# Effects of fishing during the spawning period: implications for management

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# Contents

# Summary

Avoidance of fishing during the spawning season has been proposed as a contribution to achieving sustainable exploitation. Here we review the biological effects of fishing during the spawning period and explore their implication on sustainable management. A distinction will be made between direct mortality and indirect effects. The latter will review how fishery disturbance will affect the physiology and behaviour. Based on the results, a classification scheme is presented of the vulnerability for fisheries during the spawning period. Finally the implications for the population dynamics and fisheries management are discussed.

# 1 Introduction

Worldwide there is great concern about the effect of fisheries on fish populations and the ecosystem (Jackson *et al.*, 2001; Coleman and Williams, 2002; Pauly *et al.*, 2002; Worm *et al.*, 2010). After decades of continuous increase, global landings of capture fisheries are declining (Pauly *et al.*, 2005). Important commercial stocks such as Peruvian anchovy, herring, Canadian cod and European eel have collapsed (Hutchings and Myers, 1994; Dekker, 2003; Toresen and Ostvedt, 2000; Dickey-Collas *et al.*, 2010), and despite harsh management measures, only some of the collapsed stocks have recovered (Hutchings, 2000; 2001). Moreover, fisheries adversely affects the ecosystem through the bycatch of undersized fish or unwanted organisms, by trawling impacts on benthic habitats, and evolutionary changes (Jennings and Kaiser, 1998; Jorgensen *et al.*, 2007). Fisheries is not confined to human consumption or fishmeal purposes, but also targeted at ornamental fish and invertebrates (Gerstner *et al.*, 2006; Calado *et al.*, 2003). Concern has been raised regarding sustainability and environmental impacts triggering the debate as to how best to monitor, manage and regulate the ornamental fishing industry (Shuman *et al.*, 2004; Hardin and LeGore, 2005). Fisheries management faces the difficult task to develop scenarios for the sustainable exploitation of living resources, while protecting biodiversity and maintaining the livelihood of the fishing communities.

Fisheries management generally applies a mix of management measures such as landing or effort quota, gear restrictions, size limits and closed areas or seasons. The establishment of closed areas have gained support to contribute to the protection of biodiversity (Agardy, 1994; Cote *et al.*, 2001), but may also contribute to sustainable exploitation through protection of spawning or nursery areas (Russ and Alcala, 1996; Murawski *et al.*, 2000; Pastoors *et al.*, 2000).

Spawning closures have been introduced in both freshwater and marine fisheries to protect spawning populations (e.g. Celtic Sea herring: Molloy, 1989; haddock: Halliday, 1988; Cod: Anon., 2001) or to reduce the total catch in species that build up dense aggregations during the spawning period, which makes them vulnerable for over-exploitation (e.g. Nassau grouper: Sadovy and Domeier, 2005; squid: Iwata *et al.*, 2010). It is thought that a spawning closure to protect the spawning population will enhance the reproductive output and hence improve the number of recruits in the exploited stock. However, scientific evidence supporting these closures is lacking.

In this paper we analyse how fishing during the spawning period affects the population biology of exploited populations, focusing on the reproductive output of the population and the subsequent recruitment, as well as effects on the population genetics. First, a short description of the spawning strategies is given to provide insight on the diversity of strategies that may determine their vulnerability for fishing. Thereafter the pathways how fishing may affect the reproductive success will be discussed. A distinction will be made between direct mortality and indirect effects. The latter reviews how fishery disturbance will affect the physiology and behaviour. Based on the results, a classification scheme is presented of the vulnerability for fisheries during the spawning period. Finally the implications for the population dynamics and fisheries management will be discussed.

# 2 Reproductive strategies

All organisms have to invest energy to reproduce at some point in their life with the ultimate goal of maximising their reproductive success. Organisms achieve this by practicing a wide range of reproductive strategies. A trade-off between different traits enables them to survive optimally in a specific environment. Species can be assigned to different strategies on the basis of these traits (Table 1).

**Table 1:** Summary of different reproductive strategies (Wootton, 1990; Helfman *et al.*, 1997; Murua and Saborido-Rey, 2003)

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1. Mode of reproduction
    a. Oviparous – Embryo develops outside the ovary
    b. Viviparous – Embryo develops inside the ovary

2. Number of breeding opportunities
    a. Semelparous – Species spawn once during their lifetime
    b. Iteroparous – Species spawn more than once during their lifetime
        I. Total spawner – Release offspring in a single event
        II. Batch spawner – Release offspring in multiple events

3. Gender system:
    a. Gonochoristic
    b. Hermaphroditic
        I. Simultaneous
        II. Sequential
    c. Parthenogenetic

4. Mating system
    a. Promiscuity – both sexes have multiple partners during spawning
    b. Polygamy
        I. Haremic system
        II. Lek system
    c. Monogamous – single mate during spawning

5. Spawning site
    a. Pelagic zone
    b. Benthic zone
        I. Spawning site preparation
        II. No spawning site preparation

6. Time window spawning
    a. Seasonal pattern
    b. Diel or lunar pattern

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## 2.1 Mode of reproduction

Species can be classified on the basis of their reproductive product into two opposite modes of reproduction: oviparity and viviparity (Wourms *et al.*, 1988; Wootton, 1990; Wourms and Lombardi, 1992). Most fish species are oviparous, or egg-laying organisms (Wootton, 1990). Viviparous organisms retain fertilised eggs inside the maternal reproductive system where they undergo development. At the moment of hatching or some time later the developed young are released by the female (Wourms *et al.*, 1988). The young receive nutrition from the female in various ways, i.e. through lecithotrophy or matrotrophy. The high level of energy invested by the mother enhances the survival of the offspring (Wourms and Lombardi, 1992).

There is sound evidence that older and larger spawners contribute disproportionally to the reproductive output of the population, as they produce relatively more (Kjesbu, 2009; Trippel *et al.*, 2005) as well as higher quality eggs (Marteinsdottir and Thorarinsson, 1998; Trippel and Neil, 2004) and sperm (Trippel and Neilson, 1992; Rakitin *et al.*, 1999; Rideout *et al.*, 2004).

