Implications of density-dependent juvenile growth for compensatory recruitment regulation of haddock

C. Tara Marshall and Kenneth T. Frank

Abstract: Data from bottom trawl surveys conducted by Canada and the United States were used to describe temporal trends in the length of haddock ages 1–4 on the southwestern Scotian Shelf (SWSS) and Bay of Fundy. From 1970 to 1995, the length of juvenile (age-1) haddock on the SWSS was negatively correlated with the abundance of adults (age-4+). Within year-classes temporal trends in juvenile length persisted through to the adult stage such that year-classes that were small(large) at age-1 were small(large) at age-4. These two results were combined with the positive correlation observed between recruitment and the body size characteristics of haddock on the SWSS in a conceptual model of compensatory recruitment regulation. In the model high adult abundance decreases growth of juveniles leading to smaller-sized adults and subsequently lower recruitment. Conversely, low adult abundance results in increased growth of juveniles leading to larger adults and higher recruitment. Density-dependent growth of juveniles, combined with the positive correlation between recruitment and adult body size, constitutes a compensatory mechanism for adjusting future haddock recruitment according to present adult abundance.

Résumé : On a utilisé les données de campagnes d'échantillonnage au chalut de fond réalisées par le Canada et les États-Unis pour décrire les tendances temporelles des longueurs de l'aiglefin de 1 à 4 ans dans le sud-ouest de la plate-forme néo-écossaise et la baie de Fundy. De 1970 à 1995, la longueur de l'aiglefin juvénile (âge 1) dans le sud-ouest de la plate-forme néo-écossaise était corrélée négativement avec l'abondance des adultes (âges 4+). Les tendances temporelles de la longueur des juvéniles à l'intérieur des classes d'âge ont persisté jusqu'à l'âge adulte en ceci que les poissons qui étaient petits (ou gros) à l'âge 1 étaient petits (ou gros) à l'âge 4. Ces deux résultats ont été combinés avec la corrélation positive observée entre le recrutement et les caractéristiques de taille de l'aiglefin dans le sud-ouest de la plate-forme néo-écossaise dans un modèle conceptuel de régulation compensatoire du recrutement. Selon ce modèle, une forte abondance des adultes entraîne une baisse de la croissance des juvéniles, qui deviendront des adultes de plus petite taille, d'où un recrutement subséquent réduit. Inversement, une faible abondance d'adultes augmente la croissance des juvéniles, qui deviendront des adultes de plus grande taille, d'où un recrutement subséquent accru. Le fait que le taux de croissance des juvéniles dépend de la densité, combiné avec la corrélation positive entre le recrutement et la taille des adultes, constitue un mécanisme compensatoire qui ajuste le recrutement futur des aiglefins à l'abondance présente des adultes.

[Traduit par la Rédaction]

Introduction

Investigations into the density-dependent responses of haddock (*Melanogrammus aeglefinus*) stocks have a long history. Herrington (1944) proposed that when adult haddock on Georges Bank were abundant they depleted available food resources (the macrobenthos) and then moved on to other feeding grounds, leaving the more sedentary juveniles to experience food limitations, which increased their mortal-

C.T. Marshall.[1] Department of Oceanography, Dalhousie University, Halifax, NS B3H 4J1, Canada.
K.T. Frank. Marine Fish Division, Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.

[1]Author to whom all correspondence should be addressed.
 Present address: Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway.
 e-mail: tara.marshall@imr.no

ity. Herrington suggested that the competitive interaction between juvenile and adult haddock resulted in recruitment being highest for intermediate levels of stock abundance (fig. 5 in Herrington 1944). His analysis was one of several examples used by Ricker (1954) in formulating the dome-shaped relationship between recruitment and spawner abundance. Increased competition between juveniles and adults for a shared food resource could also decrease the growth of juveniles. While density-dependent growth has been observed in a majority of studies on haddock growth (Table 1), few of these studies specifically examined the relationship between juvenile growth rate and adult abundance.

The growing appreciation of maternal effects on the recruitment dynamics of gadoid stocks (Marteinsdottir and Thorarinsson 1998; Marshall et al. 1998) introduces new possibilities for linking density-dependent responses to recruitment. The companion paper (Marshall and Frank 1999) found that recruitment to age-1 is positively correlated with length and (or) condition of spawning haddock on the southwestern Scotian Shelf portion of NAFO Division 4X. This correlation focuses attention on identifying the factors that

Table 1. Summary of studies investigating the relationship between stock abundance and growth of haddock.

Year	Time period	Correlation	Reference
North Sea	1923–1931	None	Bowman 1932
North Sea	1919–1934	Negative	Raitt 1936
Skagerak	1929,1938	Negative	Andersson 1938
North Sea	1919–1938	Negative	Raitt 1939
Georges Bank	1912–1946	Negative	Herrington 1948
Barents Sea	1945–1959	Negative	Sonina 1965
Grand Bank	1940–1975	Negative	Templeman et al. 1978
North Sea	1923–1972	Negative	Jones 1979
St. Pierre Bank	1948–1975	Negative	Templeman and Bishop 1979
Browns Bank	1970–1979	Negative	Beacham 1982
Georges Bank	1930–1980	Negative	Clark et al. 1982
North Sea	1959–1971	Negative	Jones 1983
North Sea	1960–1980	Negative	Cook and Armstrong 1984
North Sea	1977–1985	None	Bromley 1989
Georges Bank	1963–1980	Negative	Ross and Nelson 1992

generate differences in body size characteristics of adults among year-classes. The degree to which size differences observed at the juvenile stage persist through to the adult stage is of interest for the following reason: a negative correlation between stock abundance and juvenile growth that persists through to the adult stage combined with a positive correlation between adult body size and recruitment constitutes a compensatory mechanism for regulating recruitment.

