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Differential Egg Mortality of Georges Bank Cod and Haddock Inferred from Two Independent Estimates of Seasonal Egg Production

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Abstract

Georges Bank Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks have undergone significant changes over the last 40 years with the reduction of older spawners and increased incidence of young mature fish. Captive studies, from other investigations, have noted that first- and second-time spawners exhibit lower egg hatching success, and especially for haddock compared to cod. Spawning stock biomass (SSB), derived from virtual population analysis (VPA), has been considered as an overestimate of a stock's spawning potential since it does not fully account for differences in age or size of spawners. The Northeast Fisheries Science Center's (NEFSC) ichthyoplankton Surveys (1979–1999) have provided an independent estimate of seasonal egg production to compare with a VPA-fecundity based estimate. Since the early stage eggs of the two species are indistinguishable, their numbers were estimated by apportioning the total egg abundance (cod plus haddock) at a station by the late stage abundance ratio, assuming equal mortality for the two species. For cod, the Surveys overestimated the VPA-derived egg production in many years by as much as an order of magnitude. However, for haddock, the VPA-derived egg production estimates were mostly higher than those from the Surveys. Comparing the ratio of the two egg production estimates versus the total combined VPA egg production of cod and haddock, the cod ratios were high when haddock was abundant, especially during the years 1995–1999, and closer to one when cod comprised the greater part of the total. The corresponding analysis for haddock was the reverse to that of cod further supporting the hypothesis that the higher egg mortality of the reduced age population of haddock biased the seasonal egg production estimates of both haddock and cod. These ratios appear to explain 60–70% of the variability in the ratio of Survey to VPA seasonal egg production, while other factors might be related to fecundity and age-class composition of the SSB, or changes in egg mortality rates over the time series. Our Survey estimates also suggest that haddock egg mortality is greater than cod. Thus, the seasonal egg production estimates from egg Surveys based on constant egg mortality are probably inaccurate, especially since the mid-1990s. Cod egg production may have been overestimated and haddock's underestimated.

Key words: Atlantic cod, egg mortality, Georges Bank, haddock, spawning pattern.

Introduction

Spawning stock biomass (SSB), often derived from virtual population analysis (VPA), traditionally has been used as a metric of spawning potential in stock and recruitment models. It has long been known that SSB is a crude measure of stock reproductive potential since fish size, condition, and age affect fecundity (Rothschild and Fogarty, 1989). Mean length and condition of Scotian Shelf haddock (*Melanogrammus aeglefnus*) were correlated with recruitment over three decades while the traditional SSB was not (Marshall and Frank, 1999). Parental conditioning has been hypothesized to explain the very large year-classes of Georges Bank haddock over the last decade (Friedland *et al.*, 2008). Egg and larval survival and recruitment of Atlantic cod (*Gadus morhua*) were positively correlated with age diversity indices of SSB for Georges Bank cod (O'Brien *et al.*, 2003) and Icelandic cod (Marteinsdottir and Thorarinsson, 1998) indicating the importance of old age classes. Multi-year repeat

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spawners have larger and more viable eggs and larvae compared to first- and second-time spawners (Kjesbu *et al.*, 1996; Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Trippel and Neil, 2004). Recent captive studies have reported haddock to be characterized by a much lower fertilization and hatching success compared to cod (Trippel *et al.*, 1998; Trippel and Neil, 2004; Peck *et al.*, 2004; Rideout *et al.*, 2005).

The Georges Bank Atlantic cod and haddock stocks have undergone significant changes over the last 40 years. Increased fishing mortality caused a reduction of older spawners and led to earlier maturity of younger fish that have lower egg viability and larval survival (Murawski *et al.*, 2001; Brodziak *et al.*, MS 2006; O'Brien *et al.*, MS 2006). Cod exhibit peak spawning on the northeastern part of Georges Bank in February–March, and haddock in March–April and their eggs and larvae are transported south and west along the southern flank with some part of the cohort retained on the shallower, central part of the bank (Lough *et al.*, 2006). Egg development is temperature dependent and hatching is typically 2–3 weeks post-fertilization at seasonal ocean temperatures (Buckley *et al.*, 2000).

