

Impacts of fisheries bycatch on loggerhead turtles worldwide inferred from reproductive value analyses

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Summary

1. Fisheries bycatch has been implicated in declines of many long-lived marine vertebrate populations, but bycatch impacts on these populations vary according to spatio-temporal overlap in fisheries operations and critical ontogenetic habitat, as well as to characteristics of fishing gear.
2. To provide a framework for comparing the relative impacts of different fisheries on populations of loggerhead sea turtles *Caretta caretta*, we compiled published data on sizes of individual loggerheads taken as bycatch in North Atlantic, North Pacific and Mediterranean fisheries, and used Leslie matrix models to calculate reproductive values (RVs) for bycatch samples of loggerheads within these basins.
3. Sizes and RVs of loggerheads varied significantly based on spatial overlap in fisheries and ontogenetic habitat as well as on fishing gear. Thus, fisheries operating in areas occupied by larger, older turtles (e.g. trawls in neritic areas) tended to interact with more reproductively 'valuable' turtles than fisheries that operated in areas occupied by smaller, younger turtles (e.g. oceanic and pelagic longlines).
4. We also found evidence of size-selectivity among different fishing gears (e.g. wider size variation among loggerheads taken in driftnets and trawls than in longlines) and gear configuration (e.g. smaller loggerheads in shallow longline sets using small hooks).
5. These results suggest that evaluation of fishery impacts on marine megafauna require characterization of fishery activities; understanding of species biology must be considered in order to determine population impacts of fisheries bycatch. Data access and quality can be improved and uncertainty reduced by increasing independent observer coverage on fishing vessels throughout the world's oceans.
6. *Syntheses and applications.* Our analyses demonstrate that application of reproductive values can allow fisheries managers and biologists alike to identify the most influential bycatch threats to geographically widespread populations of long-lived marine vertebrates, thereby facilitating prioritization of conservation actions and successful management of these animals. For example, our results suggest that effective management of loggerhead catch in trawl gear should be one of the top priorities for conservation of loggerhead populations worldwide.

Key-words: reproductive values, fisheries bycatch, long-lived vertebrates, sea turtles, matrix population models, life history, marine conservation

Introduction

Many long-lived marine vertebrates (e.g. marine mammals, seabirds, sea turtles, elasmobranchs) occupy broad geographic

ranges traversing international boundaries and oceanographic features. Several populations of these species are declining due to combinations of different threats encountered across their ranges. Specifically, incidental capture in fishing gear (bycatch) can have profound impacts on populations of long-lived marine taxa (Reeves *et al.* 2003; Lewison, Freeman

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& Crowder 2004; Heppell *et al.* 2005). Because most large marine vertebrates occupy different ocean habitats during different life stages, spatially distinct fisheries operations can have differential impacts on the same population of animals. The relative population-level impact of bycatch depends on the frequency of interactions, lethality of the gear, and the life stage(s) most frequently affected (Crouse, Crowder & Caswell 1987; Heppell *et al.* 2005). Thus, management strategies should identify relative population-level impacts of different fisheries across a population's range to ensure effective prioritization of limited conservation resources (Crowder *et al.* 1994; Gerber & Heppell 2004).

The types and frequency of interactions between fishing gear and protected species depend not only on the extent of spatio-temporal overlap of fishing activities and critical habitat for a given species, but also on fishing methods and gear characteristics. Effective management strategies to reduce bycatch must integrate fisheries operations and protected species biology (Kraus *et al.* 1997; Epperly *et al.* 2002; Gilman *et al.* 2006). For example, studies of spatio-temporal relationships between certain fisheries and protected species habitat have led to the establishment of marine protected areas (Hooker & Gerber 2004) and time-area fishery closures (Carretta *et al.* 2004). In addition, differences in gear characteristics (e.g. longline hook size and shape, gillnet mesh size, set depth) can result in differences in species or sizes (i.e. age classes) of individuals taken as bycatch (Epperly *et al.* 2002; Watson *et al.* 2005). Consequently, management measures can include gear modifications to improve selectivity of catch and to reduce bycatch (Epperly *et al.* 2002; Heppell *et al.* 2005; Gilman *et al.* 2006).

Assessing population-level responses to bycatch requires knowledge of life stages of individuals interacting with different fisheries, and of population structure and vital rates (e.g. age/stage-based survival, growth, and fertility). Incorporating this life-history information into deterministic matrix models allows estimation of asymptotic population growth rates (λ), as well as stable age distributions and age- or stage-specific reproductive values (Caswell 2001). In particular, elasticity (proportional sensitivity) analyses of such matrix models are commonly employed to determine population responses to proportional changes in different demographic parameters – particularly those affected by anthropogenic perturbations – for the purposes of directing research or conservation efforts (Crouse, Crowder & Caswell 1987; Gerber & Heppell 2004).

