Effects of water temperature on the global distribution of tuna and billfish

By

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Abstract

Although tunas and billfishes are of large economic importance and increasing conservation concern, global distribution patterns of many species are poorly resolved. By virtue of their ability to maintain elevated body temperatures, tuna and billfish are able to swim at high speeds over great distances and inhabit a wide range of water temperatures. Here, a meta-analytic approach is used to relate water temperature preferences of tuna and billfish to global distribution patterns over the past 50 years. Data was collected for 21 species of tuna and billfish from >200 sources and categorized according to latitude, longitude, method of data collection, number of replicates, and time of year. Temperature preferences were categorized according to tolerance, preference, and range for each species in the adult and juvenile life stages. Preference data were used in conjunction with satellite-derived sea surface temperature data in order to construct predictive global ranges for individual species as well as total species richness. Comparisons of predicted ranges with Japanese long line catch per unit effort data indicated that predictions based on temperature were most accurate at the northern and southern extent of ranges, and for non-migratory, surface-dwelling species such as marlins. Cumulative species richness predictions from water temperature data were highly correlated with longline-derived richness data (R^2 = 0.956), and peaked at intermediate latitudes (20 to 40°N and S). This study provides evidence that ambient water temperature preferences of tuna and billfish can broadly predict their distribution and richness on a global scale. These predictions have potential implications for marine management efforts such as the siting of high-seas protected areas, efforts to reduce fisheries by-catch, and improvement of stock assessments.

List of Abbreviations and Symbols

ASFA: Aquatic science and fisheries abstracts

AVHRR: Advanced Very High Resolution Radiometer

BCFS: Baja California frontal system

CPUE: Catch-per-unit effort

ENSO: El-Niño southern oscillation

FAO: Food and Agricultural Organization of the United Nations

ITCZ: Inter-tropical convergence zone

IUCN: International Union for the Conservation of Nature and Natural Resources

LNSO: La-Niña southern oscillation

MPA: Marine protected areas

NASA: National Aeronautics and Space Administration

NOAA: National Oceans and Atmospheric Administration

SST: Sea surface temperature

TRCC: Tuna research and conservation centre

Database abbreviations and symbols

D: Data collection method used to gather ambient temperature information for given study. 1 = fisheries data, 2 = global positioning satellite tracking data, 3 = acoustic telemetry, 4 = ultrasonic telemetry, 5 = captive studies, 6 = aerial survey.

Lat: latitude.

Lon: longitude.

N: Number of individuals for which data were collected for a given study.

O: Ocean where specified study took place. 1 = Atlantic, 2 = Pacific, 3 = Indian.

P: Ambient water temperature where majority of time was spent during study period.

P(mn): Minimum ambient temperature where species spent majority of time.

P(mx): Maximum ambient temperature where species in study spend majority of time.

R: Maximum ambient temperature differential experienced by species for a given study.

S: Qualitative measure of source data. 1 = peer-reviewed primary literature, 2 = secondarily referenced, 3 = historical review, 4 = literature.

t: Month of study, where number corresponds to month of year.

T(mn): Minimum ambient water temperature inhabited by species for a given study.

T(mx): Maximum ambient water temperature inhabited by species for a given study.

y: decade of study, where number corresponds to decade.

°C: degrees Celsius.

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Introduction

Ranging from tropical to subpolar seas (0 to ~55° latitude), tunas (*Thunnini*) and billfishes (*Xiphidae, Istiophodidae*) comprise some of the largest and fastest bony fishes in the ocean, and have fascinated humans for centuries. The large socio-economic importance of tunas and billfishes fish coupled with the global spread of industrialized fishing has led to the reduction of global stocks to dangerously low levels (Safina, 1998). The elimination of previously unexploited refuges that were historically protected due to remoteness or expense of access, are likely contributors to this drastic decline (Jackson et al., 2001). The use of new fishing technologies such as fish aggregating devices (FADs) by purse seiners and super-cold storage by some longline vessels have increased the scope of exploitation and the rate and magnitude of declines (Lee, Chen & Tzeng, 2005; Okamoto et al., 2004). Recent analyses suggest that large, predatory fishes have declined more than 90% globally in the past 50 years (Myers & Worm, 2003; 2005), raising concerns regarding the future of many species. This is particularly troubling, as any ecosystem-wide effect is bound to be widespread and likely irreversible due to the global nature of decline (Myers & Worm, 2003). These negative trends could potentially trigger cascading effects, leading to loss of ecosystem stability and functioning (Frank et al., 2005; Jackson et al., 2001). Furthermore, as fisheries provide direct employment to ~200 million people (FAO, 1993), and account for 19% of the total human consumption of animal protein (Botsford, Castilla & Peterson, 1997), decline or collapse of these species have the potential to have drastic social and economic consequences in some fisheries-dependant regions of the globe.

It is therefore surprising, that while these ecologically and economically important species continue to decline, large-scale patterns of abundance and diversity so essential to effective conservation are relatively poorly understood. This is in part explained by the fact that tuna and billfish are highly migratory species usually found many miles offshore, making information-gathering expensive and time-consuming. Consequently, most information for these species comes from fisheries data, which may be biased, inaccurate or lacking in quality. The issue is compounded by under- and over-reporting of catches by countries reporting to the Food and Agriculture Organization (FAO) of the United Nations, the institution charged with recording global fisheries statistics (Watson & Pauly, 2001). Such lack of reliable data hinders the development of effective international management strategies for tuna and billfish. At the time of writing, there were 5 species of tuna and billfish (albacore, bigeye, swordfish, northern and southern bluefin tunas) listed on the IUCN red list for varying degrees of endangerment, 3 of which (albacore, northern bluefin tunas, and swordfish) were listed as "data deficient". Although knowledge of global distribution patterns for individual species of tuna and billfish have rapidly advanced in recent years, for example, through tagging studies (Block et al., 2001), community-wide patterns of abundance and richness remain poorly known (Worm et al., 2005). Knowledge of these patterns and the oceanographic factors which drive them are essential to effective conservation and management of global tuna and billfish populations. Understanding the oceanographic variables responsible for global distribution patterns will allow an increased understanding of the additional factors influencing global species distribution and abundance. By using oceanographic or habitat features as determinants of large-scale distribution patterns for

these species, dependence upon questionable fisheries data may be minimized. Furthermore, previous studies (Worm et al., 2005) have indicated that species richness, when considered in conjunction with species density, fine-scale information regarding habitat use, spawning areas, migration patterns, and fishing mortality (Bertrand et al., 2002; Block et al., 2001; Ferraroli et al., 2004), could be useful in identifying priority areas for marine conservation.

Tunas and billfishes are unique among teleost fishes in being thermoconserving. Vascular counter-current heat exchangers in the body and head of these species maintain internal temperatures above ambient water temperature, allowing improved locomotor muscle efficiency, especially at burst speeds and when pursuing prey into deeper and colder environments (Holland et al., 1992). This endothermic ability enables tuna and billfish to swim at high speeds over great distances and exploit a wide range of oceanic environments. For example, northern bluefin tuna (*Thunnus thynnus*) has been documented in ocean waters ranging from 2.8 to 30.6°C, while maintaining relatively constant internal body temperatures (~25°C) - up to 21°C above ambient temperatures (Block et al., 2001). In addition to water temperature, factors such as oxygen content, prey availability, ocean fronts, zooplankton, salinity, islands, seamounts, and the presence of other organisms (seabirds, porpoises) have been hypothesized to correlate with the abundance and distribution of these species (Worm et al., 2005). Of these, sea surface temperature (SST) has emerged repeatedly as the best single predictor of species density and richness (Lee et al., 2005; Worm et al., 2005). This suggests that ambient water temperature may be a key oceanographic variable driving distribution and abundance of tuna and billfish on a global scale.

In this thesis a meta-analytic analysis of tuna and billfish distribution in relation to water temperature is employed in order to analyze the role of temperature preferences for global species distribution and richness. Ambient water temperature data gathered from >200 studies were analyzed to predict individual species distribution and cumulative species richness for 21 species of tuna and billfish globally. The accuracy of predictions was tested against observed patterns of species distribution and richness as analyzed from Japanese pelagic longline logbook data (1950-2000). Japanese logbook data represent the world's largest longline fleet and the only globally consistent data source, reporting species composition, catch, and effort for all tuna (*Thunnini*), billfishes (*Istiophoridae*), and swordfish (*Xiphiidae*); (Worm et al., 2005).

Methods

Database

     All available information was gathered regarding the ambient water temperatures inhabited by tuna and billfish species. In addition to using web-based search engines to locate electronic journals, databases such as the International Centre for Living Aquatic Resources Management (FishBase), Aquatic Sciences and Fisheries Abstracts (ASFA), Food and Agricultural Organization of the United Nations (FAO), and the Tuna Research and Conservation Centre (TRCC), were used.

     A database was constructed that combined results of all available studies involving ambient temperature preferences of tuna and billfish (Appendix A). For each reference, the species studied and the ocean in which the study took place was recorded numerically: Atlantic Ocean (1), Pacific Ocean (2), and Indian Ocean (3). Location was entered in latitude (Lat) and longitude (Lon), where positive integers represent North and East coordinates and negative integers represent South and West coordinates. Data collection method (d) used in each study were coded as follows: fisheries data (1), satellite GPS tracking (2), acoustic tracking (3), ultrasonic telemetry (4), aerial surveys (5), and captive studies (6). The sampling size per study (n) was entered as the number of sets in the case of fishing data, number of individual fish in the case of tracking or captive studies and number of sighted schools in the case of aerial surveys. Month was entered (t) such that the number entered represented the month in which the study took place, 0 denoting a study that lasted for more than one year. The decade (y) of study was entered with the number representing the decade of the study (9 = 1990-1999). The data source (s) was categorized as follows: primary, peer-reviewed study (1), secondary, peer-

reviewed historical analyses (2), secondary reference (3), and literary (book) reference (4).

For each species, temperature information was categorized into minimum and maximum water temperature tolerances [T(mn)/T(mx)] and preferences [P(mn)/P(mx)] experienced by all individuals of a species in a specified study. Temperature tolerances represent the minimum and maximum water temperatures in which the species was documented to have lived. Temperature preference denotes a temperature range where the species spent the majority time for the duration of the study as well as a point estimate (P) which referred to the temperature where the species was most commonly found. As data was collected from a wide range of sources and using a range of different collection methods, water temperature preferences could not be generally entered in terms of statistical distribution. Temperature range (R) represents the maximum temperature differential experienced by all the species.

T, P, and R measurements were compiled for 21 species of tuna and billfish in both the adult (>5 years) and juvenile (.5 - 1 years)) life stages and water temperature tolerances [(T(mn)/(mx)] and overall preferences were collected for the larval (0 - .5 years) life stage of species for which data were available. Furthermore, we added bonitos (*Sarda*, spp.) to the study due to the fact that, while they lack the tuna characteristic of endothermy, they are frequently classified in the *Thunnus* genera and share many similarities with this group (Collette & Nauen, 1983). Bonitos were not, however compared against fisheries data. Temperature studies were sparse for some species (kawakawa, little tunny, bonitos), was entirely absent for the *Istiophoridae* spearfishes (shortbill, longbill, Mediterranean).

Inter-species temperature analysis

Temperature tolerance and preference averages were calculated from the database for each of 21 species of tuna and billfish in order to compare these variables between species. The same analysis was performed in order to compare these temperature variables between different life stages of tuna and billfish.

Temperature-predicted global range analysis

Global ranges were predicted using temperature tolerances and preferences for each species as calculated from the database in conjunction with fine-scale (0.5° resolution) SST data. These data were provided by the NOAA/NASA Advanced Very High Resolution Radiometer (AVHRR) Oceans Pathfinder project covering 1998-2002, with error estimates ranging from 0.3-0.5C°. By comparing SST in each 5° by 5° global cell with averaged temperature preference data from the database, predictive global ranges were constructed for each species. Temperature-predicted species ranges for 13 species were compared against patterns of catch per unit effort (CPUE) as calculated from Japanese pelagic longline logbook data, also binned on a global 5° × 5° grid. This data set encompasses the estimated global range of all tuna and billfish species excluding coastal areas which are protected by individual countries Exclusive Economic Zones. However, Australia, New Zealand and other Pacific nations have granted coastal access to Japanesse vessels through joint agreements. Depth correction of longline catches was applied to account for increasing fishing depth over time (Ward & Myers, 2005). To calculate CPUE from depth corrected data standardized subsample sizes of 1000 hooks were used because this corresponds to the average number of hooks in a single longline

set. Longline data from the 1960's and 1990s were selected for comparison due to the

fact that this period saw a large increase in fishing effort over time (Pauly et al., 2002).

Species for which there was a lack of data (bonitos, kawakawa, little tunney) and those

which were absent from Japanese longline records (white marlin, striped marlin, slender

tuna) were omitted from this comparison (Appendix C).

