Does habitat or depth influence catch rates of pelagic species?

Keith A. Bigelow and Mark N. Maunder

Abstract: The efficiency of a pelagic longline fishing operation and the species composition of the resulting catch is influenced primarily by the relationship between the distribution of hooks and species vulnerability, with vulnerability described by either depth or some suite of environmental variables. We therefore fitted longline catch rate models to determine whether catch is estimated better by vertically distributing a species by depth or by environmental conditions (e.g., temperature, thermocline gradient, and oxygen concentration). Catch rates were estimated by two methods: (*i*) monitoring longlines where the vertical distribution of hooks and catch in relation to depth and environmental conditions is known, and (*ii*) applying a statistical habitat-based standardization (statHBS) model to fishery and environmental data to develop relative abundance indices for bigeye tuna (*Thunnus obesus*) and blue shark (*Prionace glauca*). Results indicated that an understanding of gear dynamics and environmental influences are important for analyzing catch-per-unit-effort (CPUE) data correctly. Analyses based on depth-specific catch rates can lead to serious misinterpretation of abundance trends, despite the use of sophisticated statistical techniques (e.g., generalized linear mixed models). This illustrates that inappropriate inclusion or exclusion of important covariates can bias estimates of relative abundance, which may be a common occurrence in CPUE analysis.

Résumé : L'efficacité d'une pêche commerciale pélagique à la palangre et la composition spécifique de la capture sont influencées principalement par la répartition des hameçons et la vulnérabilité des espèces; la vulnérabilité peut être décrite par la profondeur ou par un autre ensemble de variables environnementales. Nous avons donc ajusté des modèles de taux de capture à la palangre afin de déterminer si les captures sont mieux estimées lorsque les espèces sont réparties verticalement en fonction de la profondeur ou en fonction des conditions du milieu (par ex., la température, le gradient de la thermocline et la concentration d'oxygène). Nous avons estimé le taux de capture par deux méthodes : (*i*) en suivant des palangres pour lesquelles la répartition verticale des hameçons et le taux de capture en fonction de la profondeur et des conditions du milieu sont connus et (*ii*) en utilisant un modèle statistique de standardisation basé sur l'habitat (« statHBS ») avec des données de pêche et de conditions environnementales afin de générer des indices d'abondance relative pour le thon ventru (*Thunnus obesus*) et le requin bleu *(Prionace glauca*). Les résultats indiquent qu'une bonne compréhension de la dynamique des engins de pêche et des influences de l'environnement sont nécessaires pour pouvoir analyser correctement les données de capture par unité d'effort (CPUE). Les analyses basées sur les taux de capture spécifiques aux différentes profondeurs peuvent mener à une interprétation sérieusement faussée des tendances dans l'abondance, malgré l'utilisation de méthodes statistiques sophistiquées (par ex., les modèles linéaires généralisés de mélange). Cela illustre comment l'inclusion ou l'exclusion non appropriée de covariables importantes peut fausser les estimations de l'abondance relative, ce qui peut se produire couramment dans les analyses de CPUE.

[Traduit par la Rédaction]

Introduction

The vertical and horizontal distributions of pelagic species are commonly believed to be influenced by temporal and spatial trends in environmental conditions (Sharp 1978; Lehodey et al. 1997), which has led to a substantial amount of research on the habitat preferences and physiological limitations of these species (Brill 1994; Brill and Lutcavage 2001). Habitat preferences and limits (i.e., habitat envelopes) have been used to evaluate the influence of the environment on catch rates of pelagic longlines (Hanamoto 1987; Hinton and Nakano 1996; Bigelow et al. 2002). Accounting for such influences is particularly important when using catch rates as indicators of relative abundance trends because unadjusted catch rates may be misleading (Hinton and Maunder 2004*a*). Catch rates are used as a critical source of information for the majority of fisheries stock assessments, and standardizing catch rates for factors other than abundance, including environmental conditions, is one of the most commonly applied analyses in fisheries science (for a review, see Maunder and Punt 2004). Analyses that do not take these factors into consideration (e.g., Myers and Worm 2003) are likely to

Received 7 December 2006. Accepted 26 July 2007. Published on the NRC Research Press Web site at cjfas.nrc.ca on 31 October 2007.
J19691

K.A. Bigelow.[1] Pacific Islands Fisheries Science Center, NOAA Fisheries, 2570 Dole Street, Honolulu, HI 96822, USA.
M.N. Maunder. Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA.

[1] Corresponding author (e-mail: Keith.Bigelow@noaa.gov).

doi:10.1139/F07-115

produce biased estimates of the status of the stocks (Hampton et al. 2005; Maunder et al. 2006*b*; Polacheck 2006).

For several years, assessments of pelagic species have taken environmental information into consideration when standardizing catch rates of pelagic longlines. In particular, the habitat-based standardization (HBS) framework (Hinton and Nakano 1996) represents a modeling approach whereby catch rates are standardized by estimating effective longline effort from information on the vertical distribution of hooks, species-specific habitat envelopes, and the vertical, horizontal, and temporal distribution of environmental conditions. Initial implementations of this method used habitat preference data collected from acoustic tracking and electronic (archival and pop-up satellite archival) tags. However, for some species, analyses have shown that the application of habitat envelope data derived from tracking or tags may not appropriately represent vulnerability to longline gear (Bigelow et al. 2003). In these analyses, HBS effort may be worse at estimating catch than the use of nominal effort. Reasons may include inaccurate assumptions about habitat envelopes and longline gear depth characteristics, or the fact that changes in motivation to feed or the ability of fish to locate baited longline hooks may well be affected by depth or specific environmental conditions.

Statistical approaches in estimating catch rates have provided superior fits to deterministic habitat modeling (Bigelow et al. 2003), and consequently, these statistical approaches have been advocated (e.g., statHBS, Maunder et al. 2006*a*; neural networks, Maunder and Hinton 2006; generalized linear models, Ward and Myers 2005, 2006). These statistical methods account for some of the previously mentioned problems with the deterministic habitat model (detHBS). Methods for testing the appropriateness of HBS effort (Maunder et al. 2002) naturally lead to a statistical approach for habitat-based standardization (statHBS, Maunder et al. 2006*a*). Rather than deterministically using the habitat envelope data, either these data can be used as a prior in a Bayesian context and updated in the analysis, or habitat-at-capture can be estimated within the analysis in a maximum likelihood context. Commercial catch and effort data are reported as the number of fish caught without information on the position of individual hooks in the water column. Modeling of these catch and effort data in a habitat context precludes the use of linear models (as used by Ward and Myers 2005, 2006) because observations sum information over multiple habitats (Maunder et al. 2006*a*). Therefore, an efficient nonlinear statistical modeling framework is required (e.g., AD Model Builder). The statHBS method has become a standard approach to analyzing catch rate data for the most commercially important billfish and tuna species in the Pacific Ocean (e.g., Bigelow et al. 2003; Hinton and Maunder 2004*b*).

Recent studies have advocated the use of depth distribution of pelagic fishes to standardize longline catch-per-unit-effort (CPUE) and generate indices of relative abundance (Ward and Myers 2005, 2006). The depth-based approach differs from the detHBS and the subsequent statistical approaches that take environmental parameters into consideration. In addition, other covariates that are typically used to standardize catch rates (e.g., year, month, and area) should also be considered (Maunder and Punt 2004). Therefore, it is important to determine if a naive depth-based standardization is adequate or if environmental and other covariates are important to standardizing longline CPUE data and generating indices of relative abundance for use in stock assessment models.

Our study compares depth- and habitat-derived catch rate estimates to ascertain if catch is estimated better by modeling the vertical distribution with a variety of environmental conditions or in a stereotyped depth preference. We apply models to bigeye tuna (*Thunnus obesus*) and blue shark (*Prionace glauca*), two ecologically diverse species in the Pacific Ocean, using two approaches to compare catch rates: (*i*) calculating CPUE from monitored longlines where the vertical distribution of hooks and fish catch in relation to environmental conditions and depth is known, and (*ii*) applying a statHBS model to fishery and environmental data to develop indices of relative abundance and comparing them with depth-based analyses (Ward and Myers 2005).

Materials and methods

Catch rate estimation from known catch and hook depth

Depth- and habitat-derived catch rates were estimated from monitored longline sets in the central North Pacific Ocean. Fishery observers of the National Marine Fisheries Service (NMFS) attached one time–depth recorder (TDR) to the presumed deepest hook in each longline set to obtain actual longline fishing depths for swordfish (n = 333 sets) and tuna (n = 266 sets) gear in the Hawaii-based fishery from February 1996 to April 1999 (Bigelow et al. 2006). This study concentrated on monitored tuna sets, and operational details can be found in table 1 of Bigelow et al. (2006). The large geographical area of the monitored tuna sets (4°N–32°N, 170°W–154°W) represents fishing in several current systems and water masses of the North Pacific (Sverdrup et al. 1942). Two data sets were produced to reflect oceanographic properties and allow catch rate comparisons with previous studies. One data set (n = 44 sets) was stratified from 4°N to 14°N, an area dominated by the north equatorial current and countercurrent and characterized by the North Pacific equatorial water mass. The second data set (n = 244 sets) was stratified from 4°N to 25°N and incorporates both the North Pacific equatorial water and central water in the subtropics. No data were used from latitudes to the north of 25°N as these 22 sets occurred within the subtropical frontal zone, an area with differing thermohaline circulation (Roden 1991).

