
Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L.

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Abstract:

The hypothesis that marine survival of Atlantic salmon *Salmo Salar* is linked to marine growth was explored by using inter-circuli distances and total numbers of circuli existing on scales from a population monitored over nearly four decades. The results suggest that marine growth controls survival, particularly during the late summer and early winter of the first year at sea. Recruitment is strongly linked to growth, described as the total number of circuli, but not to inter-circuli distances. This highlights the potential of patterns of circuli number to be considered as proxies for growth. Indications that hatchery populations might be subject to other mortality events, in addition to those experienced by wild populations, are also presented.

Keywords: Atlantic salmon, Circuli, Growth, Post-smolt, Survival

1. Introduction

The overall catches of salmon (*Salmo salar* L.) in the North Atlantic have decreased by more than 80% since the early 1970's (Anon., 2002). Management measures, taken to regulate the exploitation of the wild resource, have resulted in lower catches, but have not stemmed the decline in the levels of recruitment linked to high mortality in the marine environment (Mather *et al.*, 1998; Anon., 2003, Friedland *et al.*, 2005). The possible causes for this increase in mortality are numerous, ranging from high numbers of predators (Middlemas *et al.*, 2003; Montevecchi & Cairns, 2003), the effects of the exploitation of forage fish (Daan *et al.*, 2005), to the effects of aquaculture (Butler and Watt, 2003; McGinnity *et al.*, 2003) and overfishing (Anon., 2005). In recent decades, profound modifications of the marine environment have resulted in important changes in the dynamics of marine ecosystems in the North Atlantic (Beaugrand *et al.*, 2002; Beaugrand & Reid, 2003; Beaugrand, 2004; Richardson & Schoeman, 2004; Heath, 2005; Perry *et al.*, 2005). High levels of fishing pressure have often exacerbated the influence of changing environmental conditions on fish stocks (Jennings *et al.*, 1998). The modifications that have occurred at different trophic levels may have profoundly affected the ability of salmon to use the marine environment to achieve optimal growth and return successfully to their native rivers (Cairns, 2001).

In this context, several studies have considered the possible influence of marine conditions, particularly changes in ocean temperatures, on both sides of the Atlantic (Friedland *et al.*, 1993). Relationships between the levels of marine recruitment of European and North American stocks and the availability of specific thermal habitats in the spring have been reported (Friedland *et al.*, 1998; 2000). Survival for two salmon populations from the North Sea was compared to information on marine growth, but the intermediate link between temperature and growth was not explicitly demonstrated (Friedland *et al.*, 2000). During their marine migration, salmon exhibit rates of mortality and growth that are significantly higher than those experienced by other pelagic species (Cairns 2003). Their overall strategy seems to be based on a trade-off between these two life-history traits (Cairns 2001), thus highlighting the possible importance of marine growth in controlling the overall rates of marine survival and recruitment.

This study tests the hypothesis that rates of marine recruitment of Irish salmon are linked to scale patterns, hence providing a platform to better understand the observed reduction in recruitment. Seasonal contributions of overall marine growth are described and the effects of seasonal growth patterns on critical periods for salmon survival are tested.

2. Materials and methods

Scales from a monitored salmon population were used to explore the relationships between growth and survival over a multi-decadal time frame. Variations in fish growth rates are often recorded in scales and other hard structures such as otoliths or vertebrae (Jennings *et al.* 2001). For instance, salmon have cycloid scales, characterised by the formation, as the fish grow, of concentric ridges called circuli, which provide a permanent record of the growth history. When growth is important, the circuli are more widely spaced than when growth is poor. Narrow groups of circuli are then interpreted as winter growth and called annuli (Baglinière & Le Louarn, 1987). This property is widely used to determine the freshwater and marine ages of several salmonids species. In addition, scales are also used to back-calculate the size of the fish, based on evidence of proportionality between scale size and body size, eventhough this relationship has been found to be variable (Fukuwaka & Kaeriyama, 1997; Martinson *et al.*, 2000). Several studies have confirmed the links between body size and both inter-circuli distances and circuli number (Doyle *et al.*, 1987; Fisher & Percy, 1990; Nicieza & Brana, 1993; Fukuwaka & Kaeriyama, 1997) resulting in the widespread use of scale patterns to infer salmon growth (Friedland *et al.*, 1993; Friedland & Reddin, 2000; Beamish *et al.* 2004; Fisher & Percy, 2005; Moss *et al.*, 2005).

Scales from one-sea winter (1SW) salmon were sampled from fish returning to the Burrishoole catchment, in Western Ireland. Migration movements in freshwater for this population are entirely monitored by permanent upstream and downstream trapping facilities (Byrne *et al.*, 2003). The upstream traps are also used to capture returning fish that have previously been released as smolts from the local hatchery. Depending on availability, samples from approximately 50 fish were randomly

selected each year from 1961 to 1999. Prior to 1980, all fish were of wild origin, whereas from 1981 onward, an increasing number of the samples came from fish released from the hatchery. Scales were chosen after examination (scales showing evidence of regeneration were excluded from the analysis) and rolled onto acetate slides, which were later analysed using an image processing system. A high resolution picture of each salmon scale was saved and the presence of the circuli was recorded using differences in light intensity (circuli bands appeared as dark bands and inter-circuli periods as clearer bands). The distances between each successive circuli were recorded for the entire marine zone, that is between the circuli corresponding to the smolt seaward migration and the last circuli at the edge of the scale (time of capture of returning adults). All measurements were made along the 360° axis of the scale (Fig. 1) (Friedland & Reddin, 2000). Starting from the first indication of the marine residency, several growth measurements were computed using this information to characterize growth experienced at various stages. Time series of the first and second groups of four consecutive circuli were obtained to describe early marine growth, similarly to Clarke & Friedland (2004). In addition, measurements were also compiled for several other circuli intervals: one to 10, 11 to 20, 21 to 30, 31 to 40 and all circuli. For all these circuli intervals, both mean inter-circuli and cumulative distances were calculated.

The rates of circuli deposition during the marine residency are not known accurately for wild populations. Friedland *et al.* (1993) suggested that the mean rate of deposition is approximately four circuli per month during the spring-summer period, and two circuli per month in the autumn and winter. However, the patterns of inter-circuli distances might not always be a true representation of somatic growth. Poor growth can result in no circuli deposition, or even in the absorption of existing circuli (Bilton, 1975). This has implications for the value of growth measurements compiled over arbitrary circuli intervals, as representative proxies for growth. The growth recorded over these intervals does not necessarily occur over comparable periods of time over the years, making inter-annual comparisons potentially irrelevant. Salmon growth rates are controlled by endogenous rates, food availability, but also photoperiod cycles (Fjellidal *et al.*, 2005). Therefore, peaks of maximum and minimum inter-circuli growth are possibly linked to the times when the photoperiod is respectively maximum (summer solstice) and minimum (winter solstice). Here, the growth patterns between the seaward migration and the occurrence of First Summer Maximum growth (the point of higher Inter-Circuli Distance), First Winter minimum growth (the point of lower Inter-Circuli Distance), and Second Summer Maximum growth were considered. These temporal limits were defined for each year in terms of the numbers of circuli pairs deposited. The total number of circuli deposited between the last freshwater circuli and the edge of the scale was also computed. Finally, records of the fish body lengths were considered in addition to their scale patterns. These are forklengths, recorded to the nearest centimeter.

