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The Influence of Stock Abundance and Water Temperature upon Growth Dynamics  
of haddock and yellowtail flounder on Georges Bank

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**Abstract**

Growth rates of the yellowtail flounder (*Limanda ferruginea*) and the haddock (*Melanogrammus aeglefinus*) are highly correlated with stock abundance in the Georges Bank region of the Northwest Atlantic. We used stepwise regression and Spearman rank sum analyses to test for correlations between length at age for age-2 and age-3 fish, and both stock abundance and bottom-water temperature for the period between 1963 and 1980. Mean length at age was significantly inversely correlated with stock abundance for both species and age groups tested. Growth was more highly correlated with stock abundance during periods when abundance was high than when it was low. This supports the hypothesis that growth should be most clearly density-dependent when stock size, thus intraspecific competition, is high. Stock size was significantly correlated with growth of juvenile fish but not young adults. Temperature was not significantly correlated with all age-species groups tested. Also, when significant, temperature did not consistently explain as much or more variability in length at age as did stock abundance, even during periods when abundance was low. Annual temperature fluctuations of the magnitude studied appeared to exert only modest influence on growth rates of yellowtail flounder and haddock on Georges Bank.

Body growth of fishes is widely held to be density-dependent, but numerous studies have either reported that growth rates of fishes from particular stocks are not correlated with population density, or are less correlated with density than with density-independent factors such as water temperature. In this paper we explore a long term data set to determine the relative influence of stock abundance and of bottom-water temperature upon growth of the yellowtail flounder (*Limanda ferruginea*) and haddock (*Melanogrammus aeglefinus*) in the Georges Bank region of the Northwest Atlantic.

Analyses addressing the effect of population density upon body growth have been conducted since the first half of this century. Early experimental work such as that by Swingle and Smith (1942) established that growth rate was inversely correlated with density when growth-related environmental variables were held constant. Increased body growth within natural populations has been measured after abundance has undergone precipitous decline due to exploitation (Hile 1936; Beckman 1948; LeCren 1958; Parsons 1967; Shepherd and Grimes 1983). Some studies, such as Iles (1968), Pitt (1975), and Peterman (1984), have demonstrated that sequential changes in growth rates are significantly inversely correlated with changes in stock size, whereas others have not (Van Oosten and Hile 1949; LeCren 1958; Forney 1977; Kempinger and Carline 1977; Willemsen 1977; Akenhead et al. 1982; Carl 1983). Bowering (1989) reported an inverse relationship between mean size at age and the number of age classes in a witch flounder (*Glyptocephalus cynoglossus*) stock; he postulated that the number of age classes was proportional to stock density, thus growth was density-dependent. Carlander and Payne (1977) found that substantially greater variability in growth of walleye (*Stizostedion vitreum*) was explained by fluctuations in water level (62%) than by stock density (17%). An earlier study of the same population (Carlander and Whitney 1961) demonstrated that growth was significantly correlated with water temperature. Kreuz et al. (1982) found that annual fluctuations in growth increments for Dover sole (*Microstomus pacificus*) and English sole (*Parophrys vetulus*) were negatively correlated with water temperatures, but were not correlated with changes in stock abundance. Bromley (1989) found that North Sea populations of cod, haddock, and whiting (*Merlangius merlangus*) displayed growth rates that differed among the regions from which samples were derived, but he did not find any correlation between density and growth for these species within any particular region of his study.

Growth has been shown to be density-dependent for juvenile but not adult English sole (Peterman and Bradford 1987), North Sea haddock (Jones 1983), Atlantic menhaden (*Brevoortia tyrannus*) (Reish et al. 1985), and Atlantic herring (*Clupea harengus*) (Lett and Kohler 1976; Hubold 1978; Haist and Stocker 1985). However, water temperature explained more variability in growth of juveniles than did stock density in Peterman and Bradford's (1987) study, and similar variability to that explained by stock density in Haist and Stocker's (1985) study. Moores and Winters (1982) found that juvenile growth was related to environmental conditions but not to stock density in Atlantic herring off Newfoundland.

The results of studies investigating the relationship between density and growth have been so uneven that authors of review literature have variously concluded that:

- 1) growth is more clearly density dependent than any other characteristic of fish populations (Beverton and Holt 1957),
- 2) density is not "generally and systematically related to growth" (Weatherley 1972), and
- 3) density-dependent growth occurs regularly in natural populations, but lack of precision in measuring growth and abundance masks the relationship (Backiel and LeCren 1967).

