NPAFC

Doc. 564

Rev.

Evidence of the validity of the critical size and critical period hypothesis

by

R. J. Beamish[1], K.L. Poier[1] and C. Mahnken[2]

[1]Fisheries and Oceans Canada
Pacific Biological Station
Science Branch
3190 Hammond Bay Road
Nanaimo, B.C.
Canada V9R 5K6

[2]National Marine Fisheries Service
7305 Beach Drive East
Port Orchard, Washington
USA, 98366

Submitted to the

North Pacific Anadromous Fish Commission

by

CANADA
September 2001

This paper may be cited in the following format:
Beamish, R.J., K.L. Poier and C. Mahnken. 2001. Evidence of the validity of the critical size and critical period hypothesis. (NPAFC Doc. 564). Fisheries and Oceans Canada, Science Branch - Pacific Region, Pacific Biological Station, Nanaimo, BC, Canada, V9R 5K6 National Marine Fisheries Service, Port Orchard, WA, USA, 98366

Abstract

The critical size and critical period hypothesis identifies two distinct periods of mortality in the first ocean year of Pacific salmon. The first period is immediately after salmon enter the ocean and is believed to be primarily the result of predation. The second period occurs in the late fall and winter and is related to the ability of juvenile salmon to grow during the summer to a size that will allow them to survive in the ocean after the fall equinox. In 2001, coho salmon returned to the Strait of Georgia in the spring of their second ocean year for the first time in 6 years. The scales from these coho salmon had an average circuli width in the area corresponding to the early marine period in the previous summer (2000) that was significantly wider than observed on the scales of coho from the same brood year sampled in September and November, 2000. This indicated that mortality in the fall and winter of 2000/2001was size related with more of the larger fish surviving the winter. The survival of larger coho supports the hypothesis that growth of coho during the first marine summer is an important component of the natural processes that regulate brood-year strength.

Introduction

Beamish and Mahnken (1999a, 1999b, 2001) proposed that the natural regulation of coho (*Oncorhynchus kisutch*) and other Pacific salmon occurred in two main stages during their first year in the ocean. The first major mortality occurred very early in the marine period, primarily as a consequence of predation. This is the familiar predation-based mortality (Parker 1968, Pearcy 1992) that many biologists believe is the only major source of marine mortality. Beamish and Mahnken (1999a, 1999b, 2001), however, proposed that only part of the mortality that determines brood year strength occurs in the first few months and that there is a second and distinct period of mortality that occurs after the fall equinox. This mortality is directly related to climate and ocean conditions that affect the productivity of the particular habitat in the ocean occupied by the various species of Pacific salmon. The linkage with climate and ocean productivity is through growth. According to this hypothesis, an individual must grow to a certain size or at a certain rate to be able to survive the more stressful ocean conditions that occur in the first ocean fall and winter. Beamish and Mahnken (2001) were uncertain whether size or growth rate or both were the determining factors. Cowan et al. (2000) reviewed the results of studies of factors affecting the year class strength of freshwater and marine fishes and concluded that it was the ability of the individual to achieve a critical weight late in its first year that determined recruitment variability. The critical size and critical period hypothesis of Beamish and Mahnken appeared to be supported by some studies (Beamish and Mahnken 1999a, 1999b, 2001). However tests in the ocean were problematic because it was difficult to find populations that remained in one ecosystem

through to the fall and returned to the same ecosystem after the first fall and winter mortality occurred.

In 2000 and 2001, the behaviour of coho in the Strait of Georgia changed, providing an opportunity to test the critical size and critical period hypothesis. Large numbers of ocean age 0 coho that remained in the Strait of Georgia through to the end of September (Sweeting et al. 2001) returned to the Strait of Georgia in the spring of 2001 for the first time in 6 years. In this report we show that the larger, ocean age 0 coho in September of 2000 became more abundant in the population of ocean age 1 coho in 2001.

Methods

Ocean age 0 coho were captured in September and November 2000 during standard trawl surveys (Beamish et al 2000). Ocean age 1 coho were captured in March and June/July 2001 using troll gear. Coho were measured for fork length (to the nearest millimeter) and fish were weighed (to the nearest gram). Scales were removed from the area just below and posterior of the dorsal fin and above the lateral line. Scales were stored in scale book and later used to make acetate impressions.

