Understanding the determinate–indeterminate fecundity dichotomy in fish populations using a temperature dependent oocyte growth model

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ABSTRACT

The fecundity type (determinate vs. indeterminate) is still uncertain for many commercially important fish populations affecting accuracy in fecundity estimations and hindering the selection of appropriate egg production methods for stock assessment purposes. It is broadly considered that boreal fish populations living in colder habitats are determinate spawners whilst populations residing in warmer habitats tend to be indeterminate spawners. In the present study we modelled the determinate–indeterminate fecundity type in batch spawning fishes, i.e. fish that spawn several batches of eggs per spawning season, based on the relationship between oocyte growth period and the duration of the spawning period considering that both variables can be affected by water temperature and latitudinal distributions. Individual based models (IBMs) were developed to explore how the interaction of these variables can result in a series of patterns along the continuum from extreme determinacy, i.e. annual fecundity being recruited long before the onset of the spawning period, to indeterminacy. Model simulations showed that fish stocks with oocyte growth periods longer than the spawning period are predicted to exhibit determinate fecundity which provides a fair justification for why cold water species with slow oocyte growth and limited spawning periods are determinate spawners and vice versa.

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1. Introduction

The fecundity type of fishes can be broadly classified according to the pattern of *oocyte recruitment* from the primary growth (PG) phase to secondary growth (SG) and the time lag between oocyte recruitment and spawning (Ganias, 2013; Lowerre-Barbieri et al., 2011). In general, fishes exhibit two fecundity types: *determinate fecundity* in which all oocytes to be spawned in a reproductive cycle are recruited to SG prior to the beginning of the spawning period; and *indeterminate fecundity*, in which oocytes continue to be recruited to SG throughout the spawning season (Hunter et al., 1992; Kjesbu, 2009; Lowerre-Barbieri et al., 2011; Murua and Saborido-Rey, 2003). The knowledge of the fecundity type of a fish stock is of great importance in fisheries biology as it is used to estimate reproductive potential (Murua and Saborido-Rey, 2003) as well as spawning stock biomass when egg production methods are applied (Armstrong and Witthames, 2012; Stratoudakis et al., 2006). If fecundity type is incorrectly assigned, estimates of fecundity can be off by orders of magnitude (e.g. Hyle et al., 2014).

Despite its importance, the fecundity type of many exploited fish stocks is still uncertain. In addition, little is known about the processes driving the two fecundity types and whether they are genetically controlled or an ecophenotypic response to a variable environment

(Kjesbu and Witthames, 2007). The most general pattern which is recognized for fecundity type is the one that relates it with the thermal habitat and the latitudinal distribution of fish stocks (Ganias, 2013; Hunter et al., 1985; Lowerre-Barbieri et al., 2011). Hunter et al. (1985) first suggested that coldwater species like whiting (*Merlangius merlangus*) and haddock (*Melanogrammus aeglefinus*) with boreal geographic distributions tend to have determinate fecundity whilst temperate and tropical species are mostly indeterminate spawners. Moreover, based on the concepts of definite and indefinite spawning of Hickling and Rutenberg (1936), Hunter et al. (1985) linked determinate fecundity to species with total (isochronal) spawning and limited spawning seasons whilst indeterminate fecundity was linked to multiple spawning and extended spawning seasons.

The relationship between the duration of the spawning season and oocyte growth rate is critical to understanding phenotypic plasticity in fecundity type. This relationship was first proposed by Greer-Walker et al. (1994) for N Atlantic mackerel and subsequently evaluated for the NA population of sole, *Solea solea*, by Witthames and Walker (1995). According to this approach slow oocyte growth combined with restricted spawning seasons allow little scope for oocyte recruitment within the spawning season and thus results in determinate fecundity. On the other hand, fast oocyte growth, combined with an extended spawning season allows batches to be recruited throughout the spawning season leading to indeterminate fecundity. Indeed, as shown in Fig. 1 (data and references for this figure are provided in
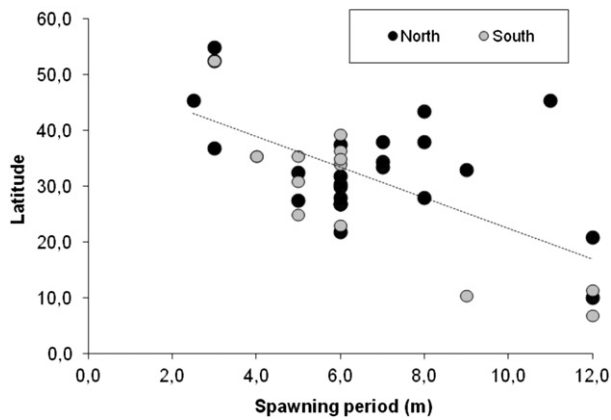
Fig. 1. Relationship between latitude and the duration of the spawning period for several stocks of multiple spawning fishes (data and references are placed in the supplement).

Supplement A) and Table 1 respectively both spawning season and oocyte growth rate of fish stocks decline with increasing latitude. Conceptually, this suggests determinate fecundity to be more common in temperate/boreal stocks in contrast to tropical/sub-tropical stocks, where indeterminate fecundity should be more common.

