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# PRELIMINARY ESTIMATES OF HISTORICAL VARIATIONS IN THE FISHING POWER AND CATCHABILITY OF PELAGIC LONGLINE FISHING GEAR

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**PETER WARD**[1]

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[1] Fisheries and Marine Sciences Program, Bureau of Rural Sciences, GPO Box 858, Canberra ACT, 2601, AUSTRALIA

# Preliminary Estimates of Historical Variations in the Fishing Power and Catchability of Pelagic Longline Fishing Gear

**Peter Ward**
Fisheries and Marine Sciences Program
Bureau of Rural Sciences
GPO Box 858
Canberra ACT 2601
AUSTRALIA
Phone: 612 6272 4163
Fax: 612 6272 3882
Email: Peter.Ward@brs.gov.au

## Abstract

I quantify the effects of 11 variables on the catchability of pelagic longlines, which are used to catch tunas and billfishes in the open ocean. Extension of the depth range and the duration of longline operations have reduced the catchability of several epipelagic species, such as mako sharks (*Isurus* spp.), since industrial longlining commenced in the tropical Pacific Ocean in the early 1950s. Reductions in the body size of many species also resulted in reduced searching for food and fewer encounters with longline hooks. By contrast, the catchability of commercially valuable species, like bigeye tuna (*Thunnus obesus*), increased substantially as a result of the extension of the depth range of longlines and the longer duration of fishing operations. Stronger and less visible line materials, new bait species, and skipper experience also contributed to increased catchability. Dedicated surveys should be used to obtain fishery independent estimates of abundance. Another option is to use surveys to measure variations in the relationship between longline catch rates and animal abundance.

## Introduction

Despite technological innovations, such as the satellite tracking of animals (Block et al. 2005), field-based sampling remains the key source of information on the status of natural animal populations, including damaging insect pests (Southwood 1966), endangered antelope (Whittaker et al. 2003), and valuable fish stocks (Cooke and Beddington 1984). Catches from scientific surveys, commercial fishing, and recreational angling are often the only data available to estimate the abundance of aquatic animals (Arregion-Sanchez 1996; Francis et al. 2003; Stoner 2004). Understanding catchability—how catches vary with sampling effort and population abundance—is critical to the accurate assessment and effective management of animal populations.

For some assessment models, catchability is assumed to be constant over time (Polacheck 1991; Arregion-Sanchez 1996). However, it is rarely constant (Murphy 1960; Paloheimo and Dickie 1964; Gulland 1964; Harley et al. 2001). Of particular concern is hyperstability in catch rate – abundance relationships, where fishers increase catchability or fishing power to maintain their catch rates, but those catch rates do not reflect the depleted state of stocks (Hilborn and Walters 1992). Discrepancies between model predictions and observed catches are often attributed to variations in catchability that are linked to changes in targeting in multi-species fisheries or environmental fluctuations. However, the causes of those variations are rarely verified with independent estimates of catchability. Of further concern is the inability of age-structured assessment models to fit the very steep declines in catch rates of many large predators soon after pelagic longline fishing commenced. Those declines are often attributed to unexplained declines in catchability (Fournier et al. 1999).

Catch rates—the catch-per-unit-of-effort (cpue)—are used as indices of abundance where fishery-independent methods of counting animals are impractical (Bishop 2006). Commercial fishers and gear manufacturers continuously experiment with fishing gear and practices to improve the catchability of target species. However, few published studies have compared the effects of variations in longline gear and practices on catchability. I review approaches to estimating catchability and fishing power then present a comparative method for estimating variations. Estimates of historical variations in the Japanese pelagic longline fishery are presented to illustrate the method.

## Definitions of Fishing Power and Catchability

Put simply, catchability is the ability to catch animals. More formally, it is defined as the probability of catching an animal with a single unit of fishing effort (Paloheimo and Dickie 1964). It is sometimes referred to as sampling efficiency—the percentage of the animals actually present that are recorded (Southwood 1966). Baranov (1918) proposed the catch equation that uses the catchability coefficient $q_i$ to link catch $c_i$, fishing effort $f_i$ for fishing operation $i$, and the local density of vulnerable animals $n_t$ at time $t$:

$$\frac{c_i}{f_i} = q_i n_t \quad (1)$$

Where $q$ is constant over time and area, eq. 1 can be generalized to the entire stock and fishery (Maunder and Punt 2004). Catch rates $c/f$ are usually presented as indices of relative abundance. The estimation of abundance from catch rates assumes that the stock's area is constant because catchability is inversely proportional to the stock's area (Paloheimo and Dickie 1964). It also assumes that the stock's full range is sampled (Walters 2003).

Catchability is the interaction of the fishing gear and animal's behaviour whereas fishing power is a property of the fishing gear and practices. It is a vessel's effectiveness in catching animals relative to the effectiveness of a standard vessel (Beverton and Holt 1957). The unit of effort used for calculating longline catch rates is the number of hooks deployed. I use the term fishing power to refer to how the number of baited hooks varies as a result of changes in gear or practices, e.g., soak time (Beverton and Holt 1957; Hovgård and Las 2000). The distinction between fishing power and catchability is often blurred. Bait type, for example, affects fishing power through its effects on bait loss rates affects catchability through its ability to attract animals (Ward and Myers 2007). Regardless, both fishing power and catchability have the potential to bias abundance indices derived from catch rates.

## Methods of Estimating Catchability

Catchability can be estimated from enclosed ponds and aquaculture facilities where absolute abundance is obtained from a complete census and compared to catch rates. Schultz and Haines (2005), for example, estimated trap-net catchability for bluegill (*Lepomis macrochirus*) by comparing catch rates with electrofishing counts of entire stocks.

More commonly, absolute abundance is not known. In this situation, survey or commercial catch rates may be compared to abundance estimates from other fishing methods (e.g., Dorn et al. 2005), mark-recapture experiments (e.g., Martell and Walters 2002), or other sampling methods. Richards and Schnute (1986), for example, used an underwater submersible to visually count reef fish. They then compared those estimates with angling catch rates. The usefulness of catch rate – abundance comparisons depends on the accuracy of those baseline estimates of abundance. Using meta-analysis to utilize information from multiple data sets has enhanced the approach. For example, Harley et al. (2001) compared 297 series of catch rates from commercial trawlers and abundance indices from surveys. They found evidence of a positive bias in estimates of catchability. The catch rate – abundance relationship for the combined data series showed a hyperstable pattern where commercial catch rates remained high while abundance declined.

