Validity of inferring size-selective mortality and a critical size limit in Pacific salmon from scale circulus spacing

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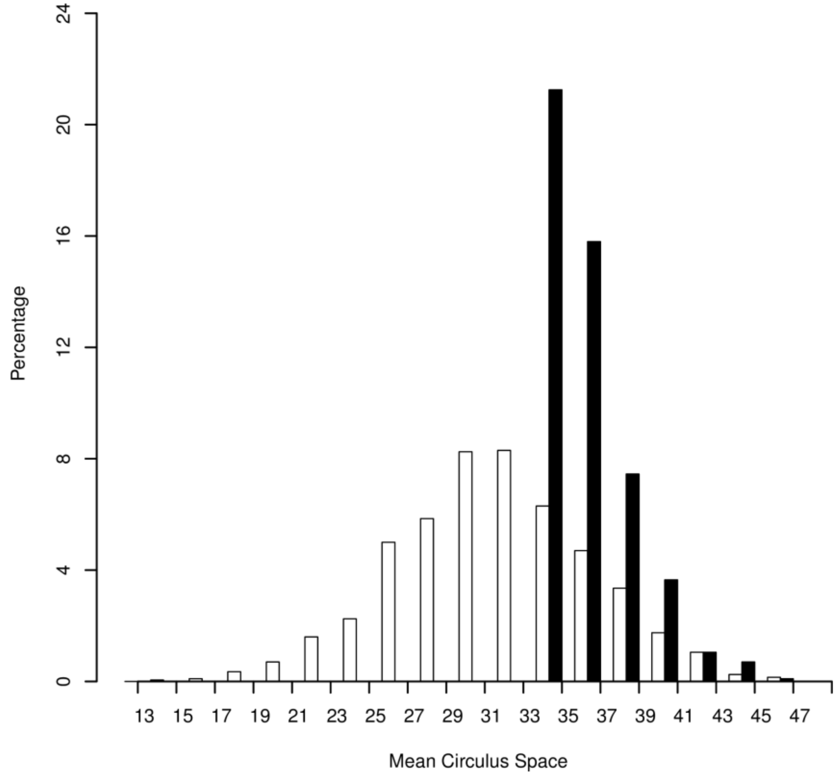
Critical size, critical period hypothesis

- Beamish and Mahnken (2001): “Juvenile salmon that fail to reach a critical size by the end of their first marine summer do not survive the following winter.” This implies a knife-edge mortality function, not any logistic function that may be a more reasonable assumption to make. Nowhere in the Beamish and Mahnken (2001) paper or in any of the subsequent papers do the authors say that there is a reduction in mortality with size and stochasticity.
- This presumed substantial size-selective mortality directed against the smaller members of the stock should result in a discernable signal in size distributions that should be detectable when comparing late summer/early fall size distributions within a stock with those observed the following year in the stock.
- If this mortality is indeed size selective, centered upon the smaller body-sized individuals during a period of presumed low growth rates, then this loss of smaller body sized individuals should have a profound effect on the distribution, range, and variance of juvenile size.

Statistical considerations

- Failure to attain a critical size implies a knife-edge function, whereby individuals failing to attain this critical size die and disappear from the population. If the scale circulus spacing index (SCSI) in the original juvenile population is normally distributed, and if the critical size hypothesis is valid, then the distribution of SCSI values in the adult population should display a truncated normal distribution such that some portion of the left side (smaller SCSI values) of the juvenile SCSI distribution is absent in the adult SCSI distribution.
- Theoretically, in a truncated normal distribution, samples from the adult population should display a larger mean and reduced variance relative to samples from the juvenile population, decreased range, and increased skewness and kurtosis.

