Interpreting catch per unit effort data to assess the status of individual stocks and communities

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Despite being one of the most common pieces of information used in assessing the status of
fish stocks, relative abundance indices based on catch per unit effort (cpue) data are noto-
riously problematic. Raw cpue is seldom proportional to abundance over a whole exploita-
tion history and an entire geographic range, because numerous factors affect catch rates.
One of the most commonly applied fisheries analyses is standardization of cpue data to re-
move the effect of factors that bias cpue as an index of abundance. Even if cpue is standard-
ized appropriately, the resulting index of relative abundance, in isolation, provides limited
information for management advice or about the effect of fishing. In addition, cpue data
generally cannot provide information needed to assess and manage communities or ecosys-
tems. We discuss some of the problems associated with the use of cpue data and some
methods to assess and provide management advice about fish populations that can help
overcome these problems, including integrated stock assessment models, management strat-
egy evaluation, and adaptive management. We also discuss the inappropriateness of using
cpue data to evaluate the status of communities. We use tuna stocks in the Pacific Ocean as
examples.

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Introduction

Assessment and management of fish stocks[1] has had a long
history, with many successes and failures. Failure to manage
a fishery appropriately can have disastrous effects on social
and economic conditions (e.g. northeastern Atlantic cod,
Gadus morhua). The reasons for failure can be attributed
to many factors, including inadequate or erroneous scientific
information, poor management decisions, and inability of
policy-makers to act (Sinclair and Murawski, 1997). Suc-
cessful management is more likely when decision-makers
are well informed. Therefore, it is important for scientists
to communicate the best available information to managers,
policy-makers, users, and the community at large. It is also
important to include information on uncertainty in scientific
advice, so that this can be taken into consideration when de-
cisions are made. Unfortunately, information that filters
through to the different sectors of the community is incom-
plete, and is often controlled or promoted by special

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[1] Stock is here defined as the proportion of a population consid-
ered to be a unit for fisheries management. This may be all or part
of the population, and may be defined on the basis of spatial distri-
bution or other characteristics. The definition of a stock may
change over time as a fishery expands into new areas. However,
for our purposes, we assume that the definition of a stock does
not change over time.

interests. In such an environment it is difficult to reconcile fisheries with conservation, and the challenge of managing human activities in aquatic ecosystems is to provide the whole picture to all sectors of the community.

One example of incomplete information filtering through to all sectors of the community, particularly to the fishery management and scientific communities, is the promotion by interested groups of a recent article (Myers and Worm, 2003) published in a high-profile scientific journal (see Polacheck, 2006, for a discussion). The specific article stated that "large predatory fish biomass today is only about 10% of pre-industrial levels". The analysis was based on raw catch per unit effort (cpue) data of, mostly, species of large tuna caught in Japanese industrial longline fisheries around the world. The catch of all species was combined to produce a single cpue measure for "communities" of large predatory fish. The article, and much of the media promotion centred around it, ignored decades of fisheries research. The result was that fundamentally flawed information (Hampton *et al.*, 2005) reached all sectors of the community. We demonstrate here that the analysis inappropriately combined data from multiple species to develop cpue trends for fish communities, depended on critical assumptions (e.g. that cpue is proportional to abundance) that are violated, provided no useful guidance for management, and ignored the wealth of other information available (e.g. biology, population dynamics, and total catches).

The development of the analysis of Myers and Worm (2003) was based on the observation that, for many species, cpue declines rapidly in the first few years of exploitation. However, the specific cpue decline was during a period of low catches, subsequent to which substantially greater levels of catch have been maintained at lower, but stable, levels of cpue. The phenomenon of large declines in tuna cpue at low catches is not consistent with population dynamics if cpue is assumed to be proportional to abundance. This has been a long-standing (Gulland, 1974), but largely unresolved, problem in fisheries. In some cases, the decline can be explained, but in others the cause has yet to be identified, although several hypotheses exist.

Despite being one of the most common pieces of information used in assessing the status of fish stocks, relative abundance indices based on cpue data, as used by Myers and Worm (2003), are notoriously problematic (Beverton and Holt, 1957; Paloheimo and Dickie, 1964; Gulland, 1974; Hilborn and Walters, 1992; Harley *et al.*, 2001; Walters, 2003). Raw cpue[2] is seldom proportional to abundance over the whole exploitation history and the entire geographic range, because many factors affect catch rates.

One of the most commonly applied fisheries analyses is standardization of cpue data to remove the effect of these factors in an attempt to make cpue proportional to abundance (Maunder and Punt, 2004). Even if cpue is standardized appropriately, the resulting index of relative abundance, in isolation, provides limited information about the effect of fishing. In addition, cpue data alone generally cannot provide information needed to assess and manage communities or ecosystems, because the relative catchability of the various species is generally unknown (Hampton *et al.*, 2005). Unfortunately, for many fish stocks, such as tuna species, it is not practical to collect fishery-independent data (e.g. trawl surveys), so cpue data are the main source of abundance information available.

Here we call attention, as does Polacheck (2006), to misinformation that has been widely spread in the fishery management and conservation community by addressing problems with the use of cpue data to assess single stocks and fish communities, and management of these populations. We also suggest how to improve the assessment advice provided to managers. First, we discuss the inherent problems with raw cpue data. Then, we discuss management of single stocks. Next, we discuss three methods that can help overcome problems with cpue data: integrated stock assessment models, management strategy evaluation, and adaptive management. We also point out the inappropriateness of the use of cpue data to assess the status of communities. We use tuna stocks in the Pacific Ocean as examples. Similar phenomena have been observed also in the Atlantic and Indian Oceans, but the Pacific Ocean is more familiar to the authors and has, in general, been where the widest range of models has been used to assess stock status of tuna.

Problems with cpue data

The use of cpue as an index of abundance is based on a fundamental relationship widely used in quantitative fisheries analysis. The relationship relates catch to abundance and effort:

$$C_t = qE_tN_t, \tag{1}$$

where C_t is catch at time t, E_t is the effort expended at time t, N_t is abundance at time t, and q is the portion of the stock captured by one unit of effort (often called the catchability coefficient). This equation can be rearranged to form the relationship between cpue and abundance:

$$C_t/E_t = qN_t, \tag{2}$$

making cpue proportional to abundance,

$$\text{cpue}_t \propto N_t, \tag{3}$$

provided q is constant over time. Unfortunately, q is seldom constant over the entire exploitation history; it can vary for many reasons. As mentioned above, one of the most

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[2] Raw cpue, also called nominal cpue, is simply the total catch divided by the sum of an observable measure of effort associated with the catch, e.g. total number of hooks for longline fisheries. Cpue is usually calculated for a defined time period (e.g. year), but can also be restricted by spatial or other strata.

frequently performed analyses in fisheries, cpue standardization (Maunder and Punt, 2004), attempts to standardize effort data to ensure that q can be assumed to be constant (i.e. to control the effects other than those caused by changes in stock size). Some of the factors that commonly cause q to change over time are the change in the efficiency of the fleet, species targeting, the environment, and dynamics of the population or fishing fleet. Each of these factors is briefly discussed below.

