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Ecological Metrics of Biomass Removed by Three Methods of Purse-Seine Fishing for Tunas in the Eastern Tropical Pacific Ocean

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Abstract: *An ecosystem approach to fisheries management is a widely recognized goal, but describing and measuring the effects of a fishery on an ecosystem is difficult. Ecological information on the entire catch (all animals removed, whether retained or discarded) of both species targeted by the fishery and nontarget species (i.e., bycatch) is required. We used data from the well-documented purse-seine fishery for tunas (*Thunnus albacares, T. obesus, *and* Katsuwonus pelamis*) in the eastern tropical Pacific Ocean to examine the fishery's ecological effects. Purse-seine fishing in the eastern tropical Pacific is conducted in 3 ways that differ in the amount and composition of target species and bycatch. The choice of method depends on whether the tunas are swimming alone (unassociated sets), associated with dolphins (dolphin sets), or associated with floating objects (floating-object sets). Among the fishing methods, we compared catch on the basis of weight, number of individuals, trophic level, replacement time, and diversity. Floating-object sets removed 2–3 times as much biomass as the other 2 methods, depending on how removal was measured. Results of previous studies suggest the ecological effects of floating-object sets are thousands of times greater than the effects of other methods, but these results were derived from only numbers of discarded animals. Management of the fishery has been driven to a substantial extent by a focus on reducing bycatch, although discards are currently 4.8% of total catch by weight, compared with global averages of 7.5% for tuna longline fishing and 30.0% for midwater trawling. An ecosystem approach to fisheries management requires that ecological effects of fishing on all animals removed by a fishery, not just bycatch or discarded catch, be measured with a variety of metrics.*

Keywords: bycatch, eastern tropical Pacific tuna, ecosystem approach, ecosystem-based fisheries management, tuna-dolphin

Métricas Ecológicas de la Biomasa Extraída por Tres Métodos de Pesca de Atún con Red de Cerco en el Océano Pacífico Oriental Tropical

Resumen: *Un enfoque ecosistémico en el manejo de pesquerías es una meta ampliamente reconocida, pero describir y medir los efectos de una pesquería sobre un ecosistema es difícil. Se requiere información ecológica de toda la captura (todos los animales extraídos, ya sea retenidos o descartados) tanto de especies objetivo de la pesquería como de especies no objetivo (captura incidental). Utilizamos datos de la pesquería de atunes (*Thunnus albacares, T. obesus *y* Katsuwonus pelamis*) con red de cerco en el Océano Pacéfico oriental tropical, bien documentada, para examinar los efectos ecológicos de la pesquería. La pesca con red de cerco en el Pacífico oriental tropical se lleva a cabo de tres formas, con distintas cantidades y composiciones de las especies objetivo y de la captura incidental. La selección del método depende de si los atunes se encuentran nadando solos (lances no asociados), asociados con delfines (lances sobre delfines) o asociados con objetos*

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flotantes (lances sobre objetos flotantes). Entre los métodos de pesca, comparamos la captura con base en el peso, número de individuos, nivel trófico, tiempo de reemplazo, y diversidad. Los lances sobre objetos flotantes extrajeron dos a tres veces más biomasa que los otros métodos, dependiendo de cómo se midió la extracción. Los resultados de estudios previos sugieren que los efectos ecológicos de los lances sobre objetos flotantes son miles de veces mayores que los efectos de otros métodos, pero estos resultados fueron derivados del número de animales descartados solamente. El manejo de la pesquería ha sido impulsado en grado sustancial por una concentración en la reducción de la captura incidental, aunque los descartes actualmente forman el 4.8% de la captura total en peso, comparado con los promedios globales de 7.5% para la pesca atunera con palangre y 30.0% para la captura con red de arrastre a media agua. Un enfoque ecosistémico al manejo de las pesquerías requiere que los efectos ecolgicos de la pesca sobre todos los animales extraídos por una pesquería, no sólo la captura incidental o captura descartada, sean cuantificados con una variedad de métricas.

Palabras Clave: atún-delfín, atún del Oriente Tropical del Pacífico captura incidental, enfoque ecosistémico, manejo de pesquerías basado en ecosistemas

Introduction

An ecosystem approach to fisheries management is a widely recognized, if not yet widely practiced, goal worldwide (Pikitch et al. 2004; Levin et al. 2009; McLeod & Leslie 2009). Fisheries can cause large perturbations of marine ecosystems (Dayton et al. 1995; Fogarty & Murawski 1998; Jennings & Kaiser 1998). Ecosystem-based fisheries management requires an understanding of the ecological effects of removing animals through fishing (Fogarty et al. 1991). The degree to which fisheries affect the structure and function of ecosystems depends on the biomass, composition, life history, and ecological role of the different species captured. For example, removal of keystone species (Paine 1966) may be associated with much larger ecological changes than would be expected on the basis of the abundances of those species (Dayton 1971; Estes & Palmisano 1974; Brown & Heske 1990), but this idea has been difficult to test in open-ocean ecosystems because controlled experiments are rarely possible. In lieu of detailed knowledge of the ecological roles of the species removed, more accessible quantities such as trophic levels and production-of-biomass to biomass ratios are used to construct models of marine food webs (Cox et al. 2002; Olson & Watters 2003).