Atlantic cod and haddock have been monitored by the Northeast Fisheries Science Center (NEFSC) annually since the 1970s by bottom trawl and plankton surveys. Time series data are available since 1978 on SSB and recruitment at age 1 (R), as well as egg and larval abundances. Ichthyoplankton surveys also have been used to provide an independent estimate of seasonal egg production (Berrien *et al.*, MS 1984) that could be compared with VPA-derived estimates of fecundity. Recent studies have attempted to account for inter-annual variability in egg and larval survival (Lough *et al.*, 2006; Mountain *et al.*, 2008).

The purpose of this study is to compare these two independent estimates of seasonal egg production over two decades (1979–1999). The relative comparison of cod and haddock egg production over the 20-year time series explores the hypothesis that higher egg mortality of the reduced age population of haddock has biased the seasonal egg production estimates of both haddock and cod.

Methods

SSB and R for Georges Bank cod and haddock during 1979–1999 were obtained from assessments conducted using the ADAPT VPA calibration method (Parrack, MS 1986; Gavaris, MS 1988; Conser and Powers, 1990). The VPAs were calibrated with indices of abundance from spring and autumn research bottom trawl surveys through 2005 (O'Brien *et al.*, MS 2006; Brodziak *et al.*, MS 2006). SSB was estimated within the software program (NOAA, 2008) as the product of VPA beginning year numbers of fish, commercial mean weight at age, and variable proportion of mature fish at age summed over all age classes. Maturation ogives were estimated with logistic regression of NEFSC spring bottom trawl research survey maturity data (O'Brien *et al.*, MS 2006; Brodziak *et al.*, MS 2006).

Fecundity estimates at length and age are known to vary annually but this information has not been collected routinely, therefore, a single fecundity model was applied for each stock. For Georges Bank cod, annual fecundity was estimated using NEFSC autumn research survey mean lengths at age in an exponential fecundity at length model from fish sampled on Georges Bank in February and March of 1999 and 2000 (McIntyre *et al.*, 2003). For Georges Bank haddock, annual fecundity was estimated using NEFSC autumn research survey mean lengths at age in a fecundity length model from fish collected on Georges Bank during January–March 1972–1973, (Livingston *et al.*, MS undated) where fecundity (F) in millions of eggs is a function of fork length (L):

$$F = 3.19L^{3.15}$$

($R^2 = 0.79$, $SE_b = 0.15$, $N = 121$, length range 50–75 cm). This fecundity-length relationship was not considered significantly different from the function derived in the Livingston study for a high stock period (1955–1956, Fig. 1). However, the mean fecundity derived for the low stock period (1970–1971) was slightly lower than that for 1972–1973, and was considered an underestimate due to the different preservation and counting methods used in their study. The Livingston fecundity-length relationship falls within the range of haddock fecundity relationships for southwest Nova Scotia (Waiwood and Buzeta, 1989) and eastern Nova Scotia (Blanchard *et al.*, 2003) and other stocks reported therein.

For both cod and haddock, annual egg production was estimated as the product of VPA beginning year numbers of fish, sex ratio (1:1), maturity, and fecundity at age, for ages one to ten.

Cod and haddock spawning and hatching abundance estimates from the NEFSC's ichthyoplankton surveys included the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) period 1977–1987 (Lough *et al.*, 2006), the Larval Herring period 1988–1994 (O'Brien *et al.*, 2003) and the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) period 1995–1999 (Mountain *et al.*, 2008). Egg data could not be located for the 1977

