

# Do habitat models accurately predict the depth distribution of pelagic fishes?

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## ABSTRACT

Habitat models are used to correct estimates of fish abundance derived from pelagic longline fishing gear. They combine information on hook depth with the species' preferences for ambient environmental conditions to adjust the gear's catchability. We compare depth distributions of bigeye tuna (*Thunnus obesus*) catch predicted by a habitat model with distributions derived from data collected by observers on longliners in the tropical Pacific Ocean. Our analyses show that the habitat model does not accurately predict the depth distribution of bigeye tuna; its predictions are worse than those from models that assume no effect of depth on catches. Statistical models provided superior fits to the observed depth distribution. The poor performance of the habitat model is probably due to (1) problems in estimating hook depth, (2) fine-scale variations in environmental conditions, (3) incomplete knowledge of habitat preferences and (4) differences between the distribution of bigeye tuna and their vulnerability to longline gear.

**Key words:** bigeye tuna, cpue standardization, habitat modeling, longline fishing, Pacific Ocean, pelagic zone, temperature, *Thunnus obesus*

## INTRODUCTION

Longline catch rates of many pelagic fish species are sensitive to hook depth and environmental conditions. Adult bigeye tuna, for example, range down to

600 m or deeper in the western Pacific Ocean. In the mid 1970s, many pelagic longliners began to target bigeye tuna with gear that ranged to 250 m (Suzuki *et al.*, 1977). Catch rates derived from shallower longlines used in earlier years will underestimate the true abundance of species like bigeye tuna because the gear did not cover the species' full depth range.

Variations in the depth range of the fishing gear and oceanographic conditions affect 'catchability', the part of a population caught by a unit of fishing effort (Murphy, 1960). A reliable estimate of catchability is required to accurately estimate abundance from catch rates. In addition to being affected by the gear's depth range, the catchability of longline gear will be affected by spatial and temporal variations in oceanographic conditions, e.g. the thermocline is much deeper in the west (approximately 175 m) than in the east (approximately 40 m) of the tropical Pacific Ocean. Oceanographic conditions also fluctuate with broad-scale events, e.g. the thermocline shoals by about 40 m during El Niño periods in the western Pacific Ocean (Philander, 1990).

Habitat models are increasingly being used to correct abundance indices derived from longline catch rates, e.g. Bigelow *et al.* (2002). They adjust catchability by combining information on hook depth, ambient environmental conditions and the species' preferences for those conditions. Bigelow *et al.* (2002) applied a habitat model to 1966–96 catch and fishing effort data reported by Japan's longline fleet. They concluded that a large proportion of adult bigeye tuna was not available to longline gear in the tropical Pacific Ocean because they were beyond the gear's depth range. Their habitat-corrected catch rates suggested greater declines in bigeye tuna abundance than those indicated by nominal catch rates. However, we found no published study that tests the depth distributions predicted by habitat models. Here we test whether habitat model predictions match the depth distribution of bigeye tuna inferred from longline catches, and we compare the model's performance with that of alternative models.

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## METHODS

### Catch and effort data

Our analyses focused on bigeye tuna in the Pacific Ocean between 5–15°N and 180°E–120°W during 1994–2001. We derived the observed depth distribution of bigeye tuna from data reported by observers on Hawaii-based longliners that targeted the species by deploying deep longlines (27–600 m) at sunrise each day. Each longline consisted of about 2000 baited hooks suspended from a buoyed mainline. They were retrieved during the afternoon and evening of the same day. The observers reported a unique identifier for each longline hook. We used the gear dimensions and individual hook data reported by observers to estimate the depth at which each bigeye tuna was caught. The data consisted of 864 daily fishing operations where at least one bigeye tuna was caught.

### Estimation of hook depth

We used longline dimensions reported by the observers to estimate the maximum settled depth  $d$  of each hook  $j$  on each longline by assuming that the mainlines formed a catenary curve (Suzuki *et al.*, 1977):

$$d_j = b + f + \frac{m}{2} \left\{ \left( 1 + \cotan^2 \varphi^o \right)^{1/2} - \left[ \left( 1 - 2 \frac{j}{n+1} \right)^2 + \cotan^2 \varphi^o \right]^{1/2} \right\}, \quad (1)$$

where  $b$  is the length of the branchline,  $f$  is the length of the floatline,  $m$  is the length of mainline between floats and  $n$  is the number of hooks between the pair of floats holding hook  $j$ , and  $\varphi^o$  is the angle of a horizontal line drawn between the tangent of the mainline and the connecting point of the floatline and mainline.

