Historical changes in the catchability of pelagic longline fishing gear

or

Evidence of historical changes in the catchability of pelagic longline fishing gear

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Abstract

Catchability of several species decreased, whereas catchability of most species increased. The removal of large sharks has resulted in reduced losses of animals hooked on the longline.

Key words: catchability, tuna, billfish, shark, pelagic, open ocean, fishing effort

Running title: Historical changes in longline catchability

Introduction

Significance

Despite technological innovations, such as satellite tracking, field-based sampling remains the key source of information on the status of wild animal populations, ranging from insect pests [Southwood, 1966 #798] to endangered antelope [Whittaker, 2003 #878] and valuable fishing industries (Cooke and Beddington, 1984).

Catch levels and sampling or “fishing” effort are often the only information available to estimate the abundance of aquatic animals [Arregion-Sanchez, 1996 #780; Francis, 2003 #778; Stoner, 2004 #842]. Abundance estimates based on catch-per-unit-effort (cpue or “catch rates”) are particularly important for non-target or “bycatch” species, where fishery-independent methods of counting fish are often impractical. Therefore, understanding the relationship between catch levels, the amount of sampling and population abundance is critical to the accurate assessment and effective management of wild populations.

Historical patterns in longline catch rates present fishery managers with a paradox. A common pattern is a sudden decline in catch rates soon after longlining commences, which implies that the populations were initially small. However, the populations subsequently support high catch levels, suggesting much larger populations than indicated by initial catch rates. Has catchability radically changed or do these patterns point to other attributes of pelagic populations that have been overlooked, e.g., population sub-structuring?

The question of whether catch rates provide unbiased measures of animal density is also important to mark-recapture studies (Seber, 1982) and to “depletion estimates” of the size of closed populations (e.g., Leslie and Davis, 1939) that examine how removals of animals affect catch rates. Both techniques assume that all individuals have an equal probability of being caught in a sample. Catchability is also important to bycatch mitigation, since if we know how to reduce catchability of certain species, then we can reduce fishing mortality. An understanding of catchability also allows catch rates from different fisheries and surveys to be combined (Ward depth ref?).

A measure of catchability is especially important for pelagic longline fisheries, where fishery-independent estimates of abundance are rare, especially for the diversity of non-target species taken. The catch (number or weight) is divided by fishing effort to estimate catch-per-unit-effort (cpue) or “catch rates” that are used as an index of abundance. In many stock assessment models catchability is assumed to be constant over time, and fishing effort is taken to be uniformly distributed and constant [Polacheck, 1991 #804; Arregion-Sanchez, 1996, p. 225–27]. However, it has long been known that the catchability coefficient, which links catch rates to abundance, is rarely constant, e.g., (Murphy, 1960), (Paloheimo and Dickie, 1964), and (Gulland, 1964).

Purpose

Longlines have been used to catch highly migratory tunas and billfishes throughout tropical and temperate waters of the world’s oceans since the 1960s. The longlines consist of a series of baited hooks attached to a mainline that is suspended from buoys floating at the sea surface. Trawlers and purse seiners actively encircle fish schools or sweep the ocean. By contrast, demersal and pelagic longlines, other hook-and-line methods and baited traps rely on animals encountering and being attracted to baits. In addition to the temporal and spatial distribution of the gear and fish, the odds of catching a fish depends on the stochastic processes of the fish attacking the bait and the probability of remaining on the hook (Deriso and Parma, 1987).

Other reviews

(Arregion-Sanchez, 1996) provides a general review of catchability in fisheries. (Løkkeborg and Bjordal, 1992) reviews factors affecting the size selectivity of longline fishing gear, concentrating on demersal longline gear. (Stoner, 2004) evaluates environmental variables that influence the availability of fishes to baited fishing gear, particularly demersal longlines. He concluded that the assumption of constant catchability is often not valid for baited fishing techniques, mainly because of the variable behavior of target species; responsiveness to baits varies in time, in space and among individuals depending on its environment and feeding history. Stoner ranked environmental variables on the basis of the natural range of conditions experienced and the strength of its affect on the animal’s active range and catchability. He concluded that temperature, light, direction and velocity of ocean currents and the density of conspecifics had the greatest potential impacts on catchability and offered the best prospects for adjustment in stock assessments. Our review complements Stoner’s review by focusing on pelagic longline gear and estimating historical changes in catchability.

[Lin, 1997 #929] compared the performance of a longliner using the contemporary “American fishing system” with that of a nearby longliner using the traditional system.

The two systems used the same longline gear, however the contemporary mainline was deployed with a hydraulically-driven line-shooter and wound onto a hydraulical spool. The longlines were deployed parallel to each other, within about 12 km. For the four fishing trips monitored, each involving about nine longline operations, catch rates of the contemporary system (1.27–3.45 animals per 1000 hooks per hour) were higher than those of the traditional system (0.76–2.08). [Lin, 1997 #929] reported that the differences in catch rates were statistically significant, attributing the difference to increased deployment and retrieval speeds (resulting in longer soak times) and the deeper depths fished by the contemporary system.

Catch equation

In other areas of ecology, catchability is often referred to as the sampling method's efficiency – "the percentage of the animals actually present that are recorded" (Southwood, 1966). (Baranov, 1918) proposed the catch equation, which introduced the catchability coefficient q to link estimates of catch, fishing effort, and the species' local abundance N:

$$U = qN \tag{1}$$

The catch rate U is the catch divided by fishing effort. The catchability coefficient q is defined as the probability of catching a fish in a single unit of fishing effort (Paloheimo and Dickie, 1964).

There are two separate aspects of the catch equation: estimating catchability and obtaining a true estimate of fishing effort. A consistent measure of fishing effort should be the product of three factors: the efficiency of the gear; the quantity of gear; and the duration of deployment (Cooke and Beddington, 1984). In longline fisheries, the unit of effort is usually 1000 hooks. The efficiency of the gear and the duration of deployment are rarely considered, although (Ward et al., 2004) found that the length of time that hooks are available vary among fleets and historically, and that soak time and the availability of hooks at dawn and dusk strongly influences the catches of many species.

Catchability usually varies with size and is termed "gear selectivity" (Seber, 1982). Selectivity is a measure of the bias in catching an animal with particular attributes, such as size or sex. Selection will influence what proportion of the population is actually caught. Factors influencing selectivity may also affect catchability.

The animal's availability and its vulnerability to the fishing gear determine the probability of capture (Figure 1). Availability is determined by its density and distribution, behavior and physiology, in relation to the fishing gear's characteristics, such as its distribution (Arregion-Sanchez, 1996, p. 222). Vulnerability is the product of availability interacting with attributes of the fishing gear, e.g., longline depth.

Whether an animal is on a hook when it is brought on board is determined by six stochastic events; its density and distribution in relation to that of the fishing gear; the availability of baited hooks; detection of the bait by the animal; attraction to the bait; and hooking (Figure 1). The sixth event – landing – is not always considered in other reviews, but is important in longline fisheries because animals may escape, fall off or are removed from the hook by scavengers before it is retrieved [Ward, 2004 #451]. We do not consider an additional event, retention and reporting practices that may affect the reporting of catches by commercial fishers in logbooks.

General approach

To estimate historical changes in catchability we first estimate the effect on catchability of each factor believed to affect catchability (Figure 1). For example, there is evidence that branchline material affects catchability. [Stone, 2001 #732] present the results of an experiment where monofilament and multifilament branchlines were alternated along a longline. Catch rates U_1 derived from monofilament branchlines are related to the species' local abundance N and catchability q through the catch equation:

$$U_1 = \alpha_1 q N$$

$$\text{and } N = \frac{U_1}{\alpha_1 q}$$

where α_1 represents the affect of monofilament on catchability. For multifilament branchlines we have α_2 resulting in catch rates U_2:

$$N = \frac{U_2}{\alpha_2 q}$$

Local abundance N is the same for both types of branchline, so we combine the two equations:

$$\frac{U_1}{\alpha_1 q} = \frac{U_2}{\alpha_2 q}$$

$$\frac{\alpha_2}{\alpha_1} U_1 = \frac{q}{q} U_2$$

$$\frac{\alpha_2}{\alpha_1} = \frac{U_2}{U_1}$$

For a controlled experiment we can therefore estimate relative catchability by dividing one catch rate by the other. In our example, [Stone, 2001 #732] deployed equal numbers of monofilament and multifilament branchlines. They caught 128 swordfish on multifilament and 260 swordfish on monofilament. We estimate the effect of monofilament on catchability as $\Delta q = 260/128 = 2.03$. In other words, monofilament catchability for swordfish is double that of multifilament.

To estimate the historical change in catchability we need an estimate of the proportion of gear types in the periods of interest. In our example, 25% of the branchlines used in a fishery were monofilament in 1980 rising to 75% monofilament in 1990, with the remainder multifilament. We estimate the change in catchability Δq between the two periods as:

$$\Delta q = \frac{(2.03 \times 0.75)}{(2.03 \times 0.25)} = 3.00$$

We conclude that the switch to monofilament has resulted in a threefold increase in catchability between 1980 and 1990. Where there was a complete change from one gear to another, we simply assign one to the denominator.

