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

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

Harriët M. J. van Overzee · Adriaan D. Rijnsdorp

Abstract While fishery closures during the spawning season are commonplace, direct evidence for their benefit is mainly restricted to species forming large spawning aggregations. This paper analyses the conditions under which spawning closures could contribute to sustainable fisheries management by reviewing how fishing during spawning may affect the physiology, behaviour and ecology of individuals and how this may influence the dynamics and the genetics of the population. We distinguish between the effects of fishing activities in relation to mortality, disturbance of spawning activity, and impact on spawning habitat. Spawning closures may be of benefit it they: (1) reduce the fishing mortality of the large and older spawners; (2) avoid negative effects on spawning habitats; (3) reduce the risk of over-exploitation in species which form large spawning aggregations; (4) reduce the evolutionary effects on maturation and reproductive investment; and (5) reduce the risk of over-

exploitation of specific spawning components. The contribution of spawning closures to sustainable fisheries will differ among species and depends on the complexity of the spawning system, the level of aggregation during spawning and the vulnerability of the spawning habitat. The importance of these closures depends on the degree of population depletion but does not cease when populations are 'healthy' (i.e. no sign that recruitment is impaired).

Keywords Spawning closures · Fish · Invertebrates · Reproduction · Spawning aggregations · Fisheries

H. M. J. van Overzee · A. D. Rijnsdorp (✉)
IMARES, Wageningen UR, PO Box 68,
1970 AB Ijmuiden, The Netherlands
e-mail: adriaan.rijnsdorp@wur.nl

A. D. Rijnsdorp
Aquaculture and Fisheries Group, Wageningen
University, PO Box 338, 6700 AH Wageningen,
The Netherlands

Introduction

There is great concern internationally about the effects of fisheries on populations of exploited species and the ecosystem in which they live (Coleman and Williams 2002; Jackson et al. 2001; Pauly et al. 2002). Although the exploitation rate has started to decline in some well-studied ecosystems, the majority of the assessed stocks worldwide still require rebuilding (Worm et al. 2009). In addition, fisheries may have an adverse effect on the ecosystem due to the bycatch of undersized fish or organisms of no commercial value, by changing or adversely impacting habitats through towed bottom gear, and evolutionary changes (Dayton et al. 1995; Jennings and Kaiser 1998; Jørgensen et al. 2007).

Fisheries management faces the difficult task of developing scenarios for sustainable exploitation while, at the same time, protecting biodiversity and the livelihood of the fishing communities. Generally, fisheries management applies a combination of measures such as landing quota, effort quota, gear restrictions, size limits and closed areas or seasons. The establishment of closed areas has gained support as contributors to the protection of biodiversity (Agardy 1994). Closed areas may also promote sustainable exploitation through the protection of spawning or nursery areas (Murawski et al. 2000; Pastoors et al. 2000; Russ and Alcala 1996; Sadovy de Mitcheson and Colin 2012).

Fishery closures during the spawning season are commonplace. Table 1 presents a selection of spawning closures illustrating their wide-spread use in terms of location and species, and the differences in objectives. First, spawning closures have been established successfully to reduce the fishing mortality in fisheries targeting large spawning aggregations that are particularly vulnerable to over-exploitation (Sadovy de Mitcheson et al. 2013) (e.g. reef fish; Table 1, #1–2). A review of spawning closures for spawning aggregating reef fish is presented by Russell et al. (2012). Secondly, spawning closures have been implemented successfully in semelparous or short-living species to allow a sufficient proportion of the spawning stock to be able to shed their eggs before dying (e.g. Southern calamary and Chokka squid; Table 1, #3–4). Thirdly, spawning closures have been put into place to protect spawning populations in order to enhance the reproductive output of spawning fish and hence improve the number of recruits in the exploited stock (e.g. European spiny lobster, Pacific halibut, cod, herring and haddock; Table 1, #5–10). However, none of the latter studies provide compelling evidence to demonstrate that spawning closures are in fact achieving their stated objectives.

Opinions in the scientific community about the usefulness of spawning closures are divided (Horwood et al. 1998; Russell et al. 2012; Sadovy de Mitcheson and Erisman 2012; Sauer 1995). Although the concept of spawning closures may be appealing as it is easy to understand, it is hard to study their effectiveness because it is very difficult, if not impossible, to carry out replicated experiments in real fisheries systems (but see (Hamilton et al. 2011)). Therefore, alternative approaches to study the effect of spawning closures on the population dynamics and sustainable management are used, such as studying the population dynamics before and after the establishment of a spawning closure (Russell et al. 2012), applying a comparative approach across species or populations (Sadovy de Mitcheson and Erisman 2012), or applying a simulation approach (Grüss et al. 2014; Gwinn and Allen 2010).

Here we analyse the conditions under which spawning closures could make a contribution to the sustainable fisheries management of fish and invertebrate species. We apply a mechanistic approach in which the effect of fishing during the spawning period on the physiology, behaviour, population dynamics and genetics is considered and compared to the effect of fishing during the non-spawning period. We distinguish between the primary effect of fishing on the target species (mortality, disturbance of spawning) and the secondary effect of fishing on the spawning habitat. Thereafter, population biological consequences of fishing during the spawning period are discussed. Finally, implications for management are considered by presenting a scoring system to infer the vulnerability of species to fisheries during the spawning period and by discussing the ecosystem based approach.

Fishing effects during the spawning period versus the non-spawning period

To evaluate the effect of fishing during the spawning period, we analyse the effect of (1) fishing mortality, (2) spawning disturbance and (3) impact on spawning habitat separately. As these factors are not restricted to the spawning period, the effects of fishing during the spawning period in comparison to the effect of fishing during the non-spawning period are discussed (Table 2).

