Developing Alternative Indices of Reproductive Potential for Use in Fisheries Management: Case Studies for Stocks Spanning an Information Gradient

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Abstract

There is accumulating evidence to suggest that spawning stock biomass (SSB) may not be directly proportional to reproductive potential. The wide-ranging implications of this conclusion necessitate that it be tested for as many stocks as possible. Undertaking such tests is complicated by the fact that fish stocks vary in the amount and type of information that is available to estimate reproductive potential. In this review, nine stocks illustrate the range of

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approaches that are being taken to developing alternative indices of reproductive potential from existing data resources. Three stocks had sufficient data to reconstruct a time series of total egg production (TEP), whereas, the remaining stocks were limited to estimating proxies for stock reproductive potential. For some of the case studies the alternative indices explained a higher amount of recruitment variation than did SSB. Other case studies provided evidence that characteristics of the spawning stock, e.g. age diversity and female-only SSB, influence recruitment in ways that are not properly accounted for by using SSB as the sole index of reproductive potential. This is further evidence that the assumption of proportionality between SSB and TEP is invalid. The data-rich stocks showed the relationship between SSB and TEP to be variable and characterized by distinct time trends. This variability will impact the ability of biomass-based reference points to conserve reproductive potential. Consequently, management protocols should be adapted to incorporate the detailed information on reproductive potential that is increasingly becoming available rather than being restricted to approaches that have been designed for data-poor situations.

Introduction

One of the basic goals of fisheries management is to conserve sufficient reproductive potential of a stock to allow for sustainable exploitation. In the precautionary approach to fisheries management harvest control rules are developed and implemented to achieve this goal (Caddy, MS 1999). For many marine fish stocks harvest control rules are defined using reference points for both spawning stock biomass (SSB) and fishing mortality (NAFO, MS 1998; ICES ACFM, MS 1998a). In simple terms, a limit reference point indicates a level that should be avoided because the probability of negative consequences (such as impaired recruitment) is unacceptably high when that level is violated. Threshold reference points indicate a value beyond which the stock is considered to be in an acceptable area and wherein management targets may be set. Reference points are frequently established from the stock-recruit relationship (Table 1). Although there appears to be a central tendency for recruitment to be related to SSB (Myers and Barrowman, 1996; Brodziak *et al*., 2001), in practice the high degree of variability that is typical of many stock-recruit relationships impedes identifying either an underlying functional form or a specific level of SSB at which recruitment is impaired. If SSB over-estimates the reproductive potential of the stock, then the reference points derived using SSB will over-estimate the resiliency of the stock to fishing (Murawski *et al*., 2001).

One source of uncertainty in the stock-recruit relationship is the assumption that SSB is proportional to the reproductive potential of the stock (Rothschild and Fogarty, 1989; Trippel, 1999). It is equivalent to assuming that the relative fecundity (number of eggs produced per unit weight) of the stock is constant both temporally and spatially and that all eggs have the same probability of survival. The former assumption has long been recognized as invalid at the individual-level (Oosthuizen and Daan, 1974; Ware, 1980). Several recent studies have documented a high degree of variability in the relative fecundity of individual Atlantic cod (*Gadus morhua*) (Kjesbu *et al.,* 1998, Kraus *et al.,* 2000, Marteinsdottir and Begg, 2002). At the stock-level, skipped spawning and atresia have been observed (Kjesbu *et al.*, 1991; Witthames and Greer Walker 1995; Ma *et al.*, 1998; Marshall *et al.,* 1998; Bromley *et al.,* 2000; Rideout *et al.,* 2000). As both are observed in fish of poor condition, a high degree of interannual variability in per capita food abundance is likely to increase the divergence between SSB and total egg production (TEP). Reproductive potential is also affected by shifts in size composition because large/old spawners have higher relative fecundities, higher egg quality, and/or specific spawning behaviours that can make a disproportionately high contribution to recruitment (Zastrow *et al.,* 1989; Lambert, 1990; Secor, 2000a, b; Marteinsdottir and Begg, 2002). Likewise, shifts in the size composition of the spawning stock towards smaller size classes can result in the sex ratios becoming progressively skewed towards males because of their earlier maturation (Ajiad *et al*., 1999; Jakobsen and Ajiad, 1999). Thus, maturity ogives that do not account for gender could cause SSB to be disproportionately influenced by males. Furthermore, spatial and/or temporal segregation of spawners of differing sizes or condition can interact with the physical environment such that the surviving eggs have a higher probability of originating from sub-units of the stock (Vallin and Nissling, 2000; Begg and Marteinsdottir, 2003).

TABLE 1. Commonly used reference points for the management of marine fisheries (adapted from ICES, MS 1997 and NAFO, MS 1997).

Reference Point	Definition
$F_{0.1}$	F at which the slope of the Y/R curve is 10% of its value near the origin
F_{max}	F giving the maximum yield on a Y/R curve
F_{low}	F corresponding to a SSB/R equal to the inverse of the 10% percentile of the observed R/SSB
F_{med}	F corresponding to a SSB/R equal to the inverse of the 50% percentile of the observed R/SSB
F_{high}	F corresponding to a SSB/R equal to the inverse of the 90% percentile of the observed R/SSB
F_{MSY}	F corresponding to a Maximum Sustainable Yield from a production model or from an age-based analysis using a stock-recruitment model
$F_{40\%SPR}$	F corresponding to a level of SSB/R which is 40% of the SSB/R obtained when $F = 0$
F_{crash}	F corresponding to the higher intersection of the equilibrium yield with the F axis as estimated by a production model; could also be expressed as the tangent through the origin of a stock-recruit relationship
F_{loss}	F corresponding to a SSB/R equal to the inverse of R/SSB at the lowest observed SSB (B_{loss})
F_{lim}	F determined either objectively (e.g. lowest observed F) or subjectively based on stock history
F_{pa}	F determined either objectively (e.g. with reference to F_{lim} value) or subjectively based on stock history
F_{buf}	F that acts as a buffer to ensure that there is a high probability that F_{lim} is not reached
F_{target}	target F which depends on management objectives; corresponds to a level below or equal to F_{buf}
B_{MSY}	biomass corresponding to Maximum Sustainable Yield from a production model or from an age-based analysis using a stock-recruitment model
MBAL	a value of SSB below which the probability of reduced recruitment increases
$B_{50\%R}$	the level of SSB at which average recruitment is one half of the maximum of the underlying stock-recruit relationship
B_{loss}	lowest observed spawning stock size
B_{lim}	in general, the SSB level that the stock should not be allowed to fall below; in some cases the level of SSB below which recruitment is impaired
B_{pa}	the level of SSB associated with a very low risk of falling below B_{lim} value
B_{buf}	SSB that acts as a buffer to ensure that there is a high probability that B_{lim} is not reached
B_{target}	the target recovery level. In accord with Annex II of the UN Agreement of the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish stocks, for overfished stocks this is the SSB which would produce maximum sustainable yield

As a result of increased knowledge about the sources and magnitude of variability in TEP, the stock-recruit relationships for several stocks are currently being re-evaluated using alternative indices of reproductive potential (Marteinsdottir and Thorarinsson, 1998; Marshall *et al.,* 1998, 2000; Köster *et al.*, 2003). Two general categories of indices are possible: i) stock-based indices estimated from attributes of the spawners which approximate *potential* TEP; and ii) survey-based indices estimated from egg abundances measured during ichthyoplankton surveys which approximate *realized* TEP. Both categories of indices can be estimated either on an absolute scale (e.g. estimates of SSB or TEP) or on a relative scale (e.g. proxies such as age diversity or relative egg abundance). Examples of stock-based indices include: i) fecundity-based estimates of potential TEP by the stock (Köster *et al.,* 2001a); ii) bioenergetic indices (Painting *et al.,* 1998; Henderson *et al.,* 2000; Marshall *et al.,* 2000); iii) refinements to SSB through the incorporation of year-, area- and/or gender-specific information on maturity- and weight-at-age (Tomkiewicz *et al.,* MS 1997); iv) proxies derived from long time series describing the condition of individual spawners (Marshall and Frank, 1999; Blanchard, MS 2000); and v) proxies, such as age diversity indices, derived from basic demographic data provided by stock assessments (Lambert, 1990; Marteinsdottir and Thorarinsson, 1998; Secor, 2000a; O'Brien *et al.*, 2003). Examples of survey-based indices include: i) estimates of egg production (Brodeur *et al.*, 1996; Köster *et al.,* 2001a); ii) relative egg abundance (Morse, MS 1994; Mukhina *et al.*, 2003); and iii) proportions of tows containing eggs (Uphoff, 1997). For some stocks a combination of stock- and survey-based indices is proving useful for evaluating the relationship between potential and realized TEP (Köster *et al.*, 2003; Mukhina *et al.*, 2003).

This review illustrates several of the approaches being used to quantify reproductive potential by

presenting separate case studies for nine stocks distributed throughout the Atlantic Ocean and in the Baltic Sea. The majority of these stocks are currently outside safe biological limits or under moratoria (Table 2) although one has recovered from an earlier collapse. The stocks span an information gradient in the sense of having variable amounts of relevant data. Data-rich stocks could be considered to be those having sufficient fecundity data to permit estimating TEP on time scales that are comparable to those represented in the traditional stock-recruit relationship. Data-poor stocks could be considered as those that are restricted to proxies that can be derived directly from the analytical assessment (e.g. age diversity indices, female-only SSB) (Lambert *et al.*, 2003). The case studies presented here were not categorized specifically according to richness because in several cases the alternative indices presented herein under-represent the databases that are available. However, the case studies are presented approximately in descending order of the number and complexity of the indices that are described for the case study in this review. A more objective approach to ranking data availability for stocks in the Northwest Atlantic can be found in Tomkiewicz *et al.* (2003).

Each case study follows a similar format: the current management protocol is summarized with specific reference to the harvest control rules used, the alternative index of reproductive potential is described, and possible approaches for incorporating this information into stock management are indicated. There are three general approaches to evaluating the alternative indices: i) the index can be compared to a survey-based estimate of egg production; ii) the index can replace SSB in the bivariate stock-recruit model; or iii) the index can be used as an additional independent variable in a multivariate stock-recruit model. Each case study used at least one of these approaches to evaluating the indices. The case studies were not pre-selected to include only cases where improvements to the stock-recruit relationship were found. Rather, both positive and negative results are presented because all results were felt to be informative at this early, exploratory stage of inquiry. The general discussion identifies several key issues that must be addressed before the alternative indices can be fully integrated with existing management protocols.

Case Studies

Baltic cod

Current management protocol. The management of cod in the central Baltic (ICES Sub-divisions 25–32) has established B_{pa} and B_{lim} values equal to 240 000 tons and 160 000 tons, respectively (ICES ACFM, MS

1998b). The B_{pa} equals the former MBAL value (ICES, MS 1996) that was calculated using a constant maturity ogive and values of weight-at-age in the stock that were constant over the whole (ages 1–3) or part of the time series (ages 4–8). The B_{lim} was estimated as follows:

$$B_{lim} = B_{pa}e^{(-1.645\sigma)} \qquad (1)$$

where σ is the standard error of a cod biomass index derived from the Baltic International Trawl Survey (BITS). In 1998, the ICES Baltic Fisheries Assessment Working Group replaced the constant maturity ogive with a time series of area- and period- or year-specific ogives resulting in a substantial downward revision of the SSB values (ICES ACFM, MS 1998b), however, the biomass reference points were not revised.

Since 1998 the stock-recruit relationship for Baltic cod (Fig. 1) has been divided into a period where oxygen conditions were favourable for egg and larval survival (1966–80) and a period of unfavorable oxygen conditions (1981 to present). The F_{pa} of 0.6 was derived from medium-term simulations applying a stock-recruit relationship fitted only to data covering the latter time period (ICES ACFM, MS 1998b). These simulations used average (1995–97) values of stock weight- and maturity-at-age and, thus, the F_{pa} value does not account for the true magnitude of interannual variability in growth and maturation. The F_{lim} corresponds to the F_{med} value of 0.96 that was derived from a stochastic stock-recruit relationship that included the 1966–95 year-classes (ICES ACFM, MS 1998b).

Estimating stock reproductive potential. Area-specific estimates of weight-at-age are available by quarter as input to a Multispecies Virtual Population Analysis (MSVPA) that discriminates between the main spawning areas (Sub-divisions 25, 26 and 28) that account for 90–98% of the annual catch (Köster *et al.*, 2001a). To correct for the shift towards later spawning time that occurred during the late-1980s and early-1990s (Wieland *et al.*, 2000), the MSVPA abundance- and weight-at-age values were adjusted so that they correspond to peak spawning times. Historical and recent data on sex ratios and gender-specific maturity have also been compiled (Tomkiewicz *et al.*, MS 1997) and show that: i) males generally mature earlier; ii) maturity at age varies spatially and temporally; and iii) the proportion of males decreases with increasing age. These data have been used to re-calculate SSB and female-only SSB for each sub-division (Köster *et al.*, 2001b). The SSB values for the aggregated stock can therefore be obtained by integrating across sub-divisions.

TABLE 2. Stock status and management protocols for stocks included as case studies (biomass and landings are in tons).

