



Variation in reproductive potential and influence on Icelandic herring recruitment

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ABSTRACT

Explaining recruitment variation in fish is essential for successful fishery management and is consequently under constant review, with an increasing focus on how maternal factors, relative to environmental influences, operate at the level of individual female spawners and extend from the spawning stock through to recruitment. We estimate total egg production (E) in Icelandic summer-spawning herring (*Clupea harengus*) from 1963 through 1999 by using sequential population analyses (SPA) and their estimates of stock biomass and recruitment, various size and maturity metrics, and individual fecundity estimates that rely on total length and the condition of the spawners. Generalized linear models indicate that maternal effects are of significance in explaining SPA-based recruitment-at-age-3 (R). The best model explained 64% of the variation in R and incorporates E constrained to the repeat spawners (40%), the NAO winter index (18%) and ocean temperature (6%). The latter two represent the winter and spring periods subsequent to year-class formation. Recruit spawner contributions to E were of no significance in explaining variation in R despite the fact that they could contribute as much as 55% of E when their contribution to E was consistently underestimated by a factor of ~ 2 , based only on their contribution to spawning stock biomass. We conclude that the spawning potential of the repeat spawners should replace total spawning stock biomass for determining recruitment potential in stock assessment. In addition to the incorporation of oceanographic factors, this

would provided a more cautious and risk-adverse approach.

Key words: condition, egg production, fecundity, herring, management, recruitment, repeat spawners

INTRODUCTION

A primary goal of fisheries science and much of fisheries oceanography is to identify the factors responsible for interannual variation in recruitment (Marshall *et al.*, 1998). Over the last century, several competing and complementary hypotheses emerged to explain the variance generally observed in recruitment within and among fish stocks. We focus here on the hypothesis that some of the variation is due to non-heritable maternal effects, i.e., the dynamic, phenotypic variation among female spawners (see overview in Solemdal, 1997). Maternal contributions to recruitment variation may derive from variations in the number of spawning females, their length composition, physiological condition, maturation as a function of size or age, egg size, fecundity, spawning time and spawning location.

Despite the above variations in maternal contributions, recruitment (R) in a fish stock (S) is most frequently described as a function of spawning stock biomass (SSB). Here R is defined as the number of recruits from a year-class of a stock that is determined at the age when the cohort becomes available to the fishery. The assumption routinely used in stock-recruitment (SR) models is that the total egg production of a stock (E), equivalent to population fecundity, is proportional to SSB. Several authors, including Rijnsdorp (1994) for flatfish; Marshall *et al.* (1998) for Atlantic cod, *Gadus morhua*; Óskarsson and Taggart (2006) for Atlantic herring, *Clupea harengus*; and most recently Marshall (2009) in a thorough review, have challenged the validity of the proportionality assumption. The challenges are founded on the other factors that contribute to variation in E above that normally have been attributed to variation in SSB or the environment, or both. For example, relative fecundity (i.e., potential fecundity, F_p , per unit whole-body weight, where potential fecundity is defined as the number of

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Received 15 February 2010

Received version accepted 5 May 2010

vitellogenic oocytes in a prespawning ovary), has been shown to increase with size (length) in Arcto-Norwegian cod (Kjesbu *et al.*, 1998; Marshall *et al.*, 1998), Norwegian spring-spawning herring (Óskarsson *et al.*, 2002) and Icelandic summer-spawning herring (Óskarsson and Taggart, 2006). In the examples above, E at a given SSB will vary according to the number and length of the spawners contributing to the SSB estimates. The assumption of proportionality is further violated when interannual variation in the average energetic reserves of a stock, typically reported as condition, changes the fecundity-at-length ratio (Blanchard *et al.*, 2003). In most fishes, the energy intake that exceeds the cost of maintenance is used for gonadal and somatic growth (Calow, 1985), and better than average physical condition results in increased fecundity. Conversely, food limitation can lead to different energy allocation schemes among individuals that become manifest in reduced egg number (Tanasichuk and Ware, 1987; Rijnsdorp, 1993, 1994; Winters *et al.*, 1993; Lobon-Cervia *et al.*, 1997).

In light of the information above, it is reasonable to expect that recruitment should be more closely related to E than to SSB. For Arcto-Norwegian cod, estimates of E that are independent of virtual population analysis (VPA), an analogue to sequential populations analysis (SPA; see overview in Megrey, 1989), are proposed as better indices of recruitment relative to the frequently employed VPA-based estimates of SSB (Marshall *et al.*, 1998). The proposition is based on the fact that E better reflects the observed variation in recruitment, and the relationship between E and recruitment-at-age approaches the origin. Similar results have been reported for Icelandic capelin (*Mallotus villosus*; Johannsdottir and Vilhjalmsón, 1999), where variation in the 0-group index was explained more by E ($r^2 = 0.46$) than by SSB ($r^2 = 0.35$), yet no relation was found between either E or SSB and recruitment. This reflects the absence of a relationship between the

0-group index and recruitment in the same stock (linear regression, $P = 0.63$; data from Johannsdottir and Vilhjalmsón, 1999).

A stock-recruitment relationship for Icelandic summer-spawning (ISS) herring has been documented by Jakobsson *et al.* (1993) using a Cushing-type SR model, and later by Óskarsson (2005) using a Beverton-Holt-type model. The former authors concluded that recruitment to the stock was influenced by the ocean temperature. In an effort to better resolve the nature of the SR relationship in ISS herring, we test the working hypothesis that non-heritable maternal variation, in combination with oceanographic variation, can be used to explain the observed variation in recruitment. We use the fecundity-at-length relation from Óskarsson and Taggart (2006) and various biological variables to estimate E and SSB among recruit- and repeat-spawners and to examine their interannual and interrelated variations. The stock-related variables we employ originate from the ISS herring database at the Marine Research Institute (MRI) in Iceland, which contains various data gathered from scientific surveys and the commercial fisheries detailed in Óskarsson and Taggart (2009). Variation in the nature of the female spawners and their contributions to the estimates of E and SSB are then used to examine the proportion of recruitment variation that can be explained in the ISS herring stock during 1963–99. The oceanographic and ecological variables we employ include the North Atlantic Oscillation (NAO) winter index, ocean temperature indices, a zooplankton abundance index, and an index of predation on herring larvae and juveniles.

MATERIAL AND METHODS

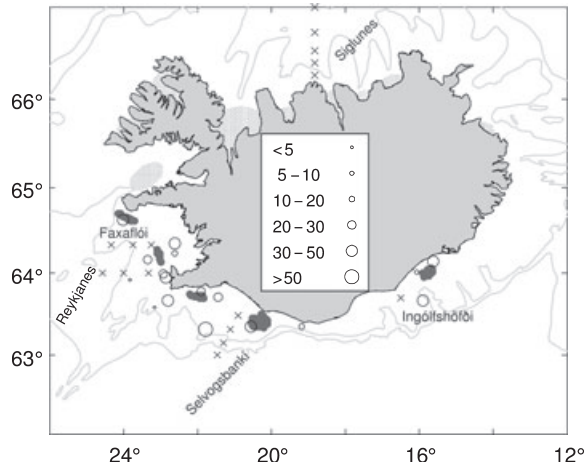
Data and sources

The estimates of E and SSB are based on data drawn from the three primary sources listed in Table 1:

Table 1. Summary of the basic variables and data sources used to estimate total egg production, E , for the Icelandic summer-spawning herring based on the Marine Research Institute (MRI), Iceland, database over the period 1962–99.

