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Potential Errors in Measuring Spawning Stock Biomass: Determining the Effects  
of Non-participatory Adults for some Atlantic Groundfish Species

M. P. M. Burton

Department of Biology, Memorial University of Newfoundland,  
St. John's, Newfoundland, Canada, A1B 3X9

**Abstract**

Using both old datasets and recent information it is possible to show that previous ideas of spawning stock biomass have been over-optimistic for several commercially important groundfish species. The concept of non-participation can be used for adults which undergo gametogenesis but fail to spawn successfully, or which have very low participation because fecundity is extremely low for an individual, in comparison to others of the same species. Interannual variability in production of fertilized eggs can also be due to the presence of adults which do not undergo gametogenesis every year and this situation may be much more common than has been previously accepted in setting up models. Re-calculations of spawning stock biomass for some groundfish species using lower and more realistic participation rates can provide better understanding of stock-recruitment relationships.

**Introduction**

Despite a long history of amassing data on spawning potential of commercially important fish species the basis for data collection has some deep flaws which have affected fisheries management. In order to identify fish which should be included in calculations of spawning stock biomass it is first necessary to know at what point, or by which criteria, a fish can be considered an adult. Usually this partitioning has been achieved by determining a size (length) or age at which 50% of the population are "mature" (Thompson, 1916; Beacham, 1983), which may give a sharp demarcation. With this information a decision can be made to assign all fish above a certain age or length to spawning stock, which may be subjected to modification with knowledge of ongoing fishing activity (Fukuda, 1962). The spawning stock can be regarded as units of individuals but generally is treated as undivided biomass. Any fluctuation in biomass can be tested for relationships with production of recruits. In such a manner spawning stock biomass/recruitment relationships have been studied for several groups of commercially important fish species and for flatfish such as halibut it has been claimed that there is no stock-recruit relationship (Cushing, 1971) whereas for haddock an inverse relationship has been stated (Ricker, 1954), which was believed to occur because cannibalism of recruits would increase with stock (Beverton and Holt, 1957). Recent reassessments of stock-recruit relationships (Hillborn and Walters, 1992) show some scepticism regarding the prevalence of non-relatedness as stocks decline, with the new view being that recruitment overfishing can be seen to occur with nearly every species studied, except flatfish. Explanation of non-relatedness, or inverse relationships of stock and recruitment besides cannibalism includes the possibility that recruitment may appear to be independent of stock but that there is an out of phase relationship caused by an unspecified environmental factor (Hillborn and Walters, 1992). This paper will suggest means to clarify

the unrelatedness of some groundfish stock/recruitment values and the possible environmental situation which can obscure the relationship.

A major problem in defining stock and recruitment relationships is the allocation of fish to spawning stock which can be a more complex matter than previously supposed; as will be shown, large or old fish do not necessarily participate in reproduction in a regular annual fashion, they may not start or maintain gametogenesis. Even if gametogenesis is maintained there may be individual or group fluctuations in gamete output for either males or females, a possibility which should be factored into recruitment modeling, to give conservative rather than optimistic values for predictions. Moreover, and perhaps most serious as a problem for data manipulation,

identification of adults and appropriate differentiation of fish which have never reproduced from adults which are not currently reproductive has given considerable confusion in the data-sets. I will show how some of the historical data can be re-evaluated using recently collected information, and how recalculations may be used to see pattern in apparently chaotic or negative stock-recruitment.

## Materials and Methods

### Maturity estimates

Data is derived from historical sources for halibut *Hippoglossus hippoglossus* (Thompson, 1916; Kohler, 1967) and Atlantic cod *Gadus morhua* (Graham, 1924; Anon., 1948; Beacham, 1983).

### Non-participation

Failure of an adult to reproduce is analyzed on the bases of a) failure to establish gametogenesis for a particular reproductive season b) failure to complete gametogenesis c) failure to achieve fertilization. Data for these are best for a), rare for b) and speculative for c). For a) I will use my own data for winter flounder (*Pleuronectes americanus*) and Atlantic cod (*Gadus morhua*), some of which is derived by calculation from Graham (1924) using his 1922 data and calculating gonadosomatic index ( $GSI = \text{gonadal weight} \times 100 / \text{body weight}$ ) where  $GSI < 1.00$  prespawning is assumed to mean a female is non-reproductive. Data were also obtained on Barents Sea cod from Shirakova (1969), for Greenland halibut or "turbot" *Reinhardtius hippoglossoides* from Fedorov (1971), for the burbot (*Lota lota*) from Pulliainen and Korhonen (1990). For b) I will use data for *R. hippoglossoides* (Fedorov, 1971). For c) fertilization rates for captive yellowtail *Pleuronectes ferrugineus* are derived from Manning and Crim (1998).

