

The effect of interannual variation in growth and condition on haddock recruitment

C. Tara Marshall and Kenneth T. Frank

Abstract: The relationship between recruitment and spawner biomass assumes that estimates of spawner biomass are proportional to total egg production by the stock. The validity of this assumption is in question for long-lived gadoid stocks; however, estimating total egg production independently of spawner biomass is seldom feasible. An alternative approach is to examine correlations between recruitment and variables likely to be proxies for total egg production by the stock. This indirect approach was used for haddock on the Scotian Shelf. Indices of growth (mean length at age-4) and condition (weight at 50 cm) were used as proxies for the reproductive potential of individual spawners. Both variables were positively correlated with recruitment over a 3-decade period (1964–1995). During the same time period, there was no relationship between recruitment and spawner biomass estimated by Virtual Population Analysis (VPA). This is further evidence that VPA-based spawner biomass is a poor index of the true reproductive potential of the stock. The results highlight the need to develop more accurate/precise measures of total egg production for use in recruitment research.

Résumé : La relation entre le recrutement et la biomasse des géniteurs s'appuie sur la prémisse selon laquelle les estimations de la biomasse des géniteurs sont proportionnelles à la production totale d'oeufs par le stock. La validité de cette hypothèse est remise en question pour les stocks de gadoïdes à longue durée de vie. Toutefois, il est rarement possible d'estimer la production totale d'oeufs sans tenir compte de la biomasse des géniteurs. Une autre façon de procéder consiste à examiner les corrélations entre le recrutement et les variables considérées comme des approximations de la production totale d'oeufs par le stock. Cette approche indirecte a été appliquée au stock d'aiglefin de la plate-forme néo-écossaise. Des indices de la croissance (longueur moyenne à l'âge de 4 ans) et de la condition (poids à 50 cm) ont été utilisés comme approximations du potentiel reproducteur des géniteurs. Une corrélation positive entre ces variables et le recrutement a été observée sur une période de plus de 30 ans (1964–1995). Durant cette même période, aucune corrélation n'a été observée entre le recrutement et la biomasse des géniteurs estimée par analyse des populations virtuelles. Ces résultats démontrent une fois de plus que l'estimation de la biomasse des géniteurs par analyse des populations virtuelles ne reflète pas fidèlement le potentiel reproducteur d'un stock. Ils font également ressortir la nécessité d'élaborer des instruments de mesure plus justes et plus précis de la production totale d'oeufs à des fins d'utilisation dans le cadre de recherches sur le recrutement.

[Traduit par la Rédaction]

Introduction

In the field of fish population dynamics the most common method of assessing the relationship between the reproductive potential of a stock and the resultant progeny has been to use theoretical models relating spawner biomass to recruitment. This approach assumes that spawner biomass is linearly related to total egg production by the stock. A recent test of this assumption for northeast Arctic (NEA) cod (*Gadus morhua*) revealed that the relationship between total egg production and spawner biomass is non-linear with non-constant variance (Marshall et al. 1998). Furthermore, the magnitude of variation in total egg production was closer to that observed in recruitment (≈ 100 -fold) and the relation-

ship between the two variables approached the origin. The corresponding lack of a relationship between recruitment and estimates of spawner biomass derived from Virtual Population Analysis (VPA) suggests that the latter is a poor measure of the true reproductive potential of the NEA cod stock. The far-reaching implications of this conclusion necessitates that it be investigated for other stocks.

Quantifying total egg production (or abundance) independently of the VPA requires highly specialized databases. For example, total egg production for NEA cod was estimated using acoustic estimates of the total abundance of spawners, demographic information describing the size, sex, and maturity composition of the stock, and year-specific fecundity-length relationships (Marshall et al. 1998). Such

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Table 1. Sampling dates (day/month) for bottom trawl surveys of NAFO Division 4X.

| Year | Spring | Summer | Fall |
|------|-------------|-------------|-------------|
| 1963 | — | — | 21/11–23/11 |
| 1964 | — | — | 22/11–22/11 |
| 1965 | — | — | 14/10–15/10 |
| 1966 | — | — | 18/10–20/10 |
| 1967 | — | — | 13/11–15/11 |
| 1968 | — | — | 06/11–07/11 |
| 1969 | — | — | 15/11–17/11 |
| 1970 | 20/03–21/03 | 07/07–16/07 | 08/11–13/11 |
| 1971 | 27/03–30/03 | 30/06–08/07 | 06/11–12/11 |
| 1972 | 10/03–10/03 | 25/06–01/07 | 08/11–14/11 |
| 1973 | — | 10/07–19/07 | 11/11–15/11 |
| 1974 | 09/03–10/03 | 09/07–23/07 | 02/11–03/11 |
| 1975 | 17/02–21/02 | 15/07–24/07 | 08/11–13/11 |
| 1976 | 21/02–27/02 | 13/07–19/07 | 15/11–15/11 |
| 1977 | 25/03–30/03 | 10/07–16/07 | 03/11–05/11 |
| 1978 | 17/03–18/03 | 10/07–13/07 | 11/11–12/11 |
| 1979 | 05/03–11/03 | 06/07–13/07 | 27/10–28/10 |
| 1980 | 20/03–26/03 | 07/07–14/07 | 31/10–01/11 |
| 1981 | 12/03–16/03 | 06/07–12/07 | 27/10–05/11 |
| 1982 | 16/03–24/03 | 10/07–18/07 | 25/10–27/10 |
| 1983 | 07/04–14/04 | 07/07–14/07 | 02/11–03/11 |
| 1984 | 17/03–26/03 | 10/07–20/07 | 21/10–22/10 |
| 1985 | 01/03–06/03 | 04/07–10/07 | 01/11–02/11 |
| 1986 | — | 08/07–14/07 | 30/10–31/10 |
| 1987 | — | 29/06–09/07 | — |
| 1988 | — | 04/07–11/07 | — |
| 1989 | — | 05/07–13/07 | — |
| 1990 | — | 04/07–12/07 | — |
| 1991 | — | 04/07–11/07 | — |
| 1992 | — | 22/06–05/07 | — |
| 1993 | — | 05/07–16/07 | — |
| 1994 | — | 04/07–15/07 | — |
| 1995 | — | 25/06–07/07 | — |