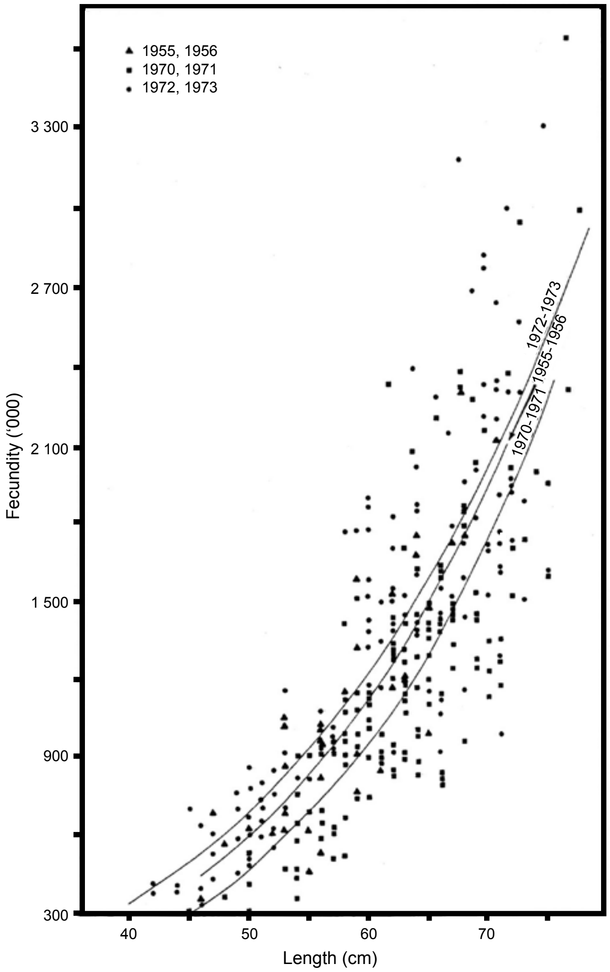

Fig. 1. Fecundity-length relationships for Georges Bank haddock collected during three periods: 1955–1956, 1970–1971, and 1972–1973 (R. Livingston *et al.*, MS undated).

and 1978 seasons. Considering survey coverage during the various sampling periods, the GLOBEC period provided the best coverage of the spawning seasons with monthly surveys from January through June, sampling the Georges Bank region with about 40 standard stations and frequently additional stations were sampled between standard stations in areas of abundant eggs and larvae. The MARMAP period sampled the region every two months with about 30 standard stations. Other years in the time series were only surveyed once or rarely twice during the spawning season so that we have the least confidence in these years to estimate seasonal spawning egg abundance.

Sampling methods and data procedures for the ichthyoplankton time series are described in full detail elsewhere (Lough *et al.*, 2006; Mountain *et al.*, 2008). Fish eggs were identified, staged and counted from quantitative 61-cm Bongo-net hauls. Counts of staged eggs were normalized to number 10 m^{-2} d^{-1} at ambient water temperature. Egg stage densities were averaged by survey (delta-mean) and survey means were expanded by the number of days represented by each survey and summed over the season's beginning and end times to estimate total number of eggs spawned 10 m^{-2}.

Distribution plots of all fish eggs collected on the MARMAP surveys are in Berrien and Sibunka (MS 1999) and on the GLOBEC surveys in Sibunka *et al.* (MS 2006). Cod and haddock eggs can only be separated as late stage eggs and both can be confused with witch flounder eggs (*Glyptocephalus cynoglossus*) during early developmental stages, so that the relative proportion of earlier stages was approximated by apportioning the total early abundance at a station in the same proportions as the older egg stages for the three species at the same or adjacent stations (Berrien and Sibunka, MS 1999). Assuming constant proportions assumes constant egg mortality for the three species. While cod and haddock eggs overlap closely with peak spawning in February–April on eastern Georges Bank, witch flounder peak spawning is in May–June and occurs along the southwest part of the Bank and in the Great South Channel (Sibunka *et al.*, MS 2006), thereby minimizing misidentification with this species.

Results

Cod SSB declined to a low in the mid-1990s with only a slight increase since the implementation of two year-round closed areas on Georges Bank in December 1994 (Fig. 2). Relatively high recruitment occurred for the 1980 and 1985 year-classes and moderate but above average recruitment occurred for the 1983, 1987 and 1990 year-classes. Since 1990, recruitment has been below average; however, the 2003 year-class was estimated to be above average in 2005 (O'Brien *et al.*, MS 2006). As cod declined on Georges Bank, a greater percentage of females matured at an earlier age (O'Brien *et al.*, MS 2006). Estimated maturity at age 1 was 8–10% for the MARMAP period 1978–1983 and 14–24% for the period 1984–1987. During the GLOBEC period 1995–1999 maturity at age 1 declined to 4–11%.

Haddock SSB also declined from a relative high during the late 1970s to a low in the early 1990s, but has steadily recovered since 1994 when the closed areas and other management measures went into effect (Fig. 3). The median size of haddock female maturity was 40 cm during 1977–1983 and declined to 34–36 cm in the