Hook depth in each tuna longline set was estimated by two methods: (*i*) catenary depth formula and (*ii*) interpolation of shallower hooks from the observed depth of the deepest settled hook from TDR monitoring. Hook depth from the catenary formula followed Ward and Myers (2005, 2006) and Bigelow et al. (2006). Briefly, the requirements for catenary depth estimation were longline dimensions reported by the observer or vessel operator such as length of branchline, length of floatline, length of mainline deployed between two floats, hook number, hook midway between floats, and the angle (ϕ) between the horizontal and tangential line of the mainline where the floatline was attached. The angle (ϕ) is based on a sag ratio or the length of the mainline deployed between two successive floats and the horizontal distance between the two floats. We followed the criterion of Ward and Myers (2006) by assuming a value of 72° for ϕ when the sag ratio could not be estimated or did not fall within reasonable bounds (sag ratio ranging from 0.20 to 0.73; $\phi = 62°–90°$, respectively). An assumed angle of 72° occurred for 147 of the 244 sets (60.2%).

TDR depths were estimated according to Boggs (1992). Hook depth was interpolated between either (*i*) the average depth of the deepest (TDR) hook and the calculated depth of the middle hook or (*ii*) the depth of the middle hook and the shallowest depth of the mainline depending on the hook position. The ratio between the middle hook and deepest hook TDR positions was assumed at 0.737 (Boggs 1992), and the shallowest depth of the mainline was assumed to be equal to the length of the floatline.

All fish caught were identified by observers to either the species level or lowest possible taxon, and the hook number associated with the fish was recorded. Capture depths and effort (hooks) were estimated for each longline deployed and binned into 40-m depth categories ranging from 0 to 800 m. We analyzed the vertical distribution in catch rates for bigeye tuna and blue shark. These species were selected because they are primarily caught when the gear is settled, thus the recorded hook number is unlikely to be substantially biased as a result of capture on longline deployment and retrieval (Boggs 1992).

Environmental covariates

Ambient temperature, thermocline gradient, and climatological oxygen at depth were used to model catch rates. TDR monitoring provided temperature and depth measurements every 5 min; however, mixed layer depth and gradients describing the upper thermocline may be poorly determined as the TDR only recorded upper ocean thermal structure while sinking or rising rapidly on longline deployment and retrieval. As an alternative, temperature at discrete depths was obtained from the Global Ocean Data Assimilation System (GODAS) developed at the National Centers for Environmental Prediction (NCEP). The model has 10 and 31 vertical layers in the upper 100 and 1000 m, respectively, and a spatiotemporal resolution of 1/3° latitude and 1° longitude by 1 month (1980–2005). The estimated temperature profile from the TDR monitoring agreed well with the GODAS model values (mean profile difference = 0.09 °C, with a root mean squared or RMS difference = 1.19). We implemented a cubic smoothing spline in R (smooth.spline; version 2.2.0 for Linux; www.r-project.org) for each temperature profile to estimate temperature and gradient (first derivative) for each metre of the profile. Mean temperature and gradient were then estimated for each 40 m depth category. Climatological dissolved oxygen (DO) profile data were obtained from Levitus and Boyer (1994), and mean estimates were interpolated for each 40 m depth category.

Modeling longline catch rates from known catch and hook depth

Generalized linear models (GLMs; S-PLUS version 6.2.1 for Linux; Insightful Corporation, Seattle, Washington) were developed to explain the vertical distribution in catch rates by depth and habitat. GLM structure and the assumption of a Poisson error distribution followed Ward and Myers (2005, 2006). In a model of catch rates by depth, the mean catch ($\mu_{i,D}$) in longline operation *i* at depth *D* is estimated with a log link:

$$\log(\mu_{i,D}) = N_i + \beta_1 D_{i,D} + \beta_2 D_{i,D}{}^2 + \beta_3 D_{i,D}{}^3 + \log(H_{i,D}) \tag{1}$$

where N_i is the mean local abundance, and $H_{i,D}$ and β are estimated parameters. The regression coefficients in eq. 1 describe how catch rates change with depth as a third-order (cubic) effect. Models were also calculated with no depth information (null model) and depth as a linear and quadratic parameterization. For modeling catch rates by habitat, the model estimates mean catch ($\mu_{i,D}$) in longline operation *i* at depth *D* using a log link:

$$\begin{aligned}\log(\mu_{i,D}) = N_i + \beta_1 T_{i,D} + \beta_2 T_{i,D}{}^2 + \beta_3 T_{i,D}{}^3 + \beta_4 \Delta T_{i,D} \\ + \beta_5 \Delta T_{i,D}{}^2 + \beta_6 \Delta T_{i,D}{}^3 + \beta_7 \mathrm{Oxy}_{i,D} + \log(H_{i,D})\end{aligned} \tag{2}$$

where *T* is the ambient temperature, ΔT is the thermocline gradient, and Oxy is the oxygen concentration. Mean catch was modeled as a function of temperature and gradient effects with up to a third-order (cubic) effect. Oxygen was modeled as a two-piece linear effect, as high values would not be expected to result in lower catches. The two linear stanzas were separated at a particular threshold (concentration), with a linear decay in catch below the threshold and no effect (slope = 0) at oxygen values above the threshold. Three oxygen thresholds were considered for each species: bigeye tuna had linear stanzas separated at 1, 2, and 3 $\mathrm{mL \cdot L^{-1}}$, whereas sharks in general are less hypoxia tolerant (Carlson and Parsons 2001), thus blue shark had stanzas separated at 2, 3, and 4 $\mathrm{mL \cdot L^{-1}}$. GLMs were fit in forward and backward selection and the order of entry into the GLM was determined by reductions in the Akaike information criterion (AIC).

Catch rate estimation from a large-scale fishery in a statistical framework

We compared catch rate estimates derived from depth and habitat with corresponding indices of relative abundance for the Japanese distant-water fishery, the largest longline fishery in the Pacific Ocean. Modeling longline catch and effort in a habitat context precluded use of the aforementioned GLMs because observations were summed over multiple habitats. Thus modeling of the catch and effort series entailed use of a standard likelihood approach that fit estimated catch to observed catch (Maunder et al. 2006*a*).

Two Japanese longline fishery data sets were analyzed. Bigeye tuna from 1980 to 2004 were grouped by month, 5° latitude × 5° longitude area, and gear configuration (hooks between floats (HBF); range 5–23) from logbook information. Blue shark captures from 1980 to 2002 were grouped by month, 1° latitude × 1° longitude area, and 5–20 HBF. Blue shark are a bycatch species and captures were not specifically reported in logbooks throughout the entire time series; thus, a filtering method was applied to remove questionable data by calculating a reporting rate per vessel cruise (Nakano and Clarke 2006). The vertical distribution of hooks within each configuration was estimated from longline characteristics and catenary geometry (K. Yokawa, National Research Institute of Far Seas Fisheries, Shimizu, Japan, personal communication; Bigelow et al. 2002).

Catch was fit to four effort series for comparison: (*i*) nominal, (*ii*) statHBS, (*iii*) depth in a deterministic context following Ward and Myers (2005, 2006), and (*iv*) depth estimated statistically. In the statHBS approach, the vertical distribution of a species was based on both habitat-at-capture and environmental data. Effective effort was calculated by summing the habitat-at-capture of the species for each hook within each stratum. This was achieved by matching the depth of the hook with the environmental data to determine the habitat fished by the hook. The estimated catch for a stratum i is

$$C_i = q_{\text{base}} I_t \sum_h \left(H_h \sum_{i,j \in h} E_{i,j} \right) \tag{3}$$

where q_{base} is the overall catchability, I_t is the year effect for year t, H_h represents the habitat effect of hook j in stratum i, and $E_{i,j}$ is the effort for observations i and j. The estimated and observed catch was then compared with a lognormal likelihood function:

$$-\ln L(\boldsymbol{\theta} | \tilde{C}) = \sum_i \ln[\sigma] + \left[\frac{(\ln[\tilde{C}_i + \delta] - \ln[C_i + \delta])^2}{2\sigma^2} \right] \tag{4}$$

where $\tilde{C}_i$ is the observed catch and C_i is the estimated catch for observation i, δ is a small constant (1.0, justification in Maunder et al. 2006*a*) that is used to avoid computational problems when the observed or estimated catch is zero, and σ^2 is the lognormal variance. The negative log likelihood was minimized to estimate q_{base}, the year effects (year effect for the initial year is fixed at 1.0 to avoid confounding with q_{base}) and the standard deviation of the likelihood function. The four effort series differ in the H_h parameterization. For nominal effort, $H_h = 1$. For the deterministic depth-based analysis, H_h is fixed based on parameter estimates for day longlining operations (Ward and Myers 2005, their appendix 1), and H_h is represented by a vector of fifteen 40 m categories from 0 to 600 m. For the statistically estimated depth-based analysis, H_h is estimated for each 40 m depth category. The statHBS model estimates H_h and the categories represented by h are based on ambient temperature and thermocline gradient at 40 m depth internals for each monthly 1° or 5° stratum from the aforementioned GODAS model. AD Model Builder (Otter Research Ltd., Sidney, British Columbia) was used to develop the model, and no priors were used in the estimated depth distribution or statHBS analysis.

