

HISTORICAL VARIATIONS IN PELAGIC FISH COMMUNITIES
AND THEIR CAUSES

by

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Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
February 2007

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ISBN: 978-0-494-31308-4

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ISBN: 978-0-494-31308-4

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Dedication

To my leading lights: Jo, Jess, Ella, and Jack

*“But how had the mystic thing been caught? Whisper it not,
and I will tell; with a treacherous hook and line...”*

Ishmael in *Moby Dick*
(Melville 1851, p. 191)

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Abstract

I explore bias in body-size and abundance indices that are derived from pelagic longline data, then describe historical variations in pelagic fish communities, and review possible causes of those variations. Most species of large, predatory tuna, billfish, and sharks, were characterized by significant declines in abundance soon after longline fishing commenced, followed by long-term stability. The largest and most abundant predators, such as sharks and large tunas, suffered the greatest declines in abundance. They also showed striking reductions in mean body-size.

I show how longline fishers have modified their fishing gear and practices to improve fishing power and catchability, which has altered the relationship between catch rates and abundance. Variations in hook depth, bait species, the local abundance of tuna, and the timing of longline operations influenced the rate of bait loss from pelagic longlines. A reduction in soak time since longlining commenced in the 1950s has introduced a systematic bias in estimates of mortality levels and abundance of most species. Habitat models are shown to be inaccurate in predicting the depth distribution of bigeye tuna. A new method that uses generalized linear mixed models is developed to infer the depth distribution of pelagic fishes. My analyses do not reveal anything unique about longline gear or pelagic animals that might explain the community variations.

I review hypotheses that explain the observed variations in pelagic fish communities. Avenues of future research that may help to explain the variations include studies of the removal of an accumulated biomass and changes in schooling behaviour related to density thresholds.

List of Abbreviations and Symbols Used

Symbol or abbreviation	Definition	Symbol or abbreviation	Definition
σ^2	Variance	N	Normal distribution
θ	Dispersion parameter	N	North
η	Linear predictor	<i>N</i>	Sample size
π	Probability of a bait being on a hook	nb	Negative binomial distribution
*	Statistically significant	NMFS	National marine fisheries service
<i>a</i>	Area	NND	Nearest neighbour distance analysis
<i>A</i>	Latitude	No.	Number
AIC	Akaike's information criterion	NP	North Pacific Ocean
ANOVA	Analysis of Variance	ns	Not statistically significant
<i>arl</i>	Autoregressive process with lag one correlation structure	<i>O</i>	Longitude (Appendix 2)
ave.	Average	<i>O</i>	Random effects distribution (Ch. 4)
<i>B</i>	Bait type (Ch. 3)	<i>O</i>	Three-month quarter (Ch. 3)
<i>bn</i>	Binomial distribution	<i>P</i>	Fishing period (Ch. 8)
<i>B</i>	Biomass index (Appendix 3)	<i>P</i>	Market price (Appendix 2)
<i>B</i>	Branchline loss rate (Appendix 2)	<i>P</i>	Pilchard (Appendix 2)
<i>b</i>	Length of the branchline	<i>P</i>	Poisson distribution
<i>B</i>	Number of hooks per buoy (Ch. 3)	<i>P</i>	Predicted proportion of species (Ch. 6)
BIC	Sawa's Bayesian information criterion	<i>P</i>	Probability
<i>C</i>	Catch	<i>P</i>	Probability distribution
<i>C</i>	Celsius	<i>P</i>	Proportion of longlining operations (Ch. 5)

Symbol or abbreviation	Definition	Symbol or abbreviation	Definition
C	Total costs	p	Vector dimension
C_{cubic}	Cubic model	P_0	Probability of capture when the hook is deployed
CI	Confidence interval	P_c	Probability density function of an animal being captured
C_{linear}	Linear model	PDO	Pacific decadal oscillation
cm	Centimetre	pers. comm.	Personal communication
coeff.	Coefficient	POFI	Pacific Oceanic Fisheries Investigations
CP	Central Pacific Ocean	P_r	Probability density function of a captured animal being retained
CPUE	Catch-per-unit-effort	q	Catchability coefficient
d	Day	Q	Squid
D	Depth	Q_0	Proportion of hooks that were vacant at the time of longline retrieval
D	Depth	Q_i	Proportion of hooks occupied by species i
d	Maximum settled depth	QQ	Quantile-quantile (plot)
D	Number of hooks per buoy	r	Correlation coefficient
D	Shark-damage rate	R	Operating profit
df	Degrees of freedom.	rd	Residual deviance
E	Cost of electronic equipment	Rel.	Released fish
E	East	Ret.	Fish that were brought on board
E	Fishing effort (Ch. 5)	S	Bait species (Ch. 3)
E	Longitude (Ch. 3, 8)	S	Proportion of mako shark (Appendix 2)
$E(y)$	Expected value of y (or mean value of y)	S	Scad (Appendix 2)
ENSO	El niño – southern oscillation	s	Second

Symbol or abbreviation	Definition	Symbol or abbreviation	Definition
eq.	Equation	S	South
exp	Exponent	<i>s</i>	Species identifier
<i>f</i>	Fishing effort	<i>S</i>	Time of longline deployment
<i>f</i>	Length of the floatline (Ch. 6)	SD	Standard deviation
<i>f(D)</i>	Depth distribution of catchability	SE	Standard error
F.	Taxonomic family	SN	Short-nosed (lancetfish)
FAD	Fish aggregating devices	SP	South Pacific Ocean
<i>g</i>	Gear configuration (Ch. 5)	SPC	Secretariat of the Pacific Community
<i>g</i>	Mean-link function (Ch. 3)	spp.	Species
GAM	Generalised additive model	SST	Sea surface temperature
GEE	Generalised estimating equation	Sword.	Swordfish
GLM	Generalised linear model	t	Metric ton
GLMM	Generalised linear mixed model	<i>t</i>	Time
<i>H</i>	Number of hooks	<i>T</i>	Time when the branchline is retrieved
<i>h</i>	Number of vacant hooks (Ch. 8)	TAO	Tropical atmosphere ocean
<i>h</i>	Proportion of hooks (Ch. 6)	TDR	Temperature–depth recorder
hk	Hooks	tot.	Total
hr	Hour	<i>u</i>	Catch rate
<i>i</i>	Longline operation identifier	<i>U</i>	Catch rate
<i>I</i>	Milkfish	US	United states
<i>i</i>	Species identifier (Appendix 2)	USD	US dollars

Symbol or abbreviation	Definition	Symbol or abbreviation	Definition
IQR	Interquartile range	V	Mean search volume
j	Hook identifier (Ch. 6)	var	Variance
j	Identifier of bait status observations (Ch. 3)	w	Mean weight
JFA	Fisheries Agency of Japan	W	West
k	Depth zone (Ch. 5)	WP	Western Pacific Ocean
K	Mackerel	x	Regressor vector
k	Sagging rate (Ch. 6)	Y	Nominal catch rate of tunas
kg	Kilogram	Y	Year
km	Kilometre	α	Capture rate
L	Body length	α	Effect of leader material on catchability
LM	Linear model	β	Estimated parameter
LN	Long-nosed (lancetfish)	B	Loss rate
log	Natural logarithm	γ	Estimated parameter
M	Month (Appendix 2)	Γ	Gamma function
M	Length of mainline between floats (Ch. 6)	δ	Shape parameter of mean-link function and regressor relationship
m	Metre	ΔA	Change in abundance
m	Total number of bait status observations	Δq	Change in relative catchability
MLL	Maximum log likelihood	μ	Mean
mm	Millimetre	π	Parameter representing variance in the binomial model
N	Latitude (Ch. 8)	π	Probability of an animal being on a hook when the branchline is retrieved (Ch. 4)
N	Local abundance	Φ	Angle of line drawn between mainline tangent and floatline-mainline intersection
		χ^2	Chi-square

Acknowledgements

I am indebted to my supervisor Ransom (“RAM”) Myers—his great ideas, enthusiasm, and perseverance remain an inspiration to me. I also thank my committee, Jeff Hutchings, Hal Whitehead, and Boris Worm for their support and guidance throughout my studies.

Observers and survey scientists are acknowledged for their tireless efforts in collecting data that were analysed in this thesis. Various fishermen, observers, and scientists provided me with the benefit of their experience and knowledge. In particular I am grateful to the help and advice provided by Bill Bayliff, Wade Blanchard, Albert Caton, Yoshimi Fukui, Kevin McLoughlin, and Richard Shomura.

Six chapters and two appendices of the thesis were submitted for publication in scientific journals. I am senior author of each of those journal articles. Each chapter of the thesis includes an Acknowledgements section that lists sources of support and contributions by colleagues. Author contributions to each article are listed in Student Contribution to Manuscripts in Thesis forms that were submitted with this thesis. Copyright Agreement Letters have been submitted separately for each published article.

Introduction

Background

Declines in Longline Catch Rates

Catch rates or catch-per-unit-of-effort (cpue) often show rapid declines soon after fishing commences (Ricker 1940; Hilborn 1985). Three recent studies have highlighted significant declines in longline catch rates of large predators in the open ocean. Baum et al. (2003) show that the catch rates of several species of large pelagic sharks have declined by 70% since 1986 in the Atlantic Ocean. Similar declines are reported in the Gulf of Mexico by Baum and Myers (2004). Analyses of commercial data from the Atlantic, Pacific and Indian oceans show a 90% decline in tuna (*Thunnus* spp.) and billfish (F. Xiphiidae and F. Istiophoridae) catch rates since pelagic longline fishing began in the 1950s (Myers and Worm 2003). Those catch rates are then relatively stable over long periods while total catches increase substantially. This presents a paradox. The initially low catch levels and rapid decline in catch rates suggest significant reductions in a relatively small population; subsequent sustained catches at high levels indicate a large population (Hampton et al. 2005a). Many researchers have attributed this pattern to an unexplained reduction in longline catchability and have dismissed or discounted those early data in assessments (Fournier et al. 1999). However, the causes of those variations have not been verified with independent estimates of fishing power or catchability. My thesis explores changes in longline fishing power and catchability, then describes variations in pelagic fish communities of the tropical Pacific Ocean, and reviews hypotheses that might explain those variations.

Longline Gear as a Sampling Tool

This thesis addresses the question of whether longline catch rates are a reliable index of abundance. Like other fishing methods, pelagic longlines are size- and species selective. This results in bias in size and abundance indices derived from longline data. It also results in the selective removal of components of animal communities.

The selectivity of longlines is determined by the gear's distribution in relation to the population's distribution ("availability") and the component of the population that the

gear can actually take (“vulnerability”). Longlines catch piscivorous animals larger than about 5 kg that are available in the mixed layer of the open-ocean (Kitchell et al. 1999). The minimum body-size is determined by the animal’s attraction to baits and its ability to ingest 20×30 mm hooks that are embedded in baits that are 100–300 mm long. There does not seem to be a limit to the maximum size of animals caught by longline because the gear provides struggling animals with considerable slack; they are eventually exhausted without breaking the line. Toothed whales (Suborder Odontoceti) sometimes remove bait or animals that are hooked on longlines. They are rarely caught because they are able to detect the gear (Bell et al. 2006).

Theory of Predator–prey Interactions

Understanding predator–prey interactions and the consequences of reductions in predator abundance is fundamental to managing natural resources. “Competitive release” is where the abundance of animals at the same trophic level increase in response to reductions in the abundance of their competitors. “Predator release” is the increase in prey abundance in response to reduced predation (Krebs 1978). The selective removal of large animals is a characteristic of human expansion into new environments (Pauly et al. 1998; Jackson et al. 2001). Many of the large animals were apex predators with ecological roles quite different to those of other animals—by eating smaller animals they influence the abundance, species composition, and size composition of lower trophic levels (Jackson and Sala 2001). In lakes, elevated predator abundance may create trophic cascades that eventually result in reduced phytoplankton abundance and improved water clarity (DeMelo et al. 1992). The idea of trophic cascades is based on a key tenet of ecology; that organisms interact. This is the basis of the “ecosystem approach” to resource management that considers the full range of flow-on effects on all ecosystem components (Krebs 1978).

It is easy to demonstrate that predators can alter prey populations on small temporal and spatial scales. The experimental manipulation of predator densities on reefs in the Bahamas, for example, resulted in significant variations in the survival of larvae of prey species (Carr and Hixon 1995). The distribution of bluegill sunfish (*Lepomis machrochirus*) contracted in the presence of predatory bass (*Micropterus salmoides*; Werner et al. 1983).

Predators can only regulate prey populations if the predator's consumption is density-dependent (Crawley 1992). In other words, the probability of an individual being removed by the predator is related to the prey's density. Mortality rates that are not density-dependent will eventually result in extirpation (where the prey's mortality rates exceed the intrinsic rate of natural increase) or will not affect prey population size (where they are below the rate of increase). By contrast, density-dependent mortality will set upper and lower bounds to prey population size (Strong 1992; Crawley 1992).

The trophic cascade is not a unified theory *per se*, but the consequence of predator–prey interactions. Prey populations may be resource-limited or they may be controlled by predation, or they may be subject to both types of controls. Trophic cascades can be viewed as a sequence of predator–prey interactions where consumption at each level depends on the density of the level below, i.e., there is regulation through density-dependent consumption at every trophic level except at the highest trophic level (Strong 1992; Larkin 1978; Crawley 1992).

Density-dependent mortality requires a feedback mechanism between prey density and mortality rates. Such mechanisms are classified as either functional responses (e.g., switching between prey species or aggregation that result in increased consumption rates at high prey densities) or numerical responses of the predator to prey density, e.g., increased predator density due to improved reproductive success or growth rates. Numerical responses involve time lags and are usually long-term, whereas functional responses are more immediate (Crawley 1992).

The term “trophic cascade” was introduced by Paine (1980), but the concept originated from two theoretical models: the Green World Hypothesis proposed by Hairston (1960) and the more general Exploitative Ecosystem Hypothesis of Oksanen et al. (1981) and Fretwell (1987). These hypotheses recognize that the population size of producers (plants) and predators is determined by density-dependent competition for resources—they are “resource-limited”. By contrast, herbivores are unlikely to compete for resources and are seldom resource-limited. Instead, they are “predator-limited”. The world is green because predators suppress herbivore populations, allowing producers to survive and grow (Polis et al. 2000).

In trophic cascades, changes in abundance are transmitted down through the system because each trophic level is inversely and directly related to adjacent trophic levels (Brett and Goldman 1996; Carpenter et al. 1992). A true trophic cascade involves three or more trophic levels so that variation in predation eventually affects the producers (Strong 1992). An increase in the abundance of piscivores, for example, reduces the abundance of their prey (planktivorous fish). In turn, the reduction in planktivores releases their prey (herbivorous zooplankton) from predation; then the increased abundance of herbivores reduces the abundance of phytoplankton (Brett and Goldman 1996).

The strength of interactions between trophic levels may dampen or magnify the cascade. There might be minimal effect on planktivores if the species of piscivore is just one of many predators that did not change in abundance. The response at each trophic level is likely to be nonlinearly related to the strength of interactions among adjacent levels (Carpenter et al. 1992).

Food webs may have “top-down” (i.e., consumer driven as in trophic cascades) or “bottom-up” control (i.e., nutrient or donor driven). Whether top-down or bottom-up controls predominate in particular systems has been extensively debated (DeMelo et al. 1992; Brett and Goldman 1996). Bottom-up processes are believed to be more important for lower trophic levels, whereas top-down processes are thought to be more important for higher levels. Top-down forces are reticulate—they have strong feedback mechanisms—whereas feedback mechanisms are weaker in bottom-up effects (Strong 1992). In more complex systems, the effects of trophic cascades may be buffered by defensive adaptations among producers, interspecific competition, omnivory, spatial and temporal heterogeneity in interactions, and prey refuges. Through “cultivation effects”, large predators may crop down the competitors and predators of their juveniles (Walters and Kitchell 2001). Consequently, variations in predator abundance affect the survival of juveniles of those same predator species. Such feedback mechanisms and the inability of ecosystem models to accurately predict the consequences of variations in predator abundance highlight the need to monitor how natural systems actually respond to reductions in the top trophic level.

Empirical Studies

Several authors assert that trophic cascades rarely occur in large, diverse ecosystems that are buffered by multiple trophic links and spatial heterogeneity. Strong (1992) argues that, in nature, trophic cascades are limited to low-diversity systems characterized by keystone species, e.g., discrete freshwater habitats where volatile algae are the producers. By contrast, Pace et al. (1999) review empirical studies of terrestrial and aquatic systems, and conclude that trophic cascades are more widespread than previously believed because it is unreasonable to simplify the systems into linear food chains and because of opportunistic feeding habits and ontogenic shifts. The relative importance of predators in structuring animal communities also depends on the scale at which it is investigated (Jennings and Kaiser 1998; Polis et al. 2000). Furthermore, predators may influence prey in some years or areas but not in others (Crawley 1992).

Fogarty and Murawski (1998) report that habitat modification and direct removals by fishing in the 1960s resulted in a reduction of over 50% in the total biomass of the fish populations of Georges Bank. They identified examples of competitive release within guilds, e.g., increased abundance of skates (F. Rajidae) and dogfishes (F. Etmopteridae) as a result of the selective removal of cods (O. Gadiformes) and flounders (F. Pleuronectidae).

A comparison of the Bering Sea ecosystem in the 1950s and 1980s highlighted the competitive release of apex predators; pollock (*Pollachius virens*) and flounders increased after a decline in Steller sea lion (*Eumetopias jubatus*) populations. Ecosystem models showed that the removal of prey by fishing quickly reduced the abundance of marine mammals, but their low reproductive potential delayed recovery when prey became abundant again (Trites et al. 1999). Other examples of in marine systems include Scheffer et al. (2005) and Frank et al. (2005).

The changes to terrestrial and coastal ecosystems are the product of habitat modification and removals by harvesting over many decades or centuries. However, population data were rarely collected at the beginning of human interaction (Jackson et al. 2001). The expansion of longline fishing to the open ocean is a relatively recent development. Previous exploitation of this ecosystem had been limited to harvesting whales, such as sperm whale (*Physeter macrocephalus*) since the early 1700s (Whitehead

2002). Data have been systematically collected since large-scale pelagic longlining began in the early 1950s in the then “pristine open oceans” (Steele 1998). Longlining rapidly expanded to high levels over enormous geographical scales. In the Pacific Ocean, total annual catches of pelagic species now amount to about 500 000 tons per year (SCTB 2004), which is taken from an area that is four times the size of the North American continent. I hypothesise that longline fishing in the 1950s resulted in the removal of large predators and an increase in prey species as a result of predator release.

Aim and Purpose

I show how the pelagic fish community of the tropical Pacific Ocean has changed since industrial longline fishing commenced in the early 1950s. To achieve this aim, methods are developed to interpret data collected by pelagic longline fishing gear. I then use those methods to describe changes in abundance, body-size, and community composition. Those variations have consequences for predator–prey interactions, which were reviewed in the preceding section.

The thesis makes the following contributions to knowledge of the ecology of open-ocean communities and longline fishing gear as a tool for sampling those communities:

- A stochastic model describing the probability of an animal being on a hook as an integral of the probability density functions of capture and retention.
- Parameter estimates that describe the effects of the day and night depth-distribution of catchability of pelagic species, which can be used to adjust abundance indices.
- Demonstration that habitat models produce misleading indices of abundance.
- The first estimates of the magnitude of variations in fishing power and catchability for a major fishing fleet.
- The first quantitative description of the abundance, body-size, and composition of pelagic fish communities in a relatively unexploited fishery, including rarely studied non-target species.

Structure

The relationship between longline catch rates and abundance is critical to understanding the variations in pelagic fish communities—whether they represent true variations in the communities or whether they are an artefact of the sampling method (longline fishing).

Chapter 2 describes variations in fishing operations since longlining commenced, focussing on Japan's distant-water longline fleet. Long time-series of catch and fishing effort data reported by this fleet are primary abundance indices for assessments of most commercially important tuna and billfish species and several other pelagic species, such as blue shark (*Prionace glauca*), in all three oceans. I quantify the effects of bait loss (Chapter 3) and timing (Chapter 4) on fishing power, and the effects of hook depth on catchability (Chapter 5). I also test "habitat models", which combine information on hook depth with the species' preferences for ambient environmental conditions to correct abundance indices (Chapter 6). Chapter 7 reviews a range of other factors that affect longline catchability.

Using the tools developed in Chapters 3–7, I describe variations in pelagic fish communities between the 1950s and recent years in the tropical Pacific Ocean (Chapter 8). Chapter 9 reviews hypotheses for the historical variations in those communities.

An Overview of Historical Changes in the Fishing Gear and Practices of Pelagic Longliners¹

Introduction

Size data and catch rates—catch-per-unit-of-effort or “CPUE”—from commercial longline fishing vessels are the primary source of information on the status of many fish species in the open ocean where fishery-independent methods of counting animals are impractical (Bishop 2006). However, improvements in fishing gear and practices will alter the relationship between catch rates and abundance, masking declines in fish stocks until they collapse (Cooke and Beddington 1984; Arregion-Sanchez 1996). Those variations will introduce serious flaws to time-series of abundance indices if the data are not adjusted or “standardized”.

Catchability is defined as the probability of catching an animal with a single unit of fishing effort (Paloheimo and Dickie 1964). It is a property of interactions between the gear and the animal’s behaviour. By contrast, fishing power or “fishing efficiency” is a property of the fishing gear and practices. It has its origins in attempts to standardize fishing effort among trawlers of various sizes, horsepower and swept area (Smith 1994). Beverton and Holt (1957) defined fishing power as a vessel’s effectiveness in catching animals relative to the effectiveness of a standard vessel. More generally, it is a measure of the catch taken by a unit of effort from a given density of fish in a specified time interval compared to the standard unit of effort (Gulland 1969; Smith 1994). For longline fishing gear, the number of hooks deployed is used as the unit of effort. Longline fishing power will be influenced by differences or changes in gear and practices that alter a

¹ This chapter has been submitted for publication as: Ward, P., and Hindmarsh, S. (submitted). An overview of historical changes in the fishing gear and practices of pelagic longliners, with particular reference to Japan’s Pacific fleet. Reviews in Fish Biology and Fisheries. The original article’s abstract is incorporated in the Conclusions of this thesis and its reference list is included in the Bibliography.

hook's effectiveness. For example, catch rates—and thus fishing power—may vary with soak time or depth of the hook.

In examining variations in fishing power and catchability it is useful to consider why fishers modify their gear and practices. Such modifications have a financial cost that fishers accept when they expect increased financial returns or savings in other areas of their operations. Increased returns can be achieved through improvements in the size, quality or catch rates of target species. Other reasons for modifying gear or practices include a reduction in operating costs, reduced labour, improved crew safety and, more recently, regulations that limit fishing effort or interactions with species of special concern e.g., seabirds. This article reviews variations that affect catch rates because they have consequences for stock assessments.

The focus is on historical developments in pelagic longline gear and practices, particularly for Japan's distant-water longline fleet. Long time-series of catch and effort data reported by this fleet are the key abundance index for assessments of most commercially important tuna and billfish species and several other pelagic species, such as blue shark (*Prionace glauca*), in all three major oceans. Pelagic longlines consist of a series of baited hooks, each attached to a branchline. The branchlines, which are also called snoods or gangions, are attached at 40–50 m intervals along a mainline. The mainline is suspended from buoys floating at the sea surface. The longlines deployed by large, distant-water longliners span 100 km of the sea's surface and consist of 3000–4000 baited hooks. They are usually deployed and retrieved within 24 hours (Ward 1996). Shorter longlines, with fewer hooks, are used by smaller vessels that land tuna and broadbill swordfish (*Xiphias gladius*) for fresh-chilled markets. The sparse and patchy spatial distribution of target species, diurnal cycles in their feeding activity and distance from port usually necessitate 24-hour operations, regardless of catch rates or vessel size.

Trends in Fishing Gear

Vessels

Prior to 1920, the relatively small size of vessels (< 20 m), their primitive propulsion (sail) and lack of refrigeration equipment limited longlining to short trips of several days in coastal waters of Japan. Fishers navigated by the position of celestial bodies and

environmental cues, such as ocean colour, surface currents and landmarks. They had no means of finding fish, other than their skills and past experience.

Steam-powered, steel longliners began operating in 1914 (Miyake 2004). The introduction of diesel-powered longliners in the early 1920s (Beverly et al. 2003) further increased fishing power by increasing the ability to remain on the fishing grounds and adjust fishing practices to local conditions and to follow target species. Large factory vessels (“motherships”), with up to 30 catcher-vessels, operated around what is now Indonesia in the early 1930s. By 1939 about 70 Japanese longline vessels of 60–270 gross registered tons (GRT) were operating from several north-western Pacific ports, with additional longliners based in Japan (Beverly et al. 2003). The offshore longliners mainly fished for albacore tuna (*Thunnus alalunga*) for canning or swordfish for domestic markets (Nakamura 1951; Wildman 1997). The area of activity contracted during the War in the Pacific and was limited by Allied Forces for the remainder of the 1940s (Nakamura 1950).

In the early 1950s, Allied Forces permitted mothership operations in an area of the equatorial western Pacific (Yamaguchi 1989). Subsequent relaxation of those restrictions and the introduction of large, freezer longliners in the mid 1950s facilitated the geographical expansion of longlining into distant waters. Within ten years the fleet had expanded across the Pacific and into the Indian and Atlantic oceans to cover all the tuna resources known today. In the late 1960s, distant-water longliners installed super-cold freezers (–40°C or lower) that allowed extended fishing trips of 12 months or longer, yet landing sashimi-quality tuna and billfish in Japan (Sakagawa et al. 1987). Trans-shipment, when practiced, also increased fishing power by allowing longliners to remain on fishing grounds for extended periods.

Longline Materials

Longliners improved catchability through progressive refinements to longline materials. Initially they used natural fibres, such as hemp (Beverly et al. 2003). More durable synthetic materials, such as kuralon, were first used for mainlines and branchlines in the 1960s. However, they were not widely used until the early 1980s (Yamaguchi 1989).

At first, longline leaders or “traces” were also made from natural fibres. The Japanese have used wire leaders since the 1920s to reduce the loss of hooked animals

from line-breaks and bite-offs (Shimada 1951b; Yamaguchi 1989). They began using nylon monofilament leaders in the mid 1980s (Mr. Peter Miyake pers. comm. 18 April 2006), which would increase catchability through their low refractive index and high tensile strength (more than 250 kg for a 2.5 mm line). On the other hand, the introduction of monofilament may have increased loss rates for several species with abrasive teeth (e.g., wahoo, *Acanthocybium solandri*), skin (e.g., sharks) or gill plates (e.g., yellowfin tuna, *Thunnus albacares*). Since the early 1980s, several fleets have used luminescent lightsticks to increase swordfish (Berkeley et al. 1981) and bigeye tuna (*Thunnus obesus*) catchability.

Early longliners used iron hooks, which sometimes broke or bent under stress and corroded, thereby reducing the hook's sharpness. The use of tin-plated, tempered iron hooks in the 1950s and galvanized high-carbon steel and stainless steel hooks in the 1980s increased fishing power (Otsu 1954; Yamaguchi 1989). Similar changes to wire leaders reduced corrosion.

Hook design has also evolved, with the Japanese tuna hook replacing "J" hooks by the early 1970s (Shimada 1972). In the 2000s, circle hooks were adopted by several fisheries to mitigate sea turtle bycatch (Figure 2.1). Field trials indicate that circle hooks do not significantly affect the catchability of tuna and sharks, but they may reduce the catchability of swordfish (Watson 2005).

Communications

Communication is essential to finding fish in the open ocean. The Japanese began using radio telegraph in 1908 for ship-to-shore communication (TBMIAC 2006). By 1927, 120 Japanese fishing vessels had installed wireless communication equipment (Yamaguchi 1989). In 1959, all Japanese vessels over 100 GRT were required to carry radio transceivers (Kodaira 1959). Distant-water longliners had a dedicated radio operator among their crew, highlighting the importance of radio communication. Since the early 1980s, weather facsimiles ("weather fax") have provided longliners with weather maps annotated with information on sea surface temperature, the position of other longliners and areas of current and past catches (Yamaguchi 1989; Whitelaw and Baron 1995). Since the 1980s, satellite-based communication systems (e.g., Inmarsat-C and satellite

telephones) have provided more reliable and secure, global communication (Inmarsat 2006).

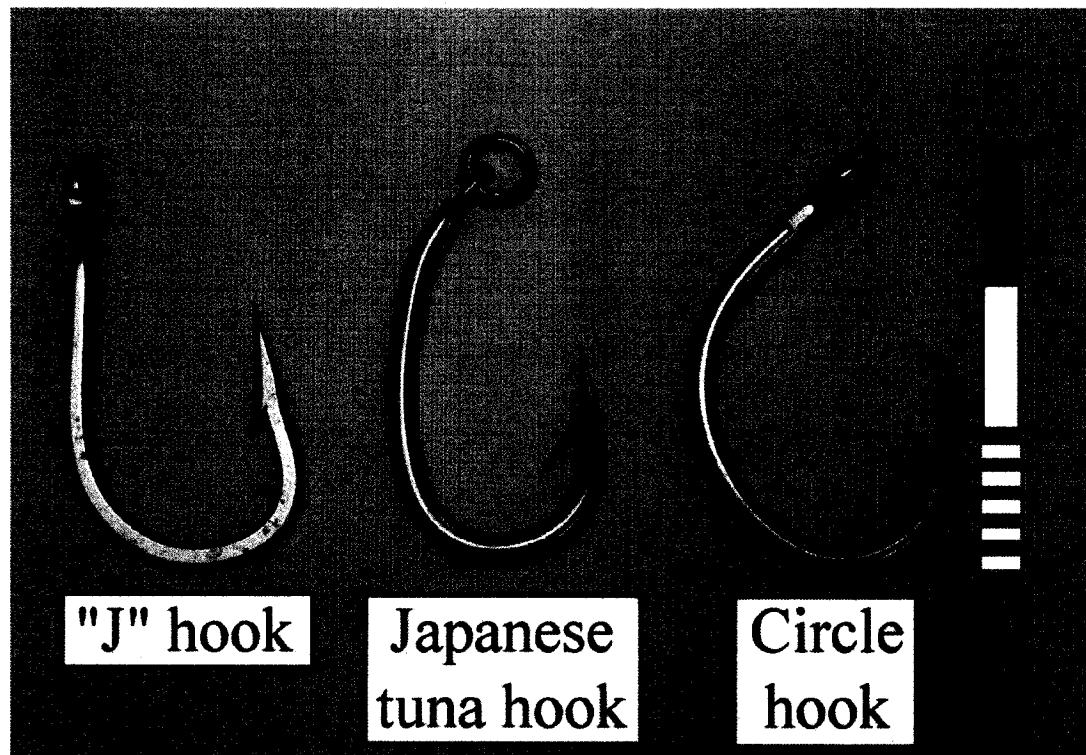


Figure 2.1. Examples of the three types of hooks used by pelagic longliners: “J” hook (manufactured by Forman Tech Co. Ltd.), Japanese tuna hook (Kabuto) and circle hook (Maruto). In recent years, US longliners have used much larger circle hooks ($\geq 16/0$) to reduce sea turtle bycatch.

Navigation

Satellite navigation (SatNav) and Global Positioning Systems (GPS) have provided longliners with frequent, very accurate fixes on their positions since the late 1970s. This allows fishers to locate bathymetric features, such as underwater seamounts. When related to satellite imagery, it allows fishers to find oceanographic features where target species are known to aggregate, e.g., temperature fronts.

Fish-finding

Since the early 1960s, Japanese longliners have used echo-sounders to detect the deep-scattering layer, concentrations of plankton and forage species, tuna schools and variations in current direction and velocity (Tominaga et al. 1963). Longliners also use echo-sounders to locate seamounts (Mr. Peter Miyake pers. comm. 15 April 2006). Multi-

directional sonar has been used by longliners to locate and target aggregations of fish, or to identify individual fish since the mid 1980s. Soon after, Doppler current profilers were introduced to determine the velocity and direction of currents at various depths. With knowledge of subsurface currents, fishers can also adjust the depth and direction of longline deployment to reduce mainline breaks and tangles and thereby maximize the availability of baited hooks to target species.

Longliners use remotely-sensed images to locate oceanographic features where target species may be abundant, thereby reducing searching time and increasing fishing power. They have used sea surface temperature imagery since the 1970s to locate temperature fronts (Mr. Johnny Aoki pers. comm. 10 October 2006). Ocean colour and sea surface height imagery has been available since 1990 for identifying biologically-rich areas of upwelling and current shear. Lyne et al. (2000) found that longline catch rates of several species were significantly correlated with ocean colour, sea surface temperature and proximity to temperature fronts. New systems integrate the various technologies. For example, satellite imagery, radar, GPS, plotters and depth sounders can be interfaced on computers to provide sophisticated, multi-dimensional images that include the location of recent catches.

Fishers on large longliners have quickly adopted the new technology, partly because the cost of such equipment represents a small proportion of their total operating budget (Figure 2.2). For a typical large longliner in the late 1990s, for example, the purchase price of electronic devices was about \$US 150 000. Over the lifetime of those devices, this amounts to a small proportion of the value of the vessel's annual operating costs (about \$US 2.850 million per year; Reid et al. 2003).

Figure 2.2. Time-line of the uptake of gear and electronic devices by pelagic longliners. Indicative purchase price is shown for equipment used on a typical distant-water longliner in the 1990s

Device or system	Cost (USD) ^a	1950	1960	1970	1980	1990	2000	Key references
Radio communication	\$8 640							Kodaira (1959)
SST monitor	\$3 200							Shapiro (1950)
Radar	\$13 900							Suiyo-Kai (1959)
Sounder	\$5 070							Tominaga et al. (1963)
Sonar	\$29 000							Simrad (2006)
Loran	—							Anon. (1987)
Decca	—							Decca (1959)
Line hauler	\$4 200							Izumi Iron Works (1959)
Radio direction finder ^b	\$21 722							Yamaguchi (1989)
Monofilament leader	—							Miyake (2004)
Plotter	\$13 500							Kawai (1995)
Circle hook	—							Montrey (1999)
Super-cold freezer	—							Miyake (2004)
Bathythermograph	—							Shea et al. (1995)
Weather facsimile	\$1 600							Yamaguchi (1989)
Japanese tuna hook	—							Shimada (1972)
Satellite navigation	—							Whitelaw and Baron (1995)
SST imagery	\$1 080							Butler et al. (1988)
Lightsticks	—							Berkeley et al. (1981)
Monofilament mainline	—							Okamoto et al. (2003)
Inmarsat communication	—							Inmarsat (2006)
Global Positioning System	\$3 590							Whitelaw and Baron (1995)
Ocean colour imagery	—							Svejkovsky (1996)
Doppler profiler	\$41 098							Whitelaw and Baron (1995)
Personal computer	\$5 800							Beverly (2001)
Sea surface height imagery	—							Orbinage (2006)
Total	\$152 400	1950	1960	1970	1980	1990	2000	
Legend:								
^a Purchase price of two units of each device in the late 1990s, excluding annual fees, installation, and maintenance costs.								
^b Includes the cost of 23 radio buoys.								
no record of use by longliners								
limited use or used by specific fleets								
used by up to 50% of longliners in many fleets								
used by most longliners								

Trends in Fishing Practices

Bait

Bait species and type (e.g., frozen, fresh, alive) affects catchability and fishing power through its ability to attract animals and to remain on the hook. Japanese longliners initially used pilchard (*Sardinops sagax*) and saury (*Cololabis saira*; Shapiro 1950; Ego and Otsu 1952). They mostly deployed frozen saury during the 1960s and 1970s in the tropical central Pacific Ocean. Other species (e.g., mackerel, *Scomber* spp.) gradually replaced saury in the late 1970s (Figure 2.3). Observers reported that Japanese longliners off eastern Australia in 1985–95 mostly used frozen mackerel (43% of baits), pilchards (23%) and squid (23%). In other areas, squid has been the most popular bait since about 1970 (Mr. Johnny Aoki pers. comm. 10 October 2006). It increases the catchability of bigeye tuna and swordfish and is less likely to be removed from hooks by scavengers or by turbulence (Murphy 1960; Ward and Myers submitted). Recent increases in squid prices have resulted in several fleets reverting to fish bait, although the Japanese distant-water fleet has continued to use squid (Mr. Peter Miyake pers. comm. 15 August 2006). Various artificial baits have been tested, but they tend to have lower catch rates than real bait, e.g., Tsurudome (1970).

Locally-based longliners used live milkfish (*Chanos chanos*) in the equatorial Pacific in the mid 1990s, which elevated yellowfin tuna catch rates (Fitzgerald 1996). Live bait continues to be used by longliners in the Gulf of Mexico and off south-eastern Australian where it improves the catchability of yellowfin tuna and billfish, e.g., blue marlin (*Makaira nigricans*; Scott et al. 2000).

Number of Hooks

In using the number of hooks as the measure of fishing effort, it is assumed that adjacent baits do not compete for catches. The number of hooks deployed in each operation by Japan's longliners increased from about 1200 hooks in the 1950s to well over 3000 by the late 1990s (Campbell 1997). Locally-based longliners deploy fewer hooks, typically ranging from 500 to 1500 hooks per operation. Appendix 2 shows that the distance between hooks (~45 m) along longlines has not changed significantly since the early 1950s. Polacheck (1991) found no statistically significant effect of hooks per operation on catch rates of bigeye or yellowfin tuna in the tropical western Pacific. Nevertheless,

particular features where target species are found, such as temperature fronts or seamounts, may be smaller than the distance covered by the longline. Hooks that are deployed in less suitable areas will have lower catch rates on average. Therefore, an increase in the distance covered by the longline may reduce overall fishing power. This may be why small, locally-based longliners often report higher catch rates than larger longliners fishing nearby.

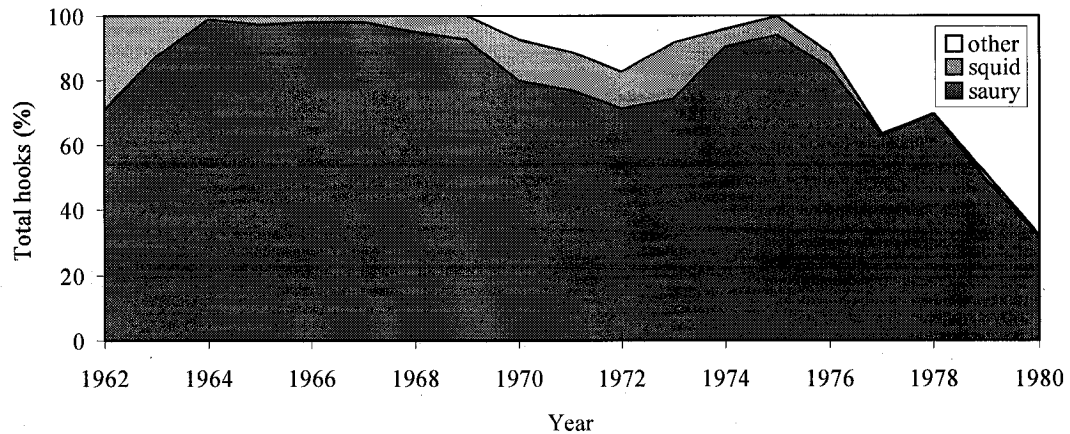


Figure 2.3. Variations in the species of bait used by Japanese longliners in the tropical central Pacific, 1962–80 (JFA 1962–80). Observer data suggest that the category “other” is likely to be mostly pilchards and mackerel.

Soak Time

The increased number of hooks per operation might be expected to result in longer soak times. However, the increases in hook numbers were accompanied by increased retrieval and deployment speeds and reduced time between the completion of deployment and commencement of retrieval (Figure 2.4). Branchline coilers and line-haulers resulted in increased retrieval speeds. Line-shooters or “line-throwers” increased setting speeds. Consequently, the average soak time of longline hooks decreased, from about 11.5 hours in the 1950s to 10.0 hours in the 1990s. Ward et al. (2004) estimated an expected catch rate for swordfish of 0.94 per 1000 hooks for a soak time of 11.5 hours compared to 0.82 per 1000 hooks for 10.0 hours. The reduction in soak time is due to increased deployment and retrieval speeds that were necessary to allow more hooks to be used each day.

There are occasional reports of longliners during the 1950s and locally-based vessels patrolling their longlines. This involved hauling branchlines that had already

caught an animal, then rebaiting the hooks and returning them to the water, thus increasing fishing power. The increased number of hooks deployed since the 1950s and subsequent contraction in the period between deployment and retrieval has precluded large longliners patrolling their longlines (Mr. Johnny Aoki pers. comm. 10 October 2006).

Time of Day

Longline catchability is closely linked to the availability of baited hooks at peak feeding times. Generally, longliners that target swordfish deploy their longlines at dusk and commence retrieval at dawn so that baited hooks are available at night and during crepuscular periods. Longlines are deployed at dawn and retrieved in the late afternoon and evening to catch tuna (Ward and Elscot 2000). Japan's longliners initially commenced deployment after midnight so that most baited hooks were available at dawn, but many were retrieved before dusk. By the 1990s they had adjusted operation times so that more hooks were available at dusk (Figure 2.3). Analyses presented by Ward et al. (2004) show that those differences would affect catch rates of target and non-target species. For example, the expected catch rate for bigeye tuna for bait that is available at dawn and dusk is about double that for bait available at dawn only (with other factors, such as depth, location and soak time, held constant).

Lunar Cycle

Fishers have long been aware of the influence of the lunar cycle on catchability through its effects on tides, currents, light levels and animal behaviour, including the timing of spawning, feeding and migration (Omori 1995). Moon phase is often a statistically significant correlate that is included in models used to standardize fishing effort, e.g., Bigelow et al. (1999). Locally-based longliners often time their trips to coincide with full moons to maximize their catch rates of swordfish. Observers also report that Japanese longliners sometimes targeted swordfish around full moons with shallow longlines deployed at night over seamounts off eastern Australia (Ward and Elscot 2000).

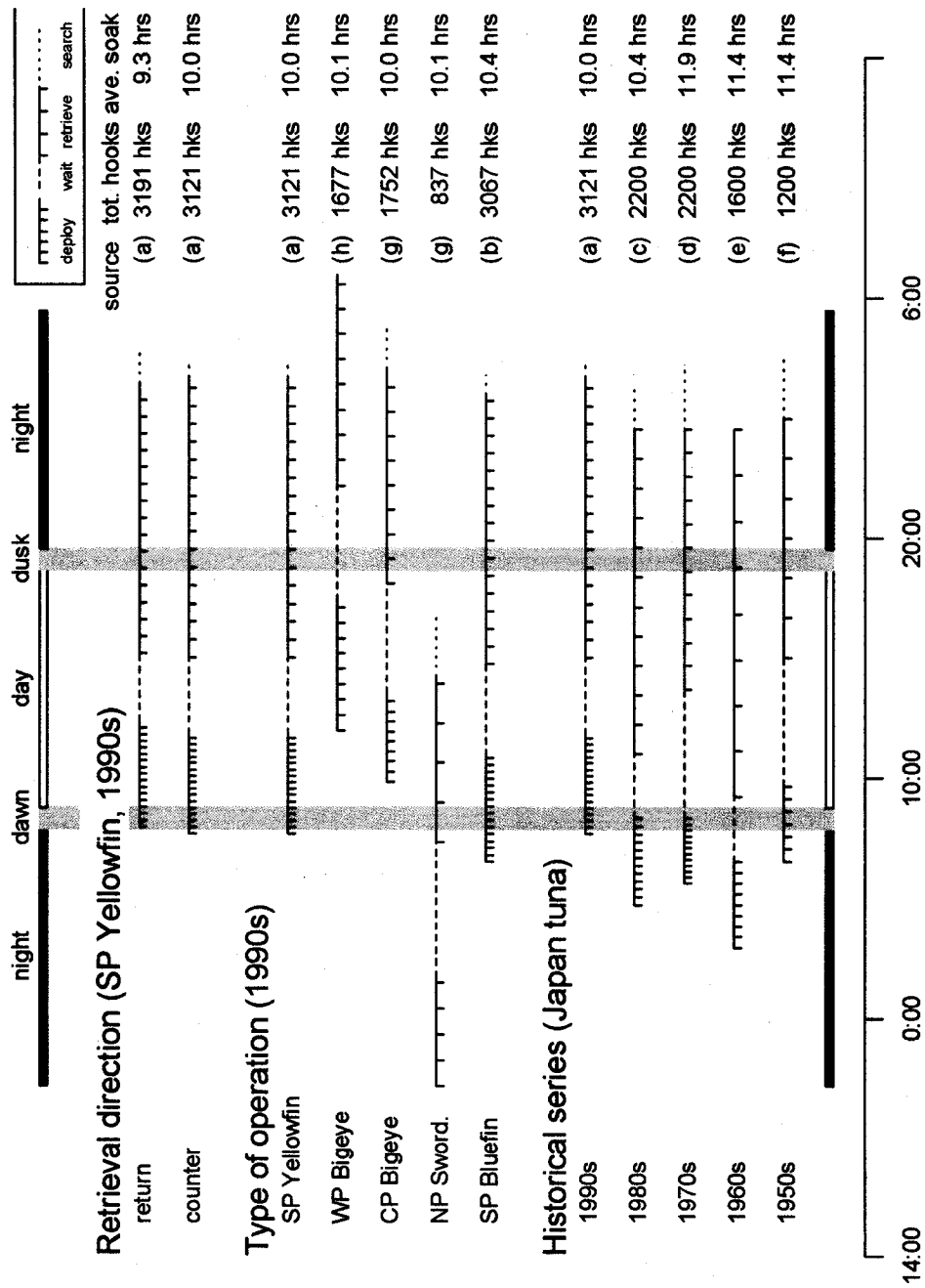
Figure 2.4. Schematic representation of the duration of various types of longline operations. Also shown is the average number of hooks deployed per operation and the average soak time for all hooks in each type of operation. Each tick mark represents 200 hooks so that the density of ticks reflects deployment and retrieval speeds. Longlines are usually counter-retrieved (retrieval begins with the last buoy deployed), except for the return retrieval shown for Japan's longliners in the South Pacific yellowfin fishery. The historical series is based on data for the South Pacific yellowfin fishery for the 1980s and 1990s. For other decades the series uses published sources for Japan's longliners fishing for yellowfin and bigeye tuna in the tropical Pacific Ocean.

Abbreviations of fishery names:

NP	North Pacific	WP	Western Pacific	Sword.	Swordfish
CP	Central Pacific	SP	South Pacific	Bluefin	Southern bluefin tuna (<i>Thunnus maccoyii</i>)

Sources:

- (a) Australian Fisheries Management Authority observer data (South Pacific yellowfin fishery, 1992–97)
- (b) Australian Fisheries Management Authority observer data (South Pacific bluefin fishery, 1992–97)
- (c) Yamaguchi (1989)
- (d) Au (1985)
- (e) Sivasubramaniam (1961) and Maéda (1967)
- (f) Shapiro (1950) and Shimada (1951b)
- (g) US National Marine Fisheries Service observer data (1994–99)
- (h) Secretariat of the Pacific Community observer data (1990–99)



Depth

The vertical distribution of many pelagic animals depends on their behavioural responses to physical and biological conditions that are depth-dependent, e.g., ambient temperature, oxygen concentration, light levels, prey and predators (Dagorn et al. 2000). The depth range of baited hooks determines which components of the pelagic community are exploited and thus longline catch rates and the species- and size-composition of catches. During deployment, fishers routinely adjust the longline's depth by varying the vessel's speed, the mainline's tension and the distance between floats. They may also increase depth range by adding weights to the mainline or branchlines and by increasing the lengths of floatlines or branchlines. Line-shooters are used in most fleets to slacken the mainline by pulling the line from the reel or bin at a rate faster than the vessel's speed. This reduces tension on the mainline, allowing it to settle at greater depths.

The number of branchlines between floats or "hooks-per-basket" is often used as an index of longline depth if the mainline is assumed to form a catenary curve between floats. Variation in longline depth has received close attention in assessments (Suzuki et al. 1977; Hinton and Nakano 1996; Bigelow et al. 2002). Before the mid 1970s the Japanese deployed their longlines at relatively shallow depths (25–170 m) by maintaining tension on the mainline and having a long distance between floats relative to the length of the mainline (about 4–6 hooks-per-basket). The Koreans were the first to use deep longlines (Koido 1985), followed by the Japanese in the Pacific and Indian Oceans in the early 1970s and in the Atlantic Ocean in the late 1970s (Suzuki et al. 1977; Sakagawa et al. 1987). Deep longlines consist of 10 or more hooks-per-basket, with a depth range of 25–300 m or deeper. They continue to be used by Japanese longliners in tropical waters and by other fleets that target bigeye tuna where the thermocline and oxycline are deep, e.g., Hawaii, Fiji, Korea and, more recently, Taiwan.

Depths obtained from depth sensors often differ from depths predicted by the catenary formula. Wind and current shear may cause hooks to rise towards the surface or "shoal". Bigelow et al. (2006), for example, estimated that the hooks adjacent to the floats on longlines with 13 hooks-per-basket shoaled by about 20% when subjected to a current velocity of $0.4 \text{ m}\cdot\text{s}^{-1}$. Observers report that fishers minimize shoaling by

deploying their longline in the same direction as currents, as determined with Doppler current profilers.

Bycatch Mitigation

Several fishery management agencies have legislated the use of weighted swivels to reduce seabird bycatch, e.g., Australia since 2005. Other mitigation measures include bird-scaring lines (“tori lines”), night-deployment of gear, complete thawing of bait, sub-surface setting chutes, side-setting, circle hooks (to reduce turtle bycatch) and the banning of wire leaders (to reduce shark bycatch). These measures will also increase fishing power by reducing bait loss and may affect the catchability of target and non-target species (see review by Bull, in press).

Measuring Fishing Power and Catchability

Commercial enterprises rarely report systematic analyses of the comparative performance of fishing gear; and there are few published studies on the effects of particular innovations on fishing power or catchability. Large companies and fleets that freely share information might gain some insights into the performance of new gear and practices. However, it is extremely difficult for individual fishers to quantitatively compare the performance of new and old gear because of the variability in the temporal and spatial distribution, abundance and availability of target species in the open ocean.

Several methods are available for estimating the effects of fishery changes. Effort standardization involves fitting models—such as generalized linear models—to data on catch, effort and covariates that might affect fishing power or catchability, such as area of activity and longline depth (Maunder and Punt 2004; Bishop 2006). However, uptake of innovations is often very rapid, reducing the overlap between the use of old and new gear and practices and thereby reducing the statistical power of analyses. Such models require large data sets, such as historical time-series of commercial longline data. Where information is not available, it may be possible to develop synthetic data series of covariates. Lee et al. (2005), for example, use species composition data to categorize the depth range of pre-1995 longline operations. Bishop (2006) highlights the need to develop estimation models for extrapolating from commercial catch and effort datasets that quantify bias in parameter estimates, rather than relying on prediction models that are subject to confounding among variables.

Empirical experiments are another way of estimating variations in fishing power or catchability. The effects of hook design on catchability, for example, can be reliably estimated by alternating the different hook types (e.g., circle and “J” hooks) along the same longline, with details recorded on the species caught on each hook. Each hook pair can be treated as a separate experiment in a conditional logistic regression. At a broader level, it is possible to gain insights into variations in fishing power by comparing the performance of two or more vessels using different gear or practices. Robins et al. (1998), for example, examined the impact of GPS and plotters on fishing power in an Australian prawn fishery. They found that vessels using GPS had 4% greater power than vessels without GPS. The addition of a plotter increased power by 7% over vessels without this equipment. Power increased by 12% when both pieces of equipment were used for at least three years (Robins et al. 1998). In one of the few studies of longliner fishing power, Lin et al. (1997) compared the performance of longliners using contemporary and traditional longline systems. For 27 pairs of longlines within about 12 km of each other, the contemporary system’s catch rates of target species were up to 1.67 times higher than those of the traditional system. Lin et al. attributed the difference to increased deployment and retrieval speeds (resulting in longer soak times) and the deeper depths reached by the contemporary system.

Gulland (1969) shows how estimates of fishing power can be combined by the summing of each unit’s fishing power multiplied by its fishing time, which is equivalent to the product of the gear’s swept area and the proportion of animals in that area that is retained by the gear. Statistically robust methods need to be developed to allow overall changes in catchability to be derived from several different experiments, e.g., the results of hook design experiments combined with bait and leader material experiments conducted in a different fishery.

Our review identifies many studies that have quantified the effects of hook depth on catchability (Table 2.1). In the 1950s several studies demonstrated the effects of bait species on catchability. Since then, however, few bait studies have been published, despite considerable variations in the bait species used by longliners. Concerns over bycatch have recently led to many experiments with mitigation measures. These have also provided estimates of the effects of those measures on fishing power and the

catchability of target and other non-target species. For example, several studies have estimated the effects of bird-scaring lines on the number of baits removed by seabirds during longline deployment (Bull, in press). Very few studies have investigated the effects of line materials or electronic devices that assist in navigation, communication or fish-finding. Of note is the absence of published comparisons of the fishing power of nylon monofilament and wire leaders. Wire leaders have been banned in several fisheries because they are believed to increase shark mortality. Our literature searches were mainly limited to publications in English. There are likely to be other studies on variables affecting fishing power and catchability that have been published in other languages, particularly by the Japanese who were particularly active in this area during 1930–80.

Further Work

The many developments in gear and practices are likely to have increased fishing power and the catchability of target species (and any non-target species that are closely associated with those target species). We need to identify which technologies have had the greatest effect on fishing power and catchability and then develop methods for monitoring and quantifying those effects. Improvements to existing equipment, such as the range and precision of sonar, and the expertise of operators, interpretation of information, the development of communication networks that enhance searching will significantly affect fishing power and catchability. There is also considerable variation in skill among fishers (Hilborn and Ledbetter 1985; Squires and Kirkley 1999). A particular device might significantly affect fishing power for one vessel, whereas it might be used incorrectly or not used at all on other vessels. Empirical comparisons of performance will therefore be complex and comparisons made when new fishing gear and practices are first introduced are likely to underestimate their true effects on fishing power and catchability.

Conclusions

The many developments in gear and practices are likely to have increased fishing power and the catchability of target species (and any non-target species that are closely associated with those target species). By the 1990s, many longliners had installed a sophisticated array of electronic communication, navigation and fish-finding equipment.

The introduction of technology based on computer-chips and satellites in the 1980s was essential for those improvements. Variations in bait, hooks, lightsticks and leader materials are likely to have changed catchability by affecting the probability of an animal attacking bait, being hooked and being landed. Other innovations have increased the availability of baited hooks (e.g., deeper longlines), improved searching efficiency (e.g., satellite imagery) and increased time on fishing grounds (e.g., freezers), providing fishers with opportunities to adapt to local conditions and to follow the fish. The establishment of major fishing companies in Japan during the 1950s provided logistical support for longliners and networks for sharing information.

Research surveys or surveys utilizing commercial fishing vessels should be considered for estimating the abundance of pelagic fish in the open ocean because of the problems in measuring fishing power and catchability in commercial longline fisheries. Assessments of several major groundfish fisheries use abundance indices derived from regular research surveys that use standard demersal fishing gear and practices at predetermined stations (Sullivan and Rebert 1998). Surveys have rarely been attempted in the open ocean apparently because of the high cost of obtaining representative samples from a system that features vast distances and high spatial and temporal variability (Bishop 2006). It will be essential to estimate variations in fishing power through surveys and experiments that compare the performance of past and current longline gear and practices if surveys or other fishery-independent methods do not prove to be feasible for estimating the abundance of pelagic fish in the open ocean.

Acknowledgements

The Bureau of Rural Sciences supported the compilation of this article. The article is largely based on the observations of fishers, observers, scientists and other experts, including Johnny Aoki, Steve Auld, Steve Beverly, Deirdre Brogan, James Findlay, Gretchen Fitzgerald, Jay Hender, David Itano, Makoto (Peter) Miyake, Dae-Yeon Moon, RAM Myers, Tim Park, Martin Scott, Bob Stanley, John Watson and Peter Williams. Albert Caton, James Findlay, Kevin McLoughlin and two anonymous referees provided comments on drafts of this article.

Table 2.1. Summary of published studies that have measured variations in the fishing power or catchability of pelagic longline fishing gear. The variables listed here are not necessarily mutually exclusive, e.g., bait type, soak time and depth may all affect the rate of bait loss. Where there is no published study, variables are not listed, e.g., fish-finding equipment. Studies that have investigated the short-term effects of environmental variables (e.g., temperature and season) on availability are not included in this table.

