

Impacts of fisheries bycatch on marine turtle populations worldwide: toward conservation and research priorities

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Abstract. Fisheries bycatch is considered the most serious threat globally to long-lived marine megafauna (e.g., mammals, birds, turtles, elasmobranchs). However, bycatch assessments to date have not evaluated population-level bycatch impacts across fishing gears. Here, we provide the first global, multi-gear evaluation of population-level fisheries bycatch impacts for marine turtles. To compare bycatch impacts of multiple gears within and among marine turtle populations (or regional management units, RMUs), we compiled more than 1,800 records from over 230 sources of reported marine turtle bycatch in longline, net, and trawl fisheries worldwide that were published between 1990–2011. The highest bycatch rates and levels of observed effort for each gear category occurred in the East Pacific, Northwest and Southwest Atlantic, and Mediterranean regions, which were also the regions of highest data availability. Overall, available data were dominated by longline records (nearly 60% of all records), and were non-uniformly distributed, with significant data gaps around Africa, in the Indian Ocean, and Southeast Asia. We found that bycatch impact scores—which integrate information on bycatch rates, fishing effort, mortality rates, and body sizes (i.e., proxies for reproductive values) of turtles taken as bycatch—as well as mortality rates in particular, were significantly lower in longline fishing gear than in net and trawl fishing gears. Based on bycatch impact scores and RMU-specific population metrics, we identified the RMUs most and least threatened by bycatch globally, and found wide variation among species, regions, and gears within these classifications. The lack of regional or species-specific patterns in bycatch impacts across fishing gears suggests that gear types and RMUs in which bycatch has the highest impact depend on spatially-explicit overlaps of fisheries (e.g., gear characteristics, fishing practices, target species), marine turtle populations (e.g., conservation status, aggregation areas), and underlying habitat features (e.g., oceanographic conditions). Our study provides a blueprint both for prioritizing limited conservation resources toward managing fishing gears and practices with the highest population impacts on sea turtles and for enhancing data collection and reporting efforts.

Key words: bycatch rates; distinct population segments; fisheries bycatch; fisheries mortality; longlines; marine megafauna; marine turtle; nets; regional management units; stock assessment; trawls.

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INTRODUCTION

Minimizing bycatch, or the unintended capture of non-target organisms during fisheries operations (Hall et al. 2000, Soykan et al. 2008), is a key component of sustainable fisheries management that maintains marine biodiversity (Veitch et al. 2012). Fisheries bycatch is recognized as perhaps the most serious global threat to highly migratory, long-lived marine taxa including turtles (Wallace et al. 2010a, 2011), birds (Croxall et al. 2012, Lewison et al. 2012), mammals (Read et al. 2006), and sharks (Dulvy et al. 2008). Marine megafauna species are susceptible to fisheries bycatch because they occupy broad geographic distributions across geopolitical boundaries and oceanographic regions that support both small- and large-scale fisheries, and because their life histories (e.g., delayed maturity, low reproductive rates) make them particularly sensitive to sources of mortality that affect late life stages (Crouse et al. 1987, Heppell et al. 2005). The nature and frequency of megafauna bycatch interactions depend on several factors, including fishing methods and gear characteristics (Lewison et al. 2009, Wallace et al. 2008, 2010a), species' life history and ecology (Žydelis et al. 2009; Lewison et al., *in press*), and spatio-temporal overlaps between fishing activities and critical habitat for given species (Peckham et al. 2007, Žydelis et al. 2011).

Marine megafauna bycatch research has increased exponentially in recent years (Soykan et al. 2008), highlighting cases of particularly acute bycatch problems (e.g., Peckham et al. 2007, Alfaro-Shigueto et al. 2011), the relative magnitude of bycatch at broad scales (e.g., Lewison et al. 2004a, b, 2005, Read et al. 2006, Casale 2010, Wallace et al. 2010a), and the need for development and implementation of bycatch reduction strategies (Cox et al. 2007, FAO Fisheries Department 2009, Gilman et al. 2009). Various types of information are necessary to characterize bycatch patterns and to understand population impacts on taxa affected by bycatch, including bycatch rates, amounts of fishing effort on which these

rates were based, rates of mortality associated with bycatch interactions, among others. However, several traits of bycatch data make comprehensive evaluations of bycatch patterns and impacts particularly challenging (for review, see Lewison et al., *in press*). First, direct observation of bycatch during normal operations—if it exists at all—typically accounts for only <5% of total fishing effort in a particular fishery (Wallace et al. 2010a, Finkbeiner et al. 2011), and rarely occurs in small-scale fisheries, thus underrepresenting the true magnitude of bycatches. Second, reported bycatch rates are highly variable within and among gears and regions (e.g., Lewison and Crowder 2007, Wallace et al. 2010a). Third, bycatch is a rare event relative to overall fishing effort, and the amount of effort observed, analogous to survey effort, can affect observed bycatch rates; high or low bycatch rates are often reported where fishing effort is relatively low, illustrating potential biases in estimates of bycatch rates based on relatively low levels of observed fishing effort (Sims et al. 2008, Wallace et al. 2010a). Finally, bycatch studies typically focus on specific areas, time periods, and gear types, thus limiting their generality (Lewison et al. 2009), or are global-scale assessments of megafauna bycatch that are unable to describe fine-scale patterns to guide effective bycatch management at local scales (e.g., Wallace et al. 2010a).

Beyond availability of bycatch data, information on the current status of the affected population(s) is crucial to characterizing demographic impacts of bycatch. However, population characteristics of widely distributed marine species can vary significantly across geographic regions (Suryan et al. 2009). Because impacts of fisheries bycatch—and other threats—also vary in space and time, and individual populations can interact with multiple fisheries across their range, bycatch impacts must be assessed at appropriate population scales, taking into account all fisheries in which bycatch occurs (Wallace et al. 2008; Lewison et al., *in press*). Specifically, a stock assessment-type approach to

evaluating cumulative and relative impacts of bycatch in multiple fishing gears on marine megafauna populations is necessary to sustainably manage fisheries bycatch of these species (Taylor 2005, Moore et al. 2009, Finkbeiner et al. 2011).

Marine turtles are impacted by bycatch and are species of conservation concern; six of seven marine turtle species are currently considered “Threatened” according to the IUCN Red List of Threatened Species (www.iucnredlist.org; accessed 26 July 2012). However, unlike marine mammals, resolving stocks or population units appropriate for status assessments has been elusive until recently. To provide a framework of spatially explicit, intra-specific population segments—analogue to distinct population segments (DPSs) defined for other species (Taylor 2005)—Wallace et al. (2010b) used multi-scale biogeography data, including all known nesting locations and in-water distribution data, that reflected population connectivity among demographic classes to define regional management units (RMUs) for all marine turtle species. A subsequent assessment of the conservation status of marine turtle RMUs evaluated the risk level of each RMU based on a range of population parameters (e.g., population size, recent and long-term population trends, rookery distribution and vulnerability, genetic diversity) and the degree of threats impacting each RMU (Wallace et al. 2011). This analysis underscored wide inter- and intra-specific variation in population risk and degree of threats, and highlighted fisheries bycatch as the most pervasive and serious threat to marine turtles globally.

In this study, we compiled a comprehensive database of reported data on marine turtle bycatch in multiple fishing gear categories worldwide from 1990–2011. Building on the RMU delineations and status assessments (Wallace et al. 2010b, 2011), our goals were to (1) describe fisheries bycatch data across fishing gears and RMUs at a global scale; (2) assess bycatch impacts across gears and among RMUs, and (3) to identify RMU-gear combinations where conservation action and/or enhanced monitoring and research is necessary. Results from this study, based on the best information available, can facilitate prioritization of conservation efforts to reduce bycatch in areas where

fisheries bycatch is likely to be having the largest impact on marine turtle populations.

METHODS

Data compilation, standardizations, and conversions

We updated an existing database of reported sea turtle bycatch globally from peer-reviewed publications, agency and technical reports, and symposia proceedings published between 1990 and 2008 (see Wallace et al. 2010a for a description; complete reference list in Appendix A) by adding records from reports that had been published between 2008 and mid-2011. We summarized only observed, reported information; we did not calculate our own estimates or extrapolations, nor did we include reported estimates or extrapolations from reviewed studies. Reported bycatch data represent bycatch information from direct observation, termed observer data, as well as from interviews with fishers (~15% of all records). It was not possible to calculate the proportion of global fishing effort represented, nor to describe temporal or spatial trends in marine turtle bycatch, as the available information was restricted spatially and temporally, and thus only represented snapshots of fishing activities and bycatch that occurred in recent decades. Furthermore, we did not weight records differently within fisheries and/or regions according to changes over time in fishing practices and/or gear configurations. Our overarching goal was to assess bycatch impacts on marine turtle populations during the most recent marine turtle generation, i.e., approximately the past 20 years; such impacts occurred regardless of changes in bycatch rates, fishing practices, or gear characteristics within fisheries.

For each study, we recorded information on the time period when and geographic region where reported bycatch occurred, species reported as bycatch, bycatch rate (bycatch per unit effort; BPUE), the metric in which BPUE was reported, observed fishing effort, the metric in which observed fishing effort was reported, and observed incidents of mortality or mortality rates. In addition, we compiled reported body sizes of turtles taken as bycatch and assigned each record to either a small (juvenile) or large (subadult or adult) category to use this variable as a proxy for reproductive value, which de-

scribes the relatively higher value of larger/older turtles than smaller/younger turtles to a population (Crouse et al. 1987, Heppell et al. 2005, Wallace et al. 2008). We based our categorization scheme on the average sizes of turtles reported in each record relative to species-specific size-at-maturity data from the literature, such that the division between small and large categories roughly coincided with the separations between small juvenile and large juvenile/sub-adult size classes reported for different sea turtle species (see Wallace et al. 2010a for definitions of size categories). Roughly 20% of records presented information on body sizes or demographic classes of turtles taken as bycatch. Although we use the term “reproductive value” in this paper to describe our proxy metric based simply on body sizes of bycaught turtles, we recognize that these are not true reproductive values derived from population models (e.g., Wallace et al. 2008).

Following Wallace et al. (2010a), bycatch data were first grouped in three general fishing gear categories—longlines, nets, and trawls—recognized by the FAO as major fishing gear categories (described as hooks and lines, gillnets and entangling nets, and trawl nets, respectively; <http://www.fao.org/fishery/topic/1617/en>). Despite the broad nature of these gear categories, this classification scheme allowed us to draw general conclusions over two decades, hundreds of studies, and multiple spatial scales, balancing relevant variation and details with a common denominator approach. To identify impacts of particular gears within these broad categories, we recorded subgear types for each record when the original study provided sufficient information to allow for such categorization. Longlines were divided into pelagic longlines, surface or drifting longlines, bottom-set longlines, or “other” longlines. Nets were divided into bottom-set nets, fixed nets (i.e., pound nets, trammels), drift nets, or “other” nets. Trawls were divided into shrimp trawls, bottom trawls, midwater trawls (although this category was later eliminated due to extremely low number of records), or “other” trawls. The “other” category was created for each subgear type to include records in which insufficient information was provided to assign the record to a particular subgear type.

To account for the fact that a single study could

report multiple bycatch rates (i.e., for each species taken as bycatch, for each year bycatch was observed), we entered each as a separate record. Thus, we present the number of records, rather than number of studies, to describe the amount of reported bycatch information. Number of records, in the present case, is analogous to a sample size, and thus can be thought of as a measure of reliability in variables recorded and analyzed throughout the paper. Our database included a total of 239 studies that yielded 1,874 records of marine turtle bycatch between 1990–2011. Numbers of records varied among sea turtle species, from 39 for the Kemp’s ridley (*Lepidochelys kempii*) to 771 records for loggerheads (*Caretta caretta*) (Table 1).

High variability in terminology and definitions of metrics among reported bycatch records, which reflected the overall lack of standardized reporting methods across fisheries and regions, required us to convert all fishing effort metrics into standardized “sets” (Wallace et al. 2010a). This conversion within each of the three main gear categories allowed us to compare bycatch rates within and among regions. We chose the “set” because it was the most commonly reported unit of observed fishing effort across the three gear categories and thus was the appropriate unit to permit straightforward evaluation of the amount of marine turtle bycatch per typical operation; i.e., when gear goes into and then is removed from the water. We defined “set” as 1,000 hooks for longlines, a net deployment for nets, and a trawl haul for trawls. Despite the high variation in fishing gear characteristics within major fishing gears, this standardization allowed us to compare bycatch rates and relative amounts of gear observed and to explore patterns in bycatch across regions and gears. Many records were excluded (15–20%) when they lacked necessary information (i.e., no BPUE or effort reported) for certain analyses, or because we were unable to convert units.

Evaluating bycatch impacts by fishing gears among RMUs

To assess population-level impacts of bycatch, we attributed each record in the database to marine turtle RMUs (as defined by Wallace et al. 2010b; polygons available for download and review at <http://seamap.env.duke.edu/swot>)

Table 1. Number of bycatch records per sea turtle species.

Species	No. records	No. records, including unidentified†
Loggerhead, <i>Caretta caretta</i>	374	771
Green turtle, <i>Chelonia mydas</i>	148	484
Leatherback, <i>Dermochelys coriacea</i>	239	239
Hawksbill, <i>Eretmochelys imbricata</i>	41	335
Kemp's ridley, <i>Lepidochelys kempii</i>	27	39
Olive ridley, <i>Lepidochelys olivacea</i>	159	388
Flatback, <i>Natator depressus</i>	2	55

† Records in which the species of marine turtle reported as bycatch was not identified; these records were attributed to the RMU(s) in which these records fell or to the RMU(s) in closest proximity.

based on the reported or inferred geographic location of the observed bycatch record relative to RMU boundaries. In cases where turtles taken as bycatch in a particular study had not been identified to species, we attributed the record to each RMU within which the record fell or to the nearest RMU(s) if a record did not fall within any RMU boundaries (Table 1). We did not assign unidentified species records to leatherback (*Dermochelys coriacea*) RMUs, as misidentification of leatherbacks is extremely unlikely. All bycatch records in our database were therefore attributed to at least one RMU, allowing for subsequent data compilations and analyses.

