Supporting Online Material for

Biomass, Size, and Trophic Status of Top Predators in the Pacific Ocean

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Background

The oceanic tuna fishery uses four principal gear types, longline, purse seine, pole and line (or baitboat), and troll, deployed by fishing vessels from approximately 25 different countries and territories. Each gear type may be deployed in a variety of configurations to target a particular species of fish. Longliners deploy numerous baited hooks arranged on lines up to 75 n. mi. in length. The number of hooks deployed and the depths at which they operate are adjusted to target different species in different regions of the ocean. The range of depths fished by tuna longliners has shifted to deeper layers during the last 50 years so that the catchability coefficient (the probability that a hook will catch a fish) has changed over time in various ways for various species. Surface fisheries generally depend on aggregations of tunas. Purse-seine fisheries operate by surrounding surface aggregations of fish with large nets that can be closed under the aggregation. Purse-seiners may target free-swimming tuna schools or dolphin associated schools composed primarily of large yellowfin tuna (*Thunnus albacares*), or they may

exploit a variety of naturally occurring and artificial floating objects, fish-aggregating devices (FADs), which attract mixed schools of skipjack (*Katsuwonus pelamis*), small yellowfin and bigeye (*Thunnus obesus*) tunas. The trend over time has been toward more use of FADs, which have become increasingly sophisticated and numerous, and to larger nets with speedier net handling gear, with the result that fishing power of individual purse seiners has increased dramatically. Pole-and-line fisheries for skipjack and albacore (*Thunnus alalunga*) operate by attracting surface schools of fish to the fishing boat with bait and use barbless hooks to catch the fish. The prevalence of the pole-and-line fishing has declined over time, mirroring the increase in the purse seine fleet. Widely dispersed troll fisheries for albacore operate in both the North and South Pacific, and small-scale troll fisheries for a variety of species are found in all coastal and insular areas. Other large pelagic species such as swordfish (*Xiphias gladius*), marlins, and sharks are taken either in fisheries specialized to target these species or as incidental catch. The data from these diverse fisheries provide insight into different aspects of the dynamics of the exploited populations and the response of the ecosystem to the removal of large predators.

The Inter-American Tropical Tuna Commission (IATTC) has been monitoring tuna fisheries in the Eastern Pacific Ocean (EPO) since 1950 (S1). In 2003, membership of the IATTC adopted the Antigua Convention for Co-operation in the Protection and Sustainable Development of the Marine and Coastal Environment of the North-East Pacific updating the 1949 IATTC Convention (S2). In 2000, twenty-five countries with tuna fishing interests in the Western and Central Pacific Ocean (WCPO) signed the

Convention on the Conservation and Management of Highly Migratory Fish Stocks in the

Western and Central Pacific Ocean (S3), and in 2004, this treaty entered into force,

creating the Western and Central Pacific Fisheries Commission (WCPFC). The

convention areas of the IATTC and the WCPFC meet at 150°W longitude, and the

commissions have agreed to coordinate fisheries management measures in the Pacific.

For the first time, it is feasible to envisage a Pacific-wide regulatory regime for the

conservation of large predatory fish in the Pacific Ocean.

Materials and methods

Stock assessment refers to the suite of statistical procedures used to reconstruct

the size and other properties of exploited fish populations by analysis of data from the

fishery (S4, S5). Current state-of-the-art stock assessment models represent the

population with an age-structured demographic model, describe dependence of catch on

age of fish, include temporal variability in recruitment of young individuals into the

population, and explicitly describe movement within the range of the stock. Integrated

assessment models incorporate statistical models of observation error that enable them to

utilize diverse data: total catch and fishing effort by gear type, size composition of the

catch, and tag release and recapture data. Integrated methods link all sources of data in a

consistent population dynamics and statistical estimation framework, taking full

advantage of the insights into population dynamics provided by data from diverse

fisheries exploiting different life history stages.

We use such a model to reconstruct trajectories of biomass and size composition

of eight stocks (S6) of large predators over the period sampled by the fishery. The model,

MULTIFAN-CL, is fully documented in the primary literature (S7), and the program, source code and user's guide are in the public domain and freely available for download (S8). MULTIFAN-CL is currently used for "official" assessments produced for the WCPFC. A derivative of MULTIFAN-CL, A-SCALA (S9) is used for assessments of eastern Pacific stocks conducted by the IATTC. The MULTIFAN-CL approach is similar to stock assessment approaches used to assess major fish stock around the world (S10).

MULTIFAN-CL is age-structured with annual or quarterly age-classes. The final age-class is an aggregate of all fish of that age and older. Spatial structure is incorporated by modeling populations separately in regions within the spatial domain of the model. These regions reflect the distribution of the various fisheries defined in the model, the bio-geographical characteristics of the stocks and the spatial resolution of some of the data. For yellowfin, bigeye and skipjack stocks, recruitment is assumed to occur at the beginning of each quarter because spawning does not invariably follow a clear annual pattern in the tropics, and may occur sporadically throughout the year. For albacore and blue shark stocks, reproduction is highly seasonal and an annual recruitment pattern is assumed. Recruitment is parameterized as the product of a spatially-aggregated average recruitment, a vector specifying the time-series variation (log-normally distributed) in spatially-aggregated recruitment, a vector specifying the average distribution of recruitment among the regions and a matrix specifying the time-series variation in the spatial distribution of recruitment. Spatially-aggregated recruitment may be assumed to have a weak association with spawning biomass via a Beverton and Holt stock–recruitment relationship (SRR). This assumption is optional, but is required if the model

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results are to be used in a yield analysis. The assumption is introduced by means of a small penalty on the objective function for deviations of recruitment from the SRR.

