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Seawater Acclimation and Parr-Smolt Transformation of Juvenile Atlantic Salmon, *Salmo salar* L.

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SUMMARY

Changes in the osmotic concentration of serum, urine and intestinal fluid of one and two-yr-old Atlantic salmon pre-smolts and smolts were examined during exposure to salinity increasing from 0.1 to 31°/∞. Both age-classes acclimated to sea water equally well, the marine osmoregulatory mechanisms being developed prior to completion of parr-smolt transformation. Acclimation to sea water was possible during the parr stage when fish exceeded a fork length of 12-13 cm. The timing of transformation was synchronous for both the one- and two-yr-old juveniles as demonstrated by changes in lipid and moisture content and condition factor (K). Condition factor of juveniles at the Mactaquac Hatchery, New Brunswick (45°58'N), decreased from February until the second half of May and lipid content from February until the second half of June. The peak of migratory activity of juveniles at this location occurred during the second half of May coincident with the attainment of minimum K values and decreased during the first half of June as K values increased. While timing of changes in lipid content and K values during transformation were similar for juveniles at Mactaquac and the Mersey Hatchery in Nova Scotia (44°10'N), lipid of fish at the more southerly station decreased at a greater rate and migratory activity was apparent earlier. This was probably attributable to the advanced temperature cycle at that location necessitating earlier liberation of smolts than at more northerly locations.

Danger exists in the practice of rearing smolts at one location then transporting them during their migratory period to distant release sites where the temperature cycle is different. In this situation, smolts would be out of phase with the river and the sea in that area. A solution may exist in transporting smolts to distant release ponds during the January to March period when water temperatures are low and the process of transformation not well advanced. Smolts could then be held until in phase with the light and thermal regimes in their new location. Particular attention should be made to release smolts earlier within the migratory period rather than later to minimize rapid loss of energy stores particularly evident at the more southerly hatcheries.

Identification of the minimum size for seawater acclimation of salmon will facilitate grading practices at Maritime hatcheries. Parr <12-13 cm during the late fall could be liberated in fresh water at that time assuming they will not be of sufficient size for release as smolts the following spring. This will reduce pond densities possibly resulting in an improvement in quality of the larger juveniles destined to undergo transformation.

Both the yearling and larger two-yr-old smolts acclimated to sea water equally well indicating the desirability of yearling smolt programs where temperature regimes are conducive to rapid growth. Not only are increases in production possible with this type of program but adult returns from the release of yearling smolts can be equal to returns from the release of the larger two-yr-old individuals (Peterson 1973; Isaksson 1976).

INTRODUCTION

Juvenile Atlantic salmon for release in the Maritimes are reared at hatcheries of diverse geographic location having different water temperature regimes. The differences in annual temperature cycle results in variation in salmon growth rate. Juveniles reared at the Charlo Hatchery in northern New Brunswick (47°58'N) are held for two years before they are sufficiently large for liberation during the spring as smolts, while a proportion of the juveniles at the Mactaquac Hatchery, New Brunswick (45°58'N) are large enough for release as yearlings. The remainder of the juveniles at this location are retained for an additional year then liberated as larger two-yr-old smolts. Because of the warmer temperature regime encountered at the Mersey Hatchery in southwest Nova Scotia (44°10'N), virtually the entire production at this location during the years 1976 and 1977 has been of yearling smolts.

Adult returns from tagged juveniles produced at the Kejimkujik Hatchery (N.S.) and released during the years 1972 to 1974 in the LaHave River, N.S., were lower from smolts released as yearlings than from those released at two years of age. The mean return rate during those years for the larger two-yr-old juveniles was three-fold greater. The lower adult return resulting from yearling liberation indicated a need for specific knowledge of the timing of parr-smolt transformation of both juvenile age-classes and of the time and size at which their marine osmoregulatory mechanisms develop. The experiment was conducted using juveniles at the Mactaquac and Mersey hatcheries because latitudinal and hence temperature differences between these locations were expected to demonstrate the influence of these variables on timing of transformation. Additionally, these hatcheries are the largest producers of smolts for release in the Maritimes, juveniles from Mactaquac being released in the Saint John River (N.B.) and those from Mersey in the LaHave River (N.S.). This information is necessary for determining juvenile release dates at the two locations and size selection practices.

Materials and Methods

Changes in the osmotic concentration of serum, urine and intestinal fluid of euryhaline teleosts during exposure to increasing salinity have been documented (Parry 1966; Conte 1969; Hickman and Trump 1969; Shehadeh and Gordon 1969) and were used in the present study as criteria for determining the success of seawater acclimation. The timing of migratory activity and of changes in condition factor and proximate composition associated with parr-smolt transformation (Wagner 1968; Fessler and Wagner 1969) were measured for yearlings at Mersey and for both juvenile age-classes at Mactaquac to allow prediction of release dates.

