Relationships between maternal body size, condition and potential fecundity of four north-west Atlantic demersal fishes

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Fecundity data for four species (American plaice Hippoglossoides platessoides, yellowtail flounder Limanda ferruginea, witch flounder Glyptocephalus cynoglossus and Atlantic cod Gadus morhua) of north-west Atlantic demersal fishes, corresponding to nine populations, were examined in relation to fish size and condition in an attempt to explain the observed variability in potential fecundity. Both relative body (K_r) and liver condition (H_r) were poor single-factor predictors of fecundity, and in almost all cases fish body mass (M) was the best single-factor predictor. Annual variability in mean K_r and H_r existed for most populations. The inclusion of K_r and H_r in total length (L_T)-based predictive models improved model fit only slightly and not significantly in all cases. Multiple regression analyses to determine the best model for explaining the variability in fecundity often excluded K_r, H_r and L_T in favour of M. The amount of variability in fecundity that could be explained by the factors analysed here was species specific, with the highest proportion explained for H. platessoides and the lowest for L. ferruginea. The highly variable, and sometimes unpredictable, nature of north-west Atlantic groundfish fecundity suggests the need to continue collecting such reproductive data on an ongoing basis.

Key words: Gadus morhua; Glyptocephalus cynoglossus; Hippoglossoides platessoides; Limanda ferruginea; reproductive potential; spawning.

INTRODUCTION

Fish population dynamics can be closely linked to stock reproductive potential (SRP) (i.e. total population egg production represents the maximum number of potential recruits to the population), and so better understanding the natural variability in SRP might lead to improved advice on fisheries management. Understanding SRP requires a detailed knowledge of the species’ reproductive strategy and factors affecting fecundity at the individual level.

From a fisheries assessment perspective, the reproductive potential of a fish population has traditionally been gauged using spawning stock biomass (SSB). This practice is based on the assumption that SSB is a direct indicator of total population egg production (TEP), an assumption that is not always correct (Marshall et al., 1998, 1999; Scott et al., 1999; Marteinsdóttir & Begg, 2002). In fact, estimating TEP

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based on individual reproductive data (i.e. maturity and fecundity) and numbers of fish at age or length can give a different perception of spawning stock size and reproductive potential (Morgan & Brattee, 2005), give different interpretations of the recruitment process at low stock size (Marshall et al., 2006) and even improve the fit of stock–recruit relationships (Kraus et al., 2002) over the use of just SSB.

The estimation of TEP requires the collection of yearly stock-specific fecundity data, which unfortunately is generally lacking for north-west Atlantic demersal fishes (Tomkiewicz et al., 2003). Part of the reason for the lack of these data is the time-consuming nature of traditional fecundity estimation techniques. Newer, more efficient methods based on automated image analysis (Thorsen & Kjesbu, 2001) should help alleviate some of the problems associated with these traditional techniques and facilitate the routine collection of fecundity data. An alternative to the yearly collection of fecundity data is the development of proxies for fecundity, i.e. easier to measure physical attributes of the fish (or environmental factors) that can be used to estimate (i.e. model) fecundity. Nevertheless, this too requires the collection of ample fecundity data to evaluate the accuracy of modelled fecundity estimates.

Controlled feeding studies have demonstrated a direct relationship between fish somatic or liver condition (or diet) and individual egg production for numerous marine fishes, including cod Gadus morhua L. (Kjesbu et al., 1991), haddock Melanogrammus aeglefinus (L.) (Hislop et al., 1978), herring Clupea harengus L. (Ma et al., 1998), plaice Pleuronectes platessa L. (Horwood et al., 1989) and winter flounder Pseudopleuronectes americanus (Walbaum) (Tyler & Dunn, 1976). Somatic and liver condition indices have thus been explored as potential proxies for fecundity in wild populations. This is usually done using a multiple regression approach, whereby the condition indices are added to a model already accounting for the influence of fish size on fecundity. The results of such analyses have been variable for G. morhua and M. aeglefinus with somatic and liver conditions explaining an additional 1–23% of the observed variability in fecundity over length alone (Kjesbu et al., 1998; Kraus et al., 2000; Lambert & Dutil, 2000; Marteinsdóttir & Begg, 2002; Blanchard et al., 2003). Less has been done to investigate potential proxies for fecundity of flatfishes but links with somatic condition have been demonstrated for a few species. Rijnsdorp (1991) reported that somatic condition explained an additional 10% of the variability in fecundity over length alone for North Sea P. platessa but length accounted for a small overall portion (18%) of the variability. For P. platessa in the Irish Sea, somatic condition generally explained <5% of the observed variability in fecundity when fish were sampled during the spawning season but as much as 15% when sampled in September (Kennedy et al., 2007). Millner et al. (1991) reported that somatic condition explained approximately an additional 7% of the variability in fecundity over length alone for North Sea sole Solea solea (L.).

