Sampling mobile oceanic fishes and sharks: Implications for fisheries and conservation planning

Running Title: *Sampling of oceanic predators*

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ABSTRACT

Tuna, billfish, and oceanic sharks (hereafter referred to as “mobile oceanic fishes and sharks”, MOFS) are characterised by conservative life-history strategies and highly migratory behaviour across large, transnational ranges. Intense exploitation over the past 65 years by a rapidly expanding high-seas fishing fleet has left many populations depleted, with consequences at the ecosystem-level due to top-down control and trophic cascades. Despite increases in both CITES and IUCN Red Listings, the demographic trajectories of oceanic sharks and billfish remain poorly quantified and resolved at geographic and population levels. Of all MOFS tunas are generally considered better understood, yet several populations remain either overfished or of unknown status. MOFS population trends and declines therefore remain contentious, partly due to challenges in deriving accurate abundance and biomass indices. Two major management strategies are currently recognised to address conservation issues surrounding MOFS: (1) internationally ratified legal frameworks and their associated regional fisheries management organisations (RFMOs); and (2) spatio-temporal fishery closures, including no-take marine protected areas (MPAs). In this context, we first review fishery-dependent studies relying on data derived from catch records and from material accessible through fishing extraction, under the umbrella of RFMO-administrated management. Challenges in interpreting catch statistics notwithstanding, we find that fishery-dependent studies have enhanced the accuracy of biomass indices and the management strategies they inform, by addressing biases in reporting and non-random effort, and predicting drivers of spatial variability across meso- and oceanic scales in order to inform stock assessments. In contrast and motivated by the increase in global MPA coverage restricting extractive activities, we then detail ways in which fishery-independent methods are increasingly improving and steering management by exploring facets of MOFS ecology thus far poorly grasped. Advances in telemetry are increasingly used to explore ontogenic and seasonal movements, and provide means to consider MOFS migration corridors and residency patterns. The characterisation of trophic relationships and prey distribution through biochemical analysis and hydro-acoustics surveys has enabled the tracking of dietary shifts and mapping of high quality foraging grounds. We conclude that while a scientific framework is available to inform initial design and subsequent implementation of MPAs, there is a shortage in the capacity to answer basic but critical questions about MOFS ecology (who, when, where?) required to track populations non-extractively, thereby presenting a barrier to empirically assessing the performance of MPA-based management for MOFS. This sampling gap is exacerbated by the increased establishment of large (>10,000 km^2) and very large MPAs (VLMPAs, >100,000 km^2) - great expanses of ocean lacking effective monitoring strategies and survey regimes appropriate to those scales. To address this shortcoming, we demonstrate the use of a non-extractive protocol to measure MOFS population recovery and MPA efficiency. We further identify technological avenues for monitoring opportune at the VLMPA scale, through the use of spotter planes, drones, satellite technology, and horizontal acoustics, and highlight their relevance to the ecosystem-based framework of MOFS management.

Keywords: Pelagic sharks, Tuna, Migratory, MPA, RFMO, Spatial management

CONTENTS

I. INTRODUCTION

(1) Pelagic predicaments

The onset of industrialised fisheries in the 1950s catalysed the widespread exploitation of mobile oceanic fish and sharks (hereafter 'MOFS') such as tuna (*Thunini*), swordfish (*Xiphiidae*), billfish (*Istiophoridae*) and pelagic sharks (e.g. oceanic white tips, *Carcharinus longimanus*; blue sharks, *Prionace glauca*). In the decades that followed, the large-scale and unregulated removal of these apex predators pushed several populations of long-living, slow-breeding and hence vulnerable MOFS species to collapse (Collette *et al.*, 2011; Worm *et al.*, 2013; Dulvy *et al.*, 2014) with direct consequences for trophic integrity (Baum & Worm, 2009; Estes *et al.*, 2011), ecosystem productivity (Srinivasan *et al.*, 2010), and resilience to environmental change (Sumaila *et al.*, 2011). In spite of evident population declines and cases of resource mismanagement, fishing effort continues to intensify to this day (Anticamara *et al.*, 2011) as fleets supported by government subsidies venture further into the high seas and away from ports (Swartz *et al.*, 2010). Management decisions remain contentious due to the trans-jurisdictional and competitive nature of numerous MOFS fisheries on the high seas, all generally unwilling to forgo a loss in resource access to the perceived benefit of others (Hardin, 1968; White & Costello, 2014).

A major challenge in quantifying the biological footprint of worldwide fisheries lies in that much of the global take goes unreported and is not subject to independent updates or verification, making MOFS catch rates notoriously hard to assess. For example, existing estimates of shark landings from the Food and Agriculture Organisation (FAO) are four times lower than those derived from available market sale statistics in the same year (Clarke *et al.*, 2006). Likewise, only four tunas (bigeye, *Thunnus obesus*, albacore, *Thunnus alalunga*, skipjack, *Katsuwonus pelamis*, and yellowfin, *Thunnus albacares*) reportedly contribute to 90% of the ca. 6 million metric tonnes (Mt) of tuna harvested annually (FAO), but this evaluation likely overlooks substantial incidental and illegal catches (surpassing quotas by approximately 300% , Gewin, 2004; Metuzals *et al.*, 2009).

As MOFS are highly mobile and generally occur in low densities (though some may form large schools), the logistical difficulties in obtaining ecologically meaningful data for these animals have fuelled heavy debates regarding the extent of population declines (Myers & Worm, 2003; Sibert *et al.*, 2006; Juan-Jordá *et al.*, 2011). The lack of consensus is further hindered by a poor grasp of the animals' distributions (Worm & Tittensor, 2011), their complex relationships with physical habitats (Morato *et al.*, 2010; Bouchet *et al.*, 2014), their intricate population dynamics compared with lower trophic levels (Blower *et al.*, 2012), and their high spatio-temporal heterogeneity (Block *et al.*, 2005).

(2) Missing management or missing data?

Regional fisheries management organizations (RFMOs) have been formed by a number of fishing nations to develop cooperative management arrangements for wild population of MOFS that primarily entail gear regulations, catch quotas, and fishing behaviour changes. In the Pacific Ocean for example, recognition of the value of the tuna fishery, which yields 50% of global annual tuna landings, led to the establishment of the Western and Central Pacific Fisheries Commission (WCPFC) in 2004 by countries with vested interests, including Australia, Palau, and Papua New Guinea. The WCPFC is primarily responsible for guaranteeing the sustainability of high seas fisheries in the western Pacific and typically sets quotas and recommended levels of effort, including those for highly migratory species. In spite of calls for restraint to curb industry expansion, purse seining efforts increased by ~20% in the equatorial Pacific between 2004 to 2007, and management successes were initially low (Langley *et al.*, 2009). The recent implementation of both the 'vessel day scheme', which restricts the number fishing days for purse-seine vessels, and shark finning bans, have been found to have little effect on fishing effort and activities (Clarke *et al.*, 2013; Havice, 2013). Incorporating socio-economic dynamics in effort and catch allocation programmes, rather than soles reliance on reported catch statistics (Bailey *et al.*, 2013), may be a more pragmatic way of reducing catches, but high-seas management remains challenging in general (Cullis-Suzuki & Pauly, 2010).

To combat the severe impact of commercial fishing bycatch, single species protection measures have also been put in place to foster MOFS recovery. Several species of commercially important elasmobranchs such as the oceanic white tip and three species of hammerhead (*Sphyrna lewini, Sphyrna zygaena, Sphyrna mokarran)* have recently become listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, www.cites.org), which restricts the international trade of these animals. Experience from migratory species in terrestrial systems indicates that the CITES listing of a single threatened species may translate to other vulnerable ones (Branton & Richardson, 2011) more efficiently than the protection of areas with high biodiversity (hotspots, Watson *et al.*, 2011), but it remains unclear whether similar mechanisms are operating in the marine realm.

Large and pelagic marine protected areas (MPAs) have been presented as a conservation strategy for a range of marine mega-vertebrates, including seabirds (Camphuysen *et al.*, 2012), turtles (Scott *et al.*, 2012), cetaceans (Gormley, Slooten, & Dawson, 2012) and MOFS (Game *et al.*, 2009; Koldewey *et al.*, 2010). While MPAs are primarily established to avert biodiversity loss, they may also provide a buffer for threatened MOFS species that would otherwise be exploited under conventional fishery management schemes or current legal frameworks. Due to the rate at which MOFS distributions change temporally and spatially, management strategies that incorporate 'moving' MPAs in order to reduce MOFS bycatch are increasingly advocated (Hobday *et al.*, 2011). Such a 'dynamic ocean management' framework may be particularly efficient for mobile species compared with static management regimes (Maxwell *et al.*, 2015) but requires real-time data from remote sensing, telemetry, and catch data (Hobday & Hartmann, 2006). Whether fisheries closures are moving or static, understanding the contribution of large (>10,000 km^2) and very large MPAs (>100,000 km, VLMPA) to MOFS management is essential given their increasing number in the last decades (from 1 to 76 large MPAs, and from 1 to 34 VLMPAs, between 1975 and 2015, Fig. 3). These areas typically contain extensive open-water habitats which may be sufficiently wide to cover the ontogenic migration routes of species such as skipjack and yellowfin tuna (Sibert & Hampton, 2003).

Critical knowledge gaps exist with respect to the overall efficiency of MPAs in protecting or supporting the recovery of MOFS (Davies *et al.*, 2012; Sibert *et al.*, 2012), particularly when MPAs are implemented 'residually' where they are easy to establish and conflict is minimised, rather than by following a rigorous scientific rationale (Devillers *et al.*, 2014). Moreover, the successful implementation and enforcement of large-scale pelagic MPAs may require a more flexible infrastructure regime than coastal MPAs to match the dynamic nature of offshore environments and the highly mobile behaviour of MOFS, presenting new challenges.