Anthony and Fogarty (1985) found that growth of the Atlantic herring was density-dependent during time periods when stock size was relatively high. However, during periods when stock abundance was low, growth was density dependent, being significantly correlated with water temperature. Ross and Almeida (1986) similarly found that growth of the silver hake (*Merluccius bilinearis*) in the Gulf of Maine was density-dependent only during time periods when stock size was high. Ross and Almeida (1986) proposed that the inconsistent results in the literature concerning the importance of stock size to growth may be due to the condition of the stocks studied, rather than to differences among species in the sensitivity of growth to population density. They suggested that stocks depleted by exploitation should not be expected to display density-dependent growth, because intraspecific competition arguably should be limited under such conditions. The studies of Anthony and Fogarty (1985) and Ross and Almeida (1986) indicate that density might be the major factor affecting rates of body growth in stocks experiencing periods of high abundance, whereas density-dependent factors such as water temperature become important when abundance is low.

In this paper, we explore a long-term time series of growth data for yellowtail flounder and haddock in the Georges Bank region in order to test whether:

- 1) growth is generally correlated with stock abundance,
- 2) growth is more clearly density-dependent in the juvenile life stage than in the adult, and
- 3) growth is more highly correlated with density during periods of high stock abundance, and with bottom-water temperatures during periods of low stock abundance.

### Methods

Data were obtained from autumn groundfish surveys conducted by the Northeast Fisheries Science Center of the National Marine Fisheries Service. Groundfish surveys employ a stratified random sampling design using standardized gear and procedures (Grosslein 1969; Azarovitz 1981). Data were taken from the Georges Bank region (survey strata 13 to 25). Specific data sets included annual mean lengths at age (cm) for age-2 and -3 fish, mean weights per tow which represented an index of mean stock biomass or abundance (Figure 1), and mean bottom-water temperatures. Mean lengths at age were calculated by applying age-length keys generated by aging subsamples from each year's survey cruises to length-frequency data compiled from all fish collected on the same year's cruises. Data sets included the years from 1964 to 1980 for yellowtail flounder and 1963 to 1980 for haddock. For both species the start of the time series represents the first year that fish were aged by the Northeast Fisheries Science Center. The final year of the time series was selected because of a change in aging protocol at the Center for yellowtail flounder in 1980. Also, due to the consistently high exploitation rates of the last several decades (Clark et al. 1982), the data sets for both species included only a few years of high relative stock abundance (Figure 1). Additional years of data after 1980 would only have biased data sets more strongly toward periods of low stock abundance.

In order to test whether growth is generally related to stock abundance or bottom-water temperatures, we first regressed growth increments on mean stock biomass indices and mean bottom-water temperatures from calendar years when the growth increments occurred. Growth increments were calculated by subtracting length at age-1 from age-2, and -2 from -3, for each year class in the data sets. No significant correlations were found in these analyses, possibly because the variances of the age-length keys used to calculate mean lengths were large in comparison to the calculated growth increments. In a

few instances, increments were represented by negative values. Negative values could result from measurement imprecision, or less likely from active fisheries that remove faster growing 2-year olds from the stock. Thus, we used length at age as the measure of growth for all analyses, because length represents accumulated growth that has occurred over the lifespan of the fish prior to capture.

We conducted stepwise linear regression analyses of mean length of age-2 and age-3 fish on mean stock biomass indices and mean bottom-water temperatures. Older ages were not considered due to the increasingly confounding effects that size-specific mortality and other factors might have upon the size distribution of older age groups. If growth was correlated with either population density or bottom-water temperatures, mean sizes attained at particular ages would be a result of stock biomass or temperature regimes to which the fish were exposed during time periods before they were captured and measured. Mean length-at-age data were compared to two forms of population biomass and temperature data. In the first set of analyses, mean lengths of age-2 and age-3 fish were regressed on mean catch per tow indices and mean temperatures taken at the time the fish were captured, as well as on measures of the same variables taken 12 and 24 months before the fish were captured. Use of these time intervals allowed us to investigate whether growth was more clearly density dependent in juvenile than in young adult life stages. Stock biomass as measured by mean weight per tow was chosen as the measure of stock abundance because it is a better measure of intraspecific competitive pressure than is numerical abundance. If food is a limiting factor, available food resources support growth in some specific biomass, rather than any particular number, of fish in a stock.