Fishing mortality

Spawning is generally limited to specific areas and times (Cushing 1990). Therefore, fishing during the spawning period may target different components of the population than during the non-spawning period. The chance of catching the older (and larger) age classes may be higher during the spawning period as they gather on the spawning grounds, which are often

Table 1 Several examples of spawning closures for different exploited species around the world

S. No.	Species	Area	Closure	Goal	Effectiveness
1	Red hind (*Epinephelus guttatus*)	St. Thomas, U.S Virgin Islands, Red Hind Bank Marine Conservation District	Closure fishery during spawning period (December until end February, implemented in 1990)[1,2]	Protection of spawning aggregations	Increase average length, normalization sex ratio, and increased fish abundance all indicated that curtailment of fishing at the spawning locale has contributed to recovery of red hind around St. Thomas[1]
			Permanent closure (since 1999)[3]	Protection of spawning aggregations and large area of critical fish habitat	Increase in average density, biomass, spawning density[3]
2	Brown-marbled grouper (*Epinephelus fuscoguttatus*), Camouflage grouper (*Epinephelus polyphekadion*)	Coral triangle (Papua New Guinea)	Two spawning aggregation sites were protected by the establishment of community-based MPA in 2004	Sustainable fisheries and protection of biodiversity	Densities of *E. fuscoguttatus* and *E. polyphekadion* increased at both MPAs, but not at the site that remained open to fishing[4]
3	Southern calamary (*Sepioteuthis australis*)	Great Oyster Bay, Tasmania	Two short closures in two-week blocks separated by two weeks October–December in 1999[5]	Protect spawning aggregations	The closure was successful in providing protection to the spawning individual[5]
4	Chokka squid (*Loligo vulgaris reynaudii*)	South African waters	No (jigging) fishery during the peak of the spawning period (November, implemented in 1988; closure period altered through time)[6]	Protection to spawning females at the peak of the breeding cycle	Modelling study revealed that biological gain of closed season is small[7]
5	European spiny lobster (*Palinurus elephas*)	Spanish Mediterranean	Annual 6-month closure fishery during the egg-bearing period (September to February)[8,9]	Protection egg-bearing females	Though the high catch rates of *P. elephas* within the protected area suggest a protection effect, no reliable assessment can be made as no baseline studies were conducted prior to closure[8]
6	Pacific halibut (*Hippoglossus stenolepsis*)	off British Columbia and the US Pacific Northwest	Closure fisheries during spawning in the winter (December–February)[10,11,12]	Protect spawning fish	–
7	Cod (*Gadus morhua*)	Icelandic waters	Closure fisheries for two weeks during Easter[13,14]	Protect spawning of cod	Hardly any evidence is available that demonstrates their effectiveness[13]
8	Atlantic herring (*Clupea harengus*)	Celtic Sea	Closure fisheries on spawning grounds during spawning peak each year on a rotational basis[15,16]	Protect spawning shoals	Effectiveness not evaluated
9	Atlantic cod (*Gadus morhua*)	West of Scotland and North Sea	Closure any fishery appropriate to catch cod from 14 Feb–30 Apr since 2001[17,18]	Protect spawning fish	Hardly any evidence that demonstrates effectiveness

Table 1 continued

S. No.	Species	Area	Closure	Goal	Effectiveness
10	Haddock (*Mlenogrammus aeglefinus*)	Georges Bank; three areas	Closure to most fishing gears from March through April implemented in 1970. Closure period altered through time[19] Closed year-round to any gears capable of retaining groundfish in US portion and Canadian closure from Jan–May since 1994[19]	Protect two spawning components of Georges Bank haddock[20,21] Protect spawning groundfish, particularly haddock[21]	Little effect in arresting the decline of haddock stock in the early 1970 s[20] In ensuing 5 years closed areas contributed significantly to reduced fishing mortality of depleted groundfish stocks[20]

[1] Beets and Friedlander (1998); [2] Sadovy (1994); [3] Nemeth (2005); [4] Moltschaniwskyj et al. (2002); [5] Hamilton et al. (2011); [6] Augustyn and Roel (1998); [7] Roel et al. (1998); [8] Gõni and Latrouite (2005); [9] Gõni et al. (2001); [10] Skud (1985); [11] Loher and Blood (2009); [12] Loher (2011); [13] Jaworski et al. (2006); [14] website by Icelandic Ministry of Fisheries and Aquaculture—www.fisheries.is; [15] Molloy (1989); [16] Molloy (2006); [17] Anon. (2001b); [18] Anon. (2001a); [19] DFO (1998); [20] Murawski et al. (2000); [21] Halliday (1988)

more confined in space than the feeding grounds. For example, in North Sea plaice (*Pleuronectes platessa*) fishing mortality rates on the older adult age groups, in particular for males, is higher in the spawning period than in the non-spawning period (Fig. 1). Consequently, the selection pattern, i.e. the relative mortality imposed by fishing on the different age groups, sexes or maturity stages, may differ between the spawning period and the non-spawning period.

An extreme example are species which form large aggregations during their spawning migration or during spawning itself. Spawning aggregations have been reported in a wide variety of fish and invertebrate species in fresh water and marine ecosystems, such as fresh water cyprinids (de Graaf et al. 2006; Tan et al. 2009), marine reef fish (Erisman et al. 2007; Sadovy de Mitcheson et al. 2008), pelagic fish (Skaret et al. 2003; Zwolinski et al. 2006), demersal fish such as gadoids (Large et al. 2010; Morgan and Trippel 1996; Rose 1993), deep sea species (Gordon 2001; Pankhurst 1988), squid (Iwata et al. 2010; Sauer 1995) and crustaceans (Sarda et al. 2003; Stevens 2003). Aggregations may occur at scales varying between 0.01 to hundreds of square kilometers (Baumberger et al. 2010; Kadison et al. 2009; Morato et al. 2006; Rose 1993).