Biomass dynamics and age-structured assessment models are another source of abundance estimates for estimating catchability (Hilborn and Walters 1992). Care is required in using model estimates of catchability because catch and natural mortality rates are assumed to be known without error (Harley et al. 2001) and because of confounding among variables—standardized catch rates are usually the key abundance index for those models. Most assessment models provide estimates of catchability. They are the difference between observed catch rates and catch rates predicted from model estimates of abundance. Labelling those differences as “catchability” is not strictly correct because they include the model’s observation and process errors.

Generalized linear models and generalized additive models are often used to derive abundance indices from catch rates that are adjusted or “standardised” for the effects of explanatory variables, such as fishing location, season, and depth (Venables and Dichmont 2004). Another approach is to use maximum likelihood equations to estimate natural mortality and catchability simultaneously from catch and effort data (Wang 1990). However, uncertainty in natural mortality estimates associated with this latter method results in a wide range of possible values for catchability.

Vast distances, combined with the patchy distribution of animals and difficulties in establishing controlled experiments present problems for estimating animal abundance in the open ocean. The prime sources of information on the relative abundance of pelagic animals are survey, observer, and logbook data from commercial fishing vessels that sample large areas over long periods. Abundance indices have been derived from longline (Fonteneau and Richard 2001), purse seine (Gaertner et al. 1999), pole-and-line (Andrade and Teixeira 2002), pelagic driftnet (Nakano et al. 1991), trolling (Kleiber and Perrin 1991), and recreational rod-and-reel catch rates (Holdsworth et al. 2003). Independent estimates of abundance are more difficult to obtain. Some have been derived from acoustic and aerial surveys (Hobday 2005), and mark-recapture experiments (Kleiber et al. 1987).

## An Empirical Method for Estimating Catchability

Pelagic longlines consist of a series of baited hooks on branchlines. The branchlines, which are also called “snoods” or “gangions”, are attached to a mainline suspended from buoys floating at the sea surface. The longline is deployed and retrieved in a daily operation. The probability of catching an animal on a hook depends on the distribution and density of animals, the distribution and intensity of fishing effort, and other stochastic processes influencing the probability of an animal attacking the bait and the probability of it remaining on the hook (Deriso and Parma 1987). I classified those processes into six events; the availability of animals (i.e., their density and distribution in relation to that of the gear); the availability of baited hooks; detection of the bait by animals; attraction to the bait; and hooking (Figure 1). A seventh event—landing—is rarely considered, but it is important in hook-and-line fisheries where animals sometimes escape, drop off, or are removed from the hook by scavengers before retrieval (Ward et al. 2004). I do not consider an additional event—retention and reporting practices—that may bias commercial and effort data.

I separately estimated the effects of 11 variables on catchability. Studying catchability in commercial fisheries is very difficult because estimation is confounded with variations in abundance; and reliable, independent estimates of abundance are rarely available. Longline experiments, where data are recorded on the status of individual hooks, provide one avenue for estimating catchability because hooks can be assumed to access the same local abundance of animals. My approach to estimating relative catchability utilizes the ratios of catch rates from experiments and other situations where fishing power and abundance are constant. For example, virtually invisible nylon branchlines have replaced rope branchlines. Those variations will affect longline catchability. Stone and Dixon (2001) present the results of an experiment where nylon monofilament and multifilament branchlines were alternated along a longline. Catch rates $u_1$ derived from monofilament branchlines are linked to the species’ local abundance $n_i$ catchability $q_i$ through the catch equation (eq. 1):

$$u_1 = \alpha_1 q_i n_i$$

and $n_i = \dfrac{u_1}{\alpha_1 q_i}$

where $i$ is the local time and area of interest and $\alpha_1$ is the effect of monofilament on catchability. For multifilament branchlines, $\alpha_2$ produces catch rates $u_2$:

$$n_i = \frac{u_2}{\alpha_2 q_i}$$

The two equations can be combined because local abundance $n_i$ is the same for both types of branchline:

$$\frac{u_1}{\alpha_1 q_i} = \frac{u_2}{\alpha_2 q_i}$$

$$\frac{\alpha_2}{\alpha_1} u_1 = \frac{q_i}{q_i} u_2$$

$$\frac{\alpha_2}{\alpha_1} = \frac{u_2}{u_1}$$

Thus, for experiments and situations where abundance and fishing power are constant, relative catchability can be inferred by dividing one catch rate by another. In my example, Stone and Dixon deployed an equal number of monofilament and multifilament branchlines. They caught 128 broadbill swordfish (*Xiphias gladius*) on multifilament and 260 swordfish on monofilament in 12 longline operations. The effect of monofilament on catchability is 260/128 or 2.03. In other words, monofilament catchability for swordfish is double that of multifilament.

The mix of gear types can then be used to estimate historical variations in catchability. In my example, 35% of the branchlines were monofilament in the early 1990s rising to 42% monofilament in the late1990s, with the remainder multifilament. The relative catchability $\Delta q$ between periods is:

$$\Delta q = \frac{(2.03 \times 0.42) + (1.00 \times 0.35)}{(2.03 \times 0.35) + (1.00 \times 0.42)} = 1.06$$

A value of 1.00 is included to standardize each estimate for multifilament catchability in the late 1990s. The introduction of monofilament resulted in swordfish catchability in the late1990s being 1.06 times the early 1990s catchability.

Several variables directly affect fishing power instead of catch, but the approach to estimating these is similar to the method described for catchability. For example, 6.1% of hooks deployed by 1950s longliners in the tropical Pacific caught an animal compared to 2.2% in the 1990s (Ward and Myers 2005c). Hooks that have caught an animal are not available to catch another animal. Therefore, fishing effort must be discounted by about 0.061 – 0.022 = 0.04 for the number of baited hooks that are actually available. This is the same as reducing the probability of catching an animal by 0.04 or reducing catchability by 0.04.

To illustrate the method, estimates of relative catchability are presented for Japan's large, distant-water longliners between the “1950s” (1950–54) and the “1990s” (1995–99) in the central tropical Pacific Ocean (20°S–20°N and 140°E–140°W). For the three oceans, long time-series of catch and effort data reported by Japan’s longliners are the prime abundance index for assessments of commercially important tuna (*Thunnus* spp.) and several other pelagic species, such as blue marlin (*Makaira nigricans*) and blue shark (*Prionace glauca*). Catchability is estimated for five frequently caught species that represent a wide range of life-histories (Table 1). A supporting document (Ward 2007) details data sources and the methods used to estimate relative catchability and fishing power. Following is a summary of historical trends in each variable and the reliability of estimates. I then review other variables that may have affected catchability over time.

