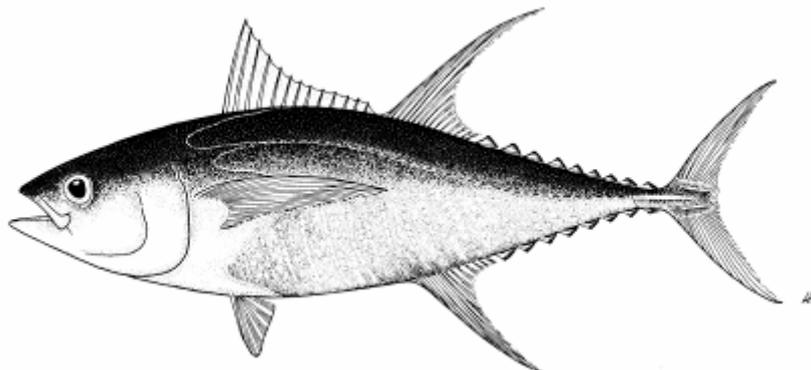




**Inferring the depth distribution of catchability for
pelagic fishes and correcting for variations in the
depth of longline fishing gear**



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August 2005

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Abstract: We introduce a new method that uses generalized linear mixed models to infer the depth distribution of pelagic fishes. It uses existing data from research surveys and observers on commercial vessels to estimate changes in catchability when longline fishing gear is lengthened to access deeper water. We infer the depth distribution of catchability for 37 fish species that are caught on pelagic longlines in the Pacific Ocean. We show how the estimates of catchability can be used to correct abundance indices for variations in longline depth. Our method facilitates the inclusion of data from early surveys in the time series of commercial catch rates used to estimate abundance. It also resolves inconsistencies in the time series caused by a rapid switch to deep longlining in the 1970s. The catchability distribution does not always match depth preferences derived from tracking studies. Therefore, depth preferences from tracking studies should not be used to correct abundance indices without additional information on feeding behavior.

Résumé : Nous présentons une nouvelle méthode qui utilise des modèles linéaires généralisés mixtes pour estimer la répartition des poissons pélagiques en fonction de la profondeur. La méthode exploite les données existantes d'inventaires scientifiques et d'observations faites sur les navires commerciaux afin d'estimer les changements de capturabilité qui se produisent lorsqu'on allonge les palangres pour pêcher en eau plus profonde. Nous estimons la répartition de la capturabilité en fonction de la profondeur chez 37 espèces de poissons récoltés à la palangre pélagique dans le Pacifique. Nous démontrons comment les estimations de capturabilité peuvent servir à corriger les indices d'abondance en fonction des variations de la profondeur des palangres. Notre méthode facilite l'inclusion de données d'inventaires plus anciens dans la série chronologique de taux de capture commerciaux utilisée pour estimer l'abondance. Elle permet aussi de résoudre les irrégularités dans la série chronologique causées par un passage rapide à la pêche à la palangre en profondeur durant les années 1970. La répartition de la capturabilité ne correspond pas toujours aux préférences de profondeur déterminées par les études qui traquent les poissons; il ne faut donc pas utiliser les préférences de profondeurs obtenues de ces études pour corriger les indices d'abondance s'il n'existe pas de renseignements supplémentaires sur le comportement alimentaire.

[Traduit par la Rédaction]

Introduction

Recent analyses indicate that the state of the world's pelagic fish stocks is much worse than previously believed. Most species of pelagic shark in the northwest Atlantic are now declining by about 10%·year⁻¹ (Baum et al. 2003). Ward and Myers (2005) found that the biomass of large sharks, tunas, and billfishes has fallen to one tenth of the level when pelagic longline fishing commenced in the tropical Pacific Ocean. Globally, the abundance of many large marine predators is now less than 10% of the pre-exploitation level (Myers and Worm 2003).

The new perspective on the status of pelagic fishes is directly linked to the recovery of historical data from longline surveys and commercial operations. However, critics have challenged conclusions based on those data, pointing to un-

certainities in using longline catch rates as indices of abundance. Longline fishing effort must be corrected or "standardized" for variations in fishing practices and oceanographic conditions if abundance indices for early years are to be comparable with indices from recent years. The timing of longlining operations in relation to peak feeding periods is an example of a historical change in fishing practices. Ward et al. (2004) found that changes in the timing of longlining operations, which now have hooks available during dusk as well as dawn, have resulted in the overestimation of abundance for many species in recent years.

Another important historical change in longlining operations is the depth range of the gear (Fig. 1), which is the topic of this article. Two methods have been used to account for changes in the depth distribution of longline hooks. One

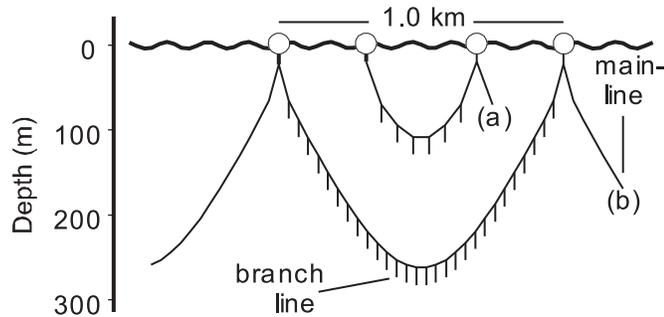
Received 26 June 2004. Accepted 31 December 2004. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 31 May 2005.
J18197

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Fig. 1. Configuration of (a) a regular longline with six hooks between floats, like the longlines deployed by the US Pacific Oceanic Fisheries Investigations survey and (b) a deep longline with 28 hooks between floats, like those deployed by Hawaii-based longliners to catch bigeye tuna. Many longliners began using deep longlines in the tropical Pacific Ocean after 1974 and in the tropical Atlantic Ocean after 1979.



method is to use generalized linear models to relate catches to longline depth and other explanatory variables. In most longline fisheries, however, a switch to deep gear was so rapid in the mid-1970s that there is inadequate temporal overlap to allow comparison of the performance of regular and deep gear (Suzuki et al. 1977). Takeuchi (2001) concluded that it was not possible to make reliable inferences about changes in abundance from historical longline catch and effort data.

The second method of correcting abundance indices for longline depth is to model the species' preferred habitat. Oceanographic information (e.g., thermocline depth) is combined with information from tracking studies (e.g., Musyl et al. 2003) to estimate the species' depth distribution in time and area strata (e.g., Hinton and Nakano 1996; Bigelow et al. 2002). The habitat-based model is then combined with the inferred depth distribution of longline hooks to adjust the fishing effort for the species' availability in each time-area stratum.

The previous methods required the estimation of an additional parameter for each longlining operation included in the analysis. Consequently, estimates become increasingly biased as the sample size increases (Kiefer and Wolfowitz 1956). The generalized linear models used the proportions of catch at depth. However, the local abundance and gear configuration vary among longlining operations, causing further biases in the interpretation of the depth distribution derived from catch proportions. This article describes a new method that uses data from individual longline hooks to estimate relative catchability at depth. The lack of an adequate statistical framework has previously precluded the use of individual hook data to derive statistically valid estimates of the depth distribution of catchability.

We use generalized linear mixed effect models (Wolfinger and O'Connell 1993), which have considerable advantages for estimating catchability at depth: (i) they allow for nonlinear relationships between independent variables and the dependent variable (mean catch), (ii) a variety of error distributions (e.g., Poisson) can be modeled, and (iii) they allow local abundance to be a random variable, providing statisti-

cally consistent estimates with improved accuracy (Robinson 1991).

Variations in fishing gear and oceanographic conditions affect catchability, the part of a stock that is caught by a defined unit of fishing effort. The catchability coefficient q relates catch C to the species' local abundance N and the amount of fishing effort E :

$$(1) \quad C = qEN$$

A reliable estimate of catchability is therefore necessary to estimate abundance from catch and effort data (Murphy 1960). Catches are the product of catchability, local abundance, and fishing effort. For longline gear, fishing effort is often measured as the number of longline hooks available at each depth. Our approach is to first estimate the depth distribution of catchability independent of availability. We then take availability into account by adjusting the number of hooks at each depth by the estimated catchability.