In addition to applications of elasticity analyses, determinations of age-specific reproductive values (RVs) of individuals from a vulnerable population can also inform conservation and management strategies. RVs represent the relative contribution of individuals within an age-class to current and future reproduction (Fisher 1930), and are a combination of estimates of age- or size-specific survival and current and future potential fecundity. Unlike elasticity analysis, which examines the effects of proportional changes in *rates* of survival, growth or reproduction, a comparative assessment of RVs can provide information about the relative 'reproductive value' of *individuals*

in distinct age- or size-classes (Caswell 2001). RVs typically are scaled to the value of newborns and are low for early life stages, reach maximum levels at or near the onset of sexual maturity, and decline with adult age (Caswell 2001).

Approaches using RVs highlight the importance of considering how threats to specific life stages affect population-level processes. RV and 'reproductive potential' – the sum of reproductive values for a population with a fixed survivorship curve – have been used to examine the effects of fishing on marine vertebrate populations (Caddy & Seijo 2002). For example, Gallucci, Taylor & Erzini (2006) examined RVs of shark populations resulting from various harvest strategies to determine optimal conservation strategies that preserved the reproductive potential of these populations. In addition, Lewison & Crowder (2007) suggested that sea turtle bycatch in pelagic longlines involve older age classes with relatively high RVs, while recognizing that there is a lack of comparable information for other gear types. Further, the Atlantic Loggerhead Recovery Plan Team, convened by the US National Marine Fisheries Service (NMFS) and the US Fish and Wildlife Service (USFWS), scaled various threats to loggerheads by RVs to compare potential population impacts and to set conservation priorities (NMFS & USFWS 2008). Thus, because geographically distinct life stages of protected marine species often interact with spatially separate fisheries, estimation of RVs of individuals taken as bycatch across a population's range, rather than in only one place or in one fishery, would facilitate comparison of population-level impacts of different fisheries.

Similar to other long-lived marine vertebrates, sea turtles occupy broad geographic ranges including separate nesting and foraging areas utilized by adults, as well as geographically distinct ontogenetic habitats (Musick & Limpus 1997). In particular, loggerhead sea turtle *Caretta caretta* (Linnaeus 1758) populations worldwide exhibit trans-oceanic life cycles in which post-hatching juveniles initially are transported by major current systems to typically oceanic feeding areas before recruiting to neritic areas as large juveniles (subadults) several years later (Bolten 2003). Fisheries bycatch has been implicated in population declines of several species of sea turtles worldwide, including loggerheads (TEWG 2000; NMFS SEFSC 2001; Bolten 2003; Lewison, Freeman & Crowder 2003; Lewison, Crowder & Shaver 2004). Due to their ocean basin-wide ranges, loggerhead populations presumably encounter different bycatch risks from distinct fisheries, depending on stage-dependent habitat use and fishing operations present in a given region. However, assessment of relative impacts of bycatch in different fisheries on a loggerhead population across its range has not been conducted, but could aid managers in setting conservation priorities.

Our primary objective was to facilitate a qualitative comparison of the relative potential effects of different fisheries on loggerhead populations around the world by determining whether size distributions and RVs of loggerheads recorded as bycatch across a population's range varied according to (i) geographic areas corresponding to overlap in different fisheries and ontogenetic habitats, and to (ii) fishing gear

characteristics. Our results, when considered with estimates of interactions and mortality rates of turtles in fisheries, reinforce the importance of integrating effects of threats to different life stages of marine vertebrates to enhance understanding of population-level responses to multiple perturbations.

Methods

BODY SIZE DISTRIBUTIONS OF LOGGERHEADS INTERACTING WITH GLOBAL FISHERIES

We used published research and fisheries observer data (obtained by official data request: US NMFS Southeast Fisheries Science Center and Pacific Island Fisheries Science Center) to compile or construct body size (carapace length) distributions of loggerheads taken as bycatch (observed interactions with fishing gear) in various global fisheries or of beach-stranded loggerheads (often used as a proxy for fisheries-related bycatch mortality; e.g. Crowder, Hopkins-Murphy & Royle 1995; TEWG 2000; Gardner & Nichols 2001; Lewison, Crowder & Shaver 2003). Loggerhead size data were available for samples from the North Atlantic (NA), the North Pacific (NP) and the Mediterranean (Table 1). Because turtle size data were recorded using multiple methods (e.g. curved and straight carapace length), we

converted all straight carapace length data to notch-to-tip standard curved carapace length (CCL) following Teas (1993).