Species	Cod					Haddock		American plaice	Striped bass
Stock	Baltic	Northeast	Icelandic Arctic	Flemish Cap	Scotian Shelf	Scotian Shelf	Georges Bank	Grand Bank	U.S. Coastal Mixed Stock
Management unit	ICES Sub-areas 25–32	ICES Sub-areas I and II		NAFO Div. 3M	NAFO Div. 4TVW	NAFO Div. 4X	NAFO Div. 5Z	NAFO Div. 3LNO	
Responsibility	ICES Baltic Fisheries Assessment WG	ICES Arctic Fisheries, WG	Marine Research Inst., Iceland	NAFO	Dept. of Fisheries and Oceans Maritimes Region	Dept. of Fisheries Fisheries Maritimes Region	Northeast Fisheries Science Center	NAFO	Atlantic States Marine Fisheries Commission
Basis for harvest	$B_{pa} = 240\,000$, $B_{lim} = 160\,000$, $F_{pa} = 0.65$, $F_{lim} = 0.96$	$B_{pa} = 500\,000$, $B_{lim} = 112\,000$, $F_{pa} = 0.42$, $F_{lim} = 0.7$	25% harvest control rule	$B_{lim} = 14\,000$	closed fishery, strict by-catch limitation	$F_{0.1} = 0.25$	$F_{0.1} = 0.26$	none	$F_{MSY} = 0.38$, $F_{target} = 0.31$
Current stock status	outside safe biological limits	outside safe biological limits	outside safe biological limits	collapsed, under moratorium	collapsed, under moratorium	overfishing not occurring, stock recovering	overfishing not occurring, stock recovering	collapsed, under moratorium	fully recovered
Average landings (time period)	175 284 (1966–2000)	671 005 (1946–2000)	350 871 (1930–1999)	23 098 (1972–1995) 1 329 (1996–2000)	15 203 (1954–1993) 104 (1994–2000: by-catch only after closure)	120 549 (1960–1999)	32 480 (1931–2000)	39 610 (1960–2000)	4 188 (1982–2000)
Current landings (year)	66 051 (2000)	414 144 (2000)	235 199 (2000)	55 (2000)	71 (2000)	7 800 (1998)	8 768 (2000)	5 176 (2000)	10 701 (2000)
Average spawner biomass (time period)	299 713 (1996–2000)	372 934 (1946–2000)	501 023 (1955–2000)	17 854 (1972–1995) 3 097 (1996–2000)	9 960 (1970–2000)	35 883 (1970–1999)	76 890 (1931–2000)	96 654 (1960–2001)	9 334 (1982–2000)
Current spawner biomass (year)	87 082 (2000)	222 703 (2000)	226 000 (2000)	3 056 (2000)	12 190 (2000)	34 994 (1999)	59 737 (2000)	22 250 (2001)	20 625 (2000)

Fecundity data are available from several sources and time periods (e.g. Shapiro, 1988; Bleil and Oeberst, MS 1996; Kraus *et al.*, 2000; 2002). Intraannually, relative fecundity is independent of size and age and does not vary between spawning areas or between early- and late-spawners within spawning seasons (Kraus *et al.*, 2000). However, relative fecundity varies significantly among years with the interannual variation being significantly related ($r^2 = 0.72$, $P = 0.01$, $n = 11$) to clupeid prey availability expressed relative to adult cod biomass (Fig. 2). Potential TEP by the stock was therefore estimated by applying modeled values of relative fecundity (Kraus *et al.*, 2000) to the female-only SSB.

Ichthyoplankton surveys have been conducted at regular intervals throughout the spawning season (Wieland, 1995). Egg abundances were high during the 1970s then declined to low levels in the 1980s and 1990s with an intervening peak in 1994-95 (Fig. 3). Abundance has always been highest in Sub-division 25. Low abundances have been observed in Sub-divisions 26 and 28 since the mid-1980s. It is unclear whether this is due to the loss of cod eggs from the water column because the low ambient salinity prevents them from reaching neutral buoyancy. Consequently, only the egg abundance data from Sub-division 25 were used to estimate egg production rates. Two different time series of the daily realized egg production during the main spawning time (RDEP) exist: i) RDEP of the earliest egg stage (IA) based on years with four to six surveys (Köster *et al.*, 2001a); and ii) RDEP of early egg stage I based on years having a minimum of three surveys (Köster *et al.*, 2003).

Because of the relative richness of the databases for Baltic cod, the analytical approach that has been taken to identifying sources of recruitment variability is to compare abundances at adjacent early life history stages in a manner similar to a Paulik diagram (Köster *et al.*, 2003). Accordingly, different stock-based indices of reproductive potential were evaluated by comparing them to RDEP estimated for Sub-division 25 (Köster *et al.*, 2003). The stock-based indices included: i) SSB based on a constant maturity ogive (ICES, MS 1996); ii) SSB based on year- (or period-) and area-specific maturity ogives (Tomkiewicz *et al.*, MS 1997; CORE, MS 1998); iii) female-only SSB (Tomkiewicz *et al.*, MS 1997; CORE, MS 1998); and iv) potential TEP estimated from the female-only SSB as described above. There was no relationship ($r^2 = 0.03$, $P = 0.488$, $n = 16$) between the SSB computed on the basis of the previously used constant maturity ogive and RDEP of egg stage I (Fig. 4a; Köster *et al.*, 2003). However, the correlation with RDEP became significant ($r^2 = 0.30$,
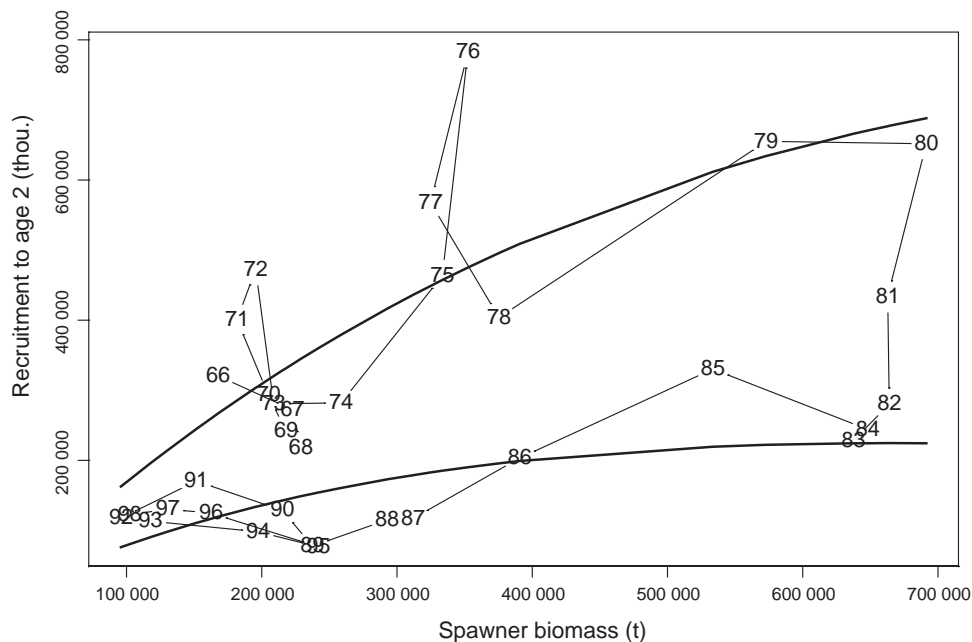

Fig. 1. Stock-recruitment relationships for the Baltic cod stock (data source: ICES ACFM, MS 2001a). The data points are labeled by year-class. The curves shown are Ricker curves fit to data from 1966–80 and 1982–2000, separately.
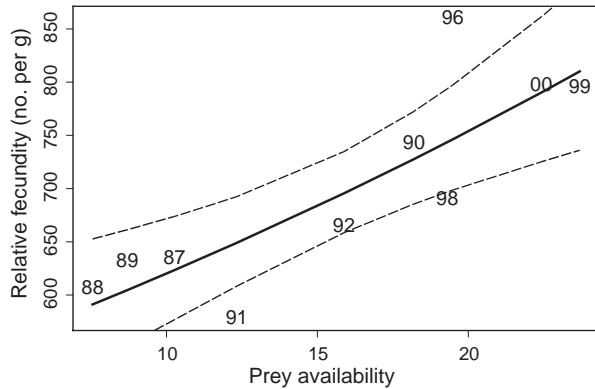
Fig. 2. The relationship between the relative fecundity of Baltic cod (number of eggs per g total body weight) and prey availability expressed as the total biomass of sprat and herring age 0–2 divided by adult cod biomass. Observations (labeled by year), modeled relationship (solid line) and 95% confidence intervals (dashed line) are shown. Fecundity relationship is from Kraus *et al.* (2002).
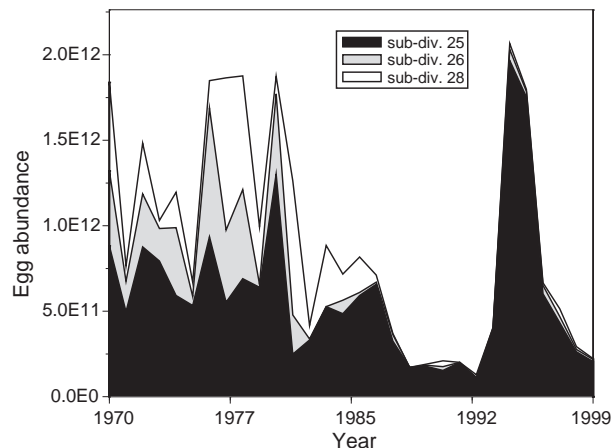

Fig. 3. Time series of the total abundance of cod eggs in ICES Sub-divisions 25, 26 and 28 of the central Baltic Sea during the main spawning period (month of peak spawning ± one month).

$P = 0.027$) when year- (or period-) and area-specific maturity ogives were used to estimate the SSB (Fig. 4b) and the significance level increased substantially ($r^2 = 0.61$, $P < 0.001$) when female-only SSB was used (Fig. 4c; Köster *et al.*, 2003). A small improvement to the fit ($r^2 = 0.63$, $P < 0.001$) was obtained using the potential TEP of the stock (Fig. 4d). These results suggest that part of the variability in the stock-recruit relationship currently used by management (Fig. 4b) results from using an index of reproductive potential that

does not properly account for the magnitude of variability in growth, maturity, sex structure and fecundity on TEP.

Incorporating this information into stock management. Most of the current biological reference points were calculated using values of SSB estimated with constant maturity ogives estimated for females and males combined. Consequently, a review of the biological reference points for this stock should be undertaken using the revised SSB time series. Substantial improvements to explaining variability in RDEP were achieved using female-only SSB or the potential TEP. These alternative indices could therefore be used to evaluate new values proposed for biomass reference points and/or establish alternative reference points.

It should be noted that the weight-at-age term is critical to estimating both female-only SSB and potential TEP (the latter being the product of two weight-dependent terms: female-only SSB and relative fecundity). The present assessment (ICES ACFM, MS 2001a) utilizes weight-at-age in the stock obtained from the BITS conducted in first quarter. Given that spawning takes place in summer, weight data from the second or third quarters are more relevant for the estimation of reproductive potential. Female-only weight data from surveys would be required to test whether the explanatory power of female-only SSB and TEP estimates could be improved by factoring in sexually dimorphic growth.

The alternative indices of reproductive potential have been used to develop environmentally-sensitive recruitment models (Fig. 5) which are of potential utility for medium-term predictions because they explain a higher portion of the recruitment variability than the models that are currently used. These models combine stock-based estimates of the potential TEP with processes such as egg mortality in relation to oxygen conditions, predation by clupeids and transport to suitable nursery areas. Models were developed for Sub-divisions 25, 26 and 28 using area-disaggregated estimates of the abundance of age groups 0 and 1 from the MSVPA as the dependent variable. The recruitment at age 0 predicted by the stock-recruit relationships summed across areas agrees well with the recruitment values from the MSVPA ($r^2 = 0.72$, $P < 0.001$, $n = 20$; Fig. 5) except for one outlying year-class (Köster *et al.*, 2001a). The predicted 0-group recruitment values from 1996 to 1999 were reasonably close to the observed (Fig. 5a; Köster *et al.*, 2003). As a further test of the models, predicted recruitment at age 1 (corrected for
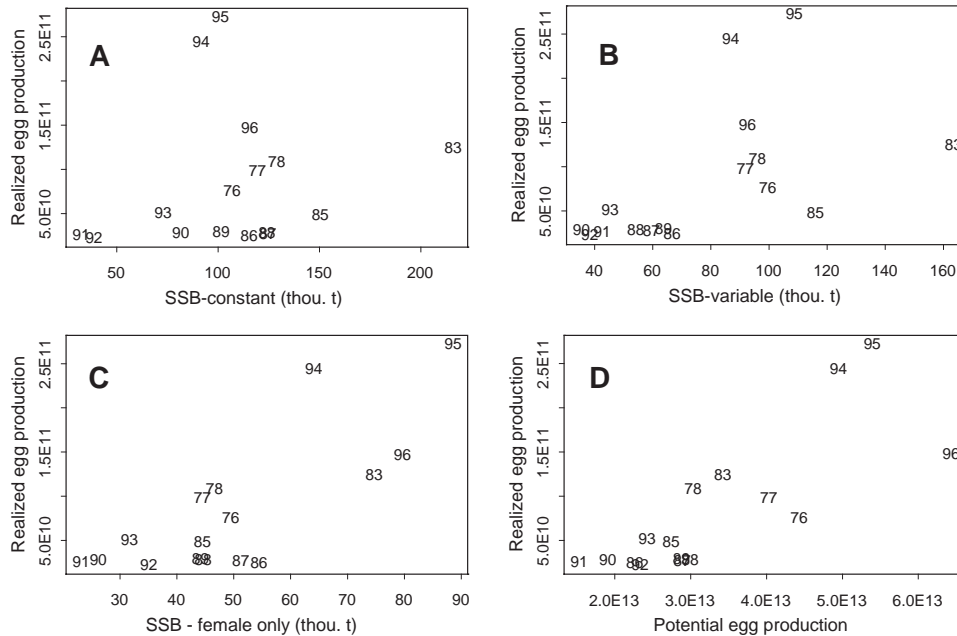
Fig. 4. The relationship between different stock-derived indices of reproductive potential and estimates of realized daily egg production of Baltic cod obtained from ichthyoplankton surveys conducted during the main spawning time (Sub-division 25 only). **a**) spawner biomass (SSB) estimated using constant maturity ogive, **b**) SSB estimated using year-(period-) specific maturity ogives, **c**) female-only SSB, and **d**) and potential TEP. Observations are labeled by year-class.

cannibalism, Köster *et al.*, 2001a, b) was compared with recruitment indices obtained from the BITS (Sparholt and Tomkiewicz, 2000). The time trends of decreasing recruitment throughout the first half of the 1980s and increasing recruitment in the 1990s are similar except for the years 1995 to 1998 (Fig. 5b). The poorer fit observed for the most recent time period may indicate that there is a problem within the recruitment index from the bottom trawl survey caused by a shift in spawning time.