The age structures of the region-specific initial populations are assumed to be at equilibria defined by the average total mortalities in each region over the initial five years of the time series. Therefore, initial populations are not assumed to be unexploited.

Movement among the regions is assumed to occur instantaneously at the beginning of each quarter, and may be age-dependent but time-invariant. We are therefore attempting to capture only the general pattern of cohort dispersal over time, and not model detailed movement dynamics, which are likely to be highly variable and affected by a range of biological and physical factors.

Natural mortality is assumed to be age-dependent, but time- and region- invariant.

Multiple fisheries are defined on the basis of gear type, set type in the case of purse-seine gear, and region. Catch and fishing mortality are fishery-, age- and time-specific, with fishing mortality partitioned into age-dependent (selectivity) and time-dependent components (catchability and effort) (S11, S12, S13, S14). A process error term (effort deviations) is included in the effort–fishing mortality relationship to acknowledge the stochastic variability that occurs in all fisheries.

Selectivity is fishery-specific and assumed to be time-invariant. Selectivity coefficients have a range of 0−1, and for the longline fisheries (which catch almost exclusively adult individuals) are assumed to be non-decreasing functions of age. The coefficients are expressed as age-specific parameters, but are smoothed according to the

degree of length overlap between adjacent age classes because selectivity is a fundamentally length-based process (S*14*). The coefficients for the last age classes are constrained to be equal, because the mean lengths for these age classes are very similar.

Catchability is allowed to vary slowly over time (akin to a random walk) for the non-longline fisheries using a structural time-series approach (S15). Seasonal variability in catchability is allowed for all fisheries for which quarterly data are available. For certain fisheries, effort is standardized using statistical (S16, S17) or habitat-based (S18) algorithms to attempt to make catch per unit of effort a reliable index of abundance. In such cases, catchability is assumed to be constant over time and among regions.

Length- and weight-frequency data are used to estimate catch age composition, and therefore some assumptions need to be made concerning the length and weight distributions of the fish (S19). These assumptions are (i) the lengths of the fish in each age-class are normally distributed; (ii) the mean lengths-at-age lie on a von Bertalanffy growth curve; (iii) the standard deviations of the lengths for each age-class are a linear function of the mean length-at-age; and (iv) the distribution of weight-at-age is a deterministic function of length-at-age as defined by a specified weight-length relationship. Regarding assumption (ii), previous analyses revealed significant departure from von Bertalanffy growth of juvenile tuna for some stocks, so the mean lengths of specified age-classes may be allowed to be independent parameters of the model.

The spawning biomass of the population is a quantity that is often monitored for management purposes. We use spawning biomass to estimate the SRR for the yield analysis and compute it as a function of numbers-at-age, the proportion of mature fish in

each age-class and the average weight of fish in each age-class.

Several modifications of this general population dynamics model are required to model the dynamics of the tagged fish. The main difference is that the tagged population is stratified by 'cohorts' (groups of tagged fish released in a particular region during a particular time period) and recruitment to the tagged population occurs when tagged cohorts are released. Tag recaptures are predicted in an equation similar to that for the general population. Because not all tag recaptures are reported, fishery-specific tag-reporting rates are estimated and used to adjust the predicted recaptures.

For the tagged population and the general population to share fishing mortality parameters, it must be assumed that the tagged fish become randomly mixed with the general population within the spatial strata being considered. As the regions defined in the model are large, it is likely that this assumption will not be satisfied soon after release. The approach taken is to define a number of initial time periods after release as 'premixed' periods and to compute fishing mortality rates for each tag release cohort during such periods based on the observed recaptures and estimated tag-reporting rates. This or similar procedures are commonly applied in analyses of tagging data (S20, S21, S22).

The model parameters are estimated by minimizing an objective function that comprises the sum of the negative log-likelihoods of the data and various penalties that constrain the parameterization. The data component of the objective function comprises the log-likelihoods of the observed total (i.e. age-aggregated) catches by time period and fishery, the observed length- and weight-frequency proportions by time period and

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fishery and the observed tag recaptures by tag-release cohort, age-class, time period and fishery.

Several penalties are added to the objective function to add additional structure to the model. Penalties based on distribution assumptions (similar to random effects) are included for recruitment, effort, and catchability. Penalties are also used to implement the non-parametric approach to model the age-specific selectivity parameters.

We refer to the reconstructed population estimated by the assessment model as the "exploited" population. The assessment model can also predict the biomass that might have occurred in the absence of fishing by setting the fishing mortality parameters to zero. We refer to this prediction as the "unexploited" population. The unexploited population trajectories include the estimated effects of temporal variability in recruitment on the dynamics of the populations, and thus incorporate environmental constraints that occurred during the history of the fishery. The unexploited biomass also incorporates the estimated effect of the additional recruitment predicted by the SRR resulting from unexploited spawning biomass. The steepness parameter of the SRR is estimated to be relatively large (>0.5) for the stocks considered here and the stocks appear not to have declined to the extent that recruitment has been adversely affected by low spawning biomass. Thus, in the context of the stock assessment, the estimated recruitment time series can be considered a unique realization of a random process. The methodology does not adjust for the impact of species interactions, which may differ between exploited and unexploited conditions. The impact of fisheries on abundance is assessed by comparing the exploited biomass trajectories with unexploited biomass trajectories.

