Influence of oceanographic variability on recruitment of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean

Adam Langley, Karine Briand, David Seán Kirby, and Raghu Murtugudde

Abstract: Recruitment estimates for yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean (WCPO), derived from a stock assessment model, are highly variable seasonally, interannually, and over decadal periods. A generalized linear model (GLM) was developed that predicts the variation in yellowfin tuna recruitment in response to a range of oceanographic variables. The GLM model accounted for 54% of the variation in quarterly recruitment for the period 1980–2003, with the inclusion of seven different oceanographic variables derived from a zone within the northwestern equatorial region of the WCPO. The robustness of the recruitment model was investigated by cross-validation. The GLM was complemented by a cluster analysis approach that identified five principal oceanographic states within the northwestern zone selected by the GLM. Incorporation of the recent GLM recruitment indices in the yellowfin tuna stock assessment model is likely to improve the precision of estimates of current and projected (next 1–2 years) biomass and exploitation rates. In a broader context, the recruitment model provides a tool to investigate how yellowfin tuna recruitment might vary in response to short- and long-term variation in the oceanographic conditions of the WCPO.

Résumé : Les estimations du recrutement de l'albacore à nageoires jaunes (*Thunnus albacares*) dans l'ouest et le centre du Pacifique (WCPO), obtenues à l'aide d'un modèle d'évaluation des stocks, varient fortement en fonction de la saison et de l'année et au cours des différentes décennies. Nous mettons au point un modèle linéaire généralisé (GLM) qui prédit la variation du recrutement de l'albacore à nageoires jaunes en réaction à une gamme de variables océanographiques. Le modèle GLM explique 54 % de la variation trimestrielle du recrutement pour la période 1980–2003 avec l'inclusion de sept variables océanographiques différentes mesurées dans une zone du nord-ouest de la région équatoriale de WCPO. Nous avons étudié la robustesse du modèle de recrutement par validation croisée. Le GLM est complété par une méthode d'analyse de groupement qui identifie cinq états océanographiques principaux dans la zone du nord-ouest retenue par le GLM. L'incorporation des indices récents de recrutement provenant du GLM dans le modèle d'évaluation des stocks des albacores à nageoires jaunes va vraisemblablement améliorer la précision des estimations de la biomasse et des taux d'exploitation courants et projetés (sur les prochaines 1–2 années). Dans un contexte élargi, le modèle fournit un outil pour déterminer de quelle manière le recrutement de l'albacore à nageoires jaunes peut changer en réaction aux variations à court et à long termes des conditions océanographiques de WCPO.

[Traduit par la Rédaction]

Introduction

Yellowfin tuna (*Thunnus albacares*) is a dominant pelagic species in equatorial waters of the world's oceans. The species is principally distributed in the epipelagic zone in areas where sea surface temperature exceeds 26 °C, with the distribution centered on tropical waters and extending to temperate waters (Suzuki et al. 1978; Maury et al. 2001). Yellowfin tuna are multiple spawners, and a reproductive behaviour appears to be related to water temperature, with the onset of spawning triggered above 24–26 °C (Ueyanagi 1969; Suzuki 1994; Wild 1994).

Yellowfin tuna in the western and central tropical Pacific Ocean (WCPO) support a large fishery that yields an annual catch of ~400 000 tonnes (Fig. 1*a*; Langley et al. 2006). Historically, yellowfin tuna were principally caught by domestic and distant-water longline vessels. Since the early 1980s, the fishery has become increasingly dominated by the purse seine method and small-scale domestic fisheries operating within the national waters of Indonesia and the Philippines (Langley et al. 2006).

In the WCPO, most of the yellowfin tuna catch is taken within the western Pacific warm pool (Fig. 1*a*), a relatively deep (~150 m depth) surface layer of warm (>28 °C) water usually confined to the western side of the ocean basin (Fig. 1*b*). The warm pool is formed by converging upper ocean currents (Fig. 1*c*) forced by the northeast trade winds in the Northern Hemisphere and the southeast trade winds in the Southern Hemisphere (McPhaden and Picaut 1990). Variability in the spatial extent of the warm pool on interannual time scales is described by the El Niño – Southern Oscillation (ENSO), with the warm pool extending into the eastern

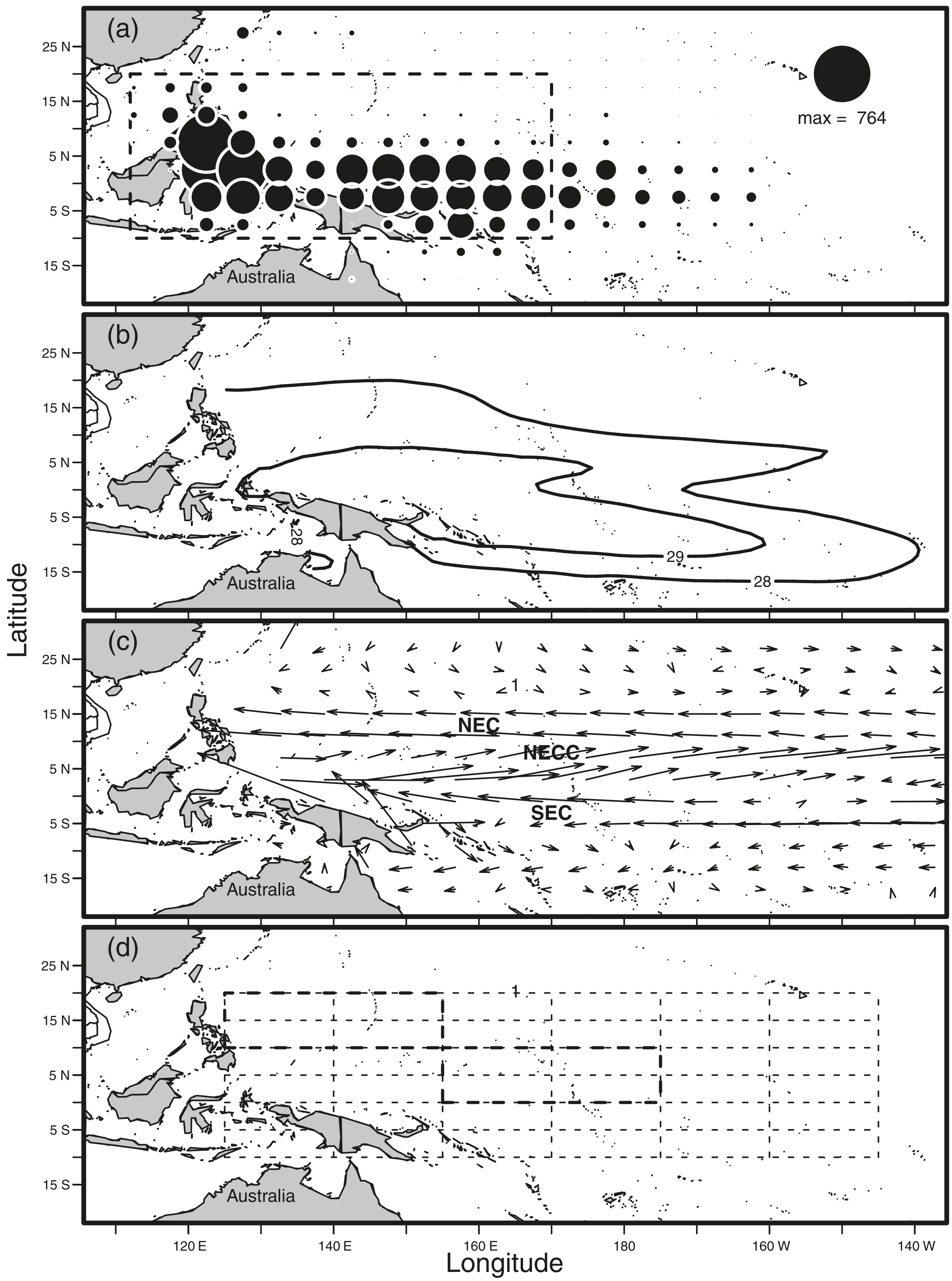
Received 10 September 2008. Accepted 30 March 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 25 August 2009.
J20769

Paper handled by Associate Editor Ray Hilborn.

A. Langley,[1] K. Briand, and D.S. Kirby. Oceanic Fisheries Programme, Secretariat of the Pacific Community, BP D5, 98848 Nouméa, New Caledonia.
R. Murtugudde. Earth System Science Interdisciplinary Center, University of Maryland, College Park, MD 20742-2465, USA.

[1]Corresponding author (e-mail: adam_langley@xtra.co.nz).

Fig. 1. Spatial distribution of (*a*) yellowfin tuna (*Thunnus albacares*) catch in the western and central Pacific Ocean (WCPO), (*b*) average sea surface temperature (SST), (*c*) average current flow, and (*d*) spatial stratification used in the generalized linear model (GLM) model. Yellowfin tuna catch is aggregated for 1980–2003; catches are in 10^3 tonnes. The broken line in panel (*a*) represents spatial domain of MULTIFAN-CL (MFCL) stock assessment model. SST and current are averaged over 1980–2003: SST is represented by 28 and 29 °C isotherms; current is represented by vectors. Major currents are labeled: NEC, North Equatorial Current; NECC, North Equatorial Counter-Current; SEC, South Equatorial Current. Panel (*d*) presents the finest scale spatial resolution used to aggregate oceanographic data (small boxes) and the larger area used in the final GLM (bold broken lines).



Pacific during the El Niño phase and contracting back to the western Pacific during La Niña (Picaut et al. 1996 and 2001). The longitudinal distribution of the equatorial tuna purse seine fishery also follows this pattern (Lehodey et al. 1997).

Variability of the pelagic environment at seasonal to decadal scales is likely to contribute directly to the observed variation in yellowfin tuna recruitment. The availability of oceanographic data at appropriate spatial and temporal resolution provides the opportunity to identify those variables that are most correlated with yellowfin tuna recruitment and, thereby, determine the relevance of oceanic variability to tuna recruitment at different spatio-temporal scales.

