

Abstract—Our analyses of observer records reveal that abundance estimates are strongly influenced by the timing of longline operations in relation to dawn and dusk and soak time—the amount of time that baited hooks are available in the water. Catch data will underestimate the total mortality of several species because hooked animals are “lost at sea.” They fall off, are removed, or escape from the hook before the longline is retrieved. For example, longline segments with soak times of 20 hours were retrieved with fewer skipjack tuna and seabirds than segments with soak times of 5 hours. The mortality of some seabird species is up to 45% higher than previously estimated.

The effects of soak time and timing vary considerably between species. Soak time and exposure to dusk periods have strong positive effects on the catch rates of many species. In particular, the catch rates of most shark and billfish species increase with soak time. At the end of longline retrieval, for example, expected catch rates for broadbill swordfish are four times those at the beginning of retrieval.

Survival of the animal while it is hooked on the longline appears to be an important factor determining whether it is eventually brought on board the vessel. Catch rates of species that survive being hooked (e.g. blue shark) increase with soak time. In contrast, skipjack tuna and seabirds are usually dead at the time of retrieval. Their catch rates decline with time, perhaps because scavengers can easily remove hooked animals that are dead.

The results of our study have important implications for fishery management and assessments that rely on longline catch data. A reduction in soak time since longlining commenced in the 1950s has introduced a systematic bias in estimates of mortality levels and abundance. The abundance of species like seabirds has been over-estimated in recent years. Simple modifications to procedures for data collection, such as recording the number of hooks retrieved without baits, would greatly improve mortality estimates.

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Fish lost at sea: the effect of soak time on pelagic longline catches

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Our knowledge of large pelagic fish in the open ocean comes primarily from tagging and tracking experiments and from data collected from longline fishing vessels since the 1950s. Abundance indices for pelagic stocks are often derived from analyses that model catch as a function of factors such as year, area, and season. However, the amount of time that baited hooks are available to fish is likely to be another important factor influencing catch rates (Deriso and Parma, 1987).

The activity of many pelagic animals and their prey vary with the time of day. Broadbill swordfish, for example, feed near the sea surface at night. They move to depths of 500 m or more during the day (Carey, 1990). Other species may be more active in surface waters during the day (e.g. striped marlin) or at dawn and dusk (e.g. oilfish). Longline fishing crews take a keen interest in the timing of their fishing operations and soak time (the total time that a baited hook is available in the water). However, assessments have not accounted for those factors in estimating the abundance or mortality levels of target species or nontarget species.

In many assessments that use pelagic longline catch rates, fishing effort is assumed to be proportional to the number of hooks deployed. The effects of soak time and timing may have been omitted because a clear demonstration of their effects on pelagic longline catch rates is not available. The few published accounts on soak time in pelagic longline fisheries have been based on

limited data and a few target species. For example, in analyzing 95 longline operations or “sets” by research vessels Sivasubramaniam (1961) reported that the catch rates of bigeye tuna increased with soak time, whereas yellowfin tuna catch rates were highest in longline segments with intermediate soak times.

In contrast to the limited progress in empirical studies, theoretical approaches are well developed for modeling factors that may influence longline catch rates. Soon after large-scale longlining commenced, Murphy (1960) published “catch equations” for adjusting catch rates for soak time, bait loss, escape, hooking rates, and gear saturation. He suggested that escape rates could be estimated from counts of missing hooks and hooks retrieved without baits. Unfortunately, such data are rarely collected from pelagic longline operations.

More recently, hook-timers attached to longline branchlines have begun to provide information on the time when each animal is hooked and also whether animals are subsequently lost, e.g. Boggs (1992), Campbell et al.^{1,2} Such data are particularly useful to under-

¹ Campbell, R., W. Whitelaw, and G. McPherson. 1997. Domestic longline fishing methods and the catch of tunas and non-target species off north-eastern Queensland (1st survey: October–December 1995). Report to the Eastern Tuna and Billfish Fishery MAC. 71 p. Australian Fisheries Management Authority, PO Box 7051, Canberra Business Centre, ACT 2610, Australia.

² See next page.

standing the processes affecting the probability of capture and escape.

The purpose of our study is to determine whether variations in the duration and timing of operations bias abundance and mortality estimates derived from longline catch rates. We present a theoretical model that is then related to empirical observations of the effects of soak time on catch rates. The strength in our approach is in applying a random effects model to large data sets for over 60 target and nontarget species in six distinct fisheries. We also investigate the survival of each species while hooked because preliminary analyses suggested that the effects of soak time on catch rates might be linked to mortality caused by hooking (referred to as “hooking mortality”).

Factors affecting catch rates

To aid interpretation of our statistical analysis of soak time effects, we first developed a simple model to illustrate how the probability of catching an animal may vary with soak time.

The probability of an animal being on a hook when the branchline is retrieved is a product of two probability density functions: first the probability of being hooked and then the probability of being lost from the hook.³ Influencing the probability of being hooked are the species’ local abundance, vulnerability to the fishing gear, and the availability of the gear. Catches will deplete the abundance of animals within the gear’s area of action, particularly for species that have low rates of movement. Movement will also result in variations in exposure of animals to the gear over time—for instance, as they move vertically through the water column in search of prey (Deriso and Parma, 1987).

Other processes that will reduce the probability of being hooked include bait loss and reduced sensitivity to the bait (Fernö and Huse, 1983). Longline baits may fall off hooks during deployment, deteriorate over time and fall off or they may lose their attractant qualities. They may be removed by target species, nontarget species, or other marine life, such as squids. Hooked animals may also escape by severing the branchline or breaking the hook. Sections of the longline may become saturated when animals are hooked, reducing the number of available baits (Murphy, 1960; Somerton and Kikkawa, 1995). After an animal has been hooked, it may escape, fall off the hook, be removed by scavengers, or it may remain hooked until the branchline is retrieved.

Some of the processes affecting the probability of an animal being on a hook when the the branchline is retrieved

are species-specific, whereas other processes may affect all species. For example, bait loss during longline deployment will reduce the catch rates of all species. In contrast, the probability of a hooked animal escaping may be species-dependent; some species are able to free themselves from the hook whereas other species are rarely able to do this.

Our simple model of the probability of an animal being on a hook is based on a convolution of the two time-related processes described above: 1) the decay in the probability of capture with the decline in the number of baits that are available; and 2) gains due to the increased exposure of baits to animals and losses due to animals escaping, falling off, or being removed by scavengers.

The probability of an animal being on a hook when the branchline is retrieved is the integral of the probability density functions of capture and retention:

$$\pi(T) = \int_{t=0}^T P_c(t)P_r(T-t)dt, \quad (1)$$

where $\pi(T)$ = the “catch rate” or probability of an animal being on a hook when the branchline is retrieved at time T (T is the total soak time of the hook);

$P_c(t)$ = the probability density function of an animal being captured at time t ; and

$P_r(t)$ = the probability density function of a captured animal being retained on the hook for a length of time t .

The probability density function of capture can be approximated with an exponential function:

$$P_c(t) = P_0 e^{-\alpha t}, \quad (2)$$

where P_0 = the probability of capture when the hook is deployed ($t=0$); and

α = a parameter determining the rate of change in capture probability over time.

After the animal is hooked, the probability density function of an animal being retained after capture can be approximated as

$$P_r(t) = e^{-\beta t}, \quad (3)$$

where β = the “loss rate,” a parameter determining the rate of change in the probability of an animal being retained after it has been captured.

Substituting approximations 2 and 3 into Equation 1 gives

$$\begin{aligned} \pi(T) &= \int_{t=0}^T P_0 e^{-\alpha t} e^{-\beta(T-t)} dt \\ &= \frac{P_0}{\beta - \alpha} [e^{-\alpha T} - e^{-\beta T}]. \end{aligned} \quad (4)$$

² Campbell, R., W. Whitelaw, and G. McPherson. 1997. Domestic longline fishing methods and the catch of tunas and nontarget species off north-eastern Queensland (2nd survey: May–August 1996). Report to the Eastern Tuna and Billfish Fishery MAC, 48 p. Australian Fisheries Management Authority, PO Box 7051, Canberra Business Centre, ACT 2610, Australia.

³ In discussing continuous variables we use the terms “probability” and “probability density function” interchangeably.