Following Wallace et al. (2010a), we computed summary statistics for BPUEs and observed effort for each RMU-gear combination using the standardized BPUE values and reported fishing effort values. To limit potential bias from BPUEs reported from low observed effort (Sims et al. 2008), we also calculated a weighed median BPUE for each RMU-gear combination, and then across RMUs within each fishing gear and subgear category. We computed weighted median BPUEs by (1) calculating the proportion of fishing effort observed in each record relative to the total amount of effort observed for that RMU-gear combination, (2) then multiplying the standardized BPUE value (i.e., individual turtles per set) by this proportion of effort to obtain a weighted BPUE (i.e., the BPUE weighted by the relative amount of effort associated with it), and (3) dividing the median of these weighted BPUEs by the median of the effort proportion values. Thus, weighted median BPUEs accounted for the relative effort observed in each record, as well as the overall effort observed for each RMU-gear combination.

To adequately assess population impacts of bycatch, once bycatch rates were associated with

the appropriate RMU-gear combinations and weighted as described above, additional information about fishing effort, mortality rates, and reproductive values of turtles caught was also necessary (Casale 2010; Lewison et al., *in press*). Therefore, we assessed weighted median BPUEs, mortality rates (not including post-release mortality estimates), and body sizes of turtles reported as bycatch to compute a bycatch impact score for all RMU-gear combinations. We compared bycatch impact scores for RMUs for each broad gear category and subgears using a Kruskal-Wallis Rank Sum test with Steel-Dwass nonparametric post-hoc comparisons. To understand what component of the bycatch impact score explained observed differences among RMUs and gears, we also compared the composite parameters used to calculate the impact score among RMUs and gear or subgears.

Identifying conservation and monitoring priorities among RMU-gear combinations

To evaluate relationships between bycatch impact scores and RMU risk scores, we adapted the scaling evaluation approach used by Wallace et al. (2011) to assess risk and threat criteria for marine turtle RMUs. Weighted median BPUE, mortality rate, and body size values were scored using a comparable low-medium-high scale (numeric values 1 to 3; see Table 2 for values). Values were assigned to low, medium, or high scores based on the complete distributions of each parameter, thus ensuring that the numeric scale reflected the distributions of all values relative to extremely low and high values. Numeric scores for weighted median BPUE, mortality rates, and body size values were averaged to yield a total bycatch impact score for each RMU-gear combination. Because this low to high (1 to 3) scale corresponded to the

Table 2. Relative scores of bycatch data parameters along a low-medium-high continuum.

Parameter	Numeric scores				
	1 (low)	1.5	2 (medium)	2.5	3 (high)
Weighted median BPUE†	<0.001	0.001 to < 0.01	0.01 to < 0.1	0.1 to <1	≥1
Median mortality rate	<0.01	0.01 to <0.1	0.1 to < 0.3	0.3 to < 0.5	≥0.5
Body sizes	No data		Small (juvenile)		Large (adult/subadult)

Note: Records with no data for body size received a numerical score of 1 so that bycatch impact scores could still be calculated in the absence of body size data, i.e., numerical values for the other variables in the equation were present, but not for body size.

† No. turtles/set.

scale used by Wallace et al. (2011) to evaluate population risk, we were able to directly compare the degree of population risk (i.e., RMU risk scores) and bycatch impact scores for each RMU. For clarification, RMU risk scores were the average scores of five criteria: population abundance, recent population trend, long-term population trend, rookery vulnerability, and genetic diversity (Wallace et al. 2011).

To compare total bycatch impact scores among marine turtle RMUs and fishing gears relative to each RMU's risk score, we plotted the bycatch impact scores of each RMU-gear combination with corresponding RMU risk scores following the quadrant-graph approach used by Wallace et al. (2011). This method allowed us to visualize the full spread of bycatch impact scores in the context of overall population vulnerability and illustrated the differences in RMU risk-bycatch impact pairs by gear types globally. For RMU-gear combinations that fell on a border between quadrants, we applied a precautionary approach to and included them within the higher risk-higher bycatch quadrant.

Because the level of bias in bycatch rates and mortality rates decreases with increasing observed effort (Sims et al. 2008, Wallace et al. 2010a), we accounted for the number of bycatch records associated with bycatch impact scores to incorporate a degree of confidence or reliability in our analyses. We used bycatch impact scores for RMU-gear (and subgear) combinations that had ≥3 records for both weighted median BPUEs and median mortality rate in comparisons across RMU-gear combinations, unless noted otherwise. Because many RMU-gear combinations failed to meet these thresholds (see *Results: Evaluating bycatch impacts by fishing gears among RMUs*), we also calculated bycatch impact scores for RMU-gear (and subgear) combinations with <3 records for these parameters to be able to highlight

where data were available, but not necessarily reliable. In particular, the majority of bycatch impact scores for RMU-subgear combinations failed to meet this reliability threshold, so we used all bycatch impact scores for RMU-subgear combinations. Overall, we had higher confidence in bycatch impact scores that met or exceeded our reliability thresholds than in scores that failed to meet these thresholds. These reliability thresholds provided a means to identify which RMU-gear combinations required enhanced monitoring and/or reporting of bycatch data.

RESULTS

Description of bycatch data across fishing gears and RMUs

Of the data records that contained both BPUE and fishing effort information ($n = 1,467$), more than 59% were longline records, while the remainder was split between nets (26%) and trawls (15%) (Fig. 1). Global distribution of bycatch data was non-uniform, with significant data gaps—especially for nets and trawls—around Africa, in the Indian Ocean, and throughout Southeast Asia (Fig. 1B,C). The highest bycatch rates and levels of observed effort for each gear category occurred in the East Pacific, Northwest and Southwest Atlantic, and Mediterranean regions. Generally, BPUEs and mortality rates were inversely related to amounts of observed fishing effort (Fig. 2) as well as the associated number of bycatch records (Fig. 3).

We then mapped georeferenced bycatch records by gear and RMUs to display species-level distributions of available bycatch data for all marine turtle RMUs globally (Figs. 4–10). Spatial distribution of available bycatch data by regions and gear categories varied among species, but also among RMUs of the same species, and generally followed similar patterns that were

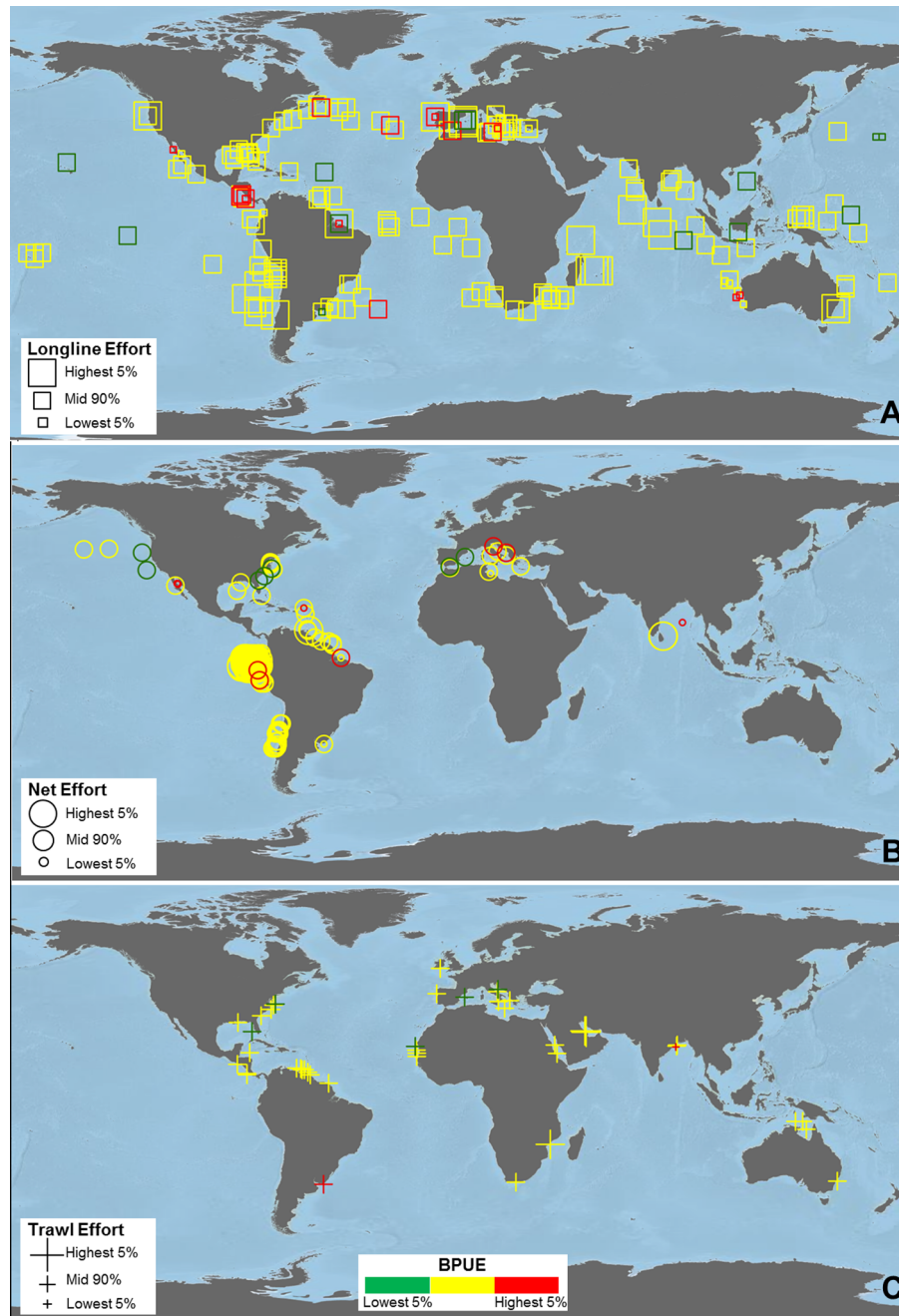


Fig. 1. Global distributions of sea turtle bycatch records for longlines (squares, A), nets (circles, B), and trawls (crosses, C) from 1990 to 2011. Symbol size is displayed in three size classes corresponding to amounts of effort (in number of sets) observed in each record; symbol color corresponds three classes of bycatch rates (bycatch per unit effort, or BPUE: number of turtles per set). Only records that reported both a bycatch rate and amount of observed fishing effort were plotted ($N = 1,467$ records; n [longlines] = 868 records, n [nets] = 377 records, n [trawls] = 222 records). Symbol sizes and colors correspond to low values (lowest 5% of total records), medium values (between lowest 5% and highest 5%), and high values (highest 5% of total records) for each gear category; display of records was prioritized to show high BPUE values, followed by low and then medium values. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

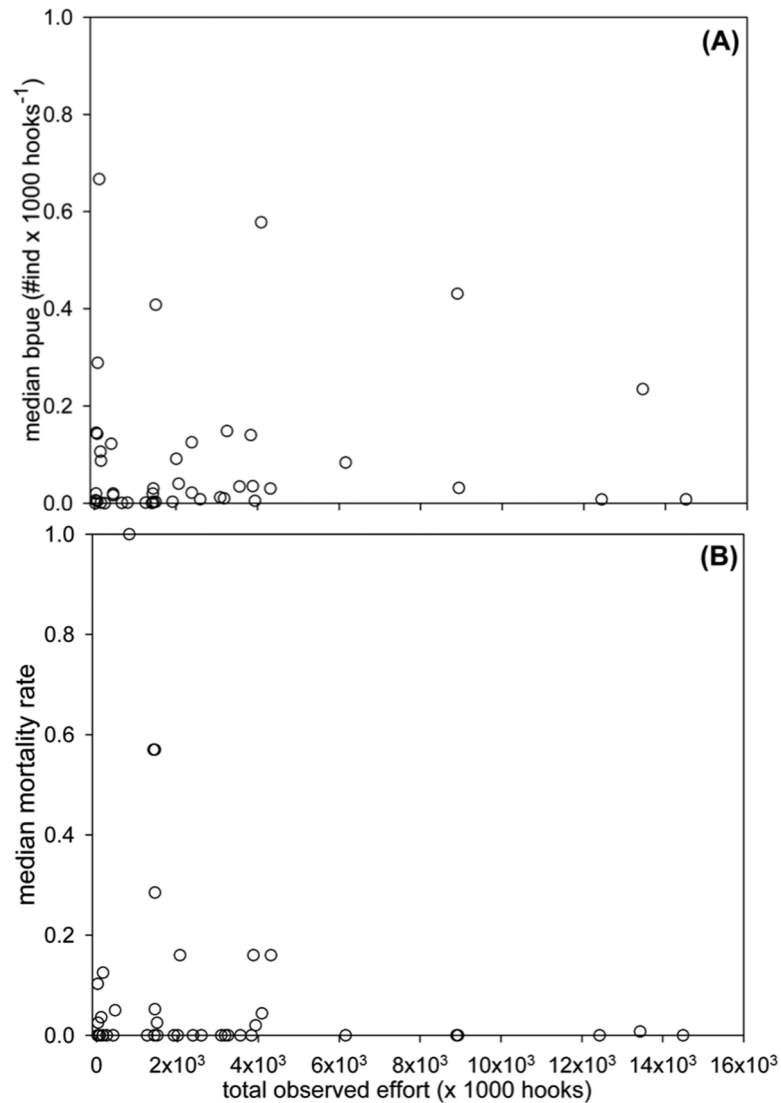


Fig. 2. Median bycatch rates (BPUEs; A) and median mortality rates (B) of marine turtles in longlines globally are inversely related to the associated total observed fishing effort. Data for nets and trawls not shown, but demonstrate similar patterns.

evident across gears globally. This pattern generally reflected the global patterns of bycatch data across gears, with more records—and highest BPUE and effort values—in the East Pacific, North and Southwest Atlantic, and Mediterranean, especially for longlines, and fewer records in the East Atlantic, North Indian, and West Pacific, especially for nets and trawls (Figs. 4–10).