## Estimates of Relative Catchability

### Area of Action and Abundance

*Animal's Movement Patterns*

Large animals swim faster, forage through a larger volume of water, and are more successful at competing for bait than are smaller animals (Ware 1978; Hart 1986; Videler 1993). Longlining has selectively removed large predators from the pelagic fish community of the tropical Pacific Ocean study area, while the mean length of several smaller species has not changed or has increased (Ward and Myers 2005c). I hypothesize that the reduction in body length resulted in fewer encounters with longline bait.

I used a length-based constant (Ware 1978) to estimate size-related variations in the volume of water searched, which is assumed to reflect longline catchability. The estimates of relative catchability were not statistically significant, partly due to small sample sizes for several species in the 1950s and large variance in body length (Table 2). Nevertheless, the results suggest that declines in body size will reduce the catchability of large predators. Elevated catchability may be expected for several small species that increased in size during the study period, e.g., long-nosed lancetfish (*Alepisaurus ferox*).

My estimates of search volume were more sensitive to variations in length than they were to the value of Ware's constant. For example, a 10% variation in the constant resulted in relative catchability varying from 0.47 to 0.51 for blue marlin. Reductions in length may contribute to reduced catchability in other ways. Visual acuity is related to length so that larger animals are able to detect prey at greater distances than can smaller animals of the same species (Ware 1978; Blaxter 1980). On the other hand, the importance of length and search volume will diminish when food is in over-supply. The reduction in catchability due to reduced length might not be as large as estimated if food availability has increased as a result of predator release or if higher densities of longline bait are present.

*Depth of Gear*

Catchability will increase as the match between the stock's distribution and the gear's distribution improves (Hanamoto 1987; Boggs 1992). Tracking studies demonstrate that bigeye tuna range down to 500 m or deeper in the warm, well-oxygenated waters of the equatorial Western Pacific Ocean (Musyl et al. 2003). The effects of variations in longline depth have received close attention in assessments (Suzuki et al. 1977; Hinton and Nakano 1996; Bigelow et al. 2002). A proportion of the stock would not have been available to the 1950s longlines, which ranged down to 120 m (Suzuki et al. 1977). By extending to 400 m or more, the longlines deployed by many fleets now access the full vertical range of most pelagic species.

I used estimates of the depth range of longline hooks and the daytime depth distribution of each species (Ward and Myers 2005a) to infer variations in catchability (Table 2). Long-term increases in longline depth range resulted in elevated catchability of mesopelagic species like bigeye tuna. Proportionally fewer hooks were available at shallow depths in the 1990s, resulting in significant reductions in catchability for epipelagic species, including skipjack tuna (*Katsuwonus pelamis*), shortfin mako shark (*Isurus oxyrinchus*), and blue marlin.

In addition to being influenced by depth range, catchability 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 rises by about 40 m during El Niño periods in the western Pacific Ocean (Philander 1990). However, catchability might not have varied significantly because ENSO conditions and thermocline depth were not markedly different in the study area between the 1950s and 1990s (Ward and Myers 2005c).

### *Fishing Master Experience*

Several studies have shown that the experience of skippers or "fishing masters" is the most important variable affecting commercial catch rates (Comitini and Huang 1967; Hilborn and Ledbetter 1985; Squires and Kirkley 1999). Skilled fishing masters are adept at anticipating when and where target species will be abundant. They synthesize past experience, knowledge of historical patterns, understanding of relationships between environmental conditions and the availability of target species, and catches by other vessels. Fishing master skill also involves adjusting fishing gear and techniques to suit local conditions.

I included the master's years of experience in fishing for tuna as a variable in a generalized linear model of catch rates for Japanese longliners operating off eastern Australia during the 1990s. The analyses show that fishing master experience resulted in significant improvements in catchability of bigeye tuna over the study period (Table 2). Interestingly, increased experience resulted in significant declines in shortfin mako shark catchability. This might be due to a decline in mako shark abundance during the 1990s. Alternatively, it might indicate that fishing masters have learnt to avoid sharks, which have a low commercial value, damage gear, and damage animals that are hooked on longlines (Sivasubramaniam 1963). There may be a separation in the distribution of mako shark and target species along fine temporal and spatial scales, so that improved experience in locating target species has inadvertently resulted in reduced mako shark encounters.

I restricted the analyses to fishing master experience in longlining for tunas, ignoring their experience in other fisheries. Furthermore, observer reports of the number of years of experience are a crude measure of fishing master skill. Kirkley et al. (1998) found that several variables, including education levels, improved catch rates in a scallop fishery. My estimates do not account for progressive improvements in the skill levels of crewmembers and the 40 years of knowledge accumulated by the fleet since the 1950s. On the other hand, the high wages demanded by Japanese crewmembers since the 1980s may have resulted in a deskilling, with increasing numbers of other nationalities—mainly Indonesians, Filipinos, and Fijians—employed on Japan's longliners (Kawai 1995).

### *Operation Time*

Diminished light levels alter the ability of prey and predators to detect one another (Boden and Kampa 1967; Hart 1986). Dietary studies show that tunas, billfishes, and sharks are generalist predators that are particularly active during crepuscular periods (Helfman 1978; Galkov 1984). Their catchability increases when baited hooks are available during peak feeding times, although the increased availability of prey at those times may compete with longline bait (Bertrand et al. 2002).

The number of hooks deployed each day by Japan's longliners has steadily increased over time, resulting in proportionally more bait being available at dusk and in the early evening (Polacheck 1991; Ward et al. 2004). I combined information on the timing of longline operations and estimates of the effects of dawn and dusk on catch rates (Ward et al. 2004) to infer variations in catchability (Table 2). The analyses suggest that the historical shifts in timing resulted in a statistically significant increase in the catchability of blue marlin.

## Availability of Baited Hooks

### *Bait Loss*

Usually, a hook must have a bait attached if it is to attract and catch an animal. Bait may be removed by target species and scavengers, or they may fall off hooks because of incorrect attachment, disintegration of the bait over time, or through wave action (Shomura 1955; Shepard et al. 1975; Bjordal 1983). Shomura (1955) observed that fewer bait were retrieved on longline hooks with long soak times, e.g., 46% of 720 bait were lost over soak times of 1.5–5.5 hr.

Ward and Myers (2007) estimated historical changes in bait loss rates from 1950s survey data. Their model predictions suggest that loss rates have significantly declined since the 1950s (Table 2). This was partly due to historical increases in the depth range of longlines—loss rates declined with depth—perhaps because of reduced turbulence or scavenger activity. Tuna abundance, bait type, and soak time also affected loss rates.