Suzuki *et al.* (1977) and many other researchers used a value of 72° for  $\varphi^o$  because they did not have data on the sagging rate  $k$ . The sagging rate is the ratio of the distance between floats and the length of mainline between floats. However, the observers sometimes collected this information on Hawaii-based longliners. We used those data to calculate  $\varphi^o$  from the sagging rate  $k$  for each longline operation with a derivation of a formula presented by Yoshihara (1954). For 74% of operations the sagging rate could not be estimated or did not fall within reasonable bounds ( $0.20 < k < 0.73$ ). For those operation we used a value of 72° for  $\varphi^o$ .

We assumed that the shape of the catenary curve formed by the mainline (and therefore the

corresponding depth of hooks) did not systematically vary along each longline or during each operation. However, observed depths and predicted depths are known to vary, with the direction and velocity of 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  $0.4 \text{ m s}^{-1}$ . To represent shoaling of longlines in our study area, which is characterized by strong equatorial currents, we reduced all depths predicted by the catenary formula by 25%. The data were then binned into 40-m depth strata, ranging from 0–40 to 560–600 m.

### Habitat predictions

Mr Keith Bigelow (NMFS Honolulu Laboratories) provided the depth distribution of bigeye tuna predicted by the habitat model of Bigelow *et al.* (2002). The model predicted the proportion of bigeye tuna in each 40-m depth – 1° latitude–longitude square – year – month stratum. The proportions sum to one in each area–time stratum. Effective fishing effort  $f_{a,t}$  is the weighted sum of longline hooks  $H_{a,t}$  over all depths  $d$  in each area  $a$  and time  $t$ :

$$f_{a,t} = H_{a,t} \sum_d h_{a,t,d} p_{a,t,d}, \quad (2)$$

where  $h_{a,t,d}$  is the proportion of hooks in the stratum. The predicted proportion of bigeye tuna  $p_{a,t,d}$  in the stratum is the product of scaled oxygen and temperature indices from Bigelow *et al.*'s model of the habitat preferences of bigeye tuna that were mapped to predicted temperature and oxygen levels to produce a depth distribution.

Bigelow *et al.* (2002) used data from physiological experiments and tracking studies to develop models of habitat preferences in relation to temperature and oxygen levels. For environmental conditions, they used a global circulation model (Behringer *et al.*, 1998) to predict the temperature at each 40-m depth – degree – year – month stratum in the study area. Levitus and Boyer (1994) estimated the mean dissolved oxygen concentrations during 1934–94 for each depth – degree – 3-month quarter in the study area. Bigelow *et al.* binned the oxygen and temperature data by depth – degree – quarter to match the resolution of the Japanese longline data that they analyzed. The longline data that we analyzed had a finer temporal stratum, so we used proportions that Mr Bigelow provided for each depth – degree – year – month stratum.

The Hawaii-based longliners deployed their longlines at dawn then retrieved throughout the afternoon and evening. Estimates of the astronomical time of sunset for each operation showed that hooks were exposed to 73% daylight on average. Consequently, we used the same 0.75 weighting factor for day and 0.25 for night that Bigelow *et al.* (2002) used.

#### Assessing model performance

To assess the performance of the habitat model (and alternative models described in the next section), we embedded model predictions in a generalized linear model that related catch to local abundance and fishing effort with a log link. This 'habitat-based model' predicted the mean catch  $\mu_{d,i}$  in depth stratum  $d$  of operation  $i$ :

$$\log(\mu_{d,i}) = N_i + \log(p_{d,i}H_{d,i}), \quad (3)$$

where  $H_{d,i}$  is the number of hooks deployed,  $p_{d,i}$  is the habitat model prediction of the proportion of bigeye tuna in the stratum and  $N_i$  is the logarithm of local abundance of the species encountered by the operation. In our analysis,  $N_i$  is a nuisance parameter and was estimated for each longline operation in a fixed effect analysis. To check robustness we repeated the analysis using a generalized linear mixed-effect model in which  $N_i$  was assumed to be a normal random variable; however, the conclusions were the same and the details are not presented here.

