SCTB13 Working Paper

BET-1

Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*)

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Introduction

Bigeye tuna (*Thunnus obesus*) is the main target species of the longline fishery in the tropical and sub-tropical Pacific Ocean, with catches of 90,000–165,000 t since 1980 (Hampton et al. 1999). Stock assessments have been conducted using indices of abundance, non-equilibrium production models, cohort analysis and yield-per-recruit analysis (Hampton et al. 1998; Miyabe 1995; IATTC 1999). Central to each method has been the use of longline fishery catch and effort statistics to construct indices of bigeye tuna abundance based on catch-per-unit-effort (CPUE).

The effectiveness of longline effort with respect to bigeye tuna catch is strongly affected by the fishing depth of the gear (Hanamoto, 1987; Boggs, 1992), with gear fishing deeper in the water column generally more effective in targeting bigeye tuna. This is thought to be due to a preference of bigeye tuna for temperatures cooler than those of the upper mixed layer (Hanamoto, 1987; Holland et al., 1990; Boggs, 1992; Brill, 1994). Since the mid-1970s, longliners began to change their setting methods from mainly ‘conventional’ sets (5–6 hooks between mainline floats) fishing a depth range of approximately 90–150 m, to ‘deep’ sets (>10 hooks between floats) fishing a depth range of approximately 100–250 m (Suzuki et al., 1977; Hanamoto, 1987). This is likely to have increased the effectiveness of longline gear in targeting bigeye tuna, with possibly greater efficiency gains in the western and central Pacific Ocean (WCPO), where the optimum temperature range of bigeye tuna is deeper than in the eastern Pacific Ocean (EPO). Also, the concentration of dissolved oxygen (DO) that limits bigeye tuna vertical distribution may be sufficiently shallow in some areas to impact the effectiveness of longline fishing.

For longline CPUE to be an unbiased estimator of bigeye tuna relative abundance, variation in the fishing depth of longlines and variation in the depth of preferred bigeye tuna habitat need to be accounted for. Hinton and Nakano (1996) presented a method of estimating effective longline effort using information on habitat preferences and constraints, in combination with environmental data. In this paper, we apply a similar, habitat-based model to estimate effective longline effort and catch-per-unit-of-effective-effort (CPEE) of Pacific bigeye tuna. The essential elements of the model are: (i) for small time and area strata, the vertical distribution of bigeye tuna is estimated by coupling general habitat (temperature and oxygen) requirements ascertained from archival tag and acoustic tracking information with oceanographic data for the strata; (ii) using information on longline gear depth, the numbers of longline hooks weighted by the relative vertical distribution of bigeye tuna (effective effort) are computed; and (iii) catch and effective effort are aggregated over appropriate spatial zones to produce time series of overall CPEE. We tested the sensitivity of our habitat assumptions using Monte Carlo simulations.

Methods

Effective fishing effort

We define effective fishing effort (f) in a particular area (indexed by a) and time (indexed by t) stratum as the weighted sum of longline hooks (E) fishing in different depth zones (indexed by d) throughout the bigeye tuna vertical habitat:

$$f_{at} = E_{at} \sum_d h_{atd} p_{atd} \quad (1)$$

where h_{atd} is the proportion of hooks fishing in depth zone d in area a during time period t and p_{atd} is the proportion of bigeye tuna in area a during time period t occurring in depth zone d . In this analysis, we used 15 depth bins of 40 m in the range 0–600 m to define the vertical stratification. The fishery data analyzed were Japanese longline data for the Pacific Ocean for the period 1966–1996 stratified by 1°-square areas and by month. Longline vessels from other nations (e.g., Taiwan, Korea and the United States) have also operated in the Pacific Ocean for several decades. We chose to use the Japanese fleet for this analysis because (i) it has consistently targeted tuna over a large area of the Pacific Ocean, (ii) the data resolution is generally better than for the other fleets, (iii) effort by this fleet is by far the largest component of the longline fishery in the Pacific Ocean, and (iv) ancillary information on approximate fishing depth is available for the Japanese fleet (see below).