### *Gear Saturation*

When an animal encounters a longline hook, the hook may be unavailable if it already holds another animal. These occupied hooks have zero fishing power. The tendency toward underestimation of abundance as a result of gear saturation will be greatest when catch rates are high (Rothschild 1967; Au 1986). Gear saturation was more frequent in the 1950s when Japan's longliners averaged 61 animals per 1000 hooks compared to 22 per 1000 hooks in the 1990s (Ward and Myers 2005c).

I used the formula developed by Rothschild (1967) and nominal catch rates for each period to estimate the effect of gear saturation on fishing power for each species. Gear saturation resulted in variations in fishing power between periods, but these were not statistically significant (Table 2). The estimates were not adjusted for the effects of localized clumping, bait loss, and hooks that were occupied by animals that were subsequently lost from the longline. On the other hand, the 1950s longliners sometimes patrolled their longlines, removing hooked animals and re-baiting the hook during the relatively long period (six hours) between the cessation of deployment and commencement of hauling (Shapiro 1950). This would reduce gear saturation in the 1950s and increase fishing power, whereas clumping and losing animals would elevate fishing power.

## Detection

### *Detection of Gear*

Animals may avoid bait that have unnatural visual cues, such as a visible hook or line (Blaxter 1980). Laboratory experiments by Cui et al. (1991) demonstrate that mackerel (*Scomber scomberus*) are better at detecting multifilament lines than monofilament lines.

The 1990s Australian observer data show that 85% of the branchlines were monofilament teteron or nylon with the remainder braided nylon or kuralon cord. They were transparent or dyed to reduce their visibility to target species (Wardle et al. 1991). By contrast, 1950s branchlines were tar-coated rope or cotton thread wound around wire cable (Shimada 1951). I combined this information with the results of an experiment that compared catch rates on monofilament and multifilament branchlines (Stone and Dixon 2001). The results suggest that the introduction of monofilament branchlines significantly increased the catchability of several species (Table 2). However, those results may not be strictly applicable to the study area because the experiment involved shallow longlines deployed at night in temperate Atlantic waters. Furthermore, it may be incorrect to use their white marlin (*Tetrapturus albidus*) estimate for blue marlin. Although the difference between multifilament and monofilaments for yellowfin tuna (*Thunnus albacares*) was reported as statistically significant, it may be an aberration related to the small number of yellowfin caught.

## Attraction to Bait

### *Hunger*

Hunger—the need to obtain energy to support activities—drives animals to feed and to attack bait (Atema 1980). 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 per unit of mass because of size-related penalties and requirements, such as growth and drag (Ware 1978).

My analyses show that the effect of daily ration on catchability was most pronounced in large predators that showed large reductions in body mass between periods. An average-size blue marlin in the 1950s would require 1.3 kg of food per day for routine metabolism (Ward 2007). They would have a higher feeding motivation than blue marlin in the 1990s, which were smaller and only required 0.5 kg per day on average. Small species like skipjack tuna showed small reductions in mass. The high daily ration of skipjack offset the effects of those size reductions on catchability.

If the historical removal of large pelagic predators has resulted in increased availability of food, then the remaining animals might be less attracted to longline bait. Historical variations in length–weight relationships may provide further insights into variations in feeding motivation. Some fishers report low condition factors for tunas caught in newly exploited areas. Competition for food would be more intense before exploitation, so more food is available per capita after stocks are reduced, resulting in "fatter, more content animals". However, analyses indicated a historical decline in the condition factor of Atlantic bluefin tuna (*Thunnus thynnus*), which is the opposite of what would be expected if food availability was increasing as stock size declined (Golet et al. 2007). Nevertheless, there are many other factors that might influence food availability and condition factor, including concurrent declines in prey, such as mackerels (MacKenzie and Myers 2007).

### *Competition among Gears*

In using the number of hooks as the measure of fishing effort it is assumed that the catchability of each bait is not affected by nearby bait. However, the catchability of each bait must eventually decline as the distance between branchlines decreases (Skud 1978).

Shomura and Murphy (1955) report catch rates of survey longlines that had alternating segments of high and low hook densities (all segments were 366 m long). Their data show that high density segments (11 hooks per 366 m) caught 53 yellowfin tuna per 1000 hooks compared to 44 per 1000 hooks on the low density segments (6 hooks per 366 m). The higher catch rates for high-density segments are the opposite of what would be expected if competition among adjacent hooks depressed catch rates. Instead, it supports hypotheses proposed by Murphy (1960) and Au (1986) that increasing the density of hooks increases the catch per school. Apparently commercial fishers use less than optimal hook densities to reduce tangles and to provide time for crewmembers to attach and detach each branchline during deployment or retrieval (Ward and Hindmarsh 2007).

I estimated a mean hook density of 45.4 m (SD ±4.5 m) from the longline dimensions of 25 longliners in the study area in 1950 (Shimada 1951). Longline dimensions reported by observers on 38 longliners in the study area (P. Williams, pers. comm.) indicate a mean density of 38.3 m (SD ±15.6 m) during 1994–2003. However, the lengthening of longlines to access deeper waters also alters the distance between bait. The 1990s longliners also used shorter branchlines (24 m on average) than the 1950s longliners (30 m). The shorter branchlines and the lengthening of longlines offset the historical reduction in hook density. The effects of variations in hook density also depend on the animal's foraging behaviour. A species foraging in a horizontal plane will less frequently encounter hooks on a deep longline than mesopelagic species like bigeye tuna that forage during ascents and descents (Bertrand et al. 2002).

At an intermediate scale, hook density will increase with the number of hooks deployed on a longline. The average number of hooks deployed by Japan's longliners increased from about 1200 in the 1950s to 3100 per operation in the 1990s (Ward and Hindmarsh 2007). Hooks along the longline must compete with adjacent hooks, whereas distal hooks are subject to less competition—they compete with hooks on only one side. I found that catch rates of distal hooks were not significantly different to those of nearby hooks (Ward 2007), which does not support the hypothesis that hooks of the same longline compete for animals. Polacheck (1991) also found no significant effect of hooks per operation on catch rates of bigeye or yellowfin tuna in the tropical western Pacific Ocean. My results are also consistent with estimates of the swept area of longline hooks of 2–6 $km^2$ that were derived from fine-scale survey records of yellowfin tuna catches in the Indian Ocean (Hirayama 1972).