Variable	Nomenclature	Data source
Annual number-at-age derived from Sequential population analysis (SPA)	$N_{A,Y}$	G. Stefánsson and J. Jakobsson, MRI, unpublished data Anonymous, 2006
Proportion females-at-age	H_A	MRI database
Proportion mature-at-age	U_A	MRI database
Average weight-at-age	W_A [g]	MRI database
Individual potential fecundity	F_P	Óskarsson and Taggart, 2006
Annual average Fulton's condition index	$K_{a,Y}$	Óskarsson and Taggart, 2009

Figure 1. Iceland shelf region illustrating spawning grounds for summer-spawning herring (solid gray), nursery grounds (stippled areas; Jakobsson and Stefánsson, 1999) locations and number (expanding open circles) of individual pre-spawning females collected for fecundity determination during 1999 and 2000, and locations (x) of repeated temperature measurements used for calculating the N Iceland (Siglunes) and SW Iceland (Faxaflói, Reykjanes, Selvogsbanki, Ingólfshöfði) ocean temperature indices.

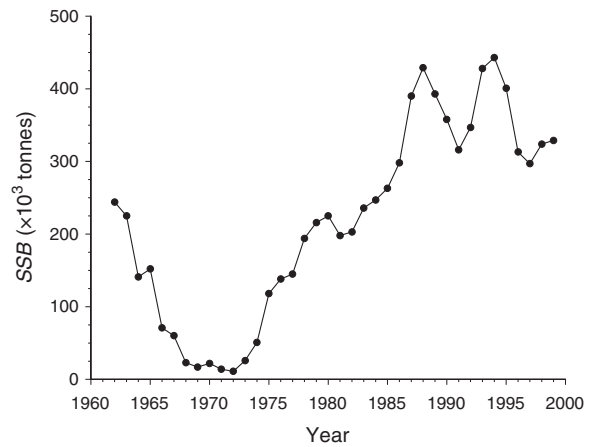


(i) stock assessment publications, reports and estimates from MRI; (ii) the historical ISS database at MRI containing herring-sample data from 1962–99; and (iii) the fecundity-at-size ratio derived from herring collections on the spawning grounds off the S and SW coasts of Iceland (Fig. 1) in 1999 and 2000 (Óskarsson and Taggart, 2006).

A 1992 SPA provided annual estimates of SSB for 1962–81 (G. Stefánsson and J. Jakobsson, MRI, unpublished data) and a 2006 SPA (Anonymous, 2006) provided estimates for 1982–99 (Fig. 2). Differences between the overlapping SPA estimates of SSB amounted to < 0.2% in 1982–86, 10% in 1987–89, 21% in 1990, and 42% in 1991, justifying the concatenation of the two series at the 1981–82 interface based on increasing convergence in estimates further back in time from the most recent SPA.

The database provided information on sex, maturity stage-1 through -8 (1–2 immature, 3–5 maturing, 6 spawning, 7 recently spawned and 8 recovering; Bowers and Holliday, 1961; Anonymous, 1962a), total length (L , ± 1.0 cm), whole-body weight (W , ± 1.0 g), ovary weight (OW, ± 1.0 g), and age in years (derived from scale annuli; Anonymous, 1962b). From these data we derived the portion of females in the stock, age-at-maturity, weight-at-age, and Fulton's K

Figure 2. The 1962–99 time series of spawning stock biomass (SSB) estimates of Icelandic summer-spawning herring derived from sequential population analyses (G. Stefánsson and J. Jakobsson; MRI, unpublished data; Anonymous, 2006).



($K = 100 \times W \times L^{-3}$). Fulton's K is considered a valid estimator of condition among herring, especially during the pre- and post-spawning periods (Óskarsson, 2008). Estimates of interannual variation in average condition of pre-spawning fish were determined using the average condition anomaly, $K_{a,Y}$, among individuals for a given year (Y) from 1962 to 1999 (Óskarsson, 2008; Óskarsson and Taggart, 2009). The average condition anomaly is used in place of individual K estimates among spawners as a strong seasonal effect in K is expected and the data are not equally represented over the pre-spawning period of February through June.

Accurate estimates of E can be superior to spawning stock biomass estimates in explaining recruitment if variation in E among spawners is well explained (Marshall *et al.*, 1998; Marteinsdottir and Begg, 2002; Blanchard *et al.*, 2003). Óskarsson and Taggart (2006) demonstrated that the fecundity relation for ISS herring meets this criterion wherein fecundity is a function of fish length and Fulton's K . The same authors also assessed atresia (oocyte degeneration), which is considered to be a primary factor in fecundity determination (Tyler and Sumpter, 1996) and is related to female condition (Rideout *et al.*, 2000; Óskarsson *et al.*, 2002). However, the frequency and prevalence of atresia declines with increasing seasonal maturation such that it becomes undetectable as spawning approaches (Óskarsson *et al.*, 2002; Kurita *et al.*, 2003). Thus, to ensure that F_P is a reliable estimator of realized fecundity, the actual numbers of eggs to be spawned by the pre-spawning herring, our analyses were restricted to mature ovaries presumed to be beyond the

effects of atresia and therefore to those collected after day-of-year 160 (Óskarsson and Taggart, 2006) and just prior to spawning (Óskarsson and Taggart, 2009).

The recruitment at age-3 estimates (R), as in Jakobsson *et al.* (1993) and Jakobsson and Stefánsson (1999), were derived from the two different SPAs detailed above. The most recent year in the data set was 1999, as the 2006-SPA estimates are very uncertain in more recent years. No other recruitment estimates or indices commensurate with our series are available for ISS herring.

The oceanographic factors examined for their contribution to explained variation in recruitment include the NAO winter index and ocean temperature indices. The NAO winter index (Climate Analysis Section, NCAR, Boulder, CO, USA; Hurrell, 1995) for 1962–2000 was chosen as it has been used to inform similar studies elsewhere (Cardinale and Arrhenius, 2000; Axenrot and Hansson, 2003; Brander and Mohn, 2004). The index represents the December through March difference in normalized atmospheric pressure measured at sea level between Lisbon, Portugal, and Stykkisholmur, Iceland. The ocean temperature index for Siglunes (Fig. 1) was derived using data collected annually during spring surveys (May–June) along the Siglunes hydrographic transect off northern Iceland (Anonymous, 2003) and is based on the depth-weighted average over the 0–200 m depth range at five stations. The annual ocean temperature index for SW Iceland (Fig. 1) was derived from hydrographic data collected annually at 50 and 100 m depth along four transects off southern Iceland, as detailed in Óskarsson and Taggart (2009).

Other oceanographic and ecological variables examined for their utility in explaining recruitment variation include a zooplankton biomass index representing potential food for herring larvae and an index of the predation rate on larval and juvenile herring. The zooplankton biomass index is the average dry weight (g m^{-2}) in the upper 50 m of zooplankton collected at the five hydrographic stations on the Siglunes transect during May of each year using a WP2 0.2-mm-mesh net (Anonymous, 2003). We used year-class strength (abundance at age-3) and SSB estimates of Icelandic cod (Anonymous, 2006) as an index of the potential predation rate on herring larvae and juveniles. As the cod spawn in spring and the herring in autumn, we assume that cod larvae and juveniles feed on herring larvae and juveniles, as observed by Pálsson (1980). Suitable indices of other known herring-larvae or -juvenile predators, such as jellyfish (Lynam *et al.*, 2005), birds (Eilertsen *et al.*, 2008) and

marine mammals (Lindstrøm *et al.*, 2002), are not available.