CALCULATION OF RVs FROM SIZE-SPECIFIC BYCATCH DATA

To calculate 'intrinsic' RVs (i.e. assuming natural survival and mortality schedules) for loggerheads taken as bycatch in a particular area and fishery, we used deterministic, female-based, age-structured (Leslie) matrix models to estimate the average RV for each age class and applied those RVs to each bycatch sample based on the estimated range of age classes affected by a particular fishery. First, we derived age distributions from the size distributions given for each bycatch sample using the von Bertalanffy growth function (VBGF). Because the vital rates for many loggerhead populations are unknown, we constructed matrix models under two different scenarios – 'slow growth–high reproduction' and 'fast growth–low reproduction' – with the intent of bracketing natural variation and uncertainty in demographic parameters. The 'slow' and 'fast' growth parameters indicated early or late onset of maturity, respectively (see Table 2 for parameter values associated with each scenario). The fecundity terms (number of female offspring adult female⁻¹ year⁻¹) were based on estimates of 4.1 clutches, 115 eggs per clutch, 0.7 egg survival, and 0.5 sex ratio (Heppell *et al.* 2003), and a 2- or a 3-year remigration interval for 'high' and 'low' fecundity, respectively. The combinations

Table 1. Data sets with reported loggerhead size distributions. Abbreviations for 'Data type': LL-ALB, albacore tuna longlines; LL-SWO, swordfish longlines; LL-BFT, bluefin tuna longlines

Population	Bycatch area	Period	Data type	Source
North Atlantic	US ATL	1992–2004	Longline	NMFS–SEFSC observer data
	US ATL	1996–1997	Strandings	TEWG 2000
	Azores	2000	Longline	Bolten 2003
North Pacific	Mexico	1999	Strandings	Gardner & Nichols 2001
	Hawaii	1999–2005	Longline	NMFS–PIFSC observer data
	North Pacific	1990–1992	Gillnet	Wetherall <i>et al.</i> 1993
Mediterranean	Spain	1999–2000	Longline	Camiñas & Valeira 2001
	Spain	1999–2000	LL-ALB	Camiñas & Valeira 2001
	Spain	1999–2000	LL-SWO	Camiñas & Valeira 2001
	Spain	1999–2000	LL-BFT	Camiñas & Valeira 2001
	Italy	1999–2000	Longline	De Metrio & Deflorio 2001
	Italy	1999–2000	LL-ALB	De Metrio & Deflorio 2001
	Italy	1999–2000	LL-SWO	De Metrio & Deflorio 2001
	Italy	1999–2000	Trawl	De Metrio & Deflorio 2001
	Turkey	1995–1996	Strandings	Oruc, Demirayak & Sat 1997

Table 2. Stage designation parameters for two different Leslie matrix models; one for North Atlantic and North Pacific loggerhead populations, and the other for Mediterranean loggerheads. See text for details on methods

Populations	Stage	Survival rates (fast–slow)	Size (cm, SCCL)	Estimated age (fast growth)	Estimated age (slow growth)
North Atlantic, North Pacific	Small oceanic juvenile	0.83–0.85	< 44	1–5	1–6
	Small neritic juvenile	0.83–0.85	44–74.9	6–13	7–18
	Large neritic juvenile (subadult)	0.83–0.85	75–98.9	14–24	19–34
Mediterranean	Adult	0.90	≥ 99	25+	35+
	Small oceanic juvenile	0.83–0.85	< 38	1–6	1–8
	Small neritic juvenile	0.83–0.85	38–69.9	7–13	9–24
	Large neritic juvenile (subadult)	0.83–0.85	70–85.9	14–24	25–34
	Adult	0.90	≥ 86	25+	35+

of 'slow' growth with high reproduction and fast growth with low reproduction give the largest difference in potential adult RV. Because we incorporated first-year survival into the fecundity term (i.e. the models are based on a pre-breeding census; Caswell 2001), we did not include an egg/hatchling stage in the model.

Our models included four life stages generally following the stage designations of the Turtle Expert Working Group (TEWG) convened by NMFS from 1995–1999 (TEWG 2000): small oceanic juveniles, small neritic ('benthic' in TEWG 2000) juveniles, large neritic juveniles (subadults), and adults (Table 2). Because juvenile survival rates are poorly known, we incorporated a standardized juvenile survival rate estimate that resulted in $\lambda = 1$ for each growth–fecundity scenario (Table 2) instead of assigning stage-specific survival rates for juveniles and subadults. We based our selection of values of age-stage relationships and adult survival rates for the matrix models on available literature values (TEWG 2000; Tiwari & Bjorndal 2000; NMFS SEFSC 2001; Heppell *et al.* 2003). Further, the final row/column of our matrices represented the adult stage because we assumed that all adult turtles had the same annual survival rate and because sea turtle life spans are unknown, following the method of Crowder *et al.* (1994). Because Mediterranean nesting females are typically smaller than nesting females from other global rookeries (Tiwari & Bjorndal 2000), we constructed a von Bertalanffy growth function and matrix model specifically for Mediterranean bycatch samples to estimate size–age relationships and RVs more appropriately for these individuals (Table 2). We then derived RVs from all matrix models to allow comparison across fisheries within basins and to prioritize relative threats of different fisheries to loggerhead populations.

RVs for each age class in the two alternative life-history models – given by the left eigenvector of the matrices – were calculated using POPTOOLS Add-in for Microsoft Excel (available through CSIRO: www.poptools.org) and scaled to the adult stage RV (adult RV = 1.0). This allowed us to compare the RVs of the bycatch samples using a common currency of 'adult equivalents,' as defined by the Atlantic Loggerhead Recovery Team (NMFS & USFWS 2008).

