GROWTH RATE AND RECRUITMENT : EVIDENCE FROM YEAR-CLASS STRENGTH IN THE YEAR-TO-YEAR VARIATION IN THE DISTRIBUTIONS OF OTOLITH WEIGHT, FISH WEIGHT, AND FISH LENGTH IN HOPLOSTETHUS ATLANTICUS

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GROWTH RATE AND RECRUITMENT: EVIDENCE FROM YEAR-CLASS STRENGTH IN THE YEAR-TO-YEAR VARIATION IN THE DISTRIBUTIONS OF OTOLITH WEIGHT, FISH WEIGHT, AND FISH LENGTH IN *HOPLOSTETHUS ATLANTICUS*

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LENGTH
WEIGHT
OTOLITH WEIGHT
HOPLOSTETHUS ATLANTICUS
FISHING-DOWN
YEAR-CLASS
GROWTH CURVE

ABSTRACT – An innovative method of differences was developed to recover year class structure from a series (1984 to 1992) of random samples of fish length, fish weight and otolith weight taken from random stratified trawl surveys of Orange Roughy, *Hoplostethus atlanticus* (Trachichthyidae: Teleostei). The apparent stability of the sample distributions over the period 1984 to 1992 was likely to be caused by stratified recruitment, not a consequence of old age. Both strong year class effects, and an estimate of the growth curve, of *H. atlanticus* were recovered using the method of differences. Strong year classes were correlated with periods of low ocean turbulence. The growth curve developed from the year class structure was highly correlated with growth curves derived from daily microincrements.

LONGUEUR
POIDS
POIDS DE L'OTOLITHE
HOPLOSTETHUS ATLANTICUS
SUREXPLOITATION
CLASSE ANNUELLE
COURBE DE CROISSANCE

RÉSUMÉ – Une méthode innovante des différences est développée pour retrouver la structure de classes par année à partir d'une série d'échantillonnages au hasard (1984 à 1992) de la longueur, du poids des Poissons, et du poids des otolithes provenant de campagnes de chalutage (random stratified samples) recueillant l'Hoplostèthe, *Hoplostethus atlanticus* (Trachichthyidae : Téléostéen). La stabilité apparente des distributions dans les prises entre 1984 et 1992 est probablement due à un recrutement stratifié, plutôt que la conséquence d'une abondance d'individus âgés. Les effets importants des classes annuelles et une estimation de la courbe de croissance de *H. Atlanticus* sont retrouvés en utilisant la méthode des différences. Les fortes classes sont corrélées aux périodes de basse turbulence de l'Océan. La courbe de croissance obtenue à partir de la structure des classes annuelles est hautement corrélée aux courbes de croissance basées sur l'analyse des stries journalières.

INTRODUCTION

The Orange Roughy, *Hoplostethus atlanticus* (Trachichthyidae: Teleostei), is a pandemic deep-water fish species occurring at depths 600 to 1200 m in many parts of the world's oceans (Paulin 1979, Merrett & Wheeler 1983, Gordon & Duncan 1987). Since the late 1970's, *H. atlanticus* has been the basis of a commercial fishery in New Zealand and Australian waters (Wilson 1982, Robertson & Grimes 1983), and recent exploration for commercial quantities of *H. atlanticus* has taken place in the North Atlantic (Anon 1994, Dubuit 1995). There are commercial fisheries for *H. atlanticus* in Namibia (Anon 1998), and off the coasts of Mada-

gascar and Chile. In less than twenty years *H. atlanticus* has gone from an obscure fish in museum collections to a popular culinary item, particularly in the United States of America. Over this period growing knowledge of the biology of *H. atlanticus* has lead to the revision of several of the earlier paradigms applied to the management of the fishery in New Zealand waters. Exploration of the sea-bed with new acoustic technologies has greatly extended the geographical range over which seamounts (the favored habitat of *H. atlanticus*) are known to occur. It is now evident that there are many spawning grounds not a single spawning ground to which all fish migrate, confirming earlier observations by Pankhurst *et al.* (1987).

Continuing exploitation of the resource has lead to a revision of the early estimates of stock size

that were made in the late 1970's and early 1980's. Apparent decline in stocks of *Hoplostethus atlanticus* has occurred in the face of what were believed to be conservative yield estimates (Robertson & Grimes 1983, Smith *et al.* 1991). Downward estimates of the virgin stock size by hind-casting techniques have also occurred over this period (Francis *et al.* 1993). Unlike most species of fish, the decline in apparent stock size was thought to have occurred without a fishing-down effect. Size distributions of *H. atlanticus* apparently remained stable without the expected preferential loss of the largest size classes (Gauldie *et al.* 1989).

The apparent stability of size classes in the face of declining numbers has had considerable impact on age estimates of *Hoplostethus atlanticus*. Age estimates based on morphological and chemical properties of the otolith have been through a progressive inflation of maximum ages from 20+ years (van den Broek 1983a b, Kotlyar 1980), through 50 years (Mace *et al.* 1990), to 150-200 years (Fenton *et al.* 1991, Smith *et al.* 1995), to extreme ages of 500+ years. It was believed that growth rates were very low because of the extraordinary antiquity of the fish, and that the consequent low recruitment and extreme age at first spawning of 30+ years resulted in sensitivity to over-fishing. Taken in isolation, ages of greater than 20+ years for a fish rarely heavier than 3 kg may seem extreme, but the paradigm of extreme old age in fishes has been used to explain declining stocks of many other species of fish. The apparent stability of size frequencies in the face of fishing pressure was widely perceived as an indicator of very old, slow growing fish, although no formal explanation of how this might occur has been published. There has also been a continuing parallel effort to estimate age in *H. atlanticus* using more conventional methods that have lead to estimates of maximum ages in the range 14 to 22 years (van den Broek 1983 a b, Gauldie *et al.* 1989); still a great age for a small fish with a maximum size of about 3 kg. Although extreme ages have been discredited (West & Gauldie 1995, Romanek & Gauldie 1996, Gauldie 1998), the problem of no apparent fishing-down effect remains. The apparent stability of the size distribution in the catch curves typical of the fishery is one of the many puzzling features of the biology of *H. atlanticus*. The estimated biomass of *H. atlanticus* in New Zealand waters was thought to have declined by 70% or more over the period 1984 to 1992 covered in this study (Smith *et al.* 1991), yet the length and weight distributions in the catch have remained superficially similar and more or less stationary, as will be shown below.

We will show that the argument for slow growth based on the apparent stability of the size distribution data for *H. atlanticus* is unlikely to be correct.

Closer examination of the size distribution data for *H. atlanticus* that was made available for this study (fish length, fish weight and otolith weight), showed evidence of year class structure in what had previously been assumed to be a more or less stationary distribution over time. We describe a variation on the method of differences that is commonly used to establish year class progressions that reveals a significant amount of year class structure embedded in the *H. atlanticus* data.

Because the samples were taken at yearly intervals, the progression of year classes allows a direct estimate of the growth curve of *H. atlanticus*. We compare this direct estimate of the growth curve with growth curves derived from other direct and indirect methods. In addition, year class structure allows us to explore possible oceanographic causes that may have influenced recruitment in *H. atlanticus*.

MATERIALS AND METHODS

1. Fish length and weight, and otolith weight data : A set of 7149 observations of fish length, weight and otolith weight of *Hoplostethus atlanticus* was prepared in 1994 for the New Zealand Exploratory Fishing Company using data and specimens held by the New Zealand Ministry of Fisheries. The data and specimens were derived from the random stratified trawl surveys of the fishery for *H. atlanticus* on the Chatham Rise, east of New Zealand, conducted by the Ministry of Fisheries. A random set of 20 samples was taken from each of a number of trawl surveys amounting to a total sample size of between 842 to 933 for each successive year from 1984 to 1990, and including 1992. There were no trawl surveys commissioned by the Ministry of Fisheries in 1991. This data is as close to a random sample of the true population characteristics of *H. atlanticus* that it is possible to obtain in the context of sampling by trawl surveys.

In the following text "otolith" refers to the sagitta. Otoliths were collected at sea and stored dry in envelopes after determination of fish lengths (standard length), sex and fish weight. Otoliths were weighed to 10 mg precision, fish weight measured to a tenth of gm, and lengths (standard length) measured to a tenth of cm. The data set consisted of 8 year class (sample sizes in parentheses), 1984 (883), 1985 (842), 1986 (894), 1987 (915), 1988 (927), 1989 (933), 1990 (894), and 1992 (860).

2. Statistical analysis of the data: This study used smoothing techniques and linear regressions in addition to the standard tests for the significance of the differences between means and medians available in the Data Desk software package. The statistical nomenclature in Data Desk is followed here.

Linear regressions were fitted using Data Desk. Recovering the underlying trend in a data of two variables *y*, *x* is usually achieved by fitting the data to a function that can range from a straight line to a complex polynomial. The appropriateness of the fit in the absence of a prior model is determined by the r^2 value of the regression which provides an estimate of the proportion of the variation in *y* that is explained by the variation in *x*. Alter-

natively, in the absence of a prior model to which the data can be regressed, one can substitute an arbitrary smoothing function that follows the trend in the data. Two smoothing techniques that are available for this purpose are the lowess and the median smooth.

The lowess technique adjusts the fit to the trend in the data by calculating a running mean value based on an adjustable window of sample points (Cleveland 1979). The more points in the window, the less sensitive the lowess smooth is to short term trends. Consequently, there is an arbitrary window size that determines the cut-off point between too sensitive to short term trends, and too insensitive to short term trends. A more arbitrary, but less adjustable, method is available in median smoothing which has the least subjective control, and from a common sense point of view describes where most of the y data points may lie over the most of the range in x. Median smoothers have the advantage of behaving as low-pass filters on equally spaced data that avoid the biasing effects of brief spikes in the data sequence (Tukey 1977). This study used the lowess and the median smoothing programs available in the Data Desk statistical package.

3. Wind-driven turbulence data: Wind-driven upper ocean mixing is estimated from observations of either anemometers or ocean wave topology (Beaufort scale), following Bakun (1990), where the upwelling (mixing downward, turbulence, etc.) is related to wind speed cubed. Derived wind velocity data for the geographical area bounded by longitudes 170°E and 170°W and latitudes 40°S to 45°S are taken from the CEOS (Climate in Eastern Ocean Systems) CD-ROM containing the COADS data set (available through NOAA, ORSTOM and FAO). This area covers the historical boundaries of the eastern Pacific Ocean stocks of New Zealand *H. atlanticus* to which the size frequency data refer.