Differences in behaviour between adult males and females, or immature and mature fish, may further

Table 2 Comparison of the possible effects of fishing during and the non-spawning period

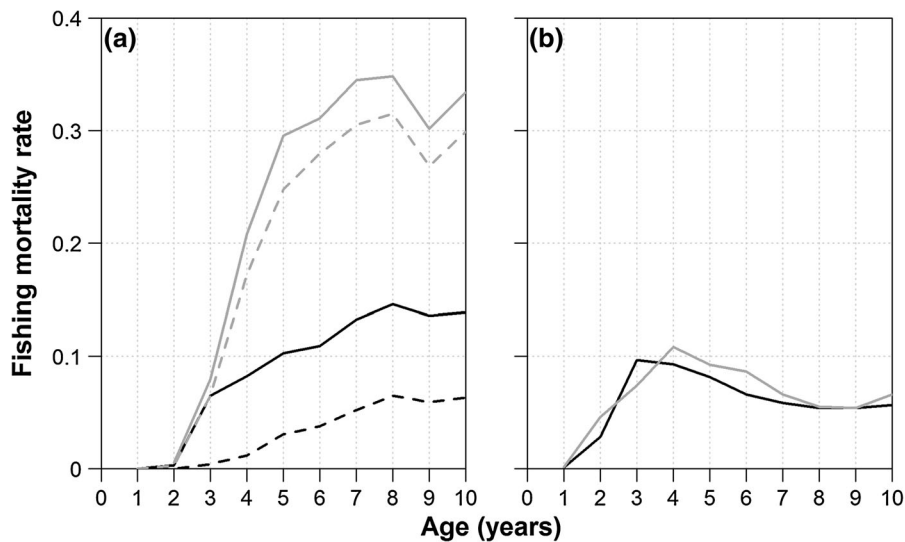|	During spawning period	During non-spawning period
Fishing mortality	Increased mortality older (and larger) mature individuals	Mortality of individuals irrespective of reproductive status
	Direct mortality demersal eggs/egg clusters	
	Increased mortality spawning aggregations	
Spawning disturbance	Affects reproductive physiology	Affects growth physiology
	Affects reproductive behaviour	Affects feeding behaviour
Impact on demersal spawning habitat	Probability spawning habitat destruction high	Probability spawning habitat destruction low–high

Fig. 1 Relationship between the fishing mortality rate (year^{-1}) and age of male (*grey lines*) and female (*black lines*) North Sea plaice (*Pleuronectes platessa*) during the spawning period (1st quarter: **a**) and the non-spawning period (2nd–4th quarter: **b**). The hatched lines in the *left panel* show the fishing mortality of spawning fish (modified from Rijnsdorp 1993b)

affect the catchability of adults during the spawning period. For example, in North Sea plaice, mature males dominate the catches on the spawning grounds, whereas the mature females are 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). In cod (*Gadus morhua*), differences between the sexes have been suggested (Robichaud and Rose 2003). Both male-dominated and female-dominated shoals have been reported during spawning (Fudge and Rose 2009; Morgan and Trippel 1996). In pelagic species the shoals depend on size or life stage and often share a similar reproductive status (Axelsen et al. 2000; Eltink 1987). In capelin (*Mallotus villosus*), 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).

Differences in catchability between adult males and females, or between immature and mature fish, will be influenced by the duration of the spawning period. In several species (e.g. Patagonian hake (*Merluccius hubbsi*), North Sea plaice) males arrive at the spawning grounds before the females, and remain there for a longer time (Pajaro et al. 2005; Rijnsdorp 1989). Furthermore, in several species it has been shown that older and larger females start spawning before the younger and smaller females and therefore arrive at

the spawning ground earlier (Lambert 1987; Ridgway et al. 1991; Rijnsdorp 1989). If fish 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) the time window for spawning will be more narrow. Synchronisation of spawning is of particular importance for a number of invertebrates that do not show courtship behaviour (Bentley et al. 1999; Counihan et al. 2001).

Selective removal may alter the sex ratio or the relative size distributions of the male and female component of the spawning population (Rijnsdorp et al. 2010; Rowe and Hutchings 2003). In non-random mating fish, such changes could affect pair formation by reducing the encounter probability of potential mates of appropriate-size. This could, in turn, reduce the reproductive output of an individual (Bekkevold 2006; Hibberd and Peckl 2007; Rowe and Hutchings 2003). For example, (Møller and Legendre 2001) have suggested that females with limited mate choice may have a lower reproductive success in comparison to females with free choice. Also, in protogynic hermaphroditic fish, show sex reversal, the removal of large dominant males could result in sperm limitation, which may lead to females being unable to spawn (Beets and Friedlander 1998; Levin and Grimes 2006; Shapiro et al. 1994).

The selective removal of older age classes during the spawning period will enhance the truncation of the age and size structure (Lambert 1990; Marteinsdottir and Thorarinsson 1998; Wright and Trippel 2009), diminishing the proportion of big old fecund fish (Boff) that produce more (Green 2008; Kjesbu 2009; Trippel et al. 2005) and larger (Kennedy et al. 2007; Kjesbu 1989; Raventos and Planes 2008) eggs per unit body weight than smaller females. Larger eggs are thought to have a survival advantage at the beginning of their life as they result in larger hatchlings which are physiologically more likely to survive (Kjesbu et al. 1996; Raventos and Macpherson 2005; Raventos and Planes 2008).

The selective removal of older, more experienced fish by a spawner fishery may disrupt spawning migrations when inexperienced recruits can no longer learn from experienced fish (Corten 2001; Levin and Grimes 2006; McQuinn 1997). The persistence of a number of migratory stocks (i.e. sardine *Sardinops sagax*, Northern cod and herring *Clupea harengus*) may rely on behavioural processes such as social interactions, as severe reductions within such stocks have often been associated with structural and social disruption (Petitgas et al. 2010).

Fishing during the spawning period may also directly impose mortality on the offspring. This applies to species that spawn their eggs into larger clusters (e.g. *Lophius* species or several Gastropoda), attach their eggs to gravel beds or other benthic features (e.g. herring, squid), or lay larger benthic egg capsules (e.g. rays and sharks). Furthermore, fishing during the spawning season may affect offspring of species that exhibit external or internal (i.e. viviparity) parental care; a brood will be lost when a parent is caught while still taking care of its young.

Spawning disturbance

Though the main aim of fisheries is to catch fish, not all fish that come into contact with the fishing gear will be caught. Fishing activities may disturb the natural behaviour of these fish during the spawning period and adversely affect the quantity or quality of the offspring produced by these disturbed fish (Sadovy de Mitcheson and Erisman 2012).