On a larger scale, the global five-degree data show that longline effort in the study area increased from 21 million hooks per year on average in the 1950s to 270 million in the 1990s. Longlines might compete for animals as the number of operations increases or some longliners might have been displaced to less productive areas as fleet size increased. The generalized linear models show that bigeye tuna catches rise linearly with the total number of hooks to an asymptote (Ward 2007). Catch then declines at higher levels of fishing effort, perhaps as a result of competition among longlines (Figure 2). The difference between the linear and cubic models might represent the effects of competition among longlines on catchability. Fishing effort of 1.5 million hooks per cell results in a 0.44 reduction in bigeye tuna catchability. However, those are extreme levels of effort; the model predicted much smaller variations in catchability at the mean 1990s effort level.

My estimates are confounded by negative correlations between fishing effort and stock abundance. The abundance of bigeye and yellowfin tuna in the 1990s is estimated to be less than half of the 1950s level (Hampton et al. 2005a). Consequently, the difference between the cubic and linear predictions is partly due to reduced abundance in the 1990s. Further work is needed to estimate the effects of gear competition on longline catchability.

*Bait Type*

Bait attracts animals by mimicking the visual (e.g., size and shape), chemical, and tactile cues (e.g., vibrations and movements) of natural prey (Blaxter 1980; Atema 1980). Fishers select bait on the basis of the expected value of catches balanced against bait costs, availability, storage and handling considerations, and how long the bait will remain on the hook (Ward and Myers 2007).

A generalized linear model of Australian observer data predicted significant declines in yellowfin tuna catchability as a result of the increased use of squid (*Loligo* spp.) and mackerel bait in the 1990s (Ward 2007). The model also predicted substantial increases in bigeye tuna and blue marlin catchability, but these were not statistically significant. There were no reports of saury (*Cololabis saira*) bait in the observer data that I modelled. I predicted 1950s catches for pilchard (*Sardinops sagax*) bait because several reports show that saury and pilchard bait have a similar catchability for a range of species, including yellowfin tuna, bigeye tuna, marlins, and sharks (Anonymous 1952; Murphy and Otsu 1954). Fishers in the 1950s frequently suggested that poor bait quality reduced their longline catch rates (Van Campen 1952). By basing parameter estimates on 1990s bait data I may have overestimated 1950s catchability relative to the 1990s situation. The effect of bait type is also confounded with bait loss, which tends to be higher for fish bait compared to squid bait (Shomura 1955; Ward and Myers 2007).

## Landing

*Breakage*

Longliners have used wire leaders or “steel traces” since the 1920s to reduce the loss of fishing gear and hooked animals that are able to sever leaders constructed from natural or synthetic fibres (Ward and Hindmarsh 2007). The materials used for longline leaders will also alter their visibility, e.g., wire is quite visible whereas nylon is almost transparent.

Nylon leaders were introduced in the 1980s, but many Japanese longliners continued to use wire leaders, at least for shallow hooks where sharks are frequently encountered (Ward and Hindmarsh 2007). Australian observers reported that 72% of the leaders deployed by Japan’s longliners were nylon in the 1990s. I combined that percentage with the results of an experiment that compared the catch rates on wire and nylon monofilament leaders on Australian longliners (Ward et al. submitted). Catch rates of sharks were significantly lower on nylon than on wire leaders, probably because some are able bite through the nylon (Table 2). Catch rates of blue marlin were also significantly lower on nylon, perhaps because their violent reaction to hooking sometimes breaks nylon leaders. By contrast, catch rates of bigeye tuna were significantly higher on nylon than on wire leaders. Bigeye may see wire leaders and avoid those hooks.

The experimental design did not allow the separate estimation of the effects of leader visibility on catchability and the effects of bite-offs on loss rates. The transparency of nylon may elevate shark catchability, for example, but this effect would be hidden by elevated loss rates. The high bite-off rates reported by Ward et al. (submitted) indicate that as many animals escape from nylon leaders as are caught on nylon leaders. Animals hooked on a longline are sometimes damaged or removed by large scavengers, such as sharks and cetaceans (Hirayama 1972; McPherson et al. 2002; Bell et al. 2006). Longline loss rates will be influenced by variations in the density and activity levels of scavengers, the number of animals available on the longline, and availability of alternative food sources.

Hirayama (1976) reported considerable geographical variation in shark-damage rates of tunas reported by longline surveys during 1954–69. The highest damage rates were in the central (10%) and eastern tropical Pacific Ocean (14%). For the central and eastern tropical Pacific Ocean in the late 1950s, Kobayashi and Yamaguchi (1978) report damage rates of bigeye tuna ranging up to 14.5%, yellowfin tuna to 21%, and blue marlin to 15%. My estimates of damaged tunas ranged between 9% in the 1990s and 20% in the 1950s. This apparent reduction in damage rates may be due to the removal of large sharks by longlining (Ward and Myers 2005c).

Anecdotal reports from observers and fishers indicate that shark-damage is more prevalent at night. Therefore, the shift to having more longline hooks available at night would further contribute to the underestimation of historical increases in catchability (Ward et al. 2004). Nevertheless, the fate of lost animals—whether they escape by biting through the leader or are consumed by large scavengers— is largely unknown. This cryptic mortality may significantly affect longline catch rates and thus abundance indices for many species.

## Other Variables

### Animals Associated with Bait

In addition to gear saturation, interference competition may occur where animals actively prevent access to bait (Stoner 2004). Torsk (*Brosme brosme*), for example, have been observed to chase smaller fish from baited hooks (Løkkeborg and Bjordal 1992). Conversely, catchability will be enhanced when animals are attracted by other animals feeding on bait or animals struggling on hooks, or animals associated with fluorescent lightsticks (Fishelson 1980; Skud 1978b).

The presence of predators is another form of interference competition; an animal that is actively involved in avoiding predators is less likely to attack bait. Werner et al. (1983) found that predation risk was an important factor in the selection of feeding habitats by bluegill sunfish (*Lepomis macrochirus*). Small size classes of several species are noticeably absent in the length data of longline catches in the early 1950s (Ward et al. 2005c). Those smaller animals would undoubtedly have been present in the early 1950s, so their absence in longline catches in the 1950s might be due to interference by large pelagic predators. The habitat of small species may have expanded in response to the removal of those predators.

## Hooks

The 1950s longliners deployed larger hooks (extended length of up to 140 mm; Shapiro 1950) than those used in the 1990s (110–120 mm). However, those large hooks are unlikely to have limited the minimum size of sharks, marlins, or large tunas taken in the 1950s because the mouth gape of those animals is considerably larger than the hook's gape (30–40 mm). Erzini et al. (1996) report increasing fishing power with decreased hook size. I therefore expect the introduction of small hooks to have extended selectivity to animals with a small gape (e.g., skipjack tuna), but not to have reduced the catchability of large animals.