4. The method of differences for establishing year class progressions: Many species of fish have clearly separated length modes evident in their catch curves, each length mode corresponding to a successive year class. Catch curves for such species readily show strong and weak year classes in which the area under the curve of a particular length mode may be much greater, or much lesser, than the other length modes in the catch curve. For example, Fig. 1 a-c show the kind of catch curves that might be sampled at three successive time intervals from a fishery based on a species with well-separated length modes, each corresponding to a different year class. Because such length modes are clearly separated, it is customary in examining such data to simply decide by eye on year class structure, and strong (or weak) year class progressions. But, in effect, the examination by eye is no more than a way of looking for differences in the location of length mode peaks between the sample at one time interval, and the sample at the next time interval. If there was no difference in the location of length modes between sampling intervals, then one would consider that no growth had occurred in the particular cohort of fish that comprise that length mode. But if there was a visible difference in location, then one would consider that growth equivalent to the separation between peaks had occurred in that particular cohort over the time between sampling. This kind of analysis is usually done intuitively, but it amounts to a subtraction from the catch curve at one time interval, of that of the previous time
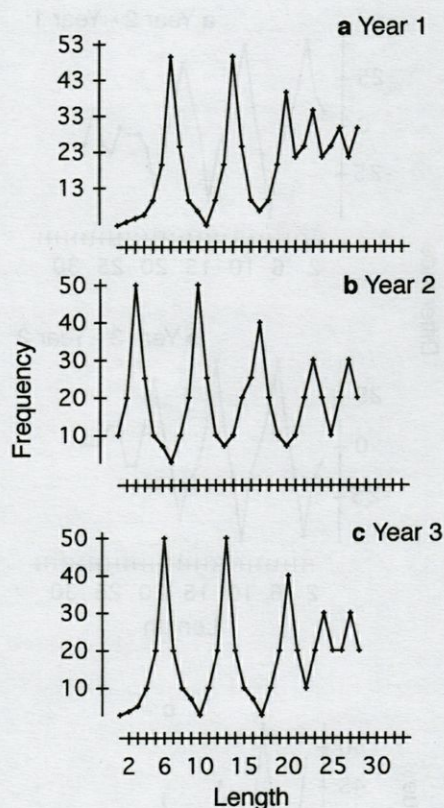

Fig. 1. – Changes in length modes over time for an idealized fishery are shown as length frequencies at time 1, time 2 and time 3.

interval. Thus, "no difference in location" by subtraction would lead to low value; and "a visible difference in location" would lead to a high value. Following the example in Fig. 1 a-c, the graphs in Fig. 2 a and b show, respectively, the differences obtained from subtracting time 1 from time 2, and time 2 from time 3 ("time" as indicated in Fig. 1 a to c). The difference graphs in Fig. 2 a and b contain further information about year class progression. If the difference between time 2 and time 3 (Fig. 2 b) is regressed against the difference between time 1 and time 2 (Fig. 2 a) at progressively lagged intervals, then the plot of the r^2 of the regression reveals the phase relations (i.e., the pattern of the change in frequency over time), between the underlying length mode structure measured at different time intervals; as is shown in the plot of r^2 against lag Fig. 2 c.

While the difference graphs are unnecessary in the case of the kind of length mode progression shown in Fig.1 a to c, they provide a useful tool for analyses of length mode progressions for data that have less obvious length modalities. For example, Fig. 3 a to c show the same length modes as in Fig. 1 a to c, but with a normally distributed overlay of non-modally distributed underlying lengths. Visual inspection of the three size distributions in Fig. 3 a to c would not indicate any underlying modality in length distribution. But, by subtracting a from b, and b from c in Fig. 3, one would recover exactly the same difference graphs as in Fig. 2 a and b, from which the same lagged regression as in Fig. 2 c
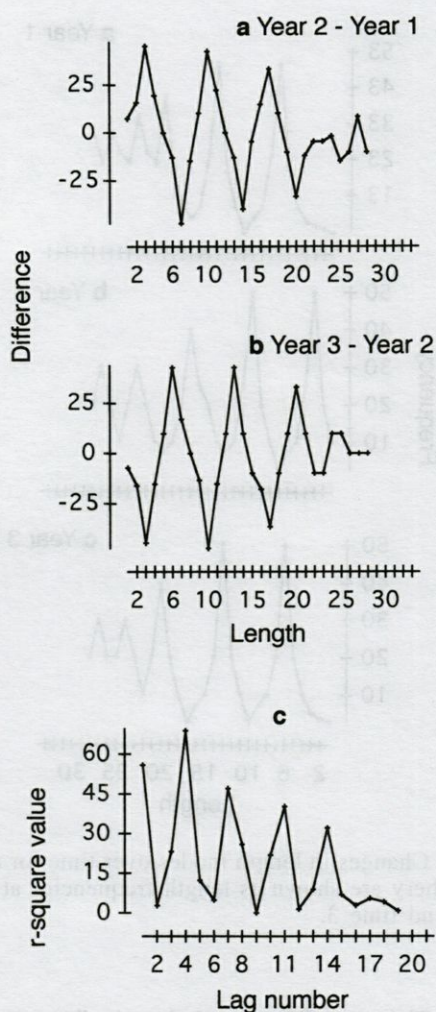
Fig. 2. – Frequencies from the method of differences resulting from (a) subtraction of time 1 from time 2 in Fig. 1; and (b) subtraction of time 2 from time 3 in Fig.1. c. The plot of r^2 of the regression of the frequencies from the method of differences (a) from Fig. 2, lagged against (b) from Fig. 2.

would show the strong length modality that was otherwise hidden in the data.

We believe that the novel approach of difference graphs to length mode analysis can be applied to the size data in the catch curves of *H. atlanticus* (fish length, fish weight and otolith weight), that have a similar appearance (see Fig 6, 9 and 11 below) to the size distributions in Fig. 3 a to c. The phase relations between different years of samples can also be established using the plots of the r^2 of the regressions of the data obtained from the method of differences.

RESULTS

General relationships in the data

Otolith weight is plotted against fish weight in Fig. 4. The graph in Fig. 4 has been fitted with a
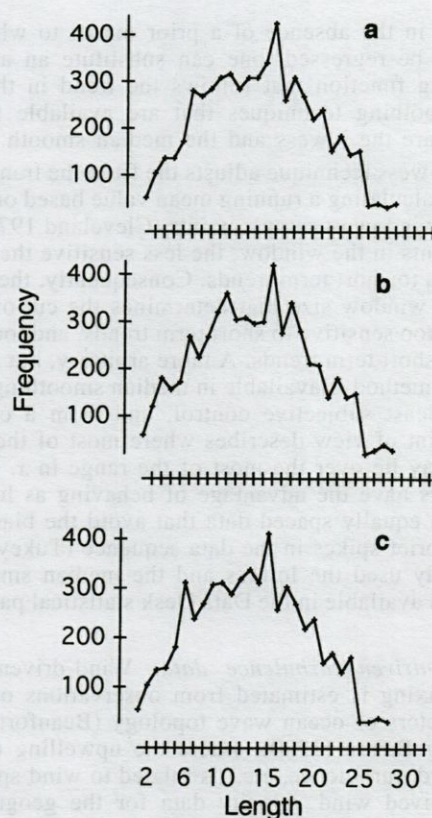

Fig. 3 a-c. – Length mode data from Fig. 1 each with the same overlay of normally distributed length frequencies.

linear regression ($r^2 = 41.4\%$). Although the plot in Fig. 4 indicates a non-linear relationship between otolith weight and fish weight, transformation of the data to provide a more linear relationship does not markedly improve the fit to the linear regression. The maximum value of $r^2 = 48.4\%$ was obtained with the transformation formula: (otolith weight)$^{0.1}$ = (fish weight)$^{1.76}$. Thus, the relationship between otolith weight and fish weight is non linear, but not markedly so. The scatter in otolith weight increased markedly with fish weight, but less than half of the variation in otolith weight is explained by the variation in fish weight in *Hoplostethus atlanticus* reflecting the de-coupling of otolith growth rate and fish growth rate seen in many species (Mosegaard *et al.* 1988, Wright *et al.* 1990).

Otolith weight is plotted against fish length in Fig. 5a, in which the graph has been fitted with a linear regression ($r^2 = 45.3\%$). Transforming the data using the formula (otolith weight)$^{0.1}$ = (fish length)$^{1.76}$, increases the value of r^2 to 58.6%. Thus, about 60% of the variation in otolith weight was explained by the variation in fish length, reflecting the de-coupling of otolith growth rate and fish growth rate. The scatter in the data increases with increasing fish length indicating a weakening of the correlation between otolith weight and fish length with increasing size.

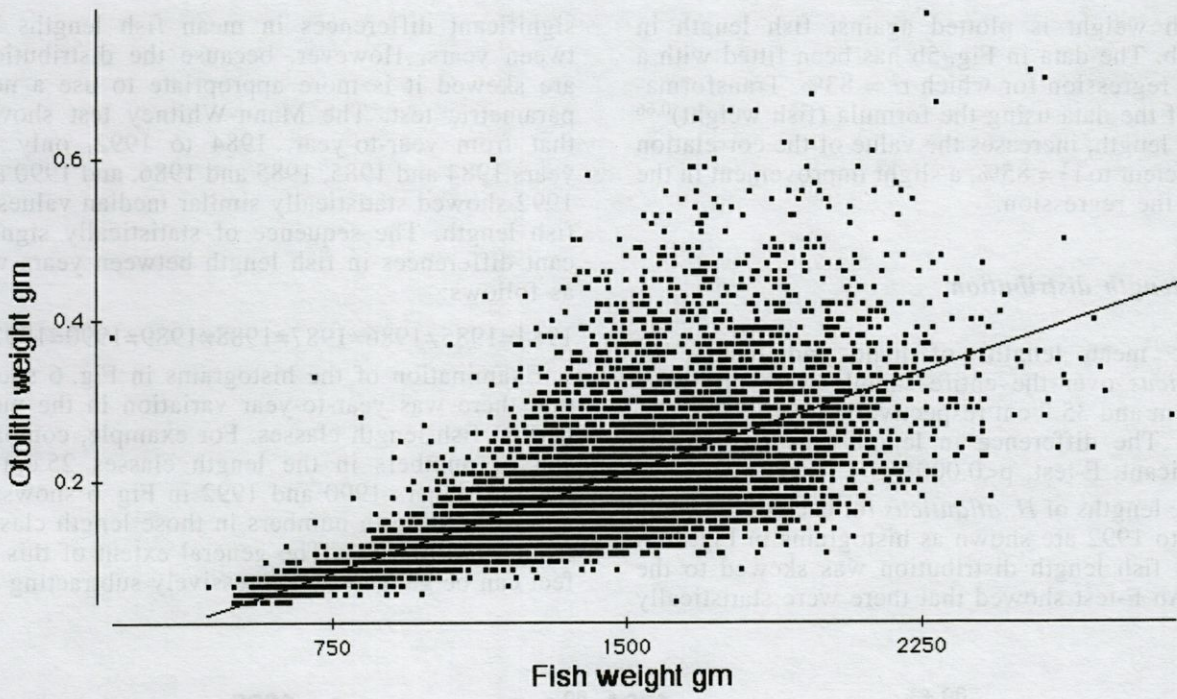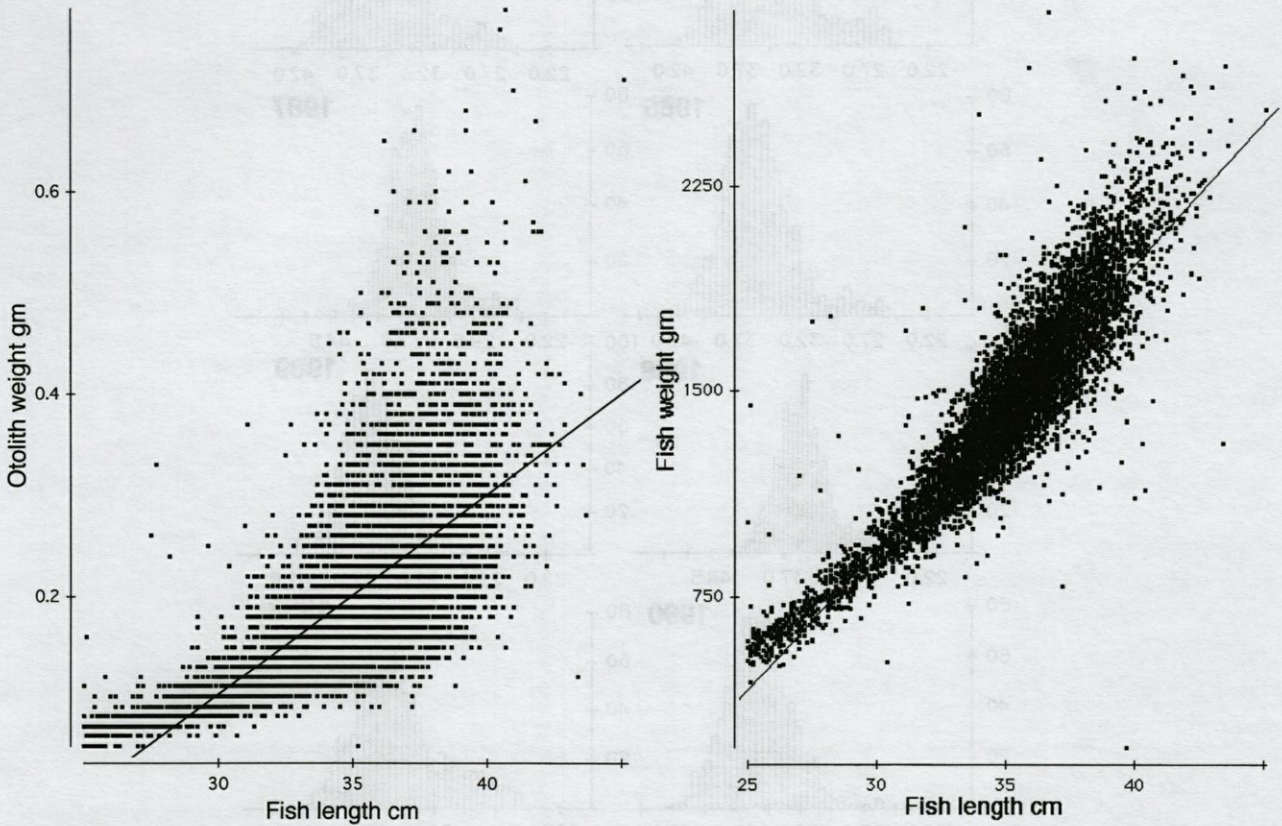Fig. 4. – Otolith weight plotted against fish weight fitted with linear regression.