Efficiency of a fleet

Catchability often increases over time as the efficiency of the fleet increases. The efficiency of a fleet can increase through fishers learning more about the location and behaviour of fish, or how to operate gear. Efficiency also increases when new technologies are obtained. For example, use of bird radar in purse-seine fisheries increased the ability to find tuna schools. Efficiency can greatly increase when a new fishing technique is introduced. For example, the cpue of bigeye tuna (*Thunnus obesus*) by purse-seiners greatly increased with the introduction of fish-aggregating devices (FADs) in the early 1990s (Watters and Maunder, 2001). The same phenomenon applies to tuna in the Atlantic and the Indian Oceans (Fonteneau *et al.*, 2004).

Targeting by a fleet

The catchability of a species can be greatly affected when a fleet changes its targeting practice from one species to another. In general, catchability increases for the new target species, and decreases for the previous target species. For example, the increase in depth of longline gear to target bigeye tuna increased the catchability for that species, but decreased the catchability of yellowfin tuna (*T. albacares*; Suzuki *et al.*, 1977; Bigelow *et al.*, 2003). The change in targeting for bigeye tuna can also be seen in the catchability of albacore (*T. alalunga*), which decreased for Japanese vessels when they changed the spatial distribution of their operations during the late 1960s to target the more valuable bigeye tuna. However, catchability did not decrease for Taiwanese vessels, which continued to target albacore in areas where that species was most abundant (Hampton *et al.*, 2005; Figure 1).

Environmental factors

The environment can have a large influence on catchability. For example, the 1981–1983 *El Niño* reduced catchability of yellowfin tuna to the purse-seine fisheries of the eastern Pacific Ocean (EPO) to such an extent that many vessels transferred their operations to the western Pacific (Joseph, 1998). Similar reductions occurred in availability of yellowfin in the Alantic Ocean purse-seine fishery. The cpues for the longline fisheries were not reduced in a similar way in either ocean, however. Current methods used for standardizing the longline cpue data for tuna in the Pacific
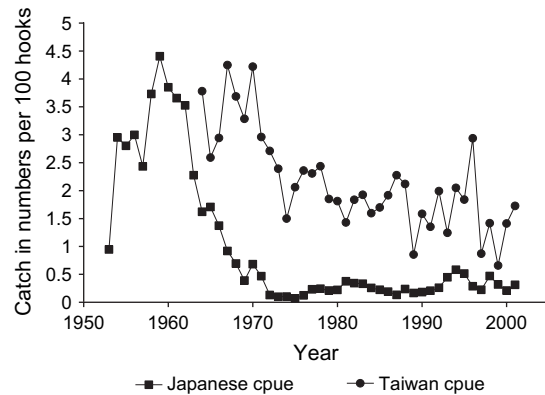

Figure 1. Comparison of albacore cpue from Japanese and Taiwanese longline vessels in Myers and Worm's (2003) area designated as the tropical Pacific Ocean (10–15°S).

Ocean use environmental data, because the distribution of tuna relative to the depth of longline gear is mediated by the environment (Hinton and Nakano, 1996; Bigelow *et al.*, 2002, 2003; Hinton and Maunder, 2003).

Dynamics of a population or fleet

The dynamics of a fish stock or a fleet can also influence how catchability changes over time (Paloheimo and Dickie, 1964; MacCall, 1990; Rose and Leggett, 1991; Rose and Kulka, 1999). Catchability is often related to abundance, and as the abundance level changes over time, so does catchability. If fish aggregate (e.g. are attracted to preferred habitat, or school), it may be just as easy to find them when abundance is low as when it is high. Therefore, as abundance decreases, the portion of the stock that one unit of effort removes may increase, even if the amount being caught decreases. This may also depend on how effort is defined. For example, each set of a purse-seine in the tuna fishery catches a school, and if the school size does not change with abundance, catch per set will remain the same. However, the time needed to find a school might change, so the measure of effort should be searching time, rather than the number of sets (Punsly, 1987). This may include removal of the time taken to conduct a set, which is not part of the searching time (Punsly, 1987).

The spatial expansion of the fleet can also cause the relationship between cpue and abundance to be non-linear. The Japanese longline fleet expanded from west to east across the Pacific. Walters (2003) showed how simple non-spatial ratio estimates, as used by Myers and Worm (2003), should not be used in such analyses. Walters (2003) argues that averaging for any time period must necessarily make some assumptions about what catch rates would have been in spatial strata that had not yet, or were no longer, being fished. He also stressed that ignoring the unfished strata (averaging only over the areas that were fished) amounts to assuming that they behaved the same as

the fished strata, leading potentially to severe hyperdepletion in abundance indices for fisheries that developed progressively over large regions, as did the Japanese longline fishery in the Pacific Ocean.

Other factors

The factors listed above are some of the most common ones that affect the relationship between cpue and abundance. However, there are numerous other factors that may influence catchability or the assumption that cpue is proportional to abundance. Examples include shark damage to target species caught on hooks (Myers and Worm, 2003), gear saturation, gear interference, misreporting (Baum *et al.*, 2003), stock structure (e.g. harvesting multiple stocks together, or fishing only a small portion of a stock), capture of more vulnerable individuals in initial stages of the fishery (Gulland, 1974; Hilborn and Walters, 1992; Nakano and Bayliff, 1992), age- or size-specific selectivity, and individual variability in natural mortality.

Management influence on cpue

Some management measures may also interfere with the assumption that cpue is proportional to effort. For example, closed seasons to restrict total catch can influence overall annual catch rates. Since 1966, the Inter-American Tropical Tuna Commission (IATTC) has used closed seasons for the surface fishery to manage the total catch of the yellowfin tuna fishery in the EPO (Joseph, 1970). The fishery was restricted when the quota was reached, resulting in a much shortened fishing season, with most effort in the first half of the year when cpue is generally higher. The result was an increase in cpue and apparent abundance when computed on an annual basis, because of concentration of effort in the high-cpue period of the year (Joseph, 1970). Effects could be similar for closed areas. In both cases, these problems can be dealt with by appropriate temporal and spatial stratification in stock assessment models.

To what portion of the stock does the cpue relate?

Cpue measures only the component of the population that is vulnerable to the gear; it may be proportional to this component of the population, but not to the total population. The proportion of the population that is vulnerable to the fishery depends on gear selectivity, size and age of fish, horizontal and vertical distribution of fish, and fishing practice of the fleet. For example, the longline cpue of bigeye represents only the abundance of large deep-dwelling fish, whereas the purse-seine cpue of bigeye covers only small surface-dwelling fish.

The amount of overlap of spatial distribution of the fish population and the fishing fleet can have a considerable influence on how cpue relates to abundance. If the fishery operates on only a fraction of the population and the mixing rates of fish among areas is low, there will be little relationship between cpue and total population abundance. Despite tuna being regarded as highly migratory, movement of most fish is limited for species like yellowfin, skipjack (*Katsuwonus pelamis*), and bigeye tuna (Sibert and Hampton, 2003), and there is a distinct possibility of local depletion and different cpue trends in different parts of a very large ocean.

Management of fish stocks

One goal of analysing data about a fish stock, including relative abundance trends from cpue data, is to provide management advice. Fisheries management can have many objectives, including conservation, political, social, and economic objectives. However, the most common advice is based on maximizing yield from a fishery. For example, maximum sustainable yield (MSY) has been included in conventions of the IATTC and the International Commission for the Conservation of Atlantic Tunas (ICCAT), and it is part of the Convention on the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean and the Magnuson–Stevens Fishery Conservation and Management Act of the United States.

