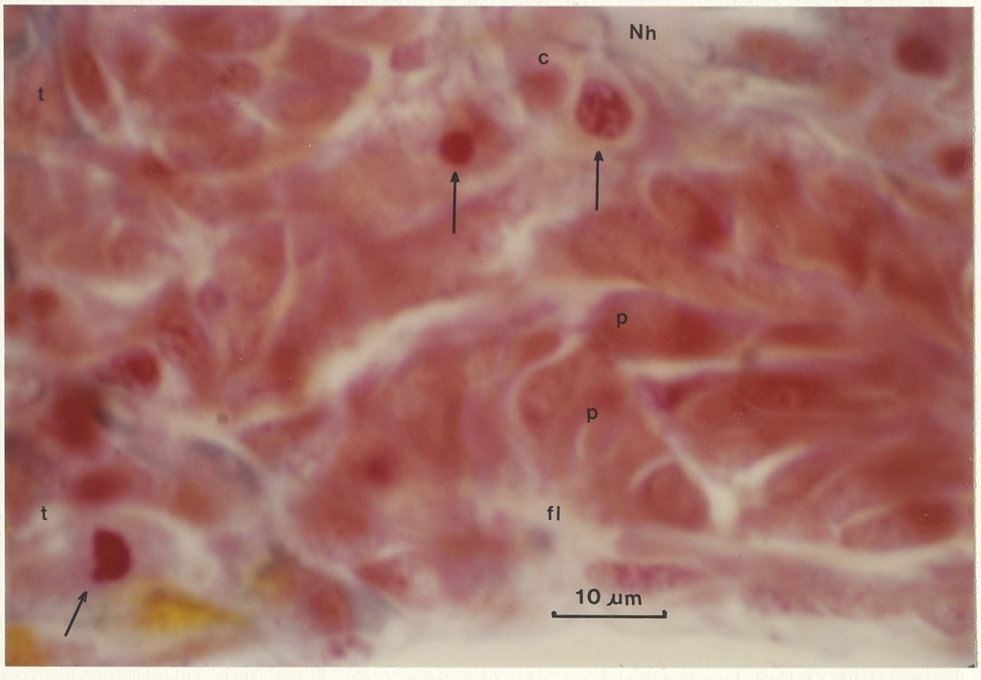

t
Nh
Nh
s
s
s
Bv
g
g
10 µm

Plate 18 Sagittal section of PPD showing a mitotic figure (arrow) amidst someatotropes (s). Bc, blood cell; Nh, neurohyopohysis. (Jafri's staining, X1250).

Plate 19 Sagittal section of the PPD showing mitotic figures (arrow) amidst chromophobes cells (c) thyrotropes (t) fl, follicular lumen; Nh, neurohypophysis; p, prolactin cell; t, thyrotropes. (Jafri(s staining, X1250).


Bc
s
Nh
10 µm


Nh
c
t
p
p
t
fl
10 µm

(Figures 67a, b), but GH and LTH cells showed significant ($p<0.05$ and $p<0.001$ respectively) differences between groups. The GH cell diamater was significantly larger for L6D and LL groups in comparison with L3D group. 8LD, L4D and nLD showed the same mean diameters, and were not difficult from L3D, nor from L6D or LL (Table 54).

The LTH cell diameter demonstrated more significant ($p<0.001$) variation, being significantly larger for the LL group and smaller for L6D when contrasted with the other four treatments. Among the latter, the 8LD group had a significantly ($p<0.05$) higher diameter than the L3D group. No differences were detectable amongst nLD, L4D, and 8LD groups (Table 54).

(b) Changes in GH and LTH cell density

The PCD of the pituitary did not differ between nLD and LL fish. (Figure 68a; Table 56). But there was a significant ($p<0.001$) disparity for SCD, where 8LD had a lower density than L4D, nLD or L3D groups but not lower than L6D or LL groups. No differences were detectable in the SCD value for L4D, nLD, L3D, L6D and LL groups (Figure 68b and Table 56).

(c) Pituitary sex differences

In order to know if there were any differences due to sex in the pituitary cytology of juvenile Atlantic salmon exposed to various photoperiodic regimes during the 1982 experiment, data from

Figure 67 Histograms showing the variation of mean pituitary cell diameter ($\pm$ 2SE) of six sibling fish populations subjected to different photoperiodic regimes. Experiment II (1982).
A. GH cells, somatotropes B. LTH cells lactotropes C. TSH cells, thyrotropes
D. GtH cells gonadotropes. ns, not significantly different.

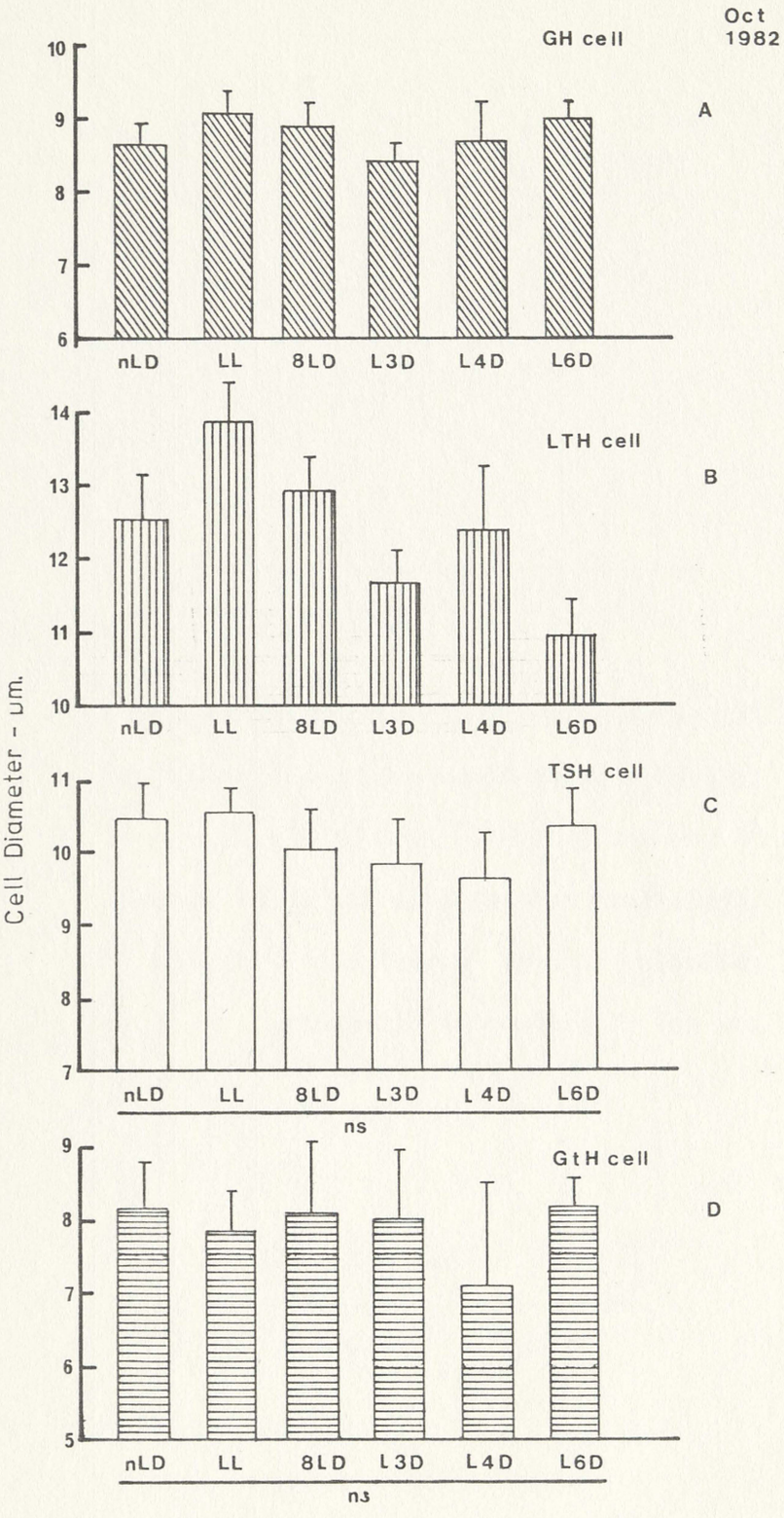
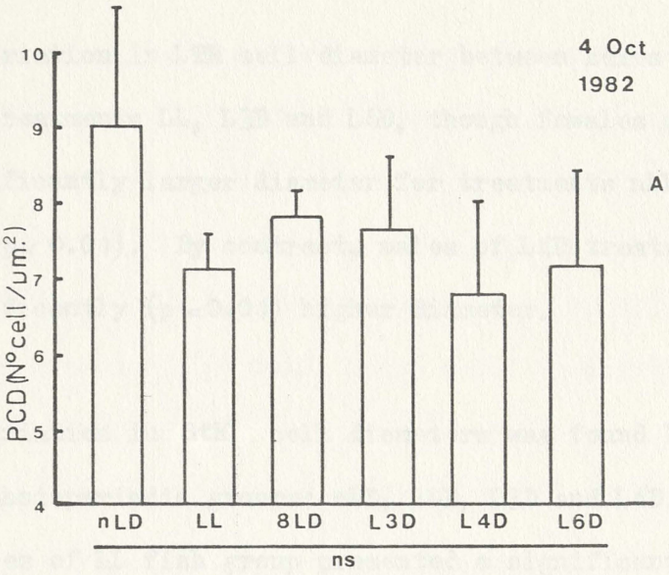
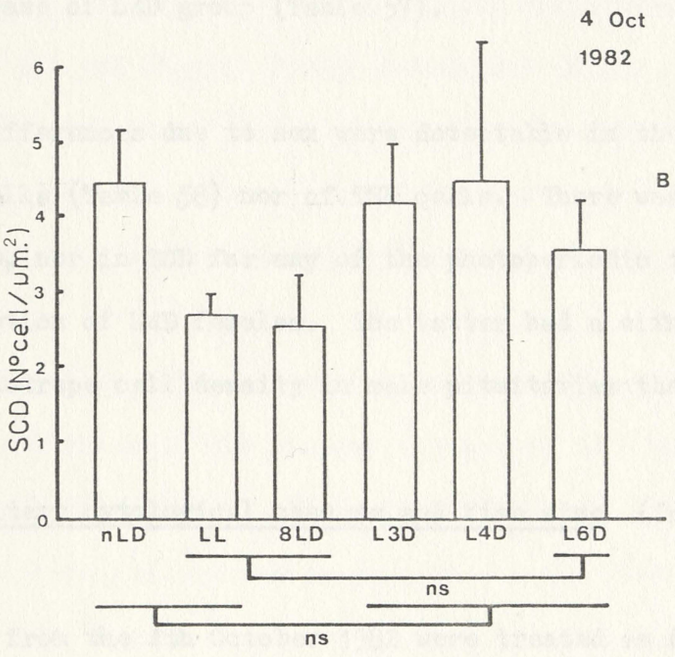

Oct
1982
GH cell
A
LTH cell
B
TSH cell
C
GtH cell
D
Cell Diameter - um.
nLD
LL
8LD
L3D
L4D
L6D
ns
ns

Figure 68 Histograms showing the variations in mean prolactin somatotrope cell density (PCD and SCD respectively) ($\pm$ 2SE) of six fish populations subjected to different photoperiodic regimes. Experiment II (1982). ns, not significantly different.


4 Oct
1982
A
PCD (Nºcell/µm²)
10
9
8
7
6
5
4
nLD
LL
8LD
L3D
L4D
L6D
ns


4 Oct
1982
B
SCD (Nºcell/µm²)
6
5
4
3
2
1
0
nLD
LL
8LD
L3D
L4D
L6D
ns
ns

4th October was segregated by sex.

No variation in LTH cell diameter between sexes was found for the treatments LL, L3D and L6D, though females showed a significantly larger diameter for treatments nLD ($p < 0.001$) and 8LD ($p < 0.01$). By contrast, males of L4D treatment showed a significantly ($p < 0.01$) higher diameter.

No variation in GtH cell diameters was found between sexes of the photoperiodic groups: nLD, 8LD, L3D and L6D. However, females of LL fish group presented a significantly larger ($p < 0.05$) GtH cell diameter, than males. No comparison was possible in the case of L4D group (Table 57).

No differences due to sex were detectable in the diameters of GH cells (Table 58) nor of TSH cells. There was no sex difference inPCD, nor in SCD for any of the photoperiodic treatment, with the exception of L4D females. The latter had a sifnificantly larger somatotrope cell density in male pituitaries than in females.

(d) Pituitary cytological changes and fish size (Table 60)

Data from the 4th October 1982 were treated as described in section 3.8.2.1d. There were no differences due to size for GH and TSH cell diameters for any of the treatment groups, with the exception of the larger LL fishes, which had a significantly ($p < 0.02$) larger TSH cell diameters. At the same time, LTH cells were significantly larger in the smaller size range, for treatments nLD ($p < 0.02$), L4D ($p < 0.001$), and L6D ($p < 0.001$). No differences

were noted for treatments LL and L3D.

GH cell nuclei did not vary between size-ranges (Table 62), nor did LTH nuclei, except for the smaller L4D fish which had a significantly ($p < 0.01$) larger nuclear diameters. The TSH nuclear diameters did not differ for photoperiod regimes nLD, L3D, and L4D, but the larger LL fish, and the smaller L6D fish had significantly larger diameters ($p < 0.001$ and $p < 0.01$ respectively).

3.9 X-ray measurement of food consumption

On the 10th December 1981, the role of light in the feeding activity of juvenile Atlantic salmon, was tested using the method of Talbot and Higgins (1983) and Talbot et al. (1983). Food labelled with iron powder as a marker was substituted for the normal diet for a 90-min period between 11.05 - 13.55 hours and offered to fishes under nLD and LL photoperiods.

From the two photoperiodic treatments only the LL group showed iron particles in the stomach (14 out of 100) 90-min after eating labelled food. These fishes had iron particles localised in the hind gut 24-h after exposure to the labelled food.

4. Discussion

4.1 Generalities

In November of both years the nLD photoperiod produced a skewed distribution with extended upper tail and not the classical bimodal distribution. However, Thorpe and Morgan (1978) and Thorpe et al (1980) have reported the appearance of this characteristic as the initial feature of the development of bimodality. Additionally the type of growth of fishes of the upper tail was different compared to those of the lower extreme of the frequency distribution (Tables 7 - 9).

Another important feature to be explained here, is the interesting fact that all treatment groups showed up a peculiar increase in specific growth rate (Gw) when transferred from 2 m to 1 m diameter radial flow tanks (see Figs 23 and 24 and section 3.3.4). These changes were due to the reduction in fish density, that in turn increased the availability of space for growth. Thorpe and Morgan (1980) reported the converse, that limiting of space restricted growth expression of juvenile Atlantic salmon.

The results reported here demonstrated that an increase in frequency of feeding regime (T-rate to 2T-rate) did not exert any important effect on growth (Fig 5 and Table 21), and suggested that for these two feeding rates, the amount of food delivered was above the fishes daily requirements. Consequently, during these experiments growth was not food limited.

4.2 Light and temperature regulation of somatic growth and development of bimodality.

4.2.1 Role in growth of the whole fish

The photoperiod exerted two different effects upon endogenous rhythms one by the length of daylight *per se*, or the proportional effect; and other by the rate of change in day-length, or the differential effect (Aschoff, 1960; Wagner, 1971; Eriksson and Lundqvist, 1980). The present experiments indicated that juvenile Atlantic salmon in relation to growth in length and weight, were physiologically sensitive to both forms of photoperiodic effects. The proportional effect seemed to be of paramount importance in fish growth, because during both experiment years, the proportion of fishes under LL photoperiod reaching the upper tail of the frequency distribution by autumn was larger, than fishes under nLD (Fig 6a, b and 7a, b). The same interpretation held for fishes under 8LD treatment, which had a shorter total exposure to light and a smaller proportion of fish in the upper tail of the frequency distribution (Figs 7a and c) than any other treatment group. Further confirmation came from the results of fish growth under different rates of photoperiodic change (L3D, L4D, and L6D). By December 1982 all of these showed better growth performance than 8LD, but at the same time, lesser skewness and fish numbers in the upper tail of frequency distribution than nLD (Figs 7 and 8). The important difference between these three photoperiodic regimes and the nLD one was the amount of light that each group of fish experienced during the growth season (Fig 3). This suggested that it was the total amount of light experienced by the fish that was the most important exogenous factor in regulating

the development of bimodality in frequency distribution of length. Recent results obtained by Thorpe (unpubl.) in this laboratory, in which not only the change of day-lengths was mimicked but the natural twilight as well, confirmed the present results and threw light on others. In the Thorpe experiment the fishes never experienced natural light but were transferred at first feeding directly from the standard alevin baskets held under constant dim red light (outside the spectral range of sensitivity of the salmon eye), into the experimental compartments.

The fish were subjected to a different photoperiodic schedule compared to the ones described here although some results can be compared. For example, fish under LL photoperiod, in his experiment showed again a larger proportion in the upper tail of the length frequency distribution, than fish under a simulated nLD regime. Similarly fishes under a standard photoperiod (simulated natural photoperiod), but 6-mo out of phase with respect to nLD, showed a pattern of bimodal growth similar to the 8LD fish group of the present experiment; in both experiments these fish had experienced relatively few hours of light during growth period.

The differential effect of photoperiod, exerted some role in growth and development of bimodality as well, because some skewing and upper tail formation appeared in the present L3D, L4D and L6D fish groups (Fig 8). Nonetheless in the two years' experiments the fishes experienced normal increase of day-length from first feeding to midsummer day when they were transferred to the experimental tanks, and this did not allow a proper gauge of the photoperiod differential

effects during this first growth phase. This is particularly important since the physiological state and responsiveness of juvenile salmon changes seasonally (Hoar, 1965 and Lundqvist, 1983); thus it may be that young salmon are more sensitive to day-length rate of change during spring and less so in summer. In this sense the experiment of Thorpe clarified the possible role of this photoperiodic effect. One of his treatments 9 mo delay, which resulted in an increase of day-length from first feeding to the end of September produced a frequency distribution similar to his nLD treatment, while his 12L:12D treatment during the same period impaired the development of bimodality compared with nLD.

However the most important finding of this study was the fact that the timing of the development of bimodality in frequency distribution in length and weight is photoperiod independent, and in accordance with the notion of genetic regulation of bimodality (Thorpe and Morgan, 1978 and Bailey et al, 1980). The photoperiod, on the other hand, affected the proportion of fishes in each modal group, from almost none under 8LD photoperiod to a higher proportion under LL, and medium values in between, all in accordance with the role of photoperiod as a synchroniser (Bünning, 1964 and Saunders, 1982). The proportion of fishes in each modal group was also influenced by genetic factors (Thorpe and Morgan, 1978 and Bailey et al, 1980). It seems likely then that the genetic mechanism that determined the fish proportions by modal group required suitable conditions for its expression; and that the day-length change was the clue that informed the fish of the forthcoming appropriate conditions for growth (e.g. food availability, optimum temperature, etc).

