

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.

Keywords: *bycatch; movement; fisheries management; marine spatial closures.*

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, 2016b¹). 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 and Cook, 2015). However, restricting fishing effort to protect non-target species 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.,

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

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 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 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-2d; 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 $(p-1)/2$ 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 $E=0 \text{ yr}^{-1}$ to $E=200 \text{ yr}^{-1}$ 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 simulations were run with no closures and annual fishing effort applied from values of $E=0 \text{ yr}^{-1}$ to $E=200 \text{ yr}^{-1}$. 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 Figs 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 (Figs 4b & 4c).

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 SSB_{MIN} of the conservation stock was calculated as being 0.5 SSB of unfished stock and the management objective was set to 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). Figs 6a-c show the proportion of which SSB_{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 SSB_{MIN} at all but the lowest of fishing efforts (Figs 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 SSB_{MIN} to be maintained at any level of fishing effort (Fig. 6a). As mobility increases (Figs 6b & c) the minimum closure necessary to meet SSB_{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 SSB_{MIN} of the conservation species had been met to consider the management objectives for the target and conservation species concurrently. Thus, when both 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 (Figs 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 territories² 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.

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

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 (Metcalf 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 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 (McCreary 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 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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669 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

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

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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)	0.6 5	1.4 0	2.4 0	3.8 0	5.4 0	7.2 3	9.2 0	11.2 5	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	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.15	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5	0.1 5
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

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FIGURE CAPTIONS:

Figure 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.

Figure 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%

Figure 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.

Figure 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.

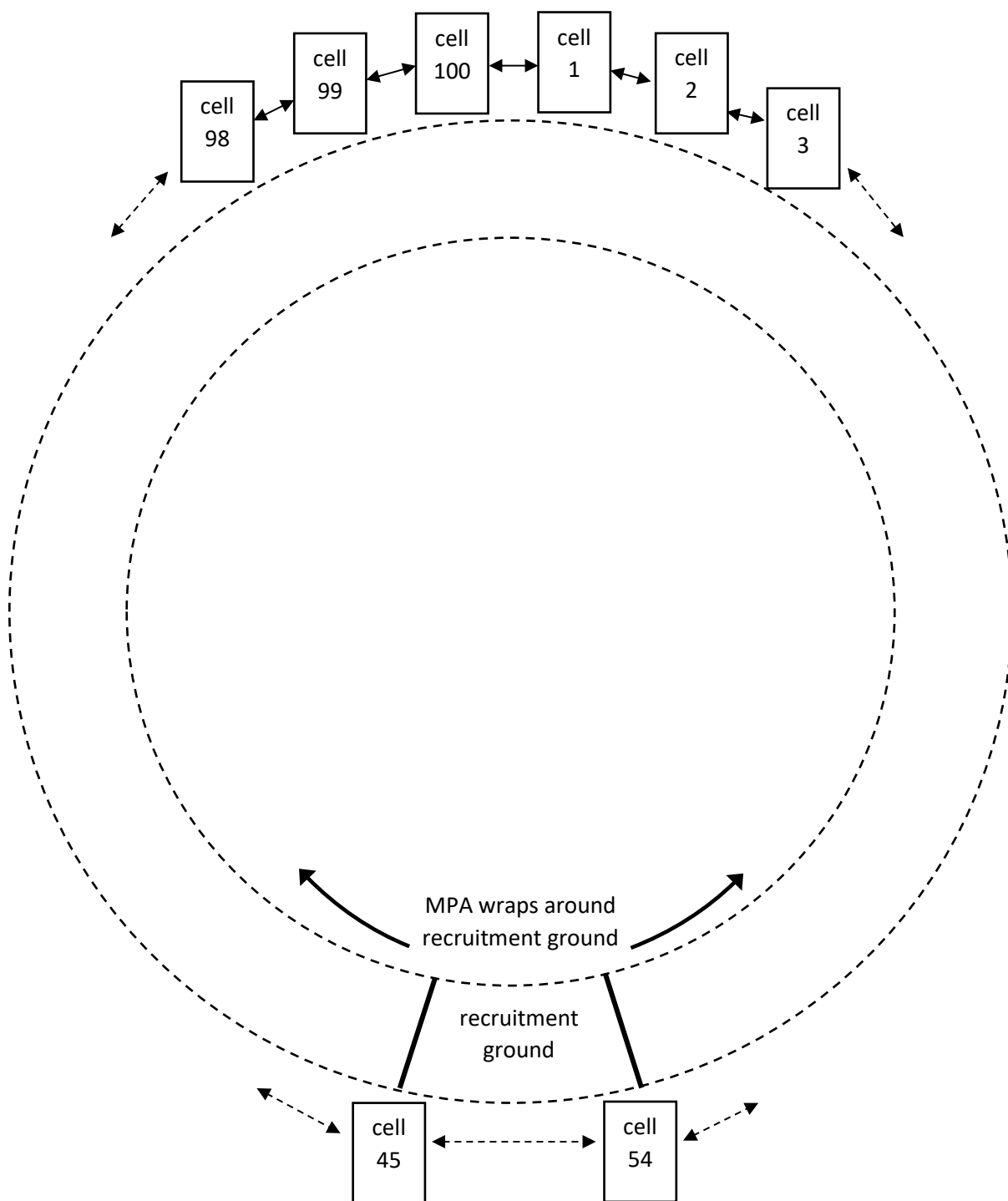
Figure 5: SSB of a bycatch conservation species in a single species fishery with no closures to fishing implemented. At each level of closure the population is exposed to annual efforts between 0 and 200. The model was run for 100 years with monthly time-steps.

