Advances in modelling the effectiveness of Marine Protected Areas (MPAs) to enhance conservation management of mobile fish stocks.

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Abstract

Marine Protected Areas (MPAs) have been proposed as beneficial for conservation of fish species and as fisheries management tools. However, there is lack of consensus about the benefit of MPAs for mobile species, which are under-represented in the literature. Empirical data in this field are lacking for mobile species so mathematical models are useful tools to explore the design and effectiveness of MPAs. A spatio-temporal, age-structured mathematical model was developed to determine whether MPAs could be used to protect biomass and sustain yield of mobile commercial stocks. It is demonstrated that the temporal resolution of models can affect the reliability of model predictions and therefore must be at an appropriate scale, appropriate to biological processes. The model is applied to a two-species fishery of mobile stocks. It is shown that stock mobility can impact the effectiveness of an MPA, potentially preventing conservation aims and fisheries goals both being met. The model is developed to examine the effect of density-dependence in the stock recruitment relationship within the model: this is found to be a key factor which affects the reliability of predictions of MPA models. The model is also used to compare the potential benefits of MPAs to seasonal closures and it is shown that while MPAs can protect more of the stock biomass, effort control over and above either type of closure can give similar management outcomes. The model is used in a case-study of the North Sea herring (*Clupea harengus*) fishery. The case-study demonstrates the need for real-world data to be used in simulations for effective MPA planning. The outcomes from each model application emphasise the need for stock mobility, life-histories and stock status to be incorporated in MPA simulations. Doing so will improve reliability of simulation predictions and aid MPA planning.

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Declaration

This thesis is a presentation of my original research work. Wherever contributions of others are involved every effort is made to indicate this clearly, with due reference to the literature, sources of data for parameterisation of the simulations, and acknowledgment of collaborative research and discussions. The model which was developed in Chapter 2 was based on and adapted from previous work by Ed Codling and Will Le Quesne (Le Quesne and Codling, 2009). This chapter is in draft paper form at time of submission and Ed Codling will be first author on the paper. The changes I have made to the model are clearly described in the methods section of Chapter 2 and have been made throughout in collaboration with Ed Codling. All changes and adaptations to the model in Chapter 2 and all subsequent chapters are my original work.

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Glossary

B_{LIM}	Limit reference point for spawning stock biomass – the point below which conservation and management action need to be implemented to facilitate stock recovery.
FSA	Fish spawning aggregation
IBM	Individual based model
IUCN	International Union for Conservation of Nature
LSMPA	Large scale marine protected area
MPA	Marine protected area
MSY	Maximum sustainable yield
NTZ	No take zone
SRR	Stock recruitment relationship
SSB	Spawning stock biomass
TAC	Total allowable catch
WWF	World Wide Fund for Nature

Chapter 1: Introduction – The theory and application of Marine Protected Areas

Restricted access to marine areas has been put in place through cultural and legal frameworks for centuries to regulate fisheries and conserve habitats and species (N.R.C., 2001). Marine conservation has been documented since at least the 14th century, when a petition was put before the English Parliament to restrict dredging gear to prevent habitat destruction (Fogarty, 2001). However, marine conservation has lagged behind that of terrestrial habitats and it was not until the late 20th century that marine conservation was recognised through legislation in many countries (Agardy, 1994). By the mid-1970s, the IUCN and WWF were seeking to identify and protect marine habitats to preserve both their biodiversity and their intrinsic value for human activities such as research and education (Björklund, 1974). The first marine areas to be afforded legislative protection in this way were Goat Island Marine Reserve in New Zealand (1975) (Ballantine and Gordon, 1979); Wrangel Island Strictly Protected Nature Reserve in Russia (1976); and the Great Barrier Reef Marine Park in Australia (1979) (Wood *et al.*, 2008).

A working definition of a marine protected area (MPA) is ‘any marine geographical area that is afforded greater protection than the surrounding waters for biodiversity conservation or fisheries management purposes’ (Kelleher, 1999). MPAs have different designations which afford varying degrees of protection within their boundaries (Dudley, 2008); these range from multiple-use marine reserves which permit some extractive activities to fully protected areas (Agardy *et al.,* 2011; Horta e Costa *et al.*, 2016). For the purposes of the current study, an MPA is considered synonymous with a marine no-take-zone (NTZ), in which no fishing is permitted; these are also termed ‘marine reserves’ in the literature.

1.1 The value of MPAs to conservation and fisheries

MPAs were originally proposed as essential for conservation in the face of habitat and species degradation from human activities. They were expected to reduce habitat loss, increase the biomass and number of the species within them, and thus proffer increased biodiversity (Dugan and Davies, 1993; Agardy, 1994; Creese and Cole, 1995; Halpern and Warner, 2002; Lubchenco *et al.,* 2003; Mora and Sale, 2011). Earlier studies of the conservation benefits reported fish populations inside MPA boundaries increasing in abundance, size and biomass (Bohnsack, 1998; Mosquera *et al*., 2000). Biodiversity in MPAs was reported to increase (Lubchenco *et al*., 2003, Micheli *et al*. 2004b; Lester *et al.,* 2009) and meta-analyses of empirical studies verified that such increases could occur within just three years of establishing MPAs in some ecosystems (Halpern and Warner, 2002; Halpern, 2003).

The increases in fish abundance and biomass within the protection of MPAs were attributed to protection from fishing within the MPA boundaries which could, therefore, also conserve commercial species (Cote *et al.,* 2001; Palumbi, 2004). As such, MPAs were also proposed as being beneficial to fisheries targets alongside conservation goals (Murray *et al.,* 1999; Agardy, 1999, 2000; Worm *et al.*, 2009, Gaines *et al.*, 2010b) and MPAs have been advocated as fisheries management tools for overexploited and poorly managed stocks for over two decades (Allison, 1998; Bohnsack, 1998; Auster and Shackell, 2000). The refuge from fishing provided within an MPA boundary allows stocks to rebuild, whilst it has been suggested spillover – the net export of juvenile and adult fish across the MPA boundary – increases biomass outside the MPA, thereby potentially maintaining or enhancing yields of commercial stocks in adjacent fisheries (Russ and Alcala, 1996; Halpern and Warner, 2002; Abesamis and Russ, 2005; Murawski *et al.,* 2005, Lester *et al*., 2009). Additionally, recent simulation findings have shown that the reproductive potential of fish within the MPA boundary may contribute disproportionately to yield (Marshall *et al*., 2019).

Spillover has been studied via simulations and some empirical studies but the underlying mechanisms of spillover and the consequent benefits to fisheries and conservation have yet to be resolved (see Di Lorenzo *et al*. (2016) for a comprehensive literature review). ‘Fishing the line’ - whereby fishers target the higher biomass at the border of the MPA (Murawski *et al.,* 2004; Goni *et al.,* 2010) – can conceal the full extent of the spillover effect (da Silva *et al*., 2015) as can poorly managed fisheries outside the MPA boundary (Buxton *et al*., 2014). It is evident that further empirical studies and fishery data are needed to draw conclusions as to the relationship between MPAs, spillover and fisheries and conservation benefits (Di Lorenzo *et al*., 2016).

Some species are not targeted by fisheries but can form the bycatch of a harvest. Due to their life-history traits such as slow-growth, late-maturity or low fecundity, some of these species become highly vulnerable when exposed to the fishing effort utilised to catch the target species (Gaines and Costello, 2013). These are termed ‘weak stocks’ and can drive the management or force the premature closure of the target fishery (Hilborn *et al*., 2004). MPAs have also been proposed as a solution which will protect these weak stocks whilst still maintaining yield for fishers (Hastings *et al*., 2017).

However, despite the reported potential of MPAs to mitigate overfishing and meet conservation and fisheries aims, less than half of MPAs globally are currently NTZ MPAs (mpaatlas.org). To achieve biodiversity and conservation goals more MPAs need NTZ designation (Costello and Ballantine, 2015; Sala *et al*., 2018), which could also confer fisheries benefits to neighbouring areas via increased biomass within the

MPA boundary, resulting in potential spillover and increased yields outside the MPA boundary (Sala and Giakoumi, 2017).

More than 30% of marine fisheries worldwide are not within biologically sustainable limits (FAO, 2018) and over half of fisheries existing for 50 years or more have been overfished at some time (Watson *et al.*, 2015). Empirical studies of the benefits of MPAs specifically to fisheries have lagged behind conservation-based studies (Vandeperre *et al*., 2010). Further research is needed whether NTZ MPAs can provide a solution which will allow depleted stocks to rebuild, conserve species and also provide a harvest via the spillover effects.

1.2 Can MPAs benefit mobile species?

Studies of MPAs originally demonstrated that MPAs produced the greatest conservation benefit for sedentary and slow-moving organisms (Hastings and Botsford, 1999; HIlborn *et al*., 2004) whose home ranges were contained within the MPA boundaries for most of their lifespans (Kramer and Chapman, 1999; Aburto-Oropeza *et al.,* 2011; Afonso *et al*., 2011). Consequently, reports of MPAs as tools in the conservation and rebuilding of commercial fish occurred commonly in earlier literature in studies of reef species (Auster and Shackell, 2000; Sweeting and Polunin, 2005), which typically exhibit low rates of movement across MPA boundaries and were therefore considered to benefit most from MPAs (Bohnsack, 1998; Almany *et al.,* 2009). Fish biomass of such species was recorded as increasing by up to 246% where MPAs had been established (Wantiez *et al*., 1997) and evidence was well documented for the increases in biomass of species with low mobility being due to the protection from fishing inside MPA boundaries (for example: Russ and Alcala, 1989; Polunin and

Roberts 1993; Ferreira and Russ, 1995; Maypa *et al.,* 2002; Lester *et al.,* 2009; La Mesa *et al.,* 2011; March *et al.,* 2011).

The conservation benefits of MPAs to temperate, pelagic species (which are typically highly migratory) have been debated (Micheli *et al.,* 2004b). MPAs were shown to enhance biomass of mobile species within the reserve boundary (Willis *et al.,* 2003) but the application of MPAs to conserve fisheries' stock biomass for mobile commercial species was criticised because, on crossing the MPA boundary, the stock no longer benefited from the protection of the MPA (Allison *et al.,* 1998). Although yield could potentially be enhanced for mobile species (Apostolaki *et al*., 2002; Stefansson and Rosenberg, 2006), MPA implementation can also result in fishing effort being displaced elsewhere rather than being reduced (Halpern *et al*., 2004). Intense 'fishing the line' for increased yields at the MPA boundary (Murawski *et al.,* 2004; Goni *et al.,* 2010) - particularly when part or all of a fishing area has been lost by the creation of an MPA (McClanahan and Kaunda-Arara, 1996; McClanahan and Mangi, 2000; Murawski *et al.,* 2005) - was considered to potentially reduce MPA effectiveness of mobile commercial species by causing a sharp decline in fish density and biomass immediately outside the MPA (Kramer and Chapman, 1999; Grüss *et al.,* 2011).

To address this, it was proposed that redistribution of effort should be coupled with MPA introduction (Stefansson and Rosenberg, 2005), particularly for species of intermediate mobility (Kellner *et al.,* 2007). The strategy of combining MPA protection with effort restrictions was used successfully to rebuild the Georges Bank (Southern New England, USA) cod (*Gadus morhua*) stock (Murawski *et al*., 2000), but the degree of adult mobility and the pattern of movement – directional, random, or seasonal migratory movements - across the boundary can potentially be confounding factors when managing redistribution of effort (Murwaski *et al.,* 2004). Effort displacement is actually suggested by Hilborn (2018) as such a failing of MPAs that it negates their purpose and he argues that it is unlikely any MPA can be designed to benefit the wide range of different species' movement types which would be evident in and around MPAs.

Another approach when developing MPAs for highly mobile species would be to strategically place MPAs so they protect habitats and locations which are important to the species' life-histories (Lauck *et al*., 1998; Game *et al*., 2009; Breen *et al*., 2015; Pérez-Jorge *et al*., 2015). For example, in a recent empirical study (Doherty *et al*., 2017), movements of basking sharks (*Cetorhinus maximus*) were tracked *a priori* of MPA site designation. The proposed MPA site (off the west coast of Scotland) was confirmed as being suitable to protect the species based on the inter-annual migrations to and movements within the MPA, which would also coincide with the key life-history event of shared foraging. Similarly, Grüss *et al*. (2019) used statistical modelling of life-history 'hotspots' to identify the optimum placement of MPAs to protect spawning and juvenile fish of migratory populations of nine grouper (Epinephelidae) and two snapper (Lutjanidae) species in United States waters. Their results indicated that expansion or stricter management of two existing MPAs in the U.S. Gulf of Mexico would be beneficial for the protection of the species studied.

Despite their potential to afford protection to mobile species, those MPAs which are sited without full consideration of the extent of species' ranges and ecological requirements will likely offer inadequate protection to those species. For example, effort-displacement on those species when their ranges cross the MPA boundary will negate protection within the MPA borders and poor management of the MPA will result in lower ecosystem health, negatively impacting the species the MPA is designed to protect (Agardy *et al.*, 2011). In their review of 40 highly mobile pelagic species in UK waters which had areas closed under fisheries legislation to protect them, Breen *et al.* (2015) found that none of the species were effectively protected. Lack of scientific knowledge about highly mobile pelagic fish was given as the key issue preventing successful MPA implementation to protect these species.

It is evident, then, that to plan and successfully predict the impact of MPAs designed to protect mobile fish, the species' movements must be a key consideration (Le Quesne and Codling, 2009; Costello *et al.*, 2010; D'Aloia *et al.*, 2017; Cabral *et al.*, 2019).

1.3 MPA design

The Aichi Biodiversity Target of 2010 (Convention on Biodiversity, 2010: Strategic Goal C, Target 11), set a target to protect 10% of the World's oceans and seas with 'ecologically representative and well-connected systems of protected areas' by 2020. By 2014, 8.4% of the marine environment within and 0.25% beyond national jurisdictions were protected and the World Parks Congress (WPC) recommended that the 10% Aichi biodiversity target should be increased to protect at least 30% of each marine habitat from extractive activities (World Parks Congress, 2014: marine conservation theme). As of 2019, 2.2% of the World's seas and oceans are protected by NTZ MPAs (mpaatlas.org).

Mean MPA size increased from 148 km^2 to 10,302 km^2 between 1994 and 2014, indicating rapid progress towards MPA targets in terms of ocean coverage (O'Leary *et al.*, 2016). Setting targets for MPA protection in terms of percentage coverage of the oceans has proven controversial (Carwardine *et al.*, 2009; De Santo, 2013; Boonzaier and Pauly, 2016) and the rate of establishment of large scale MPAs

(LSMPAs – in the order of hundreds of thousands of kilometres in size) has been questioned as a political gesture driven by the need to reach targets not conserve biodiversity (Leenhard *et al*., 2013; Devillers *et al*., 2015). The counter-argument is that targets such as these can be political drivers to take action towards biodiversity conservation (Wood, 2011; Watson *et al*., 2014) and LSMPAs can apparently offer greater conservation value than is implicit from their size alone (Russ, 2008; Toonen *et al*., 2011; Davies *et al*., 2017), particularly when their scale enables several ecosystems and habitats to be protected (Wilhelm *et al*., 2014).

However, it has been suggested by O'Leary *et al*. (2016) that protection of 10% of marine waters is insufficient and at least a third of oceans and seas should be protected for MPAs to meet sustainability aims, including those of conservation and fisheries management. There is an urgency – politically and ecologically – for the MPA target to be met but nonetheless the planning, design, and implementation of MPAs should be based on scientific principles (Lubchenco and Grorud-Colvert, 2015).

1.3.1 Is there a 'best' MPA size?

Financial analysis of start-up and maintenance costs of MPAs has shown that economies of scale are gained with increasing size of MPAs (McCrea-Strub *et al.,* 2011), although the authors acknowledge that the financial data they were supplied with could not be entirely validated in all cases. Large MPA size was also advocated by Edgar *et al*. (2014) as one of the five key 'NEOLI' features associated with successful MPAs: no-take, enforced, old, large, and isolated. However, these key features were shown to cumulatively confer conservation benefits to MPAs and size alone was not sufficient for an MPA to meet conservation targets. Their study focussed primarily on reef-dwelling species and, although they recommend that coastal MPAs are extended into deep waters beyond the limits of reefs, they do not explicitly mention the benefits to highly mobile organisms.

Studies have shown larger MPAs can increase biodiversity (Botsford *et al.,* 2003; Roberts *et al.,* 2003) and biomass of commercial stocks (Hastings and Botsford, 1999; Botsford *et al.,* 2001) more effectively because the home ranges and larval dispersal of the target species are maintained within MPA boundaries (Botsford *et al.,* 2003; Chapman and Kramer, 2000; Jennings, 2000). However, some meta-analyses showed biological measures such as population density, organism mass and biodiversity did increase within MPAs but not proportionally to MPA size (Cote *et al.,* 2001; Halpern, 2003; Guidetti and Sala, 2007; Tetreault and Ambrose, 2007). This was questioned by the findings of a meta-analysis by Claudet *et al*. (2008), which indicated that density of commercial species is directly dependent on reserve size.

An empirical study by Vandeperre *et al.* (2010) found a more complex relationship between MPA size and catch: a mixed-species fishery benefited from smaller MPAs whilst specific fisheries required larger MPAs. However, the MPAs in the studies cited above were smaller than LSMPAs and all focussed on species with lower mobility, thus they have limited applications to highly mobile species.

Species with greater adult mobility will need much larger areas to be protected than home-range species in order to effectively protect the mobile populations from harvesting over the geographic range of their life-history stages (Blyth-Skyrme *et al.,* 2006; Laurel and Bradbury, 2006; Gaines *et al*., 2010a; Roberts *et al*., 2010; Agardy *et al*., 2011). It has been suggested LSMPAs which encompass significant parts of highly migratory species' ranges will confer greater benefits than small MPAs (Wilhelm *et al.,* 2014). For example, using a simulation, Simon *et al*. (2014) demonstrated that SSB of North Sea Saithe (*Pollachius virens*) benefitted most from spatial closures which incorporated migratory routes and areas of high dispersal of *P. virens*. Game *et al.* (2009) and Breen *et al*. (2015) also propose that a whole species could benefit by protecting a specific part of a mobile species' life-history with a smaller MPA.

One challenge in developing LSMPAs is how best to protect mobile species and prove the impact of the protection. Due to their extensive ranges, tracking mobile populations in a non-extractive way can be highly demanding in terms of resources and technology (Letessier *et al*., 2015), although rapid advances in technology will make this feasible in the near future and allow much-needed movement-data to be shared, improving future marine spatial planning and fisheries management (Lowerre-Barbieri *et al*., 2019).

Despite much discussion about MPA size in the literature, there are relatively few benefits of small MPAs to mobile species due to their exposure to harvesting on crossing the MPA boundary (Breen *et al.,* 2015) and the benefits of LSMPAs to mobile species which have large ranges have not been thoroughly assessed (Davies *et al*., 2017). There is, therefore, a need to assess MPA size and effectiveness with respect to species mobility.

1.3.2 Do MPA networks offer more benefits?

The conservation benefits accrued from LSMPAs can potentially be met by combining single MPAs into networks, which can have a greater positive impact than the cumulative effect of the discrete MPAs within them (Gaines *et al*., 2010b). Networks also offer the possibility of meeting conservation targets and fisheries management aims concurrently (Le Quesne and Codling, 2009; Gaines *et al*., 2010b; Fovargue *et al*., 2017). Principles by which MPAs should be placed in a network are well-established: MPAs must be large enough and numerous enough, spaced appropriately to allow connectivity via larval and adult dispersal, be representative, and afford robust protection to the target species (Hastings and Botsford 2003; Palumbi *et al.,* 2004; Roberts *et al.,* 2003; Kaplan and Botsford, 2005; Botsford *et al.,* 2009; Anadon *et al.,* 2011). The protection of mobile species within MPA networks will require particular considerations: the species' life-histories (their age and size at maturity, fecundity and life-span), mobility (from home-range to highly mobile), distribution (the presence of spawning aggregations, nursery grounds, feeding grounds) and movement patterns (random, directional and / or seasonal) will determine the appropriate dimensions and spacing of the MPAs in the network (Smith and Metaxas, 2018).

Simulations have demonstrated the potential impact of fish movement on the success of MPA networks in meeting fishery and conservation aims. For example, D'Aloia *et al*. (2017) demonstrated that movement data at all life-history stages must be taken into account when planning effective MPA networks to protect multiple-species. Le Quesne and Codling's (2009) simulation demonstrated that the varying degrees of mobility in a multi-species fishery will affect the number and optimum size of MPAs in a network and the potential of the network to meet fisheries and conservation aims. Empirical evidence also supports the connectivity of MPA networks as particularly important for the protection of highly mobile organisms: their distribution, ranges, and migratory routes must be considered to ensure sufficient protection is afforded from the size and spacing of MPAs in networks (Pendoley *et al*., 2014; Daly *et al*., 2018).

Foster *et al*.'s (2017) analysis of the sizes and spacing of MPAs in the Celtic Seas MPA network has shown that the presence of 18 large MPAs (greater than 1000 km^2) could be of benefit to highly mobile species, but the network is dominated by small MPAs which will be of limited benefit to high-mobility species. The authors recommend that further work is needed to determine whether the MPA network supports mobile species during key life-history stages and whether additional larger MPAs would be beneficial within the network.

Gaines *et al*. (2010b) suggest that, although fisheries and management objectives can be met by well-designed MPA networks, the large MPAs needed to manage highly mobile, pelagic stocks could not be integrated into coastal MPA networks adjacent to heavily populated areas because there would be too great a cost in economic and social terms. This was also echoed by Edgar *et al*. (2014), who noted that opportunities for isolated LSMPAs in coastal areas will continue to diminish as the World population increases.

Despite the apparently conflicting opinions on MPA networks, LSMPAs and smaller MPAs do not have to be viewed as mutually exclusive, and they can be integrated into a suite of complementary management measures (Toonen *et al*., 2013; Wilhelm *et al*., 2014), which could meet signatory nations' commitment to the Aichi Biodiversity targets (Convention on Biodiversity, 2010) of designating coherent networks of MPAs. The impact of MPA networks are not being examined in the current study and will thus not be discussed further but are outlined above as context for the discussion surrounding MPA size and species mobility.

1.4 Are temporal closures a viable alternative to MPAs?

In addition to spatial closures, protection measures can take the form of seasonal closures that apply to species and/or areas. These can be used as a management tool, particularly to protect fish spawning aggregations (FSAs). FSAs are typified by a high abundance of fish in a predictable time and at a known location. Although typically used to describe reef species, spawning migrations and aggregations are also evident in temperate, pelagic species such as herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) (Sadovy de Mitcheson, 2016). Spawning migrations and aggregations provide potentially lucrative conditions for fishers (Sadovy and Domeier, 2005; Erisman *et al.,* 2012), but targeting such aggregations is likely to reduce the reproductive capacity of a stock, increase the rate of stock reduction, can lead to overfishing and, potentially, near extinction (Hutchings, 1996; Sala *et al.,* 2002; de Mitcheson *et al.,* 2008; de Mitcheson, 2016; Erisman, *et al.* 2012). For example, the short, spatially small spawning season of Atlantic bluefin tuna (*Thunnus thynnus*) coupled with poor management has been cited as a factor in the decline to endangered levels of the species (Collette *et al*., 2011). Fishing which targeted spawning aggregations of large yellow croaker (*Larimichthyes crocea*) in coastal fisheries of East Asia caused the fishery to collapse and the stock failed to recover (Liu and Sadovy de Mitcheson, 2008). Despite this, less than 35% of fish spawning aggregations are protected by any form of management (Erisman *et al.,* 2017).

Proponents of seasonal spawning closures suggest that the benefits are rapid and wide-reaching, benefiting conservation and fisheries management because the reproductive capacity of the stock is protected (Erisman *et al.,* 2017). As with permanent MPAs, spawning closures can be counter-productive if the fishing effort is then displaced either in space or time (Grüss and Robinson, 2015; Clarke *et al*., 2015). Displaced effort has been reported after the Sole (*Solea solea*) fishery closure in the Celtic Sea: daily Sole landings after the fishery reopened were double the baseline level (Sys *et al.,* 2017). Seasonal closures have also been suggested as ineffectual because of late implementation: protecting spawning areas only when a stock is on the point of collapse such as the Cod (*Gadus morhua*) closure in 2001 off the Scottish West Coast (Clarke *et al*., 2015).

The lack of consensus about spawning closures has been accredited to the lack of clear objectives associated with management decisions coupled with only a few empirical studies being available to evaluate the effectiveness of such closures (van Overzee and Rijnsdorp, 2015; Clarke *et al.*, 2015). Case-studies have highlighted the difficulty of implementing spawning closures in multi-species fisheries when there are different spawning timings and patterns between species (Samy-Kamal *et al.,* 2015). In contrast, the seasonal closure of US scallop (*Placopecten magellanicus*) harvests was successfully modified by adjusting the timing and location of closures to maximise the benefit to the associated bycatch of yellowtail flounder (*Limanda ferruginea*) (Smolowitz *et al.,* 2016). Similarly, spawning closures established to protect groundfish in the North West Atlantic also benefited the bycatch of the fishery (O'Boyle, 2011).

1.5 How effective are MPAs?

Despite the potential benefits of MPAs to conservation and fisheries goals, MPA performance thus far is highly variable (Gill *et al*., 2017). The drive to meet MPA targets of size and quantity is apparently to the detriment of the quality of the MPAs (De Santo, 2013; Watson *et al*., 2014; Boonzaier and Pauly, 2016). Failure of MPA performance is attributed to lack of enforcement of NTZs and inadequate financial and staffing commitments (Edgar *et al*., 2014; Marra *et al*., 2016; Gill *et al*., 2017; Worm, 2017). A meta-analysis by Melnychuk *et al*. (2017) revealed that the economic stability of a country is an indicator of their ability to enforce management measures. Additionally, despite the apparent potential of LSMPAs, those that are sited in remote locations may be difficult to monitor and enforce (De Santo, 2013; Wilhelm *et al*., 2014; Jones and De Santo, 2016), although technological advances could be used to counteract this (O'Leary *et al*., 2018). MPA enforcement can be complicated further when MPAs span marine territories (Agardy *et al*., 2011; Friedlander *et al*., 2016) and when mobile stocks cross the boundaries of jurisdictions or of MPAs (Bjørndal and Lindroos, 2004). Even in areas such as the North Sea – where the fishing resources are cooperatively managed via common governance – conflict between user groups, their priorities and their territorial fishing rights remains (Jentoft and Knol, 2014).

In mixed fisheries, traditional approaches of managing fisheries by total allowable catches (TACs) have not always been successful: alternative legislation to manage mixed fisheries includes individual species quotas and discard bans of bycatch species enforced via the landing obligation of the Common Fisheries Policy reform (EU, 2013). However, the species subject to the discard ban can then become a choke species in a mixed fishery (Mortensen *et al.*, 2018), causing the entire fishery to close or individual fishers to stop fishing when the discard quota is reached. Discard bans have been shown to be effective in influencing fishers to reallocate effort (in space, time or by using alternative gear) to avoid the discard-species but this can be at the expense of their revenue (Batsleer *et al*., 2013) and can result in marketable fish being discarded (Poos *et al*., 2010). Large MPAs can encompass multiple species and could potentially mitigate the conflicting priorities of fishers targeting a marketable species whilst preserving a by-catch species. However, the bioeconomic model of Ono *et al.* (2013) found that the introduction of an MPA in a mixed-fishery reduced profit for stakeholders more than TACs or discard bans, which could undermine stakeholder buy-in.

Well-manged MPAs which result in the rebuilding of biomass can yield economic benefits for the local community (Aburto-Oropeza *et al*., 2015). In communities which rely on marine resources for food security and livelihood, stakeholder buy-in of MPAs is likely to be lower (Lundquist and Granek, 2005) and when fisheries with high market value are included in an MPA the MPA effectiveness and ecosystem health are reduced (Ban *et al*., 2017).

MPAs can be considered a top-down measure to impose regulatory control on fishers in comparison to the bottom-up approach of stakeholders (fishers) participating in management decisions, but legal frameworks and governance are only as good as the human behaviour which underpins compliance: small individual decisions with respect to non-compliance can scale up to undermine management systems and sustainability of fisheries (Fulton *et al*., 2010). Successful enforcement of MPAs is thus dependent on co-operation between stakeholders, who may have differing perspectives on MPA targets and regulation such as maintenance of revenue from fisheries and access to recreational activities within the MPA (Ruiz-Frau *et al*., 2015).

1.5.1 Engagement with stakeholders

A working definition of a stakeholder can be considered as a group whose compliance (socially, economically or ecologically) with an MPA is crucial for its successful function (Giakoumi *et al*., 2018). Thus, although scientists will not necessarily be considered stakeholders, they nonetheless hold a vital responsibility in the consultation process about MPA design and outcomes. The stakeholders involved in fisheries management – via permanent MPA or seasonal closures – have a pivotal role in the success of the management strategies employed and stakeholder involvement has been identified as the most important factor in successful MPA implementation (Lundquist and Granek, 2005; Giakoumi *et al*., 2018; Laffoley *et al*., 2019). Realisation of both conservation and fisheries management decisions requires measurable benefits in terms of the resource and to the stakeholders (Erisman *et al.,* 2017) who may have conflicting objectives and priorities (Agardy, 2005; Caveen *et al.,* 2014; Rybicki *et al*., 2018).

Engaging fishers with the policy-making processes can enhance their commitment to - and thus the success - of management measures (Haapasaari *et al*., 2007). Case-studies have been documented in New Zealand and British Columbia groundfish fisheries whereby fishers have actively encouraged spatial management measures designed to promote conservation and habitat preservation (Liu *et al.,* 2018). The collapse of local fisheries also garnered support for spatial closures from reef-fishers in the Philippines (Russ and Alcala, 1996) and fishers in the groundfish fishery of the Georges Bank (Murawski *et al*., 2000). Conversely, conflict can arise if there is perceived social or financial inequity resulting from an MPA (Rees *et al*., 2010). Multiple-stakeholder investments can result in bureaucratic and legislative complexities which complicate the implementation of closed areas, for example in the establishment of a marine conservation zone (MCZ) in UK waters to protect the European native oyster (*Ostrea edulis*) (Allison, 2017). Fishers might oppose MPAs due to lost fishing grounds, both commercial (Di Lorenzo *et al*., 2016) and recreational (McNeill *et al*., 2019). There is also evidence of fishers withdrawing support from fisheries closures due to conflict between stakeholders. For example, reports were made of fishers withdrawing support for the North Sea ‘plaice box’ because of perceived management irregularities while other reports documented stakeholders claiming the plaice box was not fully enforced and therefore ineffectual (Beare *et al.,* 2013).

A recent study has recommended that a solution to balance stakeholder interests is that of ‘pulse-harvesting’ of fish, whereby MPAs are established for up to two years then lifted temporarily for a year to allow episodes of harvesting (Carvalho *et al*., 2019). This could potentially ease fishers’ resistance to MPAs, whilst allowing stock to rebuild and still providing a harvest. However, the simulation at the core of the study was based only on small-scale Pacific fisheries and results have not been extrapolated to encompass mobile species and large-scale fisheries, nor to consider the effect of this model on MPAs which have additional objectives such as habitat conservation.

To resolve potential conflicts, MPAs are increasingly identified and selected in consultation with stakeholders in order to increase MPA effectiveness (Ruiz-Frau *et al*., 2015; Dehans and Fanning, 2018; Hopkins *et al*., 2018). Although such multi-party approaches have been suggested to be less effective at conserving biodiversity due to the imposition of non-conservation focussed targets (Bogaert *et al*., 2009), the degree of cooperation and 'buy-in' from stakeholders are key to the success of an MPA (Rees *et al*., 2010; Edgar *et al*., 2014). A set of reliable models to allow stakeholders to explore MPA management options including MPAs, no take and seasonal closures may support greater participation and engagement from stakeholders who are usually separated from the methods fisheries scientists use. A purpose of the work in this thesis is to make all models' code open-source so that it may be taken on and used by a range of stakeholders.

1.6 Simulations of MPAs and mobile species

The requirement of MPAs to meet ecologically coherent targets necessitates that MPA design moves from a single-species focus to incorporate multiple species, objectives and life-stages (Gaines *et al.,* 2010a, 2010b; Edgar *et al.,* 2014; D'Aloia *et al.,* 2017; Hastings *et al.,* 2017). The complexity of studying these factors is a driver for the field to move from empirical studies towards mathematical modelling of the effectiveness and potential application of MPAs (Grüss *et al*., 2019).

The development of spatial models to inform fisheries' stock assessments and management decisions has increased rapidly in the last two decades (Berger *et al.,*

2017) with research into the design and effectiveness of MPAs being increasingly modelled via mathematical simulations. Cornejo-Donso *et al*. (2017) explain that it is difficult to directly attribute the beneficial effects of an MPA to its establishment because to do so would require many years' worth of data to show comparisons before and after and within and outside the NTZ. Therefore, simulations are an alternative way to compare and assess MPA design and impact, thereby informing more effective protected areas.

Initial simulations of mobile species showed MPAs could benefit yields and population stability, although these benefits reduced with increased mobility (Apostolaki *et al.,* 2002; Le Quesne and Codling, 2009; West *et al.,* 2009) unless large areas of the species' habitat was set aside as an MPA (Beattie *et al.,* 2002; Sumaila, 2002; Le Quesne and Codling, 2009). This was supported by Cabral *et al*. (2019) who showed that optimum MPA size for fisheries was dependent on harvesting cost and market price, with mobile species requiring a larger MPA to maximise the economic potential of a catch. In contradiction to this, the simulation of Grüss *et al*. (2011), demonstrated that yield would decrease with such large MPAs because fish would be inaccessible to fishers.

De Leo and Micheli (2015) developed a stochastic simulation based on that of Hilborn *et al.* (2006) to determine fishery performance with and without an MPA network for species considered to be sedentary and for mobile species. However, although 'sedentary' is clearly defined in the model, the degree of mobility is not similarly described. The findings are that the introduction of a network of MPAs always shows a reduction in benefits to fisheries of mobile adults, although the yields can still exceed those achieved under conventional management and further gains can be made by introducing fewer, larger MPAs. However, because the scale of adult mobility is not described, these findings have limited application to highly mobile populations without further parameterisation; additionally, this is a single-species model which does not address conflicting management objectives of multiple-species within the MPA.

The use of large MPAs as a viable fisheries management option for highly mobile species is explored by Cornejo-Donoso *et al.* (2017). The authors recognise an increased interest in individual based models (IBMs) of MPAs incorporating detailed assumptions about fish movement. They develop a model to test and compare how different movement assumptions within models affect the outcomes with respect to MPA design and predicted benefits. Their simulation indicated that MPAs smaller than 10% of the total area did not confer noticeable benefits to mobile species and larger MPAs were required as movement complexity increased. The authors conclude that simplified movement such as diffusion results in an overestimation of the benefits conferred by an MPA to stock protection and fisheries yields and causes an underestimation in the size of an MPA needed to protect a stock. However, the authors acknowledge that data-poor fisheries may require simple diffusion simulations. Overall, their results corroborate previous findings (Leo *et al.,* 2015; Gaines *et al.,* 2010b) that MPAs of approximately one third of the total area will allow stock to rebuild whilst benefiting fisheries, although they note that the more complex movement scenario indicates that an MPA of half the total area is more realistic.

By contrast, Hastings *et al*. (2017) suggest the biggest challenge facing fisheries managers is dealing with mixed stocks with differing life histories and the bycatch of weak stocks. Their simulation identifies a target species and a bycatch species (the weak stock) which does not interact biologically with the target species. Their assumption is that the management policy is to maximise the target stock whilst maintaining the weak stock. However, the adults in the simulation are non-diffusive:

implicit in this is they do not cross the MPA boundary to the harvested area as a highly mobile species would, thus the effects of spillover are not examined. The authors recognise the assumptions within their model may need to be refined and detail added to models addressing more complex management plans. The generalisations of the model in terms of space and age-structure do still confer guiding principles for managing a two-species, catch/by-catch fishery insofar as the disparity in life-histories between the target and weak stock is shown to be the driver in determining optimum reserve size and/or fishery management. However, the lack of consideration of diffusion of adults presents limitations in the applicability of the model to a fishery with highly mobile species in which there would be movement across the MPA boundary.

D'Aloia *et al*. (2017) recognise that incorporating movement types across life-stages and species is important in developing and utilising MPAs and state that post-settlement movement needs to be considered for the range of species falling within an MPA network. This multi-species, movement-based approach can be considered a similar ethos to the current study. The paper notes that the multiple species being considered in the simulation could either be commercial target species or a group of co-habiting species within that region. The model is not parameterised with life-history traits of specific species but six virtual species are simulated by modelling three different degrees of larval dispersal and two home range sizes - the large home range size being 16 times larger than the small. The model determines connectivity based on larval dispersal then modifies those results by imposing a minimum reserve size determined by the home-range size of the adults. The additional consideration of home-range size of adults altered the optimum network design derived from larval dispersal alone. As an outcome, the optimisation model could identify key reserve sites in the sea-scape of British Columbia, Canada, which would be of benefit to all species. Whilst this differs from the current study in that the model is constructed within a specific location and is not parameterised with specific life-histories, it reinforces the importance of adopting a multi-species, movement-based approach to MPA planning. In recent years, the literature detailing mathematical models of MPA design and efficacy remains dominated by simulations of species which exhibit low mobility (Grüss, 2014; Breen *et al.,* 2015). The simulations described thus far have tackled aspects of MPA effectiveness for mobile stocks, but the life-histories of the species have not been considered in conjunction with their degree of mobility. Discrepancies exist between findings in terms of optimum MPA size for fishery management and stock conservation of mobile species. This thesis seeks to explore the potential fisheries management and conservation benefits of MPAs to diffusive fish species by way of an age-structured, spatio-temporal simulation, parameterised with life history traits representative of commercial or bycatch stocks.

1.7 Thesis rationale

MPAs are a vital component of global marine conservation strategies, and signatory nations to the Convention on Biodiversity Aichi agreement (2010) have made a commitment to their establishment. However, despite considerable debate in the scientific literature, questions still remain as to the most effective design of MPAs and their potential impact. Despite empirical and theoretical studies providing evidence of MPAs benefiting conservation aims and fisheries targets, the literature remains dominated by studies of fish which exhibit low mobility. As such, the model developed in Chapter 2 incorporates the degree of mobility of a species as a model parameter, enabling home-range, moderate and highly diffusive movement to be simulated. This allows theoretical exploration of what contributes to the effectiveness of MPAs for mobile species. In Chapter 3 the model is developed further to explore the potential conflict between conservation and fisheries targets within a mixed-fishery of mobile species. It seeks to answer whether MPAs, effort restrictions or both can meet conservation targets of a bycatch species whilst still providing yield of the harvest species. This enables further consideration of how the model can potentially be used to meet conflicting stakeholder priorities.

Conflicts between theoretical applications and case-studies in the literature warrant further investigation of the relative success of MPAs vs. other management options. In addition to effort control, temporal closures are also utilised as fishery management options. Therefore, in Chapter 4, the model is adapted to compare seasonal spawning closures with permanent, NTZ MPA closures, thereby contributing to better understanding of the impact of species' mobility on fisheries management options. This enables recommendations to be made regarding the use of MPAs both as a management tool in their own right and as part of the suite of potential management options available.

The overall purpose of this PhD thesis is to explore the impacts of marine protected areas on fisheries and conservation targets for mobile species. As such, the final experimental chapter – Chapter 5 – synthesises the model developments from the previous chapters and applies the simulation to a case-study. Using historic stock data to parameterise the model, it is used to investigate whether MPAs would have been a successful management tool to prevent the collapse of North Sea herring (*Clupea harengus*) stocks. This demonstrates how the model can be used to explore the potential effectiveness of MPAs in real-world scenarios of managing mobile fish species.

1.8 Aims and objectives of the thesis

The aim of this thesis is to establish the suitability of MPAs to meet conservation and fisheries outcomes for mobile fish species via the following objectives:

Chapter 2: to develop a spatio-temporal, time-series model which can be adapted to explore the effect of fish species mobility on an MPA, thus:
Chapter 3: to explore the extent to which species mobility affects whether an MPA coupled with effort regulation can simultaneously meet potentially conflicting aims in a two-species fishery;
Chapter 4: to compare the effectiveness of an MPA with seasonal fishery closures to meet fisheries management aims of mobile species;
Chapter 5: to determine whether an MPA would have effectively prevented the past collapse of a fishery of a mobile species.

Chapter 2: Can MPA models be trusted? Temporal resolution affects the apparent performance of marine spatial closures as a fisheries management tool

Abstract: Fisheries are an important global resource, but many fish species are currently over-exploited and require protection. Many fisheries scientists have explored the use of marine spatial closures (marine protected areas, marine reserves, no-take zones, marine conservation zones) as a tool that could protect fish stocks and allow for sustainable fisheries. While some empirical case studies of fishery spatial closures exist, most studies in the literature advocating the use of spatial closures rely on a modelling approach. Most spatial fishery models use a simulation framework based on discrete annual time-steps. Only a few models in the literature use a higher temporal resolution such as weekly or daily time-steps. Here a simple generic simulation of a fishery is used with a spatial closure to demonstrate how the temporal resolution used in the model can have a dramatic effect on the apparent performance and sustainability of the fishery. In particular, it is demonstrated how models based on an annual discrete time-step are likely to over-estimate the efficacy of marine spatial closures in many scenarios, when compared to the same model scenario using a monthly or weekly discrete time-step. Conceptual problems inherent with a fishery model - where key dynamic processes occur at different spatial and temporal scales - are discussed. Suggestions are made for the design of future spatial models and potential implications for fisheries management are discussed.

2.1 Introduction

2.1.1 Spatial closures as a fisheries management tool

Although originally proposed as a conservation measure (Agardy, 1994; Halpern and Warner, 2002; Lubchenco *et al.,* 2003), marine protected areas (MPAs) have long been recognised as providing refuge from fishing, enabling an increase in stock biomass within and beyond MPA boundaries (Polunin and Roberts, 1993; Lester *et al.,* 2009; La Mesa *et al.,* 2011; March *et al.,* 2011). Such benefits have resulted in MPAs being explored as a management tool for commercial species in terms of protection of weak stocks and of maximising yield (Agardy, 1999; 2000; Auster and Shackell, 2000; Halpern and Warner, 2003; Hastings and Botsford, 2003; Abesamis and Russ, 2005; Gaylord *et al.,* 2005; Murawski *et al.,* 2005; Worm *et al.,* 2009; Gaines *et al.,* 2010b). However, consensus has not been reached as to the most effective properties of MPAs in terms of size, formation of MPA networks and management of MPAs (Game *et al.,* 2009; Gaines *et al.,* 2010a; Agardy *et al.,* 2011; McCrea-Strub *et al.,* 2011; Edgar *et al.,* 2014; Breen *et al.,* 2015; Wilhelm *et al.,* 2014; Davies *et al.,* 2017; Gill *et al.,* 2017).

2.1.2. Modelling closed areas in spatial fishery models

Empirical studies of MPA design are becoming more commonplace (in particular, see Edgar *et al.,* 2014; Gill *et al.*, 2017). However, the lack of long-term, before and after-establishment data needed to validate the impacts of an MPA means the use of spatial simulations to explore MPAs as a fisheries management tool has developed rapidly in recent years (Berger *et al.*, 2017; Cornejo-Donso *et al.*, 2017; Hastings *et al.*, 2017).

The impact of closed areas has been modelled with respect to the effect of biomass within a marine protected area (MPA or reserve), and of the yield of a stock beyond the reserve: aims which are often viewed as conflicting. Such models can be considered to fall into two categories: simple models which provide overarching principles to the establishment of MPAs or more complex models which inform MPA design in specific contexts and facilitate quantitative evaluation of MPA implementation (Gerber *et al.,* 2003; Pelletier and Mahévas, 2005). Initial models were spatially homogeneous and, as such, their application to closure policy and implementation was limited. In addition, early MPA implementation was focussed on sedentary populations or those with small home-ranges and the associated simulations of these included little or no adult movement (focussing on dispersal of eggs and larvae) and were largely single-species (Pelletier and Mahévas, 2005; Grüss, 2014; Hastings *et al.,* 2017).

Models were subsequently developed to include spatial factors such as movement of individuals beyond the boundary of the closed area. These spatial models have been used to address the role that space and spatial heterogeneity plays in affecting biological and economic processes, to assess design and siting of closed areas, and to investigate the optimum pattern of closed areas for either conservation and / or maximising yield. These models gave useful results to help determine the impact of a closed area and the associated change in fishing effort or yield, but many were based on a single-cohort approach or differentiated only between larvae and adults. To fully evaluate the impact of a closed area, further refinements were needed in order to account for stage-specific processes such as larval dispersal, recruitment, adult movement, and exploitation. Consequently, age-structured population dynamics also needed to be incorporated into models (St. Mary *et al.,* 2000; Pelletier and Mahévas, 2005). A thorough review of earlier spatial models is provided by Pelletier and Mahévas (2005), whilst comprehensive reviews of later models and the degree of movement represented within them are provided by Grüss (2014) and Breen *et al.,* (2015). A review of the spatial models extended from that published by Pelletier and Mahévas (2005) is provided in Table 2.1. As can be seen, annual time-steps dominate models.

Table 2.1: A review of spatial models, extended from that published by Pelletier and Mahévas (2005). Note, continuous models which do not use explicit time steps have not been included.

Time step	**Spatial assumptions**	**References**
One generation	Uni-directional larval dispersal between patches; sedentary adults	Tuck and Possingham, 2000
One generation	Larval dispersal; adult movement	Grüss *et al.*, 2011
Variable (time for population to increase by factor of 2.71)	Diffusion coefficient representative of sedentary to highly mobile species	Neubert, 2003
Equal to time to progress to next size-class	Sedentary adults; density dependent larval pre-dispersal or post-dispersal.	Gaylord *et al.,* 2005
Annual	Population distributed in two patches linked by non-oriented exchanges of recruited groups.	Beverton and Holt, 1957; Polacheck 1990; DeMartini 1993; Sumaila 1998; 2002
Annual	One-way oriented migrations	Die and Watson, 1992; Christensen and Lassen, 1996
Annual	One-dimensional model (linear coastline). Non-oriented dispersal of larvae and juveniles. 3 species with distinct dispersal.	Attwood and Bennett, 1995
Annual	Larval pool from which there is density-dependent migration between patches	Holland and Brazee, 1996
Annual	Random dispersion of fish	Guénette and Pitcher, 1999

Table 2.1 (cont.): A review of spatial models, extended from that published by Pelletier and Mahevas (2005). Note, continuous models which do not use explicit time steps have not been included.

Annual	Ideal Free Distribution (IFD); habitat heterogeneity.	Lundberg and Jonzen, 1999
Annual	Dispersal between patches.	Walters and Bonfil, 1999
Annual	Random dispersal of organisms.	Walters, 2000
Annual	Sedentary adults.	Nowlis and Roberts, 1999; Nowlis, 2000
Annual	Spatial heterogeneity in productivity and biomass; source sink structure. Directional and non-directional dispersal.	Crowder *et al.,* 2000
Annual	Sedentary adults.	Mangel, 2000
Annual	Juveniles and adults are sedentary and spatially segregated	St Mary *et al.,* 2000
Annual	One-dimensional (linear coastline) Four dispersal schemes for larvae; sedentary adults.	Morgan and Botsford, 2001
Annual	Sedentary adults, widely distributing larvae.	Hastings and Botsford, 2003
Annual	No differentiation between larval and adult movement, determined by normal distribution.	Hilborn *et al.,* 2004
Annual	Local recruitment; adult migration through random diffusion.	Pitchford *et al.*, 2007
Annual	Sedentary adults; larval dispersal determined by normal probability matrix.	McGilliard and Hilborn, 2008
Annual	Two-patch. Age-dependent movement.	Edwards, 2008

Table 2.1 (cont.): A review of spatial models, extended from that published by Pelletier and Mahévas (2005). Note, continuous models which do not use explicit time steps have not been included.

Annual	High larval dispersal; random dispersal of adults. Single and multiple closures. Larval pool and local recruitment.	Le Quesne and Codling, 2009; Le Quesne, 2009
Annual	Single reserve and multiple reserve; Laplacian larval distribution; uniform adult movement.	Moffitt *et al.*, 2009
Annual	Movement of juveniles and large adults.	Miethe *et al.,* 2010
Annual (with two harvesting, spawning and feeding sessions per year)	Movement of three stages between a fished and unfished area.	Miethe *et al.,* 2011
Annual	MPA Network. Larval and adult diffusion determined by Gaussian Kernel.	De Leo and Micheli, 2015
Various (daily to annual)	Sedentary population and home range movements. Recruitment distributed proportional to initial stock sizes.	Meester *et al.,* 2001
Six monthly	Migratory behaviour between spawning / nursery ground and feeding ground with and without MPA.	West *et al.,* 2009
1.5 months	Seasonal size-specific migration rates.	Apostolaki *et al.,* 2002

Table 2.1 (cont.): A review of spatial models, extended from that published by Pelletier and Mahévas (2005). Note, continuous models which do not use explicit time steps have not been included.

Monthly	Seasonal size-specific migration rates.	Sparre and Willman, 1993
Monthly	Oriented seasonal migrations of adults. Juveniles located inshore.	Pelletier and Magal, 1996
Monthly	Seasonally variable random movement rate mimicking observed ontogenic migrations.	Guénette *et al.,* 2000; Martell *et al.,* 2000
Monthly	Sedentary adult; larval dispersal via dispersal matrix.	Smith and Wilen, 2003
Monthly	Local post-larval settlement populations linked through larval dispersal. Closure based on real networks. Movement between reefs based on reef size and distance.	Little *et al.,* 2009
Monthly	Directional migration; no closures.	Poos *et al.,* 2010
Monthly	Adult movement: probability distribution based on tagging data.	Babcock *et al.,* 2012
Monthly	Fished and unfished area. Horizontal and vertical movements of fish.	Duery and Maury, 2013
15 days	Seasonal offshore migration of immature after molt; sedentary adults located offshore.	Walters *et al.,* 1993

Table 2.1 (cont.): A review of spatial models, extended from that published by Pelletier and Mahévas (2005). Note, continuous models which do not use explicit time steps have not been included.

Weekly	Monthly size-specific migration rates.	Rijnsdorp and Pastoors, 1995; Pastoors *et al.,* 2000
Weekly	Spawning ground closures.	Rijnsdorp *et al.,* 2012
5 days	Advection-diffusion. Environmental heterogeneity.	Maury and Gascuel, 1999
5 days	Seasonal oriented migrations and permanent dispersion; uniform recruitment.	Holland, 2000
5 days	1-d advection-diffusion movement. Gaussian recruitment from grid centre.	Holland, 2002
Daily	Diffusion-advection model for larvae; model forced by currents and turbulence.	Stockhausen *et al.,* 2000
Daily	2 patches linked by non-oriented exchanges of recruited groups.	Gendron and Brêthes, 2002
Daily	MPAs sited at fish feeding area / dispersal route.	Moustakas *et al.,* 2006; Moustakas and Silvert, 2011; Silvert and Moustakas, 2011; Moustakas, 2016.
Daily	Movement of larval, juvenile and adult stages within potential sites for MPA network.	D'Aloia *et al.,* 2017
1/5 of a day	Four movement types modelled. Single MPA.	Cornejo-Donoso *et al.,* 2017

The importance of appropriate time-resolution in marine models has already been highlighted in contexts other than fisheries such as habitat preference of highly mobile species (Scales *et al.,* 2016; Fernandez *et al.,* 2017), ocean-circulation dependent dispersal of marine organisms (Putman and He, 2013) and predator-prey interactions (for example: Ratikainen *et al.,* 2007; Embling *et al.,* 2012). The use of models using annual time-steps in population dynamics and fishing effort has been called into question. As a caveat to the findings from their model Guénette and Pitcher (1999) voiced concern that the full impact of an MPA needed a more realistic model in both temporal and spatial terms. Caution has been urged in using over-simplified design rules when planning and implementing MPAs (Pitchford *et al.,* 2007; Edwards *et al*., 2008) because doing so could overestimate the impact of the MPA by masking underlying processes (Stockhausen *et al.,* 2000). Indeed, biological processes are continuous and fishing effort may be seasonal but is not applied via one annual harvest event. Annual level information or equilibrium predictions in models are therefore likely to be inadequate and sub-annual processes could have great significance in determining the effectiveness of MPAs, which will induce changes in the fish biomass and fishery stock at a variety of time scales (Holland, 2002).

2.1.3 Aim and objectives

The aim of this chapter is to develop a spatio-temporal MPA model to examine the effect of temporal resolution on MPA predictions via the following objectives:

1. to compare annual with sub-annual time-steps within the model to examine whether annual time-steps are masking the effects of sub-annual processes in MPA models and their resulting predictions;

2. to represent three levels of species diffusion within the model in order to explore the extent to which mobility of species impacts the efficacy of closures at each temporal resolution.

2.2 Methods

2.2.1 Spatial and temporal structure of simulation model

A deterministic simulation model of a virtual fish stock that is restricted to a finite 1-dimensional closed spatial domain is presented. The model was programmed in R (R Core Team, 2019). The spatial domain consists of 100 cells such that cells 1 and 2 are adjacent, 2 and 3 are adjacent, and so on. The domain is 'looped' in a closed cycle such that cell 100 and cell 1 are assumed to be adjacent (Figure 2.1). This is the same spatial arrangement used by Le Quesne and Codling (2009). The original Le Quesne and Codling (2009) study ran each simulation for a total of 250 years to reach steady state. This was adapted for the current study such that each simulation was run for a burn-in time of 50 years without applying closures or fishing effort to establish initial population numbers and ensure any transient dynamics settled so the subsequent simulations started at equilibrium. Having checked the population dynamics had damped down, the resulting population of each age-class after the burn-in time was equally distributed between each of the 100 cells before the main simulation started. Each simulation was then run for 100 years (at which point the system had reached approximately steady state given the population dynamics model described below).

The previous Le Quesne and Codling (2009) model used annual time-steps to describe movement, mortality events and recruitment. The authors partially tested the effects of ascribing monthly movement and mortality events within the simulation and, as an outcome, recommended that quantitative studies should be conducted to ascertain appropriate temporal resolution in future analyses. As such, the objective of this chapter was to examine the effect of the temporal resolution used in the simulation on the observed results. Hence, the original model was developed and each year was split into either Incr = 1, Incr = 12, or Incr = 48 separate time increments corresponding to an annual, monthly or weekly time step respectively (each 'year' has 48 weeks for numerical convenience). Thus each 100-year simulation consisted of either 100, 1200 or 4800 total time steps depending on the temporal resolution used. Where the simulation used monthly or weekly increments, the population dynamics and movements were split proportionally into these smaller steps (see below). The key point to note is that, when fishing was absent from the system, the simulation produced the same net population and movement dynamics at the end of each annual cycle and over the whole 100-year simulation run, irrespective of the time-step increment used.

2.2.2 Population dynamics

A typical generic gadoid-like stock was simulated using life-history parameters based on a fast-growing species with early maturation such as cod (Table 2.2) (Codling *et al.,* 2004; Le Quesne and Codling, 2009; Pazhayamadom *et al.,* 2013). It is stressed that the intention was not to simulate a specific stock but to use a generic life-history model which could be representative of many 'typical' commercially harvested fish species that are managed using spatial closures. The population dynamics model used is age-structured: juvenile fish enter the population at age 0 (but suffer no mortality and do not move until age 1), while age classes 1-7 are part of the fishery. Fish aged 7 years or older are included together in a 'plus group'; thus, older and larger fish are maintained within the simulation compared to the assumption in the original model (Le Quesne and Codling, 2009) that fish die after reaching the oldest age-class.

Table 2.2: Life-history parameters of the simulated virtual fish stock. The life-history parameters are based on a gadoid-like stock such as cod. Recruits are not included in the simulated life-history dynamics until they reach age 1. All fish that reach 7 years or older are included in a 'plus-group'.

Age (years)	Initial population numbers (000s)	Weight (kg)	Maturity proportion	Catchability (selectivity, q)	Natural mortality (M)
0 (recruits)	4000	0.00	0.00	0.00	0.00
1	1000	0.85	0.00	0.11	0.20
2	700	1.62	0.38	1.37	0.20
3	600	3.18	1.00	1.97	0.20
4	500	5.51	1.00	2.05	0.20
5	200	7.52	1.00	2.39	0.20
6	100	10.14	1.00	2.19	0.20
7+ (plus group)	80	12.62	1.00	2.19	0.20

2.2.2.1 Fishing model

Fishing mortality was applied every time-step, s (i.e.: annually, monthly or weekly). The fishing mortality on age class *a* in *cell c* in time step *s* is given by the following, as per the earlier model used by Le Quesne and Codling (2009):

$$F_{a,c,s} = q_a E_{c,s} \qquad (1)$$

where q_a is the 'catchability' (equivalent to 'selectivity' in this model) of age class *a* and $E_{c,s}$ is the fishing effort rate in cell *c* in time step *s*. The catchability, q_a, was assumed to be fixed for each age class across all time steps in the simulation (Table 2.2). Two different models were considered for how fishing effort was distributed across the spatial domain.

In the 'basic' simulation model, fishing effort was always constant across all cells open to fishing in the spatial domain and across all time steps. Hence, in this basic model all cells open to fishing had the same fishing mortality at age across all time steps in the simulation. In the ‘modified’ simulation model, the basic level of fishing effort per cell was modified relative to the proportion of the total spawning stock biomass (SSB) available to fishing in that cell in the previous time-step. This of course assumes that fishers are able to accurately determine the biomass distribution across space in a dynamic manner. In this variant of the model, the effort in cell *c* in time step *s* was given by:

$$E_{c,s} = \frac{SSB_{c,s-1}}{\frac{(\sum SSB_{c,s-1})}{n}} \qquad (1.1)$$

where $(\sum SSB_{c,s-1})/n$ is the average biomass across all cells open to fishing (*n*) in the previous time-step (cells inside any spatial closure are not included in the calculation). In practice, this allowed the fishers to redistribute effort according to where the highest densities of available fish occurred in the previous time step. Hence, when spatial closures were in place, most of the effort was located on the edge of the closed area (Figure 2.1; ‘fishing the line’) where the highest densities of biomass occurred. Note that in a given time-step, the same total fishing effort was applied to the fishery in both the ‘basic’ and ‘modified’ simulation model, although the distribution of this effort across cells was different.

Spatial closures were modelled in a simple manner by closing a given proportion of cells to fishing: in such cells fishing effort E=0. A range of closure sizes (*p*) was considered from $0\% \leq p \leq 100\%$. For a given closure size, *p*, the closed cells were centred symmetrically on the central point of the recruitment ground (i.e. cell 50: Figure 2.1). Hence if the closure size is $p = 10\%$ then cells 45:54 were closed; if the closure size is $p = 30\%$ then cells 35:64 were closed and so on. It would be straightforward to use the model to explore the design of networks of closed areas rather than the ‘2-patch’ model described above but this has not been attempted in this chapter as the main aim is to illustrate the effect of temporal resolution on the most basic model of a spatial closure.