The current hypothesis of development of bimodality postulates that a minimum or threshold size must be reached before the decision to smoltify or mature as a parr may be made (Simpson and Thorpe, 1976; Thorpe and Morgan, 1978; Bailey et al, 1980 and Thorpe et al, 1982). In addition, the decision to mature is independent and with lower threshold, than the decision to smoltify (Thorpe, et al, 1980; Saunders et al, 1982). The present results indicate that light permitted the fish to "decide" for one or the other pattern of development accelerating or decelerating the rate of growth which in turn will allow the fish to reach one or the other size threshold, in phase with the diverse endogenous mechanisms involved in the development of the bimodal pattern of growth. It is explicitly proposed here then, that genetic mechanisms determine the rate to be achieved before any decision can be made, and that the photoperiod accelerates or delays its achievements.

In agreement with the latter statement, the specific growth rate (G_w) and the elevation of the regression line for growth in length and weight of the LL group from 1981 was significantly higher than nLD group (Fig 14, Tables 22 and 23). Although the 1982 experiment did not produce exactly the same results, the LL group grew better and showed a higher G_w than the nLD group for August and September (Figs 11, 12 and 24). This short term increase in specific growth rate was enough to increase appreciably the proportion of fish in the upper tail of the length distribution (Figs 7a, and b). Figures 9 and 10 show again that brief growth increases were responsible for the same effect for the LL group in 1981.

It is noteworthy (Figs 14 - 17) that from the beginning of August of

both years there was a significant decrease in growth rate. The same phenomenon has been noticed in juvenile salmon under natural (Allen, 1940; Gardiner and Geddes, 1980) and experimental (Lundqvist, 1980) conditions. In all these cases, as well as in the present one, growth was more rapid in the months June and July followed by a rapid decline. I propose that it is during the latter two months when the "critical photosensitive period" (CPP) occurs that enables the fish to reach the critical decision size. Additionally, the CPP is dependent on rate of change of photoperiod. In conformity, both a shortening (L3D, L4D and L6D regimes) or a lengthening day (9 mo delay in the Thorpe experiment) can increase the proportion of fishes in the upper mode. Further enhancement in size was possible under LL photoperiod, because in salmonids this treatment prolonged the period of feeding activity, which is only limited by gastric emptying time (Adron et al, 1973).

In comparison with light, temperature had a relatively unimportant role in the development of bimodality. For example under LL photoperiod there was an increase in G_w during the first half of September 1981 and 1982, (Figs 23 and 24) at a time when water temperature was rapidly declining. By contrast, under 8LD, L6D, L3D and L4D photoperiods (Figs 24 and 25) G_w declined faster during July and August 1982, than under nLD, at a time when water temperature went up (Fig. 4). Independence of seasonal growth from temperature has been recorded in Kiyi (Coregonus kiyi) (Deason and Hile, 1947) and in the bluegill sunfish (Lepomis macrochirus) (Gerking, 1966).

Once the bimodal distribution was well established photoperiod did not seem to exert any important developmental effect (Figs 9 and 10), apart from sustaining the fishes appetite under LL photoperiod (see section 3.9).

4.2.2 Role of light in regulating the number and size of muscle fibres

Before any further consideration of the role of nucleic acid and their ratios can be made, special attention must be paid to their biological meaning.

It is widely accepted that DNA synthesis is mainly confined to the interphasic nucleus, and as a rule for a given species its amount is constant and double that of the corresponding haploid nucleus (Vendrely and Vendrely, 1950; Davidson and Leslie, 1950; Thompson et al, 1953; Roels, 1954). Any attempt to understand the role of nucleic acids in growth relies upon these facts. Enesco and Leblond (1962) and Luquet and Durand (1970) have proposed that the different expressions of DNA content (concentration and total) and the ratios calculated from them reflect the number of nuclei per tissue, cell size, cell number and nuclear activity defined as follows:

In all fishes so far studied the somatic cell nucleus has a constant amount of DNA (Mirsky and Ris, 1951; Vendrely and Vendrely, 1953; Felix et al, 1956; Dixon and Smith, 1968; Hinegardner, 1968). Therefore, the total amount of DNA of a tissue or an organ is equal to the total DNA content of all the nuclei present in that tissue or organ. So the number of nuclei per tissue may be determined from the total DNA content of that tissue.

The DNA concentration, represents the amount of this acid associated with a constant amount of wet or dry tissue (e.g. µg DNA per 100 mg of dry tissue). For this reason it may be used to differentiate between the relative roles of cellular enlargement (hypertrophy) and division

(hyperplasia) in growth. Under a constant nuclear DNA content, any decrease of concentration can only be due to cellular enlargement. On the contrary DNA concentration increase represents an increase of cell number.

In a similar way the ratio Dry weight-DNA (DW-DNA), is an index of the amount of material which on average is associated with one nucleus, and therefore it is an indirect estimate of cell size, if there is not a parallel variation of intercellular material.

The Dry weight-DNA (DW-DNA), on the other hand, is also an estimate of the DNA activity in terms of protein synthesis. Finally, the RNA-DNA ratio represents the cellular growth per nucleus (Haines, 1973; Sower et al, 1983).

The scope and limitation in the application of these different biochemical estimates of cell activity and growth have been discussed extensively by Enesco and Leblond (1962). In the present work special attention was paid to their recommendation that parallel histological measurements of the muscular cell should be made in order to interpret better the role of hypertrophy and hyperplasia in the growth of juvenile Atlantic salmon.

4.2.2.1 Growth of the whole fish

The fish from first feeding to midsummer day grew through the participation of both processes, hypertrophy and hyperplasia. In some cases, one phenomenon gained precendence over the other. For

example, after first feeding in both years, the increase in DNA concentration indicated a cellular proliferation, produced by active mitosis as shown by the slight increase in total DNA in 1981 and a more marked increase in 1982, together with a cell size decrease (i.e. dry weight-DNA ratio decrease) (Figs 26, 34 and 44; Tables 2 and 11). From mid May to the beginning of June of both years, the DNA concentration decreased where as the DW-DNA ratio increased: a sign of hypertrophy (Figs 26, 28, 42 and 44). These changes were not accompanied by nuclear proliferation and so no important change of total DNA occurred (Tables 2 and 11). From the beginning of June onwards both phenomena (hypertrophy and hyperplasia) contributed to growth. However, the fact that total DNA increased consistently from June up to the beginning of July 1981, clearly suggested that cellular proliferation was the leading factor during that period.

If the growth of the whole young fish was the result of cell proliferation and enlargement, it is not surprising the RNA-DNA ratio showed a high degree of correlation with specific growth rate. Bulow (1970) in his original proposal of RNA-DNA ratio as an indicator of recent growth stated that this ratio was a more accurate index of metabolic activity than RNA concentration alone, because it was not affected by cell number. The present results agree with the Bulow assertion.

These results also agree with those of Buckley (1980) who found a similar decrease of RNA-DNA ratio of flounder (Pseudopleuronectes americanus) larvae between the yolk sac stage and feeding initiation with a subsequent rise after feeding had started. Once feeding has

been initiated a good correlation existed between growth and RNA-DNA ratio, a result consistent with those obtained in carp (Cyprinus carpio) small mouth bass (Micropterus dolomicu) (Haines, 1973), perch (Perca flavescens)(Kearns and Atchinson, 1979), black crappie (Pomoxis nigromaculatus) (Haines, 1980) and landlocked Atlantic salmon parr (Salmo salar) (Wilder and Stanley, 1983). Although, in all these cases the claim has been made that the RNA-DNA ratio represented the specific growth rate of natural and experimental fish populations, only in three cases was a proper correlation analysis made of these two variables (Haines, 1973, 1980; Thorpe et al, 1982; Wilde and Stanley, 1983).

Haines (1980) reported that the RNA-DNA ratio and specific growth rate correlation improved, if weight values were lagged a week with respect to RNA-DNA ratio values, and added that the correlation declined with further lagging. He explained his results by suggesting that as RNA was the temporal precursor of protein (i.e. growth building blocks), its increase must precede any fish weight increment. In the present work on that of Thorpe et al (1982) correlation were established between G_w (% day $^{-1}$) and the geometric mean of the RNA-DNA ratio for the relevant period (Fig 50). In other words the normalised RNA-DNA ratio values for the period under study were compared with the G_w during that particular interval. Thus in this particular way RNA synthesis is a more precise expression of its activity than otherwise. During the 1982 experiment not enough data was available for a proper correlation analysis: however, G_w of whole fish and RNA-DNA ratio for 1982 (Figs 24 and 36) clearly mirror one another, indicating again a good correlation between the two variables.

4.2.2.2 Muscle tissue growth

Muscle total DNA and concentration declined steadily from mid June to the last week of July in both years when their lowest values were reached (see sections 3.4.3.1b; 3.4.3.2; 3.4.4). From then onwards there was an increase in both values toward a plateau with a concentration value at about 600 µg/mgdt, with short term variation. This latter is likely to be due to sampling error because before October the two growth groups (i.e. future modal groups) could not be distinguished. Consequently, it is likely that the representation of future upper and lower growth mode in fishes in these late samples was varied, and this would be reflected in varying DNA levels. These tendencies in DNA synthesis permit division of the DNA changes into two phases, one of DNA content decline up to the end of July (early summer growth), and a second of constant DNA content up to the end of September (Figs 26 - 34) (late summer growth).

(a) Early summer growth

The most striking feature of this growth phase was the appearance of the lowest value of muscular total DNA and concentration (22nd July 1981 and 26th July 1982) which was independent of photoperiodic treatment.

The DNA content decline, during a period of overall somatic growth (Figs 9 - 13) can only be explained by assuming that muscular growth was due predominantly to cell enlargement rather than cell proliferation. Under these circumstances a constant total DNA and a smooth DW-DNA ratio increase must be expected. Tables 5, 6 and 15 - 20 clearly show

that none of the latter expectations were realised (see also Figs 34, and 42 - 49).

Enesco of Leblond (1962), in their excellent discussion of the significance of total DNA, indicated three limitations of this method as a way of estimating nuclei number. Firstly it does not distinguish between mono or polynuclear cells; secondly polyploid nuclei are present in some animal tissues; and finally the DNA content per nucleus increases a few hours before mitosis. The first limitation is irrelevant, since muscle fibres are polynucleate cells, so the muscle total DNA in this case is a measurement of the average number of nuclei associated to a muscle fibre. The third limitation can be excluded, because total DNA includes not only the DNA actually present in the tissue, but also that of potential nuclei to be added in a few hours.

On the other hand, the possibility that the total DNA decline may be caused by a decrease in nuclear DNA content after transient increase produced by polyploidism or a DNA segment amplification, rather than a nuclear decline (Lewin, 1983) cannot be ruled out in the light of the present results. This explanation is unlikely though, since polyploid nuclei have been reported in rat liver and fly salivary glands (Thomson et al, 1953; Enesco and Leblond, 1962; Lewin, 1983), but not in other tissues, and although DNA amplification appeared in the amphibian Xenopus laevis, it has never been described in fishes (Schröder, 1973; Kirpichnikov, 1981; Lewin, 1983). A specially designed experiment must be carried out before these two possibilities may be discarded.

Another explanation of the DNA decline is that it represented a decrease of nuclear number in connective tissue rather than in muscle. No attempt was made during the present experiments to separate skin, bone and connective tissue (myocommata) from muscle tissue. Love (1958b, 1970) has reported that in North Sea cod (Gadus morhua) the anterior myotome has a DNA content lower than the myocommata for the same area. The same author indicated simultaneously that with a doubling of fish size, the myocommata increased threefold. Assuming that something similar was happening in Atlantic salmon during early growth, then an increase rather than a decrease of nuclear number (DNA total) would be expected. Moreover if myocommata have the function of transmitting contracting forces to the vertebrae, as has been postulated by Szarski (1964), it does not make physiological sense that the active swimming freshwater young salmon should lose this tissue. It is conceivable nevertheless, that processes such as nuclear migration or degeneration, actually diminish the muscle nuclei number at a low replacement rate or simply without replacement. In both cases the total DNA would decrease. Processes like these have been described in highly mobile tissues, such as rat thymus and lung (Enesco and Leblond, 1962). The fish muscle tissue, on the contrary, is very stable and during the present histological observations no evidence of muscle degradation, or thickening of myocommata was noted (see Plate 2). Finally, this surprising DNA decline may be a methodological problem. There are two possibilities: the existence of interfering substances, or the appearance of chemical changes in the muscle that decrease the DNA release. Burton (1956) in his study of the condition and mechanisms of diphenylamine (DPA) and DNA reaction, reported that low molecular weight compounds can interfere a great deal with the reaction, but these interfering

substances were removed by a double cold trichloroacetic acid (TCA) extraction (see Bulow, 1981).

Munro and Fleck (1966) reported that lipid extraction can decrease the nucleic acid recovery, and in the present work no attempt was made to remove lipid (see also Thorpe et al, 1982). The same authors reported that a too vigorous extraction of nucleic acid with hot TCA may destroy the deoxypentosa, and that the optimum temperature is tissue dependent. Extraction was carried out as standard procedure with 5% TCA at 90°C for 20 minutes, so even though this may not be the optimum, the fact that all samples were treated in the same way standardised any error due to excessive heating.

The possible presence cannot be ruled out of some chemical compound or configurational change of nucleoprotein during the early growth phase in both years (June - July), that could have interfered with the release of DNA and in this way reduced the colour reaction. This substance must have been insoluble in cold TCA and so attached to the nucleoprotein that prevented the DNA release in hot TCA. The transient configurational change must produce exactly the same effect.

In order to discriminate between these alternatives, direct measurements of DNA nuclear content must be performed by microdensitometry or in isolated nuclei by biochemical methods. Simultaneously a detailed chemical analysis of the remaining sediment after the removal of cold-acid soluble compounds, must be carried out in O+ Atlantic salmon sampled between the months of June and July.

The DW-DNA ratio showed a huge increase in value by late July of both

years and for all treatments (Figs 42 - 49), due to this enormous DNA content decline. These results suggest that during the early summer growth season the cellular trend was represented by hypertrophy. However, because total DNA and concentration both increased from the end of July to mid August (Figs 26 - 34, see also Tables 2 and 15 - 20), cellular proliferation was also important. Morphometric evidence corroborated this explanation, since the two modal values of muscle fibre frequency distribution increased with fish length for both photoperiod treatments of 1981 and nLD photoperiod in 1982 (Figs 53, 54 and 58). Simultaneously, the fact that with fish length increase the proportion of small diameter fibres increased as well,(Figs 55a and b) indicated that recruitment of new cells was occurring parallel to cell enlargement. If DNA concentration decline expressed cell enlargement (volume increase) as was indicated above (see introduction to section 4.2.2.2), the decline of DNA concentration for the nLD fish population from the 8th - 20th July, 1981 suggested an increase in cell size of 65% (Table 5). This value can be compared with the morphometric cell measurements assuming an increase in cell diameter in all directions as a perfect sphere. For this purpose cell volume estimations were made from the mean cell diameter of both modes of the muscle fibre frequency distribution for fishes under nLD photoperiod, of lengths close to the mean size value, for the 8th and 20th July, 1981. These were compared with the estimate made from DNA concentration values for the same period. These estimations indicated that cell volume increase, calculated from biochemical data was about 65%, and from morphometric data was about 63%, and so there was good agreement between the two methods. Taking all this evidence together, it can

be concluded that during the period between midsummer day and late July muscle tissue grew by hyperplasia and hypertrophy, but that the latter cellular process was the principal factor.

The RNA-DNA ratio is considered an estimate of the synthetic activity of the nucleus, because almost all the RNA present in the cell has been transcribed from the nuclear DNA (Szekely, 1980; Lewin, 1983). It can be stated then, that the maximal nuclear synthetic activity occurred at the end of July when for both experimental years the RNA-DNA ratio was at a maximum (Figs 35 - 41). As was discussed elsewhere (see section 4.2.2.1), the rise in RNA/DNA ratio preceded the protein synthesis (translation); it seems logical then to suggest that the end of July represented the moment of building up of protein precursors.

(b) Late summer growth

From August to September of both years the DNA concentration, for all photoperiodic treatments remained constant with a few exceptions in 1982 (see section 3.4.3.2d). This suggested that during this period, cell division and enlargement contributed in constant relative proportion to fish growth. Morphometric measurements corroborated this interpretation, since the increase of muscle fibre diameters with fish length increase (hypertrophy) was accompanied by a notable recruitment of new fibres (hyperplasia)(Figs 53, 54 and 57). The important point to stress here is that by contrast with early summer growth, neither of the two cellular growth processes (hypertrophy or hyperplasia) dominated. The fact that the RNA-DNA ratio remained constant from August to September, indicated that

muscle fibres were synthesising proteins at the same rate all along (Figs 35 - 41). Transient variations were due to sampling error in DNA content estimation.

4.2.2.3 Role of light on cellular growth

Day length did not seem to affect directly the timing of the cellular processes of growth, particularly during the critical photosensitive period (CPP). Independent of light treatment of family, there was a consistent decline in DNA concentration and increase in DW-DNA ratio, indicating that throughout June and July the principal growth process was cellular hypertrophy. However, photoperiod could alter the degree of DNA concentration decline (e.g. fishes under 8LD photoperiod, Fig 30) or shift its phase (e.g. fishes under LL photoperiod in 1981, Fig 27). These results suggest that a strong endogenous seasonal cellular component existed in the growth of juvenile Atlantic salmon. It was surprising, though, that LL photoperiod did not shift the phase of the lowest DNA concentration point in 1982. Nevertheless, Bünning (1963) and Harker (1964) have pointed out that the effect of constant light on endogenous physiological processes depended on intensity and spectral light composition, factors which were not assessed during the present experiments. It can be concluded from the present study that the CPP occurred during the months of June and July, and the level at which the day-length exerted its effect will be discussed below. The relevant point was that the endogenous timing of cellular enlargement and RNA synthesis (early summer) represented the moment of cellular preparation for the peak of maximum dry weight (protein and lipids) by September. The function of photoperiod was to synchronize the endogenous time of cellular readiness for protein

Luquet and Durand (1970) have reported that in rainbow trout (Salmo gairdneri) protein comprised 90% of muscle tissue dry weight.

The RNA content of the fish body seemed to behave differently to dry weight and water percentage during the growth season. The values of total RNA and concentration in whole body increased before midsummer day for both years for fishes under nLD photoperiod, and then they declined (Figs 26 and 28). The muscular tissue showed a steady decline from midsummer day onwards for all photoperiodic treatments and years (Figs 26 - 34). These changes in RNA content were also correlated with specific growth rate (Tables 24 and 26). However, a very striking difference existed between these correlations before and after the summer solstice. Before the solstice, specific growth rate was highly correlated with RNA-DNA ratio, but after it, with the natural logarithm of RNA concentration (Figs 50 - 52). These observations indicated that during spring RNA concentration was more affected by cell size, than during summer; and additionally that at least during summer RNA concentrations alone could be used as a growth indicator.