Seawater Acclimation of Pre-smolts and Smolts

The one- and two-yr-old juvenile salmon (≥14 cm) used in the seawater acclimation study were exposed to increasing salinity during the February-March period when in the pre-smolt stage and again during May as smolts. Salmon of both age-classes were progeny of spring-run parents captured in the Saint John River and were obtained from the Mactaquac Hatchery during early February and again during late-April. Upon arrival in the laboratory, 100 juveniles of each age-class were added to each of four 3,000 l circular freshwater tanks (4±0.5°C), the two age-classes within a tank being separated by a partition of small mesh seine netting. The salmon were exposed to a natural photoperiod and fed to satiation once daily with finely chopped Atlantic cod, _Gadus morhua_. The initial weights and fork lengths of the February and May groups were:

	February		May	
Age (yrs)	Fork length[a] (cm)	Wt[a] (g)	Fork length[a] (cm)	Wt[a] (g)
1	15.4±0.6	36.4± 4.4	16.6±0.9	41.0± 6.7
2	21.9±1.1	105.8±15.4	21.0±1.0	102.2±18.9

[a] Means ±1 S.D. here and throughout text.

During the February and May studies, four yearling and four two-yr-old juveniles, deprived of food for 72 h, were randomly taken from each of the three freshwater tanks and samples of their blood, urine and intestinal fluid obtained prior to sacrificing them for proximate analysis. The salinity within each tank was increased 2‰·day^{-1} and 12 salmon of both age-classes sampled at 15.5‰ and 31‰. The salmon were then held for an additional month at 31‰ and a record made of any mortality within the tanks. Fish in the fourth tank served as controls and were held in fresh water until September at temperatures similar to those at Mactaquac. Twelve juveniles of each age-class were removed monthly from the control tank and sacrificed to follow changes in proximate composition and condition factor (Fulton 1911). The methods of proximate analysis and determination of osmolarity of the various body fluids has been previously described (Farmer et al. 1977).

Seawater Acclimation of Parr

The osmoregulatory ability of salmon parr (2-37 g) was assessed during June using 200 underyearling fish from Mactaquac. The parr were held in a 3,000 l freshwater tank at 15±0.5°C and fed chopped cod once daily. Measurements of total body moisture and osmolarity of serum and intestinal fluid were made for 15 individuals randomly taken from the tank. Salinity was then increased 2‰·day^{-1} and 15 parr sampled at 15.5‰ and after five days exposure to 31‰. The remaining parr were held for two months at that salinity and a record kept of the mortalities. This procedure was repeated during November with a different group of underyearling parr.

Parr-Smolt Transformation

The timing of migratory activity and of changes in condition factor and proximate composition associated with parr-smolt transformation was determined for salmon at the Mactaquac and Mersey hatcheries during the winter and spring. Migratory activity was assessed from the tendency for smolts to swim with the current in the rearing ponds rather than against it as observed for pre- and post-smolts. Thirty juveniles were randomly removed from each of four ponds at Mactaquac on seven sampling dates between February and June for weight and fork length measurements. Fifteen fish from each pond were sacrificed on all sampling dates for lipid and moisture determination. Two of the ponds contained two-yr-old juveniles and the other two, yearlings, all fish being progeny of spring-run parents captured in the Saint John River. Similarly, weights and fork lengths of 40 juveniles from each of two ponds at Mersey were determined on five dates between February and May. Fifteen individuals from each of the ponds were sacrificed on all dates for determination of their lipid and moisture content. All juveniles at this station were yearlings and were progeny of parents captured in the LaHave River, Nova Scotia.

Results

Seawater Acclimation

The relationship between osmolarity of the various body fluids, ambient salinity, salmon age and month of seawater exposure was determined by multiple regression analysis.

Serum osmolarity of both yearling and two-yr-old juveniles showed a gradual linear increase of about 9% as salinity increased from fresh water (0.1°/∞) to 31°/∞.. For example, values for yearlings increased from 329±9 mOsm/l in fresh water to 359±18 mOsm/l in sea water during the February-March study and for the two-yr-old juveniles from 333±11 to 351±10 mOsm/l. Similar values for both age-classes were recorded during May. The relationship between serum osmolarity and ambient salinity was described by the regression:

$$(1)\quad 0_S = 0.769S + 333.283$$

The coefficient of multiple determination (R^2) is 0.405 (1,191 d.f.) where 0_S is serum osmolarity (mOsm/l) and S is salinity (°/∞). Neither month of seawater exposure nor salmon age significantly influenced changes in serum osmolarity with increasing salinity ($P>0.05$).

