A review of tagging methods for estimating fish population size and components of mortality

Techniques to improve estimation of animal population size and mortality from tagging studies have received substantial attention from terrestrial biologists and statisticians during the last 20 years. However, these techniques have received little notice from fisheries biologists, despite the widespread applicability to fisheries research, the wide variety of tag types used in fisheries research (from traditional fin clips to telemetry tags), and the development of new computer software to assist with analyses. We present a brief review of population models based on recaptures, returns, or telemetry relocations of tagged fish that can be used to estimate population size, total mortality, and components of mortality (i.e., fishing and natural) that are frequently of interest to fisheries biologists. Recommended strategies include (1) use closed population models (e.g., Lincoln-Peterson) to estimate population size for short term studies where closure assumption can be met, (2) use the robust design to estimate population size for studies of longer duration, (3) use high-reward tags in conjunction with other methods of estimating reporting rate in tag-return studies, (4) combine a subset of telemetry tagged fish with either a high-reward tagging program or a traditional capture-recapture study to improve mortality estimates and understanding of mortality components, and (5) use pilot studies and simulation analyses to assess precision of estimated parameters to evaluate study feasibility. Incorporation of these improved techniques could lead to greater accuracy and precision of parameter estimates from tagging studies and thus to improved understanding and management of fish populations.

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Introduction

Effective fisheries management often requires reliable information on population size, survival, and mortality. For example, the population size of imperiled fish species is often a critical factor in determining its protected status, and recovery plans often focus on ways to increase species abundance by understanding mortality components and reducing mortality rates (Pine et al. 2001). Management actions such as the evaluation of marine protection areas also frequently use indices of animal abundance to assess the effectiveness of restrictions on fishing mortality (Russ and Alcala 1996). Fish stocks with commercial and recreational value are usually managed with a goal of maintaining sustainable harvests through regulation of fishing mortality (Hilborn and Walters 1992).

Capture-recapture methods with tagged animals are a primary means of estimating the abundance and survival of animal populations. These methods have received considerable attention over the last century from wildlife biologists and statisticians interested in developing applied statistical models to estimate animal abundance (Pollock 1991; Williams et al. 2002). Tag-return methods are also a primary means of estimating a population's total mortality rate, and in some fisheries settings, the natural and fishing components of mortality (Brownie et al. 1985; Hoenig et al. 1998a; Pollock et al. 2001a). Such tag return models are basically special extensions of capture-recapture models used to estimate population size, survival rates, and recruitment (i.e., "Jolly-Seber" models, Seber 1982). The key difference is, for a capture-recapture model, the biologist conducts the sampling at specific points in time to recapture tagged fish alive. For application of a tag-return model, returns of harvested fish come from one or more fisheries over an extended period of time (e.g., fishing season).

It is our observation that fisheries biologists have been less aggressive in adopting these models for estimating population size, survival rates, and mortality rates, relative to our wildlife counterparts. This may be due to unfamiliarity with the methods or software as well as practical concerns. We also have observed that tagging studies to estimate population size and survival rates (e.g., Jolly-Seber) are frequently considered separately from tagging studies used to estimate mortality rates (e.g., Brownie models). Information from both study types is useful to

fisheries managers, and the purpose of this article is to review tagging methods for estimating population size and mortality components for fisheries applications. Our review is intended to assist fisheries biologists in designing tagging studies by summarizing the underlying assumptions and basic models available within the framework of available specialized software (Box 1, Tables 1 and 2). Our hope is that this review will encourage fisheries biologists to utilize these techniques in their research efforts.

Capture-recapture versus Catch-per-unit-effort

Catch-per-unit-effort (CPUE) data are often used as a relative index of population size. However, this approach assumes that catchability or probability of capture is consistent over time. The relationship between catch rate and actual abundance is not generally considered, and it is unlikely that capture probability will be constant over time and under varying sampling conditions (Williams et al. 2002). That relationship is important, because fish sampling techniques rarely collect all animals present in an area and fish behaviors (e.g., schooling) may concentrate fish such that catches remain high, even if populations are declining (Hilborn and Walters 1992). Capture-recapture models provide direct estimates

of both population size and the probability of capturing an individual while CPUE only demonstrates trends in catches which may (or may not) be related to population abundance (Williams et al. 2002). In general, if the primary study objective is to detect large (e.g., >50%) changes in population abundance, then CPUE data may be adequate. In situations where more precise information on population size and trends, or information on mortality and its components are of interest, then a tagging study is likely the best approach.

The two approaches can be compared by considering the common situation of sampling largemouth bass (*Micropterus salmoides*) in reservoirs with shoreline electrofishing transects. Due to gear avoidance or sampling difficulties related to physical structure, it is unlikely that every largemouth bass along the shoreline is collected. Instead, we can conceptualize a model where each fish will have a capture probability (p_i), which can then be used to estimate the number of largemouth bass in the transect (N_i) from the number of fish collected in the sample (C_i), where

$$\hat{N}_i = \frac{C_i}{p_i} \qquad (1)$$

The capture probability, p_i, is the probability of a fish being caught at that time (i) and location with

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Box 1. Planning a capture-recapture study.

A key step in planning a capture-recapture study is to examine the possible precision of parameter estimates before conducting the study. This helps determine if study objectives can be met given the expected sample sizes and variances. For example, population size estimates of an endangered species may require higher precision (as part of a recovery plan) than estimates associated with an annually stocked game fish. One simple way to do this is to use estimates or assumed values for capture probability and population size to generate expected frequencies of the possible capture histories by hand (Box 1, Table 1) or on a spreadsheet. These capture histories can then be analyzed using the software and models discussed in this review to evaluate approximate precision at different capture histories, population sizes, and number of samples.

As an example, there are eight (2^3) possible capture histories in a closed population study with three samples. Excluding the case with no captures (000), there are seven of interest to us (Box 1, Table 1). If we assume the capture probability (p) to be 0.10 based either on pilot field work or published studies, and our approximate estimate of population size (N) is 1,000 individuals, then we can calculate the expected number of fish for each capture history (Box 1, Table 1). The expected frequencies of each capture history could then be analyzed in MARK or CAPTURE to evaluate precision of parameter estimates using the various closed models discussed in this review. This very simple example does not incorporate heterogeneity. But assigning different capture probabilities to portions of the estimated population size would simulate heterogeneity.