Evaluating bycatch impacts by fishing gears among RMUs

We compared bycatch impact scores among gear types to explore variation in bycatch patterns globally. Among major gear categories, bycatch impact scores for longlines were significantly lower than for nets ($p = 0.002$) and trawls ($p = 0.006$) (Table 3; Fig. 11A). Among variables used to calculate bycatch impact scores, we found no significant differences in weighted median BPUEs or body sizes of turtles caught

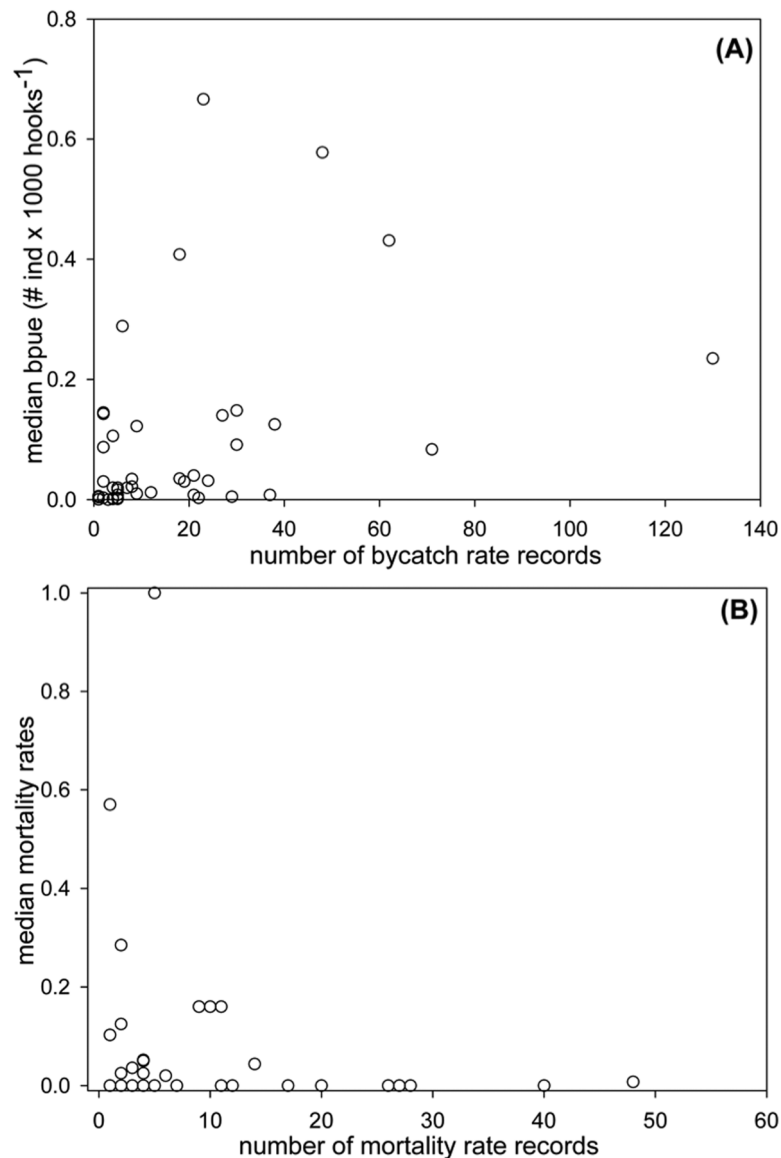


Fig. 3. Median bycatch rates (BPUEs; A) and median mortality rates (B) of marine turtles in longlines globally are inversely related to the associated number of bycatch records. Data for nets and trawls not shown, but demonstrate similar patterns.

across gears at the global scale ($p > 0.05$). However, median mortality rates of turtles caught in longlines were significantly lower than in nets ($p < 0.001$) and trawls ($p < 0.001$) globally (Table 3, Fig. 11B).

Among subgears, bycatch impact scores of “other” longlines (i.e., longlines that could not be categorized) were significantly lower than those of bottom-set nets ($p = 0.018$), “other” nets ($p <$

0.001), and shrimp trawls ($p = 0.015$) (Table 4, Fig. 12A). As with major gear categories, we found no significant differences in weighted median BPUE or body sizes of turtles caught among subgears. However, we found that, in general, mortality rates in longlines, with the exception of bottom-set longlines, were significantly lower than mortality rates in most nets and trawls (Table 4, Fig. 12B; see all significantly

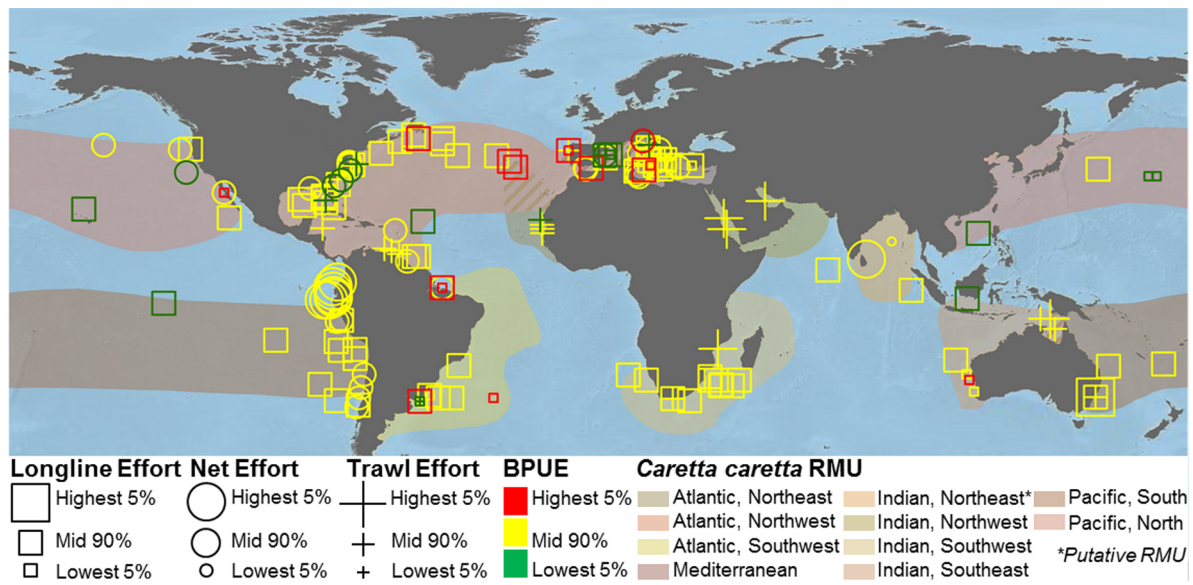


Fig. 4. Global distributions of bycatch records of loggerheads (*Caretta caretta*) in relation to their respective regional management units (RMUs; Wallace et al. 2010b). Gear and bycatch per unit effort (BPUE) symbology is identical to global gear maps (Fig. 1), but symbol sizes and colors correspond to low, medium, and high values for each gear-species category. Because many points had identical coordinates, not all points are visible; records with high BPUE values were prioritized, followed by low and then medium values, for display. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

different pairs in Appendix B). Fishing gear anchored to the ocean bottom (e.g., bottom-set longlines, bottom-set gillnets) tended to have higher mortality rates and bycatch impact scores than gear set at or near the surface (Table 4, Appendix B), though this pattern was not statistically significant.

Out of a possible 135 RMU-gear combinations with data records in our database, 93 (~69%) had sufficient data to calculate bycatch impact scores (Fig. 13), but only 71 (~53% of the total) met our data reliability thresholds and were subsequently plotted (Fig. 14). Another 22 RMU-gear combinations (~16% of the total) had sufficient data to calculate lower reliability bycatch impact scores (Fig. 13). For the remaining 42 RMU-gear combinations (~31% of the total), bycatch impacts could not be calculated due to insufficient data records (Table 5). Both lower reliability RMU-gear combinations and those for which insufficient data were available ($n = 64$) should be considered critical data needs from a bycatch assessment perspective.

Out of the 93 RMU-gear combinations as-

sessed, longlines had the highest bycatch impact scores for 18 RMUs, trawls for 13 RMUs, and nets for nine RMUs; we were unable to assess highest bycatch impact scores among gears for 18 RMUs due to insufficient data for any gear category (Table 5). Furthermore, only nine RMUs (~16%) had sufficient data to calculate bycatch impact scores for all three gear categories (Table 5). The subgear within each gear category that had the highest bycatch impact score for a given RMU included pelagic longlines, “other” nets, and “other” trawls (Appendix B).

Identifying conservation and monitoring priorities among RMU-gear combinations

To identify RMU and gear combinations that are the highest conservation and monitoring priorities, we plotted bycatch impacts scores against the RMU risk scores from Wallace et al. (2011), and generated an array of population risk-bycatch impact paired scores that fell within one of four quadrants along the risk and bycatch impact continua (Fig. 14). Among species with more than two RMUs (all but Kemp’s ridleys

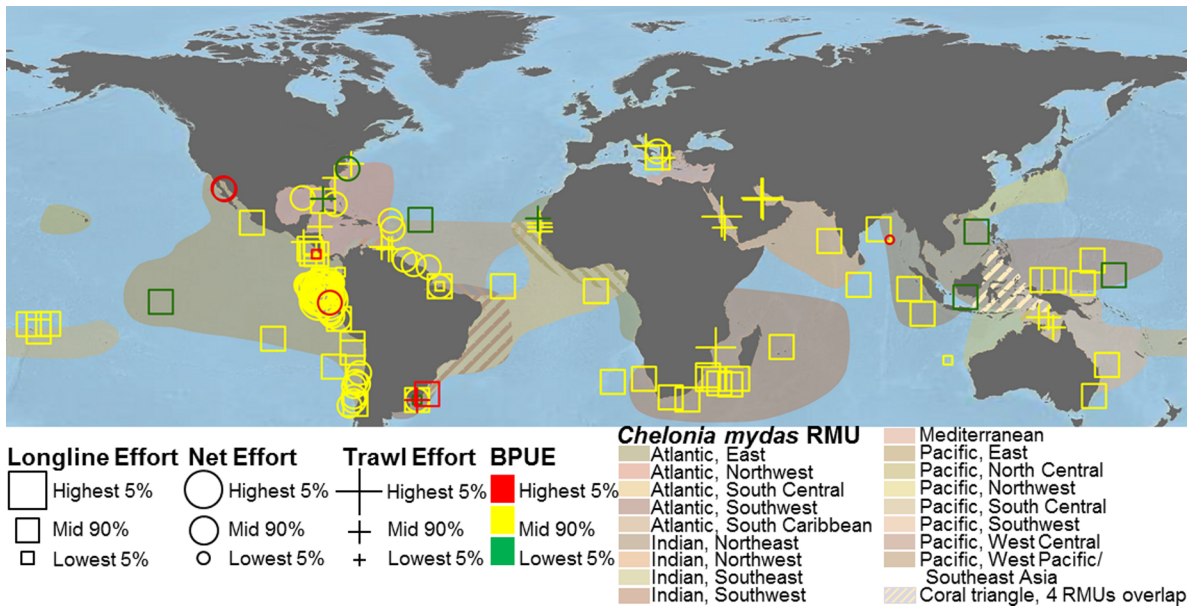


Fig. 5. Global distributions of bycatch records of green turtles (*Chelonia mydas*) in relation to their respective regional management units (RMUs; Wallace et al. 2010b). Gear and bycatch per unit effort (BPUE) symbology is identical to Fig. 4. Because many points had identical coordinates, not all points are visible; records with high BPUE values were prioritized, followed by low and then medium values, for display. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

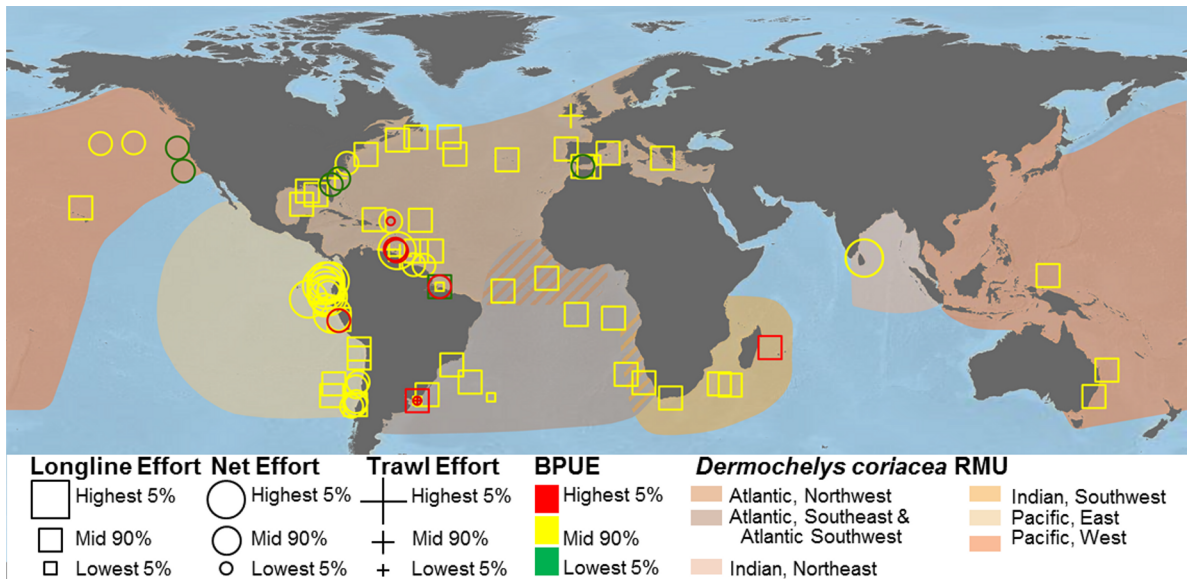


Fig. 6. Global distributions of bycatch records of leatherbacks (*Dermochelys coriacea*) in relation to their respective regional management units (RMUs; Wallace et al. 2010b). Gear and bycatch per unit effort (BPUE) symbology is identical to Fig. 4. Because many points had identical coordinates, not all points are visible; records with high BPUE values were prioritized, followed by low and then medium values, for display. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