We also compared mean lengths of fish to 12-month means of population biomass and bottom-water temperature. If growth is responsive either to stock biomass or temperature, the relationship might be better clarified by comparing length at age to time periods before capture, rather than points in time before capture. Running 12-month means may also have the effect of smoothing data, potentially reducing the impact that specific variable values with high variances might have upon the correlation between dependent and independent variables. Thus, mean lengths of age-2 fish were regressed on mean stock biomass indices and mean temperatures from time periods of 0 to 12 months, and 12 to 24 months, before capture. We compared mean length of 3-year-old fish to these time periods and to that from 24 to 36 months before capture. Mean biomass indices and temperatures were calculated by averaging the mean values recorded during consecutive autumn survey cruises, since data sets for all parameters were limited to measurements made during these cruises.

To test whether growth was more highly correlated with stock abundance during high periods of population abundance, and with temperature during low periods, data for each species and age group were stratified into periods of relatively high and relatively low stock abundance, keeping a similar number of observations in each strata. We applied stepwise linear regression analyses to the data. When applying regression to all years of data, we found that mean biomass for one particular time period before capture was significant for each species-age group tested. Subsequent separating of data sets into calendar years based upon high or low values of biomass from any particular time period did not always separate values of biomass from other time periods properly into the same high or low subsets. Thus, in all analyses that separated periods of high abundance from those of low, all biomass values representing specific time periods other than those displaying significance when comparing all years data were eliminated from the data subset for that species-age group. For example, when using 12-month means for independent variables, values representing biomass 12 to 24 months before capture were the only population abundance indices used, since this was the only biomass variable displaying

significant correlation with length at age when using full data sets for each species-age group. All temperature values were used in each subset analyses.

The Durbin-Watson test (Chatterjee and Price 1977; Draper and Smith 1981), which tests whether least square residuals are randomly distributed along the calculated regression line or display first order autocorrelation, was included in all regression analyses. When autocorrelation occurs, a linear model is not adequate to fully test the relationship between dependent and independent variables. Confidence intervals and tests of significance cannot be considered strictly valid (Chatterjee and Price 1977). We also examined residuals for the presence of heteroscedasticity (unequal variance errors). If present, unequal error variance can reduce the precision of the least square estimates (Chatterjee and Price 1977).

We analyzed all data sets with the Spearman rank correlation statistic. Only the independent variables that displayed significant correlation in regression analyses were used in the Spearman tests for each species-age group.

### Results

When all years of data were included in analyses, mean length at age was significantly correlated with stock abundance for all species-age combinations ( $P < 0.05$ ; Tables 1 and 2). When regressing length at age on specific time periods previous to capture, biomass indices taken 24 months (B-2) and 12 months (B-1) before capture accounted for the greatest amount of variability in length at age for yellowtail and haddock, respectively (Table 1). B-1 and B-0 were also significantly inversely correlated with length at age for age-2 yellowtail and age-3 haddock, respectively ( $P < 0.05$ ; Table 1). When regressing length at age on 12-month averages for biomass and temperature, mean biomass taken 12 to 24 months before capture (B12) accounted for the greatest variability in length at age for both species (Table 2). Mean temperature 12 months (T-1) before capture and the average of 0 to 12 months (T01) before capture were significant for age-3 haddock (Table 1) and age-2 yellowtail (Table 2), respectively, but accounted for less variability in length at age than did stock abundance in both instances. Because B23 and T23 were not significant for age-3 fish of either species, we eliminated these variables from the data sets and ran the regression analyses for that age group again (Table 2). This allowed one additional calendar year to be included in the data set for 3-year olds of each species (1965 for the haddock and 1966 for the yellowtail). Consistent declines in stock abundance occurred for both species from the mid-1960s onward (Figure 1); thus, this adjustment increased the already limited number of mean lengths taken during time periods of high stock abundance. We modified the data set in this manner to test whether adding one length measure from a time of high stock abundance would modify the fit of the regression, because other workers have postulated that growth should be most clearly density-dependent during periods when population abundance is high (see Ross and Almeida 1986). The amount of variability in mean length for age-3 fish that was explained by stock abundance increased somewhat for both species with the addition of this one year's data (Table 2).

