

Chapter 11

Design and Analysis of Tagging Studies

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11.1 INTRODUCTION

Tagging and marking studies of fish populations are used to examine movement patterns and estimate growth rates, demographic parameters, and abundances. The key steps in conducting an effective tagging study are (1) careful planning to ensure that study objectives are addressed, (2) selecting an appropriate tag or mark, (3) ensuring that sufficient numbers of animals are marked and recaptured to generate parameter estimates of sufficient precision to meet management needs, (4) meeting the sometimes rigorous assumptions required to provide accurate parameter estimates, (5) employing appropriate analytical methods, and (6) interpreting the results properly. This chapter provides guidance on designing simple tagging studies to calculate common fisheries estimates such as abundances, survival rates, components of mortality (fishing and natural), movement patterns, and growth rates.

Most tagging and marking studies are similar in that they create a subset of animals from the population that are “known” and identified by their tags or marks. This subset of animals is then followed through space or time (or both) by subsequent recaptures and used to provide information on the entire population. A strength of a well-planned tagging program is that multiple characteristics of interest to researchers and managers, such as movements, growth, and mortality rates, can often be addressed in the same study. Many essential questions must be considered for any tagging study, including the following.

1. What types of marks or tags are going to be used (fin clips, traditional passive tags, or telemetry tags)?
2. Who will tag the animals (biologists or cooperative recreational or commercial fishers)?
3. Are tagged fish representative of the population as a whole?
4. How will tagged animals be recaptured (collected from fishers or captured and released by biologists)?
5. Where and how often will relocations or recaptures be attempted?
6. What is the tag-shedding rate or how can it be estimated? Does tagging cause increased mortality of tagged fish?
7. Are tag-reporting rates relatively high and consistent across the study area and the duration of study?

Answers to all of these questions, and others, will affect the design of tagging studies; they are considered in detail in this chapter.

11.2 CHOICE OF MARKING TECHNIQUE

A wide variety of tagging or marking methods can be used to create a known subset of a population of fish. Marks are defined as anything recognizable that is external, internal, or incorporated into the integument of the fish, whereas a tag is usually defined as something attached externally or internally to the fish and which contains specific identification information (Jones 1979; Guy et al. 1996). Tags and marks can range from simple fin clips to technologically advanced tags that record a wide variety of spatial and biological information about an individual animal and then transmit it to the researcher by satellite (Chapter 18). Whereas no “perfect” tag exists (Nielsen 1992), it is still important to examine how the characteristics of each tag align with study objectives. For example, a tag that is highly visible would be a good choice for studies that rely on tag returns from commercial or recreational fishers. Other important considerations include not impairing the growth or survival of tagged animals, high tag retention rate, and cost (Nielsen 1992; Guy et al. 1996). Time spent in selecting the right tag, developing the study design, and thinking through the basic assumptions of the analysis will pay off in the quality of information obtained.

11.2.1 Body Marks

A fin clip is one of the simplest and oldest forms of marking a fish. The fin to be marked is selected, and a portion of it is removed in a single cut using scissors, wire cutters, or a hole punch (Figure 11.1). Partial removal of the pelvic or pectoral fin is commonly done by using scissors to remove a portion of the fin perpendicular or at an angle to the principal fin ray about half way between the end of the fin and its base (Eipper and Forney 1965; Guy et al. 1996). Clipped fins typically regenerate but often remain recognizable (Figure 11.2). Fin clips are quick and inexpensive, but the limited number of possible combinations and the uncertainty that results from regeneration limit the types of studies in which they can be used. In practice, fin clips are often used as simple distinguishing marks to separate one group of fish from another, such as in a hatchery setting.

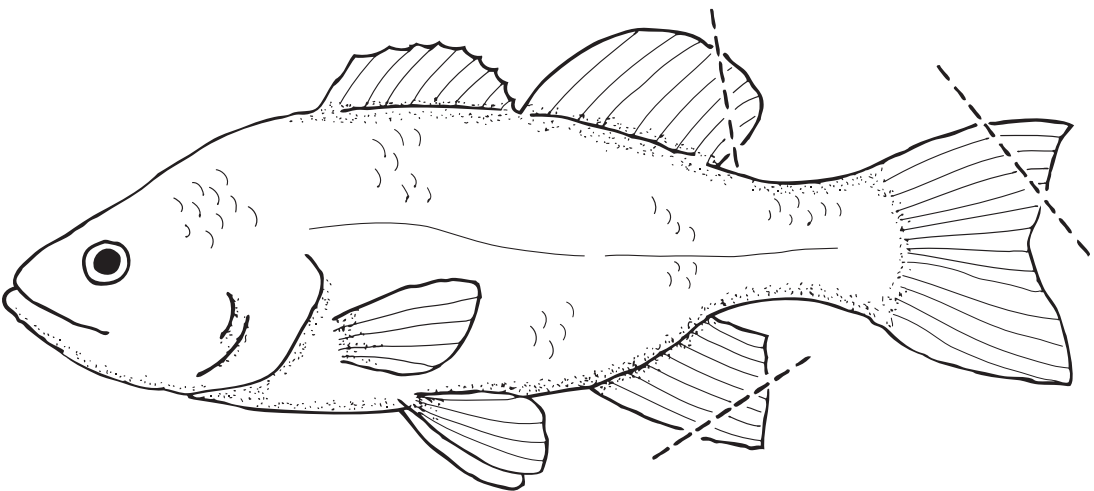


Figure 11.1 Angled clips of dorsal, anal, and caudal fins are most recognizable before and after regeneration (reprinted from Guy et al. 1996).

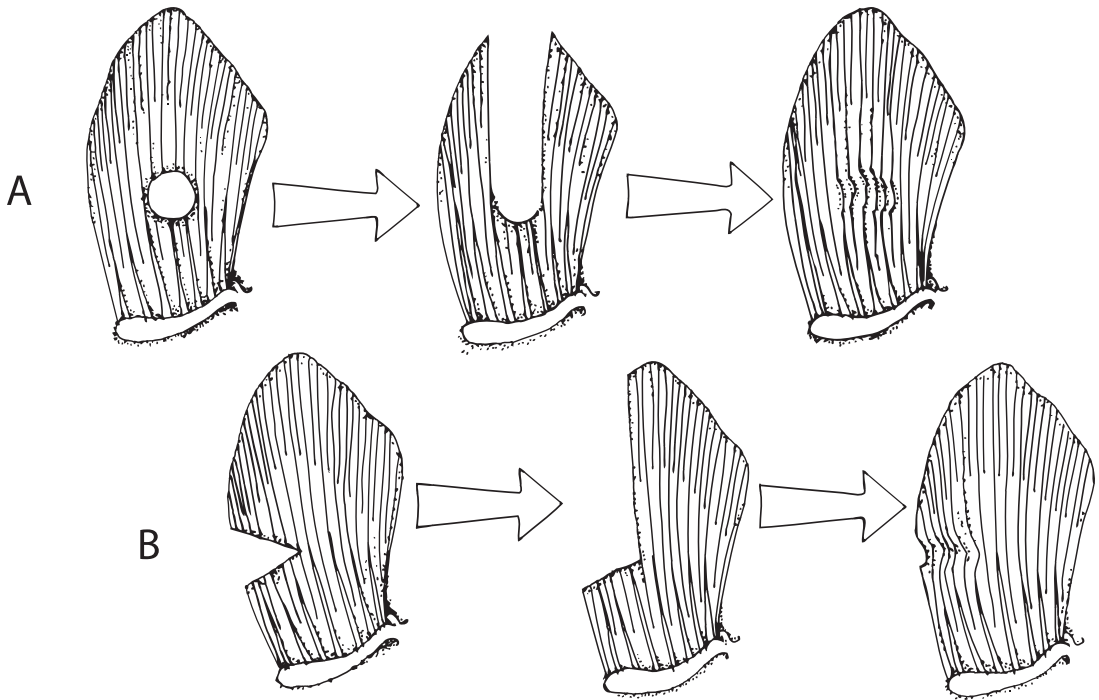


Figure 11.2 The appearance of (A) punched and (B) notched fins. Regenerated fins and fin rays will be distorted after regeneration, allowing for recognition after the original clip grows back (reprinted from Guy et al. 1996).

Both hot and cold branding create identifiable marks on the bodies of fish. Branding is rapid and can be used to mark large numbers of animals. As with fin clipping, it is best used for short-term marking because brands can fade with time or become difficult to distinguish as fish grow (Guy et al. 1996). Branding is generally used to provide a batch mark (section 11.3.1; Bryant et al. 1990) but can also create individual marks (Morrison and Secor 2004).

11.2.2 Natural Marks and Tags

Morphological and meristic marks are natural marks based on body shape, markings, size, or color (morphometric) or on counts of physical features such as scales along the lateral line (meristic). These marks are often unique to animals of specific geographic regions and allow them to be separated from conspecifics from other locations. For example, morphometric and meristic traits were used to identify stocks of Mediterranean horse mackerel and show that their migration patterns were restricted among the Black, Marmara, Aegean, and eastern Mediterranean seas (Turan 2004).

Marine mammals are often identified based on scar patterns on their bodies or fins that result from interactions with predators such as sharks, barnacle growth, or boat propeller strikes. Individuals sighted during visual surveys to estimate marine mammal abundances are photographed when they are at the surface of the water to breathe. These photos are then analyzed, and the distinguishing marks are noted and cataloged (Wilson et al. 1999). These catalogs are then examined through time to create “capture” histories that record where and when an animal was relocated (section 11.4). Photo identification requires that accurate matches are made to make certain that

the same animal is actually being observed multiple times. Scar marks can change over time from new injuries or healing, which can make unique identification of some animals difficult. Much research has been devoted to these types of analyses given the intense interest in assessing the status of threatened and endangered marine mammals (Yoshizaki et al. 2009, 2011).

11.2.3 Otolith Microchemistry

Researchers use naturally occurring isotopic and elemental markers to determine natal origins and to assess movement patterns of larvae, juveniles, and adult fish over large areas (Elsdon et al. 2008). Such information is essential in developing spatial management programs such as marine protected areas or in identifying natal rivers. Otoliths are paired calcified structures that are located in the heads of fish and function in hearing and balance. They are widely used in fisheries management to determine the ages of fish (Chapter 15), and they are also reliable natural tags (Thorrold et al. 2001). Otoliths are composed primarily of calcium carbonate and a variety of trace elements, which are usually derived from the ambient water that fish swim in; therefore, the isotopic and elemental composition of otoliths will mirror the environmental characteristics of the water the fish inhabit. These characteristics of water may vary spatially, and if a fish moves among areas as it grows, that variability will be recorded in the growth layers of its otoliths. Samples of otolith material deposited at different ages can be removed and chemically analyzed to determine where a fish lived at different points in its life.

11.2.4 Coded Wire Tags

Coded wire tags are widely used for tagging large numbers of animals, especially for distinguishing hatchery fish from wild counterparts (Bordner et al. 1990; Johnson 1990). Coded wire tags are small pieces of magnetized steel wire (1.1 mm × 0.25 mm) that are notched or imprinted with a code that can identify individual fish. Because of their small size, they must be read under a microscope. They have been used successfully to tag hundreds of millions of a wide variety of bony and cartilaginous fishes and invertebrates (see Table 5.2 in Nielsen 1992). The size of coded wire tags allows them to be used in small fish and have high retention. Coded wire tags are believed to have little effect on growth or mortality risk of tagged animals (Nielsen 1992).

Coded wire tags are injected into specific body locations, such as the head or snout, where retention rates are high (Buckley and Blankenship 1990; Nielsen 1992; Brennan et al. 2005). They are implanted using handheld or semiautomated injectors (Guy et al. 1996) that allow large numbers of animals to be tagged quickly. They are usually detected with handheld or automated detectors. Detection indicates that an animal is tagged, but it is generally not possible to decode the tag to identify the individual animal without sacrificing it and extracting the tag. An exception is to place the tag in a location (e.g., between fin rays) where it remains visible and can be surgically recovered without significant harm to the fish (Haw et al. 1990). Shallow tagging locations may have higher loss rates, so a more practical approach may be either to accept the need to sacrifice recaptured fish or to use coded wire tags for group level identification. Batches of fish can be identified by injecting tags into different body structures, such as in the cheek in one year and in the snout in the next. This allows for multiple batches of animals to be marked for use in Brownie-type survival analyses (section 11.5).

11.2.5 Visible Implant Elastomer Tags

Visible implant elastomer (VIE) tags are injected into transparent or translucent fish tissues such as the cheek. They are made of a colored elastomer and a clear catalyst that are mixed togeth-

er as a liquid and injected with a hypodermic needle. The material cures to a flexible solid after a few hours and is visible as a colored dot or short stripe. Multiple tag locations and colors can be used to create unique identifications. Visible implant tags are widely used because they have little effect on growth, survival, and behavior of fish (Phillips and Fries 2009) except for small individuals (Reeves and Buckmeier 2009). They can also be used on invertebrates (Replinger and Wood 2007) and amphibians (Phillips and Fries 2009). Retention time varies by tag location, species, and tag color as the tag material degrades or is covered over by new tissue growth (Summers et al. 2006; Bolland et al. 2009).

11.2.6 Anchor Tags

Anchor tags are composed of an internal attachment end imbedded into the body of the tagged animal and an external colored plastic tube or streamer imprinted with study-specified information. The attachment end for dart-style tags is either T-shaped (T-bar tag) or single-barbed arrowhead shaped (dart tag). Internal-anchor tags are attached to a flattened rectangular or oval plate that lies flush against the body wall (Nielsen 1992). These tags are commonly used on a wide variety of fishes and invertebrates because they are relatively easy to attach, are readily visible, and can carry a simple informational message (e.g., unique identification number, agency that tagged the fish, and return and reward information). Anchor tags have been used to gather important information on migration (Boreman and Lewis 1987) and mortality (Dorazio et al. 1994; Diodati and Richards 1996) of striped bass along the Atlantic coast to develop management plans for this species (Richards and Rago 1999). They are preferred over other external tags such as transbody Carlin tags, which may affect growth (Nielsen 1992).

Dart-style tags are typically anchored to the fish by means of a hollow-needle applicator inserted below the dorsal fin of the fish and beyond the pterygiophore bones (Figure 11.3). Dart tag applicators are reloaded with a tag for each fish whereas T-bar tag applicators can be loaded with strips of multiple tags. The key to high tag retention is proper anchor placement behind the pterygiophores (Figure 11.4) or other rigid body structure to provide a firm attachment point (Waldman et al. 1990; Sprankle et al. 1996). Failure to attach to a rigid structure will lead to tag shedding; insertion into the musculature is insufficient. Internal-anchor tags are generally attached by inserting the base through a small incision in the body wall (Nielsen 1992).

Shedding of anchor tags occurs in two ways (Ebener and Copes 1982). Initial tag shedding occurs immediately (hours to days) after tagging and is probably caused by improper attachment; long-term or “chronic” shedding is probably a result of tag wear. Tag longevity also depends on animal growth rates and environmental conditions. Structural growth within a rapidly growing animal may push a dart-style tag anchor away from the rigid structure and into soft tissue from which it is more likely to be shed. Tags on animals living in clear, productive waters may become covered with algae, making it difficult to read the tag inscription and leading to higher tag shedding rates because of increased drag. Tags covered with algae are also more likely to be overlooked, contributing to under-reporting in studies with fishery tag returns.

11.2.7 Passive Integrated Transponder Tags

Passive integrated transponder (PIT) tags are radio-frequency identification (RFID) tags injected into the body cavity or musculature of animals that are subsequently detected and read without removing them from the animals (Chapter 18). The PIT tag consists of an integrated circuit that is used for information storage, processing, and signal modulation and an antenna for receiving and transmitting a signal. An external energy source in the PIT-tag reader activates



Figure 11.3 Red grouper being tagged with a dart tag (photo by Nick Parcell, Mote Marine Laboratory).

the tag, which then transmits a unique alphanumeric code by radio signal to the reader, which decodes the tag and displays the information.

The PIT tag offers several important advantages over other tag types. Tag shedding is low because PIT tags are incorporated into the musculature or body cavity of fish and therefore cannot be lost to entanglement or affected by algal growth. They can be read without removing the tag from the fish; they are also small, which reduces swimming, survival, or growth impairment of tagged fish; and they are essentially permanent, in that the tag's power comes from the reader instead of an internal battery. The tag components are encapsulated in glass and protected within the animal. The long-life of PIT tags is beneficial for long-term population monitoring programs such as that of humpback chubs in the Colorado River (Coggins et al. 2006a). The PIT tag plays an important role in hatchery operations as hatchery managers can keep track of individual broodfish to compile breeding histories and assess performance (Jenkins and Smith 1990).