Over the past 3 decades, the abundance of adult haddock in NAFO Division 4X (see fig. 2 in Marshall and Frank (1999) for map) shows two distinct peaks (Fig. 1). The first peak was fueled by the exceptionally strong 1962 and 1963 year-classes, whereas the second peak from 1979 to 1986 reflects a sustained period of good recruitment in the 1970s and early 1980s (fig. 1B in Marshall and Frank (1999) gives the recruitment time series). The effect of adult abundance on juvenile growth specifically is unknown. Data from research vessel surveys conducted by Canada and the United States were used to address the following questions: (*i*) what is the pattern of temporal variation in juvenile body size, (*ii*) how has the growth of juveniles responded to changes in adult abundance, and (*iii*) do differences among year-classes in juvenile body size persist through to the adult stage such that small juveniles become small adults? The effect of interannual variation in bottom water temperature on juvenile growth was also evaluated. The results were combined with the relationship between recruitment and the body size characteristics of adults (Marshall and Frank 1999) in a conceptual model describing a possible form of compensatory recruitment regulation in Scotian Shelf haddock.

Methods

The data sources used to describe temporal variation in body size characteristics of juvenile haddock in Division 4X were the summer (1970–1995) and fall (1963–1986) surveys conducted by Canada (CDN) and the United States (US), respectively. Temporal and spatial coverage of these surveys are described in Marshall and Frank (1999). Because haddock in the Bay of Fundy are larger than haddock on the southwestern Scotian Shelf (fig. 4 in Marshall and Frank (1999)), the survey database was partitioned into two distinct geographic regions: the southwestern Scotian Shelf

(SWSS) and Bay of Fundy (BofF). For the CDN surveys, data from strata 70–81 were used to represent the SWSS and data from strata 85, 90, 91, and 95 were used to represent the BofF (fig. 2A in Marshall and Frank (1999)). For the US surveys, data from strata 31, 32, 41, 42, and 49 were used to represent the SWSS and data from strata 33, 34, and 35 were used to represent the BofF (fig. 2B in Marshall and Frank (1999)).

Mean length at age was used as an index of growth for haddock age-1 to age-4. For the CDN surveys, the catch-weighted mean length at age was estimated by weighting the length observations for the length frequency distribution of the trawl catches. Mean length at age for the US surveys was calculated as the arithmetic average of all of the length observations for a given age class in strata in that region (either SWSS or BofF). Correlations between the CDN and US values for the overlapping time period (1970–1986) were examined to determine if temporal trends in the unweighted US estimates of mean length at age agreed with the catch-weighted CDN estimates. The p values reported were corrected for temporal autocorrelation (p^*) using eq. 2 in Marshall and Frank (1999). There were significant ($p^* \leq 0.05$) positive correlations between CDN and US mean lengths for all four age classes on the SWSS and for haddock age-2 to age-4 in the BofF (Table 2). The correlation between CDN and US mean length at age-1 for the BofF was not significant ($p^* = 0.42$) even when the outlying observation for 1972 was excluded ($p^* = 0.54$). The weaker correlations for age-1 haddock suggest that size-dependent catchability might be introducing error into estimates of mean length for the smallest fish (Engås and Godø 1989).

The correlation between length at age-1 and adult abundance was examined using the total abundance of haddock age-4 and older as an estimate of adult abundance (Fig. 1). From 1979–1985, the ages at 50% maturity ranged from 2.8 to 3.6 years for female haddock in Division 4X and from 2.8 to 3.3 years for males (Trippel et al. 1997*a*). Thus, the total abundance of haddock age-4 and older approximates the abundance of a fraction of the stock which is >50% mature. Abundance at age for 1970–1995 was estimated using Virtual Population Analysis (VPA) (Hurley et al. 1997). Abundance at age for 1963–1969 was generated using a specialized VPA run (P.C.F. Hurley, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S., Canada).

The influence of temperature on the growth of juvenile haddock was also assessed. Water temperatures, expressed as anomalies from the long-term average (1961–1990), are available by month for 35 subareas of the Scotian Shelf (Drinkwater and Trites 1987).

358

Can. J. Fish. Aquat. Sci. Vol. 56, 1999

Fig. 1. Temporal trends (1863–1995) in total abundance of haddock age-4 and older. Values for 1970 to 1995 were obtained from Hurley et al. (1997), whereas values for 1963 to 1969 were from a specialized VPA run described in Marshall and Frank (1999).
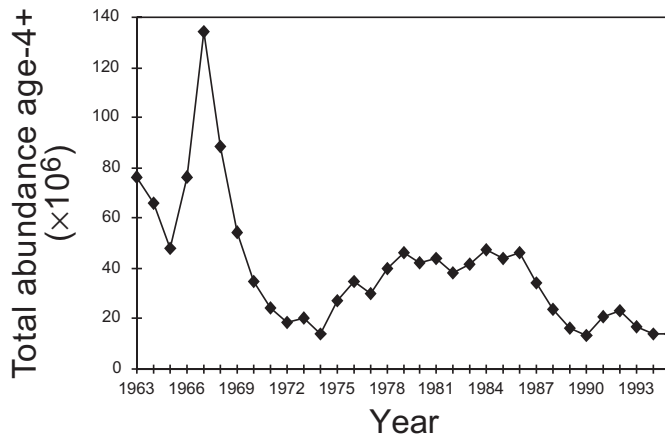
Data for subarea 22 (corresponding to stratum 80) and subarea 24 (corresponding to stratum 85) were used to represent temperatures on the SWSS and BofF, respectively. Temperature anomalies at depths of 100 and 50 m were used for subareas 22 and 24, respectively. Mean temperature anomalies for the CDN survey were calculated by pooling observations for June and July. Observations for October and November were pooled to estimate the mean temperature anomalies at the time of the US survey. There were several years of missing observations for the June–July and October–November time periods.

