First Sea Turtle Informal Intersessional Working Group Meeting (STIIWG01)
Review of CMM 2018-04 (Sea Turtles)

8 and 10 April 2026 (Pohnpei)| 10 AM-2PM
Virtual Meeting

Multifaceted effects of bycatch mitigation measures on target or non-target species for pelagic longline fisheries and consideration for bycatch management

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STIIWG01-2026-IP-31[1]
4 April 2026

[1] Reference 31

CSIRO PUBLISHING

RESEARCH PAPER
https://doi.org/10.1071/MF23148

MARINE & FRESHWATER RESEARCH

Multifaceted effects of bycatch mitigation measures on target or non-target species for pelagic longline fisheries and consideration for bycatch management

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Handling Editor:
Haseeb Randhawa

Received: 3 August 2023
Accepted: 23 December 2023
Published: 24 January 2024

Cite this:
Ochi D *et al.* (2024)
Marine and Freshwater Research **75**, MF23148.
doi:10.1071/MF23148

ABSTRACT

Context. The pelagic longline fishery has implemented bycatch mitigation measures to reduce sea turtle bycatch, but little attention has been given to their side effects on other endangered species. **Aims.** To investigate the impact of using circle hooks and whole fish bait on the fishing mortality of target and non-target fish species, as well as bycatch species. **Methods.** Long-term data collected from research cruises conducted by a pelagic longline vessel were used for analysis. A Bayesian quantitative evaluation was employed to assess the effects of the mitigation measures on the fishing mortality of various species. **Key results.** The use of circle hooks led to an increase in mouth-hooking for both target and bycatch species, and the effect was proportional to hook size. Although deploying circle hooks did not increase fishing mortality per unit effort (MPUE) for shortfin mako sharks, combining to whole fish bait had a significant increase on MPUE. **Conclusions.** The study stresses the need for considering the trade-offs of bycatch mitigation measures such as circle hooks and fish bait among multi-taxa species. **Implications.** The necessity for quantitative assessments of bycatch mitigation measures before implementation is highlighted to avoid unintended consequences on endangered species and ensure effective conservation in pelagic longline fisheries.

Keywords: bycatch mitigation measure, circle hook, finfish bait, fisheries management, pelagic longline fishery, sea turtle, sharks, swordfish.

Introduction

Unintentional catch in fisheries is known as bycatch, and bycatch of particularly endangered species can have devastating effects on these populations. Therefore, efforts to minimise bycatch of endangered species are strongly encouraged at all levels of conservation from local to international. For example, in the tuna longline fishery, concerns about the increased conservation risk for seabirds and sea turtles by unintentional and fatal catch have been a major issue among many regional fisheries management organisations (RFMOs) since the 1990s (Wallace *et al.* 2013; Dias *et al.* 2019). In recent years, some elasmobranchs, whose populations are declining further, are also treated as bycatch species. The decline of these species has focused attention at both the national and the international levels. Even for target fish that are not bycatch species, addressing the deterioration of stock status caused by overfishing requires reductions in unintentional fishing mortality (for instance, billfishes in the North Atlantic; Kerstetter and Graves 2006; Diaz 2008).

Several studies have weighed the sustainability of tuna longline fisheries against the conservation of species vulnerable to bycatch (Hall *et al.* 2000; Melvin *et al.* 2014; Clarke *et al.* 2015), particularly for seabirds and marine turtles, with the development of several effective bycatch mitigation measures (Melvin *et al.* 2014; Swimmer *et al.* 2017). Bycatch mitigation measures in longline fisheries target specific animal groups and are evaluated on the basis of their success in reducing mortality owing to bycatch of specific vulnerable species. Although the impact on the catch of the target fish is the primary consideration when evaluating bycatch mitigation measures, few studies have examined the impacts and tradeoffs on species not targeted by mitigation measures (Pacheco *et al.* 2011; Gilman *et al.* 2016). However, the introduction of bycatch mitigation measures requires an assessment of the impact not only on the target bycatch species but on the other ecologically related species prior to their introduction (Reinhardt *et al.* 2018).

Use of circle hook and whole-finfish bait are typical sea turtle bycatch mitigation measures for pelagic longline fisheries (Watson *et al.* 2005; Gilman *et al.* 2006; Yokota *et al.* 2009; Stokes *et al.* 2011). The tip of the circle hook bends inward, and when a fish or sea turtle swallows the hooked bait, the circle hook less likely to hook inside the digestive tract; instead, as the hook exits the mouth, a torque causes it to hook through the edge of the mouth. This property allows for easy hook removal and has been reported to reduce the mortality rate of bycatch sea turtles on board and after release (Cooke and Suski 2004; Kiyota *et al.* 2004; Kerstetter and Graves 2006). Reports of positive effects of circle hooks include those for other species, such as reduced haulback and post-release mortality in sharks, reduced post-release mortality in swordfish (*Xiphias gladius*), and increased catch rates in tuna, the target fish. The use of fish bait instead of squid bait potentially reduces bycatch (Watson *et al.* 2005; Yokota *et al.* 2009, 2011) and mortality rates (Stokes *et al.* 2011; Parga *et al.* 2015) of sea turtles. However, these sea turtle mitigation measures exact other costs. Several meta-analytic studies have reported the circle hook-related reduction of sea turtle mortality rate but an increase in billfish and shark catch rates (Gilman *et al.* 2016; Reinhardt *et al.* 2018; Santos *et al.* 2020). Another aspect of the circle hook effect on catch and bycatch species is that an increase in minimum hook width would alter catch rate, hooking location and mortality rate (Curran and Beverly 2012; Gilman *et al.* 2018). This effect of the hook width is assumed to be related to mouth dimensions of the species, and its effect needs to be examined separately. The use of whole-fish bait also reportedly increases the catch of several species (e.g. porbeagle shark, *Lamna nasus*, and shortfin mako shark, *Isurus oxyrinchus*, Foster *et al.* 2012; meta-analysis for multi-taxa species, Gilman *et al.* 2020; Santos *et al.* 2020). However, few studies have allowed for quantitative evaluation of the effects of these mitigation measures experimentally on species beyond sea turtles. This limited data concern is due in part to the reliance on observer data from commercial vessels, and small sample sizes, small comparison groups and lack of experimental rigour from research vessels. In addition, the impact assessment for sharks underestimates catch rates and mortality associated with missed catches owing to 'bite-off' branchline (Reinhardt *et al.* 2018). In addition, many experimental studies and meta-analyses (e.g. Diaz 2008; Pacheco *et al.* 2011; Godin *et al.* 2012; Huang *et al.* 2016) evaluate gear impacts only at significance levels, without evaluating the magnitude of the effect. Small significant differences may be judged not to matter much when assessing overall risk in bycatch species. Also, many studies use catch or bycatch rates (Watson *et al.* 2005; Gilman *et al.* 2007; Foster *et al.* 2012; Andraka *et al.* 2013) and mortality rates (at haulback or after release; Kerstetter *et al.* 2003; Horodysky and Graves 2005; Carruthers *et al.* 2009; Gallagher *et al.* 2014) as important impact indicators, without considering irreversible impacts, such as the number of organisms killed at the time of catch. Additionally, hooking location itself (mouth, swallow or external) is believed to have a strong influence on mortality rate, which demands the estimation of risk under specific hooking conditions, taking causal relationships into account.

Yokota *et al.* (2006*a*) had also conducted experimental pelagic longline operations under controlled conditions to confirm the effects of bait type, hook type and hook size on catch of blue sharks (*Prionace glauca*), and found no difference in CPUE, size or mortality rate among tuna hooks and two-sized circle hooks, and that the use of monofilament leaders reduced CPUE because of shark bite-off. However, the effects of hooking location on mortality rate, the effects of bait type, and those effects on multi-taxa species other than blue sharks had not been verified.