Reduction of bycatch is an explicit goal of the Food and Agriculture Organization's (FAO) Guidelines for Responsible Fisheries (FAO 1995) and of many national fishery management plans. Bycatch affects the probability of persistence of certain species of seabirds, cetaceans, turtles, and fishes (Lewison et al. 2004; Read et al. 2006). Bycatch is distinct from discarded catch. Catch refers to all animals captured and removed from the ocean, both species targeted and not targeted by the fishery. Landings are retained catch and discards are nonretained catch, whereas bycatch is the part of the catch that is not the target of the fishery (Kelleher 2005). Most bycatch is discarded but some may be landed, and most targeted animals are landed but some may be discarded, for example, because they are too small or damaged. We used detailed catch data from the purse-seine fishery for tunas (genera *Thunnus* and *Katsuwonus*) in the eastern tropical Pacific Ocean to examine the fishery's effect on pelagic species. An ecosystem-based approach to management of this large tuna fishery is particularly challenging because purse-seine fishing is conducted in 3 ways that differ in the amount and composition of both landings and discards. The target species in this fishery are yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye (*Thunnus obesus*) tunas. In the eastern tropical Pacific, yellowfin tuna often swim with dolphins, primarily *Stenella* spp. In dolphin sets, the net is deployed around the tuna–dolphin aggregation after the animals have been chased and corralled by speedboats. The dolphins are released after the net is pursed (drawn together at the bottom) and partially retrieved, but strong currents, wind, and gear malfunctions can result in the accidental deaths of some dolphins. Bycatch in dolphin sets is currently low, but the previously high dolphin bycatch in this tuna fishery was one of the main factors behind the passage of the U.S. Marine Mammal Protection Act in 1972.

Tunas also aggregate near the ocean surface in the vicinity of floating objects, both natural and human made. In floating-object sets, a purse seine is deployed around the flotsam and associated fauna. With this method, sharks (Chondrichthyes), billfishes (Istiophoridae and Xiphiidae), dolphin fishes (*Coryphaena* spp.), wahoo (*Acanthocybium solandri*), and other fishes are bycatch. In unassociated sets, purse seines are deployed around schools of tuna that are not associated with either dolphins or flotsam. Bycatch from unassociated sets is similar to that of floating-object sets in species composition, but consists of fewer individuals and less biomass.

Previously, researchers examined single effects of the purse-seine fishery for tunas in the eastern tropical Pacific Ocean. A series of studies focused solely on dolphin populations (Smith 1983; Gerrodette & Forcada 2005). Edwards and Perkins (1998) describe the biomass of tuna discards among different fishing methods. Hall (1998) found that, in terms of average number of individuals per set, discards in floating-object sets are thousands of times greater than in dolphin sets. However, Hall considered discarded animals only and compared the number of individuals without regard to body size, life-history characteristics, or position in the food web. Essington et al. (2002) used a bioenergetics population model to estimate the reduction in predation by yellowfin tuna because of their removal by the fishery. Their analysis suggests that the ecological effects of different fishing methods vary by changing the predation impact of yellowfin tuna. Here, we extended previous analyses by examining several metrics of biomass of both target species and bycatch removed by the fishery.

Methods

Landing records for the tuna purse-seine fishery in the eastern Pacific Ocean were collected by the Inter-American Tropical Tuna Commission from vessel logbook and cannery records for purse-seine vessels of all sizes (IATTC 2008). Since 1993, onboard observers have recorded landed and discarded bycatch and discarded tunas for class-6 vessels (>363 t carrying capacity). On the basis of discard data for class-6 vessels, we estimated that discards for smaller vessels were approximately 0.7% of total removals for vessels of all sizes. Our results were not sensitive to this minor underestimate of total discards, so we used discard data from class-6 vessels only in the analysis. We obtained estimates of bycatch and discarded tunas for trips of class-6 vessels without observers by extrapolating values from observed trips. An estimated 94% of the bycatch was recorded on observed trips during 1993–2008.

Landings of target species were recorded in biomass (metric tons) and converted to numbers of individuals on the basis of data from a comprehensive size-frequency sampling program (Tomlinson 2002). Onboard observers typically estimate bycatches and discarded tunas within 3 classes (small, medium, and large [Supporting Information]) on the basis of number of individuals and metric tons, respectively. We converted data for non-target species from biomass to number of individuals or from number of individuals to biomass (Supporting Information).