## 2.2 Number of breeding opportunities

Semelparous species devote all their energy to a single spawning event and then die (Cole, 1954). The life span of these species is therefore equal to the age of reproduction. Some well-known fish species, such as Pacific salmon (Healy, 1991; Salo, 1991), eel (Schmidt, 1923) and squid (Boyle and Boletzky, 1996), follow this strategy. However, most fish species are iteroparous, that is, they reproduce repeatedly during their lives (Cole, 1954; Helfman *et al.*, 1997). Total spawners release their offspring in a single episode during each breeding season (Murua and Saborido-Rey, 2003). This means that a whole clutch has to ovulate at the same time (Wallace and Selman, 1981). In contrast, batch spawners release their offspring in batches over a period that can last from days up to months (Murua and Saborido-Rey, 2003).

## 2.3 Gender system

Most fish species are gonochoristic, the male and female reproductive organs are in different individuals and remain fixed throughout their lifetime. A number of fish species (e.g. reef fishes), however, appear to be hermaphroditic (Sadovy de Mitchenson and Liu, 2008; Pavlov *et al.*, 2009). These species are characterized by having both male and female reproductive organs during their life span. Hermaphrodites are divided into two categories: simultaneous (or synchronous) and sequential. Simultaneous hermaphrodites develop ovarian and testicular tissues synchronously, which means they have both male and female reproductive organs. It has been shown that generally in a mating sequence sexual roles are assigned to simultaneous hermaphroditic organisms (Fischer and Petersen, 1987; Petersen, 1995). However, self-fertilization has been observed in mangrove killifish. Yet, this is considered unique. In sequential hermaphrodites, on the other hand, the ovarian and testicular tissues do not develop synchronously (Pavlov *et al.*, 2009). This means that a sex change occurs at a certain point in life (Coleman *et al.*, 1996; Beets and Friedlander, 1998; McBride and Johnson, 2007; Coulson *et al.*, 2009). The majority of sequential hermaphrodite fish species mature as females and later become males (protogyny) (Pavlov *et al.*, 2009). Fish species that mature as males and then change into females are observed less often (protandry) (Ross, 1978; Hattori, 2005). Finally, it is also possible that sex change occurs more than once in a life-time (bi-directional sex change) in order to reach maximal reproductive success (Munday *et al.*, 1998).

A few fish species are parthenogenetic (Schultz, 1971). This is a form of reproduction where sperm is needed to initiate normal development. However, the sperm only activates reproduction and does not contribute genetically to the next generation (Beukeboom and Vrijenhoek, 1998).

## 2.4 Mating system

A mating system describes the number of mates an individual acquires during the breeding season. This differs widely among species as it depends on the distribution patterns of potential mates and the key resources, such as food availability (Emlen and Oring, 1977; Reynolds, 1996). Depending on their mating system, fish species can exhibit specific behavioural interactions. Such interactions can vary from being poorly developed to elaborate and time-consuming resulting into different types of mating systems. In a number of fish species both sexes have multiple partners during the spawning period, i.e. promiscuous spawners. In such a system no obvious mate choice occurs. For example, Baltic herring (*Clupea harengus membras*) and Pacific herring (*Clupea harengus pallasi*) exhibit no particular system in the behaviour between males and females during spawning (Stacey and Hourston, 1982; Aneer *et al.*, 1983). These species form spawning aggregations that are segregated vertically into a pelagic component comprising of immature and spent fish that are contracted to a tight ball (Axelsen *et al.*, 2000). When a female is ready to spawn she swims away from the main school at high speed. She is pursued by several males. Eggs and milt are released at the end of the high speed swimming burst after which the fish immediately rejoin the main school (Geffen 2009; Aneer *et al.*, 1983). A similar spawning behaviour has been documented for mackerel (*Scomber scombrus*) (Walsh and Johnstone, 1992).

Species may also exhibit more structured behavioural routines prior to and during spawning. For example, in several flatfish species, males defend territories, which include several smaller territories that are occupied by females. The dominant male courts and mates successively with females in his territory (Moyer *et al.*, 1985; Konstantinou and Shen, 1995; Manabe *et al.*, 2000; Manabe and Shinomiya, 2001). Females seem to show mate fidelity to their dominant male (Carvalho *et al.*, 2003). It is possible for the males to control their group of females by either defending a resource that attracts the females, defending the females to other males or a combination of these two strategies (Emlen and Oring, 1977). This harem-style mating system is also very common among protogynous hermaphroditic reef fish species that change sex from female to male (e.g. Sakai and Kohda, 1997). In these systems the harem can be dominated by a large male that is able to maintain dominance over his harem with his size. For example, in the protogynous angelfish *Centropyge ferrugatus* it is known that each male is able to monopolize a harem of females (Sakai *et al.*, 1997). The female forages alone within a single home range which overlaps with the territory of the male (Sakai and Kohda, 1995). Each female spawns daily at sunset throughout the breeding season from early May to mid November. The male visits each female within his territory and performs specific courtship behavior after which mating occurs (Sakai and Kohda, 1995). The haremic mating system has also been found in the simultaneously hermaphroditic tropical reef fish *Serranus fasciatus* where the large individuals lose their female function and become male. These permanent males maintain territories where they protect a group of female-acting hermaphrodites with which pair spawning occurs. However, the female-acting hermaphrodites within this haremic group are also able to obtain low levels of male mating success through streaking, i.e. they join a spawning pair and fertilize some eggs with their functional testes (Fischer and Petersen, 1987).

Another mating system that has been observed among a number of fish species is the lek system (e.g. (Wedekind, 1996; Young *et al.*, 2009). Within this system the female specifically visits male aggregations or leks to have her eggs fertilized (Kirkpatrick and Ryan, 1991). The females often show strong preferences towards certain males. Atlantic cod (*Gadus morhua*) display the characteristics for a lekking mating system. This species is known to demonstrate complex behavioural routines during and prior to spawning. Dominance hierarchies are established among male cod through aggressive behaviour prior to spawning and females exercise mate choice by inspecting different males prior to spawning and on the basis of the short grunting sounds the males make during courtship (Brawn, 1961; Hutchings *et al.*, 1999; Nordeide and Kjellsby, 1999; Rowe and Hutchings, 2003). These specific behavioural routines will result in a spawning couple. During spawning the couple is accompanied by satellite males (i.e. “sneakers”) that are also able to fertilise a number of eggs (Bekkevold *et al.*, 2002).