There are no direct measurements of recruitment strength for yellowfin tuna. However, estimates of recruitment strength at quarterly or annual time intervals are available from assessment models for each of the main yellowfin tuna stocks: eastern Pacific Ocean (EPO) (Hoyle and Maunder 2006), WCPO (Langley et al. 2007), Atlantic Ocean (International Commission for the Conservation of Atlantic Tunas 2004), and Indian Ocean (Indian Ocean Tuna Commission 2006). The recruitment estimates are derived as parameter estimates from the statistical population models, which integrate the available biological and fisheries data, including catch, fishing effort, and the size composition of catch. For each of these stocks, recruitment is highly variable over short and long time periods, with models for some stocks (especially in the EPO) revealing decadal shifts in recruitment (Hoyle and Maunder 2006).

For the WCPO fishery, estimates of quarterly recruitment are considered to be more reliable from the early 1980s onwards (i.e., the period for which length frequency data is available from the fisheries that predominantly catch small yellowfin tuna). These data provide the stock assessment model with sufficient information to link the individual length modes to the respective quarter when spawning occurred via the estimated growth function. Conversely, quarterly recruitment estimates from the earlier period of the model (before 1980) are likely to be less precise. Size data for this period are only available from the longline fisheries, which predominantly catch large (adult) yellowfin tuna. The modal structure of these size data represents the amalgamation of many quarterly age classes, and consequently, the model has limited information with which to resolve individual age classes.

The apparent high variation in yellowfin tuna recruitment over the short- and long-term may provide sufficient contrast to link the trends in recruitment with key oceanographic indicators and, thereby, formulate a predictive model for yellowfin tuna recruitment in the WCPO. A predictive model for yellowfin tuna recruitment would have direct application in future stock assessments for yellowfin in the WCPO and the application of the assessment model in the provision of management advice.

As in most stock assessment models, the most recent estimates of recruitment are frequently the least precise, and consequently, there is a high level of uncertainty regarding current biomass levels and fishing mortality rates, particularly for those fisheries targeting smaller fish. Unfortunately, it is this information that is most crucial to fishery managers. A reliable, predictive model would considerably improve estimates of recent and current recruitment, thereby improving estimates of current biomass and increasing the accuracy of forward projections of the stock assessment model (see Langley et al. 2007).

A predictive model may also provide greater insights into trends in recruitment for the period predating the development of the fisheries whose catch is dominated by juvenile yellowfin tuna. This may assist in resolving whether historical trends in recruitment represent genuine phase changes in productivity of the stock or, rather, are due to a misspecification of the assessment model. Lastly, the development of such a predictive model may increase the understanding of the inherent relationship between yellowfin tuna recruitment and the environment and improve our ability to interpret future trends in recruitment from the stock.

Materials and methods

Overview

A series of "observed" recruitment values were derived from a stock assessment model that encompasses the core distribution of yellowfin tuna within the WCPO. Oceanographic data were obtained and configured in such a way that a generalized linear model (GLM) could be developed, relating oceanographic variability to yellowfin tuna recruitment for the period 1980–2003. This model was then hindcast to predict yellowfin tuna recruitment for the period 1948–2003. A cluster analysis was also applied to the oceanographic data set included in the GLM to discriminate the predominate categories of prevailing oceanographic conditions occurring in the study area.

Observed recruitment

The observed recruitment values for yellowfin tuna were estimated from a stock assessment conducted using MULTIFAN-CL (MFCL; Hampton and Fournier 2001). MFCL implements a statistical, size-based, age- and spatially structured model developed and used for stock assessments of Pacific tuna and other highly migratory fish species (www.multifan-cl.org). MFCL provides estimates of population parameters, including recruitment, biomass, and fishing mortality, based on observed size frequency, catch, effort, and tagging data from the fisheries. For this study, the MFCL model was configured for yellowfin tuna in a similar manner to the model formulated for the 2007 stock assessment of yellowfin in WCPO (Langley et al. 2007); however, the spatial extent of the current model was restricted to the main area of the yellowfin tuna fishery — the western equatorial region, which accounts for 80% of the total yellowfin tuna catch from the WCPO (see Fig. 1*a*) and approximately 65% of the total WCPO recruitment (Langley et al. 2007). The single region model is described in detail in Langley et al. (2007).

The population model incorporates catch, effort, and size (length and weight frequency) data from 10 fisheries: three longline fisheries, two purse seine fisheries (associated and unassociated set types), a distant-water pole-and-line fishery, the Philippine handline fishery, and the domestic fisheries in Indonesia and Philippines waters. More details on these fisheries and the associated data are given in Langley et al. (2007).

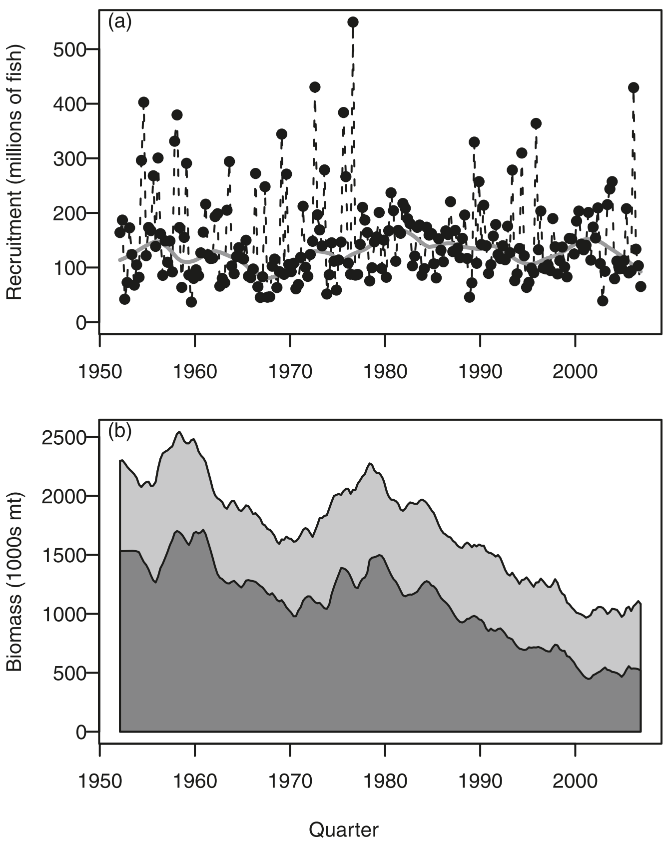
The model encompasses the 1952–2006 period, divided into quarterly time intervals. Recruitment estimates are derived for each quarter of the model period. The recruitment estimates are computed as deviates from the estimated

Table 1. Summary of oceanographic data, sources, and a description of composite variables used in the statistical approach.

Attribute	Description	Unit	Source
tempavg	Mean sea temperature within 0–100 m depth (for spatial–temporal stratum $z_{r,i}t_{j}$.)	°C	ESSIC
temprange	Range in sea temperature within 0–100 m depth	°C	
currentuavg	Mean zonal (E–W) current velocity within 0–100 m depth	m·s^{-1}	ESSIC
currentrange	Range in zonal current velocity within 0–100 m depth	m·s^{-1}	
currentvavg	Mean meridional (N–S) current velocity within 0–100 m depth	m·s^{-1}	ESSIC
currentvrange	Range in meridional current velocity within 0–100 m depth	m·s^{-1}	
currentdir	Current direction	quadrant	ESSIC
ppavg	Mean primary production within 0–400 m depth	mmol·m^{-2}·day^{-1}	ESSIC
winduavg	Mean zonal (E–W) wind speed at 10 m altitude	m·s^{-1}	NCEP
windvavg	Mean meridional (N–S) wind speed at 10 m altitude	m·s^{-1}	NCEP
turbulence	Index of turbulent kinetic energy (wind speed cubed)	m^{3}·s^{-3}	NCEP

Note: ESSIC, Earth System Science Interdisciplinary Center; NCEP, National Centers for Environmental Prediction.

Fig. 2. (*a*) Quarterly estimates of yellowfin tuna (*Thunnus albacares*) recruitment (millions of fish) and (*b*) juvenile (light grey fill) and adult (dark grey fill) yellowfin tuna biomass for 1952–2004 from the MULTIFAN-CL (MFCL) stock assessment undertaken for western subequatorial region of the western and central Pacific Ocean (WCPO). Grey line in panel (*a*) represents the smoothed trend in recruitment estimates.



Beverton–Holt stock–recruitment relationship (SRR). The model assumes an uninformative prior for the value of steepness of the stock recruitment relationship and a very low penalty for recruitment deviations from the SRR. Growth is considered to be constant for the entire model period. The model estimate of steepness, a value of 0.865, indicates a weak relationship between recruitment and spawning biomass (i.e., a reduction in spawning biomass to 20% of the unexploited equilibrium level is predicted to result in a 13.5% reduction in equilibrium recruitment).

Only recruitment estimates from 1980 to 2003 (96 quarters) were included in the subsequent analysis. Recruitment estimates from the last 12 quarters included in the model (2004–2006) were also excluded from the subsequent analysis. Recruitment estimates were expressed as numbers of fish in the first quarterly age class included in the model (3–6 months). The distribution of the recruitment estimates closely approximated a lognormal distribution (mean = 18.74, SD = 0.40).