Nominal catch rates are the catch divided by the associated fishing effort. Several factors directly affect our measure of fishing effort instead of catchability, but the result is the same. For example, one in ten hooks held a fish – were "occupied" – in the 1950s compared to one in a hundred in the 1990s. Consequently, fishing effort must be discounted by 10%. This is the same as reducing the probability of catching a fish by 10%, which is equivalent to reducing catchability by 10%. Changes in catchability due to factors that directly affect catch (e.g., drop-off) can be directly estimated in a similar way.

We present estimates of change in relative catchability for ? factors for which there is evidence of historical variations. Following is a brief summary of how each factor affects catchability, historical trends, the methods we used to estimate the factor's affect on relative catchability, and the reliability of our estimates. Reference numbers in parentheses link each factor to the estimates of catchability presented in Table 2. Our study area is the central tropical Pacific Ocean (between 20°S–20°N and 140°E–140°W). Affects are compared for Japan's large, distant-water longliners between the "1950s" (1950–54) and the "1990s" (1995–99). We also mention other significant trends in catchability for other longline fleets. We limit our analyses to five frequently caught species that represent a range of life-histories (Table 1).

Area of action and abundance

Animal's movement patterns (A.2)

Mechanism: Maximum swimming speed is closely liked to the fish's length More importantly, small fish incur relatively greater energetic costs in locomotion than are incurred by larger fish, resulting in a small feeding range [Hart, 1986 #854; Videler, 1993 #884] and reduced encounters with baits. Consequently, changes in a population's size composition will result in variations in catchability.

Evidence: Large animals can swim faster and are more successful at competing for baits than smaller animals [Ware, 1978 #888]; Hart, 1986; Løkkeborg and Bjordal, 1992). [Nottestad, 1999 #881] found statistically significant relationships between the extent of northward migrations and body length for four small pelagic fish species. Simulations by [Ware, 1978 #888] show that the optimal speed during foraging is a function of food concentration and body size. The volume of water searched in a given period is a function of the animal's swimming speed and visual acuity [Ware, 1978 #888].

Historical trend: Longlining has selectively removed large animals from the pelagic fish community, while the mean size of several smaller species has increased (Ward and Myers, in press-c).

Estimation: Optimal foraging and cruising speeds increase in proportion to $L^{0.4}$ and the volume of water searched will vary with $L^{0.26}$ [Ware, 1978 #888].

Reliability: If food is in over-supply, then the importance of body size and feeding range is diminished. It is noteworthy that visual acuity is also related to body size, so that larger animals are able to detect prey at greater distances than can smaller animals of the same species [Blaxter, 1980 #887].

Depth of gear (A.3)

Mechanism: Catchability will increase when the distribution of the fishing gear matches that of the population because a larger proportion of the population will be available to the gear [Hanamoto, 1987 #768; Boggs, 1992 #250]). Tracking studies demonstrate that bigeye tuna, for example, range down to 500 m or deeper in the tropical Pacific Ocean [Musyl, 2003 #751]. Early longlines ranged down to 120 m [Suzuki, 1977 #541]. Consequently, a proportion of the population would not have been available to the gear. By ranging down to 400 m or more [Boggs, 1992 #250] the longlines now access the full vertical range of many species.

Evidence: ~~Tracking studies combined with oceanographic measurements show that environmental conditions, ecological factors, and body size strongly influence the vertical movement patterns and the depth distribution of pelagic species. Tracking studies show that blue marlin often swim near the sea surface; they rarely venture below the thermocline. Occasionally they make rapid descents and ascents within surface waters [Yuen, 1974 #867; Holland, 1990 #756; Block, 1992 #760].~~

~~Adult mako shark [Carey, 1981 #764; Carey, 1990 #747] and yellowfin tuna [Carey, 1982 #868; Block, 1997 #755; Josse, 1998 #758] are also epipelagic species that inhabit the mixed layer above the thermocline. However, they make deeper dives than blue marlin, occasionally moving below the thermocline.~~

~~By contrast, adult bigeye tuna inhabit surface waters (<100 m) at nighttime then move to deeper depths (up to 500 m) during the day [Dagorn, 2000 #753; Musyl, 2003 #751]. During the daytime the tagged bigeye tuna also make rapid upward vertical excursions into surface waters every 2–3 hours, probably to regulate body temperature and possibly to compensate for oxygen debt [Dagorn, 2000 #753].~~

Analyses of fine-scale longline catch data (e.g., [Hanamoto, 1987 #768; Uozumi, 1997 #611; Maury, 2001 #839; Ward, in press #861]) and hook-timer experiments (e.g., [Boggs, 1992 #250; Campbell, 1997 #282]) provide information on the depth distribution of longline catchability. [Ward, in press #861], for example, inferred the depth distribution of 37 pelagic species with a generalized linear mixed effects model applied to four fine-scale datasets from observers on longliners in the tropical Pacific Ocean. Their estimates match the patterns derived from tracking studies. The daytime distribution of catchability declines with depth for blue marlin, yellowfin tuna, and mako shark, and it increases with depth for bigeye tuna. There is no tracking data for skipjack tuna; the catchability estimates show that almost all skipjack tuna are caught near the sea surface.

Historical trend: By assuming that the longline forms a catenary curve [Suzuki, 1977 #541] and reducing estimated depths by 25% for the effects of currents [Ward, in press #861], we estimated that the longlines deployed by Japan's longliners in the 1950s ranged from about 65 to 107 m. In the mid 1970s, the Japanese began to use deeper longlines to target bigeye tuna [Suzuki, 1977 #541]. We estimated an average depth range of 60–210 m in the 1990s.

Estimation: We applied the daytime catchability coefficients estimated for each species by [Ward, in press #861] to depths estimated from longline configurations typical of each period (Table 3). The longline configuration is almost always identical between floats, so that the number of depths that needs to be considered for each configuration is half the number of hooks between floats. For each species, $f(D_i)$ represents the effect of depth D on relative catchability of hook number *i* in the period:

$$f(D_i) = \exp(\alpha + \gamma_1 D_i + \gamma_2 D_i^{\ 2} + \gamma_3 D_i^{\ 3})$$

where α and the γ_j are parameters that [Ward, in press #861] estimated for the species. The change in catchability Δq between periods was then estimated as:

$$\Delta q = \frac{\overline{f(D_{1990})}}{\overline{f(D_{1950})}}$$

where $\overline{f(D_{1950})}$ is the mean depth effect $f(D_i)$ for the 1950s and $\overline{f(D_{1990})}$ is the mean $f(D_i)$ for the 1990s.

Reliability: In addition to being affected by depth range, the catchability of longline gear will be affected by spatial and temporal variations in oceanographic conditions, e.g., the thermocline is much deeper in the west (~175 m) than in the east (~40 m) of the tropical Pacific Ocean. Oceanographic conditions also fluctuate with broad-scale events, e.g., the thermocline shoals by about 40 m during El Niño periods in the western Pacific Ocean [Philander, 1990 #840]. Such oceanographic information (e.g., thermocline depth) is combined with information from tracking studies to estimate the species' depth distribution in time and area strata, e.g., [Hinton, 1996 #525; Bigelow, 2002 #565]. The “habitat-based model” is then combined with the inferred depth distribution of longline hooks to adjust the fishing effort for the species’ availability in each time–area stratum.

Our estimates ignore oceanographic variations because ENSO conditions and thermocline depth were not markedly different between the 1950s and 1990s [Ward, in press #628]. Also, [Ward, in press #861] assume that the animal was caught when the hook was at its maximum settled depth, whereas hook-timer experiments (e.g., [Boggs, 1992 #250]) show elevated catch rates for several species while the bait is moving through the water column during longline deployment and retrieval.

It is noteworthy that other fleets (e.g., Hawaii) now use longlines that range down to 400 m or more (ref).

[Ward, in press #861] note inconsistencies between their estimates of the depth distribution of catchability and depth preferences derived from tracking studies. They suggest that this might reflect differential vulnerability to longline gear. It is quite possible for a species to be abundant at depths where they have a reduced vulnerability to the gear. For example, bigeye tuna might briefly move to surface waters for thermoregulation, but not caught on longline hooks there because they are not feeding. Tracking data represent an animal’s depth preference, which may not always match its vulnerability to longline fishing gear. From an analysis of simulated data [Goodyear, 2003 #137] concluded that the propensity of blue marlin to take longline baits and the actual depth profile of the fishing gear strongly influenced habitat-based model estimates of abundance.

Location of gear (A.4)

Mechanism: The ability to locate target species has improved with experience, cooperative searching [Ruttan, 2003 #908] and the installation of electronic navigation and fish-finding equipment [Kleiber, 1991 #170; Ward and Myers, in press-c)

Evidence: [Kleiber, 1991 #170] detected historical increases in the ability of jig-fishers to locate high-density patches of albacore tuna in the North Pacific. They attributed the increases to the availability of satellite imagery and advisory bulletins. In a detailed analysis of 1971–91 logbook data, [Campbell, 1994 #909] observed that Japan's longliners rarely operated in areas where southern bluefin tuna catch rates were low; they concentrated in areas of high catch rates. He concluded that the concentration of longlining effort in areas of high catch rates resulted in an upward bias in abundance indices as population size declined.

Historical trend: [Ashenden, 1987 #915] report that the 800 Japanese longliners searched cooperatively in the tropical Pacific Ocean. Communication usually involved longliners owned by the same company or personal networks developed by vessel masters. Australian observers report that most longliners received daily facsimiles from their company illustrating sea surface temperature isotherms and annotated with current and predicted areas of high catch rates in their area.