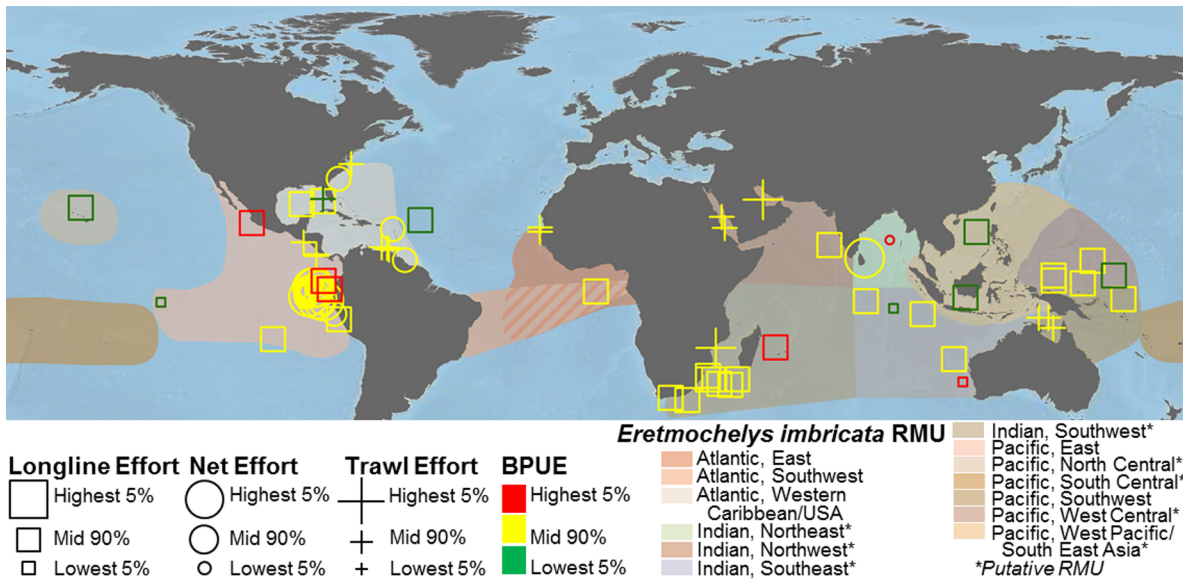


Fig. 7. Global distributions of bycatch records of hawksbills (*Eretmochelys imbricata*) in relation to their respective regional management units (RMUs; Wallace et al. 2010b). Gear and bycatch per unit effort (BPUE) symbology is identical to Fig. 4. Because many points had identical coordinates, not all points are visible; records with high BPUE values were prioritized, followed by low and then medium values, for display. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

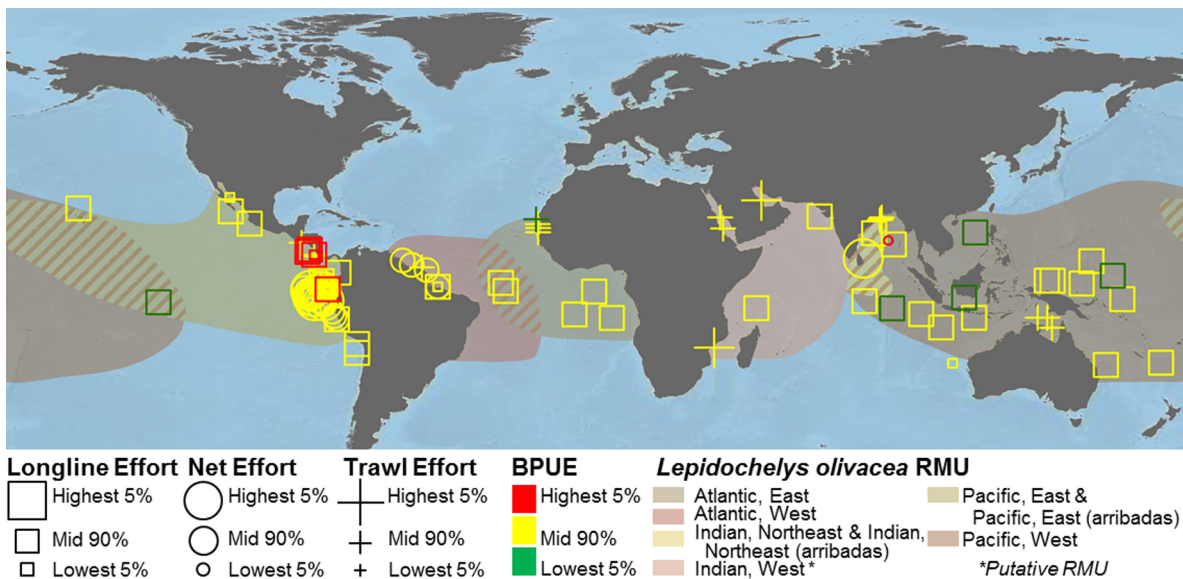


Fig. 8. Global distributions of bycatch records of olive ridleys (*Lepidochelys olivacea*) in relation to their respective regional management units (RMUs; Wallace et al. 2010b). Gear and bycatch per unit effort (BPUE) symbology is identical to Fig. 4. Because many points had identical coordinates, not all points are visible; records with high BPUE values were prioritized, followed by low and then medium values, for display. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

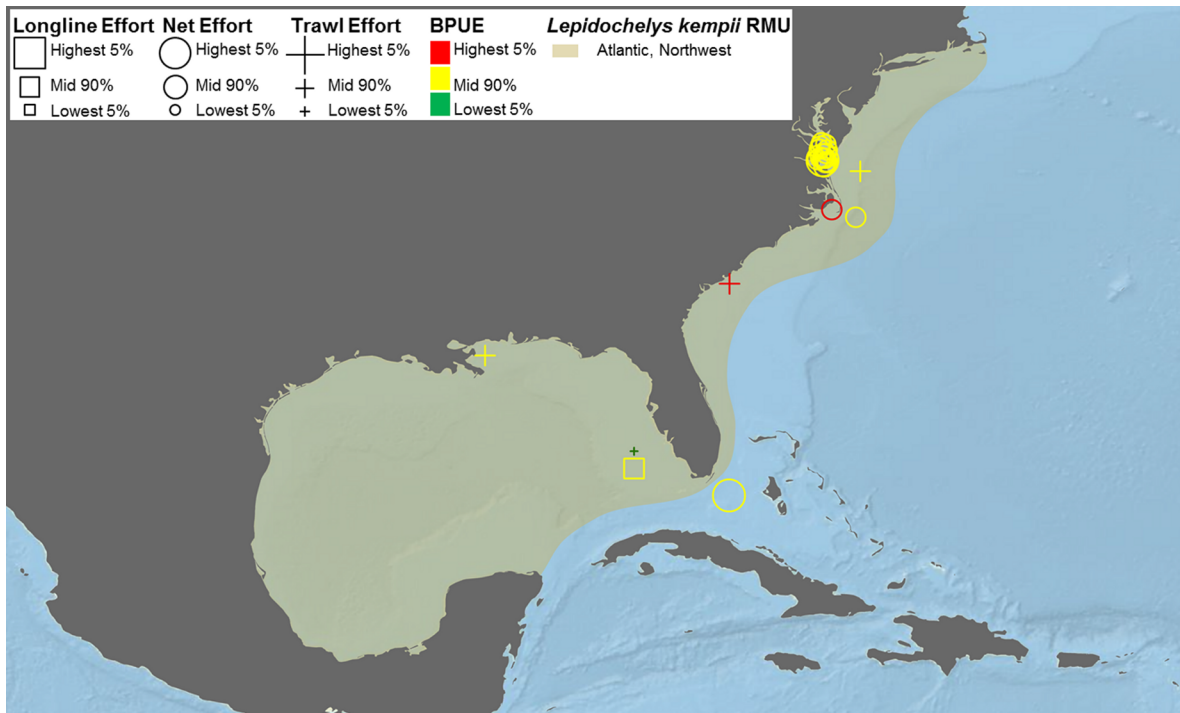


Fig. 9. Global distributions of bycatch records of Kemp's ridleys (*Lepidochelys kempii*) in relation to their respective regional management units (RMUs; Wallace et al. 2010b). Gear and bycatch per unit effort (BPUE) symbology is identical to Fig. 4. Because many points had identical coordinates, not all points are visible; records with high BPUE values were prioritized, followed by low and then medium values, for display. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

[*Lepidochelys kempii*] and flatbacks [*Natator depressus*]), all species had at least one RMU in at least three quadrants, while four of five species (leatherbacks, green turtles [*Chelonia mydas*], hawksbills [*Eretmochelys imbricata*], and loggerheads [*Caretta caretta*], but not olive ridleys [*Lepidochelys olivacea*]) had at least one RMU in each of the four quadrants (Fig. 14). All three gear categories appeared in each of the four quadrants.

We identified 11 RMUs as high risk-high bycatch (Fig. 14, upper right quadrant). These included four in longlines, three in nets, and four in trawls. We identified 18 high risk-low bycatch RMUs (Fig. 14, lower right quadrant), including 12 RMUs in longlines, four in nets, and two in trawls. We identified 19 RMUs as low risk-high bycatch (Fig. 14, upper left quadrant), including four in longlines, six in nets, and nine in trawls. A total of 23 RMUs were identified as low risk-low

bycatch (Fig. 14, bottom left quadrant). These included 15 in longlines, four in nets, and four in trawls (Table 6).

DISCUSSION

For wide-ranging, long-lived species with complex population structures, population-level threats assessments are fundamental to (1) quantifying and comparing relative impacts, and (2) designing conservation strategies that promote recovery by prioritizing limited conservation resources to reducing the threats with highest impacts. Our study is the first to evaluate, compare, and highlight relative bycatch impacts across different fishing gears to all marine turtle RMUs globally. As such, it should be considered an initial roadmap for targeted efforts to observe, report, and reduce marine turtle bycatch in specific fishing gears where

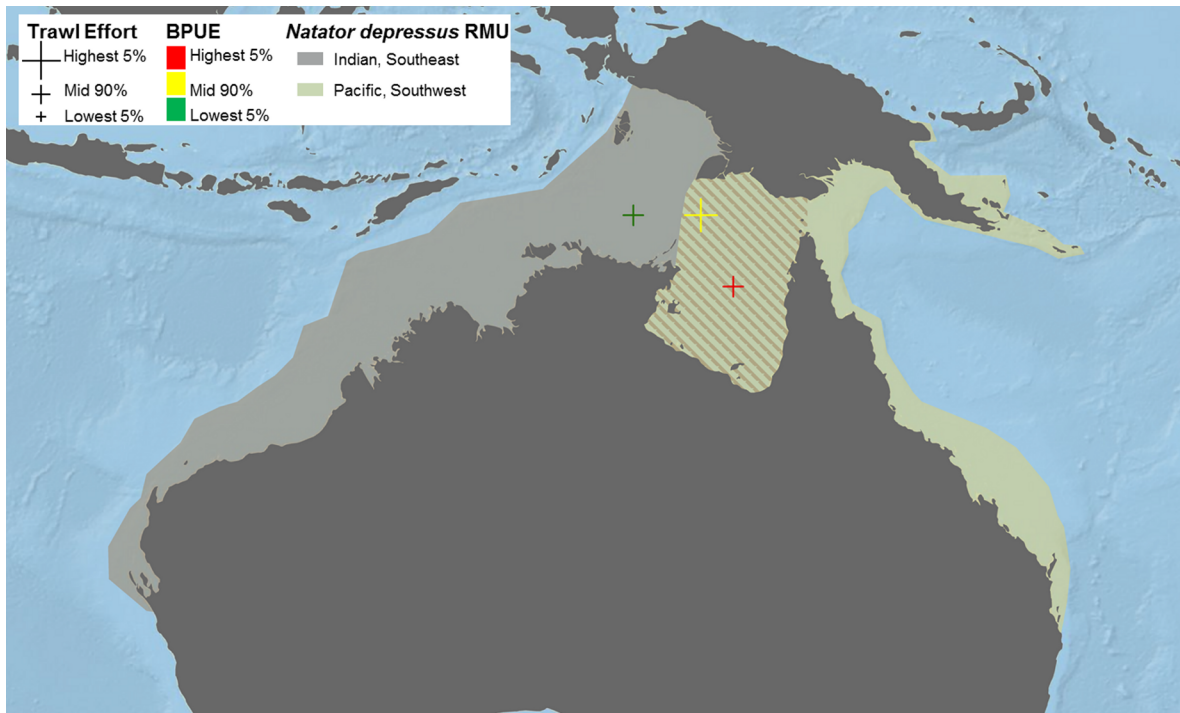


Fig. 10. Global distributions of bycatch records of flatbacks (*Natator depressus*) in relation to their respective regional management units (RMUs; Wallace et al. 2010b). Gear and bycatch per unit effort (BPUE) symbology is identical to Fig. 4. Because many points had identical coordinates, not all points are visible; records with high BPUE values were prioritized, followed by low and then medium values, for display. Where bycatch locations were not provided in the original source, records were mapped relative to general area of operation for the fishery reported.