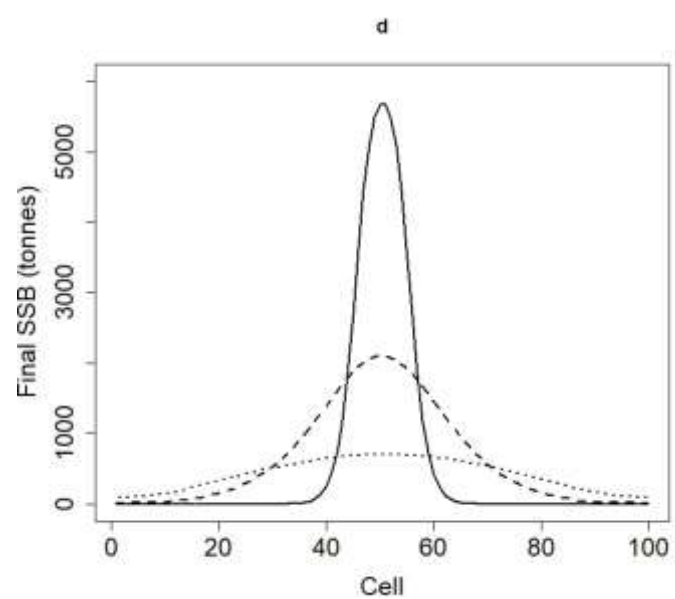
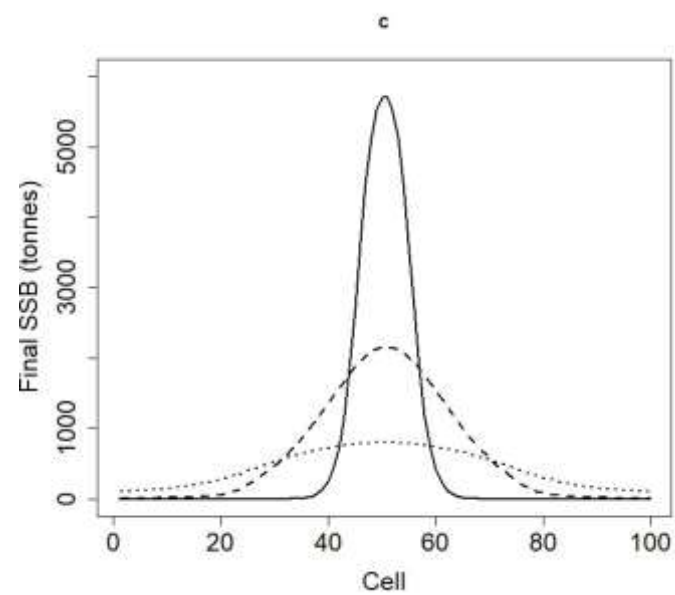
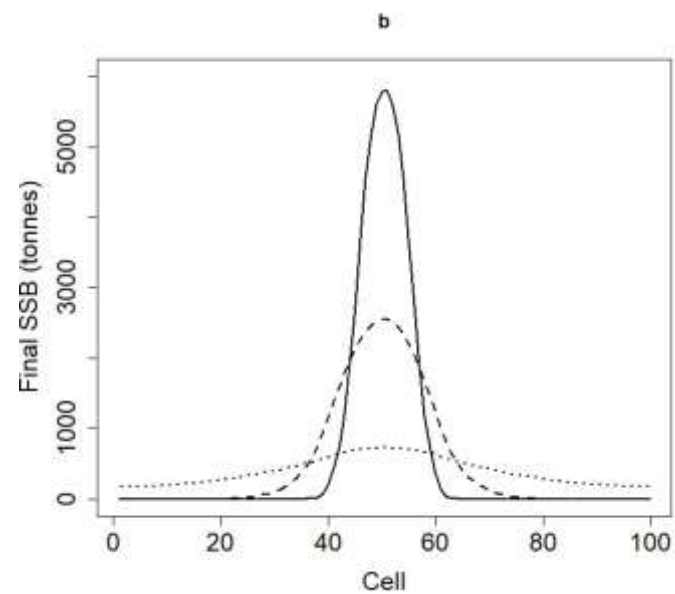
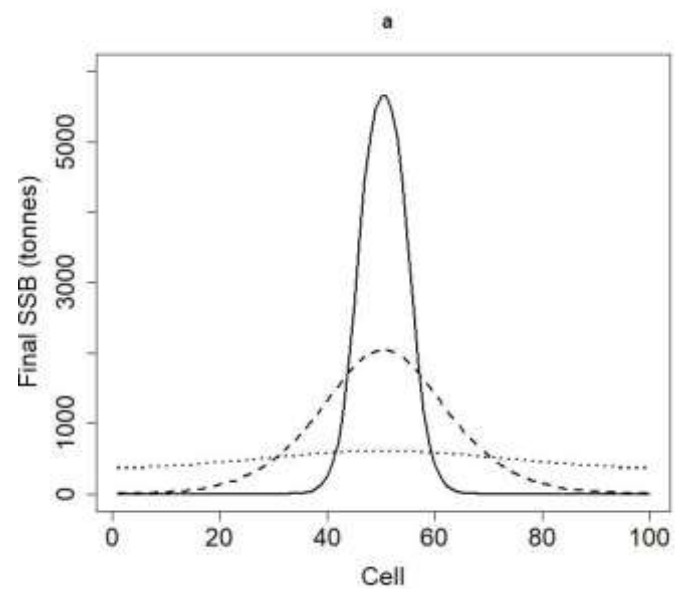
Figure 6: scaled results to show the proportion of which SSB_{MIN} (represented by a value of 1.0) of the bycatch conservation species has been met in simulations of a single species fishery protected by 0 – 100% closures to fishing and exposed to annual efforts between 0 and 200. The simulation was 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.

