REPRODUCTIVE CYCLING AND CONTROL IN SOME NW ATLANTIC TELEOSTS

M.P.M.Burton
Department of Biology and Ocean Sciences Centre, Memorial University of Newfoundland, St.John's, Newfoundland, Canada A1B 3X9, Telephone: 709-737-3515; Fax: 709-737-3018

Abstract

Variations in reproductive cycling and their control can be related to seasonal food availability, and muscle quality. Variants studied, in marine teleosts from the NW Atlantic, include short-season spawners and batch-spawners as well as fish reputed to be semelparous (single-time spawning).

Introduction

Cycles of reproduction for Northern teleosts, whether fresh-water or marine can be classified in various ways. One of the major classifications (Cole 1954) deals with whether spawning is normally repeated in an individual from year to year (iteroparous) or whether spawning is terminal event in the life-cycle (semelparous). For females it is accepted that oogenesis may be completely synchronous, group-synchronous or asynchronous (Marza 1938, Harder 1975, Wallace & Selman 1981). It is expected that semelparous females will have completely synchronous oocyte development, and it is implied that semelparous females in the final phases of oogenesis should not have immature oocytes because all oocytes should be committed to the terminal reproduction. It also makes sense that semelparous fish will have the option to draw heavily on body reserves in the last phases of gamete development if such fish are going to die shortly after reproduction anyway they might as well commit most of their energy to gamete development and only reserve sufficient to complete the final gamete deposition phase.

For iteroparous fish in habitats with highly seasonal food supply a problem of survival compatible with energy allocation to reproduction has perhaps been solved by various mechanisms in the cycles. One option is finely adjusting numbers of gametes produced both at the species and the individual level. The ultimate option is to totally omit reproduction in a facultative manner (Burton 1994) so that fish only reproduce if they have a good chance of post-spawning survival. For fish such as winter flounder, *Pleuronectes americanus*, which has to sustain a long winter fast at least in the Northern part of its range, the strategy of facultative spawning omission makes it possible for individual fish to "choose" whether to risk committing energy to a spawning season.

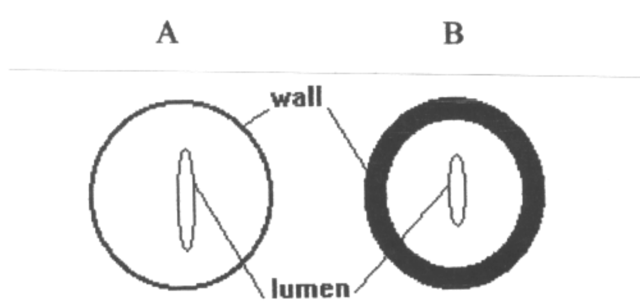
However winter flounder is an unusual flatfish in that it has short-season spawning, certainly for the females, in that all the evidence is that females deposit all their eggs in a very short time, probably much less than a week. This contrasts with other Northern flatfish such as yellowtail, *P.ferrugineus*, halibut, *Hippoglossus hippoglossus*, and American plaice (long rough dab in European waters), *Hippoglossoides platessoides*, all of which are confidently reported to be batch-spawners. Such batch-spawners will deposit sub-sets of the mature oocytes at intervals over a period of about 1 month or more to give an extended spawning period, with several advantages. One of these advantages is perhaps increasing the chance of survival for at least some of the offspring which may hatch at a better time than earlier or later groups. Another advantage is that if the final stages of maturation include considerable increase in size with pressure on the abdomen, then batch spawning staggers the effect and makes possible a larger overall production of oocytes. A considerable disadvantage would be the effect an extended spawning period would have on options for feeding. A possible effect would be a down-grading of white muscle protein content to provide materials for batch-spawners as is implied by Roff (1982).

Cycles examined

Recently, in addition to studies on winter flounder (Burton & Idler 1984, 1987a, 1987b; Burton 1991a, 1991b, 1994) and earlier work looking at aspects of salmonid reproduction (Burton et al 1985), several other NW Atlantic teleost cycles have been examined in conjunction with thesis work and summer employment of several students and assistants. Gametogenesis of male and female cod was studied (Burton et al 1996); oogenesis of American plaice is being examined in association with muscle depletion (Maddock & Burton 1995, 1996), and the reproductive cycle of capelin *Mallotus villosus* has been scrutinized (Flynn & Burton 1995, 1996) in the light of strong suggestions that it is semelparous. I am just beginning (with two students) to investigate the life cycle of the NW Atlantic "turbot", *Reinhardtius hippoglossoides*, a fish which is supposed to migrate North and spawn in deep water off the Davis Strait (Scott & Scott 1988), which makes knowledge of reproduction somewhat inaccessible. Another feature of this fish is that it has been recently under increasing commercial pressure and it has the interesting biological feature that males seem to be very rare.

Results

Winter flounder seems be an extreme case of a reproductive cycle that may be quite typical for NW Atlantic teleosts whether they be batch-spawners (cod, most Northern flatfish except winter flounder) or short-season spawners like winter flounder. In all these fish whether batch-spawners or spawners over a very compressed time period the females at least seem to have a very protracted oogenesis that may be subject to very fine control of timing and several switches and adjustments related to nutrition. Because both cod and flatfish have similar cystovarian ovaries with substantial outer muscle layers which apparently get irreversibly thicker (Fig. 1) after the first spawning (Burton & Idler 1987a, Burton et al 1996) it should be reasonably easy to identify adults at certain seasons, and particularly non-spawning adults.