Growth of secondary oocytes will be affected by metabolism, and thus water temperature in cold-blooded fishes and its relationship to thermal conditions has been previously explored using the Q_{10} temperature coefficient (e.g. Kjesbu, 1994, 2009; Witthames and Walker, 1995). However, the relationship between spawning season duration and water temperature is more complex, as a population's spawning season is controlled by ultimate factors that select for inheritable components (e.g., endogenous rhythms and energetic thresholds) and by proximate factors, which are exogenous cues used to entrain gonadal development and spawning activity (Leder et al., 2006; Munro et al., 1990; Yamahira, 2001) to synchronize reproductive effort with the optimal conditions for offspring survival (Bye, 1984; Cushing, 1971). Moreover, in their review on flatfishes Rinjdorp and Witthames (2005) described trends relating the fecundity type to seasonal patterns in temperature, with determinate fecundity more common in winter spawners and indeterminate fecundity common in summer spawners (see also Kjesbu, 2009). In that respect both large scale, geographic and small scale, seasonal climatic shifts are worth exploring since they may shed light on how the environment affects the fecundity pattern of fishes.

The present paper uses an individual based model (IBM) to evaluate how oocyte growth and spawning season duration interact to affect fecundity type in fish stocks. IBMs have proved a valuable tool to assess reproductive parameters in batch spawning fishes (e.g. Cooper et al., 2013; Lowerre-Barbieri et al., 1998). Different fecundity types were simulated ranging from extreme determinate fecundity (oocyte recruitment completed well in advance of the beginning of the spawning period) to extreme indeterminate fecundity (oocyte recruitment occurring throughout most of the spawning period). Estimates of total fecundity, mean oocyte size, and oocyte size frequency distributions are discussed in comparison to published results for various populations of determinate and indeterminate spawners.

2. Methods

There is little published data on oocyte recruitment in fishes mainly because this phenomenon is extremely difficult to assess. Only recently, the use of novel methodology such as stereology and oocyte packing density theory (Kurita and Kjesbu, 2009) has been used to quantify newly recruited oocytes in hake, *Merluccius merluccius* (Korta et al., 2010), cod, *Gadus morhua* (Kjesbu et al., 2011) and anchovy, *Engraulis encrasicolus* (Schismenou et al., 2012). As a consequence, in our model we needed to make some assumptions both on the pattern of oocyte recruitment and on how this relates to other parameters such as spawning interval (*SI*) and batch fecundity (F_b), i.e. the number of oocytes shed per spawning event. In general, our model follows the conceptual model presented in Li et al. (2011) which assumes fish recruit oocytes from primary growth (*PG*) to secondary growth (*SG*) in batches which develop and are spawned and thus are the basis of F_b. Time period between two recruitment events (batch recruitment interval, *BRI*) corresponds to *SI*.

Model parameters are illustrated in Fig. 2. The oocyte growth period (*OGP*) is the time period between recruitment to SG and the spawning of each oocyte batch (i.e., the time period necessary for oocytes to develop from cortical alveolar stage to ovulated eggs). The batch recruitment period (*BRP*) is the period between the recruitment of the first and the last batch per season. The spawning period (*SP*) is the period between the spawning of the first and the last batch per season and is a factor of *SI*, the annual number of spawns and *OGP*. Theoretically, if *OGP* does not change inside the season, the number of days in the *BRP* will be equivalent to the number of days in the *SP*. Mean seasonal spawning date (*MSD*) is the median in the range between the first and the last spawning date and is an indicator of the season in which a stock spawns. The reproductive period (*REP*) is defined as the time between the recruitment of the first batch to the date the last batch is spawned. Total fecundity, F_t, is the number of SG oocytes present at any time in the ovary whilst annual fecundity, F_a is the total number of SG oocytes produced/spawned per season (Hunter et al., 1992; Murua et al., 2003). In our model we did not account for atretic losses and thus F_a was simply calculated as F_b multiplied by the number of annual spawns.

In our model, oocytes were considered to be perfect spheres and their size was expressed by their diameter (*OD*) which in each batch was assumed to come from a normal distribution. *OD* in all batches and for all populations was set to grow from 100 μm at the onset of SG to 700 μm prior to hydration when spawning is imminent (Fig. 2). These values of oocyte sizes, that are typical for many determinate (e.g. cod; Kjesbu et al., 2011; sole: Witthames and Walker, 1995) and

Table 1
Oocyte growth rates (OG) for various populations of determinate and indeterminate fecundity species. When available, egg volume is also provided so as to standardize OG values.

Fecundity type	Species	Region	Survey	OG (mm/d)	Egg vol. (mm³)	References
Determinate	*Clupea harengus*	Norwegian Sea	Field	0.0037	1.15	Kurita et al. (2003)
	Gadus morhua	Barents Sea	Field	0.0035	1.76	Kjesbu et al. (2010)
		Barents Sea	Lab	0.0036–0.0042	1.76	
	Microstomus pacificus	California	Field	0.0024	6.37	Hunter et al. (1992)
	Reinhardtius hippoglossoides	N. Atlantic	Field	4.1096	40.19	Kennedy et al. (2011)
	Scomber scombrus	N. Atlantic	Field	0.0034	0.90	Greer-Walker et al. (1994)
		N. Atlantic	Lab	0.0002–0.0010	0.90	ICES (2012)
	Solea solea	N. Atlantic	Field	0.0032	1.02	Witthames and Walker (1995)
Indeterminate	*Encrasicholina purpurea*	Hawaii	Field	0.0900	0.23	Clarke (1987)
	Engraulis capensis	S. Africa	Field	0.0700		
	Engraulis mordax	California	Lab	0.0178	0.35	Hunter and Leong (1981)
		California	Field	0.0400	0.35	Hunter and Goldberg (1980)
	Sardina pilchardus	N. Atlantic	Field	0.0260	1.76	Ganias et al. (2011)