E and SSB

Estimates of total annual egg production (E_Y) required various data. We employed the model of potential fecundity (F_P) provided in Óskarsson and Taggart (2006) for the stock and assumed that the model-derived fecundity estimates represent realized fecundity as indicated by a simultaneous examination of the frequency of atresia (see above), and uses total length (L) and K as independent variables according to

$$F_P = -4.69 \times 10^5 + 1.60 \times 10^4 L + 9.11 \times 10^4 K \quad (r^2 = 0.849, N = 451) \quad (1)$$

However, when estimating E (Eqn 3 below) in each year (Y), we modified K in Eqn 1 to include the annual average condition anomaly by adding $K_{a,Y}$ (Óskarsson and Taggart, 2009) to the constant average K (0.92 over all years for fully mature stage-5 spawners; Óskarsson and Taggart, 2006). The temporal variation in K is assumed to be the same across all length classes as the overall individual variation in K originates mainly from seasonality and year and less so from geographic location and fish length, though both were incorporated when estimating the K anomaly (Óskarsson, 2008).

The estimation of E relied on estimating the number of mature females (N_m) at age (A) each year derived from the SPA number (N) of fish at age each year according to

$$N_{m,A,Y} = N_{A,Y} \times U_{A,Y} \times H_A \quad (2)$$

where U is the proportion of mature and H the proportion of females where the latter is not indexed by year because there is no indication of interannual differences in H for the ISS stock (Óskarsson, 2005). Subsequently, the average length-at-age estimated from the MRI database for each year was then incorporated in the fecundity relation (modified Eqn 1, see above) to calculate

$$E_Y = \sum_{i=1}^A F_P \times N_{m,L,Y} \quad (3)$$

Estimates of the annual contribution to E by recruit (rec) and repeat (rep) spawners relied on the total number of eggs spawned each year (Y) according to

$$E_{\text{rep},Y} = \sum_{i=1}^A \left(\frac{U_{A-1,Y-1}}{U_{A,Y}} \times E_{A,Y} \right) \quad (4)$$

and likewise $E_{\text{rec},Y} = E_Y - E_{\text{rep},Y}$. In this manner, the estimate of $E_{\text{rep},Y}$ is based on the ratio between U in year Y and the previous year ($Y-1$) and the matching year class ($A-1$). Sexual dimorphism in maturity-at-age was not considered in estimating E as neither the literature nor the data indicate dimorphism. We also assume that all mature females spawn every year. This assumption is difficult to validate, especially in this case where there are spring and summer spawning populations. Further, Atlantic herring appear to skip spawning only when in extremely poor condition ($K < 0.7$), when a high proportion of oocytes are atretic (Óskarsson *et al.*, 2002). There was no evidence for this in the ISS herring collected for fecundity and atresia determination (Óskarsson and Taggart, 2006).

We estimated SSB by summing over each year the stock number-at-age multiplied by average weight-at-age (W_A) and the proportion mature, which was applied to the SPA estimates (Eqn 2 above) according to

$$\text{SSB}_Y = \sum_{i=1}^A N_{A,Y} \times W_{A,Y} \times U_{A,Y} \quad (5)$$

Explaining variation in R

We used generalized additive models (GAM) and generalized linear models (GLM; S-PLUS INSIGHTFUL, V. 6.0, 2000) to examine recruitment-at-age-3 variation in ISS herring in terms of SSB, E , E_{rep} , E_{rec} , K_a , and the several oceanographic and ecological indices detailed above. The GAM and the GLM used to validate the GAM do not require a normalized response variable and homogeneous variance, and many of the data violated the normality assumptions of conventional parametric statistics. The procedure involved determination of the most appropriate GAM using Mallows' C_p statistic (Neter *et al.*, 1996), where the best model is the one with the lowest C_p statistic, relative to the full model, and is not improved by removing any term. Improvements in model fit were also evaluated on the basis of approximate F -tests (Hastie and Tibshirani, 1990). We used a cubic-B spline to estimate the smoothers (Hastie and Tibshirani, 1990) and employed Gaussian data distribution with an identity link for the calculations. To verify whether the results of the GAM were overinterpreting additive fits, each covariate in the final model was analyzed separately using GLM polynomial functions of varying degree and/or piecewise functions with varying break-points, which also determine whether smoothing is necessary. Thus, we evaluated whether the added complexity of the GAM was realistic and

necessary, and whether the GLM was more appropriate. All possible first-order interaction terms were then tested in a similar manner along with the significant covariates. Bootstrap re-sampling with 1000 replications of the obtained covariates was used to estimate whether the covariates were of significance. To assess departures from model assumptions we graphically assessed normality using residuals and quantiles and determined whether the residuals were auto-correlated. To further prevent overinterpreting the additive fits, the width of the standard errors and residuals fitted against the predictions were examined (Hastie and Tibshirani, 1990) and these provided information about the homogeneity of variance. The explanatory power of other measures of reproductive potential ended in a final model of explained recruitment variation that was used for comparative purposes.

The influence of NAO, ocean temperature and zooplankton indices at various lags associated with the year of spawning (age-0), the following year (age-1) as well as averages during the first two (age-0 through -1) and three (age-0 through -2) prerecruit years were also examined.