### Low participation

Low participation can be calculated on the basis of fecundity for determinate spawners winter flounder and Atlantic cod, and fecundity can be estimated from gonadosomatic index (GSI) for vitellogenic (exogenous, yolky) prespawning fish, excluding any females with hydrated oocytes. The assumption is made that for determinate spawners prespawning the GSI reflects fecundity. The winter flounder used were caught during the winter and killed shortly afterwards. The cod data is calculated from Graham (1924) for prespawning North Sea females or from Penney (1994) for prespawning Northwest Atlantic females

### Spawning stock biomass values

Spawning stock biomass values are adjusted for flatfish, using varying participation rates.

### Stock-recruit relationships

Adjusted spawning stock biomass values are substituted into stock-recruit curves for flatfish, from Cushing (1971). For the substitutions in the halibut curve (Area 2) based on

Pacific halibut, Fukuda (1962) recruitment is divided into three categories high (50-100, 11 points), medium (38-50, 13 points) and low (18-35, 12 points). The prediction is made that recruitment would correlate positively with stock when stock is correctly allowed to reflect reproductive participation. Participation rates are set at 50% (for high recruitment), 20% (medium) and 10% (low), justified by reference to the apparent participation rates calculated from Kohler's (1967) data. Plaice (*Pleuronectes platessa*) is treated similarly.

## Results

### Maturity estimates

Thompson (1916) studied Pacific halibut, was unable to access fish throughout the expected spawning season, but obtained sufficient mature/spent females to provide graphs of age and length at maturity: the plot for age at maturity shows that although mature fish are recorded at age VII, 50% maturity is not seen until age XII, and this stagger continues, with age XV still only showing 90% maturity. The 100% maturity level is not reached until age XVII, by which age few fish are present; from one area (Frederick Island) of three studied, no females above age XIII were recorded, and off Kodiak Island the oldest females were age XVIII.

Kohler (1967) provides tables of Atlantic halibut (males  $n = 310$ , females  $n = 292$ ) classified as immature, ripe-running or spent-recovering for spring and for late summer/fall. It is clear that the term "immature" is used uncritically as it includes large fish, for both males and females. The size range for "immature" fish for both sexes is 16-110 cm with very few fish of either sex (2 males and 9 females) in the larger size classes. Few fish (30 males and 18 females) are actually classified as reproductive i.e. ripe-running or spent-recovering. Even in the size range  $>91$  cm length 25% of the males (5 fish) are still classified as immature, while 50% (13 fish) of this size class of females are also classed as immature even though the smallest reproductive fish (male and female) are in the 41-50 cm size class. I assume therefore that this author could not differentiate non-reproductive adults from juveniles which had never spawned.

Atlantic cod records (Anon. 1948) show that there has been considerable uncertainty about maturity stages in the past for this fish. Large fish originally classed as immature have been subsequently reclassified (Fig. 1), but it is not clear whether this was done on any other basis than large size.

Graham (1924) studied North Sea cod, and the records show uncertainty about allocation of fish to classes for reproduction. Graham mentions barren cod, but he does not quantify them, nor even explain his reason for knowing or suspecting their existence. Graham also states that "it is impossible in practice to distinguish small spent fish, either male or female, from immature fish." In an extensive analysis of male and female cod obtained in January and March 1923 Graham lists 499 mature males and 155 immature males, with 324 mature females and 164 immature females. Within the immature classification he includes females up to 97 cm long and males up to 89 cm long

Beacham (1983) shows maturity ogives (length versus % mature) for Scotian shelf Atlantic cod (Subdiv. 4Vs); in 1959-64 for both males and females large fish are not necessarily 100% "mature", of approximately 11 data points for males of length  $>70$  cm only three show 100% maturity, the rest show from 75%-95% maturity. For females of length  $>70$  cm in the same time-frame 11 data points show five at 100% maturity with the remainder at 85-95% maturity. However as the time series progresses more large fish data points are at the 100% level and by 1975-79 there are no outliers for fish  $>70$  cm; all data points lie on the 100% level. Similar trends are seen for Div. 4Vn and 4W but Div. 4X retains some "immature" fish in the large size classes up to 1979.