Materials and methods

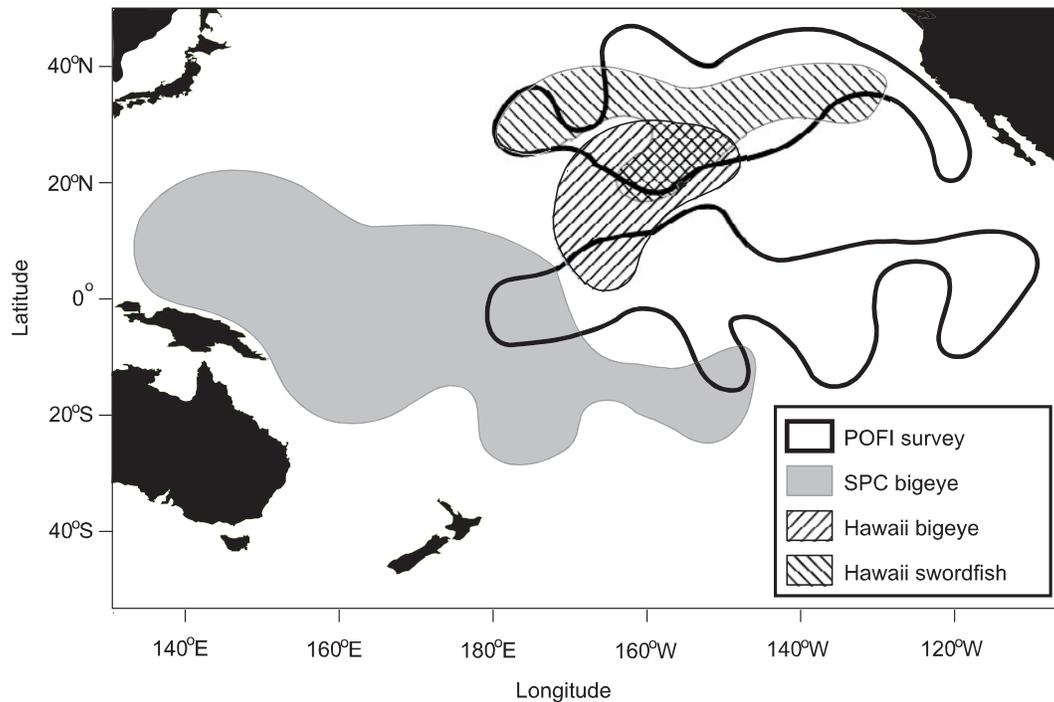
Data

We analyzed data collected by scientists involved in a research survey and by observers on commercial vessels using pelagic longlines. The data included gear dimensions for each longlining operation, which we used to estimate the maximum settled depth of each hook deployed. The scientists and observers also reported a unique identifier, a sequential number, for each longline hook. Combined with the gear dimensions, the individual hook data were used to estimate the depth at which each animal was caught.

We combined three data sets. The US Pacific Oceanic Fisheries Investigations conducted 1157 longlining operations in an area of the Pacific Ocean bounded by 175°E–115°W and 12°S–44°N during 1950–1958 (Fig. 2). Survey longliners used fishing gear and techniques adopted from Japan (Murphy and Shomura 1972). They typically deployed longlines at dawn each day and retrieved in the afternoon. They usually attached six hooks between each pair of floats, amounting to about 240 hooks in each daily longlining operation. The maximum settled depth of the hooks ranged from 18 to 103 m (unless otherwise indicated, all hook depths were estimated from the catenary formula reduced by 25% for the effects of currents). The survey longliners occasionally deployed longlines at night and deep longlines with up to 21 hooks between floats (18–144 m). They mostly used sardines (*Sardinella* spp.) as bait but also experimented with saury (*Scorpaenopsis* spp.), squids (*Illex* spp.), and various other baits.

The second data set was from US National Marine Fisheries Service observers placed on commercial longliners in the Pacific Ocean during 1994–2002. The data consisted of 8037 daily longlining operations in an area bounded by 5°N–40°N and 174°E–134°W. The longliners targeted broadbill swordfish (*Xiphias gladius*) or tunas, specifically bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*Thunnus albacares*), for domestic fresh-fish markets. To catch tunas in tropical waters, they deployed deep longlines with sardines as bait during the day with about 28 hooks between floats (40–230 m). To catch swordfish in temperate waters,

Fig. 2. Geographical ranges of data sets used to derive the depth distribution of catchability for each species. The data were collected by longline surveys under the US Pacific Oceanic Fisheries Investigations and compiled by the Secretariat of the Pacific Community from observers on commercial longliners operating in the western Pacific and by observers placed on Hawaii-based longliners by the US National Marine Fisheries Service. The Hawaii longliners targeted swordfish in the North Pacific or bigeye tuna in the tropical Pacific Ocean.



they deployed shallower longlines (39–121 m) with shortfin squid (*Illex illecebrosus*) as bait at night.

The Secretariat of the Pacific Community assembled the third data set from data collected by observers placed on commercial longliners during 1992–2002. The data consisted of 1813 longlining operations in an area of the Pacific Ocean bounded by 27°S–12°N and 138°E–172°W. Most of the longliners targeted bigeye tuna during the day with deep longlines consisting of about 30 hooks between floats (33–267 m). They used saury, sardines, or squids as bait.

The longliners used similar fishing gear, e.g., comparable hook sizes and wire leaders to connect hooks to branch lines. The longliners monitored by US National Marine Fisheries Service and Secretariat of the Pacific Community observers deployed monofilament-nylon branch lines, whereas the survey longliners used rope gear. The next section describes the random effects model that are used to account for variations in local abundance and catches among longlining operations. It was included to reduce the effects on catchability of variations in bait and fishing gear among longline operations.

Observers and survey scientists identified the species and recorded the hook number for each animal caught. Occasionally, they did not identify animals to the species level, so that species were combined into species groups. For brevity, we use the term species group to refer to individual species as well as species groups. The US National Marine Fisheries Service observers did not record the hook number for species groups other than tunas, billfishes, and sharks.

We assumed that the mainline formed a catenary curve between each pair of floats and estimated the depth of each

hook by applying the formula presented by Suzuki et al. (1977) to longline dimensions reported for each operation. We assumed that the shape of the catenary curve (and therefore the corresponding depth of hooks) did not systematically vary along each longline or during each longline operation. Observed depths and predicted depths are known to vary, with ocean currents and wind having the most important influence on hook depth. Bigelow et al. (2002) estimated that hook numbers 3 and 10 of longline gear with 13 hooks between floats shoaled by about 20% when subjected to a current velocity of 0.4 m·s⁻¹. To represent shoaling of longlines in our study area, we reduced all depths predicted by the catenary formula by 25%. The data were then binned into 40-m depth categories ranging from 0–40 to 480–520 m.

We estimated catchability distributions separately for day and night operations. Most day operations commenced at dawn (the median deployment time was 0705 (local) with 50% beginning between 0520 and 0747). Night operations often started at dusk (median time of 1817 with 50% between 1711 and 1930). We analyzed a total of 3155 night operations (13 679 animals) and 7852 day operations (32 046 animals) (Table 1).

Models

We used generalized linear mixed effect models (Wolfinger and O'Connell 1993) to estimate parameters that describe the shape of the depth distribution of catchability of each species group. The catch of each species group in longlining operation i at depth D was assumed to follow an overdispersed Poisson distribution with a mean of $\mu_{i,D}$. The assumption of a Poisson distribution is reasonable because

Table 1. Common and scientific names of each species or species group analyzed and the number of animals modeled for day and for night longlining operations.