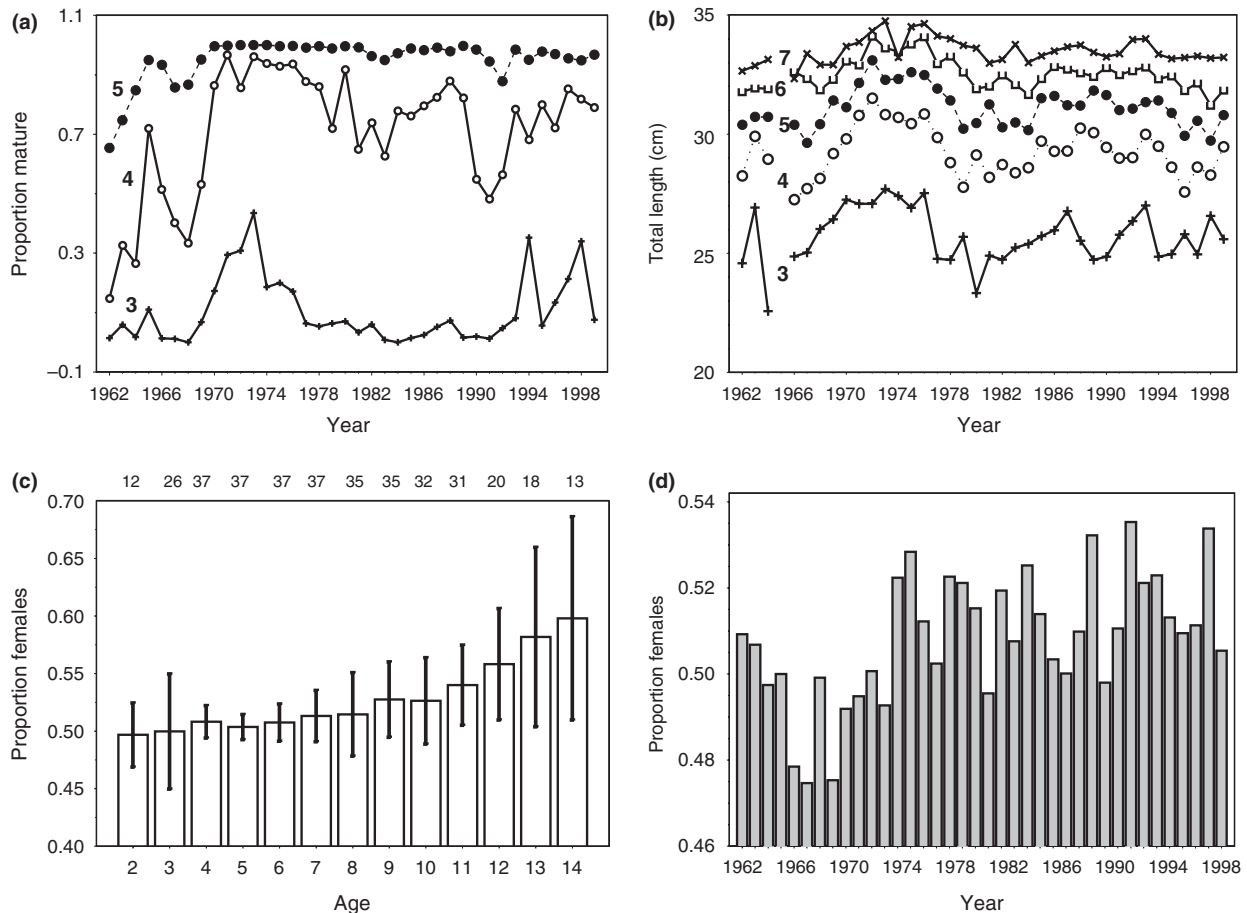
RESULTS

E and SSB

Annual estimates of the proportion of mature herring among the age-3 to age-5 classes for 1962–99 demonstrated that herring start maturing at age-3, with the proportion of mature varying among years (Fig. 3a). In all but six of the 38 years, > 90% were mature by age-5. Thus, for our analyses, all fish at age-6+ were assumed to be mature and those < age-3 were assumed to be immature. Length-at-age-3 through -7 fluctuated around relatively constant sizes (approximately ± 2 cm) with some evidence of elevated length-at-age during the 1970s (Fig. 3b). Approximately $50 \pm 2\%$ of the stock at age-3 through -8 was female and thereafter increased with the proportion of females reaching $\sim 60 \pm 6\%$ by age-14 (Fig. 3c). The differences in the proportion of female herring among age-classes (arcsine transform, ANOVA, $P < 0.001$) were attributable to the age-13 and -14 classes (*a posteriori*, $P < 0.05$). There were minor interannual variations in the sex ratio, with the proportion of females ranging from 47 to 54% (Fig. 3d). Over all length groups, and all years, 51.6% of the 159 485 herring in the MRI sample-collection data base were female.

A typical seasonal cycle was observed in the K estimates of the ISS herring (Fig. 4a), where the maximum occurred just prior to the relatively invariant spawning day-of-year 200 (Óskarsson and Taggart,

Figure 3. The 1962–99 Icelandic summer-spawning herring time series of (a) annual proportion of mature males and females among the age-3 through age-5 classes, (b) average total length (cm) at age-3 through age-7 (no data available in 1965), (c) average ± 2 SE proportion of females within each age-class where the superimposed numerals (N) indicate N -years within the series with available measures ($N < 20$ within age-class excluded; total $N = 155$ 655 among age-classes ranging from 436 at age-14 to 34 147 at age-5), and (d) annual proportion of females across age classes in the stock where the annual number of samples ranged from 1162 to 10 141.

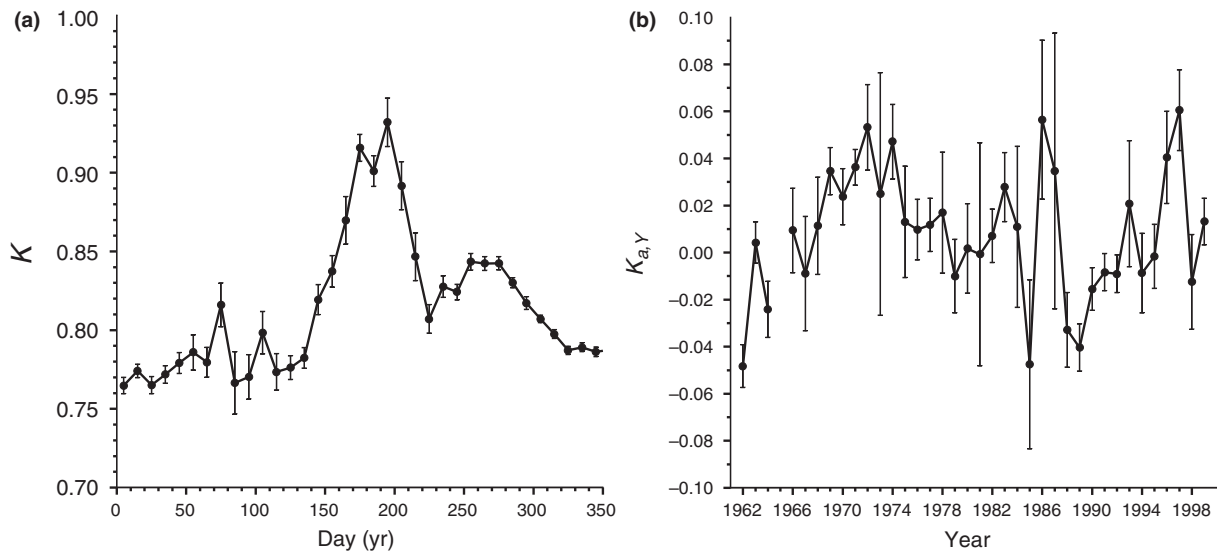


2009). The annual body condition anomaly, $K_{a,Y}$, prior to spawning, ranged from -0.05 to 0.06 (Fig. 4b). It is this variation that was incorporated in the estimates of E through the modified fecundity relation (Eqn 1). The frequency distribution of K for prespawning female herring collected over the period 1962–99 and after day-of-year 160 (when F_P is determined prior to spawning and not reduced further by atresia; Óskarsson and Taggart, 2006) was normal, with a mean of 0.924 and a median of 0.920 (Fig. 5a). The frequency distribution of K for females at maturity stage-3 to -5 and collected after day-of-year 160 for fecundity determination in 1999 and 2000 (Fig. 5b; mean and median = 0.919) was virtually identical ($P = 0.171$) to that of the 38-year data. This result confirms that the fish used for F_P determination are representative of the stock from a historical perspec-

tive. The average annual K (± 2 SE) never fell below 0.75 (Fig. 4a) and fish with $K < 0.7$ used for fecundity determination (Fig. 5b) were extremely rare, indicating that the F_P estimates are not unduly compromised by fish that may have skipped spawning. Atlantic herring with $K > 0.70$ have a nearly 100% chance of beginning ovary maturation, whereas those with $K < 0.70$ are less likely to do so (Kennedy *et al.*, 2010).

The contribution to the total annual egg production by the different age-classes varied among years (Fig. 6). During the 1960s through the early 1970s, the stock-size and age structure collapsed and consequently the older fish contributed little to total egg production. In the early- to mid-1970s there were relatively few fish older than age-8 and the spawning population was dominated by age-4 recruit spawners. During this time,

Figure 4. The 1962–99 Icelandic summer-spawning female herring time series of (a) variation in the average body condition index ($K \pm 2$ SE) aggregated across years at 10-day-of-year intervals, and (b) average body condition index anomaly ($K_{a,Y} \pm 2$ SE) for pre-spawning herring with lengths of 28–35 cm and maturity stages 3 (mature) through 5 (fully mature). No data available for 1965.