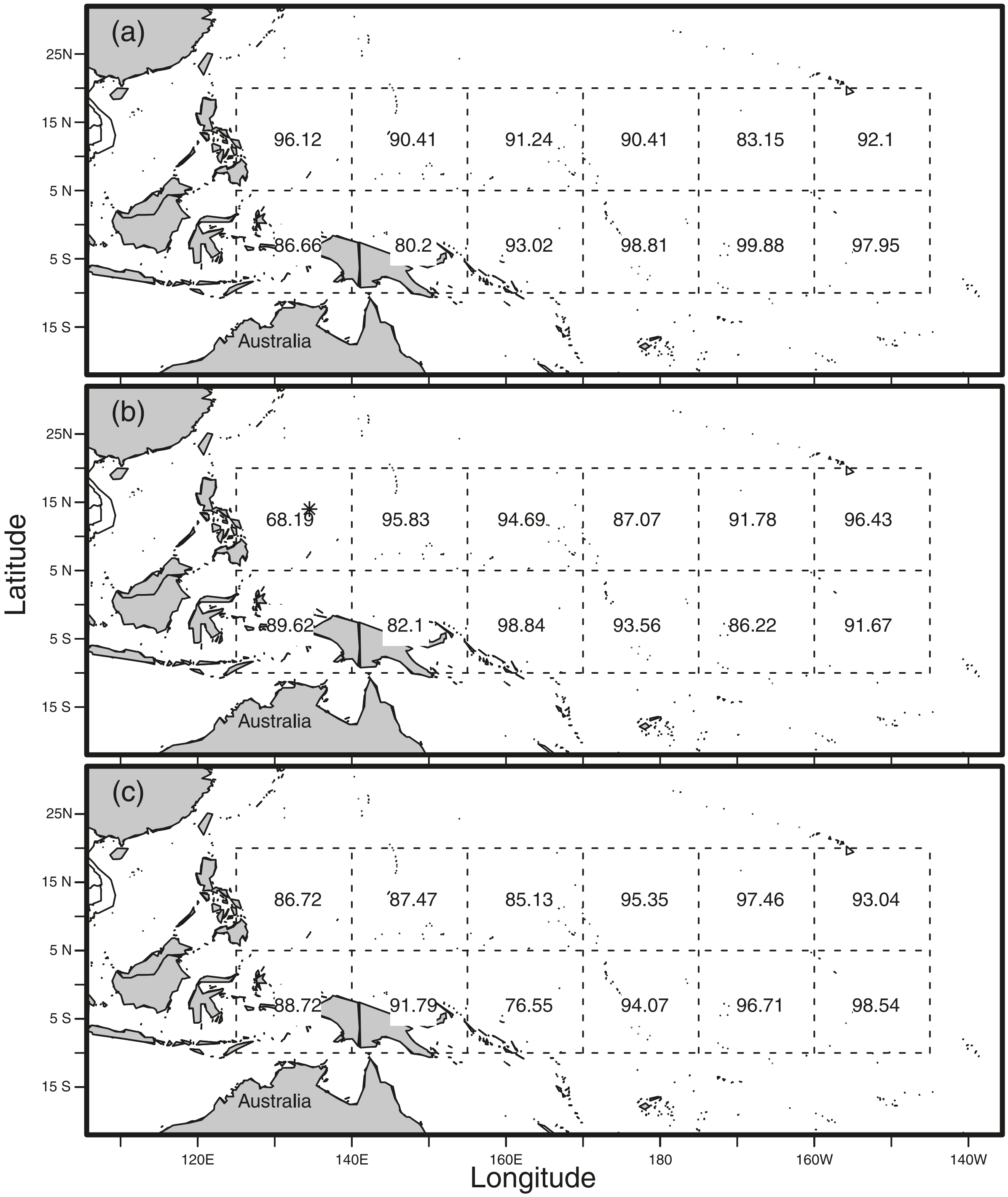
Oceanographic data

The analysis incorporated oceanographic data from two different sources. Most of the data, including sea surface temperature (averaged over 0–100 m depth), east–west (zonal, *u*) current component, north–south (meridional, *v*) current component (averaged over 0–100 m depth), and primary production (averaged over 0–400 m depth), were derived from a physical–biogeochemical model for the Pacific Ocean, developed at the Earth System Science Interdisciplinary Center (ESSIC), University of Maryland (Christian et al. 2002*a*, 2002*b*; Christian and Murtugudde 2003). In addition, *u* and *v* wind components at 10 m altitude were obtained from the National Centers for Environmental Prediction – National Center for Atmospheric Research (NCEP–NCAR) reanalysis provided by NOAA Earth System Research Laboratory from their web site (www.cdc.noaa.gov/cdc/data.ncep.reanalysis.derived.surface.html; Kalnay et al. 1996). All data were available for 1948–2004 and the spatial and temporal resolution was 1° × 1° (latitude, longitude) and 30 days for ESSIC data and 2.5° × 2.5° and 30 days for NCEP data, respectively. For each 2.5° × 2.5° and 30-day period, an index of turbulence was calculated from *u* and *v* wind components based on the fact that turbulent kinetic energy is proportional to the third power or cube of absolute wind speed (Niller and Kraus 1977).

Generalized linear model

A two-phase approach was developed to investigate the relationship between the range of available oceanographic variables and the yellowfin tuna recruitment indices for 1980–2003. The first phase involved the identification of key zones within the western equatorial Pacific Ocean for which the oceanographic data were most highly correlated with the yellowfin tuna recruitment indices.

Fig. 3. Akaike's information criteria (AIC) values from generalized linear models (GLMs) incorporating oceanographic data from 15° latitude, 15° longitude spatial strata for the three different temporal strata (*a*: quarter prior to spawning; *b*: quarter of spawning; *c*: quarter after spawning). The asterisk (*) in panel (*b*) shows the spatial cell used to define oceanographic data sets included in the final GLM.



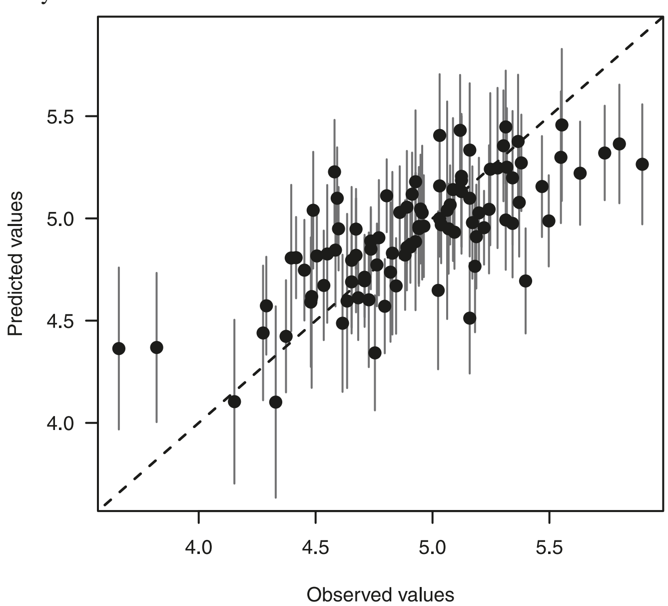
The location and spatial extent of these zones were assessed using a GLM approach with the natural logarithm of the observed recruitment values (numbers of fish) as the dependent variable with a normally distributed error structure. The oceanographic variables were included in the model in a stepwise fitting procedure. The resulting additive model incorporates the significant oceanographic variables to explain the variation in the natural logarithm of the observed recruitment values.

The western equatorial region of the Pacific Ocean (latitude 10°S to 20°N, longitude 125°E to 140°W) was divided into zones configured at six different spatial resolutions (r), resulting in 99 different spatial zones (z): 5° latitude × 15° longitude (36 zones), 10° × 15° (18 zones), 15° × 15° (12

Table 2. Proportion of the variation in observed recruitment explained by the inclusion of successive environmental variables to the final generalized linear model (GLM) (R^2) and corresponding Akaike's information criteria (AIC) value.

Variable	R^2	AIC
winduavg	0.1814	86.69
+ ppavg	0.2564	83.47
+ temprange	0.3434	77.52
+ currentvrange	0.3815	77.79
+ windvavg	0.4263	76.57
+ turbulence	0.4805	73.03
+ currenturange	0.5360	68.19

Fig. 4. A comparison of the natural logarithm of the observed recruitment indices (millions of fish) and predicted recruitment estimates from the final generalized linear model (GLM) model and associated 95% confidence interval. The broken line represents unity.



zones), 5° × 30° (18 zones), 10° × 30° (9 zones), 15° × 30° (6 zones) (see Fig. 1*d*).

For each zone, the oceanographic data included within the zone were aggregated over the spatial extent of the zone and by quarterly time period (t), and summary statistics were computed, principally the mean value and the range. The resulting list of oceanographic variables is described (Table 1). For example, for a given spatial zone of resolution r indexed by location i ($z_{r,i}$) and temporal interval t_j, the mean value of sea surface temperature was computed from the 1° × 1° latitude–longitude cells within the boundaries of the spatial zone and three monthly periods that comprised the quarterly time strata (i.e., the value of the tempavg variable, see Table 1). Similarly, the range (maximum – minimum) of sea surface temperature data from the same spatial–temporal stratum was used to calculate the value of the temprange variable. In addition, the average u and v current components (currentuavg and currentvavg, respectively) were used to derive the current direction (currentdir; in quadrants). Comparable variables were derived from the aggregated east–west and north–south current flow data (average and range) and the primary production and zonal and meridional wind components (average).

To examine the temporal influence of oceanographic conditions on recruitment, the oceanographic data for each zone were considered at three time intervals (t): the quarter prior to the quarter when spawning occurred, the quarter when spawning occurred, and the quarter following the spawning period.

In total, 297 different configurations of the oceanographic data were investigated: 99 different spatial zones (z) at the six different levels of spatial resolution (r) and the three different temporal intervals (t). For each configuration (z,t), the oceanographic variables were included as potential explanatory variables in the GLM fitting procedure. The explanatory variables were represented in the form of third-order polynomial functions, with the exception of current direction, which was categorical. The stepwise GLM was implemented using the stepAIC function in the statistical software R (Venables and Ripley 2002; R Development Core Team 2006). The forward and backward selection of significant variables was undertaken based on the Akaike's information criteria (AIC).

The initial model selection procedure can be summarized as follows. For each spatial zone (i = 1 to n), within each spatial resolution (r = 1 to 6) and each temporal interval (j = 1 to 3), (1) select spatial zone $z_{r,i}$ and temporal interval t_j; (2) determine oceanographic summary statistics for $z_{r,i}t_j$; (3) construct GLM with potential predictor variables from (2) using stepwise fitting procedure; (4) report AIC.

The spatial–temporal stratum with the lowest AIC ($z_{(r^*,i^*)}t_{j^*}$) was then selected as the base stratum for the final GLM model. The next phase of the model fitting involved testing the explanatory power of the model with the inclusion of oceanographic data from different areas (of the same spatial resolution (r^*) and temporal interval (j^*).

