Reconstructing marine ecosystem dynamics: What the pre-exploitation pelagic fish communities were really like

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Abstract–We show that declines in the abundance of apex predators in the open ocean over the past 50 years are much greater than previously believed. The declines range up to several orders of magnitude for many species of shark, tuna and billfish. We compare abundance indices derived from data collected by independent observers on commercial longliners in the central Pacific Ocean in the late 1990s with those from a scientific survey conducted in the same area in the early 1950s when exploitation first commenced.

A major shift in the abundance, species composition and size composition of the pelagic fish communities accompanied the expansion of longline fishing in the open ocean. The most abundant species, such as yellowfin tuna and silky shark, suffered the largest declines. In addition to reduced abundance, there were striking reductions in the body size of many species. During the 1950s most of the blue marlin were very large (100–300 kg), with smaller blue marlin rarely caught. By contrast, large blue marlin are now rare. For blue marlin the decline in abundance was greatest among the large size groups, whereas the abundance of small blue marlin showed no significant change.

Several small species, such as skipjack tuna, increased in abundance, perhaps as a result of the decreased abundance of their predators or competitors. However, many species showed tenfold declines in abundance, resulting in changes to trophic structure and a significant contraction in the biomass of the pelagic fish community. Assessments should now consider implications of the current state of the fish communities; whether ecosystem functions can be maintained, whether biodiversity is protected and the merits of fishing activities that remove apex predators from the fish communities.

Keywords–Ecosystem dynamics, species compensation, other ecological terms?, longline fishing, fishing effort, catch rate standardization, bycatch

Introduction

The most important question in applied ecology today is how to mitigate and repair the cumulative effects of human activities on entire ecosystems, e.g., pollution, habitat destruction and harvesting. The first step in rehabilitation is to understand how ecosystems function and how human activities have changed their structure and linkages (Krebs 1978, Jackson and Sala 2001).

The changes to terrestrial and coastal ecosystems are the product of habitat modification and removals by harvesting over many decades or centuries. However, data on population distribution, abundance and trophic interactions were rarely collected at the beginning of human interaction. Many historical studies of the early abundance of fish use commercial catch and effort data that was collected some time after the very beginning of large-scale exploitation, e.g., Fogarty and Murawski (1998), more examples?. Jackson et al. (2001, p. 629) observe that "few modern ecological studies take into account the former natural abundances of large marine vertebrates." The analyses of Fogarty and Murawski (1998), for example, are limited to commercial? fishing data that were collected after the 1950s, more than a century after large-scale fishing commenced.

By contrast, data have been systematically collected since large-scale pelagic longlining began about 50 years ago in what were "pristine open oceans" (Steele 1998). In the late 1950s longlining expanded rapidly to high levels over enormous geographical scales. In the Pacific, total annual catches of pelagic species in the open ocean now amount to about 500 000 tons per year (ref), which is taken from an area that is four times the size of the North American continent.

Two recent studies have highlighted significant declines in the abundance of large predators in the open ocean. Baum et al. (2003) show that several species of large pelagic shark have declined by 70% in the past 15 years in the Atlantic Ocean. Analyses of commercial catch rates in the Atlantic, Pacific and Indian Oceans show a decline in the abundance of tuna and billfish by a factor of 10 since fishing began (Myers and Worm, 2003). However, ecosystem models suggest that the declines may have been less pronounced (Cox et al. 2002).

The three recent studies analyzed catch and effort data that were reported by commercial fishers in logbooks. We analyze catch, effort and size data collected by independent observers during 1994–2002 and by a scientific survey in the early 1950s. For both periods the data were collected at a hook-by-hook level, allowing abundance estimates to be adjusted for variations in fishing operations, e.g., longline depth. Our analyses provide insights into the long-term changes in a wider range of pelagic species when longline fishing first commenced. They provide an opportunity to test the predictions of ecosystem models/ the predictions of ecological theory.

Data and Methods

Data sets

In 1950 the US embarked on an ambitious program of fishery monitoring and scientific surveys of Pacific tuna resources. The Pacific Oceanic Fisheries Investigations (POFI) were a response to interest in harvesting the tuna resources of newly acquired US territories and possessions in the region. The US fishing industry was interested in catching large quantities of yellowfin tuna for canning. Using longline fishing gear and techniques adopted from Japan, POFI conducted 12 longline fishing trips each of about 30 days duration in the central tropical Pacific Ocean during 1950–53. We refer to the POFI program as the "1950s survey".

The 1950s survey was conducted as a controlled experiment with gear and techniques held constant throughout the study. Survey longlines were deployed in a grid at pre-determined stations. The stations were often located at each one-degree of latitude. Murphy and Shomura (1972) and references cited therein provide details of survey fishing techniques and gear. The 1950s survey deployed longlines at dawn each day and retrieved in the afternoon (Table 1). They attached six-hooks between each float, amounting to about 342 hooks in each daily fishing operation. Within the same operation the performance of the standard gear was sometimes compared with variations in the type of bait, method of bait attachment or the number of hooks between floats (Murphy and Shomura 1972).

We compare abundance indices derived from 1950s data, with those derived from data collected by independent observers placed on Hawaii-based longliners in the same area during 1994–2002. About 90% of the Hawaii longline activities occurred in 1999–2002, but for convenience we refer to these activities as "1990s" longlining. In the study area they targeted tuna, specifically bigeye and yellowfin tuna, for commercial sale. Their bycatch of other species, such as broadbill swordfish, striped marlin, mahi mahi and wahoo was also valuable.

The scientifically trained observers placed on 1990s longliners attempted to identify all species caught, as did scientists involved in the 1950s survey. There are several species that were recorded in the 1990s, but not recorded in the 1950s. Those species had been placed in a "not identified" category in the 1950s because they were not identified to the species level on board the survey vessel, e.g., sunfish, opah, escolar, oilfish and pomfrets (Dr. Richard Shomura, pers. comm.). For both periods this category also includes catches that had not been identified for other reasons, e.g., the fish was damaged beyond recognition or had been released before it could be identified. Several species were too rare to estimate abundance (e.g., hammerhead sharks). Rare species and unidentified species were included in the estimates of total catch rates and abundance. We combined data for several rare species into larger species groups. For example, the mako sharks consisted of members of the Family Lamnidae, such as salmon sharks, mackerel sharks and longfin mako as well as the more abundant shortfin mako shark.

We used data from the two periods that overlapped in terms of deployment time (02:00–08:00 local time), season (January–November) and the area fished (0–10°N, 175°E–160°W) (Figure 1). This reduced data set is referred to as the "study area" whereas data from the entire 1950s survey that covered the area 10°S–15°N and 175°E–115°W is referred to as the "wider survey area". We used a model to derive abundance indices for each species in the study area. The model adjusted abundance estimates for operational differences (e.g., longline depth) as well as spatial and temporal variations among the periods.

Table 1 compares longline fishing gear and techniques used in the 1950s and 1990s. However, there are also differences between longlining activities in the two periods, such as the range of depths fished by longline hooks. We describe the procedures that we used to adjust abundance indices for the effects of depth, soak time, location and gear saturation then present the model used to derive those indices.

Depth and soak time estimation

We estimated the depth reached by each longline hook with the catenary formula presented by Suzuki et al. (1977). The formula uses φ^o, the angle made between a horizontal line drawn between the tangential line of the mainline and the connecting points of the float line and mainline. Suzuki et al. and many subsequent researchers selected a value of $\varphi^o = 72^o$ because they did not have data on the sagging rate *k*. The sagging rate is the ratio between the distance between floats and the length of mainline between floats, measurements that were taken by the 1950s survey and 1990s observers. We used a derivation of the formula presented by Yoshihara (1954) to calculate φ^o from k for each longline operation:

$$k = \cot\varphi^o \sinh^{-1}(\tan\varphi^o)$$

We assume that the shape of the catenary curve formed by the longline (and therefore the corresponding depth of hooks) does not systematically vary over the entire operation. We reduced the depths predicted by the catenary curve by 25% to account for the mean difference between observed and predicted depths reported by Uozumi & Okamoto (1997) and Mizuno *et al.* (1999).

The 1950s data include a unique identifier – the hook number – for each longline hook that each fish was caught on. This allowed the depth (and soak time) of each catch to be estimated. The 1990s observers reported the hook number for catches of tuna, billfish and shark, but not for other species. For the other species we used the number of hooks per float as a measure of the depth range of the entire longline operation.

We estimated soak times from records of the time when each longline hook was retrieved combined with the start and finish times of longline deployment and retrieval. In estimating soak times we assume constant rates of longline deployment and retrieval throughout each operation (the analyses were limited to operations where the longline was counter-retrieved and had no evidence of stoppages due to line breaks or mechanical failure). We used the median soak time for species that had no data on hook number.