These findings were in agreement with similar ones reported in invertebrates (Sutcliffe, 1965, 1970; Båmstedt, 1983), and fishes (Kayes, 1979). On the contrary, several researchers have reported that the RNA-DNA ratio was a better growth index than RNA concentration alone (Bulow, 1970, 1971; Haines, 1973, 1980; Wilder and Stanley, 1982). Finally Sower et al (1983) have indicated no relationship between growth and RNA concentration, nor with RNA-DNA ratio. This discrepancy could be explained assuming that muscle nucleic

acid measurements did not represent growth of the whole fish. The classical definition of growth by Bulow (1970) presupposed that fish growth was caused by an increment in fish flesh accomplished by protein synthesis, so that any increase in the synthesis of protein precursors (e.g. RNA) was an index of growth. These assumptions have been abundantly confirmed (Bulow, 1970; Bulow et al, 1978; Kayes, 1978; Kern and Atchinson, 1979; Haines, 1973, 1980; Thorpe et al, 1982; Matty et al, 1982; Wilder and Stanley, 1983). Therefore, the better explanation was that since variations in cell size during development and fasting were occurring so often these could affect the short term assessment by RNA concentration alone. For example, a close observation of the original data of Bulow (1970, Table 1), and Wilder and Stanley (1982, Table 3) clearly demonstrated that the increase in RNA-DNA ratio during growing fed fish was due to RNA concentration increase alone, since DNA concentration remained constant during the whole experiment. In other words RNA concentration was an appropriate growth index when for one reason or another it was not affected by cell size. In cases such as during starvation (Love, 1970; Bulow, 1970, 1971, Medda and Ray, 1979; Buckley, 1982; Wilder and Stanley, 1982), sexual maturation (Mustafa, 1977; Bâmsted, 1983) or during development (as during spring growth in the present case), variation in DNA concentration or cell size was a factor of paramount importance, and RNA-DNA ratio would be a better index of growth. In any case the usage of one or another indicator of growth must be validated experimentally and frequently reviewed. Thorpe and Morgan (1978) and Thorpe et al (1980, 1982) postulated that the precise level of environmental variables, range of fish size, and the timing at which the "decision" to take one

or the other pattern of modal growth occurred, was genetically determined and would assume different values between families. It was expected then to observe interfamily differences in growth rate, which in turn would modify the "decision" to smoltify early or mature, especially when these traits and growth rate are highly related (Thorpe et al, 1983). The evidence gathered here contributed to confirm these postulates, since each year the families showed significant ($p < 0.025$) differences in the slope of the regression of RNA concentration on specific growth rate (Table 25), which demonstrated that effectively each family had a different specific growth rate that in turn may modify the growth-related pattern of development. The ontogeny of DW-RNA ratio (Figs 42 and 43, section 3.4.3) for the whole fish showed, from first feeding to midsummer day, a decline or a constant value, and then an increase. This finding suggested that a great amount of RNA was involved in dry weight accumulation (e.g. protein synthesis). However, since the RNA content was calculated for the whole fish it was an expression of the synthetic activity of the diverse body compartments each one involved in active developmental modifications. In relation to this, several researchers have reported that fish liver, gut and spleen synthesise more RNA than blood and muscle (Imura and Saito, 1968, 1969; Bulow, 1971; Yavonenko et al, 1980; Kulik, 1981; Kurant et al, 1981), Buckley (1980), on the other hand has shown that RNA content of the whole body of larval flounders varied during ontogenesis. In such circumstances it must be expected that RNA would not reflect protein synthesis directly because the protein turnover rate would be highly diverse from one body compartment to another. However, if the same protein turnover rate was unlikely for all body compartments at a

particular time, the fish RNA was less efficient per unit of dry weight, since more RNA had to be synthesised for accumulation of new dry tissue. In this respect Dunn and Schotman (1981) noted that RNA increase did not necessarily imply enhancements of protein synthesis, as mRNA can be stored in cytoplasm of eukaryotic cells, so that DW-RNA ratio would not be an accurate expression of RNA metabolic activity. Further studies of the RNA content of the different body compartments of juvenile Atlantic salmon must be made in order to understand their individual contributions to fish growth. By contrast, after the summer solstice there was a tendency for the muscle tissue DW-RNA ratio to increase in all photoperiodic treatments for both experimental years. If the elevated degree of homogenity in tissue composition and cellular pattern of growth is taken into account, and the same protein turnover rate is assumed during the period under study then the muscle RNA was more active per unit of protein synthesis, since less RNA was needed to increase the dry weight accumulation.

4.2.4 Bimodal population chemical composition

Thorpe et al (1982) and Talbot (unpubl.) found that for the upper modal group of a population, winter growth was associated with higher RNA synthesis, than was the lower one. The present work confirmed and amplified these findings, in that the 1981 nLD population upper modal group showed a consistently and significantly higher dry and wet weight, total RNA and RNA concentration, total DNA DW-DNA ratio, and RNA-DNA ratio than the lower modal group. These results also suggested that upper modal fishes were synthesising protein and lipids at a higher rate than the lower ones. The water content supported this interpretation, since the upper modal population

had a lower percentage water than did the lower one (Fig 20).

On the contrary, this very same population (upper modal group) showed a lower DNA concentration and DW-RNA ratio (Figs 26, 27, 42 and 43). The upper modal group then was growing fundamentally by hypertrophy, confirmed by the morphometric results, which demonstrated that this modal group had a higher proportion of large diameter muscle fibres, than the lower one. Additional nuclei were simultaneously added, since total DNA was higher as well, possibly due to the new fibres under recruitment (Fig 57) (Higgins, personal communication).

Very surprisingly though, the DW-RNA ratio was lower for the upper modal group, at a time when it was synthesising more dry weight and showed lower water content, suggesting a less efficient protein synthesis per RNA unit than the lower modal group. This apparent contradiction between the unexpected low DW-RNA ratio and faster growth of the upper modal group, can be explained by the preliminary results of experiments under way (Higgins, personal communication). They showed that the upper modal group ate more food and consumed more oxygen than the lower modal one. It is well known that salmonids utilise protein and lipids as major sources of energy, rather than carbohydrates (Walton and Cowey, 1982). It can be argued that the upper modal fish were accumulating less dry weight per RNA unit, because the rate of protein turnover was rapid in order to cope with the antagonistic demands on energy resources for adaptation to cold and to growth.

4.3 Endocrine regulation of somatic growth and the development of bimodality

4.3.1 Role through differential allocation of resources to somatic and reproductive effort (Gonadotropes and gonadal development)

Thorpe et al (1982) in their review of the development of bimodality, concluded that sexual maturation was a primary influence, whereas smoltification was an incidental one. This conclusion was based on the findings that in a Canadian 0+ Atlantic salmon population, early stages of male sexual maturation were seen in mid June. (Bailey et al, 1980; Saunders et al, 1982). It was postulated then that the lower modal group should represent both those fishes whose initial growth was most rapid, and in which maturation had been triggered and somatic growth retarded as a consequence of gonadal growth and those whose initial growth was slowest (Thorpe et al, 1982). In such conditions it was expected firstly that early stages of spermatogenesis appeared earlier than those of oogenesis. Secondly, that higher male gonadal development must appear in the lower modal group, whereas the opposite should happen with the female gonads.

4.3.1.1 Gonadal development and somatic growth

The results previously reported clearly indicated that male gonadal development corresponded histologically to the very early stages of spermatogenesis found in other salmonids (Robertson, 1958; Henderson, 1962; Oota and Yamamoto, 1966; Drance et al, 1976; Takashima et al, 1980). These developmental stages for both photoperiodic treatments lasted from June to September, 1981, and were represented by the following characteristics: weak haematoxylin affinity, nucleus with a

single nucleolus, relatively small change in cell diameter, small size cysts and low mitotic activity (Figs 55, 60 and Tables 33 - 35). From the end of September onwards, for both photoperiodic regimes, three very important changes took place, first a significant increase in cell diameter ($p \leq 0.005$), second an enhancement of the mitotic activity and third a cyst enlargement accompanied by the appearance of a central lumen. The latter characteristics were especially conspicuous in the upper modal group (Plates 5 and 6, Table 37).

The appearance of large cysts with lumina is of fundamental importance because this feature is regarded as typical of spermatogenesis initiation (Henderson, 1962; Murza, 1978; Glebe, per communication).

The 1982 experiment confirmed these results, since no differences existed in spermatogonia cell and nucleus diameters between the nLD populations of both years (Table 41). The photoperiod seems to exert no fundamental role in spermatogenesis, as no differences in cell diameter of spermatogonia were noticed among photoperiodic treatments, with the exception of the L6D one (Table 39). The latter difference may be explained by sampling error, since the day of sampling (October 4th, 1982) corresponded to the time at which the bimodal distribution in length normally shows up, and as has been said above upper modal fish normally showed spermatogonia with significantly larger diameters. It is likely then in such conditions that fish were sampled which had disproportionally large numbers of spermatogonia with large diameters.

It can be concluded from these results that during the period of somatic growth very few resources were allocated by males to gonadal

growth; and that the upper modal group canalised more energy to gonadal growth than the lower modal one did. These conclusions are in disagreement with the original postulate of Thorpe et al (1982) (see also section 4.3.1).

The results and conclusions thus far discussed contradict those of Bailey et al (1980) and Saunders et al (1982) who found that spermatogonial proliferation appeared as early as June, that is 3-mo before the present fish populations. However, fish stock differences and temperature rearing and conditions can account for these discrepancies. For example Canadian salmon populations smoltify at larger size than the Scottish ones, and their development at the early fry stage is accelerated with heated water as standard procedure in Canadian hatcheries. (Saunders et al, 1982; Thorpe, pers communication). In Canadian populations, such conditions promote the development of fishes with an early faster growth rate and larger size than in Scottish ones. If gonadal growth in juvenile salmon is regulated by general growth rate through the action of growth hormone (GH), as is suggested below, the early appearance of advanced gonadal development in Canadian fish is more related to general body growth rather than with differential allocation of resources.

The female gonads of fishes under the same photoperiodic treatment (and period) were at the primary growth phase (Plates 7 - 10 and section 3.7.2), similar to that described for many teleosts (Yamazaki, 1965; Wallace and Selman, 1981; de Vlaming, 1983) which included a cytoplasm growing faster than the nucleus (i.e. decrease in nucleus-cytoplasm ratio), building up of cytoplasmatic RNA (yolk nucleus and increased haematoxylin affinity), the appearance of

provitelline nucleoli and no mititic activity (Figs 59, 61, 62 and Tables 33, 34 and 36). The provitelline nucleoli (Plates 7, 9 and 10) are thought to reflect ribosomal gene amplification (Chouinard, 1963; Vincent et al, 1969; Vlad, 1976; Wallace and Selman, 1981), whereas the yolk nucleus acts as a centre of organelle formation (Guraya, 1979; de Vlaming, 1983). In other words, female gonadal growth was characterised by oocyte enlargement, with accumulation of organelles, proteins and their precursors.

Because no differences existed between modal groups in oocyte and nucleus diameter (Table 37), nor amongst year groups for the nLD treatment (Table 41), it can be concluded that the ovary growth thus far described represented the normal pattern of resource allocation to reproductive effort by female juvenile salmon, and that it was larger than the male equivalent. The differences due to photoperiodic treatment (Table 39) will be discussed in the context of pituitary regulation of gonadal growth (see section 4.3.1.2). The analysis of female GSI, presented a significant inverse correlation with length (Fig 65), which suggested that the fishes when small allocated more resources to gonadal than to somatic growth, until they reached a certain critical size when they reversed these priorities. If this was so, then small female fishes (i.e. lower modal females) were investing more in reproduction at this stage than the larger (i.e. upper modal ones).

These results again clearly indicated that the notion of differential allocation of resources to somatic and gonadal growth was not a suitable explanation of development of bimodality. Several points were

at variance with the postulates of this hypothesis (see section 4.3.1): first, early stages of oogenesis preceded those of spermatogenesis; second, relatively larger gonadal development was shown by the upper modal group males, whereas the contrary happened with the females; and third, females as a whole invested more in gonadal growth than the male fish did, throughout the first year of growth.

These conclusions were confirmed by the preliminary results of experiments underway, in which fish populations obtained from embryos sterilized by Co-60 irradiation showed the same bimodal frequency distribution in length, as untreated control populations (Thorpe, unpubl.).

4.3.1.2 Pituitary control of gonadal growth

The identification of gonadotropes (GtH cells) was difficult because they showed the same tinctorial affinity as TSH cells. These difficulties were overcome by a topographical differentiation of the two cell populations in accordance with Ball and Baker (1969), Holmes and Ball (1974) and more recently by van Oordt (1982), who defined GtH cells as all those localized in the ventral PPD of the adenohypophysis. However, Lindahl (1980) has reported that RPD basophilic cells in 1+ Atlantic salmon were immunoreactive to anti-salmon gonadotropin (s GtH). This finding suggested that in the present cell measurements GtH cells of RPD were regarded as TSH cell. Follenius et al (1978), on the other hand, have indicated that there is a general cross-reaction between gonadotropin and thyrotropin, as a result of the presence of a common alpha subunit in both hormones. Similarly, Olivereau and Nagahama (1983) demonstrated that the antibody to s GtH cross-reacted with both GtH and TSH cells in five fish species

tested by them. However, Murphy (1980) has demonstrated that in precocious Atlantic salmon parr PPD basophilic cells, in opposition to the RPD ones were hypertrophic, hyperplastic and contained both large and fine granules. In other words, recent evidence tends to sustain the topographical differentiation of the two basophilic cell populations.

The GtH cells, in our study, have the smallest cell size reported in the pituitary (Figs 66a, b and 67). In agreement, in sexually immature 0+ Oncorhynchus nerka and O. keta this cell type could not be found or they were extremely small (Nagahama and Yamamoto, 1969; Nagahama, 1973) and the oocyte primary growth phase coincided with the presence of inactive GtH cells in the pituitary of Poecilia latipinna (Young and Ball, 1982). Since there was no change in GtH cell and nucleus diameters during the observation period of 1981 (Tables 44 and 45), nor between sexes (Tables 46 and 48), or photoperiod treatments (Table 54), it may be stated that young fishes were secreting a synthesising gonadtropin at the same rate all the time. The low level of the pituitary and plasma content of gonadotropin, as well as that of the plasma amount of steroid in juvenile Atlantic salmon and brown trout are in conformity with this interpretation (Dodd et al, 1978; Crim and Evans, 1978; Billard and Breton, 1978).

The gonadal development in both sexes seemed to be highly independent of gonadotropin secretion, since gonadal growth was accompanied by no cytological change of GtH cells. Different studies confirm these results, for example oocyte primary growth and spermatogonial division occur normally in hypophysectomised fish (Vivien, 1939; Barr, 1963, 1968;

Yamazaki, 1965; Lofts, 1968; Dodd, 1972; Lam et al, 1978; de Vlaming, 1983). Similarly consistent are the findings that stages of spermatogenesis very similar to those described here occurred at low secretion of gonadotropin and androgen in brown and rainbow trout (Billard and Breton, 1978).

The physiological role played by the minute amounts of plasma gonadotropin and gonadal steroids is not known but Dodd (1972) has suggested that spermatogonial mitosis in teleosts requires the presence of gonadotropin. In the same way in immature salmonids, Leydig cells show cytological evidence of secretory activity that indicates that some early stages of spermatogenesis are under androgen control (Oota and Yamamoto, 1966; Nagahama et al, 1978; Hunt et al, 1982). No similar evidence exists for the role of steroids in the oocyte primary growth phase. As a whole, the results thus far discussed suggest that small amounts of GtH are needed to maintain the morphological and physiological status of gonads.

The fact that the ovaries of fishes under nLD treatment in the 1982 experiment showed the significantly ($p < 0.005$) highest oocyte and nucleus diameter (Table 39) and at the same time the better growth performance (Figs 12 and 13) suggests that ovary growth was reflecting the general pattern of body growth. If the body growth is dependent on somatotropin (GH) and thyrotropin (TSH) secretion, it may be that primary oocyte growth is GH and TSH dependent as well, although the evidence for the importance of these cellular types on gonadal growth is scanty (for example female GH and TSH cell diameter is higher, but not significantly so than male in 1982 and the contrary in 1981). However, Higgs et al (1976) reported that bovine GH (bGH) and higher

T_4 doses increased the size of oocytes during the primary growth phase in underyearling coho salmon (Oncorhynchus kisutch). In kilifish (Fundulus heteroclitus) mammalian GH, stimulated the build up of spermatogonial cysts (Loft, 1968). Finally, in accordance with Dodd (1968) the early stage of spermatoginial development, in mammals needed GH for activation.

4.3.2 Role through variation in releasing and synthesis of hormones

According to Follénius et al (1978) pituitary cell activity is more or less independent of secretion, and the quantity of hormone stored results from changes in the ratio between elaboration and secretion. As a result, only when there is a considerable accumulation of hormone are clear cytological differences produced, and in many cases cells with low synthetic activity and high secretion rate show very few cytological changes. In the following discussion of the results obtained by cytological methods, special attention has been paid to these concepts.

4.3.2.1 Role of Somatotropes and Thyrotropes in somatic growth

Somatotropes (GH cells) and thyrotropes (TSH cells) were involved in growth regulation, since they showed a consistent and in some cases significant increases in cell and nucleus diameter, and numbers where the fishes were increasing their body weight and length during the 1981 experiment (Fig 66 and Tables 43 and 44). Further corroboration was given by the findings that the initial cell size increase was accompanied by a parallel proliferation of GH cells (SCD) particularly for fishes under nLD (Fig 66d and Table 45).

These results then indicated that GH and TSH cells were active during summer somatic growth. The tables 47 and 58 showed that there were no differences between sexes in the GH and TSG cell diameter, indicating that both sexes were synthesising GH and TSH at the same rate. The light regime was exerting some differential effect on the pituitary since the GH and TSH cell diameters were significantly larger for the LL treatment in the 1981 experiment (Figs 66a, b and Table 43) nLD, LL and L6D treatments which showed similar growth patterns (Tables 22 and 23), at the same time showed no differences in GH and TSH cell measurements (Table 54). Conversely the photoperiodic treatments which showed poorer growth performance at the end of experiment 1982 (8LD, L3D and L4D) (Tables 22 and 23) had smaller GH and TSH cell and nucleus diameters (Figs 67a, c and Tables 54 and 55).

In accordance with these findings, salmonids and the three spined stickleback (Gasterosteus aculeatus) during their rapid growth phase showed pituitaries with GH cells which were highly orangophilic, hyperplastic and hypertrophic (Olivereau, 1957a, b; Leatherland, 1970; Nagahama, 1973, Komourdjian, 1976; Higgs et al, 1976; Jalabert et al, 1982). Similarly, Leatherland (1970) reported that TSH cells of G. aculeatus increased during the period of maximal growth. The results obtained with hormonal treatments are in conformity with this evidence since bovine or fish GH administered to hypophysectomised or intact fish accelerated teleost somatic growth (Kormourdjian et al, 1976; Higgs et al, 1976; Clarke, 1976, Clarke et al, 1977; Kayes, 1977a, b, 1978 and 1979). The same effect was produced by treatment with low doses of thyroxine (T_4) or triiodothyronine (T_3) alone or in combination with GH (Piggins, 1962; Sage, 1967; Higgs et al, 1976). These results, as well as the present ones, indicate that both hormones act synergically to produce growth. Nevertheless, the actions

of GH and thyroid hormones vary from one tissue to another and between species. For example, although bGH promoted cell division in different vertebrates, it did not produce any increase in fibre input of small diameter muscle fibres in Salmo gairdneri (Weatherley and Gill, 1982). In general GH and thyroid hormone increase food consumption and conversion efficiency; finally they promote the synthesis of RNA and proteins (Thorburn and Matty, 1963; Clarke, 1976; Komourdjian et al,1976; Higgs et al, 1976; Kayes, 1977b, 1978, 1979; Medda and Ray, 1979; Jalabert et al, 1982; Leatherland, 1982; Matty et al, 1982). The GH by itself enhanced the mobilisation of body fat (Clarke, 1976; Higgs et al, 1976; Jalabert et al, 1978). Finally, thyroid hormone participated in the regulation of GH cell secretion exerting a negative feedback on it (Higgs et al, 1976; Leatherland, 1982; Jalabert et al, 1982). The opposite control occurred in Tilapia zilli (Leatherland and Hyder, 1975). Grau and Stetson (1979) on the other hand, demonstrated that GH is thyrotrophic in Fundulus heteroclitus. Some of these effects may explain some of the present results, for example the better growing populations of 1981 (LL photoperiod population) and 1982, LL and L6D ones presented at the same time larger GH cell diameters. The former population demonstrated a higher degree of food consumption as revealed by a feeding study using iron particles as markers (see section 3.9) which suggested that the GH action is exerted at least through an increase in appetite. The higher level of RNA-DNA ratio and RNA concentration for the LL group for 1981 and part of the 1982 experiment (Tables 5, 6 and 15, 16) indicated that the GH and TSH may promote the increase of protein precursors. Furthermore the L6D population that showed a better growth performance at the end of Experiment II (Fig 12) when contrasted with nLD population, had elevated GH and TSH cell diameters and RNA concentration at that particular time (Figs 33 and 41). On the

contrary the poorer growth performance populations (8LD, L3D and L4D) were associated with smaller GH and TSH cell diameters (Fig 67a and Table 54) and lower RNA concentrations (Tables 17 - 19).