The 1950s longliners deployed straight-shanked "J" hooks, whereas the tuna hooks used since the 1970s have many similarities to "circle hooks" (Shimada 1972; Ward and Hindmarsh,2007). Circle hooks have been advocated as a way of mitigating sea turtle bycatch while maintaining or increasing catch rates of target species. Experiments by Falterman and Graves (2002), for example, show that longline catch rates of yellowfin tuna on circle hooks were 2.5 times those on "J" hooks. The introduction of tuna hooks may have increased the catchability of some species but reduced the catchability of others.

## Fish-finding Equipment

The ability of fishers to locate target species has improved with the installation of electronic navigation and fish-finding equipment (Kleiber and Perrin 1991). Catches of blue-spotted mackerel (*Scomberomorus niphonius*) increased by 10–30% when fishing operations were guided by sea surface temperature imagery (Faji et al. 1990). Sonar, which is used to detect plankton layers, baitfish, and target species, tripled the fishing power of Japan's purse seiners in the 1950s (Inoue 1961). For prawn trawlers off northern Australia, Robins et al. (1998) found that the installation of global positioning systems (GPS) and plotters contributed to an increase of at least 12% in fishing power after three years.

The effects of electronic equipment are difficult to quantify, and there are few studies of the effects of electronic equipment on longline catch rates. By the 1980s, Japan's longliners had installed many electronic fish-finding aids, such as sonar, GPS, plotters, and satellite receivers for downloading sea surface temperature maps. In the 1990s, Australian observers reported that longliners also accessed satellite ocean-colour imagery and obtained thermal profiles from bathythermographs (XBTs). Other equipment, such as weather facsimiles and radio-direction finders added to the efficiency of longlining operations and extended the time that vessels could remain on fishing grounds to follow the fish (Ward and Hindmarsh, 2007). Descriptions of 1950s longlining do not mention the Japanese using electronic equipment (Shapiro 1950; Shimada 1951b; Ego and Otsu 1952; Ochi 1952; Van Campen 1952). However, I expect that they had radios to communicate with their mothership and other longliners.

## Searching

Communication and cooperative searching have been shown to influence fishing power in several fisheries (Ruttan 2003; Grant and Berkes 2007). Improvements in radio communications were estimated to double the fishing power of Japan's purse seiners during the 1950s (Inoue 1961). Cooperative searching in the 1990s involved longliners owned by the same company and the fishing master's personal networks. By contrast, fewer than 27 longliners operated at any one time in the 1950s (Van Campen 1952). They would have a much narrower temporal and spatial coverage than the 800-strong 1990s fleet (Ashenden and Kitson 1987).

### Environment

Stoner (2004) evaluates environmental variables that influence the availability of animals to baited fishing gear. He suggests that the assumption of constant catchability is often not valid because of the variable behaviour of target species and their responsiveness to bait, which depends on the animal's feeding history and environment. Stoner concludes that temperature, light, current direction, current velocity, and the density of conspecifics have the greatest impacts on catchability and offered the best prospects for adjustment in stock assessments.

Oceanographic conditions, such as temperature and oxygen concentration, alter the distribution and abundance of pelagic species through recruitment, variations in productivity, and the efficiency of longline gear. The expansion of a stock's horizontal or vertical range will result in reduced catchability because catchability is inversely proportional to the total area inhabited ( Paloheimo and Dickie 1964; MacCall 1990). In the western Pacific, El Niño conditions result in a shallow thermocline that limits the vertical distribution of many pelagic species. If abundance is unchanged, a contraction in the vertical limit of the habitat will elevate catchability and increase catch rates of hooks located above the thermocline (Bigelow et al. 2002). I did not estimate environmental effects on catchability because several key environmental variables did not vary significantly in the tropical Pacific during the study period (Ward and Myers 2005c). For other periods, historical variations in environmental conditions may be significant and abundance indices should take into account their effects. Information on each species' geographical extent would be relatively simple – though expensive – to gather through surveys of unfished areas combined with commercial catch data. Regardless, care is required in considering environmental effects because they may influence abundance rather than catchability, whereas abundance is the signal of interest in stock assessments (Kleiber and Yokawa 2002).

## Discussion

The estimates suggest substantial increases in the catchability of the five selected species, especially target species, through improvements in fishing gear, practices, and fishing master experience. Variables that strongly affect catchability include fishing master experience and bait type. Fishing power might also have increased through reduced rates of bait loss. The analyses are mostly preliminary; further work is required to provide more reliable estimates of the effects of most variables. Further experiments on the effects of those variables and the effects of electronic fish-finding equipment and cooperative searching are required to develop estimates of catchability that can be used in assessments. Historical changes and new developments in longline fishing gear and practices also need to be documented and quantified.

There is a need to estimate variations in catchability among fleets and on finer spatial and temporal scales, e.g., the introduction of fish-finding devices would result in stepwise jumps in catchability. Furthermore, catchability will be influenced by density dependent processes, such as the aggregation of target species and behaviour of fishers (Wang 1990). A shape parameter $\beta$ is often included in the catch equation to accommodate non-linear relationships between catch rates and abundance:

$$\frac{c}{f} = \alpha q^{\beta} n$$

Hyperstability in the relationship between catch rates and abundance occurs when $\beta > 1$. There are also cases of hyperdepletion ($\beta < 1$) where high concentrations of animals are removed early in the fishery's development (Hilborn and Walters 1992). Treating catchability as a random variable also holds promise (Bishop 2006). My analyses are limited to a linear relationship with a point estimate of $\alpha$ and where $\beta$ is assumed to equal one.

Methods need to be developed to combine separate estimates into a single index of relative catchability. The effects of variables on catchability are rarely additive. Most are multiplicative, but interactions among variables may be particularly important for deriving combined indices of catchability. For example, deployment time might moderate the effect of wire leaders on the catchability of species like bigeye tuna that are able to see those leaders.

The increased catchability of associated species like blue marlin is linked to the increased catchability of target species, such as yellowfin tuna. Blue marlin have a close ecological association with yellowfin tuna—they forage on the same prey aggregations (Josse et al. 2000). By contrast, longline fishers may have inadvertently become better at avoiding some non-target species. mako shark are more closely associated with swordfish than with tunas (Mejuto and Garces 1984). My estimates imply that improvements in technology and experience did not increase mako shark catchability as much as it increased the catchability of target species. Encounters between these non-target species and the fishing gear will have a strong random component with highly variable catchability.