This approach also provides insight into the amount of effort required to obtain precise parameter estimates. Precision can be improved by increasing the capture-probability (which may be difficult), increasing the number of samples, or a combination of the two. This allows biologists to examine if the potential gain in precision justifies the expense associated with increasing the sampling effort.

This approach can also be generalized in two ways. We could generate expected capture histories under a heterogeneity model and examine bias and precision of different estimators (i.e., M_t vs. M_h). We could also generate expected capture histories under an open model (i.e., Jolly-Seber) and examine precision issues under that scenario.

We encourage the use of simple pre-study evaluations such as this before conducting a capture-recapture study. Biologists should find the information from these simple simulations very useful in evaluating and planning the feasibility of a capture-recapture study. This approach should lead to savings in both time and money by implementing the most efficient study design and establishing realistic expectations for study results.

Box 1, Table 1. Approximate expected capture frequencies for a three sample closed population study with a capture probability, $p = 0.1$, and estimated population size $N_t = 1000$.

Capture history	Formula to calculate expected frequency	Approximate expected frequency
111	$p \times p \times p \times N$	1
110	$p \times p \times (1 - p) \times N$	9
101	$p \times (1 - p) \times p \times N$	9
011	$(1 - p) \times p \times p \times N$	9
100	$p \times (1 - p) \times (1 - p) \times N$	81
010	$(1 - p) \times p \times (1 - p) \times N$	81
001	$(1 - p) \times (1 - p) \times p \times N$	81

the gear employed. The use of estimates of capture probability ($\hat{p}$) to account for individuals that are not collected in an area is critical to generating precise and accurate estimates of population size.

Because capture probability is rarely constant, it is not possible to separate changes in p_i from changes in population size if CPUE is considered alone (Pollock et al. 2002; Williams et al. 2002). Returning to our example, if an electrofishing sample collected along the same transect six months later included only 10% of the number of fish caught in the previous transect, is this because fewer fish are present along the shoreline, or has CPUE changed because of a change in water temperature, vegetative cover, or some other environmental factor? Bayley and Austen (2002) demonstrated wide variation in the catchability of lentic fishes across a range of fish species, fish size, and varying environmental conditions. This is not surprising to field biologists who routinely notice changes in catch rate with changes in environmental conditions (e.g., weather) or seasonal patterns in recruitment and movement.

A key parameter in a capture-recapture study is the capture probability, which can be defined as the probability that an individual animal is captured on a sampling occasion. In practical terms, it can also be thought of as the fraction of the study population captured on that occasion. It is generally estimated from the recapture of tagged individuals, and should be as high as possible in order to obtain reliable estimates of population parameters. Unfortunately, the literature and our own experiences in conducting these types of studies have shown that capture probability is low in most fisheries studies, resulting in "sparse" data. The typically low efficiency of fisheries sampling methods is illustrated by Bayley and Austen (2002).

They sampled known populations of various species in reservoirs and ponds and reported empirical estimates of catchability (the fraction of fish collected in a single pass in an electrofishing boat) that ranged from 2–14%.

Tagging studies require that fish that are collected, tagged, and released be in good condition and as likely to be captured (or harvested) as untagged fish in a future sample. This compels biologists to use non-lethal collection techniques that may not be the most efficient gears available. Collection restrictions placed on researchers by permitting agencies may also limit the use of some techniques or sampling programs (e.g., placing limits on gillnet soak time or electrofishing settings), particularly with imperiled species (Pine et al. 2001; Holliman et al. in press). Because capture probability drives accuracy and precision of parameter estimates, biologists should design their sampling programs to maximize capture probability.

Capture-recapture models

One approach to estimating capture probability and population size is to use capture-recapture (mark-recapture) methods. These methods have been intensively studied by biostatisticians and applied widely to terrestrial wildlife populations (Lancia et al. 1994; Williams et al. 2002). In these studies, fish are recaptured alive on multiple occasions, unlike tag-return studies (described below) where there is only one "recapture" in the harvest—and the fish is dead.

Capture-recapture models can be broadly defined as open or closed population models, each with specific assumptions. Closed population models are "closed" to changes in the population due to births, deaths, emigration, or immigration, whereas

Table 1. Product name, description, and World Wide Web address for various software packages to assist with analyzing data from tagging studies.

Product name	Description	World Wide Web address
MARK	Comprehensive program for most types of capture-recapture analysis including open, closed, and robust design models. Capture probability and survival directly estimated for open, closed, and robust models and population size estimation for closed and robust models.	www.cnr.colostate.edu/~gwhite/mark/mark.htm
CAPTURE	One of the first programs for estimating population size and capture probability in closed populations. Calculates estimates using a variety of models which are able to account for heterogeneity, behavioral response, time variation, in capture probability. Only software that contains heterogeneity models. Can be run as an option within MARK.	www.mbr-pwrc.usgs.gov/software
JOLLY	Program for estimating population size, survival, and capture probability of open populations.	www.mbr-pwrc.usgs.gov/software
SURVIV	Program used to calculate survival rates from user-specified survival functions including tag-return models. Not very user-friendly.	www.mbr-pwrc.usgs.gov/software
POPAN	Program for estimating population size and number of new recruits in open populations.	www.cs.umanitoba.ca/~popan/
SPAS	Program for estimating population size in stratified two sample capture-recapture studies.	www.cs.umanitoba.ca/~popan/

open models allow for these changes. Both closed and open models estimate capture probability and population size. In addition, open models are able to estimate apparent survival, recruitment, and population change. Detailed explanations and examples of each are discussed below.

Closed Models

Models that assume equal catchability among individuals and sample dates, such as Lincoln-Peterson and Schnabel models (Figure 1), have a long history of use in fisheries applications (Ricker 1975). These models have strict assumptions that are frequently violated to varying degrees, which results in biased population estimates. The basic Lincoln-Peterson model is based on a sample of n_1 animals caught, marked with individual (e.g., Passive Integrated Transponder—PIT tag) or batch marks (e.g., fin clip), and released at time one. A second sample, n_2, is then taken at time two and the number of marked animals m_2 is noted. The equation for the population estimate (Ricker 1975) is

$$\hat{N} = \frac{n_1 n_2}{m_2} \qquad (2)$$

The rationale for this model is that the fraction of marked fish in the second sample ($\frac{m_2}{n_2}$) should on average equal the fraction of the population that is marked ($\frac{n_1}{N}$).