The fish that may be disturbed are those that escape through the meshes of the net, underneath the ground rope or above the headline, or swim away from the approaching gear (Albert et al. 2003; Godø and Walsh 1992). Furthermore, fish that are located at some distance from the gear may be influenced by a variety of stimuli generated by the vessel or the gear, or by the fish caught in the net. It is, for example, known that fish respond to the noise of a vessel by either swimming away sideways or into deeper water (de Robertis et al. 2010; Jørgensen et al. 2004). Moreover, the noise that is produced by the vessel and/or gear may interfere with the sounds produced by species during courtship. The importance of sounds in courtship has been reported for a wide variety of fish (Finstad and Nordeide 2004; Hawkins and Amorim 2000; Ladich 2007; Lindstrom and Lugli 2000; Myrberg 1997; Rowe and Hutchings 2006; Ueng et al. 2007). However, at present there is a lack of scientific studies of the possible impact of noise pollution on courting species.

It is plausible that fish exhibit a physiological response towards spawning disturbance (Table 2). During the spawning period this may have consequences for reproduction (Morgan et al. 1997). For example, escape behaviour in reaction to the fishing gear could result in an oxygen deficit which needs to be replenished before an individual can resume its spawning behaviour. Spawning disturbance may also 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). Such a response could also be induced through stress hormones produced by fish that are caught by the fishing gear. Furthermore, spawning disturbance may cause a forced delay in fertilization which again may negatively affect the reproductive output. It has been shown that when females are unable to shed their ovulated eggs, the quality of the eggs deteriorate and the fertilization rate declines, a process called overripening (Hay 1986; McEvoy 1984; Mollah and Tan 1983; Springate et al. 1984). Since the natural spawning is generally confined to a short window at a specific time (Domeier and Colin 1997; Matos-Caraballo et al. 2006; Nemeth 2005; Takemura et al. 2004), disturbance may lead to a missed opportunity to spawn. The rate of overripening differs between 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 spawning disturbance than

species in which overripening occurs after several days (e.g. Pacific herring (*Clupea harengus pallasi*) (Hay 1986)). Moreover, it is possible that even though eggs are fully ripened and ovulated, they are never released; retaining eggs is thought to be caused by unfavourable conditions during the spawning period (Rideout et al. 2000).

Spawning disturbance during the spawning period may also affect behavioural routines performed prior to or during the spawning event and disrupt social hierarchies (Levin and Grimes 2006; Rowe and Hutchings 2003; Sadovy de Mitcheson and Erisman 2012). Dean et al. (2012), who studied the response of cod in a spawning aggregation using acoustic tags, showed that the spawning aggregation was completely dispersed by the onset of the fishery. Such disruption(s) may, in turn, have negative consequences for the reproductive success. As behavioural spawning routines vary between species, we expect that the degree of disturbance will vary with the complexity of the behaviour.

The mechanisms described above suggest that spawning disturbance during the spawning period may reduce the reproductive output of the population. Since no empirical studies are available, we can only speculate about its potential effect based on the knowledge reviewed above on how fishing may disturb physiological processes and behavioural routines.

A first proxy of the potential effect is given by the probability that a species is disturbed by a fishery during the spawning period. This probability can be estimated from data readily available for many commercial fish species. Data required are the fishing mortality by age group, the proportion of spawning fish and an estimate of the catch efficiency of the gear. For example, in North Sea plaice, the fishing mortality during the spawning period that is imposed on spawning fish is around $F = 0.3$ in males and around $F = 0.05$ in females (Fig. 1). Assuming a catch efficiency of the fisheries of 95 % (Piet et al. 2009), the proportion of the fish that will be disturbed during spawning will be around 1.4 % for males (i.e. ((1 − exp-F) * ((1 − catch efficiency)/catch efficiency))) and less than 0.26 % for females. However, since fish is expected to swim away from the approaching gear (Albert et al. 2003) the actual efficiency will be less than the 95 % proposed by Piet et al. (2009). When assuming an efficiency of 75 %, the percentage of plaice disturbed by the gear will increase to 8.6 % for males and 1.6 % for females. Such calculations illustrate the sensitivity of the estimation for the catch efficiency of the commercial gear. Overall, the potential effect of spawning disturbance will be the product of the estimated probability of disturbance and the effect of the disturbance on the spawning individual which can only be qualitatively assessed.

The degree of spawning disturbance will depend on the fishing technique. Overall, it is expected that active fisheries (e.g. bottom trawls) will inflict a higher degree of disturbance than passive fisheries (e.g. gillnets or longlines). The noise disturbance from active fisheries will, for example, be continuous while the noise disturbance from passive fisheries will be smaller as the gear is not moved and the vessel is not continuously present at the fishing ground. Also, active fishing gears, where the catching principle is based on chasing fish, are expected to invoke a larger physical disturbance in comparison to passive gears, where the catching principle relies on the fish coming to the gear voluntarily. Nevertheless, passive fisheries may disturb spawning as showed by the disruption of a cod spawning aggregation after the onset of a gill net fishery (Dean et al. 2012).

Impact on spawning habitat

Although many marine fish and invertebrate species release their eggs in the pelagic zone (Russell 1976) and will not be exposed to fishing gear, several species use spawning substrate to lay their eggs. In particular inshore marine fish species and freshwater species, produce benthic eggs to avoid advection (Gross and Sargent 1985; Growns 2004; Russell 1976). For example, herring deposits its eggs on gravel beds (Geffen 2009) and many shark and ray species lay larger benthic egg capsules, while perch (*Perca fluviatilis*) attach their eggs in long threads on water plants (Riehl and Patzner 1998). There are also fish species that bury their eggs into the substratum (e.g. Atlantic salmon (*Salmo salar*) (Fleming 1996; Peterson and Quinn 1996)) or build a nest (e.g. pikeperch (*Sander lucioperca*) (Lappalainen et al. 2003)). These latter two strategies are associated with parental care. Spawning habitat structure may also play a role after hatching. It may serve as refuge for predators for the early life history stages, such as shown in coral reef systems (Costello et al. 2005) and sea grass beds (Hovel and Lipcius 2002). In addition, several

invertebrate species, such as squid and whelks, also produce benthic eggs (Himmelman and Hamel 1993; Sauer et al. 1992).