Expected distribution of adults with 80% size-selective mortality of juveniles



Descriptive statistics of adults

Mean: increase

Variance: decrease

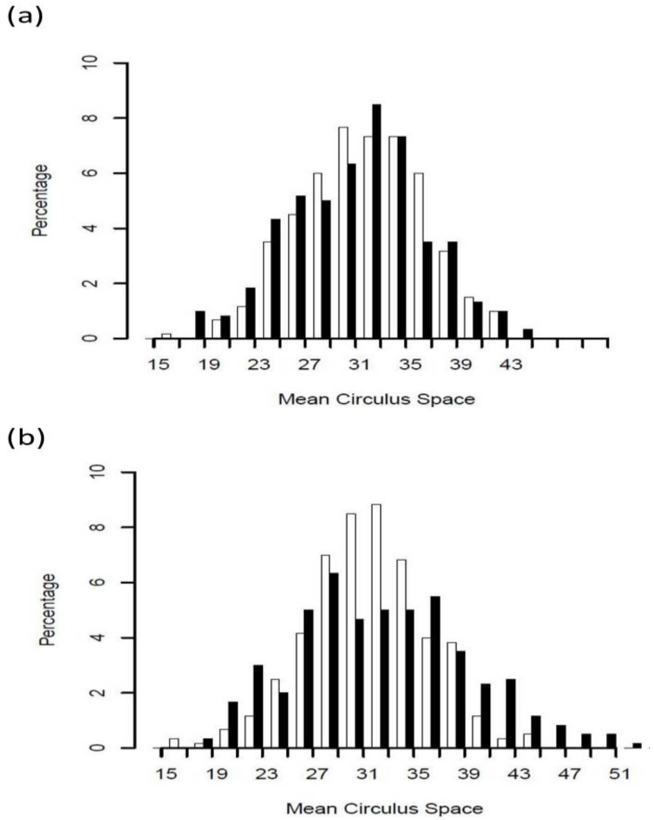
Range: decrease

Kurtosis: increase

Skewness: increase

% adults outside juvenile range:< 1%

Expected adult distribution with no mortality with 60% of adults from sampled population with mean of 30 and 40% from unsampled population with mean of (a) 35 and (b) 40, with adult samples of 50 and 200 individuals



Descriptive statistics of adults

Mean: increase

Variance: increase

Range: increase

Kurtosis: decrease

Skewness: decrease

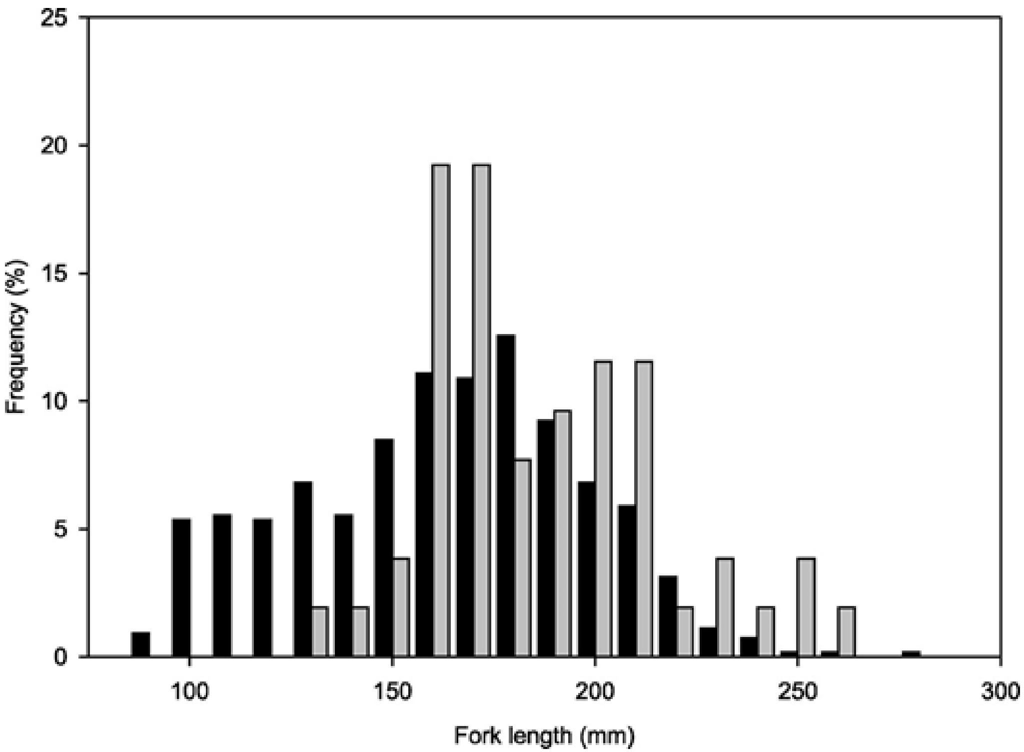
% adults > largest juvenile 5%-34%

Summary of differences

Statistic	Size selective mortality, critical size limit	Two juvenile populations
Mean	Increase	Increase
Range	Decrease	Increase
Variance	Decrease	Increase
Kurtosis	Increase	Decrease
Skewness	Increase	Decrease
% of adults > largest juvenile	< 1% with adequate juvenile sample	> 5%

Study where juveniles were sampled in fresh water prior to hatchery release

Bond et. al. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. Can J Fish Aquat Sci 65:2242–2252.