We summarized landing and discard data by year, fishing method (dolphin, floating-object, or unassociated set), and species or ecological group. Of the 38 ecological groups defined in the food-web model of Olson and Watters (2003), 26 were caught in the purse-seine fishery (Supporting Information). These included the 3 target species of tuna, functional groups such as sharks and marlins, and other taxonomic groups of conservation interest such as sea turtles and dolphins. Some taxa were included in 2 ecological groups at different ontogenetic stages because of changes in diet and changes in catch rate by fishing method at different sizes. We aggregated the 26 ecological groups into 7 categories for display purposes: yellowfin tuna, skipjack tuna, bigeye tuna, other fishes, sharks, turtles, and cetaceans (Supporting Information).

The model of Olson and Watters (2003) of the eastern tropical Pacific ecosystem estimates the trophic level of each ecological group as 1.0 plus the biomass-weighted average of the trophic levels of its prey (Supporting Information). Olson and Watters (2003) estimated production-of-biomass to biomass (P/B) ratios for each ecological group from stock assessments and other fisheries data and meta-analyses of fisheries data. We used the inverse of the P/B ratio as an index of replacement time (i.e., the time necessary to replace a unit of biomass removed by the fishery [B/P]) (Supporting Information).

From the landing and discard data, we described type of biomass removed by mean trophic level, mean replacement time, and diversity. We computed mean trophic level and mean replacement time with the biomass-weighted means of the trophic levels or replacement times of the ecological groups removed. We computed diversity with the Shannon index $-\sum_i p_i \ln p_i$, where p_i was the proportion of total biomass removed for ecological group i. The value of the Shannon index is a function of both the number of ecological groups removed and the evenness of biomass among them. In this case, the maximum possible value of the index was $\log(26) = 3.26$ if the removed biomass of each of the 26 ecological groups caught by the fishery was equal.

We described the amount of biomass removed on the basis of number of individuals, biomass, trophic-level units, and replacement-time units. The first 2 measures are standard measures of removals by fisheries, but number of individuals and biomass may not account for the ecological effects of removing animals from different trophic levels and animals with different reproductive rates. Thus, we calculated the latter 2 biomass-weighted removal metrics: trophic-level tons (mean trophic level of each ecological group times the biomass of that ecological group) and replacement-time tons (mean replacement time of each ecological group times the biomass of that ecological group).

Results

The biomass removed by the purse-seine fishery increased since its establishment around 1960 (Fig. 1). For 1993–2008 each of the methods of purse-seine tuna fishing removed between 100,000 t and 300,000 t annually. The percentage of biomass removed by dolphin sets, floating-object sets, and unassociated sets was 30%, 44%, and 26%, respectively, although the percentage of biomass removed with the 3 methods varied considerably among years (Fig. 1). The mean total annual biomass removed was >500,000 t (Fig. 2). The 3 target tuna species

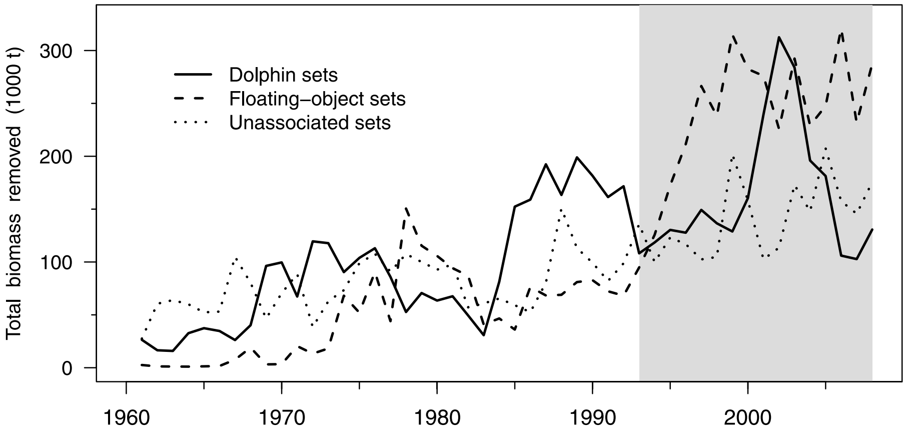

Figure 1. Total biomass removed by the purse-seine tuna fishery in the eastern tropical Pacific as a function of year and fishing method (dolphin sets, purse seine is set around the tuna–dolphin aggregation; floating-object sets, purse seine is set on the animals associated with a floating object; unassociated sets, purse seine is set on a school of tuna not associated with dolphins or floating objects). Data for 1993–2008 (shaded area) were analyzed for this paper. We calculated total removals for each of the 3 fishing methods before 1993 by multiplying catches of target species before 1993 by the mean ratio of total removals (target species and bycatch) to removals of target species for 1993–2008.