Fig. 5. – a. Otolith weight plotted against fish length fitted with linear regression; b. Fish weight plotted against fish length fitted with linear regression.

Fish weight is plotted against fish length in Fig. 5b. The data in Fig. 5b has been fitted with a linear regression for which $r^2 = 83\%$. Transformation of the data using the formula (fish weight)$^{0.66}$ = fish length, increases the value of the correlation coefficient to $r^2 = 85\%$, a slight improvement in the fit of the regression.

Fish length distribution

The mean lengths of male and female *H. atlanticus* over the entire sample were different, 34.3 cm and 35.7 cm respectively; about 4% difference. The difference in length was statistically significant, F-test, $p<0.0001$.

The lengths of *H. atlanticus* for each of the years 1984 to 1992 are shown as histograms in Fig. 6 in which fish length distribution was skewed to the left. An F-test showed that there were statistically

significant differences in mean fish lengths between years. However, because the distributions are skewed it is more appropriate to use a non-parametric test. The Mann-Whitney test showed that from year-to-year, 1984 to 1992, only the years 1984 and 1985, 1985 and 1986, and 1990 and 1992 showed statistically similar median values in fish length. The sequence of statistically significant differences in fish length between years was as follows:

$1984=1985\neq1986\neq1987\neq1988\neq1989\neq1990=1992.$

Examination of the histograms in Fig. 6 shows that there was year-to-year variation in the numbers in fish length classes. For example, comparison of numbers in the length classes 25 cm to 30 cm in years 1990 and 1992 in Fig. 6 shows an almost trebling in numbers in those length classes from 1990 to 1992. The general extent of this effect can be gauged by successively subtracting the
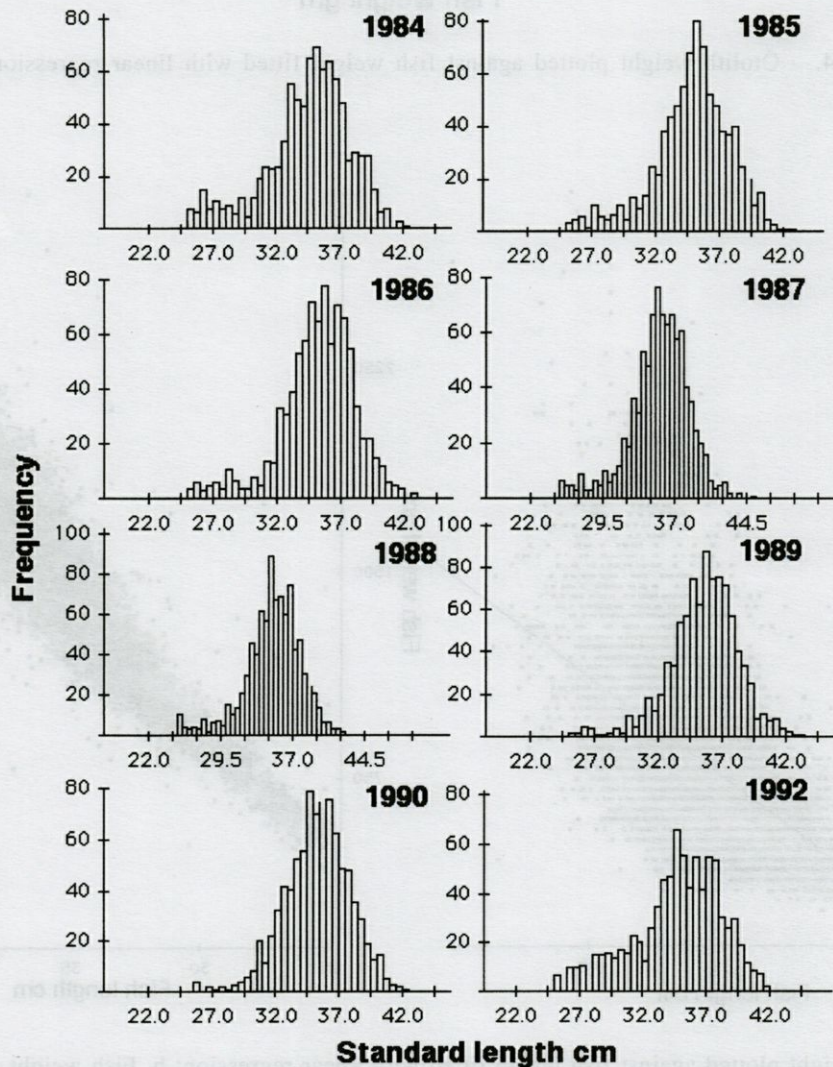

Fig. 6. – Histograms of fish length plotted by years 1984 to 1992.

numbers in each annual length class from the numbers in the same length class in the year ahead. For example, 85-84 in Fig. 7 is the difference in length classes resulting from 1984 value being subtracted from 1985 values. The seven sets of differences for the years 1992-1990, 1990-1989, 1989-1988, 1988-1987, 1987-1986, 1986-1985, and 1985-1984 are shown in Fig. 7.

The subtraction means that negative values in the difference distributions indicate a decrease in that size class with respect to the previous year,

and positive differences indicate an increase in that size class with respect to the previous year. When each of the difference graphs in Fig. 7 was fitted with median smoothed curves it was evident that there was a year-to-year oscillation in year-to-year differences around zero. However, the oscillations were out of phase from sample to sample. The sets of arrows identified from A to J show an apparently positive phase cycle, i.e. year-classes, moving through successive years before finally damping out to zero.
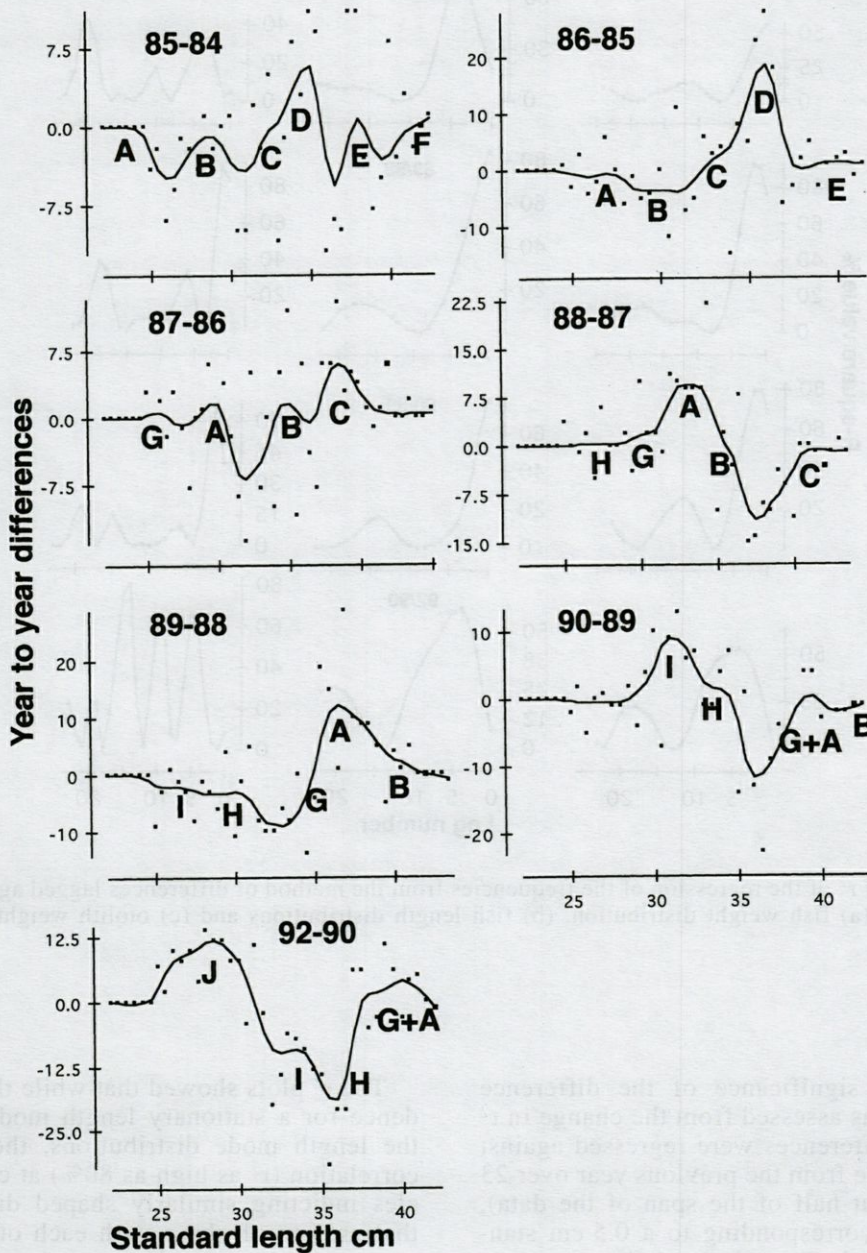

