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Biomass, Size, and Trophic Status of Top Predators in the Pacific Ocean
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24. Our calculated rates of evolutionary turnover are considered to be conservative for a number of reasons. First, the practice of integrating turnover rates over intervals of geological time (binning) necessarily yields rates of evolutionary change that are time-averaged. At BR, WL, and site 1209, the PETM is binned into two intervals: from the onset to the peak CIE (70 ky) and the recovery (150 ky) (*20*). At site 690, the record is resolved into time intervals of about 10 ky (table S3). This higher resolution is possible at site 690 because the cyclostratigraphic age model that we have used (*6*) was developed at this site. Second, there is likely to have been differential postmortem dissolution resulting in the selective removal of some delicate species, both in surface waters (*21*) and in the sediment. This in part accounts for the minor geographic variations in rates, resulting from higher species numbers in shelf and lower-latitude areas as a function of better preservation in shelf areas, and a real increase in species diversity (*20*).

25. We have used the cyclostratigraphic age model of Röhl *et al.* (2000) (*6*) rather than an alternative age model based on extraterrestrial He (³He_ET) incorporation in sediments (*13*, *20*). The choice of age model does not substantially alter our findings because the onset-to-peak interval is nearly identical in both age models (table S1 and fig. S2). Values differ for the recovery interval, but this discrepancy is not substantial to our findings because the high-resolution record from site 690 demonstrates that extinction and origination rates returned to near-background levels before carbon isotope values increased

from their PETM minimum [marking the start of recovery (*20*)], irrespective of age model (fig. S2).

26. Despite large CCD changes at the PETM, we are confident that the patterns we observed are associated with evolutionary turnover and not dissolution. We have assessed nannofossil preservation through the sections, and where substantial dissolution is present, it is confined to short intervals during the event onset to peak. All samples that exhibited substantial dissolution were excluded (*20*).

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

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Fisheries have removed at least 50 million tons of tuna and other top-level predators from the Pacific Ocean pelagic ecosystem since 1950, leading to concerns about a catastrophic reduction in population biomass and the collapse of oceanic food chains. We analyzed all available data from Pacific tuna fisheries for 1950–2004 to provide comprehensive estimates of fishery impacts on population biomass and size structure. Current biomass ranges among species from 36 to 91% of the biomass predicted in the absence of fishing, a level consistent with or higher than standard fisheries management targets. Fish larger than 175 centimeters fork length have decreased from 5% to approximately 1% of the total population. The trophic level of the catch has decreased slightly, but there is no detectable decrease in the trophic level of the population. These results indicate substantial, though not catastrophic, impacts of fisheries on these top-level predators and minor impacts on the ecosystem in the Pacific Ocean.

Industrial fisheries for tunas and associated species extend over most of the tropical and temperate Pacific Ocean and currently produce over 2.5 million tons (*1*) or about 64% of the 2004 global tuna catch (Fig. 1). These fisheries have grown continuously since the 1950s and have removed more than 50 million tons of large pelagic fish. The fishery targets four primary temperate and tropical tuna species: skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*) tuna. Other species, blue-

fin tuna (*T. orientalis*), billfishes, and oceanic sharks are also taken, but the primary tuna species make up >90% of the total catch by weight. Data derived from these fisheries (including catch, fishing effort, size composition, and tagging data) show a 50-year record of natural variability in and human impacts on open-ocean ecosystems. We analyzed all available data with state-of-the art stock assessment methods to provide estimates of fishery impacts on population biomass, size structure, and trophic status of major top-level predator stocks in the Pacific

Ocean: bigeye tuna, yellowfin tuna, skipjack tuna, albacore tuna, and blue shark (*Prionice glauca*) (*2*).

The trajectories of exploited and unexploited (*3*) biomass vary substantially among stocks (Fig. 2). Exploited western Pacific yellowfin and bigeye have declined steadily to levels near the equilibrium biomass that would produce the maximum sustainable yield (MSY) in the fishery. Skipjack tuna and blue shark appear to have increased slightly, whereas albacore have fluctuated in both directions. Current total and adult biomass range, respectively, from 36 to 91% and 12 to 89% of that predicted in the absence of fishing (Table 1 and fig. S1). The variability in biomass over time and among stocks cannot be attributed entirely to fishing. Each stock has a unique recruitment history, some with periods of several years during which recruitment is more than 1 SD above or below the long-term average for the stock (fig. S2).