were 98% of the landings and 81% of the discards by weight. Mean biomass removed was 17.0, 41.1, and 12.8 t per set for dolphin sets, floating-object sets, and unassociated sets, respectively. Of these amounts, bycatch was 0.3% for dolphin sets, 3.8% for floating-object sets, 1.4% for unassociated sets, and 2.1% for all methods combined. The discard rate was 0.7% for dolphin sets, 10.5% for floating-object sets, 2.2% for unassociated sets, and 5.4% for all methods combined. With the addition of the 0.7% estimated for smaller vessels, the overall discard rate was 4.8%.

Mean trophic levels removed by the 3 fishing methods were similar: 4.64 for dolphin sets, 4.63 for floating-object sets, and 4.59 for unassociated sets. Slight decreases in trophic levels of landings from dolphin sets and unassociated sets (Fig. 3a) resulted from increasing proportions of skipjack and decreasing proportions of yellowfin or bigeye tunas in the catch, not from increasing catches of low trophic-level species (Supporting Information). Averaged over years and fishing methods, mean trophic-level of discards (4.53) was lower than that of landings (4.63). Annual mean trophic level values of discards were more variable than those of landings (Fig. 3b). The decrease in mean trophic level of dolphin-set discards was largely because of an increase in the proportions of discarded prey fishes (bullet and frigate tunas [*Auxis* spp.]), miscellaneous epipelagic fishes (Supporting Information) and rays (Rajiformes, mostly manta rays, Mobulidae) with lower trophic levels (Supporting Information).

Mean replacement time for total removals averaged over years was lowest for dolphin sets (mean 0.48 years), intermediate for unassociated sets (0.57 years), and highest for floating-object sets (0.74 years). There were no temporal trends in mean replacement time for landings (Fig. 3c). Mean replacement times for discards were more variable than those for landings, and mean replacement times for dolphin-set discards were approximately 7 times the mean replacement times for floating-object or unassociated-set discards because dolphins have a low reproductive rate (Fig. 3d). Proportional contributions of ecological groups to the biomass-weighted replacement times revealed strong positive relations with proportions in the catch of cetaceans (dolphin sets), bigeye tuna (floating-object sets), and other fishes (unassociated sets) and strong negative relations with proportions of yellowfin tuna (dolphin sets) and yellowfin and skipjack tunas (floating-object sets) (Supporting Information).

The Shannon diversity index for total removals was lowest for dolphin sets (mean 0.62), intermediate for unassociated sets (1.22), and highest for floating-object sets (1.38). Diversity of dolphin-set landings increased by a mean of 0.023 per year from 0.45 to 0.79 (Fig. 3e) due primarily to percentages in the catch of skipjack tuna increasing from <1% to >7% and concurrent decreasing percentages of yellowfin tuna (Supporting Information). Diversity of unassociated-set landings and discards both decreased (Figs. 3e and f), and diversity of total removals decreased by a mean of 0.024/year, from 1.40 to 1.04. The number of the 26 ecological groups caught annually ranged from 17 to 22 for dolphin sets, 18 to 21 for floating-object sets, and 17 to 22 for unassociated sets.

The relative amounts and characteristics of the biomass removed by each of the fishing methods varied as a function of how removal was measured (Fig. 4). Landings