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The assessment model also reconstructs the age and size composition of the population. The impact of fisheries on the size structure of the population is assessed by comparing the size spectra of the exploited biomass with the size spectra of the unexploited biomass. Trophic level of the catch is often cited as an indicator of the ecosystem effects of fishing (S23). Tunas and other oceanic top-level predators grow very rapidly, often recruiting to the fishery in their first year. They are selective predators from the onset of feeding, and become piscivorous at approximately 6 mm in length (S24). In other words, tunas occupy trophic level 3 or greater from the start of life. We construct a simple hyperbolic relationship between size and trophic level (S25) by assuming that top predators occupy trophic level 3 at a length of 5 cm, and reach trophic levels reported in the literature (S26, S27, S28) at the size when 50% of the individuals reach sexual maturity (Figure S6). The relationship between size and trophic level allows us to map size spectra onto trophic spectra. We estimate the impact of the fishery on trophic level by comparing trophic level in the catch, the exploited population, and the unexploited population. This measure of trophic level represents documented ontogenetic shifts in trophic level. It reflects changes in trophic level in the population in response to changes in size composition, but is insensitive to changes in the trophic status of prey organisms.

Data from all documented fisheries for the period from 1950 through 2004 are included in the analysis. The data are drawn from "official" assessment documents (S29, S30, S31, S32, S33, S34, S35, S36) published by international commissions and from *ad hoc* groups established to assess the status of populations of interest. We consider the

entire Pacific Ocean where the information exists, but treat the EPO/WCPO and North/South Pacific separately as appropriate for the individual species. In some cases, we augment the official stock assessments with data recently made available or re-analyze the "official" data. The primary model implementation details for each stock in the analysis are listed briefly in Table S1.

Uncertainty is an ubiquitous concern in stock assessment. Its causes derive mostly from incomplete, inaccurate or uninformative fishery data, and from assumptions regarding biological processes (e. g. dependency of natural morality on age) and variability in fishery parameters (e. g. changes in catchability and recruitment over time). MULTIFAN-CL accommodates these sources of uncertainty in several ways. It is a flexibly parameterized likelihood method that allows statistical testing of alternative model structure. It uses robust estimation so that outliers do not have an unwarranted influence on parameter estimates. Random and autocorrelated variation in fishing mortality parameters are allowed but their variability is severely constrained. All parameters are estimated simultaneously so that the covariance matrix of the parameter estimates can be approximated by the inverse Hessian matrix to yield formal measures of uncertainty.

Results

Biomass impact

Trends in total exploited and unexploited biomass are presented in Figure 2 in the main text. The ratio of exploited to unexploited biomass for total biomass and biomass of fisher larger than the size at 50% maturity are presented in Figure S1 A and B

respectively. The final points in Figure S1 are presented in Table 1 in the main text.

Size spectra

The size spectra aggregated over all eight stocks is presented in Figure S3. Starting in the 1980s, the impact of the fishery on the size composition of the stocks can be seen by the increasing difference between the exploited and unexploited stocks at sizes greater than 100 cm. The growth of the purse-seine fishery can be seen by the increase, again beginning in the 1980s, in catch of fish around 50 cm in length. The mean length of the catch has decreased from 93 cm in the 1950s to 83 cm currently (Table S2). The mean lengths in the exploited population are less than those of the unexploited population in all decades, but neither shows a clear trend with time.

The biomass of fish larger than 100 cm has decreased to about 60% of that expected in the absence of fishing (Figure S4A). In the 1980s, the rapidly developing purse-seine fishery began to exploit the smaller fish, and the impact of the purse-seine fishery on the sizes of tunas can be seen by the decrease in biomass of fish of around 75 cm in length. Data on commercial catches of blue sharks are not available prior to 1970, and the advent of blue shark biomass estimates in 1970 masks the impact of the fishery on larger tuna. When blue shark is excluded from the analysis, the impact of the fishery on tuna stocks is more clearly evident (Figure S4B). The biomass of tuna larger than 175cm has declined to less than 20% of that that expected in the absence of fishing. The proportion of tunas greater than 175 cm in length has always been small, < 5% of the total population and has declined further to less than 1% (Figure S5).

Trophic spectra

Figure S6 shows the relationship between length and trophic level for yellowfin tuna in the WCPO (S37) in comparison to the approximate length when yellowfin tuna shift from trophic level 3 to trophic level 4 based on diet and stable isotope analyses in Hawaii (S38). The trophic spectra of the biomass aggregated over all stocks appears bimodal, with most of the biomass between trophic levels 3.5 and 4.0 and a secondary mode around trophic level 4.5 (Figure S7). Estimates of trophic level are extremely uncertain because they depend on diet data, which for highly migratory species, are sparse in both time and space. In addition, the structure of the ecosystem varies within the Pacific Ocean basin, and the trophic level of top-level predators is influenced by the diversity of processes at the base of the food web (S26) in such a way that the within-basin variation in trophic level is of the same order of magnitude as reported (S39) changes in the trophic level of the catch. We use ratios of trophic level in the catch and exploited biomass to the trophic level in the unexploited biomass as measures of the impact of fishing on trophic level. As seen in Figure 3B in the main text, the trophic level in the catch has decreased slightly, but the trophic level in the exploited population is relatively unchanged. These changes in trophic level basically reflect changes in size composition. Since this fishery exploits carnivorous fish at the top of the food chain and does not include herbivorous species, large changes in trophic level would be unexpected.