No direct evidence has been obtained here on the interaction of GH and thyroxine, but the fact that cell diameter variation of GH and TSH cells mirrored one another (Figs 66a, b and 67a, c) seemed to provide indirect support for such interaction.

The higher GH cell and nucleus diameters at the end of September 1981 (Figs 66a, b) coincided with the time at which the percentage water content began its autumn increase. Because this change is inversely correlated with lipid content, it can be suggested that GH cells and other pituitary cells (see below) are involved in the seasonal removal of muscle lipid.

4.3.2.2 Lactotropes and somatic growth

The importance of prolactin cells (LTH cells) in fish growth was suggested by Clarke (1976) who observed that bovine prolactin (bLTH) stimulated growth in juvenile sockeye salmon. Later studies demonstrated that this effect was caused by overlapping of the activity of bGH and bLTH, on fishes (Clarke et al, 1977). Other important effects exerted by prolactin are: osmoregulatory, fat mobilisation, control of gonadal and parental behaviour and thyrotropic (Olivereau, 1968; Nagahama, 1973; de Vlaming et al, 1974; Komourdjian et al, 1976; Grau and Stetson, 1977; Sage and Bern, 1978; Ensor, 1978; Brown and Stetson, 1983).

In the present study, LTH cells showed an increase in diameter during the somatic growth phase in 1981 (Figs 66a, b) but this was significantly only at the end of September for the LL population. On the other hand, no correlation existed between the growth pattern and LTH cell diameters for the 1982 experiment (Figs 67b, c and Table 54), for example the fastest growing population (nLD) showed the same cell diameter as the slower ones (8LD, L3D and L4D). During the same experiment, the LL group (which had to same growth pattern as the nLD one) had the highest LTH cell diameter. This results indicated that the LTH cells were probably not involved in the regulation of somatic growth.

From these results the involvement of LTH cells in lipid dynamics cannot be ruled out, since their diameters were larger at the time when percentage water began to increase in autumn. Nevertheless in 1982 the significant heterogenity ($p < 0.001$) of this cell type by early autumn contrasted with the uniformity of the percentage water at that time (Fig 67b and Table 14). In relation to the latter findings, de Vlaming et al (1976) demonstrated that the LTH effect on deposition and mobilisation of lipid varied seasonally. This seasonal pattern of variation appeared to be caused by changes in photoperiod (Ensor, 1978). The Figures 66, 67b and 68a clearly show that photoperiod affected the LTH cell diameter and number. Whether or not these changes due to photoperiod treatment may reflect changes in sensitivity to LTH as well is not known, but strongly suggest that the normal interaction of LTH and GH in the regulation of lipid removal and deposition can be affected by changes in photoperiodic regime. Further investigation is needed in order to clarify the role of this cell population in association with the regulation of lipid content of muscle.

In respect to the role of LTH in parental behaviour and gonadal activity, the first possibility can be ruled out for the obvious reason that no reproductive activities occur in 0+ salmon. The second role may be discounted on the grounds that it was the female fishes which normally showed differences in LTH cell diameter (except for the males of LL population in 1981 (Tables 46 and 57)) whereas the evidence so far collected associated this cell type with male gonad maturation (for review see Ensor, 1978).

The thyrotropic effect of LTH, though well recorded in teleosts (Ball and Baker, 1969; Ensor, 1978; Grau and Stetson, 1977; Leatherland, 1982) has not been demonstrated in salmonids (Milne and Leatherland, 1978). Indirect evidence in the present work corroborated the latter finding. Since in teleosts TSH secretion is under a negative feedback regulation from the secretion of the thyroid gland (Peter, 1973; Ball, 1981; Leatherland, 1982; Gorbman et al, 1983) therefore with an increase in LTH cell diameter should be accompanied by decrease in TSH cell diameters. However, in 1981 experiment a parallel increase in cell diameter was observed in both cellular types and photoperiodic treatments (Figs 66a, b). In the same way the 1982 LTH and TSH cells did not show the expected inverse pattern of cell sizes (Figs 67a, b) and whereas TSH cells for the different treatments showed no differences, the LTH ones were significantly heterogeneous ($p<0.001$) (Figs 67c, d and Table 54). It may be concluded then that no correlation existed between the TSH and LTH cell diameter variation.

The most consistent physiological role of fish LTH is the osmoregulatory one (Olivereau, 1968; Ball and Baker, 1969; Holmes and Ball, 1974;

Ensor, 1978) exerted by promoting electrolite retention in freshwater. This function seems to be associated with the regulation of the ionic balance of young Atlantic salmon.

The female fish had larger LTH cell and nucleus diameters more often than the male, in both experiments (Tables 46, 48 and 57), suggesting that for an unknown reason the females were subjected to greater osmoregulatory problems. Similarly the small sized fishes showed more frequently a significantly higher LTH cell diameter (Tables 52, 61 and 62). A two-way ANCOVA test demonstrated no interaction effect of both factors (sex and size) on LTH cell diameter ($F = 0.1050$, $p > 0.25$). The effect of size on LTH cell diameter indicated that smaller fish were subjected to a more acute osmotic stress possibly due to their higher surface area - volume ratio, which allowed passive ion losses more easily.

4.3.2.3 Synthesis and releasing of hormones and fish size

The fundamental assumption about the emergence of the bimodal frequency distribution in length and weight, was that each modal group synthesised and released pituitary hormones differentially, especially thyrotropin. It was specifically suggested that the upper modal group would have a lower threshold response to thyroxine and higher TSH secretion than the lower modal one; and that such thresholds applied at the target and secretory sites (Simpson and Thorpe, 1976; Thorpe and Morgan, 1978; Thorpe et al, 1980, 1982). In order to contribute to the elucidation of this hypothesis, data of pituitary cell diameters segregated by fish size were analysed. The result showed a consistent fish size effect on LTH and TSH cell diameters

(Tables 52, 53, 61 and 62). The meaning of LTH cell diameter variation and fish size has been discussed above.

If the fundamental difference between the two modal groups is the synthesis and release of TSH and the sensitivity threshold to it, differences in TSH cell diameters would be expected. The TSH cells indeed presented significant differences between fish size (Tables 52 and 61), but they varied with date and photoperiod treatment. Thus there was not a single and simple pattern of cell diameter change, suggesting that TSH cell activity varied with season and photoperiod for the different fish size ranges. These results then did not give a clear answer to our original question about differences in TSH secretion by the two modal groups, but indicated that these cells possessed the degree of flexibility for the functions outlined at the beginning of this section. Better designed experiments and observations must be carried out before a definitive answer may be given about the role of TSH cells in the development of bimodality.

4.4 Link between the endogenous and exogenous regulating factors on growth and development of bimodality in juvenile Atlantic salmon

Hoar (1965, 1976) postulated that fish trophic hormones of the adenohypoplysis are the link between environmental changes and the internal physiological processes associated with them. The results presented here contributed to the validation of this postulate since, somatic growth, the proportion of fish in each modal group, the amount of nucleic acid synthesised by the muscle, and the cell diameters of the various pituitary cells, are all modified by photoperiod. In some cases a good correlation has been found between

the morphometric estimate of pituitary cell activity modified by photoperiod and somatic growth and development. It may be concluded then that it was through the pituitary that the change in day-length exerted its effect on the body of juvenile Atlantic salmon. The identity of the receptor areas for light information, and the processing centres are not known. However recent evidence has suggested that the retinae and pineal organ were the probable receptors, and that information on light change was transmitted from these to a hypothalamic processing centre (Hafeez and Zerihun, 1974; Hafeez et al, 1978; Tamura and Hanyu, 1980; Kavaliers, 1980, 1982; Scharrer, 1965; Hoar, 1965; Zambrano, 1972; Peter, 1973; Poston, 1978; Ball, 1981). The regulatory role of this centre in the development of bimodality in Atlantic salmon, needs to be studied in the near future.

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TABLES

Table 1. Change in fork length, wet and dry weight, water content (in percentage); specific growth rate and condition factor (K) of whole juvenile Atlantic salmon, from first feeding to 1st July, of Experiment I (1981). Values shown are means ± standard error.

Date	N	Fork length (mm)	Wet weight (mg)	Dry weight (mg)	% water	G_w % day^{-1}	K
7/5	23		194.10 ± 5.84	36.90 ± 1.40	81.85 ± 0.80	1.98	
13/5	24		197.50 ± 3.49	31.50 ± 0.55	84.00 ± 0.30	0.28	
22/5	30		219.80 ± 4.93	36.60 ± 1.21	83.42 ± 0.18	1.89	
27/5	25		277.80 ± 10.00	47.80 ± 2.14	82.84 ± 0.22	4.68	
2/6	24	32.40 ± 0.30	230.50 ± 11.43	45.90 ± 2.35	85.83 ± 0.26	2.86	0.94
11/6	24	35.90 ± 0.30	460.00 ± 12.25	85.60 ± 2.80	81.54 ± 0.13	4.01	0.99
17/6	10	37.20 ± 0.79	526.00 ± 32.24	96.00 ± 4.49	82.24 ± 0.59	2.23	1.14
26/6	10	41.50 ± 0.40	741.00 ± 24.10	146.60 ± 11.29	79.10 ± 0.29	3.81	1.04
1/7	20	42.30 ± 0.60	734.00 ± 28.00	148.30 ± 6.24	79.83 ± 0.16	-1.89	0.97

Table 2. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of whole juvenile Atlantic salmon, from first feeding to 1st July, of Experiment I (1981). Values shown are mean ± standard error.

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
7/5	23	2558.47 ± 100.26	1634.16 ± 64.46	1.60 ± 0.06	0.921 ± 0.01	0.59 ± 0.09	40.18 ± 1.23	63.06 ± 3.56
13/5	24	2634.49 ± 86.24	2031.93 ± 56.36	1.32 ± 0.06	0.83 ± 0.01	0.64 ± 0.01	38.96 ± 1.41	50.03 ± 2.37
22/5	30	3428.36 ± 94.63	1617.85 ± 46.61	2.19 ± 0.07	1.24 ± 0.01	0.58 ± 0.01	29.87 ± 0.84	63.43 ± 1.87
27/5	25	2885.98 ± 94.61	1210.61 ± 50.48	2.44 ± 0.10	1.40 ± 0.04	0.58 ± 0.01	35.33 ± 1.30	86.17 ± 4.44
2/6	24	3296.85 ± 63.55	2321.22 ± 95.76	1.47 ± 0.05	1.50 ± 0.03	1.04 ± 0.02	30.58 ± 0.57	44.61 ± 1.64
11/6	24	5656.31 ± 206.79	1388.48 ± 33.22	3.84 ± 0.19	4.78 ± 0.07	1.18 ± 0.02	18.16 ± 0.55	73.03 ± 1.65
17/6	10	5462.81 ± 93.31	1577.25 ± 60.66	3.49 ± 0.17	5.26 ± 0.24	1.51 ± 0.06	18.45 ± 0.56	63.60 ± 1.21
26/6	10	3523.69 ± 202.49	1536.10 ± 84.37	2.33 ± 0.15	6.11 ± 0.15	2.24 ± 0.15	27.11 ± 3.84	67.17 ± 3.88
1/7	20	2401.84 ± 71.84	1865.95 ± 95.18	1.29 ± 0.06	3.55 ± 0.07	2.27 ± 0.08	42.67 ± 1.47	55.57 ± 1.83

Table 3 . Change in fork length, wet weight, specific growth rate and condition factor (K) of juvenile Atlantic salmon subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error.

	nLD				LL				
Date	N	Fork length (mm)	Wet weight (mg)	G_w % day^{-1}	K	N	Fork length (mm)	Wet weight (mg)	G_w % day^{-1}	K
8/7	50	47.50 ± 0.49	1120.0 ± 35.36	3.44	1.04	50	46.90 ± 0.41	1060.0 ± 31.11	2.98	1.03
22/7	46	51.80 ± 0.65	1450.0 ± 53.08	1.84	1.04	50	51.80 ± 0.48	1480.0 ± 42.43	2.38	1.06
5/8	50	57.00 ± 0.74	1870.0 ± 70.71	1.50	1.01	50	57.60 ± 0.53	2080.0 ± 55.15	2.00	1.09
20/8	48	61.00 ± 0.74	2180.0 ± 90.93	1.28	0.96	50	64.50 ± 0.75	2610.0 ± 100.41	1.89	0.97
4/9	51	64.40 ± 0.98	2630.0 ± 127.40	1.25	0.98	50	65.50 ± 1.06	2920.0 ± 141.42	0.94	1.04
16/9	50	65.50 ± 0.96	2810.0 ± 136.00	0.55	1.00	50	70.50 ± 1.00	3810.0 ± 172.53	2.22	1.09
30/9	44	67.20 ± 1.01	3140.0 ± 149.25	0.79	1.04	43	71.20 ± 1.34	3770.0 ± 203.65	-0.08	1.04

Table 4. Change in dry weight and water content (%) of skeletal muscle of juvenile Atlantic salmon subjected to natural photoperiod (nLD) or constant light (LL), Experiment I (1981). Values shown are means ± standard error.

	nLD			LL		
Date	N	Dry weight (mg)	% water	N	Dry weight (mg)	% water
8/7	50	100.61 ± 3.89	75.51 ± 0.17	50	89.65 ± 3.43	78.76 ± 0.18
22/7	46	142.83 ± 6.29	76.99 ± 0.11	50	136.10 ± 4.53	77.71 ± 0.32
5/8	50	172.18 ± 7.31	77.03 ± 0.61	50	184.80 ± 5.52	77.35 ± 0.09
20/8	48	185.38 ± 8.68	75.15 ± 0.13	50	212.10 ± 8.65	76.41 ± 0.13
4/9	51	166.42 ± 6.43	75.12 ± 0.10	50	161.30 ± 6.28	74.44 ± 0.11
16/9	50	168.54 ± 6.25	75.59 ± 0.06	50	188.60 ± 5.88	75.73 ± 0.12
30/9	44	160.78 ± 5.03	75.98 ± 0.17	43	180.70 ± 7.11	76.29 ± 0.12

Table 5. Change in RNA and DNA concentrations (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of juvenile Atlantic salmon subjected to natural photoperiod (nLD), Experiment I (1981). Values shown are means ± standard error.

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
8/7	50	2067.46 ± 56.08	1186.10 ± 15.92	1.90 ± 0.08	2.04 ± 0.08	1.19 ± 0.08	49.87 ± 1.20	93.46 ± 3.85
22/7	46	1406.39 ± 30.91	419.51 ± 3.59	3.40 ± 0.09*	1.95 ± 0.08	0.58 ± 0.02	72.63 ± 1.14	244.35 ± 7.47
5/8	50	1125.52 ± 24.42	655.77 ± 6.93	1.75 ± 0.04***	1.94 ± 0.09	1.09 ± 0.05	90.69 ± 1.74	158.91 ± 3.14
20/8	48	810.91 ± 13.91	633.55 ± 4.03	1.29 ± 0.03**	1.50 ± 0.08	1.16 ± 0.05	125.60 ± 2.24	160.09 ± 2.74
4/9	51	798.13 ± 21.62	603.09 ± 6.08	1.38 ± 0.05***	1.36 ± 0.07	0.95 ± 0.05	125.90 ± 2.48	192.54 ± 14.74
16/9	50	749.18 ± 21.68	641.26 ± 6.15	1.18 ± 0.03***	1.27 ± 0.06	1.07 ± 0.05	139.57 ± 4.75	160.91 ± 5.53
30/9	44	847.44 ± 16.03	628.59 ± 4.87	1.40 ± 0.05***	1.37 ± 0.06	1.00 ± 0.03	119.76 ± 2.21	164.62 ± 5.45

Significance of differences from constant light (LL)

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 6 . Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of juvenile Atlantic salmon subjected to constant photoperiod (LL). Experiment I (1981). Values shown are means ± standard error.

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
8/7	50	1814.8 ± 43.89	887.68 ± 12.46	2.08 ± 0.06	1.60 ± 0.06	0.79 ± 0.03	47.12 ± 3.99	56.68 ± 1.36
22/7	46	1483.87 ± 26.11	557.74 ± 7.44	2.97 ± 0.14*	2.01 ± 0.08	0.76 ± 0.05	68.83 ± 1.36	201.14 ± 1.36
5/8	50	1412.16 ± 32.49	379.89 ± 9.19	4.56 ± 0.26***	2.61 ± 0.09	0.69 ± 0.06	72.54 ± 1.65	327.74 ± 19.67
20/8	48	1040.43 ± 32.41	613.55 ± 9.21	1.74 ± 0.07**	2.22 ± 0.12	1.28 ± 0.05	99.98 ± 2.57	165.05 ± 4.42
4/9	51	1051.31 ± 27.48	677.04 ± 7.81	1.58 ± 0.04***	1.72 ± 0.09	1.08 ± 0.04	96.00 ± 2.91	152.73 ± 4.03
16/9	50	893.95 ± 26.80	530.98 ± 7.61	1.69 ± 0.05***	1.71 ± 0.08	0.99 ± 0.04	115.09 ± 3.98	193.72 ± 4.99
30/9	44	835.62 ± 17.88	563.97 ± 5.49	1.52 ± 0.03***	1.53 ± 0.07	1.02 ± 0.04	124.06 ± 6.75	176.92 ± 3.26

Significance of differences from natural light (nLD)

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Table 8 . Change in fork length, wet weight, specific growth rate and condition factor of separate modal groups of juvenile Atlantic salmon subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error.

nLD

Date	N	Fork length (mm)		Wet weight (mg)		G_w % day^{-1}		Condition factor	
		Upper mode	Lower mode	Upper mode	Lower mode	Upper mode	Lower mode	Upper mode	Lower mode
15/10	20	81.70 ± 0.65	59.90 ± 0.78	5850.0 ± 154.29	2130.0 ± 80.50			1.07	0.99
28/10	20	81.11 ± 0.78	60.20 ± 0.47	5530.0 ± 257.15	2190.0 ± 55.90	-0.43	0.21	1.04	1.00
11/11	20	80.80 ± 0.69	62.60 ± 0.69	5370.0 ± 129.69	2360.0 ± 64.85	-0.03	0.53	1.02	0.96
25/11	20	83.30 ± 1.07	58.70 ± 0.56	5790.0 ± 259.38	1870.0 ± 58.14	0.54	-1.66	1.00	0.92

Table 8 /Contd. Change in fork length, wet weight, specific growth rate and condition factor of separate modal groups of juvenile Atlantic salmon subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error.