The second phase of the model building process is summarized as follows. Select initial model (lowest AIC) derived from $z_{(r^*,i^*)}t_{j^*}$ oceanographic data. For the other spatial zones with an equivalent spatial resolution to the initial model ($r = r^*$; i = 1 to n; $i \neq i^*$) and the temporal interval equivalent to the initial model ($j = j^*$), (1) select spatial zone $z_{r^*,i}$; (2) determine oceanographic summary statistics for $z_{r^*,i}t_{j^*}$; (3) construct GLM using stepwise fitting procedure with potential predictor variables from initial model zone–time $z_{(r^*,i^*)}t_{j^*}$, and second zone $z_{r^*,i}t_{j^*}$ (2); (4) report model and AIC.

The iterative fitting procedure minimized the simultaneous fitting of potentially hundreds of different oceanographic variables (11 variables compiled for each time–area stratum). It may also have made the resulting model easier to interpret, as it was based on oceanographic variables derived from a relatively limited spatial range. The parameterization of the individual variables included in the final GLM was examined using the "predict" function in R. For the main oceanographic variables included in the final GLM, the influence of the individual variables was investigated by examining the fitted values for each of the individual variables included within the additive model.

Table 3. Correlation matrix for the variables included in the final generalized linear model (GLM).

	winduavg	ppavg	temprange	currentvrange	windvavg	turbulence	currenturange
winduavg	1.0000	–0.5288	–0.5013	0.4056	0.8641	–0.7640	0.2358
ppavg		1.0000	0.4540	0.0128	–0.7613	0.7677	0.0150
temprange			1.0000	0.0167	–0.5747	0.4713	0.1115
currentvrange				1.0000	0.3205	–0.1784	0.4795
windvavg					1.0000	–0.8296	0.1702
turbulence						1.0000	–0.1985
currenturange							1.0000

The robustness of the final GLM was assessed following the cross-validation approach of Francis (2006). This approach involves refitting the model iteratively, successively excluding each recruitment observation (r_i). For each iteration (i), the percentage of the variation explained (PVE) by the model is calculated as the difference between the deviation between the mean of the recruitment series (excluding r_i) and the observed value (r_i) and the deviation between the estimated recruitment value (from the refitted model) and the observed value (r_i). A PVE of zero means that the model does not perform any better than the assumption of average recruitment, while a PVE of 1.0 means that the model estimates the recruitment index without error (see Francis 2006 for further details).

Hindcasting

The final GLM was employed for a hindcast by applying the predictive model to historical oceanographic data to predict recruitment for the entire period of the oceanographic model run (1948–2003). The recruitment predictions were compared with the observed recruitment estimates from the yellowfin tuna stock assessment model. Further, for each of the main oceanographic variables included within the model, the relative influence of the variables on the short- and long-term trends in predicted recruitment was examined.

Cluster analysis

For an individual spatial zone, many of the oceanographic variables included in the model data set are likely to be highly correlated. A clustering approach was applied to the oceanographic variables included in the final GLM to attempt to discriminate predominate oceanographic conditions within the study area. The resulting categories of oceanographic conditions were then compared with the observed recruitment indices (1980–2003) from the corresponding period.

The cluster analysis was undertaken using the “clara” function in the cluster package of R. The number of specified clusters was assessed by comparing the improvement in the objective function with increasing numbers of clusters.

Results

MFCL stock assessment for yellowfin tuna

There is considerable short- and long-term variation in the quarterly yellowfin tuna recruitment estimates derived from the stock assessment model (Fig. 2). Over the longer term, the stock assessment model estimates that recruitment declined during the 1950s and 1960s, increased during the late 1960s and 1970s, and remained stable at a relatively high level in the late 1970s and 1980s. Recruitment was estimated to be relatively low during the mid 1990s and high during the early 2000s. Total yellowfin tuna biomass is predicted to have declined sharply during the 1960s, increased through the 1970s, and declined sharply over the subsequent period (Fig. 2). Recent adult biomass levels are estimated to be approximately one-third of the biomass levels in the 1950s.

GLMs

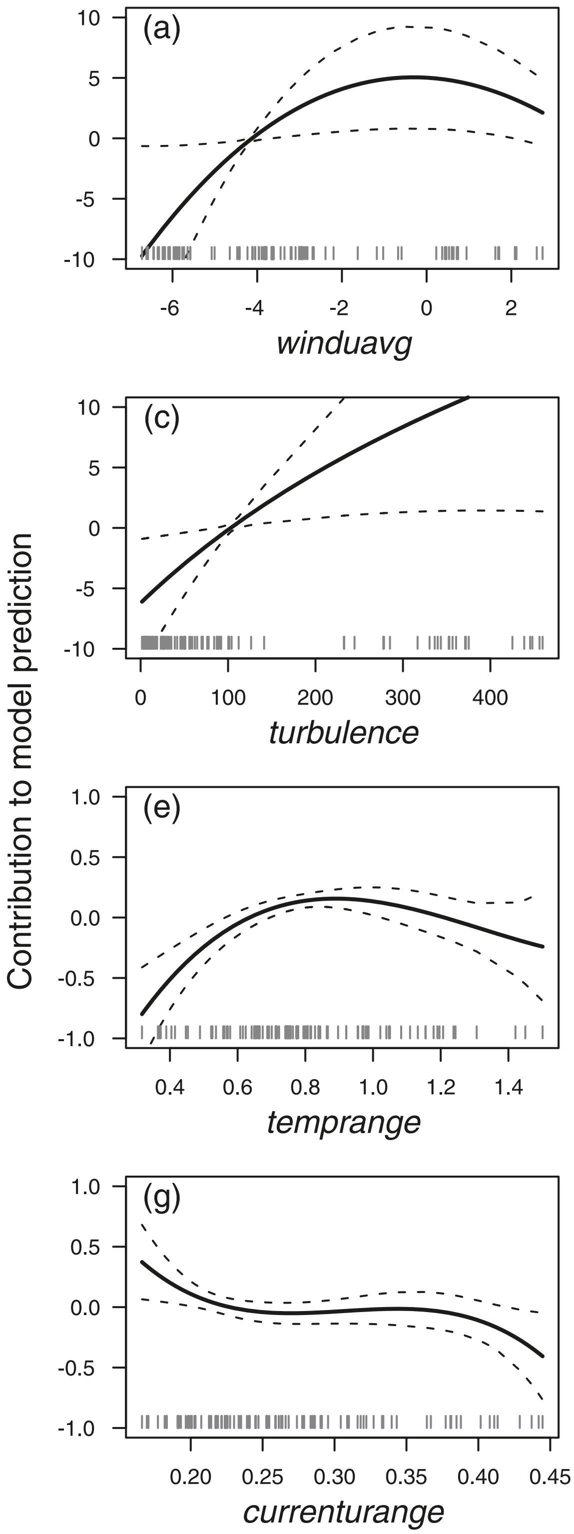
The initial GLMs, derived from oceanographic data compiled for individual spatial and temporal strata, accounted for between 4% and 54% of the observed variation in the natural logarithm of the recruitment indices (1980–2003). In general, the highest explanatory power was obtained from models comprising oceanographic data from the northwestern spatial zones. For the range of spatial resolutions investigated, higher explanatory power was generally obtained from models with a relatively coarse spatial resolution (i.e., 15° latitude, 15° longitude). In relation to the temporal stratification, the highest explanatory power (lowest AIC) was generally obtained from models comprising oceanographic variables derived from the quarterly data from the period corresponding to when the fish were spawning (rather than the quarter prior to or after spawning) (Fig. 3).

The model building process first selected a 15° latitude, 15° longitude zone in the northwest of the study area (Fig. 3) for the period corresponding to the quarter of spawning. The model was then offered each of the remaining $15^\circ \times 15^\circ$ zones and selected an additional zone in the southeast. The inclusion of the second zone resulted in a considerable improvement in the AIC; however, the two zone models included a total of 15 explanatory variables of the 22 potential explanatory variables (11 from each zone). It was considered that the added complexity of the two region models (an additional eight variables) outweighed the improvement in the explanatory power of the model.

The final GLM was restricted to the oceanographic data set from the northwestern zone and included 7 of the 11 potential explanatory variables: winduavg, ppavg, temprange, currentvrange, windvavg, turbulence, and currenturange (Table 2). The final GLM model has the following structure:

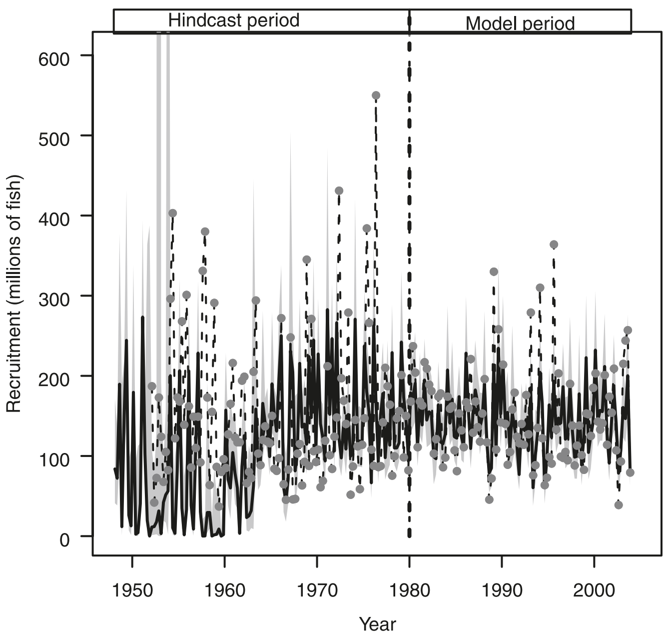
$$\begin{aligned}\log(\text{recruit}_t) = \text{mean} &+ \text{poly}(\text{winduavg}, 3) \\ &+ \text{poly}(\text{ppavg}, 3) \\ &+ \text{poly}(\text{temprange}, 3) \\ &+ \text{poly}(\text{currentvrange}, 3) \\ &+ \text{poly}(\text{winduavg}, 3) \\ &+ \text{poly}(\text{turbulence}, 3) \\ &+ \text{poly}(\text{currenturange}, 3) \\ &+ \text{error}\end{aligned}$$

Fig. 5. Predicted relationship between yellowfin tuna recruitment (natural logarithm of number of fish, in millions) and oceanographic variables included in the final generalized linear model (GLM). Broken lines represent approximate 95% confidence interval of model prediction. Distribution of data included in the model for the individual variable is presented as tick marks along the *x* axis.



