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Managing catch of marine megafauna: Guidelines for setting limit reference points

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ABSTRACT

Limit reference points (LRPs) for catch, which correspond to thresholds to undesirable population or ecosystem states, offer a consistent, objective approach to management evaluation and prioritization across fisheries, species, and jurisdictions. LRPs have been applied successfully to manage catch of some marine megafauna (elasmobranchs, marine reptiles, seabirds, and marine mammals) in some jurisdictions, such as the use of Potential Biological Removal (PBR) to manage incidental mortality of marine mammals under the U.S. Marine Mammal Protection Act. However, implementation of ecosystem-based management is still in its infancy globally, and LRPs have not yet been widely adopted for marine megafauna, particularly for incidental catch. Here, guidelines are proposed for estimating catch LRPs for marine megafauna, with particular attention to resolving common technical and political challenges, including (1) identifying management units, population thresholds, and risk tolerances that align with common conservation goals and best practices, (2) choosing catch LRP estimators, (3) estimating input parameters such as abundance and productivity, (4) handling uncertainty, and (5) dealing with mismatches between management jurisdictions and population boundaries. The problem of cumulative impacts across sectors is briefly addressed. These guidelines, grounded in marine policy, science, precedent, and lessons learned, should facilitate wider application of catch LRPs in evaluation and management of fisheries impacts on marine megafauna, in support of global commitments to conserve biodiversity and manage fisheries responsibly.

1. Introduction

Direct interactions with fisheries[1] threaten the ecological function and existence of many non-teleost marine vertebrates, including elasmobranchs, marine reptiles, seabirds, and marine mammals (henceforth “marine megafauna” regardless of size) [3–13]. Under global commitments to conserve marine biodiversity and ecosystems,[2] fisheries managers are required to conserve both target and non-target species. Several international agreements, plans of action, and guidelines suggest ways forward [1,14–16], and successes in reversing population declines of marine

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[1] For the purposes of this paper, catch (a quantity) and fishing mortality (a rate) are used to denote both intentional and incidental direct fisheries interactions leading to removal from a population, including unobserved direct interactions (e.g., animals caught in gear but lost before gear was retrieved) [1,2].

[2] Global commitments to biodiversity of relevance to marine megafauna include, with date of entry into force, the Convention on International Trade in Endangered Species (1975), and Convention on the Conservation of Migratory Species (1983), the Convention on Biological Diversity (1993), and the United Nations Convention on the Law of the Sea (1994).

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megafauna through reduction or cessation of directed harvests show that population recovery is often possible when threats are addressed [6,10,17]. However, 20 years after the adoption of the Food and Agriculture Organization's Code of Conduct for Responsible Fisheries ("the Code of Conduct"), implementation of ecosystem-based management remains in its infancy. Improvements in management are hindered, especially for non-target species, by conflicting goals and perceptions among stakeholders, shared jurisdiction over highly mobile populations among multiple management organizations, and limited time and resources [2,18,19]. To overcome these challenges, management proposals and actions must be grounded in clearly defined objectives and prioritized strategically. Yet, with some notable exceptions [12,20–24], domestic and international fisheries management organizations make most decisions affecting catch of marine megafauna without assessing impact on population status [2,19,20,24]. Continued failure to institute biologically-based benchmarks for catch of marine megafauna as a key component of ecosystem-based fisheries management risks inefficient allocation of limited resources and extirpation of overexploited populations.

Biological reference points, originally developed for target fish stocks, express broad management objectives (e.g., for population productivity) as operational objectives that can guide short-term management decisions [25]. Estimates of population size and status are often highly uncertain, while catch is often easier to measure and manage. Therefore, reference points for population status are usually projected to corresponding reference points for fishing mortality or catch, based on theoretical or empirical models of the equilibrium relationship between fishing mortality and population status (Fig. 1). A limit reference point (LRP) marks a transition point between desirable and undesirable states, defined by conservation objectives (also known as minimum management objectives) for populations. For example, Regional Fisheries Management Organizations (RFMOs) are increasingly adopting maintenance of population productivity as a conservation objective, which represents a shift from targeting maximization of

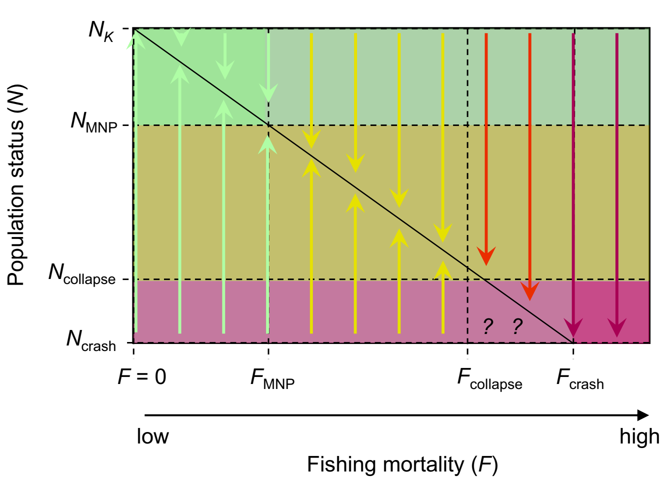


Fig. 1. Modified from Moore et al. [37]. Relationship between reference points for catch, which are based on fishing mortality (F), and population status (N), where F drives N. F is expected to be the more measurable axis in practice, and thus guides management decisions in the short-term. Arrows indicate direction of population change given F and initial N. The diagonal represents equilibrium between F and N. Equilibrium states and constant carrying capacity are a convenient simplification for the purposes of developing reference points. Arrow colors depict relative concern level (light green=low; dark red=high) associated with F. Subscripts: K=carrying capacity; N_{MNP}=maximum net productivity level; collapse=0.1 K; crash=critical level below which the population is expected to be driven to extinction ($N_{crash} > 0$). Populations in the upper left box (light green) are of low concern. Populations in the lower right box (dark red) require immediate and drastic conservation action. Positions along axes and color schemes are relational indicators only, not to scale.

population productivity. This conservation objective can be expressed as a population status LRP (henceforth "population threshold") of N_{MSY}, the maximum sustainable yield level [26], where N may be in terms of any abundance measure, such as biomass or number of individuals. The N_{MSY} population threshold can in turn be projected to a catch LRP based on estimated current population level N and the maximum fishing mortality expected to allow the population to stay at or above N_{MSY}, i.e., F_{MSY}. Tracking current population level relative to the estimated level at the population threshold, N_{MSY}, may inform long-term management evaluation and adaptation, but short-term management is guided by comparing the higher-precision indicator – the estimate of actual catch – to the corresponding catch LRP [27,28].

Estimators for catch LRPs can be tuned to buffer against risk of failure to stay above population thresholds. Risk arises from uncertainty in the knowledge of a population's response to fisheries management, due primarily to uncertainty in estimates of biomass and fishing mortality and in the underlying biological model relating fishing mortality to population status [29,30]. For example, policymakers and stakeholders might agree on a 0.10 probability as an acceptable risk of allowing a population to fall below a population threshold of N_{MSY}. The corresponding catch LRP can be reduced commensurate with uncertainty and precaution, such that the population is estimated to have a ≥ 0.90 probability of remaining at or above N_{MSY} if the catch LRP is observed. The resulting system replaces reactive management with objective, science-based management by translating predefined population conservation objectives and acceptable risk in the face of uncertainty to biologically-based precautionary benchmarks. LRPs are now widely used for target stocks and are internationally accepted as a best-practice element of precautionary fisheries management [14,25,31–33].

An ecosystem approach to fisheries management requires a broader suite of reference points and indicators that address different parts of the affected ecosystem beyond target species [27,28]. The Code of Conduct calls for minimization of unused catch and catch of threatened, endangered, and protected species [14], but complete elimination of such catch is often not feasible, necessitating minimum benchmarks to guide and evaluate management of ongoing catch. Single-species reference points have been proposed as a simple and effective tool for this purpose [1,34–38].