In some fish species (e.g. midas cichlid, filefish, Australian seahorse) the male and female are known to form exclusive pairs and stay together for a long period during which they mate (Barlow, 1992; Nakazono and Kawase, 1993; Jones *et al.*, 1998; Kvarnemo *et al.*, 2000; Takegaki, 2000; Whiteman and Côté, 2004; Egger *et al.*, 2006). Monogamous fish species are mainly found in the tropics and are associated with coral reefs that facilitate territory defense and site attachment (reviewed by: Whiteman and Côté, 2004).

## 2.5 Spawning site

The site where spawning occurs can differ between species (Balon, 1975; Wootton, 1990). Many marine offshore fish species release their eggs in the pelagic zone (Russell, 1976). The pelagic eggs drift with the water current and can therefore be passively dispersed over wide distances (Molen *et al.*, 2007). Most inshore marine fish species and freshwater species produce benthic eggs (Russell, 1976; Gross and Sargent, 1985; Growns, 2004), which generally tend to be larger than planktonic eggs (Russell, 1976). Eggs may be deposited on (Geffen, 2009), attached to (Riehl and Patzner, 1998), or hidden in (Gale and Gale, 1977) substratum. There are also fish species (e.g. Atlantic salmon, *Salmo salar*) that dig their eggs into the substratum (Fleming, 1996; Peterson and Quinn, 1996) or build a nest (e.g. pikeperch, *Sander lucioperca*) where the eggs are laid (Lappalainen *et al.*, 2003). These latter two spawning strategies are associated with parental care. It is an energy-consuming process that may be performed by one parent (uni-parental care) or by both (bi-parental care). It is also plausible that fish species externally carry their eggs instead of depositing them, e.g. by mouth breeding (Oppenheimer, 1970). This occurs only in a small number of fish species (e.g. cichlids, seahorse) and is also thought to be a form of parental care (Blumer, 1982).

When species migrate to their spawning site and/or also when they arrive at their spawning site they can form large aggregations. Such spawning aggregations have been reported in a wide variety of fish species in fresh water and marine ecosystems, such as cyprinids (de Graaf *et al.*, 2005; Tan *et al.*, 2009); reef fish (de Mitcheson *et al.*, 2008; Erisman *et al.*, 2007); marine pelagic fish (Geffen, 2009), marine demersal fish like gadoids and flatfish (Rose, 1993; Morgan and Trippel, 1996; Rijnsdorp, 1989), deep sea species (Pankhurst, 1988; Gordon, 2001) as well as squid (Iwata *et al.*, 2010) and crustaceans (Sarda *et al.*, 2003; Stevens, 2003). Aggregations may occur at scales varying between 0.01 km$^2$ to hundreds of square kilometers (Morato *et al.*, 2006; Kadison *et al.*, 2009; Baumberger *et al.*, 2010; Rose, 1993).

Behavioural differences between male and female, as well as between immature and mature fish, will result in differences in their spatial distribution. In North Sea plaice, adult males dominated the catches on the spawning grounds, whereas the adult females were more abundant along the borders of the spawning grounds, and seem to make successive visits to the spawning grounds to shed a batch of eggs (Rijnsdorp, 1989), a phenomenon also suggested for cod (Robichaud and Rose, 2003). Cod were found to form both male dominated and female dominated shoals during spawning (Morgan and Trippel, 1996; Fudge and Rose, 2009) In pelagic species, fish of particular reproductive status will aggregate in schools (Eltink, 1987; Axelsen *et al.*, 2000). In capelin, mixed-sex shoals were observed close to the coastal spawning grounds, while sex-specific shoals were observed in deeper water off the coast (Davoren *et al.*, 2006).

In several species, males arrive at the spawning grounds before the females, and remain there for a longer time, whereas older and larger females start spawning before young and spawned a larger number of batches over a longer time period than younger / smaller females (Hutchings and Myers, 1993; Pankhurst, 1988; Kjesbu, 1989; Rijnsdorp, 1989).

## 2.6 Timing of reproduction

In order to maximize reproductive success species should reproduce at the right time and right place. Reproduction within a fish stock is therefore often restricted to a certain time window. Spawning may occur during a certain period in the year when the environmental conditions are most favourable for species in maximizing their reproductive success. Some species may synchronise their spawning activity to certain times of the day or to particular phases of the moon (Domeier and Colin, 1997; Matos-Caraballo *et al.*, 2006; Nemeth, 2005; Takemura *et al.*, 2004) making the time window during which reproduction occurs much narrower.

# 3 Effects of fisheries on spawning fish

Fishing will affect fish by removing them from the spawning population, or by disturbing them. In the following sections we will discuss these effects separately.

## 3.1 Fisheries disturbance

Fisheries disturbance can act through three different pathways. The first source of disturbance may be the due to the contact between the fish and the fishing gear. It is well established that a trawl does not catch all the fish that are in its path. Not only will small fish escape through the meshes, but fish may escape below the ground rope, above the headline or escape laterally or may swim way from the approaching gear (Godø and Walsh, 1992; (Albert *et al.*, 2003).

The second source is the disturbance by the noise of the vessel and the fishing gear. It is well established that fish respond to the noise of a vessel by swimming away sideways or to deeper water (Jorgensen *et al.*, 2004; Sara *et al.*, 2007; Vabo *et al.*, 2002; de Robertis *et al.*, 2010).

Thirdly, the noise produced by vessel and fishing gear may interfere with the sounds produced by fish during their courtship. The importance of sounds in the courtship has been reported for a wide variety of fish (Myrberg, 1997; Hawkins and Amorim, 2000; Lindstrom and Lugli, 2000; Finstad and Nordeide, 2004; Rowe and Hutchings, 2006; Ladich, 2007; Ueng *et al.*, 2007). In cod, sound production is related to a special drumming muscle. In mesocosm experiments it was shown that the fertilization success is positively related to the size of the drumming muscle (Rowe and Hutchings, 2008). The possible impact of noise pollution on fish is a research area that has remained virtually untouched.