The key elements in the estimation of effective longline effort are the specification of the depth distribution of the gear (h_{atd}) and the depth distribution of bigeye tuna (p_{atd}). These aspects of the analysis are discussed in the following two sections.

Depth distribution of longline gear

Predicting depth distribution from gear configuration

The depth at which longline gear fishes is known to be influenced by the set configuration, such as floatline and branchline lengths, distance between branchlines, sagging rate of the mainline (Figure 1) and a variety of environmental factors, particularly wind and currents (Suzuki et al., 1977; Boggs, 1992). The depth of the longline is typically altered by varying the length of mainline between floats and the sagging rate of the mainline (ratio of horizontal distance between two floats and the stretched length of mainline between two floats, Suzuki et al., 1977). While actual fishing depth has been measured in several studies with time-depth-recorders (TDRs, Boggs, 1992; Uozumi and Okamoto 1997), fishing depth measurements are rarely available from commercial longline sets. However, the number of hooks between adjacent mainline floats

Figure 1. Configuration of a pelagic longline.

(HBF), which is routinely recorded on Japanese longline logbooks, can be used along with other information on set configuration to estimate the approximate depth distribution of longline hooks using catenary geometry (Suzuki et al., 1977):

$$D_j = h_a + h_b + L \left\{ \left(1 + \cot^2 \phi \right)^{1/2} - \left[\left(1 - 2 \frac{j}{N} \right)^2 + \cot^2 \phi \right]^{1/2} \right\} \quad (2)$$

where D_j is the depth of j -th hook,
 h_a is length of branch line,
 h_b is length of float line,
 L is half of the length of the mainline between two floats,
 N is HBF+1
 j is the j -th branch line from the float line, and
 ϕ is the angle between the horizontal and tangential line of the mainline.

The catenary parameters ($h_a=26.3$ m, $h_b=19.4$ m, $L=(50 \text{ m}) \cdot (\text{HBF}+1)$, $\phi=60^\circ$) were estimated from data collected by at-sea observers deployed on Japanese vessels (212 longline sets) in the 1990s (unpublished observer data, SPC, BP D5 98848, Noumea Cedex, New Caledonia). Thus, it is possible, using equation (2) to estimate the depth distribution of longline hooks for various HBF categories.

From 1966 to 1996, gear configuration in the Japanese longline fishery ranged from 3 to 22 HBF. Targeting yellowfin or bigeye tuna is characterized by daytime fishing at moderate (100–250 m) to deep depths (100–400 m) with gear of 5 HBF or greater. Data corresponding to 3–4 HBF were deleted prior to analysis because these shallow gear types are used mainly to target swordfish at night. For the purpose of determining approximate hook depth distributions, the remaining HBF information was aggregated into 6 categories: 5–6 HBF (regular gear), 7–9 HBF (intermediate gear), and 10–11, 12–15, 16–20 and 21–22 HBF (deep gear).

Between-set and within-set variability

The catenary estimation results in a single depth estimate for each longline hook; however, actual hook depths vary both between and within longline sets. We characterized between-set hook-depth variability for each HBF value by randomly generating 1000 values of ϕ from a normal distribution ($\mu = 60^\circ$, $\sigma = 11.3^\circ$, unpublished data, SPC) and computing D_j for each.

Within-set variability in longline fishing depth has been estimated using TDR data (Boggs, 1992; Yano and Abe, 1996). The deepest hook on a longline set has the greatest variation – Boggs (1992) observed a 30% variation in settled depth on a set deployed to >300 m. Similarly, Yano and Abe (1996) found a linear increase in depth fluctuation as hooks were deployed deeper. Based on data from Yano and Abe (1996), the relationship between the standard deviation of hook depth D_j and hook number j (the hooks closest to the floats are numbered 1) is ($r^2=0.64$):

$$\sigma(D_j) = 8.73 + 4.4j. \quad (3)$$

Within-set variability in D_j was characterized by generating 500 random samples of hook depth from normal distributions of mean D_j and standard deviation $\sigma(D_j)$ for each of the 1000 estimates of D_j obtained previously, thereby producing 500,000 estimates of D_j for each HBF

value of 5 through 22. Aggregate hook-depth distributions (40 m depth bins) corresponding to the six HBF categories were produced by aggregating the individual hook distributions (Figure 2).