We fit models to bigeye tuna and blue shark distributions from a spatial area analogous to that of the Ward and Myers (2005) study (Fig. 1). The area contains 91 960 strata for bigeye tuna (1.4% zero observations) in the tropical (15°S–15°N, 140°E–110°W) and temperate (25°N–40°N, 110°W–170°W) Pacific and 71 046 strata for blue sharks (5.2% zero observations) in the North Pacific Ocean (0°N–15°N, 140°E–110°W and 25°N–40°N, 110°W–170°W). The nominal effort model had a total of 26 parameters (q_{base}, σ, and 24 year effects) for bigeye tuna and 24 parameters for blue sharks. All other models had an additional 14 parameters (preferences – 1) when estimating depth or habitat-at-capture. Model results were compared by three methods: (*i*) Akaike information criterion (AIC), (*ii*) Bayesian information criterion (BIC), and (*iii*) an aggregated prediction error ($\Sigma[\ln(\tilde{C}_i + \delta) - \ln(C_i + \delta)]^2$). Bootstrapping was employed to empirically estimate the distribution of the differences between models (ΔAIC, ΔBIC, Δprediction error). Bootstrapping was conducted by block resampling each year, using a simple random sample with replacement to model temporal correlation as monthly 1° or 5° strata may not represent independent observations. The four longline effort models were then applied to each of the 25- or 23-year blocks, and a total of 500 bootstrap replications were computed. For the aggregated prediction error, a ratio (model 1 to model 2) of prediction errors was calculated from each bootstrap replication. Selecting model 1 compared with model 2 corresponds to the proportion (p) of bootstrapped ratios having a value <1.0.

Fig. 1. Geographical areas of longline catch rate analyses for the Hawaii-based tuna fishery (two areas) and Japanese distant-water tuna fishery. Hawaii-based fishery was monitored with time–depth recorders (TDRs) and has known vertical distribution of hooks and fish catch in relation to environmental conditions and depth. Japanese fishery was analyzed for bigeye tuna (*Thunnus obesus*, shaded area) and North Pacific blue sharks (*Prionace glauca*, hatched area north of the equator).

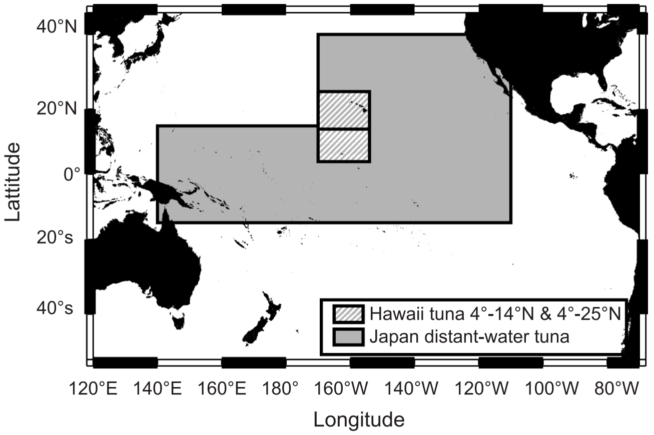


Table 1. Number of fish and effort (sets, hooks) from monitored (time–depth recorders) longline sets in the Hawaii-based fishery.

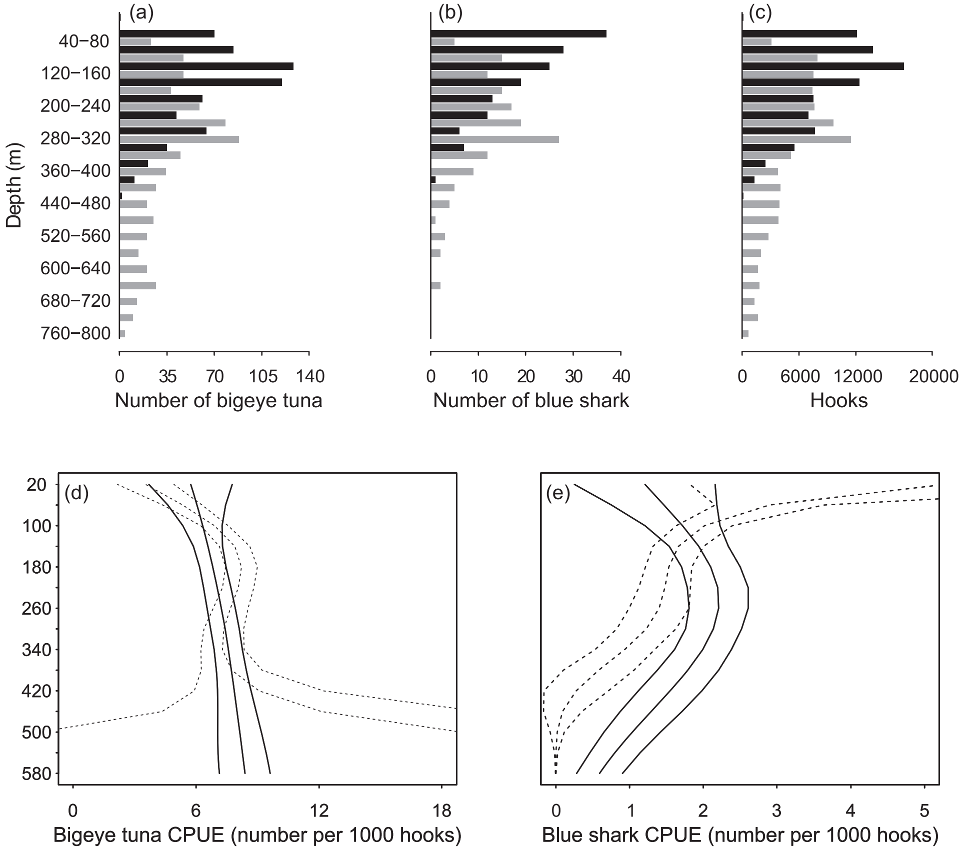
		Number modeled	
Stratum	Sets (hooks)	Bigeye tuna	Blue sharks
4°N–14°N	44 (86 888)	639	148
4°N–25°N	244 (412 834)	2509	1308

Results

Precision of depth and catch rate estimates

The vertical distribution of hooks and fish capture were known for 44 longline sets from 4°N to 14°N and 244 sets from 4°N to 25°N (Table 1). The tropical area (4°N–14°N) corresponds to data analyzed by Ward and Myers (2006, n = 864 sets). Hook depths based on the catenary formula were substantially deeper (mean = 310 m) than observed hook depths (mean = 183 m; Fig. 2*c*). Similar biases occur when estimating the vertical distribution in catch and correspond-

Fig. 2. Comparison of the bigeye tuna (*Thunnus obesus*) and blue shark (*Prionace glauca*) vertical distribution of (*a*, *b*) catch, (*c*) longline effort, and (*d*, *e*) catch rates based on catenary depth estimates (shaded bars) and observed depth (solid bars) for the Hawaii-based longline fishery (n = 44 sets, 4°N–14°N, 170°W–154°W). Estimated catch rate-at-depth with 95% confidence intervals from generalized linear models (GLMs) based on catenary (solid line) and observed depth (broken line) for (*d*) bigeye tuna and (*e*) blue sharks.



ing CPUE. Depth distribution in catch rates for bigeye tuna based on observed hook depths indicated an increase in CPUE from the surface, peaking at 180 m, and a slight decline in catch rates to a depth of 420 m (Fig. 2*d*). Few inferences can be made from TDR monitoring at depths deeper than 420 m as confidence intervals widen because of a lack of fishing effort. In contrast, bigeye tuna CPUE appears to linearly increase from the surface to a depth of 600 m based on catenary assumptions. There was a greater difference in profiles for blue sharks based on catenary and observed longline depths as indicated by the mean trend and 95% confidence intervals (Fig. 2*e*). Blue shark catch rates based on observed hook depths were high in the upper water column (0–100 m) and declined with depth, but the profile based on catenary assumptions indicated significantly lower catch rates in the upper water column, an increase to a depth of 260 m, and significantly higher catch rates at deeper depths.

Modeling catch rates from known longline catch and hook depth

Results from modeling catch rates by depth and habitat-at-capture are presented for bigeye tuna and blue sharks in two geographical areas (Tables 2–3). A latitudinal depiction from the larger area (4°N to 25°N) of the Hawaii-based longline fishery indicates that the vertical structure of temperature and oxygen is dynamic (Fig. 3). From 4°N to 14°N, the thermocline is shallow (80–280 m) with large gradients (~0.25 $°C{\cdot}m^{-1}$) and a shallow oxycline. Proceeding northward (14°N–20°N), the thermocline occurs at moderate depths (100–320 m) with smaller gradients (~0.1 $°C{\cdot}m^{-1}$) and a deepening oxycline. From 20°N to 25°N, the thermocline is diffuse (<0.1 $°C{\cdot}m^{-1}$) and the oxycline is deep with a concentration of 4 $mL{\cdot}L^{-1}$ at ~350 m.