The final GLM accounts for 54% of the observed variation in the recruitment time series. The GLM approximates the observed values over the main range of the recruitment series data, although there is considerable deviation between individual observed and predicted values, and many of the predicted values are not well estimated (i.e., relatively high standard error) (Fig. 4). Further, the GLM performs poorly in predicting recruitment values at the extremes of the range; low recruitment observations are generally overestimated by the GLM and vice versa.

Fig. 6. “Observed” quarterly estimates of yellowfin tuna recruitment from MULTIFAN-CL (MFCL) assessment model (broken line with points) and “predicted” recruitment from final generalized linear model (GLM) for 1948–2003 (solid black line). Broken vertical line indicates the start of the period used to construct predictive model. Shaded area shows 95% confidence interval of individual recruitment prediction.



A comparison of the model residuals with the MFCL estimates of adult biomass at the time of spawning revealed no trend in the residuals. This observation is consistent with the high value of steepness of the SRR estimated by the MFCL stock assessment model.

The PVE statistics calculated from the cross-validation of the final GLM indicate that the model has moderate predictive power (median value: 0.48; range: 0.45–0.51). Essentially, the model is able to account for 48% of the observed variation in the recruitment index from the long-term mean of the series. This indicates that the final GLM is capable of providing a reasonably reliable estimate of recruitment over the range of observed oceanographic conditions.

Many of the variables included in the final GLM are highly correlated (Table 3). Consequently, it is not possible to make definitive conclusions regarding the causal affect on yellowfin tuna recruitment of the specific oceanographic variables included in the model. Instead, the variables included in the model should be considered as representing a series of indices of the prevailing oceanographic conditions that are directly or indirectly influential in determining yellowfin tuna recruitment in the region. Nonetheless, an examination of the parameterization of these variables in the final GLM is likely to be informative regarding the key variables influencing yellowfin tuna recruitment (Fig. 5).

Of the seven variables included in the model, the *u* and *v* wind component variables (winduavg and windvavg) are highly correlated (Table 3) and reveal that either southwesterly (positive winduavg and negative windvavg) or northeasterly winds prevail in the northwestern zone. The parameterization of the wind variables in the GLM indicates that higher or lower recruitment occurs during southwesterly or northeasterly conditions, respectively (Fig. 5). However, this is mediated by the parameterization of the turbulence variable (calculated from *u* and *v* wind components), which predicts recruitment increases strongly with increasing values of turbulence; turbulence is highest during period of strong southwesterly winds (Fig. 5).

Primary production (ppavg) is the second most influential variable included in the GLM. Recruitment is predicted to peak at moderate values of this variable, with lower recruitment predicted at the extremes of the range (Fig. 5). The variable defining the range in the sea surface temperature (temprange) is essentially an index of the latitudinal contrast in the sea surface temperature within the spatial strata. The final GLM predicts increasing recruitment with increased values of temprange up to a threshold level.

The variables currenturange and currentvrange are relatively uninformative in the final GLM; recruitment is predicted to remain relatively constant over the range of two variables, except for the extremities of the range where the relationship is poorly determined (Fig. 5).

Model prediction

For the model building period (1980–2003), the time series of predicted recruitment from the final GLM approximates the fluctuations in the recruitment estimates from the stock assessment model (Fig. 6). Overall, 67% of the recruitment predictions from the final GLM are within ±25% of the observed recruitment estimates from the assessment model. The recruitment predictions from the final GLM have a coefficient of variation of approximately 15%, and most of the observed recruitment estimates are within the confidence interval of the recruitment predictions from the final GLM. However, the final GLM underestimates the magnitude of some of the higher observed recruitment estimates, particularly in the early 1990s (Fig. 6).

The GLM recruitment predictions are driven by strong seasonal trends in the winduavg, turbulence, and windvavg variables (Fig. 7). The deviation of the recruitment indices from these seasonal processes is largely explained by the deviations in the ppavg and temprange variables. For example, the predictions of low recruitment in the middle and late 1990s are largely attributed to low values of the temprange variable during those periods (Fig. 7). The inclusion of these additional variables contributes to the substantial improvement in the fit of the final GLM relative to a simple GLM including season (quarter) as the sole predictive variable (14.3% compared with 54% of the observed variation in recruitment).

The final GLM was also applied to predict quarterly yellowfin tuna recruitment for 1948–1979, the hindcast period for which oceanographic data were available. For the 1950s and early 1960s, there is a divergence between recruitment predicted by the GLM and the MFCL recruitment estimates (Fig. 6). For this period, the GLM predictions are highly variable; a high proportion of the predictions are very low and most are poorly determined. For a number of the oceanographic variables (temprange, currentvrange, and currenturange), the observed values from the 1950s to early 1960s are beyond the range observed during the model building period (1980–2003), and on that basis, the GLM re-

Fig. 7. Quarterly trends for each of the key environmental variables included in the final generalized linear model (GLM) model for 1948–2003 (points and grey line) and the partition of the total recruitment prediction associated with each variable presented in each panel (black line). The summation of the recruitment predictions from each variable equals the prediction of total recruitment (expressed as the natural logarithm of the number of fish, in millions).

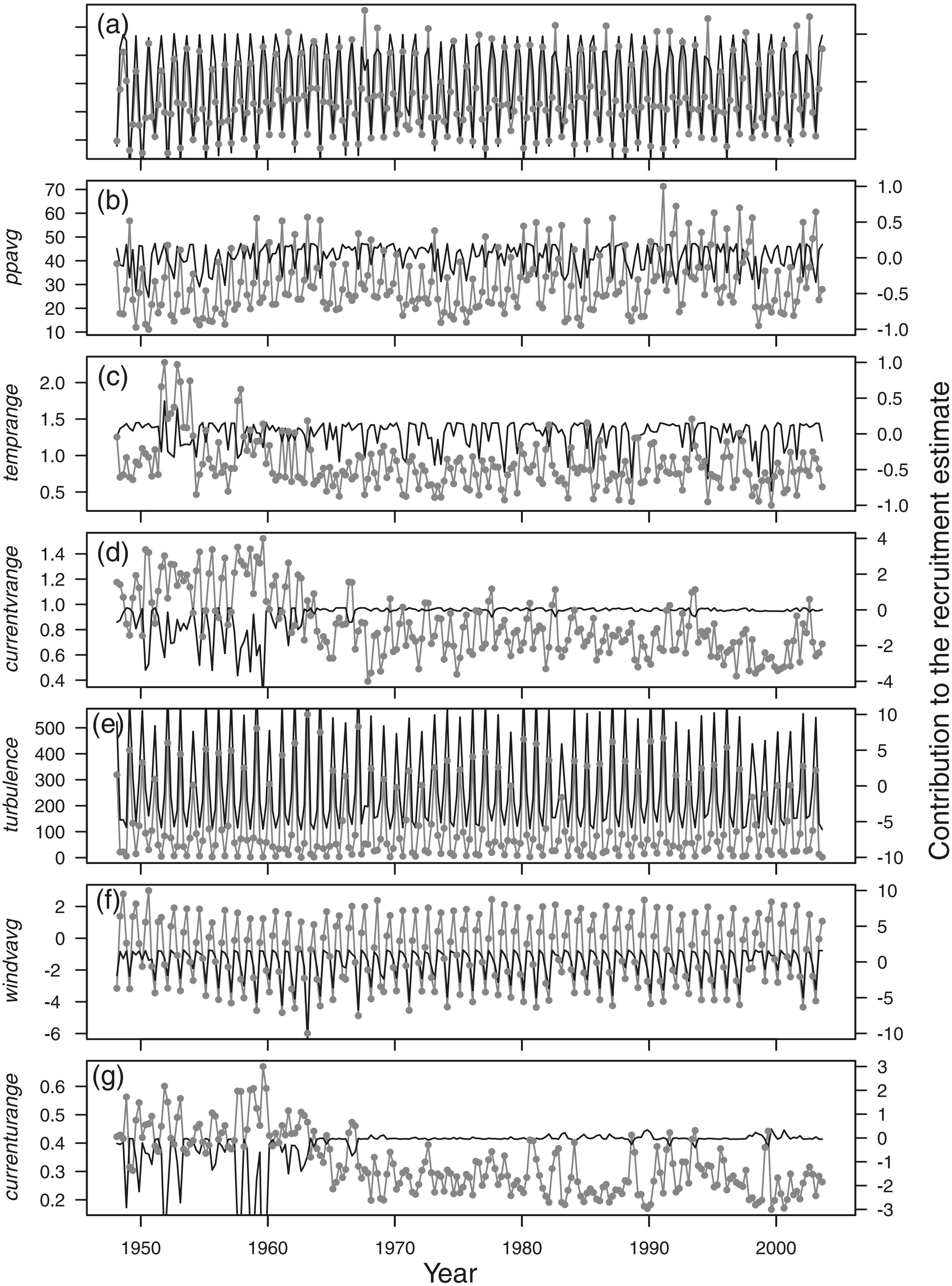
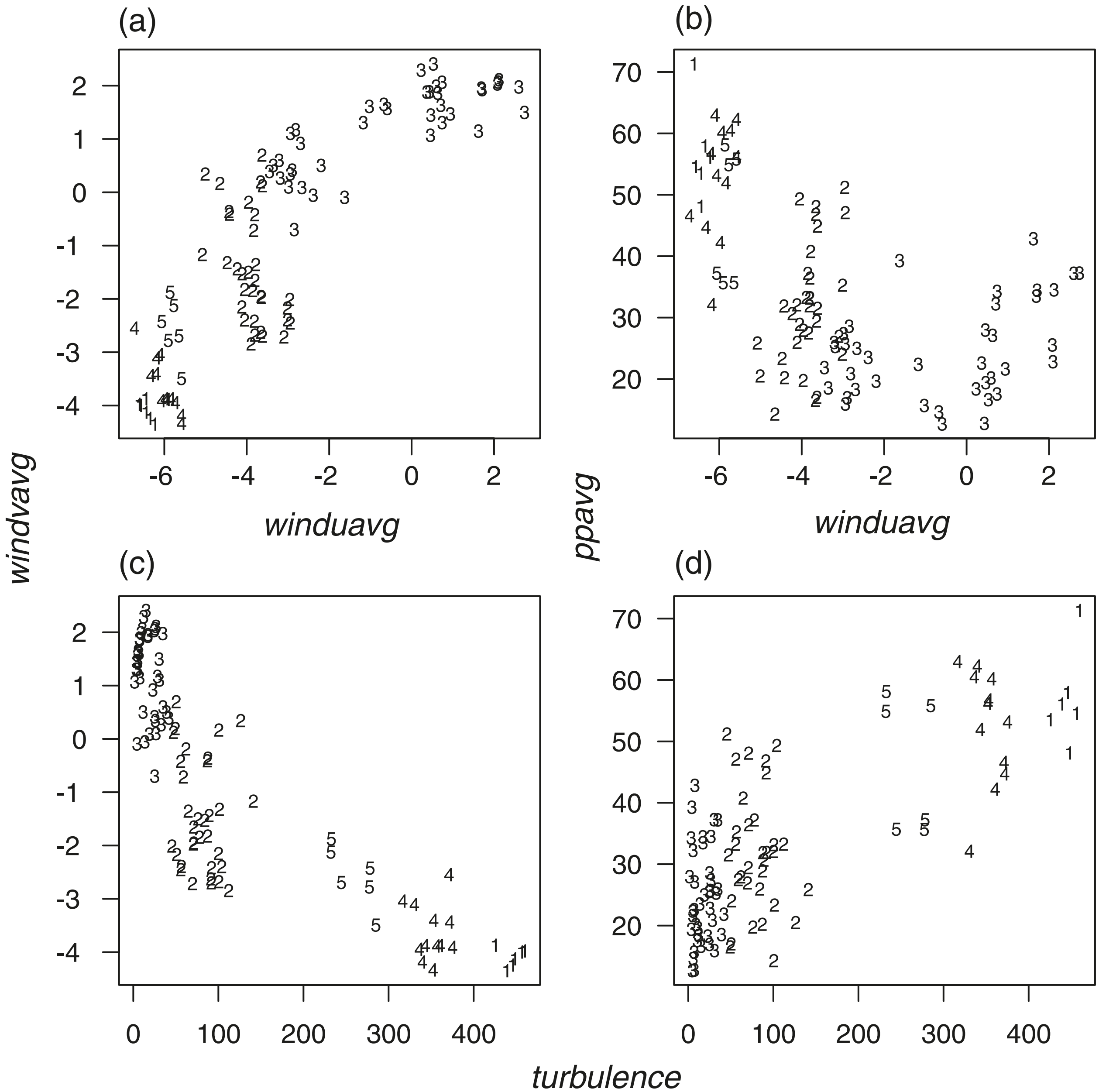