Fig. 7. – Differences from year to year in fish length plotted against fish length class. The fish length divisions on the abscissa in 85-84 have the same values in all graphs. Successive year classes values are marked alphabetically from the left.
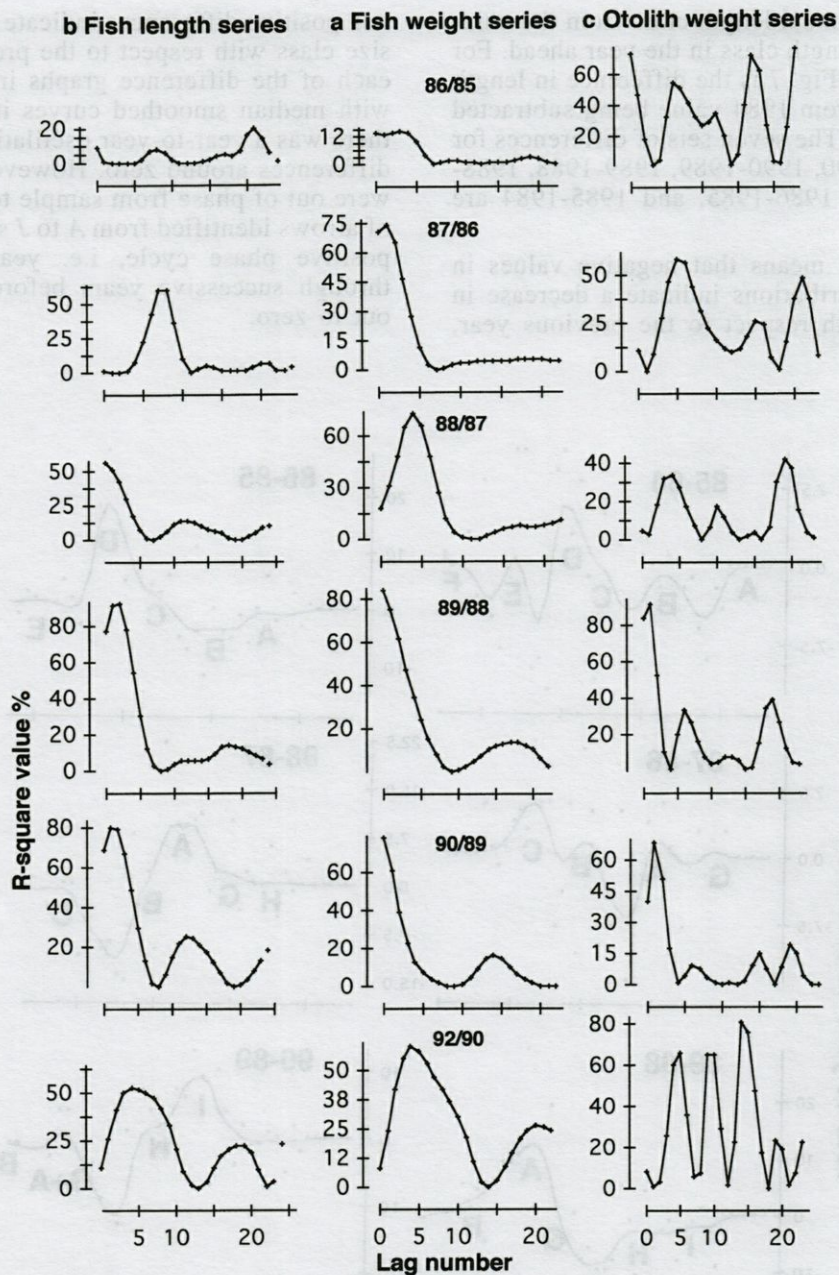
Fig. 8. – The plots of r² of the regression of the frequencies from the method of differences lagged against the previous year are shown for (a) fish weight distribution, (b) fish length distributions and (c) otolith weight distributions.

The biological significance of the difference curves in Fig. 7 was assessed from the change in r² value when the differences were regressed against the difference curve from the previous year over 23 lag intervals (about half of the span of the data), each lag interval corresponding to a 0.5 cm standard length interval. The plots of the r² values against lag interval for regressions between the median smoothed successive annual differences in Fig. 7 are shown in Fig. 8a.

The r² plots showed that while there was no evidence for a stationary length modes concealed in the length mode distributions, there were strong correlation (r² as high as 80%) at certain phase cycles indicting similarly shaped difference curves that are out of phase with each other; exactly the properties one would expect from a length mode progression representing a strong year class. In addition, the peaks in the r² values shift in respect to length in progressive years, thus supporting the in-

terpretation of a cycle of strong year classes moving through the data that was apparent from an inspection the lettered peaks in Fig. 7.

Fish weight distribution

The mean weights of male and female *H. atlanticus* of the total sample were different, 1322.3 gm and 1558.3 gm respectively; about 17.8% difference. The differences in weight was statistically significant, F-test, p ≤ 0.0001.

The weights of individual *H. atlanticus* for each of the years 1984 to 1992 are shown as histograms in Fig. 9 in which it is evident that fish weight distribution was skewed to the left, the opposite direc-

tion to the otolith weight histograms below. An F-test showed that there were statistically significant differences in mean fish weights between years; however, because the distributions are skewed it is more appropriate to use a non-parametric test. The Mann-Whitney test showed that from year-to-year, 1984 to 1992, only the years 1984 and 1985, 1985 and 1986, and 1990 and 1992 showed statistically similar median values in fish weight. The sequence of statistically significant differences in fish weight between years was as follows:

1984=1985=1986≠1987≠1988≠1989≠1990=1992.

Examination of the histograms shows that there was year-to-year variation in the numbers in fish weight classes. For example, comparison of numbers in the weight classes 600 gm to 1100 gm in
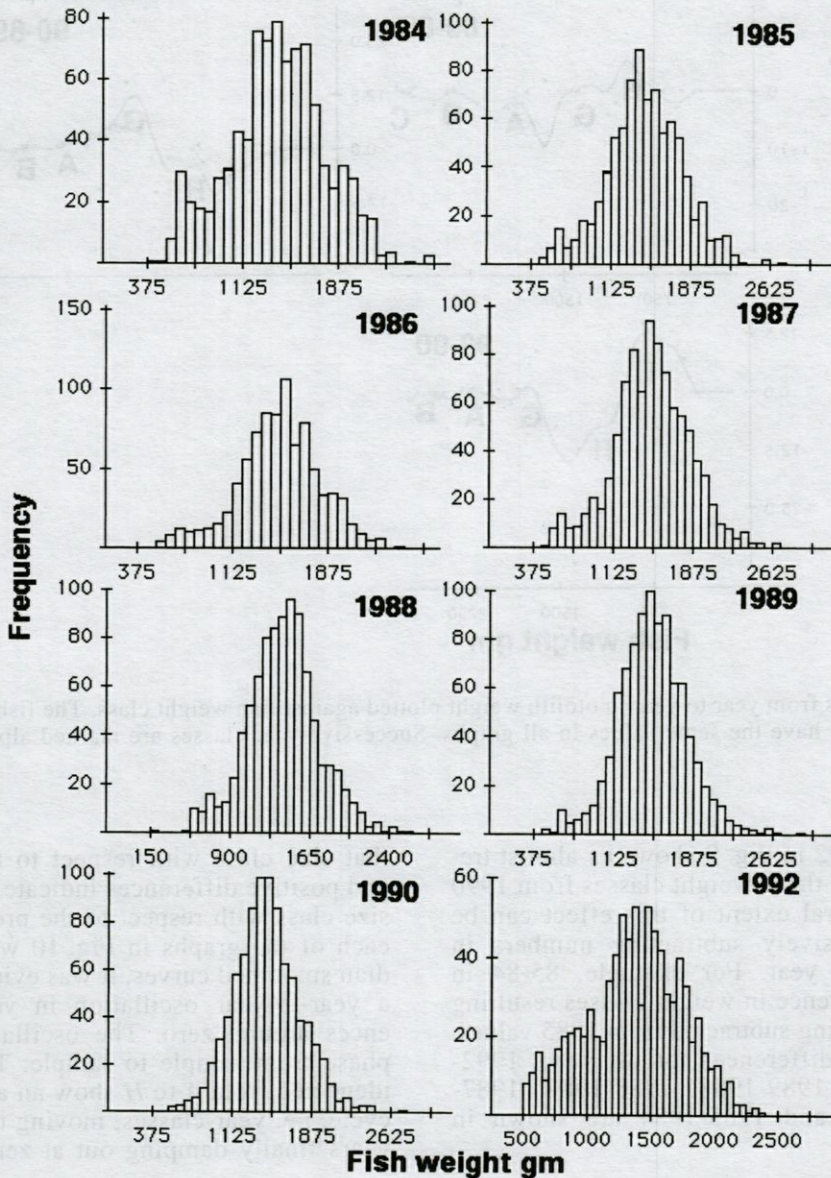

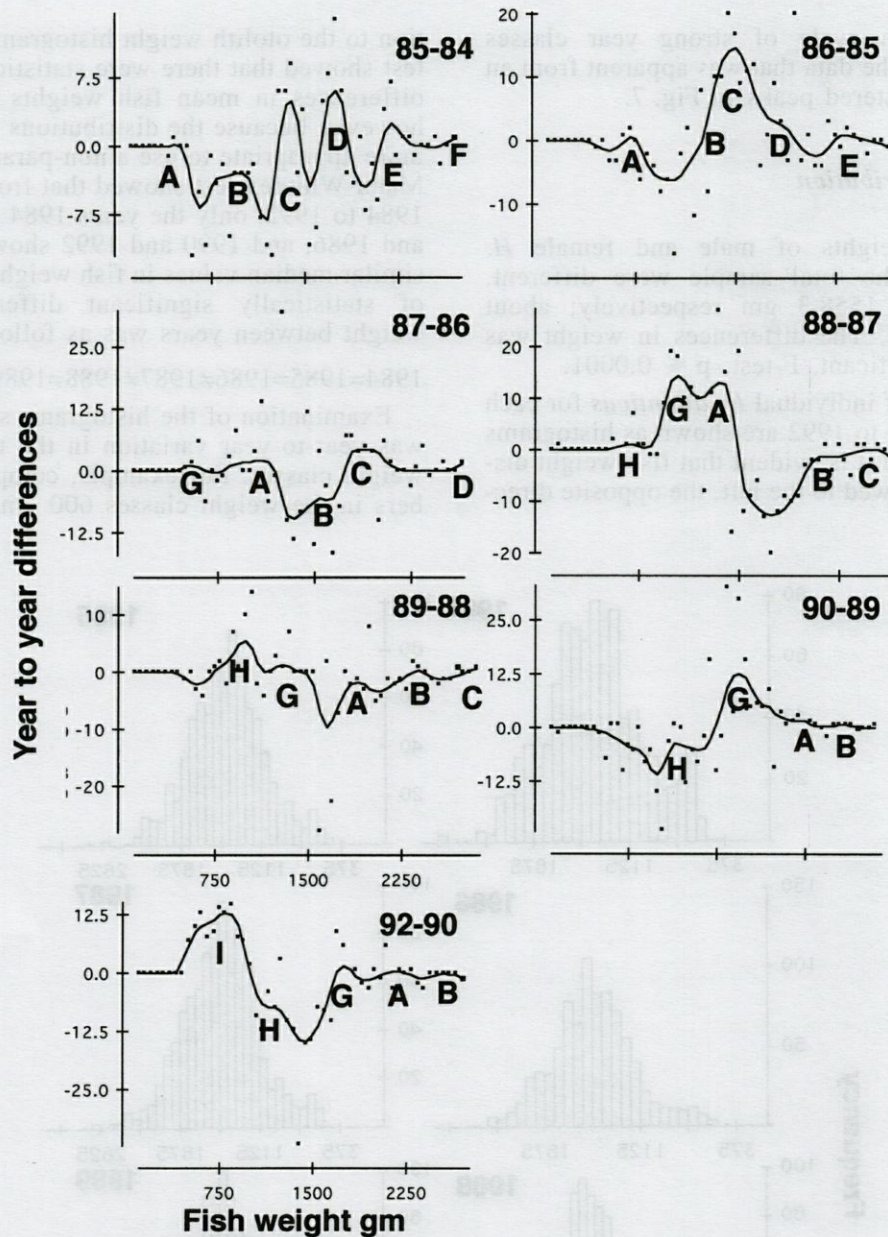Fig. 9. – Histograms of fish weight plotted by years 1984 to 1992.