Range: decrease

Variance: decrease

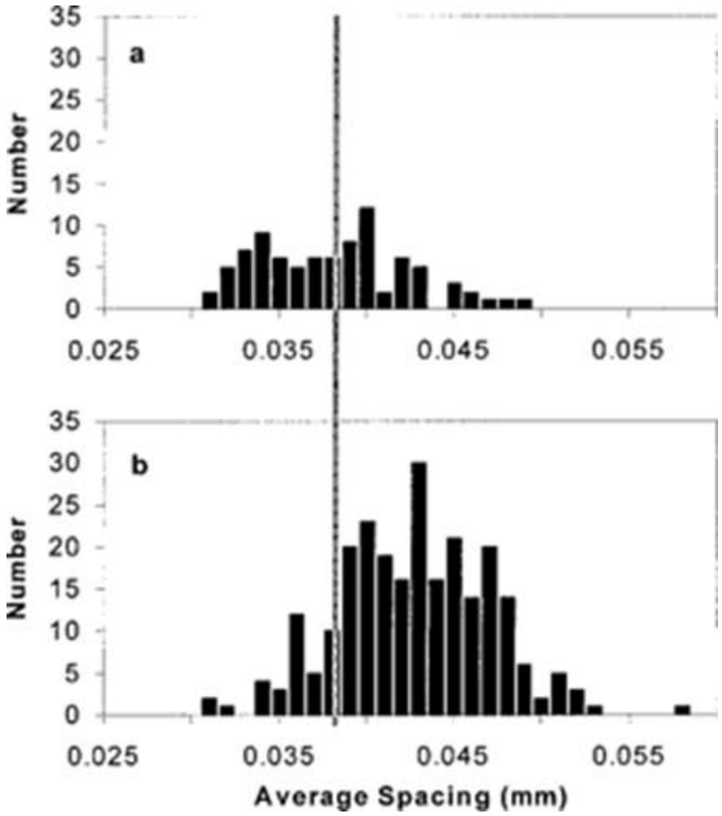
% adults > largest juvenile: 0%

N juveniles: 542 N adults: 52

Conclusion: Results consistent with size-selective mortality

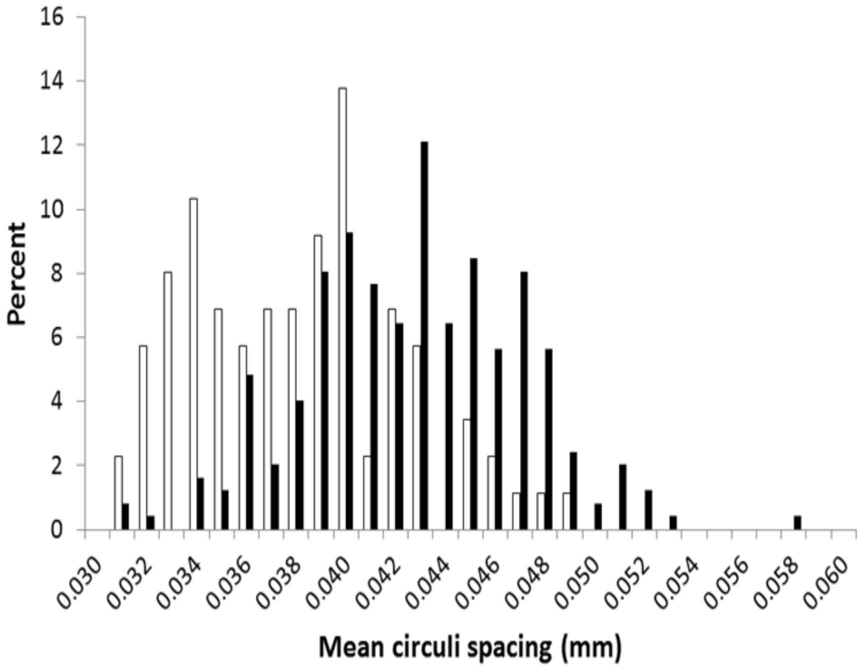
Studies where juveniles were sampled after rearing for a period in the ocean