Fig. 8. A comparison of the key oceanographic variables (from the northwestern zone) included in the cluster analysis. The cluster assigned to each data point is denoted by the number (1 to 5).



cruitment estimates from the early period should be disregarded (Fig. 7).

From the mid-1960s to 1980, the overall magnitude of the recruitment estimates predicted from the final GLM (mean value 144 million fish) is comparable to the average of the observed recruitment values for the same period (143 million fish) (Fig. 6). The predicted recruitment also appears to reflect some of the short-term variation in observed recruitment; for example, during the mid-1960s the sequences of observed and predicted recruitments are similar. However, the recruitment series are poorly correlated (correlation coefficient = 0.189); there are significant deviations between individual recruitment observations and predictions. Most notably, the GLM consistently underestimates the very high recruitments observed during the mid-1970s. Partly for this reason, the GLM does not capture the overall trend of increasing recruitment observed during the late 1960s and 1970s.

Cluster analysis

The cluster analysis of the seven oceanographic variables included in the final GLM identified five clusters. A qualitative examination of the results from the cluster analysis revealed that clusters are principally defined by four key variables: winduavg, ppavg, windvavg, and turbulence (Fig. 8, Table 4). For example, cluster 1 is characterized by year or quarters with low values for the winduavg and windvavg variables and high values for ppavg and turbulence, while the opposite is the case for cluster 3.

The MFCL recruitment observations from each year or

Table 4. Median values of the principal environmental variables for each of the five clusters defined in cluster analysis.

	Cluster				
Variable	1	2	3	4	5
winduavg	–6.45	–3.81	0.23	–6.02	–5.81
ppavg (median)	55.35	31.53	22.81	54.67	46.07
temprange	1.09	0.78	0.72	1.00	0.78
currentvrange	0.65	0.63	0.76	0.68	0.58
windvavg	–4.06	–1.65	1.45	–3.87	–2.56
turbulence	446.75	77.78	14.97	352.71	261.10
currenturange	0.22	0.26	0.26	0.24	0.27
Median recruitment	168	117	136	181.5	187.5
Mean recruitment	179.8	125.3	147.5	183.7	187.2
SD recruitment	22.8	39.4	63.9	78.1	56.1
No. of records	6	33	39	12	6

Note: The number of records (recruitment observations) and the median, mean, and standard deviation (SD) of the recruitment observations that correspond to each cluster are also presented.

quarter were grouped into the corresponding clusters. In general, observed recruitment was higher in clusters 1 and 5 and lower in cluster 2 (Table 4, Fig. 9). Observed recruitment was more variable for clusters 3 and 4, although recruitment was generally below average in the former and above average in the latter.

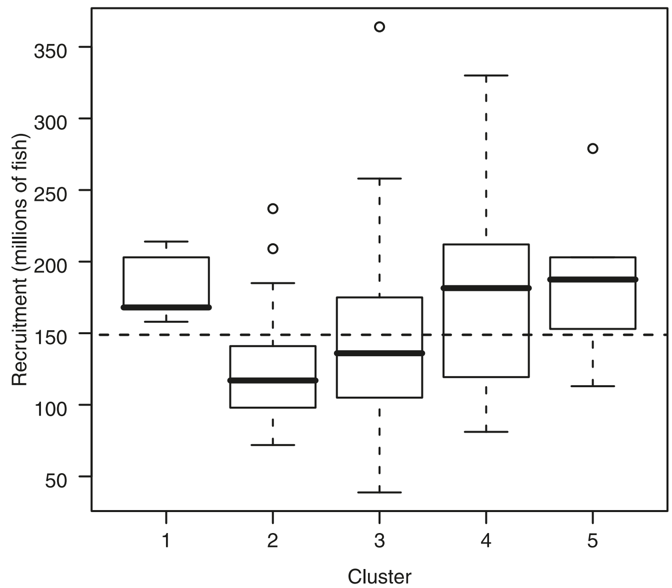
The oceanographic conditions corresponding to high recruitment (clusters 1 and 5) are typically characterized by strong northeasterly winds, a moderate northwestward current, and a relatively strong latitudinal gradient in sea surface temperature (compressed isotherms) within the northwestern area — the area used to derive the oceanographic variables included in the final GLM and cluster analysis (Fig. 10). Over the broader equatorial region, the oceanographic conditions corresponding to high recruitment are typically characterized by the presence of waters exceeding 30 °C in the proximity of northern Papua New Guinea and the location of the 28 °C isotherm west of 180° along the equator. These conditions occur more frequently during the first quarter of the year.

In contrast, lower recruitment generally corresponds to comparatively weaker winds, limited variation in sea surface temperature, and either westerly or southwesterly current flows within the northwestern area (clusters 2 and 3; Fig. 10). These conditions tend to occur in either the second and third quarters of the year (cluster 2) or third and fourth quarters (cluster 3).

Discussion

The spatial extent and variability of the spawning habitat of yellowfin tuna in the western tropical Pacific Ocean preclude the direct measurement of recruitment strength of yellowfin tuna cohorts. Recruitment estimates for yellowfin tuna are available as an output of an age-structured population model that integrates catch, effort data, and fish (length and weight) size data from the principal fisheries operating in the area. However, recruitment estimates may be biased because of incorrect specification of the assessment model or imprecise because of data limitations. More critically, from a management perspective, the most recent estimates

Fig. 9. Box plot of recruitment observations (1980–2003) grouped by the five clusters defined in the cluster analysis of the principal environmental variables. The box represents the interquantile range of the recruitment observations in each cluster, and the solid line represents the median value. The whiskers represent 1.5 times the interquantile range, and the points represent outliers in the data. The broken horizontal line represents the average of all the recruitment observations.