Table S1. Summary of model structure and data input. Size sample column indicates number of length-frequency samples and weight-frequency samples. Main abundance index column indicates the fisheries for which catchability was assumed constant and therefore catch-per-unit-effort is assumed to provide an index of abundance. Where effort standardization was applied the method used is indicated – "nominal" indicates no standardization; "GLM" indicates general linear model (S16,S17), and "statHBS" indicates statistical habitat-based standardization (S18). Size samples column shows number of length-frequency (upper) and weight-frequency (lower) samples included in the analysis. Samples typically include more than 100 measurements. Tagging data column shows numbers of tags released (upper) and recaptured (lower).

| Stock	Time Period	Spatial Domain	Regions	Fisheries	Main abundance index	Size Samples	Tagging Data
North Pacific Albacore	1952 - 2003	Pacific Ocean North of 0°N	1	27	Japan longline (nominal)	381 0	None
Pacific Bigeye	1952 - 2003	Pacific Ocean 40°S to 40°N	8	26	Japan longline (statHBS)	569 385	26,887 4,817
WCPO Yellowfin	1952 - 2003	40°S to 40°N 110°E to 170°W	6	19	Japan longline (GLM)	445 288	48,043 4,130
EPO Yellowfin	1950 - 2003	Pacific Ocean East of 150°W	1	18	Japan longline (GLM)	477 0	None
North Pacific Blue Shark	1971 - 2003	0°N to 60°N 140°E to 130°W	4	25	Japan longline (statHBSl)	94 0	None
WCPO Skipjack	1952 - 2003	40S to 40N 110°E to 170°W	6	30	Japan pole-and-line (GLM)	443 0	226,329 18,042
EPO Skipjack	1950 - 2003	Pacific Ocean East of 150°W	1	8	Purse seine (nominal)	208 0	None
South Pacific Albacore	1952 - 2003	Pacific Ocean 45°S to 0°S	1	23	Taiwan longline (GLM)	356 0	9,691 138
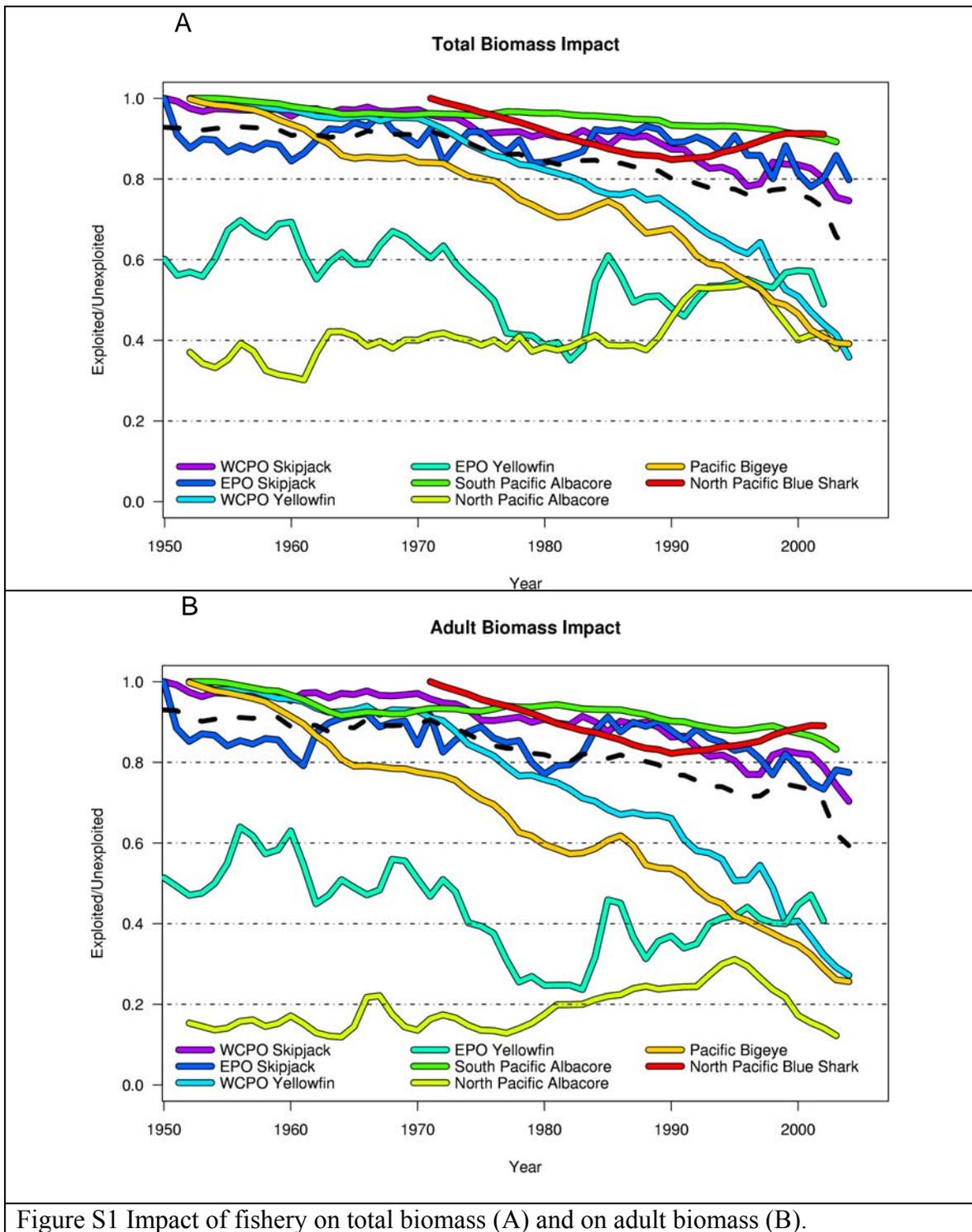
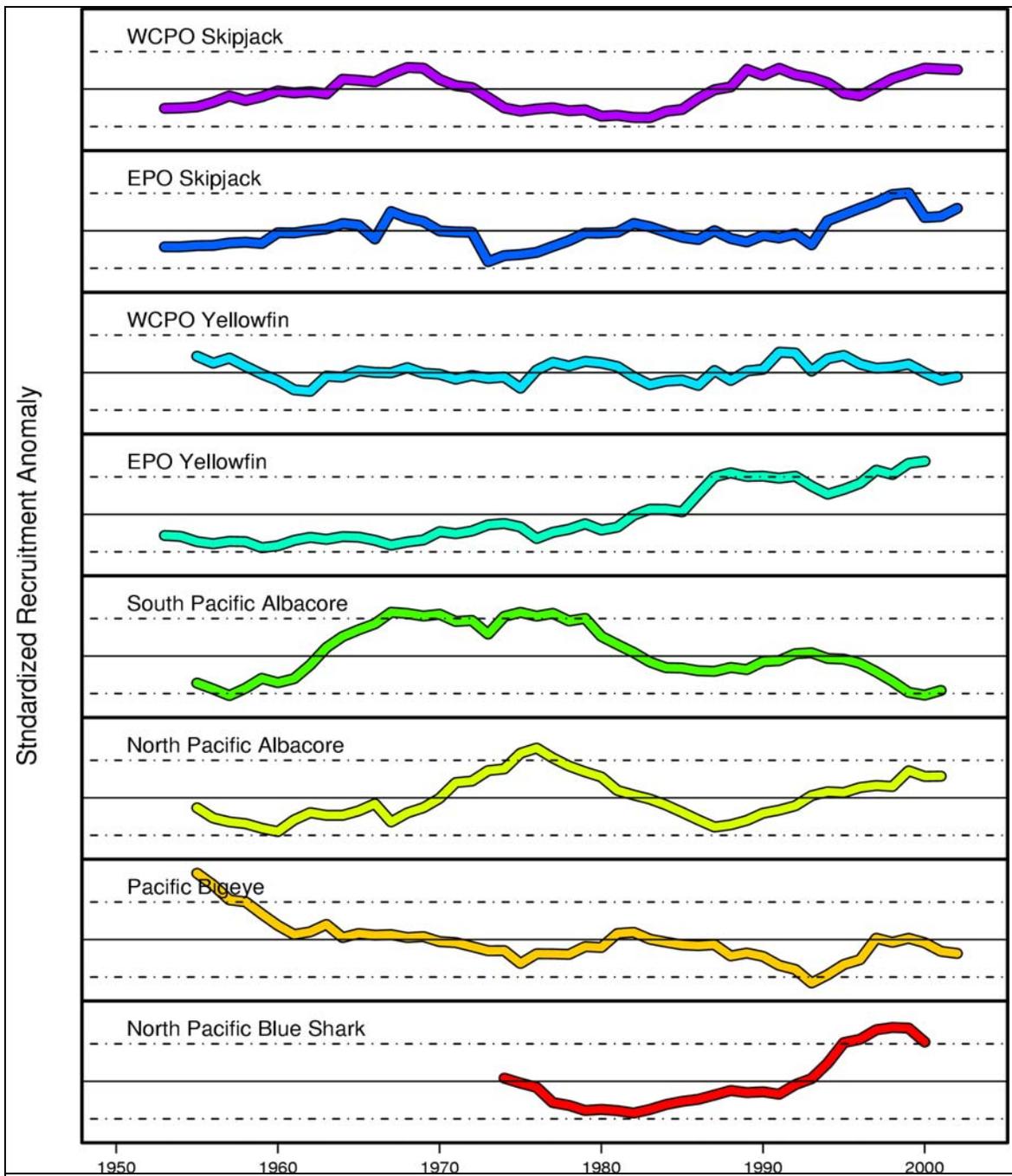Figure S1 Impact of fishery on total biomass (A) and on adult biomass (B).