The widely used "Schnabel" model (Ricker 1975) is basically an extension of the Lincoln-Peterson model that allows for more than two samples with a batch mark. The assumptions for both models are that (1) the population is closed to additions (recruitment or immigration) or deletions (deaths or emigration), (2) capture probability is equal among all animals in each sample, and (3) marks are not lost or overlooked.

Table 2. Model, type of mark required (batch or individual), source of fish used in study (research collection or fishery dependent), typical study duration, reporting rate requirement, key parameters, additional information generated, and principal software for estimating population size and mortality components from tagging models discussed in this review.

Model name	Type of mark required	Source of fish	Typical study duration	Reporting rate required?	Key demographic parameters	Additional information generated	Principal software
Lincoln-Peterson	Batch	Research	< 1 month	No	Population size		Calculator, spreadsheet, SPAS
Schnabel	Batch	Research	< 1 month	No	Population size		Calculator, spreadsheet, or CAPTURE
Removal	No mark	Research	< 1 month	No	Population size		CAPTURE or MARK
Closed-CAPTURE models	Unique individual	Research	< 1 month	No	Population size, capture probability		CAPTURE for all closed models or MARK for non-heterogeneity
Jolly-Seber and Cormack-Jolly-Seber	Unique individual	Research	>1 month	No	Population size, apparent survival	Individual growth from recaptures	POPAN, JOLLY, or MARK
Robust	Unique individual	Research	>1 month	No	Population size and growth, apparent survival, temporary emigration	Individual growth from recaptures	CAPTURE and JOLLY together or MARK
Brownie	Unique individual	Fishery	>1 year	No	Survival, total mortality		BROWNIE, MARK
Hoenig/Hearn	Unique individual	Fishery	>1 year	Yes	Survival, fishing and natural mortality		AVOCADO
Telemetry	Unique individual	Research	= 1 year	No	Survival, fishing and natural mortality	Movement, habitat use	SURVIV
Combined telemetry/ tagging	Unique individual	Research/Fishery	> 1 year	No	Survival, fishing and natural mortality	Movement, habitat use	SURVIV

In capture-recapture studies lasting longer than a few days, the closed model assumption of no additions or deletions occurring in the population may be unrealistic. Although recruitment and mortality may be negligible or low for a species over a period of time longer than a few days (perhaps even a season), movement into or out of the study area often precludes the use of closed population models. A variety of studies have revealed movement patterns in adult and juvenile fishes that would violate the closure assumption (e.g., Cleary and Greenbank 1954; Skalski and Gilliam 2000; Hightower et al. 2001; Mitro and Zale 2002).

Heterogeneity in capture probability may be an important source of bias if traditional Lincoln-Peterson and Schnabel models are used. Heterogeneity can be related to differences in fish size, sex, or social status (assumption 2, equal catchability). Many fisheries gears are strongly size selective. For example, electrofishing is known to select for larger individuals (Reynolds 1996), which likely leads to electrofishing samples containing disproportionate numbers of large individuals relative to their actual abundance. Lincoln-Peterson and Schnabel models do not account for such heterogeneity (which leads to strong negative bias in population size). Estimates may be produced separately for important strata, (size, sex, or status), to minimize heterogeneity within a stratum (Kwak 1992), but this approach results in reduced sample sizes for each estimate and corresponding reduced precision. Program SPAS can be used to analyze 2-sample capture-recapture data over several strata to account for heterogeneity provided sufficient recaptures are collected within each strata (Table 1).

An additional source of variation in capture probability is "trap response" or behavior, where capture probability depends on an animal's previous capture experience. An animal may be less or more likely to be caught in future samples because it has learned to avoid, or is attracted to, a trap. For example, fish behavior was shown to be altered for at least 24 h following electrofishing and marking (Mesa and Schreck 1989).

Tag loss is common in fisheries studies (Guy et al. 1996, violation of assumption 3) and can result in very serious bias in $\hat{N}$. Tag loss can be estimated by double tagging some individuals (Guy et al. 1996) and then adjusting the number of recaptures to account for this loss. For this approach, tag loss must be assumed to be independent for the two tags. If possible, tag type and location should be evaluated with a pilot study to ensure that tag retention will be adequate and provide the researcher with experience in tagging procedures.

The Lincoln-Peterson and Schnabel models are widely used in fisheries applications because they are easily implemented, computationally simple, and most importantly, individual fish do not have to be uniquely marked. Despite these advantages, we recommend applying individual marks to obtain the complete capture history of each fish, so that the degree of heterogeneity and trap response in capture probabilities may be assessed and accounted for. Capture histories are often recorded as a series of 1s and 0s, where 1 indicates an animal was caught in that sampling period, and 0 indicates the animal was not caught. This method of recording capture histories of individual animals is the standard means of entering data into capture-recapture software packages.

A suite of eight closed models has been developed to allow for variation in capture probability related to physical, behavioral, and temporal attributes of the study species or sampling design (Otis et al. 1978). These models are available in program CAPTURE, a computer software program