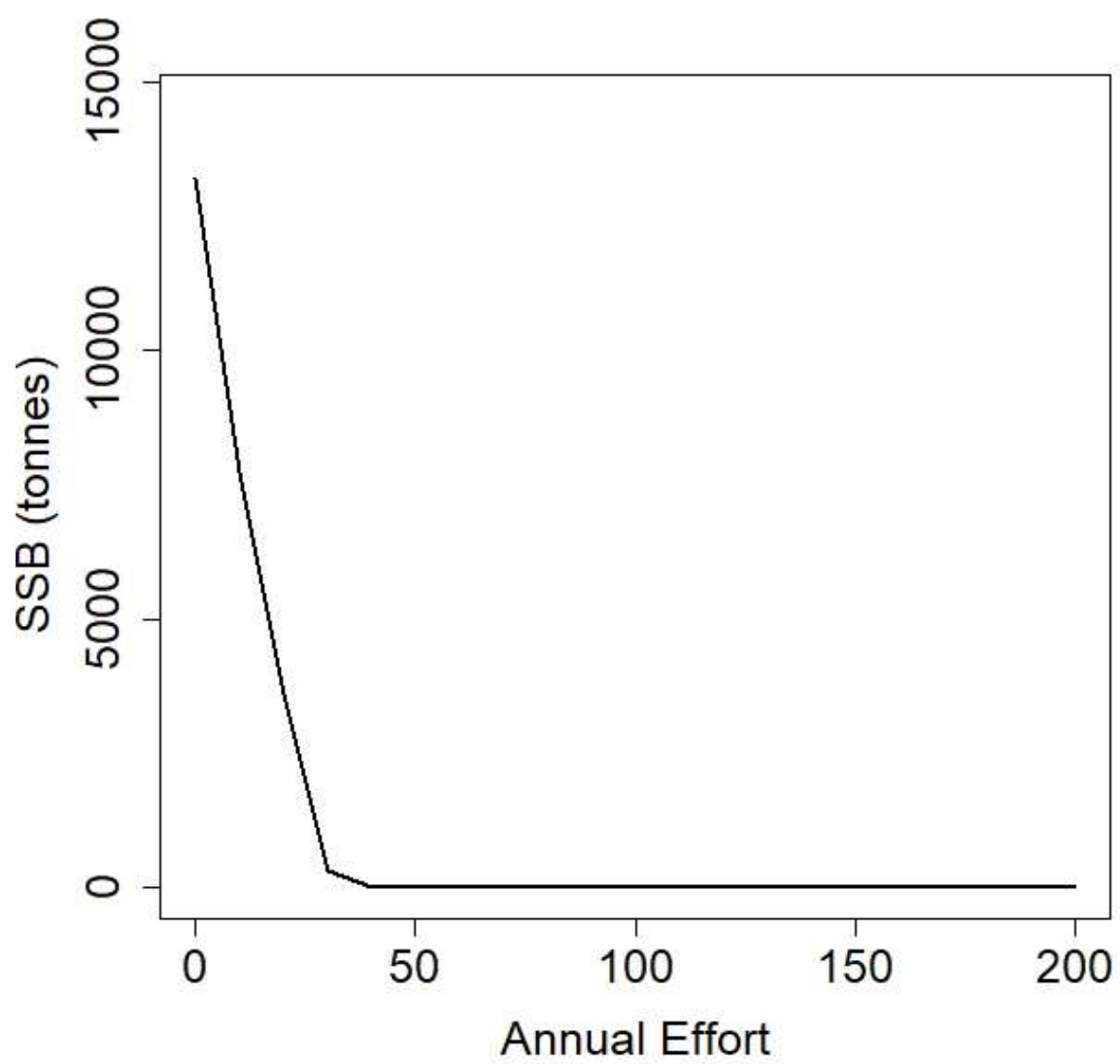
Figure 7: results to show the extent to which Y_{OPT} of the target species can be met when SSB_{MIN} of the bycatch conservation species has already been met in simulations of a two-species fishery protected by 0 – 100% closures to fishing and exposed to annual efforts between 0 and 200. The simulation was run for 100 years in monthly time steps. The levels of movement (D) within each simulation are:

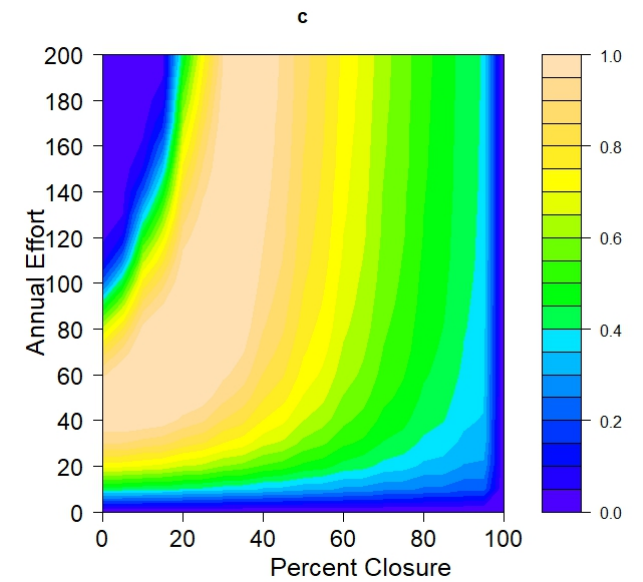
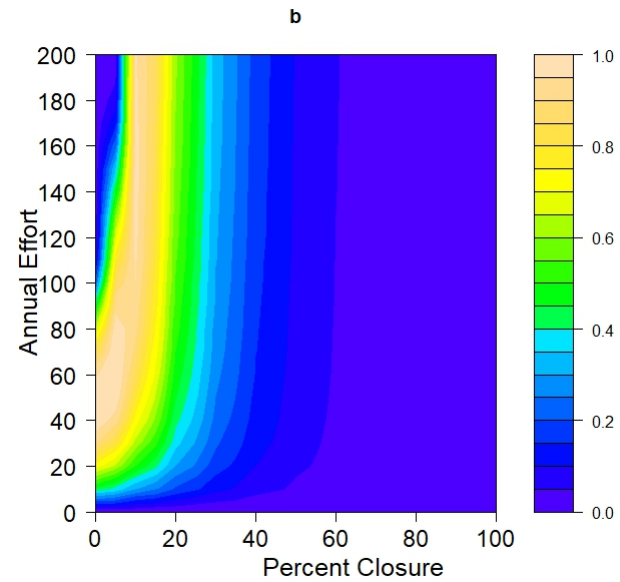
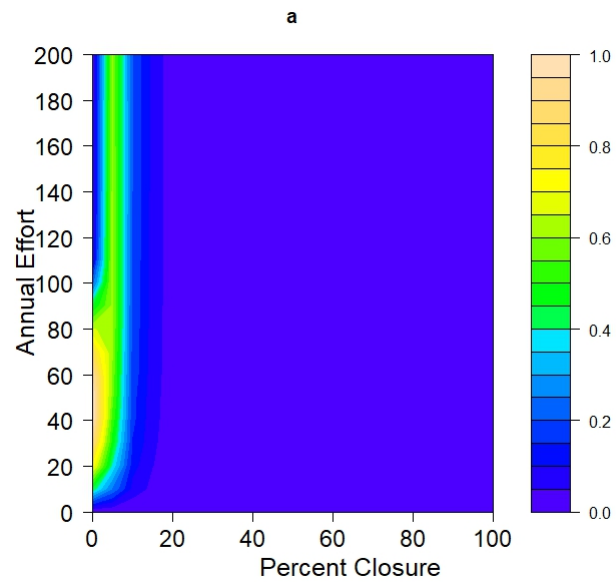
- a. both species D = 1
- b. both species D = 10
- c. both species D = 100
- d. target species D = 10, conservation species D = 1
- e. target species D = 100, conservation species D = 1
- f. target species D = 100, conservation species D = 10
- g. target species D = 1, conservation species d = 10
- h. target species D = 1, conservation species d = 100
- i. target species D = 10, conservation species d = 100

