Abstract—Catch rates for the 13 most abundant species caught in the deep-set Hawaii-based longline fishery over the past decade (1996–2006) provide evidence of a change among the top North Pacific subtropical predators. Catch rates for apex predators such as blue shark (*Prionace glauca*), bigeye (*Thunnus obesus*) and albacore (*Thunnus alalunga*) tunas, shortbill spearfish (*Tetrapturus angustirostris*), and striped marlin (*Tetrapturus audax*) declined by 3% to 9% per year and catch rates for four midtrophic species, mahimahi (*Coryphaena hippurus*), sickle pomfret (*Taractichthys steindachneri*), escolar (*Lepidocybium flavobrunneum*), and snake mackerel (*Gempylus serpens*), increased by 6% to 18% per year. The mean trophic level of the catch for these 13 species declined 5%, from 3.85 to 3.66. A shift in the ecosystem to an increase in midtrophic-level, fast-growing and short-lived species is indicated by the decline in apex predators in the catch (from 70% to 40%) and the increase in species with production to biomass values of 1.0 or larger in the catch (from 20% to 40%). This altered ecosystem may exhibit more temporal variation in response to climate variability.

Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996–2006

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The North Pacific subtropical gyre is a large oceanic gyre bounded on the south by the North Equatorial Current, on the west by the Kuroshio Current, on the north by the Kuroshio Extension Current and the North Pacific Current, and on the east by the California Current (Pickard and Emery, 1990). Although low in primary productivity, the warm, vertically stratified oligotrophic waters of the subtropical gyre contain a highly diverse food web populated by tunas, sharks, and billfishes at the top trophic levels (Seki and Polovina, 2001; Kitchell et al., 2002). Since the 1950s, the tunas, billfishes, and other large predators in this ecosystem have been targeted by large-scale fisheries. Several studies have indicated possible ecosystem impacts from fishing (Ward and Myers, 2005a; Kitchell et al., 1999; 2002). A comparison of catch, size, and species composition between a research longline survey in the 1950s and observer data from commercial longliners in the 1990s indicated a substantial decline in the abundance of large predators, in the mean size of these predators, and gave some evidence of an increased abundance of formerly rare species (Ward and Myers, 2005a). Models of the North Pacific subtropical gyre were generated with Ecopath with Ecosim, vers. 5 (EwE) modeling software (available from http://www.ecopath.org/index.php) to investigate whether the ecosystem contained any keystone species (Kitchell et al., 1999; 2002). The results indicated that there was not any single species group that functioned as a keystone, but that a broad reduction of apex predators due to fishing might result in an increase in prey (Kitchell et al., 1999; 2002). In effect, the fishing fleet is the keystone predator (Kitchell et al., 1999). However another modeling effort with an EwE model that incorporated some size-class structure revealed that although fishing decreased predator abundance, there was limited evidence (based on the decline in predators) of trophic cascades or other ecosystem impacts (Cox et al., 2002).

The longline logbook and observer data from the Hawaii-based fishery are valuable data sources for investigating the spatial and temporal dynamics of the exploited subtropical ecosystem. The fishery operates over a large portion of the central North Pacific, from the equator to 40°N latitude and from 140°W longitude to the International Date Line. Federally mandated logbooks completed by fishermen provide catch and effort

data on the landed species. A portion of the vessels, randomly selected, also carry observers who record all catches including noncommercial species.

Fishing effort in the Hawaii-based deep-set longline fishery targeting bigeye tuna (*Thunnus obesus*) increased about 250% between 1996 and 2006. The number of fishing sets increased from about 530 per month to 1370 per month, and the number of hooks deployed increased from about 850,000 per month to 2.9 million per month. The catch also increased from 161,000 to 427,000 fishes annually between 1996 and 2006.

In this article, changes in catch rates were investigated within the upper trophic levels of the subtropical ecosystem. Logbook and observer data from the Hawaii-based deep-set longline fishery provided catch and effort data that were used to describe the changes in catch rates of the most commonly caught commercial and noncommercial species from 1996 to 2006. Ecological indicators of the catch were also computed to estimate trends in the exploited ecosystem.

Material and methods

The Hawaii-based longline fishery consists of two components: the daytime deep-set fishery targeting bigeye tuna at depths, and the nighttime shallow-set fishery targeting swordfish (*Xiphias gladius*). The deep-set fishery typically sets hooks between depths of 100 m to 400 m with the median hook depth at about 250 m (Bigelow et al., 2006). Catch data recorded by fishermen in federally mandated logbooks provide daily records of fishing activity such as location, catch by species, number of hooks per set, and since 1996, the number of hooks per float for each set. Deep sets and shallow sets can be identified by a very strong bimodal distribution of the number of hooks between floats. For shallow sets, 2–6 hooks are used per float, whereas for deep sets, 20–32 hooks are used per float (Bigelow et al., 2006). For our analysis we identified deep sets as those with 10 or more hooks per float and shallow sets as those with fewer than 10 hooks per float. The shallow-set fishery operates primarily in the winter and spring within a narrow band of 28–32°N latitude. The shallow-set fishery was closed for several years to reduce interactions with sea turtles. In this article we focus exclusively on the deep-set fishery that operates throughout the year over a broad geographic region and provides an uninterrupted catch and effort time series from 1996. The restriction of our analysis to the deep-set fishery provides a relatively standardized depth range and method of gear deployment. Our analysis was further restricted to data that were obtained from the core region of the fishing ground defined as bounded by 12–27°N latitude. In some years, the fishery made excursions as far south as the equator and as far north as 32°N latitude; however, fishing in these areas was inconsistent over the period of the study.