Fig. 10. – Differences from year to year in otolith weight plotted against fish weight class. The fish weight divisions on the abscissa in 85-84 have the same values in all graphs. Successive year classes are marked alphabetically from the left.

years 1990 and 1992 in Fig. 9 shows an almost trebling in numbers in those weight classes from 1990 to 1992. The general extent of this effect can be gauged by successively subtracting numbers in weight classes by year. For example, 85-84 in Fig. 10 is the difference in weight classes resulting from 1984 value being subtracted from 1985 values. The seven sets of differences for the years 1992-1990, 1990-1989, 1989-1988, 1988-1987, 1987-1986, 1986-1985, and 1985-1984 are shown in Fig. 10.

The subtraction means that negative values in the difference distributions indicate a decrease in

that size class with respect to the previous year; and positive differences indicate an increase in that size class with respect to the previous year. When each of the graphs in Fig. 10 was fitted with median smoothed curves, it was evident that there was a year-to-year oscillation in year-to-year differences around zero. The oscillations were out of phase from sample to sample. The sets of arrows identified from A to H show an apparently positive cycle, i.e. year-classes, moving through successive years finally damping out at zero.

The biological significance of the difference curves in Fig. 10 was assessed from the change in

r^2 value when the differences were regressed against the difference curve from the previous year over 23 lag intervals (about half of the span of the data), each lag interval corresponding to a 50 gm standard weight interval. The plots of the r^2 values against lag interval for regressions between the median smoothed successive annual differences in Fig. 10 are shown in Fig. 8b.

The r^2 plots showed that while there was no evidence for a stationary length modes concealed in the weight mode distributions, there were strong correlation (r^2 as high as 80%) at certain phase cycles indicting similarly shaped difference curves that are out of phase with each other; exactly the properties one would expect from a length mode progression representing a strong year class. In ad-

dition, the peaks in the r^2 values shift in respect to length in progressive years, thus supporting the interpretation of a cycle of strong year classes moving through the data that was apparent from an inspection the lettered peaks in Fig. 10.

Otolith weight distribution

The mean weights of otoliths of males and females in the total sample were different, 0.199 g and 0.205 g respectively. The difference in weight was statistically significant, F-test, $p < 0.0027$. However, given the variation in otolith weight with fish size, this minor difference (about 3%) is probably not biologically significant.
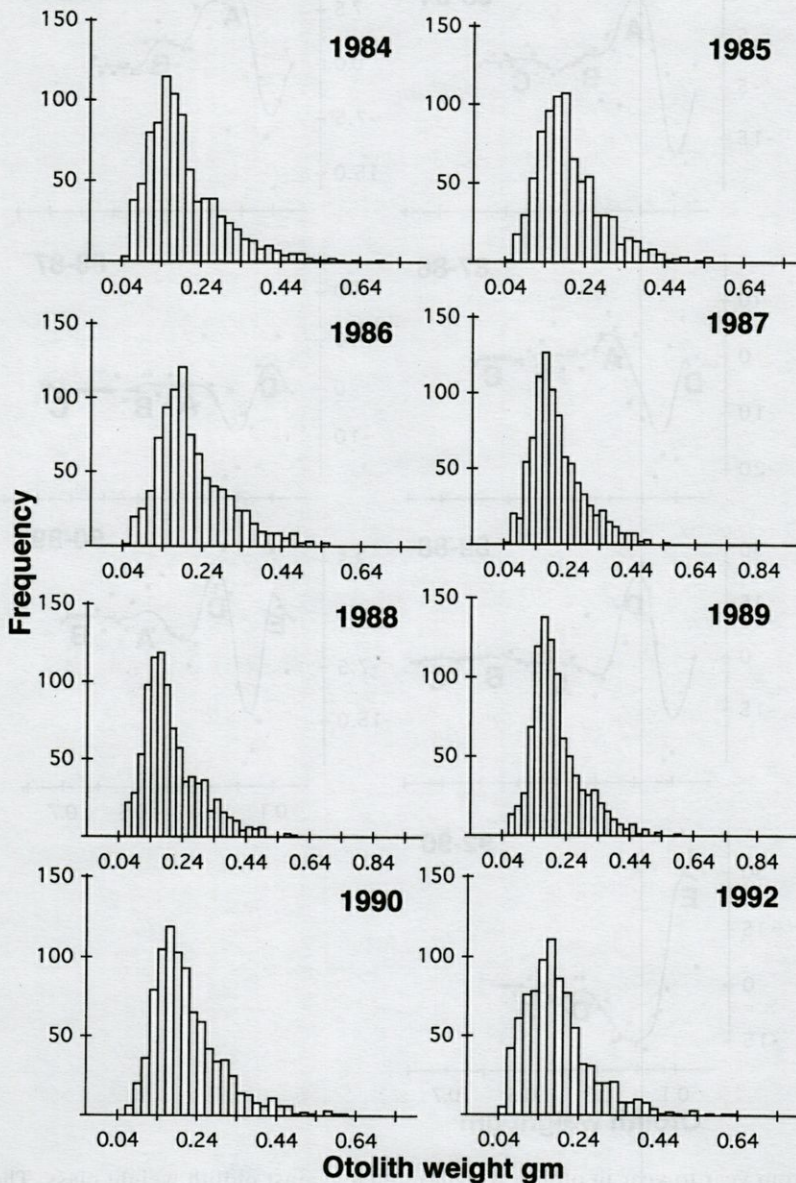

Fig. 11. – Histograms of otolith weight plotted by years 1984 to 1992.

The weights of otoliths of *H. atlanticus* for each of the years 1984 to 1992 are shown as histograms in Fig. 11. It is evident from the histograms that otolith weight distribution was skewed to the right. An F-test showed that there were statistically significant differences in mean otolith weights between years; however, because the distributions are skewed it is more appropriate to use a non-parametric test. The Mann-Whitney test showed that from year to year, 1984 to 1992, only the four-year period 1986 to 1990 showed no statistically significant year-to-year change in otolith weight. The sequence of statistically significant differences in otolith weight between years was as follows:

$$1984 \neq 1985 \neq 1986 = 1987 = 1988 = 1989 = 1990 \neq 1992.$$

Examination of the histograms shows that there was year-to-year variation of numbers in otolith weight classes. For example, comparison of the numbers in the weight classes 0.04 to 0.14 gm in years 1990 and 1992 in Fig. 11 shows an almost doubling in numbers in these weight classes form 1990 to 1992. The general extent of this effect can be gauged by successively subtracting numbers in weight classes by year. For example, 85-84 in Fig. 12 is the difference in weight classes resulting from 1984 values being subtracted from 1985 values. The seven sets of differences for the years 1992-1990, 1990-1989, 1989-1988, 1988-1987, 1987-1986, 1986-1985 and 1985-1994 are shown in Fig. 12.
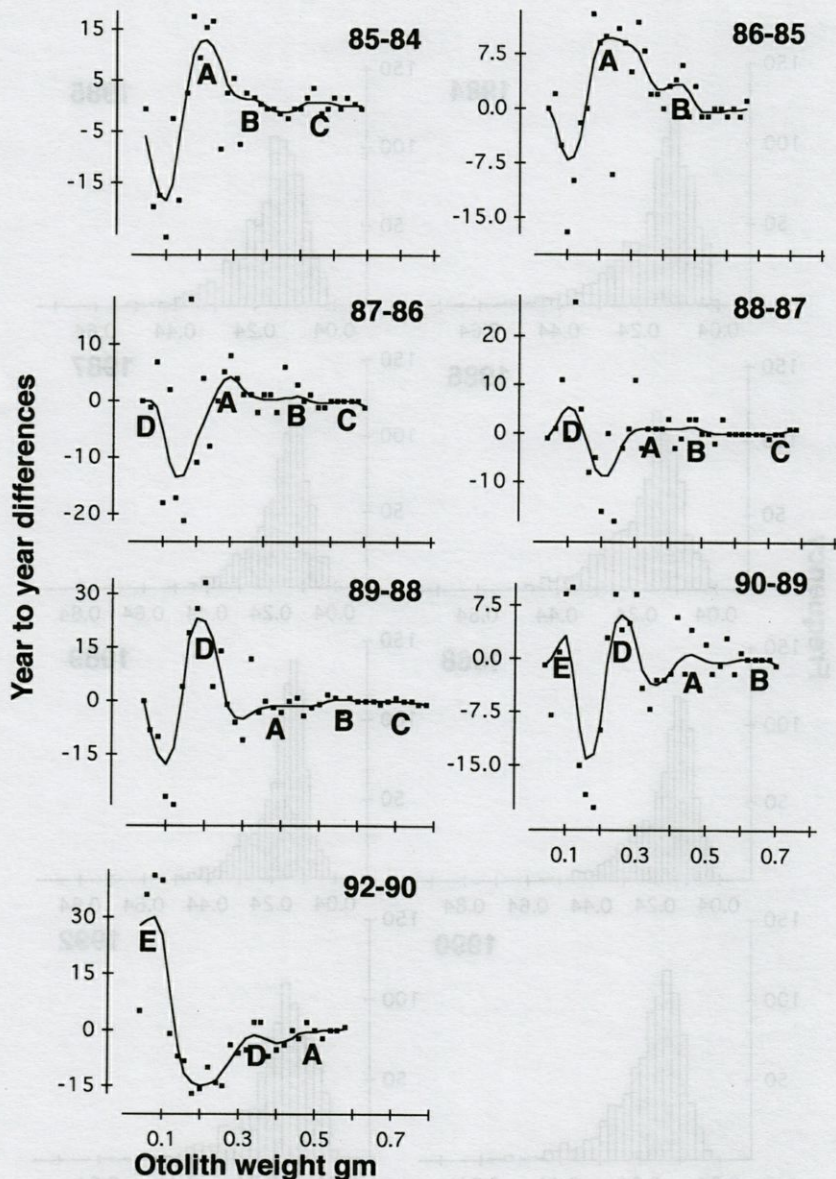

Fig. 12. – Differences from year to year in otolith weight plotted against otolith weight class. The otolith weight divisions on the abscissa in 85-84 have the same values in all graphs. Successive year classes are marked alphabetically from the left.