Figure S2. Trends in recruitment for each stock from 1950 to 2002. Ordinate is the 5-year running mean difference between the recruitment and the long-term average recruitment standardized by its standard deviation. The solid line is the mean recruitment, and the dashed lines are 1 standard deviation above and below the mean.
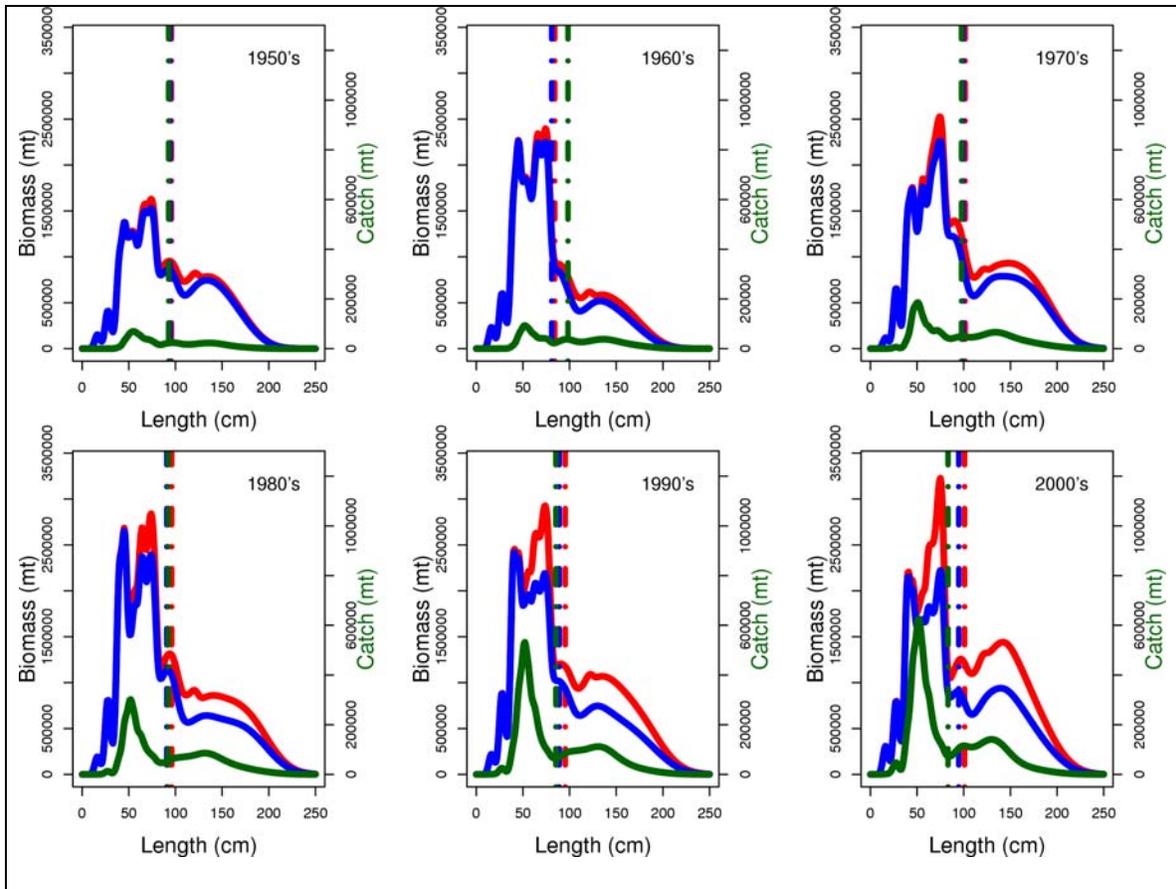
Figure S3. Decadal changes in size spectra summed over eight stocks. The ordinates are the total biomass at length summed over the decade indicated. Blue lines indicate the biomass at length estimated from the observed fishing history (the exploited population), and red lines indicate the biomass at length estimated in the absence of all fishing (the unexploited population). The green lines indicate the catch at length plotted against the right-hand ordinate. The dashed vertical lines indicate the respective mean lengths in Table S2 (below).