Broadly defined, reference points can be set for any measurable variable describing the interaction of interest, but catch LRPs provide the best and most relevant information for marine megafauna with respect to conservation goals (Table 1). For example, reference points lacking biological context, such as historical catch and catch trends, may be misleading [39], because they may fail to highlight populations whose growth rates are substantially affected by removing only a few individuals, and changes in fishing gear or practices may confound the relationship between population size and catch. Reference points and indicators based on population trend are also problematic for marine megafauna: the burden of proof generally rests on showing that a population is declining, but large declines in abundance and intensive survey effort over many years are required to detect a trend given the high uncertainty in most abundance estimates [40,41]. Finally, population status thresholds, while directly relevant to conservation goals, fail on a number of fronts for marine megafauna as a basis for guiding management. Population status indicators for marine megafauna, such as fraction of historic abundance, suffer not only from low signal-to-noise ratios [40,41], but often also from long time lags in the response of the monitored portion of the population (e.g., nesting turtles or birds) to fisheries impacts on other life stages [42]. Population status indicators also do not provide information on the relative impacts of different human-caused stressors on the population of interest nor on reduction in

Table 1
Properties of several types of limit reference points commonly employed in catch management for marine megafauna. Note that while the term "catch limit reference point" (catch LRPs) can be applied broadly to both historically and biologically based catch limit reference points, for the sake of brevity, we reserve it for biological catch limit reference points (last row). K is carrying capacity or historical abundance. N_{MNP} is maximum net productivity level, which is analogous to the maximum sustainable yield level commonly used as a limit reference point in fisheries management of target species.

Limit reference point type		Properties				
		Directly related to conservation goals	Indicator responds quickly	Indicator easily monitored	High statistical power to detect shift in indicator status	Informative about magnitude of change required to shift indicator status
Status	Population status (e.g., abundance threshold relative to K, such as N_{MNP})	X				
Trend	Population size	[a]				
	Catch			X	X[b]	
Catch	Historical		X	X	X	X
	Biological (corresponding to a population status threshold; i.e., "catch LRPs" as used here)	X	X	X	X	X

[a] Population trend is indicative of improving or deteriorating population status, but does not directly relate to long-term conservation goals for population health.
[b] Statistical power to detect a shift in catch trend depends on uncertainty in catch due to process (e.g., environmental variability) and observation (e.g., observer coverage) error.

impacts required to improve population status. Finally, assessing the current status of a population is complicated by poor knowledge of historical baselines and difficulty of estimating the true maximum net productivity level (N_{MNP}; this term is used in place of N_{MSY}, given that many marine megafauna are managed as protected species rather than harvested) [43,44]. Catch LRPs for marine megafauna therefore provide a more effective short-term management tool, and are the focus of this paper.

Despite the suitability of catch LRPs to managing catch of marine megafauna, they are currently used for only a few taxa by a limited number of management organizations [2,19,20,24]. Prominent examples of catch LRPs being adopted for marine megafauna include for marine mammals under the U.S. Marine Mammal Protection Act (MMPA) and by the International Whaling Commission (IWC), some targeted elasmobranchs in the U.S. and Australia [12], and non-target elasmobranchs in Australia [22] and in Antarctica by the Commission for the Conservation of Antarctic Marine Living Resources [45]. Increasingly, the Potential Biological Removal (PBR) estimator developed for marine mammals under the MMPA is being used by researchers and consultants to evaluate sustainability of catches for a broader range of taxa, particularly seabirds [46–50], though management application has not necessarily followed. Often, incidental catch limits established for domestic or international fisheries management are not clearly linked to conservation objectives for population status, such as for sea turtles in U.S. waters [24] or sharks under the jurisdiction of the International Commission for the Conservation of Atlantic Tunas [51].

Moore et al. [37] reviewed catch LRPs for marine megafauna, providing a taxonomy of the diversity of different tools for estimating catch LRPs, identifying their common fundamental components, highlighting the need to characterize associated uncertainty, and outlining some of the technical, logistical, and political challenges facing their implementation – in essence, providing an overview of their form, function, and current place in the management system. Here, a roadmap is laid out for their application, aimed at facilitating and informing more widespread and institutionalized use, with practical guidance on navigating the choices and challenges faced in estimating catch LRPs for marine megafauna (Fig. 2). First, management units, population thresholds, and risk tolerance are identified that align with internationally agreed principles and management goals for limiting fishing impacts on populations and ecosystems, as well as with precedent and best practice. Then guidance is provided on estimating catch LRPs that meet those performance criteria, including selecting catch LRP estimators, estimating key biological input parameters, handling uncertainty, and dealing with the mismatch between population boundaries and management jurisdictions. Where population data are limited, several practical options are identified for filling data gaps. The focus is on marine megafauna, but much of the content is relevant to other taxa with similar life histories, management contexts, and data considerations.

2. Estimating limit reference points for marine megafauna

Fig. 2 outlines the process of estimating catch LRPs, broken down into several key steps. Most of these steps are only required initially, as subsequent updates to catch LRP estimates involve one or a few of these steps (Fig. 2).

2.1. Guiding principles

The guidelines suggested here align with relevant principles for fisheries management outlined in the Code of Conduct and guidelines on the precautionary approach (Box 1) [14,52]. Further direction is provided by lessons from prior work on reference point estimator development and application [25,37,44,48,53,54], including the importance of:

- Basing reference points and corresponding indicators on biological parameters and variables that can be estimated from existing data or current sampling programs;
- Underpinning reference point estimators with straight-forward model mechanics so they are simple to understand and explain;
- Creating incentives for reducing uncertainty by setting more conservative limits for more uncertain populations (an inherent part of a precautionary approach; Box 1:9d); and
- Ensuring that reference point estimators and input parameters are defensible and robust for meeting conservation objectives (e.g., through incorporation of influential uncertainties and simulation testing).

Box 1–Guiding principles

The approach and guidance suggested here follow relevant principles for fisheries management outlined in the Code of Conduct (FAO, 1995) and pursuant guidelines on the precautionary approach (FAO, 1996), including:

1. "States and users of living aquatic resources should conserve aquatic ecosystems. The right to fish carries with it the obligation to do so in a responsible manner so as to ensure effective conservation and management of the living aquatic resources."
2. "Fisheries management should promote the maintenance of the quality, diversity and availability of fishery resources in sufficient quantities for present and future generations in the context of food security, poverty alleviation and sustainable development. Management measures should not only ensure the conservation of target species but also of species belonging to the same ecosystem or associated with or dependent upon the target species."
3. "Conservation and management decisions for fisheries should be based on the best scientific evidence available, also taking into account traditional knowledge of the resources and their habitat, as well as relevant environmental, economic and social factors."
4. "States and subregional and regional fisheries management organizations should apply a precautionary approach widely to conservation, management and exploitation of living aquatic resources in order to protect them and preserve the aquatic environment."
5. "The absence of adequate scientific information should not be used as a reason for postponing or failing to take conservation and management measures."
6. "States and users of aquatic ecosystems should minimize waste, catch of non-target species, both fish and nonfish species, and impacts on associated or dependent species."
7. "States should… cooperate … to promote conservation and management, ensure responsible fishing and ensure effective conservation and protection of living aquatic resources throughout their range of distribution, taking into account the need for compatible measures in areas within and beyond national jurisdiction."
8. "States should, to the extent permitted by national laws and regulations, ensure that decision making processes are transparent and achieve timely solutions to urgent matters."
9. "The precautionary approach involves the application of prudent foresight. Taking account of the uncertainties in fisheries systems and the need to take action with incomplete knowledge, it requires, inter alia:
   a. consideration of the needs of future generations and avoidance of changes that are not potentially reversible;
   b. prior identification of undesirable outcomes and of measures that will avoid them or correct them promptly;
   c. that any necessary corrective measures are initiated without delay, and that they should achieve their purpose promptly, on a timescale not exceeding two or three decades;
   d. that where the likely impact of resource use is uncertain, priority should be given to conserving the productive capacity of the resource"
10. "The standard of proof to be used in decisions regarding authorization of fishing activities should be commensurate with the potential risk to the resource, while also taking into account the expected benefits of the activities."