Osmolarity of intestinal fluid also showed a gradual linear increase with salinity, values recorded at 31°/∞ exceeding those at 0.1°/∞ by ≤15%. Osmolarity of this fluid for yearlings during the February-March study increased from 316±17 in 0.1°/∞ to 340±26 mOsm/l in 31°/∞ and for the two-yr-old juveniles from 317±33 to 334±15 mOsm/l. Similar values were observed during May for both age-classes. The relationship between osmolarity of intestinal fluid and ambient salinity was described by the regression:

$$(2)\quad 0_I = 1.009\ S + 305.649$$

The coefficient of multiple determination (R^2) is 0.263 (1,144 df) where 0_I is osmolarity of intestinal fluid (mOsm/ℓ). Neither month of exposure to increasing salinity nor salmon age significantly influenced changes in osmolarity of this fluid ($P>0.05$).

Increases in ambient salinity from 0.1 to 31°/∞ resulted in an exponential increase in the osmolarity of urine taken from salmon of both age-classes. Values of this fluid from juveniles in 0.1°/∞ was similar to that of their medium whereas values for juveniles in 31°/∞ were markedly higher and similar to that of serum and intestinal fluid. For example, during the February-March study, osmolarity of urine from yearlings increased from 32±9 to 331±36 mOsm/l as salinity increased from 0.1 to 31°/∞ while values for two-yr-old juveniles increased from 25±9 to 327±20 mOsm/l. Values recorded for both age-classes were slightly greater at 0.1 and 15.5°/∞ salinity during May than during the earlier study and at 31°/∞ salinity identical. The following regression of salinity and month of the year on urine osmolarity was used to describe the data.

$$(3)\quad \log_{10} O_u = 0.036\,S + 0.249M - 0.788\times10^{-2}\,(S\times M) + 1.424$$

The R^2 value is 0.943 (3,165 d.f.) where Ou is urine osmolarity, S is salinity and M month. The month term was represented by a dummy variable in the regression analysis where 0 represented the February-March experiment and 1 the May experiment. This was necessary because month is a nominal-scale variable. Salmon age was not significant.

During both acclimation studies, two-yr-old juveniles exhibited 100% survival in all experimental tanks while mortality occurred among a small percentage of the yearlings (range 0-8%) and was attributable to aggressive behaviour resulting in scale loss and wounding. Serum and intestinal fluid obtained from a number of salmon parr inadvertently included with the experimental fish indicated an elevation of these body fluids, values of 495±41 (N=22) for serum and of 471±49 (N=17) for intestinal fluid representing a 50% increase from values recorded in fresh water. Changes in osmolarity of the body fluids of juveniles and of salmon parr which accompanied increases in salinity are shown in Fig. 1.

Attempts to acclimate salmon parr to 31°/₀₀ indicated that survival was related to their size. All mortality was restricted to fish $\leq$19 g (<12 cm fork length). Within this size range, mortality was greatest among the smallest individuals. Parr, unable to acclimate to 31°/₀₀, showed elevated osmolarity of serum and intestinal fluid coupled with decreased body moisture. Values for serum and intestinal fluid were 447±29 and 422±27 mOsm/l respectively, considerably greater than the values of 351±14 and 336±14 mOsm/l recorded for the serum and intestinal fluid of acclimated parr. Total body moisture for acclimated parr was 73.7±0.7% wet weight and 69.8±1.5% for those unable to acclimate. The relationship between serum osmolarity, parr weight and ambient salinity was described by the regression:

$$(4)\quad O_S = 0.180S^2 - 0.133\times10^{-1}(S^2\times W) + 0.201\times10^{-3}(S^2\times W^2) + 315.998$$

The coefficient of multiple determination (R^2) is 0.716 (3, 92 d.f.) where O_S is serum osmolarity, S is salinity and W is parr weight (g). A response surface predicted using equation (4) is presented in Fig. 2 to aid in interpretation of the data. Serum osmolarity of parr in fresh water remained constant over the 2-37 g weight range changing little with increases in salinity to 15°/₀₀. At 31°/₀₀, elevation of osmolarity above values observed for fish in fresh water was most marked among the smallest individuals (52% increase) whereas values for the heaviest parr showed little increase (6%). For parr > 19g (12 cm fork length) no signs of osmotic stress such as extreme elevation of serum and intestinal fluid osmolarity or decreased body moisture were apparent.

Changes in Proximate Composition and Condition Factor During Parr-Smolt Transformation

Mersey Hatchery

Changes in condition factor and lipid and moisture content of juveniles at Mactaquac and Mersey were related to time of year (cumulative days from January 1) by multiple regression analysis. Because the nature of the changes in these parameters with time was size specific, fork length was made an independent variable in the analysis. This allowed comparison of juveniles of a given size at different times of the year. Additionally, all changes were modulated by time of year acting quadratically necessitating the use of the Day^2 variable.