When we used data subsets representing time periods of high stock abundance, stepwise regression analyses revealed that length was significantly inversely correlated with stock abundance (B-2 for yellowtail, B-1 for haddock, and B12 for both species when using 12-month averages,  $P < 0.05$ ; Tables 1 and 2). Length was significantly positively correlated with temperature for age-3 yellowtail and age-2 haddock (T-0 and T01, respectively). Temperature explained less variability in length than did stock biomass in both instances.

When we used data subsets representing periods of low population abundance, length was significantly correlated with temperature using either bottom water temperature values from specific time periods or 12-month means for all species-age groups (Tables 1 and 2). Length was significantly correlated with biomass during time periods of low stock abundance when using 12-month averages for age-2 and -3 yellowtail (B12; Table 2). Greater variability in length at age was explained by variability in stock abundance than by temperature for both age-2 and age-3 yellowtail within this data subset. The variability in length that was explained by variation in B12 was higher for age-2 yellowtail during periods of high stock abundance than during periods of low stock abundance ( $r^2$  of 0.75 and 0.55, respectively).

A higher percentage of the variability of mean length at age was explained more frequently by regression analyses for age-2 than for age-3 fish. Of the four instances in which the coefficient of determination ( $r^2$ ) was higher for age-3 than age-2 fish, three were from data subsets representing periods of low stock abundance, and temperature was the independent variable responsible for the higher  $r^2$  value. The use of 12-month average values did not consistently improve the variability of mean length explained by independent variables. In all regressions, the sign of the slope for biomass was negative, supporting the density-dependent relationship.

Based upon Durbin-Watson tests, the null hypothesis that  $\rho_s = 0$  ( $P < 0.05$ ) was rejected for 4 of 10 regression analyses using entire data sets, indicating the presence of first order autocorrelation for these regressions. Interpretation of the Durbin-Watson statistic for data subsets representing time periods of high or low stock abundance was difficult. Tables representing bounds of significance for the Durbin-Watson statistic do not include values for sample sizes as small as these data subsets (Durbin and Watson 1951; Draper and Smith 1981). Further, calculations of exact bounds provide only rough approximations when sample sizes are small; substantial information is lost in such instances (Durbin and Watson 1951). Although extrapolation from tables provided only limited indication for these regressions, the Durbin-Watson statistic appeared to fall well within the bounds indicating the absence of autocorrelation for most data subsets. Those that appear to be problematical are marked on Tables 1 and 2 as indicating the presence of autocorrelation. First order autocorrelation did not appear to exist in the majority of complete data sets and subsets.

Heteroscedasticity was found in several data sets. Error variance tended to be greater at lower densities than at higher ones in regressions that included all years of data. Transformation of data is frequently used to reduce or eliminate heteroscedasticity (Chatterjee and Price 1977). However, the greater error variance associated with length measures taken during time periods of low stock abundance supports one of the hypotheses examined in this study, namely, that density will have less influence on body growth during periods of low than of high stock density. Although transformations of Y values may improve the precision of the least squares analysis, the biological associations examined would not be better clarified. Thus, we applied the non-parametric Spearman rank sum test (Mendenhall and Scheaffer 1973) to all data sets. This test, generally considered less robust than regression analysis, is independent of assumptions mandated by least squares analysis.

Lengths-at-age for all species-age groups were significantly inversely correlated with stock abundance and positively correlated with bottom water temperature, based upon Spearman rank correlation analyses of all years of data ( $P < 0.05$ ; Tables 3 and 4). The rank correlation coefficient ( $r_s$ ) was higher for biomass than for temperature for all

species-age groups. Length was significantly inversely correlated to biomass for all species-age groups during time periods when stock biomass was high (either B12 as a 12-month average value, or B1 and B2 for stock abundance indices at specific times before capture; Tables 3 and 4), but was significant only for age-3 yellowtail (B12; Table 4) when stock biomass was low. Length was significantly directly correlated with temperature for age-2 and -3 haddock and age-2 yellowtail during time periods of low stock abundance (Table 3; temperature was not significant for any species-age group during low biomass time periods when temperature values represented 12-month means).