Common name	Scientific name	No. modeled	
		Day	Night
Tunas and tuna-like species			
Albacore tuna	<i>Thunnus alalunga</i>	2777	1267
Bigeye tuna	<i>Thunnus obesus</i>	2980	1819
Skipjack tuna	<i>Katsuwonus pelamis</i>	2771	241
Wahoo	<i>Acanthocybium solandri</i>	528	122
Yellowfin tuna	<i>Thunnus albacares</i>	3131	1417
Billfishes			
Black marlin	<i>Makaira indica</i>	225	98
Blue marlin	<i>Makaira nigricans</i>	1902	593
Broadbill swordfish	<i>Xiphias gladius</i>	1277	2332
Sailfish	<i>Istiophorus platypterus</i>	402	148
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	2477	269
Striped marlin	<i>Tetrapturus audax</i>	2726	743
Other teleosts			
Barracudas ^a	<i>Sphyræna</i> spp.	240	0 ^b
Escolar	<i>Lepidocybium flavobrunneum</i>	266	107
Great barracuda	<i>Sphyræna barracuda</i>	102	0 ^b
Lancetfishes ^a	<i>Alepisaurus</i> spp.	358	0 ^b
Longnosed lancetfish	<i>Alepisaurus borealis</i>	46	0 ^b
Mahi mahi	<i>Coryphaena hippurus</i>	349	157
Oilfish	<i>Ruvettus pretiosus</i>	254	96
Opah	<i>Lampris guttatus</i>	197	0 ^b
Pomfrets ^a	Family Bramidae	179	35
Shortnosed lancetfish	<i>Alepisaurus brevirostris</i>	53	7
Sickle pomfret	<i>Taractichthys steindachneri</i>	20	0 ^b
Snake mackerel	<i>Gempylus serpens</i>	102	113
Sharks and rays			
Bigeye thresher shark	<i>Alopias superciliosus</i>	956	139
Blue shark	<i>Prionace glauca</i>	3050	2444
Common thresher shark	<i>Alopias vulpinus</i>	30	0 ^b
Crocodile shark	<i>Pseudocarcharias kamoharui</i>	384	84
Dusky shark	<i>Carcharhinus obscurus</i>	54	0 ^b
Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	25	0 ^b
Long-finned mako shark	<i>Isurus paucus</i>	153	0 ^b
Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	1910	494
Pelagic stingray	<i>Dasyatis violacea</i>	356	204
Short-finned mako shark	<i>Isurus oxyrinchus</i>	665	388
Silky shark	<i>Carcharhinus falciformis</i>	1019	362
Silver-tip shark	<i>Carcharhinus albimarginatus</i>	29	0 ^b
Tiger shark	<i>Galeocerdo cuvier</i>	34	0 ^b
Whip stingray	<i>Dasyatis akajei</i>	19	0 ^b

^aOccasionally, observers did not identify animals to the species level. Consequently, we modeled data for species groups (e.g., barracudas (*Sphyræna* spp.)) separately to data for identified species (e.g., great barracuda (*Sphyræna barracuda*)).

^bInsufficient numbers caught to allow reliable parameter estimation.

only a small proportion of the hooks are occupied by a species group, e.g., the mean percentage of hooks occupied by one of the most abundant species, yellowfin tuna, was 1.7% ± 4.1% SD.

For each species group, the model predicts the mean catch $\mu_{i,D}$ using a log link:

$$(2) \quad \log(\mu_{i,D}) = \lambda_i + \gamma_1 D + \gamma_2 D^2 + \gamma_3 D^3 + \log(H_{i,D})$$

where λ_i and γ_j are parameters estimated for each species group and the offset $H_{i,D}$ is the number of hooks H deployed

at depth D of longlining operation i . Our method includes a random effects model that accounts for variations in the local abundance of each species. We assumed that the log abundance of the species group, when it is encountered, followed the random effects distribution, which we assumed to be a normal distribution,

$$\lambda_i \sim N(\mu, \sigma^2)$$

The regression coefficients γ_j in eq. 2 describe how catchability changes with depth (μ represents catch, H is

fishing effort, and the γ_j parameters represent catchability in eq. 1). For each species group, we sequentially tested increasingly complex functional forms of eq. 2 to find the most appropriate model. We initially fitted eq. 2 with $\gamma_1 = \gamma_2 = \gamma_3 = 0$ and then tested the model in which we estimated γ_1 while constraining the quadratic and cubic parameters to zero. We sequentially added other γ_j parameters until the increase in the fit of the model was not significant as judged by a likelihood ratio test. The cubic model adequately described most of the variation in depth; including additional terms had very little effect on parameter estimates.

We then used parameter estimates, denoted by the “hat” symbol, from eq. 2 to estimate the catchability of each species group as a function of hook depth D (metres):

$$f(D) = \exp(\alpha + \hat{\gamma}_1 D + \hat{\gamma}_2 D^2 + \hat{\gamma}_3 D^3)$$

where α is chosen such that the mean of $f(D)$ equals one over the depth range considered. We refer to these standardized $f(D)$ as the depth distribution of catchability or simply the catchability distribution.

Correcting abundance indices for depth effects

To correct abundance indices for variations in longline depth, we can apply our estimates to data where gear dimensions are known for each operation. They can also be used to correct indices for changes in catchability when only the proportion of gear configurations is known. In almost all cases, the longline configuration is identical between floats and symmetrical. Therefore, the number of depths k that needs to be considered for each gear configuration is half the number of hooks between floats. We then estimated q_g , which is the average catchability of the species group for gear configuration g :

$$q_g = \sum_k f(D_k) p_g(D_k)$$

where $p_g(D_k)$ is the proportion of hooks at depth D_k . For each year, the catchability averaged over all gear configurations is

$$\bar{q}_y = \sum_g P_{y,g} q_g$$

where $P_{y,g}$ is the proportion of longlining operations using gear configuration g in year y . For each species group, we standardized the average catchability \bar{q}_y by dividing it by its value in the first year of the time series.

We illustrate the effect of the depth correction by applying it to a time series of annual catch rates for Japan's longline fleet operating in the southern Atlantic Ocean. Estimation of the average annual catchability used the depth distribution of catchability combined with changes in gear configurations reported by Suzuki et al. (1977) and Uozumi and Nakano (1996). For each year, we divided the species' catch rate by our estimate of its average catchability for all gear configurations \bar{q}_y . We then standardized the estimate by dividing it by the average catchability in 1975 (the first year of the time series).

Results and discussion

Precision of depth estimates

The application of our estimates of the depth distribution of catchability should not be affected by uncertainty over the depths of longline hooks estimated by the catenary formula. It is true that observed depths (obtained using depth sensors) and predicted depths often differ. The weight of the longline causes a gradual shortening in the distance between floats during the operation. Consequently, longline hooks may sink to deeper depths than those predicted by the catenary formula. At the same time, wind and current shear may cause hooks to rise towards the surface or “shoal” (Hanamoto 1987; Mizuno et al. 1999). However, we contacted several observers and longline fishers who pointed out that commercial fishers adjust their fishing practices to maximize the availability of longline hooks to target species, such as deep-dwelling bigeye tuna. Since the 1980s, many longliners have used Doppler current profilers to monitor the velocity and direction of subsurface currents. Most fishers minimize shoaling by deploying their longline in the same direction as prevailing currents. Furthermore, the predicted depth distributions of the hooks are surrogates for their true, but unknown, depth distributions. Our approach does not require accurate depth estimates because exactly the same methods and corrections that we used to estimate depth for our models can be applied to the longline data that are being corrected. By contrast, the depth estimates from tracking studies that are used in habitat-based models are not calibrated against longline depth.