So as to analyse confounding factors, such as missing catch by bite-off and covariates related to operation, we utilised new experimental data and part of the data from Yokota *et al.* (2006*a*). Then, we developed a Bayesian statistical model to evaluate the effects of changing hook and bait type on fish species other than turtles, particularly, tuna, swordfish and sharks, and then verified the contribution of circle hooks and fish bait to mortality rate, catch rate and fatal catch rate. We also discussed the appropriate assessment of bycatch mitigation measures in fisheries management.

Methods

Experimental operations

We analysed data from the R/V *Taikei No. 2* longline research operation conducted in the Northwest Pacific Ocean between 2002 and 2010, a typical Japanese shallow-setting operation targeting mainly swordfish and sharks (set depth mean shallowest 47.44 m ± 14.22 s.d., deepest 72.41 m ± 10.87 s.d.; n = 98 operations, on the basis of the time depth recorder data, SBT500, Murayama Denki Ltd), by using four hooks per basket, a wire leader and a night soaking (Yokota *et al.* 2006*a*). In total, 286 363 hooks from 306 operations (range 400–964 hooks per operation) were deployed in the experiment (Table 1). The area of operation ranged from around the Izu Islands in Japan to off the eastern coast of north-eastern Honshu, being typical fishing ground for Japanese shallow-setting longliners (Fig. 1; Hiraoka *et al.* 2016). We deployed 11 different hooks (Table 2, and Table S1 and Fig. S1 of the Supplementary material) and we describe hook shapes

Table 1. Fishing effort (longline hooks) in experimental operations used in the analysis.

Hook type	Bait type		Total effort
	Squid	Fish	
Tuna	97 834	71 146	168 980
Small-C	70 882	7658	78 540
Large-C	31 872	6976	38 848
Total effort	200 588	85 780	286 368

and other details of these hooks in Table S1, following the measurement method of Yokota *et al.* (2006*b*). Because the degree of hook offset has been reported to affect catch and hooking location (Cooke and Suski 2004), most hooks were <10° but some were nearly 15°. The bait comprised chub mackerel (*Scomber japonicus*) and Japanese common squid (*Todarodes pacificus*) in the range of 20–30-cm fork length or dorsal mantle length. These were frozen and stored, then completely thawed before being hooked. The sequence of line setting was divided into several experimental segments, and a different combination of hook and bait type was applied for each segment, with an alternate order of segments at each operation. It should be noted that the fishing effort (i.e. hooks set) assigned to each experimental segment varied from cruise in each year, resulting in a bias in overall effort for each experimental group.

The researcher recorded catch for each operation for all catch or bycatch, and the species caught, fate of catch (alive or dead), hooking location (mouth, swallow, and external hooking), time of catch and float ID. The researchers determined whether the catch was alive or dead on the basis of the movement of the animals and the degree of injuries before being hauled. Float ID was recorded when a float was dropped during line setting and when it was retrieved to the deck during line hauling, so as to calculate soak time. Hooking locations were recorded for catches caught using squid bait. At the start of longline operations, the researcher also collected sea-surface temperature with a water thermometer (DS-1; Murayama Denki Ltd) equipped on the vessel, which we subsequently used in the analysis.

The experiment was conducted using multiple sizes of circle hooks, which varied greatly in size. However, those sample sizes were too small to analyse each hook type separately. For convenience, we have classified the hook shapes on the basis of size (threshold for straight total length was 68 mm and maximum total width was 80 mm; approximately equivalent to 5.0-sun or 18/0). This led to the following three main hook types:

1. Control (tuna hook 4.0-sun; tuna)
2. Smaller circle hook (smaller than the threshold; small-C)
3. Larger circle hook (the threshold or larger; large-C)

The width of the 4.0-sun tuna hook is a standard size for Japanese pelagic longliner, whereas it was the same or slightly narrower than the 'small-C' hook.

In Table 1, we show longline effort separated by bait and hook type, tabulated according to the above categorisation. We selected the following species on the basis of whether

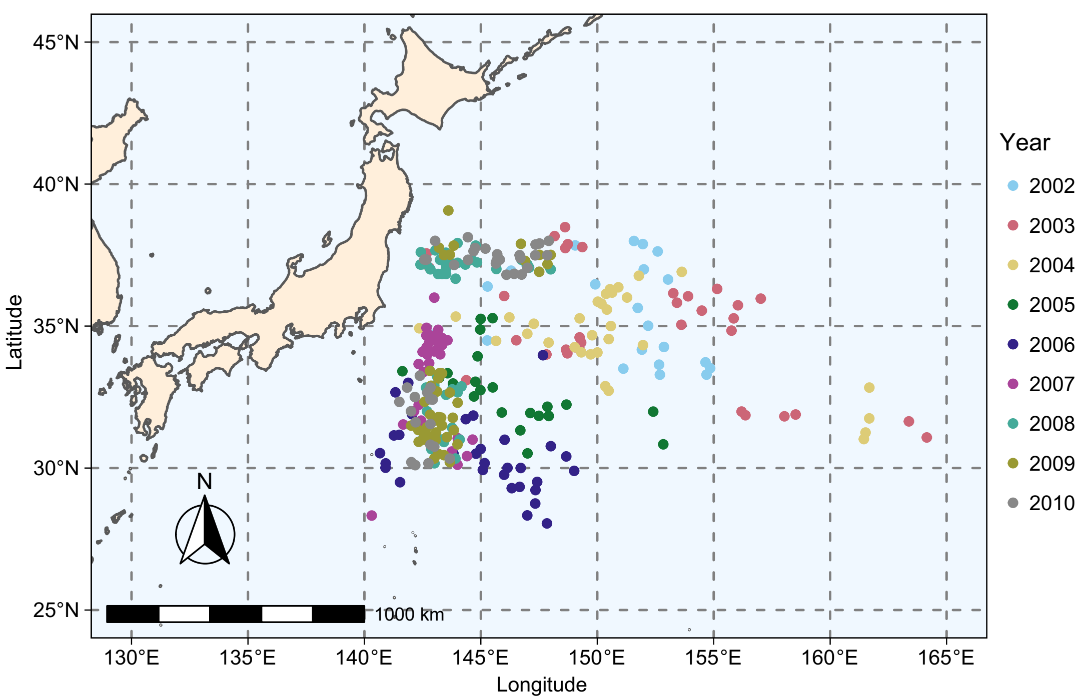

Fig. 1. Locations where the longline operation experiment was conducted.

Table 2. List of hook types used in the experiment.

Hook name	Size	Category	Straight total length (mm)	Maximum total width (mm)	Minimum total width (mm)
Komatu Keisaku tunahook	4.0 sun	Tuna	63	63	38
Doitomi Tunamutsu	4.0 sun	Small-C (circle hook)	58	69	39
Komatsu Keisaku modified	4.0 sun	Small-C (circle hook)	60	68	41
Komatsu Keisaku modified	4.5 sun	Small-C (circle hook)	63	71	45
Komatsu Keisaku modified	4.8 sun	Small-C (circle hook)	N/A	N/A	N/A
Komatsu Keisaku type Koshina	4.5 sun	Small-C (circle hook)	62	76	51
Komatsu Keisaku type North America	4.3 sun	Small-C (circle hook)	57	63	41
Tankichi Uruwa	3.8 sun	Small-C (circle hook)	56	64	36
Komatsu Keisaku modified	5.2 sun	Large-C (circle hook)	74	81	48
Komatsu Keisaku type North America	5.2 sun	Large-C (circle hook)	76	85	52
Pacific Fishing Tackle circle hook	18/0	Large-C (circle hook)	68	80	51

N/A, no measurement data were available because of the loss of the hook after the experiment.

there was a sufficient sample size to statistical analyses (especially for model convergence): bigeye tuna (*Thunnus obesus*), blue shark, common dolphinfish (*Coryphaena hippurus*), escolar (*Lepidocybium flavobrunneum*), longnose lancetfish (*Alepisaurus ferox*), shortfin mako shark, striped marlin (*Kajikia audax*), swordfish and loggerhead turtle (*Caretta caretta*).