By the mid 1980s, Japan’s longliners had installed various electronic aids to finding fish, including color sounders that are used to detect the thermocline, plankton and baitfish layers, and target species, and satellite receivers for downloading sea surface temperature maps. In the 1990s, Australian observers reported that some longliners also accessed satellite ocean-color imagery and obtained thermal profiles by deploying expendable bathythermograph (XBT). Other equipment, such as weather facsimiles and radio direction finders added to the efficiency of longlining operations and extended the time that vessels can remain on fishing grounds to follow the fish.

Estimation: We located no controlled experiments on the effects of electronic navigation and fish-finding equipment on pelagic longline catch rates. Our approach to estimating the effects of electronic equipment on catchability is based on the argument that owners would install the equipment when they expect the resulting improvements in catch rates to exceed the cost of the equipment. We estimated the annual cost of electronic equipment for a typical longliner (Table 11), then estimated the proportional increase in catch rates required to cover those costs (Table 12). The value (USD) of the catch of each of six species i is the product of its catch rate U_i (number per 1000 hooks), mean weight w_i (kg), market price P_i (USD/kg), and the total number of hooks deployed by a longliner each year H (878 802 hooks; [Reid, 2003 #934]). The longliner’s operating profit V is then the summation of the value of all species minus total costs C:

$$V = \left[\sum_{i=1}^{6} U_i H w_i P_i \right] - C$$

Catch rates must be increased by Δq to cover the additional costs of electronic equipment E:

$$V + E = \left[\sum_{i=1}^{6} \Delta q U_i H w_i P_i \right] - C$$

Reliability: We assume that the relative proportions of species remain constant as catch rates increase and that no other species contribute to financial returns. Our estimate of the effect of electronic equipment on catchability are directly linked to the value selected as the proportion of outlay that the owner will need recoup each year. Based on advice from Australian longline fishers, we set the equipment's life expectancy to seven years, so one-seventh (14.29%) of the original cost would need to be recovered each year. A lower rate of recovery would reduce the catch required to cover outlay and result in a smaller increase in catchability, whereas a higher value would require a larger increase in catchability.

We assume that increasing catch rates is the only avenue available to covering equipment costs. However, other options might be available, such as increasing the number of operations per year or limiting other costs, e.g., wages.

Regardless, we must stress that the estimates of the effects of electronic equipment on catchability are very conservative; an owner would not purchase and install a device unless he or she was convinced that a profit would be made, let alone cover costs. Many of the devices are likely to have added value to catches well beyond the equipment's initial cost. A sea surface temperature (SST) monitor, for example, is indispensable in the location of oceanic fronts. It would return far more than the initial USD733 outlay.

~~Our estimates need to be verified through controlled experiments. Need to estimate searching effect? In the 1950s a longliner, with a cruising speed of ? km.hr^{-1} searching for an average of ? hours per day for a campaign of 200 days a year would search ? km^2. Given that there were about 80 longliners operating in the tropical Pacific Ocean, at that time and assuming that each longliner communicated with about half of those, would provide a total search area of ? km^2.~~

Time of deployment and retrieval (A.5)

Mechanism: Most large pelagic predators show diel patterns in their feeding activities. Many species are especially active during the transition between day and night ("crepuscular periods"). Diminished light levels affect the ability of prey and predators to detect one another [Helfman, 1986 #872]. By exploiting diel variations in the availability of prey and their vulnerability to predation, animals maximize their energy return and minimize the time spent foraging [Hart, 1986 #854]. We expect catchability to increase for species when baited hooks are available at peak feeding times.

Evidence: [Helfman, 1978 #873] shows that most fish species forage primarily during the day or during the night. Few are active during crepuscular periods; and those that are active then are often large-mouthed, generalist predators. Dietary studies (e.g., [Galkov, 1984 #874]) and the analyses of fine-scale longline data (e.g., [Ward, 2004 #451] indicate that large pelagic predators, such as the marlin and large tunas considered in our study, are large-mouthed, generalist predators that are especially active during crepuscular periods.

[Ward, 2004 #451] used random effects models to analyze observer records of longline catches in relation to the periods when hooks were available. Their estimates for Japan's longliners that deployed during the day to target yellowfin tuna in the South Pacific Ocean show that hooks available at dusk had particularly high catch rates of bigeye tuna, yellowfin tuna and blue marlin. Those available at dawn also produced elevated catch rates of blue marlin. By contrast, skipjack tuna catch rates were highest outside those periods. Dawn or dusk did not strongly affect catch rates of mako shark.

Historical trend: The number of hooks deployed each day by Japan's distant-water longliners has steadily increased over time [Polacheck, 1991 #804]. This has resulted in relatively fewer longline baits being available at dawn and more available at dusk (Table 5).

Estimation: For each species we used the model of [Ward, 2004 #451] to predict the catch rates for the exposure of hooks to dawn and dusk in each period (Table 5). We estimated the change in catchability as the catch rate predicted for the proportions of hooks available at dawn and at dusk in the 1950s divided by the catch rate predicted for the 1990s.

Reliability: While we expect elevated catch rates during periods of peak feeding activity, it is possible for competition from natural prey might reduce the catchability of longlines. (Bertrand et al., 2002), for example, found that longline catch rates of albacore tuna and bigeye tuna were highest where prey were not distributed in dense patches.

Availability of baited hooks

Bait loss (B.1)

Mechanism: A hook must almost always have a bait attached to attract and catch an animal. In addition to being removed by other animals, baits may fall off hooks during the operation, e.g., unskilled crewmembers might incorrectly attach the bait to the hook or wave action may shake it loose.

Evidence: (Shomura, 1955) observed that fewer baits were retrieved on longline hooks with longer soak times. However, we could find no other published study of bait loss rates in pelagic longline fisheries. This is surprising given that fishers know that the availability of baits will have a direct bearing on their financial returns.

Target species, like large tunas, have been reported to steal baits from longlines, e.g., (Shomura, 1955) reports that 14% of the stomachs of 695 large tunas examined contained one bait and 2% contained two baits. In one case, a yellowfin tuna stomach contained nine baits. (Shomura, 1955) believed that the bait was normally lost (ejected by the tuna) at the time of hooking.

Historical trend: (Shomura, 1955) presents data that indicate bait loss rates of 44% over soak times of 1.5 to 5.5 hours. Soak time has declined. In addition to soak time, many variables are likely to affect bait loss rates, e.g., sea conditions, bait type, bait quality and the activities of marine life.

Estimation:

Reliability:

Gear saturation (B.2)

Mechanism: When an animal encounters a longline hook, the hook may be unavailable if it already holds another animal [Rothschild, 1967 #270]. Occupied hooks have zero catchability. The tendency toward underestimation of abundance as a result of gear saturation will be greatest when catch rates are high [Rothschild, 1967 #270].

Evidence: (Rothschild, 1967) recognized that the local abundance of target species and competitors for bait could affect longline catch rates. He developed a stochastic model to adjust catch rates for the effects of gear saturation or “exploitive competition”.

Historical trend: Gear saturation is more likely to have occurred in the 1950s because abundance was higher then than in the 1990s (Ward and Myers, in press-c). In the study area during the 1950s, Japan's longliners averaged an estimated 61 animals per 1000 hooks compared to 22 per 1000 hooks in the 1990s (Table 10).

Estimation: For each period we used the formula developed by [Rothschild, 1967 #270] to estimate the catch rate U_{0i} of each species i in the absence of all other species:

$$U_{0i} = 1 - Q_0^{\frac{Q_i}{1-Q_0}}$$

where Q_0 is the proportion of hooks that were vacant at the time of longline retrieval and Q_i is the proportion of hooks occupied by species i. For each period we then estimated relative catchability q:

$$q_i = \frac{Q_i}{U_{0i}}$$

and estimated the change in catchability Δq for each species between periods due to saturation as:

$$\Delta q = \frac{q_{i,1990}}{q_{i,1950}}$$

where $q_{i,1950}$ is the species’ relative catchability in the 1950s and $q_{i,1990}$ is its relative catchability in the 1990s.

We estimated the proportion of vacant and occupied hooks from catch and effort data reported by Japan's longliners during 1952–55 and 1995–99 in the study area (Table 10). Both datasets were provided as monthly summaries for each 5° latitude by 5° longitude square. For each species we derived the proportion of occupied hooks from the mean catch rate over all month–5° cells. The proportion of vacant hooks Q_0 was derived from the mean catch rate of all species over all cells.

The 1950s data were available for nine species of tunas and billfishes, but they did not include sharks and other non-commercial species. Therefore we divided the total catch by 0.67, which was proportion of tunas and billfishes in the total number of animals reported by the 1950s POFI survey in the tropical Pacific Ocean [Ward, in press #628].

To estimate catches of mako shark, which were not reported by Japan's longliners, we applied the proportion of mako shark in the POFI survey (0.004) to the total number of all species estimated for each cell.

The 1990s data included the number of each species of marlin, swordfish, and large tuna. It included a category for all other species combined, but we considered the other species data to be unreliable. Therefore we estimated the other species catch as the marlin, swordfish, and tuna catch divided by 0.75, which was the proportion of those species reported from four longline surveys in the tropical Pacific Ocean during the 1990s [Nakano, 1997 #539]. To estimate catches of skipjack tuna and mako shark, which were not reported by Japan's longliners, we applied the proportion of skipjack tuna (0.035) and the proportion of mako shark (0.009) in Nakano’s surveys to the total number of all species estimated for each cell.