Effect of currents

Boggs (1992) observed that hook depths were usually shallower (54–68%) than those predicted from catenary geometry especially in deep sets (>300 m). Reasons for shallow set depths include wind and currents, with current shear between the surface and thermocline being of paramount importance. Although it seems certain that wind and currents shoal longline gear, there is a paucity of published quantitative information available on this effect. However, some studies (Uozumi and Okamoto 1997) allow an estimation for a relationship between longline shoaling and surface current velocities of 0 – 60 cm sec⁻¹:

$$S = 0.95V \quad (4)$$

where S is the shoaling percentage and V is the current velocity in cm sec⁻¹.

A time-series (1980–1996) of oceanic currents was obtained from an Ocean Global Circulation Model (OGCM) developed at the National Center for Environmental Prediction (NCEP, Behringer et al., 1998). The model has 27 vertical layers (0–3000 m) and a spatio-temporal resolution of 1.5° and one month. Data for each layer were aggregated by quarter and re-gridded to 1° to correspond with the fishery data. The initial 8 layers (0–80 m) of the model were averaged to provide current velocity in the upper ocean. Prior to 1980, the OGCM was used to

Figure 2. Probability distribution of hook depth in six gear configurations within the Japanese tuna longline fishery. HBF=hooks between floats.

make an average quarterly climatological series. The generic distributions of hook depths for each HBF category shown in Fig. 2 were adjusted for each area-time stratum in the model by the following function:

$$\mathbf{D}' = \frac{S}{1 + \exp[a(\mathbf{D} - D_{0.5})]} \quad (5)$$

where $\mathbf{D}'$ is the depth distribution after adjustment for current velocity, a is a parameter defining the slope of the function, $\mathbf{D}$ is the depth distribution prior to adjustment, and $D_{0.5}$ is depth at the inflexion of the hook depth distribution. A value of -0.025 was chosen for the curvature parameter a to provide realistic results. The shoaling of longline gear was most evident from 10°S to 15°N in the area of equatorial currents and countercurrents. The application of the methodology described above produced estimates of h_{atd} that incorporated the combined effects of longline set configuration, between-set and within-set variability in hook depth distribution, and the shoaling effects of ocean currents on hook depth distribution.

Bigeye tuna habitat preferences as determinants of depth distribution

Unlike some other species of tuna and billfish (Brill et al., 1999; Block et al., 1992; Brill et al., 1993), the depth distribution of bigeye tuna appears to be related to ambient temperature preference (rather than a sea surface – ambient temperature differential) and minimum dissolved oxygen (ml l^{-1}) requirements. Therefore, a major difference in our application of the habitat-based model is that bigeye depth distribution is based on ambient temperature, rather than previous applications that distributed blue marlin (Hinton and Nakano, 1996) and swordfish (Hinton and Deriso, 1998) populations at temperatures relative to the mixed layer. Bigeye tuna temperature preferences were inferred from the results of archival (electronic data recording) tag and acoustic tracking studies on fish >30 kg which are equivalent to the size of longline-caught bigeye tuna (Dagorn et al., 2000, Boggs et al., In Review).

Both daytime and nighttime temperature distributions (Figure 3) were used to formulate temperature preference hypotheses. Japanese tuna longline gear is typically deployed in the early morning, allowed to soak for 8–10 hrs and retrieved throughout the afternoon and evening. Observer data (219 longline sets) indicates that 75% of soak time occurs during the day and 25% at night. Therefore, the bigeye tuna temperature preference distributions for day and night were combined using 0.75 and 0.25 as weighting factors for day and night respectively, to obtain an

Figure 3. Time-at-temperature histograms for adult bigeye tuna during day (A) and night (B). Data from Hawaii (Boggs et al., In review) and Tahiti (Dagorn et al., 2000).