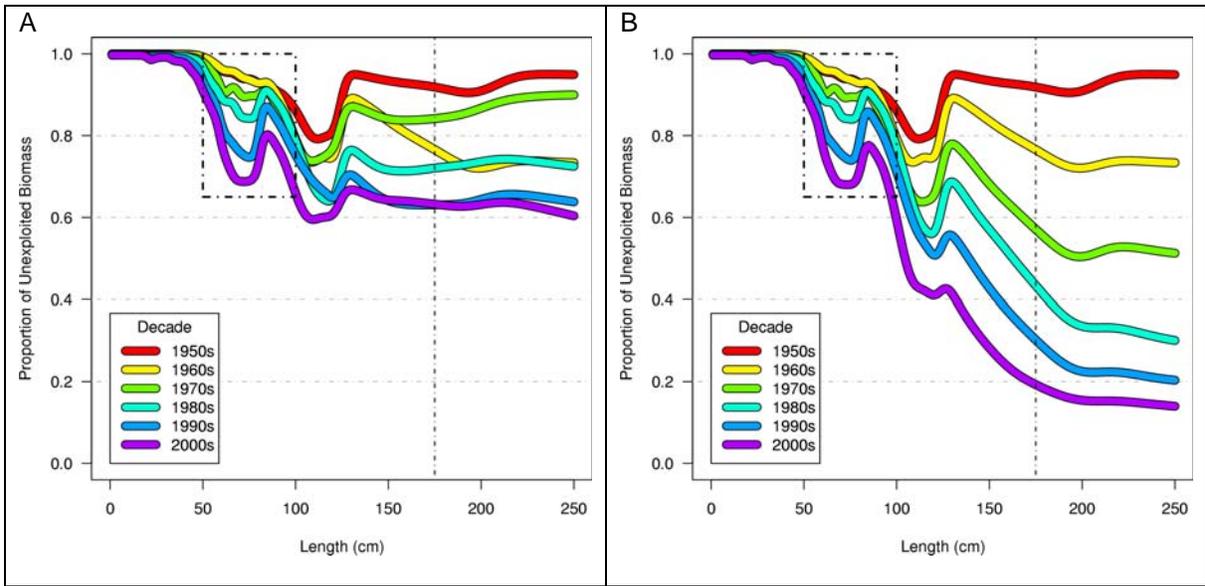| Decade	Mean Length (cm)		
	Exploited	**Unexploited**	**Catch**
1950	94.4	95.6	92.7
1960	80.8	84.1	98.3
1970	99.2	102	97.6
1980	90.7	96.0	92.2
1990	88.9	95.4	85.2
2000	94.7	101	83.2

Table S2. Mean length by decade.