Northeast Arctic cod

Current management protocol. The management for Northeast Arctic cod defines both limit and threshold reference points for both SSB and fishing mortality. The current value of B_{lim} (112 000 tons) corresponds to the lowest SSB value in the time series (i.e. B_{loss}) while the B_{pa} value has been set at the former MBAL value of 500 000 tons (ICES ACFM, MS 1999). The F_{lim} value (0.70) approximates the median value of F_{loss} (ICES ACFM, MS 1999), whereas, the F_{pa} value (0.42) corresponds to the 5th percentile of F_{loss}. These reference points influence scientific advice and management decisions through medium-term (5-year) stock projections in which the output variable is the probability of SSB falling below the B_{pa} under a variety of

harvesting scenarios including F_{pa}. Stochasticity is incorporated through uncertainty in the stock estimates of numbers-at-age and recruitment while the growth terms (maturity- and weight-at-age) are treated as constants and set equal to the average of the three most recent years.

The indeterminate nature of the biomass-based stock-recruit relationship (Fig. 6a) makes it difficult to establish a SSB value below which recruitment is impaired. For example, four years having high recruitment (1950, 1963, 1964 and 1970) are associated with SSB values considerably less than the B_{pa}. Prior to 2001, SSB values for the pre-survey time period were estimated using knife-edge maturity ogives (1946–81) and constant weight-at-age values (1946–82). Because the B_{lim} and B_{pa} have been derived from this SSB time series they are insensitive to the true effect that variation in growth has on stock dynamics.

In reality, the stock undergoes large and rapid fluctuations in growth. In 2001, the ICES Arctic Fisheries Working Group (AFWG) compiled historical Russian and Norwegian data to develop year-specific values for maturity- and weight-at-age for the pre-survey time period. Replacing the constant values with these year-
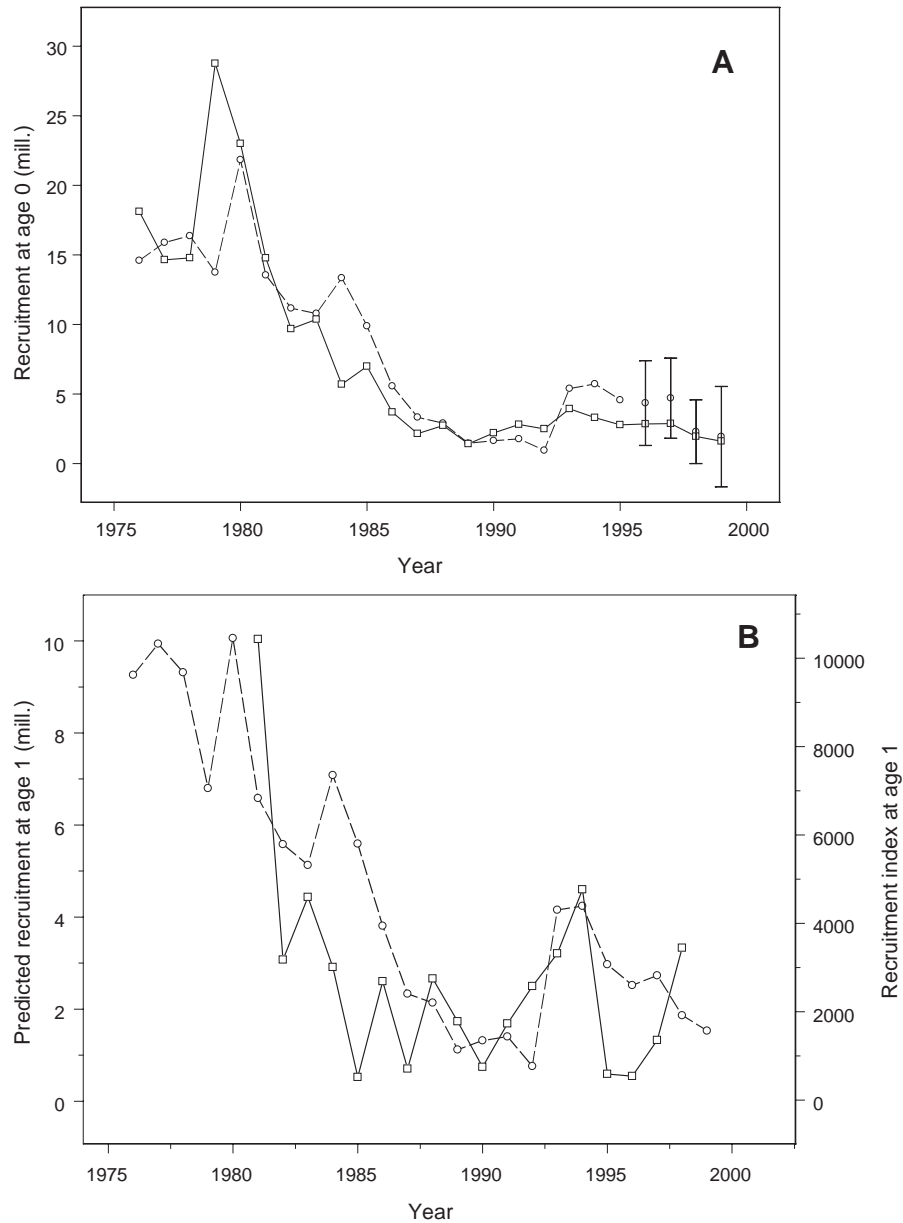
Fig. 5. Time series of recruitment of Baltic cod. **a**) recruitment at age 0 estimated from a Multi-species VPA (open squares, solid line) and predicted by a recruitment model which was developed for the time period 1976–95 based on estimated potential TEP (open circles, dashed line). Predictions for 1996–99 are shown with 95% confidence limits; and **b**) recruitment index at age 1 for Sub-divisions 25, 26 and 28 from the first quarter bottom trawl survey (open squares, solid line) and predicted recruitment estimated using a model similar to that used in the upper panel but which includes an additional term for cannibalism mortality of 0-group cod (open circles, dashed line).

specific values led to a substantial downward revision of SSB values such that the long-term mean decreased from 577 425 tons (ICES ACFM, MS 2001b) to 372 934 tons (ICES ACFM, MS 2001c).

The revision to the SSB time series as well as the high degree of variability associated with both the former and current stock-recruit relationships prompted concern about the appropriateness of the current
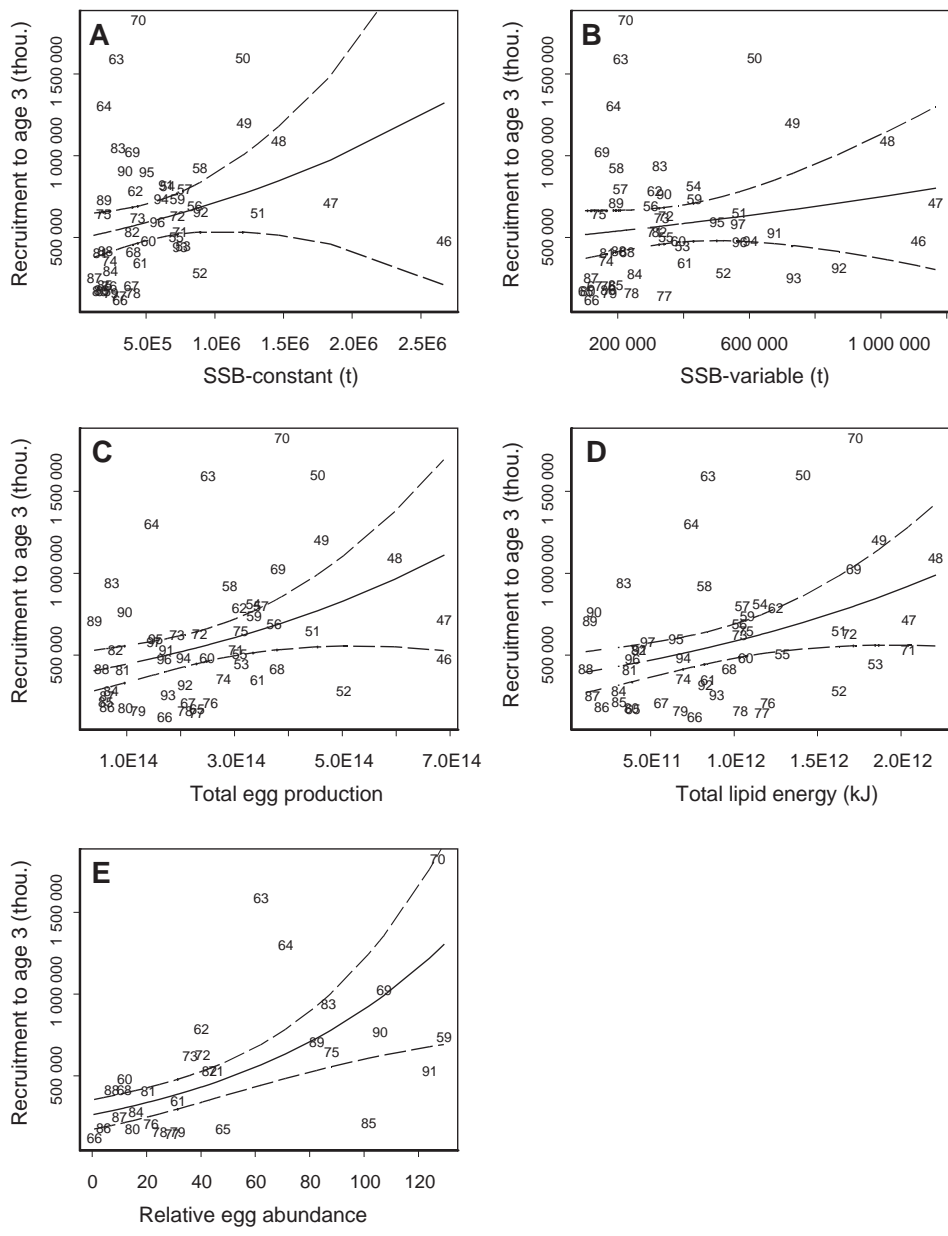
Fig. 6. The stock/recruit relationship for Northeast Arctic cod using different indices for reproductive potential. **a**) SSB calculated with constant values of proportion mature and weight-at-age for pre-survey time period (ICES ACFM, MS 2001b), **b**) SSB calculated with year-specific values of proportion mature- and weight-at-age for the full time series (ICES ACFM, MS 2001c), **c**) TEP (Marshall *et al.*, unpub. data), **d**) total lipid energy in livers of mature females (from Marshall *et al.,* 2000), and **e**) relative egg abundance (Mukhina, MS 1999). The recruitment index used is the abundance at age 3. Observations are labeled by year-class. The generalized linear model (family = gamma, link = log) and 95% confidence intervals are shown for each.

biomass reference points (ICES ACFM, MS 2001b, c). New methodology for deriving precautionary reference points (ICES ACFM, MS 2003a) was applied to derive new values of B_{lim}, B_{pa}, F_{lim} and F_{pa} using the revised SSB time series (ICES ACFM, MS 2003b). The proposed values were used in the most recent assessment of stock status (ICES ACFM, MS 2003c), however, they have yet to be formally adopted.

Estimating stock reproductive potential. As noted above, historical data from Russian and Norwegian sources were used to replace the constant values of maturity- and weight-at-age with year-specific values. The pattern of variability in the revised stock-recruit relationship (Fig. 6b) is similar to the relationship obtained using the original SSB values (Fig. 6a). As before, the high recruitment values in 1963, 1964 and 1970 are associated with values of SSB well below the B_{pa} and nearer to the B_{lim}.