Gear saturation estimation

The total number of hooks deployed is often used as a measure of fishing effort in longline fisheries. However, the measure of fishing effort should be adjusted for the number of hooks already occupied by fish because occupied hooks are no longer available for fish that might subsequently encounter the longline (Rothschild 1967). Catch rates of all species combined often exceeded 100 fish per thousand hooks in the 1950s. At those levels of abundance, gear saturation is likely to have a significant affect on observed catch rates.

To adjust fishing effort for saturation we subtracted half the number of fish caught from the number of hooks deployed in each soak time – depth zone of each operation. Information was not available on the depth and soak time for all species. Therefore we applied the ratio of those unknown catches from the entire operation to each soak time – depth zone. Our approach is likely to overestimate the number of vacant hooks because of local saturation (Rothschild 1967).

Model

We used a generalized linear model with a negative binomial error distribution and a log link to correct for the effects of differences in longline activities among operations. Catches in each longline segment s of operation i are assumed to have a negative binomial distribution with mean $\mu_{i,s}$ The negative binomial distribution is similar to a Poisson distribution with an extra parameter θ to allow for over-dispersion. It is appropriate for over-dispersed Poisson data, like the longline data where catches may be clustered along the longline and the variance is greater than the mean (Venables and Ripley 1999).

The predicted mean catch $\mu_{i,s}$ is the product of the amount of fishing effort, the fishing period and a collection of other variables, such as depth and soak time. We model the natural logarithm of the mean catch:

$$\log(\mu_{i,s}) = \beta_0 + \beta_1 F_{i,s} + \beta_2 T_{i,s} + \beta_3 D_{i,s} + \beta_4 N_{i,s} + \beta_5 E_{i,s} + \log(h_{i,s}) \qquad (1)$$

where $F_{i,s}$ is the fishing period for each longline segment *s* of operation *i*

$T_{i,s}$ is the soak time (estimated from hook number where available, median soak time otherwise)

$D_{i,s}$ is the depth (estimated from hook number where available, hooks per float otherwise)

$N_{i,s}$ is the latitude

$E_{i,s}$ is the longitude

$h_{i,s}$ is the number of vacant hooks, which are modeled as offsets

The β are parameters to be estimated. We included quadratic terms for soak time, depth, latitude and longitude, which are not shown in equation (1). *F* is a dummy variable indicating the fishing period (it is set to 0 for 1950s data and 1 for the 1990s). Its coefficient (β_1) indicates the difference between 1950s' and 1990s' abundance. The coefficient's exponent $(e^{-\beta_1})$ represents the ratio between abundance in the two periods

For tuna, billfish and sharks the models used estimated depth and soak time. For each operation, catch and fishing effort were stratified by one-hour soak time and 40-m depth zone. The analyses included soak time – depth strata where hooks were deployed but a zero catch was reported. For other species the models used hooks per float and median soak time. There was good agreement between abundance estimates that used actual depth and those that used hooks per float, although the depth-based estimates were less variable. For example, the depth model predicted 9.02 bigeye tuna (±0.97 SE) per thousand hooks in the 1950s compared to 9.96 (±2.71 SE) predicted by the model that used hooks per float for the 1950s.

Biomass estimation

To estimate changes in biomass we first estimated the mean weight of each species in each period. We estimated mean weights by applying length-weight relationships (Uchiyama and Kazama 1999, Froese and Pauly 2003) to length measurements reported in the wider area (175°E–115°W and 10°S–15°N). In this area sixty-eight percent of all fish were measured in the 1950s and 50% were measured in the 1990s. For species that were not measured in the 1990s we used length data collected by observers on longliners fishing in adjacent waters of the western Pacific during the 1990s[1]. We estimated species' biomass from the estimate of numerical abundance multiplied by its mean weight in the wider study area. Examination of plots of size against the depth of the longline hook that the fish was caught on showed that the mean weight of many species increased with

[1] The observer data were provided by Mr. Peter Williams, Secretariat of the Pacific Community (SPC). They were from vessels deploying deep longlines to targeted bigeye and yellowfin tuna in the tropical western Pacific Ocean adjacent to the western of our study area during 1990–2001.

depth. Plots of body size and estimates of biomass for tuna, billfish and sharks used the weights of fish taken from surface waters (0–200 m). Depth-stratified size data were not available for other species.

Verification

We verified 1950s catch rates with catch rates from commercial longline operations during 1952–54. The commercial operations involved several large processor vessels or "motherships" each accompanied by 12–25 smaller catcher vessels. The longline fishing gear and techniques used by catcher vessels were almost identical to those of the 1950s survey (Shapiro 1950, Niska 1953). Japanese companies were permitted to undertake nine mothership expeditions in a restricted area of the central tropical Pacific. We present catch rates for the area bounded by 20°S–10°N and 150°E–130°W. The mothership expeditions targeted tuna, specifically yellowfin tuna, for US canning markets (Van Campen 1952). The 1950s mothersip data are limited to 10 commercial species or species groups and are aggregated by month and five-degree square area.

Results

Twenty-five species or species groups were common to both periods and had adequate data to model abundance as a function of depth, soak time and location. The inclusion of quadratic terms for depth, soak time, latitude and longitude improved model fits. For all 25 species the performance of models with negative binomial error was superior to the same models with a Poisson error distribution. Selection of a value of θ can be problematic for models using negative binomial error distributions. We tested values of θ ranging from 0.1 to 1.5. A value of 0.5 produced the best fit over all species. Subsequent analyses and discussion focus on models with a negative binomial error distribution $(\theta = 0.5)$.

We investigated the sensitivity of abundance estimates to variations in the area selected as the study area. Variations in the location of the eastern boundary made little difference to abundance estimates (Table 3), whereas latitude had a greater affect. Estimates of coefficients (β) confirmed that latitude had a stronger affect on abundance estimates for most species than did longitude. Therefore we selected a study area that had a wide longitudinal range but closely matched the latitudinal range of activities in both periods.

Soak times ranged up to 10 hours in the 1950s compared to up to 19 hours in the 1990s. Coefficients for soak time that were estimated by the models support the conclusions of Ward et al. (2003); longer soak times result in increased catch rates of many species, particularly sharks and billfish, whereas the catch rates of several species, such as skipjack tuna, decrease with soak time. The long duration of longline operations would also result in about 80% of 1990s longline hooks being exposed to a dusk period as well as to dawn. By comparison, 1950s hooks were only exposed to a dawn period. Our models included terms for soak time, but did not correct for variations in exposure to dawn and dusk.

The affects of season or time of day were not included in our models because preliminary analyses showed that they did not have a significant affect on changes in abundance. The distributions of those variables in the 1950s closely matched those in the 1990s (Figure 1).

Deep longlines cover a wider depth range than shallow longlines. They produce elevated catch rates of several species, e.g., bigeye tuna. For some species, such as blue marlin, they produce lower catch rates. For others, like blue shark, they have no significant effect on catch rates (Myers and Ward in prep.). Our models adjusted abundance estimates for the effects of depth. Another important difference between the two data sets is that the commercial longliners actively searched for target species in the 1990s whereas longlines were deployed at predetermined stations along a survey grid in the 1950s. We could not correct the abundance estimates for the affects of searching, but consider its implications in the Discussion.

Table 4 shows reasonable agreement between 1950s survey and mothership catch rates. For several species (skipjack tuna?, shortbill spearfish? and especially yellowfin tuna) the motherships reported catch rates that were significantly lower than those in the 1950s survey. Their catch rates of bigeye tuna, sailfish and especially Pacific blue marlin, were significantly higher than those in the survey. Overall, the 1950s survey reported catch rates of 54 commercial species per 1000 hooks compared to 47 per 1000 hooks for the motherships.

It is noteworthy that independent observers on the motherships (e.g., Van Campen 1952) consistently reported that external factors kept catch rates well below levels that true commercial longline operations could achieve. Those factors included strict restrictions on areas of operation, catcher vessels having to remain in close proximity to their mothership and poor bait quality (Van Campen 1952).

The pelagic fish community in the 1950s was markedly different to that of the 1990s, both in terms of total biomass and the relative abundance of species. Biomass of all species combined was 8.3 t (± SD) per thousand hooks for the 1950s compared to 0.9 t (± SD) per thousand hooks for the 1990s. The species that were most abundant in the 1950s showed the largest declines in the 1990s. Most noticeable are the declines in most abundant tuna, yellowfin and bigeye tuna (for both species the 1950s biomass was about ten-times the 1990s biomass). Also showing marked declines in biomass were the three most abundant shark species (oceanic whitetip, silky and blue shark) and the most abundant billfish (blue marlin).