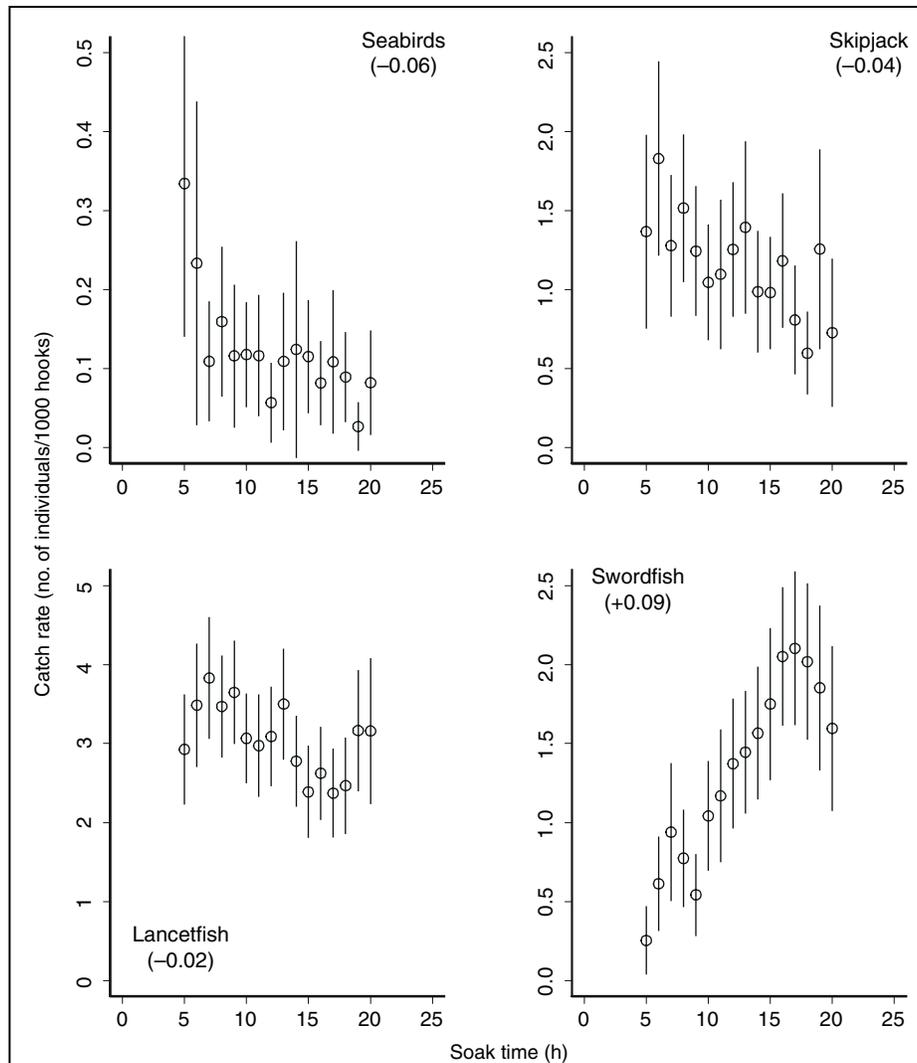


Figure 1

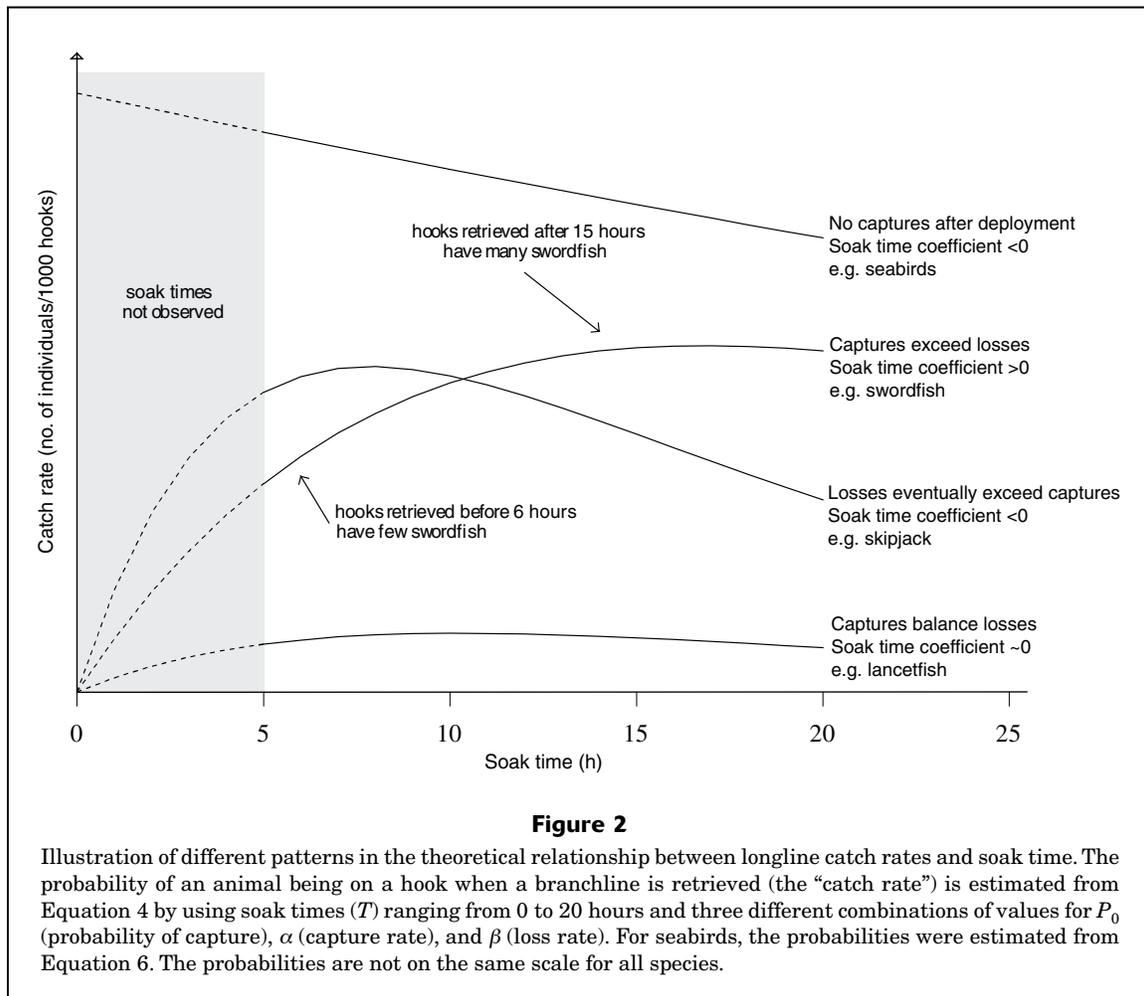
Mean catch rates plotted against soak time for skipjack tuna, long-nosed lancetfish, and swordfish in the South Pacific yellowfin tuna fishery and for “other seabirds” in the South Pacific bluefin tuna fishery. To reduce variability, the estimates were limited to longline segments with more than 25 hooks and soak times of 5–20 hours. Vertical bars are 95% confidence intervals for the mean hourly catch rate. In parentheses are the soak-time coefficients from random effects models (note that the soak-time coefficient is not the same as the slope coefficient of a regression of the data presented in this graph).

Our model is similar to the parabolic catch model examined by Zhou and Shirley (1997). It is simpler than catch equations developed by other authors because it does not include specific terms for the loss of baits, for fish competition, and gear saturation.

Preliminary plots of observer data indicated a variety of patterns in the relationship between catch rates and soak time (e.g. Fig. 1). By varying the values of P_0 (probability of capture), α (capture rate), and β (loss rate), our simple catch equation (Eq. 4) can mimic the observed patterns (Fig. 2). However, estimates of P_0 , α , and β are not available. Instead, we used the empirical approach described

in the following section to model the effect of soak time on catch rates. The relationship of soak time to catch rate represents the product of the probability of capture and the probability of being retained.

One approach to investigating the effects of soak time on catch rates is to fit linear regressions to aggregated data like those presented in Figure 1. Such an approach, however, would violate assumptions of independence (within each longline operation, catch rates in consecutive segments will be related), normality (these are binomial data), and homogeneity of variance (for binomial data, the variance is dependent on the mean).



Another approach might be to fit separate logistic regressions to each operation and then to combine the parameter estimates. This would overcome the problems of normality and homogeneity of variance. However, the separate regressions would not incorporate information that is common to all operations.

Instead, we used a logistic regression with random effects. The key advantage in using random-effects models in this situation is that they carry information on the correlation between longline segments that is derived from the entire data set of operations.

Data and methods

Fisheries

We analyzed observer data from six different fisheries in the Pacific Ocean to determine the effects of soak time and timing on longline catch rates (Table 1, Fig. 3). These fisheries involve two different types of longline fishing operation: 1) distant-water longlining involves trips of three months or longer and the catch is frozen on board

the vessel; and 2) fresh-chilled longlining, which involves small vessels (15–25 m) undertaking trips of less than four weeks duration, and the catch is kept in ice, ice slurries, or in spray brine systems. The fresh-chilled longliners deploy shorter longlines with fewer hooks (~1000 hooks) than the distant-water longliners (~3000 hooks per operation) (Ward, 1996; Ward and Elscot, 2000).

The six fisheries share many operational similarities, such as the types of bait used and soak time. However, they are quite different in terms of targeting, which is determined by fishing practices, e.g. the depth profile of the longline, timing of operations and the area and season of activity. South Pacific bluefin tuna longliners operate in cold waters (10–16°C) in winter to catch southern bluefin tuna. In the South Pacific yellowfin tuna longliners target tropical species, such as yellowfin and bigeye tuna, in warmer waters (19–22°C) (Ward, 1996). To target bigeye tuna, longlines in the Central Pacific bigeye fishery are deployed in the early morning with hook depths ranging down to about 450 m. The depths of the deepest hook are much shallower (~150 m) in the North Pacific swordfish fishery where the longlines are deployed late in the afternoon and retrieved early in the morning (Boggs, 1992).

Observer data

National authorities and regional organizations placed independent observers on many longliners operating in the six fisheries during the 1990s. The observer data consisted of records of the species and the time when each animal was brought on board. We restricted analyses to operations where the last hook that had been deployed was retrieved first (“counter-retrieved”), where there was no evidence of stoppages due to line breaks or mechanical failure, and where there was continuous monitoring by an observer. Combined with records of the number of hooks deployed and start and finish times of deployment and retrieval, the observer data allowed calculation of soak time and catch rates of longline segments. We aggregated catches and the number of hooks into hourly segments. The soak time was estimated for the midpoint of each hourly segment.