The subtraction means that negative values in the difference indicate a decrease in that size class with respect to the previous year, and positive differences indicate an increase distribution in that size class with respect to the previous year. When each of the graphs in Fig. 12 was fitted with median smoothed curves, it was evident that there was a year-to-year oscillation in year-to-year differences around zero; however, the oscillations were out of phase from sample to sample. The peaks identified from A to E showed an apparently positive cycle (i.e. year-classes), moving through successive years finally damping out at zero. Two positive cycles apparently began in 1988 and 1992 respectively.

The biological significance of the difference curves in Fig. 12 was assessed from the change in r^2 value when the differences were regressed against the difference curve from the previous year over 23 lag intervals (about half of the span of the data), each lag interval corresponding to a 15 mg standard otolith weight interval. The plots of the r^2 values against lag interval for regressions between the median smoothed successive annual differences in Fig. 12 are shown in Fig. 8c.

The r^2 plots showed that while there was no evidence for a stationary length modes concealed in the length mode distributions, there were strong correlation (r^2 as high as 60%) at certain phase cycles indicting similarly shaped difference curves that are out of phase with each other; exactly the properties one would expect from a length mode progression representing a strong year class. In addition, the peaks in the r^2 values shift in respect to length in progressive years, thus supporting the interpretation of a cycle of strong year classes moving through the data that was apparent from an inspection the lettered peaks in Fig. 12.

Estimating length at age

The samples from 1984 to 1990 were made at yearly intervals. Therefore, if the same cohort can be recognized as a peak that can be identified in two, or more, successive years, then a length-at-age relationship can be developed in the following way.

Suppose that each of the length modes recognized in each yearly sample represent successive cohorts. Then, the age in years of the first cohort is a, the age of the second cohort is $a+1$, the third $a+2$, etc. each peak represents a length mode so that the length corresponding to the first cohort is l_a, the second l_{a+i}, etc. Plotting l_{a+i} against a_i will give a specific length-at-age curve starting at age a. If it is assumed that growth from age zero to age a_i is linear, then length from zero age can be extrapolated; thereby giving the full growth curve.
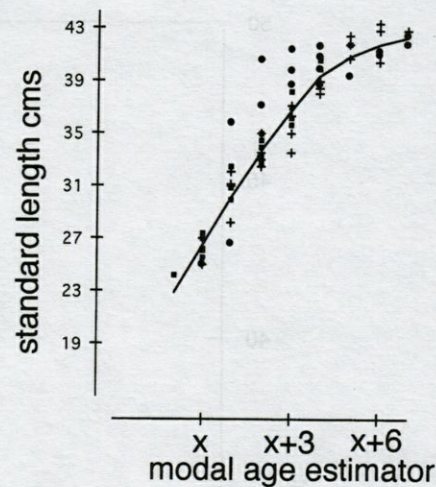

Fig. 13. – Length at age (x, $x+1$...etc) estimated from the subtraction method using otolith weight (filled circles), fish weight (filled squares) and fish length (crosses) fitted with a lowess smoothed curve.

Assuming that the lettered modes in the year to year difference curves for fish length, fish weight and otolith weight (Figs. 7, 10 and 12) are indicators of different cohorts, then the subsequent cohort lengths l_{a+i} are plotted against age class $a+i$ from each successive cohort in Fig. 13. The age and length data from cohorts in the fish length, fish weight and otolith weight data are indicated respectively by a cross, filled square and filled circle in Fig. 13.

Rather then attempt to fit a predetermined type of growth curve to the data points in Fig 13, a lowess smoothing curve was fitted, assuming zero length at zero age. The lowess curve is shown as a curved line in Fig. 13. It is evident from Fig. 13 that a has a value of 7 years by extrapolation along the lowess curve. By comparison, a length at age curve for *H. atlanticus* based on daily microincrement age is shown in Fig. 14. Lowess curves for females and males are shown as a dotted lines and a filled line respectively in Fig. 14. The similarity of the two length at age curves is evident. A direct regression of lengths at age over the size range 25 to 45 cm SL from both sets of growth curves in Figs. 13 and 14 resulted in a statistically significant regression ($p \leq 0001$) with an r^2 value of 97%.

Year class strength and recruitment

Changes in abundance of fishes are often related to changes in ocean productivity that is influenced by changing oceanographic conditions. Ocean productivity is tied to the degree of mixing of the deeper, nutrient-rich water with the water in the photic layer. One proxy for the degree of mixing between the deeper and the photic layer water is
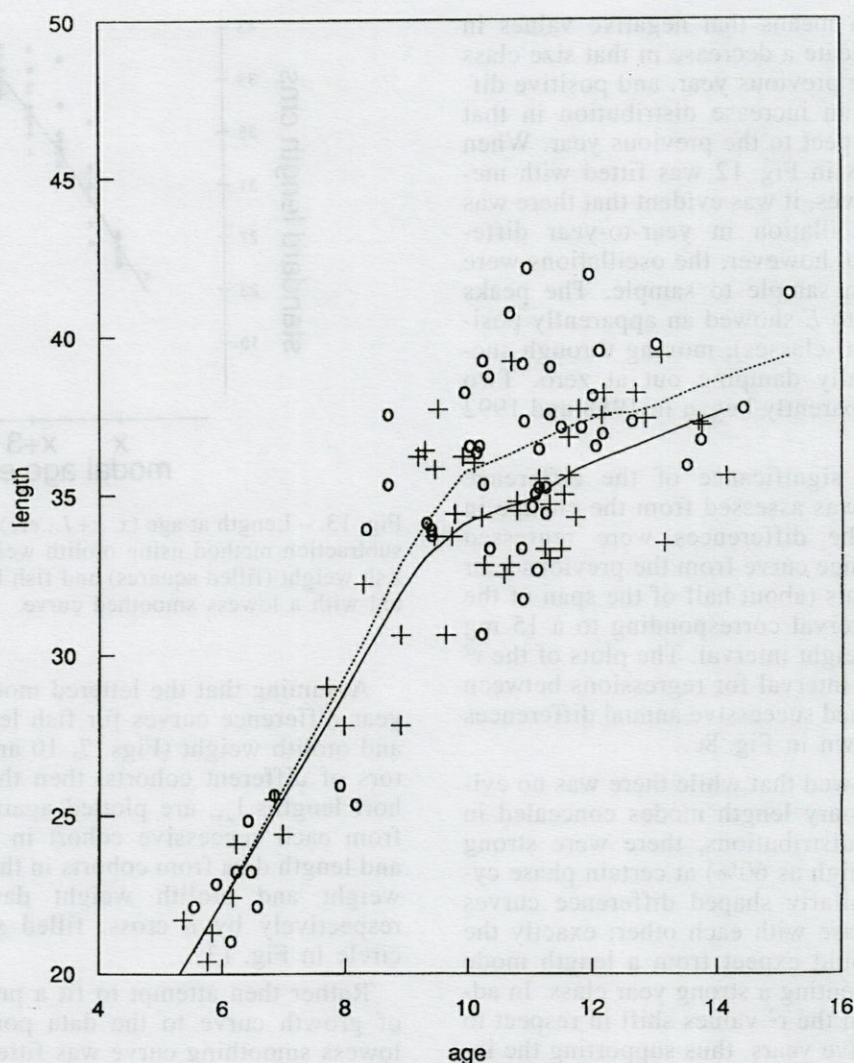
Fig. 14. – Length at age estimated by the daily microincrement method; females (open circles) and males (crosses) fitted separately with a lowess smoothing curve.

the cube of wind velocity (Backun 1990). In this study we have used the wind velocity observations in the CEOS-COADS data set. Annual turbulence effects are taken as the sum of the monthly average cubed wind speed in the region comprising the eastern New Zealand stocks of *H. atlanticus*. The annual turbulence 1970 to 1991 is plotted against year in Fig. 15a.

Following the assumption that the lettered modes in the year to year difference curves represent cohorts whose year of spawning can be identified, then it is possible to use the area under the curve of each lettered length mode as a measure of year class strength for each cohort. The average annual contribution of each cohort as area under the curve is taken as a measure of the year class strength for that cohort. The plot of year class strength is plotted against year of spawning in Fig. 15 b shows two stronger peaks in 1978/1979 and 1986, with a weaker peak in 1981. Examina-

tion of the plot of annual turbulence on year of occurrence that is also plotted in Fig. 15 b shows 1978/1979, 1981 and 1986 to be low turbulence years. The years 1973 and 1974 were also low turbulence years but are outside of the range of the cohort year class strength measure available from the 1984-1992 data.

The assumption that ocean productivity in the year of spawning determines year class strength can be tested by plotting year class strength (from area under the difference curves) against annual turbulence (Fig. 15c). The data in Fig. 15c have been fitted with a both linear and non-linear regression. The slope of the linear regression line is significantly different from zero (p=0.039) and the r^2 value is 0.36, indicating the 36% of the variation in annual year class strength is explained by the variation in ocean turbulence, which we use as an analog productivity measure. Fitting polynomial equations to year-class strength in Fig. 15c yields a
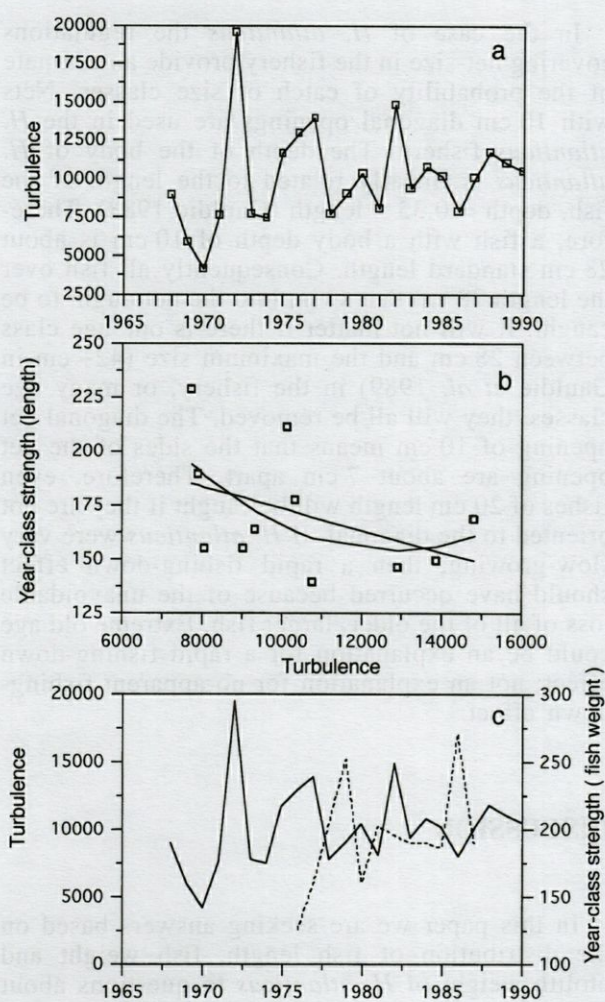
Fig. 15 – a. Annual turbulence plotted against year of spawning; b. Annual turbulence and year class strength both plotted against year of spawning; c. Fish weight year class strength plotted against year of spawning fitted with linear and non-linear regressions.

higher r^2 value, 0.44, but there is no reason to choose a non-linear over a linear regression.