2.1. Salmon recruitment

The growth measurements and the final sizes were compared on an inter-annual basis to estimates of marine survival of wild and hatchery Burrishoole salmon (Fig. 2) using Pearson correlation. These estimates are computed according to the number of smolts migrating (or released), the corresponding number of adults returning to the traps, and estimates of the levels of exploitation and unreported catches (Anon., 2003). A time series of the rate of returns to freshwater (trap returns), similar to the time series of marine survival for the Burrishoole wild fish but not corrected for unreported catches and the levels of exploitation, was also used. The rates of marine survival are available between 1980 and 1999 (smolts years), while the rates of returns to the traps are available since 1972. In addition, an estimate of Irish Pre-Fishery Abundance (PFA) for maturing 1SW fish was used (Anon., 2002; Potter *et al.*, 1998). This is an estimate of the number of fish available before exploitation starts, back-calculated from the catches, and estimates of the rates of exploitation, natural mortality and unreported catches (Potter *et al.*, 1998; 2004). For each pairwise comparison presented, the level of autocorrelation of the time series were assessed and a Pearson correlation coefficient was calculated. When autocorrelation was detected, the significance of the correlation coefficient was re-assessed following the method of Garrett & Toulany (1981), and the correlation coefficients were presented after using the “corrected” number of degree of freedom.

3. Results

3.1. Inter-circuli distances

The curves of salmon marine growth, as inferred from the scales patterns, display a characteristic shape. Typically, increasing inter-circuli distances (Fig. 3) reach a maximum early after the seaward migration (referred to as FSM: First Summer Maximum), followed by a gradual decline in growth until the First Winter minimum (FWm) is recorded. After the First Winter minimum, a new period of increasing inter-circuli distances takes place and reaches a plateau just before the fish return to freshwater (SSM: Second Summer Maximum). The growth in the last spring-summer period is considerably lower than when the fish enter the marine environment. This possibly reflects the fact that the skeletal growth has been largely completed at this stage and that energy is likely to result in increased weight or gonadal development. Growth, as inferred from the inter-circuli distances, is also most variable during a short period just before the return to freshwater, as indicated by the confidence bars in Fig. 3. The number of circuli deposited at the points of maximum and minimum inter-circuli distances showed important variations over the period of study (Fig. 4). The number of circuli deposited at the point of First Summer Maximum (Fig. 4a) was significantly higher in the 1960's than in the 1990's (t -test; $df = 793$; $P < 0.05$). The number of circuli at the point of minimum inter-circuli distances (FWm, Fig.4b) demonstrated variation over the period of study with important values recorded during the first two decades and a marked decline in the early 1980's. Pairwise t -tests between decades confirmed that at the point of minimum inter-circuli distances (FWm), there were significantly more circuli deposited in the 1960-70's than in the 1980-90's (t -test; $df = 793$; $P < 0.01$). There was no significant difference in the number of circuli deposited at the point of FWm between the 1960's and 1970's, or between the 1980's and 1990's. Finally the number of circuli deposited at the point of Second Summer Maximum (Fig. 4c), was significantly higher in the 1960's than in the 1980's (t -test; $df = 772$; $P < 0.05$). It was also higher (t -test; $df = 898$; $P < 0.05$) in the 1970's than in both the 1980's and 1990's, and the number of circuli was more variable in the last two decades.

Total inter-circuli distances (Fig. 5) were high in the late 1960's and early 1970's (highest value in 1972, 2.730 ± 0.321 mm), started to decline in the mid 1970's to reach a minimum value in 1980 (2.165 ± 0.299 mm) and then increased again, showing important inter-annual variability in the 1980's and 1990's, but remaining lower than in the earlier part of the study.

3.2. Circuli Numbers

The lowest mean number of circuli (Fig. 6) was recorded for 1980 (37.894 ± 4.279) and the highest for 1964 (49.100 ± 8.417). Overall the total number of circuli follows the pattern of the inter-circuli distances, with higher circuli number in the 1960's and 1970's, a strong decline in the late 1970's and a small recovery in the 1980's. However, and contrarily to the pattern of inter-circuli distances, the number of circuli declined again from the mid 1980's to the late 1990's. The total number of circuli was significantly higher (t -test; $df = 772$; $P < 0.01$) and less variable during the early part of the study (1960's and 1970's) than during the later years (1980's and 1990's).

The patterns of growth, derived from inter-circuli distances and circuli numbers, all indicated a decline in growth over the period of study. Generally, growth was higher in the 1960's and 1970's than in the 1980's and 1990's. The number of circuli gave slightly different results than the total inter-circuli distances with regard to the comparison between the 1980's and 1990's. The total inter-circuli distances were significantly higher (t -test; $df = 943$; $P < 0.01$) in the 1990's than in the 1980's, whereas the number of circuli was significantly higher in the 1980's than in the 1990's (t -test; $df = 943$; $P < 0.05$). The number of circuli stayed low during the 1990's while the inter-circuli distances increased during this period.

3.3. Length of returning 1SW

There was little variation in the length of returning 1SW over the period of study (Fig. 7). There was no significant difference in fish length (t -test; $df = 748$; $P > 0.05$) between the 1960's (62.591 ± 5.672 cm) and the 1970's (62.780 ± 4.861 cm). However, the length of the returning fish was significantly higher in the 1980's (63.462 ± 5.571 cm) (t -test; $df = 748$; $P < 0.05$) and lower in the 1990's (61.105 ± 5.901 cm) (t -test; $df = 748$; $P < 0.01$) than in any other decade. The total length of the fish having returned to freshwater appears relatively constant, around 63 cm, in the first part of the study,

increases in the mid-1980's, but then decreases and becomes more variable in the 1990's. The decline in the early 1990's is similar to the decline observed for the number of circuli during the same period. The lowest value is recorded in 1962 (57.650 ± 7.291 cm) and the highest in 1986 (65.414 ± 6.682 cm).

3.4. Comparison between growth and recruitment

The distances between the marine circuli 1-4 and 5-8 were not significantly correlated to Burrishoole Marine survival, of either wild or hatchery origin. However, there were significant negative correlations between the inter circuli distances for the circuli 1-4 and 5-8 and the survival rate to the traps (Table I). There was no significant correlation with the estimate of PFA. The inter-circuli distance between circuli 11-20, 21-30 and 31-40 were not correlated to any of the time series of salmon recruitment.

The mean number of circuli was highly correlated to Burrishoole wild marine survival ($r = 0.797$; $df = 18$; $P < 0.001$) (Fig. 8), to the estimate of PFA ($r = 0.669$; $df = 28$; $P < 0.05$), and to a lesser extent to the survival to the traps ($r = 0.463$; $df = 26$; $P < 0.05$) and Burrishoole hatchery marine survival ($r = 0.514$; $df = 18$; $P < 0.05$).