In the model of compensatory recruitment regulation, only CDN data for the SWSS were used. This was done because (*i*) the correlation between recruitment and mean length at age-4 was significant for the SWSS but not for the BofF (table 2 in Marshall and Frank (1999)) and (*ii*) haddock on the SWSS constitute approximately 75% of the commercial catch of the 4X haddock stock (table 3 in Hurley et al. 1997) and the recruitment dynamics of this component will have the greatest influence on the stock. Cross correlation analysis of the CDN mean length at age time series for the SWSS was used to determine whether temporal trends in length at age-1 persisted as the year-class aged. If there is a year-class effect on growth then peak correlations would occur at appropriate lags (e.g., the peak correlation between length at age-1 and length at age-4 would occur at a 3-year lag). The correlation between length at age-1 and length at age for the three older age classes was determined for six different lags (–1 to 5 years).

A key element of the conceptual model describing compensatory recruitment regulation is the relationship between recruitment to age-1 and mean length at age-4, which was developed for haddock on the SWSS in the companion paper (see fig. 6B in Marshall and Frank (1999)). Given that haddock spawn in the spring, this relationship was developed assuming that mean length at age-4 observed at the time of the CDN summer survey in year t represents the reproductive potential of spawners in year $t + 1$. Therefore, the relationship is between recruitment in year $t + 1$ (i.e., abundance of age-1 haddock in year $t + 2$) and mean length at age-4 in year t.

Results

For the CDN surveys, length at age-1 on the SWSS decreased by approximately 4 cm from the mid-1970s to a minimum in 1981 (Fig. 2A). Length at age-1 then increased such that by the 1990s lengths were comparable with those

Table 2. The coefficient of determination and corrected significance levels ($p*$ in brackets) for correlations between the US mean length at age and CDN length at age for 1970–1986 for the southwestern Scotian Shelf (SWSS) and Bay of Fundy (BofF).

| Age	SWSS	BofF
1	0.24 (0.05)	0.05 (0.42)
2	0.65 (<0.01)	0.54 (<0.01)
3	0.83 (<0.01)	0.25 (0.05)
4	0.79 (<0.01)	0.56 (<0.01)

observed earlier in the time series. The temporal trends observed for haddock age-2 to age-4 on the SWSS from 1970 to 1995 (Figs. 2B–2D) were similar to those for age-1 haddock with minimum lengths occuring in the mid-1980s. The minimum length at age-4 was observed in 1984 (i.e., 3 years after the minimum in length at age-1). Lengths for all four age classes were almost always higher in the BofF (Figs. 2A–2D) compared with the SWSS. Unlike the SWSS, length at age was not at a minimum in the BofF in the 1980s. Length at age-1 for the BofF showed no distinct temporal trend although the observation for 1972 was anomalously low relative to all other values. A slight decrease in length at age was observed during the late 1970s for older haddock in the BofF.

For the US surveys, haddock on the SWSS exhibited minimum length at age values in the 1960s for all four age classes (Fig. 3). From 1963 to 1966, length at age-1 on the SWSS decreased by approximately 6 cm (Fig. 3A) and was at a minimum in 1966 and 1967 when adult abundance was at or near maximum (Fig. 1). A slight decreasing trend in length at age-1 began on the SWSS in the late 1970s and continued through the early 1980s. The lengths for haddock age-2 to age-4 on the SWSS were also low in the mid-1960s, increased from 1967 to 1971, and then began to decrease in the late 1970s or early 1980s (Figs. 3B–3D). Length for haddock age-1 to age-4 in the BofF exhibited low values in the mid-1960s followed by a rapid increase (Figs. 3A–3D). Unlike the SWSS there was no evidence of a decrease in length at age beginning in the late 1970s.

On the SWSS, length at age-1 is negatively correlated with adult abundance ($r^2 = 0.30$, $p* < 0.01$) for the CDN survey such that length at age-1 was low in the late 1970s to mid-1980s when adult abundance was high (Fig. 4A). The correlation between length at age-1 and adult abundance for haddock on the BofF was not significant ($r^2 = 0.03$, $p* = 0.40$) for the CDN survey (Fig. 4B). For the US survey, the results were reversed: the correlation between mean length at age-1 and adult abundance was not significant for the SWSS ($r^2 = 0.07$, $p* = 0.23$, Fig. 4C) but was significant for the BofF ($r^2 = 0.26$, $p* = 0.03$, Fig. 4D).

For the SWSS, mean length at age-1 was uncorrelated with temperature anomalies in both the CDN and US surveys, irrespective of whether temperature was the only variable in a univariate model or the second variable added to a bivariate model that included adult abundance (Table 3). This was also true for the BofF for the time period covered by the CDN survey. For the US survey of the BofF, the temperature anomaly term was significant (Table 3) when it was