Recent fecundity work for north-west Atlantic G. morhua and flatfish populations in the Newfoundland and Labrador area has demonstrated significant spatial and temporal variability in the relationship between fecundity and length (Rideout & Morgan, 2007; Stares et al., 2007; Morgan & Rideout, 2008; Fudge & Rose, 2008). It has also been demonstrated that failure to account for this variability can lead to large discrepancies in estimates of TEP (Rideout & Morgan, 2007; Stares et al., 2007; Morgan & Rideout, 2008). Despite the demonstrated degree of variability in fecundity and its effect on perception of SRP, there have to date been no explanations to sufficiently account for the amount of variability in fecundity of north-west
Atlantic demersal fishes. Fudge & Rose (2008) suggested that a recent increase in fecundity of *G. morhua* in NAFO Divisions 2J3KL was a density-dependent response to population decline, whereas Stares *et al.* (2007) found that density-dependent factors could not explain temporal changes in fecundity of *G. morhua* from the Grand Bank (NAFO Divisions 3NO) and Newfoundland south coast (NAFO Subdivision 3Ps). Here, whole body and liver condition indices are examined as potential proxies (both single-factor linear predictors as well as in multiple factor models) for fecundity of north-west Atlantic demersal fishes and the hypothesis that individual fish condition is the primary factor responsible for the variability observed in fecundity of north-west Atlantic demersal fishes is tested. For the flatfishes, data were those previously used to demonstrate spatial and temporal variability in fecundity (Rideout & Morgan, 2007). For *G. morhua*, data from Stares *et al.* (2007) were used along with an additional 700 fecundity samples collected as part of Fisheries and Oceans Canada’s long-term cod fecundity project.

**MATERIALS AND METHODS**

**FISH COLLECTION**

Ovaries for fecundity determination were collected from *G. morhua* (*n* = 1266), American plaice *Hippoglossoides platessoides* (Fabricius) (*n* = 964), yellowtail flounder *Limanda ferruginea* (Storer) (*n* = 546) and witch flounder *Glyptocephalus cynoglossus* (L.) (*n* = 349) during spring stratified random surveys of NAFO areas 2J3KLNOPs (Fig. 1). Data collection covered a total of nine populations (Table I). Sampling years varied among species and areas. For the flatfishes, sampling was done between 1993 and 1998 and was limited to NAFO Divisions 3LNO and Subdivision 3Ps, as described by Rideout & Morgan (2007). *Gadus morhua* in NAFO Division 2J3KL and 3NO were sampled between 1988 and 2004 and those in 3Ps were sampled between 1993 and 2004. Sampling was confined to offshore regions and was not necessarily annual within each time period.

Only fishes with ripening ovaries that showed no signs of having commenced spawning (i.e. opaque oocytes but no clear oocytes) were selected. Total length (*L*<sub>T</sub>) was recorded for all fish sampled, while body mass, liver mass and gonad mass were recorded for a subset of the fish sampled.

**FECUNDITY DETERMINATION**

Ovaries were cut open and stored in jars of Gilson’s fluid for 2–4 months in order to digest the connective tissues that held the oocytes in place. Before the late 1970s, the Gilson’s fluid used for fecundity work contained mercuric chloride (Simpson, 1951) but was subsequently substituted with zinc chloride (Barszcz, 1976) due to safety concerns associated with the use of mercury. Eggs were rinsed through a series of sieves to separate first generation oocytes (i.e. vitellogenic oocytes that would have been spawned in the current year) from second generation oocytes (i.e. immature oocytes that are the basis for the production of vitellogenic oocytes in subsequent years) and connective tissue. First generation oocytes were stored in ethanol until counted.

Fecundity was determined volumetrically using a modified whirling vessel (Wiborg, 1951), as described by Rideout & Morgan (2007).