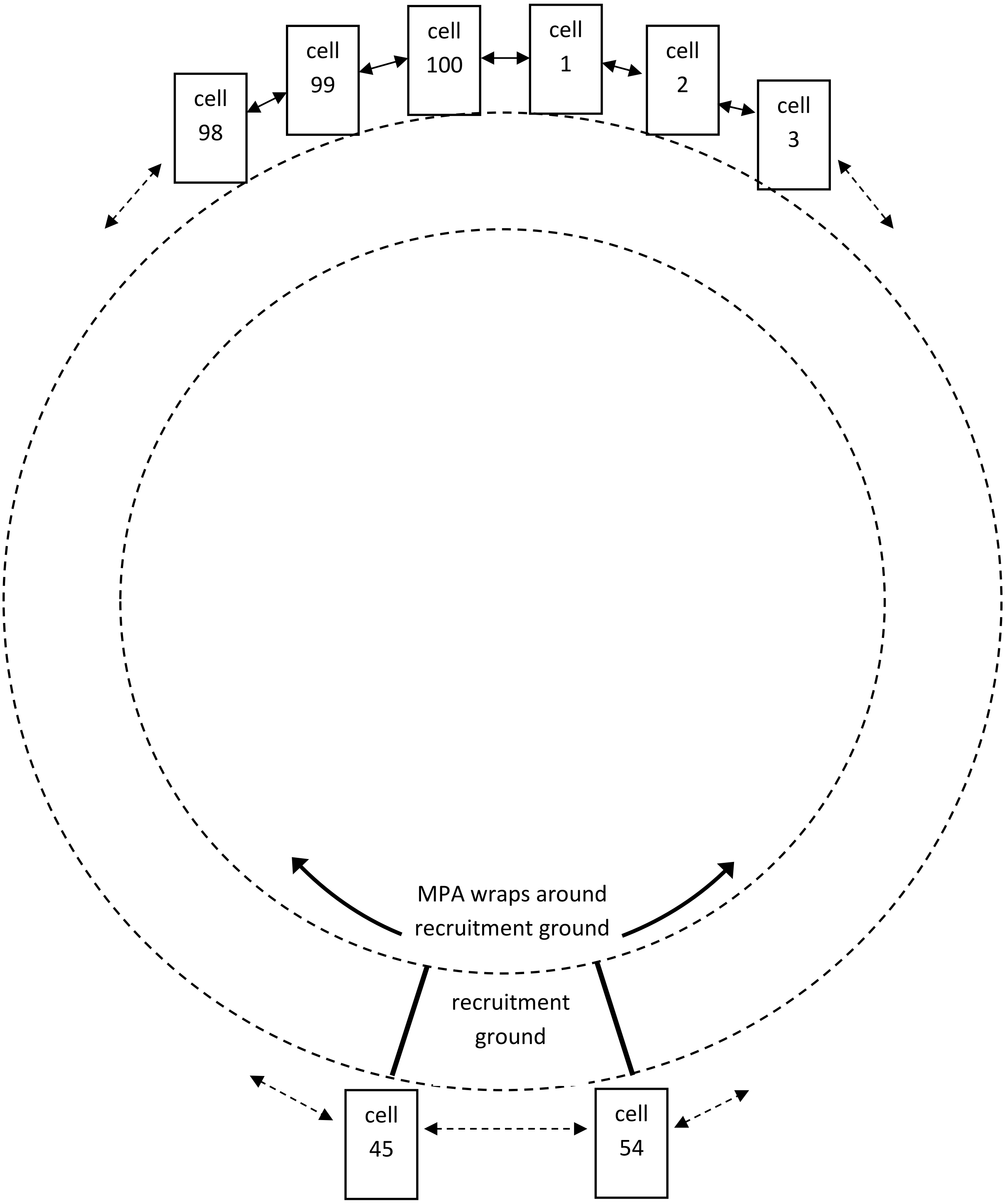

Figure 2.1: Representation of spatial domain of the simulation: the loop represents 100 discrete cells; cell 1 is adjacent to cell 100, the recruitment ground is in the middle 10 cells of the virtual loop and any MPA closures are centred at the middle of the recruitment ground. Fish can move continuously in both directions through the loop of cells.

2.2.2.2 Natural mortality

Natural mortality was age-based and modelled using a standard exponential decay function (Pitcher and Hart,1982), as per the earlier model used by Le Quesne and Codling (2009) and therefore maintained consistency between the two models.

$$N_{a,c,s+1} = N_{a,c,s}e^{-(F_{a,c,s}+M_{a,c,s})/Incr} \qquad (2)$$

where $N_{a,c,s}$ is the population numbers at age class *a* in cell *c* in time step *s*. $F_{a,c,s}$ and $M_{a,c,s}$, are respectively the fishing and natural mortalities on age-class *a* in cell *c* in time step *s*, and *Incr* is the number of time-step increments in a simulation year (the temporal resolution). Note that if fishing mortality is constant across the year then because the exponents in the exponential mortality function are additive, the same total mortality rate is applied in a given cell in a simulation year irrespective of the temporal resolution used. With zero fishing, the final steady state SSB after 100 years was given by SSB = 63,945 tonnes. This figure is hence an upper bound for the maximum long-term SSB when fishing occurred.

2.2.2.3 Yield

Yield in kg per age class *a* in cell *c* was calculated every time step, *s*, using the Baranov (1918) Catch Equation:

$$Y_{a,c,s} = \left(\frac{F_{a,c,s}}{F_{a,c,s}+ M_{a,c,s}}\right) * (N_{a,c,s+1} - N_{a,c,s}) * W_a \qquad (2.2)$$

where W_a is the mass per individual in age class *a* (Table 2.2), $F_{a,c,s}$ is as stated in (1) and $M_{a,c,s}$, *and* $N_{a,c,s}$, are as stated in (2).

At the end of each virtual year the total yields per time-step, s, across all age-classes and cells were calculated to give an annual yield.

2.2.3 Movement model

It was assumed that adult fish moved via random dispersal using a diffusion model. This is the simplest movement model that is typically used in spatial fishery models (Table 2.1); there was no attempt to model annual migrations (e.g. to/from the recruitment ground) nor more complex movement behaviour in this chapter. As in Le Quesne and Codling (2009), the movement of adult fish from each cell was modelled using a one-dimensional 'dispersal kernel', $p(x)$ given by the probability density function for a single step of a one-dimensional diffusion process (Okubo and Levin, 2001; Codling *et al.,* 2008):

$$p(x,s) = \frac{e^{\frac{-x^2}{4Ds}}}{\sqrt{4\pi Ds}} \qquad (3)$$

The probability density function for a single time-step, s, of a one-dimensional diffusion process (Okubo and Levin, 2001; Codling *et al.*, 2008), where x is the unit of distance between cell centres, s is a time step and D is the diffusion coefficient (D=10, 100 or 1000). $p(x,s)$ represents the probability that in a single time step *(s)* an individual from a given cell will have moved to another cell up to 100 distance units away in either direction. Similar to Le Quesne and Codling (2009), as $p(x,s)$ is technically a continuous probability function and x in this model was a discrete variable, at each time-step each discretely determined value of $p(x,s)$ was rescaled such that the total sum over all 100 cells was equal to 1 and it is hence a true probability distribution. In the simulations, the time step, s was determined by the time-increment being used in the model: s = 1/Incr (i.e. s = 1/48 for weekly time-steps, s = 1/12 for monthly time-steps, and s = 1 for annual time steps).

Figure 2.2 illustrates how the same dispersal profile was obtained for a fixed value of *D*, irrespective of the time-step increment used, if no fishing is present in the system. Therefore, any differences between models with different temporal resolutions were due to different fish distributions attributed to the different movement profiles.

The original Le Quesne and Codling (2009) values of D were D = 0.001, D = 0.01, D = 0.1, and D = 1.0. Although representative of low to high mobility (by virtue of the fact each is an order of magnitude greater than the previous value), integrating $p(x, s)$ (equation 3, above) with respect to these values and also D = 10, D = 100 and D = 1000 indicated that the latter three values better represented low, moderate and high degrees of mobility with respect to the virtual domain. Therefore, to represent qualitatively different types of movement behaviour, the values D = 10, D = 100 and D = 1000 were used for the diffusion coefficient. It should be stressed that these values have no real quantitative meaning beyond the simulation. Instead, the values should be interpreted in a qualitative sense: D = 10 represents low movement and dispersal between cells by adults, D = 100 represents moderate movement, and D = 1000 represents high movement. Figure 2.2 illustrates how the final steady state spatial distribution changes with different D. With D = 10 there is a clear spatial structure with the SSB distribution closely structured around the centre of the recruitment ground, while with D = 1000 there is almost complete mixing and a homogenous SSB distribution across space (D=100 gives a result in-between these extremes).

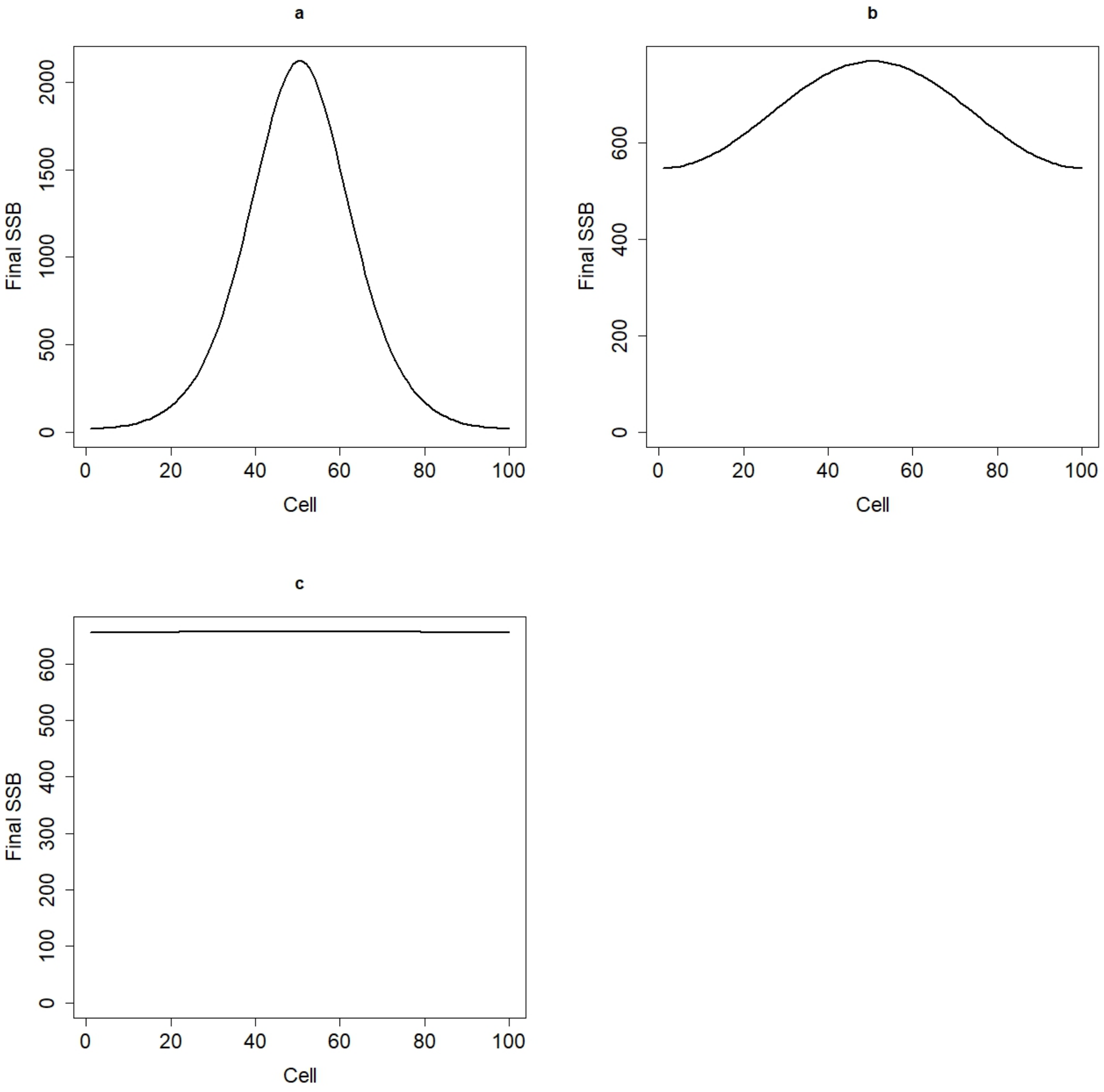

Figure 2.2: Final SSB distribution v cell number after 100 years (steady-state). All adults in the stock contribute to the SSB but recruits enter the population in a small recruitment ground situated in cells 46:55. The spatial domain is looped such that cell 1 and cell 100 are adjacent. The simulation is run for 100 years and using a time-step increment of 1 unit (100 annual steps; solid line), 12 units (1200 monthly steps; dashed line), and 48 units (4800 weekly steps; dotted lines) although note that the individual lines are not distinguishable because, without fishing, the final spatial distributions are the same. The final SSB in all cases is 65,619 tonnes. a) D = 10 (low adult mobility); b) D = 100 (medium adult mobility), c) D = 1000 (high adult mobility).

2.2.4 Recruitment

The descriptors of recruitment in the Le Quesne and Codling (2009) simulation were based on an egg-production-recruitment function. For the purposes of the current chapter, this was changed and recruitment was modelled using a standard Ricker (1954) SSB-recruitment relationship which always occurred at the end of the year. This change was made in order that the model could be readily adapted in the future to represent stocks with different stock recruitment relationships (SRR) by altering the Ricker parameters. The total number of recruits (age 0 fish) in thousands is given by:

$$R = \alpha S e^{-\beta S}, \qquad (4)$$

where S is the total SSB (tonnes) across all age classes and cells and α = 0.96031 and β = 0.00005 are Ricker parameters that represent the fecundity of a typical gadoid-like species (Kelly *et al.*, 2006). Although all spawning adults contributed to the SSB, an important assumption in the model was that juvenile fish (‘recruits’) were assumed to initially be located in cells 45:54 in the spatial domain – the recruitment ground (Figure 2.1). The recruits stayed in this recruitment ground until they reached age 1 at which point they suffered mortality and underwent movement as with all the adult age classes.

2.2.5 Simulations

Fishing effort was modelled in two ways. In simulation 1 (which was not modelled in the original Le Quesne and Codling (2009) study) effort was modelled as a rate E per cell open to fishing. Hence, in these models, there was no redistribution of lost effort from a closed cell to a cell open to fishing as the closure size increased – in effect this effort is ‘lost’. Many fisheries closures are enforced in parallel with a decrease in effort, so this was not unrealistic and allowed effort redistribution to be controlled in the study. In simulation 2 (and as per the original Le Quesne and Codling (2009) study) redistribution of effort was modelled proportional to biomass. In these models, nominal effort rate E per cell open to fishing was rescaled according to the biomass in each cell. Thus, the resultant effort could be described as density-dependent fishing effort. For each of the fishing models (simulation model 1 – constant fishing effort; simulation model 2 – density dependent fishing effort) simulations were run across a range of parameters. For each combination of dispersal, D (D = 10, D = 100, D = 1000) and temporal increments, Incr (Incr = 1, annual; Incr = 12, monthly; Incr = 48, weekly), simulations were run for a range of values of Effort ($0 \leq E \leq 4$, in steps of 0.1) and percentage spatial closure ($0\% \leq p \leq 100\%$, in steps of 5%). The maximum total yield across all simulations was 490,210 tonnes and the maximum final SSB (corresponding to zero fishing) was 65,619 tonnes.

2.3 Results

The maximum yield at D=1, Incr=1 and the maximum SSB of the unfished population were given a value of 1 so all results had a value between 0 and 1. The results from the simulations run with the other values of D and of Incr were then scaled between 0 and 1 using the D=1, Incr=1 and unfished SSB results as a baseline. This enabled heat maps to be constructed to show direct comparison between each set of results: any given value on each heat map corresponds to the same yield or SSB. In practice, unfished SSB would not be a typical management reference point but the purpose of these initial models was simply to determine the effect of temporal resolution within a simulation on the predictive capacity of the model, therefore unfished SSB was selected as the reference point to allow comparison between temporal resolutions. This is discussed further in model developments.

2.3.1 Results: simulations without fishing

With no fishing or closure, all increments give the same approximate spatial distribution of SSB after the simulation was run for the burn-in period of 50 years then an additional 100 years (see Figures 2.2a – 2.2c). As can be seen in Figures 2.2a – 2.2c, a larger value of the diffusion coefficient, D, leads to increased mixing in the population and a flatter profile of the final distribution of SSB when closures and fishing were not in place.

2.3.2 Effect of adult movement rate

The heat maps in Figure 2.3 illustrate the effects of increasing the value of the diffusion coefficient, D, in simulation 1 – constant effort per cell. Taking annual increments as the baseline from which to compare the effect of D (Figures 2.3a, 2.3d and 2.3g), it can be seen that as adult movement (D) increases, the yield without closures can be met with larger closures and higher effort. For example, when D=10 (Figure 2.3a), the yield without closures can only be met if closures are 5 – 10% of the area and effort per cell is 1.0 or greater. When D increases to 100 (Figure 2.3d) the yield without closures can be met if closure sizes increase to 25 – 35% coupled with effort per cell of 2.0 or greater. Finally, at the highest rate of diffusion (D=1000, Figure 2.3g), closure sizes of 55 – 65% coupled with effort per cell of 2.0 or greater will facilitate the same yield as that without closures. The pattern of higher D enabling larger closures to be introduced is also evident in the results from simulation 2 – density-dependent effort (Figure 2.5). The proportional relationship between effort and SSB is reflected in the fact that the combinations of closure and effort which can produce the highest yield with constant effort per cell (Figure 2.3) are not evident and one closure size is effective across all efforts.

The SSB heatmaps (Figures 2.4 and 2.6) show that as diffusion increases, and individuals cross the boundary of the closure more frequently, increasingly large closures are required for the unfished SSB to be maintained. For example, at D=1, with an annual time-step increment, with constant or density-dependent effort (Figures 2.4a and 2.6a respectively), closures of 40% are required to maintain unfished SSB but when adult movement increases to D=100 (Figures 2.4b and 2.6b) and to D=1000 (Figures 2.4c and 2.6c) closures of almost 100% are required to maintain SSB. The heat maps of SSB under density-dependent effort (Figures 2.6a–i) reflect, as they did for the yield, the proportional relationship between effort and SSB.

2.3.3 Effect of temporal resolution

Across all values of D, at constant and density-dependent effort, increasing the temporal resolution from annual to monthly recruitment and fishing effectively shifts the heat maps to the right. That is, at all values of D and increased temporal resolution, closure sizes need to increase from those at Incr =1 to reach the highest yield and to maintain unfished SSB. Of particular note is the impact of this on the SSB of a high-dispersal species. With an annual increment (Figures 2.4g and 2.6g) the simulation suggests that 80% of a highly mobile stock's SSB can be preserved at unfished levels with large closures of 80% or more. When the temporal increments of movement and fishing are increased to monthly (Figures 2.4h and 2.6h) SSB is driven to zero except at nearly 100% closures. However, a further increase in temporal resolution from monthly to weekly shows little further change in results in this and other scenarios. For example, at D=10 when Incr increases from annual (Incr = 1, Figures 2.4a and 2.6a) to monthly (Incr = 12, Figures 2.4b and 2.6b), closures needed to maintain unfished SSB increase from 40% - 60%. A further increase to weekly increments (Incr = 48, Figures 2.4c and 2.6c) shows very little change in closures required.

The same pattern is true of the yield. For example, at constant effort, D=1000, and an annual time-step (Incr = 1, Figure 2.3g), low effort with closures of 40% or less, or higher efforts with bigger closures attain highest yield. Changing the time-step to monthly increments (Incr = 12, Figure 2.3h) gives a greater variety of combinations of effort and closure to attain highest yield, although closure must increase for any given effort. Further increasing temporal resolution to weekly time-steps (Incr = 48, Figure 2.3i) makes little further change in terms of effort or closure sizes needed to reach highest yield. The equivalent simulations under density-dependent effort (Figures 2.5g–i) illustrate that an annual increment suggests highest yield can be reached with closures of 60- 70% (Figure 2.5g) but monthly and weekly increments (Figures 2.5h and 2.5i respectively) show maximum yield cannot be reached.

In summary, these results demonstrate that more extensive closures are required to preserve unfished SSB of species with higher levels of diffusion, yet the maximum yield of a highly diffusive species can still be reached when larger closures are introduced. The temporal resolution of the model affects the outcome of the predicted SSB and yield, with annual time-steps of what are sub-annual events (movement and fishing) considerably overestimating the protection afforded by an MPA compared to monthly time-steps; however, increasing the time-steps to daily increments gives no further benefit to the results.

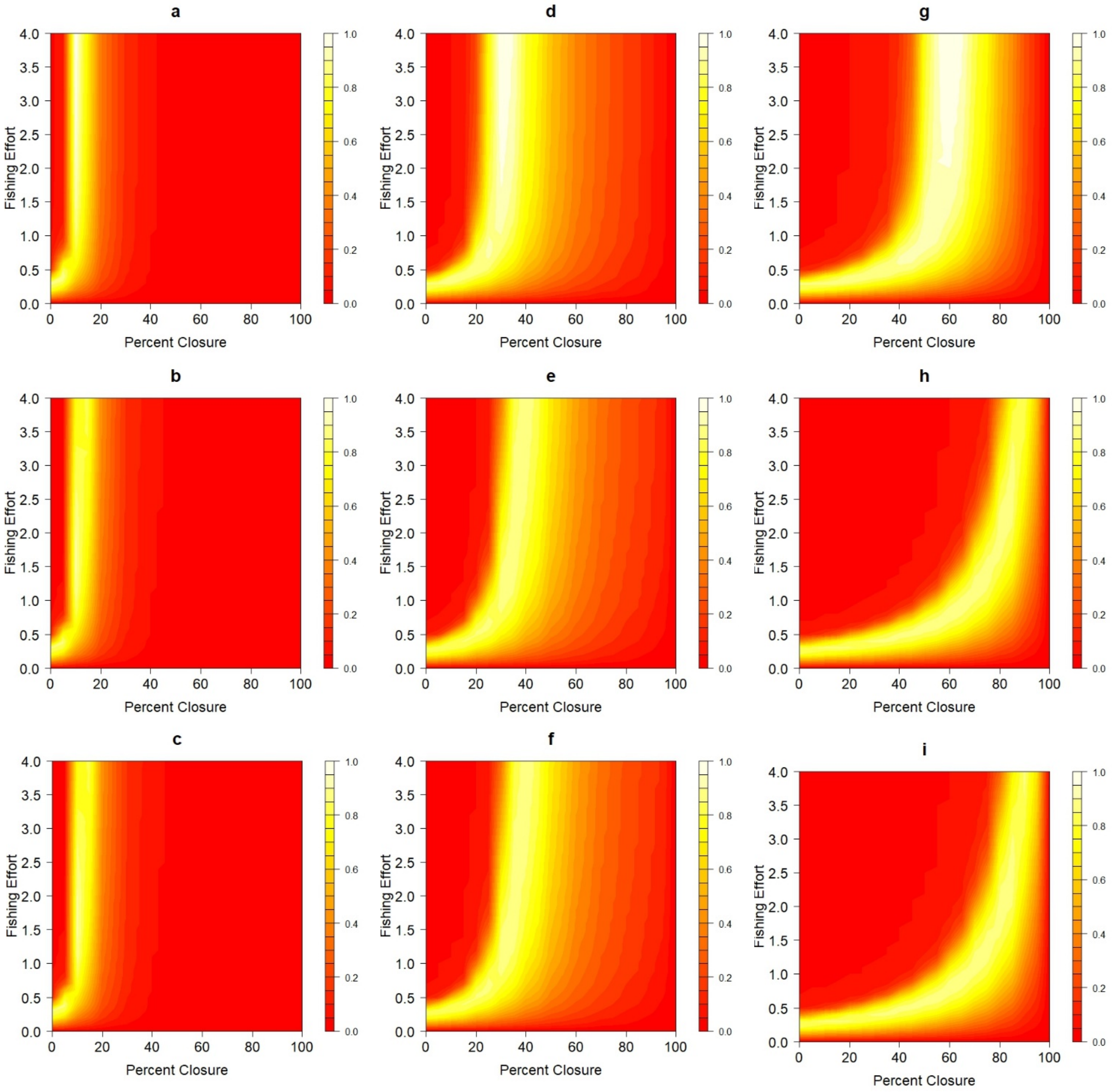

Figure 2.3: Heat maps representing the extent to which the highest yield (scale of 1) of the species modelled using annual time-steps has been met when constant fishing effort per cell is applied at the following levels of adult movement (D) and time-steps (Incr). Figures 3a-c. D=10, a) Incr=1, b) Incr=12, c) Incr=48. Figures 3-f. D=100, d) Incr=1, e) Incr=12, f) Incr=48. Figures 3-i. D=1000, g) Incr=1, h) Incr=12, i) Incr=48.

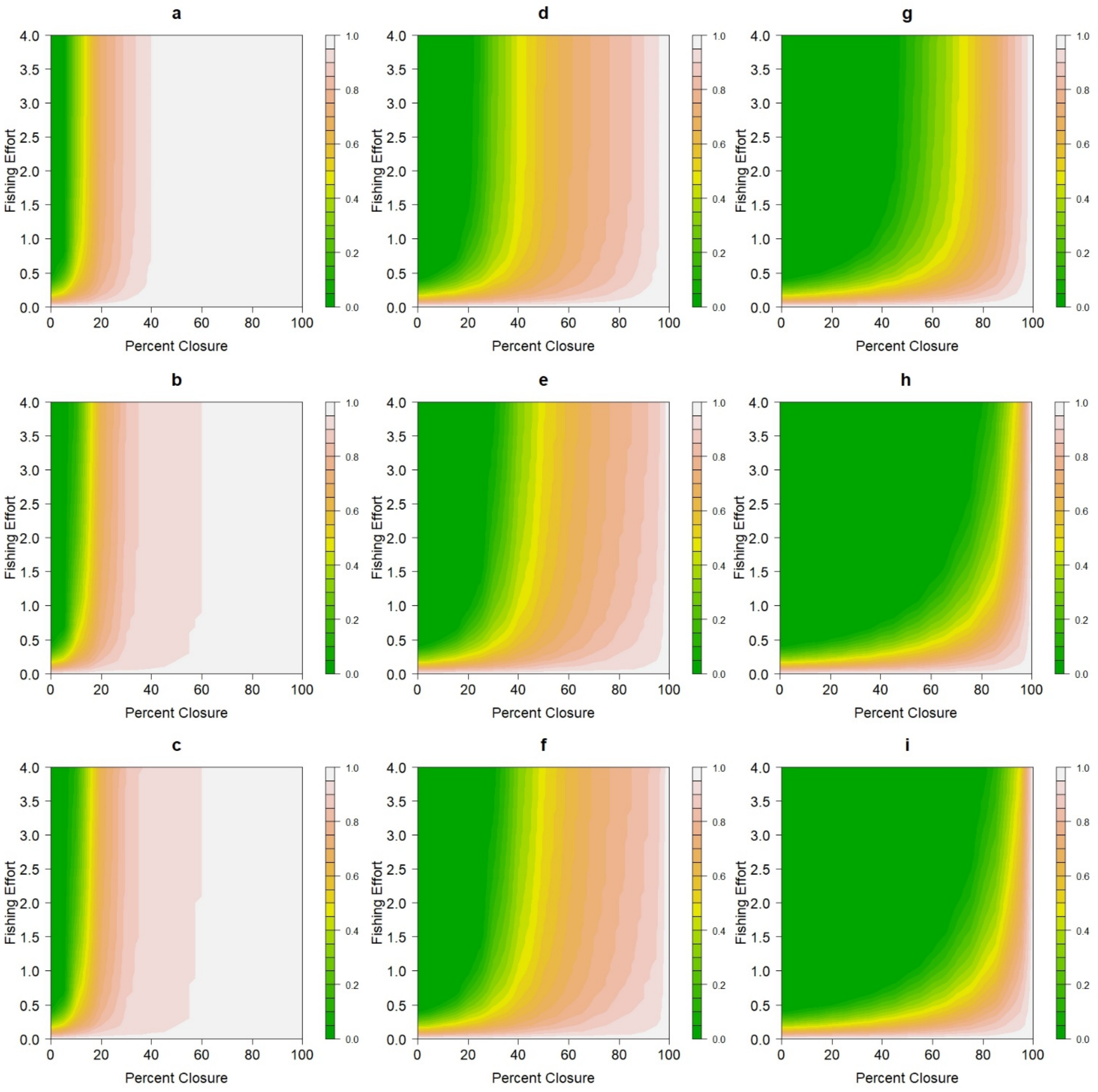

Figure 2.4: Heat maps representing the extent to which the maximum unfished SSB (scale of 1) of the population modelled using annual time-steps has been met when constant fishing effort per cell is applied at the following levels of adult movement (D) and time-steps (Incr). Figures 4a-c. D=10, a) Incr=1, b) Incr=12, c) Incr=48. Figures 4d-f. D=100, d) Incr=1, e) Incr=12, f) Incr=48. Figures 4g-i. D=1000, g) Incr=1, h) Incr=12, i) Incr=48.

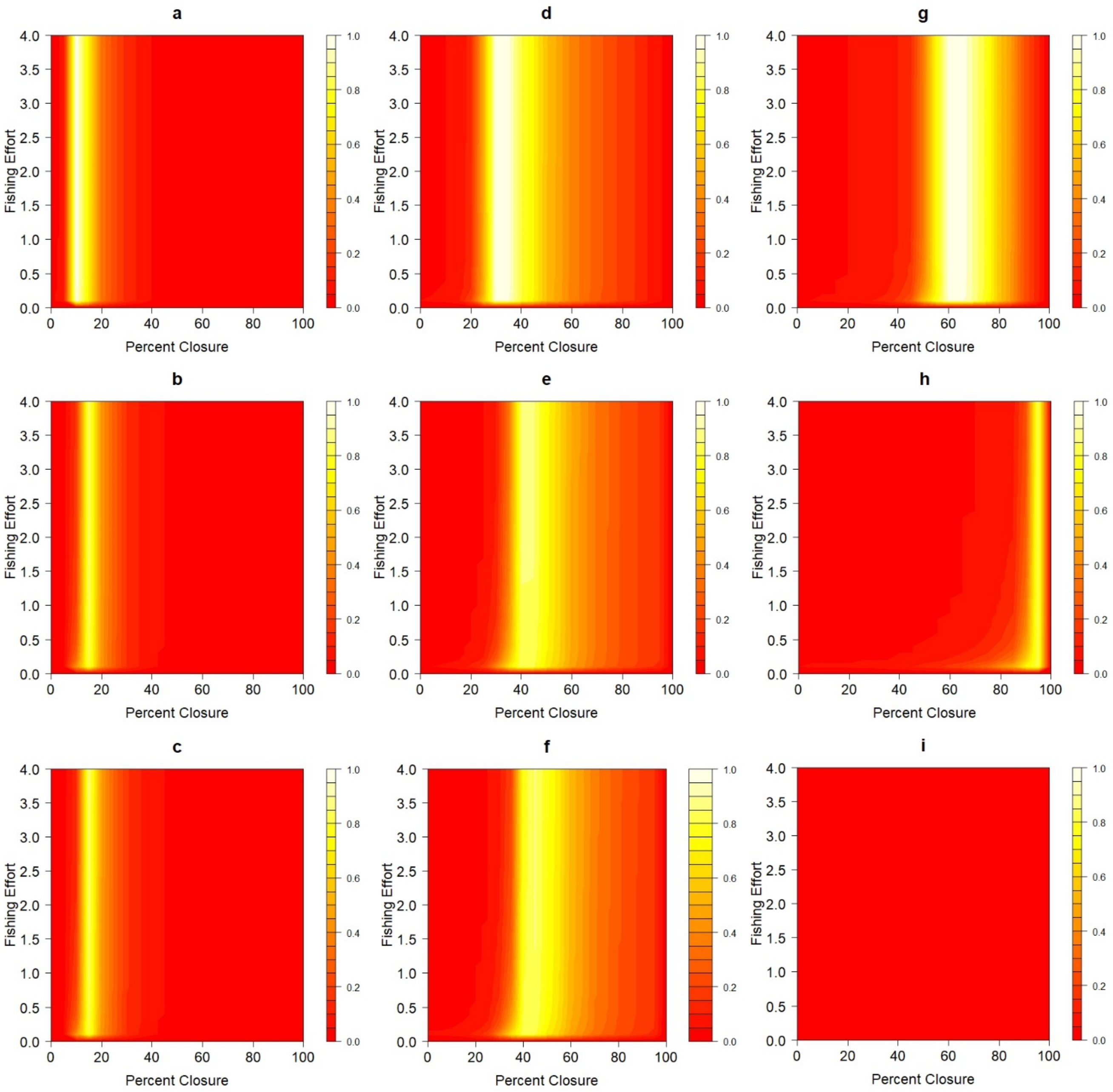

Figure 2.5: Heat maps representing the extent to which the highest yield (scale of 1) of the species modelled using annual time-steps has been met when density-dependent fishing effort is applied at the following levels of adult movement (D) and time-steps (Incr). Figures 5a-c. D=10, a) Incr=1, b) Incr=12, c) Incr=48. Figures 5d-f. D=100, d) Incr=1, e) Incr=12, f) Incr=48. Figures 5g-i. D=1000, g) Incr=1, h) Incr=12, i) Incr=48.

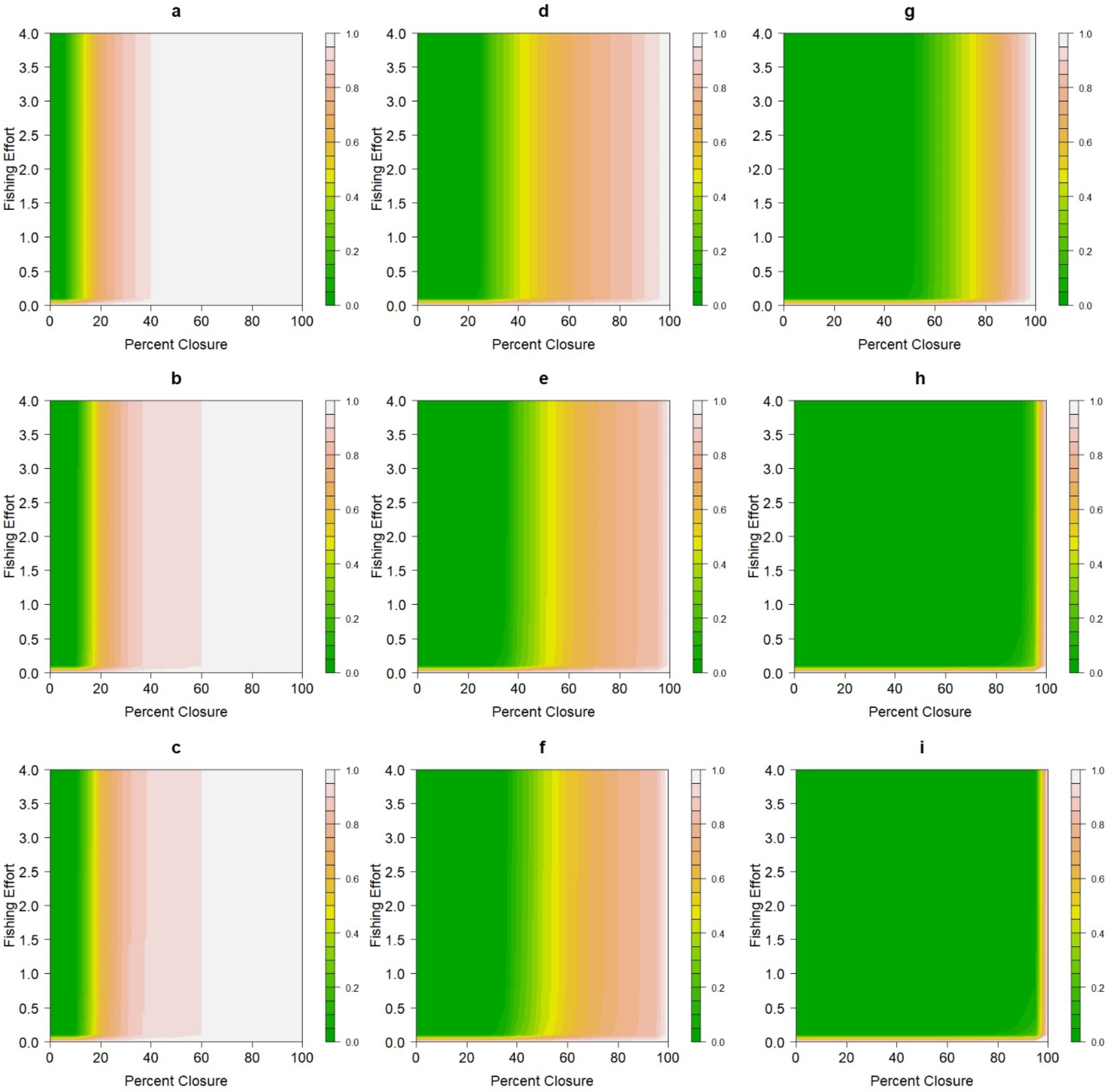

Figure 2.6: Heat maps representing the extent to which the maximum unfished SSB (scale of 1) of the population modelled using annual time-steps has been met when density-dependent fishing effort is applied at the following levels of adult movement (D) and time-steps (Incr). Figures 6a-c. D=10, a) Incr=1, b) Incr=12, c) Incr=48. Figures 6d-f. D=100, d) Incr=1, e) Incr=12, f) Incr=48. Figures 6g-i. D=1000, g) Incr=1, h) Incr=12, i) Incr=48.

2.4 Discussion

Simulations of MPA design have increased rapidly in recent years, proving useful particularly when there is a lack of long-term field data to assess the impacts of MPAs (Berger *et al.,* 2017; Cornejo-Donso *et al.,* 2017; Hastings *et al.,* 2017). Biological processes are necessarily simplified in deterministic simulations but, for some time, caution has been urged against oversimplification in simulations of what are continuous or seasonal processes due to the potential for this leading to misplaced trust in subsequent MPA design (Stockhausen *et al.,* 2000; Pitchford *et al.,* 2007; Edwards, 2008; Cornejo-Donoso *et al.,* 2017).

As reflected in the summary by Pelletier and Mahévas (2005) and the extension of this presented in Table 2.1, annual time-steps within simulations are still common-place. The results of this chapter indicate that reducing biological processes to annual events in simulations can, as cautioned, overestimate the benefits of an MPA. Predictions based on annual time-steps can underestimate the degree of protection required protect the SSB of a species.

As highlighted by Grüss (2014) and Breen *et al.,* (2015), MPA simulations remain dominated by home-range species which exhibit low degrees of movement. Results of the current simulation agree with previous simulations (Moustakas, 2016; Cornejo-Donoso *et al.,* 2017) and show that a species with a higher dispersal rate will require larger MPAs to afford protection. Additionally, the results show that using annual increments in a simulation of a highly mobile species could potentially underestimate the protection of the MPA to such a degree that the unfished SSB could be reduced to zero.

The proposed benefits of networks of MPAs to provide connected refuges from fishing is well documented (for example: Gaines *et al.,* 2010b; Moustakas and Silvert, 2011;

Edgar *et al.,* 2014), particularly for highly mobile and migratory species (Hays *et al.,* 2014; Davidson and Dulvy, 2017). However, the results of this chapter indicate that MPA network design should incorporate realistic temporal resolution of movement in order to more accurately assess the mortality of mobile species moving between closed areas in a network.

In terms of the yield, the simulation - using annual time-steps - indicates that yield of mobile species can be maintained with larger closures. This is as would be expected and in line with previous models (Le Quesne and Codling, 2009; Gaines *et al.,* 2010a; Moustakas, 2016; Cornejo-Donoso *et al.,* 2017), because the more frequently the MPA boundary is crossed, the more frequently an organism is exposed to fishing. However, decreasing the temporal resolution of the simulation from weekly to monthly produces a lower yield for a species with low diffusion. As diffusion increases, using monthly time-steps of movement and fishing decreases the effort / closure management options available (when constant effort is assumed) and requires larger closures (assuming density-dependent effort) to obtain maximum yield. This effect is amplified with the highest dispersal rate, whereby highest yield cannot be reached. Such underestimation of yield resulting from a low temporal resolution, annual model could have negative economic impacts on fishers, resulting in a reduced incentive to 'buy-in' to an MPA, thus resulting in a loss of conservation and fisheries benefits stemming from the MPA (Erisman *et al.,* 2017; Liu *et al.,* 2018).

Having explored monthly vs. annual temporal resolution in an MPA simulation, Le Quesne and Codling (2009) consequently recommended that further analysis was needed to ascertain appropriate temporal resolution in simulations of MPA design. The current study has developed this further by simulating annual recruitment coupled with annual, monthly and weekly increments in fishing and movement. As discussed above, when temporal resolution is increased from annual to monthly movement and fishing, notable changes are seen in the closure sizes and (in the case of the constant effort simulation) the closure / effort management options available to maintain unfished SSB or reach highest yield. However, the results indicate that minimal benefit is accrued from increasing the temporal resolution of the model: little further change is seen in effort regulation, closures or both when weekly time-steps underpin the simulation. The additional time taken to run the weekly time-step simulation (more than twice the time of the monthly simulations) was disproportionate to the benefits offered from the resulting data. Consequently, the time-step used in the model for the rest of this thesis is monthly and will thus forward be represented by t, rather than the variable s, used in this chapter.

2.4.1 Model Assumptions

The model in this chapter is not proposed to be any more realistic than prior simulations in biological, species-based terms and there are obvious model developments which could be implemented. The spatial domain of the model could be adapted further: a non-looping model (whereby there is less movement across the MPA boundary) would be appropriate to represent a 2D coastline. The model is purposely generalised to explore the underlying assumptions of the effects of the degree of movement and the time-step resolution within the model. As such, the life-history parameters within the model are not intended to represent a particular species; to apply the model to ‘real world’ scenarios one would need to use realistic life-history parameters and scale the extent of movement appropriately to the spatial domain to represent, for example, home-range, mobile and highly mobile species. Unfished SSB was taken as the reference point for comparison between the different simulations in the current chapter and, although the results would not qualitatively change when applied to a management reference point, future model developments should use a suitable management reference point for comparison such as 0.5 virgin SSB or B_{LIM} of a given species.

To make the model more specific, it would also be beneficial to represent non-diffusive movement such as migratory movement to spawning grounds or leptokurtic movement. However, the results demonstrate that changing the arbitrary model structure assumptions about the extent of movement and temporal resolution gives very different results in terms of size of spatial closures, fishing effort and resultant SSB and yield. It therefore highlights that consideration should be given to the temporal resolution of processes and degree of diffusion of species within any simulation of MPA design.

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Relative mobility determines the efficacy of MPAs in a two species mixed fishery with conflicting management objectives

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ABSTRACT

Marine Protected Areas (MPAs) have been used to protect species in need of conservation and as a fisheries management tool. It has been suggested MPAs can benefit mobile stocks by protecting spawning grounds whilst also allowing yields to be maintained as mature fish move out of the protected areas. However, the robustness of this claim in mixed species fisheries has yet to be established. We use a simulation model to explore the efficacy of spatial closures and effort regulation when other forms of fishery control (e.g., Total Allowable Catches) are absent or non-enforced as ways of addressing management objectives that are difficult to reconcile due to the contrasting life-histories of a target and a bycatch, conservation species in a two-species fishery. The mobility of each stock in such a fishery affects the benefits conferred by an MPA. The differing management objectives of the two species can be partially met by effort regulations or closures when the species exhibit similar mobility. However, a more mobile conservation species prevents both sets of aims being met by either management tool. We use simulations to explore how spatial closures and effort regulation can be used to seek compromise between stakeholders when the mobility of one stock prevents conflicting management objectives to be fully met. Our results demonstrate that stock mobility is a key factor in considering whether an MPA can meet conflicting aims in a multispecies fishery compromised of stocks with differing life histories and mobilities.

1. Introduction

Declines in abundance in commercial fisheries are of environmental and economic concern: over 30% of global marine fish stocks are not within biologically sustainable limits (UN, 2016). Application of single species quota management of fisheries coupled with refined effort control since 2002 is resulting in successful rebuilding of some fish stocks in north European waters (Fernandes and Cook, 2013). For example, North Sea cod (*Gadus morhua*) and flatfish have shown an increase in spawning stock biomass (SSB) since 2004 (Kirkegaard, 2015; ICES, 2016a). Management objectives of a target species and a conservation species are often in conflict within the same fishery due to the mixed nature of many fisheries, (Vinther et al., 2004; Kraak et al., 2008; Mackinson et al., 2009; Da Rocha et al., 2012; Hastings et al., 2017). For example, increased effort to catch more recovered stocks such as cod and horse mackerel *(Trachurus trachurus*) can lead to increased bycatch of species that are either not rebuilding as rapidly or are in danger of collapse (e.g., seabass *Dicentrarchus labrax*; ICES, 2016b[1]). Managing multispecies fisheries with single-species biological reference points (BRPs) can therefore worsen bycatch problems for those conservation species (Larkin, 1977; Branch et al., 2006), meaning it may not be possible to meet both conservation and yield objectives within the same fishery (Jensen, 1991; Baudron et al., 2010; Poos et al., 2010; Ulrich et al., 2011; Rijnsdorp et al., 2012; D'Aloia et al., 2017).

Stakeholders associated with a mixed fishery will have differing priorities and perspectives on how to manage their resource (Caddy, 1999; Agardy, 2005; Pascoe et al., 2009; Pulina and Meleddu, 2012). Maximising the yield of the target species is likely to cause further depletion of non-target species which may need to be conserved (Jensen, 1991; Hilborn et al., 2004; Kraak et al., 2008; Fazli et al., 2009), as is evident in high bycatch of seabass or blonde ray (*Raja brachyura*) in otherwise sustainable gill or long line cod fisheries in the southern North Sea (Gibson et al., 2006; Quirijns, 2014;Heath et al., 2015). However, restricting fishing effort to protect non-target species

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[1] http://www.trawlerphotos.co.uk/forums/showthread.php?11484-Channel-fishing-effort-threat-to-bass-stocks.

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0165-7836/

in a mixed fishery can meet conservation objectives but can also lead to loss of substantial economic benefits due to the target species being underexploited (Baum et al., 2003; Rijnsdorp et al., 2012). For example, the landing obligation introduced via the new EU Common Fisheries Policy (2013) to mitigate impacts on species most in need of protection ascribed small catch limits to vulnerable species, resulting in these becoming “choke” species in mixed fisheries (Schrope, 2010), potentially leading to loss of revenue to fishers as they fill that vulnerable species quota (Catchpole, et al., 2017; Guillen et al., 2018).

One way of addressing these conflicts is the designation of spatial closures in the form of Marine Protected Areas (MPAs) or No Take Zones (NTZs). MPAs have been advocated as feasible fisheries management tools for overexploited and poorly managed stocks (e.g., Allison et al., 1998; Edgar et al., 2014; Davies et al., 2017). However, conservation benefits of MPAs have been demonstrated to be highly variable, due to constraints in financial and staff investment (Gill et al., 2017) and trade-offs can also be a consideration when siting MPAs: for example, the potential reduction in catch of sole (*Solea solea*) to the inshore fleet following introduction of UK MPAs (Lieberknecht et al., 2011).

It has been suggested that the movement behaviour of the different species must be taken into account to better predict the likely success of using MPAs in mixed species fisheries (Le Quesne and Codling, 2009; D’Aloia et al., 2017), and that spatial closures alone will not meet fisheries and conservation objectives, but a combination of management tools is needed (Worm et al., 2009). However, it remains unclear whether spatial closures and effort management can be used simultaneously to manage multiple mobile species in a mixed fishery.

Spatially explicit mathematical models have rapidly increased in the last two decades as a way to inform fisheries’ stock assessments and management strategies in the absence of clear empirical evidence (Berger et al., 2017), although the literature remains dominated by simulations of the effects of MPAs for species with low mobility or more mobile species from tropical areas (see Grüss, 2014; Breen et al., 2015 for comprehensive literature reviews). We use a deterministic, age-structured, spatial simulation model to examine the combined efficacy of MPAs and fishing effort regulation as management tools in a mixed fishery of two species with differing life histories and potentially conflicting management objectives: ensuring sustainable exploitation of a target species coupled with maintenance of SSB of a non-target (bycatch) species requiring conservation. The target species management objective is to fish at maximum sustainable yield (MSY); the objective for the conservation species is to maximise SSB. We specifically explore how different movement (i.e., diffusion) rates for each species affect the performance of the management measures. We ask to what extent conservation and fisheries objectives can be met concurrently for mobile stocks and explore the compromises needed to obtain the optimum management policies for each.

2. Methods

To explore the extent to which the management aims of two mobile species – a target and a conservation species - with contrasting life-histories and management objectives can be met simultaneously, we developed an age-structured, spatio-temporal simulation in which fishing effort and closures could be allocated. The simulation was programmed in R (R Core Team, 2019).

2.1. Spatial domain

The spatial domain (Fig. 1) is the same as that used by Le Quesne and Codling (2009) and can be considered an extension of their model: it is one-dimensional, divided into 100 discrete cells arranged in a loop so cell 1 is adjacent to cell 100. Fish can move continuously in both directions through all cells. The simulation has one designated No Take MPA forming between 0 to 100% of the total area; the spatial closures (size p%) are modelled by closing the middle p cells to fishing. In all simulations we assume there is a juvenile recruitment ground, defined as the middle 10 cells of the virtual space. Therefore, apart from very small closures ($p < 10\%$), the MPA always covers the recruitment ground, which is always situated in as far away as possible from cells open to fishing. The sub-models for fishing, mortality, and adult and juvenile movement (described below) are applied monthly to each of the 100 cells; a recruitment sub-model is applied annually to those cells within the designated recruitment ground.

2.2. Life history parameters

The age-structured model includes two species of fish with contrasting life histories. The parameters for the target species (Table 1) are based on life-history parameters of a ‘cod-like’ species which is fast growing and exhibits early maturation (Codling et al., 2005; LeQuesne and Codling, 2009; Pazhayamadom et al., 2013). Those of the conservation species (Table 2) are based on life-history parameters of a’ ray-like’ species (Ryland and Ajayi, 1984; Codling et al., 2005; Porcu et al., 2014), which is longer-lived, exhibits slower growth and later maturation; such species have been recognised as susceptible to fishing mortality to the extent that some populations have previously been eradicated (Walker and Heessen, 1996).

The cod-like target species has 11 age classes compared to the 20 age classes for the ray-like species. In both species, the final age class is a plus-group, capturing all fish which have survived to that age. Natural mortality was established as 0.2 yr^{-1} for all age classes (Jennings et al., 2009) of the cod-like species, higher than the 0.15 yr^{-1} for the ray-like species. All fish were assumed to mature in age-class three of the cod-like species; the later maturation of the ray-like species is reflected by all fish maturing in age-class nine. The net selectivity by age class of the cod-like species (derived from Le Quesne and Codling, 2009) is lower for juvenile age-classes than mature fish, whereas in the ray-like species - due to their larger size and weight at age - the net-selectivity applied renders it vulnerable to full-exploitation from the third age-class (juveniles).

Our model is intended to be illustrative and as such we deliberately use life-history parameters that are generic and representative of typical targeted species and typical bycatch species in need of conservation.

2.3. Model structure

The technical details of the model are fully described in the flow chart and accompanying equations in Figure App.1. To establish initial population numbers and exclude transient dynamics, the model is initially run for a ‘burn-in’ period of 50 years without applying closures (MPA size = 0%) or fishing mortality (Equation App.1, Fig. App.1). The burn-in time was determined to be the time taken for the oscillations of the cyclical stock-recruitment dynamics to have damped down to a minimal level. This is explored further in the supplementary online material (Online Supplementary Figs S.1i – S.1vi). The starting population for each species was thus obtained by applying by applying natural mortality (Equation App.2, Fig. App.1) and annual recruitment (Equations App.5i and App.5ii; Fig. App.1) for the duration of the burn-in time. At the start of each simulation the resultant, unfished starting population numbers within each age class for each species are distributed evenly across the spatial domain.

2.4. Monthly population dynamics and fishing

The annual rate of fishing effort (E) is assigned a value between 10 and 200 at the start of each simulation: this is divided into equal monthly efforts that are distributed equally between cells outside the MPA; in cells within the MPA boundaries the fishing effort is always 0. Effort is exerted equally on all populations of both species in the cells open to fishing (Equation App.1, Fig. App.1). The higher net selectivity

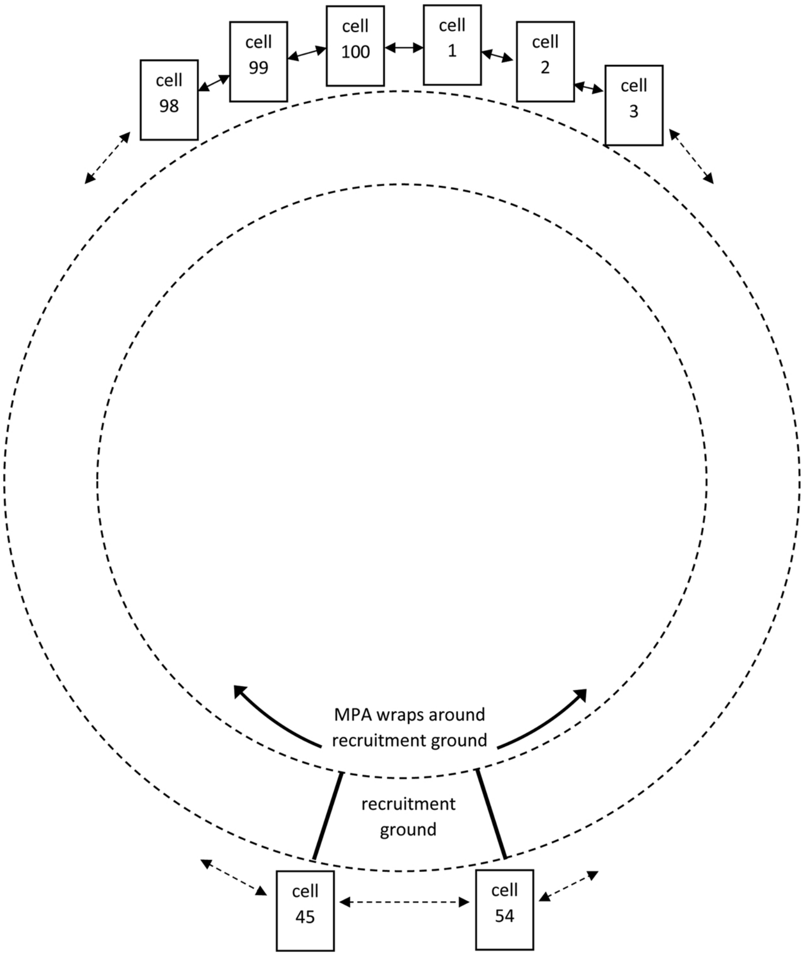

Fig. 1. Representation of spatial domain of the simulation: the loop represents 100 discrete cells; cell 1 is adjacent to cell 100, the recruitment ground is in the middle 10 cells of the virtual loop and any MPA closures are centred at the middle of the recruitment ground. Fish can move continuously in both directions through the loop of cells.

Table 1
Life history parameters of the cod-like target species.

Age	1	2	3	4	5	6	7	8	9	10	11+
Weight, W_a (kg)	0.62	0.97	2.13	4.01	6.26	8.34	10.0	11.13	12.51	13.61	14.66
Maturity, Mat_a	0	0	1	1	1	1	1	1	1	1	1
Natural mortality, M_a	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Selectivity, S_a	0.1	0.2	0.4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

Table 2
life history parameters of the ray-like conservation bycatch species.

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20+
Weight, W_a (kg)	0.65	1.40	2.40	3.80	5.40	7.23	9.20	11.25	13.4	15.5	17.7	19.8	21.9	23.9	25.8	27.8	29.5	31.2	32.8	34.3
Maturity, Mat_a	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Natural mortality, M_a	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15	0.15
Selectivity, S_a	0.4	0.7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

for juvenile classes of the conservation species coupled with the effort rate being equally applied to both species effectively makes age-averaged fishing selectivity higher on the conservation species. This assumption is explored further in Online Supplementary Figs S.2 and S.3. In the first monthly loop, mortality due to fishing per age class (Equation App.1, Fig. App.1) and the associated yield per age class per cell (Equation App.3, Fig. App.1) are calculated. The monthly population changes in each cell due to natural and fishing mortalities are applied (Equation App.2, Fig. App.1), which allows the population of each age class per cell for the current month to be obtained.

2.5. Monthly movement and population redistribution

Fish movement and population redistribution are the next monthly processes to be applied after fishing mortality and populations. As in Le Quesne and Codling (2009), we assume fish of all age classes 1 and over undergo density-independent, random movement based on the one-dimensional diffusion Equation (Equation App.4, Fig. App.1); fish can

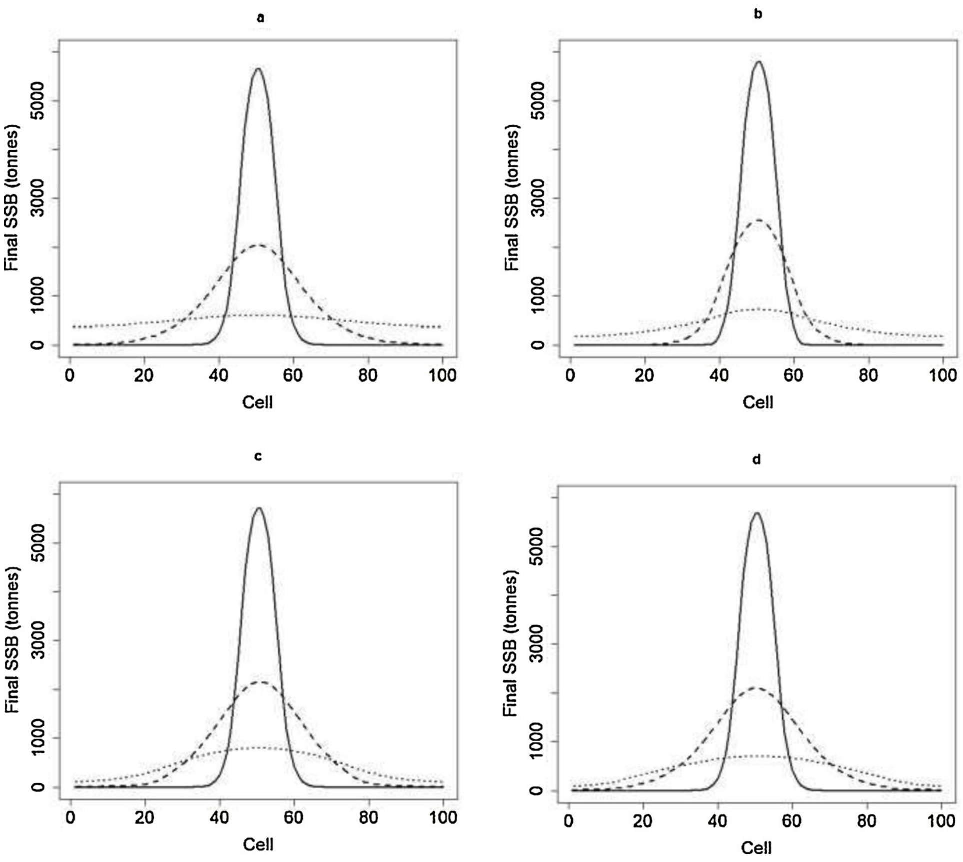

Fig. 2. Final distribution of SSB of the target species after one simulation run (50 years burn-in time plus 100 years) under the following scenarios of closure, and annual effort (E). Three levels of movement (D) are represented: ____, D = 1; _ _ _ _, D = 10;. . . . . ., D = 100.
a. unfished population.
b. E = 50, closure = 20%.
c. E = 50, closure = 40%.
d. E = 50, closure = 70%.

move in either direction through the virtual space. Values of the diffusion coefficient used in the simulations are not intended to be accurate representations of the movement of real species. Instead, in a similar approach to Le Quesne and Codling (2009), these values were used to represent qualitatively different levels of mobility relative to the extent of the spatial domain: $D = 1$ is used to represent small movements typical of ‘home range’ species; the moderate mobility of $D = 10$ represents a demersal species such as North Sea cod (Neat et al., 2006); $D = 100$ represents a wide-ranging, mobile species such as blonde ray (Morel et al., 2013). The effect of the three degrees of mobility on the final distribution of SSB are shown in Figs. 2a-d; by way of example, the final distribution of the target species is shown at three levels of mobility when unharvested (Fig. 2a), and under constant annual fishing rate (E = 50) with 20%, 40% and 70% (Figs. 2b-d) closures in place.