Figure 4. Probability distribution of temperature (A) and oxygen (B) assumptions for Monte Carlo simulation. Line with circles indicates the initial hypothesis.

initial overall temperature preference distribution (expressed on a scale of 0–1, Figure 4A).

Physiological experiments, longline monitoring and tracking studies provide information on bigeye tuna DO preferences. Physiological observations indicate bigeye tuna cardiac performance is reduced at DO concentrations $<2.1 \text{ ml l}^{-1}$ (Bushnell et al., 1990), consistent with longline monitoring studies that concluded that adult bigeye are rarely caught in water with DO ranging from $1.0\text{--}1.4 \text{ ml l}^{-1}$ (Hanamoto, 1987; Boggs, 1992). In the tropical and subtropical western and central Pacific, DO concentrations are high over most of the temperature range preferred by bigeye tuna; therefore DO is unlikely to limit vertical distribution in this region. In contrast, DO concentration in the EPO is much lower at a given depth than in the WCPO. As an initial preference hypothesis, a DO index (again on a scale of 0–1) was constructed in which the bigeye tuna population is not limited at $\text{DO} > 2.25 \text{ ml l}^{-1}$, declines linearly from 2.25 to 0.75 ml l^{-1} and is zero at $<0.75 \text{ ml l}^{-1}$ (Figure 4B).

Bigeye tuna habitat quality was defined as the product of the scaled temperature and DO indices. Values of this combined index, normalized to sum to 1 across the fifteen 40 m depth layers, was used to specify p_{atd} , the relative vertical distribution of bigeye tuna at each area-time stratum (one degree square, quarter). A time-series of temperature data obtained from the aforementioned OGCM (with pre-1980 represented by a quarterly climatology) was used to generate the temperature indices. There is good correspondence between independent temperature-at-depth measurements (mooring records) and OGCM output for the 20°C isotherm at three locations (165°E , 140°W , 110°W) along the equator (Ji and Smith, 1995).

Dissolved oxygen profile data were obtained from a World Ocean Atlas climatological database (Levitus and Boyer, 1994). These data summarize the spatial and seasonal variability of DO at depth averaged over a long period of time (1934–1994). Ultimately, it would be preferable to use time-specific data to account for inter-annual variability in DO, but such data are not currently available at the spatial and temporal coverage required for this analysis.

Computing aggregate effective effort and relative abundance

The estimates of h_{atd} and p_{atd} , obtained as described above, allow the estimation of effective effort from nominal effort using equation (1). CPEE, or relative abundance, may then be

determined at one-degree quarter resolution simply by C_{at}/f_{at} , where C_{at} is the catch (in number of bigeye tuna) in one-degree square a during quarter t .

For stock assessment purposes, it may be useful to aggregate f_{at} and C_{at} into larger area and time strata according to the requirements of the assessment. We aggregated effective effort and CPEE observations into years and according to two area aggregation schemes: (1) the WCPO and EPO separated at 150°W longitude (an informal boundary currently used for tuna stock assessment in the Pacific) and (2) eight bio-ecological provinces (Figure 5), based on primary productivity regimes (Longhurst et al., 1995). CPEE values occurring in a particular year and geographical region can be weighted by area (geographical size of a 1° cell) or fishing effort (Hinton and Nakano, 1996). We present results based on the median values of area-weighted cells, although similar results were obtained using an effort-weighted scheme. Implicit in either case is the assumption that the observations randomly sample relative abundance within that region and year.

Figure 5. Bio-ecological provinces used to spatially aggregate longline effort and relative abundance indices (after Longhurst 1995). NPST – west – North Pacific Subtropical Gyre (west), NPST – east – North Pacific Subtropical Gyre (east), NPTG – North Pacific Tropical Gyre, WARM – Western Pacific Warm Pool, PNEC – North Pacific Equatorial Countercurrent, PEQD – Pacific Equatorial Divergence, ARCH – Western Pacific Archipelagic Deep Basins, SPSG – South Pacific Subtropical Gyre.