In general, as fish are removed from a population, that population will decrease in abundance, and the average size of fish in the population will also decrease. Existence of sustainable fisheries is based on an increase in surplus production[3] as abundance decreases towards a level corresponding to MSY. In fact, standard fisheries science theory predicts that, to maximize yield, the abundance level must be reduced to below, often substantially below, half the unexploited population size (Clark, 1991; Maunder, 2003a). The required level of depletion and associated yield can change for numerous reasons, including the fishing method (and hence age- or size-selectivity) used (Maunder, 2002).

Relative abundance trends in isolation tell us nothing about levels of abundance corresponding to MSY, or abundance levels that cause risk of fishery or population collapse. Rules of thumb such as abundance level should be >20% of the unexploited level (Beddington and Cooke, 1983; Francis, 1993), or reference points (e.g. the biomass that corresponds to MSY as a fraction of unexploited biomass, B_{MSY}/B_0) calculated for similar species can be used. However, information on the biology and the dynamics of the stock is needed to produce and evaluate specific reference points and management strategies for that stock.

Several reference points (e.g. B_{MSY}/B_0) refer to unexploited abundance. This requires estimates of unexploited biomass by either (1) using cpue from the start of substantial fishing (e.g. Myers and Worm, 2003), which increases

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[3] Production through recruitment and growth is greater than the loss through natural mortality (i.e. production is greater than that required to maintain the population at its current level), so the additional, or surplus, production can be harvested.

the potential problems with interpretation of cpue data, or (2) using population dynamics to extrapolate back to the unexploited condition (e.g. Maunder and Watters, 2003), which involves several assumptions (e.g. a form of the stock-recruitment relationship or the production function) that may not be satisfied. There is also uncertainty attributable to natural fluctuations in unexploited conditions (Hampton *et al.*, 2005), or bias caused by changing baselines (Pauly, 1995). Starting stock assessment models from unexploited states (i.e. before industrial fisheries commenced) can remove some of the influence of changing baselines, but the environment can still influence that baseline.

There are several factors other than fishing that influence the abundance of fish stocks. For example, Mediterranean populations of Atlantic bluefin tuna (*T. thynnus*) have experienced substantial fluctuations in abundance for centuries while removals have been small (Ravier and Fromentin, 2001, 2004). Therefore, it is important to estimate the effect of fishing compared with other influences on the population. This requires knowledge of the total removals from the stock, rather than just those used in the cpue analysis, which may constitute only a small component of total removals (Hampton *et al.*, 2005). In addition to total removals, productivity of the stock should be incorporated into the analysis of the effect of fishing on abundance. Therefore, population dynamics models are needed to estimate the effect of fishing.

Integrated stock assessment models

Integrated stock assessment (Fournier and Archibald, 1982; Deriso *et al.*, 1985; Bergh and Butterworth, 1987) is a statistical analysis that uses all available information about a stock. It is one of the main approaches used in modern fisheries stock assessment (Quinn, 2003; Maunder, 2003b). Integrated analysis has become the dominant method for assessing tuna stocks for which there is sufficient information (e.g. Fournier *et al.*, 1998; Hampton and Fournier, 2001; Butterworth *et al.*, 2003; Maunder and Watters, 2003). The method represents scientific understanding of the dynamics of the system in equations that define how the population and its structure (e.g. the age structure) changes over time. Biological information (e.g. growth and mortality) is included in the analysis by providing or estimating values for parameters of the model. Many types of data (e.g. length frequency of the catch, tag recaptures), including relative abundance indices developed from cpue data, are used in the analysis to provide estimates of the unknown parameters. Further, some implementations (e.g. Hampton and Fournier, 2001; Maunder, 2001) of this type of model can also take into account the spatial heterogeneities of stocks and fisheries, and also age-dependent movements of fish among areas (this characteristic being of major interest for all tuna stocks). The methods used to estimate the model parameters are statistical, so they provide measures of uncertainty about estimates and predictions of the model. Unfortunately, true uncertainty in the assessment remains

difficult to estimate, so this is an area of continuing research (Parma, 2001). For example, a fitted assessment model may attribute recent increases in catch to either increases in catchability, increases in recruitment, or both (Watters and Maunder, 2001). The parametric structure of these models allows explicit statement of alternative hypotheses about population dynamics and fishery impacts, and the statistical structure of these models allows evaluation of these hypotheses with respect to available data.

Advantages of integrated stock assessment models include their ability to use cpue to represent the component of the population with which it is associated (i.e. spatial or age strata), and that they can combine cpue for multiple components of the population. For example, cpue data from longline vessels provide information on large bigeye tuna, while cpue data from purse-seiners provides information on small bigeye tuna (Maunder and Watters, 2003).

Integrated models represent knowledge of the system, so they can be used in a variety of ways to provide management advice. They can be used to estimate management reference points (e.g. MSY) and to evaluate current stock status with respect to these reference points, to determine the effect of the fishery on the stock, and to predict what will happen in future and under different management strategies. Their statistical nature allows estimation of uncertainty, which is an important consideration when making decisions. For example, integrated stock assessment models are used to estimate the rate of fishing mortality in relation to fishing mortality that produces MSY and associated uncertainty for yellowfin and bigeye tuna in the western and central Pacific Ocean (Hampton *et al.*, 2004a, b).

Integrated stock assessment models can be used to estimate the relative effects of fishing and other factors on the population. They can also be used to estimate the effect of each component of the fishery. For example, abundance of yellowfin tuna in the EPO has fluctuated over time, with the fishery and the environment having about the same amplitude of effect on abundance (Figure 2). The effect of longline fishing has been negligible (Figure 2), simply because total yellowfin catches by longlines have always been far less than those of surface gear in the area.

Integrated models use all available information, so they can be used to find inconsistencies in the data. For example, the rapid decline in cpue of yellowfin tuna in the longline fishery during the first few years of the fishery is not consistent with current understanding of population dynamics. Catches were low during the period of rapid decline of the cpue, then large catches were achieved during the period when cpue was stable at relatively low levels (Figure 3). The integrated model estimates large deviations in the relationship between effort and fishing mortality for the early years, indicating that cpue is not consistent with population dynamics and the data as a whole. In general, integrated stock assessment models show that raw cpue data from longline vessels for tuna can be misleading if not interpreted in the context of other
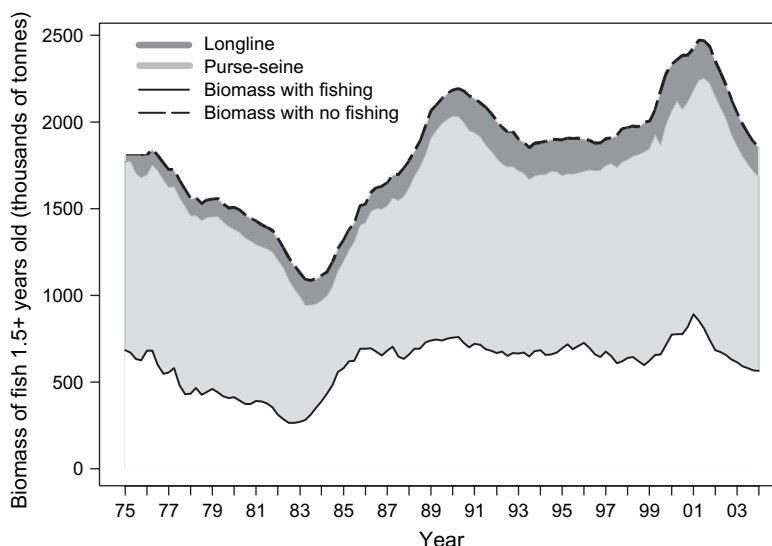
Figure 2. Abundance of yellowfin tuna in the eastern Pacific Ocean (east of 150°W), showing the impact of fishing from purse-seine and longline fisheries (after Maunder and Harley, 2006). The lower black line is the estimate of current biomass, the border between the light and dark shaded areas is the estimated biomass in the absence of purse-seine fisheries, and the upper dashed black line is the estimated biomass in the absence of all fishing.

data, biological information, and population dynamics theory (Hampton *et al.*, 2005).