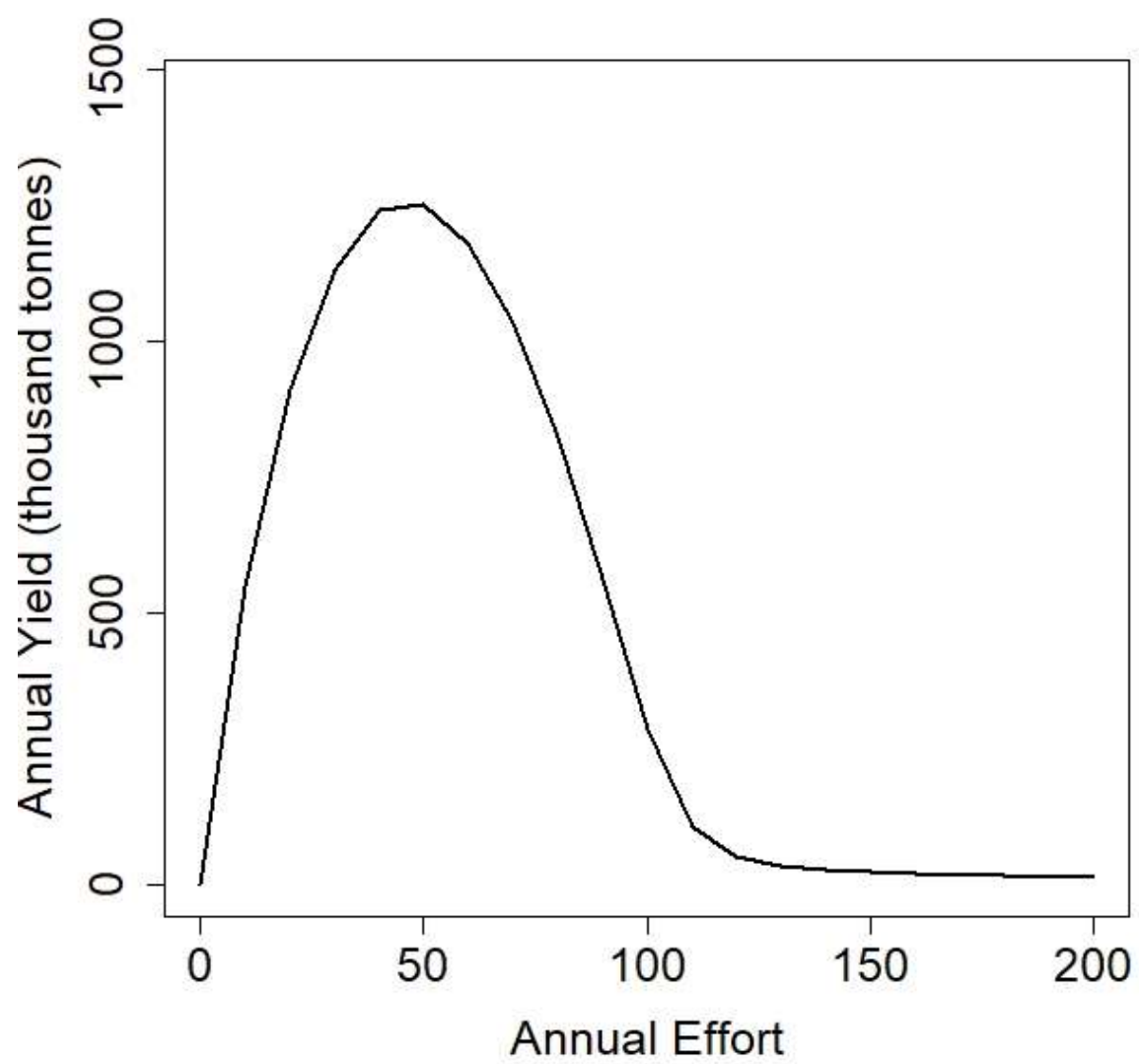
Figures 8: results to show the extent to which Y_{OPT} of a less-mobile ($D=10$) target species and SSB_{MIN} of a more mobile ($D=100$) conservation species have been met concurrently in simulations of a two-species fishery with closures to fishing implemented of a. 5%, b. 10%, c. 15%, d. 20%. At each 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 ____.