2.6. Annual recruitment and yield

At the end of every 12th monthly time-step (after the monthly sub-models of fishing, population dynamics and movement) and, as per the earlier Le Quesne and Codling (2009) model, the annual recruitment sub-model is applied using the Ricker (1954) recruitment function (Equations App.5i and App.5ii, Fig. App.1), which specifies a global density dependent stock-recruitment relationship. The Ricker function is widely applicable to temperate stocks and is used in the current simulation as a continuation from LeQuesne and Codling (2009). The values for the Ricker parameters for the target, cod-like species were obtained from ICES (2005). SSB and recruitment data is sparse for ray species (ICES, 2017) so Ricker parameters typical of a k-selected species (recognised as being particularly sensitive to overfishing and exhibiting slow recovery time from depletion) were allocated to represent the conservation species (Adams, 1980).

Although previous papers have explored local and global recruitment (e.g., Le Quesne and Codling, 2009), the current paper focuses on recruitment to an area contained within the MPA boundaries – the scenario to which MPAs are most relevant (Jones et al., 2007, 2009; Planes et al., 2009). In our simulation, the available recruits (age-0 fish) undergo density independent settlement by being equally distributed across the 10% of cells which represent the recruitment ground. Although recruitment is often highly variable in many fish species, random recruitment has been shown to have little quantitative effect when modelling effort-based management and closed areas (Le Quesne and Codling, 2009). The recruitment in the model was therefore deterministic to reduce simulation time and so that the underlying trends revealed by the model were not masked by stochastic recruitment events.

The annual yield is also obtained after each 12th monthly time-step by summing the monthly yields from all age classes across all cells open to fishing for each species.

2.7. Simulation scenarios

The model was run for 100 years after the burn-in time in monthly time-step increments. Closures of size p% were applied in 5% increments from $p =$ 0 to 100. For closures with odd values, cell 50 was closed with $(p\text{-}1)/2$ cells closed either side (e.g., 15% closure = cells 43 to 57 closed). For each closure size we considered a range of base fishing effort values in cells outside the MPA from $E = 0\ \mathrm{yr}^{-1}$ to $E = 200\ \mathrm{yr}^{-1}$ in increments of 10.

3. Results

3.1. Dynamics of target species

The yields of the target species across all annual efforts without closures are represented in Fig. 3; the extent of diffusion does not affect yield when closures are not in place. After the burn-in period, initial

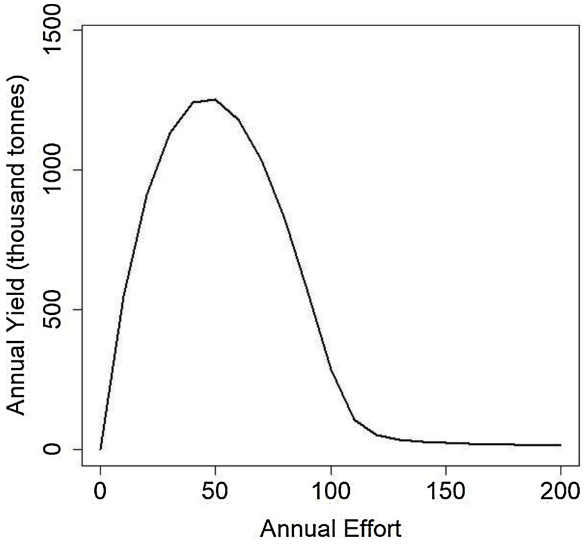

Fig. 3. Yields of a target species in a single species fishery with no closures to fishing implemented. At each level of closure the population is exposed to annual fishing efforts between 0 and 200. The model was run for 100 years with monthly time-steps.

simulations were run with no closures and annual fishing effort applied from values of $E = 0\ \mathrm{yr}^{-1}$ to $E = 200\ \mathrm{yr}^{-1}$. This enabled the maximum sustainable yield without spatial management to be obtained; this was considered to be the target or optimal yield (Y_{OPT}). The heat maps in Fig. 4a-c show the proportion of which the management objective of harvesting Y_{OPT} has been met when considering the target species as a single-species fishery.

The introduction of even a small MPA reduces the yield of a target species with low mobility. Because of the low mobility the proportion of the stock within the MPA will rarely be exposed to harvesting; additionally, new recruits will only move slowly towards and across the MPA boundary, thus Y_{OPT} cannot be met, regardless of the amount of fishing effort (Fig. 4a). Y_{OPT} can be reached if larger closures are introduced but only with increased fishing effort as target stock mobility increases (Fig. 4b & c).

3.2. Dynamics of bycatch conservation species

The SSB of the conservation species when exposed to all annual fishing efforts without closures are represented in Fig. 5; the extent of diffusion does not affect SSB when closures are not in place. The threshold of $\mathrm{SSB}_{\mathrm{MIN}}$ of the conservation stock was calculated as being 0.5 SSB of unfished stock and the management objective was set to

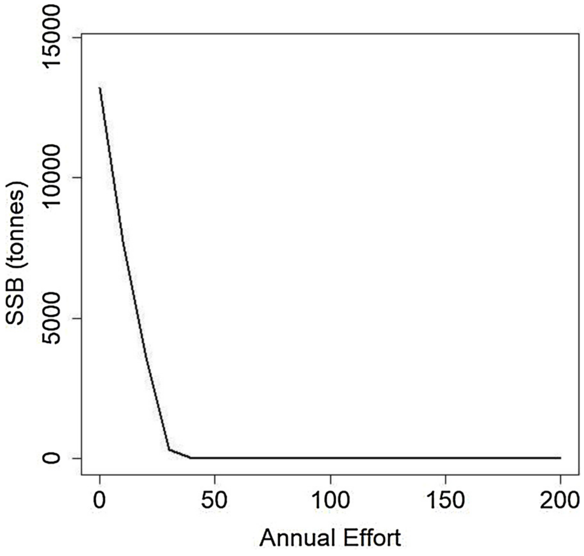

Fig. 5. SSB of a bycatch conservation species in a single species fishery with no closures to fishing implemented. At each level of closure the population is exposed to annual efforts between 0 and 200. The model was run for 100 years with monthly time-steps.

maintain SSB of the conservation stock at or above this level. This was selected as a precautionary reference point for what we have considered to be a generic vulnerable stock (Caddy, 1999). Fig. 6a-c show the proportion of which $\mathrm{SSB}_{\mathrm{MIN}}$ of the conservation species has been maintained when considering it in isolation. The results demonstrate that at all levels of diffusion the conservation species requires closures to maintain $\mathrm{SSB}_{\mathrm{MIN}}$ at all but the lowest of fishing efforts (Fig. 6a–c).

A conservation species that exhibits low diffusion will effectively be contained within the MPA boundary for its lifetime and thus benefits from closures at all levels of fishing effort; closures of 10% of the total area enable $\mathrm{SSB}_{\mathrm{MIN}}$ to be maintained at any level of fishing effort (Fig. 6a). As mobility increases (Fig. 6b & c) the minimum closure necessary to meet $\mathrm{SSB}_{\mathrm{MIN}}$ across all levels of effort also increases – the more diffusive a species, the more it crosses the MPA boundary and thereby requires greater closures to protect the SSB – and increased fishing effort necessitates still larger closures.

3.3. Dynamics of a two-species fishery

Heat maps were constructed which showed the extent to which Y_{OPT} of the target species could be attained when $\mathrm{SSB}_{\mathrm{MIN}}$ of the conservation species had been met to consider the management objectives for the target and conservation species concurrently. Thus, when both

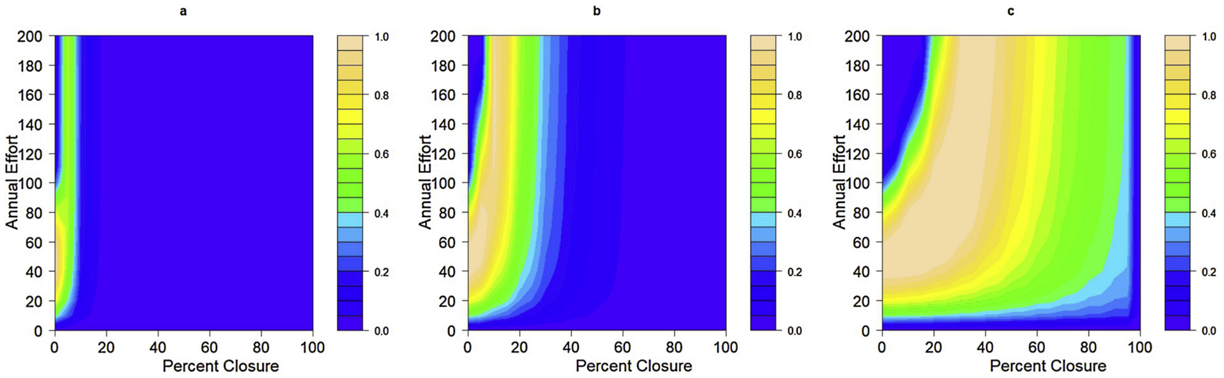

Fig. 4. Scaled results to show the extent to which Y_{OPT} (Y_{OPT} or greater is represented by a value of 1.0) of the target species has been met in simulations of a single species fishery protected by 0–100% closures to fishing and exposed to annual efforts between 0 and 200. The simulation was run for 100 years in monthly time steps and the results generated for three levels of movement (D) of the target species: a. D = 1; b. D = 10; c. D = 100.

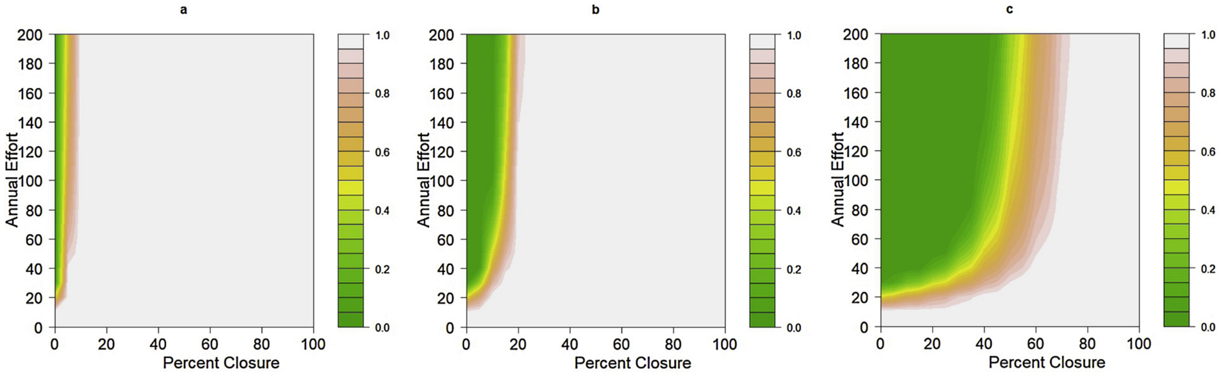

Fig. 6. Scaled results to show the proportion of which SSB_{MIN} (represented by a value of 1.0) of the bycatch conservation species has been met in simulations of a single species fishery protected by 0–100% closures to fishing and exposed to annual efforts between 0 and 200. The simulation was run for 100 years in monthly time steps and the results generated for three levels of movement (D) of the target species: a. D = 1; b. D = 10; c. D = 100.

management aims could be met concurrently the heat map value would be 1.0. These results were used to show what would happen if both species exhibited the same degree of movement (Figs. 7a–c) or the more realistic scenario of the species exhibiting different degrees of movement (Figs. 7d–i).

When both species exhibit the same mobility (Figs. 7a–c) the two management aims become mutually exclusive - SSB_{MIN} of the conservation species is met but Y_{OPT} of the target species cannot be fulfilled. Broadly, two scenarios exist when the two species exhibit different degrees of movement: the target species is more highly diffusive than the conservation species (Figs. 7d–f) or vice versa (Figs. 7g–i). Both management aims can be met by the introduction of closures When the target species is more diffusive (Figs. 7d–f). A single-species fishery of a highly diffusive target species has a wide range of management options through effort regulation and closures (Fig. 4c) whilst a conservation species with low mobility will almost always benefit from closures (Fig. 6a). Accordingly, the greatest number of management options exist in a two-species fishery when the target species is far more diffusive than the conservation species (Fig. 7e).

The larger closures required to maintain SSB_{MIN} of a diffusive conservation species decrease the yield of a target species; consequently, when a conservation species is more mobile than the target species in a two-species fishery, the management objectives for the two species cannot be fully met simultaneously (Figs. 7g–i). The best outcome that can be achieved when SSB_{MIN} of a highly diffusive conservation species is maintained is 0.4 of Y_{OPT} of a moderately diffusive target species (Fig. 7i) – this requires restricted fishing effort coupled with closures. Additional plots (Fig. 8a–d) were constructed with a view to enabling fisheries managers to explore compromises between differing management aims in such a scenario. For example, following on from Fig. 7i, Fig.8a shows that with 5% closures and low effort the yield of the less mobile target species can be increased to more than 60% of Y_{OPT} but only by decreasing SSB of the conservation species to 60% of SSB_{MIN}.

4. Discussion

This paper is an investigation of a two-species mixed fishery in which the two species are considered to have conflicting management objectives. We evaluated two fishery control tools - spatial closures and effort management - as ways of managing the conflicting objectives while considering the potential for differing levels of mobility between the two species. The results indicate that closures are an effective management tool to increase biomass of a species requiring conservation but are not needed to meet the management objectives of maintaining the yield of a highly diffusive target species. When considered as a mixed fishery, the simulation indicates that the conflicting management objectives of the two species could be met via effort regulation or by closures if both species exhibit similar mobility. However, the presence of a highly mobile, bycatch conservation species prevents both sets of management aims being met concurrently when the mobility of the species differs. The best compromise in the current simulation is found when small closures of 5% are coupled with considerable effort restrictions – 60% of both management aims (yield of the target stock and maintenance of SSB of the conservation stock) can then be met.

These results are not intended to be applied directly to any particular species, but serve as a guideline for exploring management options of species with different life-history parameters and degrees of mobility. However, the model can easily be parameterised for other species' life-histories and could be used to consider management conflicts in specific areas such as the management conflict in the southern North Sea between recovering cod and declining seabass. Seabass are known to range widely between resident, feeding, pre-spawning and spawning territories[2] while cod, although known to show a migratory tendency between feeding, spawning and homing grounds, are more limited in their movements (Neat et al., 2014).

4.1. Single objective fisheries

The primary purpose of the current simulation was to examine the potentially conflicting aims within a two-species fishery. The first step was to establish the consequences on the management decisions for each species when subjected to the primary management strategy for the other species, i.e. the effect of an NTZ MPA when imposed on the target species and the effect of fishing effort on the conservation species.

Closures are detrimental to the yield of a target species with low mobility (such as a home-range species), which is effectively contained within the MPA and therefore not exposed to harvesting (DeMartini, 1993; Gerber et al., 2003). As mobility increases a small MPA (less than 10% of the total area) does not impact the yield of a mobile target species because increased movement will facilitate enhanced yields via spillover beyond the MPA boundary (DeMartini, 1993; Russ and Alcala, 1996; Kramer and Chapman, 1999; Halpern and Warner, 2003; Abesamis and Russ, 2005; Buxton et al., 2014). However, even with highly mobile species, as MPA size increases there will be a need for fishers to increase annual fishing effort to obtain MSY (Fig. 4), thus increasing their costs (Metcalfe et al., 2015). Such socio-economic impacts can lead to conflict between stakeholders (Rees et al., 2010) and lack of adherence to enforcement of the NTZ MPA (Edgar et al., 2014).

The results for the bycatch species requiring conservation measures demonstrate that, as per previous studies (Hastings and Botsford, 1999; Hilborn et al., 2004), closures are one method of conserving SSB. The

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[2] C-Bass on the move! Marine Science Blog; https://marinescience.blog.gov.uk/2016/01/18/c-bass-on-the-move/.

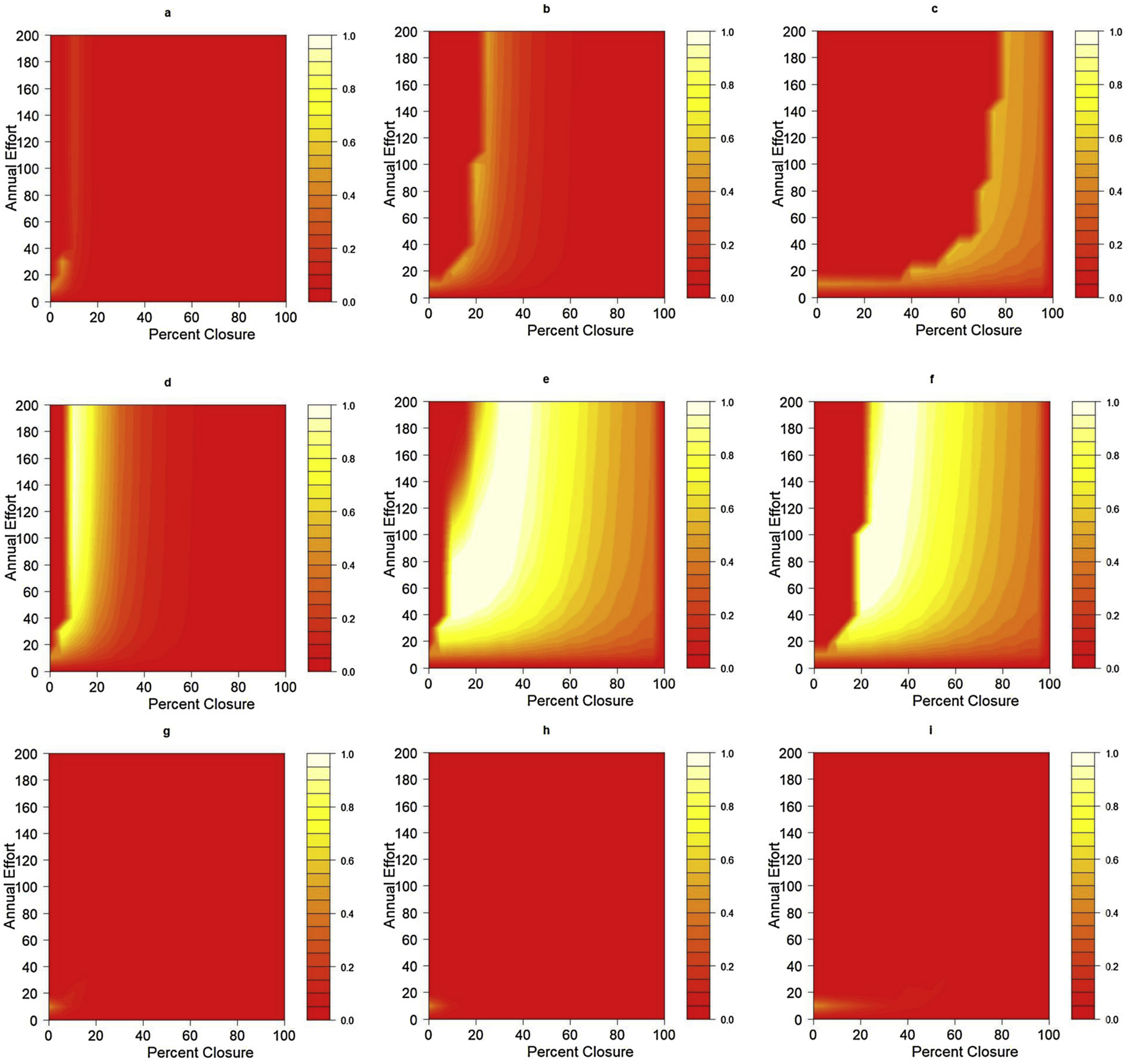

Fig. 7. Results to show the extent to which Y_{OPT} of the target species can be met when SSB_{MIN} of the bycatch conservation species has already been met in simulations of a two-species fishery protected by 0–100% closures to fishing and exposed to annual efforts between 0 and 200. The simulation was run for 100 years in monthly time steps. The levels of movement (D) within each simulation are:
a. both species D = 1.
b. both species D = 10.
c. both species D = 100.
d. target species D = 10, conservation species D = 1.
e. target species D = 100, conservation species D = 1.
f. target species D = 100, conservation species D = 10.
g. target species D = 1, conservation species d = 10.
h. target species D = 1, conservation species d = 100.
i. target species D = 10, conservation species d = 100.

size of the MPA needed to maintain SSB_{MIN} increases with increased movement of the species, with a highly mobile species exposed to moderate to high fishing effort needing extensive closures. These findings are in keeping with those of other authors: (Bohnsack, 1998; Lauck et al., 1998; Shipp, 2003; Blyth-Skyrme et al., 2006; Almany et al., 2009; LeQuesne and Codling, 2009) because a highly mobile species will cross the MPA boundary more frequently and will only be protected for the time it spends within the MPA (Gerber et al., 2005). However, the economies of scale potentially gained by establishing such large MPAs (McCrea-Strub et al., 2011) have been questioned (Gaines et al., 2010) and there can be difficulties enforcing NTZs in large MPAs (Wilhelm et al., 2014); as such, large closures may not be a viable management option.

Considering the fisheries and conservation objectives independently shows the potential challenges faced by fisheries managers when implementing MPAs. We next set out to ask whether these challenges are confounded or reduced when considering the two sets of objectives simultaneously.

4.2. Two-species, target and bycatch fisheries

The current model extends single-species findings by considering the target and bycatch conservation objectives simultaneously. The differing life-histories of the two species will present unique challenges

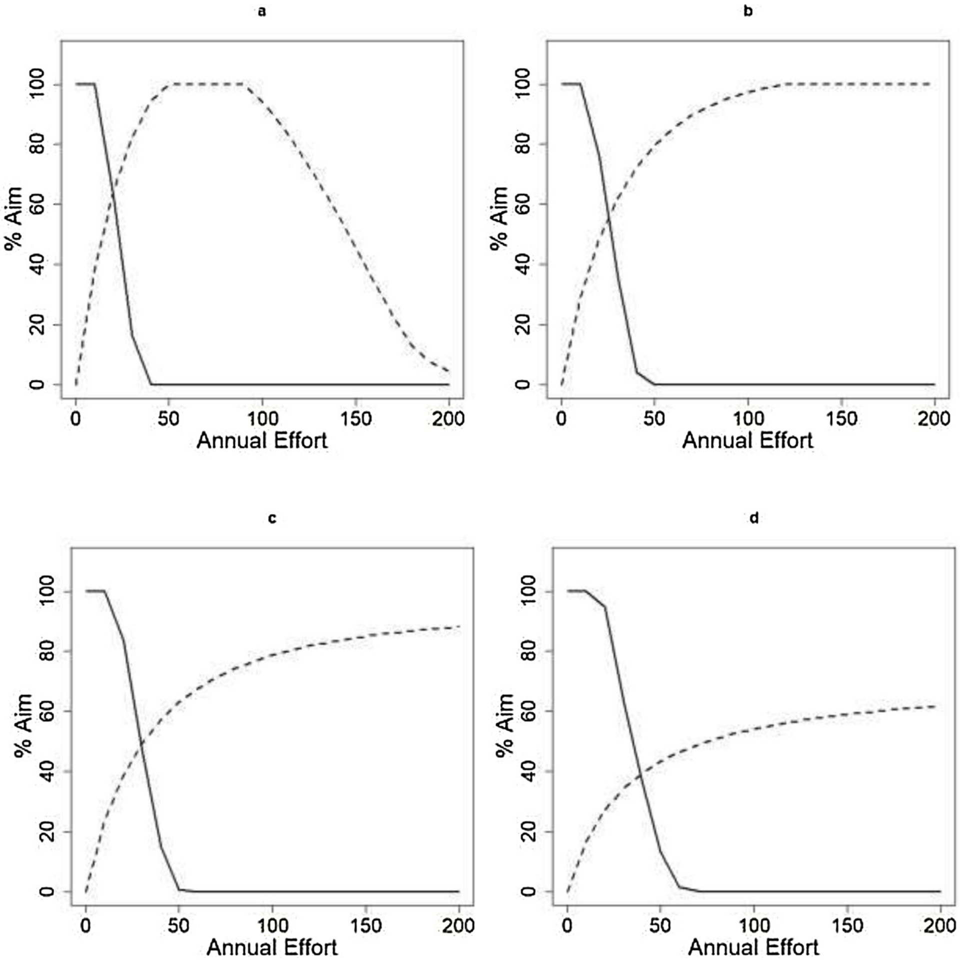

Fig. 8. Results to show the extent to which Y_{OPT} of a less-mobile (D = 10) target species and SSB_{MIN} of a more mobile (D = 100) conservation species have been met concurrently in simulations of a two-species fishery with closures to fishing implemented of a. 5%, b. 10%, c. 15%, d. 20%. At each level of closure the population is exposed to annual efforts between 0 and 200. The model was run for 100 years with monthly time-steps. Target species (D = 10) represented by _ _ _, conservation species (D = 100) represented. by __.

to fisheries managers (Hastings et al., 2017) and we explore whether these challenges will be further complicated when the mobility of the two species is also taken into account.

The 'weak stock' considerations of previous studies (Hilborn et al., 2004; Hastings et al., 2017) – whereby the aim to protect a single stock drives the management strategy of the mixed fishery – are evident in the simulation scenarios. The conservation and fisheries benefits of effort regulation and closures have previously been reported for home-range species (Hastings et al., 2017). In the current simulations when both species have low mobility, the highest combined outcome – approximately two thirds of the maximum - is obtained by effort control and introducing closures of up to 10% of the total area, which equates to protecting the recruitment grounds. When both species are more mobile or when the target species is more mobile than the conservation species, the maximum fishing effort and the minimum closure sizes required to obtain the best outcome for both species are driven by the effort and size necessary to conserve the SSB of the conservation species; when the conservation species is equally mobile or more mobile than the target species then the target stock has to be exploited at less than MSY because the management rules of implementing closures or reducing effort is driven by the conservation species (Baum et al., 2003; Rijnsdorp et al., 2012).

The size of closures needed increases with increased mobility of the conservation species (Blyth-Skyrme et al., 2006; Laurel and Bradbury, 2006), more so when fishing effort is also increased (Bohnsack, 1998; Lauck et al., 1998; Shipp, 2003; Blyth-Skyrme et al., 2006; Almany et al., 2009; LeQuesne and Codling, 2009). Spillover of mobile adults contributing to the yield of fisheries adjacent to a closed area has been well documented (Russ and Alcala, 1996; Abesamis and Russ, 2005; Murawski et al., 2005; Halpern et al., 2009). The results of the current simulations demonstrate that when species have equal mobility, or the target species is more mobile than the conservation species, maximum closure size is determined by the mobility of the target species and thus the ability of the target stock to cross the MPA boundary. Being able to determine the range of effective closure sizes in this way could be of benefit and offer flexibility to marine planners considering additional socio-economic objectives of stakeholders when siting MPAs (Lieberknecht and Jones, 2016; Agardy et al., 2011; Kelly et al., 2017). This is particularly the case in coastal areas where there may be multiple demands on space (Rees et al., 2010; Edgar et al., 2014; Abreu et al., 2017; Moore et al., 2017).

The scenarios which model a conservation species with greater mobility than a target species are more realistic to demersal species such as cod and ray or seabass. The two-species model demonstrates that, although effort and closure can be used to achieve conservation or fishery objectives in isolation, when the conservation species is more diffusive than the target species the two management objectives become mutually exclusive and the best outcome requires restricted fishing effort to be coupled with closures. The minimum closure size required for conservation of bycatch SSB prevents the less mobile target species being harvested. In such cases, no one strategy totally meets both sets of objectives simultaneously and alternative strategies (closures and/or effort regulation) will lead to a different compromise in the objectives. To seek such a compromise, the model can be used to serve as a decision-making tool for fishery and marine planning managers (Fig. 8) based on the priorities within the area and to explore compromises between stakeholders (Punt, 2017).

A simplification of the current model is the assumption of full mortality due to capture of the conservation species, although live discards can mitigate the impacts of fishing on the conservation species. However, the application of the landing obligation of the Common Fisheries Policy reform (EU, 2013) to bycatch species will mean that bycatch conservation species could present challenges as a choke-species in a mixed fishery (Mortensen et al., 2018); these challenges could potentially be mitigated by the introduction of an MPA to conserve one species whilst allowing fishing of another species to continue and the simulation could be used by stakeholders to explore satisfactory management strategies (Catchpole et al., 2017; Guillen et al., 2018).

4.3. Model assumptions

The movement of species within the model was represented as diffusion-based. Although future simulations would benefit from incorporating migratory-type and directional movements, which would ideally be parameterised for specific species, the virtual 1D space of the model was an abstract representation of the marine space that served to give a generalised representation of the extent of closures needed with respect to the differing mobility of each species. To make the model applicable to specific MPA sites it should be developed to simulate the movement types within a spatially accurate representation of a particular coastline or seascape, better enabling planners to determine the required extent and location of an MPA.

The model in its current form is meant to provide broad guiding principles to consider when managing mobile stocks. As such, the effects of introducing closures should not be considered absolute and it would be of benefit to explore the underlying mechanisms which are enhancing stocks with closure. For example, yield per recruit, enhanced survival of older fish and density dependence in the stock-recruitment-relationship could be explored in future developments.

There are key biological assumptions within the model that are simplified to give an overarching view of MPA design within a two-species fishery. Annual recruitment is deterministic but stochasticity in recruitment was previously shown to have little effect on the outcomes of fishing regulatory effects in single-species simulations of the original model (Le Quesne and Codling, 2009). There is no direct interaction between the two species within the model and incorporating such information is not always required for efficient fisheries management (Clark, 2017); a recommendation would be to incorporate biological interactions appropriate to the species for which future models are designed, particularly where any interactions between the species or with their environment leads to any spatial correlation in their movement biology, spawning or feeding areas.

Online Supplementary Figs S.2 and S.3 illustrate the effect of removing juveniles of the conservation species from the harvest. This increases the management options available in terms of effort and spatial management when a highly diffusive conservation species is considered as a single species and as part of a mixed fishery. The current model should therefore be viewed as erring on the side of caution in this respect, and future models should aim to incorporate empirical, species-based evidence on the vulnerability to fishing of age-classes of the conservation and target species. This could also include species-specific capture efficiency, which was assumed to be the same for both species represented in the simulation. Online Supplementary Figs S.4i and S.4ii illustrate the effects of altering the capture efficiency of the conservation species: including this when the model is parameterised precisely for a species will give more accurate predictions of the model and therefore management outcomes.

The value of $SSB_{MIN} = 0.5$ unfished SSB has not been based on a reference point published for a particular species, but has been selected as a precautionary limit for what is assumed to be a potentially vulnerable stock. This reference point can easily be adapted to a published value for a particular species or management option (ICES, 2015).

In summary, this model provides general principles for considering a two-species fishery - with a target and bycatch conservation stock which exhibit different life-history parameters - and for exploring the effect of the species' mobility on MPA effectiveness. The outcomes have demonstrated that species mobility in a two-species fishery is as important a determining factor as classical life history information in the success of an MPA and should be incorporated into future models of MPA design.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2019.105334.

References

Abesamis, R.A., Russ, G.R., 2005. Density-dependent spillover from a marine reserve: long-term evidence. Ecol. Appl. 15, 1798–1812.
Abreu, J.S., Domit, C., Zappes, C.A., 2017. Is there dialogue between researchers and traditional community members? The importance of integration between traditional knowledge and scientific knowledge to coastal management. Ocean Coast. Manag. 141, 10–19.
Adams, P.B., 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fish. Bull. (Wash. D. C.) 78 (1), 1–12.
Agardy, T., 2005. Global marine conservation policy versus site-level implementation: the mismatch of scale and its implications. Mar. Ecol. Prog. Ser. 300, 242–248.
Agardy, T., di Sciara, G.N., Christie, P., 2011. Mind the gap. Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar. Pol. 35 (2), 226–232.
Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecol. Appl. 8, S79–S92.
Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L., Williamson, D.H., 2009. Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs 28, 339–351.
Baudron, A., Ulrich, C., Nielsen, J.R., Boje, J., 2010. Comparative evaluation of a mixed-fisheries effort-management system based on the Faroe Islands example. ICES J. Mar. Sci. 67, 1036–1050.
Baum, J.K., Meeuwig, J.J., Vincent, A.C.J., 2003. Bycatch of lined seahorses (*Hippocampus erectus*) in a Gulf of Mexico shrimp trawl fishery. Fish. Bull. (Wash. D. C.) 101, 721–731.
Berger, A.M., Goethel, D.R., Lynch, P.D., Quinn, T., Mormede, S., McKenzie, J., Dunn, A., 2017. Space oddity: the mission for spatial integration. Can. J. Fish. Aquat. Sci. 74 (11), 1698–1716.
Blyth-Skyrme, R.E., Kaiser, M.J., Hiddink, J.G., Edwards-Jones, G., Hart, P.J.B., 2006. Conservation benefits of temperate marine protected areas: variation among fish species. Conserv. Bio. 20, 811–820.
Bohnsack, J.A., 1998. Application of marine reserves to reef fisheries management. Aust. J. Ecol. 23, 298–304.
Branch, T.A., Hilborn, R., Haynie, A.C., Fay, G., Flynn, L., Griffiths, J., Marshall, K.N., Randall, J.K., Scheuerell, J.M., Ward, E.J., Young, M., 2006. Fleet dynamics and fishermen behavior: lessons for fisheries managers. Can. J. Fish. Aquat. Sci. 63, 1647–1668.
Breen, P., Posen, P., Righton, D., 2015. Temperate marine protected areas and highly mobile fish: a review. Ocean Coast. Manage. 105, 75–83.
Buxton, C.D., Hartmann, K., Kearney, R., Gardner, C., 2014. When is spillover from marine reserves likely to benefit fisheries? PLoS One 9 (9), e107032.
Caddy, J.F., 1999. Fisheries management in the twenty-first century: will new paradigms apply? Rev. Fish Biol. Fish. 9, 1–43.
Catchpole, T.L., Riberio-Santos, A., Mangi, S.C., Hedley, C., Gray, T.S., 2017. The challenges of the landing obligation in EU fisheries. Mar. Policy 82, 76–86.
Clark, C.W., 2017. Modelling the behavior of fishers and fishes. ICES J. Mar. Sci. fsx 212https://doi.org/10.1093/icesjms/fsx212. (accessed 28 May 2018).

Codling, E.A., Kelly, C.J., Clarke, M., 2005. Comparison of the Effects of Exploitation on Theoretical Long-Lived Fish Species with Different Life-History Strategies and the Implications for Management. ICES CM 2005/N:24.

D'Aloia, C.C., Daigle, R.M., Cote, I.M., Curtis, J.M.R., Guichard, F., Fortin, M.J., 2017. A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. Biol. Cons. 216, 93–100.

Davies, T.E., Maxwell, S.M., Kaschner, K., Garilao, C., Ben, N.C., 2017. Large marine protected areas represent biodiversity now and under climate change. Sci. Rep. 7, 9569.

Da Rocha, J.M., Gutierrez, M.J., Cervino, S., 2012. Reference points based on dynamic optimization: a versatile algorithm for mixed-fishery management with bioeconomic age-structured models. ICES J. Mar. Sci. 69, 660–669.

DeMartini, E.E., 1993. Modeling the potential of fishery reserves for managing Pacific Coral-Reef fishes. Fish. Bull. (Wash. D. C.) 91, 414–427.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Forsterra, G., Galvan, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220.

EU, 2013. European Council Regulation No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations EC No 1954/2003 and EC No 1224/2009 and repealing Council Regulations EC No 2371/2002 and ECematical Sciences, University of E No 639/2004 and Council Decision 2004/585/EC. Off. J. Eur. Union 2013 (L354), 22–61. (accessed 12 October 2018). https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX%3A32013R1380.

Fazli, H., Zhang, C.I., Hay, D.E., Lee, C.W., 2009. Multi-species approach for stock management of Kilka fish (Genus: Clupeonella) in Iranian waters of the Caspian Sea. Iran. J. Fish. Sci. 8, 141–154.

Fernandes, P.G., Cook, R.M., 2013. Reversal of stock decline in the Northeast Atlantic. Curr. Bio. 8 (15), 1432–1437.

Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. Proc. Natl. Acad. Sci. U. S. A. 107, 18286–18293.

Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., Andelman, S., 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecol. Appl. 13, S47–S64.

Gerber, L.R., Heppell, S.S., Ballantyne, F., Sala, E., 2005. The role of dispersal and demography in determining the efficacy of marine reserves. Can. J. Fish. Aquat. Sci. 62, 863–871.

Gibson, C., Valenti, S.V., Fowler, S.L., Fordham, S.V., 2006. Rhe Conservation Status of Northeast Atlantic Chondrichthyans: Report of the IUCN Shark Specialist Group Northeast Atlantic Regional Red List Workshop. VIII + 76pp. IUCN SSC Shark Specialist Group.

Gill, D.A., Mascia, M.B., Ahmadia, G.N., Glew, L., Lester, S.E., Barnes, M., Craigie, I., Darling, E.S., Free, C.M., Geldmann, J., Holste, S., Jensen, O.P., White, A.T., Basurto, X., Coad, L., Gates, R.D., Guannel, G., Mumby, P.J., Thomas, H., Whitmee, S., Woodley, S., Fox, H.E., 2017. Capacity shortfalls hinder the performance of marine protected areas globally. Nature 543, 665–669.

Grüss, A., 2014. Modelling the impacts of marine protected areas for mobile exploited fish populations and their fisheries: what we recently learnt and where we should be going. Aquat. Living Resour. 27, 107–133.

Guillen, J., Holmes, S.J., Carvalho, N., Casey, J., Dorner, H., Gibin, M., Mannini, A., Vasilakopoulos, P., Zanzi, A., 2018. A review of the European Landing Obligation focusing on its implications for fisheries and the environment. Sustainability 10, 900.

Halpern, B.S., Lester, S.E., Kellner, J.B., 2009. Spillover from marine reserves and the replenishment of fished stocks. Environ. Conserv. 36, 268–276.

Halpern, B.S., Warner, R.R., 2003. Matching marine reserve design to reserve objectives. Proc. R. Soc. Lond. Ser. B-Bio. Sci. 270, 1871–1878.

Hastings, A., Botsford, L.W., 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science 284, 1537–1538.

Hastings, A., Gaines, S.D., Costello, C., 2017. Marine reserves solve an important bycatch problem in fisheries. Proc. Natl. Acad. Sci. U. S. A. 113 (34), 8927–8934.

Heath, M., Cook, R., Robin, M., 2015. Hind-casting the quantity and composition of discards by mixed demersal fisheries in the North Sea. PLoS One 10 (3), e0117078. https://doi.org/10.1371/journal.pone.0117078. (accessed 16 June 2018).

Hilborn, R., Stokes, K., Maguire, J.J., Smith, T., Botsford, L.W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K.L., Garcia, S., Hall, S.J., Kirkwood, G.P., Sainsbury, K., Stefansson, G., Walters, C., 2004. When can marine reserves improve fisheries management? Ocean Coast Manage. 47, 197–205.

ICES, 2005. Report of the Study Group on Multispecies Assessment in the North Sea. ICES Document CM 2005/d: 06.

ICES, 2015. Report of the ICES Advisory Committee 2015. ICES Advice 2015, Book 1.

ICES, 2016a. Advice on Fishing Opportunities, Catch, and Effort Greater North Sea and Celtic Seas Ecoregions; Cod (*Gadus Morhua*) in Subarea 4, Division 7.d, and Subdivision 3.a.20 (North Sea, Eastern English Channel, Skagerrak) Update Nov 2016. Book 6, Section 3.3.

ICES, 2016b. Advice on Fishing Opportunities, Catch, and Effort Greater North Sea and Celtic Seas Ecoregions; Seabass (*Dicentrarchus Labrax*) in Divisions 4.b-c, 7.a Abd 7.d-h (central and Southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea) Update July 2016. Book 5, Section 3.57.

ICES, 2017. ICES Stock Assessment Database. ICES, Copenhagen, Denmark (Accessed 16 June 2018). http://standardgraphs.ices.dk.

Jennings, S., Kaiser, M., Reynolds, J.D., 2009. Marine Fisheries Ecology. Wiley-Blackwell.

Jensen, A.L., 1991. Multiple speciemic performance of a mixed fishermic performance of a mixed fishers fisheries with no ecological interaction: two-species Schaefer model applied to lake trout and lake whitefish. ICES J. Mar. Sci. 48 167-17.

Jones, G.P., Almany, G.R., Russ, G.R., Sale, P.F., Steneck, R.S., van Oppen, M.J.H., Willis, B.L., 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28 (2), 307–325.

Jones, G.P., Srinivasan, M., Almany, G.R., 2007. Population connectivity and conservation of marine biodiversity. Oceanography 20 (3), 100–111.

Kelly, R., Pecl, G.T., Fleming, A., 2017. Social licence in the marine sector: a review of understanding and application. Mar. Policy 81, 21–28.

Kirkegaard, E., 2015. State of Fish Stocks in NE Atlantic, North Sea and Baltic Sea. ICES seminar "State of fish Stocks in European Waters (accessed 12 May 2018). https://www.slideshare.net/ICES_ASC/state-of-fish-stocks-in-the-northeast-atlantic-the-north-sea-and-the-baltic-sea-50507457.

Kraak, S.B.M., Buisman, F.C., Dickey-Collas, M., Poos, J., Pastoors, M.A., Smit, J.G.P., van Oostenbrugge, J.A.E., Daan, N., 2008. The effect of management choices on the sustainability and economic performance of a mixed fishery: a simulation study. ICES J. Mar. Sci. 65 697-693.

Kramer, D.L., Chapman, M.R., 1999. Implications of fish home range size and relocation for marine reserve function. Environ. Biol. Fishes 55, 65–79.

Larkin, P.A., 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 106, 1–11.

Lauck, T., Clark, C.W., Mangel, M., Munro, G.R., 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecol. Appl. 8, S72–S78.

Laurel, B.J., Bradbury, I.R., 2006. "Big" concerns with high latitude marine protected areas (MPAs): trends in connectivity and MPA size. Can. J. Fish. Aquat. Sci. 63, 2603–2607.

Le Quesne, W.J.F., Codling, E.A., 2009. Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. ICES J. Mar. Sci. 66, 122–131.

Lieberknecht, L.M., Hooper, T.E.J., Mullier, T.M., Murphy, A., Neilly, M., Carr, H., Haines, R., Lewin, S., Hughes, E., 2011. Finding sanctuary final report and recommendations. Annex I2. A Report Submitted by the Finding Sanctuary Stakeholder Project to Defra. the Joint Nature Conservation Committee, and Natural England (accessed 18 May 2018). http://tna.europarchive.org/*/http://www.finding-sanctuary.org/.

Lieberknecht, L.M., Jones, P.J.S., 2016. From stormy seas to the doldrums: the challenges of navigating towards an ecologically coherent marine protected area network through England's Marine Conservation Zone process. Mar. Policy 71, 275–284.

Mackinson, S., Deas, B., Beveridge, D., Casey, J., 2009. Mixed-fishery or ecosystem conundrum? Multispecies considerations inform thinking on long-term management of North Sea demersal stocks. Can. J. Fish. Aquat. Sci. 66, 1107–1129.

McCrea-Strub, A., Zeller, D., Sumaila, U.R., Nelson, J., Balmford, A., Pauly, D., 2011. Understanding the cost of establishing marine protected areas. Mar. Policy 35 (1), 1–9.

Metcalfe, K., Vaughan, G., Vaz, S., Smith, R.J., 2015. Spatial, socio-economic and ecological implications of incorporating minimum size constraints in marine protected area network design. Conserv. Biol. 29 (6), 1615–1625.

Moore, S.A., Brown, G., Kobryn, H., Strickland-Munro, J., 2017. Identifying conflict potential in a coastal and marine environment using participatory mapping. J. Environ. Manage. 197, 706–718.

Morel, G.M., Shrives, J., Bossy, S.F., Meyer, C.G., 2013. Residency and behavioural rhymicity of ballan wrasse (*Labrus bergylta*) and rays (*Raja* spp.) captured in Portelet Bay, Jersey: implications for Marine Protected Area Design. J. Mar. Biol. Assoc. U.K. 93 (5), 1407–1414.

Mortensen, L.O., Ulrich, C., Hansen, J., Hald, R., 2018. Identifying choke species challenges for an individual demersal trawler in the North Sea, lessons from conversations and data analysis. Mar. Policy 87, 1–11.

Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., Mountain, D.G., 2005. Effort distribution and catch patterns adjacent to temperate MPAs. ICES J. Mar. Sci. 62, 1150–1167.

Neat, F.C., Wright, P.J., Zuur, A.F., Gibb, I.M., Gibb, F.M., Tulett, D., Righton, D.A., Turner, R.J., 2006. Residency and depth movements of a coastal group of Atlantic cod (*Gadus morhua* L.). Mar. Biol. 148 (3), 643–654.

Neat, F.C., Bendall, V., Berx, B., Wright, P.J., O'Cuaig, M., Townhill, B., Schon, P.-J., Lee, J., Righton, D., 2014. Movement of Atlantic cod around the British Isles: implications for finer scale stock management. J. Appl. Ecol. 51 (6), 1564–1574.

Pascoe, S., Bustamante, R., Wilcox, C., Gibbs, M., 2009. Spatial fisheries management: a framework for multi-objective qualitative assessment. Ocean Coast. Manage. 52, 130–138.

Pazhayamadom, D.G., Kelly, C.J., Rogan, E., Codling, E.A., 2013. Self-starting CUSUM approach for monitoring data poor fisheries. Fish. Res. 145, 114–127.

Planes, S., Jones, G.P., Thorrold, S.R., 2009. Larval dispersal connects fish populations in a network of marine protected areas. Proc. Natl. Acd. Sci. U. S. A. 106 (14), 5693–5697.

Poos, J.J., Bogaards, J.A., Quirijns, F.J., Gillis, D.M., Rijnsdorp, A.D., 2010. Individual quotas, fishing effort allocation, and over-quota discarding in mixed fisheries. ICES J. Mar. Sci. 67, 323–333.

Porcu, C., Bellodi, A., Cannas, R., Marongiu, M., Mulas, A., Follesa, M., 2014. Life-history traits of a commercial ray, *Raja brachyura* from the central western Mediterranean Sea. Mediterr. Mar. Sci. 16 (1), 90–102 https://doi.org/10/12681/mms.898 (accessed 15 September 2018).

Pulina, M., Meleddu, M., 2012. Defining a marine protected area strategy: a stakeholder perspective. Ocean Coast. Manage. 66, 46–55.

Punt, A.E., 2017. Strategic management decision-making in a complex world: quantifying, understanding, and using trade-offs. ICES J. Mar. Sci. 74 (2), 499–510.

Quirijns, F., 2014. Discard Atlas of North Sea Fisheries. IMARES Wageningen UR 2014. 84 pp.

R Core Team, 2019. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL http://www.R-project.org/. (accessed 17 July 2019).

Rees, S.E., Attrill, M.J., Austen, M.C., Mangi, S.C., Richards, J.P., Rodwell, L.D., 2010. Is there a win-win scenario for marine nature conservation? A case study of Lyme Bay, England. Ocean Coast. Manage. 53, 135–145.

Ricker, W.E., 1954. Stock and recruitment. J. Fish Res. Board Can. 11 (5), 559–623.

Rijnsdorp, A.D., van Overzee, H.M.J., Poos, J.J., 2012. Ecological and economic trade-offs in the management of mixed fisheries: a case study of spawning closures in flatfish fisheries. Mar. Ecol. Prog. Ser. 447, 179–194.

Russ, G.R., Alcala, A.C., 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, Central Philippines. Mar. Ecol. Prog. Ser. 132, 1–9.

Ryland, J.S., Ajayi, T.O., 1984. Growth and population dynamics of three *Raja* species (*Batoidei*) in Carmarthen Bay, British Isles. J. Cons. Int. Explor. Mer 41, 111–120.

Schrope, M., 2010. Fisheries: what's the catch? Nature 465, 540–542.

Shipp, R.L., 2003. A perspective on marine reserves as a fishery management tool. Fisheries 28, 10–21.

Ulrich, C., Reeves, S.A., Vermard, Y., Holmes, S.J., Vanhee, W., 2011. Reconciling single-species TACs in the North Sea demersal fisheries using the fcube mixed-fisheries advice framework. ICES J. Mar. Sci. 68, 1535–1547.

UN, 2016. The Sustainable Development Goals Report, 2016. (accessed 27 September 2018). https://unstats.un.org/sdgs/report/2016/.

Vinther, M., Reeves, S.A., Patterson, K.R., 2004. From single-species advice to mixed-species management: taking the next step. ICES J. Mar. Sci. 61, 1398–1409.

Walker, P.A., Heessen, H.J.L., 1996. Long-term changes in ray populations in the North Sea. ICES J. Mar. Sci. 53, 1085–1093.

Wilhelm, T.A., Sheppard, C.R.C., Sheppard, A.L.S., Gaymer, C.F., Parks, J., Wagner, D., Lewis, N., 2014. Large marine protected areas – advantages and challenges of going big. Aquat. Conserv. Mar. Freshwater Ecosyst. 24, 24–30.

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., Jensen, O.P., Lotze, H.K., Mace, P.M., McClanahan, T.R., Minto, C., Palumbi, S.R., Parma, A.M., Ricard, D., Rosenberg, A.A., Watson, R., Zeller, D., 2009. Rebuilding global fisheries. Science 325, 578–585.

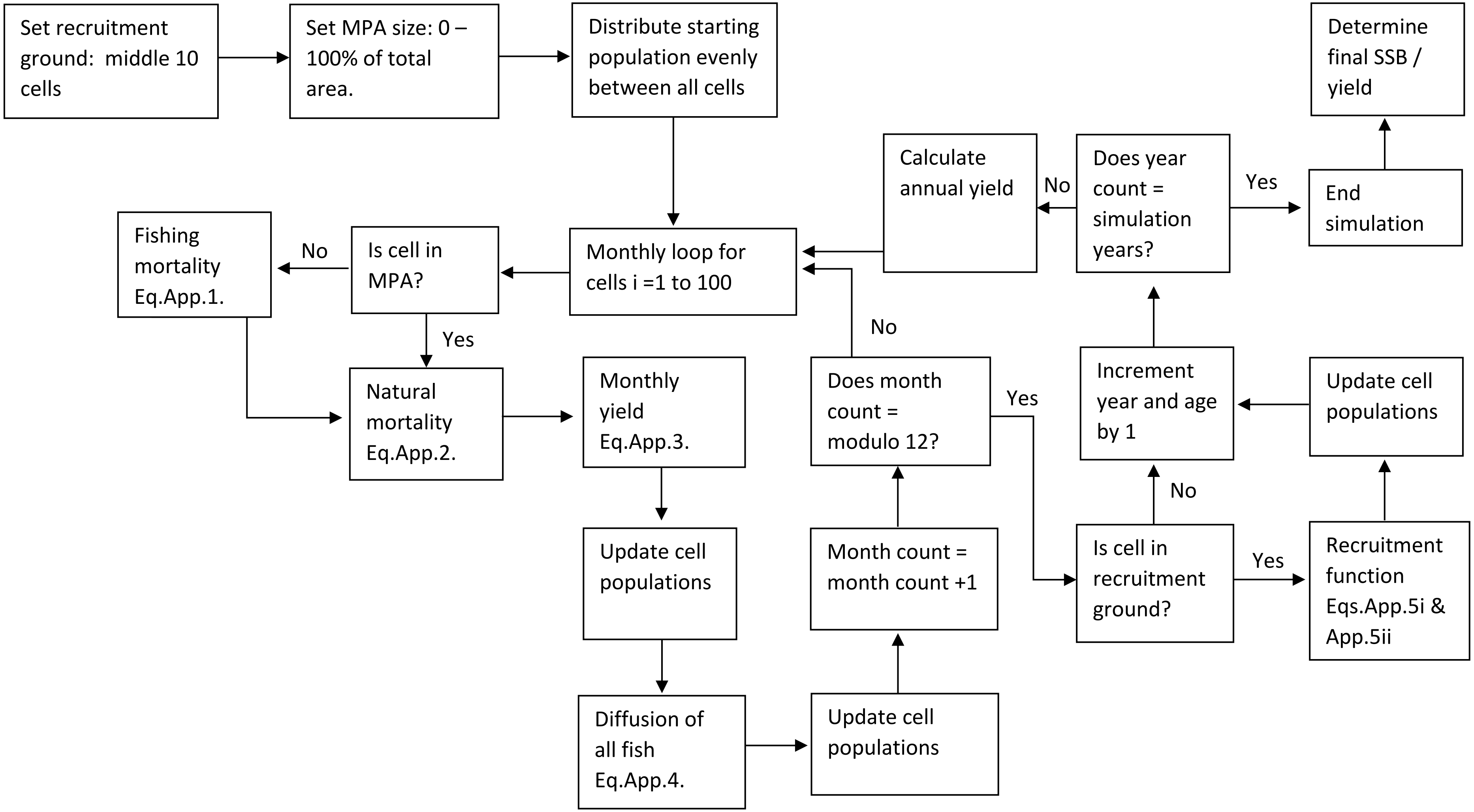


Figure App.1: Flow chart of the simulation, indicating the monthly and annual sub-processes which are fully described by the accompanying equations below the diagram.

Equations App.1 – App.5

App.1 $\mathrm{F_{a,c}} = \mathrm{E}.\frac{\mathrm{S_a}}{12x}$

$\mathrm{F_{a,c}}$ is the fishing mortality for a given age class, a, and cell, c, in the most recent month; E is the nominal annual fishing effort across all cells ($10 \le E \le 200$), x is the number of cells open to fishing, and S_a is the selectivity per age class (see Tables 1 and 2) - the same across all cells for a given age class of each species. As per Le Quesne and Codling (2009), capture efficiency (q) is assumed to be the same between species; this is explored further in supplementary material (Figures S.4i and S.4ii).

App.2 $N_{a,t+1,c} = N_{a,t,c}.\exp(-(F_{a,c} + M_a)$

The standard exponential decay model (Pitcher and Hart, 1982). $N_{a,t,c}$ is the number of individuals of age a in years, at month t, in cell c; M_a is the natural mortality rate at age a (assumed to be the same per species across all cells) and $F_{a,c}$ is the fishing mortality described in (1) applied to cells outside the MPA when t is a multiple of 12 (i.e. the end of a year) the age is updated by one year.

App.3 $Y_{a,t,c} = \left(\frac{F_{a,c}}{F_{a,c}+M_a}\right) * \left(N_{a,t+1,c} - N_{a,t,c}\right) * W_a$

The Baranov (1918) Catch Equation. $Y_{a,t,c}$ is the yield in kg for a given age class, a, and cell, c, in the most recent month, t; W_a is the mass per individual at age a (W_a is the same per species across all cells); $F_{a,c}$ and M_a are as stated in (1) and (2) respectively.

App.4 $p(x) = \frac{e^{\frac{-x^2}{4D}}}{\sqrt{4\pi D}}$.

The probability density function for a single step of a one-dimensional diffusion process (Okubo and Levin, 2001; Codling et al., 2008), where x is the unit of distance between cell centres, D is the diffusion coefficient (D=1, 10 or 100) and $p(x)$ represents the probability that an individual from a given cell will move to another cell up to 100 distance units away in either direction. Similar to Le Quesne and Codling (2009), as p(x) is technically a continuous probability function and x in our model is a discrete variable, at each monthly time-step we rescale each discretely determined value of p(x) such that the total sum over all 100 cells is equal to 1 and it is hence a true probability distribution.

App.5i. $R = \alpha . S . exp^{-(\beta . S)}$

The Ricker (1954) recruitment function. R is the total number of recruits (age 0 fish) to the population; for target, cod-like species α = 0.96, β = 0.00005; for conservation species, α = 0.5, β = 0.00025; S is the total spawning stock biomass, thus:

App.5ii. $S = \sum_{c,a} N_{c,a} * W_a * Mat_a$.

i.e.: where c is the cells in the recruitment ground, a is the age-classes, W_a is the mass per individual at age a and Mat_a is the maturity per age class (as per parameters - Tables 1 & 2

References

Baranov, F.I. 1918. On the question of the biological basis of fisheries in: Sass, G.G., Allen, M.S. (Eds.), Foundations of Fisheries Science. American Fisheries Society, Bethesda, Maryland. pp. 11-72.

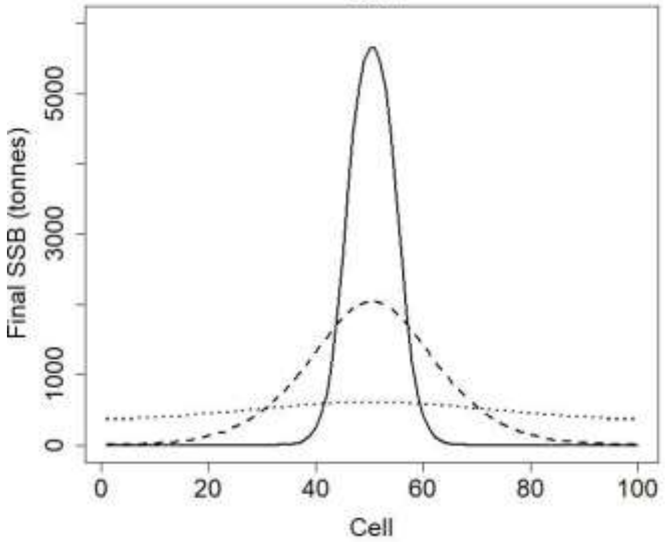
Codling, E.A., Plank, M.J., Benhamou, S. 2008. Random walk models in biology. J. R. Soc. 5, 813-834.

Le Quesne, W.J.F., Codling, E.A. 2009. Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. ICES J. Mar. Sci. 66, 122-131.