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Longline fishing, which selectively removes the largest and oldest individuals, was the primary method of fishing for the first 25 years of the tuna fishery except in some coastal areas. The biomass of tunas larger than 175 cm fork length (measured from the tip of the snout to the center of the fork in the tail) decreased by 40% by the end of the 1970s (Fig. 3A). The current biomass of tunas larger than 175 cm is less than 17% of the biomass expected in the absence of fishing, but this segment of the population never

made up more than 5% of the total tuna biomass (fig. S5). The burgeoning purse-seine fishery in the 1980s began to remove smaller fish (~75 cm in length), spreading exploitation to earlier life-history stages (Fig. 3A).

An ontogenetic model relating size to trophic level was applied to the size structure of the catch, exploited population, and unexploited population to estimate trophic levels (2). The trophic level of the catch, aggregated across the eight stocks, was about 10% higher than the troph-

ic level in both the exploited and unexploited population in the 1950s and declined steadily to the same level as the exploited population (Fig. 3B). The trophic level of the catch dropped from 4.1 to 4.0 over the past 50 years because of the increased catch of smaller fish, but the trophic level in the exploited population has remained relatively constant at 3.9 (table S3).

Stock assessment is sometimes criticized (4) for dependence on unproven assumptions and for producing uncertain results. Integrated stock assessment models are, however, the tools of choice when attempting to accommodate disparate fisheries data as opposed to selecting a single data source [for example, (5)]. Our analysis depends mainly on ratios of estimated variables, which are less variable than point estimates (6). The analysis, which used all available fisheries data, shows that the biomass of top-level predators has not declined catastrophically in spite of the continuous increase in catches since the 1950s. The biomass of four stocks is greater than 74% of their unexploited potential, and the biomass of the remaining four stocks is 36 to 49% of the unexploited potential, as expected when the catch approaches MSY.

The biomass of several stocks of primary tuna and other top predators (7–10) has declined to MSY-associated levels. The ecosystem impact of such reductions is unknown, but model studies have shown that fishing all species in an ecosystem at mortality rates yielding single-species MSY may, under some conditions, lead to the erosion of trophic structure and depensa-
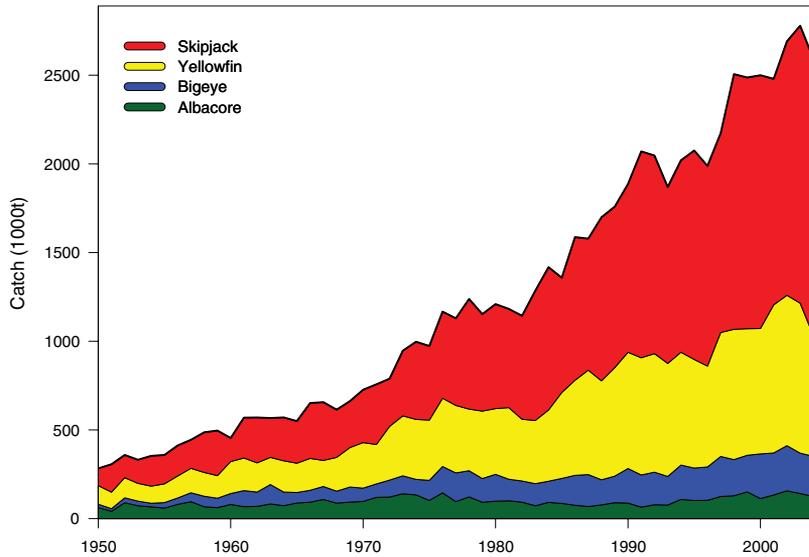

Fig. 1. Catches of major tuna species in the Pacific Ocean from 1950 through 2004 (1).

Fig. 2. Trends in total biomass for eight stocks of large predators in the Pacific Ocean, estimated from integrated stock assessment models. Blue lines indicate the biomass estimated from the observed fishing history (the exploited population), and red lines indicate the biomass estimated in the absence of all fishing (the unexploited population). The single black dash indicates the equilibrium biomass corresponding to MSY conditions, assuming current levels of recruitment and distribution of fishing mortality among fisheries. WCPO, western central Pacific Ocean; EPO, eastern Pacific Ocean.