### Discussion

Stock abundance clearly influenced growth rates of yellowtail flounder and haddock. Higher correlations occurred during time periods of highest stock abundance than at times when stocks were depleted. These results agree with analyses presented for Atlantic herring (Anthony and Fogarty 1985) and silver hake (Ross and Almeida 1986), and support the largely untested hypothesis discussed by Ross and Almeida (1986) that growth should be most density dependent during times when population density, thus intraspecific competition, is greatest. This relationship appears applicable to a variety of Northwest Atlantic species.

Length was not significantly correlated with stock abundance from the same period of the life cycle for age-2 and -3 fish. Assuming hatching in winter to early spring for both species, B12 represents the time period between 0.5 and 1.5 years of age for the 2-year-old fish in this study (in reality 2.5 years of age at autumn capture), and between 1.5 and 2.5 years of age for the 3-year olds (3.5 years at autumn capture). Similar relationships exist in data sets using data from time periods rather than 12-month means. Perhaps length was not significantly correlated with time periods as early in life for age-3 fish as for age-2, because confounding natural influences and characteristics of the fisheries may tend to mask correlations between growth and density established early in the life cycle once substantial time has passed.

Fifty percent maturity is achieved at age-2 for both of these species (Northeast Fisheries Center 1990). Thus, length appears to be most highly influenced by stock abundance to which fish are exposed while still juveniles. This agrees with analyses of haddock, English sole, Atlantic menhaden, and Atlantic herring (Lett and Kohler 1976; Hubold 1978; Jones 1983; Haist and Stocker 1985; Reish et al. 1985; Peterman and Bradford 1987). Such results may be biologically driven, an artifact of measurement precision, or a result of harvest by associated fisheries. Growth may be most highly influenced by stock abundance when individuals are experiencing the time period of greatest growth potential as juveniles (Weatherley 1972). Once a fish reaches sexual maturity, substantial energy is diverted toward reproduction and growth slows markedly. At this time, stock abundance may have less influence on growth rates, or lack of precision of measurement may not allow subtle differences in growth of adult fish created by changes in stock size to be identified (as per Backiel and LeCren 1967). Once individuals are recruited to a fishery, intraspecific competition may be markedly reduced for older fish due to reduction in abundance caused by harvest. However, this effect assumes that prerecruit juvenile and postrecruit adult fish eat different foods, thus are not competing with each other for available food resources. This condition should not apply to this study, because major dietary shifts between juvenile and young adult stages are not characteristic of yellowtail flounder or haddock (Bowman and Michaels 1984), and biomass indices for the total stock, not for cohorts, were used in our analyses.

Temperature influenced growth of the species studied, although it was not significant for all species-age combinations, nor did it consistently explain as much or more

variability in size at age than did stock biomass, even during low density time periods. The stock sizes of both species declined markedly within the time periods covered by this study (Clark and Brown 1977; Clark et al. 1982; O'Brien and Mayo 1988), providing opportunity to test whether temperature influences growth when stock abundance is low. Measurement precision probably is not masking any relationship between temperature and growth, because the coefficients of variation (CV) for mean temperatures are markedly lower than those for stock abundance, the independent variable to which growth was most highly correlated (Table 5). Annual temperature fluctuations of the magnitude examined in this study apparently exerted only modest influence upon individual growth rates of these species in the Georges Bank region.

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Table 1. Results of regression analyses comparing the length at age of yellowtail flounder and haddock with measures of stock biomass (mean catch per tow) and bottom water temperature from time periods before capture. Samples are separated into fishes captured during time periods of high population biomass, low population biomass, and all years of the study.

[illegible]

Table 1. Continued

Species and age	Relative biomass	Number	Step 1 <sup>a</sup>			Step 2			Step 3			Intercept	Durbin-Watson statistic
			Variable entered	Regression coefficient	Partial $r^2$	Variable entered	Regression coefficient	Partial $r^2$	Variable entered	Regression coefficient	Partial $r^2$		
2	low years	8	T-0	1.106	0.40							36.167	2.27
3	all years	15	B-1	-0.225	0.68	T-1	1.021	0.77	B-0	0.127	0.84	44.535	2.49 <sup>b</sup>
3	high years	8	B-1	-0.168	0.58							55.413	1.95
3	low years	9	T-1	1.446	0.70							40.044	2.59

<sup>a</sup> All regression analyses  $P < 0.05$ . Independent variables used in regression analyses when considering all years of data were: B-0, B-1, B-2 = mean catch per tow in kg in year of capture, 1 and 2 years prior to capture, respectively; T-0, T-1, T-2 = mean bottom water temperatures for the same time periods. Independent variables used in analyses focusing upon periods of either high or low population density included the biomass variable shown to be most highly correlated for each species/age group when considering all data, and all temperature variables displaying significant correlation when considering all data.