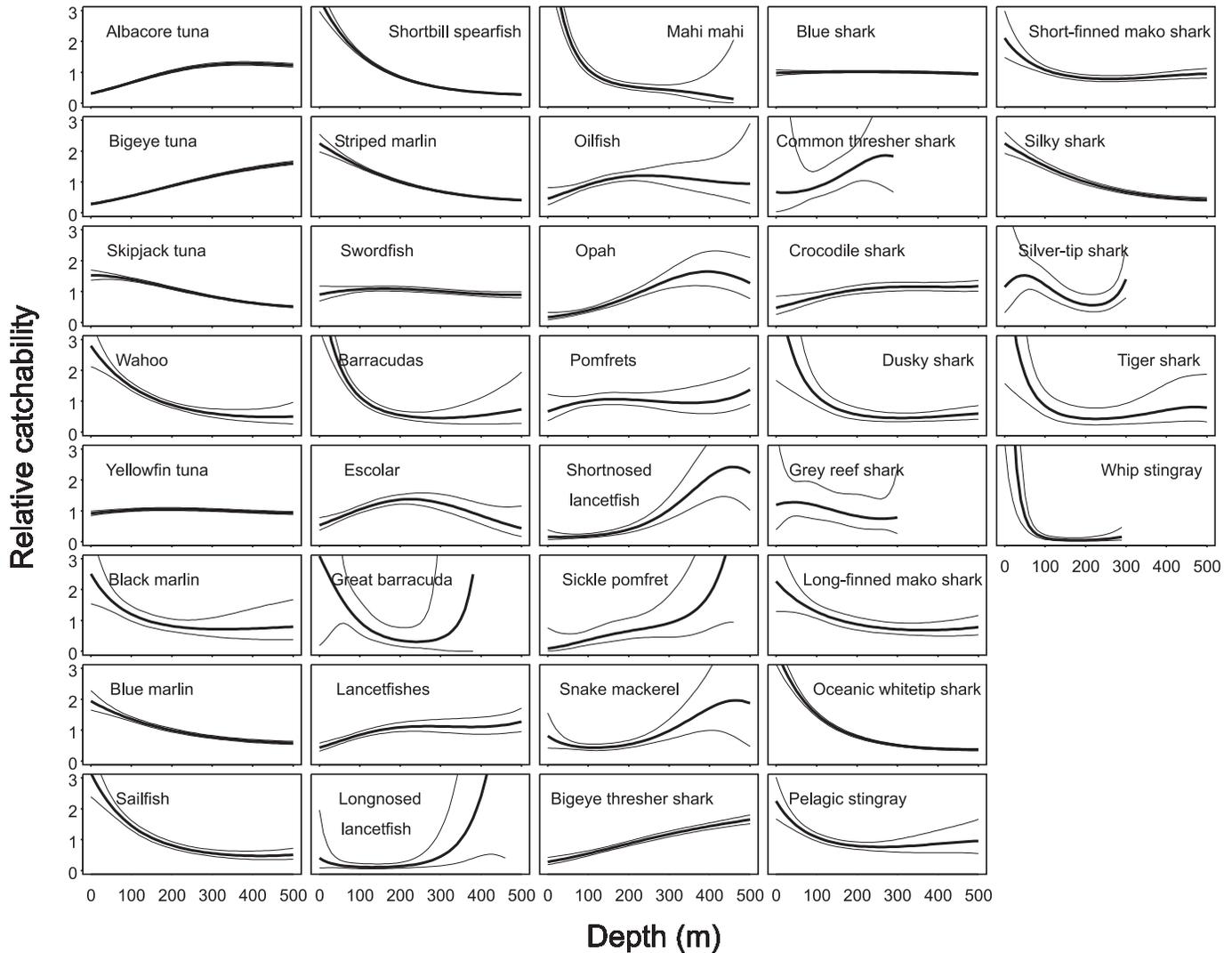
Various factors may influence the depth distribution of catchability derived from observer data, e.g., spatial and seasonal variations in wind, currents and thermal structure and differences in fishing practices and gear among fleets. Our presentation of one night and one day distribution for each species should not preclude further investigation of the importance of those influences on depth distributions.

Ecological groups

We derived reliable estimates of the depth distribution of catchability for 37 species groups over a depth range of 18–512 m for day operations (Fig. 3) and for 24 species groups over 28–504 m for night operations (Fig. 4) (Appendix A provides parameter estimates for each species). The species groups show considerable variability in the distribution of catchability. The distributions indicate at least three distinct ecological groups, which should be considered separately in ecosystem models: epipelagic species that feed in surface waters (<200 m) during the day, wide-ranging pelagic species whose catchability does not vary over the observed depth range, and mesopelagic species that feed at intermediate and deep depths (>200 m) by day and then range more widely at night. Few species groups show high catchability at intermediate depths (200–400 m).

Swordfish, blue shark (*Prionace glauca*), and yellowfin tuna are members of the wide-ranging pelagic group. Their daytime catchability shows only minor variations over the observed depth range (Fig. 3). Tracking studies indicate that they range throughout the epi- and meso-pelagic zones (e.g., Carey and Robison 1981; Carey and Scharold 1990; Holland et al. 1990a).

Fig. 3. Estimates of the depth distribution of catchability $f(D)$ (thick line) with the 95% prediction intervals (thin lines) for day long-lining operations. The mean catchability has been set to 1 to facilitate comparison between species and species groups.



The epipelagic group includes oceanic whitetip shark (*Carcharhinus longimanus*), dusky shark (*Carcharhinus obscurus*), skipjack tuna (*Katsuwonus pelamis*), mahi mahi (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), and all billfishes except swordfish. They were most often caught in surface waters above the thermocline (about 140 m in the tropical Pacific Ocean) during the day (Fig. 3). However, some were also caught on deep hooks. This is probably because animals may be caught when “deep” hooks pass through surface waters during longline deployment and retrieval (Boggs 1992).

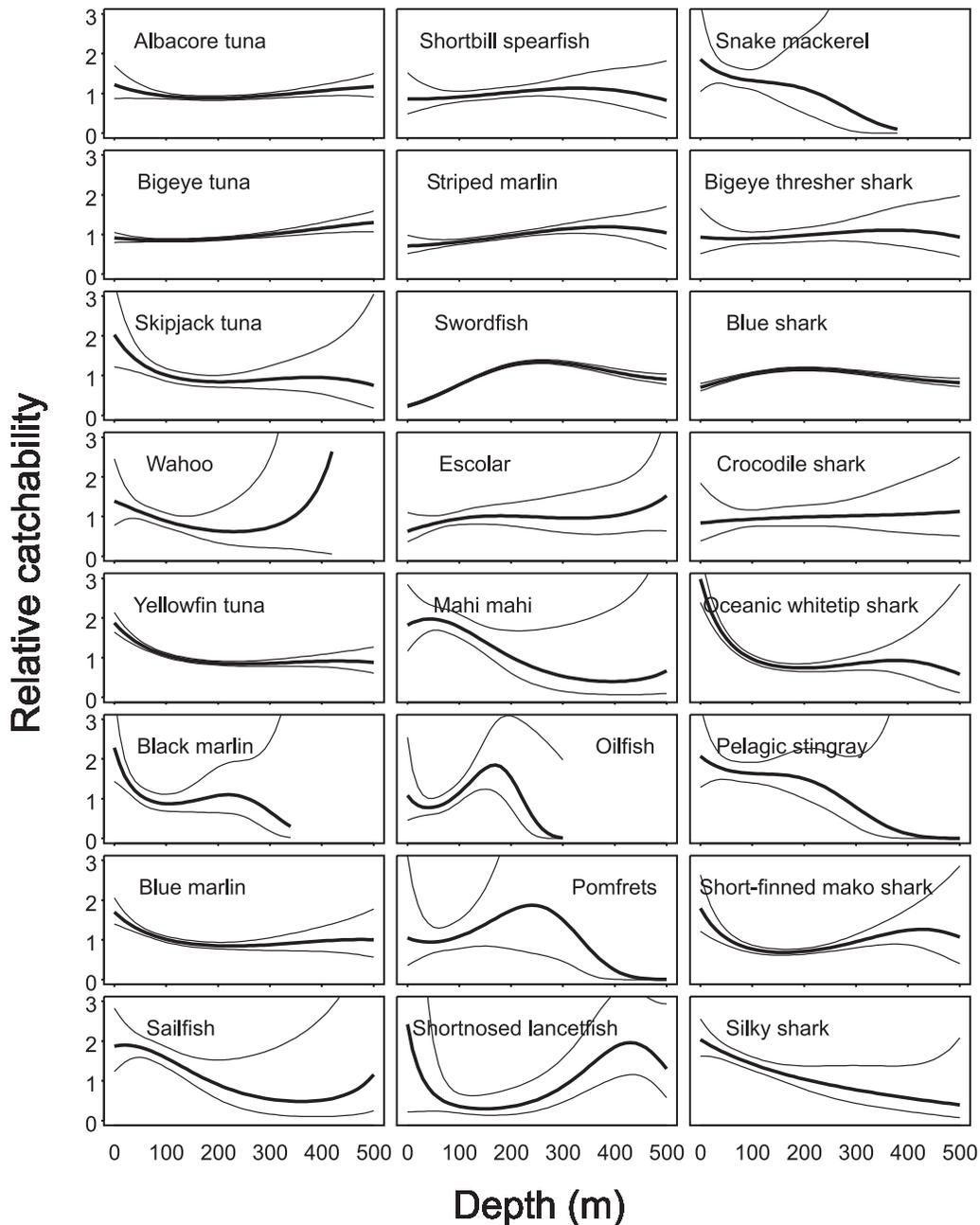
Diel variation

Comparisons of catchability for day and night operations (Figs. 3 and 4) reveal patterns of diel variation among the mesopelagic species that probably represent vertical migration. The catchability of bigeye tuna, for example, increases with depth during the day, whereas it shows a much more uniform distribution at night. Our interpretation is that visibility is critical to the vertical distribution of large predators like bigeye tuna in the open ocean. They have several physi-