Total Biomass
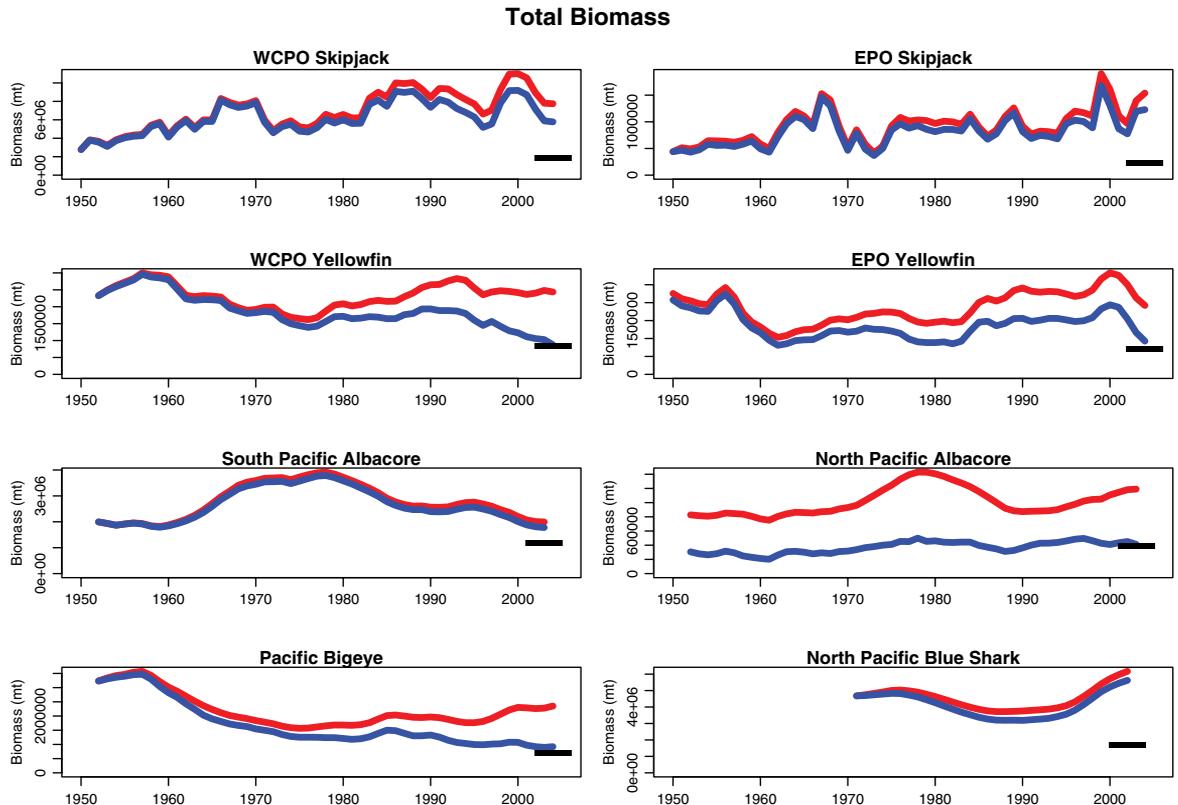
tory effects on recruitment (*11, 12*). MSY is, nevertheless, enshrined by many national and international fishery management agencies as the target level of catch to which fishery management aspires. More conservative, but ad hoc, reference points, such as maintaining adult populations above 50% of the unexploited adult biomass, may be more appropriate for an ecosystem approach to fisheries management (*13*).

Attempting to establish an unvarying initial reference point or baseline against which to evaluate changes in biomass is misleading. For example, the biomass of yellowfin in the eastern Pacific is currently about 2 times greater than the biomass at the beginning of the data time series, suggesting that the stock is in good condition. The exploited biomass is, however, only 49% of the unexploited biomass, and the current catch is near MSY (*14*). Expressing the impact of fishing as the ratio of exploited to unexploited biomass is a more sensitive indicator than comparison of current biomass to the biomass at some arbitrary date in the past at which the stock is assumed to be in a "pristine" or "virgin" state. The impact of the fishery is detectable in all stocks when the exploited-to-unexploited ratio is used.

The increase in the biomass of certain species, such as blue shark and skipjack, is a potentially important ecosystem response predicted by simple ecosystem models (*15*) and possibly attributable to a reduction in the biomass of other large predators. The possibility that the biomass of rapidly growing predators (such as *Coryphaena hippurus* and *Acanthocybium solandri*) may be also increasing should be examined. Unfortunately, complete fisheries statistics for these species are not available, and they rank low on the list of priority species for stock assessment in fishery management organizations.

Single-species assessment models do not explicitly include the effects of changes in the abundance of one species on the abundance of another. Until assessment models are able to simultaneously analyze multiple species, whether reduced abundance of larger fish has led to an increase in skipjack abundance will remain uncertain. In spite of this limitation, single-species stock assessments have an important role in the ecosystem approach to fisheries. Single-species assessment methods applied to nontarget species, such as blue shark, reveal potentially important ecosystem trends.

