Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success*

Peter J. Wright[1] & Edward A. Trippel[2]

[1]Fisheries Research Services, Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK; [2]Fisheries and Oceans Canada, St. Andrews Biological Station, 531 Brandy Cove Road, St. Andrews, NB, Canada E5B 2L9

Abstract

Demography can have a significant effect on reproductive timing and the magnitude of such an effect can be comparable to environmentally induced variability. This effect arises because the individuals of many fish species spawn progressively earlier within a season and may produce more egg batches over a longer period as they get older, thus extending their lifetime spawning duration. Inter-annual variation in spawning time is a critical factor in reproductive success because it affects the early environmental conditions experienced by progeny and the period they have to complete phases of development. By reducing the average lifetime spawning duration within a fish stock, fishing pressure could be increasing the variability in reproductive success and reducing long-term stock reproductive potential. Empirical estimates of selection on birth date, from experiments and using otolith microstructure, demonstrate that there is considerable variation in selection on birth date both within a spawning season and between years. The few multi-year studies that have linked egg production with the survival of progeny to the juvenile stage further highlight the uncertainty that adults face in timing their spawning to optimize offspring survival. The production of many small batches of eggs over a long period of time within a season and over a lifetime is therefore likely to decrease variance and increase mean progeny survival. Quantifying this effect of demography on variability in survival requires a focus on lifetime reproductive success rather than year specific relationships between recruitment and stock reproductive potential. Modelling approaches are suggested that can better quantify the likely impact of changing spawning times on year-class strength and lifetime reproductive potential. The evidence presented strengthens the need to avoid fishing severely age truncated fish stocks.

Correspondence: Peter J. Wright, Fisheries Research Services, Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK
Tel.: +44 1224 295436
Fax: +44 1224 295511
E-mail: p.wright@marlab.ac.uk

Introduction

High fishing pressure decreases the proportion of older and larger individuals within a spawning stock. This reduction is largely acknowledged to have a deleterious impact on the number of viable offspring produced due to the positive relation between maternal age/state, relative fecundity and egg viability (Kjesbu 1994; Trippel 1998; Ouellet *et al.* 2001; Clemmesen *et al.* 2003; Berkeley *et al.* 2004a). However, in addition to egg quality the loss of larger and older individuals may affect reproductive success through the impact it has on spawning time. Spawning time has long been proposed as a critical factor in the reproductive success of fish. Whilst the influence of environmental factors on spawning time is widely recognized, there is now growing evidence that phenotypic characteristics of the spawners, such as their size and age, influence the timing and duration of spawning. Consequently, by removing older and larger adults, fishing may have an appreciable effect on spawning times and thereby an adverse affect on recruitment. This review considers the importance of spawning time to reproductive success and whether fishing has a significant impact on this aspect of fitness.

To evaluate whether fishery induced changes in spawning time have a significant effect on reproductive success we consider whether:

1. there is substantial inter-annual variation in spawning time;
2. stock demography plays a significant role in this variability;
3. fishing significantly affects stock demography and thereby spawning time;
4. there is selection on birth date i.e. survivors are not a random subset of offspring from a spawning period;
5. the magnitude of any effect is at least comparable to other sources of variability in reproductive potential.

This paper addresses these objectives by drawing together evidence for extrinsic and intrinsic sources of variability in spawning time and the contribution that fishing has to this variation. Evidence for intra- and inter-annual variability in selection on birth date and the implications this has to reproductive success of harvested stocks is then presented. Before considering these questions a background about the ways in which spawning time is important to progeny survival is given.

Importance of spawning time to survival

Large temporal variation in early offspring mortality over a breeding season has been demonstrated in a wide variety of animal taxa. Hence, the probability of survival can be related to the date an individual is born. The importance of birth or hatch date as a component of selection on breeding schedules has received considerable attention in birds (Price *et al.*, 1988; Harris *et al.*, 1992; Verhulst *et al.* 1995; Christians *et al.* 2001) and mammals (Rutberg 1987; Ims 1990; Green and Rothstein 1993; Nussey *et al.* 2005), but less so in fish (Schultz 1993; Cargnelli and Neff 2006). Although Schultz (1993) found evidence of stabilizing selection on birth date in a single year-class, multiple year studies of a number of birds and mammals have demonstrated that the form of selection is likely to vary between years and with parental age and experience (Moller *et al.* 2006; Nussey *et al.* 2005). Ultimately, selection on birth date will influence the evolution of parental breeding schedules, particularly in species that reproduce only once a year (Stearns 1992).

Evidence that spawning time in fishes is, in part, a heritable trait includes the temporal stability of mother – daughter spawning times (Danzmann *et al.* 1994; Su *et al.* 1999), the expansion of the spawning season of rainbow trout (*Oncorhynchus mykiss,* Salmonidae) from 2 weeks to 8 months by means of phenotypic selection (Siitonen and Gall, 1989; Fishback *et al.* 2000) and evidence of quantitative trait loci associated with spawning time (Sakamoto *et al.* 1999; Leder *et al.* 2006). Local adaptation of spawning time has also been indicated

from differences in spawning time that continued when fish were taken from locations with differing environmental conditions in the wild and reared under a common environment (Otterå *et al.* 2006; Rogers *et al.* 2006). Differences in spawning runs of Atlantic rainbow smelt (*Osmerus mordax*, Osmeridae) (Coulson *et al.* 2006), sockeye (*Oncorhynchus clarkia*, Salmonidae Woody *et al.* 2000) and Atlantic salmon (*Salmo salar*, Salmonidae, Stewart *et al.* 2002) have been related to genetic population differences. Indeed, rapid evolution of distinct breeding periods is also apparent from investigations of chinook salmon (*Oncorhynckus tshawytscha*, Salmonidae) introduced into New Zealand (Quinn *et al.* 2000).

Reproductive timing in fish, as in other vertebrates, is commonly cyclical. This spawning periodicity is strongly connected to re-occurring, cyclical conditions favouring offspring survival. Whilst offspring survival is key to the evolution of reproductive timing there is likely to be a trade-off if there are other selective forces acting on parental spawning time. For example, timing of predation risk may differ between parents and offspring and their energetic state could limit when they are able to breed (Varpe *et al.* 2007). Various categories of reproductive timing have been suggested according to whether time of year or cyclical events are important to offspring survival. Knowledge of the timing category is important in understanding how inter-annual differences in reproductive timing arise. Absolute timing may be important when, for example, animals have to migrate to a spawning ground by a specific time of year to accrue some benefit. Timing relative to the phenology of other organisms may be important when synchronization with seasonal fluctuations of prey is important to progeny survival (Verhulst *et al.* 1995). Synchronization of reproduction with other members of a breeding group may be important in reducing predation rate (Hatchwell 1991; Johannes, 1978) and finding suitable mates (Rowe and Hutchings 2003). Synchronization of reproduction among individuals within a population generally arises through entrainment of gametogenesis with regularly occurring environmental cycles. Synchrony that evolved to reduce predation on offspring may rely additionally on mechanisms that are not correlated with seasonal environmental cycles and resource availability such as lunar cycles and social stimulation from female conspecifics (Johannes, 1978). A high degree of population synchrony

should result from cues that can be reliably used to predict the future conditions for reproductive success.

Unlike many branches of evolutionary ecology, fishery science theory has tended to consider offspring survival (recruitment) in relation to a population's peak or duration of egg production rather than the reproductive success of individual parents. As such fishery science has tended to focus on the role of environment in influencing year-class variation rather than the life history traits that fish have evolved to reproduce successfully under these varying conditions. Of course natural selection acts on the mechanisms controlling gametogenesis and therefore spawning time of individuals rather than on population-level attributes. Stock level variability in spawning times and recruitment variation should therefore be seen as emergent properties of the overall selection on individual spawning time and offspring survival. Moreover, as recruitment only considers the outcome of one spawning season it is not possible to directly link this population attribute to an individual's lifetime reproductive success. Nevertheless, the idea that reproductive timing should be related to the timing of prey and predators is central to both fishery recruitment hypotheses described below and those concerning reproductive success (e.g. 'timing' hypothesis – Verhulst *et al.* (1995); 'date' hypothesis – Verboven and Verhulst (1996); the 'environment' hypothesis – Winkler and Allen (1996)).

Synchronizing spawning times with hydrographical cycles or events has been implicated in fish survival. Advection is important to recruitment in species which have separate spawning and nursery grounds (Harden Jones 1968; Bartsch *et al.*, 1989). Dispersal may also be important for larvae to reach areas of high prey productivity (Hinrichsen *et al.*, 2003). Stability in oceanographical features which concentrate plankton prey resources has also been implicated in early survival (Lasker 1981; Peterman and Bradford 1987; Munk *et al.* 1995).

Hjort (1914) hypothesized that the time of first feeding was a critical period when year-class strength was established since starvation during this early phase could substantially reduce the number of offspring surviving. Whilst the importance of early starvation has been questioned, several hypotheses have proposed that the rates of growth and mortality are inversely related (Beyer, 1989; Houde, 1989; Anderson, 1988; Sogard 1997; Takasuka *et al.* 2003). This is because prey density and/or size limits growth and predation rate
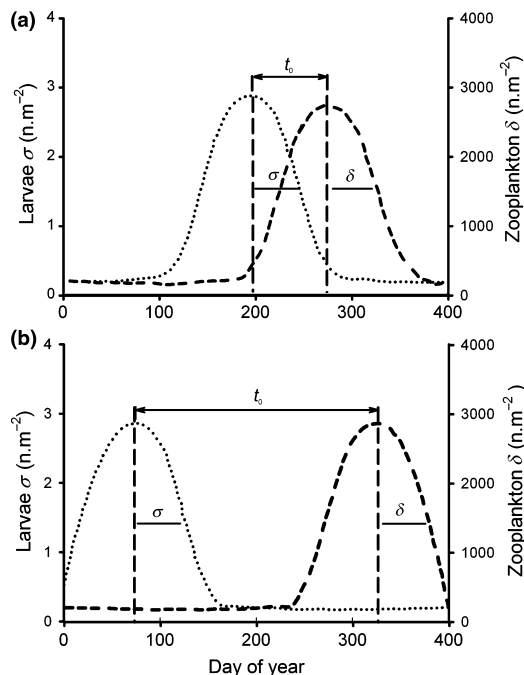
tends to be strongly negatively size selective (Peterson and Wroblewski 1984). Due to the seasonal availability of larval prey in temperate waters, Cushing (1969, 1975) proposed that the synchrony or match between hatching and an appropriate phase of the prey production cycle was an important selective influence on growth and mortality ('match–mismatch' hypothesis; Fig. 1). Similar hypotheses about synchrony have extended this concept to an optimal window for survival (Cury and Roy 1989; Bollens *et al.* 1992) and the need to complete early phases of development during favourable feeding conditions (Sinclair and Tremblay 1984). Indeed in some species, individuals need to reach a critical size before the end of their first year to survive low food conditions during winter months (Shuter *et al.*, 1980; Cargnelli and Gross, 1996; Biro *et al.* 2004).