The size of the PIT tag influences both the size of the animal that can be tagged and the detection range of the tag from the tag reader. The most common PIT tags are small (about 12 mm long \times 2 mm diameter) full-duplex PIT tags that can be implanted in a wide range of fish but must be in close proximity (generally a few centimeters) to a reader to be detected. Tagged animals must be confined (Sandford and Smith 2002) or captured and manually checked for tags. Half-duplex technology using larger 23 mm \times 3 mm tags allows greater detection range and is used where autonomous receivers and stream-spanning antennas can detect tagged fish (Jepsen et

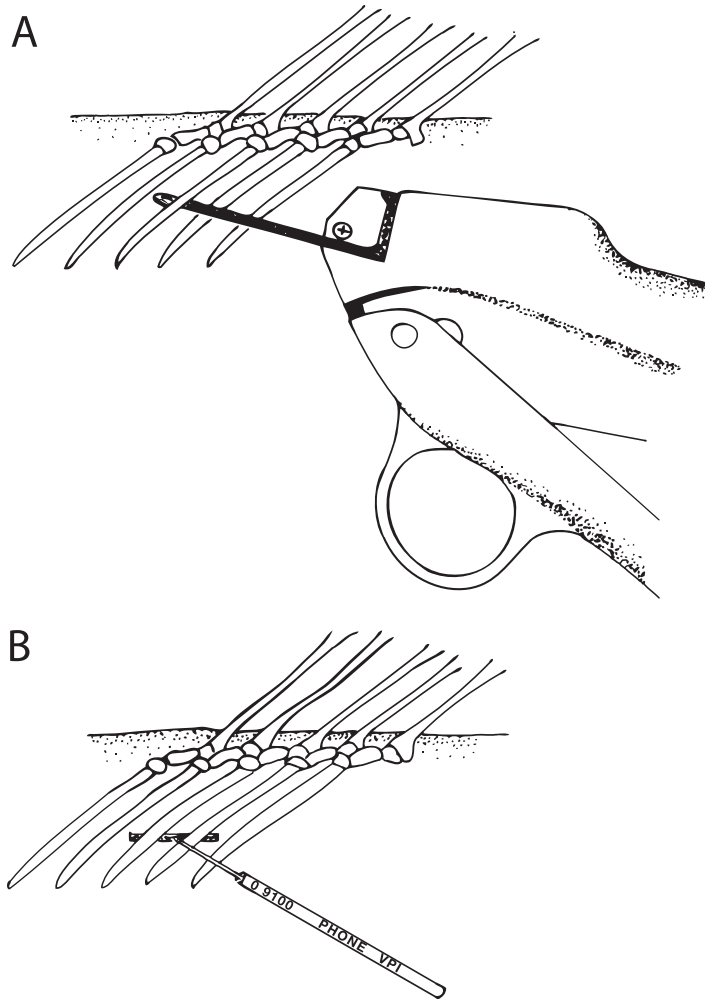


Figure 11.4 High tag retention rates of dart and T-bar anchor tags are often dependent on placement of the (A) tagging gun needle and (B) tag between the pterygiophores of fish (reprinted from Guy et al. 1996).

al. 2000; Adams et al. 2006; Zydlewski et al. 2006; Chapter 18). Enhanced detection rates and large-scale monitoring of habitats are possible because tagged animals do not have to be captured (Hewitt et al. 2010).

11.2.8 Genetic Tags

The unique DNA of an animal can serve as a tag (Waits 2004). The use of molecular genetic techniques to identify animals and estimate abundances and trends in populations is fairly widespread in wildlife management (Waits 2004) and is becoming more common in fisheries applications (Buckworth 2004). In a gene-tagging program, a tissue biopsy (usually a muscle punch or fin clip) is taken from each animal and stored in alcohol; the animals are released. The tissue sample is processed using polymerase chain reaction (PCR) to amplify 4–12 (depending

on population variation) nuclear DNA microsatellite markers, the combination of which is used to identify the individual animal. In the future, as animals are captured, biopsied, and released, their DNA is compared with the previously collected library for matches. Fishing mortality can be estimated directly by taking tissue samples from harvested fish (e.g., through a creel survey or port sampling program) and comparing them to the known (previously genetically identified) population of animals.

Genetic tags minimize some of the problems with traditional tagging studies such tag shedding and low reporting rates. However, gene tagging requires specific assumptions related to the genetic analyses that traditional tagging programs do not (Yoshizaki et al. 2009, 2011), and technical and analytical concerns must be overcome. The cost of “tagging” (analyzing the tissue sample) is high compared with most other tag types but is declining as sequencing technology advances. Another concern is amplification failure, in which PCR fails to produce sufficient copies of the intended piece of the animal’s genome, possibly because of a lack of sufficient DNA in the sample. It is most common when tissue is taken from specific body parts, such as fins or epithelial mouth cells. Pilot studies to evaluate the quality of the DNA from a variety of tissue sample locations can help avoid this problem. Allelic dropout occurs when one allele at a locus fails to amplify. It can cause a false identification because the sample appears to be homozygous at a particular locus when it is actually heterozygous. This results in incorrect genotyping of an animal, which can result in a new animal being classified as a recapture or vice versa. The key to avoiding this problem is development at the beginning of the study of a reliable library of microsatellites with sufficient power to identify animals uniquely and with a high degree of certainty (Waits 2004).

11.3 IMPORTANT CONCEPTS AND ASSUMPTIONS

11.3.1 Batch versus Individual Marks

The distinction between batch marks and individual marks is important. A batch mark indicates that a fish is from a specific group or batch but does not individually identify the fish. For example, batch marks are commonly applied in hatcheries to fish larvae or juveniles that are being reared for release into the wild. These animals can then be distinguished from wild fish by examination for the batch mark. Common batch marks include chemicals such as oxytetracycline (OTC) and calcein administered through direct injection, immersion, or feed. Exposure to these chemicals creates a mark that can be detected by examining the fish’s otoliths or other hard parts (Muncy et al. 1990; Guy et al. 1996). Batch marking is often inexpensive, can sometimes (as in hatcheries) be done to large numbers of animals quickly, and can be used to determine simple movement patterns or to estimate abundances using closed-population models (section 11.4.3).

Whereas batch marking is simple and inexpensive, the types of studies conducted using it are limited. Batch marks can be applied in only a limited number of combinations (i.e., only so many fins can be clipped), and animals usually must be killed to find chemical and coded wire tags (Guy et al. 1996). Batch marks do not allow detection of multiple recaptures of an individual, thereby precluding use of many modern capture–recapture analytical methods for estimating demographic parameters and limiting the rigor of analyses or types of research questions that can be addressed. Because of these limitations, we recommend that animals generally be individually marked using uniquely identifiable, long-life tags whenever possible.

11.3.2 Tag Retention

Tag retention must be sufficiently high to meet study objectives and must be estimated to calculate abundance estimates or mortality rates. Tag shedding can be highly variable among and within species. For example, largemouth bass anchor-tag shedding rates range from 8 to 76% (Hartman and Janney 2006). Tag retention often depends on the experience of the person doing the tagging. We recommend practicing tagging before conducting a study and estimating tag-shedding rate by double-tagging a subset of animals.

Double-tagging (Figure 11.5) provides the best information about tag loss because the estimate is specific to the study organism, location, tag type, and skill of taggers. For example, in a tagging study conducted to estimate harvest rates of redbreast sunfish by use of T-bar tags, a biologist may choose to double-tag some fish with two T-bar tags. The tag retention rate can be estimated from recaptures or tag returns of double-tagged fish based on the number retaining both or just one of the tags (Seber 1982; Barrowman and Myers 1996; Polacheck et al. 2006; Smith et al. 2009). Loss of each tag is assumed to be independent. This critical assumption can be met by sound study design. For example, if two streamer tags are inserted in close proximity to each other, the loss of one could affect retention of the other; independence would be more likely if they were inserted farther apart. A better approach for ensuring independence is to use tags of completely different types (e.g., a PIT tag and a T-bar tag).



Figure 11.5 Double-tagged Atlantic cod. Tag-loss estimates are obtained from recaptures of double-tagged fish based on the number retaining both or just one of the two tags (photo, with permission, by Shelly Tallack, Gulf of Maine Research Institute, on board FV *Elizabeth*, Maine).

Tag retention is not just an issue for external tags. Some fishes, notably channel catfish and salmonids, can expel foreign objects such as PIT or telemetry tags that have been implanted into the body cavity (Chisholm and Hubert 1985; Marty and Summerfelt 1986; Lucas 1989). Tagging such species may require special modifications, such as attaching the tag directly to bony structures (Siegwarth and Pitlo 1999) or the use of natural tags such as gene tags (section 11.2.8).

If double-tagging is not possible, another approach is to capture, tag, and hold tagged fish in cages or ponds and record the number of tags that are shed over a specific time period (Taylor et al. 2006). This approach is limited to species that can be kept in captivity and assumes that tag retention rates in the wild are the same as in cages. If none of these approaches can be used, estimates of retention for many tag types can be found in the literature (e.g., Nielsen 1992 and Clugston 1996).

11.3.3 Effects of Tagging

A key assumption of many models to estimate mortality or abundance is that tagged animals have similar movements, growth and survival rates, and capture probabilities as untagged animals. Differences in growth (Manire and Gruber 1991) and survival (Dunning et al. 1987) between tagged and untagged animals exist in some species. These can probably be minimized by carefully choosing the type and size of tag to minimize injury, effects on swimming performance, or predation risk. Tag manufacturers are an excellent source of information for selecting the best tag type for a species and can offer the most up-to-date information on tag types, sizes, and suitability for organisms of different sizes and shapes. They often also provide excellent training videos and technical reports and have many years of experience in helping to choose a tag type.

11.4 ESTIMATION OF ABUNDANCE

11.4.1 The Limitations of Population Abundance Indices

A common need is to determine the absolute abundance of a fish population, whether it is a species of commercial or recreational value, one that is endangered or threatened, or perhaps an invasive species. A simpler alternative is to use a population abundance index that is assumed to be proportional to absolute population abundance and will thus reflect trends in the population in response to management actions such as harvest regulations, habitat modifications, or eradication efforts (Williams et al. 2002).

Catch per unit effort (C/f ; Boxes 6.3 and 11.1) is a ubiquitous abundance index used in fisheries research and management. It is based on the assumption that the finite probability of capture (denoted as p in the capture–recapture literature; Williams et al. 2002) is constant over space and time. In the stock assessment literature (e.g., Hilborn and Walters 1992), similar assumptions are made based on the instantaneous catchability (q), with $p = 1 - \exp(-qf)$, where f is the amount of effort expended in obtaining a catch C . The mathematical relationship between the expected or average value (E) of C/f and population abundance (N), or expected catch and population abundance, can be expressed as

$$\begin{aligned} E(C/f) &= qN \\ \text{or} \\ E(C) &= pN. \end{aligned} \tag{11.1}$$

Despite the assumption of linearity and constant p , fisheries biologists commonly acknowledge that p (and q for a given unit of effort) varies over time and space.

Box 11.1 The Relationship between Catch Per Unit Effort and Abundance

Many fisheries monitoring programs are strongly reliant on abundance indices such as catch rate or catch per unit effort (C/f) to monitor abundance. Such indices are used both in fisheries-dependent (e.g., catch rates of commercial fishers) and fisheries-independent (e.g., electrofishing C/f by management agency personnel) monitoring programs. If C/f always provided a reliable index of abundance, many of the techniques in this chapter would not be necessary because C/f data could be used to follow trends in abundance directly, precluding the need to estimate abundance. However, catchability (q) often varies in response to changes in factors such as temperature, water clarity, or fish abundance (N), leading to bias in C/f indices and erroneous conclusions about trends in population abundances (Hilborn and Walters 1992; MacKenzie et al. 2006).

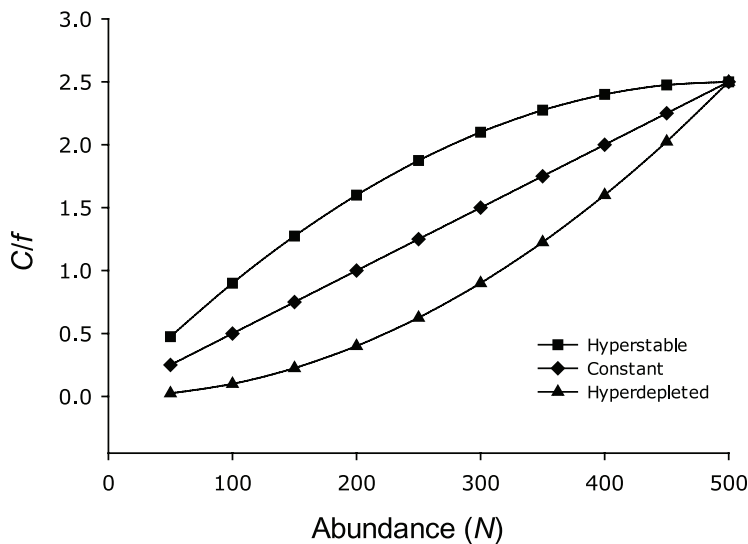


Figure Relationships between abundance and catch rate (C/f) when catch increases faster than abundance (hyperstable), catch increases at the same rate as abundance (constant), and catch increases at a slower rate than abundance (hyperdepleted).

If q is constant as abundance N changes, we would expect C/f to change at the same rate. In this case, C/f would be a good index for assessing abundance as part of a monitoring program as it would provide direct and reliable information on patterns in N . But what if q decreased as abundance increased? This situation is called hyperstability; it results in a C/f index that does not strictly follow patterns in abundance and would provide misleading information about the actual trend in fish population abundance. This pattern could show up in a gill-net survey if gear saturation occurs such that the net fills with fish and is therefore more visible and less efficient at high densities. Gear saturation can occur in traps if fish or shellfish are less likely to enter a trap because of previously caught individuals (Miller 1978). Hyperstability can also occur in commercial fisheries if fishers adjust their methods

(Box continues)

Box 11.1 Continued

to maintain high catch rates despite declines in abundance. Fish abundance may actually be declining, but the C/f index would not indicate this until abundance was critically low. What if q increases with abundance? This is called hyperdepletion. A C/f index in this case would indicate that the abundance is declining faster than in reality and could result in lost income to fishers because of overly conservative management. Hyperdepletion can occur when heterogeneity exists in catchability among individuals in a population. As a stock is depleted through exploitation, the catchability of the remaining fish decreases as the more vulnerable fish are removed. This phenomenon also tends to induce bias in removal abundance estimates (Box 11.5).

Consider a simple example. Suppose the catch of redbreast sunfish differs in two electrofishing transects conducted with equal effort in the same place along a streambank at different times. This difference can be the result of differences in capture probability (p) or abundance (N). How do we know which it is? If the first transect was electrofished on a warm, clear day whereas the second was made on cool, cloudy day, then one may suspect that the difference in catch rate was a result of differences in capture probabilities. However, one cannot be certain of this because the population abundance may also have changed because of animals leaving or entering the area. A better approach is to estimate N and p separately, allowing for variation in time. The mathematical result based on equation (11.1) is that

$$\hat{N}_i = \frac{C_i}{\hat{p}_i}, \quad (11.2)$$

where \hat{N}_i is the estimated number of redbreast sunfish in transect i , C_i is the number of redbreast sunfish actually captured in transect i , and \hat{p}_i is the estimated capture probability in transect i . The capture–recapture models that we describe in the next section provide accurate estimates and avoid the restrictive assumption that catchability is constant over time and space.

11.4.2 Capture–Recapture Models

Capture–recapture methods for estimating animal abundances and survival rates are widely used in fisheries and wildlife applications (Seber 1982; Pollock et al. 1990; Williams et al. 2002; Pine et al. 2003); they are broadly defined as either “closed” or “open” population models (Figure 11.6). Closed models assume that the population is static during the study period and is thus closed to changes from births, deaths, emigration, or immigration. In other words, both demographic and geographic closure are necessary. Therefore, they are most appropriate for short-term studies. Closed models include the Lincoln–Petersen model and the CAPTURE suite of models (Otis et al. 1978; Seber 1982). Removal or depletion models use a similar analytical approach to closed capture–recapture models although they do not involve marked animals (section 11.4.3.3). The key parameters to estimate in all closed models are population abundance and capture probability.

Open models do not assume that the population is static and allow for changes in abundance caused by births, deaths, or movements into or out of the sample area to occur. Open models include the well-known Jolly–Seber type estimators and their many variations (Williams et al. 2002).

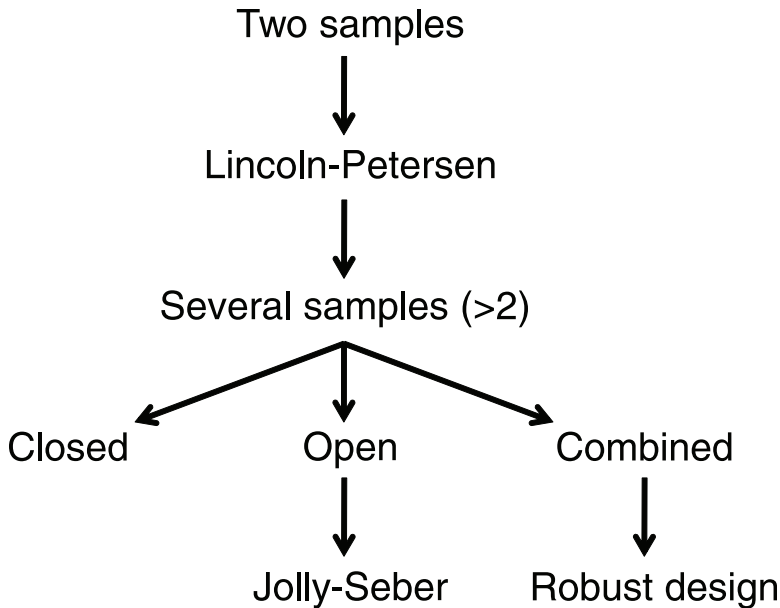


Figure 11.6 Flow chart showing possible study design options to estimate abundances based on the number of samples taken.

Open models are designed to estimate abundance, survival, recruitment, and population rate of change. Because open models are generally more complex than closed-population models (to allow for changes in the population), these models generally require larger numbers of tagged animals and higher capture probabilities. Tagging studies can sometimes be structured such that short-term studies which provide snapshot estimates of population abundance can be nested within longer-term studies that examine temporal trends in abundance or estimates of survival in an open-population framework. This approach is known as the “robust” design (section 11.4.5; Pollock 1982).