In addition to logbook records of all commercially valuable catches, a portion of the longline vessels carried observers who recorded all catches and measured a subset of the catches. Between 1996 and 2006 approximately 16% of the deep-set effort in the core fishing ground had observer coverage. The top 13 species in the catch, determined from the observer data, accounted for 90% by number of the total observed catch over the period 1996–2006 in the deep-set fishery in the core fishing ground. In descending order of their proportion in the catch they were bigeye tuna (*Thunnus obesus*), longnose lancetfish (*Alepisaurus ferox*), blue shark (*Prionace glauca*), mahimahi (*Coryphaena hippurus*), sickle pomfret (*Taractichthys steindachneri*), snake mackerel (*Gempylus serpens*), skipjack tuna (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), yellowfin tuna (*Thunnus albacares*), striped marlin (*Tetrapturus audax*), escolar (*Lepidocybium flavobrunneum*), ono (*Acanthocybium solandri*), and shortbill spearfish (*Tetrapturus angustirostris*). The local name most frequently used in Hawaii for the sickle pomfret is monchong. Other common names used for mahimahi and ono are dolphinfish and wahoo, respectively. Three species reported by observers as part of the catch but not fully reported in logbooks because of their limited commercial value were lancetfish, snake mackerel, and escolar. In recent years escolar has become a commercial species and is now reported in the logbook, but this was not the case in the early part of the time period examined. Escolar is sometimes locally called oilfish or walu, but oilfish is actually the common name for *Ruvettus pretiosus* which represents a relatively rare species in the catch of the longline fishery.

For the 10 species fully reported in the logbooks, we computed a monthly catch-per-unit-of-effort (CPUE) time series. Logbook monthly CPUEs were computed as the total number of fish of a species caught in a month divided by the total number of hooks multiplied by 1000; thus CPUE was computed as the number of fish per 1000 hooks. A generalized additive model (GAM) (Hastie and Tibshirani, 1990) was then used over the 1996–2006 period that fitted observed monthly CPUE and contained a linear function of year to model the time trend, a smoothed monthly term to model the seasonal pattern, and a smoothed spatial term computed from mean monthly latitude and longitude to incorporate any spatial contribution to CPUE.

For the three species not fully reported in the logbooks (lancetfish, snake mackerel, and escolar), we used observer catch and effort data which covered about 16% of the fishing effort over the decade. Because we had much less observer coverage than logbook coverage, we pooled the observer data over the year and computed an annual, rather than monthly, CPUE time series. Observer annual CPUEs were computed as the total number of fish of a species caught in a year on vessels carrying observers divided by the total number of hooks used by those vessels multiplied by 1000. Because of the limited data points with our annual CPUE time series, a simple linear regression was fitted to the annual CPUE data. Although the limited observer coverage was considerably less than that reflected by the logbook data

Table 1

The percentage of the observed catch, the annual percent change in catch per unit of effort (CPUE) from the linear trends, categorical values of production to biomass (P/B), and trophic level for each of the top 13 most abundant species in the observed deep-set longline catch in Hawaii, listed in order of increased annual percent change in CPUE. Trophic level and P/B values are taken from the Ecopath model of Kitchell et al. (2002).

Species	Percentage of total catch		Annual percent change in CPUE	Ratio of production to biomass (P/B)	Trophic level
	1996	2006			
Albacore (*Thunnus alalunga*)	12	2	−9.1	0.6	4.0
Striped marlin (*Tetrapturus audax*)	5	4	−4.8	0.5	4.3
Bigeye tuna (*Thunnus obesus*)	17	17	−3.4	0.8	4.0
Shortbill spearfish (*Tetrapturus angustirostris*)	3	2	−3.3	0.5	4.3
Blue shark (*Prionace glauca*)	12	10	−2.6	0.3	4.0
Skipjack tuna (*Katsuwonus pelamis*)	4	4	0.0	1.9	3.9
Yellowfin tuna (*Thunnus albacares*)	4	4	0.0	1.2	4.0
Ono (*Acanthocbium solandri*)	1	4	0.0	2.0	3.9
Longnose lancetfish (*Alepisaurus ferox*)	10	20	0.0	0.3	3.2
Sickle pomfret (*Taractichthys steindachneri*)	5	9	6.0	1.5	3.2
Mahimahi (*Coryphaena hippurus*)	3	7	6.6	3.0	3.9
Escolar (*Lepidocybium flavobrunneum*)	1	4	10.6	0.8	3.2
Snake mackerel (*Gempylus serpens*)	2	6	17.9	1.0	3.2

for those commercial species where we had both types of data, the observer-based estimates of CPUE compared well with logbook-based estimates. For example, correlations between CPUE trends for commercial species computed from both logbooks and observer data were very similar—0.93 or greater for albacore, striped marlin, shortbill spearfish, bigeye tuna, and sickle pomfret, between 0.80 and 0.89 for mahimahi, ono, and yellowfin tuna, 0.78 for skipjack, and 0.76 for blue shark.

Based on the linear trend derived from either the GAM fitted to monthly CPUE data or the regression line fitted to annual observer CPUE, the annual percent change in CPUE of each species was computed as the slope divided by the intercept multiplied by 12 to convert from monthly to annual values, if necessary, and multiplied by 100 to convert to a percentage. For those species with linear slopes that were not statistically different from zero the annual percent change was set at zero.