Note: A dash indicates that a survey was not conducted that year. The spring and summer surveys were conducted by the Canadian Department of Fisheries and Oceans and the fall survey was conducted by the U.S. National Marine Fisheries Service.

detailed information describing the abundance and reproductive potential of individual spawners is lacking for many species. Field-based estimates of total egg abundance from synoptic-scale surveys could also be used to test the proportionality assumption. With the exception of stocks assessed using the egg production method (and therefore lacking the corresponding VPA estimates of spawner biomass), field-based estimates of total egg abundance are usually available for only a small number of years. This severely limits their utility for testing the proportionality assumption.

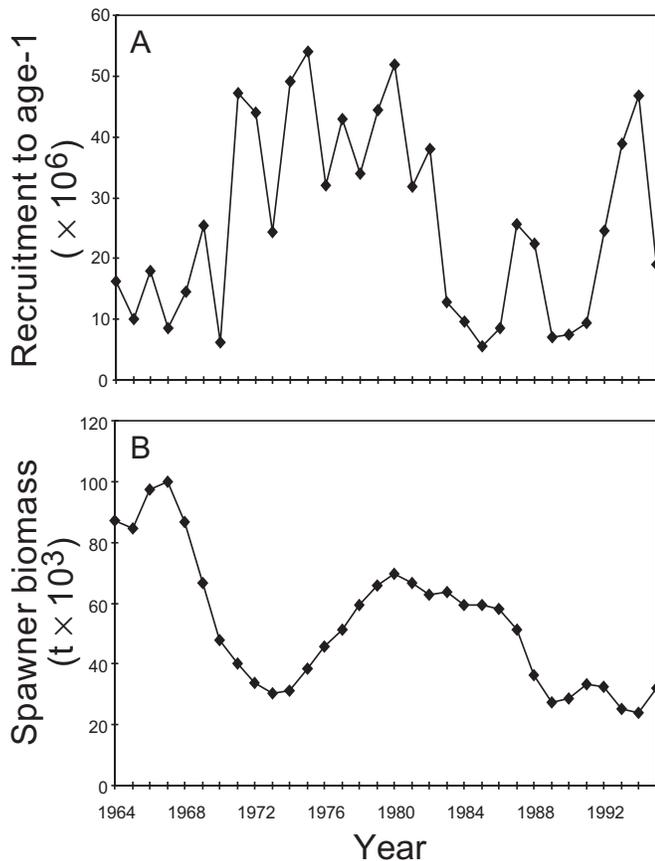
As a practical alternative, interannual variability in reproductive potential can be assessed using variables assumed to be proxies for the reproductive potential of individual spawners and (or) total egg production by the stock. For example, the Shannon diversity index has been used to describe interannual variation in the number and proportional representation of different age classes comprising the Icelandic cod stock (Marteinsdottir and Thorarinnsson 1998). A positive correlation was observed between age diversity and

recruitment to age-3 (see fig. 3b in Marteinsdottir and Thorarinnsson 1998); higher recruitment resulted when the spawning stock had a higher number and (or) proportion of older, larger cod. This suggests that recruitment is influenced by the higher reproductive potential of older cod, an interpretation supported by recent research demonstrating the age- and size-dependency of the timing and duration of spawning (Kjesbu et al. 1996) and egg and larval quality (Solemdal et al. 1993; Marteinsdottir and Steinarsson 1998). These maternal factors can affect not only the quantity of offspring produced but also their survival (Solemdal et al. 1995; Chambers and Leggett 1996; Trippel et al. 1997; Trippel 1998; Nissling et al. 1998).

Indices of the growth rate or physiological condition of spawners could potentially be used as proxies for the reproductive potential of individual spawners and possibly the stock. At the individual level, condition has been shown to influence the potential fecundity of females for a variety of species (Hislop et al. 1978; DeMartini 1991; Koslow et al. 1995; Kjesbu et al. 1998). Condition affects the realized fecundity of spawning females through atresia (Ma et al. 1998) and effects on egg and larval quality (Solemdal et al. 1993; Chambers and Waiwood 1996; Chambers and Leggett 1996; Marteinsdottir and Steinarsson 1998). Condition also affects the annual cycle of gonadal maturation. For example, a laboratory study on captive cod has shown that individuals in poor condition will skip spawning (Burton et al. 1997). At the stock level, anomalously low percentages of mature females in size classes corresponding to repeat spawners were observed in poor condition years suggesting that cod skip spawning seasons (Marshall et al. 1998). Variation in growth rates will affect the rate at which immature fish recruit to the spawning stock. This could be critical to the reproductive potential of the stock, particularly when age diversity is reduced.

In this paper, we examine the relationship between growth–condition of spawners and recruitment for haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf and Bay of Fundy (NAFO Division 4X). Over the past 30 years, recruitment to age-1 has varied by more than one order of magnitude (Fig. 1A) while spawner biomass has varied by a factor of approximately 4 (Fig. 1B). The recruitment dynamics of this stock remain unexplained despite broad-scale ichthyoplankton surveys conducted in the late 1970s to early 1980s (the Scotian Shelf Ichthyoplankton Program, O'Boyle et al. 1984), process-oriented studies in the mid-1980s (the Fisheries Ecology Program, Smith et al. 1989), population dynamic analysis of the spawner–recruit relationship (O'Boyle et al. 1989), and correlation analysis of the relationship between environmental factors and recruitment (Myers and Drinkwater 1988). The objectives of this study were to (i) describe the magnitude of interannual variation in the growth and condition of spawners, (ii) examine the relationship between growth and condition of spawners (independent variables) and recruitment (dependent variable), and (iii) contrast these relationships with the conventional relationship between VPA-based spawner biomass and recruitment. In essence, this comparison is equivalent to assessing the effects of the quality of individual spawners on recruitment relative to the effects of the quantity of spawners.