The Central Pacific bigeye tuna and North Pacific swordfish fisheries differed from the other four fisheries in the species that were recorded and the method of recording the time when each animal was brought on board. Observers reported catches according to a float identifier in the Central and North Pacific fisheries. Therefore we estimated soak times for each longline segment from the time when each float was retrieved. For those fisheries, observers reported the float identifier only for tuna, billfish, and shark (Table 2). Data are available for protected species, such as seals, turtles, and seabirds but were not sought for the present study.

We assumed a constant rate of longline retrieval throughout each operation. The number of hooks retrieved during each hourly segment was the total number of hooks divided by the duration of monitoring (decimal hours). For each species we analyzed only the operations where at least one individual of that species was caught.

Longline segments that involved a full hour of monitoring had several hundred hooks. Segments at either end of the longline involved less than an hour of monitoring and had fewer hooks. Catch rates may become inflated in segments with very small numbers of hooks. Therefore we arbitrarily excluded segments where the observer monitored less than 25 hooks.

For four of the fisheries, data were available on survival rates, allowing the investigation of the relationship between soak time and hooking mortality. For the Western Pacific and South Pacific fisheries, observers reported whether the animal was alive or dead when it was brought on board. We calculated survival rate (the number alive divided by the total number reported dead or alive) for species where data were available on the life status of more than ten individuals.

Generalized linear mixed model

Logit model We applied a generalized linear mixed model to the observer data. The model is based on a logistic regression, with the catch (y) on each hook assumed to have a binomial distribution with $y \sim b(n, \pi)$. π is the expected value of the distribution for a specified soak time. We refer to it as the probability of catching an animal or

Table 1

Summary of the six fisheries analyzed, showing the mean number of hooks per operation, mean duration of operations, mean catch rate of all species, the period of observer data, and the total number of longline operations. For the two Western Pacific fisheries, the catch rates are for the most common species only. NP = North Pacific; CP = Central Pacific; WP = Western Pacific; and SP = South Pacific.

Fishery name	Fleet	Area	Target species	Period	No. of operations	Hooks per operation	Duration (h)	Catch rate (no. of fish per 1000 hooks)
NP swordfish [†]	U.S. fresh-chilled	North Pacific	swordfish	1994–2002	1539	812	21	51
CP bigeye tuna [†]	U.S. fresh-chilled	Central Pacific	bigeye tuna, albacore	1994–2002	3243	1865	19	23
WP bigeye tuna	fresh-chilled (various flags)	Western Pacific	bigeye tuna, yellowfin tuna	1990–2001	1915	1620	21	28
WP distant	distant-water (various flags)	Western Pacific	bigeye tuna, yellowfin tuna	1990–2001	234	2347	22	30
SP yellowfin tuna	Japan distant-water	northeastern Australia	yellowfin tuna, bigeye tuna	1992–97	1419	3130	22	40
SP bluefin tuna	Japan distant-water	southeastern Australia	southern bluefin tuna	1992–97	666	3086	22	23

[†] We used the number of hooks between floats to distinguish the North Pacific swordfish fishery (<15 hooks between floats) from the Central Pacific bigeye tuna fishery (16 or more hooks between floats).

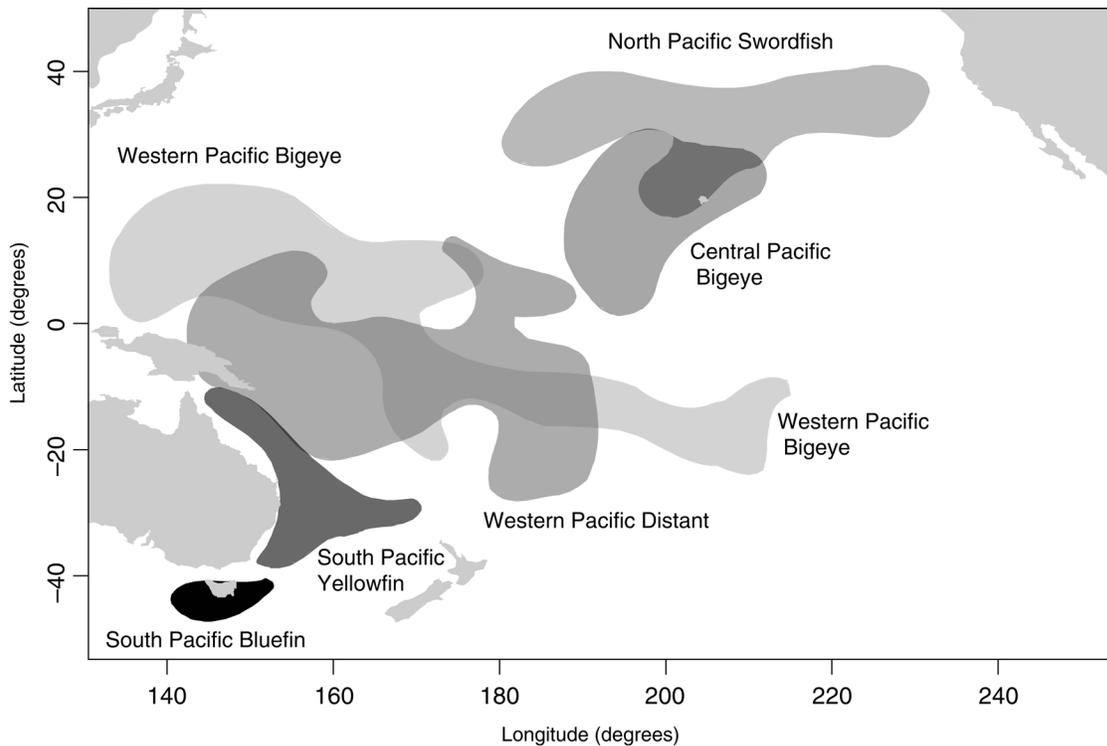


Figure 3

Geographical distribution of the observer data analyzed for each fishery.

the expected number of animals per hook. For each longline segment (j) within each operation (i), we link $\pi_{i,j}$ to a linear predictor ($\eta_{i,j}$) through the equation

$$\pi_{i,j} = \frac{e^{\eta_{i,j}}}{(1 + e^{\eta_{i,j}})}$$

η_i is then modeled as a function of soak time:

$$\eta_{i,j} = \beta_0 + \beta_1 T_{i,j}, \quad (5)$$

where $T_{i,j}$ = the hook's soak time (decimal hours) in longline segment j ;

β_0 = the intercept; and

β_1 = the slope coefficient, which we term the "soak time coefficient."

Modeling the probability of a catch on each individual hook would result in large numbers of zero observations and thus test the limits of current computer performance. Therefore we aggregated hooks and catches into hourly segments for each longline operation.

We assumed that each longline segment had the same configuration and that the probability of capture was the same for each segment within a longline operation. The assumption may be violated where segments pass through different water masses or where they differ in depth profile or baits. Saturation of segments with animals will also alter the capture probability between segments. The effects

of water masses, depth profiles, baits, and gear saturation were not analyzed in the present study.

Capture probability may also vary through the differential exposure of segments to the diurnal cycle of night and day. The addition of dawn and dusk as fixed effects allowed us to model diurnal influences on catch rates.

Fixed effects To explore factors that might affect the relationship between soak time and catch rate, we added four fixed effects to the logit model: year, season, and, as mentioned above, whether the segment was available at dawn or dusk. A full model without interaction terms would be

$$\eta_{i,j} = \beta_0 + \beta_1 T_{i,j} + \beta_2 A_{i,j} + \beta_3 P_{i,j} + \beta_4 S_{i,j} + \beta_5 Y_{i,j} + O_i,$$

where $T_{i,j}$ = the hook's soak time (decimal hours) in longline segment j ;

$A_{i,j}$ = an indicator of whether the hook was exposed to a dawn period;

$P_{i,j}$ = an indicator of whether the hook was exposed to a dusk period;

$S_{i,j}$ = the season (winter or summer);

$Y_{i,j}$ = the year;

O_i = the random effect for operation that we modeled as an independent and normally distributed variable (see "Random effects" section); and

β_0 – β_4 are parameters (fixed effects) to be estimated. We refer to β_1 as the "soak time coefficient."

Table 2

List of common and scientific names of the species analyzed. Also shown is the number of individuals of each species analyzed in each fishery. A dash indicates that the species was not analyzed in the present study; it does not necessarily mean that the species was not taken in the fishery. In particular, observer data on the time of capture were not available for “other bony fish” in the North Pacific swordfish and Central Pacific bigeye tuna fisheries. NP = North Pacific; CP = Central Pacific; WP = Western Pacific; SP = South Pacific; LN = long-nosed; and SN = short-nosed.