2.2. Steps in limit reference point estimation

2.2.1. Step 1: Define conservation objectives and risk tolerances

Estimating catch LRPs requires specific conservation objectives. The following guidelines draw on natural history and precedent to refine common conservation goals for living marine resources and ecosystems from relevant global treaties and agreements to reasonable defaults for management units, population thresholds, and corresponding risk tolerances.

2.2.1.1. Step 1.A: Define management units. Global fisheries-relevant treaties and agreements call for conservation of marine biodiversity at the ecosystem level, maintenance of ecosystem integrity, reversibility of fishing effects, and prevention of long-term harm (Box 1: 1, 2, 4, 9a) [14,31,55]. This requires identifying demographically independent units, i.e., populations whose dynamics are primarily determined by births and deaths rather than dispersal, and managing at this level [56,57]. Management for higher-level units, such as subspecies or species, may fail to achieve ecosystem-integrity goals by failing to prevent local depletions or extirpations and associated impacts to ecosystems. Moreover, LRP-based management functionally operates at the level of demographically independent populations. While a review of methods for stock delineation is beyond the scope of this paper, a broad array of techniques has been developed to aid in stock delineation, with varying levels of confidence assigned to each [58].

2.2.1.2. Step 1.B: Establish population thresholds for conservation. Using N_{MNP} as the primary population conservation threshold for both target and non-target marine megafauna – i.e., preserving the productivity of their populations – has considerable support in policy, science, and precedent. The UN Straddling Fish Stocks Agreement (UNFSA) establishes F_{MNP} (the fishing mortality corresponding to N_{MNP}) as the minimum standard for LRPs, which it specifies are relevant not only to target species but also to "associated and dependent" species (see also Box 1: 2, 9d). N_{MNP} has since been identified as the best-practice population threshold for target and non-target stocks, including species of conservation concern [59], and is increasingly used as the primary population threshold for target stocks by Regional Fisheries Management Organizations [26] and in domestic fisheries management. LRPs serve to prevent long-term or irreversible ecosystem effects of fishing, so it follows that the same population thresholds are relevant to both target and non-target species [59]. This point is underscored by studies that have found a strong correspondence in teleosts and invertebrates between stocks that fall below N_{MNP} and populations that qualify as threatened based on criteria for the International Union for the Conservation of Nature (IUCN) Red List of Globally Threatened Species [60,61]. Maintaining populations at or above N_{MNP} therefore ensures their conservation for future

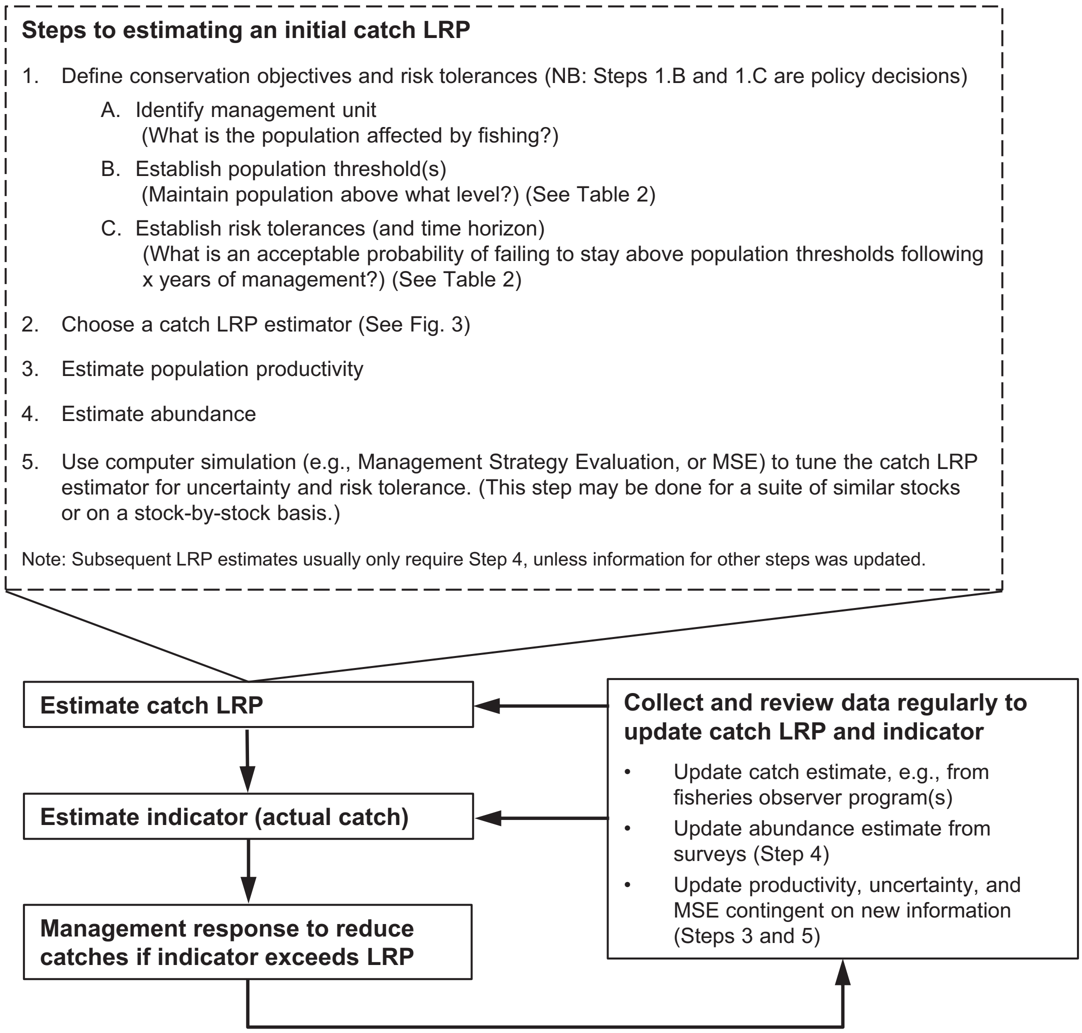


Fig. 2. Management process based on LRPs. This paper focuses on the steps involved in quantifying catch LRPs, indicated by the dashed box.

generations. Finally, greater fragmentation of management among multiple Exclusive Economic Zones (EEZs) has been shown to correspond directly with poorer population outcomes [12]. Setting N_{MNP} as a shared population threshold for marine megafauna would help address this problem by harmonizing management regimes, as called for by the United Nations and the Code of Conduct [31,55] (Box 1: 7). However, where further reductions in catch are possible beyond those that would maintain N_{MNP}, the principle of minimizing waste of non-target species (Box 1:6) should take precedence as a minimum bar.

Projecting population thresholds to catch LRPs requires care to avoid unintended negative consequences (Box 1: 9b). Considerable potential and evidence for depensatory dynamics at low population levels have been found among marine megafauna [62–69], exacerbating genetic and demographic risks to small populations [70,71]. Furthermore, in the "slow" life histories typical of marine megafauna, F_{MNP} is often close to the lowest fishing mortality expected to drive a population to extinction [72,73], so if uncertainty is high, the latter may have an appreciable chance of being exceeded using a catch LRP based on F_{MNP}. The threshold $N_{collapse}$, at 10% of carrying capacity, has been used as a critical lower reference point for fish where relevance to a wide variety of species was a priority [61,74]. A review of historic declines and subsequent recoveries of marine mammal populations also indicated that a biological threshold may occur near $N_{collapse}$ – a large proportion of populations that had declined by more than 90% have since failed to increase substantially [17]. Therefore, $N_{collapse}$ is adopted as a safeguard population threshold (Fig. 1), to be evaluated along with the N_{MNP} threshold but associated with a lower risk tolerance of being exceeded (Box 1: 10), thereby addressing the objective of avoiding "levels at which … reproduction [of associated and dependent species] may become seriously threatened" [55]. The underlying assumption, that $N_{collapse}$ is greater than the unknown critically low population abundance level below which population recovery may not be possible, should be evaluated for each species.