We assumed that bigeye tuna catches had a Poisson distribution:

$$C_{d,i} \sim P(\mu_{d,i}), \quad (4)$$

where  $C_{d,i}$  is the expected catch of bigeye tuna and  $\mu_{d,i}$  is the mean catch at depth  $d$  in operation  $i$ . We also investigated the performance of each model under a negative binomial distribution:

$$C_{d,i} \sim nb(\mu_{d,i}, \theta). \quad (5)$$

The negative binomial is similar to a Poisson distribution. It has the same mean, but it has an extra parameter  $\theta$  to allow for over-dispersion. The dispersion parameter  $\theta$  scales the estimate of binomial variance for the amount of variance in the data (Venables and Ripley, 1999).

We implemented the models in the *glm* function of S-Plus (version 6.0 SE), which uses iteratively reweighted likelihoods to fit generalized linear models (Venables and Ripley, 1999). For the negative binomial models we also used Venables and Ripley's *glm.nb* function of the MASS library (version 7.0, <http://www.stats.ox.ac.uk/pub/>) to estimate the dispersion parameter  $\theta$ . To check that each model provided a

reasonable fit to the data, we examined scatter plots of chi-square residuals against fitted values and residual plots. We used Akaike's information criterion (AIC) and residual deviance to compare model performance. The residual deviance measures the amount of variation in mean catch that is not explained by the model. AIC is based on the model's log-likelihood and number of parameters (Venables and Ripley, 1999):

$$\text{AIC} = -2\text{maximized log-likelihood} + 2\#\text{parameters}. \quad (6)$$

#### Alternative models

We compared the performance of the habitat-based model in predicting the depth distribution of bigeye tuna catches with that of four statistical models and a null model. The first statistical model, the basin-wide model, was exactly the same as eqn. 3 except that  $p_{d,i}$  was the proportion predicted for the stratum by Ward and Myers (2005). They estimated the depth distribution of bigeye tuna from a generalized linear mixed-effect model fitted to data from a longline survey and three longline fleets operating over a longer period in a wider area of the Pacific Ocean. Note that we used estimates from their model (Table 1) that specifically excluded data from the Hawaii-based fleet analyzed here. Ward and Myers modeled mean catch  $\mu_{d,i}$  using a log link:

$$\log(\mu_{d,i}) = \lambda_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \beta_3 D_{d,i}^3 + \log(H_{d,i}). \quad (7)$$

where  $\lambda_i$  and  $\beta_j$  are parameters to be estimated and  $D_{d,i}$  is the depth of depth stratum  $d$  of longline operation  $i$ . Ward and Myers assumed that the log abundance of the bigeye tuna  $\lambda_i$ , when it is encountered by the operation, followed a random effects distribution, which they nominated to be a normal distribution.

**Table 1.** Parameter estimates for the basin-wide model. The model was proposed by Ward and Myers (2005). However, parameter estimates presented in this table and used in the present article specifically excluded data from the Hawaii-based fleet in the study to avoid problems in assessing the model with data that its parameters were partly derived from.

Parameter*	Estimate	SE
$\lambda$	-6.4762	0.0465
$\beta_1$	8.7736	0.4588
$\beta_2$	-15.3437	1.4038
$\beta_3$	10.3750	1.2978

\*Equation 7 provides the model's formula and explanations of symbols.

The basin-wide and habitat-based models used external information on depth. Three statistical models fitted *in situ* depth estimates from the study area. The cubic depth model predicted the mean catch from the local abundance, number of hooks and estimated depth  $D_{d,i}$  of each stratum:

$$\log(\mu_{d,i}) = N_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \beta_3 D_{d,i}^3 + \log(H_{i,d}), \quad (8)$$

where the  $\beta_j$  are estimated parameters. The cubic depth model was the same as the basin-wide model, but its parameters were estimated from longline data from the study area (basin-wide estimates were derived from several longline data sets outside the study area). The other two statistical models were the same as eqn. 8, but had different functional forms of the depth coefficients (Table 2). The sixth model, the null model, did not have any depth coefficient. It represented the hypothesis that depth did not influence catch rates.