11.4.3 Closed-Population Models

11.4.3.1 Two-Sample Lincoln–Petersen Model

The simplest and most common capture–recapture model for estimating population abundance is the two-sample Lincoln–Petersen model (Ricker 1975; McInerny and Cross 1999; Kocovsky and Carline 2001). This model is appealing because it is simple and intuitive. A sample of animals, M , is collected from a population of unknown abundance N . These animals are marked or tagged and released back into the population (Figure 11.7). After allowing the marked animals to mix completely with the unmarked animals, a second sample of animals, C , is collected, of which R animals are recaptures of animals marked in the previous sample trip. We would expect the marked fraction in the second sample (R/C) to equal the marked fraction after the first sample (M/N) provided assumptions of the model (see below) are met. Equating the two ratios produces the standard Lincoln–Petersen estimator

$$\hat{N} = \frac{MC}{R}. \quad (11.3)$$

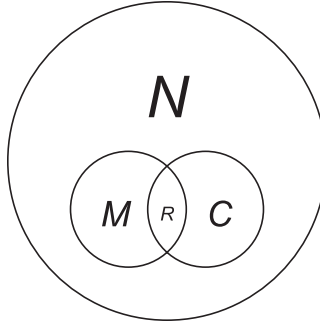


Figure 11.7 Schematic representation of a two-sample Lincoln–Petersen estimate. The objective is to estimate the population abundance N . The first step is to collect, mark, and release the first sample of fish M . The second sample C is collected later and examined for recaptures R from the first sample. An estimate of population abundance is $\hat{N} = MC/R$.

The Chapman modification of the Lincoln–Petersen estimator (Seber 1982) is

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1, \quad (11.4)$$

with a variance estimator of

$$\text{var } \hat{N} = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}. \quad (11.5)$$

The Chapman modification is routinely used in practice because it has much better statistical properties than the standard Lincoln–Petersen estimator when R is small (less than 10). The Lincoln–Petersen model has three key assumptions: (1) the population is closed to additions (births or immigration) and losses (deaths or emigration); (2) capture probability is the same for all animals in each sample (marked and unmarked); and (3) marks are not lost or overlooked. When all three assumptions are met, the model is a straightforward approach to estimating abundance (Box 11.2).

The first assumption means that the study must be of short duration such that the population is static. Otherwise, an open-population model should be used. Moreover, tagging itself may cause some mortality (directly through injury or indirectly because of increased predation), which violates the closure assumption. This serious problem should be addressed by experimentation to determine the least injurious tag type and by conducting in situ experiments to assess mortality rates; see Pollock and Pine (2007) for design considerations for cage experiments. Any mortality whatsoever induced by sampling or tagging is probably of major concern when monitoring threatened or endangered species. This is further complicated by the need to provide tight confidence intervals on abundance estimates of such species, which requires intensive sampling and possible deleterious effects on fish survival or growth—the exact opposite of what would be desired in a monitoring program for a protected species (Paukert et al. 2005).

The second assumption implies that marked and unmarked animals are equally likely to be captured (i.e., no trap response) and that no differences in capture probabilities exist among ani-

Box 11.2 Simple Closed-Population Estimates: Lincoln–Petersen

A simple approach for estimating population abundance N is the two-sample Lincoln–Petersen model. This model does not require detailed capture histories and can be calculated using batch marks. The Chapman modification of the Lincoln–Petersen estimate for N is

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1,$$

where \hat{N} is the estimate of population abundance, M is the number of animals collected and marked in the first sampling event, C is the number of animals collected in the second sample, and R is the number of animals collected in the second sample that were marked as part of M . The approximate variance estimate for \hat{N} is

$$\text{var } \hat{N} = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}.$$

Several options exist for calculating confidence intervals from this variance estimate. Ricker (1975) recommended that when R is 25 or greater, a normal distribution can be assumed such that 95% confidence intervals can be calculated using

$$\hat{N} \pm 1.96\sqrt{\text{var } \hat{N}}.$$

In instances in which R is less than 25, Ricker (1975) recommended a Poisson distribution for the variance approximation and provided tabled values for calculating the upper and lower limits directly by replacing R in the Lincoln–Petersen estimate equation with the upper and lower bounds of the Poisson distribution.

When using the Lincoln–Petersen model, the product of M and C should exceed four times the estimated population abundance (\hat{N}), multiple gears should be used for marking and recapture to reduce potential gear selectivity effects, and seven or more recaptures (R) should be made (Robson and Regier 1964; Ricker 1975). The following plot can be used to estimate needed sample sizes.

(Box continues)

mals resulting from inherent differences such as length (i.e., no capture heterogeneity). In some situations, the probability of capturing a fish may depend on its previous capture experience. For example, cutthroat trout behavior following electrofishing and marking was highly altered for 24 h after capture, thereby probably altering recapture probabilities during that period (Mesa and Schreck 1989). Differential capture probability between marked and unmarked animals can cause serious problems with a variety of closed-population sampling programs (Mahon 1980; Thurow et al. 2001). Most fisheries gears are selective such that some individuals are more likely to be collected than others, leading to heterogeneity in capture probability. For example, electrofishing is size selective for larger individuals (Chapter 8). This could cause electrofishing samples to have higher proportions of large fish than in the population as a whole. One approach to dealing with

Box 11.2 Continued

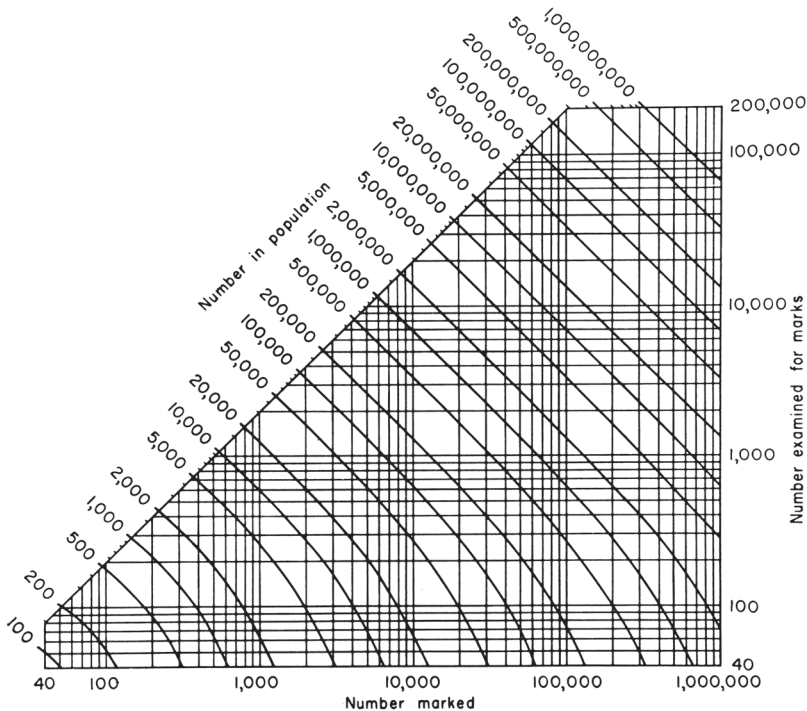


Figure Combinations of the numbers of marked animals (M) and the numbers that should be subsequently examined for marks (C) to achieve estimates within 25% of \hat{N} (Figure 5 from Robson and Regier 1964).

Use of the plot requires generation of an assumed value (best guess) of population abundance. An assumed value for a species in a lake might be based on the lake's surface area and the average density observed from historical rotenone sampling in the region. For example, if 2,000 animals are thought to be in a population, then $M = 1,000$ and $C = 70$ is one combination that should provide an estimate within 25% of the true population abundance. If a lower precision is needed (within 50% of the true population abundance) then fewer animals would need to be marked and recaptured (see Figure 4, Robson and Regier 1964).

Consider a Lincoln–Petersen abundance estimation sampling series in which 421 bluegills (M) were sampled, marked with a fin clip, and released on day 1. Five days later, another sample yielded 332 fish (C), of which 88 (R) were marked. The abundance estimate is

$$\hat{N} = \frac{(421+1)(332+1)}{(88+1)} - 1 = 1,578,$$

with an approximate variance of

(Box continues)

Box 11.2 Continued

$$\text{var } \hat{N} = \frac{(421+1)(332+1)(421-88)(332-88)}{(88+1)^2(88+2)} = 16,017.$$

The resulting 95% confidence interval (assuming a normal distribution) is 1,330 to 1,826. Adjustments to M , C , or R allow exploration of the degree to which the estimate of N might be biased by violation of assumptions. For example, if 10% of fin clips were overlooked, only 79 recaptures would be detected (reduce 88 by 10%) and \hat{N} would be 1,756. Such biases are precisely why it is important to have a well-designed and executed study that minimizes assumption violations.

such heterogeneity is to incorporate multiple gears into each sampling trip so that gear selectivity bias is reduced in the aggregate sample (Seber 1982). For example, electrofishing transects could be sampled while hoop nets were being fished to collect species (such as channel catfish) that may not be efficiently sampled by electrofishing. The combined catch from the two gears may provide a better estimate of overall abundance because of differences in gear selectivity among species. A second approach is to produce abundance estimates for strata, for example, by grouping animals into size-classes and calculating separate estimates for each size-class (Seber 1982; Kwak 1992) or by calculating the pooled estimate and then weighting the pooled estimate by the strata (Seber 1982). However, stratification reduces the number of marked and recaptured fish in each stratum, thereby potentially inflating variance in parameter estimates. Equal probability of capture also assumes that marked and unmarked fish are well mixed in the population such that individuals in one group do not have a greater chance of being captured than those in the other.

What happens when these assumptions are violated? The nature of the bias will depend on the type of violation. Heterogeneity of capture probabilities causes underestimation of the population abundance N . Put simply, this can be thought of as one portion of the population being less vulnerable (lower capture probability) than another. The population estimate is based on the entire population, so the capture probability is then biased toward the more vulnerable population, resulting in an overestimate of capture probability and an underestimate of abundance. Trap response causes an underestimate if marked animals are trap happy and an overestimate if marked animals are trap shy. Tag loss and tagging mortality directly reduce the number of marked fish M available for recapture R and therefore reduce the denominator in equation (11.3) causing an overestimate of N (Pollock et al. 1990).

Sufficiently large capture probabilities are imperative. When capture probabilities are low (generally <0.10), abundance estimates vary widely and are not sufficiently precise for detecting population trends (Figure 11.8). Note also that the distribution of estimates is not normal at low capture probabilities (Figure 11.8), which affects the choice of confidence interval estimation technique used (Seber 1982).

An advantage of Lincoln–Petersen type models is that batch marking is sufficient; fish do not need to be individually marked (section 11.3.1). Also, the second sample could involve harvest or other removal approaches instead of recapture, thereby reducing the possibility of a trap response.

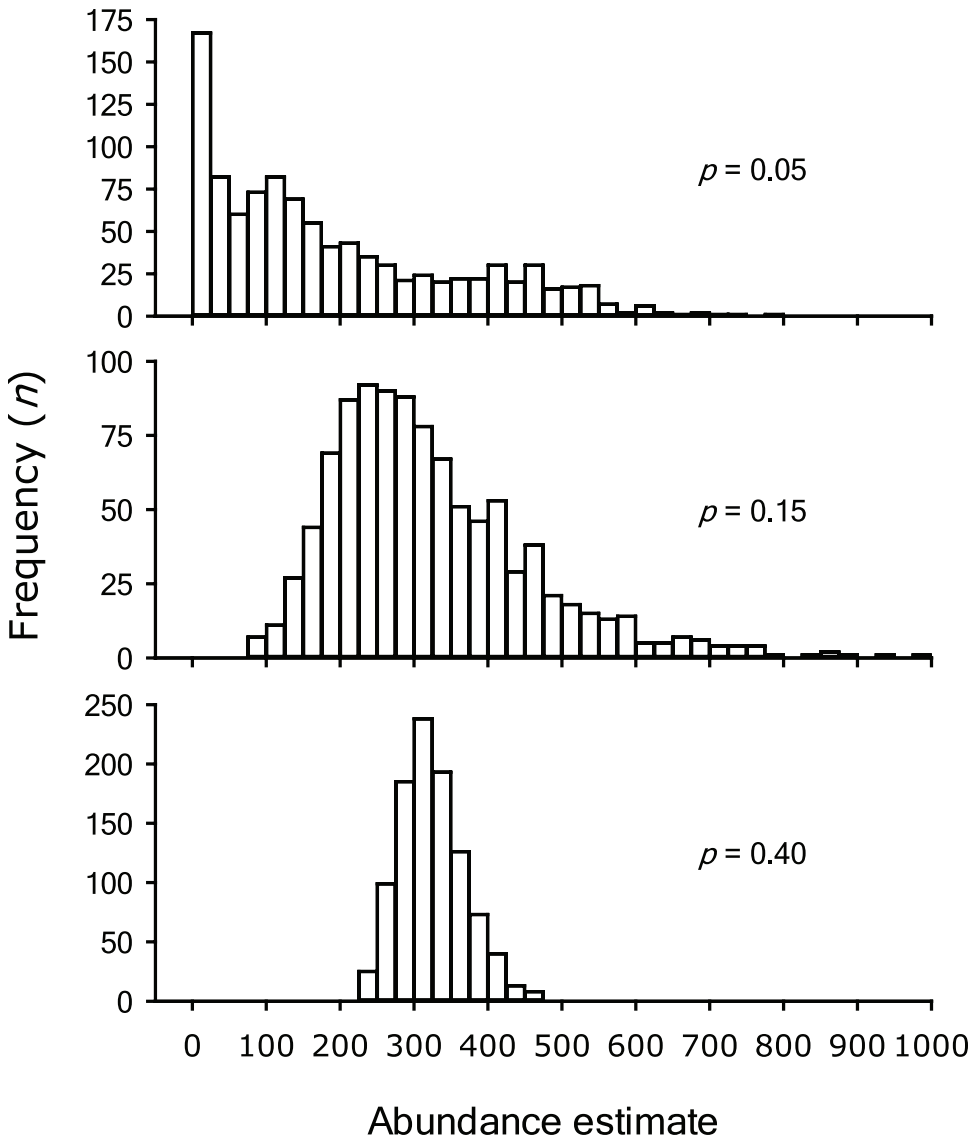


Figure 11.8 Frequency distributions of simulated abundance estimates from a two-sample Lincoln-Petersen experiment based on three different capture probabilities ($p = 0.05, 0.15$, and 0.40) and a known population abundance of 300 individuals. Frequency distributions represent the frequency of occurrence of a particular abundance estimate out of 1,000 possible trials (i.e., simulated field experiments).

Using different gears for marking and recapturing in a Lincoln-Petersen model also reduces the likelihood of a trap influence or heterogeneity in capture probability related to a single gear type.

The Lincoln-Petersen model is commonly used to monitor salmon smolt out-migration in some Alaskan rivers (Carlson et al. 1999). Typically, salmon smolts are captured while they are migrating downstream, subcutaneously marked with dye, and released back into the river (to cre-

ate the marked fish M). Fish are then resampled (C) at a second point farther downstream and examined for the dye mark (R). This simple design capitalizes on the unidirectional movement of salmon smolts and allows the estimation of both capture probability (p) and out-migrant number (N) during a particular time period based on equation (11.2). Similar designs have been used for returning adult salmon (McPherson et al. 2000).

11.4.3.2 More Than Two Samples—General Closed Models

The more general sampling scheme involves more than two sampling occasions. The fish may be recaptured multiple times and released alive each time (Box 11.3). Each capture is commonly recorded as a “capture history,” which is a series of 1s and 0s for which a 1 indicates that a fish was caught in that sampling period and a 0 indicates that it was not caught. This method of recording capture histories is widely used for summarizing data and entering it into software packages for analysis.

A suite of widely used closed-population models useful to fisheries biologists is assembled in the computer package CAPTURE (Otis et al. 1978; Pollock et al. 1990; Williams et al. 2002) and is available free on the Internet as a stand-alone program or as a module within the program MARK (www.phidot.org/software/mark/). These models were designed to account for variations in capture probability related to temporal variation, trap response, and inherent heterogeneity among individual fish. For example, the M_h model allows each animal to have a unique capture probability (e.g., because of size or sex or other more subtle differences), but this capture probability remains the same for each sample (Otis et al. 1978). The M_t model is analogous to the traditional Schnabel model (Ricker 1975) and allows capture probability to vary among sample periods but to be uniform for all individuals within each period (Box 11.3). This is the only model in CAPTURE appropriate for multiple sampling events using batch marks. The M_b model allows for trap response or behavioral changes by allowing both a capture probability for a first capture (\hat{p}) and a separate probability for recaptures (\hat{c}) to be estimated. Combinations of the above models such as the M_{th} , which allows for heterogeneity among individuals and among sampling occasions, are also possible. However, these combination models are more complex and require higher capture probabilities than do the simpler models (Norris and Pollock 1995; Pledger 2000; Williams et al. 2002).

Well-designed closed-population studies should be the first choice in fisheries applications for estimating abundance. The design should be developed by examining the model assumptions and minimizing violations to the extent possible. For example, sampling needs to occur over a short time period (days to weeks) so that births and deaths during the study period are minimized. Movement into or out of the sample area may be negligible in some systems (e.g., a lake or a stream reach blocked at each end) but can be much more difficult to control in other settings. Stretches of stream can be considered closed even though animals potentially can move into or out of the area if sampling occurs over a short period and movements are monitored (Osmundson and Burnham 1998; Mitro and Zale 2002). Immigration should be examined by tagging animals outside the sample reach and then checking to see if any of these animals are recaptured inside the sample reach or, preferably, by incorporating a telemetry component to the study to evaluate movement patterns of a small subset of animals while conducting the tagging study (Zehfuss et al. 1999).