Fig. 1. (A) Time series (1964–1995) of recruitment to age-1 for haddock. (B) Time series (1964–1995) of spawner biomass. Values for 1970 to 1995 were obtained from Hurley et al. (1997), whereas values for 1964 to 1969 were from a specialized run of the VPA described in the text.



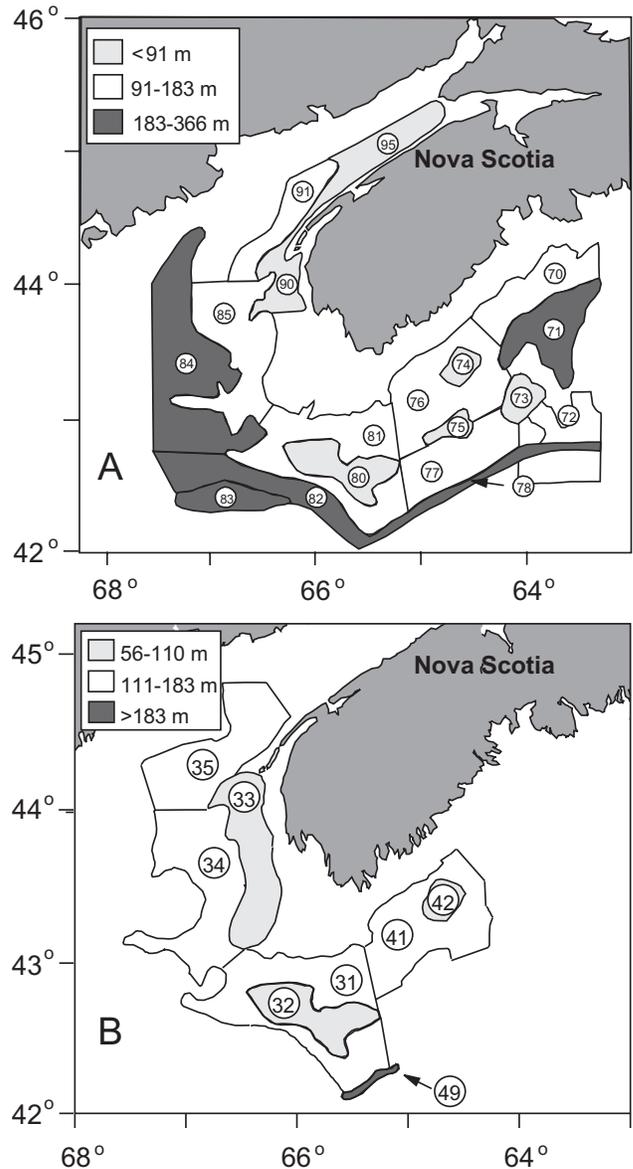
Methods

Data Sources

Indices describing the growth-condition of spawners were developed using data from bottom trawl surveys of the southwestern Scotian Shelf conducted in the spring (1970–1985, with no survey conducted in 1973), summer (1970–1995), and fall (1963–1986). The spring and summer surveys were conducted by the Canadian Department of Fisheries and Oceans (Halliday and Koeller 1981) and the fall survey was conducted by the U.S. National Marine Fisheries Service (Azarovitz 1981). Table 1 indicates the sampling dates for the different survey series. Spring surveys were conducted in February–April, just prior to or at the peak spawning period for haddock in April–May (Page and Frank 1989). Summer and fall surveys were conducted between spawning seasons (Waiwood and Buzeta 1989). For this analysis it was assumed that growth-condition in the summer and fall surveys describe reproductive potential in the subsequent spawning season rather than the preceding one. Thus, the growth-condition of spawners in spawning year $t + 1$ was assumed to be sampled by the summer survey in year t , the fall survey in year t , and the spring survey in year $t + 1$.

Spring surveys conducted prior to 1979 were based on a fixed station design. With one exception (stratum 91 in 1976), strata located in the Bay of Fundy were not sampled by spring surveys prior to 1979. Canadian (CDN) summer surveys and spring surveys from 1979 to 1985 and the United States (US) surveys use a

Fig. 2. (A) Strata from Canadian bottom trawl surveys of NAFO Division 4X included in the analysis. (B) Strata from US bottom trawl surveys included in the analysis.



stratified random design with depth as the major stratifying variable (Fig. 2). Strata boundaries for the CDN surveys were defined using three depth intervals (<100, 100–200, >200 m) that differed slightly from those used in the US surveys (56–110, 111–183, >183 m). The spatial coverage of the CDN surveys (total area 56 734 km², 18 strata) better represents the stock range. Strata from the western half of the Bay of Fundy were not included in the analysis because haddock there are considered to belong to the Gulf of Maine stock (Halliday 1974). With the exception of one shallow inshore stratum (stratum 33), the spatial coverage of the US survey (maximum area 29 345 km², 8 strata) overlaps with the area sampled by the CDN surveys (Fig. 3). Since 1987, coverage by the US surveys has been reduced to three strata located in the Bay of Fundy (strata 33, 34, and 35). Consequently, these years were not used in the analysis.