The results presented here appear to differ sharply from widely accepted views of the status of large oceanic predatory fish stocks and the ecosystem effects of fishing (*5, 16*). Our results, however, should be interpreted as extensions of previous work, providing a more realistic (*17–22*) appraisal of the effects of fishing on the pelagic ecosystem. Our estimates of biomass trends interpret all available data from all major fishing fleets in the context of well-understood population dynamics processes. The analysis extends the concept of aggregating abundance across species (*5*) by summing biomass according to length across species, concluding that the biomass of fish smaller than 175 cm is near that predicted for stocks at full exploitation and that drastic declines in abundance are detectable only in fish larger than 175 cm. Furthermore, the analysis extends the concept of "shifting baseline" (*23, 24*) by defining an empirical, quantitative reference base that depends directly on the activity being analyzed, concluding that although some predator populations have declined severely in response to fishing, others have increased. Finally, the analysis extends the notion of examining the impact of fisheries on the trophic level of the catch (*16*) by also examining the trophic level of the population at large, concluding that there is no impact on the trophic level of the population and that the apparent reduction in the trophic level of the catch is caused by the development of purse-seine fisheries targeting smaller tunas; that is, by "fishing through the food web" (*21*).

Fishery scientists have been warning of impending stock conservation problems in Pacific yellowfin and bigeye tuna in the western and central Pacific Ocean since 2001 (*25*), and the relatively depressed condition of the spawning populations of these two species has stimulated fishery managers to attempt to impose constraints on the fishery. The Western and Central Pacific Fisheries Commission and the Inter-American Tropical Tuna Commission have the responsibility to implement conservation regulations in the western and eastern Pacific Ocean, respectively. Scientists in both commissions have recommended management options, including catch and effort limits, restrictions on the use of artificial floating objects by the purse-seine fishery, and time and area closures, to maintain sustainable fisheries for these species on both sides of the Pacific (*26, 27*). Unfortunately, these options have not been fully implemented, and decreases in fishing mortality have not yet been realized. Commissioners and national delegations to these commissions need to implement effective conservation measures before stocks reach a state where draconian measures, such as complete closures, are required to preserve the fishery and sustain the ecosystem.

Table 1. Comparison of estimated impacts of fishing computed as the ratio of estimated exploited biomass to the estimated unexploited biomass in the last year of the analysis (exploited/unexploited) and as the ratio of estimated exploited biomass in the last year to that in the first year (biomass ratio).

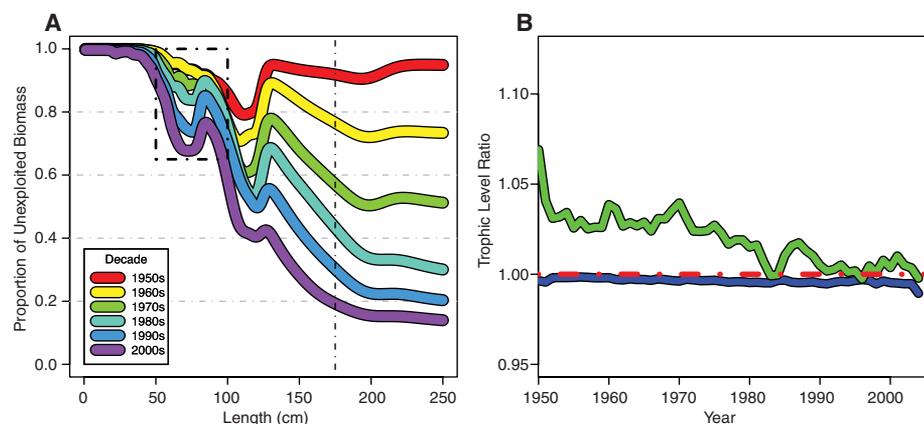| Stock	Exploited/unexploited		Biomass ratio	
	Total	Adult	Total	Adult
North Pacific albacore	0.38	0.12	1.34	0.94
Pacific bigeye	0.39	0.26	0.28	0.19
WCPO yellowfin	0.36	0.27	0.37	0.30
EPO yellowfin	0.49	0.41	2.12	2.27
North Pacific blue shark	0.91	0.89	1.20	1.16
WCPO skipjack	0.74	0.70	2.08	1.84
EPO skipjack	0.79	0.77	2.79	3.12
South Pacific albacore	0.89	0.83	0.89	0.91