### Non-participation

#### a) failure to establish gametogenesis for a particular reproductive season

Non-reproductive winter flounder, from wild populations calculated for three consecutive years showed values from 5%-35% for males, and 10-30% for females (Burton, 1991a and unpublished). For North Sea cod (Graham 1924) prespawning females,  $n = 54$ , in 1922, size range  $>50$  cm, 59% were non-reproductive. Shirakova's (1969) data for young cod shows 99% spawning for 5 year old females in 1961, with a drop to 89% spawning for the same cohort the next year. Likewise the 1957 male cohort attained 99% spawning in 1961, which dropped successively to 94% spawning in 1962 and 92% spawning in 1963. Fedorov (1971) shows 9.5% non-breeding females and 2.8% sterile fish for "turbot" (*Reinhardtius hippoglossoides*). Burbot, off Finland (Pulliainen and Korhonen (1990), can have a high level of non-maturing fish in the large size classes. Both males and females were capable of reproduction at size classes 32-30 cm, but even at sizes  $>50$ cm 30% females and 13% males were non-maturing. From Kohler's (1967) data for halibut it seems clear that a lot of the fish listed as immature in the higher size-range are actually non-reproductive adults. For the total 239 females  $>41$  cm, a size at which reproduction can occur, there are only 7.53% reproductive fish. At the greater size of  $>61$  cm ( $n = 120$ ) only 14.17% females are reproductive. For the largest females  $>91$ cm ( $n = 26$ ) only 50% are actively reproductive. To achieve the 100% reproduction level for females it is necessary to exclude all but the very large fish ( $>111$ cm,  $n = 9$ ).

#### b) failure to complete gametogenesis

Fedorov (1971) records mass gamete resorption by Greenland halibut or turbot females (*Reinhardtius hippoglossoides*) in response to temperature anomalies; but this situation is reported for a summer spawning period auxiliary to the main winter spawn. It is not clear whether Fedorov believes some fish to have two spawnings per year but he does state that once a fish has undergone a mass resorption it may subsequently miss one or more subsequent annual spawnings. His data show 8.3% females "missing the summer spawn" by resorption.

### c) failure to achieve fertilization

For captive *P. ferrugineus* individual mean (for batches) fertilization rates can vary from 87% to 5% (Manning and Crim, 1998), with two individuals <10%. Individual batches could show 0% fertilization, with huge variation for any individual female; one fish with 17 batches had from 0-87% fertilization and another with 16 batches had 1-32% fertilization. For two consecutive years (n = 11, 10) the mean fertilization was 38% and 57%.

### Low participation

Winter flounder GSI for females shows some individual variation in the prespawning season, in four different years (n = 15, 14, 10, 15) the mean and range were 14.24 (9.8-20.09), 13.56 (7.83-23.57), 11.89 (6.5-22.8) and 13.24 (9.35-18.15). Cod GSI shows considerable variation prespawning; for North Sea females (1922), n = 21, the mean was 5.32, with a range of 1.54-11.81. For cod off Newfoundland (February, 1992), n = 9, the mean was 5.92 with a range of 2.5-10.12.

### Spawning stock biomass values

Starting with usual estimates of spawning stock biomass the values can be modified by applying estimates of non-participatory adults, and perhaps also effects of low participation. For Pacific halibut where spawning stock is apparently taken (Fukuda, 1962) to include even influxes of young fish ("chickens", 7 year-olds) it is reasonable to apply corrections to the data. For Fukuda, stock is implied to be equal to spawning stock but he calculates residual stock from landed fish including small-sizes, but does not give any values for lengths of fish caught. Inspecting available length and age data for Pacific halibut Thompson's (1916) data from the North Pacific show high variation for length at age. Converting Thompson's data from inches to cm. for three locations, seven year-old fish would be 61 cm, 66 cm or 81 cm in length. Applying this to Kohler's (1971) data, for females >61cm 14.5% would be reproductive; the data cannot discriminate for the >66 cm level, but for the >81 cm size 39% would be reproductive. Given some variation in size distribution and mean fecundity interannually it is proposed that in any given year a correction of from 10% to 50% of total stock could represent the real spawning stock participating in reproduction for halibut.

