ECOSPHERE

Do static and dynamic marine protected areas that restrict pelagic fishing achieve ecological objectives?

ERIC GILMAN [iD],[1],† MICHEL J. KAISER [iD],[2] AND MILANI CHALOUPKA [iD][3]

[1]*Pelagic Ecosystems Research Group & Tuna Program, The Nature Conservancy, 3661 Loulu Street, Honolulu, Hawaii 96822 USA*
[2]*Heriot-Watt University, Edinburgh, Scotland*
[3]*Ecological Modelling Services Pty Ltd & Marine Spatial Ecology Lab, University of Queensland, St Lucia, Queensland, Australia*

Abstract.   There has been a recent proliferation of large-scale marine protected areas (MPAs) containing pelagic habitats. These contribute substantially toward meeting the area-based goal of Aichi Biodiversity Target 11 and to managing pelagic ecosystem pressures, including fishing. We assessed theoretical and empirical evidence for the achievement of ecological objectives by static and dynamic spatial management of pelagic fisheries. Exceptionally few studies have assessed ecological responses to MPAs that constrain pelagic fisheries, leaving substantial uncertainty over their efficacy. Assessments have provided a limited basis for causal inferences and have not evaluated whether other management tools would be more effective. Pelagic MPAs have relatively high promise to mitigate fisheries bycatch of species of conservation concern with "slow" life history traits and that form temporally and spatially predictable hotspots, and for some species, to protect habitats important for critical life history stages. It would be challenging to design MPAs to maintain absolute biomass levels of target stocks near targets and above limits: MPAs would need to be extensive to account for broad and variable distributions, and account for catch risk outside of the MPA, including from displaced fishing effort and fishing-the-line. For non-overexploited stocks, which is the status of most target pelagic species and their prey, there would likely be little response in absolute stock biomass to an MPA. While pelagic MPAs have a higher promise of increasing target stocks' local abundance, evidence with a robust basis for inferring causality is needed. Reducing fishing mortality of prey species might not affect the biomass of their pelagic predators because prey species experience light fishing pressure and because there may be a weak correlation between the absolute abundance of forage fish and their predators. There is an especially limited basis for predicting the effects of MPAs on fisheries-induced evolution (FIE) in pelagic species. We describe how pelagic MPAs could be designed to achieve five ecological objectives without causing cross-taxa conflicts and exacerbating FIE. To fill substantial gaps in knowledge, we prescribe counterfactual-based modeling of time series data of standardized catch records to infer causation in assessments of ecological responses to pelagic MPAs.

† **E-mail:** ericlgilman@gmail.com

INTRODUCTION

Marine protected areas (MPAs) are increasingly employed as a component of management frameworks to govern human activities in the ocean, including fishing, and to protect marine biodiversity. There is a large body of evidence demonstrating the biological community changes that occur within coastal, benthic, shallow-water MPAs and MPA networks when fishing mortality is reduced or eliminated. These responses include, on average, increases in the following (Halpern 2003, Claudet et al. 2006, Lester et al. 2009, Stewart et al. 2009, Kaiser et al. 2018, Kenchington et al. 2018): local abundance and biomass; mean length; recruitment and absolute biomass; and species richness and diversity. These increases can occur within and near the MPA, including from spillover of adults, juveniles, and larvae across the MPA seaward margin (Roberts et al. 2001, Lubchenco et al. 2003, Goñi et al. 2008, Lester et al. 2009, Christie et al. 2010). The responses are strongest for species with high site fidelity and limited mobility (Blyth-Skyrme et al. 2006, Kaiser et al. 2018, Kenchington et al. 2018).

We include the caveat "on average" because the response to protection is highly variable among taxa. This variability is due to factors such as the biology, life history and behavioral traits, trophic links such as whether increased predator abundance in the MPA increased predation pressure and reduced the abundance of their prey, and economic value. The types and magnitudes of ecological responses are also variable by MPA—depending in part on the type and magnitude of pressures that were reduced within the MPA, the MPA's size and age, the suitability of the MPA's design, and the efficacy of regulatory and management frameworks and compliance (McClanahan et al. 1999, Mosqueira et al. 2000, Halpern 2003, Micheli et al. 2004a, b, Kaiser 2005, Claudet et al. 2006, 2010, Le Quesne and Codling 2009, Grüss et al. 2011, Edgar et al. 2014, Gill et al. 2017, Kenchington et al. 2018, Gillespie and Vincent 2019).

While coastal, benthic MPAs have been shown to generate positive outcomes on average, there remains substantial uncertainty over the feasibility of pelagic MPAs to achieve these and other ecological objectives (Botsford et al. 2003, Hilborn et al. 2004a, b, Kaiser 2005, Le Quesne and Codling 2009, Kaplan et al. 2010, Davies et al. 2012, Graham et al. 2012, Hazen et al. 2013). Despite these uncertainties, over the past decade there has been a proliferation of large-scale MPAs that either include or are exclusively pelagic habitat in which pelagic fishing is restricted (Fernandes et al. 2005, Sheppard et al. 2012, Gannon et al. 2017). These pelagic MPAs support progress toward achieving the area-based goal of Aichi Biodiversity Target 11—also adopted as Sustainable Development Goal (SDG) target 14.5 —which calls for 10% of coastal and marine areas by 2020 to be conserved through ecologically representative and well-connected systems of MPAs and other effective area-based conservation approaches (CBD 2011, UNGA 2015a, Rice et al. 2018).

Reservations, however, have been raised over whether achieving MPA area-based targets will achieve biodiversity and fisheries management objectives if governance frameworks are weak or absent, and if MPA site selection is opportunistic and not based on ecological criteria (Kaiser 2005, Leenhardt et al. 2013, Edgar et al. 2014, Gill et al. 2017, Jantke et al. 2018, Sala et al. 2018, Visconti et al. 2019). Concerns have been raised over the feasibility of effectively monitoring, conducting surveillance, and enforcing management measures of pelagic MPAs, in particular in areas beyond national jurisdiction where vessels of multiple flag states occur (Fonteneau 2007, Gilman 2007, Kaplan et al. 2010).

There is large variability in the degree of protection afforded by different marine spatial management frameworks. Some are cross-sectoral in scope and prohibit all extractive activities, some prohibit a subset of extractive activities, while others temporally or spatially prohibit one or more pelagic fishery. Some fisheries spatial management frameworks meet IUCN's MPA definition of "clearly defined geographical space, recognised, dedicated, and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (IUCN 2018). Other marine areas may achieve protection of pelagic habitat as a consequence of restrictions implemented for reasons other than nature/ biodiversity conservation that may also achieve ecological benefits by constraining fishing mortality of pelagic species. Examples include: areas

zoned for defense, prohibitions on fishing to prevent damage of data buoys, areas subject to piracy, privately protected areas, and areas protected by indigenous peoples and local communities (e.g., WCPFC 2009, Chassot et al. 2010, Gannon et al. 2017). These examples, which fit IUCN's definition of Other Effective Area-based Conservation Measures, could contribute to the attainment of area-based goals for global MPAs in relation to SDG target 14 (Diz et al. 2018).

Some pelagic MPAs are static (place-based) and prohibit pelagic commercial fishing year-round, such as the Great Barrier Reef Marine Park, the first large MPA containing pelagic habitats, which prohibits pelagic longline fishing throughout the park (Australian Government 1983, GBRMPA 2004; Tom Hatley, *personal communication*), and MPAs established by some Pacific island states where pelagic longline fishing is prohibited within a specified distance of shallow submerged features (e.g., FSM Government 2014, MIMRA 2018). Others are static but seasonal, and are often species-specific, such as seasonal spatial closures to purse seining adopted by tuna regional fisheries management organizations (RFMOs) designed to reduce fishing mortality of juvenile bigeye tuna (*Thunnus obesus*), and the Mackerel Box off southwestern England established to protect juvenile mackerel (*Scomber scombrus*; Sweeting and Polunin 2005, Torres-Irineo et al. 2011, IATTC 2017). Some are spatially explicit but triggered only when seasonal thresholds are exceeded. For instance, in the Hawaii tuna longline fishery, the U.S. government has adopted a seasonal limit of catching and causing mortality or serious injury to two false killer whales (*Pseudorca crassidens*) in a portion of the fishing grounds near the main Hawaiian Islands (NMFS 2012). Others are spatially dynamic, such as near real-time dynamic spatial management of southern bluefin tuna (*Thunnus maccoyii*) bycatch by the eastern Australian pelagic longline fishery (Hobday and Hartmann 2006, Hobday et al. 2010).

The socioeconomic sustainability of marine capture fisheries and the quasi-stable state of marine ecosystems are unequivocally linked (Link 2002, FAO 2003, Gilman et al. 2011, 2017). Pressures from marine capture fisheries interact with the other main drivers of change and loss of marine biodiversity of climate change, marine pollution, habitat degradation, and the spread of invasive alien species (Kaiser and de Groot 2000, Pauly et al. 2005, Halpern et al. 2008, 2015, Leadley et al. 2010, Pereira et al. 2010, Selig et al. 2014). Direct fishing mortality by pelagic marine fisheries is the main driver of reductions in the size and abundance of pelagic apex predators, including of target stocks and incidentally caught species, although there is disagreement over the magnitude of these declines (Baum et al. 2003, Myers and Worm 2003, Burgess et al. 2005, Hampton et al. 2005, Ward and Myers 2005, Worm et al. 2005, Sibert et al. 2006, Dulvy et al. 2014). Fisheries that target tuna and tuna-like species (Scombroidei), billfishes (Xiphioidei), and other relatively fecund species can have large impacts on incidentally caught species that, due to their lower reproduction rates and other "slow" life history traits, are relatively vulnerable to increased mortality, including seabirds, sea turtles, marine mammals, elasmobranchs, and some teleosts (Goñi 1998, Hall et al. 2000, Gilman 2011, Branch et al. 2013). Pelagic fisheries selectively remove individuals based on certain traits (e.g., behavioral traits for boldness; life history traits for size-at-age; physiological traits for visual acuity; morphological traits for mouth dimensions), reducing intraspecific genetic diversity and altering fitness and evolutionary processes (Heino et al. 2015, Hollins et al. 2018). Fishing gear can alter and damage habitat (e.g., drifting fish aggregating devices (FADs) can alter the natural behavior and ecology of species that associate with the device; derelict FADs can run aground on sensitive coastal habitats; Dagorn et al. 2013, Sempo et al. 2013, Escalle et al. 2017). Fisheries targeting large, highly migratory pelagic predators of high trophic levels (TL > 4.0) indirectly modify trophic food web structure and processes and functionally linked systems (Pace et al. 1999, Stevens et al. 2000, Cox et al. 2002, Pikitch et al. 2004, Ward and Myers 2005, Baum and Worm 2009, Polovina et al. 2009, Ferretti et al. 2010, Estes et al. 2011). At this latter broad level, there is limited understanding of what magnitudes of interacting natural (e.g., large-scale climate variability) and anthropogenic pressures (including from fishing) cause pelagic ecosystems to reach a tipping point where they undergo a protracted or permanent regime shift, and how altered components of the state of

pelagic ecosystems affect functionally linked systems (Pace et al. 1999, Daskalov et al. 2007, Mollmann et al. 2009, Leadley et al. 2010, Crespo and Dunn 2017).