From the catch data for the most abundant 13 species, we computed time trends of the annual mean trophic level of the catch, the annual proportion of the catch composed of apex predators (those with trophic level at least 4.0), and the annual proportion of the catch with moderate or high production to biomass (P/B) ratio (defined as at least 1.0). Here we define trophic level 1.0 as primary producers (e.g. phytoplankton), level 2.0 as secondary producers (e.g. zooplankton), level 3.0 as mid-level consumers, and level 4.0 and above as the apex predators. The estimates of trophic level and P/B ratio for most of the 13 species came from a central North Pacific pelagic ecosystem EwE model (Kitchell et

al., 2002). The annual trophic level, annual percentage of the catch with trophic level at least 4.0, and annual percentage of catch with P/B ratio of at least 1.0 were computed as a mean weighted by the relative catch in numbers as follows:

$$M_j = \sum_{i=1}^{13} X_i(C_{ij}/CC_j), \qquad (1)$$

where M_j = annual trophic level, annual percent of the catch with trophic level at least 4.0, or annual percentage of catch with P/B ratio of at least 1.0 in year j;
X_i = trophic level of species i or binomial variable with value 0 if trophic level < 4.0 or P/B < 1.0 and 100 otherwise;
C_{ij} = catch in number of species i in year j; and
CC_j = combined catch of top 13 species in year j.

Three species—sickle pomfret, escolar, and snake mackerel—are not represented as species groups in the Kitchell et al. (2002) model. However, longnose lancetfish is assigned a trophic level of 3.2 and a P/B ratio of 0.3 in the model. Lancetfish is found from the surface to below 1000 m and feeds on a diverse assemblage of fishes, cephalopods, tunicates, and crustaceans that occupy the scattering layers (Post, 1984). Sickle pomfret, escolar, and snake mackerel all appear to feed on much of the same prey as the longnose lancetfish so it seems reasonable to assign them all to a trophic level of 3.2 (Nakamura and Parin, 1993). For the P/B ratio,

a preliminary growth-rate estimation, based on daily increments on otoliths, indicates that sickle pomfret has rapid growth and reaches 42–49 cm fork length

in 12 months (M. Seki, personal commun.[1]).The sickle pomfret growth and maximum size were estimated at just slightly less than the values for skipjack tuna, which has a P/B of 1.9 in the model; hence the sickle pomfret P/B was set at 1.5. Snake mackerel is a relatively fast-growing species with a maximum size of 1.0 m and population doubling time of less than 15 months and therefore it was assigned a P/B of 1.0 whereas escolar has a maximum size of 2 m and is slower growing than snake mackerel, and therefore it was assigned a P/B of 0.8. Recognizing that the P/B values for most of the 13 species are fairly subjective, we used them only to compute the change in the proportion of moderate and high P/B species in the catch where moderate and high P/B species are defined as those with P/B greater than or equal to 1.0.