Common to all these strategies is the need for reliable, accurate data that allow MOFS population trajectories to be resolved and their responses to geographically explicit management measures examined. This is particularly crucial in no-take MPAs where areal closures terminate the collection of fishery data. Murphy & Jenkins (2010) provided a summary of some of the non-extractive techniques available to study habitats and fish communities/assemblages inside and around MPAs. However, their review was limited to small-bodied shallow-water species and to surveys of costal environments such as seagrass meadows or coral reefs. Here, we complement this effort by reviewing the observational and analytical methods available for assessing the status of mid-water, far-ranging, pelagic MOFS and summarise their wider implications for both fishery management and conservation planning. Firstly, recognising the challenges associated with traditional fishery administration and the assessment of long-term population trajectories, we review the declines reported for MOFS through fishery catch records. We further identify fishery-dependent methodologies and the aspects in which these have supported RFMO management of MOFS through the improvement of abundance indices and the exploration of poorly known facets of MOFS ecology. Secondly, motivated by the increase in both MPA areal coverage and pelagic fishery closures, we review non-extractive methodologies currently available for ecological studies and monitoring in areas closed to fishing activities. Thirdly, with a view to the future, we highlight new protocols that show promise for application on the necessary scale of VLMPAs, and MOFS population processes.

II. CATCH RECORDS AND FISHERY-DEPENDENT SAMPLING

Contention surrounding the status of the oceans' large predators has mainly been fuelled by the restricted coverage of most monitoring datasets and the complex relationship between catch and abundance (Walker *et al.*, 2010; Pauly, Hilborn, & Branch, 2013). Fishery catch records provide some of the most spatially and temporally extensive information available (with the exception of by-caught species, Clarke *et al.*, 2006), so population assessments and, by extension, management schemes are conventionally established using fishery-dependent data derived from commercial fishing activities and monitoring programmes. Catch records are typically standardized by some overarching measure of effort such as the number of hooks (Worm *et al.*, 2013), estimates of fuel consumption (Bastardie *et al.*, 2010), or individual biomass measurements for each gear (Maunder & Punt, 2004) to derive catch-per unit effort (CPUE) indices which stand as proxies of population status. Since there are cases when catch rates are decreasing but abundance is constant, or vice versa (Hilborn & Walters, 1992), standardization models are applied to account for changes in fishing behaviour and efficiency (Maunder & Punt, 2004). For MOFS, this has resulted in several attempts to assess trends, and thus to estimate the impact of global fishing effort (Fig. 1) for decisions on management regimes. Ferretti *et al.* (2010) reviewed shark population trajectories and highlighted widespread declines in pelagic, coastal, and demersal systems. The authors further summarized the evidence pertaining to trophic cascades resulting from these declines, and suggested mechanisms in which these could be sustained. Here, we restrict our focus to species deemed truly pelagic (Dulvy *et al.*, 2008), but review both teleosts and oceanic sharks (see sources listed in the supplementary material, Fig. 1 and Fig. 2).

Our review of the primary literature documents declines for most MOFS populations for which data exist (97.5%). Of 80 population trajectories identified, 79 estimates stemmed from fishery-dependent records (supplementary material, Fig. 1 and Fig. 2). The spatial and taxonomic resolution of these trajectories are highly variable and have been estimated using CPUE-based indices at the scale of the assemblage (Myers & Worm, 2003), and stock assessment at the level of the region and species (Sibert *et al.*, 2006), and of the population (Juan-Jordá *et al.*, 2011). Broadly speaking, oceanic sharks have expressed the most substantial declines (up to a 1000-fold decrease, Fig. 2), followed by billfish (between 70 and 80%) and tunas (approx 60 %, from recent estimates Fig. 1). Geographically, the highest declines across all species were observed in the Mediterranean, probably due to a long history of human exploitation and limited geographic connectivity between source populations (Gubili *et al.*, 2011). Multiple attempts to consider the same catch records typically yielded different results, due to different decisions by the authors regarding the analytical treatment of fishing behaviour, practices in data pooling, and the inclusion of contrasting ecological parameters in stock assessment and recruitment models. The most recent estimates showing average population declines of 56% for tunas (Juan-Jordá *et al.*, 2011) were generally less pessimistic than earlier evaluations of around 90 % for the species-aggregated MOFS assemblage (Myers & Worm, 2003). The earlier estimates relied primarily upon CPUE derived indices (Myers & Worm, 2003; Baum *et al.*, 2003), whereas the later estimates typically relied upon full stock assessments. Only a single stock assessment was identified for oceanic sharks, that of the blue shark from Sibert *et al.* (2006). Stock assessments are considered superior to CPUE-based metrics in that they combine multiple sources of information (such as scientific fishery surveys, size, and age distribution, Branch *et al.*, 2011; Juan-Jordá *et al.*, 2013), although they are often unavailable for numerous important fisheries (Kleisner *et al.*, 2013). Stock assessments are thus preferentially used by RMFOs, compared with CPUE-based indices. Improvement in fishery-dependent estimates of MOFS population trajectories falls broadly in two categories: (1) through consideration of changes in catch-reporting and fishing practices and (2) through elucidation of migration behaviour and spatio-temporal variability of MOFS.

(1) Catch record accuracy and non-random effort

The utility of catch-statistics in guiding MOFS management hinges on the accurate reporting of catches. While catch record-keeping is primarily contingent upon an incentive to report, it is further complicated by the typical omission of

(1) recreational fishing, (2) illegal, unreported and unregulated (IUU) fisheries, and (3) discards, which may have considerable impacts on both commercial and non-commercial species (McPhee, Leadbitter, & Skilleter, 2002; Metuzals *et al.*, 2009; Kleiven, Olsen, & Volstad, 2011). While global discards have been estimated at 7.3 million tonnes for all fisheries and species combined (Kelleher, 2005), assessing the scale of IUU fishing is a pervasive problem with global estimates ranging between 10 million and 26 million tonnes (Agnew *et al.*, 2009). However, estimates of IUU activities are improving, for example by identifying the characteristics and flagging behaviour most typical of IUU vessels, thereby allowing for their identification (Miller & Sumaila, 2014).

Several ground-truthing protocols have been implemented to detect biases and generate error budgets for MOFS catch reports, most notably through the use of RFMO observer programmes. Successes in observer programmes have been mixed, as variability in coverage between vessel types can be high. In 2010 for instance, observer coverage in the fleet managed by the WCPFC ranged between 5-25% for long-line and 10-55% for purse-seine vessels respectively (Nicol *et al.*, 2012). Several case studies have demonstrated both observer-related effects, where the presence of observers influences fishing practices, and deployment-related effects, where the distribution of observers is non-random (Benoît & Allard, 2009). Observer programmes do not necessarily provide data with high taxonomical resolution, and spatial coverage can be low in hard-to-manage fisheries. For instance, prior to the closure of fisheries in the Chagos Marine Reserve, observers were present on only 1 to 5% of vessels (Koldewey *et al.*, 2010). The prevalence and success of observer programmes on a global scale have yet to be the topics of a dedicated review, which makes a formal assessment of their overall efficiency difficult, and arguably overdue.

With respect to reducing observer biases, recently developed quantitative training approaches where observers are provided feedback on the average of an observer group estimate, rather than the true values, may be fruitful in training surveyors (Wintle *et al.*, 2012). Possible technological solutions to low observer coverage include the further development of vessel monitoring systems (VMS), where GPS trackers are fitted to fishing vessels. Although VMS are not yet widespread on the high seas (particularly on vessels flagged to developing countries), they are extensively used in a few heavily managed fisheries (European-Commission, 2009) and show promise in enabling the correct recording of vessel locations and the particular source of the catches from logbooks, in addition to discerning fishing practises and fleet behaviours. As an alternative to VMS, Automatic Identification System (AIS) satellite data could be utilized for tracking fishing vessels (Natale *et al.*, 2015). This system was initially introduced to avoid ship collision and may be preferable from a research point of view, as AIS data access is less restricted by confidentiality than VMS (Hinz *et al.*, 2013).

Increasingly, electronic monitoring programmes are being considered in order to improve reporting accuracy, as both a complement and an alternative to observer programmes (Stanley *et al.*, 2015). Electronic monitoring of MOFS fisheries has been proposed (Piasente *et al.*, 2012), and would likely involve review of dockside and fisheries events from video records. Combined with incentives such as a government support that is conditional on improved catch-monitoring, such programmes could form part of a dual 'carrot and stick' solution1 to enforcement, with likely greater chance of success than mono-faceted approaches (Stanley *et al.*, 2015).

(2) Migration and spatio-temporal variability

Recognition of the aggregative and migratory behaviours of many MOFS species has triggered efforts to capitalise on material readily extracted from commercial catches in order to elucidate spatio-temporal variability in yearly and ontogenic time scales. For instance, observations of patterns in long-line catches suggest that billfish, skipjack and bigeye tuna as well as some species of pelagic sharks cluster around reefs, shelf breaks, seamounts (Holland & Grubbs, 2007; Morato *et al.*, 2010) and thermal fronts (Worm *et al.*, 2005) and often coincide with zooplankton and coral reef hotspots (Worm, Lotze, & Myers, 2003). The use of geomorphic variables as proxies of MOFS distributions is a budding field of research, with real-world applications for spatial planning (Bouchet *et al.*, 2015).