## RESULTS

The observed depth distributions of bigeye tuna showed substantial variation among operations. The depth coefficients of the quadratic and cubic depth models were all statistically significant ( $P \ll 0.001$ ), thus supporting the hypothesis that depth does influence catches. The residual deviance shows that the statistical models with *in situ* depth information

produced close fits to the observed distributions (Table 2). The basin-wide model also produced a good fit to the distribution observed in the study area. The habitat-based model produced the poorest fit of all models. It overestimated the observed distribution at shallow depths, but underestimated it at intermediate depths (Fig. 1).

The AIC and residual deviance of negative binomial models gave the same ranking of model performance as that indicated by Poisson models (Table 2). Fixing the dispersion parameter  $\theta$  at the same value for the negative binomial models did not change the ranking of negative binomial models as judged by the residual deviance and AIC. The Poisson models were preferred because estimates of  $\theta$  ranged up to 680 for some negative binomial models, so that the Poisson model was recovered. Consequently our discussion of results concentrates on the Poisson models.

## DISCUSSION

The fit of statistical models to data that their parameters were derived from will usually be superior to the fit of deterministic models like the habitat model. However, care is necessary when using statistical models to predict outside their data range. Variations in oceanographic conditions and changes in fishing practices will affect catchability, which was the original motivation for using habitat models. In this case,

**Table 2.** Formulae and statistics for generalized linear models. Separate statistics are shown for models that fitted a Poisson error distribution and those that fitted a negative binomial error distribution. All models fitted the same data set regardless of error distribution or formulation.

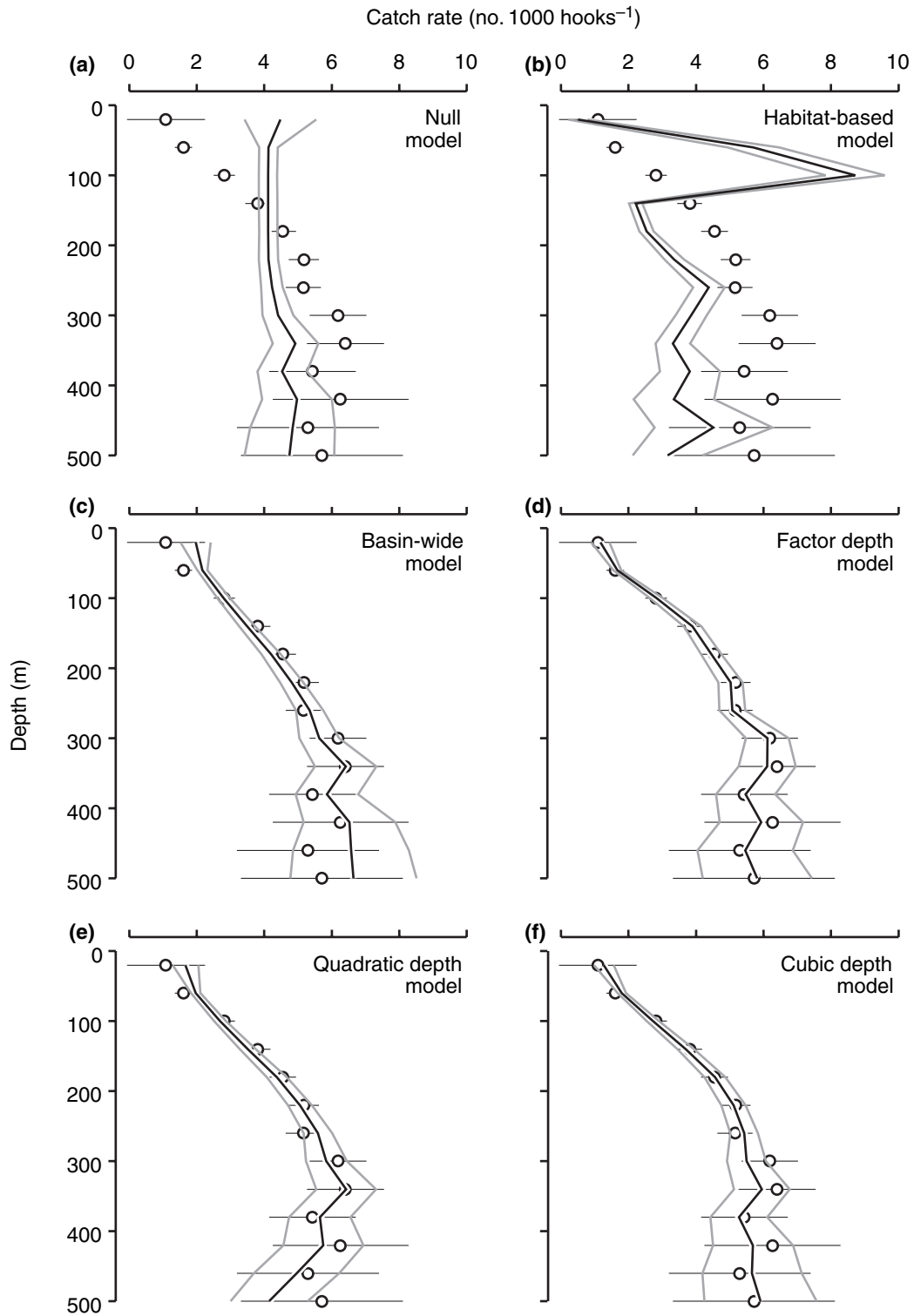
Model name	Formula	Residual, d.f.	Poisson		Negative binomial	
			rd*	AIC†	rd*	AIC†
No depth information						
Null	$\log(\mu_{d,i}) = N_i + \log(H_{d,i})$	4696	5942	7670	3344	5072
External depth information						
Habitat based	$\log(\mu_{d,i}) = N_i + \log(p_{d,i} H_{d,i})$	4696	12 154	13 882	5377	7105
Basin wide	$\log(\mu_{d,i}) = N_i + \log(p_{d,i} H_{d,i})$	4696	5223	6951	3011	4739
<i>In situ</i> depth information						
Factor depth	$\log(\mu_{d,i}) = N_i + \beta_d D_{d,i} + \log(H_{d,i})$	4682	5153	6909	2965	4721
Quadratic depth	$\log(\mu_{d,i}) = N_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \log(H_{d,i})$	4694	5196	6928	2986	4718
Cubic depth	$\log(\mu_{d,i}) = N_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \beta_3 D_{d,i}^3 + \log(H_{d,i})$	4693	5175	6909	2977	4711