Sensitivity analysis

Monte Carlo simulations were used to assess the impact of uncertainty in our habitat assumptions on estimates of effective effort and relative abundance. Ten alternative hypotheses were generated for both temperature and oxygen preferences based on our interpretation of their uncertainty (Figure 4, Table 1). Estimation of effective effort and relative abundance was repeated 1000 times, in each case randomly selecting from the ten temperature-preference and ten DO-preference hypotheses with equal likelihood. Uncertainty in relative abundance was represented by plotting the 2.5, 50 and 97.5 percentiles of the Monte Carlo replicates. The long-

term mean of the Monte Carlo trials was normalized to a value 1.0 to facilitate comparison with nominal estimates.

Table 1. Bigeye tuna temperature hypotheses used in Monte Carlo simulations. Hypotheses are based on archival tag data from Hawaii (Boggs et al. In Review) and acoustical tagging in Tahiti (Dagorn et al. 2000).

Hypothesis	Assumption
1-Hawaii	100% day + 25% night
2-Hawaii	100% day + 10% night
3-Hawaii	100% day + 40% night
4-Hawaii	100% day
5-Hawaii	100% day + 2°C
6-Hawaii	100% day with no feeding at warm temperatures
7-Tahiti	100% day + 10% night
8-Tahiti	100% day + 25% night
9-Tahiti	100% day + 40% night
10-Tahiti	100% day

Results and discussion

Modeled population distribution

Vertical profiles on two meridional sections (at 160°E and 120°W) of temperature habitat quality, DO habitat quality, combined temperature-DO habitat quality and p_{atd} are depicted in Figure 6 for the initial temperature and oxygen hypotheses. The distribution of habitat preferences agrees well with a previous fisheries oceanography study (Hanamoto, 1987). Optimum temperature is at >400 m in the western Pacific mid-latitudes (160°E section). Near the equator, optimum temperatures are found at 250–400 m. Optimum temperature is shallower in the EPO (120°W section) where it reaches to 100 m depth north of the equator. The favorable temperature at shallow depths in both sections indicates the mix of daytime (deeper, colder) and nighttime (shallower, warmer) distributions used in the analysis. Along 160°E, DO is limiting at depths >200 m at 5°N–15°N. Along 120°W, DO is limiting at depths as shallow as 100 m in tropical waters north of the equator. The combination of temperature and DO preferences indicates that good habitat is generally >300 m in the WCPO, except around the equator where it is 200–300 m. In the EPO, good habitat occurs at 100–200 m just south of the equator, and at increasing depths further to the south. North of about 5°N, the temperature-DO habitat is poor at all depths because the temperature is too warm in the top 100 m (with the exception of the narrow band representing nighttime temperature distribution) and too DO-deficient deeper than 100 m. The zonal section (at 10°N) suggests that the best bigeye tuna habitat occurs at 300–500 m in the region 150°E–180°. Moving east, bigeye habitat is progressively confined to the upper layers because of shallower DO-deficient water.

The percentage of the bigeye population in the upper 300 m, as inferred from the p_{atd} estimates, is illustrated for the entire Pacific Ocean in Figure 7. In the WCPO, the population is shallow in lower latitudes $\sim 10^\circ\text{N}$, gradually deepens at mid-latitudes and shallows again at high ($\sim 40^\circ$) latitudes. In the EPO, the predicted population is shallower than the WCPO and has little variability with latitude. Histograms of population proportions were estimated for three layers (0–200, 0–300 and 0–400 m) in the tropical WCPO (23°S – 23°N , 120°E – 150°W) and EPO (23°S – 23°N , 70° – 150°W) from the Monte Carlo simulations (Figure 8). The model predicts that the bigeye population will be distributed much deeper in the WCPO than in the EPO.

Figure 6. Meridional (160°E and 120°W) and zonal section (10°N) of bigeye tuna habitat indices for temperature, oxygen, combined temperature and oxygen and normalized habitat quality (p_{jky}). Habitat indices follow initial temperature and oxygen hypotheses in Figure 4.

Figure 7. Percentage of bigeye population from 0 to 300 m inferred from the habitat-based model. Bigeye distributed according to initial temperature and oxygen hypotheses in Figure 4.