This study reviews theoretical and observed findings on whether static and dynamic spatial management of pelagic fisheries have achieved the following ecological objectives:

1. Reduce or eliminate bycatch fishing mortality of pelagic species of conservation concern;
2. Reduce or eliminate fishing mortality at habitats that are important for critical life history stages of pelagic species;
3. Reduce the fishing mortality of target stocks to contribute to sustaining desired production levels (i.e., stay near target thresholds) and avoiding conditions where protracted or irreparable harm to the stock occurs (i.e., stay above limit thresholds);
4. Reduce fishing mortality of prey species of pelagic target stocks and species of conservation concern in order to stay near targets and above limits; and
5. Reduce trait-based selective fishing mortality and fisheries-induced evolution (FIE).

We describe how pelagic MPAs could be designed to achieve these ecological objectives and discuss what factors may have a significant influence on the performance of a pelagic MPA. We explain how counterfactual-based modeling of time series data of standardized catch records can be used for causal inference of the ecological responses to the implementation of pelagic MPAs.

THEORETICAL AND OBSERVED EVIDENCE OF PELAGIC MPAS ACHIEVING ECOLOGICAL OBJECTIVES

The following sections synthesize theoretical and empirical evidence of static and dynamic MPAs that constrain pelagic fishing in achieving ecological objectives and underlying ecological responses. For each overarching ecological objective, the study describes ecological responses, direct and indirect ecological objectives, MPA designs that enable achieving the objectives and responses, why the MPA design might not be successful, and evidence of pelagic MPAs achieving the objectives and responses. While the

ecological objectives used to structure this review could be objectives of pelagic MPAs, explicit purposes for establishing MPAs tend to be broad and vague, such as to protect marine biodiversity and representativeness, and to improve fisheries yields, and in some cases have narrow objectives, such as to protect rare, endemic, and threatened species (e.g., see Gilman et al. 2011: Figure 2).

We undertook structured and unstructured literature searches to compile peer-reviewed and gray literature with findings on observed and theoretical ecological responses to MPAs with pelagic habitats. The structured search employed Boolean searches on combinations of the following keywords in Google Scholar: area, bigeye, billfish, blue water, dynamic, fisheries-induced evolution, FIE, fishery, fishing, genetic, highly migratory, open ocean, longline, marine, marlin, monument, MPA, no-take, park, pelagic, piracy, protected, purse seine, reserve, sanctuary, skipjack, Somali, spatial, swordfish, time-area, tuna, yellowfin, and zoning. No previous systematic reviews or meta-analyses on pelagic MPAs were identified. The unstructured search reviewed reference lists of relevant publications and reports, and tuna RFMO materials from assessments of pelagic MPAs. Table 1 summarizes how MPAs could be designed to achieve these objectives, intended ecological effects, main factors that affect whether the MPA achieves the objective, and theoretical and empirical evidence that pelagic MPAs are able to achieve these intended outcomes.

Reduce fishing mortality of species of conservation concern

Intended ecological response.—Increase the absolute abundance of populations of species of conservation concern, including endangered and threatened species, that are susceptible to capture in pelagic fisheries.

Direct and indirect ecological objectives.—Reducing anthropogenic mortality levels of vulnerable populations contributes to reducing the risk of population extirpations and to recovering depleted populations. This may also contribute to maintaining populations near target and above limit thresholds, and maintaining their community and ecosystem roles. This contributes to maintaining the system in a quasi-stable and resilient state, and a state selected to maintain

Table 1. Aims and intended ecological effects from eliminating pelagic fishing in marine pelagic areas, MPA design, factors that significantly explain whether the MPA achieves the intended objective and response, and the theoretical and empirical basis for hypothesizing that pelagic MPAs can achieve the objectives.

Aim	Intended ecological effects	MPA design options	Why it may fail	Theoretical basis	Empirical basis
Reduce fishing mortality of species of conservation concern	• Reduce the risk of population extirpations • Maintain stocks/populations near target and above limit thresholds; recover depleted stocks and populations • Contribute to implementing ecosystem-level harvest strategies and maintaining a desired quasi-stable ecosystem state	• Reduce/eliminate pelagic fishing in temporal/spatial bycatch hotspots with high local abundance or high catch rates of species of conservation concern • Reduce/eliminate pelagic fishing in temporal/spatial hotspots with high bycatch:-target catch ratios • May be spatially and/or temporally static and/or dynamic	• Displaced effort has the same or higher fishing mortality rates of species of conservation concern, or displaced effort has increased catch rates of higher risk age classes. • Displaced effort (or changing effort from one fishing method to another) results in cross-taxa conflicts. • In fisheries with quotas for target species but no effort controls, if an MPA displaces effort to areas or periods with lower target species catch rates, this could increase catch and fishing mortality of bycatch species. • Depending on (1) the proportion of each age class and sex of a population that occurs within the MPA, (2) the proportion of an individual's lifetime spent within the MPA, (3) whether the MPA includes habitat critical for life history stages, and (4) the degree of risk of anthropogenic mortality outside the MPA, the protection afforded may not increase biomass. The MPA may be too small and inadequately designed to account for the extensive ranges, variable	• Hypothetical closure of an area with relatively high species richness and density of pelagic predators would reduce catch levels of some sharks and teleosts if displaced effort maintained the same level of target species catch or effort (Worm et al. 2003). • Dynamic spatial management of Hawaii's swordfish pelagic longline fishery could mitigate sea turtle bycatch (Howell et al. 2008, 2015). • Dynamic spatial management of California's swordfish driftnet fishery could mitigate bycatch of sea turtles, sea lions and sharks (Hazen et al. 2018). • Some pelagic species of conservation concern may have sufficiently long residency times at networks of aggregating features so that MPAs could protect individuals for a sufficient proportion of their lifetime during which growth and increased biomass occurs.	• High catch rates of species of conservation concern and species diversity occur at shallow submerged features and floating objects (Worm et al. 2003, Morato et al. 2008, 2010a, 2010 Gilman et al. 2012, Dagorn et al. 2013, Hall and Roman 2013). • Dynamic spatial management of Australia's eastern tuna and billfish longline fishery has mitigated southern bluefin tuna bycatch (Hobday et al. 2010).

(Table 1. Continued.)

Aim	Intended ecological effects	MPA design options	Why it may fail	Theoretical basis	Empirical basis
			distributions, and shifting distributions in response to outcomes of climate change and changes in biomass to increase highly migratory pelagic species' biomass.		
Protect habitat in locations and during periods important for pelagic species' critical life history stages	• Increase reproduction, recruitment and absolute biomass • Reduce the risk of population extirpations • Maintain stocks/populations near target and above limit thresholds; recover depleted stocks and populations • Contribute to implementing ecosystem-level harvest strategies and maintaining a desired quasi-stable ecosystem state	• Restrict pelagic fishing at spatially and temporally predictable sites used for spawning, mating, calving, pupping, nurseries, nesting, foraging and migratory pathways • May be spatially and/or temporally static and/or dynamic	• Increased recruitment does not affect absolute biomass for stocks that are not recruitment-limited. • Effort is displaced where fishing mortality rates during critical life history stages are the same or higher. • Displaced effort results in cross-taxa conflicts, benefiting some species during critical life history stages, while exacerbating fishing mortality of others during a critical life history stage. • For some species, areas important for critical life history stages may not be predictable or known, so that MPAs cannot be designed to protect them. • The MPA may be too small and inadequately designed to protect extensive critical habitat areas.	• Purse seine seasonal area closures may have reduced juvenile bigeye tuna fishing mortality (Torres-Irineo et al. 2011, IATTC 2017). • Mobile MPAs might be able to protect relatively small dynamic sites important for pelagic species' critical life history stages that are temporally and spatially predictable (e.g., seabird foraging habitat, Hyrenbach et al. 2006a, Oppel et al. 2018; sea turtle migratory corridors, Schillinger et al. 2008; eddies within bluefin tuna spawning grounds, Bakun 2012; pelagic shark aggregations, Litvinov 2006, Domeier and Nasby-Lucas 2007, Vandeperre et al. 2014a, b).	• High densities of juvenile tunas and other species occur at shallow submerged features (Fonteneau 2007, Itano and Holland 2000, Sibert et al. 2012, Adam et al. 2003, Gilman et al. 2012).
Reduce or eliminate fishing	• Reduce fishing mortality and increase	• Protect a sufficient proportion of	• The MPA may be too small and inadequately	• Lifetime displacements of tropical tunas in some	• Increased local and regional abundance of

(Table 1. Continued.)

Aim	Intended ecological effects	MPA design options	Why it may fail	Theoretical basis	Empirical basis
mortality of target stocks of large pelagic predators at a site or period in order to contribute to keeping the stock near its target and above its limit reference points	recruitment, increasing absolute stock biomass • Increase local biomass, with spillover across the MPA margin • Maintain stocks near target and above limit thresholds, recover depleted stocks • Contribute to implementing ecosystem-level harvest strategies and maintaining a desired quasi-stable ecosystem state	individuals for an adequate proportion of their lifespan and sufficient proportion of the stock's distribution to cause an increase in local and/or absolute biomass of a target stock • May be spatially and/or temporally static and/or dynamic	designed to protect extensive ranges, temporally and spatially variable distributions, account for catch risk outside the MPA, and account for shifting distributions in response to outcomes of climate change and changes in biomass to increase highly migratory large pelagic target species' local or absolute biomass. • Displaced effort has the same or higher fishing mortality rate, such that the MPA does not cause absolute biomass to increase. • Increased recruitment does not affect absolute biomass for stocks that are not recruitment-limited.	regions may be sufficiently small so that a large MPA could enable a large part of a local population to be protected for several months or longer (Sibert and Hampton 2003, Gunn et al. 2005), during which a large proportion of lifetime growth occurs, which could augment local and absolute biomass. • Some tunas exhibit long residency times at networks of aggregating features (Adam et al. 2003, Dagorn et al. 2007), suggesting that MPAs protecting these sites could protect individuals for a sufficient proportion of their lifetime to augment growth and local biomass. • 85% of the distribution of overexploited stocks of highly mobile species needs to be included in a no-take MPA in order to increase absolute biomass and yields (Le Quesne and Codling 2009). • Closed areas would not affect biomass and yields of highly migratory stocks that are not over-exploited (Le Quesne and Codling 2009).	striped marlin occurred following temporary pelagic longline closures in part of the Mexican EEZ in the eastern Pacific (Jensen et al. 2010). • Temporary high seas closure to tuna purse seine vessels in the western and central Pacific did not reduce bigeye tuna fishing mortality because effort displaced to areas outside the MPAs and effort increased (WCPFC 2010, Sibert et al. 2012). • A de-facto MPA in the Indian Ocean from Somali piracy reduced regional effort, caused vessels to rely on log associated sets in place of sets on free swimming schools, increasing catch rates of juvenile tunas (Chassot et al. 2010). • Purse seine catch rates and relative abundance of yellowfin and skipjack tunas in an area adjacent to the Galapagos Marine Reserve were higher following enforcement of the Galapagos Marine Reserve. Fishing-the-line occurred to the southwest of the reserve (Boerder et al. 2017,

(Table 1. Continued.)