Common name	Species	Fishery					
		NP swordfish	CP bigeye tuna	WP bigeye tuna	WP distant	SP yellowfin tuna	SP Bluefin tuna
Tuna and tuna-like species							
Albacore	<i>Thunnus alalunga</i>	9707	23,128	14,194	11,976	21,550	1399
Bigeye tuna	<i>Thunnus obesus</i>	5409	45,476	9814	2581	1846	—
Butterfly mackerel	<i>Gasterochisma melampus</i>	—	—	—	—	—	533
Skipjack tuna	<i>Katsuwonus pelamis</i>	546	13,882	1456	445	691	—
Slender tuna	<i>Allothunnus fallai</i>	—	—	—	—	—	28
Southern bluefin	<i>Thunnus maccoyii</i>	—	—	—	—	1030	10,537
Yellowfin tuna	<i>Thunnus albacares</i>	2811	21,654	16,029	4689	12,454	—
Wahoo	<i>Acanthocybium solandri</i>	383	5508	1345	—	308	—
Billfish							
Black marlin	<i>Makaira indica</i>	25	41	353	226	160	—
Blue marlin	<i>Makaira nigricans</i>	981	2379	1467	529	179	—
Sailfish	<i>Istiophorus platypterus</i>	49	193	706	399	151	—
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	543	5467	529	398	654	—
Striped marlin	<i>Tetrapturus audax</i>	1963	8332	681	182	724	—
Swordfish	<i>Xiphias gladius</i>	22,457	1680	1472	287	1173	92
Other bony fish							
Barracouta	<i>Thyrsites atun</i>	—	—	—	—	53	—
Barracudas	<i>Sphyræna</i> spp.	—	—	707	153	—	—
Escolar	<i>Lepidocybium flavobrunneum</i>	1208	3983	1343	878	1726	84
Great barracuda	<i>Sphyræna barracuda</i>	32	743	303	442	92	—
Lancetfish (LN)	<i>Alepisaurus ferox</i>	2788	30,136	325	419	2868	610
Lancetfish (SN)	<i>Alepisaurus brevirostris</i>	—	—	155	84	257	59
Lancetfishes	<i>Alepisaurus</i> spp.	—	—	1431	98	—	—
Long-finned bream	<i>Taractichthys longipinnis</i>	—	—	—	—	—	292
Mahi mahi	<i>Coryphaena hippurus</i>	17,463	19,090	1436	211	447	—
Oilfish	<i>Ruvettus pretiosus</i>	555	1091	420	456	653	900
Opah	<i>Lampris guttatus</i>	68	4724	527	129	80	213
Pomfrets	Family Bramidae	—	—	623	60	—	40
Ray's bream	<i>Brama brama</i>	—	—	—	—	1074	10,547
Ribbonfishes	Family Trachipteridae	—	—	—	—	—	22
Rudderfish	<i>Centrolophus niger</i>	—	—	—	—	—	90
Sickle pomfret	<i>Taractichthys steindachneri</i>	—	—	122	21	—	—
Slender barracuda	<i>Sphyræna jello</i>	—	—	—	—	121	—
Snake mackerel	<i>Gempylus serpens</i>	1971	9881	256	44	—	—
Snake mackerels	Family Gempylidae	—	—	456	10	—	—
Southern Ray's bream	<i>Brama</i> spp.	—	—	—	—	—	28
Sunfish	<i>Mola ramsayi</i>	—	—	—	—	249	99
Sharks and rays							
Bigeye thresher shark	<i>Alopias superciliosus</i>	149	1930	145	61	—	—
Blacktip shark	<i>Carcharhinus limbatus</i>	—	—	445	125	—	—
Blue shark	<i>Prionace glauca</i>	31,503	31,413	5601	1628	1689	12,797
Bronze whaler	<i>Carcharhinus brachyurus</i>	—	—	—	—	116	—
Crocodile shark	<i>Pseudocarcharias kamoharai</i>	—	—	153	73	—	—

continued

Table 2 (continued)

Common name	Species	Fishery					
		NP swordfish	CP bigeye tuna	WP bigeye tuna	WP distant	SP yellowfin tuna	SP Bluefin tuna
Sharks and rays (continued)							
Dog fishes	Family Squalidae	—	—	—	—	—	60
Dusky shark	<i>Carcharhinus obscurus</i>	—	112	—	—	20	—
Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	—	—	282	64	—	—
Hammerhead shark	<i>Sphyrna</i> spp.	—	—	142	191	22	—
Long finned mako	<i>Isurus paucus</i>	—	83	108	15	—	—
Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	568	2373	2376	384	142	—
Porbeagle	<i>Lamna nasus</i>	—	—	—	—	27	1011
Pelagic stingray	<i>Dasyatis violacea</i>	2374	2849	1212	248	534	109
Pelagic thresher shark	<i>Alopias pelagicus</i>	—	—	77	34	—	—
School shark	<i>Galeorhinus galeus</i>	—	—	—	—	—	143
Short finned mako	<i>Isurus oxyrinchus</i>	476	685	408	169	432	128
Silky shark	<i>Carcharhinus falciformis</i>	25	1433	5396	2406	8	—
Silvertip shark	<i>Carcharhinus albimarginatus</i>	—	—	168	74	—	—
Thintail thresher shark	<i>Alopias vulpinus</i>	—	74	—	—	—	31
Thresher shark	<i>Alopias superciliosus</i>	—	—	415	—	93	18
Tiger shark	<i>Galeocerdo cuvier</i>	—	—	56	18	38	—
Velvet dogfish	<i>Zameus squamulosus</i>	—	—	—	—	—	156
Whip stingray	<i>Dasyatis akajei</i>	—	—	78	15	—	—
Seabirds							
Albatrosses	Family Diomedidae	—	—	—	—	—	88
Petrels	Family Procellariidae	—	—	—	—	—	29
Other seabirds	Family Procellariidae	—	—	—	—	38	200
All operations	104,054		238,340	73,212	30,222	51,699	40,343

To maintain a focus on the effects of soak time, the models were limited to simple combinations of fixed effects and interaction terms. Dawn and dusk were added to various models of each species in each fishery. To reduce complexity, year and season were limited to models of seven species (bigeye tuna, oilfish, swordfish, blue shark, albacore, southern bluefin tuna, long-nosed lancetfish) in the two South Pacific fisheries. The seven species represented four taxonomic groups and the full range of responses observed in preliminary analyses of the soak-time–catch-rate relationship.

Random effects We added random effects to all models to allow catch rates of segments within each longline operation to be related. The random effects model assumes that there is an underlying distribution from which the true values of the probability of catching the species, π , are drawn. The distribution is the among-operation variation or “random effects distribution.” The operations are assumed to be drawn from a random sample of all operations, so that the random effects (O_i) in the relationship between catch rate and soak time for each operation (i) are

independent and normally distributed with $O_i \sim N(0, \sigma^2)$. The random effects and various combinations of the fixed effects were added to the linear predictor presented in Equation 5.

For each species in the South Pacific yellowfin tuna data set we compared the performance of models under an equal correlation structure with that of models under an autoregressive correlation structure. Under an autoregressive structure, catch rates in the different hourly segments within the operations are not equally correlated. For example, the correlation between segments might be expected to decline with increased time between segments. However, we used an equal correlation structure for all models because the Akaike’s information criterion (AIC) and Sawa’s Bayesian information criterion (BIC) indicated that there was no clear advantage in using the autoregressive structure rather than an equal correlation structure.

Implementation We implemented the models in SAS (version 8.0) using GLIMMIX, a SAS macro that uses iteratively reweighted likelihoods to fit generalized linear

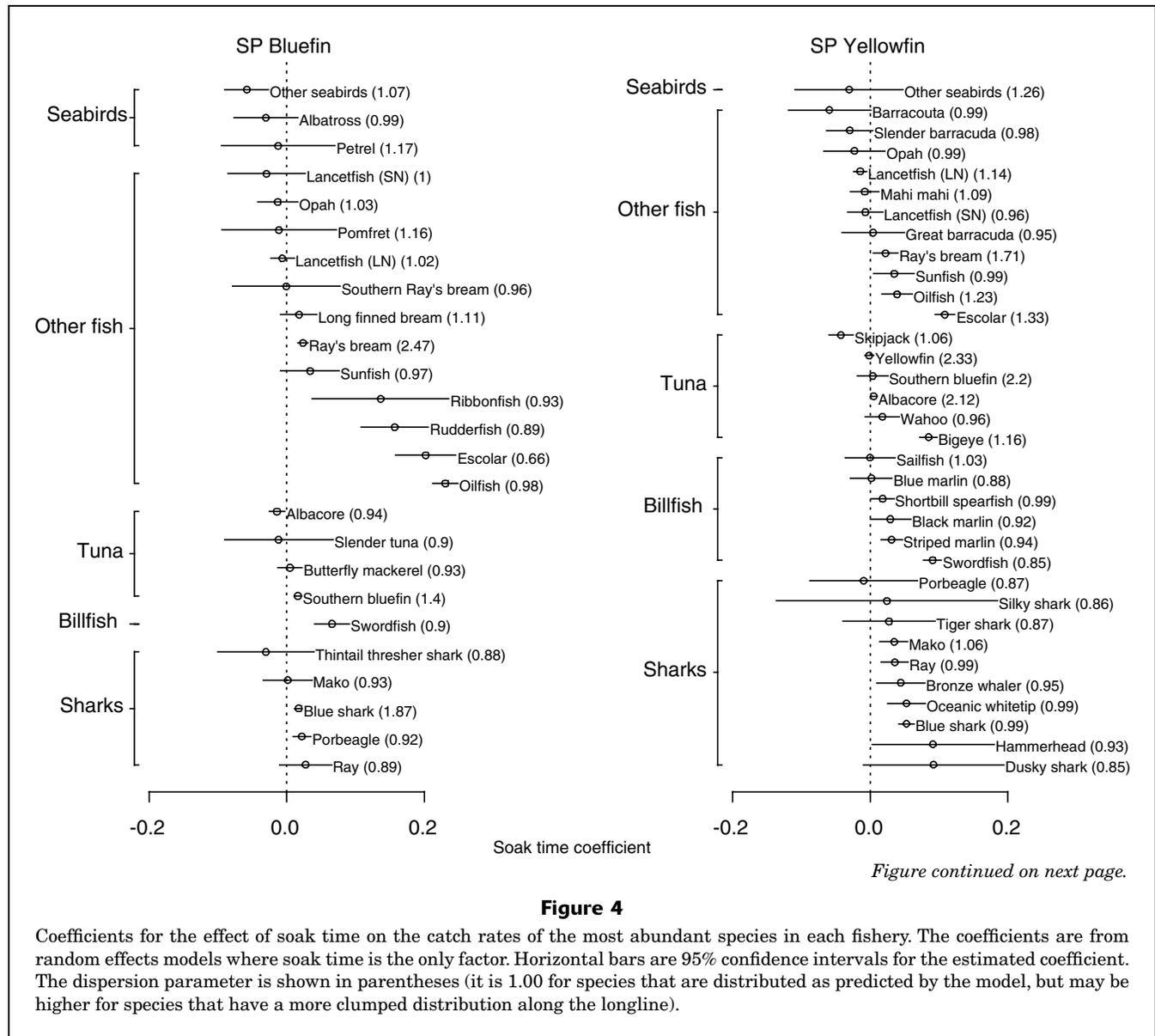


Figure 4

Coefficients for the effect of soak time on the catch rates of the most abundant species in each fishery. The coefficients are from random effects models where soak time is the only factor. Horizontal bars are 95% confidence intervals for the estimated coefficient. The dispersion parameter is shown in parentheses (it is 1.00 for species that are distributed as predicted by the model, but may be higher for species that have a more clumped distribution along the longline).