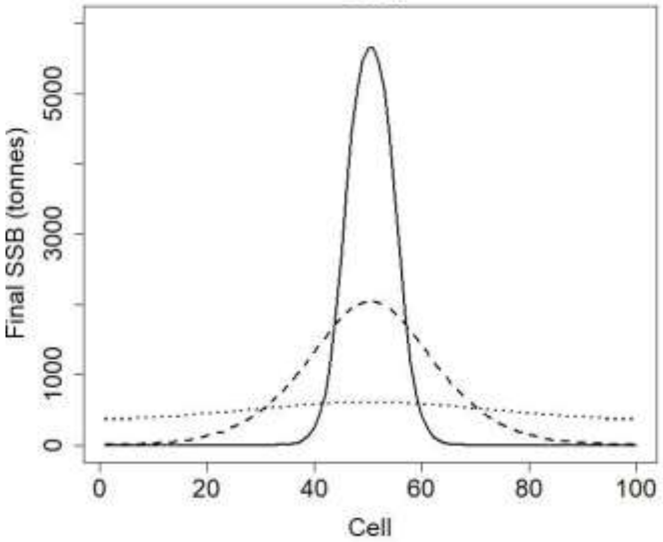
Okubo, A., Levin, S. 2001. Diffusion and Ecological Problems: Modern Perspectives. Springer Verlag, New York.

Pitcher, T.J., Hart, P.J.B. 1982. Fisheries Ecology. Chapman and Hall, London.

Ricker, W.E. 1954. Stock and Recruitment J. Fish. Res. Board of Can. 11(5), 559–623.



S.1i



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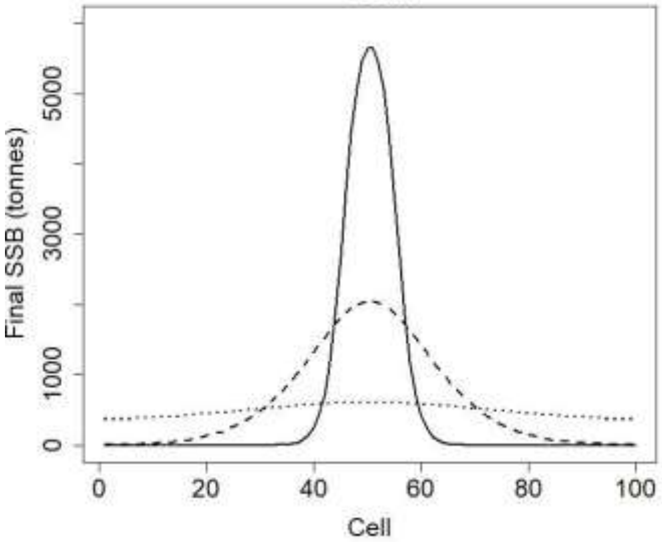

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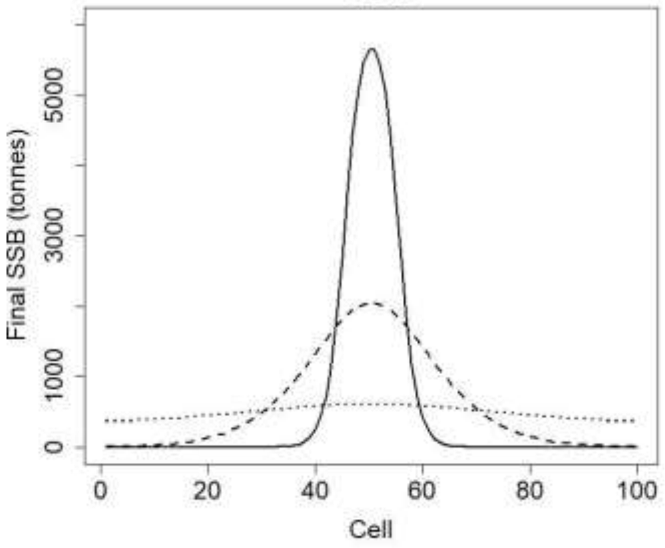

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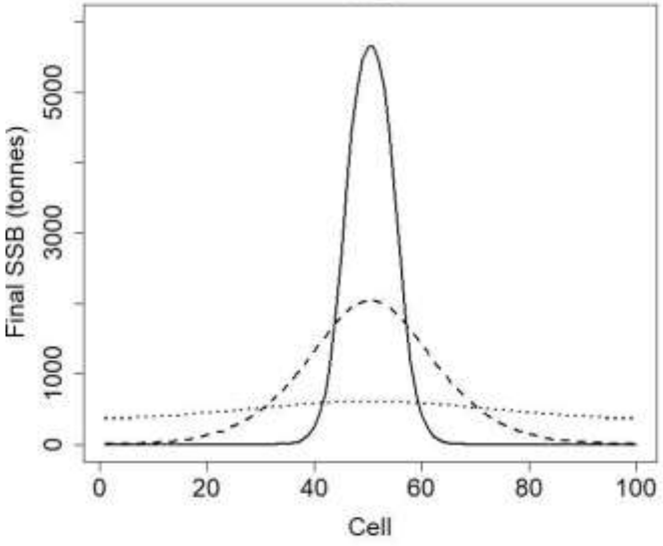

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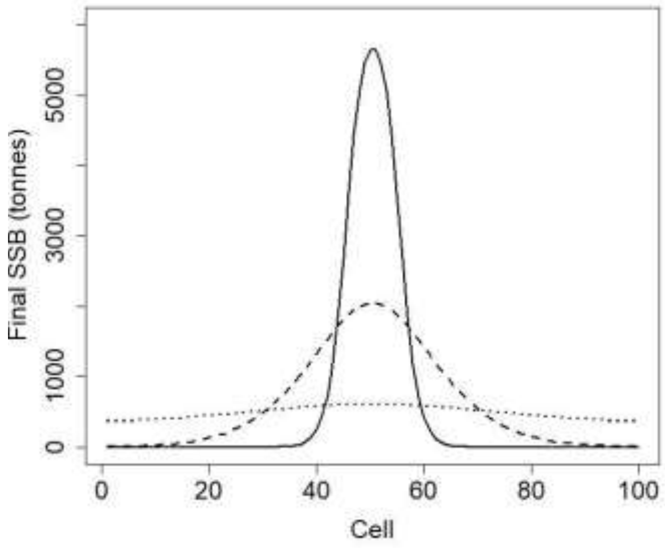


S.1vi

Figure S.1: Final distribution of SSB of the target and conservation species without harvesting or closures after a simulation of 100 years with burn-in times as described below. Three levels of movement (D) are represented: _____, D=1; _ _ _ _ , D=10; . . . . , D=100. The burn-in time between 45 – 50 years is shown not to affect final SSB of the overall stock of either species within the recruitment ground and across the spatial domain as a whole.

S.1i. target species, burn-in time = 50 years
S.1ii. target species, burn-in time = 45 years
S.1iii. target species, burn-in time = 55 years
S.1iv. conservation species, burn-in time = 50 years
S.1v. conservation species, burn-in time = 45 years
S.1vi. conservation species, burn-in time = 55 years

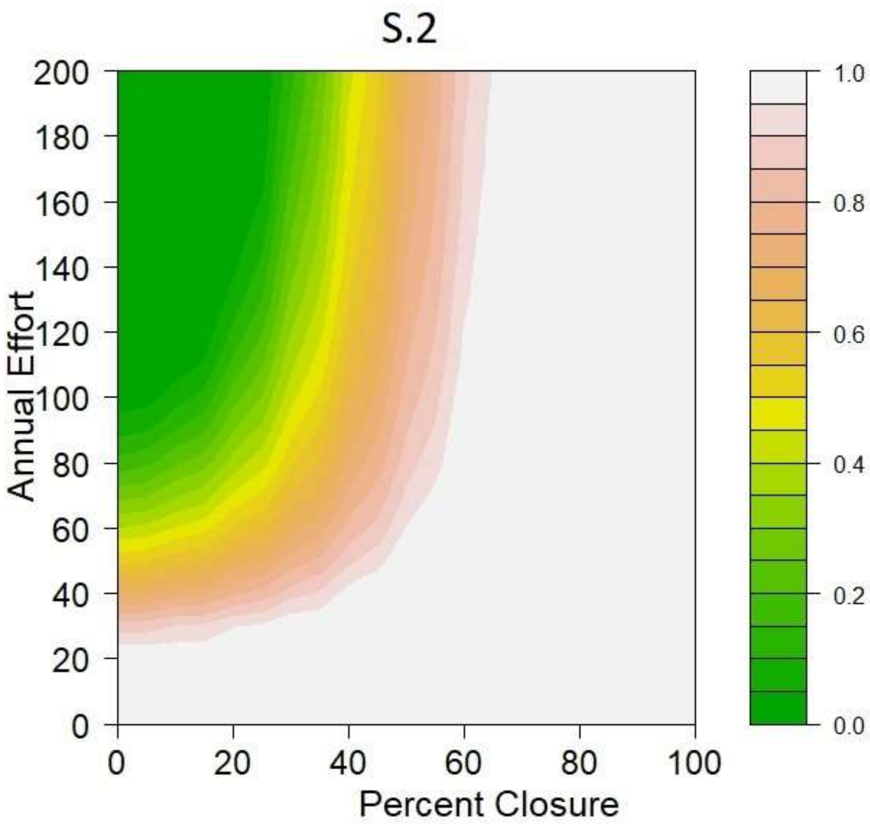


Figure S.2: Scaled results to show the extent to which SSB_{MIN} (represented by a value of 1.0) of the highly mobile (D=100) bycatch conservation species has been met in simulations of a single species fishery protected by 0 – 100% closures to fishing and exposed to annual fishing efforts between 0 and 200. The life-history parameters differ from that of the main model: here, juveniles of the bycatch are not subject to fishing mortality (vs. entering the fishery at age 3+ in the main model) and, consequently, SSBMIN of the bycatch stock can be maintained across a greater range of fishing effort and closure options (compare with Fig. 6c main text).

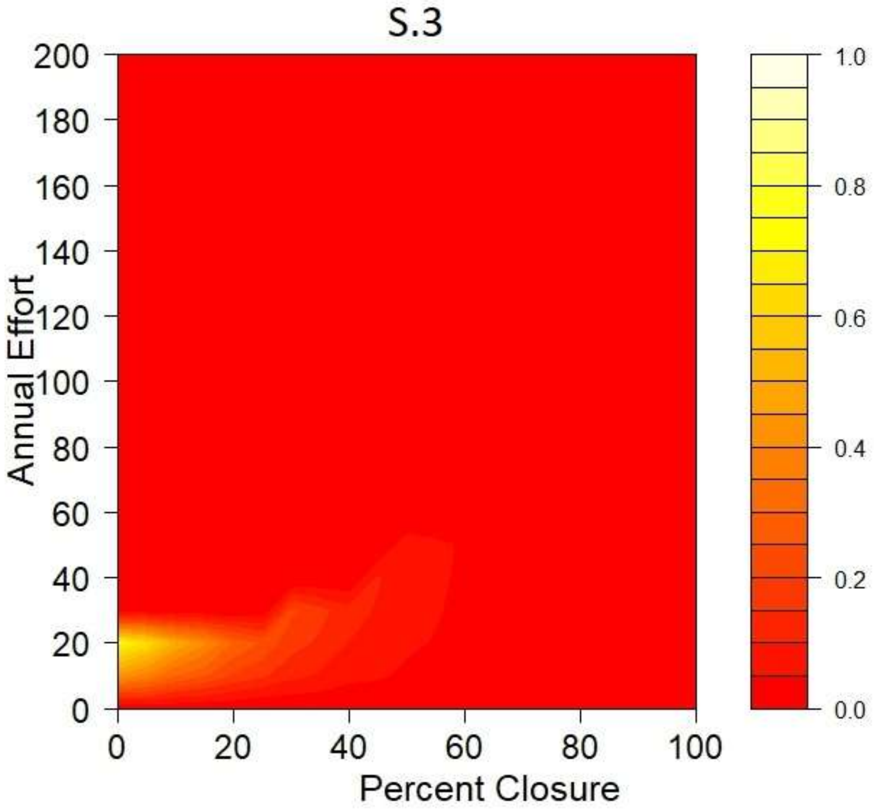
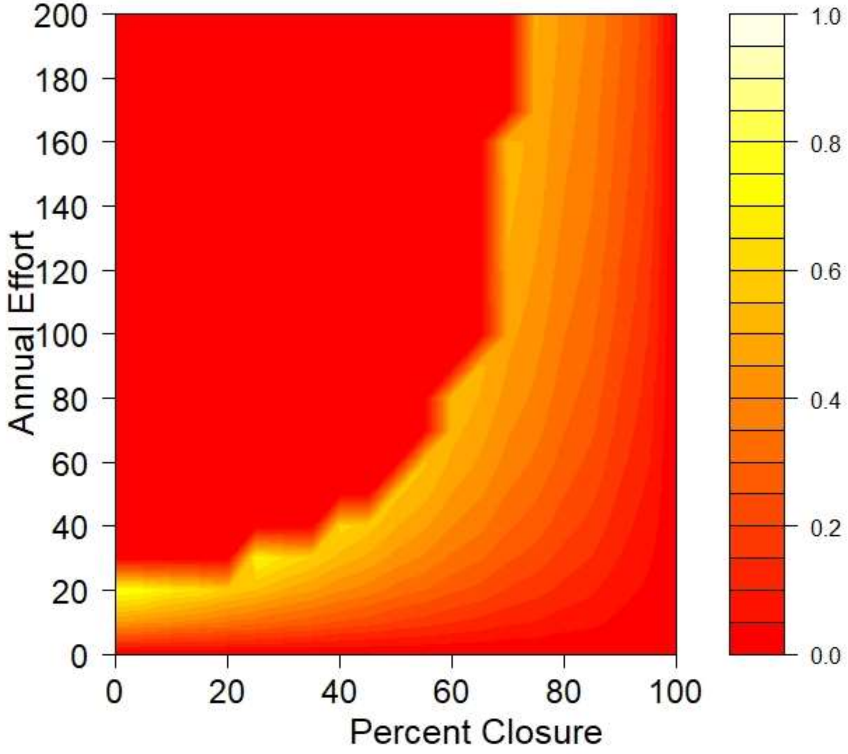


Figure S.3: Weighted results to show the extent to which Y_{OPT} of the target species can be met when SSB_{MIN} of the conservation species has been met (D=100 for both species) in simulations of a two-species fishery protected by 0 – 100% closures to fishing and exposed to annual fishing efforts between 0 and 200. The simulation was run for 100 years in monthly time steps. The simulation differed from the main model because juveniles were not subject to fishing mortality. The main model (when juveniles age 3+ were subject to fishing pressure) had a best-case scenario of 0.4 of Y_{OPT} of the target species being met (Fig. 7i); removing juveniles of the bycatch species from the harvest increases the best-case scenario to 0.6 of Y_{OPT} being met, although still with extensive closures and effort control.

S.4i


Annual Effort
200
180
160
140
120
100
80
60
40
20
0
0
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Percent Closure
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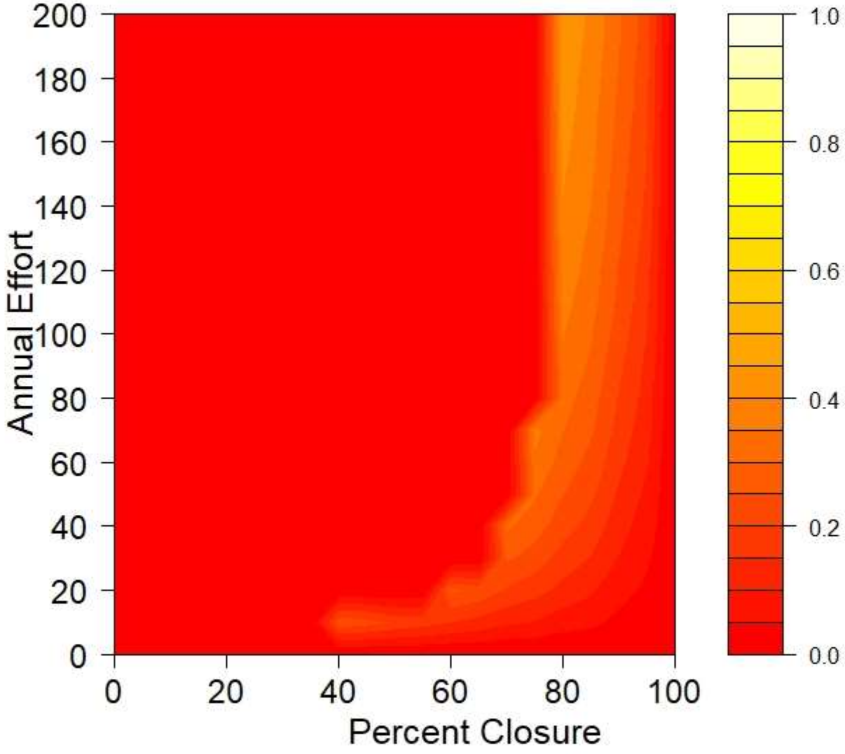
S.4ii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Percent Closure
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0.4
0.2
0.0

Figure S.4: Results to show the extent to which Y_{OPT} of a highly mobile target species can be met when SSB_{MIN} of a highly mobile bycatch conservation species (D=100 for both species) has been met in simulations of a two-species fishery protected by 0 – 100% closures to fishing and exposed to annual fishing efforts (E) between 0 and 200. The simulation was run for 100 years in monthly time steps. In the main model the catchability coefficient (q) of both species was q=1.0. In this simulation the bycatch species has a catchability coefficient of q=0.5 (Fig. S.4i) and q=2.0 (Fig. S.4ii); catchability coefficient of the target species remains as q=1.0. When the bycatch species' capture efficiency is half that of the target species (Fig. S.4i) the best-case scenario improves from 0.59 (Fig. 7c) to 0.76 (Fig. S.4i) of Y_{OPT} of the target species being met. This can be achieved with smaller closures (40% or less compared with 40% or more in the main model) coupled with effort management. When the bycatch species' capture efficiency is twice that of the target species (Fig. S.4ii), the best-case scenario is reduced to 0.44 of Y_{OPT} of the target species being met and requires more extensive closures (80% or more) coupled with effort management.

Chapter 4: How effective is an MPA compared to seasonal closures to meet the fishery management aims of a mobile species?

Abstract

Seasonal closures are a management option utilised in temperate regions to protect the spawning stock of commercial species: they can maintain reproductive capacity and theoretically prevent overfishing, but their effectiveness has been questioned due to consequent effort-displacement by fishers. Additionally, poorly-timed closures which do not match the spawning season of a species – particularly in a multi-species fishery – are thought to contribute to declines in species' biomass and overfishing. Alternatively, spatial closures (MPAs) have been used to protect fish spawning aggregations of reef-based fisheries but using MPAs to protect the spawning grounds of temperate, mobile species is more problematic due to the wide-ranging spatial variability in their spawning grounds. In this chapter, a single-species, age-structured spatio-temporal model is used to explore whether seasonal spawning closures can protect the spawning biomass and yield of a mobile species to the same extent as a year-round MPA. The extent that mobility of the species and the degree of density dependence in the stock-recruitment relationship change the effects of each type of closure are explored. The results indicate that an appropriate stock-recruitment relationship should be incorporated into future simulations of closures – both seasonal and spatial – in order for more reliable predictions to be gained. Seasonal spawning-closures are considered as an alternative management approach to MPAs to conserve biomass and produce yield of commercial species, and recommendations are given for the implantation of both seasonal closures and the siting of MPAs.

4.1 Introduction

Permanent No Take Zones (NTZ) and Marine Protected Areas (MPAs) are areas of the oceans and seas in which human activities are restricted for conservation of biodiversity and fisheries management purposes (Kelleher, 1999). As discussed more thoroughly in Chapter 1, the enhancement of biomass associated with NTZ MPAs can have benefits to meet conservation aims (for example: Lester *et* al., 2009; Costello and Ballantine, 2015; Edgar *et al*., 2014; Giakoumi *et al*., 2018) and also to meet fisheries aims (for example: Edgar *et al.,* 2014; Di Lorenzo *et al*., 2016; Davies *et al*., 2017).

4.1.1 MPA protection of mobile stocks

MPA size is a key factor in the success or failure of an MPA in contributing to conservation and fisheries aims (see Chapter 2; Edgar *et al*., 2015; Watson *et al*., 2019). Small MPAs are ineffective conservation tools when the range of the species is not encompassed by the MPA (Gaines *et* al., 2010a; Agardy *et al*., 2011) and large and very large MPAs are better matched to the spatial scales evident in marine ecosystems (Agardy *et al*., 2011; Wilhelm *et al*., 2014). Larger individual MPAs have been proposed as a way of protecting mixed stocks (Russ *et al*., 2008) and have been shown to have economic benefits when applied to commercial species with slow growth rates (Cabral *et al*., 2019). Whether the benefits to biomass and biodiversity increase proportionally to MPA size has been debated (for example: Guidetti and Sala, 2007; Claudet *et al*., 2008; Davies *et al*., 2017), and it is thought that a large spatial area must be a well-enforced NTZ for the benefits of the MPA to be realised (Agardy *et al*., 2011; Edgar *et al*., 2014; Costello and Ballantine, 2015).

The benefits of MPAs to species with low mobility (such as home-range species) have been reported as providing a refuge from harvesting for overexploited stocks and enabling biomass to rebuild within the MPA boundary for conservation purposes (for example: see Bohnsack, 1998; Almany *et al*.; 2009; Davies *et al*., 2017). The enhanced biomass can then 'spillover' to benefit the harvest of commercial stocks (Russ and Alcala, 1996; Halpern and Warner, 2002; Abesamis and Russ, 2005; Murawski *et al.,* 2005). There are fewer reports of the conservation and fisheries benefits of MPAs to mobile species typical of temperate waters (Breen *et al*., 2015). As described in Chapter 1 (section 1.2), it has long been recognised that more mobile species will cross an MPA boundary more frequently, at which point the stock will no longer have conservation benefits from the protection of the MPA (Allison *et al*., 1998; Blyth-Skyrme *et al*., 2006). As such, the mobility of a stock should be taken into account when planning MPAs (Le Quesne and Codling 2009; D'Aloia *et al*., 2017) and species' movement has been highlighted as a key consideration when predicting the success of MPAs (Le Quesne and Codling, 2009; D'Aloia *et al*., 2017; Cabral *et al*., 2019; Watson *et al*., 2019). As discussed in Chapter 1 (section 1.3.1) and as per the results in Chapter 2, large MPAs have been proposed to be of greater benefit to more mobile species (for example: Le Quesne and Codling, 2009; Agardy *et al*., 2011; Edgar *et al*., 2014; Wilhelm *et al*., 2014). Alternatively, small MPAs which protect important parts of mobile species' life-histories could also be of benefit (Game *et al*., 2009; Breen *et al*., 2015).

4.1.2 Protection of spawning stocks

Fish spawning aggregations are seen in many commercial species and have been noted as vulnerable to overexploitation because fish can either be harvested on route to the spawning site before reproduction (for example: camouflage grouper, *Epinephelus polyphekadion* (Rhodes *et al*., 2011)) or subject to aggregation fishing (for example: orange roughy, *Hoplostethus atlanticus* (Sadovy, and Domeier, 2005)). The need to protect fish spawning aggregations (FSAs) for conservation and fisheries management is recognised (Erisman *et al*., 2017) because FSAs can prove highly profitable to fishers (MPA News, 2006; de Mitcheson, 2016) and harvesting which targets aggregations can leave stocks vulnerable to overexploitation (Sadovy and Domeier, 2005; Rhodes *et al*., 2011). The application of MPAs as a protection strategy of FSAs has increased (González-Irusta and Wright, 2016); however, limited data about these largely reef-based MPAs have not, as yet, demonstrated the expected outcomes in conservation and fisheries management targets (Grüss *et al*., 2014).

FSAs in reef fish are characterised quite specifically by being predictable in time and space and forming densities at least four times greater than outside the aggregation (Domeier, 2011). Many commercial, mobile fish species in temperate areas (see Chapter 1, section 1.4) also show spawning aggregations, both behaviourally (over extensive spawning grounds) or in a limited spatial area (Ellis *et al*., 2010). Although these aggregations have been considered when siting MPAs such as the United Kingdom Marine Conservation Zones (MCZs) (Blyth-Skyrme, 2010; Ellis *et al*., 2010), there can be high variability in temperate species' spawning seasons and grounds (for example: Daan *et al*., 1990; CEFAS, 2001; Fox *et al*., 2008; Engelhard *et al*., 2014; González-Irusta and Wright, 2016). Consequently, MPAs specifically protecting spawning grounds of temperate, mobile species are challenging to situate and thus not well documented (Blyth-Skyrme *et al*., 2006; Breen *et al*., 2015).

The common alternative measure to mitigate the vulnerability of spawning stocks in temperate regions is the implementation of seasonal spawning closures, which have been discussed in Chapter 1, section 1.4. To reiterate the key points, the potential benefits of these have been shown through modelling (Wiegand *et al*., 2011) but can also result in effort-displacement (Clarke *et al*., 2015, Sys *et al*., 2017) and will fail to protect spawning stock if the closure is not in synch with the spawning season (Clarke *et al*., 2015). Multi-species fisheries present an additional complexity when the spawning times and sites differ between species (Samy-Kamal *et al*., 2015). The success of spawning closures in a fishery will be largely species dependent (van Overzee and Rijnsdorp, 2015), particularly given the varying life-history and stock-recruitment strategies within the diversity of species in temperate waters (Shepherd, 1982; Iles, 1994; Wiegand *et al*., 2011). When a spawning aggregation is harvested it could be detrimental to the reproductive capacity of the stock, which would therefore have a negative impact on conservation efforts and could potentially lead to overfishing (Sala *et al.,* 2002; de Mitcheson *et al.,* 2008; de Mitcheson 2016; Erisman *et al.,* 2012).

There remains a paucity of information in the literature regarding seasonal spawning interventions and their application in sustainable fisheries management. It is useful, then, to explore further the potential of spawning-season closures to protect stocks for conservation and fisheries aims in comparison to year-round MPAs.

4.1.3 Stock Recruitment Relationships

The stock recruitment relationship (SRR) in a population describes the number of recruits which join the fishery as a function of the size of the adult stock. It can thus be considered a predictor of the productivity of that stock and is fundamental to the understanding of management of fisheries stocks (Pitcher and Hart, 1982). As such, the choice of stock-recruitment relationship is a pivotal underlying assumption in any simulation of fisheries management.

The Ricker (1954) stock recruitment function used in the preceding chapters implies strong density-dependence in a population, producing a domed curve representing low recruitment at high stock levels. In fish populations, density-dependent mechanisms have been shown empirically to be strongest and most likely to occur on the proportion of the population which are 10% or less than the population asymptotic length (Lorenzen and Camp, 2019). Strong density-dependent mechanisms operating in a population could be, for example, cannibalism by adults on younger cohorts (Hannesson, 2018) or ‘scramble competition’ for limited resources (Bellows, 1981).

The Beverton-Holt (1957) equation is another commonly used stock-recruitment function which also describes density-dependence but represents a steady reduction in recruitment as adult stock-density increases. This results in an asymptotic upper-bound of recruitment imposed, for example, by resource limitation (Pitcher and Hart, 1982). Alternatively, Cushing’s (1971) stock-recruitment function does not show density dependence at high stock levels and can be considered ‘unbounded’ as adult stock increases (Iles, 1994).

The choice of stock-recruitment curve used can affect the outcome of a stock assessment (Kimura, 1988) and will similarly affect the predictions from simulations of fisheries stocks. As such, selecting a suitable SRR which allows density-dependence to be descried as a model parameter will enable any resulting simulations of MPA effectiveness to have more reliable predictive abilities for a given stock.

4.1.4 Chapter aim and objectives

The aim of this chapter is to determine if the application of seasonal spawning closures can have the same effects in terms of sustaining biomass and meeting fisheries yields in mobile species as an MPA.

Objectives:

1. to incorporate three degrees of mobility into the single-species model (adapted from that described in Chapter 2) to understand how the degree of the mobility in the stock affects each type of closure;
2. to determine whether the degree of density-dependence in the population stock-recruitment relationship (SRR) used in the model affects the outcomes of seasonal and of spawning closures;
3. to explore whether additional harvest control measures are effective in meeting management aims in terms of biomass conservation and fisheries yields.

4.2 Methods

An age-structured, spatio-temporal, two-patch simulation was programmed in R (R Core Team, 2019), adapted from that described in Chapter 2. Constant annual fishing effort coupled with spatial or seasonal closures were applied in the simulation in order to compare the effects of seasonal closures which protect the recruitment season with a permanent, spatial, NTZ MPA closure on biomass and on fisheries yields of the model population.

4.2.1 Spatial domain

The spatial domain (see Figure 4.1) was the same as that used by Le Quesne and Codling (2009) and can be considered an extension of their model, as per the description in Chapter 2. 100 discrete cells were arranged in a one-dimensional loop, cell 1 being adjacent to cell 100. Fish could move continuously in both directions throughout the entire space. A No Take MPA was applied which encompassed 10%, 50% or 70% of the total area (see Figure 4.1). The model differed from that described in Chapter 2 in that juvenile recruitment was assumed to be global, across the whole spatial domain. Monthly sub-models were applied to each of the 100 cells to describe fishing, mortality, and adult and juvenile movement (see below). Another development from the model described in Chapter 2 was that the recruitment sub-model for this Chapter was applied in the first three months of the year, each year.

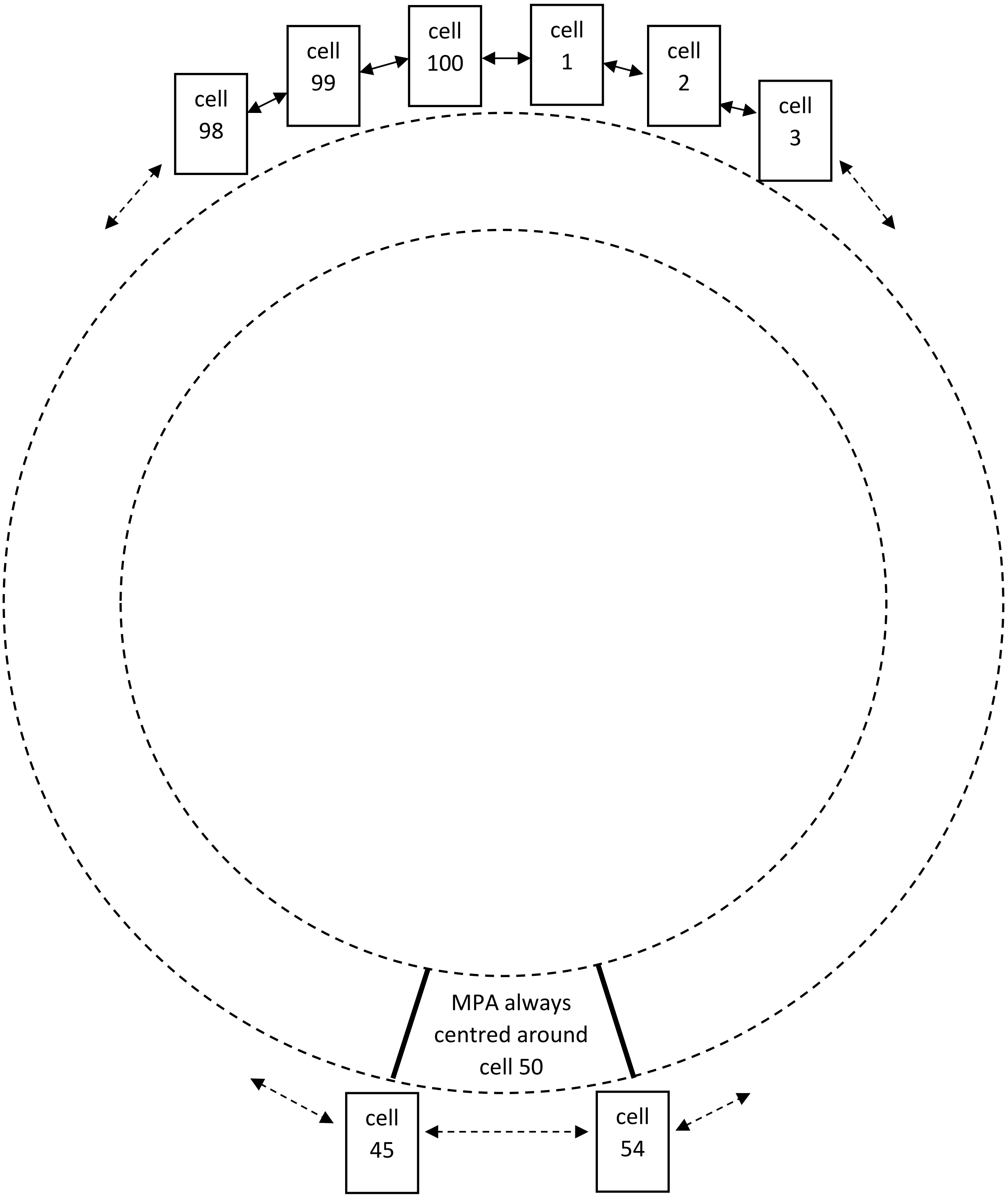


Figure 4.1: Representation of spatial domain of the simulation: the loop represents 100 discrete cells; cell 1 is adjacent to cell 100, recruitment occurs in all 100 cells of the virtual loop and the MPA closures (of 10%, 50% and 70%) are always centred around cell 50. Fish can move continuously in both directions through the loop of cells.

4.2.2 Life history parameters and stock-recruitment relationship

The model was a single-species model with 11 age classes (Table 4.1), the final age class being a plus-group which included all fish which had survived to age 11 or more. Natural mortality was set at 0.2, applied monthly, for all age classes; all fish were assumed to mature in age-class three and juveniles did not form part of the fishery. The model does not seek to compare the effect of these parameters with contrasting ones from a different species and is not therefore representative of a particular species.

Table 4.1: Life-history parameters of the model species.

Age (years)	1	2	3	4	5	6	7	8	9	10	11+
Weight, W_a (Kg)	0.4	0.9	2.4	4.3	6.3	8.5	10.0	11.4	12.4	13.6	14.3
Maturity, Mat_a	0	0	1	1	1	1	1	1	1	1	1
Natural mortality, M_a	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Selectivity, S_a	0	0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

The SRR in the model was described by Shepherd's (1982) stock-recruitment relationship (see Appendix 4A, Equation 4A.5i), in which the value of the parameter β can be altered to adjust the degree of density dependence. The values of β used in the model and the corresponding stock-recruitment curves are shown in Figures 4.2a – 4.2g. Altering the value of β enabled the effects of the spatial and seasonal closures to be explored with reference to stocks which exhibit differing density-dependent stock-recruitment mechanisms.

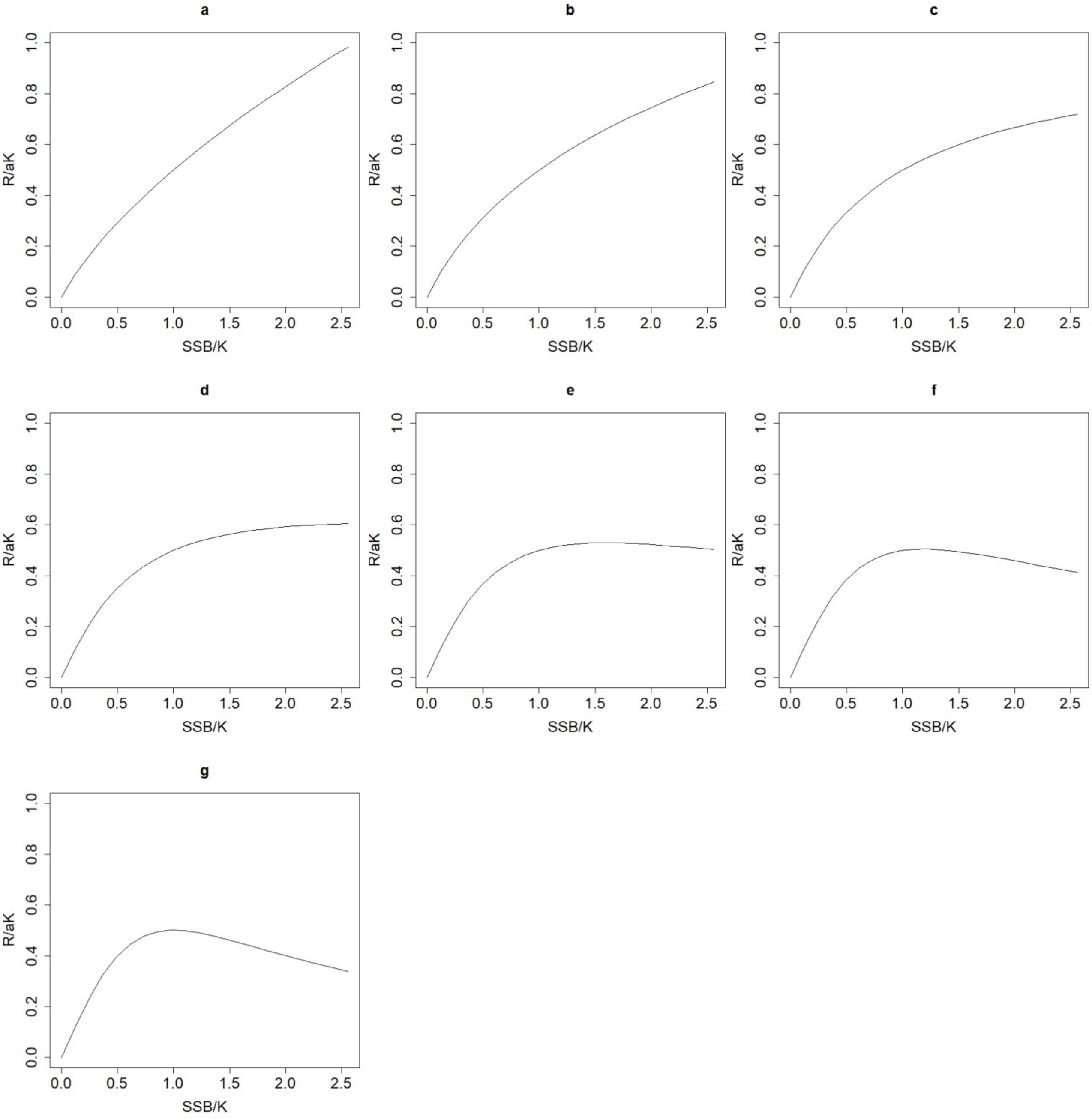


Figure 4.2: SRR relationships described by the Shepherd (1982) stock-recruitment equation where: B=spawning stock biomass; R=recruitment; a=the maximum recruitment-per-unit biomass; K=the threshold biomass; β=extent of density dependence (or ‘degree of compensation’ (Shepherd, 1982)). a. β = 0.5; b. β=0.75; c. β=1.0; d. β=1.25; e. β=1.5; f. β=1.75; g. β=2.0.

4.2.3 Model structure

The processes and equations of the two versions of the model are fully described in Appendix 4A, Figures 4A.1 and 4A.2. To allow the stock-recruitment dynamics to have damped down to a minimum, the model was initially run for a burn-in period of 50 years with zero closures and no fishing; see Chapter 3 (Watson *et al.*, 2019). Fifty years was the time taken for the oscillations of the stock-recruitment function to have damped to a minimum across all values of β in the SRR. The starting population of each model run was therefore an unexploited stock, generated by applying natural mortality (Appendix 4A: Equation 4A.2) to a population using the Shepherd (1982) recruitment function (Appendix 4A: Equations 4A.5i and 4A.5ii) at the designated value of β (Appendix 4A: parameter β). The starting population numbers within each age class were distributed equally across the 100 cells at the start of each simulation.

4.2.4 Monthly population dynamics and fishing

The annual fishing effort (E) was set at E=600 yr^{-1} and remained constant within and between all simulations. When there were spatial or seasonal closures, the total effort was redistributed in space or time respectively, i.e.: without closures E=0.5 $month^{-1}$ per cell. When spatial closures were imposed, the effort was always exerted equally on all populations in the cells outside the spatial MPA and fishing effort within the MPA was always zero. When seasonal closures were imposed, fishing effort across the whole spatial domain was zero. Fishing mortality (Appendix 4A: Equation 4A.1) was applied monthly per age class per cell and the associated yield (Appendix 4A: Equation 4A.3) was calculated. These allowed the monthly population changes per age class per cell due to natural and fishing mortalities to be applied (Appendix 4A: Equation 4A.2) and the population per age class of each cell for that month to be updated.

4.2.5 Monthly movement and population redistribution

Fish movement and population redistribution were the next monthly processes applied, after harvesting and population dynamics. As in Chapter 2 and Chapter 3 (Watson *et al.,* 2019), the movement of all fish (age 1 and over) is described by the one-dimensional diffusion equation (Appendix A: Equation A.4) used by Le Quesne and Codling (2009). The movement was density-independent, random and could result in movement in either direction through the spatial domain. Two values of the diffusion coefficient were used: D=10 and D=100 to represent a mobile and highly mobile, wide-ranging species, respectively. These were not based on empirical data of real species' movements but were representative of different levels of mobility relative to the spatial domain (Le Quesne and Codling, 2009).

4.2.6 Recruitment season and annual yield

Global recruitment was represented in the model by all age-0 fish being equally distributed across all 100 cells of the spatial domain. i.e. they underwent density independent settlement. Although MPAs in reef fish have been used to enclose spawning and recruitment grounds (Grüss *et al*., 2011; Grüss *et al*., 2014; Erisman *et al*., 2017), global recruitment was determined to be the more suitable representative (by precautionary principle) of the variability in temperate species' spawning and recruitment grounds (CEFAS, 2001; fishbase.org). Recruitment remained deterministic so the Shepherd (1982) recruitment relationships could be used to explore the impacts of density-dependence without being masked by the additional complexity of random recruitment events.

Recruitment occurred at the end of the first three monthly time steps each year, after the fishing, population dynamics and movement models had been applied. As discussed above, the recruitment sub-model was applied using the Shepherd (1982) recruitment function (Appendix 4A: Equations 4A.5i and 4A.5ii). Each simulation was run using the values of β previously described in Figure 4.2 and Appendix 4A.

The monthly yields of all age classes from all cells open to fishing within each simulation were summed to give the annual yield after each 12th monthly time-step.

4.2.7 Simulation scenarios

After the initial burn-in time of 50 years, each simulation was run for 20 years in monthly time-step increments. 20 years was chosen as a realistic time-scale in terms of impact if the simulation was to be applied to a fishery. To ensure that no longer-term effects were being disregarded, additional simulations were run for 50 years: the longer simulation run did not yield different outcomes (see Appendix 4B, Figure 4B.1).

Two groups of simulations were run: spatial closures and seasonal closures. In the simulations of spatial closures, MPAs of 10% (to represent a small MPA), 50% (a large MPA) and 70% (a very large MPA) of the total spatial domain were applied. Each of the spatial closure simulations was repeated for each value of β and for both values of the diffusion coefficient (D=10 and D=100).

Seasonal closures were simulated by closing the whole fishery for the recruitment season +/- additional months, thereby protecting the adult spawning stock and the year 0 stock during those months. To ensure that the seasonal closures were not merely acting on population density dependence, an additional simulation was run before commencing with the suite of seasonal closure simulations. The conditions were that the fishery was kept open during the recruitment season (months 1 to 3) but was closed for the three months furthest away time-wise from that recruitment season (months 7 to 9). The results demonstrated that protecting the recruitment season with seasonal closures was of greater benefit in terms of SSB than closing the fishery during a different three months of the year (see Appendix 4C, Figure 4C.1).

In the simulations of seasonal closures, the entire fishery was closed for: 1. the first two months of the recruitment season (months 1 and 2); 2. the whole recruitment season (months 1 to 3); 3. the recruitment season and an additional month (months 1 to 4); 4. the recruitment season and two additional months (months 1 to 5) and 5. the recruitment season and an additional three months (months 1 to 6). Each simulation was repeated for each value of β.

The seasonal closure simulations were not repeated for both values of the diffusion coefficient because, without spatial closures, fishing occurred throughout the spatial domain in months that harvesting was permitted and therefore all individuals (regardless of degree of mobility) were equally susceptible to harvesting.

4.2.8 Biological reference points

The maximum mean annual yield achieved without closures was calculated for each value of β to serve as a benchmark for the subsequent examination of the effect of spatial and seasonal closures on the yield. The benchmark for SSB (SSB_{MIN}) was taken as 0.4 of unfished SSB at each value of β. 0.4 of unfished SSB was selected as an appropriate benchmark in line with B_{LIM} (biomass limit) for commercial stocks (ICES, 2017). Additional SSB_{MIN} thresholds were also used as benchmarks and the results of these are available in Appendix 4C, Figures 4C.2a – 4C.2f.

4.2.9 Harvest control

Harvest control has been utilised in conjunction with other management measures to conserve fisheries stocks (Needle and Catarino, 2011; Fernandes and Cook, 2013) and was incorporated in the model as effort control. Each simulation was run multiple times, reducing the annual effort in each iteration. The final annual effort which maintained SSB at 0.4 of the unfished SSB in each scenario was taken as the effort to be applied under harvest control measures; it was distributed evenly per month (in months open to fishing) and per cell (in cells open to fishing).

4.3 Results

4.3.1 Effects of β value on raw yield and final SSB.

The effect of the value of β in the Shepherd (1982) equation on raw yield and final SSB are shown in Figures 4.3a and 4.3b, respectively. Increasing the value of β decreased both the raw total yield and the final SSB. This is to be expected due to the increasing density-dependence within the SRR as β increases (see Figures 4.2a - 4.2g); as such, SSB and yield are supressed at high values of β.

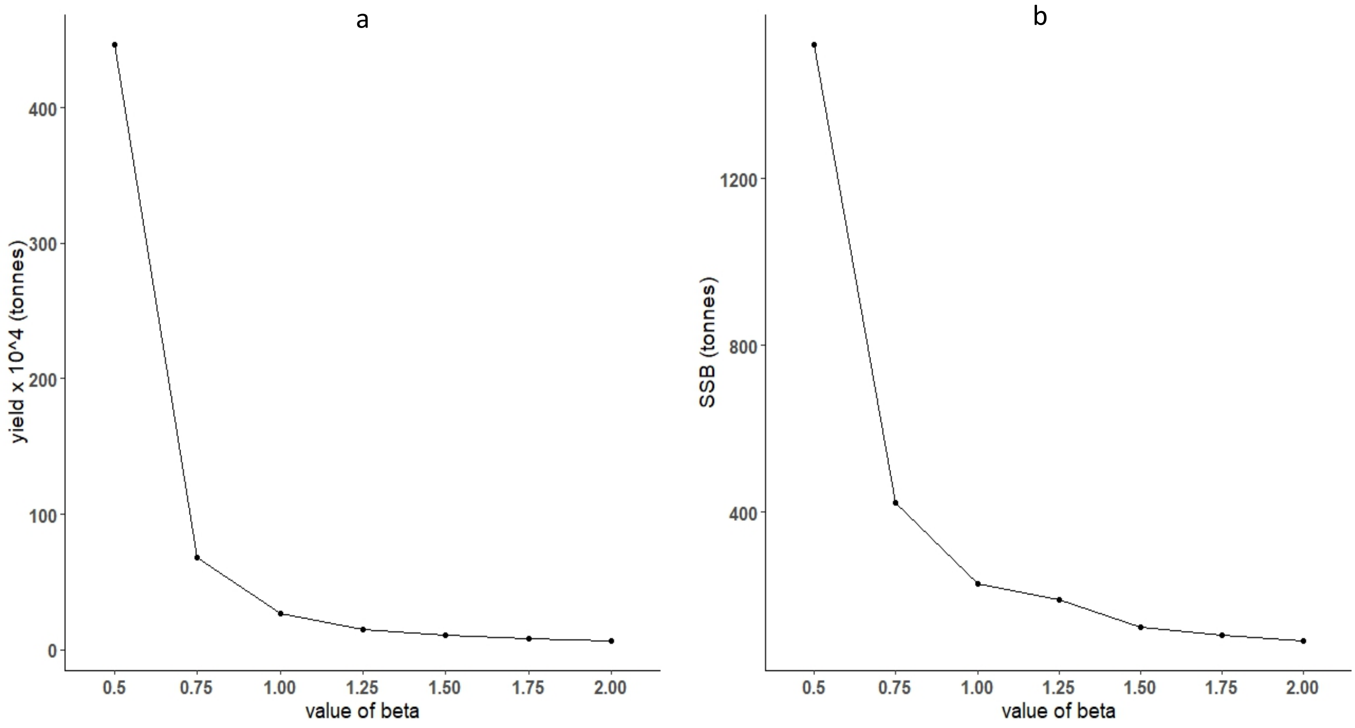


Figure 4.3: The effect of changing β value in the Shepherd (1982) stock recruitment equation on a. raw mean annual yield and b. final SSB after one simulation run (50 years burn-in time plus an additional 20 years) with no closures at constant fishing effort.

4.3.2 Effects of spatial closures

The proportion of the mean annual yield without closures which could be achieved at the MPA sizes (10%, 50%, and 70%) for the seven values of β are shown in Figures 4.4a (D=10) and 4.4b (D=100). The introduction of a small (10%) MPA only decreased mean annual yield by 2% or less. Increasing the size of the MPA decreased the proportion of mean annual yield which could be met, with a very large MPA (70%) reducing the proportion of mean annual yield by approximately half for D=10 mobility (Figure 4.4a) across all values of β. When mobility of the stock increased (D=100, Figure 4.4b), a greater proportion of the mean annual yield was met, rising to 0.75 for a very large MPA (70%) for all values of β.

At D=10 (Figure 4.4a) and D=100 (Figure 4.4b), the proportion of mean annual yield which could be met with any closures in place rises by up to 3% with increasing values of β. As shown in Figure 4.3a, increasing β decreases raw yield, so although the proportion of yield met was slightly higher at higher values of β (i.e. when there is greater density dependence in the SRR), there was still overall less yield than at lower values of β (i.e. when there is lower density dependence in the SRR).

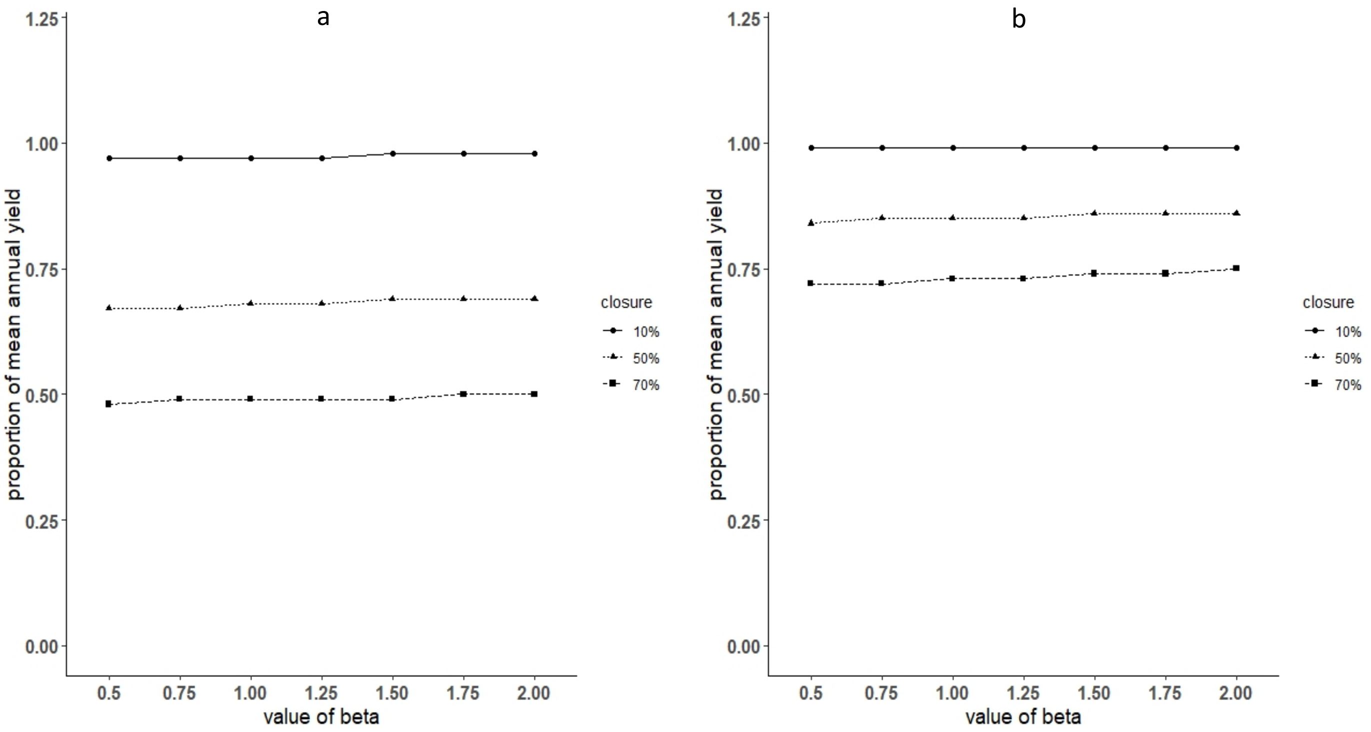


Figure 4.4: The proportion of mean annual yield (without closures) which can be met with a single MPA of size 10%, 50% or 70% in place at each β value in the Shepherd (1982) stock recruitment equation. Two levels of stock mobility are represented: a. d=10; b. d=100.

The proportion of SSB_{MIN} (0.4 unfished SSB) met with closures in place at each value of β is shown in Figure 4.5a (D=10) and 4.5b (D=100). As expected, larger closures protected more of the SSB. SSB_{MIN} could always be met with 70% closures when D=10 (Figure 4.5a) but increased mobility (Figure 4.5b) reduced SSB_{MIN} to less than half across all values of β. The stock recruitment relationship is such that closures of any size were of most benefit to the SSB of populations with β values of β=1.25 and β=1.5.

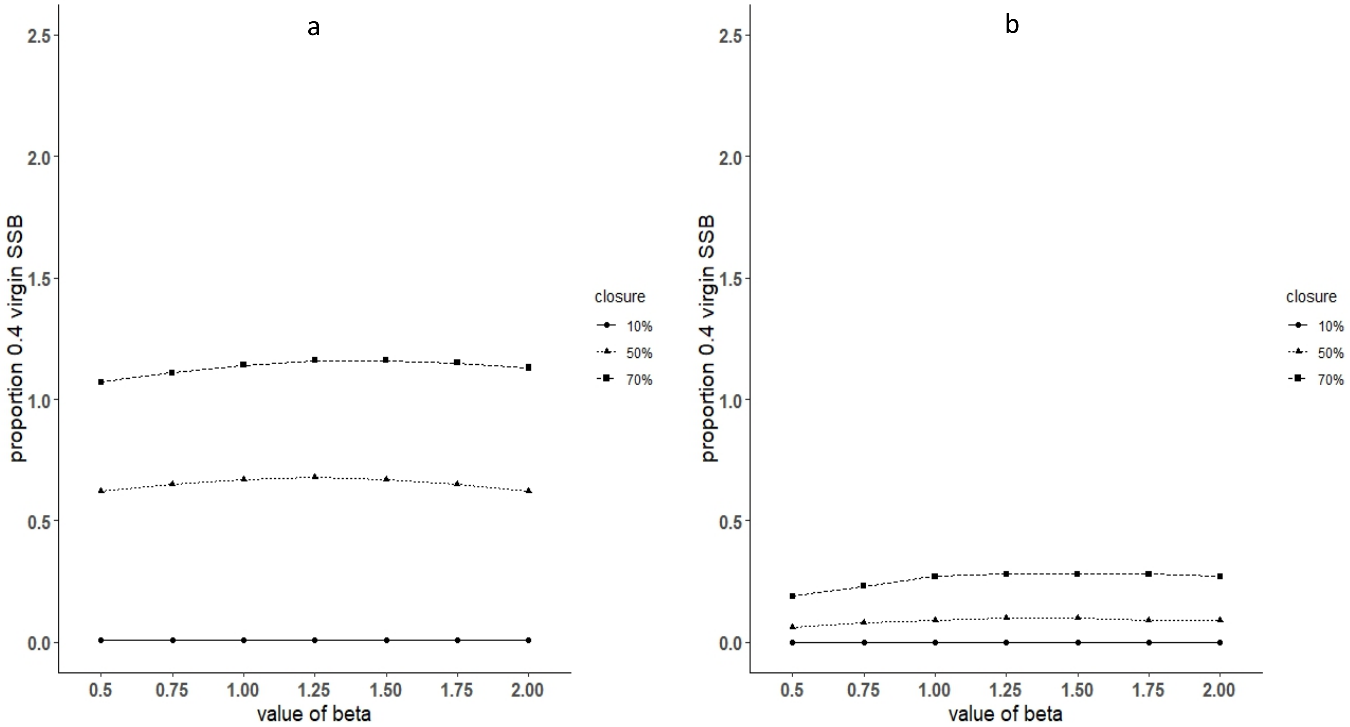


Figure 4.5: The proportion of SSB_{MIN} (0.4 of virgin SSB) which can be met with a single MPA of size 10%, 50% or 70% in place at each β value in the Shepherd (1982) stock recruitment equation. Two levels of stock mobility are represented: a. d=10; b. d=100.

4.3.3 Effects of seasonal closures

Seasonal closures of any length which contained the three-month recruitment season prevented the mean annual yield without closures being met across all values of β (Figure 4.6). However, closures of 4 – 6 months (i.e.: closure for the recruitment months plus an additional one to three months) enabled a greater proportion of the yield to be met across all values of β than both 50% and 70% closures at D=10 (Figure 4.4a) and D=100 (Figure 4.4b). Comparing the six-month closures (Figure 4.6) to the 50% closures (Figures 4.4a and 4.4b) shows that redistribution of effort in time gave a greater proportion of the mean annual yield without closures than redistribution of effort in space.

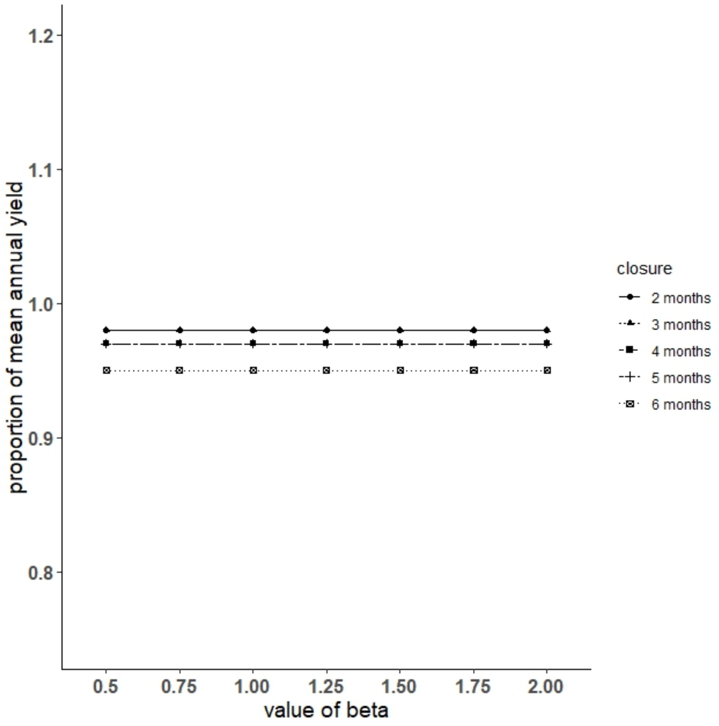


Figure 4.6: The proportion of mean annual yield (without closures) which can be met with seasonal closures of 2-6months in place at each β value in the Shepherd (1982) stock recruitment equation. Recruitment is always in months 1-3; the closures always start from the beginning of each year.