LL

Date	N	Fork length (mm)		Wet weight (mg)		G_w % day^{-1}		Condition factor	
		Upper mode	Lower mode	Upper mode	Lower mode	Upper mode	Lower mode	Upper mode	Lower mode
15/10	20	83.70 ± 0.89	60.10 ± 1.07	6380.0 ± 221.37	2180.0 ± 107.33			1.09	1.00
28/10	20	83.80 ± 0.98	61.00 ± 0.85	6150.0 ± 228.08	2190.0 ± 78.26	-0.28	0.04	1.05	0.96
11/11	20	84.20 ± 0.94	62.30 ± 0.54	6270.0 ± 194.54	2390.0 ± 55.90	0.15	0.67	1.05	0.99
25/11	20	87.60 ± 0.69	66.30 ± 0.40	6940.0 ± 169.94	2820.0 ± 64.85	0.73	1.18	1.03	0.97

Table 9 . Change in RNA and DNA concentration (in ug/100 mg of dry tissue) and RNA - DNA ratio of skeletal muscle of separate modal groups of juvenile Atlantic salmon subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error.

nLD

Date	N	[RNA] Upper mode	[RNA] Lower mode	[DNA] Upper mode	[DNA] Lower mode	RNA/DNA Upper mode	RNA/DNA Lower mode
15/10	20	830.54 ± 52.56	564.16 ± 35.60***	434.09 ± 31.00	577.43 ± 42.93 ***	2.05 ± 0.14*	0.97 ± 0.08
28/10	20	844.19 ± 52.11	647.10 ± 43.42**	448.25 ± 42.12	453.02 ± 45.61	2.08 ± 0.16*	1.57 ± 0.10
11/11	20	806.23 ± 55.47	644.50 ± 43.51*	441.77 ± 44.83	441.18 ± 28.89	2.20 ± 0.30**	1.46 ± 0.06
25/11	20	909.89 ± 21.12	873.23 ± 24.64	462.71 ± 17.75	598.31 ± 14.60 ***	2.02 ± 0.10*	1.43 ± 0.04

Table 9 /Contd. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and RNA - DNA ratio of skeletal muscle of separate modal groups of juvenile Atlantic salmon subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are mean ± standard error.

LL

Date	N	[RNA] Upper mode	[RNA] Lower mode	[DNA] Upper mode	[DNA] Lower mode	RNA/DNA Upper mode	RNA/DNA Lower mode
15/10	20	1007.05 ± 73.92	827.97 ± 36.76***	500.59 ± 38.41	586.62 ± 31.84**	2.07 ± 0.20*	1.42 ± 0.06
28/10	20	688.58 ± 64.92	675.72 ± 35.53	430.00 ± 59.50	539.32 ± 57.36*	1.74 ± 0.23	1.39 ± 0.16
11/11	20	1059.05 ± 45.32	1062.70 ± 88.64	417.35 ± 34.73	510.63 ± 38.31**	2.63 ± 0.22*	2.14 ± 0.20
25/11	20	1155.54 ± 41.17	1054.71 ± 75.52*	563.66 ± 18.24	604.35 ± 32.93	2.44 ± 0.30***	1.99 ± 0.25

Significance of differences * $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Table 10. Change in fork length (mm), wet and dry weight (mg), water content (in percentage), specific growth rate, and condition factor (K) of whole Salmo salar (O+) from first feeding to 29th June. Experiment II (1982). Values shown are means ± standard error.

Date	N	Fork length	Wet weight	Dry weight	% water	G_w % day^{-1}	K
7/5	25	28.3 ± 0.10	132.22 ± 4.06	28.20 ± 0.26			
13/5	15	28.3 ± 0.15	169.30 ± 2.19	28.70 ± 0.52	83.83 ± 0.28	4.12	0.75
25/5	25	30.4 ± 0.14	252.10 ± 4.48	41.90 ± 0.82	83.25 ± 0.18	3.32	0.897
8/6	25	33.5 ± 0.38	368.70 ± 13.40	70.70 ± 2.92	80.95 ± 0.17	2.72	0.98
29/6	22	29.9 ± 0.32	400.00 ± 10.66	41.60 ± 2.17	82.36 ± 0.20	0.39	1.50

Table 11. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, and Dry W - DNA ratio of whole juvenile Atlantic salmon, from first feeding to 29th June 1982. Experiment II (1982). Values shown are means ± standard error.

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total	DNA total	Dry W/RNA	Dry W/DNA
7/5	25	3727.45 ± 49.00	1613.20 ± 27.80	2.32 ± 0.05	1.05 ± 0.02	0.45 ± 0.01	26.98 ± 0.37	62.44 ± 1.10
13/5	15	2802.22 ± 137.36	1765.04 ± 40.54	1.62 ± 0.09	0.81 ± 0.05	0.50 ± 0.01	37.96 ± 3.53	57.42 ± 1.21
25/5	25	3247.35 ± 95.40	2183.17 ± 46.60	1.50 ± 1.56	1.36 ± 0.05	0.93 ± 0.03	31.48 ± 0.94	45.38 ± 1.47
8/6	25	3317.72 ± 96.80	1464.19 ± 53.92	2.34 ± 1.97	2.35 ± 0.12	1.02 ± 0.05	30.69 ± 0.80	70.53 ± 2.59
29/6	22	3096.99 ± 82.59	1777.89 ± 50.32	1.77 ± 2.05	1.28 ± 0.07	0.71 ± 0.02	32.51 ± 0.96	57.90 ± 1.86

Table 12. Change in fork length (mm), wet weight (mg), specific growth rate and condition factor (K) of Salmo salar (0+), subjected to natural photoperiod (nLD), constant light (LL), and constant autumn photoperiod (8LD). Experiment II (1982). Values shown are means ± standard error.

nLD

Date	N	Fork length	Wet weight	G_w % day^{-1}	K
9/7	20	42.60 ± 0.10	830.00 ± 51.43	7.30	1.07
26/7	20	48.40 ± 0.56	1200.00 ± 44.72	2.17	1.06
6/8	20	48.60 ± 0.80	1240.00 ± 58.14	0.30	1.08
20/8	20	50.90 ± 1.19	1430.00 ± 91.68	1.02	1.08
6/9	20	52.40 ± 0.92	1520.00 ± 84.97	0.36	1.06
20/9	20	54.10 ± 1.59	1710.00 ± 149.82	0.84	1.08
4/10	20	53.80 ± 1.25	1650.00 ± 138.64	-0.26	1.06

LL

Date	N	Fork length	Wet weight	G_w % day^{-1}	K
9/7	20	41.6 ± 1.12	720.00 ± 51.43	5.88	1.00
26/7	19	46.00 ± 0.60	1010.00 ± 48.18	1.99	1.04
6/8	20	47.50 ± 0.92	1140.00 ± 64.85	1.10	1.06
20/8	20	48.00 ± 1.21	1210.00 ± 80.50	0.43	1.09
6/9	20	51.90 ± 0.98	1440.00 ± 84.97	1.02	1.03
20/9	20	55.70 ± 0.12	1910.00 ± 149.82	2.02	1.10
14/10	19	51.60 ± 0.85	1440.00 ± 94.06	-2.02	1.05

Table 12/Contd. Change in fork length (mm), wet weight (mg), specific growth rate and condition factor (K) of Salmo salar (0+), subjected to natural photoperiodic (nLD), constant light (LL), and constant autumn photoperiod (8LD). Experiment II (1982). Values shown are means ± standard error.

8LD

Date	N	Fork length	Wet weight	G_w % day^{-1}	K
9/7	19	39.40 ± 0.11	630.00 ± 50.47	4.54	1.03
26/7	20	43.70 ± 0.80	830.00 ± 49.19	1.62	0.99
6/8	19	43.60 ± 0.96	950.00 ± 75.71	1.23	1.15
20/8	20	44.90 ± 1.10	1010.00 ± 67.08	0.44	1.12
6/9	20	47.00 ± 0.94	1100.00 ± 67.08	0.50	1.06
20/9	18	47.60 ± 0.12	1160.00 ± 68.35	0.38	1.08
4/10	20	47.50 ± 1.14	1090.00 ± 76.03	-0.44	1.02

Table 13. Change in fork length (mm). wet weight (mg), specific growth rate and condition factor (K) of Salmo salar (0+), subjected to three different rates of photoperiodic change (L3D, L4D, L6D). Experiment II (1982). Values shown are means ± standard error.

L3D

Date	N	Fork length	Wet weight	G_w % day^{-1}	K
9/7	20	41.10 ± 0.60	670.00 ± 33.54	5.16	0.96
26/7	20	46.40 ± 0.78	1100.00 ± 51.43	2.92	1.10
6/8	20	47.10 ± 0.85	1190.00 ± 73.79	0.71	1.14
20/8	20	48.60 ± 0.63	1220.00 ± 51.43	0.06	1.04
6/9	20	50.70 ± 0.94	1430.00 ± 78.26	1.03	1.01
20/9	20	52.20 ± 0.92	1490.00 ± 93.91	0.29	1.05
4/10	20	51.90 ± 1.25	1500.00 ± 120.75	0.05	1.07

L4D

Date	N	Fork length	Wet weight	G_w % day^{-1}	K
9/7	20	39.30 ± 0.94	590.00 ± 38.01	3.89	0.97
26/7	20	44.80 ± 1.05	980.00 ± 64.85	2.98	1.09
6/8	20	47.90 ± 0.87	1210.00 ± 69.32	1.92	1.10
20/8	20	50.00 ± 0.76	1330.00 ± 60.37	0.68	1.06
6/9	20	49.90 ± 0.98	1320.00 ± 91.68	-0.04	1.06
20/9	20	51.60 ± 0.89	1440.00 ± 76.03	0.62	1.05
4/10	20	51.60 ± 1.12	1470.00 ± 98.39	0.15	1.07

Table 13/Contd. Change in fork length (mm), wet weight (mg), specific growth rate and condition factor (K) of Salmo salar (0+), subjected to three different rates of photperiodic change (L3D, L4D, L6D). Experiment II (1982). Values shown are : means ± standard error.

L6D

Date	N	Fork length	Wet weight	G_w % day^{-1}	K
9/7	20	40.02 ± 1.23	680.00 ± 58.14	5.31	1.05
26/7	20	44.00 ± 0.92	930.00 ± 55.90	2.29	1.09
6/8	20	48.30 ± 0.67	1290.00 ± 55.90	2.97	1.14
20/8	20	50.10 ± 0.60	1400.00 ± 51.43	0.58	1.11
6/9	20	53.20 ± 1.05	1700.00 ± 116.28	1.14	1.13
20/9	20	52.80 ± 1.07	1580.00 ± 116.28	-0.52	1.07
4/10	20	56.40 ± 1.83	1880.00 ± 196.77	1.24	1.05

Table 14. Change in dry weight (mg) and water content (%) of skeletal muscle of Salmo salar (0+), subjected to different photoperiodic regime (nLD, LL, 8LD, L3D, L4D, L6D). Experiment II (1982). Values shown are means ± standard error.

	nLD			LL			8LD		
Date	N	Dry weight	% water	N	Dry weight	% water	N	Dry weight	% water
9/7	20	49.70 ± 3.64	79.57 ± 0.22	20	51.00 ± 4.49	80.84 ± 0.38	19	46.00 ± 4.63	81.04 ± 0.51
26/7	20	89.30 ± 2.95	77.38 ± 0.08	19	74.60 ± 3.19	77.96 ± 0.10	20	65.20 ± 3.94	77.34 ± 0.13
6/8	20	92.11 ± 4.67	77.66 ± 0.16(a)	20	81.30 ± 5.08	78.37 ± 0.14	19	63.30 ± 4.40	77.32 ± 0.29
20/8	20	104.70 ± 7.49	77.05 ± 0.31	20	80.40 ± 6.02	78.27 ± 0.28	20	71.80 ± 4.90	77.30 ± 0.16
6/9	20	105.80 ± 6.55	77.78 ± 0.12(b)	20	89.10 ± 5.81	76.66 ± 0.17	20	73.60 ± 5.23	77.61 ± 0.14
20/9	20	123.00 ± 11.85	76.54 ± 0.09	20	123.90 ± 9.35	78.10 ± 0.14	18	79.90 ± 5.07	76.66 ± 0.48
4/10	20	107.00 ± 8.30	77.53 ± 0.18	19	95.60 ± 7.39	77.54 ± 0.25	20	69.30 ± 5.43	78.07 ± 0.15

Table 14/Contd. Change in dry weight (mg) and water content (%) of skeletal muscle of Salmo salar (0+), subjected to different photoperiodic regime (nLD, LL, 8LD, L3D, L4D, L6D). Experiment II (1982). Values shown are means ± standard error.

	L3D			L4D			L6D		
Date	N	Dry weight	% water	N	Dry weight	% water	N	Dry weight	% water
9/7	20	48.00 ± 3.26	80.43 ± 0.18	20	38.20 ± 3.35	79.95 ± 0.28	20	41.00 ± 4.47	82.10 ± 0.57
26/7	20	85.40 ± 6.35	77.23 ± 0.15	20	67.80 ± 4.65	77.55 ± 0.15	20	72.70 ± 4.90	77.20 ± 0.17
6/8	20	89.60 ± 5.52	76.73 ± 0.12(a)	20	89.70 ± 5.84	77.61 ± 0.13(a)	20	92.60 ± 4.36	77.20 ± 0.12(a)
20/8	20	88.40 ± 4.47	77.18 ± 0.11	20	94.60 ± 4.38	77.16 ± 0.13	20	96.30 ± 3.47	76.98 ± 0.11
6/9	20	101.50 ± 6.51	77.32 ± 0.17(b)	20	96.70 ± 8.12	76.61 ± 0.18(b)	20	121.10 ± 9.55	77.00 ± 0.27(b)
20/9	20	102.30 ± 7.85	77.60 ± 0.11	20	94.80 ± 6.15	77.86 ± 0.13	20	111.80 ± 8.68	76.70 ± 0.09
4/10	20	98.30 ± 7.58	77.65 ± 0.15	20	102.20 ± 10.61	77.15 ± 0.26	20	117.70 ± 11.99	77.96 ± 0.13

(a) LD; L4D; L6D; L3D ($p<0.05$; Groups which are not significantly different by the SNK test are underlined.)

(b) LD; L3D; L6D; L4D ($p<0.005$; Groups which are not significantly different by the SNK test are underlined.)

Table 15. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of (0+) *Salmo salar* subjected to natural photoperiod (nLD). Experiment II (1982). Values shown are means ± standard error.

nLD

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
9/7	20	1862.80 ± 71.80	818.27 ± 31.47	2.29 ± 0.04	0.89 ± 0.05	0.39 ± 0.03	54.93 ± 1.76	129.90 ± 4.43
26/7	20	1042.55 ± 35.15	131.40 ± 25.63	12.88 ± 1.57	0.93 ± 0.04	0.11 ± 0.02	98.02 ± 4.27	795.66 ± 16.47
6/8	20	805.40 ± 24.51	406.61 ± 31.00	2.16 ± 0.14	0.73 ± 0.05	0.36 ± 0.03	135.46 ± 9.84	280.89 ± 22.81
20/8	20	745.51 ± 21.94	929.47 ± 60.80	0.87 ± 0.07	0.76 ± 0.05	0.94 ± 0.07	130.69 ± 5.81	115.67 ± 7.51
6/9	20	978.03 ± 47.76	508.28 ± 21.65	2.00 ± 0.14	1.03 ± 0.08	0.53 ± 0.03	106.29 ± 4.61	204.70 ± 9.37
20/9	20	861.33 ± 31.08	623.92 ± 29.07	1.42 ± 0.06	1.04 ± 0.11	0.75 ± 0.07	134.29 ± 0.36	165.42 ± 6.52
4/10	20	702.57 ± 22.81	630.91 ± 12.52	1.12 ± 0.04	0.77 ± 0.08	0.66 ± 0.04	141.97 ± 8.36	158.73 ± 3.14

Table 16. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of (0+) Salmo salar subjected to constant photoperiod (LL). Experiment II (1982). Values shown are means ± standard error.

LL

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
9/7	20	1813.27 ± 80.95	728.24 ± 32.87	2.50 ± 0.05	0.87 ± 0.06	0.35 ± 0.02	57.04 ± 2.27	142.49 ± 5.58
26/7	19	828.23 ± 18.34	184.85 ± 34.21	12.69 ± 2.73	0.62 ± 0.03	0.13 ± 0.02	119.86 ± 2.45	749.94 ± 18.10
6/8	20	861.55 ± 33.76	461.51 ± 41.37	2.16 ± 0.20	0.71 ± 0.03	0.35 ± 0.03	117.52 ± 3.58	245.90 ± 25.53
20/8	20	745.05 ± 35.55	488.63 ± 33.99	1.63 ± 0.16	0.58 ± 0.05	0.39 ± 0.04	139.22 ± 5.71	221.59 ± 13.80
6/9	20	977.97 ± 51.65	506.60 ± 49.86	2.35 ± 0.34	0.85 ± 0.06	0.45 ± 0.06	101.60 ± 6.82	237.00 ± 23.38
20/9	20	1568.03 ± 112 .25	691.70 ± 12.75	2.27 ± 0.16	1.95 ± 0.20	0.84 ± 0.05	68.37 ± 3.54	144.08 ± 3.31
4/10	19	668.63 ± 29.52	635.41 ± 25.49	1.04 ± 0.05	0.64 ± 0.06	0.60 ± 0.04	156.53 ± 7.08	160.61 ± 6.65

Table 17. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of (0+) Salmo salar subjected to autumn photoperiod (8LD). Experiment II (1982). Values shown are means ± standard error.

8LD

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
9/7	19	1981.66 ± 100.94	864.15 ± 34.87	2.44 ± 0.08	0.79 ± 0.08	0.32 ± 0.03	52.63 ± 2.42	125.86 ± 5.94
26/7	20	790.26 ± 18.56	97.69 ± 15.21	13.29 ± 2.41	0.51 ± 0.03	0.06 ± 0.01	127.84 ± 2.91	1326.10 ± 87.00
6/8	19	1131.59 ± 58.04	700.74 ± 25.24	1.63 ± 0.08	0.70 ± 0.05	0.46 ± 0.04	92.22 ± 4.40	141.27 ± 5.20
20/8	20	841.76 ± 46.29	782.12 ± 67.98	1.12 ± 0.07	0.59 ± 0.04	0.54 ± 0.05	123.27 ± 6.80	141.72 ± 9.20
6/9	20	796.87 ± 67.75	539.57 ± 25.94	1.52 ± 0.12	0.57 ± 0.05	0.39 ± 0.02	134.58 ± 6.10	184.90 ± 8.53
20/9	18	1011.20 ± 71.65	707.72 ± 53.27	1.53 ± 0.13	0.80 ± 0.07	0.57 ± 0.06	105.37 ± 5.49	150.77 ± 7.93
4/10	20	841.49 ± 34.88	590.83 ± 17.44	1.45 ± 0.08	0.57 ± 0.04	0.40 ± 0.03	123.36 ± 5.88	171.80 ± 4.62

Table 18. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of (0+) Salmo salar subjected to L3D photoperiod. Experiment II (1982). Values shown are means ± standard error.