The abundance of several species increased between the two periods. Those that increased tended to be small and were rarely encountered in the 1950s, e.g., snake mackeral and mahi mahi. The increases in small species might be evidence of competitive release or predator release.

Comparisons of size frequencies show major changes in the size composition of pelagic fish populations between the 1950s and the 1990s (Figure 4). Most tuna, billfish and sharks are much smaller on average now than they were in the 1950s. During the 1950s most of the blue marlin were very large (100–300 kg), with smaller blue marlin rarely encountered. By contrast, small blue marlin (<75 kg) now dominate longline catches of the species. Figure 3 shows that the reduction in biomass was much greater than the reduction in numerical abundance. This reflects the decline in body size that occurred between the 1950s and the 1990s.

Discussion

First we examine whether the 1950s and 1990s abundance estimates are comparable then consider the implications of the results. In brief, we believe that estimates from the two periods are comparable, but the declines are underestimated because of differences in searching, fishing gear and techniques and, possibly, removals by scavengers.

Comparison of catch rates

Competition among and between operations

Comparison of catch rates indicate marked changes between the 1950s and 1990s. Other than a massive decline in abundance, we can imagine few explanations for 1990s catch being so much lower than those in the 1950s. One possibility is competition among fishing vessels (Hilborn and Walters 1987). The increased number of longliners and other vessels fishing for pelagic species in the study area during the 1990s might have increased competition for the most productive areas, resulting in the displacement of some longliners to less productive waters. We did not investigate competition between fishing vessels, which would require accurate estimates of local fish abundance and daily catch and effort data for all vessels operating in the area. However, we do not expect competition to have a significant affect on catch rates in the open ocean where longliners rarely interact. Longline operations are measured along scales of tens of kilometers whereas fishing grounds and pelagic fish distributions are measured along much larger scales.

Another possible explanation of the differences in catch rates is competition within longline operations. The 1950s survey deployed fewer longline hooks in each operation than were deployed in the 1990s. It is conceivable that individual hooks do not fish independently within a longline operation (Rothschild 1967?). To test whether the number of hooks affected catch rates we applied linear regressions to the 1990s catch and fishing effort data, where hook numbers ranged between 660 and 3660 per operation. For 13 out of 21 species the regressions did not show a statistically significant relationship between catch rates and hooks per operation at the 95% level of significance. Although the relationship was significant for eight species, six of those had a negative slope (catch rates declined with the number of hooks). We conclude that differences in the number of hooks per operation did not affect our abundance estimates.

Searching, fishing gear and techniques

We believe that the effects of searching and improvements in longline fishing gear and techniques resulted in the underestimation of 1950s abundance relative to 1990s abundance. The 1950s survey adopted longline gear and techniques that had been used in Japan and Formosa during the 1930s (Niska 1953). As a controlled experiment, gear and techniques were not modified or refined during the survey, except for tightly controlled experimentation with various types of bait, methods of attaching the bait and longline depth (Murphy and Shomura 1972).

In contrast to 1950s operations, the longline gear and techniques used in the 1990s were the product of extensive practical experience and innovation over 40 years. Refinements range from the adoption of new technology (e.g., such as color sounders, doppler current meters and satellite imagery) to more subtle changes, such as the way baits were secured to the hook, the breaking strain of branchlines and maneuvering of the vessel to aid the landing of fish. The 1990s longliners also had the ability to modify their fishing techniques to suit conditions while on the fishing grounds, e.g., time of deployment and retrieval, longline depth and bait (ref?).

Quantity, species composition and quality largely determine the value of the catch landed by commercial longliners. The income of masters and crew are based on a commission of the value. They would use every available piece of information and equipment to maximize the value of the catch (ref?). This must have a substantial effect on catch rates.

The 1950s survey was based on a grid, whereas commercial longliners actively searched for concentrations of target species. They remained in areas of high catch rates or followed the fish as the concentrations moved. Searching also involved communication with other longliners to locate concentrations of target species; and the use of past experience in selecting fishing areas (ref?). In estimating abundance we were unable to quantify the effects of searching and improvements in longline fishing gear and techniques. One option would be to repeat the 1950s survey using exactly the same fishing gear and techniques.

Removals by sharks

There is evidence of a decline in the proportion fish that are damaged by sharks while the fish are hooked on the longline. Analysis of the 1950s survey data shows that sharks damaged 20–30% of tuna. By comparison, observers on commercial longliners reported damage rates of about 4% in the same area in the 1990s. The decline in damage rates is consistent with the decline in shark abundance highlighted by our analyses and by Myers and Worm (2003). If shark damage rates reflect the rate at which hooked fish are removed from longlines, then loss rates might have been higher in the 1950s, further adding to the underestimation of early abundance.

Oceanographic conditions

Several authors have highlighted the effects of broad-scale oceanographic events on ocean productivity (e.g., Mantua et al. 1998, Chavez et al. 2003) and the distribution of pelagic fish species (e.g., Polovina 1996, Bigelow et al. 2002, Rodriguez-Sánchez et al. 2002). We did not attempt to determine whether variations in oceanographic conditions affected the productivity of pelagic fish or their availability to longline fishing gear between the 1950s and 1990s. Nevertheless, examination of oceanographic conditions that are currently recognized as having a strong influence on productivity or availability revealed no obvious difference between the two periods. During the 1950s study period, for example, the mean monthly Pacific Decadal Oscillation (PDO) was –0.78(±0.91 SD) with a –2.93 – 0.97 range[2]. By compassion the 1990s featured a mean PDO of –0.50(±0.87 SD; –2.23 to 2.1 range).

The study periods spanned months of high and low values of the Southern Oscillation Index (SOI) corresponding to a mixture of La Niña and El Niño conditions. The 1990s did, however, feature stronger El Niño conditions than were experienced in the 1950s[3]. The study periods spanned four years in the 1950s and over four years in the 1990s,

[2] ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/PDO.latest

[3] http://www.cgd.ucar.edu/cas/catalog/climind/SOI.signal.annstd.ascii

which may smooth out the short-term affects of oceanographic events on fish availability and abundance.

On a finer scale, water temperature and oxygen concentrations are believed to influence the vertical distribution of many pelagic fish species (ref?). The depth of the thermocline, averaged ? m (±? m) during the 1950s in the study area compared to ? m (±? m) during the 1950s ranged between.

Abundance

The pelagic fish communities that we describe may have been previously exploited. Longlines and other pelagic fishing gear have been used intensively in oceanic waters of tropical western Pacific in the 1920s and 1930s (Nakamura 1969). This may have caused a reduction in the abundance of some of the highly migratory species (e.g. bigeye tuna and blue marlin) in adjacent areas, like our study area. Many of the fishing masters involved in the 1950s mothership expeditions believed that tuna abundance was substantially lower than it was in the 1930s. Adverse environmental conditions, the effects of war and stock depletion through past exploitation were popular explanations for the low catch rates among mothership crew members and fishing masters (Shimada 1951).

Our results are consistent with the tenfold decline in the total abundance of large demersal and pelagic fish in the open ocean reported by Myers and Worm (2003). We also see declines in shark abundance that are similar to those estimated by Baum et al. (2003) in the Atlantic Ocean.

We found a much greater decline than the two- or threefold decline reported by Cox et al. (2002). There are several possible explanations for this difference. Myers and Worms' maps of the global distribution of catch and effort show a pattern of serial depletion where longliners initially achieved high catch rates as they ventured into new areas. At the same time, abundance declined in heavily fished core areas like our study area. Consequently, the use of aggregated data may underestimate the true magnitude of declines in each area. Our study area is central to the distribution of most tropical fish species that are taken by pelagic longline fishing gear (Worm et al. 2003). Furthermore, the abundance indices of Cox et al. were derived from a data set that included surface fisheries (e.g. purse seine). Catch rates in surface fisheries often show hyper compensation as a result of difficulties in measuring fishing effort (Hilborn and Walters 1992).

Changes in size composition

Figure 6 illustrates the relative changes in mean size among species. The mean weights of large species, such as blue marlin and silky shark, are well below the line of equality, indicating degradation in size composition between the 1950s and 1990s. This probably reflects the lower growth rates of large species combined with the time required to reach large sizes. Increased fishing mortality since the 1950s has prevented species like blue marlin and silky shark reaching large sizes.

In contrast to the pattern for large species, the mean size of small species, such as skipjack tuna and lancetfishes, was stable or increased. These were the species that showed no decline in abundance between periods. The increase in skipjack tuna abundance is particularly noteworthy because it occurred in spite of the substantial increases in harvesting of the species by purse seine fishing gear that commenced in the study area during the mid 1970s (ref?).