A cubic depth model was preferred over null, linear, and quadratic depth effects; however, AIC and residual deviance indicated that all GLMs fit to catch with habitat as explanatory variables were preferred over models using depth (Tables 2–3). For each species, temperature variables (ambient and thermocline gradient) were the initial entrants in the GLM, but the entry of each variable was area dependent. Thermocline gradient was large in the tropics (4°N–14°N) and was the initial entry in the bigeye tuna model (not shown); however, ambient temperature was the initial entry for the larger area (4°N–25°N). The relationship between ambient temperature and catch for the larger area suggested a maximum catch at ~10 °C with a decline at increasing temperature (Fig. 4*a*), whereas the relationship with thermocline gradient indicated low catch at strong gradients (Fig. 4*b*). For blue sharks, the temperature effect was relatively flat (Fig. 4*d*), though the thermocline gradient effect was dome-shaped with high catches at moderate gradients (Fig. 4*e*). The effects of both temperature variables imply

Table 2. Summary statistics of a generalized linear model fit to bigeye tuna catch as a function of known gear depth and habitat for the Hawaii-based longline fishery.

Model name	Residual df	Δ Residual deviance	AIC
Bigeye tuna (4°N–14°N, North Pacific equatorial water mass), null deviance = 1193.5			
No depth or habitat information	266		1462.5
Depth information			
Depth (linear)	265	384.4	1080.0
Depth (quadratic)	264	386.8	1078.6
Depth (cubic)	263	390.7	1075.7
Habitat information			
Thermocline gradient (cubic)	263	421.5	1044.9
Thermocline gradient and ambient temperature (cubic)	260	518.4	951.0
Thermocline gradient, ambient temperature, and oxygen	259	523.1	947.3
Bigeye tuna (4°N–25°N, North Pacific equatorial and central water mass), null deviance = 5100.3			
No depth or habitat information	1415		6518.2
Depth information			
Depth (linear)	1414	1800.9	4719.3
Depth (quadratic)	1413	1904.3	4616.9
Depth (cubic)	1412	1906.5	4615.7
Habitat information			
Ambient temperature (quadratic)	1413	1919.2	4602.0
Ambient temperature and thermocline gradient (quadratic)	1411	1940.2	4583.0
Thermocline gradient, ambient temperature, and oxygen	1409	1947.5	4577.7

Note: Smaller values of Akaike information criterion (AIC) indicate better model performance.

Table 3. Summary statistics of a generalized linear model fit to blue shark catch as a function of known gear depth and habitat for the Hawaii-based longline fishery.

Model name	Residual df	Δ Residual deviance	AIC
Blue shark (4°N–14°N, North Pacific equatorial water mass), null deviance = 447.9			
No depth or habitat information	266		716.9
Depth information			
Depth (linear)	265	152.1	566.8
Depth (quadratic)	264	152.8	567.1
Depth (cubic)	263	156.4	564.5
Habitat information			
Ambient temperature (cubic)	263	155.7	565.1
Ambient temperature and thermocline gradient (linear)	262	158.8	563.1
Blue shark (4°N–25°N, North Pacific equatorial and central water mass), null deviance = 2614.4			
No depth or habitat information	1415		4032.4
Depth information			
Depth (linear)	1414	533.4	3500.9
Depth (quadratic)	1413	542.8	3492.5
Depth (cubic)	1412	545.9	3490.5
Habitat information			
Thermocline gradient (quadratic)	1413	599.0	3436.3
Thermocline gradient and ambient temperature (cubic)	1410	608.3	3430.0
Thermocline gradient, ambient temperature, and oxygen	1409	611.6	3427.8

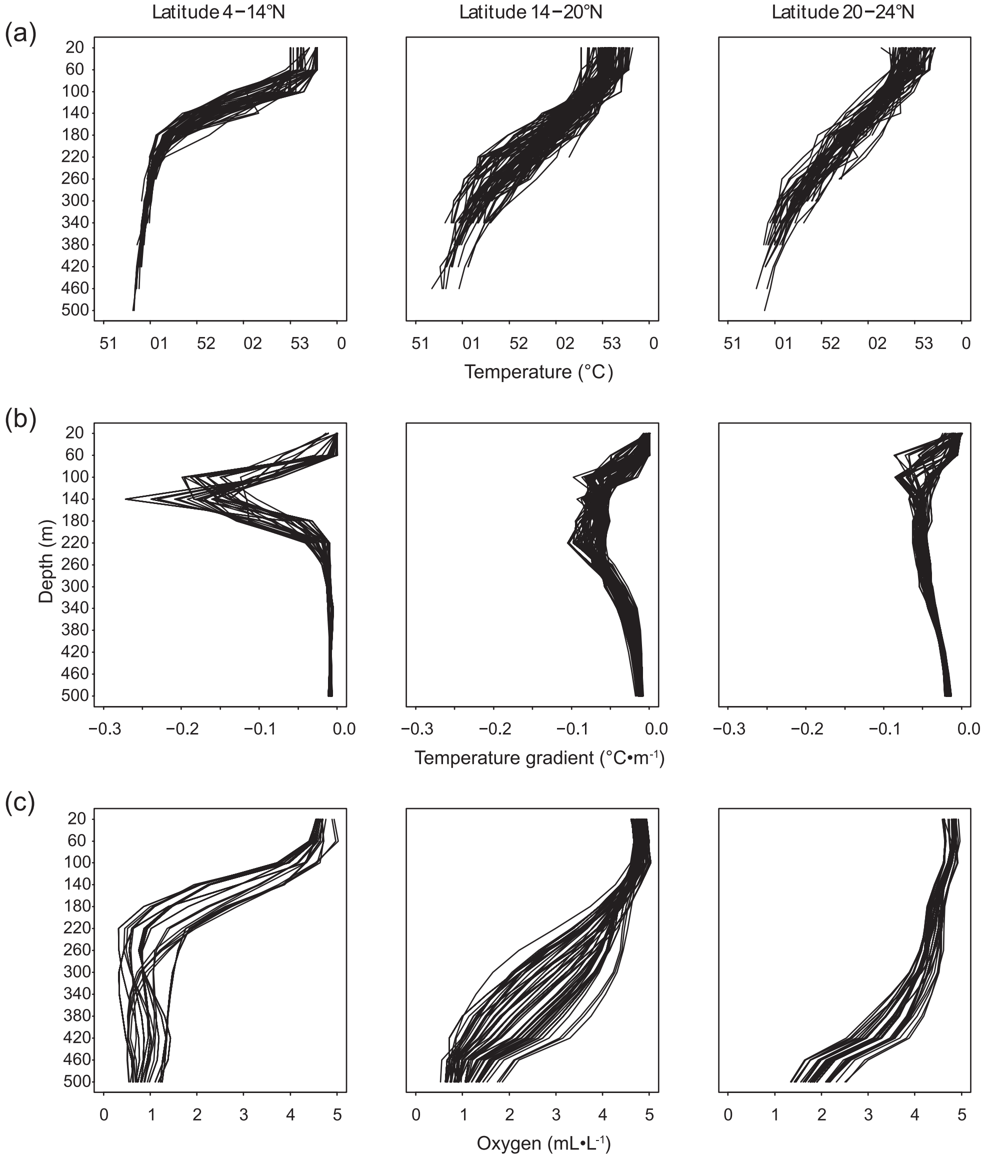
Note: Smaller values of Akaike information criterion (AIC) indicate better model performance.

that bigeye tuna catches are highest at the bottom of the thermocline, whereas high blue shark catches occur within the thermocline.

Dissolved oxygen was always the third entry in GLM, though it was not significant in one fit. AIC results indicate a linear stanza separation at 1 $mL \cdot L^{-1}$ for bigeye tuna and 4 $mL \cdot L^{-1}$ for blue shark (Figs. 4*c*, 4*f*), but AIC values were similar at other thresholds considered. Separations at these thresholds may not have been driven by oxygen but may result from a species position in the thermocline, which has more explanatory power.

Estimated catch rates at depth were generated for the four GLM models based on habitat (Fig. 5). The vertical distribution in catch rate changes markedly between the tropical

Fig. 3. Latitudinal comparison of the vertical distribution of (*a*) temperature, (*b*) temperature gradient, and (*c*) dissolved oxygen corresponding to 244 sets in the Hawaii-based longline fishery (February 1996 – April 1999).



area (4°N–14°N) and the entire area (4°N–25°N). Bigeye tuna and blue shark CPUEs peak at 180 m and 60 m; respectively, in the tropics, but CPUE peaks occur 80 m deeper when the model includes the subtropics.

Modeling catch rates from a large-scale fishery in a statistical framework

Vertically distributing a species by habitat (statHBS approach) provided the best fit to the variation in both bigeye tuna and blue shark catch in the Japanese longline fishery (Table 4; Appendix A, Table A1). Each of the statistical criteria (AIC, BIC) and the alternative prediction error statistic consistently selected the same model. The statHBS effort series based on temperature and thermocline gradient was significantly better than all other effort series based on AIC and BIC values (Table 4).