Statistical analysis

We conducted all analyses by using a Bayesian approach to estimate parameters. We adopted haulback mortality rate, catch per unit effort (CPUE, per 1000 hooks) and mortality per unit effort (MPUE, per 1000 hooks) (Afonso *et al.* 2011) as indices to evaluate the impact of hook and bait type on fishing mortality within the analyses. We used the following data as inputs to the model: number of caught (individuals), longline effort (number of hooks), fate at hauling, hooking location, year and location of operation, water temperature at operation, and soaking time.

Because of the missing data owing to not recording the hooking location when fish bait was used, we split the analysis to evaluate the impact of hook type and bait type on fishing mortality into two models. MODEL 1 evaluated only the effect of hook type on the basis of capture events with squid bait and assumed that the use of circle hooks would change to more mouth-hooking of each species, resulting in improved mortality rate. MODEL 2 evaluated both hook and bait types, and assumed that the combination of the two would result in large fluctuations in mortality rate, CPUE and MPUE for each species.

We based MODEL 1 on a logit regression by using a Bernoulli distribution. We express the observed hooking location H and haulback mortality rate M in MODEL 1 by the following equations:

$$M \sim \text{Bernoulli}\left(p_{\text{dead}}\right) \tag{1}$$

$$\text{logit}\left(p_{1,\text{dead}}\right) = \beta_{1,\text{hkloc}} + \beta_{1,\text{SST}} + \beta_{1,\text{soaktime}} \tag{2}$$

$$H \sim \text{Categorical}\left(\text{softmax}(\theta_{\text{hkloc·hook}})\right) \tag{3}$$

where β_1 is the parameter in each explanatory variable (hkloc is hooking location, SST is sea-surface temperature and soaktime is soak time), $p_{1,\text{dead}}$ is the expected haulback mortality rate, and $\theta_{\text{hkloc·hook}}$ is the expected probability of hooking location in each hook type.

We structured MODEL 2 to calculate the expected number of mortalities per effort (MPUE) on the basis of the parameters estimated in both the mortality rate and CPUE estimation subsets. In MODEL 2, owing to lack of hooking location data, we calculated the mortality rate $p_{2,\text{dead}}$ from a modified Eqn 2, as follows:

$$\text{logit}\left(p_{2,\text{dead}}\right) = \beta_{2,\text{hook}} + \beta_{2,\text{bait}} + \beta_{2,\text{SST}} + \beta_{2,\text{soaktime}} \tag{4}$$

where β_2 is the parameter in each explanatory variable (hook is hook type, bait is bait type).

The CPUE subset is based on a log-regression using a Poisson distribution as the error structure. We express the number of catches C per operation by using the expected CPUE λ, as follows:

$$C \sim \text{Poisson}\left(\lambda + \log(E)\right) \tag{5}$$

$$\lambda = \log\left(\gamma_{\text{hook}} + \gamma_{\text{bait}} + \gamma_{\text{lat}} + \gamma_{\text{SST}} + r_{\text{year}}\right) \tag{6}$$

$$r_{\text{year}} \sim N(0, \sigma^2) \tag{7}$$

where E is the longline effort (hooks per set), γ is a parameter in each explanatory variable (lat is latitude where the longline set), r_{year} is a random effect of annual fluctuation on CPUE, and σ is a standard deviation.

We obtained the expected values of hook bait-specific MPUE ζ by multiplying CPUE by at-haulback mortality rate as follows:

$$\zeta = \hat{p}_{2,\text{dead}} \times \hat{\lambda} \quad (8)$$

where $\hat{p}_{2,\text{dead}}$ denotes the expected mortality rate standardised for hook and bait type, and $\hat{\lambda}$ denotes the estimated CPUE standardised for hook and bait type. We used the standardisation method for abundance indices used in fisheries stock assessment (Maunder and Punt 2004). In this method, explanatory variables other than the factor subject to standardisation are averaged to predict the objective variable, which in stock assessment is a time scale such as years or months, but in our case, we modified the standardisation scale to reference hook type and bait type.

We calculated each parameter on the basis of a Bayesian approach with Markov-chain Monte Carlo (MCMC) sampling. For the MCMC sampling, we used cmdstan (ver. 2.28.2, see https://mc-stan.org). As a prior distribution for σ, we used a half Student's *t* distribution with 2 degrees of freedom, mean 0 and variance 2.5, and we used a uniform distribution for the other parameters (β_1, β_2, γ, θ). We computed the posterior distribution using Stan with 15 000 sampling iterations, including 10 000 warmup iterations, number of chains as 4, and no sinning. We calculated Bayesian credible intervals on the basis of the highest density interval (HDI) for the estimates. Although the Bayesian approach for the estimates precluded significance testing, we determined the difference between the estimates of the experimental group and those of the control group ('swallowing' for hooking location, 'tuna' hook for hook type and 'squid' for bait type), and if the lower and upper limits of HDI for the difference did not exceed 0, we considered the difference as a difference for convenience (assuming region of practical equivalence, ROPE, as 0; Kruschke 2015). In Fig. S2 of the Supplementary material, we show the Stan code used to estimate each parameter in MODELs 1 and 2. For other data handling, statistical analysis and plotting, we used R (ver. 4.3.0, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/) and packages 'cmdstanr' (ver. 0.6.1, J. Gabry and R. Češnovar, see https://mc-stan.org/cmdstanr/reference/cmdstanr-package.html), 'ggalluvial' (ver. 0.12.5, see https://cran.r-project.org/package=ggalluvial; Brunson 2020), 'ggthemes' (ver. 4.2.4, J. B. Arnold, see https://cran.r-project.org/package=ggthemes), 'mapdata' (ver. 2.3.1, R. A. Becker, A. R. Wilks and R. Brownrigg, see https://cran.r-project.org/package=mapdata), 'maps' (ver. 3.4.1, R. A. Becker, A. R. Wilks, R. Brownrigg, T. P. Minka and A. Deckmyn, see https://cran.r-project.org/package=maps), 'sf' (ver. 1.0-14, see https://cran.r-project.org/package=sf; Pebesma 2018), 'tidybayes' (ver. 3.0.6, see https://cran.r-project.org/package=tidybayes; Kay 2023) and 'tidyverse' (ver. 2.0.0, see https://cran.r-project.org/package=tidyverse; Wickham *et al.* 2019).

Results

Summary statistics

Sufficient catchesbycatches of blue shark, longnose lancetfish, common dolphinfish, shortfin mako shark swordfish, bigeye tuna, loggerhead turtle, escolar and striped marlin were recorded for the later analysis (Table 3). The main species listed in Table 3 as 'other species' are listed as follows: salmon shark (*Lamna ditropis*; N = 229), pelagic stingray (*Pteroplatytrygon violacea*; N = 199), pomflets (*Brama* spp.; N = 135), bigeye thresher shark (*Alopias superciliosus*; N = 89) and albacore (*Thunnus alalunga*; N = 69). The sample sizes of these 'other species' were too skewed among experimental groups to converge the later analysis.

In Table 3, we also show the number of fish caught by hook type and bait type. Bigeye tuna had extremely low catches on large-C hook, and loggerheads had low catches on fish bait. The most common hooking location at the time of catch was mouth-hooking for all nine species, with extremely few hook locations other than mouth-hooking, especially for bigeye tuna and escolar (Table 4). The proportion of mortality of captured species at haulback varied greatly by species. The haulback mortality rate was low for blue shark, common dolphinfish, escolar and shortfin mako shark, and higher for bigeye tuna, longnose lancetfish, striped marlin and swordfish. In the case of loggerhead turtles, the mortality rate was extremely low.