Predation pressure on early life stages may also be an important selective force on reproductive timing (Johannes, 1978; Sancho *et al.* 2000;

Figure 1 Schematic of the match–mismatch hypothesis in which (a) illustrates a match represented by the high overlap of fish larvae and its prey and (b) a mismatch represented by the lag in time and space between fish larvae and its prey (δ and σ represent one-half width of the production period of the match–mismatch hypothesis for larvae and zooplankton) adapted from Cushing (1990) by Johnson (2000).

Webster 2003). This has led to hypotheses linking both the importance of relative timing with prey and predators. For example, Pope *et al.* (1994) theorized that in temperate waters early survival depended on staying abreast of the seasonal wave of abundant food whilst avoiding the co-evolving wave of predators. Importantly, this hypothesis highlights that if both growth and predation mortality exhibit a seasonal trend the small gains in growth rate linked to later spawning in the spring could be counter-acted by higher predation mortality leading to lower survival rates. This concept of counteracting evolutionary responses to seasonal development of food availability and risk of predation has also been widely described in studies of reproductive success of other taxa (Naef-Daenzer *et al.* 2001).

All these hypotheses regarding recruitment imply that spawning at the right time of year, relative to other cycles within the environment, is important to offspring survival (Heath, 1992; Pope *et al.* 1994). These hypotheses also imply that fish spawning times have evolved so an individual's offspring encounter suitable conditions sufficiently often to ensure adequate levels of recruitment for populations to be sustainable. Therefore, any factor which disrupts the synchrony between reproductive timing and favourable conditions for offspring survival may affect reproductive success and thereby stock level recruitment. From an evolutionary perspective, size selective pressures from fishing mortality may ultimately select for a change in reproductive timing.

Hypotheses which focus on the relative timing of spawning imply that selection on birth date is generally stabilizing, favouring offspring originating from the peak spawning time, as for example in Cushing's match–mismatch hypothesis. Evidence for stabilizing selection was found in the only study to consider the lifetime fitness consequences of birth date selection in a fish (Schultz 1993). However, regular stabilizing selection is likely to select for short, highly synchronized spawning periods, which are rarely found in iteroparous species. Indeed, even in single batch spawners the population's spawning season can be protracted because individuals spawn at different times. The production of multiple batches may simply be a mechanism that enables fish to have a much higher fecundity than the restriction imposed by body cavity size (Garrod and Horwood, 1984; Fordham and Trippel 1999). However, according to life history theory, selection for a high number of spawnings per season and

lifetime is a response to large intra- and inter-annual variation in offspring survival rates (Stearns 1992). Thus, protracted spawning can be seen as a trade-off between the mean and variance in offspring survival since if individuals spawning larger and fewer egg batches also experience greater variance in reproductive success, then they may have lower fitness than individuals laying many smaller batches (Gillespie, 1977; Stearns 1992). Theoretical attempts to consider the consequences of a mismatch in timing at the stock level in a single year indicate that protracted spawning might help reduce the effect of short-term mortality episodes on year-class strength (Cushing 1990; Mertz and Myers, 1994). Similarly, model simulations of the effect of a stochastic and evolving environment on early mortality in haddock (*Melanogrammus aeglefinus,* Gadidae) have indicated that it is better to spawn continuously throughout the season, rather than in one distinct burst of activity (James *et al.* 2003). This is because as the hatching period is increased average recruitment increases and variance tends to decline (see Fig. 2; James *et al.* 2003).

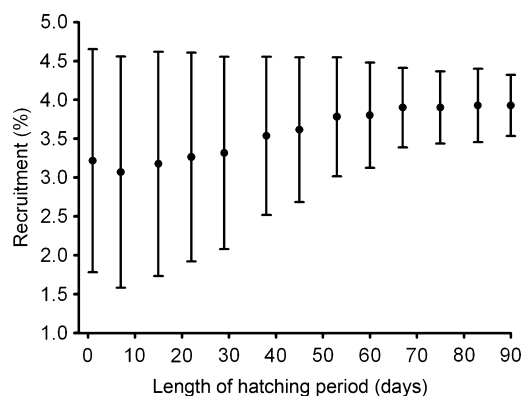## Inter-annual variation in spawning time

Early hypotheses of recruitment variation in temperate marine fishes often assumed there was no significant inter-annual variation in spawning time, an idea supported in the stocks of some species (Cushing 1969). However, there are now many examples demonstrating large inter-annual vari-

Figure 2 Mean (±SD) number of recruits as a percentage of an initial fixed total number of eggs calculated for different hatching periods based on 1000 simulation runs of survival in a stochastic and evolving environment. From James *et al.* (2003).

ability in both the peak and duration of spawning (Table 1) and so the assumption of discrete and regular spawning time is generally inappropriate. Inter-annual variability in spawning time can be expected to arise either through variability in the environmental cycles to which their reproduction is entrained or to intrinsic factors affecting when an individual can or chooses to spawn.

Spawning variability linked to the environment

Highly synchronized and discrete spawning periods have been documented for a few marine (Cushing 1969) and freshwater species (Brown and Scott 1994). Such precise timing reflects spawning synchrony with regularly re-occurring environmental cues. Eleven year cycles of spawning time in the whitefish (*Coregonus lavaretus*, Salmonidae) of Lake Constance have been correlated to sunspot activity (Hartmann, 1984). Annual reproductive cycles with a well-defined periodicity are likely to be entrained to day length, as this is the most reliable environmental signal of time (Scott, 1979). The importance of day length to reproductive timing is evident from the ability to shift or even inhibit maturation by means of photoperiod manipulation in many fish species (Shimizu *et al.*, 1994; Bromage *et al.* 2001; Norberg *et al.*, 2004). Phases of the moon are also used to synchronize reproduction in many species, including those that do not spawn annually such as many tropical reef fishes (Johannes, 1978; Takemura *et al.* 2004; Park *et al.* 2006; Gladstone 2007). Tidal cycles are especially important to species inhabiting inter-tidal habitats. For example, Yamahira (2001) demonstrated from egg translocation experiments on the inter-tidal spawning puffer fish (*Takifugu niphobles*, Tetraodontidae) that the degree of selection for diel spawning time was related to the vulnerability of eggs to seaward transport.

Synchronization of spawning with prey availability generally involves environmental cycles other than just photoperiod, at least following the onset of the secondary phase of gametogenesis (Scott, 1979). Temperature appears to be important in the onset of spawning. It may act as both an environmental cue or directly on the rate of reproductive development by modifying the levels of hormones controlling the rate of vitellogenesis (Iles, 1984; Kjesbu 1994; Bromage *et al.* 2001). As resting metabolic rate is largely dependent on environmental temperature in ectothermal animals, rates of gametogenesis would be expected to be

Table 1 Variation in spawning times and reported causes.

Species	Region	*n* years	Range in S_{50} (duration)	Cause	References
Mallotus villosus	Newfoundland	17	37	Length/temperature	Carscadden *et al.* (1997)
Mallotus villosus	Newfoundland	3	37	Length	Vandeperre and Methven (2007)
Clupea harengus	Gulf of St. Lawrence	27	45	Temperature	Sinclair and Tremblay (1984)
Clupea harengus	Newfoundland spring spawner	23	35[1] (25–78)	Temperature/ size	Winters and Wheeler (1996)
Clupea harengus	Norwegian coast	2	59	Repeat/first time	Slotte *et al.* (2000)
Engraulis enchiolus	Bay of Cadiz	4	60 (210)	Repeat/first time	Millan (1999)
Engraulis mordax	California	1	150	Age/repeat	Parrish *et al.* (1986)
Gadus morhua	NW Atlantic, NAFO areas			Temperature, age	Hutchings and Myers (1993, 1994)
	3L	30	70		
	3NO	32	65		
	3P	32	100		
Gadus morhua	Baltic	14 (before 1990)	60 (200)	Temperature, size	Wieland *et al.* (2000)
Gadus morhua	Iceland	20	34 (77)	Temperature, repeat/first time	Jónsson (1982)
Gadus morhua	Iceland	6	14 (70)	Size	Marteinsdottir and Björnsson (1999)
Melanogrammus aeglefinus	North Sea	3	20 (90)	Age	Wright and Gibb (2005)

[1]Onset of spawning.

Depending on availability, information is given on the peak or 50% spawning date (S_{50}) and the total range in spawning dates as well as the duration of stock spawning period (in parentheses). The number of years of each study is also given. The three main identified causes of spawning time variation were temperature, size or age and the proportion of first-time and repeated spawners.

highly responsive to the thermal regime during maturation. This effect of temperature on oocyte development is evident from laboratory experiments (Kjesbu 1994; Mananos *et al.* 1997) explaining why low temperature has been correlated with delayed spawning in temperate species such as Atlantic cod (*Gadus morhua*, Gadidae) and capelin (*Mallotus villosus*, Osmeridae) (Hutchings and Myers 1994; Carscadden *et al.* 1997; Wieland *et al.* 2000). Estimates of the effect of temperature on the average population spawning time for a range of species are provided in Table 1.

Factors affecting spawning migration have the potential to alter spawning times. Temperature in the spring appears to influence movements of some migratory temperate marine fish species to spawning grounds. Higher sea-surface temperatures are associated with earlier migration in Pacific herring (*Clupea harengus pallasi,* Clupeidae) and capelin (Ware and Tanasichuk 1989; Carscadden *et al.* 1997). Conversely, seaward migration of flounder (*Platichthys flesus*, Pleuronectidae) was found to be earlier and more synchronous within the population at low temperatures (Sims *et al.* 2004).

For successful breeding, animals must synchronize gamete maturity within and between genders. Teleost fishes solve this challenge by using reproductive hormones both as endogenous signals to synchronize sexual behaviour with gamete maturation, and as exogenous signals (pheromones) to synchronize spawning interactions among mature adults (Carolsfeld *et al.* 1997; Patino 1997; Kobayashi *et al.* 2002). For example, synchrony in spawning pomacentrids has been linked to facilitating interactions between nesting males and schooling females (Tzioumis and Kingsford 1995). Ovulation may also occur in response to specific factors such as temperature change or spawning substrate (Scott, 1979; Stacey 1984; Kobayashi *et al.*, 2002) and simply the presence of females, presumably through phermones, stimulate spermiation (Suquet *et al.* 1992).

Spawning variability linked to stock demography

Despite the many mechanisms by which fish can synchronize their reproductive cycles, the spawning periods of most species are not discrete, extending

over weeks and in many cases months due to individual differences in the onset and duration of spawning within the breeding population. The duration of the spawning season tends to become more extended from the polar regions to mid-latitudes with the populations of some tropical fish spawning all year (Tzioumis and Kingsford 1995; Srinivasan and Jones 2006). This asynchrony often arises because of age, size or experience related differences in spawning time (see Table 1). As a consequence, changes in spawning stock age composition can lead to a substantial shift in peak spawning time even in single batch spawners, such as herring and capelin. Age and size related differences may be linked to spawning experience with large, old repeat spawners usually spawning before young, first-time spawners (Sund *et al.*, 1938; Hay 1985; Lambert 1987; Miranda and Hubbard, 1994; Trippel and Morgan 1994; Danylchuk and Fox 1996; Trippel *et al.*, 1997; Leino and McCormick 1997; Wright and Gibb 2005) although not in all species (Morgan 2003) and stocks (Hutchings and Myers 1993). The reasons for the demographic differences are not well understood. There may be a genetically determined pre-disposition to alter the onset of spawning times with age or the difference may be related to the generally higher condition of older fish (Ellertsen *et al.*, 1989; Ridgway *et al.* 1991; Trippel *et al.*, 1997; Cargnelli and Neff 2006). Low energetic status, particularly lipid levels, can reduce the levels of hormones involved in gonadal development, such as oestradiol-17beta (Matsuyama *et al.* 1994) and 11-ketotestosterone and thereby delay spawning time (Cerda *et al.* 1994). An interesting analysis has been conducted to elucidate the relative role of female body mass and water temperature in regulating timing of spawning in Pacific herring (Ware and Tanasichuk 1989). Models based on empirical data of herring stocks along the British Columbia coast demonstrated that the instantaneous maturation rate is size dependent and that a 55 g difference in female body mass was equivalent to a 1 °C change in water temperature in affecting time to full maturity or spawn start time. In some areas, herring spawned in discrete waves such that the oldest females in the stock descending to age 4 years spawned in the first wave, while small 4-year olds and age 3 years first-time spawners in the second wave, about 16 days later (Ware and Tanasichuk 1989).