The seasonal closures did not protect SSB_{MIN} to the same extent as the spatial closures. The proportion of SSB_{MIN} retained with seasonal closures in place always yielded less than 1% of SSB_{MIN} being met and was thus not plotted. This was also true for the additional SSB thresholds which were explored: seasonal closures protected less than 1% of any SSB threshold – far less than the protection afforded by 50% and 70% MPA closures (see Appendix 4C).

4.3.4 Effects of Harvest Control

Harvest control within the model ensured that SSB_{MIN} was maintained in all simulations. When harvest control was introduced over and above spatial closures (Figures 4.7a and 4.7b), the proportion of unfished mean annual yield achieved decreased at all closure sizes and values of β compared to spatial closures alone (Figures 4.4a and 4.4b).The biggest decrease in yield was seen for the highly diffusing fish (compare Figure 4.7b with 4.4b). Although these individuals were exposed to harvesting more often because they frequently crossed the MPA boundary, the harvest-control means they cannot be extracted if doing so would force SSB to below the threshold.

Applying harvest control over and above seasonal closures also decreased the proportion of unfished mean annual yield achieved for all lengths of closure and values of β (compare Figure 4.7c with Figure 4.6). However, without harvest control SSB was effectively fished to sub-threshold levels. For mobile species, the results of imposing harvest control over and above spatial closures (Figure 4.7b) or seasonal closures (Figure 4.7c) were equitable in terms of the proportions of mean annual yield met.

In all the above scenarios of both spatial and seasonal closures, although introduction of harvest control decreased mean annual yield, the proportion which could be met increased with increased density-dependence in the SRR (Figures 4.7a - 4.7c). However, it is worth returning to the relationships between β and yield (Figure 4.3a): the actual yield always decreased with β, i.e.: with increased density-dependence in the stock.

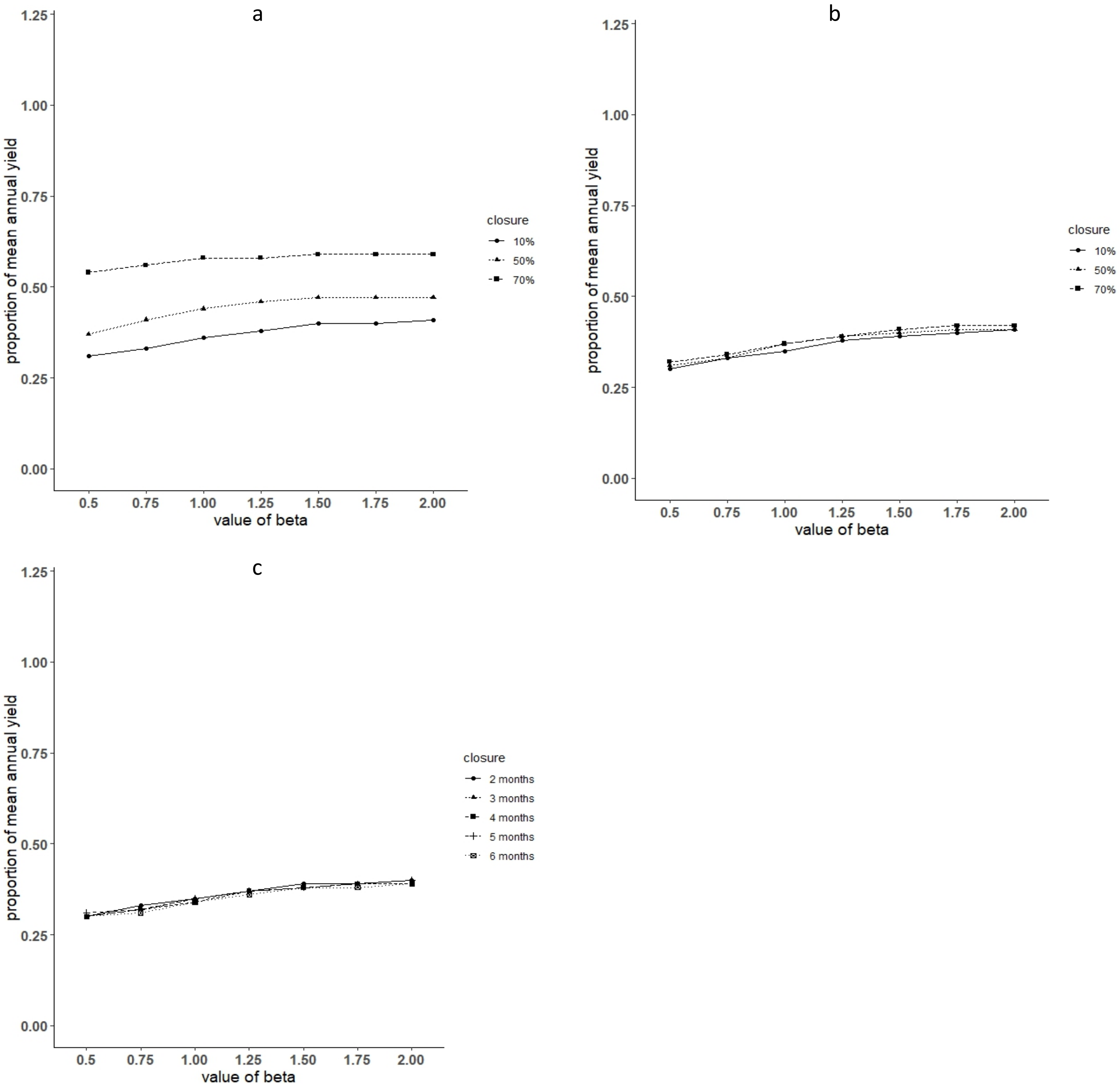


Figure 4.7: The proportion of mean annual yield (without closures) which can be met at each β value in the Shepherd (1982) stock recruitment equation when harvest control is implemented (to maintain SSB at SSB_{MIN}) in addition to:

a. a single MPA of size 10%, 50% or 70% in place; stock mobility, d=10

b. a single MPA of size 10%, 50% or 70% in place; stock mobility, d=100

c. seasonal closures of 2 to 6 months (always starting in month 1).

4.4 Discussion

The model described is a single-species model which compares the potential of spatial and seasonal closures to preserve biomass and yield in mobile stocks. The simulations explore whether the mobility of the stock and the extent of density dependence in the population stock-recruitment relationship impact the effectiveness of each type of closure. Harvest control is also explored as an additional management tool, which can be imposed over and above spatial and seasonal closures.

The results indicate that very large spatial closures are better at protecting SSB, although this is tempered by mobility of the stocks. However, applying seasonal or spatial closures without an understanding of the underlying stock-recruitment relationship could lead to fisheries and conservation management targets failing. It is suggested that, by applying harvest control in addition to closures, seasonal closures could be used as an alternative approach to an MPA to meet conservation objectives and still produce yield for fishers. These results are not intended to apply to particular species but are used to explore management options available to meet conservation and fisheries aims for mobile stocks across a range of life-history strategies.

4.4.1 Comparison of spatial closures and seasonal closures

The potential benefits of MPAs to fisheries and conservation objectives have been widely reported and debated for over two decades (Chapter 1; e.g. Bohnsack, 1998; Halpern and Warner, 2002; Worm *et al*., 2009; Gaines *et al*., 2010b). Although mobile species are less well-represented in the literature (Allison et *al.,* 1998; Micheli *et al*., 2004b; Breen *et al*., 2015), it has been proposed that whole-species benefits can be accrued from protecting crucial parts of a mobile species' life-history (Game *et al*., 2009; Breen *et al.,* 2015). In addition to spatial closures, seasonal closures which protect spawning and recruitment can also be used as a fisheries management tool and have been reported to have benefits to conservation and fisheries management aims (Erisman *et al*., 2017), although there are few empirical studies which have evaluated the impact of seasonal closures (Clarke *et al*., 2015; van Overzee and Rijnsdorp, 2015). The model described enables the theoretical benefits of recruitment-season closures to be compared to those of No Take Zone MPAs in mobile stock typical of temperate areas.

The results from the simulations of spatial closures were in keeping with Chapter 2 and previous, widely reported empirical and simulation studies which have recognised increased susceptibility of individuals when crossing the MPA boundary (Game *et al*., 2009; Agardy *et al*., 2011; Edgar *et al*., 2014; Cornejo-Donso *et al*., 2017; Watson *et al*., 2019). The larger the closure the greater proportion of SSB is protected. Increased mobility results in individuals crossing the MPA boundary more frequently, lowering SSB but increasing yields. Despite the increase in yield with increased mobility, only the smallest of MPAs modelled (10%) enabled 95% or more of the mean annual yield without closures to be maintained for mobile and highly mobile stocks. The proportion of the mean annual yield which could be maintained decreases with increased closure size. Seasonal closures consistently enable 95% - 98% of mean annual yield without closures to be met thereby facilitating more predictable yields. These yields are equivalent to a small MPA and better than both the large and very large MPA. Seasonal closure simulations did not take into account stock mobility because a whole-fishery closure does not confer different advantages to stocks based on mobility. Whilst maintaining the yield may be preferential to some stakeholders (Rees *et al*., 2010; Metcalfe *et al*., 2015; Jones *et al*., 2016) seasonal closures do so to the detriment of the stock biomass, which was driven to well-below threshold levels with all seasonal closures.

It has been suggested that temporal closures which protect spawning stocks may enhance reproductive output and recruitment to offset effort displacement by fishers (Pelc *et al*., 2010; Hamilton *et al*., 2012; Rijnsdorp *et al*., 2012), but seasonal fishery closures did not effectively protect the SSB, which was reduced under all lengths of closure to a fraction of the SSB_{MIN} threshold. Advocates of spawning season closures have proposed that rapid benefits can be seen in terms of fisheries and conservation objectives (Erisman *et al*., 2017), but these closures can also be counter-productive if effort displacement in space or time leads to over-fishing and biomass depletion (Clarke *et al*., 2015; Grüss and Robinson, 2015), e.g. after the sole (*Solea solea*) fishery closure in the Celtic Sea (Sys *et al*., 2017). Comparing 50% spatial closures to 50% (six month) seasonal closures shows that, although displacement in time is more lucrative in terms of yield, displacement in space protects more of the biomass. Nonetheless, SSB_{MIN} was only preserved for the less-mobile stock when a very large MPA of 70% was introduced; and SSB_{MIN} of the highly mobile stock could not be preserved even with a very large MPA.

The current simulation supports the standpoint that seasonal closures may not provide the expected levels of protection (Grüss and Robinson, 2015; van Overzee and Rijnsdorp, 2015) to biomass and offer no better protection than alternative management restrictions (Wiegand *et al*., 2011). Despite this, and evidence of the previous failures of seasonal closures (Clarke *et al*., 2015; Sys *et al*., 2017), seasonal closures may still be a viable real-world alternative to permanent MPA closures. The migration patterns, spawning aggregations and nursery grounds in UK and European waters can be subject to spatial and temporal fluctuations. Seasonal closures can be put in place and communicated both *a priori* and as a rapid responsive measure to such seasonal fluctuations (European Parliament, 2010; www.gov.uk a, 2019; www.gov.uk b, 2019), affording real-time protection to stocks which may otherwise be prevented by the bureaucracy which would be necessitated when re-siting an MPA.

4.4.2 Effects of density dependence

There is wide variation in the life-history strategies of marine fish, which should be considered when modelling and suggesting management options (King and McFarlane, 2003; Lowerre-Barbieri, 2019). Use of the Shepherd (1982) stock-recruitment equation within the current model enabled the effects of spatial and seasonal closures to be evaluated for different degrees of density-dependence in the SRR. A stock with high density-dependence in the SRR accrued slightly more harvest benefits in terms of the spatial closures than those without the density-dependent relationship, but only in comparison to the yield of each stock without closures. However, because the SRR which had the least density dependence gave the highest yields without closures, the net yield for highly density-dependent SRR stocks is still much lower. The positive effects of spatial closures are most evident in the populations which exhibit intermediate density-dependence in the SRR. Stocks which have the classical Ricker (1954), stock-recruitment function benefit less from the MPA. This is likely because older, mature adults are protected from harvesting and therefore suppress recruitment within the population.

The variability in life-history strategies and, thus, recruitment of exploited marine populations is well documented (for example: Shepherd, 1982; Fogarty *et al.*,1991; King and McFarlane, 2003; Ricard *et al.*, 2016; Lorenzen and Camp, 2019). Results from this study suggest that failure to assign the most appropriate SRR to a stock

(Touzeau and Gouzé 1998), or not paying heed to the variability in stock-recruitment within the stock (Myers and Cadigan, 1993; Myers, 2001; Pierre *et al*., 2017; Lorenzen and Camp, 2019), could result in inaccurate estimates of yield and SSB when an MPA is in place, potentially negating biological reference points (Piet and Rice, 2004). In summary, it is suggested that conclusions from spatially explicit movement models of fisheries are as dependent on choosing the most appropriate SRR (Hennemuth, 1980; Iles, 1994) sub-model as any other model within the simulation.

4.4.3 Effects of harvest control

The harvest control applied in the simulations was effectively a form of effort control, reducing the total annual effort to levels which allowed preservation of SSB_{MIN}. At all sizes of MPA and density dependence, applying harvest control over and above spatial closures decreased the mean annual yield. The biggest decreases compared to the yield without closures are seen in the most highly-diffusing fish, which spend least time inside the MPA and therefore do not benefit in terms of SSB to the same extent of less-diffusive (and therefore less fishable) stocks. A slightly higher proportion of mean annual yield can be met in stocks which show high density dependence in the SRR. However, the application of harvest control in addition to MPAs in highly mobile stocks resulted in very similar proportions of mean annual yields across all closure sizes. Such information could be of value when trying to meet multiple-stakeholder objectives which are sometimes conflicting (Metcalfe *et al*., 2015; Jones *et al*., 2016), particularly in coastal habitats where large and very large MPAs are not always feasible (Gaines *et al*., 2010b, Edgar *et al*., 2014).

When the stock is highly mobile, seasonal closures of any length coupled with harvest control give very similar outcomes to those achieved for harvest controls with spatial closures – an overall decrease in the proportion of mean annual yield but less-so with high density dependence in the SRR. This can potentially offer a variety of management actions: SSB_{MIN} can be maintained and the same yield produced (albeit somewhat lower than the yield without closures), by either siting a permanent MPA and controlling effort or by shutting the fishery seasonally and controlling effort. Each solution may hold incentives to different stakeholders (Liu *et al*., 2018; Caveen *et al*., 2014) and the decision can be made as to which solution holds the optimum measurable benefits to each party (Erisman *et al*., 2017). Having a suite of management tools available is sometimes needed to ensure reproductive capacity of a stock is maintained (Payne *et al*., 2009; Grüss *et al*., 2014), and having flexibility of approach in terms of effort control coupled with closures could go some way to addressing this multi-faceted approach to fisheries and conservation management. Difficulties in effective management of MPAs can lead to conservation objectives not being met (Edgar *et al*., 2014; Gill *et al*., 2017) and a short-term, seasonal closure may be more effective in terms of the management and resource-deployment (Gaines *et al*., 2010a; 2010b) needed to enforce the closure than a permanent MPA. On the other hand, seasonal closures which are poorly timed (Clarke *et al*., 2015) or fail to sufficiently protect the larger spawning stock (van Overzee and Rijnsdorp, 2015), can also be ineffective. This could be of particular concern when spawning seasons are variable and subject to changing environmental conditions (Daan *et al*., 1990; CEFAS, 2001; Ellis *et al*., 2010; Engelhard *et al*., 2014; González-Irusta and Wright, 2016). Nevertheless, in a mixed fishery with a variety of life-histories and mobilities – the extent of which may not be fully understood - seasonal closures to protect the recruitment of stock with additional effort control imposed may be the better option than MPAs, which are affected by the mobility of the stock.

4.4.4 Model assumptions and future developments

Species movement was represented in the model as diffusion-based and served to illustrate the extent of movement in relation to the one-dimensional virtual space of the model. As already outlined in previous chapters, future developments of the model will benefit from migratory-type movements to and from spawning / recruitment grounds. This is of particular relevance when examining mobility with respect to spawning season closures: additional parameterisation of movement types would allow exploration of the impact of closing part or all of the migration route as well as the spawning ground. The addition of migratory movements within the model would need to be coupled with a spatially accurate representation of the geographical area in question. The life-history parameters would also need to be made species-specific and based on empirical data.

The results of the current simulations indicate that any future models exploring spatial and seasonal closures should incorporate the stock recruitment relationship with the appropriate level of density-dependence for the stock being modelled. The findings relating to the SRR in the simulation are also of relevance to the wider ecological discussions about positive mortality effects within populations. Given the evidence that these effects are specific to life-history stages (Ratikainen *et al*., 2007; O'Connor *et al*., 2014; Schröder *et al*., 2014), a beneficial future development of the model would be to incorporate density-dependent models which are specific to the age and stage within the simulation and, ideally, accurately model the inter life-stage dynamics. Such developments would provide better representations of recruitment (Pepin, 2015) and, thus, the model would give more accurate predictions of the effects of closure.

The three-month long recruitment season has been simplified as a deterministic event within the model. Stochastic recruitment has been shown to have little effect on fisheries outcomes in single species simulations (Le Quesne and Codling, 2009) but intra-species and inter-annual variability in recruitment of stocks is well documented (for example: Ricard *et al*., 2016; Lorenzen and Camp, 2019; Pierre *et al*., 2018) and should be incorporated in future models of specific stocks.

The harvest control in the model was a simple reduction of annual effort to maintain the SSB threshold. An alternative approach would be to modify selectivity by age and / or size within the model to enable different parts of the stock to be protected and to mirror gear limitations imposed on a fleet.

In summary, the model provides overarching principles to consider when protecting a mobile stock by either a permanent MPA or seasonal closures which protect the recruitment season. The outcomes have demonstrated that an accurate understanding of density dependence within the SRR is needed in future models if yield and biomass estimates are to be valid. Additionally, effort control should be considered as an additional management tool over and above any form of closure to preserve SSB whilst also enabling some harvesting. Finally, the results suggest that, although on its own a seasonal closure is less favourable to conservation aims, when coupled with effort control it can be considered a viable alternative to a permanent MPA, thereby affording a greater variety of management options to stakeholders.

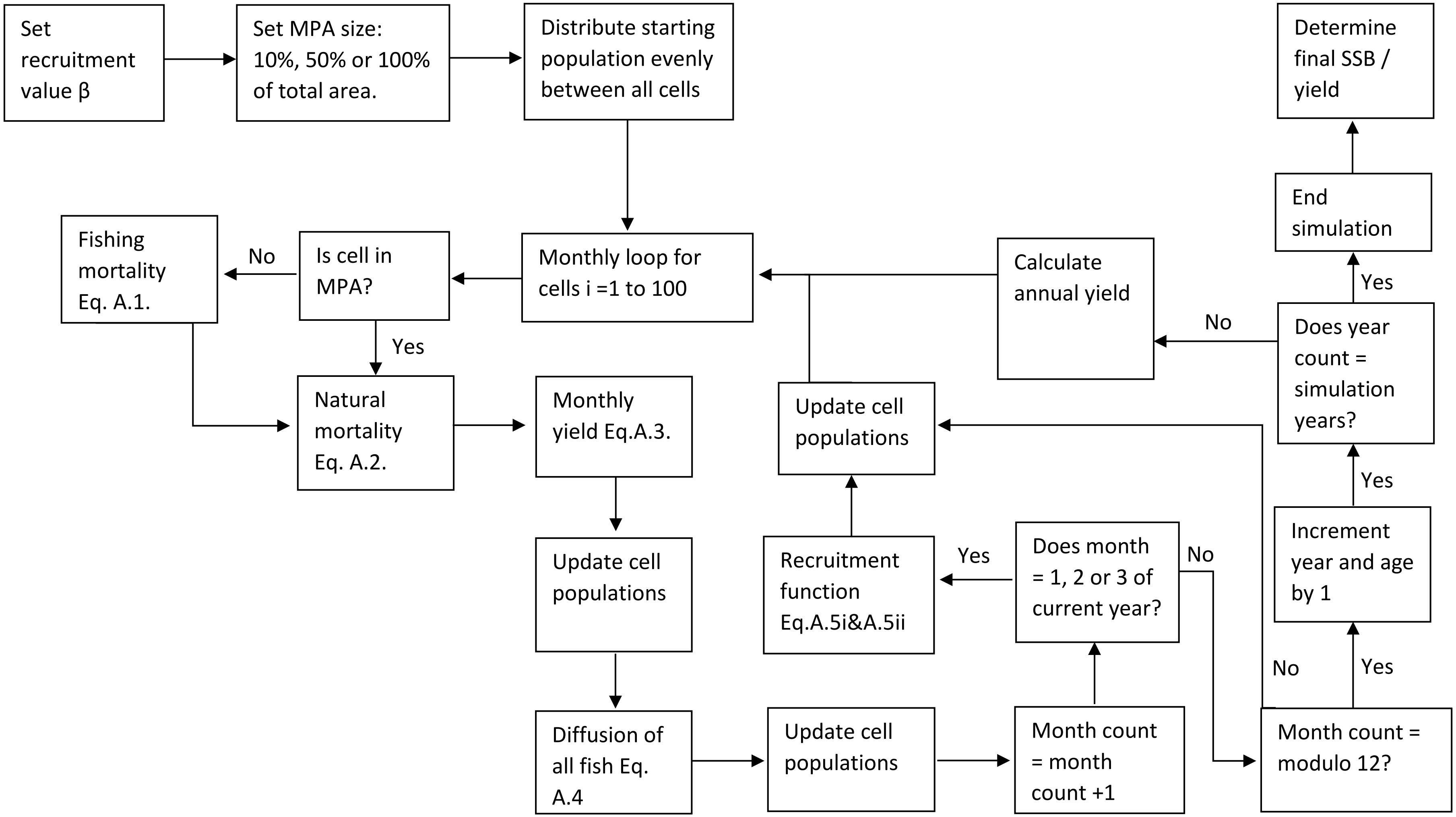


Figure 4A.1: Flow chart of the simulation when spatial closures (a single, No Take Zone MPA) are in place, indicating the monthly and annual sub-processes which are fully described by the accompanying equations below the diagram.

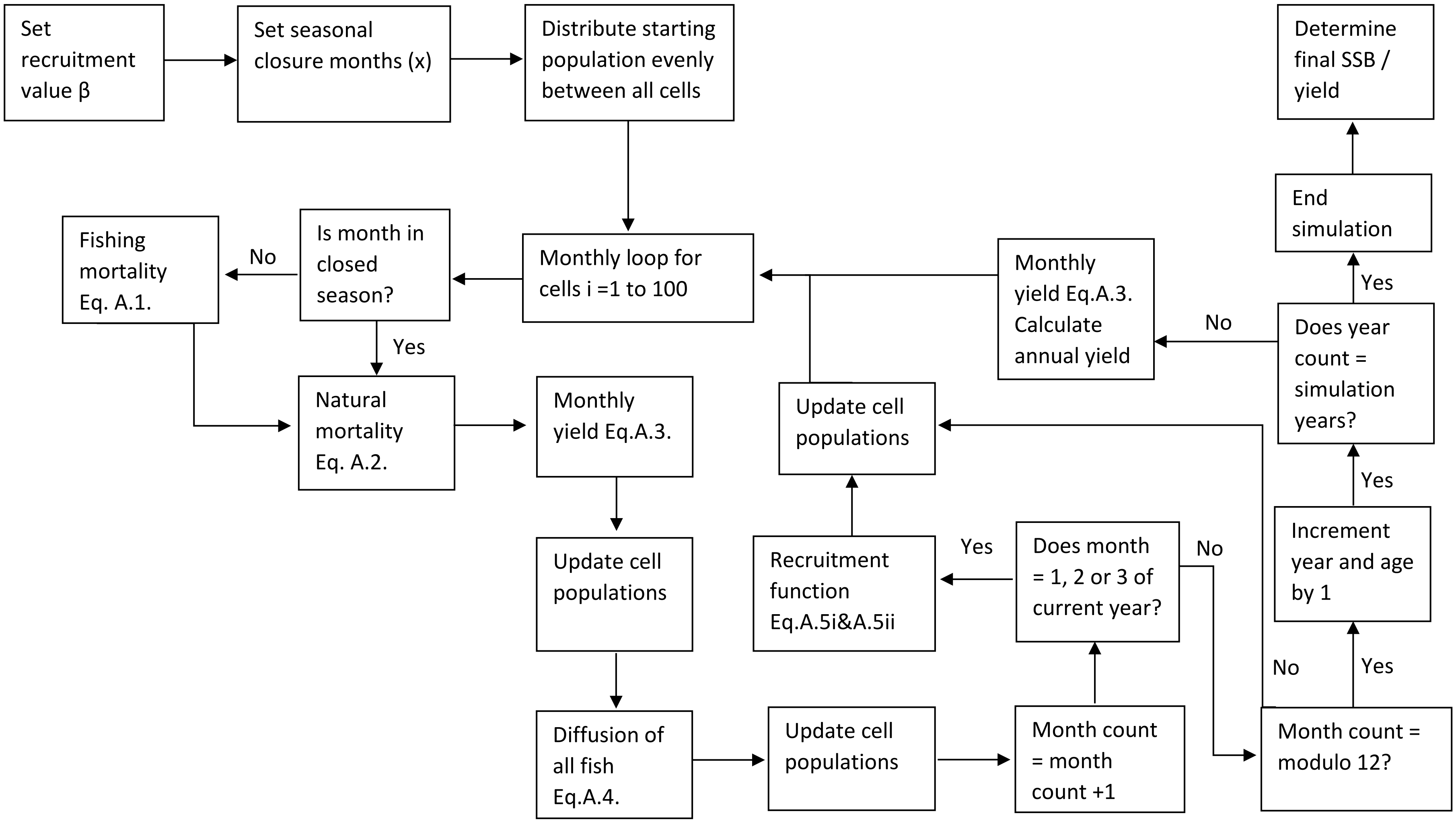


Figure 4A.2: Flow chart of the simulation when seasonal fishery closures are in place, indicating the monthly and annual sub-processes which are fully described by the accompanying equations and parameters below the diagram.

Parameters

β= 0.5; 0.75; 1.0; 1.25; 1.5; 1.75 or 2.0

x = months 1-2; 1-3; 1-4; 1-5; 1-6; 7-9

Equations 4A.1 – 4A.5

4A.1 $\mathrm{F}_{\mathrm{a,c}} = \mathrm{E}.\frac{\mathrm{S_a}}{12x}$

$F_{a,c}$ is the fishing mortality for a given age class, a, and cell, c, in the most recent month; E is the nominal annual fishing effort across all cells (E=600) and S_a is the selectivity per age class (see Table 1) - the same across all cells for a given age class of each species. As per Le Quesne and Codling (2009), capture efficiency (q) is assumed to be the same between species.

4A.2 $N_{a,t+1,c} = N_{a,t,c}.\exp(-(F_{a,c} + M_a)$

The standard exponential decay model (Pitcher and Hart, 1982). $N_{a,t,c}$ is the number of individuals of age a in years, at month t, in cell c; M_a is the natural mortality rate at age a (assumed to be the same per species across all cells) and $F_{a,c}$ is the fishing mortality described in (1) applied to cells outside the MPA when t is a multiple of 12 (i.e. the end of a year) the age is updated by one year.

4A.3 $Y_{a,t,c} = \left(\frac{F_{a,c}}{F_{a,c}+M_a}\right) * \left(N_{a,t+1,c} - N_{a,t,c}\right) * W_a$

The Baranov Catch Equation (Baranov, 1918). $Y_{a,t,c}$ is the yield in kg for a given age class, a, and cell, c, in the most recent month, t; W_a is the mass per individual at age a (W_a is the same per species across all cells); $F_{a,c}$ and M_a are as stated in (1) and (2) respectively.

4A.4 $p(x,t) = \frac{e^{\frac{-x^2}{4D}}}{\sqrt{4\pi D}}$.

The probability density function for a single step of a one-dimensional diffusion process (Okubo and Levin, 2001; Codling *et al*, 2008), where x is the unit of distance between cell centres, t is a monthly time step, D is the diffusion coefficient (D=10 or 100) and $p(x,t)$ represents the probability that in a single monthly time step (t) an individual from a given cell will have moved to another cell up to 100 distance units away in either direction. The sum of $p(x,t)$ was rescaled to 1 at each monthly time-step. The population redistribution at each monthly time step is calculated independently for each of the spatial cells so elements of the population are not redistributed more than once in a single time step.

4A.5i. $R = \frac{aB}{\left[1+\left(\frac{B}{K}\right)^{\beta}\right]}$

The Shepherd (1982) recruitment function. R is the total number of recruits (age 0 fish) to the population; α = 0.023; K=0.41x10^6; β = 0.5, 0.75, 1.0, 1.25, 1.5, 1.75 or 2.0 (defined in simulation); S is the total spawning stock biomass, thus:

4A.5ii. $S = \sum_{c,a} N_{c,a} * W_a * Mat_a$.

i.e.: where c is the cells in the recruitment ground, a is the age-classes, W_a is the mass per individual at age a and Mat_a is the maturity per age class (as per parameters - Table 1

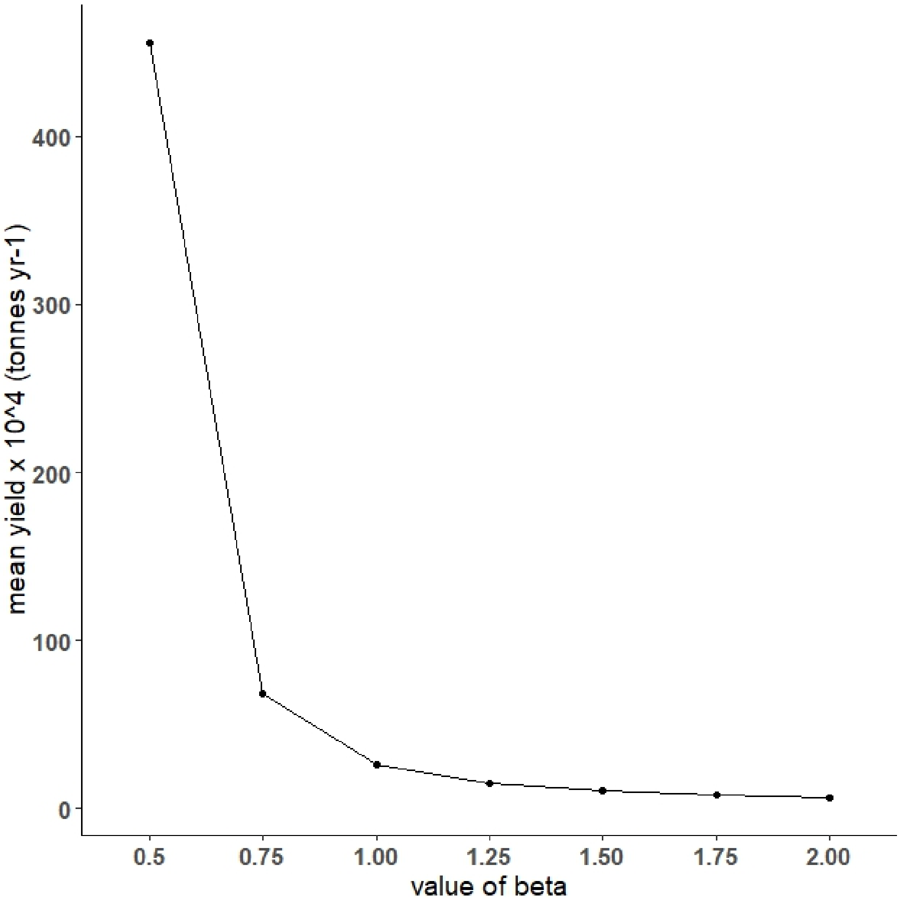


Figure 4B.1: The effect of changing β value in the Shepherd (1982) stock recruitment equation on raw mean annual yield one simulation run (50 years burn-in time plus an additional 50 years) with no closures at constant fishing effort.

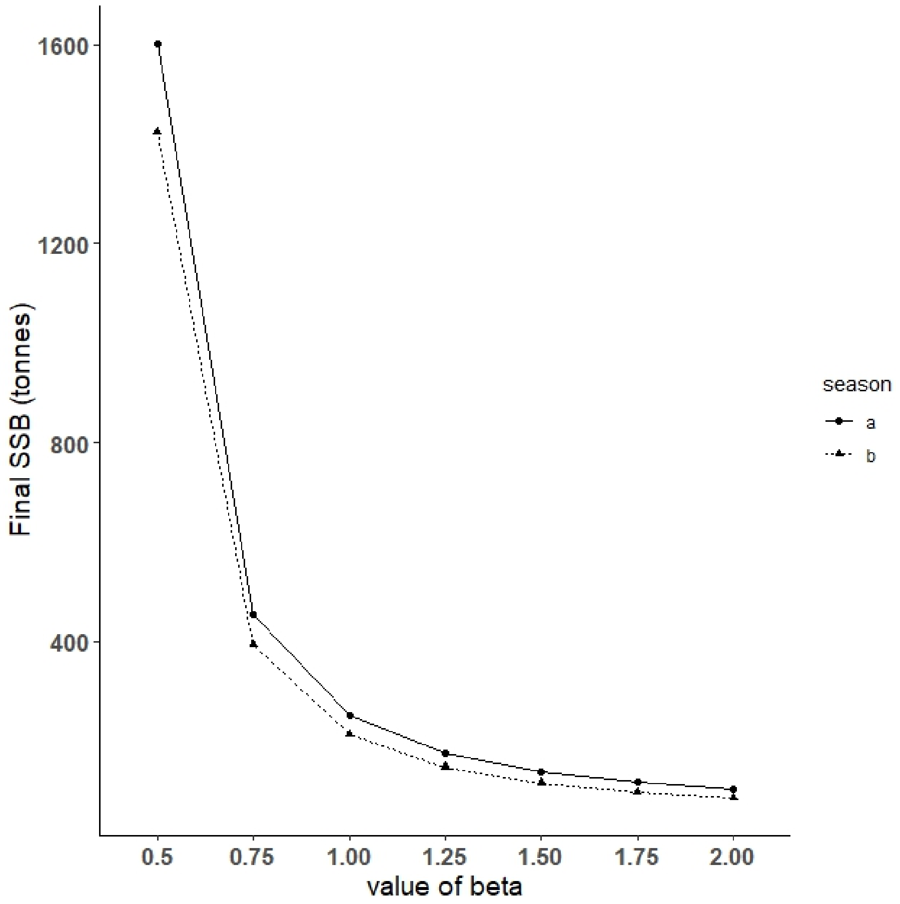


Figure 4C.1: Effect of value of β in the Shepherd (1982) stock-recruitment relationship on the final SSB under two seasonal fishery closures, both of which have the recruitment season in months 1-3:

a. fishery closed months 1 – 3

b. fishery closed months 7 – 9

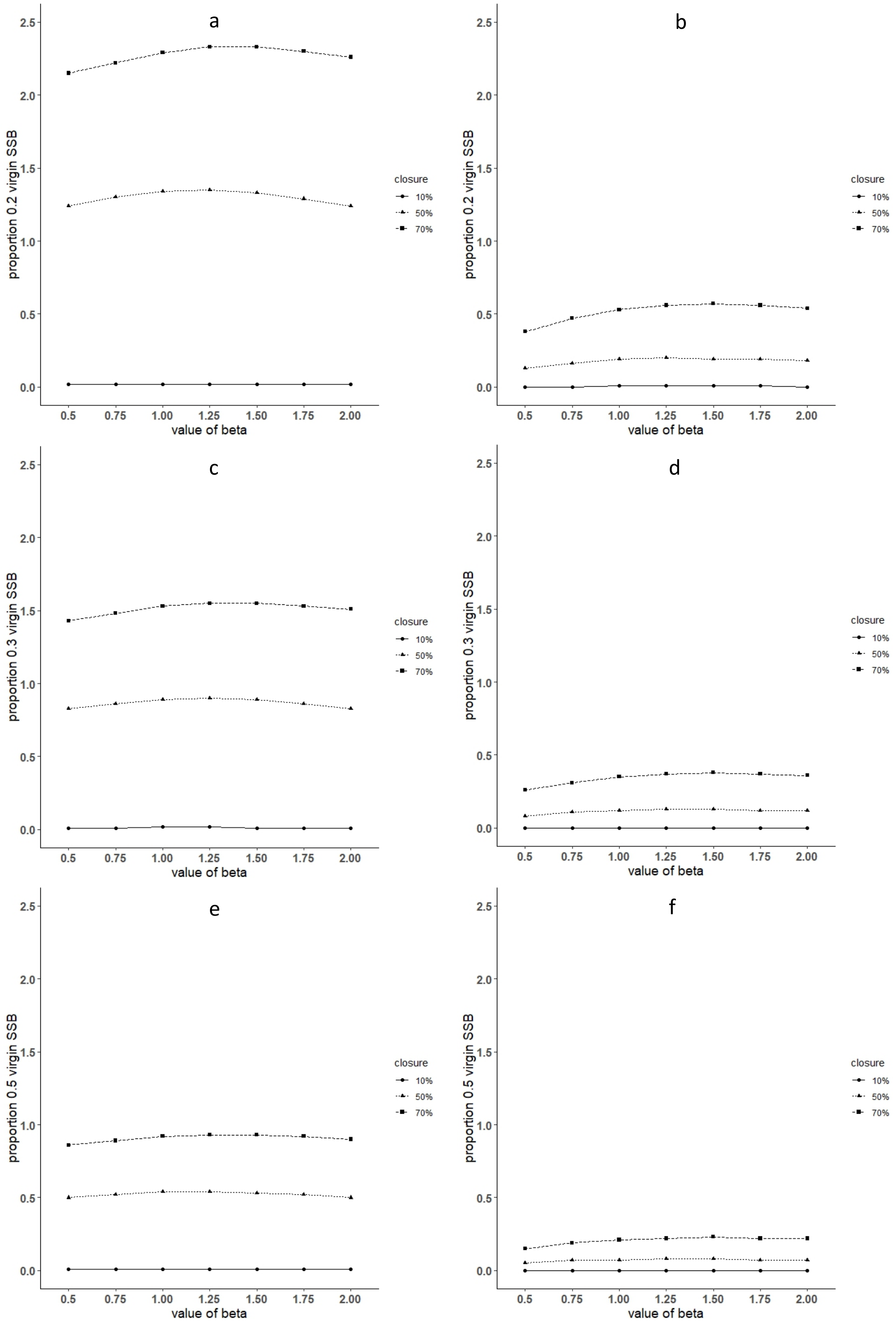


Figure 4C.2 Proportion of virgin SSB achieved with 10%, 50% and 70% closures in place at following SSB thresholds and diffusion coefficients (d): a) 0.2 virgin SSB, d=10; b) 0.2virgin SSB, d=100; c) 0.3 virgin SSB, d=10; d) 0.3 virgin SSB, d=100; e) 0.5 virgin SSB, d=10; f) 0.5 virgin SSB, d=100.

Chapter 5: Would an MPA be an effective management tool to prevent the collapse of a mobile fish stock? A case study of North Sea herring.

Abstract

Mathematical models are valuable tools for exploring the design, effectiveness and potential applications of MPAs. However, due to the constraints of empirical data-collection before and after MPA establishment – particularly for highly mobile species - the models remain largely generalised and the real effectiveness of MPAs remains untested. In this chapter the gap between empirical and theoretical studies of MPA design are addressed by coupling historic data from the North Sea herring fishery with a model of spatial and seasonal closures. Much has been written about the circumstances which brought about the collapse of the North Sea herring fishery in the 1970s and its subsequent closure. At the time, management options were exercised but these did not protect the stock. Using a single-species, spatio-temporal model parameterised with life-history data for herring and historical stock data, it is asked whether the fishery collapse could have been prevented by seasonal closures or spatial (MPA) closures. The model is then applied as a forecasting tool using contemporary stock data to assess the potential of MPAs as a tool for the future management of the fishery. The results based on historic data indicate that, if used in a timely way, well-designed MPA closures could have prevented the collapse of the fishery. In terms of applying these findings to fisheries in the future, it is recommended that MPAs can be used effectively as management tools for mobile, commercial stocks but simulations to aid with the planning of MPAs must accurately reflect the current state of the fishery.

5.1 Introduction

North Sea herring (*Clupea harengus*) are a key pelagic fish species in the North Sea, being either predator or prey to most other fish species in the area (Dickey-Collas *et al*., 2010). The North Sea stock is considered to be made up of four sub-stocks, named by their spawning locations: Downs (in the English Channel of the Southern North Sea), Banks (in the Central North Sea off the English coast), Buchan (off the North-East coast of Scotland) and Orkney-Shetland (off the coast of the Orkney and Shetland Islands) (ICES, 2019c). Whilst the sub-stock populations mix for much of the year, they each undergo Autumn spawning migrations from feeding grounds to their specific benthic spawning grounds where the females undergo simultaneous spawning, releasing eggs in a single batch (Whitehead, 1985; Ellis, *et al*., 2010). After hatching, the herring larvae drift towards nursery areas in the Eastern North Sea (Roel, 2017). Juveniles (up to 2 years old (Corten, 1986)) shoal in inshore waters, while adult herring shoals undergo diurnal migrations from deep water in the day to surface waters at night, where they disperse widely (Harden-Hones, 1968; Whitehead, 1985). Maturity and spawning of herring can occur at two years old, but most herring are aged three or four before joining adult populations for feeding and first spawning migrations (ICES, 2019c).

5.1.1 Collapse of a fishery

The North Sea herring fishery has been a valuable social, economic and political resource for over 400 years (Poulsen, 2008; Watson *et al*., 2015). However, in the 1970s the fishery collapsed due to recruitment overfishing coupled with lack of decisive, strategic management (for example: Saville and Bailey, 1980; Simmonds, 2007; Dickey-Collas *et al*., 2010; Dickey-Collas, 2016). Concerns were first raised about the decline of the North Sea fishery in 1965 when a decline in catch was noted and a working group initiated. A thorough history of the progressive collapse of the fishery and the associated management decisions which followed is given by Simmonds (2007). The account highlights the lack of consensus between and vacillation by stakeholders in the period from 1965 onwards. For example, in 1966 it was suggested one-month fishing bans should be investigated but these were rejected due to lack of agreement between the stakeholder nations. Partial and temporary closures of spawning grounds were put in place in 1967 and the fishery was closed temporarily in 1971 (Simmonds, 2007). Closed areas were agreed for 1972 and 1973 but were not enforced to the same extent across all stakeholder nations (Anon, 1972; ICNAF, 1972; Simmonds, 2007). Effort control in the form of total allowable catch (TAC) was first proposed in 1970 but disagreement between nations about equity of the TACs meant they were not enforced until 1976 (Simmonds, 2007). Ultimately, suitable measures were not put in place in a timely way to rebuild the stock, SSB dropped below B_{LIM} of 800,000 tonnes and only with closure of the fishery from 1977 to 1983 did it rebuild (Simmonds, 2007; ICES, 2018a).

5.1.2 The application of seasonal and spatial closures

As discussed in Chapter 4, seasonal closures to protect spawning seasons of commercial species are common practice (van Overzee and Rijnsdorp, 2015) and Marine Protected Areas (MPAs) have also long been cited as effective conservation and fisheries management tools due to their potential to rebuild overfished stocks by increasing biomass within the reserve and rebuilding reproductive potential of the stock (Palumbi, 2004; Lester *et al*., 2009; March *et al*., 2011; Di Lorenzo *et al*., 2016; Sala and Giakoumi, 2017). Although many studies have focused on species with low mobility, MPAs have been considered an effective part of the solution to rebuild mobile commercial stocks such as the Georges Bank cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*; Fogarty and Murawski, 2005) and could therefore be considered an appropriate management tool for a mobile, pelagic species such as herring. However, as described in Chapter 1 (section 1.2), using MPAs to manage mobile species potentially has added complexities due to the increased range of species beyond MPA boundaries and the positioning of the MPA in relation to key life-stage habitats such as nursery and recruitment grounds (Breen *et al*., 2015; Pérez-Jorge *et al*., 2015; D'Aloia *et al*., 2017). Potential proposed solutions to this have been the establishment of large or very large MPAs and networks of MPAs (Game *et al*., 2009; Agardy *et al*., 2011; Edgar *et al*., 2014; Wilhelm *et al*., 2014).

Additionally, mobile stocks such as North Sea herring can cross management boundaries and move between two management jurisdiction areas (Bjørndal and Lindroos, 2004; Dickey-Collas, 2016). North Sea herring stock is currently jointly managed through quota agreements and exchange of reciprocal fishing possibilities via the bilateral arrangement between the EU and Norway (EU, 2019), although at the time of the fishery collapse there was no such legislation in place. The North Sea stock is currently judged to be above fishery and stock reference points and ICES have advised an increase in catch in 2020 (ICES, 2019a). Long-term management strategies for the stock are under review by ICES at the time of writing (ICES, 2019b). These include consideration of effort and catch regulation and area and seasonal fishing restrictions, although the latter are primarily to minimise the impact on a separate, spring spawning stock from the West Baltic. A future decrease in stock size is predicted due to very low recruitment in 2015 and 2017 (ICES, 2019a), so selecting the appropriate and effective management strategy is vital.

5.1.3 Applying simulations to real-world scenarios

Mathematical models can be powerful tools to predict the impact of MPAs on fisheries stocks and inform management decisions. As discussed in Chapter 1 (section 1.6), these models are particularly useful when assessing MPA design in the absence of empirical data (Cornejo-Donoso *et al*., 2017). There is a need for models representing mobile species to be developed (Breen *et al*., 2015) because sedentary and low-mobility adults of species are more common in the literature (see Chapter 2, Table 1). In Chapter 1 (section 1.6) recent mathematical models are described which specifically address the impact of MPAs on mobile species. However, these models do not make predictions for specific species. De Leo and Micheli (2015) and Cabral *et al*. (2019) state that their simulations are purposely general; Cornejo-Donso *et al*. (2017) have based their model on Peru-Chile anchovy (*Engraulis ringens*) but point out the model remains theoretical. Similarly, Hastings *et al*. (2017) and D'Aloia *et al*. (2017) have estimated parameters based on the U.S. West Coast groundfish fishery and coastal species in British Colombia, Canada, respectively, but the models are not species-specific. In the same vein, the models developed in Chapters 2–4 are based on species' parameters but are intended to provide overarching principles rather than species-specific advice about MPA effectiveness. Applying the models to a real-world scenario via a case study allows the models to be tested and refined. The models can then be applied to species-specific data to test the impact of past and future management decisions, going some way to bridging the gap between theoretical and real fisheries and conservation goals.

5.1.4 Chapter aim and objectives

The aim of this chapter is to determine if lessons can be learned from previous management failings of the North Sea herring fishery and suggest alternative approaches to managing North Sea herring – and other mobile stocks - in the face of stock vulnerability. This is achieved via the following objectives:

1. to apply a single-species, time-series model to a population representative of the North Sea herring stock in the years 1965 to 1983 (encompassing the period from when concerns were first raised about the fishery, to its collapse, closure and subsequent recovery);
2. to determine whether seasonal closures would have been a suitable management option to enable the stock to recover whilst preserving some harvest for the fishers, or whether one or more MPAs would have been the better solution;
3. given the mobile nature of the stock and the dependence on enforcement of any management actions across two jurisdictions, the extent that non-compliance by one or more stakeholders could compromise the goals of SSB being maintained above B_{LIM} whilst maintaining a harvest is also examined;
4. to explore the use of the model as a forecasting tool by applying it to a population representative of the 2012 stock.

5.2 Methods

To determine whether the 1977-1983 closure of the herring fishery could have been prevented by the implementation of one or more MPAs and / or longer seasonal closures, the models described in Chapters 2 and 4 were adapted and programmed in R (R Core Team, 2019).

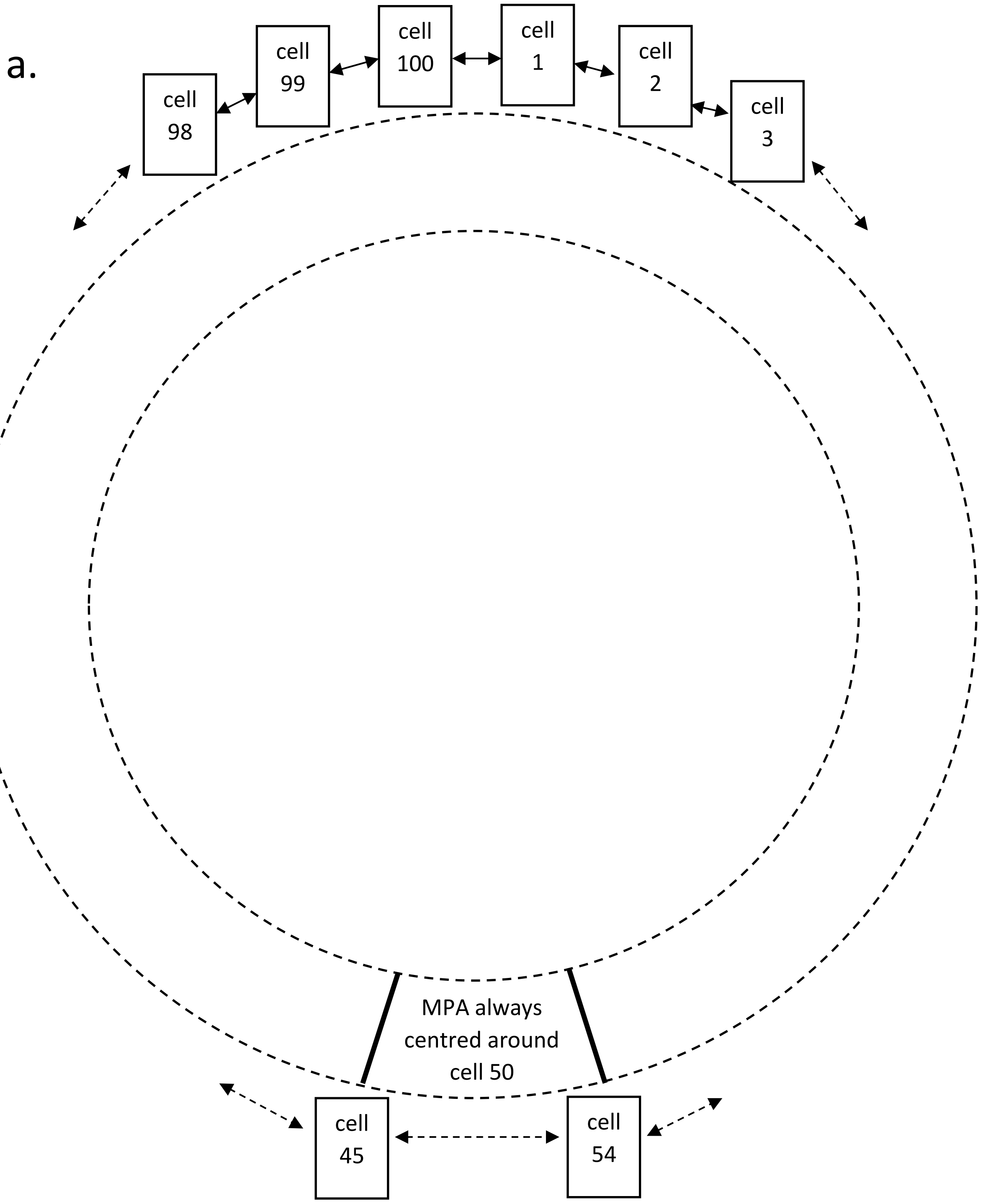
5.2.1 Spatial domain

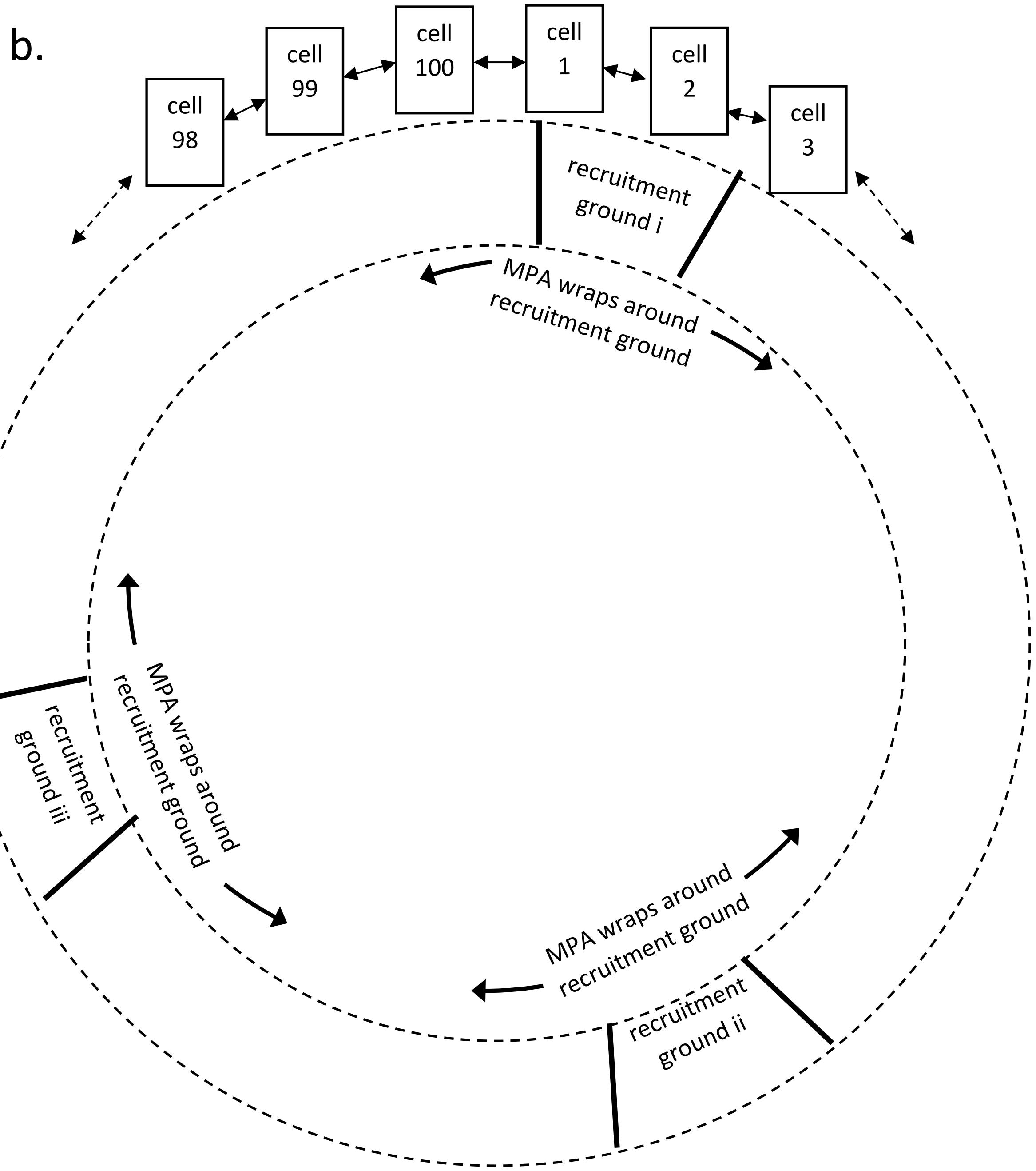
The spatial domain comprises 100 discrete cells, arranged in a one-dimensional loop with cell one adjacent to cell 100 (Le Quesne and Codling, 2009). North Sea herring is managed as a unit stock but is considered to have discrete sub-populations with at least three geographically distinct spawning and recruitment grounds (Bjørndal, 1988; Frank and Brickman, 2000; Mariana *at al.*, 2005). To represent the unit stock management and the biological sub-populations, three variants on the spatial domain were applied (see Figures 5.1a - 5.1c). In the first spatial domain (Figure 5.1a), juvenile recruitment was assumed to be global - representative of a unit stock - throughout the loop of cells, with one MPA applied in the domain. In the second variant (Figure 5.1b), juvenile recruitment took place in three, evenly spaced, separate recruitment grounds - representing spawning sub-populations - each made up of 10 cells. Three separate MPAs were applied, each centred at the middle of a recruitment ground. The third variant (Figure 5.1c) again had three juvenile recruitment grounds of 10 cells each in the domain but with one MPA which was centred outside any of the three grounds. Sub-models describing harvesting, natural mortality and movement of herring were applied monthly to each of the 100 cells in the domain. The recruitment sub-model was applied in the first three months of the year, every year.

5.2.2 Life history parameters and stock-recruitment relationship

The model is a single-species model with 10 age classes (Table 5.1). The final age class is a plus-group which includes all fish which have survived to that age. The model parameters (Table 5.1) represent those of North Sea Herring (Kunzlik and Bailey, 1986; Bjørndal, 1988; Daan *et al*., 1990; ICES, 2005 and 2018b; Roel, 2017). The three sets of parameters for selectivity represent three assumptions about juvenile fishing mortality which were tested: i. that juveniles did not form part of the catch; ii. that juveniles were half as likely to be caught as adults and iii. that juveniles were as likely to be harvested as adults. Juvenile fishing mortality has previously been shown to be a key determinant in herring stock collapse (Kunzlik and Bailey, 1986) but these assumptions were still incorporated due to the historic decisions regarding inclusion of juveniles in the catch (Simmonds, 2007) and as harvest in the sprat fishery (Corten, 1986).