**STATISTICAL ANALYSES**

Relative condition indices were calculated for all fish with available mass data. Relative body condition (*K<sub>r</sub>*) and relative liver condition (*H<sub>r</sub>*) were calculated as: *K<sub>r</sub> = MM<sup>-1</sup>* and...
\[ H_t = M_H \hat{M}_H^{-1}, \] where \( \hat{M} \) and \( \hat{M}_H \) are the predicted body mass and liver mass, respectively, from the linear \( L_T \) and body mass or \( L_T \) and liver mass relationships \[ \log_{10} M (\text{or } M_H) = a + \log_{10} L_T, \] where \( a \) is the intercept. Gutted body mass might better reflect available energy reserves than whole body mass (Lambert & Dutil, 1997), but here a very close relationship was observed between gutted and whole mass for all four species. This coupled with the fact that more fishes had whole mass data than gutted mass led to the use of whole body mass in the calculation of \( K_r \).
Table I. Summary of population structure (as used for management purposes) of Gadus morhua, Hippoglossoides platessoides, Limanda ferruginea and Glyptocephalus cynoglossus in NAFO Subareas 2 and 3

<table>
<thead>
<tr>
<th>Species</th>
<th>Populations</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. platessoides</td>
<td>Grand Bank (3LNO); southern Newfoundland (3Ps)</td>
</tr>
<tr>
<td>L. ferruginea</td>
<td>Grand Bank (3LNO); southern Newfoundland (3Ps)</td>
</tr>
<tr>
<td>G. cynoglossus</td>
<td>Northern (2J3KL); southern Grand Bank (3NO); southern Newfoundland (3Ps)</td>
</tr>
<tr>
<td>G. morhua</td>
<td>Northern (2J3KL); southern Grand Bank (3NO); southern Newfoundland (3Ps)</td>
</tr>
</tbody>
</table>

Simple linear regression analyses based on log10-transformed data were used to explore the potential of $K_r$ and $H_r$ as well as various other simple body metrics ($L_T$, body mass, liver mass, ovary mass and gonado-somatic index, $I_G$) as single-factor proxies for fecundity. Although fish age might also influence fecundity, it was not considered here due to potential unreliability issues in ageing older L. ferruginea (Dwyer et al., 2003). The utility of these metrics in predicting fecundity was evaluated by examining the $r^2$ of the observed relationships. In addition, ANCOVA were used to determine whether there was significant temporal variation in the relationships between these metrics and fecundity. Due to the actions of follicular atresia, the potential fecundity of a fish may be closer to its realized fecundity if measured close to the onset of spawning (Öskarsson & Taggart, 2006; Thorsen et al., 2006). In accordance with this, oocyte size has been used to indicate how close a fish is to the start of spawning and the inclusion of oocyte size as an explanatory variable has helped improve the fit of models explaining and predicting fecundity (Öskarsson & Taggart, 2006; Thorsen et al., 2006). Although oocyte size data were obtained here for most of the fishes examined, the oocytes had been treated for relatively uncontrolled (i.e. highly variable) amounts of time in both Gilson’s fluid and then ethanol, and so the effects on oocyte size are unknown (Klibansky & Juanes, 2007). Because of this, and because analyses suggested that the oocyte diameter data collected had no significant explanatory power when it came to fecundity, diameter data were not included in the analyses.

Forward selection multiple regression was used in two different approaches to examine the influence of $K_r$ and $H_r$ on fecundity. Analyses were not conducted for 3Ps G. cynoglossus due to a shortage of mass data. In the first approach, $L_T$ was set as the first explanatory variable a priori in order to examine whether the addition of $K_r$ and $H_r$ to a model already containing $L_T$ significantly increased the amount of explained variability in fecundity. In the second approach, $L_T$, body mass, $K_r$ and $H_r$ were all subjected to forward selection in order to determine the best model for explaining the observed variability in fish fecundity. Prey abundance data were only available for 3NO G. morhua and were examined for a relationship with relative fecundity (potential fecundity g$^{-1}$ of whole body mass).

RESULTS

LINEAR PREDICTORS OF FECUNDITY

Correlation analyses of data pooled across years and areas demonstrated that $K_r$ and $H_r$ were not strongly correlated with fecundity. Fish mass was a better predictor of fecundity than $L_T$ for the three flatfish species but the reverse was true for G. morhua (Table II). Liver mass was correlated with fecundity in all four species. Fecundity was strongly correlated with ovary mass for H. platessoides and G. cynoglossus, but surprisingly not for L. ferruginea or G. morhua. For the three
flattfish species, analyses of covariance (Table III) comparing single-factor predictors of fecundity among years revealed a high degree of variability in fecundity and $L_T$ relationships for all populations. Fecundity and body mass relationships were generally more stable, except for Division 3Ps $H. platessoides$. Fecundity and liver mass relationships showed no temporal variability but only three of the six flatfish populations had sufficient data to support these analyses. For $G. morhua$, all of the single-factor predictors of fecundity showed a high degree of temporal variability (Table III).