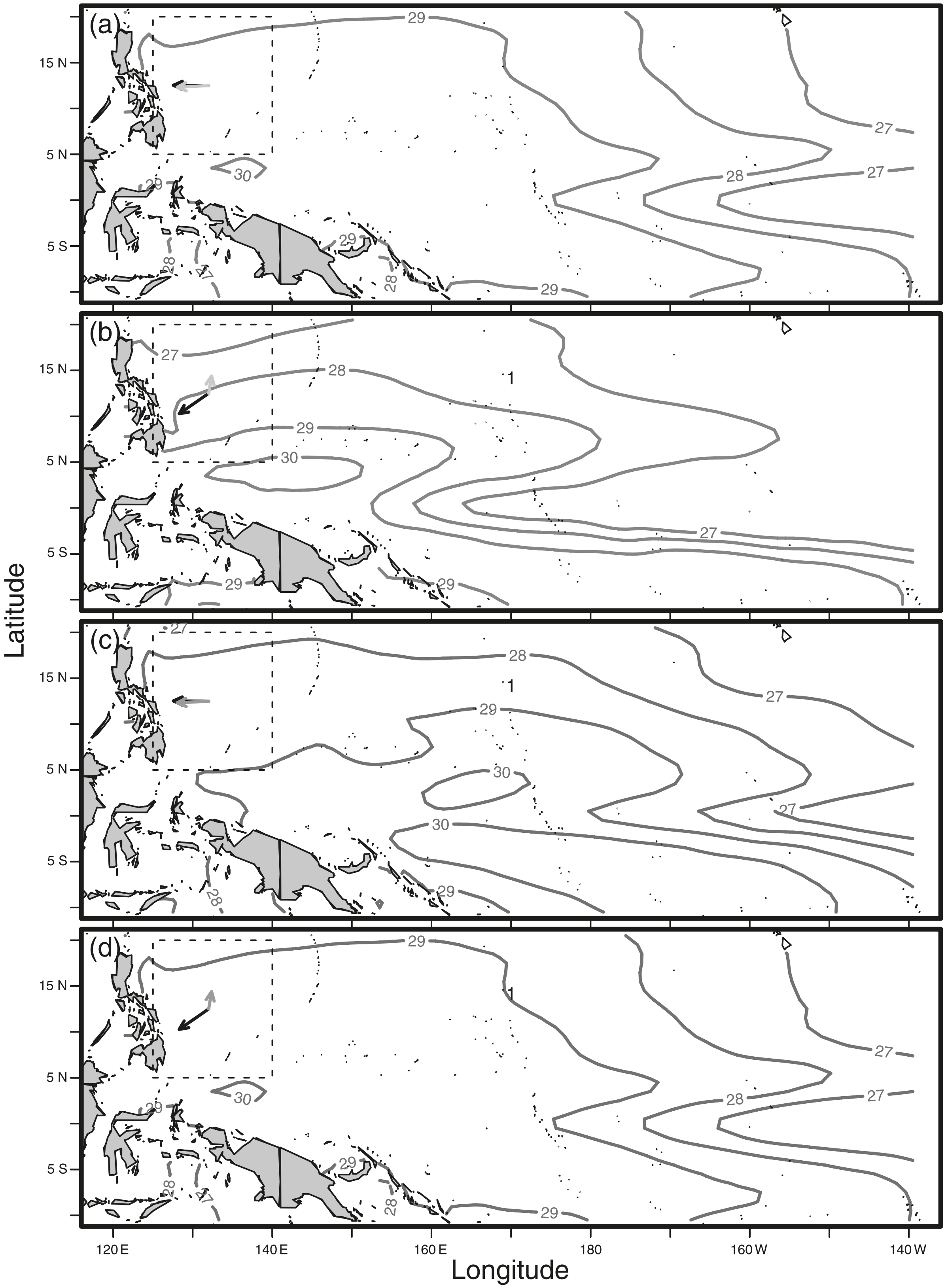
of recruitment from the assessment model tend to be the most uncertain, as there are few observations of the cohort in the fishery. Consequently, for a relatively short-lived species such as yellowfin tuna, estimates of current levels of stock biomass are also highly uncertain, as the population is dominated by a small number of cohorts. Therefore, the development of a predictive model for this species has the potential to increase the precision of the model estimates of current biomass and also improve the ability to forecast trends in biomass over the short term (1–2 years).

A moderate proportion of the variation in yellowfin tuna recruitment in the WCPO can be explained by a suite of metrics that describe the oceanographic conditions in the northwestern tropical Pacific. The results from the GLM model were also complemented by the results from the cluster analysis of the environmental data; this analysis identified five principal ocean states, and of these, higher levels of recruitment were associated with two ocean states and weaker recruitment generally corresponding to another two ocean states.

The process that links the environmental conditions in the northwestern zone with the regional variation in yellowfin tuna recruitment is unclear. There are two main hypotheses that in fact are likely to represent the extremes of a continuum. Firstly, the northwestern zone represents a major source of the total recruitment to the entire equatorial region of the western Pacific. Alternatively, the oceanography in the northwestern zone represents an indicator of the broader scale regional oceanographic conditions that influence yellowfin tuna recruitment throughout the equatorial region.

Plankton surveys have revealed that yellowfin tuna larvae are abundant throughout the western tropical region of the

Fig. 10. Examples of the prevailing oceanographic conditions from the two high recruitment clusters determined from the cluster analysis of environmental data (*a*: first quarter of 1996, cluster 1; *b*: first quarter 1999, cluster 5) and two low recruitment clusters (*c*: second quarter of 1995, cluster 2; *d*: third quarter 1996, cluster 3). The isotherms of the quarterly average sea surface temperature are plotted (solid lines). The arrows represent relative average current flow (black) and average wind flow (grey) for the zone included in the final generalized linear model (GLM) model.



Pacific Ocean, including the northwestern zone selected in the GLM analysis (Nishikawa et al. 1985). While the northwestern zone is likely to contribute to the overall level of yellowfin tuna recruitment, it appears more plausible that the oceanographic conditions observed in this area provide a broader scale index of the oceanography of the wider area crucial for yellowfin tuna spawning and the survival of early life stages.

The predictive model does not provide a direct, mechanistic link between the prevailing oceanographic conditions and yellowfin tuna recruitment, although the statistical models do provide some insights into the broader scale oceanographic conditions that may influence recruitment strength. For example, a recent study linked yellowfin tuna larval survivorship to water turbulence — experimentally determining the optimal turbulence intensity that enhances larval survival (Kimura et al. 2004). Turbulence was included as a variable in the final GLM model, although given the direct interaction between the two wind component variables, there is a high degree of confounding in the parameterization of these three variables. Nevertheless, the cluster analysis reveals that higher recruitment of yellowfin tuna is associated with stronger northwesterly winds, which are likely to increase turbulence of the surface layer.

The oceanographic conditions prevailing at the mesoscale (i.e., in the northwestern zone) are, in turn, likely to be broadly correlated with the oceanographic conditions at the regional scale. Lehodey et al. (2003) asserted that yellowfin tuna recruitment in the WCPO is driven by the variability in the spatial extent of the warm pool, which tends to occur when the North Equatorial Countercurrent becomes more dominant than the South Equatorial Current (El Niño conditions), allowing the warm pool to extend further east (Lehodey et al. 1997; Picaut et al. 2001). This assertion is consistent with the observation from many studies that relate yellowfin tuna spawning and larval survivorship to sea surface temperature (summarized in Suzuki 1994 and Wild 1994), with spawning occurring at water temperatures above 26 °C and optimal larval survivorship at 26–28 °C.

The present study reveals a more complex set of oceanographic conditions that are associated with variations in the level of yellowfin tuna recruitment. High recruitment tends to occur during periods of strong westward flow of the South Equatorial Current, dominating the North Equatorial Countercurrent, and a weak North Equatorial Current. These conditions coincide with northwestward currents and northeasterly winds in the northwestern zone, resulting in a strong latitudinal gradient in sea surface temperature in that area and a concentration of waters exceeding 30 °C in the western equatorial region. Conversely, this study reveals that low recruitment tends to occur during periods of lower flow of the South Equatorial Current and increased strength of the North Equatorial Countercurrent. These results somewhat contradict the general conclusions of Lehodey et al. (2003).

The statistical modeling approach attempts to provide a method of predicting the overall level of recruitment across a wide range of observed oceanographic conditions. For the model building period (1980–2003), the GLM appears to be capable of providing relatively good predictions of recruitment in the equatorial region of the WCPO; the cross-validation study indicates the model is capable of predicting almost 50% of the variation in future recruitment. Certainly, the potential to predict for the short term represents a substantial improvement over the previous assumption that recruitment would default to the long-term average recruitment for short-term projections of the yellowfin tuna stock assessment model (see Langley et al. 2007). However, for the earlier period (1962–1979), the model estimates are poorly correlated with the recruitment observations, suggesting (*i*) a departure from the modeled relationship between oceanographic conditions and recruitment, (*ii*) lower accuracy of the recruitment observations derived from the stock assessment for this period, and (or) (*iii*) lower reliability of the environmental variables derived from the ESSIC and NCEP–NCAR models during the earlier period.

The first explanation is plausible if the final GLM has failed to include key variables that over the long term are more crucial in determining yellowfin tuna recruitment or if the parameterization of the relationships between key oceanographic variables and recruitment are poorly determined for the model building period. The second explanation is also plausible. The higher level of statistical uncertainty associated with recruitment observations prior to 1980 (see Langley et al. 2007) is largely due to the lack of size frequency data from the fisheries catching small yellowfin tuna within the earlier period of the MFCL stock assessment model.

The statistical modeling has also assumed that the output from the ESSIC physical–biogeochemical model is without error or, at least, without major temporal biases in the key model outputs used in the final GLM model. Because of a lack of observational data, only limited validation of the output from the physical–biogeochemical model has been undertaken, and these assessments have been limited to the latter period included in the model (1990s) (Christian et al. 2002*a*). Christian and Murtugudde (2003) concluded that there was a general consistency between the modeled results and the range of observations available, although there are some important processes that the model represents imperfectly; for example, the model produces excessively high rates of primary production, especially under strong upwelling conditions.

Christian and Murtugudde (2003) also noted that the performance of the physical–biogeochemical model is quite sensitive to errors in the NCEP monthly mean wind stress data — the principally forcing data set included in the physical–biogeochemical model. The authors of this paper were unable to source published information regarding the relative accuracy of the NCEP data over the timeframe of the physical–biogeochemical model, although it is assumed that NCEP data is more accurate since the advent of global operational satellite observing systems starting in 1979 (Kalnay et al. 1996).

Overall, it is reasonable to conclude that the precision of both the recruitment observations (from the stock assessment model) and the key oceanographic variables (from the ESSIC model) are likely to be less well determined prior to 1980, and both sources of error are likely to be contributing to the discrepancy between the observed and predicted recruitments before 1980. Further refinement of the yellowfin tuna recruitment model is envisaged with the extension of the recruitment time series as additional observations are available from future stock assessments and improved oceanographic data are available from future refinements to the physical–biogeochemical model.