### 3.1.1 Response to fishery disturbance

Fishing may induce a stress response that may negatively affect the reproductive output. Laboratory studies have shown that stressed cod display less and different courtship behaviour and produce abnormal larvae more frequently (Morgan *et al.*, 1999). Similar to the communication function of reproductive hormones (Stacey, 2003), stress hormones produced by fish caught in the fishing gear could potentially induce a stress response in fish in the immediate surroundings of the fishing operation.

Disturbance may reduce the chances to spawn ovulated eggs. In aquaculture it has been shown that when females are unable to shed ovulated eggs, egg quality deteriorates as fertilization rate declines. This process is called overripening (Mollah and Tan, 1983; McEvoy, 1984; Springate *et al.*, 1984; Hay, 1986). Since the natural spawning is generally confined to a short time window at a specific time during the day (for instance during dawn or dusk), disturbance may lead to a missed opportunity to spawn. It has been suggested that the rate of overripening differs within species (Johnston *et al.*, 2008), hence species in which overripening sets in after a few hours (e.g. turbot (*Scophthalmus maximus*): McEvoy, 1984) will be more sensitive to fishery disturbance than species in which overripening occurs after several days (e.g. Pacific herring (*Clupea harengus pallasi*): Hay, 1986).

Fishing may also disturb the courtship behaviour or agonistic behaviour in spawning groups and through this influence the social hierarchies (Levin and Grimes, 2006; Rowe and Hutchings, 2003). Removal of experienced fish may affect reproduction if members of a spawning aggregation depend on each other for spawning cues (Coleman *et al.*, 1996), or if spawning migrations are disrupted because unexperienced recruits can no longer learn from experienced fish (Corten, 2001; Levin and Grimes, 2006).

Depending on the mating pattern, the behavioural routines can vary from elaborate and time-consuming in monogamous species such as midas cichlids, or lek-systems such as cod, to poorly developed in polygamous group mating species. We expect that species showing rather simple reproductive behaviour will be less sensitive for fisheries disturbance as compared to species in which sophisticated behaviour is required during courtship and spawning.

The impact of fishing disturbance will depend on the distance over which a fish will respond to the source of disturbance, as well as the response time. It is likely that the disturbance distance will differ between fishing gears and between fish species, but only limited information is available. Disturbance will be more prominent in towed gear as compared to static gear because the surface area covered by trawl will exceed those of static gears. Morgan *et al.* (1997) reported that the response time of spawning cod to an otter trawl lasted more than an hour. The response will also depend on whether the fish is feeding, spawning or resting, since these activities will differ in their trade-offs against mortality risk (Roff, 1992). Indeed, herring showed a strong avoidance reactions to survey vessels during wintering and the spawning migration, but not at a spawning site, suggesting that herring gave a high priority to reproductive activities over the avoidance responses to a passing survey vessel (Skaret *et al.*, 2005). An avoidance response during spawning was reported for capelin (Jorgensen *et al.*, 2004).

## 3.2 Direct mortality

The differences in behaviour during spawning may make the spawning population more vulnerable for fishing. This applies in particular to species that aggregate during the spawning period. The spatial aggregation attract fisheries and make populations particularly susceptible for overexploitation during (Gordon, 2001; de Graaf *et al.*, 2006; de Mitchenson *et al.*, 2008; Iwata *et al.*, 2010). The increased susceptibility is further enhanced by the higher vulnerability of spawning fish to the fishing gear (Solmundsson *et al.*, 2003; Levins and Grimes, 2006).

Many reef fish species are hermafrodites and since the larger individuals are more vulnerable to fishing gear, fishing on spawning aggregations may result in sperm limitation in protogynic hermafrodites which will lead to females being unable to spawn (Shapiro *et al.*, 1994; Levin and Grimes, 2006) or a limitation in eggs in protandrous hermafrodites.

Because of differences in behaviour and distribution between males and females, between immatures and matures, and between spawning and non spawning adults, fishing during the spawning period will selectively remove specific components of the population. Fishing may induce an evolutionary change. In order to cope with the increased mortality, fish that mature at a smaller size and/or younger age and invest more into reproduction will be more successful than fish that postpone reproduction (Rijnsdorp, 1993; Heino and Godo, 2002; Law, 2000). These expectations are supported by a number of studies of a variety of exploited fish species (see reviews in (Jorgensen *et al.*, 2007; Kuparinen and Merila, 2007) and experimental studies (Reznick *et al.*, 1993; Conover and Munch, 2002).

Fishing during the spawning period may also affect the effective population size. Though population size of commercial fish populations comprise millions of fish, genetic research has revealed that relatively few fish actually contribute to the next generation. The effective population size may be $10^2$-$10^6$ times smaller than the census size (reviewed in: Hauser and Carvalho, 2008). This can be explained by the fact that most individuals fail to reproduce because they are unable to match their reproductive activity to favourable environmental conditions (Hedgecock, 1994). Effective population size may further be reduced due to variability in fertilization success in exploited fish stocks (Rowe *et al.*, 2004; Hoarau *et al.*, 2005). A decline in the effective population size may lead to a reduction in the genetic diversity. Significant decline in genetic diversity have been found in heavily exploited populations of New Zealand snapper (*Pagrus auratus*) (Hauser *et al.*, 2002), orange roughy (Smith *et al.*, 1991), and cod (Hutchinson *et al.*, 2003), but not in thornback ray *Raja clavata* (Chevolot *et al.*, 2008). Genetic diversity may be affected on the population level, but also on the level of the individual. In plaice, the multilocus diversity has decreased since the 1970s coinciding with an increase in the exploitation rate (Hoarau *et al.*, 2005). Loss of genetic diversity may make populations less flexible in evolving adaptive responses to changing environmental conditions.