The behaviour of older members of a stock may also be important where males are territorial as larger fish are likely to displace younger fish from premium spawning sites (Ridgway *et al.* 1991; Candolin and Voigt 2003). There also seems to be a body size/age component to arrival on spawning grounds such that larger, older, experienced spawners tend to enter sites ahead of first-time spawners and this demographic element is likely to be embodied with environmental driven variation (Ridgway *et al.* 1991; Trippel *et al.*, 1997; Lawson and Rose 2000; Vandeperre and Methven 2007). Run timing in two-sea-winter Atlantic salmon has also been shown to be earlier than for one-sea-winter adults (Stewart *et al.* 2002) and early spawning stocks of chum salmon (*Oncorhynchus keta*, Salmonidae) in western Canada were comprised of older fish (Beacham and Murray 1987).

In addition to variation in the onset and peak of spawning, the duration of the spawning season in many fish populations is protracted due to multiple spawning by individuals. In multiple-batch spawners individuals may produce more batches over a longer period as they get older (DeMartini and Fountain, 1981; Parrish *et al.* 1986; Trippel, *et al.*, 1997; Secor 2000; Claramunt *et al.*, 2007). In temperate multiple-batch spawners, the peak and duration of spawning can vary by weeks to months. Spawning duration of young age-classes within a stock may only be as little as half that of older adults (Parrish *et al.* 1986; Wright and Gibb 2005). Many temperate multiple-batch spawners have determinate fecundity, where the maximum potential fecundity is established prior to the spawning season. In one such species, Atlantic cod, individual spawning can last between 2 and 7 weeks and, by individuals beginning to spawn at different times, a population may spawn from 4 to 15 weeks (Kjesbu 1989; Kjesbu *et al.* 1991; Kjesbu *et al.* 1996; Marteinsdottir and Björnsson 1999). During their lifetime individual annual spawning durations of cod can almost double (Kjesbu *et al.* 1996; Trippel 1998). The lengthening of individual spawning duration relates to both the interval between spawning and the relative scaling between potential and batch fecundity. The interval between spawning does not generally decline with age in determinate spawners such as cod and may actually lengthen (Kjesbu *et al.* 1996). Whilst the upper limit for batch fecundity is determined by female size, the slope in the batch fecundity – size relationship is lower than that of the potential fecundity – size relationship and hence large females often produce relatively small egg batches (see

Kjesbu *et al.* 1996; Marteinsdottir and Begg 2002). Even females with comparatively low realized fecundity may still commit to many egg batches (Hislop *et al.* 1978; Trippel and Neil 2004; Rideout *et al.* 2005). In indeterminate spawners where the number of eggs to be spawned is not determined prior to the onset of the spawning season such as anchovy (*Engraulis*, Engraulidae) and sardine (*Sardina*, Clupeidae) larger and older females tend to have relatively high batch fecundity and appear to spawn more frequently than smaller individuals (Claramunt *et al.* 2007).

So in summary, whilst environmental influences such as temperature can lead to significant inter-annual variation in timing of spawning, differences in demography can account for a similar additional variation in both the peak and duration. Therefore, contrary to early views of Cushing (1969), it is possible for both demography and environment to lead to a mismatch between reproductive timing and suitable conditions for offspring. The earlier onset and greater frequency of spawning with size and age also means that reproductive lifespan tends to increase non-linearly with spawning experience, which could have important consequences to fitness.

Fishing-induced changes in spawning time

The demographic influence on population spawning time and duration could be impacted by fishing in various ways. The more heavily fished a population, the more likely it is made up of only small, young population members (Law and Grey 1989; Trippel *et al.* 1997; Jennings *et al.* 1998, 1999). As a consequence of the truncation in size composition, many commercially exploited fish stocks are now dominated by a high proportion of first-time spawners (Wigley 1999; Morgan *et al.* 2003). The removal of older members of a stock could shorten the population spawning season and change the peak time of egg production. Whilst this effect may be reversed by reducing fishing mortality or counteracted by the entry of large year-classes, there is evidence that prolonged heavy exploitation has induced genetic selection for smaller and younger age at maturity in many stocks (Trippel 1995; Jørgensen *et al.* 2007). Given the relation between size, age and spawning time, long-term changes in maturity at size and age could have affected the onset of spawning in first-time spawners. The effect of size truncation and smaller size at maturity is

reflected by a decline in the average age of spawners and an increase in the proportion of first-time spawners comprising the adult stock (Jørgensen 1990; Trippel *et al.* 1997; Wigley 1999; O'Brien *et al.* 2003; Berkeley *et al.* 2004b; Beamish *et al.* 2006).

Fishing may also selectively remove components of a spawning stock if there is size or age-related spatial differences in fish distribution. For example, Marteinsdottir and Petursdottir (1995) showed that both size and age of spawning cod in the near shore area of south-west Iceland were significantly greater than on the bank and along the continental edge. This spatial segregation of size and age together with regional differences in relative fishing mortality led to a relatively high selective removal of larger spawners that tended to spawn early in the season (Begg and Marteinsdottir 2003). Fishing may also have an indirect effect on spawning time if it significantly influences prey availability and thereby reproductive developmental rates through effects on condition or the timing of spawning migrations.

It is difficult to quantify the likely impacts of changes in stock demography on reproductive output except through modelling. Murawski *et al.* (2001) developed models that incorporated the proportion of each age group spawning for the first and subsequent time (from information contained in the maturity ogive) and differences in the survival of eggs and larvae in relation to the demography of spawners (based on experimental results). Using this they modelled how the expected number of spawnings per recruit for each maturing cohort of Georges Bank cod varied as a function of fishing mortality (Fig. 3; Murawski *et al.* 2001). This simulation demonstrated that reproductive lifespans were severely curtailed as fishing mortality increased to reported levels. Lifetime expected number of spawnings per recruit was significantly reduced to 0.5 times even when age at first spawning was age 2 years.

Scott *et al.* (2006) examined the impact of fishing mortality on the temporal variation in egg production of Atlantic cod within a deterministic individual-based model. Size-specific relationships for population spawning time and experimentally derived estimates of individual inter-spawning interval were used in the model. Different simulated populations were created that had the same spawning biomass regardless of the age/size structure, allowing the assessment of relationships and parameter ranges as a function of fishery induced demo-

Figure 3 Expected number of spawnings per recruit for each platoon (age-at-maturity cohort 1–5 years) for Georges Bank cod as a function of fishing mortality (F). For example, at zero fishing mortality, an individual in this model reaching first maturity at age 2 years will spawn almost twice before dying, whereas at a $F = 1.0$ an individual would spawn slightly above 0.50 times. From Murawski *et al.* (2001).
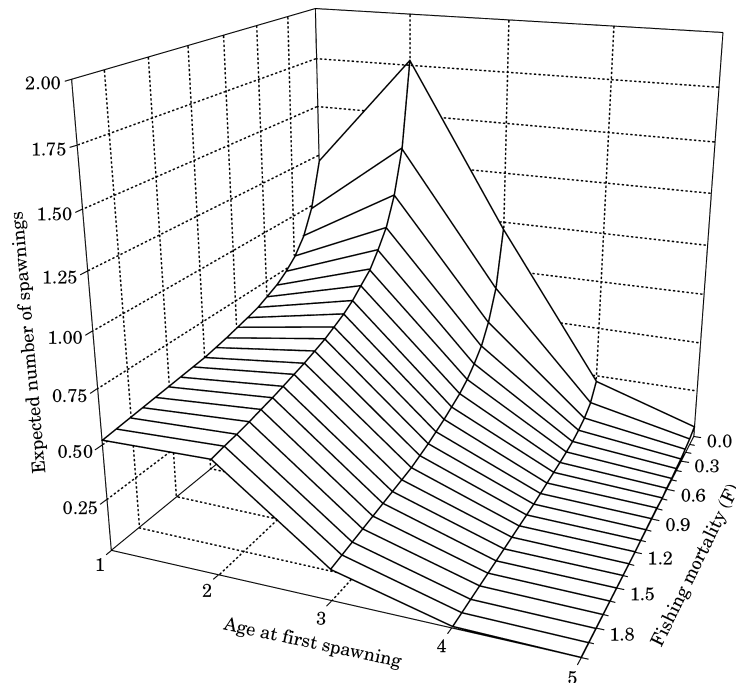
graphic changes in stock structure (Fig. 4). Because smaller cod spawn later and produce fewer egg batches, the peak and duration of spawning was 2 weeks later and 4 weeks shorter in the simulated population subject to the highest fishing mortality (i.e. most size truncated population) than the unfished population (Table 2). As most of the stock spawning period takes place over 10 weeks this estimated reduction implies that spawning periods can be substantially altered through high fishing mortality. This predicted reduction in spawning duration associated with fish size is consistent with field observations on the relation between size composition and spawning duration in Baltic cod (Tomkiewicz and Köster 1999). Scott and colleagues also considered the impact of this reduced spawning season on relative recruitment assuming no seasonal variability in environmentally induced offspring mortality. Based on this assumption, the impact of a fishing mortality of 1.0 was a 47%
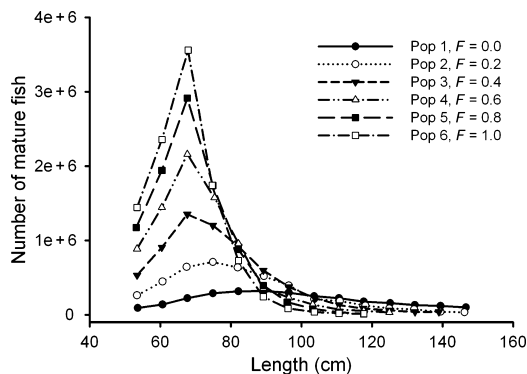
Figure 4 Simulated population length compositions of cod for a given fishing mortality (F) under a stock–recruitment scenario in which spawning biomass is constant. Redrawn from Scott *et al.* (2006).

Table 2 Simulations of the temporal characteristics of spawning with a stock of constant biomass but varying length composition due to varying F.