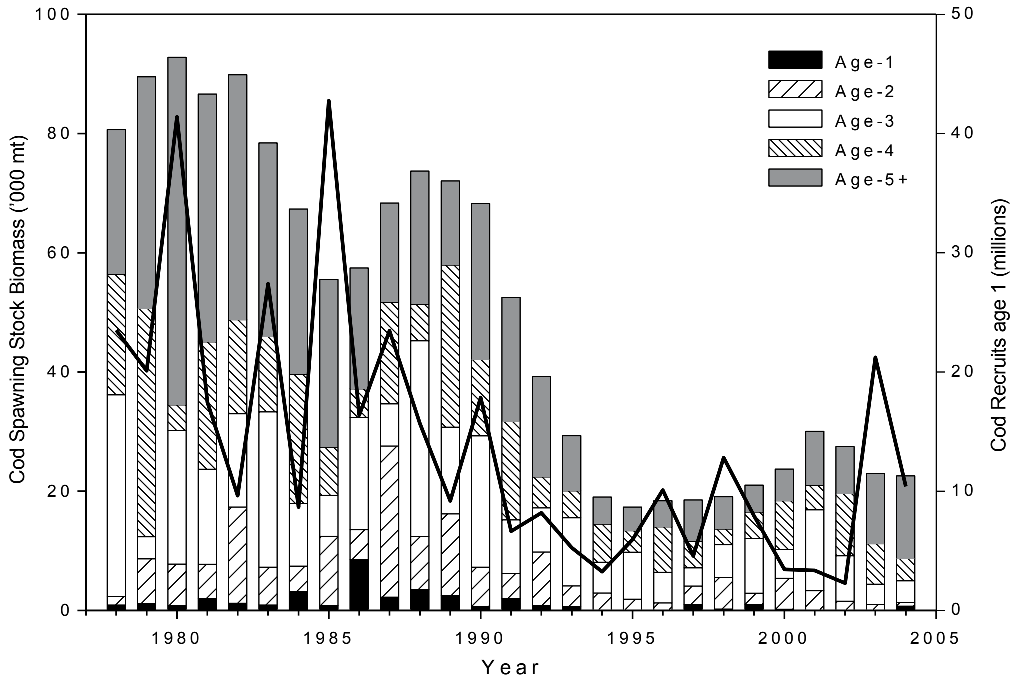

Fig. 2. Time series (1978–2004) of Georges Bank Atlantic cod VPA-derived SSB (bars) and recruitment at age 1 (solid line).

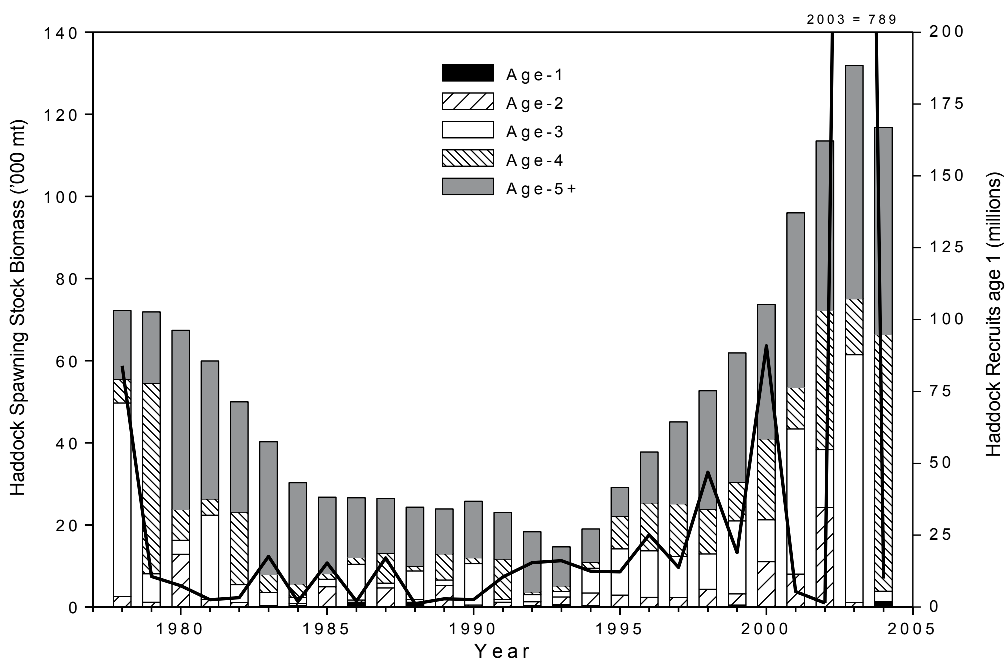

Fig. 3. Time series (1978–2004) of Georges Bank haddock VPA-derived SSB (bars) and recruitment age 1 (solid line).

early 1990s (Brodziak *et al.*, MS 2006). With older age classes entering the population, R also began to increase with the 1998 and 2000 year-classes comparable to that of 1978 and the 2003 year-class being the largest in the time series.