Figure 1. Diagram demonstrating assumptions about capture probabilities for each type of capture-recapture model discussed in this review. Each marker represents a sampling event. The solid lines connecting markers indicate closed populations with equal capture probabilities. Dashed lines between samples indicate closed populations with unequal capture probabilities. Gaps represent intervals where populations are open (see text).
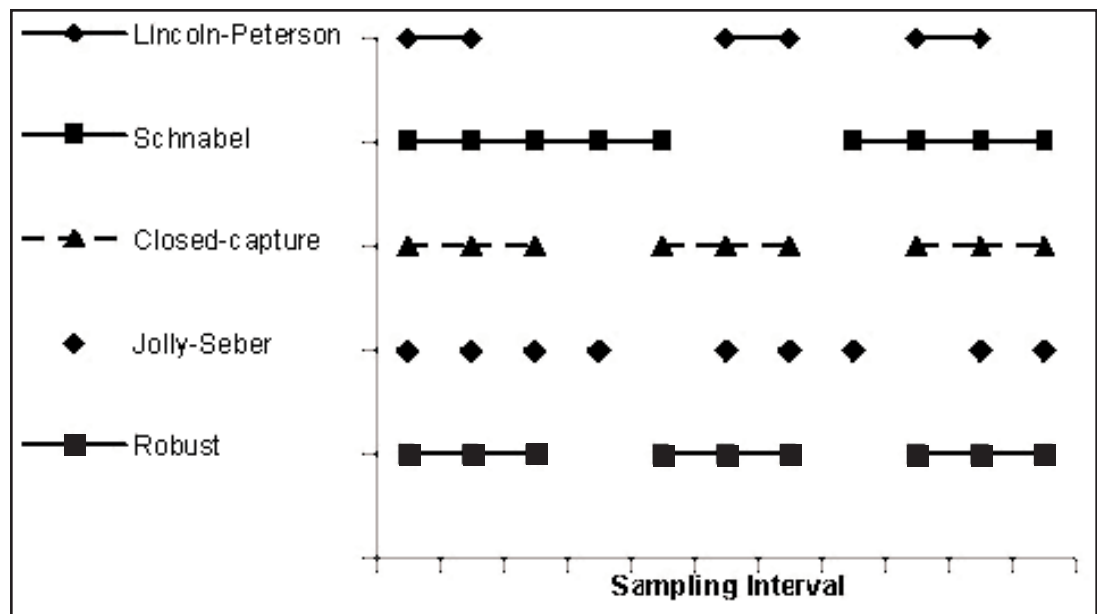
designed to assist with analyzing capture-recapture data available at no cost through the World Wide Web as a stand alone program or accessed through another free software program, MARK, discussed later (Table 1). Model M_o is the simplest model for closed populations and does not allow for changes in capture probability due to heterogeneity, behavior, or time (Pollock et al. 1990; Lancia et al. 1994). The heterogeneity model (M_h) allows each animal to have a unique capture probability (due to size, sex, etc.) but this capture probability must remain constant among all sampling periods i. The trap response/behavior model M_b estimates an initial capture probability $\hat{p}$ and recapture probability ($\hat{c}$), which may differ from each other. Model M_t allows capture probability to vary among sampling periods, but it must remain constant among individuals for each period. This model is the same as the Schnabel model. Models M_{tb}, M_{bh}, M_{th}, and M_{tbh} are combinations of the above, but require additional assumptions (for more detail see Norris and Pollock 1995; Pledger 2000; Williams et al. 2002). Program CAPTURE is the only specialized program available that can be used to fit each of these heterogeneity models to capture histories from a capture-recapture study. Program CAPTURE also uses a model selection approach based on a large number of goodness-of-fit tests to assist with choosing the model that best fits the data. However, the model selection routine in CAPTURE does not perform well with sparse data; thus, biologists should evaluate models closely in terms of meeting assumptions to select the simplest model that best describes the data (Pollock et al. 1990; Williams et al. 2002).

The Schnabel model is simple in design and analysis and has been widely used in fisheries applications (Ricker 1975; McInerny and Cross 1999; Kocovsky and Carline 2001). Capture probability can vary among sampling periods with this model (analogous to model M_t in CAPTURE). Although the Schnabel model is computationally simple (Table 2, no need for computer analysis), we suggest using program CAPTURE for analyzing such data because CAPTURE can fit and evaluate several models in addition to the Schnabel model. For example, CAPTURE can compare the M_t (Schnabel) model, which does not allow for heterogeneity, with the M_{th} model, which allows for varying capture probabilities among individuals (heterogeneity) and among sampling occasions. The M_{th} model may be more realistic because it accounts for heterogeneity, whereas the M_t is highly biased by unequal capture probabilities (heterogeneity) within each time period (Lancia et al. 1994). We consider heterogeneity in capture probability to be present in almost all fisheries applications and suggest that the Schnabel model (M_t in CAPTURE) be used only if it is chosen by a model selection procedure. However, in samples with extremely low capture probability (<0.05), M_t (or the similar Chao M_t model also available in CAPTURE, Chao 1989) may be the only model that CAPTURE is able to fit to the data for a population estimate (Mitro and Zale 2002). In this case, estimates should be evaluated in terms of the severity of potential assumption violations, particularly that for heterogeneity.

Removal Studies

Depletion or removal studies are widely used in fisheries applications and are analogous to closed capture-recapture model M_b in CAPTURE (Ricker 1975; Otis et al. 1978). M_b allows for animals that have been captured previously to demonstrate a different capture probability than those that have not been captured. This "trap response" is mathematically analogous to a removal model because only initial captures of animals are used in estimating population size (Pollock et al. 1990). Model M_b assumes that the initial capture probability is constant among animals. Model M_{bh} as applied to removal studies relaxes that equal catchability assumption by allowing individual animals to have different removal probabilities between animals but requires that the removal probability does not change over time.

Similar to closed models, accurate population size estimates from removal studies rely on minimally adequate capture probabilities and initial population size. White et al. (1982) recommended capture probabilities of 0.2 and population sizes of 200 individuals based on simulation studies for reliable population size estimates. There is also the question of the number of samples. We recommend removal studies that incorporate four or more samples to allow the possibility of accounting for heterogeneity among individuals.

CAPTURE's maximum-likelihood estimation of N generates similar estimates to those of the regression technique commonly used in removal studies (Lancia et al. 1994). A disadvantage of the regression approach is the potential for violating assumptions required for linear regression, such as homogenous variances among regressed points (Pollock 1991). Because of this and other potential violations, the wider range of models available, and model selection assistance provided in program CAPTURE, we re-emphasize the recommendation of Lancia et al. (1994) and Pollock (1991) to use CAPTURE for removal studies.

Design of short-term studies

Biologists estimating population size should carefully consider designing their study to meet the assumptions of the closed population models available in CAPTURE. Sampling areas that cannot be

closed physically might be treated as closed over short time periods (Pollock 1982), as did Osmundson and Burnham (1998) for Colorado squawfish (*Ptychocheilus lucius*) and Mitro and Zale (2002) for rainbow trout (*Oncorhynchus mykiss*). However, we strongly recommend that emigration be closely examined by either searching for tagged fish outside of the sample reach or through the use of a subset of radio-tagged individuals (e.g., Zehfuss et al. 1999).

Mitro and Zale (2002) used a pilot study and computer simulation to evaluate the precision of population size estimates using the closed models in CAPTURE before conducting the major field component of their study. We encourage careful study planning (Box 1) to help evaluate precision of population parameter estimates prior to conducting a large field study. We also believe that M_h or M_{th} often will be the most realistic models to fit in fisheries applications. Closed models are less complex (fewer parameters) than open population models and are reasonable approaches for sparse data. We caution that population estimates from closed models should be closely evaluated in terms of sensitivity to model assumptions.