Only scale impressions with a well-defined focus were used. Acetate impressions were viewed and digitized using an Optimus system. A line was drawn from the focus through the middle of the scale to the posterior edge of the scale. Individual circuli were marked electronically and the distances between circuli were calculated. An electronic image of the scale was made. The circuli formed in fresh water were counted and the distance from the focus to the first circuli formed in salt water was noted. The first saltwater circuli was distinguished by identifying the freshwater annulus and any subsequent closely spaced circuli that formed after this annulus. The first widely spaced

circuli after these narrowly spaced circuli was considered to be the first ocean circuli. Scales from ocean age 1 coho contained an ocean annulus, which could be distinguished by close spacing of circuli and the crossing over of circuli in the posterior quadrant of the scale. The length of coho when they entered saltwater was calculated by multiplying the fish length, scale length ratio at capture by the distance from the focus to the last freshwater circuli ie. the "scale length" at the time coho entered the ocean.

Results

A total of 92 ocean age 0 coho were sampled from the surveys in September and November 2000. Of these, 5 were males that were maturing in their first marine year (jacks). They were excluded from the analysis because they would not remain in salt water in the late fall and winter. The length frequency of the remaining 87 fish was compared separately for the September and November samples with the length frequency of the total catch in September and November (Figure 1A, B). The length frequencies of the fish used in the November sample for scale analysis were not significantly different from the length frequencies in the catch (t test, $p > 0.05$). However, the mean length of the fish used for scale analysis in the September sample was 256 mm which was significantly larger than the mean length of 247 mm in the total measured catch of 1482 coho (t test, $p < 0.01$).

The scale length, fish length relationship for ocean age 0 and ocean age 1 fish was strongly linear (F test, $p < 0.05$) (Figure 2). The spacing of circuli formed in salt water began to decrease around the first week in September. We identified this change in spacing as a late summer, fall check (LSF check). There was a varying number of circuli that formed from the time of entry into salt water, up to this check (average 16)

but scales from all fish had at least 10 circuli. The average spacing of the first 10 circuli was closely related to the average spacing of all circuli that formed in salt water up to the LSF check (Figure 3). Therefore, we used 10 circuli as a measure of the growth over the first marine summer. The average circuli width for this 10-circuli zone increased with increasing fork length at capture (Figure 4A). The relationship was weak, but significant (F test, p ? 0.01). We calculated the fork length at the time the individual fish entered salt water and subtracted this length from the capture length to produce a measure of saltwater growth up to the capture date. A comparison of average circuli width with saltwater growth produced a relationship very similar to the relationship with capture length (Figure 4B).

The frequency distribution of average circuli spacing of ocean age 0 coho from the September and November samples (Figure 5A) was normal with a mean of 0.038mm (SD = 0.004) (Kolmogorov-Shuntov test, $p > 0.05$). In March and June/July 2001, 82 ocean age 1 coho were sampled from the Strait of Georgia. The frequency distribution of the mean width of the first 10 ocean circuli was normal (Kolmogorov-Shuntov test, $p > 0.05$) with a mean of 0.042mm (SD = 0.004) (Figure 5B). The mean of the average circuli width of ocean age 1 coho was significantly larger than the mean average circuli width in the previous year (t test, $p < 0.01$). In the 2001 mean circuli width distribution, the circuli width of 50% of the fish with the widest average circuli spacing represented only 12% of the fish with similar circuli widths in the ocean age 0, 2000 sample.

Discussion

The comparison of circuli spacing between Strait of Georgia coho in their first and second marine years showed that a significantly larger number of the coho with the

widest circuli spacing survived the late fall and winter. The scale length-fish length and circuli width-fish length relationship showed that these fish with the widest spaced circuli were both the larger fish and the fish that grew more over the summer. Evidence of a size selective mortality in the late fall and early winter of the first ocean year for coho supports the critical size and critical period hypothesis.

Coho salmon in the Strait of Georgia traditionally returned to the Strait early in their second ocean year, contributing to a valuable recreational fishery. In 1991 and from 1995 to 2000, coho changed their behaviour and did not return (Beamish et al. 1999). Because, our project started in 1997, we could study growth of ocean age 0 coho but ocean age 1 coho stocks from the Strait of Georgia, mixed with stocks with different rates of growth off the west coast of Vancouver Island from other ecosystems. If fall and winter mortality was related to growth, we had to be able to sample the same population before and after the first ocean winter. Thus, this study was our first opportunity to test our critical size and critical period hypothesis.

