Is fecundity in plaice (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake during autumn?

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(Received 15 December 2006, Accepted 12 July 2007)

The effect of controlling food intake during the autumn, which is the time of late vitellogenesis, on fecundity, atresia and follicle and ovary growth was examined for plaice *Pleuronectes platessa*. Eighteen fish were kept in individual pens and either fed on a high or low ration diet. Fish which increased in whole body condition exhibited an increase in carcass condition which means that when food intake is sufficient to maintain whole body condition some resources are used as storage. Follicle growth rate was positively correlated with change in Fulton’s condition and total atresia was negatively correlated with change in Fulton’s condition. Thus, the rate of vitellogenesis was dependent on the availability of an exogenous food source. Fecundity at the end of the experiment was positively correlated with mass and total length. Food intake had no effect on relative fecundity; however, fish which had a lower food intake lost mass and had a greater intensity of atresia, lowering their absolute fecundity. One fish in a very low condition at the start of the experiment skipped spawning and one fish exhibited a decrease in average follicle diameter during the experiment which is hypothesized to be a prelude to mass atresia.

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Key words: atresia; fecundity; food intake; plaice; *Pleuronectes platessa*.

INTRODUCTION

In the Irish Sea, the fecundity of plaice, *Pleuronectes platessa* L., 1758, has been shown to vary over both temporal and spatial scales (Nash et al., 2000; Kennedy et al., 2007). It has been suggested that these differences are due to differences in the degree of down-regulation in different areas and years in response to
differences in the availability of food between areas and years (Kennedy et al., 2007). It is known that fecundity and maturation are affected by the availability of food (Tyler & Dunn, 1976; Horwood et al., 1989; Bromley et al., 2000) and in extreme cases low food intake can result in abortive maturation (Burton, 1994; Bromley et al., 2000). Annual changes in fecundity of Northeast Arctic cod, Gadus morhua L., 1758, have been linked to changes in environmental temperature and the availability of the main prey, capelin Mallotus villosus (Müller, 1776) (Kjesbu et al., 1998). Horwood et al. (1989) showed that fecundity differences in plaice could be generated in the laboratory by feeding different levels of food during the fecundity proliferation and subsequent maturation. They also found that plaice on low rations may make an early decision not to proceed with gonad development. This was also found by Rijnsdorp (1990) where fish that showed poor growth between June and January did not proceed with gonad development.

Plaice are an iteroparous species so must optimize their energy allocation between a minimum condition required to survive after spawning and an optimum amount of energy for reproduction (egg production and behaviour related to spawning) (Rijnsdorp, 1990). It has been estimated that up to 50% of the gonad growth in plaice is subsidized from body reserves built up during the growing period (Rijnsdorp, 1990) with the major reserve store of lipid and protein being the carcass (Dawson & Grimm, 1980). Vitellogenin (VTG), the main precursor to yolk protein (Tyler & Sumpter, 1996), is manufactured in the liver from these stored reserves and translocated to the ovary where it is incorporated as yolk granules in the vitellogenic follicles. For the optimization of sexual reproduction in female turbot Psetta maxima (L., 1758), a combination of adequate body reserves and a plentiful exogenous supply of food during the vitellogenic phase is required (Bromley et al., 2000).

In this paper, the units of fecundity are referred to as a follicle, i.e. the oocyte and its surrounding somatic tissue (Tyler & Sumpter, 1996). Prior to maturation the ovary contains previtellogenic follicles, which consist of an ooplasm surrounded by oolemma zona radiate and follicle containing no yolk protein (Tyler & Sumpter, 1996). The annual maturation cycle starts when extra-ovarian proteins, namely VTG, are sequestered, processed and packaged via the follicle into oocytes which become known as vitellogenic follicles (Tyler & Sumpter, 1996). Atresia is the degeneration and resorption of ovarian follicles with the potential fecundity being the total number of vitellogenic follicles matured per year, uncorrected for atretic losses (Hunter et al., 1992). The follicles enter final maturation in batches and after ovulation release eggs that are expelled from the ovary for fertilization. The number of eggs released being the realized fecundity.