Fitted temperatures and thermocline gradient were realistic for both species; however, results from the larger spatial area (Japanese fishery) were dissimilar to GLM results on the smaller spatial area (Hawaii-based fishery). Bigeye tuna temperature at capture was highest from 9–25 °C and declined linearly over warmer temperatures (Fig. 6*a*). Fitted thermocline effects over the larger area indicated that bigeye tuna were captured in strong gradients (~0.3 °C·m^{-1}) within the thermocline with a linear decline at weaker gradients (Fig. 6*b*). Fitted temperatures and thermocline gradient indicated that blue sharks are more epipelagic than bigeye tuna. Fitted temperatures were from 10–28 °C, with high values from 23 to 27 °C (Fig. 6*c*). Temperature gradient had a U-shaped effect on blue shark captures (Fig. 6*d*). High captures occurred at high (>0.25 °C·m^{-1}) gradients within the thermocline and low gradients such as the mixed layer. Captures were lower at intermediate gradients (0.05–0.20 °C·m^{-1}).

The use of depth distribution to infer catch rates provided no enhanced performance, as deterministic depth models were marginally better than using nominal effort for both species

Fig. 4. Generalized linear model (GLM) effects of (*a*, *d*) temperature, (*b*, e) temperature gradient, and (*c*, *f*) dissolved oxygen on catch rate of bigeye tuna (*Thunnus obesus*) and blue sharks (*Prionace glauca*) in the Hawaii-based longline fishery (n = 244 sets, 4°N–25°N, 170°W–154°W). CPUE, catch-per-unit-effort. Broken lines indicate ±1 standard error.

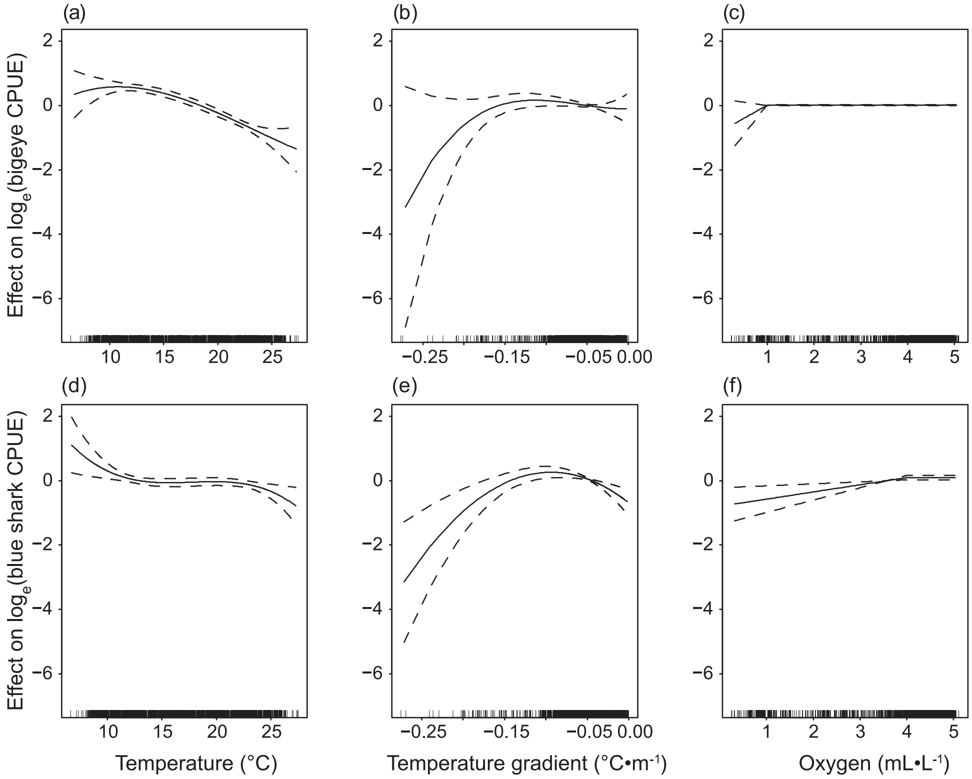
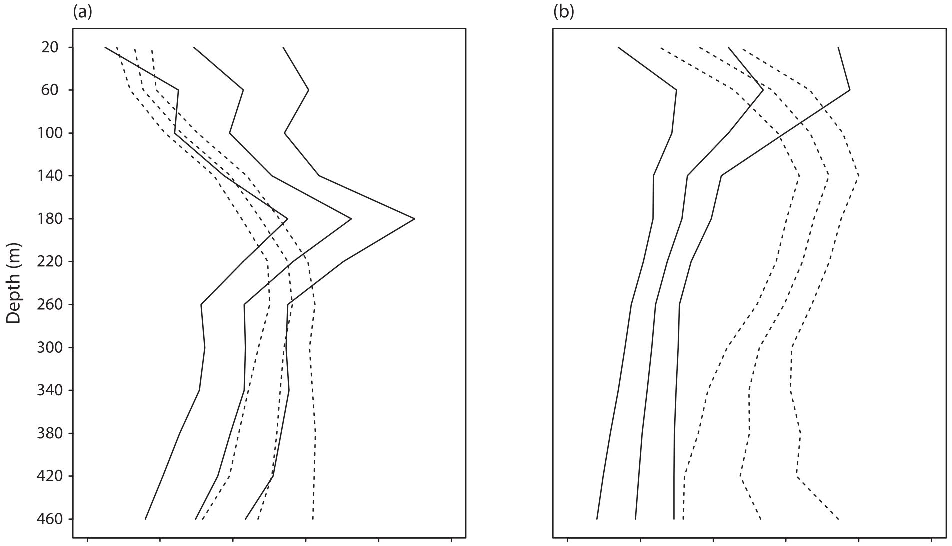


Fig. 5. Estimated catch rate at depth from generalized linear models (GLMs) based on habitat for (*a*) bigeye tuna (*Thunnus obesus*) and (*b*) blue sharks (*Prionace glauca*). Solid line with 95% confidence intervals is the tropical area (n = 44 sets, 4°N–14°N, 170°W–154°W); broken line with 95% confidence intervals is the tropical and subtropical areas (n = 244 sets, 4°N–25°N, 170°W–154°W). CPUE, catch-per-unit-effort.



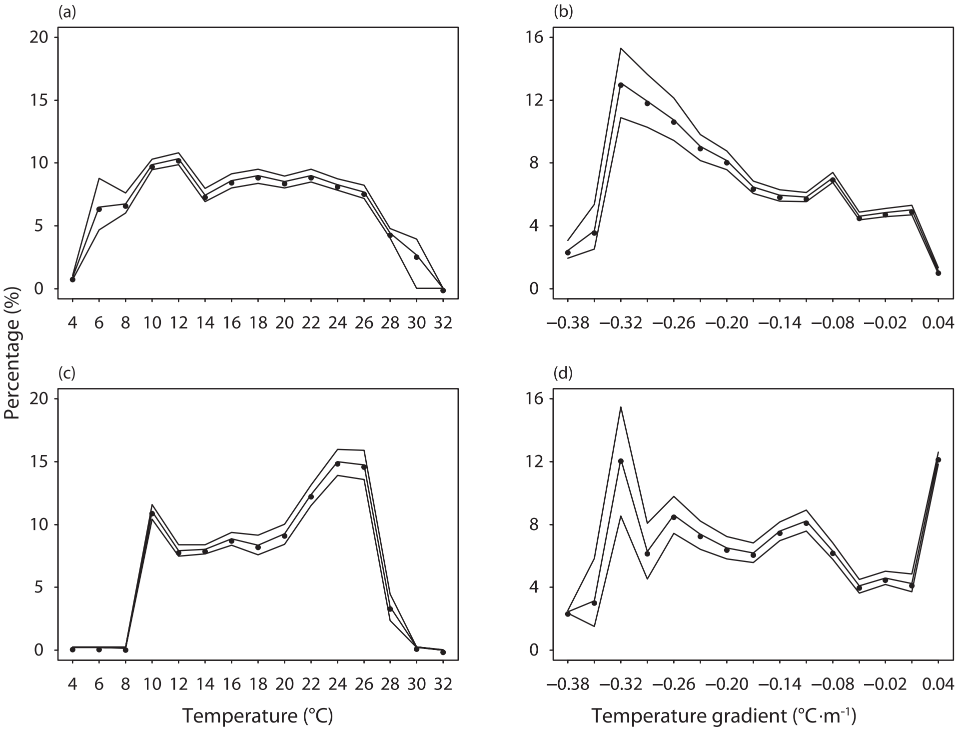
(Table 4). A model that estimated the vertical depth distribution provided intermediate explanatory ability. Two sensitivity analyses were considered: (*i*) distribution of the hooks shallowed and deepened by 10% and 25%; and (*ii*) CPUE-at-depth estimates (Ward and Myers 2005) for longlines deployed during the day (75%) and night (25%). Model results were robust to both the gear depth modifications and differential day–night catch rate assumptions (Appendix A, Table A2). The sensitivity analysis for gear depth indicated that deeper gear (25%) performed better for bigeye tuna in the

Table 4. Comparison of four longline effort models in explaining catch of bigeye tuna and blue sharks in the Japanese longline fishery in the Pacific Ocean.