Our samples used in the scale analysis in November 2000 were representative of the size distributions in the November catch. However, the fish in the September sample for scale analysis were slightly larger than in the catch. The significant difference is related to the large number of degrees of freedom and would bias the interpretation in favour of a rejection of the hypothesis. Thus, the small difference in the mean size of the sample and the catch is not viewed as an important bias.

It was important to demonstrate that both scale growth and circuli spacing was related to individual size. The fish length, scale length relationship was strongly linear as would be expected. The scale grows to protect the fish and therefore, larger fish must

have larger scales. The strong relationship, however, does show that our analyses were able to detect this expected relationship. We observed that the circuli spacing of the first 10 ocean circuli were a good measure of the average spacing of all circuli up to the capture date. Wider spaced circuli were related to larger fish and greater growth. The relationship was significantly linear, but there was considerable variation. There is irregularity in circuli formation, which results in variability in the measurement when using a fixed reference line from the focus to the posterior margin of the scale. We suspect that the use of larger samples will improve the circuli width, fish length/growth relationship.

An important assumption of the critical size and critical period hypothesis is that there must be a sufficient number of fish in the population of ocean age 0 coho in September so that mortality has a major impact on the final brood year size. We show in Beamish et al. (2000) and Beamish and Mahnken (2001) that abundances of juvenile coho in the Strait of Georgia in September are large relative to the abundances of fish that return as adults. Estimates of abundances in September are minimal estimates (Beamish et al. 2000) and vary from 2,978,000 (? 1,283,000), 3,037,000 (? 1,370,000), 4,642,000 (? 1,370,000), and 2,567,000 (?752,000) in 1997, 1998, 1999, and 2000, respectively. If the catchability of the net is not 1 as assumed, but less, as is probable, the abundance estimates will be larger, perhaps double. Total returns in 1997, 1998, and 1999 have been estimated to be 364,000, 315,000, and 328,000 respectively. If the abundance estimates that are considered to be minimal are compared to total estimated returns, then the fall and winter mortality exceeds 80%. If the true abundance estimates are double our estimate (Beamish et al. 2000), then the fall and winter mortality exceeds 90%. Thus, it

is clear that the mortality that occurs over the fall and winter is a major factor in the determination of the final brood year abundance.

Additional studies are in progress to test growth related mortalities in controlled feeding studies. Studies are also continuing to determine if it is possible to reduce the variance associated with the circuli width measurements.

Literature Cited

Beamish, R.J. and C. Mahnken. 1999a. Natural regulation of the abundance of coho and other species of Pacific salmon according to the critical size and critical period hypothesis. North Pacific Anadromous Fish Commission Doc. 319: 26 p. Dept. of Fisheries and Oceans, Science Branch, Pacific Region, Pacific Biological Station, Nanaimo, B.C., Canada, V9R 5K6. National Marine Fisheries Service, 7305 Beach Drive East, Port Orchard, WA, USA, 98366.

Beamish, R.J. and C. Mahnken. 1999b. Taking the next step in fisheries management. pp 1-21 *In* Ecosystem approaches for Fisheries Management. Proceedings of the 16th Lowell Wakefield Symposium, Anchorage Alaska. Alaska Sea Grant Report AK-SG-99-01: pp 738.

Beamish, R.J., G.A. McFarlane and R.E. Thomson. 1999. Recent declines in the recreational catch of coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia are related to climate. Can. J. Fish. and Aquat. Sci. 56 (3): 506-515.

Beamish, R.J., D. McCaughran, J.R. King, R.M. Sweeting and G.A. McFarlane. 2000. Estimating the abundance of juvenile coho salmon in the Strait of Georgia using surface trawls. N. Am. J. Fish. Mgmt. 20: 369-375.

Beamish, R.J. and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography (*in press*).

Cowan, J.H. Jr., K.A. Rose and D.R. DeVries. 2000. Is density-dependant growth in young-of-year fishes a question of critical weight? Reviews in Fish Biology and Fisheries. 10: 61-89.

Parker, R.R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, Central British Columbia. Journal of the Fisheries Research Board of Canada. 25: 757-794.