Although they are managed as a single stock, haddock on the southwestern Scotian Shelf (SWSS) grow more slowly than haddock in the Bay of Fundy (BofF). Assuming that the commercial

Fig. 3. Time series (1970–1985, 1973 missing) of mean length at age-4 (solid diamonds) and predicted weight at 50 cm (open squares) for spring surveys.

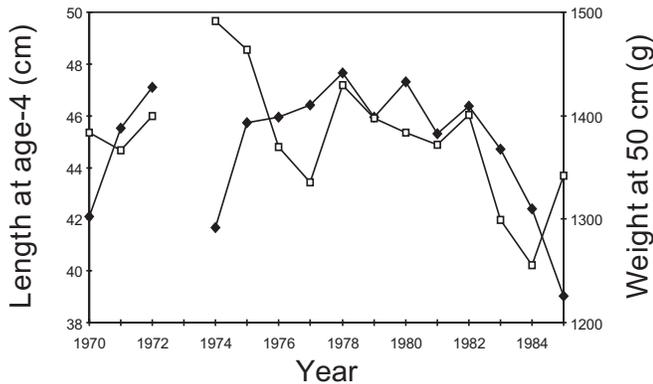
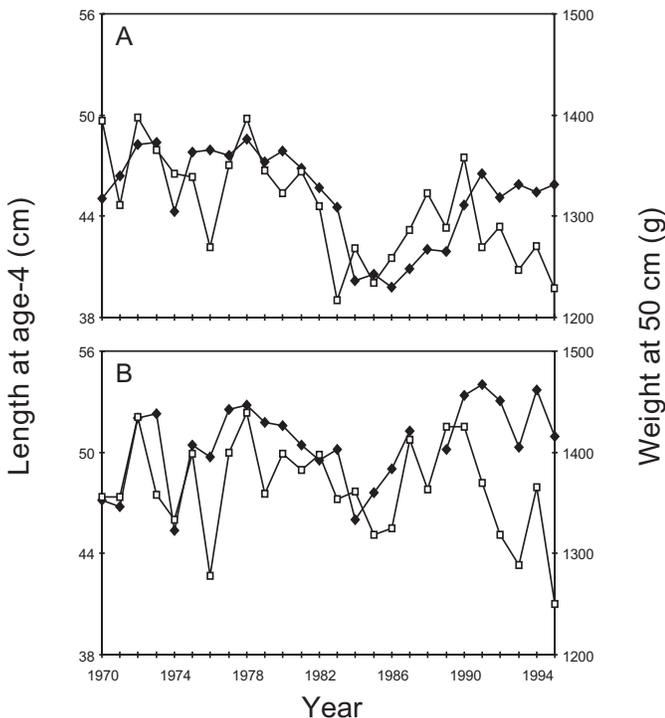
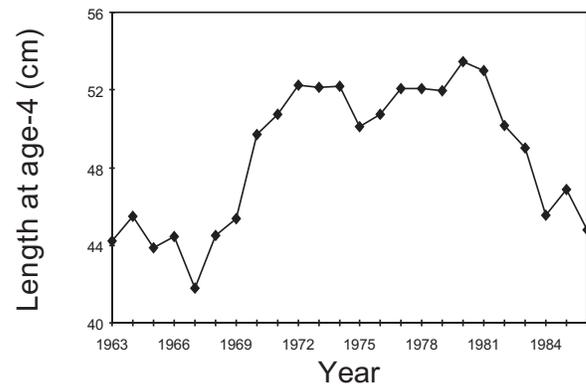


Fig. 4. Time series (1970–1995) of catch-weighted mean length at age-4 (solid diamonds) and predicted weight at 50 cm (open squares) for summer surveys. (A) Southwestern Scotian Shelf; (B) Bay of Fundy.



catch approximates the relative abundance of adult haddock in the two regions, on average 77% of the haddock stock can be found on the SWSS (table 5 in Hurley et al. 1996). Therefore, trends in growth-condition of haddock at the stock level will be dominated by trends observed on the SWSS. The spring, summer, and fall surveys differ with respect to their coverage of the SWSS and BofF regions. Growth-condition indices for the spring survey were calculated for haddock on the SWSS only because the BofF was not included in spring surveys conducted prior to 1979. Growth-condition indices for the summer surveys were calculated for the SWSS (strata 70–81) and the BofF (strata 85, 90, 91, and 95) separately. Strata 82–84 were not included in either grouping because haddock are extremely uncommon in these deep strata. Data for the fall surveys were not subdivided because of the restricted spatial coverage (Fig. 2) and correspondingly fewer observations.

Fig. 5. Time series (1963–1986) of mean length at age-4 for fall surveys.



Consequently, the fall surveys describe the growth of haddock in the SWSS and the BofF combined.

For all surveys, the fork length of individual haddock was recorded to the nearest centimetre. For the CDN surveys, weight was recorded and sagittal otoliths were removed from a length-stratified subsample of the total catch. Prior to 1985, otoliths collected during the CDN surveys were broken and burned for age determinations. Since 1985, age determinations have been made using thin sections along the dorsoventral axis (Strong et al. 1985). In 1993 it was noted that the age estimates for this stock had become systematically biased towards lower values for older haddock (Campana 1995). Consequently, otoliths collected for summer surveys conducted between 1987 and 1995 have been re-aged according to new criteria consistent with criteria used in other haddock-aging laboratories (Hurley et al. 1996). Otoliths for the spring survey have not been re-aged; however, the bias for the time period of the spring surveys (1970–1985) is thought to be minimal (Hurley et al. 1996). For the US surveys, scales were used for young fish and otoliths were used for older fish because of the difficulty in distinguishing the outer annuli on scales (Pentilla and Dery 1988).