Since their introduction in the 1950s, mark-recapture techniques have been pivotal in exploring global patterns of animal mobility (Ortiz *et al.*, 2003), travel speeds, vertical distribution, diving behaviour (Michielsens *et al.*, 2006; IOTC, 2008), seasonal movements and residency (Ortiz *et al.*, 2003), with direct implications for the development of adaptive legislation and spatial planning. For example, Sibert & Hampton (2003) showed median lifetime displacements for yellowfin and skipjack tuna ranging from 336 to 470 nautical miles, emphasizing the need for large-scale and therefore transnational resource management in the Western Pacific Ocean. However, while the simplicity of mark-recapture programmes enables long time-series to be gathered, such studies typically hinge on commercial or recreational fishers returning tags from caught specimens. For example, out of 370,000 tags deployed on billfish globally, only 1.1% have been recovered from re-captured animals (Ortiz *et al.*, 2003). In its purest form, mark-recapture therefore only provides binary information related to the presence of the individual at the point of capture and recapture, and resulting inferences on distribution and migration patterns are heavily influenced by the distribution of fishing effort and the life stages captured.

The large numbers of fish killed by commercial vessels has also enabled the collation of fish ear bones (otoliths), which would otherwise be inaccessible. These collections provide some of the largest data sets available to explore ontogenic migrations. Otoliths consist of calcium carbonate deposits that precipitate in a fish's auditory system as the animal grows, and thus provide a venue to assess the effects of different environmental conditions on physiology throughout the individual's life stages (Secor & Rooker, 2000). Classically used to assess growth, otoliths are increasingly relied up on to discern spatial structure based on variation in chemical structure. For instance, in the Pacific, the chemical analysis of otoliths extracted from commercially caught bluefin tuna has identified multiple spawning grounds from elemental differences retained in their lithium, magnesium, calcium, manganese, and strontium signatures, with juveniles hatching in the East China Sea, the Sea of Japan, and the sea of Skikoku (Rooker *et al.*, 2001). Similarly, in bluefin otoliths from the Indian Ocean, elemental concentrations of sodium, magnesium, manganese, sodium, strontium and barium are indicative of a single bluefin tuna spawning population (Wang *et al.*, 2009). In the Atlantic Ocean, the combination of elemental and isotopic otolith analyses with satellite telemetry has identified tuna populations with overlapping feeding grounds in the Eastern and Central Atlantic but disparate spawning grounds in the Mediterranean and Western Atlantic (Rooker *et al.*, 2008), helping the distinction of the two breeding populations by the International Commission for the Conservation of Atlantic Tunas (ICCAT) RFMO.

Fishery-dependent catch records have a number of restrictions, but because they are spatially and temporally extensive, they are particularly useful for inferring processes on large biogeographical scales (>100 km), and to identify areas of conservation importance such as hotspots, when these are the only data available (Morato *et al.*, 2010; Bouchet *et al.*, 2014). To address the lack of spatially consistent sampling required for temporal monitoring and the lack of resolution on the meso-scale, fishery surveys by scientific trawling vessels that employ standardized fishing gear are becoming increasingly commonplace as a monitoring tool and as an integral aspect of management in large marine ecosystems, in order to inform stock assessments (Olsen *et al.*, 2009; Needle & Catarino, 2011; Ferretti *et al.*, 2013). While most scientific sampling actively seeks to reduce or otherwise account for gear-associated biases, scientific fishery surveys use gear compliant with industry standards, looking to resolve the issues arising from non-random effort allocation by running spatio-temporally consistent and sampling designs with random effort (Conners, Hollowed, & Brown, 2002). Due to their random survey designs, the resulting CPUE indices and stock assessments are usually considered superior to those derived from commercial catch records alone. Scientific surveys commonly have a restricted spatial extent, meaning they are unable to elucidate the broad patterns observed in fishery-dependent data. Moreover, scientific fishery (and lethal) surveys are inappropriate (1) in no-take MPAs and other areas of ecological and conservation importance (Bach *et al.*, 2003), (2) for rare or Red Listed species, and (3) when the lethal take/capture of the animal raises ethical concerns.

While the capacity to generate reliable abundance indices is improving through the use of scientific survey data, sophisticated observer programmes, and advances in modelling complex catch data, robust stock assessments remain absent for many population of MOFS, as reflected in the relatively high number of 'data-deficient' species on the IUCN Red List (4 out of 39 neritic and epipelagic shark species, Dulvy *et al.*, 2014; 3 out of 9 billfish species, and 1 out of 7 tuna species, Collette *et al.* 2011). Moreover, the historical and on-going trend of increased MPA coverage (Fig. 3), is limiting the use of fisheries catch statistics and the spatial extent of extractive scientific surveys, since lethal sampling is inconsistent with the offered protection. Modelling efforts on fisheries abundance indices with hypothetical closures suggests that the presence of closed areas may lead to biases in the population indices derived from the fisheries still operating, the degree of bias being proportional to the size of the population contained within the closed area (Ono, Punt, & Hilborn, 2015). In line with the recommendations of Ono, Punt & Hilborn (2015), we agree that the development of indices based on non-extractive methodologies in the closed area is to be preferred to the alternative means of analysis that requires subsequent time-series to be restricted to areas fished continuously.

III. FISHERY INDEPENDENT AND NON-EXTRACTIVE SAMPLING

A variety of non-extractive approaches have been employed to address methodological and data gaps associated with MOFS ecology (Table 1). Some emerged in a fishery-related context, for example hydro-acoustic echosounders were initially employed as 'fish-finder' devices following the invention of military sonars, but we have opted to classify them as fishery-independent as they are appropriate for use in no-take MPAs. Moreover, while most scientific methods are invasive in the strictest sense, we pragmatically make the distinction between lethal techniques, where animals are killed, and non-extractive ones, where some degree of animal handling may be required but without consequences for the animals' survival. The gold standard of sampling is that which requires no handling and does not cause any disruption of the animals' natural behaviour, yet we recognise that very few techniques currently meet this aspiration. Here, we outline non-extractive techniques and discuss ways in which they provide information that is relevant to MOFS ecology, and how they can be used for management purposes in an MPA context.

(1) Telemetry

Telemetry is a key bio-logging technique that is increasingly supplementing traditional mark-recapture studies as a non-lethal way of examining patterns in ontogenic and seasonal MOFS migration. In contrast to mark-recapture, telemetry can be implemented independently of fishing activity, although fishing gear is still a primary way of catching MOFS to deploy tags. Satellite tagging (for a review, see Hammerschlag, Gallagher, & Lazarre, 2011) has enabled the tracking and monitoring of salmon sharks (*lamna ditropis*, Weng *et al.*, 2005), bluefin tuna (*Thunnus thynnus*, Block, 1998), white sharks (*Carcharodon carcharias*, Weng *et al.*, 2007), blue sharks (*Prionace glauca*, Queiroz *et al.*, 2012) and porbeagle sharks (*Lamna nasus*, Saunders, Royer, & Clarke, 2010) across entire ocean basins. In the Atlantic, a wealth of knowledge has been generated on the population structure and life-history of bluefin tuna, resulting in the recognition of two distinct breeding stocks by the ICCAT (Block *et al.*, 2005) analogous to those identified in isotope analyses of otoliths obtained by lethal sampling (Rooker *et al.*, 2008). Satellite telemetry has further revealed strong connectivity and behavioural sensitivity between MOFS and oceanic processes such as frontal features on meso- (Queiroz *et al.*, 2012) and ocean-basin scales (Block *et al.*, 2011), further corroborating observations stemming from catch statistics. On a smaller scale (10s km), acoustic telemetry has offered insights into the habitat use and movements of yellowfin and bigeye tuna, highlighting their associations with seamounts and floating fish aggregation devices (FADs, Holland, Kleiber, & Kajiura, 1999).

Movement data from electronic telemetry can be utilised as part of fisheries stock assessments, by informing population spatial structure. Although this field of research remains at its infancy (for a review, see Sippel *et al.*, 2015), it is showing promise for MOFS in particular, due to advances in spatial assessment models (Hampton & Fournier, 2001; Hazen, Maxwell, & Bailey, 2012). Routinely small sample sizes mean the generality of the observed behaviours in the population can be unclear, but provide important information that is key for effective management, particularly with respect to habitat usage and residency. While there has been a number of studies that consider the minimum sample size required for population level inferences of air-breather such as birds and turtles (e.g Hawkes, Witt et al. 2011; Soanes, Arnould et al., 2013), we could find none which considered MOFS, making this an important topic for future research. A recent review of telemetry studies (Hussey, Kessel, *et al.*, 2015a) highlighted the importance of global telemetry consortia such as the Ocean Tracking Network (http://oceantrackingnetwork.org/), where data-sharing necessary for effective management and conservation can be encouraged. While the long-term consequences of tagging on fitness and survival remain unknown, great care is typically taken by scientists to minimise tagging mortality related to accidental gut-hooking or by-catch, through the use of circle-hooks and the minimisation of fishing gear soaking time (Hammerschlag *et al.*, 2011).