Because reproductive traits such as maturity and fecundity are length- rather than age-dependent, TEP was estimated by converting the VPA numbers-at-age (1946–2000) to numbers-at-length using age/length keys developed from Norwegian sources. Length-dependent values of proportion of females were used to partition the stock into the numbers of females-at-length. These values were combined with year-specific values of the proportion mature females-at-length, predicted from a model that used capelin stock biomass to represent the year effect on growth (Marshall *et al.*, 2000), to estimate the numbers of mature females at length. A general fecundity model was developed using observations made during a time period when the condition of cod was changing rapidly due to the collapse and subsequent recovery of the Barents Sea capelin stock (Kjesbu *et al.*, 1998). This model was used to hindcast year-specific values of fecundity-at-length. The stock-recruit relationship having TEP as the independent variable shows a different pattern of variation than the biomass-based indices partly because the high recruitment years of 1963, 1964 and 1970 are associated with moderate values of TEP observed in these years (Fig. 6c). The low recruitment observed in the 1980s was associated with TEP values less than 1×10^{14}.

A bioenergetic index corresponding to the total lipid energy contained in the livers of mature females in the stock has also been developed (Marshall *et al.*, 2000) to take advantage of the long-term database on liver condition index (Yaragina and Marshall, 2000). The liver biomass of mature females (g) was estimated as the product of the numbers of mature females at length (estimated as for TEP), female-only weight-at-length and the length-specific value of the liver condition index. This value was then multiplied by the liver energy content (kJ per g) that is also derived from the liver condition index (Lambert and Dutil, 1997) to give total lipid energy in kJ. Total lipid energy and recruitment were both low in the late-1980s and early-1990s and the highest observed recruitment (1970) was asso-

ciated with total lipid energy in the upper 5th percentile of the time series (Fig. 6d).

Ichthyoplankton surveys of Norwegian and Barents Sea conducted between 1959 and 1993 (Mukhina *et al.*, 2003) provide a survey-based index of reproductive potential. The only index currently available for the entire survey time period expresses the mean egg abundance averaged across stations, depth strata and developmental stages (Mukhina *et al.*, 2003). This index shows that recruitment is impaired when relative egg abundance is low (Fig. 6e). Variation in recruitment increases with increasing relative egg abundance index and the maximum recruitment observed in 1970 corresponds to the second highest value in the time series.

The pattern of scatter in the different stock- and survey-based parameterizations of the stock-recruit relationship (Fig. 6a-e) was suggestive of non-constant variance. Consequently, a gamma model having a log-link function was fit to the data using a generalized linear models approach. This model assumes an exponential form to the stock-recruit relationship (i.e. Recruitment $= e^{a+b(ReproPot)}$), allows for errors to be non-normally distributed and specifies that the variability of the response variable increases with increasing mean value of the predictor. Model fit was assessed using the proportion of explained deviance (PED) as well as probabilities based on a F distribution of the test statistic. Recruitment was not significantly correlated with either of the SSB estimates (PED = 0.02, d.f. = 51, P = 0.45 for SSB with year-specific weights and maturities and PED = 0.06, d.f. = 50, P = 0.26 for SSB with constant values prior to 1981). Model fit was poor for both of these indices because variability in recruitment was highest at low levels of SSB, a property that is inconsistent with the assumption of the gamma model. Both TEP (PED = 0.13, d.f. = 51, P = 0.09) and total lipid energy (PED = 0.14, d.f. = 50, P = 0.07) had higher values of PED but were just above the P = 0.05 significance level. The correlation between relative egg abundance and recruitment was statistically significant (PED = 0.40, d.f. = 30, P <0.01). The increase in explanatory power going from the stock-based indices to the survey-based index suggests that the transition between potential and realized TEP could mark a critical stage in the development of year-class strength (Mukhina *et al.*, 2003).

In future, the estimates of TEP and total lipid energy will be refined using improved age/length keys, female-only maturity ogives and new software devel-

oped for computing TEP (ICES ACFM, MS 2003d). The Russian ichthyoplankton survey time series could also be used to generate indices of realized TEP that would be useful in assessing the accuracy of the stock-based indices.

Incorporating this information into stock management. At the present time, the alternative indices are not being used formally for stock management. However, the most recent assessment estimated the difference between female-only SSB and conventional SSB for a limited time period (1985–2001) using both Russian and Norwegian databases (ICES ACFM, MS 2003c). Both the Russian and Norwegian estimates show a strong tendency for female-only SSB to be less than half of the SSB. Females made an especially low contribution (*ca* 25%) in the years 1987 to 1989 and low proportions were also observed in 1994, 1995, 2000 and 2001. Thus, SSB overestimates the reproductive potential of the stock in those years by a considerable margin. The error is systematic in that it is driven by temporal changes in the age composition of the stock.

Introducing an alternative index of reproductive potential (e.g. female-only SSB or TEP) to stock management would require the development of alternative reference points. In principle, a limit reference point could be defined using the same methodology (segmented regression; ICES ACFM, 2003a, b) that was used to obtain the newly-proposed B_{lim} value. Implementation of alternative reference points in medium-term stock projections would require some means of projecting future values. There is a significant correlation between fecundity of cod and capelin stock biomass (Fig. 7) that is analogous to the relationship observed for Baltic cod and herring (Fig. 2). Consequently, fecundity in the upcoming year could potentially be predicted from the projections of capelin stock biomass that are now being provided annually to the AFWG (ICES ACFM, MS 2001b, c; ICES ACFM, MS 2002a) and used to forecast TEP.

Scotian Shelf haddock

Current management protocol. Two haddock (*Melanogrammus aeglefinnus*) stocks are found on the Scotian Shelf: the eastern Scotian Shelf haddock (NAFO Div. 4TVW) and southwestern Scotian Shelf haddock (NAFO Div. 4X). The Div. 4TVW haddock stock experienced a collapse in stock abundance in the early-1990s and since 1993 the stock has been closed to all fishing with the exception of a regulated by-catch in the silver hake (*Merluccius bilinearis*) fishery (Frank *et al.,* MS 1997). Reference points have not been used for management of the Div. 4TVW haddock fishery.
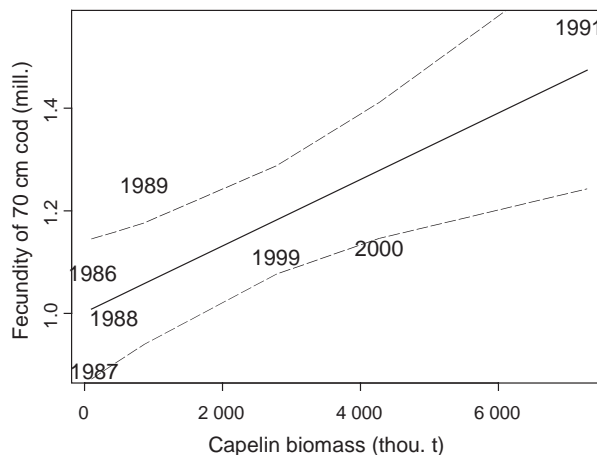

Fig. 7. The relationship between capelin stock biomass and the fecundity of a 70 cm Northeast Arctic cod. Fecundity relationships for 1986–89 and 1991 are from Kjesbu *et al.,* (1998). Fecundity data for 1999 and 2000 are courtesy of A. Thorsen and O. S. Kjesbu (Institute of Marine Research, Bergen, Norway). Observations are labeled by year. A simple linear regression line is shown as the solid line ($r^2 = 0.66$, $P = 0.02$) along with 95% confidence intervals.

The Div. 4X haddock stock is managed through spawning area closures and catch quotas (Hurley *et al.,* MS 1998). Management uses $F_{0.1} = 0.25$ as a harvest control rule (Hurley *et al.,* MS 1998) and there are currently no biomass-based reference points for this stock.

Estimating of stock reproductive potential. Fecundity determinations were made from 1997 to 1999 for Div. 4TVW haddock (Blanchard, MS 2000). Using these data, a general fecundity model was developed using both length and condition as independent variables. Both the liver condition index and Fulton's k were evaluated as terms to represent the condition effect. Liver condition explained an additional 20% ($n = 213$, $P < 0.001$) of the variation in fecundity-at-length, however, due to the absence of historical liver weight data the model could not be applied retrospectively. Fulton's k explained an additional 15% ($n = 401$, $P < 0.001$) of the variation in fecundity-at-length and was used to represent the year effect in the general fecundity model. The TEP was calculated for 1979–99 using survey-based estimates of numbers-at-length, a 1:1 sex ratio, annual maturity ogives and the aforementioned fecundity model (Blanchard, MS 2000). The correlation between TEP and recruitment (defined as the average number of individuals observed at ages 1 and 2 from the July surveys) was not significant ($r = 0.01$, $n = 21$, $P > 0.05$). Likewise, the relationship between

SSB (defined as the biomass of ages 3 and older) and recruitment was not significant ($r = -0.05$, $n = 21$, $P > 0.05$).

Condition indices derived from weight/length data are potentially a useful proxy for reproductive potential given that positive correlations with recruitment have been noted previously (Marshall and Frank, 1999). Therefore, the predicted weight at 45 cm was estimated for both Div. 4TVW and Div. 4X haddock using available survey data. For Div. 4TVW haddock mean annual pre-spawning condition (measured in March) and recruitment were not significantly correlated ($r = 0.03$, $P > 0.05$, $n = 20$). However, the correlation became significant when the strong 1999 year-class was deleted ($r = 0.57$, $P < 0.05$, $n = 19$; Fig. 8a). The condition index calculated for the July survey in the year preceding spawning was uncorrelated with recruitment either with ($r = 0.24$, $P > 0.05$, $n = 20$) or without ($r = 0.36$, $P > 0.05$, $n = 19$; Fig. 8b) the observation for 1999. A weak, positive correlation between pre-spawning condition (measured in March) and recruitment has previously been reported for the Div. 4X haddock stock (Marshall and Frank, 1999). Updating this relationship was not possible since the spring groundfish surveys have been discontinued. Condition measured in July of the year preceding spawning and recruitment was not significantly correlated with recruitment ($r = 0.038$, $P > 0.05$, $n = 29$; Fig 8c).

Incorporating this information into stock management. A recent assessment of Div. 4TVW haddock used a traffic light analysis (Caddy, MS 1999) to summarize different indicators of stock status over the time period 1970–2001 (Frank *et al.,* MS 2001). These indicators included information on condition, fecundity and TEP as well as survey abundances, distributional area, SSB, temperature, and exploitation rates. The most recent assessment of Div. 4X haddock included information on condition as a qualitative indicator of stock status (Hurley *et al.,* MS 1998). Given the relatively high degree of interannual variability in condition for both haddock stocks, further evaluation of variability in reproductive potential would be useful.

Striped bass in Chesapeake Bay

Atlantic striped bass (*Morone saxatilis*) is a long-lived, anadromous species supporting estuarine and coastal fisheries along the east coast of North America. The stock is maintained by recruitment from Chesapeake Bay sub-populations (ASMFC, MS 1998). The recreational and commercial sectors target older (females >80 cm) and younger (young males and imma-
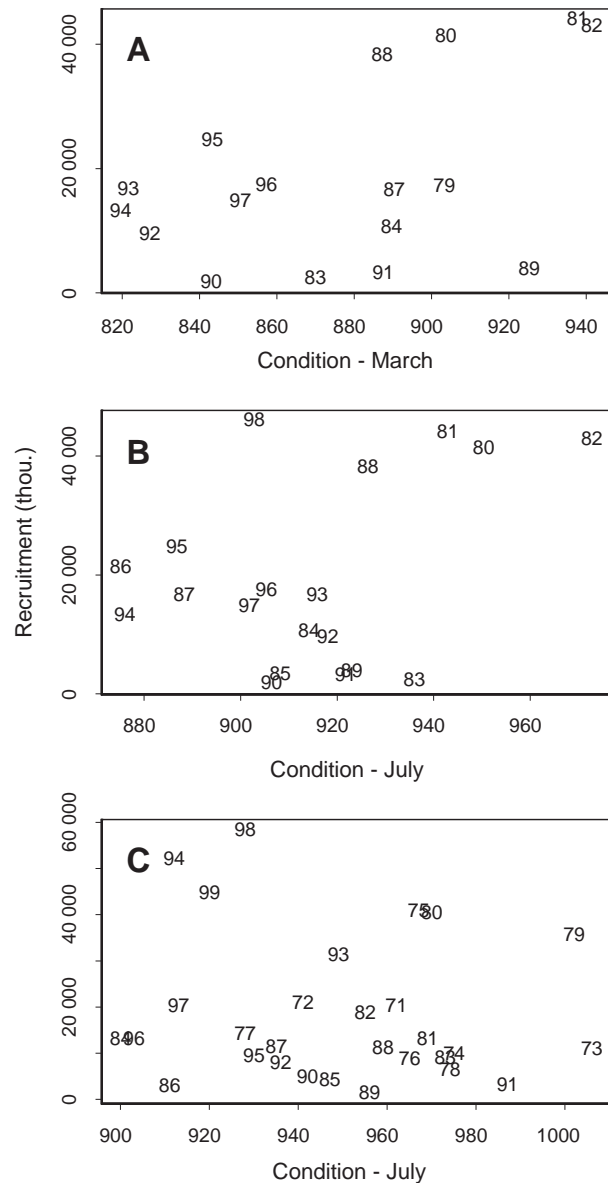

Fig. 8. Relationship between condition (expressed as the predicted weight (g) at 45 cm) and recruitment (defined as the average number, in thousands, by year-class at ages 1 and 2) for Scotian Shelf haddock. **a)** condition of Div. 4TVW haddock in July of the year preceding spawning; **b)** condition of Div. 4TVW haddock in March of the spawning year; and **c)** condition of Div. 4X haddock in July of the year preceding spawning. For Div. 4TVW the outlying observation for 1999 is not shown.

ture females 46–80 cm) individuals, respectively. In the late-1970s to early-1980s the targeting of small individuals by the commercial fishery resulted in a stock collapse (Goodyear *et al.*, 1985; Richards and Rago, 1999; Secor, 2000b). Stringent regulations enabled the

relatively strong 1982 year-class to fully recruit to the spawning population with several strong year-classes following. Thus, striped bass in Chesapeake Bay is an example of a stock that has been successfully rebuilt through effective and timely management measures (Field, 1997).