Integrated assessment models are only as reliable as the data and assumptions on which they are based. If the data or assumptions are biased, then the integrated assessment results may also be biased. However, as mentioned above, by including all information into the analysis, integrated analyses can help identify conflicts among data sets and with model assumptions, which help identify problems with data and assumptions. Often, the additional data used

in integrated analysis, such as length-composition data, do not provide additional information on exploitation rate or changes in stock size. In the case of length frequency data, this is because the information is used to determine selectivity to the gear, particularly if selectivity is allowed to change over time. Additionally, many of the data are not available at the start of the exploitation period, so do not help determine the unexploited baseline required for many management reference points. However, in some cases the additional information is vital. For example, surplus production models,
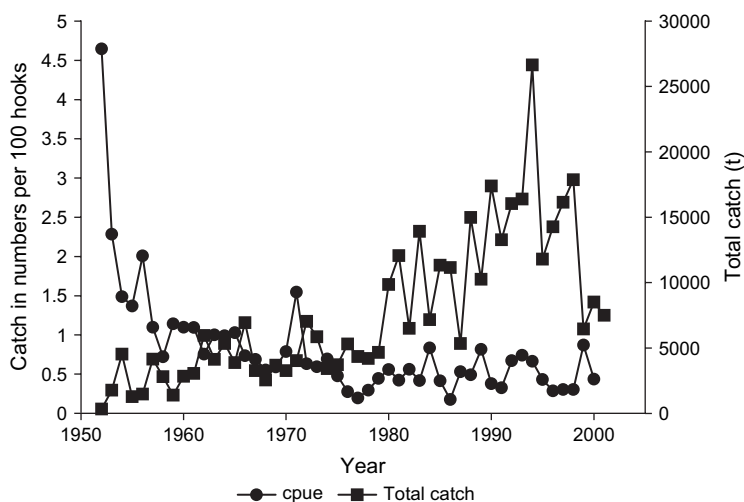

Figure 3. Total catch from all gears and longline cpue for yellowfin tuna in Myers and Worm's (2003) area designated as the tropical Pacific Ocean (10−15°S).

which do not model gear-specific selectivity and cannot include length or age frequency data, were unable to represent the change in effort distribution between fishing on dolphin-associated schools and fishing on free-swimming schools, or the regime change in productivity for the EPO yellowfin tuna stock (Tomlinson, 2001). In another example, longline cpue for the bigeye tuna stock in the EPO, which represents older fish, had a delay of several years in reflecting the recent declines in biomass, owing to the introduction of the purse-seine floating-object fishery and poor recruitment, that the integrated assessment model estimated from information in catch-at-length data from the purse-seine floating-object fishery (Maunder and Harley, in press).

Management strategy evaluation

Because of problems with cpue data, it may be beneficial to develop assessment methods and management strategies that are robust to the multiple problems and bias inherent in the use of cpue data. Current research in fisheries has focused on the use of management strategy evaluation as a tool to manage fish stocks (De Oliveira *et al.*, 1998). This involves using simulation analysis to evaluate several comprehensive management strategies under different possible states of nature, in order to define a strategy that is robust and provides a desirable outcome. A comprehensive management strategy includes a selection of which data are collected (Walters and Parma, 1996), and how they are analysed (including use of integrated stock assessment models), and then proposes management action based on the results of the analysis.

Management strategy evaluation could be used to determine management strategies that are robust to problems in cpue data for tuna fisheries. However, management strategy evaluation has only recently been applied to tuna and billfish. Punt *et al.* (2001), Kell *et al.* (2003), and Haist *et al.* (2002) used management strategy evaluations for broadbill swordfish (*Xiphias gladius*) off eastern Australia, Atlantic tuna stocks, and southern bluefin tuna (*T. maccoyii*), respectively. Below, we provide a hypothetical example for the yellowfin tuna stock in the EPO that includes the evaluation of three management strategies.

(i) Maintain fishing mortality at a level corresponding to MSY (F_{MSY}), based on the estimate from the current integrated stock assessment that begins in 1975, to eliminate uncertainties in the early cpue data. This strategy may still contain biases in the cpue since 1975.

(ii) Fish at F_{MSY}, based on estimates from the current integrated stock assessment, but extend the assessment back to 1950 so that it includes the uncertainties and biases in the early cpue data.

(iii) Define a simple decision rule that increases effort by 10% if the 3-year moving average of cpue increases by 10% or more, and decreases effort by 10% if the 3-year moving average of cpue decreases by 10% or more.

These management strategies provide a range of uses of cpue data, with Strategy 1, the current assessment method, being a compromise between Strategies 2 and 3. Management Strategy 3 does not allow one to optimize the performance of the fishery, but if the current fishery is appropriate and management objectives favour stability over optimization, it may be a good one (Hilborn *et al.*, 2002). Management Strategy 2 uses all the information (with respect to time), and allows the population model to start from an unexploited population level, an assumption that can provide substantial information to the analysis, but has a greater chance of biases in the cpue. These strategies would be tested under different states of nature, including those that assume that cpue is not proportional to abundance. The strategy that performs well with respect to management objectives, for all or most states of nature, would be chosen to manage the fishery.

Adaptive management

It is important to provide as much information as possible to allow optimal management of a stock. Unfortunately, some management strategies actually decrease the amount of information that is available to manage a stock. Many management regulations will break a continuous series of cpue data. For example, changes in the minimum legal size will change the portion of the population represented by the cpue and, as mentioned above, area or time closures can bias cpue data. Therefore, the effect of management strategies on the information available to assess the stock should be taken into consideration. The effect of information gained or lost from a management strategy could be included in the management strategy evaluation described above.

It is possible to develop management strategies that actually increase the amount of information available. This approach, often called active adaptive management, has attracted significant attention over the past 20 years (Walters, 1986). The basic concept is to design management strategies that shock the system so that a signal (contrast) can be seen in the data. For example, if the relative abundance index based on cpue data is flat, this could be because the population is only lightly exploited and fishing is not influencing cpue or because cpue is not proportional to abundance (hyperstability). By greatly increasing catch in one year, it should be possible to see whether this effects cpue data. However, one should be careful when applying this approach, because such an experiment may cause damage to the stock. Appropriate monitoring should be implemented, and contingency plans should be in place.

The IATTC implemented experimental management of the EPO yellowfin fishery by issuing an increased quota of 240 million pounds (131 000 t) for three years, beginning in 1969 (Joseph, 1970). As a safeguard, strict catch limitation would come into force if the cpue fell below a minimum safe level. At that time the fishery had expanded

spatially, and it was thought that the potential yields might be much greater than previously, when the fishery was conducted relatively close to the coast and at a few offshore islands and banks (Joseph, 1973). The assessment model (Schaefer, 1957) was used to predict the outcome of this new quota, and differences from these expectations would provide additional information for stock assessment. Results of experimental management proved that the sustainable yields were much greater than they would have been if the fishery had not expanded farther offshore (Joseph, 1973; Die *et al.*, 1990).