3.5. Number of circuli at points of maximum and minimum growth

The number of circuli at the point of First Summer Maximum and Second Summer Maximum were not correlated to salmon recruitment (Table I). The number of circuli at the point of First Winter minimum was correlated to the time series of Burrishoole wild marine survival ($r = 0.458$; $df = 18$; $P < 0.05$;) but not to the other time series of salmon recruitment.

3.6. Total circuli number versus circuli number at points of maximum and minimum growth

The total number of circuli was significantly correlated to the number of circuli at First Summer Maximum ($r = 0.388$; $df = 37$; $P < 0.001$), the number of circuli at First Winter minimum ($r = 0.732$; $df = 37$; $P < 0.001$) and the number of circuli at Second Summer Maximum ($r = 0.696$; $df = 37$; $P < 0.001$) (Fig. 9).

3.7. Fish length and salmon recruitment

There was no significant correlation between the average length of the fish and the corresponding levels of marine recruitment (Table I).

4. Discussion

Important changes in the marine ecosystems of the northeast Atlantic might be responsible for the observed decline of salmon abundance (Beaugrand *et al.*, 2003), by controlling growth, size and predation rates (Friedland *et al.*, 2000). Previous investigations have shown that marine growth has decreased over the last twenty years but no link between marine growth (as inferred from scales patterns) and marine survival was found for Irish populations (Crozier & Kennedy, 1999; McLoone, 2000).

The various growth measurements, based on scale patterns (inter-circuli distances 1-4, 5-8, 1-10, 11-20, 21-30, 31-40, circuli numbers) identified a similar pattern of decline in salmon marine growth between 1962 and 2000. The growth was generally high in the 1960's and 1970's, and then declined in the last two decades. This decline in growth is concomitant with a similar decline in catches and other time series of marine recruitment of salmon in the North Atlantic (Fig. 2) (Anon., 2002).

There were however some important differences between the measurements presented, which suggest that they might in fact have different values as proxies describing the fish growth during the marine residency. For instance, the total number of circuli in the 1980's was significantly higher than in the 1990's, while the total growth expressed in terms of cumulative inter-circuli distances was in fact significantly higher in the 1990's than in the 1980's. This could indicate that despite experiencing a poorer growth, the fish deposited more circuli in the 1980's. Alternatively, it could also suggest that

under certain circumstances, inter-circuli distances do not describe growth accurately. This second hypothesis seems to be supported by the data on fish lengths which shows that returning 1SW were significantly longer in the 1980's.

There was no significant relationship between final length and recruitment of Burrishoole salmon. In addition, there was no correlation between final length and any of the other growth patterns. The final length is the result of the synchronous effects of environmental conditions and genetic predispositions over the entire marine residency. According to the timing of their returning journey to freshwater, large adult salmon can potentially feed and grow intensively during periods of variable lengths. Final length is then unlikely to constitute a good indicator of the limiting effects of the environment on survival. If growth has a strong influence on survival, this is probably when the fish are small and the most vulnerable, not when they have reached a larger size. Hence the growth experienced between the smolts migration and the first winter at sea can have a strong influence on recruitment while making a smaller contribution to final length than growth experienced after the first winter. The "critical size and period hypothesis" of Beamish & Mahnken (2001) pointed towards the importance of growth before the first winter at sea to explain coho salmon (*Oncorhynchus kisutch*) recruitment. This hypothesis proposes that the fish must have reached a threshold size (possibly varying according to the year) by the end of the first summer/autumn at sea, to be able to face the metabolic demand of the winter.

The results of the comparison of the various growth measurements suggest that inter-circuli distances are not correlated to the rates of survival or recruitment. There was no significant relationship between the early growth (inter-circuli distances) and the rates of Burrishoole marine survival for wild or hatchery fish. Similarly, there was no significant correlation between the total growth and recruitment. The only significant relationship was found between the distances over the first 10 circuli and the rate of Burrishoole wild survival. This negative relationship would suggest that high growth during the earlier marine residency results in lower overall marine survival. Similarly, negative relationships were detected between early inter-circuli distances and the rate of wild survival to freshwater. All these relationships were significant and negative.

The time series of survival of Burrishoole salmon to freshwater (to the traps) differs from marine survival because it does not account for unreported catches and exploitation. As such, this estimate is a result of the levels of survival as well as the levels of fishing effort experienced by a cohort. Higher inter-circuli distances early during the marine phase seem to result in poorer return to the traps, perhaps indicating a higher rate of vulnerability to the size-selective coastal fishery, a phenomenon that has been reported for Norwegian populations (Jonsson *et al.*, 2003). These negative correlations might also indicate the existence of a size threshold for survival, early during the marine phase. Growth measurements derived from scale analysis are often considered as representative of the overall growth experienced by the cohort. In fact, they represent the growth rate of the fish that have survived, and perhaps also represents a threshold in growth, necessary for the fish to survive, or a "required" growth rate. These growth requirements could vary from year to year, according to the environment (e.g. the prey availability and predator types/density) which the fish will encounter during the remaining time spent at sea. Under this scenario, higher "required growth" should result in lower survival, and hence result in a negative relationship between the overall survival of the cohort and the growth displayed by the surviving fish. Alternatively, the presence of negative relationships between growth (inter-circuli distances) and recruitment may also be linked to the effects of poor growth conditions on the frequency of circuli deposition. Bilton (1975) described how under poor growing conditions, the deposition of circuli can be suspended and existing circuli can be reabsorbed. This would be detected as an increase in inter-circuli distances and a reduction of the total number of circuli.

In this study, the number of circuli was highly correlated to both rates of Burrishoole marine survival, and to the time series of pre-fishery abundance. The evidence for the control of recruitment by growth is consistent with previous work conducted with European populations (Friedland *et al.*, 2005). These relationships are interesting from a management point of view, because they suggest that the overall rate of marine survival for a cohort could be known early in the year from the pattern of circuli numbers of the first returning 1SW. Assuming that the pattern of circuli number for early returning fish is also representative of the patterns experienced by the entire cohort, growth information could be gathered from early returns, possibly from several neighbouring populations, in order to provide statistically meaningful samples to forecast the survival rates for a given brood year.

The fact that the number of circuli was less correlated to the Burrishoole hatchery marine survival than to Burrishoole wild marine survival, suggests that the fish of hatchery origin might be subject to additional mortality events than the wild fish. This is consistent with other studies where hatchery fish have been shown to not perform as well as wild fish (Jonsson *et al.*, 2003). This could be linked to poorer levels of fitness or capacity to adapt to the marine environment than their wild counterparts.

By comparing the total number of circuli to the number of circuli deposited at specific periods during the marine migration (FSM, FWm and SSM), it was possible to identify a period during which the growth experienced is linked to the final growth attainable by the fish. Growth, in terms of the number of circuli deposited, at the points of First Winter minimum and Second Summer Maximum were both significantly correlated with the total number of circuli. This was expected for the number of circuli at the Second Summer Maximum, since it occurs only few weeks before the return to freshwater and should therefore be very similar to the final number of circuli deposited. However, the number of circuli at the First Winter minimum was not expected to show a higher correlation with the final number of circuli. The fact that the total growth can be linked as far back as the First Winter minimum, but not to the First Summer Maximum, suggests that it is controlled by events taking place between these two dates. This is consistent again with the hypothesis of Beamish & Mahnken (2001). Here, the growth experienced between the First Summer Maximum (i.e. July) and by the time the First Winter minimum occurs, i.e. from October to December (Forsberg, 1995), seems to influence the final growth upon the returning migration. The growth during this period is also significantly correlated with the time series of Burrishoole wild marine survival.