Temperature-predicted global species richness analysis

Tuna and billfish species richness was predicted from temperature data using a

third-order polynomial regression fit of overall species richness (number of species)

against water temperature tolerances obtained from the database. Regressions of this type

were constructed in order to compare the amount of variability in species distribution

which was accounted for by ambient water temperature between ocean basins, genera,

and cumulatively. By inputting aforementioned satellite-derived SST data into the third-

order polynomial regression equation predicting cumulative species richness ($y=-0.007x^3$

$+ 0.29x^2 - 2.49x + 7.35$) and using map-making software (Matlab) a predictive index of

global species richness was constructed. The accuracy of temperature-predicted global

species richness was compared against spatial patterns of global species richness obtained

from Japanese logbook data in a standardized sample of 50 individuals. The accuracy of

richness predictions was further analyzed by plotting predicted species richness against

actual species richness obtained from longline data among 5° by 5° individual cells (n =

2953).

Results

Inter-species temperature analysis

Temperature preference data averaged out for and compared between 21 species of tuna and billfish in the adult life stage revealed maximum ranges of temperature tolerances among bluefin tunas and swordfish followed by bigeye and albacore tunas (Table 1; Fig.1). Also, while temperature preferences for these species were approximately centered around the tolerance mean, preferences for many species of marlin (7*sp*.) and sailfish (2*sp*.) were skewed towards the warmer extreme of their temperature tolerance. Furthermore, small tropical tunas (kawakawa, little tunny, skipjack, and bonitos) were found to be more tolerant of high water temperatures than larger species of tuna and billfish (bluefin, bigeye, yellowfin, and swordfish); (Table 1; Fig. 1). Data was not averaged for the juvenile and larval life stages for individual species, and ambient temperature preferences were not calculated for certain species due to the fact that we were unable to locate studies containing this data. Instead, data for each life stage were independently analyzed in order to compare the ambient temperature tolerances and preferences between the adult, juvenile and larval life stages for these species (Fig. 2). Results indicate that cumulatively, species spawn in waters which are much warmer ($\Delta T \sim 5°C$) than those inhabited by adults, and were actually outside of the adult temperature tolerance range in some species, such as southern and pacific bluefin tunas, and albacore tuna (Table 1; Fig. 2). The results from the juvenile life stage do not show this trend, although data for this life stage were not available for any species of *Istiophoridae* which would affect the accuracy of this comparison.

Table 1. Database summary for 21 species of tuna and billfish indicating temperature tolerances [T(mn)/T(mx)], preferences [P(mn)/P(mx)/P], and ranges (R) in °C from >200 sources. Bracketed numbers represent number of sources which support the datum. Ocean codes: 1=Atlantic, 2=Pacific, 3=Indian.

Species	Latin Name	Ocean	T(mn)	T(mx)	P(mn)	P(mx)	Preference	Range
Northern Bluefin (32)	*Thunnus thynnus*	1,	7.63	26.17	14.90	22.93	20.84	18.54
Southern Bluefin (10)	*Thunnus maccoyii*	1,2,3	7.42	22.00	13.50	17.50		14.58
Pacific Bluefin (12)	*Thunnus orientalis*	2,3	6.98	24.00	15.00	20.25	18.50	17.02
Bigeye tuna (29)	*Thunnus obesus*	1,2,3	9.25	26.45	16.95	22.32	21.56	17.20
Yellowfin tuna (18)	*Thunnus albacares*	1,2,3	16.35	27.73	20.53	25.79	23.10	11.37
Albacore tuna (24)	*Thunnus alalunga*	1,2,3	11.29	23.90	14.93	19.47	22.50	12.61
Skipjack tuna (23)	*Katsuwonus pelamis*	1,2,3	16.63	29.47	18.49	25.20	24.25	12.84
Kawakawa (2)	*Euthynnus affinis*	2,3	16.50	30.50				14.00
Slender tuna (4)	*Allothunnus fallai*	1,2,3	15.50	19.00				3.50
Striped Bonito (1)	*Sarda orientalis*	2,3	14.00	23.00				9.00
Atlantic bonito (1)	*Sarda sarda*	1,	12.00	27.00				15.00
Eastern pacific bonito (2)	*Sarda chiliensis chiliensis*	2,	18.80	30.50	21.50	25.45		11.70
Little tunny (2)	*Euthynnus alletteratus*	1,	18.00	30.00				12.00
Swordfish (18)	*Xiphias gladius*	1,2,3	8.89	27.86	14.57	22.83	18.00	18.97
Indo-pacific blue marlin (4)	*Makaira mazara*	2,3	19.75	29.05	26.00	27.00		9.30
Atlantic blue marlin (6)	*Makaira nigricans*	1,	20.68	30.05	25.00	30.00	30.00	9.37
White marlin (10)	*Tetrapturus albidus*	1,	21.33	27.57	24.80	26.85	24.00	6.23
Black marlin (3)	*Makaira indica*	1,2,3	16.17	30.17	25.50	29.50		14.00
Striped marlin (13)	*Tetrapturus audax*	2,3	16.82	25.49	21.23	24.00	23.20	8.67
Atlantic Sailfish (14)	*Istiophorus albicans*	1,	19.20	27.90	25.95	27.85	21.00	8.70
Pacific Sailfish (7)	*Istiophorus platypterus*	2,3	20.50	27.85	25.00	27.80	26.68	7.35
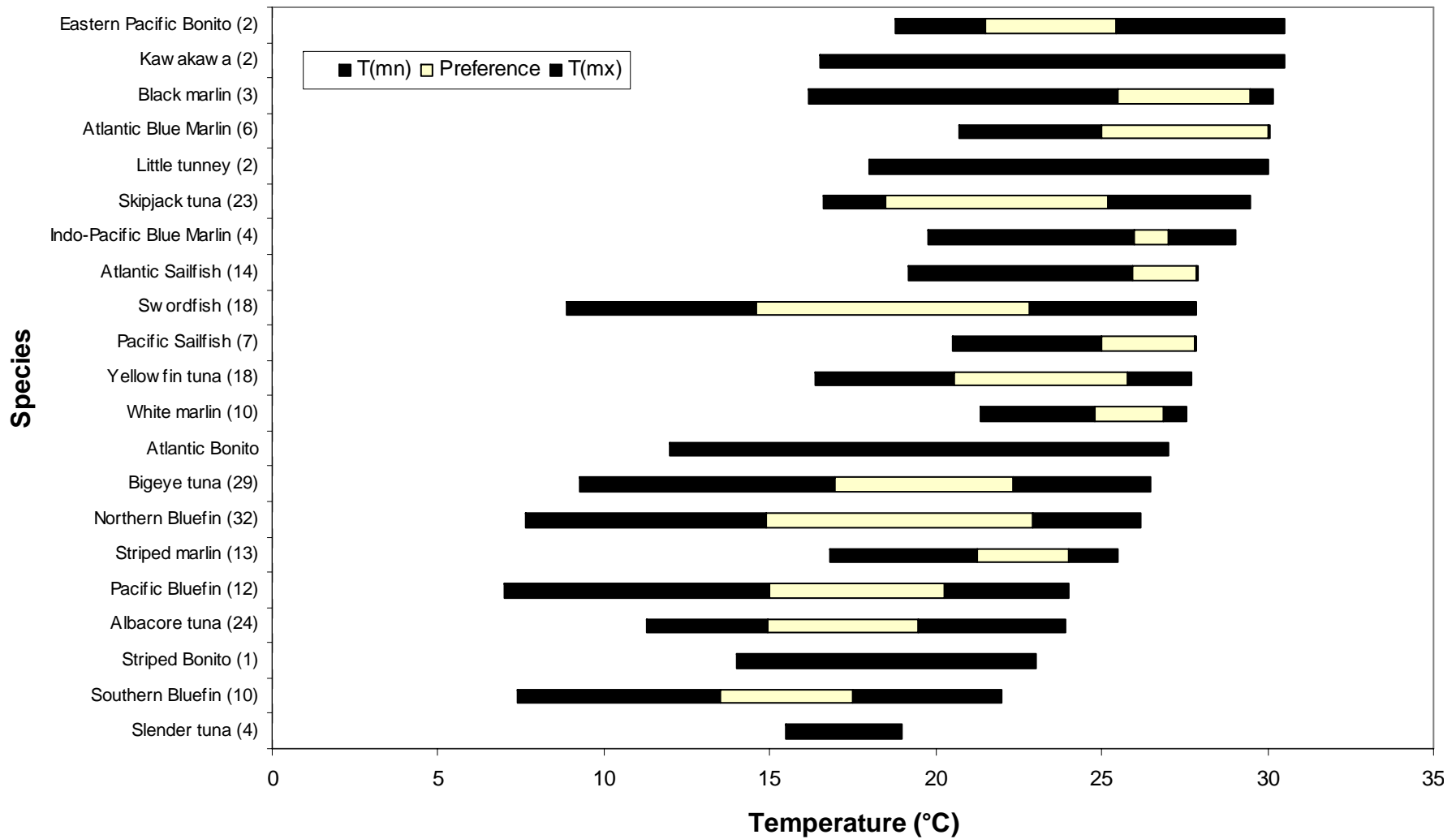
Fig. 1. Ambient water temperature tolerances [T(mn)/T(mx)] and preferences (P) for 21 species of tuna and billfish as calculated from database. Bracketed numbers represent the number of sources which support the data.
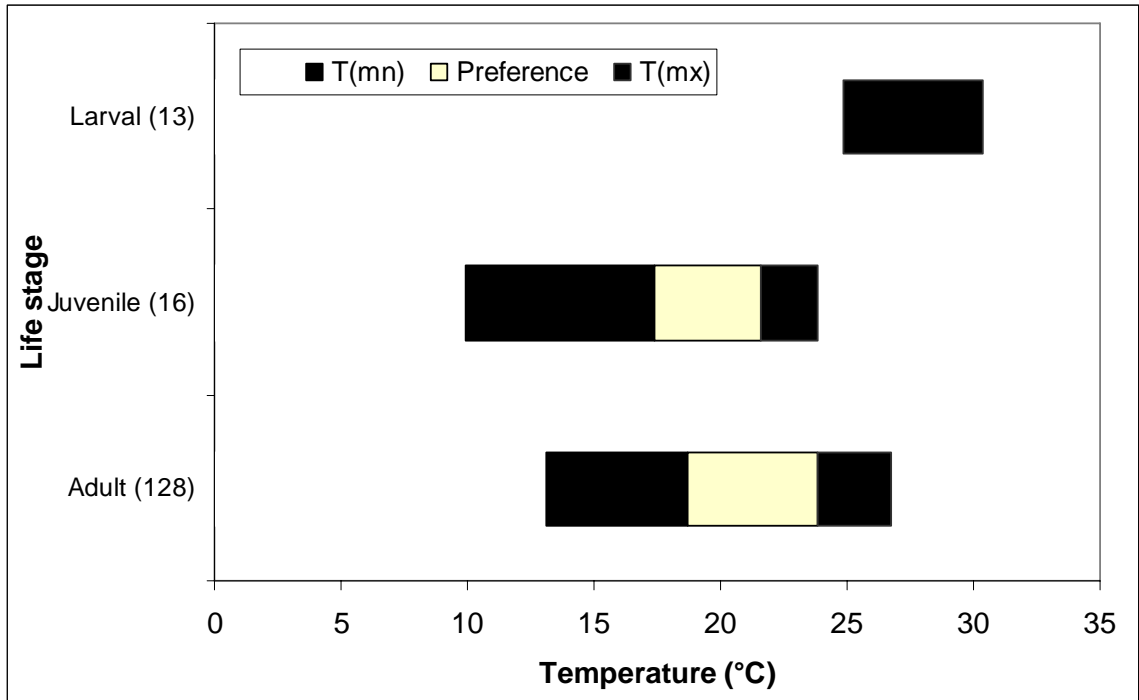
Fig. 2. Cumulative temperature tolerances [T(mn)/T(mx)] and preferences (P) compared between larval (0 - .5 yrs.), juvenile (.5 – 5 yrs.), and adult (>5 yrs.) life stages for 21 species of tuna and billfish. Bracketed numbers represent the number of studies included.

Temperature-predicted global species distribution analysis

Using individual species temperature data analyzed from the database (Table 1; Fig. 1) in conjunction with satellite-derived SST data, global species ranges were predicted for 21 species of tuna and billfish (Fig. 3A-J). The accuracy of predictions for 16 species were verified by comparing them against global species biomass distribution patterns as analyzed from Japanese pelagic longline data (Fig. 3K-T). Species that were not sampled or reported in the longline data were omitted from this comparison (Appendix C). Furthermore, as geographical ranges were discrete for some species, predicted ranges were consolidated into a single prediction for ease of analysis. Such simplifications were made for bluefin tuna (Atlantic and Pacific), blue marlin (Indo-Pacific and Atlantic), and sailfish (Pacific and Atlantic). Accuracy was found to be greatest in surface-dwelling marlin and sailfish (*Istiophoridae*) and poorest among temperate and subtropical species of tuna (albacore, bigeye, and bluefin tunas). Accuracy of predictions was further observed to be greatest at northern and southern extent of species ranges, with accuracy diminishing towards equatorial regions.