Therefore, if a species spawns in habitats that are at risk of being destroyed by specific fishing operations (e.g. towed bottom gear), the reproductive success may be affected and population persistence may be threatened. It should be noted that spawning habitats may also be altered by fisheries outside the spawning period. However, as spawning and feeding areas are often spatially segregated and fisheries follow the distribution of fish, the chance of habitat destruction will be higher during the spawning period (Table 2). It has been shown that for fish species for which coral reefs are important spawning habitat, the abundance and diversity on damaged or destroyed reefs was lower in comparison to intact habitat (Koenig et al. 2000).

Population biological consequences of fishing during the spawning period

Fishing during the spawning period may have consequences for (1) the number and quality of the eggs produced which may affect the recruitment to the population; (2) the genetics of the population due to the selective effects on individuals and distinct stock components.

Population egg production and recruitment

Above we argue that the selection pattern of fishing during the spawning period may differ from the selection pattern of fishing during the non-spawning period (see also Table 2). How this will affect the population egg production can best be illustrated with a cohort simulation model of the population egg production (PEP) as a function of the selection pattern (Rijnsdorp et al. 2012). We apply the Yield per Recruit model of Beverton and Holt (1957) to compare the PEP under a spawning closure scenario for a population spawning in either quarter 1, 2, 3 or 4 with the PEP of a year-round fishing scenario over a range of fishing mortality rates. For the baseline scenario we assume that there is no difference in the condition factor or catchability between the spawning and non-spawning period, and an isometric fecundity—body size relationship. Next, we explore how the benefits of the spawning closure are affected by a difference in body
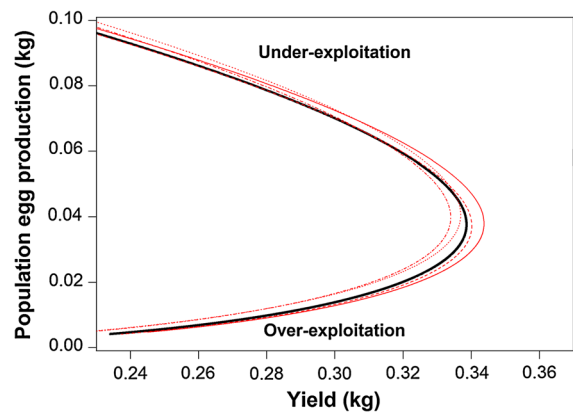

Fig. 2 Population egg production (PEP in kg) as a function of the equilibrium yield (kg) of a cohort that is exploited year-round (*thick black line*) and a cohort that is exploited with a spawning closure (*red lines*) in quarter 1 (*full*), 2 (*dashed*), 3 (*small dashed*) or 4 (*points*). Cohort simulations are fished over a range of fishing mortality rates up to F = 0.5 and assume no difference in condition or catchability during the spawning period and an isometric relationship between egg production and body size (baseline scenario). Parts of the curve that are related to a situation of under-exploitation or over-exploitation are indicated. The transition occurs at the maximum yield

condition or catchability of adult age groups during the spawning period and an allometric fecundity—body size relationship affect. Details of the model are presented in the on-line supplementary material.

A spawning closure influences the maximum yield. The baseline scenario shows that a spawning closure in quarters 1 and 2 results in an increase of the maximum yield, whereas a spawning closure in quarters 3 and 4 results in a decrease of the maximum yield (Fig. 2). The effect of a spawning closure on the PEP depends on the level of fishing mortality and the associated yield. If the population is over-exploited (i.e. the part of the curve where PEP and yield are positively related), PEP will be reduced by a spawning closure in quarters 1 and 2, and enhanced by a spawning closure in quarters 3 and 4. If the population is under-exploited (i.e. the part of the curve where PEP and yield are negatively related), the change in PEP may be positive or negative (Fig. 2). The benefits generated by a spawning closure are influenced by the biological assumptions of the condition factor, adult catchability and the assumption on the fecundity—body size relationship (Table 3). The relative benefits are evaluated for three levels of equilibrium yield in a situation of over-exploitation and one level of equilibrium yield in a situation of under-exploitation. In

Table 3 Population egg production (PEP) under a spawning closure in quarter 1 or quarter 3 expressed relative to the PEP for a year-round fishing scenario, evaluated at three different levels of equilibrium yield (kg) in a situation of over-exploitation and one level of equilibrium yield (kg) in a situation of under-exploitation

Biological assumptions			Population egg production relative to a year-round fishing scenario			
Catchability adults during spawning	Fecundity—body size relationship	Condition during spawning	Yield (kg) in a situation of over-exploitation			Yield (kg) in a situation of under-exploitation
			0.26	0.29	0.32	0.32
Spawning closure in quarter 1						
Equal	Isometric	−20 %	0.795	0.773	0.665	1.312
Equal	Isometric	Equal	0.912	0.926	0.893	1.082
Equal	Isometric	+20 %	1.030	1.080	1.161	0.912
Equal	Allometric	+20 %	1.029	1.080	1.163	0.910
+50 %	Allometric	+20 %	1.223	1.288	1.438	0.834
Spawning closure in quarter 3						
Equal	Isometric	−20 %	0.936	0.890	0.765	1.255
Equal	Isometric	Equal	1.099	1.075	1.075	0.987
Equal	Isometric	+20 %	1.253	1.264	1.406	0.831
Equal	Allometric	+20 %	1.257	1.269	1.415	0.828
+50 %	Allometric	+20 %	1.482	1.499	1.726	0.764