Condition factor of 16-20 cm juveniles declined exponentially from the first sampling date in January (day 30) until the end of May (day 150) (Fig. 3a) when the last groups of fish were released. The extent of the decline in K values was greatest for the larger juveniles. In contrast, condition of juveniles $\leq$ 12 cm showed a gradual increase throughout the experimental period.

Lipid content of 16-20 cm juveniles showed an exponential decline between January and May but remained relatively constant for fish $\leq$ 12 cm (Fig. 3b). For the larger juveniles (20 cm), lipid content was about 45% lower at the end of May(day 150) than values recorded at the end of February (day 60) while lipid of those smaller (16 cm) was 27% lower (decrease as % of initial value). More than half these changes in lipid occurred during late-April and May when migratory activity was apparent in the rearing ponds. Decreases in lipid were accompanied by increases in moisture content (Fig. 3c).

Migratory activity at Mersey was first apparent by mid-April (day 107) coincident with an increase in water temperature from 6°C to 8°C and continued until the end of May (day 150) when the last groups of juveniles were released. The largest fish demonstrated this type of activity a few days earlier than those smaller, but differences on the basis of size were not apparent later during the migratory period. Water temperatures at Mersey usually reach 10°C by the first of May and 15°C at the end of that month.

Mactaquac Hatchery

Condition factor of 16-24 cm salmon decreased from the first sampling date in February until late-May (about day 140) when values began to increase (Fig. 3d). Within this size range, the magnitude of the decrease in K was greatest for the larger fish. K values for juveniles $\leq$ 12 cm remained relatively constant until the beginning of May (day 120) when values began to increase. The response surface describing changes in condition does not show the gradual exponential decline in this parameter evident between February and May. However, more importantly, it does demonstrate that fish start to regain condition during late-May and that this parameter increased until the end of June (day 180).

Lipid content for juveniles of various size showed a gradual exponential decline during the experimental period (Fig. 3e), the magnitude of the decline being greatest for the larger salmon. For example, lipid content of 20 cm juveniles was about 16% lower at the end of May (day 150) than values recorded at the end of February (day 60) while values for 16 cm fish were 10% lower (decrease as % of initial level). Changes in moisture content during the experimental period were the inverse of those observed for lipid (Fig. 3f).

Migratory activity or reverse orientation to the current in the holding ponds occurs during May at Mactaquac, particularly the last half of that month and ceases by early June (McAskill, personal communication). Mean daily water temperatures at this location usually increase from 5°C at the beginning of May to 10°C at the end of that month reaching 15°C by mid-June.

Condition factors (K) and proximate composition of the yearling and two-yr-old juveniles used in the seawater acclimation studies have been presented in a previous report (Farmer et al. 1977). Changes in K, lipid and moisture were similar to those previously described for fish at Mactaquac while protein and ash content of both groups remained constant during the process of parr-smolt transformation.

Discussion

During both seawater acclimation studies, serum osmolarity of the one- and two-yr-old juvenile salmon increased by $\leq 9\%$ with increases in salinity from 0.1 to 31°/∞ while osmolarity of intestinal fluid showed a rise of $\leq 15\%$. In contrast, osmolarity of these fluids taken from salmon parr unable to acclimate to sea water were 50% higher than values recorded in fresh water. Gordon (1959) and Parry (1961; 1966) report that blood osmolarity of euryhaline teleosts acclimated to sea water increases by only 5-10% above freshwater concentrations. The relatively small changes in osmolarity of serum and intestinal fluid observed for juvenile salmon during the present studies indicate that both age-classes acclimated to sea water equally well and that completion of parr-smolt transformation was not requisite for acclimation. Accordingly, salinity was the only significant variable describing changes in osmolarity of serum and intestinal fluid whereas salmon age and month of seawater exposure were non-significant. While month of seawater exposure did not influence the ability of juvenile salmon to acclimate to 31°/∞, fish used in both studies were markedly different. Those employed during February-March had high lipid and K values characteristic of the pre-smolt condition (Saunders and Henderson 1970), whereas salmon used during May had low lipid and K values distinctive of smolts. Changes in osmolarity of urine obtained from both juvenile age-classes during exposure to increasing salinity also followed a pattern typical of a euryhaline teleost possessing the capacity for marine hypoosmoregulation (Hickman 1968; Hickman and Trump 1969).

Osmolarity of urine taken from juvenile salmon held in fresh water and half sea water during May and June was greater than values recorded for this fluid collected during February. Similarly, Holmes and Stainer (1966) observed during transformation of rainbow trout, Salmo gairdneri, that rate of urine flow and ionic excretion declined to half pre-smolt values and that these changes were accompanied by increases in urine osmolarity. These changes tended towards the pattern known to exist for seawater acclimated fish andwere interpreted by Holmes and Stainer (1966) as a preadaptation to the marine environment. In this context, increases in urine osmolarity during May and June for salmon held in fresh water and half sea water were coincident with their downstream migratory period.