The fecundity of plaice over its geographical range is lowest in the Southern Bight of the North Sea and radiating from there the fecundity increases (Bagenal, 1966). It was concluded by Bagenal (1966) that the geographical variability in fecundity of plaice is primarily controlled by food availability. Plaice have a determinate spawning strategy (Hunter et al., 1992), whereby the annual fecundity of an individual female is determined before the onset of the spawning season (i.e. no more follicles are recruited during spawning) (Urban, 1991). A study on plaice from the Irish Sea has shown that the maximum potential
fecundity is determined during early vitellogenesis, which is in late September to October, by the size of the fish at the end of follicle proliferation (Kennedy et al., 2007). During the period between the end of follicle recruitment and spawning, fecundity is down-regulated by atresia (Kennedy et al., 2007). Down-regulation is also known to occur in Atlantic herring Clupea harengus L., 1758, with atresia being most prevalent and intense during the early and middle stages of vitellogenesis in October and November, when they are relying on accumulated body reserves. This resorption of follicles was deemed to be a method of optimizing fecundity given available energetic reserves (Kurita et al., 2003).

Plaice feed throughout the year from the end of spawning until the beginning of the next spawning event as can be seen from the continuous rise in condition in North Sea plaice from April until December (Rijnsdorp, 1990) which implies they feed up until late vitellogenesis. The purpose of this study was to examine if food intake during late vitellogenesis can affect the degree of down-regulation, 18 individual plaice were fed on either high or low rations over a period of 4 weeks during late vitellogenesis. Ovary biopsies were taken at the start and middle of the experiment to examine the growth of vitellogenic follicles and the intensity of atresia to indicate the degree of fecundity down-regulation. The mass of the whole body ($M_T$) and ovary ($M_O$) was measured directly or estimated respectively at the start and during the experiment in order to determine the transfer rates of mass between the two body components. The $M_O$ in live fish was estimated from the area of the ovary silhouette using a calibration prepared from fish killed at the start and end of the experiment.

MATERIALS AND METHODS

EXPERIMENTAL SET-UP

Six plaice were caught off the French coast during the Cefas 2004 August beam trawl survey of the English Channel and a further 12 fish were caught by beam trawl from the southern North Sea during a charter of a commercial fishing vessel in October 2004 (Fig. 1). Ideally, all fish would have been caught at the same time, but due to poor weather during the transport of fish from the capture site to the laboratory there was a high mortality of fish. The fish were kept in holding tanks at Cefas, Lowestoft (U.K.) from the date of capture until the start of the experiment, which commenced on the 22 November 2004 (fish were acclimatized for a total of 3 months for the fish caught in August and 1 month for fish caught in October), and fed to satiation with live lugworm Arenicola marina twice a week. Lugworms were deemed a suitable feed for plaice as they make up a large part of their natural diet (Piet et al., 1999; Rijnsdorp & Vingerhoed, 2001). These fish were then divided into two groups of nine individuals for the experiment where one group was fed individually (twice weekly) on a low lugworm ration (equivalent to 0.5% of $M_T$ day$^{-1}$) and a high lugworm ration (equivalent to 1.5% of $M_T$ day$^{-1}$). Any uneaten worms were removed and weighed the following day. Any possible error in the results due to different origins of fish were compensated for in the experimental design by having an equal representation of fish from the two sources in the two feeding regimes.