Clear differences existed between species in the ability to explain the observed variability in fecundity. For example, $L_T$, mass and gonad mass all predicted fecundity with relatively good success ($r^2 = 0.73–0.80$) for $H. platessoides$ but explained a relatively small amount of the variability ($r^2 < 0.35$) in fecundity for $L. ferruginea$.

**ANNUAL VARIABILITY IN $K_r$ AND $H_r$**

Mean $K_r$ for $G. morhua$ varied significantly ($P < 0.05$) between years in all three areas (Fig. 2), with 1990 being greater than 1993 in Division 2J3KL, 1990 being greater than 1994 in Division 3NO and 1998 being greater than 2001 in Division 3Ps. Mean $H_r$ did not vary between the 2 years examined in Division 2J3KL but did vary among years in the other two areas (Fig. 2). In Division 3NO, $H_r$ was higher in 1993 than 1995, 2001, 2002 and 2003. In Division 3Ps, $H_r$ was lower in 2001 than 1993, 1998 and 2003, while 1998 was also greater than 1995 and 2000.

For $H. platessoides$ in Division 3LNO, $K_r$ was significantly lower in 1994 and 1995 than in 1996 and 1998, and 1994 was also lower than 1997 (Fig. 3). In Division 3Ps, $K_r$ for $H. platessoides$ was lower in 1993 and 1994 than 1995. $H_r$ did not vary annually for $H. platessoides$ in Division 3LNO (Fig. 3). In Division 3Ps, $H_r$ was higher in 1995 than both 1993 and 1994, and 1998 was also higher than 1993.

For $L. ferruginea$ in Division 3LNO, $K_r$ was significantly lower in 1995 than 1996 (Fig. 4). In Division 3Ps, $K_r$ in 1996 was significantly higher than both 1994 and 1995. Annual differences in $H_r$ for $L. ferruginea$ (Fig. 4) were not significant in either Division 3LNO ($P > 0.05$) or 3Ps ($P > 0.05$).
Table III. ANCOVA results examining the temporal stability of linear predictors of fecundity for north-west Atlantic demersal fish populations. P-values are given for comparisons of both slope and intercept.

<table>
<thead>
<tr>
<th>Species</th>
<th>Population</th>
<th>$L_T$ Slope</th>
<th>$L_T$ Intercept</th>
<th>$M$ Slope</th>
<th>$M$ Intercept</th>
<th>$M_H$ Slope</th>
<th>$M_H$ Intercept</th>
<th>$M_G$ Slope</th>
<th>$M_G$ Intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hippoglossoides platessoides</em></td>
<td>3LNO</td>
<td>&gt;0·05</td>
<td>&lt;0·001</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
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<td></td>
<td>3Ps</td>
<td>&lt;0·05</td>
<td>&lt;0·01</td>
<td>&lt;0·01</td>
<td>&lt;0·05</td>
<td>&lt;0·05</td>
<td>&lt;0·001</td>
<td>&lt;0·05</td>
<td>&lt;0·05</td>
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<tr>
<td><em>Limanda ferruginea</em></td>
<td>3LNO</td>
<td>&gt;0·05</td>
<td>&lt;0·001</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
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<tr>
<td></td>
<td>3Ps</td>
<td>&gt;0·05</td>
<td>&lt;0·001</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
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<tr>
<td><em>Glyptocephalus Cynoglossus</em></td>
<td>3NO</td>
<td>&gt;0·05</td>
<td>&lt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
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<tr>
<td></td>
<td>3Ps</td>
<td>&gt;0·05</td>
<td>&lt;0·05</td>
<td>&gt;0·05</td>
<td>&gt;0·05</td>
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<tr>
<td><em>Gadus morhua</em></td>
<td>2J3KL</td>
<td>&gt;0·05</td>
<td>&lt;0·01</td>
<td>&gt;0·05</td>
<td>&lt;0·01</td>
<td>&lt;0·05</td>
<td>&lt;0·001</td>
<td>&lt;0·05</td>
<td>&lt;0·001</td>
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<tr>
<td></td>
<td>3NO</td>
<td>&lt;0·001</td>
<td>&lt;0·001</td>
<td>&lt;0·001</td>
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<td>&lt;0·001</td>
<td>&lt;0·001</td>
<td>&lt;0·001</td>
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<tr>
<td></td>
<td>3Ps</td>
<td>&lt;0·01</td>
<td>&lt;0·05</td>
<td>&lt;0·001</td>
<td>&lt;0·01</td>
<td>&lt;0·05</td>
<td>&lt;0·001</td>
<td>&lt;0·05</td>
<td>&lt;0·001</td>
</tr>
</tbody>
</table>
No significant annual differences in $K_r$ were observed for Division 3NO and 3Ps *G. cynoglossus* (Fig. 5). Due to the limited available liver mass data, $H_r$ could only be compared between 2 years for each of these populations. In Division 3LNO, no difference ($P > 0.05$) in $H_r$ was observed between 1993 and 1997, and in 3Ps, no difference ($P > 0.05$) was observed between 1994 and 1998.