Variable	Region	Data source ^a	Analytical methods ^b	Key conclusions on fishing power or catchability	Author(s)
Gear saturation	Tropical Central Pacific	Experiment	Arithmetic mean	Increasing the density of hooks resulted in reductions in yellowfin tuna catch rates.	Murphy and Elliot (1954)
Gear saturation	Tropical Pacific	Survey	ANOVA, runs test, deterministic model	Longlines encounter tuna aggregations or schools, which may result in gear saturation.	Murphy and Shomura (1955); Maeda (1967)
Gear saturation	New Zealand	Observer	NND	Longlines encounter aggregations or schools of tuna and striped marlin.	Kirby et al. (2003)
Gear saturation	Tropical Central Pacific	Logbook	Deterministic model	Gear saturation unlikely to significantly affect fishing power at the catch levels encountered by pelagic longliners.	Murphy (1960); Rothschild (1967)
Bait loss	Tropical Central Pacific	Survey	ANOVA, GEE	Loss rates increased with soak time and local tuna abundance, but declined with hook depth.	Shomura (1955); Ward and Myers (submitted)
Bait species	Tropical Central Pacific	Observer	ANOVA	Saury and sardine baits do not affect tuna or marlin catch rates.	Murphy and Otsu (1954)
Bait species	Tropical Pacific and Indian Ocean	Experiment	Arithmetic mean, chi-square, ANOVA, Scheffé's test	Bait species and mixes of baits affected catch rates of most tuna and billfish species.	Anonymous (1952); Shomura (1955); Shimada and Tsurudome (1971); (Shimada 1972); Bach et al. (2000)
Bait species	Equatorial Indian Ocean	Experiment	—	Artificial bait reduced catch rates of tuna and billfish.	Tsurudome (1970)

Variable	Region	Data source ^a	Analytical methods ^b	Key conclusions on fishing power or catchability	Author(s)
Bait status	Various	Survey, experiment, observer	ANOVA	Bait status (fresh, frozen, etc) did not affect tuna catch rates, but reduced bait loss from seabirds when bait is fully thawed.	Shomura (1955), Brothers et al. (1995), Duckworth (1995), McNamara et al. (1999), Boggs (2001), Gilman et al. (2003)
Bait status	Gulf of Mexico	Observer, logbook	GLM	Catch rates of billfish are higher on live bait than on dead bait.	Scott et al. (2000)
Bait size	Tropical Pacific and Indian oceans	Experiment	–	Marlin catch rates were higher on large baits like mackerel. Tuna catch rates were higher on small saury.	Shimada and Tsurudome (1971)
Soak time	Tropical Pacific and Indian Ocean	Survey	ANOVA	Bigeye catch rates increased with soak time, whereas yellowfin catch rates were highest at intermediate soak times.	Sivasubramaniam (1961)
Soak time	Pacific Ocean	Observer	GLMM	Catch rates of sharks and billfish increased with soak time, but declined for small species, perhaps because of depredation.	Ward et al. (2004)
Depth	Tropical Oceans	Survey	ANOVA, paired t-test, multiple regression	Catch rates of epipelagic ^c species were higher on shallow hooks, whereas catch rates of mesopelagic ^c species were higher on deep hooks. Catch rates of mesopelagic species increased on shallow hooks at night.	Rey and Munoz-Chapuli (1991); Boggs (1992); Higashi and Yuwaki (1993); Nakano et al. (1997); Matsumoto et al. (2001); Musyl et al. (2003); Yokawa and Saito (2004)
Depth	Tropical Oceans	Logbook	Arithmetic mean, LM	As above.	Suzuki et al. (1977); Suzuki and Kume (1981); Koido (1985); Gong et al. (1989); Rey and Munoz-Chapuli (1991); Yokawa and Saito (2004)
Depth	Tropical Central Pacific	Observer	GLMM	As above. Parameters for day and night depth-dependent catchability estimated for 37 pelagic species.	Ward and Myers (2005)

Variable	Region	Data source ^a	Analytical methods ^b	Key conclusions on fishing power or catchability	Author(s)
Leader material	North-western Atlantic	Experiment	Chi-square goodness of fit	Catch rates of most species on nylon monofilament leaders significantly higher than that on multifilament leaders.	Stone and Dixon (2001)
Bird-scaring ("tori") line	High latitudes	Observer	–	Bird-scaring lines reduced catch rates of seabirds and increased fishing power through reduced bait loss.	Imber (1994); Duckworth (1995); Keith (1998)
Weighted swivels	High latitudes	Observer	–	Weighted swivels reduced catch rates of seabirds and increased fishing power through reduced bait loss.	Brothers et al. (2001); Baker and Robertson (2004)
Lightsticks	Eastern Australia	Experiment	Arithmetic mean	Lightsticks increased swordfish and yellowfin catch rates. Hooks with lightsticks may attract animals away from nearby hooks without lightsticks.	Williams (1993)
Lightsticks	North Pacific	Logbook	GAM	Swordfish and blue shark catch rates increased significantly with lightsticks.	Bigelow et al. (1999)
Vessel	Equatorial Western Pacific	Experiment	Chi-square	Total and target species catch rates on monofilament mainlines were significantly higher than those on kuralon mainlines	Lin et al. (1997)
Vessel	Western Atlantic	Logbook	Arithmetic mean	Swordfish catch rates of US longliners were significantly higher than those of Spanish longliners.	Hoey et al. (1987)
Vessel	Western Atlantic	Logbook	GLM	Vessel identity significantly affected blue shark catch rates.	Campana et al. (2006)
Lunar cycle	North Pacific	Logbook	GAM	Swordfish catch rates increased significantly with lunar index.	Bigelow et al. (1999)
Lunar cycle	Eastern Australia	Survey	GAM, GLM	Swordfish, bigeye and yellowfin catch rates increased with lunar index.	Lyne et al. (2000)

Variable	Region	Data source ^a	Analytical methods ^b	Key conclusions on fishing power or catchability	Author(s)
Hook shape	Various	Experiment	χ^2 analysis, GLM, paired t-test, ANOVA	Effects of circle, "J" and tuna hooks on catch rates vary among species and among fisheries. Swordfish catch rates are sometimes lower on circle hooks.	Falterman and Graves (2002); Poulsen (2004); Bolten and Bjørndal (2005); Watson et al. (2005); Kerstetter and Graves (2006); Yokota et al. (2006)
Hook size	Various	Experiment	Paired t-test, Friedman χ^2	Hook size does not affect the catchability of large predators, but will limit the minimum size of animals with a small gape, e.g., sea turtles.	Watson et al. (2004); Bolten and Bjørndal (2005)
Time of day	Various Pacific fisheries	Observer	GLMM	Catch rates of most tuna and sharks species increased during crepuscular periods, particularly at dusk.	Ward et al. (2004)
Satellite imagery	North Atlantic	Logbook	GLM	Catch rates of swordfish, were significantly correlated with distance from temperature fronts.	Podesta et al. (1993)
Satellite imagery	Eastern Australia	Survey	GLMM, GAM	Catch rates of swordfish, yellowfin and bigeye were significantly correlated with fine-scale ocean colour, sea surface temperature and distance from temperature fronts.	Lyne et al. (2000)

^aEstimates of longline fishing power and catchability have been obtained from experiments that tested the effects of two or more variables on longline catches; research surveys that used standard fishing gear and practices; or from catch, effort, and gear data reported by fishers in logbooks or by observers on commercial longliners.

^bAnalytical methods include analysis of variance (ANOVA), chi-square (χ^2), nearest neighbour distance analysis (NND), linear regression or linear models (LMs), generalized linear models (GLMs), generalized linear mixed models (GLMMs), generalized additive models (GAMs), and generalized estimating equations (GEEs).

^cEpipelagic species (e.g., blue marlin and mahi mahi, *Coryphaena hippurus*) remain in the mixed layer of the open ocean, e.g., within about 200 m of the sea surface in the tropical western Pacific. Mesopelagic species (e.g., bigeye tuna and swordfish) inhabit deeper depths (>200 m), but migrate towards the sea surface at night.

Bait Loss and Its Effects on Fishing Power in Pelagic Longline Fisheries²

Introduction

Abundance indices for pelagic fish are often derived from models that are based on long time-series of catch and fishing effort data. The models are used to adjust catch rates or “standardize” for factors that affect fishing power, the stock’s availability, and the stock’s vulnerability to the gear, e.g., time and area of fishing activity (Maunder and Punt 2004; Bishop 2006). For pelagic longlining, effort is taken to be proportional to the number of hooks deployed. However, the availability of baited hooks is another factor that is likely to influence catch rates or “catch-per-unit-effort” (CPUE) of hook-and-line fishing gear (Deriso and Parma 1987). Usually, a hook must have bait attached if it is to attract and catch an animal. Animals are caught, or they remove bait without being caught, or bait may fall off hooks (Shomura 1955). The availability of baited hooks—and thus fishing power—is expected to increase over time as fishers gain experience with different bait types, fishing methods, and gear.

Although fishers take a keen interest in the performance of their bait, data are rarely collected on bait loss. Empirical studies show that loss rates tend to increase with soak time for pelagic longlines (Shomura 1955; Shepard et al. 1975) and bottom-set “demersal” longlines (Skud 1978b; Pingguo 1996). Those studies indicate that loss rates vary among bait species, with soft-bodied mackerel (*Scomber* spp.) more likely to fall off hooks or to be torn from hooks than are squid. The studies of demersal longlines also found increasing loss rates with water depth. Demersal longline surveys use standard fishing gear and practices to limit bias from factors that affect fishing power, such as soak time and bait species (Sullivan and Rebert 1998; Sigler 2000). Standardized surveys are rarely undertaken to estimate the abundance of pelagic fish in the open ocean because of

² This chapter has been submitted for publication as: Ward, P., and Myers, R.A. (submitted). Bait loss and its potential effects on fishing power in pelagic longline fisheries. Fisheries Research. The original article’s abstract is incorporated in the Conclusions of this thesis and its reference list is included in the Bibliography.

the high cost of obtaining representative samples from a system that features vast distances and high spatial and temporal variability. As a result, assessments of pelagic species largely rely on data reported by commercial fishers in logbooks (Bishop 2006). However, the effect of bait loss on the fishing power of commercial longliners has been ignored when standardizing such data because factors affecting loss rates have been assumed to be constant over time.

This article is one in a series that examine how catch rates from hook-and-line fishing gear relate to abundance and biomass. These include articles on historical changes in longline gear and practices (Ward and Hindmarsh submitted), the timing of fishing operations (Ward et al. 2004), hook depth (Ward and Myers 2005a), biological habitats (Ward and Myers 2005b), and long-term variations in pelagic communities (Ward and Myers 2005c). The purpose of the present article is to determine what factors affect bait loss from pelagic longlines and how loss rates have varied over time. Loss rate is the number of lost baits divided by the number deployed. Fishing power or “fishing efficiency” is formally defined as 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. We use the term fishing power to refer to the relative number of baits available. We take an empirical approach in modeling variables that affect loss rates, and then use the model to extrapolate trends in historical fishing power from information on Japanese longline gear and practices. Trends in fishing power are presented relative to the number of baits available on the longlines used when industrial longlining began in the early 1950s.

Methods

Data

We analyzed data from a US program of scientific surveys known as the Pacific Oceanic Fisheries Investigations (POFI). Using pelagic longline gear and techniques adopted from Japan, POFI conducted surveys each of about two months duration in the tropical Pacific Ocean during the 1950s (Murphy and Shomura 1972). Most of the activity was during 1951–53. Survey fishing was conducted as a controlled experiment where fishing gear and techniques were held constant throughout the study. Murphy and Shomura (1972) and reports that they cite provide details of survey fishing gear and techniques. Longlines

were deployed in a grid at pre-determined stations. They were normally deployed at dawn and retrieved in the afternoon. Usually, six hooks were attached to the mainline between each buoy, amounting to several hundred hooks in each daily fishing operation (Table 3.1).

Table 3.1. Description of the longline fishing gear deployed by the 1950s survey. Table entries are based on survey data supplemented with information from Murphy and Shomura (1972).

Characteristic	Details
Mainline material	Hard-lay cotton twine
Branchline material	12-strand cotton twine with wire leader
Level of fishing effort	185 daily operations 48 249 hooks
Hooks per operation	343 hooks (± 269 SD)
Hook type	9/0 or 8/0 Mustad flattened tuna hooks
Lightsticks	No
Buoyline length	19.2 m (± 6.42 SD)
Branchline length	20.7 m (± 7.02 SD)
Hooks per buoy	Usually 6, ranging from 5 to 11
Line shooter	No

Bait species included sardine (*Sardinia melanosticta*), squid (*Loligo opalescens*), and herring (*Clupea pallasii*). Missing operational details precluded the analysis of data from survey operations that deployed other bait species. Fresh, salted, or brined bait was occasionally used, but most was frozen (Figure 3.1). Frozen bait was thawed and placed in rock salt or brine for several days to make it firm before deployment (Shomura 1955). The survey tested several hooking methods, but we restricted our analyses to fish bait that were hooked through the head and squid bait that were hooked through the mantle, which is the practice on commercial longliners (Whitelaw and Baron 1995).

Survey scientists recorded details of each longline operation (e.g., branchline length) and the time when each hook was deployed and retrieved, along with its status when retrieved (bait intact, bait missing, tangled branchline, or animal caught). We entered data for eight trips, consisting of 185 daily longline operations and 48 249 records of bait status, in the study area (16°S–21°N, 119–170°W). The US NMFS Pacific Islands Regional Office now holds a copy of the dataset. For the analyses

presented in this article, we classified remnant bait as “intact”. Missing branchlines, tangled branchlines, and hooks that caught an animal were excluded from the analyses.

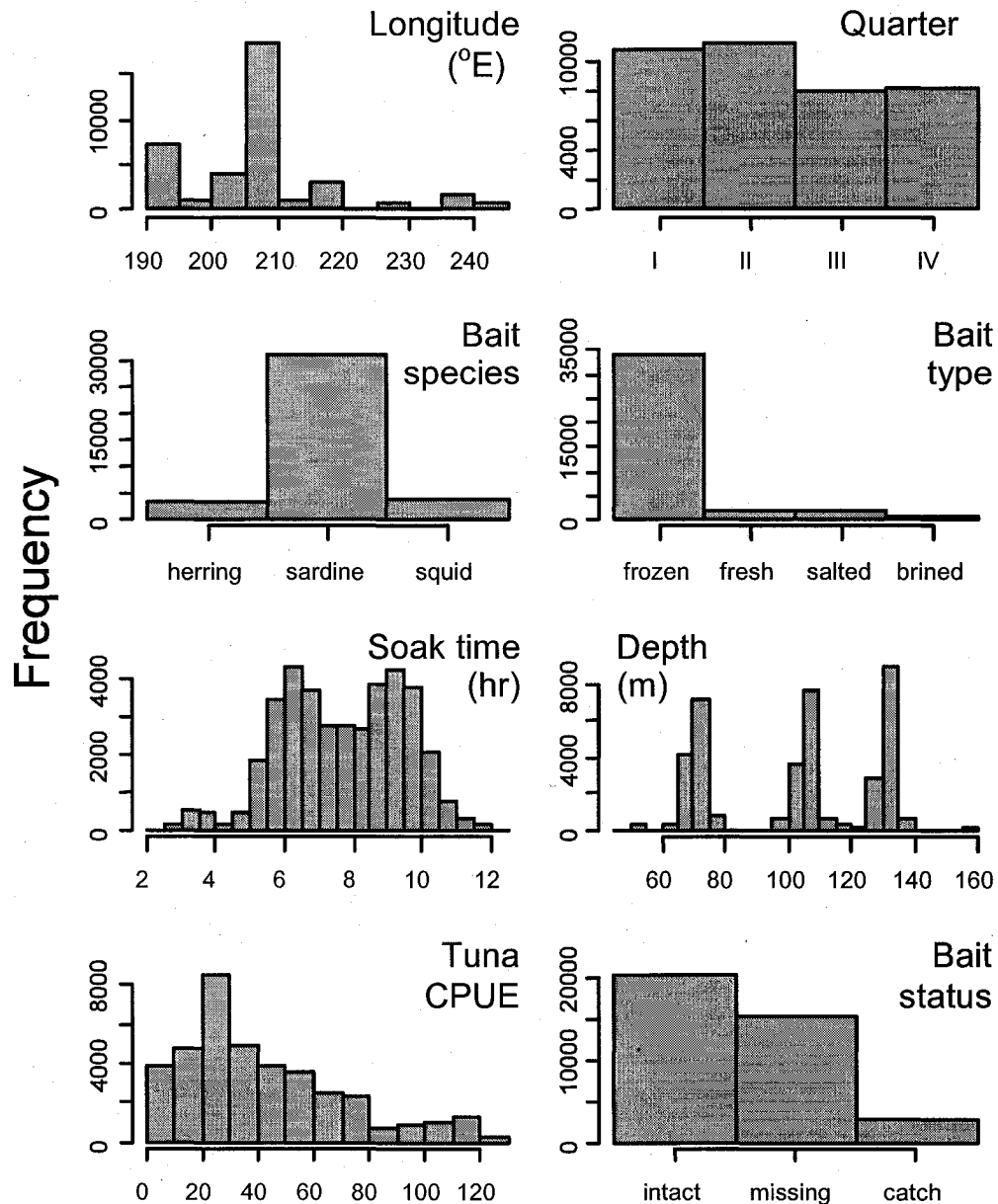


Figure 3.1. Frequency histograms of variables in the survey dataset that were included in the final model (N = 36 829 hooks). Tuna CPUE is the number of tuna per 1000 hooks.

We estimated the soak time of each hook from survey records of the time when each hook was retrieved, combined with the start and finish times of longline

deployment. The speed of longline deployment was assumed to be constant throughout each operation. We assumed that the mainline formed a catenary curve between each pair of floats and estimated the depth of each hook by applying the formula presented by Suzuki et al. (1977) to longline dimensions reported for each operation. The estimation of hook depth from the catenary formula provides only an approximation to the true depth of hooks (Bigelow et al. 2006), but we expect the estimates to represent the average depth distribution of hooks.

Generalized Estimating Equations

We used generalized estimating equations (GEEs; Liang and Zeger 1986) to model bait loss rates. GEEs are a method for analyzing data that are collected in clusters where observations within a cluster may be correlated, but observations in separate clusters are independent (Halekoh et al. 2006). They can account for spatial and temporal correlations, which are common in fisheries data that do not adhere to strict sampling regimes (Bishop et al. 2000). Like generalized linear models (GLMs), GEEs allow for non-linear relationships between independent variables and the dependent variable (bait status), and accommodate the dependent variable's non-normal distribution.

The survey data consist of $i = 1, \dots, n$ daily longline operations ("clusters"), each consisting of $j = 1, \dots, m_i$ observations of the bait status of hooks y . The observations can be represented in vector notation as:

$$y = (y_{1,1}, \dots, y_{1,m_1}, \dots, y_{i,1}, \dots, y_{i,m_i}, \dots, y_{n,1}, \dots, y_{n,m})$$

We assumed that observations from different longline operations were independent, and that observations from hooks on the same longline followed an "ar1" (autoregressive process with lag 1) correlation structure. The *ar1* structure provides the highest correlation between observations for hooks that are close together along the longline and lower correlation for hooks that are further apart. Exchangeable and independence correlation structures resulted in a poorer fit to the data.

The expectations of bait loss $E(y) = \mu$ are related to the p dimensional regressor vector $x_{i,j}$ by the mean-link function g :

$$g(\mu_{i,j}) = x_{i,j}'\delta$$

The parameter δ determines the shape of the relationship between the mean-link function and the regressor vector (t indicates that this is the transposed matrix).

We assumed that the presence of a bait on each retrieved hook has a binomial distribution with $y \sim b(n, \pi)$, where π is the probability of a bait being on a hook, n is the number of hooks observed, and $g(\mu) = \mu(1-\mu)$ with $\mu \approx (0,1)$. For each hook j in longline operation i , we linked the probability of a bait being present $\pi_{i,j}$ to a linear predictor $\eta_{i,j}$ through the logistic formula:

$$\pi_{i,j} = \frac{e^{\eta_{i,j}}}{(1 + e^{\eta_{i,j}})} \quad (3.1)$$

The linear predictor $\eta_{i,j}$ is the log odds of a bait being present on a retrieved hook. We modeled the log odds as a function of several covariates:

$$\eta_{i,j} = \beta_0 + \beta_1 S_{i,j} + \beta_2 B_{i,j} + \beta_3 T_{i,j} + \beta_4 D_{i,j} + \beta_5 Y_i + \beta_6 M_i + \beta_7 Q_i + \beta_8 E_i + \beta_9 E_i^2 + I_i \quad (3.2)$$

where $S_{i,j}$ is the bait species (sardine, squid, or herring), $B_{i,j}$ is the bait type (fresh, frozen salted, or brined), $T_{i,j}$ is the soak time, and $D_{i,j}$ is the estimated depth of hook j in longline operation i ; and Y_i is the nominal catch rate of tunas, Q_i is the three-month quarter (i.e., season), E_i is the longitude, and I_i is the unique identifier of longline operation i . The β are estimated parameters.

The GEE model was implemented in the *R* statistical language (*R* Development Core Team 2006) using *geeglm* from library *geepack* (Yan and Fine 2004). Model selection was based on the significance of the Wald statistic for each coefficient. We explored various combinations of variables and interaction terms, and linear, quadratic, and cubic forms of each variable. Model selection also explored the effects of other variables, including latitude, month, moon phase, sea surface temperature, thermocline depth, the time of longline deployment and retrieval, the availability of bait at dawn and dusk, and catch rates of other taxonomic groups (e.g., sharks), individual species (e.g., yellowfin tuna, *Thunnus albacares*), and all species combined. However, those variables were not included in the final model because they did not explain significant variation or because they were highly correlated with other variables. Latitude and sea surface temperature were significant in several models, but they were not included in the final model because they substantially reduced the number of observations and the model's predictive power. The final model (3.2) used 36 829 of the 48 249 observations. All parameters in the final model were statistically significant ($P < 0.10$).

Table 3.2. Sources of data for the synthetic time-series. We used the time-series to extrapolate historical trends in loss rates from the final model (Figure 3.3).

Variable	Stratification	Description	Source(s)
Bait species	year × quarter	Bait species from published reports and observers ^a on Japanese longliners.	Shimada (1951b), Nakamura and Kamimura (1958), JFA (1962–80) ^b , Au (1986), Yamaguchi (1989)
Bait type	year	Bait type from published reports and observers ^a on Japanese longliners.	Shimada (1951), Nakamura and Kamimura (1958), Yamaguchi and Kobayashi (1974), Au (1986), Yamaguchi (1989)
Soak time	year × hook	Soak time of each hook estimated from observer ^a data and from published reports of longline operation times.	Ward et al. (2004), Ward and Hindmarsh (submitted)
Depth	year × hook	Depth of each hook estimated from the catenary formula applied to longline dimensions reported for Japanese longliners in the tropical Atlantic Ocean.	Yokawa and Uozumi (2000)
Tuna catch rate	year × quarter	Nominal catch rates reported by Japanese longliners in the study area.	Miyabe (pers. comm.), SCTB (2004)
Quarter	year × quarter	3-month quarter weighted by the number of hooks reported by Japanese longliners in the study area.	Miyabe (pers. comm.), SCTB (2004)
Longitude	year × quarter	Longitude weighted by the number of hooks reported by Japanese longliners in the study area.	Miyabe (pers. comm.), SCTB (2004)

^aAustralian observer data, 1992–97.

^bJFA (1962–80) present data for three bait species: squid, saury (*Cololabis saira*), and “other”. Based on the species composition of bait reported by Australian observers, we coded the “other” category as mackerel. To illustrate historical trends in fishing power, we assumed that mackerel had the same loss rates as herring and that saury had the same loss rates as sardine.

We also fitted a generalized linear mixed effects model with the logistic formula (3.1) and a binomial distribution to the same dataset. The mixed effects model gave very similar results to the GEE model. We present results of the GEE model because its correlation structure matches the pattern of clustering in bait status expected along a longline and because it gave smaller standard errors for parameter estimates than the mixed model.

We used the final model to illustrate potential variations in fishing power for Japan’s longliners in the study area during 1952–2004. For all 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 species (except skipjack tuna, *Katsuwonus pelamis*) and several other major pelagic species, such as blue marlin *Makaira indica*). We created a synthetic time-series consisting of multiple longline operations of 3000 hooks for each year–quarter (Table 3.2). Within each year–quarter stratum, each hook was assigned a value for each model variable. Loss rates were then extrapolated from the final model and the synthetic time-series.

Results and Discussion

Significant quantities of bait were lost from longlines deployed by the 1950s survey. Predicted loss rates averaged 0.44 or 44% of baits deployed in the survey, where soak times averaged 7.78 hr. An extrapolation from the model when baits are initially deployed shows a loss rate that is greater than zero, i.e., the loss rate is 0.16 when soak time is 0.0 hr. It is not unusual to observe high initial loss rates during deployment. In an analysis of research vessel data from the North Pacific salmon fishery, Shepard et al. (1975) attributed high initial loss rates (0.25) to inadequate attachment of bait to hooks and the agitation of the longline during deployment. High initial loss rates might also be due to elevated hooking rates for several species during longline deployment, as reported by Boggs (1992).

We could not determine exactly when bait was lost during longlining operations; whether it was lost during deployment, during the soak, or during retrieval. Our model will overestimate the effect of soak time on loss rates if bait is lost during retrieval. However, model selection showed that quadratic and cubic coefficients for soak time were not statistically significant, indicating that loss rates during retrieval were not particularly high. Hook-timers placed on longlines have begun to provide information on the time when an animal is hooked and also whether it is subsequently lost (Boggs 1992). However, those studies do not indicate whether animals removed baits, whether an animal was hooked but then escaped, or whether the bait fell off the hook.

Removals by scavengers or target species, disintegration, and physical stresses from wave action and longline deployment and retrieval, are common causes of bait loss (Shomura 1955). The variables included in our model are proxies for those three mechanisms. Our analyses show that soak time, bait species, and depth had the greatest effects on loss rates (Table 3.3, Figure 3.2). Loss rates increased with soak time, probably

as a result of a combination of all three mechanisms. Loss rates for squid bait were low, confirming observations by other authors that firm-fleshed bait are less likely to be torn off hooks by scavengers or break apart and fall off hooks than are soft-bodied species (Shomura 1955). Our analyses did not show a statistically significant difference between loss rates for fresh and frozen bait. Only the loss rates of brined bait were significantly higher than the other bait types. Note, however, that survey scientists fully thawed bait before deployment.

Table 3.3. Parameter estimates and statistics for the final model of bait loss.

Coefficient	Estimate	SE	Wald statistic	p(>W)
(Intercept)	-33.596	9.538	12.4058	0.0004
Tuna CPUE	-0.0023	0.0013	3.1513	0.0759
Quarter II	0.2799	0.1456	3.6970	0.0545
Quarter III	-0.2457	0.1296	3.5960	0.0579
Quarter IV	0.3206	0.1544	4.3124	0.0378
Soak time	-0.1241	0.0161	59.3977	0.0000
Depth	0.0087	0.0006	186.5607	0.0000
Longitude	0.2919	0.0903	10.4485	0.0012
Longitude ²	-0.0006	0.0002	9.2107	0.0024
Bait species sardine	1.5170	0.1798	71.2162	0.0000
Bait species squid	2.1195	0.2587	67.1172	0.0000
Bait type fresh	-0.0182	0.1625	0.0125	0.9109
Bait type salted	-0.1495	0.1633	0.8385	0.3598
Bait type brined	-0.8094	0.1892	18.2995	0.0000

Studies of bait loss in demersal fisheries show that loss rates increase with water depth (Skud 1978b). By contrast, our analyses show that loss rates from pelagic longlines decrease with hook depth. The high loss rates on shallow hooks might be due to the mechanical effects of surface waves. Several longline fishers and observers that we contacted believed that loss rates are high during rough weather. Turbulence, which is a function of wind velocity, declines with depth (Niiler and Kraus 1977), so that bait may be more likely to be lost from shallow hooks. However, we were unable to obtain adequate data to model the effects of ambient wind velocity on loss rates. We fitted a

generalized linear model with a normal error distribution to mean monthly wind velocity in the study area during 1957–2003 (ECMWF 2006). The model's month coefficient was highly significant ($P < 0.001$), but the year coefficient was not significant ($P > 0.845$). We conclude that, regardless of the effect of wind on loss rates, bait loss caused by turbulence would not have influenced fishing power in the long-term.

Removals by scavengers, like wahoo (*Acanthocybium solandri*), and target species that are active near the sea surface may also contribute to high loss rates on shallow hooks. Small scavengers and predators, including tuna, billfish, sharks, and cetaceans, are reported to remove bait from longlines. Shomura (1955), for example, reported that 85% of the stomachs of 822 large tuna contained no bait, 14% contained one bait, and 2% contained two baits. The remainder contained multiple baits, including one yellowfin tuna that contained nine baits. Shomura's observations are consistent with our results, which show that tuna catch rate affected loss rates. Tuna catch rate is a proxy for the local abundance of tuna. However, it may be confounded with the observations of bait loss, because loss rates will affect those catch rates.

Several factors that were not included in our model might significantly affect loss rates. Thermocline depth, moon phase, month, sea surface temperature, and the availability of hooks at dawn or dusk, were not included in the final model because they did not significantly affect loss rates. The activities of scavengers should vary with the time of day, season, illumination in the water column, and ambient temperature. Time of day was not significant in our model, probably because survey longlining rarely extended into night. However, several longline fishers and observers that we contacted believed that loss rates are high at night when scavengers, like squid, are active in the mixed layer. The timing of longlining operations is also known to affect catch rates of several species, probably as a result of increased feeding activity of many predators during crepuscular periods (Maéda 1967; Ward et al. 2004). It may also affect bait loss rates in swordfish fisheries, which deploy longlines at night, and in tuna fisheries that have progressively increased the availability of baited hooks after dusk (Ward and Hindmarsh submitted).

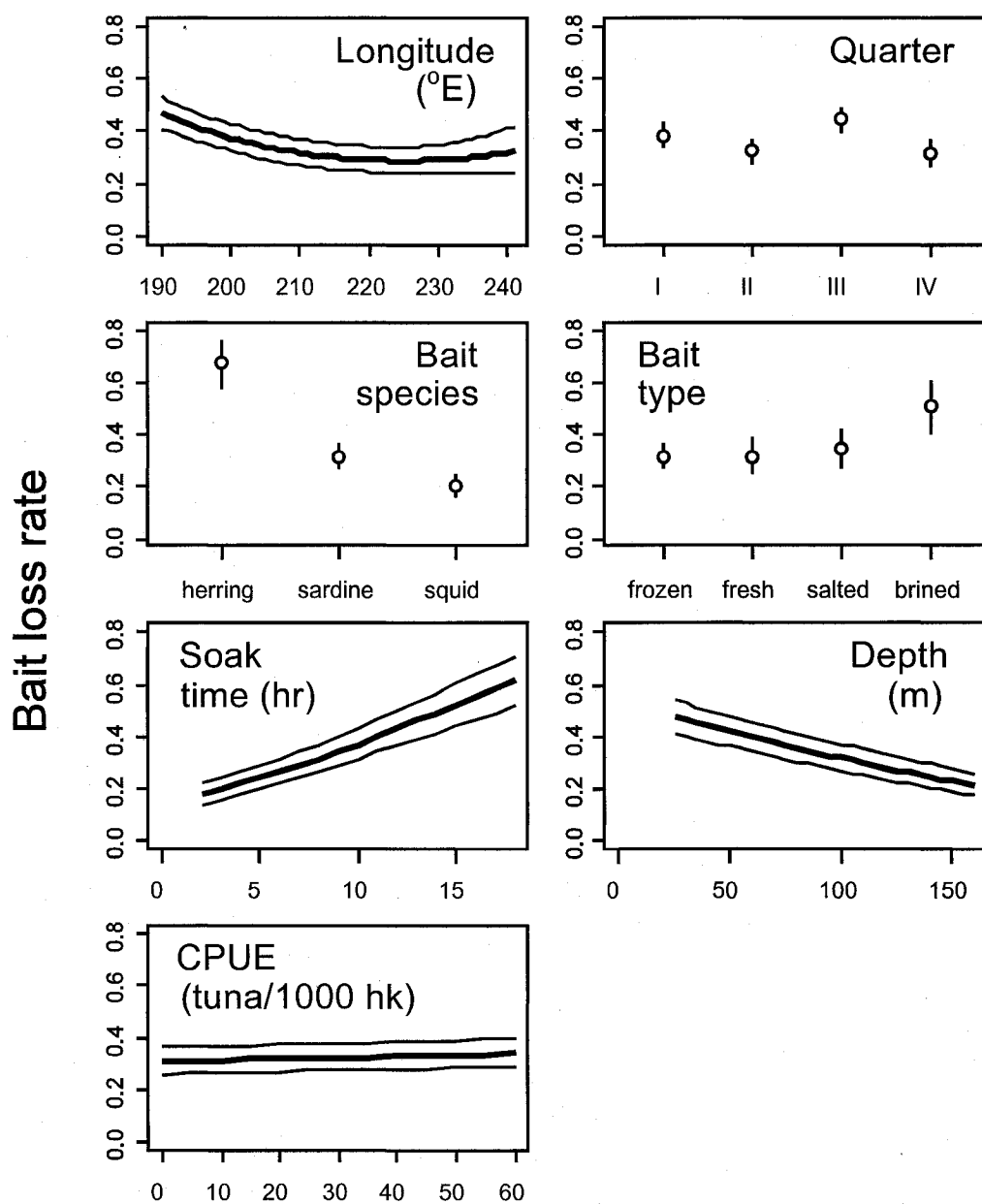


Figure 3.2. Model predictions of bait loss. We used the final model to predict loss rates over the range of each variable while holding other variables constant at their mean value in the dataset. Heavy lines are mean predictions (light lines are approximate 95% confidence intervals).

Investigations of loss rates in other pelagic longline fisheries would broaden our understanding of the effects of temperature and different pelagic communities on loss rates. Seabirds are known to steal bait during longline deployment and retrieval at high latitudes (Brothers 1991). Measures, such as bird-scaring “tori” lines, thawed bait, and nighttime longline deployment, have been instituted to reduce the bycatch of seabirds since the early 1990s (Ward and Hindmarsh submitted). Such measures will also reduce the removal of bait by seabirds. Løkkeborg and Robertson (2002), for example, reported that bird-scaring lines reduced loss rates by 13–14% during deployment of demersal longlines off Norway.

Murphy (1960) and others have developed catch equations for adjusting longline catch rates for soak time, bait loss, gear saturation, hooking, and escape. The results of our analyses combined with data from hook-timers and observer or survey data on the catch on each hook almost complete the parameter estimates required to solve such equations. Escape rate is the only parameter that has not been studied in pelagic longline fisheries. Hook-timer experiments often retrieve large numbers of triggered hook-timers without catching an animal (Boggs 1992). It is often unclear, however, whether the triggering of hook-timers was due to equipment malfunction or whether it indicates high escape rates. Escape rates could be estimated through direct observation (e.g., underwater cameras), although large sample sizes are required because of the apparently low rates of interaction between animals and longlines in the open ocean.

We do not discuss the actual values of extrapolated loss rates because of uncertainties in using a model that is based on data collected 50 years ago. Increased depth range, a switch to squid bait, an eastwards shift in the centre of longlining activity, and decreased tuna abundance contributed to a hypothesised increase in fishing power until the late 1990s (Figure 3.3). It is unlikely that other changes in longline fishing power would balance the increases caused by reduced bait loss. Ward and Hindmarsh (submitted), for example, identify several significant changes in pelagic longline gear and practices since longlining commenced, all contributing to increased fishing power and catchability.

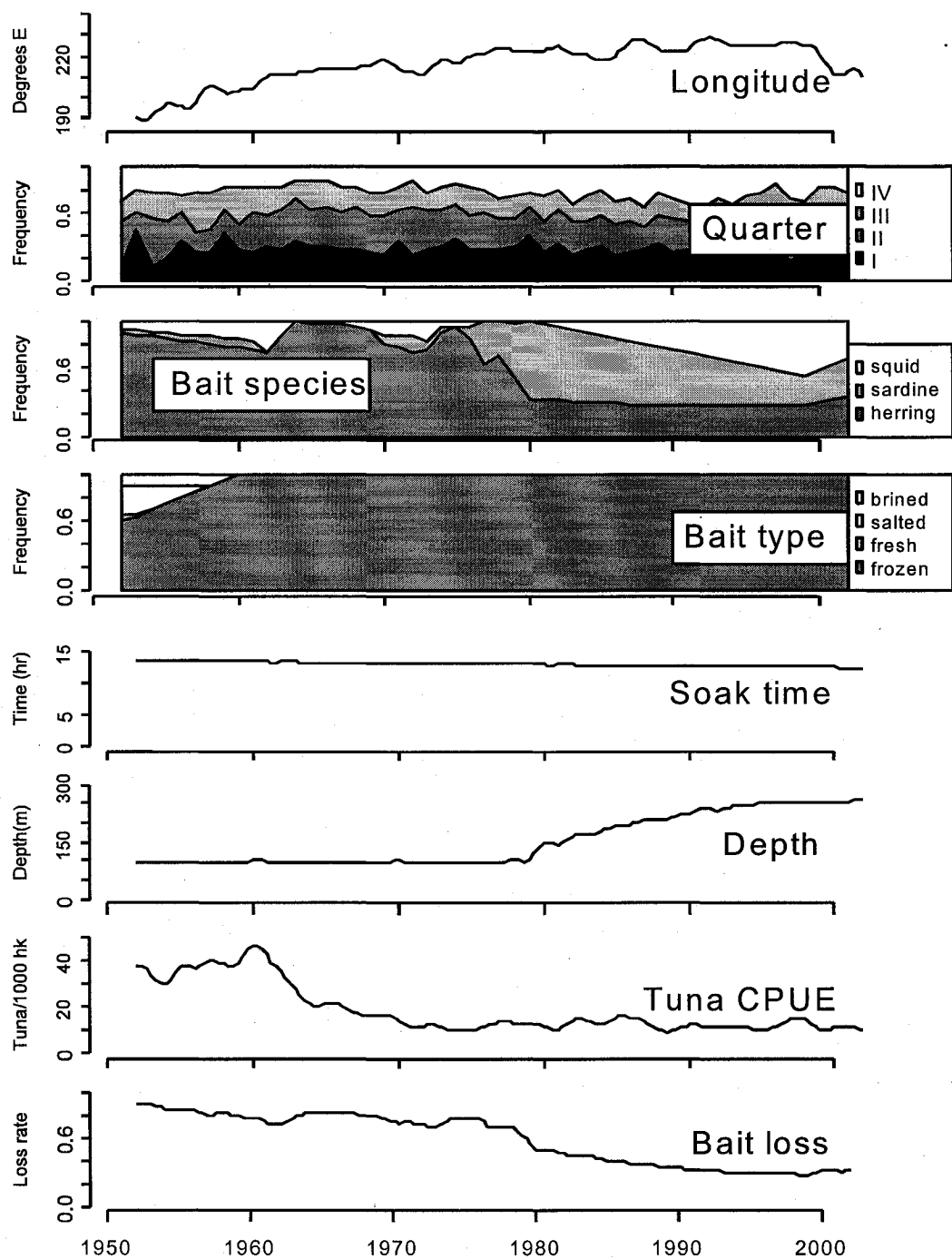


Figure 3.3. Illustration of possible historical trends in longline bait loss. We extrapolated loss rates (bottom panel) from the final model and a synthetic time-series of values for each variable. The upper panels show annual means for each variable in the synthetic time-series.

Loss rates since the early 1950s and among fisheries might vary from the extrapolated levels depending on bait treatment. During the survey, bait was soaked in brine for a several days before deployment, which is not the practice in contemporary longline fisheries. Other variables that were not included in the model, or which had limited contrast in the survey dataset, may also influence loss rates among fisheries and over time. These include variations in fishing gear (e.g., hook design and leader material), fishing practices (e.g., operations that extended into night), the physical environment (e.g., the Pacific Decadal Oscillation), and the biological environment (e.g., abundance of scavengers).

Conclusions

This article provides a baseline for a relatively unexploited fishery, highlighting the importance of compiling and analyzing more information on bait loss so that historical trends in fishing power can be estimated. Our results imply that loss rates will decline over time as fishing depletes tuna populations. This increase in fishing power might result in a pattern of hyperstability where nominal catch rates are maintained by an increase in fishing power as abundance declines (Hilborn and Walters 1992). Less competition among target species for bait would increase catchability and further add to hyperstability (Sinoda 1981; Au 1986). On the other hand, the removal of large pelagic predators in the 1950s may have resulted in predator release—an increase in the abundance of small species as predation declined (Ward and Myers 2005c). An increase in the abundance of scavengers, which are mostly small species, might result in increased bait loss and reduced fishing power. Further work is required to determine whether predator release has resulted in reduced fishing power or whether the removal of large predators has resulted in increased fishing power and hyperstability.

Acknowledgements

Grants from the Pew Charitable Trust, Pelagic Fisheries Research Program, and the Killam Foundation supported this work. Bert Kikawa provided copies of the original data sheets. David Gill and Sheree Hindmarsh helped to enter data. Karine Briand, David Kirby, and Brent Miyamoto assisted with oceanographic data. Steve Auld and Jay Hender provided observer and fisher information. Bill Clark gave advice on longline surveys. Wade Blanchard provided advice on statistical analyses. Three anonymous referees provided comments on the manuscript.

The Effect of Soak Time and Timing on Pelagic Longline Catches³

Introduction

Our knowledge of large pelagic fish in the open ocean comes primarily from data collected from longline fishing vessels since the 1950s. Abundance indices for pelagic stocks are often derived from analyses that model catches as a function of factors, such as year, area and season. However, the amount of time that baited hooks are available to animals is likely to be another important factor that influences catch rates (Deriso and Parma 1987).

The activity of many pelagic animals and their prey vary with the time of day. Broadbill swordfish⁴, for example, feed near the sea surface at nighttime. They move to depths of 500 m or more during the day (Carey and Scharold 1990). Other species may be more active in surface waters during the daytime (e.g., striped marlin) or at dawn and dusk (e.g., oilfish). Longline fishers take a keen interest in the timing of their fishing operations and soak time (the total time that a baited hook is available in the water). However, assessments have not accounted for those factors in estimating the abundance or mortality levels of target species or non-target species.

Many assessments that use longline catch rates have assumed that fishing effort is proportional to the number of hooks deployed. The omission of the effects of soak time and timing may be due to the absence of a clear demonstration of their effects on pelagic longline catch rates. The few published accounts on soak time in pelagic longline fisheries have been based on limited data and a few target species. For example, in analyzing 95 longline operations or “sets” by research vessels Sivasubramaniam (1961)

³ This chapter was originally published as: Ward, P., Myers, R.A., and Blanchard, W. 2004. Fish lost at sea: the effect of soak time and timing on pelagic longline catches. *Fishery Bulletin* 102: 179–195. The original article’s abstract is incorporated in the Conclusions of this thesis and its reference list is included in the Bibliography.

⁴ Table 2 lists the scientific names of each species mentioned in the text.

reports that the catch rates of bigeye increased with soak time, whereas yellowfin catch rates were highest in longline segments with intermediate soak times.

In contrast to empirical studies, the theory is well developed for longline catch equations. Murphy (1960), for example, develops equations for adjusting longline catch rates for soak time, bait loss, escape, hooking rates and gear saturation. Estimation of escape rates can be derived from counts of missing branchlines or hooks retrieved without baits. Unfortunately, data are rarely collected on missing baits or branchlines for pelagic longline operations.

More recently, hook-timers placed on longlines by researchers have begun to provide information on the time when an animal is hooked and also whether the animal was subsequently lost, e.g., Boggs (1992), Campbell et al. (1997a, b). Such data are particularly useful to understanding the processes affecting the probability of capture and escape.

The purpose of the present paper is to determine whether variations in the duration and timing of operations have biased abundance and mortality estimates that are derived from longline catch rates. We take an empirical approach in describing the effects of soak time on catch rates. The strength in our approach is in applying a random effects model to large data sets for over 70 target and non-target species in six distinct fisheries. We also investigate the survival of each species while hooked because preliminary analyses suggested that the effects of soak time on catch rates might be linked to hooking mortality.

Factors Affecting Catch Rates

To assist interpretation of the statistical analysis of the effects of soak time on catch rates, we first develop a simple model to illustrate how the probability of catching an animal may vary with soak time.

The probability of an animal being on a hook when the branchline is retrieved is a product of two probability density functions: first the probability of being hooked and then the probability of being lost from the hook⁵. Influencing the probability of being

⁵ In discussing continuous variables we use the terms “probability” and “probability density function” interchangeably.

hooked are the species' local abundance, vulnerability to the fishing gear and the availability of the gear. Catches will deplete the abundance of animals within the gear's area of action, particularly for species that have low movement rates. Movement will also result in variations in exposure of the animals to the gear over time, for instance as they move vertically through the water column in search of prey (Deriso and Parma 1987).

Other processes that will reduce the probability of being hooked include bait loss and reduced sensitivity to the bait (Fernö and Huse 1983). Longline baits may fall off hooks during deployment, deteriorate over time and fall off or they may lose their attractant qualities. They may be removed by target species, non-target species or other marine life, such as squids. Hooked animals may also escape by severing the branchline or breaking the hook. Sections of the longline may become saturated when animals are hooked, reducing the number of available baits (Murphy 1960; Somerton and Kikkawa 1995).

After an animal has been hooked, it might escape, fall off the hook, scavengers might remove it or it may remain hooked until the branchline is retrieved.

Some of the processes affecting the probability of an animal being on a hook are species-specific, whereas other processes may affect all species. For example, bait loss during longline deployment will reduce the catch rates of all species. In contrast, the probability of a hooked animal escaping may be species-dependent, with some species able to free themselves from the hook whereas other species are rarely able to do this.

Our simple model of the probability of an animal being on a hook is based on a convolution of the two, time-related processes described above: (a) the decay in the probability of capture with the decline in the number of baits that are available; and (b) gains due to the increased exposure of baits to animals and losses due to animals escaping, falling off or being removed by scavengers.

The probability of an animal being on a hook when the branchline is retrieved is the integral of the probability density functions of capture and retention:

$$\pi(T) = \int_{t=0}^T P_c(t) P_r(T-t) dt \quad (4.1)$$

where $\pi(T)$ is the "catch rate" or probability of an animal being on a hook when the branchline is retrieved at time T (T is the total soak time of the hook); $P_c(t)$ is the

probability density function of an animal being captured at time t ; and $P_r(t)$ is the probability density function of a captured animal being retained at time t .

The probability density function of capture can be approximated with an exponential function:

$$P_c(t) = P_0 e^{-\alpha t} \quad (4.2)$$

where P_0 is the probability of capture when the hook is deployed ($t = 0$) and α is a parameter determining the rate of change in capture probability over time. After the animal is hooked, $P_0 = 1$ and the probability density function of an animal being retained after capture can be approximated as:

$$P_r(t) = e^{-\beta(t)} \quad (4.3)$$

where β is the “loss rate”, a parameter determining the rate of change in the probability of an animal being retained after it has been captured.

Substituting approximations (4.2) and (4.3) into equation (4.1) gives:

$$\begin{aligned} \pi(T) &= \int_{t=0}^T P_0 e^{-\alpha t} e^{-\beta(T-t)} dt \\ &= \frac{P_0}{\beta - \alpha} [e^{-\alpha T} - e^{-\beta T}] \quad (4.4) \end{aligned}$$

Our model is similar to the parabolic catch model examined by Zhou and Shirley (1997). It is simpler than catch equations developed by other authors because it does not include specific terms for the loss of baits, competition and gear saturation.

The next section describes observer data that we used to analyze the effects of soak time on catch rates. Plots of the raw data indicated a variety of patterns in the relationship between catch rates and soak time (e.g., Figure 4.1). By varying the values of P_0 (probability of capture), α (capture rate) and β (loss rate), our simple catch equation (4.4) can mimic the observed patterns (Figure 4.2). However, estimates of P_0 , α and β are not available. Instead, we used the empirical approach described in the following section to model the effect of soak time on catch rates. The soak time – catch rates relationships represent the product of the probability of capture and the probability of being retained.

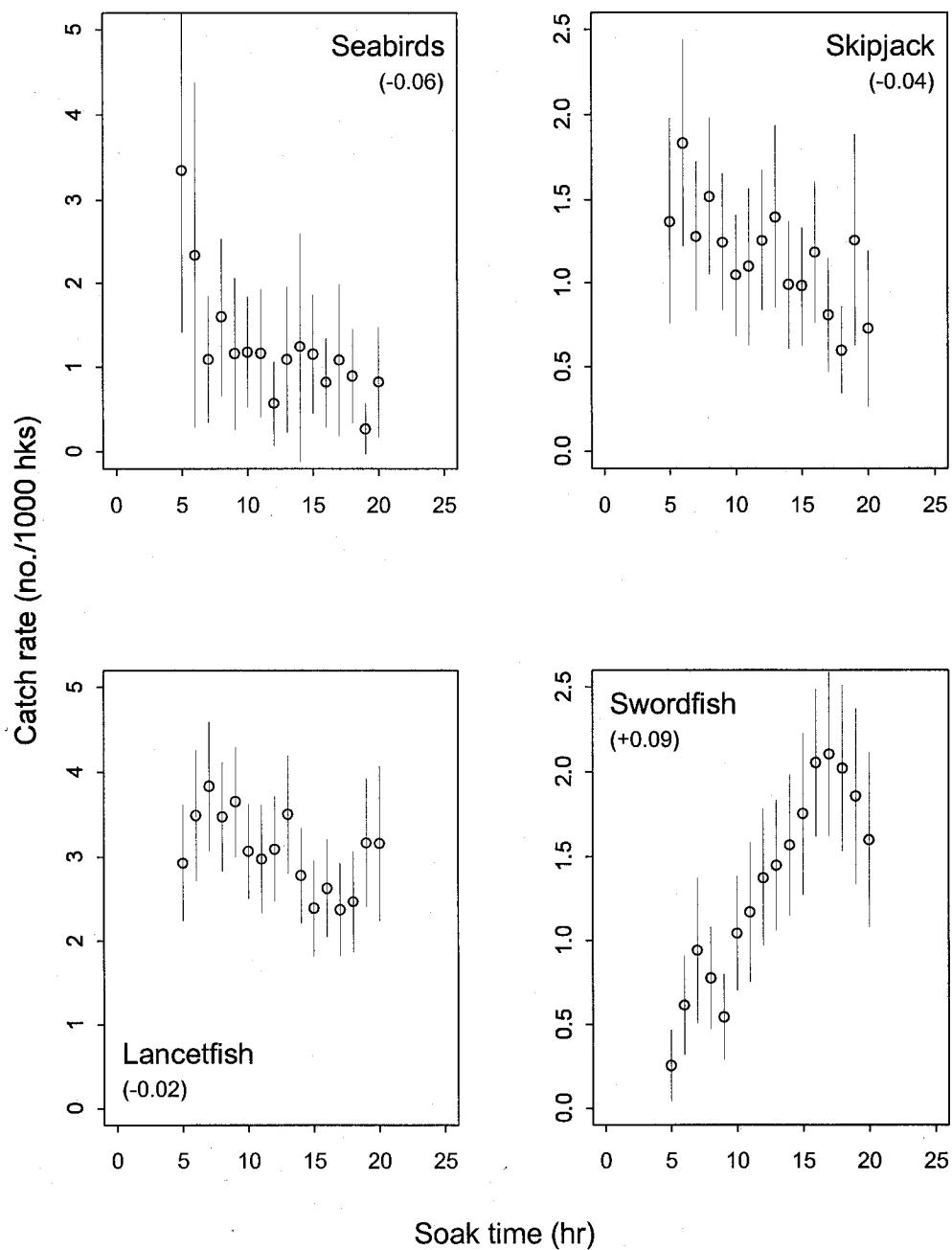


Figure 4.1. Mean catch rates plotted against soak time for skipjack, long-nosed lancetfish and swordfish in the South Pacific Yellowfin fishery and for “other seabirds” in the South Pacific Bluefin fishery. To reduce variability, the estimates are limited to longline segments with more than 25 hooks and soak times of 5–20 hours. Vertical bars are 95% confidence intervals for the mean hourly catch rate. In parentheses are the soak time coefficients from random effects models (note that the soak time coefficient is not the same as the slope coefficient of a regression of the data presented in this graph).

One approach to investigating the effects of soak time on catch rates is to fit linear regressions to aggregated data like those presented in Figure 4.1. Such an approach, however, would violate assumptions of independence (within each longline operation, catch rates in consecutive segments will be related), normality (these are binomial data) and homogeneity of variance (for binomial data the variance is dependent on the mean). Another approach might be to fit separate logistic regressions to each operation and then to combine the parameter estimates. This would overcome the problems of normality and homogeneity of variance. However, the separate regressions would not utilize information that is common to all operations. Instead, we used a logistic regression with random effects. The key advantage in using random effects models in this situation is that they utilize information on the correlation between longline segments that is derived from the entire data set of operations.

Data and Methods

Fisheries

We analyzed observer data from six different fisheries to determine the effects of soak time and timing on longline catch rates (Figure 4.2). They involve two different types of longline fishing operation. Distant-water longliners undertake trips of three months or longer. They freeze their catches. Fresh-chilled longliners store their catches in ice, slurries or in spray brine systems. They are usually small longliners (15–25 m) that undertake trips of less than four weeks duration. The fresh-chilled longliners have about six crew members and deploy shorter longlines with fewer hooks (~1000 hooks) than the distant-water longliners (~20 crew members and ~3000 hooks per operation; Ward et al. 1996; Ward et al. 2000).

The six fisheries share many operational similarities, such as the types of bait used and soak time. However, they are quite different in terms of targeting, which is determined by fishing practices, e.g., the depth profile of the longline, timing of operations and the area and season of activity. South Pacific Bluefin longliners, for example, operate in cold waters (10–16°C) in winter to catch southern bluefin. In the South Pacific Yellowfin fishery, by contrast, longliners target tropical species, such as yellowfin and bigeye, in warmer waters (19–22°C; Table 4.2; Ward 1996). To target

bigeye, longlines in the Central Pacific Bigeye fishery are deployed in the early morning with hook depths ranging down to about 427 m. The depths of the deepest hook are much shallower (~153 m) in the North Pacific Swordfish fishery where the longlines are deployed late in the afternoon and retrieved early in the morning (Boggs 1992).

Observer Data

National authorities and regional organizations placed independent observers on many longliners operating in the six fisheries during the 1990s. The observer data consist of records of the species and the time when each animal was brought on board. For the Central Pacific Bigeye and North Pacific Swordfish fisheries, the observer data were reported according to a float identifier. In those fisheries the observers reported the time when each float was retrieved on board, so we estimated soak times from the float times.

The Central Pacific Bigeye and North Pacific Swordfish data included tuna, billfish and shark catches, but not catches of other species. Data are available for protected species, such as seals, turtles and seabirds, but were not sought for the present study.

We analyzed operations where the longline was counter-retrieved, had no evidence of stoppages due to line breaks or mechanical failure and had continuous monitoring by an observer. Combined with records of the number of hooks deployed and start and finish times of deployment and retrieval, the observer data allowed calculation of soak time and catch rates of longline segments. We aggregated catches and the number of hooks into hourly segments. The soak time was estimated for the mid-point of each hourly segment.

We assumed a constant rate of longline retrieval throughout each operation. The number of hooks retrieved during each hourly segment was the total number of hooks divided by the duration of monitoring (decimal hours). For each species we analyzed only the operations where at least one individual of that species was caught.

Longline segments that involved a full hour of monitoring had several hundred hooks. Segments at either end of the longline involved less than an hour of monitoring and had fewer hooks. Catch rates may become inflated in segments with very small numbers of hooks. Therefore we arbitrarily excluded segments where the observer monitored less than 25 hooks.