<sup>b</sup>  $d < d_U$  at  $P < 0.05$ ; autocorrelation exists. Autocorrelation absent from other data sets.

<sup>c</sup> Small sample size prevented direct comparison to significance bounds for Durbin-Watson statistic. Value suggests autocorrelation.

Table 2. Results of regression analyses comparing the length at age of yellowtail flounder and haddock with the 12-month means of population biomass and bottom water temperature from time intervals before capture. Samples are separated into fishes captured during time periods of high population biomass, low population biomass, and all years of the study.

Species and age	Relative biomass	Number of years	Variables tested <sup>a</sup>	Step 1			Step 2			Intercept	Durbin- Watson statistic
				Variable entered	Regression coefficient	Partial R <sup>2</sup>	Variable entered	Regression coefficient	Partial R <sup>2</sup>		
Yellowtail											
2	all years	15	B01,B12, T01,T12	B12	-1.398	0.76	T01	-0.629	0.82	44.100	1.70
2	high years	8	B12,T01,T12	B12	-1.524	0.75				38.808	1.93
2	low years	8	B12,T01,T12	B12	-0.768	0.55				35.575	1.66
3	all years	14	B01,B12,B23 T01,T12,T23	B12	-0.758	0.45				39.478	2.31
3	all years	15	B01,B12 T01,T12	B12	-0.810	0.58				39.624	2.29
3	high years	8	B12,T01,T12	B12	-0.819	0.49				39.886	3.12 <sup>b c</sup>
3	low years	8	B12,T01,T12	B12	-3.052	0.54	T01	-1.708	0.89	63.368	1.80
Haddock											
2	all years	14	B01,B12 T01,T12	B12	-0.167	0.74				49.403	2.71 <sup>c</sup>
2	high years	7	B12,T01,T12	B12	-0.194	0.86	T01	-0.953	0.94	59.670	2.07
2	low years	6	B12,T01,T12	none							
2	low years	7	B12,T01,T12	none							
2	low years	8	B12,T01,T12	none							
3	all years	14	B01,B12,B23 T01,T12,T23	B12	-0.182	0.62				56.163	1.88
		15	B01,B12 T01,T12	B12	-0.190	0.73				56.261	1.86
3	high years	7	B12,T01,T12	B12	-0.176	0.71				55.473	2.22
3	low years	8	B12,T01,T12	T01	1.279	0.43				41.511	2.43

<sup>a</sup> B01 and T01 = the average of biomass indices (mean catch per tow; B) and bottom water temperatures (T) taken at capture and 12 months before capture; B12 and T12 = the average of biomass indices and temperatures taken 12 and 24 months before capture; B23 and T23 = the average from 24 and 36 months before capture.

<sup>b</sup>  $P < 0.06$ ; all other regression analyses  $P < 0.05$ .

<sup>c</sup>  $d < d_u$  at  $P < 0.05$ ; autocorrelation exists. Autocorrelation absent from other data sets.

Table 3. Spearman rank correlation statistics for length at age of yellowtail flounder and haddock compared to measures of population biomass and bottom water temperature during high and low population biomass time periods, and all periods combined. Measures of biomass and temperature are taken from specific time periods before capture of the fish.