Fig. 2. Temporal trends in catch-weighted mean length at age of haddock for CDN surveys (1970–1995). Open squares are for values for the southwestern Scotian Shelf and closed diamonds are values for the Bay of Fundy. (A) Age-1; (B) age-2; (C) age-3; (D) age-4.
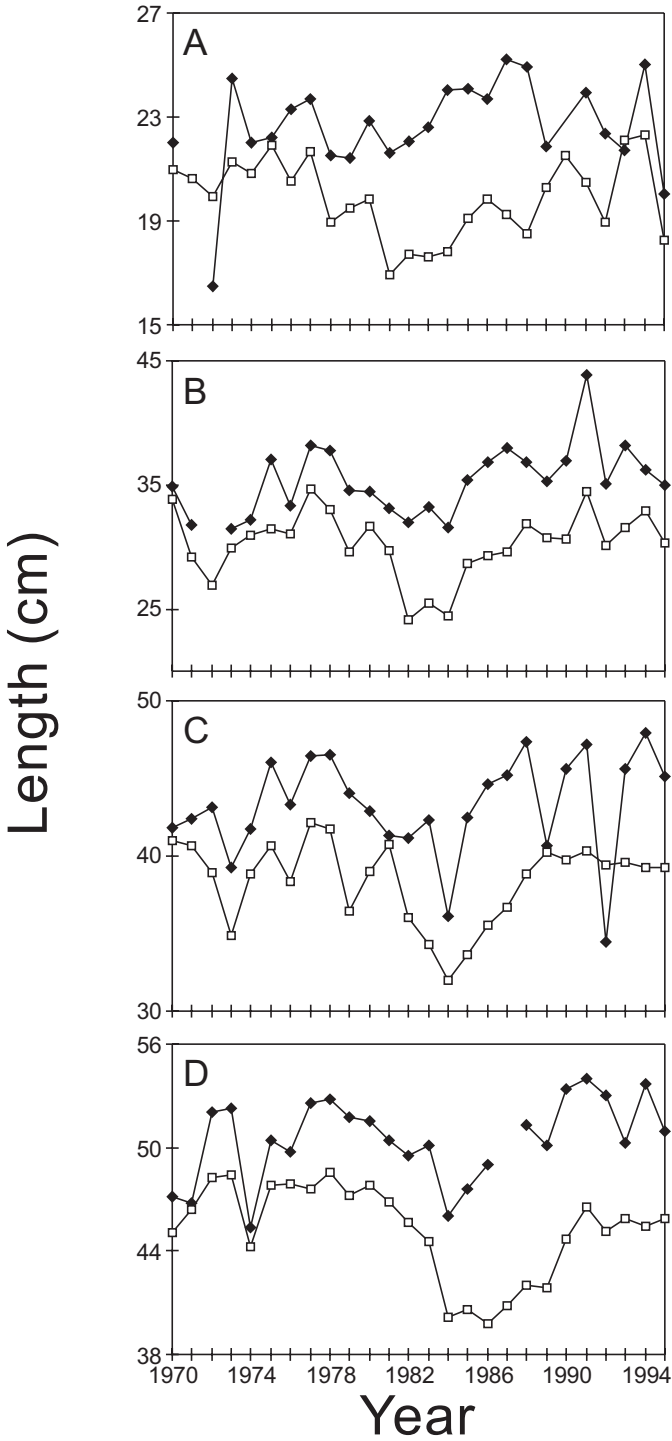
Fig. 3. Temporal trends in mean length at age of haddock for US surveys (1963–1986). Open squares are values for the southwestern Scotian Shelf and closed diamonds are values for the Bay of Fundy. (A) Age-1; (B) age-2; (C) age-3; (D) age-4.
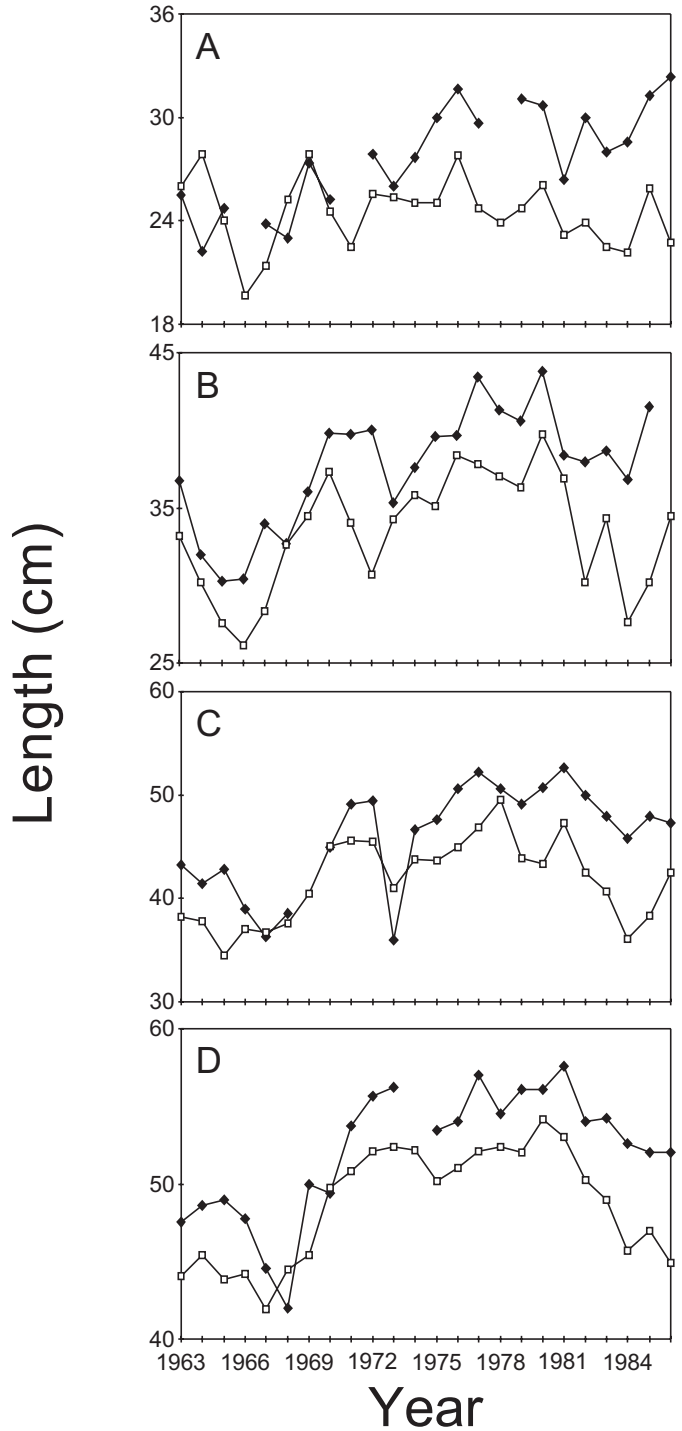

the only variable in a univariate model. It was not significant in a bivariate model that included adult abundance.