Population	Peak date spawning	Start of spawning	End of spawning	Total duration
2	3	12	0	−12
3	6	26	0	−26
4	10	35	−1	−36
5	13	40	−1	−41
6	15	44	−1	−45

The difference in days between the peak, start, end dates and total duration of the season for all populations relative to the virgin population (population 1 in Fig. 3) is displayed. A negative value represents earlier dates and positive values are later dates (from Scott *et al.* 2006).

reduction in the number of survivors compared to a population subject to no fishing mortality. In the next section we consider how changes in spawning time actually impacts early survival.

Evidence for selection on birth date

To demonstrate that spawning time is an important factor influencing fitness it is necessary to show that survivors are not just a random subset of offspring from a spawning period. It is also important to consider whether there is a direct relation between spawning time and reproductive success or one linked to a mutual relationship such as the individual quality of spawners at any given time (i.e. the quality hypothesis; Verhulst *et al.* 1995). Individual quality could be determined by a variety of factors such as age and condition. Given the known demographic effects on fish spawning times this alternative hypothesis clearly has relevance. Experimental manipulation provides the most powerful means of detecting selection on the timing of reproduction but only small fish species with a limited home range are generally amenable to such an approach. Experiments have indicated that offspring from early spawning tend to accrue a size advantage that can lead to earlier maturation and spawning than those spawned later (Saito and Nakano 1999; Reznick *et al.* 2006; Divino and Tonn 2007). For example, Reznick *et al.* (2006) examined the probability of survival to maturity and fecundity of offspring as a function birth date in the mosquito fish (*Gambusia affinis*, Poeciliidae) by rearing cohorts of young born early-, mid- or late in the reproductive season in replicate field enclosures. Early-born young had a significantly higher probability of survival to maturity and also attained maturity early enough to reproduce in their first year while late-born young had to overwinter before reproduction. As a result females most often gained fitness by not producing one last litter and instead storing fat and reproducing the following spring. If, however, the overwinter survival of offspring was not influenced by their size at the end of the season, as could happen under mild winter conditions, then a female's fitness could be enhanced by producing one more litter late in the season. This variation in selection on birth date implies that varying environmental conditions can favour differences in breeding time and duration.

Einum and Fleming (2000) were able to distinguish between parental and temporal spawning effects in Atlantic salmon by fertilizing eggs from the same mating/cross on different dates and then examining the growth and survivorship of offspring for the first month after emergence. They also undertook mark and recapture experiments on emerging juveniles in the wild over several months. Both approaches indicated that the majority of mortality occurred soon after emergence and resulted in a significant phenotypic shift toward an earlier date and increased length at emergence. Standardized selection gradients indicated that selection was more intense on date than on body size at emergence. Egg size also appeared to have fitness consequences independent of the effects of emergence time that directly affected body size at emergence and, in turn, survival and size at later life stages. Therefore, this study suggests that reproductive timing alone can be important to offspring survival but that maternal traits affecting offspring quality also influence fitness.

Although large and wide ranging fish species are not amenable to experimentation the presence of daily increments in the otoliths of most fish species has enabled selection on birth date to be examined in the field. By comparing birth date composition of survivors between two or more periods in the life history it is possible to identify the direction and magnitude of selection (Miller 1997). This approach to survivorship analysis has demonstrated there generally is temporal variability in mortality of progeny originating over a spawning period, with examples of selection for both early and late birth date (Table 3). Schultz (1993) suggested that the different forms of birth date selection reported for temperate species were related to the stage of development considered. Most studies of juveniles have found selection for early- or mid-hatched offspring (Methot 1983; Cargnelli and Gross 1996; Narimatsu and Munehara 1999; Wright and Gibb 2005) whilst those sampled between the hatching and larval metamorphosis period have found selection for late-hatched individuals (Crecco and Savoy 1985; Rice *et al.* 1987; Moksness and Fossum 1991; Wright and Bailey 1996; Hare and Cowen 1997; Pine and Allen 2001). Whilst early spawned/hatched individuals should have a substantial size advantage compared to those that spawn/hatch later (Folkvord *et al.* 1994; Phillips *et al.* 1995; Cargnelli and Gross 1996; Yamamoto *et al.* 1997), early spawned cohorts will probably experience higher mortality rates than late spawned fish due to unfavourable temperatures (Crecco and Savoy,

Table 3 Summary of otolith studies demonstrating evidence of selection on birth date.

Species	*n* cohorts	Spawn time	LH stage	Selection	References
Micrometrus minimus	1	Late spring temperate	1 and 2 spawning	Negative directional – stabilizing	Schultz (1993)
Coregonus hoyi	1	Winter temperate	Larvae	Positive directional	Rice *et al.* (1987)
Lepomis macrochirus	1	Late spring temperate	Juvenile	Negative directional	Cargnelli and Gross (1996)
Lepomis macrochirus	1	Late spring temperate	Juvenile	Positive directional	Garvey *et al.* (2002)
Lepomis macrochirus	3	Late spring temperate	Juvenile	Positive directional	Santucci and Wahl (2003)
Lepomis macrochirus	1	Late spring temperate	Juvenile	Stabilizing	Cargnelli and Neff (2006)
Micropterus salmoides Centrarchidae	2	Late spring temperate	Juvenile	Negative directional	Pine *et al.* (2000)
Pomoxis nigromaculatus Centrarchidae	1	Late spring temperate	Juvenile	Positive directional	Pine and Allen (2001)
Melanogrammus aeglefinus (Georges Bank)	5	Spring temperate	Juvenile	Negative directional	Lapolla and Buckley (2005)
Melanogrammus aeglefinus (North Sea)	3	Early spring temperate	Demersal juvenile	Negative/stabilizing	Wright and Gibb (2005)
Pleuronectes platessa	3	Winter–spring	Post-settled juvenile	Stabilizing/negative in last quarter of spawning	Fox *et al.* (2007)
Lutjanus griseus Lutjanidae	2	Semi-tropical	Juvenile	Positive/stabilizing	Allman and Grimes (2002)
Mugil curema Mugilidae	2	All year	Juvenile	Disruptional	Marin *et al.* (2003)

Information is given for species, number of cohorts/year-classes examined, final life history stage sampled, form of birth date selection and reference. Stabilizing and directional refers to selection against or for the extremes of the birth date distribution respectively. Disruptional selection refers to the selection for individuals at both extremes of the birth date distribution.

1985; Rice *et al.* 1987; Rutherford and Houde 1995) and mismatch with plankton production (Cushing 1990) or predation pressure (Santucci and Wahl 2003). Consequently, if attaining a specific size is important because of over winter survival or earlier age at maturation there must be a trade-off between size, growth rate, mortality and hatch date.

Although most studies of birth date have been limited to larval stages there are some studies that have considered selection on birth date from spawning to the juvenile stage and in some cases beyond (Table 3). Schultz (1993) examined survival in 1 year-class of female dwarf perch (*Micrometrus minimus*, Embiotocidae) from birth through to reproductive success in their second breeding season. He found that early born females were more successful in their first breeding season than late born females (negative directional selection on birth date) but were less likely to survive the period between birth and first reproduction, relative to females born in the middle of the season. As a consequence of birth date and survival in the first year, overall selection on female birth date was stabilizing. Whilst this study appears unique in considering lifetime fitness it is also important to know whether the form of selection varies from year

to year as this will shape parental breeding schedules. Two studies each following a single year-class of bluegill sunfish (*Lepomis macrochirus*, Centrarchidae) from the same lake found different survival patterns, with either the early (Cargnelli and Gross 1996), mid- (Cargnelli and Neff 2006) or late (Garvey *et al.* 2002) hatched progeny having the lowest mortality. Another study of this species in a different lake over 3 years found consistently higher relative survival in late hatched offspring up until autumn of their first year (Santucci and Wahl 2003). Other studies have found evidence for positive (Rice *et al.* 1987; Allman and Grimes 2002), stabilizing (Allman and Grimes 2002; Fox *et al.* 2007) and even disruptive (Marin *et al.* 2003) selection for birth date (see Table 3). Wright and Gibb (2005) examined selection for birth date in haddock from the North Sea, in years of high, low and average year-class size. They found persistent selection against the late spawning period which is the period when most 2-year-old spawn and suggests that these first-time spawners make little contribution to recruitment (Fig. 5). This difference in survival rates between age 2 and 3+ years haddock spawning times may be consistent with the quality hypothesis as the younger females
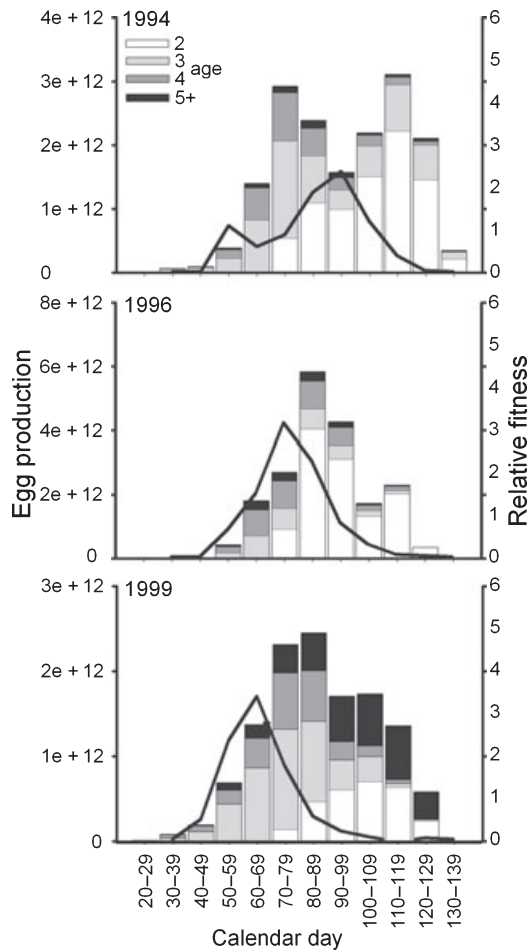
Figure 5 Temporal changes in age-stratified egg production of North Sea haddock and relative fitness (bold curve) based on the difference in proportions of eggs produced (by ages 2 to 5+ years haddock) and demersal juveniles for a given date from the years 1994, 1996 and 1999. Redrawn from Wright and Gibb (2005).

produce smaller eggs (Hislop and Bell, 1987). However, the timing of spawning would also appear to have been important as the relative contribution of early and mid-spawned progeny differed among years. Birth date selection for early and mid-season hatching has also been reported in another study of haddock comparing relative egg densities around Georges Bank and Gulf of Maine with birth date distributions of settled juveniles (Lapolla and Buckley 2005). Factors favouring early spawning in a spring-spawning species like haddock could include seasonal predation pressure (Lapolla and Buckley 2005) or the match with the timing of the spring bloom. With respect to the latter, Platt *et al.*

(2003) observed that high recruitment in haddock from the eastern Nova Scotian shelf coincided with relatively early spring blooms.