These results validate the hypothesis that growth, as defined by the number of circuli deposited during the marine phase, is central to the mechanism controlling marine recruitment for European salmon. This provides a significant improvement of our understanding of the mechanisms controlling marine recruitment and opens the way for further investigations onto the factors controlling growth and their effects on salmon survival. This could be particularly relevant in the context of observed changes in climate and ocean conditions in the northeast Atlantic. This also confirms the value of long term monitoring programs, such as the census taking place in the Burrishoole station, to understand recruitment variability. These results also highlight the importance of considering circuli number as a proxy for salmon growth rather than to solely rely on inter-circuli distances. This is particularly relevant, and perhaps restricted, to regimes of poor growing conditions, as observed during the last two decades, for which inter-circuli distances might not entirely capture the growth signal.

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Table I. Correlation between patterns of growth (as inferred from scales) and salmon recruitment.

		Recruitment 1SW Salmon			
		MSBH	MSBW	Traps	PFA
Inter-Circuli Distances (mm)	1 to 4	-0.416	-0.453	-0.576**	-0.244
	5 to 8	-0.332	-0.412	-0.612**	-0.374
	1 to 10	-0.396	-0.456*	0.657***	-0.279
	11 to 20	0.036	0.044	-0.168	0.301
	21 to 30	-0.407	-0.209	-0.198	-0.593
	31 to 40	-0.147	0.177	-0.055	-0.475
Circuli Number	FSM	-0.037	-0.065	-0.065	0.296
	FWm	0.279	0.458*	0.431	0.471
	SSM	0.147	0.419	0.415	0.249
Size (cm)	FL	0.302	0.268	0.222	0.276

The significant correlation coefficients are in bold font, and the levels of significance (following correction of the degrees of freedom to account for autocorrelation) are indicated (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$). The significant correlations between the total number of circuli and the four recruitment time-series are reported in Fig. 8. Recruitment 1SW : MSBH (Marine Survival Burrishoole Hatchery); MSBW (Marine Survival Burrishoole Wild); Traps (Marine Survival rate to the Burrishoole traps, without correction for marine exploitation); PFA (Pre-Fishery Abundance for 1SW Irish salmon). Circuli Number: FSM (Number of Circuli at First Summer Maximum); FWm (Number of Circuli at First Winter Minimum); SSM (Number of Circuli at Second Summer Maximum). Size: FL (Final Fork Length measurement of 1SW Burrishoole fish, captured following return to Freshwater).

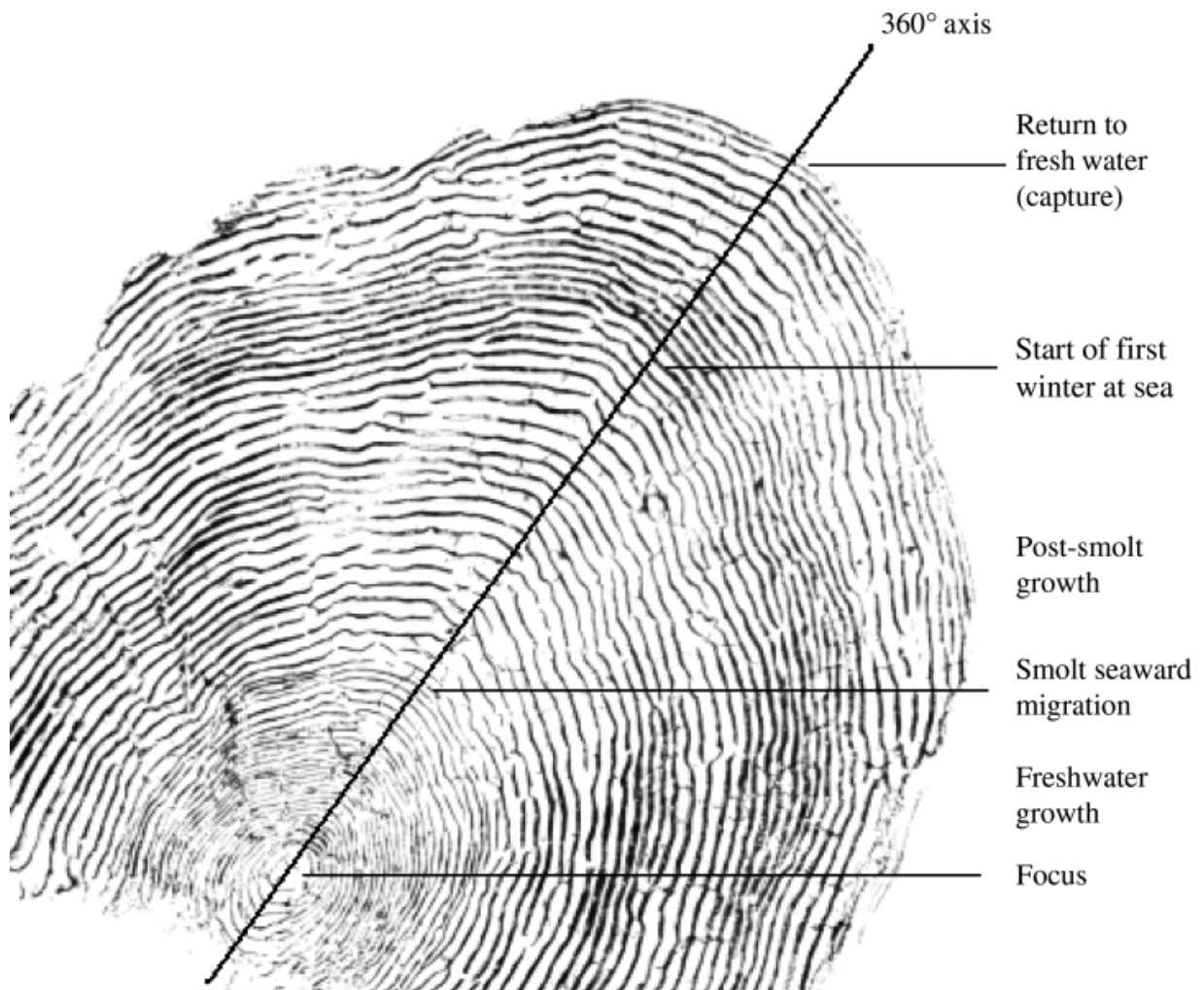


Figure 1. Magnified Salmon scale obtained by image processing, showing freshwater and marine growth (from the smolt seaward migration to the return to freshwater). Circuli measurements and counting were made starting with the first indication of the seaward migration, along the 360° axis, and towards the outer edge of the scale. Lower growth during freshwater residency results in the deposition of narrow circuli. The distances between circuli greatly increase during marine residency, reflecting better growth than in freshwater.