Changes in management that provide information about the status of a stock can be planned, unplanned, or natural. One of the greatest fisheries experiments was unplanned; World War II showed that stocks can rebuild if catches are reduced. Tuna stocks in the Pacific Ocean experienced only limited effect attributable to WWII simply because catches of tuna were relatively low prior to the war, and tuna stocks were still at or near virgin condition during this period. However, other unplanned experiments took place, including introduction of the 200-mile Exclusive Economic Zones and movement of purse-seiners from the EPO to the west and central Pacific Ocean (WCPO), owing to reduced catchability in the EPO caused by the 1981−1983 *El Niño*. In addition to the increased quota described above, the IATTC developed a closed area for management of yellowfin tuna (the Commission Yellowfin Regulatory Area, CYRA), which forced the fleet to develop fisheries in other areas, and in some years provided experimental fishing areas within the CYRA. Data associated with these planned and unplanned experiments were used, and could be further investigated, to determine the potential gain in information from adaptive management and aid in the design of future adaptive management programmes.

Problems with the use of cpue data to assess communities

Myers and Worm's (2003) analysis of large pelagic fish implicitly assumed that the catchability coefficient (q in Equation (1)) is the same for each species. This is a fundamental flaw in their analysis, because species coexist by occupying different niches. Therefore, different species have different characteristics and therefore different catchabilities to the gear. For example, skipjack tuna constitute the most abundant commercially important tuna in the world's oceans, and yet they comprise only a very small portion of the longline catch. It can be shown mathematically, using simplifying assumptions, that more often than not, the cpues of combined species will decrease more rapidly than the total abundance of the individual populations, given that no other factor influences the relationship between cpue and abundance. This is because the population with the highest catchability often contributes a greater portion to the cpue, and is the population that is most depleted. In general, if q

is not similar for all the species being combined, cpue will not be proportional to community abundance. For example, the composition of species in the Pacific Ocean predicted from longline cpue data is very different from that estimated by methods that include estimates of catchability (Figure 4). Often a single species can dominate the decline in cpue. To exacerbate this problem, catchability is seldom constant over time.

Faced with differences in catchability, the only way to combine cpue for multiple species would be to develop a measure of community abundance, which would require estimates of age-specific catchability for each species. In general, direct measurement or estimation of catchability is not possible, so stock assessment models must be used to estimate catchability and total abundance. Estimates of total species abundance can then be summed and trends in total abundance examined over time. Unfortunately, integrated models are relatively data-intensive, so may not be applicable for all situations. However, the problem of lack of data cannot be solved by simply using methods that hide the need for information on implicit assumptions. In these situations, Bayesian methods (Punt and Hilborn, 1997), used in conjunction with integrated analyses (Maunder, 2003b), which explicitly describe the assumptions in the prior distributions, may be appropriate.

Management of communities and ecosystems

Management of communities and ecosystems is quite different from single-species management (Mace, 2001; Link *et al.*, 2002; Maunder, 2002; Sainsbury and Sumaila, 2003). For example, it would be impossible to maximize the yield of two species caught simultaneously by the same gear unless their productivities and catchabilities are the same, which is highly unlikely. In the EPO purse-seine fishery on FADs, bigeye tuna are exploited at a rate that exceeds MSY, while skipjack tuna are exploited at a rate well below MSY. Only a change in fishing technology might rectify this problem. Another example is the trade-off between bycatch of dolphins in the dolphin-associated fishery for yellowfin tuna and the bycatch of many other species in the FAD fishery (Hall, 1998).

Several specific questions arise when considering management of ecosystems. For example, what would be the impact on the ecosystem if all commercially valuable stocks were fished at their single-species MSY levels? Do apex predators in the pelagic system play a role that is greater than their absolute abundance? Is it possible that declines in abundance of large predators have increased the survival of juveniles, which sustain the large catches at (apparently) low levels of abundance? Such questions cannot be answered by single-species approaches. Analyses using multispecies (e.g. Stefansson and Palsson, 1998; Hollowed *et al.*, 2000; Stefansson, 2003) and ecosystem (e.g.
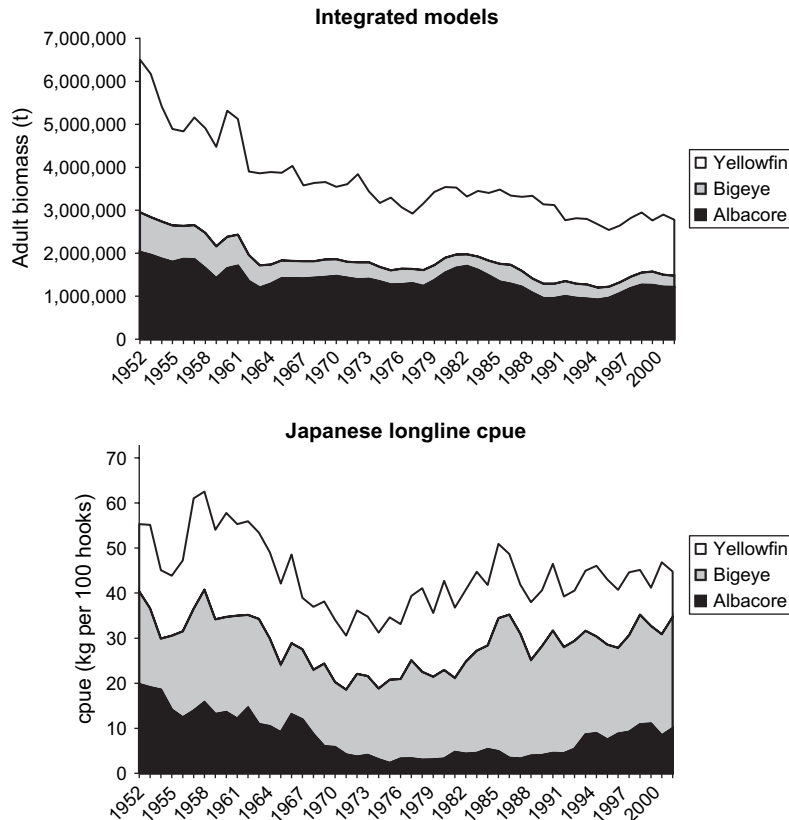
Figure 4. The composition of species in the Pacific Ocean predicted from longline cpue data (lower panel) and integrated stock assessments that estimate the catchability (upper panel) (Labelle and Hampton, 2003; Hampton *et al.*, 2004a, b).

Polovina, 1984; Walters *et al.*, 1997, 1999; Christensen and Walters, 2000; Olson and Watters, 2003) models have been used to address some of these questions (May *et al.*, 1979; Pauly *et al.*, 2000; Watters *et al.*, 2003). For example, using Ecosim models, Walters *et al.* (2005) showed that widespread application of single-species MSY-based policies would, in general, cause severe deterioration in ecosystem structure, in particular, the loss of top predator species. Their result supports the practice of protecting some forage species specifically for their value in supporting larger piscivores (Walters *et al.*, 2005).