Open Population Capture-Recapture Models

The Jolly-Seber model (Jolly 1965; Seber 1965) and its variations (Cormack 1964; Pollock et al. 1990; Williams et al. 2002) are the primary open population capture-recapture models suitable for fisheries applications. Three computer programs, JOLLY (Pollock et al. 1990), MARK (White and Burnham 1999), and POPAN (Arnason and Schwarz 1999), are capable of analyzing capture-recapture data from open populations (Table 2). These programs are also available at no cost through the World Wide Web (Table 1). The Jolly-Seber model allows population size estimation at each sampling date (excluding the first and last), estimation of apparent survival between samples, and the addition of new recruits between samples. Survival rates and recruitment numbers apply to the pool from which marked animals are sampled. For example, if tagged individuals are adults, then recruits into this population are juveniles entering the pool of tagged adult fish and not new individuals being born into the population. The "survival" estimated here actually is apparent survival (F = 1–mortality–emigration); for apparent survival to be true survival (S), emigration must not occur (Pollock et al. 1990). It is not possible to estimate true survival and emigration separately unless one collects additional data on emigration. For example, a telemetry study could be simultaneously conducted with the tagging study to help determine the rate and extent of emigration from the study site. The differences between true and apparent survival should be considered when comparing survival estimates from capture-recapture studies with traditional fisheries estimates (e.g., catch-curves, Fabrizio et al. 1997).

The Jolly-Seber model assumes the following: (1) every animal present in the population at sampling time *i* has an equal probability of capture, (2) survival is equal for every marked animal that is present from one sampling period to the next, (3) tags or marks are not overlooked or lost, (4) all animals are released immediately after the sample and all sample periods have a short duration (i.e., instantaneous) (Seber 1982). Violation of the equal catchability (no heterogeneity) assumption (number one above) will overestimate the actual proportion of marked animals in the population and lead to a negative bias in population size (Pollock et al. 1990). Negative bias in the estimated survival rate occurs when survival is affected by the tag or tagging procedure (assumption 2 above) (Arnason and Mills 1981). In fisheries applications, tagging trauma may cause lower survival for newly tagged fish. Models have been developed to detect this initial decrease in survival and adjust estimates accordingly (Brownie and Robson 1983). Tag loss can lead to serious underestimation of survival rates and overestimation of population size by decreasing the number of recaptures in the population. Double-tagging experiments can help estimate and adjust for tag loss (Arnason and Mills 1981).

An assumption of the Jolly-Seber model is that all emigration is permanent. Natural movement patterns of the study animal can lead to "temporary" emigration, where the animal is entering and leaving the study site repeatedly. There are two types of temporary emigration, "Markovian" emigration where an animal "remembers" that it has left the study area and returns based on some time-dependent function, and "random" emigration where the animal randomly leaves and returns on a continual basis (Kendall et al. 1997). The presence of a Markovian emigrant in a sample depends on the location of the animal in the previous sampling period (i.e., was the animal available for capture in the sampled area?), whereas a random emigrant does not depend on its location in the previous sample period. Temporary emigration may occur in some fisheries studies, resulting in biased survival and population size estimates. Zehfuss et al. (1999) showed that unbiased estimates of *N* could be obtained from Jolly-Seber models, even with random temporary emigration, if capture probabilities remained high ($\hat{p}_i > 0.5$, unlikely in most field applications). However, in situations with low $\hat{p}_i$ values and Markovian temporary emigration, estimates of *N* can be negatively biased (Zehfuss et al. 1999).

Several fisheries examples of Jolly-Seber model applications for imperiled fish species appear in the literature. Douglas and Marsh (1998) used Jolly-Seber and Cormack-Jolly-Seber models (which emphasize survival estimation, Cormack 1964) to estimate population size and survival for rare catostomids in the Little Colorado River over a four-year period. Fabrizio et al. (1997) estimated survival of a recovering lake trout (*Salvelinus namaycush*) population using Jolly-Seber and catch-curve methods in Lake Michigan. They found similar estimates for survival between the two methods. Jolly-Seber models have also been successfully applied in several studies of Gulf of Mexico sturgeon (*Acipenser oxyrinchus desoti*) to estimate population size, population growth, and survival (Chapman et al. 1997; Zehfuss et al. 1999; Pine et al. 2001).

Combined open and closed models

There are several major distinctions between closed and open models that we should now reiterate. Closed models are more likely to provide useful estimates from sparse data than open models. Closed models are also able to account for heterogeneity in capture probability and trap response. However, the "closure" assumption of these models generally restricts their applicability to short-term studies (i.e., < 1-month, Table 2). Open models such as the Jolly-Seber model are appealing because they are "open" to population changes due to movement, mortality, and recruitment. The difficulty in applying open models is that there are many parameters to be estimated, so these models perform poorly with sparse data. Pollock (1982) presented a sampling design that combines the strengths of both closed and open models and has widespread potential use in fisheries studies. This "robust design" is a series of short-term closed population studies (which allow for heterogeneity and trap response in capture probability) linked by open population models (which are used to estimate survival). This design allows population size to be estimated during the short-term studies (with closed population models) and survival and recruitment to be estimated with a Jolly-Seber model for the intervals between the closed periods (Figure 2). Versions of the robust design model in MARK allow for random or Markovian temporary emigration (Kendall et al. 1997).

The robust design approach performs well for fisheries studies composed of a series of short-term samples (secondary sampling periods) clustered within primary sampling periods that occur at longer time intervals. For example, a typical robust-design study would be a series of short-term population studies where fish are collected three times per week (noted l_1–l_3), once per month, over a four-month sampling season (K_1–K_4). During the "closed" portion of the study (three samples within a week), the closed population models in CAPTURE or MARK would be used to estimate population size for each of the one-week samples. We would then use a Jolly-Seber open model (in JOLLY or MARK) to estimate survival between each of the primary periods (Figure 2).

Incorporation of additional information

Another improvement on a standard capture-recapture study would be the use of auxiliary information. For example, capture probabilities could be estimated empirically by using known numbers of a species in the sampling area (e.g., radio-tagged individuals present) or using a model to predict catchability for a sampling gear given various species, habitats, and environmental conditions (Bayley and Austen 2002). These empirical estimates can then be compared to capture-probability estimates from capture-recapture studies. Individual covariates (e.g., fish length) can also be used to help reduce bias due to capture heterogeneity (Pollock 2002). The use of individual covariates is also appealing to biologists because it allows study of the relationship between the covariate and independent model parameters such as survival. These covariates can be fit in program MARK.