Additional considerations for choosing population thresholds include their relationship to ecosystem objectives and to long-term changes or variability in carrying capacity. Population reductions from historic levels may adversely affect population distribution and ecosystem function [75–77], so alternative or additional population thresholds might be required as the basis for evaluating catch with respect to ecosystem objectives for marine megafauna (Box 1: 1, 4). For example, populations near carrying capacity may be more likely to increase their range than ones near N_{MNP}, so an objective of limiting fisheries impacts on the range of a population relative to historic levels may call for a more conservative LRP, such as $N_{0.9K}$. Another consideration is that the assumption of constant carrying capacity is likely to be violated in reality. Where changes in carrying capacity are due to environmental variability, two possible approaches are to define population thresholds with respect to long-term mean unfished abundance, which will likely lead to lower catch LRPs, or to let population thresholds track predicted unfished abundance over time [59]. Most taxa of marine megafauna are long-lived, so their populations integrate over much environmental variability. On the other hand, where changes in carrying capacity are caused by humans, management must establish whether population thresholds are to be anchored to historical abundance, potentially requiring lower catch LRPs and separate action to restore carrying capacity in order to achieve population conservation objectives, or to be estimated relative to changing carrying capacity [78]. The principles of avoiding irreversible harm to ecosystems and limiting changes to those reversible within a human generation (Box 1: 9 a, 9 c) suggest that such anthropogenic changes in carrying capacity should be minimized or reversed where they can be managed, for example by limiting fisheries on prey species [59,79]. Setting catch LRPs in an ecosystem context remains a major challenge in effective management.

2.2.1.3. Step 1.C: Establish risk tolerance and time horizon. Operationalizing LRPs requires establishing risk tolerances for falling below population thresholds and time horizons over which risk is evaluated, forming the basis for performance criteria used to tune catch LRP estimators [25]. Population dynamics are stochastic, and components of a catch LRP estimate (Steps 3 and 4) and catch itself are measured with error, so the probability of catch being low enough to maintain a population above the corresponding population threshold must be estimated, and managers must define how much risk they are willing to accept of not achieving those objectives given the uncertainties at hand. This is the risk tolerance, which is defined as a probability threshold. The probability of achieving conservation objectives given uncertainty in catch and catch LRPs is time-dependent, so time horizons need to be explicitly defined too. Specifying acceptable risk and the time horizon over which risk should be integrated allows for transparent, impartial, repeatable, and consistent estimation of reference points [80–82].

The UNFSA states that the risk of overstepping LRPs should be “very low”, but does not specify a risk tolerance. The risk tolerances for overstepping population thresholds that are currently used for target and non-target species in a variety of contexts range from 5 to $<50\%$ [53,59,83]. Sainsbury [59] identifies a best-practice maximum risk tolerance for target stocks of 10% risk of failing to stay above a population threshold, integrated over a minimum time horizon of two generation lengths. For depleted populations, time horizons for population recovery to a population threshold may be defined relative to the length of time that would be required for recovery with zero fishing mortality [59,83], thereby quantifying a limit on the extent to which fishing mortality delays recovery. For example, Sainsbury [59] identified as best practice a maximum time for recovery of depleted target stocks of no more than 10 years longer than would be required without fishing mortality. The U.S. MMPA regulations are based on a standard of 5% risk tolerance for a population requiring more than a 10% increase in the time to recover to N_{MNP} [83].

Current population status may be used to modulate the risk tolerance for falling below a population threshold [84] to enhance protection against further decreases and promote recovery of threatened populations (Box 1: 3, 9c, 10). One approach has been to include an adjustment factor in catch LRP estimators, which corresponds to population status [83,85] and can be tuned to achieve an adjusted risk tolerance or relative recovery rate objective [83]. Threat status may be assessed by applying the IUCN Red List criteria [86] at the stock level to determine relative threat of extirpation. Although the IUCN Red List criteria were designed to capture the probability of species going extinct, they have been applied at the level of genetically defined management units [87–90], and can be further extended to provide a precautionary assessment of status at the stock level. For populations that qualify as Critically Endangered, which are likely already below the level at which depensatory dynamics set in, the catch LRP should be set to zero. One exception to the zero recommendation is for populations that are reproducing successfully and whose ongoing declines or lack of recovery are primarily attributable to harvest or incidental fishing mortality (other direct human-caused mortality sources such as vessel strikes may also be relevant here; see Section 3.2). In such cases, catch LRPs above zero may provide a basis for negotiating improved conservation outcomes by replacing complete cessation of an activity with improved management, which may be easier to achieve. For species classified as Data Deficient as a whole according to IUCN Red List criteria, individual stocks may have sufficient data to support risk classification and estimation of catch LRPs.

Table 2 proposes default population thresholds, risk tolerances, and time horizons to use in estimating operational catch LRPs for marine megafauna that reflect the considerations, precedents, and best practices reviewed above.

2.2.2. Step 2: Choose a catch LRP estimator

Estimating catch LRPs requires biological data on population-level abundance and potential productivity (i.e., maximum population growth rate). For many target fish species, estimates of abundance and productivity are informed primarily by fishery-dependent data, specifically catch histories. A large body of literature exists on the subject of assessing stocks and estimating reference points based on catch data, including a growing library of data-poor methods [91–97], which are relevant to many elasmobranch populations. Critical reviews and guidelines for the application of these fishery-dependent reference point estimators are available elsewhere [98–100]. The focus here is on fishery-independent estimators for catch LRPs, reviewed by Moore et al. [37], which are relevant to many non-target taxa without catch histories.

The most appropriate type of catch LRP estimator depends largely on the data types available and assumptions about the importance of age-structured demography or fishing mortality to population dynamics (Fig. 3).

For those species for which only presence–absence data are available rather than survey-based abundance estimates, which is the predominant situation among elasmobranchs and sea snakes, an alternative means of estimating LRPs – in this case for fishing mortality rather than catch – is a Sustainability Assessment for Fishing Effects (SAFE) [101,102].

For species with periodic abundance estimates, the simplest estimator is PBR, which has been used for marine mammals and seabirds [44,47,83,103]. For PBR, an estimate of total-population abundance is used, because age- or sex-specific estimates of abundance are generally not feasible for most cetaceans. All individuals killed by fisheries are assumed to have a similar impact on population dynamics, either because fishing mortality is relatively sex- and age-independent, or because the contribution of different-aged individuals to population productivity is fairly similar relative to other potential sources of bias or uncertainty. Such assumptions are often necessary in practice when the age and sex of individuals killed is unknown. Modified PBR estimators by Dillingham and Fletcher [48] and Richard and Abraham [50], developed for application to seabirds, retain the simplifying assumptions concerning impacts of fishery selectivity, but are useful for situations where only a segment of the population, such as breeding pairs, can be surveyed.

For species such as sea turtles, for which fishing mortality is often strongly age-dependent and the importance of individuals to population dynamics varies tremendously with age, an estimator like RVLL (Reproductive Value Loss Limit) may be more

Table 2
Suggested default limit reference points (LRPs) for population status (also termed population thresholds), risk tolerances, and time horizons on which to base evaluation of catch of marine megafauna, based on policy, precedent, and scientific knowledge. Population status is determined using IUCN Red List Criteria. Risk tolerances for the N_{MNP} threshold and population status better than Endangered reflect best practices for target species [59]. The next lower tier of risk tolerances follows from precedent for protected species set by application of the Potential Biological Removal (PBR) estimator under the U.S. Marine Mammal Protection Act (MMPA) [83]. If the catch LRP corresponding to the safeguard population threshold of $N_{collapse}$ is lower than that for remaining at or above N_{MNP}, the catch LRP corresponding to $N_{collapse}$ takes precedence.