Seawater acclimation of Atlantic salmon was possible during the parr stage for fish in excess of 12 cm fork length in agreement with Wagner's (1974) observation that seawater acclimation of juvenile rainbow trout preceded the completion of parr-smolt transformation occurring when trout reached a length of 12 or 13 cm. Conte (1969) has suggested that transformation is associated with a type of biological clock informing smolting species of the time to seek the marine environment rather than representing the development of the marine hypoosmoregulatory mechanisms. However, Saunders (personal communication) has observed that median survival time of juvenile Atlantic salmon transferred directly to 40°/‰ salinity from fresh water on various dates between January and June increases as they undergo parr-smolt transformation. Thus, while Atlantic salmon are apparently able to acclimate to sea water as parr, further development of the osmoregulatory mechanisms enabling them to withstand osmotic stress may occur during transformation. In this context, Saunders and Henderson (1970) concluded that although pre-smolt Atlantic salmon tolerate high salinity, those salmon of comparable size judged to be smolts grew better in sea water because transformation provided some additional capacity enabling them to thrive in this medium.

Condition factor of juveniles at Mactaquac remains above 1.0 during January, February and most of March then decreases to <1.0 during April. Liberation prior to the second half of April could result in lower rates of adult returns as a proportion of the juveniles are non-migratory at that time. In this context, Wagner (1968) observed that rate of returning adults from the release of steelhead smolts in the Alsea River, Oregon, during April was greater than from February and March releases. The early liberation groups had higher K values than those released during April and the lower rates of return were attributed to greater proportions of non-migrants which resulted in higher rates of freshwater post-liberation mortality (Wagner 1968).

The influence of timing of smolt release on subsequent adult return was first investigated at Mactaquac during 1975 when two groups of 6,000 smolts were forced from the station on May 2 and two identical groups on May 26. Returns of one-sea-winter salmon were equal for the early and late release groups suggesting that liberation dates maximizing rate of return are relatively flexible within the month of May. The flexibility in release date during May at Mactaquac is presumably attributable, in part, to the relatively small lipid losses ($\leq$10%) during this period and to the occurrence of migratory activity throughout the month. In this context, increased energy reserves at time of release has been shown to increase the survival of cultured salmonids (Burrows 1969; Peterson 1973). Condition factor of smolts at Mactaquac began to increase during the late-May to early-June period coincident with cessation of migratory activity indicating that liberation during June could result in lower adult return as a proportion of the juveniles are non-migratory at that time.

At Mersey, K values and lipid content continued to decrease at the end of May when the last groups of juveniles were released. Presumably condition factor would have increased during June as at Mactaquac marking the cessation of migratory activity at this location. In contrast, lipid content of smolts at Mersey decreased at three times the rate as observed at Mactaquac and migratory activity was apparent three weeks earlier. Water temperatures at Mersey usually reach 10°C by the first of May and 15°C at the end of that month, whereas these temperatures are not attained until late-May and mid-June respectively at Mactaquac. Although day length was slightly longer at Mersey (+10 minutes on May 1), the advanced temperatures cycle at that location is probably responsible for the earlier onset and extended period of migratory activity which results in a greater rate of lipid utilization. Because of this rapid loss of lipid among smolts at Mersey, the period of release at that location is more critical and less flexible than the month of May recommended for smolts at Mactaquac. Judging from the onset of migratory activity and from changes in K values and lipid content, late-April to early-May appears to be an appropriate period for smolt liberation at Mersey. In this context, observations of downstream movements of smolts released during the last week of April, 1971, in the LaHave River indicated that fish began migration prior to mid-May. Subsequent liberation of yearling smolts in this river during the late-May to early-June period (1972-1974) resulted in markedly lower adult returns than resulted from the release of two-yr-old smolts during early-May. Results from the present study indicate that transformation is synchronous for juveniles of various size (age) and that liberation in southwest Nova Scotia should occur during the late-April to early-May period. The lower returns from yearling smolts cannot be attributed to failure of development of the marine osmoregulatory mechanisms or totally to their relatively smaller size but rather to the late period of liberation.

Since energy reserves continually decrease during transformation, smolt liberation earlier within the migratory period ensures energy availability which may reduce mortality during acclimation to drastically different conditions of survival and feeding in a new environment. In this context, Peterson (1973) reports a higher rate of returning adult Atlantic salmon when smolts were fed a diet containing 16% marine lipid for one month prior to release rather than the usual diet having 6% lipid content. Similarly, Burrows (1969) observed greater adult returns of chinook salmon, O. tshawytscha, resulting from the release of fingerlings having 7.9% lipid content than from the group whose lipid level was 4.1%. Subsequent recovery of fingerlings in the estuary 7 days following release indicated lipid losses of 4% to 40% reflecting food deprivation and stress associated with the period immediately following liberation.