Results

The results from the logbook and observer CPUE time series for the 13 species revealed statistically significant linear trends in slopes ($P<0.05$) for 9 species—5 declining and 4 increasing trends (Table 1, Figs. 1–4). Albacore tuna, bigeye tuna, blue shark, shortbill spearfish, and striped marlin all showed declining CPUE trends; skipjack tuna, yellowfin tuna, ono, and lancetfish showed no significant trends; and mahimahi, sickle pomfret, escolar, and snake mackerel showed increasing trends (Table 1, Figs. 1–4). CPUE trends for albacore tuna, striped marlin, shortbill spearfish, bigeye tuna, and blue shark all decreased from 3% to 9% annually, CPUE trends for yellowfin tuna, skipjack tuna, ono, and lancetfish remained unchanged, whereas CPUE trends for mahimahi, sickle pomfret, escolar, and snake mackerel increased from 6% to 18% annually (Table 1, Fig. 4). For reference, the combined CPUE of all species caught in the deep-set fishery recorded in the observer data declined 4% annually. The species with declining trends had trophic levels of 4.0 or larger and the species with increasing trends had trophic levels of 3.9 or less (Table 1).
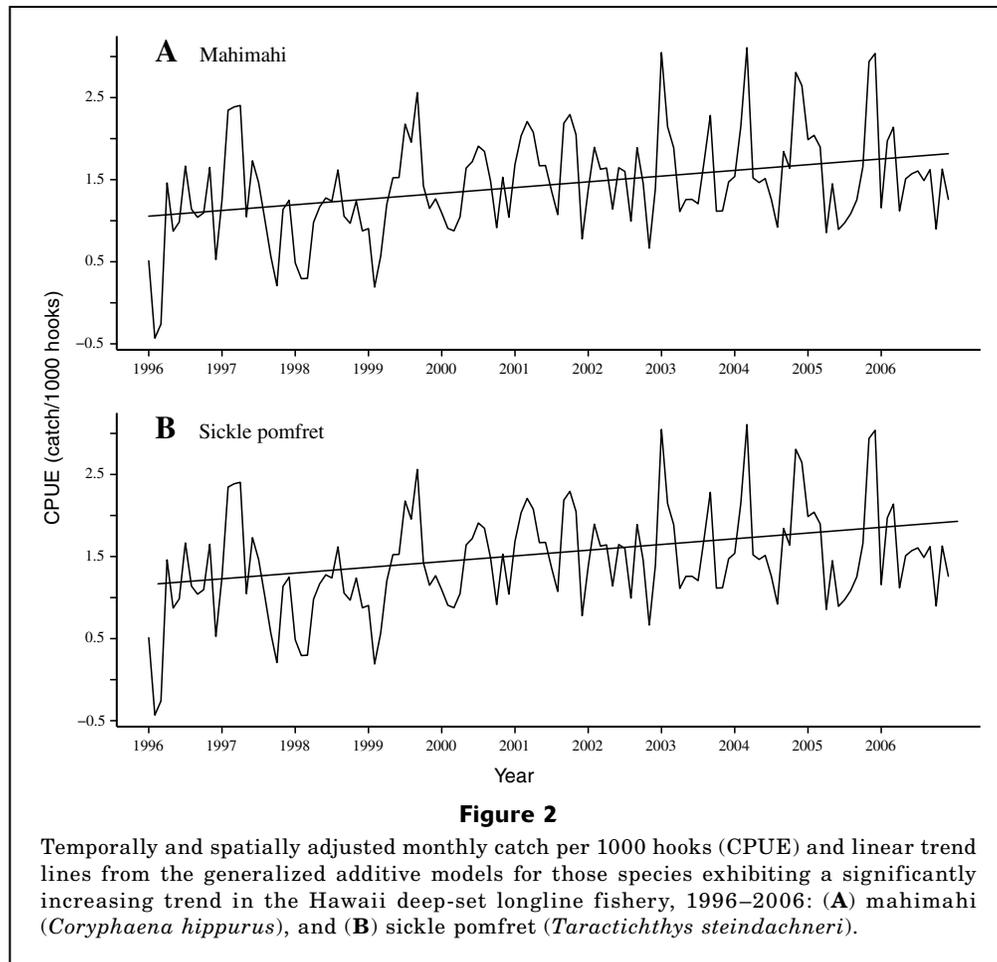
The mean annual trophic level of the top 13 species in the catch, weighted by number of fish caught, has declined over the time series by about 0.19 (or 5%), from about 3.85 to 3.66 (Fig. 5). The percentage of the catch of the top 13 species composed of apex predators (trophic level 4 and higher) has declined from about 70% to 40% (Fig. 5). The percentage of the catch of the top 13 species with relatively high P/B,
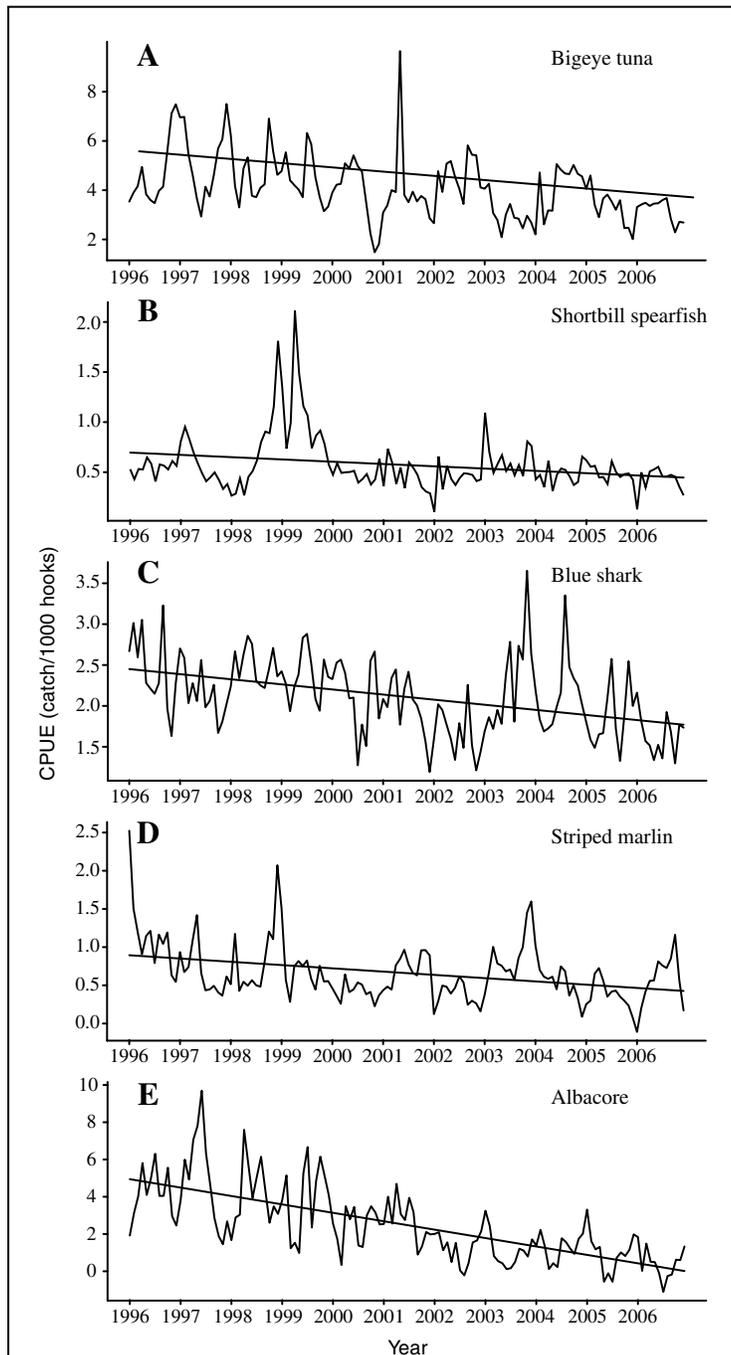
Figure 1

Temporally and spatially adjusted monthly catch per 1000 hooks (CPUE) and linear trend lines from the generalized additive models for those species exhibiting a significantly declining trend in the Hawaii deep-set longline fishery, 1996–2006: (**A**) bigeye tuna (*Thunnus obesus*), (**B**) shortbill spearfish (*Tetrapturus angustirostris*), (**C**) blue shark (*Prionace glauca*), (**D**) striped marlin (*Tetrapturus audax*), (**E**) albacore (*Thunnus alalunga*).