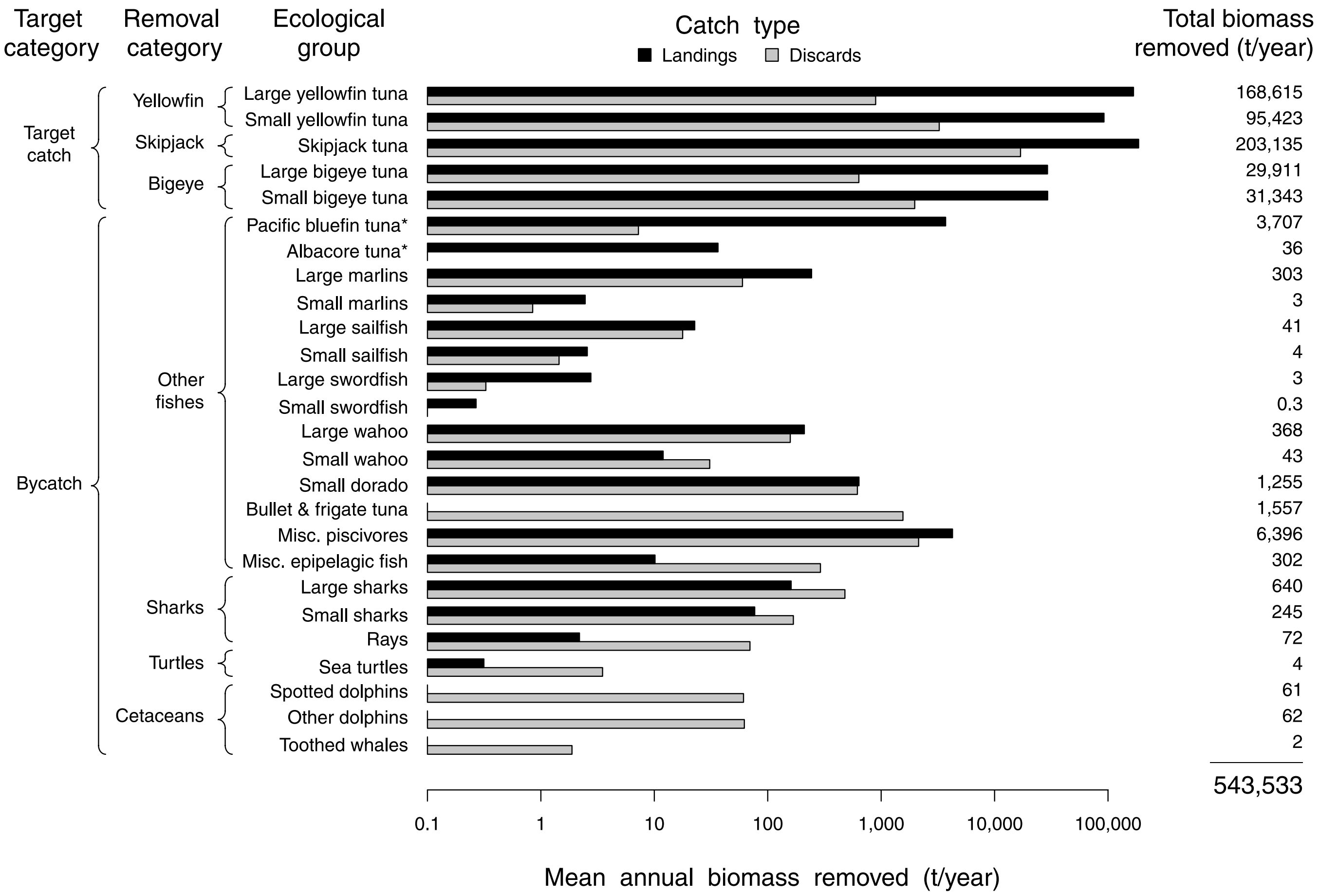

*Figure 2. Mean annual biomass removed by the tuna purse-seine fishery of the eastern tropical Pacific, 1993–2008, as a function of ecological group (Olson & Watters 2003) (misc., miscellaneous), pooled removal category, target category (target or bycatch), and catch type (landings, retained catch, discards, nonretained catch). Total biomass does not equal sum of biomass of each ecological group because of rounding. *Pacific bluefin tuna and albacore tuna can be target species in unassociated sets in the northern part of the fishing area, but are never the principal target species of this fishery.*

from floating-object sets were greatest by all 4 measures of removal, but were particularly high when removal was measured on the basis of number of individuals or replacement time. Landings of dolphin sets were almost all yellowfin tuna; landings of floating-object sets were a mixture of yellowfin, skipjack, and bigeye tunas; and landings of unassociated sets were composed of approximately equal proportions (in biomass) of yellowfin and skipjack tunas (Fig. 4).

The amount and composition of discards varied among the fishing methods (Fig. 4). Discards of the target tuna species were the greatest proportion of removed animals whether measured in biomass, number of individuals, or trophic-level units. Discards of cetaceans in dolphin sets and sharks in floating-object and unassociated sets were greater when measured in replacement-time units than when measured in other units because of the low reproductive rates of these animals.

Discussion

Commercial fisheries can alter marine ecosystems by removing predators and species with low reproductive rates and by reducing habitat quality (Dayton et al. 1995). Ecosystem-based fisheries management requires metrics that provide information about those changes (Rochet & Trenkel 2003; Cury et al. 2005; Link 2005). Assessment of the effects of fisheries on ecosystems is still in its infancy. We examined effects of a fishery on an ecosystem with a variety of relatively simple, but comprehensive metrics that we based on total removals by the fishery.