**MULTIPLE REGRESSION ANALYSES**

Multiple regression results showed that $K_r$ and $H_r$ at the time of sampling explained little more of the variability in fecundity than that which was already accounted for by differences in $L_T$ (Table IV). For *G. morhua*, $K_r$ explained a significant amount of variability in fecundity for all three populations, with the amount of explained variability ranging from $<1\%$ in Subdivision 3Ps to 5% in Division 2J3KL. The effect of $H_r$ was only significant for Division 2J3KL, where it accounted for slightly $<1\%$ of the observed variability in fecundity. For Division 3LNO *H. platessoides*,

![Diagram](image)
Fig. 3. Mean ± s.d. annual relative condition indices ($K_r$) for north-west Atlantic *Hippoglossoides platessoides* (see Fig. 1).
DISCUSSION

The fecundity of north-west Atlantic demersal fishes has, in general, been poorly studied (Tomkiewicz et al., 2003). Recent work on G. morhua, H. platessoides, L. ferruginea and G. cynoglossus has demonstrated significant temporal and spatial variability in fecundity in this region and demonstrated that failure to account for this variability can result in large differences in estimates of stock reproductive potential (Rideout & Morgan, 2007; Stares et al., 2007; Morgan & Rideout, 2008). A comparison of G. morhua fecundity in this region between different time periods suggested that changes in fecundity could not be solely explained by changes in population density (Stares et al., 2007). The potential link between individual fish condition and fecundity in this region as a potential explanation of the variable nature of fecundity, however, has not previously been examined in detail. The analyses presented here are the most extensive to date with respect to the effect of both body and liver conditions on fecundity for north-west Atlantic demersal fishes. The data, covering a total of nine populations, suggest that $K_r$ and $H_r$ do not have a large effect on fecundity above and beyond that of fish size. In those cases where the effect of one or both of the condition indices were significant, they generally explained $<5\%$ of the variability in fecundity not accounted for by fish size. These results might be considered surprising considering a large body of evidence linking egg production of captive fishes to somatic and liver conditions. The results, however, are not completely without precedent when it comes to analyses of condition and fecundity in wild populations. For example, the amount of additional variability

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Fig. 4. Mean ± s.d. annual relative condition indices ($K_r$) for north-west Atlantic Limanda ferruginea (see Fig. 1).
in fecundity that was explained by either condition factor or liver condition was 1% for G. morhua from the north-east Arctic (Kjesbu et al., 1998) and Baltic Sea (Kraus et al., 2000), 1.5% for C. harengus (Oskarsson & Taggart, 2006) and 4–13% for G. morhua from around Iceland (Marteinsdóttir & Begg, 2002). On the other hand, Lambert & Dutil (2000), working with experimental northern Gulf of St Lawrence G. morhua, reported condition to explain 23% of the variability in fecundity not accounted for by length. Results presented for other flatfish populations were similar to those obtained here for north-west Atlantic flatfish populations, with somatic condition explaining an additional 7% of the variability in fecundity at length (Millner et al., 1991) for North Sea S. solea and typically <10% for North Sea and Irish Sea P. platessa (Rijnsdorp, 1991; Kennedy et al., 2007).