The length-based size composition of the nine species (precaudal length for blue sharks and shortfin mako sharks, straight-line carapace length for loggerhead turtles, eye-to-fork length for striped marlin and swordfish, and fork length for all other species) used in the analysis was not statistically compared in this study and was not included in the model because it did not contribute to haulback mortality rate; however, in Fig. S3, we have included histograms.

Almost all parameters in the models for the nine species were successfully converged ($\hat{R} < 1.1$) but the whole models were not converged for bigeye tuna, common dolphinfish, escolar in the MODEL 1, and some of the parameters in the MOEDL 1 and the whole model in the MODEL 2 for loggerhead turtle were not converged, as we describe below.

Output of MODEL 1

We observed differences in hooking location by hook type, with an increase in mouth-hooking and a decrease in hook-swallowing for large-C for loggerhead turtle and a clear increase in mouth-hooking for small-C for shortfin mako shark and swordfish (Fig. 2, Table S2 of the Supplementary

Table 3. Number of individuals caught by hook and bait type in the experimental operation.

Species	Total catch	Hook type			Bait type	
		Tuna	Small-C	Large-C	Squid	Fish
Blue shark	13 018	8084	3562	1372	8903	4115
Longnose lancetfish	1297	945	257	95	692	605
Common dolphinfish	505	206	181	118	363	142
Shortfin mako shark	485	298	134	53	262	223
Swordfish	288	129	112	47	249	39
Bigeye tuna	269	114	146	9	201	68
Loggerhead turtle	268	128	113	27	259	9
Escolar	163	79	56	28	108	55
Striped marlin	145	70	53	22	126	19
Other species	1578	–	–	–	–	–

Table 4. Composition of hooking location and fate at haulback.

Species	Hooking location				Fate at haulback		
	Swallowed	Mouth	External	Unknown	Alive	Dead	Unknown
Blue shark	2270	2608	66	8074	11 701	1066	251
Longnose lancetfish	25	288	16	968	165	1010	122
Common dolphinfish	39	159	4	303	398	87	20
Shortfin mako shark	66	68	18	333	363	118	4
Swordfish	59	118	18	93	55	226	7
Bigeye tuna	7	128	2	132	83	183	3
Loggerhead turtle	109	116	14	29	256	5	7
Escolar	1	62	1	99	108	40	15
Striped marlin	12	80	8	45	68	76	1

Unknown includes catches that dropped off before reseachers checked or lack of survey.

material). In blue sharks, the frequency of hook-swallowing decreased in both small-C and large-C.

We observed clear differences in haulback mortality rate by hooking location for blue shark, shortfin mako shark, striped marlin and swordfish (Fig. 3, Table S3 of the Supplementary material). Haulback mortality rate after mouth-hooking for blue sharks was lower, and that of external hooking was higher than those for hook-swallowing. We observed lower haulback mortality rates for shortfin mako shark, striped marlin and swordfish from mouth-hooking than from hook-swallowing.

Output of MODEL 2

Haulback mortality rate was higher for large-C than for tuna hook in bigeye tuna, but did not differ among hook types in other species (Fig. 4, Table S4 of the Supplementary material). However, the mortality rate varied with the bait type among species. In bigeye tuna and blue shark, the rate decreased when using fish bait, whereas in shortfin mako shark, it increased.

In Fig. 5 and 6, we show the effects of two covariates, namely, sea-surface temperature (SST) and soak time, on haulback mortality rate. The response to SST differed by species, with haulback mortality rate increasing with higher SST for common dolphinfish, escolar, shortfin mako sharks and swordfish, and, conversely, increasing with lower SST for bigeye tuna and longnose lancetfish. We observed little fluctuation in haulback mortality rate with SST in blue shark and striped marlin. In general, haulback mortality rate increased with an increasing soak time. However, for blue sharks, haulback mortality rate increased only slightly with an increased soak time.

We observed higher CPUE for only small-C in blue shark, bigeye tuna, common dolphinfish and escolar (Fig. 7, Table S5 of the Supplementary material). We observed differences in standardised CPUE by bait type in bigeye tuna, blue shark, common dolphinfish, escolar and shortfin mako shark. CPUE decreased with whole fish bait in bigeye tuna and blue sharks, but increased in common dolphinfish, escolar and shortfin mako shark. In the case of blue shark, escolar and shortfin

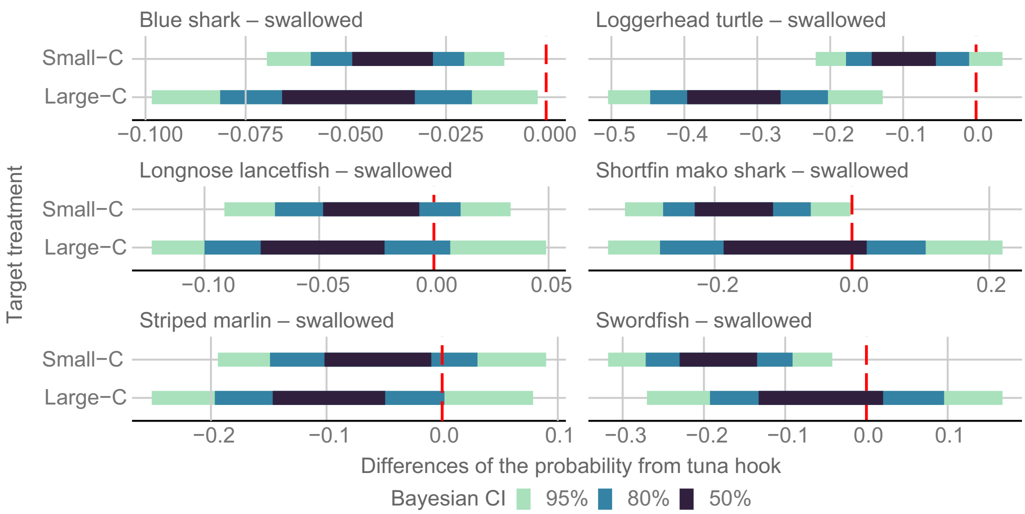

Fig. 2. Differences in the estimated probability of the 'swallowed' hooking of each circle hook type from tuna hook when squid bait is used. The red dotted line indicates that the difference is zero.

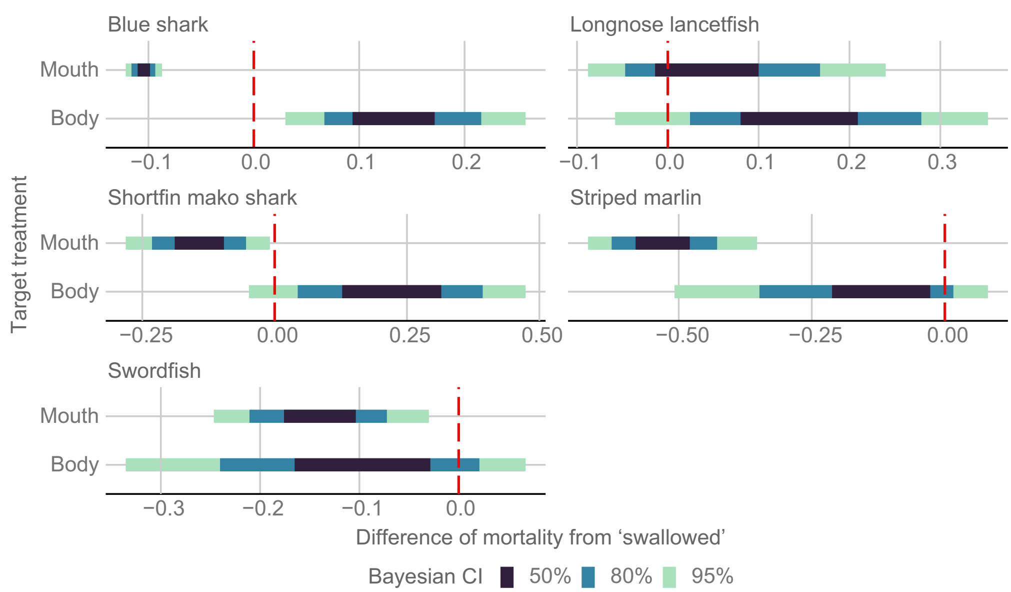

Fig. 3. Differences in the estimated haulback mortality rate of each target hooking from 'swallowed' hooking when squid bait is used. The red dotted line indicates that the difference is zero.

mako shark, the bait effect could be varied with circle hooks, suppressing the CPUE-increasing effect by fish bait in bigeye tuna, and blue shark with the use of circle hooks, whereas, conversely, this combination boosted increase of CPUE in common dolphinfish, escolar and shortfin mako shark.