Aim	Intended ecological effects	MPA design options	Why it may fail	Theoretical basis	Empirical basis
				• High seas closures to purse seining and pelagic longline fisheries in the western and central Pacific Ocean were simulated to result in a small increase in absolute biomass of adult bigeye tuna, with largest gains within and near the MPAs (Sibert et al. 2012).	Bucaram et al. 2018).
				• Model simulations found the Chagos MPA had a minor effect on absolute skipjack biomass. A hypothetical MPA covering a large portion of the western Indian Ocean caused a large reduction in fishing mortality and stabilized spawning biomass (Dueri and Maury 2013).	
				• Model simulations found that the Chagos MPA, Indian Ocean Tuna Commission spatio-temporal closures, and a closed area in part of the Maldives' EEZ, with spatial displacement of effort, have had little effect on the biomass of yellowfin tuna (Martin et al. 2011).	
				• Reducing or eliminating pelagic fishing at shallow seamounts, other discrete static natural features that aggregate apex pelagic predators, and networks of FADs would	

(Table 1. Continued.)

Aim	Intended ecological effects	MPA design options	Why it may fail	Theoretical basis	Empirical basis
				reduce fishing mortality (Worm et al. 2003, Dagorn et al. 2013; Hall and Roman 2013, Gilman et al. 2012), assuming that displaced effort would have lower catch rates than at these features.	
Protect prey of pelagic predators (including target species and species of conservation concern) to maintain prey and predator stocks near target and above limit thresholds	• Reduce fishing mortality and increase recruitment, increasing absolute prey stock biomass • Increase local biomass of prey stocks • Increase local and absolute biomass of predator stocks/populations • Maintain prey and predator stocks/populations near targets and above limits • Contribute to implementing ecosystem-level harvest strategies and maintain a desired quasi-stable ecosystem state	• Protect a sufficient proportion of individuals for an adequate proportion of their lifespan and sufficient proportion of the stock's distribution to cause an increase in local and/or absolute biomass of the prey stock • May be spatially and/or temporally static and/or dynamic	• Because prey of large pelagic predators are generally under-exploited, and because there is a weak correlation, if any, between absolute abundance of forage fish and their predators, reduced fishing mortality and increased biomass of prey will not likely affect the absolute population sizes of their predators. • Effort is displaced spatially or temporally where fishing mortality rates of prey species are the same or higher. • Displaced effort results in cross-taxa conflicts, benefiting some prey species but exacerbating catch rates of others. • The MPA may be too small and inadequately designed to account for the extensive ranges, temporally and spatially variable distributions, and shifting	• Reduced fishing mortality of forage fish may increase their local abundance, increasing the local availability of seabirds' prey, seabird populations' reproductive success and population abundance (Gremillet et al. 2008, Cury et al. 2011).	• Penguins immigrated into a recently established MPA closed to fishing, and there was a 30% decrease in penguin foraging effort three months after the fishery closure was established, possibly because the local abundance of their prey increased (Pichegru et al. 2010).

(Table 1. Continued.)

Aim	Intended ecological effects	MPA design options	Why it may fail	Theoretical basis	Empirical basis
			distributions in response to out-comes of climate change to increase the local or absolute bio-mass of highly migratory prey species.		
Reduce, halt or reverse FIE resulting from heritable, trait-selective fishing mortality	• Maintain a population's diversity of heritable traits and adaptive genetic varia-tion, fitness, and evolution-ary processes, reducing the risk of popula-tion extirpa-tions • Maintain a desired quasi-stable ecosys-tem state	• Depends on species-speci-fic traits and concomitant evolutionary responses to different forms of reductions in trait-based selective fish-ing mortality, and for which heritable traits a fishery has been selec-tively remov-ing • Protect areas where a large proportion of the local bio-mass of a spe-cies is made up of individ-uals with heri-table traits that cause them to be selectively harvested. • Protect areas where the full diversity of variation in heritable traits of a popula-tion are repre-sented, pre-serving natu-ral genetic variation in a portion of the population • Design the MPA to reduce fishing mortality of the population subject to FIE.	• Intraspecific changes in genetic diversity from FIE may be irreversible. • An MPA can have nominal effect, and in some cases might exacerbate FIE, depending on the MPA design and the life history traits of affected pelagic species, including if the MPA is not a source for recruits to the population and if density-depen-dent processes within the MPA strengthen FIE. • Fishing effort may be displaced temporally or spatially, where it exacerbates the magnitude of FIE that the MPA was intended to reduce, or exacer-bates FIE in other taxa. • The MPA may be too small and inadequately designed to sig-nificantly affect the magnitude of FIE. • Not all pelagic species may have spatially and temporally pre-dictable areas that meet either of the MPA designs predicted	No theoretical basis of the efficacy of MPAs at reducing, halting or reversing FIE in pelagic marine species. Theoretical Basis for Non-Pelagic Species: • Model-based studies predicted that no-take MPAs mitigated FIE for matura-tion at a younger age, smaller size and slower growth in demersal and coastal fishes. Assumed MPA was a source of recruits to the population. • Using a model calibrated for life history traits for Atlantic cod, a no-take MPA in foraging grounds reduced the mag-nitude of FIE, but an MPA in spawning grounds had nominal effect or exacerbated the magnitude of FIE for earlier matu-ration and smal-ler size (Trexler and Travis 2000, Baskett et al. 2005, Dunlop et al. 2009, Miethe et al. 2009). These studies assumed the MPA was a	No empirical basis of the efficacy of MPAs at reducing, halting or reversing FIE in pelagic marine species

(Table 1. Continued.)

Aim	Intended ecological effects	MPA design options	Why it may fail	Theoretical basis	Empirical basis
		Because the rate of FIE is determined in part by the intensity of fishing that selectively removes individuals from a stock, an MPA that reduces the fishing mortality rate will contribute to reducing the magnitude of FIE, and possibly to recovering from previous FIE	to alleviate pressures for FIE in pelagic marine organisms.	source of recruits to the population.	

Notes: EEZ, exclusive economic zone; FIE, fisheries-induced evolution; MPA, marine protected area.

desired provision of ecosystem services. Population extirpations result in the permanent loss of unique genotypes, which can reduce species resilience and concomitant resistance to extinction, as well as cause broad changes in community structure and functioning (Carlton et al. 1999, Dulvy 2006).

MPA design.—The ecological objectives and response could be achieved by prohibiting fishing with gear types in which the species of interest is susceptible to capture in spatially and/or temporally predictable hotspots of local abundance (Hays et al. 2019) and of catch rates (Gilman et al. 2012). Or, fishing could be prohibited in areas or periods with relatively high ratios of bycatch to target catch levels.

These pelagic MPAs could be spatially and temporally static (fixed in location and year-round), such as at anchored floating objects, a shallow seamount, shelf break, or other bathymetric feature that concentrates, and enhances the residency time, of pelagic predators and their prey (Worm et al. 2003, Genin 2004, Morato et al. 2008, 2010a, b, Gilman et al. 2012, Kaplan et al. 2014). Alternatively, the MPA, or network of MPAs, could be spatially static but temporally dynamic, such as a migratory corridor leading to a breeding area, or a site with variable periods of upwelling (Schillinger et al. 2008). The MPA could be spatially dynamic but temporally static, protecting features such as fronts and eddies that can be temporally predictable but variable spatially and in intensity. Or, the MPA could be both spatially and temporally variable, such as an MPA designed to protect hydrographic features (fronts, eddies) and drifting floating objects whose locations vary in space and time (Hyrenbach et al. 2000, Hobday and Hartmann 2006, Game et al. 2009, Hobday et al. 2010, Hall and Roman 2013, Gaertner et al. 2016).

Why the MPA design might not achieve ecological objectives and responses.—The response of fishers to the establishment of an MPA can affect MPA efficacy. MPAs designed to mitigate the bycatch of a species of conservation concern may, in some cases, cause the displacement of fishing effort to areas or periods that inadvertently exacerbate bycatch rates of this species or of other at-risk taxa (Gilman et al. 2019). In some cases, marine area closures have resulted in the spatial or temporal displacement of bycatch of an individual species or age classes (Murray et al. 2000, Powers and Abeare 2009, Diamond et al. 2010, SPC 2010, Suuronen et al. 2010, Sibert et al. 2012). Fishing effort can be displaced to other sites or seasons where mortality rates and levels are the same or

higher than they had been at the protected site, or where there is higher mortality of age classes with greater risk of causing irreparable harm or population extirpations than the age classes that are caught in the closed area (Ardron et al. 2008, WCPFC 2010, FAO 2011).

Although less well documented, there are also examples of closed areas designed to reduce the bycatch of one species of conservation concern that then lead to an increase in the bycatch of another species of conservation concern (Abbott and Haynie 2012, Gilman et al. 2019). For example, Baum et al. (2003) modeled the effects on catch rates from the closure of areas to the U.S. north Atlantic swordfish longline fishery. A portion of the fishing grounds was closed for about three years to reduce loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtle by catch. Spatially displaced effort was modeled to simulate constant levels of swordfish catch and effort. Both of the closure scenarios predicted reduced catch rates of loggerhead and leatherback sea turtles and blue and shortfin mako sharks, the latter being categorized as Low Risk by the IUCN Red List. However, there was a predicted increase in the catch rates of 10 shark species, including two categorized as Vulnerable by the IUCN Red List (Baum et al. 2003).

In fisheries with quotas for target species (e.g., bigeye tuna annual quotas for longline fisheries in the western and central Pacific; WCPFC 2018) but no effort controls, MPAs could displace fishing effort to areas or periods with relatively lower target species catch rates, resulting in increased effort to maintain target species catch levels. This could result in increased catch levels and fishing mortality of bycatch species, including of endangered, threatened, and protected species (Kaiser 2005).

For some populations, including those of endangered species, fisheries discards can be an important food subsidy (Oro et al. 2013, Fondo et al. 2015). An abrupt discontinuation of discarding offal, spent bait, and dead catch, such as might occur from the establishment of a no-take reserve that displaces fishing effort, may result in precipitous declines in local biomass and absolute population sizes of seabirds, dolphins, and other at-risk taxa (Fondo et al. 2015). Elimination of one fishing gear type in an MPA might increase scavenging from another gear type that poses a larger bycatch risk (e.g., eliminating trawling increases seabird bycatch in pelagic longline fisheries; Soriano-Redondo et al. 2016).

MPAs with time/area restrictions on pelagic fishing may be too small and inadequately designed to account for the extensive ranges, temporally and spatially dynamic distributions, and shifting distributions in response to outcomes of climate change. As a result, there may be no increase in local or absolute biomass of highly migratory pelagic species in response to an MPA. Depending on (1) the proportion of each age class and sex of a population that occurs within the MPA (more likely to be effective for species with small ranges), (2) the proportion of an individual's lifetime that they spend within the MPA, (3) whether the MPA includes habitat critical for certain life history stages (section *Reduce Fishing Mortality at Pelagic Habitats Critical for Life History Stages*), and (4) the risk of mortality outside of the MPA from anthropogenic sources, including from fishing, the protection afforded to a population of conservation concern from an MPA may not be adequate to cause an increase in biomass, locally or stock-wide (e.g., Botsford et al. 2003, Hilborn et al. 2004b, Blyth-Skyrme et al. 2006, Le Quesne and Codling 2009, Moffitt et al. 2009, Grüss et al. 2011, Graham et al. 2012, Rosenbaum et al. 2014). These issues are applicable across migratory pelagic species, and not just species of conservation concern. This is discussed in more detail in the section *Maintain the Condition of Target Stocks of Large Pelagic Predators* as it pertains to large pelagic target species.