Growth and condition indices

The indices used to represent growth and condition of spawners were mean length at age 4 (\bar{l}_4) and the predicted weight at a standard length of 50 cm (\hat{w}_{50}), respectively. Maturity ogives, constructed by pooling all data for the spring surveys, indicated that the lengths at 50% maturity for haddock in the SWSS and BofF were approximately 37 and 43 cm for males and females, respectively (Waiwood and Buzeta 1989). Values of \bar{l}_4 ranged between 38 and 48 cm (spring survey), 38 and 50 cm (summer survey), and 40 and 54 cm (fall survey). Thus, the majority of haddock that are either age-4 or 50 cm in length are mature. Choosing different standard ages or lengths had no effect on any of the general trends observed.

Values of \bar{l}_4 were estimated using the length observations for age-4 haddock, including both males and females. Values of \bar{l}_4 estimated for the spring and fall surveys were the arithmetic mean of all lengths, uncorrected for the length frequency distribution of the catch. Values of \bar{l}_4 for the summer surveys were estimated by correcting for the length distribution of the catch on a stratum-by-stratum basis. The catch-weighted values of \bar{l}_4 for the summer survey were significantly different from arithmetic means estimated for the same surveys for both the SWSS (paired *t*-test, $p = 0.01$, $n = 22$) and the BofF (paired *t*-test, $p < 0.01$, $n = 22$). The r^2 values for correlations between the catch-weighted and unweighted values of \bar{l}_4 were 0.91 and 0.58 for the SWSS and BofF, respectively. Using unweighted values will therefore have a greater effect on analysis of data from the BofF relative to the SWSS.

Table 2. Summary statistics for regressions describing the relationship between recruitment to age-1 (thousands) and body size characteristics of adult haddock for spring, summer, and fall surveys of the southwestern Scotian Shelf (SWSS) and Bay of Fundy (BofF).

| Survey/source | Indep. var. | Region | Year-classes | r^2 | p^* |
|---------------|----------------|-----------|-------------------------|-------|-------|
| Spring | \bar{l}_4 | SWSS | 1970–1985 | 0.41 | 0.01 |
| Spring | \bar{l}_4 | SWSS | 1970–1985, exc. 1974 | 0.66 | <0.01 |
| Summer | \bar{l}_4 | SWSS | 1971–1995 | 0.35 | <0.01 |
| Fall | \bar{l}_4 | SWSS/BofF | 1964–1987 | 0.51 | <0.01 |
| Spring | \hat{w}_{50} | SWSS | 1970–1985 | 0.37 | 0.01 |
| Summer | \hat{w}_{50} | SWSS | 1971–1995 | 0.18 | 0.04 |
| Summer | \hat{w}_{50} | SWSS | 1971–1991 | 0.28 | 0.02 |
| Summer | \bar{l}_4 | BofF | 1971–1995 | <0.01 | 0.85 |
| Summer | \hat{w}_{50} | BofF | 1971–1995 | 0.09 | 0.15 |
| Summer | \hat{w}_{50} | BofF | 1971–1991 | 0.05 | 0.35 |
| VPA | ssb | SWSS/BofF | 1964–1995 | 0.07 | 0.15 |

Note: The independent variables are mean length at age-4 (\bar{l}_4) and predicted weight at a standard length of 50 cm (\hat{w}_{50}). Values of p^* have been corrected for temporal autocorrelation as described in the text. Statistics are also given for the relationship between recruitment and the VPA estimate of spawner biomass (ssb).

To estimate \hat{w}_{50} , length (l) and weight (w) observations were used to fit the equation

$$(1) \quad \log_{10}(w) = \log_{10}(\alpha) + \beta \log_{10}(l)$$

for each survey. For this index, only observations for female haddock were used. For spring surveys, only ripening and spawning females (maturity stages 3–5; Waiwood and Buzeta 1989) were included in the weight–length regressions for the spring surveys. For the summer surveys, all females age-3 and older were considered mature. Where age estimates were missing, observations for female haddock 37 cm in length or larger were included in the data set. No temporal trend in the length range of observations included in the regression data sets was noted although the number of observations varied according to total abundance. Trends in \hat{w}_{50} could not be examined for the fall surveys because the US surveys did not systematically record individual weight.

Recruitment and spawner biomass

The abundance of age-1 haddock from 1970 to 1995 (Hurley et al. 1997) was used as an index of recruitment for the 1969–1994 year-classes. The abundance of age-1 haddock from 1965–1969 was obtained from a specialized VPA run described below. For the spring surveys, growth–condition in survey year t was correlated with the recruitment index for spawning year t . Correlations for the summer and fall surveys were lagged by 1 year such that growth–condition in survey year t was correlated with the recruitment index for spawning year $t + 1$.

A specialized run of the age-based VPA was used to generate estimates of spawner biomass for the time period 1962–1969 (P.C.F. Hurley, Marine Fish Division, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, N.S., Canada). Because the CDN research survey series did not begin until 1970, commercial weight at age was used to calculate spawner biomass. As in Hurley et al. (1997), a constant maturity ogive (O’Boyle et al. 1989) was used to estimate spawner biomass.

Autocorrelation correction

In estimating the statistical significance of the correlations between recruitment and growth–condition the number of observations in the time series was corrected for autocorrelation by

$$(2) \quad n^* = \frac{n}{1 + 2r_1r'_1 + 2r_2r'_2}$$

where n is the number of observations in each of the two time series, r_1 and r'_1 are the lag-one autocorrelations of the two series, and r_2 and r'_2 are the lag-two autocorrelations of the two series (Quenouille 1952). Higher-order autocorrelations were not included in the correction. Corrected p values reported here (p^*) have been estimated using the corrected degrees of freedom.