11.4.3.3 Removal Models

These models are applied widely in fisheries research to estimate population abundances and can also be used to estimate capture probabilities (Ricker 1975; Hilborn and Walters 1992). These studies involve repeated sampling (e.g., electrofishing passes) of a particular location such that

Box 11.3 Closed Models for More than Two Sample Occasions: Program CAPTURE

If sampling to estimate abundance is planned to extend beyond two sampling events, the closed-population CAPTURE models (Otis et al. 1978) should be used. The tags or marks generally must be individually unique (not batch marks) because most of these models require individual capture histories. All of the CAPTURE models are closed to changes in the population caused by animals entering (births or immigration) or leaving (mortality or emigration) the population. Closed models are powerful when their assumptions are met (section 11.4.3). They can account for variation caused by trap response, time, and inherent heterogeneity of capture probability. An important attribute of closed models in general is that they are able to fit sparse data (most often caused by low capture probabilities) much better than open models. The following example presents two simple closed models in program CAPTURE (Otis et al. 1978) available through MARK (www.phidot.org/software/mark/).

Sampling of Gulf sturgeon occurs routinely below the Jim Woodruff Dam on the Apalachicola River, Florida, to monitor population status and trends (Zehfuss et al. 1999). Gulf sturgeon were sampled using gill nets on 16 occasions during the summer of 1985. All Gulf sturgeon collected were uniquely tagged with a combination of T-bar and passive integrated transponder (PIT) tags. Occasion-specific individual captures were entered into the program. The first model (M_0) to estimate population abundance (\hat{N}) does not allow for changes in capture probability. The following table presents the M_0 model results from program CAPTURE.

Table Constant capture probability model M_0 .

Number of sampling occasions	16
Number of animals captured	76
Total number of captures	123
Estimated probability of capture, \hat{p}	0.0695
Population estimate, \hat{N}	111
Standard error	10.7
95% lower limit	96
95% upper limit	138

The M_0 output contains estimates of two parameters, capture probability (\hat{p}) and population abundance, \hat{N} . It also includes the number of sampling occasions (16), the number of unique animals collected (76), and the total number of captures (unique captures + recaptures = 123). On average, about 7% (0.0695) of the study population was captured on each sampling occasion. The population within the study area was estimated to be 111 individuals, with a 95% confidence interval of 96 to 138. This simple model assumes constant capture probability and no behavioral effects or heterogeneity in capture probability.

Because of variation in river discharges that may have affected efficiency of the sampling gear, capture probability was expected to vary with time. The second model (M_t) allows for variation in capture probability across sampling events. The following table presents the M_t model output from program CAPTURE.

(Box continues)

Box 11.3 Continued**Table** Time-dependent capture probability model M_t .

Number of sampling occasions	16
Number of animals captured	76
Total number of captures	123
Estimated probability of capture, event 1	0.01
Estimated probability of capture, event 2	0.03
Estimated probability of capture, event 3	0.08
Estimated probability of capture, event 4	0.03
Estimated probability of capture, event 5	0.01
Estimated probability of capture, event 6	0.04
Estimated probability of capture, event 7	0.01
Estimated probability of capture, event 8	0.20
Estimated probability of capture, event 9	0.11
Estimated probability of capture, event 10	0.05
Estimated probability of capture, event 11	0.10
Estimated probability of capture, event 12	0.09
Estimated probability of capture, event 13	0.07
Estimated probability of capture, event 14	0.05
Estimated probability of capture, event 15	0.10
Estimated probability of capture, event 16	0.11
Population estimate, \hat{N}	114
Standard error	15.4
95% lower limit	94
95% upper limit	157

The M_t model estimates 17 parameters, including 16 capture probabilities, \hat{p}_j (1 for each sample occasion), and \hat{N} . The output contains the number of sampling occasions, the number of unique animals captured, and the total number of captures. The \hat{p}_j for each occasion ranged from 0.01 to 0.20. Population abundance was estimated to be 114 with a 95% confidence interval of 94 to 157.

The estimates of \hat{N} generated by the models were similar, but the standard error was smaller from the simpler M_o model. This makes sense given that the same data are being used to estimate only two parameters in M_o compared with 17 parameters in M_t . Whereas the precision of M_o is greater, is it more accurate? Biologists conducting the fieldwork believed that the model with time-dependent capture probabilities was more realistic because of differences in dam discharge among sampling occasions. Thus, M_t made more sense, even though it results in a larger confidence interval around \hat{N} . One approach for choosing among alternative models is to use Akaike's Information Criterion (AIC, Akaike 1974; section 2.6.8.4, this volume). This numeric value, an estimate of how well the model fits the data, is widely used to compare competing models. It can be used to select the best model or to construct a weighted estimate of population abundance that takes into account the likelihood of each model (Burnham and Anderson 1998).

fish caught during each pass are excluded from being caught in subsequent passes. The exclusion is accomplished by physically removing fish from the sampling location following each pass, for example, by holding them in a streamside bucket or cage. Removal models are similar statistically to closed capture–recapture models and can be analyzed with the same software such as CAPTURE and MARK or in a spreadsheet (Box 11.4; White et al. 1982; Williams et al. 2002); removed fish are essentially “marked” by their absence. The key data are the number of fish caught (C_i) during each pass (i). For example, suppose that a particular stream section contains N fish before a removal experiment begins and that no fish can enter or leave this section (i.e., the reach is spatially and temporally closed). The only way that the abundance of uncaught fish can change during the experiment is by removal by sampling. This closure assumption guarantees that fish are not lost because of natural mortality or emigration nor are fish added to the population because of immigration or recruitment. The traditional approach to analyzing removal data is a simple linear regression method based on plotting catch versus cumulative catch (Leslie and Davis 1939; Moran 1951; Zippin 1956). In practice, the assumption required by linear regression of constant variance in the catches with each removal pass is usually not met, such as when catch declines erratically with each pass. In these instances, maximum likelihood approaches (model M_b in CAPTURE; Otis et al. 1978; White et al. 1982) are used because they are often less biased and more precise than regression methods (Gould and Pollock 1997). Maximum likelihood approaches have the same assumptions as closed-population capture models including a common removal probability for all fish throughout the experiment.

Capture probability frequently changes with time or is different among individuals (Otis et al. 1978; Hilborn and Walters 1992; Pierce 1997). Heterogeneity among individuals can be addressed using M_{bh} in CAPTURE (Otis et al. 1978; White et al. 1982). If the source of the heterogeneity can be identified (e.g., size), stratify the removals into groups (size categories) and estimate the abundance of each group (Kwak 1992). No estimation model is readily available for changing capture probabilities over time in a removal framework in CAPTURE. More sophisticated removal methods exist to deal with heterogeneity in capture probability (e.g., Dorazio et al. 2005 and Mäntyniemi et al. 2005). This can occur in practice, for example, if water clarity decreases in a stream between the first and second pass because silt was disturbed by the sampling crew. The change in water clarity probably decreases the capture probability during the second pass. Violating this assumption would cause population abundance to be underestimated.

Removal models have great practical appeal despite their rigid assumptions because they can be conducted quickly and at lower cost than capture–recapture methods and they provide snapshot estimates of abundance for discrete spatial areas. These snapshots can be linked over larger spatial or temporal scales (see for example Gould and Pollock 1997). We recommend that biologists considering a removal study carefully assess whether the constant catchability assumption will be met. If not, more complex methods as described below may be needed to obtain valid estimates. Note that although our examples involve removal sampling with constant effort, closely related catch–effort models exist for short, intense fisheries with known but variable effort (Delury 1947; Ricker 1975; Seber 1982).

11.4.4 Open-Population Models

Jolly–Seber type models are open-population capture–recapture models used in fisheries tagging studies when multiple recaptures are possible (Box 11.5). This group of models has been actively used and modified by a diverse group of fisheries, wildlife, and statistics professionals

Box 11.4 Removal Models

Removal (depletion) models have a long history of fisheries applications in a diverse range of settings including small streams and large commercial fisheries. Removal sampling provides an estimate of capture probability and abundance for a closed population. Removal estimation methods are useful when repeated sampling of a population occurs and captured individuals are not returned to the population. Various methods are available for estimating population abundance from removal sampling (Williams et al. 2002). Here, we use the Leslie regression method of plotting catch per pass versus cumulative catch of previous passes (Leslie and Davis 1939) and a maximum likelihood approach (Gould and Pollock 1997) to estimate the abundance of largemouth bass in a small lake sampled by boat electrofishing. Five electrofishing passes of the lake shoreline were completed over consecutive days, and all fish captured were removed from the population. Equal effort was applied during each pass, measured as distance of shoreline sampled. The daily catches of largemouth bass were 95, 78, 85, 67, and 42. Using the Leslie regression method, we acquired an abundance estimate of 589 largemouth bass (y -intercept of the linear regression model in the figure on the next page) and a mean capture probability of 0.18; capture probabilities for each pass were calculated by dividing catch by the estimated number of fish in the lake as shown in the following table. Numbers present are calculated by subtracting the cumulative catch of previous passes from the abundance estimate ($\hat{N} = 589$).

Table Capture probability estimation.

Pass and statistic	Catch (n)	Cumulative catch of previous passes	Estimated number present	Capture probability (\hat{N})
1	95	0	589	0.16
2	78	95	494	0.16
3	85	173	416	0.20
4	67	258	331	0.20
5	42	325	264	0.16
Mean				0.18

(Box continues)

(Cormack 1964; Jolly 1965; Seber 1965; Pollock et al. 1990; Williams et al. 2002). The closely related Brownie models are used if tag returns from harvest are used for recapture (see Brownie et al. 1985; Hoenig et al. 1998a, 1998b, and section 11.5). The Jolly–Seber model allows population abundance estimation at each sampling event (excluding the first and last), estimation of “apparent survival” (true survival $S \times$ fidelity rate) between samples, and estimation of new recruits to the tagged population between sampling events. If the focus is only on survival estimation, we use the Cormack–Jolly–Seber model, which uses information from only marked animals. Both Jolly–Seber and Cormack–Jolly–Seber procedures are included in MARK (White and Burnham

Box 11.4 Continued

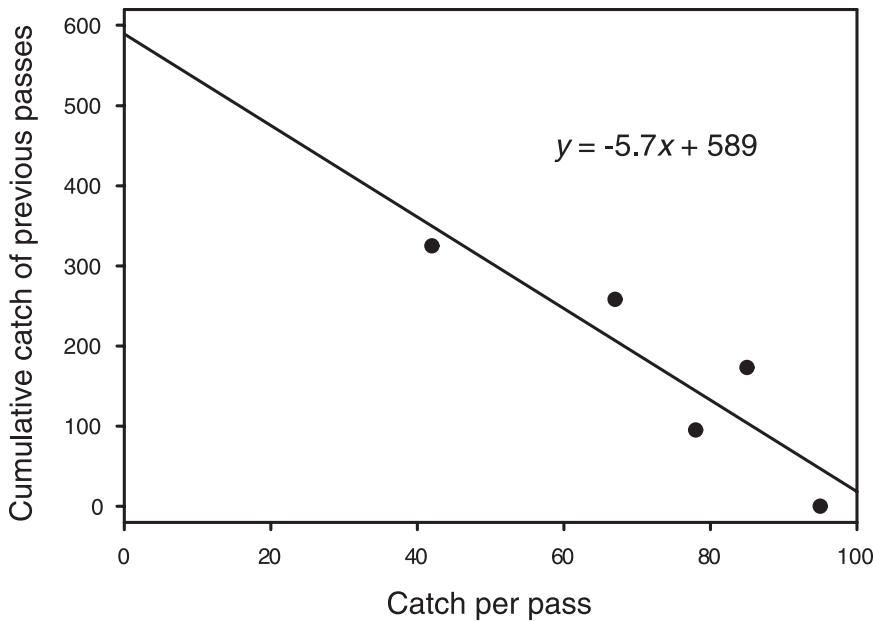


Figure Leslie regression method for estimating the abundance of largemouth bass in a small lake.

A Microsoft Excel template for the maximum likelihood removal model is available from the lead author, as well as pseudocode for the model in Program R and other programming languages. Using the maximum likelihood estimation method, we acquired an abundance estimate of 654 largemouth bass and a capture probability of 0.15. The maximum likelihood approach is more robust to imperfect removal data (e.g., increases in catches on subsequent passes) than the Leslie regression method, which may fail to produce a valid estimate given such suboptimal depletions. Behavioral responses of organisms (e.g., trap avoidance) can cause bias in removal abundance estimates; researchers should be cautious of animals avoiding the sampling gear during consecutive samples that disturb the environment (Peterson 2004). For example, if largemouth bass avoided the gear after the initial day of sampling, we would observe an artificial decline in catches over time, resulting in a negative bias in our abundance estimates.

1999). A special “superpopulation” version of the Jolly–Seber model (POPAN) fits models of survival and capture rates and estimates numbers of animals and new recruits (Schwarz and Arnason 1996); it is also accessible in MARK.

The assumptions of the Jolly–Seber model are (1) every animal present in the population on each sampling occasion has the same probability of being captured; (2) every animal present in the population on each sampling occasion has the same probability of surviving to the next sampling period; (3) marks are not lost or overlooked; (4) all animals are released immediately after

Box 11.5 Open-Population Jolly–Seber Type Models

Jolly–Seber type models are the primary “open” population models for estimating survival ($\hat{\phi}$) and abundance (\hat{N}). They can also be used to estimate the number of new animals entering a population. Open models are generally used for studies lasting longer than a few weeks, during which population changes caused by births, deaths, emigration, and immigration can occur. Jolly–Seber models can be readily fit using software available on the Internet.

This example is based on Gulf sturgeon data from the Suwannee River, Florida, and uses a Cormack–Jolly–Seber model to estimate annual survival by means of program MARK (White and Burnham 1999). Gulf sturgeon longer than about 1,000 mm in total length were tagged as they migrated into the river during the spring spawning run. Sampling effort and conditions varied over the 8-year sample period. Models in which survival is allowed to vary over time as well as those in which survival is fixed as an average parameter value through time are both biologically reasonable. Variable capture probability over time is also possible because of changes in sampling effort and sampling conditions. The following output from MARK is from a model in which single survival and capture probabilities were fit over the entire time series; they can be thought of as average values for this time period.

Table Model 1: fixed survival and capture probability. Number of parameters estimated = 2.

Parameter	Estimate	Standard error	95% confidence interval	
			Lower	Upper
$\hat{\phi}$	0.87	0.02	0.83	0.91
\hat{p}	0.12	0.01	0.11	0.13

The annual survival estimate (87%) is relatively high, as would be expected for a long-lived species such as Gulf sturgeon. The capture probability estimate (12%) is higher than in many fisheries studies. Whereas these parameter estimates seem reasonable, this model may not be the most appropriate because of the possibility that capture probability changed over time because of changes in sampling effort and in sampling conditions.

(Box continues)

the sampling event and sampling events are discrete or instantaneous; and (5) any emigration is permanent.

The Jolly–Seber model is less flexible in dealing with heterogeneity of capture probabilities or trap response than are the closed models. Heterogeneity of capture probabilities (e.g., because of fish sizes) will cause the estimated number of marked animals at large to be overestimated, leading to underestimation of the population abundance (Pollock et al. 1990). To account for this, separate analyses (and estimates of capture probability) could be included for different strata of fish (such as males and females or adults and juveniles) that represent the factor causing the heterogeneity in capture probability. Trap response could cause either a positive or a negative bias.

Box 11.5 Continued

The following output from MARK is from a model in which capture probability was allowed to vary among years.

Table Model 2: fixed survival and time-dependent capture probability. Number of parameters estimated = 8.

Parameter	Estimate	Standard error	95% confidence interval	
			Lower	Upper
$\hat{\phi}$	0.94	0.02	0.87	0.98
\hat{p}_1	0.10	0.02	0.07	0.14
\hat{p}_2	0.13	0.02	0.10	0.17
\hat{p}_3	0.13	0.02	0.11	0.17
\hat{p}_4	0.16	0.02	0.13	0.20
\hat{p}_5	0.10	0.01	0.08	0.12
\hat{p}_6	0.08	0.01	0.06	0.11
\hat{p}_7	0.03	0.01	0.02	0.04

In this example, eight parameters were estimated, including one survival rate and seven capture-probability values for years 1 through 7. Estimated survival in this model (94%) is higher than in model 1, and the estimated changes in capture probability through time make sense given the changing sampling effort and conditions. The survival and capture probability estimates appear reasonable, but note that the estimated survival rate is outside the 95% confidence interval for the survival estimate from model 1. This illustrates that confidence intervals are conditional on the model being fit, and they assume that the fitted model is correct. They provide some guidance about the precision of model estimates but need to be interpreted cautiously.

Which model is “best?” As described in Box 11.3, AIC scores can be used for model selection (Burnham and Anderson 1998), but any model selection criterion should be used only as a guide to assist the researcher and not as the singular criterion for choosing the best model. In this example, model 2 is supported by the expectation that it is more biologically reasonable, and the AIC score for this model (from MARK) is also lower (better) than the score for model 1. Therefore, we conclude that model 2 is the better model.

The original Jolly–Seber model assumes that survival is equal for every tagged fish from one sampling occasion to the next. Considerable effort has been directed toward development of models that allow for covariates (e.g., sex or size) and age-classes (Pollock et al. 1990; Coggins et al. 2006b) such that survival, and in some cases abundance, can be estimated for classes or groups of animals. Negative bias in the estimated survival rate and overestimation of abundance can occur if the tag or tagging procedure reduces survival or if the tags are shed (Arnason and Mills 1981; Brownie and Robson 1983).