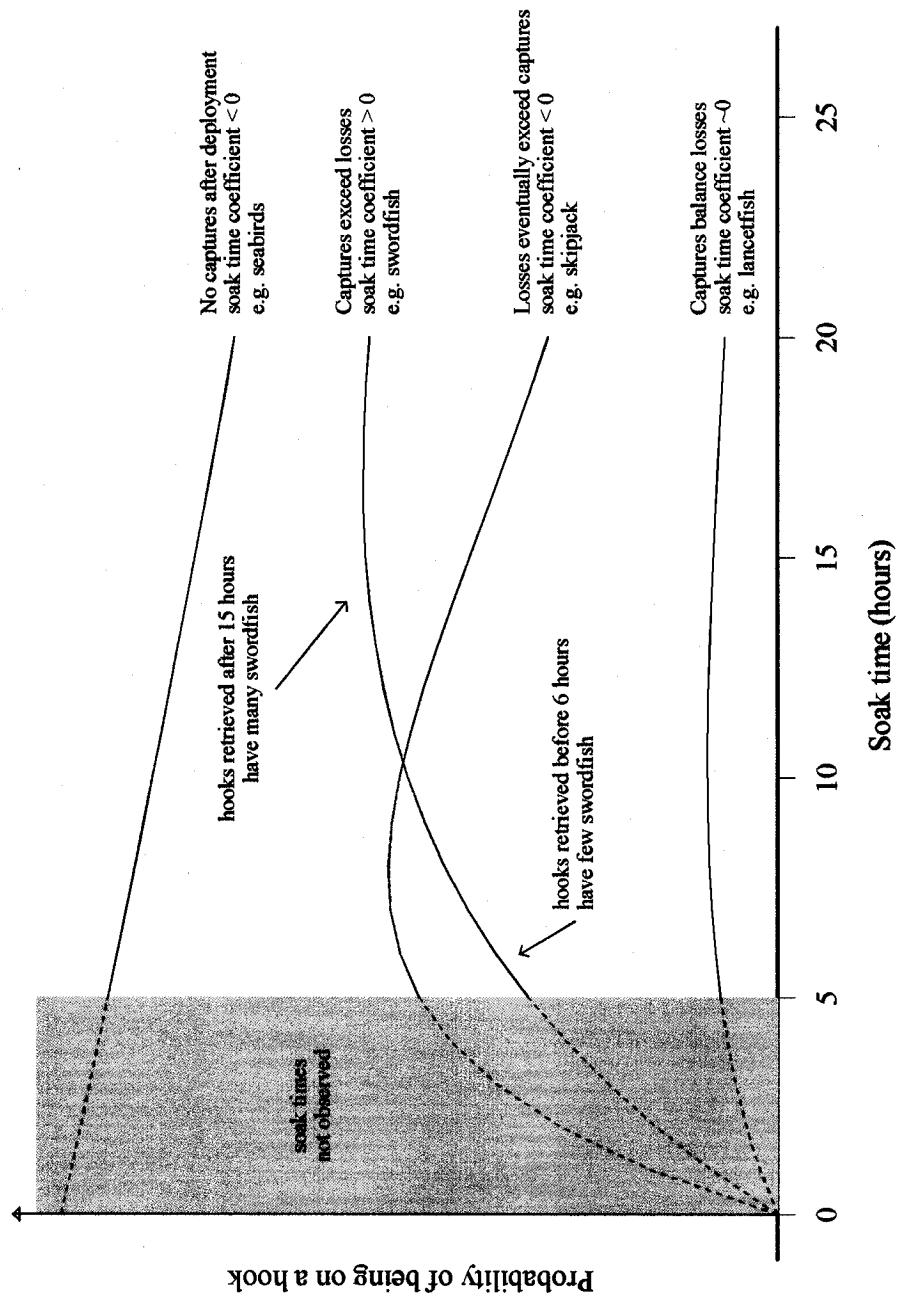


Figure 4.2. Illustration of different patterns in the theoretical relationship between longline catch rates and soak time. The probability of an animal being on a hook when a branchline is retrieved (the "catch rate") is estimated from equation (4.4) using soak times (T) ranging from 0 to 20 hours and three different combinations of values for P_0 (probability of capture), α (capture rate) and β (loss rate). For seabirds, the probabilities are estimated from equation (4.6). The probabilities of being on a hook are not intended to be comparable between species.

Table 4.1. Summary of the six fisheries analyzed. The mean number of hooks per operation, mean duration of operations, mean catch rate of all species, the period of observer data and the total number of longline operations ("ops") are given. For the two Western Pacific fisheries, the catch rates are for the most common species only.

Fishery name ^a	Fleet	Area	Target species	Period	No. ops	Hooks per op.	Duration (hrs)	Catch rate (no. per 1000 hooks)
NP Swordfish ^b	US fresh-chilled	North Pacific	swordfish	1994–2002	1539	812	21	51
CP Bigeye ^b	US fresh-chilled	Central Pacific	bigeye, albacore	1994–2002	3243	1865	19	23
WP Bigeye	fresh-chilled	Western Pacific	bigeye, yellowfin	1990–2001	1915	1620	21	28
	(various flags)							
WP Distant	distant-water	Western Pacific	bigeye, yellowfin	1990–2001	234	2347	22	30
	(various flags)							
SP Yellowfin	Japan distant-water	north-eastern Australia	yellowfin, bigeye	1992–97	1419	3130	22	40
SP Bluefin	Japan distant-water	south-eastern Australia	southern bluefin	1992–97	666	3086	22	23

^aThe following abbreviations are used in fishery names in this table and several other tables and figures:

NP North Pacific WP Western Pacific
 CP Central Pacific SP South Pacific

^bWe used the number of hooks between floats to distinguish the North Pacific Swordfish fishery (<15 hooks between floats) from the Central Pacific Bigeye fishery.

Table 4.2. List of common and scientific names of the species analyzed. Also shown is the number of individual animals of each species analyzed in each of the six fisheries. A dash indicates that the species was not analyzed in the present study; it does not necessarily mean that the species is not taken in the fishery. In particular, observer data on the time of capture were not available for “other bony fish” in the North Pacific Swordfish and Central Pacific Bigeye fisheries.

Common name	Species	NP	CP	WP	WP	SP	SP
		Swordfish	Bigeye	Bigeye	Distant	Yellowfin	Bluefin
Tuna and tuna-like species							
Albacore	<i>Thunnus alalunga</i>	9 707	23 128	14 194	11 976	21 550	1 399
Bigeye	<i>Thunnus obesus</i>	5 409	45 476	9 814	2 581	1 846	—
Butterfly mackerel	<i>Gasterochisma melampus</i>	—	—	—	—	—	533
Skipjack	<i>Katsuwonus pelamis</i>	546	13 882	1 456	445	691	—
Slender tuna	<i>Allothunnus fallai</i>	—	—	—	—	—	28
Southern bluefin	<i>Thunnus maccoyii</i>	—	—	—	—	1 030	10 537
Yellowfin	<i>Thunnus albacares</i>	2 811	21 654	16 029	4 689	12 454	—
Wahoo	<i>Acanthocybium solandri</i>	383	5 508	1 345	—	308	—
Billfish							
Black marlin	<i>Makaira indica</i>	25	41	353	226	160	—
Blue marlin	<i>Makaira nigricans</i>	981	2 379	1 467	529	179	—
Sailfish	<i>Istiophorus platypterus</i>	49	193	706	399	151	—
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	543	5 467	529	398	654	—
Striped marlin	<i>Tetrapturus audax</i>	1 963	8 332	681	182	724	—
Swordfish	<i>Xiphias gladius</i>	22 457	1 680	1 472	287	1 173	92
Other bony fish							
Barracouta	<i>Thyrsites atun</i>	—	—	—	—	53	—

Common name	Species	NP		CP		WP		WP		SP	SP
		Swordfish		Bigeye		Bigeye		Distant		Yellowfin	Bluefin
Barracudas	<i>Sphyræna</i> spp.	—	—	—	—	707	153	—	—	—	—
Escolar	<i>Lepidocybium flavobrunneum</i>	1 208	3 983	1 343	878	1 726	84	—	—	—	—
Great barracuda	<i>Sphyræna barracuda</i>	32	743	303	442	92	—	—	—	—	—
Lancetfish (LN)	<i>Alepisaurus ferox</i>	2 788	30 136	325	419	2 868	610	—	—	—	—
Lancetfish (SN)	<i>Alepisaurus brevirostris</i>	—	—	155	84	257	59	—	—	—	—
Lancetfishes	<i>Alepisaurus species</i>	—	—	1 431	98	—	—	—	—	—	—
Long-finned bream	<i>Taractichthys longipinnis</i>	—	—	—	—	—	292	—	—	—	—
Mahi mahi	<i>Coryphaena hippurus</i>	17 463	19 090	1 436	211	447	—	—	—	—	—
Oilfish	<i>Ruvettus pretiosus</i>	555	1 091	420	456	653	900	—	—	—	—
Opah	<i>Lampris guttatus</i>	68	4 724	527	129	80	213	—	—	—	—
Pomfrets	Family Bramidae	—	—	623	60	—	40	—	—	—	—
Ray's bream	<i>Brama brama</i>	—	—	—	—	1 074	10 547	—	—	—	—
Ribbonfishes	Family Trachipteridae	—	—	—	—	—	22	—	—	—	—
Rudderfish	<i>Centrolophus niger</i>	—	—	—	—	—	90	—	—	—	—
Sickle pomfret	<i>Taractichthys steindachneri</i>	—	—	122	21	—	—	—	—	—	—
Slender barracuda	<i>Sphyræna jello</i>	—	—	—	—	121	—	—	—	—	—
Snake mackerel	<i>Gempylus serpens</i>	1 971	9 881	256	44	—	—	—	—	—	—
Snake mackerels	Family Gempylidae	—	—	456	10	—	—	—	—	—	—
Southern Ray's bream	<i>Brama species</i>	—	—	—	—	—	28	—	—	—	—
Sunfish	<i>Mola ramsayi</i>	—	—	—	—	249	99	—	—	—	—

Sharks and rays

Common name	Species	NP		CP		WP		WP		SP	
		Swordfish	Bigeye	Bigeye	Distant	Bigeye	Yellowfin	Bluefin	Bluefin	Bluefin	Bluefin
Bigeye thresher shark	<i>Alopias superciliosus</i>	149	1 930	145	61	—	—	—	—	—	—
Blacktip shark	<i>Carcharhinus limbatus</i>	—	—	445	125	—	—	—	—	—	—
Blue shark	<i>Prionace glauca</i>	31 503	31 413	5 601	1 628	1 689	12 797	—	—	—	—
Bronze whaler	<i>Carcharhinus brachyurus</i>	—	—	—	—	—	—	—	—	—	—
Crocodile Shark	<i>Pseudocarcharias kamoharui</i>	—	—	153	73	—	—	—	—	—	—
Dog fishes	Family Squalidae	—	—	—	—	—	—	—	—	—	60
Dusky shark	<i>Carcharhinus obscurus</i>	—	112	—	—	—	20	—	—	—	—
Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	—	—	282	64	—	—	—	—	—	—
Hammerhead sharks	<i>Sphyrna</i> spp.	—	—	142	191	22	—	—	—	—	—
Long finned mako	<i>Isurus paucus</i>	—	83	108	15	—	—	—	—	—	—
Oceanic white tip	<i>Carcharhinus longimanus</i>	568	2 373	2 376	384	142	—	—	—	—	—
Porbeagle	<i>Lamna nasus</i>	—	—	—	—	27	1 011	—	—	—	—
Pelagic ray	<i>Dasyatis violacea</i>	2 374	2 849	1 212	248	534	109	—	—	—	—
Pelagic thresher shark	<i>Alopias pelagicus</i>	—	—	77	34	—	—	—	—	—	—
School shark	<i>Galeorhinus galeus</i>	—	—	—	—	—	—	—	—	—	143
Short finned mako	<i>Isurus oxyrinchus</i>	476	685	408	169	432	128	—	—	—	—
Silky shark	<i>Carcharhinus falciformis</i>	25	1 433	5 396	2 406	8	—	—	—	—	—
Silver-tip shark	<i>Carcharhinus albimarginatus</i>	—	—	168	74	—	—	—	—	—	—
Thintail thresher shark	<i>Alopias vulpinus</i>	—	74	—	—	—	—	—	—	—	31
Thresher shark	<i>Alopias superciliosus</i>	—	—	415	—	93	18	—	—	—	—
Tiger shark	<i>Galeocerdo cuvier</i>	—	—	56	18	38	—	—	—	—	—

Common name	Species	NP		CP		WP		WP		SP	SP
		Swordfish		Bigeye		Bigeye		Distant		Yellowfin	Bluefin
Velvet dogfish	<i>Zameus squamulosus</i>	-	-	-	-	-	-	-	-	-	156
Whip stingray	<i>Dasyatis akajei</i>	-	-	-	-	78	15	-	-	-	-
Seabirds											
Albatrosses	Family Diomedidae	-	-	-	-	-	-	-	-	-	88
Petrels	Family Procellariidae	-	-	-	-	-	-	-	-	-	29
Other seabirds	Family Procellariidae	-	-	-	-	-	-	-	-	38	200
All operations		104 054	238 340	73 212	30 222	51 699	40 343				

Abbreviations

LN long-nosed

SNshort-nosed

For four fisheries data were available on survival rates allowing the investigation of the relationship between soak time coefficients and hooking mortality. For the Western and South Pacific fisheries, observers reported whether the animal was alive or dead when it was brought on board. We calculated the survival rate (simply the number alive as a proportion of the total reported dead or alive) for species where data were available on the life status of more than ten individuals.

Generalized Linear Mixed Model

Logit Model

We applied a generalized linear mixed model to the observer data. The model is based on a logistic regression, with the catch (y) on each hook assumed to have a binomial distribution with $y \sim b(n, \pi)$. π is the expected value of the distribution for a specified soak time. We refer to it as the probability of catching an animal or the expected number of animals per hook.

For each longline operation (i), we link π_i to a linear predictor (η_i) through the equation:

$$\pi_i = \frac{e^{\eta_i}}{(1 + e^{\eta_i})}$$

η_i is then modeled as a function of soak time:

$$\eta_i = \beta_0 + \beta_1 T_{i,j} \quad (4.5)$$

where $T_{i,j}$ is the hook's soak time (decimal hours) in longline segment j ; β_0 is the intercept; and β_1 is the slope coefficient, which we term the “soak time coefficient”.

Modeling the probability of a catch on each individual hook would result in large numbers of zero observations, testing the limits of current computer speed. Therefore we aggregated hooks and catches into hourly segments for each longline operation.

We assume that each longline segment has the same configuration and that the probability of capture is the same for each segment within a longline operation. The assumption may be violated where segments pass through different water masses or where they differ in depth profile or baits. Saturation of segments with animals will also alter the capture probability between segments. The effects of water masses, depth profiles, baits and gear saturation were not analyzed in the present study.

Capture probability may also vary through the differential exposure of segments to dawn and dusk. The addition of dawn and dusk as fixed effects allowed modeling of variations resulting from the timing of operations.

Fixed Effects

To explore factors that might affect the relationship between soak time and catch rate, we added four fixed effects to the logit model: year, season (summer or winter), whether the segment was exposed to dawn and whether it was exposed to dusk. To maintain a focus on the effects of soak time, the models were limited to simple combinations of fixed effects and interaction terms. Dawn and dusk were added to various models of each species in each fishery. To reduce complexity, year and season were limited to models of seven species (bigeye, oilfish, swordfish, blue shark, albacore, southern bluefin, long-nosed lancetfish) in the two South Pacific fisheries. The seven species represented four taxonomic groups and the range of responses observed in preliminary analyses of the soak time – catch rate relationship.

Random Effects

In addition to adding fixed effects to several models, we added random effects to all models. Inclusion of random effects allows catch rates of segments within each operation to be related. The random effects model assumes that there is an underlying distribution from which the true values of π are drawn. The distribution is the among-operation variation or “random effects distribution”. We assume that the operations are drawn from a random sample of all operations, so that the random effects (O_i) in the relationship between catch rate and soak time for each operation (i) are independent and normally distributed with $O_i \sim N(0, \sigma^2)$. The random effects and various combinations of the fixed effects were added to the linear predictor presented in equation (4.5).

For each species in the South Pacific Yellowfin data set we compared the performance of models under an equal correlation structure with that of models under an autoregressive correlation structure. Under an autoregressive structure, catch rates in the different hourly segments within the operations are not equally correlated. For example, the correlation between segments might be expected to decline with increased time between segments. However, we used an equal correlation structure for all models because the Akaike's information criterion (AIC) and Sawa's Bayesian information

criterion (BIC) indicated that there was no clear advantage in using the autoregressive structure compared to an equal correlation structure.

Implementation

We implemented the models in SAS (version 8.0) using GLIMMIX, a SAS macro that uses iteratively reweighted likelihoods to fit generalized linear mixed models (Wolfinger and O'Connell 1993).

To judge the performance of the various model formulations, we checked statistics, such as deviance and dispersion, and examined scatter plots of chi-square residuals against the linear predictor (η) and QQ plots of chi-square residuals. We used the AIC and BIC to compare the performance of the various model formulations.

Variance in the binomial model depends on only one parameter, π . A dispersion parameter is therefore necessary to allow the variance in the data to be modeled. In effect, the dispersion parameter scales the estimate of binomial variance for the amount of variance in the data. The dispersion parameter will be near one when the variance in the data matches that of the binomial model. Values greater than one ("over-dispersion") imply that the species may have a clumped distribution along the longline.

Results

Soak Time

The dispersion parameters from random effects models were about 1.00 for most species, indicating that the variance predicted by the models matched the variance in the data. The models were over-dispersed for several species, particularly for abundant species, such as Ray's bream in the South Pacific Bluefin fishery (dispersion parameter of 900) and yellowfin in the South Pacific Yellowfin fishery (1 030). The dispersion of black marlin and yellowfin in our models agrees with Murphy and Elliot's (1954) conclusion from research surveys in the equatorial Pacific. They found that yellowfin catches were much more clumped along the longline compared to those of black marlin.

Soak time had a small or statistically insignificant effect on catch rates for several species, such as yellowfin and shortbill spearfish (Figure 4.5).

For some species (e.g., seabirds, skipjack and mahi mahi), soak time had a negative effect on catch rates that was often statistically significant. For skipjack in the Western

Pacific Distant fishery, for example, catch rates decreased from $1.3(\pm 0.2)$ per 1000 hooks⁶ for a soak time of 5 hours to $1.0(\pm 0.1)$ per 1000 hooks (20 hours).

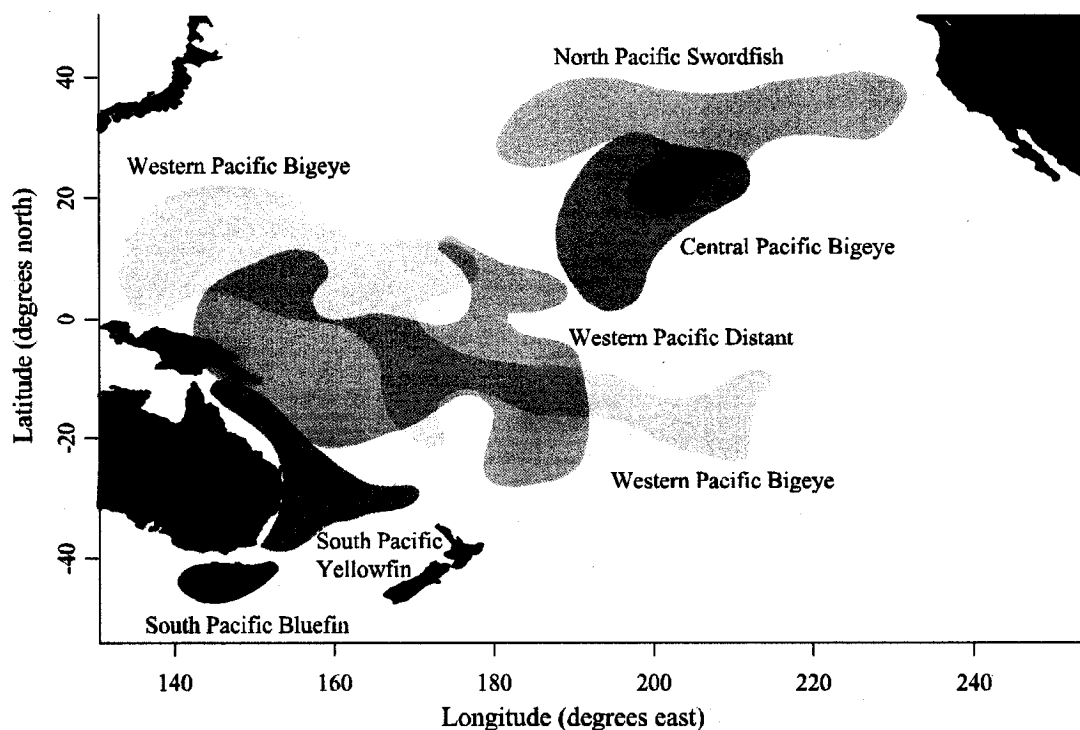


Figure 4.3. Geographical distribution of the observer data available for the six longline fisheries.

For most species, soak time had a positive effect on catch rates (Figure 4.5). In addition to being statistically significant, the effect of soak time made a large difference to catch rates at opposite ends of the longline. In the South Pacific Yellowfin fishery, for example, the expected catch rates of swordfish increase from $0.6(\pm 0.1)$ per 1000 hooks (5 hours) to $1.9(\pm 0.3)$ per 1000 hooks (20 hours; Figure 4.5; Table 4.3). A soak time of 5 hours and 3500 hooks (if that were possible) would result in a total catch of about two swordfish. By contrast, almost seven swordfish are expected from a longline operation of the same number of hooks with 20 hours of soak time.

⁶ Unless otherwise indicated, statistics preceded by \pm are the estimate's 95% confidence intervals.

Table 4.3. Examples of the effect of soak time on expected catch rates of species in the South Pacific Yellowfin fishery. The expected catch rates (number of animals per 1000 hooks) are predicted from the species' soak time coefficient for longline segments exposed to a dusk period with a soak time of 5 or 20 hours. 95% confidence intervals for catch rate estimates are available, but are not presented here.

Species	Soak time (hrs)		Species	Soak time (hrs)	
	5	20		5	20
Tuna and tuna-like species			Billfish		
Albacore	15.5	13.4	Black marlin	0.4	1.6
Bigeye	1.1	2.3	Blue marlin	1.2	0.4
Skipjack	1.3	1	Sailfish	0.8	1
Southern bluefin	5.2	5.5	Shortbill spearfish	1	1.6
Yellowfin	8.4	7.7	Striped marlin	0.8	1
Other bony fish			Swordfish	0.6	1.9
Barracouta	0.8	0.7	Sharks and rays		
Escolar	0.8	3.1	Blue shark	1.1	2
Great barracuda	0.9	1.1	Bronze whaler	0.7	0.8
Lancetfish (LN)	2.7	2.4	Dusky shark	0.4	0.8
Lancetfish (SN)	1.6	1.4	Hammerhead	0.2	1.8
Mahi mahi	1	0.9	Mako	0.6	0.8
Oilfish	0.8	2.2	Oceanic white tip	0.5	0.9
Opah	0.7	0.5	Porbeagle	1.2	1.1
Ray's bream	1.8	2	Ray	0.9	1.2
Slender barracuda	1.7	1.6	Thresher shark	0.6	1
Sunfish	0.6	1.3	Tiger shark	0.5	0.5
Wahoo	1	1.1			

Fixed Effects

Exposure to dusk had a positive effect on the catch rates for most species (Figure 4.4). Dusk often had a negative effect on the catch rates of billfish, such as striped marlin and sailfish. For most species the effect of dawn was weaker and it influenced the catch rates of fewer species.

Like soak time, timing made a substantial difference to catch rates (Table 4.4). For a soak time of 12 hours in the South Pacific Yellowfin fishery, for example, longline segments exposed to both dawn and dusk have a catch rate of $2.0(\pm 0.5)$ escolar per 1000 hooks. The catch rate is $0.8(\pm 0.1)$ per 1000 hooks for segments that were not exposed to either period.

The effects of timing on catch rates were most pronounced in the South Pacific Bluefin fishery. The fishery also showed the greatest range in soak time coefficients, with the coefficients tending to be larger than the other fisheries (Figure 4.5).

Table 4.4. Examples of the effect of timing on expected catch rates of species in the South Pacific Yellowfin fishery. The expected catch rates (number of animals per 1000 hooks) are predicted from the species' soak time coefficient for a longline operation with a soak time of 12 hours. The different catch rates are for longline segments exposed to a dawn period, both a dawn and a dusk period or neither period.

Species	Period		
	neither period	dawn only	dawn + dusk
Tuna and tuna-like species			
Albacore	12.3	14.0	16.5
Bigeye	0.9	1.2	2.1
Skipjack	1.4	1.2	1.0
Southern bluefin	3.8	2.9	4.1
Yellowfin	7.7	7.6	8.0
Billfish			
Black marlin	1.2	0.6	0.4
Blue marlin	0.4	1.0	1.4
Sailfish	0.8	0.7	0.7
Shortbill spearfish	1.3	0.9	0.9
Striped marlin	0.8	0.9	0.9
Swordfish	0.5	0.7	1.3

Species	Period		
	neither period	dawn only	dawn + dusk
Other bony fish			
Barracouta	1.1	1.2	0.7
Escolar	0.8	1.0	2.0
Great barracuda	1.0	0.8	0.8
Lancetfish (LN)	2.8	2.7	2.5
Lancetfish (SN)	1.2	1.1	1.3
Mahi mahi	1.2	1.3	1.1
Oilfish	0.8	1.1	1.8
Opah	0.5	0.5	0.6
Ray's bream	0.8	0.7	1.6
Slender barracuda	2.0	1.5	1.2
Sunfish	0.8	0.6	0.7
Wahoo	1.2	1.3	1.1
Sharks and rays			
Blue shark	1.3	1.4	1.4
Bronze whaler	0.6	0.9	1.0
Dusky shark	0.1	0.1	0.6
Hammerhead	0.4	0.2	0.3
Mako	0.7	0.8	0.8
Oceanic white tip	0.7	0.8	0.7
Porbeagle	1.0	0.6	0.6
Ray	0.9	0.9	1.1
Thresher shark	0.6	0.6	0.7
Tiger shark	0.4	0.5	0.7

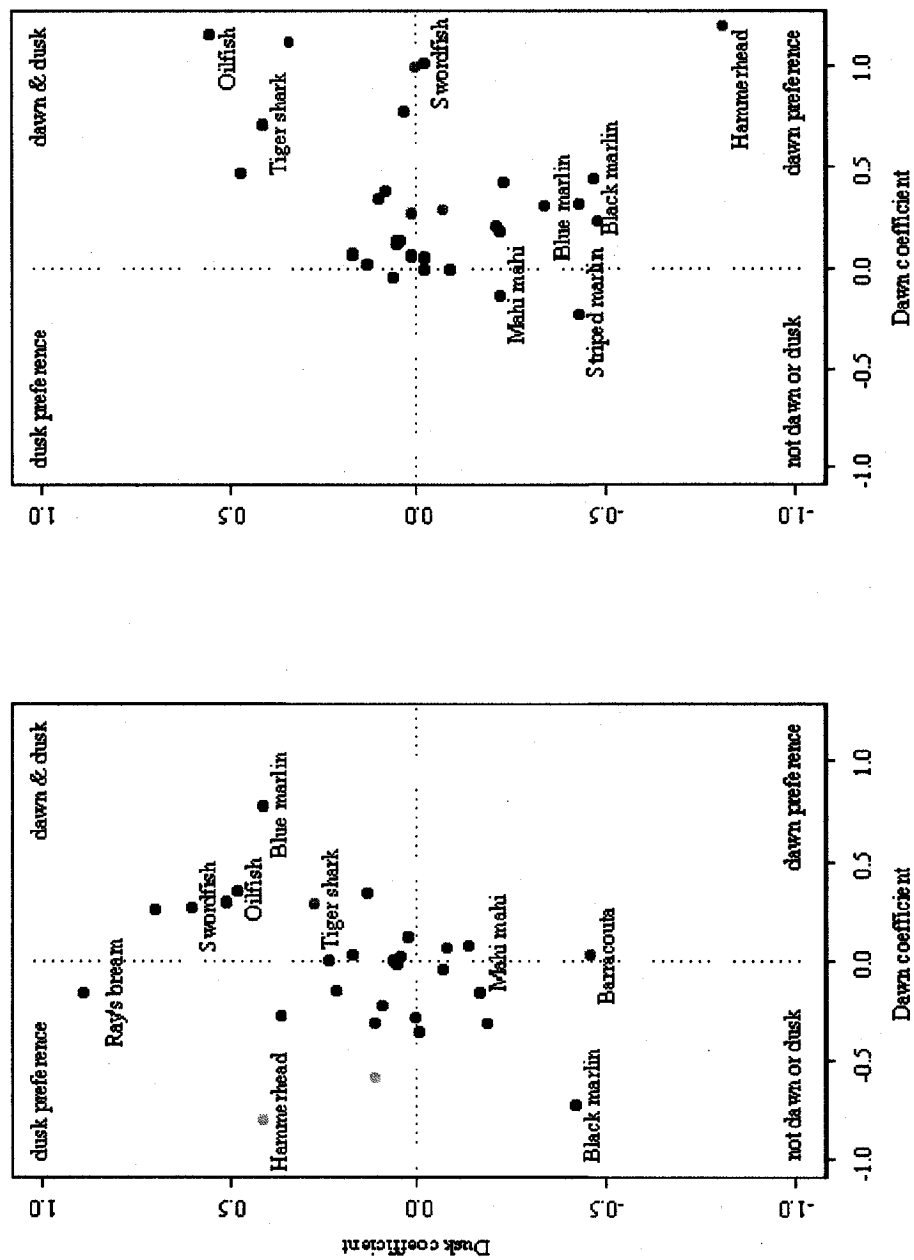


Figure 4.4. Coefficients for the effects of dawn on catch rate plotted against that of dusk for two fisheries. The shading of each symbol represents the sum of the standard errors of the dawn and dusk estimates (heavy shading for the lowest standard errors; light shading for large standard errors). Not all species names are shown.

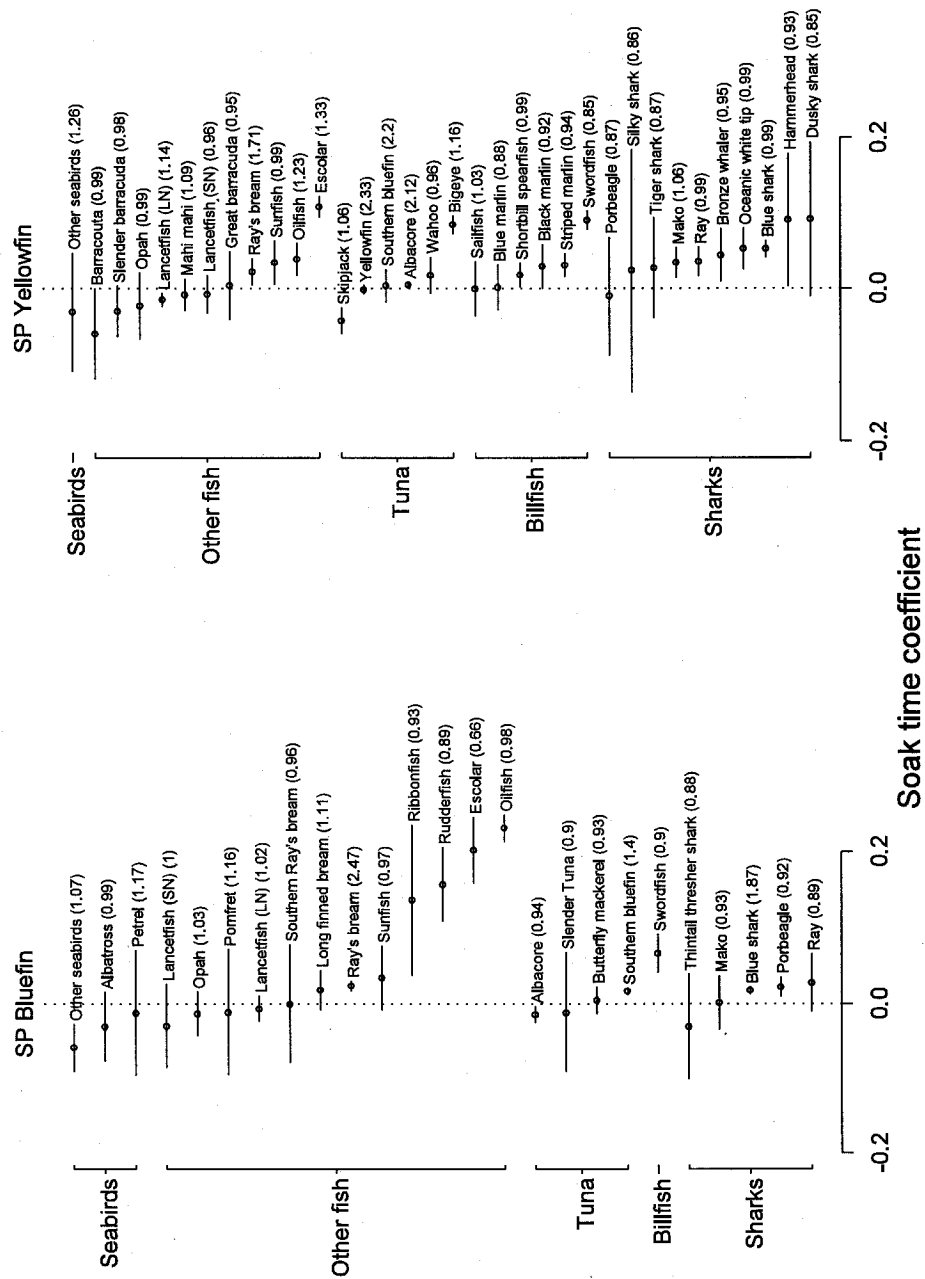
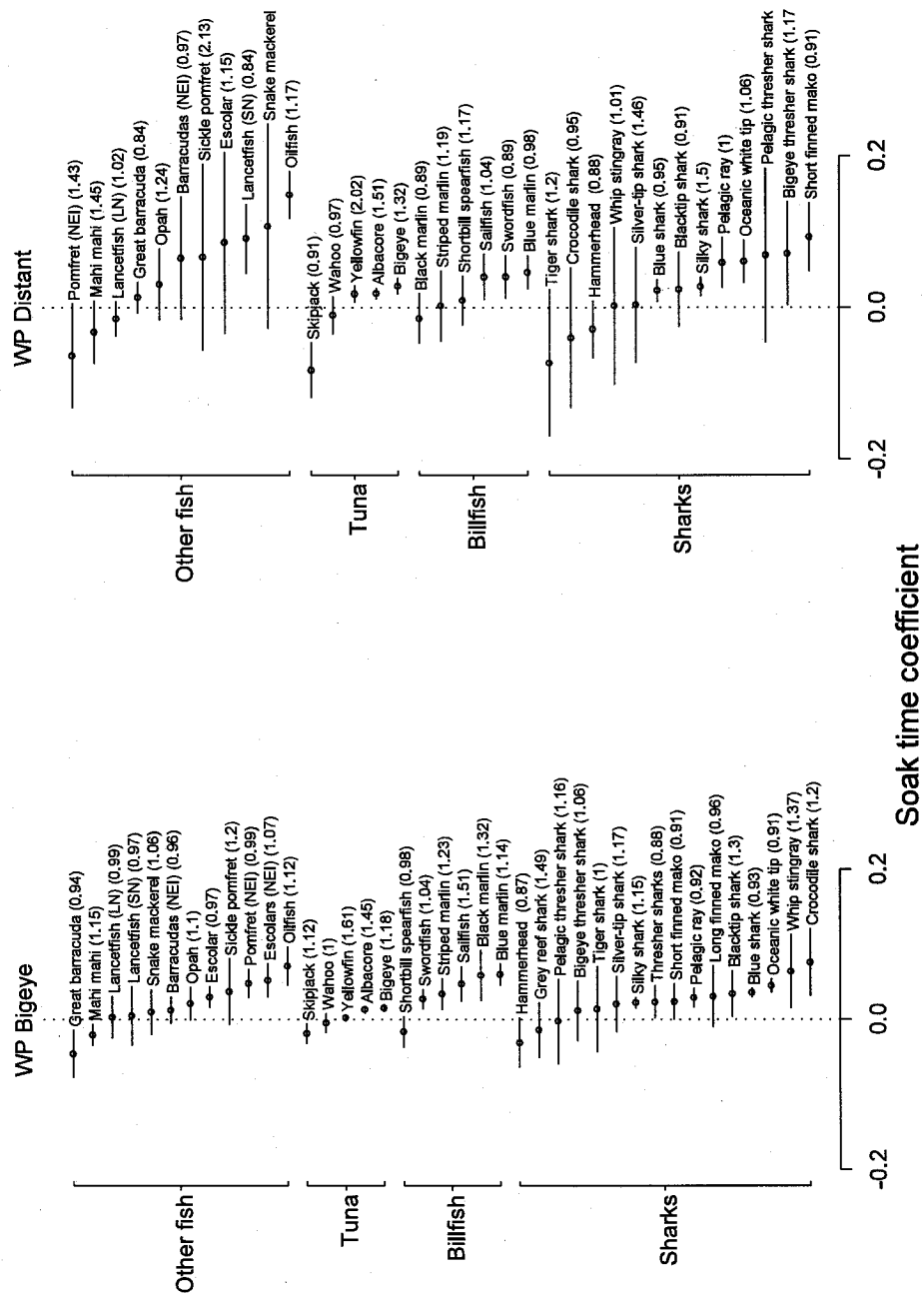


Figure 4.5. Coefficients for the effect of soak time on the catch rates of the most abundant species in each fishery. The coefficients are from random effects models where soak time is the only factor. Horizontal bars are 95% confidence intervals for the estimated coefficient. The dispersion parameter is shown in parentheses. Dispersion is 1.00 for species that are distributed as predicted by the model, but may be higher for species that have a more clumped distribution along the longline.



Separately, the fixed effects often had statistically significant relationships with catch rates of the seven species that we investigated in detail. However, the interaction between soak time and each fixed effect was less frequently significant. Season was significant, for example, in none of the six models that included a soak time – season interaction term. By comparison, season was significant in 6 of the 18 models that included season as a factor but not with a soak time – season interaction term. The effect of soak time was not significant for southern bluefin in any model for the South Pacific Bluefin fishery. It was significant in 36 of the 48 models for the other six species. We conclude that the fixed effects modified the intercept of the soak time – catch rate relationship, but they rarely altered the relationship's slope.

Akaike's information criterion (AIC) and Sawa's Bayesian information criterion (BIC) both indicated that models with soak time as the only variable are the most or second most parsimonious model. This was the case for all models, except for several models of albacore and long-nosed lancetfish. Therefore the following discussion concentrates on the effects of soak time and timing on catch rates.

Discussion

In considering results of the random effects models, we examine patterns in the effects of soak time and timing among taxonomic groups, the mechanisms that may cause the patterns and their implications. First, however, we investigate whether the effects are consistent for the same species between fisheries.

Comparison of Fisheries

The effect of soak time was consistent for several species between the fisheries, despite the wide range of areas, seasons and fishing practices that the fisheries represented. For example, the soak time coefficients for species in the South Pacific Yellowfin fishery were very similar to those of the same species in the Central Pacific Bigeye fishery ($r = 0.79$; Figure 4.6).

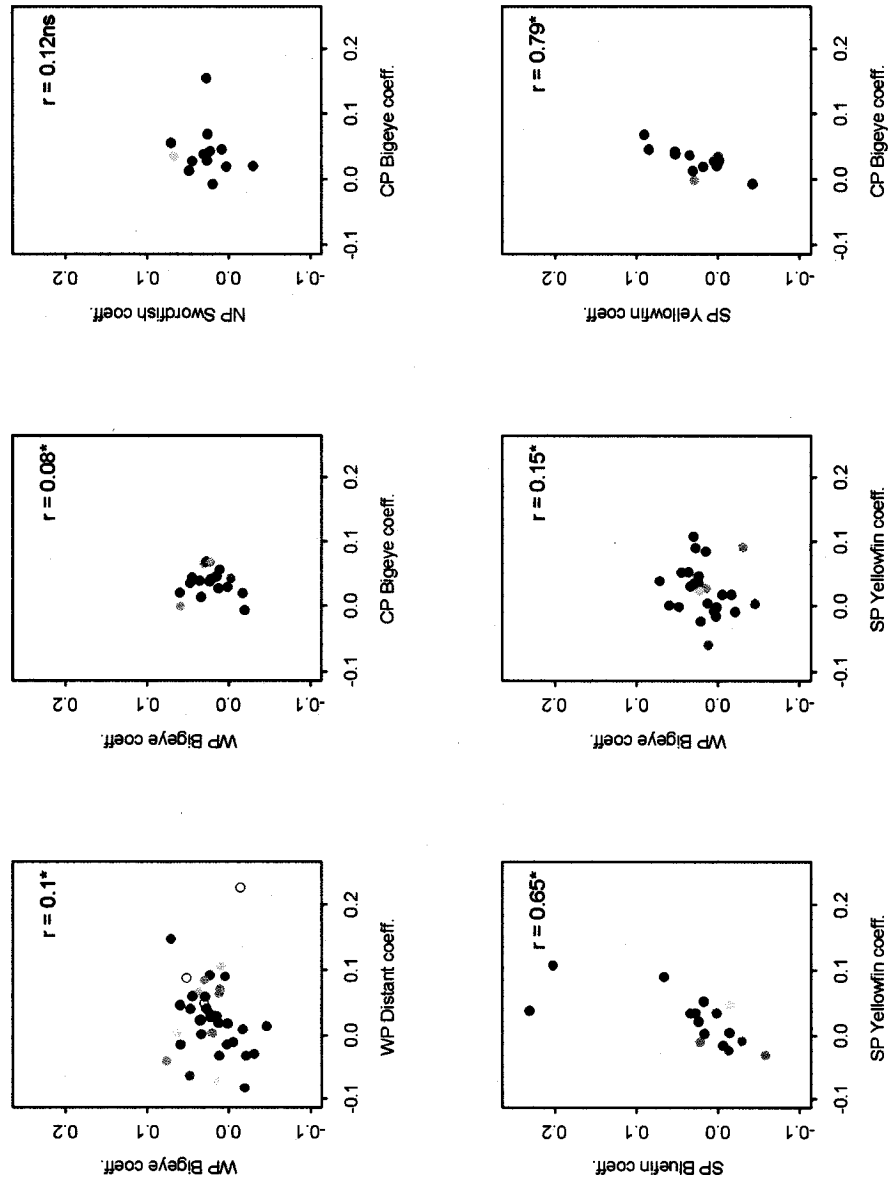


Figure 4.6. Pair-wise relationships of soak time coefficients for species that were common to fisheries. The coefficients are from random effects models where soak time is the only factor. The shading of each symbol represents the size of the standard error of the estimate. " r " is the correlation coefficient of a linear regression of coefficients (* indicates that the regression slope is significantly different from zero at the 95% level of whereas "ns" indicates that the null hypothesis, that the regression slope equals zero, cannot be rejected).

Several species have a narrow range of soak time coefficients over all the fisheries analyzed. Estimates of the coefficient of yellowfin, for example, range from $0.00(\pm 0.01)$ in the South Pacific Yellowfin fishery to $0.04(\pm 0.01)$ in the North Pacific Swordfish fishery. A coefficient of 0.04 is equivalent to a difference of 1.3 yellowfin per 1000 hooks between longline segments with soak times of 5 and 20 hours. The range in coefficients is also small for other abundant and widely distributed species, such as albacore (0.00–0.05) and blue shark (0.01–0.05).

For many species, however, the correlation between soak time coefficients from different fisheries was poor (Figure 4.6). For a few species (e.g., tiger shark) the poor correlation may be a function of small sample sizes and the wide confidence intervals of the coefficient estimates. For other species the estimates were well determined yet poorly correlated, e.g., the coefficient for short-nosed lancetfish was $0.09(\pm 0.05)$ in the Western Pacific Distant fishery compared to $0.01(\pm 0.04)$ in the Western Pacific Bigeye fishery. Therefore, we urge caution in applying our estimates of soak time coefficients to the same species in longline fisheries in other areas.

Underlying Mechanisms

The broad taxonomic groups taken by longline each represent a wide range of life history strategies and feeding behaviors. Nevertheless, the results show a tendency for soak time to have a positive effect on catch rates of most shark species (Figure 4.5). It also had a positive effect on catch rates of many billfish species, including striped marlin, black marlin and swordfish. There is no clear pattern in the effect of soak time on catch rates of tuna or other bony fish. It had a negative effect on the four seabird groups.

The results imply that the ability to stay alive and to escape or avoid scavengers while hooked are important factors that determine the catch that is actually brought on board. The effect of soak time is significantly correlated with the species' ability to survive while hooked on the longline in three of the four fisheries for which we had data on survival (Figure 4.7). Soak time has a strong, positive effect on catch rates of species like blue shark, which are almost always alive when branchlines are retrieved. Species like skipjack and seabirds are usually dead. Soak time had a negative effect on their catch rates. The opposite trend is expected if escape is a significant process that affects catch rates (if escape is important, soak time should have a *negative* affect on the catch rates of

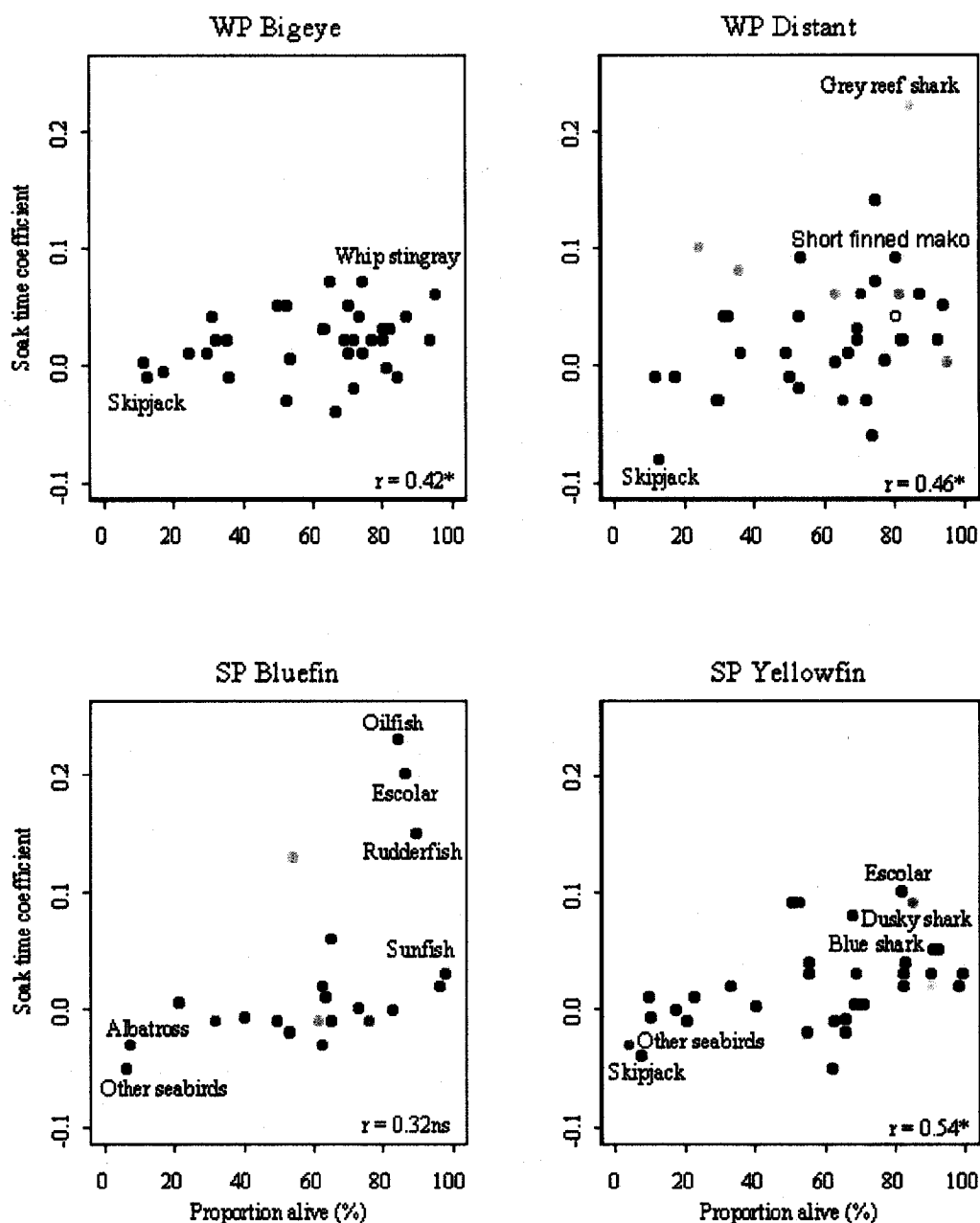


Figure 4.7. Soak time coefficients plotted against the proportion of each species reported to be alive when brought on board. Not included are species where less than ten individuals for the fishery had a record of life status. The coefficients are from random effects models where soak time is the only factor. The shading of each symbol represents the size of the standard error of the estimate. The proportion alive is assumed to be measured without error. "r" is the correlation coefficient of a linear regression of coefficients (* indicates that the regression slope is significantly different from zero at the 95% level).

the most active species). We therefore conclude that removal by scavengers is likely to be more important than escape in determining catch rates for many species.

Longline branchlines are usually 20–30 m in length, allowing considerable room for a live, hooked animal to evade predators or scavengers. Or, scavengers might be attracted by an immobile (dead) fish. The scavenger avoidance hypothesis is seductive, but it is difficult to test with the observer data. Data from hook-timer experiments might help to elucidate the number of animals that are lost or removed from the longline. Data presented by Boggs (1992) show a large number of hook-timers that were triggered, but which did not hold an animal when the branchline was retrieved, e.g., 2–4% of hook-timers on 10 236 branchlines that had “settled” were activated but did not have an animal. It is unclear whether the triggering of hook-timers was due to equipment malfunction or whether it represents high loss rates. Furthermore, current technology does not identify the species that were lost and whether they are alive or dead.

We noticed that soak time coefficients tended to be poorly correlated between fisheries and that the effects of soak time on catch rates were most pronounced in the South Pacific Bluefin fishery. Our scavenging hypothesis might explain those observations as evidence that the activities of scavengers vary between fisheries. For example, blue shark are likely to be one of the most important scavengers. They are most abundant in cool waters, such as the South Pacific Bluefin fishery (Last and Stevens 1994).

Nevertheless, there are other plausible explanations for the differences in soak time effects between fisheries. The movement of branchlines caused by wave action will cause animals to fall off hooks, especially when branchlines are near the sea surface. Rough seas are frequently experienced in the North Pacific Swordfish, and South Pacific Bluefin fisheries where the soak time effects were most pronounced. The branchline material might be subject to breakages due to abrasion by the animal’s teeth or rostrum, resulting in variations in loss rates of certain species between fisheries. For example, Central Pacific Bigeye longliners often use wire for the end of branchlines or ‘leader’ whereas North Pacific Swordfish longliners use monofilament nylon (Mr. Russell Ito, personal commun. 22 August 2002).

Mortality Estimates

The results show that longline data underestimate the level of mortality of several species because they are lost after being hooked. The soak time effect was negative for albatrosses and other seabirds. This agrees with field observations (e.g., Brothers 1991) that most seabirds are taken during longline deployment in the brief period after the bait is cast from the vessel until it sinks beyond the depth that seabirds can dive to. Those observations indicate that counts of seabirds when they are brought on board do not cover the total number hooked because many fall off or are removed by scavengers during the operation or are lost or cut free by crewmembers during longline retrieval.

Seabirds provide a unique case for estimating loss rates because they are only caught when the longline is deployed (Brothers 1991). Within minutes of the branchline being deployed, the capture rate (α in equation 4.4) falls to zero whereas the loss rate (β) might be constant or it might vary. Therefore, the probability of a seabird being on a hook when the branchline is retrieved is:

$$\pi(T) = e^{-\beta T} \quad (4.6)$$

We estimated a soak time coefficient of $-0.0302(\pm 0.0462)$ for albatrosses in the South Pacific Bluefin fishery. Substituting 0.0302 for β in equation (4.6) and 10.4 hours for T (the average soak time of hooks deployed by the longliners) shows that about 27% of albatrosses are lost after being hooked but before the branchlines are retrieved. The loss rate is about 12% for petrels ($\beta = 0.0123$) and 45% for other seabirds ($\beta = 0.0582$). It is about 26% for other seabirds in the South Pacific Yellowfin fishery ($\beta = 0.0307$, $T = 10.0$ hours).

For other species we do not know how the probability of capture or capture rate or loss rate vary during a longline operation. However, hook-timer experiments and observer programs might provide insights into those parameters. Broad limits for the probability of capture might also be obtained if observers were to report the number of branchlines that are retrieved with missing baits or missing hooks.

For most species, capture rates must balance or outweigh loss rates. In this case, captures result from the increased exposure of animals to the longline as a result of movement and, perhaps, the dispersal of chemical attractants during the operation. However, we must stress that losses are also likely to be occurring for the species that

have positive coefficients. The analyses indicate the relative levels of loss between longline segments of varying soak time. Other than for seabirds, we cannot estimate the levels of catch that are lost.

Added to the uncertainty over loss rates is the unknown fate of lost animals. For seabirds it is known that most drown soon after being hooked. The few seabirds that survive while hooked eventually drown during longline retrieval (Brothers 1991). However, it is not known whether other lost animals are dead or alive.

Results of the analysis also have implications for monitoring programs. Observers are increasingly being placed on longliners to collect data on bycatch and to independently verify data reported in logbooks. A sampling approach is necessary in some fisheries because observers are often unable to monitor the entire longline retrieval. Indications that catch rates of some species at the end of the retrieval are double those at the beginning demand care in designing observer monitoring protocols and in the interpretation of the data. Observers could also collect information on the number of hooks retrieved without baits. Such data would greatly improve the estimates of α and β required for the theoretical model. For the empirical model, catch rate data from research surveys where longline segments have very short (<4 hour) soak times would improve estimates of soak time coefficients.

Historical Changes

The interaction of year and soak time was rarely significant for the random effects models of seven species that included fixed effects. This might suggest that soak time – catch rate relationships are stable over time. Note, however, that the range of years that we analyzed is limited to 1992–97. Over larger time scales there have been large variations in the abundance of individual species and the mix of species comprising the pelagic ecosystem. We cannot predict how soak time – catch rate relationships would change with those long-term variations.

Our original motivation for examining the effects of soak time was the hypothesis that the number of hooks per operation and soak time have increased since longlining commenced and that this may have resulted in an overestimation of billfish catch rates in early years. Ward and Hindmarsh (submitted) present information on temporal trends in soak time and timing for several longline fleets. Although there is uncertainty over the

early operations, the available information indicates significant historical changes in the timing of Japan's distant-water longline operations. Average soak time shows a decline from over 11.5 hours before 1980 to 10.0 hours in the 1990s. For species with a negative soak time coefficient, this apparently modest reduction in soak time would inflate catch rate estimates for recent years. It would result in reduced catch rate estimates for species with positive coefficients. For example, the expected catch rate for swordfish is $0.94(\pm 0.06)$ per 1000 hooks for a soak time of 11.5 hours compared to $0.82(\pm 0.06)$ per 1000 hooks for 10.0 hours.

More significant may be changes in the timing of operations. During 1960–80 most baits deployed by Japan's distant-water longliners were available at dawn whereas about 50% were also available at dusk. They deployed and retrieved their longlines at later times in the 1990s so that about 30% of baits were available at dawn and about 70% available at dusk. In the case of swordfish, the changes in timing would moderate the effects of reduced soak time. The expected catch rate for swordfish is 0.89 per 1000 hooks in the early operations compared to 0.83 per 1000 hooks in the later operations.

There is more uncertainty over changes in soak time and in the timing of other longline operations. Relatively small changes in soak time will have major effects on whether species abundance has been over- or under-estimated in recent years.

Conclusions

The results have important implications for fishery management and assessments that rely on longline catch data. Modifications to data collection, such as recording the number of hooks with missing baits during longline retrieval, would greatly improve mortality estimates. The mortality of species like seabirds is significantly higher than previously estimated. Such underestimation may be particularly critical for the assessment and protection of threatened seabirds. Furthermore, the changes in timing and reduction in soak time have resulted in a systematic bias in estimates of mortality levels and abundance indices for many species. For species like swordfish where soak time has a positive effect on catch rates, the stocks might be in better shape than predicted by current assessments if they were solely based on catch and effort data from Japan's longline fisheries. The opposite situation would occur for species with negative soak time coefficients: assessments that use long time series of Japan's longline catch data will

over-estimate the species' abundance so that population declines are more severe than previously believed.

Acknowledgements

Grants from the Pew Charitable Trust, the Killam Foundation provided financial support for this work. Thim Skousen (Australian Fisheries Management Authority), Peter Williams (Secretariat of the Pacific Community) and US National Marine Fisheries Service staff (Kurt Kawamoto, Brent Miyamoto, Tom Swenarton and Russell Ito) provided observer data and operational information on the fisheries. We are especially grateful to the observers who collected the data used in this study and thank the masters, crew members and owners of longliners for their cooperation with the observers. Ian Jonsen, Boris Worm and an anonymous referee kindly provided comments on the manuscript.

Inferring the Depth Distribution of Catchability for Pelagic Fishes and Correcting for Variations in the Depth of Longline Fishing Gear⁷

Introduction

Recent analyses indicate that the state of the world's pelagic fish stocks is much worse than previously believed. Most species of pelagic shark in the northwest Atlantic are now declining by about 10% per year (Baum et al. 2003). Ward and Myers (2005c) found that the biomass of large sharks, tunas, and billfishes has fallen to one-tenth of the level when pelagic longline fishing commenced in the tropical Pacific Ocean. Globally, the abundance of many large marine predators is now less than 10% of the pre-exploitation level (Myers and Worm 2003).

The new perspective on the status of pelagic fishes is directly linked to the recovery of historical data from longline surveys and commercial operations. However, critics have challenged conclusions based on those data, pointing to uncertainties in using longline catch rates as indices of abundance. Longline fishing effort must be corrected or "standardized" for variations in fishing practices and oceanographic conditions if abundance indices for early years are to be comparable to indices from recent years. The timing of longlining operations in relation to peak feeding periods is an example of a historical change in fishing practices. Ward et al. (2004) found that changes in the timing of longlining operations, which now have hooks available during dusk as well as dawn, have resulted in the overestimation of abundance for many species in recent years.

⁷ This chapter was originally published as: Ward, P., and Myers, R.A. 2005. A method for inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1130–1142. The original article's abstract is incorporated in the Conclusions of this thesis and its reference list is included in the Bibliography.