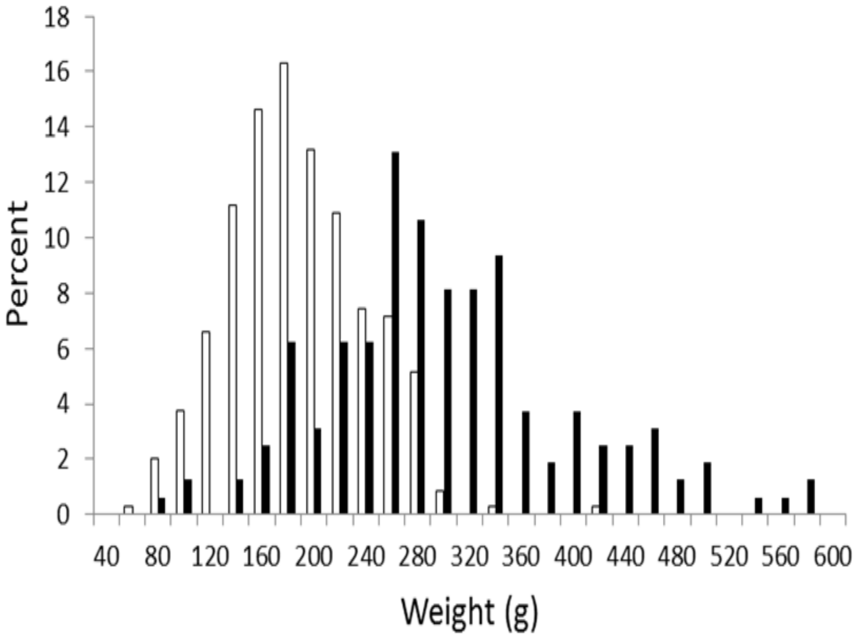
Beamish, R.J., et. al.. 2004. Evidence that early marine growth is associated with lower marine survival of coho salmon. Trans Am Fish Soc 133:26-33.



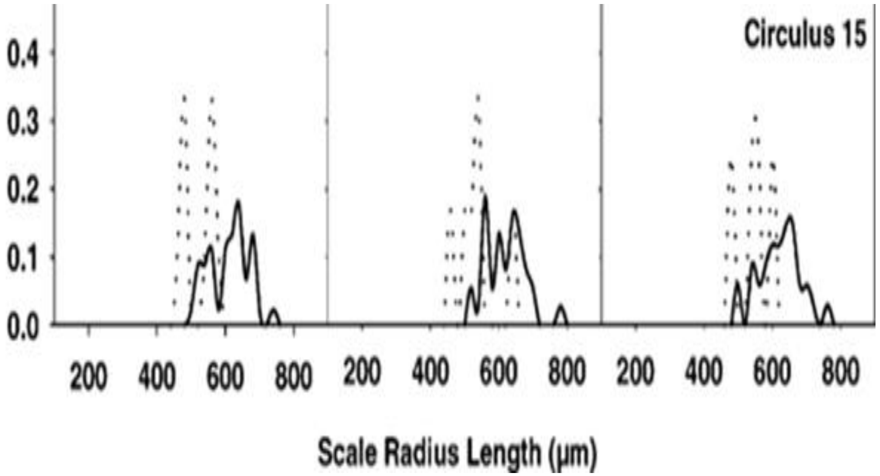
- Range: increase
- Variance: increase
- Skewness: decrease
- % adults > largest juvenile: 5%
- N juveniles= 87, N adults= 286
- Results consistent with second unsampled juvenile population with larger individuals
- Results not consistent with a critical size limit

Left: juveniles clear bar, adults black bar, Beamish et al. 2004
Right: Fall SOG Fraser and ECVI juveniles clear bar, Fall outside SOG Fraser and ECVI juveniles black bar, Beacham et al. 2017





Moss, J.H. et. Al. 2005. Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. Trans Am Fish Soc 134:1313-1322.