We estimated that discards in the purse-seine fishery for tunas in the eastern tropical Pacific Ocean were 4.8% by weight, compared with global estimates of 7.5% for tuna longlines, 30.0% for tuna midwater trawls, and 8.0% for all fisheries (Kelleher 2005). Despite the present moderate quantity of discards and bycatch in this tuna

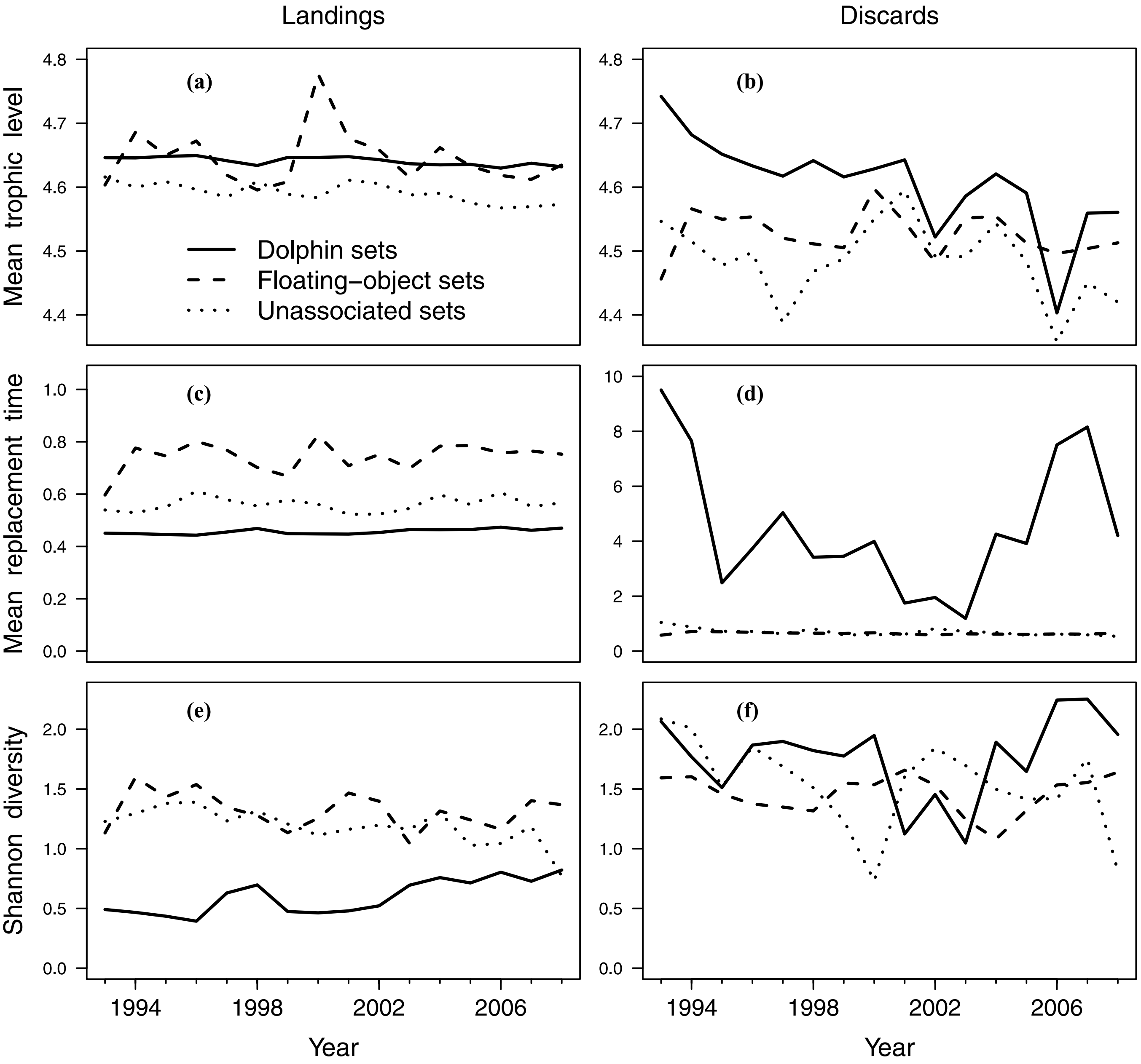

Figure 3. Three measures—(a, b) mean trophic level, (c,d) mean replacement time, (e,f) Shannon diversity index—of type of biomass removed by the purse-seine tuna fishery of the eastern tropical Pacific as a function of catch type (landings or discards) and fishing method (dolphin, floating-object, or unassociated sets [defined in legend of Fig. 1]). All measures were weighted by biomass of ecological groups caught.

fishery by global standards, management has largely focused on reducing bycatch. Past actions have successfully reduced dolphin bycatch, whereas current management is focused on reducing bycatch of other species in addition to dolphins. Previous discussions of ecological effects of the fishery have centered on discarded bycatch as measured by numbers of animals. Joseph (1994), Scott (1996), Hall (1998), and Hall et al. (2000) argue that catching tunas in dolphin sets is preferable to catching tunas in floating-object or unassociated sets. Authors of articles in popular magazines (Norris 2002; Eaves 2008) advance the contrarian idea that on the whole, management designed to protect dolphins has undesirable effects on the ecosystem. However, those who argue that the ecological effects of dolphin sets are much less than floating-object sets compared fishing methods on the basis of discards only, which are only 4.8% of total removals. Moreover, they compared methods on the basis of numbers of individuals without regard to the animals' sizes, trophic levels, or life histories. Hall (1998) suggests that the