Current management protocol. Spawner abundances are monitored for major sub-populations and used to tune the VPA. Recruitment is measured by a young-of-the-year juvenile index (1957–present) for several nursery habitats throughout Chesapeake Bay (Goodyear, 1985). The stock-recruit relationship for striped bass can be fit using either a Ricker model (Crecco, MS 2001) or a Beverton-Holt model (G. Shepherd, National Marine Fisheries Service, Woods Hole, MA, pers. comm.). There are no biomass reference points, however, the stock-recruit relationship shows clear evidence of impaired recruitment at low levels of SSB (Fig. 9). The current threshold reference point for F ($F_{MSY} = 0.38$) is based on a Shepherd stock-recruit model and a Thompson-Bell Y/R model (ASMFC, MS 1998). The effects of varying exploitation rates are evaluated under the constraint of maximizing recruitment per spawner.

Estimating stock reproductive potential. A proxy for reproductive potential was constructed by estimating the fecundity-weighted age diversity (H_{obs}) for three
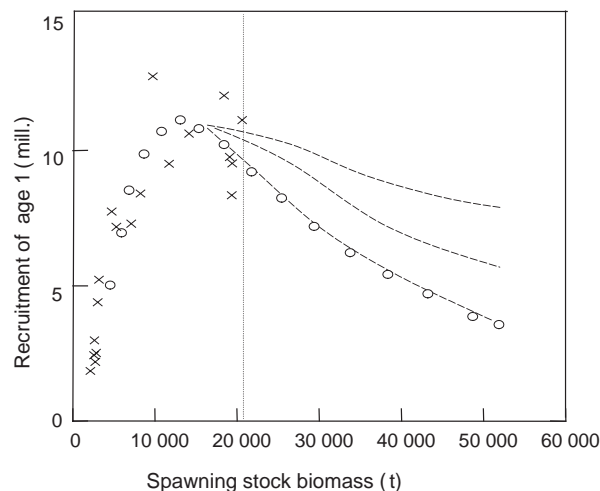

Fig. 9. The stock-recruit relationship for U.S. Atlantic striped bass (1982–2000). The vertical line indicates the boundary between regions with and without observations. Data from virtual population analysis (ASMFC, MS 2001) are shown as crosses. Values from a Ricker model fit by Crecco (MS 2001) are shown as circles. Dashed lines are alternate extrapolations of the Ricker model.

sub-populations (Choptank River, Potomac River, and Upper Bay) for the time period 1985–2000 as:

$$H_{obs} = \sum q_t \times \log_2 q_t \qquad (Eq. 2)$$

where q_t, the proportional egg production at age t, is estimated as:

$$q_t = CPUE_{ft} \left(\sum_{t=5}^{K} CPUE_{ft} \right) \qquad (Eq. 3)$$

and where $CPUE_{ft}$ is estimated as $CPUE_t \times mt$ with mt representing the fecundity schedule and K corresponds to the maximum age (35 years). Fecundity schedules were fit for two separate age stanzas (Secor, 2000a). Adjustments were made to the $CPUE_{ft}$ values for gear efficiency and to age estimates for discrepancies resulting from the use of scales (Secor *et al.*, 1995). Consequently, the values of H_{obs} reported here differ slightly from those given in Secor (2000a).

To provide a benchmark against which H_{obs} could be judged the fecundity-weighted age diversity of an unexploited population (H_{max}) was estimated as:

$$H_{max} = -\sum p_t \times \log_2 p_t \qquad (Eq. 4)$$

where p_t, the proportional egg production at age t, is estimated as:

$$p_t = R_t \left(\sum_{t=5}^{K} R_t \right) \qquad (Eq. 5)$$

and where o_t is the reproductive rate at age t ($o_t = l_t \times mt$) with l_t being the survivorship schedule for an unexploited population of striped bass (Vetter, 1988). In an unexploited population the proportional egg production by age (p_t) reaches a maximum at age 8 and then declines (Fig. 10). The proportional egg production by age (q_t) for the Potomac River sub-population in 1998 is similar to the pt for an unexploited population, whereas, the values of q_t for 1989 are highly skewed towards younger ages (Fig. 10). The degree of similarity between fecundity-weighted age diversity in exploited and unexploited stocks (%H_{max}) was then estimated for each year and sub-population as the ratio of H_{obs} to H_{max}. The %H_{max} provides ancillary information that is specific to population resiliency. The index is similar to egg production per recruit (EPR) indices (Boreman, 1997).

In the Potomac River and Upper Bay sub-populations, %H_{max} varied between 31 and 95% during the period of collapse and recovery (Fig. 11). The
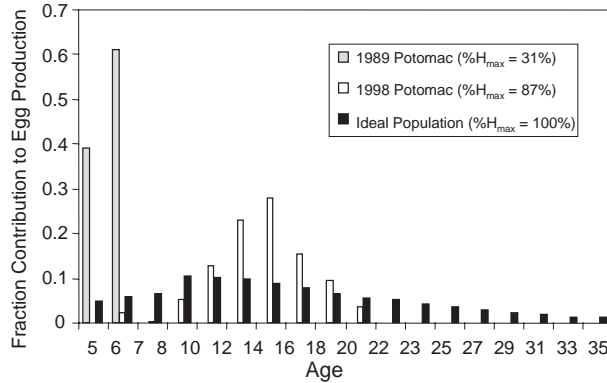
Fig. 10. Comparison of the proportional egg production by age in an unexploited (ideal) striped bass population and the observed proportional egg production by age for the Potomac River stock in 1989 and 1998.

Fig. 11. Time trends in %H_{max} for three Chesapeake Bay striped bass spawning stocks (Choptank and Potomac Rivers and Upper Bay), as monitored by the Maryland Department of Natural Resources (MD DNR, MS 2001).

Choptank River sub-population showed less variation, ranging between 60 and nearly 100%. In 1985 and 1986 SSB was low in all three sub-populations, however, %H_{max} was high (Fig. 11) due to the presence of older age-classes. From 1987 to 1989 the strong 1982 year-class dominated the age structure of spawners, lowering the value of %H_{max}. Furthermore, the contribution from age-classes older than 20 years decreased during this time period (Secor, 2000b).

Maximum recruitment in the Choptank River was consistently associated with high spawning stock abundances. However, under some circumstances fecundity-weighted age diversity could influence recruitment independently of SSB. For example, in Upper Bay (Fig. 12) there were several >50% percentile recruitment years that were well below median spawning stock size but for which %H_{max} exceeded 50%. This suggests that there is spatial variation in how age structure impacts the reproductive potential of the sub-populations.

Additional evidence of the role of reproductive potential in recruitment dynamics of striped bass is provided by ichthyoplankton surveys of Chesapeake Bay. The proportion of tows in which striped bass eggs were caught has been used as a proxy for reproductive potential (Uphoff, 1993; 1997). Recruitment is correlated with the proportion of tows with eggs for the Choptank River sub-population ($n = 11$, $r = 0.45$, for the years sampled between 1985–2000; J. Uphoff, MD Department of Natural Resources, pers. comm.). Pooling information across sub-populations suggested that strong year-classes were only produced in those years
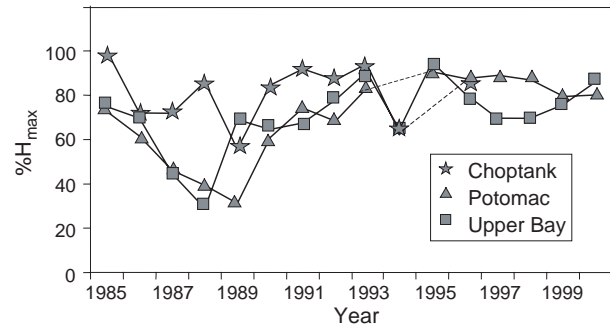
for which egg presence/absence ratio was higher than 60% (Uphoff, 1997).

Incorporating this information into stock management. The alternative indices of reproductive potential are not used in management, however, developing alternative indices of reproductive potential has highlighted limitations in current knowledge. The fecundity schedules are poorly known and estimates of p_t and q_t were obtained from a North Carolina population (Olsen and Rulifson, 1992). Research is now underway to model age-specific fecundity in the Chesapeake Bay (R.A. Richards, National Marine Fisheries Center, Woods Hole, pers comm.). Estimates of reproductive rate schedules deviate substantially among researchers depending on whether scales or otoliths are used to age striped bass. In large/old fish, the annuli in scales form at non-annual rates (Secor *et al.*, 1995), however, assessments still rely on scale-based ages. Consequently, the striped bass stock is likely to be comprised of individuals that are substantially older than is currently recognised in the assessment. This longevity may be critical in conferring population resiliency.

American plaice

Current management protocol. The American plaice (*Hippoglossoides platessoides*) stock in NAFO Div. 3LNO has been under moratorium since 1995. In 1998, a preliminary B_{lim} value was proposed based on analysis of the stock-recruit relationship (NAFO MS 1998). The SSB values used in the stock-recruit relationship were derived from a VPA from the early-1990s and used a knife-edge (9+) age at maturity. The
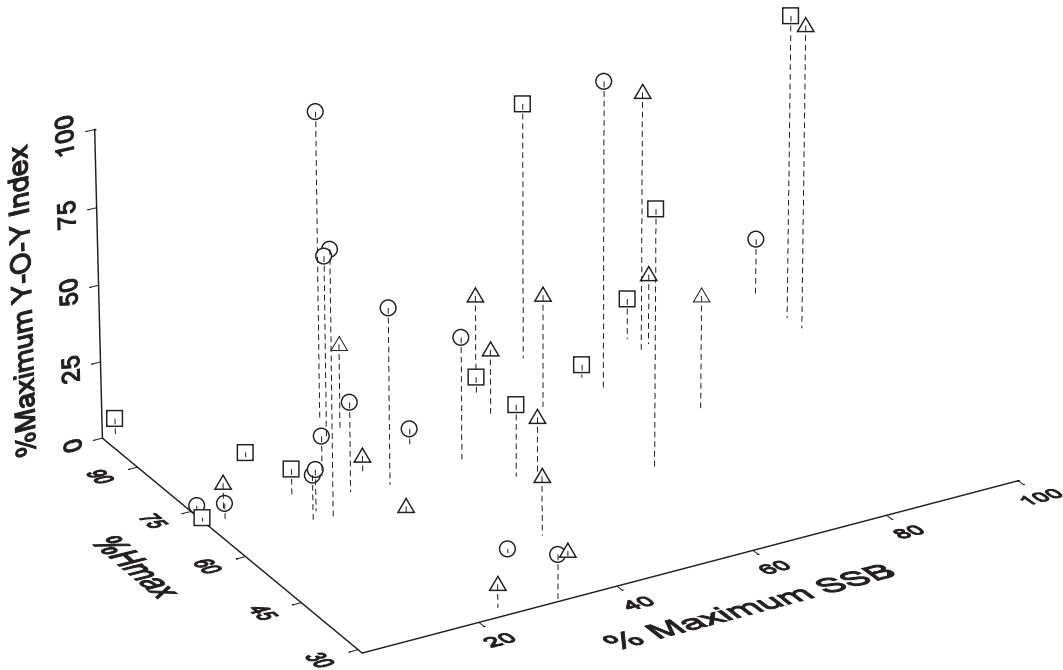
Fig. 12. Recruitment index of young-of-the-year (Y-O-Y) striped bass versus SSB and %H_{max} for Choptank (square), Potomac River (triangle) and Upper Bay (circle) systems. Measures of recruitment and SSB are expressed as % of maximum values for period 1985–2000. SSB and striped bass recruitment are from Maryland Department of Natural Resources fishery independent assessments of each system (MD DNR, MS 2001).

knife-edge maturity ogive overestimated SSB in the early part of the time series and it was later determined that this preliminary B_{lim} was too high (Morgan *et al.,* MS 1999). A recent assessment of this stock (Morgan *et al.,* MS 2001) used annual estimates of weight-at-age and estimates of maturity-at-age by cohort to estimate SSB resulting in a new stock-recruit relationship (Fig. 13). Various stock-recruit models were evaluated but all were found to over-estimate recruitment in recent years. Although poor recruitment is observed below a SSB of 50 000 tons, this value was not accepted as a B_{lim} because of time trends in the recruitment data (NAFO, MS 2001).