The strongest evidence of a negative correlation between juvenile growth and adult abundance is for the SWSS during

the time period covered by the CDN survey (1970–1995; Fig. 4A). This time period on the SWSS is also character-ised by a positive correlation between recruitment and length at age-4 (fig. 6B in Marshall and Frank (1999)). To link these two relationships together it was necessary to ex-

Fig. 4. Relationship between mean length at age-1 and adult abundance. Labels denote the observational year. Note the difference between left- and right-hand panels with respect to the magnitude of the x axis. (A) Southwestern Scotian Shelf (CDN survey); (B) Bay of Fundy (CDN survey); (C) southwestern Scotian Shelf (US survey); (D) Bay of Fundy (US survey).
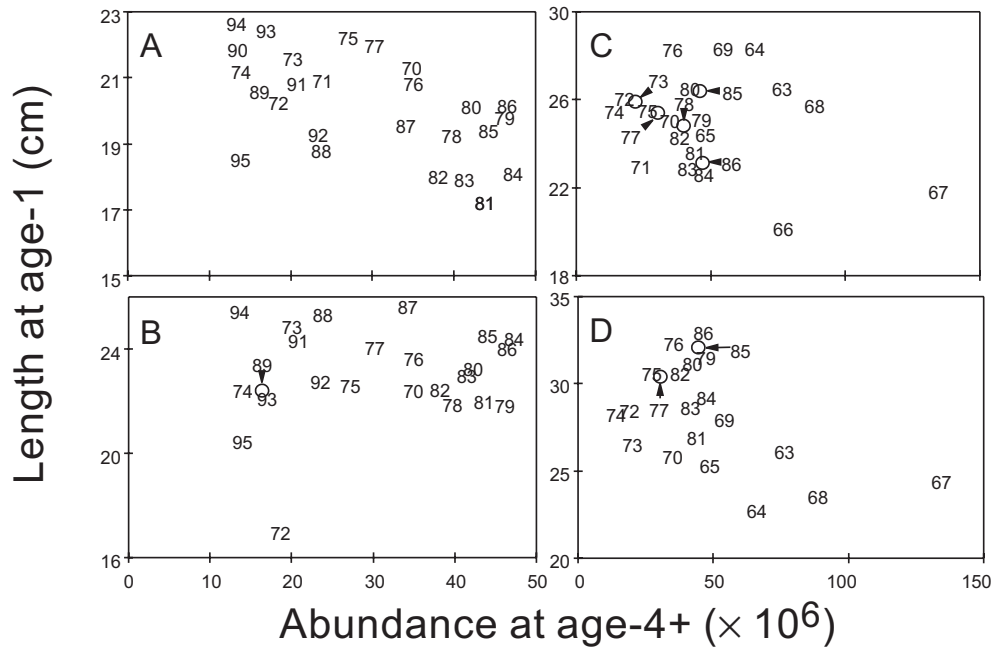
amine whether size differences established at the juvenile stage persist through to the adult stage. For haddock on the SWSS (CDN survey), temporal trends in length at age-1 persisted as the year-class aged (Fig. 5). The peak correlations between length at age-2 and length at age-1 and between length at age-4 and length at age-1 occurred at the expected lags (1 and 3 years, respectively) although the peak lag for the correlation between length at age-1 and length at age-3 occurred 1 year earlier than expected. Thus, from 1970 to 1995, the differences in body size observed at the juvenile stage for SWSS haddock persisted through to the adult stage.

The interrelationships between adult abundance, juvenile and adult body size, and recruitment were combined in a conceptual model of compensatory recruitment regulation (Fig. 6). The trajectories for juvenile haddock in years 1973 and 1981 are depicted by the dotted and dashed lines, respectively. Low adult abundance in 1973 resulted in faster juvenile growth (quadrant A) leading to larger adults in 1976 (quadrant B), higher recruitment in 1978 (quadrant C), and increased adult abundance in 1981 (quadrant D). Conversely, high adult abundance in 1981 reduced the growth of juvenile haddock (quadrant A) resulting in smaller-sized adults in 1984 (quadrant B), lower recruitment in 1986 (quadrant C), and decreased adult abundance in 1989 (quadrant D). The total time lag between application of the stress (adult abundance) and the feedback response (recruitment to age-4) is 8 years. However, this time lag could be decreased by 2 years if the total number of haddock age-3 and older were used as an index of adult abundance (quadrant A) and length at age-3 was used as the proxy for the reproductive potential of spawners (quadrants B and C).

Discussion

A significant, negative correlation between the length of

juvenile haddock on the SWSS and adult abundance was observed for the time period covered by the CDN survey (1970–1995; Fig. 4A). Inverse correlations were not observed consistently through time (Fig. 4A versus Fig. 4B or Fig. 4C versus Fig. 4D) or space (e.g., SWSS versus BofF), which suggests that density-dependent growth is a weak effect and (or) that our ability to detect it is limited. The inverse correlation for the SWSS from 1970 to 1995 was consistent with the significant negative correlation observed between length at age-2 and total stock abundance for the Georges Bank haddock stock (Ross and Nelson 1992), which suggests that intercohort competition for food is characteristic of haddock. Spatial and dietary overlap between juveniles and adults is a pre-requisite for intercohort competition. High densities of age-1 haddock are typically found on offshore banks and stratum 90 (Marshall and Frank 1995), which also have high densities of adults (Frank et al. 1990). Juveniles feed on a size fraction of the macrobenthos that can also be utilized by adult haddock (Wildish et al. 1989). Databases describing interannual variation in food availability and (or) consumption would be required to examine intraspecific competition more directly.