ASSUMPTIONS AND CAVEATS

Given the formidable gaps in knowledge of loggerhead demography and ecology, we were required to make several assumptions regarding fisheries-related mortality, size–age relationships, class-specific fisheries mortality estimates, and the degree of geographic overlap of distinct reproductive populations.

Strandings data as a proxy for fisheries-related turtle mortality

Beach strandings of dead sea turtles represent a sub-sample of the total number of dead turtles present in a given region, including those associated with fisheries-related mortality (Lewison, Crowder & Shaver 2003). As such, beach strandings data can be useful metrics in population assessments because they accurately represent body size distributions of the in-water population (TEWG 2000; NMFS SEFSC 2001). However, parsing the relative contribution of fisheries-related mortalities from the overall number of beach strandings is not straightforward. Nonetheless, several studies have correlated patterns of beach strandings with seasonality and intensity of trawl fishing (Crowder, Hopkins-Murphy & Poyle 1995; TEWG 2000; Epperly *et al.* 2002; Lewison, Crowder & Shaver 2003). With these issues in mind, we discuss with caution our analyses of strandings data as a proxy for fisheries-related mortality.

Size-at-age relationships and mortality estimates

Size-specific growth rates and mortality rates are known in relatively few cases for sea turtles, but have enormous implications for understanding size–age relationships and population dynamics in different species (Chaloupka & Musick 1997). Stage designations (according to size) in our models were set rigidly, thus eliminating variability in age and size at which ontogenetic shifts occur. This resulted in disproportionately large differences in RVs corresponding to small differences in size of loggerheads taken as bycatch (see Results). Additionally, recent findings regarding behavioural dichotomies of juvenile (McClellan & Read 2007) and adult loggerheads (Hatase *et al.* 2002; Hawkes *et al.* 2006) highlight the potential importance of within-stage variation in several life-history traits, including growth rates and mortality rates. Incorporating such variability would more realistically approximate size and RV distributions of wild populations of loggerheads. Thus, given the uncertainty associated with assigning stage-specific juvenile survival rates, we chose to incorporate an average juvenile and subadult survival rate for all age classes in our models (Table 2).

Further, our analyses included all interactions between loggerheads and fisheries, without incorporating differential mortality rates associated with distinct fisheries based on size or stage. Because general trends in variability in size–age relationships and appropriate stage-specific mortality rates for loggerheads are poorly understood, we chose to simplify our models to approximate 'intrinsic' RVs of loggerheads according to reported values from empirical studies.

Geographic overlap of Mediterranean and Atlantic loggerhead populations

Juveniles of both western Atlantic and eastern Mediterranean nesting populations occur in the western Mediterranean (Laurent *et al.* 1998) and their geographic ranges are influenced by ocean surface current dynamics (Carreras *et al.* 2006). Despite this well-established sympatry, we designated all loggerheads caught in Spanish longlines in the western Mediterranean to the Mediterranean population because reported size data from Camiñas & Valeira (2001) were not accompanied by data on the geolocations of interactions nor genetics for individual turtles upon which a valid geographic separation could be based.

Results

SIZES AND RVs OF LOGGERHEAD BYCATCH SAMPLES

As expected, RVs derived from our matrix models and scaled to the adult stage increased from minimum values for small, young turtles to maximum values at the onset of sexual maturity (Fig. 1). North Atlantic (NA) and North Pacific (NP) loggerhead RVs peaked at larger sizes than did RVs of Mediterranean loggerheads (Fig. 1a) due to the observed differences in adult body size and the growth functions and matrix models that we applied to these populations. With respect to size (Fig. 1a) and age (Fig. 1b), RVs increased more rapidly in the fast growth–low reproduction scenarios (i.e. where turtles reached sexual maturity at younger ages) than in slow growth–high reproduction scenarios. Thus, both changes in fecundity and age at sexual maturity can affect RVs considerably. To simplify the remainder of this study, we