The GLM includes no information regarding the magnitude of the spawning biomass of yellowfin tuna in the WCPO; essentially the model attributes all the short- and long-term variation in recruitment to the prevailing oceanographic conditions and assumes there is no relationship between recruitment and adult biomass, at least at the levels of stock biomass observed within the model domain. This is consistent with various stock assessments for yellowfin tuna that have tended to assume high values of steepness for the spawning stock–recruitment relationship (SRR); (i.e., there is no decline in recruitment until spawning biomass falls to very low levels; Hoyle and Maunder 2006). Hilborn and Walters (1992), in summarizing available information on SRRs, noted that tuna species are one of the major species groups where good relationships between stock abundance and recruitment have failed to appear and concluded that this is almost certainly due to the fact that the stocks are generally not fished sufficiently hard for an SRR to be evident.

There is also a circularity in the estimation of SRR for species such as yellowfin tuna that are relatively short-lived and have a short generation time, particularly when recruitment and, therefore, spawning biomass are highly autocorrelated with prevailing oceanographic conditions. For example, a period of favourable oceanographic conditions will result in high recruitment followed (within a generation) by an increase in spawning biomass. Conversely, a period of less favourable conditions will result in lower recruitment and, therefore, lower spawning biomass. If the periods of more or less favourable oceanographic conditions persist for considerably longer than the generation time of the species, then the resulting observations of recruitment and spawning biomass may be misconstrued as a strong SRR. The premise of this paper is that at the range of biomass levels observed over the history of the fishery, the variation in recruitment is essentially attributable to variation in oceanographic conditions. Nevertheless, this relationship may erode at lower biomass levels, as recruitment may become more strongly influenced by the level of spawning biomass.

The development of a reliable predictive model for yellowfin tuna recruitment has direct application to the ongoing stock assessment of yellowfin tuna in the WCPO. There is also potential to apply a similar approach to the stock assessment of yellowfin tuna and other pelagic species in other oceans, particularly for short-lived species such as skipjack tuna (*Katsuwonus pelamis*). Principally, the predictive model enables recent (last 1–2 years) recruitments to be estimated more precisely, thereby increasing the precision of estimates of current biomass and exploitation rates. The increased precision of the current age structure of the population also improves the accuracy of any short-term (next 1–2 years) stock projections from the assessment model. In a broader ecological context, the recruitment model provides a tool to investigate how yellowfin tuna recruitment may vary in response to short- and long-term variation in the oceanographic conditions in the WCPO.

Acknowledgements

This work was carried out as part of the project “Regime shifts and recruitment in western and central Pacific Ocean tuna fisheries” funded by the Pelagic Fisheries Research Program, University of Hawai’i, with additional support from the European Community funded Pacific Regional Oceanic and Coastal Fisheries (PROCFish) Project and with AusAID and NZAID programme funding to Oceanic Fisheries Programme, Secretariat of the Pacific Community. The authors acknowledge John Hampton for his guidance in the use of the MFCL software and comments on the manuscript. Keith Bigelow and two anonymous reviewers provided useful comments on a draft version of the paper.

References

Christian, J.R., and Murtugudde, R. 2003. Tropical Atlantic climate variability in a coupled physical–biogeochemical ocean model. Deep Sea Res. Part II Top. Stud. Oceanogr. **50**(22-26): 2947–2969. doi:10.1016/j.dsr2.2003.07.005.

Christian, J., Verschell, M., Murtugudde, R., Busalacchi, A., and McClain, C. 2002*a*. Biogeochemical modeling of the tropical Pacific Ocean I: Seasonal and interannual variability. Deep Sea Res. Part II Top. Stud. Oceanogr. **49**(1-3): 509–543. doi:10.1016/S0967-0645(01)00110-2.

Christian, J., Verschell, M., Murtugudde, R., Busalacchi, A., and McClain, C. 2002*b*. Biogeochemical modeling of the tropical Pacific Ocean II: Iron biogeochemistry. Deep Sea Res. Part II Top. Stud. Oceanogr. **49**(1-3): 545–565. doi:10.1016/S0967-0645(01)00111-4.

Francis, R.I.C.C. 2006. Measuring the strength of environment recruitment relationships: the importance of including predictor screening within cross-validations. ICES J. Mar. Sci. **63**(4): 594–599. doi:10.1016/j.icesjms.2006.01.001.

Hampton, J., and Fournier, D.A. 2001. A spatially-disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. Mar. Freshw. Res. **52**(7): 937–963. doi:10.1071/MF01049.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Chapman and Hall, London, UK.

Hoyle, S., and Maunder, M. 2006. Status of yellowfin tuna in the eastern Pacific Ocean in 2004 and outlook for 2005. Inter-American Tropical Tuna Commission, San Diego, Calif. Stock Assess. Rep. 6.

Indian Ocean Tuna Commission. 2006. Report of the ninth session of the Scientific Committee, Victoria, Seychelles, 6–10 November 2006 [online]. Indian Ocean Tuna Commission, Victoria, Seychelles. IOTC-2006-SC-R[EN]. Available from www.iotc.org/files/proceedings/2006/sc/IOTC-2006-SC-R[EN].pdf.

International Commission for the Conservation of Atlantic Tunas. 2004. 2003 ICCAT Atlantic yellowfin stock assessment session. SCRS/2003/016 Col. Vol. Sci. Pap. ICCAT 56. pp. 443–527.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Leetmaa, A., Reynolds, R., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Jenne, R., and Joseph, D. 1996. The NCEP/NCAR 40-year reanalysis project. Bull. Am. Meteorol. Soc. **77**(3): 437–471. doi:10.1175/1520-0477(1996)077<0437:TNYRP>2.0.CO;2.

Kimura, S., Nakata, H., Margulies, D., Suter, J., and Hunt, S.L. 2004. Effect of oceanic turbulence on the survival of yellowfin tuna larvae. Nippon Suisan Gakkai Shi, **70**(2): 175–178 . [In Japanese with English abstract.] doi:10.2331/suisan.70.175.

Langley, A., Williams, P., and Hampton, J. 2006. The western and central Pacific tuna fishery: 2005 overview and status of stocks. Tuna Fisheries Assessment Report 7. Secretariat of the Pacific Community, Noumea, New Caledonia.

Langley, A., Hampton, J., Kleiber, P., and Hoyle, S. 2007. Stock assessment of yellowfin tuna in the western and central Pacific Ocean, including an analysis of management options. Honolulu, Hawai'i, 13–24 August 2007. WCPFC-SC3-SA SWG/WP-1. Available from www.wcpfc.int/system/files/documents/meetings/scientific-committee/3rd-regular-session/stock-assessment-swg-working-papers/WCPFC-SC3%20SA-SWG%20WP-01.pdf.

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**(6652): 715–718. doi:10.1038/39575.

Lehodey, P., Chai, F., and Hampton, J. 2003. Modelling climate-related variability of tuna populations from a coupled ocean–biogeochemical–populations dynamics model. Fish. Oceanogr. **12**(4-5): 483–494. doi:10.1046/j.1365-2419.2003.00244.x.

Maury, O., Gascuel, D., Marsac, F., Fonteneau, A., and De Rosa, A. 2001. Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (*Thunnus albacares*) distribution to the environment in the Atlantic Ocean. Can. J. Fish. Aquat. Sci. **58**(3): 458–469. doi:10.1139/cjfas-58-3-458.

McPhaden, M.J., and Picaut, J. 1990. El Nino–Southern Oscillation displacements of the western equatorial Pacific warm pool. Science (Washington, D.C.), **250**(4986): 1385–1388. doi:10.1126/science.250.4986.1385. PMID:17754983.

Niller, P.P., and Kraus, E.B. 1977. One-dimensional models of the upper ocean. *In* Modelling and prediction of the upper layers of the ocean. *Edited by* E.B. Kraus. Pergamon Press, New York. pp. 143–172.

Nishikawa, Y., Honma, M., Ueyanagi, S., and Kikawa, S. 1985. Average distribution of larvae of oceanic species of scrombroid fishes, 1956–1981. Far Seas Fish. Res. Lab, Shimizu, Japan.

Picaut, J., Ioualalen, M., Menkes, C., Delcroix, T., and McPhaden, M.J. 1996. Mechanism of the zonal displacement of the Pacific warm pool: implications for ENSO. Science (Washington, D.C.), **274**(5292): 1486–1489. doi:10.1126/science.274.5292.1486. PMID:8929400.

Picaut, J., Ioualalen, M., Delcroix, T., Masia, F., Murtugudde, R., and Vialard, J. 2001. The oceanic zone of convergence on the eastern edge of the Pacific warm pool: a synthesis of results and implications for El Niño–Southern Oscillation and biogeochemical phenomena. J. Geophys. Res. **106**(C2): 2363–2386. doi:10.1029/2000JC900141.

R Development Core Team. 2006. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from www.R-project.org.

Suzuki, Z. 1994. A review of the biology and fisheries for yellowfin tuna, *Thunnus albacares*, in the western and central Pacific Ocean. *In* Proceedings of the FAO Expert Consultation on Interactions of Pacific Tuna Fisheries, 3–11 December 1991, Noumea, New Caledonia.. *Edited by* R.S. Shomura, J. Majkowski, and S. Langi. FAO Fish. Tech. Pap. 336/2. pp. 108–137.

Suzuki, Z., Tomlinson, P.K., and Honma, M. 1978. Population structure of Pacific yellowfin tuna. Bull. I-ATTC, **17**(5): 273–441.

Ueyanagi, S. 1969. Observations on the distribution of tuna larvae in the Indo-Pacific Ocean with emphasis on the delineation of the spawning areas of albacore, *Thunnus alalunga*. Bull. Far Seas Fish. Res. Lab, **2**: 177–256.

Venables, W.N., and Ripley, B.D. 2002. Modern applied statistics with S. 4th ed. Springer, New York. ISBN 0-387-95457-0.

Wild, A. 1994. A review of the biology and fisheries for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean. *In* Proceedings of the FAO Expert Consultation on Interactions of Pacific Tuna Fisheries, 3–11 December 1991, Noumea, New Caledonia.. *Edited by* R.S. Shomura, J. Majkowski, and S. Langi. FAO Fish. Tech. Pap. 336/2. pp. 52–107.