Another important historical change in longlining operations is the depth range of the gear (Figure 5.1), which is the topic of this article. Two methods have been used to account for changes in the depth distribution of longline hooks. One method is to use generalized linear models to relate catches to longline depth and other explanatory variables. In most longline fisheries, however, a switch to deep gear was so rapid in the mid 1970s that there is inadequate temporal overlap to allow comparison of the performance of regular and deep gear (Suzuki et al. 1977). Takeuchi (2001) concluded that it was not possible to make reliable inferences about changes in abundance from historical longline catch and effort data.

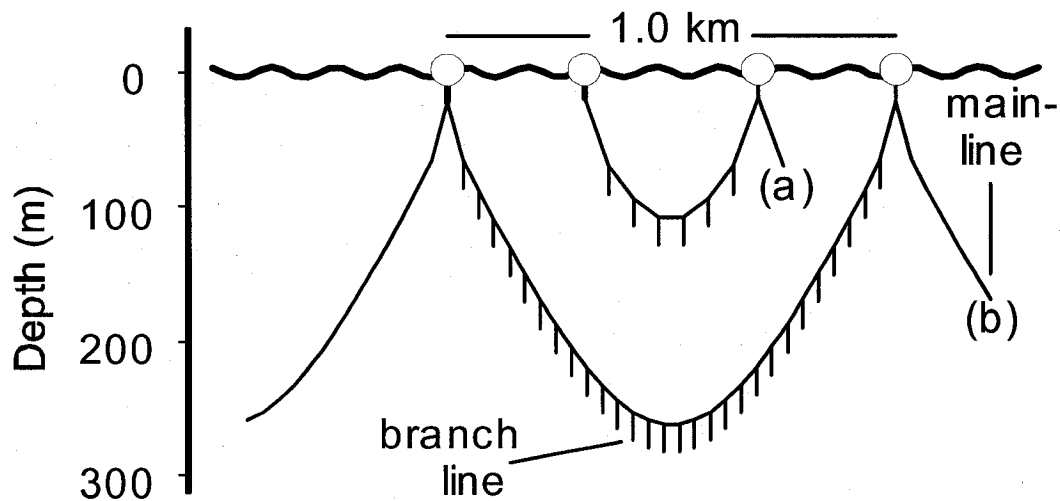


Figure 5.1. Configuration of (a) a regular longline with six hooks between floats, like the longlines deployed by the POFI survey, and (b) a deep longline with 28 hooks between floats, like those deployed by Hawaii-based longliners to catch bigeye tuna. Many longliners began using deep longlines in the tropical Pacific Ocean after 1974 and in the tropical Atlantic Ocean after 1979.

The second method of correcting abundance indices for longline depth is to model the species' preferred habitat. Oceanographic information (e.g., thermocline depth) is combined with information from tracking studies (e.g., Musyl et al. 2003) to estimate the species' depth distribution in time and area strata, e.g., Hinton and Nakano (1996), Bigelow (2002). 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.

The previous methods required the estimation of an additional parameter for each longlining operation included in the analysis. Consequently, estimates become increasingly biased as the sample size increases (Kiefer and Wolfowitz 1956). The generalized linear models used the proportions of catch at depth. However, the local abundance and gear configuration vary among longlining operations, causing further biases in the interpretation of the depth distribution derived from catch proportions. This article describes a new method that uses data from individual longline hooks to estimate relative catchability at depth. The lack of an adequate statistical framework has previously precluded the use of individual hook data to derive statistically valid estimates of the depth distribution of catchability.

We use generalized linear mixed effect models (Wolfinger and O'Connell 1993), which have considerable advantages for estimating catchability at depth: (1) they allow for non-linear relationships between independent variables and the dependent variable (mean catch); (2) a variety of error distributions (e.g., Poisson) can be modeled; and (3) they allow local abundance to be a random variable, providing statistically consistent estimates with improved accuracy (Robinson 1991).

Variations in fishing gear and oceanographic conditions affect “catchability”, the part of a stock that is caught by a defined unit of fishing effort. The catchability coefficient q relates catch C to the species' local abundance N and the amount of fishing effort E :

$$C = qEN \quad (5.1)$$

A reliable estimate of catchability is therefore necessary to estimate abundance from catch and effort data (Murphy 1960). Catches are the product of catchability, local abundance and fishing effort. For longline gear, fishing effort is often measured as the number of longline hooks available at each depth. Our approach is to first estimate the depth distribution of catchability independent of availability. We then take availability into account by adjusting the number of hooks at each depth by the estimated catchability.

Materials and Methods

Data

We analyzed data collected by scientists involved in a research survey and by observers on commercial vessels using pelagic longlines. The data included gear dimensions for each longlining operation, which we used to estimate the maximum settled depth of each hook deployed. We assumed that all animals were caught at the maximum depth, although hook–depth monitors indicate that animals are sometimes caught while the hook is settling during deployment or rising during retrieval (Boggs 1992). The scientists and observers also reported a unique identifier—a sequential number—for each longline hook. Combined with the gear dimensions, the individual hook data were used to estimate the depth at which each animal was caught.

We combined three datasets. The US Pacific Oceanic Fisheries Investigations (POFI) conducted 1157 longlining operations in an area of the Pacific Ocean bounded by 175°E–115°W and 12°S–44°N during 1950–1958 (Figure 5.2). Survey longliners used fishing gear and techniques adopted from Japan (Murphy and Shomura 1972). They typically deployed longlines at dawn each day and retrieved in the afternoon. They usually attached six hooks between each pair of floats, amounting to about 240 hooks in each daily longlining operation. The maximum settled depth of the hooks ranged from 18 m to 103 m (unless otherwise indicated, all hook depths were estimated from the catenary formula reduced by 25% for the effects of currents). The survey longliners occasionally deployed longlines at night and deep longlines with up to 21 hooks between floats (18–144 m). They mostly used sardines (*Sardinella* spp.) as bait, but also experimented with saury (*Scomberesox* spp.), squids (*Illex* spp.), and various other baits.

The second dataset was from US National Marine Fisheries Service (NMFS) observers placed on commercial longliners in the Pacific Ocean during 1994–2002. The data consisted of 8037 daily longlining operations in an area bounded by 5–40°N and 174°E–134°W. The longliners targeted broadbill swordfish (*Xiphias gladius*) or tunas, specifically bigeye tuna (*Thunnus obesus*) and yellowfin tuna (*T. albacares*), for domestic fresh-fish markets. To catch tunas in tropical waters they deployed deep longlines with sardines as bait during the day, with about 28 hooks between floats (40–

230 m). To catch swordfish in temperate waters, they deployed shallower longlines (39–121 m) with shortfin squid (*Illex illecebrosus*) as bait at night.

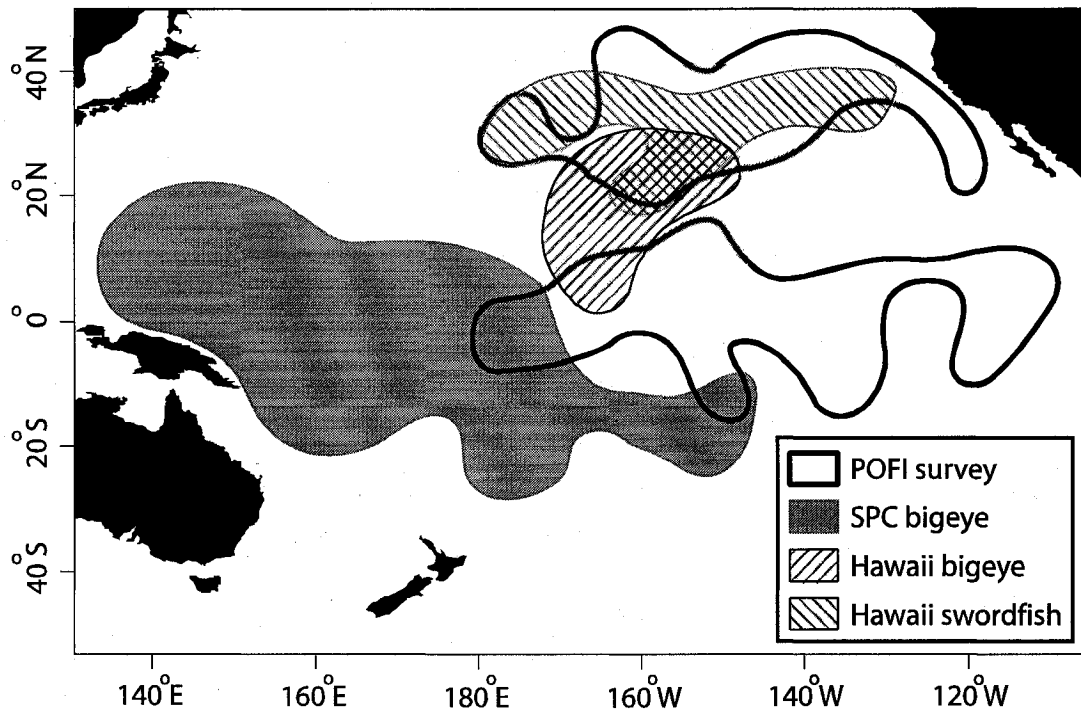


Figure 5.2. Geographical ranges of datasets used to derive the depth distribution of catchability for each species. The data were collected by longline surveys under the US Pacific Oceanic Fisheries Investigations (POFI), compiled by the Secretariat of the Pacific Community (SPC) from observers on commercial longliners operating in the western Pacific, and by observers placed on Hawaii-based longliners by the US National Marine Fisheries Service. The Hawaii longliners targeted swordfish in the North Pacific or bigeye tuna in the tropical Pacific Ocean.

The Secretariat of the Pacific Community (SPC) assembled the third dataset from data collected by observers placed on commercial longliners during 1992–2002. The data consisted of 1813 longlining operations in an area of the Pacific Ocean bounded by 27°S–12°N and 138°E–172°W. Most of the longliners targeted bigeye tuna during the day with deep longlines consisting of about 30 hooks between floats (33–267 m). They used saury, sardines or squids as bait.

The longliners used similar fishing gear, e.g., comparable hook sizes and wire leaders to connect hooks to branch lines. The longliners monitored by NMFS and SPC

observers deployed monofilament-nylon branch lines, whereas the survey longliners used rope gear. The next section describes the random effects model that are used to account for variations in local abundance and catches among longlining operations. It was included to reduce the effects on catchability of variations in bait and fishing gear among longline operations.

Observers and survey scientists identified the species and recorded the hook number for each animal caught. Occasionally they did not identify animals to the species level, so that species were combined into species groups. For brevity, we use the term “species group” to refer to individual species as well as species groups. The NMFS observers did not record the hook number for species groups other than tunas, billfishes, and sharks.

We assumed that the mainline formed a catenary curve between each pair of floats and estimated the depth of each hook by applying the formula presented by Suzuki et al. (1977) to longline dimensions reported for each operation. We assumed that the shape of the catenary curve (and therefore the corresponding depth of hooks) did not systematically vary along each longline or during each longline operation. Observed depths and predicted depths are known to vary, with ocean currents and wind having the most important influence on hook depth. Bigelow et al. (2002) estimated that hook numbers three and ten of longline gear with 13 hooks between floats, shoaled by about 20% when subjected to a current velocity of $0.4 \text{ m}\cdot\text{s}^{-1}$. To represent shoaling of longlines in our study area, we reduced all depths predicted by the catenary formula by 25%. The data were then binned into 40-m depth categories, ranging from 0–40 m to 480–520 m.

We estimated catchability distributions separately for day and night operations. Most day operations commenced at dawn (the median deployment time was 07:05, with 50% beginning between 05:20 and 07:47). Night operations often started at dusk (median time of 18:17 with 50% between 17:11 and 19:30). We analyzed a total of 3155 night operations (13 679 animals) and 7852 day operations (32 046 animals; Table 5.1).

Table 5.1. Common and scientific names of each species or species group analyzed. Also shown are the number of animals modeled for day and for night longlining operations.

Common name	Scientific name	Number modeled		
		Day	Night	
Tunas and tuna-like species				
Albacore tuna	<i>Thunnus alalunga</i>	2777	1267	
Bigeye tuna	<i>Thunnus obesus</i>	2980	1819	
Skipjack tuna	<i>Katsuwonus pelamis</i>	2771	241	
Wahoo	<i>Acanthocybium solandri</i>	528	122	
Yellowfin tuna	<i>Thunnus albacares</i>	3131	1417	
Billfishes				
Black marlin	<i>Makaira indica</i>	225	98	
Blue marlin	<i>Makaira nigricans</i>	1902	593	
Broadbill swordfish	<i>Xiphias gladius</i>	1277	2332	
Sailfish	<i>Istiophorus platypterus</i>	402	148	
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	2477	269	
Striped marlin	<i>Tetrapturus audax</i>	2726	743	
Other teleosts				
Barracudas ^a	<i>Sphyræna</i> spp.	240	0 ^b	
Escolar	<i>Lepidocybium flavobrunneum</i>	266	107	
Great barracuda	<i>Sphyræna barracuda</i>	102	0 ^b	
Lancetfishes ^a	<i>Alepisaurus</i> spp.	358	0 ^b	
Longnosed lancetfish	<i>Alepisarus borealis</i>	46	0 ^b	
Mahi mahi	<i>Coryphaena hippurus</i>	349	157	
Oilfish	<i>Ruvettus pretiosus</i>	254	96	
Opah	<i>Lampris guttatus</i>	197	0 ^b	
Pomfrets ^a	F. Bramidae	179	35	
Shortnosed lancetfish	<i>Alepisaurus brevirostris</i>	53	7	
Sickle pomfret	<i>Taractichthys steindachneri</i>	20	0 ^b	
Snake mackerel	<i>Gempylus serpens</i>	102	113	
Sharks and rays				
Bigeye thresher shark	<i>Alopias superciliosus</i>	956	139	
Blue shark	<i>Prionace glauca</i>	3050	2444	
Common thresher shark	<i>Alopias vulpinus</i>	30	0 ^b	
Crocodile shark	<i>Pseudocarcharias kamoharai</i>	384	84	

Common name	Scientific name	Number modeled	
		Day	Night
Dusky shark	<i>Carcharhinus obscurus</i>	54	0 ^b
Grey reef shark	<i>Carcharhinus amblyrhynchos</i>	25	0 ^b
Long-finned mako shark	<i>Isurus paucus</i>	153	0 ^b
Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	1910	494
Pelagic stingray	<i>Dasyatis violacea</i>	356	204
Short-finned mako shark	<i>Isurus oxyrinchus</i>	665	388
Silky shark	<i>Carcharhinus falciformis</i>	1019	362
Silver-tip shark	<i>Carcharhinus albimarginatus</i>	29	0 ^b
Tiger shark	<i>Galeocerdo cuvier</i>	34	0 ^b
Whip stingray	<i>Dasyatis akajei</i>	19	0 ^b

^aOccasionally observers did not identify animals to the species level. Consequently we modeled data for species groups (e.g., barracudas, *Sphyræna* spp.) separately to data for identified species (e.g., great barracuda, *Sphyræna barracuda*).

^bInsufficient numbers caught to allow reliable parameter estimation.

Models

We used generalized linear mixed effect models (Wolfinger and O'Connell 1993) to estimate parameters that describe the shape of the depth distribution of catchability of each species group. The catch of each species group in longlining operation i at depth D was assumed to follow an over-dispersed Poisson distribution with a mean of $\mu_{i,D}$. The assumption of a Poisson distribution is reasonable because only a small proportion of the hooks are occupied by a species group, e.g., the mean percent of hooks occupied by one of the most abundant species, yellowfin tuna, was $1.7 \pm 4.1\%$ standard deviations (SD).

For each species group, the model predicts the mean catch $\mu_{i,D}$ using a log link:

$$\log(\mu_{i,D}) = \lambda_i + \gamma_1 D + \gamma_2 D^2 + \gamma_3 D^3 + \log(H_{i,D}) \quad (5.2)$$

where λ_i and γ_j are parameters estimated for each species group, and the offset $H_{i,D}$ is the number of hooks H deployed at depth D of longlining operation i . Our method includes a random effects model that accounts for variations in the local abundance of each species. We assumed that the log abundance of the species group, when it is encountered, followed the random effects distribution, which we assumed to be a normal distribution,

$$\lambda_i \sim N(\mu, \sigma^2)$$

The regression coefficients γ_j in eq. 5.2 describe how catchability changes with depth (μ represents catch, H is fishing effort, and the γ_j represent catchability in eq. 5.1). For each species group we sequentially tested increasingly complex functional forms of eq. 5.2 to find the most appropriate model. We initially fitted eq. 5.2 with $\gamma_1 = \gamma_2 = \gamma_3 = 0$, then tested the model in which we estimated γ_1 , while constraining the quadratic and cubic parameters to zero. We sequentially added other γ_j parameters until the increase in the fit of the model was not significant as judged by a likelihood ratio test. The cubic model adequately described most of the variation in depth; including additional terms had very little effect on parameter estimates.

We then used parameter estimates, denoted by the “hat” symbol, from eq. 5.2 to estimate the catchability of each species group as a function of hook depth D (in meters):

$$f(D) = \exp(\alpha + \hat{\gamma}_1 D + \hat{\gamma}_2 D^2 + \hat{\gamma}_3 D^3)$$

where α is chosen such that the mean of $f(D)$ equals one over the depth range considered. We refer to these standardized $f(D)$ as the “depth distribution of catchability” or simply the “catchability distribution”.

Correcting Abundance Indices for Depth Effects

To correct abundance indices for variations in longline depth, our estimates can be applied to data where gear dimensions are known for each operation. They can also be used to correct indices for changes in catchability when only the proportion of gear configurations is known. In almost all cases, the longline configuration is identical between floats and symmetrical. Therefore, the number of depths k that needs to be considered for each gear configuration is half the number of hooks between floats. We then estimated q_g , which is the average catchability of the species group for gear configuration g :

$$q_g = \sum_k f(D_k) p_g(D_k)$$

where $p_g(D_k)$ is the proportion of hooks at depth D_k . For each year, the catchability averaged over all gear configurations is

$$\bar{q}_y = \sum_g P_{y,g} q_g$$

where $P_{y,g}$ is the proportion of longlining operations using gear configuration g in year y . For each species group, we standardized the average catchability \bar{q}_y by dividing it by its value in the first year of the time series.

We illustrate the effect of the depth correction by applying it to a time series of annual catch rates for Japan's longline fleet operating in the southern Atlantic Ocean. Estimation of the average annual catchability used the depth distribution of catchability combined with changes in gear configurations reported by Suzuki et al. (1977) and Uozumi and Nakano (1996). For each year, we divided the species' catch rate by our estimate of its average catchability for all gear configurations \bar{q}_y . We then standardized the estimate by dividing it by the average catchability in 1975 (the first year of the time series).

Results and Discussion

Precision of Depth Estimates

The application of our estimates of the depth distribution of catchability should not be affected by uncertainty over the depths of longline hooks estimated by the catenary formula. It is true that observed depths (obtained using depth sensors) and predicted depths often differ. The weight of the longline causes a gradual shortening in the distance between floats during the operation. Consequently, longline hooks may sink to deeper depths than those predicted by the catenary formula. At the same time, wind and current shear may cause hooks to rise towards the surface or "shoal" (Hanamoto 1987; Mizuno et al. 1999). However, we contacted several observers and longline fishers who pointed out that commercial fishers adjust their fishing practices to maximize the availability of longline hooks to target species, such as deep-dwelling bigeye tuna. Since the 1980s, many longliners have used Doppler current profilers to monitor the velocity and direction of subsurface currents. Most fishers minimize shoaling by deploying their longline in the same direction as prevailing currents. Furthermore, the predicted depth distributions of the hooks are surrogates for their true, but unknown, depth distributions. Our approach does not require accurate depth estimates because exactly the same methods and corrections that we used to estimate depth for our models can be applied to the longline

data that is being corrected. By contrast, the depth estimates from tracking studies that are used in habitat-based models are not calibrated against longline depth.

Various factors may influence the depth distribution of catchability derived from observer data, e.g., spatial and seasonal variations in wind, currents and thermal structure, and differences in fishing practices and gear among fleets. Our presentation of one night and one day distribution for each species should not preclude further investigation of the importance of those influences on depth distributions.

Ecological Groups

We derived reliable estimates of the depth distribution of catchability for 37 species groups over a depth range of 18–512 m for day operations (Figure 5.3), and for 24 species groups over 28–504 m for night operations (Figure 5.4; Appendix 1 provides parameter estimates for each species). The species groups show considerable variability in the distribution of catchability. The distributions indicate at least three distinct ecological groups, which should be considered separately in ecosystem models: epipelagic species that feed in surface waters (< 200 m) during the day; wide-ranging pelagic species whose catchability does not vary over the observed depth range; and mesopelagic species that feed at intermediate and deep depths (> 200 m) by day then range more widely at night. Few species groups show high catchability at intermediate depths (200–400 m).

Swordfish, blue shark (*Prionace glauca*), and yellowfin tuna are members of the wide-ranging pelagic group. Their daytime catchability shows only minor variations over the observed depth range (Figure 5.3). Tracking studies indicate that they range throughout the epi- and mesopelagic zones, e.g., Carey and Robinson (1981), Carey and Scharold (1990), and Holland et al. (1990).

The epipelagic group includes oceanic whitetip shark (*Carcharhinus longimanus*), dusky shark (*C. obscurus*), skipjack tuna (*Katsuwonus pelamis*), mahi mahi (*Coryphaena hippurus*), wahoo (*Acanthocybium solandri*), and all billfishes except swordfish. They were most often caught in surface waters above the thermocline (about 140 m in the tropical Pacific Ocean) during the day (Figure 5.3). However, some were also caught on deep hooks. This is probably because animals may be caught when “deep” hooks pass through surface waters during longline deployment and retrieval (Boggs 1992).

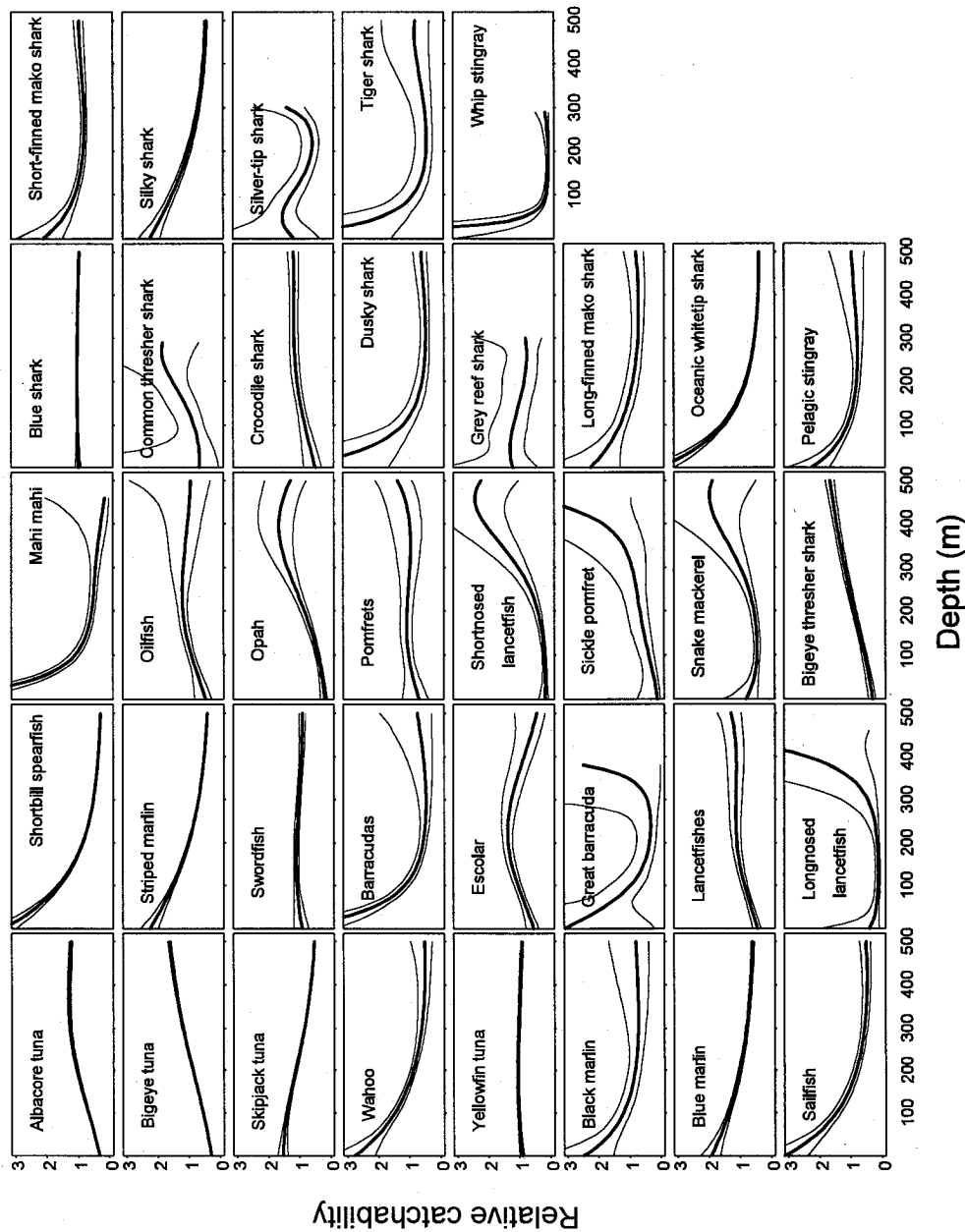


Figure 5.3. Estimates of the depth distribution of catchability $f(D)$ (thick line) with the 95% prediction intervals (thin lines) for day longlining operations. The mean catchability has been set to one to facilitate comparison between species and species groups.

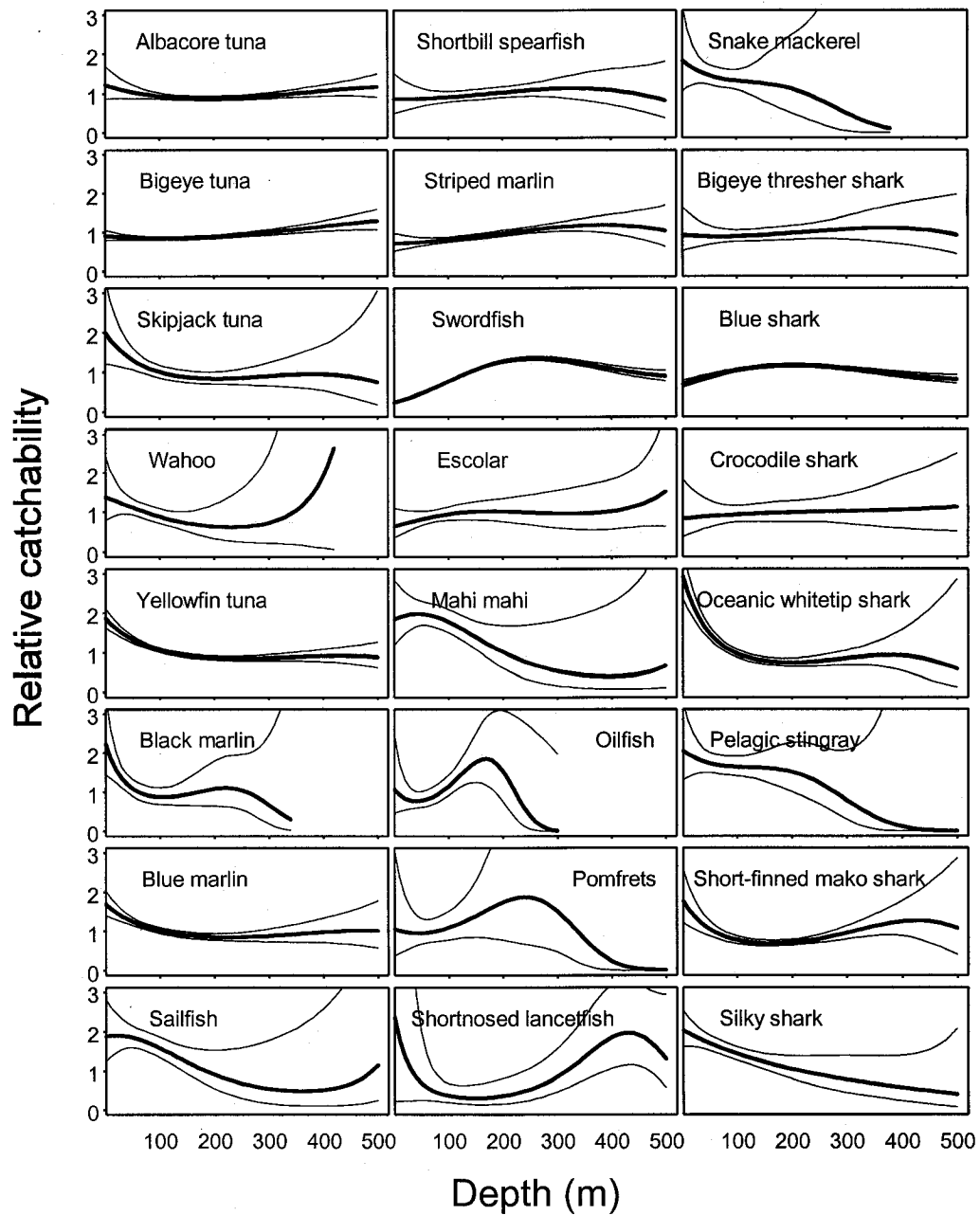


Figure 5.4. Estimates of the depth distribution of catchability $f(D)$ (thick line) with the 95% prediction intervals (thin lines) for night longlining operations. The mean catchability has been set to one.

Diel Variation

Comparisons of catchability for day and night operations (Figure 5.3, Figure 5.4) reveal patterns of diel variation among the mesopelagic species that probably represent vertical migration. The catchability of bigeye tuna, for example, increases with depth during the day, whereas it shows a much more uniform distribution at night. Our interpretation is that visibility is critical to the vertical distribution of large predators like bigeye tuna in the open ocean. They have several physiological adaptations, such as large eyes, that provide acute vision and allow them to hunt at low light levels (Pereira 1996). They feed below the sunlit zone during the day where they can avoid detection by their prey. At night they range more widely because the ocean is almost uniformly dark. The distributions of other large predators indicate patterns of vertical migration that are similar to that of bigeye tuna, e.g., albacore tuna (*Thunnus alalunga*), escolar (*Lepidocybium flavobrunneum*), and bigeye thresher shark (*Alopias superciliosus*).

Visibility is also critical for predator avoidance by small species, such as snake mackerel (*Gempylus serpens*), which are the prey of large tunas, billfishes, and sharks (Kitchell et al. 1999; Rosas-Alayola et al. 2002). These small species concentrate at deep depths, below the sunlit zone during the day, where they can avoid their predators. At night they venture into surface waters. Several epipelagic species show the opposite pattern, concentrating in surface waters during the day then ranging more widely at night, e.g., shortbill spearfish (*Tetrapturus angustirostris*) and striped marlin (*T. audax*).

The depth distribution of catchability does not change markedly between day and night for several species, e.g., skipjack tuna, mahi mahi, and sailfish (*Istiophorus platypterus*). These epipelagic species are most abundant in surface waters. Hook-timer experiments (e.g., Boggs 1992) confirm that they are often caught in surface waters, particularly during longline deployment and retrieval. Night longlining operations caught fewer species groups than day operations, and the night depth distributions for several epipelagic species are poorly estimated compared to the estimates of their daytime distributions. This is partly due to differences in sample sizes (we analysed 3155 night operations compared to 7852 day operations). The poor estimates of night distributions might also be related to diel variations in feeding activity. Stomach-content analyses indicate reduced feeding activity among many epipelagic species at night. Analyses of

the stomach contents of sailfish by Rosas-Alayola et al. (2002), for example, show that this species feeds mainly in surface waters during the day.

Comparison with Tracking Studies

For several species groups, the depth preferences derived from acoustic telemetry in the open ocean can be compared with the catchability distributions that we derived from longline data. The tracking studies are mostly limited to large, commercially important species of tunas and billfishes and several shark species (Table 5.2). Each study involved small numbers fitted with acoustic transmitters and tracked for several days. Recent studies using archival tags (e.g., Musyl et al. 2003) have allowed the depth preferences of animals to be estimated over longer periods, thereby providing a more complete understanding of their behavior.

Table 5.2. Details of tracking data used to estimate the proportion of time spent at each depth (Figure 5.5).

Species	Device	No. of animals	Time at liberty	Location	Reference
Bigeye tuna	archival tags	4	9–76 days	southwestern Hawaii	Musyl et al. (2003)
Yellowfin tuna	ultrasonic transmitters	11	5 h – 6 days	Hawaii	Holland et al. (1990)
Blue marlin	ultrasonic transmitters	5	24–42 hr	Hawaii	Holland et al. (1990)
Black marlin	ultrasonic transmitters	4	18–24 hr	northeastern Australia	Pepperell and Davis (1999)

Our estimates of catchability distributions from longlining operations provide a good match to the tracking data in several cases (Figure 5.5). For example, tagged black marlin spent most of the day in surface waters, which matches the catchability distribution (Figure 5.5g). For bigeye tuna, however, the tracking data show different patterns to the catchability distribution (Figure 5.5a, b). The inconsistencies between catchability distributions and depth preferences may be due to the small numbers of animals tracked or differences in behaviour and oceanographic conditions between our broad study area and the areas where the animals were tracked. Eight of the yellowfin tuna tracked by Holland et al. (1990; Figure 5.5c), for example, were associated with

fish-aggregating devices. Those animals were found to behave quite differently to yellowfin tuna in the open ocean.

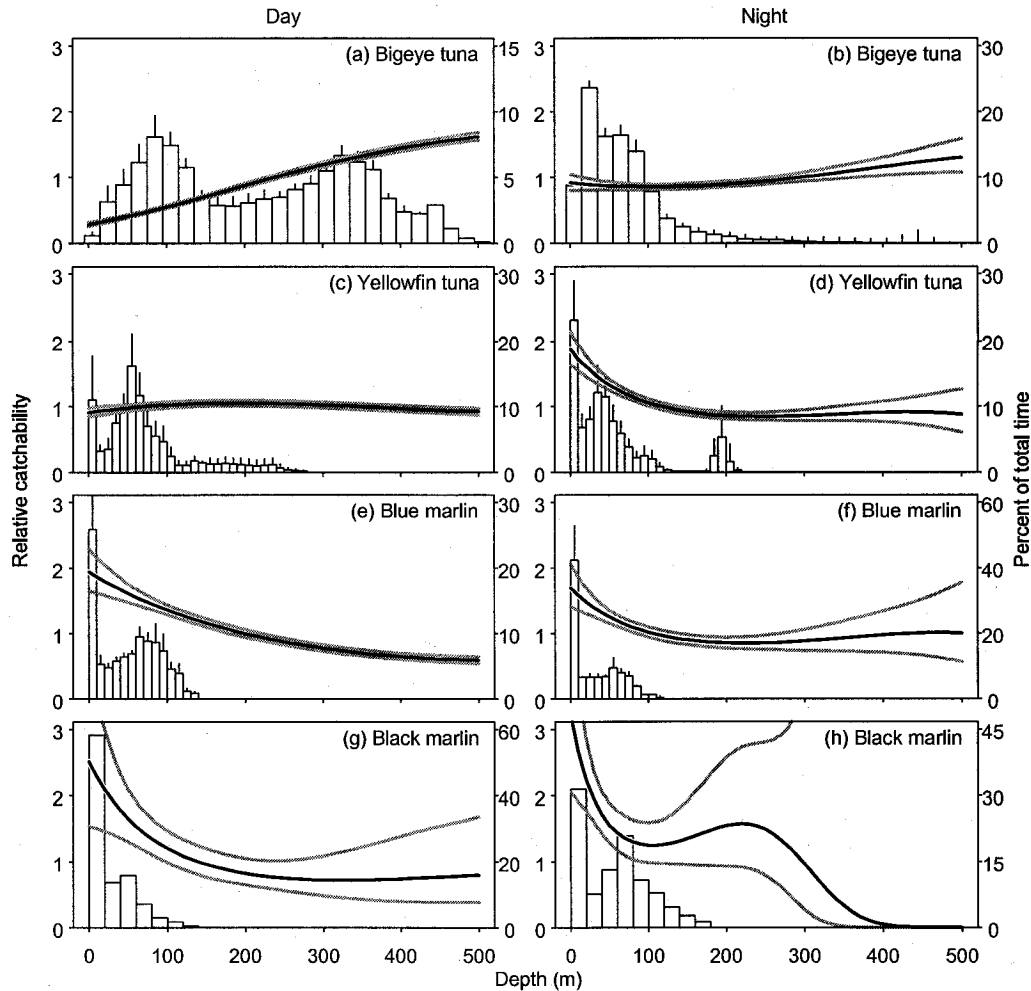


Figure 5.5. Estimates of the depth distribution of catchability $f(D)$ of longline-caught fishes (thick line) compared with the percent of time at each depth for tracked animals (histograms) for day and night periods (Table 5.2). Where available, standard errors (vertical lines) are shown for the mean percent of time at depth. Thin lines are 95% prediction intervals for catchability.

The inconsistencies between the depth distribution of catchability and depth preferences derived from tracking studies might also reflect a mismatch between the estimated depth of longline hooks and tracking depths or differential vulnerability to longline fishing 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 be present in

surface waters during the day, but not caught on longline hooks there because they are not feeding or cannot detect the baits. This is not of concern because we intend the estimates of catchability to be used to correct abundance indices derived from longline data. However, the mismatch between catches on longline hooks and the species' depth preference is a flaw in habitat-based models that are solely based on tracking data. Tracking data show an animal's depth preference, which may not always match the species' vulnerability to longline fishing gear. From an analysis of simulated data for blue marlin (*Makaira nigricans*), Goodyear (2003) concluded that the propensity of the species to take longline baits and the actual depth profile of the fishing gear strongly influenced habitat-based model estimates of abundance. The development of statistical habitat-based models, which fit observed catches (Hinton and Maunder 2003), may help to correct for differences between depth preferences and vulnerability.

An alternative to our approach is to use hook-timers that record the time and depth when each animal was caught, e.g., Boggs (1992). However, a very large number of hook-timer experiments are required to derive reliable estimates of depth preference. For example, Matsumoto et al. (2001) analyzed over 300 longlining operations, each deploying 10–163 hook-timers. However, that number of experiments was not large enough to obtain reliable estimates of depth preference.

Environmental Constraints on Depth Distribution

The tracking studies show that environmental conditions set broad limits to the vertical distribution of each species. Those limits will also apply to the depth distribution of catchability. For example, Brill et al. (1993) concluded that sharp gradients in water temperature between the mixed layer and deeper waters represented a barrier to vertical migrations of striped marlin near Hawaii. Other conditions, such as oxygen concentration, are also known to limit the vertical distribution of pelagic fishes (Hanamoto 1987). The efficacy of those thresholds will vary seasonally, spatially, among species, and with body-size (Dagorn et al. 2000). Caution is required in applying our estimates of catchability distributions to regions outside the study area. For example, the shallow thermocline in the tropical eastern Pacific Ocean results in very low catch rates of striped marlin on longline hooks below about 100 m (Matsumoto and Miyabe 2002).

By contrast, our estimates indicate an average level of catchability for striped marlin below 100 m (Figures 5. 3, 5. 4).

Further work is required to determine whether our estimates can be applied to other regions. Several organizations hold hook-level data that we could not access, e.g., data collected by British observers on longliners in the Indian Ocean and surveys by Japan's National Research Institute of Far Seas Fisheries. Such datasets should be used to test the hypothesis that the shape of a species' catchability distribution does not vary among regions or seasons, but is compressed or extended by local conditions that limit the species' depth range. Data were not available to model the effects of body-size on the depth distribution of each species, but we expect further work to show that larger animals generally have a wider depth range.

Correcting Longline Catch Rates

There are two ways that our estimates of the depth distribution of catchability can be used to improve estimates of abundance. First, correction factors can be applied to operation-level data where gear dimensions and the number of hooks between floats are known for each operation. Such data exist for a large number of longline surveys conducted before commercial fishing commenced (e.g., Wathne 1959) and for more recent research cruises and monitoring programs. Ward and Myers (2005c) illustrate how the correction factors can adjust abundance indices derived from longline surveys in the 1950s and commercial operations in the 1990s.

The second application of our estimates is to correct abundance indices for changes in depth when only the proportion of gear configurations is known. Japan's longliners rapidly switched from regular longlining (< 120 m) to deep longlining (deepest hooks ranging beyond 120 m) in the Atlantic Ocean in the late 1970s (Figure 5.6a). The introduction of deep longlining had virtually no effect on the catchability of yellowfin tuna and swordfish (Figure 5.6b, 5.6c). Catchability declined for marlins and sailfish, but increased by 60% for bigeye tuna and by 40% for albacore tuna. While these changes warrant their inclusion in assessment models, they are less than those estimated by the early non-statistical habitat-based models, e.g., Hinton and Nakano (1996).

The application of our depth correction to annual catch rates of longliners in the southern Atlantic Ocean illustrates how variations in gear configurations can affect

estimates of abundance. We have previously advised caution in applying our estimates of catchability to regions outside the study area; this application to the southern Atlantic Ocean is only intended to illustrate how the estimates can be used. The introduction of deep longlines resulted in the overestimation of bigeye tuna abundance, but had a relatively small effect on abundance indices for other species (Figure 5.7). There are several reasons why deep longlining had an apparently small effect on estimates of blue marlin, sailfish, and albacore tuna abundance. First, the effect is small in absolute terms because of the significant decline in the abundance of those species well before the switch to deep longlining (Myers and Worm 2003). Second, adding more hooks between floats increases the longline's depth range, but many hooks remain at shallow and intermediate depths. Third, deep hooks take about 30 min to move through shallow and intermediate depths during longline deployment and retrieval. Consequently, catches are smeared over a range of depths (Boggs 1992). Again, we stress that a complete assessment of the magnitude of the effect of deep longlining on catchability would require more detailed analysis than that presented (Figure 5.7).

The effects of the increased depth range on catchability indicate that the 90% decline in the abundance of tunas and billfishes reported by Myers and Worm (2003) would be an underestimate. This is because most of the biomass is now concentrated in target species like swordfish, bigeye tuna, and yellowfin tuna that have declined less dramatically than other species. The catchability of target species has not changed or it has increased. Although the catchability of marlins and sailfish has declined, they now constitute only a small part of the pelagic fish community available to longline fishing gear.

In summary, we have demonstrated a method where abundance indices derived from longline catch rates can be corrected for historical variations in the depth range of the fishing gear. The method is relatively simple to apply and uses existing data that previously lacked the appropriate statistical framework for analysis. It can be applied to bycatch species that have not been the subject of tracking studies and it accommodates early data where only approximate gear characteristics are known and detailed oceanographic data are not available. Our method also eliminates the confounding in other statistical methods caused by the rapid switch to deep longline gear in the 1970s.

Thus, we reject the claim by Takeuchi (2001) that abundance indices cannot be corrected for historical changes in the depth of longline hooks.

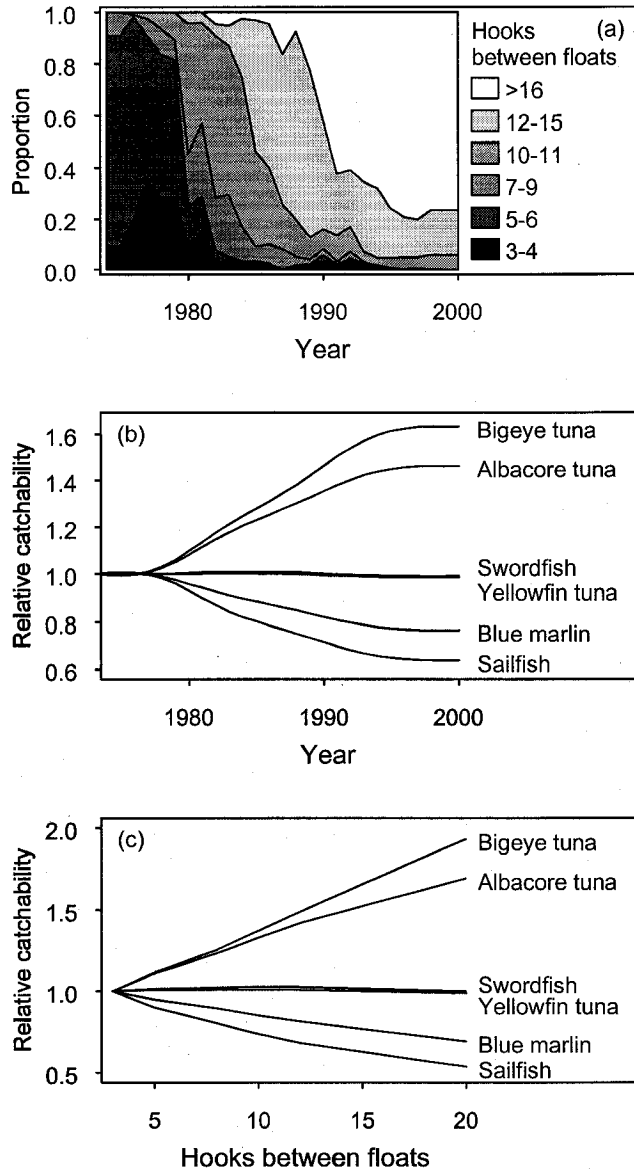


Figure 5.6. Historical variations in gear configurations and catchability. (a) The number of hooks between floats deployed by Japan's longline fleet in the tropical Atlantic Ocean (from Yokawa and Uozumi 2001). Hooks between floats is a rough indicator of longline depth range (for these operations, six hooks between floats produces a depth range of about 50–150 m compared to 50–300 m for a configuration with 14 hooks between floats). (b) The estimated change in average catchability over all gear configurations q_y used by the tropical Atlantic fleet relative to the 1975 gear configuration. (c) The change in the depth distribution of catchability q_g relative to the gear configuration with three hooks between floats for six species taken by the tropical Atlantic fleet.

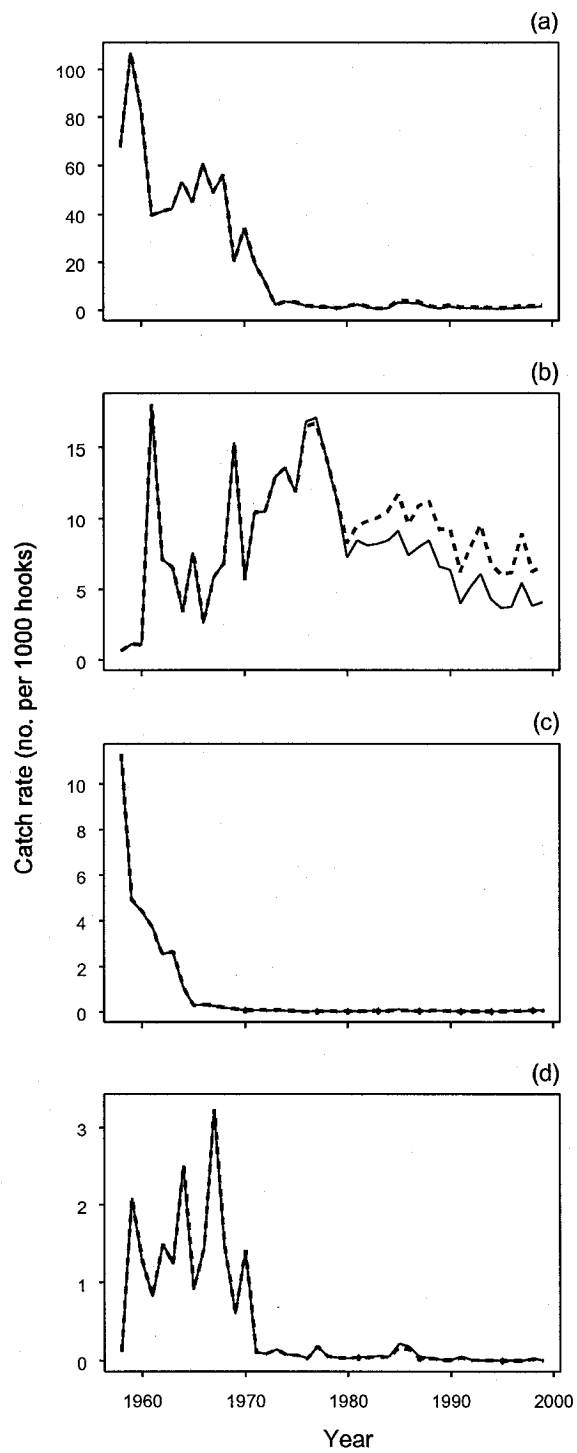


Figure 5.7. Abundance indices of four species in the southern Atlantic Ocean estimated by Myers and Worm (2003) with (solid line) and without (dashed line) the depth correction from Figure 5.6c. Species are as follows: (a) albacore tuna, (b) bigeye tuna, (c) blue marlin, and (d) sailfish.

Longliners have maintained catch rates of target species by improving the efficiency of their fishing gear (Stone and Dixon 2001), increasing soak time, ensuring that hooks are available at peak feeding periods (Ward et al. 2004), and by extending the geographical limits of fishing grounds (Myers and Worm 2003). In the 1970s, they also began to exploit a much greater depth range. Our analyses show that deep longlining has resulted in the underestimation of the abundance of several epipelagic species (e.g., sailfish). However, it has resulted in the overestimation of the abundance of several pelagic species, including target species like bigeye tuna. Those large predators not only support valuable fishing industries; they have unique ecological roles, influencing the diversity and abundance of lower trophic levels.

Acknowledgments

The work is part of a larger project on pelagic longlining that was initiated and sponsored by The Pew Charitable Trusts. We also thank the Pelagic Fisheries Research Program (PFRP), NSERC and the Future of Marine Animal Populations (FMAP) project of the Sloan Foundation Census of Marine Life for financial support. Tim Davis, Brent Miyamoto, Mike Musyl, Tom Swenarton, and Peter Williams provided data and information on the fisheries. Wade Blanchard and Darren Swan provided technical advice. Two reviewers provided comments on the manuscript.

Do Habitat Models Accurately Predict the Depth Distribution of Pelagic Fishes?⁸

Introduction

Longline catch rates of many pelagic fish species are sensitive to hook depth and environmental conditions. Adult bigeye tuna, for example, range down to 600 m or deeper in the western Pacific Ocean. In the mid 1970s, many pelagic longliners began to target bigeye tuna with gear that ranged to 250 m (Suzuki et al. 1977). Catch rates derived from shallower longlines used in earlier years will underestimate the true abundance of species like bigeye tuna because the gear did not cover the species' full depth range.

Variations in the depth range of the fishing gear and oceanographic conditions affect "catchability", the part of a population caught by a unit of fishing effort (Murphy 1960). A reliable estimate of catchability is required to accurately estimate abundance from catch rates. In addition to being affected by the gear's 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).

Habitat models are increasingly being used to correct abundance indices derived from longline catch rates, e.g., Bigelow et al. (2002). They adjust catchability by combining information on hook depth, ambient environmental conditions and the species' preferences for those conditions. Bigelow et al. (2002) applied a habitat model to 1966–96 catch and fishing effort data reported by Japan's longline fleet. They concluded that a large proportion of adult bigeye tuna was not available to longline gear in the

⁸ This chapter was originally published as: Ward, P., and Myers, R.A. 2006. Do habitat models accurately predict the depth distribution of pelagic fishes? *Fisheries Oceanography* 15: 60–66. The original article's abstract is incorporated in the Conclusions of this thesis and its reference list is included in the Bibliography.

tropical Pacific Ocean because they were beyond the gear's depth range. Their habitat-corrected catch rates suggested greater declines in bigeye tuna abundance than those indicated by nominal catch rates. However, we found no published study that tests the depth distributions predicted by habitat models. Here we test whether habitat model predictions match the depth distribution of bigeye tuna inferred from longline catches, and we compare the model's performance with that of alternative models.

Methods

Catch and Effort Data

Our analyses focused on bigeye tuna in the Pacific Ocean between 5–15°N and 180°E–120°W during 1994–2001. We derived the observed depth distribution of bigeye tuna from data reported by observers on Hawaii-based longliners that targeted the species by deploying deep longlines (27–600 m) at sunrise each day. Each longline consisted of about 2000 baited hooks suspended from a buoyed mainline. They were retrieved during the afternoon and evening of the same day. The observers reported a unique identifier for each longline hook. We used the gear dimensions and individual hook data reported by observers to estimate the depth at which each bigeye tuna was caught. The data consisted of 864 daily fishing operations where at least one bigeye tuna was caught.

Estimation of Hook Depth

We used longline dimensions reported by the observers to estimate the maximum settled depth d of each hook j on each longline by assuming that the mainlines formed a catenary curve (Suzuki et al. 1977):

$$d_j = b + f + \frac{m}{2} \left\{ (1 + \cotan^2 \varphi^o)^{1/2} - \left[\left(1 - 2 \frac{j}{n+1} \right)^2 + \cotan^2 \varphi^o \right]^{1/2} \right\} \quad (6.1)$$

where b is the length of the branchline, f is the length of the floatline, m is the length of mainline between floats and n is the number of hooks between the pair of floats holding hook j ; and φ is the angle of a horizontal line drawn between the tangent of the mainline and the connecting point of the floatline and mainline.

Suzuki et al. (1977) and many other researchers used a value of 72° for φ because they did not have data on the sagging rate k . The sagging rate is the ratio of the distance between floats and the length of mainline between floats. However, the observers

sometimes collected this information on Hawaii-based longliners. We used those data to calculate ϕ from the sagging rate k for each longline operation with a derivation of a formula presented by Yoshihara (1954). For 74% of operations the sagging rate could not be estimated or did not fall within reasonable bounds ($0.20 < k < 0.73$). For those operations we used a value of 72° for ϕ .

We assumed that the shape of the catenary curve formed by the mainline (and therefore the corresponding depth of hooks) did not systematically vary along each longline or during each operation. However, observed depths and predicted depths are known to vary, with the direction and velocity of ocean currents and wind having the most important influence on hook depth. Bigelow et al. (2002) estimated that hook numbers 3 and 10 of longline gear with 13 hooks between floats, shoaled by about 20% when subjected to a current velocity of 0.4 m s^{-1} . To represent shoaling of longlines in our study area, which is characterized by strong equatorial currents, we reduced all depths predicted by the catenary formula by 25%. The data were then binned into 40-m depth strata, ranging from 0–40 to 560–600 m.

Habitat Predictions

Mr. Keith Bigelow (NMFS Honolulu Laboratories) provided the depth distribution of bigeye tuna predicted by the habitat model of Bigelow et al. (2002). The model predicted the proportion of bigeye tuna in each 40-m depth – one-degree latitude-longitude square – year – month stratum. The proportions sum to one in each area–time stratum. Effective fishing effort $f_{a,t}$ is the weighted sum of longline hooks $H_{a,t}$ over all depths d in each area a and time t :

$$f_{a,t} = H_{a,t} \sum_d h_{a,t,d} p_{a,t,d} \quad (6.2)$$

where $h_{a,t,d}$ is the proportion of hooks in the stratum. The predicted proportion of bigeye tuna $p_{a,t,d}$ in the stratum is the product of scaled oxygen and temperature indices from Bigelow et al.'s model of the habitat preferences of bigeye tuna that were mapped to predicted temperature and oxygen levels to produce a depth distribution.

Bigelow et al. (2002) used data from physiological experiments and tracking studies to develop models of habitat preferences in relation to temperature and oxygen levels. For environmental conditions, they used a global circulation model (Behringer et al. 1998) to predict the temperature at each 40-m depth – degree – year – month stratum

in the study area. Levitus and Boyer (1994) estimated the mean dissolved oxygen concentrations during 1934–94 for each depth – degree – 3-month quarter in the study area. Bigelow et al. binned the oxygen and temperature data by depth – degree – quarter to match the resolution of the Japanese longline data that they analyzed. The longline data that we analyzed had a finer temporal stratum, so we used proportions that Mr. Bigelow provided for each depth – degree – year – month stratum.

The Hawaii-based longliners deployed their longlines at dawn then retrieved throughout the afternoon and evening. Estimates of the astronomical time of sunset for each operation showed that hooks were exposed to 73% daylight on average. Consequently, we used the same 0.75 weighting factor for day and 0.25 for night that Bigelow et al. (2002) used.

Assessing Model Performance

To assess the performance of the habitat model (and alternative models described in the next section), we embedded model predictions in a generalized linear model that related catch to local abundance and fishing effort with a log link. This “habitat-based model” predicted the mean catch $\mu_{d,i}$ in depth stratum d of operation i :

$$\log(\mu_{d,i}) = N_i + \log(p_{d,i} H_{d,i}) \quad (6.3)$$

where $H_{d,i}$ is the number of hooks deployed, $p_{d,i}$ is the habitat model prediction of the proportion of bigeye tuna in the stratum and N_i is the logarithm of local abundance of the species encountered by the operation. In our analysis, N_i is a nuisance parameter and was estimated for each longline operation in a fixed effect analysis. To check robustness we repeated the analysis using a generalized linear mixed effect model in which N_i was assumed to be a normal random variable; however, the conclusions were the same and the details are not presented here.