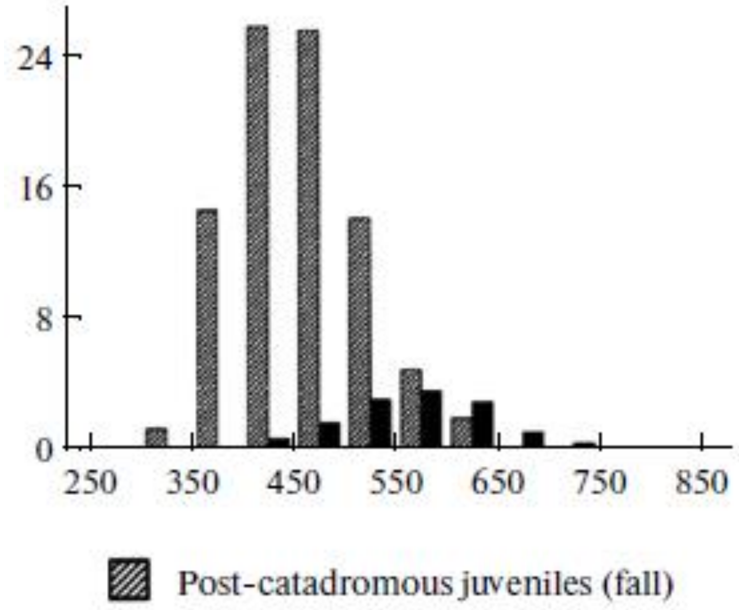
- Range: increase
- Variance: increase
- % adults > largest juvenile: 18%-58%
- N juveniles= 26-37, N adults= 26-45
- Results consistent with second unsampled juvenile population with larger individuals
- Results not consistent with a critical size limit

Zavolokin, A.V, and E.V. Strezhneva. 2013. Size-selective mortality of Sea of Okhotsk pink salmon in the ocean in the winter and spring. Russ J Mar Biol 39:501-508.

- In the 2007 year class, which had a low overwinter survival level in the ocean, the average scale increments for the first year of life were considerably smaller than those in adult fish that returned to the spawning grounds. In the pink salmon of 2008, which had a very high level of overwinter survival, the values of scale increments in juveniles and adults were similar. This confirms the hypothesis of a critical size and a critical period, according to which slowly growing juveniles that do not accumulate enough energy reserves for summer are eliminated in the winter to a greater extent as compared to fast growing fish.

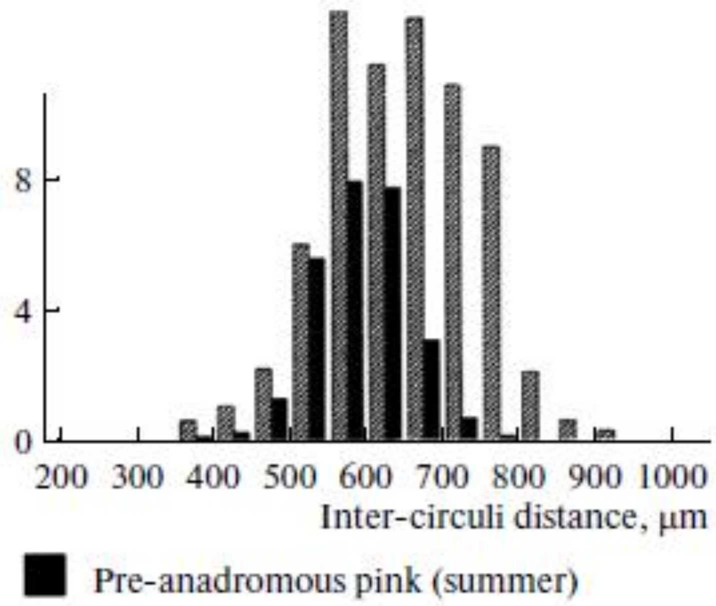
- Our interpretation of the results is that there is no evidence of a critical size limit directed at the smaller individuals in the population. Why? Let us examine the data presented:

Zavolokin, A.V, and E.V. Strezhneva. 2013. Size-selective mortality of Sea of Okhotsk pink salmon in the ocean in the winter and spring. Russ J Mar Biol 39:501-508.