Fig. 3. Two ecosystem indicators of the effects of fishing. (**A**) Impact of fishery on size. The ratio of exploited to unexploited biomass at increasing fork lengths by decade from 1950 through 2004 for all tuna stocks is shown. The dashed box indicates the size range of skipjack caught by the purse-seine fishery. The vertical dashed line indicates 175 cm fork length. (**B**) Impact of fishery on the trophic level of exploited tuna biomass and catch. The blue line is the ratio of the trophic level of exploited biomass to the trophic level of the unexploited biomass, and the green line is the ratio of the trophic level of the catch to the trophic level of the unexploited biomass. The dashed red line indicates 1.0, the relative trophic level in the unexploited biomass.

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2. Background material and analytical methods are available as supporting material on *Science* Online.
3. The "exploited" biomass is defined here as the biomass of the population estimated by the assessment model. The "unexploited" biomass is defined as the biomass that might have existed in the absence of fishing, estimated by setting the fishing mortality parameters to zero in the model. The unexploited population trajectories include the estimated effects of temporal variability in recruitment on the dynamics of the populations, thus incorporating environmental constraints that occurred during the history of the fishery and the estimated effect of the additional recruitment resulting from a larger spawning biomass (*2*).
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A Secreted Serine-Threonine Kinase Determines Virulence in the Eukaryotic Pathogen *Toxoplasma gondii*

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Toxoplasma gondii strains differ dramatically in virulence despite being genetically very similar. Genetic mapping revealed two closely adjacent quantitative trait loci on parasite chromosome VIIa that control the extreme virulence of the type I lineage. Positional cloning identified the candidate virulence gene *ROP18*, a highly polymorphic serine-threonine kinase that was secreted into the host cell during parasite invasion. Transfection of the virulent *ROP18* allele into a nonpathogenic type III strain increased growth and enhanced mortality by 4 to 5 logs. These attributes of ROP18 required kinase activity, which revealed that secretion of effectors is a major component of parasite virulence.

*T*oxoplasma gondii is a widespread protozoan parasite that chronically infects ~25% of the world's human population (*1*). *T. gondii* is dominated by three widespread, clonal lineages, which rapidly expanded following a severe genetic bottleneck ~10,000 years ago (*2*, *3*). Despite ~98% genetic identity, dramatic differences in virulence exist between *T. gondii* strains (*4*). Type I strains cause lethal infection in all strains of laboratory mice even at low inocula [lethal dose (LD$_{100}$) ≈ 1] (*4*, *5*), whereas types II and III strains are much less virulent [median lethal dose (LD$_{50}$) ≥ 10^3] (*4*). Acute virulence is associated with rapid dissemination, high parasite burdens, and overproduction of T helper cell type 1 cytokines (*6*, *7*). Toxoplasmosis has primarily been associated with type II strains, whereas type III strains are rarely associated with disease (*8*, *9*). Although less prevalent, type I can cause severe congenital infections (*10*), ocular toxoplasmosis (*11*, *12*),

and encephalitis in AIDS patients (*13*). Acute virulence of *T. gondii* in the mouse model is genetically determined (*14*), although the genes involved in this phenotype are unknown.

The extreme linkage disequilibrium of *T. gondii* populations (*4*, *9*) limits the use of association or population-based studies for identifying virulence genes. Therefore, we used forward genetic mapping to identify genes that determine natural differences in virulence. The recently completed genome map of the 14 chromosomes of the *T. gondii* ~65-megabase haploid genome provided a framework for quantitative trait locus (QTL) mapping with 175 informative genetic markers (*15*, *16*). Genomewide QTL mapping was used to analyze the genetic basis of acute virulence in 34 independent progeny from a genetic cross between the virulent type I strain GT-1 and the nonvirulent type III strain CTG (*14*). These parental strains differ in a number of virulence-related phenotypes including (i) migration under soft agarose, (ii) transmigration across polarized epithelia, (iii) intracellular replication, (iv) acute mortality in the mouse model, and (v) serum response of animals surviving low-dose infection (*17*).

Toxoplasma gondii and related apicomplexan parasites actively invade mammalian cells by using actin-based motility (*18*), which also enables passage across polarized epithelia and through tissues. Migration is enhanced in type I strains, and this may contribute to dissemination and, hence, acute virulence (*19*). In the present study, migration was monitored with two in vitro assays: migration under soft agarose and transmigration across polarized epithelia (*17*, *19*). The progeny from the cross showed correlated responses for migration (MIG) and transmigra-

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