(2) Genetic and biochemical analyses

While conventionally associated with lethal sampling, molecular genetics and biochemical analyses are increasingly performed non-lethally on species of conservation concern using fin clips, tissue punches and blood samples (Cunjak *et al.*, 2005; Hanisch *et al.*, 2010). Although these methods may require the capture and physical handling of the animal, the molecular analysis of tissue samples can yield important information on population connectivity, structure, and abundance. For instance, despite decades of protection, the effective population size of white sharks in Australia is estimated to be ca. 1500 individuals based on mitochondrial microsatellite DNA (mtDNA) markers (one or two order below historical size estimates, Blower *et al.*, 2012). The study of Blower *et al* (2012) relied in part upon samples stemming from accidentally captured individuals by commercial and recreational fishers (63% of all samples) and was therefore not strictly speaking fisheries independent and non-extractive, but their analytical approach (mtDNA analysis) did not in itself require the killing of the animals. While mtDNA studies have demonstrated little genetic heterogeneity in yellowfin tuna across the Indo-Pacific Ocean (Appleyard *et al.*, 2001), further analysis around Sri Lanka have revealed very complex population structures on the meso-scale in the Indian Ocean (Dammannagoda, Hurwood, & Mather, 2008). These results suggest that low apparent heterogeneity between populations in the Western Indian Ocean (Seychelles) and in the Western Pacific (Taiwan, see Wu *et al.*, 2010) may mask fine population structures and connectivity barriers important for assessing recruitment levels and for spatial planning.

Stable isotope analysis can provide important information on trophic and functional ecology (Popp *et al.*, 2007) and, in the context of MOFS, may help identify dietary relationships and functional roles (Hussey, MacNeil, *et al.*, 2015b). For instance, niche partitioning has been identified between silky and blue sharks, with the former having a more substantial inshore dietary component to their diet. When movement and prey distribution data are available, Bayesian mixing models (Moore & Semmens, 2008) have been developed to elucidate the relative importance of different focal habitats for foraging behaviours. Such information is particularly important when assessing the residency of animals inside MPAs, and can be combined with telemetry information (Carlisle *et al.*, 2012). Moreover, change in dietary components can be assessed over time, thus providing sensitive means with which to detect trophic and functional shifts (Utne-Palm *et al.*, 2010).

(3) Active hydro-acoustics

Active hydro-acoustics such as sonars and echosounders are utilized in marine studies as fishery-independent monitoring tools. During hydroacoustic surveys, sound is emitted vertically at regular intervals (usually 1 s) and fish abundance is estimated by integrating the intensities of the returning echo, enabling abundances and distribution of target species to be assessed. Acoustic data are increasingly collected from ships of opportunity, and data access is further facilitated through publically available online databases, such as the Australian Integrated Marine Observing System's Bio-Acoustic Ship Of Opportunity Programme (IMOS, Ryan, 2011).

Historically, concerns were raised that fish would avoid acoustic survey vessels thereby resulting in biased biomass or abundance indices, however, a study using autonomous underwater vehicle fitted with echosounders observed that fish responses to both vessel and echosounder noise were minimal, and that hydroacoustics survey were therefore appropriate for non-extractive sampling (Fernandes *et al.*, 2000). Translating acoustic data into biomass indices requires knowledge of the acoustic properties of the focal animals, which are typically summarised by target strength models (Josse & Bertrand, 2000). In the presence of multiple species, these models can be used to identify a single species from the acoustic record and then scale acoustic data to biomass estimates (Bertrand, 2003). Acoustic target strength models have been obtained for commercially important, schooling MOFS such as yellowfin and bigeye tuna (Bertrand & Josse, 2000; Josse & Bertrand, 2000), and have facilitated estimation of school biomass. In some systems, this has further enabled estimates of total regional biomass, assuming the distribution and size of the target species is sufficiently known to inform survey design (Atkinson *et al.*, 2009).

In addition to provision of biomass indices, acoustic data can offer quantitative descriptions of density and aggregation characteristics (Fig. 4 and 5, Josse & Dagorn, 2000; Brierley & Cox, 2015). Both the fishing industry (Trenkel, Mazauric, & Berger, 2008) and scientists (see Chu, 2011 for a review) have utilized hydroacoustics to monitor MOFS populations, for example using sounders fitted on fish aggregation devices (FAD, Dagorn, Holland & Restrepo 2012. Since ground-truthing the acoustic signals is required when the exact nature of the target is unknown, acoustics surveys of MOFS have been conducted in tandem with scientific longline surveys or trawl catches (Bertrand & Josse, 2000), allowing for better interpretation of the resulting indices.

Because they lack swim bladders and are weak acoustic scatterers, elasmobranchs (and therefore oceanic sharks) remain poorly studied using hydroacoustics. *Ex situ* work to date has been limited to large species (> 5 m) such as the basking shark (*Cetorhinus maximus)* using specialty sounders like sector scanning sonars (Harden Jones, 1973) or more recently, multibeam imaging sonars (Lieber *et al.*, 2014). Parsons *et al.* (2014) demonstrated that multibeams like the Gemini 20i 300M (Tritech, UK) can be used in the detection of smaller elasmobranchs (1.4-2.7 m), particularly when the seafloor backscatter is low or absent, as is the case in the open ocean. This experimental field of research has therefore potential applications for the monitoring of oceanic sharks.

While enabling target species to be surveyed, echosounders also provide important insights into the distributions of prey fields (Irigoien *et al.*, 2014), which are themselves good predictors of predator habitat quality, providing spatial cues to predator foraging grounds (Boersch-Supan *et al.*, 2012). Yellowfin and bigeye tuna both feed on mesopelagic micronekton (Sabatié *et al.*, 2004; Flynn & Paxton, 2012), which are important components of shallow and deep scattering layers (Fig. 4). Many species of oceanic sharks, such as blue and mako sharks (*Isurus* spp.) feed directly on prey with well-known acoustic targets (such as clupeids). The identification of the distribution, intensity, and characteristics of scattering layers (and automation thereof, see Proud *et al.*, 2015) and the observation of fish schools provide strong clues to the distribution and presence of MOFS, and can further guide MPA designation.

(4) Baited remote underwater video systems

Baited remote underwater video systems (BRUVS) have been extensively used to document the structure of demersal fish assemblages, and more recently have been applied to MOFS in the mid-water (Letessier, Meeuwig, *et al.*, 2013b; Bouchet & Meeuwig, 2015). Impact on the target animals is minimal and requirement for bait is typically low (Hardinge *et al.*, 2013), making them attractive for non-extractive sampling in MPAs. Originally developed for *in situ* studies of deep-sea organisms (Isaac & Schwarzlose, 1975; Mallet & Pelletier, 2014), videos from BRUVS enable species identification and the computation of relative abundance metrics such as Max*N* (see Bailey, King, & Priede, 2007). Other important indices include time-of-first-arrival, which is a highly sensitive proxy for low abundance species such as some deep sea fish, and which has been successfully correlated with CPUE-derived abundance from demersal trawls (Priede & Merrett, 1996). Baited cameras are effective in sampling predators because of their preferential attraction to the bait (Langlois *et al.*, 2010) and their use is thus particularly relevant for monitoring MOFS. BRUVS can also be fitted with stereo cameras (Letessier *et al.*, 2015), allowing for body lengths to be measured with high precision using specialised computer software. These individual length estimates can in turn be used to determine demographic characteristics such as size structure (Mclean, Harvey, & Meeuwig, 2011; Langlois *et al.*, 2012) and therefore spawning stock biomass indices. The relatively low cost of novel stereo-camera technology (Letessier, Kawaguchi, *et al.*, 2013a) means that multiple units can be deployed simultaneously and repeatedly. In demersal systems, this has so far yielded sufficient power to detect temporal and spatial changes in coral trout (Mclean *et al.*, 2011) and population structure (Langlois *et al.*, 2012) of fish assemblages. Trials in pelagic environments indicate that, assuming adequate sampling regimes, stereo-BRUVS can provide information on the diversity, abundance and size structure of MOFS with similar power (Fig. 4 and 5, Letessier, Meeuwig, *et al.*, 2013b) and yield distribution models with predictive capacity (Bouchet & Meeuwig, 2015). Mid-water stereo-BRUVS may therefore be a promising avenue to investigate the spatial and temporal distribution of MOFS.

The capacity to determine spatial patterns in the pelagic zone has received little attention to date (Heagney *et al.*, 2007; Letessier, Meeuwig, *et al.*, 2013b) and several questions related to spatio-temporal trends and camera sampling catchment due to bait plume variability are largely unanswered (Bouchet & Meeuwig, 2015). Such questions form key targets to establish robust population indices appropriate for MOFS monitoring. A future avenue of research may arise from combining both stereo-BRUVS and hydroacoustic surveys, with the former providing the information required to inform the acoustic models (Fig. 4, 5, and 6), and the latter estimating the sampling range and catchment of the individual stereo-BRUVS. Indeed, mid-water BRUVS can provide observations of species diversity, relative abundance and population length structure, thereby enabling the parameterisation of acoustic target strength models and the estimation of total MOFS biomass at increased temporal and spatial resolution.

Non-extractive sampling methods exploring unknown aspects of MOFS ecology, such as those described here (Table 1), have direct benefits for both fishery management and conservation planning. By addressing temporal and spatial variability, these methods have refined catch-derived CPUE indices and stock assessments, and helped facilitate spatial management by identifying population connectivity, key spawning and nursery habitats, and by estimating effective breeding population size. However, while our review has provided an exhaustive list of such methodologies, we could identify no study employing these methods to unravel MOFS population trajectories through time. A single study reporting on MOFS trajectories obtained by non-extractive methods was published at the time of submission of this review (2015). It stemmed from a remarkable time series (1993-2013) resulting from a unique set of circumstances: pelagic shark observations made by dive masters conducting underwater visual census at an oceanic archipelago in a large-scale MPA (White *et al.*, 2015). This study demonstrated the power of citizen science when combined with the foresight of accurate, long-term record keeping. However, the exceptional circumstances required for the analysis mean that the study is unlikely to be replicated in other locations. Of the many species of sharks considered, the authors identified declines in the species considered most migratory (scalloped hammerheads and silky sharks) and further hypothesised that this was due to low residency of these species inside the MPA. As has previously been reported for demersal fish species in small-scale MPAs (McCook *et al.*, 2010) the response of MOFS to reduced fishery-dependent mortality in large-scale MPAs was identified as species-specific, with the greatest response to protection realised by those species subjected to highest fishing mortality and lowest rate of movement. Considering the overwhelming evidence for the benefits of MPAs in enhancing demersal and benthic species diversity and abundance (Lester, Halpern, & Grorud-Colvert, 2009; MacNeil *et al.*, 2015), methodologies establishing non-extractive baselines and subsequent time-series of MOFS population indices are an urgent requirement to study responses to different management regimes and for the informed and successful administration of an expanding global network of MPAs.