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Figure S4. Ratio of exploited to unexploited biomass at length by decade from 1950 through 2004 for all eight stocks (A) and excluding blue shark (for which the data time series begins in 1970) (B). The dashed box indicates the size range of skipjack caught by the purse-seine fishery. The vertical dashed line indicates 175 cm.
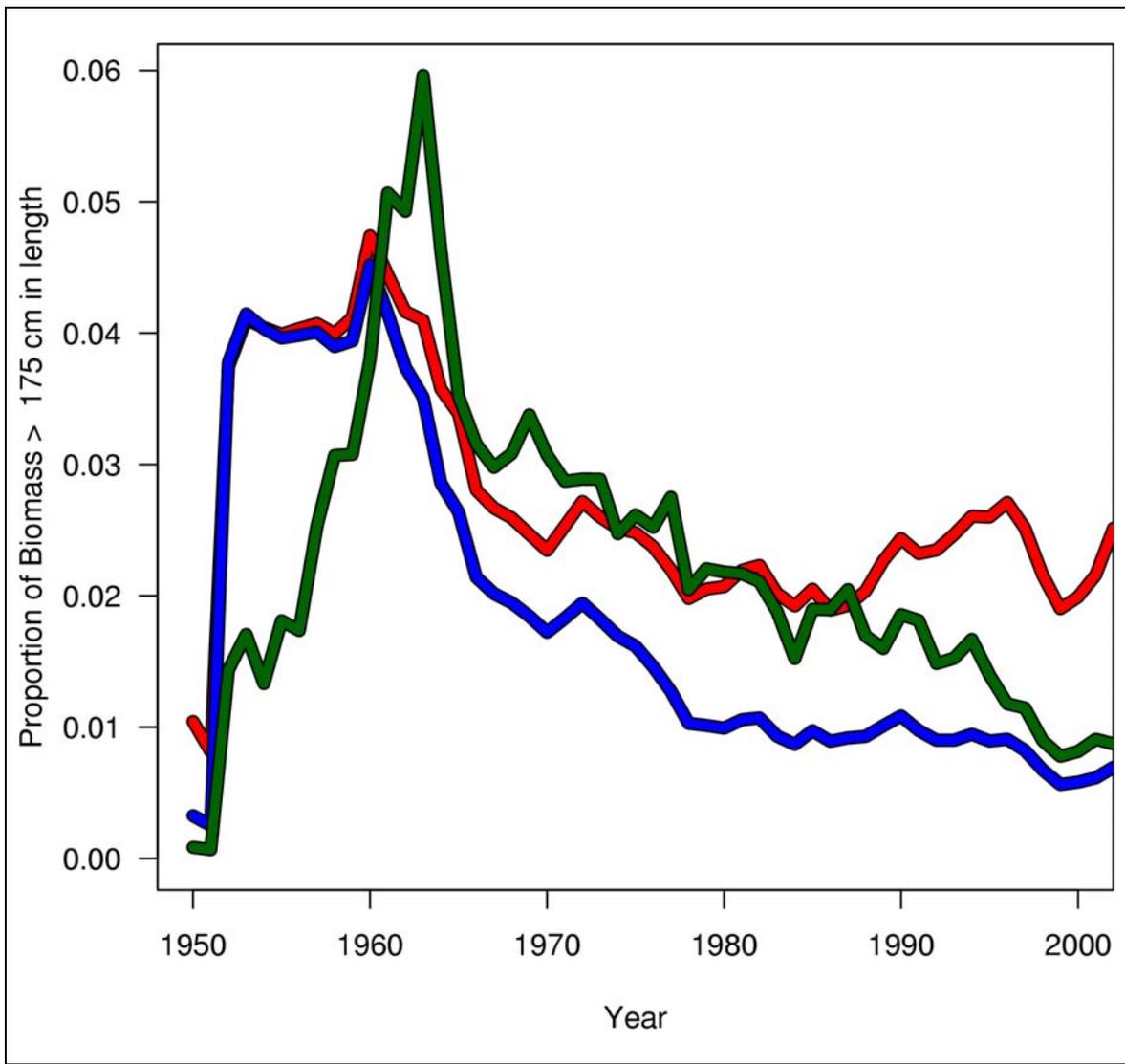
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Figure S5. Proportions of tuna greater than 175 cm in length in the exploited (blue), unexploited (red) populations and the catch (green).
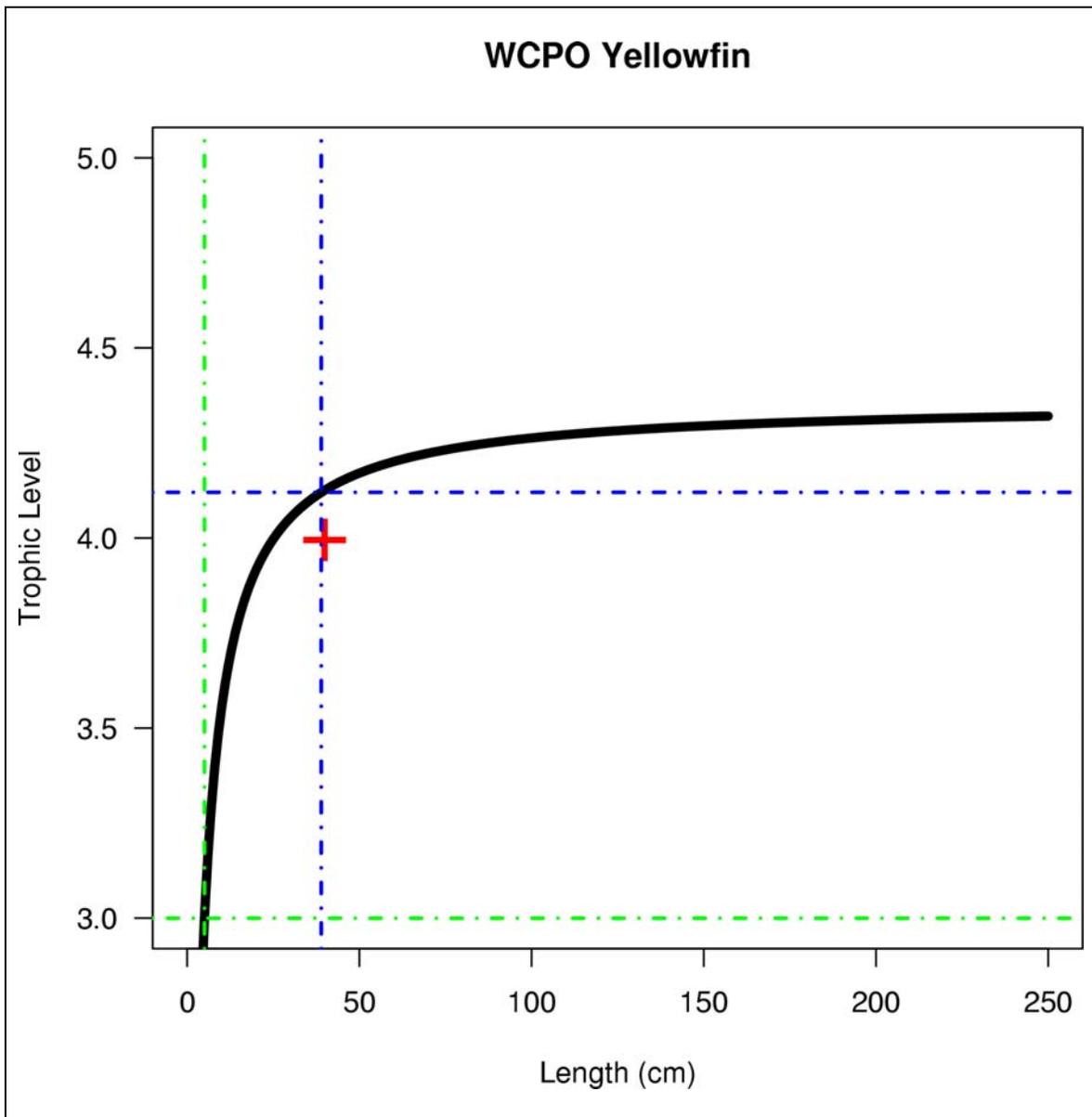
Figure S6. Relationship between length and trophic level for WCPO yellowfin tuna. The dashed green lines indicate trophic level 3 and a length of 5 cm. The dashed blue lines indicate the trophic level estimated for the WCPO yellowfin (S37) at the length when 50% of the population is sexually mature. The solid black curve is a rectangular hyperbola passing though these two points. The