Figure 2

Temporally and spatially adjusted monthly catch per 1000 hooks (CPUE) and linear trend lines from the generalized additive models for those species exhibiting a significantly increasing trend in the Hawaii deep-set longline fishery, 1996–2006: (**A**) mahimahi (*Coryphaena hippurus*), and (**B**) sickle pomfret (*Taractichthys steindachneri*).
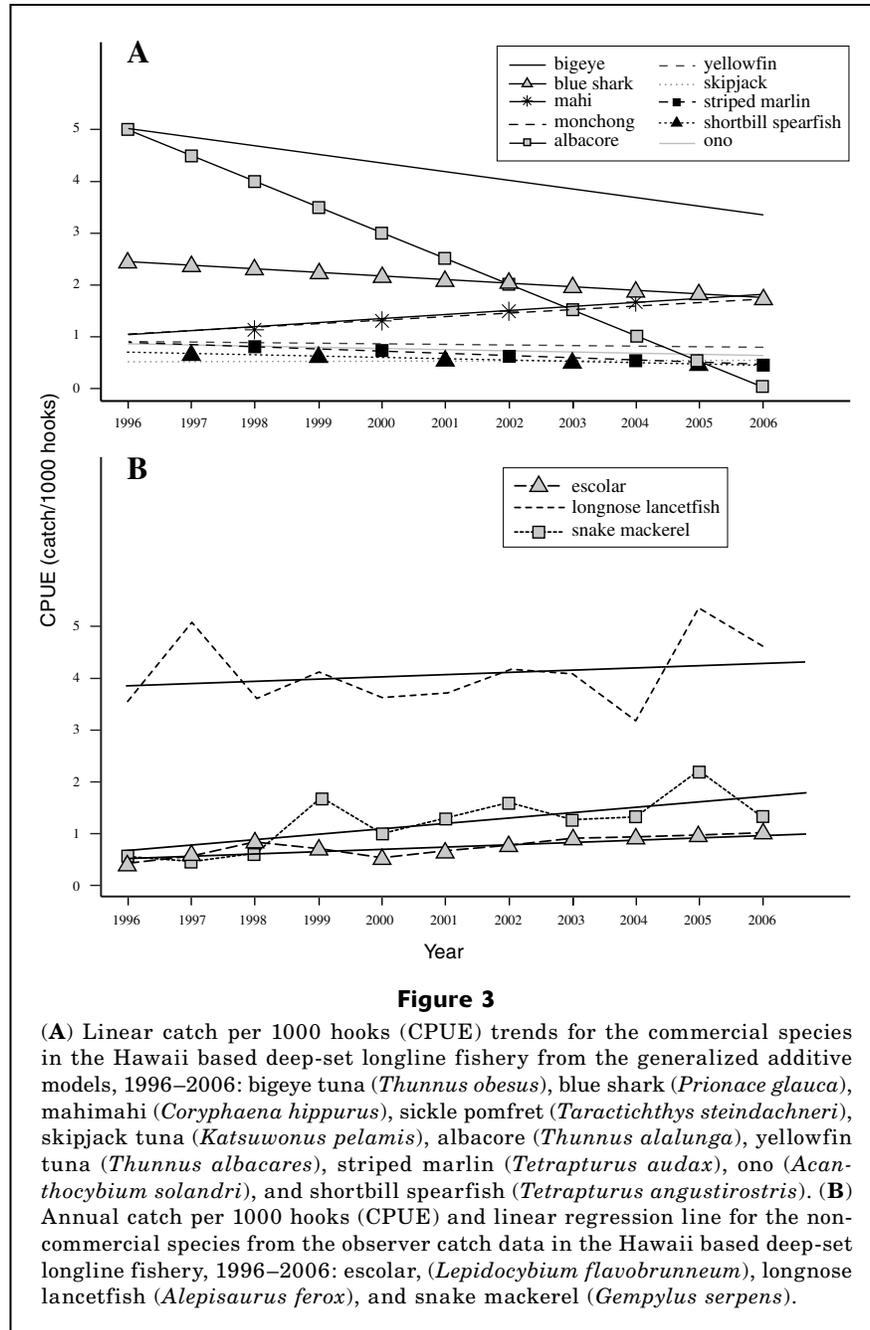
greater than or equal 1.0, has approximately doubled from about 20% to 40% (Fig. 5).

Discussion

The longline CPUE, like most fishery-dependent data, responds to a variety of factors that include changes in species targeted, gear changes that impact species catchability, changes in season, and area fished. It is likely that some of these factors have affected the Hawaii-based longline fishery. In an attempt to limit the effect of some of these factors we used only data from the deep-set fishery and from the core geographic region of the fishing ground. Further, for the 10 species for which we had logbook data we used a GAM to account for seasonal and spatial effects. However, in the case of albacore tuna, the 9.1% decline per year may be, at least in part, a result of a shift in targeting. On a basin-wide level the albacore stock, although reduced by fishing, has not exhibited the collapse seen in the deep-set fishery catches (Sibert et al., 2006). Albacore CPUE is greatest in the summer months, and since 2002 a summer fishery for large bigeye tunas has developed at 30°N latitude outside the core area covered in this study. This may