Table 3. Summary bycatch data for longlines, nets, and trawls. Significant differences between pairs are represented by different letter superscripts.

Parameter	Longlines	Nets	Trawls
Weighted median BPUE†			
Mean	0.075	0.145	0.278
SD	0.145	0.389	0.954
No. records	53	29	40
Median mortality rate			
Mean	0.07 ^A	0.32 ^B	0.26 ^B
SD	0.19	0.31	0.29
No. records	46	24	26
Body size			
Mean	2.42	2.61	2.61
SD	0.46	0.46	0.48
No. records	21	22	23
Bycatch impact score			
Mean	1.66 ^C	1.94 ^D	2.02 ^D
SD	0.33	0.35	0.37
No. RMUs	35	17	19

†No. individuals/set.

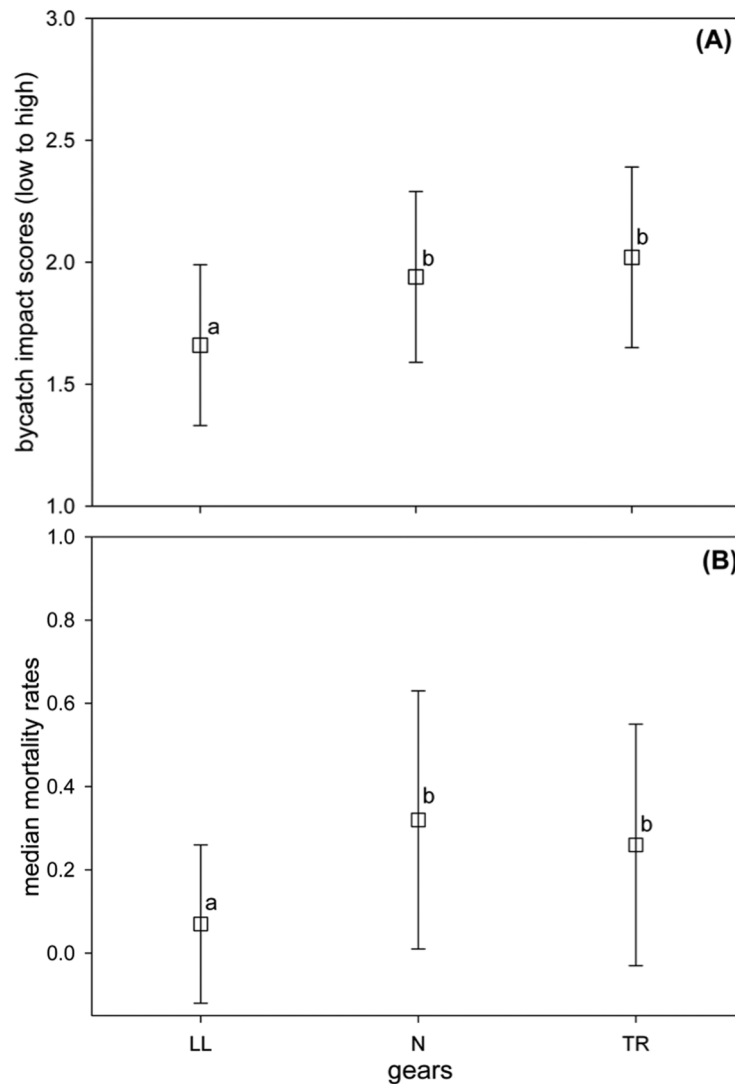


Fig. 11. Bycatch impact scores (A) and median mortality rates (B) by major gear category (codes: LL, longlines; N, nets; TR, trawls). Different superscripts denote statistically significant differences.

doing so will have the greatest benefit for population recovery.

Description of marine turtle bycatch data among fishing gears and RMUs

Our synthesis demonstrated important marine turtle bycatch patterns across regions and fishing gears. Spatial distribution of bycatch records, bycatch rates, and fishing effort varied by fishing gear and across regions. Our database contained more records of marine turtle bycatch in longlines than in nets and trawls combined; longline records occurred in near-shore as well as oceanic

areas, whereas records of marine turtle bycatch in nets and trawls were most prevalent in near-shore areas (Figs. 1, 4–10). Overall, records containing information on bycatch rates and fishing effort were most abundant in the East Pacific, North Atlantic, Southwest Atlantic, and Mediterranean. This pattern was more apparent for nets and trawls than for longlines, due to relative paucity of available information for nets and trawls in certain geographic regions (Fig. 1, Table 6). Likewise, the highest values for BPUEs and observed fishing effort occurred in the same regions (Figs. 1, 4–10).

Table 4. Summary of sea turtle bycatch data observed in all subgear types globally from 1990–2011. Bycatch impact scores for subgears included all RMU-subgear combinations that had all three variables used to compute the bycatch impact score: weighted median BPUE (no. individuals/set), median mortality rate, and body size. Significant differences among bycatch impact scores are represented by different letter superscripts.

Parameter	Longlines				Nets				Trawls		
	Bottom	Pelagic	Surface/ drift	Other	Bottom	Drift	Fixed	Other	Bottom	Shrimp	Other
Weighted median BPUE											
Mean	1.375	0.171	0.109	0.149	0.209	0.132	0.087	0.154	0.538	0.049	0.035
SD	4.950	0.498	0.131	0.281	0.396	0.256	0.316	0.386	1.393	0.108	0.050
No. records	14	39	18	42	14	17	15	24	18	26	25
Median mortality rate											
Mean	0.23	0.06	0.01	0.10	0.54	0.21	0.34	0.41	0.19	0.23	0.30
SD	0.29	0.16	0.01	0.18	0.32	0.25	0.32	0.36	0.34	0.21	0.32
No. records	9	38	16	33	14	17	17	16	8	19	15
Body size											
Mean	2.38	2.49	2.43	2.00	2.50	2.61	2.13	2.55	2.14	2.55	3.00
SD	0.52	0.49	0.47	0.00	0.58	0.49	0.25	0.49	0.24	0.52	0.00
No. records	8	17	11	2	4	7	4	11	7	11	5
Bycatch impact score											
Mean	1.94	1.68	1.64	1.45 ^A	1.93 ^B	1.72	1.71	2.07 ^B	1.71	1.81 ^B	1.81
SD	0.75	0.37	0.44	0.33	0.51	0.29	0.40	0.34	0.42	0.38	0.45
No. RMUs	9	36	16	32	14	17	15	16	8	18	15

Note: See Appendix B for detailed statistical results of comparisons among the median mortality rates shown above.

In addition to spatial heterogeneity, our analyses confirmed a nearly universal pattern wherein high bycatch and mortality rates typically were based on low observed effort and research coverage, and the higher the observed effort and reporting in a given region, the narrower the range of BPUEs and mortality rates reported (Figs. 2 and 3). These trends reflect both the relative rarity (and generally low observation rate) of bycatch events (Sims et al. 2008), as well as the disproportionately high frequency of bycatch events where fishing activities overlap with high turtle densities (see *Discussion: Evaluating bycatch impacts by fishing gears among RMUs*). Regardless, we recommend caution when interpreting high bycatch rates based on low observed effort and research coverage.

Not surprisingly, similar patterns of spatial variation and relationships among bycatch variables were reported previously by Wallace et al. (2010a), whose analyses relied upon many of the same data records as those in the present study. These persistent patterns highlight the imbalanced distribution of available marine turtle bycatch data records among gear categories and geographic regions, which directly affects our ability to adequately and quantitatively assess relative bycatch impacts across gear types and populations. Although our analyses clearly iden-

tified regions where both population risk and bycatch impacts are high, thus highlighting the need for bycatch reduction (see *Discussion: Evaluating bycatch impacts by fishing gears among RMUs*), we have limited insights into what bycatch impacts are where data are limited or non-existent. Despite our efforts to make the database as complete as possible, we recognize the possibility that bycatch data exist that were not included in our analyses. For all of these reasons, enhanced assessments and reporting of bycatch impacts in areas with limited data are fundamental to producing robust assessments of bycatch impacts on widespread species whose distributions expose them to risks from several fisheries in multiple jurisdictions.

Evaluating bycatch impacts by fishing gears among RMUs

Longlines were most frequently found to have the highest bycatch impact scores for individual RMUs, but this result was likely due to the higher availability of longline records that allowed calculation of bycatch impact scores for a greater number of RMUs; indeed, for many RMUs, bycatch impact scores could only be calculated for longlines due to insufficient records for the other gear categories (Table 5). In contrast, when records for each gear category (and subgears)

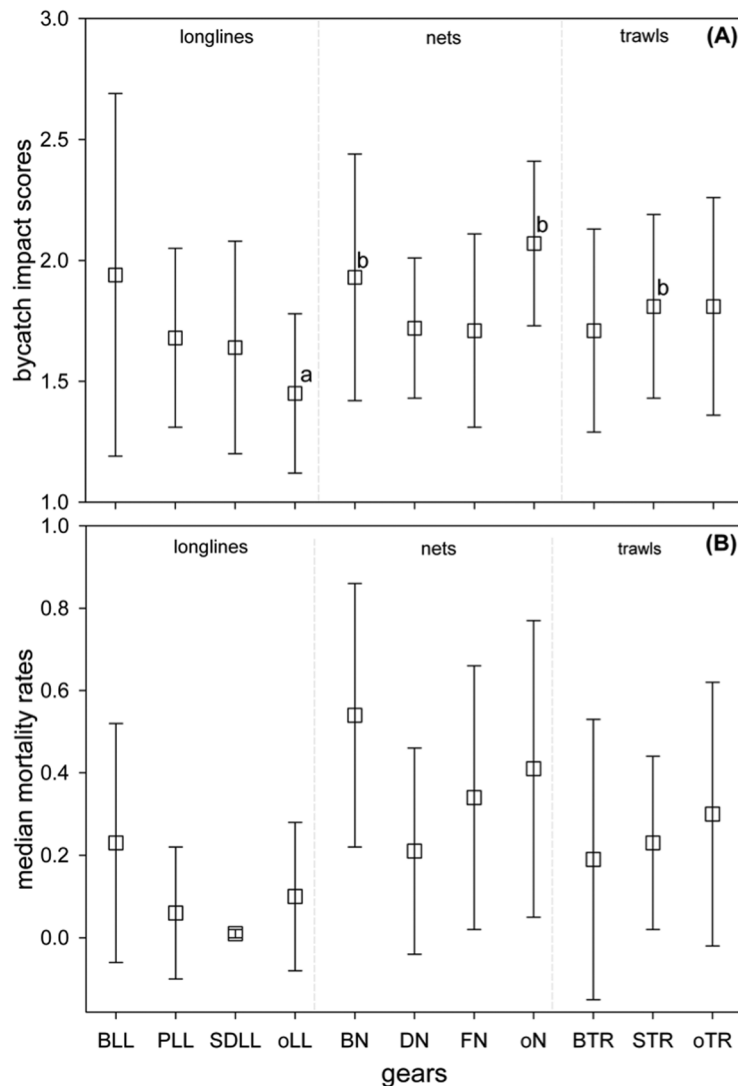


Fig. 12. Bycatch impact scores (A) and median mortality rates (B) by subgear categories (C and D; codes: BLL, bottom-set longline; PLL, pelagic longline; SDLL, surface/drift longline; oLL, “other” longline; BN, bottom-set gillnet; DN, driftnet; FN, fixed net; oN, “other” net; BTR, bottom trawl; STR, shrimp trawl; oTR, “other” trawl). Different superscripts denote statistically significant differences (see Appendix B for significant differences in (B)).

were considered together, bycatch impact scores and mortality rates in longlines were significantly lower than bycatch impacts and mortality rates in nets and trawls (Figs. 11 and 12). Although improved estimates of post-release mortality would further refine evaluation of bycatch impacts in different fishing gears (e.g., Swimmer et al. 2006), these findings illustrate that while efforts to observe and reduce marine turtle bycatch in longlines should continue,

increased efforts and resources should be invested in observation and reduction of turtle bycatch in nets and trawls.