	Base model — bigeye tuna			Base model — blue sharks		
Model	Parameters	–ln[likelihood]	AIC	Parameters	–ln[likelihood]	AIC
Nominal	26	25 058	50 168	24	21 818	43 684
Depth	26	24 924	49 900	24	21 809	43 666
Depth-fitted	40	24 739	49 558	38	21 322	42 720
statHBS (ambient)	40	24 682	49 444	38	20 538	41 152
statHBS (gradient)	40	24 611	49 302	38	20 469	41 014
statHBS (ambient and gradient)	54	24 251	48 610	52	20 219	40 542

Note: Smaller values of Akaike information criterion (AIC) indicate better model performance. Bayesian information criterion results are not shown, but models had the same ranking as AIC results.

Fig. 6. Estimated catch rate at temperature and temperature gradient for (*a*, *b*, respectively) bigeye tuna (*Thunnus obesus*) and (*c*, *d*, respectively) blue shark (*Prionace glauca*) based on a statistical habitat-based standardization (statHBS). The statHBS model was fit to the area of Ward and Myers (2005). Mean effect is illustrated as points and lines illustrate 95% confidence intervals from bootstrapping.



statHBS analysis (AIC = 47 632) compared with the base case (AIC = 48 610). Gear that was 10% shallower performed better in the statHBS blue shark analysis (AIC = 39 974) compared with the base case (AIC = 40 542). Depth-based results were relatively insensitive for both bigeye tuna and blue shark, especially blue shark where little catch rate variation with depth is assumed (Ward and Myers 2005). The sensitivity analysis of differential vulnerability indicated a slight improvement for bigeye tuna (AIC = 49 842) compared with the base case, but including a night vulnerability component performed much worse for blue shark (AIC = 76 426).

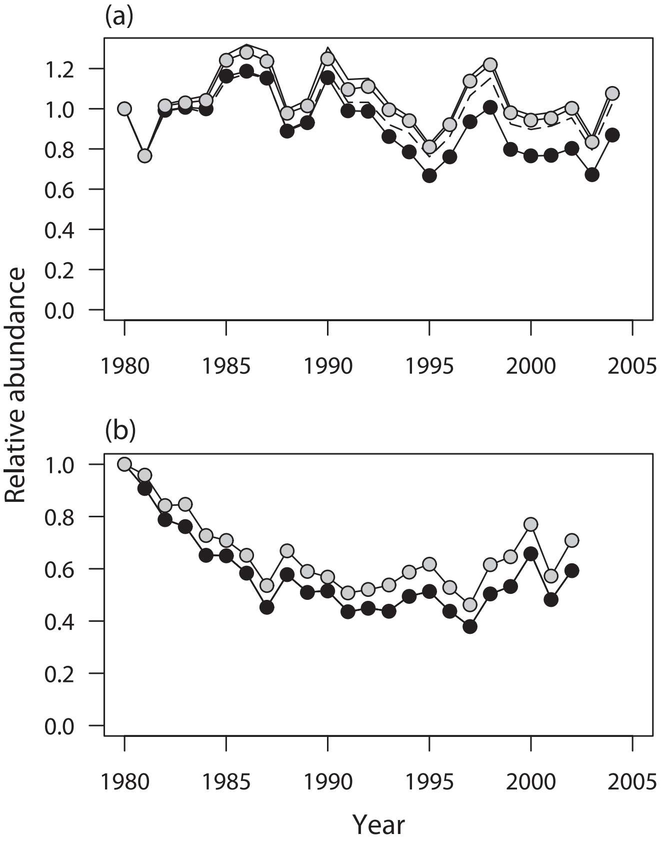
Time-series trends in relative abundance (standardized CPUE) differed markedly for each species, depending on the assumption of vertical distribution by depth or habitat (Fig. 7). Relative abundance indices based on depth or habitat were ~20% different at the end of the time series for both species. The statHBS trend was similar to nominal CPUE for bigeye (Fig. 7*a*) but indicated a greater increase in relative blue shark abundance (Fig. 7*b*) because of reduced catchability that resulted from a time-series shift to deeper gear coincident with less longline effort in the upper water column. The time-series trend based on deterministic depth was the most pessimistic for bigeye tuna, but almost identical to nominal effort for blue sharks, owing to little catch rate variation with depth. Analyses that estimated the vertical depth distribution were more optimistic than deterministic models for bigeye tuna and similar for blue shark, though the improvement over nominal effort was much less than that for statHBS.

Discussion

Precision of depth and catch rate estimates

Longline catchability models require an understanding of gear behavior and hook depth distributions. The vertical dis-

Fig. 7. Trends in relative abundance of (*a*) bigeye tuna (*Thunnus obesus*) and (*b*) blue sharks (*Prionace glauca*) based on four longline effort models: nominal (solid line), deterministic depth-based (solid circles), depth-fitted (broken line), and statistical habitat-based standardization (statHBS; shaded circles). Relative abundance estimates correspond to the area of Ward and Myers (2005) but are not representative of indices used for stock assessment because data are not included from all geographical areas pertaining to the stock. Nominal, deterministic depth-based, and depth-fitted trends for blue shark are almost identical.



tribution of longline hooks is central to estimating species-specific habitat-at-capture and depth-specific catch rates. Monitored longlines indicated that catenary estimates of hook depth were not robust because they are highly sensitive to the assumed sag angle (72°) used when the sag ratio could not be estimated or did not fall within reasonable bounds (0.20–0.73; ϕ = 62°–90°). Our reanalysis of the Ward and Myers (2006) study indicates that their mean angle was 71.8° (95% confidence interval (CI) 66.6°–77.2°) for the Hawaii-based tuna fishery with 74% of the angles assumed as 72°. In contrast, Bigelow et al. (2006) estimated angles substantially less (mean 60.2°) for the same fishery. These smaller angles result in shallower gear; however, actual gear depth was still 39% shallower than empirical catenary estimates because of shoaling (Bigelow et al. 2006). Ward and Myers (2005, 2006) reduced all depths by 25% to account for shoaling. Hook depths, however, remain biased because the commonly used catenary angle of 72° is not appropriate for the Hawaii-based tuna fishery or for other fisheries as well.

The statHBS model contains two submodels: (*i*) hook depth distribution of the longline gear and (*ii*) habitat-at-capture. The current version of the statHBS model implements a deterministic gear distribution and statistically estimates habitat or depth. Goodyear et al. (2002) noted that the weakest component in HBS models might be a quantitative understanding of hook depth distributions and gear behaviors. Our statistically estimated habitat or depth-at-capture for the Japanese distant-water fishery is contingent on assumed hook depths. Although gear depth is generally unknown in longline fisheries, our sensitivity analyses of shallower and deeper gear provide consistent results that predicting vertical distributions based on habitat-at-capture is preferable to using models on depth preferences. The statHBS model can be extended to include a gear submodel for which the parameters are estimated in the statHBS framework (Maunder et al. 2006*a*).

Catch rate comparisons with previous longline monitoring studies

Several longline monitoring studies have investigated depth and habitat relationships for bigeye tuna and blue sharks in the Pacific Ocean. Hanamoto (1987) hypothesized that the optimum bigeye tuna habitat occurred between 10 and 15 °C, but that vertical distribution was limited by temperatures below 10 °C and DO concentration below 1 $mL{\cdot}L^{-1}$. Boggs (1992) conducted longline monitoring in a similar area (14°N–20°N) to our study and demonstrated that bigeye tuna CPUE was low (<2 fish per 1000 hooks) in shallow depth strata (40–120 and 120–200 m) but much higher (8–10 fish per 1000 hooks) in deeper depth strata (200–280 m and 280–400 m). High bigeye tuna CPUE occurred at DO concentrations of 1.4–2.1 $mL{\cdot}L^{-1}$, but no fishing occurred at concentrations of <1 $mL{\cdot}L^{-1}$ to test the hypothesized limitations. There are few studies on depth and habitat relationships for blue sharks in the tropical and subtropical Pacific for comparison. There was no evidence of a depth effect on CPUE between the equator and 30°N (Strasburg 1958) or in equatorial waters and the central Pacific (Nakano et al. 1997), albeit each longline study developed relationships based on catenary formula.

Habitat- and depth-derived catch rate estimates differ by species and fish size because of physiological requirements (Brill 1994). Habitat gradients have been hypothesized to be more important in determining catch rates than ambient values (Cayré and Marsac 1993; Bach et al. 2003). Cayré and Marsac (1993) postulated that gradients (e.g., temperature and oxygen) had a greater effect on the vertical distribution of yellowfin tuna than ambient values, though gradients had to occur within the range of ambient values based on physiological limitations. Bach et al. (2003) characterized bigeye tuna catch rates in the Society Archipelago (French Polynesia) in relation to ambient values and gradients of temperature, DO, and micronekton biomass. Bigeye captures occurred near high thermocline gradients and 50 to 100 m above the maximum micronekton biomass. No inferences could be made with respect to oxygen because fishing occurred in relatively well-oxygenated (>3 $mL{\cdot}L^{-1}$) water. Our results indicate that the catch rate for bigeye tuna in the Hawaii-based fishery is highest at the bottom of the thermocline, in contrast to results of Bach et al. (2003). Differences between geographical areas may relate to the position and strength of the thermocline, which is shallower (100–320 m) and stronger (1–4 °C per 20 m) in areas covered by our study (4°N–24°N) than in the Society Archipelago at 14°S–20°S (100–400 m, 1 °C per 20 m). Alternatively, other factors such as the deep scattering layer may be paramount in explaining bigeye tuna catch rates as several studies have demonstrated an overlap between the vertical distribution of bigeye tuna and micronekton biomass during the day and night (Josse et al. 1998; Dagorn et al. 2000). The depth of the deep scattering layer could be included in the statHBS model as a habitat variable.