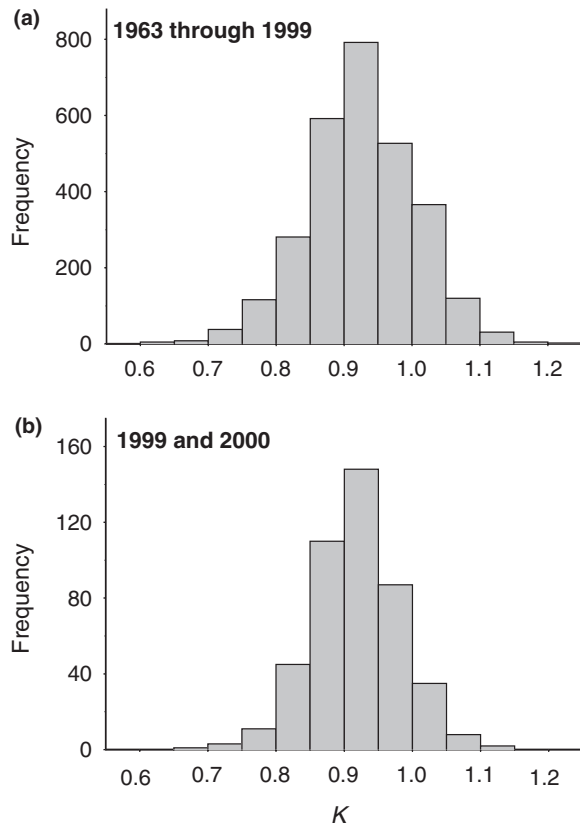
between 25 and 55% of the total egg production was derived from recruit spawners and the total number of eggs produced had declined to about 3×10^{12} ; ~ 33 -fold fewer than in the 1990s (Fig. 7). In other periods, the majority of eggs were produced by the older age-5+ repeat spawners, even when egg production was dominated by the occurrence of large year-classes, such as the 1983 year-class at age-4 in 1987, which dominated E until age-10 in 1993. From 1976 onwards, the SSB (Fig. 2) increased at a relatively constant rate of $\sim 10 \times 10^3$ tonnes annually ($r^2 = 0.57$, $P < 0.0001$) as the age structure was slowly rebuilding (Fig. 6). This was paralleled by a relatively constant increase in the number of eggs contributed by repeat spawners ($r^2 = 0.745$, $P < 0.0001$, Fig. 7) at 2.6×10^{12} eggs annually, in contrast to that contributed by recruit spawners increasing at 0.64×10^{12} eggs annually ($r^2 = 0.228$, $P = 0.014$). The relative contribution to E from recruit spawners, which reached a maximum in the early 1970s, subsequently ranged between ~ 10 and 45%. There was a positive linear relation ($r^2 = 0.984$) between the proportions of E and SSB that were contributed by recruit spawners, indicating that the contribution of recruit spawners to the reproductive potential is underestimated when using SSB by a factor of approximately two (slope = 1.86, Fig. 8).

Examining explained variation in recruitment

When examining recruitment (R) variation among the various stock-related and oceanographic variables

using GAM, with different degrees of freedom and polynomial functions of varying degree, the final model indicated that all the significant variables were linearly related to R (\log_2 -transformed). The final model was based on a stepwise elimination of variables, Mallows' C_P and F-statistics, and a bootstrap analysis, which indicated that the variables made significant ($P < 0.05$) contributions to the explained variance. Due to the linear effects in the GAM, we considered the GLM to be the most appropriate. The results of the final GLM model (with Gaussian distribution; Table 2) indicated a positive nonlinear effect of E_{rep} on recruitment (Fig. 9a) that explained 39.6% of the variation in R ($P < 0.001$). At $E_{\text{rep}} \geq 30 \times 10^{12}$, approximately 82% of the recruitment anomalies were positive. Positive linear effects on R were associated with the NAO winter index, with a 1-year lag ($\text{NAO}_{\text{lag}1}$; winter following hatching) that explained an additional 18.2% ($P < 0.001$) of the recruitment variation (Fig. 9b). The Siglunes ocean temperature anomaly in the winter following hatching ($T_{a,\text{Sigl},\text{lag}1}$) explained a further, though marginal ($P = 0.021$), 6.4% of the variation (Fig. 9c). Overall, the model (Fig. 9d) explained 64.1% of the observed variation in R ($P < 0.001$). Graphical examinations indicated no model departures from the assumptions according to residual deviance, the quantiles of the standard normal distribution of residuals and the first-order autocorrelation function of the residuals. Other stock-related variables (SSB, E , E_{rec} and K_a) made no significant

Figure 5. Frequency distributions of body condition index (K) for mature pre-spawning Icelandic summer-spawning herring collected after day-of-year 160 for (a) 1962–99 ($N = 2885$) and (b) 1999–2000 ($N = 450$).



contribution to explained variance ($P > 0.05$), or were not selected in the final model due to lower predictive power relative to other variables (e.g., $SSB < E_{rep}$). None of the other oceanographic and ecological variables, including the ocean temperature index for SW Iceland, the zooplankton biomass index on the Siglunes transect, and year-class strength and SSB of Icelandic cod (potential predators), contributed significantly to explaining the variance in R , leaving approximately 36% of the variance unexplained by the range of variables and associated lags that we examined.

DISCUSSION

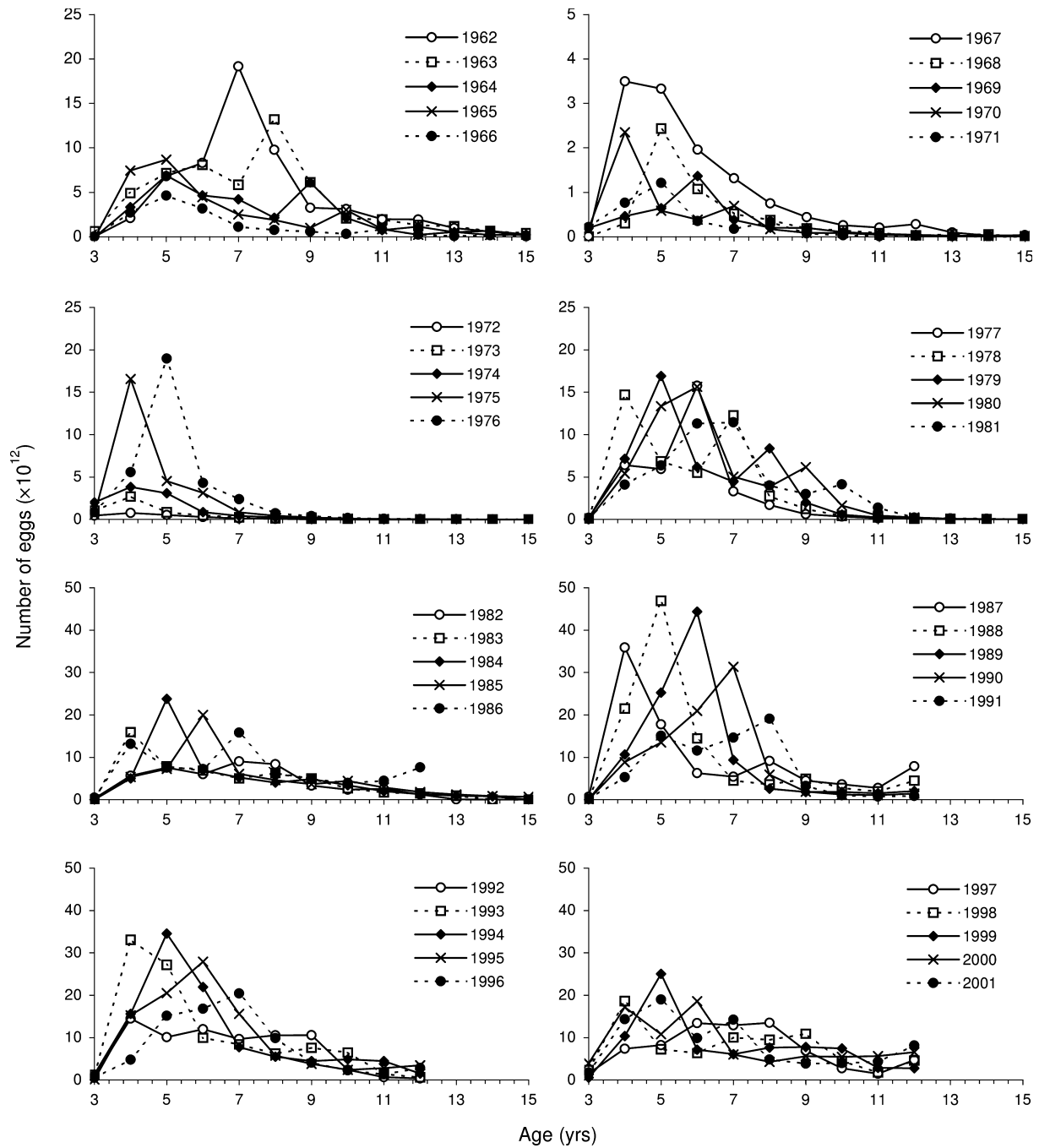
The results above provide new information regarding maternal effects, expressed via spawning experience, on recruitment potential for the Icelandic summer spawning herring that are likely applicable to similar stocks and other species. Egg production contributed by repeat spawners (E_{rep}) explained more variation in recruitment at age-3 than did total egg production (E).