A comparison of Georges Bank cod seasonal egg production estimates from plankton Surveys and VPA did not indicate similar patterns (Fig. 4). One would expect the VPA-derived estimates to be higher than the estimates derived from the Surveys reflecting the differ-

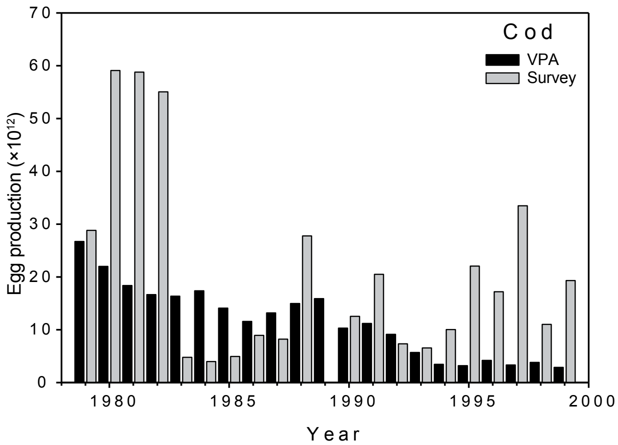

Fig. 4. Comparison of cod seasonal egg production from ichthyoplankton Survey (gray bars) and VPA-derived SSB fecundity data (black bars).

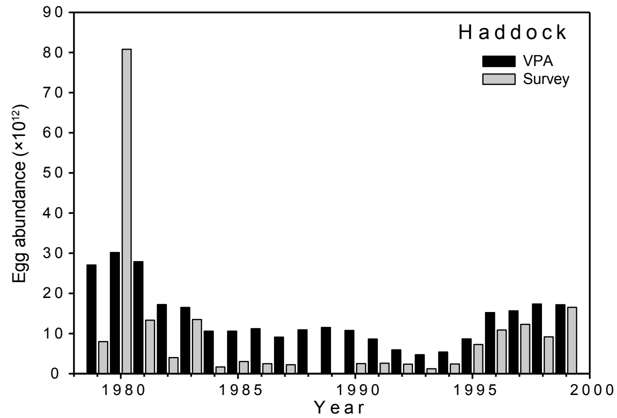

Fig. 5. Comparison of haddock seasonal egg production from ichthyoplankton Survey (gray bars) and VPA-derived SSB fecundity data (black bars).

ence between potential and realized fecundity. However, the Survey estimates were considerably higher than the VPA estimates, except for the years 1983–1987, 1990 and 1992, when they were slightly lower.

The comparison of haddock egg production from Surveys and VPA generally tracked each other over the time series with some exceptions such as for the 1980 Survey estimate, an obvious outlier (Fig. 5). In nearly all other years, the Survey estimates were lower than the VPA estimates. The Survey and VPA estimates were very close during the GLOBEC years 1995–1999 that had the best survey coverage.

The variability between the two independent estimates of cod egg production can better be seen when their ratios (Survey/VPA) are plotted against year (Fig. 6). The two estimates of egg production agree when their ratio equals unity. Also, the ratio of the VPA derived cod egg production to the combined VPA-derived cod and haddock egg production was plotted on the same figure for comparison. The Survey/VPA egg ratio was high during 1980–1982 and especially so during 1995–1999, when haddock was abundant and cod made up less than 50% of the combined egg production. When cod comprised a larger proportion of the combined egg production based on VPA, the Survey/VPA egg ratio was closer to one. It appears that when haddock is abundant, the Survey estimates of cod are inflated due to assigning a portion of the haddock egg mortality to cod. For cod, a regression plot of the ratio of seasonal production of Survey/VPA against the ratio of cod eggs/cod + haddock eggs VPA indicated a significant negative relationship (Fig. 7) where 68% of the variability (as determined