Fishing during the spawning period may also affect the offspring (Figure 1). This will not apply to the many commercial species (such as anchovies, scombridae, gadidae and flatfish) that spawn relatively small pelagic eggs of around 1 mm which will pass through the meshes of the commercial fish nets. However, in species that glue their eggs into larger clusters such as Lophius species, attach their eggs on gravel beds or other benthic features such as herring (*Clupea harengus*), or lay larger egg capsules such as certain ray and shark species, fishing during the spawning period may impose mortality of eggs. It may also apply to fish species that are viviparous, or have parental care. A brood will be lost when one of the parents is caught while still taking care of there young.

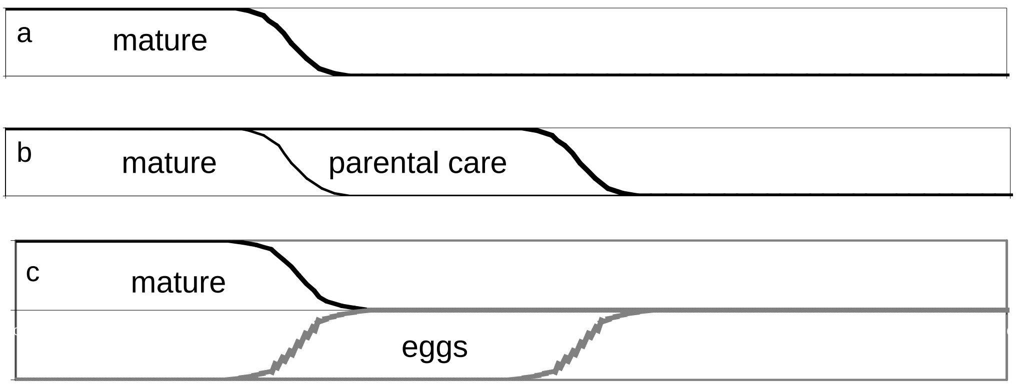

**Figure 1:** Differences in the exposure time to fishing mortality during the spawning period and its effect on the reproductive potential. In contrast to species spawning pelagic eggs, where the effect is restricted to the adult fish during their ripening and spawning stage (a), the duration of the sensitive period is larger in species with parental care (b), while in species that produce aggregations of eggs or egg capsules, also the eggs may suffer from fishing mortality (c).

## 3.3 Classification of vulnerability to spawning fisheries

In the previous paragraphs it has been made clear how fishery removal and fishery disturbance during the spawning season may affect the number of fertilized eggs that are produced. The level of effect on the number of fertilized eggs is in this review referred to as vulnerability. The degree in which fishing during the spawning season will **directly** affect the reproductive success of a population, i.e. the production of fertilized eggs, depends on to what extent species form aggregations during the spawning season; the direct effects will be higher among species that form spawning aggregations in comparison to species that do not. The degree in which species aggregate can therefore serve as a measure to determine how vulnerable species are. However, **indirect** effects also need to be considered when determining species vulnerability. The intensity of the disturbance, measured in the number of eggs fertilized, depends on to what extent a species follows a specific mating behaviour. This can vary from species exhibiting no particular system during spawning to species that exhibit elaborate and time-consuming behavioural routines during spawning. All species lie somewhere between these two extremes. Behavioural routines followed prior to and during reproduction can therefore also be used to determine the degree of vulnerability within a species.

The degree of aggregation in combination with the complexity of mating behaviour can be used in classifying species into different vulnerability groups when it comes to determining the effect of fisheries during the spawning season (Figure 2). For example, species may form spawning aggregations, while they do not exhibit any particular mating system during spawning (e.g. herring). According to the classification scheme (Figure 2) the level of vulnerability of such species will be mediocre, as they will be highly vulnerable to the direct removal of fish while they will be less vulnerable to fishery disturbance. However, other species may demonstrate complex behavioural routines during and prior to spawning and form spawning aggregations (e.g. cod), making them extremely vulnerable to fisheries during the spawning season. Clearly, the presented classification scheme provides insight on why spawning closures can be beneficial for some species, while they may be of less importance for others.

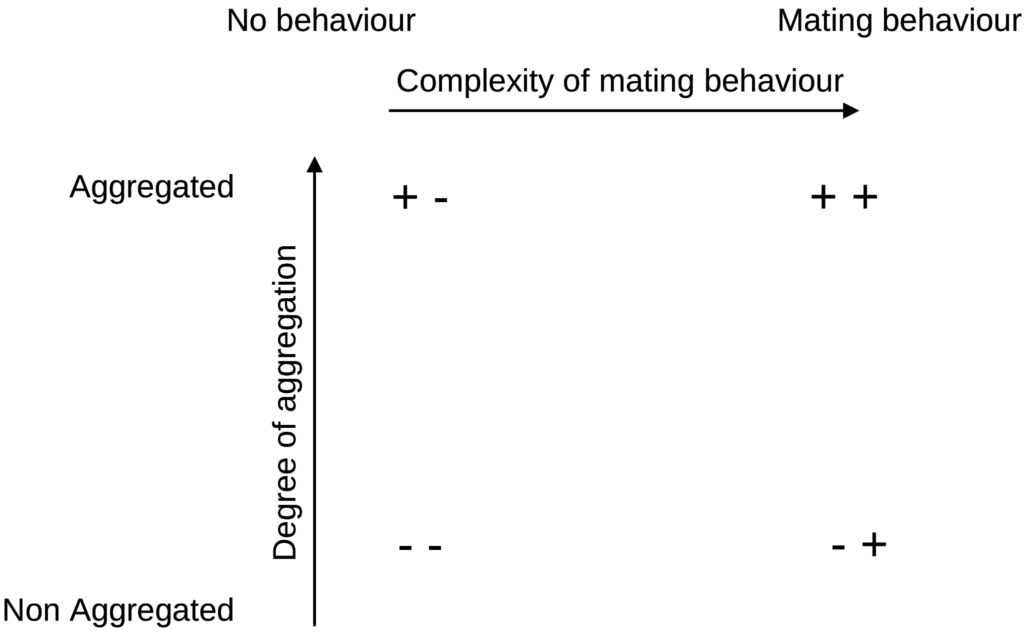

**Figure 2:** Classification scheme presenting the degree of vulnerability with - - indicating low, - + mediocre and + + high vulnerability

# 4 Population biological consequences of fishing during the spawning period

The effects of fishing during the spawning period may affect the production of recruits, but may also affect the genetics of the population.