L3D

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
9/7	20	1959.05 ± 64.40	631.69 ± 18.78	3.13 ± 0.10	0.87 ± 0.05	0.28 ± 0.02	59.83 ± 8.50	160.88 ± 4.60
26/7	20	968.25 ± 37.34	181.44 ± 22.81	6.84 ± 0.85	0.80 ± 0.05	0.14 ± 0.01	105.87 ± 3.59	570.04 ± 36.01
6/8	20	1067.30 ± 35.55	639.37 ± 17.66	1.66 ± 0.06	0.96 ± 0.07	0.56 ± 0.03	96.11 ± 37.02	159.00 ± 4.46
20/8	20	875.89 ± 26.83	407.59 ± 34.21	2.98 ± 0.74	0.77 ± 0.04	0.35 ± 0.03	116.46 ± 3.75	251.52 ± 17.04
6/9	20	999.25 ± 21.47	526.11 ± 19.90	1.94 ± 0.08	1.02 ± 0.07	0.52 ± 0.03	98.56 ± 2.68	196.86 ± 6.86
20/9	20	714.58 ± 12.97	628.55 ± 12.97	1.14 ± 0.03	0.73 ± 0.06	0.64 ± 0.04	141.12 ± 2.84	159.20 ± 3.75
4/10	20	757.55 ± 25.27	660.40 ± 17.22	1.15 ± 0.04	0.75 ± 0.07	0.65 ± 0.05	135.02 ± 4.13	153.26 ± 3.91

Table 19. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of (♀) Salmo salar subjected to L4D photoperiod. Experiment II (1982). Values shown are means ± syandard error.

L4D

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
9/7	20	1417.16 ± 49.64	971.74 ± 26.83	1.46 ± 0.03	0.52 ± 0.03	0.36 ± 0.02	72.09 ± 2.32	104.30 ± 2.72
26/7	20	1111.11 ± 21.47	145.20 ± 19.45	10.96 ± 1.46	0.75 ± 0.05	0.09 ± 0.01	90.58 ± 1.66	800.95 ± 6.92
6/8	20	1101.76 ± 61.72	631.46 ± 17.66	1.77 ± 0.08	0.96 ± 0.06	0.56 ± 0.03	95.56 ± 4.30	160.63 ± 4.31
20/8	20	940.50 ± 36.00	479.49 ± 28.17	2.06 ± 0.13	0.89 ± 0.05	0.56 ± 0.03	109.32 ± 4.26	217.37 ± 15.56
6/9	20	959.47 ± 28.17	443.00 ± 63.28	3.39 ± 0.08	0.93 ± 0.09	0.33 ± 0.02	105.91 ± 3.14	246.90 ± 14.29
20/9	20	727.26 ± 21.69	612.75 ± 7.83	1.19 ± 0.03	0.68 ± 0.04	0.58 ± 0.03	137.76 ± 3.51	163.25 ± 2.20
4/10	20	707.00 ± 22.14	674.87 ± 20.57	1.05 ± 0.04	0.73 ± 0.06	0.69 ± 0.05	144.75 ± 4.47	148.38 ± 4.15

Table 20. Change in RNA and DNA concentration (in µg/100 mg of dry tissue) and total amount (in mg), RNA - DNA ratio, Dry W - RNA ratio, Dry W - DNA ratio of skeletal muscle of (0+) Salmo salar subjected to L6D photoperiod. Experiment II (1982). Value shown are means ± standard error.

L6D

Date	N	[RNA]	[DNA]	RNA/DNA	RNA total (mg)	DNA total (mg)	Dry W/RNA	Dry W/DNA
9/7	20	1760.29 ± 81.17	909.94 ± 50.76	2.04 ± 0.09	0.66 ± 0.06	0.36 ± 0.04	59.14 ± 2.68	113.07 ± 6.97
26/7	20	996.70 ± 42.04	193.36 ± 30.86	8.88 ± 1.39	0.69 ± 0.03	0.10 ± 0.07	90.89 ± 4.22	617.94 ± 48.29
6/8	20	887.96 ± 31.08	286.63 ± 17.89	3.38 ± 0.25	0.82 ± 0.04	0.26 ± 0.02	114.99 ± 3.56	374.37 ± 26.40
20/8	20	1142.81 ± 36.22	494.80 ± 51.65	2.85 ± 0.31	1.05 ± 0.07	0.46 ± 0.05	98.40 ± 9.76	256.43 ± 29.12
6/9	20	1054.25 ± 54.11	516.64 ± 25.71	2.16 ± 0.17	1.32 ± 0.16	0.61 ± 0.05	102.57 ± 8.76	204.78 ± 10.92
20/9	20	702.62 ± 15.88	606.21 ± 11.18	1.17 ± 0.03	0.78 ± 0.06	0.67 ± 0.05	143.67 ± 3.12	166.76 ± 3.24
4/10	20	903.19 ± 20.80	740.02 ± 29.52	1.25 ± 0.05	1.07 ± 0.12	0.84 ± 0.07	112.61 ± 3.05	139.89 ± 5.15

Table 21. Regression equation for $\log_e$ of length (mm) or weight (mg) against time (days) for Experiment I (22nd July - 3rd September 1981) of juvenile Atlantic salmon, subjected to natural light (nLD) or constant light (LL) and T-rate (food delivered at 10-min interval) or 2T-rate (food delivered at 5-min interval), throughout 24 hours.

$$\text{Log}_e L = a + b\,t$$

Photoperiod	Feeding rate	a	b	r^2(1)
nLD	2T	3.8594	0.0047	0.9543
nLD	T	3.9200	0.0037	0.9010
LL	2T	3.8565	0.0054	0.9728
LL	T	3.9111	0.0048	0.9238

$$\text{Log}_e W = a + b\,t$$

Photoperiod	Feeding rate	a	b	r^2(1)
nLD	2T	6.9905	0.0140	0.9720
nLD	T	7.1812	0.0105	0.9332
LL	2T	6.9847	0.0164	0.9267
LL	T	7.1733	0.0145	0.9480

(1) Elevation or slope not significantly different between the two feeding rate for each photoperiod .

Table 22. Regression equation for $\log_e$ of weight (mg) against time (days), for Experiment I (22nd July - 30 September 1981) and Experiment II (26th July - 4th October 1982) of juvenile Atlantic salmon, subjected to different photoperiod regimes.

$$\text{Log}_e W = a + b\,t$$

(1981)

Photoperiod	Feeding rate	a	b (1)	r^2	N	Significance (p)
nLD	T + 2T	7.1836	0.0108	0.97	6	< 0.001
LL	T + 2T	7.1979	0.0135	0.94*	6	< 0.001

(1982)

Photoperiod	Feeding rate	a	b (1)	r^2	N	Significance (p)
nLD	T	7.0053	0.0052	0.92	6	< 0.01
LL	T	6.8292	0.0072	0.70	6	< 0.05
8LD	T	6.7151	0.0040	0.79***	6	< 0.02
L3D	T	6.9268	0.0048	0.93***	6	< 0.01
L4D	T	6.8979	0.0049	0.80**	6	< 0.02
L6D	T	6.8231	0.0085	0.83	6	< 0.02

(1) Slope not significantly different from natural photoperiod. Significance of differences in elevation from natural photoperiod (nLD).

* $p < 0.025$

** $p < 0.010$

*** $p < 0.005$

Table 23. Regression equation for $\log_e$ of length (mm) against time (days) for Experiment I (22nd July - 30th September 1981) and Experiment II (26th July - 4th October 1982) of juvenile Atlantic salmon, subjected to different photoperiod regimes.

$$\text{Log}_e\ L = a + b\ t$$

(1981)

Photoperiod	Feeding rate	a	b (1)	r^2	N	Significance (p)
nLD	T + 2T	3.9745	0.0029	0.95	5	< 0.01
LL	T + 2T	3.9716	0.0037	0.91*	5	< 0.02

(1982)

Photoperiod	Feeding rate	a	b (1)	r^2	N	Significance (p)
nLD	T	3.8466	0.0018	0.94	6	< 0.01
LL	T	3.7942	0.0023	0.73	6	< 0.05
8LD	T	3.7458	0.0015	0.91***	6	< 0.01
L3D	T	3.8059	0.0018	0.95***	6	< 0.001
L4D	T	3.8026	0.0018	0.82**	6	< 0.02
L6D	T	3.7641	0.0031	0.91*	6	< 0.01

(1) Slope not significantly different from natural photoperiod. Significance of differences of elevation from natural photoperiod (nLD)

* $p < 0.05$

** $p < 0.01$

*** $p < 0.005$

Table 24. Regression equations for $\log_e$ of the harmonic mean of RNA concentration (ug/100 mg dry tissue) of the relevant period against specific growth rate (G_w % day^{-1}), for Experiment I (1 July - 30 September 1981) and Experiment II (9 July - 4 October 1982), of juvenile Atlantic salmon, subjected to different photoperiodic regimes.

$$\text{Log}_e \overline{RNA} = a + b\, G_w \text{ \% day}^{-1}$$

Photoperiod	Feeding rate	a	b	r^2	N	Significance (p)
nLD	T + 2T	6.42	0.37	0.81	7	< 0.01
LL	T + 2T	6.67	0.25	0.69	6	< 0.05

(1982)

Photoperiod	Feeding rate	a	b	r^2	N	Significance (p)
nLD	T	6.67	0.15	0.92	6	< 0.001
LL	T	6.56	0.20	0.98	6	< 0.001
8LD	T	6.59	0.26	0.97	6	< 0.010
L3D	T	6.68	0.20	0.93	7	< 0.001
L4D	T	6.59	0.23	0.91	6	< 0.010
L6D	T	6.63	0.15	0.68	6	< 0.050

Table 25. Equation regression for $\log_e$ of the harmonic mean RNA concentration (µg/100 mg dry tissue) of the relevant period against specific growth rate (G_w % day^{-1}) of data of different photoperiod pooled (Table 24).

$$\text{Log}_e \overline{[RNA]} = a + b\ G_w\ \%\ day^{-1}$$

Year	Photoperiod	a	b (1)	r^2	N	Significance (p)
1981 (Exp I)	Pooled data	6.46	0.34	0.64	13	< 0.001
1982 (Exp II)	Pooled data	6.64	0.19	0.86	37	< 0.001

(1) Significance of differences $p < 0.025$

Table 26. Equation regression for geometric mean of RNA - DNA ratio for the relevant period against specific growth rate (G_w % day^{-1}) for Experiment I (27 April - 11 June 1981) of juvenile Atlantic salmon, subjected to natural photoperiod (nLD).

$$RNA/DNA = a + b\ G_w\%day^{-1}$$

Year	Photoperiod	a	b	r^2	N	Significance (p)
1981	LD	1.27	0.19	0.82	6	< 0.05

Table 27. Changes in RNA and DNA concentration (ug/100 mg dry tissue), RNA – DNA ratio and water content (%) of the whole body or the skeletal muscle of juvenile Atlantic salmon subjected to natural photoperiod (nLD). Values shown are mean ± standard error (No of fish).

Date	[RNA]		[DNA]		RNA/DNA		% water	
	Whole fish	Muscle	Whole fish	Muscle	Whole fish	Muscle	Whole fish	Muscle
17/6	(9) * 5462.81 ± 131.96	(20) 5001.58 ± 93.31	(9) * 1577.35 ± 60.66	(20) 1776.35 ± 33.95	(9) *** 3.49 ± 0.17	(20) 2.84 ± 0.08	(10) * 82.24 ± 0.59	(20) 83.47 ± 0.28
26/6	(10) 3523.69 ± 202.49	(19) 3442.03 ± 157.13	(10) ** 1536.10 ± 84.32	(19) 1788.99 ± 31.78	(10) * 2.33 ± 0.15	(19) 1.94 ± 0.09	(10) 79.62 ± 0.29	(19) 78.59 ± 1.68

Significance of differences * $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 28. Percentage and mean (µm) of fibre present in each modal group of the frequency distribution of white muscle fibre diameter of female Salmo salar (0+), subjected to natural photoperiod (nLD). Experiment I (1981).

Date	Length (cm)	Lower mode (%)	Lower mode mean	Upper mode (%)	Upper mode mean	No of cells
8/7	3.6	11.8	20.8	88.2	50.4	51
	4.2	26.0	20.2	74.0	54.7	50
	4.5	58.2	22.1	41.8	59.0	67
	4.9	56.9	27.3	43.1	58.9	58
	4.9	29.5	29.8	70.5	58.5	44
	5.2	51.0	30.2	49.0	64.1	51
	5.5	61.3	29.3	38.7	63.5	62
22/7	4.8	68.4	26.4	31.6	53.5	76
	4.9	59.8	23.9	40.2	50.2	82
	5.2	63.1	22.3	36.9	47.3	84
	5.4	60.8	22.5	39.2	39.4	97
5/8	5.4	63.3	24.1	36.6	52.2	68
	5.8	61.0	27.1	39.0	62.5	41
	6.0	68.2	25.7	31.8	51.1	66
	6.7	64.7	27.5	35.3	57.2	51

Table 29. Percentage and mean (µm) of fibre present in each modal group of the frequency distribution of white muscle fibre diameter of male Salmo salar (0+), subjected to natural photoperiod (nLD). Experiment I (1981).

Date	Length (cm)	Lower mode (%)	mean	Upper mode (%)	mean	No of cells
8/7	4.3	21.6	24.8	78.4	52.4	51
	4.7	50.0	19.6	50.0	52.8	66
	4.9	60.0	26.9	40.0	55.4	65
22/7	4.9	57.4	28.3	42.6	52.9	54
	5.0	68.3	29.2	31.7	57.0	60
	5.3	57.8	23.0	42.2	47.6	90
5/8	5.0	59.8	20.6	40.2	47.3	82
	5.2	55.8	27.9	44.2	59.3	43
	5.7	60.4	26.8	39.6	58.6	48
	5.9	63.3	25.4	36.7	55.3	49
	6.2	54.1	35.0	45.9	66.3	37

Table 30. Percentage and mean of fibre present in each modal group of the frequency distribution of white muscle fibre diameter of female Salmo salar (0+), subjected to constant light (LL). Experiment I (1981).

Date	Length (cm)	Lower mode (%)	mean	Upper mode (%)	mean	No of cells
8/7	4.5	54.7	24.5	45.3	55.4	64
	4.7	60.5	21.2	39.5	50.7	86
	4.7	51.4	25.8	48.6	51.3	74
	4.9	70.1	26.0	29.9	52.3	77
	4.9	45.0	27.1	55.0	50.8	60
	5.2	39.0	21.0	61.0	50.6	59
22/7	4.3	63.9	21.5	36.1	43.4	97
	4.9	48.9	23.3	51.1	44.4	92
	5.3	69.8	25.3	30.2	44.7	106
	5.5	52.2	21.3	47.8	41.5	92
5/8	5.8	64.1	37.5	35.9	62.1	39
	6.0	67.9	25.6	32.1	57.0	53

Table 31. Percentage and mean (µm) of fibre present in each modal group of the frequency distribution of white muscle fibre diameter of male Salmo salar (0+), subjected to constant light (LL). Experiment I (1981).

Date	Length (cm)	Lower mode (%)	mean	Upper mode (%)	mean	No of cells
8/7	4.4	41.2	15.0	58.8	42.5	68
	4.8	36.4	29.25	63.6	51.9	55
	4.9	47.5	27.9	52.5	56.9	59
	5.1	45.7	22.0	54.3	43.8	70
22/7	4.5	42.4	21.1	57.6	47.4	66
	5.4	66.6	25.7	33.3	58.0	57
	5.4	60.7	24.2	39.3	49.9	84
5/8	4.2	37.9	18.9	62.1	46.2	66
	5.7	60.4	29.1	39.6	52.8	48
	5.9	66.1	23.9	33.9	58.6	56
	6.0	52.2	26.5	47.8	59.8	46
	6.1	61.9	24.7	38.1	51.7	63
	6.2	59.6	25.4	40.4	59.9	47

Table 32. Changes in the intensity of oocyte cytoplasm staining (%) of (♀) *Salmo salar*, subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Staining intensities are represented as weak (+), moderate (++), intense (+++).

nLD

Date	No fish	No cell	+	++	+++
8/7	7	190	65.79	34.21	——
22/7	5	122	21.31	41.80	36.89
5/8	6	142	14.08	14.79	71.13
30/9	6	151	9.93	1.32	88.74
15/10	4	99	26.26	4.04	69.70

LL

Date	No fish	No cell	+	++	+++
8/7	6	128	40.63	57.81	1.56
22/7	3	73	20.55	60.27	19.18
20/8	8	173	21.97	2.31	75.72
30/9	4	98	13.27	4.08	82.65
15/10	5	127	15.75	——	84.25

Table 33. Changes in cell and nucleus diameter (µm), large nucleolous (µm) and nucleus-cytoplasm ratio of oocytes and spermatogonia of (0+) Salmo salar subjected to natural photoperiod (nLD). Experiment I (1981). Values shown are means ± standard error.

			Female			
Date	No fish	No cell	cell-diameter	nucleus diameter	Large nucleolus diameter	Nucleus/cytoplasm
8/7	7	180	16.49 ± 0.48	10.67 ± 0.23	3.23 ± 0.08	0.65
22/7	5	125	31.30 ± 1.29	18.63 ± 0.70	4.40 ± 0.10	0.60
5/8	6	149	36.58 ± 1.55	20.83 ± 0.83	3.83 ± 0.10	0.57
30/9	6	150	64.47 ± 2.34	34.96 ± 1.20	4.43 ± 0.13	0.54
15/10	4	98	49.25 ± 2.98	27.76 ± 1.56	5.06 ± 0.20	0.53

Table 33Contd. Changes in cell and nucleus diameter (µm), large nucleolus (µm) and nucleus–cytoplasm ratio of oocyte and spermatogonia of (0+) Salmo salar subjected to natural photoperiod (nLD). Experiment I (1981). Values shown are means ± standard error.

Male

Date	No fish	No cell	cell diameter (a)	Nucleus diameter	nucleus/cytoplasm
8/7	5	125	9.50 ± 0.16	6.62 ± 0.11	0.70
22/7	3	70	12.17 ± 0.42	8.00 ± 0.17	0.66
5/8	1	25	13.14 ± 0.27	9.42 ± 0.29	0.72
20/8	2	50	11.35 ± 0.24	7.90 ± 0.14	0.70
30/9	6	150	12.61 ± 0.23	8.57 ± 0.14	0.68
15/10	6	150	14.60 ± 0.15	9.66 ± 0.07	0.66

(a) 15/10; 5/8; 30/9; 22/7; 20/8; 8/7 ($p < 0.005$ Groups which are not significantly different by the SNK test are underlined.)

Table 34. Changes in cell and nucleus diameter (µm), large nucleolus (µm) and nucleus–cytoplasm ratio of oocyte and spermatogonia of (♀) Salmo salar subjected to constant light (LL). Experiment I (1981). Values shown are means ± standard error.

