Évaluation de l'efficacité des aires marines protégées pour les populations de poissons exploitées mobiles et leurs pêcheries : approches de modélisation

Les aires marines protégées (AMPs), soulèvent un intérêt croissant pour leur capacité à améliorer la conservation des ressources marines et, potentiellement, les captures des pêcheries au travers de l'export de poissons et de larves vers les zones pêchées. Des lacunes importantes subsistent dans nos connaissances des impacts du mouvement des poissons sur le fonctionnement des AMPs, et sur la manière dont les AMPs protégeant les populations de poissons modérément à fortement mobiles pourraient être efficaces sans être extrêmement larges. Différents modèles sont utilisés ici afin de combler ces lacunes de connaissances.

Tout d'abord, un modèle conceptuel a été développé afin d'explorer les impacts du mouvement des poissons sur l'efficacité des AMPs comparativement à ceux de la dispersion larvaire. Les résultats de ce modèle démontrent que le mouvement des poissons a un impact négatif plus fort sur la persistance d'une population dans les réseaux d'AMPs que la dispersion larvaire. La redistribution de l'effort de pêche anciennement dans les AMPs et la concentration des pêcheurs en bordure d'AMPs réduisent de façon significative la persistance et les captures des populations se dispersant dans le stade adulte, tandis qu'elles n'ont qu'un effet marginal pour les populations se dispersant dans le stade larvaire.

Deux modèles appliqués ont été ensuite développés afin d'examiner les impacts des AMPs protégeant des fractions spécifiques de populations migratrices. Un modèle spatialement explicite a été utilisé afin d'étudier les effets des AMPs pour deux populations de merlus sud africaines effectuant des migrations ontogéniques. Les résultats de ce modèle montrent que les AMPs ciblant les juvéniles entraînent une augmentation considérable de la biomasse féconde. Cette augmentation de biomasse conduit à une amélioration des captures de certaines, mais pas de toutes les flottes de pêche. Un modèle par recrue est utilisé afin d'évaluer les effets des AMPs pour les populations récifales effectuant des migrations pour former des agrégations de ponte transitoires. L'application de ce modèle à deux populations de poissons des Seychelles révèle que les AMPs protégeant les agrégations de ponte augmentent le potentiel reproductif des poissons en général, mais pas les captures par recrue.

MOTS-CLÉS

Aires marines protégées (AMPs) Modélisation Mouvement d'adultes et de juvéniles Migrations AMPs ciblées Redistribution de l'effort de pêche Systèmes complexes

Evaluation of the effectiveness of marine protected areas for mobile exploited fish populations and their fisheries: Modeling approaches

ABSTRACT

Marine protected areas (MPAs) are increasingly considered for their ability to improve species conservation and, potentially, fisheries yields via the export of fish and larvae to fished areas. Critical knowledge gaps remain on the impacts of fish movement for MPA functioning and on how MPAs protecting moderately to highly mobile populations may be effective without being extremely large. Here, different models are used to address these knowledge gaps.

First, a conceptual model was developed to explore the impacts of fish movement versus larval dispersal on MPA effectiveness. Results demonstrate that fish movement has a stronger negative impact on population persistence in MPA networks than larval dispersal. Redistribution of the fishing effort formerly in MPAs and concentration of fishers on MPA borders dramatically reduce persistence and yields for mobile populations, while they marginally change results for populations with dispersing larvae. Two applied models examining the effects of MPAs targeting specific fractions of migratory populations were then developed. A spatially-explicit model was used to study the effects of MPAs on two South African hake populations undergoing ontogenetic migrations. Results show that MPAs targeting juveniles considerably increase hake spawning biomass. This increase in biomass improves the yields of some, but not all fishing fleets. A per-recruit model was used to assess MPA effects for reef populations migrating to form transient spawning aggregations. Applying the model to two populations from Seychelles, MPAs protecting spawning aggregations are found to improve fish reproductive potential in general, but not yield-per-recruit.

KEYWORDS

Marines protected areas (MPAs) Modeling Adult and juvenile movement Migrations Targeted MPAs Fishing effort redistribution Complex systems

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and their fisheries: **Modeling** approaches

Evaluation of the effectiveness of marine protected areas for mobile exploited fish populations Thèse de doctorat

École doctorale Sibaah Systèmes intégrés en biologie, agronomie ences, hydrosciences et environnement) Spécialité Biologie des populations et Écologie, présentée devant l'Université Montpellier II par

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Evaluation de l'efficacité des aires marines protégées pour les populations de poissons exploitées mobiles et leurs pêcheries : Approches de modélisation

Soutenue le 23 Mars 2012

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ABSTRACT

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Marine protected areas (MPAs) are increasingly considered for their ability to improve species conservation and, potentially, fisheries yields via the export of fish and larvae to fished areas. Critical knowledge gaps remain on the impacts of fish movement for MPA functioning and on how MPAs protecting moderately to highly mobile populations may be effective without being extremely large. Here, different models are used to address these knowledge gaps.

First, a conceptual model was developed to explore the impacts of fish movement versus larval dispersal on MPA effectiveness. Results demonstrate that fish movement has a stronger negative impact on population persistence in MPA networks than larval dispersal. Redistribution of the fishing effort formerly in MPAs and concentration of fishers on MPA borders dramatically reduce persistence and yields for mobile populations, while they marginally change results for populations with dispersing larvae.

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Keywords: Marine protected areas (MPAs), modeling, adult and juvenile movement, migrations, targeted MPAs, fishing effort redistribution, complex systems.

RESUME

<u>Titre:</u> Evaluation de l'efficacité des aires marines protégées pour les populations de poissons exploitées mobiles et leurs pêcheries : Approches de modélisation

Les aires marines protégées (AMPs), soulèvent un intérêt croissant pour leur capacité à améliorer la conservation des ressources marines et, potentiellement, les captures des pêcheries au travers de l'export de poissons et de larves vers les zones pêchées. Des lacunes importantes subsistent dans nos connaissances des impacts du mouvement des poissons sur le fonctionnement des AMPs, et sur la manière dont les AMPs protégeant les populations de poissons modérément à fortement mobiles pourraient être efficaces sans être extrêmement larges. Différents modèles sont utilisés ici afin de combler ces lacunes de connaissances.

Tout d'abord, un modèle conceptuel a été développé afin d'explorer les impacts du mouvement des poissons sur l'efficacité des AMPs comparativement à ceux de la dispersion larvaire. Les résultats de ce modèle démontrent que le mouvement des poissons a un impact négatif plus fort sur la persistance d'une population dans les réseaux d'AMPs que la dispersion larvaire. La redistribution de l'effort de pêche anciennement dans les AMPs et la concentration des pêcheurs en bordure d'AMPs réduisent de façon significative la persistance et les captures des populations se dispersant dans le stade adulte, tandis qu'elles n'ont qu'un effet marginal pour les populations se dispersant dans le stade larvaire.

Deux modèles appliqués ont été ensuite développés afin d'examiner les impacts des AMPs protégeant des fractions spécifiques de populations migratrices. Un modèle spatialement explicite a été utilisé afin d'étudier les effets des AMPs pour deux populations de merlus sud africaines effectuant des migrations ontogéniques. Les résultats de ce modèle montrent que les AMPs ciblant les juvéniles entraînent une augmentation considérable de la biomasse féconde. Cette augmentation de biomasse conduit à une amélioration des captures de certaines, mais pas de toutes les flottes de pêche. Un modèle par recrue est utilisé afin d'évaluer les effets des AMPs pour les populations récifales effectuant des migrations pour former des agrégations de ponte transitoires. L'application de ce modèle à deux populations de poissons des Seychelles révèle que les AMPs protégeant les agrégations de ponte augmentent le potentiel reproductif des poissons en général, mais pas les captures par recrue.

Mots-clés: Aires marines protégées (AMPs), modélisation, mouvement d'adultes et de juvéniles, migrations, AMPs ciblées, redistribution de l'effort de pêche, systèmes complexes.

RESUME ETENDU

Les aires marines protégées (« AMPs »), zones où la pêche et les autres activités d'extraction humaines sont partiellement ou totalement interdites, soulèvent un intérêt croissant pour leur capacité à améliorer la conservation des ressources marines et, potentiellement, les captures des pêcheries au travers de l'export d'adultes et de juvéniles (le « spillover ») et de larves (l' « export larvaire ») vers les zones de pêches. Le nombre d'études consacrées aux AMPs a explosé au cours des 20 dernières années, et notre connaissance des effets des AMPs s'est considérablement améliorée. Cependant, il existe encore des lacunes dans nos connaissances et des incertitudes critiques concernant les impacts de la mise en place d'AMPs, en particulier sur les zones adjacentes non protégées. Si elles sont conçues de manière inadéquate ou si les conséquences de leur création sont mal anticipées, les AMPs ont de grandes chances d'être inefficaces écologiquement et/ou économiquement, voire de faire plus de mal que de bien. Par conséquent, une analyse scientifique minutieuse de l'efficacité des AMPs doit avoir lieu avant que la surface des eaux nationales et internationales protégées ne soit considérablement augmentée. En particulier, des modèles appropriés doivent être développés afin d'évaluer les conditions dans lesquelles les AMPs pourraient avoir des effets bénéfiques à la fois sur la ressource et sur les pêcheries dans des contextes spécifiques.

La plupart des AMPs ont été mises en place en domaine côtier, où la majorité des populations marines sont sédentaires ou relativement peu mobiles aux stades adulte et juvénile. De ce fait, les études de modélisation ont essentiellement évalué les impacts des AMPs pour des populations marines se déplaçant exclusivement au stade larvaire, et pour les pêcheries qui en dépendent. Durant ces dernières années, des AMPs de plusieurs centaines de kilomètres carrés ont été mises en place (e.g., le monument national marin de Papahānaumokuākea, la réserve marine des Chagos). Ces AMPs protègent partiellement des populations marines se déplaçant sur des distances importantes, parmi lesquelles des populations de poissons hautement migratrices (e.g., des populations de thons tropicaux dans les cas de la réserve marine des Chagos). En outre, les AMPs ont été de plus en plus envisagées, parfois même utilisées, pour la gestion d'espèces de poissons modérément à fortement mobiles aux stades adulte et juvénile, telles que, par exemple, des espèces de mérous, de morues, de merlus et de thons. Ces développements récents soulèvent des questions sur l'efficacité des AMPs pour les populations de poissons exploitées mobiles et leurs pêcheries, et en particulier deux questions fondamentales qui n'ont été que très peu abordées jusqu'à présent : « Comment le mouvement des adultes et des juvéniles influence-til les effets des AMPs sur la ressource et sur les pêcheries ? »; et : « Dans quelles conditions les AMPs visant à protéger des populations de poissons exploitées modérément à fortement mobiles pourraient-elles être bénéfiques à la fois en termes de conservation et pour les pêcheries sans être extrêmement larges ? »

La présente thèse se propose d'aborder ces questions en utilisant différentes approches de modélisation. Dans un premier temps, un modèle général spatialement explicite est développé afin d'apprécier les impacts du mouvement des poissons sur l'efficacité des réseaux d'AMPs comparativement à ceux de la dispersion larvaire (Chapitre 1). Dans un second temps, des modèles appliqués sont utilisés afin d'évaluer les conséquences de la mise en place d'AMPs ciblant des fractions spécifiques de populations de poissons migratrices, les « AMPs ciblées » (Chapitres 2, 3 et 4). Le chapitre 2 explore l'efficacité des AMPs ciblées pour les populations récifales effectuant des migrations pour former des agrégations de ponte transitoires dans des zones situées à plusieurs dizaines, voire centaines de kilomètres de leur zone de résidence. Les chapitres 3 et 4 portent sur les effets des AMPs ciblées pour deux populations démersales qui effectuent des migrations ontogéniques, i.e., qui changent d'habitat au fur et à mesure de leur croissance, les populations sud-africaines des deux espèces de merlus du Cap (Merluccius paradoxus et Merluccius capensis). Le chapitre 3 décrit la méthodologie qu'il a été nécessaire de mettre en place pour estimer les paramètres des relations stock-recrutement locales du modèle. Le chapitre 4 évalue les impacts d'AMPs protégeant préférentiellement les adultes ou les juvéniles de merlus du Cap.

Impacts du mouvement des poissons sur l'efficacité des AMPs comparativement à ceux de la dispersion larvaire

Le modèle général développé dans le *Chapitre 1* fournit une conceptualisation des impacts du mouvement des poissons, comparativement à ceux de la dispersion larvaire, sur l'efficacité des réseaux d'AMPs pour différents scénarios d'évolution de l'effort de pêche suite à la mise en place d'AMPs. Pour réaliser cette conceptualisation, nous avons considéré deux populations de poissons identiques si ce n'est que l'une se déplace uniquement au stade adulte, dans un home range, tandis que l'autre se déplace uniquement au stade larvaire, et nous avons utilisé une seule et même forme fonctionnelle pour représenter le mouvement des poissons et la dispersion larvaire. Nous avons fait différentes hypothèses en ce qui concerne la distribution spatiale de l'effort de pêche, et le devenir de l'effort de pêche qui était dans les

AMPs avant qu'elles ne soient instituées. Suite à la mise en place d'AMPs, l'effort de pêche dans les zones demeurant accessibles à la pêche est soit distribué uniformément, soit distribué préférentiellement dans les zones où des fortes captures ont été réalisées au pas de temps précédent. Ce second scénario conduit à terme à une concentration des pêcheurs sur les bords des AMPs (le « fishing-the-line »). En ce qui concerne le devenir de l'effort de pêche qui était dans les AMPs avant qu'elles ne soient instituées, soit cet effort disparaît après la création des AMPs, soit il est entièrement redistribué dans les zones non protégées.

Les résultats du modèle indiquent que le mouvement des poissons a un effet négatif plus fort sur la persistance d'une population dans un réseau d'AMPs que la dispersion larvaire. Par conséquent, une fraction d'habitat beaucoup plus grande devrait être placée en AMPs et/ou des AMPs beaucoup plus larges devraient être créées afin d'assurer la persistance d'une population se déplaçant au stade adulte. En effet, la dispersion larvaire a pour effet de « mélanger » la production d'œufs entre les zones protégées et les zones non-protégées. La persistance des populations dont les adultes sont sédentaires et les larves sont dispersées par les courants est assurée si suffisamment de larves s'installent dans les zones protégées, et la dynamique spatiale de l'effort de pêche dans les zones non protégées n'a pas d'impact significatif sur les chances de persistance de ces populations dans les réseaux d'AMPs. Le mouvement des poissons a lui pour effet de « mélanger » les taux de mortalité par pêche entre les zones de pêche et les AMPs. Etant donné que la relation entre le taux de mortalité par pêche et la capacité reproductive des poissons est convexe, « mélanger » ces taux de mortalité est plus préjudiciable pour la persistance d'une population que de « mélanger » la production d'œufs. La persistance des populations dont les adultes sont mobiles est assurée si suffisamment de poissons demeurent inaccessibles à la pêche une fraction significative du temps, afin de maintenir la capacité reproductive au-dessus d'un seuil critique dans les zones protégées. Le « fishing-the-line » et la redistribution de l'effort de pêche réduisent considérablement les chances de persistance de ces populations dans les réseaux d'AMPs. En particulier, lorsque qu'une fraction d'habitat relativement large est protégée et l'effort de pêche anciennement dans les AMPs est entièrement redistribué dans les zones non protégées, les AMPs devraient être plusieurs fois plus larges que les échelles spatiales du mouvement des poissons. La pression de pêche devient tellement élevée dans les zones non protégées dans cette situation que des individus de la population doivent être totalement inaccessibles à la pêche afin de préserver la capacité reproductive au-dessus d'un seuil critique dans les zones protégées.

En outre, les résultats du modèle montrent que les impacts du mouvement des poissons, comparativement à ceux de la dispersion larvaire, sur les captures des pêcheries dépendent essentiellement de la fraction d'habitat protégée et du devenir de l'effort de pêche anciennement dans les AMPs. L' « export larvaire » a un plus grand potentiel pour améliorer les captures des pêcheries que le « spillover » lorsqu'une petite fraction d'habitat est placée en AMPs. En revanche, en l'absence de redistribution de l'effort de pêche, des captures élevées sont obtenues pour un plus grand nombre de configurations de réseaux d'AMPs dans le cas du mouvement des poissons que dans celui de la dispersion larvaire lorsqu'une fraction relativement importante d'habitat est fermée à la pêche. La redistribution de l'effort de pêche diminue considérablement la capacité des AMPs à améliorer les captures des pêcheries dans le cas du mouvement des poissons, tandis qu'elle n'a qu'un effet mineur sur les captures dans le cas de la dispersion larvaire. Les captures maximales dans le cas des populations se dispersant au stade adulte sont faibles quand l'effort de pêche anciennement dans les AMPs est redistribué dans les zones protégées, et sont réalisées quand la quasi-totalité de l'habitat est placée en AMPs et les AMPs individuelles sont plusieurs fois plus larges que les échelles spatiales du mouvement des poissons. Ceci est dû au fait que la persistance d'une population est assurée dans cette situation en établissant des AMPs qui soient suffisamment larges afin que certains individus soient totalement inaccessibles à la pêche, comme expliqué précédemment.

Par ailleurs, les résultats du modèle indiquent que le mouvement des poissons et la dispersion larvaire combinés ont souvent un effet négatif plus fort sur la persistance d'une population dans un réseau d'AMPs que le mouvement des poissons seul. Ce résultat tient vraisemblablement au fait que la dispersion larvaire réduit le niveau de recrutement larvaire à l'intérieur des AMPs en même temps que le mouvement des poissons réduit le potentiel reproductif des individus ayant recruté dans la population au sein des AMPs. D'un autre côté, le « spillover » a le potentiel d'améliorer uniquement les captures des pêcheurs opérant dans les sites proches des AMPs. Quand la dispersion larvaire se superpose au mouvement d'adultes, les AMPs ont la capacité d'améliorer également les captures des pêcheurs opérant dans des sites plus éloignés.

Impacts des AMPs ciblées pour les populations de poissons migratrices

Dans le cas des populations de poissons migratrices, les AMPs devraient être de très grande taille et/ou les réseaux d'AMPs devraient couvrir une large fraction de l'habitat afin d'offrir une protection efficace aux juvéniles et aux adultes. Mais comme la mise en place de très grandes AMPs ou de larges réseaux d'AMPs est potentiellement extrêmement coûteuse, la recherche halieutique s'intéresse de plus en plus à la mise en place d'AMPs protégeant des zones plus petites où les poissons passent une partie de l'année et sont hautement vulnérables à la pêche et/ou associées à un stade de développement spécifique, telles que les zones de ponte et les zones de nourricerie. Ces AMPs sont mentionnées sous le terme d' « AMPs ciblées » parce qu'elles visent à protéger des fractions spécifiques de populations migratrices plutôt que leur cycle de vie tout entier. Nous avons développé différents modèles appliqués afin d'évaluer l'efficacité d'AMPs ciblées pour deux types de populations de poissons migratrices : les populations récifales formant des agrégations de ponte (*Chapitre 2*); et les populations sud-africaines des deux espèces de merlus du Cap, qui effectuent des migrations ontogéniques (*Chapitres 3 et 4*).

Efficacité des AMPs ciblées pour les populations récifales formant des agrégations de ponte

Dans le cas des populations récifales formant des agrégations de ponte, les géniteurs sont la cible des efforts de protection étant donné que la mortalité par pêche dans les sites de ponte est généralement extrêmement élevée par rapport à celle dans les zones de résidence, et que les zones de ponte couvrent une surface relativement petite. Un effort de pêche élevé dans les zones de ponte peut entraîner une réduction importante de l'abondance et de la biomasse de l'ensemble de la population. Il peut aussi conduire dans le cas des populations protogynes (i.e., les populations dont les individus sont d'abord femelles puis changent de sexe) à un déclin rapide du nombre relatif de males, et par conséquent, à une diminution considérable du taux de fertilisation des œufs.

Les connaissances sur les populations récifales formant des agrégations de ponte et leurs pêcheries (e.g., les relations stock-recrutement, le degré de fidélité des poissons aux sites de ponte, les routes de migration entre les sites de ponte et les zones de résidence) sont généralement limitées, et tout particulièrement dans les pays en voie de développement. Dans ce contexte, dans le *Chapitre 2*, nous avons développé un modèle simple, non spatial, par

recrue, structuré en âge, pour évaluer les effets des AMPs ciblant les agrégations de ponte transitoires, qui peut être appliqué à une large gamme de populations de poissons. Les variables de sortie de ce modèle sont la biomasse féconde par recrue (mesure de la capacité reproductive de la population) et les captures par recrue, ainsi que le sex-ratio (ici le ratio du nombre de femelles matures sur le nombre de mâles matures) dans le cas des populations protogynes. Des hypothèses alternatives ont été faites dans ce modèle sur la fraction des sites de ponte placée en AMPs, la fidélité des poissons aux sites de ponte (fidèle ou infidèle) et le devenir de l'effort de pêche qui était dans les AMPs avant qu'elles ne soient instituées (disparaît, est redistribué dans les sites de ponte demeurant accessible à la pêche, ou est redistribué dans les zones de résidence si tous les sites de ponte sont placés en AMPs). Nous avons appliqué ce modèle à deux populations de poissons récifaux de l'archipel des Seychelles : la population de mérou marbré (*Epinephelus fuscoguttatus*) de l'atoll de Farquhar, qui est protogyne, et la population de poisson-lapin à tâches blanches (*Siganus sutor*) des îles granitiques principales, qui est gonochorique.

Les résultats du modèle suggèrent que la mise en place d'AMPs ciblant les agrégations de ponte conduit à une amélioration de la capacité reproductive de la population, et ce quel que soit le devenir de l'effort de pêche qui était dans les AMPs avant qu'elles ne soient instituées. En règle générale, la mise en place d'AMPs ciblant les agrégations de ponte conduit aussi à une normalisation du sex-ratio des populations protogynes, et par conséquent probablement à une augmentation de leur production d'œufs fertilisés. Cependant, quand les poissons sont fidèles aux sites de ponte, la redistribution de l'effort de pêche anciennement dans les AMPs dans les zones de ponte non protégées conduit à une augmentation considérable du sex-ratio de la sous-population pêchée. Néanmoins, en parallèle, le sex-ratio de la sous-population protégée est ramené à sa valeur naturelle et, par conséquent, l'augmentation du sex-ratio de la sous-population pêchée n'aura qu'un effet mineur sur la production d'œufs fertilisée de la population dans son ensemble si suffisamment de sites de ponte sont placés en AMPs. Par ailleurs, les résultats du modèle indiquent que la création d'AMPs ciblant les agrégations de ponte n'améliorera pas les captures par recrue, quel que soient le devenir de l'effort de pêche qui était dans les AMPs avant qu'elles ne soient instituées et le degré de fidélité des poissons aux sites de ponte. Cependant, il est raisonnable de penser que la mise en place d'AMPs dans les sites de ponte puisse améliorer les captures des pêcheries via un export larvaire lié à l'amélioration de la capacité reproductive de la population, à condition qu'une fraction significative de sites de ponte soit placée en AMPs.

La pertinence d'instituer des AMPs dans les zones de ponte plutôt que de mettre en place d'autres mesures de gestion dépend des traits d'histoire de vie des populations étudiées et de leur taux de mortalité par pêche dans les zones de ponte comparativement à celui dans les zones de résidence. Les traits d'histoire de vie du mérou marbré (vie longue, croissance lente et hermaphrodisme protogyne) lui confèrent une grande vulnérabilité à la pêche, et son taux de mortalité par pêche dans les zones de ponte est extrêmement élevé. Par conséquent, dans le cas du mérou marbré, il est sensé de cibler des niveaux de captures par recrue modérés tout en empêchant un déséquilibre important du sex-ratio en faveur des femelles, et la fermeture d'un nombre significatif de sites de ponte à la pêche est certainement la meilleure mesure de gestion dans ce contexte. En contraste, le poisson-lapin à tâches blanches possède des traits d'histoire de vie qui lui confèrent un degré fort de résilience à la pêche (vie courte, croissance rapide et gonochorisme), et son taux de mortalité par pêche dans les zones de ponte est similaire à celui dans les zones de résidence. La mise en place d'AMPs dans les zones de ponte n'a qu'un effet modéré sur la capacité reproductive et les captures par recrue du poisson-lapin à tâches blanches pour une large gamme de niveaux d'effort de pêche, et d'autres mesures de gestion (e.g., une réduction de l'effort de pêche global) seraient certainement plus bénéfiques à la fois en termes de conservation et pour les pêcheries. Une analyse supplémentaire a révélé que la mise en place d'AMPs dans les zones de résidence conduirait à des niveaux plus élevés de biomasse féconde par recrue et de captures par recrue pour cette espèce. Cependant, en pratique, l'institution d'AMPs dans les zones de résidence est difficilement envisageable du fait que ces zones couvrent une surface très importante comparativement aux zones de ponte et que les pêcheries récifales ciblent un nombre considérable d'espèces dans les sites de résidence.

Efficacité des AMPs ciblées pour les populations sud-africaines de merlus

Dans le cas de la majorité des populations de poissons migratrices, les zones de nourricerie et de ponte couvrent toutes les deux des surfaces importantes. En pratique, il est difficile d'établir des AMPs à la fois dans les zones de nourricerie et dans les zones de ponte (e.g., parce que les coûts associés seraient beaucoup trop importants) et, par conséquent, il est nécessaire de déterminer si les adultes ou les juvéniles devraient être les cibles des efforts de protection. Quelques études utilisant des modèles généraux en deux patchs (zones de ponte et zones de nourricerie) (e.g., Pelletier & Magal 1996; Edwards & Plaganyi 2011) ont montré

que les AMPs devraient protéger en priorité les juvéniles, afin d'augmenter l'âge moyen de la population, et ainsi la biomasse de géniteurs et les captures des pêcheries. Ces études indiquent qu'à l'opposé, la fermeture des zones de ponte pourrait diminuer la biomasse des géniteurs et les captures en déplaçant un effort de pêche élevé sur les juvéniles.

Dans le *Chapitre 4*, nous avons développé un modèle spatialement et saisonnièrement explicite afin d'évaluer les impacts d'AMPs protégeant préférentiellement les adultes ou les juvéniles d'une population migratrice démersale, la population sud-africaine de merlu profond du Cap (*Merluccius paradoxus*). La dynamique des deux espèces de merlus présentes dans les eaux sud-africaines (le merlu profond du Cap et le merlu côtier du Cap, *Merluccius capensis*) a été représentée dans le modèle, ainsi que celle de la flotte palangrière, de la flotte chalutière hauturière, et de la flotte chalutière côtière. Les deux premières flottes citées capturent les deux espèces de merlu du Cap, tandis que la troisième ne capture que *M. capensis*. Les deux espèces de merlus du Cap migrent au large et en profondeur au fur et à mesure de leur croissance. Un sous-modèle basé sur un système d'information géographique a été utilisé pour simuler ces migrations ontogéniques. Par ailleurs, un sous-modèle biophysique individucentré a été utilisé pour estimer des matrices de connectivité larvaire des deux espèces pour chacun des mois de l'année.

Un pré-requis nécessaire avant le développement et l'utilisation de ce modèle a été la mise en place dans le *Chapitre 3* d'une méthodologie pour estimer les relations stock-recrutement locales de chacune des deux populations sud-africaines de merlus du Cap. En effet, une étude récente (White 2010) a démontré que la pente à l'origine des relations stock-recrutement doit être ajustée quand on passe d'un modèle non-spatial d'évaluation des stocks à un modèle spatialement explicite afin de ne pas surestimer ou sous-estimer les chances de persistance d'une population dans un système d'étude donné. Cette étude a aussi proposé une méthodologie analytique pour réaliser l'ajustement en question. Hélas, la méthodologie proposée ne peut pas être utilisée pour des modèles spatialement explicites complexes, en particulier quand les adultes et les juvéniles de la population d'étude effectuent des mouvements autres que de simples mouvements dans un home range. Par conséquent, nous avons développé une méthodologie numérique pour estimer la pente à l'origine des relations stock-recrutement locales. Cette méthodologie permet aussi d'estimer le niveau de recrutement larvaire maximal local, un autre paramètre crucial des relations stock-recrutement locales.

Une fois les relations stock-recrutement et les patterns de connectivité estimés pour M. paradoxus et M. capensis, le modèle a pu être utilisé pour explorer les conséquences de la mise en place d'AMPs protégeant préférentiellement les adultes ou les juvéniles de M. paradoxus. Des hypothèses alternatives ont été faites sur le devenir de l'effort de pêche qui était dans les AMPs avant qu'elles ne soient instituées (disparaît, ou est redistribué dans les zones restant ouvertes à la pêche et préférentiellement dans les zones de forte intensité de pêche), et la fraction d'habitat placée en AMPs. En accord avec les résultats des modèles généraux en deux patchs, les résultats de notre modèle pour M. paradoxus indiquent que les AMPs ciblées conduiront à une augmentation significative de la biomasse féconde quand les juvéniles vulnérables à la pêche sont les cibles prioritaires des efforts de protection. Dans cette situation, l'augmentation de la biomasse féconde de M. paradoxus conduit à une augmentation considérable des captures de cette espèce par la flotte palangrière, qui ne cible que les adultes. En revanche, la flotte chalutière hauturière cible à la fois les juvéniles et les adultes de *M. paradoxus*, et la perte de biomasse exploitable pour cette flotte due à la création d'AMPs ne sera pas compensée par une augmentation de la biomasse féconde de M. paradoxus. En contraste, les captures de M. paradoxus par les flottes palangrières et chalutières hauturières sont relativement inchangées quand les adultes de grande taille sont les cibles prioritaires des efforts de protection.

Lorsqu'à la fois *M. paradoxus* et *M. capensis* sont pris en considération, les AMPs ciblées apparaissent moins efficaces à la fois en terme de conservation et pour la pêcherie. Quand l'effort de pêche anciennement dans les AMPs est redistribué dans les zones demeurant accessibles à la pêche et que les juvéniles de *M. paradoxus* sont les cibles prioritaires des efforts de protection, la biomasse féconde de *M. capensis* est diminuée légèrement à modérément. Pour les autres scénarios d'AMPs examinés, la biomasse féconde de *M. capensis* est relativement inchangée ou bien modérément améliorée. En outre, le potentiel des AMPs ciblées d'améliorer les captures de la pêcherie apparaît plus limité. Quand les efforts de protection ciblent prioritairement les juvéniles de *M. paradoxus* et que l'effort de pêche qui était dans les AMPs avant qu'elles ne soient instituées est redistribué dans les zones demeurant accessibles à la pêche, les captures totales de merlus du Cap de la flotte palangrière augmentent modérément, tandis celles des autres flottes diminuent. Pour les autres scénarios d'AMPs parmi une multitude possible ont été évalués ici, et la mise en place d'AMPs ciblées pourrait être bénéfique à certaines flottes dans

d'autres circonstances. Cependant, il y a de grandes chances pour qu'il existe plus de conditions dans lesquelles les captures totales de merlus du Cap diminueront suite à la création d'AMPs que le contraire. Les résultats d'un autre modèle de simulation spatialement explicite, ISIS-FISH (Pelletier et al. 2009), indiquent également que les impacts des AMPs ciblées pour les pêcheries mixtes (i.e., multi-espèces multi-flottes) sont complexes, et que les AMPs ciblées n'ont des effets bénéfiques sur ces pêcheries que dans un nombre limité de cas.

Conclusions et perspectives

Le mouvement des poissons a un impact négatif fort sur la persistance d'une population et impose des contraintes importantes sur le design des réseaux d'AMPs. Etant donné que le « fishing-the-line » et la redistribution de l'effort de pêche sont la règle plutôt que l'exception dans le monde réel, les AMPs doivent être plusieurs fois plus larges que les échelles spatiales du mouvement des poissons afin de pouvoir protéger efficacement les populations se déplaçant dans un home range. En outre, les AMPs ne couvrent généralement en pratique qu'une petite fraction de l'aire d'habitat des populations de poissons. Ainsi, dans le cas de la majorité des populations de poissons se déplaçant dans un home range, le « spillover » n'est bénéfique qu'aux pêcheurs opérant à proximité des AMPs et l'« export larvaire » a un plus grand potentiel pour améliorer les captures globales des pêcheries que le « spillover ».

Dans le cas des populations migratrices, les AMPs ciblant des fractions spécifiques de la population peuvent être efficaces en termes de conservation sans être extrêmement larges. Dans le cas des populations récifales formant des agrégations de ponte, les AMPs ont plus de chances d'être mises en place dans les sites de ponte du fait que ces zones couvrent des surfaces relativement faibles et que les pêcheries récifales ciblent un nombre très important d'espèces dans les sites de résidence. La fermeture d'un grand nombre de sites de ponte à la pêche conduit à une augmentation significative du potentiel reproductif des poissons et, éventuellement, à une amélioration des captures au travers de l' «export larvaire ». Dans le cas des populations migratrices dont les zones de ponte et de nourricerie couvrent toutes les deux des surfaces importantes, les AMPs doivent cibler préférentiellement les juvéniles recrutés dans la pêcherie. La mise en place d'AMPs protégeant les juvéniles conduit à une augmentation significative de la population et de sa biomasse féconde. Cette augmentation de la biomasse féconde peut compenser les pertes de biomasse exploitable de

certaines, mais pas de toutes les flottes de pêche. Les AMPs ciblées n'ont un effet bénéfique sur les captures globales des pêcheries que dans un nombre limité de cas.

La présente thèse a abordé la problématique du fonctionnement et de l'utilité des AMPs pour les espèces de poissons exploitées mobiles et leurs pêcheries. Il s'agit là d'une problématique large et complexe, et les efforts de modélisation doivent être poursuivis pour traiter de questions importantes rattachées à cette problématique n'ayant pas été abordées ici. En particulier, l'efficacité des « AMPs dynamiques », zones protégées suivant les populations hautement migratrices (i.e., effectuant des migrations sur des centaines ou des milliers de kilomètres telles que, e.g., les thons et poissons porte-épée) dans l'espace et le temps, est présentement incertaine et devrait être examinée attentivement dans les études de modélisation futures. Par ailleurs, il existe une grande diversité de patrons de mouvement (e.g., le nomadisme, les mouvements densité-dépendants) dans les systèmes d'AMPs, qui chacun pourraient avoir des impacts spécifiques sur les effets des AMPs. En outre, le mouvement des poissons peut être influencé par des modifications de la qualité de l'habitat. Une exploration minutieuse des conséquences des différents patrons de mouvement existants et du comportement de mouvement des poissons sur le fonctionnement des AMPs est essentielle pour pouvoir créer des réseaux d'AMPs efficaces pour les populations de poissons exploitées mobiles.