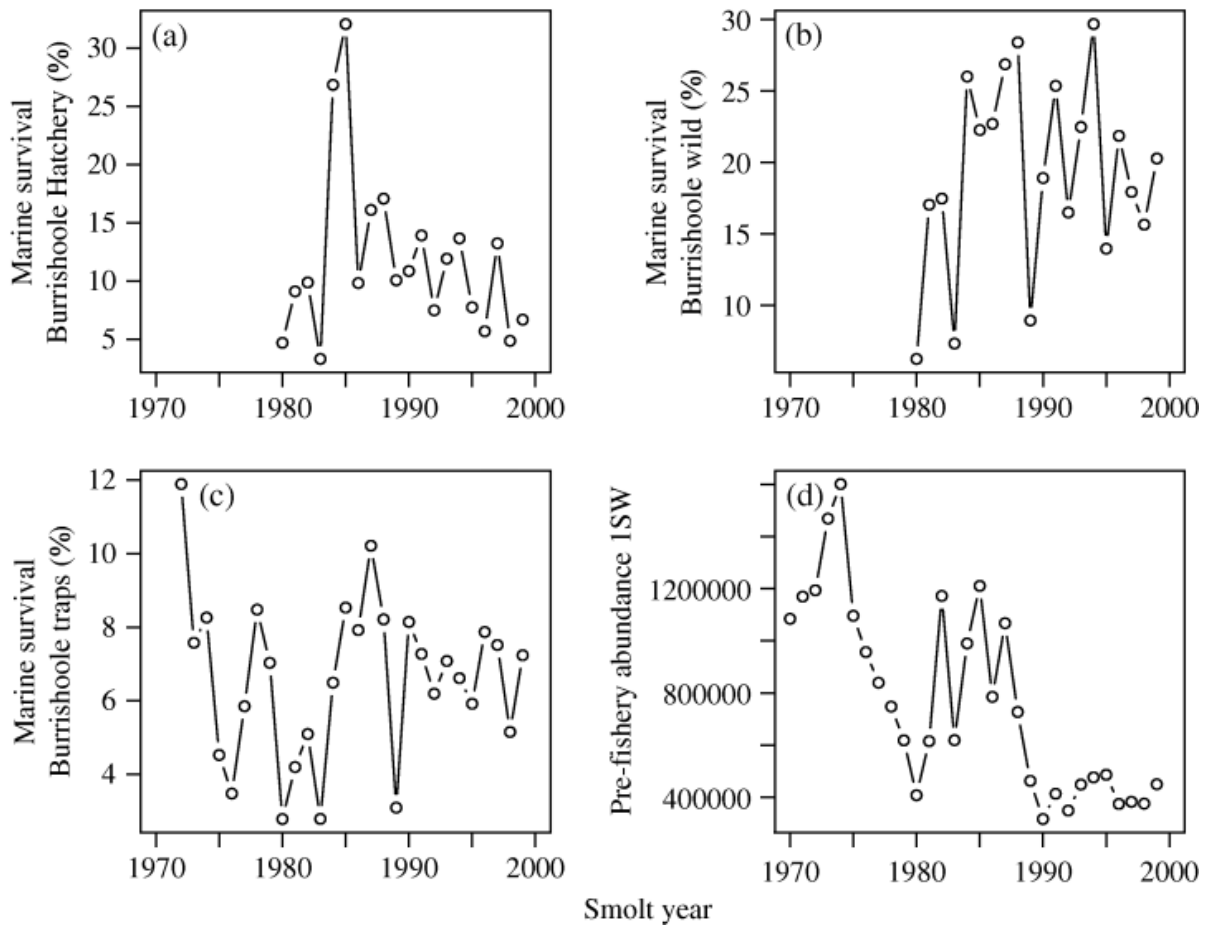


Figure 2. Time series of recruitment of Irish 1SW salmon: a) Marine survival (%) for Burrishoole Hatchery salmon; b) Marine survival (%) for Burrishoole Wild salmon; c) Marine survival (%) to the traps (after exploitation by the coastal fishery) for Burrishoole salmon; d) Estimate of Pre-Fishery Abundance for 1SW Irish salmon (Anon. 2002).