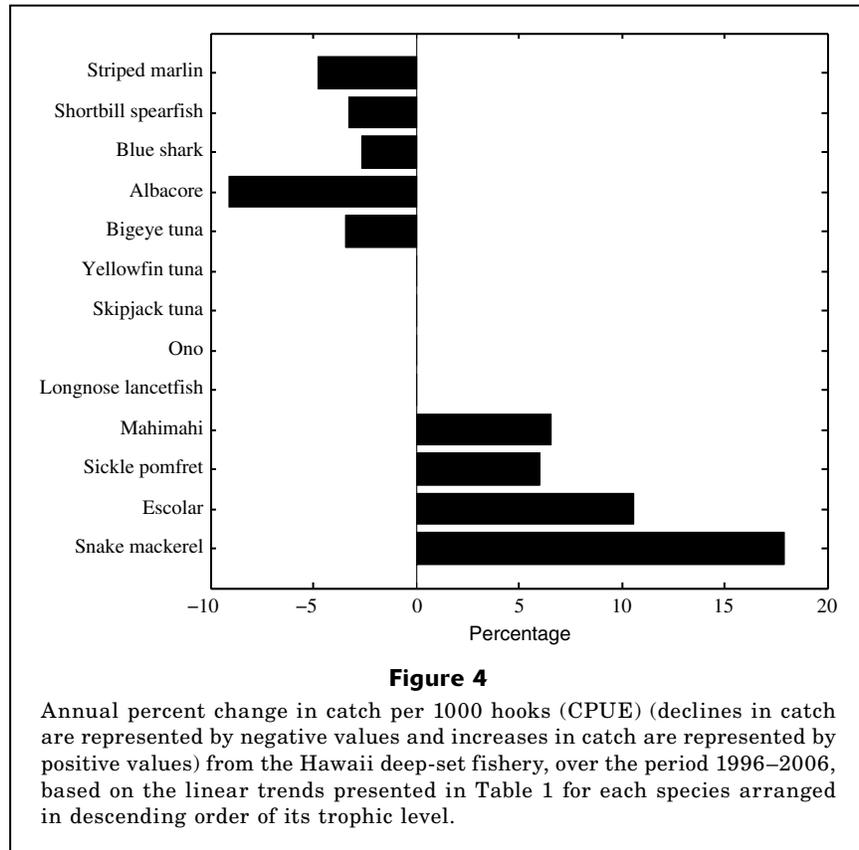have contributed to a shift in targeting from albacore to bigeye tuna.

We observed declines in CPUE trends of large high-trophic-level and lower P/B species, including striped marlin, shortbill spearfish, bigeye tuna, albacore tuna, and blue shark. Increasing CPUE trends were observed for mahimahi, sickle pomfret, escolar, and snake mackerel that are midtrophic-level species with higher P/B values. The increasing trends for mahimahi, escolar, and snake mackerel are most likely not due to increased targeting because snake mackerel has no commercial value, escolar has limited commercial value, and mahimahi is not caught efficiently with deep-set gear (it is generally only caught when the gear is being recovered and hooks are at the surface). The increasing trend is also not likely a response to more hooks being available from the decline in apex species because total catch rates are in the range of 10–20 fish per 1000 hooks and hence hook saturation is not likely a cause. However, the observed increase in catch rates of midtrophic level species concurrent with a decrease in catch rates of apex species is consistent with top-down control where fishing has reduced the abundance of apex species and mid-trophic level species have increased in abundance in response to decreased predation. Mahimahi is an epi-

Figure 3

(**A**) Linear catch per 1000 hooks (CPUE) trends for the commercial species
in the Hawaii based deep-set longline fishery from the generalized additive
models, 1996–2006: bigeye tuna (*Thunnus obesus*), blue shark (*Prionace glauca*),
mahimahi (*Coryphaena hippurus*), sickle pomfret (*Taractichthys steindachneri*),
skipjack tuna (*Katsuwonus pelamis*), albacore (*Thunnus alalunga*), yellowfin
tuna (*Thunnus albacares*), striped marlin (*Tetrapturus audax*), ono (*Acan-
thocybium solandri*), and shortbill spearfish (*Tetrapturus angustirostris*). (**B**)
Annual catch per 1000 hooks (CPUE) and linear regression line for the non-
commercial species from the observer catch data in the Hawaii based deep-set
longline fishery, 1996–2006: escolar, (*Lepidocybium flavobrunneum*), longnose
lancetfish (*Alepisaurus ferox*), and snake mackerel (*Gempylus serpens*).

pelagic species and its predators (billfishes, sharks, and
large tunas) have decreased concurrently. An increase
in troll and handline CPUE for mahimahi has been
observed in the Hawaii fishery since the 1980s (Boggs
and Ito, 1993). Sickle pomfret and escolar are mesope-
lagic species whose predators that include deep-foraging
bigeye and albacore tunas, swordfish, and large sharks
(Ward and Myers, 2005b). Snake mackerel inhabit both
the epipelagic and mesopelagic depths and have many
of the same predators as mahimahi in the epipelagic,
and sickle pomfret in the mesopelagic depths. We have
documented declines in relative abundance of bigeye