Large fish dominated the 1950s catches of most species of tuna, billfish and sharks; small fish were rarely caught. The absence of small fish in the 1950s might be an artifact of sample size or it might indicate variations in availability to longline fishing gear. An interesting possibility is that the selective removal of large fish since the 1950s has allowed small fish to move into habitats that were originally the domain of large fish.

Contraction of biomass

Our index of the biomass of pelagic fish available to longline fishing gear in the 1990s is less than 10% of that in the 1950s. The question then arises as to how the ecosystem's trophic interactions and energy flow have changed. Ultimately, the amount of energy entering an ecosystem through primary production and immigration must balance the energy lost through growth, emigration, respiration and waste products?.

The energy that once supported populations of large predators might now be utilized by other pelagic species. Through predator release the population sizes of prey species, such as squid and lanternfish, might have expanded in response to the removal of large tuna, billfish and sharks. However, Jennings and Kaiser (1998) suggest that the removal of predators rarely results in the proliferation of prey species because of the complexity of predator–prey interactions and the diversity of species in marine ecosystems. This is likely to be the case in the pelagic fish communities of the open ocean where diversity is high (Worm et al. 2003?) and species are highly opportunistic in their feeding habits (Collette and Nauen 1983).

Through competitor release species, such as skipjack tuna, might be considerably more abundant now than they were before longline fishing commenced (Cox et al. 2002). Our results support the prediction of Cox et al.'s models, that the abundance of skipjack tuna and small yellowfin tuna should increase in response to exploitation. Longline gear samples only a small fraction of the entire pelagic fish community in the open ocean, yet there are few other sources of information on the current or past abundance of other species (e.g., squid, lanternfish and pomfrets) that might have increased in abundance as a result of predator release. In the absence of higher trophic levels, the energy produced by those lower levels might be lost to the pelagic ecosystem. It might now sink to abyssal depths to be utilized by animals there or to be eventually locked into sediments (Jackson and Sala? 2001).

Implications

The substantial reduction in the abundance of large pelagic species since the 1950s does not necessarily mean that the productivity of the system has changed. In fact, we would expect a fish community consisting of many small fish to sustain higher harvesting rates than a community dominated by large, old fish. But, there are now fewer fish and what remains are smaller. Smaller fish will have a different trophic role than large fish. Competitive release might now mean that non-commercial species now dominate catches. Certainly, catch rates and thus profitability would be higher if the pelagic community could be maintained at its former state.

Beyond those economic considerations are implications for the functioning of pelagic ecosystems. Cox et al. (2002) highlight some of the potential ecosystem interactions that might result from those declines in abundance. Their ecosystem models are able to predict the general direction of the changes in community composition, but might fail to predict the magnitude of the changes. We have no experience with how the low abundance of large predators in the open ocean might affect the overall stability, persistence and productivity of the system. Neither is it clear whether the abundance of pelagic fish has now stabilized or whether reductions in abundance and body size are continuing.

Conclusions

Current assessments and management plans are dealing with a remnant fish community that is only a fraction of its former abundance and composed of fewer larger predators. Pelagic longline catch rates, once measured in "numbers of fish per 100 hooks", are now measured in "numbers per 1000 hooks". Our results underestimate the extent of the decline in large pelagic fish because they do not take into account the effects of searching and technological improvements over many years. We did not attempt to predict how those changes might affect ecosystem stability, persistence or productivity and sustainable harvest levels.

There are a range of possible causes of the declines, such as broad-scale changes in oceanographic conditions and competition among longliners. Until evidence is presented to indicate otherwise, the simplest and most unambiguous explanation should be accepted: that exploitation has caused massive declines in the abundance and size of pelagic fish in the open ocean.

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Table 1. Comparison of 1950s (POFI survey) and 1990s (Hawaii observer) longline gear and techniques in the wider study area (10°S–10°N, 175°E–115°W). Standard deviations are shown in parentheses. Supplemented with information from Niska (1953) and Murphy and Shomura (1972) for the 1950s and Mr. Paul Bartram (4 December 2002) for the 1990s.

Characteristic	**1950s**	**1990s**
Source	US Pacific Oceanic Fisheries Investigations (1950–53)	US NMFS observers on Hawaii-based longliners (1994–2002)
Target species	No targeting, but aimed to prove commercial quantities of canning tuna	Bigeye and yellowfin tuna
Mainline material	Hard-lay cotton twine	Monofilament
Branchline material	12-strand cotton twine with wire leader	400 kg breaking strain monofilament, 92% of operations used wire leaders
Level of fishing effort	242 operations 78 161 hooks	1003 operations 2 055 948 hooks
Hooks per operation	340(±147) hooks	1988(±371) hooks
Hook type	9/0 or 8/0 "Mustad flattened tuna"	"Asian ring"
Bait	Frozen sardine, occasionally fresh or salted herring, milkfish and squid	Frozen saury or sardine
Lightsticks	No	No
Floatline length	19.2(±6.4) m	22.3(±5.2) m
Branchline length	20.7(±7.0) m	13.3(±3.7) m
Hooks per float	6, occasionally 5, 9, 11 or 21	26–30, ranging from 12 up to 38
Line shooter	No	Yes
Depth range	26–200 m	27–600 m
Deployment time	1 hour before dawn	dawn
Median soak time	7 hours	12 hours
Retrieval time	1 hour after noon	1–2 hours before dusk

Table 2. List of common and scientific names of the species reported in the 1950s and 1990s. Catch rates, estimates of numerical abundance, biomass, mean weight and the type of model used to estimate abundance are shown for each species in the study area.

Common name	**Species**	**Catch rate (no./1000 hooks)**		**Mean weight (kg)**		**Number measured**		**Model**		**Number modeled**		**Est. abundance (no./1000 hooks)**		**Est. biomass (kg/1000 hooks)**	
		1950s	**1990s**	**1950s**	**1990s**	**1950s**	**1990s**	**type**	**dispersion**	**1950s**	**1990s**	**1950s**	**1990s**	**1950s**	**1990s**
Tuna and tuna–like species															
Albacore tuna	*Thunnus alalunga*	0.68	0.03	17	26	247	2044	depth	0.85	35	16	1.96	0.08	34.33	2.01
Bigeye tuna	*Thunnus obesus*	6.26	2.82	74	37	463	8825	depth	1.03	319	1464	11.71	1.89	863.70	70.50
Skipjack tuna	*Katsuwonus pelamis*	2.23	3.23	9	8	189	3300	depth	1.41	393	544	8.47	0.94	80.14	7.87
Wahoo	*Acanthocybium solandri*	0.86	0.64	15	13	46	41	float	0.66	47	640	0.95	0.53	14.30	6.86
Yellowfin tuna	*Thunnus albacares*	40.51	10.55	50	27	2865	13390	depth	1.35	2007	5596	111.96	22.28	5638.96	608.42
Billfish															
Black marlin	*Makaira indica*	0.15	0.00	138	35	15	14	float	0.89	8	1	0.00	0.00	0.10	0.03
Blue marlin	*Makaira mazara*	1.99	0.45	157	41	115	714	depth	1.06	93	251	1.24	0.44	194.81	18.24
Broadbill swordfish	*Xiphias gladius*	0.02	0.14	65	19	2	10	depth	2.75	1	82	0.04	0.10	2.85	1.92
Sailfish	*Istiophorus platypterus*	0.02	0.02	19	9	18	77	float	1.42	195	1473	0.22	11.17	4.31	99.19
Shortbill spearfish	*Tetrapturus angustirostris*	0.05	0.04	10	7	6	552	depth	1.52	15	8	0.05	0.00	0.48	0.01
Striped marlin	*Tetrapturus audax*	0.46	0.19	125	24	33	727	float	1.15	12	1332	0.15	0.43	19.36	10.21
Other bony fish															
Barracudas	*Sphyraena* species	0.07	0.10	8	7	11	3	float	0.92	4	100	0.14	0.35	1.10	2.52
Lancetfishes	*Alepisaurus* species	1.08	1.54	3	3	13	476	float	0.75	59	1549	0.69	0.92	1.92	2.65
Mahi mahi	*Coryphaena hippurus*	0.53	0.18	19	16	24	2	float	1.33	29	183	0.02	3.10	0.32	50.88
Ocean ? sunfish	*Mola ramsayi?*	0.05	0.02	–	198	0	25	depth	1.28	23	115	0.21	0.14	–	27.23
Snake mackerels	Family Gempylidae	0.22	1.33	2	2	2	1	depth	2.04	113	2028	1.67	4.97	2.56	12.23
Blue shark	*Prionace glauca*	4.16	0.95	75	39	25	730	depth	1.12	206	505	2.78	0.50	208.45	19.75