Liver and body conditions are often considered together when estimating a fish’s nutritional status (or its energy reserves) because they have the potential to represent different types of stored energy, depending on the species. For example, for G. morhua it has been well documented that surplus lipids are stored in the liver while proteins are stored primarily in the carcass, and thus indices of body condition reflect protein stores while indices of liver condition reflect lipid stores (Eliassen & Vahl, 1982a, b; Black & Love, 1986; Lambert & Dutil, 1997). In G. morhua, liver lipids are the major energy source to support egg production and other energetically demanding processes (Holdway & Beamish, 1984), but this can be supplemented with protein stored in the carcass (Black & Love, 1986). Many flatfishes, on the other hand, have small livers with a relatively low fat content (Tyler & Dunn, 1976) and so the
Table IV. Results from forward-selection stepwise regression to determine if the addition of condition indices to a model already containing total length ($L_T$) explained a significantly higher proportion of the variability in potential fecundity than the model based on $L_T$ alone. $L_T$ was included a priori as the first variable in the model. Variables available for selection to the model were relative condition ($K_r$) and relative liver condition ($H_r$).

<table>
<thead>
<tr>
<th>Species</th>
<th>Population</th>
<th>Variables selected*</th>
<th>$r^2$ ($L_T$)</th>
<th>$\Delta r^2$ ($K_r$)</th>
<th>$\Delta r^2$ ($H_r$)</th>
<th>$r^2$ (total)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hipoglossoides platessoides</em></td>
<td>3LNO</td>
<td>$\log_{10} L_T$, $K_r$</td>
<td>0.724</td>
<td>0.048</td>
<td>0.772</td>
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<tr>
<td></td>
<td>3Ps</td>
<td>$\log_{10} L_T$</td>
<td></td>
<td></td>
<td></td>
<td>0.693</td>
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<tr>
<td><em>Limanda ferruginea</em></td>
<td>3LNO</td>
<td>$\log_{10} L_T$, $H_r$</td>
<td>0.224</td>
<td>0.026</td>
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<td></td>
<td>0.259</td>
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<tr>
<td><em>Glyptocephalus cynoglossus</em></td>
<td>3NO</td>
<td>$\log_{10} L_T$, $K_r$</td>
<td>0.373</td>
<td>0.092</td>
<td>0.465</td>
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<tr>
<td><em>Gadus morhua</em></td>
<td>2J3KL</td>
<td>$\log_{10} L_T$, $K_r$, $H_r$</td>
<td>0.735</td>
<td>0.052</td>
<td>0.008</td>
<td>0.795</td>
</tr>
<tr>
<td></td>
<td>3NO</td>
<td>$\log_{10} L_T$, $K_r$</td>
<td>0.775</td>
<td>0.020</td>
<td>0.795</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3Ps</td>
<td>$\log_{10} L_T$, $K_r$</td>
<td>0.675</td>
<td>0.004</td>
<td>0.679</td>
<td></td>
</tr>
</tbody>
</table>

* $\log_{10} L_T$ was set a priori as the first variable in the models.

The principal source of energy to fuel gamete production is thought to be the carcass, not the liver (Dawson & Grimm, 1980). Indices of liver and body conditions are not equivalent measures of bioenergetic condition for any one species (Pardoe et al., 2008) and any single index of fish condition will not necessarily measure the same thing across multiple species. Given the differences in energy allocation patterns, it was expected that differential relationships between fecundity and condition would be observed among the species examined here but that did not turn out to be the case; body and liver condition had little effect on fecundity in either *G. morhua* or the three flatfish species.

Although there was significant interannual variation in condition indices, failure to observe any meaningful relationship between condition indices and fecundity could have potentially been caused by insufficient range in the condition data. Lambert & Dutil (2000) found that condition factor had a strong influence on Gulf of St Lawrence *G. morhua* fecundity but this population is known to have fish with low condition factors (0.7–1.1). If no such low condition fish were present in the data used here, then the effect of body condition on fecundity may have been reduced. The indices of condition used here were relative (rather than Fulton’s $K$ and hepato-somatic index), which alleviated the problem of both condition indices increasing with fish size. The use of relative condition indices, however, makes it impossible to identify a single value for body condition that divides poor from good condition, since the condition of individuals is expressed relative to the best-fit regression line between length and body mass (or liver mass). As such, poor-condition fishes are simply the lowest condition fishes among those used in the analyses but that is not equivalent to saying that these fishes are in physiologically poor condition.