Management goal	Population threshold	Population status	Risk tolerance	Time horizon
Maintain or restore non-threatened status, population productivity, and recruitment; permit recovery to unfished abundance within a human generation (20-30 y); harmonize management across jurisdictions	N_{MNP}	Least Concern	10%	≥ 2 generation lengths for species in question or at most 10% greater recovery time than if unfished[a]
		Near Threatened	10%	
		Vulnerable	10%	
		Endangered	5%	
		Critically Endangered	5%	
Avoid serious reproductive harm	$N_{collapse}$	Least Concern	5%	≥ 2 generation lengths for species in question
		Near Threatened	5%	
		Vulnerable	5%	
		Endangered	2.5%	
		Critically Endangered	2.5%	

[a] Risk of falling below a population threshold should be integrated over a minimum of two generation lengths for the species in question, while time for recovery to a population threshold should be defined relative to that required without fishing mortality. The cutoff of 10% longer recovery time was used to tune the PBR estimator under the MMPA [83].

appropriate [54,104]. RVLL scales abundance by the reproductive value of component ages or stages relative to adults, thus defining a catch LRP in terms of how much productivity can be removed from a population. RVLL may be more appropriate than simple PBR estimators in many other cases with age-dependent fishing mortality, including for some marine mammal populations [105], but RVLL depends on estimates of population age structure (e.g., from a model or from observation) and age distribution captured by fisheries, so its application is limited by what types of data can be collected.

Sex-selective fishing mortality is another important deviation from the PBR assumption of no selectivity [105,106]. One approach to this type of catch bias may be to estimate catch LRPs and catch for the portion of the population most heavily affected, e.g., for adult females only if they are caught disproportionately. This approach is similar to a calculation of PBR for adult turtles only, suggested by Gerrodette [107].

2.2.3. Step 3: Estimate productivity

For the fishery-independent catch LRP estimators that are the focus of this article, the theoretical maximum fishing mortality or fraction of abundance that can be removed annually while remaining at or above the corresponding population threshold can be expressed as the population's productivity at that threshold: $F = b \cdot R_{max}$, where R_{max} is the population's maximum net population growth rate (i.e., when population growth is not resource limited) and b is the fraction of R_{max} corresponding to the population threshold based on an assumed or inferred model of density-dependent population growth (Fig. 4). For example, if a simple logistic growth model is assumed and the population threshold is N_{MNP}, then $b=0.5$, because $0.5R_{max}$ is the expected net population growth rate at N_{MNP}. In other words, removing $\leq 0.5R_{max}$ of the population per year will result in maintaining the population at $\geq N_{MNP}$. Defining alternative population growth models to the logistic or alternative population thresholds (e.g., maintaining abundance above $0.75K$ or only above $0.1K$, i.e., $N_{collapse}$) will likely result in different values for b (Fig. 4). For example, the density-dependent relationship for many long-lived, late-maturing species is expected to be convex, such that a population threshold of N_{MNP} would allow for $b > 0.5$. However, uncertainty in density-dependent responses of most taxa is high [108], and $0.5R_{max}$ is likely a precautionary choice for population productivity at N_{MNP} for low-productivity marine megafauna [54,83] (Box 1: 9d). Choice of population threshold similarly affects reference point estimates using the SAFE approach [101,102].

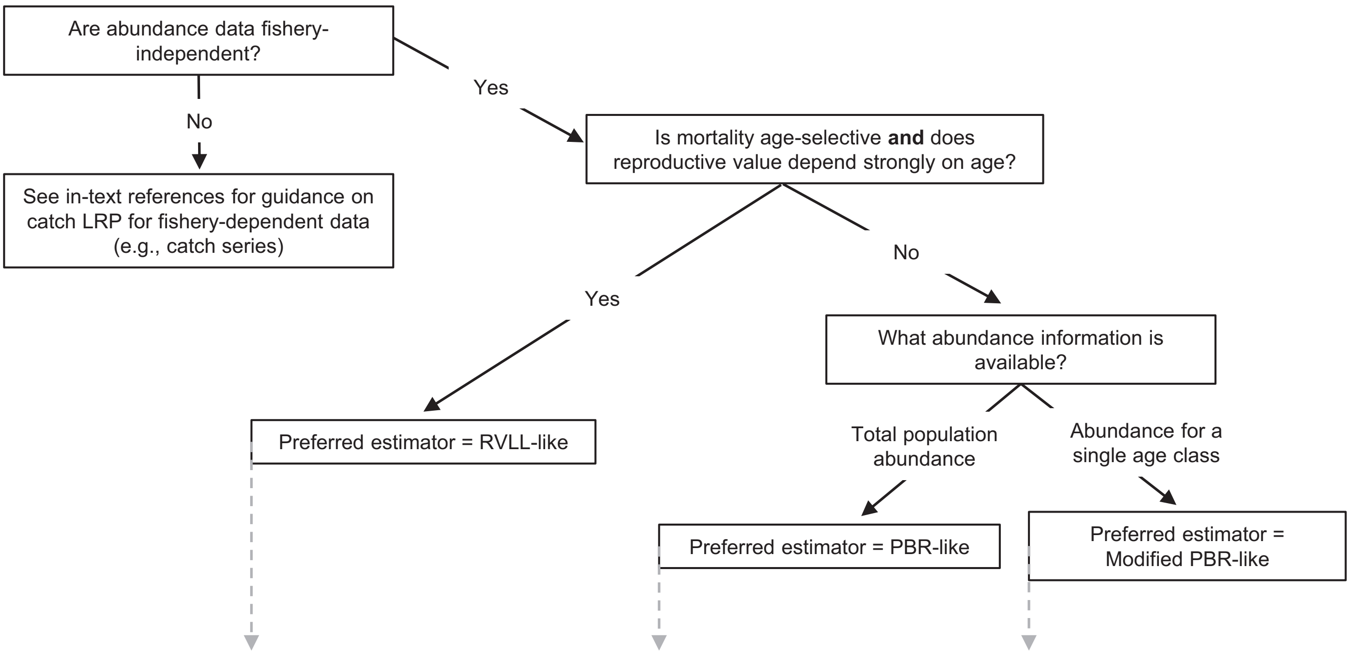
Direct estimation of R_{max} is rarely feasible, as it requires long time series of abundance for rapidly growing populations recovering from a depleted state, or estimates of survival and fertility for such a population. Alternatives include using default values (e.g., 0.04 for R_{max} for most cetaceans under the U.S. MMPA [83]) or values from other populations of the same species or other species within similar taxa [48,109,110], or estimating R_{max} from vital rate parameters derived indirectly from life history or allometric models [47,50,85,103,111]. Meta-analyses incorporating life-history or evolutionary theory can provide more robust estimates of R_{max} for data-poor species by drawing on data for better known species. Fagan et al. [112] used phylogenetic relationships to predict R_{max} for species within two broad mammalian groups, and Dillingham et al. [113] used a Bayesian approach that combines conventional population-matrix techniques with allometric scaling theory to improve estimates of R_{max} for data-poor species. Meta-analytical approaches such as these underscore a need for synthetic global databases of life history parameters and phylogenetic information.

2.2.4. Step 4: Estimate current abundance

The SAFE approach indirectly estimates abundance from spatial presence–absence data in research trawl surveys, inferred catchability given life history and gear characteristics, intensity and spatial distribution of fishing effort, and catch [101,102].

Many methods are available for estimating abundance of marine vertebrate populations, from aerial to ship-based, ground-based and underwater surveys of animals in water or hauled out at rookeries and nesting beaches. Analytical methods include mark-resight/recapture, strip transect estimation, and distance sampling, among others. A review of these methods is beyond the scope of this paper, but there are a few basic issues associated with abundance that need to be factored into reference point estimation. First, even for air-breathing taxa, only a demographic subset may be reliably surveyed for many populations (e.g., nesting sea turtles, seabird breeding pairs, pinniped pups or adults depending on species, a particular age class of shark that uses a management area). Dillingham and Fletcher [48], Richard and Abraham [50], and Curtis and Moore [54] provide examples of extrapolating estimates for reproductive adults to population-wide estimates, in terms of individuals or reproductive value, that can be used to estimate a catch LRP.

