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# Methodological challenges to examining the causes of variation in stock reproductive potential

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ABSTRACT

Understanding the causes of variation in stock reproductive potential (SRP) is challenging due to the difficulty in assessing the relative contribution of environmental, demographic and genotypic influences. This review explores how experimental and comparative field studies have been used to disentangle sources of variation in maturity, fecundity and the timing of spawning. By comparing reproductive parameters and corresponding environmental conditions among stocks of a species it is clear that demography, energetic state and temperature are important factors affecting variation in SRP. Common garden and environment experiments have confirmed that there is also a substantial genetic component to regional differences in reproductive investment and timing of spawning. Environmental manipulation experiments have helped to elucidate the proximate mechanisms underlying many reproductive processes. Together these different sources of information have provided a foundation for the development of statistical and individual based modelling approaches that help explain variation in SRP. In the near future, genomic investigations may provide a direct means to account for genetic influences on reproductive variation. Given that the age and size structure of many fish stocks has become truncated through fishing, a greater focus on the contribution of reproductive life span to SRP is also needed.

## 1. Introduction

A fish stock's ability to produce viable eggs and larvae has been termed stock reproductive potential (SRP) and is a function of maturity, fecundity, egg quality, and spawn timing (Trippel, 1999). Both environmental change and fishing can impact components of SRP in various ways and the effects of these factors can be difficult to distinguish. Rising sea temperatures will generally promote growth rate if food is not limiting and could have a direct affect on gonad developmental rates (Tobin and Wright, 2011). Fishing can impose levels of mortality on juveniles and adults that far exceeds natural mortality (Mertz and Myers, 1998), leading to a truncation in age and size structure and a reduction in reproductive life span (Murawski et al., 2001) and spawning time (Scott et al., 2006). In addition to the immediate affect that demographic change has on SRP, persistent changes in the pattern of size selectivity mortality may act as a strong agent for genetic selection on maturation schedules (Law, 2000). However, similar maturity changes may arise due to the reduction in stock biomass caused by fishing, since reductions in intra-specific competition can lead to faster growth rates and so earlier attainment of the threshold state for maturation (Trippel, 1995). Hence, it is important to be able to distinguish between the various sources of variability affecting reproductive parameters.

Estimating and understanding variation in SRP is clearly challenging because of the interaction between environmental, demographic and genetic influences on reproductive traits. Whilst there have been important advances in disentangling these effects during the last decade, there are still many limitations imposed by the data collected and the techniques available. This paper explores the challenges and progress made in understanding changes in SRP. The importance of integrating field, experiment and modelling approaches in the investigation of SRP variation is discussed. For simplicity, some of the key components of SRP are considered separately; namely maturation (puberty), fecundity and spawning time. Examples are largely drawn from studies on temperate deterministic spawners and most notably Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.). This review starts by highlighting some of the simplifying assumptions inherent in most field investigations of SRP, since these affect whether statistically significant results are actually biologically meaningful.

## 2. Relevance of physiology to the measurement of reproductive traits

Correlative based field studies using data on reproductive parameters, measures of energy storage and information on region wide environmental conditions have long been the main approach

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to investigating variability in SRP. Most such investigations depend on recognisable macroscopic features of gonads together with length, somatic and occasionally liver and gonad weight. Ovaries for potential fecundity analysis are usually sampled when vitellogenesis is in an advanced state because they are easy to distinguish macroscopically. The data derived from these collections are then used to correlate maturity and fecundity with size and condition (e.g. Kjesbu et al., 1998; Marteinsdottir and Begg, 2002; Blanchard et al., 2003; Yoneda and Wright, 2004). Environmental data for comparison with reproductive parameters are usually based on average conditions prevailing during sampling or over some time period experienced by a stock. The challenges to interpreting cause and effect from such information becomes clear when the underlying reproductive physiology is considered.

Photoperiod is generally the major entraining cycle in fish reproductive physiology (Bromage et al., 2001). For temperate species that spawn in late winter and early spring, such as haddock, the decline in day length following the summer solstice is the key cue for individuals to assess their energetic state for maturation (Davie et al., 2007). The nutritional or energetic state signal to continue gametogenesis appears to involve insulin-like growth factor (IGF-I) that is produced in the liver (Campbell et al., 2003, 2006). IGF-I acts on the brain-pituitary-gonad axis, probably via kisspeptin, which in turn stimulates pituitary follicle stimulating hormone (FSH) and then sex steroids involved with early gametogenesis (Campbell et al., 2003, 2006; Migaud et al., 2010). Environmental conditions between the summer solstice and the rise in FSH production are thus likely to have the greatest influence on maturation.