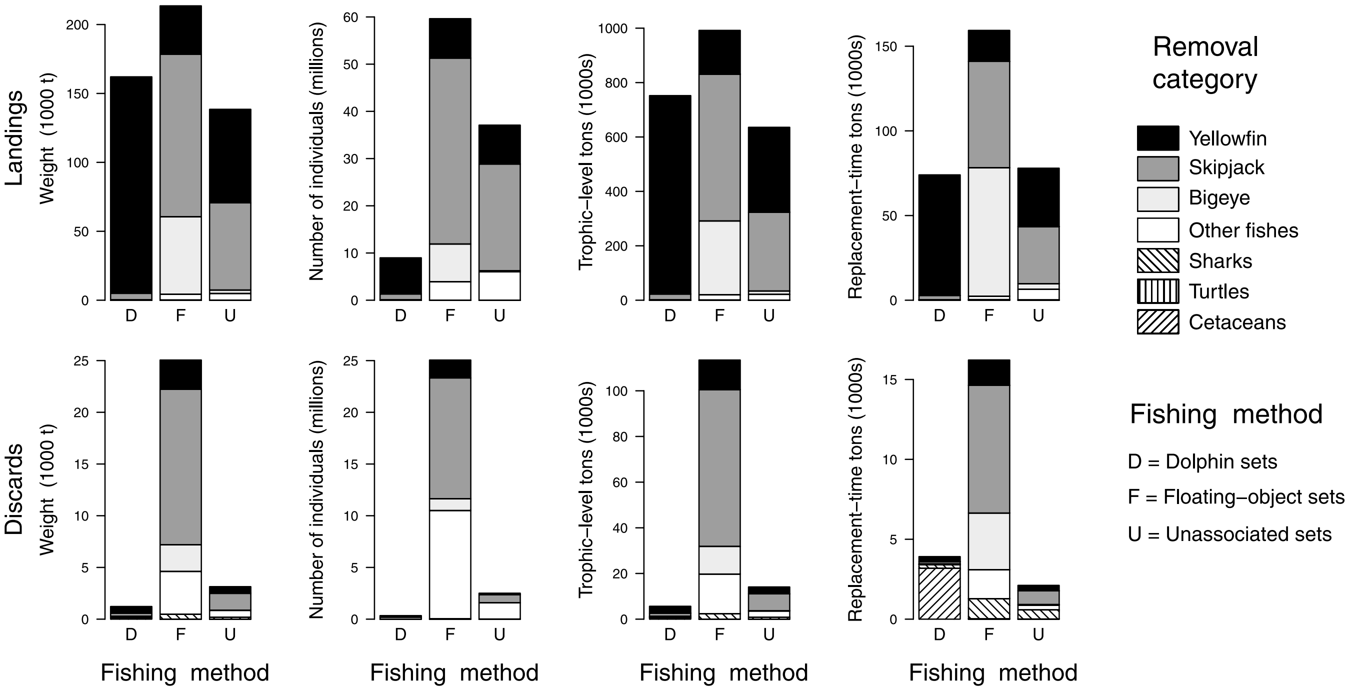

Figure 4. Four measures (weight, number of individuals, trophic-level tons, and replacement-time tons) of amount of biomass removed annually by the tuna purse-seine fishery of the eastern tropical Pacific as a function of catch type (landings or discards) and fishing method (defined in legend of Fig. 1). The y-axes differ for landings and discards. Trophic level and replacement time were weighted by biomass of ecological groups caught.

ecological effect of a floating-object set is thousands of times greater than the effect of a dolphin set. We found much smaller differences. Removals by floating-object sets were at most twice the removals by dolphin and unassociated sets when compared on the basis of weight, trophic level, and replacement time (Fig. 4). On an average per-set basis, a floating-object set removed 2.4 times as much biomass as a dolphin set and 3.2 times as much as an unassociated set.

Biomass is a more informative metric than number of individuals because it accounts for differences in sizes of animals removed from the ecosystem. Biomass is the most easily measured and widely used measure of fisheries catch. However, biomass can be misleading when comparing animals that differ in trophic level, growth rate, and reproductive rate.