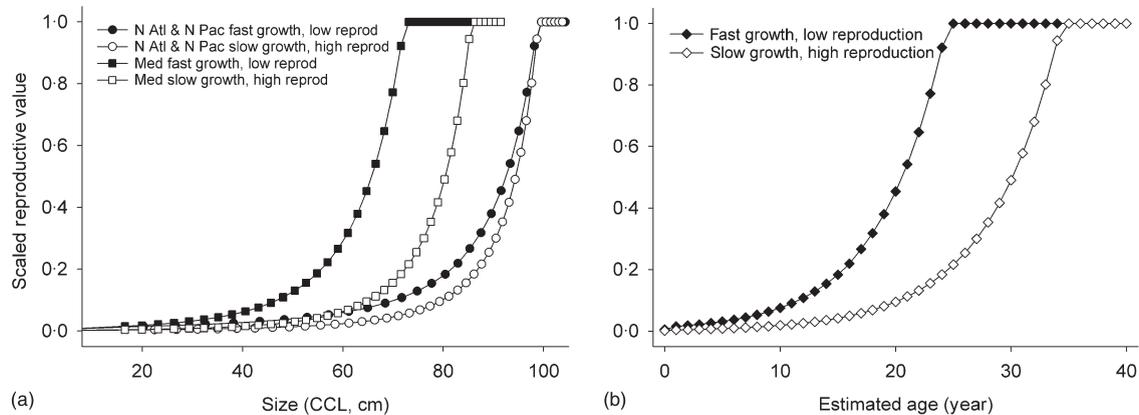


Fig. 1. Reproductive values (scaled to adults) of North Atlantic, North Pacific, and Mediterranean loggerhead populations relative to (a) size [curved carapace length (SCCL)] and to (b) estimated age with two different growth-fecundity scenarios.

Table 3. Mean sizes, estimated ages, and reproductive values of loggerheads taken as bycatch in global fisheries arranged by geographic population. Ages were derived from von Bertalanffy growth functions under 'fast' and 'slow' growth scenarios, respectively, and reproductive values (scaled to the adult stage) were calculated based on 'slow growth, high reproduction' and 'fast growth, low reproduction' scenarios, respectively. See text and Table 1 for details on methods and input parameters. Mortality rates and estimated total interactions were from *NMFS (2001); †Epperly *et al.* (2002) for US trawl fishery; ‡Gilman *et al.* (2006). Mortality rates in bold indicate inclusion of post-release mortality estimates. NA, not available

Population	Bycatch area	N (body sizes)	Mean size (SCCL; cm) (±SD)	Size range (SCCL; cm)	Mean estimated ages (year)	Mean reproductive values	Reported mortality rate (%)	Estimated total interactions (no. of turtles year ⁻¹)
North Atlantic	US ATL-LL	319	75.2 (15.2)	39–118	14.4–19.8	0.20–0.25	17–42*	989*
	US ATL-strandings	2583	78.5 (16.6)	49–120	16.1–22.3	0.28–0.32	39†	10 000–60 000†
	Azores-LL	232	50.0 (7.4)	25–75	6.1–8.5	0.02–0.04	NA	NA
North Pacific	Mexico-strandings	141	58.8 (12.6)	23–86	8.6–11.6	0.03–0.07	NA	NA
	Hawaii-LL	44	64.8 (9.9)	51–91	10.2–13.8	0.05–0.10	15‡	300‡
	North Pacific-driftnet	144	47.6 (20.1)	12–90	6.3–8.4	0.03–0.06	27	5000
Mediterranean	Spain-LL (ALL)	671	54.4 (11.6)	20–80	11.1–15.4	0.07–0.12	4.0	NA
	Spain-LL ALB	117	39.1 (9.6)	20–79	6.6–8.8	0.02–0.05	4.3	NA
	Spain-LL BFT	217	59.8 (8.2)	40–79	12.8–17.8	0.09–0.14	3.9	NA
	Spain-LL SWO	337	56.3 (9.5)	31–80	11.6–16.1	0.07–0.12	4.1	626–3090
	Italy-LL (ALL)	216	41.1 (10.3)	19–77	7.1–9.5	0.02–0.05	NA	NA
	Italy-LL ALB	85	36.9 (7.3)	20–61	5.9–7.8	0.01–0.04	0	74–132
	Italy-LL SWO	131	43.8 (11.1)	19–77	7.9–10.7	0.03–0.06	0	36–106
	Italy-trawl	61	53.9 (11.4)	25–85	10.8–15.0	0.07–0.12	14	613–6563
Turkey-trawl	86	56.5 (20.9)	30–110	12.0–17.0	0.17–0.21	13	NA	

present RV results for only the slow growth, high fecundity scenario from each population because it most closely represents reported population means for these parameters (Tiwari & Bjorndal 2000; Heppell *et al.* 2003).

NORTH ATLANTIC

Sizes of loggerheads taken as bycatch in the NA were smallest in Azores longlines, larger in US Atlantic longlines, and largest in US Atlantic strandings (presumed to partially represent interactions with the US shrimp trawl fishery; Crowder, Hopkins-Murphy & Royle 1995; TEWG 2000) ($F_{2,3230} = 272.7$, $P < 0.0001$; Table 3). Over 98% of loggerheads that interacted with the Azores longline fishery were small juveniles (< 75 cm), whereas only about 50% of loggerheads in US Atlantic longlines and US Atlantic strandings were

small juveniles, with the remainder comprised of large neritic juveniles (subadults) and adults (Fig. 2a). RVs increased following the size and life-stage distribution patterns for NA loggerhead bycatch (stranding) samples (Fig. 2b).

NORTH PACIFIC

Sizes of loggerheads caught in the NP driftnet fishery were significantly smaller than the other bycatch (strandings) samples in the NP ($F_{2,326} = 27.2$, $P < 0.0001$; Table 3). Whereas nearly 32% of the loggerheads that interacted with the NP driftnet fishery were oceanic juveniles (< 44 cm SCCL), only 0–12% of loggerheads in Mexico strandings and caught in the Hawaiian longline fishery were oceanic juveniles (Fig. 2c). RVs increased following the size and life-stage distribution trends for NP loggerhead bycatch (strandings) samples (Fig. 2d).