Pearcy, W.G. 1992. Ocean Ecology of the North Pacific Salmonids. University of Washington Press. Seattle, WA. 179pp.

Sweeting, R.M., R.J. Beamish, D.J. Noakes and C.M. Neville. 2001. Replacement of wild coho salmon by hatchery-reared coho in the Strait of Georgia over the past 3 decades. Proceedings B Editorial Office, The Royal Society 6 Carlton House, Terrace, London, SWIY 5AG, UK (*submitted*).

Figure Captions

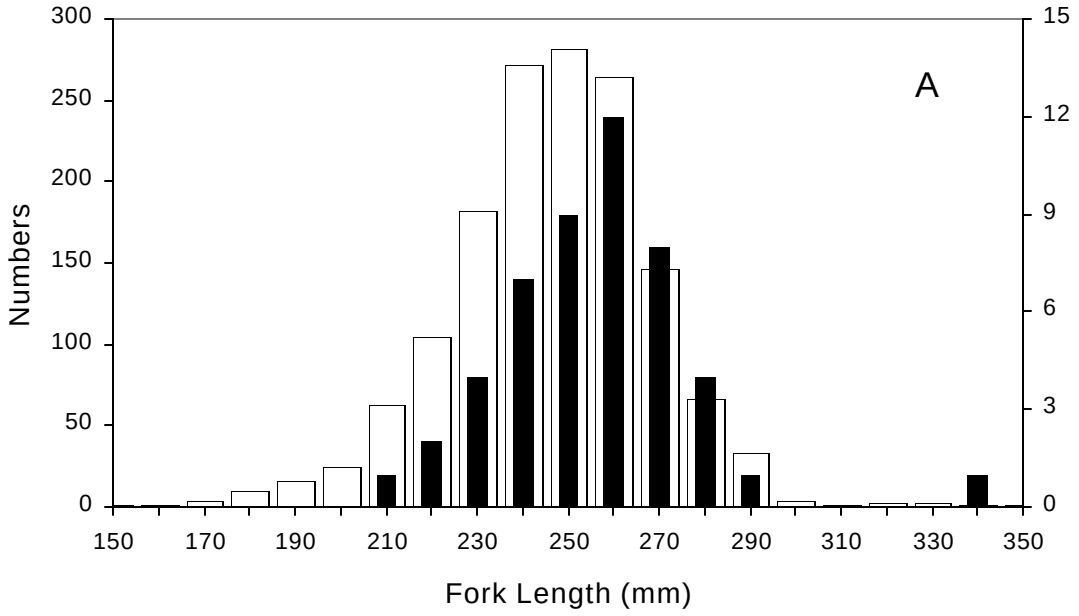
Figure 1(A) The length frequency of coho caught in the September 2000 survey (open bars, left axis) and the sample used for scale circuli spacing analysis (solid bars, right axis). (B) The length frequency of coho caught in the November 2000 survey (open bars) and the sample used for scale analysis (solid bars).

Figure 2 The relationship between scale length (focus to posterior edge) and fork length for all ocean age 0 and ocean age 1 coho used in this study.

Figure 3 The relationship between the average spacing of the first 10 circuli formed in the ocean and the average spacing of all ocean circuli that formed prior to the late summer fall check (LSF check) that occurred, usually in early to mid-September.

Figure 4 (A) The relationship between the average spacing of the first 10 ocean circuli and the capture length, and (B), between the estimate of total growth in length in salt water prior to capture.

Figure 5 (A) The average circuli spacing frequency for ocean age 0 coho in 2000 and (B) for the same population after the first marine winter (ocean age 1).


A
Numbers
Fork Length (mm)
300
250
200
150
100
50
0
15
12
9
6
3
0
150
170
190
210
230
250
270
290
310
330
350