ological adaptations, such as large eyes, that provide acute vision and allow them to hunt at low light levels (Pereira 1996). They feed below the sunlit zone during the day where they can avoid detection by their prey. At night, they range more widely because the ocean is almost uniformly dark. The distributions of other large predators indicate patterns of vertical migration that are similar to that of bigeye tuna, e.g., albacore tuna (*Thunnus alalunga*), escolar (*Lepidocybium flavobrunneum*), and bigeye thresher shark (*Alopias superciliosus*).

Visibility is also critical for predator avoidance by small species, such as snake mackerel (*Gempylus serpens*), which are the prey of large tunas, billfishes, and sharks (Kitchell et al. 1999; Rosas-Alayola et al. 2002). These small species concentrate at deep depths, below the sunlit zone during the day, where they can avoid their predators. At night, they venture into surface waters. Several epipelagic species show the opposite pattern, concentrating in surface waters during the day and then ranging more widely at night, e.g., shortbill spearfish (*Tetrapturus angustirostris*) and striped marlin (*Tetrapturus audax*).

Fig. 4. Estimates of the depth distribution of catchability $f(D)$ (thick line) with the 95% prediction intervals (thin lines) for night longlining operations. The mean catchability has been set to 1.



The depth distribution of catchability does not change markedly between day and night for several species, e.g., skipjack tuna, mahi mahi, and sailfish (*Istiophorus platypterus*). These epipelagic species are most abundant in surface waters. Hook-timer experiments (e.g., Boggs 1992) confirm that they are often caught in surface waters, particularly during longline deployment and retrieval. Night longlining operations caught fewer species groups than day operations, and the night depth distributions for several epipelagic species are poorly estimated compared with the estimates of their daytime distributions. This is partly due to differences in sample sizes (we analyzed 3155 night operations compared with 7852 day operations). The poor estimates of night distributions might also be related to diel

variations in feeding activity. Stomach content analyses indicate reduced feeding activity among many epipelagic species at night. Analyses of the stomach contents of sailfish by Rosas-Alayola et al. (2002), for example, show that this species feeds mainly in surface waters during the day.

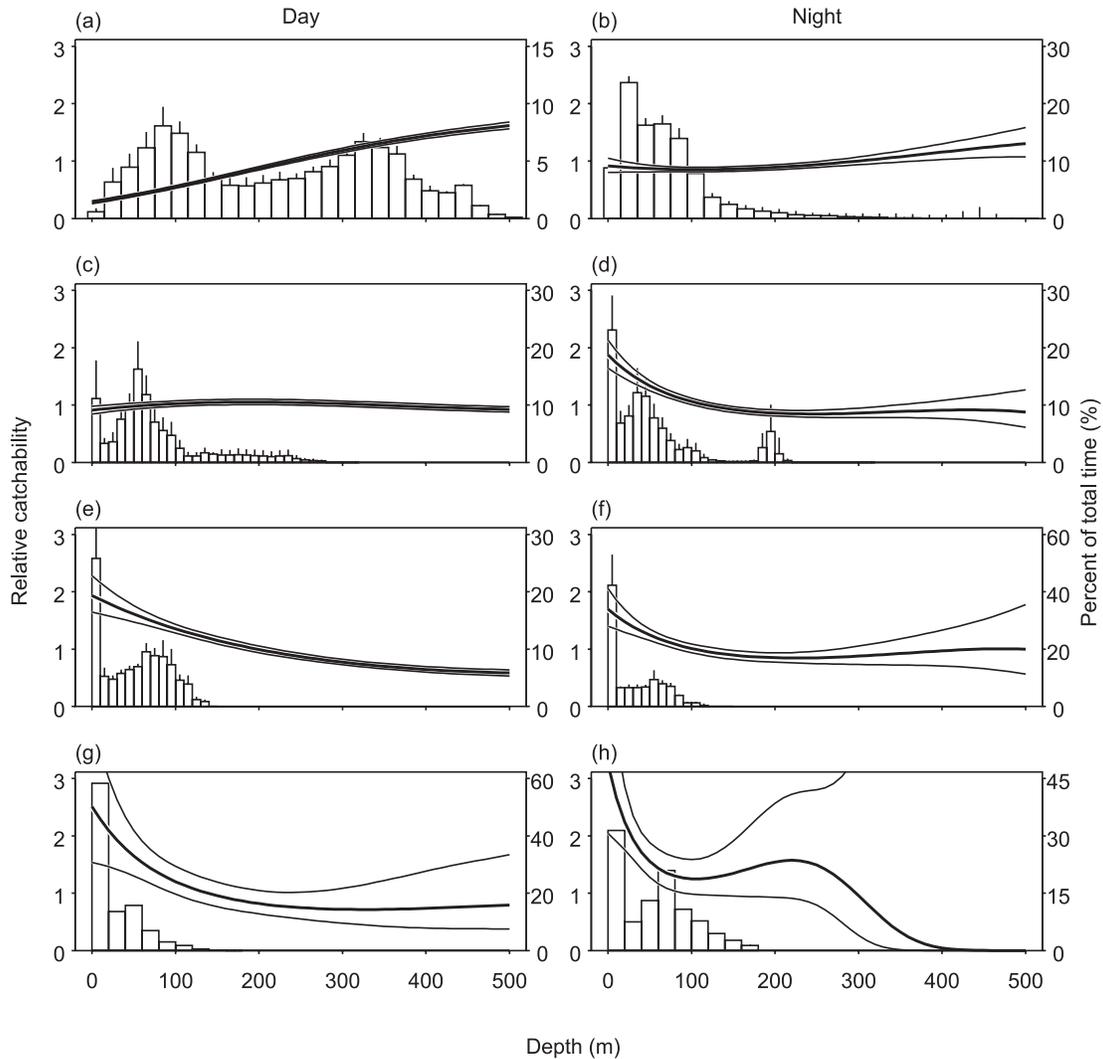
Comparison with tracking studies

For several species groups, the depth preferences derived from acoustic telemetry in the open ocean can be compared with the catchability distributions that we derived from longline data. The tracking studies are mostly limited to large, commercially important species of tunas and billfishes and several shark species (Table 2). Each study involved small numbers fitted with acoustic transmitters and tracked for

Table 2. Details of tracking data used to estimate the proportion of time spent at each depth.

Species	Device	No. of animals	Time at liberty	Location	Reference
Bigeye tuna	Archival tags	4	9–76 days	Southwestern Hawaii	Musyl et al. 2003
Yellowfin tuna	Ultrasonic transmitters	11	5 h – 6 days	Hawaii	Holland et al. 1990a
Blue marlin	Ultrasonic transmitters	5	24–42 h	Hawaii	Holland et al. 1990b
Black marlin	Ultrasonic transmitters	4	18–24 h	Northeastern Australia	Pepperell and Davis 1999

Fig. 5. Estimates of the depth distribution of catchability $f(D)$ of longline-caught fishes (thick line) compared with the percentage of time at each depth for tracked animals (histograms) for day and night periods: (a, b) bigeye tuna, (c, d) yellowfin tuna, (e, f) blue marlin, and (g, h) black marlin. Where available, standard errors (vertical lines) are shown for the mean percentage of time at depth. Thin lines are 95% prediction intervals for catchability.



several days. Recent studies using archival tags (e.g., Musyl et al. 2003) have allowed the depth preferences of animals to be estimated over longer periods, thereby providing a more complete understanding of their behavior.