A more fundamental problem, particularly for widely ranging



Catch LRP estimator (basic form):	$(b\ R_{max}\ N\ f\ )_{min}$	$(b\ R_{max}\ N\ f\ )_{min}$	$(b\ R_{max}\ g(\eta)\ f\ )_{min}$
Notes:	N = abundance scaled by reproductive value	N = total abundance across ages	η = abundance for an age class; $g(\eta)$ is a function to obtain total abundance from η
Indicator:	Removals scaled by reproductive value	Removals	Removals
Data requirements:	Life table data to construct a population transition matrix corresponding to optimal population-growth conditions, estimates of abundance for a particular age or stage class (e.g., reproductive adults), age- or stage-specific estimates of human-caused removals	Estimates of R_{max} (from life table or other methods), survey estimates of total population abundance, estimates of human-caused removals	Estimates of R_{max} (from life table or other methods), survey estimates of η, demographic parameters to convert η to N, estimates of human-caused removals

What is *b?* Determined by population threshold. Corresponds to the fraction of maximum net productivity, R_{max}, that can be removed while still remaining above population thresholds (see Fig. 4). A recommended default is b = 0.5, which assumes logistic density-dependence and an N_{MNP} (Maximum Net Productivity Level) population threshold.

What is R_{max}? Maximum annual population growth rate achievable by a population (when resources are not limiting, e.g., at very small population size relative to carrying capacity) in its real environment (e.g., conditional on natural predation rates). Can be obtained from abundance time series (for recovering or founder populations), life table analysis, or life-history theory.

What is *f* ? Adjustment factor, has also been termed recovery factor (F_r) or uncertainty factor (f_u). Value between 0 and 1. Provides a precautionary buffer against potential biases, assumption violations, or model structural uncertainty that might otherwise result in resulting catch LRPs allowing for too much mortality to achieve population status objectives. Also can be used to allow for more rapid recovery of depleted populations. Computer-simulation evaluation, such as MSE (Fig. 5), is used to determine an appropriate value of *f*.

Why the subscript "min" on the estimator? The catch LRP is given by a lower-percentile estimate of the catch LRP distribution, which results from distributions for the constituent inputs (e.g., N and R_{max}) (alternatively, LRP_{min} has been derived from a lower-percentile estimate for just one particular input such as N_{min}). Computer-simulation evaluation, such as MSE, is used to find the appropriate percentile of the catch LRP distribution (that which maintains populations above their thresholds with the specified risk tolerances) to use for the catch LRP.

Fig. 3. Flowchart for selecting a catch LRP estimator.

marine species, is defining the management unit for which abundance – and catch – should be estimated [44]. Complexity of population structure is often underestimated [68,114]. In some cases, the taxonomy of animals being caught has not even been resolved to species level [115]. Attributing abundance survey data or catches to the correct population can be difficult, although these issues are increasingly being addressed through genetic approaches [106,116]. Uncertainty about population units necessitates more precautionary catch LRPs (Box 1: 9d). One way to tackle the problem of population structure for cases where populations do not co-occur is proposed in Section 3.2.

2.2.5. Step 5: Tune catch LRP estimators for uncertainty and risk tolerance

If abundance, productivity and underlying population dynamics, and catch were known perfectly and equilibrium states

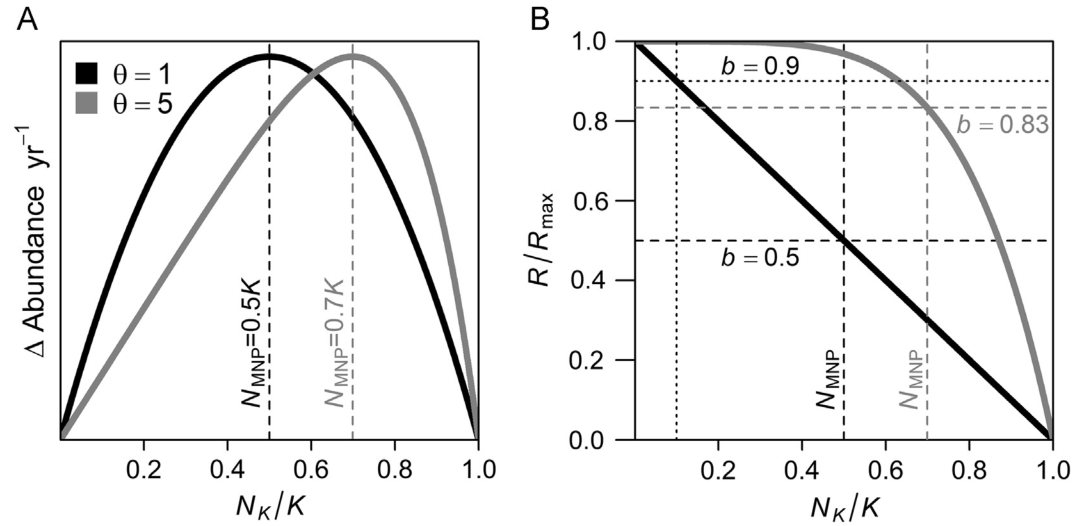


Fig. 4. Modified from Curtis and Moore [54]. (A) Net population growth rate as a function of increasing abundance (N/K) for a generalized logistic (or theta-logistic) population model with different values for the parameter controlling the shape of the density-dependent response (θ). Vertical dashed lines mark abundances at N_{MNP} under two different values of θ. (B) Corresponding standardized per-capita net population growth rate (R/R_{max}) with population size (solid lines) and solutions for parameter b, the maximum fraction of R_{max} that can be used in the catch LRP estimator to maintain N_{MNP} (dashed lines). Alternative objectives for population abundance, e.g., an objective of maintaining abundance above 0.1K (black dotted lines) or population growth models (gray dashed lines) would correspond to different solutions for b than the suggested default value of 0.5.

were a reality, then catch LRPs corresponding to specific population thresholds – and whether catch exceeds these – would be known exactly. But inputs to catch LRPs and catch itself are measured with error, population dynamics are stochastic, and each catch LRP estimator is based on assumptions that can be difficult to evaluate (e.g., the underlying population growth model). Catch LRP estimates are also prone to systematic biases due to uncertainty in inputs that are used repeatedly over many years; for example, overestimated productivity would lead to consistently high catch LRP estimates. As a result, there is considerable uncertainty in expected population outcomes from maintaining catches below a given catch LRP. The final step in estimating a catch LRP is to tune the catch LRP estimator. The catch LRP estimator may be tuned by including an adjustment factor, or by using a lower percentile for a component of the estimator, such as abundance, or for the estimated catch LRP distribution itself if more than one component has a probability distribution. The catch LRP estimator is tuned such that the expected probability of staying above the specified population thresholds falls within the respective risk tolerances for each threshold, given quantifiable uncertainties and other plausible sources of error that can be modelled.

The true probability of staying above a population threshold given a particular catch LRP is impossible to estimate accurately. A typical approach is to simulate many plausible realities over a range of tunings of the catch LRP estimator, and evaluate the resulting probability of management success (whether population thresholds are maintained) at each tuning, given the researcher's best attempt to characterize the most important uncertainties. Management strategy evaluation (MSE) [117] is a formal approach for doing this, wherein the biological, estimation, and management processes are represented in separate, interacting models (Fig. 5). MSE may also include additional elements, such as evaluating different catch LRP estimators or abundance estimation methods, or exploring economic-conservation trade-offs [118]. The "true" population state is simulated via an operating model. Variation in true dynamics among simulations and over time within each simulation reflects uncertainty in the knowledge of the biological process (e.g., estimated population productivity) and in the biological process itself (e.g., environmental stochasticity), respectively. The sampling model mimics the process by which managers or researchers estimate the variables needed to calculate a catch LRP (typically abundance), along with estimation uncertainty. The management model simulates application of a control rule, for example by limiting catch to the catch LRP, with management uncertainty resulting from, for example, catch estimation. Uncertainty may be characterized by drawing random values from probability distributions (e.g., for vital rates, abundance estimates, true catch and discard mortality, etc.), simulating plausible biases (e.g., in abundance or catch estimation), or simulating structural model uncertainties (e.g., different forms of density dependence, age-dependent fishing mortality, etc.) [37,54]. Moore et al. [37] provide a brief review of MSE in the context of managing catch of marine megafauna. Wade [83], Tuck [39] and Richard and Abraham [50], Curtis and Moore [54], and Curtis et al. [119] provide examples of MSE or MSE-like approaches for marine mammals, seabirds, and sea turtles, respectively. Several broad reviews of MSE also exist in the fisheries literature [120,121].