We assumed that bigeye tuna catches had a Poisson distribution:

$$C_{d,i} \sim P(\mu_{d,i}) \quad (6.4)$$

where $C_{d,i}$ is the expected catch of bigeye tuna and $\mu_{d,i}$ is the mean catch at depth d in operation i . We also investigated the performance of each model under a negative binomial distribution:

$$C_{d,i} \sim nb(\mu_{d,i}, \theta) \quad (6.5)$$

The negative binomial is similar to a Poisson distribution. It has the same mean, but it has an extra parameter θ to allow for over-dispersion. The dispersion parameter θ scales the estimate of binomial variance for the amount of variance in the data (Venables and Ripley 1999).

We implemented the models in the *glm* function of S-Plus (version 6.0 SE), which uses iteratively reweighted likelihoods to fit generalized linear models (Venables and Ripley 1999). For the negative binomial models we also used Venables and Ripley's *glm.nb* function of the MASS library (version 7.0) to estimate the dispersion parameter θ . To check that each model provided a reasonable fit to the data, we examined scatter plots of chi-square residuals against fitted values and residual plots. We used Akaike's information criterion (AIC) and residual deviance to compare model performance. The residual deviance measures the amount of variation in mean catch that is not explained by the model. AIC is based on the model's log-likelihood and number of parameters (Venables and Ripley 1999):

$$\text{AIC} = -2 \text{ maximized log - likelihood} + 2 \times \text{parameters} \quad (6.6)$$

Alternative Models

We compared the performance of the habitat-based model in predicting the depth distribution of bigeye tuna catches with that of four statistical models and a null model. The first statistical model, the basin-wide model, was exactly the same as eq. 6.3 except that $p_{d,i}$ was the proportion predicted for the stratum by Ward and Myers (2005a). They estimated the depth distribution of bigeye tuna from a generalized linear mixed effect model fitted to data from a longline survey and three longline fleets operating over a longer period in a wider area of the Pacific Ocean. Note that we used estimates from their model (Table 6.1) that specifically excluded data from the Hawaii-based fleet analyzed here. Ward and Myers modeled mean catch $\mu_{d,i}$ using a log link:

$$\log(\mu_{i,d}) = \lambda_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \beta_3 D_{d,i}^3 + \log(H_{d,i}) \quad (6.7)$$

where λ_i and β_j are parameters to be estimated and $D_{d,i}$ is the depth of depth stratum d of longline operation i . Ward and Myers assumed that the log abundance of the bigeye tuna λ_i , when it is encountered by the operation, followed a random effects distribution, which they nominated to be a normal distribution.

Table 6.1. Parameter estimates for the basin-wide model. The model was proposed by Ward and Myers (2005a). However, parameter estimates presented in this table and used in the present article specifically excluded data from the Hawaii-based fleet in the study to avoid problems in assessing the model with data that its parameters were partly derived from.

Parameter ^a	Estimate	SE
λ	-6.4762	0.0465
β_1	8.7736	0.4588
B_2	-15.3437	1.4038
β_3	10.3750	1.2978

^aeq. 6.7 provides the model's formula and explanations of symbols.

The basin-wide and habitat-based models used external information on depth. Three statistical models fitted *in situ* depth estimates from the study area. The cubic depth model predicted the mean catch from the local abundance, number of hooks and estimated depth $D_{d,i}$ of each stratum:

$$\log(\mu_{d,i}) = N_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \beta_3 D_{d,i}^3 + \log(H_{i,d}) \quad (6.8)$$

where the β_j are estimated parameters. The cubic depth model was the same as the basin-wide model, but its parameters were estimated from longline data from the study area (basin-wide estimates were derived from several longline data sets outside the study area). The other two statistical models were the same as eq. 6.8, but had different functional forms of the depth coefficients (Table 6.2). The sixth model, the null model, did not have any depth coefficient. It represented the hypothesis that depth did not influence catch rates.

Table 6.2. Formulae and statistics for generalized linear models. Separate statistics are shown for models that fitted a Poisson error distribution and those that fitted a negative binomial error distribution. All models fitted the same dataset regardless of error distribution or formulation.

Model name	Formula ^a	Residual		Poisson		Negative binomial	
		df ^b	rd ^c	rd ^c	AIC ^d	rd ^c	AIC ^d
No depth information							
Null	$\log(\mu_{d,i}) = N_i + \log(H_{d,i})$	4 696	5 942	7 670		3 344	5 072
External depth information							
Habitat-based	$\log(\mu_{d,i}) = N_i + \log(p_{d,i}H_{d,i})$	4 696	12 154	13 882		5 377	7 105
Basin-wide	$\log(\mu_{d,i}) = N_i + \log(p_{d,i}H_{d,i})$	4 696	5 223	6 951		3 011	4 739
In situ depth information							
Factor depth	$\log(\mu_{d,i}) = N_i + \beta_d D_{d,i} + \log(H_{d,i})$	4 682	5 153	6 909		2 965	4 721
Quadratic depth	$\log(\mu_{d,i}) = N_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \log(H_{d,i})$	4 694	5 196	6 928		2 986	4 718
Cubic depth	$\log(\mu_{d,i}) = N_i + \beta_1 D_{d,i} + \beta_2 D_{d,i}^2 + \beta_3 D_{d,i}^3 + \log(H_{d,i})$	4 693	5 175	6 909		2 977	4 711

^aSymbols and subscripts:

d	depth stratum	H	number of hooks
i	longline operation	D	depth (m)
log	natural logarithm	β	estimated parameter
μ	mean catch	p	proportion of catch predicted for the stratum by Bigelow et al. (2002) for the habitat-based model or by Ward and Myers (2005) for the basin-wide model
N	log of local abundance		
^b Degrees of freedom.			

^cResidual deviance, a measure of the amount of variation in mean catch that is not explained by the model.

^dAkaike's information criterion, used for model selection (smaller is better).

Results

The observed depth distributions of bigeye tuna showed substantial variation among operations. The depth coefficients of the quadratic and cubic depth models were all statistically significant ($P < 0.001$), thus supporting the hypothesis that depth does influence catches. The residual deviance shows that the statistical models with *in situ* depth information produced close fits to the observed distributions (Figure 6.1). The basin-wide model also produced a good fit to the distribution observed in the study area. The habitat-based model produced the poorest fit of all models. It overestimated the observed distribution at shallow depths, but underestimated it at intermediate depths (Figure 6.1).

The AIC and residual deviance of negative binomial models gave the same ranking of model performance as that indicated by Poisson models (Table 6.2). Fixing the dispersion parameter θ at the same value for the negative binomial models did not change the ranking of negative binomial models as judged by the residual deviance and AIC. The Poisson models were preferred because estimates of θ ranged up to 680 for some negative binomial models, so that the Poisson model was recovered. Consequently our discussion of results concentrates on the Poisson models.

Discussion

The fit of statistical models to data that their parameters were derived from will usually be superior to the fit of deterministic models like the habitat model. However, care is necessary when using statistical models to predict outside their data range. Variations in oceanographic conditions and changes in fishing practices will affect catchability, which was the original motivation for using habitat models. In this case, however, the habitat model failed to provide useful predictions; it was worse than the null model, which assumed no change in catch with depth.

The basin-wide model used data from other fisheries and for Hawaii-based longliners operating outside the study area. Its estimates of depth distribution were better than those of the habitat-based model, suggesting that this statistical model may provide reliable predictions of bigeye tuna distribution outside the model's data range. The very

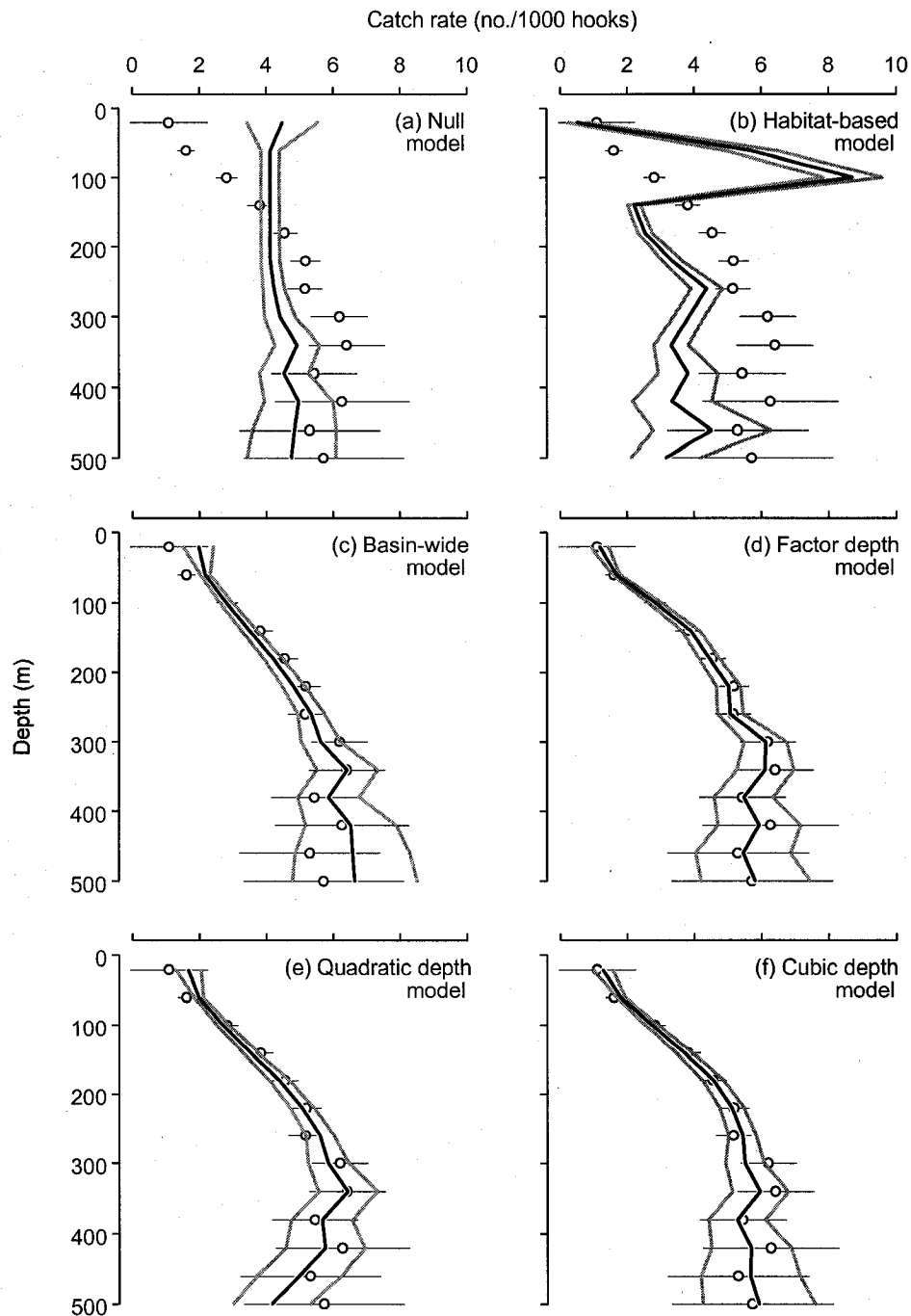


Figure 6.1. Comparison of observed catch rates of bigeye tuna (circles are means, horizontal bars are 95% confidence intervals) and fitted values for each Poisson model (heavy lines connect means, light lines connect 95% confidence intervals). Fitted values for the null model (which assumes that catchability does not change with depth) are not constant because of random variations in the nominated local abundance.

good fit of the basin-wide model (Figure 6.1c) suggests that the depth dependent catchability may be similar on average over a wide region.

There are four possible explanations of the poor fit of the habitat-based model. First, there is uncertainty in calibrating the model with hook depths. Habitat models use habitat preferences and environmental data that have accurate depth estimates. However, they must be matched to hook depths, which are known to vary with ocean currents and wind (Bigelow et al. 2002). Bigelow et al. used a method to adjust for the effects of currents on longline depth that was more sophisticated than our method. However, quite extreme—and unreasonable—estimates of depth would be required to force the observed depth distribution to match that of the habitat-based model.

Second, the environmental conditions used in habitat models were estimated on a scale that might not be relevant to bigeye tuna. Temperatures were predicted from a circulation model for each stratum. Oxygen concentrations were monthly averages for each 40-m depth – latitude-longitude – month stratum for all years combined during 1934–94. However, the temperatures and oxygen concentrations that bigeye tuna respond to would have varied significantly over much smaller spatial and temporal scales (Philander 1990).

Third, information on habitat preferences derived from tracking studies might not be representative of the bigeye tuna taken by longline in our study area. Temperature preferences were derived from four bigeye tuna released off French Polynesia and tracked for a total of 53 h (Dagorn et al. 2000) and 11 bigeye tuna near Hawaii at liberty for a total of 934 d (Musyl et al. 2003). Thirteen of those 15 bigeye tuna were smaller than the mean size taken by longliners in our study area (46 kg) and 9 were below the fifth percentile (11 kg). Dagorn et al. (2000) found that the vertical movement patterns of small bigeye tuna were distinct from those of large individuals. Furthermore, the tags themselves might affect the animal's behaviour.

Note that Bigelow et al. considered ten depth distributions that they generated from different hypotheses about the depth distribution of bigeye tuna in relation to temperature levels and oxygen concentrations. Our analyses use only one of those distributions, which was the distribution preferred by Bigelow et al. and used in the 2003 stock assessment of bigeye tuna in the Pacific Ocean. Subsequent assessments have used statistical habitat

models that include more information on depth distributions in relation to environmental determinants.

The fourth possible explanation of the habitat model's poor fit is that the distribution predicted by habitat models might not match the species' vulnerability to longline gear. Using simulations, Goodyear (2003) found that the propensity of blue marlin (*Makaira nigricans*) to take longline baits and the actual depths reached by the hooks biased abundance estimates derived from habitat models. Blue marlin and other species like bigeye tuna may be present at shallow depths during the day, but not caught there because they are not feeding. Statistical habitat models, which combine observed and predicted catch distributions (e.g., Hinton and Maunder 2003), might help to overcome this problem. However, considerable research is required to address the other problems that we have identified.

The status of the world's pelagic fishes is of considerable concern and controversy. The adjusted abundance indices produced by the habitat model indicate substantial reductions in the population size of bigeye tuna. However, our analyses show significant discrepancies between observed distributions and the model's predictions. The status of bigeye tuna may be quite different to that indicated by habitat models if our conclusions are valid for the wider Pacific Ocean over the period of exploitation.

Acknowledgements

The Pelagic Fisheries Research Program, Pew Charitable Trusts, NSERC and the Future of Marine Animal Populations project of the Sloan Census of Marine Life supported this work. Keith Bigelow, Wade Blanchard, Brent Miyamoto, Tom Swenarton and Chris Taggart provided advice and access to data.

Preliminary Estimates of Changes in the Catchability of Pelagic Longline Fishing Gear

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). Catch and sampling effort are often the only information 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. Information on variations in catchability can also be used to mitigate catches of non-target or “bycatch” species (Kitchell et al. 2004)

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 are able to increase catchability or fishing power to maintain their catch rates, but those catch rates do not reflect the depleted state of the stocks (Hilborn and Walters 1992). Discrepancies between model predictions and observed catches are often attributed to variations in catchability, such as changes in targeting in multi-species fisheries or environmental fluctuations (Fournier et al. 1999). 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 several species in most regions 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)—from surveys or commercial fishing 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 pelagic longline gear and practices on catch rates. I review approaches to estimating catchability then present a comparative method for estimating variations in the catchability of this gear.

Catchability Defined

Catchability 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 catching efficiency or the sampling method's efficiency—the percentage of the animals actually present that are recorded (Southwood 1966). Baranov (1918) proposed the catch equation that uses the catchability coefficient⁹ q_i to link catch c_i , fishing effort f_i for fishing operation i , and the local density of vulnerable animals n_i at time t :

$$\frac{c_i}{f_i} = q_i n_i \quad (7.1)$$

Where q is constant, eq. 7.1 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 and not multiplied by the stock's area to produce an estimate of absolute abundance. The use of abundance indices implicitly assume that the stock's area is constant because catchability is inversely proportional to the stock's area (Paloheimo and Dickie 1964).

Whereas catchability is the interaction of the fishing gear and animal's behaviour, fishing power or “fishing efficiency” 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 available baits 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

⁹ I use the terms catchability and catchability coefficient interchangeably.

catchability is blurred. Soak time, for example, may affect fishing power through bait loss and also affect catchability through its effects on the availability of hooks at peak feeding times. 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 farms 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 populations.

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 novel sampling approaches. Richards and Schnute (1986), for example, used an underwater submersible to visually count reef fish. They then compared these estimates with angling catch rates. The usefulness of catch rate – abundance comparisons depends on the accuracy of those abundance estimates. The approach has been enhanced by using meta-analysis to utilize information from multiple data sets. 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.

Generalized linear models and generalized additive models are often used to derive abundance indices from catch rates that are adjusted for the effects of covariates, 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 method results in a wide range of possible values for catchability.

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 the catch and natural mortality are assumed to be known without error (Harley et al. 2001) and because of confounding among variables—standardized catch rates are usually a key index of abundance 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.

Vast distances, combined with the patchy distribution of animals and difficulties in establishing controlled experiments present particular problems to 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. Catch rate – based abundance indices have been derived from longline (e.g., 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 fishing gear (Holdsworth et al. 2003). Independent estimates of abundance are more difficult to obtain. Some have been derived from acoustic and aerial surveys (e.g., Hobday 2005), and mark-recapture experiments (Kleiber et al. 1987).

My Approach

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 density and distribution of animals 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 7.1). A seventh event—landing—is rarely considered, but it is important in longline fisheries where animals sometimes escape, drop off, or are removed from the hook by scavengers before it is retrieved (Ward et al. 2004). I do not consider an

Figure 7.1. Flow chart of events that determine the fate of animals encountering a pelagic longline. Variables are classified according to whether they are determined by the animal's availability or by vulnerability to the fishing gear. Some variables may affect more than one step, e.g., bait type may influence detection as well as attraction. Reference numbers in parentheses link variables to the estimates of catchability presented in Table 7.2.

OUTCOME	EVENT	FACTORS AFFECTING PROBABILITY OF EVENT	
		Animal availability	Gear vulnerability
animal escapes alive	A. Animal is within longline's area of action	<ul style="list-style-type: none"> • density and distribution • movement patterns (A1) 	<ul style="list-style-type: none"> • depth (A2) • fish-finding equipment (A3) • skipper experience (A4) • operation time (A5)
	B. Baited hook is available		<ul style="list-style-type: none"> • bait loss (B1) • gear saturation (B2)
	C. Animal detects baited hook	<ul style="list-style-type: none"> • sensory perception • feeding history and memory 	<ul style="list-style-type: none"> • bait type (C1) • animals associated with bait
	D. Animal attacks baited hook	<ul style="list-style-type: none"> • hunger (D1) • feeding history and memory • interference competition 	<ul style="list-style-type: none"> • gear competition (D2) • detection of fishing gear (D3) • availability of competing foods
	E. Animal is hooked	<ul style="list-style-type: none"> • gape 	<ul style="list-style-type: none"> • shape and sharpness of hook • size of bait and hook • pressure on line
	F. Animal is landed	<ul style="list-style-type: none"> • breakage (F1) • animal's strength 	<ul style="list-style-type: none"> • drop off • removal by scavengers (F2) • strength of gear • skill of crew
animal perishes	G. Animal is retained	<ul style="list-style-type: none"> • animal's size and quality 	<ul style="list-style-type: none"> • market prices • vessel's catch history • safety • convenience
	animal perishes		

additional event—retention and reporting practices—that may affect the reporting of catches by commercial fishers.

I separately estimated the effects of 13 variables on catchability. Estimating catchability in commercial fisheries is very difficult because it is confounded with variations in abundance; and 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 catchability change utilizes ratios of catch rates in situations where there is evidence of fishing power and abundance being constant. For example, there is evidence that branchline material affects 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_i derived from monofilament branchlines are linked to the species' local abundance n_i at and catchability q_i through the catch equation (7.1):

$$u_1 = \alpha_1 q_i n_i$$

$$\text{and } n_i = \frac{u_1}{\alpha_1 q_i}$$

where i is local time-area of interest and α_1 is the effect of monofilament on catchability. For multifilament branchlines, α_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:

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

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

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

For controlled experiments where abundance and fishing power are constant, relative catchability can be inferred from one catch rate divided by another. In my

example, Stone and Dixon deployed an equal number of monofilament and multifilament branchlines, catching 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.

I then use the proportion of gear types in each period of interest to estimate historical changes in catchability. In my example, 25% of the branchlines used in a fishery were monofilament in 1980 rising to 75% monofilament in 1990, with the remainder multifilament. The change in catchability Δq between periods is:

$$\Delta q = \frac{(2.03 \times 0.75) + (1.00 \times 0.25)}{(2.03 \times 0.25) + (1.00 \times 0.75)} = 1.41$$

A value of 1.00 is included to standardize each estimate for multifilament catchability. I conclude that the introduction of monofilament resulted in swordfish catchability in 1990 being 1.41 times the 1980 catchability.

Several variables directly affect fishing power instead of catch, but the approach to estimating relative catchability is the same. 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). Consequently, fishing effort must be discounted by about 0.04 for the number of hooks actually available. This is the same as reducing the probability of catching an animal by 0.04 or reducing catchability by 0.04. I use a similar approach to estimating changes in catchability due to variables like loss rates that directly affect catch. I did not attempt to combine all 13 estimates into a single index of catchability change for each species because their effects on catchability are unlikely to be additive, and more complex than multiplicative.

Appendix 2 details data sources and the methods that I used to estimate relative catchability and fishing power. To illustrate the method, estimates of relative catchability are compared 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 all 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 species (except skipjack tuna, *Katsuwonus pelamis*) and several other

major pelagic species, such as blue marlin and blue shark (*Prionace glauca*). Catchability is estimated for five frequently caught species that represent a wide range of life-histories (Table 7.1). Following is a brief summary of historical trends in each variable and the reliability of my estimates. I then consider other important variables that were not estimated.

Table 7.1. Species for which I estimated changes in longline catchability. Body-size ranges are from the 1950s POFI survey and 1990s Hawaii longline data. 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 et al. (2002).

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

^aFor brevity, I refer to shortfin mako shark as mako shark throughout this chapter.

Estimates

Area of Action and Abundance

Animal's Movement Patterns (A.1)

Large animals swim faster, forage through a larger volume of water, and are more successful at competing for bait than smaller animals (Ware 1978; Hart 1986; Videler 1993). Longlining has selectively removed large predators from the pelagic fish community of my study area, while the mean body-size of several smaller species did not change or increased (Ward and Myers 2005c). The reduction in body-size of large predators will result in fewer encounters with longline baits and reduced catchability.

Table 7.2. Estimates of historical changes in catchability for 13 variables for Japan's distant-water longliners. Estimates are the ratio of relative catchability in the 1990s to that in the 1950s in the tropical Pacific Ocean. 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 one ($\alpha = 0.05$) are in bold. Also shown are estimates of change in fishing power that I extrapolated from a model of bait loss and a synthetic dataset of historical changes in longline gear (Ward and Myers submitted).

Variable		Reliability ranking ^a	Estimated change in catchability ^b				
			mako shark	blue marlin	bigeye tuna	yellowfin tuna	skipjack tuna
A. Area of action and abundance							
1.	Movement patterns	6	>0.59	>0.49	>0.64	>0.58	>0.83
2.	Depth of gear	3	0.83	0.84	1.39	1.01	0.89
3.	Fish-finding equipment	12	>1.01	>1.01	>1.01	>1.01	>1.01
4.	Skipper experience	9	>0.31	>1.52	>2.55	>2.11	>1.44
5.	Operation time	2	1.10	1.86	1.06	0.94	0.96
B. Availability of baited hooks							
1.	Bait loss	5	<4.92	<4.92	<4.92	<4.92	<4.92
2.	Gear saturation	1	>1.03	>1.02	>1.01	>1.01	>1.02
C. Detection							
1.	Detection of gear	4	>1.26	>1.70	>1.73	<7.65	–
D. Attraction to baits							
1.	Hunger	8	>0.54	>0.42	>0.60	>0.55	>0.80
2.	Gear competition	7	–	>0.98	>0.95	>0.95	–
3.	Bait type	10	0.94	4.66	1.94	0.48	0.65
F. Landing							
1.	Breakage	13	<7.56	>1.00	>1.00	>1.00	>1.00
2.	Removal by scavengers	11	1.05	1.16	1.09	1.09	0.97

^aOn the basis of the reliability of parameter estimates and plausibility of assumptions, I ranked estimates from 1 (most reliable) to 13 (least reliable).

^bGreater-than (“>”) and less-than (“<”) signs show the likely direction of bias in estimates.

I estimated that catchability declined for all five species as a result of reductions in the volume of water searched for food, which was a function of reduced body-size. The largest predators, such as blue marlin, showed the greatest reductions in catchability (Table 7.2). The body-size and catchability of the smallest species, skipjack tuna, also

declined. However, elevated catchability may be expected for several small species that increased in size, e.g., long-nosed lancetfish (*Alepisaurus ferox*).

My estimates of search volume were more sensitive to variations in body-size than they were to the value of Ware's constant, which was used to derive search volume from body-size. For example, a 10% variation in the constant resulted in catchability change varying from 0.47 to 0.51 for blue marlin. Reductions in body-size may contribute to reduced catchability in other ways. 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 (Ware 1978; Blaxter 1980). On the other hand, the importance of body-size and search volume will diminish when food is in over-supply. The reduction in catchability due to reduced body-size 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 (A.2)

Catchability will increase as the match between the population's distribution and the gear's distribution improves (Boggs 1992; Hanamoto 1987). Tracking studies demonstrate that bigeye tuna range down to 500 m or deeper in the relatively warm, well-oxygenated waters of equatorial Pacific Ocean (Musyl et al. 2003). A proportion of the population 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.

My analyses indicated that extending the depth range of longlines increased the catchability of mesopelagic species like bigeye tuna (Table 7.2). At the same time, proportionally fewer hooks are available at shallow depths, resulting in decreased catchability for epipelagic species, including skipjack tuna, mako shark, 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).

Fish-finding Equipment (A.3)

The ability of fishers to locate target species has improved with cooperative searching (Ruttan 2003) and the installation of electronic navigation and fish-finding equipment (Kleiber and Perrin 1991). Campbell (2004) observed that Japan's longliners rarely operated in areas where catch rates of southern bluefin tuna (*Thunnus maccoyii*) were low. 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. 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. Sonar, which are used to detect plankton layers, baitfish, and target species, tripled the fishing power of Japan's purse seiners in the 1950s (Inoue 1961).

By the 1980s, Japan's longliners had installed various 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, submitted).

Descriptions of 1950s longlining did 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.

I estimated the effects of electronic fish-finding equipment on catchability by calculating the proportional increase in catch rates required to cover the annual cost of electronic equipment. A 0.01 increase in catchability was required to offset the annual cost of the equipment. There are several reasons why this estimate is likely to be conservative. First, estimation depends on the outlay that owners need to recoup each year. Based on advice from Australian longline fishers, I fixed the equipment's life span

at seven years. Catchability must increase by 0.07 to cover the outlay if the life span is set to one year. Second, my estimate is also sensitive to the price differential between catches and equipment costs. The price of tuna remained fairly stable after 1970, whereas the cost of electronic equipment declined substantially (Campbell and McIlgorm 1997; FFA 1998). Catchability must increase by 0.02 to cover equipment costs if estimates are based on pre-1980 equipment costs. Third, an owner would not purchase and install a device unless they were convinced that it would contribute to profit, let alone cover the outlay. Many of the devices are likely to have increased profits 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 USD733 outlay. Catches of blue-spotted mackerel (*Scomberomorus niphonius*) have been shown to increase by 10–30% when fishing operations were guided by sea surface temperature imagery (Faji et al. 1990).

Skipper Experience (A.4)

Several studies have shown that skipper experience 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 where and when target species will be abundant. They synthesize their past experience, knowledge of historical patterns, understanding of relationships between environmental conditions and the availability of target species, and catches by other vessels. Skipper skill also involves adjusting fishing gear and techniques to suit local conditions.

My analyses show that differences in fishing master experience resulted in substantial improvements in catchability for most species between the 1950s and 1990s. However, increased experience resulted in decreased catchability of mako shark. This might be evidence of fishing masters learning to avoid low-value species like mako shark, which are also responsible for damaging animals 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.

My estimate of the average years of experience (two years) of 1950s fishing masters was highly uncertain. I do know that Japan's longliners had not operated in the

study area before the 1950s. On the other hand, commercial longliners operated in south-eastern Asia and the north-western Pacific Ocean in the 1920s and 1930s and around Japan since the early 1900s (Nakamura 1950). I restricted my 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 likely to be a crude measure of skipper skill. Kirkley et al. (1998) found that several variables, including skipper education levels, provided significant improvements in 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 (A.5)

Diminished light levels affect the ability of prey and predators to detect one another (Boden and Kampa 1967; Hart 1986). Fish that forage during crepuscular periods are usually large-mouthed, generalist predators (Helfman 1978). Dietary studies show that tunas, billfishes, and sharks are generalist predators that are particularly active during crepuscular periods (Galkov 1984). Analyses of tracking data suggest that their catchability increases when baited hooks are available during peak feeding times (Bertrand et al. 2002).

The number of hooks deployed each day by Japan's longliners has steadily increased over time (Polacheck 1991), resulting in proportionally more baits being available at dusk and in the early evening (Ward et al. 2004). I found that this change in timing resulted in decreased catchability of visual predators, such as yellowfin and skipjack tuna, which are most active during the day. While I expect elevated catch rates during periods of peak feeding activity, it is possible that the increased availability of natural prey at those times might reduce longline catchability. Bertrand et al. (2002) observed high catchability of albacore and bigeye tuna in areas where those species' prey were rare.

Availability of Baited Hooks

Bait Loss (B.1)

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

Bait loss increased at shallow depths, perhaps through elevated turbulence or increased scavenger activity in surface waters (Chapter 3). All else being equal, 1950s longlines are predicted to have higher bait loss rates than the deeper longlines used in the 1990s. Loss rates also increased with tuna abundance, soft-bodied bait; e.g., sardine, *Sardinia melanosticta*), and with soak time.

Gear Saturation (B.2)

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 is more likely 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).

My estimates indicate that gear saturation resulted in a relatively small increase in catchability between periods. I may have underestimated the increase in catchability because I did not take into account localized clumping and did not include hooks that were occupied by animals that were lost from the longline before retrieval. 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 end of deployment and commencement of hauling (Shapiro 1950). This would reduce gear saturation in the 1950s, slightly increasing fishing power and catchability.

Detection

Detection of Gear (C.1)

Animals may avoid baits that present 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 cord (nylon or kuralon). They were transparent or dyed certain colours, which would reduce their visibility to target species (Wardle et al. 1991). By contrast, 1950s branchlines were tar-coated rope (cotton, hemp or Manila) or cotton thread wound around wire cable, attached to a wire leader (Shimada 1951b).

I used the results of the experiment reported by Stone and Dixon (2001) to estimate the effect of changes in branchline material on catchability. However, those results may not be strictly applicable to Japanese operations in the study area because the experiment involved shallow longlines deployed at nighttime in temperate Atlantic waters. Furthermore, it may be incorrect to use their white marlin estimate for blue marlin and their swordfish estimate for bigeye tuna. Although their estimate for yellowfin tuna (9.00) was reported as statistically significant, I consider it to be an aberration related to the small number caught.

Nevertheless, I believe that Stone and Dixon's results significantly underestimate the improvements to catch rates provided by nylon branchlines. The 1950s longliners used tar-coated, rope branchlines, whereas the experiment used nylon branchlines. 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 1951b) and on 31% of branchlines in the 1990s (Australian observer data). The branchlines were also thicker (5–7 mm; Shimada 1951) than those used in the 1990s (2–4 mm; Australian observer data). The branchlines and leaders used by Stone and Dixon would be more visible to animals than the 1950s gear. This would decrease the catchability of many species, particularly large predators like blue marlin that use vision for daytime foraging (Fritsches et al. 2000).

Attraction to Baits

Hunger (D.1)

Hunger—the need to supply energy to support activities—drives animals to feed and to attack baits (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 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-size between periods. An average-size blue marlin in the 1950s would require 1.3 kg of food per day for routine metabolism (Appendix 2). 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 body-size. These effects on the catchability were largely offset by the high daily ration of skipjack tuna ($0.0551 \text{ kg} \cdot \text{day}^{-1} \cdot \text{mass}^{-1}$ compared to 0.0125 for blue marlin).

If the removal of large pelagic predators (Ward and Myers 2005c) has resulted in increased availability of food, then the remaining animals might be less attracted to longline baits. 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 compared to tunas from the same areas after several years of exploitation. Competition for food would be more intense before exploitation, and I hypothesize that more food is available per capita after populations are reduced, resulting in “fatter, more content animals”.

Competition among Gears (D.2)

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 baits. However, the catchability of each bait must eventually decline as the distance between branchlines decreases (Skud 1978a). Shomura and Murphy (1955) report catch rates of survey longlines that had alternating segments of high and low hook densities, with all segments 366 m in length. My analysis of 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.

I estimated a mean distance between adjacent hooks of 45.4 m (SD ± 4.5 m) from the longline dimensions of 25 longliners in the study area in 1950 (Shimada 1951b). 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. However, the lengthening of longlines to access deeper waters also affects the distance between baits. 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 reduced distance between hooks so that hook density did not change between periods. Nevertheless, the effects of variations in hook density will 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 that forage during ascents or descents, e.g., bigeye tuna (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 1200 in the 1950s to 3121 hooks per operation in the 1990s. 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 (Appendix 2), which does not support the hypothesis that hooks of the same longline compete for animals. Polacheck (1991) also found no significant affect 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 km² 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 the total number of longline hooks 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. My generalized linear models show that bigeye tuna catches rise linearly with the total number of hooks to an asymptote (Appendix 2). Catch then declines at higher levels of fishing effort, perhaps as a result of competition among longlines (Figure 7.2). I contend that the difference between the linear and cubic models represents 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; at the mean 1990s level, competition resulted in much smaller variations in catchability. At these intermediate levels of fishing effort the linear model often predicts lower catches than the cubic model. This is probably an artefact of model structure because residual plots indicate that the cubic model overestimates catches at intermediate levels in attempting to fit catch declines at high effort levels.

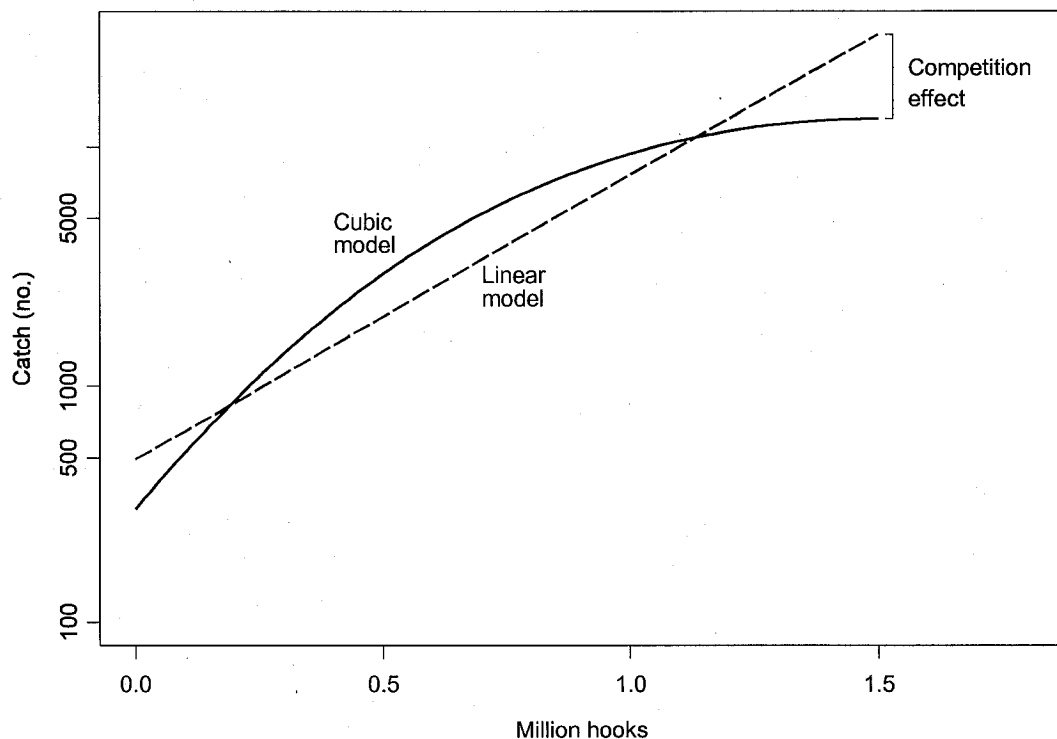


Figure 7.2. Effect of gear competition on catch rates. Using the global five-degree data, I inferred catchability change as the difference between catch predictions of a generalized linear model that included quadratic and cubic terms for fishing effort (the cubic model) and one that did not include those terms (the linear model).

My estimates are likely to be confounded by negative correlations between fishing effort and population 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.

Bait Type (D.3)

Baits attract animals by mimicking the visual (e.g., size and shape), chemical odours that leach from baits, and tactile cues (e.g., vibrations and movements) of natural prey (Blaxter 1980; Atema 1980). Fishers select bait on the basis of the expected financial return of catches balanced against bait costs, availability, storage and handling considerations, and how long the bait will remain on the hook.

My generalized linear models of Australian observer data show that variations in bait type resulted in substantial increases in the catchability of bigeye tuna and blue marlin between periods while yellowfin and skipjack tuna catchability declined. There were no reports of saury baits in the observer data that I modeled. I predicted 1950s catches for pilchard baits because several reports show that saury and pilchard baits produce similar catch rates of 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 confounded with bait loss. Shomura (1955) concluded that sardine and herring produced higher catch rates of tunas than those produced by squid (*Loligo opalescens*) because of high loss rates of squid over time, especially in rough seas.

Landing

Breakage (F.1)

Longline fishers and observers report that sharks often sever monofilament branchlines after they have been hooked. Although the fate of lost animals is unknown, I consider it here because it will affect catchability. Wire leaders are used to reduce gear loss from abrasion of the leader by the rostrums of billfishes or the teeth of many species, including tunas and sharks.

By assuming that mako shark losses were proportional to the number of severed branchlines that are retrieved, I estimated a large increase in mako shark catchability between the 1950s and 1990s. Large variations in branchline loss rates are necessary to significantly affect my estimates, e.g., for 1950s catch and effort data, a 1% loss rate results in a 0.83 catchability change compared to 0.88 for a 5% loss rate. More reliable estimates of branchline loss rates could easily be obtained by counting the number of missing branchlines at the completion of longline retrieval. Loss rates will be overestimated if the same mako shark is responsible for more than one branchline loss, but this will not affect the estimate of catchability change unless the number of branchlines removed by each mako shark varied between periods. I assumed that the switch to monofilament in the 1990s did not affect the loss rates of tunas and blue marlin.

Removal by Scavengers (F.2)

Animals hooked on a longline are sometimes damaged or removed by large scavengers, such as sharks and, in some areas, 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) reports 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 historical reduction in damage rates may be due to the removal of large sharks by longlining (Ward and Myers 2005c).

I used the ratio of damage rates in each period as an index of catchability change. This assumes that damage rates are directly proportional to removals of hooked animals—a hypothesis that has not been tested. Shark damage rates decreased between the 1950s and 1990s for all species except skipjack tuna. The situation with skipjack tuna is unclear because many may be completely removed from longlines by large scavengers (Ward et al. 2004).

Shark catch rates tend to be lowest on shallow hooks (Ward and Myers 2005a). If damage rates also decline with depth, I may have overestimated damage rates for 1990s operations that used deeper longlines (61–231 m) compared to the 1950s (66–111 m). The trend to deeper longlines would result in an underestimation of catchability change. I expect that the deeper longlines now deployed by several fleets will have even lower damage rates, e.g., the Hawaii fleet deploys longlines that range down to 500 m to catch tunas (Boggs 1992).

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 (Ward et al. 2004) would further contribute to the underestimation of historical increases in catchability.

Other Variables

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, affect the abundance of pelagic species through recruitment, variations in productivity, and the efficiency of longline gear (Chapter 8). However, I did not consider their effects on catchability because conditions 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 their effects should be included in effort standardization. Regardless, care is required in considering environmental effects because they may affect abundance rather than catchability, whereas abundance is the signal of interest to analyses related to stock assessment (Kleiber and Yokawa 2002).

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 baits or struggling on hooks (Fishelson 1980; Skud 1978b) or by fluorescent lightsticks (Flanagan 1996).

The presence of predators is another form of interference competition; an animal that is actively involved in avoiding predators is less likely to attack baits. Werner et al. (1983) found that relative 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 body-size 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.

Bait size may be more important. 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).

The 1950s longliners deployed straight-shanked “J” hooks, whereas the tuna hooks used in the 1990s have many similarities to “circle hooks”. 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.

Strength of Gear

Animals may fall off the hook as a result of violent movements of the longline during retrieval, during storms, or when struggling to be free. Improvements in skill levels among crewmembers and the introduction of more flexible gear have probably reduced the frequency of such losses. The nylon branchlines used in the 1990s were more elastic than the rope and wire used in the 1950s, resulting in reduced losses from snapped branchlines, bent hooks, or from hooks being torn free of the animal. Australian observers report the use of small (~300 mm diameter) plastic buoys in the 1990s that allow more vertical movement than the large glass or steel buoys deployed in the 1950s (Shimada 1951a). Japan’s longliners used tin-plated iron hooks in the 1950s (Shapiro 1950) that are more likely to break than the stainless-steel or hi-carbon steel hooks used since the 1980s. Furthermore, the selective removal of large animals would also contribute to reduced losses through line breakage.

Discussion

My analyses show significant increases in the catchability of the five selected species, especially target species, through improvements in technology and skipper experience. Furthermore, the effects of several variables were likely to have been underestimated and those that I did not estimate are likely to have increased catchability. In particular, communication and cooperative searching will strongly influence catchability.

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. Less 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). A declining trend in catch rates is cause for concern in commercial fisheries. A static or increasing pattern does not necessarily indicate a healthy stock because effort standardization might not have fully adjusted for increased catchability or fishing power.

My analyses are mostly preliminary, and I expect further work to provide more reliable estimates of catchability. In particular, evidence is emerging that catchability may vary significantly among fleets and with area and season. Variables that have a strong effect on catchability include skipper experience, bait type, and bait loss. 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. Additionally, historical changes and new developments in longline fishing gear and practices need to be documented and quantified. Observers need to collect hook-level data that can be linked to size measurements of each animal. Selection of variables was determined by the availability of comparable catch and effort data between periods and also evidence of historical variations. I did not estimate the effects of other variables (e.g., hook size and offset) that might have quite different effects on catchability or fishing power.

There is also a need to estimate variations in catchability on finer temporal scales since it is unlikely that catchability changed linearly between the 1950s and 1990s, e.g., the introduction of electronic fish-finding equipment would result in sudden, stepwise jumps in catchability. Furthermore, catchability is likely to be affected by density dependent processes, such as the aggregation of target species and behaviour of fishers (Wang 1990). Several authors include a shape parameter β in the catch equation to represent hyperstability ($\beta > 1$):

$$\frac{C}{F} = \alpha q^{\beta} N$$

There are cases of hyperdepletion ($\beta < 1$) where high concentrations of animals are removed early in the development of the fishery (Hilborn and Walters 1992). My analyses are limited to a linear relationship where I estimate α and assume that $\beta = 1$. Treating catchability as a random variable also holds promise (Bishop 2006).

Neither did I estimate interactions between variables. For example, I found that longline depth had a significant affect on catch rates of most species. It also affects bait loss rates. However, I estimated the catchability change due to those two variables separately.

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. Conversely, blue marlin have a close ecological association with target species—they forage on the same prey aggregations (Josse et al. 2000). The increased catchability of associated species like blue marlin is linked to the increased catchability of target species, such as bigeye tuna

Particularly noteworthy were the effects of the historical reduction in the abundance of large animals. 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 biomass rather than the number of animals. Large tuna tend to have a wider depth range than small tuna (Neill et al. 1976) through the effects of water temperature on heart rates (Brill et al. 1998). The extension of longlines to access a wider depth range may therefore be significant in increasing the catchability of tunas and other large pelagic animals (Au 1985).

Conclusions

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 true fishing effort and measuring variations in fishing power. Several major groundfish fisheries (e.g., Pacific halibut, *Hippoglossus stenolepis*) do not attempt to derive abundance indices from commercial catch and effort data (Sullivan and Rebert 1998). Instead they rely on regular research surveys that use standardized fishing gear and practices along a predetermined grid. Such an approach to estimating the abundance of pelagic fish in the open ocean should be considered given the daunting problems with measuring variations in catchability and fishing power in commercial longline fisheries. Research surveys have rarely been attempted in the open ocean because of the high cost in obtaining representative samples from a system that features vast distances and high spatial and temporal variability (Bishop 2006). If

abundance surveys are not feasible, it will be essential to estimate changes in catchability and fishing power through experiments that compare the performance of past and current longline gear and practices.

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, although I have refuted the notion that catchability has declined.

Acknowledgments

The Pelagic Fisheries Research Program (PFRP), Future of Marine Animal Population Project of the Census of Marine Life, NSERC, and the Killam Foundation supported this work, which is part of a larger project initiated and supported by the Pew Charitable Trusts. The views expressed in this chapter are those of the author and do not necessarily reflect the views of funding bodies. Peter Williams provided observer data, Steve Beverley estimated the costs of electronic fish-finding equipment, Ziro Suzuki released Japanese on-line data. Rob Ahren, Wade Blanchard, RAM Myers, and Allan Stoner provided technical advice and comments on this chapter.

Shifts in Open-ocean Fish Communities Coinciding with the Commencement of Commercial Fishing¹⁰

Introduction

There is a growing realization of the magnitude of ecosystem changes caused by the expansion of human activities into new areas and the mechanization of exploitation that began in the eighteenth century (McCann 2000). The selective removal of large animals is a characteristic of human expansion into new environments (Pauly et al. 1998; Jackson et al. 2001). Many of the large animals were apex predators with ecological roles quite different to those of other animals—by eating smaller animals they influence the diversity and abundance of lower trophic levels (Jackson and Sala 2001).

Trophic cascades occur when a reduction in predator abundance results in alternating increases and declines in lower trophic levels. Most documented cases of trophic cascades are from streams, lakes, kelp forests, and intertidal zones, or they have been created in experiments (Pace et al. 1999). Several authors (e.g., Strong 1992) assert that trophic cascades rarely occur in large, diverse ecosystems that are buffered by multiple trophic links and spatial heterogeneity.

The open ocean is a complex ecosystem. Its high species diversity, patchiness in productivity, and highly mobile and opportunistic predators should buffer against trophic cascades (Steele 1985; Angel 1993; Jennings and Kaiser 1998; Kitchell et al. 1999). However, several features of the open ocean warrant closer scrutiny of that prediction. For example, large predators, such as tunas (Scombridae) and billfishes (Istiophoridae and Xiphiidae), must themselves survive intense predation as juveniles before reaching a size at which predation pressure diminishes. Through “cultivation effects”, large

¹⁰ This chapter was originally published as: Ward, P., and Myers, R.A. 2005. Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* 86: 835–847. The original article’s abstract is incorporated in the Conclusions of this thesis and its reference list is included in the Bibliography.

predators crop down the competitors and predators of their juveniles (Walters and Kitchell 2001). Consequently, variations in predator abundance affect the survival of juveniles of those same predator species. Such feedback mechanisms and the inability of ecosystem models to accurately predict the consequences of variations in predator abundance highlight the need to monitor how natural systems actually respond to reductions in the top trophic level.

Industrial fishing represents large-scale experiments in the manipulation of trophic levels because fishing is often size-selective (Pace et al. 1999). Since the 1960s, pelagic longlines have been used throughout tropical and temperate waters of the world's oceans to catch highly migratory, piscivorous tunas and billfishes. The longlines consist of a series of baited hooks attached to a mainline that is suspended from buoys floating at the sea surface. Over 50 species larger than about 5 kg are caught by the gear. Most of the species reach that size in their first year and mature by their fourth year. Some, such as sharks and rays (Elasmobranchii), are slower-growing and mature later (Last and Stevens 1994). Consequently, many species are vulnerable to the gear throughout a large part of their lives. By contrast, the prey of longline-caught fish (e.g., squids, Cephalopoda) are rarely if ever caught by longline (Kitchell et al. 1999).

Three recent studies have examined changes in the abundance of large predators in the open ocean. Baum et al. (2003) show that several species of pelagic sharks declined by 70% during 1986–2000 in the Atlantic Ocean. Myers and Worm (2003) found a tenfold decline in the abundance of tunas and billfishes since fishing began in the Atlantic, Pacific, and Indian Oceans. However, the analyses of Cox et al. (2002) show less pronounced declines.

The three studies analyzed data that commercial fishers reported in logbooks. Unfortunately, logbook programs often do not capture the true magnitude of community changes because they are limited to commercially valuable species, do not collect reliable body-mass data, and are not implemented until well after the start of exploitation (Jackson et al. 2001). We analyze data collected by observers on commercial longliners during 1994–2002 and by a scientific survey in the early 1950s. For both periods, the data were collected at a level of detail that allowed indices of abundance and biomass to be adjusted for variations in fishing operations, e.g., the depth of each longline hook. Our

analyses quantify the abundance, biomass, and body-mass of a wide range of species that constituted the pelagic fish community at the beginning of exploitation.

Methods

Data

We compare estimates of body-mass and indices of abundance and biomass derived from data collected in recent years by observers on commercial longliners in the tropical Pacific with those from a scientific survey conducted in the same region in the early 1950s (Figure 8.1). The US National Marine Fisheries Service provided copies of the two datasets. Conducted during 1951–58, the 1950s survey used standardized longline fishing gear and techniques. Most of the survey activities were along a survey grid during 1951–54. Commercial longliners were chartered towards the end of the survey. Several hundred baited hooks were deployed each morning and then retrieved in the afternoon (Murphy and Shomura 1972).

Observers on commercial longliners collected the recent data. Most of these activities occurred in 1999–2002, but for convenience are referred to as the “1990s”. The data consist of 505 daily longline operations compared to 880 operations in the 1950s. The 1990s longliners targeted large tunas. They deployed more hooks (averaging 2240 hooks per day compared to 322 hooks in the 1950s) over a wider depth range (down to 600 m compared to 200 m) for longer periods (Figure 8.2). The median soak time—the amount of time that baited hooks are available in the ocean during a daily operation—was 12 hours in the 1990s compared to 7 hours in the 1950s. We limited analyses to data from the two periods that provided the greatest overlap in terms of deployment time (02:00–08:00 local time) and month (January–November), within a broad region of the Pacific Ocean (10°S–11°N, 175°E–115°W; Figure 8.1).

The scientifically trained observers on 1990s longliners attempted to identify all species caught, as did scientists involved in the 1950s survey. However, the 1950s survey did not distinguish the various species of hammerhead sharks (*Sphyrna* spp.), thresher sharks (*Alopias* spp.), mako sharks (*Isurus* spp.), or snake mackerels (Gempylidae). For those species, we present indices for higher-level groups, e.g., all *Alopias* species

together as “thresher sharks”. For brevity, we use the term “species” to refer to species groups as well as individual species.

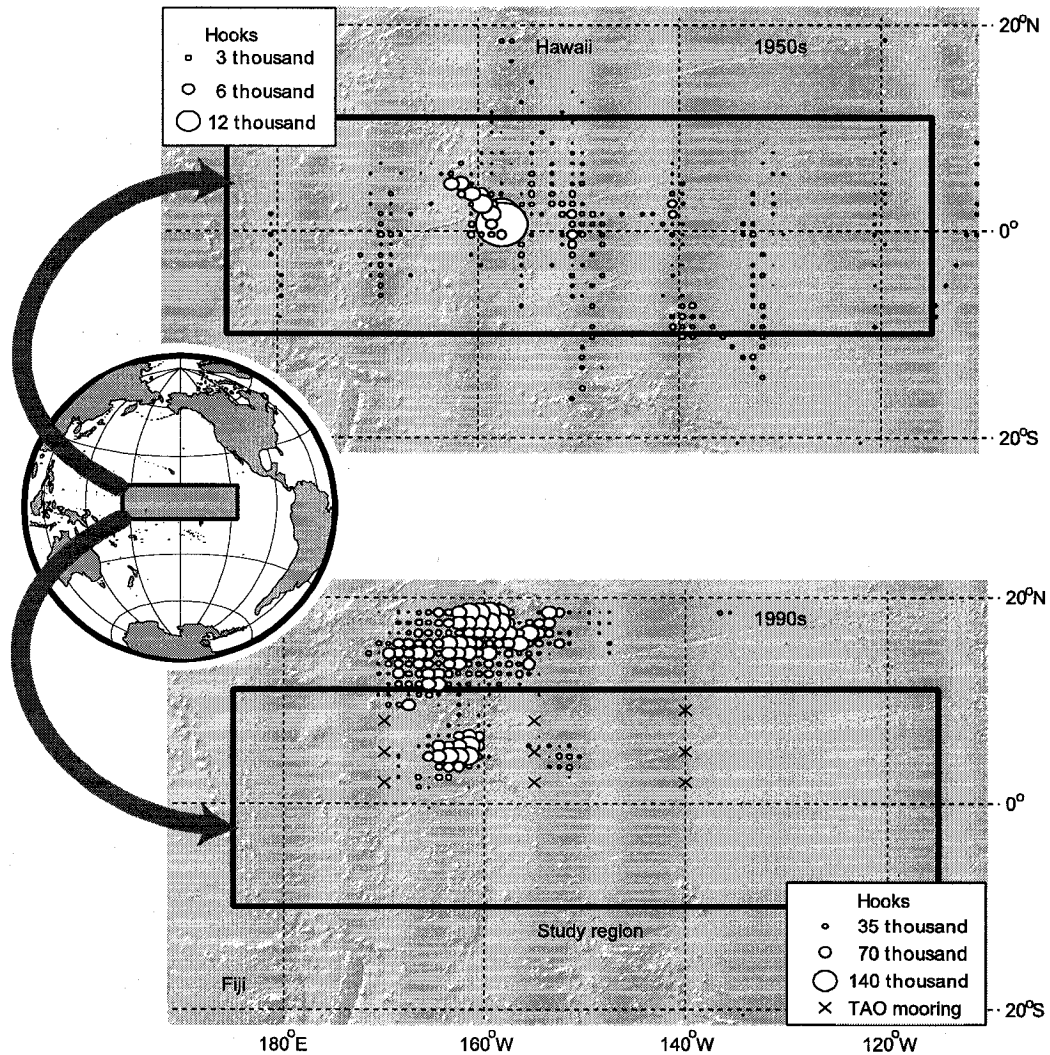


Figure 8.1. Bathymetric map of the study region showing the distribution of longline fishing in each period. Circles represent the level of longline fishing effort in each one-degree square. Crosses indicate the positions of Tropical Atmosphere Ocean (TAO) moorings that we used to obtain data on thermocline depth for the 1990s. Only data gathered within the rectangle were analyzed. Catch rates for 1990s activities outside the study region in the north were at similar levels to those for 1990s activities in the study region.