From a population dynamics perspective, the density-dependent growth of juvenile haddock is of interest because it facilitates the compensatory recruitment regulation depicted in Fig. 6. Figure 6 applies only to time periods characterised by both density-dependent growth (Fig. 4A) and a positive correlation between recruitment and length at age-4 (fig. 6B in Marshall and Frank (1999)). When these two features of the stock dynamics are present, shifts towards either high abundance (e.g., because of anomalously high recruitment) or low abundance (e.g., because of high levels of fishing mortality) could induce cyclical variation in haddock recruitment at frequencies dependent on growth and maturation rates of the year-classes comprising the stock. Several stud-

Table 3. Significance levels associated with sequential and partial sums of squares (SS) for models having length at age-1 as the dependent variable and adult abundance (total 4+) and (or) temperature (T) in either subarea 22 or subarea 24 as the independent variables.

| Region	Time period	Independent variables	Sequential SS	Partial SS
SWSS	1970–1995	T (subarea 24)	0.52	0.29
SWSS	1963–1986	T (subarea 24)	0.28	0.53
BofF	1970–1995	T (subarea 22)	0.57	0.30
BofF	1963–1986	T (subarea 22)	0.02	0.21

Note: The sequential SS were calculated assuming that T was the first variable to enter the model. The partial sums of squares were calculated for temperature assuming that adult abundance was already in the model.

Fig. 5. Cross correlation analysis for the southwestern Scotian Shelf (1970–1995). Arrows indicate the expected lag for a strong year-class effect. Solid bars indicate correlations significant at the $p* \leq 0.05$ level, whereas open bars indicate correlations not significant. (A) Length at age-1 and age-2; (B) length at age-1 and age-3; (C) length at age-1 and age-4.

ies have suggested that haddock exhibit cyclical variation in recruitment. For example, North Sea haddock have followed a 3- to 4-year cycle in recruitment throughout most of this century (Jones and Hislop 1978; Sahrhage and Wagner 1978) with very strong year-classes being frequently followed by very weak ones (Cook and Armstrong 1984). Hislop (1996) has suggested that this cyclical pattern originates in density-dependent mechanisms. The faster growth and maturation rates of North Sea haddock stock (age at 50% maturity is between 2 and 3 years; Cook and Armstrong 1984) would decrease the feedback time relative to SWSS haddock.

Although there are differences in both the processes and the time scales represented, the compensatory recruitment regulation model for haddock resembles the well-known Paulik diagram (Paulik 1973). The starting point for a Paulik diagram is the quadrant depicting the relationship between the quantity (or biomass) of spawners and total egg production. The Paulik diagram proceeds through time to describe the effect that mortality during egg and larval stages has on recruitment. The time lag between stock abundance and recruitment corresponds to the time taken to recruit (t_ρ). A Paulik diagram therefore describes the effect that the quantity of spawners has on recruitment via total egg production. Figure 6 describes the effect that the quantity of adults has on juvenile growth (quadrant A) and subsequently the effect that quality of spawners has on recruitment (quadrant C). The time lag is longer (approximately $2 \times t_\rho$) because two generations of haddock are represented in the model: the juveniles negatively impacted by adult abundance (the density-dependent effect) and the progeny produced by those juveniles once they mature (the maternal effect).

In the real world, the processes described by Fig. 6 and Paulik diagrams act in combination to determine recruitment. A conceptual model combining elements of both Fig. 6 and the Paulik diagram has been proposed to explain the recruitment dynamics of the Far Eastern sardine (*Sardinops sagax*) (fig. 5 in Kawasaki and Omori 1995). Like Fig. 6, this model incorporates both density-dependent and maternal effects on total egg production. Compensation occurs through the dependency of spawner condition on stock abundance; high stock abundance results in poor condition spawners and lower total egg production, which in turn reduces recruitment. Like a Paulik diagram, the survivorship of eggs was influenced by density-independent environmental processes.
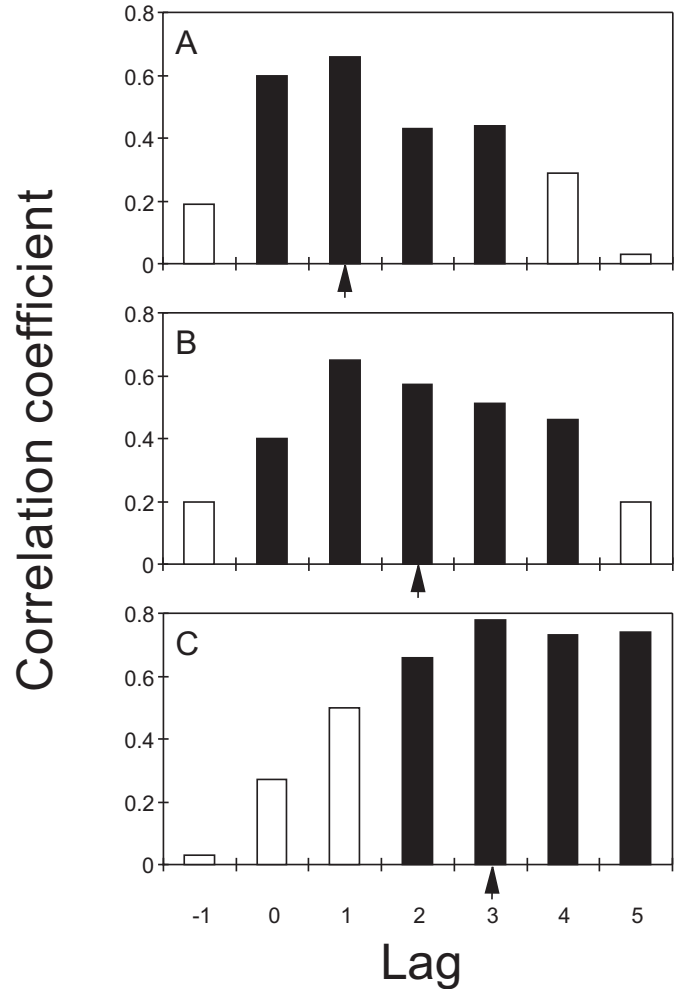
One of the earliest reported examples of density-dependent growth in haddock suggested that North Sea haddock compensate for low abundance by increasing growth rates thereby adjusting the "fertility" of the stock (Raitt 1939). Raitt (1936) presaged modern research on the effects of spawning experience on both egg viability (Solemdal et al. 1995) and population dynamics (Trippel et al. 1997*b*) by noting the potential for fishing mortality to remove repeat spawners from the population "forcing the brunt of recruitment upon two and three-year old fish much less well provided by nature to do so." This argues for the development of growth-based management strategies that consider both the current reproductive potential of adults and the short-term forecasts of growth and maturation rates of juveniles.