Common name	Species	Catch rate (no./1000 hooks)		Mean weight (kg)		Number measured		Model		Number modeled		Est. abundance (no./1000 hooks)		Est. biomass (kg/1000 hooks)	
		1950s	**1990s**	**1950s**	**1990s**	**1950s**	**1990s**	**type**	**dispersion**	**1950s**	**1990s**	**1950s**	**1990s**	**1950s**	**1990s**
Dusky shark	*Carcharhinus obscurus*	0.00	0.00	–	25	0	22	depth	0.64	0	11	0.00	0.00	–	0.05
Mako sharks	Family Laminidae	0.66	0.07	85	40	8	39	depth	0.83	19	39	0.50	0.05	42.36	2.15
Oceanic white tip shark	*Carcharhinus longimanus*	7.52	0.75	67	27	51	327	depth	1.47	391	407	3.95	0.65	263.32	17.62
Silky shark	*Carcharhinus falciformis*	7.96	1.07	84	25	22	366	depth	1.04	3	23	0.02	0.02	1.28	0.46
Thresher sharks	*Alopias* species	0.31	0.41	17	5	2	275	depth	1.32	15	225	0.26	0.11	4.44	0.52
Other and unidentified species		3.56	1.47	–	–	–	–	float	1.26	3	19	0.03	0.05	–	–
All species		79.39	25.99	53	28	4157	31402	–	–	–	–	133.36	46.76	7007.65	1305.75

Table 3. The affect of longitude on estimates of abundance for eight species. We applied the generalized linear model (1) to catch and effort data for five progressively smaller areas of the Pacific Ocean. Values are the ratio of 1950s to 1990s numerical abundance (standard errors are shown in parentheses). For all areas the western boundary was held constant at 175°E and latitudinal boundaries were 10°S–20°N. A similar analysis, with constant longitude and variable latitude, resulted in larger variations in abundance estimates.

Species	**245°E**	**235°E**	**225°E**	**215°E**	**205°E**
Yellowfin tuna	4.7	5.1	5.2	5.8	4.0
	(0.93)	(0.93)	(0.93)	(0.92)	(0.9)
Bigeye tuna	3.8	4.0	4.1	4.3	3.8
	(0.91)	(0.91)	(0.91)	(0.91)	(0.88)
Silky shark	9.6	9.4	10.2	11.5	11.2
	(0.89)	(1)	(0.88)	(0.88)	(0.86)
Oceanic white tip shark	7.5	6.8	7.0	6.8	5.9
	(0.89)	(0.89)	(0.89)	(0.89)	(0.86)
Blue shark	5.1	4.5	4.6	4.7	4.0
	(0.9)	(0.89)	(0.89)	(0.88)	(0.85)
Skipjack tuna	0.3	0.2	0.3	0.2	0.1
	(0.83)	(0.83)	(0.82)	(0.8)	(0.71)
Albacore tuna	4.8	4.9	4.9	4.8	5.1
	(0.84)	(0.84)	(0.84)	(0.81)	(0.77)
Blue marlin	2.5	2.4	2.2	1.9	4.2
	(0.84)	(0.83)	(0.83)	(0.82)	(0.77)

Table 4. Comparison of mean catch rates of commercial species reported by the POFI survey and mothership expeditions during the early 1950s in the central tropical Pacific Ocean (numbers in parentheses are standard

Species	Mothership[a]	Survey
Yellowfin tuna	25.83	38.35
	(19.55)	(44.61)
Bigeye tuna	9.01	6.36
	(8.23)	(11.81)
Albacore tuna	4.01	2.87
	(10.51)	(8.79)
Skipjack tuna	0.37	2.59
	(1.09)	(6.35)
Pacific blue marlin	6.00	1.97
	(3.50)	(3.44)
Striped marlin	0.42	0.63
	(2.29)	(2.39)
Sailfish + spearfish	0.72	0.32
	(1.06)	(1.40)
Black marlin	0.33	0.23
	(0.89)	(3.44)
Broadbill swordfish	0.08	0.11
	(0.21)	(1.07)
All commercial	46.75	53.83
species	(20.79)	(46.74)

[a]Standard deviations may not represent the true variance among operations because the original data were aggregated by month and five-degree square.

errors). check? reduce to 1 decimal place? change footnote to SEs?

Figure captions

Figure 1. Comparison of the spatial and temporal distribution of 1950s survey and 1990s commercial longline operations. The density histograms and map summarize the catch and effort data used in estimating species abundance (January–November, 2:00–8:00 am deployment; 0–10°N, 175–245°E).

Figure 2. Catch rates of species reported in the 1950s and 1990s in the study area. Horizontal bars are approximate 95% confidence intervals for the mean catch rate. The estimates of total catch rates include rare and unidentified species that are not shown in the figure.

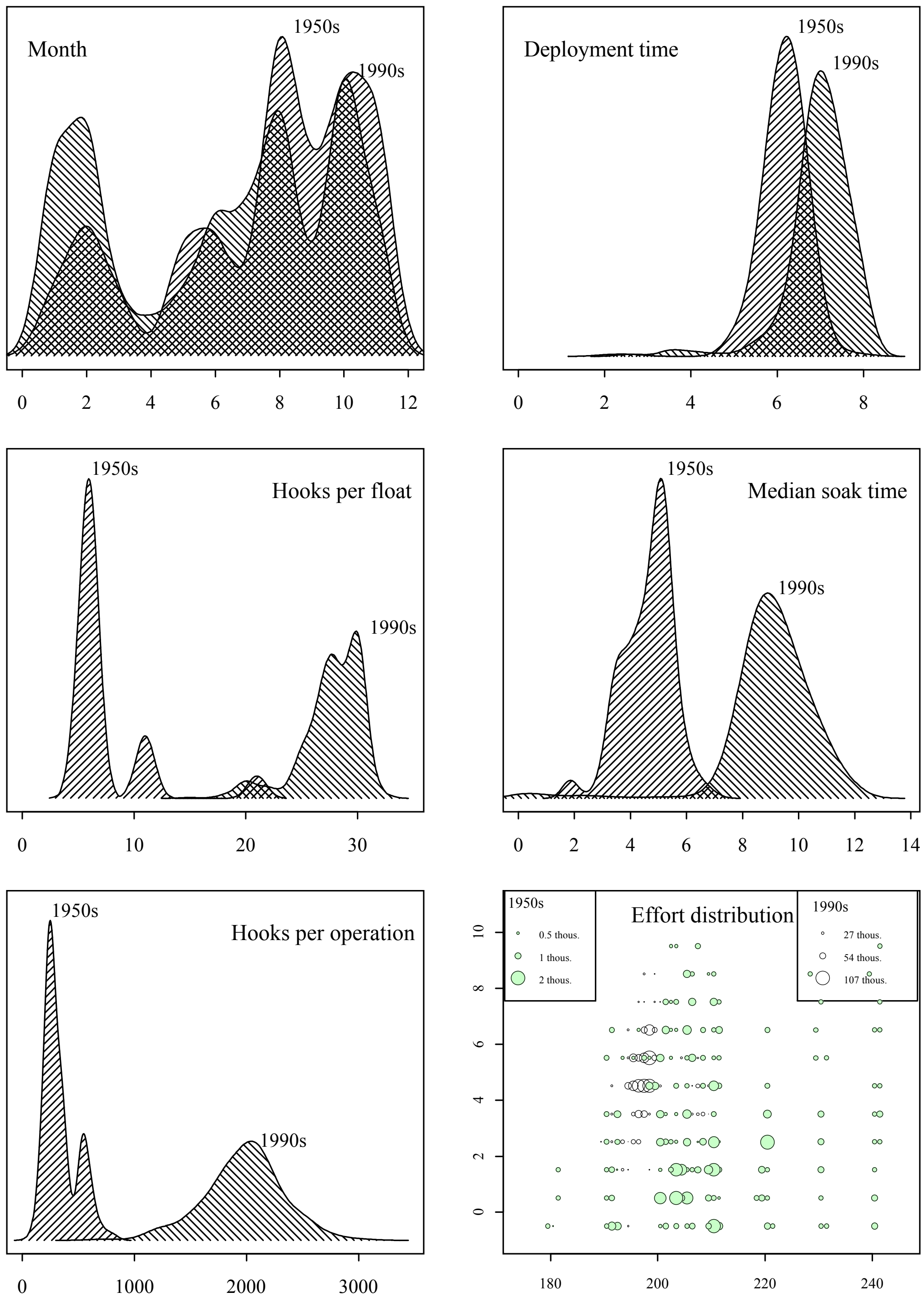
Figure 3. Change in abundance between the 1950s and 1990s. Solid circles are the ratio of 1950s to 1990s biomass estimated from generalized linear models and (horizontal bars are 95% confidence intervals). Also shown is the ratio in terms of number of individuals (open circles, confidence intervals not shown). Species are listed in order of the most abundant species in the 1950s (yellowfin tuna) to less abundant species (shortbill spearfish).