Noteworthy were the possible effects of the historical reduction in the abundance of large predators. By reducing catchability and availability to the gear, those community changes partly offset the effects of improved technology. I did not attempt to estimate variations in vulnerability with body size or age. The increases in catchability would have been much larger if catch was expressed as mass rather than the number of animals. Large tuna tend to have a wider depth range than small tuna through the effects of water temperature on heart rates (Neill et al. 1976; Brill et al. 1998). The extension of longlines to access deeper depths may therefore be significant in increasing the catchability of tunas and other large pelagic animals (Au 1985).

## Concluding Remarks

At first glance, a baited hook appears to be a simple unit of fishing effort. Closer inspection, however, reveals many variables that may alter a hook's catchability and fishing power. A declining trend in catch rates is cause for concern in commercial fisheries. However, a static or increasing pattern does not necessarily indicate a healthy stock because standardization might not have fully adjusted for increased catchability or fishing power. My analyses show that catchability has increased for several pelagic species. I did not find anything unique about longline gear or pelagic animals that might explain the rapid decline in catch rates soon after the commencement of longlining. The cause of that pattern remains unresolved.

Few researchers have attempted to derive abundance indices from catch and effort data reported by other tuna fishing methods, such as purse seine and pole-and-line, because of problems in defining the unit of fishing effort and measuring variations in fishing power. Several major groundfish fisheries (e.g., Pacific halibut, *Hippoglossus stenolepis*) rely on regular surveys that use standardized fishing gear and practices along a predetermined grid. This approach is preferable because it avoids problems with measuring variations in catchability and fishing power in commercial longline fisheries. However, abundance surveys have rarely been attempted in the open ocean because of the prohibitive cost in obtaining representative samples from a system that features vast distances and high spatial and temporal variability (Bishop 2006). If such surveys are not feasible, it will be essential to estimate variations in catchability and fishing power through experiments that compare the performance of past and current longline gear and practices.

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**Table 1.** Characteristics of species selected to illustrate estimates of relative catchability. Body size estimates are from a 1950s survey and 1990s commercial longline data (Ward and Myers 2005c). The indication of longline catchability is based on a qualitative assessment of the species' habitat, size range, and proportion of the population likely to be vulnerable to longline fishing gear. Trophic positions are ECOSIM model estimates reported by Kitchell et al. (2002).

| Common name | Latin binomial | Longline target | Trophic position | Habitat | Longline catchability | Mass (kg) | |
|---|---|---|---|---|---|---|---|
| | | | | | | mean | range |
| Blue marlin | *Makaira nigricans* | no | 4.6 | epipelagic | high | 100 | 6–274 |
| Shortfin mako shark | *Isurus oxyrinchus* | no | 4.6 | epipelagic | high | 74 | 4–164 |
| Bigeye tuna | *Thunnus obesus* | yes | 4.0 | mesopelagic | medium | 76 | 4–153 |
| Yellowfin tuna | *Thunnus albacares* | yes | 4.0 | epipelagic | medium | 52 | 6–90 |
| Skipjack tuna | *Katsuwonus pelamis* | no | 3.9 | epipelagic | low | 10 | 2–24 |

**Table 2.** Estimates of historical variations in catchability for 11 variables for Japan's distant-water longliners. 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. Estimates that are significantly different from parity ($\alpha = 0.05$) are in bold.

| | Variable[a] | Estimated change in catchability[b] | | | | Source of estimates |
|---|---|---|---|---|---|---|
| | | mako shark | blue marlin | bigeye tuna | skipjack tuna | |
| 1 | Gear saturation | >1.03 | >1.02 | >1.01 | >1.02 | Saturation formula (Rothschild 1967) applied to nominal catch rates. |
| 2 | Operation time | 1.10 | 1.86 | 1.06 | 0.96 | Mixed model of observer data (Ward et al. 2004). |
| 3 | Depth of gear | **0.83** | **0.84** | **1.39** | **0.89** | Mixed model of observer data (Ward and Myers 2005a). |
| 4 | Breakage | [c]**0.62** | **0.51** | **1.14** | 1.71 | Experiment comparing catch rates on wire and nylon leaders (Ward et al. submitted) |
| 5 | Bait loss | **<3.09** | **<3.09** | **<3.09** | **<3.09** | Generalized estimating equation analysis of survey data (Ward and Myers 2007). |
| 6 | Detection of gear | **>1.34** | [d]**>2.44** | – | – | Experiment comparing catch rates on mono- and multifilament branchlines (Stone and Dixon 2001). |
| 7 | Movement patterns | >0.59 | >0.49 | >0.64 | >0.83 | Length measurements (Ward and Myers 2005c) multiplied by Ware's constant (Ware 1978). |
| 8 | Gear competition | – | >0.98 | >0.95 | – | Cubic and linear generalized linear model of catch and effort (Ward 2007). |
| 9 | Hunger | >0.54 | >0.42 | >0.60 | >0.80 | Size (Ward and Myers 2005c) and daily ration estimates (Menard et al. 2000; Junior et al. 2004) |
| 10 | Fishing master experience | **>0.31** | >1.52 | **>2.55** | >1.44 | Generalized linear model of years of fishing master experience and catch rates (Ward 2007). |
| 11 | Bait type | 0.94 | 4.66 | 1.94 | 0.65 | Generalized linear model of bait species and catch rates (Ward 2007). |

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[a] On the basis of the reliability of parameter estimates and plausibility of assumptions, I ranked estimates from 1 (most reliable) to 11 (least reliable).

[b] Greater-than signs (">") indicate that relative catchability is likely to have been underestimated; less-than signs ("<") indicate that it is likely to have been overestimated.