Results

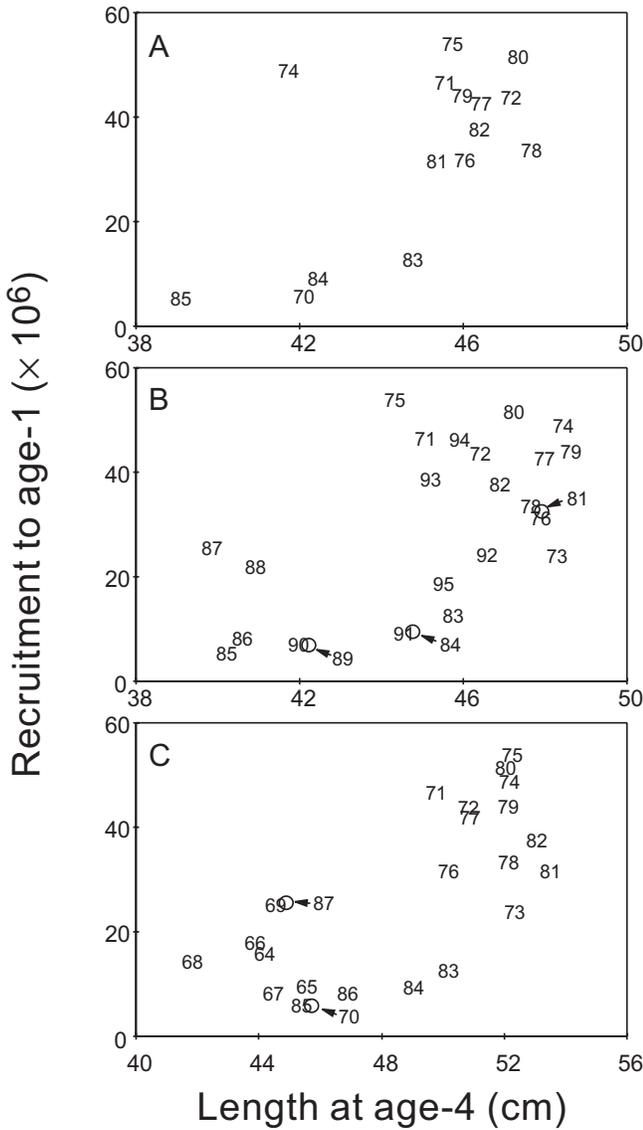
Temporal trends in growth and condition

The spring survey for the SWSS shows that both \bar{l}_4 and \hat{w}_{50} were relatively stable until 1982 when both indices began to decrease (Fig. 3). The differences between maximum and minimum values in the time series expressed as a percentage of the minimum ($\Delta\%$) were 22 and 19% for \bar{l}_4 and \hat{w}_{50} , respectively. The value of \bar{l}_4 in 1974 was unusually low relative to adjacent years and at odds with the trend observed in \hat{w}_{50} .

The summer survey for the SWSS (Fig. 4A) confirms that \bar{l}_4 and \hat{w}_{50} were relatively high and stable from 1972 to 1980, then decreased during 1981–1983, and remained low until 1986 when the values began to increase. As in the spring survey, \bar{l}_4 in 1974 was low relative to adjacent years. Over the entire time period, the values of $\Delta\%$ were 22 and 15% for \bar{l}_4 and \hat{w}_{50} , respectively. The temporal trends observed in \bar{l}_4 and \hat{w}_{50} are reasonably synchronous until the most recent years (1991–1995) when the trends diverged. During this time period, \bar{l}_4 increased to values that are near those observed between 1972 and 1980, while \hat{w}_{50} decreased to values that are nearly 200 g lower than those observed in 1972–1980.

Growth rates differ between the BofF and the SWSS both with respect to magnitude and temporal trends (Fig. 4B). Haddock in the BofF are longer at age and heavier at length compared with haddock on the SWSS. Over the entire time period, values of \bar{l}_4 in the BofF show an increasing trend and in recent years (1991–1995) have been at or near historical highs. The \bar{l}_4 value for 1974 was again low relative to adjacent values. Unlike the SWSS, the mid-1980s were not characterized by historical lows in both \bar{l}_4 and \hat{w}_{50} . Values of $\Delta\%$

Fig. 6. Relationship between recruitment to age-1 and mean length at age-4 of haddock on the southwestern Scotian Shelf. Observations are identified by the spawning year. (A) Spring survey; (B) summer survey; (C) fall survey.



were 19 and 15% for \bar{l}_4 and \hat{w}_{50} , respectively. After a period of relatively synchronous variation, a divergence between \bar{l}_4 and \hat{w}_{50} has occurred in recent years (1991–1995). Values of \bar{l}_4 are near historical highs, whereas values of \hat{w}_{50} are at or near historical lows. The decoupling of trends in \bar{l}_4 and \hat{w}_{50} for both the SWSS and BofF cannot be attributed to a change in timing of the summer survey because there was no systematic shift towards earlier or later surveys during that time period (Table 1).

The fall survey for southernmost portions of both SWSS and the BofF (SWSS–BofF) shows low values of \bar{l}_4 from 1963–1967, suggesting that conditions for growth of haddock were poor during this time period (Fig. 5). Values of \bar{l}_4 increased rapidly from 1967 to 1972, were high throughout the 1970s, and then began to decrease in 1981, a temporal trend that is consistent with those observed in the spring and summer surveys. The value of $\Delta\%$ for \bar{l}_4 was 28%.

Fig. 7. Relationship between recruitment to age-1 and predicted weight at 50 cm of haddock on the southwestern Scotian Shelf. Observations are identified by the spawning year. (A) Spring survey; (B) summer survey.