Because the relative impacts of any threat—especially bycatch—to marine turtle populations depend on the magnitude, mortality rates, and reproductive values of individuals affected relative to amounts of fishing effort, a threat that incurs high mortality and occurs in areas of high density of reproductively valuable individuals

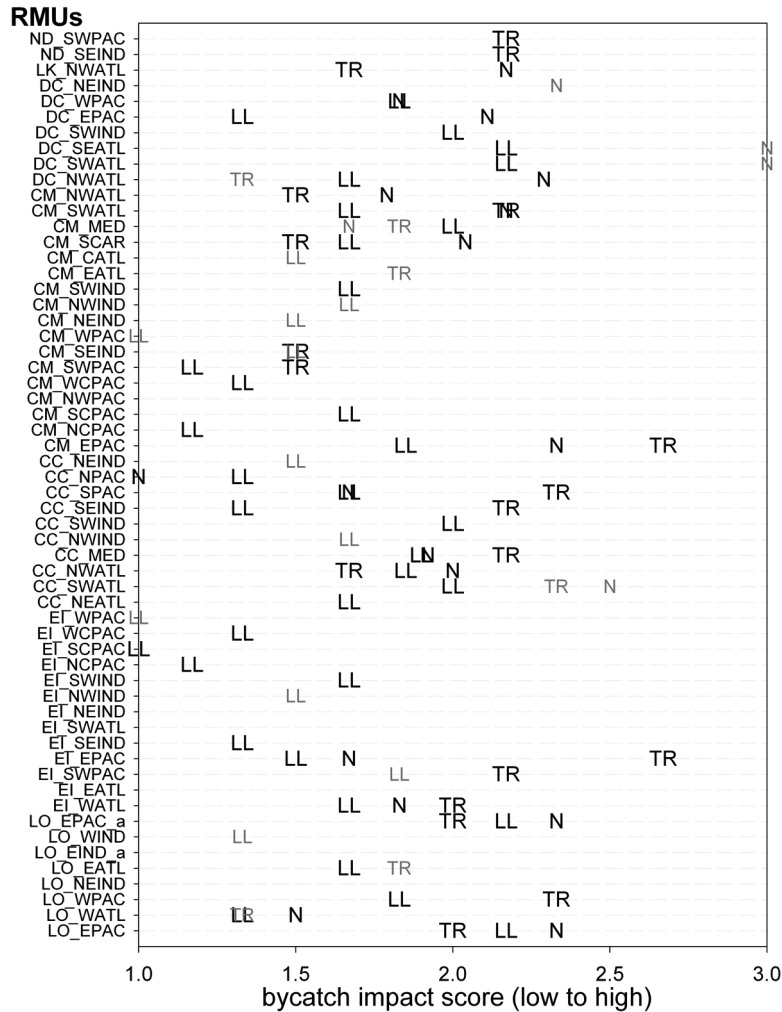


Fig. 13. Bycatch impact scores for each RMU-gear combination, showing scores with higher reliability (those with ≥ 3 records for weighted median BPUEs and median mortality rates; larger, black font) and those with lower reliability (those with < 3 records for weighted median BPUEs and median mortality rates; smaller, grey font). Codes: LL, longlines; N, nets; TR, trawls.

will have a negative population-level impact. In this context, small-scale fisheries operating in near-shore areas (Stewart et al. 2010) that often overlap with high-use areas for turtles (e.g., breeding or feeding areas) can have particularly high bycatch impacts on affected populations (Lee Lum 2006, Peckham et al. 2007, Alfaro-Shigueto et al. 2011, Humber et al. 2011). In this study, bycatch records for nets and trawls tended to occur in near-shore areas (Figs. 1, 4–10), and were associated with higher mortality rates and bycatch impact scores than longlines overall (Figs. 11 and 12). In the East Pacific Ocean, for

example, which hosts breeding and/or feeding areas of RMUs of five different species (Wallace et al. 2010b), high levels of bycatch have been reported in small-scale fisheries in multiple locations (e.g., Baja California, Mexico: Peckham et al. 2007; Costa Rica: Arauz 1996; Peru: Alfaro-Shigueto et al. 2011). Likewise, we found high bycatch impacts for 10 RMU-gear combinations in this region (Figs. 13 and 14). Coastal areas off Africa, within the North Indian Ocean, and throughout Southeast Asia are also known to host numerous nesting colonies belonging to RMUs that are under high threat from various

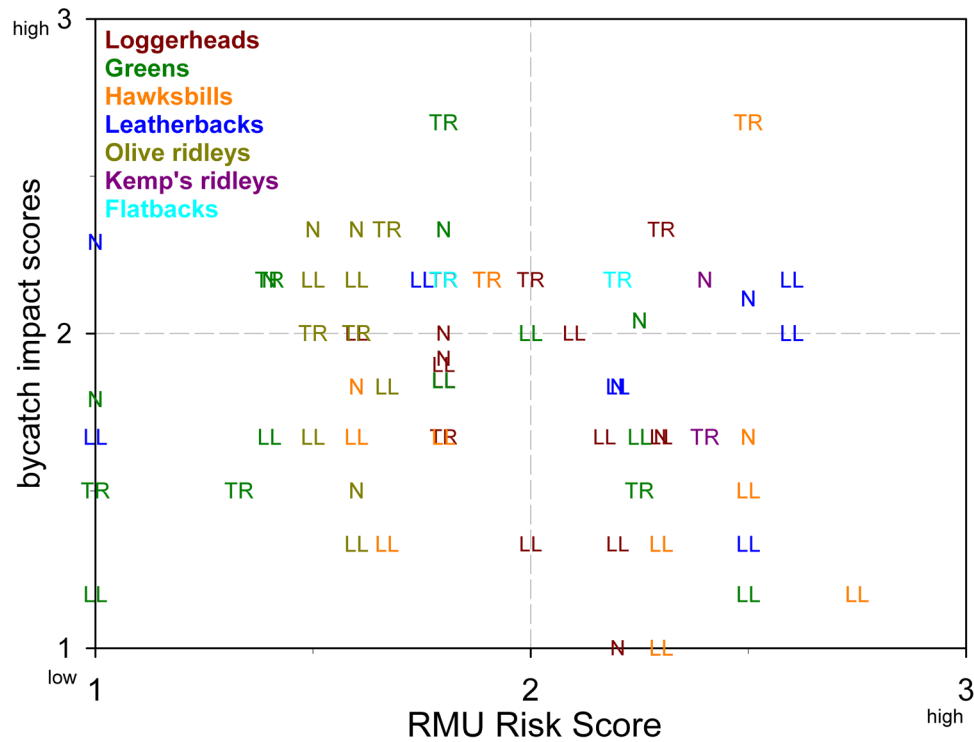


Fig. 14. Bycatch impact scores for each RMU-gear combination plotted against RMU risk scores of all RMUs in longlines (LL), nets (N), and trawls (TR). Only higher reliability scores shown in Fig. 13 are displayed (see text for details).

human activities, including bycatch in small-scale fisheries (Moore et al. 2010, Humber et al. 2011, Wallace et al. 2011). However, RMU-gear combinations in this region were found to be largely data deficient in this study (Table 5), underscoring the need to prioritize future bycatch assessments in these regions. Because of known and unknown levels of impacts, monitoring and reducing marine turtle bycatch in nets and trawls—particularly in small-scale fisheries operating in or close to critical turtle habitats where high risk RMUs identified by Wallace et al. (2011) occur—should be a top priority for resource managers and conservation groups around the world.

Gear fixed to the ocean bottom appeared to have higher mortality rates and bycatch impact scores than gear close to the surface, free of bottom-set anchoring, although these differences were not statistically significant, possibly because of limited sample size and reduced statistical power (Figs. 11 and 12, Tables 3 and 4). This general pattern can be attributed to the air-

breathing nature of marine turtles; when turtles become hooked, entangled, or trapped in fishing gear that prevents them from reaching the surface to breathe, the likelihood that these interactions result in mortality will be higher (Poiner and Harris 1996). This phenomenon is likely the case for other air-breathing vertebrates taken as bycatch in these gears (e.g., Żydelski et al. 2009). Thus, one straightforward action to reduce bycatch impacts on marine turtles and other air-breathing species would be to limit or eliminate gear that prevents bycaught animals from reaching the surface, or optimize soak times of such gear to avoid lethal bycatch interactions while maintaining target catch per unit effort.

Our results showed that high bycatch impact scores varied globally across and within gear categories (Figs. 11 and 12), as well as within RMUs (Table 5; Appendix B). However, adapting successful mitigation measures across gear types requires understanding specific gear configurations, fishing practices, and turtle biology, and how these factors interact to result in observed

Table 5. Summary table showing number of records (*N*), total fishing effort, weighted median BPUEs, median mortality rates (MR), and bycatch impact scores (BIS) for longlines, nets, and trawls for marine turtle regional management units (RMUs). Weighted median BPUEs (BPUE) displayed for only those RMU-gear combinations with ≥ 3 records of both BPUE and observed fishing effort values (number of records in parentheses). Median mortality rates displayed only for those RMU-gear combinations with ≥ 3 records of mortality rate data (range of median mortality rates in parentheses). Bycatch impact score (BIS) is the average of BPUE score, mortality rate score, and body size score for each RMU-gear combination; value shown is for RMU-gear combinations that had ≥ 3 records for both BPUEs and mortality rates.

RMU	Longlines				Nets				Trawls			
	<i>N</i>	BPUE	MR	BIS	<i>N</i>	BPUE	MR	BIS	<i>N</i>	BPUE	MR	BIS
<i>Caretta caretta</i>												
NE Atlantic	23	0.871 (23)	0.04 (0.02–0.04)	1.67	ND	ND	ND	ND	(4)	0.008 (4)	ND	ND
NW Atlantic	144	0.274 (130)	0.01 (0–1)	1.85	51	0.012 (47)	0.17 (0–1)	2.00	31	0.007 (26)	0.06 (0–0.5)	1.67
SW Atlantic	48	0.407 (47)	0.04 (0–0.14)	2.00	4	0.182 (3)	0.58 (0.17–1)	ND	4	5.5 (4)	0.188 (0.16–0.22)	ND
Mediterranean	70	0.409 (62)	0 (0–0.23)	1.90	13	0.069 (11)	0.05 (0–0.69)	1.92	14	0.011 (12)	0.06 (0–0.5)	2.17
NE Indian	4	0.009 (4)	0.29 (0–0.57)	ND	2	0.008 (2)	ND	ND	ND	ND	ND	ND
NW Indian	1	ND	ND	ND	ND	ND	ND	ND	4	0.025 (4)	ND	ND
SE Indian	6	0.023 (6)	0 (0–0)	1.33	ND	ND	ND	ND	8	0.002 (8)	0.28 (0.22–0.38)	2.17
SW Indian	25	0.040 (21)	0.16 (0–0.80)	2.00	ND	ND	ND	ND	3	0.042 (3)	ND	ND
N Pacific	36	0.011 (24)	0 (0–0.92)	1.33	56	0.001 (34)	0 (0–1)	1.00	1	ND	ND	ND
S Pacific	23	0.020 (21)	0 (0–0.25)	1.67	14	0.005 (14)	0.33 (0–1)	1.67	9	0.024 (8)	0.28 (0.22–0.38)	2.33
<i>Chelonia mydas</i>												
Central Atlantic	18	0.139 (18)	ND	ND	1	ND	ND	ND	4	0.008 (4)	ND	ND
E Atlantic	1	ND	ND	ND	ND	ND	ND	ND	5	0.008 (4)	ND	ND
NW Atlantic	1	ND	ND	ND	9	0.003 (9)	0 (0–0.2)	1.79	10	0.004 (9)	0 (0–0.19)	1.50
S Caribbean	29	0.006 (27)	0.02 (0–0.07)	1.67	26	0.041 (14)	0.17 (0–1)	2.04	5	0.001 (3)	0 (0–0.19)	1.50
SW Atlantic	30	0.071 (30)	0 (0–0.07)	1.67	19	0.056 (7)	0.38 (0–1)	2.17	6	2.600 (4)	0.08 (0–0.22)	2.17
Mediterranean	7	0.103 (4)	0 (0–0)	2.00	1	ND	ND	ND	2	0.1210 (2)	0	ND
NE Indian	4	0.037 (4)	0.03 (0–0.05)	ND	1	ND	ND	ND	ND	ND	ND	ND
NW Indian	2	ND	ND	ND	2	ND	ND	ND	9	0.002 (9)	ND	ND
SE Indian	2	ND	ND	ND	ND	ND	ND	ND	8	0.003 (8)	0.22 (0.09–0.38)	1.50
SW Indian	23	0.030 (19)	0.16 (0–0.78)	1.67	ND	ND	ND	ND	2	ND	ND	ND
E Pacific	30	0.098 (27)	0 (0–1)	1.85	43	0.009 (40)	0.34 (0–0.67)	2.33	7	0.041 (4)	0.75 (0.25–1)	2.67
W Pacific	3	0 (3)	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
N Central Pacific	13	0.001 (4)	0 (0–0)	1.17	ND	ND	ND	ND	ND	ND	ND	ND
S Central Pacific	6	0.0008 (5)	1 (0.18–1)	1.67	ND	ND	ND	ND	ND	ND	ND	ND
W Central Pacific	5	0.003 (5)	0.05 (0–0.27)	1.33	ND	ND	ND	ND	ND	ND	ND	ND
NW Pacific	1	ND	ND	ND	6	ND	0 (0–0.97)	ND	1	ND	ND	ND
SW Pacific	6	0.001 (5)	0 (0–0.25)	1.17	ND	ND	ND	ND	10	0.007 (10)	0.22 (0.09–0.38)	1.50

Table 5. Continued.