Fishing-down effect

Most fisheries scientists refer to the progressive loss of larger size classes in a new or expanding fishery as a fishing-down effect because of the decrease in numbers involved. However, it is also referred to by the less intuitively obvious term "fishing-up effect" which is in the sense of the Russian equivalent: 'juvenation of the age structure'. A discussion of the origins and applications of the 'fishing-up effect' is in Ricker (1975: 262-264).

The fishing down effect results in the progressive loss of larger, presumably older, size classes. In most fisheries with size limits on net openings (including the *H. atlanticus* fishery) the specific

probability that a fish going into the net will be caught is mostly a function of size. The general probability of a fish being available to go into the net is more complex, but the simplified in-net model will suffice for our discussion of the fishing-down effect. Consequently, at any particular size distribution, the larger size classes have a disproportionately higher probability of being caught. The fishing-down effect is similar whether age classes and size classes are congruent or not; congruent meaning each size comprises a discrete age class. The fishing-down effect does not markedly decrease when age classes and size classes are not congruent because of the spread of ages within size classes.

The Congruent Model matrix is shown in Table Ia. The rows are size classes and the columns are age classes. The number of cells is arbitrary and does not have to be symmetrical. Each cell in the matrix can contain two numbers. The lower number is the probability, p_s, that the size class, irrespective of age, will be caught; bearing in mind that the mechanism of the fishing-down effective will be size-selective. The upper number is the proportion of fish in each age class within each size class. This proportion represents the proportion of fish in the ith age class that are in the jth size class. This proportion, p_{age}, gives the spread of an age class over different size classes. This is the column marked p_{sum} is the size class probability, the horizontal sum of the products [$p_s * p_{age}$] within each cell. The probability p_{sum} represents the proportion of each size class lost in each fishing pass. A similar treatment is presented in Ricker (1975).

The values for the probability of being caught, p_{sum} for each size class is the same for each of Table Ia b and has been chosen arbitrarily to reflect the increasing probability of catch with size. In the congruent model (Table Ia) age classes are identical with size classes, so that p_{age} has a constant value of one. In the absence of any fishing effect, in the congruent model the size frequency distribution of a thousand fish would comprise a series of non-overlapping, equal-sized length modes in each age class. The matrix in Table Ia can be used to simulate the fishing down effect by removing the numbers of fish in each size class corresponding to the size-class probabilities in column p_{sum}. After each pass, the remaining fish are all moved up one length class, and another 143 fish corresponding to the new cohort are added as size class 1. Constant recruitment is not likely to occur in nature, but simplifies the example. A series of length distributions corresponding to each successful pass for 7 passes using the congruent model are shown in Fig. 16a. After 7 passes the size distribution has stabilized to a new level in which the larger size classes are greatly reduced. The total population has stabilized at 683 out of the original 1000 fish.

Table I – The rows are size classes, the columns are age classes within each size class. Each cell in the row/column matrix has two numbers. The lower number is the probability that the fish in that size class (irrespective of age) will be caught. This is the probability p_s. The upper number is the proportion of fish the total population of fish that is in each age class within each size class. This proportion represents the probability p_{class} The column marked p_{sum} is the size class probability, the horizontal sum of the product of $p_s.p_{age}$. a. Congruent model matrix: in the congruent model each size class is an age class as well, so that proportion p_{age} is 1, and there is no spread of ages among size classes. b. Non.congruent model matrix: in the non-congruent model age classes are spread over more than one size class and the size class probability p_{sum} is non-linear on size.

a

Age Size	1	2	3	4	5	6	7	P_{sum}
1	*1*							
	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
2		*1*						
	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
3			*1*					
	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
4				*1*				
	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
5					*1*			
	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
6						*1*		
	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
7							*1*	
	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

b

Age Size	1	2	3	4	5	6	7	P_{sum}
1	*0.3*	*0.2*						
	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.005
2	*0.3*	*0.3*	*0.2*	*0.15*				
	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.0475
3	*0.3*	*0.3*	*0.3*	*0.25*	*0.25*	*0.2*	*0.1*	
	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.18
4		*0.25*	*0.3*	*0.3*	*0.3*	*0.25*		
	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.34
5		*0.05*	*0.2*	*0.25*	*0.25*	*0.2*	*0.3*	
	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.75
6					*0.5*	*0.2*	*0.25*	
	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.56
7					*0.1*	*0.1*	*0.1*	
	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.3

The Non-congruent Model matrix is shown in Table Ib. The lower numbers in the cells are the same as for Table 1a, but the upper numbers reflect a spread of ages within each size class. Consequently, the relation between p_{sum} the size class catch probability and size is non-linear. However, the effects of a series of fishing passes over a population with a constant annual recruitment of 143 fish into the smallest year class shows a similar fishing-down effect to the congruent model (Fig. 16 b). The only difference is that the non-linear relation between p_{sum} and size that results in a one-pass phase delay in the approach to equilibrium of the largest size class.

It is evident from Fig. 16a b that the probability of a size-class being taken determines the approach to fishing-down equilibrium, not the distribution of age classes within size classes.

In the case of *H. atlanticus* the regulations covering net-size in the fishery provide an estimate of the probability of catch of size classes. Nets with 10 cm diagonal openings are used in the *H. atlanticus* fishery. The depth of the body of *H. atlanticus* is linearly related to the length of the fish, depth = 0.35 x length (Gauldie 1988). Therefore, a fish with a body depth of 10 cm is about 28 cm standard length. Consequently all fish over the length 28 cm that swim into the net ought to be caught. It will not matter if there is one age class between 28 cm and the maximum size (42+ cm in Gauldie *et al.* 1989) in the fishery, or many age classes, they will all be removed. The diagonal net opening of 10 cm means that the sides of the net opening are about 7 cm apart. Therefore, even fishes of 20 cm length will be caught if they are not oriented to the diagonal. If *H. atlanticus* were very slow-growing, then a rapid fishing-down effect should have occurred because of the unavoidable loss of all of the older, larger fish. Extreme old age could be an explanation for a rapid fishing-down effect; not an explanation for no apparent fishing-down effect.

DISCUSSION

In this paper we are seeking answers based on the distribution of fish length, fish weight and otolith weight of *H. atlanticus* to questions about fishing down effects, growth rates, and strong year classes, as well as their cause. Before examining the answers that we have obtained, there is a need to be sure that the materials and methods that we have used are adequate to the task.

The samples of fish length, fish weight and otolith weight were as near to representative of the population of *H. atlanticus* as it is possible to obtain in the context of trawl surveys. It is unlikely that we will ever have access to data of better quality than that used in this study.

The general relationships between fish length, fish weight and otolith weight of *H. atlanticus* have the same basic form as in other species of teleosts, so that there is no reason to expect any unusual biological properties in the catch curves of fish length, fish weight and otolith weight that are unique to *H. atlanticus*. The scatter in the length-weight relationship increases with increasing size which accounts for the over-lap in year class size modes, as well as the increasing scatter in the length-at-age curve.

There have been a number of attempts to associate age with otolith weight (Brander 1974, Fletcher 1991), but they have usually been confounded by the need to assign prior ages to otolith weight size classes from an age estimation procedure not di-
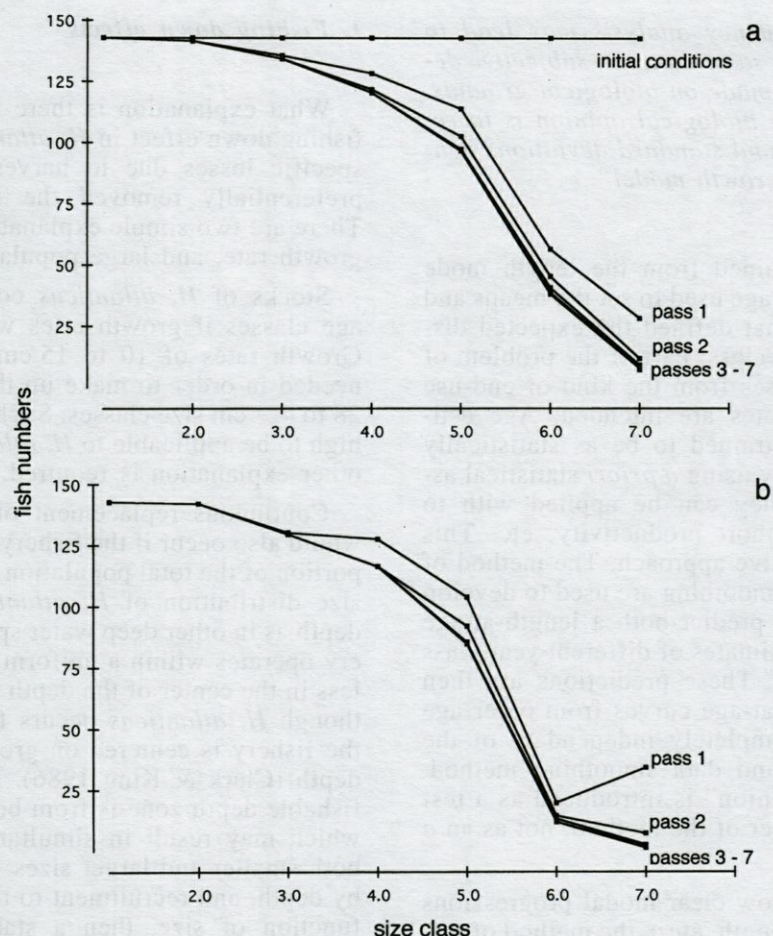
Fig. 16 – The fishing-down effect for the congruent model (a) and non-congruent model (b).

rectly related to weight (e.g., Boehlert 1985). Age estimation methods based on otolith weight generally use weight as a key to ages determined by other methods. This paper describes a new method of year-to-year differences aimed at directly assessing year-class strength, (and by implication age), from weight distributions of otoliths of *H. atlanticus* that does not require prior age estimation.

The statistical methods used in this study, F-test, Mann-Whitney tests and regression are all part of the standard suite of statistical tools used by fish biologists. Smoothing is widely applied to data sets both when the underlying functional relationship in known (Hinton & Campbell 1974, Tessler *et al.* 1993, Riggs & Tessler 1994), and when it is not known (Tukey 1977, Lancaster & Salkauskas 1986). In this study an arbitrary median smooth (Tukey 1977) was applied to the year-to-year subtraction data. This approach avoids the prior biological assumptions required by statistical fitting of modes in size class distribution, and provides a temporal progression of size modes that can be compared with other sources of information about

growth in *H. atlanticus*. We have also used standard lowess smoothing (Cleveland 1979) to establish trend lines in growth curves.