Pelagic apex predators, and in some cases different size classes and sexes within species, utilize different static and dynamic pelagic habitats (Hyrenbach et al. 2000, 2006a, b, Polovina et al. 2004, Bailey and Thompson 2010, Muhling et al. 2011, Vandeperre et al. 2014a, b, Gilman et al. 2016). Their geospatial and vertical distributions are determined, in part, by prey availability and primary environmental variables of hydrostatic pressure, temperature, and dissolved oxygen (Musyl et al. 2003, 2011, Beverly et al. 2009, Bernal et al. 2010, Lehodey et al. 2011, 2015, Muhling et al. 2011, Brodziak and Walsh 2013). The distributions of pelagic predators, and when and where they aggregate, are also determined, in part, by physical features that determine their

biophysical structure (e.g., gyres, fronts). These features structure the distribution of nutrients, levels of primary productivity, and the distributions and aggregations of prey species of pelagic apex predators (Hyrenbach et al. 2000, *a*, *b*, Selles et al. 2014, Vandeperre et al. 2014*b*, Kavanaugh et al. 2016). The different categories of these features differ in their amenability for management through spatial restrictions such as MPAs.

Some pelagic species aggregate at bathymetric structures, which have fixed (static) geospatial locations. Such structures include shallow submerged features like seamounts and reefs, areas with steep seabed gradients such as shelf breaks, and near islands and coastal features that create small-scale eddies and fronts (i.e., island mass effect; Doty and Oguri 1956, Worm et al. 2003, Genin 2004, Hyrenbach et al. 2000, Bailey and Thompson 2010, Gilman et al. 2012, Kavanaugh et al. 2016). Depending on their physical characteristics and location, these features alter local currents and possibly isotherm distributions, create oceanographic perturbations, such as through advection and dispersion, and increase upwelling and mixing (Pitcher et al. 2007, White et al. 2007). The influence of these static features in concentrating productivity, and aggregating pelagic predators, can be coupled with hydrodynamic conditions, such as current direction and strength. In other words, the feature is fixed in location, but its concentration of productivity can be temporally variable. This class of pelagic features is relatively suitable for management through spatially static MPAs due to our ability to predict the physical parameters that lead to variation in the intensity, extent, and position of these features.

Other habitats of pelagic apex predators are much more challenging to manage through the use of MPAs. Spatially dynamic hydrographic features affect the distribution of pelagic predators. Some are broadscale, such as currents and frontal systems that are temporally persistent, occurring over years to decades, and over entire ocean basins. Others are meso-scale, such as upwelling plumes, eddies, and frontal systems, persisting over tens to hundreds of days and occurring over tens to hundreds of kilometers. Others are fine scale, including fronts and eddies, which are ephemeral, lasting for days, and occurring over 100s of meters to kilometers

(Hyrenbach et al. 2000, McGlade and Metuzals 2000, Polovina et al. 2001, Hazen et al. 2013, Kavanaugh et al. 2016). Aggregations of pelagic species at ephemeral, dynamic, pelagic habitats are difficult to map and manage in real time for the exclusion of fishing effort, especially for high seas areas where vessels of multiple flag states occur and in some cases target species that are not covered by RFMOs (e.g., Kaiser 2005, Fonteneau 2007, Gilman 2007, Kaplan et al. 2010). As with static habitats, dynamic but persistent habitats are relatively predicable, enabling dynamic pelagic MPA boundaries to be defined more easily, but as discussed above, they may need to be extremely large to achieve ecological objectives, especially if they are used without other management measures (Horwood et al. 1998).

Pelagic MPA designs need to account for other sources of variability in the ranges of mobile pelagic predators. This includes inter-annual, decadal, and multidecadal variability in the distributions, recruitment, and biomass of pelagic species in response to large-scale climate cycles (Lehodey et al. 1997, 2006, Lu et al. 1998, Lehodey 2000, Menard et al. 2007, Gilman et al. 2012, Baez et al. 2018, Faillettaz et al. 2019). Distributions and abundance of pelagic predators are also shifting in response to the outcomes of human-induced climate change (Perry et al. 2005, Dufour et al. 2010, Lehodey et al. 2010, 2013, 2015, Muhling et al. 2011, Gilman et al. 2016). Climate change outcomes include decadal and longer-term trends in: ocean surface and subsurface temperature, dissolved CO_2 and O_2 concentrations, pH, ocean circulation patterns, vertical mixing, and eddies, as well as outcomes from indirect effects such as alterations to functional links between ecosystems (Brander 2010, Le Borgne et al. 2011, Lehodey et al. 2011). Ranges may also change in response to variations in abundance, where it is hypothesized that, as a population's abundance declines, its distribution will contract toward the center of their ranges, where density remains stable (Collette and Russo 1984, Pitcher 1995, Brodie et al. 1998, Worm and Tittensor 2011).

Expanding on the categorizations of Hyrenbach et al. (2000) and Kavanaugh et al. (2016) of physical features that determine pelagic ecosystems' biophysical structure, we add a category of individual and networks of natural and artificial

drifting and anchored floating objects (Hall and Roman 2013, Gaertner et al. 2016). Some pelagic species associate near and aggregate at natural and artificial floating objects, including FADs, possibly because the floating objects provide shelter, foraging opportunities, and meeting points (Freon and Dagorn 2000, Castro et al. 2002, Hall and Roman 2013). Floating objects that aggregate pelagic marine organisms include drifting logs, drifting algae, live and dead large marine organisms, marine debris (e.g., crates, pallets, nets), vessels, and anchored and drifting FADs, which are artificial floating objects that are built and deployed by fishers and are designed specifically to aggregate pelagic fishes (Castro et al. 2002, Hall and Roman 2013, Gaertner et al. 2016).

FADs have modified pelagic habitat by increasing the density of floating objects in regions where natural floating objects already were present, and possibly by introducing floating objects to areas where they did not naturally occur. FADs may detrimentally alter the natural behavior and ecology of species that associate with the device. Drifting FADs have been hypothesized to change the spatial distributions, migration patterns, schooling dynamics, and vertical habitat use of aggregated organisms. In turn, by altering their distributions and movement, drifting FADs may modify the aggregated organisms' diet, condition, growth, reproductive success, and other biological characteristics (Marsac et al. 2000, Hallier and Gaertner 2008, Amandè et al. 2010, Dagorn et al. 2013, Sempo et al. 2013). As with natural static features, anchored floating objects, including networks of anchored FADs, could feasibly be managed through the use of spatially static MPAs. Given adequate monitoring and surveillance, managing tuna purse seine fishing on drifting FADs and other drifting floating objects is feasible through temporally and spatially dynamic MPAs (e.g., seasonal tuna purse seine FAD closure; WCPFC 2018). Otherwise, for tuna purse seine fisheries with limited observer coverage and surveillance, drifting floating objects would face similar issues constraining the utility of management through dynamic MPAs as occurs with dynamic hydrographic features.

Theoretical and empirical basis.—There is empirical evidence of higher bycatch rates of at-risk taxa, as well as higher pelagic species diversity, at shallow submerged features, including seamounts and submerged reefs (Worm et al. 2003, Morato et al. 2008, 2010a, b, Gilman et al. 2012). Protecting these static sites might reduce bycatch. Furthermore, bigeye and yellowfin tunas have residency times at networks of static aggregating features (shallow seamounts, anchored FADs, and buoys, banks, and ledges) of between days (Ohta and Kakuma 2004) and as long as possibly two years (Adam et al. 2003). In some locations with networks of natural and non-natural aggregating features, these tuna species, and possibly pelagic species of conservation concern, may have sufficient persistence such that MPAs could provide protection to individuals for an adequate proportion of their lifetime to augment growth and local biomass within the MPA.

Restrictions on purse seine fishing on FADs and other anchored and drifting floating objects could reduce bycatch of some species of conservation concern. There is empirical evidence of a larger number of species in the catch and higher bycatch rates of silky and oceanic white tip sharks in tuna purse seine sets on drifting FADs and logs than occurs in sets in unassociated free-swimming school sets (Dagorn et al. 2013, Hall and Roman 2013, Gilman et al. 2019). School sets, however, have higher catch rates of mobulid rays and leatherback sea turtles (Dagorn et al. 2013, Hall and Roman 2013, Gilman et al. 2019). Therefore, if restrictions on associated sets (i.e., sets on FADs and other floating objects) increased school set effort, this would result in cross-taxa conflicts by displacing bycatch issues onto other species of conservation concern (Gilman et al. 2019).

Using a closed-area model to analyze historical catch data from a U.S. swordfish longline fishery in the northwest Atlantic, Worm et al. (2003) assessed what the effect would have been if the fishery had been banned in a hotspot of pelagic species richness and density (an area with a high number of species per unit of number of catch and a high number of species per unit of fishing effort). The area closure would have reduced catch levels of some species of pelagic sharks and teleosts without reducing swordfish catch levels, when assuming displaced effort maintained either swordfish catch levels or effort (Worm et al. 2003).

Theoretical approaches have been developed for dynamic temporal and spatial fisheries management based on the variable position of pelagic habitats and variable ecosystem processes. The objectives of these theoretical approaches to fisheries dynamic spatial management include protecting and recovering depleted target species, mitigating fisheries bycatch of species of conservation concern, mitigating ecosystem effects of pelagic fisheries, contributing to the protection of representative habitats nationally and globally, and protecting processes that maintain and produce biodiversity (e.g., Hyrenbach et al. 2000, Alpine and Hobday 2007, Lombard et al. 2007, Pressey et al. 2007, Nel and Omardien 2008). A retrospective analysis of the efficacy of a dynamic fisheries management system for the eastern Australian yellowfin and bigeye tuna and billfish longline fishery that uses a habitat model found that it is successfully mitigating bycatch of southern bluefin tuna (Hobday and Hartmann 2006, Hobday et al. 2009, 2010). A similar approach provides maps of near real-time locations of predicted thermal habitat of loggerhead and leatherback sea turtles to Hawaii longline swordfish vessels, information that could, theoretically, enable them to avoid loggerhead bycatch hotspots (Howell et al. 2008, 2015). A comparable tool for the California drift swordfish gillnet fishery identifies near real-time areas with high ratios of bycatch to target catch for leatherback sea turtles, California sea lions, and blue sharks (Hazen et al. 2018).

In summary, only two studies were identified that assessed pelagic MPA effects on species of conservation concern. Both were retrospective analyses, one of a hypothetical closure (Worm et al. 2003) and the other of the efficacy of a dynamic fisheries management system (Hobday et al. 2010).

Reduce fishing mortality at pelagic habitats critical for life history stages

Intended ecological response.—Increase recruitment and absolute biomass of populations of species that are susceptible to capture in pelagic fisheries.

Direct and indirect ecological objectives.—Pelagic MPAs may protect habitat in locations and during periods that are important for critical life history stages of pelagic species (Kaiser 2005, Game et al. 2009, Davies et al. 2012). In addition to the ecological objectives described in the section *Reduce Fishing Mortality of Species of Conservation Concern*, protecting spawning, mating, calving/pupping, nursery, and nesting sites, and migratory corridors leading to these sites, may increase reproduction. Fish eggs and larvae, and juvenile fish, seabirds, sea turtles, and marine mammals, are exported from the protected area. This in turn may cause an increase in stock/population recruitment and total stock/population biomass.