The resilience of fish populations to exploitation is determined by the relationship between the spawning stock – recruitment (Ricker, 1954; Beverton and Holt, 1957). Fish produce many more eggs than are needed to replace themselves. This surplus in reproductive output is the basis for the fishing yield, as it would otherwise die of natural causes. The study of the stock-recruitment relationship deals with the question about the processes determining the functional relationship as well as the processes determining the interannual variability in recruitment (Fogarty and O'Brien, 2009; Houde, 2009).

Figure 3 shows two typical stock – recruitment relationships which illustrate that the increase in recruitment levels off when spawning stock biomass increase. The Beverton and Holt gradually increases to a maximum recruitment at high spawning stock biomass. This relationship will apply to species in which the habitat determines the carrying capacity of the population. In the Ricker curve, the recruitment decreases at high spawning stock biomass, for instance due to cannibalism. The high variability in recruitment (Houde, 2009) and the possibility of long term variations in recruitment (Koster *et al.*, 2005; Mantzouni and MacKenzie, 2010), hampers the study of the processes that determine the stock – recruitment relationship. It is often impossible to determine statistically which functional relationship gives the best fit to the observations (Iles, 1994; Fogarty and O'Brien, 2009). Nevertheless, an analysis of 364 stock-recruitment relationships revealed that when there is a sufficient range in spawner abundance recruitment is positively affected and recruitment overfishing appears to be a common problem (Myers and Barrowman, 1996). At very low levels population levels, a positive correlation between population density and the per capita population growth rate is expected due to depensatory processes (Allee effect: Stephens *et al.*, 1999), but due to the high variability in recruitment, the statistical evidence is thin (Myers *et al.*, 1995). This Allee effect may be responsible for the lack of recovery of depleted fish population despite the strong compensatory population dynamcis (Frank and Brickman, 2000).

The variability in recruitment will be affected by the demography of the spawning population (Lambert, 1990; Marteinsdottir and Thorarinsson, 1998; Wright and Trippel, 2009). Fishing will lead to a truncation of the age and size composition by removing the larger and more experienced spawners. Since the quality of eggs and sperm is positively related to size, it will also lead to a reduction in quality of the spawning products. In multiple batch spawners, the older fish will spawn over a longer time period and may increase the chance that a batch of eggs will hit the appropriate conditions to survive, which may result in a reduction in reproductive success as well as an increase in the variability in recruitment.

A second mechanism that may affect recruitment is related to the possibilities for size-assortive mating. In non-random mating fish, the changes in sex ratio or size distribution may affect the pair formation of the appropriate sized fish (Rowe and Hutchings, 2003; Bekkevold, 2006). Experiments with cod revealed that females and males achieved their highest reproductive success when breeding with mates that were larger than themselves (Rowe *et al.*, 2007). Observations of spawning of captive Dover sole suggested that spawning pairs were of similar size, despite the clear sexual dimorphism (Baynes *et al.*, 1994). As before, it has been notoriously difficult to provide empirical support for the hypothesis that fishing result in an increase in recruitment variability. In an analysis of stock-recruitment relationships in 39 northeast Atlantic fish stocks, Brunel (2010) found evidence for a significant effect in the expected direction for a few stocks, but significant correlations in the opposite direction were also found. Meta-analyses combining the stock-level tests revealed that none of the effects were significant overall. The lack of support may be due to the large variability in recruitment relative to the variation in spawning stock biomass, but not necessarily refute the hypothesis. Support for the hypothesis stems from the 55 year long ichtyoplankton sampling off California, which revealed that recruitment variability of exploited stocks was significantly higher than of unexploited stocks (Hsieh *et al.*, 2006; Anderson *et al.*, 2008).

The stock-recruitment relationship provides the theoretical background against which we can assess the population dynamic consequences of a fishery during the spawning period. Fishing reduces the reproductive output of the population due to removals of mature fish before they have been able to shed their eggs and to the disturbance of the spawning process. Further, it may increase the mortality of eggs and larvae. Whether the decrease in reproductive output due to spawning fisheries will affect recruitment depends on the degree of density-dependent processes affecting the survival of the fertilised eggs to recruitment to the spawning stock.

In this view, it does not matter whether fish are caught during the spawning period or during any other period of the year (Horwood *et al.*, 1998). Only at levels of spawning stock biomass where recruitment increases with stock size as density-dependent processes are weak, a reduction in the number of fertilised eggs due to fishing during the spawning period will result in a reduction in recruitment (Figure 3).

Above, we assumed that the reproductive output can be estimated as the total egg production by the population. Although this may be reasonable for species where the reproductive output is constrained by the total egg production, it may be inappropriate for species where sperm limitation may occur due the loss of large individuals (primarily males) like in the red hind *Epinephelus guttatus*, a protogynopus hermaphrodite, a commercially important reef fish (Beets and Friedlander, 1999). Also in species with male parental care, the male reproductive investment may constrain the reproductive potential of the population. Species where the reproductive potential is constrained by the total egg production, the biomass of the spawning population may be a poor proxy of the reproductive output (Marshall *et al.*, 1998; Cardinale and Arrhenius, 2000). The egg production per unit of spawning biomass varies due to inter-annual variations in the fecundity – size relationship (Rijnsdorp, 1994; Kjesbu *et al.*, 1998) and variations in the proportion of adult fish that skip spawning (Rideout *et al.*, 2000; Jorgensen *et al.*, 2006).