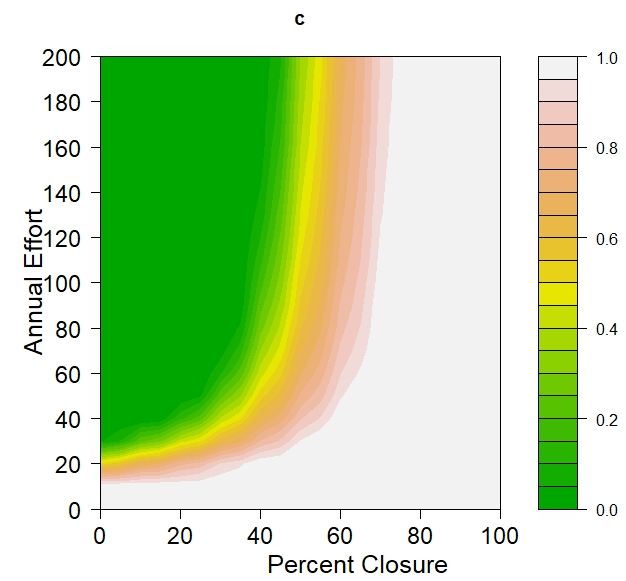
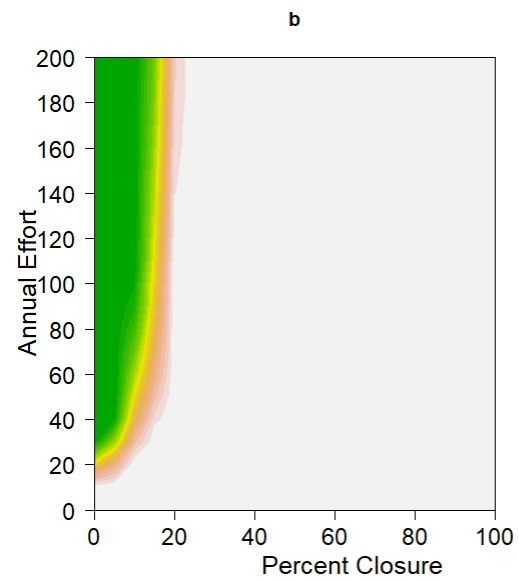
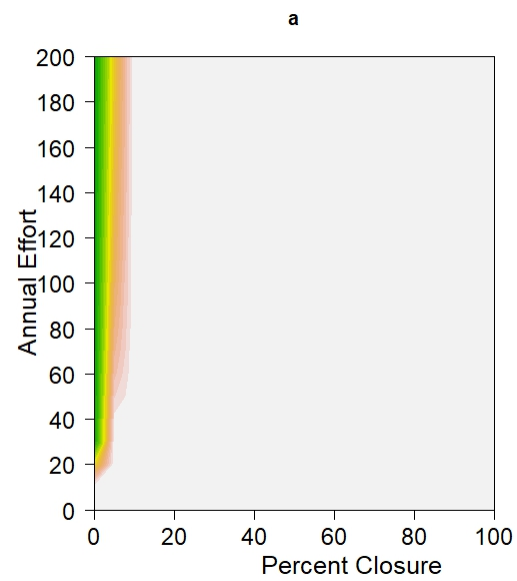