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GENERAL INTRODUCTION

Marine protected areas ('MPAs'), places where fishing and other human extractive activities are partially or totally restricted, are increasingly being considered and used for their ability to improve species conservation and, potentially, fisheries yields through adult and juvenile export ('spillover') and larval export ('recruitment subsidy') (Lubchenco et al. 2003; Gell & Roberts 2003; Russ et al. 2004; Claudet 2011). Their number is going to rapidly increase worldwide so as to try to meet the conservation targets established for 2020 (10% of the world's ecological regions in MPAs; CBD 2010; Wood 2011; Marinesque et al. 2012). The number of studies devoted to MPAs has grown substantially during the last 20 years and our knowledge of the conservation and fisheries effects of protected areas has considerably increased (Halpern & Duffy 2008; Claudet 2011). However, critical knowledge gaps and uncertainties remain about the impacts of MPA implementation, especially on adjacent fished areas (Hilborn et al. 2004; Sale et al. 2005; Grüss et al. 2011). If they are inadequately designed or the consequences of their establishment are poorly anticipated, MPAs are likely to be ecologically and/or economically ineffective and, eventually, may do more harm than good (Agardy et al. 2003, 2011; Kaiser 2005; Kaplan et al. 2010). Therefore, before moving too quickly towards conservation targets, a thorough and science-driven analysis of the effectiveness of MPAs needs to take place (Sale et al. 2005; Kaplan et al. 2010; Edgar 2011). In particular, appropriate models should be used to evaluate whether and under what conditions MPAs may produce conservation and fisheries benefits in specific contexts (Gerber et al. 2003; Pelletier & Mahévas 2005; Little et al. 2007).

MPA implementation has long been concentrated in coastal and nearshore areas, where many fish populations are sedentary or have relatively low mobility (Roberts *et al.* 2005; Roberts 2007; Gaines *et al.* 2010). For this reason, until recently, modeling efforts have been essentially directed to evaluating the impacts of larval dispersal on the functioning of MPAs (e.g., Tuck & Possingham 2000; Botsford *et al.* 2001; Gaines *et al.* 2003; Hastings & Botsford 2006), and the consequences of MPAs for populations dispersing exclusively in the larval phase and their fisheries (e.g., Sladek Nowlis & Roberts 1999; Stockhausen *et al.* 2000; Kahui & Alexander 2008; Kaplan *et al.* 2009). During the last 5-6 years, several large-scale MPAs have been created, among which the Papahānaumokuākea Marine National Monument in the northwestern Hawaiian Islands (362 000 square kilometers), and the Chagos Island marine reserve in the Indian Ocean (544 000 square kilometers) (Koldewey *et al.* 2010;

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Nelson & Bradner 2010; Jones 2011). In December 2010, the imminent creation of a 5 million square kilometer partial-take MPA around Bermuda (north-west Atlantic) was announced (Jones 2011). These large-scale MPAs may offer protection to fish populations exhibiting extensive movement, including some highly migratory populations (e.g., tropical tuna populations in the case of the Chagos Island marine reserve; Koldewey et al. 2010). Furthermore, MPAs primarily aimed at protecting moderately to highly mobile exploited species such as migratory groupers (Rhodes & Warren-Rhodes 2005; Sadovy & Colin 2012), cods and haddocks (Murawski et al. 2005; Roberts & Mason 2008), hakes (Sink & Attwood 2008; Machado-Schiaffino et al. 2011), and tunas and billfishes (Norse et al. 2005; Pala 2009, 2010), are increasingly being considered and used. These recent developments raise questions regarding the effectiveness of MPAs for mobile exploited fish populations and the fisheries depending on them and, in particular, two fundamental questions that have been only partially addressed and understood until now: "How adult and juvenile movement affects the conservation and fisheries effects of MPAs?"; and: "Under what conditions may MPAs be beneficial both for the conservation of moderately to highly mobile exploited fish populations and for their fisheries without being extremely large?"

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In the present thesis, I propose to address these two questions, using several different fundamental and applied modeling approaches. Below, I briefly overview what is currently known about the impacts of adult and juvenile movement on MPA effectiveness and what remains to be further explored. Then, I introduce the concept of 'targeted MPAs', namely MPAs aimed at protecting specific fractions of moderately to highly mobile fish populations. I review the few modeling studies that have evaluated the effectiveness of this type of MPA and identify important avenues for research. Finally, I give an outline of the contents and objectives of the different chapters of the thesis.

Impacts of adult and juvenile movement on MPA effectiveness

Existing modeling studies show that adult and juvenile movement (hereafter often referred to as 'fish movement') reduces overall protection of the population by MPAs¹ as individuals moving between fished areas and MPAs are effectively protected only for the percentage of time they spend inside closed areas (Kramer & Chapman 1999; Gerber *et al.*

¹ MPA models have usually explored the effects of no-take MPAs (Pelletier *et al.* 2009; White *et al.* 2011). Therefore, unless otherwise specified, the term 'MPAs' hereafter refers to 'no-take MPAs'.

2005), and only to the extent that fishing effort is unmodified to take advantage of spillover. This reduction of protection is in general unbalanced by movement of individuals from nonprotected to protected areas since abundance outside MPAs is typically lower (Polacheck 1990; Walters 2000; Walters *et al.* 2007). More specifically, if enough habitat area is closed to fishing to ensure that in the absence of fish movement larval supply would be at or near the carrying capacity of the system, then moderate spillover can improve fisheries yields at little cost to population persistence (e.g., Guénette & Pitcher 1999; Stefansson & Rosenberg 2005; Moffitt *et al.* 2009; Le Quesne & Codling 2009). On the other hand, if MPAs are too small and/or fish export is too great, then spillover has a negative effect on population persistence and eventually fisheries yields (e.g., Polacheck 1990; Walters 2000; Walters *et al.* 2007; Moffitt *et al.* 2009).

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The way fish movement impacts MPA effects is dependent on fishing pressure and the spatial distribution of fishing mortality in non-protected areas. MPAs are likely to have positive fisheries effects only when fish populations were already overexploited in adjacent fished areas, so that spillover and recruitment subsidy due to increased fish biomass in protected areas are sufficiently large that they offset the loss of fishing grounds due to MPA establishment (e.g., Holland & Brazee 1996; Guénette & Pitcher 1999; Hart 2006; Hilborn *et al.* 2006; Little *et al.* 2009). Furthermore, high concentration of fishers on MPA boundaries to take advantage of spillover ('fishing-the-line') and redistribution of the fishing effort formerly in closed areas to remaining fished areas ('fishery squeeze') have the potential to significantly reduce protected population size and, later, to alter the capacity of MPAs to replenish adjacent fished waters through larval, adult and juvenile export (e.g., Beattie *et al.* 2002; Salomon *et al.* 2002; Kellner *et al.* 2007; Walters *et al.* 2007).

Only two modeling studies have examined the relative impacts of fish movement versus larval dispersal on fish conservation and fisheries yields with MPAs (Moffitt *et al.* 2009; Le Quesne & Codling 2009). Moffitt *et al.* (2009) used a spatially-explicit model to examine persistence and fisheries yields for a fish population with dispersing larvae and adults moving within a home range, where fishery squeeze and the tendency of fishers to fish-the-line are not considered. The authors showed that home range movement has a strong negative impact on population persistence in MPA networks relative to larval dispersal, even for movement spatial scales considerably smaller than MPA size. Their results also suggest that recruitment subsidy has greater potential to increase fisheries yields than spillover. Le Quesne & Codling (2009) found the opposite using a spatially-explicit model representing

fish movement as a diffusive process and accounting for fishery squeeze and the tendency of fishers to fish-the-line, but only the special cases of non-dispersing larvae and a uniform spatial distribution of larvae were considered in that study. While these two studies provide

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spatial distribution of farvae were considered in that study. While these two studies provide some insights into the impacts of adult and juvenile movement on MPA effectiveness relative to those of larval dispersal, the underlying mechanisms driving differences in the effects of larval dispersal and fish movement as well as the generality of these effects have not been clearly identified. Furthermore, the implications of fish movement and larval dispersal for MPA effectiveness relative to those of 'fishing-the-line' and 'fishery squeeze' have never been rigorously examined.

'Targeted MPAs'

General modeling studies suggest that for moderately to highly mobile populations individual MPAs should be very large and/or MPA networks should cover a large fraction of total habitat area to offer effective protection to juveniles and adults (e.g., Polacheck 1990; Stefansson & Rosenberg 2005; Moffitt *et al.* 2009; Le Quesne & Codling 2009). But as the implementation of very large MPAs or extensive MPA networks is potentially extremely costly, research has shown increasing interest in strategies for protecting smaller areas where fish spend an inordinate fraction of time and/or are highly vulnerable to fishing (e.g., areas associated with specific developmental stages, such as nursery or spawning areas). These more limited MPAs are referred to as 'targeted MPAs' because they aim to protect specific fractions of the fish population rather than their entire life cycle (Kaplan *et al.* 2010; Grüss *et al.* 2011).

Targeted MPAs have been addressed in several modeling studies (e.g., Horwood *et al.* 1998; Apostolaki *et al.* 2002; Heppell *et al.* 2006; Edwards & Plaganyi 2011), usually using patch models, each representing a specific developmental stage (spawning and nursery areas) or a specific seasonal habitat (spawning and feeding areas), with explicit or implicit migrations of fish between patches. Apostolaki *et al.* (2002), using a patch model to examine the consequences of MPAs for the Mediterranean hake (*Merluccius merluccius*) resource, found that the greatest conservation and fisheries benefits are likely to be obtained when both some nursery and spawning areas to fishing (e.g., because it is too costly), some authors suggest that spawning areas should be protected to preserve older, larger, more fecund individuals and

significantly increase recruitment success (e.g., Berkeley *et al.* 2004a, 2004b; Birkeland & Dayton 2005). On the other hand, several modeling studies indicate that fish juveniles should be the targets of protection efforts (e.g., Pelletier & Magal 1996; Roberts & Sargant 2002; Edwards & Plaganyi 2011).

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Edwards & Plaganyi (2011) developed a two-patch (spawning areas, nursery areas) model to investigate the impacts of protecting preferentially the older or the younger sections of a South African population of deep water Cape hake, Merluccius paradoxus. M. paradoxus is a demersal species that undergoes ontogenetic migrations, i.e., moves from one habitat to another as it grows older (Payne 1989). The authors found that protecting preferentially the older, more fecund individuals without reducing overall catches at the time of MPA establishment would likely displace very high fishing effort onto sites occupied by young individuals, consequently preventing most of these individuals to grow older to improve the productivity of hake-directed offshore trawl fleet. On the other hand, Edwards & Plaganyi (2011) showed that fishing the older sections of the population while protecting the younger individuals would likely increase the mean age of the population and its reproductive capacity and improve the catches of the hake-directed offshore trawl fleet. Roberts & Sargant (2002) developed a four-patch (spawning areas, feeding areas and two migration routes), agestructured model to assess the potential benefits of MPAs for a theoretical migratory fish population. The authors demonstrated that closing spawning areas to fishing would likely displace high fishing effort on young and vulnerable life stages and dissipate the conservation benefits resulting from MPA establishment. Results, e.g., from Pelletier and Magal (1996) and Horwood et al. (1998), also indicate that spawning area closures may do more harm than good for migratory fish populations since high fishing effort may then be redirected into nursery areas.

Relatively important modeling efforts have been undertaken so far to evaluate the effectiveness of targeted MPAs for migratory fish populations, and existing modeling studies concur on the fact that juveniles of these populations should be the preferential targets of protection efforts. However, existing studies generally use two-patch models that provide only general insights into the potential effects of spawning area or nursery area closures. More complex spatially- and, eventually, seasonally-explicit models representing migrations between feeding and spawning areas and/or ontogenetic migrations and fleet dynamics are needed to provide detailed assessments for specific populations and gain insights regarding

the interaction between different fish movement types, fishing fleet dynamics and the spatial distribution of MPAs (Pelletier & Mahévas 2005; Grüss *et al.* 2011).

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The specific case of aggregation-forming reef fish populations

Numerous coral reef fish populations migrate to form transient spawning aggregations at sites located a few to hundreds of kilometers from their normal residence areas (Domeier & Colin 1997; Sadovy & Domeier 2005). For these populations, spawning individuals are usually the targets of protection efforts as spawning aggregation areas are of relatively small size and fishing mortality at spawning sites is in general extremely high (Rhodes & Warren-Rhodes 2005; Sadovy & Domeier 2005). In the case of aggregation-forming reef fish populations, it is of interest to evaluate whether spawning area closures may improve fish reproductive capacity, but also whether they may normalize sex ratio when the study population is protogynous (i.e., matures first as a female and then changes to male), since for protogynous populations a decrease of the relative number of males is thought to significantly reduce egg fertilization rates (Coleman *et al.* 1996; Koenig *et al.* 1996; Rhodes & Warren-Rhodes 2005).

Only two modeling studies have to date examined the potential impacts of 'spawning aggregation-based MPAs' (Alonzo & Mangel 2004; Heppell et al. 2006). Heppell et al. (2006) developed a two-patch, age-structured model to evaluate the conservation effects of spawning area closures for a protogynous aggregation-forming grouper population, alone or in combination with nearshore area closures (protecting juveniles and mature females outside of the spawning season) and conventional management tools. The authors found that nearshore area closures lead to the highest female spawning stock biomass (SSB) and most rapid population recovery but has limited effect on sex ratio, while year-round closure of all spawning sites result in sex ratio normalization but is less effective at improving fish reproductive capacity than nearshore area closures or fishing effort reduction, especially when fishing effort is redistributed at the time of MPA establishment. Alonzo and Mangel (2004) used a size-structured, individual-based model to evaluate the effects of closing 10-30% of spawning sites to fishing for aggregation-forming gonochoristic and protogynous populations, using parameter estimates from previous research on a rocky reef species. The authors found that spawning aggregation-based MPAs increased mean population size and production of fertilized eggs, but that the redistribution of fishing effort previously in protected areas to remaining fished areas decreased MPA benefits for the protogynous population. For the scenarios examined, spawning aggregation-based MPAs did not increase harvestable biomass (Alonzo & Mangel 2004).

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Results from Alonzo and Mangel (2004) and Heppell et al. (2006) concur on the fact that spawning aggregation-based MPAs may significantly improve fish reproductive capacity and/or reduce sex-ratio bias, unless fish mortality outside spawning sites and/or outside of the spawning season is considerably increased due to fishing effort displacement. However, critical knowledge gaps remain on the effectiveness of MPAs protecting transient reef fish spawning aggregations (Sale et al. 2005; Sadovy et al. 2008). In particular, the effects of spawning site fidelity, or lack thereof, and fishing effort displacement on the efficacy of spawning aggregation MPAs have not been satisfactorily explored. Models should be developed to fully explore the potential conservation and fisheries effects of closing a fraction or all spawning sites to fishing for gonochoristic and protogynous aggregation-forming reef fish populations. However, data and knowledge are limited for most coral reef fish populations forming spawning aggregations (e.g., stock-recruitment relationships, critical values of sex ratio, migration routes between spawning sites and normal residence areas) and their fisheries, especially in developing nations (Johannes 1998; Nemeth 2005; Sadovy & Domeier 2005; Sadovy et al. 2008). This limited availability of information imposes important constraints on models.

Contents and objectives of the thesis

In the present thesis, I propose to evaluate how adult and juvenile movement affect the conservation and fisheries benefits of MPAs relative to larval dispersal, and whether and under what conditions targeted MPAs may be beneficial for the conservation of migratory fish populations and their fisheries.

Central to accurately assessing MPA effectiveness and deciding where to invest limited scientific resources when planning MPA networks is determining the relative importance of fish movement and larval dispersal for the dynamics of exploited fish populations in MPA networks. *Chapter 1* provides the first general, rigorous conceptualization of the impacts of fish movement within a home range on the effectiveness of MPA networks relative to those of diffusive larval dispersal. In order to carry out this conceptualization, a theoretical spatially-explicit metapopulation model was developed. A

single functional form was used for both fish movement and larval dispersal, providing a comparative platform for assessing which form of ecological connectivity has greater impact on population persistence and fisheries yields for different configurations of MPA networks. The consequences of fish movement versus larval dispersal on MPA effectiveness were investigated in presence or absence of fishery squeeze (i.e., concentration of fishing effort in areas outside MPAs so as to maintain total fishing effort constant) and/or movement of fishers to take advantage of spillover (i.e., fishing-the-line), so as to rigorously examine how economic connectivity affects the impacts of ecological connectivity on MPA effectiveness. This work was done in collaboration with D.M. Kaplan (Institute of Research for Development of Sète, France) and D. R. Hart (Northeast Fisheries Science Center, Woods Hole, USA), and was published in PLoS ONE in 2011.

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Our knowledge of the effectiveness of 'spawning aggregation-based MPAs' is currently limited, just as is the information available for most aggregation-forming reef fish populations, calling for the development of simple models to identify the conditions under which spawning area closures may be beneficial for the conservation of aggregative reef fish populations and their fisheries. In Chapter 2, a non-spatial per-recruit MPA model was designed, which was intended to be parsimonious and flexible in order to be applicable to a wide range of aggregation-forming populations. This model assesses the impacts of spawning aggregation-based MPAs on female spawning stock biomass-per-recruit (a proxy of fish reproductive capacity), yield-per-recruit and sex ratio. Alternative possible scenarios for the fidelity of fish to spawning aggregation sites and the fate the fishing effort that was in MPAs before they were closed were explored. The model was applied to populations of two species forming transient spawning aggregations in Seychelles: the brown-marbled grouper (Epinephelus fuscoguttatus) population of Farquhar Atoll, which is protogynous, and the shoemaker spinefoot rabbitfish (Siganus sutor) population of the main granitic islands, which is gonochoristic. This work was done in collaboration with D.M. Kaplan and J. Robinson (Seychelles Fishing Authority, Mahé, Seychelles), and was submitted for publication to Marine Ecology Progress Series on January 3, 2012.

Central to the dynamics of most stock assessment models is density-dependence during recruitment of larvae into the fish population. In the context of spatially-explicit MPA models, one issue is how to translate population-level stock-recruitment relationships into settler-recruit relationships ('SRRs') valid at the level of a single grid cell. A recent study demonstrated that the initial slope of local SRRs should be adjusted so as to correctly estimate population persistence, and proposed an analytical methodology to carry out the adjustment (White 2010). Unfortunately, this methodology cannot be used to evaluate small-scale SRRs for more complex spatially-explicit models, in particular when adults of the study population are mobile beyond simple home range movements. *Chapter 3* introduces a numerical methodology to estimate the initial slope of local SRRs and local maximum recruitment levels for complex spatially- and seasonally-explicit MPA models. Development of this methodology was necessary so as to be able to implement a complex spatially-explicit model for evaluating the potential effects of targeted MPAs for the South African Cape hake resource. This work was done in collaboration with D.M. Kaplan and C. Lett (Institute of Research for Development of Sète, France), and was submitted for publication to Fisheries Research on December 16, 2011.

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Because the spatio-temporal dynamics of migratory fish populations and their fisheries are usually complex, the impacts of targeted MPAs are likely to be much more complicated than predicted by simple patch models. Central to accurately predicting the conditions under which MPAs may reach their conservation and fisheries objectives is the improvement of the spatial and temporal structuring of MPA model dynamics, using the best available scientific knowledge. In *Chapter 4*, a complex spatially- and seasonally-explicit simulation model was developed to examine the potential conservation and fisheries effects of targeted MPAs designed for the South African population of deep-water Cape hake (Merluccius paradoxus). Two species with overlapping spatial distributions are considered: M. paradoxus and the shallow-water Cape hake, Merluccius capensis. These two species undertake ontogenetic migrations during their life cycle. The simulation model represents the dynamics of M. paradoxus and M. capensis within a spatial grid where hake-directed inshore and offshore trawl and longline fleets operate. Migration and larval connectivity matrices were estimated for this model using a GIS-based submodel and an individual-based biophysical submodel, respectively. Several MPA scenarios were examined to assess the impacts of MPAs targeting the older or younger sections of the *M. paradoxus* population on the SSB of *M. paradoxus* and *M. capensis* and the catches of the different hake-directed fleets. This work was done in collaboration with D.M. Kaplan, D.T. Fischer (USA), C.T.T. Edwards (Imperial College, London, UK), M. Smith (Capricorn Fisheries, Cape Town, South Africa), C. Lett, P. Verley (Institute of Research for Development of Sète, France) and L. Garavelli (Institute of Research for Development of Sète, France). It is to be submitted for publication in Marine Ecology Progress Series.



CHAPTER 1. Relative Impacts of Adult Movement, Larval Dispersal and Harvester Movement on the Effectiveness of Reserve Networks

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Abstract - Movement of individuals is a critical factor determining the effectiveness of reserve networks. Marine reserves have historically been used for the management of species that are sedentary as adults, and, therefore, larval dispersal has been a major focus of marinereserve research. The push to use marine reserves for managing pelagic and demersal species poses significant questions regarding their utility for highly-mobile species. Here, a simple conceptual metapopulation model is developed to provide a rigorous comparison of the functioning of reserve networks for populations with different admixtures of larval dispersal and adult movement in a home range. We find that adult movement produces significantly lower persistence than larval dispersal, all other factors being equal. Furthermore, redistribution of harvest effort previously in reserves to remaining fished areas ('fishery squeeze') and fishing along reserve borders ('fishing-the-line') considerably reduce persistence and harvests for populations mobile as adults, while they only marginally changes results for populations with dispersing larvae. Our results also indicate that adult home-range movement and larval dispersal are not simply additive processes, but rather that populations possessing both modes of movement have lower persistence than equivalent populations having the same amount of 'total movement' (sum of larval and adult movement spatial scales) in either larval dispersal or adult movement alone.

Keywords: marine reserves, larval dispersal, adult movement, per recruit egg production, population persistence, harvester behavior, fishery squeeze, modeling.

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INTRODUCTION

Spatial management of natural resources via the implementation of reserves has recently received significant attention in marine environments [1-3]. Movement of individuals among reserves and between reserves and surrounding unprotected areas is a major factor for determining population persistence in reserve networks [4-7]. Marine reserve implementation has historically concentrated on coastal environments, characterized by a larger proportion of populations with dispersing larvae and a relatively sedentary adult phase [8-10]. For this reason, considerable research effort has been directed towards the impact of larval dispersal on the functioning of marine reserve networks [4,11-13]. However, the large scale implementation of marine reserve networks [14-17] and, in particular, the increasing interest in using reserves for populations that possess considerable adult mobility [18-20] have pushed questions of persistence for populations with different levels and forms of mobility to the forefront [21,22]. The relative importance of larval dispersal versus adult movement for persistence and harvest of populations in the presence of reserve networks has not, to our knowledge, been rigorously examined in a comparative framework. In this paper, a simple conceptual metapopulation model is developed to compare the functioning of reserve networks for populations with different admixtures of larval dispersal and adult movement in a home range. Using populations that move exclusively in the larval phase, exclusively as adults or both, we develop analytic and numerical results to assess the relative impact of each on persistence and harvest, and to identify the driving forces underlying differences.

A number of modeling studies suggest that even relatively moderate adult spillover has a strong negative impact on reserve effectiveness in terms of persistence [23-26] and a positive impact on harvest under a relatively limited set of conditions [21,27-29]. Moffitt et al. [25] develop a spatially-explicit model to examine persistence and harvest of a population that has dispersing larvae and adults moving within a home range. They find that adult movement has a significant impact on persistence in reserve networks, often for movement spatial scales significantly smaller than the reserve size. In particular, 'network persistence' (i.e., persistence due to the collective impact of a network of reserves as opposed to that due to any single reserve) is significantly and rapidly reduced by adult movement. Moffitt et al. [25] also suggest that larval spillover has greater potential to improve harvest than adult spillover. Le Quesne and Codling[29] find the opposite using a model including harvester movement in response to prey density, but only the special cases of non-dispersing larvae and a uniform spatial distribution of larvae are considered.

While these results indicate the importance of adult movement for population dynamics in reserve networks, the underlying mechanisms driving differences in the effects of larval and adult connectivity and the generality of these effects have not been clearly identified. In this paper, we build on the approach of Moffitt *et al.*[25] by including a number of key modifications that provide a rigorous general conceptualization of the impacts of these different forms of connectivity on the conservation and harvest effects of marine reserves. A single functional form is used for both larval dispersal and adult movement, providing a comparative platform for evaluating which process has a greater impact on persistence and harvest. Analytic results identify the underlying mechanism behind differences between the two, as well as the universality of this mechanism. Furthermore, we examine in detail consequences of the movement of harvesters to take advantage of spillover and the redistribution of harvest effort previously in reserves to remaining non-reserves areas, both of which have been widely recognized as important for population dynamics and harvest in reserve networks[13,30-32]. In particular, harvester behavior potentially interacts differently with adult movement and larval dispersal because individuals that have spilled over are exposed to harvest at different points in their life history. Our results indicate that harvester movement changes not only quantitatively, but also qualitatively, differences in the impact of reserves on populations moving as adults versus as larvae.

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METHODS

We begin the development of our spatial metapopulation model by first considering a simple *non-spatial* population where each individual produces on average a certain number of eggs, b(f). Individual egg production is a function of life-history parameters and the instantaneous harvest rate, f. These eggs become larvae that experience intra-cohort, density-dependent interactions before entering the adult population. This population structure is represented by:

$$S_{t+1} = N_t \cdot b(f) N_{t+1} = s(S_{t+1})$$
(1)

where N_t is the number of adult individuals at time t, S_t is the number of pre-recruits (i.e., fish individuals that are prepared to recruit into the adult population, but have not yet done so; also referred to as 'settlers'), and the function s represents intra-cohort density-dependent processes that connect the number of pre-recruits with the final number of adult individuals. While directly applicable to semelparous populations that reproduce once before dying, this
population structure is commonly used in fisheries to represent age-structured populations at equilibrium [12]. In this latter case, b(f) represents the average egg production of a recruit over its lifetime, here referred to as the per recruit egg production, N represent the number of new recruits to the population, and t is a generational time step, as opposed to a physical unit of time.

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This population structure is adapted to spatially-distributed, sedentary populations with dispersing larvae through the introduction of a dispersal matrix [12]:

$$S_{t+1}(x) = \int_{t+1}^{t} N_t(y) b(f(y)) D_L(x, y) dy$$

$$N_{t+1}(x) = s(S_{t+1}(x))$$
(2)

where the dispersal function, $D_L(x,y)$, expresses the probability that larvae produced by adults at one location, y, will eventually settle in another location, x. Intra-cohort density-dependent mortality, represented by the function s, is applied to pre-recruits after they have arrived in their future adult habitat and, therefore, is only a function of the local number of settling larvae S. The function s does not explicitly depend on location, implying that settlement habitat is assumed of uniform quality over space. Note that the harvest rate, f, varies as a function of location due to the presence or absence of reserves.

In order to integrate the movement of adults in a home range in this model, we must first differentiate between two concepts of the harvest rate. The first is 'harvest rate', f(x), the rate of removals at location x, which depends on the distribution of harvesters. The second is the harvest rate experienced by fish individuals as a function of the center of their home range. If individuals move in a home range, then they may be caught away from the center of their home range, and therefore the biological consequences of this harvest will be felt elsewhere than the actual location of capture. This 'effective' harvest rate [24,25], $f_{eff}(x)$, of individuals whose home range is *centered* at a location, x, is given by:

$$f_{eff}(x) = \int D_A(y, x) f(y) dy$$
(3)

where $D_A(y,x)$ represents the probability that an individual whose home range is centered at x is found at a given moment at location y. This 'effective harvest rate' determines the biological dynamics of the system and is integrated into the model by replacing f with f_{eff} in Equation (2):

$$S_{t+1}(x) = \int_{t+1}^{t} N_t(y) b(f_{eff}(y)) D_L(x, y) dy$$

$$N_{t+1}(x) = s(S_{t+1}(x))$$
(4)

Equation (4) implicitly assumes that adult individuals produce their eggs at the center of their home range, as is the case for breeding sea birds and many terrestrial animals, but likely not the case for many mobile marine species (e.g., live-bearing sharks). Larval dispersal via the movement of adults would be included in the model in an identical fashion to other forms of larval dispersal (Equation (2)), and, therefore, is not separately addressed here. Nevertheless, this possibility is implicitly addressed by examining populations with different mixes of both larval dispersal and home-range movement.

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Harvest and the spatial (re)distribution of harvest effort

As with harvest rate, we can distinguish between two measures of the harvest at a location, one as perceived by harvesters, the other as perceived by biological populations. We assume that each recruit contributes on average a certain harvestable biomass over its lifetime, here referred to as the harvest-per-recruit h (also known as yield-per-recruit in the fisheries literature). The total harvest of the system is the product of harvest-per-recruit and the number of recruits to the system:

$$H_{total,t} = \int H_{eff,t}(x) dx = \int N_t(x) h(f_{eff}(x)) dx$$
(5)

where $H_{eff,t}(x)$, the effective harvest at a location, represents the biomass caught whose home-range center is at *x*. The actual biomass caught by harvesters at a given location, $H_t(x)$, is obtained from the effective harvest by inverting the adult home-range distribution:

$$H_{t}(x) = \int H_{eff,t}(y) \frac{f(x)D_{A}(x,y)}{f_{eff}(y)} dy$$
(6)

We consider two different scenarios for the spatial distribution of effort in the presence of reserves. For both scenarios, harvest effort, which is assumed proportional to the harvest mortality rate, f(x), is zero inside reserves. Outside reserves, effort can either be uniform (i.e., f(x)=f for all x not in a reserve), or the effort distribution can change in response to the expected harvests at a location. This latter effect is modeled using a gravity model [26]:

$$f_{t+1}(x) = f_{total} \frac{H_t(x)^{1/\gamma}}{\int H_t(y)^{1/\gamma} dy}$$
(7)

where f_{total} is the total harvest mortality integrated over all locations and γ is a measure of the difference among harvesters in perception of benefits of operating at a location. Small values of γ produce effort that is highly concentrated in areas of increased harvests.

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We also consider two different scenarios for the fate of effort that was in reserves before they were closed. Either this effort 'disappears' or it is fully redistributed to the remaining non-protected areas at the time of reserve creation (the 'fishery squeeze' assumption, [13,31]). Combining these two scenarios of harvest redistribution after reserve implementation with the two scenarios for the spatial distribution of harvest effort produces a total of four scenarios for the response of effort to reserve implementation, ranging from uniform effort distribution that diminishes after reserve creation in proportion to the amount of area in reserves, to total harvest effort that is conserved before and after reserve creation and effort that changes spatially in response to expected harvests. The last scenario evoked is the most likely to occur in the real world except in cases of extremely low mobility fisheries and/or simultaneous changes in conventional harvest management to reduce total harvest effort. However, uniform effort distribution and effort disappearance after reserve creation have generally been the norm in marine reserve modeling studies until relatively recently [21]. Furthermore, consideration of these two scenarios allows us to analyze the relative impacts of harvester movement on the effectiveness of reserve networks and to highlight the erroneous conclusions that could be made if 'fishery squeeze' and/or harvester behavior are ignored when they actually occur.

Model application

In order to gauge the sensitivity of model results to life-history traits of the populations modeled, we apply our spatial metapopulation model to three different life-history configurations, each of which is roughly modeled on a real population. It is important to emphasize that for each population only growth, reproduction and natural mortality parameters are modeled after the corresponding real population. Both larval dispersal and adult home-range movement are considered for each irrespective of the type and nature of connectivity in the real populations.

The three populations that serve as the basis for our model simulations are: U.S. canary rockfish (*Sebastes pinniger*) and skipjack (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) populations of the Atlantic Ocean. U.S. canary rockfish is a long-lived,

iteroparous fish population whose first reproduction occurs at approximately eight years old, 3 years after initial vulnerability to harvest [33], making the population particularly susceptible to overexploitation [34] and a target for management with reserves. Rockfish are often territorial and their movements are generally well represented by a home range [35,36]. Skipjack and yellowfin tunas of the Atlantic Ocean are relatively short-lived, iteroparous fish populations whose reproduction occurs, respectively, before and after age of first harvest [37]. Tuna movements are far more complex than a simple home range, including significant migratory behavior [38], though there is some precedent for representing their large-scale movements as diffusive [39,40] and some argue that over long time scales diffusive movements can be approximated as a home range [21,22]. Here we make *absolutely* no claim to be representing tuna movement. Rather we are using non-movement life-history parameters of these species so as to have three significantly different patterns of growth, mortality and reproduction to test sensitivity of model results to these non-movement parameters. So as to make clear that we are not attempting to model all aspects of the life-history of these species, we hereafter refer to canary rockfish, skipjack tuna and yellowfin tuna as the 'long-lived', 'harvest-first' and 'spawn-first' species, respectively.

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For the long-lived species, individuals are assumed here to recruit to the population at age 0 and to grow according to a von Bertalanffy growth function:

$$L = L_{\infty} \left(1 - e^{-kA} \right) \tag{8}$$

where A is the age of the individual, k is the Brody growth coefficient, and L_{∞} is the maximum length. For the other two species, empirical relationships from the literature are used to relate length to age (Appendix S1, [41,42]). For all three populations, biomass and reproductive capacity at a given age are assumed to be allometic functions of length (i.e., each is proportional to L^n for some exponent *n*). See Table 1 for a list of population parameter values, and Figures 1 and prior literature [12,43] for the per recruit egg production and harvest-per-recruit as a function of harvest rate.