Reliability: Our estimates do not include hooks that were occupied by an animal that escaped or was removed before the longline was retrieved. The proportion of occupied hooks may have been underestimated in the 1990s because three of the four 1990s surveys reported few or no teleosts. It is unclear whether those surveys did not catch those species or whether they were not recorded for some reason.

Hook design

Mechanism: Pelagic longliners have switched to “circle” hooks (ref?) that improve hooking efficiency by channeling the force applied by the animal in the direction of the hook’s eye. Consequently, circle hooks often attach to the corner of the jaw whereas the traditional “J” hook design sometimes attach to soft tissue that can tear loose Cooke. A hook that sets in soft tissue may tear free when under pressure. The introduction of circle hooks in the 1970s reduced losses by hooking through the animal’s jaw.

Evidence: Prince report catch rates of blue marlin on recreational trolling of 0.174 for circle hooks compared to 0.167 for “J” hooks. Those differences were not, however, statistically significant (we think, because of the high variability in catch rates and the model used). Circle hook catch rates of sailfish were significantly higher than those for “J” hooks. Falterman and Graves (2002) compared circle hook and J hook hooking efficiency in pelagic longline fisheries. Catch rates were higher using circle hooks, both for target species (yellowfin tuna) and bycatch (15 other species).

Historical trend: “J” hooks were used in all operation in the 1950s, whereas observers report that about ?% of the hooks deployed off eastern Australia were “circle” hooks (ref?). We applied that percentage to the ratio of catch rates reported for blue marlin by Prince and yellowfin tuna, ? reported by Falterman and Graves (2002).

Estimation:

Reliability: The size of hooks used by Japan's longlines has also declined, from size ? in the 1950s to ? in the 1990s. This should not affect the size range of tunas and billfishes, since those species have a relatively narrow maxillae.

Detection of baits

Bait appeal (C.1)

Mechanism: Chemical attractants will be leached from baits over time. The appearance of baits will deteriorate with soak time. Scavengers will consume or remove baits with soak time.

Evidence: Bait qualities are important for demersal species - bait species and even the source of the bait (e.g., herring or salmon from different locations) and condition of the bait.

Historical trend: Some authors (e.g., [Polacheck, 1991 #804] surmise that the historical increase in the number of hooks per operation has resulted in increased soak time. [Ward, 2002 #871], however, shows that increased deployment and retrieval speeds accompanied the increased number of hooks. Consequently, the mean soak time declined, from 11.5 hours in the 1950s to 10.0 hours in the 1990s [Ward, 2002 #871].

Experiments have shown that dying baits certain colors increases catchability and observers report some longliners using blue-green dyed baits to increase swordfish catch rates (J. Hender, pers. comm.). They also report the use of “slammers”; foam soaked in fish oil placed above the hook to attract marine life and target species.

Estimation:

Reliability:

Other animals associated with bait (C.2)

Mechanism: The presence of competitors for baits does not always have a negative affect on catchability. Animals will more easily detect, and be attracted to, the activities of other marine life around a bait [Blaxter, 1980 #887].

Evidence: Fluorescent artificial bait produced elevated catch rates on demersal longlines [Yamaguchi, 1983 #281]. (Stoner, 2004) lists several studies that found increased attack rates by demersal species in the presence of conspecifics and other competitors. Lightsticks are chemically luminescent cylinders attached to longline branchlines several meters above the hook. They attract small marine animals to the branchline, which in turn attract larger predators (Gaw and Flanagan, 1997).

Historical trend: Japan’s longliners have not routinely used lightsticks in the study area. Since the late 1980s, however, they have used fluorescent beads and chafe tubes (senior author’s pers. obs.), which may attract other marine life to the longline and target species. Australian longliners are also known to use battery-operated lights to their branchlines. Australian longliners are also known to use battery-operated lights to their branchlines.

Estimation: Using a mixed effects model on 88 000 logbook(?) records for US longliners targeting swordfish in the north-western Atlantic Ocean, we estimated that lightsticks increased swordfish catchability by a factor of 3.52. Deploying longlines with fluorescent beads may have improved catch rates in our study area in the 1990s, especially at deep depths and after dusk. However, we do not expect as strong an effect as that demonstrated for lightsticks.

We have no information on historical variations in the density of animals associated with longlines, but note that the abundance of large pelagic predators declined significantly between periods.

Reliability:

Attraction to baits

Feeding motivation (E.2)

Mechanism: Hunger – more formerly the need to supply energy to support activities – is a major motivation driving animals to feed. A satiated animal will be less likely to attack a bait.

Evidence: Feeding history can affect level of satiation (obviously) and willingness to search & locate, but also search image. A large animal will require a greater mass of food than a small animal of the same species. However, small animals require relatively more food when the daily ration is expressed in terms of body-size because of size-related requirements, such as growth and drag.

Historical trend:

Estimation: Ration and growth rates of pelagic predators should increase in proportion to $W^{0.8}$ [Ware, 1978 #888]. [Stillwell, 1982 #889] estimated that the daily food ration for mako shark was about 27.9 g kg^{-1} d^{-1} for routine metabolism. To compensate for energy expended during active metabolism (e.g., foraging, migration), food consumption would increase by at least 25–50%, 3.47–4.27% of body weight per day. We used the mid point of that range (3.88%). We used estimates of daily ration presented by [Menard, 2000 #943] for skipjack tuna, bigeye tuna, and large (>90 cm) yellowfin tuna from free-swimming schools. For blue marlin we used?

We applied those estimates to estimated weights by number for the 1950s and 1990s (Ward and Myers, in press-c), and then averaged them.

Reliability: If the removal of large pelagic predators (Ward and Myers, in press-c) has resulted in increased availability of food, then remaining animals might be less attracted to longline baits.

Competition between gears (E.3)

Distance between hooks (A.4)

Mechanism: In using the number of hooks as the measure of fishing effort for the catch equation it is assumed that the catchability of each hook is not affected by other hooks. However, hooks will begin to compete for the same animal as hook density increases. Hook density may vary as a result of: (1) changes in the spacing between hooks [Skud, 1978 #271]; (2) the number of hooks deployed on each longline [Polacheck, 1991 #804]; or (3) the number of longlines in the area [Hilborn, 1987 #325]. The catchability of each hook will decline as the density of competing baits increases.

Evidence:

Historical trend: The spacing of branchlines along longlines declined over the study period. We estimated a mean distance between branchlines of 45.4 m (SD $\underline{+}$4.5 m) from the longline dimensions of 25 longliners in the study area in 1950 [Shimada, 1951 #330]. Longline dimensions reported by observers on 38 longliners in the study area (P. Williams, pers. comm.) indicate a mean spacing of 38.3 m (SD ±15.6 m) during 1994–2003. These estimates do not account for changes in the distance between hooks resulting from the lengthening of longlines to access deeper waters. However, we found that the effect of deeper longlines on hook spacing was largely offset by the shorter branchlines (24 m on average) used in the 1990s compared to 30 m in the 1950s.

Reliability:

Number of hooks deployed (A.5)

Mechanism:

Evidence: [Campbell, 1994 #909] found no effect for southern bluefin tuna. [Polacheck, 1991 #804] analyzed operation-level data from longliners in the tropical western Pacific Ocean to investigate the effect on catch rates of the number of hooks deployed per operation. He found no statistically significant affect of hooks per operation on catch rates of bigeye tuna or yellowfin tuna. It is noteworthy, however, that Polacheck's analysis did not take into account variables, such as area, season, and longline depth, that often affect longline catch rates.

Competition between longliners (A.6)

Evidence: [Campbell, 1994 #909] suggested that the positive effect of vessel concentrating on areas of high southern bluefin tuna abundance almost always outweighed any negative effect stemming from competition among vessels.

(3) Historical trend: The number of hooks deployed in the study area has increased more than tenfold, from an average of 21 million hooks per year in the 1950s (Z. Suzuki, unpublished data) to 270 million in the 1990s [OFP, 2004 #880].

Estimation:

(3) Reliability: Purse seiners, which commenced fishing in the region in the late 1960s, now take large amounts of small skipjack tuna (~586 000 t per year in the 1990s), about 176 000 t per year of a wide size range of yellowfin tuna (95% between ? and ? kg, cf. ?–? kg for yellowfin tuna) and lesser amounts of small bigeye tuna (95% between ? and ? kg) [OFP, 2004 #880]. Pole-and-line fishing vessels have fished with love-bait for skipjack tuna and yellowfin tuna in the region over the same period as longliners. However, we do not expect pole-and-line activities to strongly affect the availability of those species to longline because they select smaller animals.

Detection of gear (E.4)

Mechanism: Animals may avoid baits that present unnatural visual cues (), such as a visible hook or branchline. During the 1980s many longliners adopted monofilament branchlines and mainlines that are less visible to target species (Stone and Dixon, 2001).

Evidence: [Stone, 2001 #732] deployed longlines with alternate mono- and multifilament branchlines in ten operations each consisting of about 1440 hooks. For each species, catch rates on monofilament were considerably higher than those on multifilament (Table ?). For all species combined, monofilament catch rates were double those of multifilament.

Experiments by [Cui, 1991 #922] demonstrated that mackerel (*Scomber scomberus*) were better able to detect multifilament nylon than multifilament. Experiments by [Cui, 1991 #922] demonstrated that mackerel (*Scomber scomberus*) were better able to detect multifilament nylon than multifilament. Including colored dyes in the monofilament make the line more or less invisible to human observer [Wardle, 1991 #923].