A)

Albacore tuna

B)

Bluefin tuna

C)

Southern Bluefin

D)

Bigeye tuna

K)

Albacore Tuna / 1000 hooks 1960

L)

Bluefin Tuna / 1000 hooks 1960

M)

Southern bluefin tuna / 1000 hooks 1960's

N)

Bigeye Tuna / 1000 hooks 1960

15

E)

Yellowfin tuna

F)

Skipjack tuna

G)

Swordfish

H)

Blue Marlin

O)

Yellowfin tuna / 1000 hooks 1960's

P)

Skipjack tuna / 1000 hooks 1960's

Q)

Swordfish / 1000 hooks 1960's

R)

Blue Marlin / 1000 hooks 1960

I)

S)

J)

T)
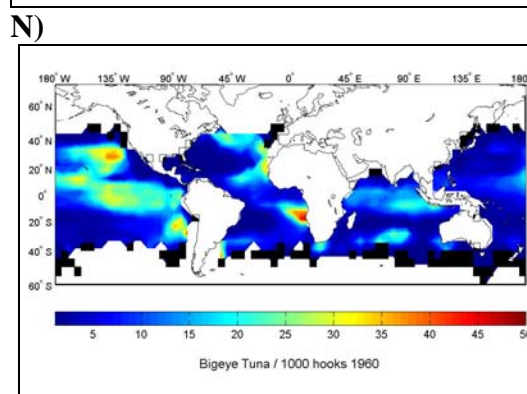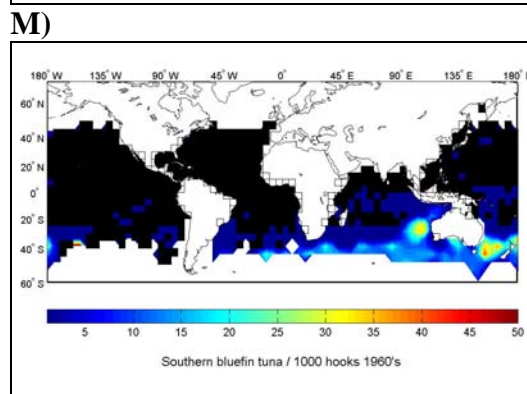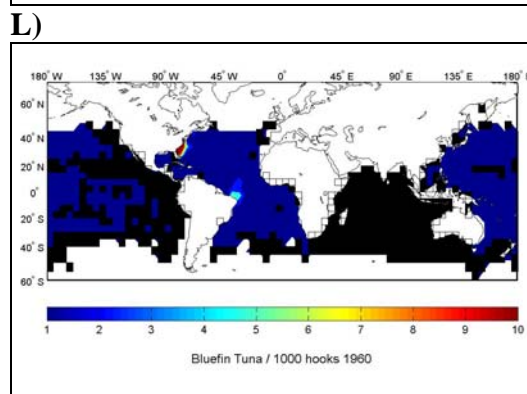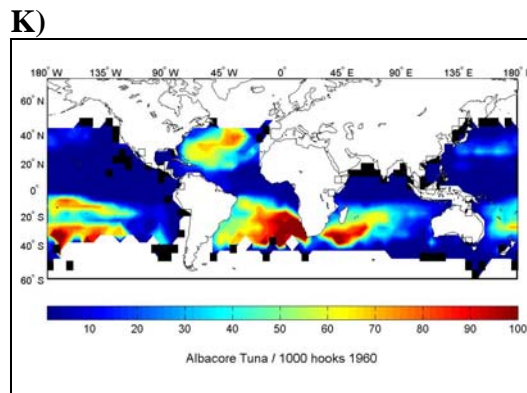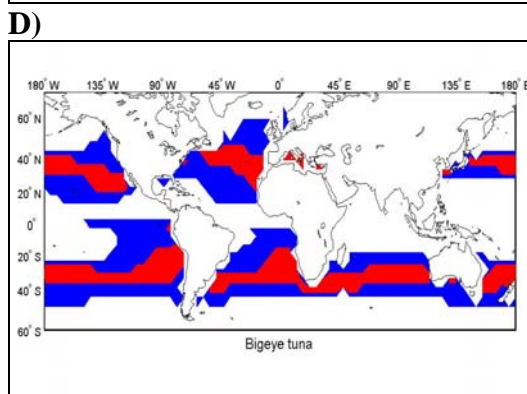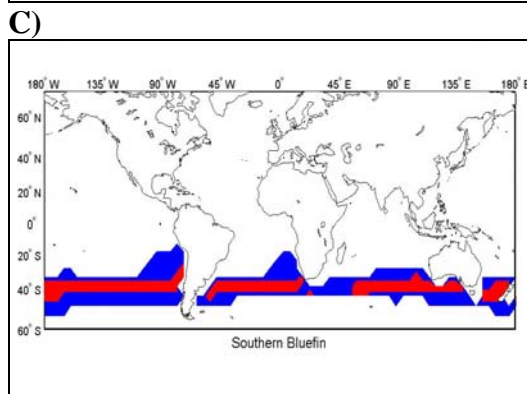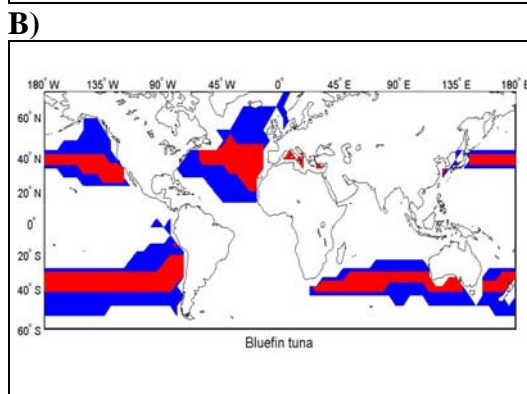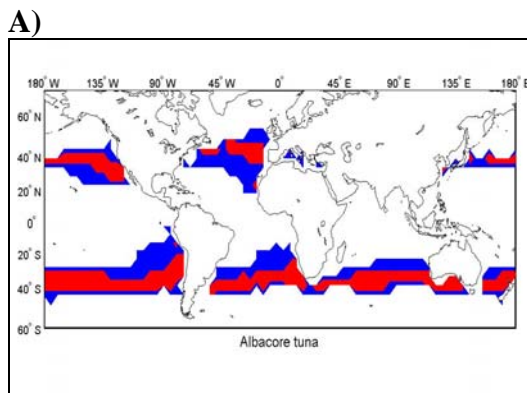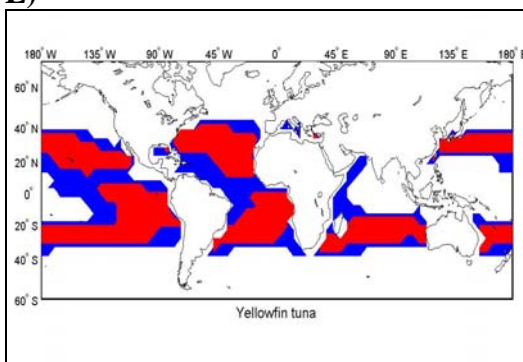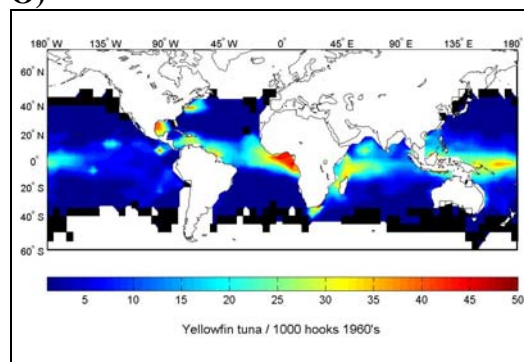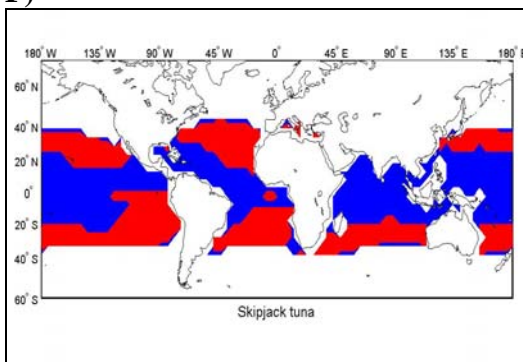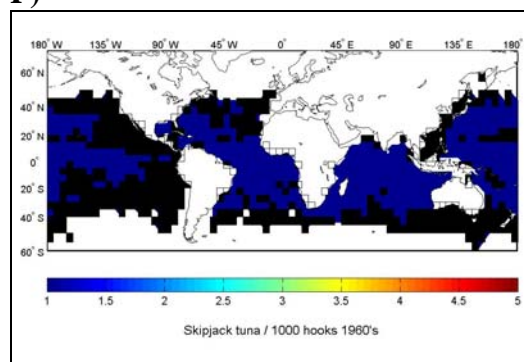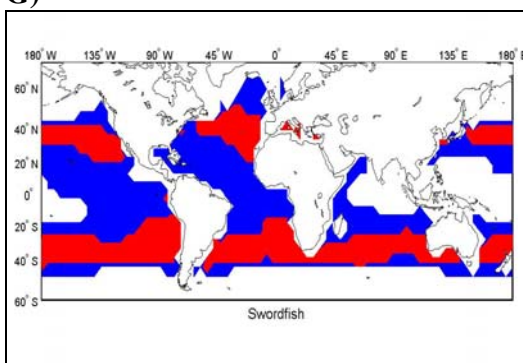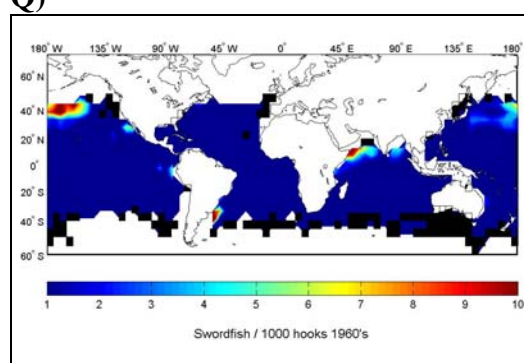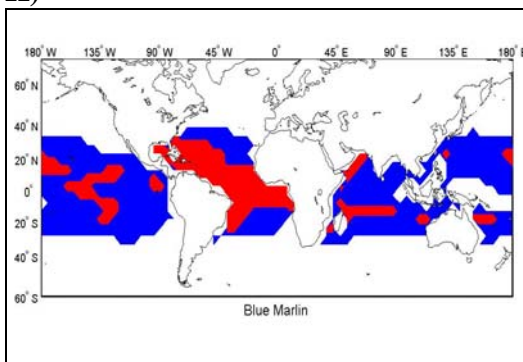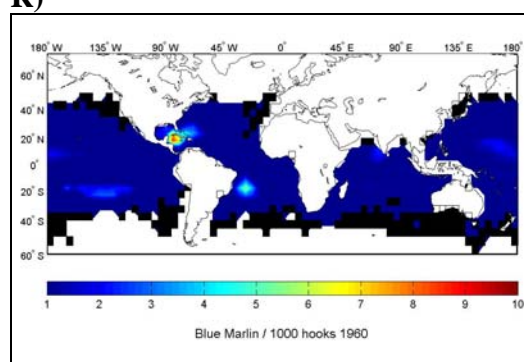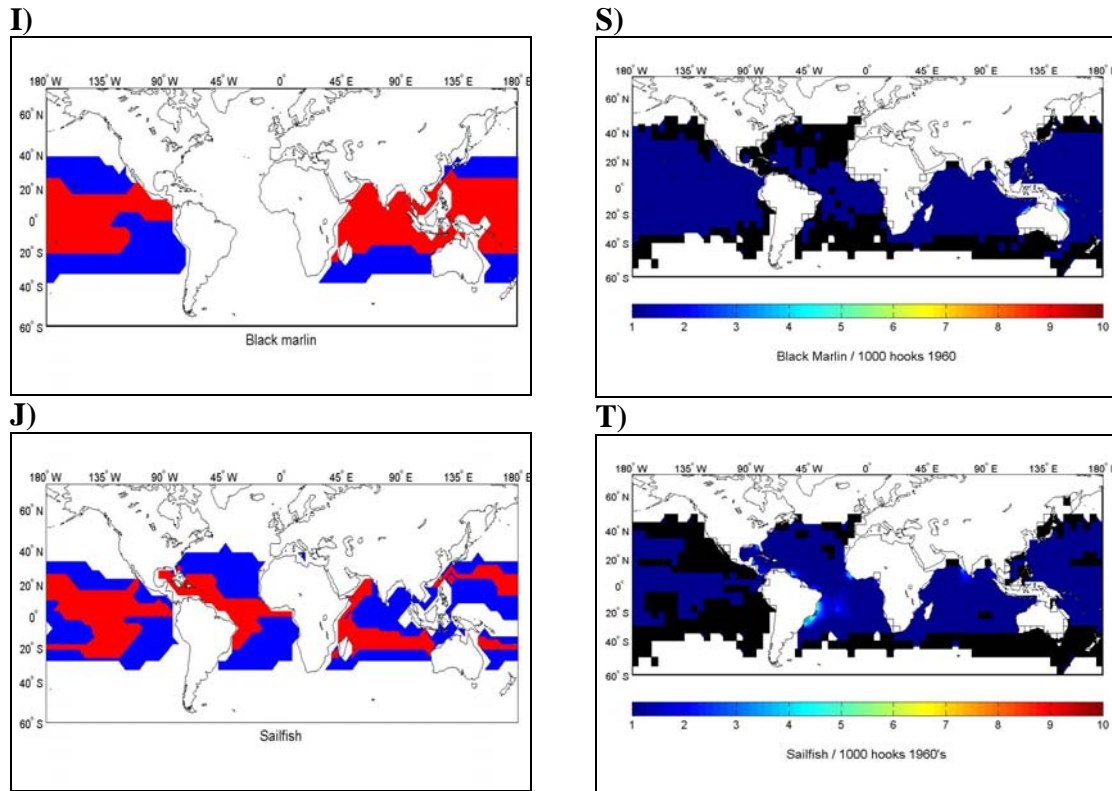
Fig. 3. (A-J)Spatial patterns of predicted species distribution for 16 species of tuna and billfish based on temperature database and satellite-derived SST. Red indicates preferred SST, blue indicates tolerated SST. Spatial patterns of tuna and billfish catch per unit effort in the 1960's. Colors depict the number of fish caught/1000 hooks on pelagic longlines set by the Japanese fleet. Black indicates complete absence of the species from catch (K-T); (Worm & Tittensor, unpublished data).