and albacore tunas, striped marlins, shortbill spearfish-
es, and blue sharks, all predators of these midtrophic
level species. Further, on a Pacific basin scale, biomass
of top-level predators, tunas and blue shark, has been
estimated to be at 36–91% of the level they would be in
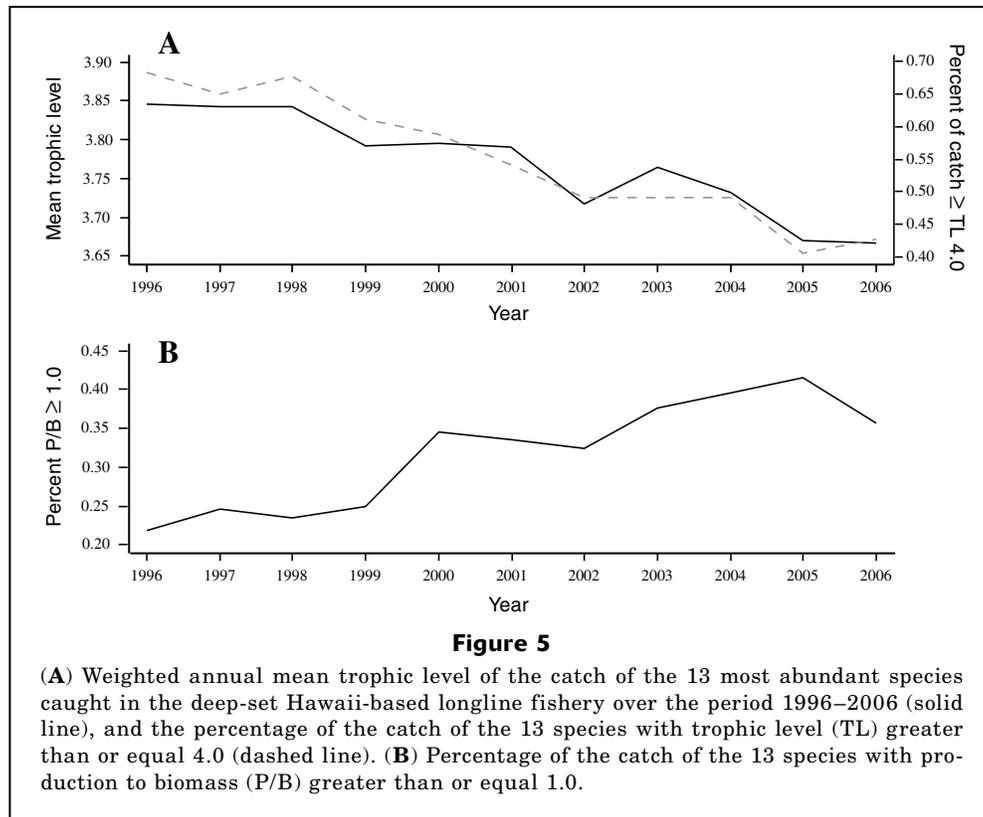the absence of fishing (Sibert et al., 2006).

In a central Pacific EwE model, a top-down control
was observed in the simulation (Kitchell et al., 2002;
Fig. 3). When an increase in longline fishing was simu-
lated, the biomasses of blue shark, large sharks, brown
shark, bigeye tuna, yellowfin tuna, albacore, swordfish,
blue marlin, and other marlins all declined; however,

Figure 4

Annual percent change in catch per 1000 hooks (CPUE) (declines in catch are represented by negative values and increases in catch are represented by positive values) from the Hawaii deep-set fishery, over the period 1996–2006, based on the linear trends presented in Table 1 for each species arranged in descending order of its trophic level.

the biomass of mahimahi, flying squid, and lancetfish increased (Kitchell et al., 2002; Fig. 3). The pattern reversed when fishing was eliminated: the biomass of mahimahi, flying squid, and lancetfish all decreased as their predators increased (Kitchell et al., 2002; Fig. 3). Lancetfish CPUE in our analysis showed an increasing trend, but because of its large interannual variation, it was not statistically significant (Fig. 3). Flying squid is not caught in the longline gear. However, as previously discussed, sickle pomfret, escolar, and snake mackerel, although not specifically identified in the Kitchell et al. (2002) model, appear to occupy a very similar prey role in the food web as lancetfish and flying squids. Hence, the observed increase in CPUE for mahimahi, sickle pomfret, escolar, and snake mackerel is consistent with the top-down control seen in the Kitchell et al. (2002) model simulation. Considering an earlier and somewhat different central North Pacific Ecopath model (Kitchell et al., 1999) we concluded that there is no single species that serves as a keystone species in this ecosystem but rather the longline fishery may function as a keystone species.

One additional piece of evidence supporting top-down control for sickle pomfret is that this species was absent in the longline sets of the 1950s but present in the 1990s (Ward and Myers, 2005a). This finding was interpreted as a possible population response to a reduction in predators that included tunas, billfishes and sharks (Ward and Myers, 2005a).

Top-down controls have been observed in temperate ocean ecosystems. A meta-analysis showed shrimp population abundance was controlled by the abundance of its predator, the Atlantic cod (*Gadus morhua*), in eight regions in the North Pacific (Worm and Myers, 2003). Further, at least in one ocean system, the eastern Scotian Shelf, removal of the top predator, the Atlantic cod, resulted in a trophic cascade impacting four trophic levels (Frank et al., 2005). In our pelagic ecosystem, if we considered the longline fleet functioning at the top trophic level, then we have top-down controls spanning three trophic levels: the longline fleet, the apex fishes, and the midtrophic level fishes. Our knowledge of the feeding ecology of many of the midtrophic level fishes that appear to have increased—sickle pomfret, escolar, and snake mackerel—is very limited and therefore we do not know the impacts on the ecosystem from their increased abundance. The juveniles of many of the tunas also occupy the midtrophic level but whether they benefit from the reduction in apex predators or suffer from increased competition or an increase in other predators is unknown but is a critical question for fisheries management. For example, if juvenile tunas are adversely impacted by the increase in other midtrophic level species then a reduction in fishing effort may not result in an increase in adult tunas. Lastly, we do not have data on changes in cetacean abundance and cetaceans have not been included in previous central Pacific models. However, cetaceans are apex predators and if they are

Figure 5

(**A**) Weighted annual mean trophic level of the catch of the 13 most abundant species caught in the deep-set Hawaii-based longline fishery over the period 1996–2006 (solid line), and the percentage of the catch of the 13 species with trophic level (TL) greater than or equal 4.0 (dashed line). (**B**) Percentage of the catch of the 13 species with production to biomass (P/B) greater than or equal 1.0.

not adversely impacted by fishery interactions they may experience less competition because of reduced numbers of apex predator fishes and because more prey would be available with the increase in midtrophic level fishes.