Our estimates of catchability distributions from longlining operations provide a good match to the tracking data in several cases (Fig. 5). For example, tagged black marlin (*Makaira indica*) spent most of the day in surface waters, which matches the catchability distribution (Fig. 5g). For bigeye tuna, however, the tracking data show patterns different from the catchability distribution (Figs. 5a and 5b). The

inconsistencies between catchability distributions and depth preferences may be due to the small numbers of animals tracked or differences in behavior and oceanographic conditions between our broad study area and the areas where the animals were tracked. Eight of the yellowfin tuna tracked by Holland et al. (1990a) (Fig. 5c), for example, were associated with fish-aggregating devices. Those animals were found to behave quite differently from yellowfin tuna in the open ocean.

The inconsistencies between the depth distribution of catchability and depth preferences derived from tracking studies might also reflect a mismatch between the estimated

depth of longline hooks and tracking depths or differential vulnerability to longline fishing gear. It is quite possible for a species to be abundant at depths where they have a reduced vulnerability to the gear. For example, bigeye tuna might be present in surface waters during the day but not caught on longline hooks there because they are not feeding or cannot detect the baits. This is not of concern because we intend the estimates of catchability to be used to correct abundance indices derived from longline data. However, the mismatch between catches on longline hooks and the species' depth preference is a flaw in habitat-based models that are solely based on tracking data. Tracking data show an animal's depth preference, which may not always match the species' vulnerability to longline fishing gear. From an analysis of simulated data for blue marlin (*Makaira nigricans*), Goodyear (2003) concluded that the propensity of the species to take longline baits and the actual depth profile of the fishing gear strongly influenced habitat-based model estimates of abundance. The development of statistical habitat-based models, which fit observed catches (Hinton and Maunder 2003), may help to correct for differences between depth preferences and vulnerability.

An alternative to our approach is to use hook-timers that record the time and depth when each animal was caught (e.g., Boggs 1992). However, a very large number of hook-timer experiments are required to derive reliable estimates of depth preference. For example, Matsumoto et al. (2001) analyzed over 300 longlining operations, each deploying 10–163 hook-timers. However, that number of experiments was not large enough to obtain reliable estimates of depth preference.

Environmental constraints on depth distribution

The tracking studies show that environmental conditions set broad limits to the vertical distribution of each species. Those limits will also apply to the depth distribution of catchability. For example, Brill et al. (1993) concluded that sharp gradients in water temperature between the mixed layer and deeper waters represented a barrier to vertical migrations of striped marlin near Hawaii. Other conditions, such as oxygen concentration, are also known to limit the vertical distribution of pelagic fishes (Hanamoto 1987). The efficacy of those thresholds will vary seasonally, spatially, among species, and with body size (Dagorn et al. 2000). Caution is required in applying our estimates of catchability distributions to regions outside the study area. For example, the shallow thermocline in the tropical eastern Pacific Ocean results in very low catch rates of striped marlin on longline hooks below about 100 m (Matsumoto and Miyabe 2002). By contrast, our estimates indicate an average level of catchability for striped marlin below 100 m (Figs. 3 and 4).

Further work is required to determine whether our estimates can be applied to other regions. Several organizations hold hook-level data that we could not access, e.g., data collected by British observers on longliners in the Indian Ocean and surveys by Japan's National Research Institute of Far Seas Fisheries. Such data sets should be used to test the hypothesis that the shape of a species' catchability distribution does not vary among regions or seasons but is compressed or extended by local conditions that limit the species' depth

range. Data were not available to model the effects of body size on the depth distribution of each species, but we expect further work to show that larger animals generally have a wider depth range.

Correcting longline catch rates

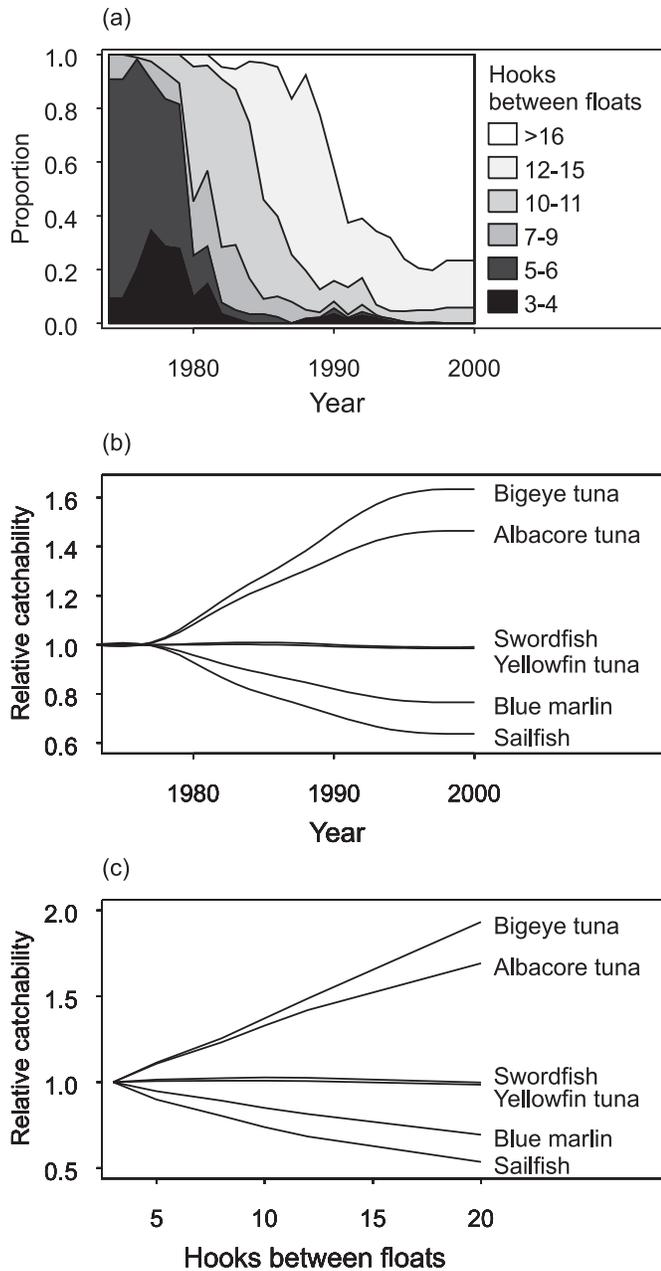
There are two ways that our estimates of the depth distribution of catchability can be used to improve estimates of abundance. First, correction factors can be applied to operation-level data where gear dimensions and the number of hooks between floats are known for each operation. Such data exist for a large number of longline surveys conducted before commercial fishing commenced (e.g., Wathne 1959) and for more recent research cruises and monitoring programs. Ward and Myers (2005) illustrated how the correction factors can adjust abundance indices derived from longline surveys in the 1950s and commercial operations in the 1990s.

The second application of our estimates is to correct abundance indices for changes in depth when only the proportion of gear configurations is known. Japan's longliners rapidly switched from regular longlining (<120 m) to deep longlining (deepest hooks ranging beyond 120 m) in the Atlantic Ocean in the late 1970s (Fig. 6a). The introduction of deep longlining had virtually no effect on the catchability of yellowfin tuna and swordfish (Figs. 6b and 6c). Catchability declined for marlins and sailfish but increased by 60% for bigeye tuna and by 40% for albacore tuna. While these changes warrant their inclusion in assessment models, they are less than those estimated by the early nonstatistical habitat-based models (e.g., Hinton and Nakano 1996).