Harvest mortality is gauged in this paper in terms of its effect on per recruit egg production. For all three species, a pre-reserve harvest mortality rate that reduces per recruit egg production to 25% of the unfished value is used. This value represents a heavily exploited species and is consistent with levels for several California rockfish species [44] A hockey-stick density-dependent recruitment relationship [45] is parameterized so that in the absence of reserves the population collapses (i.e., population size becomes too small to support a

fishery) when harvest mortality reduces the per recruit egg production below a certain value (hereafter referred to as the 'critical per recruit egg production') [46]. The value of this collapse point may range between 10 and 60% depending on the species [47]. A value of 35% is consistent with those found for several rockfish species [47] and will be used here when not explicitly varying this parameter. Given this collapse point, harvests are not sustainable in the absence of reserves. Qualitative aspects of our results are generic and not tied to the particular settler-recruit relationship or collapse point used. So as to be able to oppose the effects of adult movement to those of larval dispersal, we assume that the larval dispersal kernel and the adult home-range have identical functional forms. Reserves occur periodically along an infinite, one-dimensional space, and dispersal and home-range functions are given by a Laplacian distribution:

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$$D(x, y) = \frac{e^{-|x-y|/a}}{2a}$$
(9)

where *a* is the mean movement distance.

Parameter	Definition	Estimate	References
Long-lived species			
α	Allometric biomass parameter	3.03	[63,64] (estimate of α for a related species, <i>Sebastes alutus</i>)
β	Allometric reproductive-capacity parameter	4.1416	[33]
L_{∞} (cm)	Maximum length	53.4	[33]
k (year ⁻¹)	Brody growth coefficient	0.183	[33]
m (year ⁻¹)	Natural mortality rate	0.06	[33]
A _F (years)	Age of first harvest	5	[33]
A ₅₀ (years)	Age of first reproduction	8	[33]
Harvest-first species			
α	Allometric biomass parameter	2.976	[65]
β	Allometric reproductive-capacity parameter	2.9861	[66] (estimate of β for the yellowfin tuna population of the Indian Ocean)
m (year ⁻¹)	Natural mortality rate	0.6	[67]
A _F (years)	Age of first harvest	0.28	[68]
A ₅₀ (years)	Age of first reproduction	2.63	[37]
Spawn-first species			
α	Allometric biomass parameter	3.253	[69]
β	Allometric reproductive-capacity parameter	2.5704	[70]
m (year ⁻¹)	Natural mortality rate	0.8	[71]
A _F (years)	Age of first harvest	2.13	[68]
A ₅₀ (years)	Age of first reproduction	2.08	[37]

Table 1. Non-movement parameter estimates for the long-lived (canary rockfish - Sebastes pinniger), harvest-first (yellowfin tuna - Thunnus albacares) and spawn-first (skipjack tuna - Katsuwonus pelamis) species.



Figure 1. Fraction of lifetime egg production (FLEP, i.e., per recruit egg production / natural per recruit egg production) ((**a**)) and harvest-per-recruit over maximum harvest-per-recruit (h/h_{max}) in function of harvest mortality over fishing mortality ((**b**)) when lifetime egg production is at 25% of its unfished value (f/f_{25}) for the three species studied in the present study. The dashed lines represent the harvest mortality above which the studied species collapse in the absence of reserves (i.e., the harvest mortality for which lifetime egg production is at 35% of its unfished value in the context of this paper).

RESULTS

Before proceeding to numerical evaluation of the model, we begin with some general analytic results that provide insights into how larval dispersal and adult movement affect persistence. Consider first the system immediately after reserve creation, so that adult density and harvest effort are still uniform over space. For populations with only larval dispersal, the number of settlers arriving at a given location at the next time step is:

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$$S_{t+1}(x) = N_t [b(0)(1 - \nu_L(x)) + b(f)\nu_L(x)]$$
(10)

where *f* is the harvest rate outside protected areas after reserve implementation and $v_L(x)$ is the fraction of larvae arriving at *x* from fished areas Ω_F :

$$\nu_L(x) = \int_{\Omega_F} D_L(x, y) dy \tag{11}$$

If we now consider the same system with only adult home-range movement, the number of settlers becomes:

$$S_{t+1}(x) = N_t b(f \nu_A(x) + 0(1 - \nu_A(x))) = N_t b(f \nu_A(x))$$
(12)

where $v_A(x)$ is the fraction of time an individual centered at x spends in fished areas Ω_F :

$$\nu_A(x) = \int_{\Omega_F} D_A(y, x) dy$$
(13)

Assuming that the larval dispersal and adult movement distributions are the same, symmetric around *x* and uniform over space (as is the case for the Laplacian distribution in Equation (9)), Equations (10) and (12) are similar except that larval dispersal linearly mixes egg production inside and outside reserves, whereas adult home-range movement linearly mixes the harvest rate inside and outside reserves. As the relationship between harvest rate and per recruit egg production is decreasing and convex (see proof in Appendix S2), the number of eggs produced in the adult movement case will necessarily be lower than in the larval dispersal case by Jensen's inequality (Figure 2), suggesting that final equilibrium persistence will also be lower for adult movement.



Harvest Mortality

Figure 2. Per recruit egg production as a function of harvest mortality rate for the long-lived species (dasheddotted curve). Immediately after reserve implementation, changing the fraction of habitat in reserves moves the average reproductive capacity on the full curve for a population with dispersing larvae and sedentary adults. For a population with adults moving within a home range and non-dispersing larvae, changing the fraction in reserves moves the reproductive capacity on the dashed-dotted curve. Consequently, when lifetime egg production is a decreasing, convex function of harvest mortality, adult movement leads to lower egg production immediately after reserve implementation than larval dispersal. Per recruit egg production functions are, respectively, more and less convex for the harvest-first and spawn-first species, but similar qualitative results are obtained for these species.

Next consider the limiting cases of large dispersal distance or home-range size (or equivalently, very small reserves). In this limit, $v_L = v_A = 1 - C$, where *C* is the fraction of habitat in reserves, and settlement is uniform over space so that global persistence is guaranteed if the number of settlers in Equations (10) and (12) exceeds the fraction of natural settlement necessary to avoid collapse (e.g., 35%). As we have just shown that the number of eggs produced will be greater for larval dispersal than adult movement, persistence of these populations will occur at lower closure fractions for the larval dispersal case than for the adult movement case. For larval dispersal, persistence occurs if [12]:

$$C_{L} \ge \frac{b(f_{c}) - b(f)}{b(0) - b(f)}$$
(14)

where f_c is the harvest rate that reduces per recruit egg production to the critical level in the absence of reserves. For adult movement one finds:

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$$C_A \ge \frac{f - f_c}{f} \tag{15}$$

The same fraction of habitat in reserves is required for the two cases only if reproductive capacity is a linear function of harvest rate (e.g., ${}^{b(f)}/{}_{b(0)} = 1 - f$). For more realistic scenarios (i.e., decreasing, convex functions), more habitat is required in reserves for adult movement than for larval dispersal. For example, for the long-lived species with 25% natural per recruit egg production remaining in fished areas, persistence for large dispersal distances occurs if greater than 13% of habitat is in reserves, whereas for large home ranges persistence requires at least 31% in reserves.

Consider these results for the case when harvest effort redistributes uniformly in nonprotected areas after reserve implementation (i.e., 'fishery squeeze' occurs). In such a system the harvest mortality rate in non-protected areas is:

$$f = \frac{f_0}{1 - C} \tag{16}$$

where f_0 is the pre-reserve harvest rate [13,27]. Replacing f by $\frac{f_0}{1-C}$ in Equation (14) logically yields that persistence in the larval dispersal case requires more habitat area in reserves when fishery squeeze is considered. However, even with effort redistribution, there is always a value of C < 1 for which persistence occurs. For example, for the long-lived species, persistence for large larval dispersal distances occurs if at least 19% of habitat is in reserves versus 13% when fishery squeeze is ignored. Replacing f by $\frac{f_0}{1-C}$ in Equation (15), it follows after simplification that for large home-range sizes, persistence requires that:

$$(1-C)f_0 \le (1-C)f_c$$
 (17)

Since $C \le 1$, persistence is ensured if and only if $f_0 < f_c$. Hence, no fraction of habitat in reserves (<1) will cause persistence if the pre-reserve harvest rate is greater than the collapse point (vertical axes of Figures 3d-f).

Analytic results can be found for persistence for arbitrary reserve widths and fractions in reserves for both the larval dispersal [12,48] and adult movement cases. Whereas in the larval dispersal case, persistence is a complex function of the connectivity between reserve and non-reserve areas [48], in the adult movement case, subpopulations are not connected through dispersal and, therefore, global persistence is guaranteed whenever there is at least one location where $f_{eff} < f_c$. As reserve centers are the locations of the system where persistence is most likely, whether the population of interest will ultimately be persistent can be determined by evaluating if $f_{eff} < f_c$ at reserve centers (Appendix S3). For all species lifehistories examined, persistence requires considerably larger total fraction in reserves and/or larger individual reserves for a given home range than for an equivalent larval dispersal distance (Figures 3a-c), particularly in the limit of large dispersal distances or home-ranges discussed above (along vertical axes in Figures. 3). Perhaps most importantly, if fishery squeeze occurs (Figures 3d-f), patterns of persistence are qualitatively different for the larval dispersal case than the adult home-range case, with the latter requiring large reserve widths and, paradoxically, small fractions of habitat in reserves.



Figure 3. Border between persistence and collapse in the adult movement case (black curves) versus the larval dispersal case (grey curves) as a function of reserve width (in units of the dispersal distance or home-range size) and fraction of habitat in reserves. In all cases, collapse occurs for very small reserves covering a small fraction of habitat (lower, left corner of panels). Harvest effort is uniformly distributed outside reserves. (**a,d**) are for the long-lived species, (**b,e**) for the harvest-first species and (**c,f**) for the spawn-first species. For (**a,b,c**), it is assumed that the effort that had previously been in the reserves disappears at the time of reserve creation, while for (**d,e,f**) it is assumed that the total effort does not change before and after reserve creation. Per recruit egg production is 25% of its unfished value in harvested areas, and three different values of the critical per recruit egg production below which collapse occurs in the absence of reserves are shown (27, 35 and 45% of the natural per recruit egg production).

In the limit of a single isolated reserve (along the horizontal axes in Figures 3), differences are also significant, except for when the value of per recruit egg production in fished areas is close to the critical per recruit egg production (e.g., 25 and 27% of the unfished per recruit egg production, respectively). Examining in more detail the limit of a single isolated reserve (Appendix S3 and Figures 4), one finds that minimum reserve widths for persistence are generally smaller for larval dispersal than adult movement for realistic values of the critical per recruit egg production (i.e., 0.1-0.6), but can be larger for high critical values and/or per recruit egg production in harvested areas close to the critical value (Figure 4c).

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Patterns of persistence in reserve networks are qualitatively similar for the three species studied. There are somewhat more reserve configurations leading to persistence for the harvest-first species than for the two other species (Figures 3b and e), and slightly fewer for the spawn-first species than for the two other species (Figures 3c and f). These quantitative differences are tied to the functional dependence of reproductive capacity of each species on harvest mortality rate (Figures 1a and 2).



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Figure 4. Minimum reserve width (in units of the dispersal distance or home-range size) required for persistence of an isolated reserve as a function of critical per recruit egg production and per recruit egg production in harvested areas for the long-lived species. (a) is for larval dispersal alone, (b) is for adult movement alone, and (c) gives the ratio of these two quantities, with values greater than one indicating larger reserves are needed to ensure persistence for the larval dispersal case than for adult movement. Here harvest effort is assumed uniformly distributed outside reserves and the effort that had previously been in the reserves disappears at the time of reserve creation. Note that similar qualitative results are obtained for the harvest-first and spawn-first species.

Persistence and harvest for different scenarios of harvester movement

Numerical model evaluation is required to examine patterns of persistence when harvest effort is non uniform outside reserves and to obtain total harvest levels. Given the qualitative similarities in patterns of persistence (Figures 3) between the three species studied, we focus on the results for the long-lived species (Figures 5), for which patterns of persistence appear to be intermediate between those of the two other species. Results for the other species showed only relatively minor quantitative differences (Figures 6).

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Non-uniform harvest effort in response to expected harvests at each location reduces the set of reserve network configurations that produce persistent populations for both the case of exclusive larval dispersal and that of exclusive adult movement in a home range (Figures 5c-d). Nevertheless, the reductions in persistence are considerably more drastic for adult movement. For the larval dispersal case, spatial heterogeneity in recruitment is capped by the density-dependent settler-recruit relationship (Figure 7a). This limits the extent of effort concentration in areas along reserve borders (Figure 7c) and therefore only marginally changes persistence. For the adult movement case, there is no cap in our model on the number of individuals using a particular location as part of their home range. Furthermore, harvests along reserve edges are driven by the spillover of individuals from reserves, and therefore effort concentration continues even after the locally resident population becomes overexploited and collapses (Figs. 7b, d and e). In the worst of cases, this produces serial collapse of the areas surrounding reserves and eventually the collapse of the entire population.

In the absence of fishery squeeze, patterns of persistence and harvest are qualitatively similar for larval dispersal and adult movement. At small fractions of habitat in reserves (bottom half of Figures 5a-d), harvests are relatively insensitive to reserve width so long as reserves are of sufficient size to ensure persistence [46] and harvest increases with fraction of habitat in reserves. As noted by Moffitt et al. [25], harvests for a given small fraction of total habitat in reserves are considerably greater for the larval dispersal case than the adult movement case. Nevertheless, for both cases maximum harvests occur when the fraction of habitat in reserves is sufficient to ensure persistence for all reserve widths (i.e., network persistence occurs, top half of Figures 5a-d). In this case, maximum harvests occur for a network of many small reserves that cover just enough habitat to produce network persistence (i.e., along vertical axes of Figures 5a-d just above the area of non-persistence) [49,50]. Maximum harvests are higher for the adult movement case, though differences are slight and most likely driven by the particulars of the functional relationship between harvest rate and harvest-per-recruit (Figure 1b). More importantly, high harvests are produced for a larger set of reserve configurations for adult movement than larval dispersal, though at greater overall fraction of habitat in reserves.

When fishery squeeze is included (Figures 5e-h and 6a-b), both persistence and harvest are qualitatively different for the adult movement than for larval dispersal. For the adult movement case, persistence requires reserves at least as large as the home range, and maximum harvests are lower than in the absence of fishery squeeze (e.g., ~30-40% for the long-lived species and ~35-45% for the spawn-first species). Furthermore, maximum harvests for the adult movement case occur at fractions in reserves approaching one and for reserves widths several times the home-range size (e.g., ~4-7 times for all species). Le Quesne and Codling [29] also found maximum harvests require large reserve fractions, though their maximal harvests were higher for adult movement than larval dispersal. This discrepancy is due principally to their use of lower pre-reserve harvest rates, though a precise comparison is difficult due to differences in model formulation.



Figure 5. Equilibrium harvest as a function of reserve width (in units of the dispersal distance or home-range size) and fraction of habitat in reserves for the long-lived species. Panels to the left are for populations with sedentary adults and dispersing larvae, while panels to the right are for populations with mobile adults and non-dispersing larvae. For (**a**,**b**,**c**,**d**), it is assumed that the effort that had previously been in the reserves disappears at the time of reserve creation, while for (**e**,**f**,**g**,**h**) it is assumed that the total effort does not change before and after reserve creation. For (**a**,**b**,**e**,**f**), harvest effort distribution is uniform outside reserves, while for (**c**,**d**,**g**,**h**), it depends on local expected harvests and the value of γ is 1.2. The light grey area represents reserve configurations leading to a collapsed population and for (**b**,**c**,**d**,**e**,**f**,**g**,**h**) the dash-dotted grey line represents the border between persistence and collapse when harvester behavior and effort redistribution after reserve creation are ignored.



Figure 6. Equilibrium harvest as a function of reserve width (in units of home-range size) and fraction of habitat in reserves for populations with mobile adults and non-dispersing larvae. (a) is for the harvest-first species and (b) for the spawn-first species. Here it is assumed that the total effort does not change before and after reserve creation and that harvest effort distribution depends on local expected harvests, and the value of γ is 1.2. The light grey area represents reserve configurations leading to a collapsed population the grey line represents the border between persistence and collapse when harvester behavior and effort redistribution after reserve creation are both ignored. Harvest values shown are relative to the maximum value for the adult movement case when harvester behavior and effort redistribution after reserve creation are ignored.



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Figure 7. Spatial patterns of (**a**,**b**) recruitment, (**c**,**d**) real harvest mortality rate (*f*), and (**e**) effective harvest mortality rate (f_{eff}) for a system of periodically-spaced, uniformly-sized reserves (grey areas) at equilibrium for the long-lived species. (**a**,**c**) are for populations possessing only larval dispersal, whereas (**b**,**d**,**e**) are for populations that only have adult movement in a home range. The effective mortality rate is not shown for the larval dispersal case as it is identical to the real harvest mortality rate. Harvest effort is uniform outside reserves for red curves. For the green and blue curves, the harvest effort distribution in the non-protected areas depends on local expected harvests, with the value of γ being 1.2 for green curves and 2.4 for blue curves. The units of recruitment are arbitrary, but consistent between simulations. The dashed black line on

(c) and (d) represents the harvest mortality rate above which the population collapses in the absence of reserves.

Persistence with both adult movement and larval dispersal

As larval dispersal and adult movement often occur together, we examine their combined effects by comparing populations with varying levels of both processes. For simplicity, we consider only uniform effort distribution outside reserves. Populations are characterized by a total movement spatial scale given by the larval dispersal distance plus the adult home-range size. The adult home-range represents different fractions of this total movement scale, ranging from no adult movement (fraction of zero) to all adult movement (fraction of one).

Persistence occurs for fewer reserve configurations when larval dispersal and adult movement are combined (but each having a smaller spatial scale) than for exclusively one or the other process (Figures 8), rather than being intermediate between results for larval and adult cases, as might have been expected. At small reserve sizes (towards the left of Figures 8), the closure fraction necessary for persistence is the same for all cases but that of no adult movement. In this limit, any home-range size other than zero is always greater than the reserve size and persistence is driven by adult movement (Equation 15) irrespective of the amount of larval dispersal. This explains the rapid decrease in 'network persistence' when adults movement is added to a population with larval dispersal noted by Moffitt *et al.* [25]. For a single isolated reserve (horizontal axes in Figures 8), persistence requires larger reserves for most mixtures of adult and larval movement than for adult movement alone, except for rather small fractions in adult movement (< 20% of the total movement scale).



Figure 8. Border between persistence and collapse as a function of reserve width (in units of the 'total movement scale') and the fraction of habitat in reserves for the long-lived species. The 'total movement scale' is the sum of the larval dispersal distance and the adult home-range size. Blue to red curves are for different fractions of the total movement scale in adult home-range movement, ranging from larval dispersal only (0) to adult home-range movement only (1). In all cases, harvest effort is uniform outside reserves. In (**a**), there is no harvest effort redistribution after reserve creation, whereas in (**b**) total harvest effort is conserved before and after reserve implementation. Per recruit egg production is 25% of its unfished value in harvested areas.

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DISCUSSION

Our results indicate that persistence of a population whose adults move within a home range requires significantly more area in reserves and/or larger reserves than for an equivalent population with larvae dispersing over the same spatial scale. Results are more pronounced for species beginning reproduction before first harvest ('spawn-first' species) since their reproductive capacity is more sensitive to harvest rate, though differences are relatively slight over the range of growth and reproduction configurations examined. The differences between adult movement and larval dispersal are accentuated when harvester movement is taken into account, producing patterns of persistence and harvest that are qualitatively different for the two movement processes. For example, even if harvest effort formerly in reserve areas is redistributed into non-reserve areas (i.e., 'fishery squeeze') and harvest effort concentrates spatially in response to increased prey densities near reserve edges (i.e., 'fishing-the-line'), persistence of sedentary populations with dispersing larvae can always be achieved by creating either a single large reserve or placing more than a critical fraction of habitat in reserves (the latter being referred to as 'network persistence') (Figure 5g). For populations with mobile adults, persistence cannot be achieved solely by increasing the percentage in reserves, but rather requires individual reserve size be several times the adult home-range (e.g., >2 times for 50% in reserves in Figure 5h, for the long-lived species). Furthermore, though maximum harvests are roughly equivalent for the two movement types without fishery squeeze, they are considerably lower (e.g., ~30-45% for the three species we considered) for populations with mobile adults when harvest effort redistribution is included, and require large fractions of habitat in reserves, producing extreme levels of harvest effort concentration. As harvester movement to areas of higher expected harvest and 'fishery squeeze' are likely to occur in the real world, our results highlight that ignoring harvester movement when it actually occurs can lead to dangerous overestimation of persistence in reserve networks.

The underlying cause of these differences in persistence for larval dispersal versus adult movement is more subtle than it might appear. One could assume that it is due to the fact that adult movement operates over the entire lifespan of an individual, whereas larval dispersal generally represents a small fraction of the lifespan. However, larvae dispersing outside of reserves are subject to harvest their entire lifetime, potentially having a greater negative effect on persistence. Which process is more detrimental is fundamentally linked to the results in Equations (10) and (12). Larval dispersal has the effect of averaging over egg production inside and outside reserves, whereas adult movement averages over harvest rate.

As the relationship between harvest rate and reproductive capacity is convex, averaging over harvest rate is more detrimental. In biological terms, this is saying that persistence is better if some fraction of individuals are protected over their entire lifespan than if all individuals are protected a fraction of the time. As such, the result that adult movement is more detrimental for persistence than larval dispersal is general to all age-structured populations. Changes to model assumptions (such as, e.g., the type of density-dependent recruitment) are unlikely to alter this overall trend.

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The results presented here include two aspects that appear at first glance paradoxical. The first is that fishery squeeze combined with adult mobility produces scenarios where no network of small reserves, no matter how dense, will lead to persistence and increasing the density of reserves can lead to collapse of networks that would have been persistent if the effort that was in closed areas had disappeared at the time of reserve creation. Effort redistribution, which will likely occur in the absence of effort restrictions or low harvester mobility, increases the harvest rate outside reserves as the fraction in reserves increases. With adult movement, as the fraction in reserves increases, fish spend more time inside protected areas but are also more likely to be harvested outside reserves due to increased fishing pressure . This leads to a net increase in effective harvest rate, even inside reserves, impeding persistence for networks of small reserves and eventually collapsing networks of larger reserves. This also explains the low maximum harvests for mobile adults with fishery squeeze because persistence is achieved by creating reserves of sufficient size that some individuals are inaccessible to harvest. These results highlight once more the need to effectively control harvest effort in non-protected areas for reserve implementation to be successful [8,27,51].

The second paradoxical result is that when both types of movement are present in the same population, persistence results are often worse than those for a population possessing just one of the two processes, even if the 'total movement scale' (the sum of larval dispersal distance and adult home-range size) is the same (Figures 8). The likely explanation for this is that larval dispersal reduces self-recruitment needed for persistence inside reserves at the same time that adult movement reduces the lifetime reproductive capacity of individuals recruiting to reserves. For populations whose larvae are indirectly dispersed through adult movement, such as some live-bearing sharks or species that do not separate feeding and reproductive habitats, these two movement processes are inevitably coupled and persistence will be negatively impacted.

These results have important consequences for spatial conservation efforts targeting mobile species. Larval dispersal has been a major focus of marine-reserve research, with significant effort being devoted to estimating larval dispersal scales [21,52,53], whereas adult movement has received less attention because many coastal species are sedentary and it is felt that long-distance larval dispersal is the dominant process affecting marine reserves. While the attention devoted to larval dispersal is by no means misplaced, the results here suggest that adult movement cannot be ignored in many cases. Home-range sizes of order 1-10 km cited for many California rockfish species [26,35], for example, may be significant in terms of their effects on persistence for reserves that are often the same order of magnitude in size [25], particularly when the distribution and amount of harvest effort is not controlled.

Furthermore, conservationists and researchers have recently proposed using reserves for managing highly-mobile pelagic (e.g., tunas) and demersal (e.g., hakes) species [18-20]. These species undertake complex nomadic and migratory movements over hundreds to thousands of kilometers on monthly timescales [38,54,55]. Proposed solutions to creating effective reserve networks for these species include static or dynamic reserves that target certain sectors of spatially-structured populations (e.g., juveniles or spawners) [18,22]. Though we have by no means examined the rather complex set of spatial migrations that may produce the spatial structure necessary for such 'targeted' approaches and marine reserve models indicate significant sensitivity of results to the precise temporal and spatial nature of movements [22,29,56], it is reasonable to assume that these results set a fairly high bar for the effective use of such approaches. Even relatively limited movement of individuals outside of pelagic reserves may significantly decrease reserve effectiveness, particularly if harvesters specifically target spillover (Figures 5d and h and 6a-b).

Despite these results, there is some evidence that marine reserves benefit mobile species [57-59]. These positive results have often been sources of new insights regarding the behavior of marine organisms and the interaction between behavior and conservation. For example, if habitat regeneration occurs inside reserves (e.g., through increased prey density), then residency time inside reserves may increase, thereby improving the value of reserves for mobile species. There are at least two cases where this is thought to have occurred involving emperor penguins in South Africa [58] and snappers in New Zealand [60]. Furthermore, it is now recognized that many mobile marine species possess specific subpopulations that are relatively sedentary (referred to as 'behavioral polymorphism') [22,61]. Our results indicate that reserves may only protect these sedentary subpopulations, raising the possibility of strong

selection for sedentarism [62]. It is our hope that the results presented in this paper will serve as a baseline for predicting responses of mobile species to reserve implementation and identifying when non-trivial species behaviors alter these predictions.

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SUPPORTING INFORMATION

Appendix S1. Length-at-age relationships for yellowfin (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) populations of the Atlantic Ocean.

Gascuel *et al.* [1] established for yellowfin tuna population of the Atlantic Ocean that length (*L*) can be predicted from the relationship:

$$L(A) = 37.8 + 8.93A + (137 - 8.93A)(1 - e^{-0.808A})^{7.49}$$
(S1.1)

where *A* is the age in years.

Hallier and Gaertner [2] established the following length-at-age relationship for skipjack tuna population of the Atlantic Ocean:

$$L(A) = 97.258 \left(1 - e^{-0.251A}\right) \tag{S1.2}$$

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It will be assumed for simplicity that harvest mortality rate f and natural mortality rate m are constant with age, though this assumption is not essential to the argument. The per recruit egg production function b is given by:

$$b(f) = \int_{A0}^{\infty} e^{-(m+f)A} w(A) dA$$
 (S2.1)

where w(A) dA is the (expected) egg production of a recruit between ages A and A + dA. Differentiating with respect to f yields:

$$b'(f) = -\int_{A0}^{\infty} A e^{-(m+f)A} w(A) dA$$
 (S2.2)

and

$$b''(f) = \int_{A0}^{\infty} A^2 e^{-(m+f)A} w(A) dA$$
 (S2.3)

Since the integrands are always positive, b'(f) < 0 and b''(f) > 0, i.e., b is decreasing and convex.

Appendix S3. Border between persistence and collapse when harvest effort is uniformly distributed outside reserves.

Previous studies [1,2] demonstrated that, for a population with sedentary adults and larvae dispersing over finite distances, the border between persistence and collapse is:

$$0 = \left(\frac{1}{c^{2}} - c^{2}\right) \sinh\left(\frac{G}{c}\frac{(s-w)}{a}\right) \sin\left(Gc\frac{w}{a}\right) + 2\left[\cosh\left(\frac{G}{c}\frac{(s-w)}{a}\right)\cos\left(Gc\frac{w}{a}\right) - 1\right]$$
(S3.1)

with:

$$c = \left(\frac{b(0) - b(f_c)}{b(f_c) - b(f)}\right)^{\frac{1}{4}}$$
(S3.2)

and

$$G = \left[\frac{(b(0) - b(f_c))(b(f_c) - b(f))}{b(f_c)^2}\right]^{\frac{1}{4}}$$
(S3.3)

where *b* is the per recruit egg production *f* the instantaneous harvest rate, f_c the harvest rate that reduces per recruit egg production to 35% of its unfished value in the absence of reserves, *m* the natural mortality rate, *a* the mean larval dispersal distance, *s* the spacing between reserves and *w* the width of a reserve.

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In the limit of a single isolated reserve (i.e., in the limit $s \rightarrow \infty$) when the width of a reserve and the mean larval dispersal distance remain finite, the border between persistence and collapse in the larval dispersal case becomes:

$$0 = \left(\frac{1}{c^2} - c^2\right) \sin\left(Gc\frac{w}{a}\right) + 2\cos\left(Gc\frac{w}{a}\right)$$
(S3.4)

In this limit, the width of a reserve over the mean larval dispersal distance can be expressed as:

$$\frac{w}{a} = \frac{1}{Gc} \tan^{-1} \left(\frac{2c^2}{c^4 - 1} \right)$$
(S3.5)

In the case of mobile adults and non-dispersing larvae, when adult home range is finite, there is population collapse when collapse occurs in all the locations, i.e., when $f_{eff} \ge f_c$ in all locations (f_{eff} is the effective harvest mortality rate experienced by mobile adult individuals). In other words, persistence is guaranteed when there is at least one location where $f_{eff} < f_c$. As reserves centers are the locations of the system where persistence is most likely, whether the population of interest will ultimately be persistent can be determined by evaluating if $f_{eff} < f_c$ there, i.e., $f_{eff} \left(x = \frac{w}{2} \right) < f_c$. Therefore, the border between persistence and collapse in the adult movement case when home range is finite is:

$$[[1]] = \nu \binom{w}{2} f - f_c = 0$$
(S3.6)

It then comes that:

$$\begin{split} & [[1]] = f \int_{\Omega_F} D_A(y, \frac{w}{2}) dy - f_c \\ &= \frac{f}{2a} \int_{-\infty}^{+\infty} e^{-|y - \frac{w}{2}|/a} dy - f_c \\ &= \frac{f}{2a} \sum_{-\infty}^{+\infty} \int_{ks+w}^{ks+s} e^{-|y - \frac{w}{2}|/a} dy - f_c \forall k \in \mathbb{Z} \end{split}$$
(S3.7)

where a is here the mean distance travelled from home range center.

After making a change of coordinate from y to $y - \frac{w}{2}$, [[1]] becomes:

$$[[1]] = \frac{f}{2a} \sum_{-\infty}^{+\infty} \int_{ks+\frac{w}{2}}^{ks+s-\frac{w}{2}} e^{-|y|/a} dy - f_c \,\forall k \in \mathbb{Z}$$
(S3.8)

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Splitting the sum into integrals over positive and negative values and switching y with -y in the negative integrals, [[1]] becomes:

$$\llbracket 1 \rrbracket = \frac{f}{2a} \Biggl[\sum_{1}^{\infty} \int_{ks+\frac{w}{2}}^{ks+s-\frac{w}{2}} e^{-y/a} dy + \sum_{0}^{\infty} \int_{ks+\frac{w}{2}}^{ks+s-\frac{w}{2}} dy \Biggr] - f_c \forall k \in \mathbb{Z}$$
(S3.9)

The two integrals are readily evaluated:

$$\llbracket 1 \rrbracket = \frac{f}{2} \left[e^{-\frac{w}{2a}} - e^{-\frac{(s-\frac{w}{2})}{a}} \right] \sum_{0}^{\infty} e^{-\frac{(k+1)s}{a}} + \frac{f}{2} \left[e^{-\frac{w}{2a}} - e^{-\frac{(s-\frac{w}{2})}{a}} \right] \sum_{0}^{\infty} e^{-\frac{ks}{a}} - f_c \forall k \in \mathbb{Z}$$
(S3.10)

Using the identity $\sum_{0}^{\infty} x^{\alpha} = (1 - x)^{-1} \forall 0 < x < 1$, it finally comes that the border between

persistence and collapse in the adult movement case when home range is finite is:

$$0 = f \frac{e^{-\frac{w}{2a}} \left(1 - e^{-\frac{(s-w)}{a}}\right)}{1 - e^{-\frac{s}{a}}} - f_c$$
(S3.11)

In the limit of a single isolated reserve (i.e., in the limit $s \rightarrow \infty$) when the width of a reserve and the mean distance travelled from home range center remain finite, the border between persistence and collapse in the adult movement case becomes:

$$0 = f e^{-w/_{2a}} - f_c \tag{S3.12}$$

In this limit, the width of a reserve over the mean distance travelled from home range center can be expressed as:

$$\frac{w}{a} = 2\log\left(\frac{f}{f_c}\right) \tag{S3.13}$$

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CHAPTER 2. Evaluation of the effectiveness of marine protected areas for transient spawning aggregations in data-limited situations

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Abstract - Numerous coral reef fish species form predictable, short-lived spawning aggregations. Many of these aggregations are overfished, making them a target for management with marine protected areas (MPAs). Here we develop a parsimonious model for evaluating the impacts of no-take MPAs protecting transient spawning aggregations on spawning stock biomass-per-recruit, yield-per-recruit and sex ratio. The model requires limited data on fish life history and exploitation patterns and, therefore, can be applied to a wide variety of aggregation-forming species in data-limited situations. Applying the model to a protogynous grouper population and a gonochoristic rabbitfish population from Seychelles, we find that spawning aggregation-based MPAs are generally effective at improving spawning stock-biomass-per-recruit and reducing sex ratio bias whatever the degree of fish spawning-site fidelity and the fate of fishing effort formerly in MPAs. Nonetheless, when fish of the protogynous population are faithful to spawning sites and fishing effort is redistributed at the time of MPA creation, sex ratio of the fished subpopulation may be considerably biased, thereby potentially impairing population-wide egg fertilization rates unless a significant fraction of spawning sites is protected. Increase in yield-per-recruit with spawning aggregation-based MPAs did not occur. However, long-term yield increases may occur in populations that are recruitment limited by means of recruitment subsidy due to increased spawning stock biomass if a significant fraction of spawning sites is protected. Model results also demonstrated the sensitivity of sex ratio in protogynous populations to numerous lifehistory traits. Improved understanding of the mechanisms driving sex change is essential to accurately predicting MPA effects.