It should be noted that the almost threefold increase in the domestic fishery over the past decade is not the only change in the ecosystem. Over the same period, satellite-derived estimates of surface chlorophyll showed a decline in surface chlorophyll in the Hawaii-based longline fishing ground (Polovina et al., 2008). A change in productivity at the base of the food web could result in bottom-up control that could reduce the abundance of apex predators. Thus it is possible that the substantial changes we have observed in the pelagic ecosystem over the past decade are due to a combination of both bottom-up and top-down controls.

A decline in mean trophic level that exceeds 0.15 has been suggested as representing an ecologically significant fishing down of the food web (Essington et al., 2006). According to this definition the change in the annual mean trophic level of the catch we observed—a decline by 0.19 from 3.85 to 3.66—represents a significant fishing down of the food web in the central North Pacific subtropical gyre. However, an analysis of changes in biomass and trophic level for tunas and blue shark revealed a slight drop in the trophic level of the catch but showed no detectable change in the trophic level of the population (Sibert et al., 2006). A likely reason that we found a more substantial decline in mean trophic level

of the catch is that our study encompassed not just the top predators but also midtrophic level fishes.

The decline in the percentage of apex predators from 70% to 40% of the catch and the increase in midtrophic level species from about 20% to 40% of the catch, as well as moderate and high P/B values illustrate the significant increase in the contribution of short-lived, fast-growing, high-fecundity species in the catch and presumably in the exploited population. These species increase their population size rapidly under favorable conditions but given their short life spans, decline quickly in unfavorable conditions. As a result, the current ecosystem will likely exhibit greater temporal variation in response to climate variation.

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Literature cited

Bigelow, K. A., M. K. Musyl, F. Poisson, and P. Kleiber.
  2006. Pelagic longline gear depth and shoaling. Fish. Res.77:173–183.
Boggs, C. H., and R. Y. Ito.
  1993. Hawaii's pelagic fisheries. Mar. Fish. Rev. 55(2): 69–82.
Cox, S. P., T. E. Essington, J. F. Kitchell, S. J. D. Martell, C. J. Walters, C. Boggs, and I. Kaplan.
  2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. Can. J. Fish. Aquat. Sci. 59:1736–1747.
Essington, T. E., A. H. Beaudreau, and J. Wiedenmann.
  2006. Fishing through marine food webs. Proc. Natl. Acad. Sci. 103(9):3171–3175.
Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett.
  2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308:1621–1623.
Hastie,T., and R. Tibshirani.
  1990. Generalized additive models, 352 p. Chapman and Hall. London.
Kitchell, J. F., T. E. Essington, C. H. Boggs, D. E. Schindler, and C. J. Walters.
  2002. The role of sharks and longline fisheries in a pelagic ecosystem of the central Pacific. Ecosystems 5:202–216.
Kitchell, J. F., C. Boggs, X. He, and C. J. Walters.
  1999. Keystone predators in the Central Pacific. In Ecosystem approaches to fisheries management, p. 665–683. Univ. Alaska Sea Grant Rep. AL-SG-99-01, Anchorage, Alaska.
Nakamura, I., and N. V. Parin.
  1993. FAO species catalogue. Vol. 15. Snake mackerels and cutlassfishes of the world (families Gempylidae and Trichiuridae). An annotated and illustrated catalogue of the snake mackerels, snoeks, escolars, gemfishes, sackfishes, domine, oilfish, cutlassfishes, scabbardfishes, hairtails, and frostfishes known to date. FAO Fish. Synop. 125(15), 136 p. FAO, Rome.
Pickard, G. L., and W. J. Emery.
  1990. Descriptive physical oceanography: an introduction, 5th ed., 336 p. Pergamon Press, Oxford, UK.
Polovina, J. J., E. A. Howell, and M. Abecassis.
  2008. The ocean's least productive waters are expanding. Geophys. Res. Lett., 35(3):1–5.
Post, A.
  1984. Alepisauridae. In Fishes of the north-eastern Atlantic and the Mediterranean, vol. 1 (P. J. P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese, eds.), p. 494–495. UNESCO, Paris.
Seki, M. P., and J. J. Polovina.
  2001. Ocean gyre ecosystems. In The encyclopedia of ocean sciences, vol. 4 (J. H. Steele et al., eds.), p. 1959–1964. Academic Press, San Diego, CA.
Sibert J, J. Hampton, P. Kleiber, and M. Maunder.
  2006. Biomass, size, and trophic status of top predators in the Pacific Ocean. Science 314:1773–1776.
Ward, P., and R. A. Myers.
  2005a. Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86(4):835–847.
  2005b. Inferring the depth distribution of catchability for pelagic fishes and correcting for variation in the depth of longline fishing gear. Can. J. Fish. Aquat. Sci. 62:1130–1142.
Worm, B., and R. A. Myers.
  2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology 84(1):162–173.