Acknowledgements

362

Can. J. Fish. Aquat. Sci. Vol. 56, 1999

Fig. 6. A conceptual model for haddock on the southwestern Scotian Shelf illustrating compensatory responses in recruitment operating during the period 1970–1995. As in a Paulik diagram, the ordinate of one stage becomes the abscissa of the next, beginning here in the top right quadrant (quadrant A) and ending in the bottom right quadrant (quadrant D). The dotted line indicates the trajectory for *t* equal to 1973. The dashed line indicates the trajectory for *t* equal to 1981. Note the difference between the abscissa of quadrant A and the ordinate of quadrant D in both the magnitude (50 and 30 million, respectively) and the time scale (year *t* and year *t* + 8, respectively).
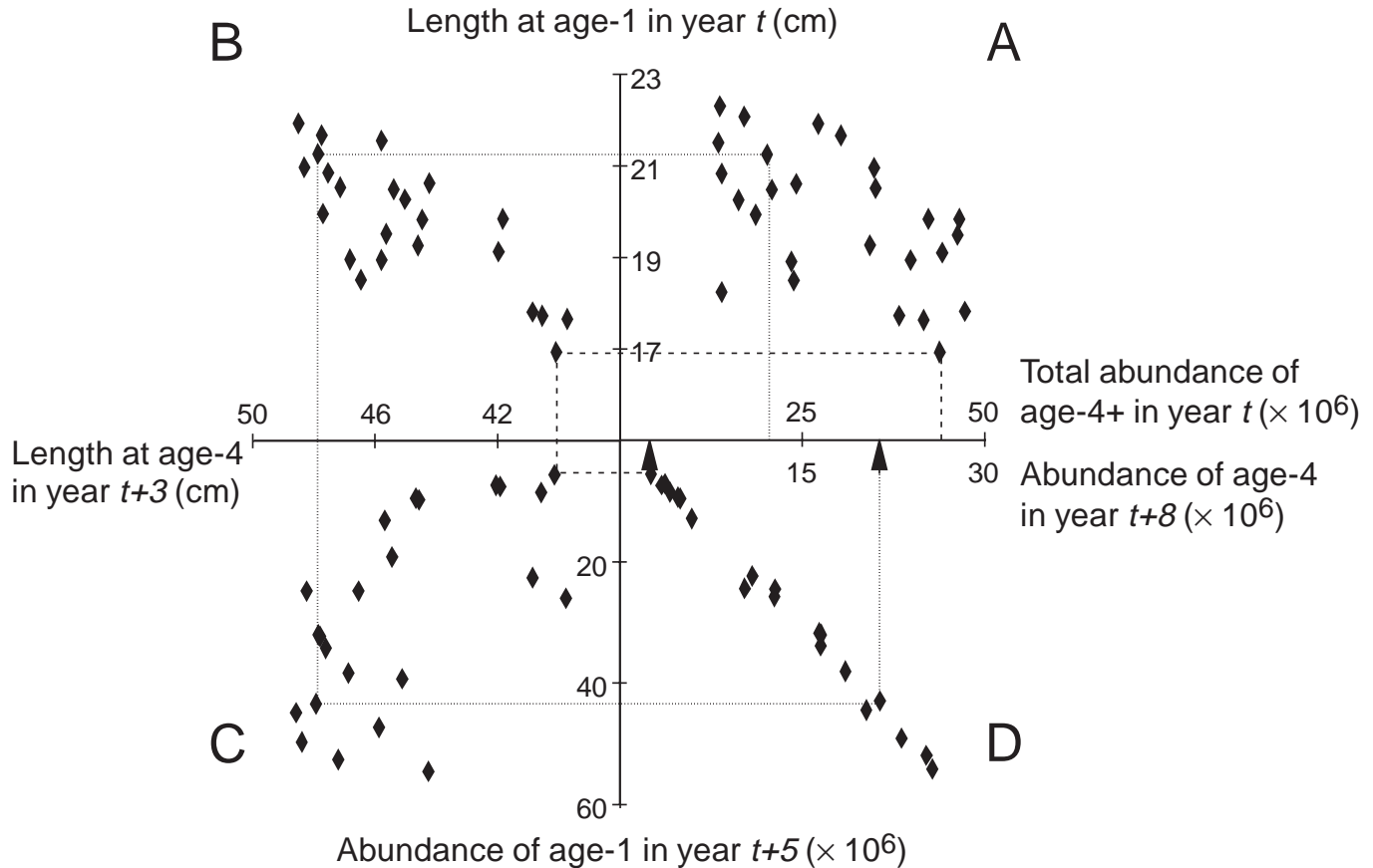
References

Andersson, K.A. 1938. An investigation into the alterations in the growth-rate of the haddock. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **108**: 85–87.

Beacham, T.D. 1982. Some aspects of growth and Canadian exploitation of haddock (*Melanogrammus aeglefinus*) on Browns and Georges Bank in the Northwest Atlantic Ocean. Can. Tech. Rep. Fish. Aquat. Sci. 1066.