IV. FUTURE PROSPECTS FOR OCEANIC MONITORING

In the last decades, global MPA coverage has been expanded primarily by the contribution of a growing number of large-scale MPAs (Fig. 3). A subset of these can be classified as very large MPAs (Singleton & Roberts, 2014), which typically include the entire EEZ of remote islands, themselves often overseas territories of developed nations. Examples of these now include the Papahānaumokuākea Marine National Monument in 2006 (360,000 km^2), the Chagos/British Indian Ocean Territory in 2010 (640,000 km^2), and the Coral Sea Marine Reserve in 2012 (990,000 km^2), which forms part of the Australian Commonwealth marine reserve network (Devillers *et al.*, 2014). Seventeen VLMPAs are now in place, with many more likely to follow, such as those declared in New Caledonia, the Cook Island, and the Pitcairn Islands (Singleton & Roberts, 2014). Additionally, far-reaching MPA proposals have been put forward, including closing the entire high-seas to fishing (White & Costello, 2014; Sumaila *et al.*, 2015).

Common to all sampling methods that we identify (both extractive and non-extractive, Table 1) is that areal coverage scales relatively linearly with sampling effort. For example, fishery-dependent CPUE indices are scaled up by virtue of the great level of fishing effort reported globally. Telemetry tracking is limited by the behaviour of the tagged animals and number of tags (satellite tracking typically require surface swimming) but can be mitigated by intense effort and tagging of more individuals and species (Block *et al.*, 2011). Hydroacoustics surveys are limited by the speed at which high quality data are collected by the vessel but can be scaled up through more vessel time (Kloser *et al.*, 2009; Irigoien *et al.*, 2014). Therefore, while non-extractive methods are a necessary requirement for successful monitoring of MOFS, they will likely under-sample the ocean in time and space (Maclennan & Simmonds, 2005), particularly at the scale of VLMPAs, unless very intense effort can be mobilised.

Modelling proxies of MOFS distribution provide some means to predict areas of high usage and diversity, such as hotspots, in locations that are data poor and across distances requiring long survey times. Several studies have observed that MOFS aggregate in topographically complex areas (Morato *et al.*, 2008; 2010;

Bouchet *et al.*, 2014), and around frontal features with strong sea-surface height and temperature gradients (Worm *et al.*, 2005; Game *et al.*, 2009). These variables are considered good predictors of high quality, prey-rich feeding grounds (Alpine & Hobday, 2007) and areas of high MOFS residency (Humphries *et al.*, 2010). Remote environmental observations derived from satellite sensing as well as geomorphic (Yesson *et al.*, 2011; Bouchet *et al.*, 2014) or biological indices (such as seabird foraging events, Maxwell & Morgan, 2013) and long running plankton sampling programmes such as the continuous plankton survey (Letessier, Cox, & Brierley, 2009) all provide important yet indirect proxies of MOFS distribution and hotspots. Though they are unlikely to substitute monitoring and time-series containing direct observations, they are useful alternatives to real observations in data-poor environments.

While we identify data shortage as a challenge for non-extractive monitoring of MOFS spatial management, some emerging methods of observation have been devised specifically for use at the necessary scale (>100,000 km^2) and may therefore be promising for consideration as monitoring tools inside VLMPAs. Spotter planes have been used to conduct aerial surveys for identifying ocean life, because of their ability to cover large areas. Planes have to date been involved primarily in the observation of conspicuous wildlife that leave clear surface clues, such as marine mammals (Koski *et al.*, 2009). Monitoring programmes have in some cases relied on airborne visual surveys to elucidate associations between tunas and frontal features (and as so has the fishing industry, Lutcavage & Kraus, 1995; Eveson, Farley, & Bravington, 2011; Schick, Goldstein, & Lutcavage, 2004). While the requirements of person-hours may be high for manned aircraft, robotic and satellite technologies originally developed for remote military observations are increasingly employed in commercial and scientific settings, with the potential to substantially cut down on personnel time and costs. Example of such usage for observation of marine mammals includes unmanned aerial vehicles (such as drones, Hodgson, 2007) and very high resolution satellite imagery (VHRSI, Fretwell, Staniland, & Forcada, 2014). If drones and VHRSI were used for the identification of tuna schools at the surface, several avenues of research would thus become available, theoretically allowing aerial transects to be scaled up to the level of an ocean basin.

Aerial and remote satellite observation techniques are necessarily limited to animals that are visible at the surface, and provide little information on deeper-living species and greater depth horizons. Toward this purpose, autonomous underwater and ocean gliders (Leonard *et al.*, 2010) are increasingly being utilised for long-term (>1 year) environmental monitoring of temperature, salinity, chlorophyll fluorescence and currents. Gliders have recently been fitted with both passive and active acoustics sensors (Send, Regier, & Jones, 2013), with applications toward the assessment of free-ranging MOFS (Bingham *et al.*, 2012). Gliders are slow-moving by design, and thus face similar limitations with respect to scale compared with traditional sampling methods. However, they can be operated remotely and at depth, and often for long periods of time (up to 4-5 years), making them attractive in remote and hard-to-access VLMPAs.

The novel use of 'horizontal' hydro-acoustics arrays, or Ocean Acoustics Waveguide Remote Sensing (OAWRS, Makris *et al.*, 2006) has also enabled instantaneous mapping of fish schools and their behaviour over thousands of km^2. The OAWRS can resolve fish schools at the order of tens of meters in range and 1° in bearing and studies have so far been focused on clupeid fish with very well known acoustic properties, in environments where water column stratification enables the ocean to function as an acoustic waveguide (such as on continental shelves, Makris *et al.*, 2006; 2009). The OAWRS is theoretically capable of observing a variety of animals, such as Antarctic krill (*Euphausia superba*) or Alaskan pollock (*Theragra chalcogramma*), in other habitats such as seamounts (Makris, Jagannathan, & Ignisca, 2010), as long as certain key parameters like typical population density, average target strengths, and seafloor scattering are known (see Jagannathan *et al.*, 2009 for a review). The array could therefore be utilised for the instantaneous mapping of tuna schools, allowing insights into the animals' migration patterns and habitat use over seasonal cycles. Using acoustic parameters from Atlantic bluefin tuna, Jagannathan *et al.* (2009) determined that OAWRS would be able to detect tuna densities ranging from 0.25 to 3 x 10^{-6} m^{-2}. Moreover, Jagannathan *et al.* (2009)

observed a school of fish with swimming speed and behaviour consistent with that of tuna, and estimated densities of the school at 5 x 10^{-4} m^{-2}. This school was spotted during instantaneous acoustic imagining of 8000 km^2, suggesting a potential of OAWRS in MOFS monitoring in VLMPAs. Monitoring regimes of large-scale areas such as those sampled by OAWRS and aerial surveys are simplified by reports that average school size distribution appears independent of total regional biomass (Brierley & Cox, 2015). Using a combination of multibeam sonars and traditional echosounders, Brierley & Cox (2015) reported consistent school size for krill and pelagic fish across increasing regional biomass. This has substantial implication for monitoring: a sufficiently robust abundance index may be reached by simply counting the numbers of school across the desired area.

Increased VLMPA implementation has received criticism for a variety of reasons (for a review of the arguments, see Singleton & Roberts, 2014), but their popularity is bolstered by suggestions that bigger closures, such as closing the high seas to fishing, may increase yield and profits (White & Costello, 2014), reduce income inequality between fishing nations (Sumaila *et al.*, 2015), and offer rebuilding potential for MOFS (Armsworth *et al.*, 2010). There is currently considerable debate and controversy surrounding the best course of action. For example, a modelling study exploring constant effort scenarios in response to MPA closure suggested that high seas MPAs will result in very little tangible effects on bigeye tuna populations in the Western Pacific (Sibert *et al.*, 2012), whereas another study suggested substantial species-specific responses in catches of both tunas and oceanic sharks in the North Atlantic and Gulf of Mexico (Baum *et al.*, 2003). These studies and those of White *et al.* (2014) or Sumaila *et al.* (2015) typically rely on spatial models of fleet behaviour or ecosystem models (such as SEAPODYM, Lehodey, Senina, & Murtugudde, 2009) to predict the responses of MOFS populations to different high seas management regimes, thus forming an integral part in highlighting the consequences of fisheries closures. However, in the absence of empirical evidence, the provision of which may well stem from methods outlined in this review, the benefits of MPAs to

MOFS will remain uncertain and the paradigm of the large marine reserve unresolved.