A key assumption of the Jolly–Seber model is that all emigration is permanent. This assumption can be difficult to meet because fish may move in and out of a study area naturally. Such behavior can be described as temporary emigration (Kendall et al. 1997; Zehfuss et al. 1999). Temporary emigration can be further distinguished as “Markovian,” in which a fish “remembers” its previous location and returns to that location at some discrete time interval, or “random,” in which the fish randomly comes and goes on a continuous basis (Kendall et al. 1997). Temporary emigration can result in biased survival and abundance estimates and is especially problematic if Markovian. Unbiased estimates of abundance can be obtained with temporary emigration if capture probabilities are high ($\hat{p} > 0.5$; Zehfuss et al. 1999), but such values are difficult to achieve in fisheries studies. In most cases, temporary emigration would negatively bias abundance estimates (Zehfuss et al. 1999). The robust design (Kendall et al. 1997; Williams et al. 2002; section 11.4.5) allows for temporary emigration.

The standard Jolly–Seber model cannot be used to estimate survival and emigration because the two rates are confounded. For example, if a fish is not collected, is it because the fish died or because it emigrated from the sample area? Because of this, survival estimates (ϕ) from a Jolly–Seber model are actually apparent survival ($\phi = S \times \text{fidelity rate}$). True survival (S) can be calculated if additional information on fish emigration ($1 - \text{fidelity rate}$) is available, for example, from a telemetry study or if tagged individuals are collected outside the sample area. Note that the survival estimates apply to only the tagged component of the population. For example, if only adults are tagged, then the apparent survival rate estimate is for adults only. As with studies to estimate abundance, tag retention is important in survival estimation studies; PIT tags are a good choice because they have high retention rates, are uniquely identifiable, and have no external streamer that may attract piscivores, thereby minimizing differential survival between marked and unmarked fish.

If the intensity of sampling remains constant over all sampling occasions, confidence limits from a Jolly–Seber model will be “trumpet” shaped, with the most precise estimates from the middle sampling occasions (Figure 11.9). During the sample occasions that take place in the middle of the study, the number of tagged fish is large, and sampling occasions remain during which these animals can be recaptured. As with Lincoln–Petersen estimates (Figure 11.8), the precision of Jolly–Seber abundance estimates increases with higher capture probabilities.

Jolly–Seber models are commonly used for long-term (>10 year) tagging programs for estimating trends in abundance and survival of imperiled fishes such as humpback chub (Douglas and Marsh 1998; Coggins et al. 2006a) and Gulf sturgeon (Chapman et al. 1997; Zehfuss et al. 1999; Pine et al. 2001). The humpback chub tagging program has evolved to play a central role in developing and evaluating water allocation plans for Glen Canyon Dam and management of much of the aquatic component of Grand Canyon National Park (Coggins et al. 2006b). Jolly–Seber models have also been used to estimate survival of lake trout in important recreational and commercial fisheries (Fabrizio et al. 1997). Simulation results from a largemouth bass study using the Jolly–Seber model (Hightower and Gilbert 1984) can be used in planning these types of studies in cases where population abundance is large and survival is high. The free Microsoft Excel add-in “PopTools” available on the Internet (www.poptools.org) is useful for simulating Jolly–Seber data sets and analyzing simple capture–recapture experiments.

11.4.5 Combined Open and Closed Models—The Robust Design

Attributes of both the closed and open models make each appealing for fisheries applications. Open models allow for changes in the population (e.g., permanent emigration, births, and

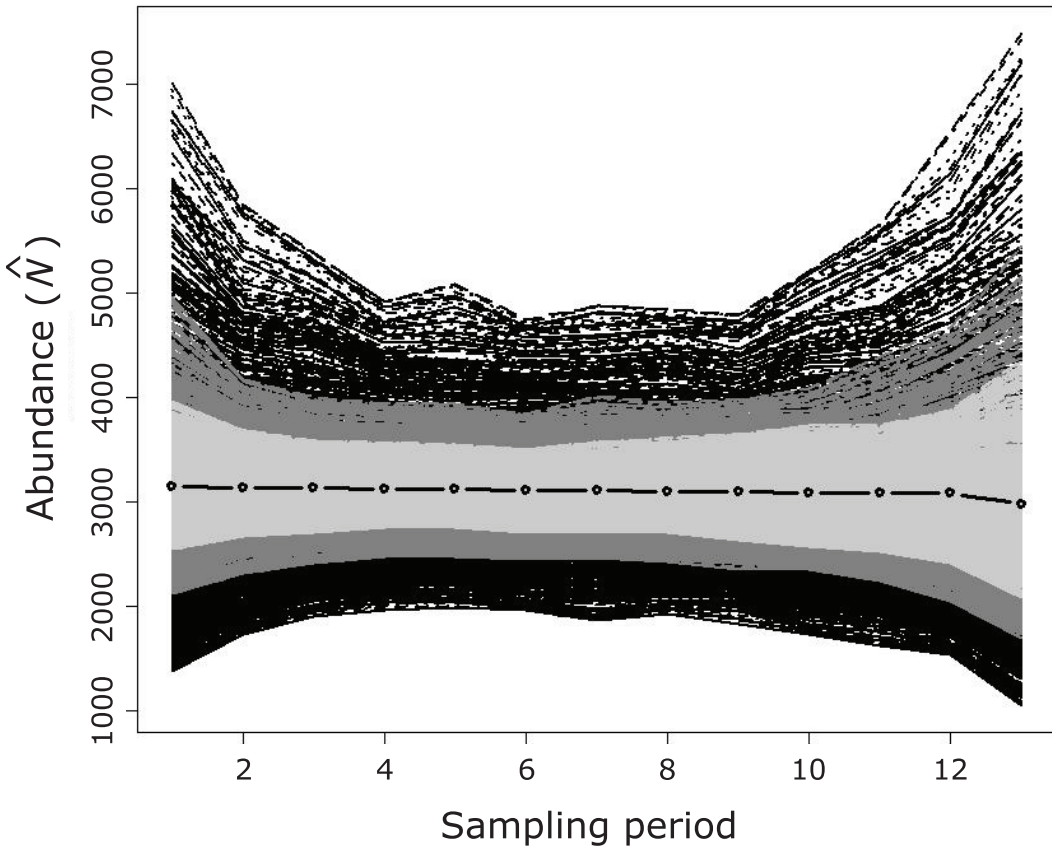


Figure 11.9 Confidence intervals of simulated Jolly–Seber population estimates based on three different mean capture probabilities (light gray, $p = 0.15$; dark gray, $p = 0.10$; black, $p = 0.05$). The dark dash-circle line indicates true population abundance ($N = 3,150$). Distributions are based on 1,000 replicate trials such that each trial represents a field experiment. Note the wide range in possible abundance estimates, \hat{N} , with low capture probabilities as indicated by the wide range of results for the $p = 0.05$ case.

deaths) that are likely to occur naturally over time. However, this flexibility requires estimation of more parameters, so open models often perform poorly with sparse data (small sample sizes). Closed models do not allow for population changes but are more likely to provide abundance estimates with sparse data and can also account for heterogeneity and behavioral responses of capture probabilities of individual fish.

The robust design (Pollock 1982) is a sampling design and analysis framework that incorporates aspects of both closed and open models. It works by linking a series of discrete, closed-population studies to estimate population abundance with an open-population model to estimate survival. For example, monthly closed-population abundance estimates could be obtained by sampling daily during a 1-week period each month (Figure 11.10). Survival between months could be estimated using the Jolly–Seber model. Additionally, the data set could be analyzed in a fully open model by collapsing the monthly samples into single sampling events (1 per month,

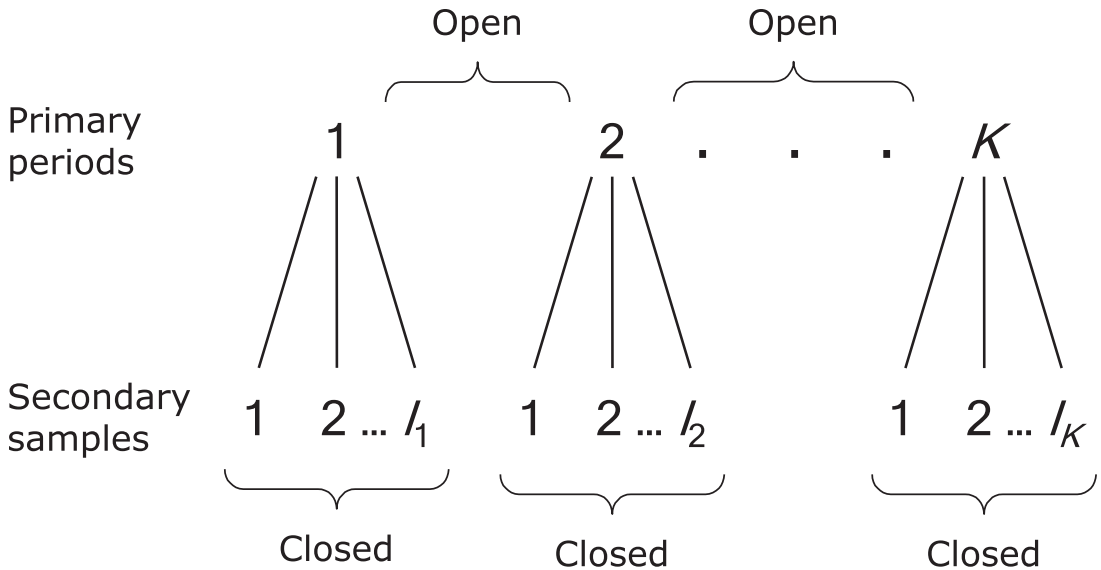


Figure 11.10 Schematic representation of the robust design. Abundance is estimated in the secondary sampling periods by means of closed-population models and survival is estimated between the primary periods based on open models (redrawn from Pine et al. 2003).

12 samples total) to get another estimate of abundance based on the Jolly–Seber model for comparison. The advantages of the robust design are that it allows for unequal capture probabilities and also temporary emigration of fish (Williams et al. 2002).

11.4.6 Multistate Models

Multistate models are similar to Cormack–Jolly–Seber models and are used to estimate movement probabilities among “states” and state-specific survival and capture probabilities. Survival and capture probability are defined as the probability of being alive and captured in state r , and the probability of transitioning from one state to another is estimated as ψ . States can be defined in a variety of ways including spatial location (e.g., tributary and main-stem river or inside and outside a marine protected area) and age-class (e.g., juvenile and adult). For example, fish may move between two patches of preferred habitat in which fishing mortality rates differ. A biologist may be interested in the mortality rates in the two areas, as well as the transition probability between the two locations. Such questions are common in fisheries (e.g., marine reserve evaluations), and a variety of approaches exist for examining them (Hilborn 1990; Schwarz et al. 1993; Quinn and Deriso 1999), yet the use of multistate models in fisheries is not common (Newman 1998; Whitehead 2001).

The sampling design for multistate models is similar to that of Cormack–Jolly–Seber models but with the addition of sampling the different states and estimating the transition probability between them. In practice, multistate models require large amounts of data because sufficient recaptures need to be made to determine if an animal is present and simply not captured in state r or if it has transitioned to another state (Joe and Pollock 2002; Coggins et al. 2006a). For example, if states are geographic regions, then sampling is conducted in multiple regions. The transition probability is often difficult to estimate because the number of marked and recaptured animals

is essentially reduced by a factor equal to the number of regions. Essentially, separate Cormack–Jolly–Seber studies to estimate survival must be conducted in each state. Moreover, low capture probabilities and return rates are not unusual in fisheries tagging programs (Pine et al. 2003). Recent advances in PIT tag antennas (Adams et al. 2006; Hewitt et al. 2010) and the combination of multiple types of tagging approaches (e.g., tagging and telemetry; Pollock et al. 2004) may be useful for providing sufficient capture information. Such approaches can also provide empirical estimates of ψ based on observations of animals moving between sites.

11.4.7 Sampling Effort

The most important step in planning a tagging study is to ensure that sampling effort for both marking and recapturing will provide sufficient precision to answer the research question. The capture probability that will be achieved by a sampling program is difficult to estimate in advance, but pilot studies or published estimates can be helpful in estimating capture probability and the level of sampling necessary to generate parameter estimates of sufficient precision. Bayley and Austen (2002) empirically estimated capture probabilities in small ponds and reservoirs in Illinois for a range of species, sampling gears, and conditions. Not surprisingly, capture probability estimates were generally low (most less than 0.2) and variable across the species sampled. In our experience, capture probabilities in closed- and open-population models are generally 0.2 or lower (often much lower). Accurate population abundance estimation using closed models generally requires capture probabilities greater than 0.1 and population abundances of at least 200–300 individuals (Otis et al. 1978).

A powerful tool in planning a capture–recapture study is to create simulated data that represent the expected number of sampling trips, possible capture probabilities, and, depending on the model used, survival and other parameters. White et al. (1982) used simulations to recommend capture probabilities of 0.2 and population abundances of at least 200 individuals to generate reliable population abundance estimates. The classic Robson and Regier (1964) sampling plot (Box 11.2) remains useful for estimating the number of fish that must be marked in the first sample and examined for marks in the second sample to estimate population abundance reliably using the Lincoln–Petersen model.

11.5 ESTIMATION OF FISHING AND NATURAL MORTALITY WITH TAG-RETURN MODELS

Estimating the rate of survival (S) or total finite mortality ($1 - S$) of a fish population is an essential step in understanding what regulates its structure and abundance. Most fisheries management activities are directed at monitoring exploitation rates of fish populations and how fishing mortality combined with natural mortality affects population change. Studies on imperiled species are often focused on trends in survival to assess the long-term viability of populations.

In exploited fish populations, instantaneous mortality rates are used more often than survival rates because fisheries regulations are usually designed to limit fishing mortality (F). The sum of fishing mortality and natural mortality (M) equals the total instantaneous mortality rate (Z), which can be converted to S as

$$S = e^{-Z}. \quad (11.5)$$

The Cormack–Jolly–Seber model based on multiple captures and recaptures can be used to estimate survival of a species that is not exploited, such as an imperiled species (section

11.4.4). A related approach based on tag returns of exploited species can be used to estimate survival or mortality rates and, in some cases, to partition total mortality into fishing and natural components. The estimates are based on tag-return models, which are commonly referred to as the Brownie models (Brownie et al. 1985). The models were originally developed for analyzing band-return data from migratory waterfowl in the USA and have been widely applied to a variety of fisheries applications (Youngs and Robson 1975; Hoenig et al. 1998a, 1998b). Fisheries managers are keenly interested in partitioning mortality ($1 - S$) into fishing (F) and natural (M) mortality in most recreational and commercial fisheries. Brownie models estimate total mortality, which when combined with tag shedding, tag-induced mortality (δ), and tag-reporting (λ , the probability that a tag on a harvested fish is reported) rates, can be used to estimate F and M (Hoenig et al. 1998a, 1998b; Pollock et al. 2001). The advantage of this approach is that F and M can be estimated without all of the tags having to be reported.

11.5.1 Biologist-Based Tagging Programs

Many tagging studies, whether to estimate abundance (section 11.4), mortality, or movements (section 11.7) are carried out completely by biologists who capture, tag, release, and recapture the animals of interest. These studies most often take place in situations where the biologists can sample all of the population of interest (e.g., largemouth bass in a small lake) or a large portion of it (e.g., one particular salmon stock during a spawning run). In these situations, biologists have great control over the fates of fish that are caught (i.e., they can be tagged and released rather than harvested), which allows for multiple mark–recapture analysis methods to be used (section 11.4.2).

Researcher-sampled tag returns can come from a variety of sources including onboard observers on large vessels, shore-based port samplers, or creel clerks. Estimates of survival based on biologist recaptures of previously tagged fish are based on Cormack–Jolly–Seber type models, and high capture probabilities are critical for estimating survival precisely (section 11.4.4). Primary advantages of this biologist-based approach are maintaining data quality and being able to acquire additional information such as detailed spatial information on catch that might not be readily available from most fishers. Another advantage is that the reporting rate is 100% for the fraction of the harvest examined by the biologist. Meeting this assumption allows for the separation of total mortality into fishing and natural mortality components (Pollock et al. 2002). In addition, estimates of migration rates would be unaffected by spatial or temporal differences in reporting rate. The disadvantages of using biologists to recover tags are the additional staff cost and often limited coverage (vessels, ports, or ramps) where staff can be based.

The International Pacific Halibut Commission (IPHC) tagging program is a noteworthy example of scientific sampling for tag returns (Forsberg 2004; Kaimmer and Geernaert 2004). The IPHC concluded that prior tagging studies were of limited value because of variable reporting by fishers, so it started a new program using PIT tags that would be recovered by IPHC port samplers. In the first year, 44,000 Pacific halibut were tagged and 584,000 landed Pacific halibut were scanned for tags. Tag recoveries enabled IPHC staff to estimate fishing and natural mortality as well as migration rates among areas (Clark and Chen 2005).

11.5.2 Angler-Based Tagging Programs

Angler-based tagging programs are an increasingly important way of marking marine fishes and obtaining tag returns (Loftus et al. 2000; Prince et al. 2002). They are an example of the “citizen science” widely used in many areas of natural resource management (e.g., citizen-based bird

counts and the REEF program, www.reef.org), which can be cost-effective and provide broader spatial and temporal coverage than could be achieved by agency staff (Lucy and Davy 2000). However, such programs must be carefully managed to minimize bias and uncertainty in the data collected. A major benefit is that the interaction between agency staff and participating fishers tends to build public support for agency management efforts (Lucy and Davy 2000). Most successful angler-based tagging programs have well-defined scientific or management objectives, a training program for taggers, and dedicated commitment from the agencies and organizations involved (Loftus et al. 2000).