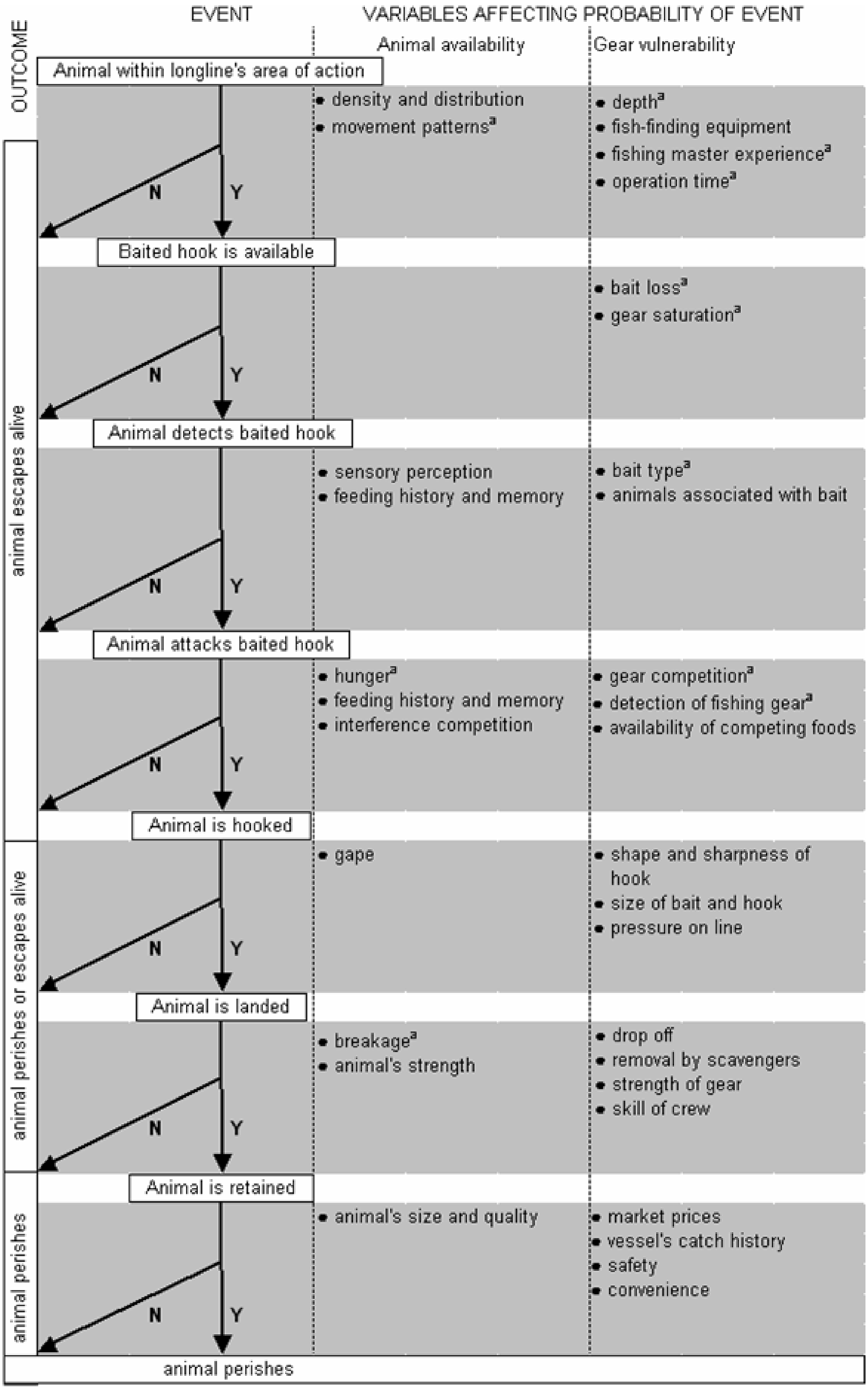
[c] Estimate is for all shark species combined.

[d] Estimate is for white marlin (*Tetrapturus albidus*).

## Figure legends

**Figure 1.** Flow chart of events that determine the fate of animals encountering pelagic longlines. Variables are classified according to whether they are linked to the animal’s availability or its vulnerability to the fishing gear. Several variables affect more than one step, e.g., bait type may influence detection as well as attraction.

**Figure 2.** Effect of gear competition on catch rates. Using the global five-degree data, I inferred relative catchability as the difference between catch predictions of a generalized linear model that included quadratic and cubic terms for fishing effort (the cubic model) and one that did not include those terms (the linear model).



[a]Present article presents estimates of variations in relative catchability for these variables.

Fig. 1

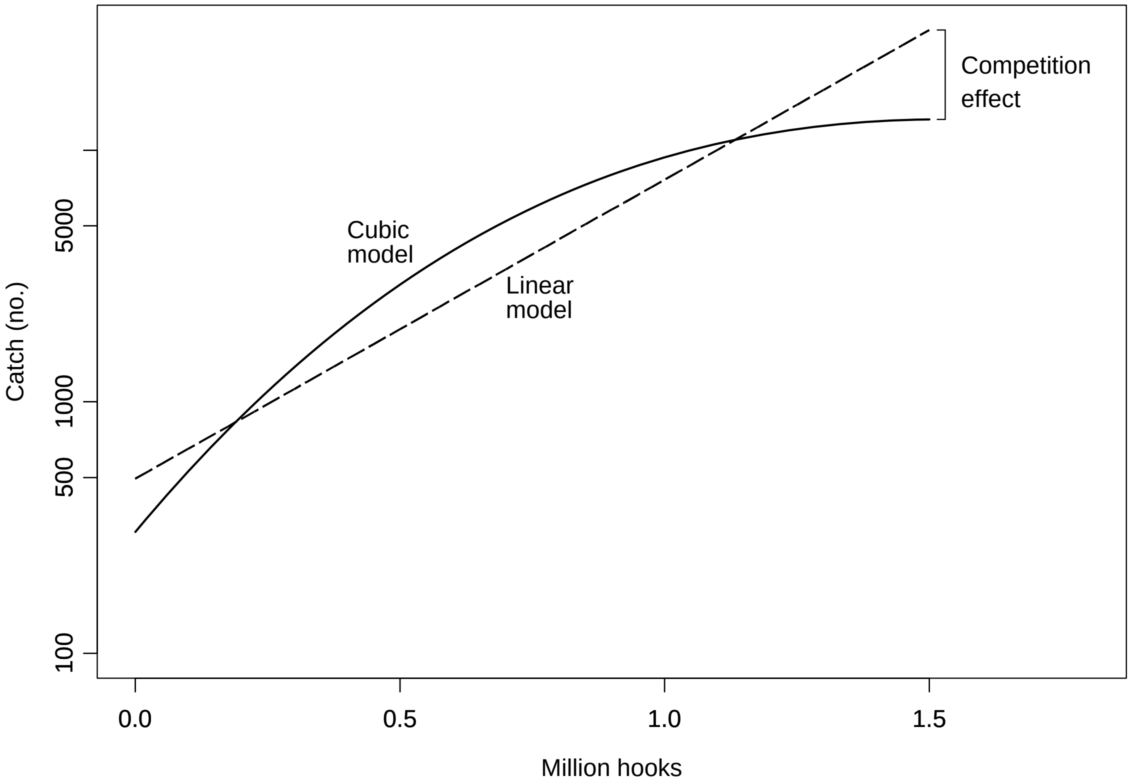

Catch (no.)
100
500
1000
5000
0.0
0.5
1.0
1.5
Million hooks
Cubic model
Linear model
Competition effect

Fig. 2