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When to count your eggs: Is fecundity in Greenland halibut (*Reinhardtius hippoglossoides* W.) down-regulated?

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ABSTRACT

Fecundity in several fish species is subjected to down-regulation by atresia so if fecundity is estimated many months before spawning, this will be an overestimation of the realised fecundity (actual number of eggs spawned). In order to get accurate measurements of fecundity it is important to have knowledge on when potential fecundity (estimated fecundity at time of sampling) closely resembles the realised fecundity. Down-regulation of fecundity for Greenland halibut (*Reinhardtius hippoglossoides* W.) was assessed using fish caught off East Greenland in 1998, 1999 and 2000. The fish caught in 1998 and 1999 were in early and late stages of vitellogenesis, respectively of the same maturation cycle. The fish caught in 2000 were also in an early stage of vitellogenesis. Fecundity decreased by 43% between early and late vitellogenesis. Fecundity in 1999 appeared to be the second lowest recorded for Greenland halibut but it is believed to be due to developmental stage rather than low productivity. There was no difference in fecundity between 1997 and 1998. It is believed that differences in fecundity between years only become apparent in late maturation as size during oocyte recruitment has a very large influence on fecundity. Neither Fulton's condition nor hepatosomatic index had any significant influence on fecundity.

1. Introduction

Greenland halibut (*Reinhardtius hippoglossoides* W.) is a deep-water boreal species inhabiting large areas of the North-Atlantic. It has the biological characteristics of a typical deep-water species: slow growth and late maturation. Even though Greenland halibut are an important commercial resource, knowledge of its reproductive biology is relatively sparse. Males mature at lengths of about 40–50 cm while females mature at about 50–60 cm (Morgan et al., 2003). They have a low fecundity (Gundersen et al., 1999) with very large eggs; developing oocytes have been documented as large as 2.4 mm (Gundersen et al., in press) and eggs collected in the field have been documented as large as 4.17 mm (Magnússon, 1977). Greenland halibut populations are known to exhibit a yearly maturation cycle with an extended spawning season; in the area around Iceland this runs from January until March (Morgan et al., 2003). Several studies have examined fecundity in Greenland halibut from several areas including the Northwest Atlantic (Lear, 1970; Bowering, 1980; Serebryakov et al., 1992; Junquera et al., 1999), Northeast Arctic (Gundersen et al., 1999, 2000) and Iceland (Gundersen et al., 2009). However, sampling time in respect to time of year varies considerably between these studies.

In respect to fecundity development, fish are divided into two groups, indeterminate and determinate spawners (Hunter et al., 1992). The fecundity of indeterminate spawners is not fixed with a continuous recruitment of pre-vitellogenic oocytes to the developing pool of oocytes, even during spawning (Hunter et al., 1992). This is opposed to determinate spawners which recruit a batch of oocytes to the developing pool and then there is no more recruitment until the next maturity cycle (Hunter et al., 1992). It is now known that the fecundity in determinate spawners is not fixed but subject to down-regulation (Kurita et al., 2003; Thorsen et al., 2006; Kennedy et al., 2007). Down-regulation is a process in which the fecundity is reduced to match the energy and/or food availability of the fish (Kjesbu and Witthames, 2007; Kennedy et al., 2008). Down-regulation happens by a process known as atresia which is the re-absorption of a developing oocyte (Hunter and Macewicz, 1985).

In order to calculate stock reproductive potential (Trippel, 1999) it is essential to have accurate estimations of fecundity. The use of inaccurate values of fecundity can result in inaccurate perceptions on the state and productivity of a stock (Lambert, 2008). However, the collection of fecundity samples can be very difficult and expensive in terms of man hours, ship time and logistics. This is especially true when studying deep-water species which can spend many parts of the year under ice covered seas so making their capture difficult. It is therefore important to know when the potential fecundity (standing stock of oocytes when sampled)

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is equal to, or very close to realised fecundity (actual number of eggs spawned). This is known to vary among species and depends on their life history. In herring (*Clupea harengus*) a large part of the down-regulation occurs during the autumn when herring switch from feeding to subsisting on stored reserves (Kurita et al., 2003). In plaice (*Pleuronectes platessa*) and cod (*Gadus morhua*) this is a gradual process happening over several months in response to reduced available energy (Kennedy et al., 2008; Witthames et al., 2009). In general it is considered that potential fecundity estimates taken very close to spawning will closely reflect the realised fecundity (Óskarsson and Taggart, 2006). Atresia has been witnessed previously in Greenland halibut and can be seen throughout the entire maturation process (Fedorov, 1971; Walsh and Bowering, 1981; Junquera et al., 1999; Tuene et al., 2002; Gundersen, 2003; Cooper et al., 2007) but this is generally of a low prevalence or intensity in fish in an advanced stage of ovary maturation. Over an extended period, continuous small levels of atresia could result in a substantial reduction in fecundity (Kurita et al., 2003).

It is known that energy reserves can influence fecundity in several fish species, i.e., fish of equal length but greater energy reserves will have a higher fecundity. Several proxies are commonly used for energy reserves in fishes such as Fulton's condition (which is a measure of weight at length) (see Nash et al., 2006) and hepatosomatic index (HSI) (Marshall et al., 1998). However Koops et al. (2004) argues that weight is the most important decider of fecundity and that length based models of fecundity overinflate the variance in fecundity attributed to maternal condition. Weight can be a good measure of energy and protein reserves in fish which store these substances in the muscle; a high percentage of the total weight of fish is made up of muscle so changes in weight can reflect changes in available energy. It is known that the muscle is the main source of protein used for ovary development in plaice, a closely related species of flatfish (Dawson and Grimm, 1980).