The study by Platt and colleagues showing a fivefold increase in survival rate in haddock coinciding with just a 2- to 3-week difference in spring bloom is typical of many such studies that have correlated intra-annual variability in environmental conditions to recruitment variation. However, the contribution of temporal events to offspring survival and recruitment is difficult to assess except by considering the relative magnitude of intra- and inter-annual survival rates. If large year-classes were characterized by exceptionally high survival for just a short period within the spawning season then this would suggest that factors linked to time could be having a first order effect on recruitment. In contrast, if large year-classes were found to be associated with high survivorship over the entire spawning period then within-season timing would probably be a second order effect. Few studies provide the necessary comparison between birth date selection and year-class strength to consider the importance of timing on recruitment. Santucci and Wahl (2003) found that variation in larval mortality between the first and second half of the breeding season of bluegill sunfish was greater than between years, although mortality beyond this life-stage determined year-class strength. Wright and Gibb (2005) found that a 6-fold difference in year-class strength in North Sea haddock corresponded to differences in survival during only the first half of the spawning season. In contrast, for a different haddock stock, Lapolla and Buckley (2005) indicated that the largest year-class was associated with generally higher survival throughout the spawning period. From these few studies we can infer that birth date may be a primary factor influencing recruitment variation in some circumstances. Given that demographic changes have the potential to shift spawning by a matter of weeks any impact on the peak and duration of spawning could be expected to have a significant impact on recruitment.

Theory suggests that spawning intermittently just prior to and across the larval growing season can improve fitness in unpredictable environments by increasing the likelihood that at least some offspring survive to maturity. Studies of birth date selection indicate that most fish do have to cope with a temporally unpredictable environment and hence the generally protracted nature of spawning

would appear to be adaptive. In addition, parents might not be able to spawn at the optimal time for their offspring if they are constrained by energetic pressures. The latter has been termed an 'internal life history mismatch' (Varpe *et al.* 2007) and this could be particularly relevant to the often low conditioned first-time spawners that tend to spawn later and for a shorter period than older fish. Thus, the extended reproductive lifespan brought about by spawning at different times and for longer as fish get older would appear to be important to reproductive success. Through the selective removal of large old fish, fishing may be having a significant impact on reproductive timing and as a consequence may have reduced the inherent resiliency of many exploited stocks (Pine *et al.* 2000; Secor 2000; Wright and Gibb 2005).

Relevance to stock reproductive potential

Current management advice regarding the reproductive potential of many stocks is generally based on the relationship between recruitment and spawning stock biomass, a proxy for egg production. The present study suggests that fishery induced changes in spawning times could be an important but presently unquantified source of variation in the stock–recruit relationship. Several other factors related to the reproductive potential of spawning stocks (SRP) have been identified, including relative/weight-specific fecundity, maternal effects of egg size and larval viability (Trippel 1999). Impacts of demographic variation in spawning characteristics on reference points for fishery management have been modelled for Georges Bank cod (Murawski *et al.* 2001). The reference points F_{med} and F_{crash} were used in the model as these represent recruitment-based fishing mortality reference points at intermediate levels of exploitation that permit replacement (F_{med}) and heavy exploitation levels that lead to stock extinction (F_{crash}) (Mace 1994). They found that although point estimates of F_{med} and F_{crash} were similar using spawing stock biomass (SSB) and viable larval production the median F_{crash} estimate for viable larvae was much lower than that from SSB. The results suggested that traditional approaches of *F*-based reference points using SSB systematically overestimate the resiliency of stocks to fishing. The model strategy used relevant variation in hatching success to maternal experience, and variation in larval viability to age/size effects. The effect of varying spawning time relative to other measures of stock reproductive potential on survival, although not used in the model, could be large because the impact of poor synchrony between spawn date and favourable conditions for larvae may overwhelm other components of reproductive value. However, due to the variable nature of selection on birth date it is not possible to give a value to spawn date that is related to offspring survival on an annual basis (e.g. in contrast to egg quality). It is also difficult to disentangle the fitness consequences of spawn date and parent quality as these can co-vary. The act of spawning and its timing also impact the seasonal energetics that is important in re-conditioning of an individual after spawning ends (i.e. prey availability and water temperature).

The combination of low egg viability and unfavourable spawning time of young, first-time spawners may explain the apparent low survival of their progeny (Pine *et al.* 2000; Wright and Gibb 2005) and the inverse relation between spawner age diversity and recruitment reported for some stocks (Lambert 1990; Marteinsdottir and Thorarinsson 1998; O'Brien *et al.* 2003). Indeed, recent modelling and meta-analysis estimates of the difference in reproductive rate between periods of growth and decline indicated that maximum reproductive rate increases with the reproductive lifespan of a population (Venturelli *et al.* 2009). Given the large changes in spawning stock demography over the period that most stock-recruitment time series are based, biomass reference limits and targets may be biased by the relative contribution of first-time spawners.

Whilst high fishing mortality clearly has the potential to affect recruitment via alteration of spawning times it is unlikely that this will be easy to quantify from traditional stock-recruitment relationships. This is because it is difficult to identify the negative effects of reduced or altered spawning time in any one year relative to other factors contributing to early mortality. Rather demographic changes in the peak and duration of spawning are likely to be seen as an increase in the probability of low recruitment for a given spawning biomass. Examining the residuals in the stock–recruitment relationship may give an indication of the potential magnitude of any stock demographic effect. However, any recruitment relation with stock demography will encompass effects related both to spawning time and offspring quality. Therefore, simulation modelling is required to estimate the potential

magnitude of this effect relative to other measures of SRP.

State-based modelling of reproductive parameters similar to that used by Scott *et al.* (2006) coupled to estimates of environmentally induced selection inferred from studies of birth date selection could provide a way forward in evaluating the impact of fishery induced changes in stock demography on reproductive potential. A relatively simple illustration of how such an approach may be developed is given below based on available information for North Sea haddock. A set of five simulated populations with different age structures were produced by calculating the number that would remain with a constant instantaneous total mortality rate (Z). The total instantaneous mortality (Z) was made up of a sum of natural mortality (based on ICES, 2007) and fishing mortality for ages 2–10 years (F = 0.2, 0.4, 0.7, 1.0 and 1.2). The daily egg production for each population was then calculated for a 10-year lifespan based on known age-specific spawning relationships (Wright and Gibb 2005). The contribution of first-time spawning age 2 years group to lifetime egg production ranged from 8% for the population with the lowest fishing mortality to 42% in the population subject to an F of 1.2. Assuming that empirical estimates of selection for birth date reflected environmental conditions rather than parental influences, daily survivorship patterns for a good and poor year-class were used to determine the number of survivors from estimates of daily egg production (see Wright and Gibb 2005). The infrequency of highly favourable conditions for survival in haddock stocks was mimicked by subjecting only 1 year of the 10-year lifespan to a daily survivorship pattern representative of a strong year-class whilst in other years survivorship reflected a poor year-class (see Wright and Gibb 2005). For comparison, a constant survivorship pattern for all years was also considered. By this means the model gave an indication of how the age at which a favourable year was encountered affected the lifetime survival potential of a population. This simulation helps to illustrate the potential benefits to stock rebuilding via protecting a large cohort from high fishing pressure and enabling the positive traits associated with longevity to improve recruitment.

Output from this simple model is presented in Fig. 6. As 2-year-old haddock spawn late, there are always relatively few survivors from this age-class according to the model. With fishing mortality <0.4, very good survival was generated when the
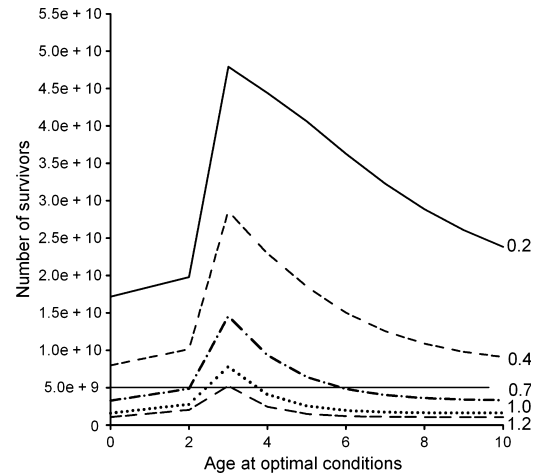
Figure 6 Simulation exploring the benefits of reducing fishing pressure to enable a rarely occurring good environment year to replenish a population. Plotted is the relation between survivorship over a 10-year lifespan of a population and the age at which it encounters favourable conditions for survival. Results are presented for simulated haddock populations subjected to F_{2-10} of; 0.2, 0.4, 0.7, 1.0 and 1.2 where 0.7 and 1.0 are the International Council for the Exploration of the Sea (ICES) precautionary and limit reference points respectively. Survivorship (*S*) was estimated as: $S = S_p/e$, where *e* is the daily egg production and S_p is the daily proportion of a year-class surviving to 6 months old based on estimates from Wright and Gibb (2005) for a good (1999) and poor (1996) year-class. Age-specific estimates of *e* were determined from; $e = nmf$ where *n* is the number of fish surviving from an initial starting number of 5×10^9 of 6-month-old haddock subject to natural mortality (according to ICES, 2007) and fishing mortality, *m* is maturity at age and *f* is the age-specific fecundity derived from Wright and Gibb (2005). The solid horizontal line represents the number of survivors (5×10^9) needed to replace the population.

high survival year was present from any age between 3 and 10 years. In fished populations, the highest lifetime survival occurred when the favourable year coincided with the age when most eggs were produced and early spawning occurred. Importantly however, the rate of decline in lifetime number of survivors from this peak was positively related to fishing mortality. As such, in age-truncated populations the survivorship over the lifetime of the cohort was highly dependent on the single chance coincidence between good environmental conditions and young repeat spawners. Reducing fishing mortality clearly increases the probability that the year-class will produce at least

1 year of high recruitment due to the extended distribution of egg production over the spawning season and lifetime. This provides one possible explanation of why age-truncated populations have been found to be subject to unstable population dynamics (Anderson *et al.* 2008).

The high potential for inappropriate spawning time means that the probability of a lifetime mismatch is generally greater for short-lived individuals and age-truncated populations. Where demographically related changes in spawning time are found to be a likely source of recruitment variability then the scientific advice to fishery managers should encourage the build up of a balanced age structure to increase the occurrence of strong year-classes as opposed to maintaining a young spawning stock with below average recruitment. Thus, the current management focus on spawning biomass reference limits and targets needs to be expanded to promote the mitigation effect of a long reproductive lifespan and protracted spawning. Developing on from the model described in Fig. 6, more realistic simulations of the temporal periodicity of birth date survival patterns over many generations could be used to estimate the level of fishing mortality at which there is a high probability of year-classes producing sufficient recruits for replenishment. Reference targets based on such a probability would enhance the opportunity for any recovering stock to benefit from a strong incoming year-class. This type of approach would also provide a basis for defining appropriate age compositions that increase the long-term likelihood of strong year-classes.

Young spawners, as noted previously, also develop smaller eggs and thus may strengthen the rationale for management to recognize age structure in conservative resource exploitation. Clearly, further modelling is needed to understand variation in reproductive success that integrates the effects of offspring quality with the onset, termination and seasonal breadth of spawning. Varpe *et al.* (2007) provides a possible approach to examine temporal patterns of egg fitness, using a dynamic state variable model, which they applied to a boreal copepod. In their model they included detail of the relevant life history and the species environment such that life history trade-offs emerged from built-in physiology and environmental constraints.