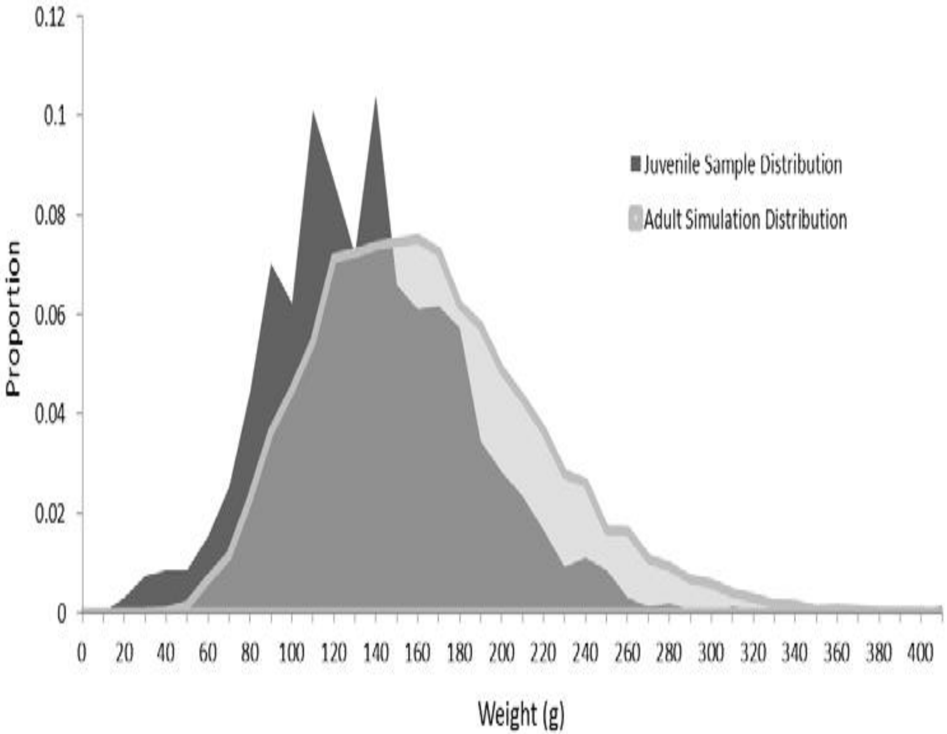
- Odd year (2007) broodline
- Range: increase
- Variance: increase
- % adults > largest juvenile: 11%
- N juveniles= 1122, N adults= 329
- Results consistent with second unsampled juvenile population with larger individuals
- Results not consistent with a critical size limit

Zavolokin, A.V, and E.V. Strezhneva. 2013. Size-selective mortality of Sea of Okhotsk pink salmon in the ocean in the winter and spring. Russ J Mar Biol 39:501-508.



- Even year (2008) broodline
- Range: decrease
- Variance: decrease
- % adults > largest juvenile: 0%
- N juveniles= 476, N adults= 418
- Results consistent with a critical size limit, but mortality directed at largest juveniles in the population, not the smallest

Howard et al. 2016. Size-selective mortality of chinook salmon in relation to body energy after the first summer in nearshore marine habitats. N Pac Anad Fish Comm Bull 6:1-11



- Range: increase
- Variance: increase
- % adults > largest juvenile: 6%
- N juveniles= 1,040, N adults= 829
- Results consistent with second unsampled juvenile population with larger individuals
- Results not consistent with a critical size limit

Summary

- In order to invoke size selection as an important driver of mortality during the first year of ocean rearing, it is necessary to demonstrate not only that size-selective mortality is directed towards the smaller members of the population, but that the selective nature of the mortality can account for a substantial portion of the observed mortality.
- If the assumption is made that a random sample of a single juvenile population has been obtained, then studies that employ a scale circulus spacing index (SCSI) to infer size-selective mortality coupled with a critical size must demonstrate a shift toward larger values of the SCSI, but also a concomitant reduction in the variance and range of the SCSI and an increase in the skewness and kurtosis of the SCSI values.
- Geographical distributions of juvenile Pacific salmon can be stratified by size, with larger individuals migrating earlier from local ocean entry locations than smaller individuals, and thus differential timing migration of juveniles based upon body size prior to the collection of the marine juvenile sample may be a more plausible explanation of published trends in the SCSI, rather than invoking substantial size-selective mortality and a critical size limit.

Overall conclusion

- Empiricists are supposed to only believe in what they see. However, they are far better at believing than in seeing!
- Source: An unknown philosopher