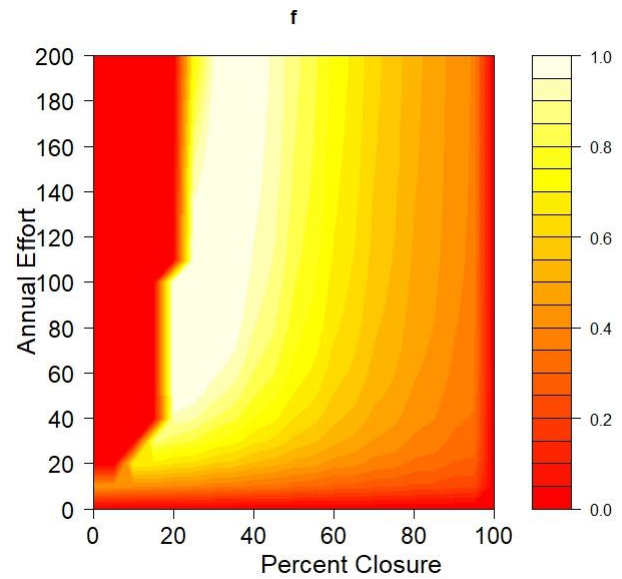
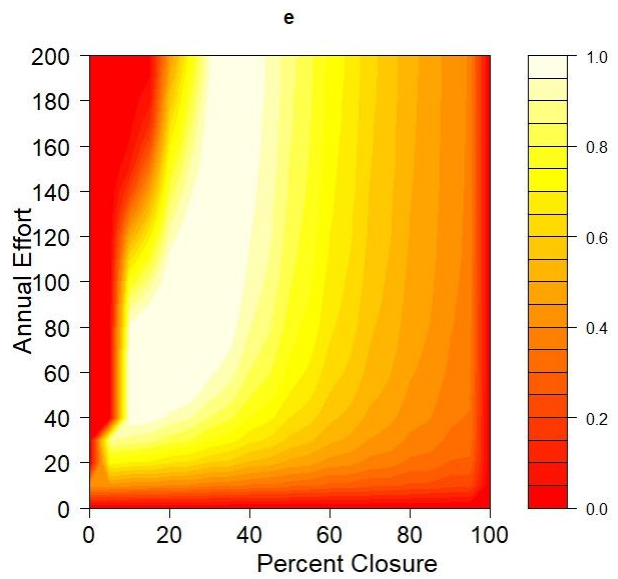
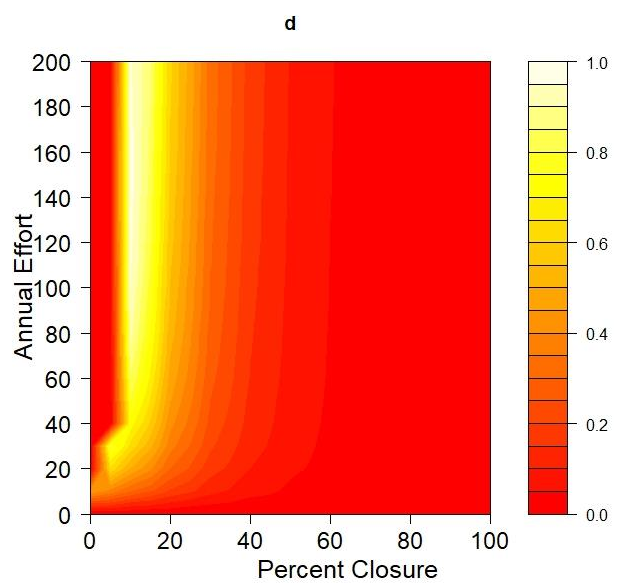
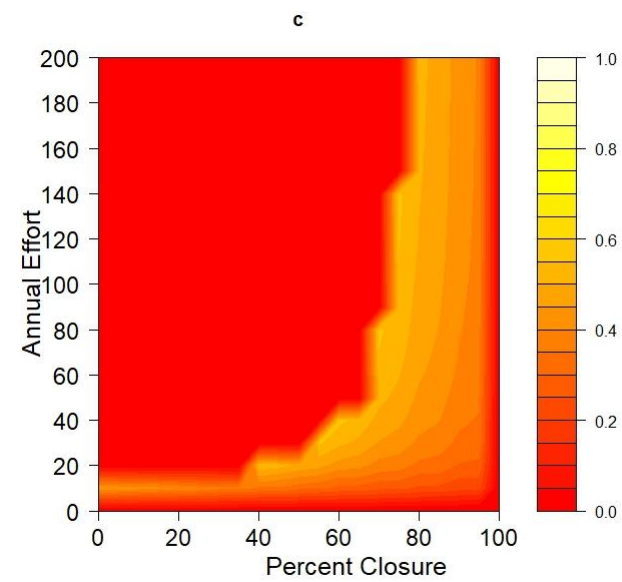
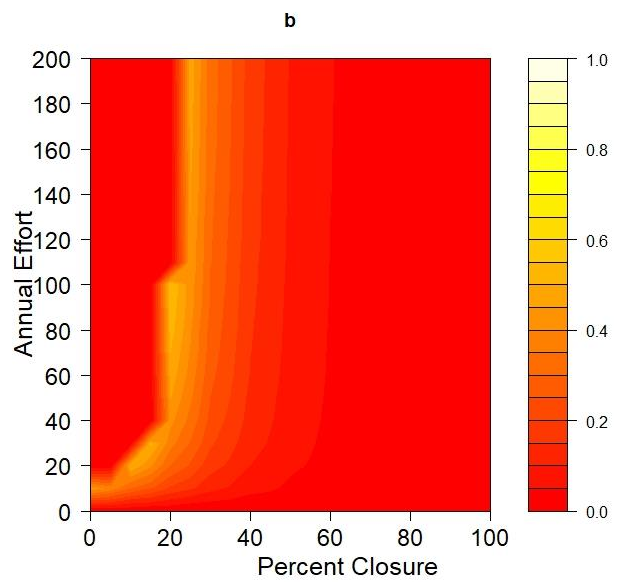
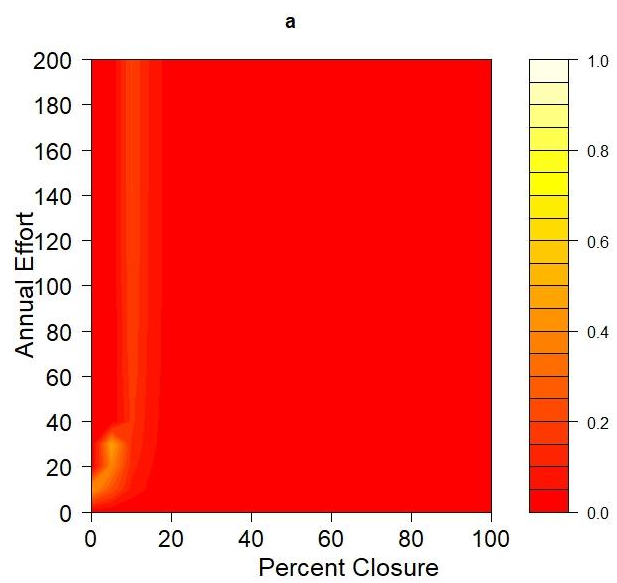