In order to examine if there is a reduction in Greenland halibut fecundity during ovary development, fecundity was estimated for Greenland halibut during early and late stages of ovary development in East Greenland. This data was also compared to previously published data from 1997 (Gundersen et al., 2001). The effect of energy reserves on fecundity was also examined using Fulton's condition factor and HSI as proxies.

2. Materials and methods

2.1. Sample collection

The year, depth, area and number of fish sampled is summarised in Table 1. In 1998 ovaries were collected during a joint Norwegian–Greenland trawl survey during July and August in locality B (Fig. 1) in the waters off East Greenland. Trawling was conducted at depths 690–930 m, using a commercial Greenland halibut trawl (mesh size 140 mm). Ovaries which had begun maturation (ovaries containing oocytes >1 mm in diameter and visible to the naked eye) were sampled, stratified to total length with a maximum of 15 fish in each 5 cm length group sampled. Ovaries were preserved in 3.6% buffered formaldehyde at sea.

In 1999 samples were collected from the German commercial trawl fishery in East Greenland waters in March (localities A and B, Fig. 1). The fishery was mainly carried out at depths 1280–1430 m. Ovaries were collected randomly from the catches and frozen at sea. These were transported to the laboratory and thawed slowly at 4 °C, before being preserved in 3.6% buffered formaldehyde. Most ovaries contained large oocytes with diameter of 2–4 mm. However, in some of the ovaries some of the oocytes had started hydration indicating spawning would have started shortly. Ovaries containing hydrated oocytes were excluded from all analysis. The samples from the two areas were pooled as area did not have a significant effect on fecundity (see results). A total of 42 ovaries were analysed for fecundity.

Table 1
Details of the year, month, depth, area (see Fig. 1) and number of fecundity samples taken for Greenland halibut in East Greenland.

Year	Month	Depth	Area	*N*
1998	July–August	690–930	B	74
1999	March	1280–1430	A + B	42
2000	August	1100–1500	A	112

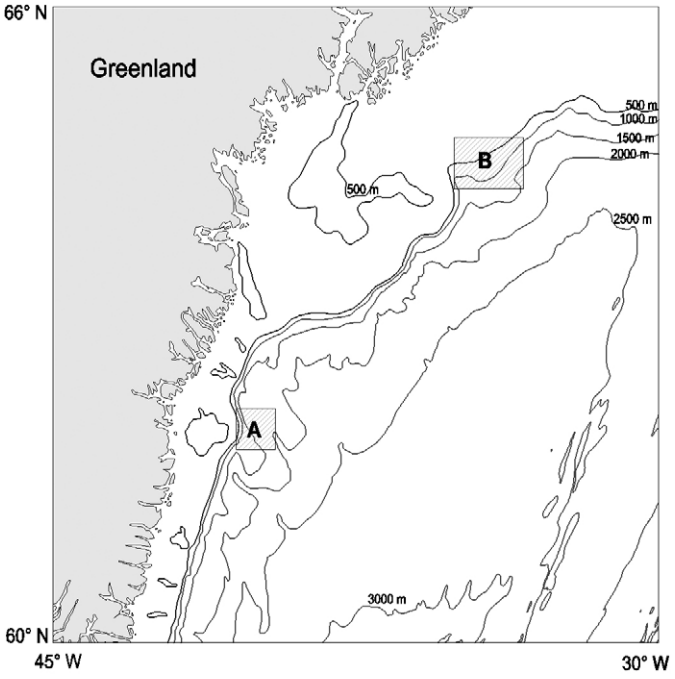

Fig. 1. Localities of sampling of Greenland halibut ovaries in 1998–2000.

In 2000, 112 ovaries were collected near Kap Bille Banke (locality A, Fig. 1) from Greenland halibut caught on longlines in the commercial fishing area during a joint Norwegian–Greenland survey in August at depths between 1100 and 1500 m. Ovaries were collected in a similar manner to 1998.

From each female of which ovaries were taken, total length, total weight, gonad weight and liver weight were measured. The length range sampled was similar between years (see Table 2).

2.2. Fecundity analysis

Analyses of potential fecundity were carried out using the gravimetric method modified for Greenland halibut described by Gundersen et al. (1999, 2000). From each ovary four sub-samples of tissue of approximately 0.75–2.00 g were taken from the middle section of the right lobe of the ovary. Greenland halibut ovaries are known to be homogenous in oocyte packing density (Gundersen et al., 2001), hence samples were taken from only one location in the ovary. Of the three classes of oocytes found in this study only fully vitellogenic oocytes that will be spawned in the next spawning season (G1 oocytes) were counted. Classification of the oocytes is described in detail by Gundersen (2003). These oocytes appear dark when visualized under binocular microscope. Ovaries which did not contain vitellogenic oocytes were excluded from any analysis. Two sub-samples were counted and used in the fecundity estimates if the coefficient of variation of the estimates per unit ovary weight were below 5% for the two samples, otherwise all four samples were counted and analysed. The sub-sample count ranged from