A. Immature B. Post-spawning or non-reproductive adult

Figure1. Changes in the cystovarian ovary after spawning

It is certain that winter flounder, and perhaps cod, and probably many of the other flatfish do not necessarily spawn every year after the first spawning (Burton 1994, Burton et al 1996) and it is clear that spawning omission can be primarily related to recent poor feeding conditions. Experiments (Burton 1991a,b, 1994) have confirmed that winter flounder reproduction is very sensitive to feeding conditions and that winter flounder have a critical period, close to the normal spawning season, during which nutritional status can influence whether a fish will begin or maintain gametogenesis for the next spawning season. In studying factors controlling this "decision" it is interesting that Burton & Burton (1989) noted that non-reproductive adults at the normal spawning time showed evidence of some seasonal steroidogenesis. Recent examination of pituitaries of some non-reproductive fish shows that there is some synthetic activity in the DR (distinct region Burton et al 1981) normally associated with reproductive fish and the production of carbohydrate-rich gonadotropins.

Winter flounder, because it has a very short spawning period is easier to study, from the point of the inter-relationships between reproduction and nutrition and early gametogenesis, than the batch-spawners which have an extended spawning season and at least the possibility of variable late recruitment into vitellogenesis (indeterminate gametogenesis). Studies on American plaice, a fish noted for its propensity to sacrifice muscle condition (Templeman & Andrews 1956, Roff 1982) are ongoing, with timing of gametogenesis (Maddock & Burton 1996) and development of jellied muscle (Maddock & Burton 1995) compared to the situation in winter flounder (Burton & Idler 1984, Maddock & Burton 1994). The main interest on the nutrition-reproduction interaction is whether American plaice does undergo late vitellogenesis which draws on muscle protein (Maddock & Burton 1996). For batch-spawners generally there may be problems with nutrition in that protracted spawning can interfere with feeding, which may necessitate drawing on somatic stores. Winter flounder which, off Newfoundland, undergoes a protracted winter fast (Kennedy & Steele 1971, Fletcher & King 1980) but does start feeding both in the wild and in the laboratory before spawning, even though the temperatures may be below the temperatures at which flounder generally stop feeding in the late fall, then stops feeding for a very short time (about a week) around the spawning time for females (unpublished records, Burton).

Capelin, *Mallotus villosus*, has the general reputation (Nakashima 1987, Shelton et al 1993) of being a one-season spawner, ie is semelparous. The post-spawning ovaries however (Flynn & Burton 1995, 1996) contain immature oocytes and it is possible to keep females, though not males, alive after spawning. Such post-spawned females will develop vitellogenic oocytes for the next spawning season (Flynn & Burton 1995, 1996) so it is evident that at least the females are not semelparous. The situation with the males remains puzzling. I have not been able to persuade them to resume feeding after spawning, whereas the females feed readily on *Artemia*. However it is entirely possible that they die partly at least partly because the spawning period for males is protracted (Templeman 1948). Conversely, the females have a short spawning (Templeman 1948) period similar to that of winter flounder. It will probably not be possible to use simple ovarian structure to detect repeat-spawners in wild females because the ovary is not of the cystovarian type. Neither is it of the simple gymnovarian type such as is found in salmonids (Flynn & Burton 1996). Detection of repeat-spawning males in the wild would be possible if the testicular structure changes with spawning as occurs with winter flounder (Burton & Idler 1987a). As male capelin are generally larger and more robust than females it was somewhat surprising to find that females survive much better than males, even though Templeman (1948) and more recently Shackell et al (1993) had indicated this could be so. This life cycle requires more study, particularly as this small species is such an important prey item in the NW Atlantic.

Work with turbot (Greenland halibut *Reinhardtius hippoglossoides*) has just started, with initial data collection already showing we are going to need considerable revision of published accounts of where the fish spawn. It is also evident that clearly identifiable males continue to be very rare in samples collected.

Conclusions

For fish with cystovarian ovaries it may be possible to obtain sound data on spawning omission for adult females in the wild populations of the NW Atlantic. For any fish, marine or freshwater, which is subject to nutritional constraints because of short feeding seasons perhaps compounded by long spawning periods there are various adaptations that may have arisen. Nutritionally controlled and irregular spawning omission for individuals is one possibility while for others it may be possible to maintain batch-spawning by short-term sacrifice of white muscle. Surprisingly however the small pelagic capelin females do not deplete their soma to the point of obligate semelparity unlike the Pacific coast and much larger fish of the *Onchorhynchus* grouping in the same taxon (Protacanthopterygii). Although I do not have firm data yet on the batch-spawning flatfish there is evidence in the literature (Pitt 1966, Bagenal 1957, Templeman & Andrews 1956) that some of these flatfish may show periodic spawning omission as individuals. Cod, *Gadus morhua*, is also a batch-spawner, and although it may show some muscle depletion (Love 1960) it seems more likely that it responds to poor nutrition by down-grading its fecundity (also found for flatfish species, Burton 1994), and by spawning omission (Burton et al 1996), also reported for Barents Sea cod by Oganesyan (1993).

The inter-relationship of muscle as protein (or fat) store, and the fine control of seasonal allocation or depletion of materials to or from gonads and muscle, may be shifted towards conservation of soma in the case of the winter flounder or muscle depletion in the case of American plaice.

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