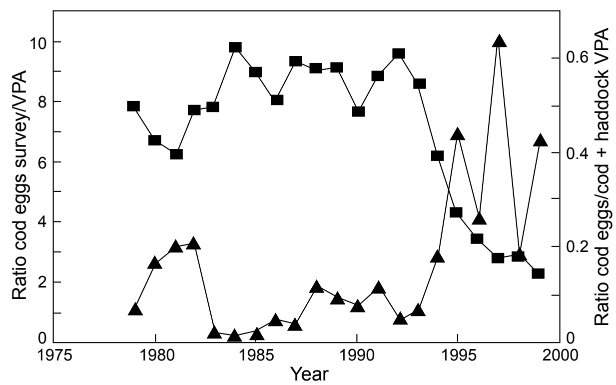

Fig. 6. Ratio of seasonal production of cod eggs Survey/VPA 1979–1999 (triangles). Ratio of cod eggs/cod + haddock eggs VPA (squares).

by R^2) in the ratio of seasonal production of cod eggs Survey to VPA may be explained by their contribution to the combined VPA egg production. The corresponding analysis for haddock (Fig. 8) showed the opposite trend (R^2 = 63%), that is when haddock egg abundance increased relative to cod VPA, the Survey/VPA ratio also increased. The slope observed in the cod regression is opposite of the expected positive slope as observed in haddock. The negative slope for cod and the ratio of realized: potential fecundity being greater than one suggests that the Survey estimate of number of cod eggs was overestimated when haddock abundance was high. Conversely, when cod abundance was high relative to haddock based on VPA, haddock egg production based on the Survey was greatly overestimated.

Given the uncertainty in the assumed egg mortality rates, the seasonal egg production could have been

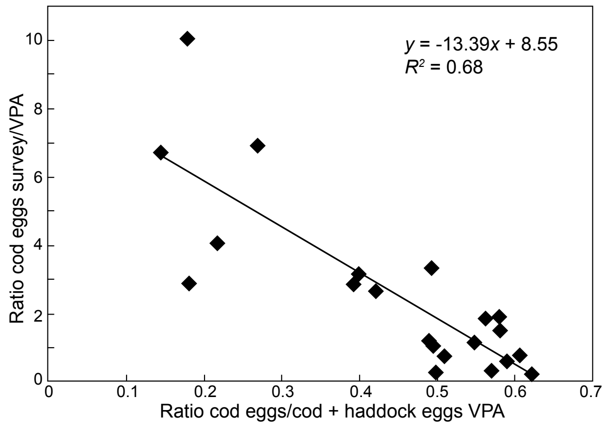

Fig. 7. Regression of ratio of seasonal production of cod eggs Survey/VPA to ratio of cod eggs/cod + haddock eggs VPA for the years 1979–1999.

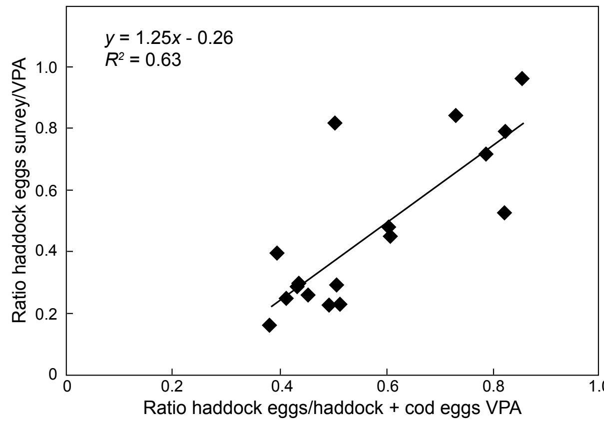

Fig. 8. Regression of ratio of seasonal production of haddock eggs Survey/VPA to ratio of haddock eggs/ haddock + cod eggs VPA for the years 1979–1999.

overestimated for cod and underestimated for haddock, especially since the mid 1990s. The unexplained variability may be related to other factors such as fecundity, age-class composition of the SSB, or change in mortality rates over the time series.

Discussion

Both egg production methods used in the present study have inherent uncertainty in their estimates. Coefficients of variation (CV's) for NE Atlantic cod stocks, SSB, and recruits are similar to those derived from ichthyoplankton surveys (Brander, 2003). The CV for age 1 in the terminal year of the assessment is about 58% for both cod and haddock (O'Brien *et al.*, MS 2006; Brodziak *et al.*, MS 2006). The CV for ages prior to the terminal year are not readily available but are expected to decrease each year as more of the year-class is accounted for and the model approaches convergence. Estimates of fish egg and larval production are imprecise and even for the most comprehensive surveys the average CV is about 30% (Pennington and Berrien, 1984; Hauser and Sissenwine, 1991).