Uncertainty can then be factored into catch LRPs based on MSE results by tuning the catch LRP estimator to a specific risk tolerance. For example, a 20th percentile estimate (rather than point estimate) of abundance is used for N_{min} in the original PBR estimator because this value was deemed sufficient, based on simulations, to ensure a ≥ 0.95 probability of a population being at or above N_{MNP} after 20 years of LRP-based management, given typical levels of uncertainty in cetacean and pinniped catch and abundance [83]. By analogy, the Xth percentile estimate of the catch LRP may be found sufficient, based on MSE simulations, to ensure a $1 - \alpha$ management success probability given typical levels of uncertainty in the abundance, productivity, and catch estimates for a particular species or taxonomic group. An adjustment factor f (also termed recovery or uncertainty factor in applications of PBR and RVLL) can be incorporated in the estimator and tuned to a value less than one to buffer against sources of error that do not lend themselves to quantification as an uncertainty distribution or to achieve an objective for limiting human-caused delays of population rebuilding.

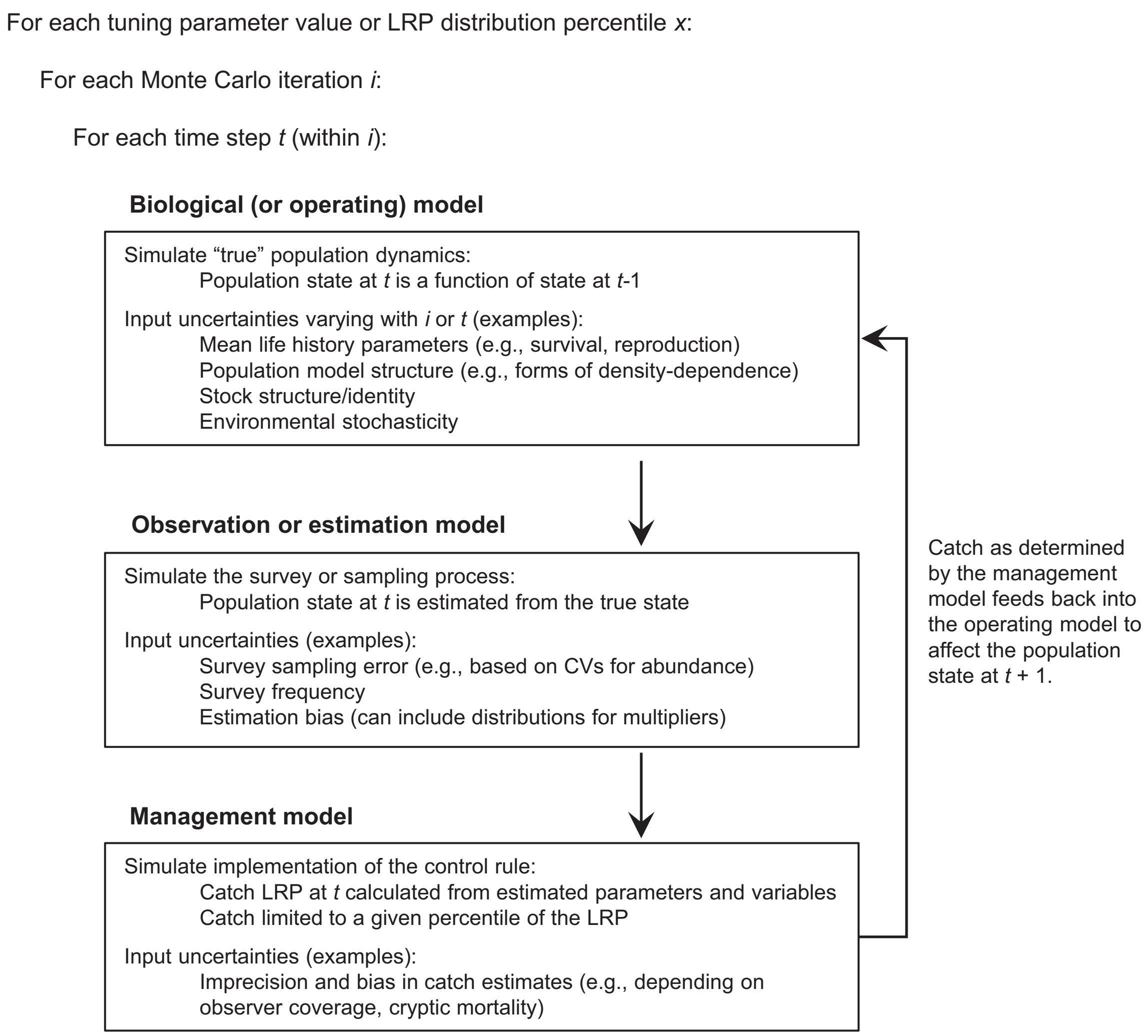


Fig. 5. Flowchart for a basic MSE to tune a catch LRP estimator. MSE is a Monte Carlo simulation process. For each of a range of tunings of the catch LRP estimator being tuned, many hypothetical "realities" are simulated, each one representing the outcome through time of a population and management process. Cumulatively, these outcomes represent management success (i.e., proportion of simulations for which population thresholds are maintained at a specified time horizon) for each tuning, enabling the catch LRP estimator to be tuned appropriately to the specified population thresholds and corresponding risk tolerances. Other variations of the management procedure in addition to tunings of an individual catch LRP estimator (e.g., different catch LRP estimators or abundance estimation approaches) may also be compared among sets of simulations.

Tuning parameter values can either be tailored to each population and management context or assigned based on general rules that are sufficiently precautionary for most situations based on an initial MSE that covers important sources of variation for a group of populations. The latter approach of using pre-specified tuning parameter values, followed for PBR estimation under the MMPA, eliminates the need for case-specific analyses, greatly increasing ease of use, e.g., across multiple species. However, a one-size-fits-all approach can also be problematic. Factors such as uncertainty or underlying processes may differ in a particular population or fishery from those underlying a catch LRP estimator's development to an extent not easily captured in a generalized MSE. Curtis and Moore [54] found that the extensive variation in life histories and uncertainties in information among populations of sea turtles warrants customized tuning for each application. Likewise, Richard and Abraham [50] customized separate correction and recovery factors for each seabird species.

A recent study that estimated LRPs for western Pacific leatherbacks in the U.S. West Coast EEZ provides a demonstration of the guidelines proposed here for estimating catch LRPs [119].

3. Addressing key challenges

Moore et al. [37] reviewed various challenges to implementing catch LRPs, categorized as being technical, operational, or political in nature. Here, two issues are addressed: (1) applying LRP-based management where the boundaries of a management jurisdiction do not coincide with a population's range and (2) applying a catch LRP for a population affected by multiple sources of human-caused mortality across sectors.

3.1. Local management to address scientific and political uncertainty

Boundaries of management jurisdictions rarely coincide with population ranges of marine megafauna. In some cases, management jurisdictions may subsume multiple populations of the same species. Where demographically independent populations are well-defined, it should be relatively straight-forward to treat each population separately. But where demographic independence among geographically separate groups of animals of the same species is uncertain, as is often the case [56,122], setting catch LRPs separately for each group that persists or recurs across years provides a precautionary solution that may help avoid unwittingly

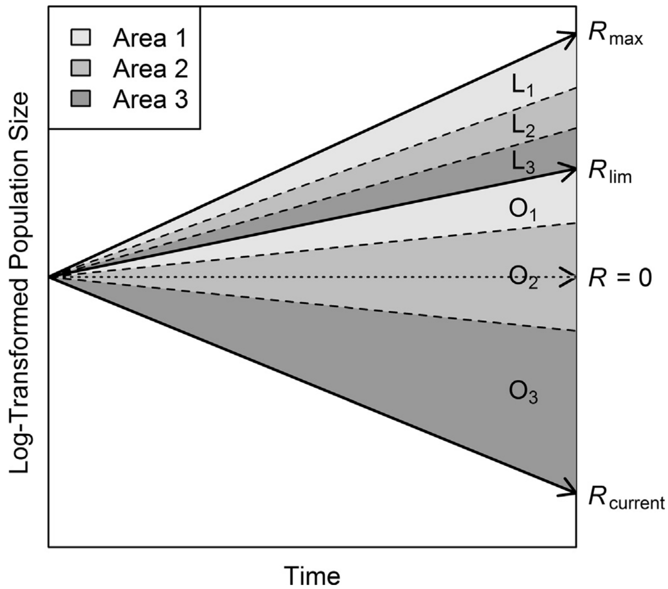


Fig. 6. Illustration of "take reduction wedges" corresponding to local LRPs as a means to achieve population conservation objectives for a hypothetical declining stock. Solid black lines represent, from bottom to top, current population trend, expected population growth rate if LRP-based management were in place in all jurisdictions (with identical population thresholds and risk tolerances), and maximum possible population growth rate without fishing (or other human-caused) mortality; respective slopes for these lines are $R_{current}$, R_{lim}, and R_{max}. Current catch in each management jurisdiction i in which the population occurs is L_i plus O_i, where L_i is the local catch LRP and O_i is the "take reduction wedge", or amount by which the stock is being overharvested in that jurisdiction. The dotted line equals zero population growth (i.e., $R=0$).

eliminating an unresolved population [56,123].