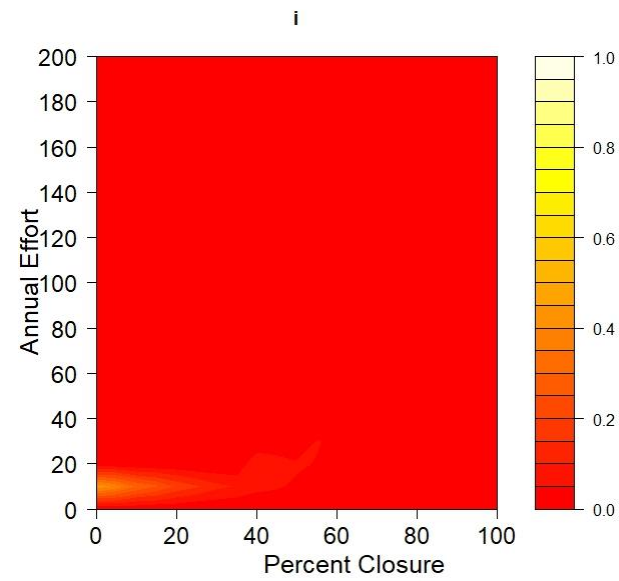
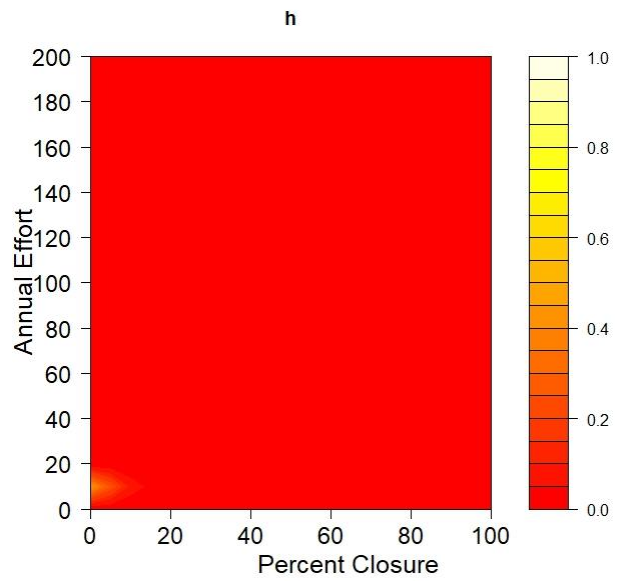
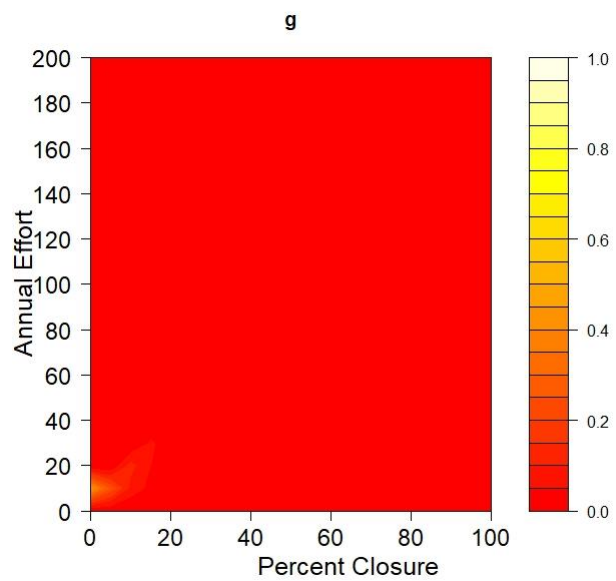


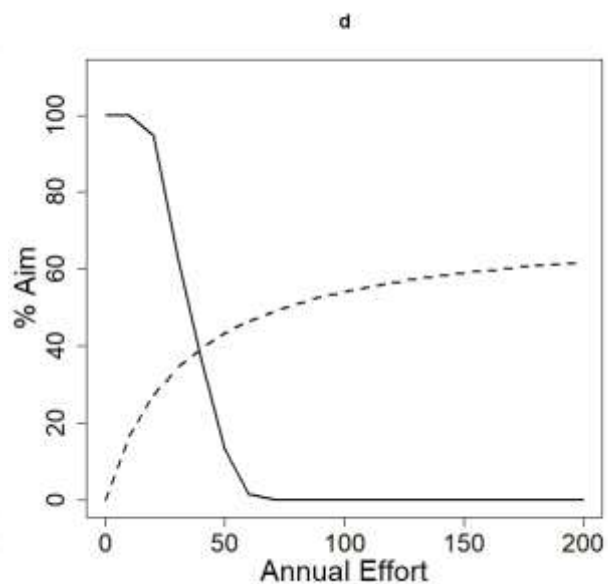
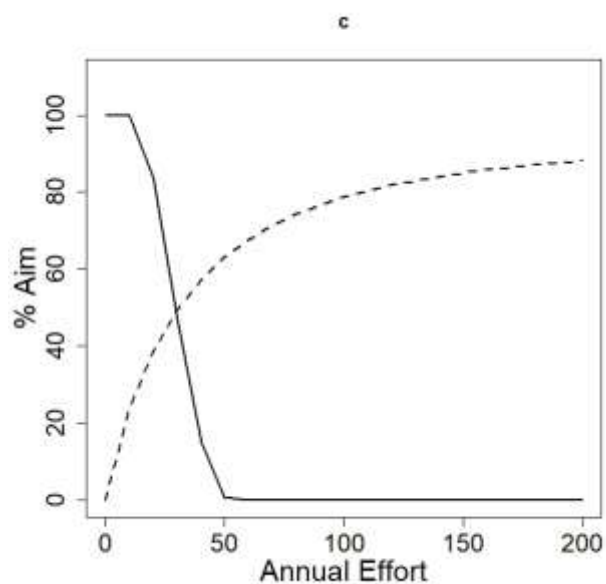
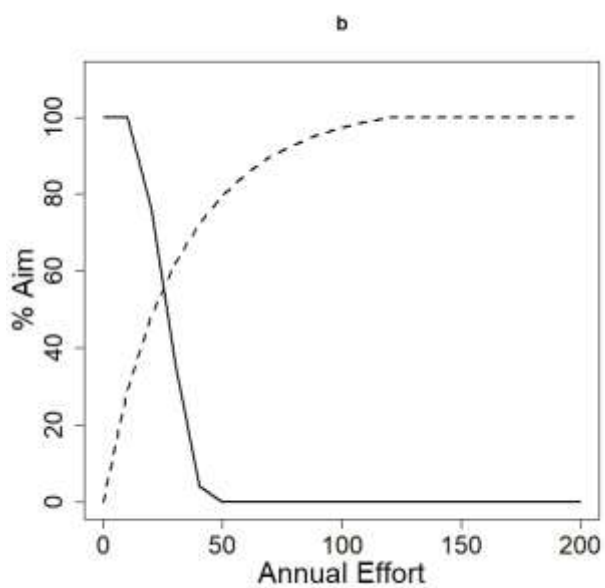
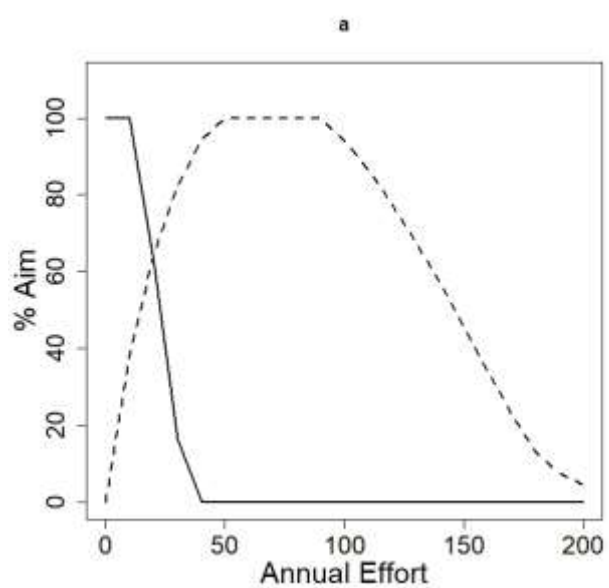