$d$ , depth stratum;  $H$ , number of hooks;  $i$ , longline operation;  $D$ , depth (m);  $\log$ , natural logarithm;  $\beta$ , estimated parameter;  $\mu$ , mean catch;  $p$ , proportion of catch predicted for the stratum by Bigelow *et al.* (2002) for the habitat-based model or by Ward and Myers (2005) for the basin-wide model;  $N$ , log of local abundance.

\*Residual deviance, a measure of the amount of variation in mean catch that is not explained by the model.

†Akaike's information criterion, used for model selection (smaller is better).

**Figure 1.** Comparison of observed catch rates of bigeye tuna (circles are means, horizontal bars are 95% confidence intervals) and fitted values for each Poisson model (heavy lines connect means, light lines connect 95% confidence intervals). Fitted values for the null model (which assumes that catchability does not change with depth) are not constant because of random variations in the nominated local abundance.



however, the habitat model failed to provide useful predictions; it was worse than the null model, which assumed no change in catch with depth.

The basin-wide model used data from other fisheries and for Hawaii-based longliners operating outside the study area. Its estimates of depth distribution were better than those of the habitat-based model, suggesting that this statistical model may provide reliable predictions of bigeye tuna distribution outside the model's data range. The very good fit of the basin-wide model (Fig. 1c) suggests that the depth-dependent catchability may be similar on average over a wide region.

There are four possible explanations of the poor fit of the habitat-based model. First, there is uncertainty in calibrating the model with hook depths. Habitat models use habitat preferences and environmental data that have accurate depth estimates. However, they must be matched to hook depths, which are known to vary with ocean currents and wind (Bigelow *et al.*, 2002). Bigelow *et al.* used a method to adjust for the effects of currents on longline depth that was more sophisticated than our method. However, quite extreme – and unreasonable – estimates of depth would be required to force the observed depth distribution to match that of the habitat-based model.