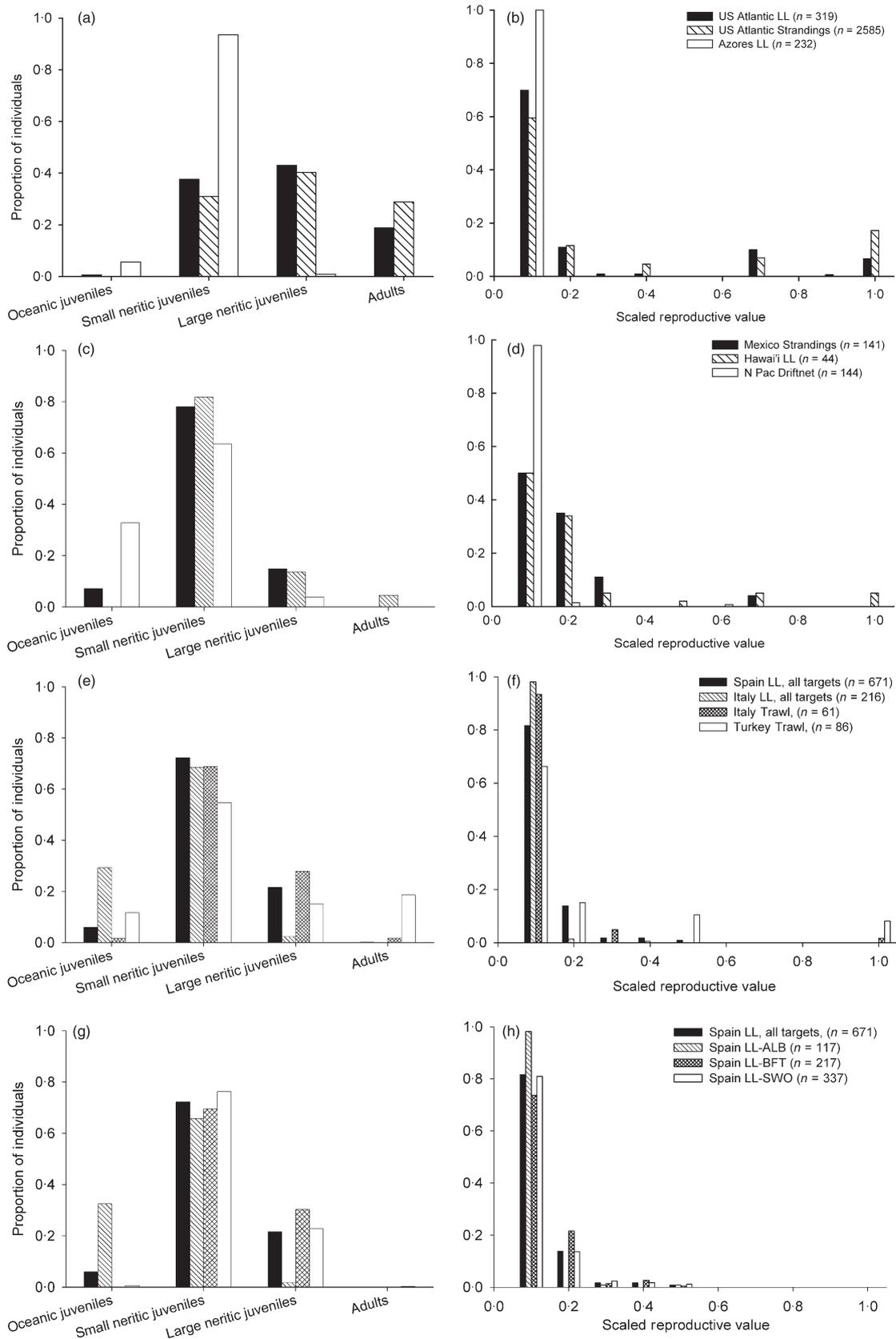


Fig. 2. Relative proportions of life stages (left column) and reproductive values (scaled to adults; right column) of loggerhead bycatch samples from fisheries in the (a, b) North Atlantic, (c, d) North Pacific, (e, f) Mediterranean, and (g, h) Spanish longline fisheries.

MEDITERRANEAN

Sizes of loggerheads increased across bycatch samples from Italian longlines to Spanish longlines and Italian trawls to Turkish trawls; however, only Italian longline loggerhead sizes were significantly smaller than the other Mediterranean groups ($F_{3,1030} = 68.2$, $P < 0.0001$; Table 3). Loggerheads taken as bycatch in the Italian longline fishery yielded the lowest average RVs (> 40% oceanic juveniles), whereas loggerhead RV increased from Spanish longline (9% oceanic juveniles) and Italian trawl fisheries (8% oceanic juveniles) to the Turkish trawl fishery (34% subadults and adults) (Table 3; Fig. 2e,f).