RMU	Longlines				Nets				Trawls			
	N	BPUE	MR	BIS	N	BPUE	MR	BIS	N	BPUE	MR	BIS
<i>Dermochelys coriacea</i>												
NW Atlantic	77	0.062 (71)	0 (0–0.72)	1.67	27	0.015 (23)	0.21 (0–1)	2.29	5	0.001 (5)	ND	ND
SE Atlantic	31	0.171 (30)	0 (0–0.33)	2.17	2	ND	ND	ND	2	ND	ND	ND
SW Atlantic	31	0.171 (3)	0 (0–0.33)	2.17	2	ND	ND	ND	2	ND	ND	ND
NE Indian	ND	ND	ND	ND	2	ND	ND	ND	ND	ND	ND	ND
SW Indian	8	0.014 (8)	0 (0–0.20)	2.00	ND	ND	ND	ND	ND	ND	ND	ND
E Pacific	9	0.016 (8)	0 (0–0.05)	1.33	20	0.006	0.33	2.11	ND	ND	ND	ND
W Pacific	22	0.005 (9)	0 (0–0.16)	1.83	38	0.003 (27)	0 (0–1)	1.83	ND	ND	ND	ND
<i>Eretmochelys imbricata</i>												
E Atlantic	1	ND	ND	ND	ND	ND	ND	ND	4	0.008 (4)	ND	ND
SW Atlantic	1	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
W Atlantic	22	0.003 (22)	0 (0–0.5)	1.67	11	0.008 (9)	0.5 (0–1)	1.83	6	0.001 (5)	0.19 (0–1)	2.00
NE Indian	ND	ND	ND	ND	4	ND	ND	ND	1	ND	ND	ND
NW Indian	2	ND	ND	ND	ND	ND	ND	ND	4	0.024 (4)	ND	ND
SE Indian	5	0.004 (5)	0.03 (0–0.57)	1.33	ND	ND	ND	ND	1	ND	ND	ND
SW Indian	22	0.034 (18)	0.16 (0–0.78)	1.67	ND	ND	ND	ND	2	ND	ND	ND
N Central Pacific	4	0.002 (4)	0 (0–0)	1.17	ND	ND	ND	ND	ND	ND	ND	ND
S Central Pacific	3	0.00 (3)	0 (0–0.18)	1.00	ND	ND	ND	ND	ND	ND	ND	ND
W Central Pacific	5	0.002 (5)	0.05 (0–0.27)	1.33	ND	ND	ND	ND	ND	ND	ND	ND
E Pacific	9	0.118 (9)	0 (0–0.95)	1.50	21	0.005 (19)	0.39 (0.25–1)	1.67	6	0.011 (3)	0.63 (0–1)	2.67
SW Pacific	3	ND	ND	ND	ND	ND	ND	ND	7	0.003 (7)	0.28 (0.22–0.38)	2.17
W Pacific	4	0.000 (3)	ND	ND	6	ND	0 (0–1)	ND	1	ND	ND	ND
<i>Lepidochelys kempii</i>												
NW Atlantic	1	ND	ND	ND	24	0.004 (24)	0.5 (0–1)	2.17	5	0.014 (5)	0 (0–0)	1.67
<i>Lepidochelys olivacea</i>												
E Atlantic	8	0.014 (7)	0 (0–0.25)	1.67	ND	ND	ND	ND	5	0.008 (4)	ND	ND
W Atlantic	12	0.022 (12)	0 (0–0.14)	1.33	8	0.038 (5)	0.08 (0.05–0.17)	1.50	3	ND	0 (0–0.33)	ND
NE Indian†	2	ND	ND	ND	3	ND	ND	ND	3	0.041 (3)	ND	ND
W Indian	5	ND	0.05 (0–0.57)	ND	ND	ND	ND	ND	7	0.035 (6)	ND	ND
E Pacific‡	50	0.127 (38)	0 (0–1)	2.17	31	0.007 (28)	0.35 (0–0.93)	2.33	6	0.047 (4)	0.44 (0.25–1)	2.00
W Pacific	49	0.007 (37)	0 (0–1)	1.83	3	ND	ND	ND	13	0.011 (13)	0.22 (0.19–0.38)	2.33
<i>Natator depressus</i>												
SE Indian	ND	ND	ND	ND	ND	ND	ND	ND	8	0.004 (8)	0.22 (0.14–0.38)	2.17
SW Pacific	ND	ND	ND	ND	ND	ND	ND	ND	7	0.005 (7)	0.22 (0.14–0.38)	2.17

† NE Indian, *L. olivacea* arribada RMU and solitary RMU have identical bycatch results.‡ E Pacific *L. olivacea* arribada RMU and solitary RMU have identical bycatch results.

Table 6. Classification of RMU-gear combinations according to population risk scores and bycatch impact scores, as displayed in quadrants of Fig. 14 indicated in parentheses.

Fishing gear by impact	n	RMU (species, region)
High risk–high bycatch impact (upper right quadrant)	11	
Longline	4	Leatherbacks, Southwest Indian Ocean Leatherbacks, Southwest Atlantic Ocean Loggerheads, South Pacific Ocean Green turtles, Mediterranean
Nets	3	Leatherbacks, East Pacific Ocean Kemp's ridleys, Northwest Atlantic Ocean Green turtles, South Caribbean
Trawls	4	Hawksbills, East Pacific Ocean Flatbacks, Southwest Pacific Ocean Loggerheads, Southeast Indian Ocean Loggerheads, Southwest Indian Ocean
Low risk–high bycatch impact (upper left quadrant)	19	
Longlines	4	Olive ridleys, East Pacific Ocean† Leatherbacks, Southeast Atlantic Ocean Loggerheads, Southwest Atlantic Ocean
Nets	6	Olive ridleys, East Pacific Ocean† Leatherbacks, Northwest Atlantic Ocean Green turtles, East Pacific Ocean Green turtles, Southwest Atlantic Ocean Loggerheads, Northwest Atlantic Ocean
Trawls	9	Olive ridleys, East Pacific Ocean† Olive ridleys, West Pacific Ocean Green turtles, East Pacific Ocean Green turtles, Southwest Atlantic Ocean Hawksbills, West Atlantic Ocean Hawksbills, Southwest Pacific Ocean Flatbacks, Southeast Indian Ocean Loggerheads, Mediterranean
High risk–low bycatch impact (lower right quadrant)	18	
Longlines	12	Leatherbacks, East Pacific Ocean Leatherbacks, West Pacific Ocean Green turtles, North Central Pacific Ocean Green turtles, South Caribbean Hawksbills, East Pacific Ocean Hawksbills, North Central Pacific Ocean Hawksbills, South Central Pacific Ocean Hawksbills, West Central Pacific Ocean Loggerheads, North Pacific Ocean Loggerheads, South Pacific Ocean Loggerheads, Northeast Atlantic Ocean Loggerheads, Southeast Indian Ocean
Nets	4	Leatherbacks, West Pacific Ocean Hawksbills, East Pacific Ocean Loggerheads, North Pacific Ocean Loggerheads, South Pacific Ocean
Trawls	2	Kemp's ridleys, Northwest Atlantic Ocean Green turtles, South Caribbean
Low risk–low bycatch impact (lower left quadrant)	23	
Longlines	15	Olive ridleys, West Atlantic Ocean Olive ridleys, West Pacific Ocean Leatherbacks, Northwest Atlantic Ocean Green turtles, East Pacific Ocean Green turtles, South Central Pacific Ocean Green turtles, West Central Pacific Ocean Green turtles, Southwest Pacific Ocean Green turtles, Southwest Atlantic Ocean Green turtles, Southwest Indian Ocean Hawksbills, West Atlantic Ocean Hawksbills, Southeast Indian Ocean Hawksbills, Southwest Indian Ocean Loggerheads, Northwest Atlantic Ocean Loggerheads, Mediterranean Sea

Table 6. Continued.

Fishing gear by impact	n	RMU (species, region)
Nets	4	Olive ridleys, West Atlantic Ocean Green turtles, Northwest Atlantic Ocean Hawksbills, West Atlantic Ocean Loggerheads, Mediterranean Sea
Trawls	4	Green turtles, Southwest Pacific Ocean Green turtles, Southeast Indian Ocean Green turtles, Northwest Atlantic Ocean Loggerheads, Northwest Atlantic Ocean

†Solitary and arribada RMUs.

bycatch (FAO Fisheries Department 2009; Lewison et al., *in press*). For example, Wallace et al. (2008) showed that body sizes of loggerheads taken as bycatch in Mediterranean longlines varied according to hook sizes and set depths, indicating that within the category of longline gear, relative bycatch impacts depended on target species and associated gear characteristics. Furthermore, mitigation measures are only successful if implemented properly and if compliance remains high (Cox et al. 2007, Finkbeiner et al. 2011). Nonetheless, successful mitigation testing and implementation efforts to reduce marine turtle bycatch in various fishing gears have increased greatly in recent years (see FAO Fisheries Department 2009 for review), including creative approaches to reducing small-scale fisheries bycatch (e.g., Wang et al. 2010, Alfaro-Shigueto et al. 2012), providing managers with numerous possible solutions to bycatch problems in various gears.

By combining bycatch rates with information on amounts of fishing effort associated with bycatch rates, mortality rates, and body sizes (i.e., proxy for reproductive values) of turtles taken as bycatch, we generated the most comprehensive assessment of bycatch population impacts on marine turtles to date. Bycatch impact scores varied within and among species, as well as within and among fishing gears, as most species and all gears appeared in each of the four risk-bycatch impact categories (Figs. 13 and 14, Table 5). This finding demonstrates that bycatch impacts are not necessarily related to generalities of broad gear categories or species-level life history traits, but rather vary based on region- or site-specific characteristics of fishing gear and practices, marine turtle habitat use, and underlying oceanographic features. Furthermore, just

as spatial distribution of observer coverage influences the accuracy of bycatch estimates (Sims et al. 2008), adequate spatial distribution of bycatch data in relation to turtle distribution within RMUs is necessary to produce accurate assessments of bycatch impacts on individual RMUs. Thus, detailed characterization of variation in fishing gear configurations and methods, as well as greater understanding of turtle responses to static and dynamic habitat features (e.g., Kobayashi et al. 2008, Shillinger et al. 2011) are necessary to improve understanding of marine turtle bycatch patterns (Watson et al. 2005, FAO Fisheries Department 2009, Gilman et al. 2009).

Identifying conservation and monitoring priorities among RMU-gear combinations

Only three of the 11 most endangered RMUs in the world (East Pacific leatherbacks and hawksbills, South Pacific loggerheads; Wallace et al. 2011) were categorized as high risk-high bycatch impacts for at least one of the three major gear categories (Fig. 14, Table 6). Yet, many RMU-gear combinations were not included in these analyses due to failure to meet our data reliability thresholds. Thus, our results and their implications are primarily limited to RMUs and regions that are relatively data-rich (Figs. 1, 4–10, Tables 5 and 6). Although we were not able to evaluate all RMU-gear combinations, the RMU-gear combinations identified as high risk-high bycatch impacts in this analysis should still be considered important targets for bycatch reduction efforts. For high risk RMUs with insufficient bycatch data to be included in the present analyses (e.g., West Indian and North Indian olive ridleys, North Indian green turtles, hawksbills, and loggerheads), efforts to enhance bycatch moni-

toring must occur simultaneously with bycatch reduction, given the acute conservation situation of these populations (Wallace et al. 2011).

On the other hand, low risk-low bycatch impact RMU-gear combinations also provide important insights for conservation strategies because they might represent areas where successful mitigation efforts have occurred that could be applicable elsewhere. For example, several RMUs that interact with longline gear in the Northwest Atlantic Ocean and North Pacific Ocean fell into this category, which could reflect the substantial efforts in these regions to monitor and reduce turtle bycatch through on-board observer programs and the implementation and compliance of several mitigation measures, including changes to hooks, bait, and spatio-temporal distribution of fishing effort (Watson et al. 2005, Gilman et al. 2006, Howell et al. 2008). Regionally focused analyses of bycatch patterns over time in response to mitigation efforts would shed light on this possibility, although the “snapshot” nature of the bycatch studies makes such analyses challenging. Regardless, where data exist to compare how marine turtle bycatch rates might have changed over time in relation to mitigation techniques, changes in fishing effort, gear configurations, etc., a description of these patterns would be very useful for subsequent efforts to reduce bycatch.

Caveats and assumptions of our methods

Our methods were intended to balance the inclusion of as much bycatch data as possible with the need for scientific rigor and confidence in results of data analyses. By using the number of records for RMU-gear combinations as a proxy for sample size, we were able to provide a rough estimate of reliability in results of our analyses. A disadvantage to using number of records as reliability thresholds was that many RMU-gear combinations were excluded from analyses (Figs. 13 and 14, Table 5), thus limiting our interpretation of bycatch impact globally. Nonetheless, these data reliability thresholds allowed us to highlight not only more reliable, possibly actionable results, but also underscore the need for enhanced observer effort and reporting to increase the reliability of bycatch impact estimates.

Another consequence of our methodological attempts to convert, standardize, weight, and

synthesize bycatch data across fishing gears and populations was the apparent failure to corroborate widely held perceptions about bycatch impacts in certain regions, gears, or RMUs. For example, Finkbeiner et al. (2011) found that shrimp trawl bycatch in the Northwest Atlantic (i.e., Gulf of Mexico and Southeast USA) accounted for >90% of all turtle bycatches across U.S. fisheries since 1990. However, reliable estimates of marine turtle bycatch in these fisheries based on thorough observer coverage are virtually non-existent. We only included observed—not extrapolated or estimated—bycatch rates in our analyses, and reported BPUE values in this fishery were evaluated to be low relative to other trawl bycatch rates. As a result, trawl bycatch impact scores for Northwest Atlantic loggerheads and Kemp’s ridleys were moderate (Table 5), in apparent contradiction to estimated impacts on these RMUs (Epperly et al. 2002, Finkbeiner et al. 2011).

Likewise, bycatch impact scores for North Pacific loggerheads appear low relative to what might be expected based on a published study of extraordinarily high bycatch rates in small-scale fisheries in Baja California Sur, Mexico (Peckham et al. 2007) (Figs. 1, 4–10, Table 5, Appendix B). In fact, this study was included in our dataset, but it was considered together with other records of bycatch that impacted this North Pacific loggerhead RMU. Therefore, despite these bycatch rates for longlines and nets being extremely high, the amounts of effort on which these bycatch rates were based were relatively very low compared to other bycatch records for this RMU. As a result, the weighted median BPUEs for this study were weighted down relative to raw values, which permitted a less biased comparison of these bycatch rates with others for similar gears impacting the same RMU. In addition, although body size data were available for loggerheads in the same study area (off Baja California Sur, Mexico) (Peckham et al. 2007), these body sizes were not reported for turtles observed as bycatch, so were excluded from our analyses.