The use of length modes, to assign ages to length classes is one of the oldest "common-sense" approaches to fish age estimation (see Ricker 1975: 203-207). Many fishes species show distinct length modes in the early life of the fish that have been used to estimate age. In many species of fish, including *H. atlanticus*, the older year classes do not show such obvious modalities. Nonetheless, the justification for a maximum age of 150+ years for *H. atlanticus* has been based on extrapolation of apparent length modes of the first three age classes (Gauldie 1998).

There have been many attempts to overcome the subjectivity of length mode recognition from size distributions of mixed-mode older year classes by using statistical methods (Cassie 1954, Tanaka 1953, Hasselblad 1966, McNew & Summerfelt 1978, Schnute & Fournier 1980, Macdonald & Green 1988). Such methods are not always as objective as they may seem. In the words of Schnute & Fournier (1980: 1348):

"Because length-frequency analysis may lead to many solutions for the same data set, subjective decisions must often be made on biological grounds. One way to introduce biological opinion is to require that the means and standard deviations conform to an assumed growth model".

Thus, the age obtained from the length mode analysis is always the age used to set the means and standard deviations that defined the expected distribution of each year class. Part of the problem of prior assumptions arises from the kind of end-use for which age estimates are intended. Age estimates are often constrained to be as statistically rigorous as possible by using *a priori* statistical assumptions, so that they can be applied with to length/age curves, cohort productivity, etc. This paper uses an alternative approach. The method of differences and data smoothing are used to develop estimates of age that predict both a length-at-age curve, and provide estimates of different year class recruitment strengths. These predictions are then tested against length-at-age curves from other age estimates that are completely independent of the original subtraction and data smoothing method. Thus, "biological opinion" is introduced as a test of the predictive power of the method, not as an *a priori* definition.

In fisheries that show clear modal progressions in fish size (weight, length, etc.), the method of differences by subtraction between year classes is applied routinely although indirectly, and visually, by the progressive absence of a year class in successive years at a particular size class. The method of differences used here is, in principal, no different to the widely used visual method of identifying modal progression. Instead of the difference between years being the subtraction of a positive mode from what amounts to a "zero" mode, the difference is between a larger mode and a smaller mode. However, the application of the method of subtraction used here is a departure from common fisheries practice. The method of differences was applied directly in this study and median smooth curves fitted to the subtracted data yielded evidence of year class progressions through the fishery from 1984 to 1992 in the three categories otolith weight, fish weight and fish length.

The method of differences is the quantitative application of the qualitative visual method routinely used by fish biologists to distinguish both year classes, and year class progressions. The extent to which the method of differences is robust is determined by the same criterion by which the qualitative visual method is judged: are the result supported by other, entirely independent, observations? Against this background, we can now examine the answers to the question of fishing down effects, year class strength and growth rate.

1. Fishing down effects

What explanation is there for the absence of a fishing down effect in *H. atlanticus* when the size-specific losses due to harvesting ought to have preferentially removed the larger size classes? There are two simple explanations: relatively rapid growth rate, and large population size.

Stocks of *H. atlanticus* could replenish larger age classes if growth rates were relatively rapid. Growth rates of 10 to 15 cm per year would be needed in order to make up the loss of fish in the 28 to 42+ cm size classes. Such growth rates are too high to be applicable to *H. atlanticus*, therefore another explanation is required.

Continuous replacement of larger size classes would also occur if the fishery was sampling only a portion of the total population of *H. atlanticus*. The size distribution of *H. atlanticus* is stratified by depth as in other deep water species, while the fishery operates within a uniform depth range more or less in the center of the depth range of the fish. Although *H. atlanticus* occurs from 600 to 1200 m, the fishery is centered on grounds at about 800 m depth (Clark & King 1986). Recruitment into the fishable depth zone is from both above and below, which may result in simultaneous recruitment of both smaller and larger sizes. If size was stratified by depth, and recruitment to the 800 m zone was a function of size, then a stable size distribution would result under any levels of fishing pressure. Thus, the lack of an apparent fishing down effect in the size distribution of *H. atlanticus* can be explained by size partitioning by depth. This would result in only a relatively small proportion of both smaller and larger fish in the population being exposed to capture.

Size partitioning by depth is a simple explanation for stability of size frequencies. However, there still remains the possibility that factors related to the deep-water habitat of *H. atlanticus* contribute to the stability of size classes. Stability of length classes under fishing pressure in Cichlids and Coregonids has been attributed to extreme environments with inherently low energy inputs (Johnson 1983). As such, these fishes fall into the general class of K-selected species. In such species, size is usually poorly correlated with age. In K-selected life history strategies, organisms tend to be promoted from an unstable pool of smaller organisms to a stable pool of larger organisms only when depletions of large organisms occur. K-selection life history strategies appear to be fairly common in deep water fishes (Merrett 1994, Merrett & Haedrich 1997), including *H. atlanticus* (Gauldie *et al.* 1989). Part of the reason may be a uniformly low energy input into the deep ocean.

Size is the causal factor in most fishing down effects, not age. Age can only be a causal factor in

circumstances where growth rates are so high that smaller fish are promoted into larger size classes rapidly enough to match losses due to fishing. An argument that no apparent fishing down effect is related to great age in *H. atlanticus* is unsupportable.

2. Year class strength

Year class strength in most fish species is a function of many variables. Most of the variables that control year class strength cannot be measured over the period for which the commercial fishery for *Hoplostethus atlanticus* has existed. However one variable, upper ocean turbulence, that has a strong impact on ocean productivity (Bakun *et al.* 1982, Bakun 1990, Cury *et al.* 1995), can be recovered from the historical climate and meteorology data.

When the average year class strength based on fish weight and fish length modes is plotted against wind-driven turbulence measurements the coefficients of determination (r^2 values) show that 36% of the variation in year class strength can be explained by the variation in ocean turbulence in the linear model; and a higher proportion of the variation in year class strength, 44%, can be explained by the variation in ocean turbulence in the non-linear (polynomial) model. Year class strength is likely to be affected by many variables. It may be possible in low turbulence conditions that there is lower cloud cover and higher sunshine that compensates for lower nutrients; and, conversely, at high turbulence conditions there are more storm clouds and more nutrients compensating for lower sunshine, resulting in a non-linear relation. Nonetheless, the more conservative linear regression model indicates an increase in year class strength with low turbulence.

The plot of fish-weight year class strength against year of spawning showed stronger year classes in 1978/1979, 1981 and 1986. The effect of the 1986 year class should reach a peak in 1995 as nine-year olds, the dominant age class in the fishery for *Hoplostethus atlanticus* following the microincrement aging method (Gauldie *et al.* 1989). However, the 1986 year class followed three years of weaker recruitment and as far as we know has been followed by nine years of neither high nor low turbulence. It is possible that weak recruitment from 1980 to 1985, and from 1987 to 1994 has contributed to the apparent decline in stocks of *H. atlanticus*. In addition, the low turbulence recorded in 1973 and 1974 may have resulted in a particularly strong recruitment that would have been evident in the fishery when commercial exploitation of stocks of *H. atlanticus* began in 1977. The decline in stocks from 1977 estimated by hind-casting techniques may reflect variability in recruitment strength as much as the effects of fishing pressure.

Examination of modes derived from the method of differences showed that within years and between years over the period of 1984 to 1987 there were seven-year classes in the *H. atlanticus* fishery. Length modes in raw size data from the *H. atlanticus* fishery are usually more-or-less bimodal, with one large adult mode and a much smaller, apparently juvenile, mode (Gauldie *et al.* 1989, Mace *et al.* 1990). The three length modes in small (< 10 cm SL) *H. atlanticus* used by Mace *et al.* (1990) to validate ages up to 56 years may be artifacts of sampling (Gauldie 1998). However, Gordon & Duncan (1987) reported clearly recognizable length modes in *H. atlanticus* sampled from the Porcupine Sea Bight in the North Atlantic at 19, 24, 26, 29, 33 and 36 cm (standard length). The 19 cm mode is missing in the *H. atlanticus* subtraction data reported here, but the remaining length modes (24, 26, 29, 33 and 36 cm) appeared in the subtraction data corresponding to ages 6, 7, 8, 9 and 10 years respectively calculated from the growth curve.

The passage of year classes evident from the subtraction method points to the 1978 spawning as a strong recruitment year that appeared in the 85-94 data as seven-year-old fish and persisted until at least 1992. There was possibly another successful spawning in 1976 that appeared as 9-year-old fish in 85-84, and there was also another possible successful spawning in 1985 that appeared a seven-year-old fish in 92-90.

3. Growth rate

Age estimation for *H. atlanticus* has been difficult to test because of the lack of conventional length modes (or other modalities) in the catch curves from the fishery (as shown in this paper), but comparison of length-at-age curves from length mode progressions, derived from the subtraction method, with length-at-age curves estimated from a daily microincrement method showed similarly shaped curves. Alternative ages of 150+ years for *H. atlanticus* have been proposed by Fenton *et al.* (1991); Mace *et al.* (1990) claimed maximum ages of 29 years. The length-at-age curve derived from the method of differences were clearly dissimilar to the length-at-age curves of both Fenton *et al.* (1991) and Mace *et al.* (1990). However, the growth curves obtained from the method of differences are not only similar to those obtained from daily microincrements (verified by the Gauldie-Romanek model, Romanek & Gauldie 1996, Gauldie & Romanek 1998, Payan *et al* 1997, 1998); but are also give similar maximum ages to the original growth curves of *H. atlanticus* obtained from assumed annual marks in otoliths de-

scribed in van den Broek (1983 a, b) and Kotlyar (1980). The microincrement method of aging shows that the fishery for *H. atlanticus* is dominated by the age classes 4-12 years (Gauldie *et al.* 1989). The method of differences indicates 6 year classes in the fishery of 4 to 10 year old fish, with the age groups 11 to 16 represented by a small number of size classes.

Common practice usually requires that an age estimation method be shown a priori to be correct before it is applied to a fisheries problem. The methods used to establish *a priori* correctness inevitably contain assumptions that can lead to circularities. The method of differences is free of any prior biological assumptions, but requires an *a posteriori* test of its potential value. Growth curves obtained by the method of differences matched closely ($r^2 = 97\%$) the shape of growth curves generated by microincrement ageing of the otolith of *H. atlanticus*. It is unlikely that two completely independent estimates of the growth curve could be so similar just by chance.

Conclusions

1. The absence of a fishing down effect in the catch curves of *H. atlanticus* cannot be explained as a consequences of old age. The most likely explanation is that there are considerable reserves of *H. atlanticus* that migrate into the fishable zone. This would account for both the stability of the size distribution and the decline in apparent biomass within the fishable zone.

2. The method of differences provides information about year class structure of *H. atlanticus* that is correlates recruitment with ocean productivity. The correlation of recruitment with productivity provides prediction of future recruitment patterns that can be used as a direct experimental test of the robustness of both the prediction of recruitment and the method of differences itself.

3. The high correlation between the growth curve obtained by the method of differences and the growth curves based on daily microincrements is remarkable. It is even more remarkable when one considers that there is little or no correlation between the published growth curves of *H. atlanticus* that are all supposedly based on the same annual marks from otolith sections.

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