There were also significant differences in sizes and RVs of loggerheads taken as bycatch in Spanish and Italian longlines depending upon target species of sets. In the Spanish longline fishery, loggerhead sizes were smallest in albacore tuna *Thunnus alalunga* (ALB) sets, larger in swordfish *Xiphias gladius* (SWO) sets, and largest in bluefin tuna *Thunnus thynnus* (BFT) sets ($F_{2,668} = 208.9$, $P < 0.0001$; Table 3). RVs increased following the size distribution patterns among these target species in Spanish longline sets, with ALB sets catching nearly 50% oceanic juveniles and SWO and BFT sets catching < 2% oceanic juveniles (Fig. 2g,h). Likewise, loggerheads caught in Italian longlines targeting SWO were significantly larger than those caught in ALB longlines ($F_{1,215} = 49.4$, $P < 0.0001$; Table 3). Italian longlines targeting ALB caught significantly fewer reproductively valuable loggerheads (~60% oceanic juveniles) than did Italian longlines targeting SWO (~30% oceanic juveniles) (Table 3).

Discussion

Patterns of size distributions and RVs of loggerhead turtles taken as bycatch (or beach-stranded) generally reflected overlap between fisheries activities and ontogenetic habitats for different life stages of loggerheads and also revealed how different gear types influence the size of turtles taken as bycatch. Our approach combining published field data with basic life-history models provides a useful framework for conservation decision-makers to compare population-level impacts of fishery activities that disproportionately affect certain life stages. Application of this approach could also improve conservation strategies for populations of other long-lived marine vertebrates.

It is important to point out that evaluating the relative impact of several fisheries on marine megafauna populations requires consideration of the total number of interactions with each fishery, the estimated mortality rate for that gear type, and the mean RV for the size- or age-distribution of animals caught and killed. By itself, the RV calculation simply allows the effects of bycatch to be compared with a 'common currency'; a fishery that kills a large number of low RV animals may have a greater impact than one that kills a small number of high RV animals. There is considerable uncertainty in empirical estimates of interactions and mortality rates for many fisheries; such data are unavailable for many fisheries (Table 3).

This uncertainty could be addressed, in part, by enhancing the extent and quality of independent fisheries observer coverage in most of the world's fishing fleets because most observer programmes cover only a small proportion of the total effort in a given fishery across its geographic range of operation (NMFS 2001). Additionally, although there are relatively few available post-release mortality rates of turtles released alive after interactions with fishing gear, improved estimates are possible through strategic deployment of satellite transmitters on turtles taken as bycatch and subsequently released (Swimmer *et al.* 2006). Nonetheless, our analysis of RVs of loggerheads in bycatch is the first global comparison of fisheries' impacts on widespread marine vertebrate populations, and thus serves as an important starting point for further research.

RVS ACROSS GEOGRAPHIC AREAS

Differences in sizes and RVs of loggerheads taken as bycatch in distinct geographic areas varied significantly with ontogenetic habitats in each ocean basin we examined. In general, loggerheads caught in trawl gear were larger and had higher RVs than those caught in longlines (Table 3), probably reflecting spatial overlaps between these fisheries operations and differences in habitat use (i.e. larger juveniles and adults interacting with trawls in neritic habitats and smaller juveniles interacting with longlines in oceanic and pelagic habitats). Small loggerhead sizes and low RVs corresponded to longline bycatch in oceanic waters that are well-established developmental habitats for small juvenile loggerheads near the Azores in the NA (Bjorndal, Bolten & Martins 2000a; Bolten 2003) and in the Mediterranean (Laurent *et al.* 1998; Carreras *et al.* 2006). In contrast, larger juveniles and adults tend to occupy neritic habitats on the North American continental shelf (Crouse, Crowder & Caswell 1987; Bjorndal *et al.* 2000b; Bolten 2003) and in the eastern Mediterranean basin (Margaritoulis *et al.* 2003) where trawl fisheries tend to operate (Oruc, Demirayak & Sat 1997; Epperly *et al.* 2002; De Metrio & Deflorio 2001). While the overall impact of these fisheries on loggerhead populations depends on the total number of interactions, we speculate that loggerhead bycatch in trawls has a larger impact than longline gear in both basins because the estimated total loggerhead mortality in the US Atlantic trawl fishery is thought to exceed that estimated for the US Atlantic longline fishery by more than two orders of magnitude, and reported loggerhead mortality rates in the Mediterranean were higher in trawls than in longlines (Table 3). Thus, our results suggest that effective management of loggerhead bycatch in trawl gear should be one of the top priorities for conservation of loggerhead populations worldwide.