MPA design.—The ecological objectives and responses could be achieved by prohibiting fishing with gear types in which the species in question is susceptible to capture in spatially and temporally predictable sites important for critical life history stages. This includes periods and areas used for spawning, mating, and calving/pupping, as well as nursery and nesting areas, areas important for foraging, and migratory pathways. The MPA or network of MPAs may be spatially and/or temporally static and/or dynamic, as with MPAs designed to mitigate bycatch of at-risk taxa (section *Reduce Fishing Mortality of Species of Conservation Concern*).

Why the MPA design might not achieve ecological objectives and responses.—Displaced effort could have higher catch rates during critical life history stages. Displaced effort could also produce cross-taxa conflicts, benefiting some species during critical life history stages, but exacerbating fishing mortality rates of others during a critical life history stage (Gilman et al. 2019).

Areas important for critical life history stages are not known for many populations of pelagic species, and not all pelagic species may have spatially and temporally predictable pelagic areas of critical habitat that are relatively small, where overlap with problematic fisheries can be eliminated (e.g., Fernandez et al. 2001, Hyrenbach et al. 2002, Oppel et al. 2018). For instance, with the exception of bluefin tuna species, discussed below, there is very limited documentation of spawning aggregations for large pelagic target species (SCRFA 2019), with, for example, a handful identified for istiophorid billfishes (e.g., black marlin, *Istiompax indica*; Domeier and Speare 2012, Erisman et al. 2015) and dolphinfish (*Coryphaena hippurus*; Alejo-plata et al. 2011). This

may be because there have been too few larval studies, or it may be that most large pelagic species do not spawn in discrete sites or during discrete time periods. For instance, bigeye, yellowfin, skipjack, and albacore tunas are believed to have extensive spawning grounds in tropical and subtropical waters with long spawning seasons relative to bluefin species (Schaefer et al. 2005, Collette et al. 2011, Muhling et al. 2011, Dueri, and Maury 2013). In addition, if the MPA does result in increased recruitment, this will increase total stock biomass only if the stock was recruitment-limited (Hilborn et al. 2004*b*).

Theoretical and empirical basis.—There is empirical evidence of relatively high catch rates of undersized and juvenile tunas and other fish species at shallow seamounts and other features (Fonteneau 1991, Itano and Holland 2000, Sibert et al. 2000, Adam et al. 2003, Gilman et al. 2012). Protecting these sites could reduce catch rates of these age classes.

Tuna RFMO seasonal closures to purse seine fishing in areas with a high density of juvenile bigeye tunas, in the eastern Pacific and Atlantic Oceans, may have reduced juvenile bigeye tuna catch rates (Torres-Irineo et al. 2011, IATTC 2017).

Theoretically, mobile MPAs might be able to protect relatively small, dynamic sites that are important for critical life history stages of pelagic species if the sites are temporally and spatially predictable. For example, mobile MPAs designed to protect eddies within bluefin spawning grounds during spawning periods hold promise. The three bluefin tuna species, which are categorized as IUCN Threatened (Collette et al. 2011), spawn in small areas (Muhling et al. 2011). Bluefin tunas also have relatively short spawning periods of 1–2 months (Collette et al. 2011, Muhling et al. 2011). Bluefin tunas may depend heavily on eddies to produce spawning schools that are above a density threshold needed for successful reproduction (Bakun 2012).

Theoretically, for those species that exhibit consistent at-sea aggregating behavior, where the individuals of the same population aggregate during the same periods and at the same areas, mobile or static MPAs may be highly effective, such as for predictable pelagic foraging hotspots of some seabird species (Hyrenbach et al. 2006*a*, Louzao et al. 2006, Oppel et al. 2018). Similarly,

pelagic MPAs could theoretically be designed to protect predictable pelagic foraging hotspots of pelagic shark pupping, nursery, and mating aggregations (Litvinov 2006, Domeier and Nasby-Lucas 2007, Vandeperre et al. 2014*a*, *b*). Pelagic MPAs could protect areas where pelagic juvenile loggerhead sea turtles have prolonged residence (e.g., the Kuroshio Extension Bifurcation Region, Kobayashi et al. 2008; an area off Baja California, Peckham et al. 2007; and an area in the East China Sea, Kobayashi et al. 2011). Pelagic MPAs could protect predictable, well-defined pelagic migratory corridors (Block et al. 2011), for example, for post-nesting leatherback sea turtles between their nesting beaches in Costa Rica and foraging grounds in the South Pacific Gyre (Schillinger et al. 2008). Such an application has been applied to migratory right whales off the coast of New England with considerable success (Schick et al. 2009). Although this is not a fishery example, it has reduced mortality through an area avoidance approach (i.e., by excluding the source of mortality—shipping).

Of the above-reviewed studies, only one assessed the effect of a pelagic MPA established in habitat important for critical life history stages. A one-month annual closure to a pelagic fishery in an area with a high density of juvenile tunas was assessed using a Before–After-Control–Impact (BACI) study design (discussed in the section *Counterfactual Reasoning*), but without after sampling in the closure (Torres-Irineo et al. 2011). During an annual one-month closure, purse seine vessels making free school sets fished-the-line. In the control area, juvenile tuna catch levels increased after the closure was established, possibly due to fishing-the-line by the displaced effort, or possibly due to various other variables.

Maintain the condition of target stocks of large pelagic predators to sustain desired production levels

Intended ecological response.—Increase local biomass, and maintain the absolute biomass of stocks of principal market species near targeted levels.

Direct and indirect ecological objectives.—Pelagic MPAs may reduce or eliminate the fishing mortality of target stocks of large pelagic predators

at a site or time period in order to contribute to maintaining biomass levels and exploitation rates near target reference points (TRPs) so as to sustain desired production levels, and above limit reference points (LRPs) in order to avoid causing protracted or irreparable harm to the stock.

Defined in Annex II of the United Nations Fish Stocks Agreement, "Limit reference points set boundaries which are intended to constrain harvesting within safe biological limits within which the stocks can produce maximum sustainable yield. Target reference points are intended to meet management objectives" (UNFSA 1995). Stock-specific and multispecies TRPs are designed to meet long-term socioeconomic objectives of managing target stocks, but also contribute to addressing ecological risks, as the TRP establishes biomass and fishing morality rate levels at or above the level that is predicted to produce maximum sustainable yields, and also may avoid a spiral to LRPs and other biological reference points where increased fishing effort and mortality risk irreparably damaging a fish stock (e.g., F_{crash}, the fishing mortality rate that will drive a population to 1/1000 of virgin biomass, B_{crit}, the minimum viable population size below which population extirpation is imminent, threshold for minimum viable density) (Mace 1994, White et al. 2007, Gilman et al. 2014). When current biomass falls below B_{msy} for a sufficiently long period, this could trigger a decrease in market supply. In turn, this could increase both the market value and demand and concomitantly incentivize increasing fishing effort (Cinner et al. 2011). Thus, TRPs can be seen as checks against market forces that could drive the biomass of an overexploited stock to a critical level or lead to Allee effects (Stephens and Sutherland 1999, Gilman et al. 2014). Stock-specific TRPs can be designed to be consistent with ecosystem-level target and limit thresholds (Gilman et al. 2017).

The reduction or elimination of fishing mortality of target species in the MPA increases recruitment and reduces fishing mortality risk due to diminished catch risk of individuals who spend a proportion of their lifetime in the MPA. These outcomes, in turn, contribute to the intended ecological response of maintaining absolute stock biomass at a targeted level, or increasing biomass

if it is below the target (e.g., Christie et al. 2010). This contributes to maintaining the stock near its TRP, to recovering depleted stocks, and to implementing stock-specific as well as ecosystem-level harvest strategies (Sainsbury et al. 2000, Link 2005, Gilman et al. 2017).

The reduction or elimination of fishing mortality of target species in the MPA results in an increase in local biomass (number of individuals and size) within the MPA. This, in turn, results in spillover, benefiting fisheries adjacent to the seaward margin of the MPA, through emigration of target (as well as non-target) species from within to outside the protected area (Roberts et al. 2001, Goñi et al. 2008).

MPA design.—The ecological objectives and responses could be achieved by creating temporal and/or spatial closures to historical fishing grounds where target species were caught, designed to protect a sufficient proportion of individuals of a stock of a target species for an adequate proportion of their life span, and protect a sufficient proportion of the distribution of the stock. The MPA or network of MPAs may be spatially and/or temporally static and/or dynamic, as with MPAs designed to mitigate bycatch of at-risk taxa (section *Reduce Fishing Mortality of Species of Conservation Concern*).

Why the MPA design might not achieve ecological objectives and responses.—As discussed in the section *Reduce Fishing Mortality of Species of Conservation Concern*, time/area restrictions applied to pelagic fisheries attempting to protect highly migratory large pelagic predators may not be sufficiently large to account for their extensive ranges and designed to account for their temporally and spatially variable distributions and catch risk outside of the MPA, as well as account for permanent shifts in distributions due to the outcomes of climate change. Large pelagic target species on average are highly migratory (however, see Sibert and Hampton 2003 and Gunn et al. 2005, discussed below). A pelagic MPA, or network of pelagic MPAs, would need to cover extremely large areas in order to enable an individual pelagic fish to be at significantly reduced risk of capture throughout its lifetime (i.e., the protected area or areas need to cover a large proportion of the stock's distribution), and to protect a substantially large proportion of the individuals of the stock (Botsford et al. 2003, Blyth-

Skyrme et al. 2006, Le Quesne and Codling 2009, Grüss et al. 2011, Dueri and Maury 2013). If individuals of the target species are transient, remaining relatively short time periods (days, weeks) in the MPA, especially if fishing-the-line occurs, then there would not be an increase in biomass from the MPA, locally or stock-wide (Moffitt et al. 2009, Grüss et al. 2011, Graham et al. 2012).

If effort is displaced, temporally or spatially, so that it increases the catch risk and fishing mortality rate, then the pelagic MPA might act to reduce biomass. And, as discussed in the section *Reduce Fishing Mortality at Pelagic Habitats Critical for Life History Stages*, if the MPA increases recruitment, this will increase absolute stock biomass only if the stock was recruitment-limited.

Where MPAs have been documented to result in spillover of fished species that increase in local abundance as a result of site-based protection from fishing mortality, the spillover effect was detectable over very small distances (100s of meters) from the MPA boundary (Halpern et al. 2009). However, it is possible that the spatial extent of a spillover effect could extend over tens to hundreds of km (e.g., see Boerder et al. 2017, Bucaram et al. 2018).

Theoretical and empirical basis.—Tropical skipjack and yellowfin tunas had median lifetime displacements (net distance moved) of between about 400 and 500 nm, and median residence times (the time it would take for half of the local population to emigrate outside of the exclusive economic zone (EEZ) of a Pacific island country) of about 6 months (Sibert and Hampton 2003). In contrast, bigeye tuna in the Coral Sea off the northeastern coast of Australia showed limited horizontal movements: 90% of 83 bigeye tunas that were recaptured between 16 and 1441 days following release were within 150 nm of their release locations (Gunn et al. 2005). Adult bigeye tuna in the Pacific made home range movements of between 100 and 700 nm (Schaefer and Fuller 2009). Mark–recapture studies of juvenile skipjack, bigeye, and yellowfin tunas in the Indian Ocean have shown much larger-scale movements of 400–1000 nm within three months (not lifetime displacements; IOTC 2008, Kaplan et al. 2014). Thus, while a large proportion of a local population of tropical tunas occurs in more than one EEZ and/or high seas area, the findings of

Sibert and Hampton (2003) and Gunn et al. (2005) suggest that it might be feasible to establish a large pelagic MPA within which a large part of the local population of tropical tunas remains for several months or longer, a period of time during which a large proportion of the total growth of these species occurs. It is unclear, however, what effect protecting areas of high tuna persistence/residency might have on local biomass within the MPA or absolute biomass of the population.