The tagging program for highly migratory marine species developed by the Cooperative Tagging Center is a notable example of an angler-based tagging program (Prince et al. 2002). Its recreational and commercial fishing constituents have tagged more than 245,000 fish, and the program has provided information about movement and biology of these species that has contributed substantially to stock assessment and management. The Suntag program coordinated between the Australian National Sportfishing Association, Queensland, and the Queensland Fisheries Service is another large-scale recreational tagging program (www.info-fish.net/). It links recreational fishers with fisheries management agencies to work together to develop a greater understanding of Australia's fisheries resources.

11.5.3 Fishery-Dependent Tag-Return Programs

Fishery-dependent tag-return programs are common in freshwater and marine recreational and commercial fisheries. They depend on fishers to report tagged fish that are found in their catch and use Brownie-type models (Brownie et al. 1985) to estimate fishing and natural mortality rates. Generally, annual cohorts of fish are tagged, and tags from harvested fish are collected for several years. These tag returns are then used to estimate S and f , which is the recovery rate or the probability that a tagged fish is harvested and reported. The assumptions for these models are similar to capture-recapture models (section 11.4) but also assume that the tags are reported in the correct time period and that all fish in a tagging cohort have the same annual survival and reporting rates. For example, natural and fishing mortality of southern rock lobster in Tasmania were estimated in a tagging program dependent on fisher returns (Frusher and Hoenig 2001). The study was originally designed to evaluate southern rock lobster growth and movement patterns, but the information collected could also be used to estimate mortality. Southern rock lobsters were tagged during three research cruises and were released immediately after capture and tagging. Reporting rate estimates were generated by means of a lottery reward system with entries compiled from completed tag-return information cards. Instantaneous fishing mortality was high ($F = 1.0$ – 1.2 annually) and comparable to estimates obtained using other methods such as catch-effort models. Natural mortality estimates were difficult to generate, low (generally $M < 0.02$ annually), and relatively imprecise. In this example, estimates of fishing and natural mortality that were independent of catch-based estimates were useful in effectively managing the fishery.

Estimating reporting rate accurately is not easy; methods include using high-reward tags, tags secretly planted in a fisher's catch, angler surveys, and catch information from multiple components of a fishing fleet (Pollock et al. 2001). The high-reward method is the most common in fisheries studies (Murphy and Taylor 1991; Denson et al. 2002; Taylor et al. 2006). In it, messages on tags indicate various reward amounts for returning tags to the researchers. A portion of the tags offer a high reward, usually US\$100 or more, and the expectation is that a

recreational or commercial fisher that encounters a fish bearing one will return it with 100% certainty. The reporting rate of the non-high-reward standard tags is estimated as their return rate divided by the return rate of the high-reward tags (Pollock et al. 2001; Taylor et al. 2006). If high-reward tags are not reported 100%, then the reporting rate of the standard tags is positively biased (Pollock et al. 2001).

The high-reward method was used to estimate reporting rate of recreational anglers fishing for common snook in southeastern Florida as part of a tagging program to estimate common snook harvest rates (Taylor et al. 2006; Box 11.6). Legal-size common snook were tagged with anchor tags during the closed-harvest season (summer); anglers returned tags during the remainder of the year. Tags ranged in value from \$5 to \$200, which was assumed to be sufficiently large to elicit 100% return. The reporting rate of the standard tags differed between years (73% in the first year and 56% in the second), possibly because anglers were more aware of the high-reward tags in the second year and less likely to report the lower-valued tags. The reporting rates were higher than those in other fisheries (Matlock 1981), possibly because the highly specialized common snook anglers were actively concerned with the management of the fishery, making them more likely to participate in a tag-return program.

Estimating a reporting rate is difficult because of the numerous factors affecting whether a fisher will report a tag. Some effort on the fisher's part is generally involved, such as calling a tag-reporting hotline, logging in to a reporting Web site, or mailing the tag to the agency. Fishers may be reluctant to report tags if they perceive that the management agency will use the information to limit future harvest. In such case, no reasonable reward may be sufficient to elicit fishers to report all tags. Low reporting rates motivated the IPHC to implement a large-scale PIT-tagging program with port agents checking landed Pacific halibut for tags (Forsberg 2004; Kaimmer and Geernaert 2004). Recreational fishers may be more likely to participate in a reward tagging program than commercial anglers because their motivation for fishing is often intrinsic rather than economic (Schmalz et al. 2004). Regular estimation of reporting rate is imperative in any tagging program so that return rates from fishers can be better interpreted.

11.5.4 Estimation of Survival by Means of Telemetry

"Known fate" survival models applied to telemetry studies (Chapter 18) are another approach to estimating survival (White and Garrott 1990). The fate of each tagged individual (alive or dead) is determined on each search occasion. A mortality rate is estimated for each interval between search occasions, based on the number of deaths that occurred (relative to the number alive on the previous search occasion). Relocation probabilities are generally much higher for telemetry studies than are capture probabilities for passive tagging studies; that is, it is usually easier to know whether or not a telemetered fish is in an area than it is to collect a sample of fish and check them for traditional tags. Therefore, the fates of individual animals can be determined more easily. Repeated relocations of a tag in an anomalous habitat (e.g., an anoxic hypolimnion) or lack of movements can be inferred as a likely mortality (Lee and Bergersen 1996; Bettoli and Osborne 1998; Heupel and Simpendorfer 2002). Mortality sensors incorporated into transmitters (Chapter 18) can also be used to infer fate. A key assumption of these models is that telemetered animals are not affected by the tag.

Use of telemetry to estimate fishing and natural mortality rates extends the methods originally used to estimate only total mortality of terrestrial wildlife species (White 1983; White and

Box 11.6 Estimation of Exploitation Rates

Estimation of exploitation rates is a common purpose of tagging programs. However, proper design of an exploitation study requires careful planning and evaluation of potential biases such as tag loss and nonreporting. Many of the same assumptions that apply to the Jolly–Seber model (section 11.4.4) apply to tagging studies to estimate exploitation rates. A key consideration is how many animals to tag. This question is difficult to answer and depends on the method of retrieving the tags. If tag returns are dependent on commercial or recreational fishers, reporting rates must be estimated. Unless all tags have a high reward, the reporting rate will be less than 100% and may be quite low.

A good practical approach for deciding how many animals to tag is to conduct an analysis of tagging data based on expected tag returns. This analysis will show what level of precision can be achieved with a certain number of tagged fish, given assumed values for the exploitation rate and reporting rate. To begin, use a calculator or construct a simple spreadsheet model to calculate the number of expected tag returns. For example, assume a sample size of 300 fish tagged in each of 3 years, a survival rate of 0.4, an exploitation rate of 0.3, and a reporting rate of 0.5. The number of returns expected in the first year is the product of the number tagged, the exploitation rate, and the reporting rate ($300 \times 0.3 \times 0.5 = 45$). The number of returns of fish tagged in the first year expected in the second year is the product of tagged fish remaining ($300 \times 0.4 = 120$), the exploitation rate, and the reporting rate ($120 \times 0.3 \times 0.5 = 18$). Returns in the third year are calculated similarly, except that the expected number of tagged fish remaining is $300 \times 0.4 \times 0.4 = 48$. The matrix of expected returns can be used to construct a tag-return model, which can be fitted using a spreadsheet or software developed for tagging models such as MARK (www.phidot.org/software/mark/) or SURVIV (www.mbr-pwrc.usgs.gov/software.html). For this 3-year study, if we assume that λ (the reporting rate) is known from a separate study to be 0.5, we obtain 95% confidence intervals of 0.29 to 0.51 for annual survival rate (S) and 0.25 to 0.35 for exploitation rate (u) from SURVIV. Tagging only 100 fish each year results in confidence intervals of 0.21 to 0.59 for S and 0.22 to 0.38 for u . Varying the number of tagged fish allows the investigator to select a sample size that will achieve a desired level of precision. Use of this approach assumes that the survival, exploitation, and reporting rates are constant and that the reporting rate is known. In reality, the reporting rate would need to be estimated, and the precision of that estimate would affect precision of the estimates of survival and exploitation rates. To use this approach in planning a field study, trial values for S , u , and λ can be obtained from studies in other areas or years or from other species.

Ricker Approach

The key to this approach (Ricker 1975) is to design the study so that potential sources of error (tagging mortality, tag loss, and nonreporting) can be assessed. For example, Crawford and Allen (2006) addressed these key concerns in a tagging study to estimate exploitation and natural mortality rates of bluegill and redear sunfish in Lake Panasoffkee, Florida, a large natural lake in central Florida. The focus of the 2-year study was to evaluate the potential of length limits to increase the proportions of large fish in the populations. All captured

(Box continues)

Box 11.6 Continued

bluegill and redear sunfish 15 cm or longer were tagged with individually numbered T-bar tags just below the dorsal fin.

Long-term tag loss was estimated by double-tagging (two tags of the same type placed in each fish). Long-term tag loss was 25% per year in both years (e.g., in year 2, 2 of 8 double-tagged fish that were returned had lost a tag; $2/8 = 25\%$). Short-term (6 d) tag loss and tagging mortality were evaluated in a cage study; none of either occurred.

Reporting rates were estimated with two methods. The first was done in conjunction with a creel survey; the creel clerk discreetly noted the tag numbers of tagged fish before returning them to anglers (making no mention of the tags to the anglers). Reporting rate was calculated as the proportion of observed tags returned. The second approach used \$50 high-reward tags to estimate return rates of standard tags (Pollock et al. 2001). The reporting rates determined using the two methods differed; the creel estimate was 83% and the high-reward estimate was 55%. Both approaches have limitations. The likelihood that an angler will report a tag may be altered simply by the creel clerk measuring a fish that was tagged, and the high reward may not have been sufficient to elicit 100% reporting, which is a key assumption of the method (Pollock et al. 2001; Taylor et al. 2006). Crawford and Allen (2006) therefore evaluated a range of reporting rates in their assessment and examined the possible implications to mortality estimation.

Exploitation rate \hat{u} was calculated as

$$\hat{u} = \frac{N_r}{\left[N_o (1 - t)(1 - m)(\hat{\lambda}) \right]},$$

where N_r is the number of tags returned by anglers, N_o is the number of fish tagged, t is the tag loss rate, m is the tagging mortality rate, and $\hat{\lambda}$ is the tag reporting rate. The estimated annual exploitation rate of redear sunfish in 1999 was

$$\hat{u} = \frac{55}{\left[(753) \times (1 - 0.25) \times (1 - 0) \times (0.83) \right]} = 0.12.$$

Total annual mortality estimates (A) were derived from catch curves ($A = 0.68$) and annual natural mortality (v) was estimated by subtracting u from A :

$$\hat{v} = 0.68 - 0.12 = 0.56.$$

Brownie Tag-Return Models

Brownie (Brownie et al. 1985) models are the standard method for analyzing tag-return data in wildlife studies and should be more widely used in fisheries (Hoenig et al. 1998a, 1998b; Pine et al. 2001). In a Brownie study, annual cohorts of fish are tagged in multiple years, and tags from harvested fish (commercial or recreational returns) are collected from fishers over several years. Various computer programs including MARK, SURVIV, and R can be used to calculate survival estimates. Brownie models are based on discrete rates (e.g.,

(Box continues)

Box 11.6 Continued

annual survival rate) but can be reformulated using instantaneous rates of fishing (F) and natural (M) mortality, which are common in stock assessment (Hoenig et al. 1998a, 1998b).

Consider the following tag-return study designed to estimate F and M of common snook in Florida (Taylor et al. 2006). Common snook were tagged for 10 years with internal anchor tags. The instantaneous tag loss rate ($\hat{\phi}$) was estimated at 3% annually in a separate study in holding ponds. A high-reward tagging study was used to estimate reporting rate ($\hat{\lambda}$) as 0.58 (SE = 0.06). Fish were tagged with either high-reward or standard-reward (standard) tags in 1995; return rates for the standard tag were calculated in 1995, and this rate was assumed for other years (Taylor et al. 2006). This approach allows estimation of M and annual F .

Table Tag-return matrix for a portion of a common snook study in Florida (Taylor et al. 2006).

Tagging year	Standard tags	High-reward tags	Return year					
			1995	1996	1997	1998	1999	2000
1995		246	45	42	10	7		
	248		36	24	5	6		
1996	1,120			217	30	29	6	4
1997	1,238				156	45	20	8

For example, 1,120 common snook were tagged and released during the closed angling season prior to harvest in 1996. Of these, 217 were returned in 1996, 30 in 1997, 29 in 1998, 6 in 1999, and 4 in 2000. It is easy to see how survival rates can be estimated using these data. For example, similar numbers of fish were tagged in 1996 and 1997, but the 1996 cohort was at large for one additional year; the differences in returns of the two cohorts from 1997 to 2000 represent the additional mortality incurred.

Estimated instantaneous rates of fishing (F) for 1995 through 2000 were 0.28 (SE = 0.03), 0.51 (0.07), 0.26 (0.04), 0.21 (0.05), 0.12 (0.04), and 0.09 (0.04). The estimated instantaneous natural mortality rate (M) of 0.37 (0.06) was assumed constant over the study. These estimates have good precision and should be valuable for guiding management.

Garrott 1990). For example, telemetry tags were used to estimate fishing and natural mortality rates of striped bass in Lake Gaston, North Carolina (Hightower et al. 2001). Relocations of telemetered fish were used to determine if fish died because of natural mortality (multiple relocations at the same site or in anomalous habitat), were alive (movement between relocations), or had been harvested (not relocated within the reservoir or adjacent reservoirs). Identification of live animals and those newly dead because of natural mortality allows the separation of fishing and natural mortality without external information on reporting rate. Combination of tag-return and telemetry models provides robust estimates of fishing and natural mortality rates and eliminates the need for high-reward tags to estimate reporting rate (Pollock et al. 2004).

11.6 GROWTH OF TAGGED FISH

11.6.1 Biological Questions That Can Be Addressed

Fish growth is a fundamental biological process that must be reliably measured to understand population dynamics and to develop effective management strategies. The most common approach for examining growth is to use age data from otoliths or other hard tissues (Chapter 15), but this is not always feasible. Some species are difficult to age using hard tissues (e.g., sablefish; Kimura et al. 1993) and others are imperiled and cannot be killed to extract hard parts. In these instances, tagging studies can be an effective way to fit the von Bertalanffy growth curve relating length to age (Box 11.7; Fabens 1965; James 1991; Wang 1998; Quinn and Deriso 1999; Walters and Essington 2010). The widespread use of this curve makes it possible to compare parameter estimates among populations, years, or areas. A growth curve based on tag-return data played a key role in assessment of Atlantic bluefin tuna (Lucy and Davy 2000) and in assessing ontogenetic shifts in growth of humpback chub in the Colorado River (Coggins and Pine 2010). Tagging studies can also be used to validate age and growth data obtained from hard tissues by comparing a growth curve based on age-length data to one based on tag returns or by calculating aging errors for fish tagged at a known age, such as hatchery releases (e.g., Kimura et al. 1993 and Dwyer et al. 2003).

An advantage of using tag returns to study growth is that more than one observation is obtained per individual (Eveson et al. 2004). This is useful for examining how much of the overall variability in growth is caused by measurement error versus different growth trajectories among individuals (Sainsbury 1980; James 1991; Smith et al. 1997; Smith and Botsford 1998). Individual fish might grow at different rates toward a single maximum size, at the same rate toward different maximum sizes, or at different rates toward different maximum sizes. For example, this approach showed that maximum size varied significantly among individual sablefish (Kimura et al. 1993). Variation among individuals in asymptotic size can result in biased estimates of growth parameters depending on the analysis method used (Wang 1998).

11.6.2 Design Considerations for a Growth Study

Information about growth of tagged fish is generally based on the growth increment (change in size from tagging to recapture) and the time at large (e.g., Rountree and Able 1992). When tagged fish are released and recaptured within a single season, this approach provides useful and unambiguous information about seasonal growth rates. The recommended approach is to tag the widest possible distribution of initial sizes (Smith et al. 1997) with individually identifiable tags. Small individuals are more informative about the growth rate whereas larger individuals (or small ones at liberty for a long time) provide information about maximum size (Smith and McFarlane 1990). Tagging all sizes also reduces the study duration needed to fit a growth curve or carry out an age validation study compared with a study done by tagging only young fish. However, tagging older individuals may sometimes be impractical; in such cases, the study should be continued until returns are obtained from the oldest ages (e.g., Neilson et al. 2003).

A key assumption in growth studies is that tagging does not affect fish growth. This can be examined through short-term laboratory or cage studies or field trials in which fish are marked with different types of tags (Malone et al. 1999). A common approach is to compare growth of fish marked with an internal tag versus an external tag, which has greater potential for injury (e.g., Mourning et al. 1994).

Box 11.7 Use of Tagging Data to Fit a Growth Curve

Growth in fishes is often modeled using a von Bertalanffy curve (Figure 15.19A, this volume):

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)} \right],$$

where L_t is length at time t , with t typically measured in years (Quinn and Deriso 1999). The three model parameters are the asymptotic length L_∞ , the growth rate k , and t_0 , the theoretical age when length = 0. Typically, the model is fitted using measured lengths and ages derived from scales or otoliths. However, the model can also be fitted using information obtained from a capture–recapture study. The data required are size when tagged, time at large, and the growth increment (change in size) over the time at large. A key advantage of this approach is that age information is not used in fitting the growth curve. Thus, this approach could be used to validate a growth curve developed from size and age data or could be used for species that are difficult to age.

The von Bertalanffy equation is rearranged to describe the growth increment (ΔL) as a function of the size at tagging (L_t) and time at large (Δt) (Quinn and Deriso 1999):

$$\Delta L = (L_\infty - L_t)(1 - e^{-k\Delta t}) + \varepsilon_i.$$

Two of the three parameters for the von Bertalanffy curve (L_∞ and k) can be estimated using this approach. The third parameter, t_0 , cannot be estimated without additional information, such as an estimate of size at age 1; ε_i is an error term.