### Stock-recruit relationships

The recalculated stock recruitment plot for Pacific halibut (Fig. 2) shows a shift from the original which had little stock dependency, towards dependency of recruitment on stock. The same effect is obtained with plaice (Fig. 3).

## Discussion

Recruitment variability may indeed have a great deal to do with factors such as food and predation directly affecting larval and juvenile survival rather than variability in stock, as Miller *et al.* (1991) imply. However analysis of stock relative to spawners in the stock may help understand why some stock-recruit relationships have been so difficult to clarify. Clear stock-recruit plots have been obtained for anadromous salmonids (Cushing, 1971), presumably because stock analyzed has only been migrating fish, and therefore reproductive fish. Stock analysis for groundfish however has been based on landings, the values of which may then be used to calculate residual stock (Fukuda, 1962), but which do not allow for the fact that not all fish in a stock are actively or maximally reproductive in any one year.

In 1979 a review (Bull and Shine) of iteroparous (repeat reproducing) animals which may "skip reproduction" listed only six species of fish, in comparison to 27 amphibia and 18 reptiles. The fish species did not include any fully marine teleosts, but we now know that reproductive omission can be found in Northern pleuronectids and gadids. Recent papers have also shown that reproductive omission occurs in a Southern gadoid *Macruronus novaehollandiae* (Livingston *et al.*, 1997); for females reproductive participation varied interannually from 67% to 82%. Another southern fish, the commercially important orange roughy (*Hoplostethus atlanticus*) also shows spawning omission Bell *et al.* (1992), with an estimate of 45% non-reproductive females for 1990.

Although Pulliainen and Korhonen (1990) believe that for burbot (*Lota lota*) spawning omission is not nutrition related their data are based on current condition rather than condition which might have evoked spawning omission. In general it is possible to relate spawning omission to varying food supplies, and experimentally it is possible to evoke or reverse the non-reproductive state in winter flounder (Burton, 1991b, 1994). Given that varying nutrition will also affect fecundity there is the possibility that it is feeding success which drives the stock-recruitment

relationship from the stock side. In the case of Northwest Atlantic cod lack of capelin (*Mallotus villosus*) at critical points in the reproductive cycle may affect both fecundity and participation for males and females.

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NO.	DATE 1948	POSITION & LOCALITY	WEIGHT Lbs.	SEX	MATURITY	A	Black O. Sp.	Yrks. Eye	Eye DIA.
0.880	Nov. 18	Parsons Ground 70FM	3.6	F	Immature	57	✓	5	0
0.872			1.63	F	Immature	70	✓	7	T0
0.779			4.8	F	Immature	77	✓	7	0
0.754			2.18	F	Immature	7	✓	10	T*
0.903			5.4	F	Immature	74	✓	6	10
0.915			2.45	F	Spent	67	✓	6	0
0.872			7.3	F	Maturing A	77	✓	8	T0
0.943			3.31	F	Spent	77	✓	9	T10
0.883			4.3	F	Spent	77	✓	7	0
0.904			1.95	F	Spent	77	✓	7	0
0.861			4.8	F	Spent	77	✓	9	T10
1.03			2.18	F	Spent	77	✓	7	T10
0.824			4.8	F	Spent	77	✓	7	T10
0.925			2.18	F	Spent	77	✓	9	T10
			5.7	F	Spent	77	✓	7	T10
			2.59	F	Spent	77	✓	7	T10
			5.4	F	Spent	77	✓	7	T10
			2.54	F	Spent	77	✓	7	T10
			6.0	F	Spent	77	✓	7	T10
			2.72	F	Spent	77	✓	7	T10
			6.7	F	Spent	77	✓	7	T10
			2.59	F	Spent	77	✓	7	T10
			7.5	F	Spent	77	✓	7	T10
			3.40	F	Spent	77	✓	7	T10
			6.5	F	Spent	77	✓	7	T10
			2.95	F	Spent	77	✓	7	T10
			3.31	F	Spent	77	✓	7	T10
			3.31	F	Spent	77	✓	7	T10

Fig. 1. Part of a page from Anon. (1948). Additions to this page include age data in January 1951, at which time the change of status for fish S-546 probably occurred. Left marginal notes giving condition factor and metric values for the weight are not on the original. This page is representative of other changes in the notebook, which also has comments on small "spent" fish, as "looks immature".