SSB used as a metric for fishery management is generally considered as an overestimate of potential reproductive output particularly if the reduced age structure of a population includes a greater proportion of first or second time spawners that produce significantly less viable eggs and larvae (*e.g.*, Trippel, 1998; Murawski *et al.*, 2001). Cod is a batch spawner with egg size declining during the spawning season, but the number of batches and egg size are related to the female size and spawning history (Trippel *et al.*, 1997; Lambert *et al.*, 2003). Smaller cod eggs generally have higher mortality, especially for first-time spawners due to lower fertilization and hatching rates (Trippel, 1998). Six first- and six second-time spawner pairs of Bay of Fundy Atlantic cod collected during 1991–1992 were monitored for egg size and viability by Trippel (1998). Mean fertilization rates were only 20% for first-time spawners and 84% for second-time spawners. Hatching success of fertilized eggs from first-time spawners was only 57% verses 75% for second-time spawners. Seasonal composite hatching rates for first- and second-time spawners were 13% and 62%, respectively. Average seasonal egg diameters of first-time spawners were 1.43 ± 0.03 mm (mean ± SE) and for second-time spawners, 1.53 ± 0.01 mm. First-time spawners' average egg diameters declined between initial and terminal batches, whereas second-time egg diameters increased slightly from mid-February to March and then decreased through April.

Haddock also is a batch spawner and within a female the fecundity and mean egg diameter declines over the season (Hislop, 1988; Buckley *et al.*, 2000; Trippel and Neil, 2004; Rideout *et al.*, 2005). Haddock has a much lower fertilization rate and hatching rate of the fertilized eggs compared to cod. Batch-specific fertilization rates of six adult pairs of Bay of Fundy haddock had a mean seasonal composite of 38.5% compared to a mean of 70% for six adult pairs of Atlantic cod (Trippel *et al.*, 1998). Another study by Trippel and Neil (2004) of 22 captive Bay of Fundy adult haddock pairs (female mean length 53.4 cm, mostly second-time spawners) observed over the 1997–1999 spawning periods only had 57% of eggs fertilized, and of these only 31% hatched, resulting in only 20 ± 4% of the initial eggs spawned successfully hatched. Their low fertilization and hatching success was attributed not only to poor egg quality but also the male haddock had a much lower sperm output and density (spermatocrit) than cod (Trippel *et al.*, 1998). Better conditioned males had higher fertilization rates for captive Bay of Fundy haddock (Trippel and Neil. 2004). Rideout *et al.*'s (2005) study of haddock broodstock from the Bay of Fundy monitored during 2001–2003 also observed the wide variability in fertilization and hatching success that ranged 30–80%. And, Peck *et al.* (2004) collected cod and haddock broodstock from the Great South Channel for experimental purposes and noted the mean percent hatch in controls was significantly less for haddock (35%) than cod (75%). They also found that viable eggs made up a much larger portion of total eggs produced for cod compared to haddock.

Buckley *et al.* (2000) maintained Atlantic cod and haddock broodstock caught off Chatham, Massachusetts and evaluated the production and quality of eggs under altered temperature and photoperiod regimes during 1995–1997. Cod produced eggs from October through June and haddock, from December through May. Egg size of both species was similar with a mean diameter 1.45 mm for cod and 1.53 for haddock, range 1.25–1.76 mm. Egg diameters of both species increased in the autumn-winter as temperatures declined and decreased in the spring as temperatures increased (Chambers, 1997).

In regards to using VPA-based SSB to estimate total egg production, Trippel (1998) recommended multiplying the egg production of first-time spawners by about 0.10 and of second-time spawners by about 0.60 to account for differences in egg viability based on experimental results of Bay of Fundy cod. Other attributes of first-time spawners such as shorter spawning time, smaller eggs and less viable larvae also should be incorporated into spawner-recruitment models (Trippel, 1999). For haddock, the lower fertilization and hatching rates reported in Trippel and Neil (2004) were mostly based on second-time spawners. Based on the Trippel (1998) results, it might be reasonable to multiply the haddock egg production of second-time spawners by 0.20, and first-time spawners proportionately by 0.033.