Discussion

Our review of the available literature, including our own published analyses, has shown that simple cpue-based analyses used to determine the status of fish communities, particularly for tuna and other large pelagic predators, are inappropriate and almost certain to lead to erroneous conclusions. Raw cpue data can be misleading, because there are many factors that can cause catchability to change and so prevent cpue from providing accurate indices of abundance. To use cpue data in isolation of the wealth of data that are available on the biology and fisheries for these

species is not common sense. Even if cpue could potentially monitor the relative abundance of some part of a stock or community, models based solely on cpue data cannot be used to provide predictions for the future, or to evaluate different management strategies. Even the simplest stock assessment models (biomass dynamic or surplus production models), which have been applied to tuna stocks (Schaefer, 1954, 1957; Pella and Tomlinson, 1969), despite their limitations (Maunder, 2003a), include catch data and information about population dynamics that can help interpret cpue data and identify contradictions. Moreover, it is generally inappropriate to combine the cpue across species to monitor community abundance, because overall trends in cpue can be misleading, reflecting changes in abundance of one or a few dominant species in the catch.

The concerns we raise about the use of raw Japanese longline cpue to infer abundance trends of tuna, as done by Myers and Worm (2003), are not new. Several scientific papers by researchers who studied tuna in the different oceans have previously identified these issues. For example, the IATTC Bulletin series contains several contributions produced jointly by Japanese and IATTC scientists, starting with Suda and Schaefer (1965), which describe the Japanese longline fishery in the eastern Pacific Ocean.

In particular, the contribution of Nakano and Bayliff (1992) identifies some of these concerns and issues.

It is possible to use all available information with integrated assessments. Integrated stock assessment has been applied for more than two decades, and several general computer programs have been developed to implement integrated analysis. For example, Stock Synthesis (Methot, 1990) and its successor Stock Synthesis II have been used to assess numerous fish stocks in the United States, Coleraine (Hilborn *et al.*, 2000; http://www.fish.washington.edu/research/coleraine/) has been used to assess fish stocks in several countries, CASAL (Bull *et al.*, 2004) has become the main stock assessment tool used in New Zealand, and MULTIFAN-CL (Fournier *et al.*, 1998; Hampton and Fournier, 2001; http://www.multifan-cl.org/) is becoming the standard for tuna stock assessment. By integrating all available information, integrated analysis shows where information is in conflict, which helps identify areas that require more research.

Integrated stock assessment is not the solution to all fisheries management problems. It cannot create information that is not already available; it can only synthesize information into a form that is usable. In many cases, additional information is required to provide the management advice required, requiring collection of more data. It is preferable to obtain data that are independent of the fishery and collected using a standard protocol each year. However, such surveys may not be appropriate for every fish stock. For example, appropriate survey techniques are yet to be developed for most tuna stocks and that situation is not likely to change in the foreseeable future, because oceans are too wide and too deep, and tuna are, on an ocean-basin scale, too dilute. In these cases, other methods, such as comprehensive tagging programmes, may be appropriate. In other cases, adaptive management may provide the additional information needed to interpret cpue data.

In many cases, available data may result in integrated stock assessment producing results that are too uncertain to provide the management advice asked for (e.g. is the current level of fishing mortality greater than that which would support MSY?). In such cases, use of prior information using Bayesian analysis (Punt and Hilborn, 1997) provides a means of including information borrowed from other species or the inclusion of common-sense (hopefully) "information" into assessments where specific data might not be available. Many assessments of tuna stocks now use integrated stock assessment in a Bayesian framework (Fournier *et al.*, 1998; Maunder, 2003b; Maunder and Watters, 2003). Bayesian analysis also provides a framework for estimation of uncertainty. Unfortunately, full Bayesian integration for the types of integrated stock assessment models used for tuna is not currently feasible owing to computational demands (Maunder, 2003b), so approximations are required (Fournier *et al.*, 1998; Hampton and Fournier, 2001; Maunder *et al.*, 2006).

In cases for which information is inadequate to provide the required management advice, management strategy evaluation may be a good option. This will, hopefully, provide a management strategy that will perform reasonably well with respect to management objectives while providing protection against stock collapse. Even when information is abundant, management strategy evaluation may be a useful tool.

Ecosystem management is becoming popular as a concept and has been applied to varying degrees (e.g. restrictions on forage fish). However, science has not yet reached the stage where reasonable whole ecosystem management can be applied. There are still many questions to be answered, especially in management of pelagic ecosystems. Currently, only management of trade-offs among a few important species can be made. Multispecies models show promise, but whole ecosystem models have far too many unknowns to provide appropriate management advice. We consider the current ecosystem models to be hypothesis-generators, providing important hypotheses to test by collection and analysis of new data. Unfortunately, many scientists naively use them as hypothesis tests. However, in some cases, the results of ecosystem models are robust to uncertainties and can be used to provide management advice. Ecosystem-based management policies are necessarily based on quantification of the expected impact of alternative policy choices; the issue is not whether or not to use models but only which models to use.

Despite the pessimism of Quinn (2003), who considers the golden age of stock assessment to have ended, we believe that there is still huge potential to improve stock assessment and fishery management based on integrated stock assessment, management strategy evaluation, adaptive management, and multispecies models. As computers become more powerful, improved statistical methods are developed, and routine collection of previously inaccessible data (e.g. archival tagging) becomes possible, much better understanding of fish stocks and their exploitation and management will be possible. However, unless there is a change in the willingness of policy-makers to act with appropriate management measures, all these efforts will be wasted (Maunder and Harley, in press).

We have portrayed a bleak picture of cpue data and analyses dependent solely on them. However, this does not mean that cpue-based analyses are useless. They are not an alternative to integrated stock assessments, but they do provide useful information about fisheries changes, discussion points, and indicate areas of future research, e.g. more careful examination of the utility of historical fisheries data. They also provide a component of information analysed by integrated models, and interpretation of such information is important. In instances in which full stock assessments are not possible, e.g. when catch time-series are not available, cpue-based analyses will play an important role in management, but we have shown here that there are many factors that must be considered, and that great caution is necessary

in interpreting results. In these cases, decision rules or management strategy evaluation are important.

In conclusion, while one recent analysis based solely on cpue data (Myers and Worm, 2003), suggesting that the worldwide community of large pelagic fish has become highly depleted since the late 1960s, has received much media attention, we believe that we have demonstrated that the analysis was based on flawed methodology and misinterpretation of the data, as already demonstrated by other authors (Walters, 2003; Hampton *et al.*, 2005; Polacheck, 2006). We propose that assessment of fish stocks and communities be based on considering all available data, and that historical data be carefully examined before being included so as to preclude invalid assumptions and erroneous conclusions. Methods should be developed to better analyse current information and to use it in management, additional data should be collected, and methods to improve information extracted from data should be investigated.

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References

Baum, J. K., Kehler, D., Myers, R. A., Worm, B., Harley, S. J., and Doherty, P. A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science, 299: 389−392.

Beddington, J. R., and Cooke J. G. 1983. The potential yield of fish stocks. FAO Fisheries Technical Paper, 242. 47 pp.

Bergh, M. O., and Butterworth, D. S. 1987. Towards rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. South African Journal of Marine Science, 5: 937−951.

Beverton, R. J. H., and Holt, S. J. 1957. On the Dynamics of Exploited Fish Populations. Ministry of Agriculture, Fisheries and Food, London. 533 pp.