Figure 4. Boxplots of the size composition of each species in the 1950s and 1990s. For the 1990s, weights were predicted from length-weight relationships applied to length measurements. For wahoo and lancetfishes the 1990s size data are from SPC observers. The lower right-hand panel is an explanatory key. Each "box" contains 50% of observations and the interquartile range (IQR) is the difference between the first and third quartiles.

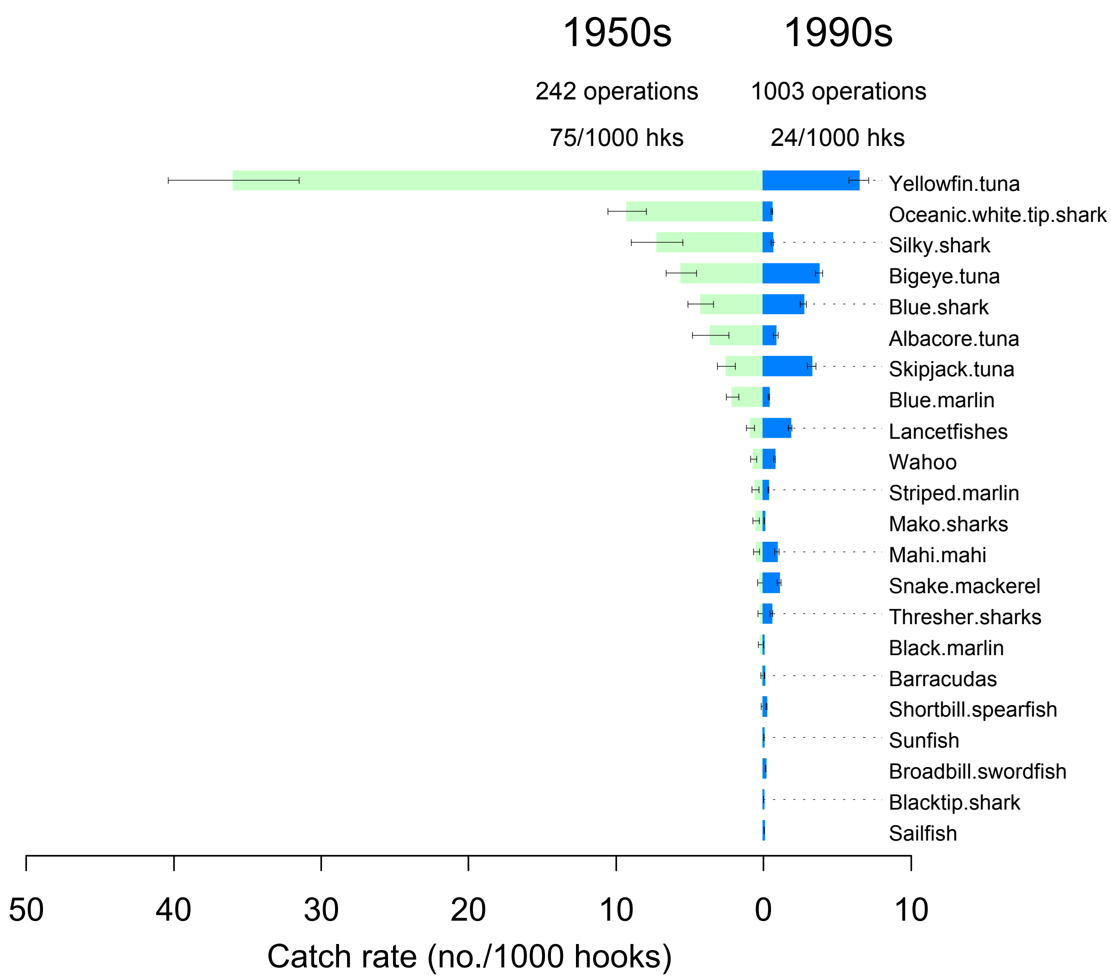
Figure 5. Relationship between mean weights of each species in the 1950s and 1990s. 95% confidence intervals are shown for mean weights of the 1950s (horizontal bars) and 1990s (vertical bars). The broken line is the line of equality where mean weight 1950s equal 1990s mean weight. Figure 4 provides an indication of the variance in weight for each period; sample sizes are shown in Table 2.

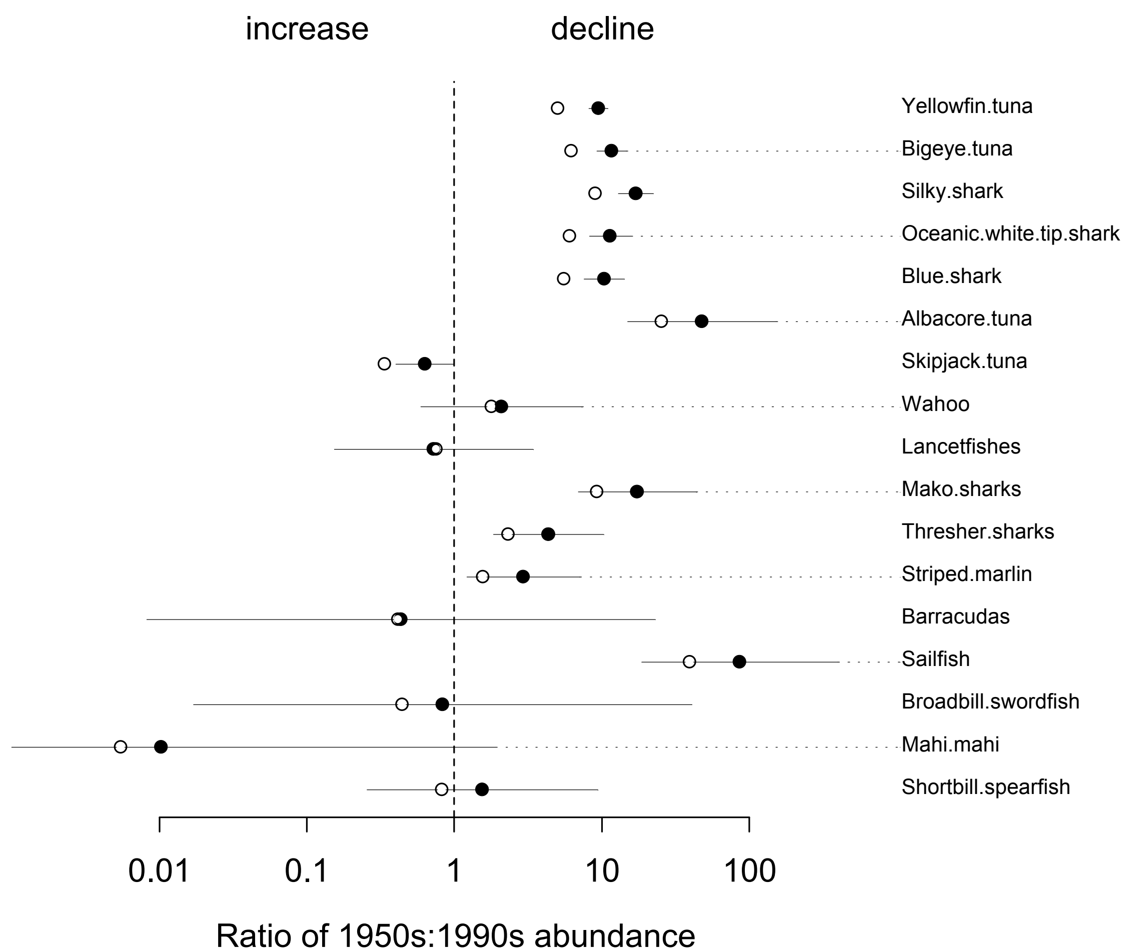
Figure 6. Relationship between body size and the subsequent change in biomass for each species. Figure 4 provides an indication of the variance in weight for each period; sample sizes are shown in Table 2.