Historical trend: In the 1950s Japan's longliners used branchlines made of tar-coated rope (cotton, hemp or Manila) or cotton thread wound around a core of wire or fiber, attached to a wire leader [Shimada, 1951 #330]. Off eastern Australia in the 1990s, by contrast, 85% of their branchlines were monofilament teteron or nylon with the remainder braided nylon cord or kuralon. The branchlines are thinner (2–4 mm), but stronger (>300 kg; POP) than the 1950s rope gear (5–7 mm, ? kg), and are transparent or dyed certain colors to reduce their visibility to target species (gillnet ref?).

Estimation: [Stone, 2001 #732] provide a reliable estimate for the effect of monofilament on mako shark catch rates (). They did not estimate an effect for bigeye tuna, skipjack tuna, or blue marlin. Adult bigeye tuna inhabit a similar ecological niche to swordfish so we used Stone and Dixon’s swordfish estimate for bigeye tuna; and, for similar reasons, we used their white marlin estimate for blue marlin. We used Stone and Dixon’s estimate for all species combined (2.00) for skipjack tuna. Although their estimate for yellowfin tuna (9.00) is statistically significant, we considered it to be an aberration related to the small number caught. Therefore we also used 2.00 for yellowfin tuna. We applied those estimates to the proportion of monofilament branchlines in the tropical Pacific in the 1950s (0%; [Shapiro, 1950 #329; Shimada, 1951 #330] and in the tropical Indian Ocean in the 1990s (~90%; [Okamoto, 2004 #920].

Reliability: Stone and Dixon’s results are not strictly applicable to Japanese operations in the study area. For example, they deployed shallow longlines at nighttime in temperate waters of the north-western Atlantic. We believe that their results significantly underestimate the improvements to catch rates provided by nylon branchlines. The tar-coated, rope branchlines used in the 1950s would be much more visible than the monofilament and multifilament nylon branchlines deployed by Stone and Dixon. Furthermore, both their gear configurations used a 3.6 m monofilament leader, whereas the Japanese used wire leaders on all branchlines in the 1950s [Shimada, 1951 #330] and on 31% of branchlines in the 1990s. The wire leaders used in the 1950s would be much more visible than the monofilament leaders attached to Stone and Dixon’s multifilament branchlines.

Hooking

Taste (F.1)

Mechanism: Animals will reject baits that have an unattractive taste. Longliners have developed baits that are attractive, easy to store and handle, readily available, cost-effective.

Evidence: An experiment by a Japanese research vessel suggested no differences in catch rates of tunas and billfishes for frozen saury (*Colalabis* saira) and salted sardine (*Sardina maelanostica*) baits [Anonymous, 1952 #931]. [Murphy, 1954 #516], in an analysis of 1950s Japanese mothership catch rates, also concluded that there was no difference in catch rates between those baits for bigeye tuna and yellowfin tuna. In an analysis of 1950s POFI survey data, however, [Shomura, 1955 #277] concluded that sardine and herring produced higher catch rates of yellowfin tuna and probably bigeye tuna and skipjack tuna than those produced by squid (*Loligo opalescens*). he attributed the different catch rates to high loss rates of squid over time, especially in rough seas. More recently, [Bach, 2000 #810] investigated various combinations of small, medium, and large-sized herring, sardines, and squids (*Loligo sloani* and small *Illes* sp.) in longline operations with average soak times varying from 7.9 to 10.3 hours. They found no significant difference between tuna hooking success among the different bait types.

Historical trend: Japan's longliners used a combination of saury and sardine as bait in the 1950s [Murphy, 1954 #516], but in the 1990s they used saury exclusively (ref?). [Murphy, 1954 #516] presents nominal catch rates of bigeye tuna and yellowfin tuna for a range of bait combinations.

Estimation:

Reliability:

Size of bait and hook (F.3)

Mechanism: There is a range of species-specific preferences for bait size [Hart, 1986 #854]. A small animal will be unable to swallow a large bait or hook [Karpouzi, 2003 #898]. Prey are usually 7% of the predator’s length, however, the size range of prey is related to the body-size of predators (large fish have a wider range, since they also feed on very small prey).

(a) The use of smaller hooks and baits has extended the gear’s size selectivity. (b) The selective removal of large animals (Ward and Myers, in press-c) has increased the relative abundance of small animals.

Evidence: There may be a relationship between body size and optimal prey size [Løkkeborg, 1994 #200]. Observations reveal that a wide size range of haddock preferred smaller baits, whereas small bait size resulted in increased catch rates of small cod [Løkkeborg, 1994 #200].

Historical trend:

Estimation:

Reliability:

Landing

Abrasion by teeth or rostrum (G.1)

Mechanism: Animals with sharp teeth or rostrums are more likely to escape by cutting through the leader. Reduced usage of wire leaders has increased losses through line cutting.

Evidence: Longline fishers and observers report that branchlines are often severed by sharks after they have been hooked. ? reports that the stomachs of ? sharks caught on longlines often contained longline baits or had hooks embedded in their jaws. The loss of branchlines to sharks is expensive because of the cost of the fishing gear (~USD150 per operation), the loss of a valuable bycatch (shark carcasses and fins), and reductions in the number of baited hooks available to catch target species. Many longline fishers believe that reducing the local abundance of sharks will lessen shark-damage of their catch and competition for longline baits.

Historical trend: Using the same gear as the Japanese in the 1950s, the POFI survey reported a loss rate of 1% of 65 417 branchlines. Discussions with various Australian observers and longline fishers indicated that 2–3% of monofilament branchlines are severed when longlines are retrieved.

Estimation: We estimated the number of mako shark U_i per 1000 hooks that would have bitten through monofilament leaders and escaped in each period *i*:

$$U_i = \frac{C_i + S_i B_i f_i}{f_i}$$

where B_i is the branchline loss rate, S_i is the proportion of mako shark in the total shark catch, and f_i is the number of hooks deployed by Japan's longliners in each period (Table ?). We use the same catch and effort for both periods so that variations in abundance do not affect our estimate of change in catchability. The change in catchability Δq is then:

$$\Delta q = \frac{U_{1990}}{U_{1950}}$$

Reliability: Branchline loss rates are likely to depend on the use of wire leaders to attach longline hooks to each branchline. The Japanese used wire leaders on all branchlines in the 1950s [Shimada, 1951 #330]. By contrast, observers reported that in the 1990s the Japanese attached wire leaders to the four shallowest branchlines between each float to reduce gear lose while maximizing catch rates of target tunas. Therefore the monofilament branchline loss rate that we used may be too high. If we use a loss rate of 2.0% instead of 2.5% the change in catchability is reduced to ?

Branchline loss rates might be underestimated because shark damage rates are often higher in our study area than off eastern Australia. More reliable estimates of branchline loss rates could easily be obtained by counting the number of missing branchlines at the completion of longline retrieval. The loss rates might be correlated with shark abundance, e.g., on one trip an observer, J. Hender (pers. comm.), reported that for each shark caught on a monofilament leader, an equivalent number of branchlines are missing when the longline is retrieved. Variations in branchline loss rates will have a significant effect on catchability, e.g., a 1% loss rate results in a 0.83 change in catchability compared to 0.88 for a 5% loss rate.

We assume that the switch to monofilament did not affect the loss rates of tunas and blue marlin. However, wire leaders are less likely to be severed by those species, so that the tendency towards monofilament would have reduced their catchability by a small, amount that we were unable to quantify.

We assume that the loss rate of mako shark is equal to their share of the shark catch.

We are using catch rates as an index of abundance, however abundance (and change in catchability) will be overestimated if mako sharks sever and escape, then return to attack another hook

Removal by scavengers (G.3)

Mechanism: Longline loss rates will be influenced by variations in the density and activity levels of scavenger, such as sharks and killer whales.

Evidence: Blue? and mako? sharks are believed to be responsible for most of the removals of animals caught on longlines [Hirayama, 1976 #510].

Historical trend: The removal of large sharks by fishing (Ward and Myers, in press-c) probably reduced losses to scavengers by the 1990s.

Estimation: We derived the proportion of each species damaged from Australian observer data for the 1990s D_{1990s} and from the POFI survey for the 1950s D_{1950s} (Table 9). For each species, we estimated the change in catchability Δq between periods due to removals by scavengers as:

$$\Delta q = \frac{(1 + D_{1990s})}{(1 + D_{1950s})}$$

One is added to the damage rate because this is the quantity that catches should be raised by to obtain an estimate of the total number of animals actually hooked.

Reliability: We assume that shark damage rates are directly proportional to removals of hooked animals. However, [Ward, 2004 #451] hypothesized that small species, like skipjack tuna, were completely removed by large predators so that severed branchlines are the only evidence of removals.

Our estimates may be unreliable for mako sharks because of small sample sizes (34 checked for damage in the 1950s and 122 checked in the 1990s).

A global study by [Hirayama, 1976 #510] on research longlines during 1954–69 shows considerable geographical variation in shark-damage rates of tunas. The highest damage rates were in the central (10%) and eastern tropical Pacific Ocean (14%). Those rates are lower than the rates we estimated for yellowfin tuna (17%) and bigeye tuna (21%), but may reflect a reduction in the abundance of large sharks over their 14 year study period.