At the beginning and 2 weeks after the start of the experiment, the fish were anaesthetized using phenoxy-ethanol (at a concentration 0.4 mol l$^{-1}$), weighed to the nearest g ($M_T$) and measured for total length ($L_T$) to the nearest 10 mm (Table I), photographed over a light-box for the assessment of ovary size, and an ovary sample was taken using
a catheter with an internal bore of 2.0 mm (Bromley et al., 2000). The catheter was inserted through the oviduct into the ovary and c. 0.15–0.3 g of tissue was extracted from the ovary and preserved in 3.6% formaldehyde. The gonad biopsies were deemed to have no effect on the results as biopsies were carried out on both groups with only a small amount of tissue removed and there was no mortality or other apparent adverse effects. To avoid bias in the measurement of follicle sizes [plaice ovaries are not homogenous
in respect to follicle diameter (Kennedy et al., 2007) the catheter was inserted a standard distance into the ovary which took a sample from the middle section. The follicle size between the dorsal and ventral ovaries in the middle portion are not significantly different (Kennedy et al., 2007), so there was no requirement to take the sample from a specific ovary.

During the experiment, the fish were housed individually in a compartmentalized tank with a flow-through system of filtered sea water at ambient temperature (range 9.5–13.7 °C, mean 12.1 °C). The fish were divided into a high and low feeding group by ranking the fish according to their mean follicle diameter and putting alternate fish into each group to ensure that the range of follicle development at the start of the experiment was spread between both groups.

The fish were killed after 4 weeks (with an overdose of anaesthetic and subsequent severing of the CNS), measured to the nearest 10 mm and dissected to determine the mass of the liver, gut, ovaries and carcass to the nearest 0.01 g. Three follicle samples were taken from the middle section of the ovaries and analysed using the image analysis system and histology.

### OVARY AREA AND MASS RELATIONSHIP

A relationship between ovary area \(A_O\) and \(M_O\) was constructed using 40 fish. These consisted of (1) four fish that were caught at the same time as the fish from the southern North Sea and kept in the same tank until the start of the experiment and killed at the start of the experiment, (2) 18 frozen fish caught at the same time as the fish from the southern North Sea, which died before the start of the experiment and (3) the 18 fish that were used in the experiment. The area of the shadow created by the ovary, posterior to the body cavity, was measured in the fish by placing them over strong

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**Table I.** Details of the individual *Pleuronectes platessa* used in the experiment with fish number, origin (N, North Sea; F, French coast), total length \((L_T)\), mass at the beginning of the experiment \((M)\), ration level \((RL)\) (H, high; L, low) and success of gonad sampling at the start and middle of the experiment (S, successful; N, non-successful).
illumination and taking a photograph. The \( A_0 \) was then measured from the picture using a polygon function provided by image analysis software (Myrmica; Pilkington Image Analysis Systems, London, U.K.) and plotted against the total \( M_O \) of the fish. The growth of the ovaries in the experimental fish throughout the experiment was then reconstructed from the \( A_0 \) measured at the beginning of the experiment. The equation for the calculation of \( M_O \) was: \[ M_O = 0.049A_0 + 6.67. \]

**ANALYSIS OF OVARY SAMPLES**

The ovary samples were analysed by the auto-diametric method (Thorsen & Kjesbu, 2001), which involves the use of image analysis to measure the diameter of individual follicles. The follicle density (\( D_F \)) and fecundity (\( F \)) could then be calculated from the mean follicle diameter (\( F_{MD} \)) using the equations from Kennedy et al. (2007) which was calibrated using plaice from the Irish Sea [this equation is robust in the same species at different stages of maturity (Kennedy et al., 2007) and across species (unpubl. data)]; \[ D_F = 54.506e^{-3.3807F_{MD}} \] and \[ F = D_F M_O. \]

The image analysis was performed as described in Kennedy et al. (2007). This involved using a PC-based image analysis system Aphelion (ADCCIS, Hérouville Saint-Clair, France) with commercially available software GFA (Pilkington Image Analysis Systems). Follicle samples were stained with periodic acid and Schiff’s reagent to improve the identification of follicles during image analysis. The measurements of follicles using image analysis after staining were not significantly different from measurements made manually before staining (\( t \)-test for dependent samples, \( n = 31, P > 0.05 \)).