Similarly, bigeye and yellowfin tunas have residency times at networks of static aggregating features (e.g., shallow seamounts, anchored FADs, and buoys, banks, and ledges) of between days to months (Ohta and Kakuma 2004, Dagorn et al. 2007) and as long as approximately two years (Adam et al. 2003). In some locations with networks of natural and non-natural aggregating features, these tuna species, and perhaps other pelagic predators, may have sufficient persistence such that MPAs could provide protection to individuals for an adequate proportion of their lifetime to augment growth and local biomass within the MPA. Bigeye and yellowfin tunas, however, have short residency times at individual static aggregating features of days to months (Holland et al. 1999, Itano and Holland 2000, Sibert et al. 2000, Adam et al. 2003, Ohta and Kakuma 2004, Richardson et al. 2018), and residency times of days at drifting FADs (Schaefer and Fuller 2002).

Jensen et al. (2010) modeled the response in abundance of striped marlin (*Kajikaia audax*) to two temporary closures to longline fishing established in part of the Mexican EEZ in the eastern Pacific. During the closures, local and regional abundance of striped marlin increased. This may have been a response to the MPA, as a large proportion of the stock's range might have occurred inside the MPA. Alternatively, other factors, such as effects on recruitment and stock distribution in response to large-scale climate cycles, and effects of changes in fishing gear and methods that affect fishing efficiency and species selectivity that were not accounted for in standardizing the catch time series, may have had significant influences on striped marlin catch rates.

High seas closures to purse seine fishing in the western and central Pacific Ocean did not reduce bigeye tuna fishing mortality because purse seine

effort was displaced to areas adjacent to the closures, and effort increased by 10% following the creation of the MPAs (WCPFC 2010, Sibert et al. 2012). A de facto pelagic MPA from Somali piracy in the Indian Ocean resulted in reduced effort regionally. However, this also resulted in a switch to log-associated sets in place of sets on free-swimming schools, which increased the catch rate of juvenile bigeye and yellowfin tunas (Chassot et al. 2010).

Boerder et al. (2017) observed that nominal tuna purse seine catch rates, fishing effort, and catch levels in an area adjacent to and down current of the Galapagos Marine Reserve were higher after enforcement of a ban on industrial tuna fishing within 40 nautical miles around the Galapagos Islands began than during a period before enforcement of the closure occurred. Analyses of Automatic Identification System data from purse seine vessels also detected a higher density of sets near the reserve (fishing-the-line). Based on these observations, the authors hypothesized that the MPA caused an increase in the local abundance of tropical tunas, with spillover across the MPA boundary. However, the authors recognized that other variables may have contributed to causing these observed changes (Boerder et al. 2017). The study did not assess whether there was a local or absolute response in stock biomass to the MPA.

Similar to Boerder et al. (2017), Bucaram et al. (2018) assessed the effects of the Galapagos Marine Reserve on Ecuadorian tuna purse seine catch rates, relative local abundance of tuna species, and the spatial distribution of fishing effort. Following enforcement of the reserve, fishing-the-line was observed southwest of the reserve. In the Ecuador EEZ adjacent to the Galapagos Islands, and on the high seas in El Corralito, an area to the west of the Galapagos that is seasonally closed to tuna purse seine vessels (IATTC 2017), significantly smaller sized yellowfin tuna were caught relative to yellowfin caught by tuna purse seine vessels throughout the eastern Pacific Ocean. After the reserve was established, yellowfin and skipjack tuna catch rates with standardized effort significantly increased in the Ecuadorian EEZ adjacent to the reserve and in El Corralito, indicating that their local abundance may have increased. These studies did not assess absolute abundance responses to the MPA. Thus,

the findings of Boerder et al. (2017) and Bucaram et al (2018) support possible tuna local abundance responses to the Galapagos Marine Reserve, where a counterfactual assessment approach would provide a more certain understanding (section *Counterfactual Reasoning*).

While not an assessment of responses of pelagic predators to fishery closures, the findings of Le Quesne and Codling (2009) have implications for highly migratory pelagic species. Using a population model parameterized for North Sea cod (*Gadus morhua*), the authors predicted that, for overexploited stocks of highly mobile species, 85% of the distribution of the stock would need to be included in a no-take MPA in order to increase absolute biomass and yields. Furthermore, a closed area would not affect biomass and yields of stocks that are not overexploited (i.e., are fully exploited and achieving maximum sustainable yields or are underexploited; Le Quesne and Codling 2009).

Theoretical, model-based results of the effect of high seas closures to purse seine fishing in the western and central Pacific Ocean, with effort displaced outside the closed areas, predicted a very small (0.1%) increase in stock-wide adult bigeye biomass (Sibert et al. 2012). High seas closures to both purse seine and pelagic longline fisheries, such that the longline closures were located within part of the known bigeye spawning area, with effort displacement, would result in a 1% increase in absolute adult bigeye biomass (Sibert et al. 2012). This spatially explicit population model accounted for the limited lifetime spatial movements estimated by Sibert and Hampton (2003). The effect of the closures on adult bigeye biomass was predicted to be largest within the closed areas and adjacent areas from a spillover effect (Sibert et al. 2012).

Dueri and Maury (2013) modeled the effect of the Chagos Archipelago/British Indian Ocean Territory MPA and of a hypothetical MPA covering a large portion of the western Indian Ocean where most skipjack catches currently occur, employing various assumptions on the displacement of fishing effort. The Chagos MPA had a very minor effect on absolute skipjack biomass, while the hypothetical extremely large MPA was projected to cause a large reduction in fishing mortality and stabilization of skipjack spawning biomass (Dueri and Maury 2013). Martin et al.

(2011) used an age-structured model to assess the effects of the Chagos MPA, Indian Ocean Tuna Commission one-month closures of an area off the coast of Somalia to pelagic longline and tuna purse seine fisheries, and a longline closure in part of the Maldives EEZ, with spatial displacement of fishing effort from the Chagos and IOTC MPAs. They found that the MPAs have been associated with little change in yellowfin tuna absolute stock biomass, and may be causing a decrease in biomass. These findings support the idea that a static pelagic MPA would need to be larger than Chagos and located to encompass a much larger proportion of the distribution of the skipjack stock in order to affect absolute biomass. For instance, the Chagos MPA covers about 2.5% of longline and 5.5% of purse seine fishing grounds in the Western Indian Ocean (Dunne et al. 2014) and does not include areas with high concentrations of juvenile and adult spawning tunas (Kaplan et al. 2014).

Davies et al (2017) conducted a counterfactual analysis of the Indian Ocean Tuna Commission's one-month closure and the Chagos MPA to assess effects on the distribution of effort. They found inconsistent short-term responses to the closures by different tuna purse seine fleets. The study did not assess ecological responses to the two MPAs.

As reviewed in the section *Reduce Fishing Mortality of Species of Conservation Concern* for at-risk taxa, there is empirical evidence of higher catch rates and species diversity at shallow submerged features as well as at natural and artificial floating objects (Worm et al. 2003, Gilman et al. 2012, 2019, Dagorn et al. 2013, Hall and Roman 2013). This suggests that protecting these discrete static sites and floating objects would reduce fishing mortality, assuming that displaced effort would have lower catch rates of principal market species than occur at these features.

Of the eight studies that assessed effects of pelagic MPAs on the biomass of stocks of large pelagic target species, five were retrospective observational studies without controls (Chassot et al. 2010, Jensen et al. 2010, WCPFC 2010, Sibert et al. 2012, Boerder et al. 2017, Bucaram et al. 2018). The other three studies modeled historical catch data to assess retrospective, and in one case prospective, effects of hypothetical and existing pelagic fishery closures, with model runs that

included no MPAs, that is, serving as controls (Martin et al. 2011, Sibert et al. 2012, Dueri and Maury 2013).

Protect prey species of large pelagic apex predators

Intended ecological response.—Maintain the absolute biomass of stocks of prey and principal market species near targeted levels.

Direct and indirect ecological objectives.—Pelagic MPAs may protect stocks of prey species of pelagic target species and species of conservation concern in order to contribute to maintaining biomass levels and exploitation rates of the prey stocks near TRPs and above LRPs, and in turn keep the biomass of their pelagic predators near targets and above limits.

Similar to the section *Maintain the Condition of Target Stocks of Large Pelagic Predators*, the intended ecological effects are to reduce fishing mortality and increase recruitment, increasing absolute stock biomass of prey stocks. This would increase the local biomass of the prey stock. The increase in local and absolute biomass of large pelagic predators' prey would in turn cause an increase in local and absolute biomass of pelagic predator stocks/populations. The resulting ecological response would be to maintain stocks of prey, as well as of their predators, near target and above limit thresholds. Maintaining prey and predator stocks near target levels in turn contributes to implementing ecosystem-level harvest strategies and maintaining a desired quasi-stable ecosystem state.

MPA design.—Similar to the section *Maintain the Condition of Target Stocks of Large Pelagic Predators*, the ecological objectives and responses could be achieved by establishing temporal and/or spatial closures to historical fishing grounds where prey species of large predatory pelagic species were subject to fishing mortality, designed to protect a sufficient proportion of individuals of the prey stocks for an adequate proportion of their life span, and protect a sufficient proportion of the distribution of the stock. The MPA or network of MPAs could be spatially and/or temporally static and/or dynamic.

Why the MPA design might not achieve ecological objectives and responses.—In addition to the points covered in sections *Reduce Fishing Mortality of*

Species of Conservation Concern and *Maintain the Condition of Target Stocks of Large Pelagic Predators*, there is little evidence of a strong correlation between the total abundance of forage fish and their predators (Hilborn et al. 2017). This suggests that reducing fishing mortality on prey species would unlikely affect the population sizes of their pelagic predators. The prey for large pelagic predators includes micronekton and macrozooplankton, including small schooling fishes, cephalopods, and small scombrids, which are at intermediate TL. These species generally experience light fishing pressure (Young et al. 1997, Olson and Watters 2003, Lansdell and Young 2007, Potier et al. 2007, Le Borgne et al. 2011).

Theoretical and empirical basis.—Pichegru et al. (2010) observed the immigration of African penguins (*Spheniscus demersus*) into a recently established MPA closed to fishing by purse seine vessels that target small pelagic fishes. There was also a 30% decrease in penguin foraging effort within three months following the establishment of the fishery closure. The local abundance of prey resources may have increased in the MPA as a result of the cessation of fishing mortality. Alternatively, other factors may have caused the observed change in the penguins' distribution and foraging behavior. This was the only study that reported findings related (albeit indirectly and inconclusively) to how the abundance of stocks of prey of pelagic target species or species of conservation concern responded to a pelagic MPA.