The relative PEP is compared for different biological assumptions on the catchability of adults during spawning relative to the non-spawning period (equal, +50 %), the condition during the spawning period (−20 %, equal, +20 %), and the relationship between fecundity and body size (isometric β = 3, allometric β = 3.3)
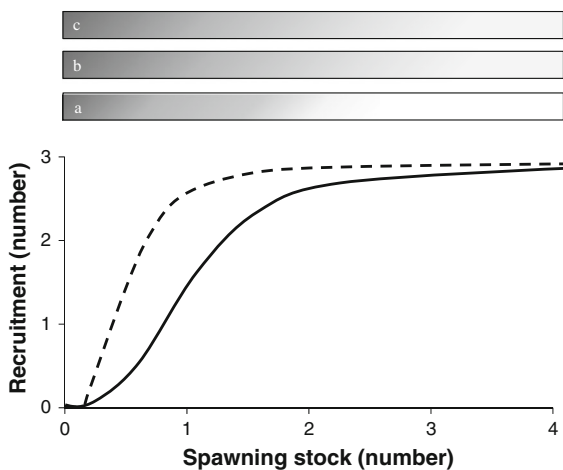

Fig. 3 Stock—recruitment relationships for a species with high (*hatched line*) and low (*solid line*) population growth rate. At low levels of spawning stock, recruitment is impaired by depensatory processes. The greyscales illustrate the contribution of a spawning closure to sustainable management in terms of (*a*) population egg production, (*b*) habitat structure and (*c*) genetics, where white codes no importance and *dark grey codes* high importance

the situation of over-exploitation, a spawning closure will enhance PEP, except when the body condition during the spawning period is lower (quarters 1 and 3) or equal (only quarter 1) than during the non-spawning period. Furthermore, the benefits of a spawning closure are highest when the body condition or adult catchability during the spawning period is higher than during the non-spawning period. An increase in relative fecundity with body size (allometric scaling) has only a small effect. In a population that is under-exploited, the benefits of a spawning closure on PEP are smaller and may even be negative (Table 3).

The simulation model thus shows that a spawning closure will not always result in an increase in PEP, in particular when the population is over-exploited and the body condition of the fish during the spawning period is lower than during the non-spawning period. If fish have a higher condition factor or higher catchability (adults only) during spawning, a spawning closure will enhance PEP but only when the population is over-exploited. The benefits of a spawning closure suggested by the simulation model, although quantitatively dependent on the parameter values chosen, will qualitatively apply to species matching the model assumptions.

The next question is whether an increase in PEP will enhance recruitment. This will depend on the state of the spawning stock. The stock-recruitment relationship provides the background against which the

population dynamic consequences of a fishery can be assessed (Beverton and Holt 1957; Ricker 1954). Figure 3 shows an example of a stock-recruitment relationship which applies to populations in which pre-recruit mortality increases with stock size (Beverton and Holt 1957). If adult stock size has a strong negative effect on their young, for instance through cannibalism, the stock-recruitment relationship is dome-shaped (Ricker 1954).

In practice, the high inter-annual variability in recruitment (Houde 2009) and the possibility of long-term fluctuations in recruitment (Koster et al. 2005; Mantzouni and MacKenzie 2010) hampers the study of the processes that determine the stock-recruitment relationship (Fogarty and O'Brien 2009; Iles 1994). Nevertheless, a meta-analysis of 364 stock-recruitment relationships shows that recruitment is related to spawner abundance and that recruitment is reduced at high levels of exploitation (Myers and Barrowman 1996). At very low population levels, a positive relationship is expected between the per capita population growth rate and population density due to depensatory processes (Allee effect: Stephens et al. 1999), though the statistical evidence is thin (Myers et al. 1995). The Allee effect may prevent depleted fish population from recovering despite the strong compensatory population dynamics (Frank and Brickman 2000; Rowe et al. 2004).

Against this background, we may infer how a reduction in the number (PEP) and quality of the eggs and their fertilisation probability caused by fishing during the spawning period could affect recruitment (Fig. 3). If the spawning stock is at a very low level, fishing during the spawning period is expected to increase the risk of stock collapse due to depensation. When a stock is at a level where recruitment increases with stock size, density-dependent processes will be weak and a reduction in the number and quality of the eggs or their fertilisation probability is expected to lead to a decline in recruitment. When a stock is at the level where an increase in egg production has no effect on recruitment, fishing during the spawning period is expected to have no effect on recruitment.

Population genetics

Stock structure

Within the distribution area of a fish species, distinct spawning components may occur (Hauser and Carvalho 2008; Sinclair 1988). Though 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 (Beacham et al. 2002; Hutchinson et al. 2001; Pampoulie et al. 2006; Ruzzante et al. 1999). The scale of the biological stock structure may not match with the scale of the management unit for which stock assessment is carried out, and depletion of local spawning components may go unnoticed when the stock assessment is carried out for the total management unit (Reiss et al. 2009).

If a fishery is exploiting a stock comprising of spawning components that spatially segregate during spawning, fishing during the spawning period will aggravate the risk of over-exploitation of stock components and increase the risk of a loss of genetic diversity.

Fisheries-induced evolution

Theoretically it is argued that under increased mortality due to fishing, individuals that mature at a smaller size and/or younger age and invest more in reproduction will be more successful than fish that postpone reproduction (Heino and Godo 2002; Law 2000; Rijnsdorp 1993a). This hypothesis is supported by a number of studies on various exploited fish species (see reviews in (Jørgensen et al. 2007; Kuparinen and Merila 2007) and experimental studies (Conover and Munch 2002; Reznick et al. 1993; van Wijk et al. 2013). In particular, the selective removal of the larger (and older) individuals, who may be more vulnerable to fishing during the spawning period than outside the spawning period (see also fishing mortality), may induce evolutionary change. Simulation studies have shown that a dome-shaped exploitation pattern, where fishing pressure exerted on the older age or size classes is reduced, will reduce the selection pressure on reproductive traits (Jørgensen et al. 2009; Laugen et al. 2012). How the differences in selection between males and females, in particular in sex dimorphic species, affect fisheries-induced evolution remains to be studied. In the very specific case where fishing is exclusively on the spawning grounds, fishing may select for a delay in maturation as has been suggested for Northeast Arctic cod (Jørgensen et al. 2009). Apparently, the direction of fisheries-induced evolution depends on how a population is harvested; it is advantageous either to grow and mature as late as possible or to stay small and mature early.