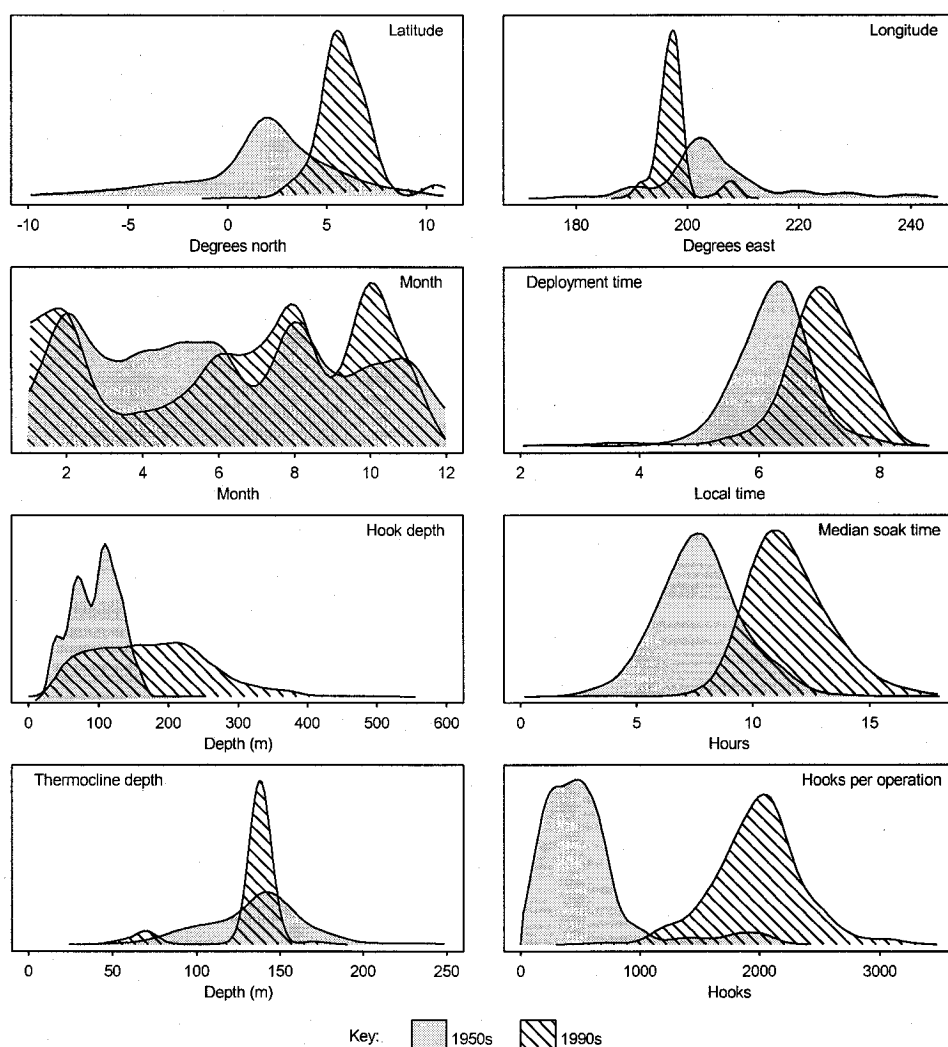


Figure 8.2. Comparison of 1950s survey (shaded) and 1990s commercial longline operations (cross-hatched) in the study region. For each period, the area of the density histogram sums to one. Densities were smoothed with running medians. Our analyses excluded operations in December and those where the longline was deployed before 2:00 am or after 8:00 am local time. We derived the thermocline depth (20°C isotherm) from Tropical Atmosphere Ocean data for the 1990s. For the 1950s, it was estimated from temperature profiles taken by survey longliners during 1950–53.

Much of the 1990s activity was near seamounts and islands in northwestern waters of the study region (Figure 8.1), which resulted in the capture of several species that do not usually inhabit the open ocean, e.g., dusky shark (*Carcharhinus obscurus*).

Consequently, we limited analyses to species that were not strongly associated with land masses (Appendix 2).

The survey and observer data consist of daily records of gear dimensions, the number of hooks deployed, times of deployment and retrieval, the species caught, and the hook on which each fish was caught. The data enabled us to estimate the maximum depth of each hook and its soak time. Many of the fish were also measured or weighed.

To verify that commercial and survey longliners sampled similar components of the pelagic fish community, we compared 1950s catches with those of commercial longliners operating in nearby areas during 1952–54 (Appendix 2).

Models for Estimating Abundance

We derived indices of species abundance from generalized linear models with a negative binomial error distribution and a log link. Generalized linear models were used because they allow for non-linear relationships between independent variables and the dependent variable (the number of a species caught), and accommodate the non-normal distribution of the number caught. Catches were highly skewed, with many longline strata having a zero catch, a few having a catch of one, and so on. The negative binomial distribution is appropriate for overdispersed data like longline catches where the variance is greater than the mean (Venables and Ripley 1999).

We assumed that the number of each species caught is proportional to their abundance, after corrections are made for differences in sampling among periods and operations. We divided the data for each longline operation into one-hour soak time strata and 40-m depth-zone strata. The probability distribution p of catching $C_{i,s}$ of a given species in stratum s of operation i is assumed to follow a negative binomial distribution with mean catch $\mu_{i,s}$:

$$p(C_{i,s}; \theta; \mu_{i,s}) = \frac{\Gamma(\theta + C_{i,s})}{\Gamma(\theta) C_{i,s}!} \frac{\mu_{i,s}^{C_{i,s}} \theta^\theta}{(\mu_{i,s} + \theta)^{\theta + C_{i,s}}}, \text{ for } C_{i,s} = 0, 1, 2, \dots, (8.1)$$

where Γ is the gamma function. The parameter θ is a measure of the aggregation of the data. It represents the amount of overdispersion relative to the Poisson distribution. Small values of θ indicate larger variance than that predicted by the Poisson model, i.e.,

$\text{var}(Y) = \mu + \frac{\mu^2}{\theta}$. As θ approaches infinity, the Poisson model is recovered, i.e.,

$\text{var}(Y) = \mu$ (Venables and Ripley 1999).

The mean catch $\mu_{i,s}$ of a species is assumed to be the product of the fishing effort and a combination of other variables:

$$\log(\mu_{i,s}) = \beta_0 + \beta_1 P_i + \beta_2 N_i + \beta_3 N_i^2 + \beta_4 E_i + \beta_5 E_i^2 + \beta_6 T_{i,s} + \beta_7 T_{i,s}^2 + \beta_8 D_{i,s} + \beta_9 D_{i,s}^2 + \log(h_{i,s}) \quad (8.2)$$

where P_i is the fishing period (it is set to zero for the 1950s and one for the 1990s), N_i is the latitude, and E_i is the longitude of longline operation i ; and $T_{i,s}$ is the soak time, $D_{i,s}$ is the depth below the sea-surface, and $h_{i,s}$ is the number of vacant hooks of each stratum s of operation i . The β_j are estimated parameters. We fitted the models separately to the data for each species. We included quadratic terms for soak time, depth, latitude, and longitude because scatter plots showed that relationships were not always linear.

The exponent of β_1 represents the ratio of abundance in the two periods, which we refer to as the change in abundance. We use the term “catch rate” for the number of fish actually reported per 1000 hooks, “abundance index” for the standardized catch rate expressed in terms of number of fish per 1000 hooks, and “biomass” for the abundance index multiplied by the mean mass of the species (kg) in each period. The index of community biomass is the sum of biomass indices of all species.

Abundance indices are model predictions of the number of the species caught by a standard unit of longline fishing effort (1000 hooks) at a standard location, depth, and time in the study region. The models adjusted abundance indices for several factors that are known to affect the efficiency of the fishing gear (e.g., hook depth), which is otherwise assumed to be constant among operations and periods. Biomass and abundance are relative indices that do not take into account differences in vulnerability to longline gear among species. The efficiency of longline gear or “catchability” generally increases with body-mass (Kleiber et al. 2003). Consequently, the true abundance of small species, such as skipjack tuna (*Katsuwonus pelamis*), is likely to be much greater than indicated by our abundance index.

We used three forms of eq. 8.2, corresponding to the level of information available on soak time and hook depth. We used the “hook model” described in eq. 8.2 for most

species of tunas and sharks because estimates of the hook's soak time and depth were available for each animal caught.

We applied the “operation model” to species where the hook was not identified. It has the same form as eq. 8.2, but terms are combined for each operation:

$$\log(\mu_i) = \beta_0 + \beta_1 P_i + \beta_2 N_i + \beta_3 N_i^2 + \beta_4 E_i + \beta_5 E_i^2 + \beta_6 T_i + \beta_7 T_i^2 + \beta_8 B_i + \beta_9 B_i^2 + \log(h_i) \quad (8.3)$$

where T_i is the median soak time of operation i and B_i is the number of hooks per buoy, a commonly used index of longline depth. Preliminary analyses showed good agreement between the depth distribution predicted by the hook model and that of the operation model for most tunas and sharks. However, results for several species indicated that the operation model sometimes provided poor predictions of fish distribution at shallow depths. The third form of eq. 8.2, the “offset model”, replaced depth terms with a second offset:

$$\log(\mu_i) = \beta_0 + \beta_1 P_i + \beta_2 N_i + \beta_3 N_i^2 + \beta_4 E_i + \beta_5 E_i^2 + \beta_6 T_i + \beta_7 T_i^2 + \log[h_i \overline{f(D_i)}] \quad (8.4)$$

where the mean depth effect $\overline{f(D_i)}$ is based on depth distributions derived from a wider study by Ward and Myers (2005a). They inferred the depth distribution of 37 pelagic species with a generalized linear mixed effects model applied to four datasets from longline activities in the Pacific Ocean. We used their coefficients for ten species that did not have the hook-level data required by the depth model. For each species,

$\overline{f(D_i)}$ represents the mean effect of hook depth D on relative catch rate over all hooks deployed in operation i :

$$\overline{f(D_i)} = \frac{\exp(\alpha + \gamma_1 D_i + \gamma_2 D_i^2 + \gamma_3 D_i^3)}{\exp(\alpha + \gamma_1 0.175 + \gamma_2 0.175^2 + \gamma_3 0.175^3)} \quad (8.5)$$

where α and the γ_j are parameters that (Ward and Myers 2005a) estimated for the species. For each operation, the offset was the mean depth effect multiplied by the number of hooks. The depth effect is standardized so that it equals one at a hook depth of 175 m, which is the median depth of hooks deployed by 1990s longliners. The inclusion of the depth effect scales the number of hooks in each operation, reducing the offset where the mean depth of the operation resulted in increased catchability and inflating the offset where catchability was low.

The models used only catch records where data were available for all variables, e.g., 262 of the 323 albacore tuna (*Thunnus alalunga*) caught in the 1950s had data on all variables used in the hook model. Consequently, we raised the abundance index of each species in each period by multiplying it by the ratio of the numbers caught and modeled. This article focuses on the 21 species most frequently caught by longline in the study region. They represented 97.8% of the fish caught in the 1950s and 99.7% of those caught in the 1990s. They included 19 species caught in both periods and two species that were caught only in the 1990s (pelagic stingray, *Dasyatis violacea*, and pomfrets, Bramidae). Body-mass estimates were not available for pelagic stingray, pomfrets, or snake mackerels. For those species we used body-mass estimates from a wider area of the Pacific Ocean during the 1990s (Appendix 3).

Results

The 19 species caught in the study region in both periods consisted of 12 species of sharks, large tunas (*Thunnus* spp.), and billfishes, which we refer to as “large predators”, and 7 “small species” with a mean body-mass less than 17 kg (Table 8.1). The 1990s survey caught more species than were caught in the 1950s. The extra species caught in the 1990s all had a mean mass of less than 17 kg.

The mean body-mass of most large predators declined between the 1950s and the 1990s, whereas the mean mass of small species showed minor variations or increased (Figure 8.3). The 1990s longliners deployed 1.103 million hooks and caught 24 208 fish (25 fish per 1000 hooks) compared to 17 439 fish caught from 0.302 million hooks in the 1950s. Abundance indices reflected the differences in catch rates, with the indices of all large predators declining between periods (Figure 8.4). Both the abundance index and mean mass of large predators declined between periods, resulting in reductions in their biomass index (Figure 8.4). By contrast, biomass indices of several small species increased because their abundance index or mean mass increased between periods. The relationship between change in biomass and mean mass was statistically significant ($P = 0.002$; Figure 8.5a), as was the relationship between change in biomass and the 1950s biomass index ($P = 0.031$; Figure 8.5b). The large predators, which dominated the pelagic fish community in the 1950s, showed the greatest declines in biomass.

Table 8.1. Common and scientific names of the 21 species most frequently caught in the study region. We classified species as either “small species” (1950s mean body-mass less than 17 kg, common names in regular font) or “large predators” (bold font). Classification of species that were not caught in the 1950s is based on their 1990s mean mass. Habitat categories^a are based on Froese and Pauly (2005) and are listed in decreasing order of importance for each species.

Common name	Scientific name	Habitat ^a	No. caught		Mean body-mass (kg)	
			1950s	1990s	1950s	1990s
Tunas and tuna-like species						
Albacore tuna	<i>Thunnus alalunga</i>	I, II	323	31	19	24
Bigeye tuna	<i>Thunnus obesus</i>	I, II	694	2 975	76	46
Skipjack tuna	<i>Katsuwonus pelamis</i>	I	438	1 668	10	8
Wahoo	<i>Acanthocybium solandri</i>	I	100	683	14	13
Yellowfin tuna	<i>Thunnus albacares</i>	I, II	10 636	10 625	52	28
Billfishes						
Black marlin	<i>Makaira indica</i>	I	38	2	134	35
Blue marlin	<i>Makaira nigricans</i>	I	325	459	100	42
Sailfish	<i>Istiophorus platypterus</i>	I	25	31	23	10
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	I	15	55	12	7
Striped marlin	<i>Tetrapturus audax</i>	I	55	215	59	28
Other teleosts						
Great barracuda	<i>Sphyrna jello</i>	I, A	19	97	14	7
Longnosed lancetfish	<i>Alepisaurus ferox</i>	II, I	100	1 699	3	3
Mahi mahi	<i>Coryphaena hippurus</i>	I	53	190	6	7
Pomfrets	Bramidae	III, I	0	637	—	3

Common name	Scientific name	Habitat ^a	No. caught		Mean body-mass (kg)	
			1950s	1990s	1950s	1990s
Snake mackerels	Gempylidae	II, I, III	23	933	—	4
Sharks and rays						
Blue shark	<i>Prionace glauca</i>	I, II	696	1 081	52	22
Mako sharks	<i>Isurus</i> spp.	I	51	72	74	38
Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	I	1 149	794	36	18
Pelagic stingray	<i>Dasyatis violacea</i>	I	0	302	—	3
Silky shark	<i>Carcharhinus falciformis</i>	I, II	2 210	1 080	53	33
Thresher sharks	<i>Alopias</i> spp.	I, A, II	112	511	17	12

^aHabitat categories:

- I epipelagic zone of the open ocean (0–200 m)
- II mesopelagic zone of the open ocean (200–1000 m)
- III bathypelagic zone of the open ocean (immediately above the sea floor)
- A associated with land masses, such as seamounts, reefs, and islands

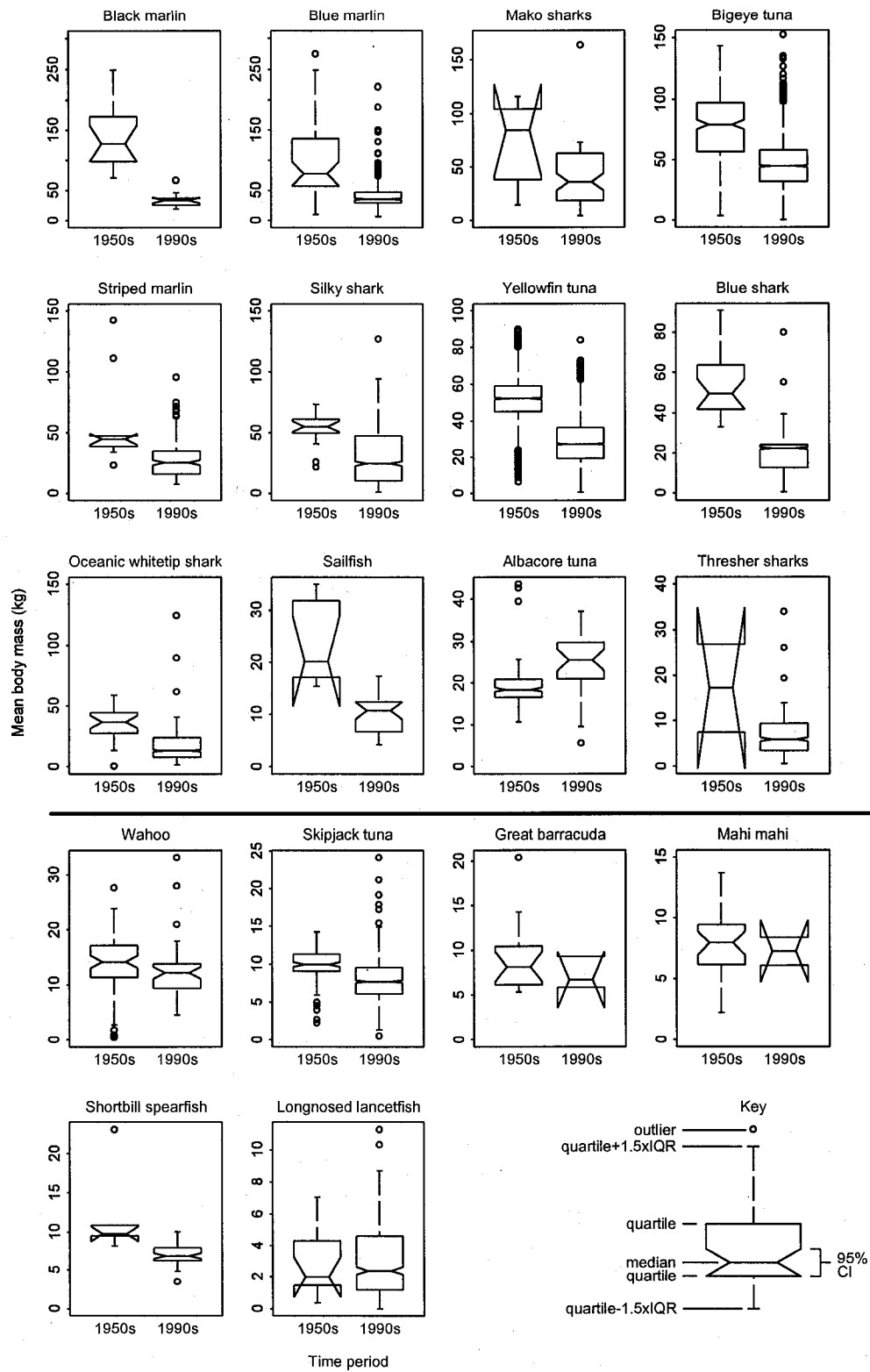
Variations in body-mass between the two periods tended to be more important than variations in abundance in driving changes in biomass. For all species combined, body-mass reductions contributed 66% of the decline in the index of community biomass.

The index of community biomass for the 1950s was ten-times the 1990s index (Figure 8.6). In terms of biomass, yellowfin tuna (*Thunnus albacares*) and bigeye tuna (*T. obesus*) were the dominant species in both periods. However, there was a reordering among the other species. Several small species rose in dominance, e.g., skipjack tuna ranked tenth in the 1950s, then ranked third in the 1990s. The rank of several large predators, such as mako sharks, fell below that of many small species in the 1990s.

We applied the three models (eq. 8.2–4) to data for each species. For simplicity, we presented the model that provided the most reliable estimate of change in abundance between the two time periods. The results from stepwise model selection were not qualitatively different from the models with all parameters estimated. Depth or hooks between floats was statistically significant for 73% of the models, followed by soak time (62%) and latitude (62%). Quadratic terms and longitude (38%) were less frequently significant (Appendix A1).

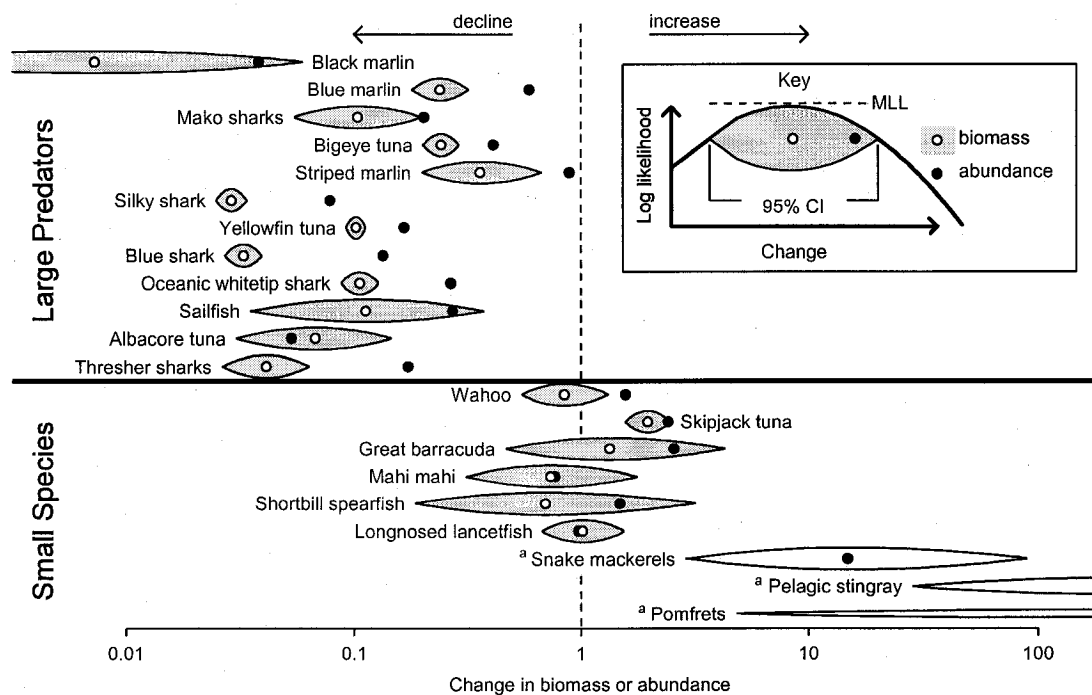
We investigated the robustness of abundance indices to the location of the study region's boundaries and the difference in longline depth range between periods (Appendix 3). Most species showed latitudinal gradients in abundance indices, but weaker longitudinal effects. Reducing the extent of the study region down to a small area of overlap had no systematic effect on abundance indices of most species, other than increasing their confidence intervals. Consequently, we included terms for latitude and longitude in the models and used a region that had a wide geographical range. Hook depth significantly modified the estimate of change in abundance for 5 of the 12 species investigated. However, restricting the analyses to strata where depth was less than 200 m made only a small difference to the estimates.

Figure 8.3. Variations in the body-mass of 18 species between periods. In this article, we present indices for the 21 most frequently caught species, but body-mass estimates were not available for 3 of those species in the 1950s and they are not shown in Figure 8.4 or 8.5a. Species are in descending order of their 1950s mean mass. The scientists involved in the 1950s weighed fish, whereas we predicted mass from length–mass relationships applied to length measurements reported by observers in the 1990s. The boxplots show the interquartile range (IQR), which is the difference between the first and third quartiles, thus containing 50% of observations. Boxplots are sometimes inside-out where the sample size is small and the confidence interval (CI) is wider than the interquartile range.



Large Predators

Small Species



^aConfidence intervals are for change in abundance because no body-mass data were available for the species in the 1950s.

Figure 8.4. Change in indices of biomass (open circles) and abundance (solid circles) between periods. The 21 species are in descending order of their mean body-mass. A value of 1.0 indicates no change in the biomass (or abundance) index, a value of 0.1 indicates a tenfold decline, and a value of 10 indicates a tenfold increase. The shaded regions are “raindrop plots” (Barrowman and Myers 2003) representing approximate 95% confidence intervals (CI) of the change in biomass obtained from profile likelihoods. The maximum log likelihood (MLL) estimate of biomass change is shown at the vertical centre of the raindrop. Indices could not be estimated for pelagic stingray or pomfrets because they were not caught in the 1950s. However, the lower limits of their confidence intervals for abundance could be estimated and are shown.

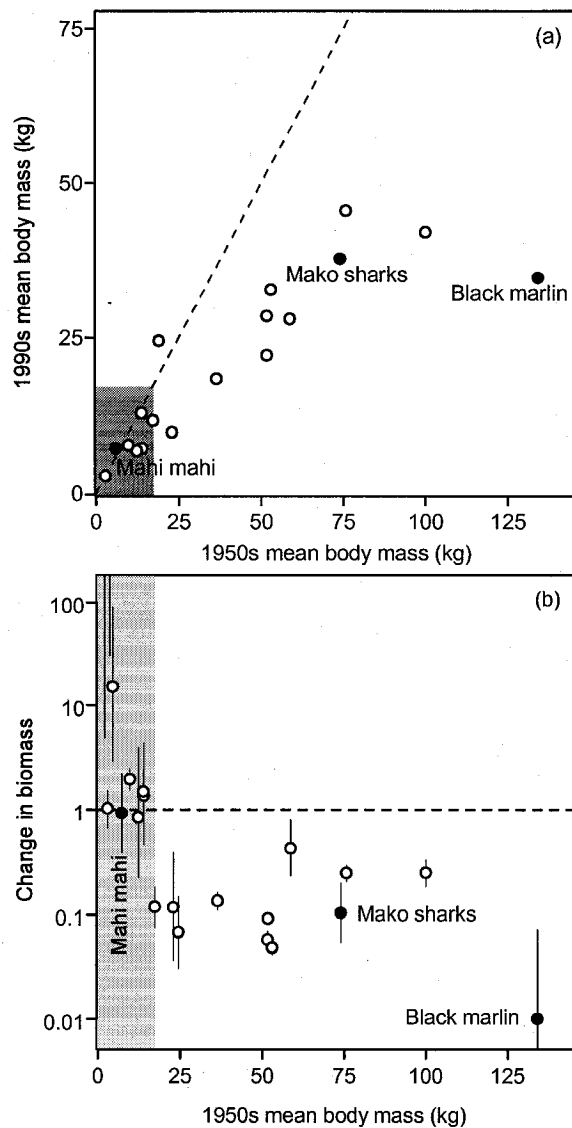


Figure 8.5. Body-mass relationships. Several species are labelled and have solid symbols to assist comparison between panels. Background shading indicates small species (<17 kg). (a) The mean mass of each species in the 1950s plotted against its 1990s mean mass. Pomfrets, pelagic stingray, and snake mackerels are not plotted because estimates of their mean mass were not available for the 1950s. The broken line is the line of equality between mean mass in the two periods. (b) The relationship between the change in biomass for 21 species and 1950s mean mass (or 1990s mean mass for the three species that did not have body-mass data in the 1950s). The vertical bars are approximate 95% confidence intervals for the change in biomass. Only the lower limits of the confidence intervals for change in abundance of pomfrets and pelagic stingray are shown at the top left-hand corner of panel (b).

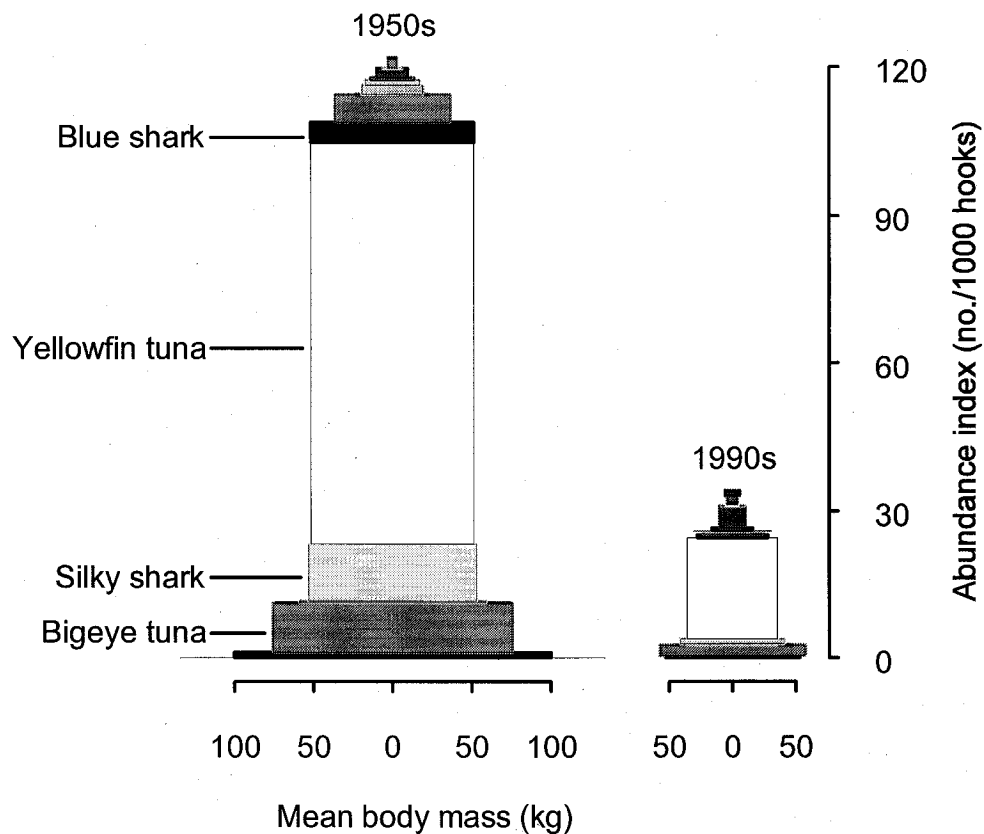


Figure 8.6. Change in biomass of the pelagic fish community. Each bar represents one species (species associated with land masses are excluded). The height of each bar is scaled to the abundance index and its width is scaled to mean body-mass so that the bar's area represents biomass (kg per 1000 hooks). The four most abundant species in the 1950s are labelled. The shading and the order in which each species is shown are the same for both periods.

For most tunas and billfishes, there was no statistically significant difference between catch rates reported by the 1950s survey (48 tunas and billfishes per 1000 hooks) and those of commercial longliners fishing in and adjacent to the study region in 1952–54 (47 per 1000 hooks; Appendix 3). It is noteworthy that observers on the commercial longliners during 1952–54 consistently reported that external factors, such as limitations on the area of activity, kept catch rates well below levels that true commercial operations could achieve (Van Campen 1952).

Discussion

Our analyses of longline data indicate significant reductions in the abundance and body-mass of large predators and changes in the species composition of the pelagic fish community since the 1950s. Possible explanations of the changes include the effects of fishing, variations in oceanographic conditions, or that they are a sampling artifact. We review evidence pertinent to those hypotheses then consider how the pelagic fish community may have compensated for the changes.

Hypothesis I: Differences in Sampling

We used available data and generalized linear models to standardize abundance estimates between the 1950s and 1990s, e.g., longline depth. However, there were other differences in sampling between periods that we could not correct, e.g., searching for target species and gear saturation. Could our results be an artifact of those differences? Several independent lines of evidence show that this is unlikely and, if anything, we have underestimated the decline in large predators.

The density of hooks in the 1990s (40 m between hooks) was about 80% that in the 1950s (50 m). It is not known how increased hook density might affect catch rates. Neither did we investigate the possibility that the increased number of vessels fishing for pelagic species in the study region after the 1950s increased competition for the most productive areas. Such competition may result in the displacement of some longliners to less productive waters.

There is firmer evidence that differences in sampling resulted in the underestimation of the extent of the decline in abundance. First, the 1990s longliners actively searched for target species, whereas the 1950s data were mostly from a predetermined survey grid. Abundance is overestimated in the 1990s because longliners concentrated on areas where fish-finding equipment (e.g., sea-surface temperature imagery), recent catches, and past experience indicated that fishing would yield the highest financial returns. Operating costs, such as distance from port, were a consideration. However, the expected catch of bigeye tuna and yellowfin tuna was the main factor determining the location of 1990s activities within the study region (T. Swenarton, pers. comm.).

Second, the concentration of 1990s activity near seamounts and islands resulted in elevated catch rates for many species. Several studies have shown that proximity to land masses influences the local abundance of pelagic fish species, e.g., Murphy and Shomura (1972). Our models adjusted abundance indices for latitude and longitude, but did not include a specific term for distance from land.

Third, detailed descriptions of the fishing and sampling show many similarities between the periods, e.g., similar hook sizes, wire leaders, sardines as bait, and the time of longline deployment. However, the 1990s longliners connected hooks to mainlines with monofilament-nylon branchlines. They produce higher catch rates than the rope branchlines used in the 1950s (Stone and Dixon 2001). We were unable to adjust indices for these improvements in fishing gear, the effects of fishing near seamounts and islands, or for searching and experience. However, those differences would have resulted in 1990s abundance being overestimated rather than underestimated.

Hypothesis II: Variations in Oceanographic Conditions

There is no doubt that changes in oceanographic conditions affect the recruitment of marine fishes (Myers 1998; Ravier and Fromentin 2004), variations in productivity (Mantua and Hare 2002; Chavez et al. 2003), and the efficiency of longline gear (Bigelow et al. 2002). Oceanographic conditions certainly caused some of the variation in abundance seen in our study. Moreover, the effects of oceanographic conditions are difficult to dismiss because they may involve time-lags, and they may range from long-term affects like regime shifts to short-term affects. However, there are two reasons to believe that they were not the major cause of the changes observed in the pelagic fish community of the tropical Pacific.

First, there was no obvious difference between periods in several oceanographic indices that are often associated with variations in productivity and fish distribution (Appendix 3). Second, there is no reason to believe that changes in oceanographic conditions would exactly mimic the changes predicted by fishing. The oceanographic hypothesis must demonstrate a mechanism that explains a pattern where the body-mass and abundance of large predators declined while small species increased in abundance. Those changes occurred among 12 species of large predators and 9 small species that have diverse life histories. The large predators, for example, range from fast-growing

yellowfin tuna that mature at two years of age, through to mako sharks that mature at eight years or older and may live for decades (Froese and Pauly 2005). The pattern of changes in community composition, body-mass, and abundance are not consistent with any known oceanographic changes.

Nevertheless, it is difficult to assess hypotheses without a time-series of indices. Repeating the 1950s survey would provide an empirical test of hypotheses I and II. Such a survey would need to cover similar oceanographic conditions and replicate the 1950s sampling design, fishing gear, and techniques. In many other fisheries, regular surveys are used to gather information for assessments because of problems in standardizing commercial logbook data, e.g., searching and variations in fishing gear.

Hypothesis III: Ecosystem Effects of Fishing

Fishing has been extensively documented as a cause of fish population declines. It affects populations directly through removals or indirectly by modifying the ecosystem's trophic structure or habitats (Jennings and Kaiser 1998). Longliners have removed millions of large predators from the study region each year, with many more tunas removed by other fishing gears, such as purse seine. Furthermore, the 1950s fish community was not pristine. Pelagic fish species, such as albacore tuna and yellowfin tuna, had been commercially harvested in the Pacific Ocean since the early 1900s (Nakamura 1950).

Nevertheless, there are several inconsistencies between our results and those of other assessments. Cox et al. (2002) found smaller changes in large predators than we observed. They used an ecosystem model to investigate changes in populations of tunas and billfishes in a much wider area of the Pacific Ocean. Our results also contradict accepted age-based stock assessments for commercially important tuna and billfish species. The substantial decline in abundance indicated by our analyses suggests that the original populations were relatively small. However, the populations subsequently supported much higher catch levels since the 1950s, indicating that they may have been much larger than indicated by our estimates.

However, those analyses did not include sharks, the group that showed the largest declines in our study. Also contributing to the inconsistencies are the non-linear relationship between commercial catch rates and abundance, particularly for purse-seine catch rates, and the fact that the populations were already exploited by the start of their

study period. Our analyses require fewer assumptions than age-structured assessments and ecosystem models. Our findings are consistent with those of Myers and Worm (2003) and the strong, size-dependent patterns predicted by many models of the effects of fishing (Myers and Mertz 1998b). The changes in body-mass are typical of a demographic change known as the “fishing down of an accumulated biomass” (Hilborn and Walters 1987). The initial reduction in biomass by size-selective fishing takes the form of a disproportionate reduction in large animals that had few natural enemies. Increased fishing mortality since the 1950s has prevented large predators, particularly sharks, from reaching a large mass because of their low growth rates combined with the time required to reach that size.

Although our study is limited to two snapshots of the community, the similarity of the changes to declines in large sharks reported in the northwestern Atlantic (Baum et al. 2003), Gulf of Mexico (Baum and Myers 2004), and global declines in commercial catch rates (Myers and Worm 2003) indicate that it is linked to fishing.

Compensatory Responses

Our analyses did not reveal any clear evidence of species extirpation, but several species that were caught in the 1990s were not reported in the 1950s. The additional species included: (1) mesopelagic and benthopelagic species caught by the deep longlines used in the 1990s (e.g., escolar, *Lepidocybium flavobrunneum*); (2) species caught by 1990s longliners fishing near land masses (e.g., dusky shark); (3) rare species that were probably an artifact of the larger sample size in the 1990s (e.g., Pacific bluefin tuna, *Thunnus orientalis*); and (4) extra species that were caught in large numbers, are not associated with deep longlining or land masses, and are easily distinguished from other species. The extra species included pelagic stingray, slender sunfish (*Ranzania laevis*), and pomfrets. We contacted a former survey scientist, R. Shomura (pers. comm.), who confirmed that the 1950s survey did not encounter the extra species in the study region.

Increases in the biomass indices of several small species and the appearance of extra species are consistent with release from predation. Pomfrets, for example, may have increased because of the reduction in the abundance of their predators, which include large tunas (Collette and Nauen 1983), billfishes (Nakamura 1985), and sharks (Last and Stevens 1994). Most small species would have a very low catchability due to their small

gape. Skipjack tuna, for example, are not caught by longline until they are mature, affording some protection from overexploitation by the gear (Myers and Mertz 1998a; Hampton 2000). They increased despite a substantial expansion in their harvesting by purse-seine fishing gear in the tropical Pacific (Cox et al. 2002). Pelagic stingray were caught in considerable numbers in the 1990s, but are unlikely to have been an artifact of deep longlining or activities near land masses because they inhabit the epipelagic zone of the open ocean (Mollet 2002). It is also noteworthy that pelagic stingray were not marketed. They are often alive when longlines are retrieved, and they might survive when released alive.

Expansion in the distribution of prey in response to reductions in the abundance of their predators is another possible explanation of the increased abundance of small species observed in the study region. Many studies have reported changes in the microhabitat utilization of prey species following the introduction or removal of predators, e.g., Werner et al. (1983). A change in depth distribution may have contributed to the increases in abundance that we estimated for small species. The removal of large predators would allow small species to move into habitats (e.g., epipelagic waters during the day) that were originally the domain of large predators.

Contraction of Biomass

The index of the biomass of pelagic fish available to longline gear in the 1990s was less than 10.3% of that in the 1950s. The large predators were 9.7% of their 1950s biomass index, which agrees with the 88.5% decline in the abundance of tunas and billfishes estimated by Myers and Worm (2003) for all oceans.

The amount of energy entering an ecosystem through primary production balances the energy lost through waste products, decay, respiration, and other activities (Valiela 1995). A small portion of the energy that once supported populations of large predators is now removed as commercial catches. The balance must be consumed by other pelagic species or it might sink to abyssal depths to be utilized by other animals and detritivores or eventually become buried in sediments. Our analyses revealed relatively minor increases in the biomass of small pelagic species (e.g., pelagic stingray), which may represent release from predation. We would also expect the competitive release of species at the same trophic level as large predators, e.g., false killer whale (*Pseudorca*

crassidens). Alternative sources of information must be investigated to determine how other components of the ecosystem have compensated for the reduction in larger predators because their competitors and prey are rarely, if ever, caught by longline fishing gear.

Implications of Reductions

The changes in the pelagic fish community might not have reduced the harvest levels that the system can sustain. A fish community consisting of many small fish will sustain higher exploitation rates than a community dominated by large, old fish (Myers and Mertz 1998a).

Beyond the economic considerations of the community changes are implications for the functioning of the ecosystem and biodiversity. The substantial reduction in the biomass of large pelagic predators since the 1950s follows the global pattern of reduction in mean trophic level identified by Pauly et al. (1998). Ecosystem models (e.g., Steele and Schumacher 2000; Cox et al. 2002) can predict many community changes. The addition of early survey data, like that analyzed in the present paper, will help those models to predict the magnitude of changes caused by the selective reduction of large predators. However, we have no experience with how those changes may have affected the overall stability and persistence of the system. Neither is it clear whether the pelagic fish community has stabilized or whether reductions in predator abundance, community biomass, and body-mass are continuing.

Conclusions

Our analyses show that only a remnant of the original fish community remains in a large region of the tropical Pacific. The index of community biomass is about 10% of its former level and the community is composed of smaller fish and fewer large predators. The changes are typical of a large and fundamental reordering of the pelagic ecosystem of the world's open oceans. The advent of industrial longline fishing coincided with these changes. The 1950s longlining survey could be repeated to determine the exact extent of the community changes and whether they were due to variations in oceanographic conditions or sampling. The implications of the changes in open-ocean fish communities on ecosystem stability and persistence are highly uncertain.

Acknowledgments

The Pelagic Fisheries Research Program (PFRP), Future of Marine Animal Population Project of the Census of Marine Life, NSERC, and the Killam Foundation supported this work. This research is part of a larger project initiated and supported by the Pew Charitable Trusts. The views expressed in this article are those of the authors and do not necessarily reflect the views of funding bodies. Kurt Kawamoto, Naozumi Miyabe, Brent Miyamoto, Ziro Suzuki, Tom Swenarton, and Peter Williams provided data and information on the fisheries. Julia Baum, Wade Blanchard, Justin Breen, Albert Caton, Ian Jonsen, Dan Kehler, Ramzi Mirshak, Aswea Porter, Richard Shomura, Wilvan Van Campen, Boris Worm, and two reviewers provided technical advice and comments on the manuscript.

Hypotheses Explaining Community Variations

Introduction

My comparison of 1950s survey and 1990s observer data indicate significant declines in abundance and body-size indices for most species of large tuna, billfish, and sharks in the tropical Pacific Ocean (Chapter 8). The body-size and abundance of small species did not decline. I show that the declines in large species are unlikely to be the result of variations in fishing; longline fishers have modified their fishing gear and practices to improve fishing power and catchability (Chapters 3–7). Earlier, unpublished analyses recognised the rapid decline in initial catch rates as a feature of pelagic longline fishing (Nakamura 1951). Recent studies link this phenomenon to the depletion of apex predators in the open ocean and draw parallels with historical changes in animal communities in other environments. In investigating the relationship between species diversity and ecosystem productivity and stability, Worm et al. (2006) highlight population collapses and extinctions in a variety of marine ecosystems, including the pelagic ecosystem of the open ocean. Myers and Worm (2003) reported a 90% reduction in the abundance of large tuna and billfishes since fishing began in the Atlantic, Pacific, and Indian oceans. They also noted an increase in swordfish abundance, which they may have been caused by the serial depletion of large predators and competitors, such as blue marlin. Pelagic shark abundance also declined by up to 90% during 1986–2000 in the Atlantic Ocean (Baum et al. 2003). A third study (Baum and Myers 2004) reported even higher rates of decline in shark populations in the Gulf of Mexico. Age-structured stock assessment models, which largely depend on longline catch rates and size data, show similar rapid declines in biomass, e.g., bigeye tuna in the tropical Western Pacific (Hampton et al. 2005a).

Many of the studies described above relied on catch and effort data reported by commercial fishers in logbooks. Under-reporting of catches by commercial fishers might explain the rapid decline in longline catch rates. Japan, for example, recently disclosed significant under-reporting of southern bluefin tuna catches by its longline fleet in 2005

(CCSBT 2006). The under-reporting is related to attempts to avoid taxation and limits on catches since 1985. Similar under-reporting of catches of other species is possible, although catch limits have not been introduced for other target species until the late 1990s or 2000s. On the other hand, southern bluefin tuna catches might have been reported as other species (e.g., bigeye tuna), resulting in over-reporting of catches of those species. The early data are based on logbook reports from a small number of longliners, which were raised to provide an estimate of total catch and effort. The estimates would be biased upwards if only the high performers submitted logbooks. Regardless, concerns about under-reporting and misreporting do not apply to the variations in pelagic fish communities identified in my thesis because I analysed scientific survey and observer data that are considered much more reliable.

Other fishing methods used to take tuna in the open ocean (e.g., pole-and-line and purse seine) do not tend to show rapid declines when fishing first commenced. This might be due to the small body-size of tuna taken by those methods (they are very fast-growing at that age and fishing mortality rates are relatively low compared to natural mortality). The absence of clear catch-rate declines might also be due to problems in measuring fishing effort for those methods, which involve considerable searching and handling time for schooling fish.

Here I review seven hypotheses that may explain the observed community changes documented in my thesis. For each hypothesis I describe the mechanism that could be involved, evidence of that mechanism from pelagic fish and other communities, and ways that the hypothesis could be tested. I then consider the plausibility of each hypothesis in relation to specific characteristics of the community variations. Many of the hypotheses address the question of whether longline catch rates are a useful index of abundance. Chapter 8 shows that the community changes are unlikely to be an artefact of sampling bias. Earlier Chapters show that fishing power has increased over time. I identified very few fishery-related factors that could have decreased fishing power or catchability over time. I did not investigate the form of the relationship between longline catch rates and abundance; whether it is linear or shows a hyperdepletion or hyperstability pattern.

Review of Hypotheses Explaining Community Variations

Hypothesis 1: Sub-populations

Ricker (1973) shows that a constant harvest ratio applied to a mixed stock may result in the increased abundance of productive sub-populations and reductions in less productive sub-populations. Less productive sub-populations may persist at low levels or they may be extirpated because environmental variability combined with lower productivity will result in lower recruitment on average. Hilborn (1985) suggests that the reduction of less productive sub-populations may not be of concern because the fishery is now exploiting a subset of the original stock that is truly more productive. However, the loss of genetic diversity through the removal of sub-populations may have detrimental effects on adaptability, population persistence, and ecosystem links (Patrick 1997). In particular, the loss of diversity will reduce the ability of the remaining sub-populations to utilize all available habitats and to respond to environmental changes.

Most examples of the removal of sub-populations involve anadromous species, such as salmon (F. Salmonidae), that return from common marine forage areas to their natal stream to spawn with other members of their sub-population, e.g., Skeena River sockeye salmon (*Oncorhynchus nerka*; Ricker and Smith 1975). Few biochemical genetic analyses of tuna and billfishes have reported homogenous populations. Instead, those analyses show substantial genetic heterogeneity among ocean basins and among samples from the same ocean basin, suggesting that mixing is not instantaneous or that distinct sub-populations may exist (Ward et al. 1994; Graves and McDowell 1995; Chow et al. 2000).

MacKenzie (2005) presents evidence of the simultaneous decline in catch rates of bluefin tuna (*Thunnus thynnus thynnus*) to commercial extinction in three widely separated areas of the Atlantic Ocean. Past tagging studies indicate that those regions were once linked by migration. He suggests that this is evidence of the extirpation of a sub-population of bluefin tuna. This is circumstantial evidence of sub-population removal that needs to be linked to biochemical analyses that identify genetically independent or semi-independent sub-populations within each stock. Those analyses should also demonstrate spawning-site fidelity and include estimates of mixing rates among sub-

populations because it is unlikely that sub-populations will be completely isolated. It would be particularly difficult to demonstrate that the removal of sub-populations is the cause of rapid declines in longline catch rates because the sub-populations—if they existed—would have been removed many years ago; the necessary material is unlikely to be available for genetic analysis. Chemical analyses of calcified tissues, which provide an environmental history of animals, held potential for determining spawning-site fidelity (Proctor et al. 1995), but progress in this area has been slow.

Hypothesis 2: Artificial Selection

Artificial Selection is also known as the “Dumb Fish Hypothesis” (Miller 1959). The idea is that fishing will selectively remove the members of a population that are most vulnerable to the gear. Individuals with adaptations for avoiding capture will have a competitive advantage in the same way that natural selection will favour individuals with a successful mix of risk-sensitive foraging and predator-avoidance behaviours (Walters 2000). Typical predator-avoidance responses, for example, will lead to evasion of an approaching trawl net (Heino and Godoe 2002). Hutchings (2000) observes that “...the potential for fishing to effect significant evolutionary change within a population is no different than that of any form of predator-induced mortality that differentially affects the survival of individuals of different ages and sizes.” Longlining is a potentially significant evolutionary force for some heavily exploited species. This might be expected for bigeye tuna, for example, where fishing now accounts for over 20% of the total adult mortality (Hampton et al. 2005).

Artificial selection is closely related to the Sub-populations Hypothesis, but it requires additive genetic variation in the traits selected by the fishing gear. Changes in genetic life-history traits can be measured indirectly through analyses of phenotypic variability or “reaction norms” (Rijnsdorp 1993). Although there are many studies of the effects of fishing on marine populations, few have examined its effects on behavioural traits that may help animals to avoid capture (Stokes and Law 2000; Hauser et al. 2002). The genetic basis for behavioural traits is poorly understood, and evidence is scanty and correlative for marine species (Heino and Godoe 2002). Phenotypic behavioural traits, such as the avoidance of fishing gear, are extremely difficult to measure, particularly for

large pelagic species that are hard to maintain in captivity, and in the open ocean where controlled experiments are not feasible.

Hypothesis 3: Removal of an Accumulated Biomass

Fishing has been extensively documented as a cause of fish population declines.

Longliners have removed millions of large predators from the open ocean each year, with many more removed by other fishing gears, such as purse seines. Nevertheless, this does not explain the contradictory evidence of the rapid decline in catch rates with low catch levels, which suggests that the original populations were relatively small. The catch rates declines are then followed by a period of stability in catch rates with much higher catch levels, which suggests that the populations are very large (Hampton et al. 2005b).

A demographic shift, known as the “fishing down of an accumulated biomass”, might explain the paradoxical patterns in catches and catch rates. The initial reduction in biomass takes the form of a disproportionate reduction in the older age-classes. Baranov (1918) showed that the commencement of exploitation involves a period when the population’s age-structure adjusts to increasing mortality rates. The first few units of effort remove the more vulnerable animals, producing rapid declines in catch rates and other abundance indices, e.g., body-size. After this initial removal, the remaining animals have lower catchability, so that catch rates decline as the fishery develops (Ricker 1973; Hilborn and Walters 1992)¹¹. Increased abundance of juveniles as a result of the removal of old adults (the “accumulated biomass”) is consistent with the idea of predator release.

The reduction of an accumulated biomass and changes in catchability are rarely documented because data collection programs are seldom in place when fishing commences. Nevertheless, the strong, size-dependent patterns like the depletion of an accumulated biomass are easily demonstrated with age-structured models (Myers and Mertz 1998b). It would be useful to verify that the predicted age-structure of pristine pelagic populations is consistent with the effects of parasitism and senility on very old animals.

¹¹Hilborn and Walters (1992) suggest that catchability is initially elevated because animals comprising the accumulated biomass are “dumber, slower or more accessible to the fishing gear”. I consider those other factors under separate hypotheses, reserving accumulated biomass for initial size-dependent patterns of depletion.

Hypothesis 4: Local Depletion

The idea behind the Local Depletion Hypothesis is that pelagic species have a patchy distribution, and that initial longline activities depleted areas of high density. Fishing an area of high density will cause local depletion when growth and recolonisation rates are less than fishing mortality rates (Shackell et al. 2005). Local depletion is essentially a matter of scale; whether depletion is considered at the level of a single hook, a fishing operation, around a bathymetric feature, or a large portion of an ocean basin; and whether the period of interest is on a scale of hours through to decades. Depletion depends on the “viscosity” of the population—how rapidly mixing fills the vacancy created by the removal of animals (MacCall 1990). It is not surprising, then, that most examples of local depletion are from slow-growing, sessile species in small, isolated habitats, e.g., abalone (*Haliotis* spp.) and crustacea on reefs (Haaker et al. 1996; Orensanz et al. 1998). Serial depletion occurs where fishers maintain catch rates by successively moving on to newer fishing grounds as fish abundance becomes depleted on existing grounds (Orensanz et al. 1998; Berkes et al. 2006).

The distribution of large predators is characteristically patchy in the open ocean. Japanese longliners, for example, initially targeted spawning aggregations of large adult southern bluefin tuna south of Java in the Indian Ocean. In the late 1950s they shifted their longlining operations to southerly waters (20–45°S) where more valuable, sashimi-grade southern bluefin tuna are taken. The tuna in those waters are more dispersed than the spawning aggregations, resulting in a decline in nominal catch rates (Caton 1991). Such expansion in effort distribution may result in catch rate declines, but this is not included in my definition of local depletion because the data that demonstrate the early catch rate declines are stratified or adjusted for spatial and seasonal effects.

Although tuna and billfish are considered highly migratory species, Hilborn and Sibert (1986) pointed out that most tagged tuna and billfish move relatively small distances. The median lifetime displacement of yellowfin tuna, for example, is about 340–380 nautical miles (Sibert and Hampton 2003). Tracking studies show that most yellowfin and bigeye tuna reside for several months in the vicinity of bathymetric features, such as seamounts, and fish aggregating devices (FADs; Itano and Holland 2000; Musyl et al. 2003). There is also evidence of local depletion of swordfish in several

longline fisheries (Ward et al. 2000) and reports of the disappearance of large yellowfin tuna (called “home guards”) around reefs or seamounts off California and south-eastern Australia. Testing the Local Depletion Hypothesis requires fine-scale data on movement rates and patterns, growth rates, fishing and natural mortality rates, and the distribution of fishing effort and targeting practices.

Hypothesis 5: Learning

Catch rates may have declined because animals have learnt to avoid longline fishing gear. García et al. (1974) identified 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., Atlantic cod (*Gadus morhua*; Mackay 1977). The effect of learning on catchability in the wild is unknown, but laboratory studies suggest that it may be significant (Brown and Warburton 1999).

Encounters with longlines have probably increased since the 1950s with increased fishing effort, although this is partly offset by the size-dependent reductions in search volume described in Chapter 7. Analyses of missing branchlines suggest that a significant proportion of animals escape from longlines. Catchability might decline if those animals remember to avoid longline baits. Tracking studies, for example, often show abnormal behaviour among marlin in the first few days after release (Orbesen et al. 2005), indicating that they do respond to the stress of being hooked or being tagged, albeit for brief periods. On the other hand, recreational tagging data shows that 1% of tuna (N = 398), 2% of marlins (N = 755), and 8% of mako shark (N = 144) recaptures are made within 24-hours of release (Mr. Tim Park, pers. comm., 12 October 2005). This implies that some pelagic animals, particularly mako sharks, do not learn to avoid baited fishing gear. Fishers and observers often report catches of sharks that have several hooks from past longline encounters embedded in their jaws.

Hypothesis 6: Schooling

The behaviour of fishers interacting with a species' aggregating behaviour may result in catch rates deviating from a linear function of abundance. Hyperstability occurs when searching by fishers is highly efficient and target species concentrate in schools, shoals,

or other aggregations¹², e.g., purse seining for clupeids. Nominal catch rates consequently remain high while abundance declines. Hyperdepletion is where catch rates decline more rapidly than abundance. It occurs in situations where fishers initially fish-down a small yet highly vulnerable component of the stock, then expand to more dispersed components, e.g., initial harvesting of high densities of rock lobsters (*Jasus* spp.) on reefs followed by harvesting of lower densities in other habitats (Hilborn and Walters 1992). Swartzman (1991) predicted that decreased abundance will alter the size-composition of schools, but will only affect the number of schools through the removal of large animals. School sizes of sardine off Senegal declined with increasing fishing effort (Fréon and Misund 1999).

Size-selective schooling is widespread among fish (Hoare et al. 2000). Tuna often school with conspecifics and other tuna species of the same size. Even large tuna, like 50 kg yellowfin, form schools of similarly sized animals (Dagorn et al. 1997). Several authors note that catches along a longline have a contagious distribution, indicating that longlines encounter schools of tuna and billfish (Murphy and Elliot 1954; Maéda 1967; Kirby et al. 2003). I hypothesise that catch rates were initially high in the 1950s because longliners harvested multi-species schools of large pelagics. Fishing then reduced the populations to a density threshold at which they no longer aggregated. This reduced availability resulted in significantly lower catch rates as longliners began to harvest more dispersed individuals.

To explore the Schooling Hypothesis, historical time-series of data on the size-and species composition, school size, and frequency of schools could be assembled from existing literature and reports. Dell (2004), for example, found significant trends in body-size and school metrics of small (5–30 kg) southern bluefin tuna taken by pole-and-line fishing gear during 1960–2003. He attributed those trends to a decline in the abundance of juvenile southern bluefin tuna since 1960. In the 1950s, large Atlantic bluefin tuna formed substantial feeding aggregations off Norway that were exploited by purse seine (Tiews 1978).

¹² Shoals, aggregations and schools describe similar patterns, but may have different causes and functions (Kirby et al. 2003). I use “schools” to refer to all three patterns.

Broadhead and Orange (1960) concluded that the size of yellowfin tuna schools did not decline with abundance. However, their study might not reflect the true effects of reduced density because it was undertaken during the late 1950s when exploitation rates were relatively low (Dagorn et al. 1997). Shomura and Murphy (1955) found that increasing the density of hooks along survey longlines elevated the catch per yellowfin tuna school by about 20% (Murphy 1960). That experiment could be repeated to determine whether the frequency and size of schools encountered by longlines has varied since the 1950s. Kirby et al. (2003), for example, analysed fine-scale longline data in New Zealand during 1993–98. He concluded that several tuna and billfish species formed schools or aggregations with a nearest neighbour distance of 100–200 m. Note, however, that the prolonged soak times of longlines, their broad depth range, and the high swimming speeds of most pelagic species pose problems for estimating school size and distribution from longline data. The use of time-depth recorders (TDRs) would mitigate the problems of longline depth and soak time (Kirby et al. 2003). Testing of the Schooling Hypothesis for pelagic species would also require further exploration of the functions of schooling, the relationship between abundance and school metrics, and the factors influencing their formation, e.g., the distribution of prey.

Hypothesis 7: Regime Shift

Broad-scale oceanographic events, such as the El Niño – Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO), affect global weather, oceanography and productivity, and the ecology of animal communities (Polovina 1996; Lehodey 2001; Worm 2005). Chapter 8 acknowledged that such events influence the abundance of pelagic species through recruitment, variations in productivity, and the catchability of longline gear. The term regime shift is also used for switches between ecosystem states, e.g., a system dominated by top-down processes switching to one dominated by bottom-up processes (Krebs 1978).