Figure 8. Histogram of population proportions for 0–200, 0–300 and 0–400 m in the tropical western and central Pacific and eastern Pacific Ocean based on 1000 Monte Carlo simulations.

Effective effort

Trends in effective effort have increased in both the WCPO and EPO (Figure 9). In the WCPO, effective effort increased 43% from the late 1960s to the late 1980s. Over the same period, effective effort increased 250% in the EPO. Effective effort has declined in the EPO since the early 1990s due to vessels leaving the fishery. Effective effort as a percentage of nominal effort increased ~50% in the WCPO over the time-series (Figure 9). In contrast, effective effort as a percentage of nominal effort in the EPO has remained stable. Nominal effort in the WCPO has declined since the 1960s; however, effective effort actually increased due to greater targeting of the bigeye habitat. There was a steady increase in nominal effort within the EPO until the early 1990s.

Throughout the time-series there was an increase in effective effort in four of the bio-ecological provinces and stability in the remaining four provinces (Figure 10). Annual estimates of effective effort were highest for the equatorial provinces (PNEL & PEQD), moderate for the warm pool and tropical and subtropical gyres in the north Pacific (WARM, NPTG & NPST-east) and lowest in the western subtropical gyres in the western north Pacific and subtropical south Pacific (NPST-west, ARCH, SPSG). The greatest effective effort is expended in the Pacific Equatorial Divergence (PEQD), a traditional fishing ground for the Japanese longline fleet. Effective effort in this province increased five-fold between the late 1960s and early 1990s. Gear modifications in four provinces (NPST-west, NPST-east, NPTG and WARM) indicated that the longline was more efficient in the bigeye habitat after 1980.

Figure 9. Annual effective longline effort (shaded area is 95% confidence band) and effective effort as a percentage of total nominal effort (line with circles) in the bigeye tuna habitat for the western and central Pacific Ocean (A) and eastern Pacific Ocean (B).

Relative abundance

The north Pacific shows the greatest temporal changes with a substantial CPEE reduction in the subtropical (18°-32°N) area during the 1980-90s. The subtropical south Pacific does not show a similar decline, but the interpretation is complicated because the Japanese fleet has not actively fished this area due to limited fishing access arrangements and presumably because of the thermal profile, whereby bigeye are more difficult to catch.

Trends in CPEE differed from nominal CPUE for the WCPO, but were similar for the EPO (Figure 11). The 95% confidence intervals are wider for the WCPO. For the WCPO, median annual CPEE from the simulations declined continuously since 1978 (Figure 11). The divergence

Figure 10. Annual effective longline effort (shaded area is 95% confidence bands) and effective effort as a percentage of total nominal effort (line with circles) in the bigeye tuna habitat in the eight bio-ecological provinces in the Pacific Ocean.

between CPEE and nominal CPUE in the WCPO results from progressive changes in longline setting behavior (deeper sets) of the Japanese fleet, which resulted in longline effort becoming more efficient in the WCPO because of better targeting of optimal bigeye habitat. For the EPO, both nominal and standardized indices show similar trends – a decline during the 1960s, a period of stability in the 1970s, high values during 1985 and 1986 and a decline thereafter. The similarity between indices in the EPO results from at least two factors. First, DO is the predominant factor determining the effectiveness of longline effort in the EPO. Therefore, a shallower optimal temperature layer in the EPO would mean that the change from conventional to deeper longline sets would have had a smaller relative impact on effort efficiency in the EPO compared to the WCPO. Secondly, given the shallower optimal habitat for bigeye in the EPO, there has not been as dramatic a change to deeper sets as in the WCPO.

Stratification by the bio-ecological provinces may be preferable to a simple east-west stratification as it may better characterize large-scale spatial variation in bigeye tuna abundance. Of the eight provinces, nominal CPUE was stable in six and declined in two (Figure 12). In comparison, CPEE declined in four and was stable in four. Within the subtropical gyres of each hemisphere (NPST-east & SPSG), the decline in CPEE from the 1970s to the 1990s was more precipitous (~70%) than nominal CPUE (~50%). There was no apparent decline in CPEE in the subtropical gyre in the western north Pacific (NPST-west) or the western Pacific archipelagic basin (ARCH); however these regions have the lowest catch rates of the eight provinces. Nominal CPUE was stable in the north Pacific tropical gyre (NPTG) and western Pacific warm pool (WARM); however, CPEE declined at a rate similar to the subtropical gyres (~70%). The two provinces in the equatorial central and western Pacific (PNEL & PEQD) had high CPUE in the 1980s, though values in the 1990s were below average levels for the entire time-series.