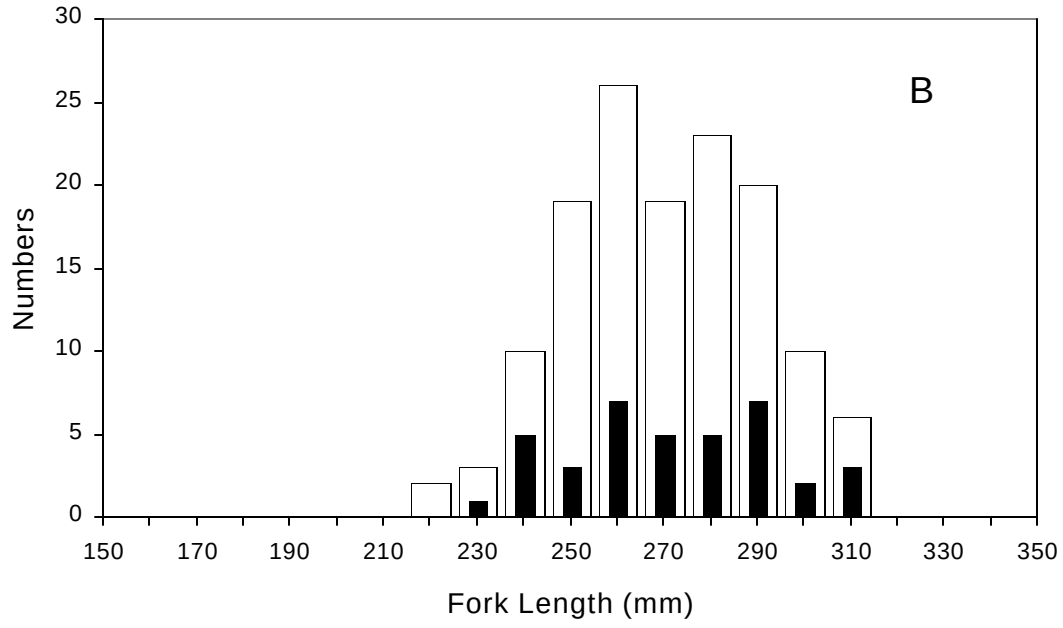

B
Numbers
Fork Length (mm)
30
25
20
15
10
5
0
150
170
190
210
230
250
270
290
310
330
350

Figure 1

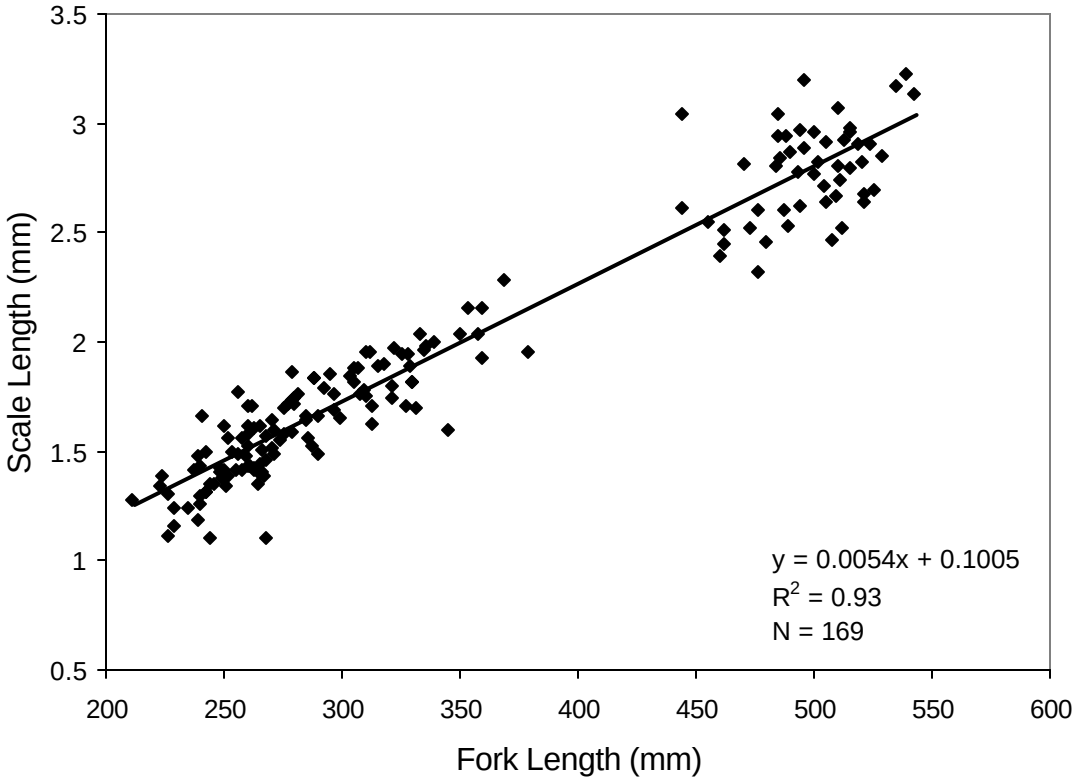

3.5
3
2.5
2
1.5
1
0.5
Scale Length (mm)
200
250
300
350
400
450
500
550
600
Fork Length (mm)
y = 0.0054x + 0.1005
R2 = 0.93
N = 169