Temperature-predicted global species richness analysis

Polynomial regression fit of tuna and billfish species richness against water temperature compared between genera (Fig. 4) indicates a lower predicted optimal water temperature for *Thunnini* (~21°C; R^2 = 0.9328) than for *Istiophoridae* and *Xiphidae* (~25°C; R^2 = 0.8902). Richness comparisons across ocean basins (Fig. 5) predict highest species richness in the Pacific (~22°C; R^2 = 0.9445) followed by the Atlantic (~23°C; R^2 = 0.8979) and Indian Oceans (~20-26°C; R^2 = 0.5879). Polynomial regression fit of cumulative species richness against water temperature (Fig. 6) yielded a predicted optimal water temperature of ~23°C (R^2 = 0.9566). Across these analyses, a very high amount of variation (89-96%) was explained by water temperature, except for the Indian Ocean, where data for only 2 species were available.

These predicted patterns of species richness (Fig. 7) were compared against actual species richness distribution analyzed from Japanese longline logbook data (Worm et al., 2005); (Fig. 8). Discrepancies were noted particularly in the Indian Ocean where latitudinal patterns of predicted species richness are opposite to what longline data indicate. Predictions were accurate for the Gulf Stream region in the northeast Atlantic, but less accurate for the southern Atlantic, where peak patterns of observed richness at equatorial regions were not matched by our predictions. Furthermore, predictions were accurate for the western Pacific region, and diminished towards the eastern Pacific. Predicted and observed global species richness, however, were found to occur at intermediate latitudes (20 to 40°N and S), with a negative trend towards polar and equatorial regions. Linear regression analysis of predicted species richness against actual

species richness as calculated from Japanese longline logbook data per 5° by 5° cell (Worm et al., 2005), indicated some significant overlap (R=0.3893; P<0.0001); (Fig. 9).
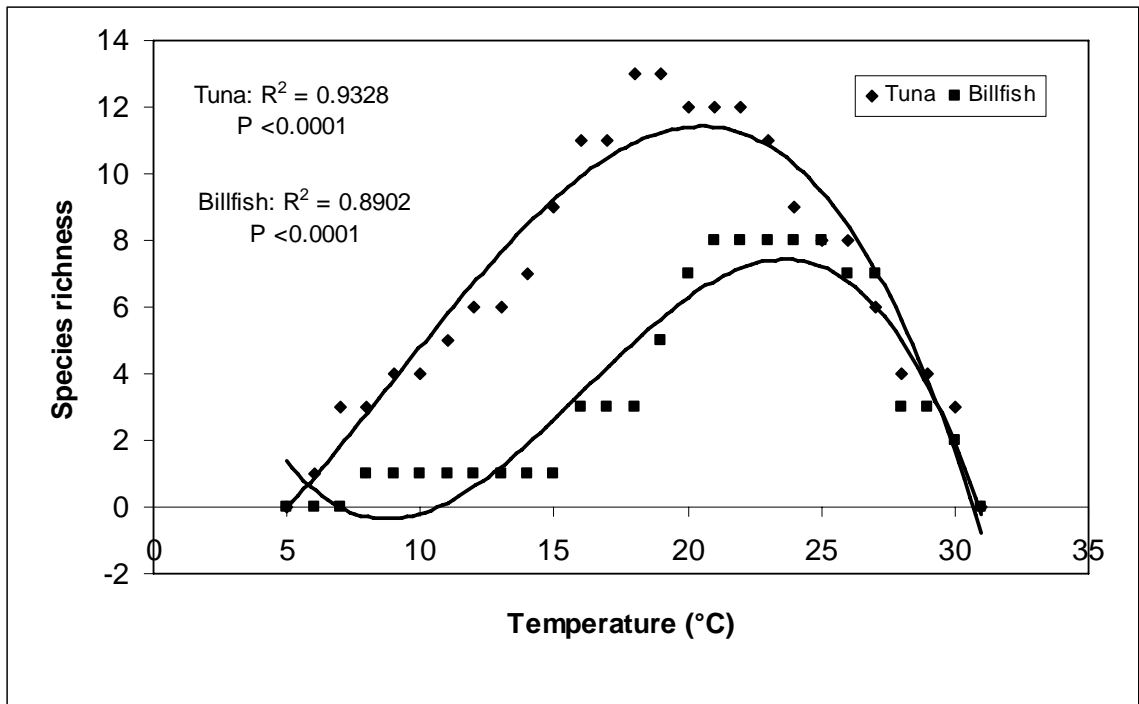
Fig. 4. Polynomial regression fits of predicted species richness against water temperature compared between genera, *Thunnini*: $y = -0.0024x^3 + 0.0644x^2 + 0.4312x - 3.502$, *Istiophoridae, Xiphidae*: $= -0.0047x^3 + 0.2294x^2 - 2.9266x + 10.856$
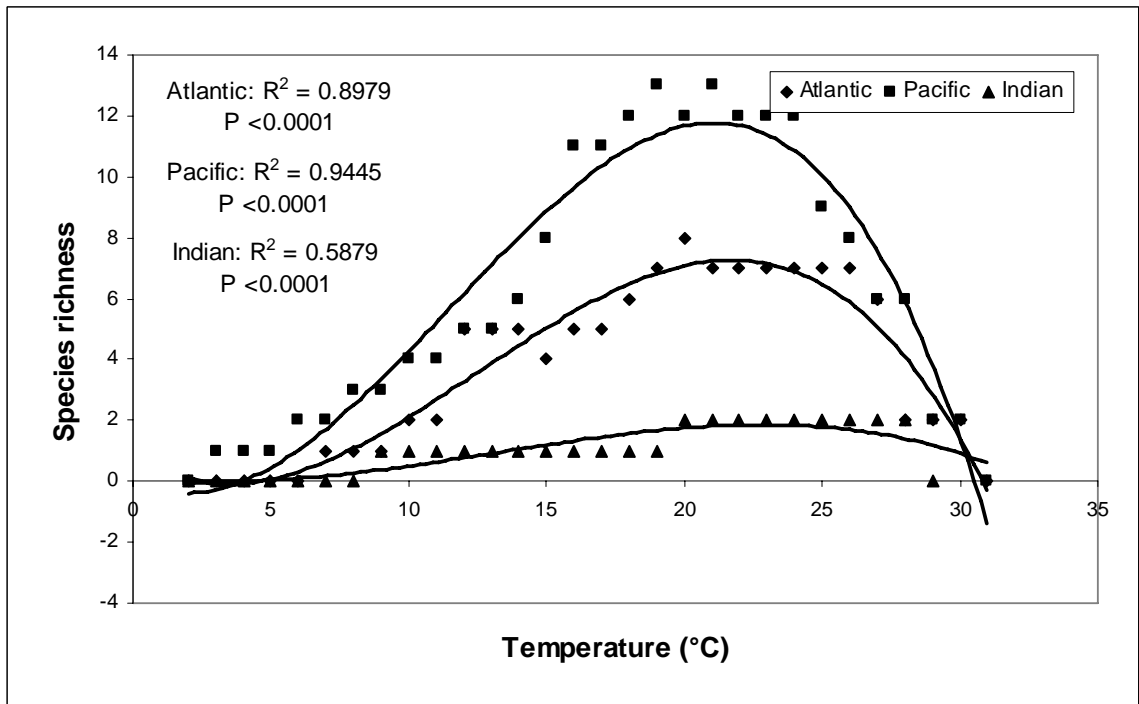
Fig. 5. Polynomial regression fits of predicted species richness against water temperature compared across oceans, Pacific: $y = -0.004x^3 + 0.15x^2 - 0.89x + 2.07$; Atlantic: $y = -0.002x^3 + 0.08x^2 - 0.44x + 0.3$; Indian: $y = -0.001x^3 + 0.06x^2 - 0.92x + 4.76$.
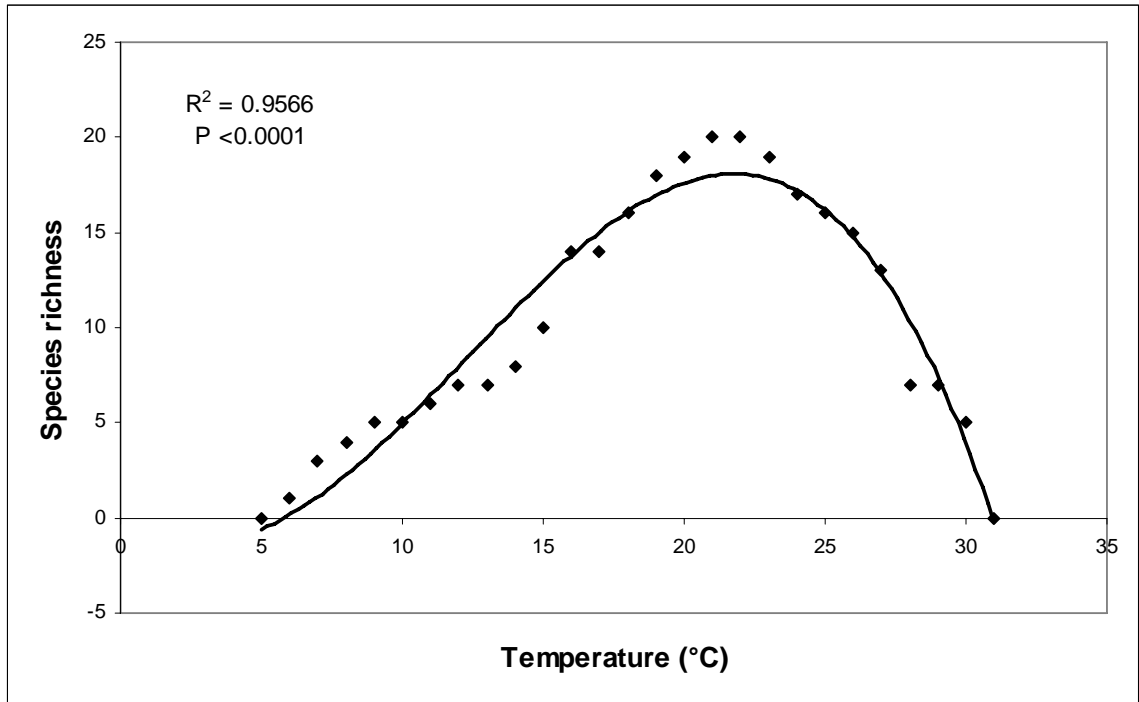
Fig. 6. Polynomial regression fit of total predicted species richness against ambient water temperature: $y = -0.007x^3 + 0.29x^2 - 2.49x + 7.35$.
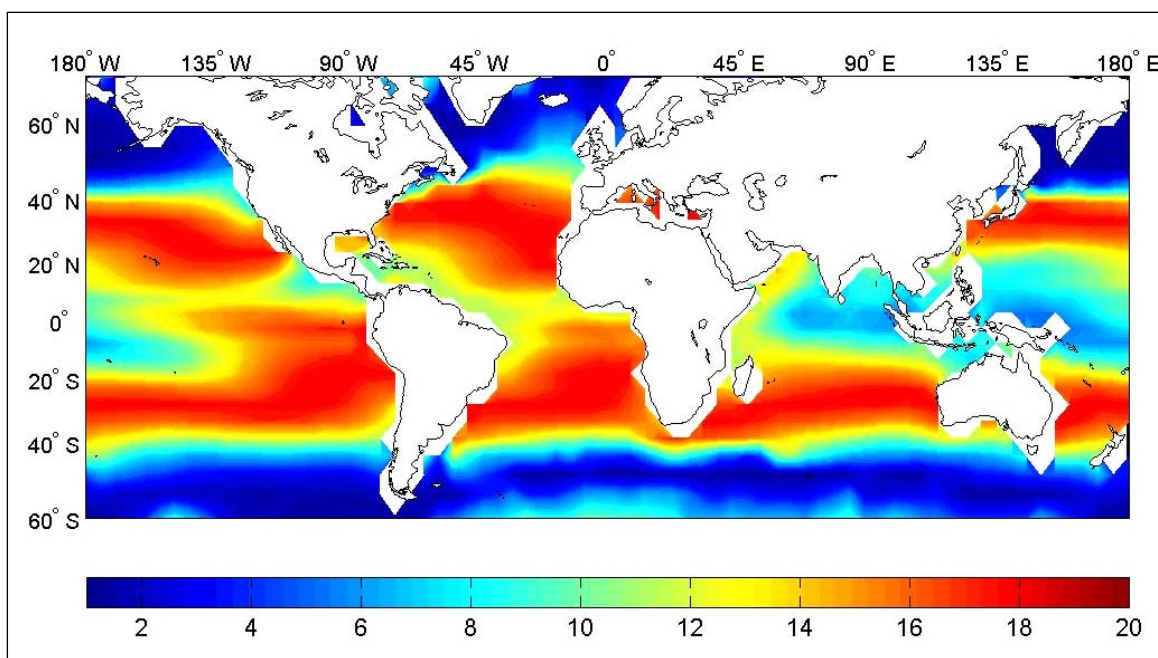
Fig. 7. Predicted spatial patterns of tuna and billfish species richness as a function of SST as defined by polynomial regression fit of total species richness against water temperature ($y=-0.007x^3 + 0.29x^2 - 2.49x + 7.35$). Color codes depict the number of species predicted to occur.
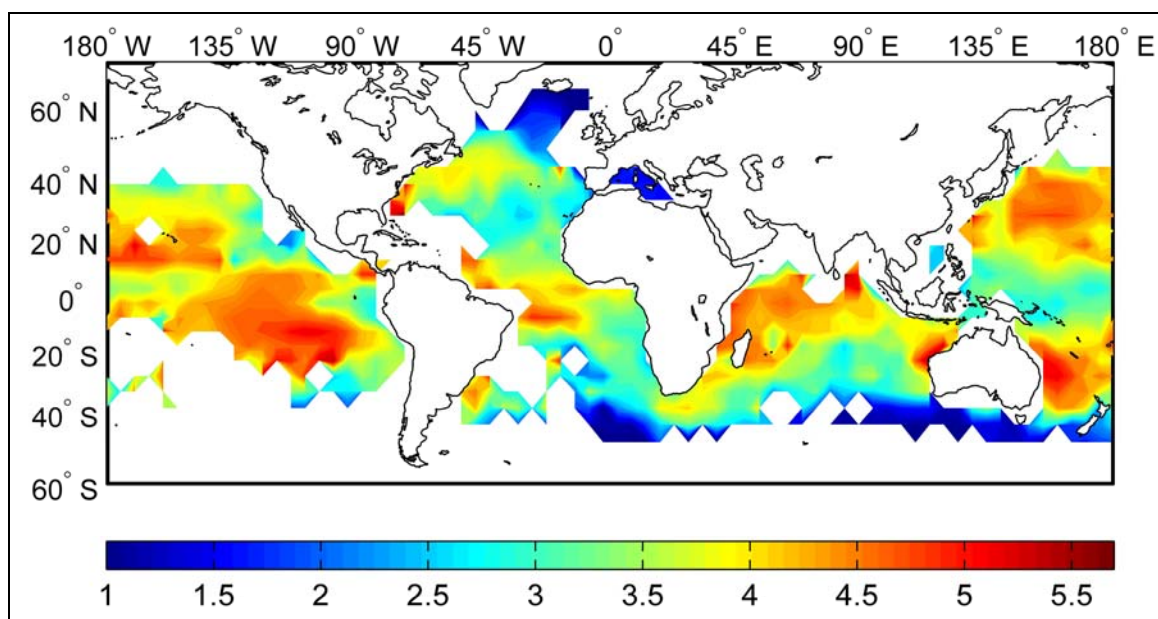
Fig. 8. Actual observed pattern of species richness from Japanese pelagic longline data. Colors indicate the number of species in a standardized sample of 50 individuals (Worm et al., 2005).
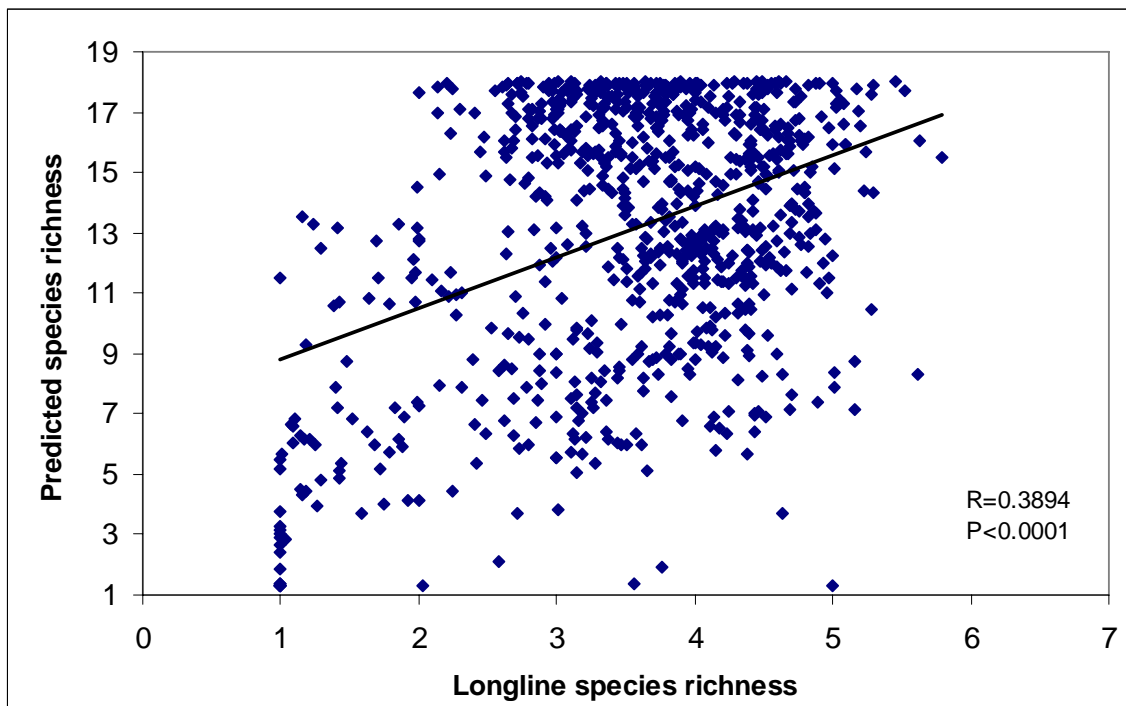
Fig. 9. Correlation between predicted and observed species richness as analyzed from longline data in a standardized sample of 50 individuals. Data points correspond to individual 5° by 5° cells, regression line to best linear fit (Worm et al., 2005).