Catch rate comparisons with electronic tracking information

There are numerous studies providing data on time-at-depth and time-at-habitat for pelagic species based on acoustic tracking or electronic tags. These have been invaluable for determining the processes and habitat variables to use when standardizing CPUE data. However, statistical tests have indicated that the data obtained from these sources are generally not appropriate for inclusion in the statHBS and similar approaches to standardize CPUE (Maunder et al. 2006*a*). Essentially, tagging data provide information on depth and habitat limits but may not accurately reflect the vulnerability to longline capture, feeding motivation, or a species' ability to locate baited hooks. The main problems with using these data in the statHBS approach include the following. (*i*) The data are from a restricted geographical scale compared with the requirements for analysis of CPUE data. Bigeye tuna, for example, have been tagged in the eastern Pacific Ocean, Japan, Coral Sea, and Hawaii, yet the interest is in basin-scale stock assessments. A greater spatiotemporal coverage of tagging data and finer spatial scale statHBS applications may address this problem. (*ii*) Differential vulnerability aspects due to day and night. The statHBS integrates over the longline set, which occurs during the day and night. (*iii*) Temporal and spatial mismatch between habitat preference and environmental data. Habitat data are taken from electronic tags that measure the near-real-time habitat of the fish, whereas the environmental data are usually model-based (e.g., ocean general circulation model) and averaged over time (month) and space (1°) strata. A mismatch may occur because an individual fish may follow particular environmental conditions within the strata that differ from the average. (*iv*) In general, the historical tag data do not record when an individual is feeding. The consequence is that habitat envelopes may not adequately represent vulnerability to capture. Use of internal temperatures to identify feeding events may address this problem. Alternatively, problems with the assumptions of the statHBS model (e.g., an incorrect gear depth assumption) may result in the poor performance of the detHBS model.

Depth- and habitat-derived catch rate estimates were similar for electronic tracking and monitored longlines for bigeye tuna in French Polynesia at a time when the entire depth and habitat range was targeted by longline gear (Bach et al. 2003). Similarity in catch rate results in this study may relate to daytime vulnerability of bigeye tuna as the longline was deployed in the early morning and retrieved in the early afternoon. Direct comparison of catch rates in the Hawaii-based fishery with electronic tag information is problematic for at least two reasons: (*i*) the longline fishes during the entire daytime and a portion of the night and (*ii*) our monitored longline results are only valid to a depth of ~420 m. A large bigeye tuna (131 cm fork length, 44 kg) tagged in Hawaii showed a characteristic W-shaped pattern in vertical movements during the day with a peak of time-at-temperature from 6–8 °C with a skew towards warmer values resulting from vertical migrations into the upper thermocline (Musyl et al. 2003). During the night, the bigeye was distributed in near-surface waters from 22–26 °C. Our results indicate a maximum catch at ~10 °C with a decline at increasing temperatures, but this relationship is based on a composite of day and night vulnerability. Our monitored longline results are only valid to a depth of ~420 m and no inferences can be made regarding catch rates at deeper depths or cooler temperatures, although bigeye tuna occupy these strata at least occasionally given that the 44 kg individual near the Hawaiian Islands had a descent to 817 m at 4.7 °C (Musyl et al. 2003).

Adjusting longline catch rates

We argue that depth-specific catch rate estimates should not be used for the following reasons. First, we have demonstrated that hook depths calculated according to the assumptions of Ward and Myers (2005, 2006) differed significantly from depth-specific catch rate estimates based on observed hook depths. Hence, Ward and Myers (2005) assertion that the depth distribution of catch rates will not be affected by uncertainty in longline hook depth is untenable.

Second, we argue that their depth-derived catch rate estimates should not be used to adjust abundance indices given the poor performance in estimating catch from depth in their study area. The poor model performance is probably related to the size of the study area, which corresponded to ~61 million km^2 (approximately one-third of the entire Pacific Ocean). This area spans the tropical Pacific, an area characterized by high oceanographic variability. The assumption that a species would have the same vertical depth distribution throughout this oceanographically diverse area is unreasonable. We fit the statHBS model to Japanese longline data in the Ward and Myers (2005) study area for comparison only, but advocate that future statHBS applications consider finer spatial scales that reflect ocean structure. Ward and Myers (2005) advised caution in applying their estimates of catchability to regions outside their study area. Despite such cautions, however, their catchability estimates have been applied to bigeye tuna in the South Atlantic (Ward and Myers 2005) and oceanic sharks in the Gulf of Mexico (Baum and Myers 2004). Given the current depth-based modeling results, the application of the Ward and Myers (2005) Pacific catchability estimates to other areas appears unjustified. Additionally, adjustments based on catchability in each of the South Atlantic and Gulf of Mexico applications were applied externally to the CPUE standardization. We encourage that catchability aspects be estimated within the modeling framework.

Our analyses indicate that gear dynamics and environmental conditions are important in understanding catch rates for pelagic species; analyses solely dependent on vertically distributing a species by depth will be misleading. This can be generalized to all aspects of CPUE standardization. It is important to understand the system being modeled and to avoid extrapolating outside the range of the data. Omitting important covariates, or inclusion of inappropriate covariates, can bias estimates of relative abundance, which may be a common occurrence in CPUE analysis.

The version of statHBS presented here is a simple application. Other applications include the use of additional covariates and habitat types such as ambient light and movements of the deep scattering layer. Additional research is currently underway or proposed to improve the performance of the statHBS methodology, including the following: fish size, which for most pelagic species reflects an ontogenetic change in habitat and depth; consideration of total habitat as it expands and contracts; statistical estimation of hook depths; inclusion of shoaling and retrieval of the longline; and additional validation tests with longline monitoring experiments.

Acknowledgements

The authors gratefully acknowledge the National Research Institute of Far Seas Fisheries for access to commercial fisheries data, M. McCracken for statistical advice, and W. Walsh, C. Lennert, and R. Brill for reading and commenting on the manuscript. GODAS data were provided by the National Centers for Environmental Prediction. This project was partially funded by Cooperative Agreement NA17RJ1230 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Oceanic and Atmospheric Administration (NOAA). The views expressed herein are those of the authors and do not necessarily reflect the views of the NOAA or any of its subdivisions.

References

Bach, P., Dagorn, L., Bertrand, A., Josse, E., and Misselis, C. 2003. Acoustic telemetry versus monitored longline fishing for studying the vertical distribution of pelagic fish: bigeye tuna (*Thunnus obesus*) in French Polynesia. Fish. Res. **60**: 281–292.

Baum, J.K., and Myers, R.A. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. Ecol. Lett. **7**: 135–145.

Bigelow, K.A., Hampton, J., and Miyabe, N. 2002. Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). Fish. Oceanogr. **11**: 143–155.

Bigelow, K., Maunder, M.N., and Hinton, M. 2003. Comparison of deterministic and statistical habitat-based models to estimate effective longline effort and standardized CPUE for bigeye and yellowfin tuna. *In* 16th Meeting of the Standing Committee on Tuna and Billfish, Mooloolaba, Australia, 2003. http://www.spc.int/OceanFish/Html/SCTB/SCTB16/RG3.pdf.

Bigelow, K., Musyl, M.K., Poisson, F., and Kleiber, P. 2006. Pelagic longline gear depth and shoaling. Fish. Res. **77**: 173–183.

Boggs, C.H. 1992. Depth, capture time, and hooked longevity of longline-caught pelagic fish: timing bites of fish with chips. Fish. Bull. U.S. **90**: 642–658.

Brill, R.W. 1994. A review of temperature and oxygen tolerence studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. Fish. Oceanogr. **3**: 204–216.

Brill, R.W., and Lutcavage, M.E. 2001. Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments. *In* Island in the stream: oceanography and fisheries of the Charleston Bump. *Edited by* G.R. Sedberry. Am. Fish. Soc. Symp. **25**: 179–198.

Carlson, J.K., and Parsons, G. 2001. The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. Environ. Biol. Fishes, **61**: 427–433.

Cayré, P., and Marsac, F. 1993. Modelling the yellowfin tuna (*Thunnus albacares*) vertical distribution using sonic tagging results and local environmental parameters. Aquat. Living Resour. **6**: 1–14.

Dagorn, L., Bach, P., and Josse, E. 2000. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean determined using ultrasonic telemetry. Mar. Biol. **136**: 361–371.

Goodyear, C.P., Die, D., Kerstetter, D.W., Olson, D.B., Prince, E., and Scott, G. 2002. Habitat standardization of CPUE indices: research needs. Inter. Comm. Cons. Atlan. Tunas, Coll. Vol. Sci. Pap. **55**: 613–623.