Keywords: Transient spawning aggregations; marine protected areas (MPAs); coral reef fish; modeling; marine conservation; fisheries management; protogynous hermaphroditism.
INTRODUCTION

Numerous coral reef fish species migrate to form spawning aggregations at sites located a few to hundreds of kilometers from their normal area of residence (Domeier & Colin 1997). These 'transient' spawning aggregations are often highly vulnerable to fishing due to their spatial and temporal predictability and to the large increase in catchability that may occur when fish aggregate (Sadovy & Domeier 2005). High levels of fishing effort can lead to rapid depletion of transient spawning aggregations (e.g., Colin 1992, Sala et al. 2001, Hamilton & Matawai 2006). Protogynous species (i.e., species that mature first as females and then change sex to males) may also experience reductions in egg fertilization rates due to declines in the relative number of males (e.g., Coleman et al. 1996, Koenig et al. 1996, Armsworth 2001). Many transient spawning aggregations are currently declining in size while others have collapsed and no longer form due to fishing (e.g., Sadovy & Eklund 1999, Aguilar-Perera 2007, Sadovy et al. 2008). Management measures are therefore urgently needed to ensure the persistence of transient spawning aggregations, the populations from which they form, and the long-term viability of the fisheries depending on them (Domeier et al. 2002, Sadovy & Domeier 2005). A range of management tools have been proposed and/or applied for the protection of spawning aggregations, of which marine protected areas (MPAs, hereafter also referred to as 'marine reserves'), zones where fishing and other human extractive activities are restricted, are a commonly applied measure (Rhodes & Warren-Rhodes 2005, Sadovy et al. 2008).

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'Spawning aggregation-based MPAs' seem at first glance a promising management tool. Moderately to highly mobile species can be protected for part of the year by the establishment of relatively small closures (Domeier et al. 2002, Grüss et al. 2011a). Furthermore, closing spawning sites to fishing may preserve older, larger individuals that contribute disproportionately to larval production via maternal age effects, potentially enhancing recruitment success and, eventually, fisheries yield (Berkeley et al. 2004, Birkeland & Dayton 2005). Relatively few empirical studies on the effects of spawning aggregationbased MPAs currently exist. Burton et al. (2005) reported increased aggregation size for mutton snapper (*Lutjanus analis*) only two years after the establishment of a spawning aggregation-based MPA. The closure of a spawning aggregation site for a protogynous red hind (*Epinephelus guttatus*) population off St. Thomas Island (U.S. Virgin Islands) resulted in considerable increases in fish size, aggregation density and biomass, as well as sex-ratio normalization (Beets & Friedlander 1999, Nemeth 2005). Negative results have been mostly attributed to ineffective design and implementation (e.g., Rhodes & Sadovy 2002, Pet et al. 2005, Rhodes & Warren-Rhodes 2005), and to excessive fishing outside protected spawning sites (e.g., Claro & Lindeman 2003, Coleman et al. 2004, Rhodes & Tupper 2007).

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To our knowledge, only two biological models have explored the consequences of spawning aggregation-based MPAs (Alonzo & Mangel 2004, Heppell et al. 2006). Heppell et al. (2006) developed a non-spatial, stage-structured model to evaluate the conservation effects of various management measures for the gag (Myctperoperca microlepis) population of the Gulf of Mexico. Gags are protogynous and relatively unusual in that males stay year-round in spawning sites, whereas mature females migrate to these sites in winter and stay the rest of the year in nearshore habitats that they share with juveniles. Seasonal spawning area closures led to increased biomass and moderate population growth but did not reduce sex ratio bias, whereas year-round closure of all spawning areas improved the sex ratio but had limited effect on population recovery compared to nearshore area closures or fishing effort reduction. In a further scenario, year-round closure of all spawning areas together with increased fishing mortality in nearshore habitats resulted in sex ratio normalization but very slow population recovery (Heppell et al. 2006). Alonzo & Mangel (2004) used a size-structured, individualbased model to evaluate the conservation and fisheries effects of closing 10-30% of spawning sites to fishing for gonochoristic populations and protogynous populations with size-mediated sex change (i.e., with sex change under endogenous control), using parameter estimates for a rocky reef species, California sheephead (Semicossyphus pulcher). The authors found that spawning area closures enhanced mean population size and production of fertilized eggs, but that the redistribution of fishing effort formerly in reserves decreased MPA benefits for the protogynous population. For the scenarios examined, MPAs did not increase harvestable biomass. Consistent with previous studies (e.g., Bannerot et al. 1987, Hunstman & Schaaf 1994), if sex change occurred after recruitment into the fishery, the protogynous population was more sensitive to fishing than the gonochoristic population. Alonzo and Mangel (2004) also found that the gonochoristic population derived greater conservation benefits from MPA protection, even under low fishing pressure, because of the protection of large fecund females.

Existing studies concur on the fact that MPAs protecting spawning aggregation sites can lead to significant increases in population size and biomass and/or to sex-ratio normalization, unless fish suffer high fishing mortality outside spawning sites or in spawning sites outside of the period of MPA implementation. However, critical knowledge gaps remain regarding the effectiveness of spawning aggregation-based MPAs, in particular with respect to their impacts on fisheries (Sale et al. 2005, Grüss et al. 2011a). MPA establishment can incur significant socio-economic impacts for fishing communities (McClanahan et al. 2006). Consequently, there is a need for the development of tools for assessing the potential conservation and fisheries effects of spawning aggregation-based MPAs. Unfortunately, data and knowledge are limited for the majority of the aggregative species and their fisheries, especially in developing countries. Fisheries data are scarce and often not available at the species level (Bannerot et al. 1987, Johannes 1998, Sadovy 2005), relationships between spawning stock and recruitment (Sadovy 2001, Sadovy & Domeier 2005) and between population sex ratio and egg fertilization rate (Hunstman & Schaaf 1994, Armsworth 2001, Alonzo & Mangel 2004) are typically unknown, and the degree of spawning-site fidelity of individual fish is poorly described (Nemeth 2005, Sadovy & Domeier 2005, Sadovy et al. 2008).

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In recognition of these information constraints, we developed a parsimonious, nonspatial, per-recruit model for evaluating the conservation (spawning stock biomass-perrecruit, sex ratio) and fisheries (yield-per-recruit) effects of spawning aggregation-based MPAs for gonochoristic populations and protogynous populations with age-mediated sex change. Being a per-recruit model, it avoids the need for inclusion of a stock-recruitment relationship and a relationship linking egg fertilization success to the proportion of males in the population, relationships that are often unknown or uncertain. The information needed to run the model is relatively easy to obtain: the level of annual fishing effort exerted on fish populations and the fraction of this annual effort directed towards spawning aggregations, estimates (by proxy) of catchability at spawning and non-spawning sites, and estimates for a limited set of life-history parameters. Our model is therefore highly flexible and can be widely applied for examining the effects of MPAs on aggregation-forming populations and their fisheries in data-limited situations.

The specific objectives of the present study are to: (1) develop a general model that can be applied to a variety of gonochoristic and protogynous fish populations forming transient spawning aggregations; (2) apply the model to two aggregation-forming populations from Seychelles and analyze MPA scenarios for these two populations; (3) derive general observations on the conservation and fisheries effects of spawning aggregation-based MPAs; and (4) discuss the potential effects of parameters not included in the model. For simplicity, the MPAs considered are entirely no-take during periods of spawning (i.e., closures could be year-round or seasonal so long as they remove all fishing mortality on protected spawning aggregations) though partial-take reserves could also be examined in the model with few modifications.

MATERIAL AND METHODS

The age-structured model we developed here includes two life history stages for gonochoristic populations: juveniles and adults, and three life history stages for protogynous populations: juveniles, adult females and males. Adults can either be in a spawning or a non-spawning state, and catchability differs between spawning and non-spawning sites.

We assume that fish spawn on timescales that are considerably shorter than those for other biological processes such as growth, so that spawning and non-spawning events can be treated as continuous processes acting on individuals. Juveniles are considered not to be harvestable at spawning sites because they are deterred from these areas by the high adult abundance, or the spawning sites are not their normal habitat. There is significant evidence that, for many protogynous species, males remain longer than females at spawning sites (e.g., Zeller 1998, Nemeth et al. 2007, Robinson et al. 2008). This is incorporated in the model by considering the fraction of the spawning aggregation period females spend at spawning sites.

Mortality/survival in the absence of MPAs

We assume that fish recruit to the fishery at or before sexual maturation, due to the wide size selectivity in multi-gear reef fisheries and the late maturity in many aggregation-forming species (Sadovy 1994, Sadovy & Eklund 1999, Rhodes & Tupper 2008). As juveniles are not harvested during spawning periods, the total mortality rate of juveniles is:

$$Z_{j} = M + (1 - C_{s})q_{ns}E \tag{1}$$

where *M* is the natural mortality rate (yr⁻¹), C_s the fraction of annual fishing effort on spawning aggregations, q_{ns} the catchability at non-spawning sites and *E* the total annual fishing effort (yr⁻¹). Note that C_s may be taken proportional to time fish spends spawning, but this is not obligatory and C_s may take into account fishing intensification during spawning and/or targeting of spawning individuals over periods shorter than the full spawning period. The probability of survival of an individual to sexual maturity is:

$$p(a_{50}) = e^{-[M + (1 - C_s)q_{ns}E](a_{50} - a_F)}$$
(2)

where a_{50} is the age at 50% fecundity, which for simplicity we equate with the age of sexual maturity, and a_F the age of recruitment to the fishery.

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Adult individuals are exposed to fishing mortality at both spawning and non-spawning sites. For gonochoristic populations, the total mortality rate of adult individuals is:

$$Z_{mat} = M + ((1 - C_s)q_{ns} + C_s q_s)E$$
(3)

where q_s is the catchability at spawning sites. Natural mortality, M, is assumed the same for adults and juveniles, though changes in natural mortality with age could be included in the model.

For protogynous populations, as females often spend less time at spawning sites than males, the total mortality rate of adult females is:

$$Z_f = M + \left(\left(1 - C_s \right) q_{ns} + C_f C_s q_s \right) E \tag{4}$$

where C_f is the fraction of the spawning period females spend at spawning sites. This fraction is 1 in cases where males and females experience the same level of fishing effort at spawning sites. The probability of survival of adult females to sex change is:

$$p(a_{sx}) = e^{-[M + (1 - C_s)q_{ns}E](a_{50} - a_F)} e^{-[M + ((1 - C_s)q_{ns} + C_f C_s q_s)E](a_{sx} - a_{50})}$$
(5)

where a_{sx} is the age of sex change. Sex change is often a gradual process in populations of protogynous species, occurring over a wide range of sizes and ages, but for mathematical simplicity we use a single mean age at sex change.

Finally, in the case of protogynous populations, the total mortality rate of males (Z_m) is identical to that of gonochoristic populations and, therefore, given by Eq. 3.

Mortality/survival in the presence of MPAs

Fishing mortality with MPAs will depend on spawning-site fidelity and on the fate of the fishing effort previously in reserves before closure. We examine cases where all fish are either completely faithful or completely unfaithful to spawning sites and consider several scenarios for the evolution of effort after reserve creation: (1) effort previously in reserves disappears, (2) pre-reserve effort is redistributed to spawning sites remaining open to fishing, and (3) pre-reserve effort is fully redistributed to non-spawning sites for cases where all spawning sites are closed to fishing. Underlying these scenarios for fishing effort evolution with MPAs is the assumption that fishers will preferentially move to other spawning sites if any remain open to fishing, only resorting to intensifying fishing in non-spawning areas if they have no other alternative.

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If effort previously in reserves disappears at the time of MPA creation and fish are not faithful to spawning sites, then the fishing mortality rate of spawning individuals is simply reduced by a factor of $(1-C_r)$, the fraction of time fish spawn outside protected spawning areas. For example, in the case of gonochoristic populations, the total mortality rate of adult individuals will become:

$$Z_{mat} = M + ((1 - C_s)q_{ns} + (1 - C_r)C_sq_s)E$$
(6)

If, on the other hand, individuals are faithful to spawning sites, then there will essentially be two subpopulations, one that experiences no fishing mortality while spawning (representing a fraction C_r of the population assuming complete mixing of recruits between the two subpopulations) and one that does experience fishing mortality while spawning (representing a fraction $(1-C_r)$ of the population).

If the effort previously in reserves is fully redistributed to the spawning sites remaining open to fishing and fish are not faithful to spawning sites, then the fishing mortality rate of spawning individuals will be both reduced by a factor of $(1-C_r)$ compared to the prereserve situation and increased by a factor of $\frac{1}{(1-C_r)}$, so that global fishing mortality will be unchanged by protection.

If, on the other hand, fish are faithful to spawning sites, then there will again be two subpopulations, one that experiences no fishing mortality during spawning periods and one that has the normal fishing mortality during that time of the year increased by a factor of

$$\frac{1}{\left(1-C_r\right)}.$$

Considering the case where all spawning sites are closed, if effort previously in reserves is fully redistributed to non-spawning sites, all the annual fishing effort is exerted in

non-spawning areas and all individuals (juveniles and adults) are assumed subject to the same total mortality rate:

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$$Z_{i} = M + q_{ns}E \tag{7}$$

On the other hand, if effort previously in reserves disappears at the time of MPA creation (which can occur if the redistribution of effort to normal residence areas is unprofitable), the total mortality rate for all fish individuals is:

$$Z_{i} = M + (1 - C_{s})q_{ns}E \tag{8}$$

Metrics

To evaluate the effectiveness of spawning aggregation-based MPAs, we use two metrics: female spawning stock biomassper-recruit (female SSBR) and yield-per-recruit (YPR). For protogynous populations, we also examine sex ratio (SR), defined here as the number of mature females over the number of males. Female SSBR is an indicator of reproductive capacity, whereas SR is an indicator of the chances of egg fertilization for protogynous populations. Given sufficient disparity in prevalence of the two sexes, it is assumed that egg fertilization rate will decrease. Implicit in the calculation of average female SSBR and YPR for scenarios with MPAs and absolute site fidelity, for which the system is essentially represented by two subpopulations experiencing different mortality rates, is the assumption that recruitment rates per unit habitat area are the same in the two subpopulations.

Female SSBR and YPR are obtained by integrating the product of survival to age and weight-at-age over the relevant age range. For the site fidelity case, these are weighted averages of the corresponding per recruit quantities for the two subpopulations (MPA spawners and non-MPA spawners) making up the population.

If fish are faithful to spawning sites, the population-wide average sex ratio and the sex ratio of the fished subpopulation are different. In this case, it is important to estimate local sex ratio experienced by individuals at fished spawning sites since that is a limiting factor for reproduction in the fished subpopulation.

The relevant equations can be found in Appendix A1.

Model application

The model is applied to populations of two species that form transient spawning aggregations in Seychelles: the brown-marbled grouper (*Epinephelus fuscoguttatus*) population of Farquhar Atoll (Robinson et al. 2008) and the shoemaker spinefoot rabbitfish (*Siganus sutor*) population of the main granitic islands (Robinson et al. 2011). Brown-marbled grouper is long-lived (maximum reported age ~42 yrs, Pears et al. 2006), slow-growing and protogynous, while shoemaker spinefoot rabbitfish is short-lived (natural life expectancy ~2.5 yrs, Grandcourt 2005), fast-growing and gonochoristic. Both populations are assumed to grow according to a von Bertalanffy growth function, and weight is an allometric function of growth (Table 1 and Fig. A2).

At Farquhar Atoll, the fishery for brown-marbled grouper and other species is subsistence and/or small-scale commercial, typically involving three fishing boats that are each only used a fraction of the year. Total annual effort for brown-marbled grouper is approximately 169 fishing boat days per year, of which roughly 12 occur during spawning aggregations (JR, pers. obs.). Shoemaker spinefoot rabbitfish and other siganid species are fished using traps mainly set from small outboard-powered boats. The trap fishery is subject to minimum mesh size requirements but otherwise is not managed (Robinson et al. 2011). Mean annual effort in the trap fishery for 2000-2006 was 95 000 sets (Seychelles Fishing Authority, unpubl. data). The number of days the trap fishery spent fishing on spawning aggregations is estimated at 30 (Robinson et al. 2011).

The absolute values of catchability are currently highly uncertain for both grouper and rabbitfish and quite difficult to precisely estimate. So as to obtain approximate values for absolute catchability, it is assumed that total annual fishing mortality on spawning aggregations is roughly equivalent to the annual natural mortality rate (note this is different from the instantaneous spawning-aggregation fishing mortality, which would be much greater than natural mortality, but only occurs over a small fraction of the year). Given this assumption, spawning-site catchability is obtained as:

$$q_s = \frac{M}{C_s E} \tag{9}$$

The ratio of catch-per-unit-effort (CPUE) at non-spawning sites to CPUE at spawning sites is then used to estimate relative catchability between these two periods. The assumption that annual fishing mortality at spawning sites is equivalent to the annual natural mortality rate is extremely approximate. We address this uncertainty by varying total fishing effort, which can alternatively be interpreted as varying catchability as these two quantities always appear together in the model.

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The age of recruitment to the fishery is unknown for brown-marbled grouper at Farquhar. Since juvenile catch is negligible for this population (JR pers. obs.), the age of recruitment to the fishery is taken equal to the age of sexual maturity. Sex ratio is assumed to be 1:1 for rabbitfish (Robinson et al. 2011). All other model parameters are obtained from the literature relating to the study populations or to populations of the same species in other regions (see Table 1). The model assumes that sex change takes place at a fixed age for grouper. The potential implications of exogenous control of sex change on the effects of fishing and MPAs are considered in the Discussion.

Parameter Definition		Siganus sutor	Epinephelus fuscoguttatus	
М	Natural mortality rate	0.63 yr ^{-1 a}	0.1 yr ^{-1 b}	
E	Total annual fishing effort	95.10^3 trap sets per yr ^c	169 fishing days per yr ^d	
C_s	Fraction of annual fishing effort on spawning aggregations	0.0822 °	0.0329 ^d	
C_{f}	Fraction of the spawning period females spend at spawning sites	-	0.45 °	
q_s	Spawning-site catchability	$1.0758.10^{-4}$	6.5447.10 ⁻³	
q_{ns}	Non-spawning site catchability	q_s / 10 $^{ m e}$	$q_s/140^{ m e}$	
a_F	Age of recruitment into the fishery	0.34 yr [°]	9.2 yr ^e	
<i>a</i> ₅₀	Age of sexual maturity	0.79 yr ^d	9.2 yr ^f	
a_{sx}	Age of sex change	-	25.5 yr ^f	
k	Instantaneous growth rate at small size	0.65 yr ^{-1 a}	0.16 yr ^{-1 f}	
L_{∞}	Maximum size	43.3 cm ^a	80.7 cm ^f	
a_0	Theoretical age at zero length	-0.379 yr ^a	-0.2 yr ^f	
α	Constant of proportionality of the allometric length-weight relationship	5.9.10 ^{-3 g}	6.10 ^{-6 h}	
β	Exponent of the allometric length-weight relationship	2.75 ^g	3.28 ^h	

Table 1. Parameter estimates for shoemaker spinefoot rabbitfish (*Siganus sutor*) and brown marbled grouper (*Epinephelus fuscoguttatus*).

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^aGrandcourt 2002; ^bHoenig 1983; ^cRobinson et al. 2011; ^dJR, pers. obs. ; ^eSeychelles Fishing Authority, unpubl. data; ^gPears et al. 2006; ^gSamboo & Mauree 1988; ^hGrandcourt 2005. The six scenarios of spawning aggregation-based MPAs described above were assessed for both grouper and rabbitfish (see Table 2 for a summary). To facilitate the discussion of our results, we assumed that reproduction of grouper may fail when sex ratio is superior to 50:1, a reasonable assumption considering sex ratio estimates reported for heavily exploited aggregation-forming serranid populations (Beets & Friedlander 1992, Sadovy et al. 1994a, Coleman et al. 1996). The value of the 'critical sex ratio' for brown-marbled grouper under the assumption of age-mediated sex change may in reality be higher or lower than 50:1, but qualitative comparisons between the effect of different MPA scenarios on sex ratio normalization are unchanged for a wide range of critical sex ratios.

To be able to disentangle the effects of long life and slow growth from those of the sexual mode, the model was also applied to a theoretical *gonochoristic* grouper population. This theoretical population has exactly the same characteristics as brown-marbled grouper population (described in Table 1), except that it does not change sex and its sex ratio is 1:1.

The basic MATLAB code to run the model can be found in Appendix A3.

MPA Scenario	Description
#1	Some spawning sites are closed to fishing; the fishing effort formerly in reserves disappears at the time of MPA creation; fish are completely unfaithful to spawning sites
#2	Some spawning sites are closed to fishing; the fishing effort formerly in reserves disappears at the time of MPA creation; fish are completely faithful to spawning sites
#3	Some spawning sites are closed to fishing; the fishing effort formerly in reserves is fully redistributed to spawning sites remaining open to fishing at the time of MPA creation; fish are completely unfaithful to spawning sites
#4	Some spawning sites are closed to fishing; the fishing effort formerly in reserves is fully redistributed to spawning sites remaining open to fishing at the time of MPA creation; fish are completely faithful to spawning sites
#5	All spawning sites are closed to fishing; the fishing effort formerly in reserves disappears
#6	All spawning sites are closed to fishing; the fishing effort formerly in reserves is fully redistributed to non-spawning sites at the time of MPA creation

Table 2. Description of the marine protected area (MPA) scenarios simulated in the present study.

RESULTS

Model in the absence of MPAs

For the grouper population, the default annual effort estimate used in the model (hereafter referred to as E_{base}) is around thirteen times less than the level of annual effort at which YPR reaches a maximum, E_{max} (Fig. 1a). By comparison, E_{base} is close to E_{max} for the rabbitfish population (Fig. 1b). Due to the plateau in length- and weight-at-age relationships beyond the age of sex change (Figs. A2a and b), the yield-per-recruit curve for grouper has a 'flat-top' shape, making the precise value of E_{max} less distinctive than for rabbitfish (e.g., for grouper, YPR is approximately maximal for effort levels 3-4 times greater than E_{base}). YPR is at around 63% and 99% of its maximum value for grouper and rabbitfish, respectively (Figs. 1a-b), and female SSBR is at 65.76% of its natural value for grouper and to 14.24% of its natural value for rabbitfish (Figs. 1c-d). These values of values of SSBR likely represent populations that are lightly and heavily exploited, respectively, given that population collapse points typically are in the range of 10-60% of natural SSBR (Myers et al. 1999). Given uncertainty in the absolute value of catchability mentioned above, we cannot determine how well these results depict the status of the real populations. As such, various levels of fishing effort are explored. Nevertheless, differences between the two species are convenient because they allow us to explore model behavior under different scenarios of exploitation level.

Although the default annual effort exerted on brown-marbled grouper is relatively low, grouper sex ratio in the model is approximately 5 times greater than under unfished conditions (approximately 19:1 female to male ratio vs. approximately 4:1 female to male ratio) (Fig. 1e). Thus, even low levels of effort significantly skew the demography of the grouper population towards smaller and younger female individuals, potentially impacting egg fertilization rates. Since the relationship between fishing effort and sex ratio is roughly exponential (Fig. 1e), any small increase in fishing leads to a considerable increase in sex ratio. Sex ratio is particularly sensitive to changes in model parameters and especially to changes in the age of sex change (Table 3).

For the default set of parameter values, annual fishing mortality rates at spawning sites (i.e., $C_s q_s E$) were higher than fishing mortality in normal residence areas (i.e., $(1-C_s)q_{ns}E$) for both adult female and male groupers, by factors of around 2 and 5, respectively. For rabbitfish, mortality rates at spawning and non-spawning sites are approximately equal. The contrast between the two populations was essentially due to the ratio of catchabilities for

spawning and non-spawning periods (a 140-fold difference for grouper vs. a 10-fold difference for rabbitfish).



Figure 1. (**a**,**b**) Yield-Per-Recruit (YPR), (**c**,**d**) fraction of female spawning stock biomass per recruit (FNSSBR, i.e., the ratio of female spawning stock biomass per recruit over natural female spawning stock biomass per recruit) and (**e**) sex ratio (i.e., the number of adult females over the number of adult males) as a function of annual fishing effort, for (**a**,**c**,**e**) grouper and (**b**,**d**) rabbitfish populations. The dashed grey lines indicates the default value of annual fishing effort exerted on the population, E_{base} , and the corresponding value of the per recruit quantity, whereas the dashed black lines indicates the value of annual fishing effort at which yield-per-recruit reaches a maximum for the population, E_{max} , and the corresponding value of the per recruit quantity.

Table 3. Sensitivities of per recruit quantities and sex ratio to changes in natural mortality rate (*M*), fraction of annual fishing effort on spawning aggregations (C_s), spawning-site catchability (q_s), non-spawning site catchability (q_{ns}), age of recruitment into the fishery (a_F), age of sexual maturity (a_{50}) and age of sex change (a_{sx}), for brown-marbled grouper and shoemaker spinefoot rabbitfish. Sensitivities greater than 0.5 in magnitude are indicated in bold.

		Female spawning stock biomass per recruit	Yield-per-recruit	Sex ratio
Μ	Grouper	-0.57	-0.75	1.61
	Rabbitifsh	-0.73	-0.62	-
C_s	Grouper	-0.25	0.32	0.97
	Rabbitfish	-0.38	0.02	-
q_s	Grouper	-0.26	0.32	0.98
	Rabbitfish	-0.45	0.02	-
q_{ns}	Grouper	-0.12	0.14	0.34
	Rabbitfish	-0.82	-0.09	-
a_F	Grouper	1.12	0.82	0
	Rabbitfish	0.45	0.34	-
<i>a</i> ₅₀	Grouper	-0.66	-0.23	-1.63
	Rabbitfish	-0.40	0.07	-
a _{sx}	Grouper	0.42	-0.13	4.64

Effects of spawning-aggregation based MPAs

The scenarios of spawning aggregation-based MPAs (Table 2) are assessed for different levels of annual effort. We focus primarily on results for grouper since patterns of female SSBR and YPR in the presence of MPAs are qualitatively similar for grouper and rabbitfish.

When a fraction of spawning sites is in reserves, greatest conservation benefits are obtained when effort formerly in reserves disappears at the time of MPA creation (MPA scenarios #1-2) (Figs. 2a, 3a-b, A4a-b and full and dashed black curves in Figs. 4, 5 and A5).

As the relationship between annual fishing effort and female SSBR is decreasing and convex (Figs. 1c-d) and the relationship between annual effort and sex ratio is increasing and concave (Fig. 1e), conservation benefits are expected to be greater in the site fidelity situation than in the non-site fidelity situation according to Jensen's inequality (Grüss et al. 2011b). However, we do not observe here marked differences of female SSBR or sex ratio between the site fidelity and the non-site fidelity situations. As is to be expected, increasing the fraction of spawning sites in reserves, C_r , only produces significant changes in female SSBR and sex ratio for high effort levels (Figs. 2a, 3a-b, A4a-b and full and dashed black curves in Figs. 4, 5 and A5).

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When effort previously in reserves is fully redistributed to the spawning sites remaining open to fishing (MPA scenarios #3-4), MPA effects on female SSBR and sex ratio vary qualitatively depending on whether fish are faithful to spawning sites or not. In the nonsite fidelity situation, per recruit quantities and sex ratio are independent of the fraction of spawning sites in reserves, because any reduction on mortality of an individual while in protected spawning sites will be recuperated on that same individual when it uses a different spawning site (Eq. 7; Fig. 3c and A4c, and full violet curves in Figs. 4, 5 and A5). In the site fidelity situation, SSBR results are qualitatively similar to those when effort disappears (MPA scenarios #1-2), but more spawning sites need to be in reserves to produce a given increase in SSBR when effort is redistributed (Fig. 3d and dashed violet curves in Fig. 5). On the other hand, MPA effects on sex ratio are qualitatively different if effort is redistributed (compare Fig. 2a with Fig. 2b), in that sex ratio of the fished subpopulation is predicted to increase with both annual effort and C_r . Therefore, sex ratio at fished spawning sites is likely to rise above the critical level when a relatively high proportion of spawning sites is protected for effort levels that, in the absence of MPAs, maintained sex ratio below the critical level (Fig. 2b and A4d and dashed violet curves in Figs. 4 and A5).

When all spawning sites are in MPAs (MPA Scenarios #5 and 6), conservation benefits are only slightly changed by the fate of effort formerly in reserves (full and dashed green curves in Figs. 4, 5 and A5). Conservation benefits are obtained when effort is displaced to non-spawning sites because catchability is much lower, significantly reducing fishing pressure on adults, and especially males in the grouper case. Differences in female SSBR between the MPA and the no-MPA situations are stronger for grouper than rabbitfish as adult fishing mortality rates are much higher at spawning sites than in normal residence areas for grouper. Differences in sex ratio between the MPA and the no-MPA situations are

large for grouper due to the complete protection of males during spawning periods (full and dashed green curves in Figs. 4 and A5).

For all the MPA scenarios examined, closing spawning sites to fishing has zero or even negative effects on YPR (Figs 6 and 7). YPR is relatively insensitive to the fraction of spawning sites in MPAs, and is identical to YPR in the no-MPA situation at values of annual effort around two times E_{max} for rabbitfish (Fig. 7c-d). For any given effort level on grouper, YPR decreases with the fraction of spawning sites in reserves and, the higher the value of effort, the more YPR decreases with C_r (Figs 6 and 7a-b). When all spawning sites are in reserves, YPR is significantly reduced compared to the no-MPA situation for grouper (full and dashed green curves in Figs. 7a-b) since the annual fishing mortality rate is 2-5 times higher at spawning sites than at non-spawning sites and fishing mortality rates in the absence of reserves are already below those that maximize YPR.



Figure 2. Grouper sex ratio (i.e., the number of mature females over the number of males) for the fished subpopulation as a function of multiplier of fishing effort (mE_{base} , i.e., fishing effort in units of E_{base}) and fraction of spawning sites in reserves (C_r). Results are only shown for MPA scenarios (**a**) #1 and (**b**) #4. For MPA scenarios #2 and #3 sex ratio of fished subpopulations is invariant with C_r , and, for these scenarios, sex ratio of fished subpopulations as a function of fishing effort is given by Fig. 1e (see Table 2 for the description of the different MPA scenarios). For all panels, the light grey area represents combinations of mE_{base} and C_r for which sex ratio of the fished subpopulation is superior to 50:1. E_{base} is indicated by a vertical dashed-dotted line.



Figure 3. Grouper fraction of female spawning stock biomass-per-recruit (FNSSBR, i.e., the ratio of female spawning stock biomass-per-recruit over natural female spawning stock biomass-per-recruit) as a function of multiplier of fishing effort (mE_{base}) and fraction of spawning sites in reserves (C_r), for MPA scenarios #1-4 (see Table 2 for the description of the different MPA scenarios). For all panels, the light grey area represents combinations of mE_{base} and C_r for which sex ratio at fished sites is superior to 50:1. E_{base} is indicated by a vertical dashed-dotted line.



Figure 4. Grouper sex ratio for the fished subpopulation as a function of multiplier of fishing effort (mE_{base}), for the 6 MPA scenarios analyzed in the present study (see Table 2 for a description of all MPA scenarios). The fraction of spawning sites in reserves, C_r , is 30% and 60% for MPA scenarios #1-4 for (**a**) and (**b**), respectively, while all spawning sites are set aside as reserves for MPA scenarios #5-6. E_{base} is indicated by a dashed-dotted blue line.



Figure 5. Fraction of female spawning stock biomass-per-recruit (FNSSBR) as a function of multiplier of fishing effort (mE_{base}), for the 6 MPA scenarios analyzed in the present study (see Table 2 for the description of the different MPA scenarios). (**a**,**b**) is for grouper, while (**c**,**d**) is for rabbitfish. The fraction of spawning sites in reserves, C_r , is 30% and 60% for MPA scenarios #1-4 for (**a**,**c**) and (**b**,**d**), respectively, while all spawning sites are set aside as reserves for MPA scenarios #5-6. E_{base} is indicated by a dashed-dotted blue line. E_{max} is indicated by a dashed-dotted red line for rabbitfish. Note the horizontal scales differ for grouper and rabbitfish.



Figure 6. Yield-per-recruit normalized by maximum YPR in the absence of reserves (YPR/YPR_{max}) as a function of multiplier of fishing effort (mE_{base}) and fraction of spawning sites in reserves (C_r), for the grouper population, for MPA scenarios #1-4 (see Table 2 for the description of the different MPA scenarios). For all panels, the light grey area represents combinations of mE_{base} and C_r for which sex ratio at fished sites is superior to 50:1. E_{base} is indicated by a vertical dashed-dotted line. Note the horizontal scales differ for grouper and rabbitfish.



Figure 7. YPR normalized by maximum YPR in the absence of reserves (YPR/YPR_{max}) as a function of multiplier of fishing effort (mE_{base}) for the 6 MPA scenarios (see Table 2 for the description of the different MPA scenarios). (**a**,**b**) is for grouper, while (**c**,**d**) is for rabbitfish. The fraction of spawning sites in reserves, C_r , is 30% and 60% for MPA scenarios #1-4 for (**a**,**c**) and (**b**,**d**), respectively, while all spawning sites are set aside as reserves for MPA scenarios #5-6. E_{base} is indicated by a dashed-dotted blue line. E_{max} is indicated by a dashed-dotted red line for rabbitfish.

Relative impacts of sex change under endogenous control on MPA effects

Comparing the theoretical gonochoristic with the protogynous grouper population, the patterns of female SSBR and YPR for the different scenarios examined are qualitatively similar (results not shown here). The gonochoristic grouper population experiences greater increases in female SSBR and relatively similar decreases in YPR than the protogynous population when MPAs are created, regardless of the assumptions made on spawning site fidelity and the fate of the effort previously in reserves (Fig. 8).





Figure 8. MPA effects on fraction of female spawning stock biomass-per-recruit (FNSSBR) and normalized YPR (YPR/YPR_{max}) for (**a**,**b**) the theoretical gonochoristic grouper population and (**c**,**d**) the protogynous grouper population, for the 6 MPA scenarios analyzed in the present study (see Table 2 for the description of the different MPA scenarios). (**a**,**c**) Ratio of FNSSBR to FNSSBR in the status quo situation ((*FNSSBR*)/(*FNSSBR*)_{sq}) as a function of multiplier of fishing effort (mE_{base}). (**b**,**d**) Ratio of YPR/YPR_{max} to YPR/YPR_{max} in the status quo situation ((*YPR/YPR_{max}*)/(*YPR/YPR_{max}*)_{sq}) as a function of mPA scenarios #1-4, while all spawning sites are set aside as reserves for MPA scenarios #5-6. E_{base} is indicated by a dashed-dotted blue line.