Plankton surveys generally would be expected to underestimate seasonal egg abundance due to the wide spatial and temporal sampling and egg mortality processes. In April 1982, most eggs and larvae appeared to have been transported off Georges Bank and lost as a result of a strong storm (Lough *et al.*, 1994, 2006). The exceptionally high 1980 survey estimate of haddock eggs appeared to have been caused by the expansion of a few very high density stations sampled during recent spawning. Circulation modeling studies have indicated that haddock spawning on Browns Bank (Scotian Shelf) at times could be an important upstream source of eggs and larvae for Georges Bank (Brickman, 2003), although Scotian Shelf water overflows are only observed sporadically (Bisagni *et al.*, 1996; Smith *et al.*, 2003). Mountain *et al.* (2008) in an analysis of cod and haddock egg mortality from the GLOBEC Georges Bank surveys, 1995–1999, estimated that annual egg mortality might be attributed in part to off the bank wind-driven transport. The intercept from the regressions between annual observed egg mortality and modeled wind-loss mortality suggested a ~8–9% d^{-1} mortality due to other causes. Predation on eggs is always a contributing mortality process that may have been accentuated when the pelagic species Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) increased in the early 1980s (Garrison *et al.*, 2000; Segers *et al.*, 2007).

Egg diameters were measured from subsamples taken during the GLOBEC surveys (Mountain *et al.*, 2008). A sample of 50 eggs was taken from the March survey each year for cod and from the April surveys for haddock. Haddock had no significant change in median diameters (1.47 mm) each year, but cod decreased from 1.54 mm in 1995 to 1.47 mm in 1998 and 1999. The smaller egg size in cod may have been related to an increase in first- or second-time spawners after 1997.

There was a marked increase in the cod Survey egg estimates from 1980 to 1982 (Fig. 4) that could be partially attributed to the inflated egg estimates due to the moderate increase in haddock egg abundance during this period (Fig. 6). In 1983 a high fishing mortality (*F*) was reported on the 4–7 year old cod, decreasing from 48 395 mt in 1982 to 34 268 mt in 1983 (O'Brien *et al.*, 2005). Even though the total SSB did not decrease much from 1982 to 1983, the loss of these older fish reduced the potential number and viability of eggs spawned. Cod egg production estimated from VPA data did not track the year to year variability of the Survey data. In terms of having a reliable SSB-R relationship, it does not appear that we can use the VPA-derived seasonal egg production for cod for interannual comparisons because of the lack of yearly estimates of stock fecundity among other factors. Studies have shown that cod fecundity is very variable between stocks and years as a result of environment, fishing and genetics (Lambert *et al.*, MS 2005). On the other hand, haddock fecundity may be more stable for fish beyond first- and second-time spawning based on the fact that the Livingston fecundity-length relationships for three different periods of Georges Bank stock abundance were essentially the same. The haddock VPA-derived seasonal egg production based on the Livingston relationship generally paralleled the survey estimates, especially for the GLOBEC years. Nevertheless, there is still the need for age-specific annual measures of fecundity to estimate egg production from SSB.

For cod the significant relationship between the ratio of the two egg production estimates (Survey/VPA) (Fig. 7) and the ratio of VPA-derived cod eggs/cod + haddock eggs, was not just based on the five data points of high haddock abundance from the GLOBEC years, 1995–1999, but also the moderately high abundances during the MARMAP years, 1980–1982 (Fig. 6). These three years were the result of the large 1978 year-class coming into maturity as age 2, 3 and 4 before being fished down. Also, in the corresponding ratio analysis for haddock (Fig. 8), the significant reverse regression was based on a more even progression of data points. Therefore, there is credible evidence to state that differences in egg mortality between cod and haddock have introduced a systematic error into Survey derived estimates of yearly egg production for the two species that varies with their relative biomass. This error has implications to estimates of egg mortality rates among years and life stages.

This study indicates more uncertainty in previously published estimates of initial egg abundance and egg stage mortality rates of cod and haddock based on the assumption of constant mortality. One cannot assume that the eggs of related species have the same survival probabilities even under similar environmental conditions and stock structure. Molecular techniques have been used to resolve the problem of early stage egg identification of related species such as cod, haddock and whiting (*Melangius merlangus*) in Norwegian waters (Mork and Giaever, 1999), Irish Sea (Heffernan *et al.*, 2004) and North Sea (Taylor *et al.*, 2002); however, with the development of DNA-based genetic probes for rapid sample processing, an entire spawning ground has only recently been mapped in conjunction with ichthyoplankton surveys (Fox *et al.*, 2008).

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