Figure 2

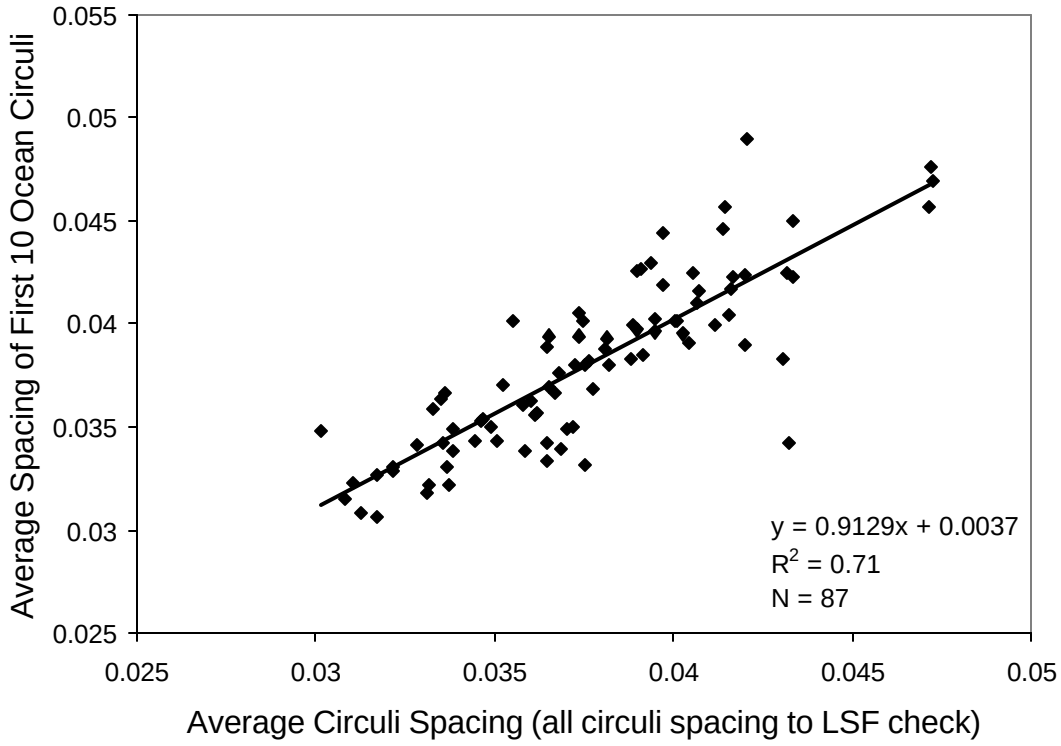
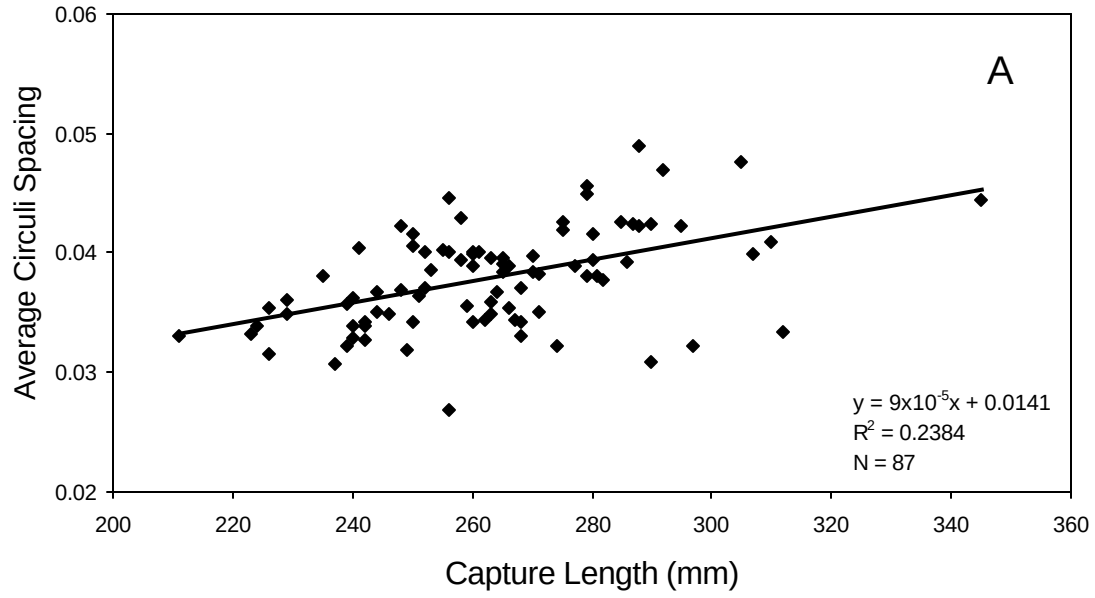