Model Selection

One useful approach for evaluating estimates from a capture-recapture study is to compare results of several different models used to analyze the same data set. The different estimates of population size can be evaluated in part by examining how well the assumptions for each model are met and how well each model fits the data. MARK evaluates how well each model fits the data using Akaike's Information Criterion (Akaike 1973; White and Burnham 2002; Burnham and Anderson 2002), which in many cases is a better model selection approach than the goodness-of-fit tests used in CAPTURE. For the typical fisheries situation with limited data, we recommend using the model selection criteria in conjunction with the biologist's knowledge of the system to select the most biologically meaningful and parsimonious model.

Tag return models

Tag-return models use harvest of previously tagged fish to estimate total mortality or survival rate (S) and tag-recovery rates (f). For a multi-year

tag-return study, these "Brownie" models (Brownie et al. 1985) are the standard method of analyzing wildlife tag-return data (Williams et al. 2002) and can be widely applied in fisheries settings (Youngs and Robson 1975; Hoenig et al. 1998a, b).

Many of the assumptions for tag-return models are the same as capture-recapture models, namely that the tagged fish sample is representative of the target population, tags are not lost, survival rates are not affected by tagging, and the fates of each tagged fish are independent. In addition, tag-return models assume (1) the year of the tag recoveries is correctly reported, (2) all tagged fish within a cohort have the same annual survival and recovery rates, and (3) fishing and natural-mortality are additive.

In this type of study, annual cohorts of fish are tagged in different years, and then the tags from harvested fish (commercially or recreationally) are collected from fishers over a period of years. These tag returns are then used to estimate mortality parameters. Assuming that the individual cohorts are independent, then the overall likelihood function for the model is the product of each of the individual cohort likelihoods (Brownie et al.

1985). Programs MARK and SURVIV can be used to generate mortality estimates for multiple groups (ages, sexes) and examine dependence in S and f. Although an estimate of survival can theoretically be obtained from only two years of tagging and recovery, in practice at least three and preferably five years are needed (Brownie et al. 1985; Williams et al. 2002). The number of fish tagged each year will depend on the tag-recovery rate and desired precision, and can be explored using the methods outlined in Box 1. Brownie et al. (1985) suggest that tagging 300 individuals per year is a useful minimum sample size in order to obtain reliable estimates of survival for waterfowl.

By combining total mortality estimates from a Brownie model with information about the tag-reporting rate, mortality can be partitioned into fishing and natural-mortality rates (Pollock et al. 1991; Hoenig et al. 1998a, b). The tag-return rate f is defined as

$$f = 1u \qquad (3)$$

where 1 is the probability that a tag on a harvested fish is reported, and u is the exploitation rate. If 1

Figure 2. Schematic drawing of the robust-design model demonstrating open and closed periods as well as estimable parameters at each period.
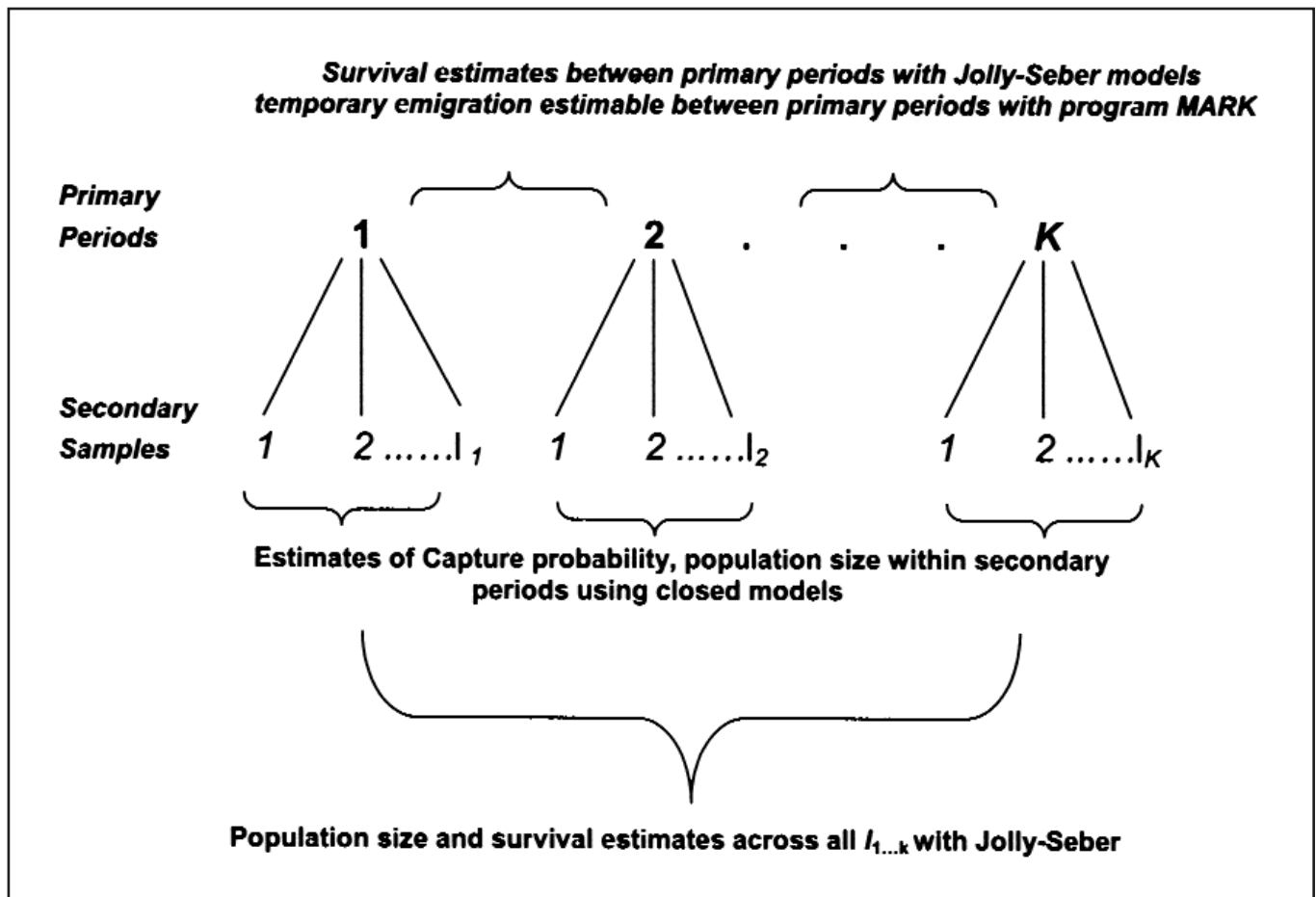
can be estimated, then an estimate of the exploitation rate u can be solved for.