Bigelow, K. A., Hampton, J., and Miyabe, N. 2002. Application of the habitat-based model to estimate effective longline effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*). Fisheries Oceanography, 11: 143−155.

Bigelow, K., Maunder, M. N., and Hinton, M. 2003. Comparison of deterministic and statistical habitat-based models to estimate effective longline effort and standardized cpue for bigeye and yellowfin tuna. Standing Committee on Tuna and Billfish, 16, RG-3. 18 pp.

Bull, B., Francis, R. I. C. C., Dunn, A., McKenzie, A., Gilbert, D. J., and Smith, M. H. 2004. CASAL (C++ algorithmic stock assessment laboratory): CASAL User Manual v2.06−2004/09/26. NIWA Technical Report, 126. 261 pp.

Butterworth, D. S., Ianelli, J. N., and Hilborn, R. 2003. A statistical model for stock assessment of southern bluefin tuna with temporal changes in selectivity. South African Journal of Marine Science, 25: 331−362.

Christensen, V., and Walters, C. 2000. Ecopath with Ecosim: methods, capabilities and limitations. University of British Columbia Fisheries Center Research Report, 8: 79−105.

Clark, W. G. 1991. Groundfish exploitation rates based on life history parameters. Canadian Journal of Fisheries and Aquatic Sciences, 48: 734−750.

De Oliveira, J. A. A., Butterworth, D. S., and Johnston, S. J. 1998. Progress and problems in the application of management procedures to South Africa's major fisheries. *In* Fishery Stock Assessment Models. Proceedings of the International Symposium on Fishery Stock Assessment Models for the 21st Century, October 1997, Anchorage, Alaska, pp. 513−530. Ed. by F. Funk, T. J. Quinn, J. Heifetz, J. N. Ianelli, J. E. Powers, J. J. Schweigert, P. J. Sullivan, and C. I. Zhang. University of Alaska, Fairbanks. Alaska Sea Grant College Program Report No. AK-SG-98−01.

Deriso, R. B., Quinn, T. J., and Neal, P. R. 1985. Catch-age analysis with auxiliary information. Canadian Journal of Fisheries and Aquatic Sciences, 42: 815−824.

Die, D. J., Restrepo, V. R., and Fox, W. W. 1990. Equilibrium production models that incorporate fished area. Transactions of the American Fisheries Society, 19: 445−454.

Fonteneau, A., Ariz, J., Delgado, A., Pallares, P., and Pianet, R. 2004. A comparison of bigeye stocks and fisheries in the Atlantic, Indian and Pacific Oceans. Collective Volume of Scientific Papers ICCAT, 57: 41−66.

Fournier, D. A., and Archibald, C. 1982. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences, 39: 1195−1207.

Fournier, D. A., Hampton, J., and Sibert, J. R. 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore *Thunnus alalunga*. Canadian Journal of Fisheries and Aquatic Sciences, 55: 2105−2116.

Francis, R. I. C. C. 1993. Monte Carlo evaluation of risks for biological reference points used in New Zealand fishery assessments. Canadian Special Publication in Fisheries and Aquatic Sciences, 120: 221−230.

Gulland, J. 1974. Catch per unit effort as a measure of abundance. Collective Volume of Scientific Papers ICCAT, 3: 1−11.

Haist, V., Parma, A. M., and Ianelli, J. 2002. Initial specifications of operating models for southern bluefin tuna management procedure evaluation. Commission for the Conservation of Southern Bluefin Tuna. CCSBT-ESC/0209/07. 42 pp.

Hall, M. A. 1998. An ecological view of the tuna−dolphin problem: impacts and trade-offs. Reviews in Fish Biology and Fisheries, 8: 1−34.

Hampton, J., and Fournier, D. A. 2001. A spatially disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. Marine and Freshwater Research, 52: 937−963.

Hampton, J., Kleiber, P., Langley, A., and Hiramatsu, K. 2004a. Stock assessment of yellowfin tuna in the western and central Pacific Ocean. Standing Committee on Tuna and Billfish, 17, SA-1. 76 pp.

Hampton, J., Kleiber, P., Langley, A., and Hiramatsu, K. 2004b. Stock assessment of bigeye tuna in the western and central Pacific Ocean. Standing Committee on Tuna and Billfish, 17, SA-2. 70 pp.

Hampton, J., Sibert, J. R., Kleiber, P., Maunder, M. N., and Harley, S. J. 2005. Changes in abundance of large pelagic predators in the Pacific Ocean. Nature, 434: E2−E3.

Harley, S. J., Myers, R. A., and Dunn, A. 2001. A meta-analysis of the relationship between catch-per-unit-effort and abundance. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1705−1772.

Hilborn, R., and Walters, C. J. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York. 570 pp.

Hilborn, R., Maunder, M. N., Parma, A., Ernst, B., Payne, J., and Starr, P. J. 2000. Documentation for a General Age-structured

Bayesian Stock Assessment Model: Code named Coleraine. Fisheries Research Institute, University of Washington. FRI/UW 00/01.

Hilborn, R. H., Parma, A., and Maunder, M. N. 2002. Exploitation rate reference points for west coast rockfish: are they robust and are there better alternatives? North American Journal of Fisheries Management, 22: 365–375.

Hinton, M. G., and Maunder, M. N. 2003. Methods for standardizing CPUE and how to select among them. Collective Volume of Scientific Papers ICCAT, 56: 169–177.

Hinton, M. G., and Nakano, H. 1996. Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints and environmental data, with an application to blue marlin (*Makaira nigricans*) catch and effort data from Japanese longline fisheries in the Pacific. Inter-American Tropical Tuna Commission Bulletin, 21: 169–200.

Hollowed, A. B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J., and Rice, J. C. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES Journal of Marine Science, 57: 707–719.

Joseph, J. 1970. Management of tropical tunas in the eastern Pacific Ocean. Transactions of the American Fisheries Society, 99: 629–648.

Joseph, J. 1973. Scientific management of the world stocks of tunas, billfishes, and related species. Journal of the Fisheries Research Board of Canada, 30: 2471–2482.

Joseph, J. 1998. On scientific advice and tuna management. Collective Volume of Scientific Papers ICCAT, 50: 855–861.

Kell, L. T., Die, D. J., Restrepo, V. R., Fromentin, J-M., Ortiz de Zarate, V., and Pallares, P. 2003. An evaluation of management strategies for Atlantic tuna stocks. Scientia Marina, 67(Suppl. 1): 353–370.

Labelle, M., and Hampton, J. 2003. Stock assessment of albacore tuna in the western and central Pacific Ocean. Standing Committee on Tuna and Billfish, 16, ALB-1. 30 pp.

Link, J. S., Brodziak, J. K. T., Edwards, S. F., Overholtz, W. J., Mountain, D., Jossi, J. W., Smith, T. D., and Fogarty, M. J. 2002. Marine ecosystem assessment in a fisheries management context. Canadian Journal of Fisheries and Aquatic Sciences, 59: 1429–1440.

MacCall, A. D. 1990. Dynamic Geography of Marine Fish Populations. University of Washington Press, Seattle. 153 pp.

Mace, P. M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries stock assessment and management. Fish and Fisheries, 2: 2–31.

Maunder, M. N. 2001. Integrated Tagging and Catch-at-Age ANalysis (ITCAAN). *In* Spatial Processes and Management of Fish Populations, pp. 123–146. Ed. by G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell. University of Alaska, Fairbanks. Alaska Sea Grant College Program Report, AK-SG-01–02.