Estimating stock reproductive potential*. A Beverton-Holt stock-recruit model was fit to the SSB and recruitment data using maximum likelihood. The residuals were then plotted against: a) the weighted mean age of the SSB; b) the proportion of first-time spawners; and c) the proportion of female spawners. The proportion of first-time spawners (P_f) was calculated as:

$$P_f = \frac{\sum_{a=b}^{n} B_a P_a Pfi Ust_a}{\sum_{a=b}^{n} B_a P_a} \qquad \text{(Eq. 6)}$$

where B_a is the biomass-at-age from the VPA, P_a is the female proportion mature-at-age, P_{fa} is the proportion of first-time spawners at age estimated for individual cohorts, and b and n are the first and last ages (5 and 15+, respectively). For example, if 10% of the fish in a given cohort are mature at age 4 and 20% are mature at age 5 then one-half of the mature age 5 fish are first-time spawners.

The Beverton-Holt model tends to over-estimate recruitment from 1986–92, particularly relative to the years prior to 1986 (Fig. 13). There is a positive relationship between the residuals from the stock-recruit model and the weighted mean age of the SSB ($r = 0.55$, df = 35, $P <0.001$, Fig. 14a). There was no significant relationship with the proportion of female spawners
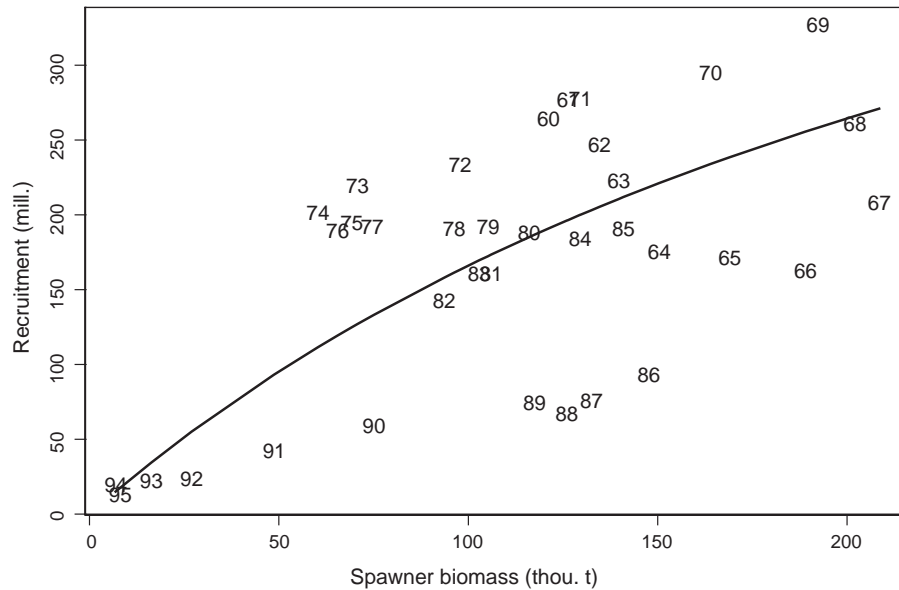
Fig. 13.   The stock-recruit relationship for American plaice in NAFO Div. 3LNO showing
observed (symbols) and recruitment to age 5 predicted from a Beverton-Holt
stock-recruit model (line). Observations are labeled by year-class.

(r = 0.36, df = 19, NS, Fig. 14b) or with the proportion of first-time spawners (r = -0.07, df = 35, NS; Fig. 14c). These results indicate that variations in sex ratio and in the proportion of first-time spawners have no effect on recruitment beyond that already accounted for by the stock-recruit relationship. It is notable that the proportion of female spawners is considerably less than half and in several years is less than 0.2 (Fig. 14c).

Incorporating this information into stock management. Some progress has already been made in the sense that SSB is now calculated using estimates of maturity-at-age rather than using a knife-edge maturity-at-age. The stock-recruit relationship could potentially be improved by including information on weighted mean age of the SSB either by adjusting the estimate of SSB or by including a term for weighted mean age as an extra parameter in the stock-recruit model.

Icelandic cod

Current management protocol. Management of the Icelandic cod stock uses a harvest control rule that sets the TAC for the next fishing year (beginning September 1) to 25% of the mean of the available biomass in the beginning of the current calendar year and the beginning of next year with the constraint that the TAC is never less than 155 000 tons. Available biomass is defined as the number of age 4 and older at the beginning of the year multiplied by the weight of those age

groups in the commercial catch. This biomass is considerably higher than the true biomass because the mean weight-at-age in the catch is higher than in the stock. Stochastic simulations indicated that the 25% harvest control rule would lead to an average fishing mortality of ages 5 to 10 of 0.4 with less than a 1% risk of stock collapse where stock collapse was defined as a SSB less than 100 000 tons (Jakobsson and Stefánsson, 1998).

The 25% harvest control rule was first implemented in 1994. Retrospective analyses done in 2000 and 2001 indicated that the stock had been overestimated and that the 25% harvest control rule had actually been followed only for the first two years (Anon., MS 2001). In the years that followed, the TAC had actually been 27–42% of the available biomass. Severe reductions in the TAC became necessary and the original 25% harvest control rule was amended to limit interannual changes in TAC to 30 000 tons and the 155 000 tons minimum TAC constraint was removed (Anon., MS 2001). Although the original 25% harvest control rule had been accepted by ICES as being in accordance with the precautionary approach, the subsequent amendment was not accepted (Anon., MS 2001).

Biological reference points have been proposed for this stock (Anon., MS 1998) but not adopted. Below-median recruitment occurs more frequently when SSB is below the long-term median 500 000 tons (Fig.
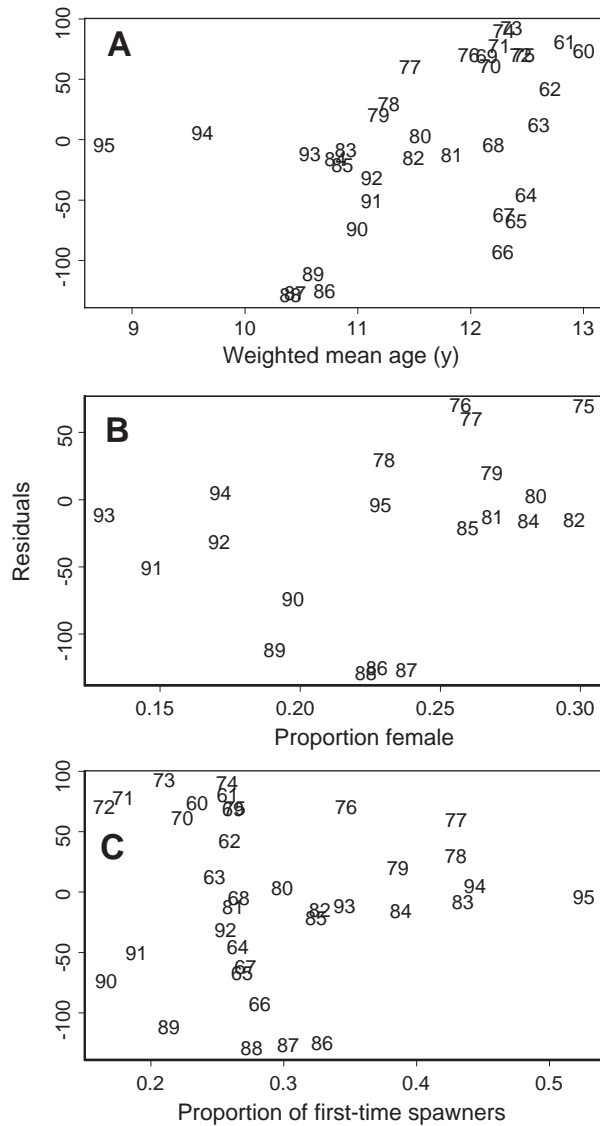
Fig. 14. Residuals from Beverton-Holt stock-recruit model for American plaice in Div. 3LNO plotted against potential proxies of reproductive potential. **a)** weighted mean age of the SSB, **b)** proportion of adults that are female and **c)** proportion of first-time spawners. Observations are labeled by year-class.

15). The proposed B_{pa} (300 000 tons) was based on the observation that the five weakest year-classes in the time period 1955–94 were generated in years having SSB values less than 300 000 tons (Fig. 15). The proposed B_{lim} value corresponds to the lowest observed SSB (200 000 tons).

Estimating stock reproductive potential. The proxy representing age diversity of the mature fish (H)

is estimated as:

$$H = (nlog_{10}(n) - \sum_{i=1}^{k} f_i log_{10}(f_i)) / n \qquad \text{(Eq. 7)}$$

where k is the number of age groups, n is the total number of mature fish in all age groups, and f_i is the number of mature fish in each age group (Marteinsdottir and Thorarinsson, 1998). The H shows a stronger degree of linear correlation with recruitment ($r^2 = 0.17$, $n = 43$, Fig. 16) than does SSB ($r^2 = 0.06$, $n = 43$, Fig. 15). A positive relationship between H and recruitment is consistent with observations that the size and age composition of spawners has a major impact on the amplitude of potential egg production, time and duration of spawning as well as offspring viability (Scott *et al*., 1999; Marteinsdottir and Björnson, MS 1999; Marteinsdottir *et al*., 2000a; Marteinsdottir and Begg, 2002).

In future, historical trends in egg production will be reconstructed from available data sources. Information on length distributions has been collected since the early-1900s. Fecundity determinations have been made intermittently (Joakimsson, MS 1969; Schopka, MS 1971; Marteinsdottir *et al*., 2000a; Marteinsdottir and Begg, 2002) and a relationship between atresia and female size, spawning stage and condition has recently been established (Hardardottir, MS 2001). Because the Icelandic cod stock consists of multiple spawning aggregations (Marteinsdottir *et al*., 2000b; Begg and Marteinsdottir, 2000; Begg and Marteinsdottir, 2002) the potential egg production has been estimated for 18 offshore and inshore areas separately (Begg and Marteinsdottir, 2003). Additional data on temporal variation in size and quality of eggs and larvae in relation to female size, age and condition (Marteinsdottir and Steinarsson, 1998; Marteinsdottir and Begg, 2002) will be used to further refine these estimates.

Incorporating this information into stock management. With respect to the management of Icelandic cod, no attempts have been made to incorporate information on age diversity or the influence of maternal size and condition on the timing, quality and amplitude of egg production into management. In recent years, large cod have been specifically targeted by the fishery due to a combination of high price for the cod and high cost of rental quota in the Icelandic quota system. This has led to severe reduction in the abundance of large cod. In coming years most of the spawning stock will be composed of the 1997 or younger year-classes thereby increasing risk of poor recruitment.
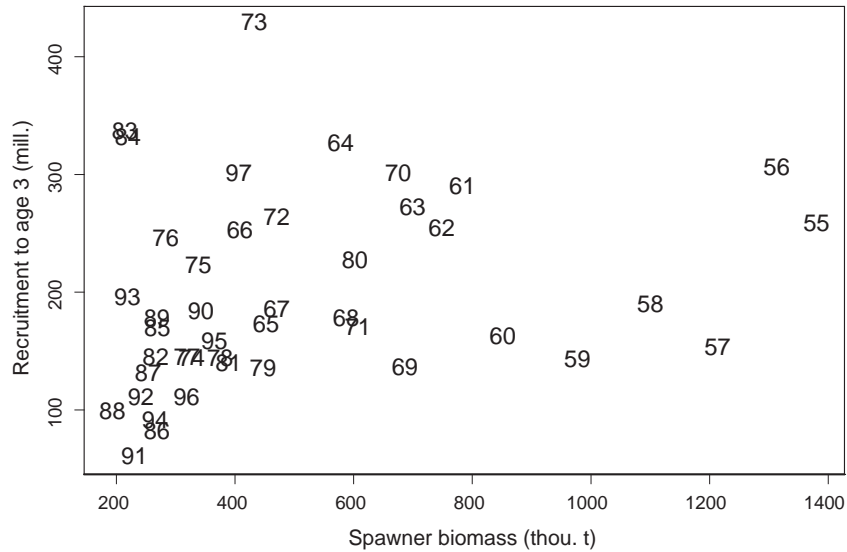
Fig. 15.   The scatterplot of SSB *versus* recruitment for Icelandic cod based on data from the most recent assessment (Anon., MS 2001). Observations are labeled by year-class.
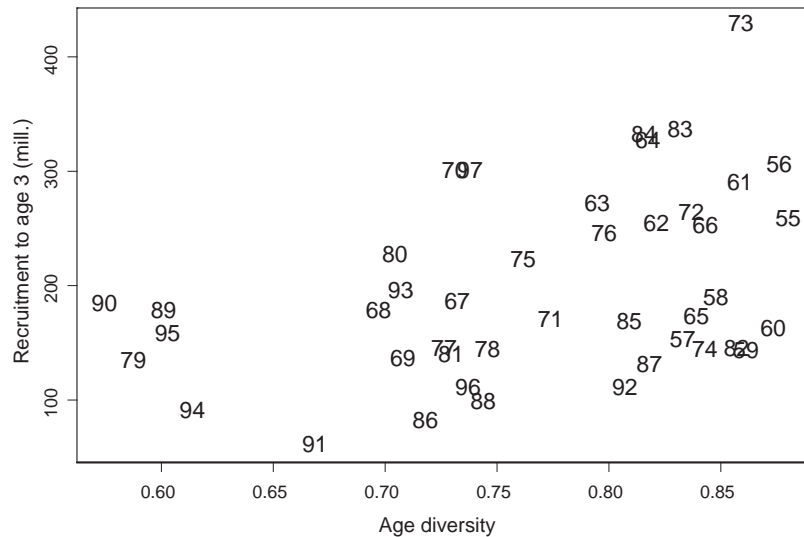

Fig. 16.   Relationship between age diversity and recruitment for Icelandic cod (updated from Marteinsdottir and Thorarinsson, 1998). Observations are labeled by year-class.