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 responses to bait, which depends on the animal's feeding history and environment. Stoner concludes that temperature, illumination, current direction, and current velocity have the greatest

impacts on catchability. Chapter 8 did not consider the effects of oceanographic variables that are commonly associated with variations in fish populations because those variables did not vary noticeably between the early 1950s and late 1990s in the study area. For other periods, historical variations in environmental conditions may be significant and their effects should be included in effort standardization. Regardless, care is required in considering environmental effects because they may affect abundance rather than catchability, whereas abundance is the signal of interest to stock assessments (Kleiber and Yokawa 2002).

Discussion and Conclusions

The historical variations in pelagic fish communities, which are evident in the time-series of commercial catch and effort data and in the analyses presented in Chapter 8, have six fundamental characteristics:

1. magnitude (corrected longline catch rates of most large predators declined by about 90%)
2. rate (the catch rates declined to low levels within about 10 years of longline fishing commencing)
3. stability (the corrected catch rates were static in subsequent years)
4. body-size (the average body-size of large predators declined in longline catches, whereas small species increased or did not change in size)
5. diversity (the declines involved large tuna, billfish, and sharks that have diverse life histories, habitats, and behaviour)
6. asynchrony (the declines coincided with the commencement of industrial-scale longline fishing, but did not occur at the same time in each ocean basin or region)

I scored the seven hypotheses outlined earlier against each of the six characteristics listed above (Table 9.1). To be plausible, hypotheses must be consistent with all six characteristics. Schooling and removal of an accumulated biomass are the only hypotheses that are consistent with—or at least not ambiguous across—all six characteristics. Except for Regime Shifts, the other hypotheses are not consistent with the diversity of species involved in the variations. Further evidence relevant to each hypothesis is discussed below.

Table 9.1. Summary of hypotheses that may explain the variations in pelagic fish communities. Hypotheses are scored against six characteristics of the variations. The Learning Hypothesis, for example, is consistent with the magnitude of the declines and is given a “+” for that characteristic. This hypothesis scores a “–” for diversity because it is unlikely that the diverse array of species would show the same ability to learn to avoid longline fishing gear.

Hypothesis	Characteristic ^a					
	Magnitude	Rate	Stability	Size	Diversity	Asynchrony
Accumulated biomass	+	+	+	+	o	+
Schooling	+	+	o	+	o	+
Local depletion	+	+	o	+	–	+
Learning	+	+	o	+	–	+
Sub-populations	+	o	+	o	–	+
Regime shift	+	+	o	o	o	–
Artificial selection	+	–	+	o	–	+

^aPlausibility scores:

- + hypothesis is consistent with characteristic
- o support for hypothesis is unclear or ambivalent
- hypothesis is not consistent with characteristic

In addition to being inconsistent with the diversity of species involved in the community variations, Local Depletion contradicts the theory of density-dependent habitat selection. Density-dependent habitat selection is a mechanism where members of a population saturate the ideal habitats or ‘blocks’. When population size increases, the excess stock overflows into adjacent blocks. Catch rates are low on the fringes when population size declines, although density remains at saturation levels in the ideal habitats. The population’s range will expand and contract with variations in population size, but optimal density will be maintained in core habitats (MacCall 1990). The expansion of a population’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; Hilborn and Walters 1987). Densities and thus catch rates would fluctuate with the range of the population if fishing occurred outside the core areas, and there are other situations where density may change proportionally throughout the population’s range (Myers and Stokes 1989). Furthermore, density-dependent habitat

selection will be difficult to detect in situations where there are multiple populations or if core areas are unsaturated (Shackell et al. 2005). Nevertheless, local depletion is unlikely for the diverse assemblage of pelagic species taken by longline, which range from landmass-associated sharks (e.g., dusky shark, *Carcharhinus obscurus*) to highly mobile tuna species (e.g., yellowfin tuna) with very different geographical distributions and habitat preferences.

Likewise, the Artificial Selection Hypothesis was not consistent with the diversity of species involved in the community variations. Miller (1959) highlights many examples of vertebrate populations that have undergone catastrophic declines, yet show no apparent genetic change. Since Miller's review, clear evidence of selection for life-history traits, such as size at maturity, has emerged for both wild and captive populations (Heino and Godoe 2002). Long-lived species, such as sharks, should evolve more slowly than species, like skipjack tuna, that have shorter generations times. I would therefore expect different rates of evolution among the diverse species involved in the community variations.

Although there is clear evidence of oceanographic regime shifts along a range of spatial and temporal scales in the open ocean (Polovina 1996; Steele 1998; Anderson and Piatt 1999), this hypothesis is not consistent with the asynchrony of the variations in different ocean basins or regions. Chapter 8 reviews evidence of regime shifts causing the community variations. In brief, there was no obvious difference between periods in several oceanographic indices that are often associated with variations in productivity and fish distribution. Furthermore, it is unclear how variations in oceanographic conditions or productivity would result in the observed patterns in body-size variations in this diverse group of large predators and small species.

Chapter 8 did not consider variations in the vertical dimension of the habitat because thermocline depth did not vary significantly in the study area between the 1950s and 1990s (Ward and Myers 2005c). However, Chapter 6 showed that availability is likely to be more complex than that suggested by a simple metric, such as thermocline depth. Information on each species' vertical and horizontal extent would be relatively simple—though expensive—to gather through surveys of unfished areas combined with commercial catch data.

The seven hypotheses reviewed here are not mutually exclusive. Animals learning to avoid longlines, for instance, would not preclude artificial selection. Furthermore, there are other hypotheses that might explain the community variations, e.g., pollution, environmental effects on larval mortality, and competition among fishing gears.

Empirical studies that track changes in the abundance and composition of pelagic communities are required to verify predator release. Unfortunately data are rarely collected on pelagic communities when those communities are first exploited (Jackson et al. 2001). Mass-balance ecosystem models, such as *EcoSim*, hold potential for exploring community responses to the removal of large predators (Pauly et al. 2000).

Predator release—which can cause increases in the abundance of prey in response to reductions in the abundance of their predators—is a likely consequence of the observed variations in the pelagic communities, regardless of the causes of those variations. Foerster and Ricker (1941), for example, reported increased survival rates of juvenile sockeye salmon (*Oncorhynchus nerka*) in a lake as a result of decreased predator abundance. Their survival rates declined when the predator populations recovered. Merrick (1997) suggests that the overharvesting of whale and seal populations in the Bering Sea may have resulted in an increase in the population sizes of their prey, e.g., walleye pollock (*Theragra chalcogramma*). Predator–prey interactions will be more complex in the open ocean because of omnivory, spatial and temporal heterogeneity in interactions, trophic levels consisting of many species, and cultivation effects (Walters and Kitchell 2001). The removal of large predators from the pelagic community may have reduced mortality rates among juveniles of many species. This would result in the increased abundance of small animals that maintained longline catches. Those animals would include small, highly productive tuna and billfish that sustained subsequent longline catches.

Conclusions

I have presented evidence of significant historical variations in pelagic fish communities. The variations are characterized by substantial declines in the abundance and the size composition of apex predators, including large tuna, billfish, and sharks. Those indices reached low levels within about 10 years of the commencement of industrial-scale longline fishing. The community variations did not occur at the same time in different ocean basins or regions.

Pelagic longline fishers have continuously modified their fishing gear and practices to improve fishing power and catchability, which has altered the relationship between catch rates and abundance. Advances in technology resulted in the introduction of many electronic devices to assist in navigation, communication, and finding target species. The development of synthetic materials allowed improvements to lines and hooks that increased the probability of hooking target species and landing them. Other changes increased fishing power by improving searching efficiency (e.g., satellite imagery, fleet fishing) or the time spent on fishing grounds (e.g., freezers).

The number of hooks deployed in daily longlining operations has steadily increased since 1950. However, soak time did not change significantly because faster longline retrieval and deployment speeds balanced the increased hook numbers. There has been a shift from having all baits available at dawn to having more available at dusk and at night. In the 1970s, several longline fleets began to exploit a much greater depth range, resulting in increased catchability for deep-dwelling species (e.g., bigeye tuna) and reduced catchability for epipelagic species like blue marlin. The information on gear and practices suggest significant increases in fishing power and catchability that will result in the overestimation of abundance since longlining commenced. Progressive improvements in expertise and technological improvements in the gear will also affect fishing power, but are particularly difficult to quantify.

Hook depth, bait species, the local abundance of tuna, and the timing of longline operations strongly influenced the rate that bait was lost from pelagic longlines. Loss rates rose with increased tuna abundance and soak time. They declined with hook depth

and were low for firm-bodied bait, such as squid. Many longliners began targeting bigeye tuna with deep longlines in the mid 1970s and have used squid bait since the 1980s. This may have resulted in significant variations in fishing power, with important implications for the estimation of abundance from catch and fishing effort data.

Analyses of observer records of the time when each animal was brought on board longliners revealed that abundance estimates are strongly influenced by soak time and the timing of longline operations in relation to dawn and dusk. Longline catch data will underestimate the total mortality of several species because the animals fall off, are removed, or escape from the hook. For example, longline hooks with soak times of 20 hours were retrieved with fewer skipjack tuna and seabirds than hooks with soak times of 5 hours. The mortality of some seabird species is up to 45% higher than previously estimated.

The effects of soak time and timing of operations vary considerably between species. Soak time and exposure to dusk periods have strong positive effects on the catch rates of many species. In particular, the catch rates of most shark and billfish species increase with soak time. At the beginning of longline retrieval, for example, swordfish catch rates are four times those at the end of retrieval.

Survival of the animal while it is hooked on the longline is likely to be an important factor determining whether it is eventually brought on board. Catch rates of species that survive being hooked (e.g., blue shark) increase with soak time. In contrast, seabirds are usually dead at the time of retrieval. Their catch rates decline with time, probably because scavengers can easily remove small, hooked animals that are dead.

The results have important implications for fishery management and assessments that rely on longline catch data. A reduction in soak time since longlining commenced in the 1950s has introduced a systematic bias in estimates of mortality levels and abundance. The abundance of species like seabirds will have been over-estimated in recent years. Simple modifications to data collection, such as recording the number of hooks retrieved without baits, would greatly improve mortality estimates.

I introduce a new method that uses generalized linear mixed models to infer the depth distribution of pelagic fishes. It uses existing data from research surveys and observers on commercial vessels to estimate changes in catchability when longline

fishing gear is lengthened to access deeper water. The depth distribution of catchability is presented for 37 fish species that are caught on pelagic longlines in the Pacific Ocean. I show how the estimates of catchability can be used to correct abundance indices for variations in longline depth. The method facilitates the inclusion of data from early surveys in the time series of commercial catch rates used to estimate abundance. It also resolves inconsistencies in the time series caused by a rapid switch to deep longlining in the 1970s. The catchability distribution does not always match depth preferences derived from tracking studies. Therefore, depth preferences from tracking studies should not be used to correct abundance indices without additional information on feeding behaviour.

Other researchers have used habitat models to correct estimates of fish abundance derived from pelagic longline fishing gear. Those models combine information on hook depth with the species' preferences for ambient environmental conditions to adjust the gear's catchability. I compared depth distributions of bigeye tuna catch predicted by a habitat model with distributions derived from data collected by observers on longliners in the tropical Pacific Ocean. My analyses show that the habitat model does not accurately predict the depth distribution of bigeye tuna; its predictions are worse than those from models that assume no effect of depth on catches. Statistical models provided superior fits to the observed depth distribution. The poor performance of the habitat model is probably due to (1) problems in estimating hook depth; 2) fine-scale variations in environmental conditions; 3) incomplete knowledge of habitat preferences, and (4) differences between the distribution of bigeye tuna and their vulnerability to longline gear.

I quantified the effects of 13 variables on the catchability of pelagic longlines that 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 large sharks, 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, increased substantially as a result of the extension of longline depth and duration, combined with improved materials, bait, and skipper experience. Ideally, fishery independent methods

should be used to verify the relationship between longline catch rates and animal abundance, e.g., acoustic surveys. Nevertheless, my analyses did not reveal anything unique about longline gear or pelagic animals that would explain the rapid decline in catch rates soon after longlining commenced.

I used these insights into the relationship between longline catch, effort, and abundance to quantify variations in the pelagic fish community of the tropical Pacific Ocean. This involved comparisons of recent data collected by observers on longline fishing vessels with data from a 1950s scientific survey when industrial fishing commenced. A major shift in size composition and indices of species abundance and community biomass accompanied the start of fishing. The largest and most abundant predators, such as sharks and large tuna, showed the greatest declines in abundance (21% on average). They also showed striking reductions in mean body-mass. For example, the mean mass of blue shark was 52 kg in the 1950s compared to 22 kg in the 1990s. The estimated abundance of this species was 13.4% of that in the 1950s. Overall, the biomass of large predators fell by a factor of ten between the periods. By contrast, several small and rarely caught species increased in abundance, e.g., pelagic stingray. However, the increases in the biomass of small species did not balance the reductions in the biomass of large predators.

There are various hypotheses that may explain the historical variations in pelagic animal communities, and more will emerge as further insights are gained into the biology of pelagic species, their ecological relationships, and their interactions with fishing gear. Pelagic fish communities have changed, perhaps as a result of removal of an accumulated biomass or reduced schooling, yet longline fishers have adapted and maintained catch rates by improving their fishing gear, practices, communication, and knowledge.

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Estimates of Depth Distribution Parameters Derived from Pelagic Longline Data¹³

We used generalized linear mixed effect models with a Poisson distribution to model the mean catch μ of each species or species group in longline operation i at depth D . The model predicted the mean catch using a log link:

$$\log(\mu_{i,D}) = \lambda_i + \gamma_1 D + \gamma_2 D^2 + \gamma_3 D^3 + \log(H_{i,D})$$

where the “offset” $H_{i,D}$ is the number of hooks deployed at depth D in longline operation i , and λ_i is the random effects distribution for the species in operation i (we assumed that the log abundance of the species encountered by each operation follows a normal distribution). The regression coefficients γ_j describe how the species’ catchability varies with depth. For each species, we used the GLIMMIX macro in SAS (version 8.0) to fit the models separately to day (Table A1.1) and night longlining operations (Table A1.2). We also investigated the alternative assumption of extra-binomial variation, which gave very similar results to the Poisson distribution. We report only the Poisson results because they are simpler to interpret.

¹³ This Appendix was originally published as: Ward, P., and Myers, R.A. 2005. Appendix A. A method for inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of longline fishing gear. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 1130–1142.

Table A1.1. Parameter estimates and the number of each species or species group modelled for day longlining operations (standard errors of each estimate are in parentheses).

Common name	Number	Parameter			
	modeled	λ	γ_1	γ_2	γ_3
Tunas and tuna-like species					
Albacore tuna	2 777	−6.47 (0.04)	9.44 (0.43)	−20.34 (1.39)	13.81 (1.34)
Bigeye tuna	2 980	−6.44 (0.05)	7.83 (0.48)	−12.25 (1.45)	7.20 (1.33)
Skipjack tuna	2 771	−5.38 (0.06)	−0.09 (0.63)	−9.69 (2.12)	10.97 (2.10)
Wahoo	528	−5.68 (0.14)	−6.88 (2.51)	4.46 (12.34)	4.95 (15.94)
Yellowfin tuna	3 131	−5.48 (0.04)	1.73 (0.39)	−6.05 (1.35)	5.32 (1.37)
Billfishes					
Black marlin	225	−6.06 (0.25)	−9.48 (4.28)	22.77 (19.67)	−16.81 (23.33)
Blue marlin	1 902	−5.81 (0.08)	−3.77 (1.06)	1.83 (3.78)	1.86 (3.89)
Sailfish	402	−5.81 (0.14)	148.00 (2.22)	8.61 (9.28)	2.61 (10.43)
Shortbill spearfish	2 477	−4.79 (0.07)	−7.95 (0.84)	4.31 (2.97)	3.34 (3.03)
Striped marlin	2 726	−5.11 (0.06)	−3.82 (0.77)	−2.30 (2.62)	6.29 (2.61)

Common name	Number modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Swordfish	1 277	-6.94 (0.14)	2.74 (1.61)	-11.45 (5.38)	11.84 (5.24)
Other teleosts					
Barracudas	240	-5.45 (0.20)	-19.17 (3.87)	47.12 (19.04)	-32.90 (23.27)
Escolar	266	-6.71 (0.19)	8.72 (3.24)	-21.67 (16.64)	6.73 (24.41)
Great barracuda	102	-4.91 (1.44)	-8.86 (33.83)	-45.90 (232.52)	178.29 (482.91)
Lancetfishes	358	-6.20 (0.15)	9.50 (2.22)	-30.57 (9.56)	31.86 (11.61)
Longnosed lancetfish	46	-6.27 (0.81)	-20.84 (16.97)	93.31 (92.41)	-74.91 (136.92)
Mahi mahi	349	-4.41 (0.18)	-25.17 (4.32)	86.37 (29.58)	-108.34 (58.60)
Oilfish	254	-7.72 (0.30)	9.58 (4.95)	-29.23 (24.06)	25.94 (32.87)
Opah	197	-8.24 (0.33)	8.81 (4.78)	-0.74 (20.18)	-17.56 (24.37)
Pomfrets	179	-6.95 (0.31)	6.69 (4.92)	-29.87 (21.93)	38.71 (26.09)
Shortnosed lancetfish	53	-7.41 (0.45)	-2.93 (6.33)	51.76 (27.49)	-70.62 (35.01)

Common name	Number modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Sickle pomfret	20	-8.87 (1.08)	20.50 (17.01)	-73.37 (79.15)	102.60 (106.75)
Snake mackerel	102	-6.34 (0.33)	-11.78 (6.06)	63.10 (30.00)	-72.36 (42.00)
Sharks and rays					
Bigeye thresher shark	956	-8.08 (0.21)	7.88 (1.98)	-12.95 (5.69)	8.52 (4.98)
Blue shark	3 050	-5.43 (0.05)	0.35 (0.52)	-0.77 (1.68)	-0.16 (1.62)
Common thresher shark	30	-7.67 (1.52)	-2.40 (27.45)	59.64 (149.25)	-135.85 (247.22)
Crocodile shark	384	-7.79 (0.30)	7.17 (3.18)	-18.88 (9.83)	16.39 (9.14)
Dusky shark	54	-4.55 (0.57)	-19.05 (7.22)	47.48 (25.06)	-35.91 (25.48)
Grey reef shark	25	-6.51 (0.56)	3.43 (16.68)	-46.59 (130.00)	101.53 (283.53)
Long-finned mako shark	153	-6.00 (0.29)	-6.66 (4.00)	9.83 (14.42)	-1.46 (14.66)
Oceanic whitetip shark	1 910	-4.92 (0.07)	-9.85 (0.97)	11.61 (3.48)	-2.09 (3.56)
Pelagic stingray	356	-5.85 (0.15)	-9.97 (2.65)	28.78 (12.82)	-24.50 (16.14)

Common name	Number modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Short-finned mako shark	665	-6.14 (0.18)	-9.11 (2.33)	26.32 (8.22)	-22.57 (8.45)
Silky shark	1 019	-5.17 (0.08)	-3.56 (1.00)	-4.43 (3.76)	9.90 (4.02)
Silver-tip shark	29	-6.34 (0.66)	12.75 (15.51)	-162.55 (105.60)	407.47 (211.62)
Tiger shark	34	-5.03 (0.69)	-27.92 (10.81)	91.35 (43.29)	-87.35 (49.00)
Whip stingray	19	-2.69 (0.86)	-75.92 (15.42)	298.97 (64.83)	-322.17 (76.22)

Table A1.2. Parameter estimates and the number of each species or species group modelled for night longlining operations (standard errors of each estimate are in parentheses).

Common name	Number modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Tunas and tuna-like species					
Albacore tuna	1 267	-4.92 (0.17)	-3.99 (2.17)	14.44 (8.43)	-13.26 (9.83)
Bigeye tuna	1 819	-5.53 (0.07)	-1.50 (1.00)	8.32 (4.10)	-7.84 (4.76)
Skipjack tuna	241	-5.63 (0.26)	-10.47 (4.74)	39.32 (24.12)	-44.72 (34.83)
Wahoo	122	-6.12 (0.29)	-3.83 (8.24)	-12.18 (64.44)	59.35 (128.00)

Common name	Number modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Yellowfin tuna	1 417	-5.00 (0.07)	-7.97 (1.14)	25.43 (5.58)	-25.02 (7.89)
Billfishes					
Black marlin	98	-5.57 (0.24)	-21.65 (8.46)	151.63 (77.45)	-310.27 (189.09)
Blue marlin	593	-5.70 (0.10)	-7.35 (1.91)	24.06 (9.64)	-22.96 (13.05)
Sailfish	148	-6.19 (0.21)	1.58 (5.16)	-39.99 (34.39)	69.81 (47.04)
Shortbill spearfish	269	-6.56 (0.29)	-0.08 (4.34)	8.10 (18.86)	-16.20 (23.66)
Striped marlin	743	-6.35 (0.16)	0.88 (2.37)	6.05 (10.39)	-12.54 (13.72)
Swordfish	2 332	-6.22 (0.07)	16.38 (0.95)	-47.07 (3.54)	39.58 (3.87)
Other teleosts					
Escolar	107	-6.55 (0.28)	6.57 (5.19)	-28.51 (26.10)	37.79 (35.79)
Mahi mahi	157	-6.09 (0.23)	3.88 (5.65)	-48.80 (37.60)	74.12 (51.85)
Oilfish	96	-6.25 (0.43)	-17.73 (14.76)	268.21 (144.36)	-854.80 (410.20)
Pomfrets	35	-6.58 (0.54)	-5.46 (13.57)	75.28 (99.03)	-177.15 (195.89)

Common name	Number modeled	Parameter			
		λ	γ_1	γ_2	γ_3
Shortnosed lancetfish	7	-4.76 (1.18)	-32.04 (17.98)	145.64 (69.78)	-168.07 (79.16)
Snake mackerel	113	-5.99 (0.29)	-6.92 (9.85)	48.80 (95.07)	-133.89 (243.15)
Sharks and rays					
Bigeye thresher shark	139	-6.58 (0.29)	-1.20 (4.43)	10.49 (18.75)	-16.13 (22.29)
Blue shark	2 444	-5.00 (0.07)	5.79 (0.84)	-19.62 (3.15)	17.38 (3.34)
Crocodile shark	84	-6.55 (0.40)	1.44 (5.97)	-4.02 (24.39)	4.66 (27.48)
Oceanic whitetip shark	494	-4.97 (0.11)	-17.14 (2.39)	66.41 (14.78)	-77.27 (26.39)
Pelagic stingray	204	-6.00 (0.24)	-5.54 (6.86)	43.57 (56.22)	-119.38 (127.20)
Short-finned mako shark	388	-5.74 (0.20)	-13.66 (3.31)	58.33 (16.64)	-66.17 (24.42)
Silky shark	362	-4.99 (0.12)	-3.90 (2.71)	3.82 (19.07)	-5.10 (30.97)

Estimates of Change in the Catchability of Pelagic Longline Fishing Gear

Data Sources and Estimation

The sources of data used to estimate relative catchability are listed in Table A2.1. I used generalized linear models to estimate the effects of several variables on catchability. The models were implemented in S-Plus (version 6.1) using *glm*, *glmmPQL*, and *glm.nb* from library MASS (Venables and Ripley 1999). Model selection was based on residual deviance and stepwise regression using Akaike's information criterion (AIC). The residual deviance measures the amount of variation in catch that is not explained by the model. The AIC is based on the model's log-likelihood and number of parameters (Venables and Ripley 1999). Model selection explored various error distributions (e.g., Gaussian, Poisson and negative binomial), combinations of variables and interaction terms, and linear, quadratic, and cubic forms of each variable. I used the MASS function *predict.gam* to predict catch rates of each species in each period.

The variance of catchability change was estimated from the formula presented by Kendall and Stuart (1977):

$$\text{var}(\Delta q) = \frac{\text{var}(U_{1990})}{U_{1950}^2} + U_{1990}^2 \frac{\text{var}(U_{1950})}{U_{1950}^4}$$

where U_{1950} is the catch rate in the 1950s, U_{1990} is that in the 1990s, and relative catchability q is assumed to be independent in each period.

Area of Action and Abundance

Animal's Movement Patterns

I combined body-size – velocity relationships with size data from each period to estimate changes in catchability. Simulations by Ware (1978) show that the volume of water searched is a function of the animal's swimming speed. The search volume increases in proportion to body length L raised to the power of 2.6 (Ware 1978). For each species I estimated the mean search volume V from the length of each animal reported in the 1950s POFI survey and 1990s Hawaii observer data, raised by Ware's constant (Table A2.3):

$$V = \frac{\sum_{i=1}^n L_i^{2.6}}{n}$$

where n is the number of animals measured. The change in relative catchability Δq is the ratio of the search volumes in each period:

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

Depth of Gear

Ward and Myers (2005a) used a generalized linear mixed effects model to estimate the depth distribution of catchability from longline observer data in the tropical Pacific Ocean. For each species, $f(D_i)$ represents the effect of depth D on relative catchability for hook number i :

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

where α and the γ_j are parameters that Ward and Myers estimated for the species. I then inferred the daytime depth distribution of catchability for each species for longline configurations typical of each period (Table A2.2). The depth of each longline hook was estimated from a catenary formula (Suzuki et al. 1977) and reduced by 25% for the effects of currents (Ward and Myers 2005a). The longline configuration is almost always identical between buoys, so the number of depths that needs to be considered for each configuration is the number of hooks between buoys. The catchability change Δq between periods is then:

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

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

Fish-finding Equipment

My approach to estimating the effects of such equipment was based on the argument that owners would install the equipment when they expected the financial return to exceed the cost of the equipment. I estimated the annual cost of electronic equipment for a typical longliner (Table A2.10), then calculated the proportional increase in catch rates required

to cover those costs (Table A2.11). The value of the catch of each 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 each year H (878 802 hooks; Reid et al. 2003). The longliner's operating profit R is then the summation of the market value of all species minus total costs C :

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

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

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

Skipper Experience

The 1990s Australian observer data included the number of years of longlining experience for 82 fishing masters over 307 daily longlining operations. Using generalized linear models with a log-link and Poisson error distribution, I modeled the number of a species caught C in each longlining operation j as a function of experience, fishing effort, and a combination of other variables that influence catches:

$$\log(C_j) = \beta_0 + \beta_1 M_j + \beta_2 A_j + \beta_3 O_j + \beta_4 S_j + \beta_5 D_j + \beta_6 D_j^2 + \beta_7 T_j + \beta_8 T_j^2 + \beta_9 X_j + \log(h_j)$$

where M_j is the month, A_j is the latitude, O_j is the longitude, S_j is the time of longline deployment, D_j is the number of hooks per buoy (a commonly used index of longline depth range), T_j is the years of experience fishing for yellowfin tuna or bigeye tuna, X_j is the years of experience fishing for southern bluefin tuna, and h_j is the number of hooks deployed in each operation j . The β_k are estimated parameters.

I used the model to predict catch rates for each species in the 1950s and the 1990s, with only the years of experience modified between periods. I did not obtain data on the years of experience of fishing masters in the 1950s, but believed they were relatively inexperienced because the Japanese did not longline in the study area before 1950 and because of the lapse in activity in most other areas during the 1940s. I arbitrarily used a value of two years of experience to predict 1950s catch rates.

Operation Time

Ward et al. (2004) used mixed 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 catch yellowfin tuna in the South Pacific Ocean show that hooks available during crepuscular periods had particularly high catch rates of bigeye tuna and blue marlin. By contrast, skipjack tuna catch rates were highest outside those periods. Crepuscular periods did not strongly affect catch rates of mako shark or yellowfin tuna. For each species I used the model of Ward et al. (2004) to predict the catch rates for the dawn and dusk exposure of hooks of a typical longline in each period (Table A2.4). I estimated the catchability change as the catch rate predicted for a typical 1950s operation divided by the mean catch rate predicted for 1990s operations.

Availability of Baited Hooks

Bait Loss

I used the Generalized Estimating Equations of Ward and Myers (submitted) to estimate the change in fishing power due to variations in bait loss between the 1950s and 1990s. Loss rates were predicted for operational details (e.g., location, soak time, hook depth, and bait species) that were typical of Japan's longliners operating in the study area in each period.

Gear Saturation

For each period I estimated the catch rate U_{0i} of each species i in the absence of all other species (Rothschild 1967):

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

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 I estimated relative catchability q_i :

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

and estimated the catchability change Δq between periods due to saturation:

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

The proportions of vacant and occupied hooks were from Japanese five-degree data (Table A2.10). For each species I derived the proportion of occupied hooks from the mean catch rate over all five-degree – month – year cells. The proportion of vacant hooks Q_0 was 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 I divided the total catch by 0.67, which was the proportion of tunas and billfishes in the total catch of the 1950s POFI survey. To estimate catches of mako shark, which were not reported by Japan's longliners, I multiplied the proportion of mako shark in the POFI survey (0.004) by the total number of all species estimated for each cell.

For the 1990s I estimated the other species catch as the marlin, swordfish, and tuna catch divided by 0.75, which was the proportion of those species reported in the 1990s Japanese survey data. To estimate catches of skipjack tuna and mako shark, which were not reported by Japan's longliners, I multiplied the proportion of skipjack tuna (0.035) and the proportion of mako shark (0.009) in the surveys by the total number of all species estimated for each cell.

Detection

Detection of Gear

I estimated the effect of branchline material on catchability from the results of an experiment by Stone and Dixon (2001), which is described in Chapter 8. Stone and Dixon did not estimate an effect for bigeye tuna, skipjack tuna, or blue marlin (Table A2.7). I used their swordfish estimate for bigeye tuna because adult bigeye tuna and swordfish inhabit similar ecological niches. For similar reasons, I used the white marlin estimate for blue marlin. I applied those estimates to the proportion of monofilament branchlines deployed in the tropical Pacific in the 1950s (0%; Shimada 1951) and the 1990s Australian observer data (85%).

Attraction to Baits

Hunger

Stillwell and Kohler (1982) estimated that the daily food ration for mako shark was about $27.9 \text{ g kg}^{-1} \text{ d}^{-1}$ for routine metabolism. To compensate for energy expended during active metabolism (e.g., foraging and migration), they predicted that daily ration would increase by at least 25–50% (3.47–4.27% of body weight). To obtain an index of feeding motivation for mako shark, I multiplied the midpoint of the daily ration (3.88%) by individual body-mass in the 1950s POFI survey and 1990s Hawaii observer data. The catchability change was then the mean 1990s index divided by the 1950s mean. I used estimates of daily ration presented by Menard et al. (2000) for skipjack tuna, bigeye tuna, and large (>90 cm) yellowfin tuna from free-swimming schools. For blue marlin I used estimates from Junior et al. (2004).

Competition among Gears

I estimated the distance between hooks from the catenary formula (Suzuki et al. 1977) and the dimensions reported for longlines in each period. I also used the POFI survey data to compare catch rates of distal hooks with those from the next closest buoy. Distal and nearby hooks will have almost identical soak times, depth ranges, and local abundance of animals. A Fisher exact test indicated that there was no significant difference in the catch rates of distal hooks and those of those of nearby hooks (Table A2.14).

On a larger scale, I inferred the effects of gear competition on catchability as the difference between catch predictions of a cubic model and a linear model. My cubic model was a generalized linear model with a log-link and Poisson error distribution, with the number of bigeye tuna caught C in each cell j of the global five-degree data modeled as a function of fishing effort and other variables that influence catches:

$$C_j = \beta_0 + \beta_1 Y_j + \beta_2 M_j + \beta_3 A_j + \beta_4 O_j + \beta_5 N_j + \beta_6 D_j + \beta_7 D_j^2 + \beta_8 D_j^3 + \beta_9 H_j + \beta_{10} H_j^2 + \beta_{11} H_j^3$$

where Y_j is the year, M_j is the month, A_j is the latitude, O_j is the longitude, D_j is the number of hooks per buoy, and H_j is the number of hooks deployed in each cell j in the study area. I developed a time-series of the number of hooks per buoy from published and unpublished reports. Monthly population abundance N_j is the number of bigeye tuna

predicted by an age-structured stock assessment model (Hampton et al. 2005a) for the region that approximates my study area. The β_k are estimated parameters.

My linear model was identical to the cubic model, but it did not include the quadratic H_j^2 and cubic H_j^3 terms and it excluded cells where fishing effort exceeded the effort corresponding to the maximum catch predicted by the cubic model. Catchability change was the ratio of catches predicted by the linear model C_{linear} and the cubic model C_{cubic} at the mean monthly 1990s level of fishing effort (213 527 hooks per cell):

$$\Delta q = \frac{C_{cubic}}{C_{linear}}$$

I applied the same method to estimate the effect of gear competition on yellowfin tuna and blue marlin catchability. The effects of gear saturation were not estimated for mako shark or skipjack because abundance estimates were not available for those species.

Bait Type

The 1950s longliners deployed South American pilchard (*Sardinops sagax*) or Pacific saury (*Colalabis saira*) baits almost exclusively (Ego and Otsu 1952; Shapiro 1950). I used 1990s eastern Australia observer data to estimate the effect of bait type on catchability. Those data consist of various combinations of baits, including mackerels (34% of all baits), squid (21%), pilchards (20%), scad (3%) and milkfish (2%). Using generalized linear models with a log-link and Poisson error distribution, the number caught C in each longlining operation j was modeled as a function of bait type, fishing effort, and a combination of other variables that influence catches:

$$\log(C_j) = \beta_0 + \beta_1 A_j + \beta_2 O_j + \beta_3 M_j + \beta_4 S_j + \beta_5 T_j + \beta_6 D_j + \beta_7 K_j + \beta_8 P_j + \beta_9 S_j + \beta_{10} Q_j + \beta_{11} I_j + \log(h_j)$$

where A_j is the latitude, O_j is the longitude, M_j is the month, S_j is the time of longline deployment, T_j is the maximum soak time (minutes elapsing between the commencement of deployment and completion of retrieval), D_j is the number of hooks per buoy, and h_j is the number of hooks deployed in each operation j . The model included the proportion of hooks with the five most frequently used baits: mackerel (K_j), squid (Q_j), pilchard (P_j), scad (S_j), and milkfish (I_j). I fitted the models separately to the data for each species and predicted catch rates for the 1950s combination of baits (all pilchard) and the various combinations of bait types deployed in each operation in the 1990s.

Landing

Breakage

Using 1950s Japanese longline gear, the POFI survey reported a loss rate of 1% of 65 417 branchlines. Anecdotal reports from Australian observers and longline fishers indicated that 2–3% of monofilament branchlines are severed when longlines are retrieved. I used those estimates of branchline loss rate to correct the reported catch rate of mako shark for the number estimated to have bitten through monofilament leaders and escaped:

$$U_j = \frac{C + S_j B_j f}{f}$$

where U_j is the corrected catch rate, S_j is the proportion of mako shark in the total shark catch, and B_j is the branchline loss rate in each period j (Table A2.14). I used the mako shark catch C and fishing effort f from the 1990s Japanese surveys so that variations in abundance did not affect my catchability estimates. The catchability change was the 1990s corrected catch rate divided by that for the 1950s.

Removal by Scavengers

I assumed that loss rates are directly proportional to damage rates reported for the species (Table A2.8). For each species, I estimated the catchability change Δq between periods due to removals by scavengers:

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

where D_{1990s} is the damage rate from the 1990s Australian observer data and D_{1950s} is the rate from the 1950s POFI survey. One is added to each damage rate to represent catches of undamaged animals.

Table A2.1. Datasets used to estimate catchability change. Unless otherwise indicated, analyses were limited to data from the tropical Pacific Ocean study area (20°S–20°N and 140°E–140°W) for the 1950s (1951–55) or 1990s (1995–99).

Dataset name	Period	Target species	Characteristics	Data features	No. of ops	Source	Key reference(s)
POFI survey	1950s	[scientific survey]	26–200 m, daytime, Japanese rope gear with wire leaders	gear details, hook-level catch, effort, operational data, individual lengths, weights, damage	880	Pacific Oceanic Fisheries Investigations (US National Marine Fisheries Service)	Murphy and Shomura (1972)
POFI bait status	1950s	[scientific survey]	[as above]	[as above], details of the status of each hook	208	entered by author from original POFI data sheets	Shomura (1955)
Hawaii observer	1990s	bigeye, yellowfin tuna	27–600 m, daytime, monofilament gear with wire leaders,	gear details, hook-level catch, effort, operational data, individual lengths and damage	505	US National Marine Fisheries Service	http://swr.nmfs.noaa.gov/pir/qreports/qreports.htm
Eastern Australian observer	1990s	bigeye, yellowfin tuna	20–200 m, daytime, monofilament branchlines, one-third with wire leaders, eastern Australian fishing zone (10–40°S, 140–175°E)	gear details, catch, effort, operational data, individual lengths, weights, damage, fishing master experience	307	Australian Fisheries Management Authority	Ward (1996)
Japanese surveys	1992, 1995	[scientific surveys]	70–290 m, daytime, monofilament branchlines	catch, effort, operational summaries for three trips, including east of Hawaii	108	Table A2.3 of Nakano et al. (1997)	Nakano et al. (1997)

Dataset name	Period	Target species	Characteristics	Data features	No. of ops	Source	Key reference(s)
Japanese five-degree	1950s, 1990s	bigeye, yellowfin tuna	20–500 m, night and day, monofilament branchlines, some wire leaders	monthly catch and effort summaries for each 5° latitude-longitude cell	39 485 month – 5-degree cells	Japan's National Research Institute of Far Seas Fisheries	Shimada (1951), Ego and Otsu (1952), Van Campen (1952), Suzuki et al. (1977)
Global five-degree	1950s, 1990s	bigeye, yellowfin tuna	20–500 m, night and day, monofilament branchlines, some wire leaders	monthly catch and effort summaries for each 5° cell (all flags combined)	51 069 month – 5-degree cells	Secretariat of the Pacific Community	http://www.spc.int/oceanfish/html/SCTB/Data/index.asp

Table A2.2. Longline dimensions used to estimate the depth of each hook. Dimensions for the 1950s are from Shapiro (1950) and Shimada (1951). The 1990s dimensions are means derived from 721 day-operations during 1994–2003 (P. Williams, pers. comm.). Depth estimates were derived from a catenary formula (Suzuki et al. 1977) and reduced by 25% for the effects of currents.

Period	1950s	1990s
Number of hooks between buoys	6	18
Buoyline length (m)	20.0	21.7
Branchline length (m)	30.0	24.1
Mainline between buoys (m)	280	726
Distance between buoys (m)	180	502
Minimum depth (m)	66	61
Maximum depth (m)	111	231

Table A2.3. Changes in mean body length L (m; Ward and Myers 2005c), mean volume of water searched per second $L^{2.6}$ (m^3 ; Ware 1978), and catchability change for five species in the study area (standard deviation in parentheses).

Common name	1950s			1990s			Catchability change	
	no.	L	$L^{2.6}$	no.	L	$L^{2.6}$	estimate	p-value
Mako shark	6	1.82	5.15	80	1.46	3.04	0.59	0.78
		(0.41)	(2.46)		(0.37)	(2.13)	(1.43)	
Blue marlin	38	2.13	7.86	421	1.65	3.87	0.49	0.73
		(0.47)	(4.42)		(0.25)	(1.72)	(1.46)	
Bigeye tuna	253	1.52	3.12	2 652	1.27	1.98	0.64	0.66
		(0.22)	(1.04)		(0.22)	(0.79)	(0.82)	
Yellowfin tuna	1 536	1.41	2.49	6 333	1.13	1.45	0.58	0.63
		(0.15)	(0.73)		(0.19)	(0.60)	(0.87)	
Skipjack tuna	135	0.76	0.49	1 168	0.70	0.41	0.83	0.68
		(0.07)	(0.10)		(0.08)	(0.11)	(0.41)	

Table A2.4. Historical changes in mean body-mass (1950s POFI survey and 1990s Hawaii observer data) and mean daily ration. Catchability change is the ratio of mean daily ration between periods (standard deviation in parentheses).

Common name	Daily ration constant source (kg.day ⁻¹ .mass ⁻¹)	1950s			1990s			Catchability change	
		N	mean mass (kg)	daily ration (kg.day ⁻¹)	N	mean mass (kg)	daily ration (kg.day ⁻¹)	estimate	p-value
Mako shark	0.0388 Stillwell (1982)	6	74 (40)	2.9 (1.6)	80	40 (35)	1.6 (1.4)	0.54 (1.89)	0.81
Blue marlin	0.0125 Vaske (2004)	38	100 (67)	1.3 (0.8)	421	43 (24)	0.5 (0.3)	0.42 (2.05)	0.78
Bigeye tuna	0.0482 Menard (2000)	253	76 (28)	3.7 (1.3)	2652	45 (20)	2.2 (1.0)	0.60 (0.96)	0.68
Yellowfin tuna	0.0259 Menard (2000)	1536	52 (18)	1.3 (0.5)	6333	28 (13)	0.7 (0.3)	0.55 (1.05)	0.67
Skipjack tuna	0.0551 Menard (2000)	135	10 (2)	0.5 (0.1)	1168	8 (3)	0.4 (0.1)	0.80 (0.52)	0.70

Table A2.5. Performance of nylon monofilament and multifilament branchlines. This table is reproduced from Stone and Dixon (2001) who deployed longlines with alternate mono- and multifilament branchlines, in ten longline operations of 1440 hooks each. Relative catchability is the number caught on monofilament divided by the number on multifilament. The p-values are for a chi-square test that Stone and Dixon used to determine whether catchability differed from 1.0.

Common name	Latin binomial	Number caught		Relative catchability	p-value
		multifilament	monofilament		
Swordfish	<i>Xiphias gladius</i>	128	260	2.03	0.000
Yellowfin tuna	<i>Thunnus albacares</i>	1	9	9.00	0.011
Mako shark	<i>Isurus oxyrinchus</i>	39	58	1.49	0.054
Blue shark	<i>Prionace glauca</i>	116	225	1.94	0.000
White marlin	<i>Tetrapturus albidus</i>	13	47	3.62	0.000
Mahi mahi	<i>Coryphaena hippurus</i>	10	27	2.70	0.005
Pelagic stingray	<i>Dasyatis violacea</i>	31	63	2.03	0.001
Loggerhead turtle	<i>Caretta caretta</i>	26	40	1.54	0.085
Total	—	364	729	2.00	0.000

Table A2.6. Historical changes in shark-damage rates reported in the 1950s (POFI survey) and 1990s (Hawaii observer data) in the tropical Pacific Ocean. Catchability change is the ratio of 1950s and 1990s shark-damage rates.

Common name	1950s			1990s			Catchability change	
	examined damaged			examined damaged			estimate	p-value
	(no.)	(no.)	(%)	(no.)	(no.)	(%)		
Mako shark	34	2	6	123	1	1	1.05	1.00
Blue marlin	247	54	22	1 246	65	5	1.16	1.00
Bigeye tuna	663	110	17	13 429	958	7	1.09	1.00
Yellowfin tuna	4 442	935	21	8 121	905	11	1.09	1.00
Skipjack tuna	285	28	10	3 866	500	13	0.97	0.08

Table A2.7. Estimates of the effect of gear saturation on catchability. I used the formula of Rothschild (1967) to correct the reported fishing effort and catch rate of each species for the baits made unavailable through known catches. Reported catch rates (mean number per 1000 hooks) are from Japan's longliners in the study area during 1995–99 (1384 million hooks) and 1952–55 (123 million hooks), supplemented with species composition data from the 1950s POFI and 1990s Japanese surveys. Relative catchability is the corrected catch rate divided by reported catch rate. The catchability change is the 1950s relative catchability divided by that in the 1990s.

Common name	1950s			1990s			Catchability change	
	reported catch rate	corrected catch rate	relative catchability	reported catch rate	corrected catch rate	relative catchability	estimate	p-value
Mako shark	0.23 (0.10)	0.24 (0.11)	1.04 (0.63)	0.20 (0.14)	0.21 (0.14)	1.01 (0.91)	1.03 (1.25)	0.98
Blue marlin	4.57 (3.51)	4.71 (3.62)	1.03 (1.05)	0.48 (0.71)	0.48 (0.72)	1.01 (2.09)	1.02 (5.54)	0.99
Bigeye tuna	8.26 (9.13)	8.43 (9.27)	1.02 (1.53)	4.60 (3.96)	4.64 (4.00)	1.01 (1.21)	1.01 (3.77)	1.00
Yellowfin tuna	18.73 (16.43)	19.16 (16.85)	1.02 (1.21)	5.48 (6.89)	5.54 (7.01)	1.01 (1.77)	1.01 (4.59)	1.00
Skipjack tuna	0.24 (0.79)	0.25 (0.82)	1.04 (4.55)	0.77 (0.52)	0.78 (0.54)	1.01 (0.96)	1.02 (21.21)	1.00

Table A2.8. Estimates of the annual cost of electronic navigation, communication, and fish-finding equipment used by a typical Japanese longliner off eastern Australia, 1995-97 (Mr. Steve Beverley, Secretariat of the Pacific Community). Purchasing and installation costs were estimated as a fixed percentage (20%) of the purchase price. The cost of maintenance was estimated as 5% of the purchase price. To estimate annual costs, I depreciated total costs by 14% per year.

Device	Model	Purchase price (USD)	Purchasing 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	3 484
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	20 549	4 110	3 523	1 027	2	9 100
NOAA satellite receiver	Garmin GDL 30	540	108	93	27	2	239
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	24 018

Table A2.9. Estimates of the additional catch required to meet the annual cost of electronic equipment (USD24 018) installed on Japan's longliners during the 1990s. Equipment costs are itemized in Table A2.10. Annual catches are based on catch rates multiplied by the mean number of hooks per operation (2949 hooks) and the mean number of operations per year (298 operations; Reid 2003). Catch rates are from data reported by Japan's longliners in the study area, except for mako shark and other species, which are from the 1990s Japanese surveys. Mean weights were estimated from 1990s Hawaii observer data. Prices are from Vannuccini (1999) for mako shark, Uozumi and Matsumoto (2002) for blue marlin, FFA (1998) for bigeye and yellowfin tuna, and Sabatini (2003) for skipjack tuna. The value for other species was arbitrarily set at 5% of the total value of those five species.

Common name	Market Mean		Without electronics				With electronics			
			price (USD/kg)	wt. (kg)	catch rate (no./1000 hks)	annual catch (no.)	total value (t) ('000 USD)	catch rate (no./1000 hks)	annual catch (no.)	total value (t) ('000 USD)
Mako shark	1.96	18.9	0.20	178	3.4	7	0.21	180	3.4	7
Blue marlin	1.89	51.9	0.48	419	21.8	41	0.48	424	22.0	42
Bigeye tuna	10.10	36.4	4.64	4 076	148.2	1 497	4.68	4 116	149.7	1 512
Yellowfin tuna	5.40	28.7	5.48	4 819	138.3	747	5.54	4 866	139.7	754
Skipjack tuna	1.04	6.7	0.77	680	4.6	5	0.78	687	4.6	5
Other species	1.11	12.4	9.48	8 331	103.5	115	9.57	8 413	104.5	116
						total 2 411			total 2 435	

Table A2.10. Financial analysis of annual income and expenditure of a Japanese longliner during the 1990s. All estimates are based on FFA (1998), except for income from sale of catch, which is based on the catch rates and prices presented in my Table A2.11. The estimated annual cost of electronic equipment (USD24 018) is included in vessel maintenance in the “With electronics” column.

Component	Without electronics (USD 000s)	With electronics (USD 000s)
Income		
Sale of catch		
Mako shark	7	7
Blue marlin	41	42
Bigeye tuna	1 497	1 509
Yellowfin tuna	747	753
Skipjack tuna	5	5
Other species	609	614
total income	2 905	2 929
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	193
fishing gear maintenance	83	83
support and management	178	178
total fixed costs	430	454
Total costs	2 353	2 376
Operating profit	553	553

Component	Without electronics (USD 000s)	With electronics (USD 000s)
Depreciation	400	400
Net profit	153	153
Replacement cost	5 000	5 000
Net return to investment	3%	3%

Table A2.11. Estimates of the effects of fishing master experience on change in catchability. I used generalized linear models to estimate the effect of experience on catch rates of each species from 1990s eastern Australia observer data. I then used the models to predict catch rates of each species for the mean years of experience in the 1990s (15 years) and that assumed for the 1950s (2 years). Catch rates are the mean number predicted per 1000 hooks (standard deviation in parentheses).

Common name	Number modeled	Model residual deviance	AIC	Predicted catch rate (no./1000 hooks)		Catchability change estimate p-value	
				1950s	1990s		
Mako shark	487	297	435	1.92 (0.61)	0.60 (0.04)	0.31 (0.01)	0.00
Blue marlin	41	297	162	0.02 (0.03)	0.04 (0.01)	1.52 (3.33)	0.78
Bigeye tuna	1 900	297	1 760	0.89 (0.37)	2.28 (0.17)	2.55 (1.15)	0.15
Yellowfin tuna	6 896	297	4 004	3.21 (1.20)	6.76 (0.53)	2.11 (0.65)	0.17
Skipjack tuna	442	297	689	0.29 (0.16)	0.42 (0.04)	1.44 (0.65)	0.59

Table A2.12. Estimates of the effects of bait type on change in catchability. I used generalized linear models to estimate the effect of bait type on catch rates of each species from 1990s eastern Australia observer data. I then used the models to predict catch rates of each species for bait combinations in the 1950s (all pilchards) and the mean proportion of each bait type reported for the 1990s. Catch rates are the mean number predicted per 1000 hooks (standard deviation in parentheses).

Common name	Number modeled	Model		Predicted catch rate		Catchability change	
		residual	AIC	(no./1000 hooks)		estimate	p-value
		deviance		1950s	1990s		
Mako shark	545	434	458	0.66 (0.15)	0.62 (0.04)	0.94 (0.22)	0.79
Blue marlin	46	130	154	0.01 (0.00)	0.03 (0.01)	4.66 (4.61)	0.43
Bigeye tuna	2 340	1 825	1 849	1.24 (0.40)	2.41 (0.18)	1.94 (0.63)	0.14
Yellowfin tuna	8 811	3 982	4 006	15.47 (3.66)	7.36 (0.51)	0.48 (0.12)	0.00
Skipjack tuna	580	745	769	0.92 (0.31)	0.60 (0.06)	0.65 (0.22)	0.12

Table A2.13. Estimates of the catchability change of mako shark derived from branchline loss rates. The estimation procedure used identical values for the reported mako shark catch and fishing effort for each period.

Parameter	Symbol	1950s	1990s
Nominal mako shark catch (no.)	C	238 543 ^a	238 543 ^a
Nominal fishing effort ('000 hooks)	f	1 172 657 ^b	1 172 657 ^b
Nominal mako shark catch rate	—	0.20	0.20
Branchline loss rate	B	0.01 ^c	0.03 ^d
Proportion of mako shark	S	0.03 ^e	0.10 ^f
Lost mako shark (no.)	SBf	195 422	3 062 910
Corrected mako shark catch rate	U	0.37 ^g	2.82 ^g
Catchability change	Δq	0.13 ^h	

^aMako shark catch as a proportion of the tuna and billfish catch (1990s Japanese survey data) multiplied by the tuna and billfish catch reported by Japan's longliners in 1995–99.

^bJapanese longline data, tropical Pacific Ocean, 1995–99.

^cPOFI longline survey, tropical Pacific Ocean, 1950–54 where 384 of 65 417 branchlines were reported missing or severed.

^dAnecdotal reports from Australian longline fishers and observers.

^ePOFI survey data.

^f1990s surveys.

$$^g U = \frac{(C + SBf)}{f(1 - B)}$$

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

Table A2.14. Comparison of catch rates on distal hooks and hooks at the next nearest buoy (POFI survey data). Also shown is the p-value for an approximation to the Fisher exact test (Zar 1984) that tests whether the proportions of hooks with a catch are the same.

Statistic	Distal Nearby	
	hooks	hooks
Vacant (no.)	379	386
Catch (no.)	37	30
Catch (%)	10	8
P-value	0.1461	

Table A2.15. The effects of competition among longlines on catchability change. Catchability change was estimated as the ratio of catches predicted by a model that included cubic terms for fishing effort C_{cubic} and a linear model C_{linear} for the number of hooks corresponding to the mean monthly – five-degree catch in the 1990s. Standard errors are in parentheses.

Common name	Predicted catch (no.)		Catchability change	
	C_{cubic}	C_{linear}	estimate	p-value
Blue marlin	30	30	0.98	0.001
	(2.06)	(2.01)	(0.01)	
Bigeye tuna	930	886	0.95	0.000
	(4.25)	(4.05)	(0.00)	
Yellowfin tuna	935	890	0.95	0.000
	(4.11)	(4.31)	(0.00)	

Estimation of Relative Abundance and Biomass using Longline Data from Surveys and Observers¹⁴

Introduction

This appendix provides details of the data that we used in models to develop indices of abundance and biomass, which are presented in our *Ecology* article. We also examine the robustness of abundance indices and consider whether indices from different periods are indeed comparable. A separate document¹⁵ presents parameter estimates and diagnostic statistics for each model.

Data Sources

1950s Survey

In 1950, the US embarked on an ambitious program of fishery monitoring and scientific surveys of Pacific tuna resources. The Pacific Oceanic Fisheries Investigations (POFI) was a response to interest in harvesting the tuna resources of newly acquired US territories and possessions in the region. The US fishing industry sought large quantities of yellowfin tuna (*Thunnus albacares*) for canning. Using longline fishing gear and techniques adopted from Japan, POFI conducted 24 longline fishing trips each of about two months duration in the tropical Pacific Ocean during 1951–58 (Murphy and Shomura 1972). Most of the activity was during 1951–54. We refer to the POFI program as the “1950s survey”.

The 1950s survey was conducted as a controlled experiment where fishing gear and techniques were held constant throughout the study. Murphy and Shomura (1972) and

¹⁴ This Appendix was published as: Ward, P., and Myers, R.A. 2005. Appendix A. A description of the estimation of relative abundance and biomass using longline data from surveys and observers. Ecological Archives E086-043-A1. <http://esapubs.org/archive/ecol/E086/043/appendix-A.htm>. The original document's reference list is included in the Bibliography of this thesis.

¹⁵ Ward, P., and Myers, R.A. 2005. Appendix B. Parameter estimates and diagnostic statistics for generalized linear models used to estimate relative abundance. Ecological Archives E086-043-A1. <http://esapubs.org/archive/ecol/E086/043/appendix-B.htm>

reports that they cite provide details of the fishing gear and techniques. Longlines were deployed in a grid at pre-determined stations, e.g., at each one-degree of latitude. They were deployed at dawn each day and retrieved in the afternoon. Usually, six hooks were attached to the mainline between each buoy, amounting to about 342 hooks in each daily fishing operation (Table A3.1). Within the same operation, the performance of the standard gear was sometimes compared with that of gear with different types of bait, methods of bait attachment, or longline depth (Murphy and Shomura 1972). After the mid 1950s, POFI chartered commercial longliners that were encouraged to search for tunas for US canning markets.

1990s Observer Data

Our Ecology article examines changes in the pelagic fish community by comparing estimates from the 1950s with those from data collected by observers on Hawaii-based longliners in the tropical Pacific Ocean during 1994–2002. In the study region, the 1990s longliners targeted bigeye tuna (*Thunnus obesus*) and yellowfin tuna for commercial sale. Their catch of other species, such as broadbill swordfish (*Xiphias gladius*), striped marlin (*Tetrapturus audax*), mahi mahi (*Coryphaena hippurus*), and wahoo (*Acanthocybium solandri*) was also valuable. The markets pay a premium for large individuals of most species (T. Swenarton, pers. comm.).

For each period, we used data that overlapped in terms of deployment time (02:00–08:00 local time) and month (January–November), within a broad region of the Pacific Ocean (10°S–11°N, 175°E–115°W; Figure A3.1). Table A3.1 highlights several similarities between the fishing gear and techniques used in the 1950s and 1990s. However, there are also differences such as the depth range, soak time, number of hooks per operation and areas fished.

Species Identification

Our analyses revealed several species that were caught in the 1990s, but were not reported in the 1950s, e.g., pelagic stingray (*Dasyatis violacea*). Differences in sample size, catchability, and the level of species identification prevented us determining the exact number of extra species that appeared in the 1990s. We were confident, however, that the extra species would have been reported if they were caught in the 1950s. Scientists involved in the 1950s survey had access to taxonomic keys that covered the

extra species. Furthermore, survey activities outside the study region reported several of the extra species, e.g., pelagic stingray. We contacted a scientist involved in the survey, R. Shomura (pers. comm.), who confirmed that they would have identified and reported the extra species if they had been caught in the study region.

Data for both periods included fish that were not identified because they were released or broke free before being identified or, more rarely, fish that were damaged beyond recognition. In the 1950s, 1883 (9%) of the 17 439 fish caught were not identified, compared to 482 (2%) of the 24 208 caught in the 1990s. A check of the original data sheets revealed that 99% of the unidentified fish in the 1950s were unidentified sharks. Few, if any, unidentified fish could have been the extra species. We used generalized linear models to derive indices of abundance and biomass for each species or species group in the study region. For brevity, we use the term “species” in this appendix to refer to species groups as well as individual species. The models adjusted estimates for operational differences and spatial and temporal variations among the longline operations and periods. Following is a description of the procedures used to estimate hook depth, soak time, and fishing effort for the models.