Management under conditions of age truncation, particularly for long-lived teleosts exceeding age longevities of 30 years, needs to be precautionary as poor recruitment may persist for decades as a population may be incapable of rebuilding even when favourable conditions return due to the absence of older fish (Leaman and Beamish 1984; Beamish *et al.* 2006). In Pacific rockfishes (Sebastidae), it has been suggested that perhaps the only way to ensure old-growth age structure and complex spatial structure is through interconnected networks of marine reserves (Berkeley *et al.* 2004b).

This review highlights the importance of managing stocks for age and size composition as well as biomass. Whilst interest in the alteration of timing of spawning with depleted longevity has primarily arisen during the previous two decades, this has been an issue for some time as documented for Atlantic herring in the Bay of Fundy in the late 1880s (Huntsman 1953) and for North Sea haddock in the 1920s (Graham 1956). The downturn of fish stocks in the past decade at a global scale, however signifies a heightened concern over the reproductive capacity of the young, remnant parental fish of these stocks. The studies we have reviewed reveal that this dimension of spawning, tied in with the variability in survival linked to birth date, can at times be an important mechanism influencing cohort strength and thus population intrinsic rate of increase. Consequently, this adult life history trait needs to be considered further in studies of recruitment variation and where significant be a part of the provision of scientific advice to fishery managers.

Acknowledgements

References

Allman, R.J. and Grimes, C.B. (2002) Temporal and spatial dynamics of spawning, settlement, and growth of gray snapper (*Lutjanus griseus*) from the West Florida shelf as determined from otolith microstructures. *Fishery Bulletin* **100**, 391–403.

Anderson, C.N.K., Hsieh, C.-H., Sandin, S.A. *et al.* (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* **452**, 835–839.

Anderson, J. (1988) A review of size dependent survival during pre-recruit stages of fishes in relationship to recruitment. *Journal of Northwest Atlantic Fisheries Science* **8**, 55–66.

Bartsch, J., Brander, K., Heath, M., Munk, P., Richardson, K. and Svensen, E. (1989) Modelling the advection of herring larvae in the North Sea. *Nature* **340**, 632–636.

Beacham, T.D. and Murray, C.B. (1987) Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 244–261.

Beamish, R.J., McFarlane, G.A. and Benson, A. (2006) Longevity overfishing. *Progress in Oceanography* **68**, 289–302.

Begg, G.A. and Marteinsdottir, G. (2003) Spatial partitioning of relative fishing mortality and spawning stock biomass of Icelandic cod. *Fisheries Research* **59**, 343–362.

Berkeley, S.A., Chapman, C. and Sogard, S.M. (2004a) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**, 1258–1264.

Berkeley, S.A., Hixon, M.A., Larson, R.J. and Love, M.S. (2004b) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* **29**, 23–32.

Beyer, J.E. (1989) Recruitment Stability and Survival - Simple Size-Specific Theory with Examples from the Early Life Dynamics of Marine Fish. *Dana - A Journal of Fisheries and Marine Research* **7**, 45–147.

Biro, P.A., Morton, A.E., Post, J.R. and Parkinson, E.A. (2004) Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 1513–1519.

Bollens, S., Frost, B.W., Schwaninger, H.R., Davis, C.S., Way, K.J. and Landsteiner, M.C. (1992) Seasonal plankton cycles in a temperate fjord and comments on the match-mismatch hypothesis. *Journal of Plankton Research* **14**, 1279–1305.

Bromage, N., Porter, M. and Randall, C. (2001) The environmental regulation of maturation in farmed finfish with special reference to the role of photoperiod and melatonin. *Aquaculture* **197**, 63–98.

Brown, E. and Scott, D.B.C. (1994) Life histories of the powan, *Coregonus lavaretus* (L.) (Salmonidae, Coregoninae) of Loch Lomond and Loch Eck. *Hydrobiologia* **290**, 121–133.

Candolin, U. and Voigt, H.R. (2003) Size-dependent selection on arrival times in sticklebacks: why small males arrive first. *Evolution* **57**, 862–871.

Cargnelli, L.M. and Gross, M.R. (1996) The temporal dimension in fish recruitment: Birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 360–367.

Cargnelli, L.M. and Neff, B.D. (2006) Condition-dependent nesting in bluegill sunfish *Lepomis macrochirus*. *Journal of Animal Ecology* **75**, 627–633.

Carolsfeld, J., Scott, A.P. and Sherwood, N.M. (1997) Pheromone-induced spawning of Pacific herring, 2. Plasma steroids distinctive to fish responsive to spawning pheromone. *Hormones and Behavior* **31**, 269–276.

Carscadden, J., Nakashima, B.S. and Frank, K.T. (1997) Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Science* **54**, 781–787.

Cerda, J., Carrillo, M., Zanuy, S. and Ramos, J. (1994) Effect of food ration on estrogen and vitellogenin plasma-levels, fecundity and larval survival in captive sea bass, *Dicentrarchus labrax* – preliminary observations. *Aquatic Living Resources* **7**, 255–266.

Christians, J.K., Evanson, M. and Aiken, J.J. (2001) Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. *Journal of Animal Ecology* **70**, 1080–1087.

Claramunt, G., Serra, R., Castro, L.R. and Cubillos, L. (2007) Is the spawning frequency dependent on female size? Empirical evidence in *Sardinops sagax* and *Engraulis ringens* off northern Chile. *Fisheries Research* **85**, 248–257.

Clemmesen, C., Bühler, V., Montgomery, C. J. *et al.* (2003) Variability in condition and growth of Atlantic cod larvae and juveniles reared in mesocosms: environmental and maternal effects. *Journal of Fish Biology* **62**, 706–723.

Coulson, M.W., Bradbury, I.R. and Bentzen, P. (2006) Temporal genetic differentiation: continuous vs. discontinuous spawning runs in anadromous rainbow smelt *Osmerus mordax* (Mitchill). *Journal of Fish Biology* **69**, 209–216.

Crecco, V. and Savoy, T.F. (1985) Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 1640–1648.

Cury, P. and Roy, C. (1989) Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Science* **46**, 670–680.

Cushing, D.H. (1969) The regularity of the spawning season of some fishes. *Extrait Du Journal du Conseil International pour L'exploration de la Mer* **33**, 81–92.

Cushing, D.H. (1975) *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge.

Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update of the match/

mismatch hypothesis. *Advances in Marine Biology*, **Vol. 26**, pp. 249–293.

Danylchuk, A.J. and Fox, M.G. (1996) Size and age-related variation in the seasonal timing of nesting activity, nest characteristics, and female choice of parental male pumpkinseed sunfish (*Lepomis gibbosus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **74**, 1834–1840.

Danzmann, R.G., Ferguson, M.M. and Heculuck, D.M. (1994) Heterogeneity in the distribution of mitochondrial-DNA haplotypes in female rainbow trout spawning in different seasons. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 284–289.

DeMartini, E.E. and Fountain, R.K. (1981) Ovarian Cycling Frequency and Batch Fecundity in the Queenfish, Seriphus-Politus - Attributes Representative of Serial Spawning fishes. *Fishery Bulletin* **70**, 547–560.

Divino, J.N. and Tonn, W.M. (2007) Effects of reproductive timing and hatch date on fathead minnow recruitment. *Ecology of Freshwater Fish* **16**, 165–176.

Einum, S. and Fleming, I.A. (2000) Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* **54**, 628–639.

Ellertsen, B., Fossum, P., Solemdal, P. and Sundby, S. (1989) Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.). *Rapports et Procesverbaux des Reunions du Conseil international pour l'Exploration de la Mer* **191**, 209–219.

Fishback, A.G., Danzmann, R.G. and Ferguson, M.M. (2000) Microsatellite allelic heterogeneity among hatchery rainbow trout maturing in different seasons. *Journal of Fish Biology* **57**, 1367–1380.

Folkvord, A., Øiestad, V. and Kvenseth, P.G. (1994) Growth patterns of three cohorts of Atlantic cod larvae (*Gadus morhua* L.) studied in a macrocosm. *ICES Journal of Marine Science* **51**, 325–336.

Fordham, S. and Trippel, E.A. (1999) Feeding behaviour of cod (*Gadus morhua*) in relation to spawning. *Journal of Applied Ichthyology* **15**, 1–9.

Fox, C.J., Geffen, A.J., Taylor, N., Davison, P., Rossetti, H. and Nash, R.D.M. (2007) Birth-date selection in early life stages of plaice *Pleuronectes platessa* in the eastern Irish Sea (British Isles). *Marine Ecology-Progress Series* **345**, 255–269.

Garrod, D. and Horwood, J.W. (1984) Reproductive strategies and the response to exploitation. In: *Fish Reproduction: Strategies and Tactics*. Academic Press, London, pp. 367–384.

Garvey, J.E., Herra, T.P. and Leggett, W.C. (2002) Protracted reproduction in sunfish: the temporal dimension in fish recruitment revisited. *Ecological Applications* **12**, 194–205.

Gillespie, J.H. (1977) Natural selection for variances in offspring numbers: a new evolutionary principle. *American Naturalist* **111**, 1010–1014.

Gladstone, W. (2007) Temporal patterns of spawning and hatching in a spawning aggregation of the temperate reef fish *Chromis hypsilepis* (Pomacentridae). *Marine Biology* **151**, 1143–1152.

Graham, M. (1956) *Sea Fisheries*. Edward Arnold Publishers Ltd, London, pp. 487.

Green, W.C.H. and Rothstein, A. (1993) Persistent influences of birth date on dominance, growth and reproductive success in bison. *Journal of Zoology* **230**, 177–186.

Harden Jones, F. (1968) *Fish Migration*. Edward Arnold, London, 325 pp.

Hare, J.A. and Cowen, R.K. (1997) Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). *Ecology* **78**, 2415–2431.

Harris, M., Halley, D.P. and Wanless, S. (1992) The post-fledging survival of young Guillemots *Uriaaalge* in relation to hatching date and growth. *IBIS* **134**, 335–339.

Hartmann, J. (1984) 11-year cycle of spawning time and growth of the whitefish (Coregonus lavaretus) of Lake Constance. *Aquatic Sciences - Research Across Boundaries* **46**, 163–170.

Hatchwell, B. (1991) An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*). *Journal of Animal Ecology* **60**, 721–736.

Hay, D.E. (1985) Reproductive biology of Pacific herring (*Clupea harengus pallasi*). *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 111–126.

Heath, M. (1992) Field investigations of the early life stages of marine fish Vol. 28. *Advances in Marine Biology*. Academic Press, London, pp. 2–174.

Hinrichsen, H.H., Lehmann, A., Mollmann, C. and Schmidt, J.O. (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. *Fisheries Oceanography* **12**, 425–433.

Hislop, J.R.G. and Bell, M.A. (1987) Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. *Journal of Fish Biology* **31**, 1–20.

Hislop, J.R.G., Robb, A. P. and Gauld, J. A. (1978) Observations on effects of feeding level on growth and reproduction in haddock, Melanogrammus aeglefinus (L.) in captivity. *Journal of Fish Biology* **13**, 85–98.

Hjort, J. (1914) Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **20**, 1–228.

Houde, E. (1989) Subtleties and episodes in the early life of fishes. *Journal of Fish Biology* **35**, Special Issue A, 29–38.