V. CONCLUSION

1) Top-down forcing by apex predators is increasingly recognised as a fundamental process of ecological change in nature (Estes *et al.*, 2011), on land as well as in the sea. There is now a growing body of evidence that stable and abundant populations of apex predators serve to promote diversity in meso-predators and herbivores and that their removal may provoke trophic cascades (Myers *et al.*, 2007; Baum & Worm, 2009; Ferretti *et al.*, 2010) with consequence for ecosystem function (D'agata *et al.*, 2014), and resilience (Llope *et al.*, 2011). Complex trophic structure in MOFS (Hussey, MacNeil, *et al.*, 2015b) leaves these mechanisms poorly understood and difficult to predict, but their implications are likely severe given the low functional redundancy in marine apex predators (Heithaus *et al.*, 2013).

2) Due to their conservative life-history characteristics, and transnational distributions, MOFS are particularly prone to over-fishing (Collette *et al.*, 2011; Davidson, Krawchuk, & Dulvy, 2015; Juan-Jorda *et al.*, 2015). Their ecological and conservation status is further complicated by their wide-ranging nature, clumped distributions, and migratory behaviour, which delay and challenge their effective management on the high seas and across jurisdictional boundaries. There is therefore a critical need to understand MOFS population trajectories, particularly for sharks and billfish, whose current status is generally less well known than that of tunas.

3) Improvements in catch record-keeping and fleet supervision are leading to a greater understanding of spatio-temporal patterns, superior abundance indices and stock assessments for RFMO-based management strategies. However, fundamental limitations in data quality related to sampling biases, fishery practises, and gear use leave several aspects of MOFS ecology understudied. The advent of fisheries-independent sampling regimes in conjunction with advances in fisheries-dependent modelling techniques has enabled the predictions of MOFS distribution (Morato *et al.*, 2010; Bouchet *et al.*,

2014) and that of their prey (Letessier *et al.*, 2009), providing scientific rationale for spatial planning and the designation of pelagic MPAs.

4) The review of Murphy & Jenkins (2010) concerning monitoring demersal species and habitats highlight numerous methodologies that are available for determining the efficiency of coastal MPAs. In contrast, we find that methods available for determining MOFS conservation outcomes inside pelagic MPAs are lacking, primarily owing to a dearth of non-extractive monitoring techniques. However, the general recommendation of Murphy & Jenkins (2010) of a multifaceted approach to monitoring and ecological study still applies to the mid-water realm and to the predators that reside there. Motivated by this incentive we recommend that MOFS populations potentially benefitted by MPAs be monitored using a combination of mid-water stereo-BRUVS, hydro-acoustics, and telemetry. Mid-water BRUVS and acoustic surveys run in tandem would enable the tracking of MOFS biomass and abundance, and important aspects surrounding MOFS residency patterns and connectivity between populations inside and outside the reserves can be explored through the use of satellite telemetry and genetic analysis.

5) The expanding global MPA network is bolstered primarily by the disproportionally high contribution of large and very large MPAs (>10,000 km^2 and >100,000 km^2). Several techniques show promise for monitoring at the necessary scales such as horizontal acoustics and satellite imagery analysis, yet the elusive nature of MOFS behaviour and the spatio-temporal dimensions of their ecology will likely necessitate further technological innovation. Mapping of MOFS status and distribution required for assessment of spatial management regimes of the high seas and VLMPAs will remain sporadic and at the experimental level until such technological advances are forthcoming, or until extremely high survey efforts of non-extractive sampling can be mobilised.

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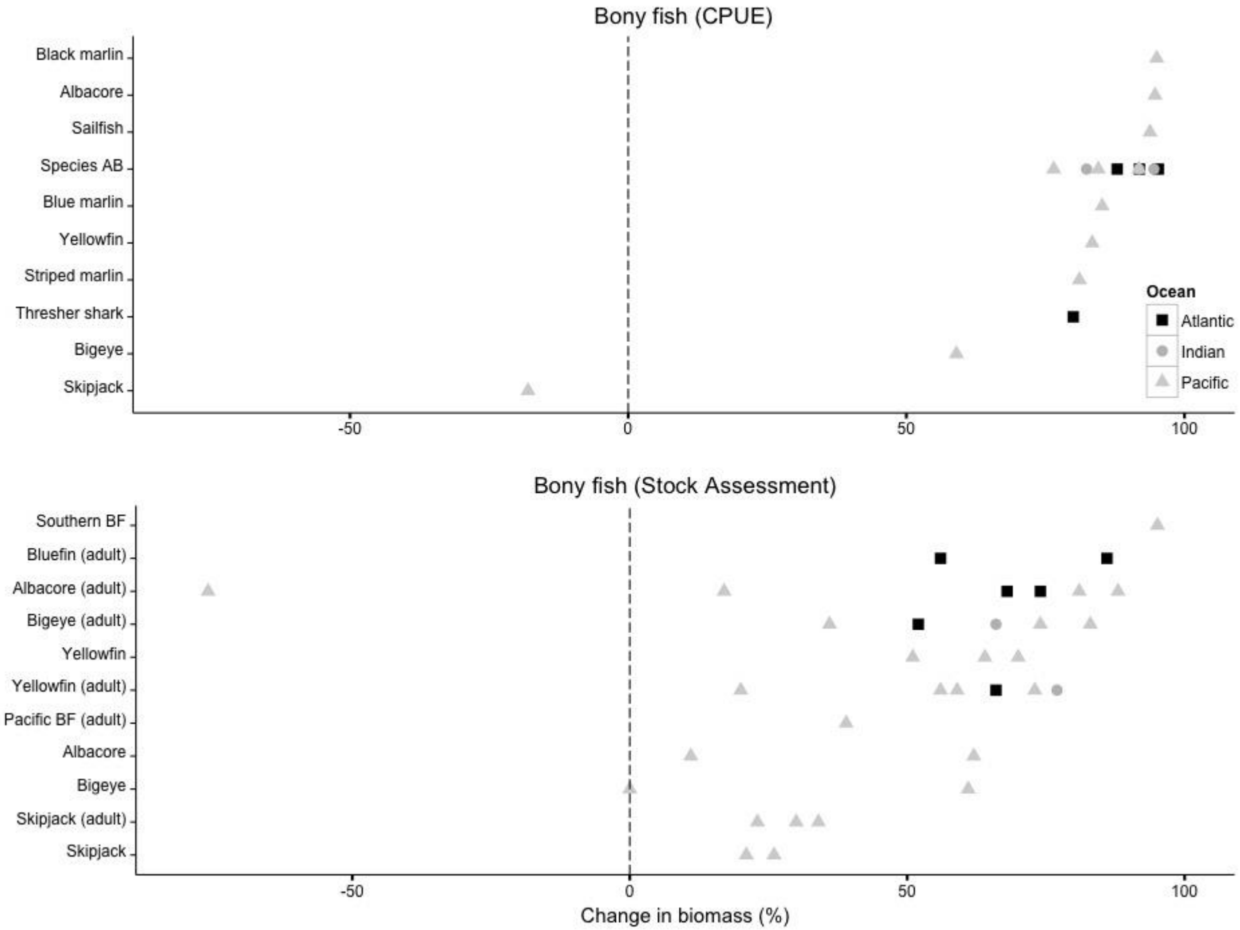
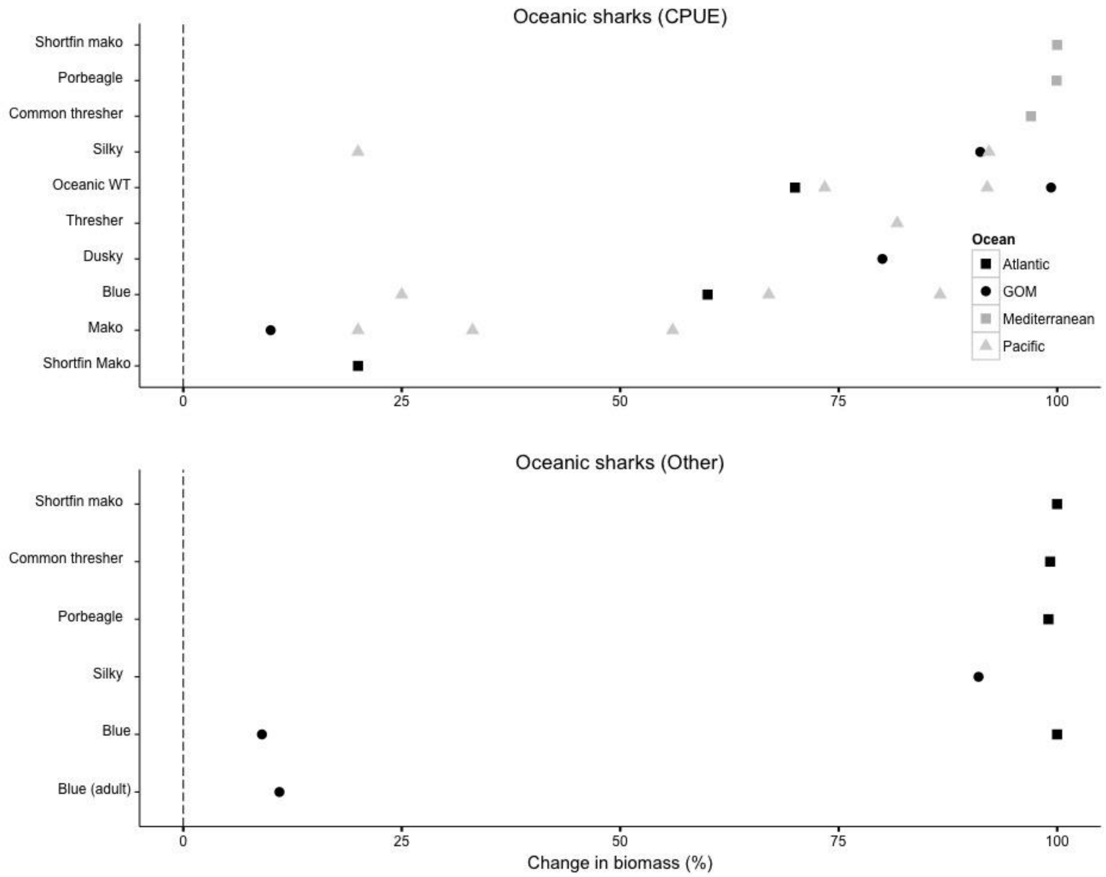


Fig 1. Declines in tuna and billfish reported by CPUE and stock assessment in the literature over the last 12 years globally, in order of declining median (See supplementary material for data and sources). Abbreviation for species and ocean names: BF, Bluefin; AB, aggregated assemblage biomass; WT, Whitetip; GOM, Gulf of Mexico. For sources see (Myers & Worm, 2003; Baum & Myers, 2004; Ward & Myers, 2005; Hampton *et al.*, 2005; Sibert *et al.*, 2006; Juan-Jordá *et al.*, 2011).