Egg production from recruit spawners (E_{rec}) made no significant contribution to the explained variance in recruitment at age-3. These findings indicate that the use of recruit spawners, in terms of either E or SSB, as E_{rec} and SSB_{rec} , are strongly correlated (Fig. 8), should be judiciously considered prior to their incorporation in SR models. Wigley (1999) obtained similar results for haddock (*Melanogrammus aeglefinus*), where the exclusion of recruit spawners improved the SR relation by a whopping 39%. The modeling work of Carr and Kaufman (2009) also showed that more offspring of repeat cod spawners survive compared with offspring of recruit spawners.

We suggest that the limited influence E_{rec} has on recruitment in ISS herring is related to egg size and spawning time associated with recruit spawners. Egg size in ISS herring is a function of spawner weight, or length and K (Óskarsson, 2005). Thus, the smaller (< 30 cm) recruit spawners produce fewer eggs of a reduced quality and survivorship – assuming that egg quality and the survival of the eggs or hatching larvae or both are some function of egg size, as has been determined by others (e.g., Blaxter and Hempel, 1963; Duarte and Alcaraz, 1989; Rijnsdorp and Vingerhoed, 1994; Berkeley *et al.*, 2004). Spawning among ISS recruit spawners is, on average, delayed by 17 days relative to repeat spawners, where the latter have a spawning time that is independent of their size or age (Óskarsson and Taggart, 2009). Hence, delayed spawning by recruit spawners may contribute to decreased survival of eggs and/or larvae (Wright and Gibb, 2005); the latter being due to a ‘mis-match’ between emergent larvae and suitable larval food resources (e.g., Cushing, 1967; Bagenal, 1971; Ware, 1975; Rothschild, 1986; Kjesbu *et al.*, 1996), and thus little or no influence on recruitment. The insignificant contribution of recruit spawners to R may also be related to lower fertilization rates. Observations on Baltic herring provide some evidence that fertilization declines as the spawning season protracts (Rajasilta *et al.*, 1997).

Our results indicate that E_{rep} is the most appropriate stock-related variable for estimating R in the ISS stock. Further, if E_{rec} is of no significance in explaining R as demonstrated above, then the use of either SSB or E , each of which include E_{rec} , is inappropriate in modeling the variation in R . We have also shown that the interannual estimates of the proportions of E that are contributed by the recruit spawners, and which vary from year to year, are greater than the corresponding proportions of SSB that are contributed by the same recruit spawners (Fig. 8) and vice versa for repeat spawners. This implies that when estimating the reproductive potential based on SSB instead of E ,

Figure 6. Variation in the annual age-class (year) contribution to the total number of eggs produced by Icelandic summer-spawning herring during 1962–99. Note varying scales on the ordinate. From 1986 onward, age 12 is actually 12+.



the contribution of recruit spawners is underestimated (e.g., 30 versus 55%, respectively; Fig. 8), and thereby the contribution from the repeat spawners is overestimated (e.g., 70 versus 45%). The primary reason for the discrepancy in the estimates of the interannual

contributions is related to the manner in which they are calculated, even if the calculations appear biologically justified.

SSB is typically estimated using weight-at-length and disregards fecundity-at-length (and the

Figure 7. The 1962–99 time series of Icelandic summer-spawning herring total annual egg production by recruit (E_{rec} ; open symbols) and repeat (E_{rep} ; filled symbols) spawners and the annual percent (crosses, right ordinate) of total egg production contributed by recruit spawners (sp).

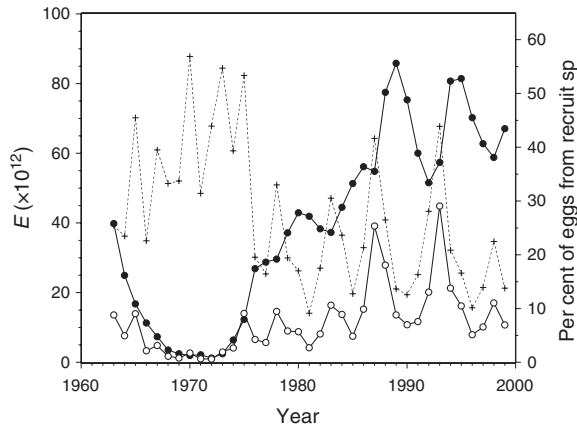
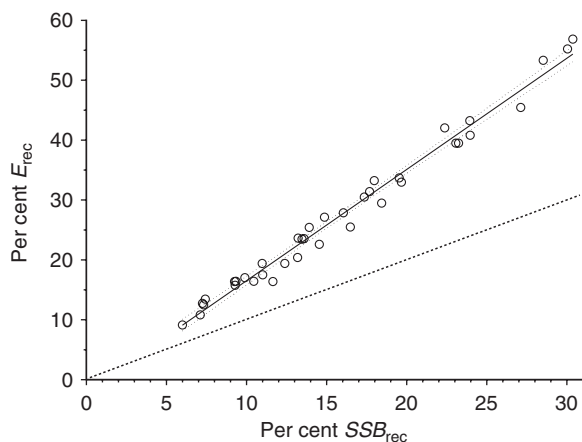


Figure 8. Scattergram of observed (open symbols) and least squares regression (solid line) with 95% confidence interval (dotted lines) for the model ($E_{\text{rec}} = 1.86 \text{SSB}_{\text{rec}} - 2.04$; $r^2 = 0.984$, $N = 37$, $P < 0.001$) showing total egg production of recruit spawners (E_{rec}) as a function of the per cent recruit spawners in the spawning stock biomass (SSB_{rec}) for Icelandic summer-spawning herring over 1963–99. Broken line represents a 1 : 1 ratio.



associated K) ratios that are used to estimate E . Body weight increases as a power function of length in the ISS stock, while the most appropriate fecundity relation for the stock is a linear increase in F_P with length (Óskarsson and Taggart, 2006). This explains why, in the example above, the repeat spawners that account for 70% of SSB , account for only 45% of E . We suggest that similar results are to be expected among those stocks or species where fecundity increases linearly

with length, and weight increases as a power function of length, as in Norwegian spring-spawning herring (Óskarsson *et al.*, 2002) and Pacific herring (Hay and Brett, 1988). Alternatively, where power functions are appropriate for a fecundity-at-length relation (e.g., cod: Kraus *et al.*, 2000; Kjesbu *et al.*, 1998 and haddock: Blanchard *et al.*, 2003), the difference between the relative contributions of recruit spawners to SSB and E should be reduced. In summary, the metrics (e.g., SSB , E , E_{rec} , etc.) used to estimate the reproductive potential and recruitment in herring are of importance – simply due to differences in the repeat- and recruit-spawner contributions to recruitment potential. Correspondingly, E likely reflects recruitment potential better than SSB when the repeat- and recruit-spawners contributions are variable.