Atretic follicles were counted during the analyses; these were distinguished in the whole mount from normal follicles by their non-round shape. The final atretic counts were determined by identification in the whole mount and compared with a histological method where the follicles were dispersed into a layer one follicle deep and polymerized in hydroxymethyl methacrylate. A section was then taken 250 \( \mu \)m from the block face and the numbers of atretic and normal follicles were counted. The total atresia for a fish was calculated as the number of atretic follicles from the second sampling and the number at the termination of the experiment divided by the total number of normal and atretic vitellogenic follicles measured in these two samples. The fecundity of the fish was adjusted for the level of atresia present in the ovary samples taken at the termination of the experiment. Fulton’s condition (\( K \)) was calculated for each fish at each sampling date with the equation: \[ K = 100M_T L_T^{-3}. \] Carcass condition (\( K_C \)) was calculated using the same equation but using carcass mass (\( M_C \)) in the place of \( M_T \).

**STATISTICAL ANALYSIS**

All statistical tests were carried out using Statistica (StatSoft Inc., 2002). The food conversion efficiency among fish was assumed to be constant during the experiment. Measured variables were converted into relative change over the 4 week period. Carcass size at the start of the experiment was calculated from \( M_T \) minus estimated \( M_O \) and the mass of gut and liver at the end. The gut mass was assumed to be constant during the experiment and the effect of the change in liver mass (\( M_L \)) on estimated \( M_C \) was assumed to be insignificant as \( M_L \) makes up c. 1–2% of mass of pre-spawning plaice (unpubl. data), so any change in \( M_L \) would have only a very small effect on estimated \( M_C \). The \( L_T, \) mass and \( F \) measurements were normalized by a ln-transformation.

**RESULTS**

The fish in the experiment ranged in \( M_T \) from 274 to 497 g with an average of 384 g (Table I). Twelve of the fish were 3 years old and the other six 4 years old. All fish re-established feeding after being moved to the individual pens;
however, not all fish consumed all the food they were given. The fish from the high-ration group consumed a mean ± s.d. of 125 ± 35 g of food each throughout the experiment which amounted to a mean ± s.d. of 35 ± 13% of their $M_T$. The fish from the low-ration group consumed 47 ± 4 g each which amounted to 12 ± 2% of their $M_T$. One fish from the high-ration group consumed only 33·6 g of food which was the lowest of all the fish.

The combined mass of both ovaries in each fish was positively correlated with the area of the ovary posterior to the body cavity ($r^2 = 0·85$, $n = 40$, $P < 0·001$) (Fig. 2). A total of 14 biopsy samples were successfully taken at the beginning of the experiment and 11 during the second sampling. A successful biopsy from a fish at the beginning of the experiment did not always result in a second successful biopsy and vice versa (due to the small size of the fish it was difficult to get a sample without keeping the fish out of the water for too long). All fish survived to the end of the experiment. One fish went into mass atresia during the experiment. This fish was on the high-ration diet but had the lowest $K$ of all fish in the experiment.

The $M_T$ at the end of the experiment was positively correlated with $M_T$ at the start of the experiment (linear regression, $r^2 = 0·96$, $n = 18$, $P < 0·001$). Total mass gain or loss was related to the amount of food each fish consumed relative to its own body mass (linear regression, $r^2 = 0·35$, $n = 18$, $P < 0·05$) (Fig. 3). The value of $F$ at the end of the experiment was positively correlated with $L_T$ (linear regression, $r^2 = 0·45$, $n = 17$, $P < 0·05$) and $M_T$ at the beginning (linear regression, $r^2 = 0·52$, $n = 17$, $P < 0·001$) and end of the experiment (linear regression, $r^2 = 0·51$, $n = 17$, $P < 0·001$) (Fig. 4) with no influence of condition. The $M_O$ increased in 14 of the 18 fish with the average percentage

![Fig. 2. Relationship between the area of Pleuronectes platessa ovary shadow posterior to the body cavity and the total mass ($M_O$) of both ovaries. The curve was fitted by: $y = 0·05x + 6·67$.](image-url)
Fig. 3. The relationship between the average amounts of food consumed per day by each individual Pleuronectes platessa expressed as a percentage of total body mass ($M_T$) at the start of the experiment and the percentage change in $M_T$ during the experiment. The curve was fitted by: $y = 4.54x - 3.59$.