Table 4 Semi-quantitative scoring system to classify the potential vulnerability of aquatic species for the negative impact of fishing during the spawning period

Characteristics	Score		
	1	2	3
Aggregation during spawning	No aggregation	Moderate aggregation	Large aggregation
Spawning behaviour complexity	Broadcast spawner, no courtship	Simple courtship	Social hierarchy, size-assortive mating, pair bond, or parental care
Spawning habitat	Pelagic	Attached and dispersed	Attached and aggregated

The impact of fishing will differ between fishing gears: passive gears such as gill nets or long lines will generally have less impact than active gears such as bottom trawl (see text). Level of aggregation during spawning is considered relative to the aggregation during the non-spawning period

Management

The contribution of a spawning closure to the sustainable management will depend on the status of the fish stock and will differ among species given their reproductive characteristics and type of fishing gear used. Spawning closures may be particularly relevant in over-exploited stocks where there is a risk that recruitment is impaired. Any measure to protect the spawning stock by restricting fishing on the spawning population will warrant that all fish that survived until the start of the spawning period will be allowed to spawn. As recruitment increases with stock size, the benefit of a spawning closure will reduce (Fig. 3). However, for stocks for which there is no indication that recruitment is impaired, spawning closures may still be relevant to protect the older (and larger) individuals, protect spawning habitat structure, or reduce genetic effects.

Scoring system

The potential vulnerability of a species to fishing during the spawning period can be assessed by a simple semi-quantitative scoring system. The scoring system evaluates (1) the degree of aggregation during the spawning period, (2) the complexity of the spawning behaviour and (3) the vulnerability of the spawning habitat to fishing (Table 4).

If a species aggregates in spawning schools prior to and/or during spawning it will be more vulnerable to the impact of fisheries (Sadovy de Mitchenson et al. 2012). The degree of aggregation of a species can be estimated from seasonal variations in commercial catch statistics, such as the landed catch, catch-per-unit-effort, and timing and size of large catch anomalies (Tobin et al. 2013). This vulnerability may be further enhanced due to a difference in spawning behaviour affecting their catchability (Levin and Grimes 2006; Solmundsson et al. 2003).

The impact of fishing on species during the spawning period also depends on the complexity of their spawning system. When a species exhibits a broadcast spawning type that is triggered by environmental cues or chemical signals (e.g. many invertebrate species), the effect of spawning disturbance will not play a role. Species that perform more complicated behavioural routines during spawning, such as courtship, pair formation, social hierarchies, size-assortive mating and/or external or internal (i.e. viviparity) parental care, will be more vulnerable to disturbance during the spawning period. The degree of disturbance will depend on the type of fishing gear that is used; active gear will cause a higher degree of disturbance than passive gear.

If species spawn in habitats that are at risk of being destroyed by specific fishing operations during the spawning season (e.g. towed bottom gear), the effect on the reproductive potential will be high. Demersal spawning habitats will be vulnerable, in particular if species are highly selective and spawning habitats are restricted to relatively small localities. Pelagic spawning habitats, on the other hand, will not be affected.

We have applied the scoring system on a selection of commercially exploited invertebrate and fish species (Table 5). According to the scoring system there is no biological reason for a spawning closure for sea cucumber or bivalves as they score 1 for the three criteria. For crustaceans, that may carry their eggs during incubation, specific measures to reduce fishing on egg-bearing females may be relevant. There are several examples where fishermen are indeed obliged to release egg-bearing females (Comeau and Savoie 2002; Ennis 2011). For the semelparous Cephalopods (e.g. chokka squid) that form dense spawning aggregations, spawning closures may protect the spawning

Table 5 Semi-quantitative assessment of the potential vulnerability of a number of exploited aquatic species for the negative impact of fishing during the spawning period

Species	Aggregation during spawning	Spawning behaviour complexity	Spawning habitat
Sea cucumber	1	1	1
Bivalves	1	1	1
Lobster	1	3	2
Chokka squid	3	3	2
Common skate	1	2	2
Lesser spotted dogfish	1	2	2
Herring	2	2	3
Anchovy	2	2	1
Plaice	2	3	1
Red hind	3	3	2
Labeobarbus spp.	3	3	1
Pike perch	1	3	2
Cod	2	3	1

The scoring of the different criteria is given in Table 4

population to allow for successful reproduction (Sauer 1995) and to reduce the impact of selective removals of males (Hibberd and Peckl 2007; Moltschaniwskyj et al. 2002). A spawning closure may also be an effective measure to protect stocks that show large spawning aggregations from over-exploitation such as red hind (Sadovy de Mitchenson et al. 2012; Sadovy de Mitcheson et al. 2008; Sadovy and Domeier 2005) Among the fish species exploited in Lake Tana (Ethiopia), only the Labeobarbus species that migrated to the rivers to form large spawning aggregations, showed signs of recruitment overfishing (de Graaf et al. 2006). A spawning closure may also be beneficial for species that show intermediate spawning aggregations, such as cod and plaice (Dean et al. 2012; Rijnsdorp et al. 2012). Spawning closures are expected to be less useful in fish species such as common skate, lesser spotted dogfish or pike perch, which do not form spawning aggregations and do not require a spawning habitat that is highly vulnerable for fishing. Also for pelagic fish species such as anchovy and herring, spawning closures may not necessarily provide additional protection during spawning as these species school throughout their life. Within the scoring system each criterium stands individually. Therefore, it is not possible to sum up the effects of the three criteria when predicting the degree of vulnerability of a species to fisheries during the spawning period.

Ecosystem based approach

Since fisheries management is embedded in a broader ecosystem approach, the benefits of a spawning closure for a particular species need to be traded-off against the ecosystem effects of the effort re-allocation (Jennings 2005; Rice 2008). The spawning closure to protect North Sea cod that was imposed in 2001 by the fisheries ministers of the European Union illustrates the need to include ecosystem considerations. In this specific case analysis of the response of the fisheries to the spawning closure showed that the fishing fleet reallocated their activities to areas which were more vulnerable with regard to trawling impacts on the benthic ecosystem and the occurrence of threatened fish species (Dinmore et al. 2003; Rijnsdorp et al. 2001).