Changes in lipid and moisture content and K values occurring during transformation at both Mactaquac and Mersey were greater for larger smolts than for those smaller, suggesting that energy expenditure associated with transformation is size specific. It is not known if these size specific differences are manifest in greater migratory activity of larger cultured smolts, but larger wild smolts have been observed to show downstream migration earlier than those smaller (Saunders and Allen 1967; Österdahl 1969), a phenomenon observed in the present study for smolts at Mersey.

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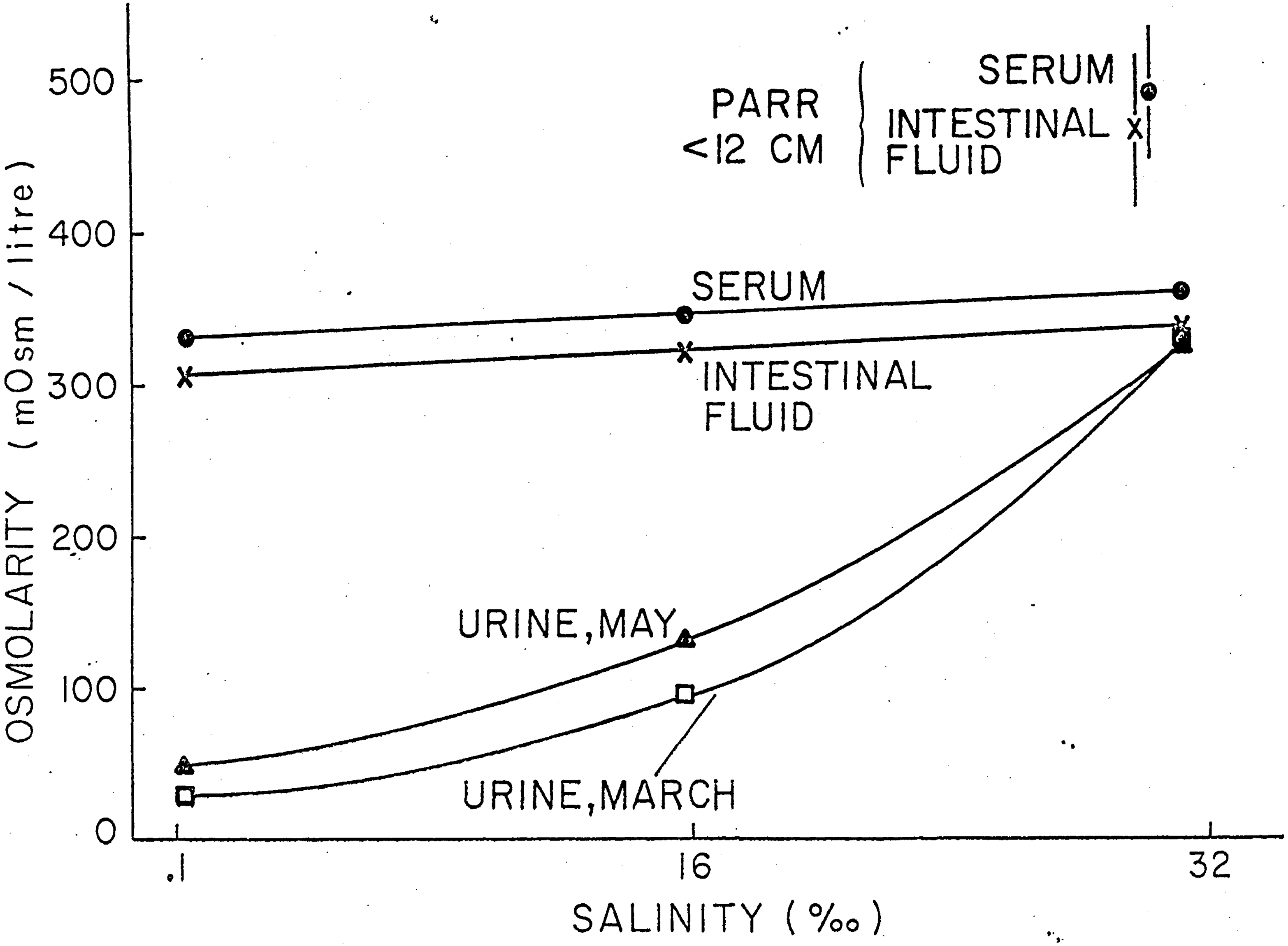
Captions for Illustrations

Figure 1. Changes in the osmotic concentration of serum, urine, and intestinal fluid of juvenile Atlantic salmon exposed to increasing salinity. Values obtained from equations 1, 2 and 3. Mean values ±1 S.D. for parr of <12 cm in 31°/‰ salinity are given for comparison.