The approach can be illustrated using information from a North Carolina Division of Marine Fisheries tagging study of red drum conducted from 1985 to 2003 (Ross et al. 1995). Data from 1993 releases illustrate the approach. Information on size at tagging and recapture was available for 77 fish recaptured after 60 or more days at large.

Table Example observations of red drum captures and recaptures (arranged by length at capture) for fish at liberty more than 60 days in coastal North Carolina.

Date of initial capture and release	Length at capture (mm)	Date of recapture	Length at recapture (mm)	Time at large (years)	Growth increment (mm)
24 Aug 1993	300	18 Nov 1993	394	0.236	94
24 Aug 1993	305	16 Apr 1994	406	0.644	101
18 Aug 1993	307	20 Oct 1993	421	0.173	114
02 Sep 1993	325	24 Oct 1994	610	1.142	285
11 Aug 1993	333	03 Nov 1993	457	0.230	124

Nonlinear regression using frequentist (e.g., SAS, JMP, or R) or Bayesian (OpenBUGS) statistical software can be used to estimate the von Bertalanffy parameters and confidence or credible intervals that show the level of uncertainty in the parameter estimates.

(Box continues)

Box 11.7 Continued**Table** Von Bertalanffy equation parameter estimates for red drum data.

Parameter	Estimate	Lower 95% interval	Upper 95% interval
L_{∞} (mm)	1084	1018	1156
k	0.33	0.27	0.40

This tagging approach works best when fish of a wide range of sizes are tagged and when fish are at large for different amounts of time. Measurement error should be considered in such studies, especially when fishers report the sizes of recaptured fish. It could be a bias or simply an added source of variability. Measurement error should have less effect when fish are at large for longer periods.

The choice of tag depends on the fish species, level of funding, and who will recover tagged fish. Individually numbered tags are generally used for growth and some age validation studies. If the age of released fish is not known, hard tissues may be marked with a batch tag or chemical mark such as oxytetracycline (OTC) to compare the number of annuli outside the OTC mark to the years at large (Leaman and Nagtegaal 1987; Smith et al. 2003).

The primary concern about estimating growth from fishery-dependent returns is that information about fish size is less reliable than when researchers measure recaptured fish lengths. Variability in model residuals was substantially greater for measurements of recapture length provided by fishers than by researchers (Laslett et al. 2002). Such a potential difference in reliability can be addressed by incorporation of different error terms for fish measured by scientific staff versus fishery participants into the analysis (Laslett et al. 2002; Hearn and Polacheck 2003; Eveson et al. 2004).

11.6.3 The Future of Tagging Data in Growth Studies

Integrated analysis of multiple sources of growth information is an area of active research. Sources include length-frequency distributions, growth increments from tag returns, and size-at-age data (Kirkwood 1983; Smith and McFarlane 1990; Smith and Botsford 1998; Eveson et al. 2004). Length-frequency data are readily collected and can provide good information about growth rates when year-class modes are relatively distinct but may not be informative about maximum size (Smith and McFarlane 1990; Eveson et al. 2004). The individual growth trajectories from tagging data aid in identifying the key sources of variation. Size-at-age data based on otoliths or other hard tissues are sometimes the only information about growth of older individuals (Eveson et al. 2004). An integrated analysis of these complementary data sources provides the most reliable approach for understanding growth. A joint analysis can also be helpful in identifying data sources that are inconsistent.

Flexible growth models are another area of active research. The standard von Bertalanffy equation assumes that growth rate decreases monotonically as a function of age (Figure 15.19A, this volume). This pattern fits many size-at-age data sets well, but in some situations a marked change in growth is evident. For example, a two-phase von Bertalanffy growth model was de-

veloped for southern bluefin tuna to account for an apparent change in growth at the transition from the juvenile to subadult phases of the life cycle that may be caused by a change in occupied habitat (Hearn and Polacheck 2003). The model used different von Bertalanffy parameters for the first ($L_{\infty 1}$, k_1) and second ($L_{\infty 2}$, k_2) growth phases, with the transition occurring at size L^* . Another modification is a two-phase von Bertalanffy curve that allows for a smooth transition in growth rate between phases (Laslett et al. 2002). These models should be more biologically meaningful than standard models but can require more observations to estimate the additional parameters. Incorporation of seasonal growth may also refine models. For example, a seasonal pattern in residuals from tag-return (growth increment) data for lingcod was noted (Smith and McFarlane 1990), as was evidence of seasonal growth differences in bimonthly length-frequency distributions of southern bluefin tuna (Eveson et al. 2004). In both cases, model fit was significantly improved by modifying the standard von Bertalanffy equation to incorporate a sinusoidal cycle of annual growth.

11.7 ESTIMATION OF MOVEMENT

11.7.1. Biological Questions That Can Be Addressed

Fish movements are often studied to understand habitat preferences and requirements for growth and reproduction. Knowing when and how fish use key habitats is essential for understanding the factors that regulate population abundance and for developing management policies such as protected areas. This knowledge is also important for predicting the effects of changes in habitat quantity or quality (e.g., caused by dam construction on a river or shoreline alterations in a lake). For exploited species, changes in spatial distribution can affect vulnerability to fishing. Fishers continually strive to understand fish movements to increase their catch rates. For a biologist, knowing where fish are located versus where fishing effort is concentrated can help judge the effect of fishing. For example, Atlantic Coast migratory striped bass occur in inland and marine waters of a number of east coast U.S. states as well as marine waters under U.S. and Canadian jurisdiction. Because they migrate across state and federal boundaries, they are managed on a coastwide basis.

11.7.2. Design Considerations

The distance over which movement occurs is one consideration affecting the type of tag to be used. Small-scale (m or km) movements within a stream, lake, or river are often studied using telemetry methods (Chapter 18). Conventional tags can also be used in small-scale movement studies, such as when a biologist regularly samples throughout a study area. In such cases, internal tags such as PIT tags or combinations of elastomer colors could be used. Larger-scale movements within a river, estuary, or ocean are typically studied using conventional external tags that are returned by fishers. Typical tags for these studies include T-bar, dart, and internal-anchor tags (Guy et al. 1996) or the use of telemetry tags and large arrays of acoustic receivers (Welch et al. 2003, 2004; section 18.7.2.1, this volume).

Durations of tagging studies that rely on fishery tag returns to characterize movements are usually greater than one year because the tags are returned gradually and the information about the date of capture may be imprecise. Another reason for using a long study period is that tagged and untagged fish may not be well mixed initially (Hoenig et al. 1998a). Biased information about movements (and mortality rates) would be obtained from tagged fish until they are completely mixed with the untagged part of the population. Studies using fishery tag returns are less

labor-intensive than telemetry studies because the fishery generates the data, but in most cases relatively little information (often only approximate location and date of capture) is obtained about each fish for which a tag is returned.

Electronic archival tags (Chapter 18) store time series of environmental data about habitat conditions at occupied locations, such as water temperature, depth, and light level, and can be used to infer movements if habitat conditions vary spatially. Light level, day length, and water temperature data from an archival tag can be used with sea surface temperature data to reconstruct migration routes for species that migrate over long distances (Itoh et al. 2003; Block et al. 2005; Domeier et al. 2005). Archival tags are usually returned by fishers. They may be attached externally or implanted, but an additional external tag is required to identify fish with implanted tags so that the tag can be recovered. Archival tags are roughly similar in cost to telemetry tags, but they become more valuable with time because of the information they contain. A high reward is therefore sometimes paid for their return (e.g., \$1,000 for return of an archival tag from an Atlantic bluefin tuna; Block et al. 2005).

A fish's otolith can be thought of as a natural archival tag (section 11.2.3). Trace elements deposited over a fish's lifetime can be used to determine the habitats occupied at different life stages (Lucas and Baras 2000). For example, because strontium is much more abundant in salt than freshwater, strontium : calcium ratios can be used to determine the timing of movements among fresh, brackish, and salt water (Morrison et al. 2003; Zlokovitz et al. 2003). Differences in otolith microchemistry have also been used to determine river of origin of anadromous fishes (Thorrold et al. 1998).

Another approach for getting tag "returns" that is not dependent on fishers is the use of satellite tags (Chapter 18). These large tags are suitable for marine fishes that migrate extensively. They are programmed to detach on a specific date, pop to the surface, and transmit archived data to satellites. The information obtained from satellite tags has been used to define seasonal migration patterns, foraging and spawning grounds, and stock structure (Block et al. 2005; Domeier et al. 2005; Wilson et al. 2005).

11.7.3. Analytical Approaches

The most common approach for analyzing movements from fishery tag returns is to generate simple graphic summaries showing when and where tags were returned. These summaries provide basic information about range, spawning grounds, and seasonality of movement, provided that tagged fish are encountered and reported throughout the species' geographical range (Melvin et al. 1986). This approach was used to characterize the coastal migration and homing of American shad (Talbot and Sykes 1958; Melvin et al. 1986). Findings showed the need for multi-state management and how harvest in one area affected spawning abundances in another. The endangered humpback chub tagging program in the Colorado River used capture–recapture methods to provide movement and distribution information (Gorman and Stone 1999; Paukert et al. 2006). Because researchers both tagged and recaptured the fish, they could be marked with individually coded internal PIT tags, which have a low shedding rate. This allowed individual fish to be monitored over multiple seasons and years by use of trammel nets, hoop nets, and boat electrofishing. Most fish remained close to where they were captured, and the Little Colorado River was the primary aggregation and spawning location (Figure 11.11).

A tagging program, if carefully planned, can provide more than just information on range and seasonality of movement. For example, a tag-return model can be used to estimate rates of

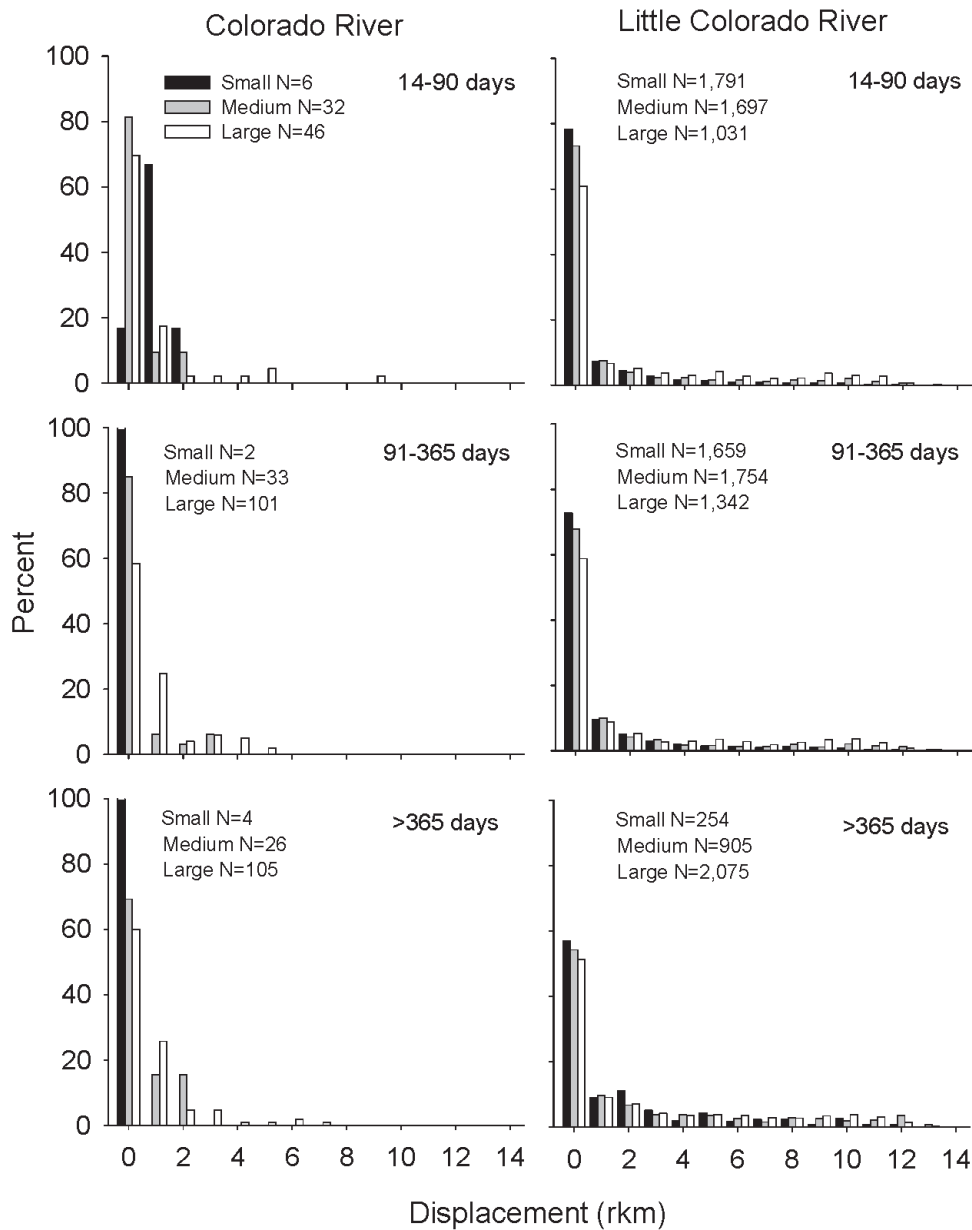


Figure 11.11 Displacement (distance moved in river kilometers [rkm]) between capture and recapture events of three sizes of fish at three different temporal scales in the Colorado River and the Little Colorado River (a major tributary), Arizona (reprinted from Paukert et al. 2006).

fishing and natural mortality for stock assessment purposes as well as migration rates among areas (Hilborn 1990; Hilborn and Walters 1992; Schwarz et al. 1993; Schweigert and Schwarz 1993; Williams et al. 2002). The basic design requires that tagged fish be released in each area. Fish both tagged and caught in the same area provide information about the intensity of fishing. Fish

tagged in one area but caught in another provide information on migration rates. For example, if different-colored tags are deployed in two areas and if tags of both colors are returned from one area but only locally deployed tags are returned from the other, it would suggest that migration occurs from one area to the other but not the reverse.

Any analysis of movement data should consider whether the observations are statistically independent (White and Garrott 1990). For example, multiple observations of an individual fish in a specific habitat are not independent, especially if spaced closely in time; its previous location influences the next. Similarly, if tagged individuals move as a group (e.g., in a school), the sampling unit is the group and not the individual (White and Garrott 1990). When individual animals are recaptured multiple times, analyses such as habitat use should be done individually because of among-animal differences and the lack of independence among observations associated with an individual (White and Garrott 1990).

11.8 SUMMARY

Many tagging studies are conceptually simple, yet implementation, execution, and subsequent data analyses require careful planning to maximize the likelihood of success. Simple simulation and pilot studies are an essential component of good study design; they provide experience with field and tagging techniques and data analyses and allow examination of model assumptions. Pilot and simulation studies can help to establish realistic expectations of study results and help determine sampling requirements.

The choice of whether to use a batch mark or uniquely identifiable tag is important because each provides different types of data about recaptured fish. In general, batch marks can be made on small fish at low cost, allowing many fish to be marked. Some individual tags can also be applied to small animals (e.g., coded wire tags), but most internal (e.g., PIT tag) or external (e.g., T-bar) individual tags require that animals be large to preclude effects on growth or survival. Whereas both tag types can be used in certain situations to estimate survival and abundance, individual marks are preferable because of the much broader range of analyses that can be conducted with individual capture histories (e.g., incorporating heterogeneity in capture probability). All analyses that can be conducted on data from batch marks can be done with data from individual marks, but not vice versa. Again, pilot studies are critical to match tag types with research objectives and budgets.

When the objective is to estimate fish abundance over a short time period, closed-population study designs are appropriate if the assumption of closure can be met. Heterogeneity in capture probability caused by fish size is common in most fisheries sampling, and closed models can account for it (e.g., model M_h in CAPTURE or length-stratified Lincoln–Petersen estimates). If unaccounted for, heterogeneity in capture probability can lead to underestimation of population abundance. Time-dependent closed-population models should also be considered for many fisheries applications because capture probability often varies over time. Model performance in both removal and mark–recapture studies often improves with increasing numbers of sampling events; five or more are often required in fisheries applications because of low capture probability.

In studies lasting longer than a few weeks or in which survival is a parameter of interest, open-population capture–recapture studies based on the Cormack–Jolly–Seber model are appropriate. Open-population models estimate apparent survival, which includes emigration away from the study site. If temporary emigration occurs, as when an animal leaves and returns to the area during the study, large biases in parameter estimates can occur. Temporary emigration can be assessed

by telemetry. Robust design capture–recapture models use attributes of both closed- and open-population models to account for heterogeneity and temporary emigration. This sampling and analysis framework reduces bias of estimates of abundance and survival. The design is straightforward and can be incorporated into many standard fisheries sampling programs.

Reporting rate must be estimated in tagging studies designed to estimate fishing and natural mortality by use of passive tags. If fishing and natural mortality are estimated using telemetry techniques, uncertainty associated with relocations of telemetered fish should be minimized through multiple searches or use of mortality sensors in tags. These estimates can also be positively biased by emigration and hooking mortality. Accuracy and precision of mortality estimates are probably best in studies in which both active and passive tags are used in combination.

The evolution of tagging techniques and technology includes use of gene tags, self-reporting tags that uplink to satellites, and autonomous receiver networks. Such developments link basic fisheries management data needs with innovative technology, novel engineering, and applied statistics to find original approaches to improve resource management. We encourage readers to make use of the wide range of tagging models available.