The stock-recruitment considerations apply to a population where the density-dependent feed back mechanisms operates on the level of the total population. However, in many species, the population is comprised of a number of spawning components (Hauser and Carvalho, 2008). In reef fish, mature fish aggregate in particular spawning sites after a migration over distances between 0.001 to $10^2$ kilometers (Levin and Grimes, 2006). In cod, coastal and offshore populations mix during part of the year but show distinct biological characteristics and spawning ground (Beacham *et al.*, 2002; Pampoulie *et al.*, 2006). The scale of the biological stock structure may not match with the scale of the management unit for which the stock-recruitment relationships are constructed. This has important implications for management (Reiss *et al.*, 2009; Kritzer and Sale, 2004). If a fish stock, defined pragmatically by the management area, comprises of multiple spawning units, the dynamics is not well represented by the stock-recruitment relationship of the total population (Frank and Brickman, 2000). The mismatch between the biological stock units and the management unit may jeopardize sustainable exploitation, because the fishery may successively deplete local spawning components, which may go on unnoticed in the stock assessment carried out on the total aggregated stock (Reiss *et al.*, 2009). Although the stock structure may not necessarily be expressed on the genetic level, genetic differences have been observed within management areas in species such as cod (Ruzzante *et al.*, 1999; Hutchinson *et al.*, 2001; Beacham *et al.*, 2002; Pampoulie *et al.*, 2006). Hence, fishery removals during the spawning period or disturbance of the spawning process, may aggravate the risk of overexploitation of localized stock components.

Removal or disturbance of spawning fish at high quality spawning sites may increase the susceptibility of the population to population genetic effects. Fishing disturbance during spawning may affect the variability in fertilization success, and hence contribute to a reduction in effective population size. With regard to the evolutionary effect, the expected response to fishing during the spawning period will be dependent on the selection patterns during the spawning period as well as during the non-spawning period. If a stock is only fished on the spawning ground, we expect that fishing will select for a delay in maturation, because this will allow the fish to become bigger and hence gain a higher fecundity. This expectation is corroborated by the changes in maturation in Northeast Arctic cod. During the during the 1st half of the 20th century, when the population was mainly exploited during the spawning period, the maturation did not change much. Only after the fishery on the feeding grounds in the Barents Sea developed, a gradual downward shift in the maturation reaction norm was observed, consistent with a fisheries-induced evolutionary change (Jorgensen *et al.*, 2009). In most fisheries, the stock will not be exclusively exploited during the spawning period. In those situations, spawning fisheries may increase the selection for earlier maturing genotypes, since all mature age groups aggregate at the spawning ground. This will result in a sigmoid exploitation pattern with highest mortality on the larger mature stock component, whereas this mortality may be lower during the non-spawning period. Eco-genetic simulations have shown that a dome-shaped exploitation pattern will reduce the evolutionary effects on the maturation and reproductive output (Jorgensen *et al.*, 2009; Mollet, 2010). How the differences in selection between males and females, in particular in sex dimorphic species, affect fisheries-induced evolution remains to be studied.

In conclusion, our analysis shows that fishing during the spawning period may have negative effects on the population biology of the exploited stock. The main impacts are related to the reduction in the production of fertilized eggs, both due to fishing mortality imposed on mature fish that have not yet spawned, and due to disturbance. The negative effect of disturbance is inferred from an analysis of the spawning behaviour and the effects of fishing. This analysis is hampered by the lack of studies on the response of fish to fisheries, as well as by the lack of knowledge on mating systems. Nevertheless, the biological insight allows us to infer that both the degree of aggregation during the spawning period, as well as the complexity of the spawning behaviour will influence the vulnerability of populations for fishing during the spawning period. In addition, fishing during the spawning period may affect the population genetics, in particular the effective population size and the evolutionary changes in reproductive traits, as well as the stock structure within management units. Finally, the observations that only few fish contribute to the next generation, that large spawners disproportionally contribute to the reproductive output, and that these large spawners may be particular vulnerable for fishing mortality during the spawning period, emphasize the need to protect the spawning stock. The impact of fishing during the spawning period will be highest at low levels of spawning stock, and will gradually decrease with an increase in spawning stock size (Figure 3).

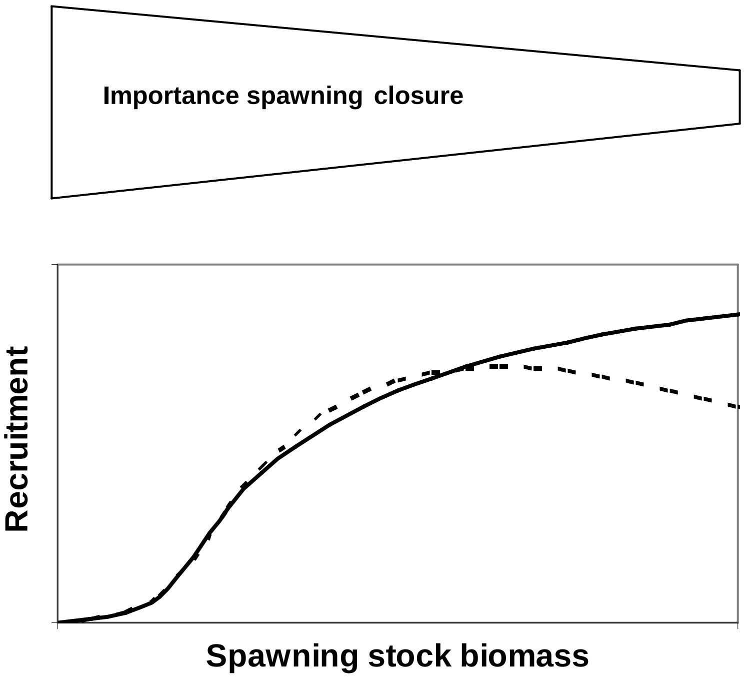

**Figure 3:** Stock – recruitment relationships describing the effect of the reproductive output (spawning stock biomass) on the recruitment. At low levels of spawning stock biomass, recruitment is impaired by depensatory processes. The full line shows the Beverton and Holt relationship. The dotted line shows the Ricker relationship assuming an increase in density-dependent mortality at high population biomass. The wedge shows the decreasing effect of a spawning closure on recruitment (see text)

# 5 Management implications

Our review supports the view that specific management measures are needed to protect the adult population. The urgency of specific measures will differ among stocks (degree of aggregation during spawning and complexity of the spawning behaviour) and will depend on the characteristics of the fisheries. Because of the disturbance effects, trawl fisheries are expected to have larger impacts than gill net fisheries or hook and line fisheries. The main arguments to restrict spawning fisheries are: (i) maximize the production of fertilized eggs by warranting all mature fish, that survived until the start of the spawning period, to shed their eggs undisturbed; (ii) reduce the fishing mortality of the large and older spawners that are most valuable for reproductive output of the population; (iii) avoid negative genetic effects; (iv) minimise the risk of over-exploitation in species which form large spawning aggregations.