DISCUSSION

Overall, model results indicate that spawning aggregation-based MPAs increase female spawning stock biomass-per-recruit, i.e., fish reproductive capacity regardless of the fate of the fishing effort formerly in reserves. An exception to this general pattern occurs if

fish are not faithful to the fraction of spawning sites protected, which results in unchanged reproductive capacity if effort is redistributed to non-protected spawning sites. However, this scenario is unlikely to be fully met in real cases as spawning site fidelity appears to be high for a majority of aggregative species (e.g., Zeller 1998, Bolden 2000, Starr et al. 2007), though results of tagging studies on shoemaker spinefoot rabbitfish aggregations in Seychelles indicate that infidelity may be as high as 15% (J. Bijoux, unpubl. data).

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Setting aside spawning sites as reserves generally improves the sex ratio of protogynous populations, thereby potentially increasing the chances of egg fertilization. However, when fish are faithful to spawning sites, effort displacement onto non-protected spawning areas increases sex ratio for the subpopulation using the non-protected spawning sites. Nevertheless, individuals using protected spawning sites experience the natural sex ratio in this case, and, therefore, the effects of increased sex ratio on the fished subpopulation may be relatively minor for population-wide average production of fertilized eggs if a sufficient number of spawning sites are protected. Consistent with Heppell et al. (2006), the greatest reduction in sex ratio bias is obtained when all spawning sites are closed to fishing yearround, whatever the fate of the fishing effort previously in spawning areas, due to considerable reduction of fishing mortality of males (Fig. 4). We also found that the greatest increase in fish reproductive capacity occurs in this case (Fig. 5), while Heppell et al. (2006)'s results indicate that this management measure has a limited effect on population growth. This discrepancy essentially stems from the fact that fishing mortality of grouper females is higher at spawning than at non-spawning sites in our model, while the opposite occurs in Heppell et al. (2006)'s model.

In our model, sex change is assumed to take place at a fixed age, though a recent empirical study suggests that sex change in brown-marbled grouper from Great Barrier Reef occurs over a wide range of ages and sizes, and may be socially mediated, i.e., under exogenous control (Pears et al. 2006). The existence of exogenous mechanisms controlling sex change may render fish populations less vulnerable to the effects of fishing on sex ratio (Hunstman & Schaaf 1994, Alonzo & Mangel 2004, 2005). This would reduce the need for the creation of MPAs to balance sex ratio as age at sex change will adjust to compensate for any imbalance introduced by fishing. In the absence of precise information on patterns of sex change (as is the case for the brown-marbled grouper population of Farquhar Atoll), assuming sex change occurs at a fixed age is conservative in the sense that the model will indicate the maximum possible increase in sex ratio that is likely to occur as a result of fishing.

Fishery benefits of spawning aggregation-based MPAs through an increase in yieldper-recruit did not occur in our model. Rather, benefits for fishing would need to occur via an increase in recruitment due to increased reproductive capacity, provided that a sufficient fraction of spawning sites is placed in reserves. Fishery benefits also did not occur in Alonzo and Mangel (2004)'s individual-based model, which integrates recruitment. Nevertheless, as with MPAs for non-aggregative populations (Hart 2006), fisheries benefits are likely to occur for certain scenarios of high fishing pressure and fidelity to spawning sites for whom the population collapses in the absence of reserves, but is persistent with reserves.

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We found that levels of site fidelity had a surprisingly minor impact on spawning stock biomass-per-recruit with MPAs (Figs. 3a vs. 3b, and to a lesser extent 3c vs. 3d). Grüss et al. (2011b) demonstrated that movement in a home range, which, similar to a lack of spawning site fidelity, exposes 'reserve' individuals to fishing, dramatically reduces persistence benefits of MPAs. Therefore, one would naively expect a significant decrease in MPA benefits due to a lack of spawning site fidelity. Here, this effect is weak because the implementation of spawning aggregation-based MPAs eliminates some, but not all, fishing mortality on reserve individuals. Therefore, the difference in total mortality of individuals using protected spawning sites versus those using non-protected spawning sites is relatively minor (e.g., total mortality of individuals using protected sites is only 0.6 times that of individuals using non-protected spawning sites for grouper fished at the default effort level), and both are relatively close to the average mortality rate experienced by fish that lack site fidelity. These relatively small differences in mortality explain both the need for placing significant fractions of spawning sites in reserves to see marked changes in fish reproductive capacity and the fact that site fidelity has a relatively small impact. If the fraction of annual fishing effort on spawning aggregations was much greater and/or the difference between spawning-site catchability and non-spawning site catchability was very large (e.g., a 600-fold difference), as could be envisaged for some groupers that are predominantly fishable at spawning aggregations (e.g., tiger grouper, Mycteroperca tigris (Sadovy et al. 1994b)), differences between the site fidelity and non-site fidelity situations would be more marked.

As it to be expected, we found that the positive effects of spawning aggregation-based MPAs on fish reproductive capacity and their negative effects on yield-per-recruit are stronger for long-lived, slow-growing populations than for short-lived, fast-growing populations. Furthermore, consistent with Alonzo & Mangel (2004), our results suggest that gonochoristic populations experience greater increases in reproductive capacity and similar

decreases in yield-per-recruit than protogynous populations when spawning aggregationbased MPAs are created if sex change occurs after recruitment into the fishery (as is the case for the majority of protogynous aggregation-forming populations; e.g., Sadovy 1994, Rhodes & Warren-Rhodes 2005).

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Potential implications of spawning aggregation-based MPAs for the shoemaker spinefoot rabbitfish and brown-marbled grouper populations from Seychelles

The shoemaker spinefoot rabbitfish is short-lived, fast-growing and gonochoristic. These life history traits promote a degree of resilience to fishing (Robinson et al. 2011). Therefore, high yield-per-recruit levels can be targeted while reproductive capacity of the species is kept at a low level. As shoemaker spinefoot rabbitfish is not entirely faithful to spawning sites (J. Bijoux, unpubl. data), our findings of only moderate changes in spawning stock biomass-per-recruit and yield-per-recruit for a wide range of fishing levels suggest that reducing global fishing effort would likely be more beneficial to the population than creating spawning aggregation-based MPAs.

In contrast, the life history traits of the brown-marbled grouper population of Farquhar Atoll (long life, slow growth and protogynous hermaphroditism) confer much greater vulnerability to fishing (Grandcourt 2005, Robinson et al. 2008). Therefore, for brown-marbled grouper, it would be cautious to target moderate yield-per-recruit levels while ensuring that the sex ratio is maintained below a critical level at a maximum number of spawning sites. Brown-marbled grouper appears to show fidelity to spawning aggregation sites (Robinson et al. 2008, J. Bijoux, unpubl. data). In this context, and conservatively assuming effort redistribution after MPA establishment, our model results suggest that a significant fraction of spawning sites should be protected so as to ensure population-wide egg fertilization rates.

Since approximate values of absolute catchability were used for the two study populations, it is not possible to assess the exact current status of these populations. Nevertheless, model results are qualitatively similar for a wide range of fishing mortality levels. It is feasible to obtain more reliable estimates of absolute spawning-site catchability and the relative catchability in non-spawning periods, for example, through the parallel estimation of spawning aggregation CPUE and biomass (e.g., from on-site observation of fishing), compared to non-aggregation estimates of CPUE in normal residence areas measured immediately prior to the spawning season.

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Conclusions

Using a parsimonious model, spawning aggregation-based MPAs are found to be an effective conservation measure under a wide range of conditions. Nonetheless, for protogynous populations, when fish are faithful to spawning sites and fishing effort is redistributed at the time of MPA creation, sex ratio of the fished subpopulation may dramatically increase, thereby impairing population-wide average chances of egg fertilization unless a significant fraction of spawning sites is set aside in reserves. Moreover, increase in yield-per-recruit with spawning aggregation-based MPAs did not occur in the model. However, spawning aggregation-based MPAs may benefit yield through an increase in recruitment. For the rare aggregation-forming populations for which a stock-recruitment relationship is known, per recruit quantities could be combined with that relationship to assess whether and under what conditions yield may increase with spawning aggregation-based MPAs (Guénette & Pitcher 1999, Hart 2006).

In this study, annual fishing effort was unchanged or decreased after MPA establishment. If annual effort was significantly increased and/or the efficiency of fishing gears was improved after MPA creation, the conservation benefits of spawning aggregation-based MPAs may be considerably reduced. Therefore, it is important to emphasize that, in practice, management measures aiming at limiting levels of annual fishing effort and the efficiency of fishing gears in non-protected areas are needed for spawning aggregation-based MPAs to be effective (Nemeth 2005, Rhodes & Warren-Rhodes 2005).

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SUPPLEMENTARY MATERIAL

Appendix A1. Equations for female spawning stock biomass-per-recruit, yield-per-recruit and sex ratio.

Female spawning stock biomass-per-recruit (female SSBR) and yield-per-recruit (YPR) are obtained by integrating the product of survival to age and weight-at-age over the relevant age range. For instance, in the absence of marine protected areas, female SSBR for gonochoristic populations is given by:

$$SSBR = \frac{SR}{1+SR} \int_{a_{50}}^{\infty} e^{-[M+(1-C_s)q_{ns}E](a_{50}-a_F)} e^{-[M+((1-C_s)q_{ns}+C_sq_s)E](a-a_{50})} w(a) da$$
(A1.1)

where SR is the fixed sex ratio for gonochoristic populations; *M* the natural mortality rate (in yr⁻¹); C_s the fraction of annual fishing effort that is directed towards spawning aggregations; q_{ns} the catchability at non-spawning sites; q_s is the catchability at spawning sites; *E* the total annual fishing effort (yr⁻¹); a_{50} the age at 50% fecundity equated here to the age of sexual maturity; a_F the age of recruitment to the fishery; and w(a) the biomass per adult female at a certain age *a*. For protogynous populations, SSBR is given by:

$$SSBR = \int_{a_{50}}^{a_{50}} e^{-[M + (1 - C_s)q_{ns}E](a_{50} - a_F)} e^{-[M + ((1 - C_s)q_{ns} + C_f C_s q_s)E](a_{50} - a_{50})} w(a) da$$
(A1.2)

where C_f is the fraction of the spawning aggregation period females spend at spawning sites; and a_{sx} the age of sex change. Still in the situation where none of the spawning sites is set aside as marine protected areas, YPR for gonochoristic populations is given by:

$$YPR = (1 - C_{s})q_{ns}E\int_{a_{F}}^{a_{50}}e^{-[M + (1 - C_{s})q_{ns}E](a - a_{F})}w(a)da$$

$$+ [((1 - C_{s})q_{ns} + C_{s}q_{s})E]\int_{a_{50}}^{\infty}e^{-[M + (1 - C_{s})q_{ns}E](a_{50} - a_{F})}e^{-[M + ((1 - C_{s})q_{ns} + C_{s}q_{s})E](a - a_{50})}w(a)da$$
(A1.3)

and for protogynous populations by:

$$YPR = (1 - C_{s})q_{ns}E \int_{a_{F}}^{a_{50}} e^{-[M + (1 - C_{s})q_{ns}E](a - a_{F})}w(a)da$$

+ $[((1 - C_{s})q_{ns} + C_{f}C_{s}q_{s})E]\int_{a_{50}}^{a_{sx}} e^{-[M + (1 - C_{s})q_{ns}E](a_{50} - a_{F})}e^{-[M + ((1 - C_{s})q_{ns} + C_{f}C_{s}q_{s})E](a - a_{50})}w(a)da$
+ $[((1 - C_{s})q_{ns} + C_{s}q_{s})]E$
 $\int_{a_{sx}}^{\infty} e^{-[M + (1 - C_{s})q_{ns}E](a_{50} - a_{F})}e^{-[M + ((1 - C_{s})q_{ns} + C_{f}C_{s}q_{s})E](a - a_{sx})}w(a)da$ (A1.4)

In the absence of marine protected areas, sex ratio of the protogynous populations is given by:

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$$SR = \frac{\int_{a_{50}}^{a_{5x}} e^{-[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a-a_{50})} da}{\int_{a_{5x}}^{\infty} e^{-[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a_{5x} - a_{50})} e^{-[M + ((1-C_s)q_{ns} + C_s q_s)E](a-a_{5x})} da}$$
(A1.5)

Eq. A.1.5 can be simplified and then solved:

$$SR = \frac{\int_{a_{50}}^{a_{5x}} e^{-[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a-a_{5x})} da}{\int_{a_{5x}}^{\infty} e^{-[M + ((1-C_s)q_{ns} + C_s q_s)E](a-a_{5x})} da}$$

$$= \frac{M + ((1-C_s)q_{ns} + C_s q_s)E}{M + ((1-C_s)q_{ns} + C_f C_s q_s)E} \left[e^{[M + ((1-C_s)q_{ns} + C_f C_s q_s)E](a_{5x} - a_{50})} - 1 \right]$$
(A1.6)

Figure A2. Length-at-age and weight-at-age relationships for (**a**,**b**) brown marbled grouper (*Epinephelus fuscoguttatus*) and (**c**,**d**) shoemaker spinefoot rabbitfish (*Siganus sutor*). a_{50} is the age of sexual maturity, a_F the age of recruitment into the fishery and a_{sx} the age of sex change.



Appendix A3. Basic MATLAB code to run the model.

```
rabbitfish.E = 95000 ; % in trap sets per year
grouper.E = 169 ; % in fishing days per year (number of days *
% number of boat trips)
% Fraction of fishing effort on spawning aggregations
% (Number of days spent fishing on spawning aggregations
% per year)
rabbitfish.Cs = 30./365;
grouper.Cs = 12./365;
% Fraction of spawning-site fishing effort that females are
% subject to
rabbitfish.Cf = 1 ;
grouper.Cf = 15./33;
% Spawning-site catchability
rabbitfish.gs = rabbitfish.M./ rabbitfish.E./ ...
    rabbitfish.Cs ;
grouper.qs = grouper.M./ grouper.E./ ...
    grouper.Cs ;
% Non-spawning site catchability
rabbitfish.qns = rabbitfish.qs./ 10 ;
grouper.qns = grouper.qs./ 140 ;
%% Classic von Bertalanffy growth function and
%% corresponding inverse function
vb_growth = @( a , p ) p.Linf .* ( 1 - exp(-p.k.* ( a - p.a0 ) ...
    ));
vb inv = @ ( L , p ) p.a0 + ( log(p.Linf) - log(p.Linf-L) ) ./ ...
    p.k
rabbitfish.Linf = 43.3 ; % in cm
rabbitfish.k = 0.65; % in year^-1
rabbitfish.a0 = -0.379;
grouper.Linf = 80.7 ; % in cm
grouper.k = 0.16; % in year^-1
grouper.a0 = -0.2;
% Age of recruitment into the fishery
rabbitfish.aF = vb inv( 16.15, rabbitfish ) ; % Size of first
% capture is 16.15 cm
grouper.aF = grouper.a50 ;
% Age of sexual maturity
rabbitfish.a50 = vb inv( 23 , rabbitfish ) ; % Size at maturity
% is 23 cm
grouper.a50 = 9.2;
% Age of sexual maturity and maximum age
rabbitfish.asx = 100 ; % Use very high value to indicate none
rabbitfish.amax = rabbitfish.asx ;
grouper.asx = 25.5;
grouper.amax = inf ;
% Necessary parameters for weight-at-length relationships
rabbitfish.wa = 5.9e-3;
rabbitfish.wb = 2.75;
grouper.wa = 6e-6;
grouper.wb = 3.28;
% Weight-at-length relationships
```

```
weight from length = @( L , p ) p.wa .* L.^( p.wb ) ;
length from weight = @(w, p) (w ./ p.wa).^{(1./ p.wb)};
%% Basic functions for doing calculations
fishing_mort_juvenile = @( p ) p.qns .* p.E .* ( 1 - p.Cs ) ;
fishing mort ns female = @( p ) p.E .* p.qns .* ( 1 - p.Cs ) ;
fishing_mort_s_female = @( p ) p.E .* p.qs .* p.Cs .* p.Cf ;
fishing mort female = @(p) fishing mort ns female(p) + \dots
   fishing mort s female( p ) ;
fishing mort ns male = Q(p) fishing mort ns female(p);
fishing mort s male = @( p ) p.E .* p.qs .* p.Cs ;
fishing mort male = @( p ) fishing_mort_ns_male( p ) + ...
   fishing mort s male( p ) ;
mortality juvenile = @( p ) p.M + fishing mort juvenile( p ) ;
mortality female = @( p ) p.M + fishing mort female( p ) ;
mortality_male = @( p ) p.M + fishing_mort_male( p ) ;
%% Basic functions that calculate mean weights
%% per recruit into each life phase
weight juvenile = @( p ) ...
   quadgk( (@( a ) exp( -mortality_juvenile( p ).* ( a - ...
   p.aF ) ).* weight from length( vb growth( a , p ) , p ) ...
   ), p.aF, p.a50);
weight female = Q(p) ...
   quadgk( (@( a ) exp( -mortality female( p ).* ( a - p.a50 ...
   )).* weight from length( vb growth( a , p ) ,p )), ...
   p.a50 , p.asx ) ;
weight male = Q(p) ...
   quadgk( (@( a ) exp( -mortality_male( p ).* ( a - p.asx ) ...
   ).* weight from_length( vb_growth( a , p ) , p ) ) , ...
   p.asx , p.amax ) ;
%% Probabilities of survival
prob survival female = @( p ) exp( -mortality juvenile( p ).* ...
   (p.a50 - p.aF));
prob survival female male = @( p ) ...
   exp( -mortality female( p ).* ( p.asx - p.a50 ) );
prob survival male = @( p ) prob survival female( p ).* ...
   prob survival female male( p ) ;
%% Combine all to get final per recruit quantities
EPR = @(p) prob survival female( p ).* weight female( p ) ;
YPR_juvenile = @( p ) fishing_mort_juvenile( p ).* ...
   weight_juvenile( p ) ;
```
```
YPR_female_ns = @( p ) fishing_mort_ns_female( p ).* ...
   prob_survival_female( p ).* weight_female( p ) ;
YPR_female_s = @( p ) fishing_mort_s_female( p ).* ...
   prob_survival_female(p) .* weight_female(p) ;
YPR_female = @( p ) fishing_mort_female( p ).* ...
prob_survival_female( p ).* weight_female( p ) ;
YPR male ns = @(p) fishing mort ns male(p).* ...
   prob survival male( p ).* weight male( p ) ;
YPR male s = Q(p) fishing mort s male(p).* ...
   prob survival male( p ).* weight male( p ) ;
YPR_male = @(p) fishing_mort male(\overline{p}).* ...
   prob survival male( p ).* weight male( p ) ;
YPR ns = @( p ) YPR juvenile( p ) + YPR male ns( p ) + ...
   YPR female ns( p ) ;
YPR_s = @( p ) YPR_male_s( p ) + YPR_female_s( p ) ;
YPR = Q(p) YPR juvenile(p) + YPR male(p) + ...
   YPR female( p ) ;
%% Sex-ratios
fished_sex_ratio = @( p ) mortality_male( p )./ ...
   mortality_female(p).* ( exp( mortality_female( p ).* ...
   (p.asx - p.a50)) - 1);
natural sex ratio = Q(p) \exp(p.M.* (p.asx - p.a50)) - 1;
%% Functions for estimating marine protected area effects
%% Functions that modify parameter structures in useful ways
mod params_no_eff_no_site = @( p , Cr ) setfield( p , 'qs', ...
   p.qs.* (1 - Cr));
mod_params_no_eff_site = @( p , Cr ) setfield( p , 'qs' , 0 ) ;
mod params eff no_site = @( p , Cr ) p ;
mod params eff site = @( p , Cr ) setfield( p, 'qs', p.qs./ ...
   (1 - Cr));
mod params eff ns = @( p ) setfield( p, 'Cs', 0 ) ;
mod params eff ns 2 = @( p ) setfield( p, 'qs', 0 ) ;
%% Marine protected area scenarios
*****
%% Scenario 1: Effort disappears; no spawning site fidelity
per recr no eff no site = @( p , Cr ,f ) ...
   feval( f , mod params no eff no site( p , Cr ) );
%% Scenario 2: Effort disappears; spawning site fidelity
per recr no eff site = @( p , Cr , f ) ...
   feval(f, p).* (1 - Cr) + ...
   feval( f , mod params no eff site( p , Cr ) ).* Cr ;
per recr no eff site protected = @( p , Cr , f ) ...
   feval( f , mod_params_no_eff_site( p , Cr ) ) ;
per_recr_no_eff_site_nonprotected = @( p , Cr , f ) ...
   feval(f,p);
```

```
%% Scenario 3: Effort displaced to other spawning sites;
%% no spawning site fidelity
per_recr_eff_no_site = @( p , Cr , f ) feval( f , p ) ;
%% Scenario 4: Effort displaced to other spawning sites;
%% spawning site fidelity
per recr_eff_site = @( p , Cr , f ) ...
    feval( f, mod params no eff site( p , Cr ) ).* Cr + ...
    feval( f , mod params eff site( p , Cr ) ).* ( 1 - Cr ) ;
per_recr_eff_site_protected = @( p , Cr , f ) ...
    feval( f , mod params no eff site( p , Cr ) ) ;
per recr eff site nonprotected = @( p , Cr , f ) ...
    feval( f , mod params eff site( p , Cr ) ) ;
%% Scenario 5: All spawning sites closed to fishing and effort
%% that was in spawning sites disappears
per recr eff ns 2 = 0(p, f) feval(f, ...
    mod params eff ns 2( p ) );
%% Scenario 6: All spawning sites closed to fishing and effort
%% displaced to non-spawning periods
% Cr should be 1 in this case
per_recr_eff_ns = @( p , f ) feval( f , ...
    mod params eff ns( p ) );
```

Figure A4. Population-wide average sex ratio (i.e., the number of mature females over the number of males) as a function of multiplier of fishing effort (mE_{base}) and fraction of spawning sites in reserves (C_r), for the grouper population, for MPA scenarios #1-4 as a function of multiplier of fishing effort (mE_{base}) (see Table 2 for the description of the different MPA scenarios). For all panels, the light grey area represents combinations of mE_{base} and C_r for which sex ratio of the fished subpopulation is superior to 50:1. E_{base} is indicated by a vertical dashed-dotted line.



Figure A5. Population-wide average sex ratio (i.e., the number of mature females over the number of males) of grouper as a function of multiplier of fishing effort (mE_{base}), for the 6 MPA scenarios analyzed in the present study (see Table 2 for the description of the different MPA scenarios). The fraction of spawning sites in reserves, C_r , is 30% and 60% for MPA scenarios #1-4 for (**a**) and (**b**), respectively, while all spawning sites are set aside as reserves for MPA scenarios #5-6. E_{base} is indicated by a dashed-dotted blue line. The description of all 6 scenarios is given in Table 2.

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CHAPITRE 3. Estimating local settler-recruit relationship parameters for complex spatially-explicit models

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Abstract – Applied spatially-explicit models are needed to thoroughly evaluate the potential effectiveness of marine protected areas in particular locations. These models have traditionally parameterized a spatially non-varying settler-recruit relationship (SRR), which is often the large-scale, non-spatial stock-recruitment or egg-recruit relationship used for stock assessments. A recent study demonstrated that the initial slope of local SRRs should be adjusted so as to correctly estimate population persistence, and proposed an analytical methodology to carry out the adjustment. This methodology can not be used to evaluate small-scale SRRs for more complex applied spatially-explicit models, in particular when adults of the study population are mobile beyond simple home range movements. Here we propose a numerical methodology for estimating the parameters of local SRRs for complex spatially- and seasonally-explicit population models, from parameters of a large-scale, nonspatial SRR. The consideration of spatial and seasonal patterns of fishing mortality rates, reproduction and larval dispersal results in discrepancies between spatial monthly models and equivalent non-spatial annual models in terms of global spawning stock biomass. The adjustment of the initial slope of small-scale SRRs is necessary so as not to underestimate population persistence, and also reduces discrepancies between spatially- and seasonallyexplicit models and their non-spatial annual counterparts.

Keywords: Settler-recruit relationships, complex systems, spatially-explicit population models, spatial resource management.

INTRODUCTION

Marine protected areas (MPAs) have become a central tool for the conservation and sustainable use of marine resources. Nevertheless, MPAs are unlikely to be effective management tools if they are inappropriately planned or the impacts of their implementation are poorly anticipated (Agardy et al., 2003, 2011; Kaiser, 2005; Kaplan et al., 2010). Applied models (also referred to as 'tactical models' in the MPA literature) based on the best available scientific knowledge are needed to evaluate the potential conservation and fisheries effects of proposed MPAs in particular locations (Gerber et al., 2003; Pelletier and Mahévas, 2005; Little et al., 2007; White, 2010).

If sufficient knowledge is available to develop them, spatially- - and eventually seasonally- - explicit population models will best address the possible consequences of spatial management scenarios (Mahévas and Pelletier, 2004; Pelletier and Mahévas, 2005; Mapstone et al., 2008). Applied spatially-explicit models are generally extensions of non-spatial models used in fisheries management (e.g., Edwards et al., 2009; Kaplan et al., 2009; White, 2010). The construction of spatially-explicit models is often complicated since it requires a consistent representation of patterns of larval dispersal, adult movement, and fleet distributions, as well as adequate parameterization of small-scale settler-recruit relationships (i.e., relationships between the number of larvae arriving at settlement locations and the subsequent recruitment level) (Pelletier and Mahévas, 2005; Little et al., 2007; Botsford et al., 2009). Spatially-explicit models have traditionally used a spatially non-varying settler-recruit relationship (e.g., Attwood and Bennett, 1995; Walters et al., 2007; Kaplan et al., 2009; White et al., 2010). This spatially non-varying relationship is often the large-scale, non-spatial stock-recruitment, or egg-recruit, relationship used for stock assessments of the study population (e.g., Walters et al., 2007; Kaplan et al., 2007; Kaplan et al., 2009; White et al., 2010).

White (2010) developed a methodology to estimate small-scale settler-recruit relationships from a large-scale, non-spatial egg-recruit relationship. The author established that the initial slope of the local settler-recruit relationships, α , is obtained by dividing the slope at the origin of the large-scale, non-spatial egg-recruit relationship by the dominant eigenvalue of the larval dispersal matrix of the study population. This correction ensures that some sources of larval mortality (such as larval advection away from recruitment areas) are not double counted and, consequently, that population persistence is not underestimated (White, 2010). White (2010)'s analytical methodology can not be used however to evaluate



small-scale settler-recruit relationships ('SRRs') for cases where adults of the study population are mobile beyond simple home range movements. Moreover, maximum recruitment, another crucial parameter in SRRs, is expected to vary spatially since recruitment areas usually have different carrying capacities. If information about the proportion of suitable habitat in each recruitment zone is available, it should be used to estimate local maximum recruitment.

Here we propose a numerical methodology for estimating local SRR parameters for complex, spatially- and seasonally- explicit population models, from parameters of a large-scale, non-spatial SRR. We apply this methodology to the South African population of deepwater hake (*Merluccius paradoxus*) in a theoretical study system. We then investigate differences between estimates of global annual spawning stock biomass (SSB) obtained from the parameterized spatially-explicit model, when the initial slope of the SRRs is adjusted versus when it is not, and its non-spatial counterpart, for different levels of fishing mortality.

THEORY

The relationship between the spawning stock, or larval production, and the subsequent recruitment, is one of the most fundamental components in marine population dynamics (Beverton and Holt, 1957; Sissenwine and Shepherd, 1987; Mace and Sissenwine, 1993; Myers and Barrowman, 1996). Stock-recruitment relationships (also abbreviated SRRs where there is no confusion with settler-recruit relationships) are highly uncertain for most marine populations and the issue of its estimation has been subject to intense debates (see, e.g., Francis (1997) and Myers (1997) vs. Gilbert (1997)). Nevertheless, to be in line with the precautionary approach to fisheries management, it is wise to accept the 'stock recruitment paradigm', that is that recruitment is positively related to spawning stock biomass, at least at low SSB (Shepherd, 1982; Francis, 1997). Traditionally, SRRs are represented using functions that follow the stock recruitment paradigm: Beverton and Holt (1957) and Ricker (1954) functions, or generalizations of them. Beverton-Holt-like and Ricker-like functions respectively plateau and decrease at high values of SSB. Beverton-Holt-like functions are usually used for marine populations for which intra-cohort density-dependent processes occur at high SSB (e.g., competition among recruits for food or habitat), and Ricker-like functions when inter-cohort density-dependent processes take place when SSB becomes large (e.g., cannibalism).

Shepherd (1982) established a versatile functional form relating SSB to recruitment R:

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$$R = \frac{\alpha_0 SSB}{1 + \left(\frac{SSB}{K_0}\right)^{\beta}}$$
(1)

where α_0 is the slope of the SRR at low levels of SSB, K_0 the value of SSB above which compensatory density-dependent effects start dominating over density-independent effects (Shepherd, 1982; Barrowman and Myers, 2000), and β represents the degree of compensation (Shepherd, 1982). If $\beta = 1$, Eq. (1) becomes the classical Beverton-Holt function. If $\beta > 1$, Eq. (1) mimics the Ricker function (quasi-Ricker SRR) (Shepherd, 1982). It can be demonstrated that the maximum of the Shepherd function (R_0) is given by:

$$R_0 = \frac{\alpha_0 K_0 (\beta - 1)^{(\beta - 1)/\beta}}{\beta}$$
(2)

Fig. 1 shows large-scale Beverton-Holt and quasi-Ricker SRRs sharing α_0 and R_0 parameters. For a specific level of fishing mortality, *F*, equilibrium global recruitment is found at the intersection of the SRR curves with the 'replacement line' (Shepherd, 1982; Sissenwine and Shepherd, 1987; Goodyear, 1993; Mace and Sissenwine, 1993). The 'replacement line' is the line of slope 1/ (*SSB_{eq}*), where *SSB_{eq}* is the equilibrium SSB when the fishing mortality *F* is exerted on the fish population. Fishing reduces SSB and thus increases 1/ (*SSB_{eq}*) and shifts equilibrium recruitment to the left along the SRR curve. If 1/ (*SSB_{eq}*) becomes higher than α_0 , equilibrium recruitment is zero and the fish population collapses (Goodyear, 1993; Botsford et al., 2009) (Fig. 1).



Figure 1. Relationships between Spawning Stock Biomass (SSB) and Recruitment. The full curve is a Beverton-Holt relationship for which the initial slope α_0 and maximum value R_0 are indicated. The dashed and dotted curves are quasi-Ricker relationships, with, respectively $\beta = 1.5$ and $\beta = 2$, and the same α_0 and R_0 parameters as the Beverton-Holt curve. Equilibrium recruitment can be found at the intersection of the curves and a line with slope $1/(SSB_{eq})$ where SSB_{eq} is the equilibrium SSB when a specific level of fishing mortality is exerted on the fish population. Fishing reduces SSB, and thus increases $1/(SSB_{eq})$ and shifts

equilibrium recruitment to the left along the dashed curves. If 1/ (SSB_{eq}) becomes larger than α_0 , recruitment is zero and the fish population collapses.

Consider now an age-structured population with dispersing larvae, mobile adults, knife-edge maturity and seasonal patterns of reproduction, larval dispersal and recruitment. Individuals move from one age class to another each month. Spawning occurs at the beginning of each month, natural and fishing mortalities are continuous events taking place after spawning, and adult movement between zones of the study system is supposed to occur at given ages before spawning events. Fishing mortality rates for the different fleets vary across space and months. Population dynamics is given by (Edwards et al., 2009):

$$N_{z,t+1,0} = R_{z,t+1}$$

$$N_{z,t+1,a} = \left[N_{z,t,a-1} + N_{z,t,a-1}^{IMIG} - N_{z,t,a-1}^{MIG}\right]e^{-Z_{z,t,a-1}} \quad for \ 0 < a < p$$

$$N_{z,t+1,p} = \left[N_{z,t,p-1} + N_{z,t,p-1}^{IMIG} - N_{z,t,p-1}^{MIG}\right]e^{-Z_{z,t,p-1}} + \left[N_{z,t,p} + N_{z,t,p}^{IMIG} - N_{z,t,p}^{MIG}\right]e^{-Z_{z,t,p}}$$
(3)

where $N_{z,t,a}$ is the number of fish of age *a* in zone *z* at the start of time period *t* (i.e., at the start of a given month of a given year); $R_{z,t}$ the number of recruits (0 year old fish) in zone *z* at the start of time period *t*; N^{MIG} and N^{IMIG} are respectively the number of migrants (fish leaving the zone) and immigrants (fish entering the zone); *p* is the age plus group; and $Z_{z,t,a}$ the total mortality rate at age *a* in zone *z* at the start of time period *t*, which is equal to:

$$Z_{z,t,a} = \sum_{f} F_{z,f}^{Month} s_{f,a} + M_{a} \quad if \ t = Month$$

$$\tag{4}$$

where $F_{z,f}^{Month}$ represents the fishing mortality in zone z for fleet f a given month; $s_{f,a}$ the selectivity-at-age a for fleet f, which is assumed to be constant across space and months; and M_a the natural mortality rate at age a, which is taken to be constant across space and months.

Larval settlement in zone z at time $t(S_{z,t})$ is given by:

$$S_{z,t} = \sum_{z'} D_{zz'}^{Month} \left(\sum_{a=a_{mat}}^{p} \eta^{Month} N_a^{BATCHES} w_a \left[N_{z',t,a} + N_{z',t,a}^{IMIG} - N_{z',t,a}^{MIG} \right] \right) \quad if \ t = Month$$
(5)

where $D_{zz'}^{Month}$ is the probability of larval dispersal from zone z' to zone z a given month; $N_a^{BATCHES}$ represents the number of batches spawned per year at age a; η^{Month} the probability to spawn a given month relatively to the other months of the year; w_a the weight-at-age a; and a_{mat} the age of sexual maturity. Here, we assume for simplicity that weight-at-age is proportional to individual egg production, though egg production could equally well be an arbitrary function of age and weight (Berkeley et al., 2004; O'Farrell & Botsford, 2006). Then, local recruitment is related to local larval settlement by the Shepherd function:

$$R_{z,t} = \frac{\alpha S_{z,t}}{1 + \left(\frac{S_{z,t}}{K_z}\right)^{\beta}}$$
(6)

where α is the slope of the SRR at low levels of larval settlement; and K_z the level of larval settlement above which compensatory density-dependent effects start dominating over density-independent effects in zone z, which can be obtained from α and maximum recruitment in zone z ($R_{\max z}$):

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$$K_{z} = \frac{\beta R_{\max z}}{\alpha (\beta - 1)^{(\beta - 1)/\beta}}$$
(7)

To evaluate the parameters of small-scale SRRs, we propose a methodology in three steps: (1) the global annual natural SSB (i.e., global annual SSB in pristine conditions), $NSSB^{nonspatial}$, and the critical annual fishing mortality rate for the different fleets operating in the study system (i.e., the annual fishing mortality rate for the different fleets making the fish population collapse), $F_{crit}^{nonspatial}$, are estimated from the global population model; (2) the slope of SRRs at low levels of larval settlement, α , is adjusted so that the fish population collapses when the annual fishing mortality rate for the different fleets is at $F_{crit}^{nonspatial}$; and (3) the value of local maximum recruitment, $R_{max z}$, is adjusted so that global annual natural SSB in the spatial monthly model, $NSSB^{spatial}$, equals $NSSB^{nonspatial}$.