The application of our depth correction to annual catch rates of longliners in the southern Atlantic Ocean illustrates how variations in gear configurations can affect estimates of abundance. We have previously advised caution in applying our estimates of catchability to regions outside the study area; this application to the southern Atlantic Ocean is only intended to illustrate how the estimates can be used. The use of longline catch rates as indices of abundance is also subject to debate (R.A. Myers and A.M. Edwards, unpublished data). The introduction of deep longlines resulted in the overestimation of bigeye tuna abundance but had a relatively small effect on abundance indices for other species (Fig. 7). In absolute terms, the effect is small on estimates of blue marlin, sailfish, and albacore tuna because of the significant decline in the abundance of those species well before the switch to deep longlining (Myers and Worm 2003). Furthermore, deep hooks take about 30 min to move through shallow and intermediate depths during longline deployment and retrieval. Consequently, catches are smeared over a range of depths (Boggs 1992).

The effects of the increased depth range on catchability indicate that the 90% decline in the abundance of tunas and billfishes reported by Myers and Worm (2003) would be an underestimate. This is because the animal community has been modified so that most of the biomass is now concentrated in swordfish, bigeye tuna, and yellowfin tuna, which declined less dramatically than other species. The catchability of target species has not changed or it has increased. Although the catchability of marlins and sailfish has declined,

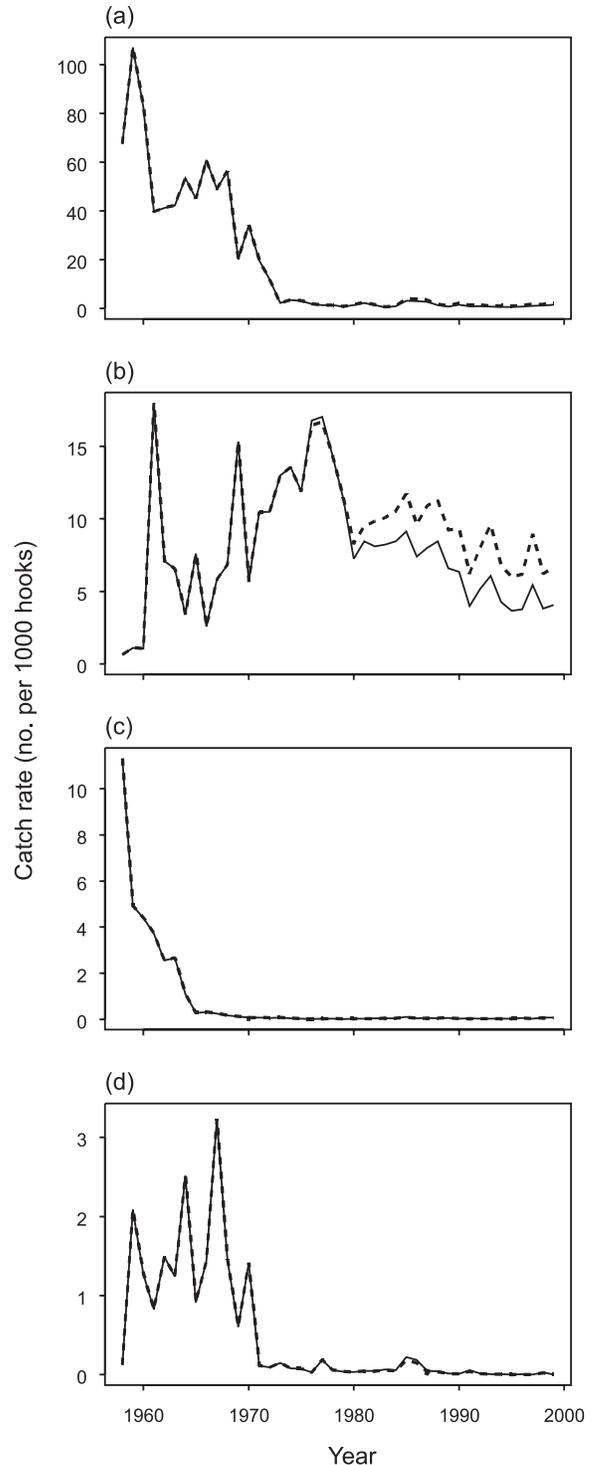
Fig. 6. Historical variations in gear configurations and catchability. (a) Number of hooks between floats deployed by Japan's longline fleet in the tropical Atlantic Ocean (modified from Yokawa and Uozumi (2001)). Hooks between floats is a rough indicator of longline depth range (for these operations, six hooks between floats produces a depth range of about 50–150 m compared with 50–300 m for a configuration with 14 hooks between floats). (b) Estimated change in average catchability over all gear configurations q_y used by the tropical Atlantic fleet relative to the 1975 gear configuration. (c) Change in the depth distribution of catchability q_g relative to the gear configuration with three hooks between floats for six species taken by the tropical Atlantic fleet.



they now constitute only a small part of the pelagic fish community available to longline fishing gear.

In summary, we have demonstrated a method where abundance indices derived from longline catch rates can be cor-

Fig. 7. Abundance indices of four species in the southern Atlantic Ocean (modified from Myers and Worm (2003)) with (solid line) and without (broken line) the depth correction from Fig. 6c. Species are as follows: (a) albacore tuna, (b) bigeye tuna, (c) blue marlin, and (d) sailfish.



rected for historical variations in the depth range of the fishing gear. The method is relatively simple to apply and uses existing data that previously lacked the appropriate statistical framework for analysis. It can be applied to bycatch spe-

cies that have not been the subject of tracking studies and it accommodates early data where only approximate gear characteristics are known and detailed oceanographic data are not available. Our method also eliminates the confounding in other statistical methods caused by the rapid switch to deep longline gear in the 1970s. Thus, we reject the claim by Takeuchi (2001) that abundance indices cannot be corrected for historical changes in the depth of longline hooks.

Longliners have maintained catch rates of target species by improving the efficiency of their fishing gear (Stone and Dixon 2001), increasing soak time, ensuring that hooks are available at peak feeding periods (Ward et al. 2004), and by extending the geographical limits of fishing grounds (Myers and Worm 2003). In the 1970s, they also began to exploit a much greater depth range. Our analyses show that deep longlining has resulted in the underestimation of the abundance of several epipelagic species (e.g., sailfish). However, it has resulted in the overestimation of the abundance of several pelagic species, including target species like bigeye tuna. Those large predators not only support valuable fishing industries, they have unique ecological roles, influencing the diversity and abundance of lower trophic levels.

Acknowledgments

The work is part of a larger project on pelagic longlining that was initiated and sponsored by the Pew Charitable Trusts. We also thank the Pelagic Fisheries Research Program, the Natural Sciences and Engineering Research Council of Canada, and the Future of Marine Animal Populations project of the Sloan Foundation Census of Marine Life for financial support. Tim Davis, Brent Miyamoto, Mike Musyl, Tom Swenarton, and Peter Williams provided data and information on the fisheries. Wade Blanchard and Darren Swan provided technical advice. Two reviewers provided comments on the manuscript.

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Appendix A. Estimates of depth distribution parameters derived from pelagic longline data.

We used generalized linear mixed effect models with a Poisson distribution to model the mean catch μ of each species or species group in longline operation i at depth D . The model predicted the mean catch using a log link:

$$\log(\mu_{i,D}) = \lambda_i + \gamma_1 D + \gamma_2 D^2 + \gamma_3 D^3 + \log(H_{i,D})$$

where the “offset” $H_{i,D}$ is the number of hooks deployed at depth D in longline operation i , and λ_i is the random effects distribution for the species in operation i (we assumed that the log abundance of the species encountered by each operation follows a normal distribution). The regression coefficients γ_j describe how the species’ catchability varies with depth. For each species, we used the GLIMMIX macro in SAS (version 8.0) to fit the models separately to day (Table A1) and night longlining operations (Table A2). We also investigated the alternative assumption of extrabinomial variation, which gave results very similar to those of the Poisson distribution. We report only the Poisson results because they are simpler to interpret.

Table A1. Parameter estimates and the number of each species or species group modeled for day longlining operations (standard errors of each estimate are in parentheses).