If not designed properly spawning closures may select for particular spawning components. For example, (Loher 2011) showed that the spawning closure for Pacific halibut (*Hippoglossus stenolepsis*) over the past 20 years has been consistently too short. He noted that failure to fully protect spawning migrations may allow the selective removal of early and late spawners which could result in changes in stock demographics, restrict effective spawning, and influence long-term stock productivity. Support for a genetic control of the timing of spawning is suggested for cod (Otterå et al. 2012).

In addition to the biological arguments supporting the use of spawning closures as a tool to enhance the sustainable use of the aquatic resources, there are economic consequences to consider. Spawning closures will result in the reallocation of the fisheries catch over different seasons and different fishing grounds. The establishment of a spawning closure will result in a change in the cost and revenues of fishing. In the case of a fisheries which utilises spawning aggregations, the reallocation of fishing effort away from the spawning grounds will likely result in a decrease in revenue of fishing due to the lower catch rate. The lower catch rate, however, may be compensated to some degree by the higher market value of the fish caught outside the spawning period. Figure 4 shows the seasonal variations in the fish price of four different demersal fish species distinguishing between
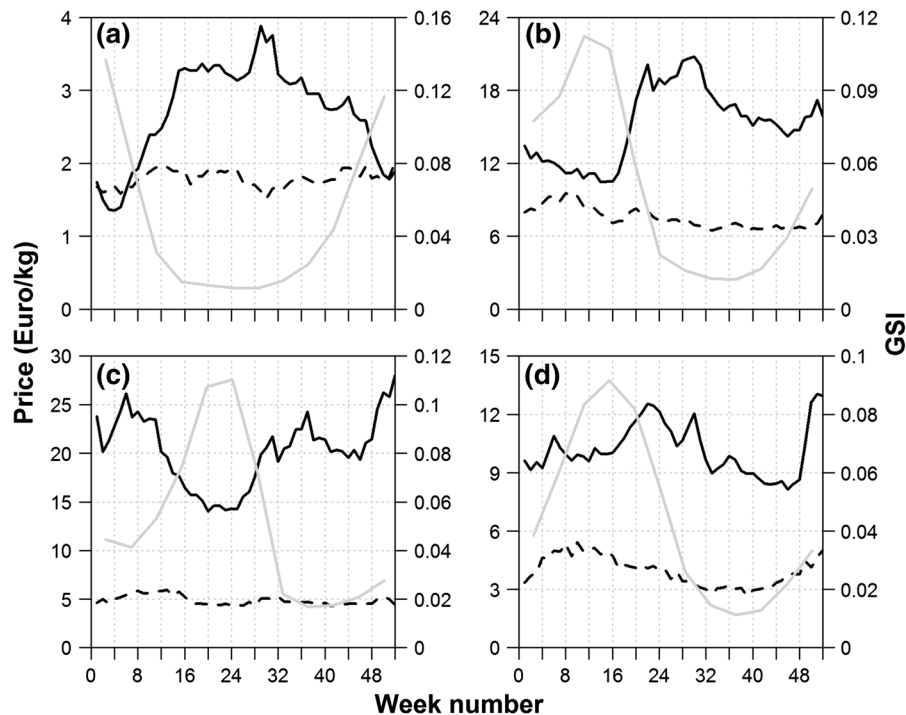
Fig. 4 Seasonal variation in first sale price of adults (*solid black line*) and juveniles (*hatched black line*) in relation to the gonado somatic index (GSI, *grey line*) for **a** plaice, **b** sole, **c** turbot and **d** brill (adapted from (Rijnsdorp et al. 2012))

the smallest size class (mainly juveniles) and the largest size class (adult fish). Although these results corroborate the effect of fish size on the ex-vessel price (Zimmerman and Heino 2013), the price of the adult fish shows seasonal variations that coincide with the seasonal cycle in gonado-somatic index. These patterns are expected to be applicable for fisheries targeting species for their meat. However, fisheries targeting roe, such as in sturgeon (caviar) and lumpsucker, will show a different relationship with the highest price expected just prior to and during the spawning period.

In a first exploration of an integrated approach, the implications of spawning closures in the North Sea flatfish fishery (Rijnsdorp et al. 2012) were assessed in terms of indicators of stock status (spawning stock biomass) of the four main target species of the fisheries, economic performance of the fishery (yield, revenue) and ecosystem impact (discards of under-sized fish, bycatch of sensitive species, seabed integrity and fisheries-induced evolution). This study shows that in a single species context, spawning closures may be beneficial for plaice and sole, while in a mixed

fisheries and ecosystem context, negative effects may occur. Tailor made solutions are required that need to be developed in stakeholder consultation to trade-off the ecological and economic objectives.

Conclusion

This review shows that empirical support for the contribution of spawning closures to sustainable fisheries management is mainly restricted to fish species forming large spawning aggregations and also provides insight about the conditions under which spawning closures may be of benefit for other species. The analysis of the processes by which fishing affects the biology of a population suggests that spawning closures may be beneficial if they: (1) reduce fishing mortality on the older and larger individuals that are most valuable for the reproductive output of the population; (2) avoid negative effects of fishing on spawning habitats; (3) reduce the risk of over-exploitation in species which form large spawning aggregations; (4) reduce the evolutionary effects on

maturation and reproductive investment; (5) reduce the risk of over-exploitation of specific spawning components.

Spawning closures 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 fisheries systems, no general recommendation can be given and the relevance should be considered on a case by case basis. In order to assess whether a spawning closure could make a valuable contribution, research should focus on whether, and to what extent, the five conditions specified above apply. Suggestions for topics for future research are: (1) studies on how fishing disturbs spawning and its consequences for the production of viable offspring; (2) studies on the selectivity of the fishery during the spawning season in relation to the age structure, gender and spawning stage of the fish and specific spawning components; (3) modelling studies of the potential effect of spawning closures for a variety of spawning types. The latter may provide quantitative insight into the contribution of spawning closures to sustainable exploitation, and the relative importance of the various mechanisms by which fishing may impact the population, in relation to spawning type.

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