Species	Age	Relative biomass	Number of years	Independent variable <sup>a</sup>	Rank correlation coefficient ( $r_s$ )
yellowtail	2	all years	15	B-2	- 0.764* <sup>b</sup>
			17	T-0	0.567*
			15	T-2	0.682*
	3	all years	16	B-1	- 0.552*
			15	B-2	- 0.809*
			17	T-0	0.325
	2	high years	15	T-2	0.550*
			8	B-2	- 0.429
			8	T-0	0.167
	3	high years	8	T-2	0.333
			8	B-2	- 0.455
			8	T-0	- 0.180
	2	low years	8	T-2	- 0.060
			7	B-2	- 0.643
			7	T-0	0.286
	3	low years	7	T-2	0.750*
			7	B-2	- 0.595
			7	T-0	- 0.036
	2	all years	7	T-2	0.288
			15	B-1	- 0.743*
			16	T-0	0.662*
haddock	3	all years	15	T-1	0.079
			16	B-1	- 0.685*
			17	T-0	0.592*
	2	high years	16	T-1	0.542*
			8	B-1	- 0.762*
			8	T-0	0.429
	3	high years	8	T-1	0.190
			8	B-1	- 0.690*
			8	T-0	0.548
	2	low years	8	T-1	0.405
			9	B-1	- 0.417
			9	T-0	0.617*
	3	low years	9	T-1	0.133
			9	B-1	- 0.517
			9	T-0	0.500
	2	all years	9	T-1	0.700*

<sup>a</sup> B-0 and T-0 = mean catch per tow and bottom water temperature at the time of capture; B-1 and T-1 = mean catch per tow and bottom water temperature 12 months prior to capture; B-2 and T-2 = 24 months prior to capture.

<sup>b</sup> asterisk signifies  $P < 0.05$  (significance levels from Mendenhall and Scheaffer 1973).

Table 4. Spearman rank correlation statistics for length at age of yellowtail flounder and haddock compared to 12-month means of population biomass and bottom water temperature during high and low population density time periods, and all periods combined. Measures of biomass and temperature represent 12-month means of time intervals before capture.

Species	age	relative biomass	number of years	independent variable <sup>a</sup>	Rank correlation coefficient ( $r_s$ )
Yellowtail	2	all years	15	B12	-0.832 * <sup>b</sup>
				T01	0.531 *
	3	all years	15	B12	-0.786 *
				T01	0.486 *
	2	high	8	B12	-0.714 *
				T01	-0.119
	3	high	8	B12	-0.667 *
				T01	-0.357
	2	low	8	B12	-0.548
				T01	0.357
	3	low	8	B12	-0.833 *
				T01	0.619
haddock	2	all years	14	B12	-0.679 *
				T01	0.238
	3	all years	15	B12	-0.746 *
				T01	0.550 *
	2	high	8	B12	-0.786 *
				T01	0.036
	3	high	7	B12	-0.714 *
				T01	0.214
	2	low	8	B12	-0.286
				T01	-0.132
	3	low	8	B12	-0.048
				T01	0.524

<sup>a</sup> B12 = mean catch per tow from 12 and 24 months before capture; T01 = mean bottom water temperature from 0 to 12 months before capture.

<sup>b</sup> asterisk signifies  $P < 0.05$  (Significance levels from Mendenhall and Scheaffer 1973).

Table 5. Means and coefficients of variation (CV) for catch per tow (kg) of yellowtail flounder and haddock, and for bottom water temperature ( $0^{\circ}$  C) from Northeast Fisheries Science Center survey strata 13 to 25. CV = (standard deviation / mean) (100).

Year	haddock		yellowtail flounder		temperature	
	mean	CV	mean	CV	mean	CV
1963	51.29	21.4	8.16	18.9	8.06	1.8
1964	75.15	19.4	8.43	39.2	8.12	2.4
1965	56.08	16.4	5.61	32.0	9.92	2.3
1966	21.42	21.1	2.44	32.5	8.78	2.6
1967	19.99	23.1	4.41	27.0	7.47	3.1
1968	9.32	35.1	6.69	22.8	10.07	2.9
1969	5.76	32.1	5.45	25.9	8.06	6.3
1970	10.62	39.3	3.05	28.3	9.53	3.5
1971	3.65	34.1	3.68	20.7	10.82	3.5
1972	5.11	20.4	4.03	26.4	10.31	2.9
1973	7.17	30.0	3.83	30.1	11.30	2.8
1974	2.79	28.4	2.23	18.6	11.35	1.5
1975	2.60	21.7	1.39	16.1	10.42	1.3
1976	27.55	46.4	1.17	20.9	12.50	1.2
1977	23.78	39.8	3.16	21.1	11.31	1.1
1978	11.83	23.3	1.90	17.0	10.15	1.5
1979	25.21	59.7	1.39	21.3	11.47	0.9
1980	11.91	33.4	4.97	19.6	11.27	2.6