The North Atlantic Oscillation winter anomaly index was of some significance in explaining recruitment variation in ISS herring, and in a manner similar to that determined for recruitment in Icelandic cod (Brander and Mohn, 2004). Positive NAO anomalies are a function of lower atmospheric pressure over Iceland, stronger than average westerly winds across the North Atlantic (Hurrell *et al.*, 2003), and increased flow of the North Atlantic current into the NE Atlantic and Norwegian Sea (e.g., Wanner *et al.*, 2001). The Irminger Current, a branch of the North Atlantic Drift (current), brings warm, high-salinity water to the southern Iceland shelf, where part of it is subsequently transported cyclonically around Iceland, although the magnitude of the flow varies due to factors other than simply the NAO. We are unable to identify easily the reason for the positive effects of the NAO on ISS herring recruitment and can only suggest some relation to, or combination of, generally warmer waters (but see below), enhanced vertical mixing due to increased wind-stress, and increased advection of prerecruits to favourable nursery grounds. Knowledge concerning the temporal and spatial variation in the drift of the larvae from spawning grounds and their distribution among the different nursery grounds is limited (Einarsson, 1956; Gudmundsdottir *et al.*, 2007). Warmer conditions off northern Iceland during periods of a positive NAO index have been inferred (Malmberg and Valdimarsson, 2003), despite the lack of statistical association between the NAO index and ocean temperature on the Siglunes transect (Ólafsson, 1999). Enhanced vertical mixing results in more naupliar stages of *Calanus finmarchicus* being transported upwards from deeper waters (e.g., Durbin *et al.*, 2000), which increases prey availability (Fiksen *et al.*, 2002), resulting in increased larval survival and thus increased R . Increased mixing (turbulence) also

Table 2. Summary of parameter estimates (a) for recruitment variation at age-3 ($\log_2 R; \times 10^6$) of Icelandic summer-spawning herring from the generalized linear model (Gaussian distribution: $\log_2 R = a + b \times \log_2 E_{\text{rep}} + c \times \text{NAO}_{\text{lag1}} + d \times T_{\text{a., Sigl.,lag1}}$) over the period 1963–99 and (b) the corresponding analysis of deviance table (terms added sequentially). The explanatory variables are total egg production of repeat spawners ($E_{\text{rep}}; \times 10^{12}$; \log_2 -transformed), the North Atlantic Oscillation winter index (NAO_{lag1} ; Hurrell, 1995) in the winter following hatching and the temperature anomaly at Siglunes ($T_{\text{a., Sigl.,lag1}}$) in the spring following hatching.

(a)		Value	SE	t-value	
Intercept		4.374	2.940×10^{-1}	14.87	
$\log_2 E_{\text{rep}} (\times 10^{12})$		3.786×10^{-1}	8.760×10^{-2}	4.322	
NAO_{lag1}		2.054×10^{-1}	4.734×10^{-2}	4.338	
$T_{\text{a., Sigl.,lag1}}$		2.419×10^{-1}	1.001×10^{-1}	2.416	
(b)	df	Deviance residuals	df	Residual deviance	% explained
Null			36	36.18	
$\log_2 E_{\text{rep}} (\times 10^{12})$	1	14.31	35	21.86	39.58
NAO_{lag1}	1	6.571	34	15.29	18.16
$T_{\text{a., Sigl.,lag1}}$	1	2.298	33	12.99	6.36

implies the possibility of increased larval feeding (e.g., Fiksen *et al.*, 2002 and refs. therein), although *in situ* estimates of turbulence do not necessarily indicate increased prey encounter and larval feeding success as a result of increased turbulence (Reiss *et al.*, 2002). Nevertheless, the zooplankton index on the Siglunes transect made no significant contribution to explained variance in R , nor did the potential predation index expressed through cod SSB and year-class strength.

Increased wind-stress may also influence the advection of larvae to more favourable nursery grounds (Ottersen and Sundby, 1995), although no data are available to verify this suggestion for ISS herring. Instances of greater than average recruitment in ISS herring, as well as other herring stocks in the NE Atlantic (e.g., Norwegian spring-spawning herring; Toresen and Østvedt, 2001) and NW Atlantic (e.g., Scotia-Fundy herring; Óskarsson, 2005) and other fish stocks such as cod (Ottersen and Sundby, 1995; Anonymous, 2006) in 1983 or in the late 1970s and early 1980s, suggest relatively large-scale oceanic or climate-related phenomenon that may favour larvae survival.

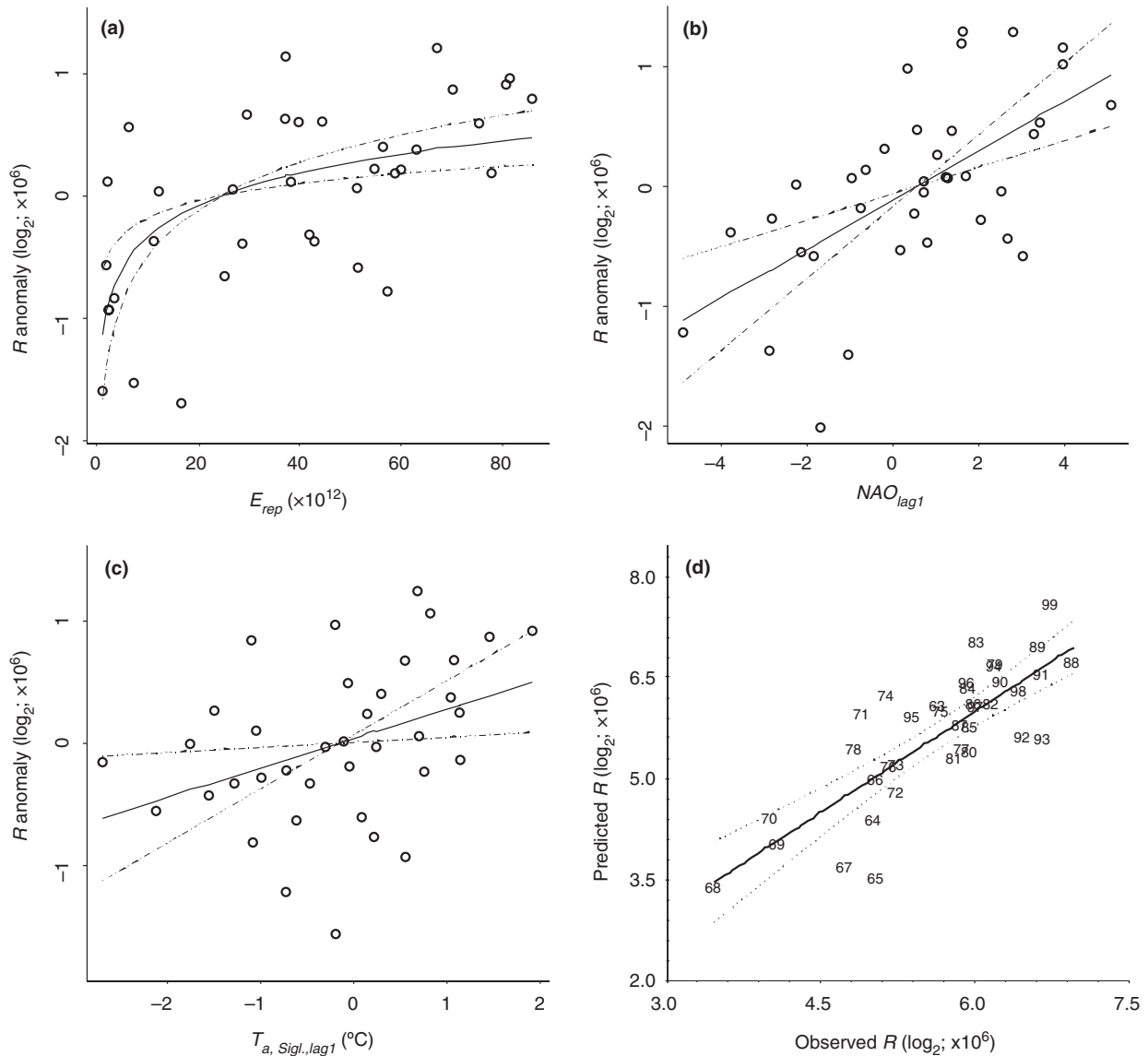
Ocean temperature off northern Iceland (Siglunes) was found to have a marginal effect on the ISS recruitment; consistent with the results of Jakobsson *et al.* (1993), where average R was reduced during the relatively cold period of 1965–71. The primary nursery grounds for the stock are off northern Iceland (Fig. 1), although larvae and juveniles are also found elsewhere (Gudmundsdottir *et al.*, 2007). In general, we conclude that oceanographic variability, as reflected in the lagged winter NAO index and ocean temperature indices, influences recruitment through the survival of