The importance of specific protection during the spawning period will depend on the exploitation level of the fish stock. Spawning closures[1] may be particularly relevant in overexploited stocks where there is a risk that recruitment may be impaired by the low level of spawning stock biomass. Any measure to protect the spawning stock by restricting fishing on the spawning population will warrant that all fish that survived till the start of the spawning period will be allowed to spawn without any fishing disturbance. Spawning closures may also be a measure to avoid depensation at low abundance (Rowe *et al.*, 2004).

For stocks, for which there is no indication that recruitment is impaired, spawning closures may still be relevant to protect the larger and older fish or protect spawning habitat structure. In stocks with a complex stock structure within a management area, spawning closures may provide protection to the specific spawning components, which would otherwise be at risk because the indicators of the population dynamics of the aggregated stock may be misleading about the dynamics of the stock components (Frank and Brickman, 2000). Also, a lack of empirical evidence for a positive relationship between recruitment and spawning stock, does not imply that no such relationship exist. Under the precautionary approach, the possibility of a positive relationship should be the basis for management. This refutes the conviction of many fisheries biologists, that it makes no difference for stocks for which there is no indication that recruitment is impaired, when a fish is being caught in the spawning period or in the non-spawning period (Horwood *et al.*, 1998).

Irrespective of the state of the stock, spawning closures may contribute to a dome-shaped exploitation pattern, and hence lead to a reduction in the evolutionary response of fishing, in particular in species where spawning fisheries select for a particular traits (Jorgensen *et al.*, 2009; Mollet *et al.*, 2010).

Special attention should be given to the management of fisheries resources that build up large spawning aggregations that may attract intensive fisheries. A closure of the fishery during (part of) the spawning period may be an effective measure to protect the stocks from overexploitation (de Graaf *et al.*, 2006; de Mitchenson *et al.*, 2008; Iwata *et al.*, 2010). De Graaf *et al.* (2006) showed that of the several species exploited in Lake Tana (Ethiopia), only the species that migrated to the rivers to form large spawning aggregations, showed signs of recruitment overfishing.

The evidence for these conclusions are mainly based on mechanistic understanding of the processes how fishing will impact fish populations. Direct evidence for the impact of fishing during the spawning period is unavailable and will be almost impossible to obtain given the complexity of the problems. For several of the mechanisms discussed, the scientific evidence is thin. In particular, there is a lack of information how fishing may disturb fish during the spawning period and how quick the will recover from the disturbance, and on the mating systems of the important commercial species (Rowe and Hutchings, 2003).

Current fisheries management trades off the sustainable exploitation of stocks against the ecosystem effects of the fisheries (Jennings, 2005; Rice, 2008). A spawning closure should be evaluated against multiple ecologic and economic objectives. Ecological objectives could include the protection and conservation of sensitive and threatened species or habitats, or bycatch reduction. The following example shows how ecosystem objectives may be jeopardized, if fisheries managers restrict themselves to single species considerations. Fisheries ministers of the European Union, imposed a spawning closure to protect spawning North Sea cod in 2001. Analysis of the response of the fisheries to the spawning closure showed that the fleets re-allocated their fishing

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[1] spawning closures indicate any management measures that reduce fishing during the spawning period.

effort to areas which were more vulnerable with regard to trawling impacts on the benthos and on the threatened thornback ray *Raja clavata* and possibly on undersized cod (Rijnsdorp *et al.*, 2001; Dinmore *et al.*, 2003). Finally, the economic consequences need to be considered as well. From an economic point of view, spawning aggregation fisheries may be highly profitable because of the high catch rates obtained. A spawning closure will re-allocate the fishing effort to other periods of the year when it may be more costly to fish the resource. However, spawning fish may have a lower market value because of the considerable weight of the gonads. The fish quality will deteriorate during spawning due to the increase in the proportion of spent fish in the catch. It is well known that fish lose considerable amounts of lipids and protein during spawning. The above does not apply to all fisheries, since there are some fisheries that specifically target roe.

The growing concern about the overexploitation of the worlds fish stocks and the negative impact of fisheries on aquatic ecosystems (Jackson *et al.*, 2001; Coleman and Williams, 2002; Pauly *et al.*, 2002; Worm *et al.*, 2010), has led to the development of various certification scheme for sustainably produced fish products. The Marine Stewardship Council, a joint initiative of WWF and Unilever, operates on a global scale, whereas in several countries, local initiatives are developing. The certification schemes allow consumers to influence the development towards sustainable fisheries. In order to gain public support for sustainable fisheries, spawning closures could provide an attractive measure to incorporate in the certification schemes, since it is easy to explain and is likely to be favourably be received by the consumer. Although spawning closures are not a panacea for solving the crisis in fisheries management, they may provide a useful component in a management system aiming at a balance between the profitable utilization of the productivity of the aquatic system against a minimal cost in terms of ecosystem effects. Since multiple objectives will differ across ecosystem and across fisheries systems, no general recommendation can be given. The relevance should be considered on a case by case basis.

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# 7 Quality Assurance

IMARES utilises an ISO 9001:2000 certified quality management system (certificate number: 08602-2004-AQ-ROT-RvA). This certificate is valid until 15 March 2010. The organisation has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Environmental Division has NEN-AND-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 27 March 2013 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

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# Justification

Rapport C077/10
Project Number: 4301104701

The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department of IMARES.

Approved: Dr. M. de Graaf
Researcher

Signature:

Date: 29 June 2010

Approved: Dr. ir. T.P. Bult
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Date: 29 June 2010

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