The notion of a link between fish condition and fecundity persists because it makes sense from an energetics perspective. Less energy available for reproduction should result in fewer eggs being produced. For the north-west Atlantic populations studied here, $K_r$ and $H_r$ rarely explained variability in fecundity that was not accounted...
for by fish mass and when they did, the amount of variability explained was <2%. Koops et al. (2004) concluded from similar findings that length-based analyses of fecundity can ‘overestimate the effects of condition factor on fecundity’ and that indices of condition may not be ‘as biologically important as previously thought’. Because body condition can be partitioned into both growth in length and growth in terms of mass, changes in body condition (and hence available energy to allocate to reproduction) may simply be accounted for by changes in fish mass. In fact, relationships between fish fecundity and fish mass or liver mass, as were observed here, can be considered evidence that energy stores do have a strong influence on fecundity (Kennedy et al., 2007).

There were obvious species differences in the amount of variability in fecundity that could be explained by the factors analysed here. For example, fish size was a good predictor of fecundity for *H. platessoides* but a very poor predictor for *L. ferruginea*. These populations of *L. ferruginea* are in the northernmost extreme of their range, leading to the possibility that the effects of environmental and other abiotic factors on egg production might be high. Temperature has been shown to influence and even prevent reproduction in other species (Hodder, 1965; Kjesbu et al., 1998; Rideout et al., 2005; Yoneda & Wright, 2005a, b). Intrapopulation spatial variability in fecundity for north-west Atlantic flatfish populations, however, did not appear to be related to temperature (Morgan & Rideout, 2008). Perhaps somewhat surprising was the poor relationship between ovary mass and fecundity for *L. ferruginea*, when the same relationship for *H. platessoides* and *G. cynoglossus* was quite strong. The reason for the poor relationship for *L. ferruginea* is not known at this time but it is unlikely that such high variability could have been generated by counting error since samples from all three species were processed simultaneously and in the same manner.

Despite evidence for only a minimal impact of $K_r$ and $H_r$ on fecundity, there does appear to be a positive relationship between *M. villosus* (the major prey item
for *G. morhua* in this region) abundance in the previous year and fecundity of 3NO *G. morhua* in the current year. The disagreement between results may be indicative of a problem with sampling time. Vitellogenesis in *G. morhua* is a lengthy process, taking several months to complete. Down-regulation of fecundity can occur throughout this period via follicular atresia of vitellogenic oocytes. The realized fecundity of a fish may therefore be best estimated when sampled just before spawning (Oskarsson & Taggart, 2006; Thorsen *et al*., 2006). Sampling earlier may mask the relationship between indices of condition and fecundity if the effects of condition (through an effect on intensity of atresia) have not yet been fully expressed. On the other hand, important reproductive decisions such as whether to spawn and how many eggs to produce may be made several months before spawning when energy is initially allocated to egg production (Eliassen & Vahl, 1982a; Millner *et al*., 1991; Burton, 1994), and so sampling too close to spawning may also mask the effect of condition on fecundity. Skjæraasen *et al*. (2006) determined that lipid energy best estimated the fecundity of captive Norwegian coastal *G. morhua* when measured 3–4 months before the onset of spawning. Kennedy *et al*. (2007) found the timing of sampling to be an important aspect of the relationship between somatic condition and fecundity for Irish Sea *P. platessa* as well. When sampled during the spawning season, condition explained <5% of the observed variability in fecundity. Condition, however, explained 15% of the variability in fecundity when sampled earlier in September. In the present study, autumn sampling, where available, is many months before spawning so that decisions about fecundity are unlikely to be complete by that time and there are certainly no fecundity measurements to correspond to autumn sampling.

The analyses presented here should not be misinterpreted as indicating that neither body nor liver condition influence reproduction in these fish populations. The effects of condition on reproductive biology are not just with respect to fecundity but can also be felt in terms of changes in the probability of being an adult (Ajiad *et al*., 1999; Bromley *et al*., 2000; Marteinsdóttir & Begg, 2002; Morgan, 2004; Morgan & Lilly, 2006), the probability of skipped spawning (Rideout *et al*., 2006), gamete...
and progeny quality (Kjesbu et al., 1991; Marteinsdóttir & Steinarsson, 1998) and postspawning survival (Lambert & Dutil, 2000). If variability in stock reproductive potential is to be understood and predicted, continued work should aim to understand the effect of both body and liver condition on all these aspects of fish reproduction as well as the interactions among them.

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