There is evidence of competition for forage fish between fisheries and seabirds, where the local (not total) abundance of prey affects seabird reproductive success (Gremillet et al. 2008, Cury et al. 2011).

Reduce, halt, or reverse trait-based selectivity and fisheries-induced evolution

Intended ecological response.—The magnitude of FIE is reduced, halted, or reversed.

Direct and indirect ecological objectives.—Pelagic MPAs may reduce, halt, or reverse FIE resulting from a fishery's intraspecific heritable trait-selective mortality, thus sustaining genetic diversity, fitness, and evolutionary characteristics of affected populations (Dunlop et al, 2009; Heino et al. 2015, Hollins et al. 2018). Ecological

objectives of reducing, halting, or reversing FIE include maintaining the diversity of a population's heritable traits, fitness, resistance and resilience to stressors, and ability to evolve, and avoiding ecosystem-wide changes in structure and functioning through trophic links.

Marine fisheries that selectively remove individuals within populations based on certain traits that are highly heritable and vary within the population can cause FIE (Heino et al. 2015, Tuck et al. 2015, Audzijonyte et al. 2016, Lennox et al. 2017, Hollins et al. 2018). The relative catchability of individuals of a population susceptible to capture by a fishing gear type is explained, in part, by various heritable traits that vary within a population. This includes, for example, behavioral traits for shyness/boldness; life history traits such as age and size at maturation and growth rate (size-at-age); physiological traits such as metabolic rate (which may be correlated with shyness/boldness), visual acuity, and swimming performance; and morphological traits such as mouth dimensions (e.g., gape width and height) and body shape (Heino et al. 2015, Lennox et al. 2017, Hollins et al. 2018).

Selective mortality on heritable traits reduces the range of phenotypes for these traits within the populations. In other words, a fishery that causes intraspecific heritable trait-based selectivity reduces genetic diversity of affected populations by reducing the occurrence of phenotypes for traits associated with higher catch risk. These intraspecific changes in genetic diversity can be protracted or irreversible (Kuparinen and Merila 2007, Heino et al. 2015). Reduced intrapopulation genetic diversity compromises population fitness, weakens resistance and resilience to natural pressures, and reduces the population's natural selection and ability to evolve in response to changes in environmental conditions (Saccheri et al. 1998, Westemeier et al. 1998, Reed and Frankham 2003, Jorgensen et al. 2007, Evans and Sheldon 2008). This reduction in adaptive genetic variation increases the risk of population loss (Ehlers et al. 2008, Evans and Sheldon 2008).

For example, many fisheries target and selectively catch large individuals of species. This creates (unnatural) selection for maturation at a younger age, smaller size, and slower growth (i.e., "fast" life history traits) by reducing the proportion of the population made up of individuals

with "slow" life history traits (Law 2000, Kuparinen and Merila 2007, Swain et al. 2007, Fenberg and Roy 2008, van Wijk et al. 2013). In addition to compromised fitness and altered evolutionary processes, this reduces fecundity and duration of the spawning season and decreases larva survival potential, size, and growth rate, which in turn reduces reproductive potential and fisheries yields (Heino 1998, Law 2000, Ernande et al. 2004, Swain et al. 2007, Fenberg and Roy 2008, Miethe et al. 2009). These altered life history traits result in cascading effects through trophic food webs (Jennings et al. 1999, Polovina et al. 2009). Furthermore, selectively removing larger individuals changes the community's size structure and predator–prey interactions by reducing the relative abundance of species that grow to large sizes, and releasing pressure and increasing abundance of smaller sized species (Kuparinen and Merila 2007, Polovina and Woodworth-Jefcoats 2013).

MPA design.—MPA designs that effectively counter FIE will depend in part on species-specific traits and concomitant evolutionary responses to different forms of reductions in trait-based selective fishing mortality. This will also depend on which heritable traits a fishery has been selectively removing (e.g., Dunlop et al. 2009).

Protection would be desirable for areas where a large proportion of the local biomass of a species is made up of individuals with heritable traits that cause them to be selectively harvested by a fishery (Kuparinen and Merila 2007, Dunlop et al. 2009). For instance, an MPA designed to reduce, halt, or reverse FIE caused by fisheries that selectively remove large, mature individuals of a stock could select temporally and spatially predictable habitat where large, old individuals of the stock make up a large proportion of the local biomass, in essence creating a genetic reservoir for individuals in the population with traits for late maturation and large size (Law 2007). Alternatively, establishing no-take MPAs where the full diversity of variation in heritable traits of a population is represented, such as foraging grounds that are used by all age classes of a population, might effectively preserve natural genetic variation in the portion of the population that is protected by the MPA (Conover and Munch 2002, Baskett et al. 2005, Kuparinen and Merila 2007, Dunlop et al. 2009, Miethe et al. 2009).

Because the rate of FIE is determined in part by the intensity of fishing by a fishery that selectively removes individuals from a stock, an MPA that effectively reduces the fishing mortality rate will contribute to reducing the magnitude of FIE, and possibly recovering from previous FIE (Baskett et al. 2005, Kuparinen and Merila 2007).

Why the MPA design might not achieve ecological objectives and responses.—Intraspecific changes in genetic diversity from FIE may already be irreversible (Kuparinen and Merila 2007, Heino et al. 2015).

An MPA can have nominal effect and in some cases might exacerbate FIE depending on the MPA design and the life history traits of affected pelagic species, including if the MPA is not a source for recruits to the population and if density-dependent processes within the MPA strengthen FIE, such as for earlier maturation (Trexler and Travis 2000, Dunlop et al. 2009). For instance, an MPA may select in favor of individuals of a population with traits for less mobility, where individuals with traits for high mobility suffer higher fishing mortality rates (which would improve the likelihood that the MPA increases local population abundance within the MPA; Miethe et al. 2009, Mee et al. 2017). However, it is not well understood whether behavioral differences in mobility are heritable in pelagic predators (Kaplan et al. 2014).

Fishing effort may be displaced temporally or spatially, where it exacerbates the magnitude of FIE that the MPA was intended to reduce, or exacerbates FIE in other taxa. A time–area closure might displace fishing effort to times or areas where a narrower proportion of the variations of a trait that occurs for an affected population occurs. For example, because many marine species exhibit temporal and spatial variability in habitat use by size (e.g., sharks, Stevens and McLoughlin 1991; teleosts, Solmundsson et al. 2015), an MPA that displaces fishing effort to an area with a narrower length frequency distribution of a species could result in an increase in size selectivity by a fishery. If small size classes of a species predominantly occur nearshore while larger individuals are largely distributed offshore, an MPA that displaces fishing to offshore waters would increase selection for larger organisms, favoring heritable traits for earlier maturation and other "fast" life histories (Heino et al. 2015).

Similarly, a no-take reserve that protects a spawning site that predominantly protects mature age classes might contribute to FIE through increased size selectivity (Dunlop et al. 2009).

The MPA may be too small and inadequately designed to significantly affect the magnitude of FIE. And, not all pelagic species may have spatially and temporally predictable areas that meet either of the MPA designs predicted to alleviate pressures for FIE in pelagic marine organisms.

Theoretical and empirical basis.—MPAs are hypothesized to provide broad protection for genetic diversity (Perez-Ruzafa et al. 2006, Gilman et al. 2011). More specifically, there are several model-based studies that provide a theoretical basis for MPAs offsetting pressures for FIE in demersal and coastal fishes from selective fishing mortality of individuals with genotypes for delayed maturity, described below. These model-based assessments assume that the MPA serves as a source of recruits to the population, which would be a more challenging assumption to meet when modeling pelagic fishes. No studies were identified with model- or empirical-based evidence of the efficacy of MPAs at reducing, halting, or reversing FIE in pelagic marine species.

Dunlop et al. (2009) modeled the effect of alternative locations of no-take MPAs on FIE of life history traits for growth, maturation, and reproductive investment using life history characteristics typical of northern populations of Atlantic cod (*G. morhua*). An MPA located in foraging grounds, where all age classes occur, was simulated to reduce FIE. Fishing in foraging areas, where both juveniles and adults are caught, selects for individuals with traits for earlier maturation with relatively little investment in energy for growth (Law and Grey 1989, Heino and Godø 2002, Dunlop et al. 2009). An MPA protecting spawning grounds where only breeding-aged classes occur had either a nominal effect or exacerbated FIE (Dunlop et al. 2009). This is because fishing in spawning grounds benefits (selects for) individuals with traits for delayed maturity (i.e., individuals that are larger and more fecund when they reach maturity and begin to occur at spawning grounds; Law and Grey 1989, Heino and Godø 2002, Dunlop et al. 2009). In other words, protecting spawning

grounds could favor life history traits for maturing and moving to the protected spawning grounds at an earlier age. With increased mobility of individuals in the population, the larger the feeding ground no-take MPA needs to be to reduce FIE (Dunlop et al. 2009).

Trexler and Travis (2000) modeled the effect of no-take MPAs on the evolution of the size at maturation, where the model was calibrated using life history parameters for Gulf of Mexico populations of red snapper (*Lutjanus campechanus*), and the population was subject to size-selective fishing mortality outside of the MPA. The MPA increased the age at maturity of the population, assuming that the MPA was a source of recruits. The effect was larger when recruitment is not limited by density-dependent mortality (Trexler and Travis 2000).

Baskett et al. (2005) also modeled the effect of no-take MPAs on the evolution of the size at maturation of stocks subject to size-selective fishing mortality. No-take MPAs protected against strong FIE for earlier maturation when the model was calibrated using life history parameters for cod, red snapper, and rockfishes (*Sebastes* spp.).

Miethe et al. (2009) modeled the effect of no-take MPAs on the evolution of the size at maturation and behavioral changes in mobility from size-selective fishing mortality. No-take MPAs could prevent FIE for earlier maturation within the MPA and could decrease mobility. As discussed above, this latter finding may result if the MPA increases the fitness and local abundance of less mobile individuals of a population within the MPA, where individuals with traits for high mobility suffer higher fishing mortality rates. Both the protection from FIE to small maturation size and reduced mobility are stronger the larger the size of the MPA (Miethe et al. 2009).

DISCUSSION AND CONCLUSIONS

Given the recent proliferation of very large MPAs, we can be optimistic that area-based goals of Aichi Biodiversity Target 11 and SDG target 14.5 (CBD 2011, UNGA 2015*a*) will be achieved. The United Nations has committed to develop a legally binding treaty to improve management of marine biodiversity in the 64% of the ocean that lies beyond national jurisdictions (UNGA 2015*b*,

United Nations 2018), which may strengthen political will to establish, as well as allocate adequate resources to enable effective management, of additional large pelagic MPAs.

But there remains a tremendous lag in rigorous scientific research to assess whether pelagic MPAs are achieving ecological objectives of marine biodiversity conservation and management of fishing and other human ocean activities. This concluding section summarizes the key findings and identifies research priorities, and presents counterfactual-based modeling as a robust approach to infer causation in assessments of ecological responses to pelagic MPAs.