Average Spacing of First 10 Ocean Circuli
0.055
0.05
0.045
0.04
0.035
0.03
0.025
0.025
0.03
0.035
0.04
0.045
0.05
Average Circuli Spacing (all circuli spacing to LSF check)
y = 0.9129x + 0.0037
R2 = 0.71
N = 87

Figure 3


A
Average Circuli Spacing
0.06
0.05
0.04
0.03
0.02
200
220
240
260
280
300
320
340
360
Capture Length (mm)
y = 9x10-5x + 0.0141
R2 = 0.2384
N = 87

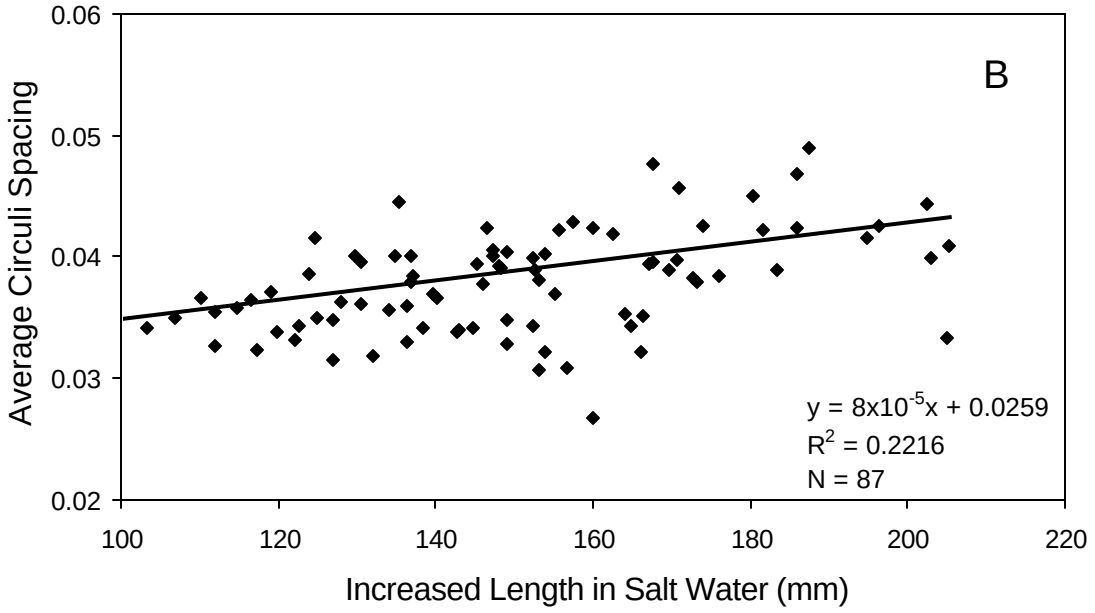
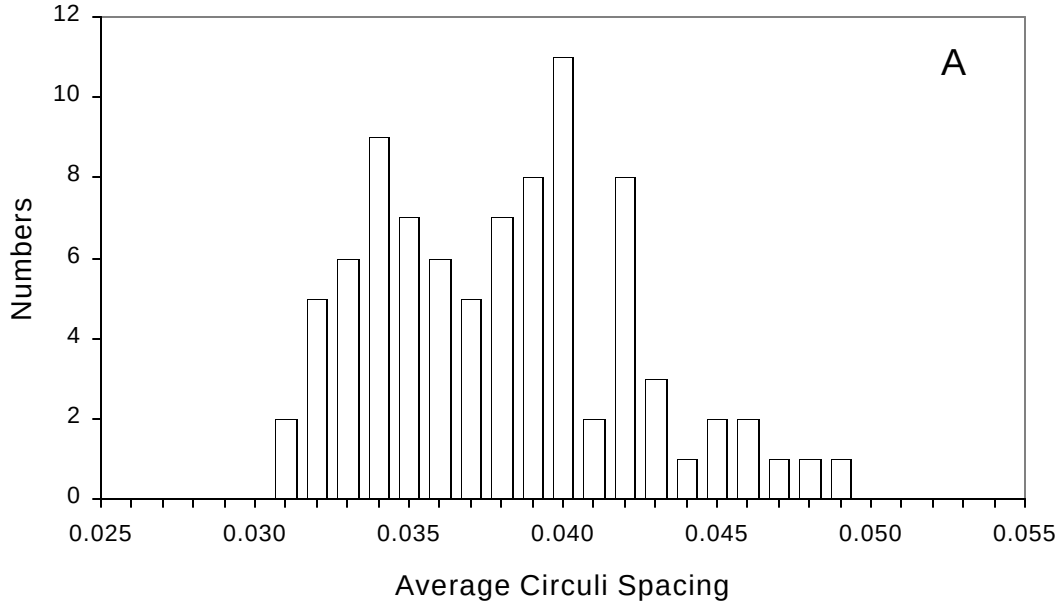