Bowman, A. 1932. The effect on the stock of the capture of under-sized fish. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **80**: 1–19.

Bromley, P.J. 1989. Evidence for density dependent growth in North Sea gadoids. J. Fish. Biol. **35**(Suppl. A): 117–123.

Clark, S.H., Overholtz, W.J., and Hennemuth, R.C. 1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. J. Northw. Atl. Fish. Sci. **3**: 1–27.

Cook, R.M., and Armstrong, D.W. 1984. Density effects in the recruitment and growth of North Sea haddock and whiting. ICES C.M. 1984/G:68.

Drinkwater, K.F, and Trites, R.W. 1987. Monthly means of temperature and salinity in the Scotian Shelf region. Can. Tech. Rep. Fish. Aquat. Sci. 1539.

Engås, A., and Godø, O.R. 1989. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. J. Cons. Int. Explor. Mer, **45**: 269–276.

Frank, K.T., Hurley, P.C.F., and Simon, J. 1990. Assessment of 4X haddock in 1989. CAFSAC Res. Doc. 90/58.

Herrington, W.C. 1944. Factors controlling population size. *In* Transactions of the 9th North American Wildlife Conference. *Edited by* E.M. Quee. American Wildlife Institute, Washington, D.C. pp. 250–263.

Herrington, W.C. 1948. Limiting factors for fish populations: some theories and an example. Bull. Bingham Oceanogr. Coll. **11**: 229–283.

Hislop, J.R.G. 1996. Changes in North Sea gadoid stocks. ICES J. Mar. Sci. **53**: 1146–1156.

Hurley, P.C.F., Black, G.A.P., Mohn, R.K., and Comeau, P. 1997. Assessment of 4X haddock in 1996 and the first half of 1997. Can. Stock Assess. Secretariat Res. Doc. 97/108.

Jones, R. 1979. Relationship between mean length and year class strength in North Sea haddock. ICES C.M. 1979/G:45.

Jones, R. 1983. An investigation of North Sea haddock (*Melanogrammus aeglefinus*) length-at-age data, with particular reference to the effects on growth of the outstanding year classes of 1962 and 1967. J. Cons. Int. Explor. Mer, **41**: 50–62.

Jones, R., and Hislop, J.R.G. 1978. Changes in North Sea haddock and whiting. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **172**: 58–71.

Kawasaki, T., and Omori, M. 1995. Possible mechanisms underlying fluctuations in the Far Eastern sardine population inferred from time series of two biological traits. Fish. Oceanogr. **4**: 238–242.

Marshall, C.T., and Frank, K.T. 1995. Density-dependent habitat selection by juvenile haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf. Can. J. Fish. Aquat. Sci. **52**: 1007–1017.

Marshall, C.T., and Frank, K.T. 1999. The effect of interannual variation in growth and condition on haddock recruitment. Can. J. Fish. Aquat. Sci. **56**. This issue.

Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod (*Gadus morhua*)? Can. J. Fish. Aquat. Sci. **55**: 1766–1783.

Marteinsdottir, G., and Thorarinsson, K. 1998. Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. Can. J. Fish. Aquat. Sci. **55**: 1372–1377.

Paulik, G.J. 1973. Sudies of the possible form of the stock–recruitment curve. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **164**: 302–315.

Raitt, D.S. 1936. Stock replenishment and fishing intensity in the haddock of the North Sea. J. Cons. Int. Explor. Mer, **11**: 211–218.

Raitt, D.S. 1939. The rate of mortality of the haddock of the North Sea stock 1919–1938. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **110**: 65–79.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Board Can. **11**: 559–623.

Ross, M.R., and Nelson, G.A. 1992. Influences of stock abundance and bottom-water temperature on growth dynamics of haddock and yellowtail flounder on Georges Bank. Trans. Am. Fish. Soc. **121**: 578–587.

Sahrhage, D., and Wagner, G. 1978. On fluctuations in the haddock population of the North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **172**: 72–85.

Solemdal, P., Kjesbu, O.S., and Fonn, M. 1995. Egg mortality in recruit- and repeat-spawning cod—an experimental study. ICES C.M. 1995/G:35.

Sonina, M.A. 1965. Relationship between the growth rate and population density of haddock in the Barents Sea. Int. Comm. Northwest Atl. Fish. Spec. Publ. **6**: 565–570.

Templeman, W., and Bishop, C.A. 1979. Age, growth, year-class strength, and mortality of haddock, *Melanogrammus aeglefinus*, on St. Pierre Bank in 1948–75 and their relation to the haddock fishery of this area. Int. Comm. Northwest Atl. Fish. Res. Bull. **14**: 85–99.

Templeman, W., Hodder, V.M., and Wells, R. 1978. Age, growth, year-class strength, and mortality of haddock, *Melanogrammus aeglefinus*, on the southern Grand Bank in 1948–75 and their relation to the haddock fishery of this area. Int. Comm. Northwest Atl. Fish. Res. Bull. **13**: 31–52.

Trippel, E.A., Morgan, M.J., Fréchet, A., Rollet, C., Sinclair, A., Annand, C., Beanlands, D., and Brown, L. 1997*a*. Changes in age and length at sexual maturity of Northwest Atlantic cod, haddock and pollock stocks, 1972–1995. Can. Tech. Rep. Fish. Aquat. Sci. 2157.

Trippel, E.A., Kjesbu, O.S., and Solemdal, P. 1997*b*. Effects of adult age and size structure on reproductive output in marine fishes. *In* Early life history and recruitment in fish populations. *Edited by* R.C. Chambers and E.A. Trippel. Chapman and Hall, New York. pp. 31–62.

Wildish, D.J., Wilson, A.J., and Frost, B. 1989. Benthic macrofaunal production of Browns Bank, Northwest Atlantic. Can. J. Fish. Aquat. Sci. **46**: 584–590.