Compared with differences in CPUE among hook and bait type, those in MPUE were relatively small (Table S6 of the Supplementary material). We observed differences with higher MPUE for only small-C in bigeye tuna and escolar (Fig. 8). We confirmed decreases in MPUE by fish bait in bigeye tuna and blue shark, and, conversely, increases in MPUE in common dolphinfish, shortfin mako shark. The effect of the combination of whole-fish bait and circle hook varied in bigeye tuna, blue shark, common dolphinfish, escolar and shortfin mako shark. In bigeye tuna and blue shark, the effect of the circle hook on MPUE was suppressed by fish bait, whereas in common dolphinfish, escolar and shortfin mako shark, MPUE increased significantly when whole-fish bait and circle hook were used together.

Hook and bait effect for sea turtle bycatch

We failed to complete our analysis for loggerhead turtles throughout the models because the bias in frequency of capture events among the experimental groups was too

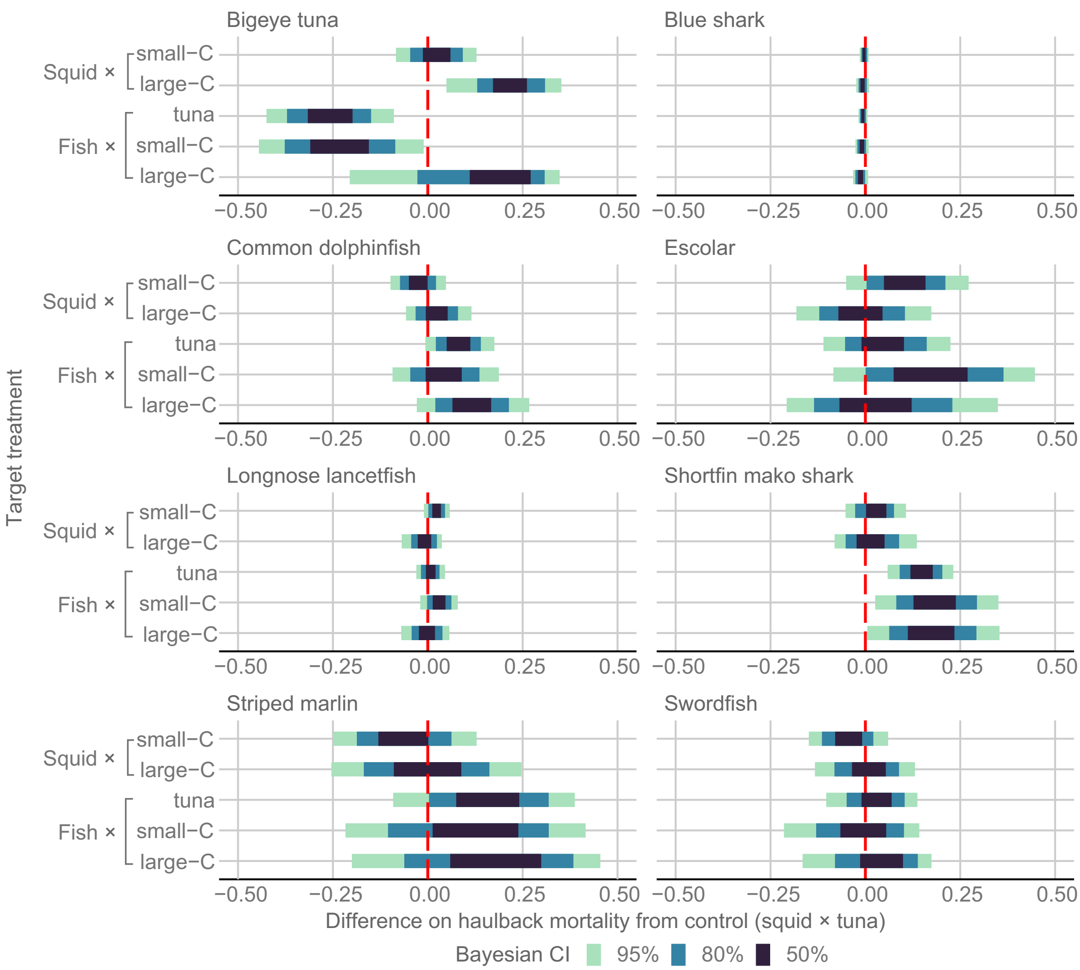

Fig. 4. Differences in estimated haulback mortality between each experimental group and the control group (squid × tuna hook). The red dotted line indicates that the difference is zero.

large and did not converge, except for only a part of MODEL 1. Instead, we show the nominal CPUE, haulback mortality rate, and MPUE for each experimental group in Table 5, and hooking location and haulback mortality rate by each hook type with squid bait in Fig. S4. Most individuals survived regardless of hooking location. When whole-fish bait was used, haulback mortality rate and associated MPUE were zero. For squid bait, large-C had the smallest CPUE, mortality and MPUE.

Discussion

Our experimental comparisons showed that the hook shape, size and bait type, all considered as effective bycatch mitigation measures for sea turtles, have extremely multifaceted effects for teleost fishes and sharks and, in some species, the direction of the effects was conflicted. The results provided significant insight into two aspects of the management of vulnerable bycatch species in tuna fisheries, namely, how the confrontational effect of bycatch mitigation measures should be managed, and in which processes of fishing mortality intervention in the management of vulnerable species should occur. As a specific concern regarding the former, when considering shortfin mako shark, which is experiencing significant stock depletion in the North Atlantic (Sims *et al.* 2018; Anon. 2019), the implementation of bycatch mitigation measures for sea turtles, which are also required to reduce fishery bycatch, could conversely increase fishing mortality and become a conservation risk. Previously, most of bycatch mitigation measure assessments have focused on whether they reduce the impact of vulnerable bycatch species of concern being bycaught, with the secondary impact being from an economic perspective; that is, in other words, whether the catch rate of commercial species is reduced or not. Where both loggerhead turtle and shortfin mako with opposing effects are at low abundance, management measures should be based on a thorough discussion identifying the optimal combination of mitigation measures, accompanied by scientific evidence. With regard to