Fig. 1 illustrates how common field measurements relate to reproductive physiology, using results from a laboratory experiment on haddock as an example. The last sample point in this figure corresponds to the time of year when most surveys begin collecting data on reproductive development. In immature females, oocyte development is arrested before or at the cortical alveoli (yolk vesicle) stage by the September before spawning (Tobin et al., 2010). Whilst the length and condition of individuals in this example were found to differ with maturity state throughout the experimental period, the magnitude of this difference varied. Length explained <14% of the variation in proportion mature at the start and end of the sampling period compared to 21% during the mid-point in summer. This was because faster growing individuals in spring and summer had a greater tendency to mature (see also Tobin and Wright, 2011). The importance of such seasonal growth differences to maturation has also been found in the lesser sandeel, *Ammodytes marinus* (Boulcott and Wright, 2008) and in chum salmon, *Oncorhynchus keta* (Morita et al., 2009). Somatic condition was also a significant proxy of energetic state prior to maturation commitment but not later in the year suggesting the growing energetic cost of reproduction may reduce the signal from such a measure by the time fish are sampled close to spawning. Similarly, high relative liver mass around the onset of the maturation assessment might be a signal of energetic state. A similar temporal variation in liver mass has also been reported in Gulf of St. Lawrence cod (Lambert and Dutil, 2000). Substantial changes in gonadosomatic index are not seen until well into vitellogenesis after the surge in FSH (Tobin et al., 2010). Hence, the size and condition at maturity relationships commonly reported in the literature may not accurately reflect those that would be obtained at the times of maturity and fecundity commitment (Wright, 2007). As it is impractical to move away from field based proxies as the primary source of information on SRP variability, it is important to consider the uncertainty that arises from the use of these proxies.

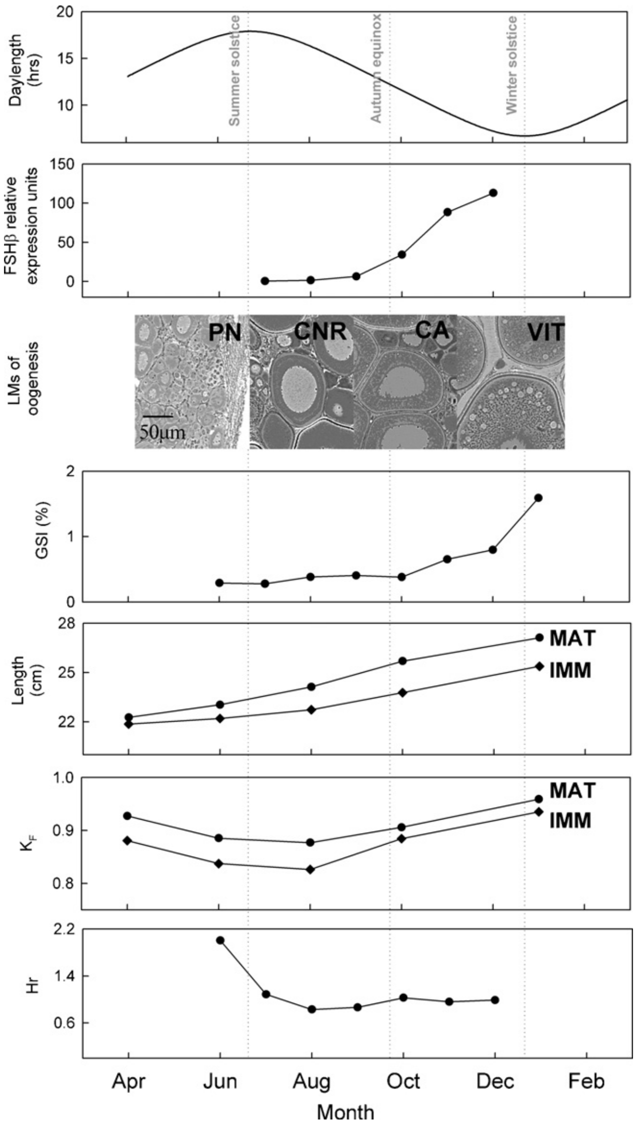

**Fig. 1.** Relation between daylength, oogenesis and changes in length, condition and relative liver index in haddock, *Melanogrammus aeglefinus*. Light micrographs (LM) show oogonia surrounded by perinucleolar (P) stages, circum-nuclear ring (CNR), cortical aveoli (CA) and early vitellogenic oocytes. Daylength based on latitude (57°N), oocyte stage, FSH expression, gonado-somatic index, GSI and relative liver index (Lr) of maturing individuals based on Tobin et al. (2010). Length and Fulton's condition ($K_F$) was based on individual haddock data from a similar unpublished study.

Increasingly, various meta-analysis approaches are being used to compare variability in SRP across ecosystems in a semi-comparative type approach. This information is vital in identifying trends in the relationships between SRP components and stock demography. However, the varying relationship between reproductive stage and an individual's size, age and energetic state show that it is important to standardise for developmental state (e.g. first time spawner and pre-, early or late vitellogenesis) when making comparisons among individuals and across ecosystems. For example, the inability to distinguish first from repeat spawners can bias maturity–size relationships, leading to a source of bias in year based maturity ogives. Histological analysis of gamete stages or measurements of ovarian and testes wall thickness may indicate if a fish has previously spawned (Burton et al., 1997) although this is rarely used (but see Pérez-Rodríguez et al., 2009). Whilst potential fecundity can be determined prior to spawning in determinate species, atretic down regulation following the initial recruitment of vitellogenic oocytes means that this measure will decline as oocyte size increases (Kurita et al., 2003; Witthames et al., 2010). As such it is desirable to standardise for possible down regulation by the