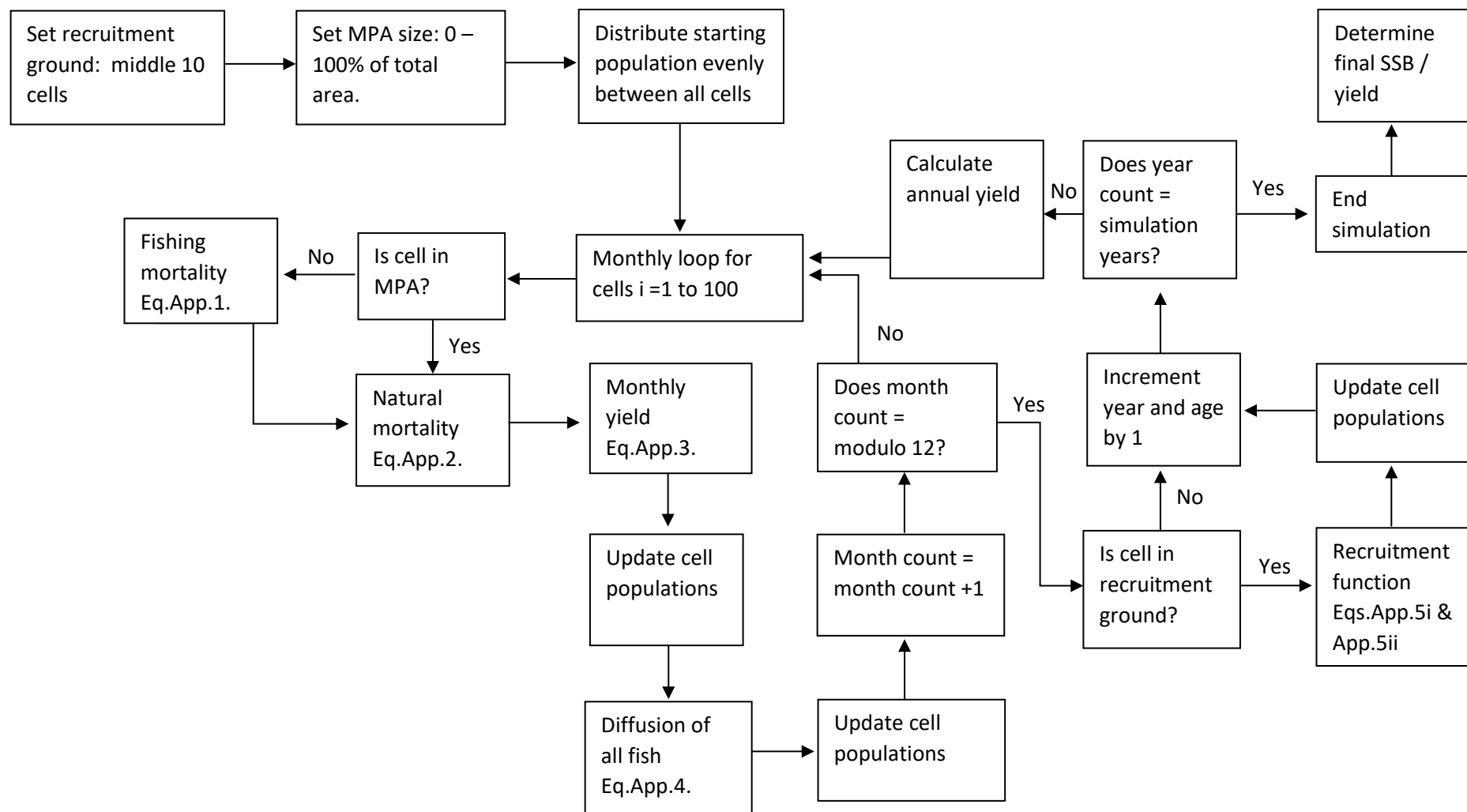


Figure App.1: Flow chart of the simulation, indicating the monthly and annual sub-processes which are fully described by the accompanying equations below the diagram.

Equations App.1 – App.5

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

$F_{a,c}$ 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 ($10 \leq E \leq 200$), 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).

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

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.

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

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 $\alpha = 0.96$, $\beta = 0.00005$; for conservation species, $\alpha = 0.5$, $\beta = 0.00025$; 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

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