Georges Bank haddock

Current management protocol. The Georges Bank haddock stock (NAFO Div. 5Z) is a transboundary resource shared by the USA and Canada. The USA assessment is for the entire stock area, whereas, the Canadian assessment is for NAFO Subdiv. 5Zj and 5Zm only. In the USA, Div. 5Z haddock is managed by a target total allowable catch (TTAC) based on $F_{0.1}$. In

Canada, Subdiv. 5Zjm haddock is managed by a TAC, also based on $F_{0.1}$.

The stock-recruit relationship for Georges Bank haddock encompasses a 70-year time period (Fig. 17a). The data show a fan-shaped scatter of points with poor recruitment generally observed at values of SSB less than 75 000 tons and higher and more variable recruit-
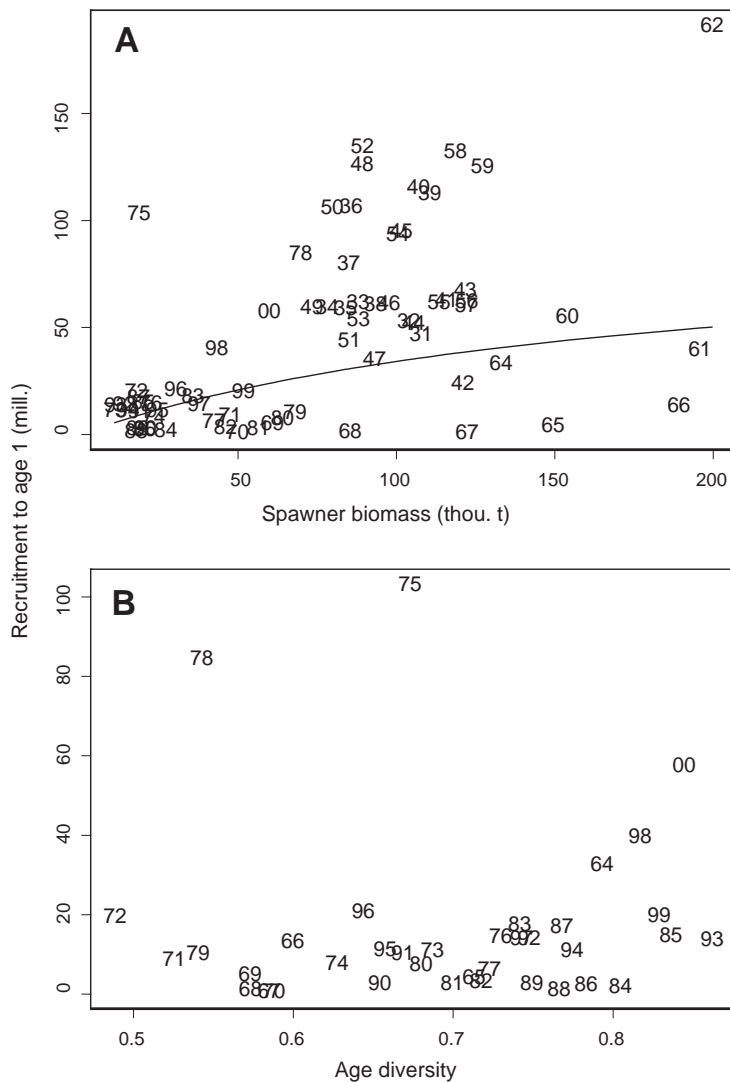
Fig. 17.   Relationship between two indices of reproductive potential and
recruitment to age 1 for Georges Bank haddock in NAFO Div.
5Z. **a**) spawner biomass (1931–2000, outlying observation for
1963 omitted); and **b**) age diversity (1964–2000). Observations
are labeled by year-class.

ment observed above that level. A Beverton-Holt model
provides the best parametric fit to this data (Fig. 17a),
however, because of a non-stationary pattern in the
residuals the model parameters were not accepted and
a non-parametric approach was used to obtain the B_{MSY}
estimate (NEFSC, MS 2002). B_{MSY} was estimated to be
250 300 tons at F40% of maximum spawning potential.
For the stochastic age-based projections of spawning
stock biomass and catch, recruitment is modelled by
re-sampling observed recruitments from SSB greater
than 75 000 tons.

Estimating stock reproductive potential. Data
from the most recent analytical assessment (R. Brown,
National Marine Fisheries Service, Northeast Fisher-
ies Science Center, Woods Hole, Massachusetts, 02543
USA, pers. comm.) were used to estimate age diversity
for the full time series (1963–2000). Linear regression
analysis of recruitment and age diversity for the time
series did not show a significant relationship, in part
because of outlying values of recruitment (Fig. 17b).
However, the data indicate a trend towards higher re-
cruitment with higher age diversity particularly during

1990–2000. This suggests that multivariate models including factors such as age diversity, spawning time, conditions might explain more of the variation in recruitment than the bivariate relationship between SSB and recruitment.

In future, alternative indices of reproductive potential can be developed using egg abundance data that are available from ichthyoplankton surveys conducted under three programs: i) Marine Resource Monitoring Assessment and Prediction (MARMAP) surveys (1977 to 1987); ii) larval herring surveys (1988 to 1994); and iii) Global Ocean Ecosystems Dynamics (GLOBEC) surveys (1995 to 1999). Furthermore, several time series of condition exist including: i) NEFSC bottom trawl surveys conducted during spring and autumn surveys (1992–2002); and ii) Canadian spring surveys which have been conducted since 1986. However, it should be noted that this stock might not exhibit poor condition given the high productivity of Georges Bank and the relatively rapid growth rate of the haddock residing there.

Incorporating this information into stock management. Currently, management is based strictly on status determinations of SSB and F. Ancillary information about the stock such as condition or age structure of the stock could be considered. If future analyses of data provide a quantitative change in the perception of the stock-recruit relationship then the current MSY reference points would need to be reconsidered. However, reference points that are not based on MSY would be difficult to implement in the U.S.-based fishery given existing legal protocols specified by the Sustainable Fisheries Act (US Department of Commerce, MS 1998).

Flemish Cap cod

Current management protocol. The Flemish Cap cod stock (NAFO Div. 3M) has been under moratoria since 1999. Its collapse has been attributed to overfishing, an increase in catchability and a sustained period of poor recruitment (Vázquez *et al.,* MS 1999). The most recent assessment indicated that SSB is currently at a historical low and that since 1992 recruitment has been at or near the historical low (Vázquez and Cerviño, MS 2001). Substantial changes in the structure of the spawning stock have occurred such that from 1978 to 1985 the oldest age-class observed in the stock ranged between 13 and 19 years, whereas, from 1995 to 1999 it was between 7 and 10 years. In addition, considerable reductions in age- and size-at-maturity were observed in the first half of 1990s (Saborido-Rey and Junquera, 1998).

Although the fishery is closed for the foreseeable future, biomass reference points have nevertheless been developed. The stock-recruit relationship (Fig. 18a) was the basis for establishing a B_{lim} value of 14 000 tons (NAFO, MS 2000).

Estimating stock reproductive potential. The most recent assessment (Vázquez and Cerviño, MS 2001) used knife-edge maturity-at-age from 1972 to 1990 and average values of catch weight at age from 1972 to 1987 to estimate SSB. The stock-recruit relationship shows recruitment values to peak at intermediate values of SSB (Fig. 18a). It was possible to refine the SSB estimates from 1978 to 1985 by replacing the constant weight- and proportion mature-at-age with observed values from Canadian surveys. The proportion of mature at age for 1986 and 1987 was estimated as the mean for adjacent years (1985 and 1988) for each age. This resulted in the SSB values for 1984 and 1985 shifting towards higher values that were more consistent with observed levels of recruitment (Fig. 18c). Incorporating sex ratio information to estimate the female-only SSB did not alter the pattern of variability substantially (Fig. 18e).

The residuals from fitting a non-linear model to the stock-recruit relationship were estimated for each of the three formulations of SSB. Residuals for SSB values estimated using fixed values for the weights and maturities (Fig. 18a) show a significant positive relationship with the age diversity index ($r^2 = 0.18$, $P = 0.04$; Fig. 18b). The residuals calculated using SSB estimated with year-specific weights and maturities was not significant ($r^2 = 0.11$, $P = 0.12$; Fig. 18d) while the relationship estimated using female-only SSB was nearly signficant ($r^2 = 0.16$, $P = 0.06$; Fig. 18f). Thus, the analysis of residuals suggests that the reproductive and recruitment potential of the stock is enhanced by the presence of older individuals.

Additional data are available for refining estimates of reproductive potential in the future. Condition, ovary weight and liver weight are available from Canadian surveys conducted from 1978 to 1985. Since 1988 condition and ovary weights have been measured during EU surveys conducted in the summer, however, the timing of this survey (post-spawning period) is problematic for obtaining data that are suitable for estimating reproductive potential.

Incorporating this information into stock management. Progress towards this goal has been made given that SSB is now calculated using year-specific values of maturity-at-age rather than using
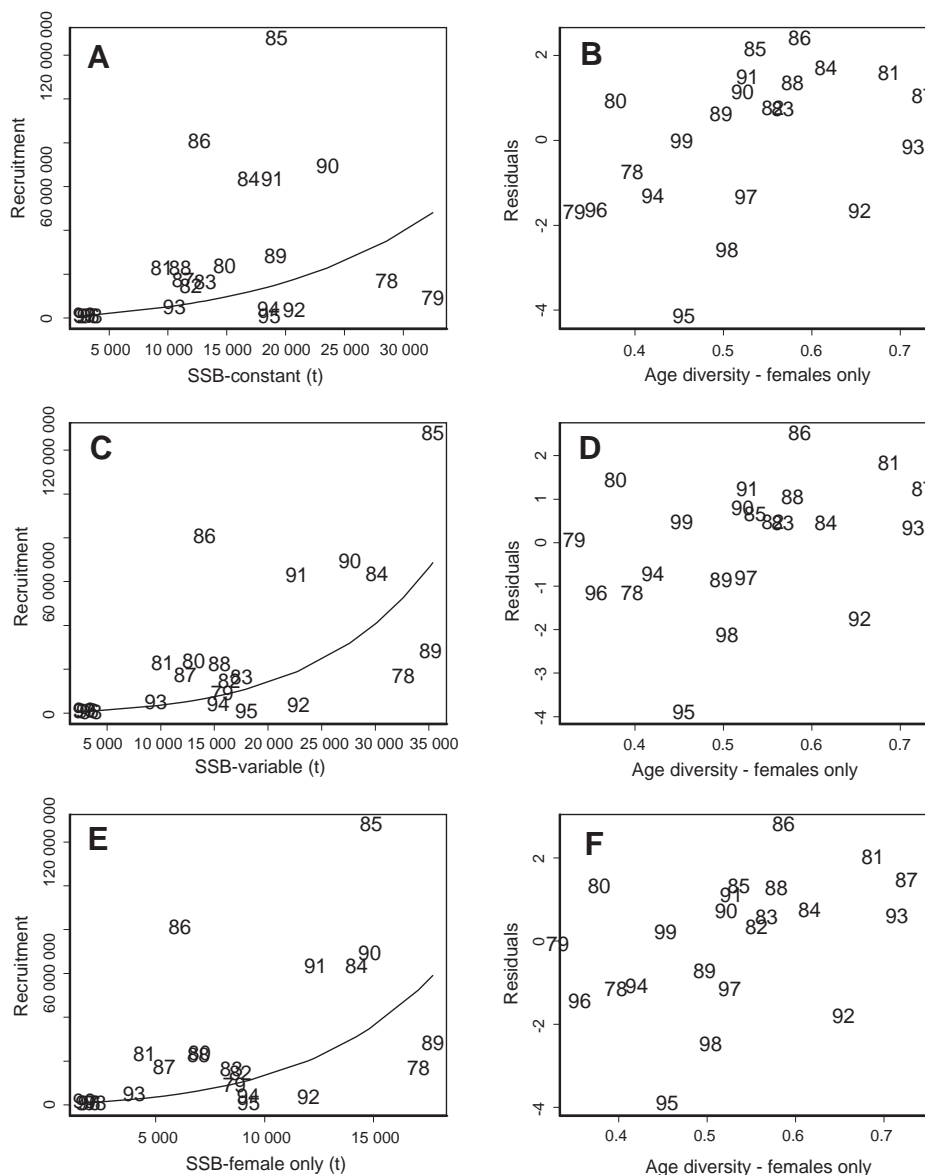
Fig. 18. Panels on the left show different parameterizations of the stock-recruit relationship
for Flemish Cap cod. Panels on the right show the residuals from a non-linear model
(shown in the left-hand panels as a solid line) plotted against age diversity. **a**) SSB
estimated using constant maturity and weight, **b**) residuals from a) plotted against
age diversity, **c**) SSB estimated using year-specific maturity and weight, **d**) residuals
from c) plotted against age diversity, **e**) female-only SSB, and **f**) residuals from e)
plotted against age diversity.

knife-edge values. Unlike many cod stocks, the
biomass-based stock-recruit relationships show clear
evidence of impaired recruitment at low levels of SSB
(Fig. 18a, c, e). Depending on the estimate of SSB used,
age diversity explained a significant or nearly signifi-
cant portion of the residual variance in the stock-re-
cruit relationship which suggests that the maternal ef-
fect on recruitment is not being fully captured by

biomass-based measures alone. However, any further
evaluation of how long-term changes in spawning
structure (both in age diversity and maturity-at-age)
have affected the reproductive potential is complicated
by serious data limitations or deficiencies. The time
series for condition is discontinuous with respect to
spawning stage at which the weight measurements were
taken (February for Canadian surveys, summer for EU

surveys). Some fecundity data are available for 1979 and 1982–85 (G. Lilly, Science Branch, Dept. of Fisheries and Oceans, Canada, unpub.data). However, collecting new data is difficult given both the timing of the annual survey (post-spawning period) and the present moratorium on fishing.