Discussion

This thesis set out to analyze the effects of ambient temperature on global species distribution and species richness patterns for tunas (*Thunnini*) and billfishes (*Istiophoridae, Xiphiidae*). We found that widest temperature ranges occurred among swordfish, bigeye, albacore and bluefin tunas (Fig. 1). This is likely due to the fact that these species have unique adaptations for temperature regulation. Hence they can occur from subtropical to temperate waters and show longer migrations and deeper dives than other species of tuna and billfish (Fromentin & Fonteneau, 2001; Sund, Blackburn & Williams, 1981). For example, bigeye tuna are capable of diving to depths of 600 m (Brill & Lutcavage, 2001; Hanamoto, 1987), and northern bluefin tunas are known to make frequent trans-Atlantic migrations (Block et al., 2005). Furthermore, while temperature preferences for these species were normally distributed about the temperature tolerance mean, temperature preferences for most marlins and sailfishes (*Istiphoridae*) were largely distributed on the warm extreme of the temperature tolerance distribution. This is due to the fact that these species are predominantly epipelagic, remaining within 8°C of the upper mixed layer above the thermocline, (Brill et al., 1993) making only occasional dives to depths of up to 209 m (Block, Booth & Carey, 1992). This is a stark contrast to previously-mentioned subtropical or temperate species, all of which are capable of diving to depths in excess of 200 m where temperatures are much lower. Northern bluefin tuna for example, are able to dive to depths in excess of 1000 m, encountering an exceptionally wide range of temperatures (Block et al., 2005). Small, tropical tuna species (kawakawa, little tunny, eastern pacific bonito, skipjack tuna) were found to posses a higher tolerance for warm waters. This is possibly a result of their large surface-

area-to-mass ratio leading to endothermic limitations, thus making warmer water temperatures essential for survival.

Temperature predicted global range distributions for tunas (*Thunnini*) and swordfish (*Xiphiidae*); (Fig. 3A-G) were consistently accurate at predicting the northern and southern extent of species distribution (Fig. 3K-Q), but less accurate at predicting equatorial range boundaries. Via increased physiological regulation, tunas and swordfish are able to make larger horizontal and vertical excursions than marlins and sailfishes. This high mobility, specifically the vertical movements into cooler subsurface waters are likely to reduce the correlation with SST (Zagaglia, 2004). This suggests that the maximum temperature tolerance prediction is possibly low for these species. This may be the result of issues such as depth of sampling effort and/or habitat features. Also, the spawning behavior of some species, such as northern bluefin which spawn in very warm waters in the Gulf of Mexico (Schaefer, 2001), is a likely factor influencing the accuracy of predictions. The effect of these features on the accuracy of predictions is discussed below. Furthermore, temperature predicted preference ranges did not coincide with spatial patterns of high species biomass. However, this is not particularly meaningful as patterns of high species biomass may be the result of a variety of factors irrespective of temperature. Furthermore, similar studies (Worm, Lotze & Myers, 2003), have documented low longline catches recorded in areas of high species diversity, and high catch rates in areas of low species diversity. This may indicate low fish productivity in areas of high species richness and density.

While temperature predicted distribution of swordfish (*Xiphiidae*) was accurate at predicting patterns of high species biomass, it was less accurate at predicting distributions at equatorial region (Fig. 3Q). Although swordfish and other billfishes share a common ancestry and have many convergent features in external morphology, the behavior of swordfish is very different from other billfish (Block, 1990). In the open ocean, swordfish make large vertical excursions, coming close to the surface at night and diving as deep as 600 m during the day (Carey, 1990). Moreover, though all billfish possess a unique thermogenic organ in their head, this is expressed to a much greater extent among swordfish, allowing it to inhabit colder water (Block et al., 1992).

Temperature predicted species ranges for marlins and sailfish (*Istiophoridae*); (Fig. 3H-J) were a good match with patterns of species biomass (Fig. 3R-T). Furthermore, regions of peak species CPUE (and by inference, biomass) were covered or closely approximated by temperature preference predictions for all species. The accuracy of these predictions is likely due to the facts that these species are surface dwelling, dive less deeply, and spawn year round in waters within their temperature tolerances.

Predicted species richness as a nonlinear function of ambient temperature compared between tuna and billfish (Fig. 4) appeared highly correlated, with optimal temperature predicted at 21°C for tunas and 24°C for billfishes. Given that tuna as a group are generally more temperate, more migratory and deeper-diving than billfish (except swordfish), these results are expected. Similar regression analysis compared across ocean basins (Fig. 5) were also positively correlated, with peak species richness predicted to occur in the Pacific Ocean, followed closely by the Atlantic. Due to the near absence of temperature tolerance data for Indian Ocean tuna and billfish, results for this

region were less credible. As it is known that the Indian Ocean has four dominant tuna species (albacore, bigeye, yellowfin, and skipjack tunas) and 4 billfish species (sailfish, blue marlin, striped marlin, and swordfish), predictive peak species richness of two species is a result of data deficiency, rather than low species richness (Anonymous, 2004; Nakamura, 1985). Cumulative species richness plotted against water temperature was highly correlated, with optimal water temperature predicted at ~22.5°C (R^2 = 0.9566; P<0.0001); (Fig. 6).

Temperature-predicted global richness peaked at intermediate latitudes (20 to 40° N or S), with declining richness towards the poles and equator (Fig. 7). Interestingly, this functional form is very similar for observed species richness of tuna and billfishes as well as foraminifera (Worm et al., 2005) and other zooplankton groups (Rutherford, D'Hondt & Prell, 1999). This suggests that the pattern of global species richness predicted here may be similar across numerous trophic levels, and diverge from patterns on land, where diversity universally peaks around the equator (Hillebrand, 2004). A decrease in species richness was documented in the western Pacific "warm pool", where exceptionally high temperatures (>30°C) are found (Worm et al., 2005). These extreme temperatures are likely unsuitable for tunas, which generate large amounts of metabolic heat. For example, Bluefin tuna spawning in the similarly warm Gulf of Mexico were observed to make repeated, brief excursions to warm surface waters to release eggs followed by extended 'cooling' dives to deeper waters (Block, personal communication). This is theorized to be a mechanism to tolerate extreme warm temperatures, which are likely unsuitable for adults of the species, but essential for rapid larval development. When compared against global species richness data analyzed from Japanese pelagic longline catch records (Fig.