Figure 2. The influence of ambient salinity on the serum osmolarity of underyearling Atlantic salmon parr of various size. Values were obtained from equation 4.

Figure 3. a, b, c, d, e, f. The relationship between time of year (cumulative number of days from January 1) and changes in condition factor and lipid and moisture content of juvenile Atlantic salmon of various size at the Mactaquac and Mersey hatcheries.

FIGURE 1



SERUM
PARR
<12 CM
INTESTINAL FLUID
500
400
300
200
100
0
OSMOLARITY (mOsm / litre)
SERUM
INTESTINAL FLUID
URINE, MAY
URINE, MARCH
.1
16
32
SALINITY (‰)

FIGURE 2

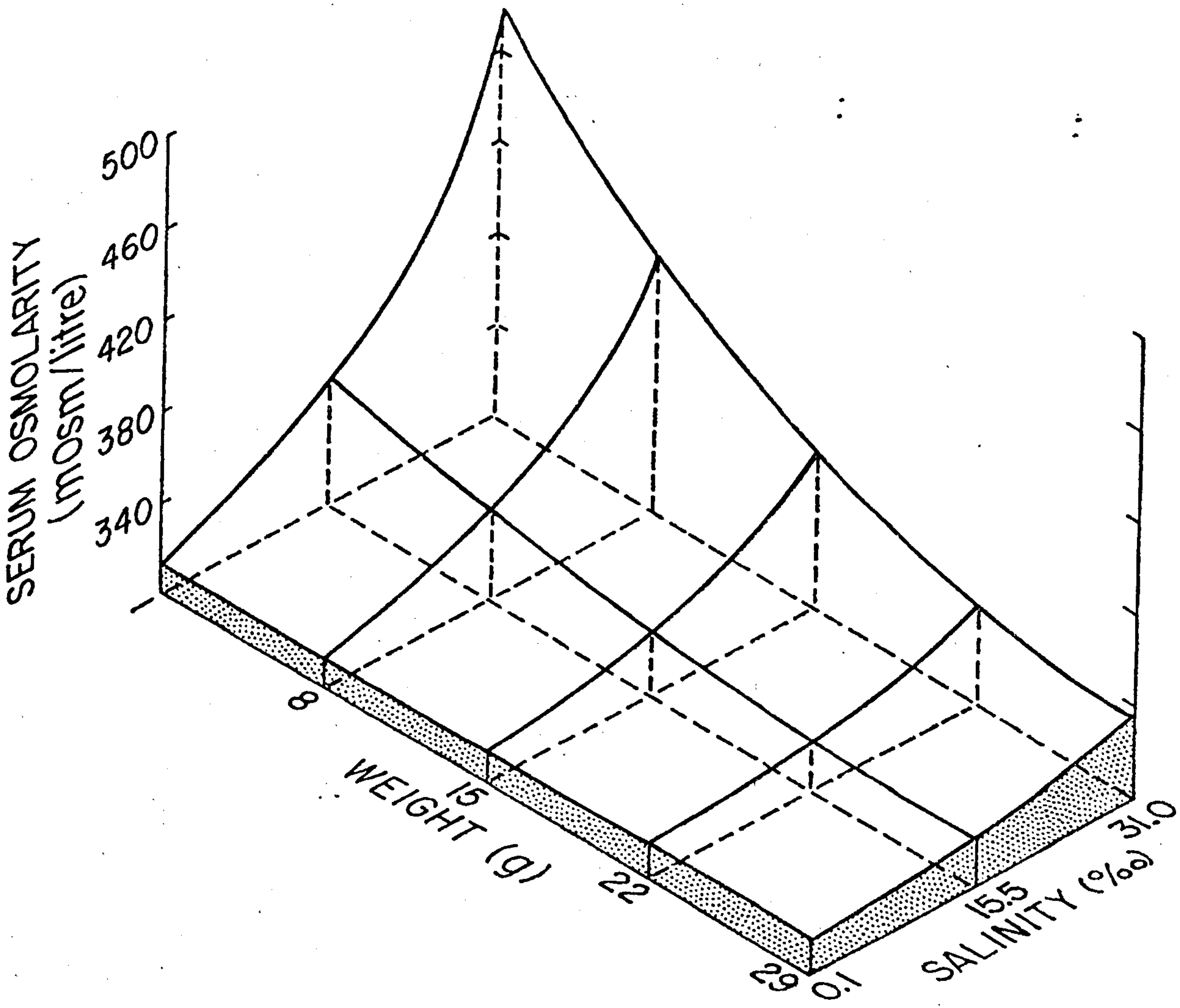
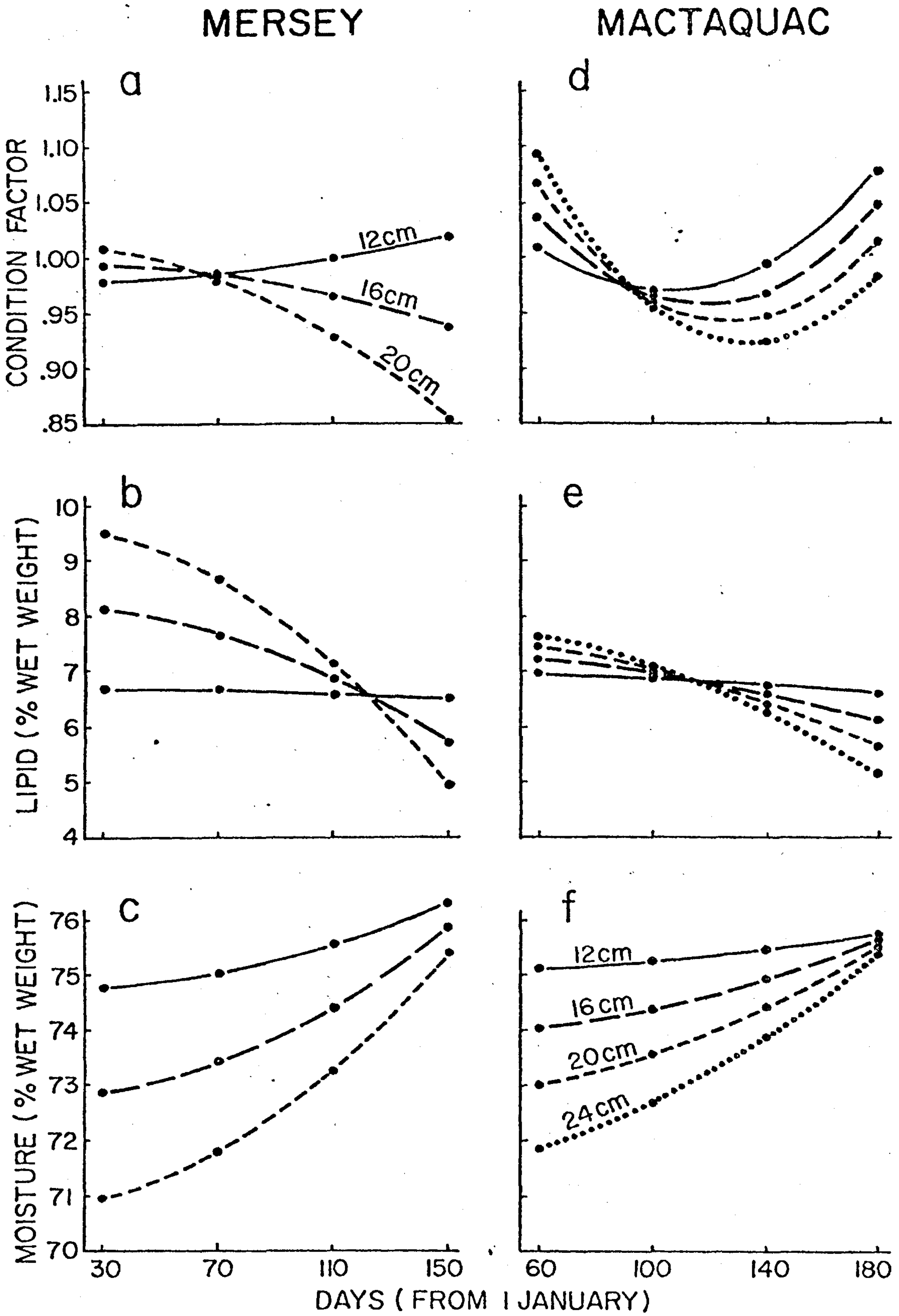

SERUM OSMOLARITY (mOsm/litre)
500
460
420
380
340
8
15
22
29
WEIGHT (g)
0.1
15.5
31.0
SALINITY (‰)

FIGURE 3


MERSEY
MACTAQUAC
a
d
CONDITION FACTOR
1.15
1.10
1.05
1.00
.95
.90
.85
12cm
16cm
20cm
b
e
LIPID (% WET WEIGHT)
10
9
8
7
6
5
4
c
f
MOISTURE (% WET WEIGHT)
76
75
74
73
72
71
70
12cm
16cm
20cm
24cm
30
70
110
150
60
100
140
180
DAYS (FROM 1 JANUARY)