Maunder, M. N. 2002. The relationship between fishing methods, fisheries management and the estimation of maximum sustainable yield. Fish and Fisheries, 3: 251–260.

Maunder, M. N. 2003a. Is it time to discard the Schaefer model from the stock assessment scientist's toolbox? Fisheries Research, 61: 145–149.

Maunder, M. N. 2003b. Paradigm shifts in fisheries stock assessment: from integrated analysis to Bayesian analysis and back again. Natural Resource Modeling, 16: 465–475.

Maunder, M. N., and Harley, M. N. Evaluating tuna management in the eastern Pacific Ocean. Bulletin of Marine Science (in press).

Maunder, M. N., Harley, S. J., and Hampton, J. 2006. Including parameter uncertainty in forward projections of computationally intensive statistical population dynamic models. ICES Journal of Marine Science, 63: 969–979.

Maunder, M. N., and Punt, A. E. 2004. Standardizing catch and effort data: a review of recent approaches. Fisheries Research, 70: 141–159.

Maunder, M. N., and Watters, G. M. 2003. A-SCALA: an age-structured statistical catch-at-length analysis for assessing tuna stocks in the eastern Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin, 22: 433–582.

May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J., and Laws, R. M. 1979. Management of multispecies fisheries. Science, 205: 267–277.

Methot, R. D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data. International North Pacific Fishery Commission Bulletin, 50: 259–277.

Myers, R. A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature, 423: 280–283.

Nakano, H., and Bayliff, W. H. 1992. A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1981–1987. Inter-American Tropical Tuna Commission Bulletin, 20: 187–237.

Olson, R. J., and Watters, G. M. 2003. A model of the pelagic ecosystem in the eastern tropical Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin, 22: 133–218.

Paloheimo, J. E., and Dickie, L. M. 1964. Abundance and fishing success. Journal du Conseil International pour l'Exploration de la Mer, 155: 152–163.

Parma, A. M. 2001. Bayesian approaches to the analysis of uncertainty in the stock assessment of Pacific halibut. American Fisheries Society Symposium, 24: 111–132.

Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution, 10: 1994.

Pauly, D., Christensen, V., and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science, 57: 697–706.

Pella, J. J., and Tomlinson, P. K. 1969. A generalized stock production model. Inter-American Tropical Tuna Commission Bulletin, 13: 421–458.

Polacheck, T. 2006. Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? Marine Policy, 30: 470–482.

Polovina, J. J. 1984. Model of a coral reef ecosystems 1. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs, 3: 1–11.

Punsly, R. 1987. Estimation of the relative annual abundance of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean during 1970–1985. Inter-American Tropical Tuna Commission Bulletin, 19: 263–306.

Punt, A. E., Campbell, R. A., and Smith, A. D. M. 2001. Evaluating empirical indicators and reference points for fisheries management: application to the broadbill swordfish fishery off eastern Australia. Marine and Freshwater Research, 52: 819–832.

Punt, A. E., and Hilborn, R. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Reviews in Fish Biology and Fisheries, 7: 35–63.

Quinn, T. J. 2003. Ruminations on the development and future of population dynamics models in fisheries. Natural Resource Modeling, 16: 341–392.

Ravier, C., and Fromentin, J-M. 2001. Long-term fluctuations in the eastern Atlantic and Mediterranean bluefin tuna population. ICES Journal of Marine Science, 58: 1299–1317.

Ravier, C., and Fromentin, J-M. 2004. Are the long-term fluctuations in Atlantic bluefin tuna (*Thunnus thynnus*) population related to environmental changes? Fisheries Oceanography, 13: 145–160.

Rose, G. A., and Kulka, D. W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Canadian Journal of Fisheries and Aquatic Sciences, 56(Suppl. 1): 118–127.

Rose, G. A., and Leggett, W. C. 1991. Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 48: 843–848.

Sainsbury, K., and Sumaila, U. R. 2003. Incorporating ecosystem objectives into management of sustainable marine fisheries, including 'best practice' reference points and use of marine protected areas. *In* Responsible Fisheries in the Marine Ecosystem, pp. 343−361. Ed. by M. Sinclair, and G. Valdimarsson. FAO, Rome.

Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-American Tropical Tuna Commission Bulletin, 1: 25−56.

Schaefer, M. B. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin, 2: 245−285.

Sibert, J. R., and Hampton, J. 2003. Mobility of tropical tunas and the implications for fisheries management. Marine Policy, 27: 87−95.

Sinclair, A. F., and Murawski, S. A. 1997. Why have groundfish stocks declined? *In* Northwest Atlantic Groundfish: Perspectives on a Fishery Collapse, pp. 71−93. Ed. by J. Boreman, B. Nakashima, J. Wilson, and R. Kendall. American Fisheries Society, Bethesda, MD.

Stefansson, G. 2003. Issues in multispecies models. Natural Resource Modeling, 16: 415−437.

Stefansson, G., and Palsson, O. K. 1998. A framework for multispecies modeling of Arcto-boreal systems. Reviews in Fish Biology and Fisheries, 8: 101−104.

Suda, A., and Schaefer, M. B. 1965. General review of the Japanese tuna long-line fishery in the eastern tropical Pacific Ocean. Inter-American Tropical Tuna Commission Bulletin, 9: 1956−1962.

Suzuki, Z., Warashina, Y., and Kishida, M. 1977. The comparison of catches by regular and deep tuna longline gears in the western and central equatorial Pacific. Bulletin of the Far Seas Fisheries Research Laboratory, 15: 51−89.

Tomlinson, P. K. 2001. Production model analysis of yellowfin tuna in the eastern Pacific Ocean. Inter-American Tropical Tuna Commission Stock Assessment Report, 1: 321−340.

Walters, C. J. 1986. Adaptive Management of Renewable Resources. Macmillan, New York. 374 pp.

Walters, C. J. 2003. Folly and fantasy in the analysis of spatial catch rate data. Canadian Journal of Fisheries and Aquatic Sciences, 60: 1433−1436.

Walters, C. J., Christensen, V., Martell, S. J., and Kitchell, J. F. 2005. Possible ecosystem impacts of applying MSY policies from single-species assessment. ICES Journal of Marine Science, 62: 558−568.

Walters, C. J., Christensen, V., and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7: 139−172.

Walters, C. J., and Parma, A. M. 1996. Fixed exploitation rate strategies for coping with effects of climate change. Canadian Journal of Fisheries and Aquatic Sciences, 53: 148−158.

Walters, C. J., Pauly, D., and Christensen, V. 1999. ECOSPACE: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems, 2: 539−554.

Watters, G. M., and Maunder, M. N. 2001. Status of bigeye tuna in the eastern Pacific Ocean. Inter-American Tropical Tuna Commission Stock Assessment Report, 1: 109−211.

Watters, G. M., Olson, R. J., Francis, R. C., Fiedler, P. C., Polovina, J. J., Reilly, S. B., Aydin, K. Y., Boggs, C. H., Essington, T. E., Walters, C. J., and Kitchell, J. F. 2003. Physical forcing and the dynamics of the pelagic ecosystem in the eastern tropical Pacific: simulations with ENSO-scale and global-warming climate drivers. Canadian Journal of Fisheries and Aquatic Sciences, 60: 1161−1175.