8); (Worm et al., 2005) species richness predictions appeared positively correlated. The authors found peak tuna and billfish species richness and density at intermediate latitudes (15 to 30°N or S), with optimal water temperature around 25°C. Similar analysis of scientific-observer records from pelagic longline fisheries in the Atlantic and Pacific oceans (Worm et al., 2003) also recorded peak predator richness and density at intermediate latitudes (20 to 30° N and S) with optimal water temperature between ~20 to 26°C. While patterns of species richness are similar in all three studies, our temperature-predicted richness appeared distributed at slightly higher and lower latitudes than those of Worm et al. (2003, 2005). Discrepancies were also noted between optimal water temperatures found among the three studies. Optimal water temperature predicted in this study (~22.5°C) was lower than aforementioned studies indicate. For example, longline data indicated species richness declines around cooler upwelling regions in the eastern Atlantic and Pacific Oceans (Worm et al., 2005). These same regions are predicted to be areas of high species richness in our analysis, reflecting variation in assumed optimum temperatures. Furthermore, while longline data indicate high species richness in the equatorial Indian Ocean region, our data indicate high species richness as far as 40°S. Cumulatively, these comparisons suggest that our predicted global species richness distributions peak at about ~2°C lower than fisheries data indicate. The fact that this error pattern is consistent throughout the results, indicate that this discrepancy may be the result of a variety of factors irrespective of water temperature. Differences relating to methods used to collect and analyze the different datum, depth, spawning behavior, or habitat features are not incorporated directly into any temperature predictions and may be partially responsible for variations between temperature predictions and longline data.

Yet, linear regression analyses of these two data sets (Fig. 9) still revealed a strongly positive correlation between temperature predicted species richness and richness obtained from longline data (R= 0.3894; P<0.0001). It is important to note that longline data included spearfish (*Tetrapturus spp.*) and excluded many smaller tunas (kawakawa, little tunny, slender tuna, and bonitos), as opposed to the predicted data set. Such variation may have influenced the accuracy of predicted global species richness distribution.

Spatiotemporal spawning patterns of tuna and billfish are likely to influence the accuracy of predicted distributions, especially among tunas. All species of tuna are reported to spawn in water temperatures above 24°C (Schaefer, 2001), a behavior believed to be related to an initial existence as tropical, inshore organisms (Sharp, 1978). This would likely not affect accuracy of range predictions for tropical species such as skipjack, yellowfin, marlins, and sailfishes, as they typically inhabit temperatures within this temperature range. However, 24°C is outside or at the upper limit of temperature tolerances for many subtropical or temperate species such as bigeye, albacore, and bluefin tunas. Furthermore, albacore and bluefin tunas exhibit distinct distributions and seasons (Bartoo & Foreman, 1994; Fonteneau & Marcille, 1988; Murray, Dennison & Kempf, 1992; Nishikawa et al., 1985). Peak spawning for albacore apparently occurs in equatorial waters centered around 15°N and 15°S latitudes (Nishikawa et al., 1985; Ueyanagi, 1969). Northern bluefin tuna spawning occurs between 18 to 35°N in the Pacific (Collette & Nauen, 1983), and in the Mediterranean and Gulf of Mexico regions in the Atlantic Ocean (Clay, 1991). Southern Bluefin tuna spawning is restricted to a small area off northwestern Australia (Caton, 1991; Nishikawa et al., 1985). Except for the Mediterranean region, none of these spawning areas are within the predicted habitat

for these species. They do however appear on longline catch records, indicating that the accuracy of predicted ranges for these species may be affected by spawning behavior. These findings further suggest that those species may be vulnerable to fishing pressure during their spawning season. While bigeye tuna do not have restricted spawning regions or seasons, suitable environmental conditions for spawning are significantly warmer than those found within this species normal range. In fact, previous studies (Kikawa, 1966) have indicated that ambient temperatures in excess of 23 to 24°C are essential to reproduction for bigeye tuna. As ~26°C represents the maximum ambient temperature tolerance for bigeye tuna (Table 1; Fig. 1), it is possible that spawning distributions for this species would be outside of predicted distributions. Thus, accuracy of predictions for bigeye tuna would be affected by temporal spawning behavior. Tropical tunas (yellowfin and skipjack) and *Istiophoridae* (marlins and sailfishes) spawn year round in warm equatorial waters in all major oceans (Matsumoto, Skillman & Dizon, 1984; Nishikawa et al., 1985; Stequert & Marsac, 1986). Due to the fact that these species spawn in waters typically within their documented temperature tolerances and in many case preferences (Table 1; Fig. 1), spawning behavior would likely not affect the accuracy of predictions to such an extent. This idea is supported by the fact that known spawning areas for these species (Gunn, Patterson & Pepperell, 2003; Post et al., 1997; Sponaugle et al., 2005), are represented by both longline data and predicted distribution data.

In conclusion, spawning behavior is not directly incorporated into species distribution and richness predictions. As such, the accuracy of predictions was likely affected for species which exhibit distinct spatial and/or temporal spawning distributions, such as temperate and subtropical tunas. Spawning patterns may help to explain the fact

that optimal water temperature predicted for all species was found to be a few degrees lower than that obtained from longline records. In predicting species distribution or richness as a function of water temperature it would be essential to consider spawning areas.

Furthermore, the accuracy of predicted distributions was likely affected by the fact that data collection methods in our database and the Japanese pelagic longline fishery were not standardized. As pelagic longlines were set to an average depth of 100 m and maximum depth of 400 m, a specific range of temperature habitats and species was sampled (Sund et al., 1981; Worm et al., 2005). Swordfish, for example are known to exhibit diel vertical migration from surface waters to depths of over 650 m (Carey, 1990; Sedberry & Loefer, 2001). Diel vertical migration has also been documented in skipjack, yellowfin, bigeye and bluefin tunas and may be a common characteristic among all tuna (Cayre, 1991; Dizon, Brill & Yuen, 1978; Holland, Brill & Chang, 1990a; Kitagawa et al., 2000). While some longline gear fishes at these aforementioned depths, SST represent only surface waters rather than the depth of capture, introducing a marked positive bias. This idea is supported by the fact that discrepancies were found to exist between the optimal species water temperatures obtained in this study (23°C) with that found in a similar study (25°C) where pelagic longline data were analyzed (Worm et al., 2005). These differences corroborate that temperature data obtained from pelagic longline fisheries may be slightly biased. It should be noted that while the majority of the species of both studies were common, there was variation in a small number of species between studies. It is possible that this is also partially responsible for the disagreement between results. Hence, due to limitations such as variable vulnerability of individuals to fishing

gear, random distribution of fishing effort, and random distribution of individuals, variations in CPUE are not purely related to biomass distribution (Zagaglia, 2004).

Variation between the depth at which database temperature information was recorded and that which was used to make predicted ranges (SST) is another possible source of error. The vast majority of information within the database were collected from subsurface tracking experiments such as satellite-tracking (Block et al., 2001), ultrasonic telemetry (Brill et al., 2002), and acoustic tracking (Bach et al., 2003). Such methods accurately record ambient water temperature regardless of depth. Using SST data to predict the occurrence of species for which temperature information was gathered at depth would not fully represent true distribution patterns for these species. Furthermore, it has been claimed that the position of tracking vessels can influence diving behavior and thus temperature inhabited for fish in tracking studies (Holts & Bedford, 1990).

Variation in vertical distribution does not only occur between species but also within species. For example, bigeye tuna catch rates as a function of depth have been shown to vary with latitude in the eastern tropical pacific, possibly relating to zonal currents (Hanamoto, 1974). This variation between the depth at which pelagic longline gear is set and the actual vertical distribution of each species is an additional probable source of error.

In addition to seasonal variation in water temperature, there are more irregular fluctuations such as ENSO (El Niño-Southern Oscillation) in the Pacific (Botsford et al., 1997). ENSO results from atmospheric pressure changes in the central and eastern Pacific that lead to a change in wind patterns, reduced coastal upwelling, and above-normal temperatures across the Eastern Pacific. Additionally, changes in thermocline depth affect

vertical temperature gradients across the eastern tropical pacific (Anda-Montanez et al., 2004). Ecological costs associated with ENSO include reduced primary productivity near the equator (Barber & Chavez, 1986), lower zooplankton productivity in the California Current (Chelton, Bernal & McGowan, 1982), and decreased survival of fish such as salmon, mackerel, and anchoveta (Johnson, 1988; Murphy, 1977) all of which are potential prey of tuna and billfish. Alternatively, ENSO events in the western Pacific cause large zonal displacements of the equatorial warm pool, an oligotrophic region characterized by extremely warm surface waters (>30°C) and high catch rates of skipjack tuna (Lehodey et al., 1997). The relationship between ENSO and the zonal displacement of the warm pool is apparently linked to spatial shifts in skipjack abundances. This suggests that ENSO events are important for skipjack tuna in this region and may be used to predict regions of highest skipjack abundances (Lehodey et al., 1997). A consistent effect of ENSO on tuna and billfish species richness in longline catches 1950-2000 could also be seen across the entire Pacific, indicating massive changes in species distribution associated with ENSO events (Worm et al., 2005). SST data was averaged over a four year period in order to account for long-term variation is SST caused by ENSO. However, the magnitude of such events is unpredictable and difficult to account for. It has been shown that while moderate ENSO events have minimal effects on tuna spatial-temporal patterns, strong ENSO events may have negative effects (Anda-Montanez et al., 2004). Strong ENSO events result in much lower catches recorded for certain surface fisheries, suggesting horizontal migration may be decreasing fish vulnerability (Anda-Montanez et al., 2004). Variation in the depth of the mixed layer caused by ENSO events varies between region, affecting the recorded landings of different species of tuna and

billfish to different extents. The effect of such environmental variation is not accounted for in this analysis and a possible source of error. As sea surface temperatures vary monthly and seasonally in many regions of the world, suitable temperatures for various species are subject to short-term fluctuations. At equatorial regions one of the most important environmental forcing mechanisms is the Intertropical convergence Zone (ITCZ), resulting from the boundary between the southeast and northeast trade winds (Zagaglia, 2004). Strong seasonal cycles are associated with the ITCZ which results in changes in ocean variables such as depth of mixed layer, SST, currents and chlorophyll concentration, all of which influence distribution and abundance of pelagic species (Zagaglia, 2004). Small scale spatial-temporal variation could be corrected for by using SST data to calculate species distribution patterns in both short and long-term intervals. For this to be accurate, detailed, short-term water temperature data would be required for individual species. Hence, a larger database with more detailed information would be required. As the database used here represents a large amount of what is currently available in this field, it may not be feasible at this point in time.

This aforementioned fact raises another important limitation of using temperature as the sole predictor of species distribution. While temperature is a possible strong predictor of distribution for these species (Worm et al., 2005), it is not the only factor. Habitat features such as ocean fronts, reefs, shelf breaks, and seamounts have been shown to be areas of high tuna and billfish abundance and diversity (Worm et al., 2003).

Presumably due to the fact that they concentrate food, enhance local production and increase habitat heterogeneity (Hyrenbach, 2000; Oschilies & Garcon, 1998), fronts and eddies frequently attract large numbers of tuna, and billfish (Fiedler & Bernard,

1987; Laurs, Fiedler & Montgomery, 1984; Santos, 1994; Sund et al., 1981). Persistent fronts also form vital orientation points along ocean-wide migration routes for these species (Polovina et al., 2001). Modeling of tuna behavior supports the conclusion that movements of individuals at fronts are influenced by a multitude of external factors (ambient temperature, prey availability, etc.) which drive internal factors (thermal stress, stomach fullness, etc.); (Kirby, Fiksen & Hart, 2000). For instance, analysis of the Baja California Frontal System (BCFS) has revealed extremely high abundances of swordfish and striped marlin, among many other species (Etnoyer et al., 2004). Cumulatively, these observations support the theory that fronts and eddies are important features contributing to global tuna and billfish abundance and richness. Unfortunately, while SST gradients at persistent ocean fronts are identified, the additional oceanographic features which likely contribute to productivity and richness are not. As such, ocean fronts are not directly incorporated into species distribution or richness predictions.

Topographic features such as reef islands, shelf breaks, and seamounts are characterized by increased turbulence, mixing and mesoscale eddies, which can enhance local production by transporting nutrients into the euphotic zone (Oschlies & Garçon, 1998; Wolanski & Hamner, 1988). These areas are also key feeding areas for pelagic species such as tuna and billfish by virtue of their tendency to concentrate food (Fonteneau, 1998; Haney, 1986; Weimerskirch et al., 2002). Like fronts, these features also form important landmarks during ocean-wide movements of these species. Apparently, these species are able to sense interferences caused by these topographic features in the Earth's magnetic field (Zagaglia, 2004). Areas of high predator diversity have also been identified within or directly adjacent to recently identified coral reef

hotspots (Roberts et al., 2002). Due to the fact that these habitat features attract and concentrate food supply, they are typically areas of elevated tuna and billfish density and richness. Unfortunately, as SST is not directly related to the occurrence of these habitat features, their positive effects on tuna and billfish abundance and richness would not be taken into account.