Key findings and research priorities

The main findings from this review, and research priorities to fill key gaps in knowledge of whether static and dynamic spatial management of pelagic fisheries achieve ecological objectives, are as follows:

1. The empirical and theoretical evidence for ecological responses to pelagic MPAs is extremely limited and inconclusive. Pelagic MPAs remain extremely underrepresented in the body of literature assessing ecological responses to MPAs—in particular for assessments that provided a strong basis for causal inferences. Only 12 studies were identified that assessed ecological responses of pelagic MPAs: 8 on effects on the local and absolute biomass of stocks of target species, 2 on effects of protecting bycatch hotspots for species of conservation concern, 1 on protecting habitat important for critical life history stages of pelagic predators, and 1 on protecting prey species of pelagic predators. No studies were identified that provided observational or theoretical evidence of an effect of a pelagic MPA on FIE in pelagic marine species. There likewise is a gap in research observing and simulating the broad community- and ecosystem-level effects of pelagic MPAs, including how this management tool might contribute to robust ecosystem-level harvest strategies. This highlights the need for investment in robust assessments of ecological effects of the growing number of pelagic MPAs.

2. Assessments of pelagic MPAs have not evaluated whether other management approaches would be more effective at achieving objectives. If MPAs are to successfully contribute to meeting objectives of fisheries management, they likely need to be one component of a suite of management tools (Hilborn et al. 2004*a*, *b*). For some ecological and socioeconomic objectives of fisheries management and biodiversity conservation, tools other than MPAs that constrain fishing may be more effective (Hilborn et al. 2004*a*, *b*, Kaiser 2005, Hilborn 2016). MPAs can result in substantial adverse effects on fishing communities. Conventional fisheries management tools might avoid these adverse effects while achieving the same ecological objectives (Agardy et al. 2003, Hilborn et al. 2004*a*, *b*, Kaiser 2005). Conventional fisheries management tools may also effectively avoid adverse unintended consequences that may result from pelagic MPAs, including cross-taxa conflicts and exacerbated FIE (Dunlop et al. 2009, Miethe et al. 2009, Mee et al. 2017, Gilman et al. 2019). In fisheries where conventional management methods have failed, the underlying causes for failure (management measures do not follow scientific advice, lack of compliance, high levels of illegal fishing, etc.) may also prevent MPAs from meeting objectives (Hilborn et al. 2004*a*, *b*, Kaiser 2005, Hilborn 2016). For example, if overfishing is occurring, establishment of an MPA might displace effort without addressing underlying management deficits and socioeconomic conditions responsible for overfishing.

3. Displaced effort can prevent MPAs from achieving objectives. Effort displacement in response to MPAs, if it occurs, affects ecological responses. Retrospective observational studies demonstrated that displaced fishing effort, including fishing-the-line, prevented pelagic MPAs from meeting management objectives for target stocks (WCPFC 2010, Martin et al. 2011, Torres-Irineo et al. 2011, Sibert et al. 2012).

4. Pelagic MPAs have the highest promise of contributing to managing problematic bycatch and to protecting habitat for critical

life history stages. Of the five conservation issues assessed here, pelagic MPAs have relatively high promise to mitigate bycatch of species of conservation concern and to protect areas important for critical life history stages of some pelagic species at spatially and temporally predictable hotspots (Worm et al. 2003, Hyrenbach et al. 2006a, Peckham et al. 2007, Schillinger et al. 2008, Hobday et al. 2010, Collette et al. 2011, Oppel et al. 2018). Unlike the highly fecund target species of pelagic fisheries, many at-risk bycatch species in pelagic fisheries (1) have "slow" life history traits, where even small changes in anthropogenic mortality levels can cause large changes in population sizes (Goñi 1998, Hall et al. 2000); and (2) form bycatch hotspots of spatially and temporally predictable aggregations at manageable spatial and temporal scales (Hyrenbach et al. 2006a, Louzao et al. 2006, Peckham et al. 2007, Morato et al. 2008, Schillinger et al. 2008, Block et al. 2011, Vandeperre et al. 2014a, b).

5. Pelagic MPAs are less likely to contribute to managing target stocks of pelagic predators. Pelagic MPAs need to cover extremely large areas to significantly reduce the risk of capture of an individual pelagic fish throughout its lifetime (i.e., the protected area would need to cover a large proportion of a stock's distribution) and to protect a substantially large proportion of the individuals of a stock (Botsford et al. 2003, Le Quesne and Codling 2009, Grüss et al. 2011, Dueri and Maury 2013). If the target species remain relatively short time periods in the MPA, and especially if fishing-the-line occurs, then the MPA would not likely cause an increase in absolute biomass of a stock (Moffitt et al. 2009, Grüss et al. 2011, Graham et al. 2012). Theoretical analyses indicate that there will likely be no regional stock-level benefits for stocks that are not overexploited (Le Quesne and Codling 2009), which is the case for most target pelagic species as well as for prey of pelagic predators (Olson and Watters 2003, Le Borgne et al. 2011, ISSF 2018). Furthermore, there is little evidence of a strong correlation between the total abundance of forage fish and their predators

(Hilborn et al. 2017). Pelagic MPAs have higher promise of causing increased local abundance of target stocks of pelagic fisheries. While the findings of Boerder et al. (2017) and Bucaram et al (2018) support possible increased tuna local abundance responses to the Galapagos Marine Reserve, stronger evidence is needed through counterfactual assessments (section *Counterfactual Reasoning*). Pelagic MPAs may need to be one element of a robust governance framework to achieve stock management objectives.

6. Pelagic MPA effects on FIE are highly uncertain. There is no evidence, empirical or theoretical, of effects of MPAs on FIE in pelagic species. Pelagic MPAs will affect FIE only in pelagic species for which an MPA serves as a source of recruits, which may exclude most pelagic fishes. Because of the high mobility of pelagic species, pelagic MPAs at foraging grounds are unlikely to affect FIE in pelagic marine species (Dunlop et al. 2009). Pelagic MPAs located in spawning grounds, for pelagic species that spawn at discrete sites where predominantly breeding-aged classes occur, could exacerbate FIE for earlier maturation and select for traits for lower mobility (Dunlop et al. 2009, Miethe et al. 2009).

Counterfactual reasoning

An important issue in conservation management is how to infer the causal ecological impact attributable to a specific policy intervention (Ferraro and Hanauer 2014, Bull et al. 2015) —such as the implementation of large pelagic MPAs (Boerder et al. 2017, White et al. 2017). The most common way to evaluate the effect of an intervention is to use some form of BACI study design (Stewart-Oaten and Bence 2001, Conner et al. 2016, Smokorowski and Randall 2017). In its simplest form, BACI is a before/after sampling at the impact site compared with a simultaneous before/after sampling at a control site (Stewart-Oaten and Bence 2001). Before means sampling during the pre-intervention period, and after means sampling during the post-intervention period. The impact is then assessed by the difference-

of-differences method: Calculate the difference between the pre- and post-intervention periods for the control and the difference between the pre- and post-intervention periods for the impact site and then calculate the difference between those two differences.

The approach is then used to detect a large, abrupt, and permanent change in the mean response of the monitored system (Underwood 1994, Stewart-Oaten and Bence 2001). However, an ecological or environmental response to a management intervention such as an MPA might be small and not large, gradual and not abrupt, and temporary and not permanent (Underwood 1994, Fujitani et al. 2012, Smokorowski and Randall 2017). Moreover, the mean system response might not be the most appropriate metric to assess any impact—the intervention might affect the temporal variability of the impacted system rather than just the mean response (Underwood 1994).

So, what is the best approach to account for such temporal dependence in a BACI-type monitoring scheme and one where there might not be clear and randomly assigned treatment and control sites? One approach is based on inferring causality that takes into account the temporal and uncertain nature of any ecological response to a major intervention by using counterfactual reasoning (Hofler 2005, Coffman and Noy 2012). Counterfactuals are the main framework for causal inference in several disciplines such as medicine and epidemiology (Hofler 2005), economics (Coffman and Noy 2012), ecology (McConnachie et al. 2016), and environmental impact assessment (Ferraro and Hanauer 2014). Counterfactual reasoning is the process of evaluating conditional claims about alternate possibilities and their consequences. Here, it is about inferring what might have happened if the MPA under review had not in fact been established (Smith et al. 2006, Fujitani et al. 2012, Davies et al. 2017).

The simplest way of using counterfactuals to infer causal impact in this specific setting, where there were no pre- and post- intervention and control sites, is to model time series of standardized pelagic species catches in the region of the MPA (see Boerder et al. 2017). A suitable synthetic control could also be an environmental factor such as ocean temperature that drives regional fisheries productivity—or some macro-scale regional environmental proxy such as the Pacific Decadal Oscillation or Multivariate ENSO Index (Wolter and Timlin 2011). It is assumed that the pelagic MPA has no impact on the environmental factor, or else it is not a valid synthetic control. If we know that factor and we have a reliable time series of that factor pre- and post-intervention, then that would be a suitable synthetic control to compare with the standardized catch time series.

The two series are then (1) the standardized catch time series (Venables and Dichmont, 2004) that reflects any potential impact since that fishery was exposed to the MPA, and (2) a synthetic control time series based on the relationship between fisheries productivity and the driving environmental factor fitted to the pre-intervention data and then predicted post-intervention (Smith et al. 2006). The synthetic control can also comprise multiple time series such as other target species not impacted by the MPA (were never caught within the MPA prior to establishment), spatially replicated standardized catch series, and other regional environmental series that affect the dynamics of the fisheries.

The synthetic control comprising a single series or multiple related series that are not impacted by the MPA can then be fitted using Bayesian structural time series state-space modeling techniques with weakly informative or non-informative priors (Brodersen et al. 2015) on the data series prior to the intervention. The potential temporal and spatial correlation of the data series can then be accounted for as well—which has not been accounted for in previous assessments of marine spatial closures (Davies et al. 2017). The fitted structural time series model is then predicted well beyond the intervention to derive the counterfactual prediction (the temporal trend without any MPA). The same structural time series model is also fitted to the standardized catch times series exposed to the intervention. The difference between the two time series (the standardized catch and the synthetic control) is the measure of the effect (if any) of the MPA.

This Bayesian inference approach then supports probabilistic statements about intervention-attributable impact once a suitable model has been fit to adequate pre- and post-intervention time series (see also Conner et al. 2016). This

approach is also informative about the apparent temporal evolution of any post-intervention effect—for instance, was it abrupt or gradual, was it temporary or permanent, and was there a delay before any apparent effect?

The counterfactual-based scenario modeling approach is readily extended to evaluate retrospective (what ecological effects did an MPA cause?) and prospective (what ecological effects would an MPA cause?) changes in ecosystem structure and dynamics attributable to an MPA (Fulton et al. 2015). Population, stock, multi-species, and ecosystem models can be fit to data, for example, on biomass of functional groups, species- and ontogenetic stage-specific biomass, diet/trophic interactions, oceanographic variables, life history attributes, components of total fishing mortality, size structure of the catch, and immigration and emigration to assess ecological effects of actual and theoretical MPAs (e.g., Salomon et al. 2002, Le Quesne et al. 2008, Sibert et al. 2012, Brochier et al. 2013, Dueri and Maury 2013, Plaganyi et al. 2014). Models can also evaluate socioeconomic and ecological effects from alternative management strategies, such as various MPA designs (Christensen and Walters 2004, Le Quesne et al. 2008, Weijerman et al. 2016). The challenge is to fit such process-based ecosystem models to long-term datasets of standardized catch records (an index of relative, local abundance)—preferably within a Bayesian modeling framework to derive probabilistic statements about any intervention-attributable impacts at the ecosystem scale.

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