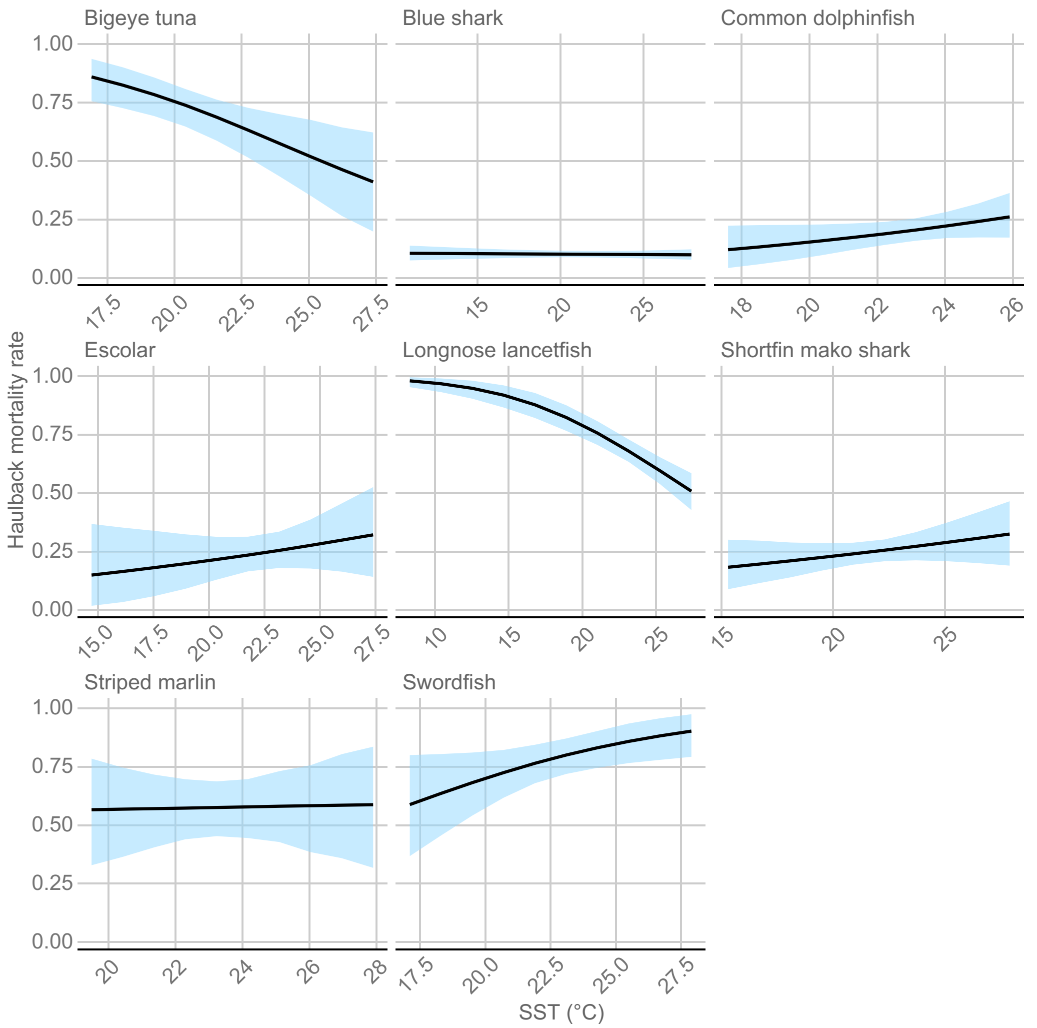

Fig. 5. Relationship between sea-surface temperature (SST) variability and haulback mortality rate at longline operations. Solid lines indicate median; masked areas indicate 95% Bayesian credible interval.

the latter issue, the mortality reduction expected from circle hooks is not very promising, especially for species with a high catch mortality, because the main effect of circle hooks is to minimise internal organ damage, which is of little use for species that have died from other causes, such as heat stress or suffocation. For such species, consideration of methods to reduce the catch itself or reduced soak time (Gallagher *et al.* 2014; Reinhardt *et al.* 2018) will be of greater benefit.

Increased mouth-hooking of loggerhead turtle by large circle hooks is consistent with existing studies. The circle hook prevents internal organ damage and improves the probability of live release (Cooke and Suski 2004); the impact of circle hooks on haulback mortality in this study could not be evaluated due to skewed data about mortality events. For the same reason, the MODEL 2 analysis could not evaluate the effects of circle hook and bait type on CPUE, mortality rate and MPUE of loggerhead turtle. However, because mortality event of loggerhead turtle did not occur at all when fish bait was used, it may be assumed that there is an effect of mortality reduction by using fish bait. This result is also consistent with existing studies, and is related to the lower attractant effect of whole-fish bait on marine turtles and the increased probability of swallowing caused by the difficulty to bite off the bait (Stokes *et al.* 2011; Parga *et al.* 2015).

Our study indicated that reduced hook-swallowing with circle hooks and increased haulback mortality after hook-swallowing were found for sharks and swordfish. Hook-swallowing has been reported to increase the likelihood of fatal damage to internal organs. Although previous studies have reported that studies to attach satellite tags to white marlin (*Kajikia albida*) caught by recreational fishing by using circle hooks, and subsequently released, have reduced the post-release mortality rate (Horodysky and Graves 2005); unfortunately, the present study did not corroborate this information. Our results also presented different effects of hooking location by hook types, with more frequent mouth-hooking by small circle hooks in many species. Few studies

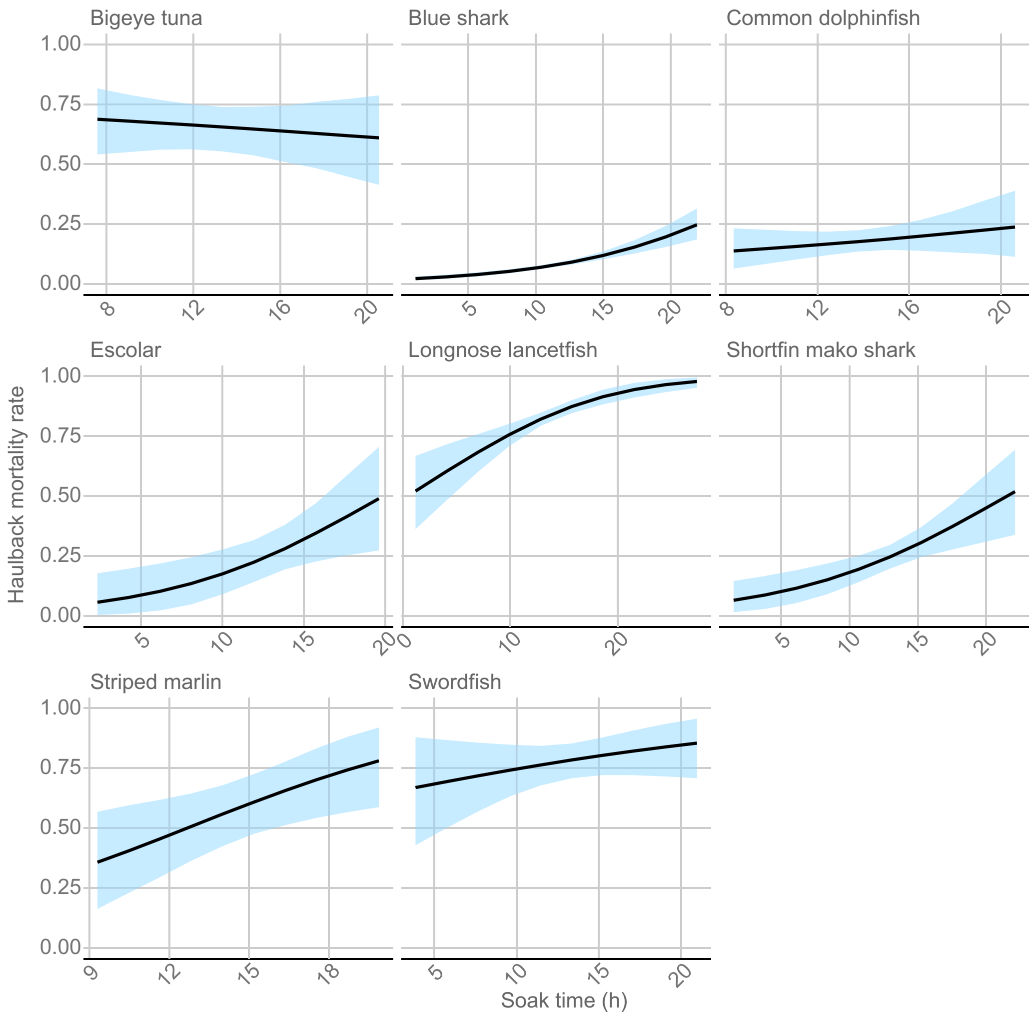

Fig. 6. Relationship between soak time (time from setting the branch line to hauling) variability and haulback mortality rate at longline operations. Solid lines indicate median; masked areas indicate 95% Bayesian credible interval.

have examined the relationship among size of circle hook, hooking location and haulback mortality of non-turtle species. However, two studies discussed the possibility that relative differences in mouth and hook size, and differences in feeding behaviour toward prey (swallowing the prey whole or biting it off) may affect the hooking location (Epperly *et al.* 2012; Gilman *et al.* 2020).