red + symbol indicates the approximate length when yellowfin tuna shift from trophic level 3 to trophic level 4 based on diet and stable isotope analyses in Hawaii (S38).
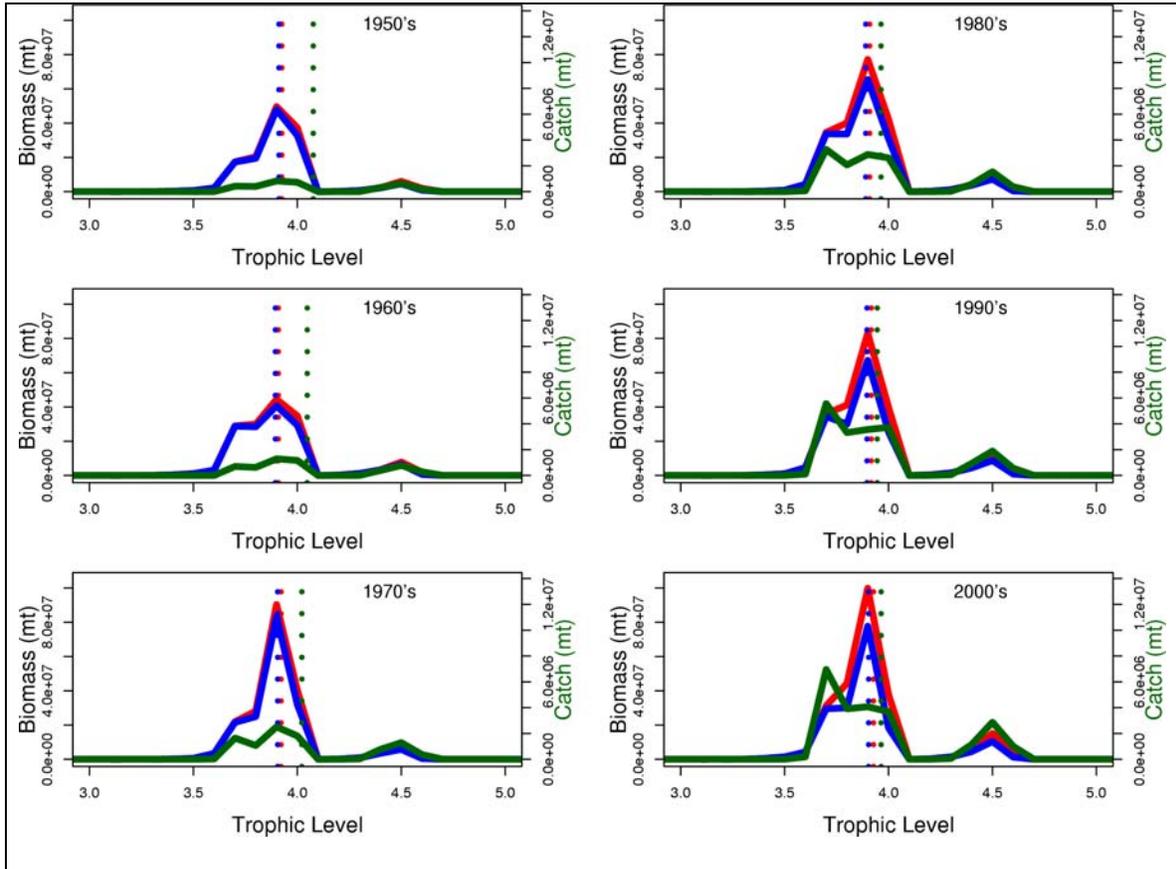
Figure S7. Decadal changes in the resulting trophic spectra aggregated over 8 species. The ordinates are the total biomass at trophic level summed over the decade indicated. The blue line is the trophic spectrum of the exploited population, the red line is the trophic spectrum of the unexploited population, and the green line is the trophic spectrum of the catch. The dashed vertical lines indicate the respective mean trophic levels given in the table below.

Decade	Mean Trophic Level		
	Exploited	Unexploited	Catch
1950	3.91	3.93	4.08
1960	3.89	3.91	4.05
1970	3.91	3.92	4.02
1980	3.89	3.91	3.96
1990	3.90	3.92	3.95
2000	3.90	3.93	3.96

Table S3. Mean trophic level by decade.

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Supporting References and Notes

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