Consequently, the potentially positive effects of numerous habitat features on tuna and billfish distribution and richness are not directly incorporated into these predictions and could be possible sources of error. Accounting for these features is essential for any attempt to accurately predict distribution and abundance of large oceanic predators.

Having identified the limitations of this analysis, several positive conclusions can be drawn. This report represents the most comprehensive review of the effects of ambient temperature on global distribution patterns of tuna and billfish to date. As such, the database and inter-species temperature analysis represents a valuable source of information regarding ambient temperatures for these species and provides a starting point to further research in this area. Additionally, information regarding the temperatures inhabited by specific species of tuna and billfish may be useful to fisheries management. Vertical distribution related to temperature may indicate ways of reducing bycatch of non-targeted, epipelagic species such as marlin and sailfish.

The ability to accurately identify the oceanographic variables explaining large-scale tuna and billfish movements have several implications for conservation and management. As the global human population continues to increase, human activities have greater impacts on the ocean environment. The effective conservation and management of ocean species will hinge on resolving the effects of impacts on marine

regimes and marine species. For example, recent research suggests that greenhouse gas emissions are causing sea temperatures to rise, causing polar ice caps to melt and sea levels to rise at faster rates than previously believed (Overpeck et al., 2006). The effects of such changes could be detrimental to many ecosystems, both terrestrial and marine. Determining the effects of such human-induced environmental changes on important species such as tuna and billfish depends on the ability to isolate the oceanographic variables which drive global distribution and species richness. Furthermore, as the majority of data regarding tuna and billfish distribution and richness is obtained decades following human alteration of ocean ecosystems (Myers & Worm, 2003), it is often difficult to determine what these patterns were in a pristine ocean. Knowledge of where species ought to exist and perhaps did at one time exist, speaks to the effects of human impacts such as industrialized fishing on global distribution and abundance of these species. Knowledge of where tuna and billfish may have once existed could allow fisheries management authorities to distinguish between changes in abundance caused by movement to other areas, and changes resulting from the impacts of fishing. As it is believed that global biomass of these species is ~10% of pre-industrial levels, improved information regarding the factors driving global movements and distribution patterns of these species are both timely and vital to conservation efforts (Myers & Worm, 2003).

While accuracy of global range predictions varied among genera, it is believed that much of the discrepancy observed in tuna and swordfish was likely due to spawning behavior or depth of data collection. By resolving these two issues and considering additional habitat features it is believed that the accuracy of species distribution and richness predictions based on ambient temperature for tunas and swordfish would be

greatly improved. With improved range prediction accuracy, comparisons of these predictions against pre and post-industrialization patterns of species biomass would be interesting.

Tuna and billfish richness predictions have implications for the siting of marine protected areas (MPAs). MPAs function to protect a portion of an exploited population by defending part of the population's range. This approach eliminates dependence on questionable assumptions regarding the relationship between fishing effort and future biomass. MPAs may effectively reduce uncertainty concerning the effects of fishing pressure on ecosystems, due to the fact that portions of the ecosystem remain unaltered (Botsford et al., 1997; Clark, 1996). Furthermore, MPAs have been shown to aid in rebuilding depleted or declining stocks (Mosquera et al., 2000; Murawski, 2000; Roberts et al., 2001). Previous studies (Worm et al., 2005) have suggested that species richness, when considered in conjunction with species density, fine-scale information regarding habitat use, spawning areas, migration patterns, and fishing mortality (Bertrand et al., 2002; Block et al., 2001; Ferraroli et al., 2004), could be useful in identifying priority areas for marine conservation. Migratory species such as tunas would not experience large benefits from the local reduction in fishing mortality caused by a randomly placed MPA (Guenette, Pticher & Walters, 2000; Lipicus et al., 2001), but could benefit from targeted MPAs that protect spawning and aggregation sites or migration routes for multiple species (Lindholm, Auster & Kauffman, 1999). As such, accurate species richness predictions represent valuable information for conservation efforts such as the International High-Seas Marine Protected Area Initiative (IUCN, 2004).

While the development of satellite tagging technology has made significant contribution to our understanding of the distribution patterns of tunas and billfishes (Block et al., 2005; Boustany et al., 2002; Graves, Luckhurst & Prince, 2002; Sedberry & Loefer, 2001), additional data is required. Information regarding water temperature tolerances or preferences was unavailable for any species of spearfish and sparse for at least 8 species of tuna and billfish studied here. While these data are difficult and time-consuming to obtain, it is essential in order to accurately identify factors responsible for tuna and billfish distribution patterns, ultimately leading to improved targeting of conservation efforts. Lastly, the accuracy of large-scale tuna and billfish distribution predictions will depend on resolving the effects of spawning behavior and depth variation in relation to water temperature.

Appendix A – Database

Species	Source	o	Lat	Lon	d	n	t	y	cat	Adult						Juvenile						Larval		
										Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	P
N. Bluefin	Lutcavage et al., 2000	1	42	-70	4	11	10	9	1	6	22	11.5	22			9	26							
	Block et al., 2001	1			2	140	6	9	1	2.8	30.6													
	Brill et al., 2002	1	37	-74	4	5	6	8	1							10	28	20	25	23.2	13			
	Sharp, 1978	1							3	6														
	Anonymous, 1997	1							2	11	30													
	Cort, 1997	1							2															
	Farrugio, 1981	1							2															
	Mather et al., 1995	1							2															
	Humston et al., 2000	1	42	-68	2			9	3	9	24			18										
	Mather et al., 1995	1							3															
	Cort and Liarzov, 1991	1							3	6	30													
	Tiews, 1963	1							3	5	30													
	Block, Dewar et al., 1998	1	40	-60	2	26	6	9	1	6	24													
	Block, Dewar et al., 1998	1	35	-76	2	9	3	9	1	17.5	21			21.3										
	Blank et al., 2002	1			2			10	3	2.8	31													
	Brill, NMFS	1	42	-72	4				3	8					14	8				23.5				
	Altringham, 1997	1							1	7	25													
	Lutcavage et al., 1999	1	35	-50	2	17	2	9	1	11	26	17	21											
	Lutcavage et al., 1999	1	35	-50	2	17	6	9	1	13.9	27	18	24											
	Stokesbury, 2004	1	40	-70	2	35	9	10	1	6	26	14	26											
	Stokesbury, 2004	1	40	-70	2	35	2	10	1	8	24	18	24											
	Schick et al., 2004	1	43	-67	5	1600	9	9	1			10.9	20.6	18.1										
	Block et al., 1998	1	39	-65	2	9		9	1					21.3										
	Block et al., 2005	1	35	-70	2	29	0	9	1					25.5										
	Inagake et al., 2001	1							3							18.5	20.5	18.5	20.5					
	Marcinek et al., 2001	1							1												8			
	Roffer, 1987	1						8	3									18.5	20.5					
	Carey and Gibson, 1983	1						8	3	6														
	Lutcavage et al., 1997	1	43	-68				9	3	10	22													
	Carey and Teal, 1966	1			2			6	3	3														
	Carey and Teal, 1969	1							3															
	Carey and Lawson, 1973	1							3															
S. Bluefin	Collette and Nauen, 1983								4	5	20													
	Nakamura, 1969	3	-52		1				1	8														
	Caton, 1991								3	9														
	Atringham, 1997								1	7	25													
	Olson, 1980								3	5														
	Robins, 1963	2							2	10.5	21													

										Adult						Juvenile						Larval		
Species	Source	o	Lat	Lon	d	n	t	y	cat	Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	P
	Hanamoto, 1986								3			10	15											
	Mohri et al., 1996								3															
	Hynd and Robins, 1967	2	-25	155					2			17	20											
	Williams, 1977								2															
	Yukinawa, 1987								2														24		
P Bluefin	Marcinek et al., 2001	2	30	-116	2	5	0	9	1	9.5	22	15	19	18										
	Block et al., unpub.	2							3															
	Kitagawa et al., 2002	2	35	133	2	4	5	9	1	5	23.6													
	Itoh et al., 2003	2	35	160	2	30	0	9	1	1.4	28.4	14	20	19										
	Uda, 1957	2							2	12	21	14	19											
	Bell, 1963	2						6	3			17	23											
	Kitagawa et al., 2004	2	40	140	2	24	0	9	1							5	23	18	21					
	Kitagawa et al., 2000	2	35	127	2	15	12	9	1							12	23	16.3	21.5	17				
	Kitagawa et al., 2001	2	34	132	2			9	2							5	12	22		17				
	Kitagawa et al., 2002	2	33	135	2	18	12	9	1							4.9	23.6			17				
	Altringham, 1997	2							1	7	25													
	Inagake et al., 2001	2	-		3			10	3									18.5	20.5					
Bigeye tuna	Holland et al., 1992	2	20	-158	4	2		9	1	12	25													
	Holland and Sibert, 1994	2							3	7														
	Collette and Nauen, 1983								4	13	29	17	22											
	Alves et al., 1998	1							2	16														
	Anonymous, 1998								2															
	Cayre and Diouf, 1984								2															
	Cayre et al., 1988								2															
	Champagnat, 1974								2															
	Weber, 1980								2															
	Holland et al., 1990	2	20	-158	4	4		8	1	8.5	27	14	17	24.5	18	4	27							
	Brill et al., 1999	2	20	-158					1												10			
	Musyl, NMFS	2	20	-158	2				3	5	27			24.5	18	4	27				10			
	Altringham, 1997								1	7	25													
	Musyl et al., 2003	2	19	-156	2	10	0	9	1	4.7	29	23	25	23.8										
	Dagorn et al., 2000	2	-16	-149	4	4	0	9	1	8.9	25.6	10	25											
	Bach et al., 2003	2	-17	-150	4	76	0	9	1	6	27				11									
	Mohri and Nishida, 1999	3			1			9	3		28	27	28											
	Bo, 2003	3			1				3		28	27	28											
	Uda, 1957	2							2	11	28													
	Alverson, 1963	2							2	13	29													
	Liming et al., 2005	1	4	-24	1		9	10	1	9.8	14.3	12	13											

Species	Source	o	Lat	Lon	d	n	t	y	cat	Adult						Juvenile						Larval		
										Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	P
	Lee et al., 2005	3	-5	60	1		0	9	1	9.8	29	27	28											
	Brill et al., 2005	2							1	5	25	5	25		20									
	Brill et al., 2001	2							1						18						19			
	Nakamura, 1969	2							4						24									
	Hanamoto, 1975	2							2	12	27													
	Hampton et al., 1998	2						9	3			9.5	17.5											
	Holland et al., 1985	2	20	-158	2	1		8	1	14.8	24.2	15	17											
	Parks, PFRP	2	20	-160	2		5	9	1	3	29													
	Hisada, 1979								2													24		
yellowfin tuna	Collette and Nauen, 1983								1	18	31													
	Nakamura, 1969	2							4	18					24									
	Aloncle and Delaporte	1							3						15	20								
	Bard, 1984	1							2	18														
	Capisano, 1991								2															
	Cayre et al., 1988								2															
	Coan, 1976								2															
	Diouf, 1991								2															
	Fonteneau, 1980								2															
	Fonteneau, 1998	1	43	-67					3	21														
	Stretta, 1991	1							3	18	31	22	29											
	Zagaglia, 2004	1	0	-30	1		0	9	1	25	29.6	26	28.5											
	Block et al., 1997	2			2			9	3	11														
	Holland et al., 1990	2	20	-158	4	11		8	1	18	26			25.5	8						8			
	Brill et al., 1999	2	19	-156	4	5	8	9	1	13	27.9	22	27.9								8			
	Musyl, NMFS	2	20	-158	2				3	11	26			25.5	8						8			
	Holland et al., 1992	2	20	-158	4			9	3	19	28													
	Block and Keen, 1997	2	32	-118	3	3	9	9	1	7	20.5	17.5	20.5	19										
	Carey and Olson, 1982	2							3	19	26	20	27											
	Blackburn, 1965	2							2	18	31	20	30											
	Bini, 1952	2							2	15														
	Uda, 1957								2															
	Graham, 1981								3	11.5		11.5	18											
	Brill et al., 2005								1						8									
	Brill et al., 2001								1						8									
	Altringham, 1997	2	32	-118					1	17.5	28													
	Barrett and Conner, 1962				6			6	3			22	23											
	Barrett and Conner, 1964				6			6	3															
	Itano et al.	2	26	-154	1			9	1			23.8	28.2											

| Species | Source | o | Lat | Lon | d | n | t | y | cat | Adult | | | | | | Juvenile | | | | | | Larval | | |
										Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	P
	Parks, PFRP	2			4			9	1					21.5										
	Nishikawa, 1985								2													24		
	Stequert, 1986								2															
	Fonteneau, 1988								2															
	Suzuki, 1994								2															
	Wild, 1994								2															
	Richards, 1971								2													24		
	Boehlert, 1994								2															
	Schaefer, 1998								2													26	30	
Albacore tuna	Collette and Nauen, 1983								1	9.5	25.2													
	Hart, 1973	2							3	10	25													
	Aloncle, 1973	1							2							15	20							
	Altringham, 1997								1	7	25													
	Anonymous, 1996	1							2	15														
	Bard, 1981								2															
	Bard, 1980								2															
	Bard, 1991								2															
	Coan, 1976								2															
	Laevastu, 1963	2							2	14	23													
	Blackburn, 1965								2															
	Laurs and Lynn, 1977								2															
	Saito, 1973	2							2	13.5	25.2													
	Beamish et al., 2005	2	40	-160	1		8	10	1			16	18											
	Graham, 1981	1							3	10	20	10	20											
	Laura, 1991								3															
	Johnson, 1961	1							3			14	20											
	Santiago, 2004	1							3			16	21											
	Talbot, 1962	1							3			16	20											
	Clemens, 1961								3			16	19											
	H. Nakamura, 1969	1	30	-25	1				4							18								
	Hazin, 1993	1	0						3							27								
	Laveastu and Hela, 1970								3															
	Fiedler and Bernard, 1987	2	33	-122	1	89	8	8	1			16.5	18.3											
	Ueyanagi, 1969								2													24		
Skipjack tuna	Collette and Nauen, 1983								4	14.7	30													
	Robins, 1951	2	-43	-148	1	1500	0	5	1	14.7	20.8	16	18											
	Antoine et al., 1982	1							2	20														
	Bard et al., 1983								2															