Shepherd's (1982) stock recruitment relationship (SRR) was used to describe the SRR in the model. The value of the parameter β in this relationship is used to adjust the degree of density dependence in the SRR and was set to 1.0 in the simulation, as described for herring by Shepherd (1982).


a.
cell 98
cell 99
cell 100
cell 1
cell 2
cell 3
MPA always centred around cell 50
cell 45
cell 54


b.
cell 98
cell 99
cell 100
cell 1
cell 2
cell 3
recruitment ground i
MPA wraps around recruitment ground
recruitment ground iii
MPA wraps around recruitment ground
MPA wraps around recruitment ground
recruitment ground ii

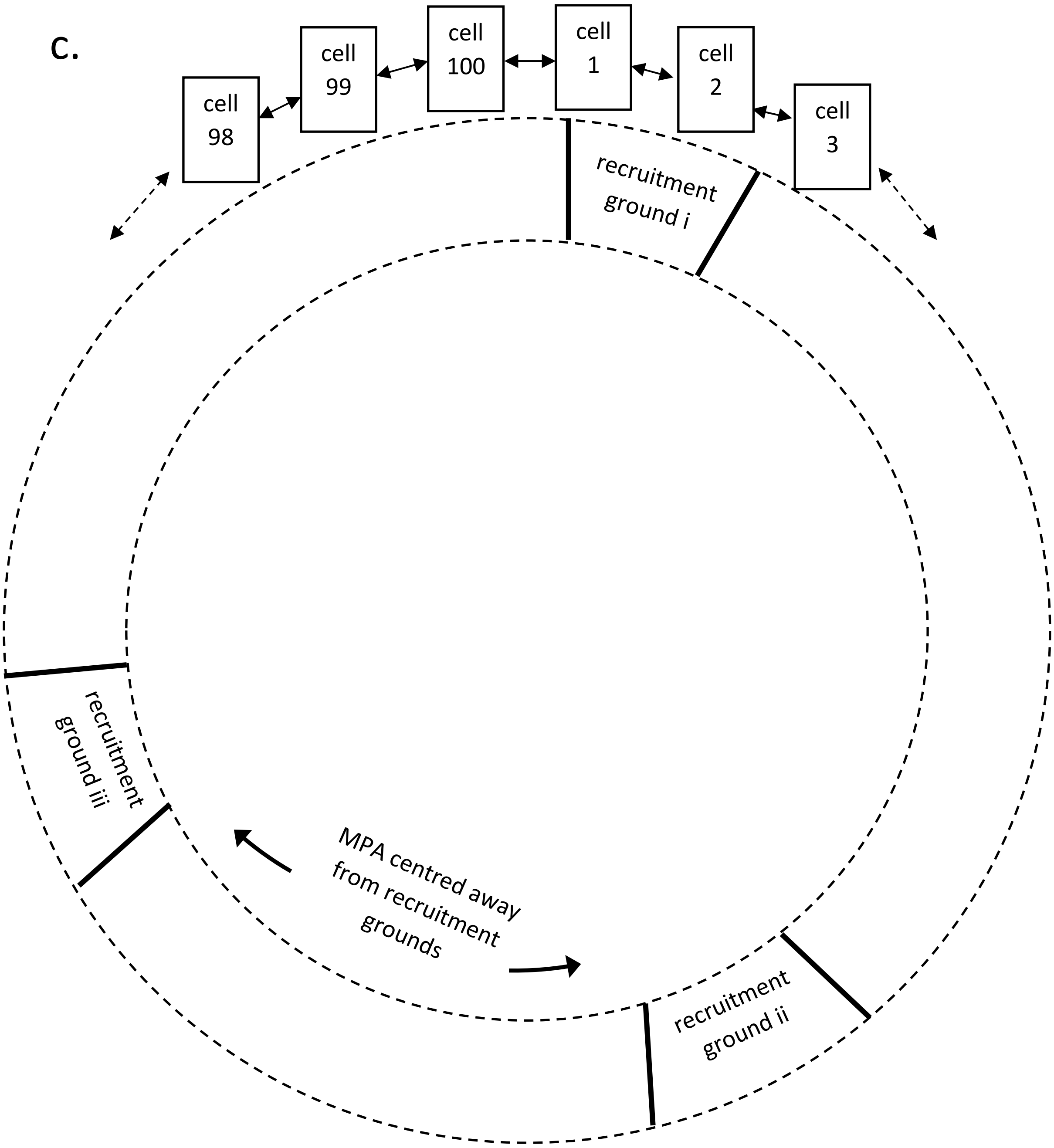


Figure 5.1: Representation of spatial domain of the simulation: the loop represents 100 discrete cells; cell 1 is adjacent to cell 100. Fish can move continuously in both directions through the loop of cells. a. recruitment occurs in all 100 cells of the virtual loop and one MPA closure is centred around cell 50. b. recruitment occurs in three separate recruitment grounds (i. cells 1-10, ii. cells 34-43 and iii. cells 67-76); an MPA closure is centred at the middle of each recruitment ground. c. recruitment occurs in three separate recruitment grounds (i. cells 1 to 10, ii. cells 34:43 and iii. cells 67 to 76) and one MPA closure is centred outside any of the recruitment grounds.

Table 5.1: Life-history parameters of the model species.

Age	1	2	3	4	5	6	7	8	9	10
Weight, W_a (Kg)	0.013	0.026	0.120	0.137	0.182	0.206	0.221	0.229	0.241	0.265
Maturity, Mat_a	0	0	1	1	1	1	1	1	1	1
Natural mortality, M_a	0.30	0.25	0.20	0.20	0.20	0.20	0.20	0.20	0.20	0.20
Selectivity, S_a i	0.0	0.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Selectivity, S_a ii	0.5	0.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Selectivity, S_a iii	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

5.2.3 Model structure and calibration

Two versions of the model were used: one in which spatial, MPA closures could be applied continuously and one whereby seasonal closures could be put in place at specific times for the full area. The descriptions of simulation scenarios are below, and processes and equations are described in full in Appendix 5A, Figures 5A.1 and 5A.2. The total annual fishing effort (E) in the simulation was calibrated to the effort within the fishery between 1965 and 1977 as follows (see Figure 5.2). The simulation was run, without closures, for 12 years, using the starting population numbers and stock structure reported for the 1965 Herring fishery (stock biomass=2.4m tonnes) (Bjørndal, 1988; ICES, 2005, 2019a; Simmonds, 2007; Roel, 2017). Simulation runs were repeated and annual fishing effort was increased with each simulation run from E=600 to E=2000 in increments of 20. The empirical decrease in stock biomass (SSB) between 1965 and 1977 is widely reported in the literature as dropping to 0.1m tonnes (for example: ICES, 2018a; Simmonds, 2007). The annual fishing effort in the simulations which was found to produce the same SSB decrease in the same period of time, and to most accurately reflect the trends in the actual SSB was determined to be E=1620. Figure 5.2 shows that between 1965 and 1977 the simulation SSB is lower than the actual SSB by, at most, 0.1%. The overall trend in reported decrease in SSB is reflected in the simulation results. The simulation shows less inter-annual fluctuation in the trend, which is discussed further in model assumptions.

This calibration process was checked by running the simulation again using the final population numbers from the previous calibration run (i.e.: the 1977 biomass numbers of 0.1m tonnes) for seven years with no closures and a minimal annual fishing effort of E=60 to represent the bycatch fishery which was permitted during the 1977 to 1983 fishery closure (Simmonds, 2007). Figure 5.2 shows the SSB in the simulation regenerated to the published levels within the simulation time frame and the overall trend in SSB between 1977 and 1983 is reflected in the simulation results. Thus, the starting biomass for the subsequent simulation scenarios was established as per the 1965 data: 2.4m tonnes (Bjørndal, 1988; ICES, 2005, 2019a; Simmonds, 2007; Roel, 2017) and fishing effort in the simulations was set at E=1620.

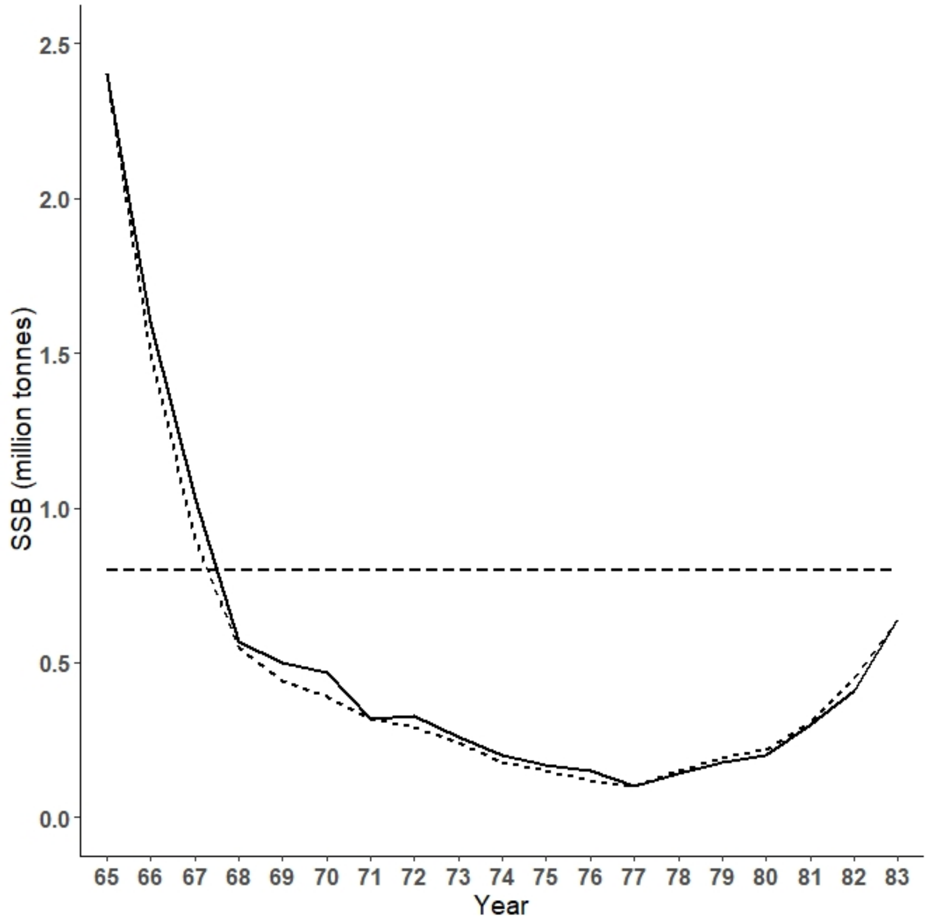


Figure 5.2: Calibration of the simulation compared to published data (ICES, 2019d) of SSB of North Sea Autumn spawning herring. The SSB of North Sea Autumn spawning herring as reported by ICES (2019d) (____) provides the benchmark for the simulation. SSB of the model population (…….) was given when the simulation was run with no closures and fishing effort, E=1620 from 1965 – 1977. The simulation was continued from 1977 – 1983 with no closures and fishing effort, E=60 to represent the bycatch fishery operating at that time. B_{LIM} (- - - -) is 800,000 tonnes.

5.2.4 Harvest and population dynamics

The annual fishing effort (E) remained constant at the calibration level (E=1620) within each simulation and was redistributed when spatial or seasonal closures were applied. Redistribution of the fixed effort can be considered to be the equivalent of imposing effort restrictions within the fishery, an assumption which is explored further in the 'compliance' scenarios. Within the boundaries of any MPA in the model, E was always zero; beyond the boundaries of the MPA the effort was applied equally to all populations in all cells. During seasonal closures, E=0 in all cells in the domain. The fishing mortality (Appendix 5A: Equation 5A.1) was applied monthly per age class per cell and the resultant yield was then calculated (Appendix 5A: Equation 5A.3). The population of each age class in each cell was subject to monthly natural and fishing mortalities (Appendix 5A: Equation 5A.2), which then enabled the population of each age class per cell to be updated monthly.

5.2.5 Monthly movement and population redistribution

After harvesting and population dynamics were applied, the fish movement sub-model was applied monthly and the redistribution of the population in the virtual space was calculated. The movement of all fish was density-independent, random, and could result in movement in both directions within the spatial domain. Because the spatial domain is a loop, movement can result in individuals moving throughout the spatial domain. As in previous chapters and in the model from which the simulation was developed (Le Quesne and Codling, 2009), the movement of all fish was described using the one-dimensional diffusion equation (Appendix 5A: Equation 5A.4). The diffusion coefficient, D, was given a value of D=10 to represent the mobility of herring relative to the size of the spatial domain (Whitehead, 1985).

5.2.6 Recruitment season, recruitment grounds and annual yield

The model scenarios which represented global recruitment did so by all age-0 fish being distributed equally throughout the 100 cells of the model. In the scenarios which represented local recruitment, recruitment grounds were specified as being cells 1-10, 34-43, and 67-76; the age-0 fish were distributed equally throughout the specified recruitment cells. The effect of global vs. local recruitment grounds on the final distribution of SSB is shown in Figure 5.3, which shows the final SSB after one simulation run of 12 years with no closures nor harvest with global recruitment (Figure 5.3a) and with three local recruitment grounds (Figure 5.3b).

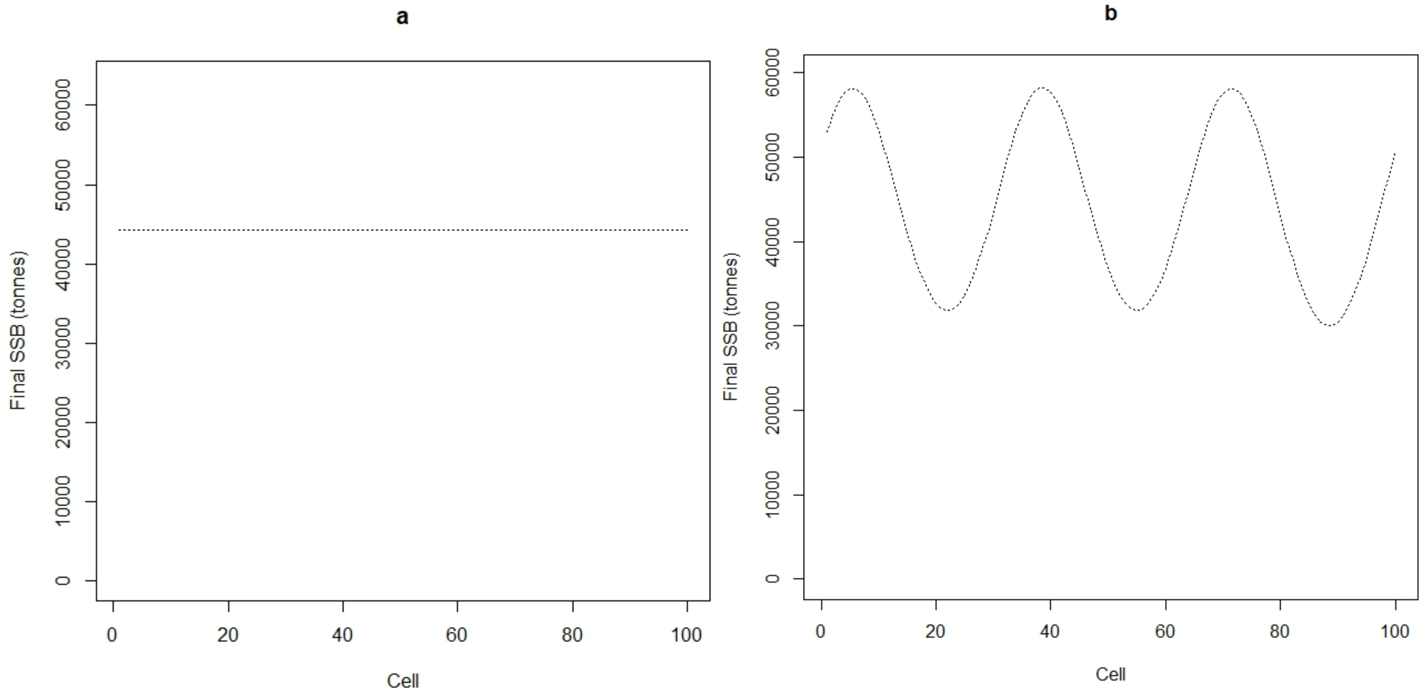


Figure 5.3: The final SSB distribution across the 100 cells of the spatial domain after one simulation of 12 years in monthly time steps with no closures and no fishing with a. global recruitment across all 100 cells of the spatial domain and b. three local recruitment grounds (cells 1-10; 34-43; 67-76).

The recruitment sub-model (Appendix 5A: Equations 5A.5i and 5A.5ii (Shepherd, 1982)) was applied at the end of each of the first three monthly time steps each year and after all other monthly processes and sub-models had been applied. For the main suite of simulations recruitment was deterministic but this assumption is explored further in model developments (below). These three months are not intended to specifically represent January to March but are a nominal three-month recruitment season which could be considered representative of North Sea herring (ICES, 2019a). The annual yield was calculated after every 12th monthly time-step by summing all monthly yields from all age classes across all cells.

5.2.7 Simulation scenarios to determine the potential impact of spatial and seasonal closures

After the initial calibration of the model, described above, each simulation was run for 12 years to represent the period from 1965 - when the North Sea herring fishery was first identified as being compromised (Saville and Bailey, 1980; Simmonds, 2007; ICES 2019a) – to 1977 when the fishery was closed. In all simulations, the assumption was made that mean fishing effort would continue as per the published data from 1965. Thus, annual fishing effort in the simulation was maintained at E=1620, as determined by the initial calibration. Four sets of simulations were run to explore the potential impact of spatial and seasonal closures on the herring fishery.

The simulations of spatial closures modelled an MPA by closing from 5% to 95% of the total spatial domain to fishing, increasing the MPA size by 1% per model run. The first set of simulations of spatial closures had a global recruitment ground with one MPA (see Figure 5.1a). The second set of simulations had three designated, evenly spaced, local recruitment grounds of 10 cells each (see Figure 5.1b). The total size of the MPA within the spatial domain was split equally between three smaller MPAs, each of which was centred on the middle of a recruitment ground. e.g.: a total MPA size of 30% would be made up of three MPAs of 10% of the total area, each one in the same cells as the three recruitment grounds. The third set of simulations had the three designated recruitment grounds, but one MPA which was always centred away from the recruitment grounds (see Figure 5.1c). Due to the structure of the model (see Figure 5.1c), a single MPA of 25% or more placed centrally between any two recruitment grounds will overlap with at least one recruitment ground. Therefore, to ensure the results of the latter simulation were not due to the placement of the MPA with respect to the recruitment grounds, the simulation was repeated 70 times, each time with the MPA centred on a different cell which was not part of a recruitment ground.

Seasonal closures were applied in the fourth set of simulations; no spatial, MPA closures were put in place. Recruitment in these simulations was designated as global and the fishery was closed between two months (months one and two) to six months (months one to six).

5.2.8 Assessing SSB and yield

B_{LIM} for the North Sea herring stock has been identified as 800,000 tonnes (ICES, 2019a). The final SSB at the end of each simulation run of 12 years was calculated as a proportion of B_{LIM} to determine the extent to which B_{LIM} had been maintained. The mean annual yield per simulation was calculated as a proportion of the yield achieved without closures with annual fishing effort set at E=1620 (i.e.: the effort established from the calibration run) to determine whether the stakeholder objective could be met of maintaining the same yield as before spatial or seasonal closures were enforced.

5.2.9 Compliance scenarios

The difficulty of enforcing MPAs and ensuring full stakeholder compliance has been widely discussed (for example, Agardy *et al*., 2011; Edgar *et al*., 2014; Rees *et al*., 2010; Laffoley *et al*., 2019). Therefore, all MPA simulations of the adult herring fishery were run again to determine the effect of non-compliance on the management objective of maintaining B_{LIM}. To model non-compliance in terms of effort management (Dickey-Collas *et al*., 2010), the optimum MPA size determined by each previous scenario was applied and annual fishing effort was increased above the calibration level, E=1620, in 5% increments from E+5% to E+100% (i.e.: up to a doubling of annual fishing effort).

Non-compliance with the MPA was modelled under the assumption that although fishers complied with effort regulations they encroached on the MPA boundaries, thereby effectively reducing the MPA size. Therefore, non-compliance in terms of spatial management was modelled by decreasing the optimum MPA size by 5% - 95% whilst maintaining annual fishing effort at the calibration level (E=1620). When three MPAs (each localised to a recruitment ground) were in place, each was considered to represent a separate MPA jurisdiction or management area; therefore, each discrete MPA was reduced in size by 5% - 95%; this was repeated three times such that one, two and all three MPAs were reduced in size in separate simulations.

5.2.10 The model as a forecasting tool

After all the above simulations, the model was set up using the population numbers published for 2012 as the starting population (SSB = 2.7m tonnes) (ICES, 2019a). The fishing effort for 2012 was 0.323 of that in 1965 (E=0.47 in 1965 vs E=0.152 in 2012, (ICES, 2019a)) so E in the model was recalibrated to be E= 0.323 x 1620; E=523.26. The model was run again for 20 years, in monthly increments with constant annual fishing effort and local recruitment grounds in place. The final SSB and mean annual yield were calculated to assess the future impact of placing local MPAs at the centre of each of the recruitment grounds or a single MPA between the recruitment grounds.

5.3 Results

5.3.1 The use of MPAs to protect B_{LIM} and maintain yield

In all results of full compliance, the same annual fishing effort was applied as before closures were enforced. When recruitment occurred throughout the spatial domain, one MPA of 30% of the total area conserved B_{LIM} and maintained the mean annual yield which would have been met without closures, assuming juveniles were not part of the harvest (Figure 5.4a). A larger MPA was needed to protect B_{LIM} when juveniles were also included in the fishery: when juveniles were included in the harvest, the required MPA size rose to up to 36% when juveniles were equally as susceptible to harvesting (Figures 5.4b and 5.4c).

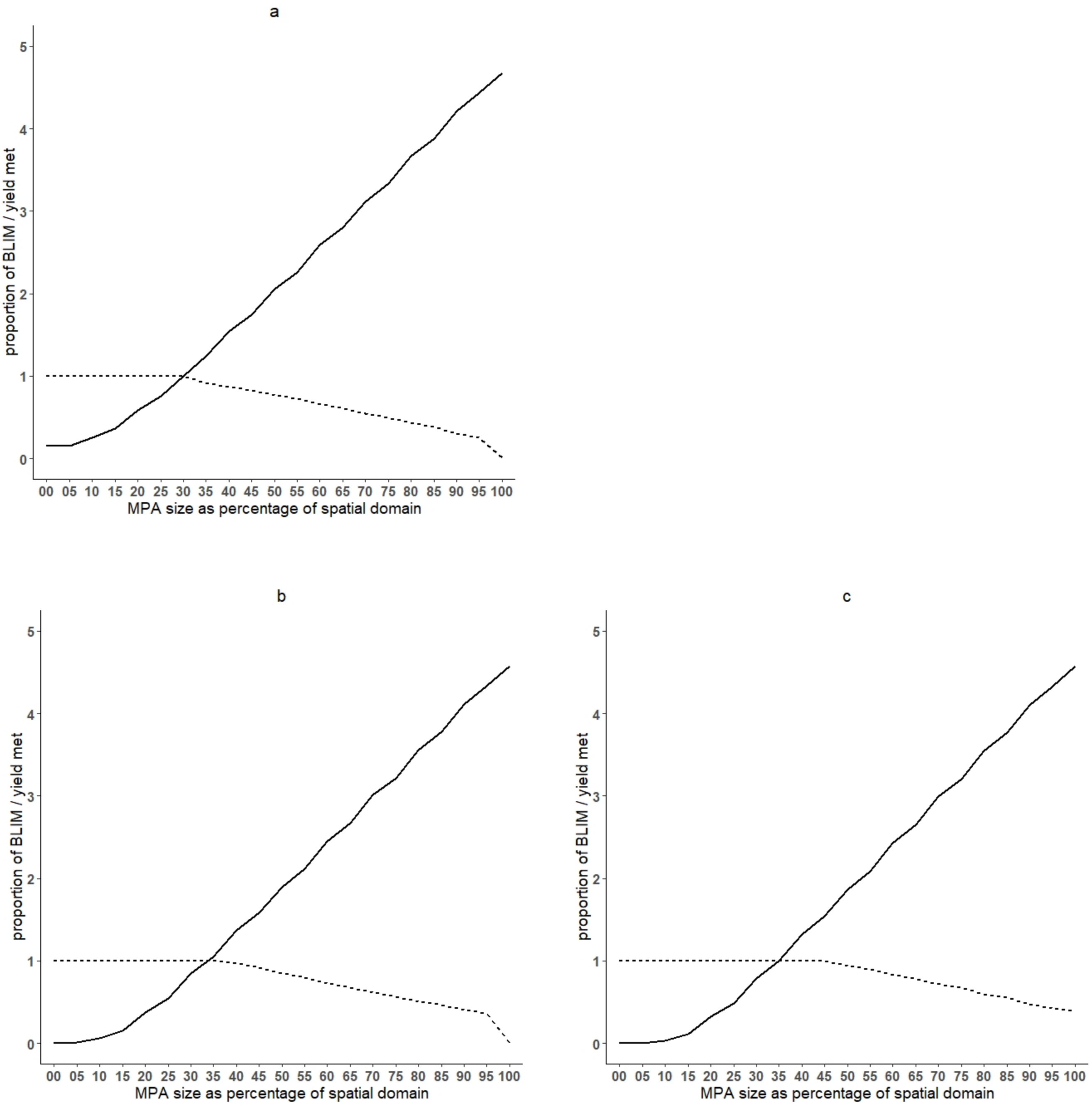


Figure 5.4: The proportion of B_{LIM} and mean annual yield (without closures) which were met when one MPA was in place protecting 5% - 95% of the total spatial domain. The simulation was run for 12 years in monthly time steps with global recruitment and a constant annual fishing effort (E=1620), determined as the equivalent of that in the 1965 fishery. _____ = SSB; ……… = mean annual yield.

a. juveniles were not part of the fishery,
b. juveniles were half as likely to be harvested as adults,
c. Juveniles were equally as likely to be harvested as adults.

By comparison, local recruitment coupled with three MPAs, each centred in a local recruitment ground, required a larger total percentage of the spatial domain to be closed to fishing to conserve B_{LIM} and maintain the yield (Figure 5.5). A total (across the three MPAs) of 36% of the spatial area - i.e.: three 12% MPAs each wrapped around a 10-cell recruitment ground - needed to be closed to fishing when juveniles were not part of the fishery (Figure 5.5a). Again, when juveniles were included in the fishery the MPA area needed increased, in this case to up to 40% of the spatial domain (Figures 5.5b and 5.5c).

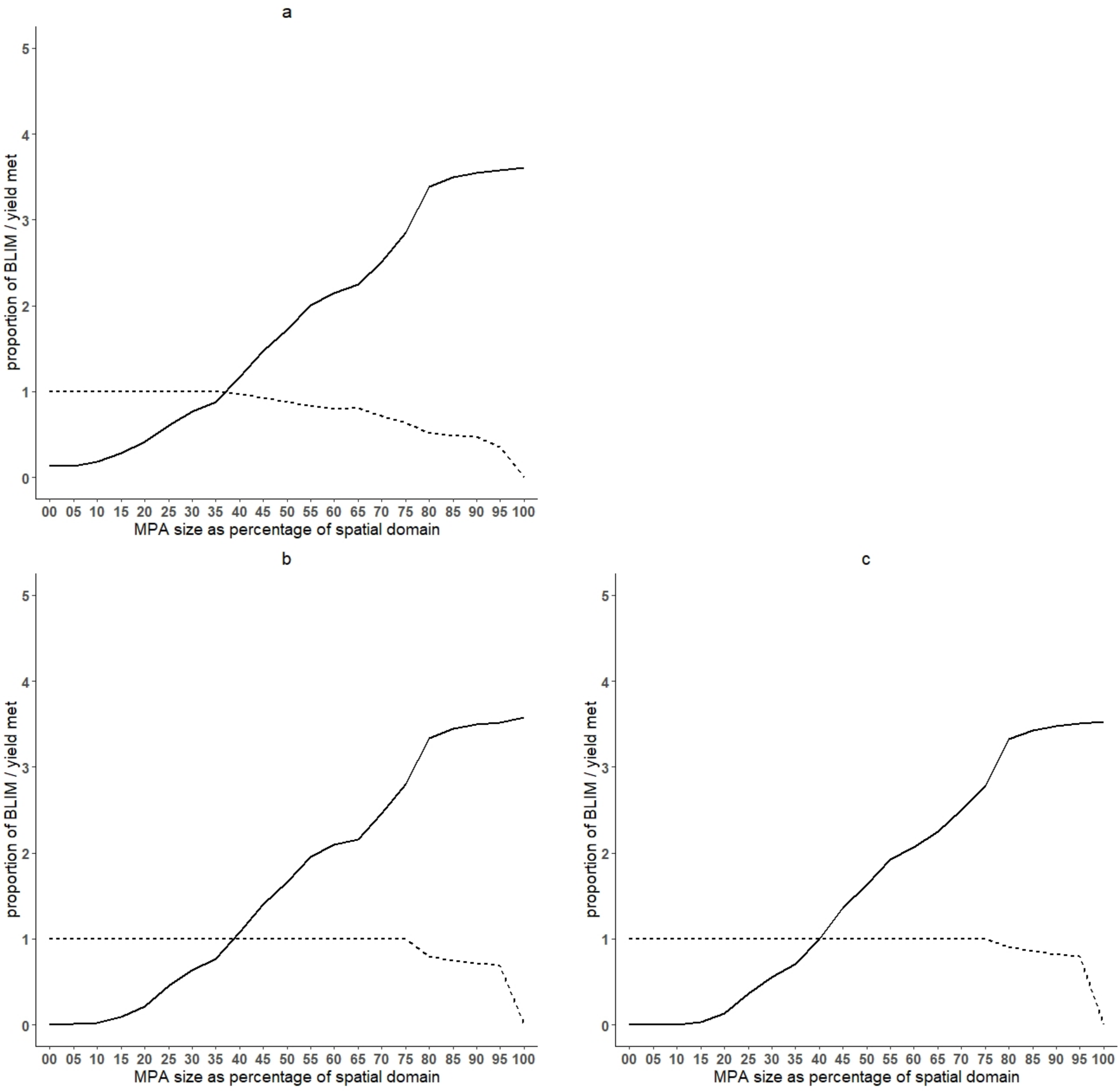


Figure 5.5: The proportion of B_{LIM} and mean annual yield (without closures) which were met when three MPAs were in place protecting 5%-95% of the total spatial domain cumulatively. The centre of each MPA was at the centre of one of the three local recruitment grounds. The simulation was run for 12 years in monthly time steps with local recruitment to three recruitment grounds and a constant annual fishing effort (E=1620), determined as the equivalent of that in the 1965 fishery. The centre of each MPA was at the centre of one of the three local recruitment grounds. _____ = SSB; ……… = mean annual yield.

a. juveniles were not part of the fishery,
b. juveniles were half as likely to be harvested as adults,
c. Juveniles were equally as likely to be harvested as adults.

When there were three local recruitment grounds and one MPA centred away from any one ground (Figure 5.6), a 36% MPA protected B_{LIM} and maintained the yield when no juveniles were harvested (Figure 5.6a). Including juveniles in the harvest again increased the MPA size required to up to 40% (Figures 5.6b and 5.6c). The impact of where the single MPA was placed between recruitment grounds was assessed by calculating the 95% confidence intervals of the proportions of B_{LIM} and yield met: at MPA sizes from 5% up to 40%, confidence intervals were 0.0; at 40% and greater, the confidence intervals were +/- 0.1. From this, it can be determined that the placement of the single MPA did not affect outcomes and there was no empirical difference between the effect of the three localised MPAs vs. one MPA outside the recruitment grounds on SSB and yield.

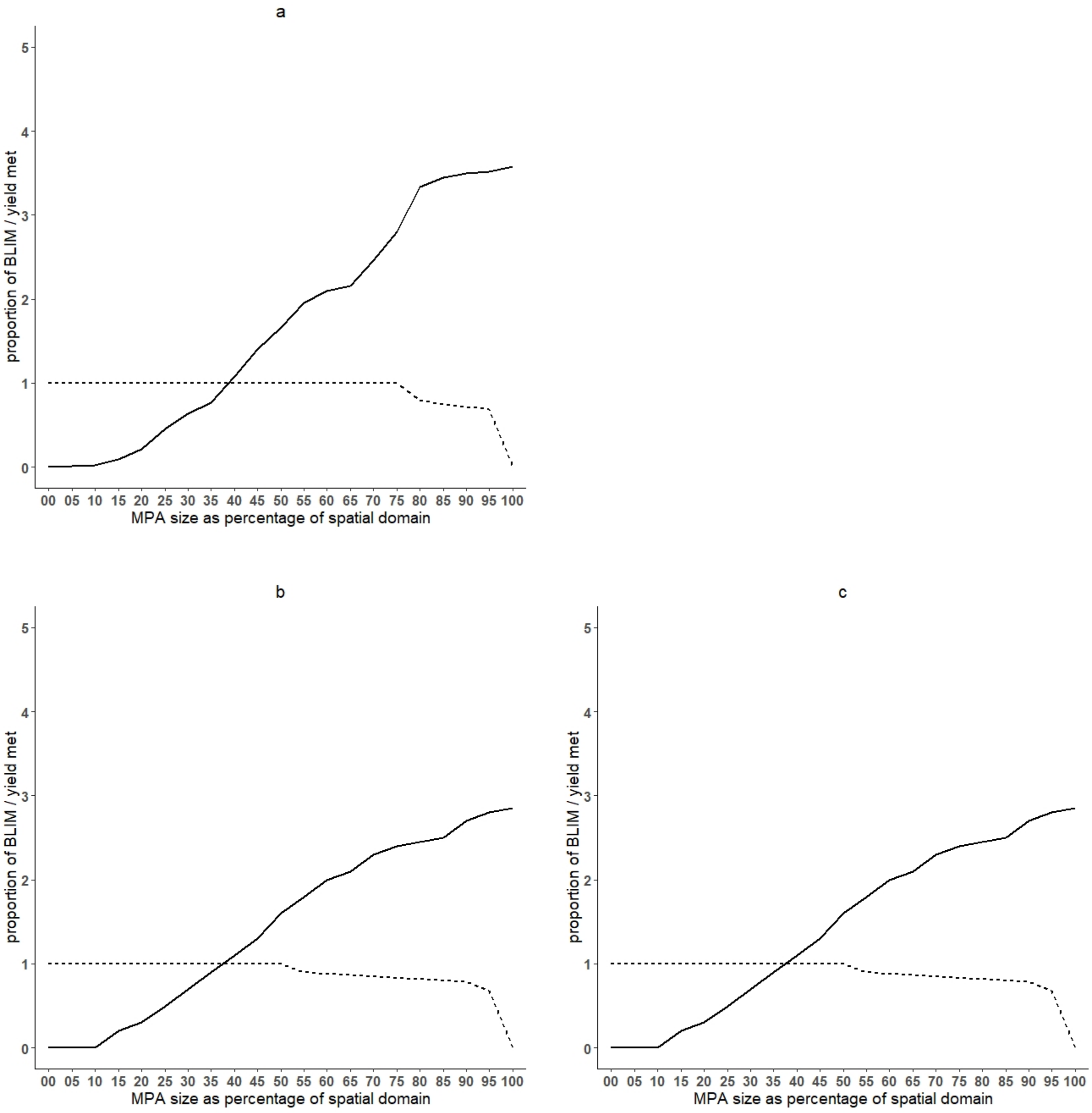


Figure 5.6: The proportion of B_{LIM} and mean annual yield (without closures) which were met when one MPA was in place protecting 5%-95% of the total spatial domain. The simulation was run for 12 years in monthly time steps with local recruitment to three recruitment grounds and a constant annual fishing effort (E=1620), determined as the equivalent of that in the 1965 fishery. The centre of the MPA was placed between two of the three recruitment grounds. _____ = SSB; ……… = mean annual yield.

a. juveniles were not part of the fishery,
b. juveniles were half as likely to be harvested as adults,
c. Juveniles were equally as likely to be harvested as adults.

5.3.2 Use of seasonal closures to protect B_{LIM} and maintain yield

When juveniles were not part of the harvest, seasonal closures of any length (which protected at least two of the three recruitment seasons) could maintain the mean annual yield which would have been achieved without closures (assuming annual fishing effort remains constant). This was to the detriment of SSB, which was reduced to 0.1 of B_{LIM} (Figure 5.7a). When juveniles formed part of the harvest (Figures 5.7b and 5.7c), mean annual yield was depleted by up to half that without closures and SSB was reduced to less than 0.1 of B_{LIM}. Due to the lack of protection of SSB afforded by seasonal closures these scenarios did not form part of the non-compliance studies.

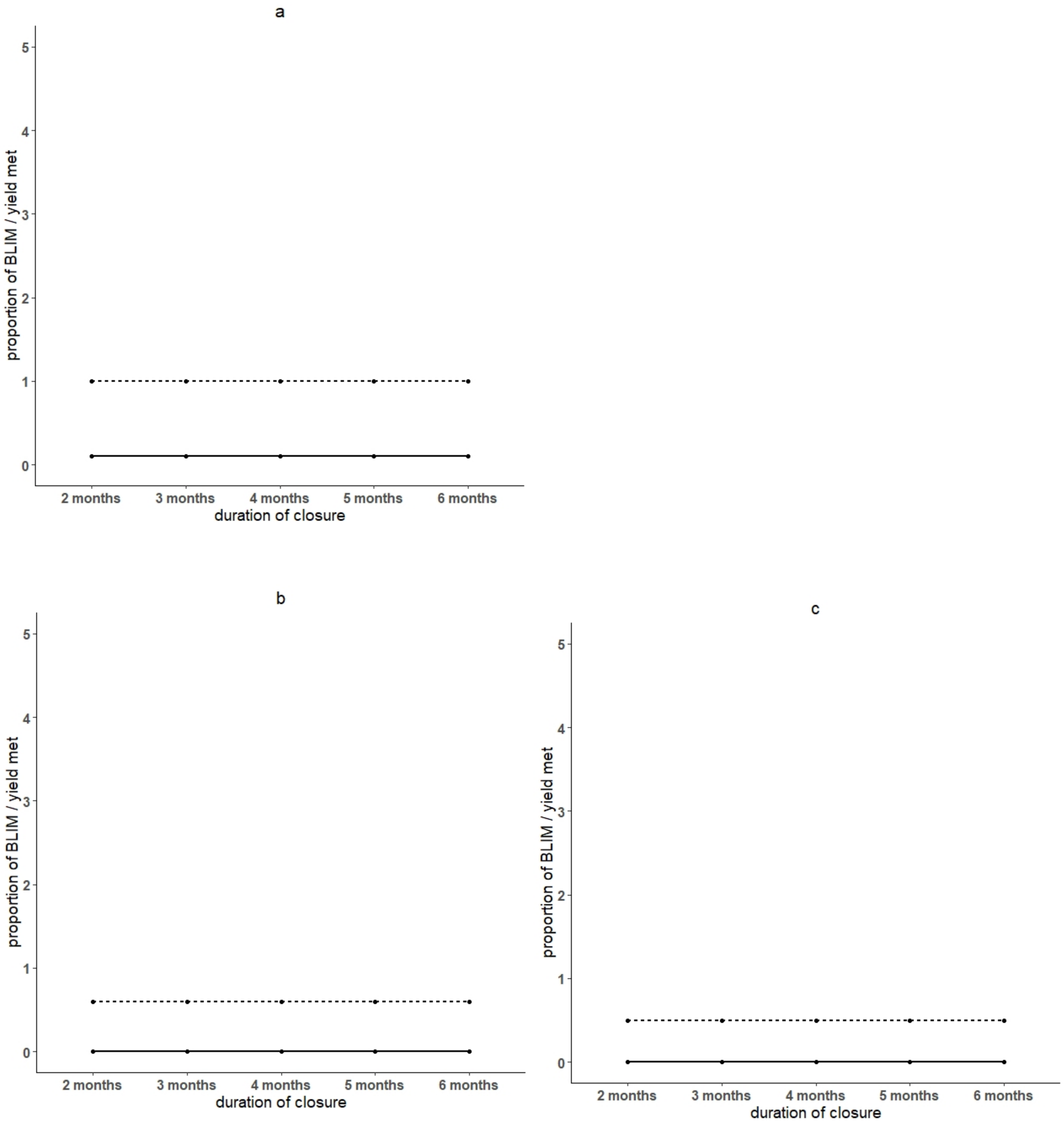


Figure 5.7: The proportion of B_{LIM} (represented by _____) and mean annual yield (without closures) (represented by ……) which could be met with seasonal closures of 2-6 months in place. Recruitment was always in months 1-3; the closures always started from the beginning of each year. The simulation was run for 12 years in monthly time steps with global recruitment and a constant annual fishing effort (E=1620), determined as the equivalent of that in the 1965 fishery.

a. juveniles were not part of the fishery,
b. juveniles were half as likely to be harvested as adults,
c. Juveniles were equally as likely to be harvested as adults.

5.3.3 Impact on MPAs of non-compliance with effort regulations

As described above, in the global recruitment scenario a single, optimum-sized MPA of 30% of the total spatial domain was able to preserve B_{LIM} and maintain mean annual yield (Figure 5.4a). Simulations of non-compliance with effort regulations showed that when effort outside the 30% MPA boundary increased by 15% or more the MPA could no longer preserve B_{LIM} (Figure 5.8a). With three local recruitment grounds, the optimum total MPA size to preserve B_{LIM} was established as 36% of the total spatial domain, either with three 12% MPAs (each centred at the middle of a recruitment ground) or with one MPA of 36% (centred away from any recruitment ground). Simulations of non-compliance with effort regulation showed that when three local MPAs were in place, increasing annual fishing effort by 10% outside the three MPA boundaries prevented B_{LIM} being preserved (Figure 5.8b) whereas when one MPA was in place annual fishing effort could be increased by 15% (Figure 5.8c) before B_{LIM} was compromised.

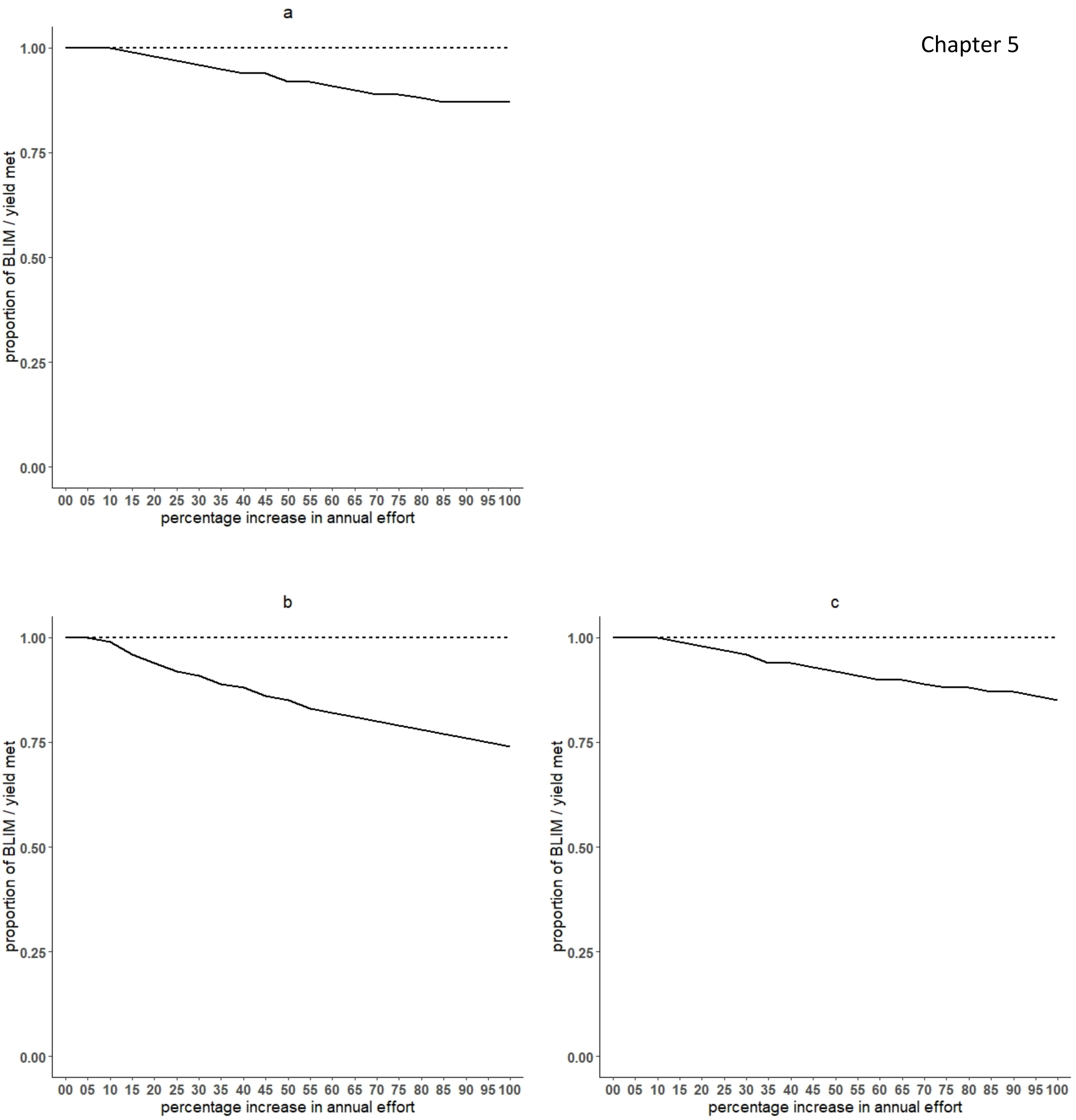


Figure 5.8: The proportion of B_{LIM} (represented by ______) and mean annual yield (without closures) (represented by ……) which were met with non-compliance of effort regulation. The simulation was run for 12 years in monthly time steps with one optimal sized MPA in place and without juveniles being harvested. Annual fishing effort was constant within each simulation and was increased between simulations from the base value of E=1620 in 5% increments from E+5% to E+100%.

a. global spawning with one MPA. MPA optimal size = 30%
b. three local recruitment grounds with three MPAs, each centred at the middle of a recruitment ground. MPA optimal size = 36%
c. three local recruitment grounds with one MPA, centred between two recruitment grounds. MPA optimal size = 36%

5.3.4 Impact on MPAs of non-compliance with MPA boundaries

Non-compliance with MPA size had the most marked effect in all simulations, with any decrease in the optimum size causing a rapid decline in SSB in all simulations (Figures 5.9a – 5.9c). When global recruitment was modelled, a 5% reduction in size of the single optimum MPA reduced SSB to 0.94 of B_{LIM} (Figure 5.9a).

When recruitment occurred at three recruitment grounds, each protected by a separate, local MPA, SSB declined when one or more of the three individual MPAs was reduced in size. In this spatial configuration, each MPA was 12% of the total spatial domain, therefore a 5% decrease of one of the MPAs was equivalent to 1.67% reduction in the total MPA area, yet just reducing one MPA by this amount reduced total SSB to 0.98 of B_{LIM} (Figure 5.9bi). When two or more MPAs were each reduced by 5% (Figures 5.9bii and 5.9biii) SSB was reduced to 0.87 of B_{LIM}. However, a 5% reduction of each of the three MPAs is equivalent of a reduction in total MPA size of 5%. This, then, is a useful benchmark to compare the effects of reducing the size of a single MPA when local recruitment was modelled. In doing so, it was noted that a single MPA was more effective at conserving SSB, maintaining 0.99 of B_{LIM} with a 5% reduction in size and 0.95 of B_{LIM} when the size was reduced by 10% (Figure 5.9c).

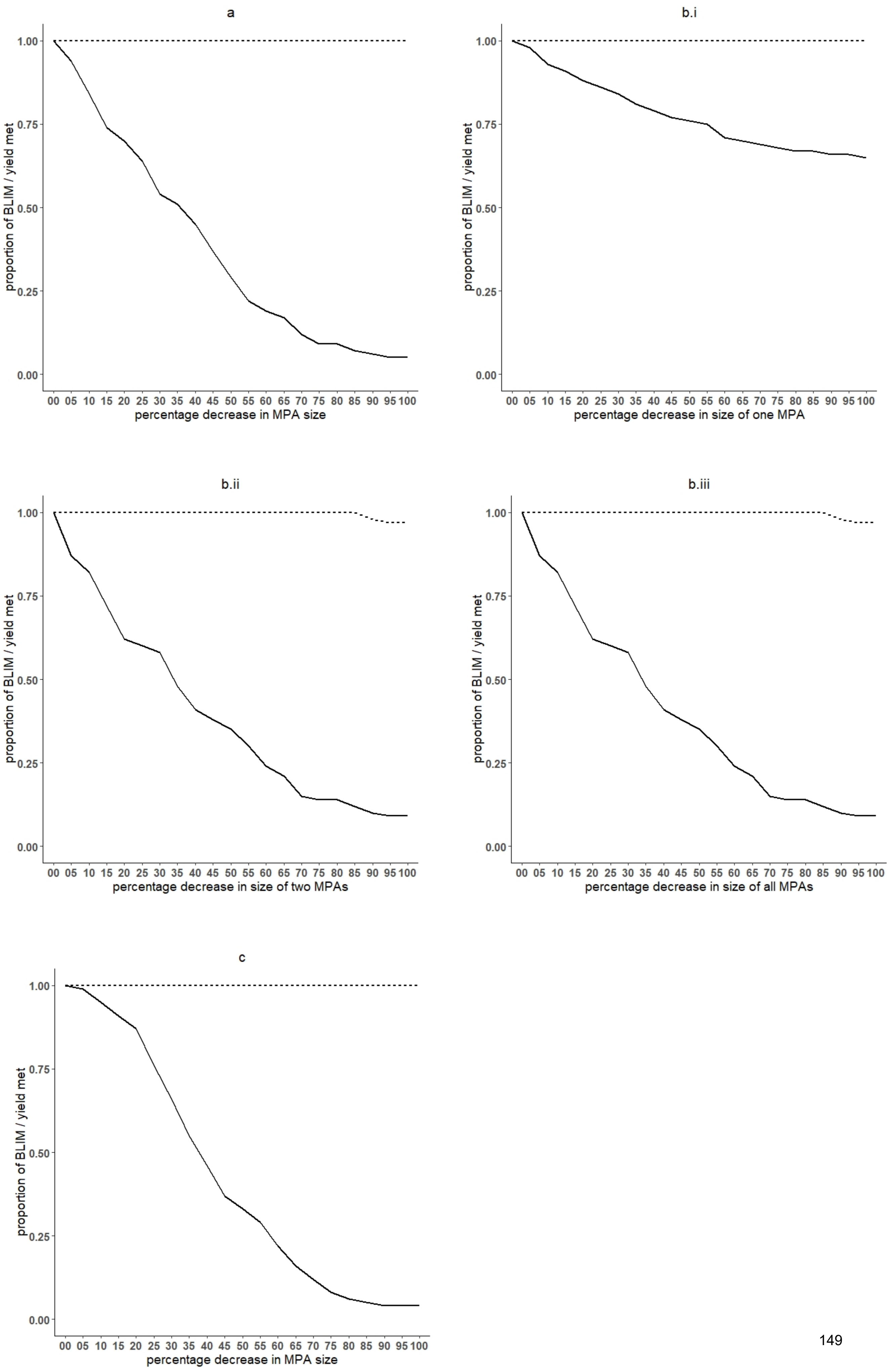

a
b.i
b.ii
b.iii
c
proportion of BLIM / yield met
0.00
0.25
0.50
0.75
1.00
00 05 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
percentage decrease in MPA size
percentage decrease in size of one MPA
percentage decrease in size of two MPAs
percentage decrease in size of all MPAs
percentage decrease in MPA size

Figure 5.9: The proportion of B_{LIM} (represented by _____) and mean annual yield (without closures) (represented by ……) which were met with non-compliance of MPA boundaries. The simulation was run for 12 years in monthly time steps with a constant annual fishing effort (E=1620), determined as the equivalent of that in the 1965 fishery. Juveniles did not form part of the harvest. Each optimal MPA size was reduced between simulations by 5% to 95% in 5% increments.

a. global spawning with one MPA. MPA optimal starting size = 30%
b. three local recruitment grounds with three MPAs, each centred at the middle of a recruitment ground. MPA optimal size = 36%
    i. one of the three MPAs is reduced in size
    ii. two of the three MPAs are reduced equally in size
    iii. all three MPAs are reduced equally in size.
c. three local recruitment grounds with one MPA, centred between two recruitment grounds.MPA optimal starting size = 36%

5.3.5 The model as a forecasting tool

The forecast simulations of 2012 to 2032 (Figures 5.10a and 5.10b) indicated that an MPA of 18% of the total area could be used to protect SSB and yield (assuming annual effort remains constant). The total protected area could be divided equally between three MPAs - each of which were centred in the middle of a recruitment ground (Figure 5.10a) – or could be one MPA centred between the recruitment grounds (Figure 5.10b). Comparing these results to the 1965 simulation (Figures 5.5a and 5.6a), it can be seen that the total effective MPA size was smaller in the forecast simulations (which had a higher starting biomass) compared to the historic simulations.

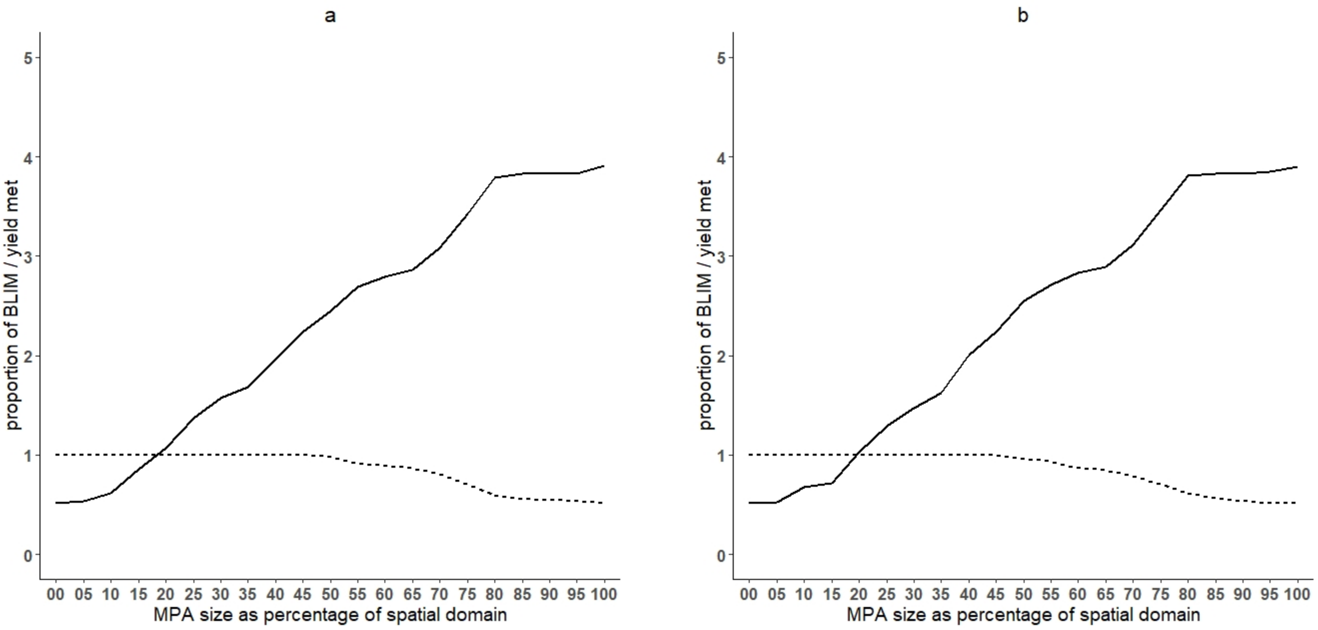


Figure 5.10: The proportion of B_{LIM} and mean annual yield (without closures) which were met with MPA spatial closures protecting 5% - 95% of the spatial domain. The simulation was run for 12 years in monthly time steps with local recruitment to three recruitment grounds and a constant annual fishing effort (E=523.26), determined as the equivalent of that in the 2012 fishery. _____ = SSB; ……… = mean annual yield.

a. three MPAs were in place, the centre of each MPA was at the centre of one of the three local recruitment grounds

b. one MPA was centred between recruitment grounds

5.4 Discussion

Using historical data of the North Sea herring fishery, a spatio-temporal model was applied to explore what – if any – management options could have prevented the collapse of the fishery. The simulations explored whether seasonal or spatial closures could maintain the stock within safe biological limits whilst also providing a harvest. Also explored was to what extent non-compliance of management decisions compromised the biological stability and yield of the fishery. The results are intended to give a fresh perspective on a historic problem but one that has the potential to recur due to poor year classes entering the fishery (ICES, 2019b): how to conserve the North Sea herring stock biomass and facilitate the continuation of the fishery.

5.4.1 Use of seasonal closures to maintain SSB

Temporary, seasonal area closures were imposed in the herring fishery between 1965 and 1977 (Anon, 1972; ICNAF, 1972; Simmonds, 2007) but the simulation results have confirmed what happened at that time – these were unsuccessful and the stock was not protected sufficiently to allow recovery. As demonstrated in Chapter 4, seasonal closures are insufficient to conserve mobile stocks unless coupled with other measures such as gear restrictions and harvest controls. Seasonal closures are therefore part of a suite of measures which have been imposed (EU, 2018; MMO, 2018, 2019) to bring the herring fishery to current, sustainable levels (ICES, 2018b), but could a permanent MPA be a viable solution to management of the fishery?

5.4.2 Use of MPAs to maintain SSB and yield

All three simulations of an MPA being put in place indicated that the North Sea herring fishery could have been prevented from collapsing if, when the fishery was first identified as being compromised, an MPA of approximately one third of the area of the spatial domain had been enforced. This is in agreement with MPA size recommended by non-species-specific studies (Gaines *et al*., 2010b; De Leo and Micheli, 2015).

The simulation which modelled global recruitment indicated that a smaller MPA (30% of the total area) was required to preserve stock and yield rather than the single MPA of 36% of the total area which was needed when local recruitment was modelled. Local recruitment is the more realistic scenario, given that at least three sub-stocks are recognised in the North Sea (ICES, 2019c). Data which is aggregated across sub-stocks can cause uncertainty around biological reference points (Frank and Brickman, 2000). As demonstrated by the case-study model, if future simulations of North Sea herring management consider the spawning sub-stocks as one (Bjørndal, 1988), it could lead to an underestimation of the MPA size required to maintain SSB and yield, therefore potentially exacerbating any vulnerabilities in the stock.

It is therefore more beneficial to compare the effects of simulations with the same underlying, local recruitment structure. i.e.: a single MPA vs. three smaller MPAs which each protect a local recruitment ground of a sub-stock. Mobile, pelagic stocks such as herring could benefit less from smaller MPAs because they cross the boundaries more frequently (Allison *et al.,* 1998; Micheli *et al.,* 2004b; Blythe-Skyrme *et al*., 2006) and a solution to this could be the establishment of large MPAs (Edgar *et al*., 2014; Wilhelm *et al*., 2014; Ban *et al*., 2017). However, smaller MPAs could still be of benefit to mobile species if strategically placed to protect key life-history stages (Game *et al*., 2009; Breen *et al*., 2015). As such, the siting of three local MPAs around recruitment grounds is intuitively beneficial to conservation of the stock. This is representative of a network of MPAs: well-designed networks of MPAs can potentially enhance conservation of stocks more than the total benefit of the individual MPAs within them (Botsford *et al*., 2003; Gaines *et al*., 2010b; Anadon *et al*., 2011; Edgar *et al*., 2014), although this can be to the detriment of fisheries yields (De Leo and Micheli, 2015). However, in the simulations where three local recruitment grounds are defined, the results indicate that there is no real difference in the MPA size needed to meet the conservation and fisheries targets when a single MPA is put in place compared to three local MPAs being used to protect the recruitment grounds.

It must be considered, though, that due to the spatial arrangement of the model, a single MPA of 36% (established as the optimal size to protect SSB and meet yield) will encompass between 11% and 17% of the total recruitment ground areas depending on its placement between recruitment grounds (see Figure 5.1c). This result leads us to re-examine the MPA not in absolute terms of size but in terms of strategic placement. When local recruitment grounds are each protected by an MPA, all new recruits are immediately protected, but fish enter the harvest on crossing the recruitment ground boundary. When a single MPA is centred between local recruitment grounds only 11% - 17% of the new recruits are afforded immediate protection, however the larger single MPA confers additional conservation advantages. Because the MPA borders at least one recruitment ground, it can be thought of as providing safe transit out of the recruitment ground which protects more individuals for longer, in addition to providing protection to all age-groups which are in the MPA at a given time (LeQuesne and Codling, 2009; West *et al.,* 2009). Furthermore, it does so without compromising fisheries yields (Grüss *et al*., 2014).