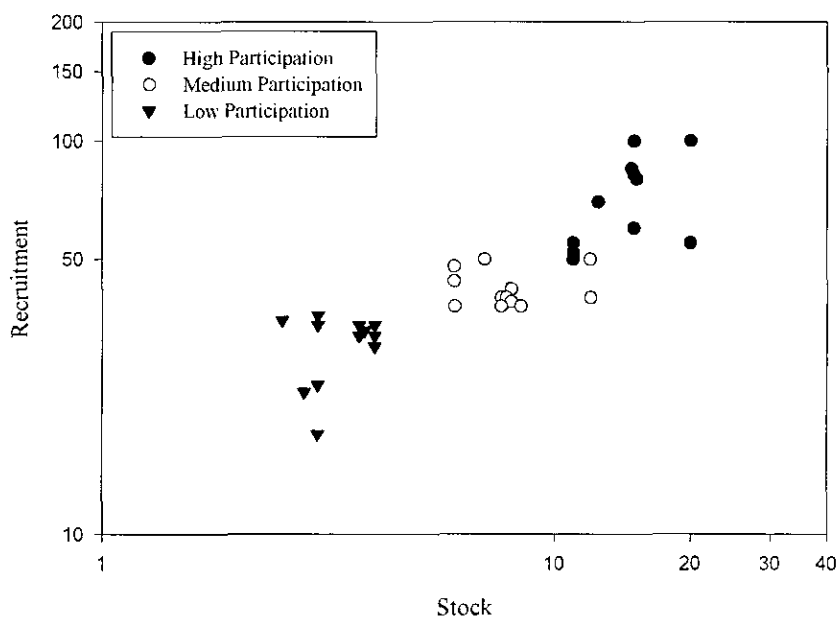


Figure 2: Halibut stock recruitment relationship (in logs) from Cushing (1971) after Fukuda (1962), recalculated with varying participation rates based on levels of recruitment.

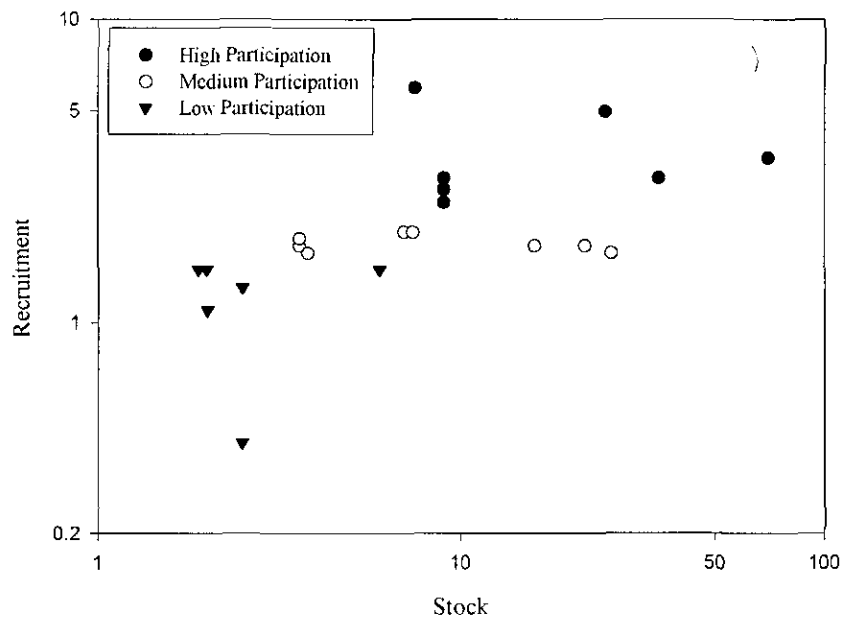


Figure 3: Plaiice stock recruitment relationship (in logs) from Cushing (1971) after Beverton (1962), recalculated with varying participation rates based on levels of recruitment.