Fig. 4. The relationship between total mass ($M_T$) and fecundity ($F$) of Pleuronectes platessa at termination of the experiment. The curve was fitted by: $y = 358x - 42552$. 

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change being a 10% increase. Sixteen of the 18 fish exhibited an increase in \( D_F \); however, the fish with the highest \( F \) exhibited a decrease of 7%. The growth of follicles (increase in \( F_{MD} \)) varied between 0.7 and 22% with one fish exhibiting a decrease of 8%.

There was a positive correlation between change in \( K \) and \( K_C \) between the start and end of the experiment (linear regression, \( r^2 = 0.66, n = 18, P < 0.01 \)) (Fig. 5). Oocyte growth was positively correlated to change in \( K \) (linear regression, \( r^2 = 0.32, n = 18, P < 0.05 \)) (Fig. 5).

Atresia levels estimated in the whole mount and by histological methods were not significantly different (\( t \)-test for dependent samples, \( n = 8, P > 0.05 \)); however, there were small differences in individual fish. Atresia was present in all fish varying from 0 to 43% (mean ± s.d. 14 ± 11%) at the start of the experiment, 2 to 25% (8 ± 7%) at the second sampling date and 2 to 19% (9 ± 5%) at the end of the experiment. The intensity of atresia was not affected by the date of capture of the fish. Total atresia for each fish was negatively correlated with the percentage change in \( K \) between the start of the experiment and the end (linear regression, \( r^2 = 0.78, n = 11, P < 0.001 \)) (Fig. 6).

**DISCUSSION**

The method for estimating ovary size was very successful and gave a reliable measurement of ovary growth although it was not accurate enough for the estimation of fecundity. It was not possible to estimate the area of the whole ovary due to difficulty in discerning the anterior of the ovary as it was obscured by organs in the abdominal cavity. The estimation of atresia from whole mounts and histological methods gave similar results, the average for all the fish estimated by both methods was not significantly different; however, there was a slight difference in individual fish. Estimation of atresia using the whole mounts was much more time efficient as it could be undertaken during the analysis of follicle diameter; however, as these two methods were compared using only a small number of samples this method should be investigated further. It is unknown whether the frequency of feeding in the present experiment is consistent with wild fish as there are very few data on feeding frequency in plaice. It has been shown that intermittent feeding of plaice does not affect fat storage when compared with fish that are fed every day (Jobling, 1982). There was a high variance in the relationship between food intake and total mass gain or loss, which is probably due to differential absorption efficiency. This could not be confirmed as the energy in the faeces was not recorded, it could be due also to stress altering the metabolic rate of the fish. The fish were of a very small size range and all results were converted to percentage change so differences in fish size are presumed to have no effect on the results. Age has only a small influence on plaice fecundity with the major influence on fecundity being mass (Horwood et al., 1986) so the fact that two age classes were present in the experiment is assumed to have no influence on the results.

The fecundity of the fish at the end of the experiment was positively correlated with the \( M_T \) and \( L_T \) of the fish at the beginning and end of the experiment. There was very little difference between the predicative power of mass...
as a proxy for fecundity between the start and end of the experiment. This is because the duration of the experiment was not great enough to bring about large differences in mass between the two feeding groups, so did not alter the correlation between mass and fecundity. Mass was the best predictor of

FIG. 5. The relationship between change in Fulton’s condition ($K$) and (a) carcass condition ($K_C$) and (b) change in follicle diameter ($D_F$) of *Pleuronectes platessa* between the start and end of the experiment. The curve was fitted by: (a) $y = 1.00x - 2.56$ and (b) $y = 1.00x + 10.8$.