In the NP, juvenile loggerheads from Japanese nesting beaches tend to settle in coastal foraging habitats off México before returning to the western Pacific as neritic subadults (Peckham *et al.* 2007), making the subtropical transition zone current system north of Hawai'i an important corridor for developmental migrations of loggerheads (Polovina *et al.* 2006). While total estimated loggerhead mortality appeared to be greatest in the NP driftnet fishery (Table 3) (~90% were

small juveniles), Peckham *et al.* (2007) recently reported that artisanal fisheries off México are likely to have a similar or greater impact because of the high mortality of large juvenile and subadult loggerheads ($> 1000 \text{ year}^{-1}$) documented in just two small fleets. Fortunately, ongoing efforts to reduce bycatch on juvenile foraging grounds and reproductive areas in the NP show promise for increasing juvenile and adult recruitment in these populations (Peckham *et al.* 2007). Considering the findings discussed in this section, adequate quantification of sea turtle–fishing gear interactions – especially in trawls and artisanal fisheries – is vital to rigorous evaluation of relative impacts of different fisheries to sea turtle populations.

RVS ACROSS FISHERIES METHODS AND GEAR TYPES

Spatio-temporal differences in fisheries operations and characteristics of fishing gear can determine catch selectivity, including size of individuals taken as bycatch (TEWG 2000; Epperly *et al.* 2002; Lewison & Crowder 2007). In the Mediterranean, the apparent geographic separation of fishing activity by target (ALB, SWO, BFT; Camiñas & Valeira 2001) corresponds roughly to the geographic separation of eastern Mediterranean- and western Atlantic-origin juvenile loggerheads in the same area (Carreras *et al.* 2006). Because eastern Mediterranean adult loggerheads are typically smaller than their western Atlantic counterparts (Tiwari & Bjørndal 2000), it is possible that juveniles from these two populations also reflect this size difference, thus resulting in BFT and SWO sets interacting with larger turtles of western Atlantic origin and ALB sets interacting with smaller turtles of eastern Mediterranean origin. Unfortunately, concomitant size, genetic, and location data were not available for individual turtles taken as bycatch in these fisheries, thus precluding a thorough analysis of this question. Future studies that elucidate relative impacts of fisheries affecting different loggerhead populations simultaneously would be highly relevant to current conservation efforts, especially considering the declining status of many loggerhead nesting rookeries in both of these regions (Ehrhart, Bagley & Redfoot 2003; Margaritoulis *et al.* 2003).

In addition to spatio-temporal factors, differences in fishing gear characteristics also influence size distributions and RVs of animals taken as bycatch. For example, hook size and shape in longline sets can be primary factors in determining frequency and severity of sea turtle bycatch (Watson *et al.* 2005). Interestingly, the bycatch size distribution of Azorean loggerheads in longline sets targeting SWO was significantly larger than the overall size distribution of turtles present in Azorean waters in 2000 (Bolten 2003); this pattern persisted over 4 years of data collection (A.B. Bolten, personal communication). In addition, within the Spanish and Italian longline fisheries, sets targeting ALB were shallower (in depths frequently inhabited by small juvenile loggerheads; Bolten 2003), used smaller hooks and smaller baits, and caught smaller, earlier life stage turtles than sets targeting SWO and BFT (Camiñas & Valeira 2001; De Metrio & Deflorio 2001)

(Table 3; Fig. 2g,h). Similarly, although the Hawaiian longline and NP driftnet operations occurred in roughly the same geographic area of the NP (Wetherall *et al.* 1993; Gilman *et al.* 2006), loggerheads caught in driftnets were significantly smaller and had lower RVs (Table 3; Fig. 2c,d). Further, standard deviations of loggerhead sizes associated with driftnet and trawl fisheries (or beach-stranded loggerheads) were greater than those associated with longline gear (Table 3). Our results demonstrate that loggerhead size and RV patterns were related to (i) spatio-temporal overlap of loggerhead habitat use and fisheries, and to (ii) size-selectivity of gear characteristics, including a hook size–body size relationship that precluded bycatch of smaller juvenile loggerhead turtles on large longline hooks (Bolten 2003; Watson *et al.* 2005; Gilman *et al.* 2006) and lower size-selectivity of driftnet and trawl gear relative to longline gear. Therefore, knowing both the size classes of animals present, as well as the size classes of animals interacting with fisheries in an area, can facilitate identification of gear-specific characteristics that drive size-selectivity of bycatch.

Conclusions

Fisheries bycatch has contributed to declines of several populations of long-lived marine vertebrates. Our findings underscore the importance of integrating spatio-temporal patterns of fisheries activities, gear characteristics, and animal life history and biology to assess the relative impacts of different fisheries operations on geographically widespread populations of marine megafauna. We recommend further applications of this approach to identify conservation priorities for populations of other marine vertebrates with life history (e.g. late maturity, long lifespan) and life-cycle traits (e.g. distinct ontogenetic habitats, separate breeding/feeding grounds) similar to sea turtles, such as seabirds, marine mammals and sharks. Future work should combine improved estimates of the relative magnitude of protected species bycatch in different fisheries with age-specific RVs to improve across-fisheries comparisons of population impacts.

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