larvae during their first winter–spring. The conclusion is substantiated by the positive relation between age-3 recruitment and larval and post-larval abundance indices at age-1 and -2 in the ISS stock, which indicates year-class strength is determined during the first year of larval development (Gudmundsdottir *et al.*, 2007).

Interannual variation in spawner body condition ($K_{\text{a,y}}$) did not contribute to explained variation in recruitment to the ISS stock. This is to be expected given that spawner condition at length is incorporated in the F_P estimates (and thus E and E_{rep}) using the modified Eqn 1 above, which also incorporates inter-annual variation in K . Such a result can be used to infer that the influence of spawner condition on future recruitment is directly moderated through potential fecundity.

In our approach, we have assumed that the only factor determining F_P , beside fish length, was fish condition, where the latter is based on ISS herring fecundity (Óskarsson and Taggart, 2006). We acknowledge suggestions in the literature that F_P can vary with stock size and can appear independent of fish condition (e.g., Stares *et al.*, 2007), yet differences in length-specific F_P determinations for Norwegian spring-spawning herring some 30–40 years apart were thought to reflect differences in average body condition (Óskarsson *et al.*, 2002). Others, such as Kelly and Stevenson (1985), argue that twofold differences in SSB in autumn-spawning herring in the western Gulf of Maine between 1969 and 1982 may explain the associated length-specific differences in F_P . Their argument was based on different log–log fecundity-at-length regressions applied to the herring collected in

Figure 9. Generalized linear model (GLM) results illustrating the 1963–99 age-3 Icelandic summer-spawning herring recruitment (R ; \log_2 -transformed) anomaly as a function of (a) total egg production attributed to repeat spawners (E_{rep}), (b) the NAO winter index for the following winter (lag-1; NAO_{lag1}), and (c) the ocean temperature anomaly at Siglunes the following spring (lag-1; $T_{a,\text{Sigl.},\text{lag1}}$). (d) The linear relation ($\log_2 R_{\text{GLM}} = 0.641 \log_2 R_{\text{obs}} + 2.03$; $r^2 = 0.641$, $N = 37$, $P < 0.0001$) between the observed and GLM recruitment estimates based on the variables illustrated in (a–c). The dotted lines denote the 95% confidence intervals for the model.



1969 and 1982. We question this ‘density-dependent’ argument, presumably and somehow related to condition, as an examination of the residuals (Fig. 2 in Kelly and Stevenson, 1985) indicates that the data are better conditioned for simple linear regression as in Óskarsson and Taggart (2006). In fact, based on linear regression, the differences between F_P at length in the 1969 and 1982 Gulf of Maine herring data are mar-

ginal. Perhaps, and more importantly, these same linear relations are only marginally different from those in Óskarsson and Taggart (2006), which represent an entirely different stock with an entirely different SSB history. Further, the intercept of the power relation (Kelly and Stevenson, 1985) is biologically meaningless, whereas the intercept of the linear relation clearly reflects size at first maturity.

We argue that Eqn 1 above adequately reflects the effect of K on fecundity among ISS herring, as the fish used in the fecundity determination in 1999 and 2000 (Fig. 5b) had a K distribution representative of the stock from a 1962–99 historical perspective (Fig. 5a). It is possible that condition estimates over a narrower sampling period, for example from around the start of vitellogenesis to spawning time, may provide greater accuracy in determining the effect on reproductive potential, as suggested by Skjæraasen *et al.* (2006), but the temporal distribution and resolution of the data available to us limit our ability to validate this possibility.

Some of the life history traits examined above have been addressed earlier using the MRI data in Iceland. Our results are similar in terms of length-at-age and maturity-at-age over the period 1960–92 to those reported by Jakobsson *et al.* (1993), particularly the relatively constant length-at-age for ages 3 and 4 and the greater than average proportion mature for these two age-classes in the early 1970s (Fig. 3a,b). We note here that a greater than average proportion of the age-3 fish were mature in the mid-1990s, as also observed in the 1970s. However, during the 1970s, the length-at-age increased together with the maturity ogive, whereas this did not occur in the 1990s. We propose that the maturity ogive in the 1990s may be exaggerated due to changes in migration or a corresponding change in the commercial fishery, which was located further offshore during the 1990s (Óskarsson *et al.*, 2009), or both, although we have no means of easily testing this proposition.

Our study of ISS herring recruitment is one of the few to demonstrate the impact of maternal factors on a wild stock. The insights reported here could prove useful for the management of the ISS stock and similar stocks. Recruitment in ISS herring increased continuously with increases in E_{rep} and there is no indication of density-dependence even as SSB and E_{rep} increased above historical estimates (e.g., Óskarsson, 2005; Anonymous, 2006). The result is that the ISS herring stock has been more or less continuously increasing in biomass since the collapse around 1970 (e.g., Jakobsson *et al.*, 1993, and see Fig. 2). This presumably reflects successful management, perhaps in addition to favourable oceanographic conditions. Based on our analyses above, it appears that when assessing, modeling and predicting recruitment in the face of oceanographic variation, it is more appropriate to use size-structured estimates of F_P as well a spawning experience (e.g., E_{rep}) in place of simply E or SSB. From a management perspective it is especially important to do so at low SSB and when the size structure is truncated, and to do so prior to assessing

potential oceanographic influences. Doing so should result in more accurate short-term predictions of R . This suggestion is particularly relevant to stock management because it infers new precautionary reference points directly related to the reproductive output of a size- and maturity-structured spawning stock and the prevailing oceanographic conditions.

ACKNOWLEDGEMENTS

We are grateful to R. Stephenson, K. Frank, J. Jakobsson, the Marine Research Institute in Iceland (MRI), T. Marshall and G. Marteinsdottir for various suggestions and critical appraisals as well as several anonymous Referees and the Editor for their valuable suggestions. The research was supported by MRI, the Fishery Ministry of Iceland, the Icelandic Research Fund for Graduate Students, a NATO Science Fellowship, and the Natural Sciences and Engineering Research Council of Canada. The research has also benefitted from the EU funded project *IN EX FISH* (proposal/contract no.: FP6-022710).

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