Huntsman, A.G. (1953) Movements and decline of large Quoddy herring. *Journal of Fisheries Research Board of Canada* **10**, 1–50.

Hutchings, J.A. and Myers, R.A. (1993) Effect of age on the seasonality of maturation and spawning of Atlantic Cod, *Gadus morhua*, in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Science* **50**, 2468–5474.

Hutchings, J.A. and Myers, R.A. (1994) Timing of cod reproduction: inter-annual variability and the influence of temperature. *Marine Ecology Progress Series* **108**, 21–31.

ICES (2007). *Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak*. ICES CM 2007\ACFM:18, Copenhagen.

Iles, T. (1984) Allocation of resources to gonad and soma in Atlantic herring, *Clupea harengus*. In: *Fish Reproduction: Strategies and Tactics* (eds G. Potts and R.J. Wootton). Academic Press, London, pp. 331–348.

Ims, R. (1990) The ecology and evolution of reproductive synchrony. *Trends in Ecology and Evolution* **5**, 135–140.

James, A., Pitchford, J.W. and Brindley, J. (2003) The relationship between plankton blooms, the hatching of fish larvae, and recruitment. *Ecological Modelling* **160**, 77–90.

Jennings, S.C., Reynolds, J.D. and Mills, S.C. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London: Series B* **265**, 333–339.

Jennings, S.C., Greenstreet, S.P.R. and Reynolds, J.D. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* **68**, 617–627.

Johannes, R. (1978) Reproductive strategies of coastal marine fishes in the tropics. *Environmental Biology of Fishes* **3**, 65–84.

Johnson, D.L. (2000) Preliminary examination of the match-mismatch hypothesis and recruitment variability of yellowtail flounder, *Limanda ferruginea*. *Fishery Bulletin* **98**, 854–863.

Jónsson, E. (1982) A survey of spawning and reproduction of the Icelandic cod. *Rit Fiskideildar* **VI**, 1–45.

Jørgensen, T. (1990) Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **46**, 235–248.

Jørgensen, C., E, K., Dunlop, E.S. *et al.* (2007) Managing evolving fish stocks. *Science* **318**, 1247–1248.

Kjesbu, O.S. (1989) The spawning activity of cod, *Gadus morhua* L. *Journal of Fish Biology* **34**, 195–206.

Kjesbu, O.S. (1994) Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. *Journal of Fish Biology* **45**, 719–735.

Kjesbu, O.S., Klungsøyr, J., Kryvi, H., Witthames, P.R. and Walker, M.G. (1991) Fecundity, atresia, and egg size of captive atlantic cod (*Gadus morhua*) in relation to proximate body compositions. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 2333–2343.

Kjesbu, O.S., Solemdal, P., Bratland, P. and Fonn, M. (1996) Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 610–620.

Kobayashi, M., Sorensen, P.W. and Stacey, N.E. (2002) Hormonal and pheromonal control of spawning behavior in the goldfish. *Fish Physiology and Biochemistry* **26**, 71–84.

Lambert, T.C. (1987) Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. *Marine Ecology-Progress Series* **39**, 209–220.

Lambert, T.C. (1990) The effect of population structure on recruitment in herring. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **47**, 249–255.

Lapolla, A. and Buckley, L.J. (2005) Hatch date distributions of young-of-year haddock *Melanogrammus aeglefinus* in the Gulf of Maine/Georges Bank region: implications for recruitment. *Marine Ecology-Progress Series* **290**, 239–249.

Lasker, R. (1981) The role of a stable ocean in larval fish survival and subsequent recruitment. In: *Marine Fish Larvae: Morphology, Ecology, and Relation to Fisheries*. University of Washington Press, Seattle, WA, pp. 80–88.

Law, R. and Grey, D.R. (1989) Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology* **3**, 343–359.

Lawson, G.L. and Rose, G.A. (2000) Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Canadian Journal of Fisheries and Aquatic Science* **57**, 1011.

Leaman, B.M. and Beamish, R.J. (1984) Ecological and management implications of longevity in some northeast Pacific groundfishes. *International North Pacific Fisheries Commission Bulletin* **42**, 85–97.

Leder, E.H., Danzmann, R.G. and Ferguson, M.M. (2006) The candidate gene, Clock, localizes to a strong spawning time quantitative trait locus region in rainbow trout. *Journal of Heredity* **97**, 74–80.

Leino, R.L. and McCormick, J.H. (1997) Reproductive characteristics of the ruffe, *Gymnocephalus cernuus*, in the St Louis River estuary on western Lake Superior: A histological examination of the ovaries over one annual cycle. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 256–263.

Mace, P.M. (1994) Relationships between common biological reference points used as threshold and targets of fisheries management strategies. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 110–122.

Mananos, E.L., Zanuy, S. and Carrillo, M. (1997) Photoperiodic manipulations of the reproductive cycle of sea bass (*Dicentrarchus labrax*) and their effects on gonadal development, and plasma 17 beta-estradiol and vitellogenin levels. *Fish Physiology and Biochemistry* **16**, 211–222.

Marin, B.J., Quintero, A., Bussiere, D. and Dodson, J.J. (2003) Reproduction and recruitment of white mullet (*Mugil curema*) to a tropical lagoon (Margarita Island, Venezuela) as revealed by otolith microstructure. *Fishery Bulletin* **101**, 809–821.

Marteinsdottir, G. and Begg, G.A. (2002) Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* **235**, 235–256.

Marteinsdottir, G. and Björnsson, H. (1999) Time and duration of spawning of cod in Icelandic waters. *ICES* CM1999/Y: **34**, 1–14.

Marteinsdottir, G. and Thorarinsson, K. (1998) Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Science* **55**, 1372–1377.

Marteinsdottir, G. and Petursdottir, G. (1995) Spatial and temporal variation in reproduction of Icelandic cod at Selvogsbanki and nearby coastal areas. *ICES CM 1995/ G:15*. Copenhagen.

Matsuyama, M., Fukuda, T., Ikeura, S., Nagahama, Y. and Matsuura, S. (1994) Spawning characteristics and steroid-hormone profiles in the wild female Japanese sardine *Sardinops melanostictus*. *Fisheries Science* **60**, 703–706.

Mertz, G. and Myers, R.A. (1994) Match/mismatch predictions of spawning duration versus recruitment variability. *Fisheries Oceanography* **3**, 236–245.

Methot, R.D. (1983) Season variation in survival of larval northern anchovy, *Engraulis mordax*, estimated from the age distribution of juveniles. *US Fisheries Bulletin* **81**, 741–750.

Millan, M. (1999) Reproductive characteristics and condition status of anchovy *Engraulis encrasicolus* L. from the Bay of Cadiz (SW Spain). *Fisheries Research* **41**, 73–86.

Miller, T.J. (1997) The use of field studies to investigate selective processes in fish early life history. In: *Early Life History and Recruitment in Fish Populations* (eds R.C. Chambers and E.A. Trippel). Chapman & Hall, London, pp. 197–224.

Miranda, L.E. and Hubbard, W.D. (1994) Length-Dependent Winter Survival and Lipid Composition of Age-0 Largemouth Bass in Bay Springs Reservoir, Mississippi. *Transactions of the American Fisheries Society* **123**, 80–87.

Moksness, E. and Fossum, P. (1991) Distinguishing spring and autumn spawned herring larvae (*Clupea harengus* L.) by otolith microstructure. *ICES Journal of Marine Science* **48**, 61–66.

Moller, A.P., Flensted-Jensen, E. and Mardal, W. (2006) Rapidly advancing laying date in a seabird and the changing advantage of early reproduction. *Journal of Animal Ecology* **75**, 657–665.

Morgan, M.J. (2003) Variation with age in the timing and duration of spawning in American plaice. *Journal of Fish Biology* **62**, 464–473.

Morgan, M.J., Burnett, J., Tomkiewicz, J. and Saborido-Rey, F. (2003) The availability of data for estimating reproductive potential for selected stocks in the North Atlantic. *NAFO Scientific Council Studies* **37**, 1–3.

Munk, P., Larsson, P.O., Danielsen, D. and Moksness, E. (1995) Larval and small juvenile cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. *Marine Ecology-Progress Series* **125**, 21–30.

Murawski, S.A., Rago, P.J. and Trippel, E.A. (2001) Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES Journal of Marine Science* **58**, 1002–1014.

Naef-Daenzer, B., Widmer, F. and Nuber, M. (2001) Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70**, 730–738.

Narimatsu, Y. and Munehara, H. (1999) Spawn date dependent survival and growth in the early life stages of *Hypoptychus dybowskii* (Gasterosteiformes). *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1849–1855.

Norberg, B., Brown, C.L., Halldorsson, O., Stenslandd, K. and Bjornsson, B.T. (2004) Photoperiod regulates the timing of sexual maturation, spawning, sex steroid and thyroid hormone profiles in the Atlantic cod (Gadus morhua). *Aquaculture* **229**, 451–467.

Nussey, D.H., Clutton-Brock, T.H., Elston, D.A., Albon, S.D. and Kruuk, L.E.B. (2005) Phenotypic plasticity in a maternal trait in red deer. *Journal of Animal Ecology* **74**, 387–396.

O'Brien, L., Rago, P.J., Lough, R.G. and Berrien, P. (2003) Incorporating early-life history parameters in the estimation of the stock-recruit relationship of Georges Bank Atlantic cod (*Gadus morhua*). *Journal of Northwest Atlantic Fishery Science* **33**, 191–205.

Otterå, H., Agnalt, A.L. and Jørstad, K.E. (2006) Differences in spawning time of captive Atlantic cod from four regions of Norway, kept under identical conditions. *ICES Journal of Marine Science* **63**, 216–223.

Ouellet, P., Lambert, Y. and Bérubé, I. (2001) Cod egg characteristics and viability in relation to low temperature and maternal nutritional condition. *ICES Journal of Marine Science* **58**, 672–686.

Park, Y.J., Takemura, A. and Lee, Y.D. (2006) Lunar-synchronized reproductive activity in the pencil-streaked rabbitfish *Siganus doliatus* in the Chuuk Lagoon, Micronesia. *Ichthyological Research* **53**, 179–181.

Parrish, R.H., Mallicoate, D.L. and Klingbeil, R.A. (1986) Age dependent fecundity, number of spawning per year, sex ratio and maturation stages in northern anchovy, *Engraulis mordax*. *Fishery Bulletin* **84**, 503–516.

Patino, R. (1997) Manipulations of the reproductive system of fishes by means of exogenous chemicals. *Progressive Fish-Culturist* **59**, 118–128.

Peterman, R.M. and Bradford, M.J. (1987) Wind speed index and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). *Science* **235**, 354–356.

Peterson, I. and Wroblewski, J.S. (1984) Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1117–1120.

Phillips, J.M., Jackson, J.R. and Noble, R.L. (1995) Hatching date influence on age-specific diet and growth of age-0 largemouth bass. *Transactions of the American Fisheries Society* **124**, 370–379.

Pine, W.E. and Allen, M.S. (2001) Differential growth and survival of weekly age-0 black crappie cohorts in a Florida lake. *Transactions of the American Fisheries Society* **130**, 80–91.

Pine, W.E., Ludsin, S.A. and DeVries, D.R. (2000) First-summer survival of largemouth bass cohorts: is early spawning really best? *Transactions of the American Fisheries Society* **129**, 504–513.