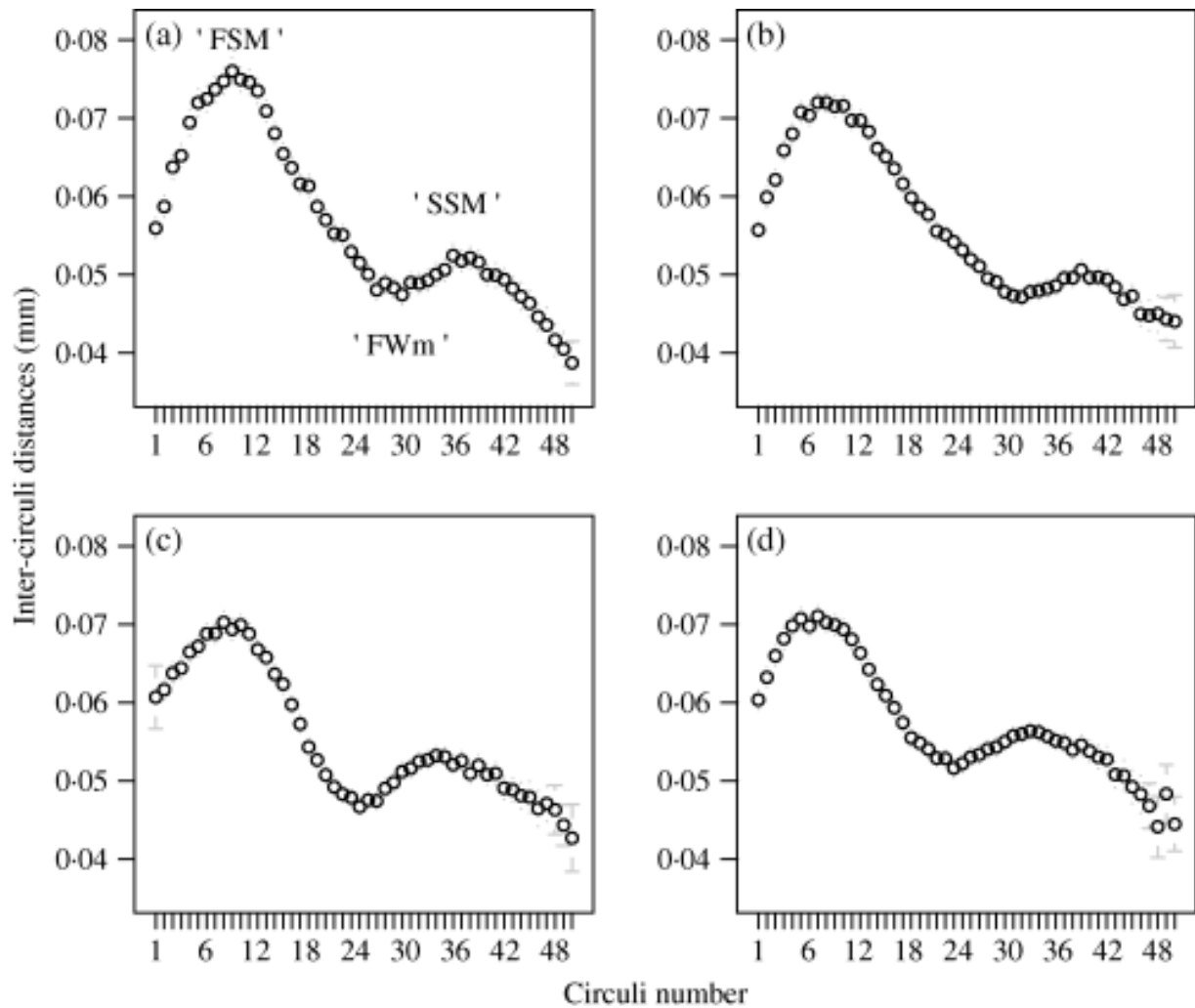


Figure 3. Mean Inter-Circuli Distances (mm) for Burrishoole Salmon, for the 1960's; 1970's; 1980's and 1990's, according to the number of circuli. These plots display the number of circuli deposited at the points of First Summer Maximum (FSM: circuli 7 to 11), First Winter minimum (FWm: circuli 25 to 32) and Second Summer Maximum (SSM: circuli 33 to 40). The confidence level for the error bars is $P = 0.95$.

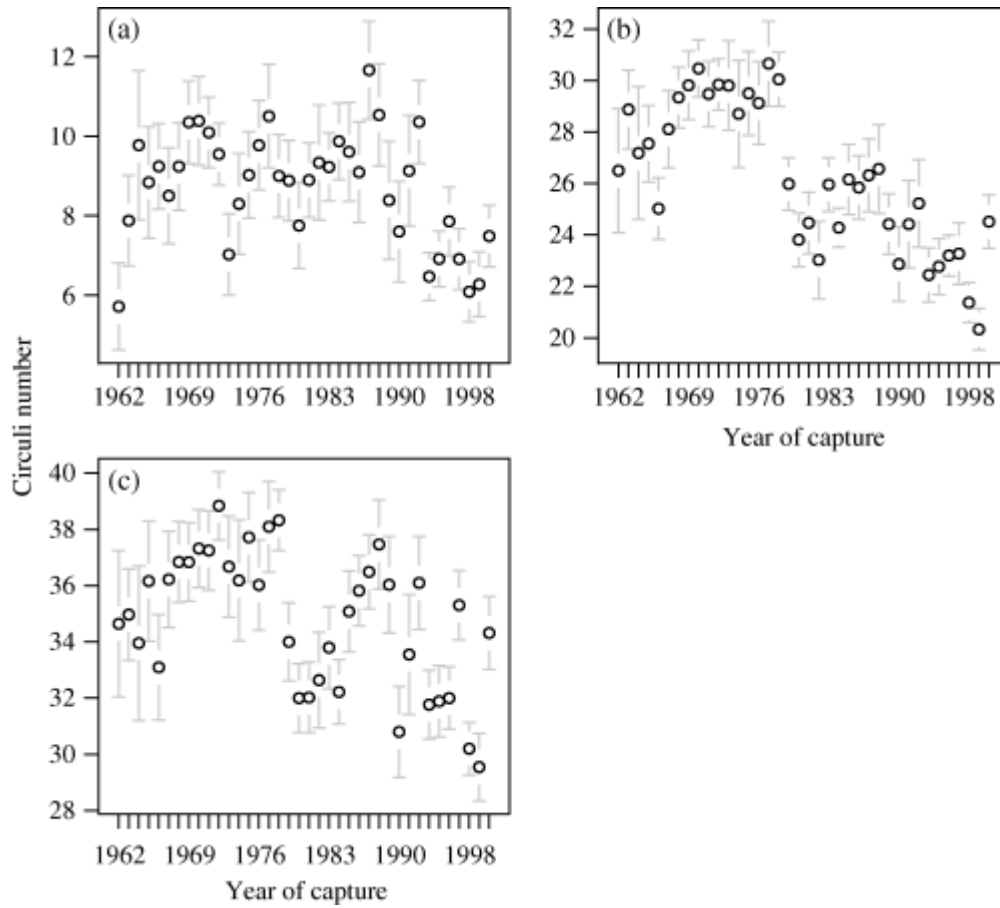


Figure 4. Mean number of circuli at a) First Summer Maximum, b) First Winter minimum and c) Second Summer Maximum. The confidence level for the error bars is $p = 0.95$.

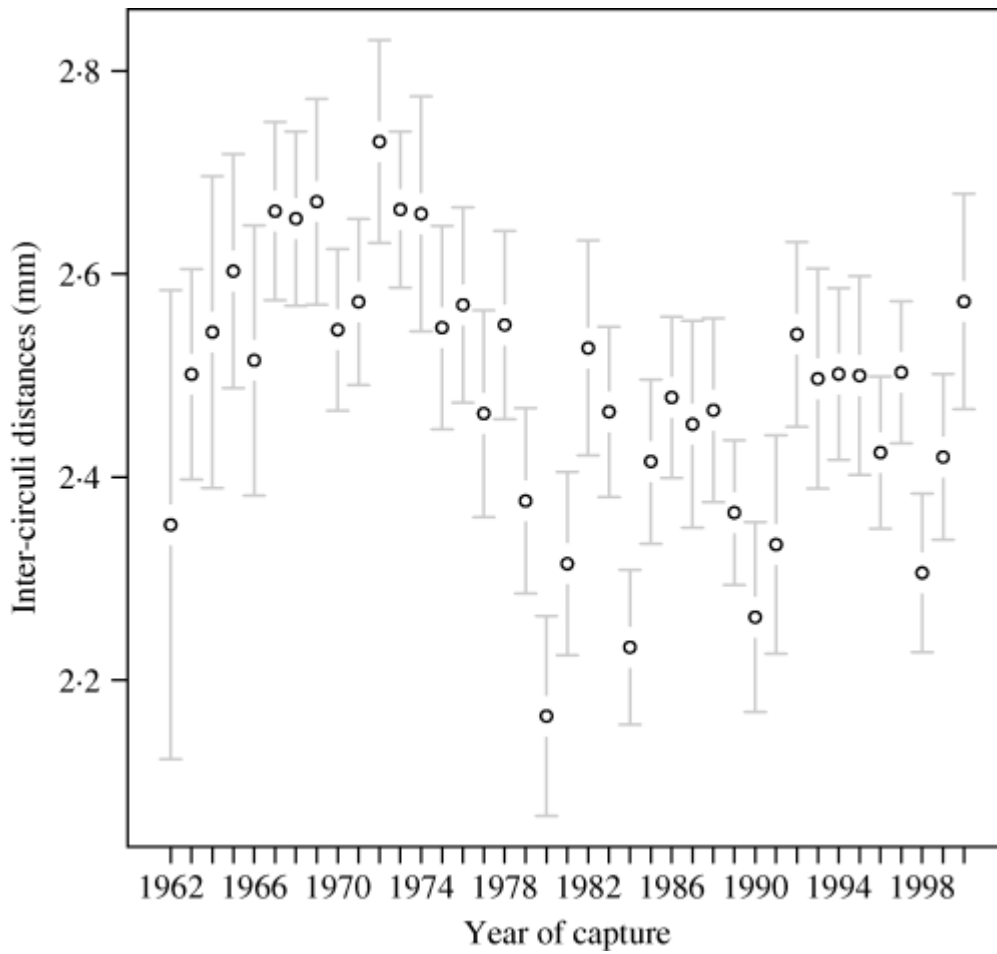


Figure 5. Mean cumulative Inter-Circuli Distances (mm), measured on scales of Burishoole 1SW salmon. Measurements were made between the last freshwater circuli and the edge of the scale. The confidence level for the error bars is $P = 0.95$.