Data Processing

Depth and Soak Time Estimation

We used the formula for a catenary curve to estimate the maximum depth reached by each longline hook (Suzuki et al. 1977). The formula uses ϕ , the angle made between a horizontal line drawn between the tangential line of the mainline and the connecting points of the buoy line and mainline. Suzuki et al. and many other researchers selected a value of 72° for ϕ because they did not have data on the sagging rate k . The sagging rate is the ratio of the distance between buoys and the length of mainline between buoys, measurements that were available for the 1950s survey and 1990s longlining activities. We used a derivation of the formula presented by Yoshihara (1954) to calculate ϕ from k for each longline operation:

$$k = \cot \phi^\circ \sinh^{-1}(\tan \phi^\circ) \quad (\text{A3.1})$$

We assumed that the shape of the curve formed by the longline (and therefore the corresponding depth of hooks) does not systematically vary over the entire operation.

Local conditions (e.g., the direction and velocity of wind and current), the buoyancy of the gear, the pull of hooked fish, and shortening of the distance between buoys over time are factors known to affect the actual depth range of longline hooks. Bigelow et al. (2002), for example, estimated that hook numbers 3 and 10 of longline gear with 13 hooks per buoy, shoaled by about 20% when subjected to a current velocity of 0.4 m s^{-1} . Strong equatorial currents characterize our study region. To represent the likely shoaling of the longline, we reduced all depths predicted by the catenary curve by 25%. The application of a 25% constant would not affect comparisons between periods because hook depth was used as a relative index in our analyses.

The data for both periods included a unique identifier—the hook number—for each longline hook deployed. The 1950s survey reported the hook number for each fish caught, allowing the estimation of its likely depth of capture. The 1990s observers reported the hook number for most catches of tunas, billfishes, and sharks, but not for other species. For the other species we used information on depth from a wider study (see “Depth”) or the number of hooks per buoy as a measure of the depth range of the entire longline operation.

We estimated the soak time of each hook from records of the time when each hook was retrieved, combined with the start and finish times of longline deployment and retrieval. The speed of longline deployment and retrieval was assumed constant throughout each operation (the analyses were limited to operations that had no evidence of stoppages due to line breaks or mechanical failure). The data were binned into 40-m depth – 1 hr soak time strata. However, we used the median soak time for species where the hook number was not reported. The analyses included soak time – depth strata where hooks were deployed but a zero catch was reported.

Estimation of Fishing Effort

The total number of hooks deployed is often used as a measure of fishing effort in longline fisheries. However, the measure of fishing effort should be adjusted for the number of hooks occupied by fish during the operation because occupied hooks are no longer available for fish that might subsequently encounter the longline (Rothschild 1967). Gear saturation would have affected our indices of abundance and

biomass, particularly for the 1950s when total catch rates often exceeded 100 fish per 1000 hooks (Figure A3.2).

To adjust fishing effort for gear saturation, we subtracted half the number of fish caught from the number of hooks deployed in each soak time – depth stratum of each operation. Information was not available on the depth and soak time for all species. Therefore we also subtracted half the mean number of those species per longline stratum from the number of hooks deployed. This approach is likely to overestimate the number of vacant hooks because of local saturation and bait loss (Rothschild 1967).

Body-mass and Biomass Estimation

We estimated the biomass index of each species by multiplying its abundance index by its mean mass in each period. The 1950s survey weighed 25% of all fish caught in the study region. The observers did not routinely weigh fish in the 1990s. However, they measured 57% of all fish, so we estimated the mass of each fish by applying length–mass relationships to length measurements (Strasburg 1957; Uchiyama and Kazama 1999; Froese and Pauly 2005). For ten species that were not measured in the 1990s, we used length data collected by Secretariat of the Pacific Community (SPC) observers on commercial longliners fishing in adjacent waters of the western Pacific during 1990–2001 (P. Williams, pers. comm.). For those species we used 1950s estimates from a wider region (10°S–15°N, 175°E–115°W).

The 1950s survey attempted to land and weigh all fish, regardless of species or body-mass (R. Shomura, pers. comm.). By contrast, the 1990s longliners sometimes released fish before observers could measure them. Fortunately, observers visually estimated the length before the fish was released or broke free from the longline. The visual estimates were to the nearest 12 inches (25.4 cm). We included both retained and released fish in our indices of abundance and biomass. For most species, retained individuals tended to be larger than those released (Figure A3.3). Our interpretation is that crewmembers released valuable species that were below a marketable size. There might be an element of bias in the visual estimates of length, although a study by Gillanders et al. (2001) concluded that recreational fishers were just as likely to underestimate the lengths of fish alongside their boat, as they were to overestimate them.

The inclusion of visual estimates made little difference to our indices of biomass and body-mass for most species because few were released (Table A3.2). However, more than half of the length data on sharks came from visual estimates. The declines in body-mass and biomass indices presented in the *Ecology* article would be much larger if the mass of released sharks had not been included.

Our index of community biomass excluded species that were caught in the 1990s as a result of longlining near land masses (Table A3.3). Those species would have accounted for less than 1% of the 1990s biomass. The index of community biomass was based on estimates of 21 species with well-determined indices of biomass. For each period, we raised the biomass index by the proportion of species with unreliable indices of abundance:

$$B_T = \frac{C_T}{C_w} B_w \quad (\text{A3.2})$$

where C_w is the catch (kg) and B_w is the biomass index (kg) of well-determined species, C_T is the catch of all species, and B_T is the index of community biomass. For the 1950s, the well-determined species accounted for 90% of the total catch, compared to 89% for the 1990s.

Robustness of Abundance Indices

Model Selection

We derived abundance indices from generalized linear models that accounted for bias caused by the effects of hook depth, soak time, location, season, and fishing effort. The models were implemented in SAS (version 8.0) using the GENMOD function and S-Plus (version 6.1) using *glm* and *glm.nb* from library MASS (Venables and Ripley 1999).

Model building examined the type of error distribution (e.g., Poisson or negative binomial model), the inclusion of variables (e.g., latitude and longitude), and functional relationships for each variable (e.g., linear or quadratic). We used Akaike's information criterion (AIC), deviance residuals, and the negative binomial model parameter θ to check the performance of the various model formulations. We also used stepwise model selection using the AIC criterion holding the negative binomial parameter θ fixed, but they did not produce estimates of change in abundance that were significantly different to

the estimates from the model with all variables included (Table A3.4). We presented indices for the models with the lowest standard error, excluding indices for species where the standard error of the estimate was greater than one or where the change in biomass was not significantly different from one (Table A3.5). For 19 species, the performance of models with negative binomial error was superior to the same models with a Poisson error distribution. The Poisson model was recovered for several rare species, e.g., striped marlin. The inclusion of quadratic terms for depth, soak time, latitude, and longitude provided the best fit for most species (Appendix A1).

Area

Commercial longliners often concentrate over deep-sea canyons and seamounts where target species are abundant (Bigelow et al. 1999). The 1990s longline activity was in the vicinity of seamounts and islands of the Christmas Ridge in northwestern waters of the study region. By contrast, the 1950s activity had a much wider distribution, including relatively featureless parts of the eastern study region (Figure A3.1). We investigated the sensitivity of abundance indices to variations in the boundaries of the study region. Variations in the longitudinal boundary made little difference to abundance indices, whereas latitude had a greater effect (Table A3.6). Estimates of model coefficients (β s) confirmed that latitude had a stronger effect on abundance indices for most species than did longitude. We drew on the power of a larger data set by using a study region that had a wide longitudinal range and a narrower latitudinal range.

Figure 1 of the *Ecology* article shows considerable activity in northern waters outside the study region during the 1990s. The exclusion of those activities from analyses did not affect our indices because the mean catch rate for 1990s activity in the study region (24.5 animals per 1000 hooks) was similar to that in northern waters (26.7 per 1000 hooks).

We also explored the joint effects of latitude and longitude on abundance indices by including a latitude–longitude interaction term in the hook model. The interaction term was significant at the 95% level for six of the nine species investigated (Table A3.7). Regardless, inclusion of the interaction term did not make a significant difference to estimates of the change in abundance between periods. For example, the model that included the interaction term estimated that the abundance of blue shark in the 1990s was

0.14 times that in the 1990s. By contrast, it was 0.13 times that for the model without the interaction term. We concluded that adding a joint measure of latitude and longitude does not significantly alter estimates of change in abundance.

Soak Time and Timing

Soak times ranged up to 8 hours in the 1950s compared to 12 hours or longer in the 1990s. Parameter estimates indicated that catch rates increased with soak time for many species, particularly sharks and billfishes. The catch rates of several species, such as skipjack tuna (*Katsuwonus pelamis*), decreased with soak time.

We adjusted estimates for the effects of soak time, but did not correct them for variations in exposure to dawn or dusk. Ward et al. (2004) found that exposure of longlines to dawn and dusk produced elevated catch rates of many pelagic species. In our study, the long duration of 1990s operations resulted in about 80% of longline hooks being available at dusk as well as at dawn. By comparison, 1950s hooks were only available at dawn. Therefore the abundance and biomass of several species may have been underestimated in the 1950s.

Depth

By covering a wider depth range than shallow longlines (<200 m), deep longlines (<600 m), produce elevated catch rates of several species, e.g., bigeye tuna (Bigelow et al. 2002). For some epipelagic species, such as blue marlin (*Makaira nigricans*), they produce lower catch rates than shallow longlines (Hinton and Nakano 1996). We explored the limited overlap in depth range between periods by adding an interaction term for fishing period – hook depth and adding a dummy variable to the hook model for 12 species (Table A3.8). The dummy variable indicated whether hook depth was less than 200 m. The interaction term was significant at the 95% level for 5 of the 12 species, indicating that hook depth modifies the estimate of change in abundance (i.e., fishing period) for those five species. However, restricting input data to strata where depth was less than 200 m made only a small difference to estimates of the change in abundance between periods (Table A3.9). For example, the model fitted to data with hook depths less than 200 m estimated that the abundance of blue shark in the 1990s was 0.15 times that in the 1950s. By contrast, the change in abundance was 0.13 times for the model that included all depths.

We applied the “offset model” to ten species where an estimate of the depth of capture was not available (Table A3.10). It used information on depth distributions from the wider study by (Ward and Myers 2005a). Their analyses included the 1950s and 1990s data, and data from 1990s longline operations that targeted broadbill swordfish in the North Pacific, and those that targeted bigeye tuna and yellowfin tuna in the western Pacific. The offsets we used were those for longlines deployed in the morning.

Verification of Catch Rates

We compared 1950s survey catch rates with those from commercial longline operations during 1952–54. The commercial operations involved several large processor vessels or “motherships”, each accompanied by 12–25 smaller catcher vessels. Japanese companies were permitted to undertake nine mothership expeditions in a restricted area of the tropical Pacific (Shapiro 1950). The mothership expeditions targeted tunas for canning markets (Van Campen 1952). The fishing gear and techniques used by catcher vessels were almost identical to those of the 1950s survey (Niska 1953). The 1950s mothership data were available for nine commercially valuable species of tunas and billfishes, aggregated by month and five-degree square area.

We compared mothership catch rates in the area bounded by 20°S–10°N and 150°E–130°W with 1950s survey catch rates in the study region (Table A3.11). Overall, the 1950s survey reported catch rates of 48 tunas and billfishes per 1000 hooks compared to 47 per 1000 hooks for the motherships. The catch rates of two species (skipjack tuna and yellowfin tuna) were higher in the 1950s survey, whereas the catch rates of bigeye tuna and blue marlin were lower. We might expect the mothership catch rates to have been significantly higher than survey catch rates because the survey was restricted to often predetermined stations along a grid. However, observers on the motherships reported that external factors kept catch rates below levels that true commercial longline operations could have accomplished. Those factors included restrictions on areas of operation, catcher vessels having to remain in close proximity to their mothership, and poor bait quality (Van Campen 1952).

Possible Causes of Variations among Indices

Competition among and within Operations

Our comparison of abundance indices that were derived from catch rates indicated marked differences between the pelagic fish community of the 1950s and that of the 1990s (Figure A3.2). Other than a massive decline in abundance, we can imagine few plausible explanations for 1990s catch rates being so much lower than 1950s catch rates. One alternative explanation is competition within longline operations. The 1950s survey deployed fewer longline hooks in each operation than were deployed in the 1990s. Individual hooks might not fish independently within a longline operation (Rothschild 1967). However, competition might not be a concern because commercial longliners would not increase the number of hooks deployed, or shorten the distance between hooks, if it reduced the day's catch of target species (Hirayama 1969; Hamley and Skud 1978).

A second possible explanation of the decline in catch rates is competition among fishing vessels (Hilborn and Walters 1987). The increased number of longliners and other vessels fishing for pelagic species in the study region after the 1950s might have increased competition for the most productive areas, resulting in the displacement of some longliners to less productive waters. However, it is noteworthy that longliners rarely sight each other, let alone physically interact in the open ocean. Longline operations are measured on scales of hours and tens of kilometres whereas pelagic fish distributions are measured on much broader scales. Angel (1993) suggests that 1000 km is an appropriate horizontal scale for the distribution of pelagic communities of the open ocean. In the next section, we discuss the ability of 1990s longliners to find concentrations of target species. This mobility would have enabled them to maintain catch rates by moving to alternative areas if competition was a problem. We did not investigate competition between fishing vessels, which would require accurate estimates of local fish abundance, mixing rates, and fine-scale data on catch and fishing effort of all vessels in the region.

Searching, Fishing Gear, and Techniques

There is strong evidence that searching and technological improvements resulted in the underestimation of 1950s abundance relative to 1990s abundance. The 1950s survey

adopted longline gear and techniques that had been used in Japan and Formosa (now Taiwan) during the 1930s (Niska 1953). They were not modified or refined during the survey, except for tightly controlled experiments with bait type, attachment methods, and longline depth (Murphy and Shomura 1972).

In contrast to the 1950s survey, the longline gear and techniques used in the 1990s were the product of 40 years of practical experience and innovation. Refinements ranged from the adoption of new technology (e.g., colour sounders, Doppler current meters, and satellite imagery) to more subtle changes, such as the materials used for branchlines and mainlines. The 1990s longliners also had the ability to modify their fishing techniques to suit conditions while on the fishing grounds, e.g., longline depth, time of deployment, and time of retrieval (T. Swenarton, pers. comm.).

Quantity, species composition, body-mass, and quality largely determine the value of the catch landed by commercial longliners. The incomes of masters and crew were based on a proportion of the value of the catch. They would use every available piece of information and equipment to maximize the value of the catch (T. Swenarton, pers. comm.).

Perhaps the most important difference between the data sets is that the 1950s survey often deployed longlines at predetermined stations along a survey grid, whereas the 1990s longliners actively searched for concentrations of target species. The 1990s longliners remained in areas of high catch rates or followed the fish as the concentrations moved. Searching also involved the use of past experience to select fishing areas and communication with other longliners to locate concentrations of target species (T. Swenarton, pers. comm.). In estimating abundance, we were unable to quantify the effects of searching or improvements in fishing gear and techniques. One option would be to repeat the 1950s survey using exactly the same survey grid, fishing gear, and techniques.

Removals by Sharks

There is evidence of a long-term decline in the proportion of fish that is damaged by sharks while the fish are hooked on the longline. The 1950s data indicate that sharks damaged 20–30% of tunas caught by survey longliners in the study region. By comparison, 1990s observers reported damage rates of about 4% (which is consistent

with the decline in shark abundance shown by our indices). If shark-damage rates reflect the rate at which hooked fish are removed from longlines by scavengers, then loss rates might have been higher in the 1950s, further adding to the underestimation of early abundance.

Influence of Oceanographic Conditions

Various authors have highlighted the effects of broad-scale oceanographic events on ocean productivity (e.g., Mantua and Hare 2002; Chavez et al. 2003) and the distribution of pelagic fish species (e.g., Polovina 1996; Bigelow et al. 1999; Rodriguez-Sanchez et al. 2002; Ravier and Fromentin 2004). Strong equatorial currents and undercurrents that flow eastwards or westwards characterize our study region. They produce areas of divergent upwelling where relatively cold, nutrient-rich water is drawn to the sea surface. West of about 180°E lies the “warm pool” of less productive waters. The location, strength and direction of currents, and associated areas of upwelling vary with El Niño – Southern Oscillation events (Lehodey 2001).

We checked oceanographic conditions that are known to strongly influence the productivity of pelagic fish or their availability to longline gear (Table A3.12). During the 1950s study period, the mean monthly Pacific Decadal Oscillation (PDO) for November–March was $-0.98 (\pm 0.89 \text{ SD})$. With a mean PDO of $-0.28 (\pm 1.07 \text{ SD})$, conditions in the 1990s were not markedly different to those in the 1950s. By comparison, the PDO ranged between -3.60 and 2.65 during November–March in the twentieth century (mean $0.00 \pm 1.04 \text{ SD}$).

The study periods spanned months of high and low values of the Southern Oscillation Index corresponding to a mixture of La Niña and El Niño conditions. The 1990s featured stronger El Niño conditions than were experienced in the 1950s. The study periods spanned six years or more, which may smooth out the short-term effects of oceanographic events on fish availability and abundance. Furthermore, unusually high recruitment in the early years would need to be synchronized across various species with quite different life histories. Exceptionally high abundance of large predators in 1953, for instance, would require strong cohorts of tunas from the early 1950s combined with strong cohorts of sharks from the mid 1940s.

On a finer scale, water temperature and oxygen concentrations are known to influence the vertical distribution of many pelagic fish species (Bigelow et al. 2002). We were unable to obtain data on oxygen concentrations in the study region during the 1950s. The mean depth of the thermocline, as indicated by the 20°C isotherm, was 135 m (± 28 SD) in the 1950s compared to 131 m (± 22 SD) in the 1990s. In conclusion, there was no obvious difference between periods in the oceanographic conditions that we examined.

Temporal and Spatial Variation

Our indices of relative abundance and biomass represent a snapshot of the pelagic fish community in space and time; they might not represent trends over longer time periods or more broadly in areas outside the study region. The fish community is unlikely to have been static in the study region before fishing commenced. Variations in abundance caused by fishing may be magnified or moderated by broad-scale oceanographic events that affect the species' distribution, recruitment, and vulnerability to the gear (Steele 1998; Jennings and Kaiser 1998). The periods that we analyzed might have coincided with years of particularly high (or low) abundance in the study region. The study region is at the margins of the distribution of several species, e.g., albacore tuna (*Thunnus alalunga*), striped marlin and blue shark (*Prionace glauca*). Estimates of those species might be confounded by geographical contractions or expansions of the populations that are driven by oceanographic conditions as well as population abundance (MacCall 1990). Nevertheless, the study area is a significant portion of the core habitat of most of the other pelagic fish species (Collette and Nauen 1983; Nakamura 1985; Last and Stevens 1994). The uncertainties outlined here might contribute to underestimation or overestimation of community changes.

Exploitation

The 1950s pelagic fish community was markedly different to that of the 1990s in terms of indices of abundance and biomass, and size composition. We believe that fishing is the most likely cause of the community changes. Industrial-level fishing began in the open ocean with open-boat whaling in the seventeenth century (Whitehead 2002). A second wave of expansion began in the latter half of the twentieth century when Japanese fishers combined pelagic longline gear with new technology for preserving fish. Low-

temperature refrigeration systems enabled longliners to remain at sea for several months and to harvest highly mobile tunas and billfishes thousands of miles from ports (Sakagawa et al. 1987).

The study region is a relatively large section of the Pacific Ocean that is central to the distribution of many of the species that we analyzed (Collette and Nauen 1983; Nakamura 1985; Last and Stevens 1994). Therefore, fluctuations in the mean mass of those species should not be due to size-related expansions and contractions in range linked to variations in ocean productivity and environmental conditions. The mean mass of only one large predator, albacore tuna, increased between periods. This pattern might reflect the fact that the study region is at the margins of this species' distribution. An alternative explanation is that heavy exploitation of albacore tuna by a longline fishery that had exclusively targeted the species in the North Pacific since the 1920s (Nakamura 1950) had reduced the abundance of large albacore tuna well before the 1950s.

Pelagic fish species, such as albacore tuna and yellowfin tuna, have been commercially harvested in the Pacific Ocean off California since the 1920s, around Hawaii since 1917, and in the northwestern Pacific and southeastern Asia since the 1920s. By the late 1940s, catches of yellowfin tuna amounted to at least 136 708 t per year (Nakamura 1950; Otsu 1954; Mais and Jow 1960). Fishing would have reduced the abundance of these highly migratory species over a wide area of the Pacific Ocean before the 1950s. Many of the masters of commercial longliners in the early 1950s believed that tuna abundance was substantially lower than it was in earlier years (Shimada 1951a).

Soon after the 1950s survey, longlining expanded rapidly to high levels over large geographical scales (Sakagawa et al. 1987). Catches of most pelagic species have been high in the Pacific Ocean since the 1970s. Longline catches of yellowfin tuna in the study region, for instance, reached about 50 000 t per year by 1979, with few caught by other fishing gears (Secretariat of the Pacific Community *public communication*, <http://www.spc.org.nc/OceanFish/Html/SCTB/Data>, accessed 10 June 2003). In subsequent years, the longline catch of yellowfin tuna averaged 30 000 t in the study region, with an additional 20 000 t of smaller yellowfin tuna caught by pole-and-line and purse-seine gear each year. We expect future analyses to demonstrate that, by the early

1960s, those levels of exploitation were sufficient to have caused the changes in the pelagic fish community identified by our study.

Table A3.1. Comparison of 1950s and 1990s fishing gear and techniques. This table is based on survey and observer data, supplemented with information from Niska (1953) and Murphy and Shomura (1972).

Characteristic	1950s	1990s
Source	Pacific Oceanic Fisheries Investigations (1951–58), US National Marine Fisheries Service, Pacific Islands Regional Office	Observers on Hawaii-based longliners (1994–2002), US National Marine Fisheries Service, Pacific Islands Regional Office
Target species	No targeting	Bigeye tuna and yellowfin tuna
Mainline material	Hard-lay cotton twine	Monofilament
Branchline material	12-strand cotton twine with wire leader	400 kg breaking strain monofilament, 92% of operations used wire leaders
Level of fishing effort	880 operations 301 520 hooks	505 operations 1 002 637 hooks
Hooks per operation	343 (± 269 SD) hooks	1985 (± 361 SD) hooks
Hook type	9/0 or 8/0 “Mustad flattened tuna” hooks	“Asian ring” hooks
Bait	Frozen sardine, occasionally herring, milkfish, or squid	Frozen sardine or saury
Lightsticks	No	No
Buoyline length	19.2 (± 6.42 SD) m	22.3 (± 5.2 SD) m
Branchline length	20.7 (± 7.02 SD) m	13.3 (± 3.72 SD) m
Hooks per buoy	Usually 6, ranging up to 21	26–30, ranging from 12 up to 38
Line shooter	No	Yes
Depth range	26–200 m	27–600 m
Deployment time	One hour before dawn	About one hour before dawn
Median soak time	7 hours	12 hours
Retrieval time	One hour after noon	About two hours before dusk

Table A3.2. Sources of 1990s length data. The number of individuals measured (“retained”) and the number visually estimated (“released”) in the study region are shown for the 21 species that had reliable biomass indices. Also shown are the number of each species measured by Secretariat of the Pacific Community observers in the wider area (10°S–15°N, 175°E–115°W).

Common name	Study region		Wider area	Total
	Retained	Released		
Tunas and tuna-like species				
Albacore tuna	30	0	0	30
Bigeye tuna	2 627	12	0	2 639
Skipjack tuna	1 133	17	0	1 150
Wahoo	0	0	41	41
Yellowfin tuna	6 241	41	0	6 282
Billfishes				
Black marlin	1	1	12	14
Blue marlin	411	5	0	416
Sailfish	30	0	0	30
Shortbill spearfish	50	3	0	53
Striped marlin	191	5	0	196
Other teleosts				
Great barracuda	0	0	3	3
Longnosed lancetfish	0	0	476	476
Mahi mahi	0	0	2	2
Pomfrets	0	1	0	1
Snake mackerels	20	0	1	21
Sharks and rays				
Blue shark	317	252	0	569
Mako sharks	31	23	0	54
Oceanic whitetip shark	281	231	0	512
Pelagic stingray	0	1	0	1
Silky shark	431	214	0	645
Thresher shark	272	126	0	398

Table A3.3. Scientific name, numbers caught, numbers of body-mass measurements, and mean mass of each species. Unless otherwise indicated, the number measured is for the study region. For the 1990s, the number measured includes visual estimates of the mass of released fish (Table A3.2). Habitat categories are based on Froese and Pauly (2005) and are listed in decreasing order of importance for each species.

Common name	Scientific name	Habitat ^a	Caught		Measured	
			1950s (no.)	1990s (no.)	1950s (no.)	1990s (no.)
Tunas and tuna-like species						
Albacore tuna	<i>Thunnus alalunga</i>	I, II	323	31	208	30
Bigeye tuna	<i>Thunnus obesus</i>	I, II	694	2 975	291	2 639
Pacific bluefin tuna	<i>Thunnus orientalis</i>	I	0	1	0	0
Skipjack tuna	<i>Katsuwonus pelamis</i>	I	438	1 668	163	1 150
Wahoo	<i>Acanthocybium solandri</i>	I	100	683	29	41 ^b
Yellowfin tuna	<i>Thunnus albacares</i>	I, II	10 636	10 625	3 358	6 282
Unidentified tunas	—	—	0	191	0	0
Billfishes						
Black marlin	<i>Makaira indica</i>	I	38	2	19	14 ^b
Blue marlin	<i>Makaira nigricans</i>	I	325	459	70	416
Broadbill swordfish	<i>Xiphias gladius</i>	I, II	11	159	1	139
Sailfish	<i>Istiophorus platypterus</i>	I	25	31	8	30
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	I	15	55	11	53
Striped marlin	<i>Tetrapturus audax</i>	I	55	215	15	196
Unidentified billfishes	—	—	11	54	5	44

Common name	Scientific name	Habitat ^a	Caught		Measured		
			1950s (no.)	1990s (no.)	1950s (no.)	1990s (no.)	
Other teleosts							
Crestfish	<i>Lophotus lacepede</i>	II	0	4	0	0	
Great barracuda	<i>Sphyræna jello</i>	I, A	19	97	5	3 ^b	
Longnosed lancetfish	<i>Alepisaurus ferox</i>	II, I	100	1 699	13	476 ^b	
Mahi mahi	<i>Coryphaena hippurus</i>	I	53	190	9	2 ^b	
Opah	<i>Lampris guttatus</i>	I, II	0	5	0	1 ^b	
Pomfrets			0	637			
Bigscale pomfret	<i>Taractichthys steindachneri</i>	III	0	559	0	0	
Dagger pomfret	<i>Taractes rubescens</i>	III	0	48	0	0	
Pacific pomfret	<i>Brama japonica</i>	I	0	13	0	1	
Rainbow runner	<i>Elagatis bipinnulata</i>	A, I	0	17	0	2 ^b	
Snake mackerels			23	933			
Escolar	<i>Lepidocybium flavobrunneum</i>	II, I, A	0	171	0	1	
Oilfish	<i>Ruvettus pretiosus</i>	A, II, III, I	0	66	0	19 ^b	
Unid. snake mackerels ^c	F. Gempylidae	II, I	23	696	1	1	
Sunfishes							
Common sunfish	<i>Mola mola</i>	I	0	4	0	25 ^b	
Pelagic puffer	<i>Lagocephalus lagocephalus</i>	I	0	3	0	0	
Slender sunfish	<i>Ranzania laevis</i>	I	0	12	0	0	

Common name	Scientific name	Habitat ^a	Caught		Measured	
			1950s (no.)	1990s (no.)	1950s (no.)	1990s (no.)
Unidentified sunfishes	<i>F. Tetradontidae</i>	I	4	0	2	0
Yellowtail amberjack	<i>Seriola lalandei</i>	A	0	4	0	0
Unidentified teleosts	—	—	0	7	0	0
Sharks and rays						
Blacktip shark	<i>Carcharhinus limbatus</i>	A, I	5	1	0	1
Blue shark	<i>Prionace glauca</i>	I, II	696	1 081	32	569
Cookiecutter shark	<i>Isistius brasiliensis</i>	I, II	0	3	0	2
Crocodile shark	<i>Pseudocarcharias kamoharui</i>	I, II	0	103	0	76
Dusky shark	<i>Carcharhinus obscurus</i>	A	0	53	0	25
Galapagos shark	<i>Carcharhinus galapagensis</i>	A, I	0	2	0	3 ^b
Hammerhead sharks						
Scalloped hammerhead	<i>Sphyrna lewini</i>	A, I	0	4	0	3
Smooth hammerhead	<i>Sphyrna zygaena</i>	A, I	0	2	0	2
Unidentified hammerhead	<i>Sphyrna</i> spp.	—	5	1	0	0
Mako sharks						
Longfin mako	<i>Isurus paucus</i>	I	21	32	5	23
Shortfin mako	<i>Isurus oxyrinchus</i>	I	0	37	0	31
Unidentified mako ^f	<i>Isurus</i> spp.	—	30	3	2	0
Oceanic whitetip shark	<i>Carcharhinus longimanus</i>	I	1 149	794	37	512
Rays						
Manta ray	<i>Manta birostris</i>	A, I	0	12	0	1

Common name	Scientific name	Habitat ^a	Caught		Measured	
			1950s (no.)	1990s (no.)	1950s (no.)	1990s (no.)
Pelagic stingray	<i>Dasyatis violacea</i>	I	0	302	0	1
Unidentified rays	-	-	0	1	0	0
Silky shark	<i>Carcharhinus falciformis</i>	I, II	2 210	1 080	23	645
Thresher sharks			112	511		
Bignose thresher	<i>Alopias superciliosus</i>	A, I, II	0	333	0	293
Pelagic thresher	<i>Alopias pelagicus</i>	I, II	0	105	0	94
Thintail thresher	<i>Alopias vulpinus</i>	A, I, II	0	18	0	11
Unidentified thresher	<i>Alopias</i> spp.	-	112	55	2	0 ^b
Tiger shark	<i>Galeocerdo cuvier</i>	A	0	6	0	3
Unidentified sharks	-	-	1 482	226	0	0
Other unidentified species	-	-	8	4	0	0
Total			17 439	24 208	4 309	13 860

^aHabitat categories:

- I epipelagic zone of the open ocean (0–200 m)
- II mesopelagic zone of the open ocean (200–1000 m)
- III bathypelagic zone of the open ocean (immediately above the sea floor)
- A associated with land masses, such as seamounts, reefs, and islands

^bInclude measurements reported by Secretariat of the Pacific Community observers in the western Pacific Ocean in the 1990s. 1950s data from a wider area (10°S–15°N, 175°E–115°W).

^cMost unidentified snake mackerels were probably *Gempylus serpens*.

^dThe 1950s survey originally identified these mako sharks as salmon shark (*Lamna ditropis*). That identification is questionable because salmon shark are distributed between 22°N and 66°N, generally over shelf waters (Froese and Pauly 2005).

Table A3.4. Stepwise regression of hook models for nine species. Statistics for the most parsimonious model derived from the MASS function *stepAIC* are compared with those from the full model that included all variables. The full model was the most parsimonious model for yellowfin tuna and blue shark.

Common name	Variables dropped in parsimonious model ^a	Statistic ^b	Parsimonious model	Full model
Tunas and tuna-like species				
Albacore tuna	E	Δ_A	0.040	0.053
		SE	0.351	0.402
		AIC	1 384	1 385
Bigeye tuna	E	Δ_A	0.413	0.410
		SE	0.093	0.094
		AIC	10 771	10 773
Skipjack tuna	D^2	Δ_A	2.445	2.415
		SE	0.118	0.118
		AIC	7 706	7 707
Yellowfin tuna	none	Δ_A	0.166	0.166
		SE	0.052	0.052
		AIC	24 253	24 253
Billfish				
Blue marlin	D^2+N+E^2	Δ_A	0.529	0.591
		SE	0.135	0.148
		AIC	3 873	3 874
Sharks				
Blue shark	none	Δ_A	0.134	0.134
		SE	0.098	0.098
		AIC	7 878	7 878
Oceanic whitetip shark	N^2	Δ_A	0.266	0.267
		SE	0.095	0.099
		AIC	7 503	7 505

Common name	Variables dropped in parsimonious model ^a	Statistic ^b	Parsimonious model	Full model
Silky shark	D^2+N	Δ_A	0.077	0.078
		SE	0.079	0.080
		AIC	9 317	9 319
Thresher sharks	N	Δ_A	0.205	0.173
		SE	0.218	0.219
		AIC	2 602	2 602

^aThe full model was:

$$\log(\mu_{i,s}) = \beta_0 + \beta_1 P_i + \beta_2 N_i + \beta_3 N_i^2 + \beta_4 E_i + \beta_5 E_i^2 + \beta_6 T_{i,s} + \beta_7 T_{i,s}^2 + \beta_8 D_{i,s} + \beta_9 D_{i,s}^2 + \log(h_{i,s})$$

where $\mu_{i,s}$ is the mean catch of the species, P_i is the fishing period, N_i is the latitude, and E_i is the longitude of longline operation i ; and $T_{i,s}$ is the soak time, $D_{i,s}$ is the depth below the sea-surface, and $h_{i,s}$ is the number of vacant hooks of each stratum s of operation i . The β_j are estimated parameters.

^bSymbols and abbreviations:

Δ_A	Estimated change in abundance between the 1950s and 1990s
SE	Standard error
AIC	Akaike's information criterion (smaller is better).

Table A3.5. Input data and parameter estimates for 21 species that had well-determined indices of abundance and were not associated with land masses. The negative binomial model parameter θ is the amount of overdispersion in the data relative to the Poisson distribution (very large values of θ indicate a Poisson distribution).

Common name	Model	No. modeled ^b		Abundance change		θ	
	type ^a	1950s	1990s	Estimate	SE	Estimate	SE
Tunas and tuna-like species							
Albacore tuna	hook	262	31	0.053	0.402	0.364	0.628
Bigeye tuna	hook	599	2 573	0.410	0.094	0.237	0.239
Skipjack tuna	hook	311	1 570	2.413	0.118	0.190	0.420
Wahoo	offset	99	646	1.514	0.298	1.285	0.162
Yellowfin tuna	hook	6 284	9 739	0.166	0.052	0.254	0.080
Billfishes							
Black marlin	offset	32	1	0.050	1.393	0.698	0.881
Blue marlin	hook	234	421	0.591	0.148	0.154	1.276
Sailfish	offset	16	26	0.062	0.208	0.261	0.179
Shortbill spearfish	offset	15	51	0.015	0.275	0.345	0.144
Striped marlin	offset	47	179	0.189	0.131	27.473	0.047
Other teleosts							
Great barracuda	offset	16	93	0.556	0.649	0.732	0.969
Longnosed lancetfish	offset	91	1 618	2.596	0.325	1.016	0.136
Mahi mahi	offset	42	177	0.501	0.666	0.223	1.144
Pomfrets	operation	0	561	>1.000	–	0.351	0.355
Snake mackerels	operation	22	870	4.212	0.569	0.712	0.153
Sharks and rays							
Blue shark	hook	618	942	0.134	0.098	0.398	0.325
Mako sharks	offset	37	65	0.319	0.669	0.193	2.367
Oceanic whitetip shark	hook	1 031	713	0.266	0.099	0.206	0.404
Pelagic stingray	offset	0	301	>1.000	–	2.366	0.222
Silky shark	hook	1 872	972	0.078	0.080	0.247	0.241
Thresher sharks	hook	108	468	0.183	0.219	0.125	1.221

^aHook models used information on the depth and soak time of each hook; offset models used the median soak time of each operation and an offset based on the number of hooks per buoy and the species' depth distribution (Table A3.10); operation models used the median soak time and the number of hooks per buoy as an indicator of the operation's depth range.

^bWe limited modeling to records that had complete input data, e.g., hook depth was required for the depth model. Consequently, the number modeled is often less than the number caught.

Table A3.6. The effect of latitude and longitude on abundance indices of ten species. We fitted the hook model to catch and effort data from seven progressively smaller areas of the tropical Pacific. Values are the change in abundance between the 1990s and 1950s (standard errors in parentheses). Shading indicates the designated study region.

Common name	Area									
	10°S-11°N 175-245°E	10°S-11°N 175-235°E	10°S-11°N 175-225°E	10°S-11°N 175-215°E	10°S-11°N 175-205°E	0-11°N 183-217°E	3-8°N 194-200°E			
Tunas										
Albacore tuna	0.053 (0.999)	0.049 (0.984)	0.051 (0.965)	0.059 (0.857)	0.046 (0.904)	0.047 (0.537)	—			
Bigeye tuna	0.410 (0.119)	0.397 (0.122)	0.362 (0.127)	0.331 (0.140)	0.683 (0.309)	0.200 (0.176)	0.688 (0.361)			
Skipjack tuna	2.415 (0.230)	2.412 (0.226)	2.465 (0.225)	2.427 (0.266)	2.263 (0.451)	3.406 (0.469)	2.837 (3.734)			
Yellowfin tuna	0.166 (0.068)	0.163 (0.069)	0.165 (0.070)	0.122 (0.075)	0.140 (0.100)	0.100 (0.086)	0.179 (0.195)			
Billfish										
Blue marlin	0.591 (0.179)	0.583 (0.182)	0.624 (0.182)	0.643 (0.185)	0.236 (0.239)	0.432 (0.222)	0.297 (0.648)			
Sharks										
Blue shark	0.134 (0.102)	0.132 (0.103)	0.133 (0.105)	0.135 (0.114)	0.143 (0.144)	0.106 (0.143)	0.100 (0.179)			
Oceanic whitetip shark	0.267 (0.117)	0.269 (0.118)	0.277 (0.121)	0.322 (0.121)	0.354 (0.159)	0.402 (0.168)	0.418 (0.833)			

Common name	Area						
	10°S-11°N 175-245°E	10°S-11°N 175-235°E	10°S-11°N 175-225°E	10°S-11°N 175-215°E	10°S-11°N 175-205°E	0-11°N 183-217°E	3-8°N 194-200°E
Silky shark	0.078 (0.087)	0.080 (0.088)	0.082 (0.091)	0.060 (0.105)	0.034 (0.109)	0.052 (0.103)	0.027 (0.196)
Thresher sharks	0.138 (1.722)	0.138 (1.920)	0.139 (1.821)	0.106 (0.697)	0.125 (0.864)	0.117 (0.687)	0.347 (7.568)

Table A3.7. The joint effects of latitude and longitude on abundance indices. We applied hook models that included a latitude-longitude interaction term to nine species. The table shows statistics for the interaction term ("LatxLon") and estimates of the change in abundance between periods for models with and without the interaction term.

Common name	Estimate of LatxLon	Standard error	Confidence limits		Chi- square	P>Chi-square	Estimated change in abundance		
			lower	upper			with LatxLon	without LatxLon	
Tunas									
Albacore tuna	0.0027	0.0021	-0.0015	0.0068	1.5900	0.2069	0.058	0.053	0.053
Bigeye tuna	0.0002	0.0008	-0.0015	0.0019	0.0500	0.8158	0.412	0.410	0.410
Skipjack tuna	-0.0019	0.0011	-0.0041	0.0004	2.6200	0.1055	2.303	2.413	2.413
Yellowfin tuna	-0.0037	0.0006	-0.0048	-0.0026	40.1000	<.0001	0.152	0.166	0.166
Billfishes									
Blue marlin	0.0058	0.0011	0.0036	0.0080	26.7200	<.0001	0.732	0.591	0.591
Sharks									
Blue shark	0.0017	0.0007	0.0003	0.0031	5.9400	0.0148	0.144	0.134	0.134
Oceanic whitetip shark ^a	-0.9311	0.0899	-1.1073	-0.7550	107.3400	<.0001	0.394	0.266	0.266
Silky shark	-0.0039	0.0010	-0.0059	-0.0020	16.0600	<.0001	0.072	0.078	0.078
Thresher sharks ^a	-1.8080	0.2153	-2.2299	-1.3860	70.5100	<.0001	0.173	0.183	0.183

^aFor models that included the interaction term, the convergence criterion exceeded the limit. Therefore, parameter estimates may be unreliable for oceanic whitetip shark and thresher sharks.

Table A3.8. The effects of hook depth on abundance indices in which we applied hook models that included a fishing period – hook depth interaction term and a dummy variable to 12 species. The dummy variable indicated whether hook depth was less than 200 m. The table shows statistics for the interaction term (“PeriodxDepth”).

Common name	Estimate of	Standard	Confidence		Chi-	P>Chi-square
	PeriodxDepth	error	limits		square	
			lower	upper		
Tunas						
Albacore tuna	1.6416	0.4976	0.6664	2.6168	10.8900	0.0010
Bigeye tuna	0.4363	0.0809	0.2779	0.5948	29.1200	<.0001
Skipjack tuna	0.3755	0.1064	0.1670	0.5839	12.4600	0.0004
Yellowfin tuna	0.2486	0.0504	0.1497	0.3474	24.2700	<.0001
Billfishes						
Blue marlin	0.1981	0.1791	-0.1530	0.5492	1.2200	0.2687
Shortbill spearfish	-0.5620	0.6571	-1.8498	0.7258	0.7300	0.3924
Striped marlin	0.1972	0.2769	-0.3456	0.7400	0.5100	0.4764
Sailfish	-0.2744	0.7031	-1.6525	1.1037	0.1500	0.6963
Sharks						
Blue shark	0.1585	0.1111	-0.0593	0.3762	2.0300	0.1537
Mako sharks	0.5945	0.4196	-0.2280	1.4170	2.0100	0.1566
Silky shark	0.2549	0.1144	0.0307	0.4790	4.9700	0.0258
Thresher sharks	-1.7228	1.3611	-4.3904	0.9448	1.6000	0.2056

Table A3.9. The effects of hook depth on abundance indices in which we applied hook models to 10 species, restricting input data to strata where depth was less than 200 m. The table shows statistics for the fishing period term, which represents the change in abundance between the two periods. Also shown are estimates of abundance change derived from the same models that used all depth strata.

Common name	Estimate of fishing period	Standard error	Confidence limits		Chi-square	P>Chi-square	Estimated change in abundance	
			lower	upper			depth<200m	all depths
Tunas								
Albacore tuna	-1.7889	0.4243	-2.6206	-0.9573	17.77	<.0001	0.136	0.053
Bigeye tuna	-0.7895	0.1041	-0.9935	-0.5855	57.54	<.0001	0.453	0.410
Skipjack tuna	1.1928	0.1228	0.9520	1.4335	94.3	<.0001	2.487	2.413
Yellowfin tuna	-1.2389	0.0523	-1.3414	-1.1365	561.54	<.0001	0.187	0.166
Billfishes								
Blue marlin	-0.4064	0.1343	-0.6696	-0.1431	9.15	0.0025	0.523	0.591
Sharks								
Blue shark	-1.8911	0.1044	-2.0957	-1.6865	328.31	<.0001	0.154	0.134
Mako sharks	-1.3492	0.3701	-2.0746	-0.6238	13.29	0.0003	0.208	0.319
Oceanic whitetip shark	-1.2059	0.1030	-1.4077	-1.0041	137.17	<.0001	0.299	0.266
Silky shark	-2.4797	0.0829	-2.6422	-2.3172	894.85	<.0001	0.079	0.078
Thresher sharks	-1.4610	0.2517	-1.9544	-0.9677	33.69	<.0001	0.244	0.183

Table A3.10. Parameters used in the estimation of depth effects. We used the parameters in offset models to derive abundance indices of ten species. Ward and Myers (2005) estimated the parameters from four longline datasets.

Common name	Coefficient ^a			
	α	γ_1	γ_2	γ_3
Tuna-like species				
Wahoo	-5.68	-6.88	4.46	4.95
Billfishes				
Black marlin	-6.06	-9.48	22.77	-16.81
Sailfish	-5.81	-8.58	8.61	2.61
Shortbill spearfish	-4.79	-7.95	4.31	3.34
Striped marlin	-5.07	-3.99	-2.14	6.38
Other teleosts				
Great barracuda	-4.91	-8.86	-45.90	178.29
Longnosed lancetfish	-6.27	-20.84	93.31	-74.91
Mahi mahi	-4.41	-25.17	86.37	-108.34
Sharks and rays				
Mako sharks	-6.14	-9.11	26.32	-22.57
Pelagic stingray	-5.85	-9.98	28.79	-24.50

^aFor each species, the coefficients were used to estimate the depth effect $\overline{f(D_i)}$ in operation i .

$\overline{f(D_i)}$ is the mean effect of hook depth D on catch rate relative to that at a depth of 0.175 km over all hooks deployed in the operation:

$$\overline{f(D_i)} = \frac{\exp(\alpha + \gamma_1 D_i + \gamma_2 D_i^2 + \gamma_3 D_i^3)}{\exp(\alpha + \gamma_1 0.175 + \gamma_2 0.175^2 + \gamma_3 0.175^3)}$$

Table A3.11. Comparison of mean catch rates of tunas and billfishes reported by the 1950s survey in the study region (10°S–11°N, 175°E–115°W; 1951–58) and mothership expeditions during 1952–54 in the area bounded by 20°S–10°N and 150°E–130°W. Standard deviations are in parentheses.

Common name	Mothership ^a (no./1000 hooks)	Survey (no./1000 hooks)
Tunas		
Albacore tuna	4.0 (10.5)	2.1 (8.1)
Bigeye tuna	9.0 (8.2)	3.9 (10.3)
Skipjack tuna	0.4 (1.1)	1.7 (4.5)
Yellowfin tuna	25.8 (19.6)	35.8 (48.5)
Billfishes		
Black marlin	0.3 (0.9)	0.2 (1.1)
Blue marlin	6.0 (3.5)	3.4 (9.9)
Broadbill swordfish	0.1 (0.2)	0.1 (0.7)
Sailfish and spearfish	0.7 (1.1)	0.2 (1.5)
Striped marlin	0.4 (2.3)	0.3 (1.6)
Total	46.8 (20.8)	47.6 (52.8)

^aStandard deviations may not represent the true variance among operations because the original data were aggregated by month and five-degree square.

Table A3.12. Sources of information on oceanographic conditions in the study region. We derived statistics presented in the text from oceanographic data and indices for 1951–58 (1950s study period) and 1999–2002 (1990s study period).

Index name	Description	Source
Pacific Decadal Oscillation	An index based on anomalies in sea-surface temperature and sea-level pressure in the North Pacific.	Joint Institute for the Study of the Atmosphere and Oceans ftp://ftp.atmos.washington.edu/mantua/pnw_impacts/INDICES/PDO.latest accessed 9 April 2003
Southern Oscillation Index	An index of the difference in air pressure between Tahiti and Darwin.	Climate and Global Dynamics Division http://www.cgd.ucar.edu/cas/catalog/limind/SOI.signal.annstd.ascii accessed 9 April 2003
Thermocline depth (1950s)	Depth of the 20°C isotherm derived from bathythermographs taken by survey longliners during 1950–53.	NOAA Satellites and Information http://www.nodc.noaa.gov accessed 16 May 2003
Thermocline depth (1990s)	Depth of the 20°C isotherm from nine Tropical Atmosphere Ocean moorings in our study region.	NOAA Pacific Marine Environmental Laboratory http://www.pmel.noaa.gov/tao/ accessed 23 May 2003

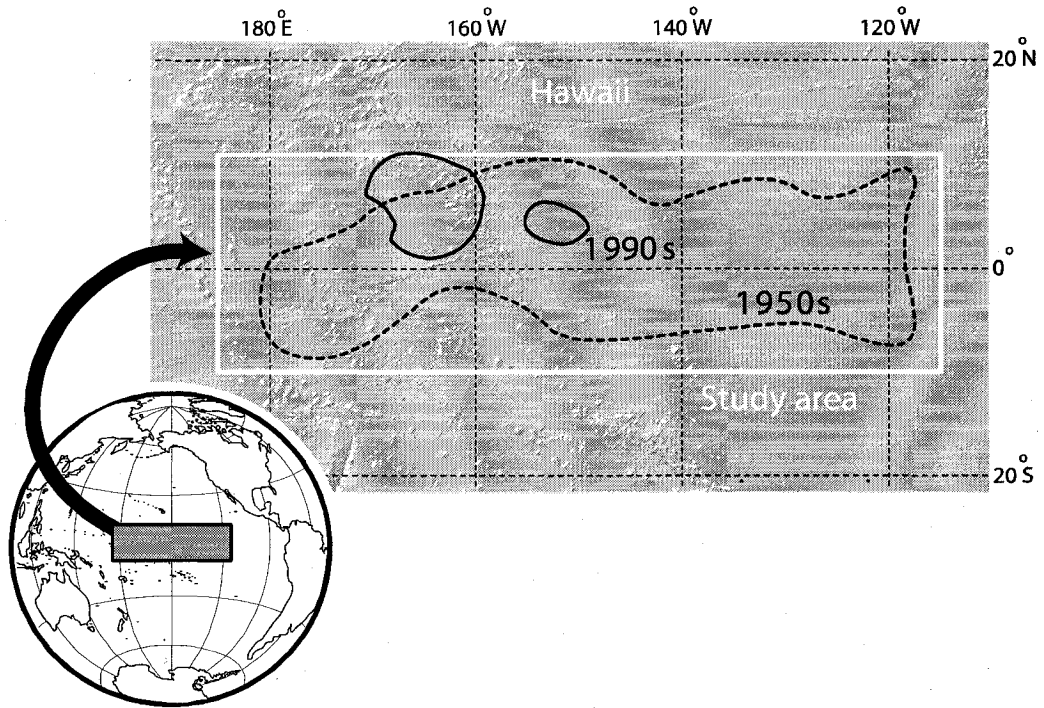


Figure A3.1. Bathymetric map of the central tropical Pacific, indicating the study region and the extent of 1950s (broken line) and 1990s (solid line) fishing activity.

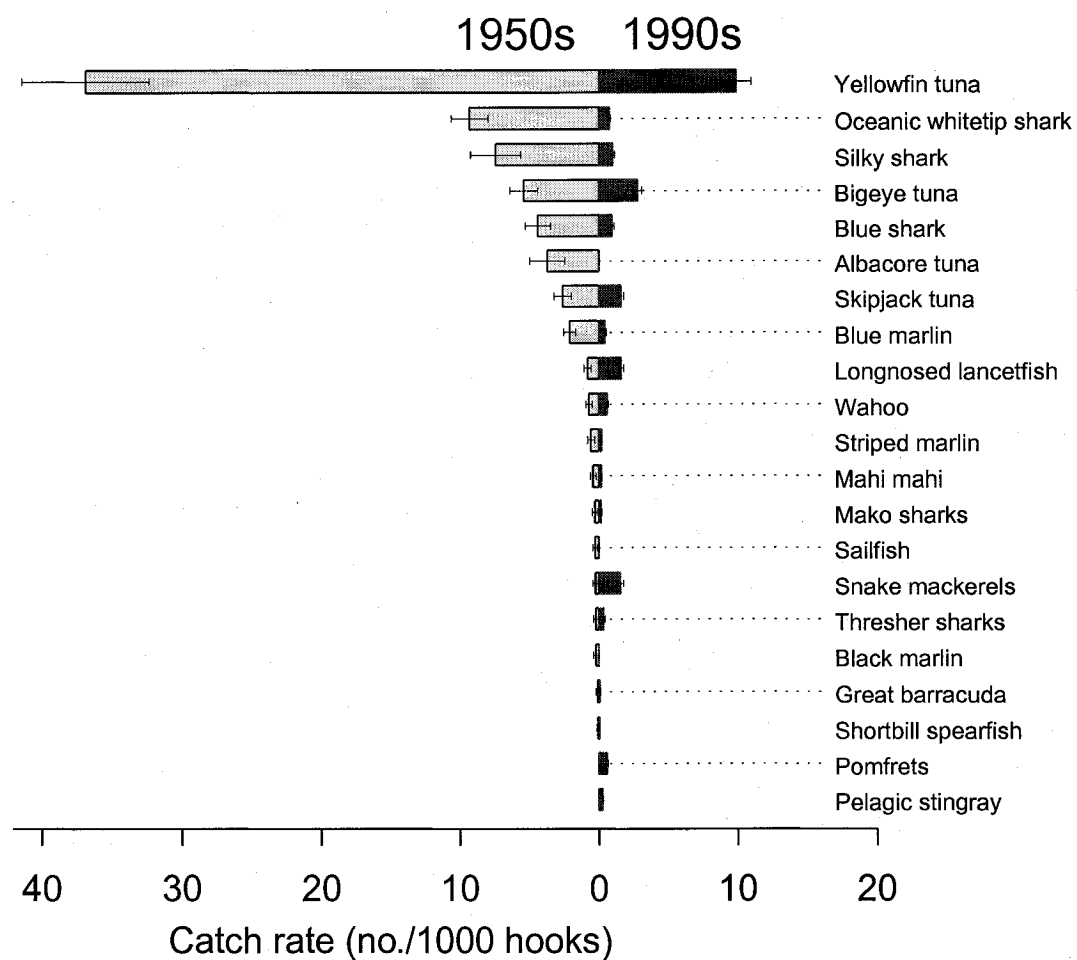


Figure A3.2. Catch rates of the 21 species most frequently caught in the study region. Horizontal bars are 95% confidence intervals for the mean catch rate in each period. Catch rates are not standardized for variations in fishing activities.

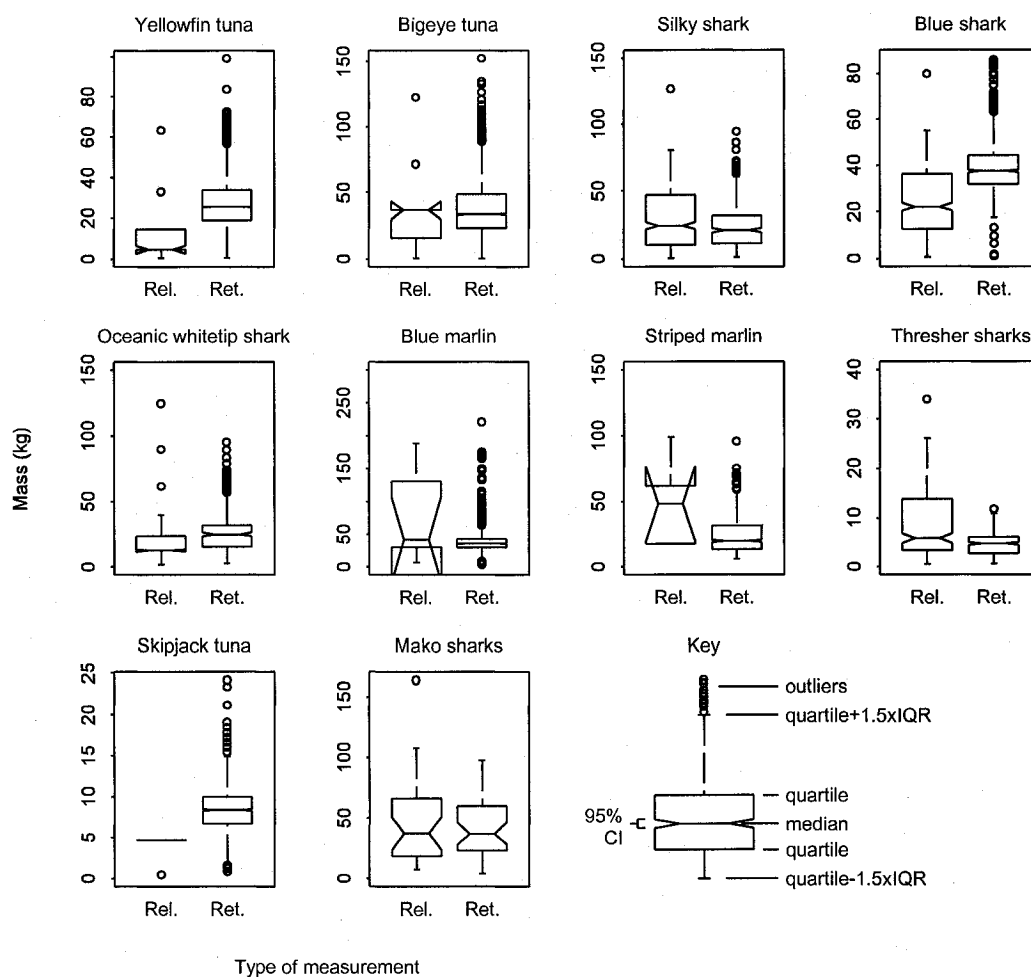


Figure A3.3. Comparison of the size composition of species measured and estimated by observers in the 1990s in the wider study area (10°S–15°N, 175°E–115°W). Visual estimates of the body-mass of released fish (“Rel.”) are compared to measurements of fish that were brought on board (“Ret.”). We predicted mass from length–mass relationships applied to length measurements. The boxplots show the interquartile range (IQR), which is the difference between the first and third quartiles. Boxplots are inside-out where the sample size is small and the confidence interval (CI) is wider than the interquartile range.