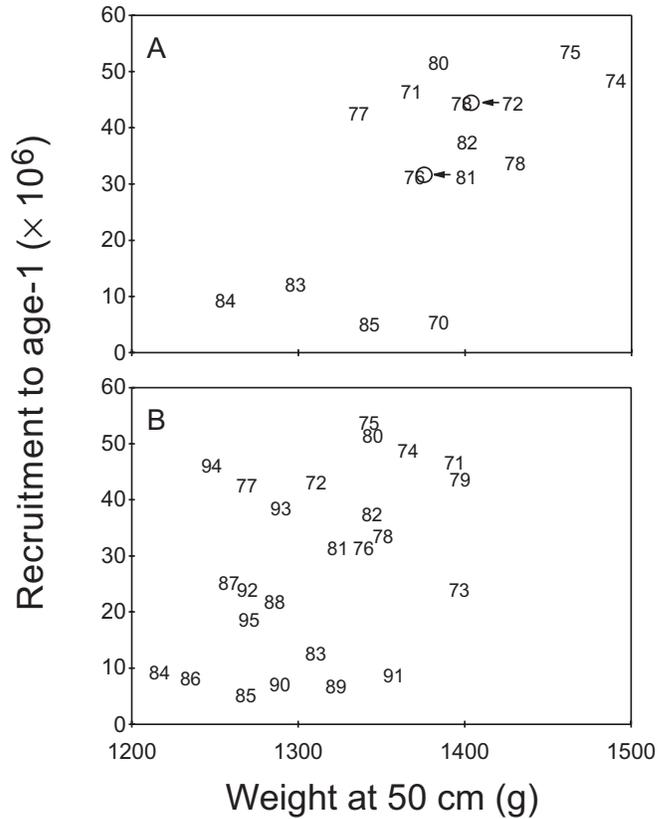
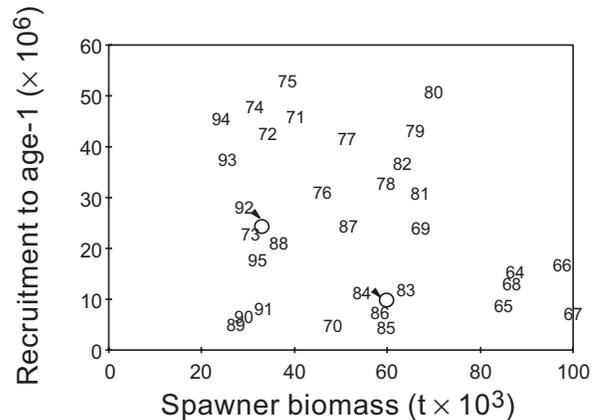


Fig. 8. Relationship between recruitment to age-1 and spawner biomass. Observations are identified by the spawning year.



Relationship between recruitment and body size of spawners

For haddock on the SWSS there were significant ($p^* \leq 0.01$) positive correlations between recruitment and \bar{l}_4 for the spring, summer, and fall surveys (Table 2). Time periods associated with poor growth and low values of \bar{l}_4 (the 1960s and mid-1980s) had low values of recruitment, whereas recruitment was high in periods when haddock were larger (the 1970s and early 1980s) (Fig. 6). The 1974 year-class

Table 3. Significance levels associated with the partial (Type II) sums of squares for a multivariate model having a body size variable (either \bar{L}_4 or \hat{w}_{50}) and a stock abundance variable (either spawner biomass (ssb) or total abundance of haddock age-4 and older (total 4+)) as the independent variables.

| Survey | Time period | Body size variable | Stock abundance variable | Partial SS |
|--------|-------------|--------------------|--------------------------|--------------|
| Spring | 1970–1985 | \bar{L}_4 | ssb | 0.06 (<0.01) |
| | | | total 4+ | 0.02 (<0.01) |
| Summer | 1971–1995 | \bar{L}_4 | ssb | 0.74 (<0.01) |
| | | | total 4+ | 0.54 (<0.01) |
| Fall | 1964–1987 | \bar{L}_4 | ssb | 0.55 (<0.01) |
| | | | total 4+ | 0.54 (<0.01) |
| Spring | 1970–1985 | \hat{w}_{50} | ssb | 0.92 (0.03) |
| | | | total 4+ | 0.41 (0.07) |
| Summer | 1971–1995 | \hat{w}_{50} | ssb | 0.99 (0.04) |
| | | | total 4+ | 0.73 (0.04) |

Note: Recruitment to age-1 is the dependent variable. The partial SS was calculated for each stock abundance variable assuming that the body size variable was already in the model. The partial SS for the body size variable is given in brackets (i.e., the significance of the body size variable assuming the stock abundance variable was already in the model).

was an outlier for the spring survey (Fig. 6A) but not the summer (Fig. 6B) or fall surveys (Fig. 6C). Excluding this observation from the correlation increased the r^2 value for the spring survey from 0.41 to 0.66 (Table 2).

Recruitment was also significantly, positively correlated (Table 2) with \hat{w}_{50} for haddock on the SWSS for both the spring (Fig. 7A) and summer surveys (Fig. 7B). Compared with the relationship between recruitment and \bar{L}_4 (Fig. 6), the relationship between recruitment and \hat{w}_{50} was weaker (Table 2). The stronger relationship between recruitment and \hat{w}_{50} for the spring survey (Fig. 7A) compared with the summer survey (Fig. 7B) suggests that the condition of spawners at or near the time of spawning would be a better proxy for reproductive potential and therefore a stronger correlate of recruitment. Given that there has been a divergence between \bar{L}_4 and \hat{w}_{50} in recent years (Fig. 4), observations for the 1991–1995 year-classes were deleted from the correlation between recruitment and \hat{w}_{50} for the summer survey. This had the effect of increasing the r^2 value from 0.18 to 0.28 (Table 2), which is still lower than the r^2 values for the correlation between recruitment and \bar{L}_4 for the summer survey.

There were no significant correlations between recruitment and either \bar{L}_4 or \hat{w}_{50} for haddock in the BofF (Table 2). Deleting the observations for 1991–1995 had a negligible effect on the level of significance for the relationship between recruitment and \hat{w}_{50} (Table 2).