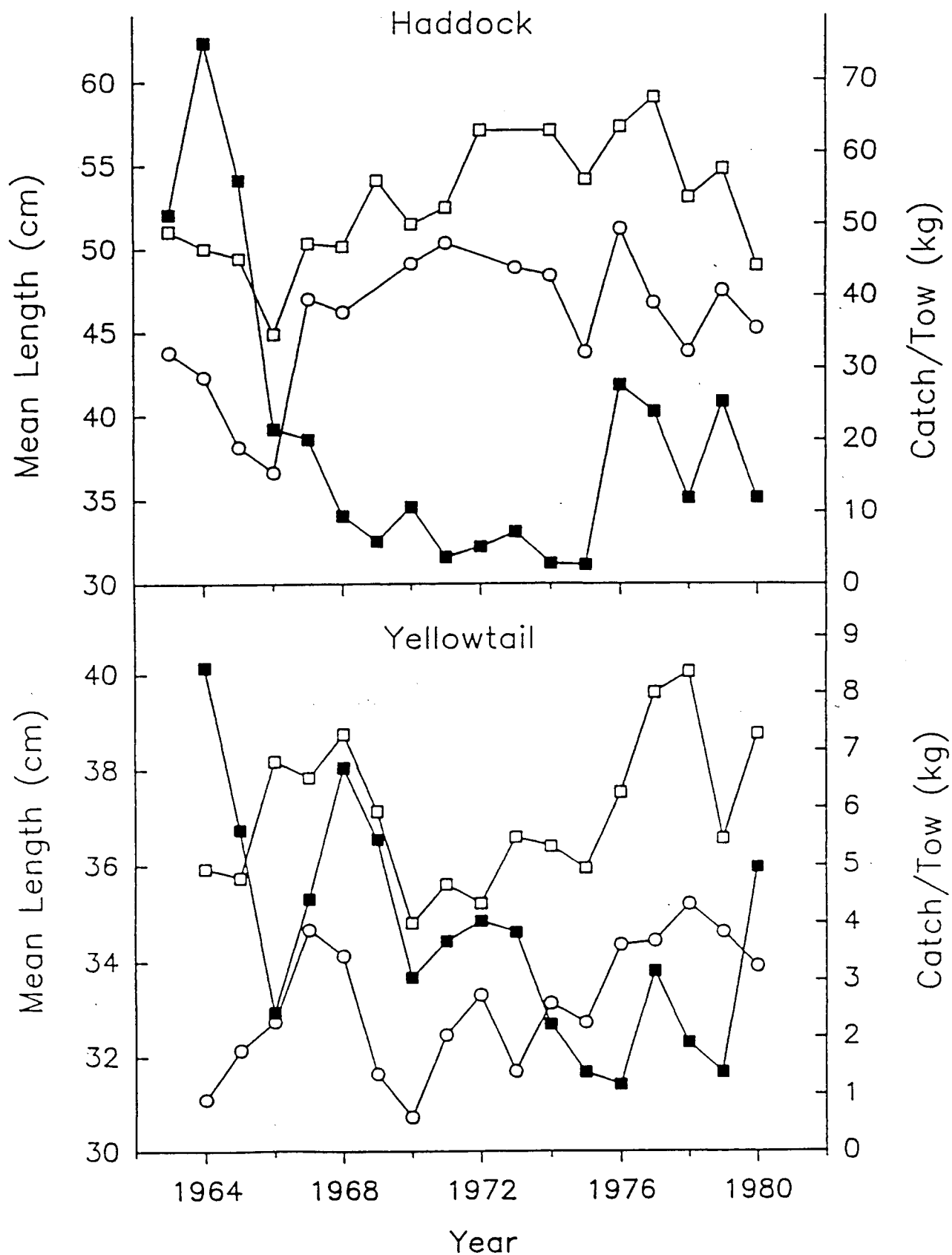


Figure 1. Measures of length at age and catch per tow for the haddock and yellowtail flounder on Georges Bank, 1963 to 1980. Samples were collected by the Northeast Fisheries Science Center groundfish survey cruises. Open circles = length at age for age-2 fish; open squares = age-3 fish; filled squares = catch per tow.