B
Average Circuli Spacing
0.06
0.05
0.04
0.03
0.02
100
120
140
160
180
200
220
Increased Length in Salt Water (mm)
y = 8x10-5x + 0.0259
R2 = 0.2216
N = 87

Figure 4


A
Numbers
0
2
4
6
8
10
12
0.025
0.030
0.035
0.040
0.045
0.050
0.055
Average Circuli Spacing

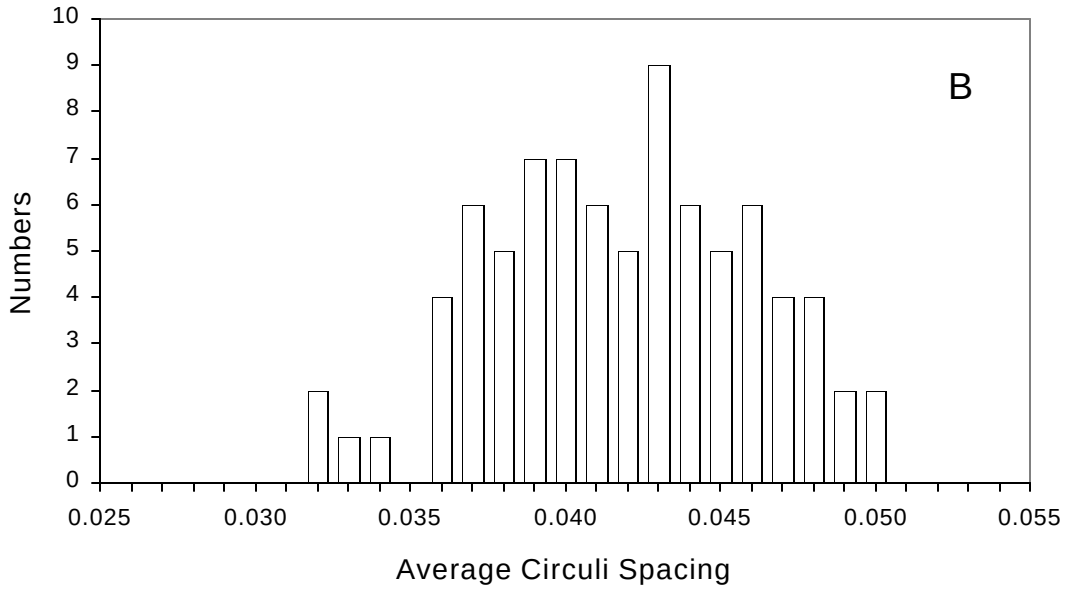

B
Numbers
0
1
2
3
4
5
6
7
8
9
10
0.025
0.030
0.035
0.040
0.045
0.050
0.055
Average Circuli Spacing

Figure 5