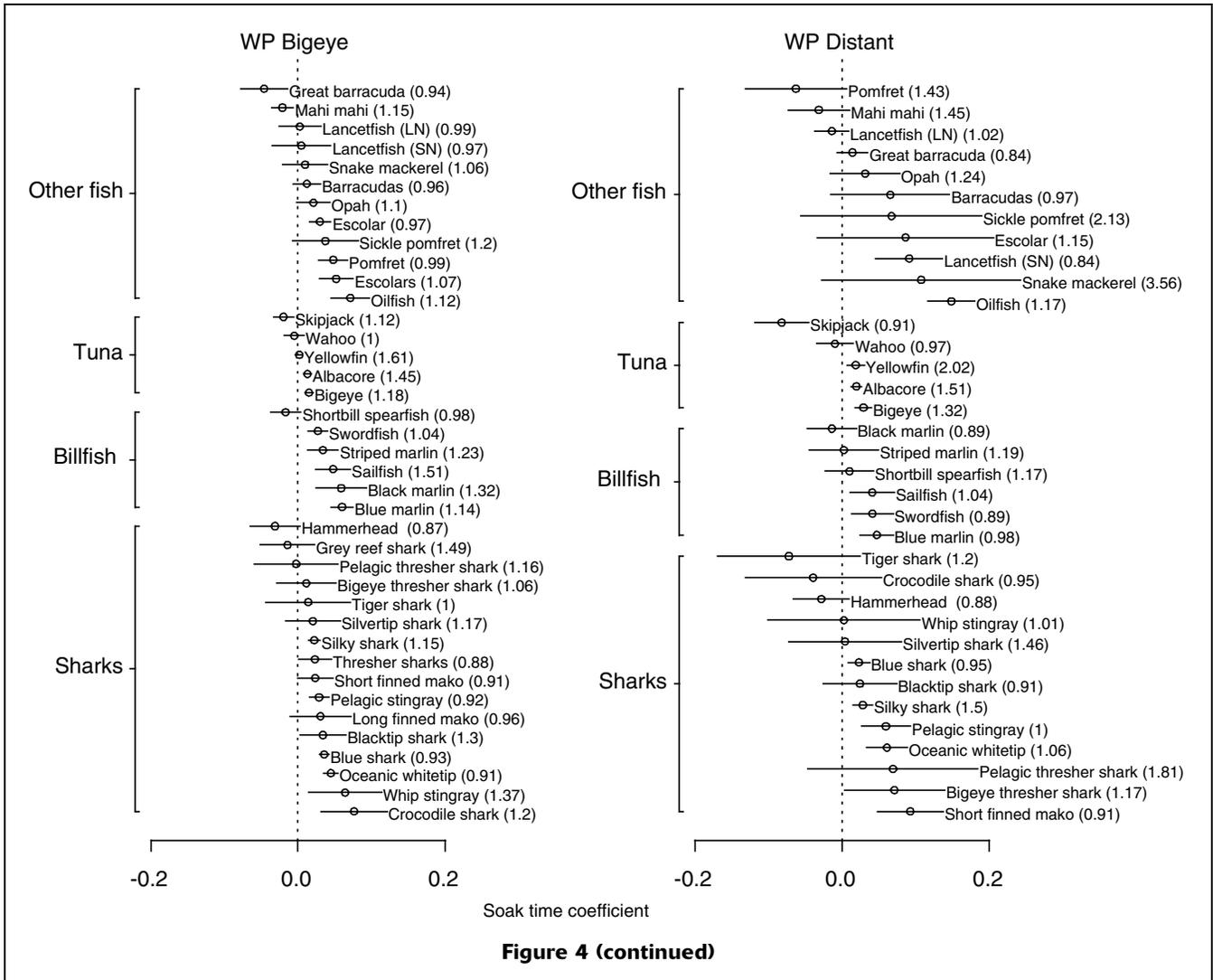
mixed models (Wolfinger and O’Connell, 1993). To judge the performance of the various model formulations, we checked statistics, such as deviance and dispersion, and examined scatter plots of chi-square residuals against the linear predictor (η) and QQ plots of chi-square residuals. We used the AIC and BIC to compare the performance of the various model formulations.

Variance in the binomial model depends on only one parameter, P . A dispersion parameter is therefore necessary to allow the variance in the data to be modeled. In effect, the dispersion parameter scales the estimate of binomial variance for the amount of variance in the data. The dispersion parameter will be near one when the variance in the data matches that of the binomial model. Values greater than one (“over-dispersion”) imply that the species may have a clumped distribution along the longline.

Results

Soak time

For most species, soak time had a positive effect on catch rates (Fig. 4). In addition to being statistically significant, the effect of soak time made a large difference to catch rates at opposite ends of the longline. In the South Pacific yellowfin tuna fishery, for example, the expected catch rates of swordfish can vary from 0.6 (CI \pm 0.1) per 1000 hooks (5 hours) to 1.9 (CI \pm 0.3) per 1000 hooks (20 hours) (Table 3). A soak time of 5 hours and 3500 hooks (if that were possible) would result in a total catch of about two swordfish. In contrast, almost seven swordfish are expected from a longline operation of the same number of hooks with 20 hours of soak time.



For some species (e.g. seabirds, skipjack tuna, and mahi mahi), soak time had a negative effect on catch rates that was often statistically significant (Fig. 4). For skipjack tuna in the Western Pacific distant fishery, for example, catch rates decreased from 1.3 (CI ± 0.2) per 1000 hooks for a soak time of 5 hours to 1.0 (CI ± 0.1) per 1000 hooks (20 hours). Soak time had a small or statistically insignificant effect on catch rates for several species, such as yellowfin tuna and shortbill spearfish.

Fixed effects

Exposure to dusk had a positive effect on the catch rates for most species (Fig. 5). Dusk often had a negative effect on the catch rates of billfish, such as striped marlin and sailfish. For most species, however, the effect of dawn was weaker, and it influenced the catch rates of fewer species.

Like soak time, timing made a substantial difference to catch rates (Table 4). For a soak time of 12 hours in the South Pacific yellowfin fishery, for example, longline seg-

ments exposed to both dawn and dusk have a catch rate of 2.0 (CI ± 0.5) escolar per 1000 hooks. The catch rate is 0.8 (CI ± 0.1) per 1000 hooks for segments that were not exposed to dawn or dusk.

The effects of timing on catch rates were most pronounced in the South Pacific bluefin tuna fishery. The fishery also showed the greatest range in soak time coefficients, and the coefficients tended to be larger than those of other fisheries (Fig. 4).

Separately, the fixed effects often had statistically significant relationships with catch rates of the seven species that we investigated in detail. However, the interaction between soak time and each fixed effect was less frequently significant. Season was significant, for example, in none of the six models that included a soak-time–season interaction term. By comparison, season was significant in six of the 18 models that included season as a factor but not with a soak-time–season interaction term. The effect of soak time was not significant for southern bluefin tuna in any model for the South Pacific bluefin tuna fishery. It was significant