An increase in CPUE and MPUE was observed only with small circle hooks among the two types of circle hooks. This indicates that the increase in CPUE owing to small circle hooks had a greater impact on MPUE than did the haulback mortality rate. There have been many previous findings on the effects of circle hook use on CPUE, with elevated CPUE for tunas and no consistent trend for other teleosts and sharks. Interestingly, we did not observe an increased CPUE and MPUE with large circle hooks. Although few previous studies have focused on hook size and made comparisons, catch rates for skipjack, shortbill spearfish, escolar and lancetfish are reported to have decreased when larger hooks were used (Curran and Beverly 2012; Gilman *et al.* 2018). Considering the effect of hook size in terms of the catch process, it is unlikely that catch rates increased as a result of swallowing, with the results of MODEL 1 indicating an increase in mouth-hooking for many species. In the case of blue shark and shortfin mako shark, the increase was observed in CPUE for small circle hook, but this increase was not observed in MPUE. It may be explained by that the effect of the circle hook on MPUE may have been masked by the uncertainty of haulback mortality rate. Several studies have examined the effects of fish bait without circle hook and have reported reduced catch rates for tropical tunas, blue sharks and escolar and increased catch rates for shortfin mako, porbeagle shark and white marlin (Watson *et al.* 2005; Yokota *et al.* 2009; Foster *et al.* 2012; Fernandez-Carvalho *et al.* 2015). In swordfish, some previous studies evaluating the effect of switching to whole-fish bait from squid bait have reported conflicting effects (increase, Foster *et al.* 2012;

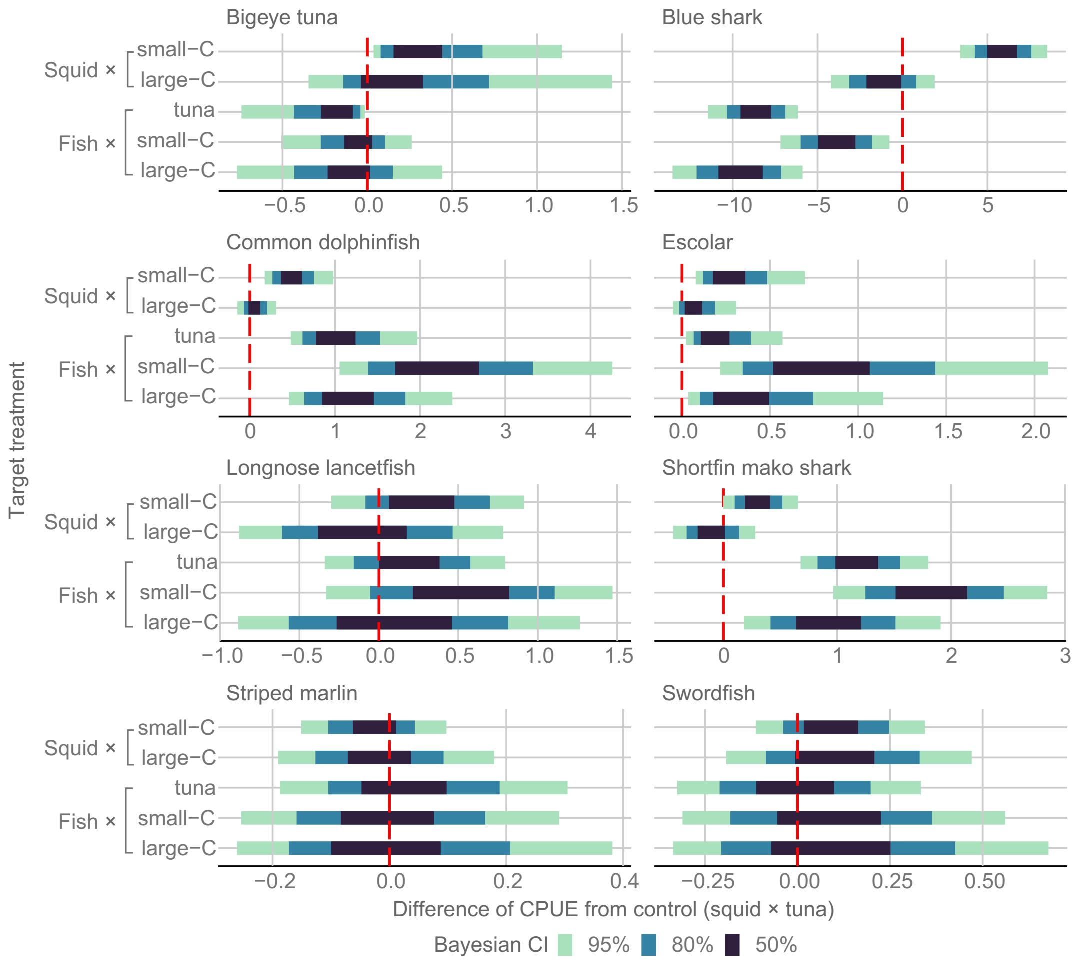

Fig. 7. Differences in the standardised catch per unit effort (CPUE) for each experimental group from those for the control group (squid × tuna hook). The red dotted line indicates that the difference is zero.

Santos *et al.* 2012; decrease, Fernandez-Carvalho *et al.* 2015), but few studies have referred to haulback mortality rate by bait types other than those on sea turtles. The catch rates of the target species, as previously noted, were affected by bait texture, but a mechanistic explanation for mortality effects is lacking. Because the likelihood that differences in feeding behaviour among species have an effect is high, this issue could be resolved through comparative studies based on observations of feeding behaviour, as in the case of circle hooks.

When the effects of hook and bait types were considered simultaneously, it was found that the bait type had a more significant impact on CPUE, mortality rate, and MPUE than did the hook type. However, whether this impact was beneficial or detrimental varied greatly depending on the species. Although the combination of circle hooks and fish bait is effective for avoiding sea turtle bycatch, this combination may pose a high mortality risk for endangered species such as shortfin mako shark, and even in the case of target fishes such as bigeye tuna, may counteract the expected positive effect of the circle hook on catch rate. In the case of shortfin mako, for example, changing the bait from squid to fish increases MPUE by ~4.0 times, and changing from tuna hooks to small circle hooks further increases MPUE by ~5.9 times (Table S6), and in the case of bigeye tuna, the CPUE estimate, which increased by 1.9 times with small circle hooks, returned to the same level as tuna hooks by changing from squid to fish bait (Table S5). Such substantial changes in CPUE and MPUE would not be ignored when managing fisheries for those species. Although very limited studies have simultaneously examined the inter-relationship between hook and bait types, all studies support the conclusion that the combination of hook type and bait type causes fluctuations in catch rates and that the direction of response varies among species (Coelho *et al.* 2012; Foster *et al.* 2012; Fernandez-Carvalho *et al.* 2015).