In other cases, management jurisdictions may include only a portion of a population's range. In this situation, catch LRPs can be approached similarly to climate stabilization wedges [124], with "take reduction wedges" for each jurisdiction estimated based on local abundance estimates and prorated by the fraction of the year the animals spend in that jurisdiction, as outlined in the guidelines for calculating PBR under the U.S. MMPA [125] (Fig. 6). The resulting local catch LRPs allow for incremental progress towards limiting mortality for the total population to the overall catch LRP (Box 1: 7). If local abundance estimates are lacking, prorating an estimate of total population abundance by the fraction of the population's range area that a management jurisdiction constitutes would provide incentive for improved abundance estimates in frequented areas. Known abundances from specific management jurisdictions and the areas of those jurisdictions can be subtracted from the total abundance and area, respectively, to calculate local catch LRPs for areas where abundance has not been estimated. Taking the localized management approach also permits precautionary management in the inverse situation of a population whose local abundance is known, but whose broader abundance is unknown. Management strategy evaluation of local catch LRPs should account for uncertainty in local abundance and human-caused mortality. Curtis et al. [119] provide a non-marine-mammal example of this approach, which they used to estimate a local LRP for western Pacific leatherbacks in the U.S. West Coast EEZ.

A more general approach developed by the IWC is to manage whaling impacts in "small areas" at a high enough resolution that all affected animals in each area are expected to belong to the same stock [44]. The IWC "small areas" approach may also be useful for other taxa to address management of impacts over large expanses on the high seas where little information is available on aggregations.

Local catch LRPs provide a sound basis for linking local management to population-scale conservation objectives, and may therefore also serve as a common standard for internationally relevant assessments of local management, such as non-detriment findings under the Convention on International Trade in Endangered Species, or to evaluate fisheries for eco-certification or for compliance with domestic environmental protections under import certification schemes.

3.2. Accounting for non-fisheries anthropogenic impacts

Many stocks of marine megafauna face multiple threats in addition to fishing mortality [10,126]. Managing catch to stay within LRPs for these stocks must account for and be balanced with other anthropogenic impacts. Anthropogenic impacts are diverse in nature and cause, but, drawing on pollution literature, they can generally be classified into diffuse and point sources. If nation states are characterized as the basic management unit within coastal waters, point source impacts are those that, like fishing mortality, can be ascribed to one state. Mortality due to power plant intakes is an example of point source mortality. Diffuse impacts are those for which multiple states collectively are responsible, such as climate change effects on population growth. These impacts may either affect vital rates directly or change the carrying capacity of the population. Extending the local management model, diffuse impacts to vital rates can be accounted for in estimating catch LRPs, e.g., by reducing estimated maximum population productivity accordingly, while point source impacts to vital rates can be summed and managed cumulatively to stay within an LRP for human-caused removals. For example, removals due to vessel strikes are counted against PBR of marine mammals under the MMPA. In reality, difficult cross-sector decisions will have to be made to effect this approach. Indeed, balancing impacts on a population from multiple fisheries is in itself a prevalent challenge [24]. However, this approach provides a starting point for accounting for cumulative impacts on vital rates of marine megafauna.

4. Management context for application of LRPs

The emphasis of this article is on providing guidance for the technical process of estimating catch LRPs for marine megafauna, but a few issues related to LRP-based management are briefly reviewed here.

A management response to exceeding a catch LRP may be formalized into a control rule, prompting semi-automated management action to prevent further exceeding the limit, such as a fishery closure or a spatial shift in shipping activity. Control rules enhance transparency and predictability of decision-making [127] and reduce implementation uncertainty. However, sudden, drastic changes in management are undesirable [28,128]. Catch and catch LRPs for marine megafauna should be evaluated and applied on a multi-annual basis if catch LRPs are low (e.g., tens of individuals per year) to reduce the effects of process error (variation in the true number of interactions per year) and observation error (variation due to incomplete sampling by observer programs) at small sample sizes on the management process [125,129]. Management responses to approaching or overshooting catch LRPs should be designed carefully to minimize unintended biological and socioeconomic effects, for example due to effort displacement [130]. Effort displacement resulting from unilateral management action on transboundary populations may be difficult to avoid, so it is also imperative to balance local or regional advances in catch management of marine megafauna with a population-wide perspective and find avenues for improving catch management in other jurisdictions.

As catch of marine megafauna garners increased attention, and especially where catch LRPs become institutionalized as output control rules, greater investment in planning and monitoring should follow. Agreement in advance on how to adapt to improved information or analytical techniques is advisable to minimize disagreements among stakeholders and managers down the road [131,132]. At-sea observer coverage or electronic monitoring is needed to support implementation of catch LRPs [21,127,133], even where discard mortality is low, since restrictions on landings alone may not sufficiently limit mortality for unproductive species [134]. Post-catch methods to further increase data availability and quality and decrease bias include dockside genetic sampling [135] and data correction [136,137].

Additional priority areas for improvement are quantifying all sources of direct and indirect fishing mortality [4,138] and long-term impacts of fishing on marine megafauna populations and life histories [84,139,140], and estimating and accounting for non-fishing human-caused impacts on carrying capacity and vital rates of marine megafauna.

5. Conclusions

Progress towards attaining management goals for the conservation of elasmobranchs, marine reptiles, seabirds, and marine mammals threatened by direct fishing mortality requires establishing meaningful minimum benchmarks upon which management decisions can be based and evaluated. Effective benchmarks make biological sense within the context of overall conservation goals, are relevant to the time frames over which management decisions are made and evaluated, and account for and are robust to uncertainty. Catch LRPs are designed to meet these criteria, can be directly incorporated into a more comprehensive ecological risk management framework, and are already being used to manage catch of many species of marine megafauna by both domestic and international fisheries management organizations. Importantly, catch LRPs are meant to complement rather than supplant management targets. Where possible, unused catch and catch of threatened, endangered, and protected species should be minimized beyond LRPs, as called for by the Code of Conduct. Reducing catch beyond catch LRPs also serves to increase population resiliency in the face of future or unquantified risks.

Current ecological science, precedent, and internationally agreed goals provide a basis for setting shared population conservation objectives for upper limits on population impacts and associated risk tolerances, potentially expediting the process of agreeing on and implementing LRP-based management. Scaling down LRP-based management to the scale of jurisdiction or potential population units can address otherwise difficult technical and political hurdles to its effective implementation. Recent advances in tools underlying reference point estimation, such as innovative meta-analytic techniques to improve productivity estimates for data-limited populations, address many key challenges that have hindered the estimation and subsequent implementation of catch LRPs to date. Finally, catch LRPs may be adapted to address cumulative mortality across multiple human activities by quantifying other mortality sources and adjusting LRPs accordingly. As demonstrated here, catch LRPs provide a means to move towards accountable, robust management of fisheries impacts on marine megafauna with a consistent approach across fisheries, species, and jurisdictions, and in line with global commitments.

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