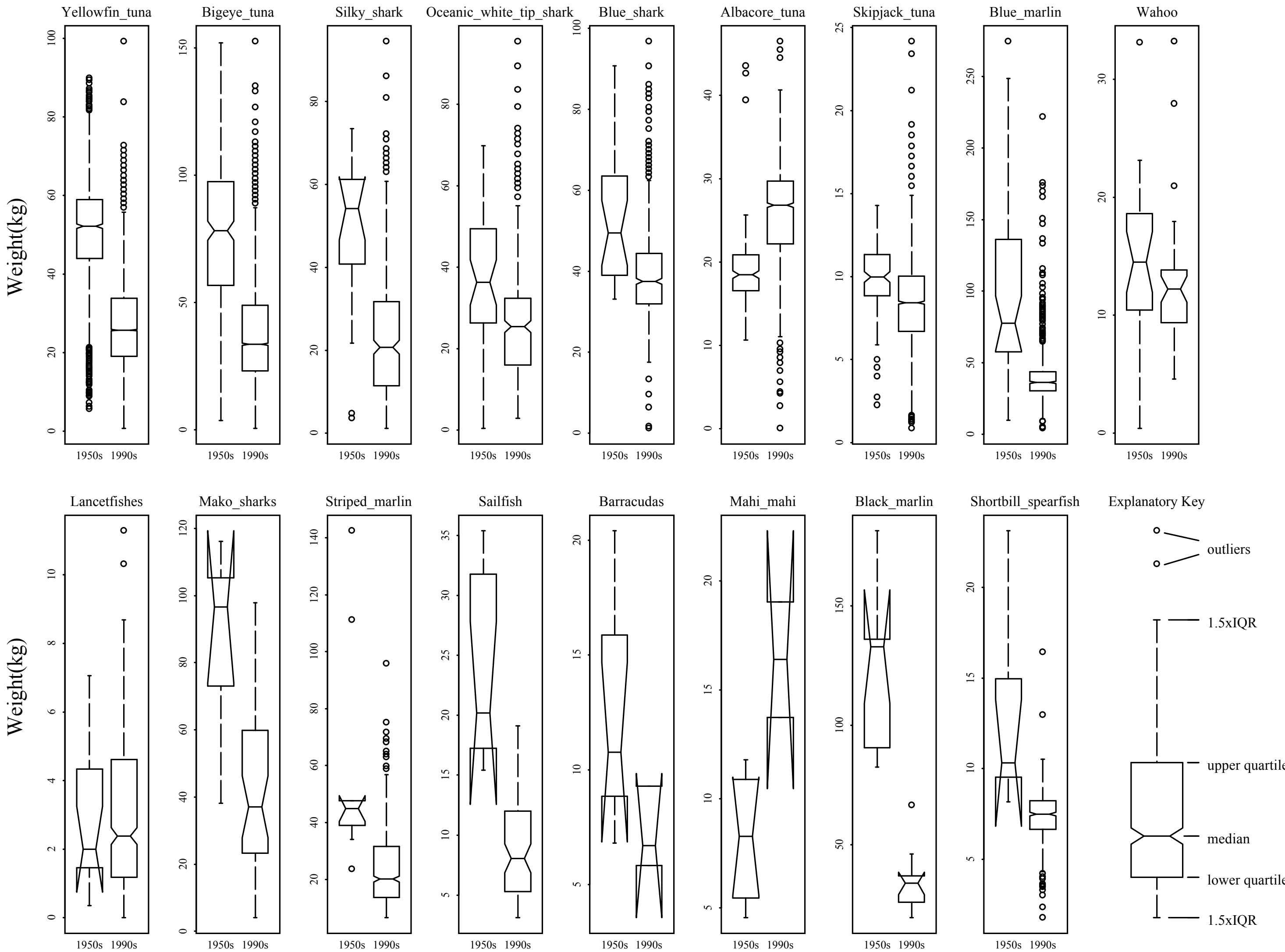
Figure 7. The change in biomass of the pelagic fish community. Each shaded bar represents one species. The five most abundant species are labeled. The area of each bar is scaled to the total biomass (kg per 1000 hooks) of the catch in each period, the horizontal dimension is scaled to numerical abundance (number per 1000 hooks) and the vertical dimension is scaled to the mean weight (kg) of all species combined.