Female

Date	No fish	No cell	cell-diameter	Nucleus diameter	Large nucleolus diameter	nucleus/cytoplasm
8/7	6	154	14.26 ± 0.44	9.16 ± 0.24	3.02 ± 0.08	0.64
22/7	3	75	26.02 ± 1.39	15.67 ± 0.84	4.00 ± 0.21	0.60
20/8	7	200	42.85 ± 1.57	24.68 ± 0.84	3.88 ± 0.11	0.58
30/9	4	100	61.52 ± 2.79	33.22 ± 1.47	4.67 ± 0.21	0.54
15/10	5	125	59.45 ± 2.47	31.75 ± 1.29	4.45 ± 0.14	0.53

Table 34. Contd. Changes in cell and nucleus diameter (µm), large nucleolus (µm) and nucleus-cytoplasm ratio of oocyte and spermatogonia of (0+) Salmo salar subjected to constant light (LL). Experiment I (1981). Values shown are means ± standard error.

			Male		
Date	No fish	No cell	cell-diameter	Nucleus diameter	nucleus/cytoplasm
8/7	3	75	9.37 ± 0.19	6.67 ± 0.12	0.71
22/7	4	100	10.93 ± 0.16	7.22 ± 0.10	0.66
5/8	3	75	9.88 ± 0.16	7.08 ± 0.09	0.72
20/8	8	199	10.13 ± 0.11	7.12 ± 0.06	0.70
30/9	2	50	12.66 ± 0.18	8.32 ± 0.12	0.66
15/10	5	150	14.60 ± 0.13	11.93 ± 0.12	0.82

Table 35. Changes in mitotic activity, and the range and mean in number of cells per cyst of testis of (0+) Salmo salar, subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981).

nLD

Date	No fish	Mitotic activity	No cyst	No cell/cyst Range	No cell/cyst mean (± SE)(a)
8/7	3	———	53	1 - 4	1.45 ± 0.11
22/7	4	2/4	112	1 - 4	1.55 ± 0.08
5/8	3	2/3	49	1 - 3	1.53 ± 0.11
20/8	8	5/8	116	1 - 7	1.76 ± 0.10
30/9	2	———	26	1 - 4	1.92 ± 0.22
15/10		6/7	53	1 - 11	3.63 ± 0.12

Table 35/Contd. Changes in mitotic activity (%), and the range and mean in number of cells per cyst of testis of (0+) Salmo salar, subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981).

LL (Male)

Date	No fish	Mitotic activity	No cyst	No cell/cyst Range	No cell/cyst mean (± SE)(b)
8/7	5	2/5	79	1 - 3	1.65 ± 0.09
22/7	3	3/3	110	1 - 4	1.55 ± 0.08
5/8	1	1/1	15	1 - 3	1.60 ± 0.19
20/8	2	1/2	29	1 - 4	1.76 ± 0.18
30/9	6	2/6	83	1 - 5	1.87 ± 0.12
15/10	6	4/6	54	1 - 14	3.40 ± 0.37

(a) 8/7; 22/7; 5/8; 20/8; 30/9; 15/10 ($p < 0.005$ Groups which are not significantly different by the SNK test are underlined.)

(b) 8/7; 22/7; 5/8; 20/8; 30/9; 15/10 ($p < 0.001$ Groups which are not significantly different by the SNK test are underlined.)

Table 36. Changes in range, mean in number of small nucleolous, and the ranges and mean in number of cells per cyst of ovary of Salmo salar (0+), subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981).

nLD (Female)

Date	No fish	No Small nucleolous		No cyst	No cell/cyst	
		Range	Mean ± SE (No cells)		Range	Mean (± SE)
8/7	7	1 - 9	4.26 ± 0.41 (31)	103	1 - 11	1.93 ± 0.19
22/7	5	1 - 10	5.65 ± 0.28 (60)	120	1 - 3	1.07 ± 0.02
5/8	6	1 - 10	4.66 ± 0.24 (89)	144	1 - 3	1.09 ± 0.02
30/9	6	1 - 19	9.97 ± 0.47 (96)	141	1 - 3	1.10 ± 0.04
15/10	4	1 - 25	13.86 ± 1.05 (59)	92	1 - 3	1.04 ± 0.02

Table 36 Contd. Changes in range, mean in number of small nucleolous, and the ranges and mean in number of cells per cyst of ovary of Salmo salar (0+), subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981).

nLD (Female)

Date	No fish	No Small nucleolous		No cyst	No cell/cyst	
		Range	Mean ± SE (No cells)		Range	Mean (± SE)
8/7	6	1 - 9	4.30 ± 0.59 (20)	38	1 - 11	2.11 ± 0.34
22/7	3	2 - 9	5.21 ± 0.35 (34)	62	1 - 6	1.21 ± 0.09
20/8	7	1 - 18	8.68 ± 0.39 (97)	160	1 - 4	1.12 ± 0.04
30/9	4	1 - 22	10.66 ± 0.61 (61)	97	1 - 2	1.04 ± 0.02
15/10	5	1 - 39	16.85 ± 0.77 (98)	125	1 - 1	1.00 ± 0.01

Table 37. Comparison between lower and upper modal groups, of the cell and nucleus diameter (µm), and mean and range of cells per cyst of female and male juvenile Atlantic salmon, subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are mean ± standard error and (N = number of cells).

nLD

	Female (N = 49)			Male (N = 75)		
	No fish	Upper mode	Lower mode	No fish	Upper mode	Lower mode
Cell diameter	2	51.30 ± 4.28	46.46 ± 4.18	3	15.42 ± 0.23	13.77 ± 0.19***
Nucleus diameter	2	27.94 ± 2.16	26.57 ± 2.24	3	12.10 ± 0.22	11.76 ± 0.13
No cell/cyst	2	1.02 ± 0.08	1.07 ± 0.08	3	4.70 ± 0.09	2.63 ± 0.17**
Range of cell/cyst	2	1 - 3	1 - 3	3	1 - 11	1 - 6

Table 37 Contd. Comparison between lower and upper modal groups, of the cell and nucleus diameter (um), and mean and range of cells per cyst of female and male juvenile Atlantic salmon, subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are mean ± standard error and (N = number of cells).

LL

	Female (N = 75)			Male (N = 75)		
	No fish	Upper mode	Lower mode	No fish	Upper mode	Lower mode
Cell diameter	3	60.69 ± 3.09	58.45 ± 3.34	3	14.76 ± 0.17	14.39 ± 0.19
Nucleus diameter	3	31.26 ± 1.49	32.33 ± 1.90	3	9.70 ± 0.10	9.62 ± 0.10
No cell/cyst	3	1.00 ± 0.06	1.00 ± 0.06	3	4.27 ± 0.39	2.53 ± 0.23*
Range of cell/cyst	3	1 - 1	1 - 1	3	1 - 14	1 - 8

Significance of differences * $p < 0.050$
** $p < 0.010$
*** $p < 0.001$

Table 38. Changes in the intensity of oocyte cytoplasm staining (%) of (0+) Salmo salar, sampled in October, 1982 (Experiment II).

Staining intensity is represented as weak (+), moderate (++) and intense (+++).

Photoperiodic regime	No fish	No cell	+	++	+++
nLD	4	97	5.15	3.09	91.75
LL	4	101	7.00	3.00	90.00
8LD	2	50	8.00	——	92.00
L3D	2	50	18.00	2.00	80.00
L4D	3	75	17.33	——	82.67
L6D	3	75	12.00	2.67	85.33

Table 39. Effect of photoperiodic regime on cell and nucleus diameter (μm), large nucleolus diameter (μm), and nucleus-cytoplasm ratio of oocyte and spermatogonia of Salmo salar, sampled in October, 1982 (Experiment II). Values shown are means ± standard error and (No of cells).

	Female					
Photoperiodic regime	No fish	No cell	(a) cell diameter	Nucleus diameter	Large nucleolus diameter	Nucleus/cytoplasm
nLD	4	98	66.54 ± 2.28	33.54 ± 0.58	4.23 ± 0.21	0.54
LL	4	100	51.20 ± 5.12	27.95 ± 1.25	4.56 ± 0.10	0.55
8LD	2	50	51.03 ± 2.63	27.29 ± 1.48	4.18 ± 0.17	0.53
L3D	2	50	45.84 ± 3.40	25.67 ± 1.81	4.23 ± 0.17	0.56
L4D	3	75	48.82 ± 2.73	27.71 ± 1.55	4.33 ± 0.14	0.57
L6D	3	75	53.61 ± 2.86	28.67 ± 1.54	3.99 ± 0.15	0.53

Table 39 Contd. Effect of photoperiodic regime on cell and nucleus diameter (μm), large nucleolus diameter (μm), and nucleus-cytoplasm ratio of oocyte and spermatogonia of Salmo salar, sampled in October, 1982 (Experiment II). Values shown are means ± standard error and (No of cells).

Male

Photoperiodic regime	No fish	No cell	(b) cell diameter	Nucleus diameter	Nucleus/cytoplasm
nLD	1	25	12.53 ± 0.27	8.14 ± 0.18	0.65
LL	1	25	12.32 ± 0.29	8.32 ± 0.18	0.68
8LD	3	74	12.04 ± 0.24	8.35 ± 0.14	0.69
L3D	2	50	12.38 ± 0.20	8.45 ± 0.14	0.65
L4D	2	50	11.78 ± 0.13	7.99 ± 0.10	0.68
L6D	2	50	13.77 ± 0.20	9.01 ± 0.14	0.68

(a) nLD; LL; 8LD; L3D; L4D; L6D. ($p < 0.005$ Groups which are not significantly different by the SNK test are underlined.)

(b) nLD; LL; 8LD; L3D; L4D; L6D ($p < 0.005$ Groups which are not significantly different by the SNK test are underlined.)

Table 40. Effect of photoperiodic regime on mitotic activity and the range and mean number of cells per cyst of oocyte (female) and spermatogonia (male) of (0+) Salmo salar, sampled in October, 1982 (Experiment II).

Female

Photoperiodic regime	No fish	No cyst	No cell/cyst Range	mean
nLD	4	98	1	1.00
LL	4	100	1	1.00
8LD	2	50	1	1.00
L3D	2	75	1	1.00
L4D	3	75	1	1.00
L6D	3	50	1	1.00

Table 40/Contd. Effect of photoperiodic regime on mitotic activity and the range and mean in number of cells per cyst of oocyte (female) and spermatogonia (male) of (0+) Salmo salar, sampled in October, 1982 (Experiment II).

Male

Photoperiodic regime	No fish	Mitotic activity	No cyst	No cell/cyst Range	No cell/cyst mean (± SE)
nLD	1	———	14	1 - 4	2.21 ± 0.24
LL	1	1/1	17	1 - 3	1.82 ± 0.21
8LD	3	———	39	1 - 6	2.10 ± 0.19
L3D	2	1/2	22	1 - 6	2.32 ± 0.21
L4D	2	———	26	1 - 5	2.00 ± 0.21
L6D	2	1/2	25	1 - 4	2.28 ± 0.27

Table 41. Comparison between cell and nucleus diameter (µm) of spermatogonia and oocyte of Salmo salar (0+) sampled in September, 1981 (Experiment I) with that of October, 1982 (Experiment II). Values shown are means ± standard error and (No of cells).

nLD

	Female			Male		
	No fish	cell diameter	nucleus diameter	No fish	nucleus diameter	nucleus diameter
30/9/81	6	64.46 ± 2.33 (150)	34.81 ± 1.20 (150)	2	12.75 ± 0.17 (50)	8.32 ± 0.12 (50)
4/10/81	4	66.54 ± 2.28 (98)	36.34 ± 1.31 (98)	1	12.53 ± 0.27 (25)	8.14 ± 0.18 (25)
Significance		ns	ns		ns	ns

Table 42. Gonadosomatic index (%) and the proportion of females and male present in the sample sacrificed on 4th February 1982 (Experiment I). GSI value shown are mean $\pm$ standard error.

Photoperiodic regime	No fish	Female GSI	Female (%)	Male (%)	X^2
nLD	269	0.35 ± 0.01***	47.94	52.06	0.16 ns.
LL	194	0.31 ± 0.01	48.33	51.67	0.11 ns.

Significance of differences *** $p < 0.001$

Table 43. Change in cell diameter (µm) of GH, TSH, LTH and GtH cells of pituitary of (0+) Salmo salar, subjected to natural photoperiod or constant light (LL). Experiment I (1981). Values shown are means ± standard error and number of cells.

nLD

Date	No fish	GH	TSH	LTH	GtH
8/7	7	8.32 ± 0.12 (114)***	8.67 ± 0.17 (72)	11.98 ± 0.16 (157)*	8.67 ± 0.2 (46)**
22/7	6	8.30 ± 0.30 (25)	8.88 ± 0.17 (117)	12.07 ± 0.23 (141)***	———
30/9	6	8.81 ± 0.13 (93)*	9.42 ± 0.17 (79)***	12.64 ± 0.20 (120)	8.31 ± 0.17 (43)

LL

Date	No fish	GH (a)	TSH (b)	LTH (b)	GtH
8/7	6	9.10 ± 0.19 (57)	9.05 ± 0.17 (80)	11.40 ± 0.21 (107)	7.57 ± 0.22 (19)
22/7	5	8.66 ± 0.19 (54)	8.79 ± 0.21 (45)	11.18 ± 0.20 (104)	———
30/9	8	9.24 ± 0.15 (167)	10.18 ± 0.18 (111)	13.26 ± 0.22 (163) *	8.32 ± 0.24 (43)

Significance of differences (nL versus LL)

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

(a) $\underline{30/9;\ 8/7;\ 22/7}$ ($p < 0.05$, SNK test, underline connect groups which are not significantly different)

(b) $\underline{30/9;\ 8/7;\ 22/7}$ ($p < 0.005$, SNK test, underline connect groups which are not significantly different)

Table 44. Change in nucleus diameter (µm) of GH, TSH, LTH and G t H cells of pituitary of (0+) Salmo salar subjected to natural photoperiod or constant light (LL). Experiment I (1981). Values shown are means ± standard error, and (No. of cells).

nLD

Date	No fish	GH	TSH	LTH	GtH
8/7	7	5.45 ± 0.10 (114)*	5.92 ± 0.11 (70)*	6.03 ± 0.10 (130)	6.06 ± 0.15 (34)***
22/7	6	5.70 ± 0.19 (25)	6.17 ± 0.10 (117)	6.05 ± 0.09 (140)	
30/9	6	6.16 ± 0.11 (85)	6.50 ± 0.12 (70)***	6.26 ± 0.09 (113)*	5.83 ± 0.18 (30)

LL

Date	No fish	GH	TSH	LTH	GtH
8/7	6	6.24 ± 0.13 (61)	6.47 ± 0.10 (81)	6.28 ± 0.10 (106)	5.45 ± 0.23 (19)
22/7	5	5.66 ± 0.13 (54)	6.03 ± 0.15 (45)	5.96 ± 0.11 (103)	
30/9	8	6.28 ± 0.07 (168)	6.94 ± 0.10 (111)	6.79 ± 0.08 (164)	6.02 ± 0.15 (48)

Significance of differences * p 0.05
(nLD versus LL) *** p 0.001

Table 45. Change in the lactotrope and somatotrope cell density (PCD and SCD) expressed as No cell nuclei/μm^2 of the pituitary of (0+) Salmo salar subjected to natural photoperiod (nLD) and constant light (LL). Experiment I (1981). Values shown are mean ± standard error, and (No of ocular grid).

Date	No of fishes		PCD		SCD	
	LD	LL	LD (a)	LL	LD	LL (b)
8/7	7	6	5.48 ± 0.34 (74)***	7.74 ± 0.44 (45)	4.26 ± 0.26 (63)**	2.84 ± 0.34 (29)
22/7	6	5	8.29 ± 0.43 (57)	7.45 ± 0.39 (45)	2.92 ± 0.25 (14)	2.88 ± 0.35 (32)
30/9	6	8	7.28 ± 0.33 (66)**	8.62 ± 0.36 (66)	4.26 ± 0.37 (60)	4.31 ± 0.29 (73)

Significance of differences ** $p < 0.01$

*** $p < 0.001$

(a) 8/7; 22/7; 30/9 ($p < 0.005$; Groups which are not significantly different by the SNK test are underlined.)

(b) 30/9; <u>22/7; 8/7</u> ($p < 0.005$; Groups which are not significantly different by the SNK test are underlined.)

Table 46. Change in cell diameter (µm) of LTH and GtH cells of the pituitary of (♀) Salmo salar, segregated by sex, and subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error and (No of cells).

nLD

Date	No fish		LTH		G t H	
	Female	Male	Female	Male	Female	Male
8/7	4	3	11.79 ± 0.20 (69)	12.12 ± 0.25 (88)	8.85 ± 0.30 (21)	8.88 ± 0.37 (13)
22/7	3	3	11.74 ± 0.31 (68)	12.38 ± 0.33 (73)	———	———
30/9	4	2	13.00 ± 0.29 (64)	12.24 ± 0.27 (56)	7.95 ± 0.26 (13)	8.45 ± 0.22 (30)

LL

	No fish		LTH		G t H	
	Female	Male	Female	Male	Female	Male
8/7	3	3	11.13 ± 0.25 (70)	11.92 ± 0.38 (37)	7.50 ± 0.41 (4)	7.84 ± 0.38 (15)
22/7	3	2	11.09 ± 0.23 (60)	11.28 ± 0.36 (45)	———	———
30/9	4	4	13.81 ± 0.36 (86)	12.65 ± 0.22 (77)**	8.68 ± 0.29 (33)	7.68 ± 0.27 (15)*

Significance of differences * $p < 0.05$

** $p < 0.01$

Table 47. Change in cell diameter (µm) of TSH and GH cell of the pituitary of (♀) *Salmo salar*, segregated by sex, and subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error, and (No of cells).

nLD

Date	No fish		TSH		GH	
	Female	Male	Female	Male	Female	Male
8/7	4	3	8.45 ± 0.22 (45)	9.05 ± 0.26 (27)	8.36 ± 0.14 (73)	8.42 ± 0.20 (41)
22/7	3	3	8.88 ± 0.24 (49)	8.88 ± 0.23 (68)	8.30 ± 0.44 (16)	8.30 ± 0.37 (9)
30/9	4	2	8.79 ± 0.20 (48)	10.39 ± 0.21 (31)***	8.52 ± 0.15 (48)	9.11 ± 0.22 (45)*

LL

Date	No fish		TSH		GH	
	Female	Male	Female	Male	Female	Male
8/7	3	3	9.34 ± 0.23 (51)	8.51 ± 0.22 (29)*	9.34 ± 0.26 (37)	8.59 ± 0.21 (25)*
22/7	3	2	8.71 ± 0.29 (28)	8.93 ± 0.32 (17)	8.89 ± 0.21 (35)	8.28 ± 0.35 (19)
30/9	4	4	10.48 ± 0.26 (57)	9.86 ± 0.26 (54)	9.39 ± 0.15 (86)	9.00 ± 0.16 (82)

Significance of differences * $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Table 48. Change in nucleus diameter (µm) of LTH and GtH cell of the pituitary of (0+) Salmo salar, segregated by sex, and subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error and (No of cells).