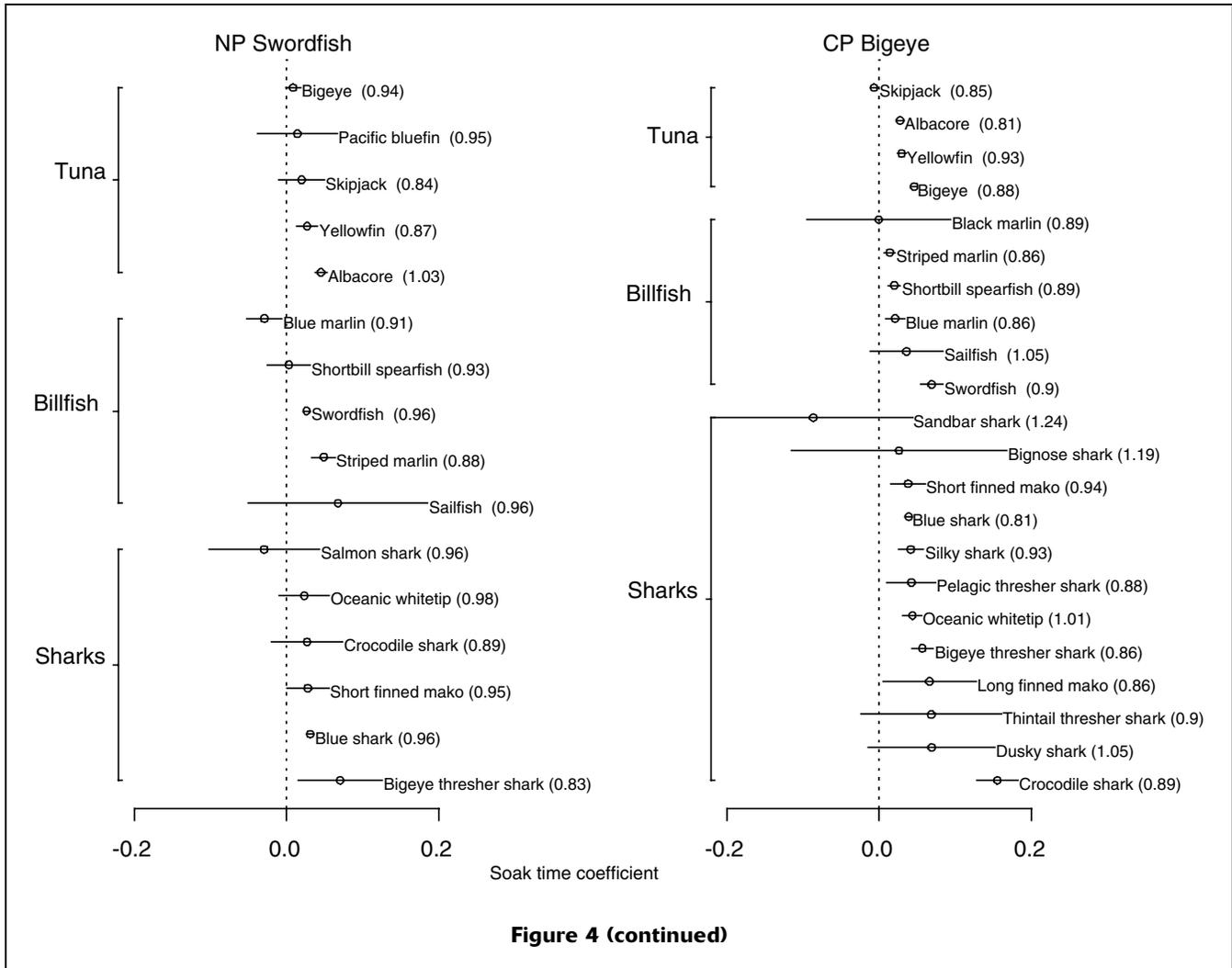


Figure 4 (continued)

in 36 of the 48 models for the other six species. We concluded that the fixed effects modified the intercept of the soak-time–catch-rate relationship, but they rarely altered the slope of the relationship.

Akaike’s information criterion (AIC) and Sawa’s Bayesian information criterion (BIC) both indicated that models with soak time as the only variable were the most or second most parsimonious model. This was the case for all models, except for several models of albacore and long-nosed lancetfish. Therefore the following discussion concentrates on the effects of soak time and timing on catch rates.

Discussion

In considering results of the random effects models, we examined patterns in the effects of soak time and timing among taxonomic groups, the mechanisms that may cause the patterns, and their implications. First, however, we investigated whether the effects were consistent for the same species between fisheries.

Comparison of fisheries

The effect of soak time was consistent for several species between the fisheries, despite significant differences in fishing practices and area and season of activity. For example, the soak time coefficients for species in the South Pacific yellowfin tuna fishery were very similar to those of the same species in the Central Pacific bigeye tuna fishery ($r=0.79$) (Fig. 6).

Several species had a narrow range of soak time coefficients over all the fisheries analyzed. Estimates of the coefficient of yellowfin tuna, for example, ranged from 0.00 (CI ± 0.01) in the South Pacific yellowfin fishery to 0.04 (CI ± 0.01) in the North Pacific swordfish fishery. A coefficient of 0.04 is equivalent to a difference of 1.3 yellowfin tuna per 1000 hooks between longline segments with soak times of 5 and 20 hours. The range in coefficients is also small for other abundant and widely distributed species, such as albacore ($r=0.00-0.05$) and blue shark ($r=0.01-0.05$).

For many species, however, the correlation between soak-time coefficients from different fisheries was poor (Fig. 6).

Table 3

Examples of the effect of soak time on expected catch rates of species in the South Pacific yellowfin tuna fishery. The expected catch rates (number per 1000 hooks) are predicted from the soak-time coefficient for each species for longline segments exposed to a dusk period with a soak time of 5 or 20 hours. Figure 4 shows the 95% confidence intervals for soak-time coefficients used to calculate the expected catch rates. LN = long-nosed; SN = short-nosed.

Species	Soak time (h)	
	5	20
Tuna and tuna-like species		
Albacore	15.5	13.4
Bigeye tuna	1.1	2.3
Skipjack tuna	1.3	1.0
Southern bluefin tuna	5.2	5.5
Yellowfin tuna	8.4	7.7
Billfish		
Black marlin	0.4	1.6
Blue marlin	1.2	0.4
Sailfish	0.8	1.0
Shortbill spearfish	1.0	1.6
Striped marlin	0.8	1.0
Swordfish	0.6	1.9
Other bony fish		
Barracouta	0.8	0.7
Escolar	0.8	3.1
Great barracuda	0.9	1.1
Lancetfish (LN)	2.7	2.4
Lancetfish (SN)	1.6	1.4
Mahi mahi	1.0	0.9
Oilfish	0.8	2.2
Opah	0.7	0.5
Ray's bream	1.8	2.0
Slender barracuda	1.7	1.6
Sunfish	0.6	1.3
Wahoo	1.0	1.1
Sharks and rays		
Blue shark	1.1	2.0
Bronze whaler	0.7	0.8
Dusky shark	0.4	0.8
Hammerhead	0.2	1.8
Mako	0.6	0.8
Oceanic whitetip	0.5	0.9
Porbeagle	1.2	1.1
Pelagic stingray	0.9	1.2
Thresher shark	0.6	1.0
Tiger shark	0.5	0.5

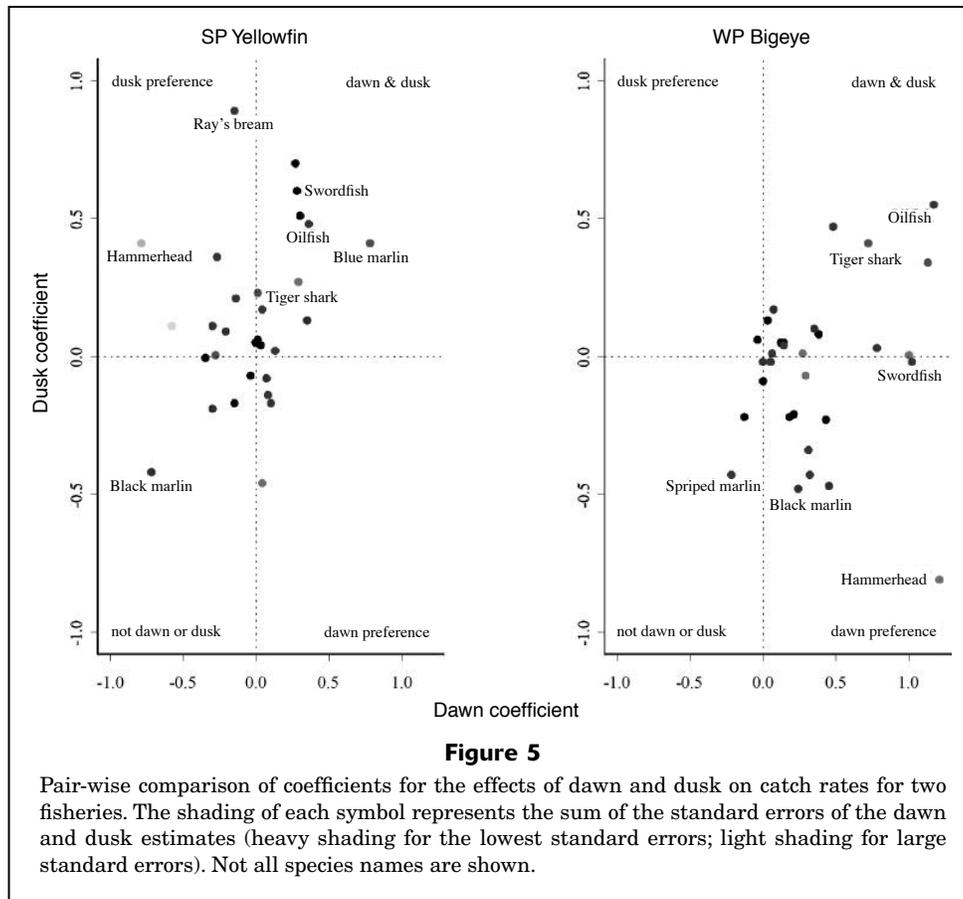
Table 4

Examples of the effect of timing on expected catch rates of species in the South Pacific yellowfin tuna fishery. The expected catch rates (number per 1000 hooks) are predicted from the soak-time coefficient for each species for a longline operation with a soak time of 12 hours. The different catch rates are for longline segments exposed to neither the dawn or dusk period, for dawn only, and for dawn and dusk periods. LN = long-nosed; SN = short-nosed.