Platt, T., Fuentes-Yaco, C. and Frank, K.T. (2003) Spring algal bloom and larval fish survival. *Nature* **423**, 398–399.

Pope, J., Shepherd, J.G. and Webb, J. (1994) Successful surf-riding on size spectra - the secret of survival in the sea. *Philosophical transactions of the Royal Society of London Series B-Biological Sciences* **343**, 41–49.

Price, T., Kirkpatrick, M. and Arnold, S.J. (1988) Directional Selection and the Evolution of Breeding Date in Birds. *Science* **240**, 798–799.

Quinn, T.P., Unwin, M.J. and Kinnison, M.T. (2000) Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution* **54**, 1372–1385.

Reznick, D., Schultz, E., Morey, S. and Roff, D. (2006) On the virtue of being the first born: the influence of date of birth on fitness in the mosquitofish. *Gambusia affinis* Oikos **114**, 135–147.

Rice, J.A., Crowder, L.B. and Holey, M.E. (1987) Exploration of mechanisms regulating larval survival in Lake Michigan bloater: A recruitment analysis based on characteristics of individual larvae. *American Fisheries Society* **116**, 703–718.

Rideout, R.M., Trippel, E.A. and Litvak, M.K. (2005) Effects of egg size, food supply and spawning time on early life history success of haddock *Melanogrammus aeglefinus*. *Marine Ecology Progress Series* **285**, 169–180.

Ridgway, M., Shuter, B.J. and Post, E.E. (1991) The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass *Micropterus dolomieui* Lacépède (Pices, Centrachidae). *Journal of Animal Ecology* **60**, 665–681.

Rogers, M.W., Allen, M.S. and Porak, W.F. (2006) Separating genetic and environmental influences on temporal spawning distributions of largemouth bass (*Micropterus salmoides*). *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2391–2399.

Rowe, S. and Hutchings, J.A. (2003) Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution* **18**, 567–572.

Rutberg, A. (1987) Adaptive Hypotheses of Birth Synchrony in Ruminants: An Interspecific Test. *American Naturalist* **130**, 692–710.

Rutherford, E.S. and Houde, E.D. (1995) The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. *Fishery Bulletin* **93**, 315–332.

Saito, T. and Nakano, S. (1999) Reproductive-timing-dependent alternation of offspring life histories in female threespine sticklebacks. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **77**, 1314–1321.

Sakamoto, T., Danzmann, R.G., Okamoto, N., Ferguson, M.M. and Ihssen, P.E. (1999) Linkage analysis of quantitative trait loci associated with spawning time in rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* **173**, 33–43.

Sancho, G., Solow, A.R. and Lobel, P.S. (2000) Environmental influences on the diel timing of spawning in coral reef fishes. *Marine Ecology-Progress Series* **206**, 193–212.

Santucci, V.J. and Wahl, D.H. (2003) The effects of growth, predation, and first-winter mortality on recruitment of bluegill cohorts. *Transactions of the American Fisheries Society* **132**, 346–360.

Schultz, E. (1993) The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). *Evolution* **47**, 520–539.

Scott, B.E., Marteinsdottir, G., Begg, G.A., Wright, P.J. and Kjesbu, O.S. (2006) Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling* **191**, 383–415.

Scott, D. (1979) Environmental timing and the control of reproduction in teleost fish. In: *Fish Phenology: anabolic adaptiveness in teleosts*. Vol. 44 (ed P. Miller). Academic Press, Symposium of the zoological Society of London, pp. 105–132.

Secor, D.H. (2000) Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake Bay striped bass. *ICES Journal of Marine Science* **57**, 403–411.

Shimizu, A., Aida, K. and Hanyu, I. (1994) Effects of photoperiod and temperature on gonadal activity and plasma steroid levels in an autumn-spawning bitterling, Acheilognathus rhombea, during different phases of its annual reproductive cycle. *General and Comparative Endocrinology* **93**, 137–150.

Shuter, B.J., MacLean, J.A., Fry, F.E.J. and Regier, H.A. (1980) Stochastic Simulation of Temperature Effects on First-Year Survival of Smallmouth Bass. *Transactions of the American Fisheries Society* **109**, 1–34.

Siitonen, L. and Gall, G.A.E. (1989) Response to selection for early spawn date in rainbow trout, *Salmo gairdneri*. *Aquaculture* **78**, 153–161.

Sims, D.W., Wearmouth, V.J., Genner, M.J., Southward, A.J. and Hawkins, S.J. (2004) Low-temperature driven early spawning migration of a temperate marine fish. *Journal of Animal Ecology* **73**, 333–341.

Sinclair, M. and Tremblay, M.J. (1984) Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. *Canadian Journal of Fisheries and Aquatic Science* **41**, 1055–1065.

Slotte, A., Johannessen, A. and Kjesbu, O.S. (2000) Effects of fish size on spawning time in Norwegian spring-spawning herring. *Journal of Fish Biology* **56**, 295–310.

Sogard, S.M. (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**, 1129–1157.

Srinivasan, M. and Jones, G.P. (2006) Extended breeding and recruitment periods of fishes on a low latitude coral reef. *Coral Reefs* **25**, 673–682.

Stacey, N. (1984) Control of the timing of ovulation by exogenous and endogenous factors. In: *Fish Reproduction: Strategies and Tactics* (eds G.W. Potts and R.J. Wootton), Academic Press, London, pp. 207–222.

Stearns, S. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, pp. 249.

Stewart, D., Smith, G.W. and Youngson, A.F. (2002) Tributary-specific variation in timing of return of adult Atlantic salmon (*Salmo salar*) to fresh water has a genetic component. *Canadian Journal of Fisheries and Aquatic Science* **59**, 276–281.

Su, G.S., Liljedahl, L.E. and Gall, G.A.E. (1999) Estimates of phenotypic and genetic parameters for within-season date and age at spawning of female rainbow trout. *Aquaculture* **171**, 209–220.

Sund, O. (1938) 'Biological and oceanographic investigations. 8. Cod stocks in 1938. Fish movements and replacements' (in Norwegian). *Årsberetning Norges Fiskerier* **1938**, 87–102.

Suquet, M., Omnes, M.H., Norma, Y. and Fauvel, C. (1992) Influence of photoperiod, frequency of stripping and presence of females on sperm output in turbot, *Scophthalmus maximus* (L.). *Aquaculture and Fisheries Management* **23**, 217–225.

Takasuka, A., Aoki, I. and Mitani, I. (2003) Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. *Marine Ecology-Progress Series* **252**, 223–238.

Takemura, A., Rahman, S., Nakamura, S., Park, Y.J. and Takano, K. (2004) Lunar cycles and reproductive activity in reef fishes with particular attention to rabbitfishes. *Fish and Fisheries* **5**, 317–328.

Tomkiewicz, J. and Köster, F.W. (1999) Maturation processes and spawning time of cod in the Bornholm Basin of the Baltic Sea: preliminary results. *ICES* CM 1999/Y: 25, Copenhagen.

Trippel, E.A. (1995) Age at maturity as a stress indicator in fisheries. *BioScience* **45**, 759–771.

Trippel, E.A. (1998) Egg size and viability and seasonal offspring production of young Atlantic cod. *Transactions of the American Fisheries Society* **127**, 339–359.

Trippel, E.A., Kjesbu, O.S. and Solemdal, P. (1997) Effects of adult age and size structure on reproductive output in marine fishes. In: *Early Life History and Recruitment in Fish Populations* (ed R.C. Chambers and E.A. Trippel). Chapman & Hall, London, pp. 31–62.

Trippel, E.A. and Morgan, M.J. (1994) Age-specific paternal influences on reproductive success in Atlantic cod (*Gadus morhua*) of the Grand Banks, Newfoundland. *ICES Marine Science Symposia* **198**, 414–422.

Trippel, E.A. (1999) Estimation of stock reproductive potential: history and challenges for Canadian Atlantic Gadoid stock assessments. *Journal of Northwest Atlantic Fishery Science* **25**, 61–81.

Trippel, E.A. and Neil, S.R.E. (2004) Maternal and seasonal differences in egg sizes and spawning activity of northwest Atlantic haddock (*Melanogrammus aeglefinus*) in relation to body size and condition. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 2097–2110.

Tzioumis, V. and Kingsford, M.J. (1995) Periodicity of spawning of two temperate damselfishes: *Parma microlepis* and *Chromis dispilus*. *Bulletin of Marine Science* **57**, 596–609.

Vandeperre, F. and Methven, D.A. (2007) Do bigger fish arrive and spawn at the spawning grounds before smaller fish: Cod (*Gadus morhua*) predation on beach spawning capelin (*Mallotus villosus*) from coastal Newfoundland. *Estuarine Coastal and Shelf Science* **71**, 391–400.

Varpe, O., Jorgensen, C., Tarling, G.A. and Fiksen, O. (2007) Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos* **116**, 1331–1342.

Venturelli, P., Shuter, B.J. and Murphy, C.A. (2009) Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. *Proceedings of the Royal Society B* **276**, 919–924.

Verboven, N. and Verhulst, S. (1996) Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. *Journal of Animal Ecology* **65**, 264–273.

Verhulst, S., Vanbalen, J.H. and Tinbergen, J.M. (1995) Seasonal decline in reproductive success of the Great Tit - variation in time or quality. *Ecology* **76**, 2392–2403.

Ware, D.M. and Tanasichuk, R.W. (1989) Biological basis of maturation and spawning waves in Pacific herring (*Clupea harengus pallasi*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 1776–1784.

Webster, M. (2003) Temporal density dependence and population regulation in a marine fish. *Ecology* **84**, 623–628.

Wieland, K., Jarre-Teichmann, A. and Horbowa, K. (2000) Changes in the timing of spawning of Baltic Cod:

possible causes and implications for recruitment. *ICES Journal of Marine Science* **57**, 452–464.

Wigley, S.E. (1999) Effects of first-time spawners on stock-recruitment relationships for two groundfish species. *Journal of Northwest Atlantic Fishery Science* **25**, 215–218.

Winkler, D.W. and Allen, P.E. (1996) The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment? *Ecology* **77**, 922–932.

Winters, G.H. and Wheeler, J.P. (1996) Environmental and phenotypic factors affecting the reproductive cycle of Atlantic herring. *ICES Journal of Marine Science* **53**, 73–88.

Woody, C., Olsen, J.B., Reynolds, J. and Bentzen, P. (2000) Temporal variation in phenotypic and genotypic traits in two sockeye salmon populations, Tustumena Lake,

Alaska.. *Transactions of the American Fisheries Society* **129**, 1031–1043.

Wright, P.J. and Bailey, M.C. (1996) Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. *Marine Biology* **126**, 143–152.

Wright, P.J. and Gibb, F.M. (2005) Selection for birth date in North Sea haddock and its relation to maternal age. *Journal of Animal Ecology* **74**, 303–312.

Yamahira, K. (2001) Experimental examination of inter-population variation in reproductive timing of a fish. *Oecologia* **128**, 389–399.

Yamamoto, S., Shinomi, H. and Goto, A. (1997) The effect of birth date on growth of juvenile white-spotted charr *Salvelivtus leucomaenis. Fisheries Science* **63**, 931–933.