Trophic level and replacement time indicate energy or mass flow through communities (Murawski 2000; Cury et al. 2005). Fisheries that target large piscivorous fishes act as apex predators. The mean trophic level of the fishes and invertebrates landed globally was reported to have decreased between 1950 and 1994 (Pauly et al. 1998). The most common mechanism for the decrease in trophic level was the serial addition of low trophic-level fisheries, not declining catches of upper trophic-level species or sequential fishery collapses and replacements with fisheries targeting lower trophic levels (Essington et al. 2006). However, mean trophic level of catch may not reliably predict changes in mean trophic level of marine ecosystems (Branch et al. 2010). Nevertheless, we presented mean trophic level of catch to allow comparison with other ecosystems and with tuna fisheries worldwide. We found no evidence of decreasing trophic levels of catch; minor declines in mean trophic levels of dolphin and unassociated sets were because of changing proportions of yellowfin, skipjack, and bigeye tunas, all target species of the purse-seine fishery since its inception (Supporting Information). Pauly et al. (1998) based their analysis of mean trophic level on landings alone; we included both landings and discards.

Replacement time is a measure of the length of time required for replacement of biomass removed by the fishery. Unsustainable levels of harvest may lead to greater decreases in probabilities of persistence of long-lived animals with low fecundity and late age of maturity than of fast-growing, highly fecund species. In contrast to trophic-level metrics, replacement-time metrics were sensitive to categories of animals with relatively high *B/P* values, such as bigeye tunas, sharks, and cetaceans. Biomass replacement times were longest for floating-object sets (Fig. 3) because that method captures a relatively high proportion of bigeye tunas, which have lower production rates than yellowfin and skipjack tunas (IATTC 2010). On the one hand, dolphin-set landings had shorter replacement times than those of unassociated and floating-object sets because of the relatively high productivity of yellowfin tuna (Fig. 3c). On the other hand, dolphin-set discards had replacement times 7 times longer than the replacement times of the discards of unassociated and floating-object sets due to the low reproductive rate of mammals (Fig. 3d). Measuring biomass removal in terms of replacement-time units showed dolphins and sharks were high proportions of the discards of dolphin and floating-object sets, respectively (Fig. 4). Their proportions were large because their reproductive rates are low. During most of the history of the fishery, but before the period considered in this study (approximately 1960–1990), replacement times of dolphin-set discards were 1–2 orders of magnitude greater than replacement times shown in Figure 4 because of the formerly much higher bycatch of dolphins.

Fishing alters diversity by selectively removing target species. The relation between diversity of species removed and effects on the diversity and stability of the ecosystem from which they were removed may be complex. Higher diversity of catch may be associated with fewer undesirable effects on the ecosystem, although the complexity of competitive and trophic interactions among species makes the relation between diversity of catch and diversity and stability of the ecosystem difficult to predict. A fishery that removes equal proportions of many species may be more effective than traditional highly selective fisheries to maintain the diversity, structure, and function of ecosystems (Garcia et al. 2011). The diversity of species removed by dolphin sets was low because both landings and discards were almost all yellowfin tuna (i.e., the catch was highly selective), but dolphin-set diversity has been changing (Fig. 3e & Supporting Information). Floating-object sets removed the greatest diversity of species.

Multispecies metrics are unlikely to show substantial effects of a fishery on individual species. For the tuna purse-seine fishery in the eastern tropical Pacific, the groups or species of greatest conservation concern are dolphins, sharks, and bigeye tunas. The bycatch of eastern spinner (*Stenella longirostris orientalis*) and northeastern spotted (*Stenella attenuata attenuata*) dolphins was up to 100 times higher between 1960 and 1990 than it is currently. The bycatch per unit effort of silky (*Carcharhinus falciformis*) and oceanic whitetip (*Carcharhinus longimanus*) sharks in floating-objects sets has decreased markedly during the period of our study (Minami et al. 2007), which suggests their abundance is decreasing. Abundance of bigeye tunas may be decreasing because immature individuals of this species are being caught in the floating-object fishery (Aires-da-Silva & Maunder 2011). For species of high conservation concern, multispecies metrics can be supplemented with individual stock assessments or with indices focused on such species.

Managing commercial fisheries on an ecosystem basis is a challenging task requiring new policies and procedures (Gerrodette et al. 2002; Pikitch et al. 2004; McLeod & Leslie 2009) and estimates of both target and nontarget (bycatch) removals. Because the methods of purse-seine fishing that we examined removed large amounts of biomass annually, but the fishing methods differed in the types (Fig. 3) and amounts (Fig. 4) of both landings and discards, these methods are likely to have different ecological effects (Essington et al. 2002; Olson & Watters 2003). Determining the optimal mix of fishing methods depends on a clear statement of management objectives and on the development of metrics to gauge progress in reaching the objectives (Murawski 2000).

Acknowledgments

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Supporting Information

Length–weight and weight–length conversions (Appendix S1); taxonomic composition, trophic level, and B/P ratios of ecological groups (Appendix S2), and details of the contribution of each ecological group to the ecological measures (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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