Species	Period		
	Neither period	Dawn only	Dawn + dusk
Tuna and tuna-like species			
Albacore	12.3	14.0	16.5
Bigeye tuna	0.9	1.2	2.1
Skipjack tuna	1.4	1.2	1.0
Southern bluefin tuna	3.8	2.9	4.1
Yellowfin tuna	7.7	7.6	8.0
Billfish			
Black marlin	1.2	0.6	0.4
Blue marlin	0.4	1.0	1.4
Sailfish	0.8	0.7	0.7
Shortbill spearfish	1.3	0.9	0.9
Striped marlin	0.8	0.9	0.9
Swordfish	0.5	0.7	1.3
Other bony fish			
Barracouta	1.1	1.2	0.7
Escolar	0.8	1.0	2.0
Great barracuda	1.0	0.8	0.8
Lancetfish (LN)	2.8	2.7	2.5
Lancetfish (SN)	1.2	1.1	1.3
Mahi mahi	1.2	1.3	1.1
Oilfish	0.8	1.1	1.8
Opah	0.5	0.5	0.6
Ray's bream	0.8	0.7	1.6
Slender barracuda	2.0	1.5	1.2
Sunfish	0.8	0.6	0.7
Wahoo	1.2	1.3	1.1
Sharks and rays			
Blue shark	1.3	1.4	1.4
Bronze whaler	0.6	0.9	1.0
Dusky shark	0.1	0.1	0.6
Hammerhead	0.4	0.2	0.3
Mako	0.7	0.8	0.8
Oceanic whitetip	0.7	0.8	0.7
Porbeagle	1.0	0.6	0.6
Pelagic stingray	0.9	0.9	1.1
Thresher shark	0.6	0.6	0.7
Tiger shark	0.4	0.5	0.7

For a few species (e.g. tiger shark) the poor correlation may have been a function of small sample sizes and the wide confidence intervals of the estimates. For other species the estimates were well determined, yet poorly correlated, e.g. the coefficient for short-nosed lancetfish was 0.09

(CI ± 0.05) in the Western Pacific distant fishery compared to 0.01 (CI ± 0.04) in the Western Pacific bigeye tuna fishery. Therefore, we urge caution in applying our estimates to the same species in longline fisheries in other areas.



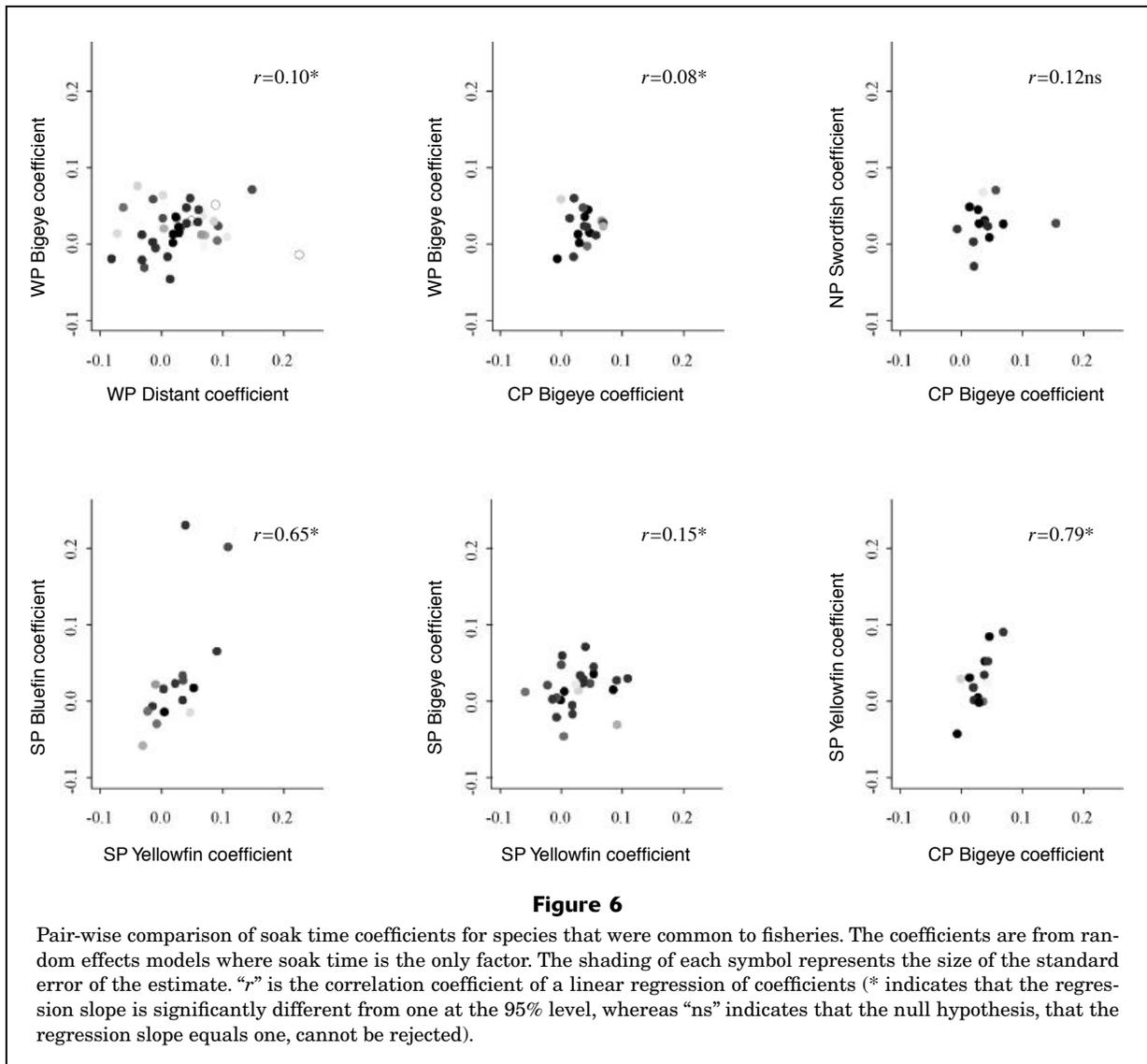
Underlying mechanisms

The broad taxonomic groups taken by longline each represent a wide range of life history strategies and feeding behaviors. Nevertheless, the results show a tendency for soak time to have a positive effect on catch rates of most shark species (Fig. 4). It also had a positive effect on catch rates of many billfish species, including striped marlin, black marlin, and swordfish. There is no clear pattern in the effect of soak time on catch rates of tuna or other bony fish. It had a negative effect on the four seabird groups.

The results imply that the ability of a species to stay alive and to escape or avoid scavengers while hooked is important in determining the catch that is actually brought on board. The effect of soak time is significantly correlated with the ability of a species to survive while hooked on the longline in the four fisheries with data on survival (Fig. 7). Soak time has a strong, positive effect on catch rates of species like blue shark, which are almost always alive when branchlines are retrieved. Species like skipjack tuna and seabirds are usually dead. Soak time had a negative effect on their catch rates. The opposite trend would be expected if escape is a significant process that affects catch rates; if escape is important, soak time should have a *negative* affect on the catch rates of the most active species. Therefore removal by scavengers is likely to be more important than escape in determining catch rates for many species.

Longline branchlines are usually 20–30 m in length, allowing considerable room for a live, hooked animal to evade predators or scavengers. Or, scavengers may be attracted by immobile and dead animals. The scavenger avoidance hypothesis is attractive, but it is difficult to test with observer data. Data from hook-timer experiments may help to estimate the total number of animals that are lost or removed from the longline. Data presented by Boggs (1992) showed a large number of hook-timers that were triggered but which did not hold an animal when the branchline was retrieved, e.g. his data show that 2–4% of hook-timers on 10,236 branchlines that had “settled” were activated but did not have an animal. It is unclear whether the triggering of hook-timers was due to equipment malfunction or whether it represents high loss rates. Of particular significance to the question of loss rates is the fact that current hook-timer technology does not identify the species that were lost and whether they were alive or dead.

We noticed that soak-time coefficients tended to be poorly correlated between fisheries and that the effects of soak time on catch rates were most pronounced in the South Pacific bluefin tuna fishery. Our scavenging hypothesis might explain those observations as evidence that the activities of scavengers vary between fisheries. For example, blue shark might be an important scavenger. They are most abundant in temperate areas (Last and Stevens, 1994). Our analyses showed a predominance of negative soak-time coefficients



in the South Pacific bluefin tuna fishery—perhaps indicating that loss rates may be particularly high where blue shark are abundant.

Nevertheless, there are other plausible explanations for the differences in soak-time effects between fisheries. The movement of branchlines caused by wave action will cause animals to fall off hooks, especially when branchlines are near the sea surface. Rough seas are frequently experienced in the North Pacific swordfish and South Pacific bluefin tuna fisheries where the soak-time effects were most pronounced.

Another source of loss might be the breakage of longline branchlines. The animal’s teeth or rostrum might abrade the branchline causing the branchline to fail and allowing the animal to escape. In this regard it is noteworthy that Central Pacific bigeye tuna longliners often use wire for the end of branchlines or “leader” whereas North Pacific swordfish longliners use monofilament nylon leaders (Ito⁴).

Mortality estimates

The results of our study show that longline catch rates that are not adjusted for the effects of soak time will underestimate the level of mortality of several species because they are lost after being hooked. The soak time effect was negative for albatrosses and other seabirds. This finding agrees with field observations (e.g. Brothers, 1991) that most seabirds are taken during longline deployment in the brief period after the bait is cast from the vessel until the bait sinks beyond the depth that seabirds can dive to. Those observations indicate that counts of seabirds when they are brought on board do not cover the total number hooked because many fall off or are removed by scavengers or are lost during the operation.