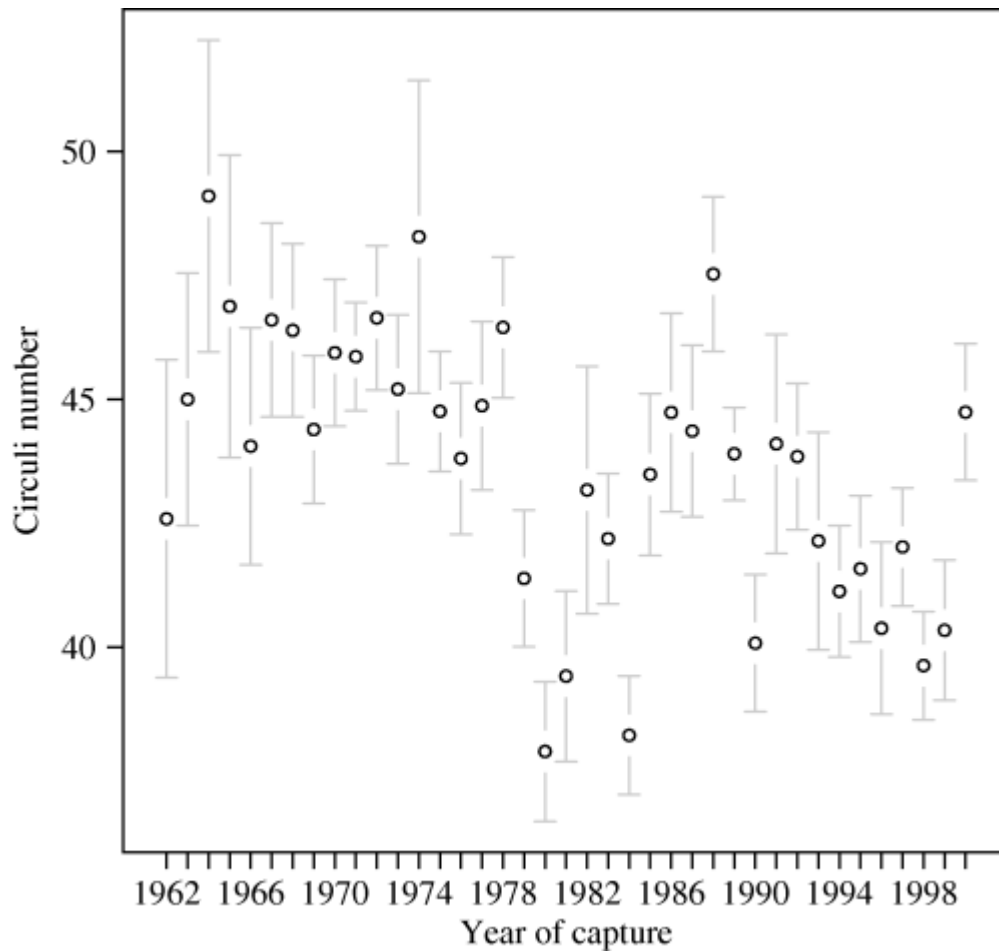


Figure 6. Mean number of circuli deposited on scales of Burrishoole 1SW salmon. The number of circuli were measured between the last freshwater circuli and the edge of the scale. The confidence level for the error bars is $P = 0.95$.

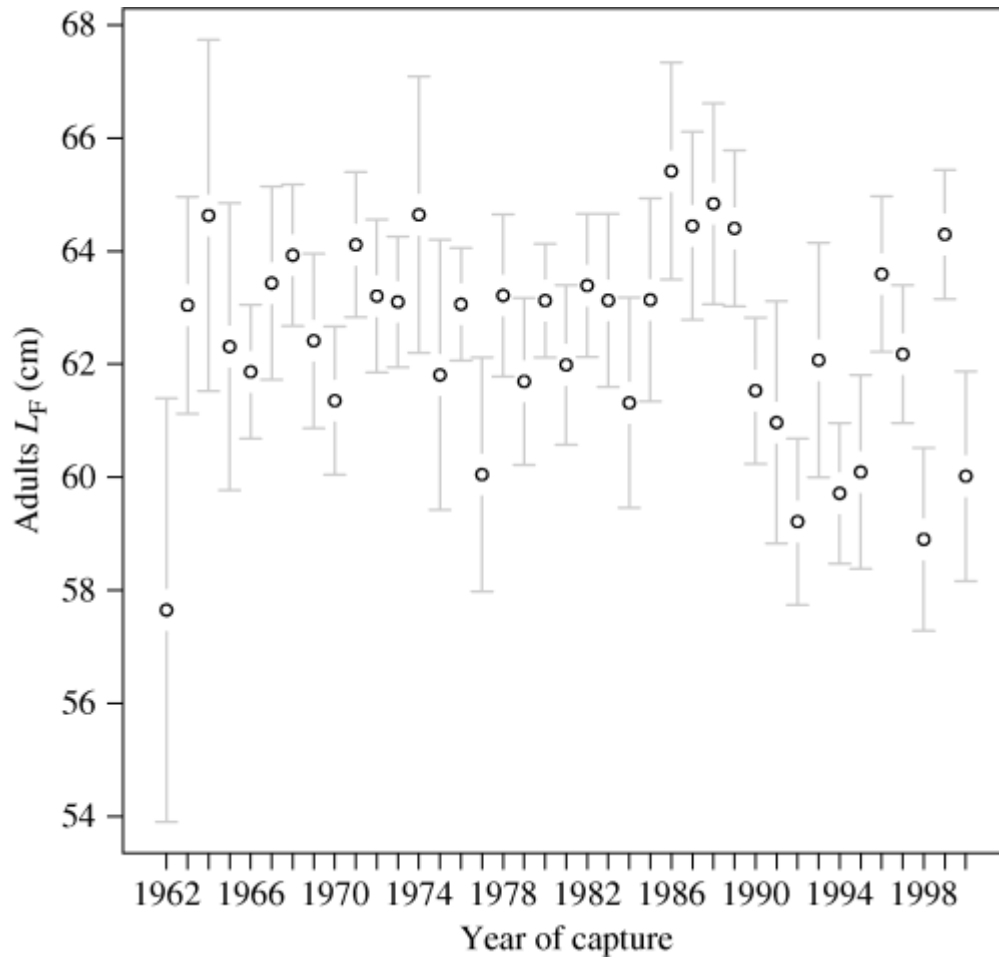


Figure 7. Mean length (cm) of 1SW Burrishoole salmon, measured upon capture in freshwater. The confidence level for the error bars is $P = 0.95$.