Common name	No. modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Tunas and tuna-like species					
Albacore tuna	2777	-6.47 (0.04)	9.44 (0.43)	-20.34 (1.39)	13.81 (1.34)
Bigeye tuna	2980	-6.44 (0.05)	7.83 (0.48)	-12.25 (1.45)	7.20 (1.33)
Skipjack tuna	2771	-5.38 (0.06)	-0.09 (0.63)	-9.69 (2.12)	10.97 (2.10)
Wahoo	528	-5.68 (0.14)	-6.88 (2.51)	4.46 (12.34)	4.95 (15.94)
Yellowfin tuna	3131	-5.48 (0.04)	1.73 (0.39)	-6.05 (1.35)	5.32 (1.37)
Billfishes					
Black marlin	225	-6.06 (0.25)	-9.48 (4.28)	22.77 (19.67)	-16.81 (23.33)
Blue marlin	1902	-5.81 (0.08)	-3.77 (1.06)	1.83 (3.78)	1.86 (3.89)
Sailfish	402	-5.81 (0.14)	148.00 (2.22)	8.61 (9.28)	2.61 (10.43)
Shortbill spearfish	2477	-4.79 (0.07)	-7.95 (0.84)	4.31 (2.97)	3.34 (3.03)
Striped marlin	2726	-5.11 (0.06)	-3.82 (0.77)	-2.30 (2.62)	6.29 (2.61)
Swordfish	1277	-6.94 (0.14)	2.74 (1.61)	-11.45 (5.38)	11.84 (5.24)
Other teleosts					
Barracudas	240	-5.45 (0.20)	-19.17 (3.87)	47.12 (19.04)	-32.90 (23.27)
Escolar	266	-6.71 (0.19)	8.72 (3.24)	-21.67 (16.64)	6.73 (24.41)
Great barracuda	102	-4.91 (1.44)	-8.86 (33.83)	-45.90 (232.52)	178.29
Lancetfishes	358	-6.20 (0.15)	9.50 (2.22)	-30.57 (9.56)	31.86 (11.61)
Longnosed lancetfish	46	-6.27 (0.81)	-20.84 (16.97)	93.31 (92.41)	-74.91 (136.92)
Mahi mahi	349	-4.41 (0.18)	-25.17 (4.32)	86.37 (29.58)	-108.34 (58.60)
Oilfish	254	-7.72 (0.30)	9.58 (4.95)	-29.23 (24.06)	25.94 (32.87)
Opah	197	-8.24 (0.33)	8.81 (4.78)	-0.74 (20.18)	-17.56 (24.37)

Table A1 (concluded).

Common name	No. modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Pomfrets	179	-6.95 (0.31)	6.69 (4.92)	-29.87 (21.93)	38.71 (26.09)
Shortnosed lancetfish	53	-7.41 (0.45)	-2.93 (6.33)	51.76 (27.49)	-70.62 (35.01)
Sickle pomfret	20	-8.87 (1.08)	20.50 (17.01)	-73.37 (79.15)	102.60 (106.75)
Snake mackerel	102	-6.34 (0.33)	-11.78 (6.06)	63.10 (30.00)	-72.36 (42.00)
Sharks and rays					
Bigeye thresher shark	956	-8.08 (0.21)	7.88 (1.98)	-12.95 (5.69)	8.52 (4.98)
Blue shark	3050	-5.43 (0.05)	0.35 (0.52)	-0.77 (1.68)	-0.16 (1.62)
Common thresher shark	30	-7.67 (1.52)	-2.40 (27.45)	59.64 (149.25)	-135.85 (247.22)
Crocodile shark	384	-7.79 (0.30)	7.17 (3.18)	-18.88 (9.83)	16.39 (9.14)
Dusky shark	54	-4.55 (0.57)	-19.05 (7.22)	47.48 (25.06)	-35.91 (25.48)
Grey reef shark	25	-6.51 (0.56)	3.43 (16.68)	-46.59 (130.00)	101.53 (283.53)
Long-finned mako shark	153	-6.00 (0.29)	-6.66 (4.00)	9.83 (14.42)	-1.46 (14.66)
Oceanic whitetip shark	1910	-4.92 (0.07)	-9.85 (0.97)	11.61 (3.48)	-2.09 (3.56)
Pelagic stingray	356	-5.85 (0.15)	-9.97 (2.65)	28.78 (12.82)	-24.50 (16.14)
Short-finned mako shark	665	-6.14 (0.18)	-9.11 (2.33)	26.32 (8.22)	-22.57 (8.45)
Silky shark	1019	-5.17 (0.08)	-3.56 (1.00)	-4.43 (3.76)	9.90 (4.02)
Silver-tip shark	29	-6.34 (0.66)	12.75 (15.51)	-162.55 (105.60)	407.47 (211.62)
Tiger shark	34	-5.03 (0.69)	-27.92 (10.81)	91.35 (43.29)	-87.35 (49.00)
Whip stingray	19	-2.69 (0.86)	-75.92 (15.42)	298.97 (64.83)	-322.17 (76.22)

Table A2. Parameter estimates and the number of each species or species group modeled for night longlining operations (standard errors of each estimate are in parentheses).

Common name	Number modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Tunas and tuna-like species					
Albacore tuna	1267	-4.92 (0.17)	-3.99 (2.17)	14.44 (8.43)	-13.26 (9.83)
Bigeye tuna	1819	-5.53 (0.07)	-1.50 (1.00)	8.32 (4.10)	-7.84 (4.76)
Skipjack tuna	241	-5.63 (0.26)	-10.47 (4.74)	39.32 (24.12)	-44.72 (34.83)
Wahoo	122	-6.12 (0.29)	-3.83 (8.24)	-12.18 (64.44)	59.35 (128.00)
Yellowfin tuna	1417	-5.00 (0.07)	-7.97 (1.14)	25.43 (5.58)	-25.02 (7.89)
Billfishes					
Black marlin	98	-5.57 (0.24)	-21.65 (8.46)	151.63 (77.45)	-310.27 (189.09)
Blue marlin	593	-5.70 (0.10)	-7.35 (1.91)	24.06 (9.64)	-22.96 (13.05)
Sailfish	148	-6.19 (0.21)	1.58 (5.16)	-39.99 (34.39)	69.81 (47.04)
Shortbill spearfish	269	-6.56 (0.29)	-0.08 (4.34)	8.10 (18.86)	-16.20 (23.66)
Striped marlin	743	-6.35 (0.16)	0.88 (2.37)	6.05 (10.39)	-12.54 (13.72)
Swordfish	2332	-6.22 (0.07)	16.38 (0.95)	-47.07 (3.54)	39.58 (3.87)
Other teleosts					
Escolar	107	-6.55 (0.28)	6.57 (5.19)	-28.51 (26.10)	37.79 (35.79)
Mahi mahi	157	-6.09 (0.23)	3.88 (5.65)	-48.80 (37.60)	74.12 (51.85)
Oilfish	96	-6.25 (0.43)	-17.73 (14.76)	268.21 (144.36)	-854.80 (410.20)
Pomfrets	35	-6.58 (0.54)	-5.46 (13.57)	75.28 (99.03)	-177.15 (195.89)
Shortnosed lancetfish	7	-4.76 (1.18)	-32.04 (17.98)	145.64 (69.78)	-168.07 (79.16)
Snake mackerel	113	-5.99 (0.29)	-6.92 (9.85)	48.80 (95.07)	-133.89 (243.15)
Sharks and rays					
Bigeye thresher shark	139	-6.58 (0.29)	-1.20 (4.43)	10.49 (18.75)	-16.13 (22.29)
Blue shark	2444	-5.00 (0.07)	5.79 (0.84)	-19.62 (3.15)	17.38 (3.34)
Crocodile shark	84	-6.55 (0.40)	1.44 (5.97)	-4.02 (24.39)	4.66 (27.48)
Oceanic whitetip shark	494	-4.97 (0.11)	-17.14 (2.39)	66.41 (14.78)	-77.27 (26.39)
Pelagic stingray	204	-6.00 (0.24)	-5.54 (6.86)	43.57 (56.22)	-119.38 (127.20)
Short-finned mako shark	388	-5.74 (0.20)	-13.66 (3.31)	58.33 (16.64)	-66.17 (24.42)
Silky shark	362	-4.99 (0.12)	-3.90 (2.71)	3.82 (19.07)	-5.10 (30.97)