Relationship between recruitment and spawner biomass

There was no discernable relationship between recruitment and spawner biomass (Fig. 8; Table 2), which is consistent with all previous studies of the stock–recruit relationship for 4X haddock. This result contrasts with the significant, positive correlations observed between recruitment and body size characteristics of spawners (Figs. 6 and 7). For example, the 1964–1969 year-classes were weak despite high spawner biomass (Fig. 8). However, this time pe-

riod was associated with poor growth and smaller body size of spawners (Fig. 5). This appears to have had a greater influence on recruitment (Fig. 6C). Similarly, the 1970s are associated with low to intermediate spawner biomass (Fig. 8); however, haddock were larger and recruitment was high (Figs. 6 and 7).

The effect of variation in the quantity of spawners on the recruitment–body size relationships in Figs. 6 and 7 was investigated using multivariate models that included a term for the body size of individual spawners (\bar{L}_4 or \hat{w}_{50}) and stock abundance (VPA-based estimates of spawner biomass or total abundance of haddock age-4 and older). With the sole exception of the model for spring survey having \bar{L}_4 and the total abundance of haddock age-4 and older (total 4+) as the independent variables, the addition of a stock abundance variable to a model already containing the body size variable did not significantly decrease the model sum of squares (Table 3). However, the addition of the body size variable to a model already containing the stock abundance variable always resulted in a significant decrease in the model sum of squares. Thus, the effect of the quantity of spawners on recruitment is less significant than the effect of the body size characteristics (quality) of spawners.

Discussion

A significant, positive correlation between recruitment and the body size characteristics of mature haddock on the SWSS was observed for spring, summer, and fall surveys, which in combination, cover a period of approximately 3 decades (1964–1995). The recruitment–body size correlation is analogous to the positive correlation between recruitment and age diversity noted for Icelandic cod (Marteinsdottir and Thorarinnsson 1998) in that it implicates interannual variation in the reproductive potential in the recruitment dynamics of gadoid stocks. When contrasted with the indeterminate relationship between recruitment and VPA-based spawner biomass for haddock (Fig. 8), it suggests that spawner biomass is an inaccurate and (or) biased measure of the reproductive and hence recruitment potential. This conclusion is consistent with the recent studies for Icelandic cod (Marteinsdottir and Thorarinnsson 1998) and NEA cod (Marshall et al. 1998).

In the absence of estimates of total egg production or abundance, proxy variables describing the growth–condition of spawners may provide insight into the recruitment dynamics of a stock. At the individual level there is ample evidence that the fecundity of long-lived gadoids such as cod and haddock varies according to growth and condition. For example, the fecundity of captive haddock has been shown to be positively correlated with condition and food ration (Hislop et al. 1978). Interannual variation in the fecundity–length relationship for wild NEA cod has been attributed to variation in condition (Kjesbu et al. 1998). There is a higher incidence of atresia in cod that are in poor condition because of food limitation (Kjesbu et al. 1991). Egg quality also varies according to body size characteristics of spawners. Egg size of haddock is positively correlated with length (Hislop 1988). Similarly, the egg diameter of cod was correlated with length (Solemdal et al. 1993) and (or) condition (Chambers and Waiwood 1996; Marteinsdottir and Stein- arsson 1998). Both the body size of larval fish and their abil-

ity to withstand starvation may also be influenced by maternal condition (Chambers and Leggett 1996).

At the stock level, variation in the growth–condition of individual fish could influence the reproductive potential of gadoid stocks in several different ways. Growth–condition determines the rate at which immature fish become recruit (first-time) spawners. This will obviously affect the reproductive potential of the stock, particularly as smaller fish generally have the advantage of higher numerical abundance. Faster growth and maturation could increase the probability that fish survive long enough to contribute to total egg production both as recruit and as repeat spawners. A positive, non-linear relationship between the proportion of eggs produced by repeat spawning NEA cod and recruitment (Marshall et al. 1998) suggests that this variation in this demographic feature of gadoid stocks might contribute to recruitment variation. Similarly, Hislop (1988) recommended downweighting the egg contribution of recruit-spawning North Sea haddock because they produce significantly smaller eggs. Variation in growth–condition may affect the seasonal maturation dynamics of repeat spawners disproportionately because relative to recruit spawners repeat spawners experience more severe depletion of body reserves and are therefore more sensitive to variations in feeding regimes (Kjesbu and Holm 1994). Skipped spawning seasons have been suggested for NEA cod in poor condition (Marshall et al. 1998). Likewise, mature female walleye (*Stizostedion vitreum*) in poor condition are unlikely to ripen and spawn (Henderson et al. 1996). Spawner biomass values estimated using knife-edge or sigmoidal maturity ogives do not allow for the possibility of skipped spawning seasons (Trippel and Harvey 1991). This will overestimate the effective spawner biomass when a substantial portion of the repeat spawners are non-reproductive (Burton et al. 1997).

The quantity of spawners obviously determines reproductive potential when stock abundance is extremely low (e.g., stock collapse). In more usual circumstances (e.g., the range in spawner biomass depicted in Fig. 1B), the effect of quantity may not be straightforward. Future recruitment research must clearly differentiate the effects of quality of individual spawners on growth, condition, maturation rates, and fecundity from the effects of quantity of spawners when assessing the reproductive potential of a stock (MacKenzie et al. 1998). This study has shown how routinely collected body size information can be used as proximate measures of reproductive potential. Other proxy variables are easily envisaged, e.g., liver condition index, gonadosomatic index. Examining the relationships between recruitment and proxy variables is a cost-effective interim measure for examining stock effects on recruitment variation. Estimates of total egg production or abundance, which account for both the quantity and quality of spawners, constitute the ultimate test.

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