When the model was used as a forecasting tool, the total MPA size needed to keep stock within biological limits and maintain yield was less when the starting stock biomass was greater – i.e.: at 2012 levels. Additionally, fishing effort in 2012 was lower than in 1965 (ICES, 2019b) and this has also been reflected in the simulation. There was still no real difference in size of MPA needed between three smaller, recruitment-ground based MPAs and the one larger MPA. Again, optimum size of MPA needed (18%) means the MPA borders directly onto a recruitment ground when placed as a single MPA. However, the reduction in optimum size of the MPA when coupled with lower effort and a more buoyant stock shows that any future models used as forecasting tools must accurately reflect these variables.

5.4.3 Inclusion of juveniles in the fishery

In 1965, the decision was made not to reduce the catch of juveniles in the herring fishery and concerns about the juvenile catch were raised again between 1989 and 1992 (Simmonds, 2007). Results from the simulation mirror previous findings that selective removals of juveniles in the fishery resulted in a more rapid collapse of the stock (Corten, 1986; Kunzlik and Bailey, 1986). Harvesting and bycatch of juveniles has been recognised as a significant contributory factor to the collapse of fisheries worldwide, for example the Atlantic cod fishery (Myers *et al*., 1997), coastal fisheries of India (Mohamed *et al*., 2014) and tuna (*Thunnus sp.*) fisheries in the Pacific (Bailey *et al*., 2013). The incentive to discard undersize, juvenile fish (Catchpole *et al*., 2005) has been tempered by the introduction of the discard ban under the Common Fisheries Policy reform (EU, 2013). Gear restrictions and landing regulations are also enforced to mitigate the impact of juvenile fishing mortality (EU, 1998, 2018; MMO, 2018), but it has been suggested that, in addition to these management measures, intended outcomes of the discard ban will need reinforcing via closures (Gullestad *et al*., 2015) or limited fishing opportunities which can take the form of spatial closures (Condie *et al*., 2014).The results from this chapter support these proposals and it is suggested that protection of juveniles could be bolstered further by increasing the MPA size above that derived for the adult fishery.

5.4.4 Non-compliance with management

Prior to the 1977 herring fishery collapse there was dissent between stakeholders as to what were acceptable management options (Simmonds, 2007). Current legislation and cooperative working (Dickey-Collas *et al*., 2016; EU, 2019) will ideally prevent such disagreements being detrimental to the overall management of the stock. However, if stakeholders withdraw support of management decisions (Beare *et al*., 2013), or compliance is not well enforced, the potential benefits of an MPA will be lost (Agardy *et al*., 2011; Edgar *et al*., 2014; Marra *et al*., 2016).

Lack of compliance with an MPA is not an unrealistic scenario with a mobile stock in a common-access resource such as the North Sea (Benjamin, 2001). Enforcing the multiple boundaries of a network of smaller MPAs or the bigger area of a large MPA both present challenges (De Santo, 2013; Wilhelm *et al*., 2014; Agardy, 2018). The results of this chapter indicate that a well-enforced MPA can buffer some non-compliance with effort restrictions, but the reverse is not true.

Even with strict controls on fishing-efforts (Dickey-Collas *et al*., 2010), encroachment on the simulated MPA by fishers was detrimental to preservation of the stock within biologically safe limits (Sala *et al*., 2018). When the separate recruitment grounds of the herring were protected by separate MPAs in the simulation, encroachment on one or more rapidly caused the stock to drop below safe biological limits, but the results indicate that a well-placed single MPA which partially overlaps at least one recruitment ground can buffer non-compliance to a greater extent than separate MPAs.

When locations of spawning and recruitment grounds of a stock are known (as is the case for the sub-stocks of North Sea herring), placing a single, large MPA at the border of a known key life-history area (Pérez-Jorge *et al*., 2015; D'Aloia *et al*., 2017) could be a viable and attractive management option to stakeholders with differing goals (Beare *et al*., 2013; Caveen *et al*., 2014; Erisman *et al*., 2017; Liu *et al*., 2018; Rybicki, 2018). As discussed, biomass and yield can both be conserved, proving biologically and economically lucrative (Rybicki, 2018) and it will also buffer a small degree of non-compliance with effort restrictions. Historically and in the future, a well-sited MPA such as this could provide the 'win-win' solution needed in a resource such as North Sea herring (Rees *et al*., 2010).

5.4.5 Model assumptions and future developments

In its present form, the model enables investigation of the broad principles of the use of MPAs to manage the North Sea herring stock. The model has enabled the reexamination of past management decisions and has also been applied as a forecasting tool.

The life-history parameters (age at maturity, age and size structure of the population) have been applied uniformly within the model. To make the model more representative of the ecology of North Sea herring, the life-history parameters should be refined by sub-stock because, although mixing of sub-stocks occurs at population level (Whitehead, 1985), each sub-stock has been identified as having characteristic life-history traits (Dickey-Collas *et al*., 2010): for example, age-at-maturity and length at age can differ between sub-stocks (ICES, 2019c).

It would also be preferable to utilise the flexibility of the Shepherd (1982) SRR equation to describe the SRR in each sub-stock discretely. Setting β=1.0 in the Shepherd

(1982) SRR equation across the duration of the simulations and between sub-stocks was an oversimplification of the model. It has been recognised that pooling data from across sub-stocks in this way can mask underlying stock-recruitment relationships - which can differ between populations (Frank and Brickman, 2000) - and stock-recruitment relationships are not static (Dickey-Collas *et al*., 2010; Corten, 2013). Density-dependence has been identified as a significant factor underlying the variability in herring recruitment since the fishery collapse of the 1970s (Heath *et al*., 1997) and variability in recruitment between sub-stocks has been evidenced (ICES, 2019a). The advantage of using the Shepherd (1982) SRR equation is that in future developments of the model the value of β can be changed to make the model more dynamic between years and between sub-populations.

Developing the model in this way will better reflect the life history variation seen within the Autumn spawning North Sea herring stock. The model could also be developed further to encompass other herring populations such as the North Sea Norwegian Spring-spawning stock - which are temporally and spatially separate from the Autumn-spawners (ICES, 2019c) – and the model findings could then be extended to examine the effects of intra-species variation in life-histories on the design and efficacy of MPAs.

In the model, recruitment was deterministic. The effects of this are seen in Figure 5.2, the calibration of fishing effort in the simulation: there is less inter-annual variation between SSB in the simulation compared to the real-world population. Stochastic recruitment was shown to have little effect on fisheries outcomes in the model on which the current simulations were based (Le Quesne and Codling, 2009). However, North Sea herring has undergone extended periods of poor recruitment to the fishery (Estrella-Martinez *et al*., 2019) and the variability of recruitment adds a high degree of uncertainty to estimates of yield and biological reference points (Dickey-Collas *et al.*, 2010). Therefore, additional simulations were run which explored the effect of the assumptions in the model about recruitment (See Appendix 5B, Figures 5B.1a – 5B.1c). The overall trend was the same when stochastic recruitment was introduced into the model, but the results did show that variability in recruitment could cause misplaced trust in the designated MPA size being able to protect biological reference points. Future versions of the model will need to incorporate accurate recruitment variability which reflect real-time data.

The model in its current form does not explicitly contain a larval phase, which has been identified as being the life-history stage which most influences year class strength of North Sea herring (Nash and Dickey-Collas, 2005). To model this correctly would require that the model was developed along the ecosystem approach so that those factors identified as having a strong correlation with larval to year 1 abundance could be incorporated into the model. For example, competition for food (Lynam *et al.*, 2005), temperature (Nash and Dickey-Collas, 2005) or larval transport (Corten, 1986).

Movement and the spatial domain were also simplified within the model. In reality, the North Sea is geographically more complex than is represented here and herring undergo migrations to spawning and feeding grounds within the North Sea (ICES, 2005; 2019c). The model in its current form identified three sub-stocks and allocated three recruitment grounds. Whilst some management regimes have recognised three sub-stocks (the Buchan and Shetland sub-stocks being treated as one sub-stock (Whitehead, 1985; ICES, 2005)), current advice (ICES, 2019c) is that four distinct spawning sub-stocks exist. As such, the model could be developed in complexity to more accurately reflect the geography of the North Sea and the location of spawning and nursery grounds.

Herring distribution can change in response to temperature and prey distribution (Corten, 2000 and 2001). The ecosystem approach of incorporating additional biotic, geographic and environmental factors would enable better understanding of these complex interactions.

Annual fishing effort was determined in the model by calibration and was static throughout the model. In reality, fishers will alter effort in real-time which will have a more dynamic effect on SSB than is currently represented in the simulation. The model could be enhanced to reflect this. A range of management options exist which can restrict effort or enforce harvest-control (MMO, 2018; ICES, 2019b). Additional parameters could be included in the model to reflect, for example, gear restrictions, quotas, days at sea or fisher behaviour: these would enable more detailed non-compliance scenarios to be explored.

The improvements outlined above will serve to make the model a more realistic in terms of ecology and life-history structure of North Sea herring stocks and, consequently, the model can be used as a more powerful forecasting tool to aid management decisions.

5.4.6 Conclusions and recommendations

MPAs can aid recovery of biologically compromised stocks and can conserve SSB of stocks within safe biological limits, but the more vulnerable the stock in terms of biomass, the larger the MPA will need to be to facilitate recovery. An MPA will also need to be larger to mitigate for juvenile harvesting. When the location of spawning or recruitment grounds is known, a single MPA bordering at least one of the grounds may protect stock equally as well as MPAs protecting each ground.

An MPA can buffer against changes in fishing effort but lack of enforcement of the MPA boundaries will compromise stock protection and it is therefore recommended that any implementation of an MPA will need to be coupled with an achievable enforcement plan and cooperation from stakeholders. Also recommended is that future models will need to accurately represent the spatial-resolution of sub-populations so the effects of an MPA can be more accurately predicted.

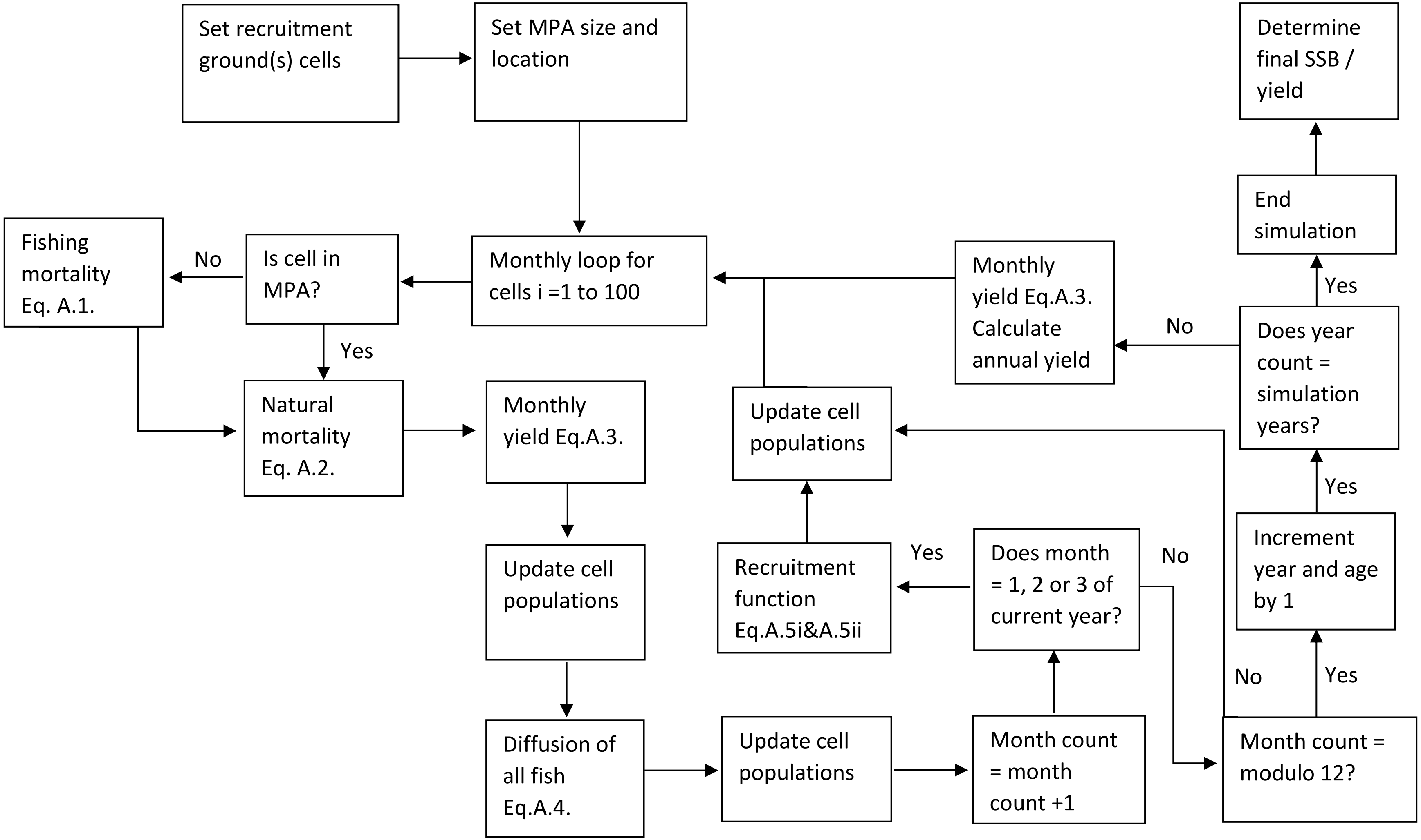


Figure 5A.1: Flow chart of the simulation when spatial closures are in place, indicating the monthly and annual sub-processes which are fully described by the accompanying equations below the diagram.

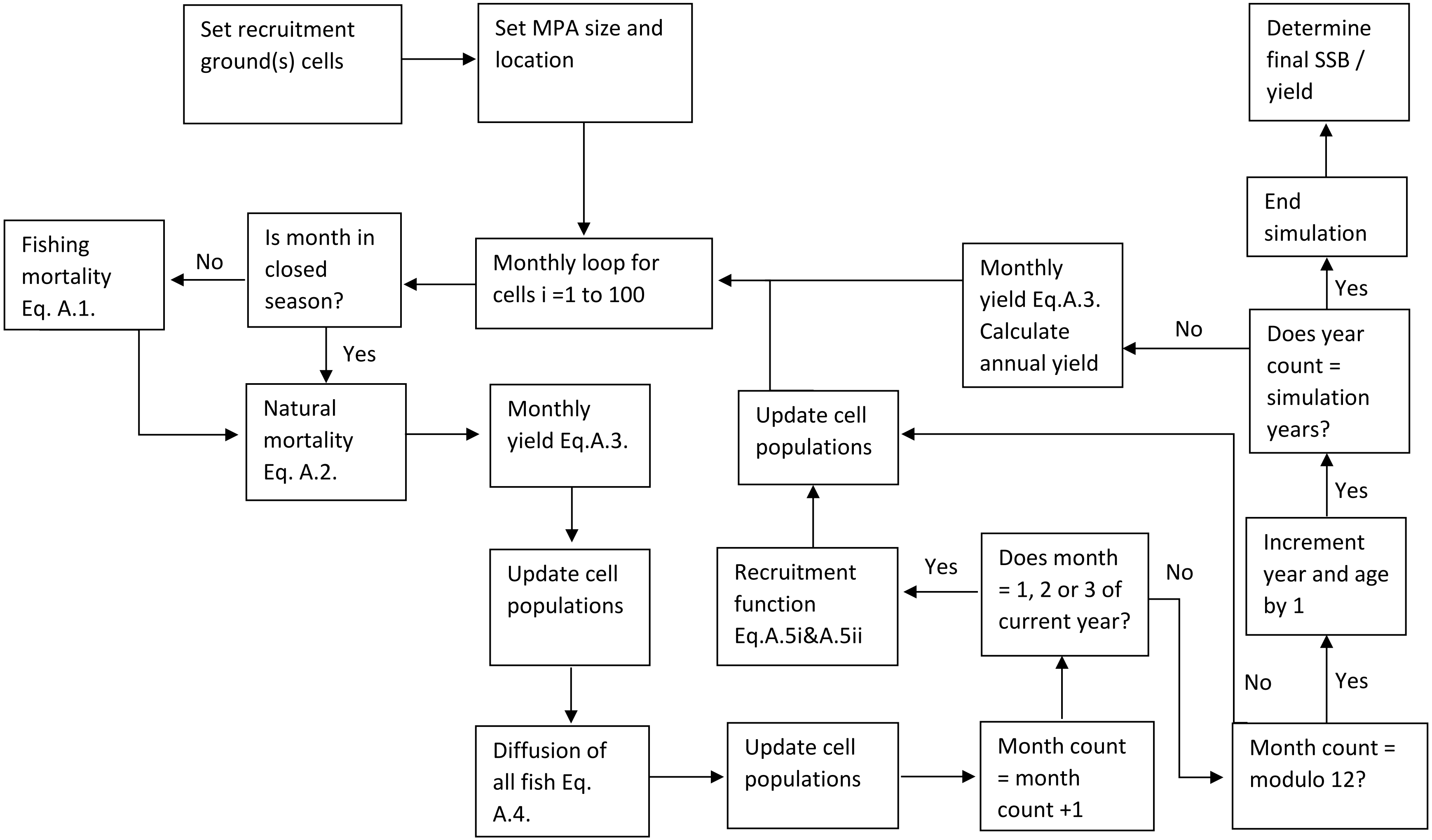


Figure 5A.2: Flow chart of the simulation when seasonal fishery closures are in place, indicating the monthly and annual sub-processes which are fully described by the accompanying equations and parameters below the diagram.

Equations 5A.1 – 5A.5

5A.1 $\mathrm{F_{a,c}} = \mathrm{E}.\frac{\mathrm{S_a}}{12x}$

$F_{a,c}$ is the fishing mortality for a given age class, a, and cell, c, in the most recent month; E is the nominal annual fishing effort across all cells (600 ≤ E ≤ 2000), x is the number of cells open to fishing, and S_a is the selectivity per age class (see Tables 1 and 2) - the same across all cells for a given age class of each species. As per Le Quesne and Codling (2009), capture efficiency (q) is assumed to be the same between species

5A.2 $N_{a,t+1,c} = N_{a,t,c}.\,\mathrm{exp}(-(F_{a,c} + M_a)$

The standard exponential decay model (Pitcher and Hart, 1982). $N_{a,t,c}$ is the number of individuals of age a in years, at month t, in cell c; M_a is the natural mortality rate at age a (assumed to be the same per species across all cells) and $F_{a,c}$ is the fishing mortality described in (1) applied to cells outside the MPA when t is a multiple of 12 (i.e. the end of a year) the age is updated by one year.

5A.3 $Y_{a,t,c} = \left(\frac{F_{a,c}}{F_{a,c}+M_a}\right) * \left(N_{a,t+1,c} - N_{a,t,c}\right) * W_a$

The Baranov Catch Equation (Baranov, 1918). $Y_{a,t,c}$ is the yield in kg for a given age class, a, and cell, c, in the most recent month, t; W_a is the mass per individual at age a (W_a is the same per species across all cells); $F_{a,c}$ and M_a are as stated in (1) and (2) respectively.

5A.4 $p(x,t) = \frac{e^{\frac{-x^2}{4D}}}{\sqrt{4\pi D}}$.

The probability density function for a single step of a one-dimensional diffusion process (Okubo and Levin, 2001; Codling *et al.*, 2008), where x is the unit of distance between cell centres, t is a monthly time step, D is the diffusion coefficient (D=10) and $p(x,t)$ represents the probability that in a single monthly time step (t) an individual from a given cell will have moved to another cell up to 100 distance units away in either direction. The sum of $p(x,t)$ was rescaled to 1 at each monthly time-step. The population redistribution at each monthly time step is calculated independently for each of the spatial cells so elements of the population are not redistributed more than once in a single time step.

5A.5i. $R = \frac{aB}{\left[1+\left(\frac{B}{K}\right)^{\beta}\right]}$

The Shepherd (1982) recruitment function. R is the total number of recruits (age 0 fish) to the population; α = 0.023; K=0.41x10^6 ; β = 0.5, 0.75, 1.0, 1.25, 1.5, 1.75 or 2.0 (defined in simulation); S is the total spawning stock biomass, thus:

5A.5ii. $S = \sum_{c,a} N_{c,a} * W_a * Mat_a$.

i.e.: where c is the cells in the recruitment ground, a is the age-classes, W_a is the mass per individual at age a and Mat_a is the maturity per age class (as per parameters - Table 1

Appendix 5B

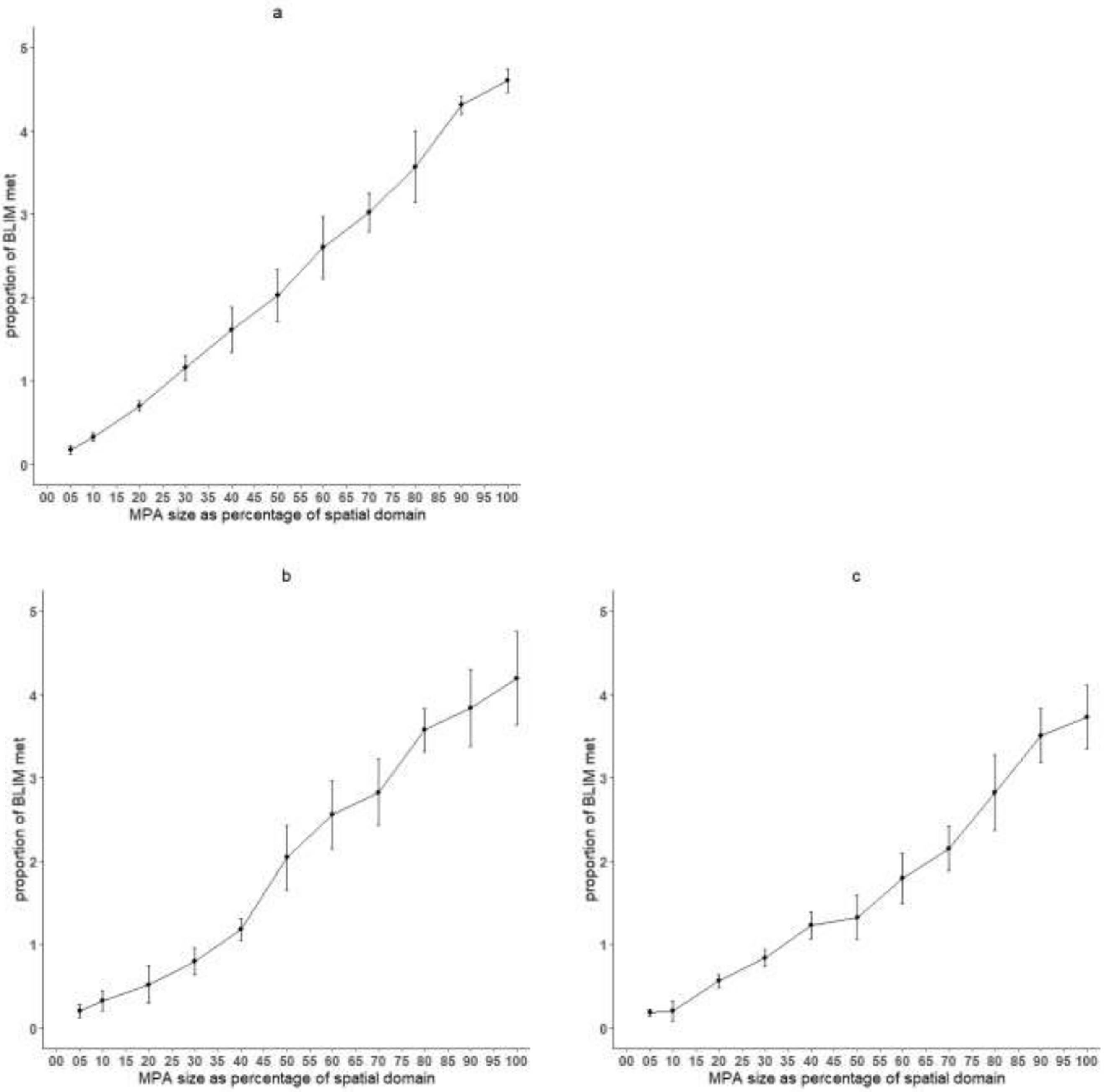

a
b
c
proportion of BLIM met
MPA size as percentage of spatial domain
0
1
2
3
4
5
00 05 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100

Figure B.1: The proportion of B_{LIM} and mean annual yield (without closures) which were met when MPA spatial closures protected 5% - 95% of the total spatial domain. The simulation was run for 12 years in monthly time steps with stochastic recruitment and a constant annual fishing effort (F=1620), determined as the equivalent of that in the 1965 fishery. SE bars represent 95% confidence limits. _____ = SSB; ……… = mean annual yield.

a. global recruitment, one MPA

b. three local recruitment grounds, three MPAs, each centred at the middle of one of the three recruitment grounds (MPA size is cumulative between the three)

c. three local recruitment grounds, one MPA centred between two of the three recruitment grounds.

Chapter 6: Discussion, recommendations and conclusions for the use of MPAs to protect mobile species.

A wealth of literature exists about the design and application of MPAs as conservation and fisheries management tools. However, mobile species remain under-represented in the literature in both empirical and simulation studies. Facilitated by the development and application of a spatio-temporal mathematical model, this thesis aimed to address this gap in the literature and inform future MPA planning and implementation for conservation and management of mobile stocks. The results have given clarity to the parameterisation of future simulations and also provide guidelines for the design and implementation of MPAs in the future.

6.1. Determining an appropriate temporal resolution when modelling spatial closures.

The model in this thesis was developed from a previous model by Le Quesne and Codling (2009) who recommended that the temporal resolution of models of spatial closures should be investigated further. The review (in Chapter 2) of spatial models developed to test MPA effectiveness showed that the time-steps within these models ranged from one generation-time to annual increments. Mathematical models necessarily condense biological process which are synchronous and continuous to linear sequences of discrete events. It was therefore important to determine an appropriate level of temporal resolution within the model to be used in this thesis. Testing the model using annual, monthly, and weekly time-steps, I found that there was little qualitative difference between the results from monthly and weekly time-steps, but in terms of processing time, the weekly time-steps made the computational time of the simulation unwieldy. Therefore, I recommended the sub-models of population dynamics, movement and harvesting were applied monthly. This was important to ensure that the sub-models were at a temporal scale which would not mask predictive results of MPA effectiveness and ensured the model was robust so it could be adapted for application to different scenarios and contexts, both within this thesis and in any future studies.

6.2 Species mobility limits the effectiveness of MPAs in a mixed-fishery

Mixed-species fisheries present unique challenges to fisheries managers (Hastings *et al*., 2017). The species will have varying life-histories, single-species biological reference points cannot be applied across the fishery, and there may be conflicting aims such as conservation of SSB for a bycatch species compared with maintaining yield for a commercial species. Maximising the yield of the target species within the fishery can lead to a faster decline of any associated bycatch species, as has been evidenced by the seabass (*Dicentrarchus labrax*) bycatch in the cod (*Gadus morhua*) and horse-mackerel (*Trachurus trachurus*) fisheries (ICES, 2017). Bycatch and vulnerable stocks can be protected via restrictions of fishing effort through gear selection or legislative means. For example, the landing obligation of the EU Common Fisheries Policy (EU, 2013) apportions small quotas of vulnerable stocks and prohibits discards, but when these quotas are reached the stock can become a ‘choke-species’ (Schrope, 2010) and cause premature closure of the fishery, leading to loss in yield and revenue to fishers.

Whether MPAs could help to resolve these conflicts within mixed-species fisheries has yet to be resolved. Whilst there is empirical and modelling evidence for the capacity of MPAs to protect biomass and potentially enhance yields of stocks for species with low mobility, there is not a similar body of evidence for species of high mobility. Large scale

MPAs could afford effective protection to mobile species and benefit biomass conservation, but such large areas could make mobile stock inaccessible to fishers. This debate remains unresolved in the literature and the constraints of collecting empirical evidence for mobile species (Letessier *et al*., 2015) means mathematical modelling lends itself well to addressing the issues.

In Chapter 3, I adapted the spatio-temporal mathematical model to represent a two-species mixed fishery of mobile species. When considered on a single-species basis, the results of this chapter confirmed findings of other authors, that the extent of mobility of the species impacted the effectiveness of MPA protection: larger MPAs are needed for conservation of biomass and effort control can be used in conjunction with or as an alternative to MPAs to maintain biomass.

Recent spatio-temporal simulations in the literature have included single-species models of mobility, MPAs and yield (De Leo and Micheli, 2015; Cornejo-Donso *et al*., 2017); a two-species model with conflicting management aims but with non-diffusive (i.e. low or no mobility) adults (Hastings *et al*., 2017); and a multi-species model of mobile individuals but without conflicting management aims (D'Aloia *et al*., 2017). What was novel about Chapter 3 was the extension of the single-species findings to consideration of the bycatch and target species management aims concurrently, whilst considering whether the degree of mobility of each species compromised the effectiveness of the MPA. When both species exhibited a similar degree of mobility, fisheries and conservation aims could be met using an MPA, effort regulation or both. It is more likely in a mixed fishery that the two species will have relatively different degrees of mobility and I concluded that when a bycatch species is more mobile than the target species, it limits the management options because the large MPA needed to maintain the bycatch biomass prevents fishers reaching their target yield. This corroborates the ‘weak stock’ findings of previous studies (Hilborn *et al*., 2004; Hastings *et al*., 2017) but from a fresh perspective – that of mobility.

This finding will be an important consideration in future planning and implementation of MPAs and consequently I recommend that models which predict MPA effectiveness for multi-species fisheries need to consider the mobility of each stock within the fishery.

In terms of fishery management, the outcome of this chapter leads to the recommendation that the harvest of a target species will need to be reduced in order to give MPA protection to a bycatch species which is at or near biological limits and has high conservation value.

6.3 The stock-recruitment relationship in a model affects predictions of MPA effectiveness

Marine populations exhibit a wide range of life-history strategies and recruitment relationships and a mathematical model must represent each as accurately as possible to trust in the predictive ability of the model. In Chapter 4 I revised the stock recruitment relationship (SRR) used in the model and replaced the Ricker (1954) stock-recruitment function with that of Shepherd (1982).

Use of the Shepherd (1982) function enabled me to alter the degree of density-dependence in the stock-recruitment function by changing the beta parameter (β). I was then able to explore the impact of MPAs on mobile stocks with different degrees of density-dependence in their SRR.

The results showed that the density-dependence in the SRR did impact the effectiveness of an MPA: stocks with intermediate density-dependence in their SRR benefited most from spatial closures. Stocks which exhibited classical Ricker (1954) density dependence benefited less from the MPA. Density-dependent mechanisms in ecology have been discussed at length in the literature (for example, see Ratikainen *et al*., 2007) and within the context of MPA studies (for example, see Micheli *et al*., 2004a; Abesamis and Russ, 2005). The findings of Chapter 4 have supplemented the discussion in the literature, showing that MPAs are most beneficial to stocks in which strong density-dependent mechanisms do not operate. Additionally, the results of Chapter 4 demonstrated that future mathematical models of MPA effectiveness must determine the most appropriate SRR in the simulated stock if MPA benefits to that stock are to be accurately predicted.

6.4 Seasonal (spawning) closures are not as effective as MPAs for mobile stocks

Seasonal closures are a common management option to protect the stock during spawning seasons in temperate areas and modelling studies have highlighted the potential benefits of these. However, there is a lack of empirical evidence as to their success and they can also be an inefficient management option if they result in effort-displacement. Additionally, the variability in temperate spawning seasons means the closures can be enforced at the wrong time. Spawning and recruitment seasons and grounds in temperate waters are not only variable but also species-specific, meaning that seasonal spawning and recruitment closures in a multi-species fishery present additional management challenges in terms of planning and enforcement.

MPAs could be an alternative to seasonal spawning closures: they can be sited permanently and could therefore be in place *a priori* to the spawning season rather than established as a responsive measure to the predicted spawning season. If sited at spawning grounds, permanent MPAs can not only protect the spawners during season but afford year-round protection to all individuals within their boundaries. Counteracting this is that mobile species will cross the MPA boundary more often and therefore lose the protection of the MPA. In Chapter 4, I asked the question whether MPAs or seasonal closures protecting a recruitment season potentially confer more benefits to the conservation of SSB and protection of yields of a mobile, temperate stock.

The outcome of the model was that an MPA consistently protected SSB to a greater degree; seasonal closures of any length allowed more yield to be maintained but failed to protect SSB, which was driven below biological reference points. This calls into question the claim (Erisman *et al*., 2017) that seasonal closures can be beneficial to both conservation and fisheries goals. Concerns have been raised that seasonal closures can result in effort displacement which then leads to overfishing. My results supported this argument: when effort was displaced due to a 50% MPA more of the biomass was preserved than when a six-month seasonal closure was in place. I then demonstrated that harvesting regulations needed to be imposed over and above seasonal closures if they were to protect SSB to the same extent that the MPA did.

Protecting the spawning stock in a commercial fishery is important to ensure the reproductive capacity of the stock is not impaired and yields can be maintained. The results of this analysis have illustrated that a suite of management options – spatial, temporal and effort-control – can and should be exercised to achieve this goal.

6.5 Models of MPA effectiveness should be applied to real-world scenarios.

The mathematical models used in Chapters 2 to 4 were parameterised with life-history data derived from the literature and the model was refined from its starting point to include appropriate temporal resolution and SRR relationships. The next stage in developing the model was to apply it to real-world data via a case study of the North Sea herring (*Clupea harengus*) fishery. Using biomass and fishing effort data from stock assessments was an important step in the model development because, although theoretical models are important to provide overarching principles for MPA design, testing and refining any model against empirical data makes the predictions from the model more certain.

Fisheries collapses worldwide are well documented and MPAs have been used to rebuild the stocks of mobile target species. A range of other management options which limit fishing effort on a stock are also available, such as total allowable catches (TACs), seasonal closures, and gear restrictions. However, these traditional management measures have been questioned as to their effectiveness (Villasante *et al*., 2010; O'Leary *et al*., 2016).

In Chapter 5, I sought to go some way to closing the gap between theoretical and empirical studies of MPAs and alternative management measures. I used historic and contemporary stock data for North Sea herring to determine what impact these management options could have on a vulnerable stock.

Spatial, MPA closures were not used at the time to prevent the 1970s stock collapse of North Sea herring, but a total fishery closure was enforced after collapse. By applying my model to historic stock data from that period (ICES, 2005, 2019a), I demonstrated that MPA closures enforced when the stock was first identified as being vulnerable could have prevented the subsequent collapse of the fishery. This would have preserved the stock biomass as well as some harvest for the fishers. I then applied the model to contemporary data from the 2012 fishery stock assessment (ICES, 2019b) and demonstrated that MPA closures could also preserve SSB of the fishery in the future. A key finding in these results was that the MPA size needed to preserve SSB when the stock was more buoyant (2012) was smaller than the MPA size needed to prevent the fishery collapse when the stock was nearing biological limits (1965). As discussed above and throughout this thesis, there is much debate about the best size of MPAs, but there is little empirical work to support the proposed size of closed areas for mobile species. The findings within this thesis suggest that real-time stock data is needed when planning MPAs to ensure that spatial closures are of a scale which will protect the stock and also ensure continued yield. Future models of MPA effectiveness should therefore incorporate biomass and fishing effort data about the stock to have more faith in the predictions of the models to real-world scenarios.

6.6 Decision Making

In Chapter 3, I showed that MPA protection of a more mobile conservation species prevented a target species being harvested fully. In any mixed fishery, similar trade-offs in priorities will be evident: key decisions to protect one stock will have implications for another stock due to, for example, associated impact on invertebrate species, catch and by-catch and predator-prey interactions. For example, as recently as January 2020, the Sussex Inshore Fisheries and Conservation Authority banned trawling along the Sussex coast to protect kelp forests in the inshore waters (Sussex IFCA, 2020). The spawning season closures explored in subsequent chapters are targeted at one species' spawning season, but the spawning seasons in a mixed-species fishery will not be synchronous in time nor space. As such, fishery managers will need to prioritise the species most in need of protection during their spawning season. In the case of stocks such as North Sea Herring – where sub-stocks have discrete spawning grounds and different spawning seasons – decisions can be based on the ecology of the population but, as explored in Chapter 5, this risks masking sub-population level effects which can negate the management decisions made. The complexity of life-histories, movement types and spawning types and seasons in a mixed-species fishery involves a series of hierarchical decisions which assess the merits for each species against the potential trade-offs for another. A suite of management techniques is available to mitigate these trade-offs such as TACs, discard bans, limited fishing effort, gear restrictions, seasonal and spatial closures. The model and subsequent simulations developed for this thesis can be developed further and parameterised with real-world data to explore the theoretical trade-offs which are necessitated in multi-species fishery management, allowing *a priori* assessment of the optimum suite of management options before implementation.

6.7 Future Developments

6.7.1 Stakeholder involvement

The stakeholders in fisheries management are vital to successful implementation of any management actions. There is evidence that gear restrictions, TACs and landing obligations cannot effectively protect stocks without being bolstered by additional measures such as MPAs (Villasante *et al*., 2010; O'Leary *et al*., 2016) and stakeholder buy-in and cooperation with these measures is vital for them to be effective.

Stakeholder compliance with fisheries management necessitates appreciation of a complex set of social, cultural and economic considerations. In many tropical areas the oceans are a source of food-security. Reducing harvests via fisheries regulation can have an immediate and negative effect on nutrition and income of fishers and their communities in those areas. This makes it challenging to garner stakeholder buy-in, despite potential long-term ecological and economic gains. In areas such as the North Sea fish is not the only source of protein, but fishing is nonetheless a long-standing industry: fishers' revenues – and those of associated industries – depend on regular and sustainable harvests. Culturally, Britain's coastal towns have centuries' long traditions of fishing and, whilst the fishers operate under EU fishing policy, their knowledge of and rights to access their home-waters are often fiercely guarded. This is currently very apparent with respect to Britain's negotiations with the EU regarding post-Brexit fishing rights (Brunsden *et al*., 2020).

Beyond those that rely on the fishing industry for their income, stakeholders can also be members of pressure groups, conservationists, or recreational users of the waters. The interests and voices of the stakeholders are many and varied and lack of compliance by just one group, or failure to find consensus between the groups can undermine management decisions.

In a multi-species fishery, non-compliance with fishing management decisions can have effects beyond those on the target species. Ignoring the discard-ban to increase yield of a target species incurs heavy fines, but if lack of investment means the discard ban can go unheeded then the fines will not be enforced and – as illustrated in Chapter 3 - the SSB of the bycatch or 'choke species' of a multi-species fishery will be driven down. Non-compliance can also take the form of not observing restricted fishing areas. In a small MPA, boundary enforcement is more practicable than in large and very large MPAs. At the scale of 100s and 1000s of kms, the investment needed to patrol MPA boundaries can be prohibitive and result in poorly enforced MPAs.

Compliance with management decisions was explored in Chapter 5 and the results demonstrated that non-compliance with fishing effort could be buffered by an MPA but non-compliance with the MPA could result in the stock biomass being driven below safe limits. MPA enforcement – particularly for the large-scale MPAs needed for mobile species – is challenging because of the financial and human resources needed to patrol MPA boundaries. A future application of the model could be to explore non-compliance issues further and present these results to stakeholders to garner buy-in from groups with potentially conflicting objectives. This could encourage collaboration between the fishing industry and science (Ford and Beukers-Stewart, 2019). For example, Figure 8 in Chapter 3 and Figures 5.4 - 5.6 in Chapter 5 show the balance between SSB and yield at different MPA sizes. These could be developed to demonstrate to fishers the true rather than perceived amount of yield which would be lost when closures were enforced. This will be particularly important when the model is used as a forecasting tool, as it was in Chapter 5, because the success of any fisheries management decisions - including future MPA planning and implementation - will be dependent on stakeholder buy-in and compliance.

6.7.2 Choosing MPA location

In Chapter 5 I explored the benefits of protecting three virtual recruitment-grounds with three separate MPAs compared to one MPA situated away from the recruitment grounds. The results showed that one MPA which was the equivalent total size of the three separate closures would protect stock equally as well if it bordered one of the recruitment grounds. This result is a spring-board for future work, particularly given the mass of literature given to debate about the benefits of MPA networks vs. large MPAs for mobile organisms and the benefits of protecting key life-history stages if a species' whole range cannot be protected. Previous theoretical models have explored the spatial arrangement of MPAs for mobile stocks (for example: Le Quesne and Codling, 2009; De Leo and Micheli, 2015) but there is still a need for simulations based on stock assessments, mobility and life-history of real species (Foster *et al.*, 2017). The model should be developed in the future to explore spatial arrangements of MPAs in relation to mobile species' spawning, nursery and feeding areas and, as recommended in Chapter 4, should incorporate stage-specific density dependent relationships in the stock at each stage. As such, the research field will benefit from additional studies of the ecology and life-history of species which are currently under-represented in the literature and can be incorporated into this and other future simulations.

6.7.3 Model Considerations

Mathematically, the model required a burn-in time to allow the fluctuations of the population dynamics described by the stock-recruitment relationship to damp down. Application of a Leslie-Matrix (Leslie, 1945) is a common approach for age-structured models in population ecology and the model could be adapted to utilise this or a Lefkovitch (1965) matrix to represent, for example, larval, juvenile and adult stock. A matrix approach would also enable density-dependence in and between life stages to be incorporated into the model efficiently but requires large amounts of data, which are not always available in data-poor fisheries (Cornejo-Donoso *et al*., 2017). As such, the structure I have used takes longer computationally in terms of the burn-in time but is appropriate for predicting the outcome of MPAs, particularly for scenarios where little empirical data is available.

The simple diffusive movement in the model is another aspect I would aim to refine. Adult migratory movements are common in temperate species and should be incorporated, as should different movement patterns at different life-history stages. Further field research tracking the migratory movements of highly mobile species will be of benefit when designing MPAs. Empirical data of this type can be incorporated into the model to make the movements realistic in time and space. The spatial domain is simplified as a loop and a logical development would be to explore different spatial representations so that, coupled with different movement patterns, migratory routes (for example: to / from spawning grounds or between legislative areas) could be represented at realistic scales.

As outlined in this thesis, the model used is deterministic and does not contain interactions between species nor abiotic factors. By comparison, ecosystem models are far more complex, representing biotic and abiotic variables to a fine degree of detail. The model I have used will benefit from incorporating different movement types and species interactions. Nonetheless, there remains a place for deterministic models in the MPA literature to unpick underlying factors which affect MPA size, so they can then be accurately represented in more complex models. This is particularly the case for mobile species for which the benefits of MPAs are unproven, and predictions about MPA effectiveness rely largely on theoretical applications and simulations to enhance understanding.

6.8 Conclusions

No Take Zone Marine Protected Areas have been commended as tools to help rebuild overexploited fisheries stocks and to facilitate conservation of vulnerable species. To date, the literature regarding the effectiveness of MPAs has focussed on species with low mobility. This study has explored the potential benefits of MPAs as fisheries management and conservation tools for mobile species via a spatio-temporal model. It has highlighted the importance of considering mobility of species when designing MPAs and I have made recommendations for the development of simulations to provide more accurate predictions of MPA effectiveness. Over-arching principles are provided which, as demonstrated in the final chapter, can be applied to real-life scenarios to inform the planning of MPAs to protect mobile species.

The literature has previously lacked evidence that MPAs can be used to protect highly mobile stocks. This study has shed light on the fact that MPAs can be a suitable management option to protect key life-stages of mobile stocks and can also be used to buffer harvesting of bycatch species in mixed-species fisheries. I have recommended that MPAs can be used as a stand-alone measure to protect mobile by-catch species in need of conservation but the necessary trade-off in a mixed fishery will be that the harvest of the target species will need to be compromised. Additionally, I have recommended that MPAs are considered as a suitable management option for stocks which do not have strong density-dependent mechanisms. The simulations have also shown that MPAs can be effective as part of the suite of fisheries management interventions available: they can be used in conjunction with more traditional management options such as seasonal closures, effort restriction and quotas to maintain stocks within biological limits. In conclusion, MPAs confer a greater choice of management options in multi-species and mobile-species fisheries and give greater flexibility in being able to find a suitable management solution to meet potentially conflicting stakeholder priorities.

References

Note: references are for chapters 1,2 & 4-6. Those for chapter 3 are within the published paper.

Abesamis, R. A. and Russ, G. R. (2005) Density-dependent spillover from a marine reserve: Long-term evidence. Ecological Applications, **15**, 1798-1812.

Aburto-Oropeza, O., Erisman, B., Galland, G. R., Mascarenas-Osorio, I., Sala, E. and Ezcurra, E. (2011) Large Recovery of Fish Biomass in a No-Take Marine Reserve. PLOS ONE: e0023601. https://doi.org/10.1371/journal.pone.0023601 *accessed on 12th May 2015.*

Afonso, P., Fontes, J. and Santos, R. S. (2011) Small marine reserves can offer long term protection to an endangered fish. Biological Conservation, **144**, pp. 2739-2744.

Agardy, M. T. (1994) Advances in marine conservation - the role of marine protected areas. Trends in Ecology & Evolution, **9**, pp. 267-270.

Agardy, T. (1999) Creating havens for marine life. Issues in Science and Technology, **16**, pp. 37-44.

Agardy, T. (2000) Information needs for marine protected areas: scientific and societal. Bulletin of Marine Science, **66**, pp.875-888.

Agardy, T. (2018) Justified ambivalence about MPA effectiveness. ICES Journal of Marine Science, **75**(3), pp. 1183-1185.

Agardy, T., di Sciara, G. N. and Christie, P. (2011) Mind the gap. Addressing the shortcomings of marine protected areas through large scale marine spatial planning. Marine Policy, **35**, pp. 226-232.

Allison, G. W., Lubchenco, J. and Carr, M. H. (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications, **8**, S79-S92.

Allison, S. (2017) *The endangered European native oyster Ostrea edulis (L) and creation of Marine Conservation Zones: a win—win scenario for fisheries and conservation?* Thesis submitted for the degree of Doctor of Philosophy. Department of Biological Sciences. University of Essex. 226pp.

Almany, G. R., Connolly, S. R., Heath, D. D., Hogan, J. D., Jones, G. P., McCook, L. J., Mills, M., Pressey, R. L. and Williamson, D. H. (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs, **28**, pp. 339-351.

Anadon, J. D., D'Agrosa, C., Gondor, A. and Gerber, L. R. (2011) Quantifying the Spatial Ecology of Wide-Ranging Marine Species in the Gulf of California: Implications for Marine Conservation Planning. PLOS ONE: e0028400. https://doi.org/10.1371/journal.pone.0028400 *accessed on 28th December 2017.*

Anon. (1972) The Herring (North Sea Fishing) Licensing Order 1972. Statutory Instruments 1972 No. 470. http://www.legislation.gov.uk/uksi/1972/470/pdfs/uksi_19720470_en.pdf *accessed on 9th July 2019*.

Apostolaki, P., Milner-Gulland, E. J., McAllister, M. K. and Kirkwood, G. P. (2002) Modelling the effects of establishing a marine reserve for mobile fish species. Canadian Journal of Fisheries and Aquatic Sciences, **59**, pp. 405-415.

Attwood, C. G. and Bennett, B. A. (1995) Modelling the effect of marine reserves on the recreational shore-fishery of the South-Western Cape, South Africa. South

African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap, **16**, pp. 227-240.

Auster, P. J. and Shackell, N. L. (2000) Marine protected areas for the temperate and boreal Northwest Atlantic: The potential for sustainable fisheries and conservation of biodiversity. North Eastern Naturalist, **7**, pp. 419-434.

Babcock, R. C., Egli, D. P. and Attwood, C. G. (2012) Incorporating behavioural variation in individual-based simulation models of marine reserve effectiveness. Environmental Conservation, **39**(3), pp. 282–294.

Bailey, M., Sumaila, U. R. and Martell, S. J. D. (2013) Can cooperative management of tuna fisheries in the western Pacific Solve the growth overfishing problem? Strategic Behaviour and the Environment, **3**, pp.31-66.

Ballantine, W. J. and Gordon, D. P. (1979) New Zealand's 1st marine reserve, Cape Rodney to Okakari Point, Leigh. *Biological Conservation,* **15**, pp. 273-280.

Ban, N. C., Davies, T. E., Aguilera, S. E., Brooks, C., Cox, M., Epstein, G., Evans, L. S., Maxwell, S. M. and Nenadovic, M. (2017) Social and ecological effectiveness of large marine protected areas. Global Environmental Change, **43**, pp. 82-91.

Baranov, F. I. (1918) On the question of the biological basis of fisheries in: Sass, G.G., Allen, M.S. (Eds.), *Foundations of Fisheries Science*. American Fisheries Society, Bethesda, Maryland. pp. 11-72.

Batsleer, J., Rijnsdorp, A. D., Hamon, K. G., van Overzee, H. M. J. and Poos, J. J. (2016) Mixed fisheries management: Is the ban on discarding likely to promote more selective and fuel efficient fishing in the Dutch flatfish fishery? Fisheries Research, **174**, pp. 118-128.

Beare, D., Rijnsdorp, A. D., Blaesberg, M., Damm, U., Egekvist, J., Fock, H., Kloppmann, M., Rockmann, C., Schroeder, A., Schulze, T., Tulp, I., Ulrich, C., van Hal, R., van Kooten, T. and Verweij, M. (2013) Evaluating the effect of fishery closures: Lessons learnt from the Plaice Box. Journal of Sea Research, **84**, pp. 49-60.

Beattie, A., Sumaila, U. R., Christensen, V. and Pauly, D. (2002) A model for the bioeconomic evaluation of marine protected area size and placement in the North Sea. Natural Resource Modeling, **15**, pp. 413-437.

Bellows, R. S. (1981) The descriptive properties of some models for density dependence. Journal of Animal Ecolog, **50**(1), pp. 139-145.

Benjamin, D. K. (2001) Fisheries are a classic example of the “Tragedy of the Commons”. PERC reports, **19**(1): 15.

Berger, A. M., Goethel, D. R., Lynch, P. D., Quinn, T., Mormede, S., McKenzie, J. and Dunn, A. (2017) Space oddity: The mission for spatial integration. Canadian Journal of Fisheries and Aquatic Sciences, **74**, pp. 1698-1716.

Beverton, R. J. H. and Holt, S. J. (1957) On the dynamics of exploited fish populations. *Fishery Investigations Series II,* Vol. XIX, Ministry of Agriculture. London.

Björklund, M. I. (1974) Achievements in marine conservation, I. marine parks. Environmental Conservation **1**(3) pp. 205 – 217.

Bjørndal, T. (1988) The optimal management of North Sea herring. Journal of Environmental Economics and Management, **15**, pp. 9-29.

Bjørndal, T. and Lindroos, M. (2004) International management of North-Sea herring. Environmental and Resource Economics, **29**(1), pp.83-96.

Blyth-Skyrme, R. E., Kaiser, M. J., Hiddink, J. G., Edwards-Jones, G. and Hart, P. J. B. (2006) Conservation benefits of temperate marine protected areas: Variation among fish species. Conservation Biology, **20**, pp. 811-820.

Bogaert, D., Cliquet, A. and F. Maes (2009) Designation of marine protected areas in Belgium: A legal and ecological success? Marine Policy, **33,** pp. 878-886.

Bohnsack, J. A. (1998) Application of marine reserves to reef fisheries management. Australian Journal of Ecology, **23**, pp. 298-304.

Boonzaier, L. and Pauly, D. (2016) Marine protection targets: an updated assessment of global progress. Oryx, **50**(1), pp. 27-35.

Botsford, L. W., Brumbaugh, D. R., Grimes, C., Kellner, J. B., Largier, J., O'Farrell, M. R., Ralston, S., Soulanille, E. and Wespestad, V. (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. Reviews in Fish Biology and Fisheries, **19**(1), pp. 69-95.

Botsford, L. W., Hastings, A. and Gaines, S. D. (2001) Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. Ecology Letters, **4**, pp. 144-150.

Botsford, L. W., Micheli, F. and Hastings, A. (2003) Principles for the design of marine reserves. Ecological Applications, **13**, S25-S31.

Breen, P., Posen, P. and Righton, D. (2015) Temperate Marine Protected Areas and highly mobile fish: A review. Ocean & Coastal Management, **105**, pp. 75-83.

Brunsden, J., Dickie, M., Mallett, V. and Hughes, L. Brexit: why fishing threatens to derail EU-UK trade talks. The Financial Times, January 28th 2020.

https://www.ft.com/content/96ebfb1a-3ea6-11ea-a01a-bae547046735 *accessed on 22nd February 2020.*

Buxton, C.D., Hartmaan, K., Kearney, R. and Gardner, C. (2014) When is spillover from marine reserves likely to benefit fisheries? PLOS ONE: e0111774. https://doi.org/10.1371/journal.pone.0111774 *accessed on 18th May 2018*

Cabral, R. B., Gaines, S, D., Johnson, B. A., Bell, T. W. and White, C. (2019) Designing MPAs for food security in open-access fisheries. Scientific Reports, **9**, article number 8033.

Carvalho, P. G., Jupiter, S. D., Januchowski-Hartley, F. A., Goetze, J., Claudet, J., Weeks, R., Humphries, A. and White, C. (2019) Optimized fishing through periodically harvested closures. Journal of Applied Ecology https://doi.org/10.1111/1365-2664.13417 *accessed on 14th September 2019.*

Carwardine, J., Klein, C.J., Wilson, K.A., Pressey, R.L. & Possingham, H.P. (2009) Hitting the target and missing the point: target based conservation planning in context. Conservation Letters, **2**, pp. 3-10.

Catchpole, T. L., Frid, C. L. J. and Gray, T. S. (2005) Discards in North Sea fisheries: causes, consequences and solutions. Marine Policy, **29**, pp. 421-430.

Caveen, A. J., Fitzsimmons, C., Pieraccini, M., Dunn, E., Sweeting, C. J., Johnson, M. L., Bloomfield, H., Jones, E. V., Lightfoot, P., Gray, T. S., Stead, S. M. and Polunin, N. V. C. (2014) Diverging Strategies to Planning an Ecologically Coherent Network of MPAs in the North Sea: The Roles of Advocacy, Evidence and Pragmatism in the Face of Uncertainty. In: Johnson, M. L. and Sandell, J.

(eds.) *Marine Managed Areas and Fisheries*. San Diego: Elsevier Academic Press Inc. 666 pp.

CEFAS (2001) Technical Report TR_003 Technical report produced for Strategic Environmental Assessment – Sea 2 North Sea Fish and Fisheries

Chapman, M. R. and Kramer, D. L. (2000) Movements of fishes within and among fringing coral reefs in Barbados. Environmental Biology of Fishes, **57**, pp. 11-24.

Christensen, S. and Lassen, H. (1996) Optimal management of the Iceland-Greenland transboundary cod stock. Journal of Northwest Atlantic Fishery Science, **19**, pp. 21-29.

Clarke, J., Bailey, D. M. and Wright, P. J. (2015) Evaluating the effectiveness of a seasonal spawning area closure. ICES Journal of Marine Science, **72**, pp. 2627-2637.

Claudet, J., Osenberg, C. W., Benedetti-Cecchi, L., Domenici, P., Garcia-Charton, J.-A., Perez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.-M., Dimech, M., Falcon, J. M., Guala, I., Milazzo, M., Sanchez-Meca, J., Somerfield, P. J., Stobart, B., Vandeperre, F., Valle, C. and Planes, S. (2008) Marine reserves: size and age do matter. Ecology Letters, **11**, pp. 481-489.

Codling, EA., Hill, NA., Pitchford, JW. and Simpson, SD., (2004) Random walk models for the movement and recruitment of reef fish larvae. Marine Ecology Progress Series, **279**, pp. 215-224.

Codling, E. A., Plank, M. J., Benhamou, S. (2008) Random walk models in biology. Journal of the Royal Society, **5**, pp. 813-834.

Collette, B.B., Carpenter, K.E., Polidoro, B.A., Juan-Jordȧ, M.J., Boustany, A., Die, D.J., Elfes, C., Fox, W., Graves, J., Harrison, L.R., McManus, R., Minte-Vera, C.V., Nelson, R., REstrepo, V., Schratwieser, J., Sun, C-L., Amorim, A., Brick Peres, M., Canales, C., Cardena, G., Chang, S.-K., Chiang, W.-C., de Oliverira Leite Jr., N., Harwell, H., Lessa, R., Fredou, F.L., Oxenford, H.A., Serra, R., Shao, K-T., Sumaila, R., Wang, S-P., Watson, R. and Yáňez, E. (2016) High value and long life – double jeopardy for tunas and billfishes. Science, **333**(6040), pp. 291-292.

Condie, H. M., Grant, A. and Catchpole, T. L. (2014) Incentivising selective fishing under a policy to ban discards; lessons from European and global fisheries. Marine Policy, **45**, pp.287-292.

Convention on Biodiversity. (2010) W.P.C. plan for biodiversity 2011–2020. Montreal, Canada: Secretariat of the Convention on Biological Diversity. https://www.cbd.int/sp/targets/#GoalC *accessed on 25th October 2018*.

Corten, A. (1986) On the causes of the recruitment failure of herring in the central and northern North Sea in the years 1972-1978. ICES Journal of Marine Science, **42**(3), pp.281-294.

Corten, A. (2000) A possible adaptation of herring feeding migrations to a change in timing of the *Calanus finmarchius* season in the eastern North Sea. ICES Journal of Marine Science, **57**, pp. 1261-1271.

Corten, A. (2001) Northern distribution of North Sea herring as a response to high water temperatures and / or low food abundance. Fisheries Research, **50,** pp. 189-204.

Corten, A. (2013) Recruitment depressions in North Sea herring. ICES Journal of Marine Science, **70**(1), pp. 1-15.

Costello, M. J. and Ballantine, B. (2015) Biodiversity conservation should focus on no-take Marine Reserves: 94% of Marine Protected Areas allow fishing. Trends in Ecology and Evolution **30** (9) pp. 507–509.

Costello, C., Rassweiler, A., Siegel, D., De Leo, Giulio, Micheli, F. and Rosenberg, A. the value of spatial information in MPA network design. (2010) PNAS, **107**(43), pp. 18294–18299.

Cornejo-Donoso, J., Einarsson, B., Birnir, B. and Gaines, S. D. (2017) Effects of fish movement assumptions on the design of a marine protected area to protect an overfished stock. PLOS ONE: e0186309. https://doi.org/10.1371/journal.pone.0186309 *accessed on 28th December 2018.*

Cote, I. M., Mosqueira, I. and Reynolds, J. D. (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. Journal of Fish Biology, **59**, pp. 178-189.

Creese, R. G. and Cole, R. G. (1995) Marine conservation in New Zealand. Pacific Conservation Biology, 2, pp. 55-63.

Crowder, L. B., Lyman, S. J. Figueira, W. F. and Priddy, J. (2000) Source-sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science, **66**, pp. 799-820.

Cushing, D. H. (1971) The dependence of recruitment on parent stock in different groups of fishes. Journal du Conseil Permanent International pour l’Exploration de la Mer, **33**, pp. 340-362.

D'Aloia, C. C., Daigle, R. M., Cote, I. M., Curtis, J. M. R., Guichard, F. and Fortin, M. J. (2017) A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. Biological Conservation, **216**, pp. 93-100.