Species	Source	o	Lat	Lon	d	n	t	y	cat	Adult						Juvenile						Larval		
										Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	P
	Cayre, 1981								2															
	Cayre and Diouf, 1981								2															
	Cayre and Farrugio, 1986								2															
	Cayre and Laloe, 1986								2															
	Cayre et al, 1988								2															
	Chur eta l, 1980								2															
	Fiedler and Bernard, 1987	2	33	-122	1		8	8	1			20.9	22.4											
	Broadhead, 1964	2							2	17	30	20	29											
	Williams, 1970								2															
	Blackburn, 1965, 1969								2															
	Uda, 1957	2	33	133					2	18	30													
	Dizon et al., 1977				6			7	2	17	33	15	35		5									
	Barkley et al., 1978								2															
	Nakamura, 1969	2							1			18	28											
	Schaefer, 2001	2	0	-100	1	65	0	9	1			20	28.2	27										
	Brill et al., 2005								1						8									
	Barrett and Conner, 1962				6			6	3			22	23											
	Barrett and Conner, 1964				6			6	3															
	Parks, PFRP	2			4			9	1			21.5												
	Boehlert, 1994								2													22		
	Matsumoto, 1984								2															
	Ueyanagi, 1969								2													24		
	Cayre, 1986								2															
	Schaefer, 2001								2													25		
Kawakawa	Collette and Nauen, 1983								4	18	29													
	Dizon, Neill, 1977	2							2	15	32													
Slender tuna	Wolfe, 1974	2	-42	148	1		6	7	1	12	14													
	Collette and Nauen, 1983	2							4	19	24													
	Mori, 1967	2	-27						3							19	24							
	Watanabe et al., 1966								3															
Striped Bonito	Collette and Nauen, 1983	2							4	14	23													
Atlantic Bonito	Collette and Nauen, 1983	1							4	12	27													
E.P. Bonito	Collette and Nauen, 1983	2							4	21.6	30.5	27	27.9											
	Altringham, 1997	2							1	16		16	23											
Little tunney	Cayre and Diouf, 1981	1							3	18	30													
	Cayre et al., 1988	1							3															

Species	Source	o	Lat	Lon	d	n	t	y	cat	Adult						Juvenile						Larval		
										Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	Pmn	Pmx	P	R	Tmn	Tmx	P
Swordfish	Carey, 1990	1			3	1	11	8	1	7	27				19									
	Nakamura, 1985								4	5	27	13												
	Nakamura, 1985	2							4	5		18	22											
	Arocha, 1996	1							2	15														
	Draganik, 1988								2															
	Ehrardt, 1991								2															
	Farber, 1988								2															
	Hoey, 1988								2															
	Mejuto, 1997								2															
	Ovchinnikov et al., 1980								2															
	Porter, 1991								2															
	Takahashi et al., 2003	2	37	142	2	1	6	9	1	2	28	3	25											
	Carey and Robison, 1981								3	6	26				19									
	Sedberry, 2001	1	32	-70	2	23	5	10	1	10	28	14	23											
	Palko et al., 1981								3	18	30													
	Bigelow et al., 1999	2	30	-160	1	27901	0	9	1			16	19	15										
	Bigelow et al., 1999	2	42	-155	1	27901	0	9	1			13	19	15										
	Ovchinnikov, 1971								1	12	29	25	29	24										
Indo-pac B.M.	Nakamura, 1985	2							4	21	31													
	Block, Booth et al., 1992	2	20	-156	3	6	7	8	1	17	27.2	26	27											
	Holland et al., 1990	2	20	-158	4	6		8	2	19	27	26	27		8									
	ABFPA								2	22	31													
Atlantic B.M.	Graves et al., 2002	1	33	-65	2	8	7	9	1	22	31	26	30	30	9									
	Nakamura, 1985	1							4	22	31	24												
	Sponaugle et al., 2005	1	24	-78	7	188	0	10	1													28.2	29.7	29
	Block unpublished data	1	35	-76					2	24.4	27.2													
	ABFPA	1							2	22	31													
	Saito, 2005					8		10	1	13														
White marlin	Amorim et al., 1998	1							2	20														
	Anonymous, 1998b	1							2															
	Baglin, 1977	1							2															
	Baglin, 1979	1							2															
	Nakamura, 1985	1							4	22	29											20	29	
	Horodysky et al., 2004	1			2	24	8	10	1		27	24	27		13									
	Ovchinnikov, 1971	1							1					24										
	Gibbs, 1957	1	25	-90					4		26.7	25.6	26.7											
	DeSylva and Davis, 1963	1																						
	ABFPA	1							2	22														

Species	Source	o	Lat	Lon	d	n	t	y	cat	Adult Tmn	Adult Tmx	Adult Pmn	Adult Pmx	Adult P	Adult R	Adult Tmn	Juvenile Tmx	Juvenile Pmn	Juvenile Pmx	Juvenile P	Juvenile R	Larval Tmn	Larval Tmx	Larval P
Black marlin	Nakamura, 1985								4	15	30													
	Pepperell, 1999	2	-16	146	4	8	11	9	1	21.5	29	24	29		8									
	Gunn, 2003	2	-20	-155	2	5	12	10	1	12	31.5	27	30											
Striped marlin	Nakamura, 1985	2							4	20	25											24		
	Howard and Ueyanagi, 1965	2						6	3	20	25													
	Brill, Holts et al., 1999	2	20	-158	4			9	3	18	27	25.1	27											
	Domeier et al., 2003	2	19	-110	2	65	0		1	11.6														
	Ortega-garcia, 2003	2	23	-110	1	110000	0	9	1	20.8	30.4	22	24	23										
	Holts and Bedford, 1990	2	33	-122	4	11		9	2	11	21	19	21											
	Brill et al., 1993	2	20	-156	4	6	11	9	1	18	27	25.1	27		8									
	Squire, 1985	2	33	-122	1	10700	0	6	1	16.7	22.2	18.9	21.1	18.9										
	Uda, 1957	2			1		0	5	2	16	29	18.5	24											
	Armas et al., 1999	2	20	-106	7	68	8	9	1													27.8	31.5	29
	Squire, 1971	2	33	-122	5	3595		6	2	16.1	22.8													
	Ortega-garcia, 2005	2	30	-120	1			10	2				27.7											
	Sippel et al., 2005	2	-40	170	2	2	5	10	1			20	23.9											
Atlantic Sailfish	Nakamura, 1985	1			1				4	21	28													
	Anonymous, 1998b	1							2	22														
	Capisano, 1989	1							2															
	Souza et al., 1994	1							2															
	Jolley and Irby, 1979	1	27	-80	4	9	0	7	1	22	26.6													
	Ovchinnikov, 1966	1							3		29	28	29											
	Ovchinnikov, 1971	1							4					21										
	Luthy et al., 2005	1	27	-77	7	70	0	10	1													26.1	30.6	28
	Post et al., 1997	1	27	-77	7	288	0	9	1													27	30.4	28.7
	Voss, 1952	1	25	-90					2	10		23.9	26.7											
	DeSylva and Davis, 1963	1							2															
	Morrow and Harbo, 1969	1							2															
	Jolley, 1974	1							2															
	ABFPA	1							2	21	28													
Pacific Sailfish	Hoolihan, 2004	3	25	54	4	8	0	10	1	20	27.7	21	25.6	23										
	Rosas-Alayola, 2001	2	15	-108	1			10	1					28										
	Armas et al., 1999	2	20	-106	7	68	8	9	1													27.8	31.5	29
	ABFPA								2	21	28													
	Ortega-garcia, 2005	2	30	-120	1			10	1					27.7										
	Nakamura, 1985	2							4					28										
	Nakamura, 1985	3							4			29	30											

Appendix B – Database references

Habitat provisions and essential fish habitat. *Atlantic billfish FMP amendment* **chapter 4,** 96.

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Appendix C - Temperature-predicted global species distribution analysis

Atlantic Bonito

Little tunney

E.P. Bonito

Slender tuna

Kawakawa

Striped bonito
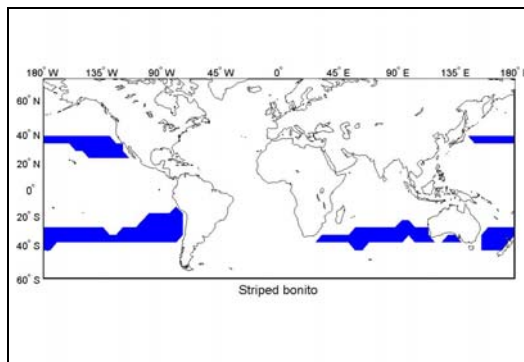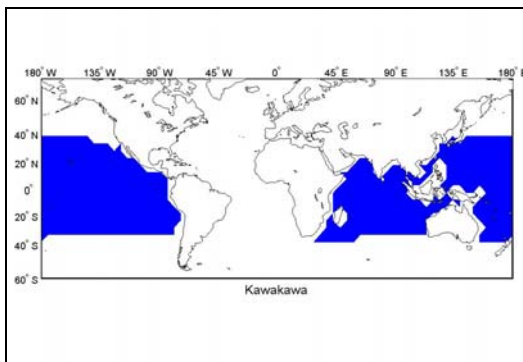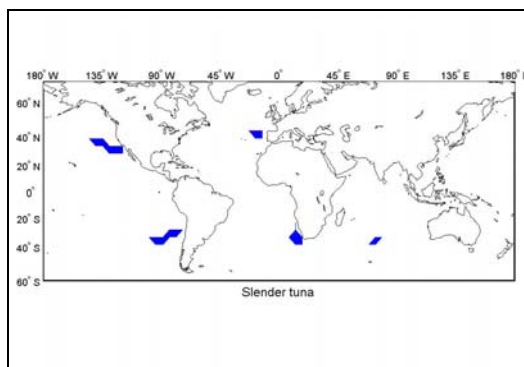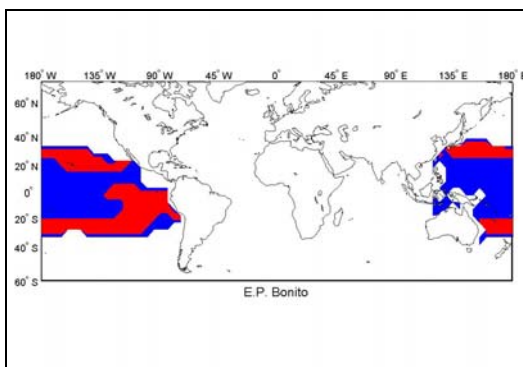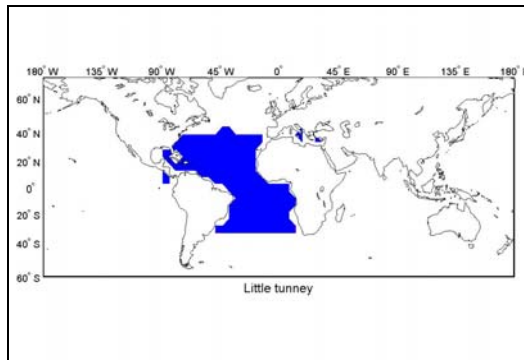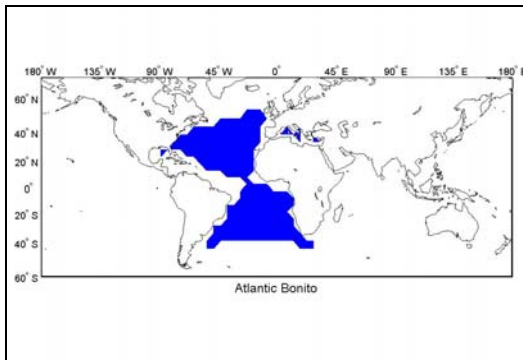
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