To separate components of mortality, we do not need to assume that all tags are reported (Table 2), but we require an estimate of the tag-reporting rate. Methods for estimating reporting rate vary widely and include relying on surreptitiously planted tags, angler or port surveys, high-reward tags, or catch information from multi-component fisheries. These methods are reviewed in Pollock et al. (2001a), and each has their own assumptions that may be difficult to meet. Exploitation rates should be examined across a range of possible reporting rates to assess how errors in reporting rate influence the estimates of exploitation and alter possible management strategies.

One common method of estimating tag reporting rate in wildlife and fisheries studies is to use two tag types, standard tags and high-reward tags, and assume 100% reporting rate for the high-reward tags (Henny and Burnham 1976; Conroy and Blandin 1984; Pollock et al. 1991). The standard tag-return rate can then be estimated as the relative recovery rate of standard tags to the recovery rate of the high-reward tags. If high-reward tags are not 100% reported, then the standard tag-reporting rate is positively biased (Pollock et al. 2001a). Angler behavior may also change as a result of the high reward tags. Anglers may report regular tags at a higher rate due to publicity associated with the high-reward tags. Pollock et al. (2001a) recommended that reward tags be used every year of tagging so that angler behavior is not altered. Although this may increase the cost of the tagging program, the tradeoff of having more accurate estimates may justify the higher cost. Denson et al. (2002) used the high reward tagging method and estimated the reporting rate for red drum (*Sciaenops ocellatus*) was approximately 60%.

Exploitation rate (u) can also be estimated from a single release of tagged fish, based on the fraction of tags that are returned from harvested individuals. The most important assumption of this method is that all recovered tags are reported, or that a precise external estimate of the reporting rate is available (see above). For the typical fishery in which fishing mortality (F) and natural mortality (M) are operating concurrently, the exploitation rate is defined as

$$u = \frac{F\,(1\text{-exp}^{(-F\text{-}M)})}{Z} \qquad (4)$$

Because the instantaneous total mortality rate (Z) is defined as $F + M$, the only two unknowns in this equation are F and M. If an estimate or (more likely) an assumed value of M is available, the estimate of u from a tagging study can be used to calculate an estimate of Z. Alternatively, if Z had

been estimated externally (e.g., through a catch-curve analysis), then the equation can be solved for F and M. In situations where catch-curves cannot reliably estimate Z, the multi-year approach (above) would be required to obtain direct estimates of total mortality. Henry (2002) conducted an annual tagging program on Rodman Reservoir, Florida, to estimate tournament exploitation rate for largemouth bass. Variable reward tags of US $5 to $100 were used to estimate the reporting rate and F, a catch-curve was used to estimate Z, and then equation 4 was solved for M.

Telemetry methods

Telemetry methods have been widely used to estimate survival rates in terrestrial systems (White and Garrott 1990). They are becoming important in aquatic systems as well, largely because of improvements in transmitter and receiver technology that have increased reliability and dramatically decreased cost (see Voegeli et al.

Snowy grouper from the Bahamas uniquely identified with a T-bar tag.

2001). For example, remote sonic receivers are now available that allow continuous automatic monitoring of an area for several months and operate simply on one lithium cell battery (e.g., Heupel and Simpfendorfer 2002).

Transmitter characteristics that are important for mortality studies include (1) small size for implantation with no effect on the fish, allowing full recovery from capture and handling; (2) relatively long battery life; (3) adequate detection range, so that relocation probability is high; and (4) unique signal so that individuals can be distinguished.

The approach is to release a sample of telemetered animals, then locate each individual until it dies or is censored (e.g., excluded from the study because the animal is harvested, leaves the study area, or transmitter battery life is exceeded). An important difference between aquatic and terrestrial studies is that it is not generally possible to observe telemetered fish, so viability of the fish is inferred from movement between relocations.

Skalski et al. (2001) used radio telemetry to estimate survival rates of outmigrating salmon smolts in the Columbia River. They released radio-tagged smolts between successive dams and used automated receivers to estimate the fraction of fish that survived and passed each dam. Similar to the multiyear tagging approach, the ratio of detected transmitters from successive upstream release sites was an estimate of the survival rate because the "older" group of tagged fish would have passed one additional dam.

Telemetry methods are also effective for estimating components of the total mortality rate, including non-harvest rate (Hightower et al. 2001). An important advantage of this approach is that information about the tag reporting rate is not required. Also, unlike traditional tagging studies that provide information only through return of tags from harvested fish, telemetry studies can provide direct information about natural mortalities as well as fish that are alive (and moving between relocations).

The information that can be gained about sources of mortality depends on the study site and organism. Direct information about natural mortality can sometimes be obtained from telemetered fish that stop moving, whereas fishing mortality may be detected indirectly through the disappearance of telemetered fish from the study area (Hightower et al. 2001; Heupel and Simpfendorfer 2002). Natural mortality can also be detected from an atypical movement pattern or change in signal strength. For example, Jepsen et al. (1998, 2000) detected predation on radio-tagged Atlantic salmon (*Salmo salar*) and brown trout (S. *trutta*) smolts by a decrease in transmitter signal strength (after telemetered smolts were eaten by northern pike [*Esox lucius*] or pikeperch [*Stizostedion lucioperca*]) or by tracking a transmitter into shallow water typically occupied by pike. Jepsen et al. (1998, 2000) confirmed that predation had occurred by electrofishing to capture pike and pikeperch with ingested transmitters. Predation by birds was established by tracking birds with ingested transmitters, locating a transmitter at an avian colony, or by disappearance of transmitters
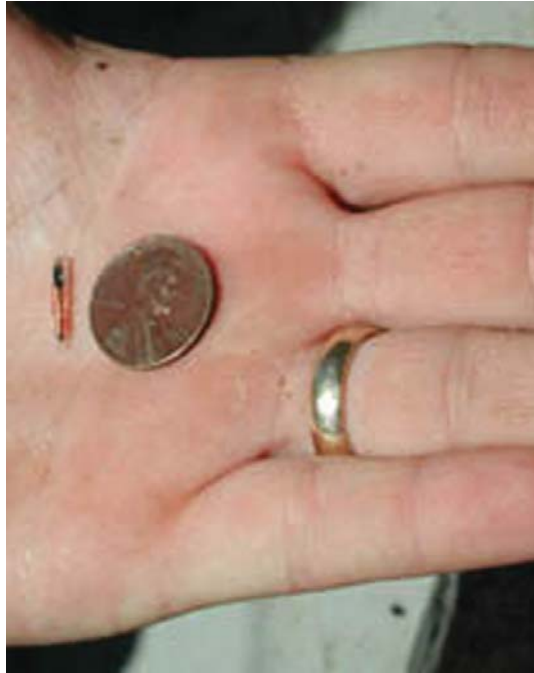
The small size of PIT tags make them useful to individually tag a large size range of fish.