A detailed description of the non-spatial annual model used as the starting point in our parameterization of the spatial model (Step 1) can be found in Appendix A.

The local fishing mortality rate for fleet f for a given month that, summed over space and months, corresponds to the global fishing mortality rate that causes population collapse is calculated based on the observed fraction of the total fishing mortality that occurs in a grid cell-month:

$$F_{crit\ z,f}^{Month} = F_{crit\ f}^{nonspatial} \frac{F_{z,f}^{Month}}{\sum_{z} \sum_{Month} F_{z,f}^{Month}}$$
(8)

Underlying Eq. (8) is the assumption that the spatial distribution of the different fleets operating in the study system remains stationary as fishing mortality is adjusted to the collapse point. The monthly spatial model is run with these values of fishing mortality, considering that at low levels of larval settlement (i.e., near the point of population collapse) density-dependent processes can be ignored and local recruitment is a linear function of local

larval settlement (i.e., that: $R_{z,t} = \alpha S_{z,t}$) (Hastings and Botsford 2006; White 2010). Iteration is used to adjust α until the fish population collapses when local fishing mortality rates for the different fleets *f* are set to $F_{crit z, f}^{Month}$.

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To complete Step (3), the monthly spatial model is run to natural equilibrium, considering that local recruitment is determined by Eq. (6), and using the estimate of α obtained at the completion of Step (2). $R_{\max_{\alpha} z}$ is initially set to:

$$R_{\max z} = \frac{R_0}{12} \left(\frac{h_z}{\sum_{z'} h_{z'}} \right)$$
(9)

where h_z is the proportion of suitable habitat for recruitment in each zone. The model is then iterated, globally increasing or decreasing the values of $R_{\max z}$ until *NSSB*^{spatial} is equal to *NSSB*^{nonspatial}, with *NSSB*^{spatial} = $\sum_{Month} \eta^{Month} NSSB$ ^{spatialMonth}, where *NSSB*^{spatialMonth} is the global natural SSB in the spatial monthly model for a given month. Finally, K_z is estimated from α and $R_{\max z}$, using Eq. (7).

APPLICATION

We propose to apply our methodology to the South African population of deep-water hake in the theoretical spatial system depicted in Fig. B.

Merluccius paradoxus is a slow-growing and long-lived demersal species (Payne, 1989) which starts reproducing at around 4 years (Botha, 1986; Punt and Leslie, 1991). Hake reproduction occurs throughout the year, essentially on the shelf edge of South Africa (Botha, 1986; Hutchings et al., 2002), primarily from June to October (Crawford et al., 1987; Grote et al., 2007). Hake larvae are then carried by currents to nearshore recruitment areas (Hutchings et al., 2002; Grote et al., 2007; Stenevik et al., 2008). Juvenile hakes stay in recruitment areas for around 9 months (Payne, 1989). Individuals then gradually move into deeper waters as they grow older ('ontogenetic migrations'; Crawford et al., 1987; Payne, 1989). It is thought that the spawning frequency of *M. paradoxus* considerably increases with age until age 15 where it plateaus (Field et al., 2008). In South African waters, the deep-water hake resource is

exploited by demersal trawlers and longliners. The demersal trawl fleet catches mainly 3+ aged fish (Butterworth and Rademeyer, 2005), whereas the longline fleet catches mainly 6+ aged fish (Butterworth and Rademeyer, 2005; Fairweather et al., 2006).

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Our theoretical study system consists of eight zones. We consider that the hake population includes 181 monthly age classes. Individuals move from one age class to another each month until reaching the 181th age class, which is a plus age class representing all individuals 15 years old and older. Hake larvae recruit in zones 1 and 2. Hake individuals undergo two ontogenetic migrations during their life cycle: the former from zones 1-2 to zones 3-5 when they reach 9 months of age, and the latter from zones 3-5 to zones 3-8 when they reach 34 months of age. Spawning takes place in zones 3-8 and hake larvae are then dispersed to zones 1-2 (Fig. B). This configuration provides sufficient structure to demonstrate our methodology, though a full model of hake dynamics would have more complicated spatial and temporal structure. Details of the dynamics of the modeled system and parameter values are given in Appendix C.

The oceanic proportion of each recruitment zone is used as an index of the proportion of suitable habitat for recruitment in these areas. α_0 and R_0 are taken from the latest baseline stock assessment for *M. paradoxus* (Rademeyer et al., 2008). In the stock assessments, hake recruitment is related to SSB by means of a Beverton-Holt SRR (Rademeyer et al., 2008).

As a check of the consistency of our approach, we compare estimates of global annual SSB obtained from the spatial monthly model and its non-spatial annual counterpart for different levels of fishing mortality and three different forms of the SRRs (Beverton-Holt, or quasi-Ricker with a value of β of 1.5 or 2). We also examine values of global annual SSB obtained from the spatially explicit model when α is not adjusted to account for larval mortality during dispersal (i.e., when all the steps of our methodology but step 2 are followed).

RESULTS AND DISCUSSION

The methodology we developed allowed us to estimate the parameters of small-scale SRRs for a spatial monthly model designed for South African deep-water hake. When the initial slope of SRRs, α , is adjusted, the fish population collapses at the same level of total annual fishing mortality in the spatial monthly model and in the equivalent non-spatial annual

model (Fig. 2a). However, for fishing mortality rates below that making the fish population collapse, global annual SSB is lower in the spatial monthly model than in the non-spatial annual model (dashed red curves in Fig.2). Discrepancies between the spatial monthly model and its non-spatial annual counterpart are mainly due to heterogeneity in the spatial distribution of fishing mortality rates. Given the fleet distributions considered here, total annual fishing mortality rate in the zones where adults are concentrated is higher than that in the equivalent non-spatial model (Fig. 3). As a result, the adult survival rate is lower in the spatial monthly model than that in the non-spatial annual model (Fig. 4). Discrepancies between the spatial monthly model and its non-spatial annual counterpart are also due to spatial and seasonal patterns of reproduction and larval dispersal. Due to density-dependence in recruitment, mean recruitment levels for a seasonally variable population are not the same as and will generally be lower than those for a non-varying model (Kaplan 2006). Under alternative configurations of the study system, global annual SSB could be higher in the spatial monthly model than in the non-spatial annual model (e.g., if fishing effort is concentrated in recruitment areas, everything else equal), or at the same level (e.g., if fishing effort is uniformly distributed in spawning areas and the spatial and temporal patterns of reproduction and larval dispersal are ignored) (results not shown here).

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When α is not adjusted, larval mortality due to advection away from recruitment areas is double counted, leading to lower larval recruitment and an overestimation of the effects of fishing on global SSB (dashed-dotted blue curves in Fig. 2) (White 2010). Furthermore, fish population collapse occurs at lower levels of total annual fishing mortality in the spatial monthly model than in the equivalent non-spatial annual model. Discrepancies between when α is adjusted versus when it is not increase with the degree of compensation of the SRR, i.e., when β increases (Fig. 2).

In our methodology, we assumed a stationary spatial distribution of the different fleets operating in the study system as fishing mortality is increased or decreased, which is usually untrue in reality. In particular, when fish populations are severely depleted, fishing effort tends to concentrate towards high fish density areas, potentially hastening population collapse (Hilborn & Walters 1992; Hutchings 1996). Generally the goal of applied spatially-explicit models is to evaluate the long-term relative conservation and fisheries effects of spatial management measures, and to compare long-term relative population persistence and fisheries yields with and without MPAs (e.g., Mapstone et al. 2008; Kaplan et al. 2009; White et al. 2010). In this context and in the absence of models capable of accurately predicting the

response of fishers to population collapse, the spatially stationary approach used here is appropriate for estimating the dynamics of local recruitment processes from global stock assessment models.



Figure 2. Fraction of Natural Spawning Stock Biomass (FNSSB, i.e., SSB over Natural SSB) as a function of total annual fishing mortality rate (expressed in % of total critical annual fishing mortality rate, $F_{crit total}$), for the non-spatial model (full black curves), the spatial model when α , the initial slope of the stock-recruitment relationships, is adjusted (dashed black curves), and the spatial model when α is not adjusted (dashed-dotted black curves). For (**a**,**b**), a Beverton-Holt function was used to relate recruitment to larval settlement, while, for (**c**,**d**), a quasi-Ricker settler-recruit was used. For (**c**), $\beta = 1.5$, whereas, for (**d**), $\beta = 2$. For (**a**), blue and red arrows indicate the value of total annual fishing mortality rate above which the fish population collapses in the spatial model when α is adjusted and when it is not adjusted, respectively.



Figure 3. Spatial distribution of (**a**) Spawning Stock Biomass (expressed in fraction of total Spawning Stock Biomass in the study system) when global annual fishing mortality rate is at 15% of its critical value and (**b**) total annual fishing mortality rate (expressed in % of total annual fishing mortality rate in the equivalent non-spatial model); Spawning areas are colored in dark grey, while recruitment areas are colored in light grey.



Figure 4. Proportionate age structure of *Merluccius paradoxus* relative to age 0 (*P0*) in the non-spatial and the spatial model (full and dashed black curve, respectively) when total annual fishing mortality rate is at 15% of its critical value, and weight-at-age for the species (full grey curve). Note that the x-axis starts at 4 years (age of sexual maturity for *M. paradoxus*).

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SUPPLEMENTARY MATERIAL

Appendix A. Equivalent non-spatial annual model.

In the equivalent non-spatial annual model, individuals move from one age class to another each year, spawning occurs at the beginning of each year, and natural and fishing mortalities are continuous events taking place after spawning. Population dynamics is given by:

$$N_{t+1,0} = R_{t+1}$$

$$N_{t+1,a} = N_{t,a-1}e^{-Z_{t,a-11}} \quad for \ 0 < a < p$$

$$N_{t+1,p} = N_{t,p-1}e^{-Z_{t,p-1}} + N_{t,p}e^{-Z_{t,p}}$$
(A.1)

where $N_{t,a}$ is the number of fish of age *a* at the start of year *t*; R_t the number of recruits (0 year old fish) the start of year *t*; *p* is the age plus group; and $Z_{t,a}$ the total mortality rate at age *a* at the start of year *t*, which is equal to:

$$Z_{t,a} = \sum_{f} F_{f} s_{f,a} + M_{a}$$
(A.2)

where F_f represents the annual fishing mortality for fleet f; $s_{f,a}$ the selectivity-at-age a for fleet f; and M_a the natural mortality rate at age a.

Spawning Stock Biomass at year t (*SSB*_t) is given by:

$$SSB_t = \sum_{a=a_{mat}}^p w_a N_{t,a} \tag{A.3}$$

where w_a the weight-at-age *a*; and a_{mat} the age of sexual maturity. Then, annual recruitment is related to SSB though the Shepherd function:

$$R_{t} = \frac{\alpha_{0}SSB_{t}}{1 + \left(\frac{SSB_{t}}{K_{0}}\right)^{\beta}}$$
(A.4)

where α_0 is the slope of the SRR at low levels of SSB; K_0 the value of SSB above which compensatory density-dependent effects start dominating over density-independent effects; and β represents the degree of compensation.

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Figure B. The study system consists of eight zones. Zones 1 and 2 are recruitment areas (colored in light grey). Fish undergo ontogenetic migrations during their life cycle (i.e., move offshore and into deeper waters as they grow older), indicated by red and blue arrows. Spawning takes place in zones 3-8 (colored in dark grey) and ichthyoplankton is then dispersed to zones 1-2. Both trawl and longline fleets operate in all the zones of the study system.



Appendix C. Details of the modeled system.

South African deep-water hakes (*Merluccius paradoxus*) are assumed to reach sexual maturity at 4 years old (Botha, 1986; Punt and Leslie, 1991).

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We consider that the number of fish of age a undergoing an ontogenetic migration and consequently leaving zone z at time period t is given by:

$$N_{z,t,a}^{IMIG} = \sum_{z'=1, z' \neq z}^{TZ} N_{zz',t,a}^{mig} = \sum_{z'=1, z' \neq z}^{TZ} A_{z'z,a} N_{z,t,a}$$
(C.1)

where TZ is the total number of zones; $N_{zz',t,a}^{mig}$ the number of fish of age *a* migrating from zone *z* to zone *z*' at time period *t*, and $A_{z'z,a}$ the probability for individuals of age *a* to migrate from zone *z* to zone *z*'. It is considered that the number of fish of *a* entering zone *z*' from zone *z* at time period *t* ($N_{z'z,t,a}^{imig}$) is equal to the number fish of age *a* leaving zone *z* for zone *z*' at

time period *t*:

$$N_{z'z,t,a}^{imig} = N_{zz',t,a}^{mig} \tag{C.2}$$

That is, none of the fish that leaves zone z for zone z' at time period t dies from natural mortality or is caught during this time period. The probabilities of migration at age 9 and 32 months are given in Table C.1. At other ages, $N_{zz',t,a}^{mig}$ and $N_{z'z,t,a}^{imig}$ are equal to zero.

The probability for larvae to be dispersed from zone z' to zone z a given month is detailed in Table C.2. Following Field et al. (2008), we assume that the number of batches spawned by *M. paradoxus* increases linearly from once a year at age 2 to 14 per year at age 15, and thereafter remains constant at 14 batches per year. The probability for *M. paradoxus* to spawn a given month relatively to the other months of the year was determined from the results of Grote et al. (2007) (Table C.3).

Weight-at-age a is calculated from the combination of the von Bertalanffy growth equation and the mass-at-length function. The mass-at-length is obtained as:

$$w_a = \psi l_a^{\ \omega} \tag{C.3}$$

where l_a is the total length-at-age a, and ψ and ω are parameters of the mass-at-length function (see Table C.4). l_a is given by the following von Bertalanffy growth equation:

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$$l_{a} = l^{\infty} \left(1 - e^{-\frac{\rho(a-a^{0})}{12}} \right)$$
(C.4)

where l^{∞} , ρ and a^0 are the parameters of the von Bertalanffy growth equation, which are detailed in Table C.4.

For each fleet f, fishing mortality is assumed to be linearly proportional to fishing effort. Hence, local fishing mortality rate for fleet f a given month can be evaluated as:

$$F_{z,f}^{Month} = F_f^{nonspatial} \frac{E_{z,f}^{Month}}{\sum_{z} \sum_{Month} E_{z,f}^{Month}}$$
(C.5)

where $E_{z,f}^{Month}$ is the value of fishing effort in zone z for fleet f a given month. The values chosen for $E_{z,f}^{Month}$ are detailed in Table C.5.

Natural mortality-at-age *a* is given by:

$$M_{a} = \begin{cases} M_{2} / 12 & \text{for } a < 24 \\ \gamma^{M} + \tau^{M} / a + 1 & \text{for } 24 \le a \ge 72 \\ M_{5} / 12 & \text{for } a > 72 \end{cases}$$
(C.6)

with $\tau^{M} = \frac{1}{2} (M_{2} - M_{5})$ and $\gamma^{M} = \frac{M_{2}}{12} - \frac{\tau^{M}}{3}$. M_{2} and M_{5} (natural mortality at age 2 and 5 years, respectively) were taken directly from the results of baseline assessments in Rademeyer et al. (2008) (Table C.6).

The selectivity-at-age a for the different fleets was taken directly from the results of baseline assessments in Rademeyer et al. (2008) (Table C.6).

The slope of the large-scale SRR at low levels of SSB (α_0) and maximum annual recruitment (R_0) are taken from the latest baseline stock assessment for *M. paradoxus* (Rademeyer et al., 2008). The oceanic proportion of each recruitment zone is used as an index

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of the proportion of suitable habitat for recruitment in these areas. All these different parameters are given in Table C.7.

Table C.1.	Probabilities	of migration	at age 9 a	and 32 months.
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Age at which migration occurs	Source areas	Destination areas	Probability of migration
9 months	Zone 1	Zone 3	0.5
9 months	Zone 1	Zone 4	0.3
9 months	Zone 1	Zone 5	0.2
9 months	Zone 2	Zone 3	0.3
9 months	Zone 2	Zone 4	0.2
9 months	Zone 2	Zone 5	0.5
32 months	Zone 3	Zone 3	0.1
32 months	Zone 3	Zone 4	0.1
32 months	Zone 3	Zone 5	0.05
32 months	Zone 3	Zone 6	0.4
32 months	Zone 3	Zone 7	0.2
32 months	Zone 3	Zone 8	0.1
32 months	Zone 4	Zone 3	0.1
32 months	Zone 4	Zone 4	0.1
32 months	Zone 4	Zone 5	0.05
32 months	Zone 4	Zone 6	0.4
32 months	Zone 4	Zone 7	0.2
32 months	Zone4	Zone 8	0.15
32 months	Zone 5	Zone 3	0.1
32 months	Zone 5	Zone 4	0.1
32 months	Zone 5	Zone 5	0.05
32 months	Zone 5	Zone 6	0.4
32 months	Zone 5	Zone 7	0.2
32 months	Zone 5	Zone 8	0.15

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Source	Destination	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
areas	areas												
Zone 3	Zone 1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Zone 3	Zone 2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Zone 4	Zone 1	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14
Zone 4	Zone 2	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
Zone 5	Zone 1	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14
Zone 5	Zone 2	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06
Zone 6	Zone 1	0.1	0.04	0.02	0.02	0.02	0.02	0.1	0.04	0.02	0.1	0.14	0.17
Zone 6	Zone 2	0.1	0.16	0.18	0.18	0.18	0.18	0.1	0.16	0.18	0.1	0.06	0.03
Zone 7	Zone 1	0.14	0.08	0.19	0.19	0.19	0.19	0.14	0.08	0.19	0.1	0.15	0.1
Zone 7	Zone 2	0.06	0.12	0.01	0.01	0.01	0.01	0.06	0.12	0.01	0.1	0.05	0.1
Zone 8	Zone 1	0.14	0.17	0.1	0.1	0.1	0.1	0.14	0.17	0.1	0.1	0.08	0.06
Zone 8	Zone 2	0.06	0.03	0.1	0.1	0.1	0.1	0.06	0.03	0.1	0.1	0.12	0.14

Table C.2. Probability for larvae to be dispersed from the different spawning areas of the study system to the different recruitment areas for each of the months of the year.

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Month	Probability to spawn
January	0.01
February	0.01
March	0.02
April	0.01
May	0.01
June	0.05
July	0.37
August	0.11
September	0.23
October	0.05
November	0.03
December	0.1

Table C.3. Relative monthly probability for South African deep-water Cape hake to spawn (estimated from the results of Grote et al., 2007).

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Table C.4. Estimates of the parameter values of the von Bertalanffy growth and mass-at-length equations for deep-water Cape hake (Punt et al., 1992).

Parameter	Estimate
ψ(g)	0.00615
ω	3.046
l^{∞} (cm)	219.4
κ (year ⁻¹)	0.049
a^0 (years)	-0.914

Table C.5. Mon	thly values of fi	ishing effort for t	he trawl and	longline flee	ts in the	different z	ones of the	study sys	stem (in
units of month ⁻¹).								

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Fleet	Zone	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Trawl fleet	1	0.0625	0.0625	0.0625	0.0625	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313
	2	0.0625	0.0625	0.0625	0.0625	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313
	3	0.0625	0.0625	0.0625	0.0625	0.125	0.125	0.125	0.125	0.0625	0.0625	0.0625	0.0625
	4	0.0625	0.0625	0.0625	0.0625	0.125	0.125	0.125	0.125	0.0625	0.0625	0.0625	0.0625
	5	0.0625	0.0625	0.0625	0.0625	0.125	0.125	0.125	0.125	0.0625	0.0625	0.0625	0.0625
	6	0.0625	0.0625	0.0625	0.0625	0.125	0.125	0.125	0.125	0.0625	0.0625	0.0625	0.0625
	7	0.05	0.05	0.05	0.05	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	8	0.05	0.05	0.05	0.05	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Longline fleet	1	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0625	0.0625	0.0625	0.0625
	2	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0313	0.0625	0.0625	0.0625	0.0625
	3	0.0625	0.0625	0.0625	0.0625	0.125	0.125	0.125	0.125	0.0625	0.0625	0.0625	0.0625
	4	0.0625	0.0625	0.0625	0.0625	0.125	0.125	0.125	0.125	0.0625	0.0625	0.0625	0.0625
	5	0.0625	0.0625	0.0625	0.0625	0.125	0.125	0.125	0.125	0.0625	0.0625	0.0625	0.0625
	6	0.125	0.125	0.125	0.125	0.25	0.25	0.25	0.25	0.125	0.125	0.125	0.125
	7	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2
	8	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.2	0.2

Table	C.6.	Estimates	of natur	al morta	lity at a	nges 2	(M_2) and	l 5 yea	$rs(M_2)$	5), and	d sele	ctivity	-at-age	e for the di	fferent
fleets	(<i>s_{f,a}</i> ,	with $f = 1$: trawl	fleet and	l with <i>f</i>	f = 2:	longline	fleet,	and a	<i>i</i> in y	ears)	taken	from 1	Rademeye	r et al.
(2008)															

Parameter	Estimate
M2	0.51
M5	0.33
$s_{1,a}$ for $a = 1,2$	0
$s_{I,a}$ for $a = 3$	0.1839
$s_{I,a}$ for $a = 4$	0.8
$s_{1,a}$ for $a = 5,, 15 +$	1
$s_{2,a}$ for $a = 1,, 4$	0
$s_{2,a}$ for $a = 5$	0.0143
$s_{2,a}$ for $a = 6$	0.2857
$s_{2,a}$ for $a = 7$	0.8286
$s_{2,a}$ for $a = 8, \dots, 15+$	1

Table C.7. Estimates of parameters necessary for estimating small-scale stock-recruitment relationship parameters. Estimates for the two first parameters were taken from Rademeyer et al. (2008).

Parameter	Definition	Estimate
$R_0(10^9)$	Global annual recruitment in pristine conditions	1.2344
$K_0 (10^3 t)$	Global SSB at which density-dependent effects start dominating density-independent effects	18.5607
$h_{l}(\%)$	Proportion of waters in zone 1	0.75
$h_{2}(\%)$	Proportion of waters in zone 2	0.5
h_2 (%)	Proportion of waters in zone 2	0.5

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CHAPITRE 4. Evaluation of the long-term effects of marine protected areas for South African Cape hakes under different scenarios of fishing effort redistribution

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Abstract - The long-term conservation and fisheries effects of marine protected areas (MPAs) for South African Cape hakes were evaluated using a spatially-explicit population model. Our model represents the dynamics of shallow-water Cape hake, Merluccius capensis, and deepwater Cape hake, Merluccius paradoxus, within a spatial grid where inshore and offshore trawl and longline hake-directed fleets operate. The spatial grid of the model matches that used for Cape hake assessments in the South African Economic Exclusive Zone. The monthly time scale of the model allows us to describe seasonal patterns of reproduction, larval dispersal, recruitment and fleet distributions. Ontogenetic migrations (i.e., movements of juveniles and young adults into deeper water as they grow older) are represented in the model via migration matrices built using a GIS-based submodel. Rules describing the probabilities of migration of hake individuals at certain ages were implemented based on the bathymetry and alongshore direction for each zone. Monthly larval connectivity matrices for both Cape hake species were generated using an individual-based biophysical submodel, Ichthyop, integrating current variability and reproductive and recruitment information for each species (e.g., recruitment zones, pelagic larval durations, etc.). A number of MPA scenarios representing preferential protection for juveniles or adults of *M. paradoxus* were explored. Overall, MPAs increase Cape hake spawning stock biomass (SSB). Redistribution of the fishing effort formerly in MPAs to remaining fished areas reduces the conservation benefits of MPAs, and even leads to decreases in the SSB of *M. capensis* when protection efforts primarily target the younger sections of the *M. paradoxus* population. Our results suggest that increases in SSB will be greater for *M. paradoxus* when fishable juveniles of the species are the primary targets of protection efforts. In this situation, catches of M. paradoxus for the longline fleet are considerably increased while those for the offshore trawl fleet decrease. Moreover, we found that losses in total hake catches due to MPA creation will generally not be compensated by

increases in SSB, and that trade-offs between conservation benefits and catches of the different hake-directed fleets will be incurred by the creation of MPAs designed to protect M. *paradoxus*.

Keywords: South African hakes, marine protected areas (MPAs), ontogenetic migrations, fishing effort redistribution, spatially-explicit population model.

INTRODUCTION

The shallow-water Cape hake, *Merluccius capensis* (Castelnau, 1861), and the deepwater Cape hake, Merluccius paradoxus (Franca, 1960), are economically the most important marine resources in South Africa (Payne & Punt 1995, Sumaila et al. 2003, von der Heyden et al. 2007). Both hake species inhabit the waters of Namibia and South Africa - but management for the two countries remains separate - and they share a number of life history characteristics, such as nearshore recruitment zones and migrations offshore and into deeper waters with age ('ontogenetic migrations'; Botha 1971; Crawford et al. 1987; Payne 1989; Payne & Punt 1995; Le Clus et al. 2005a, b). Nevertheless, M. paradoxus is generally found in deeper waters than M. capensis (Botha 1985, Bianchi et al. 1999, Cohen 1999). Furthermore, *M. paradoxus* is predominant along the western coast of South Africa, whereas *M. capensis* is more numerous along the southern coast (Payne 1989; Payne & Punt 1995; Sumaila et al. 2003; Le Clus et al. 2005a, b). Concerns have recently been raised that the steady exploitation of deep fishing grounds could have detrimental effects on the recruitment success of Cape hakes and their long-term productivity (especially for *M. paradoxus*) because of the considerable contribution of large, old individuals to reproduction (Hutton & Sumaila 2002, Field et al. 2008). Due to the socioeconomic significance of the hake fishery in South Africa, management and sustainability measures have been proposed, among which the establishment of marine protected areas (MPAs) (Field et al. 2008, Sink & Attwood 2008). Because the spatial distributions of *M. paradoxus* and *M. capensis* only partially overlap, it is unclear whether MPAs may be effective for the conservation of both species without being extremely large, while at the same time improving the catches of hake-directed fleets.

Edwards et al. (2009) examined the consequences of creating a MPA for *M. paradoxus* in a zone that was previously heavily trawled, using a two-patch model (MPA, fished areas) with an annual time step. Edwards et al. (2009)'s model is based on the agestructured approach used for current assessments of Cape hakes. The hake-directed offshore trawl fleet is integrated in the model, but the other hake-directed fleets, namely the inshore trawl, longline and handline fleets, are not. The model assumes single instantaneous spawning and diffusive movement between the MPA and the fished areas before the time of reproduction. It also assumes that the catches of *M. paradoxus* formerly taken from the MPA are taken from remaining fished areas after MPA creation. Edwards et al. (2009)'s results suggested that the establishment of a no-take MPA would not improve the total SSB of *M. paradoxus*, regardless of the rate of hake movement from the MPA to the fished areas.
However, this model has a number of important weaknesses. In particular, larval dispersal and recruitment are uniform over space and adult movement is purely diffusive and spatially homogeneous. Observed spatial structuring of adult age classes of both species consistent with coherent offshore ontogenetic migrations (Crawford et al. 1987, Le Clus et al. 2005a, b) and spatial heterogeneity in the currents presumably driving larval dispersal (Hutchings et al. 2002, Stenevik et al. 2008) suggest that these assumptions of spatially homogeneous adult and larval movements may differ significantly for reality. As movement patterns have been regularly shown to significantly alter the results of MPA models (e.g., Walters et al. 2007, Moffitt et al. 2009, Grüss et al. 2011), it is logical to assume that altering these assumptions may have a non-negligible impact on the benefits MPAs potentially offer to Cape hakes.

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Edwards and Plaganyi (2011) developed a two-patch model quite similar to that of Edwards et al. (2009), in which they integrated the fecundity per unit mass at age of hakes, to explore the impacts of MPAs targeting preferentially the older or the younger sections of a population of *M. paradoxus*. Consistent with previous studies conducted for other demersal species (e.g., Pelletier & Magal 1996, Horwood et al. 1998, Beattie et al. 2002), the authors found that protecting preferentially the older, more fecund individuals without reducing overall catches at the time of MPA creation would likely displace high fishing effort onto sites occupied by young individuals, thereby reducing or eliminating MPA benefits for population reproductive capacity and catches of the offshore trawl fleet. On the other hand, fishing the older sections of the population and improve the productivity of the offshore trawl fleet.

In the present study, we take a significantly different approach to modeling the effects of MPAs on South African Cape hake resources. Though the model is based on the agestructured approach developed for the current Cape hake stock assessment described by Rademeyer et al. (2008), which is also the basis of the models developed in Edwards et al. (2009) and Edwards and Plaganyi (2011), detailed migratory movements and spatiallyexplicit larval dispersal patterns have been integrated with the goal of examining whether targeted MPAs (i.e., MPAs targeting specific age classes of the population) may be beneficial to the conservation of both *M. paradoxus* and *M. capensis* and to the fishing fleets depending on them. Furthermore, the monthly time scale of our model allows us to resolve seasonal patterns of reproduction, larval dispersal, recruitment and fleet distributions, further increasing the spatial structuring of model dynamics and, therefore, potentially contributing to MPA effects.

MATERIAL AND METHODS

Overview of the spatial distribution, life history and exploitation patterns of South African Cape hakes

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M. capensis is found between 0 and approximately 1000 m water column depth, while the distribution of *M. paradoxus* extends from roughly 100 to almost 1100 m depth (Botha 1985, Bianchi et al. 1999, Cohen 1999). Juveniles of *M. capensis* are abundant inshore (< 150 m of water depth), and a significant overlap occurs between large *M. capensis* and small *M. paradoxus* between 150 m and 400 m of water depth (Botha 1973, 1985, Pillar & Barange 1995). Based on catch and survey data, *M. paradoxus* is believed to be more abundant than *M. capensis* on the west coast of South Africa, whereas *M. capensis* is believed to be dominant over the Agulhas Bank west of 25°E (Payne 1989; Payne & Punt 1995; Sumaila et al. 2003; Le Clus et al. 2005a, b). Only a few Cape hakes live east of 25°E (Payne 1989) (Fig. 1). The distribution of Cape hakes appears to be determined by a combination of depth and substrate type (Payne 1989; Fairweather et al. 2006).



Figure 1. Distribution of the shallow-water (left) and deep-water (right) Cape hakes in the Southern Benguela region (redrawn from Payne 1989).

Reproduction of both *M. paradoxus* and *M. capensis* occurs throughout the year (Kono 1980, Shelton 1986), but intensifies from late winter to spring (June - October) (Botha 1986; Crawford et al. 1987; Grote et al. 2007), coinciding with a minimum in offshore Ekman transport (Hutchings et al. 2002). *M. capensis* and *M. paradoxus* are serial spawners, producing a large number of small eggs and larvae (Osborne et al. 1999; Hutchings et al. 2002). Batch fecundity of Cape hake females is positively correlated to their ovary-free mass and total length (Osborne et al. 1999), and it is expected that the number of batches per year and the larval survival rate are positively correlated with female age (Field et al. 2008). The number of batches spawned per season is thought to be the primary determinant of maternal recruitment effects (Field et al. 2008; Edwards & Plaganyi 2011).

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M. capensis and *M. paradoxus* seem to have different recruitment areas both on the west and south coasts of South Africa (Stenevik et al. 2008). According to current evidence, the main recruitment areas of *M. capensis* are located in shallow water (< 100 m) on the west coast of South Africa, between St. Helena Bay and Hondeklipbaai, and north of Port Nolloth, as well as on the south coast of South Africa between Hermanus and Plettenberg Bay, while the main recruitment areas of *M. paradoxus* are located in deeper water (> 100 m) northwest of Cape Town as far as Doringbaai and further north over Oranjemund (Crawford et al. 1987; Hutchings et al. 2002; Field et al. 2008; Stenevik et al. 2008) (Fig. 2).

Cape hake juveniles stay in the recruitment areas for approximately 8-9 months (fingerlings). Once they have reached about 15-20 cm, juveniles migrate offshore and become demersal (Botha 1971). There is evidence that both *M. paradoxus* and *M. capensis* undergo several other ontogenetic migrations during their early life (Botha 1971; Crawford et al. 1987; Payne 1989; Payne & Punt 1995; Le Clus et al. 2005a, b). Research surveys are conducted each year on the west and south coasts of South Africa from which the distribution areas of successive life stages of *M. capensis* and *M. paradoxus* can be determined (e.g., Le Clus *et al.* 2005a, 2005b). The distribution areas of the different life stages of *M. capensis* and *M. paradoxus* approximately parallel contours of bathymetry (Crawford et al. 1987; Payne 1989; Le Clus et al. 2005a, 2005b). Moreover, some authors suggest that mature Cape hakes may stay most of the year in offshore feeding grounds and undertake seasonal spawning migrations shorewards (Crawford et al. 1987; Olivar et al. 1988; Hutchings et al. 2002). Yet, there is currently no concrete evidence of such migrations (Botha 1973, Payne 1989, Payne & Punt 1995). *M. paradoxus* and *M. capensis* reach sexual maturity at approximately 4-5 years old (Botha 1986, Punt & Leslie 1991).



Figure 2. Study area of the model. Grids represent the 20' x 20' rectangles (minutes of latitude and longitude) covering the South African Economic Exclusive Zone that are used for Cape hake assessments. The border between the South and West coast components of South African Cape hakes is represented by a bold line.