Figure 11. Annual nominal CPUE (line with circles) and relative abundance (CPEE) estimates for bigeye tuna in the WCPO (A) and EPO (B). Monte Carlo simulations show the CPEE median for each year and 95% confidence intervals (shaded area). Time-series of CPEE is

Conclusion

The application of habitat-based models to the estimation of effective fishing effort and relative abundance involves several assumptions. The most critical of these is that the tagging (archival and acoustic) and physiological data adequately characterize the adult bigeye habitat. Monte Carlo simulation quantified the model outputs given the effects of uncertainty in habitat assumptions, though the inputs were based on few observations. By using a variety of habitat assumptions, one can assess how these uncertainties progress through the model and affect trends in relative abundance. Within the model, habitat assumptions and associated oceanographic data

specify the bigeye tuna vertical distribution. This underscores the value of physiological, behavioural, and environmental data in interpreting longline fishery catch and effort. We framed our bigeye tuna temperature preference hypothesis on the basis of archival or acoustic tracking studies from three geographical areas in the Pacific, but additional data are needed to adequately characterize behavioral variability related to the environment, fish size and other factors.

The current application of the model is based on a longline fishery operating mainly during the daytime. The model could be applied to other fleets which conduct night longline fishing, such as the Hawaii-based longline fleet and the mainland Chinese fleet operating in Micronesia. The probability distributions on the habitat assumptions would need to be altered to reflect the nighttime behavior of bigeye.

If our estimates of CPEE accurately reflect relative abundance, then we have observed substantial reductions of bigeye tuna abundance in some regions in the Pacific, while other regions remain stable. Despite a concentration of effective longline effort in the Pacific equatorial divergence (PEQD), both nominal CPUE and CPEE declined by only 25%, suggesting that fishing performance has been maintained while fishing effort dramatically increased. In contrast, CPEE has declined severely in other areas (WARM, NPTG & NPST-east), with modest increases in effective effort. The CPEE reduction in the subtropics concurrent with stability in equatorial areas may represent a contraction in the range of the population resulting from a decline in population abundance.

Several species groups (e.g. fish, birds, insects, and mammals) have shown differential habitat utilization given changes in abundance. MacCall (1990) reviewed the concept of “density-dependent habitat selection”, in which population size is an important factor that influences the choice of ecological habitat or the relative distribution of the population. Population expansion or contraction can depend on population size. Population contractions usually occur at the frontiers of the population, which for bigeye tuna would be high latitude areas such as the subtropical gyres. Similar to skipjack and yellowfin tunas, the center of the bigeye tuna population may reside in equatorial waters where local density can be maintained (PNEL & PEQD) despite contractions or expansions in other habitats.

In conclusion, the use of effective, rather than nominal, effort for longline fisheries should provide better information on changes in abundance. In the present model, effective effort accounted for changes fishing depth through the effects of targeting and current velocity, and variability in bigeye tuna habitat, as reflected by temperature and DO concentrations. Habitat variability on seasonal, inter-annual (e.g. *El Niño* Southern Oscillation) and possibly longer time scales was accounted for in the model. The model suggests that a large portion of the adult bigeye population is not amenable to capture in some areas of the Pacific (tropical and subtropical gyres) because they are distributed deeper than the exploitation capability of most longline gear.

Figure 12. Annual nominal CPUE (line with circles) and relative abundance (CPEE) estimates for bigeye tuna in eight bio-ecological provinces in the Pacific Ocean. Monte Carlo simulations show the CPEE median for each year and 95% confidence intervals (shaded area). Time-series of CPEE is normalized to a value of 1.0.

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