Hampton, J., Sibert, J.R., Kleiber, P., Maunder, M.N., and Harley, S.J. 2005. Decline of Pacific tuna populations exaggerated? Nature (London), **434**: E1–E2.

Hanamoto, E. 1987. Effect of oceanographic environment on bigeye tuna distribution. Bull. Jpn. Soc. Fish. Oceanogr. **51**: 203–216.

Hinton, M.G., and Maunder, M.N. 2004*a*. Methods for standardizing CPUE and how to select among them. Int. Comm. Cons. Atl. Tunas, Coll. Vol. Sci. Pap. **56**: 169–177.

Hinton, M.G., and Maunder, M.N. 2004*b*. Status of striped marlin in the eastern Pacific Ocean in 2002 and outlook for 2003–2004. Inter-Am. Trop. Tuna Comm. Stock Assess. Rep. No. 4. pp. 287–310.

Hinton, M.G., and Nakano, H. 1996. Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints and environmental data, with an application to blue marlin (*Makaira nigricans*) catch and effort data from Japanese longline fisheries in the Pacific. Inter-Am. Trop. Tuna Comm. Bull. **21**: 171–200.

Josse, E., Bach, P., and Dagorn, L. 1998. Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. Hydrobiologia, **371/372**: 61–69.

Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., and Picaut, J. 1997. El Niño Southern Oscillation and tuna in the western Pacific. Nature (London), **389**: 715–718.

Levitus, S., and Boyer, T. 1994. World ocean atlas 1994. Vol. 2. Oxygen. NOAA Atlas NESDIS 2. US Government Printing Office, Washington, D.C.

Maunder, M.N., and Punt, A.E. 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. **70**: 141–159.

Maunder, M.N., and Hinton, M.G 2006. Estimating relative abundance from catch and effort data, using neural networks. Inter-Am. Trop. Tuna Comm. Spec. Rep. No. 15.

Maunder, M.N., Hinton, M.G., Bigelow, K.A., and Harley, S.J. 2002. Statistical comparisons of habitat standardised effort and nominal effort. *In* 15th Meeting of the Standing Committee on Tuna and Billfish, Honolulu, Hawaii, USA, 2002. http://www.spc.int/OceanFish/Html/SCTB/SCTB15/MWG-7.pdf

Maunder, M.N., Hinton, M.G., Bigelow, K.A., and Langley, A.D. 2006*a*. Developing indices of abundance using habitat data in a statistical framework. Bull. Mar. Sci. **79**: 545–559.

Maunder, M.N., Sibert, J.R., Fonteneau, A., Hampton, J., Kleiber, P., and Harley, S. 2006*b*. Interpreting catch-per-unit-of-effort data to assess the status of individual stocks and communities. ICES J. Mar. Sci. **63**: 1373–1385.

Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Kazama, T.K., and Seki, M.P. 2003. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. Fish. Oceanogr. **12**: 152–169.

Myers, R.A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature (London), **423**: 281–283.

Nakano, H., and Clarke, S. 2006. Filtering method for obtaining stock indices by shark species from species-combined logbook data in tuna longline fisheries. Fish. Sci. **72**: 322–332.

Nakano, H., Okazaki, M., and Okamoto. H. 1997. Analysis of catch depth by species for tuna longline fishery based on catch by branch lines. Bull. Nat. Res. Inst. Far Seas Fish. **34**: 43–62.

Polacheck, T. 2006. Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? Mar. Pol. **30**: 470–482.

Roden, G. 1991. Subarctic–subtropical transition zone of the North Pacific: large-scale aspects and mesoscale structure. *In* Biology, oceanography, and fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone. *Edited by* J.A. Wetherall. NOAA Tech. Rep. NMFS No. 105. pp. 1–38.

Sharp, G.D. 1978. Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. *In* The physiological ecology of tunas. *Edited by* G.D. Sharp and A.E. Dizon. Academic Press, New York. pp. 397–450.

Strasburg, D.W. 1958. Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. Fish. Bull. U.S. **58**: 335–361.

Sverdrup, H.U., Johnson, M.W., and Fleming, R.H. 1942. The oceans, their physics, chemistry, and general biology. Prentice-Hall, New York.

Ward, P., and Myers, R.A. 2005. Inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. Can. J. Fish. Aquat. Sci. **62**: 1130–1142.

Ward, P., and Myers, R.A. 2006. Do habitat models accurately predict the depth distribution of pelagic fishes? Fish. Oceanogr. **15**: 60–66.

Appendix A

Tables A1 and A2 appear on the next page.

Table A1. Bootstrap comparisons of longline effort models (nominal, depth, depth-fitted, and statistical habitat-based standardization (statHBS)) in explaining catch of bigeye tuna and blue sharks in the Japanese longline fishery in a Pacific Ocean area analogous to Ward and Myers (2005).

Model comparison		Bigeye tuna		Blue sharks	
Model 1	Model 2	ΔAIC, mean (range)	Prediction error ratio, mean (range)	ΔAIC, mean (range)	Prediction error ratio, mean (range)
Nominal	Depth	262 (–70–581) $p = 0.006$	1.003 (0.999–1.006) $p = 0.006$	16 (13–18)*	1.000 (1.000–1.000)*
Nominal	Depth-fitted	603 (252–941)*	1.007 (1.003–1.011)*	966 (798–1180)*	1.014 (1.012–1.017)*
Nominal	statHBS (ambient)	735 (504–942)*	1.018 (1.014–1.021)*	2543 (2258–2838)*	1.046 (1.041–1.052)*
Nominal	statHBS (gradient)	882 (672–1117)*	1.008 (1.006–1.011)*	2678 (2291–3051)*	1.037 (1.033–1.041)*
Nominal	statHBS (ambient and gradient)	1580 (1266–1893)*	1.010 (1.008–1.013)*	3161 (2781–3536)*	1.039 (1.033–1.044)*
Depth	Depth-fitted	341 (295–394)*	1.004 (1.004–1.005)*	951 (783–1162)*	1.014 (1.011–1.017)*
Depth	statHBS (ambient)	473 (140–797)*	1.005 (1.002–1.009)*	2527 (2243–2822)*	1.037 (1.032–1.041)*
Depth	statHBS (gradient)	620 (238–982)*	1.007 (1.003–1.011)*	2662 (2275–3035)*	1.039 (1.033–1.044)*
Depth	statHBS (ambient and gradient)	1318 (878–1702)*	1.015 (1.010–1.019)*	3146 (2765–3520)*	1.046 (1.041–1.052)*
Depth-fitted	statHBS (temperature)	132 (–214–475) $p = 0.124$	1.001 (0.998–1.005) $p = 0.124$	1576 (1273–1949)*	1.022 (1.018–1.028)*
Depth-fitted	statHBS (gradient)	278 (–133–660) $p = 0.008$	1.003 (0.999–1.007) $p = 0.008$	1711 (1333–2072)*	1.024 (1.019–1.030)*
Depth-fitted	statHBS (ambient and gradient)	977 (506–1380)*	1.011 (1.006–1.015)*	2195 (1823–2562)*	1.032 (1.026–1.037)*
statHBS (ambient)	statHBS (gradient)	147 (–123–437) $p = 0.064$	1.002 (0.999–1.005) $p = 0.064$	135 (–189–382) $p = 0.062$	1.002 (0.997–1.005) $p = 0.062$
statHBS (ambient and gradient)	statHBS (ambient)	–845 (–1130 – –584)**	0.991 (0.988–0.993)**	–619 (–798 – –477)**	0.991 (0.988–0.993)**
statHBS (ambient)	statHBS (gradient)	–698 (–864 – –492)**	0.992 (0.990–0.994)**	–484 (–671 – –371)**	0.993 (0.990–0.994)**

Note: ΔAIC is AIC (Akaike information criterion) for model 1 minus AIC for model 2, and larger values indicate greater difference in explanatory power between models. Negative values of ΔAIC indicate that model 1 is better than model 2. Bayesian information criterion (BIC) results are not shown as p values were identical to those of the AIC results. Prediction error statistic is the ratio (model 1 to model 2) of the aggregated prediction error. p values correspond to the proportion of model 1 that are better than model 2. *, $p < 0.002$; **, $p > 0.998$.

Table A2. Summary of sensitivity analyses for comparing longline effort models (depth-based and statistical habitat-based standardization (statHBS)) in explaining catch of bigeye tuna and blue sharks in the Japanese longline fishery in the Pacific Ocean.

	Bigeye tuna					Blue shark				
	Shallower gear		Deeper gear			Shallower gear		Deeper gear		
Model	10%	25%	10%	25%	75% day – 25% night	10%	25%	10%	25%	75% day – 25% night
Depth	50 072	50 016	49 948	49 902	49 842	43 658	43 656	43 668	43 670	76 426
statHBS (ambient and gradient)	48 308	48 658	48 004	47 632	NA	39 974	40 254	40 414	40 688	NA

Note: Analyses were conducted with shallower and deeper longline gear and catch rate-at-depth estimates for longlines deployed during the day (75%) and night (25%). Illustrated AIC values indicate explanatory power and smaller AIC values indicate better model performance. NA, not applicable.