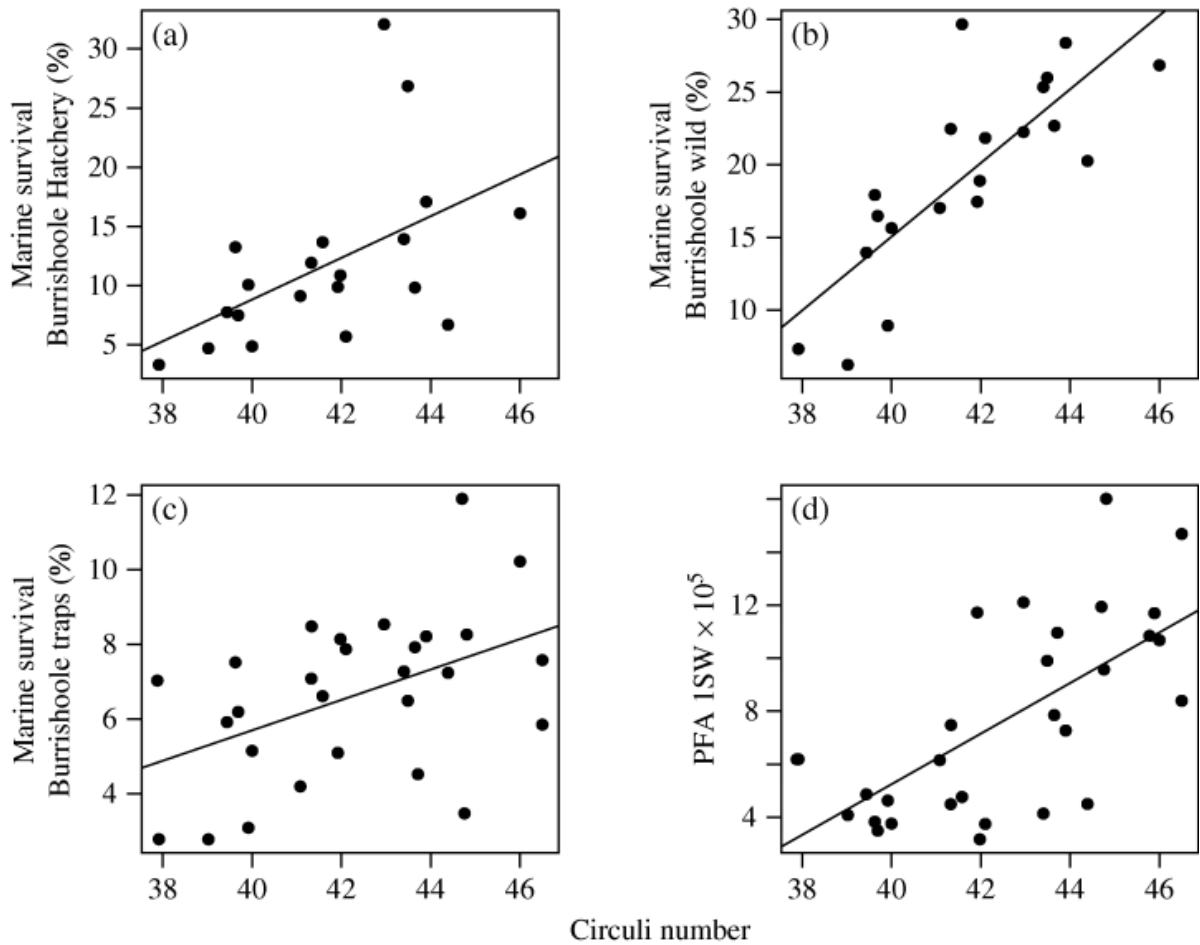


Figure 8. Scatterplots and regression lines of circuli number versus Burrishoole salmon recruitment: a) Marine Survival Burrishoole Hatchery; b) Marine Survival Burrishoole Wild; c) Marine Survival Burrishoole Traps; d) Pre-Fishery abundance 1SW.

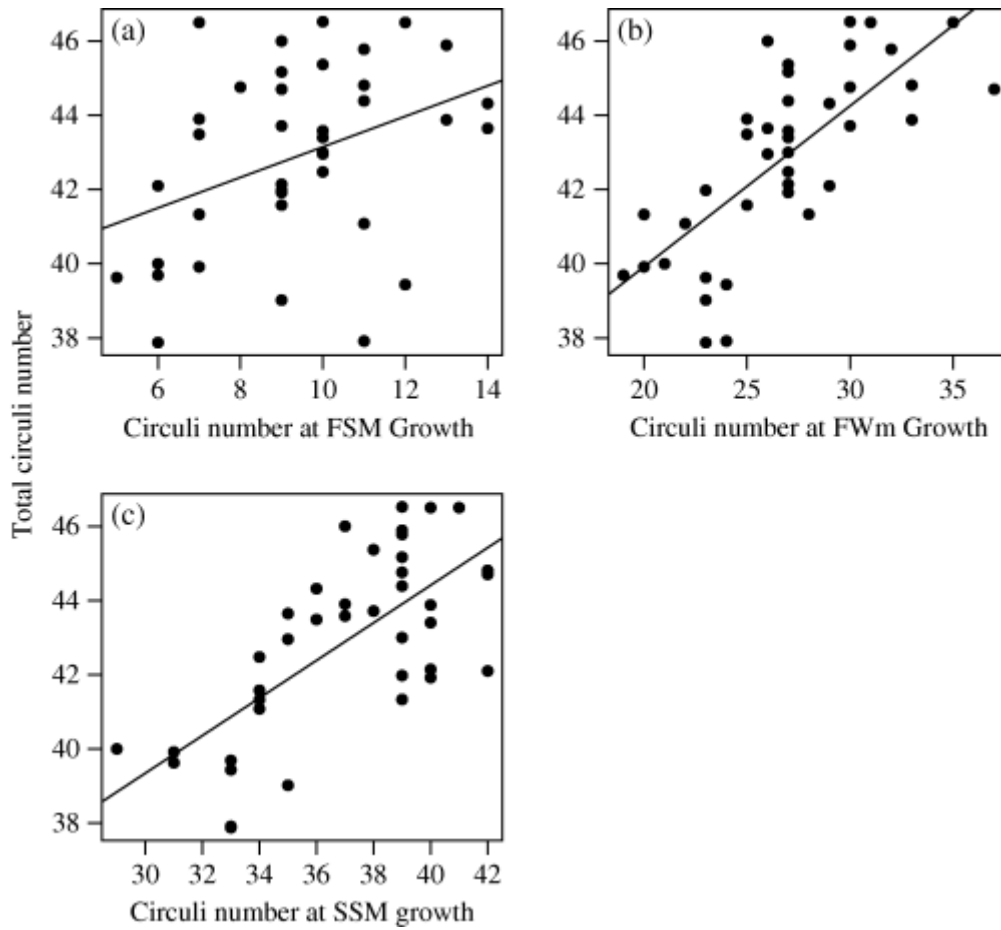


Figure 9. Scatterplots and regression lines of the total number of circuli versus the number of circuli at: a) First Summer Maximum; b) First Winter minimum and c) Second Summer Maximum.