Discussion

Collectively, the nine case studies illustrate how the collation of historical data and acquisition of new information on fecundity can be used to develop alternative indices of stock reproductive potential. Incorporating maternal effects on egg viability is the obvious next step in developing indices that more closely approximate the realized TEP of a stock (e.g. Solemdal, 1997; Vallin and Nissling, 2000; Murawski *et al.*, 2001). Further refinements can be expected in the near future given the number of research projects undertaking experimental, field and modelling studies on reproduction and recruitment (Table 3). Serious consideration of such indices by fisheries management is warranted, given the tractable nature of reproductive biology and its clear import for recruitment (Marteinsdottir and Begg, 2002).

There were no examples among the case studies of the alternative indices influencing management advice either directly or indirectly. Close scrutiny of the relationship between SSB and TEP is the first step in determining whether fundamental changes to current management protocols are necessary (Marshall *et al.*, 1998). As several of the case studies illustrated, it is possible to model historical trends in fecundity by representing the year-effect with a term, e.g. condition or prey availability, explaining a significant amount of the variability in interannual fecundity (Kjesbu *et al.*, 1998; Blanchard, MS 2000) or relative fecundity (Kraus *et al.,* 2000, 2002). Using such a modelling approach, TEP was estimated for Baltic cod, Northeast Arctic cod, and eastern Scotian Shelf haddock (Fig. 19). The relationships between SSB and TEP were highly variable for all three stocks (r^2 values were 0.80, 0.26 and 0.44, respectively, for Baltic cod, Northeast Arctic cod, eastern Scotian Shelf haddock). All three relationships showed distinct time trends with relatively rapid shifts towards either higher (Baltic cod since 1994) or lower (Northeast Arctic cod since the 1980s, eastern Scotian Shelf haddock since the 1990s) values of TEP for a given level of SSB (Fig. 19). Thus, the relationship between SSB and TEP is not directly proportional for these stocks. This result alone could justify the application of alternative indices to stock management.

Incorporating an alternative index of reproductive potential in management could also be justified if it explained a higher proportion of recruitment variability compared to SSB. This was not the case for eastern Scotian Shelf haddock; neither SSB nor TEP were significantly correlated with recruitment. However, the incorporation of more highly resolved biological data in the stock-based index of potential TEP increased the correlation with the survey-based index of daily egg production for Baltic cod that was used as a proxy of realized TEP (Köster *et al.*, 2003). The stock-based index that was most highly correlated with realized TEP was included in a recruitment model that also included variables representing environmental effects on survival (Fig. 5). For Northeast Arctic cod, the proportion of explained deviance in recruitment was higher for TEP than for SSB but the correlation was still not significant. Given that an analysis of abundance estimates for early life history stages identified at least two critical stages at which recruitment undergoes substantial modification prior to age 3 (Mukhina *et al.*, 2003), the explanatory power of the stock-recruit relationship may be low irrespective of the index used to represent stock reproductive potential.

Alternative parameterizations of the stock-recruit relationship might be better for identifying levels of reproductive potential at which recruitment is impaired, a property that is critical for defining limit biomass reference points (ICES ACFM, MS 2002b). For example, many stock-recruit relationships contain observations having low or intermediate values of SSB and relatively high recruitment. Such observations undermine conservation efforts by suggesting that good recruitment can result even when the reproductive potential of stocks is low. The case studies provided several examples of strong year-classes that shifted their position in the stock-recruit relationship from relatively low values of SSB to relatively high values of the alternative index. For example, the 1994 and 1995 year-classes for Baltic cod (Fig. 4), the 1963, 1964, 1969 and 1970 year-classes for Northeast Arctic cod (Fig. 6), and the 1984, 1985 and 1989 for Flemish Cap cod (Fig. 18) shifted from the left-hand side of the stock-recruit plot towards the right-hand side when the alternative indices were used instead of SSB. These shifts improve the ability of the stock-recruit relationship to identify impaired recruitment and help to refute the notion that recruitment is independent of the reproductive potential of a stock.

Developing TEP estimates is often hindered by the lack of fecundity data both on historical and con-

TABLE 3.   A partial selection of recent and ongoing research projects that were relevant to either quantifying reproductive potential at the stock-level or utilizing this information in management.

Acronym	Title	Project period	Funding agency	Participating countries
STORE	Environmental and fisheries influences on fish stock recruitment in the Baltic Sea	1999–2002	EU	Germany, Denmark, Finland, Sweden, Estonia, Latvia, Poland, Russia
STEREO	An operational model of the effects of stock structure and spatio-temporal factors on recruitment	1999–2002	EU	Denmark, Scotland, Norway, Iceland, Germany
MACOM	Demonstration of maternal effects of Atlantic cod: combining the use of unique mesocosm and novel molecular techniques	2000–2002	EU	Norway, UK, Germany, Denmark
GADOLIFE	Growth dynamics and regulation of energy allocation in gadoids of different life strategies and in different environments	2001–2004	Department of Fisheries and Oceans	Canada
METACOD	The role of sub-stock structure in the maintenance of cod meta-populations	2002–2005	EU	Iceland, Scotland, Denmark, Germany
RASER	Reproduction and stock evaluation for recovery	2002–2005	EU	Norway, UK, Spain

temporary time scales (Tomkiewicz *et al*., 2003). Several published studies have estimated TEP using fecundity models that have been developed for other stocks. Such a practice is inadvisable given that across stocks the fecundity of cod of a given length can vary by more than 100% (Marteinsdottir and Begg, 2002). Furthermore, it masks the real need for stock-specific data. Closed fisheries and inappropriately timed surveys are serious impediments to routine fecundity monitoring, however, they do not justify failing to collect information on a key life history parameter that has been largely overlooked since the inception of standardized sampling programs (Tomkiewicz *et al*., 2003). It has been hypothesized that factors affecting growth and reproduction will be critical in rebuilding depleted cod stocks (Rose and O'Driscoll, 2002). Testing this hypothesis will obviously require new data describing the degree of interannual variation in fecundity (Murua *et al*., 2003). The development of methodology for rapid

fecundity determinations (e.g. Thorsen and Kjesbu, 2001) makes routine fecundity monitoring considerably less labour intensive.

In the absence of detailed fecundity information, useful information on reproductive potential can be inferred from basic information about the age, gender and/or size composition of the stock. Age diversity indices showed promise in explaining recruitment levels directly (e.g. Icelandic cod) or in explaining residual variation from the stock-recruit relationship (e.g. striped bass in Chesapeake Bay, Flemish Cap cod). Female-only SSB can also lead to improvements in the stock-recruit relationship (e.g. Baltic cod, Flemish Cap cod). This index is both conceptually appealing and easily estimated from existing data resources. It may also be possible to construct bioenergetic indices of reproductive potential when historical data describing the lipid content of the stock are available (e.g.
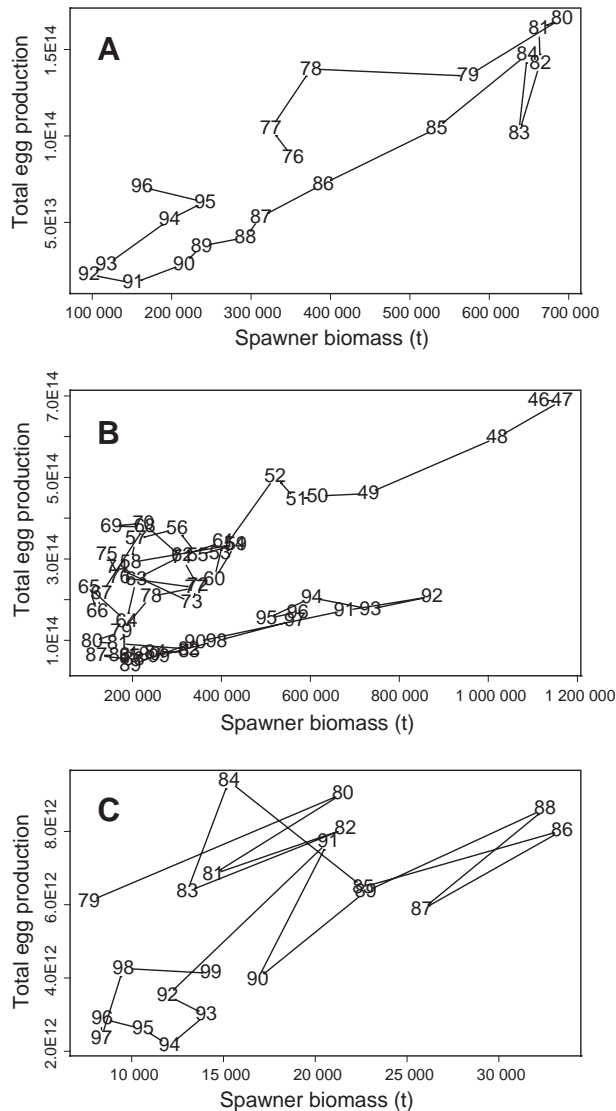
Fig. 19. Relationships between SSB and potential TEP. **a**) Baltic cod, **b**) Northeast Arctic cod, and **c**) eastern Scotian Shelf haddock. Observations are labeled by year and the time trajectory is shown by the solid line.

that oscillate between prolonged periods of unfavourable and favourable conditions. Stocks having a high age diversity may be more likely to withstand periods of unfavourable environmental conditions and experience the combination of high reproductive potential and favourable conditions giving rise to strong year-classes. The resiliency conferred by a broad age structure has been termed the "storage effect" (Chesson, 1994; Secor, 2000a) and it is increasingly regarded as a key attribute for the sustainability of fisheries resources (Fromentin and Fonteneau, 2001; Francis, 2003). High age diversity also results in increased diversity in spawning behaviour. For example, older females spawn often at different times than younger ones (Lambert, 1990; Secor, 2000a). This potentially increases the opportunities to match spawning with favourable conditions for larval survival (Kjesbu *et al*., 1998). Consequently, to accurately estimate the realized reproductive potential of a stock it may be necessary to collect and/or report information on spawners at finer temporal and spatial scales than are currently used by management (Begg and Marteinsdottir, 2003).

In addition to their practical importance to fisheries management, more precise estimates of TEP are of considerable interest for fisheries research because they allow for estimation of egg mortality rates during early and potentially critical life history stages (Nash, 1998). Similarly, expressing survival rates for individual cohorts as the ratio of recruits to TEP is preferable to the procedure in common use which assumes that SSB is directly proportional to TEP (Barrowman and Myers, 2000). The fecundity data collected in support of TEP estimates will also allow for more highly resolved investigations of the relationships between maximum population growth rates and key life history traits (Hutchings, 1999; Denney *et al*., 2002). Lastly, fecundity data can help to elucidate trophodynamic linkages between growth (*sensu* reproductive potential of individuals) and food availability to the stock (e.g. Fig. 2 and 7).

Northeast Arctic). Such databases are often collected systematically for industrial purposes (Schülein *et al*., 1995) and constitute a relatively underutilized data source.

Given that all of the case study species are relatively long-lived, it is also worth considering the management implications of a truncated age structure resulting from high fishing mortality. Due to the cyclical nature of marine ecosystems (Stenseth *et al*., 2002) fish stocks often experience environmental conditions

The precautionary approach, as applied to fisheries management, emphasizes incorporating uncertainty wherever knowledge is limiting. However, fisheries management must be equally able to accommodate the obverse situation, i.e. incorporating knowledge when it is available. Alternative indices of reproductive potential were available for the nine stocks included here as case studies. Three comparatively data-rich stocks having time series for TEP provided clear evidence that SSB is not directly proportional to TEP. The remaining case studies showed that properties of the spawning

stock (e.g. age diversity, condition) can influence recruitment in ways that are not properly accounted for by using SSB as the sole measure of reproductive potential. It is reasonable to expect further progress towards resolving whether SSB is a sufficiently sensitive index of reproductive potential given the number of dedicated studies that are either completed or ongoing (Table 3). Such targeted research will help to develop consensus regarding the nature and scope of changes that will be required of fisheries management. It is already clear that, rather than being constrained to using approaches designed for data-poor situations, management protocols should be sufficiently flexible to accommodate the use of detailed information on reproductive potential whereever it is felt to promote resource sustainability. The direct application of data on reproductive potential to fisheries management would have the corrollary benefit of stimulating the acquisition of information for data-poor stocks, and over time, reducing the large information gradient that currently exists.

Acknowledgements

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