from the study area. Heupel and Simpfendorfer (2002) used an array of automated monitors to maintain continuous contact with telemetered juvenile blacktip sharks (*Carcharhinus limbatus*) in a nursery area. They inferred predation by a larger shark on two telemetered juveniles, based on the change in swimming speed and the location of both juveniles at exactly the same (moving) position.

Unlike traditional tagging studies, telemetry methods can also provide detailed information about the timing and spatial location of mortalities. For example, Jepsen et al. (1998) conducted daily searches for radio-tagged salmonid smolts and established that predation mortality was concentrated in several areas, including a narrow constriction where a bridge crossed the reservoir. Heupel and Simpfendorfer (2002) monitored juvenile blacktip sharks during their first six months of life and established that natural and fishing mortality were concentrated within the first 12–15 weeks. Waters (1999) used telemetry methods to document that largemouth bass natural mortality varied seasonally in concert with seasonal patterns of spawning activity. Hightower et al. (2001) showed that natural mortality of striped bass (*Morone saxatilis*) was restricted to periods in summer and fall when suitable habitat was lacking.

Combined tagging-telemetry methods

A new approach that has considerable promise for estimating mortality rate is a combination of the tag-return and telemetry methods (Pollock et al. in press). The tag-return method can be based on a large sample of fish, because tags are inexpensive, and it provides direct information about harvest from returned tags. The telemetry method is restricted to a small sample size (because transmitters are expensive) and is more labor-intensive, but provides direct information about natural mortality and does not require an estimate of the reporting rate. In simulation studies based on an annual sample size of 500 conventional tags and 50 transmitters, Pollock et al. (in press) demonstrated that the combined method draws on the strengths

of both and results in improved estimates of fishing and natural mortality rates, as well as an estimate of the reporting rate. For this combined method, estimates of M are best when F is low, but estimates of the reporting rate are best when F is high. Telemetry and capture-recapture models can also be combined to improve the precision of survival and emigration estimates (Nasution et al. 2001, 2002).

Conclusions

We emphasize the use of pilot and simulation studies prior to conducting a large-scale field study to help evaluate precision of parameter estimates. As described in Box 1, this can provide a good indication of whether study objectives can be met with the available sampling resources, and will establish realistic expectations for study results.

In planning a closed capture-recapture study, the assumption of closure should be carefully evaluated through preliminary field studies if possible. Careful consideration should be granted to heterogeneity models (M_h and M_{th}), given that heterogeneity in capture probability is likely in fisheries sampling and can lead to strong negative bias in population size estimates. Five or more sampling periods are recommended for any closed capture-recapture experiment, particularly if heterogeneity models are to be used.

In planning an open capture-recapture study, temporary emigration should be evaluated because it can lead to large biases in parameter estimates. Apparent survival estimates from Jolly-Seber models are not highly biased by heterogeneity, so that is less of an issue here than for closed models. If the capture-recapture experiment will be longer-term (e.g., > 1-month), the assumptions of an open population model are more likely to be met than those of closed models. Temporary emigration can be assessed with a sub-set of telemetry tagged animals.

We strongly encourage the use of the robust capture-recapture design because (1) both heterogeneity and temporary emigration can be accounted for, resulting in less biased estimates of population parameters; (2) it utilizes strengths of both closed and open population models; and (3) the design is simple and easily incorporated into many standard fisheries sampling programs.

Key points related to tagging studies to estimate mortality include (1) information on reporting rate is not required if total mortality is the primary parameter of interest, and (2) if total mortality is partitioned into F and M then reporting rate must be estimated (e.g., reward tagging). Important aspects of telemetry methods for estimating mortality are (1) uncertainty associated with relocations of telemetered fish can be minimized by conducting multiple searches over short time intervals to locate every tagged fish or by combining searches with remote receivers to assist with documenting location (or absence) of tagged fish, (2) an estimate of the reporting rate is not required in order to partition total mortality into F and M, (3) researchers should attempt to account for emigration and hooking mortality (sources of positive bias for F and M, respectively), and (4) combining multiple methods such as tagging with telemetry studies should be considered to improve mortality estimates and provide a complete assessment of mortality components.

We hope that this review will encourage fisheries biologists to consider making broader use of the wide array of tagging models available. We covered only a few of the principal approaches to estimating population parameters from tagging data. The design, implementation, and analysis of tagging studies are a dynamic field that exists at the interface between management and applied statistics. Both of these fields can benefit via increased communication between the two groups of scientists to better define the needs of management biologist and increase the application of the statistical modeler's efforts. ▰▰

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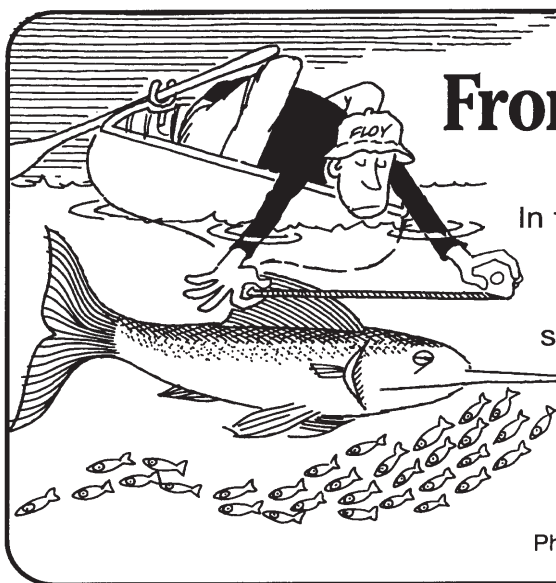
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