Historically, *M. capensis* and *M. paradoxus* were exploited almost exclusively by demersal trawlers operating inshore and offshore. However, due to the heavy European demand for large fresh hakes in top condition, demersal longlining was introduced in 1998 (Fairweather et al. 2006; Field et al. 2008). The longlining industry represented around 10% of the South African Cape hake landings in 2006 (Rademeyer & Butterworth 2006). The longline fleet primarily targets *M. capensis* and catches mainly 6+ years old fish (Butterworth & Rademeyer 2005; Fairweather et al. 2006), whereas the trawling fleets primarily targets *M. paradoxus* and catches mainly 3+ years old fish (Butterworth & Rademeyer 2005). South African Cape hakes are also caught by the handline fishery (2% of the total catch) (Sumaila et al. 2003, Edwards et al. 2009). *M. capensis* and *M. paradoxus* have been assessed separately in South Africa since 2007 (Rademeyer & Glazer 2007; Field et al. 2008). The most recent baseline stock assessment suggests that the spawning stock biomass (SSB) of *M. paradoxus* is at a relatively low level (Rademeyer & Butterworth 2010). *M. paradoxus* SSB is estimated to be at about 15% of its natural value, whereas *M. capensis* stock is in a somewhat healthier

state since its SSB is estimated to be at about 54% of its natural value (Rademeyer & Butterworth 2010).

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Model description

We developed an age-structured model with a monthly time step representing the dynamics of both *M. paradoxus* and *M. capensis* within a spatial grid where inshore and offshore trawl and longline hake-directed fleets operate. The zones of our model are the grids covering South African Economic Exclusive Zone used for Cape hake assessments which are located west of 27°66E (20'x20' rectangles, minutes of latitude and longitude, Fig. 2). Ontogenetic migrations are represented in the model via migration matrices built using a GIS-based submodel. Monthly larval connectivity matrices for both Cape hake species were generated using an individual-based biophysical submodel, Ichthyop, integrating current variability and reproductive and recruitment information for each species. For each hake species, local monthly values of fishing mortality rates for each fleet were estimated from fishing effort data over the period 2004-2008 provided by the Department of Agriculture, Forestry and Fisheries (DAFF), South Africa.

Overall model structure

We consider that each hake species includes 180 monthly age classes. Individuals move from one age class to another each month until reaching the 181^{th} age class, which is a plus age group representing all individuals 15 years old and older. Natural mortality-at-age, selectivity-at-age and catchability for each fleet are assumed to be the same across zones and constant over time. We consider that spawning takes place at the beginning of each month and that natural and fishing mortalities are continuous events occurring after spawning. Ontogenetic migrations are supposed to occur at certain ages before spawning events. Both *M. paradoxus* and *M. capensis* are assumed to reach sexual maturity at 4 years old (Botha 1986, Punt & Leslie 1991).

The resource dynamics of the two populations of South African Cape hakes are given by the following equations (Edwards et al. 2009):

$$N_{s,z,t+1,0} = R_{s,z,t+1}$$

$$N_{s,z,t+1,a} = \left[N_{s,z,t,a-1} + N_{s,z,t,a-1}^{IMIG} - N_{s,z,t,a-1}^{MIG}\right]e^{-Z_{s,z,t,a-1}} \quad for \ 0 < a < p_s$$

$$N_{s,z,t+1,p_s} = \left[N_{s,z,t,p_s-1} + N_{s,z,t,p_s-1}^{IMIG} - N_{s,z,t,p_s-1}^{MIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,t,p_s} + N_{s,z,t,p_s}^{IMIG} - N_{s,z,t,p_s}^{MIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,t,p_s} + N_{s,z,t,p_s}^{IMIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,t,p_s} + N_{s,z,t,p_s}^{IMIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,t,p_s} + N_{s,z,t,p_s}^{IMIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,t,p_s} + N_{s,z,t,p_s}^{IMIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,t,p_s-1} + N_{s,z,t,p_s-1}^{IMIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,p_s-1} + N_{s,z,p_s-1}^{IMIG}\right]e^{-Z_{s,z,t,p_s-1}} + \left[N_{s,z,p_s-1} + N_{s,z,p_s-1}^{IMIG}\right]e^{-Z_{s,z,p_s-1}} + \left[N_{s,z,p_s-1} + N_{s,z,p_s-1}^{IMIG}\right]e^{-Z_{s,z,p_s-1}} + \left[N_{s,z,p_s-1} + N_{s,z,p_s-1}^{IMIG}\right]e^{-Z_{s,z,p_$$

where $N_{s,z,t,a}$ is the number of fish of species *s* and age *a* in zone *z* at the start of time period *t* (i.e., at the start of a given month of a given year); $R_{s,z,t}$ the number of recruits (0 year old fish) of species *s* in zone *z* at the start of time period *t*; N^{MIG} and N^{IMIG} are respectively the number of migrants (fish leaving the zone) and immigrants (fish entering the zone); p_s is the plus age group of species *s*; and $Z_{s,z,t,a}$ the total mortality rate of species *s* at age *a* in zone *z* at time period *t*, which is equal to:

$$Z_{s,z,t,a} = \sum_{f} F_{s,z,f}^{Month} S_{s,f,a} + M_{s,a} \quad if \ t = Month$$
⁽²⁾

where $F_{s,z,f}^{Month}$ is the fishing mortality rate of species *s* in zone *z* for fleet *f* for a given month; $S_{s,f,a}$ the selectivity-at-age *a* for species *s* and fleet *f*; and $M_{s,a}$ the natural mortality rate of species *s* at age *a*.

For each fleet, fishing mortality rate is linearly proportional to fishing effort since catchability for each fleet is assumed to be the same across zones and constant over time. Therefore, local fishing mortality rate for species s and fleet f for a given month is evaluated as:

$$F_{s,z,f}^{Month} = F_{s,f}^{Total} \frac{E_{s,z,f}^{Month}}{\sum_{z}^{TZ} \sum_{Month} E_{s,z,f}^{Month}}$$
(3)

where *TZ* is the total number of zones; $F_{s,f}^{Total}$ the annual fishing mortality rate for species *s* and fleet *f* over all zones; and $E_{s,z,f}^{Month}$ the value of fishing effort in zone *z* for species *s* and fleet *f* for a given month.

The selectivity-at-age a for the different species and fleets was taken directly from the results of baseline stock assessments in Rademeyer et al. (2008) (Table 1).

Natural mortality-at-age *a* for species *s* is given by:

$$M_{s,a} = \begin{cases} M_{s,2} / 12 & \text{for } a < 24 \\ \gamma^{M_s} + \tau^{M_s} / a + 1 & \text{for } 24 \le a \ge 72 \\ M_{s,5} / 12 & \text{for } a > 72 \end{cases}$$
(4)

with $\tau^{M_s} = \frac{1}{2} (M_{s,2} - M_{s,5})$ and $\gamma^{M_s} = \frac{M_{s,2}}{12} - \frac{\tau^{M_s}}{3}$. $M_{s,2}$ and $M_{s,5}$ (natural mortality of species *s* at age 2 and 5 years, respectively) were taken directly from the results of baseline stock assessments in Rademeyer et al. (2008) (Table 1).

Table 1. Estimates of natural mortality at ages 2 (M_2) and 5 years (M_5), and selectivity-at-age for the different fleets ($S_{f,a}$, with f = 1: inshore trawl fleet, f = 2: offshore trawl fleet, f = 3: longline fleet, and a in years) for *Merluccius paradoxus* and *M.capensis*, taken from Rademeyer et al. (2008).

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Parameter	Estimate for Merluccius paradoxus	Estimate for Merluccius capensis
M2	0.51	0.75
M5	0.33	0.34
$S_{1,a}$ for $a = 1,2$	-	0
$S_{I,a}$ for $a = 3$	-	0.0613
$S_{I,a}$ for $a = 4$	-	0.4429
$S_{I,a}$ for $a = 5$	-	0.8857
$S_{I,a}$ for $a = 6$	-	1
$S_{I,a}$ for $a = 7$	-	0.3714
$S_{I,a}$ for $a = 8$	-	0.1286
$S_{1,a}$ for $a = 9$	-	0.0571
$S_{1,a}$ for $a = 10$	-	0.0143
$S_{I,a}$ for $a = 11,,15+$	-	0
$S_{2,a}$ for $a = 1,2$	0	0
$S_{2,a}$ for $a = 3$	0.1839	0
$S_{2,a}$ for $a = 4$	0.8	0.0613
$S_{2,a}$ for $a = 5$	1	0.4571
$S_{2,a}$ for $a = 6$	1	0.8857
$S_{2,a}$ for $a = 7,, 15+$	1	1
$S_{3,a}$ for $a = 1,,4$	0	0
$S_{3,a}$ for $a = 5$	0.0143	0.0143
$S_{3,a}$ for $a = 6$	0.2857	0.2857
$S_{3,a}$ for $a = 7$	0.8286	0.8286
$S_{3,a}$ for $a = 8,, 15+$	1	1

Total length-at-age *a* for species s, $l_{s,a}$, is given by the following von Bertalanffy growth equation:

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$$l_{s,a} = l_s^{\infty} \left(1 - e^{\frac{-\rho_s \left(a - a_s^0 \right)}{12}} \right)$$
(5)

where l_s^{∞} , ρ_s and a_s^0 are the parameters of the von Bertalanffy growth equation, which are detailed in Table 2.

Weight-at-age a for species s is then calculated from the combination of the von Bertalanffy growth equation and the mass-at-length function:

$$w_{s,a} = \psi_s l_{s,a}^{\omega_s} \tag{6}$$

where ψ_s and ω_s are parameters of the mass-at-length function for species s (see Table 2).

Parameter Merluccius **Merluccius** capensis paradoxus ψ(g) 0.00505 0.00615 3.113 3.046 ω l^{∞} (cm) 270.6 219.4 ρ (year⁻¹) 0.039 0.049 a^0 (years) -0.73 -0.914

Table 2. Estimates of the parameter values of the von Bertalanffy growth and mass-at-length equations for *Merluccius capensis* and *Merluccius paradoxus* (Punt & Leslie 1991).

The Spawning Stock Biomass (SSB) of species *s* in zone *z* at time period *t*, and commercial catches-at-age *a* for species *s* and fleet *f* in zone *z* at time period *t* ($C_{s,z,f,t,a}$) are evaluated, respectively as:

$$SSB_{s,z,t} = \sum_{a=48}^{p_s} w_{s,a} \left[N_{s,z,t,a} + N_{s,z,t,a}^{IMIG} - N_{s,z,t,a}^{MIG} \right]$$
(7)

and:

$$C_{s,z,f,t,a} = w_{s,a} \Big[N_{s,z,t,a} + N_{s,z,t,a}^{IMIG} - N_{s,z,t,a}^{MIG} \Big] \frac{F_{s,z,f,t} S_{s,f,a}}{Z_{s,z,t,a}} \Big(1 - e^{-Z_{s,z,t,a}} \Big)$$
(8)

Larval settlement and recruitment

The number of recruits of species *s* in zone *z* at the start of time period *t*, $R_{s,z,t}$, is obtained from larval settlement of species *s* for zone *z* at time *t* ($LS_{s,z,t}$) using a Beverton-Holt settler-recruit relationship:

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$$R_{s,z,t} = \frac{\alpha LS_{s,z,t}}{1 + \begin{pmatrix} LS_{s,z,t} \\ K_{s,z} \end{pmatrix}}$$
(9)

where α is the slope of the settler-recruit relationship at low levels of larval settlement; and K_z the level of larval settlement above which compensatory density-dependent effects start dominating over density-independent effects in zone *z*, which can be obtained from α and maximum recruitment in zone *z* ($R_{\max z}$):

$$K_z = \frac{R_{\max z}}{\alpha} \tag{10}$$

Larval settlement for species *s* in zone *z* at time period *t* is given by:

$$LS_{s,z,t} = \sum_{z'} D_{s,zz'}^{Month} \left(\sum_{48}^{p} \eta_{s}^{Month} N_{s,a}^{BATCHES} w_{s,a} \left[N_{s,z',t,a} + N_{s,z',t,a}^{IMIG} - N_{s,z',t,a}^{MIG} \right] \right) \quad if \ t = Month$$
(11)

where $D_{s,zz'}^{Month}$ is the probability of larval dispersal from zone z' to zone z for a given month for species s; $N_{s,a}^{BATCHES}$ represents the number of batches spawned by species s per year at age a; η_s^{Month} the probability for species s to spawn a given month relatively to the other months of the year. Here, we assume for simplicity that weight-at-age is proportional to individual egg production, though egg production could equally well be an arbitrary function of age and weight (e.g., Berkeley et al. 2004, O'Farrell & Botsford 2006).

Following Field et al. (2008), we assume that the number of batches spawned by M. *paradoxus* increases linearly from once a year at age 2 to 14 per year at age 15, and thereafter

remains constant at 14 batches per year. Values for η_s^{Month} are determined from the results of Grote et al. (2007) (Table 3).

Month	Probability to spawn
January	0.01
February	0.01
March	0.02
April	0.01
May	0.01
June	0.05
July	0.37
August	0.11
September	0.23
October	0.05
November	0.03
December	0.1

Table 3. Relative monthly probabilities for South African Cape hakes to spawn (estimated from the results of Grote et al. 2007).

The monthly probabilities of larval dispersal between zones were estimated from simulations of an offline Lagrangian individual-based model distributed as a free Java tool, Ichthyop (Lett et al. 2008), Ichthyop's simulations tracked larval individuals from defined spawning zones to defined recruitment zones. Larval individuals were considered to be entirely passive during their drift period and were characterized by their latitude, longitude and depth. Larval locations were updated every hour (time-step of the Lagrangian model) via a forward-Euler integration scheme using the three-dimensional velocity fields from the ouputs of a ROMS (Regional Ocean Modeling System) model developed by Chang (2009). A detailed description of the ROMS model is provided in Garavelli et al. (submitted). Egg buoyancy and larval vertical migration were ignored since previous studies on Cape hakes or related hake species showed that these factors had negligible impacts on larval settlement patterns (Sabatés 2004, Sakuma et al. 2007, Garavelli et al. submitted).

We estimated the extent of recruitment zones for each hake species from maps of the distribution areas of 'juvenile' individuals (i.e., individuals < 20 cm) in Le Clus et al. (2005a, 2005b) since Cape hakes undertake their first ontogenetic migrations when they reach approximately 17 cm (Botha 1971). We considered that recruitment zones cover all areas where 'juvenile' abundance is high (i.e., >3.5 per 30-minute trawl over the period 1990-2003 in Le Clus *et al.* (2005a, 2005b)). These zones corresponded well with bathymetric ranges of 0-100 m and100-200 m for *M. capensis* and *M. paradoxus*, respectively. One could consider that recruitment zones for *M. paradoxus* are located on the west coast only as the survey data in Le Clus et al. (2005a, 2005b) indicates little evidence of *M. paradoxus* recruits along the south coast. However, given evidence that *M. paradoxus* recruits on the south coast as well (Crawford et al. 1987, Hutchings et al. 2002), we considered that recruitment zones of *M. paradoxus* were located on both the west and the south coasts.

For both hake species, it was assumed that spawning can occur in all the zones of the model provided reproductively mature individuals are present in a given zone. For both *M. paradoxus* and *M. capensis*, we considered that spawning depth ranges between 0 and 300 m (Botha 1973; Sundby et al. 2001; Grote et al. 2007; Stenevik et al. 2008) and that larvae settle in recruitment zones after 26 to 30 days of passive drift (i.e., during the last five days of the Ichthyop simulations) (Stenevik et al. 2008).

The horizontal extension of the spawning and recruitment zones was defined by a quadrilateral (specified by the horizontal coordinates of four points) and a superimposed bathymetric mask that limits the area to the portion of the quadrilateral for which bottom depth was within lower and upper bathymetric limits. A fixed number of larval individuals was homogeneously distributed over the spawning zones in all simulations (400 000; this value was selected for being high enough to provide robust simulated patterns). Egg release occurred at the beginning of each month, from climatology years 4 to 9 of the ROMS model. For the different months of the year, the probability of larval dispersal from a given spawning zone z1 to a given recruitment zone z2 at some point during the last five days of larval drift simulations.

Ontogenetic migrations

Ontogenetic migrations are simulated via age-specific connectivity matrices quantifying the movement of individuals of a given species and age from one zone to other zones. We consider that the number of fish of species s and age a undergoing an ontogenetic migration and consequently leaving zone z at time period t is given by:

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$$N_{s,z,t,a}^{MIG} = \sum_{z'=1, z'\neq z}^{TZ} N_{s,zz',t,a}^{mig} = \sum_{z'=1, z'\neq z}^{TZ} A_{s,z'z,a} N_{s,z,t,a}$$
(12)

where $N_{s,zz',t,a}^{mig}$ is the number of fish of species *s* and age *a* migrating from zone *z* to zone *z*' at time period *t*; and $A_{s,z'z,a}$ the probability for individuals of species *s* and age *a* to migrate from zone *z* to zone *z*'. It is considered that the number of fish of species *s* and age *a* entering zone *z*' from zone *z* at time period *t* ($N_{s,zz',t,a}^{mig}$) is equal to the number fish of species *s* and age *a* leaving zone *z* for zone *z*' at time period *t*:

$$N_{z'z,t,a}^{imig} = N_{zz',t,a}^{mig} \tag{13}$$

That is, none of the fish that leaves zone z for zone z' at time period t dies from natural mortality or is caught during this time period.

For each Cape hake species, the probabilities of migration of individuals of age *a* between zones ($A_{s,z'z,a}$) were estimated from simulations of a GIS-based submodel. The ages at which ontogenetic migrations occur were determined from the size-category boundaries used in Le Clus et al. (2005a, 2005b) to separate hake life stages (Table 4). The probability of an individual migrating from one area to another during one of these migration events was based on rules that are a function of local bathymetry and alongshore direction. These rules were generated so that the spatial distribution of the different life stages would roughly reproduce the mean depth and depth range found in Le Clus et al. (2005a, 2005b) and so that individuals would have a greater probability of migrating 'close' to their starting locations, as opposed to distant areas. 'Close' in this context is defined using a distance calculation algorithm that avoids land and favors movement along isobaths centered on the mean depth for a given life stage (see following paragraphs for more details).

Table 4. Estimated ages at which ontogenetic migrations occur for South African deep-water Cape hake (*Merluccius paradoxus*) and shallow-water Cape hake (*Merluccius capensis*), corresponding size categories (*sensu* Le Clus et al. 2005a, 2005b), and mean depth of the of the distribution areas of individuals of the post-migration life stage.

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Species	Length	Age	Size category undertaking migration	Mean depth of the distribution areas of the post-migratory life stage
Merluccius paradoxus	17 cm	9 months	'Juveniles'	344 m
	35 cm	2 years and 8 months	'Small'	375 m
	45 cm	3 years and 9 months	'Medium small'	390 m
	55 cm	5 years	'Medium large'	400 m
Merluccius capensis	17 cm	11 months	'Juveniles'	165 m
	35 cm	2 years and 10 months	'Small'	234 m
	45 cm	3 years and 11 months	'Medium small'	306 m
	55 cm	5 years and 1 month	'Medium large'	386 m

Bathymetry data were extracted from the GEBCO 1-minute global bathymetry dataset (http://www.gebco.net - Accessed 21 Jun 2011). From these data, we calculated the aspect (i.e., the horizontal direction to which a slope faces) for each cell of the model. Local alongshore direction was then obtained by subtracting 90° from each cell's aspect. Using these maps of bathymetry and local alongshore direction, ontogenetic migration matrices were estimated in four steps. First, we determined all potential destination areas from estimates of the depth range of the distribution areas of individuals of the given post-migration life stage (Fig. 3a). Second, it was necessary to determine the location of the center of the postmigration distribution of individuals originating from each source cell, here referred to as the 'destination centroid'. All model zones with depth at or greater than the mean depth of the post-migration distribution of individuals were considered potential destination centroids (Fig. 3b). The final 'destination centroid' used for each point of origin was the cell that minized the 'path distance' between origin and destination (i.e., the distance along a curvilinear trajectory connecting two grid cells that takes into account costs for the different types of directional movement), where path distance was calculated using the 'Path Distance' module of ArcGIS 9.3 (ESRI 2009) configured so as to heavily favor downslope movements over upslope movements (by a factor of 100:1) and over along isobaths movement (10:1) (Fig. 3c).

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(a)

Figure 3. Different steps for estimating the probabilities of migration of Cape hakes at certain ages between 'source' and 'destination' areas (i.e., between the distribution areas of individuals of age a_1 and those of individuals of age a_2). Here is an example with the first ontogenetic migration of *Merluccius capensis* from the zone with GRID ID 426. (a) Determination of all potential destination areas (blue areas). Source areas are indicated by red crosses. (b) Determination of the most likely destination cells (brown areas). (c) Determination of the destination centroid, the most likely destination cell with minimum path distance from the source cell. (d) Evaluation of the path distance from the source cell.

Once these first two steps were completed and the destination centroid was determined, probabilities of migrating to specific zones from each origin were determined based on a second path distance calculation from the destination centroid to surrounding cells (Fig. 3d). In this case, the path distance algorithm was configured so that alongshore movements from the destination centroid were favored over cross-shore movements by a factor of 5:1. This ratio was chosen because the distribution areas of the different hake life stages were approximately parallel to bathymetric contours, suggesting stronger alongshore than cross-shore movement (Crawford et al. 1987; Payne 1989; Le Clus et al. 2005a, 2005b), and so that the final migration probabilities would qualitatively correspond with the set of depth ranges for the different life stages. In the final step, path distances from the destination centroids were transformed into migration probabilities as the negative exponential of the distance normalized so that the mean distance of movement from the destination centroid would be 100 km in terrain with constant bathymetry. This distance of 100 km was chosen because it roughly agrees with the extremely limited data regarding the distance of migratory movements (Botha 1973, 1980). Final migration probabilities were normalized so that the sum over all destination locations yields a probability of 1.

Estimation of local settler-recruit relationship parameters

Central to the dynamics of most stock assessment models is density-dependence during recruitment of larvae into the adult population. In the context of spatially-explicit MPA models, one issue is how to translate population-level stock-recruitment relationships into settler-recruit relationships (SRRs) valid at the level of a single grid cell (White 2010). Here, we follow the methodology proposed by Grüss et al. (submitted) to scale down from the global stock-recruitment relationship found in Cape hake stock assessments (Rademeyer et al. 2008): (1) the global annual natural SSB (i.e., global annual SSB in pristine conditions), *NSSB*^{nonspatial}, and the critical level of annual fishing mortality rate (i.e., the annual fishing mortality rate for the different fleets that produces population collapse, assuming constant ratio of fishing effort among the fleets), $F_{crit f}^{nonspatial}$, were estimated from the global stock assessment model; (2) the slope of SRRs at low levels of larval settlement, α , was adjusted so that the fish population collapses when the annual fishing mortality rate for the different fleets larval settlement, $R_{max z}$, was adjusted so that global annual natural SSB in the spatial monthly model, *NSSB*^{spatial}, equals *NSSB*^{nonspatial}.

A detailed description of the non-spatial annual model used as the starting point in our parameterization of the spatial model (Step 1) can be found in Appendix A.

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The local fishing mortality rate for fleet f for a given month that, summed over space and months, corresponds to the global fishing mortality rate that causes population collapse was calculated based on the observed fraction of total fishing effort that occurs in a grid cellmonth:

$$F_{crit\ z,f}^{Month} = F_{crit\ f}^{nonspatial} \frac{E_{z,f}^{Month}}{\sum_{z\ Nonth}^{TZ} \sum_{z\ Month} E_{z,f}^{Month}}$$
(14)

Underlying Eq. (14) is the assumption that the spatial distribution of the different fleets operating in the study system remains stationary as fishing mortality is adjusted to the collapse point.

As mentioned above, absolute values of $R_{\max z}$ were fixed so that spatial and nonspatial natural SSB levels agreed. Relative values of $R_{\max z}$ (i.e., differences in maximum possible recruitment levels between sites), on the other hand, were based on the volume of each zone with bathymetry in the range of that of recruitment areas (i.e., 0-100 m and 100-200 m for *M. capensis* and *M. paradoxus*, respectively). In essence, it was assumed that this volume was a reasonable index of carrying capacity for each zone. The volume of each zone with bathymetry in the range of that of recruitment areas was estimated from bathymetry data extracted from the GEBCO 1-minute global bathymetry dataset (<u>http://www.gebco.net</u> – Accessed 2011 Jun 21).

Evaluation of the long-term effects of MPAs

We used the model described above to evaluate the long-term conservation and fisheries effects of MPAs for South African Cape hakes. First, local monthly values of fishing mortality rates for the different fleets were adjusted so that in the absence of MPAs global annual SSB are at 15% and 54% of its natural value for *M. paradoxus* and *M. capensis*, respectively. Then, scenarios where fishing activities are not permitted year-round in certain zones of the model were considered and the model was run to equilibrium to evaluate the

long-term impacts of MPAs on the SSB of *M. paradoxus* and *M. capensis* and the catches of the inshore and offshore trawl and longline fleets.

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Adjustment of local monthly values of fishing mortality rates before MPA creation

For each hake species, local monthly values of fishing mortality rates for each fleet over the period 2004-2008 were estimated from local monthly values of fishing effort over the period 2004-2008 (provided by the DAFF, South Africa) and estimates of annual fishing mortality rate over all zones ($F_{s,f}^{Total}$) over the same time period (estimated from Rademeyer & Butterworth (2010)), using Eq. (3).

Trawl effort data were available for each of the zones represented in the model for the period 2004-2008. From these data, for each of the trawl fleets, the average value of fishing effort over the period 2004-2008 was calculated for each zone and month (Figs. A2 and A3). By contrast, spatialized longline effort data were only available for the period prior to 2003. We made the assumption that the mean seasonal spatial distribution of longline effort over the period 2004-2008 is identical to that over the period 1998-2002. We then estimated average longline effort for each zone and month from estimates of monthly relative longline effort over the period 2004-2008 (Fig. A3). Total annual fishing effort for the different hake-directed fleets in the different zones of the model is given in Figure 5. The zones where the inshore and offshore trawl fleets, longline fleet, and at least one the different hake-directed fleets operate at least one month every year over the period 2004-2008 are shown in Fig. 5.

Then, the model was iterated, globally increasing or decreasing the value of annual fishing mortality rates for each species and fleet over all zones (keeping relative fishing mortalities among different fleets for the same species constant), $F_{s,f}^{Total}$, until global annual SSB was at 15% and 54% of its natural value for *M. paradoxus* and *M. capensis*, respectively. Following Rademeyer et al. (2008), we made the assumption that *M. paradoxus* is not targeted by the inshore trawl fleet, i.e., fishing mortality rate of *M. paradoxus* by the inshore trawl fleet was set to zero in all zones and for all months.

25[°] E

163

3000 of hours)

2500 agunu) 2000 totta

1500 iui

500

0

(c)

15[°] E

30[°] S

32[°] S

34[°] S

36[°] S

South Africa

20[°] E

Figure 4. Total annual fishing effort for the (**a**) inshore trawl, (**b**) offshore trawl, (**c**) longline fleet over the period 2004-2008.

Figure 5. Zones where the (a) inshore trawl, (b) offshore trawl, (c) longline and (d) the different hake-directed fleets operate at least one month every year over the period 2004-2008 (black areas).

MPA scenarios

Eight MPA scenarios were assessed. These scenarios were designed to evaluate the long-term impacts of protecting preferentially the older or younger sections of the *M*. *paradoxus* population on the SSB of *M. paradoxus* and *M. capensis* and the catches of the inshore and offshore trawl and longline fleets. Here, MPAs are designed to protect preferentially *M. paradoxus* since the SSB of this species is at a low level while the *M. capensis* stock is in a relatively healthy state (Rademeyer & Butterworth 2010).We assumed that the fishing effort that was in MPAs before they were closed either disappeared ('effort disappearance case') or was fully redistributed to remaining fished areas at the time of MPA creation ('effort redistribution case'). For each MPA scenario, the location of MPAs was determined after running the model in the absence of MPAs. The different MPA scenarios are described in Table 5.

When the fishing effort that was in MPAs before they were closed disappears at the time of MPA creation, fishing mortality for species s and fleet f in zone z after MPA creation is given by:

$$F_{s,z,f,t} = \begin{cases} F_{s,z,f}^{Month} & \text{if } z \in \Omega_F & \text{if } t = Month \\ 0 & \text{if } z \notin \Omega_F \end{cases}$$
(15)

where Ω_F represents the areas remaining fished after MPA creation. When the fishing effort that was in MPAs before they were closed does not disappear at the time of MPA creation, we assume that this effort is preferentially redistributed to high fishing effort areas. Therefore, in this case, fishing mortality rate for species *s* and fleet *f* in zone *z* after MPA creation is given by:

$$F_{s,z,f,t} = \begin{cases} F_{s,z,f}^{Month} + \sum_{z'=1,z'\neq z}^{CZ} F_{s,z',f}^{Month} \frac{E_{s,z,f}^{Month}}{\sum_{z=1}^{FZ} E_{s,z,f}^{Month}} & \text{if } z \in \Omega_F & \text{if } t = Month \\ 0 & \text{if } z \notin \Omega_F \end{cases}$$

$$(16)$$

where CZ represents the total number of zones set aside as MPA.

MPA scenario	Description	Fate of the fishing effort that was in MPAs before they were closed
#1	The 50 zones with highest abundance of large adults of <i>M. paradoxus</i> (5+ years old individuals) are closed year-round to all fishing activities	Disappearance
#2	The 50 zones with highest abundance of large adults of <i>M. paradoxus</i> (5+ years old individuals) are closed year-round to all fishing activities	Full redistribution to the remaining fished areas
#3	The 100 zones with highest abundance of large adults of <i>M. paradoxus</i> (5+ years old individuals) are closed year-round to all fishing activities	Disappearance
#4	The 100 zones with highest abundance of large adults of <i>M. paradoxus</i> (5+ years old individuals) are closed year-round to all fishing activities	Full redistribution to the remaining fished areas
#5	The 50 zones with highest abundance of fishable juveniles of <i>M. paradoxus</i> (2-4 years old individuals) are closed year-round to all fishing activities	Disappearance
#6	The 50 zones with highest abundance of fishable juveniles of <i>M. paradoxus</i> (2-4 years old individuals) are closed year-round to all fishing activities	Full redistribution to the remaining fished areas
#7	The 100 zones with highest abundance of fishable juveniles of <i>M. paradoxus</i> (2-4 years old individuals) are closed year-round to all fishing activities	Disappearance
#8	The 100 zones with highest abundance of fishable juveniles of <i>M. paradoxus</i> fi (2-4 years old individuals) are closed year-round to all fishing activities	Full redistribution to the remaining fished areas

Table 5. Description of the marine protected area (MPA) scenarios simulated in the present study.

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RESULTS

Distribution of fishable juveniles and large adults in the absence of MPAs, and definition of MPA scenarios

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The spatial distribution of Cape hakes predicted by our model is consistent with that described in previous studies (Payne 1989; Payne & Punt 1995; Sumaila et al. 2003; Le Clus et al. 2005a, b): *M. paradoxus* is distributed in deeper waters and relatively more abundant on the west coast of South Africa than *M. capensis*, while *M. capensis* is relatively more abundant than *M. paradoxus* on the south coast of South Africa (Fig.6). For both *M. paradoxus* and *M. capensis*, fishable juveniles (2-4 year old individuals) and large adults (5+ year old individuals) are not totally spatially separated. The distribution areas of the two age classes strongly overlap in some parts of study system (e.g., on the western part of the west coast for *M. paradoxus*; Figs.6b and d).

For the different MPA scenarios assessed in the present study, the location of MPAs was determined from the spatial distribution of fishable juveniles and large adults of *M. paradoxus* (Fig. 7). Due to the partial spatial overlap of the two age classes, the preferential protection of the younger or older sections of *M. paradoxus* does not imply the closure of totally distinct zones to fishing activities. Nevertheless, as large adults of *M. paradoxus* generally occur in deeper waters than juveniles of the species, MPAs designed for protecting preferentially the older sections of South African *M. paradoxus* are often located further offshore than those designed for protecting preferentially the younger sections of the population (Fig. 7). For the different MPA scenarios, the percentages of fishing grounds lost by hake-directed fleets are given in Table 6.

(a) Fishable juveniles of Merluccius capensis

(c) Large adults of Merluccius capensis

(d) Large adults of Merluccius paradoxus

Figure 6. Relative abundance of fishable juveniles of (**a**) *M. capensis* and (**b**) *M. paradoxus* (2-4 years old individuals), and large adults of (**c**) *M. capensis* and (**d**) *M. paradoxus* (5+ years old individuals) in the study area in the absence of MPAs.

(a) MPA scenarios #1-2

(c) MPA scenarios #5-6

(b) MPA scenarios #3-4

(d) MPA scenarios #7-8

Figure 7. Zones of the study system closed to fishing for MPA scenarios (**a**) #1-2 (**b**) #3-4, (**c**) #5-6, and (**d**) #7-8.

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Table 6. Percentage of the study system in marine protected areas (MPAs) and of the fishing grounds lost by hake-directed fleets for the 8 MPA scenarios assessed in the present study. MPA scenarios are described in Table 7.

MPA Scenarios	Percentage of the study system in MPAs	Percentage of fishing grounds lost by the offshore trawl fleet	Percentage of fishing grounds lost by the inshore trawl fleet	Percentage of fishing grounds lost by the longline fleet
#1-2	7%	13.23%	10.26%	7.45%
#3-4	14%	33.07%	23.72%	19.88%
#5-6	7%	14.81%	17.20%	15.23%
#7-8	14%	28.62%	35.26%	32.92%

Long-term effects of MPAs

When the fishing effort formerly in protected areas disappears at the time of MPA creation, SSB increases for both *M. paradoxus* and *M. capensis* (MPA scenarios #1, #3, #5 and #7; Figs. 8a-b). Increases in SSB are small for the latter species relative to the former. For the fishing effort disappearance case, the greatest conservation benefits are obtained when fishable juveniles of *M. paradoxus* are the primary targets of protection efforts (MPA scenarios #5 and #7). In this situation, the mean age of the *M. paradoxus* population increases inside MPAs and is relatively unchanged outside MPAs (Figs. 9e-f). In contrast, the mean age of the *M. paradoxus* population is relatively unchanged both inside and outside MPAs when large adults are preferentially targeted by protection efforts (MPA scenarios #1 and #3; Figs. 9a-b).