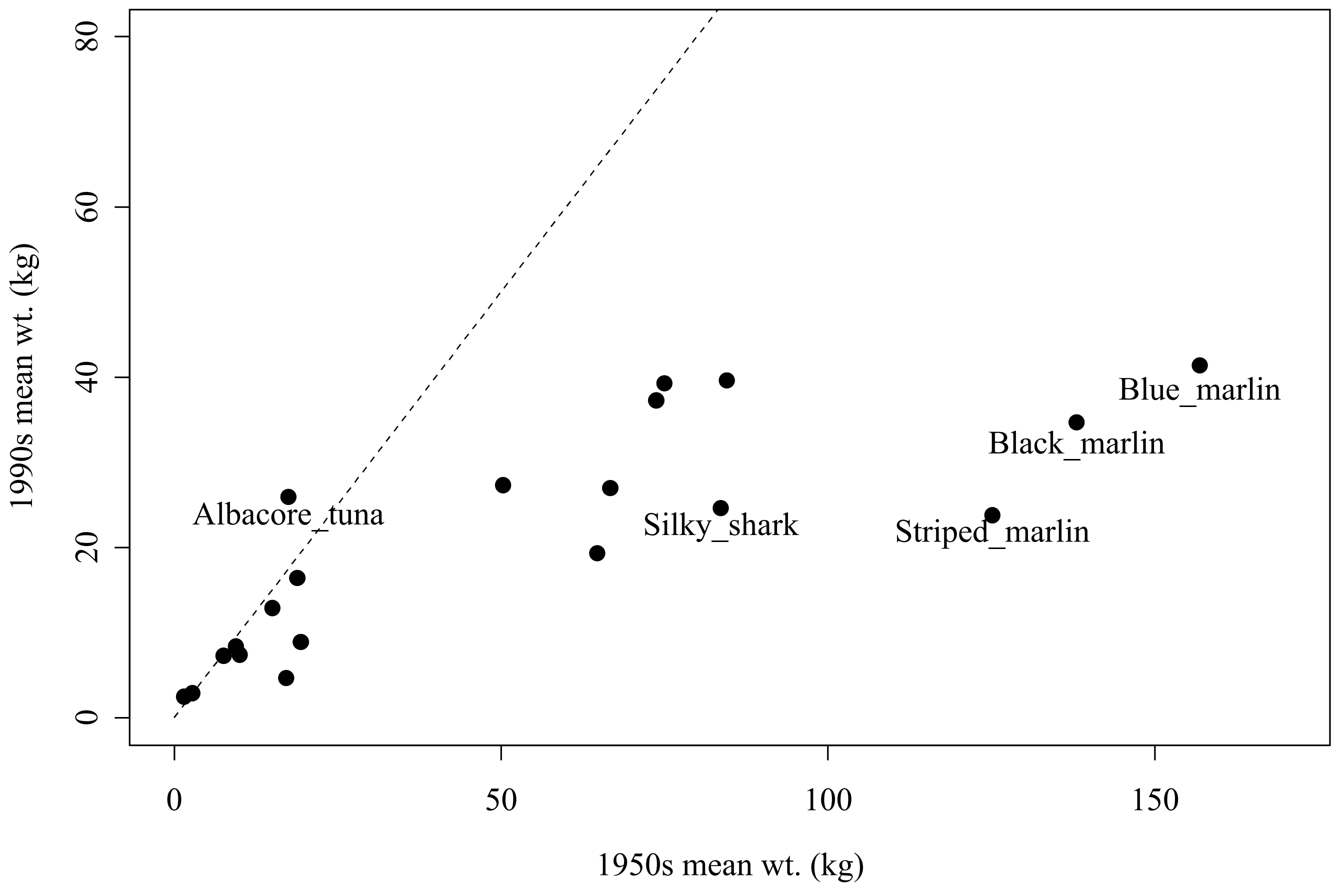


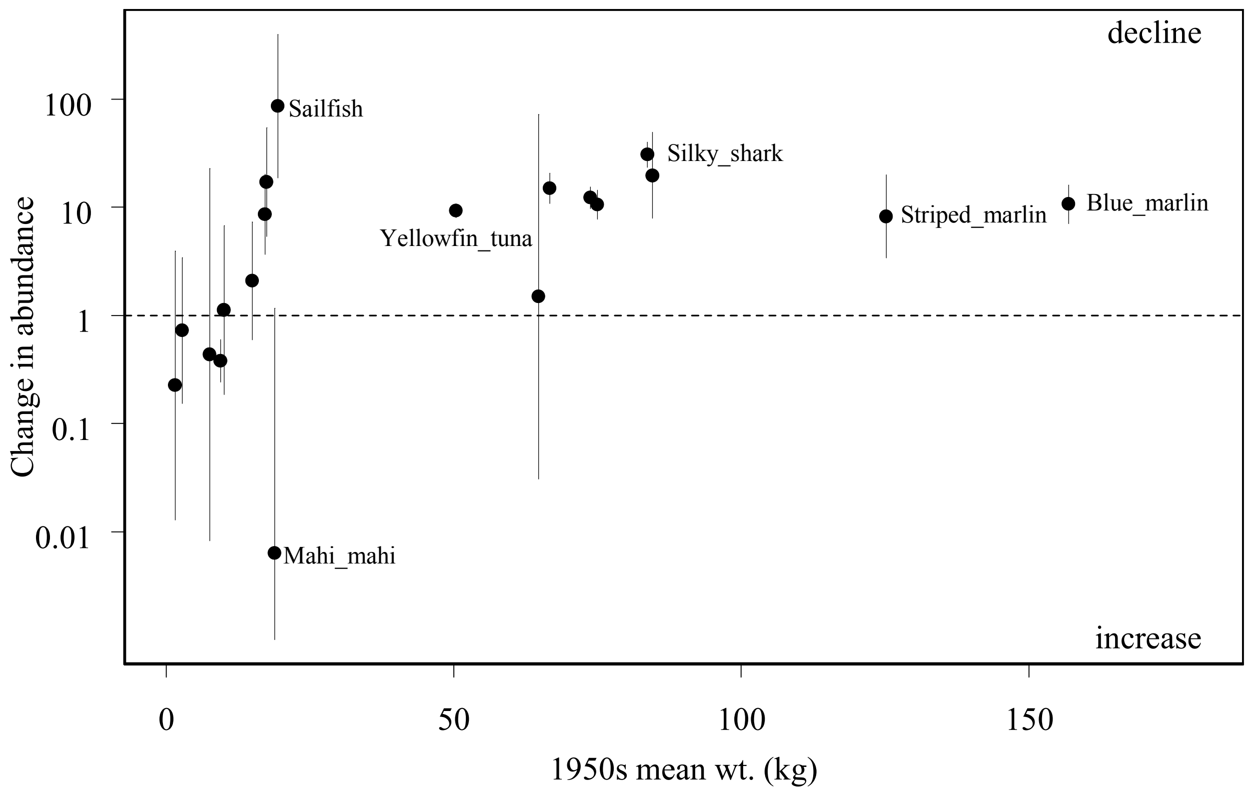
Month
1950s
1990s
0 2 4 6 8 10 12
Deployment time
1950s
1990s
0 2 4 6 8
Hooks per float
1950s
1990s
0 10 20 30
Median soak time
1950s
1990s
0 2 4 6 8 10 12 14
Hooks per operation
1950s
1990s
0 1000 2000 3000
Effort distribution
1950s
0.5 thous.
1 thous.
2 thous.
1990s
27 thous.
54 thous.
107 thous.
0 2 4 6 8 10
180 200 220 240

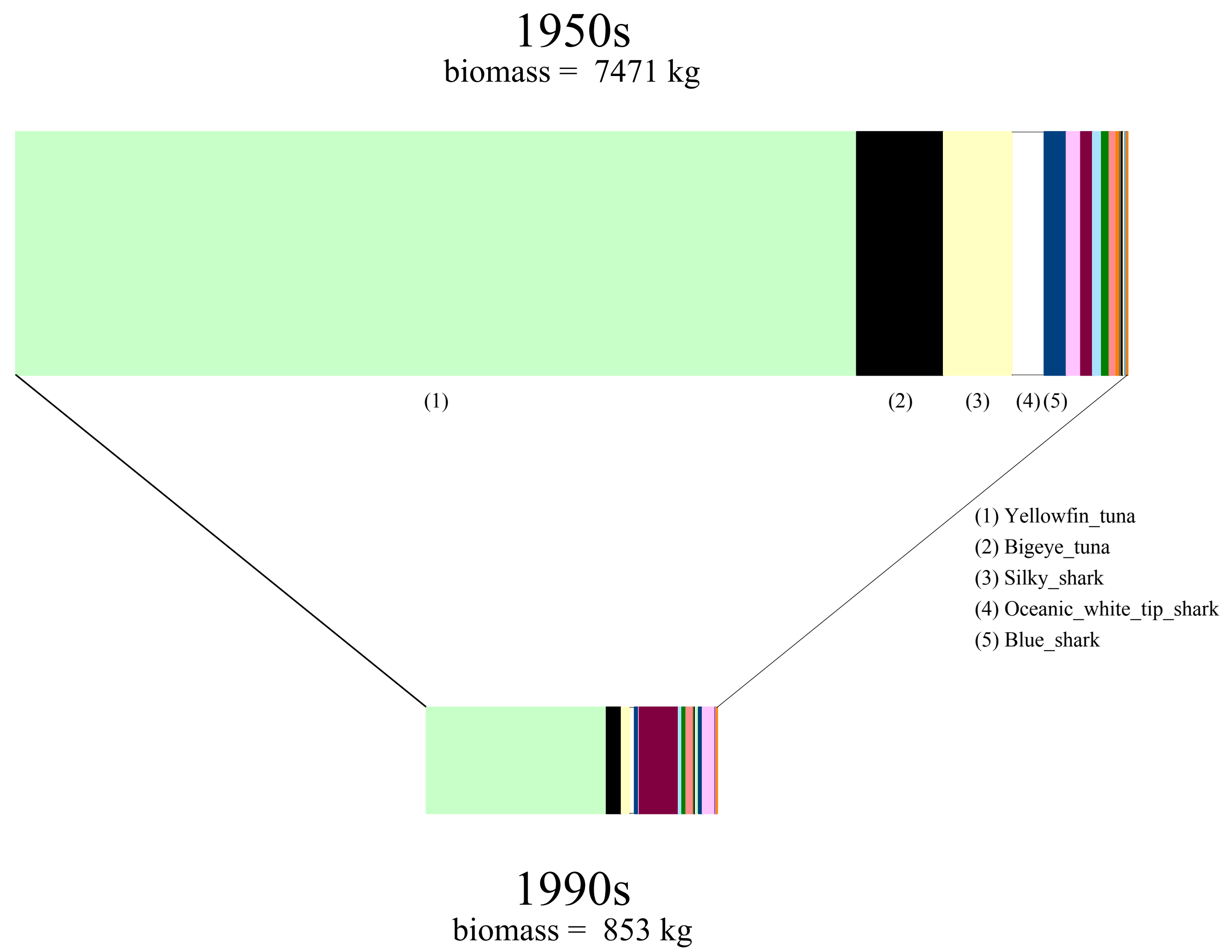

1950s
1990s
242 operations
1003 operations
75/1000 hks
24/1000 hks
Yellowfin.tuna
Oceanic.white.tip.shark
Silky.shark
Bigeye.tuna
Blue.shark
Albacore.tuna
Skipjack.tuna
Blue.marlin
Lancetfishes
Wahoo
Striped.marlin
Mako.sharks
Mahi.mahi
Snake.mackerel
Thresher.sharks
Black.marlin
Barracudas
Shortbill.spearfish
Sunfish
Broadbill.swordfish
Blacktip.shark
Sailfish
50
40
30
20
10
0
10
Catch rate (no./1000 hooks)


increase
decline
Yellowfin.tuna
Bigeye.tuna
Silky.shark
Oceanic.white.tip.shark
Blue.shark
Albacore.tuna
Skipjack.tuna
Wahoo
Lancetfishes
Mako.sharks
Thresher.sharks
Striped.marlin
Barracudas
Sailfish
Broadbill.swordfish
Mahi.mahi
Shortbill.spearfish
0.01
0.1
1
10
100
Ratio of 1950s:1990s abundance


Yellowfin_tuna
Bigeye_tuna
Silky_shark
Oceanic_white_tip_shark
Blue_shark
Albacore_tuna
Skipjack_tuna
Blue_marlin
Wahoo
Lancetfishes
Mako_sharks
Striped_marlin
Sailfish
Barracudas
Mahi_mahi
Black_marlin
Shortbill_spearfish
Explanatory Key
Weight(kg)
1950s
1990s
outliers
1.5xIQR
upper quartile
median
lower quartile
1.5xIQR


1990s mean wt. (kg)
80
60
40
20
0
Albacore_tuna
Silky_shark
Striped_marlin
Black_marlin
Blue_marlin
0
50
100
150
1950s mean wt. (kg)


decline
increase
Sailfish
Silky_shark
Yellowfin_tuna
Striped_marlin
Blue_marlin
Mahi_mahi
100
10
1
0.1
0.01
Change in abundance
0
50
100
150
1950s mean wt. (kg)


1950s
biomass = 7471 kg
(1)
(2)
(3)
(4)(5)
(1) Yellowfin_tuna
(2) Bigeye_tuna
(3) Silky_shark
(4) Oceanic_white_tip_shark
(5) Blue_shark
1990s
biomass = 853 kg