Oceanic sharks (CPUE)

Oceanic sharks (Other)

Fig 2. Declines in oceanic sharks reported by CPUE and other means in the literature over the last 12 years globally, in order of declining median (See supplementary material for data and sources). Abbreviation for species and ocean names: WT, Whitetip; GOM, Gulf of Mexico. For sources see Baum *et al.* (2003), Ward & Myers (2005), Sibert *et al.* (2006) Ferretti *et al.* (2008), Clarke *et al.* (2013), White *et al.* (2015).

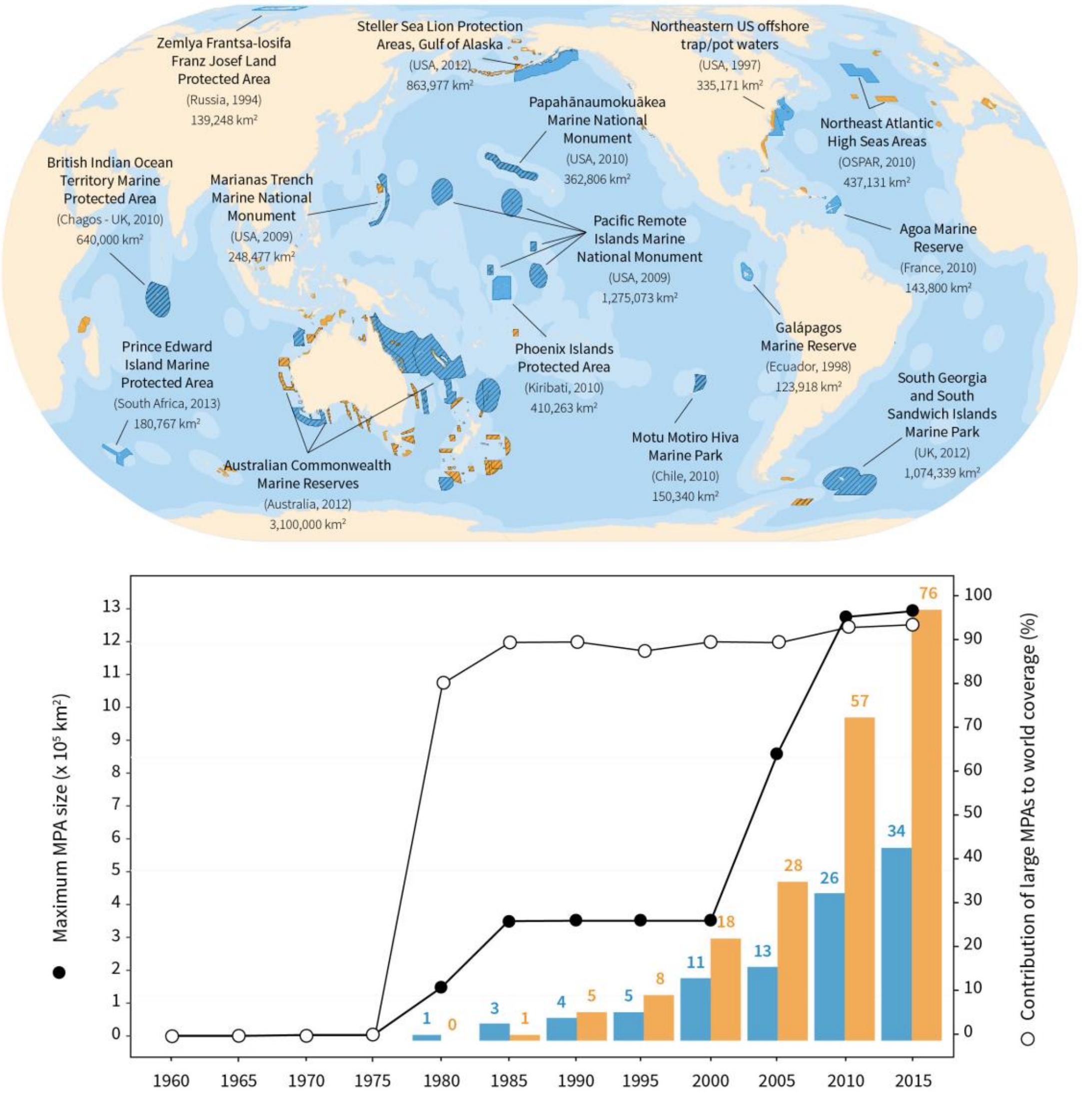


Fig 3. Historical trends in global marine protected area (MPA) coverage. The top panel is adapted from Maxwell, Ban & Morgan (2014) and shows the geographic distribution of large (>= 10,000 km^2, in orange) and very large MPAs (>=100,000 km^2, in blue). Stripe fills denote areas that are partially or entirely no-take (where all extractive activities are prohibited). The bottom panel displays the cumulative number of large and very large MPAs, using the same colour coding. Also shown are trends in maximum MPA size, and percentage contribution to worldwide coverage (data obtained from IUCN-UNEP, 2015).

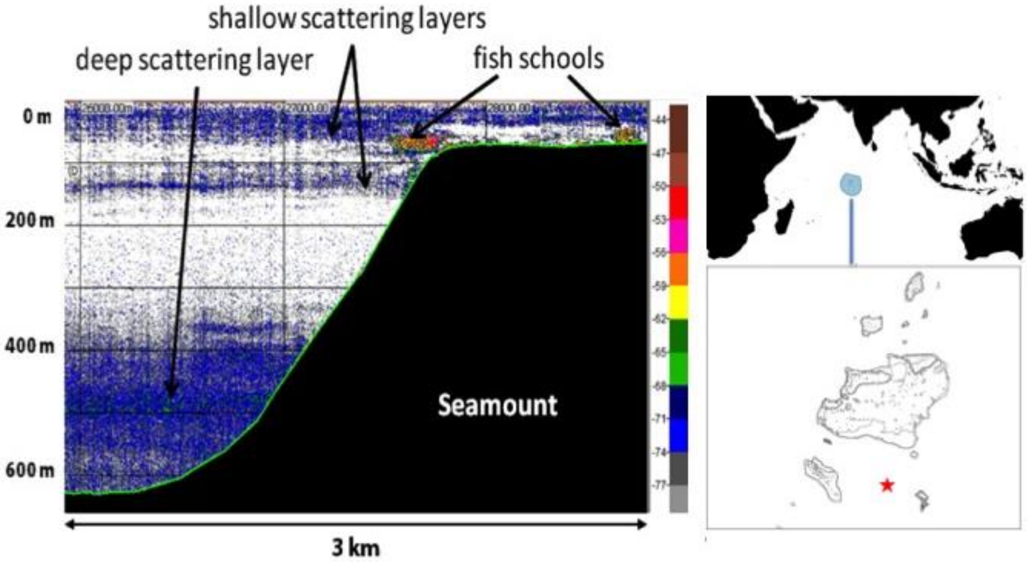


Fig 4. Non-lethal and non-extractive sampling of MOFS using hydro-acoustics inside the Chagos Marine Reserve. A calibrated split-beam echosounder (Simrad EK60, Kongsberg Maritime AS, Horten, Norway) was deployed from a rigid hulled inflatable boat using an overside mount (deployment depth = 1 m) to investigate prey field and fish schools across a shallow seamount (denoted by a red star in the inset map). The operating frequency was 38 kHz with a ping interval of 4 s, and with a pulse duration of 1.024 ms and a beam width of 12°. Colour scale on the echogram is in dB. Image courtesy of Dr Martin Cox, and Dr Phillip Boersch-Supan).