Redistribution of the fishing effort previously in protected areas to remaining fished areas reduces the conservation benefits of MPAs (MPA scenarios #2, #4, #6 and #8), especially when protection efforts preferentially target fishable juveniles of *M. paradoxus* (MPA scenarios #6 and #8). In this latter situation, SSB of *M. capensis* decreases moderately (Fig. 8b), but that of *M. paradoxus* is still at a higher level than when large adults of *M. paradoxus* are the primary targets of protection efforts (MPA scenarios #1-4) (Fig. 8a). As it to be expected, when given sections of the *M. paradoxus* population are targeted by protection efforts, increases in Cape hake SSB are more marked when a larger fraction of South African waters is set aside as MPAs (MPA scenarios #1 vs. #3, #2 vs. #4, #5 vs. #7, and #6 vs. #8; Figs. 8a-b).

Catches of *M. paradoxus* are relatively unchanged when protection efforts primarily target large adults (MPA scenarios #1-4; Figs. 8c-d). On the other hand, when fishable juveniles are the primary targets of protection efforts, catches of *M. paradoxus* by the longline fleet are considerably increased while catches of the species by the offshore trawl fleet are relatively unchanged or significantly decreased (MPA scenarios #5-8). Larger increases in catches of *M. paradoxus* by the longline fleet and larger decreases in catches of the species by the offshore trawl fleet are obtained in the fishing effort redistribution case (MPA scenarios #6 and #8). In this situation, catches of *M. paradoxus* by the longline fleet increase by 150.92% and 282.39% when, respectively, 7 and 14% of the study system is closed to fishing (Figs. 8d).

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MPA creation generally leads to decreases in total hake catches for the different fleets (Figs. 8e-h). Total hake catches of all fleets diminish in the fishing effort disappearance case (MPA scenarios #1, #3, #5 and #7). When large adults of *M. paradoxus* are the primary targets of protection efforts (MPA scenarios #1-4), total hake catches of all fleets are reduced or are relatively unchanged compared to the pre-MPA situation. When MPAs are designed to preferentially protect the older sections of the *M. paradoxus* population, declines in total hake catches are insignificant to slight for all fleets when 7% of the study system is closed to fishing (MPA scenarios #1-2). Decreases in total hake catches become more pronounced when double the fraction of the study system is set aside as MPAs (MPA scenarios #3-4).

When the younger sections of the *M. paradoxus* population are the primary targets of protection efforts and the fishing effort formerly in protected areas is redistributed at the time of MPA creation, total hake catches of the longline fleet are moderately increased compared to the pre-MPA situation (MPA scenarios #6 and #8; Fig. 8f). When 7% of the study system is closed to fishing (MPA scenario #6), total hake catches for the longline fleets increase by 13.78%, whereas the inshore and offshore trawl fleets incur, respectively, slight and significant losses in total hake catches (-1.90% and -39.12%, respectively). When the fraction of the study system in MPAs is doubled (MPA scenario #8), total hake catches for the longline fleets increase by 15.19%, while total hake catches for the inshore and offshore trawl fleets both decrease significantly (by 28.78% and 55.15%, respectively) (Figs. 8e-g).

(c) Offshore trawl catches of *M. paradoxus*

(e) Total hake catches for the offshore trawl fleet

(g) Total hake catches for inshore trawl fleet

(f) Total hake catches for the longline fleet

(h) Total hake catches summed over all fleets

Figure 8. Consequences of 8 marine protected area (MPA) scenarios on the Spawning Stock Biomass (SSB) of *(a) Merluccius paradoxus* and **(b)** *Merluccius capensis*; the annual catches of *M. paradoxus* for the **(c)** offshore trawl and **(d)** longline fleets; and total annual hake catches of the **(e)** offshore trawl **(f)** longline, and **(g)** inshore trawl fleets, and **(h)** summed over all fleets. The description of the different MPA scenarios is given in Table 5.

Figure 9. Age structure of the *M. paradoxus* population (**a,c,e,g**) inside and (**b,d,f,h**) outside marine protected areas (MPAs) for MPA Scenarios (**a,b**) #3, (**c,d**) #4, (**e,f**) #7 and (**g,h**) #8. The description of the different MPA scenarios is given in Table 5.

DISCUSSION

In the present study, we developed a spatially-explicit population model for evaluating the long-term conservation and fisheries effects of MPAs for South African Cape hakes. For the scenarios examined, we found that MPAs increase the SSB of *M. paradoxus* and *M. capensis* when the fishing effort formerly in protected areas disappears at the time of MPA creation. Increases in SSB are greater for *M. paradoxus* than for *M. capensis*, in part because the former species is here the primary targets of protection efforts, but also because the *M. paradoxus* resource is relatively depleted while the *M. capensis* resource is in a relatively healthy state (Apostolaki et al. 2002, Hart 2006, Rademeyer et al. 2008, Rademeyer & Butterworth 2010). In general, redistribution of the fishing effort formerly in MPAs to remaining fished areas reduces the conservation benefits of MPAs (Horwood et al. 1998, Grüss et al. 2011). In the effort redistribution case, SSB of *M. capensis* is even decreased moderately when fishable juveniles of *M. paradoxus* are the primary targets of protection efforts, since in this situation most zones with high abundance of *M. capensis* are not protected and subject to increased fishing pressure after MPA establishment (compare Figs. 6a and 6c with 7c-d).

Consistent with Edwards and Plaganyi (2011), we found that increases in SSB of *M. paradoxus* are greater when the younger sections of the population are the primary targets of protection efforts. The zones of the study system where the abundance of Cape hake juveniles vulnerable to fishing is the highest coincides with high fishing effort areas (Figs. 7d, A2, A3 and A4 and Table 7). Therefore, closure of the zones with highest abundance of fishable juveniles of *M. paradoxus* leads to significant increase in the number of individuals surviving to the age of sexual maturity (Figs. 9e and g). Moreover, for the scenarios examined, we found that MPAs designed to protect preferentially juveniles vulnerable to fishing considerably increase longline catches of *M. paradoxus* but decrease offshore trawl catches of the species. This partly stems from the fact that the longline fleet primarily targets 6+ year-old individuals while the offshore trawl fleet primarily targets 3+ year-old individuals (Table 1; Butterworth & Rademeyer 2005, Fairweather et al. 2006). The loss of harvestable biomass of *M. paradoxus* due to MPA creation for the offshore trawl fleet is higher than that for the longline fleet, and is not compensated by increases in SSB.

For the MPA scenarios explored, we also found that MPAs generally decrease total hake catches of all fleets. Total hake catches of the longline fleets are increased compared to

the pre-MPA situation only when the younger sections of the *M. paradoxus* population are the primary targets of protection efforts and the fishing effort formerly in MPAs is redistributed to remaining fished areas. In contrast, total hake catches of the offshore and/or inshore trawl fleets are significantly reduced compared to the pre-MPA situation in this context. Thus, our results suggest that the losses in total hake catches due to MPA creation will generally not be compensated by increases in Cape hake biomass, and that trade-offs between conservation benefits and total hake catches of the different fleets will be incurred by the creation of MPAs designed to protect *M. paradoxus*. For example, if 14% of South African waters are set aside as MPAs to protect preferentially fishable juveniles of *M. paradoxus* and fishing effort is not redistributed (MPA scenario #7), increases in Cape hake SSB will be optimal (+330.37% for *M. paradoxus* and +28.05% for *M. capensis*), whereas total hake catches for the inshore trawl fleet will slightly decrease (-7.60%) and the offshore trawl and longline fleets will incur significant losses in total hake catches (-56.50% and -22.38%, respectively). If 7% of South African waters are set aside as MPAs to protect preferentially fishable juveniles of M. paradoxus and fishing effort is redistributed (MPA scenario #6), increases in SSB will be suboptimal for *M. paradoxus* (+43.62%), SSB of *M. capensis* will slightly decrease (-7.41%), while total hake catches for the longline fleet will moderately increase (+13.78%) and total hake catches for the inshore and offshore trawl fleets will, respectively, slightly and significantly decrease (-1.90% and-39.12%, respectively) (Fig. 8).

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In the present study, larval and adult connectivity matrices were built from simulations of an individual-based biophysical submodel and a GIS-based submodel, respectively. The parameterization of these submodels was carried out using best available scientific knowledge. However, current knowledge on Cape hake larval and adult connectivity is very limited and relatively uncertain (Botha 1973, Stenevik et al. 2008, Smith & Japp 2009, Garavelli et al. submitted). Therefore, the sensitivity of the predictions of our model to alternative connectivity patterns should be tested and, in particular, examinations of the effects of using alternative ontogenetic migration patterns are needed.

Here we tested only a limited number of MPA scenarios among the many possible. All the MPAs tested in the present study were no-take and implemented year-round. Future studies should investigate the consequences of other MPA scenarios, where some or all MPAs are partial-take (e.g., trawling is forbidden while longlining is allowed). The impacts of implementing MPAs seasonally versus year-round could also be evaluated. Moreover, the South African coastal MPA network may soon be expanded to offshore areas to protect

pelagic and demersal species, from the systematic biodiversity planning analyses undertaken by the South African National Biodiversity Institute (SANBI) (Sink & Attwood 2008, Sink et al. 2010). Thus, it would be interesting to use the model developed in the present study to assess the long-term impacts of MPA scenarios defined from the results of the analyses undertaken by SANBI for South African Cape hakes and the fishing fleets depending on them.

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SUPPLEMENTARY MATERIAL

Appendix A1. Equivalent non-spatial annual model.

For each Cape hake species, in the equivalent non-spatial annual model, individuals move from one age class to another each year, spawning occurs at the beginning of each year, and natural and fishing mortalities are continuous events taking place after spawning. Population dynamics is given by:

$$N_{t+1,0} = R_{t+1}$$

$$N_{t+1,a} = N_{t,a-1}e^{-Z_{t,a-11}} \quad for \ 0 < a < p \tag{A1.1}$$

$$N_{t+1,p} = N_{t,p-1}e^{-Z_{t,p-1}} + N_{t,p}e^{-Z_{t,p}}$$

where $N_{t,a}$ is the number of fish of age *a* at the start of year *t*; R_t the number of recruits (0 year old fish) the start of year *t*; *p* is the age plus group; and $Z_{t,a}$ the total mortality rate at age *a* at the start of year *t*, which is equal to:

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$$Z_{t,a} = \sum_{f} F_{f} S_{f,a} + M_{a}$$
(A1.2)

where F_f represents the annual fishing mortality for fleet f; $S_{f,a}$ the selectivity-at-age a for fleet f; and M_a the natural mortality rate at age a.

Spawning Stock Biomass at year t (*SSB*_t) is given by:

$$SSB_t = \sum_{a=4}^p w_a N_{t,a} \tag{A1.3}$$

where w_a the weight-at-age *a*. Then, annual recruitment is related to SSB though the Beverton-Holt function:

$$R_{t} = \frac{\alpha_{0}SSB_{t}}{1 + \begin{pmatrix} SSB_{t} \\ K_{0} \end{pmatrix}}$$
(A1.4)

where α_0 is the slope of the SRR at low levels of SSB; and K_0 the value of SSB above which compensatory density-dependent effects start dominating over density-independent effects, which can be obtained from α and annual recruitment in pristine conditions (R_0):

$$K_0 = \frac{R_0}{\alpha_0} \tag{A1.5}$$

Estimates for α_0 and R_0 are given in Table A1.

Parameter	Definition	Estimate for Merluccius paradoxus	Estimate for Merluccius capensis
$\alpha_0 (10^7 t^{-1})$	Initial slope of the stock-recruitment relationship	2.1898	9.0691
$R_0(10^9)$	Global annual recruitment in pristine conditions	1.23441	3.64313

Table A1. Estimates of stock-recruitment parameters for *Merluccius paradoxus* and *Merluccius capensis* from baseline stock assessments (Rademeyer et al. 2008).

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Figure A2. Seasonality of fishing effort for the inshore trawl fleet over the period 2004-2008.

Movie available on:

http://www.amped.ird.fr/IMG/avi/Movie_Seasonality_Inshore_Trawl_Effort_Cape_hakes.avi

Figure A3. Seasonality of fishing effort for the offshore trawl fleet over the period 2004-2008.

Movie available on:

http://www.amped.ird.fr/IMG/avi/Movie_Seasonality_Offshore_Trawl_Effort_Cape_hakes.a vi

Figure A4. Seasonality of fishing effort for the longline fleet over the period 2004-2008

Movie available on:

http://www.amped.ird.fr/IMG/avi/Movie_Seasonality_Longline_Effort_Cape_hakes.avi



GENERAL DISCUSSION

Impacts of fish movement on MPA effectiveness relative to those of larval dispersal

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Chapter 1 confirms that adult and juvenile movement has a considerable impact on the conservation and fisheries effects of MPAs, and provides the first general conceptualization of the impacts of fish movement on MPA effectiveness relative to those of larval dispersal. Results of Chapter 1 demonstrate that persistence of a population with mobile adults requires significantly more habitat area in MPAs and/or larger MPAs than for an equivalent population with larvae dispersing over the same spatial scale. Differences in persistence for fish movement versus larval dispersal are accentuated in presence of fishing-the-line (i.e., high concentration of fishers on MPA borders) and fishery squeeze (i.e., redistribution of the fishing effort formerly in MPAs to remaining fished areas).

Larval dispersal and fish movement are fundamentally different in how they expose 'reserve individuals' to fishing pressure. Larval dispersal exposes young produced by individuals residing in MPAs but transported out of protected areas to fishing pressure, but those larvae that do manage to settle in MPAs are protected over their entire life span. Fish movement, on the other hand, exposes reserve individuals to fishing during the period they spend in fished areas, and, therefore, given sufficient movement, all individuals will be accessible to fisheries at some point. This accessibility explains both the need for larger MPAs and the fact that the reallocation of fishing effort is much more effective at reducing MPA protection when fish are mobile. The conceptual model developed in Chapter 1 indicates that individual MPAs should be several times larger than fish movement spatial scales to ensure population persistence in this situation.

Results of Chapter 1 show that which of fish movement and larval dispersal is more beneficial to fisheries yields depends essentially on the fraction of habitat area covered by MPAs and the fate of the fishing effort previously in protected areas. Recruitment subsidy has greater potential to improve fisheries yields than spillover when a small fraction of habitat area is protected. On the other hand, in absence of fishery squeeze, high fisheries yields are produced for a larger set of MPA configurations for fish movement than larval dispersal when a significant fraction of habitat area is set aside in MPAs. Fishery squeeze considerably alters the fisheries benefits of MPAs for mobile fish populations. Maximum fisheries yields are low in this situation, and occur when almost all the habitat area is set aside in MPAs and for MPA 186

widths several times larger than fish movement spatial scales. This is due to the fact that population persistence is achieved in this situation by establishing large MPAs to ensure some individuals have very little exposure to extremely high fishing pressure outside protected areas. This has the effect of rendering many individuals inaccessible to fishing and, therefore, limiting fishery yields. In contrast, fishery squeeze has only a marginal effect on fisheries yields for fish populations with sedentary adults and dispersing larvae, so that recruitment subsidy has usually greater potential to improve fisheries yields than spillover in presence of fishery squeeze.

Moreover, results of chapter 1 indicate that population persistence often occurs for fewer MPA configurations when fish movement and larval dispersal are combined rather than for exclusively one or the other form of connectivity. This likely stems from the fact that larval dispersal reduces self-recruitment needed for persistence inside MPAs at the same time that fish movement reduces the reproductive potential of individuals recruiting in MPAs. On the other hand, spillover may only improve the yields of fishers operating in proximity to protected area borders. When larval dispersal superposes to vessels fishing close to protected area borders, MPAs have the potential to also improve the yields of fishers operating in more distant areas (Halpern & Warner 2003; Roberts *et al.* 2005) (Figure 1).



Y₁ Y₂ = 2 Y₁ in o harvester behavior

Figure 1. Spatial patterns of (**a**,**b**) recruitment, (**c**,**d**) fishing mortality rate (*f*), and (**e**,**f**) fisheries yields for a system of periodically-spaced, uniformly-sized marine protected areas (MPAs; grey areas) at equilibrium. (**a**,**c**,**e**) are for populations possessing with adult movement moving within a home range and non-dispersing larvae, whereas (**b**,**d**,**f**) are for populations with adults moving within a home range and larvae dispersing over the same spatial scale as the adults. Fishing effort is uniform outside MPAs for red curves. For the green and blue curves, the fishing effort distribution in the non-protected areas depends on local expected fisheries yields, with the value of γ being 1.2 for green curves and 2.4 for blue curves. The units of recruitment are arbitrary, but consistent between simulations. The dashed black line on (**c**) and (**d**) represents the fishing mortality rate above which the population collapses in the absence of MPAs.

Findings of Chapter 1 provide benchmarks on the use and functioning of MPAs for fish populations that move within a home range. Moreover, these results serve as a useful baseline for investigating the impacts of migrations on MPA functioning. In the case of migratory populations with spatially segregated adult and juvenile stages and/or that clearly separate feeding and reproductive habitats, targeted MPA approaches are likely to be implemented. The rather complex set of spatial migrations that may produce the spatial structure necessary for targeted MPA approaches has not been examined in Chapter 1, yet it is reasonable to assume that results of this chapter set a conservative high bar for the effective use of these approaches. Indeed, the fidelity of migratory populations to specific sites ensures that a fraction of the population will be offered full protection by targeted MPAs. On the other hand, lack of site fidelity exposes individuals targeted for protection to fishing, similarly to fish movement within a home range. Therefore, fishery squeeze may considerably reduce the conservation and fisheries benefits of targeted MPAs when the populations targeted by protection efforts show low site fidelity, whereas it may have only minor effects for migratory populations that are faithful to specific sites.

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Effectiveness of targeted MPAs for aggregation-forming reef fish populations

Chapter 2 examines the effects of spawning area closures for coral reef fish populations migrating to form transient spawning aggregations. Given the limited availability of data and knowledge for most aggregation-forming reef fish populations, a parsimonious non-spatial, per-recruit model was developed. The model was applied to a rabbitfish population (gonochoristic) and a grouper population (protogynous) from the Seychelles Archipelago. Model results indicate that spawning aggregation-based MPAs will improve fish reproductive capacity whatever the fate of the fishing effort previously in protected areas, although improvements are often marginal when the reallocation of fishing effort to areas not protected is taken into account. Spawning aggregation-based MPAs also reduce sex ratio bias for protogynous populations and, therefore, may improve their production of fertilized eggs when the fishing effort formerly in protected areas disappears at the time of MPA creation. On the other hand, when fish are faithful to spawning sites and the fishing effort formerly in MPAs is redistributed to non-protected spawning sites, sex ratio of fished protogynous subpopulations is dramatically increased. In this situation, population-wide production of fertilized eggs of protogynous populations may only be assured if egg production from individuals spawning at protected aggregation sites is sufficient to compensate for failed reproduction in non-protected areas (presumably requiring that MPAs cover a significant fraction of spawning sites). Fisheries benefits via an increase in yield-per-recruit with spawning aggregation-based MPAs did not occur in the model, whatever the fate of the fishing effort formerly in protected areas. Nonetheless, closing a significant fraction of spawning aggregation sites to fishing may improve fish reproductive capacity. This increase in reproductive capacity may, in the longer term, lead to an increase in recruitment for fish populations that are recruitment limited due to overfishing and, eventually, to an increase in fisheries yields.

Interestingly, it was found that the degree of fidelity of fish to spawning sites did not significantly affect the conservation and fisheries effects of spawning aggregation-based

MPAs. This result was not expected as in Chapter 1 it was demonstrated that fish movement within a home range, which similar to a lack of spawning site fidelity, exposes 'reserve individuals' to fishing, considerably reduces the chances of persistence of mobile fish populations in MPA networks. The degree of fish spawning-site fidelity has a weak effect on MPA effects because spawning aggregation-based MPAs does not eliminate all fishing mortality on 'reserve individuals'. As a result, the total mortality rate of individuals using protected spawning aggregation sites quite similar to that of individuals using fished spawning sites, and these two mortality rates are relatively close to the average mortality rate of individuals that are unfaithful to spawning sites. These weak differences in mortality rates produce relatively small differences in results with and without site fidelity, and consequently the effects of spawning aggregation-based MPAs are predominantly determined by the fraction of reproductive habitat that is protected.

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The relevance of using spawning aggregation-based MPAs rather than other management tools depends on the life history traits of the reef fish populations targeted by protection efforts and its relative annual fishing mortality rate at spawning sites. Grouper possess life history traits conferring a great vulnerability to fishing (long life, slow growth and protogynous hermaphroditism) and differences between spawning and non-spawning accessibility to the fishery are large. Therefore, for grouper, it would be sound to target moderate yield-per-recruit levels while preventing strong bias in sex ratio, and the closure of a significant fraction of spawning sites is likely the best management option in this context. On the other hand, rabbitfish possess life history traits promoting a high degree of resilience to fishing (short life, rapid growth and gonochorism) and its annual mortality rate at spawning and non-spawning sites are relatively similar. For rabbitfish, reproductive capacity and yield-per-recruit were only moderately changed in presence of spawning aggregation-based MPAs under a wide range of fishing effort levels, and other management measures (e.g., fishing effort reduction) would likely be more beneficial both in terms of conservation and fisheries management.

Given the conflicting views expressed in the literature on the use of targeted MPAs, I also examined the effects of MPAs implemented in normal residence areas, i.e., targeting juveniles and non-spawning adults. This supplementary analysis suggests that, for grouper, MPAs implemented in normal residence areas will not improve yield-per-recruit (Figures 2ab), and will be less effective at improving fish reproductive capacity (Figures 3a-b) and reducing bias in sex ratio (results not shown here) than spawning aggregation-based MPAs. In

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contrast, for rabbitfish, MPAs implemented in normal residence areas may increase yield-perrecruit when the population is overexploited in remaining fished areas (Figures 2c-d) and be more effective at improving fish reproductive capacity than spawning aggregation-based MPAs (Figures 3c-d). These results suggest that it would be more beneficial to implement MPAs in normal residence areas rather than at spawning sites for aggregation-forming populations that are highly resilient to fishing and/or suffer relatively low fishing mortality at spawning sites. However, in practice, the implementation of MPAs in normal residence areas may be less practical given that these areas are extensive compared to spawning areas, and that coral reef fisheries usually target a very large number of species at non-spawning sites (Bannerot *et al.* 1987; Johannes 1998; Sadovy 2005).

- x Status quo
- MPAs at spawning sites, effort formerly in MPAs disappears
- -- MPAs at spawning sites, effort formerly in MPAs redistributed to non-protected spawning sites

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— MPAs in normal residence areas, effort formerly in MPAs disappears





Figure 2. Yield-per-recruit normalized by maximum yield-per-recruit in the absence of MPAs (YPR/YPR_{max}) as a function of multiplier of fishing effort (mE_{base}), for different MPA scenarios. (**a**,**b**) is for rabbitfish, while (**c**,**d**) is for grouper. The fraction of spawning sites or normal residence areas in MPAs, C_r , is 30% and 60% for (**a**,**c**) and (**b**,**d**), respectively. E_{base} is the default level of annual fishing effort exerted on the population and is indicated by a dashed-dotted blue line. The level of annual effort at which yield-per-recruit reaches a maximum in the absence of MPAs is indicated by a dashed-dotted red line for rabbitfish.

x Status quo

MPAs at spawning sites, effort formerly in MPAs disappears

-- MPAs at spawning sites, effort formerly in MPAs redistributed to non-protected spawning sites

MPAs in normal residence areas, effort formerly in MPAs disappears

MPAs in normal residence areas, effort formerly in MPAs redistributed to non-protected normal residence areas



Figure 3. Fraction of female spawning stock biomass per recruit (FNSSBR, i.e., the ratio of female spawning stock biomass per recruit) as a function of multiplier of fishing effort (mE_{base}), for different MPA scenarios. (**a**,**b**) is for rabbitfish, while (**c**,**d**) is for grouper. The fraction of spawning sites) or normal residence areas in MPAs, C_r , is 30% and 60% for (**a**,**c**) and (**b**,**d**). E_{base} is the default level of annual fishing effort exerted on the population and is indicated by a dashed-dotted blue line. The level of annual effort at which yield-per-recruit in the absence of MPAs reaches a maximum is indicated by a dashed-dotted red line for rabbitfish.

Effectiveness of targeted MPAs for South African hakes

Chapter 4 investigates the consequences of the implementation of targeted MPAs for a migratory fish population whose spawning and nursery areas are both relatively extensive and partially overlap, the South African population of *Merluccius paradoxus*. This chapter examines the impacts of protecting preferentially the younger or the older sections of *Merluccius paradoxus* for the conservation of South African hake stocks (*M. paradoxus* and *M. capensis*) and the catches of inshore and offshore trawl and longline hake-directed fleets. A complex spatially-explicit model was developed, which represents hake ontogenetic migrations. The use of realistic connectivity patterns for both larval dispersal and fish movement represents a particularly important advancement in this model, though additional work is needed to assess the sensitivity of model results to changes in assumptions underlying the calculation of these connectivity patterns.

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Consistent with results of simple two-patch models (e.g., Pelletier & Magal 1996; Roberts & Sargant 2002; Edwards & Plaganyi 2011), the results of the spatially-explicit model for *M. paradoxus* indicate that targeted MPAs are more effective at improving the mean age and the SSB of a migratory fish population when juveniles vulnerable to fishing are the primary targets of protection efforts. In this situation, improvement of SSB leads to a considerable increase of the catches of *M. paradoxus* for the longline fleet, which only targets large adults. On the other hand, the offshore trawl fleet targets both juveniles and adults, and the loss of harvestable biomass for this fleet due to MPA creation is not offset by an increase in SSB. In contrast, catches of *M. paradoxus* for both the longline and offshore trawl fleets are relatively unchanged when large adults are the primary targets of protection efforts.

When both *M. paradoxus* and *M. capensis* are considered, targeted MPAs are found to be less effective both in terms of conservation and fisheries management. When the fishing effort formerly in protected areas is redistributed to remaining fished areas and fishable juveniles of *M. paradoxus* are preferentially targeted by protection efforts, the SSB of *M. capensis* is found to decrease slightly to moderately. For the other MPA scenarios examined, SSB of *M. capensis* is relatively unchanged or moderately increased. Moreover, the potential of targeted MPAs to produce fisheries benefits appeared very limited. When juveniles of *M. paradoxus* are the primary targets of protection efforts and fishing effort is redistributed at the time of MPA creation, total hake catches of the longline fleet are moderately increased, whereas the other fleets incur losses in total hake catches. For the other MPA scenarios explored, all fleets incur losses in total hake catches. In Chapter 4, a set of MPA scenarios

among the many possible ones was considered, and targeted MPAs may be beneficial to some fleets in other circumstances. Nonetheless, there are likely much more conditions under which losses in total hake catches due to MPA establishment will not be compensated by an increase in hake biomass than the opposite.

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The spatially-explicit simulation model ISIS-Fish (Integration of Spatial Information for Simulation of Fisheries; Pelletier & Mahévas 2005; Pelletier et al. 2009) was also used to evaluate the consequences of targeted MPAs for migratory fish populations and multi-species multi-fleet (mixed) fisheries (Kraus et al. 2008; Pelletier et al. 2009; Mahévas & Lehuta 2012). ISIS-Fish relies on three interacting submodels pertaining, respectively, to fish population, exploitation and management, and takes into account fishers' behavior in response to management measures (Pelletier et al. 2009). Mahévas and Lehuta (2012) applied ISIS-Fish to the Bay of Biscay anchovy (Engraulis encrasicolus) fishery. E. encrasicolus is a short-lived pelagic species whose cohorts are spatially segregated for most of the year. The authors also found that protection efforts should preferentially target juveniles. Seasonal MPAs designed to protect juveniles improved both SSB and catches of E. encrasicolus, whatever the fate of the fishing effort formerly in protected areas. In contrast, seasonal MPAs designed to protect adults reduced both SSB and catches of E. encrasicolus when the fishing effort previously in protected areas is redistributed to the areas adjacent to MPAs. When the fishing effort formerly in MPAs is uniformly redistributed to non-protected areas, seasonal MPAs designed to protect adults only slightly improved SSB and catches of E. encrasicolus (Mahévas & Lehuta 2012). Pelletier et al. (2009) used ISIS-Fish to investigate the consequences of an MPA aimed at protecting hake (M. merluccius) juveniles for the French Norway lobster (Nephrops norvegicus)-hake multi-fleet fishery of the Bay of Biscay. Under the most conservative assumption about Norway lobster larval dispersal, the authors found that this MPA improved the status of the Norway lobster stock but not the overall economic return for the Norway lobster-hake fishery. In comparison, restrictions on fishing gears (twin trawl ban) improved both Norway lobster stock status and the economic return for the fishery. The results from Pelletier et al. (2009), combined with the results for South African Cape hakes, highlight the complexity of the impacts of targeted MPAs for fisheries when their mixed nature is taken into account, as well as the need to evaluate the effects of targeted MPAs versus other management measures to fully gauge their relative performances.

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Conclusions and perspectives

Fish movement has a strong negative impact on MPA effectiveness in terms of population persistence and imposes considerable constraints on MPA design. Given that fishing-the-line and fishery squeeze typically occur in the real world, MPAs should be several times larger than fish movement spatial scales to offer effective protection to populations moving within a home range. Moreover, in practice, MPAs generally cover a relatively small fraction of the total habitat area of fish populations. Based on the results presented here, this suggests that, in most practical cases, for fish populations moving within a home range, spillover benefits only fishers operating close to MPA borders and recruitment subsidy has greater potential to improve overall fisheries yields than spillover.

In the case of migratory populations, MPAs designed to protect specific fractions of the population can be effective in conservation terms without being extremely large. In the case of aggregation-forming reef fish populations, MPAs covering a substantial fraction of spawning areas produce significant conservation benefits (e.g., increased SSB and improved sex ratio) and are likely to be preferred to MPAs implemented at non-spawning sites due to their relatively small size and the fact that coral reef fisheries target a very large number of species in non-spawning areas. Results presented here indicate that spawning aggregationbased MPAs may eventually produce fisheries benefits only through recruitment subsidy provided that the population is in an overexploited state and that a significant fraction of spawning sites is protected. In the case of migratory populations whose spawning and nursery areas are both relatively extensive, MPAs should preferentially target fishable juveniles so as to significantly increase the mean age of the population and its spawning stock biomass. This significant increase in biomass may compensate some fleets for losses in catches due to MPA establishment. However, the majority of fisheries targeting migratory fish populations are mixed fisheries, and the overall impacts of targeted MPAs for these fisheries are complex. The results presented here for South African Cape hakes and those obtained with the ISIS-Fish model indicate that targeted MPAs may be beneficial overall for these fisheries only in a limited number of situations.

In the case of highly migratory populations (i.e., moving over distances ranging from hundreds to thousands of kilometers; e.g., tunas and billfishes), individuals are expected to move around within the full range of suitable habitat occupied during a specific season, and targeted MPAs may be so large as to be impractical (Hobday *et al.* 2011; Rice & Houston

2011). The direction and extent of the movements of these populations is highly influenced by the strength and direction of oceanic currents, which determine the locations of convergence zones, fronts and eddies where these populations often preferentially forage (e.g., tunas, billfishes, ocean sunfish, Humboldt squid; Lehodey *et al.* 1997; Norse *et al.* 2005; Block *et al.* 2011). Thus, some authors very recently proposed the implementation of 'dynamic' MPAs that follow highly migratory populations in space and time (e.g., Norse *et al.* 2005; Game *et al.* 2009; Hobday *et al.* 2011). Dynamic MPAs are not unlike existing concepts, such as rotational harvests, except that the location and configuration of MPAs are not entirely predictable, but rather linked to changing ecosystem conditions (e.g., sea surface isotherms) and population recovery status. The efficacy and feasibility of dynamic MPAs has only begun to be explored, though initial results results on the use of dynamic spatial zoning to manage southern bluefin tuna (*Thunnus maccoyii*) capture in eastern Australia are relatively promising (Hobday *et al.* 2010). Modeling studies are needed to examine the potential conservation and fisheries effects of dynamic MPAs in diverse ecosystems.

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In the present thesis, three patterns of fish movement were considered: movement within a home range, ontogenetic migrations and adult migrations. However, there exist many other patterns of fish movement in MPA systems: 'nomadism', 'behavioural polymorphism', and density-dependent movements (density-dependent spillover, density-dependent spill-in, and movement arising from predator to prey interactions) (see Grüss et al. (2011) for a description of the different patterns). Furthermore, fish movement may be influenced by changes in habitat quality (e.g., Roberts & Sargant 2002; Horwood et al. 2006; Van Keeken et al. 2007; Parsons et al. 2010). Nomadism, behavioural polymorphism, density-dependent movements and movement behavior in relation to habitat quality have received little or no attention in modeling studies, though they may significantly impact the conservation and fisheries effects of MPAs in a specific way (Grüss et al. 2011). For example, predator to prey interactions may in some cases trigger excessive spillover, thereby considerably decreasing the conservation benefits of MPAs (Walters 2000; Salomon et al. 2002). On the other hand, habitat quality improvement may reduce the propensity of fish to move out of protected areas, thereby improving the conservation value of MPAs for mobile populations (Roberts & Sargant 2002; Parsons et al. 2010). Thoroughly assessing how and how well the different patterns of fish movement and fish movement behavior affect MPA functioning will be essential to creating effective MPA networks for mobile populations.

Overall, results of the present thesis confirm that, while MPAs may enhance conservation of mobile exploited fish populations in a relatively wide range of situations, the extent of these benefits relative to those of other more conventional management techniques (e.g., fishing effort limitation), as well as the possibility of increased fisheries yields, depends on numerous aspects of fish life-history and fishery dynamics. Modeling efforts must be continued to identify the conditions under which MPAs may produce both conservation and fisheries benefits on a case-by-case basis (i.e., for specific species or group of species in particular geographical areas) and help decision makers to implement management strategies satisfying both conservationists and those whose livelihoods depend on fishing. 2020 is near, so much more resources should be invested in MPA modeling rapidly.



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ANNEXES

ANNEXE A: Grüss A, Kaplan DM, Guénette S, Roberts CM, Botsford LW. (2011). Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation* **144**: 692-702.

ANNEXE B: List of communications