Shark catch rates tend to be highest on shallow hooks, e.g., Australian observer data show that Japan's longliners typically used wire leaders for the four shallowest hooks between each float to reduce gear loss to sharks. Therefore we may have overestimated damage rates for 1990s operations that used deeper longlines (50–250 m?) compared to the 1950s (26–200 m). The trend to deeper longlines would therefore result in an underestimation of increases in catchability. Other fleets deploy much deeper longlines that are predicted to have lower damage rates, e.g., in the 1990s the Hawaii fleet deployed longlines that ranged down to 600 m to catch tunas.

Anecdotal reports from observers and fishers indicate that shark-damage is more prevalent at night (use data to check this). More longline hooks were available at night in the 1990s, which would have added to the underestimation of historical increases in catchability.

Fishers report that marine mammals, such as false killer whale (*Pseudorca crassidens*), have damaged many animals hooked on longlines (ref?) in recent years. Data presented by Hirayama? indicate that marine mammal-damage is temporally and geographically patchy. Those damage rates are claimed to have increased in recent years.

Discussion and conclusions

Potentially important factors not estimated (turn into a table?)

Catchability may well vary with other factors, but there was insufficient reason to believe that those factors changed over our study period. For example, turbidity may affect an animal's ability to detect a baited hook. However, we did not estimate the change in catchability linked to turbidity because there is no evidence that turbidity varied between the 1950s and 1990s.

Population density and distribution (A.1)

The active space for foraging is determined by the release rate of bait odour, its spatial dispersal, and the animal's response threshold, which may vary with the situation, e.g., satiation [Løkkeborg, 1994 #200]. Vision may be more important in alerting animals to baited hooks, e.g., yellowfin tuna [Atema, 1980 #821; Sivasubramaniam, 1961 #251]. Decreased abundance may be reflected in smaller than average school sizes, a greater distance between schools or a reduction in the total area inhabited by the stock ("range contraction") [Paloheimo, 1964 #742; MacCall, 1990 #341]. Skipjack tuna form schools throughout most of their juvenile and sub adult lives, whereas bigeye tuna and yellowfin tuna tend to school until just above the size at which they are vulnerable to longline fishing gear (>15 kg?). Blue marlin and mako shark are not known to school. Nevertheless, yellowfin tuna [Murphy, 1954 #265] and bigeye tuna are often landed in clumps along the longline, suggesting some level of schooling or aggregation.

Weather

Fishers report that catch rates often improve in rough weather, perhaps because it introduces a jigging motion to baits that attracts predators. Improvements in vessel design, hauling equipment and skill levels now allow longliners to operate in rough weather, resulting in an increase in catchability that we have not quantified.

Movement of bait

Animals will avoid baits that move unnaturally in the water column. The introduction of swivels has reduced the unnatural movement of baits (Bjordal, 1983). Japan's longliners were using swivels on their branchlines as early as 1950 [Shapiro, 1950 #329]. On the other hand, moving baits are more likely to attract visual predators [Shomura, 1955 #277]. Improvements in vessel design, hauling equipment and skill levels now allow longliners to operate in rough weather, that results in a jigging motion to baits.

Other animals associated with bait

Animals will more easily detect, and be attracted to, the activities of other marine life around bait. The use of fluorescent beads and chafe tubes attached to longlines since the late 1980s has probably increased catchability.

Hook sharpness

Sharp hooks are more likely to penetrate flesh and bony structures. The iron hooks used until the early 1980s are more likely to become blunt or to break than the galvanized hooks used in the 1990s.

Drop-off

Animals are more likely to fall off the hook as a result of violent movements of the longline. Improvements in skill levels and more flexible gear have probably reduced the frequency of such losses. Nylon is much more elastic than kuralon, resulting in reduced losses through snapped branchlines, bent hooks and hooks torn loose. Furthermore, Australian observers report the use of small (~300 mm) plastic floats in the 1990s that allow more vertical movement than the large glass floats deployed in the 1950s. On the other hand, longliners do not tend to “patrol the line” like they sometimes did in the 1950s [Shimada, 1951 #330], landing some animals soon after they were hooked and then redeploying the baited hook.

Strength and elasticity of gear

Weak or inflexible branchlines will result in animals breaking the line and escaping. The introduction of monofilament and smaller floats has provided longlines with more elasticity. The durability of branchlines has been improved by the introduction of monofilament, brass swivels and stainless steel hooks. Furthermore, the selective removal of large animals would have also contributed to reduced losses through line breakage.

Skill of crewmembers

Careful retrieval of large and powerful animals will reduce losses. Crewmember skill levels have improved.

Bait shyness

An animal that survives hooking will remember to avoid longlines in future. Encounters with longlines have increased over time. [García, 1974 #885] established a mechanism in vertebrates where the last food item consumed prior to sickness is subsequently avoided. “Conditioning”, involving chemical senses, has been demonstrated in a variety of marine species, e.g., in Atlantic cod (*Gadus morhua*) [Mackay, 1977 #886]. We were unable to determine whether pelagic fish exhibit a similar response to stress or injury associated with escaping from a longline hook.

Interference competition

In addition to gear saturation, interference competition may occur where animals actively prevent access to baits (Stoner, 2004). Intra- and interspecific competition may occur among animals attracted to a bait. For example, large cod frighten small cod away from baited hooks. Torsk (*Brosme brosme*) have been observed to chase smaller fish from baited hooks [Løkkeborg, 1992 #792].

The presence of the animal’s predators is another form of interference competition; an animal that is actively involved in predator avoidance is less likely to attack baits. [Werner, 1983 #620], for example, found that relative predation risk was an important factor in the selection of feeding habitats by bluegill sunfish (*Lepomis macrochirus*).

Social facilitation may sometimes be important in both demersal and pelagic fishes - enhancing catchability in some species.

Small size classes of several species are noticeably absent in the size data of longline catches in the early 1950s. Those smaller animals would undoubtedly have been present in the early 1950s, so their absence in longline in those years might be due to interference by large pelagic predators.

"Natural" selection

Fishing selects animals with adaptations for avoiding capture. Heavy exploitation has removed animals that are vulnerable to the gear.

Hook sharpness (F.2)

Japan's longliners used iron hooks in the 1950s [Shapiro, 1950 #329] that are more likely to become blunt or to break than stainless steel hooks since the 1980s (ref?)], whereas stainless-steel or hi-carbon steel hooks with special coatings (e.g., duratone) are used these days Also, in the 1950s they used wire that rusted [Shapiro, 1950 #329], whereas stainless-steel wire has been used since the 1980s.

Other stuff

The estimate of change in overall catchability becomes more stable with the number of factors estimated. So these estimates are quite robust, provided that the factors are accurately estimated and the factors that are estimated are the important ones.

Several factors relating to loss do not take into account the ability of animals to steal baits or escape from the longline, then have an opportunity to attack another bait. After all, we are adjusting catch rates for changes in catchability to obtain a precise estimate of abundance. An animal repeatedly attacking a bait will result in an inflatable estimate of abundance. Therefore the estimation of the frequency and species involved in attacks is a high priority area of future research.

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References

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Table 1. Species selected for historical comparisons of longline catchability. Size ranges are from the 1950s survey and 1990s Hawaii longline data analyzed by [Ward, 2005 #628]. The indication of longline catchability is based on the species' habitat and proportion of the population likely to be vulnerable to longline fishing gear. Trophic positions are Ecosim model estimates reported by [Kitchell, 2002 #940]. Epipelagic species inhabit the surface waters of the open ocean. Some epipelagic species, like mako shark, occasionally move below the thermocline (about 175 m in the tropical Pacific Ocean). Mesopelagic species live at deeper depths, although some, like bigeye tuna, regularly migrate into shallower waters.

Common name	Latin binomial	Longline target	Trophic position	Habitat	Longline catchability	Longline size range (kg)
Short-finned mako shark	*Isurus oxyrinchus*	no	[a]4.6	epipelagic	high	4–164
Blue marlin	*Makaira nigricans*	no	4.6	epipelagic	high	6–274
Bigeye tuna	*Thunnus obesus*	yes	4.0	mesopelagic	high	4–153
Yellowfin tuna	*Thunnus albacares*	yes	4.0	epipelagic	medium	6–90
Skipjack tuna	*Katsuwonus pelamis*	no	3.9	epipelagic	low	2–24

[a] Using stable isotope analysis, [Estrada, 2003 #938] estimated a trophic position of 4.0 for mako shark.

Table 2. Factors likely to have resulted in historical variations in catchability in pelagic longline fisheries. Estimates of changes in catchability are for the Japan's distant-water longliners in the central tropical Pacific Ocean. They are the ratio of relative catchability in the 1990s to that in the 1950s. A value greater than one indicates that a unit of fishing effort will catch a larger proportion of the species in the 1990s than in the 1950s; a value less than one indicates a smaller proportion in the 1990s.