Secondly, the environmental conditions used in habitat models were estimated on a scale that might not be relevant to bigeye tuna. Temperatures were predicted from a circulation model for each stratum. Oxygen concentrations were monthly averages for each 40-m depth – latitude–longitude – month stratum for all years combined during 1934–94. However, the temperatures and oxygen concentrations that bigeye tuna respond to would have varied significantly over much smaller spatial and temporal scales (Phillander, 1990).

Thirdly, information on habitat preferences derived from tracking studies might not be representative of the bigeye tuna taken by longline in our study area. Temperature preferences were derived from four bigeye tuna released off French Polynesia and tracked for a total of 53 h (Dagorn *et al.*, 2000) and 11 bigeye tuna near Hawaii at liberty for a total of 934 days (Musyl *et al.*, 2003). Thirteen of those 15 bigeye tuna were smaller than the mean size taken by longliners in our study area (46 kg) and nine were below the fifth percentile (11 kg). Dagorn *et al.* (2000) found that the vertical movement patterns of small bigeye tuna were distinct from those of large individuals.

Note that Bigelow *et al.* (2002) considered ten depth distributions that they generated from different hypotheses about the depth distribution of bigeye

tuna in relation to temperature levels and oxygen concentrations. Our analyses use only one of those distributions, which was the distribution preferred by Bigelow *et al.* and used in the 2003 stock assessment of bigeye tuna in the Pacific Ocean. Subsequent assessments have used statistical habitat models that include more information on depth distributions in relation to environmental determinants.

The fourth possible explanation of the habitat model's poor fit is that the distribution predicted by habitat models might not match the species' vulnerability to longline gear. Using simulations, Goodyear (2003) found that the propensity of blue marlin (*Makaira nigricans*) to take longline baits and the actual depths reached by the hooks biased abundance estimates derived from habitat models. Blue marlin and other species like bigeye tuna may be present at shallow depths during the day but not caught there because they are not feeding. Statistical habitat models, which combine observed and predicted catch distributions (e.g. Hinton and Maunder, 2003), might help to overcome this problem. However, considerable research is required to address the other problems that we have identified.

The status of the world's pelagic fishes is of considerable concern and controversy. The adjusted abundance indices produced by the habitat model indicate substantial reductions in the population size of bigeye tuna. However, our analyses show significant discrepancies between observed distributions and the model's predictions. The status of bigeye tuna may be quite different than that indicated by habitat models if our conclusions are valid for the wider Pacific Ocean over the period of exploitation.

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## REFERENCES

- Behringer, D.W., Ji, M. and Leetmaa, A. (1998) An improved couple model for ENSO prediction and implications for ocean initializations. Part I: The ocean data assimilation system. *Mon. Wea. Rev.* **126**:1013–1021.
- 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.

- Dagorn, L., Bach, P. and Jossé, 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. (2003) Tests of the robustness of habitat-standardized abundance indices using simulated blue marlin catch-effort data. *Mar. Freshwat. Res.* **54**:369–381.
- Hinton, M.G. and Maunder, M.N. (2003) *Methods for Standardizing C<sub>pue</sub> and How to Select Among Them*. ICCAT Coll. Vol. Sci. Pap. SCRS/2003/034.
- Levitus, S. and Boyer, T. (1994) *World Ocean Atlas. 1994, Vol. 2: Oxygen*. NOAA Atlas, NESDIS 2. Washington, DC: U.S. Government Printing Office, 186 pp.
- Murphy, G.I. 1960. Estimating abundance from longline catches. *J. Fish. Res. Board Can.* **17**:33–40.
- 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.
- Philander, S.G. (1990) *El Niño, La Niña, and the Southern Oscillation*. San Diego: Academic Press, 293 pp.
- Suzuki, Z., Warashina, Y. and Kishida, M. (1977) The comparison of catches by regular and deep tuna longline gears in the western and central equatorial Pacific. *Bull. Far Seas Fish. Res. Lab.* **15**:51–89.
- Venables, W.N. and Ripley, B.D. (1999) *Modern Applied Statistics with S-Plus*, 3rd edn. New York: Springer, 501 pp.
- Ward, P. and Myers, R.A. (2005) A method for 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.
- Yoshihara, T. (1954) Distribution of catch of tuna longline. IV – On the relation between  $k$  and  $f$  with a table and diagram. *Bull. Jpn Soc. sci. Fish* **19**:1012–1014.