⁴ Ito, R. 2002. Personal commun. National Marine Fisheries Service (NOAA), 2570 Dole Street, Honolulu Hawaii 96822-2396.

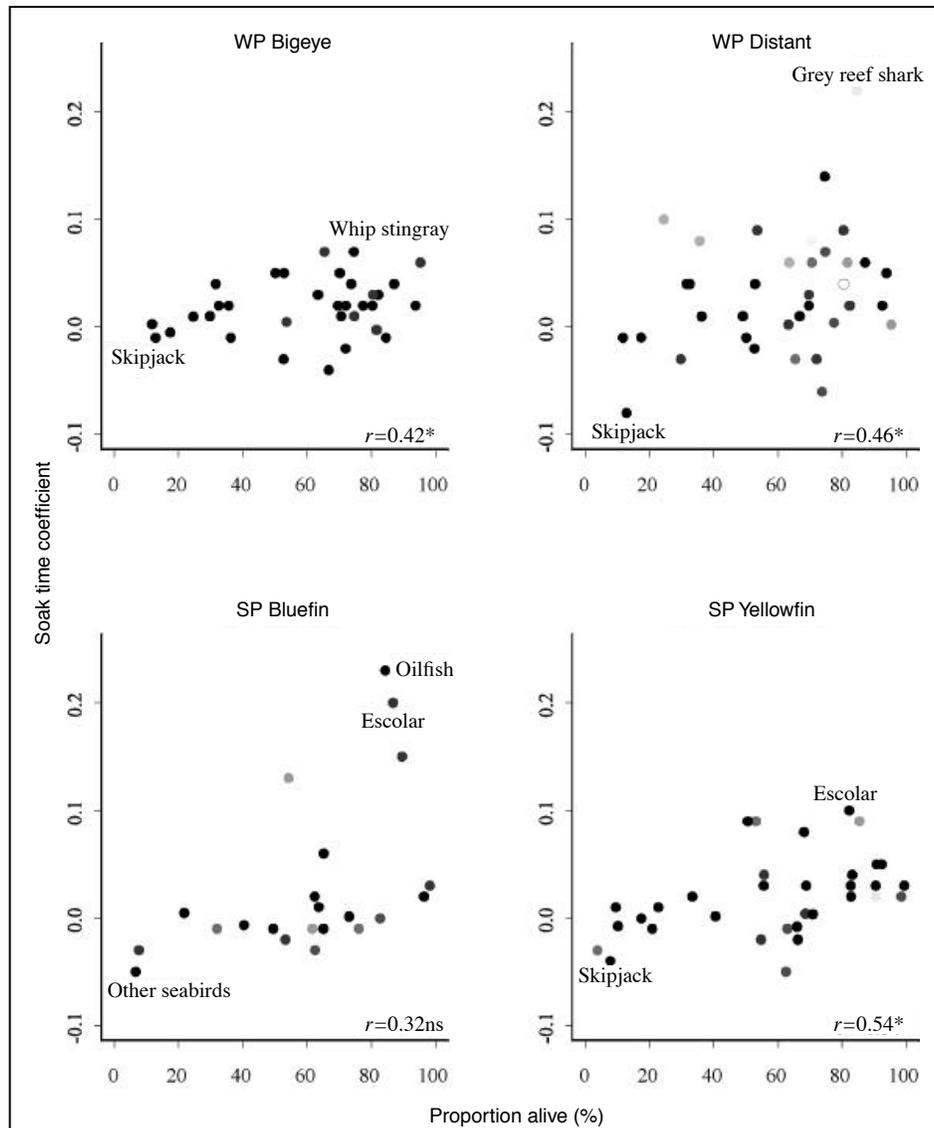


Figure 7

Soak-time coefficients plotted against the proportion of each species reported to be alive when brought on board. Not included are species where less than ten individuals for the fishery had a record of life status. The coefficients are from random effects models where soak time is the only factor. The shading of each symbol represents the size of the standard error of the estimate. The proportion alive is assumed to be measured without error. “r” is the correlation coefficient of a linear regression of coefficients (* indicates that the regression slope is significantly different from zero at the 95% level).

Seabirds provide a unique case for estimating loss rates because they are only caught when the longline is deployed (Brothers, 1991). Within minutes of the branchline being deployed, the capture rate (α in Eq. 4) falls to zero whereas the loss rate β might be constant or it might vary. Therefore, the probability of a seabird being on a hook when the branchline is retrieved is

$$\pi(T) = e^{-\beta T}. \tag{6}$$

We estimated a soak-time coefficient of -0.0302 (CI ± 0.0462) for albatrosses in the South Pacific bluefin tuna

fishery. Substituting 0.0302 for β in Equation 6 and 10.4 hours for T (the average soak time of hooks deployed by the longliners), we estimated that 27% of albatrosses are lost after being hooked but before the branchlines are retrieved. The loss rate is about 12% for petrels ($\beta=0.0123$) and 45% for other seabirds ($\beta=0.0582$). It is about 26% for other seabirds in the South Pacific yellowfin tuna fishery ($\beta=0.0307$, $T=10.0$ hours).

For fishes and sharks, we do not know how the probability of capture, or capture rate, or loss rate varies during a longline operation. However, hook-timer experiments

and observer programs may provide estimates of those parameters. Broad limits for the probability of capture may also be obtained if observers were to report the number of branchlines that are retrieved with missing baits or missing hooks.

For most species, capture rates must balance or outweigh loss rates. In this case, captures result from the increased exposure of animals to the longline as a result of movement and, perhaps, the dispersal of chemical attractants during the operation. However, we must stress that losses are also likely to be occurring for the species that have positive coefficients. The analyses indicate the relative levels of loss between longline segments of varying soak time. Other than those for seabirds, we cannot estimate the levels of catch that are lost.

Adding to the uncertainty over loss rates is the unknown fate of lost animals. For seabirds it is known that most drown soon after being hooked. The few seabirds that survive while hooked eventually drown during longline retrieval (Brothers, 1991). However, it is not known whether other lost animals are dead or alive.

Results of our analyses may also be useful for monitoring programs. Observers are increasingly being placed on longliners to collect data on bycatch and to independently verify data reported in logbooks. A sampling approach is necessary in some fisheries because observers are often unable to monitor the entire longline retrieval. Indications that catch rates of some species at the end of the retrieval are double those at the beginning necessitate care in designing observer monitoring protocols and in the interpretation of the data. Observers could also collect information on the number of hooks retrieved without baits. Such data would greatly improve the estimates of α and β required for the theoretical model. For the empirical model, catch rate data from research surveys where longline segments have very short (<4 hour) soak times would improve estimates of soak-time coefficients.

Historical changes

The interaction of year and soak time was rarely significant for the random effects models of the seven species examined in detail. This might suggest that soak-time–catch-rate relationships are stable over time. However, the range of years that we analyzed was limited to 1992–97. Over larger time scales there have been large variations in the abundance of individual species and the mix of species comprising the pelagic ecosystem. We cannot predict how soak-time–catch-rate relationships would change with those long-term variations.

Our original motivation for examining the effects of soak time was the hypothesis that the number of hooks per operation and soak time have increased since longlining commenced and that this may have resulted in an overestimation of billfish catch rates in early years. Ward⁵ presented information on temporal trends in soak time

and timing for several longline fleets. Although there is uncertainty over the early operations, the available information indicates significant historical changes in Japan's distant-water longline operations. Average soak time shows a decline from over 11.5 hours before 1980 to 10.0 hours in the 1990s. For species with a negative soak-time coefficient, this apparently modest reduction in soak time would inflate catch rate estimates for recent years. It would result in reduced catch-rate estimates for species with positive coefficients. For example, the expected catch rate for swordfish is 0.94 (CI \pm 0.06) per 1000 hooks for a soak time of 11.5 hours compared to 0.82 (CI \pm 0.06) per 1000 hooks for 10.0 hours.

More significant may be changes in the timing of operations. During 1960–80 most baits used with Japan's distant-water longliners were available to fish at dawn whereas about 50% were also available at dusk. Longlines were deployed and retrieved at later times in the 1990s so that about 30% of baits were available at dawn and about 70% available at dusk. In the case of swordfish, the changes in timing would moderate the effects of reduced soak time. The expected catch rate for swordfish is 0.89 per 1000 hooks in the early operations compared to 0.83 per 1000 hooks in the later operations.

Conclusions

The results have important implications for fishery management and assessments that rely on longline catch data. Modifications to data collection, such as recording the number of hooks with missing baits during longline retrieval, would greatly improve mortality estimates. The mortality of species like seabirds is significantly higher than previously estimated. Such underestimation may be particularly critical for the assessment and protection of threatened species of seabirds. Furthermore, the changes in timing and reduction in soak time have resulted in a systematic bias in estimates of mortality levels and abundance indices for many species. For species like swordfish, where soak time has a positive effect on catch rates, the stocks might be in better shape than predicted by current assessments (if assessments were solely based on catch and effort data). The opposite situation would occur for species with negative soak-time coefficients: assessments that use long time-series of longline catch data will over-estimate the species' abundance so that population declines are more severe than previously believed.

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⁵ Ward, P. 2002. Historical changes and variations in pelagic longline fishing operations. <http://fish.dal.ca/~myers/pdf/papers.html>. [Accessed 22 February 2003.]

cially grateful to the observers who collected the data used in this study and thank the masters, crew members, and owners of longliners for their cooperation with the observer programs. Pierre Kleiber, Ian Jonsen, Julia Baum, Boris Worm and an anonymous referee provided many useful comments on the manuscript.

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