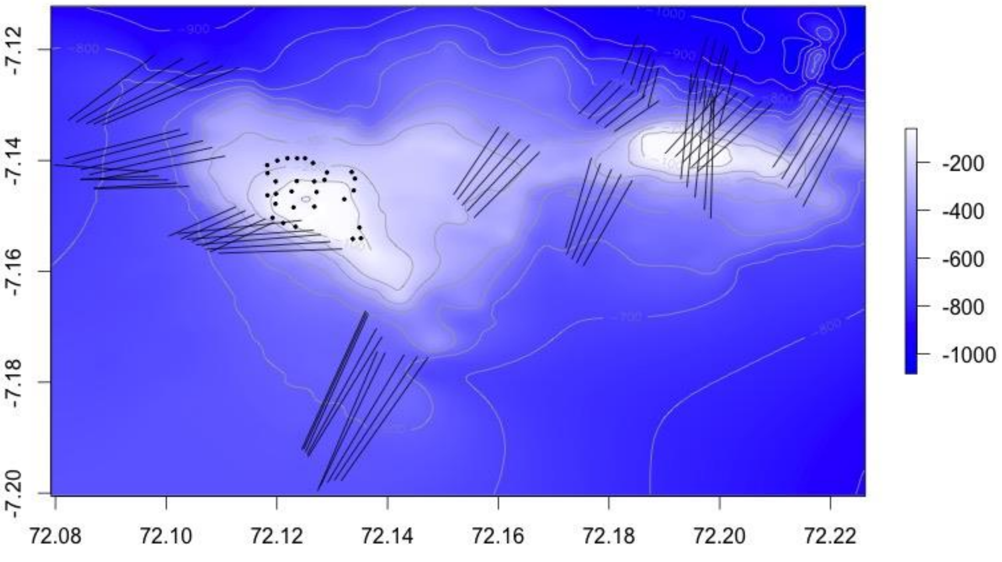


Fig 5. Two approaches to the non-extractive sampling of MOFS using mid-water BRUVS, over the seamount represented in Fig. 4. Dots represent individual mid-water BRUVS moored to the seabed using an anchor as per Letessier *et al.* (2013). Lines represent individual drifting mid-water cameras as per Bouchet & Meeuwig (2015). Two longlines of 5 mid-water BRUVS were deployed simultaneously, 200 meters apart and suspended at 10 m, and were allowed to drift freely for 2 hrs.

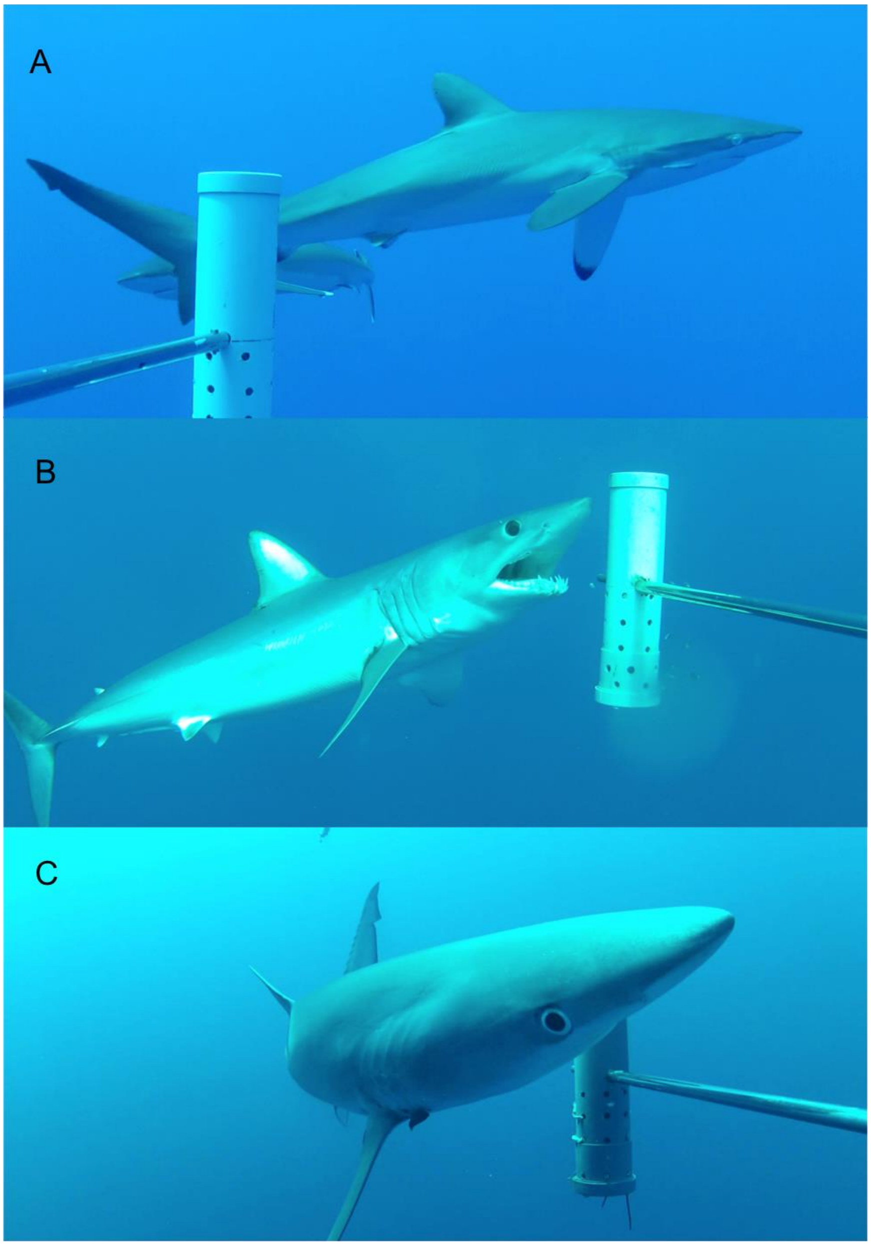


Fig 6. MOFS observed on mid-water BRUVS. The silky shark (*Carcharinus falciformis*, A), and shortfin mako shark (*Isurus oxyrinchus,* B) were observed in the Chagos Marine Reserve (7.12°S, 72.11°E) on deployments conducted simultaneously to the hydroacoustics survey described in Fig. 2. The blue shark (*Prionace glauca*, C) was observed in Western Australia (32°S, 115°E).

Table 1. Methodologies available for assessing MOFS population status, practical benefits and shortcomings, and implication for managerial regimes

Source of data	Emerging or in-use in the MOFS context	Information derived	Benefits	Shortcomings	Non-extractive	Example study and implication for MOFS management and conservation
Active Hydro-acoustics	In-use	Biomass, density, prey fields, schooling behaviour	Method is of relative low cost in consideration of volume of water sampled.	Provide limited information in the absence of independent ground-truthing. Biased toward species with well understood acoustic properties	✓	Monitoring and population assessment (Josse, Bertrand, & Dagorn, 1999). Schooling behaviour (Josse & Dagorn, 2000)
Mid-water BRUVS	In-use	Habitat association, relative abundance and biomass	Relatively low cost, easy to standardize and deploy and generate large data sets.	Does not, in it self, capture the migratory aspect of MOFS.	✓	Monitoring of MPA efficiency. Oceanographic characteristics are important for MPA zoning (Heagney *et al.*, 2007; Letessier, Meeuwig, *et al.*, 2013b; Bouchet & Meeuwig, 2015)
Catch-per-unit effort from commercial and scientific survey catch statistic	In-use	Long term abundance patterns, population structure.	Most spatially and temporally extend data set currently available	High sampling and reporting bias. Most long term and spatially extent data set available		Long term assessment of abundance (Myers & Worm, 2003) (Baum & Myers, 2004)

				are of variable quality.		
Stock assessment	In-use	Population status	Reliable	High data requirements, which are absent for many stocks		Long term and reliable assessment of abundance (Sibert *et al.*, 2006; Juan-Jordá *et al.*, 2011)
Satellite Telemetry	In-use	Habitat association, horizontal range. Ontogenic migration, distribution, behaviour, energetics	Long distance tracking, suited to migratory species	Satellite tagging is labour intensive and tags are expensive	✓	Identification of area suitable for fishery closure (Alpine & Hobday, 2007; Block *et al.*, 2011)
Acoustic Telemetry	In-use	Habitat association, homing range, behaviour	Provide high-resolution data on movement and residency patterns.	Labour intensive to deploy acoustic recorders, and to catch and perform invasive surgery.	✓	Determination of fishing practise (Girard, Benhamou, & Dagorn, 2004), provision of spatial assessment models (Hampton & Fournier, 2001)
Archival tags	In-use	Habitat association, behaviour, ontogenic changes	Low cost to recover data. High resolution data collected for several years	Labour intensive		Assessment of fishery practices, stock assessment (Block *et al.*, 2005)
Molecular genetics	In-use	Relatedness	Relatively low cost, only way to assert genetic relations	Difficult to get tissue samples from rare species	✓	IOTC recognising multiple yellowfin tuna population in the Indian Ocean (Dammannagoda *et al.*, 2008). Assessment of spill-

						over effect (Harrison *et al.*, 2012).
Stable isotopes	In-use	Trophology	Only non-lethal way of investigating diet	Labour intensive to collect samples		Identification of feeding habitats valuable for MPA protection of great white sharks (Carlisle *et al.*, 2012)
Aerial surveys/Spotter plane	In-use	Biomass/abundance index	Ability to cover large areas of VLMPAs	Linking visual cues with true abundance is still at its infancy	✓	Monitoring of MOFS population abundance (Eveson *et al.*, 2011)
Aerial surveys/Drones	Emerging	Biomass/abundance index	Ability to cover large areas of VLMPAs	Linking visual cues with true abundance is still at its infancy	✓	Monitoring of MOFS population abundance and distribution (Hodgson, 2007)
Ocean/Underwater Gliders (fitted with echosounders)	Emerging	Biomass/abundance measurement	Ability to cover remote areas of VLMPAs	Provide limited information in the absence of independent ground-truthing. Biased toward species with strong and well understood acoustic properties	✓	Monitoring of MOFS population (Send *et al.*, 2013)
Horizontal	Emerging	Biomass/abundance	Ability to	Very high power	✓	Behavioural mechanics and

Acoustics OAWRS	measurement	instantaneously visuals large areas (thousands of km^2)	requirements. Need for very specific oceanographic conditions.	population monitoring (Makris *et al.*, 2009)

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