nLD

Date	No fish		LTH		G t H	
	Female	Male	Female	Male	Female	Male
8/7	4	3	5.98 ± 0.16 (61)	6.08 ± 0.12 (69)	6.02 ± 0.20 (21)	6.14 ± 0.22 (13)
22/7	3	3	6.15 ± 0.13 (68)	5.98 ± 0.12 (72)	———	———
30/9	4	2	6.31 ± 0.12 (64)	6.21 ± 0.15 (49)	6.15 ± 0.19 (33)	5.74 ± 0.23 (15)

LL

	No fish		LTH		G t H	
	Female	Male	Female	Male	Female	Male
8/7	3	3	6.26 ± 0.13 (70)	6.26 ± 0.16 (36)	5.35 ± 0.30 (9)	6.09 ± 0.58 (4)
22/7	3	2	6.29 ± 0.14 (58)	5.54 ± 0.15 (45)***	———	———
30/9	4	4	6.92 ± 0.11 (85)	6.68 ± 0.11 (77)	6.15 ± 0.19 (33)	5.74 ± 0.23 (15)

Significance of difference *** $p < 0.001$

Table 49. Change in nucleus diameter (µm) of TSH and GH cell of the pituitary of (0+) Salmo salar, segregated by sex, and subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error (No of cells).

nLD

Date	No fish		TSH		GH	
	Female	Male	Female	Male	Female	Male
8/7	4	3	5.79 ± 0.15 (43)	6.11 ± 0.18 (27)	5.47 ± 0.13 (74)	5.42 ± 0.14 (41)
22/7	3	3	6.23 ± 0.15 (49)	6.16 ± 0.13 (68)	5.88 ± 0.22 (16)	5.37 ± 0.30 (9)
30/9	4	2	6.35 ± 0.17 (48)	7.02 ± 0.16 (23)*	6.04 ± 0.15 (48)	6.31 ± 0.16 (37)

LL

Date	No fish		TSH		GH	
	Female	Male	Female	Male	Female	Male
8/7	3	3	6.50 ± 0.12 (52)	6.41 ± 0.20 (29)	6.30 ± 0.19 (37)	6.22 ± 0.18 (24)
22/7	3	2	6.02 ± 0.17 (28)	6.07 ± 0.28 (17)	5.56 ± 0.21 (35)	5.63 ± 0.18 (19)
30/9	4	4	7.11 ± 0.12 (57)	6.77 ± 0.16 (54)	6.40 ± 0.10 (86)	6.14 ± 0.12 (82)

Significance of differences * $p < 0.02$

Table 50. Change in the lactotrope and somatotrope cell density (PCD and SCD) expressed as No cell nuclei/μm^2 of pituitary of (0+) Salmo salar, segregated by sex and subjected to natural photoperiod (nLD) and constant light (LL). Experiment I (1981). Values shown are means ± standard error (and No of ocular grid).

nLD

Date	No fish		PCD		SCD	
	Female	Male	Female	Male	Female	Male
8/7	4	3	5.81 ± 0.33 (43)	4.96 ± 0.45 (30)	4.33 ± 0.35 (39)	4.15 ± 0.40 (24)
22/7	3	3	7.03 ± 0.59 (28)	9.51 ± 0.55 (29)**	3.06 ± 0.37 (8)	2.72 ± 0.43 (6)
30/9	4	2	6.36 ± 0.39 (33)	8.20 ± 0.48 (33)**	3.89 ± 0.45 (34)	4.74 ± 0.63 (26)

LL

Date	No fish		PCD		SCD	
	Female	Male	Female	Male	Female	Male
8/7	3	3	8.18 ± 0.52 (30)	6.85 ± 0.77 (15)	2.45 ± 0.39 (12)	3.12 ± 0.50 (17)
22/7	3	2	7.17 ± 0.45 (29)	7.96 ± 0.73 (16)	3.55 ± 0.47 (20)	1.77 ± 0.61 (12)*
30/9	4	4	9.30 ± 0.62 (26)	8.16 ± 0.43 (40)	3.99 ± 0.40 (37)	4.64 ± 0.41 (36)

Significance of differences: * $p < 0.02$
** $p < 0.01$

Table 51. Size range and (Number) of fish selected for measurement of pituitary cell and nucleus diameter (Tables 52 and 53).

Date	Small size (mm)		Large size (mm)	
	nLD	LL	nLD	LL
8/7	42 - 43 (2)	44 - 45 (2)	52 - 55 (2)	51 (2)
22/7	45 - 48 (2)	43 - 45 (2)	52 - 54 (2)	51 - 54 (2)
30/9	58 - 61 (2)	58 - 63 (2)	73 - 81 (2)	73 - 74 (2)

Table 52. Change in cell diameter (μm) of TSH, GH and LTH cells of the pituitary of (0+) Salmo salar, segregated by size (large and small), and subjected to natural photoperiod (nLD) or constant light (LL), Experiment I (1981). Values shown are means ± standard error and (No of cells).

nLD

Date	TSH		GH		LTH	
	Small	Large	Small	Large	Small	Large
8/7	9.09 ± 0.29 (18)**	7.95 ± 0.27 (21)	8.52 ± 0.19 (42)	8.23 ± 0.22 (31)	11.94 ± 0.23 (38)	11.72 ± 0.31 (49)
22/7	8.52 ± 0.25 (41)	8.91 ± 0.26 (40)	8.30 ± 0.30 (25)	———	11.32 ± 0.39 (41)	12.48 ± 0.41 (50)
30/9	8.43 ± 0.39 (18)**	9.73 ± 0.30 (32)	8.51 ± 0.23 (22)	8.79 ± 0.18 (39)	12.50 ± 0.37 (39)	13.26 ± 0.32 (50)

LL

Date	TSH		GH		LTH	
	Small	Large	Small	Large	Small	Large
8/7	9.10 ± 0.26 (35)	8.58 ± 0.27 (19)	8.69 ± 0.31 (28)	8.72 ± 0.24 (16)	10.96 ± 0.43 (25)	11.92 ± 0.38 (37)
22/7	8.32 ± 0.30 (19)*	9.22 ± 0.31 (17)	8.77 ± 0.33 (18)	8.14 ± 0.32 (16)	11.81 ± 0.37 (39)*	10.82 ± 0.30 (43)
30/9	11.21 ± 0.32 (37)***	8.65 ± 0.28 (20)	9.73 ± 0.30 (42)	9.21 ± 0.19 (43)	14.40 ± 0.33 (43)***	11.98 ± 0.37 (33)

Significance of differences * $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Table 53. Change in nucleus diameter (µm) of TSH, GH and LTH cells of the pituitary of (0+) Salmo salar, segregated by size (large and small) and subjected to natural photoperiod (nLD) or constant light (LL). Experiment I (1981). Values shown are means ± standard error and (No of cells).

nLD

Date	TSH Small	TSH Large	GH Small	GH Large
8/7	6.43 ± 0.29 (17)*	5.52 ± 0.24 (20)	5.53 ± 0.17 (42)	5.40 ± 0.20 (31)
22/7	6.02 ± 0.15 (41)	6.23 ± 0.16 (40)	5.70 ± 0.19 (25)	———
30/9	6.15 ± 0.21 (18)	6.63 ± 0.16 (31)	6.09 ± 0.25 (23)	6.30 ± 0.15 (39)

LL

Date	TSH Small	TSH Large	GH Small	GH Large
8/7	6.42 ± 0.16 (35)	6.61 ± 0.24 (19)	6.14 ± 0.21 (28)	6.25 ± 0.22 (15)
22/7	5.55 ± 0.22 (19)*	6.49 ± 0.25 (17)	5.82 ± 0.22 (19)	5.68 ± 0.25 (16)
30/9	7.38 ± 0.13 (38)***	6.01 ± 0.21 (20)	6.61 ± 0.15 (42)*	6.15 ± 0.12 (43)

Significance of differences * $p < 0.05$

*** $p < 0.001$

Table 54. Effect of photoperiodic regime on cell diameter (um) of GH, LTH, TSH and GtH cell of the pituitary of (0+) Salmo salar, sampled in October, 1982 (Experiment II). Values shown are means ± standard error, and (No of cells).

Photoperiodic regime	No fish	GH (a)	LTH (b)	TSH (c)	G t H (c)
nLD	4	8.67 ± 0.15 (86)	12.51 ± 0.32 (71)	10.48 ± 0.21 (42)	8.16 ± 0.29 (16)
LL	5	9.08 ± 0.14 (77)	13.87 ± 0.24 (103)	10.56 ± 0.17 (58)	7.86 ± 0.24 (23)
8LD	3	8.90 ± 0.16 (45)	12.93 ± 0.20 (76)	10.07 ± 0.23 (37)	8.07 ± 0.48 (10)
L3D	4	8.43 ± 0.14 (89)	11.69 ± 0.21 (87)	9.87 ± 0.29 (38)	8.01 ± 0.45 (11)
L4D	2	8.71 ± 0.25 (29)	12.39 ± 0.42 (48)	9.64 ± 0.29 (18)	7.08 ± 0.70 (7)
L6D	4	9.04 ± 0.12 (96)	10.96 ± 0.24 (78)	10.34 ± 0.24 (47)	8.19 ± 0.20 (25)

(a) L6D; LL; 8LD; L4D; LD; L3D. ($p < 0.05$, Groups which are not significantly different by the SNK test are underlined.)

(b) LL; 8LD; LD; L4D; L3D; L6D ($p < 0.001$ Groups which are not significantly different by the SNK test are underlined.)

(c) n.s.

Table 55. Effect of photoperiodic regime on nucleus diameter (µm) of GH, LTH, TSH and GtH cell of the pituitary of (O+) Salmo salar, sampled in October, 1982 (Experiment II). Values shown are means ± standard error and (No of cells).

Photoperiodic regime	No fish	GH	LTH	TSH	G + H
nLD	4	6.18 ± 0.10 (85)	7.47 ± 0.46 (70)	7.15 ± 0.12 (42)	5.70 ± 0.25 (16)
LL	5	6.45 ± 0.10 (77)	7.08 ± 0.12 (103)	7.23 ± 0.12 (58)	5.98 ± 0.19 (23)
8LD	3	6.18 ± 0.13 (45)	7.12 ± 0.14 (75)	6.96 ± 0.76 (37)	5.87 ± 0.33 (10)
L3D	4	5.65 ± 0.12 (89)	6.27 ± 0.14 (87)	6.37 ± 0.14 (38)	5.39 ± 0.27 (11)
L4D	2	6.02 ± 0.18 (29)	7.35 ± 0.21 (48)	6.96 ± 0.26 (18)	5.05 ± 0.42 (7)
L6D	4	6.43 ± 0.09 (96)	6.80 ± 0.12 (78)	7.20 ± 0.24 (39)	6.15 ± 0.23 (25)

Table 56. Effect of photoperiodic regime in the lactotrope and somatotrope cell density (PCD and SCD) expressed as No cell nuclei/μm^2 of the pituitary of (0+) Salmo salar, sampled in October, 1982 (Experiment II). Values shown are means ± standard error, and (No of ocular grid).

Photoperiodic regime	No fish	PCD (a)	SCD (b)
nLD	4	9.07 ± 0.76 (27)	4.41 ± 0.36 (40)
LL	5	7.16 ± 0.19 (39)	2.70 ± 0.22 (42)
8LD	3	7.83 ± 0.47 (27)	2.54 ± 0.24 (28)
L3D	4	7.65 ± 0.51 (32)	4.15 ± 0.39 (35)
L4D	2	6.80 ± 0.63 (18)	4.49 ± 0.91 (14)
L6D	4	7.19 ± 0.63 (25)	3.52 ± 0.31 (41)

(a) n.s.

(b) L4D; LD; L3D; L6D; LL; 8LD; ($p < 0.001$ Groups which are not significantly different by the SNK test are underlined.)

Table 57. Effect of photoperiodic regime on cell diameter (µm) of LTH and GtH cell, of the pituitary of (0+) Salmo salar, segregated by sex, sampled in October, 1982 (Experiment II). Values shown are mean ± standard error and (No of cells.)

Photoperiodic regime	No of fish		LTH		G t H	
	Female	Male	Female	Male	Female	Male
nLD	3	1	13.45 ± 0.34 (50)	10.26 ± 0.41 (21)***	8.19 ± 0.34 (13)	8.03 ± 0.57 (3)
LL	3	2	13.65 ± 0.29 (77)	14.61 ± 0.10 (25)	8.25 ± 0.26 (17)	7.04 ± 0.41 (6)*
8LD	1	2	13.72 ± 0.36 (24)	12.56 ± 0.24 (52)**	7.77 ± 0.67 (7)	8.76 ± 0.22 (3)
L3D	2	2	11.47 ± 0.24 (35)	11.85 ± 0.29 (52)	7.52 ± 0.33 (6)	8.61 ± 0.88 (5)
L4D	1	1	10.75 ± 0.36 (26)	13.79 ± 0.87 (22)**	———	7.08 ± 0.70 (7)
L6D	2	2	11.19 ± 0.35 (47)	10.61 ± 0.27 (31)	8.46 ± 0.27 (15)	7.04 ± 0.41 (6)

Signifcance of differences * $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

Table 58. Effect of photoperiodic regime on cell diameter (µm) of LTH and GTH cell of the pituitary of (0+) Salmo salar, segregated by sex, and sampled in October, 1982 (Experiment II). Values shown are means ± standard error and (No of cells).

Photoperiodic regime	No of fish		GH (a)		TSH (a)	
	Female	Male	Female	Male	Female	Male
nLD	3	1	8.72 ± 0.18 (65)	8.52 ± 0.26 (21)	10.70 ± 0.26 (31)	9.87 ± 0.34 (11)
LL	3	2	9.14 ± 0.16 (66)	8.68 ± 0.14 (11)	10.49 ± 0.20 (39)	10.73 ± 0.35 (18)
8LD	1	2	8.92 ± 0.22 (12)	8.89 ± 0.20 (33)	10.73 ± 0.85 (61)	9.94 ± 0.22 (31)
L3D	2	2	8.46 ± 0.20 (47)	8.40 ± 0.19 (42)	9.37 ± 0.40 (17)	10.28 ± 0.39 (21)
L4D	1	1	8.91 ± 0.23 (16)	8.47 ± 0.27 (13)	9.44 ± 0.63 (7)	9.84 ± 0.33 (11)
L6D	2	2	9.11 ± 0.18 (50)	8.95 ± 0.19 (46)	10.45 ± 0.31 (32)	10.03 ± 0.35 (15)

(a) n.s.

Table 59. Effect of photoperiodic regime on lactotrope and somatotrope cell density (PCD and SCD) expressed as No cell nuclei/μm^2 of the pituitary of (0+) Salmo salar, segregated by sex, and sampled in October, 1982. (Experiment II). Values shown are means ± standard error and (No of ocular grid.)

Photoperiodic regime	No of fish		PCD		SCD	
	Female	Male	Female	Male	Female	Male
nLD	3	1	9.14 ± 0.95 (21)	8.85 ± 1.32 (6)	4.44 ± 0.45 (30)	4.33 ± 0.50 (10)
LL	3	2	7.65 ± 0.58 (29)	5.78 ± 0.66 (10)	2.86 ± 0.25 (34)	2.04 ± 0.35 (8)
8LD	1	2	7.02 ± 0.67 (10)	8.31 ± 0.62 (17)	2.27 ± 0.38 (9)	2.62 ± 0.30 (19)
L3D	2	2	7.84 ± 0.70 (15)	7.83 ± 0.66 (20)	4.49 ± 0.77 (16)	3.87 ± 0.39 (19)
L4D	1	1	6.33 ± 1.16 (8)	7.18 ± 0.69 (10)	2.90 ± 0.63 (9)	7.35 ± 1.75 (5)**
L6D	2	2	7.49 ± 1.21 (7)	6.33 ± 1.11 (8)	4.08 ± 0.43 (20)	3.00 ± 0.43 (21)

Significance of differences ** $p < 0.02$

Table 60. Range size and (number) of fish selected for measurement of pituitary cell and nucleus diameter (Tables 61 and 62).

Photoperiodic regime	Small size	Large size
nLD	47 - 48 (2)	55 - 67 (2)
LL	47 - 51 (2)	54 - 61 (2)
L3D	45 - 46 (2)	52 - 59 (2)
L4D	39 (1)	57 (1)
L6D	52 - 56 (2)	66 - 71 (2)

Table 61. Effect of photoperiodic regime on cell diameter (µm) of GH, LTH, TSH cells of the pituitary of (0+) Salmo salar, segregated by size (small and large), sampled in October, 1982 (Experiment II). Values shown are means ± standard error and (No of cells).

Photoperiodic regime	GH (a)		LTH		TSH	
	Small	Large	Small	Large	Small	Large
nLD	8.73 ± 0.23 (41)	8.59 ± 0.23 (43)	13.69 ± 0.44 (26)	11.82 ± 0.39 (45)**	9.80 ± 0.33 (11)	10.72 ± 0.26 (31)
LL	9.07 ± 0.18 (45)	9.29 ± 0.22 (45)	13.74 ± 0.36 (52)	14.06 ± 0.32 (51)	10.03 ± 0.22 (24)	10.95 ± 0.23 (33)*
L3D	8.46 ± 0.20 (47)	8.40 ± 0.19 (47)	11.53 ± 0.28 (34)	11.85 ± 0.29 (52)	9.37 ± 0.40 (17)	10.28 ± 0.39 (21)
L4D	8.47 ± 0.27 (13)	8.91 ± 0.40 (16)	14.32 ± 0.58 (22)	10.75 ± 0.36 (26)***	9.84 ± 0.33 (11)	9.44 ± 0.63 (7)
L6D	8.80 ± 0.14 (44)	9.24 ± 0.19 (52)	11.95 ± 0.36 (37)	10.06 ± 0.26 (41)***	10.47 ± 0.36 (25)	10.14 ± 0.30 (22)

(a) n.s.

Significance of differences ** $p < 0.02$

*** $p < 0.001$

Table 62. Effect of photoperiodic regime on nucleus diameter (µm) of GH, LTH, TSH cells of the pituitary of (0+) Salmo salar, segregated by size (small and large), sampled in October, 1982 (Experiment II). Values shown are means ± standard error and (No of cells).

Photoperiodic regime	GH (a)		LTH		TSH	
	Small	Large	Small	Large	Small	Large
nLD	6.30 ± 0.15 (39)	6.08 ± 0.14 (45)	7.03 ± 0.24 (26)	7.08 ± 0.18 (45)	6.96 ± 0.20 (11)	7.21 ± 0.15 (31)
LL	6.41 ± 0.13 (45)	6.64 ± 0.19 (24)	7.15 ± 0.16 (52)	7.01 ± 0.18 (51)	6.82 ± 0.14 (24)	7.54 ± 0.17 (33)***
L3D	5.62 ± 0.13 (47)	5.91 ± 0.14 (42)	6.46 ± 0.21 (35)	6.08 ± 0.16 (52)	6.32 ± 0.23 (17)	6.41 ± 0.18 (21)
L4D	6.17 ± 0.30 (13)	5.90 ± 0.22 (16)	8.41 ± 0.18 (22)	6.46 ± 0.24 (26)***	7.11 ± 0.29 (11)	6.72 ± 0.49 (7)
L6D	6.40 ± 0.11 (44)	6.46 ± 0.13 (51)	6.93 ± 0.17 (37)	6.68 ± 0.16 (41)	7.43 ± 0.13 (25)	6.71 ± 0.24 (21)**

(a) n.s.

Significance of differences ** $p < 0.01$

*** $p < 0.001$