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fecundity as found by Koops et al. (2004) for G. morhua and brook trout Salvelinus fontinalis (Mitchill, 1814). The reason for this is that during the non-breeding season when plaice are building up reserves and fecundity proliferation has started, they will produce an amount of eggs proportional to their body size, increasing fecundity as their mass increases (Rijnsdorp, 1990; Kennedy et al., 2007). After fecundity proliferation has ended, fecundity can then be down-regulated by atresia, which can occur when food intake or stored reserves are insufficient to bring all follicles to full development. In order to optimize the use of energy during reproduction, it would be expected that the fecundity would be decreased to a level that would reflect available energy reserves. This appears to be the case as the intensity of atresia during the experiment was negatively correlated with change in $K$ [condition being a reflection of energy reserves in plaice (Costopoulos & Fonds, 1989), which was affected by food intake].

There was no effect of food intake on relative fecundity as fish which ate less lost mass and also fecundity through down-regulation, this is in contrast to an earlier experiment by Horwood et al. (1989), also on plaice. During their experiment, there was sufficient time (406 and 30 days for the previous and present study respectively) for the fish to exhibit fluctuations in mass. This was probable as the fish were kept in communal tanks resulting in the ration that each fish received would vary due to competition for food. As fecundity decreases with decreases in mass, but cannot increase with an increase in mass after fecundity proliferation has ended, the observed differences in relative fecundity would result. A similar result to the present study has been seen in first-time spawning G. morhua where fish fed on a high–high, high–low and low–high
ration, during the follicle recruitment and vitellogenic phase respectively, over a year showed no difference in relative fecundity and fecundity differences were due to differences in the final mass of the fish (Kjesbu & Holm, 1994).

The level of atresia decreased from the start to the end of the experiment which is consistent with the idea that atresia is highest during the early part of maturation and decreases towards spawning (Kurita et al., 2003; Oskarsson & Taggart, 2006). From previous studies on plaice, it has been shown that atresia in spawning plaice is of low prevalence and intensity (Armstrong et al., 2001; Kennedy et al., 2007), therefore, plaice potential fecundity, when spawning commences, should equal their realized fecundity. The total level of atresia during the experiment was between 10 and 30%. Plaice in the Irish Sea are known to reduce their fecundity from 20 to 50% between September and February. It is unknown exactly when this occurs but it is known that it does not occur during the spawning season (Kennedy et al., 2007). The level of atresia seems to be of a similar level from fish under natural conditions in the Irish Sea, unfortunately there appears to be no available estimates of atresia for North Sea plaice.

It was clear from the present results that the rate of vitellogenesis is controlled by the availability of an exogenous food source and the amount of energy gained from this food source. Change in $K$ was a better predictor of follicle growth than food intake as changes in $K$ is a reflection of the net energy gained from food, i.e. energy available after metabolic costs. When food intake was sufficient for increases in $K$, there was an increase in $K_C$ meaning that when food intake is sufficient to maintain $K$, energy is stored in the carcass as well as used for follicle growth. When food intake was no longer sufficient to maintain $K$, stored energy was used for follicle growth as seen by the decrease in $K_C$ but follicle growth still takes place, albeit at a slower rate. This is consistent with the findings of Rijnsdorp (1990) who estimated that 50% of gonad growth in plaice was subsidised from body reserves built up during the growing period. There was no effect of $K$ on changes in the gonado-somatic index, this is probably due to atretic losses which were negatively correlated with changes in $K$. This shows that fecundity is being sacrificed for increased growth of individual follicles. It was surprising to see that fish which increased in $K$ still had atretic follicles. The reason for this may be that, even though there was adequate food to increase body condition, it still may not have been sufficient for the fish to have enough reserves to complete development at its present fecundity and have sufficient resources to survive the spawning season, hence, they decreased their fecundity by atresia.