Factor		Mechanism	Estimation	Estimated change in catchability				
				mako shark	blue marlin	bigeye tuna	yellowfin tuna	skipjack tuna
A. Area of action and abundance								
	2. Animal's movement patterns	Smaller fish have lower swimming speeds, resulting in reduced encounters with baits.	Body-size – swimming speed relationships applied to size composition data from each period.	0.59	0.49	0.64	0.58	0.83
	3. Depth of gear	Deeper longlines access the full vertical range of many species.	Daytime depth-dependent catchability applied to the depth distribution of hooks in each period.	0.83	0.84	1.39	1.01	0.89
	4. Location of gear	Catchability increases when gear deployment coincides with the animals' distribution.	Increase in catch rates required to offset the cost of electronic equipment.	1.02	1.02	1.02	1.02	1.02
	5. Time of deployment and retrieval	Catchability increases when hooks are available at peak feeding times.	Model of crepuscular effects on catchability applied to the mean exposure of longline hooks to dawn and dusk in each period.	0.91	0.54	0.95	1.06	1.04
B. Availability of baited hooks								

Factor		Mechanism	Estimation	Estimated change in catchability				
				mako shark	blue marlin	bigeye tuna	yellowfin tuna	skipjack tuna
	1. Bait loss	Baits will fall off hooks or scavengers will remove baits over time.	Bait loss – soak time relationship applied to mean longline soak time in each period.	1.00	1.00	1.00	1.00	1.00
	2. Gear saturation	Occupied hooks have zero catchability.	Stochastic model of competition for hooks applied to proportion of vacant hooks and catch rates of each species in each period.	1.03	1.02	1.01	1.01	1.02
C. Detection of baits								
	1. Bait appeal	Chemical attractants will be leached from baits or the visual appearance of baits will deteriorate with time.	Catch rate – soak time relationship applied to mean longline soak time in each period. NB These estimates also include an element of Drop-off (G.4) and Removals (G.5).	0.96	1.05	0.91	1.00	1.04
E. Attraction to baits								
	1. Movement of bait *check swivel paper	Animals will avoid baits that move unnaturally in the water column.	The introduction of swivels has probably reduced line tangling and the unnatural movement of baits.	1.00	1.00	1.00	1.00	1.00
	2. Feeding motivation	Catchability increases with body size because size determines the animal's minimum daily ration.	Size-dependent daily ration applied to body-size data from each period.	0.54	0.42	0.60	0.55	0.80

Factor		Mechanism	Estimation	Estimated change in catchability				
				mako shark	blue marlin	bigeye tuna	yellowfin tuna	skipjack tuna
	3. Competition between gears	Catchability of each bait decreases as the density of competing baits increases.	Estimates of the spacing of branchlines indicate that the density of longline hooks has not changed.	1.00	1.00	1.00	1.00	1.00
	4. Detection of gear	Animals will avoid baits that have unnatural visual cues.	Estimates of the effect of branchline material on catchability applied to the proportion of those materials deployed in each period.	1.34	1.80	1.83	1.80	1.80
F. Hooking								
	1. Taste	Animals will reject baits that have an unattractive taste.	Bait – catch rate relationships applied to the mix of baits used in each period.	1.00	1.00	1.00	1.00	1.00
	3. Size of bait and hook	A small animal will be unable to swallow a large bait or hook.	Body-size – gape relationships related to differences in hook sizes between the periods.	1.00	1.00	1.00	1.00	1.00
G. Landing								
	1. Abrasion by teeth or rostrum	Animals with sharp teeth or rostrums are more likely to escape by cutting through the leader.	Branchline loss rates pro rated by species composition and applied to the proportion of wire leaders in each period.	1.00	1.00	1.00	1.00	1.00
	3. Removal by scavengers	Longline loss rates will be influenced by scavenger densities and activity.	Ratio of species-specific shark-damage rates for each period.	0.95	0.86	0.92	0.92	1.03

Factor		Mechanism	Estimation	Estimated change in catchability				
				mako shark	blue marlin	bigeye tuna	yellowfin tuna	skipjack tuna
	4. Animal’s strength	Large, powerful animals are more likely to escape by breaking the branchline or bending the hook.	Body-size – power relationships applied to size composition and line breaking strength data for each period.	1.00	1.00	1.00	1.00	1.00
			Product	0.31	0.16	0.79	0.59	1.24
			Mean	0.95	0.94	1.02	1.00	1.03
				🟩	yet to be estimated			

Table 3. Longline dimensions used to estimate the depths of each hook. Dimensions for the 1950s are from [Shapiro, 1950 #329] and [Shimada, 1951 #330]. For the 1990s, dimensions are means derived from 721 day-operations during 1994–2003 (P. Williams (pers. comm.). are these distant-water operations?

Period	1950s	1990s
Number of hooks between floats	6	18
Floatline length (m)	20.0	21.7
Branchline length (m)	30.0	24.1
Length of mainline between floats (m)	280	726
Distance between floats (m)	180	502

Table 4. Coefficients used to estimate changes in catchability with depth (standard errors in parentheses). [Ward, in press #861] estimated the parameters from four longline datasets.

Common name	Number modeled	Coefficient[a]			
		α	γ_1	γ_2	γ_3
Short-finned mako shark	665	–6.14	–9.11	26.32	–22.57
		(0.18)	(2.33)	(8.22)	(8.45)
Blue marlin	1 902	–5.81	–3.77	1.83	1.86
		(0.08)	(1.06)	(3.78)	(3.89)
Bigeye tuna	2 980	–6.44	7.83	–12.25	7.20
		(0.05)	(0.48)	(1.45)	(1.33)
Yellowfin tuna	3 131	–5.48	1.73	–6.05	5.32
		(0.04)	(0.39)	(1.35)	(1.37)
Skipjack tuna	2 771	–5.38	–0.09	–9.69	10.97
		(0.06)	(0.63)	(2.12)	(2.10)

[a] We used the coefficients to estimate the depth effect $f(D_i)$ for each species. It represents the effect of depth D on relative catch rate of hook number i:

$$f(D_i) = \exp(\alpha + \gamma_1 D_i + \gamma_2 D_i^{\ 2} + \gamma_3 D_i^{\ 3})$$

Table 5. Longline operation times used to estimate changes in catchability with the availability of baits during dawn and dusk. Also shown is the percentage of time that hooks were exposed to a dawn period (i.e., deployed before 06:30 local time) and to a dusk period (i.e., retrieved after 18:00). Estimates for 1994–2003 are means derived from 721 day-operations (standard deviation in parentheses) (P. Williams (pers. comm.). The 1950–51 times are based on [Shapiro, 1950 #329] and [Shimada, 1951 #330].

Period	Deployment time		Dawn	Retrieval time		Dusk
	start	end	(%)	start	end	(%)
1950–51	03:30	06:30	100	12:30	01:00	44
1994–2003	06:15	11:33	13	14:45	04:16	77
	(1:40)	(1:48)	(22)	(3:08)	(3:42)	(15)

Table 6. Historical changes in mean body length *L* (cm; Ward and Myers, in press-c), mean volume of water searched per second $L^{1.26}$ (cm^3; [Ware, 1978 #888], and change in relative catchability Δq based on the volume searched for five species in the study area. Standard deviations are in parentheses.

Common name	1950s			1990s			Δq
	N	L	$L^{1.26}$	N	L	$L^{1.26}$	
Mako shark	6	182	214	80	146	163	0.76
		(41)	(59)		(37)	(53)	
Blue marlin	38	213	262	421	165	189	0.72
		(22)	(31)		(22)	(29)	
Bigeye tuna	253	152	171	2652	127	136	0.80
		(22)	(31)		(22)	(29)	
Yellowfin tuna	1536	141	154	6333	113	117	0.76
		(15)	(20)		(19)	(25)	
Skipjack tuna	135	76	71	1168	70	64	0.91
		(7)	(8)		(8)	(9)	

Table 7. Historical changes in mean body size *W* (Ward and Myers, in press-c) and the mean daily ration as a proportion of body size $W^{0.8}/W$. For each species, change in

relative catchability Δq is the ratio of $W^{0.8}/W$ between periods. Standard deviations are in parentheses.

Common name	1950s			1990s			Δq
	N	W (kg)	$W^{0.8}/W$ (%)	N	W (kg)	$W^{0.8}/W$ (%)	
Mako shark	6	74	41	80	40	46	1.10
		(40)	(19)		(35)	(31)	
Blue marlin	38	100	39	421	43	46	1.20
		(67)	(21)		(24)	(19)	
Bigeye tuna	253	76	42	2652	45	46	1.10
		(28)	(13)		(20)	(17)	
Yellowfin tuna	1536	52	45	6333	28	50	1.12
		(18)	(11)		(13)	(19)	
Skipjack tuna	135	10	63	1168	8	66	1.04
		(2)	(12)		(3)	(18)	

Table 8. Performance of monofilament and multifilament branchlines (reproduced from [Stone, 2001 #732] who deployed longlines with alternate mono- and multifilament branchlines, in ten operations each consisting of about 1440 hooks). For each species, relative catchability Δq is estimated as the number caught on monofilament branchlines

divided by the number on multifilament. The P-values are for a chi-square test that [Stone, 2001 #732] used to determine whether catchability differed from the expected 1:1 ratio.

Common name	Number caught		Δq	P-value
	multi	mono		
Swordfish	128	260	2.03	0.000
Yellowfin tuna	1	9	9.00	0.011
Mako shark	39	58	1.49	0.054
Blue shark	116	225	1.94	0.000
White marlin	13	47	3.62	0.000
Dolphinfish	10	27	2.70	0.005
Stingray	31	63	2.03	0.001
Loggerhead turtle	26	40	1.54	0.085
All species	364	729	2.00	0.000

Table 9. Historical changes in shark-damage rates reported in the 1950s (POFI survey) and 1990s (Hawaii observer data) in the tropical Pacific Ocean. We derived estimates of change in relative catchability Δq by dividing 1990s shark-damage rates by those in the 1950s.