Water temperature and soak time emerged as significant factors affecting haulback mortality rate, which had been reported in sharks (Carruthers *et al.* 2009; Gallagher *et al.* 2014) and sea turtles (Watson *et al.* 2005). This indicates that these covariates need to be controlled statistically or experimentally when assessing the effects of hook and bait

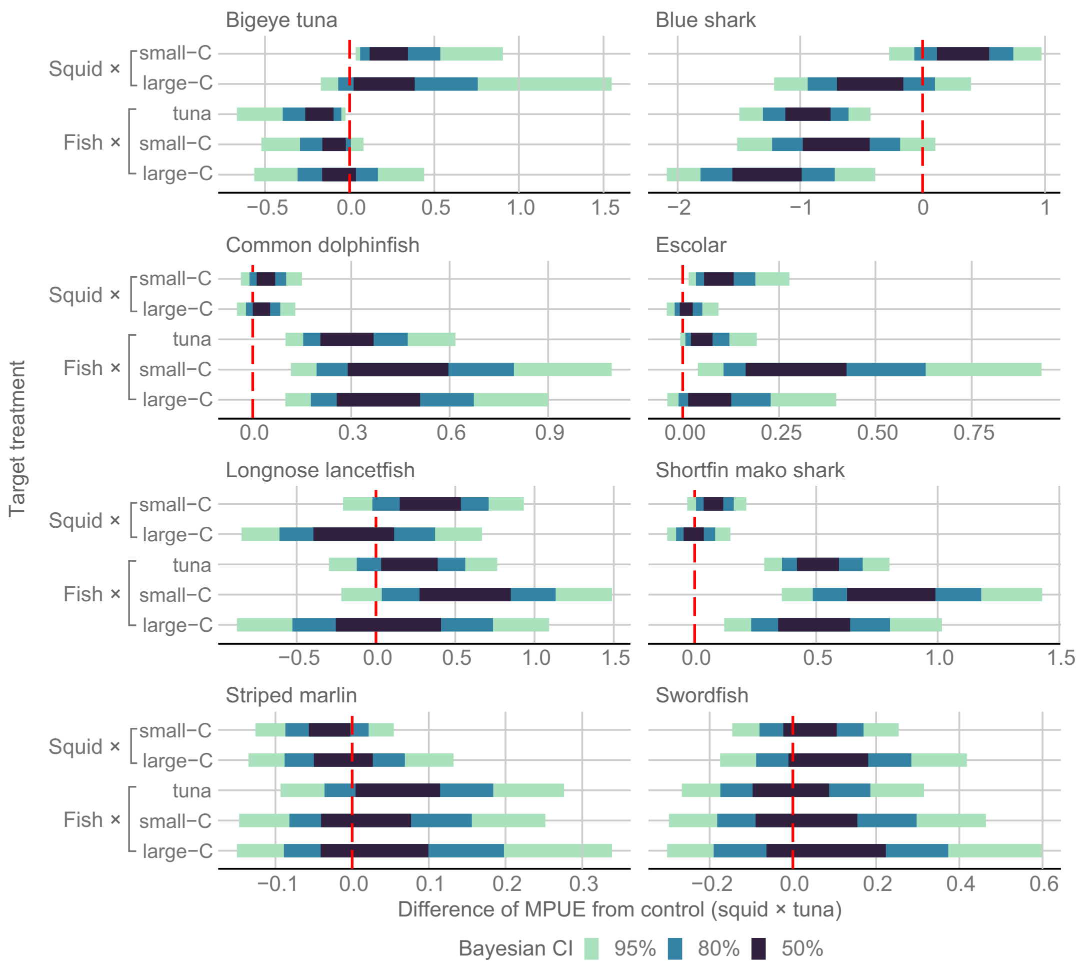

Fig. 8. Differences in the estimated MPUE (mortality per unit effort) between those for each experimental group and those for the control group (squid × tuna hook). The red dotted line indicates that the difference is zero.

Table 5. Nominal CPUE, haulback mortality rate and MPUE of loggerhead turtle; all figures are based on aggregated operational data, not estimates.

Hook type	CPUE		Haulback mortality		MPUE	
	Squid	Fish	Squid	Fish	Squid	Fish
Tuna	1.247	0.084	0.0385	0.000	0.0480	0.000
Large-C	0.816	0.143	0.0090	0.000	0.0073	0.000
Small-C	1.566	0.261	0.0246	0.000	0.0385	0.000

type on mortality rate. The effect of water temperature, particularly during the depth and time of day when hooked, and changes in water temperature up to the time the fish is landed, are considered to be influential. In addition, in high water-temperature environments, studies have identified an increased risk of suffocation as a result of decreased dissolved oxygen in water and increased physiological metabolic rate (Skomal and Bernal 2010). Gallagher *et al.* (2014) reported an increase in haulback mortality rate for four shark species when caught during high water temperatures. In addition, for the species that adopt rum ventilation, prolonged soak time inevitably increases the risk of suffocation because of the restriction of swimming behaviour by being hooked. Mortality rates of tuna, swordfish and sharks reportedly increased with an increasing soak time (Epperly *et al.* 2012; Gallagher *et al.* 2014).

We quantified our data through experimental operations that standardised the various conditions, but not all aspects were completely controlled. For example, whereas previous studies on hook size have examined the correspondence with actual measurements (Gilman *et al.* 2016), several shapes of circle hook were used in the experiment in this study, precluding examination of effects of individual hook types because of sample size issues. We were also unable to examine hooking location of the catch when fish bait was used. These omissions, although having a limited impact on the present conclusions, are probably variables that should be considered for a deeper examination of the effects of terminal gear on catch and bycatch.

Wire rather than nylon monofilament leaders were used on all branch lines to avoid missed catches owing to shark bite-offs. Although some studies have described that wire leader has the effect of increasing the catch rate of sharks (Ward *et al.* 2008; Afonso *et al.* 2011), it is considered essential for at least experimentally verifying accurate catch and mortality rates for shark species. Bite-off is more likely to occur when sharks swallow hooks, as suggested by previous studies (Yokota *et al.* 2006*a*; Afonso *et al.* 2011, 2012; Gilman *et al.* 2016). In the present study, tuna hooks were more likely to be swallowed by sharks, suggesting that their CPUE and MPUE may have been underestimated when nylon leaders were used. We know from this and previous studies that haulback mortality rates for sharks are much lower than those for teleosts (Afonso *et al.* 2012; Reinhardt *et al.* 2018), and the implementation of safe release protocols, even with wire leaders, allow for the reduction of risk for vulnerable shark species.

Here, on the basis of a Bayesian approach, we succeeded in presenting a quantitative impact assessment of terminal gear on teleosts, sharks and sea turtles by directly calculating the expected values for mortality rate, CPUE and MPUE with each terminal gear. Calculating MPUE by using this model can be a very useful tool because it provides a more direct estimate of catch or bycatch risk to populations of those species than does CPUE or mortality rate alone. Although we did not include post-release mortality rate in the model because of lack of data, it would be possible to estimate overall fishing mortality in the model by designing additional experiments so that mark–recapture is conducted at the same time. Even if it is not possible to use wire leaders for the proportion of 'cryptic catch' owing to bite-off, it is possible to extrapolate this proportion into the model to make predictions regarding mortality, a development we anticipate. The statistical control for relevant covariates would allow for an evaluation of adverse effects without the confounding factors described in previous studies. Although the data used in the analysis relied solely on the results of an Asian-style longline experiment in the Pacific Ocean and may therefore contain inherent biases, the same analysis method can be used in conjunction with data from other experiments conducted in other areas and fishing styles to provide a more integrated assessment.

Supplementary material

Supplementary material is available online.

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Data availability. There are no publicly accessible data used in this study other than the statistical model codes listed in the supplementary material. A preprint version of this article is available in Ochi *et al.* (2022).

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. This research was conducted as a part of the research and assessment program for internationally managed fisheries resources, the Fisheries Agency of Japan.

Acknowledgements. We greatly appreciate for the crew of the R/V *Taikei No. 2*, especially Fishmaster O. Asano, who was very helpful in coordinating the research operations, and members of the Fisheries Resources Institute (formerly known as the National Research Institute of Far Seas Fisheries), especially Y. Inoue, Y. Semba, A. Kurashima, Y. Fujinami, N. Katsumata, K. Yokota, K. Oshima, H. Minami, who also assisted with the research and analysis, and Y. Takeuchi who assisted model running using the computer cluster. The authors thank Enago (www.enago.jp) for English language review.

Author contributions. All authors collected data; D. Ochi designed the study, analysed data and wrote the draft of the paper. All authors reviewed the paper.

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