Slowing the growth of the follicles during periods of low food availability may allow plaice the time to find the adequate amounts of food needed to complete vitellogenesis before reabsorbing follicles by atresia, which would decrease their reproductive output for that year. With the increase in the growth rate of follicles with increased energy gain, there will be a decrease in the time to reach spawning condition. This has been noted in *G. morhua* where the timing of spawning can be predicted (for fish kept under constant conditions) from the mean diameter of the most advanced oocytes. *Gadus morhua* fed with lower rations took longer to bring their oocytes to spawning stage than fish fed with higher rations (Kjesbu, 1994). There are contrasting results, however, for this relationship. Kjesbu & Holm (1994) showed that high feeding in first-time
maturing *G. morhua* led to earlier spawning; however, this was not found in a later experiment (Karlsen *et al.*, 1995). A study by Yoneda & Wright (2005), also on first-time spawning *G. morhua*, showed that faster growing individuals entered into vitellogenesis earlier relative to the slower growing fish, though there was no effect of food ration on follicle growth rate. It was suggested that these inconsistencies may be attributable to differences in food intake among individuals within a feeding group (Yoneda & Wright, 2005).

It is interesting to note that the fish with the highest fecundity exhibited a decrease in the average follicle diameter. This fish also had the highest intensity of atresia at the end of the experiment and also had decreased in condition between the start and end of the experiment. There appears to be no previous record of a decrease in follicle size in the literature. It is hypothesized that the resorption of smaller follicles requires less energy than larger follicles (Kurita *et al.*, 2003), thus, smaller follicles should be selected preferentially before larger follicles for resorption. In this particular fish, this was not the case with the larger follicles becoming atretic. It is hypothesized that this could be a prelude to mass atresia which was seen in one other fish in the experiment. The fish that had mass atresia was on the high ration, however, this fish had a low *K* and for the successful completion of vitellogenesis a high exogenous food source and a high availability of stored reserves is believed to be essential (Bromley *et al.*, 2000). Plaice (Horwood *et al.*, 1989) and also winter flounder *Pseudopleuronectes americanus* (Walbaum, 1792) (Burton, 1994) have previously been witnessed to make an ‘early decision’ to skip spawning when under low food rations.

It was hypothesized in Kennedy *et al.* (2007) that fecundity differences between areas and years in the Irish Sea are the result of differences in the degree of down-regulation of fecundity which was a result of different feeding conditions experienced by the fish in the different areas. The results from the present study support this hypothesis as food intake affected the condition of the fish and subsequently affected the level of atresia. Thus, the availability of food will affect total egg production (TEP) in plaice in two different ways depending on the time of year. High food availability during the summer and early autumn, when follicle recruitment is taking place, means that the potential TEP will increase due to an increase in the size of the fish resulting in an increase in absolute fecundity (Rijnsdorp, 1990; Kennedy *et al.*, 2007). After follicle proliferation has ended food availability will affect TEP by affecting the down-regulation of fecundity in individual fish.

J.K. was in receipt of a NERC CASE award studentship (NER/S/A/2002/10491) with additional support from the European Community through the Energy, Environment and Sustainable Development programme, the Bergen Advanced Training site for Marine Ecology contract (EVK3-CT-2000-57129) and the University of Bergen. Parts of this work were made possible through a Defra-funded project MF0423 [Development of models of plaice (*Pleuronectes platessa* L.) population dynamics incorporating biological processes for use in risk assessment of management options] to C.J.F. (Cefas, Lowestoft), R.D.M.N. (University of Liverpool and IMR), A.J. Geffen (University of Liverpool and UiB) and G. Kirkwood (Imperial College, London). The authors would like to thank the crew of the R.V. *Corystes* and M.F.V. *St John* for help in the collection of fish and S. Hetherington and M. Smith for help in the maintenance of aquaria. This work was performed to strict Home Office guidelines under the authority of licence PPL80/1893.
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