Daan, N., Bromley, P. J., Hislop, J. R. G. and Nielsen, N. A. (1990) Ecology of North Sea Fish Netherlands Journal of Sea Research, **26**(2-4), pp. 343-386.

da Silva, I. M., Hill, N., Shimadzu,H., Soares, A. M. V. M. and Dornelas, M. (2015) Spillover effects of a community-managed marine reserve. PLOS ONE: e0111774. https://doi.org/10.1371/journal.pone.0111774 *accessed on 29th November 2019.*

Daly, R., Smale, M. J., Singh, S., Anders, Darrell., Shivji, M., Daly, C. A. K., Lea, J. S. E., Sousa, L. L. Wetherbee, B. M., Fitzpatrick, R., Clarke, C. R., Sheaves, M. and Barnett, A. (2018) Refuges and risks: evaluating the benefits of an expanded MPA network for mobile apex predators. Biodiversity Research, **24**(9), pp. 1217-1230.

Davidson, L. N. K. and Dulvy, N. K. (2017) Global marine protected areas to prevent extinctions. Nature: Ecology and Evolution, **1** article number 40.

Davies, T. E., Maxwell, S. M., Kaschner, K., Garilao, C. and Ban, N. C. (2017) Large marine protected areas represent biodiversity now and under climate change. Scientific Reports, **7**, article number: 9569.

De Leo, G. A. and Micheli, F. (2015) The good, the bad and the ugly of marine reserves for fishery yields. Philosophical Transactions of the Royal Society B-Biological Sciences, **370**:20140276.

de Mitcheson, Y. S. (2016) Mainstreaming Fish Spawning Aggregations into Fishery Management Calls for a Precautionary Approach. Bioscience, **66**, pp. 295-306.

de Mitcheson, Y. S., Cornish, A., Domeier, M., Colin, P. L., Russell, M. and Lindeman, K. C. (2008) A Global Baseline for Spawning Aggregations of Reef Fishes. Conservation Biology, **22**, pp. 1233-1244.

De Santo, E. M. (2013) Missing marine protected area (MPA) targets: how the push for quantity over quality undermines sustainability and social justice. Journal of Environmental Management, **124**, pp. 137-146.

Dehans, L. A. and Fanning, L. M. (2018) What counts in making marine protected areas (MPAs) count? The role of legitimacy in MPA success in Canada. Ecological Indicators, **86**, pp. 45-57.

DeMartini, E. E. (1993) Modeling the potential of fishery reserves for managing pacific coral-reef fishes. Fishery Bulletin, **91**, pp. 414-427.

Devillers, R., Pressey, R. L., Grech, A., Kittinger, J. N., Edgar, G. J., Ward, T. and Watson, R. (2015) Reinventing residual reserves in the sea: are we favouring ease of establishment over need for protection? Aquatic Conservation, **25**(4), pp. 480-504.

Di Lorenzo, M., Claudet, J. and Guidetti, P. (2016) Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. Journal for Nature Conservation. **32,** pp. 62–66.

Dickey-Collas, M., Nash, R. D. M., Brunel, T., van Damme, C. J. G., Marshall, C. T., Payne, M. R., Corten, A., Geffen, A. J., Peck, M. A., Hatfield, E. M. C., Hintzen, T., Enberg, K., Kell, L. R. and Simmonds, E. J. (2010) Lessons learned from stock collapse and recovery of North Sea herring: a review. ICES Journal of Marine Science, **67**(9), pp. 1875-1886.

Dickey-Collas, M. (2016) North Sea herring: longer term perspective on management science behind the boom, collapse and recovery of the North Sea herring fishery. Edwards C. T. T. and Dankel D. J. (Eds) In *Management Science in Fisheries: An Introduction to Simulation-Based Methods,* London. pp. 397-410.

Die, D. J. and Watson, R. A. (1992) A per-recruit simulation model for evaluating spatial closures in an Australian penaeid fishery. Aquatic Living Resources, **5**, pp. 145-153.

Doherty, P. D., Baxter, J. M., Godley, B. J., Graham, R. T., Hall, G., Hall, J., Hawkes, L. A., Henderson, S. M., Johnson, L., Speedie, C. and Witt, M. J. (2017) Testing the boundaries: seasonal residency and inter-annual site fidelity of basking sharks in a proposed Marine Protected Area. Biological Conservation, **209,** pp. 68-75.

Domeier, M. L. (2011) *Reef Fish Spawning Aggregations: Biology, Research and Management.* (Eds. De Mictcheson, Y. S. and Colin, P. L.) Springer. New York. pp. 1-20.

Dudley, N. (Editor) (2008) Guidelines for Applying Protected Area Management Categories. Gland, Switzerland: IUCN. x + 86pp. WITH Stolton, S., P. Shadie and N. Dudley (2013) IUCN WCPA Best Practice Guidance on Recognising Protected Areas and Assigning Management Categories and Governance Types, Best Practice Protected Area Guidelines Series No. 21, Gland, Switzerland: IUCN.

Duery, S. and Maury, O. (2013) Modelling the effect of marine protected areas on the population of skipjack tuna in the Indian Ocean. Aquatic Living Resources, **26**(2) pp.171-178.

Dugan, J. E. and Davis, G. E. (1993) Applications of marine refugia to coastal fisheries management. Canadian Journal of Fisheries and Aquatic Sciences, **50**, pp. 2029-2042.

Edgar, G. J., Stuart-Smith, R. D., Willis, T. J., Kininmonth, S., Baker, S. C., Banks, S., Barrett, N. S., Becerro, M. A., Bernard, A. T. F., Berkhout, J., Buxton, C. D., Campbell, S. J., Cooper, A. T., Davey, M., Edgar, S. C., Forsterra, G., Galvan, D. E., Irigoyen, A. J., Kushner, D. J., Moura, R., Parnell, P. E., Shears, N. T., Soler, G., Strain, E. M. A. and Thomson, R. J. (2014) Global conservation outcomes depend on marine protected areas with five key features. Nature, **506**, pp. 216–220.

Edwards, C. T. T., Rademeyer, R. A., Butterworth, D. S. and Plagányi, E. E. (2008) Investigating the consequences of Marine Protected Areas for the South African deep-water hake (Merlucius paradoxus) resource. ICES Journal of Marine Science, **66**, pp. 72–81.

Ellis, J. R., Milligan, S., Readdy, L., South, A., Taylor, N. and Brown, M. (2010) MB5301 Mapping spawning and nursery areas of species to be considered in Marine Protected Areas (Marine Conservation Zones) Report No 1: Final Report on development of derived data layers for 40 mobile species considered to be of conservation importance. Department for Environment Food and Rural Affairs. 89pp.

Embling, C. B., Illian, J., Armstrong, E., van der Kooij, J., Sharples, J., Camphuysen, K. C. J. and Scott, B. E. Investigating fine-scale spatio-temporal predator-prey patterns in dynamic marine ecosystems: a functional data analysis approach. Journal of Applied Ecology, **49**(2), pp. 481-492.

Engelhard, G. H., Righton, D. A. and Pinnegar, J. K. (2014) Climate change and fishing: a century of shifting distribution in North Sea cod. Global Change Biology, **20**, pp. 2473-2483.

Erisman, B., Aburto-Oropeza, O., Gonzalez-Abraham, C., Mascarenas-Osorio, I., Moreno-Baez, M. and Hastings, P. A. (2012) Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. Scientific Reports, **2**(284). doi:10.1038/srep00284 *accessed on 14th September 2019.*

Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O. and Nemeth, R. S. (2017) Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. Fish and Fisheries, **18**(1), pp. 128-144.

Estrella-Martinez, J., Schöne, B. R., Thursdan, R. H., Capuzzo, E., Scourse, J. D. and Butler, P. G. (2019) Reconstruction of Atlantic herring (*Clupea harengus*) recruitment in the North Sea for the past 455 years based on the $\delta^{13}C$ from annual shell increments of the ocean quahog (*Arctica islandica*). Fish and Fisheries, **20**(3), pp. 537-551.

EU. (1998) Council Regulation (EC) No 850/98 of 30 March 1998 for the conservation of fishery resources through technical measures for the protection of juveniles of marine organisms. http://www.legislation.gov.uk/eur/1998/850/contents *accessed on 19th October 2019.*

EU. (2013) European Council Regulation No1380/2013 of the European Parliament and of the Council of 11December 2013 on the Common Fisheries Policy https://eur-lex.europa.eu/legal-content/EN/TXT/? uri=CELEX%3A32013R1380. *accessed on 18th October 2018.*

EU. (2018) Commission Delegated Regulation (EU) 2018/189 of 23 November 2017 amending Delegated Regulation (EU) No 1395/2014 establishing a discard plan for certain small pelagic fisheries and fisheries for industrial purposes in the North Sea. Official Journal of the European Union, **L 36**, 09.02.2018, pp. 4-7.

EU. (2019) Agreed record of fisheries consultations between Norway and the European Union for 2019 https://ec.europa.eu/fisheries/cfp/international/agreements/norway *accessed on 12th July 2019.*

European Parliament. (2010) Real-time closures of fisheries. Note for the Directorate General for Internal Policies, Policy Department B: Structural and Cohesion Polices, Fisheries. IP/B/PECH/IC/2009_091, 15 June 2010. 56 pp. http://www.europarl.europa.eu/studies *accessed on 12th May 2019*.

FAO. (2018) *The State of World Fisheries and Aquaculture 2018 - Meeting the sustainable development goals.* Rome. Licence: CC BY-NC-SA 3.0 IGO.

Fernandes, P. G. and Cook, R. M. (2013) Reversal of fish stock decline in the Northeast Atlantic. Current Biology, **23**(15), pp. 1432-1437.

Fernandez, M., Yesson, C., Gannier, A., Miller, P.I., Azevedo, J. M. N. (2017) The importance of temporal resolution for niche modelling in the dynamic marine environments. Journal of Biogeography, **44**(12), pp. 2816–1827.

Ferreira, B. P. and Russ, G. R. (1995) Population-structure of the leopard coral grouper, plectropomus-leopardus, on fished and unfished reefs off townsville, central great-barrier-reef, Australian Fishery Bulletin, **93**, pp. 629-642.

fishbase.org https://fishbase.org *accessed on 4th May 2019.*

Fogarty, M. J. (2001) An Introduction to the Concept and Application of Marine Protected Areas *www.whoi.edu/fileserver.do?id=19703&pt=2&p=23914 accessed on 17th July 2019.*

Fogarty, M. J. and Murawski, S. A. (2005) Do marine protected areas really work? Oceanus, **43**(2), pp. 1-3.

Fogarty, M. J., Sissenwine, M. P. and Cohen, E. B. (1991) Recruitment variability and the dynamics of exploited marine populations. Trends in Evolution and Ecology, **6**(8), pp. 241-246.

Ford, E. and Beukers-Stewart, B. D. (2019) Building a bridge over troubled waters: an analysis of fishers' trust in UK fisheries management. Report. Marine Ecosystem Management Report. University of York http://eprints.whiterose.ac.uk/148186/ *accessed on 1st August 2019.*

Foster, N. L., Rees, S., Langmead, O., Griffiths, C., Oates, J. and Attrill, M. J. (2017) Assessing the ecological coherence of a marine protected area network in the Celtic Seas. Ecosphere 8(**2**) e01688 https://doi.org/10.1002/ecs2.1688 *accessed on 23rd July 2019.*

Fovargue, R., Bode, M., Armsworth, P. R. (2017) Size and spacing rules can balance conservation and fishery management objectives for marine protected areas. Journal of Applied Ecology, **55**(3), pp. 1050-1059.

Fox, C. J., Taylor, M., Dickey-Collas, M., Fossum, P., Kraus, G., Rohlf, N., Munk, P., van Damme, C. J. G., Bolle, L. J., Maxwell, D. L. and Wright, P. J. (2008) Mapping the spawning grounds of North Sea cod (*Gadus morhua*) by direct and indirect means. Proceedings of the Royal Society B, **275**(1642), pp.1543-1548.

Frank, K. T. and Brickman, D. (2000) Allee effects and compensatory population dynamics within a stock complex. Canadian Journal of Fisheries and Aquatic Sciences, **57**(3), pp. 513-517.

Friedlander, A. M., Wagner, D., Gaymer, C. F., ‘Aulani Wilhelm, T., Lewis, N., Brooke, S., Kikiloi, K. and Varmer, O. (2016) Co-operation between large-scale MPAs: successful experiences from the Pacific Ocean. Aquatic Conservation, **26**(52), pp. 126–141.

Fulton, E. A., Smith, A. D., M., Smith, D. C. and van Putten, I. E. (2010) Human behaviour: the key source of uncertainty in fisheries management. Fish and Fisheries **12**(1) pp.2-17.

Gerber, L R., Botsford, L.W., Hastings, A., Possingham, H.O., Gaines, S.D., Palumbi, S.R. Andelman, S. (2003) Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications, **13**(1), pp.47-64.

Gaines, S. D. and Costello, C. (2013) Forecasting fisheries collapse. PNAS **110**(40) 15859 – 15860 https://doi.org/10.1073/pnas.1315109110 *accessed on 16th June 2018.*

Gaines, S. D., Lester, S. E., Grorud-Colvert, K., Costello, C. and Pollnac, R. (2010a) Evolving science of marine reserves: New developments and emerging research frontiers. Proceedings of the National Academy of Sciences of the United States of America, **107**, pp. 18251-18255.

Gaines, S. D., White, C., Carr, M. H. and Palumbi, S. R. (2010b) Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences of the United States of America, **107**, pp. 18286-18293.

Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., Gjerde, K., Bustamante, R., Possingham, H. P. and Richardson, A. J. (2009) Pelagic protected areas: the missing dimension in ocean conservation. Trends in Ecology & Evolution, **24**, pp. 360-369.

Gaylord, B., Gaines, S. D., Siegel, D. A. and Carr, M. H. (2005) Marine reserves exploit population structure and life history in potentially improving fisheries yields. Ecological Applications, **15**, pp. 2180-2191.

Gendron, L. and Brêthes, J. C. (2002) Simulations of the impact of different temporal and spatial allocations of fishing effort on fishing mortality in a lobster (Homarus americanus) fishery. Canadian Journal of Fisheries and Aquatic Sciences, **59**, pp. 899-909.

Giakoumi, S., McGowan, J., Mills, M., Beger, M., Bustamante, R. H., Charles, A., Christie, P., Fox, M., Garcia-Borboroglu, P., Gelcich, S., Guidetti, P., Mackelworth, P., Maina, J., McCook, L., Michele, F., Morgan, L. E., Mumby, P. J., Reyes, L. M., White, A., Grorud-Colvert, K. and Possingham, H. (2018) Revisiting “success” and “failure” of marine protected areas: a conservation scientist perspective. Frontiers in Marine Science, **5,** pp. 223–226.

Gill, D. A., Mascia, M. B., Ahmadia, G. N., Glew L., Lester, S. E., Barnes, M., Craigie, I., Darling, E. S., Free, C. M., Geldmann, J., Holst, S., Jensen, O. P., White, A. T., Basurto, X., Coad, L., Gates, R. D., Guannel, G., Mumby, P. J., Thomas, H., Whitmee, S., Woodley, S. and Fox, H. E. (2017) Capacity shortfalls hinder the performance of marine protected areas globally. Nature, **543**, pp. 665–669.

Goni, R., Hilborn, R., Diaz, D., Mallol, S. and Adlerstein, S. (2010) Net contribution of spillover from a marine reserve to fishery catches. Marine Ecology Progress Series, **400**, pp. 233-243.

González-Irusta, J. M. and Wright, P. J. (2016) Spawning grounds of haddock (*Melanogrammus aeglefinus*) in the North Sea and West of Scotland. Fisheries Research, **183**, pp. 180-191.

Grüss, A. (2014) Modelling the impacts of marine protected areas for mobile exploited fish populations and their fisheries: what we recently learnt and where we should be going. Aquatic Living Resources, **27**(3-4), pp. 107-133.

Grüss, A. and Kaplen, D. M. and Hart, D. R. (2011) Relative Impacts of Adult Movement, Larval Dispersal and Harvester Movement on the Effectiveness of Reserve Networks. PLOS ONE: e0019960. https://doi.org/10.1371/journal.pone.0019960 *accessed on 12th May 2018.*

Grüss, A., Robinson, J., Heppel, S. S., Heppell, S. A. and Semmens, B. X. (2014) Conservation and fisheries effects of spawning aggregation marine protected areas: What we know, where we should go, and what we need to get there. ICES Journal of Marine Science, **71**(7), pp. 1515-1534.

Grüss, A. and Robinson, J. (2015) Fish populations forming transient spawning aggregations: should spawners always be the targets of spatial protection efforts? ICES Journal of Marine Science, **72**, pp. 480-497.

Grüss, A., Biggs, C. R., Heyman, W. D. and Erisman, B. (2019) Protecting juveniles, spawners or both: a practical statistical modelling approach for the design of marine protected areas. Journal of Applied Ecology, httpe://doi.org/10.1111/1365-2664.13468 *accessed on 14th September 2019.*

Guénette, S. and Pitcher, T. J. (1999) An age-structured model showing the benefits of marine reserves in controlling overexploitation. Fisheries Research, **39**, pp. 295-303.

Guenette, S., Pitcher, T. J. and Walters, C. J. (2000) The potential of marine reserves for the management of northern cod in Newfoundland. Bulletin of Marine Science, **66**, pp. 831-852.

Gullestad, P., Blom, G., Bakke, G. and Bogstad, B. (2015) The "discard ban package": experiences in efforts to improve the exploitation patterns in Norwegian fisheries. Marine Policy, **54**, pp. 1-9.

Guidetti, P. and Sala, E. (2007) Community-wide effects of marine reserves in the Mediterranean Sea. Marine Ecology-Progress Series, **335**, pp. 43-56.

Haapasaari, P., Michielsens, C. G. J., Karjalainen, T. P., Reinikainen, K. and Kuikka, S. (2007) Management measures and fishers' commitment to sustainable exploitation: a case study of Atlantic salmon fisheries in the Baltic Sea. ICES Journal of Marine Science, **64**(4), pp. 825-833.

Halpern, B. S. (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecological Applications, **13**, S117-S137.

Halpern, B. S., Gaines, S. D. and Warner, R. R. (2004) Confounding effects of the export of production and the displacement of fishing effort from marine reserves. Ecological Applications, **14**, pp. 1248-1256.

Halpern, B. S. and Warner, R. R. (2002) Marine reserves have rapid and lasting effects. Ecology Letters, **5**, pp. 361-366.

Hamilton, R., Sadovy de Mitcheson,Y. and Aguilar-Perera, A. (2012) The role of local ecological knowledge in the conservation and management of reef fish spawning aggregations. In: *Reef Fish Spawning Aggregations: Biology, Research and Management* (Eds. Y. Sadovy de Mitcheson and P. L. Colin) Spring, New York. pp. 331-369.

Hannesson, R. (2018) Density-dependent growth and cannibalism in Northeast Arctic cod: Some implications for fishing strategies. Fisheries Research, **204**, pp. 1-7.

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

Hastings, A. and Botsford, L. W. (1999) Equivalence in yield from marine reserves and traditional fisheries management. Science, **284**, pp. 1537-1538.

Hastings, A. & L. W. Botsford (2003) Comparing designs of marine reserves for fisheries and for biodiversity. Ecological Applications, **13**, S65-S70.

Hastings, A., Gaines, S. D. and Costello, C. (2017) Marine reserves solve an important bycatch problem in fisheries. Proceedings of the National Academy of Sciences of the United States of America, **114**, pp. 8927-8934.

Hays, G. C., Mortimer, J. A., Lerodiaconuo, D. and Esteban, N. (2014) Use of long-distance migration patterns of an endangered species to inform conservation planning for the World’s largest marine protected area.

Conservation Biology, **28**(6), pp. 1636-1644.

Heath, M., Scott, B. and Bryant. A. D. (1997) Modelling the growth of herring from four different stocks in the North Sea. Journal of Sea Research, **38**(3-4), pp. 413-436.

Hennemuth, R. C., Palmer, J. E. and Brown, B. E. (1980) A statistical description of recruitment in eighteen selected fish stocks. Journal of Northwest Atlantic Fisheries Science, **1**, pp. 101-111.

Hilborn, R. (2018) Are MPAs effective? ICES Journal of Marine Science, **75**(3), pp. 1160-1162.

Hilborn, R., Micheli, F. and De Leo, G. A. (2006) Integrating marine protected areas with catch regulation. Canadian Journal of Fisheries and Aquatic Sciences, **63**, pp. 642-649.

Hilborn, R., Stokes, K., Maguire, J. J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., Cochrane, K. L., Garcia, S., Hall, S. J., Kirkwood, G. P., Sainsbury, K., Stefansson, G. and Walters, C. (2004) When can marine reserves improve fisheries management? Ocean & Coastal Management, **47**, pp. 197-205.

Holland, D. S. (2000) A bioeconomic model of marine sanctuaries on Georges Bank. Canadian Journal of Fisheries and Aquatic Sciences, **57**, pp. 1307-1319.

Holland, D. S. (2002) Integrating marine protected areas into models for fishery assessment and management. Natural Resource Modeling, **15**, pp. 369-386.

Holland, D. S. and Brazee, R. J. (1996) Marine Reserves for Fisheries Management. Marine Resource Economics, **11**, pp. 157-171.

Hopkins, C. R., Bailey, D. M. and Potts, T. (2018) Navigating futre uncertainty in marine protected area governance: lessons from the Scottish MPA network. Estuarine, Coastal and Shelf Science, **207**, pp. 303-311.

Horta e Costa, B., Claudet, J., Franco, G., Erzini, K., Caro, A and Gonçalves, E. J. (2016) A regulation-based classification system for Marine Protected Areas (MPAs) Marine Policy 72 pp. 192-198.

ICES. (2005) ICES FishMap http://www.ices.dk/explore-us/projects/EU-RFP/EU%20Repository/ICES%20FIshMap/ICES%20FishMap%20species%20factsheet-herring.pdf *accessed on 2nd July 2019.*

ICES. (2017) ICES Stock Assessment Database. ICES, Copenhagen, Denmark http://standardgraphs.ices.dk *accessed on 16 June 2018*.

ICES. (2018a) ICES advice on fishing opportunities, catch, and effort Greater North Sea Ecoregion version 2:24 her.27.3a47d https://www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/GreaterNorthSeaEcoregion_FisheriesOverview.pdf *accessed on 4th July 2019.*

ICES. (2018b) Advice for Herring (Clupea harengus) in Subarea 4 and divisions 3.a and 7.d, autumn spawners (North Sea, Skagerrak and Kattegat, eastern English Channel) http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2018/2018/her.27.3a47d.pdf *accessed on 2nd July 2019.*

ICES. (2019a) ICES advice on fishing opportunities, catch, and effort Greater North Sea Ecoregion version. Published 29 May 2019.

http://www.ices.dk/sites/pub/Publication%20Reports/Advice/2019/2019/her.27.3a47d.pdf *accessed on 12th July 2019.*

ICES. (2019b) EU and Norway request concerning the long-term management strategy of cod, saithe, and whiting, and of North Sea autumn-spawning herring. *In* Report of the ICES Advisory Committee, 2019. ICES Advice 2019, sr.2019.06, s *accessed on 10th July 2019.*

ICES. (2019c) Herring Assessment Working Group For the Area South of 62°N (HAWG). **Vol 1**, Issue 2. ICES Scientific Reports.

ICES. (2019d) Stock assessment graphs: her.27.3147d http://standardgraphs.ices.dk/ViewSourceData.aspx?key=10365 *accessed on 17th July 2019.*

ICNAF. (1972) North-East Atlantic Fisheries Commission, Tenth Meeting. Press Notice. 15th May 1972. https://www.nafo.int/icnaf/library/docs/1972/com-30.pdf *accessed on 9th July 2019.*

Iles, T. C. (1994) A review of stock-recruitment relationships with reference to flatfish populations. Netherlands Journal of Sea Research, **32**(3/4), pp. 399-420.

Jennings, S. (2000) Patterns and prediction of population recovery in marine reserves. Reviews in Fish Biology and Fisheries, **10**, pp. 209-231.

Jentoft, S. and Knol, M. (2014) Marine spatial planning: risk or opportunity for fisheries in the North Sea? Maritime Studies **12**(13) https://doi.org/10.1186/2212-9790-12-13 *accessed on* 21st February 2020.

Jones, P. J. S. and De Santo, E. M. (2016) *Viewpoint* – Is the race for remote, very large marine protected areas (VLMPAs) taking us down the wrong track? Marine

Policy, **73**, pp. 231-234.

Kaplan, D. M. and Botsford, L. W. (2005) Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability. Canadian Journal of Fisheries and Aquatic Sciences, **62**, pp. 905-912.

Kelleher, G. (1999) Guidelines for Marine Protected Areas. IUCN, Gland, Switzerland and Cambridge, UK.

Kellner, J. B., Tetreault, I., Gaines, S. D. and Nisbet, R. M. (2007) Fishing the line near marine reserves in single and multispecies fisheries. Ecological Applications, **17**, pp. 1039-1054.

Kelly, C. J., Codling, E. A. and Rogan, E., (2006) The Irish Sea cod recovery plan: some lessons learned. ICES Journal of Marine Science, **63**(4), pp. 600-610.

Kimura, D. K. (1988) Stock-recruitment curves as used in the stock-reduction analysis model. ICES Journal of Marine Science, **44**(3)**,** pp. 253-258.

King, J. R. and McFarlane, G. A. (2003) Marine fish life history strategies: applications to fishery management. fisheries Management and Ecology, **10**, pp. 249-264.

Kramer, D. L. and Chapman, M. R. (1999) Implications of fish home range size and relocation for marine reserve function. Environmental Biology of Fishes, **55**, pp. 65-79.

Kunzlik, P. A. and Bailey, R. S. (1986) Harvesting North Sea herring: results of a stochastic simulation model. ICES Document CM 1986/H: 9

La Mesa, G., Molinari, A., Bava, S., Finoia, M. G., Cattaneo-Vietti, R. and Tunesi, L. (2011) Gradients of abundance of sea breams across the boundaries of a Mediterranean marine protected area. Fisheries Research, **111**, pp. 24-30.

Laffoley, D., Baxter, J. M., Day, J. C., Wenzel, L., Bueno, P. and Zischka, K. (2019) Chapter 29 – Marine Protected Areas in Sheppard, C. (Ed) *World Seas: An Environmental Evaluation (Second Edition) Volume III: Ecological Issues and Environmental Impacts.* San Diego: Elsevier Academic Press Inc. pp. 549–569.

Lauck, T., Clark, C. W., Mangel, M. and Munro, G. R. (1998) Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications, **8**(1), pp. S72-S78.

Laurel, B. J. and Bradbury, I. R. (2006) "Big" concerns with high latitude marine protected areas (MPAs): trends in connectivity and MPA size. Canadian Journal of Fisheries and Aquatic Sciences, **63**, pp. 2603-2607.

Le Quesne, W. J. F. (2009) Are flawed MPAs any good or just a new way of making old mistakes? ICES Journal of Marine Science, **66**, pp. 132-136.

Le Quesne, W. J. F. and Codling, E. A. (2009) Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. Ices Journal of Marine Science, pp. **66**, 122-131.

Leenhardt, P., Cazalet, B., Salvat, B., Claudet, J. and Feral, F. (2013) The rise of large-scale marine protected areas: conservation or geopolitics? Ocean and Coastal Management, **85**(A), pp. 112–118.

Lefkovitch, L. P. (1965) The study of population growth in organisms grouped by stages. Biometrika, **35,** pp. 183-212.

Leslie, P. H. (1945) The use of matrices in certain population mathematics. Biometrika, **33**, pp. 183-212.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., Airame, S. and Warner, R. R. (2009) Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series, **384**, 33-46.

Letessier, T. B., Bouchet, P. J. and Meeuwig, J. J. (2015) Sampling mobile oceanic fishes and sharks: implications for fisheries conservation and planning. Biological Reviews, **92**(2), pp. 627–646.

Little, L. R., Punt, A. E., Mapstone, B. D., Begg, G. A., Goldman, B. and Ellis, N. (2009) Different responses to area closures and effort controls for sedentary and migratory harvested species in a multispecies coral reef linefishery. ICES Journal of Marine Science **66**, pp. 1931-1941.

Liu, M. and Sadovy de Mitcheson, Y. (2008) Profile of a fishery collapse: why mariculture failed to save the large yellow croaker. Fish and Fisheries, **9**(3), pp. 219-242.

Liu, O. R., Kleisner, K. M., Smith, S. L. and Kritzer, J. P. (2018) The use of spatial management tools in rights-based groundfish fisheries. Fish and Fisheries, **19**, pp. 821-838.

Lorenzen, K. and Camp, E. V. (2019) Density-dependence in the life history of fishes: when is a fish recruited? Fisheries Research, **217**, pp. 5-10.

Lowerre-Barbieri, S. K., Kays, R., Thorson, J. T., Wikelski, M. and Browman, H. (2019) The ocean's movescape: fisheries management in the bio-logging decade (2018 – 2028). ICES Journal of Marine Science, **76**(2) pp. 477-488.

Lubchenco, J. and Grorud-Colvert, K. (2015) Making waves: the science and politics of ocean protection. Science, **350**(6259), pp. 382–383.

Lubchenco, J., Palumbi, S. R., Gaines, S. D. and Andelman, S. (2003) Plugging a hole in the ocean: The emerging science of marine reserves. Ecological Applications, **13**, S3-S7.

Lundberg, P. and Jonzen, N (1999) Spatial population dynamics and the design of marine reserves. Ecology Letters, 2(**3**) pp. 129-134.

Lundquist, C. J. and Granek, E. F. (2005) Strategies for successful marine conservation: integrating socioeconomic, political and scientific factors. Conservation Biology, **19**, pp. 1771–1778.

Lynam, C. P., Heath, M. R., Hay, S. J. and Brierley, A. S. (2005) Evidence for impacts by jellyfish on North Sea herring recruitment. Marine Ecology Progress Series, **298**, pp. 156-167.

Mangel, M. (2000) Irreducible uncertainty, sustainable fisheries and marine reserves. Evolutionary Ecology Research, **2**, pp. 547-557.

March, D., Alos, J., Grau, A. and Palmer, M. (2011) Short-term residence and movement patterns of the annular seabream Diplodus annularis in a temperate marine reserve. Estuarine Coastal and Shelf Science, **92**, pp. 581-587.

Mariana, S., Hutchinson, W. F., Hatfield, E. M. C., Ruzzante, D. E., Simmonds, E. J., Dahlgren, T. G., Andre, C., Brigham, J., Torstensen, E. and Carvalho, G. R. (2005) North Sea herring population structure revealed by microsatellite analysis. Maine Ecology Progress Series, **303**, pp. 245-257.

Marshall, D. J., Gaines, S., Warner, R., Barneche, D. R. and Bode, M. (2019) Underestimating the benefits of marine protected areas for the replenishment of fished populations. The Ecological Society of America: Frontiers in Ecology and the Environment. https://doi.org/10.1002/fee.2075 *accessed on 13th July 2019.*

Marra, S., Coppa, S., Camedda, A., MAzzoldi, C., Wrachien, F., Massaro, G. and de Lucia, G. A. (2016) Recovered trends of commercial fish: the case of an underperforming Mediterranean marine protected area. PLOS ONE: e0146391. doi:10.1371/ journal.pone.0146391 *accessed on 18th October 2017.*

Martell, S. J. D., Walters, C. J. and Wallace, S. S. (2000) The use of marine protected areas for conservation of lingcod (Ophiodon elongatus) Bulletin of Marine Science, **66**, pp. 729-743.

Maury, O. and Gascuel, D. (1999) SHADYS ('simulateur halieutique de dynamiques spatiales'), a GIS based numerical model of fisheries. Example application: the study of a marine protected area. Aquatic Living Resources, **12**, pp. 77-88.

Maypa, A. P., Russ, G. R., Alcala, A. C. and Calumpong, H. P. (2002) Long-term trends in yield and catch rates of the coral reef fishery at Apo Island, central Philippines. Marine and Freshwater Research, **53**, pp. 207-213.

McClanahan, T. R. and KaundaArara, B. (1996) Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conservation Biology, **10**, pp. 1187-1199.

McClanahan, T. R. and Mangi, S. (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. Ecological Applications, **10**, pp. 1792-1805.

McCrea-Strub, A., Zeller, D., Sumaila, U. R., Nelson, J., Balmford, A. and Pauly, D. (2011) Understanding the cost of establishing marine protected areas. Marine Policy, **35**, pp. 1-9.

McGilliard, C. R. and Hilborn, R. (2008) Modeling no-take marine reserves in regulated fisheries: assessing the role of larval dispersal. Canadian Journal of Fisheries and Aquatic Sciences, **65**, pp. 2509-2523.

McNeill, A., Clifton, J. and Harvey, E. S. (2019) Specialised recreational fishers reject sanctuary zones and favour fisheries management. Marine Policy, **107**, article number:103592.

Meester, G. A., Ault, J. S., Smith, S. G. and Mehrotra, A. (2001) An integrated simulation modeling and operations research approach to spatial management decision making. Sarsia, **86**, pp. 543-558.

Melnychuk, C. M., Peterson, E., Elliott, M. and Hilborn, R. (2017) Fisheries management impacts on target species status. PNAS **114**(1) pp. 178-183.

Metcalfe, K., Vaz, S., Engelhard, G., Villanueva, M. C., Smith, R. J. and Mackinson, S. (2015) Evaluating conservation and fisheries management strategies by linking spatial prioritization software and ecosystem and fisheries modelling tools. Journal of Applied Ecology, **52**, pp. 665-674.

Micheli, F., Amarasekare, P., Bascompte, J. and Gerber, L. R. (2004a) Including species interactions in the design and evaluation of marine reserves: Some insights from a predator-prey model. Bulletin of Marine Science, **74**, pp. 653-669.

Micheli, F., Halpern, B. S., Botsford, L. W. and Warner, R. R. (2004b) Trajectories and correlates of community change in no-take marine reserves. Ecological-Applications, **14**, pp. 1709-1723.

Miethe, T., Dytham, C., Dieckmann , U. and Pitchford, J. W. (2010) Marine reserves and the evolutionary effects of fishing on size at maturation. ICES Journal of Marine Science, **67**, pp. 412-425.

Miethe, T. C., Pitchord, J. W. and Dytham, C. (2011) Modelling the evolutionary effects of a coastal marine reserve on different ecological guilds of fish. Journal of the Marine Biological Association of the United Kingdom **91**(6) pp.1369–1380.

MMO. (2018) Closed fishing areas https://www.gov.uk/government/collections/closed-fishing-areas-in-english-waters *accessed on 14th July 2019.*

MMO. (2019) Seasonal Closures 2019 https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/770503/Seasonal_Closures_2019.pdf *accessed on 14th July 2019.*

Moffitt, E. A., Botsford, L. W., Kaplan, D. M. and O'Farrell, M. R. (2009) Marine reserve networks for species that move within a home range. Ecological Applications, **19**, pp. 1835-1847.

Mohamed, K S., Zacharia, P. U., Maheswarudu, G., Sathianandan, T. V., Abdussamad, E. M., Ganga, U., Pillai, S., Lakshmi, Sobhana, K. S., Nair, R. J., Josileen, J., Chakraborty, R. D., Kizhakudan, S. J. and Najmudeen, T. M. (2014) Minimum Legal Size (MLS) of capture to avoid growth overfishing of commercially exploited fish and shellfish species of Kerala. Marine Fisheries Information Service; Technical and Extension Series, **220**, pp. 3-7.

Mora, C. and Sale, P. F. (2011) Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. Marine Ecology-Progress Series, **434**, pp. 251-266.

Morgan, L. E. and Botsford, L. W. (2001) Managing with reserves: Modeling uncertainty in larval dispersal for a sea urchin fishery. Spatial Processes and Management of Marine Populations, **17**, pp. 667-684.

Mortensen, L. O., Ulrich, C., Hansen, J., Hald, R. (2018) Identifying choke species challenges for an individual demersal trawler in the North Sea, lessons from conversations and data analysis. Marine Policy, **87**, pp.1-11.

Mosquera, I., Côté, I. M., Jennings, S. and Reynolds, J. D. (2000) Conservation benefits of marine reserves for fish populations. Animal Conservation, **4**, pp. 321-332.

Moustakas, A. (2016) The effects of marine protected areas over time and species dispersal potential: a quantitative conservation conflict attempt. Web Ecology, **16**, pp. 113-122.

Moustakas, A., Silvert, W. and Dimitromanolakis, A. (2006) A spatially explicit learning model of migratory fish and fishers for evaluating closed areas. Ecological Modelling, **192**(1-2) pp. 245-258.

Moustakas, A. and Silvert, W. (2011) Spatial and temporal effects on the efficacy of marine protected areas: implications from an individual based model. Stochastic Environmental Research and Risk Assessment, **25**, pp. 403-413.

MPA Atlas (2018) http://mpatlas.org/ *accessed on 12th February 2018.*

MPA news (2006) https://mpanews.openchannels.org/news/mpa-news/protecting-spawning-and-nu rsery-habitats-fish-use-mpas-safeguard-critical-life-history *accessed on 11th May 2019.*

Murawski, S. A., Brown, R., Lai, H. L., Rago, P. J and Hendrickson, L. (2000) Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. Bulletin of Marine Science*,* **66,** pp. 775-798.

Murawski, S., Rago, P. and Fogarty, M. (2004) Spillover effects from temperate marine protected areas. In: Shipley, J. B. (ed.) *Aquatic Protected Areas as Fisheries Management Tools.* American Fisheries Society. Symposium 42.

Murawski, S. A., Wigley, S. E., Fogarty, M. J., Rago, P. J. and Mountain, D. G. (2005) Effort distribution and catch patterns adjacent to temperate MPAs. Ices Journal of Marine Science, **62**, pp. 1150-1167.

Murray, S. N., Ambrose, R. F., Bohnsack, J. A., Botsford, L. W., Carr, M. H., Davis, G. E., Dayton, P. K., Gotshall, D., Gunderson, D. R., Hixon, M. A., Lubchenco, J., Mangel, M., MacCall, A., McArdle, D. A., Ogden, J. C., Roughgarden, J., Starr, R. M., Tegner, M. J. and Yoklavich, M. M. (1999) No-take reserve networks: Sustaining fishery populations and marine ecosystems. Fisheries, **24**, pp. 11-25.

Myers. R.A. (2001) Stock and recruitment: generalizations about maximum reproductive rate, density-dependence, and variability using meta-analytic approaches. ICES Journal of Marine Science, **58**(5), pp. 937-951.

Myers, R.A. and Cadigan, N. G. (1993) Density-dependent juvenile mortality in marine demersal fish. Canadian Journal of Fisheries and Aquatic Sciences, **50**(8), pp. 1576-1590.

Myers, R. A., Hutchings, J. A. and Barrowman, N. J. (1997) Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications, **7**(1), pp. 91-106.

N.R.C. (National Research Council) 2001. *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems*. National Academy Press, Washington, D.C.

Needle, C. L. and Catarino, R. (2011) Evaluating the effect of real-time closures on cod targeting. ICES Journal of Marine Science, **68**(8), pp. 1647-1655.

Nash, R. D. M. and Dickey-Collas, M. (2005) The influence of life history dynamics and environment on the determination of year class strength in North Sea herring (*Clupea harengus* L.) Fisheries Oceanography, **14**(4), pp. 279-291.

Neubert, M. G. (2003) Marine reserves and optimal harvesting. Ecology Letters, **6**, pp. 843-849.

Nowlis, J. S. (2000) Short- and long-term effects of three fishery-management tools on depleted fisheries. Bulletin of Marine Science, **66**, pp. 651-662.

Nowlis, J. S. and Roberts, C. M. (1999) Fisheries benefits and optimal design of marine reserves. Fisheries Bulletin, **97**, pp. 604-616.

O'Boyle, R. (2011) Benefits of marine protected areas and fisheries closures in the Northwest Atlantic. Canadian Technical Report Fisheries and Aquatic Sciences. **2948**: iii 68 pp.

O'Connor, C. M., Norris, D. R., Crossin, G. T. and Cooke, S. J. (2014) Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. Ecosphere, **5**(3), pp. 1-11.

O'Leary, B. C., Winther-Janson, M., Bainbridge, J. M., Aitken, J., Hawkins, J. P. and

Roberts, C. M. (2016) Effective coverage targets for ocean protection. Conservation Letters, **9**(6), pp. 398-404.

Okubo, A., Levin, S. (2001) *Diffusion and Ecological Problems: Modern Perspectives*. Springer Verlag, New York.

Ono, K., Holland, D. S. and Hilborn, R. (2013) How does species association affect mixed stock fisheries management? A comparative analysis of the effect of marine protected areas, discard bans and individual fishing quotas. Canadian Journal of Fisheries and Aquatic Sciences, **70**(12), pp.1792-1804.

Palumbi, S. R. (2004) Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. Annual Review of Environment and Resources, **29**, pp. 31-68.

Pastoors, M. A., Rijnsdorp, A. D. and Van Beek, F. A. (2000) Effects of a partially closed area in the North Sea (plaice box) on stock development of plaice. ICES Journal of Marine Science, **57**, pp. 1014-1022.

Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaug, T., Gallegro, A., Gröger, J., Licandro, P., Llope, M., Munk, P., Röckmann, C., Schmidt, J. O. and Nash, R. D. M. (2009) Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. ICES Journal of Marine Science, **66**(2), pp. 272-277.

Pazhayamadom, D. G., Kelly, C. J., Rogan, E. and Codling, E. A. (2013) Self-starting CUSUM approach for monitoring data poor fisheries. Fisheries Research, **145**, pp. 114-127.

Pelc, R. A., Warner, R. R., Gaines, S. D. and Paris, C. B. (2010) Detecting larval export from marine reserves. Proceedings of the National Academy of Sciences, **107**, pp. 18266-1827.

Pelletier, D. and Magal, P. (1996) Dynamics of a migratory population under different fishing effort allocation schemes in time and space. Canadian Journal of Fisheries and Aquatic Sciences, **53**, pp. 1186-1199.

Pelletier, D., Mahévas, S. (2005) Spatially explicit fisheries simulation models for policy evaluation. Fish and Fisheries, 6(**4**), pp.307-349.

Pendoley, K. L., Schofield, G., Whittlock, P. A., Ierodiaconou, D. and Hays, G. C. (2014) Protected species use of a coastal marine migratory corridor connecting marine protected areas. Marine Biology, **161**(6), pp. 1455-1466.

Pepin, P. (2015) Reconsidering the impossible – linking environmental drivers to growth, mortality, and recruitment of fish. Canadian Journal of Fisheries and Aquatic Sciences, **73**(2), pp. 205-215.

Pérez-Jorge, S., Pereira, T., Corne, C., Wijtten, Z., Omar, M., Katello, J., Kinyua, M., Oro, D. and Louzao, M. (2015) Can Static Habitat Protection Encompass Critical Areas for Highly Mobile Marine Top Predators? Insights from Coastal East Africa. PLOS ONE: e0133265. https://doi.org/10.1371/journal.pone.0133265 *accessed on 19th June 2018.*

Palumbi, S. R. (2004) Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. Annual Review of Environment and Resources, **29**, pp. 31-68.

Pierre, M., Rouyer, T., Bonhommeau, S. and Fromentnin, J. M. (2018) Assessing causal links in fish stock-recruitment relationships. ICES Journal of Marine Science, **75**(3), pp. 903-911.

Piet, G. and Rice, J. (2004) Performance of precautionary reference points in providing management advice in North Sea fish stocks. ICES Journal of Marine Science, **61**(8), pp. 1305-1312.

Pitcher, T. J. and Hart, P. J. B. (1982) *Fisheries Ecology*. Chapman and Hall, London.

Pitchford, J. W., Codling, E. A. and Psarra, D. (2007) Uncertainty and sustainability in fisheries and the benefit of marine protected areas. Ecological Modelling, **207**, pp. 286-292.

Polacheck, T. (1990) Year round closed areas as a management tool. Natural Resource Modeling **v4**., pp. 327-354.

Polunin, N. V. C. and Roberts, C. M. (1993) Greater biomass and value of target coral-reef fishes in 2 small Caribbean marine reserves. Marine Ecology Progress Series, **100**, pp. 167-176.

Poos, J. J., Bogaards, J. A., Quirijns, F. J., Gillis D. M. and Rijnsdorp, A. D. (2010) Individual quotas, fishing effort allocation, and over-quota discarding in mixed fisheries. ICES Journal of Marine Science, **67**(2) pp. 323-333.

Poulsen, B. (2008) *Dutch Herring – An Environmental History, c. 1600 – 1860* Amsterdam University Press 266pp.

Putman, N. F. and He, R. (2013) Tracking the long-distance dispersal of marine organism: sensitivity to ocean model resolution. Journal of the Royal Society

Interface, **10**(81) https://doi.org/10.1098/rsif.2012.0979 *accessed on 1st September 2019.*

R Core Team. (2019) R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 2-900051-07-0. URL http://www.r-project.org/ *accessed on 14th August 2019.*

Ratikainen, I. I., Gill, J. A., Gunnarsson, T. G., Sutherland, W. J. and Kokko, H. (2007) When density dependence is not instantaneous: theoretical developments and management implications. Ecology Letters, **10**, pp.1-15.

Rees, S. E., Attrill, M. J., Austen, M. C., Mangi, S. C., Richards, J. P. and Rodwell, L. D. (2010) Is there a win-win scenario for marine nature conservation? A case study of Lyme Bay, England. Ocean & Coastal Management, **53**, pp. 135-145.

Rhodes, K. L., Taylor, B. M. and McIlwain, J. L. (2011) Detailed demographic analysis of an *Epinephelus polyphekadion* spawning aggregation and fishery. Marine Ecology Progress Series **421** pp. 183-198.

Ricard, D., Zimmermann, F. and Heino, M. (2016) Are negative intra-specific interactions important for recruitment dynamics? A case study of Atlantic fish stocks. Marine Ecology Progress Series, **547**, pp. 211-217.

Ricker, W. E. (1954) Stock and Recruitment Journal of the Fisheries Research Board of Canada, **11**(5), pp. 559–623.

Rijnsdorp, A. D. and Pastoors, M. A. (1995) Modeling the spatial dynamics and fisheries of north-sea plaice (pleuronectes-platessa l) based on tagging data. ICES Journal of Marine Science, **52**, pp. 963-980.

Rijnsdorp, A. D., van Overzee, H. M. J. and Poos, J. J. (2012) Ecological and economic trade-offs in the management of mixed fisheries: a case study of spawning closures in flatfish fisheries. Marine Ecology-Progress Series, **447**, pp. 179-194.

Roel, B. A. (2017) Herring in the North Sea, exploitation and conservation. https://u3asites.org.uk/files/h/halesworth/docs/2017-04herringinthenorthseabr.pdf *accessed on 4th July 2019.*

Roberts, C. M., Andelman, S., Branch, G., Bustamante, R. H., Castilla, J. C., Dugan, J., Halpern, B. S., Lafferty, K. D., Leslie, H., Lubchenco, J., McArdle, D., Possingham, H. P., Ruckelshaus, M. and Warner, R. R. (2003) Ecological criteria for evaluating candidate sites for marine reserves. Ecological Applications, **13**, S199-S214.

Roberts, C. M., Hawkins, J. P., Fletcher, J., Hands, S., Raab, K. and Ward, S. (2010) Guidance on the size and spacing of marine protected areas in England. Natural England Commissioned Report NECR037. Natural England, Worcester, UK.

Ruiz-Frau, A., Possingham, H. P., Edwards-Jones, G., Klein, C. J., Segan, D. and Kaiser, M. J. (2015) A multidisciplinary approach in the design of marine protected areas: integration of science and stakeholder-based methods. Ocean and Coastal Management, **103**, pp. 86-93.

Russ, G. R. and Alcala, A. C. (1989) Effects of intense fishing pressure on an assemblage of coral-reef fishes. Marine Ecology-Progress Series, **56**, pp. 13-27.

Russ, G. R. and Alcala, A. C. (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series, **132**, pp. 1-9.

Russ, G. R., Cheal, A. J., Dolman, A. M., Emslie, M. J., Evans, R. D., Miller, I., Sweatman, H. and Williamson, D. H. (2008) Rapid increase in fish numbers follows creation of world's largest marine reserve network. Current Biology, **18**, R514-R515.

Rybicki, S., Simons, S. L. and Temming, A. (2018) The influence of climate variabilities on management performance – A Northeast Atlantic pelagic fisheries case study. CERES, 2018. https://ceresproject.eu *accessed on 11th July 2019.*

Sadovy, Y. and Domeier, M. (2005) Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. Coral Reefs, **24**, pp. 254-262.

Sadovy de Mitcheson, Y. (2016) Mainstreaming fish spawning aggregations into fishery management calls for a precautionary approach. BioScience, **66**(4), pp.295-306.

Sala, E., Aburto-Oropeza, A., Parades, G., Parra, I., Barrera, J. C. and Dayton, P. K. (2002) A general model for designing networks of marine reserves. Science, **298**(5600), pp. 1991-1993.

Sala, E. and Giakoumi, S. (2017) No-take marine reserves are the most effective protected areas in the ocean. ICES Journal of Marine Science, **75**(3), pp. 1166–1168.

Sala, E., Lubchenco, J., Grorud-Colvert, K., Novelli, C., Roberts, C., Sumaila, U. R. (2018) Assessing real progress towards effective ocean protection) Marine Policy **91,** pp. 11-13.

Samy-Kamal, M., Forcada, A. and Lizaso, J. L. S. (2015) Effects of seasonal closures in a multi-specific fishery. Fisheries Research, **172**, pp. 303-317.

Saville, A. and Bailey, R. S. (1980) The assessment and management of the herring stocks in the North Sea and to the west of Scotland. ICES Marine Science Symposia, **117**, pp.112-142.

Scales, K. L., Hazen, E. L., Jacox, M. G., Edwards, C.A., Boustany, A.M., Oliver, M.J. and Bograd, S.J. (2016) Scale of inference: on the sensitivity of habitat models for wide-ranging marine predators to the resolution of environmental data. Ecography, **40**(1), pp. 210-220.

Schröder, A., van Leeuwen, A. and Cameron, T. C., (2014) When less is more: positive population-level effects of mortality. Trends in Ecology & Evolution, **29** (11), pp. 614-624.

Schrope, M. (2010) Fisheries: what's the catch? Nature, **465**, pp.540-542.

Shepherd, J. G. (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. ICES Journal of Marine Science, **40**(1), pp. 67-75.

Silvert, W. and Moustakas, A. (2011) The impacts over time of marine protected areas: A null model. Ocean & Coastal Management, **54**, pp. 312-317.

Simmonds, E. J. (2007) Comparison of two periods of North Sea herring stock management: success, failure, and monetary value. ICES Journal of Marine Science, **64**(4), pp. 686-692.

Simon, S. L, Ralf, D. and Axel, T. (2014) Combining area closures with catch regulations in fisheries with spatio-temporal variation: bio-economic implications for North Sea saithe fishery. Marine Policy, **41**, pp. 281-292.

Smith, J. and Metaxas, A. (2018) A decision tree that can address connectivity in the design of Marine Protected Area Networks (MPAn). Marine Policy, **88**, pp. 269–278.

Smith, M. D. and Wilen, J. E. (2003) Economic impacts of marine reserves: the importance of spatial behavior. Journal of Environmental Economics and Management, **46**, pp. 183-206.

Smolowitz, R., Siemann, L. A., Huntsberger, C. and Boelke, D. (2016) Application of seasonal closures to reduce flatfish bycatch in the US Atlantic sea scallop fishery. Journal of Shellfish Research, **35**, pp. 475-480.

Sparre, P. J. and Willmann, R. (1993) Software for bio-economic analysis of fisheries. BEAM4. Analytical Bio-economic Simulation of Space-structured Multispecies and Multi-fleet Fisheries. Vol 1: Description of the model. Computerized information series (fisheries) FAO, 186pp.

St. Mary, C. M., Osenberg, C. W., Frazer, T. K. and Lindberg, W. J. (2000) Stage structure, density dependence and the efficacy of marine reserves. Bulletin of Marine Science, **66**, pp. 675-690.

Stefansson, G. and Rosenberg, A. (2005) Combining control measures for more effective management of fisheries under uncertainty: quotas, effort limitation and protected areas. Philisophical Transactions of the Royal Society B., **260**(1453), pp. 133-146.

Stockhausen, W. T., Lipcius, R. N. and Hickey, B. M. (2000) Joint effects of larval dispersal, population regulation, marine reserve design, and exploitation on production and recruitment in the Caribbean spiny lobster. Bulletin of Marine Science, **66**, pp. 957-990.

Sumaila, U. R. (1998) Protected marine reserves as fisheries management tools: a bioeconomic analysis. Fisheries Research, **24**, pp. 287-296.

Sumaila, U. R. (2002) Marine protected area performance in a model of the fishery. Natural Resource Modeling, **15**, pp. 439-451.

Sussex IFCA. (2020) https://www.sussex-ifca.gov.uk/trawling-exclusion-byelaw *accessed on 22nd February 2020.*

Sweeting C .J. and Polunin N. V. C. (2005) Marine Protected Areas for Management of Temperate North Atlantic Fisheries: Lessons learned in MPA use for sustainable fisheries exploitation and stock recovery. London. DEFRA. www.defra.gov.uk/marine/pdf/science/mpareportnorthatlantic.pdf *accessed on 13th November 2015.*

Sys, K., Van Meensel, J., Polet, H. and Buysse, J. (2017) A temporal race-for-fish: The interplay between local hotspots of flatfish and exploitation competition between beam trawlers after a seasonal spawning closure. Fisheries Research, **193**, pp. 21-32.

Tetreault, I. and Ambrose, R. F. (2007) Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. Ecological Applications, **17**, pp. 2251-2267.

Toonen, R. J., Wilhelm, T. A., Maxwell, S. M., Wagner, D., Bowen, B. W., Shappard, C. R. C., Taei, S. M., Teroroko, T., Moffitt, R., Gaymer, C. F., Morgan, L., Lewis, N., Sheppard, A. L. S., Parks, J., Friedlander, A. M. and The Big Ocean Think Tank.

(2013) One size does not fit all: the emerging frontier in large-scale marine conservation. Marine Pollution, **77**(1–2), pp. 7–10.

Touzeau, S. and Gouzé, J-L. (1998) On the stock-recruitment relationships in fish population models. Environmental Modeling and Assessment, **3**(1-2), pp.87-93.

Tuck, G. N. and Possingham, H. P. (2000) Marine protected areas for spatially structured exploited stocks. Marine Ecology-Progress Series, **192**, pp. 89-101.

van Overzee, H. M. J. and Rijnsdorp, A. D. (2015) Effects of fishing during the spawning period: implications for sustainable management. Reviews in Fish Biology and Fisheries, **25**, pp. 65-83.

Vandeperre, F, Higgins, R. M., Sanchez-Meca, J., Maynou, F., Goni, R., Martin-Sosa, P., Perez-Ruzafa, A., Afonso, P., Bertocci, I., Crec;hriou, R., D'Anna, G., Dimech, M., Dorta, C., Esparza, O., Falcón, J., Forcada, A., Guala, I., Le Direach, L., Marcos, C., Ojeda-Martínez, C., Pipitone, C., Schembri, P., Stelzenmüller, V., Stobart, B. and Santos, R. S. (2010) Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. Fish and Fisheries, **12**(4), pp. 412–426.

Villasante, S., García-Negro, M. d. C., González-Laxe, F. and Rodríguez, G. R. (2010) Overfishing and the Common Fisheries Policy: (un)successful results from TAC regulation? Fish and Fisheries, **12**(1), pp. 34-50.

Walters, C. (2000) Impacts of dispersal, ecological interactions, and fishing effort dynamics on efficacy of marine protected areas: how large should protected areas be? Bulletin of Marine Science, **66**(3), pp.745-757.

Walters, C. J. and Bonfill, R. (1999) Multispecies spatial assessment models for the British Columbia groundfish trawl fishery. Canadian Journal of Fisheries and Aquatic Sciences, **56**, pp. 601-628.

Walters, C. J., Hall, N., Brown, R. and Chubb, C. (1993) spatial model for the population-dynamics and exploitation of the western-Australian rock lobster, Panulirus cygnus. Canadian Journal of Fisheries and Aquatic Sciences, **50**, pp. 1650-1662.

Wantiez, L., Thollot, P. and Kulbicki, M. (1997) Effects of marine reserves on coral reef fish communities from five islands in New Caledonia. Coral Reefs, **16**, pp. 215-224.

Watson, J. E. M., Dudley, N., Segan, D. B. and Hockings, M. (2014) The performance and potential of protected areas. Nature, **515,** pp. 67-73.

Watson, F. M., Hepburn, L. J., Cameron, T., Le Quesne, W. J. F. and Codling, E. A. (2019) Relative mobility determines the efficacy of MPAs in a two species mixed fishery with conflicting management objectives. Fisheries Research, **219**, 105334. https://doi.org/10.1016/j.fishres.2019.105334 *accessed on 14th September 2019.*

Watson, R. A., Pitcher, T. J. and Jennings, S. (2015) Plenty more fish in the sea? Fish and Fisheries, **18**(1) pp. 105-113.

West, C. D., Dytham, C., Righton, D. and Pitchford, J. W. (2009) Preventing overexploitation of migratory fish stocks: the efficacy of marine protected areas in a stochastic environment. ICES Journal of Marine Science, **66**, pp. 1919-1930.

Whitehead, P.J.P**.** (1985) FAO Species Catalogue. Vol. 7. Clupeoid fishes of the world (suborder Clupeoidei) An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, shads, anchovies and wolf-herrings. FAO Fisheries Synopsis **125**(7/1), pp. 1-303. Rome: FAO.

Wiegand, J., Hunter, E. and Dulvy, N. K. (2011) Are spatial closures better than size limits for halting the decline of the North Sea thornback ray, *Raja clavata*? Marine and Freshwater Research, **62**, pp. 722-733.

Wilhelm, T. A., Sheppard, C. R. C., Sheppard, A. L. S., Gaymer, C. F., Parks, J., Wagner, D. and Lewis, N. (2014) Large marine protected areas - advantages and challenges of going big. Aquatic Conservation Marine and Freshwater Ecosystems, **24**, pp. 24-30.

Willis, T. J., Millar, R. B., Babcock, R. C. and Tolimieri, N. (2003) Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environmental Conservation, **30**, pp. 97-103.

Wood, L. J., Fish, L., Laughren, J. and Pauly, D. (2008) Assessing progress towards global marine protection targets: shortfalls in information and action. Oryx*,* **42**, pp. 340-351.

Wood, L. (2011) Global marine protection targets: how S.M.A.R.T are they? Environmental Management, **47**: 525. https://doi.org/10.1007/s00267-011-9668-6 *accessed on 18th February 2017.*

World Parks Congress (2014) Marine Theme https://www.worldparkscongress.org/wpc/programme/marine *accessed on 7th November 2018.*

Worm, B. (2017) How to heal an ocean. Nature, **543**, pp.630-631.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D., Rosenberg, A. A., Watson, R. and Zeller, D. (2009) Rebuilding Global Fisheries. Science, **325**, pp. 578-585.

www.gov.uk a (2019) https://www.gov.uk/government/publications/bass-industry-guidance-2019 *accessed on 12th May 2019.*

www.gov.uk b (2019) https://www.gov.uk/government/publications/seasonal-closures-for-cod *accessed on 12th May 2019.*