Conclusions

This study is the first attempt to quantify potential impacts of fisheries bycatch on marine turtle RMUs worldwide by compiling and

analyzing available bycatch data from multiple fishing gears in a population context. Our analyses revealed an urgent need for increased monitoring of marine turtle bycatch in fisheries in several places (e.g., East Atlantic, Indian Ocean, Southeast Asia) and fishing gears (e.g., small-scale, coastal fisheries; nets and trawls) to enhance our ability to assess the population-level impacts of fisheries bycatch, and to identify priority fisheries in which conservation interventions are necessary. Regardless, where evidence for extremely high bycatch exists for RMUs (e.g., loggerheads and Kemp's ridleys in Northwest Atlantic trawls; North Pacific loggerheads in nets and longlines; olive ridleys in North Indian trawls [Gopi et al. 2006]), reduction of that bycatch should be a priority, especially if a RMU was identified as high risk by Wallace et al. (2011).

Prioritization of resources for bycatch reduction and monitoring across fishing gears for all marine turtle RMUs is a fundamental need for managers, funders, and researchers alike. Our analyses are not intended to replace or contradict ongoing conservation efforts to reduce bycatch of marine turtles. Where sufficient information and resources exist to support bycatch reduction efforts, we recommend that these efforts continue. However, if bycatch reduction is not currently occurring, or is still insufficient to reverse population impacts, especially for RMUs that we have highlighted as being threatened by high bycatch, we recommend that bycatch reduction strategies be developed, specifically for the fishing gears having the highest impacts (Fig. 14, Table 5). We recommend that our assessment framework be adapted to finer spatial and biological scales (e.g., within RMUs, geographic regions, oceanographic features) to improve evaluations of relative bycatch impacts and to effectively prioritize bycatch reduction measures for the fishing gears with highest impacts on marine turtle populations. We also encourage further application of comparable stock-assessment approaches to other megafauna taxa with similar life histories that are also threatened by fisheries bycatch, as is done for marine mammals in the U.S. (Taylor 2005, Moore et al. 2009). As more information on marine turtle bycatch becomes available in the future, this methodology can be updated for improved results to ensure

that conservation decision-making is based on the most current and accurate information possible.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Complete list of sources containing bycatch data used in the present study. Regional management units (RMUs; Wallace et al. 2010b) for which data were reported in each reference appear in **bold** at the end of the reference.

- Abdulqader, E. A. A. 2010. Turtle captures in shrimp trawl nets in Bahrain. *Aquatic Ecosystem Health and Management* 13:307–318. **Chelonia mydas Indian, Northwest**
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Captura de grandes peces pelagicos (pez espada y atunes) en el Atlantico Sudoccidental, y su interaccion con otras poblaciones. INAPE-Uruguay. **Caretta caretta Atlantic, Southwest; Chelonia mydas Atlantic, Southwest; Dermochelys coriacea Atlantic, Southeast; Dermochelys coriacea Atlantic, Southwest**

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APPENDIX B

Table B1. Results of Kruskal-Wallis Rank Sums test, with Steel-Dwass comparisons post-hoc test, of median mortality rates across subgears. Means \pm SD (number of records in parentheses) are shown in bold in the diagonal. Below the diagonal, test statistic results are shown for each pairwise comparison (significant differences $q > 3.268$; $p < 0.5$); above the diagonal, all significant pairwise comparisons with p -values < 0.05 are shown.

Subgear	Longlines				Nets				Trawls		
	Bottom	Pelagic	Surface/ drift	Other	Bottom	Drift	Fixed	Other	Bottom	Shrimp	Other
Longlines											
Bottom	0.23 \pm 0.29 (9)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Pelagic	2.267	0.06 \pm 0.16 (38)	NS	NS	<0.0001	NS	NS	0.0003	NS	0.0065	0.0051
Surface/ drift	2.653	1.780	0.01 \pm 0.01 (16)	NS	0.0006	NS	NS	0.0003	NS	0.0053	0.0042
Other	1.673	0.325	1.740	0.10 \pm 0.18 (33)	0.0009	NS	NS	0.005	NS	NS	NS
Nets											
Bottom	2.470	4.864	4.405	4.336	0.54 \pm 0.32 (14)	NS	NS	NS	NS	NS	NS
Drift	0.110	2.795	2.972	1.993	2.799	0.21 \pm 0.25 (17)	NS	NS	NS	NS	NS
Fixed	0.831	2.622	2.941	2.193	1.411	1.396	0.34 \pm 0.32 (17)	NS	NS	NS	NS
Other	1.193	4.577	4.585	3.921	1.188	1.576	0.889	0.41 \pm 0.36 (16)	NS	NS	NS
Trawls											
Bottom	0.591	1.644	2.359	1.252	2.577	0.597	0.842	1.537	0.19 \pm 0.34 (8)	NS	NS
Shrimp	0.050	3.855	3.909	2.999	3.255	0.387	0.824	1.185	1.548	0.23 \pm 0.21 (19)	NS
Other	0.840	3.918	3.964	3.022	2.301	1.029	-0.459	0.614	1.464	1.086	0.30 \pm 0.32 (15)

Table B2. Highest impact gear (i.e., longlines, nets, trawls) and subgears for sea turtle RMUs globally. Bycatch impact score (last column) is the average of weighted median BPUE score, mortality rate score, and body size score for each RMU-gear combination. All values are on low-medium-high scales, where low = 1, medium = 2, and high = 3 (see Table 2 for clarification). Bycatch impact scores calculated for RMU-gear combinations with ≤ 3 records both BPUEs and mortality rates are denoted with an asterisk (*).

RMU	Highest impact		Score			Bycatch impact
	Gear	Subgear	Weighted median BPUE	Mortality rate	Body size	
<i>Caretta caretta</i>						
NE Atlantic	Longlines	Pelagic longlines	2.50	1.50	1.00	1.67*
		Other longlines	2.50	1.50	1.00	1.67*
NW Atlantic	Nets	Fixed nets	2.00	3.00	2.00	2.33
		Bottom nets	2.00	3.00	1.00	2.00
		Other nets	1.50	1.50	3.00	2.00
SW Atlantic	Longlines	Bottom longlines	2.00	2.50	2.00	2.17
		Pelagic longlines	3.00	1.50	2.00	2.17
		Other longlines	3.00	1.50	2.00	2.17*
		Surface longlines	2.50	1.50	2.00	2.00*
		Other nets	2.00	3.00	2.00	2.33*
		Bottom trawls	3.00	2.00	2.00	2.33*
NE Indian	NA	Other longlines	1.50	2.00	1.00	1.50*
NW Indian	NA	Other longlines	1.00	3.00	1.00	1.67*
SE Indian	Trawls	Other trawls	1.50	2.50	3.00	2.33*
SW Indian	Longlines	Surface longlines	2.00	1.50	2.00	1.83*
		Pelagic longlines	2.00	2.00	1.00	1.67
Mediterranean	Trawls	Bottom trawls	1.50	1.50	2.00	1.67
		Other trawls	2.00	1.50	2.00	1.50
		Pelagic longlines	3.00	1.00	2.00	2.00
N Pacific	Longlines	Bottom longlines	3.00	3.00	1.00	2.33*
		Bottom net	2.00	3.00	1.00	2.00*
S Pacific	Trawls	Other trawls	2.00	2.50	3.00	2.50*
		Shrimp trawls	2.00	2.00	1.00	1.67*
<i>Chelonia mydas</i>						
Central Atlantic	NA	Other longlines	2.50	1.00	1.00	1.50*
E Atlantic	NA	Other trawls	1.50	3.00	1.00	1.83*
NW Atlantic	Nets	Other nets	1.50	1.00	2.86	1.79
S Caribbean	Nets	Other nets	2.00	2.00	2.20	2.07
		Fixed nets	2.00	3.00	1.00	2.00*
		Bottom nets	1.50	2.00	2.00	1.83
SW Atlantic	Nets, Trawls	Drift nets	2.50	1.00	2.00	1.83
		Other nets	2.50	3.00	2.00	2.50
		Drift nets	2.50	1.00	2.00	1.83
		Bottom nets	1.00	1.00	2.00	1.33
		Bottom trawls	3.00	2.00	2.00	2.33*
Mediterranean	Longlines	Surface longlines	2.50	1.00	3.00	2.17*
E Pacific	Trawls	Pelagic longlines	1.50	1.00	2.00	1.50
		Shrimp trawl	2.00	3.00	3.00	2.67
		Bottom longlines	2.50	2.00	3.00	2.50*
		Other nets	2.00	2.00	3.00	2.33
W Pacific	Longlines	Other longlines	1.50	1.00	1.00	1.17*
			1.00	1.00	1.00	1.00*
N Central Pacific	Longlines	Pelagic longlines	1.50	1.00	1.00	1.17*
		Other longlines	1.00	1.00	1.00	1.00*
S Central Pacific	Longlines	Pelagic longlines	1.00	3.00	1.00	1.67
W Central Pacific	Longlines	Pelagic longlines	2.00	1.50	1.00	1.50
NW Pacific	NA	NA	ND	ND	ND	ND
SW Pacific	Trawls	Shrimp trawls	2.00	2.00	1.00	1.67*
		Other trawls	2.00	2.00	1.00	1.67*
<i>Dermochelys coriacea</i>						
NW Atlantic	Nets	Other nets	2.00	2.00	3.00	2.33
		Drift nets	2.00	2.00	1.00	1.67
		Pelagic longlines	2.50	1.00	2.90	2.13
SE Atlantic	Longlines	Pelagic longlines	2.15	1.00	3.00	2.17
		Surface longlines	2.00	1.00	3.00	2.00*
		Bottom net	3.00	3.00	3.00	3.00*
SW Atlantic	Longlines	Pelagic longlines	2.15	1.00	3.00	2.17
		Surface longlines	2.00	1.00	3.00	2.00*

Table B2. Continued.

RMU	Highest impact		Score			
	Gear	Subgear	Weighted median BPUE	Mortality rate	Body size	Bycatch impact
		Bottom net	3.00	3.00	3.00	3.00*
NE Indian	NA	Other nets	1.00	3.00	3.00	2.33*
SW Indian	Longlines	Surface longlines	2.00	1.00	3.00	2.00*
		Pelagic longlines	2.00	2.00	1.00	1.67*
E Pacific	Nets	Drift nets	1.50	2.50	2.50	2.17
		Other nets	2.00	2.50	2.00	2.17
		Bottom nets	1.50	3.00	1.00	1.83*
W Pacific	Longlines	Pelagic longlines	1.50	1.00	3.00	1.83
		Drift nets	1.50	2.00	3.00	2.17
<i>Eretmochelys imbricata</i>						
E Atlantic	NA	NA	ND	ND	ND	ND
SW Atlantic	NA	NA	ND	ND	ND	ND
W Atlantic	Trawls	Shrimp trawls	1.50	1.50	2.50	1.83*
		Bottom trawls	1.00	3.00	1.00	1.67*
		Drift nets	2.00	3.00	1.00	2.00*
NE Indian	NA	NA	ND	ND	ND	ND
NW Indian	NA	NA	ND	ND	ND	ND
SE Indian	Longlines	Other longlines	2.50	1.00	1.00	1.50
		Pelagic longlines	1.50	1.50	1.00	1.33*
SW Indian	Longlines	Pelagic longlines	2.00	2.00	1.00	1.67
		Surface longlines	2.00	1.00	1.00	1.33*
E Pacific	Trawls	Shrimp trawl	2.00	3.00	3.00	2.67
		Other nets	2.00	3.00	1.00	2.00*
SW Pacific	Trawls	Other trawls	1.50	2.50	3.00	2.33
		Shrimp trawls	2.00	2.00	1.00	1.67
W Pacific	NA	Other longlines	1.50	1.00	1.00	1.17*
		Surface longlines	1.00	1.00	1.00	1.00*
N Central Pacific	Longlines	Pelagic longlines	1.50	1.00	1.00	1.17*
		Other longlines	1.00	1.00	1.00	1.00*
S Central Pacific	Longlines	Pelagic longlines	1.00	1.00	1.00	1.00
W Central Pacific	Longlines	Pelagic longlines	2.00	1.50	1.00	1.50
		Bottom longlines	1.00	1.00	1.00	1.00*
<i>Lepidochelys kempii</i>						
NW Atlantic	Nets	Other nets	2.00	2.00	2.00	2.00
		Fixed nets	3.00	1.50	1.00	1.83
<i>Lepidochelys olivacea</i>						
E Atlantic	Longlines	Pelagic longlines	2.00	1.00	2.00	1.67*
		Other longlines	2.00	2.00	1.00	1.67*
W Atlantic	Nets	Drift nets	2.50	2.00	1.00	1.83
		Other nets	2.00	1.50	1.00	1.50*
NE Indian†	NA	NA	ND	ND	ND	ND
W Indian	NA	Other longlines	1.50	3.00	1.00	1.83*
E Pacific‡	Nets	Other nets	2.00	3.00	1.00	2.00
		Bottom longlines	2.50	2.00	3.00	2.75*
		Pelagic longlines	2.50	1.00	3.00	2.17
W Pacific	Trawls	Shrimp trawls	2.00	2.00	3.00	2.33*
		Other trawls	1.50	1.50	3.00	2.00
<i>Natator depressus</i>						
SE Indian	Trawls	Other trawls	2.00	2.00	3.00	2.33*
		Shrimp trawls	2.00	2.00	1.00	1.67*
SW Pacific	Trawls	Other trawls	2.00	2.00	3.00	2.33*
		Shrimp trawls	2.00	2.00	1.00	1.67*

† NE Indian, *L. olivacea* arribada RMU and solitary RMU have identical bycatch results.

‡ E Pacific *L. olivacea* arribada RMU and solitary RMU have identical bycatch results.