Common name	1950s			1990s			Δq
	N	damaged		N	damaged		
		(no.)	(%)		(no.)	(%)	
Mako shark	34	2	6	123	1	1	0.95
Blue marlin	247	54	22	1 246	65	5	0.86
Bigeye tuna	663	110	17	13 429	958	7	0.92
Yellowfin tuna	4 442	935	21	8 121	905	11	0.92
Skipjack tuna	285	28	10	3 866	500	13	1.03

Table 10. Estimates of the effects of gear saturation on catchability. We used the formula of [Rothschild, 1967 #270] to correct the catch rate of each species for the effects of competition for hooks by other species. We derived mean catch rates (number per 1000 hooks) from Japan's longliners in the study area during 1995–99 (1384 million hooks deployed in 6731 month – 5° cells) and 1952–55 (123 million hooks in 1850 cells),

supplemented with species composition data from [Ward, 2005 #628] and [Nakano, 1997 #539].

Common name	1950s			1990s			Δq
	mean catch rate	corrected catch rate	relative q	mean catch rate	corrected catch rate	relative q	
Mako shark	0.15	0.16	0.962	0.00	0.00	0.989	1.03
Blue marlin	4.57	4.71	0.971	0.48	0.48	0.989	1.02
Bigeye tuna	8.26	8.43	0.981	4.60	4.64	0.992	1.01
Yellowfin tuna	18.73	19.16	0.977	5.48	5.54	0.990	1.01
Skipjack tuna	0.24	0.25	0.965	0.77	0.78	0.989	1.02
All species	61.29	–	–	22.18	–	–	

Table 11. Estimates of the annual cost of electronic navigation, communication and fish-finding equipment installed on a typical Japanese longliner in the 1990s (Mr. Steve Beverley, ?). The models were those most frequently reported by observers (or equivalent) on Japan's longliners operating off eastern Australia, 1995–97. Research and installation costs are estimated as a fixed percentage (20%) of the purchase price. The cost of maintenance was estimated as 5% of the purchase price. We depreciated the purchase price, research and installation costs by 14.29% per year so that the lifetime would be seven years.

Device	Model	Purchase price (USD)	Research and installation (USD)	Depreciated cost (USD)	Annual maintenance cost (USD)	No. of units	Annual cost (USD)
Global position system	Furuno GP-70	1 795	359	308	90	2	795
Radio-direction finder	Taiyo RDF TD-L110	2 995	599	513	150	2	1 326
Radio beacons	PR-30	684	137	117	34	23	303
Echo sounder	Furuno FCV-271	2 535	507	435	127	2	1 123
Radar	JRC-JMA 527	6 950	1 390	1 191	348	2	3 078
Colour plotter	JRC-NWU-51	6 750	1 350	1 157	338	2	2 989
SST monitor	Furuno T-2000	695	139	119	35	2	308
Doppler current meter	JRC JLN-616	19 999	4 000	3 428	1 000	2	8 857
NOAA satellite receiver	JRC JCV - 26		0	0	0	2	0
High frequency radio	Simrad RS86F	2 160	432	370	108	2	957
Weather facsimile	JRC JAX-79	1 400	280	240	70	2	620
						Total	20 355

Table 12. Estimates of the additional annual catch required to meet the cost of electronic equipment (USD20 355) installed on Japan's longliners during the 1990s. Equipment costs are itemized in Table 11. Profits were estimated using the approach of [FFA, 1998 #944]; Table 13.Catch rates and mean weights are from catch and effort data for Japan's longliners in the study area, except for mako shark, which are from [Nakano, 1997 #539]; prices are from [Vannuccini, 1999 #936] for mako shark, [Uozumi, 2002 #937] for blue marlin, [FFA, 1998 #944] for bigeye tuna, yellowfin tuna, and [Sabatini, 2003 #935] for skipjack tuna; annual catches are based on catch rates multiplied by the fleet's mean number hooks per operation (2949 hooks) and the mean number of operations per year (298 operations; Reid 2003).

Common	Market	Mean		Without electronics					With electronics			
name	price	wt.		catch rate	annual catch		total value		catch rate	annual catch		total value
	(USD/kg)	(kg)		(no./1000 hks)	(no.)	(t)	(USD)		(no./1000 hks)	(no.)	(t)	(USD)
Mako shark	1.96	18.9		0.20	178	3.4	6 608		0.32	279	5.3	10 323
Blue marlin	1.89	51.9		0.48	419	21.8	41 211		0.75	655	34.0	64 377
Bigeye tuna	8.07	36.4		4.64	4 076	148.2	1 195 406		7.25	6 367	231.5	1 867 356
Yellowfin tuna	4.82	28.7		5.48	4 819	138.3	666 695		8.57	7 528	216.1	1 041 451
Skipjack tuna	1.04	6.75		0.77	680	4.6	4 751		1.21	1 062	7.2	7 421
						total	2 970 552				total	2 990 928

Table 13. Financial analysis of annual income and expenditure of a Japanese longliner during the 1990s. All estimates are based on [FFA, 1998 #944] Table 14, except for income from sale of catch, which is based on the catch rates and prices presented in our

Table 12. In the "With electronics" column, vessel maintenance includes the estimated annual cost of electronic equipment (USD20 355; Table 11).

Component			Without electronics (USD 000s)	With electronics (USD 000s)
Income				
	Sale of catch			
		Mako shark	7	10
		Blue marlin	41	64
		Bigeye tuna	1 195	1 867
		Yellowfin tuna	667	1 041
		Skipjack tuna	5	7
		total income	2 971	2 991
Expenditure				
	Variable costs			
		crew expenses	1 145	1 145
		fuel and oil	358	358
		bait	288	288
		other	132	132
		total variable costs	1 922	1 922
	Fixed costs			
		vessel maintenance	169	190
		fishing gear maintenance	83	83
		support and management	178	178
		total fixed costs	430	450
		Total costs	2 353	2 373

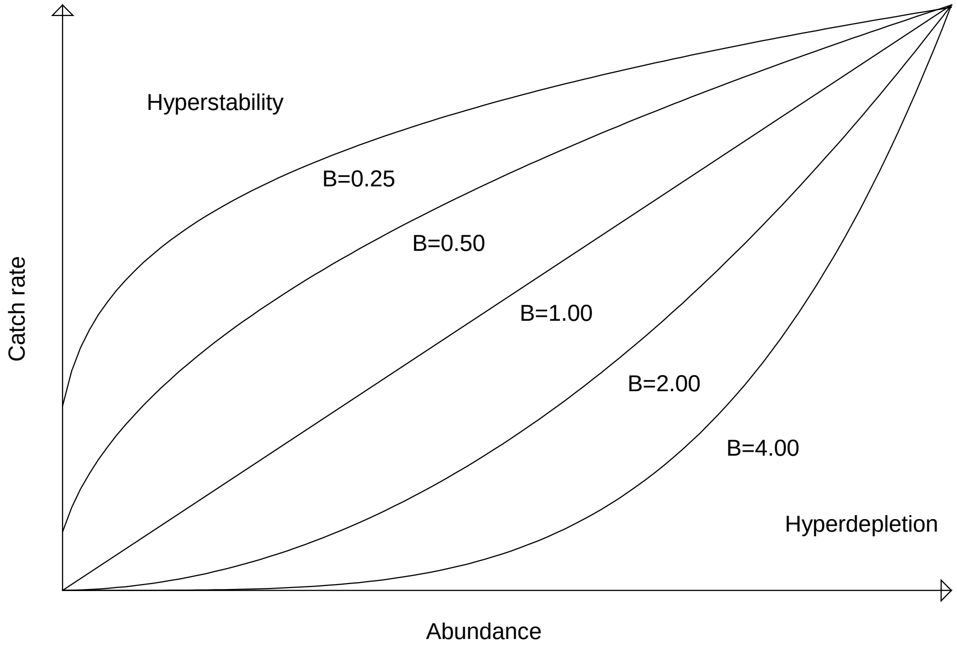
Component	Without electronics (USD 000s)	With electronics (USD 000s)
Operating profit and loss	618	618
Depreciation	400	400
Net profit	218	218
Replacement cost	5 000	5 000

Figure captions

Figure 1. Flow chart of events determining whether an animal is caught on a pelagic longline. Some factors may affect more than one step, e.g., the appearance of the bait might influence detection as well as attracting the animal.

Figure 2. Relationship between catch rates and abundance based on a power curve with various values of the shape parameter (after (Harley et al., 2001).

Figure 3. Configuration of (a) a regular longline with six hooks between floats, like the longlines deployed by longliners in the 1950s, and (b) a deep longline with 18 hooks between floats, like those deployed in the 1990s.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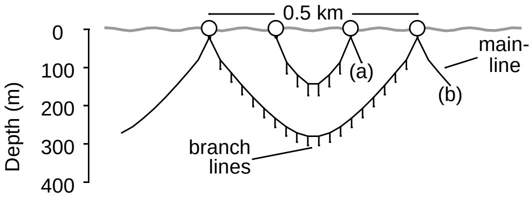
B=1.00
B=2.00
B=4.00
Hyperdepletion
Catch rate
Abundance


0.5 km
0
100
200
300
400
Depth (m)
(a)
(b)
main-
line
branch
lines