11.9 REFERENCES

- Adams, A. J., R. K. Wolfe, W. E. Pine, III, and B. L. Thornton. 2006. Efficacy of PIT tags and an autonomous antenna system to study the juvenile life stage of an estuarine-dependent fish. *Estuaries and Coasts* 29:311–317.
- Arnason, A. N., and K. H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly–Seber estimates for mark–recapture experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1077–1095.
- Barrowman, N. J., and R. A. Myers. 1996. Estimating tag-shedding rates for experiments with multiple tag types. *Biometrics* 52:1410–1416.
- Bayley, P. B., and D. J. Austen. 2002. Capture efficiency of a boat electrofisher. *Transactions of the American Fisheries Society* 131:435–451.
- Bettoli, P. W., and R. S. Osborne. 1998. Hooking mortality and behavior of striped bass following catch and release angling. *North American Journal of Fisheries Management* 18:609–615.
- Block, B. A., S. L. H. Teo, A. Walli, A. Boustany, M. J. W. Stokesbury, C. J. Farwell, K. C. Weng, H. Dewar, and T. D. Williams. 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434:1121–1127.
- Bolland, J. D., I. G. Cowx, and M. C. Lucas. 2009. Evaluation of VIE and PIT tagging methods for juvenile cyprinid fishes. *Journal of Applied Ichthyology* 25:381–386.
- Bordner, C. E., S. I. Doroshov, D. E. Hinton, R. E. Pipkin, R. B. Fridley, and F. Haw. 1990. Evaluation of marking techniques for juvenile and adult white sturgeons reared in captivity. Pages 293–303 *in* N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. *Fish-marking techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Boreman, J., and R. R. Lewis. 1987. Atlantic coastal migrations of striped bass. Pages 331–339 *in* M. J. Dadswell, R. J. Klauda, C. M. Moffitt, and R. L. Saunders, editors. *Common strategies of anadromous and catadromous fishes*. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Brennan, N. P., K. M. Leber, H. L. Blankenship, J. M. Ransier, and R. DeBruiler. 2005. An evaluation of coded wire and elastomer tag performance in juvenile common snook under field and laboratory conditions. *North American Journal of Fisheries Management* 25:437–445.
- Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. Statistical inference from band recovery data: a handbook. U.S. Fish and Wildlife Service Resource Publication 156, Washington, D.C.
- Brownie, C., and D. S. Robson. 1983. Estimation of time-specific survival rates from tag-resighting samples: a generalization of the Jolly–Seber model. *Biometrics* 41:411–420.

- Bryant, M. D., C. A. Dolloff, P. E. Porter, and B. E. Wright. 1990. Freeze branding with CO₂: an effective and easy-to-use field method to mark fish. Pages 30–35 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Buckley, R. M., and H. L. Blankenship. 1990. Internal extrinsic identification systems: overview of implanted wire tags, otolith marks, and parasites. Pages 173–182 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. Fish-marking techniques. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Buckworth, R. C. 2004. Effects of spatial stock structure and effort dynamics on the performance of alternative assessment procedures for the fisheries of northern Australia. Doctoral dissertation. University of British Columbia, Vancouver.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Carlson, S. R., L. G. Coggins, Jr., and C. O. Swanton. 1999. A simple stratified design for mark–recapture estimation of salmon smolt abundance. Alaska Fishery Research Bulletin 5:88–102.
- Chapman, F. A., C. S. Hartless, and S. H. Carr. 1997. Population size estimates of sturgeon in the Suwannee River, Florida, USA. Gulf of Mexico Science 2:88–91.
- Chisholm, I. M., and W. A. Hubert. 1985. Expulsion of dummy transmitters by rainbow trout. Transactions of the American Fisheries Society 114:766–767.
- Clark, W. G., and D. G. Chen. 2005. Preliminary estimates based on 2004 PIT tag recoveries. International Pacific Halibut Commission. Report of Assessment and Research Activities 2004:199–209.
- Clugston, J. P. 1996. Retention of T-bar anchor tags and passive integrated transponder tags by Gulf sturgeons. North American Journal of Fisheries Management 16:682–685.
- Coggins, L. G., Jr., and W. E. Pine, III. 2010. Development of a temperature-dependent growth model for endangered humpback chub using capture–recapture data. The Open Fish Science Journal 3:122–131.
- Coggins, L. G., Jr., W. E. Pine, III, C. J. Walters, and S. J. D. Martell. 2006b. Age-structured mark–recapture analysis: a virtual-population-analysis-based model for analyzing age-structured capture–recapture data. North American Journal of Fisheries Management 26:201–205.
- Coggins, L. G., Jr., W. E. Pine, III, C. J. Walters, D. R. Van Haverbeke, D. Ward, and H. C. Johnstone. 2006a. Abundance trends and status of the Little Colorado River population of humpback chub. North American Journal of Fisheries Management 26:233–245.
- Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 5:429–438.
- Crawford, S., and M. S. Allen. 2006. Fishing and natural mortality for bluegill and redear sunfish at Lake Panasoffkee, Florida: implications for size limits. North American Journal of Fisheries Management 26:24–31.
- Delury, D. B. 1947. On the estimation of biological populations. Biometrics 3:145–167.
- Denson, M. R., W. E. Jenkins, A. G. Woodward, and T. I. J. Smith. 2002. Tag-reporting levels for red drum (*Sciaenops ocellatus*) caught by anglers in South Carolina and Georgia estuaries. U.S. National Marine Fisheries Service Fishery Bulletin 100:35–41.
- Diodati, P. J., and A. R. Richards. 1996. Mortality of striped bass hooked and released in saltwater. Transaction of the American Fisheries Society 125:300–307.
- Domeier, M. L., D. Kiefer, N. Nasby-Lucas, A. Wagschal, and F. O'Brien. 2005. Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. U.S. National Marine Fisheries Service Fishery Bulletin 103:292–306.
- Dorazio, R. M., K. A. Hattala, C. B. McCollough, and J. E. Skjveland. 1994. Tag recovery estimates of migration of striped bass from spawning areas of the Chesapeake Bay. Transactions of the American Fisheries Society 123:950–963.
- Dorazio, R. M., H. L. Jelks, and F. Jordan. 2005. Improving removal-based estimates of abundance by sampling a population of spatially distinct subpopulations. Biometrics 61:1093–1101.

- Douglas, M. E., and P. C. Marsh. 1998. Population and survival estimates of *Catostomus latipinnis* in northern Grand Canyon, with distribution and abundance of hybrids with *Xyrauchen texanus*. *Copeia* 1998:915–925.
- Dunning, D. J., Q. E. Ross, J. R. Waldman, and M. T. Mattson. 1987. Tag retention by, and tagging mortality of, Hudson River striped bass. *North American Journal of Fisheries Management* 7:535–538.
- Dwyer, K. S., S. J. Walsh, and S. E. Campana. 2003. Age determination, validation and growth of Grand Bank yellowtail flounder (*Limanda ferruginea*). *ICES Journal of Marine Science* 60:1123–1138.
- Ebener, M. P., and F. A. Copes. 1982. Loss of Floy anchor tags from lake whitefish. *North American Journal of Fisheries Management* 2:90–93.
- Eipper, A. W., and J. L. Forney. 1965. Evaluation of partial fin clips for marking largemouth bass, walleyes, and rainbow trout. *New York Fish and Game Journal* 12:233–240.
- Elsdon, T. S., B. K. Wells, S. E. Campana, B. M. Gillanders, C. M. Jones, K. E. Limburg, D. H. Secor, S. R. Thorrold, and B. D. Walther. 2008. Otolith chemistry to describe movements and life history parameters of fishes: hypotheses, assumptions, limitations, and inferences. *Oceanography and Marine Biology: an Annual Review* 46: 297–330.
- Eveson, J. P., G. M. Laslett, and T. Polacheck. 2004. An integrated model for growth incorporating tag-recapture, length-frequency, and direct aging data. *Canadian Journal of Fisheries and Aquatic Sciences* 61:292–306.
- Fabens, A. J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265–289.
- Fabrizio, M. C., M. E. Holey, P. C. McKee, and M. L. Toney. 1997. Survival rates of adult lake trout in northwestern Lake Michigan, 1983–1993. *North American Journal of Fisheries Management* 17:413–428.
- Forsberg, J. E. 2004. Portside sampling for recovered PIT tags in Pacific halibut. International Pacific Halibut Commission. Report of Assessment and Research Activities 2003:361–376.
- Frusher, S. D., and J. M. Hoenig. 2001. Estimating natural and fishing mortality and tag reporting rate of southern rock lobster (*Jasus edwardsii*) from a multiyear tagging model. *Canadian Journal of Fisheries and Aquatic Sciences* 58:2490–2501.
- Gorman, O. T., and D. M. Stone. 1999. Ecology of spawning humpback chub, *Gila cypha*, in the Little Colorado River near Grand Canyon, Arizona. *Environmental Biology of Fishes* 55:115–133.
- Gould, W. R., and K. H. Pollock. 1997. Catch-effort maximum likelihood estimation of important population parameters. *Canadian Journal of Fisheries and Aquatic Sciences* 54:890–897.
- Guy, C. S., H. L. Blankenship, and L. A. Nielsen. 1996. Tagging and marking. Pages 353–383 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Hartman, K. J., and E. C. Janney. 2006. Visual implant elastomer and anchor tag retention in largemouth bass. *North American Journal of Fisheries Management* 26:665–669.
- Haw, F., P. K. Bergman, R. D. Fralick, R. M. Buckley, and H. L. Blankenship. 1990. Visible implanted fish tag. Pages 311–315 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. *Fish-marking techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Hearn, W. W., and T. Polacheck. 2003. Estimating growth rate changes of southern bluefin tuna (*Thunnus maccoyii*) from two periods of tag-return data. *U.S. National Marine Fisheries Service Fishery Bulletin* 101:58–74.
- Heupel, M. R., and C. A. Simpfendorfer. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Canadian Journal of Fisheries and Aquatic Sciences* 59:624–632.
- Hewitt, D. A., E. C. Janney, B. S. Hayes, and R. S. Shively. 2010. Improving inferences from fisheries capture–recapture studies through remote detection of PIT tags. *Fisheries* 35(5):217–231.
- Hightower, J. E., and R. J. Gilbert. 1984. Using the Jolly–Seber model to estimate population size, mortality, and recruitment for a reservoir fish population. *Transactions of the American Fisheries Society* 113:633–641.

- Hightower, J. E., J. R. Jackson, and K. H. Pollock. 2001. Use of telemetry models to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society* 130:557–567.
- Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* 47:635–643.
- Hilborn, R., and C. J. Walters. 1992. *Quantitative fisheries stock assessment: choice, dynamics, and uncertainty*. Chapman and Hall, New York.
- Hoening, J. M., N. J. Barrowman, W. S. Hearn, and K. H. Pollock. 1998a. Multiyear tagging studies incorporating fishing effort data. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1466–1476.
- Hoening, J. M., N. J. Barrowman, K. H. Pollock, E. N. Brooks, W. S. Hearn, and T. Polacheck. 1998b. Models for tagging data that allow for incomplete mixing of newly tagged animals. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1477–1483.
- Itoh, T., S. Tsuji, and A. Nitta. 2003. Migration patterns of young Pacific bluefin tuna (*Thunnus orientalis*) determined with archival tags. *U.S. National Marine Fisheries Service Fishery Bulletin* 101:514–534.
- James, I. R. 1991. Estimation of von Bertalanffy growth curve parameters from recapture data. *Biometrics* 47:1519–1530.
- Jenkins W. E., and T. I. J. Smith. 1990. Use of PIT tags to individually identify striped bass and red drum brood stocks. Pages 341–345 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. *Fish-marking techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Jepsen, N., S. Pedersen, and E. Thorstad. 2000. Behavioural interactions between prey (trout smolts) and predators (pike and pikeperch) in an impounded river. *Regulated Rivers: Research & Management* 16:189–198.
- Joe, M., and K. H. Pollock. 2002. Separation of survival and movement rates in multi-state tag-return and capture–recapture models. *Journal of Applied Statistics* 29:373–384.
- Johnson, J. K. 1990. Regional overview of coded wire tagging of anadromous salmon and steelhead in northwest America. Pages 782–816 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. *Fish-marking techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration-stochastic model. *Biometrika* 52:225–247.
- Jones, R. 1979. Material and methods used in marking experiments in fisheries research. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper 190, Rome.
- Kaimmer, S. M., and T. O. Geernaert. 2004. 2003 PIT tagging: tagging equipment and protocol, and tag shedding studies. International Pacific Halibut Commission. Report of Assessment and Research Activities 2003:351–360.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology* 78:563–578.
- Kimura, D. K., A. M. Shimada, and S. A. Lowe. 1993. Estimating von Bertalanffy growth parameters of sablefish *Anoplopoma fimbria* and Pacific cod *Gadus macrocephalus* using tag-recapture data. *U.S. National Marine Fisheries Service Fishery Bulletin* 91:271–280.
- Kirkwood, G. P. 1983. Estimation of von Bertalanffy growth curve parameters using both length increment and age–length data. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1405–1411.
- Kocovsky, P. M., and R. F. Carline. 2001. Dynamics of the unexploited walleye population of Pymatuning Sanctuary, Pennsylvania, 1997–1998. *North American Journal of Fisheries Management* 21:178–187.
- Kwak, T. J. 1992. Modular microcomputer software to estimate fish population parameters, production rates, and associated variances. *Ecology of Freshwater Fish* 1:73–75.
- Laslett, G. M., J. P. Eveson, and T. Polacheck. 2002. A flexible maximum likelihood approach for fitting growth curves to tag-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* 59:976–986.

- Leaman, B. M., and D. A. Nagtegaal. 1987. Age validation and revised natural mortality rate for yellowtail rockfish. *Transactions of the American Fisheries Society* 116:171–175.
- Lee, W. C., and E. P. Bergersen. 1996. Influence of thermal and oxygen stratification on lake trout hooking mortality. *North American Journal of Fisheries Management* 16:175–181.
- Leslie, P. H., and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. *The Journal of Animal Ecology* 8:94–113.
- Loftus, A. J., J. Waldon, V. Fay, K. Davy, and J. Lucy. 2000. Overview of angler-based tagging programs and management issues. *Fisheries* 25(4):8–13.
- Lucas, M. C. 1989. Effects of implanted dummy transmitters on mortality, growth, and tissue reaction in rainbow trout, *Salmo gairdneri* Richardson. *Journal of Fish Biology* 35:577–587.
- Lucas, M. C., and E. Baras. 2000. Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish and Fisheries* 1:283–316.
- Lucy, J., and K. Davy. 2000. Benefits of angler-assisted tag and release programs. *Fisheries* 25(4):18–23.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, San Diego, California.
- Mahon, R. 1980. Accuracy of catch-effort methods for estimating fish density and biomass in streams. *Environmental Biology of Fishes* 5:343–360.
- Malone, J. C., G. E. Forrester, and M. A. Steele. 1999. Effects of subcutaneous microtags on the growth, survival, and vulnerability to predation of small reef fishes. *Journal of Experimental Marine Biology and Ecology* 237:243–253.
- Manire, C. A., and S. H. Gruber. 1991. Effect of M-type dart tags on field growth of juvenile lemon sharks. *Transactions of the American Fisheries Society* 120:776–780.
- Mäntyniemi, S., A. Romakkaniemi, and E. Arjas. 2005. Bayesian removal estimation of a population size under unequal catchability. *Canadian Journal of Fisheries and Aquatic Sciences* 62:291–300.
- Marty, G. D., and R. C. Summerfelt. 1986. Pathways and mechanisms for expulsion of surgically implanted dummy transmitters from channel catfish. *Transactions of the American Fisheries Society* 115:577–589.
- Matlock, G. C. 1981. Nonreporting of recaptured fish by saltwater recreational boat anglers in Texas. *Transactions of the American Fisheries Society* 110:90–92.
- McInerney, M. C., and T. K. Cross. 1999. Comparison of three mark–recapture sampling designs for estimating population size of largemouth bass in Minnesota lakes. *North American Journal of Fisheries Management* 19:758–764.
- McPherson, S. A., D. R. Bernard, and J. H. Clark. 2000. Optimal production of Chinook salmon from the Taku River. Alaska Department of Fish and Game, Fishery Manuscript 00-2, Anchorage.
- Melvin, G. D., M. J. Dadswell, and J. D. Martin. 1986. Fidelity of American shad, *Alosa sapidissima* (Clupeidae), to its river of previous spawning. *Canadian Journal of Fisheries and Aquatic Sciences* 43:640–646.
- Mesa, M. G., and C. B. Schreck. 1989. Electrofishing mark–recapture and depletion methodologies evoke behavioral and physiological changes in cutthroat trout. *Transactions of the American Fisheries Society* 118:644–658.
- Miller, R. J. 1978. Saturation of crab traps: reduced entry and escapement. *Journal du Conseil International pour l'Exploration de la Mer* 38:338–345.
- Mitro, M. G., and A. V. Zale. 2002. Estimating abundances of age-0 rainbow trout by mark–recapture in a medium-sized river. *North American Journal of Fisheries Management* 22:188–203.
- Moran, P. A. P. 1951. A mathematical theory of animal trapping. *Biometrika* 38:307–311.
- Morrison, W. E., and D. H. Secor. 2004. Abundance of yellow-phase American eels in the Hudson River estuary. *Transactions of the American Fisheries Society* 133:896–910.
- Morrison, W. E., D. H. Secor, and P. M. Piccoli. 2003. Estuarine habitat use by Hudson River American eels as determined by otolith strontium : calcium ratios. Pages 87–99 in D. A. Dixon, editor. *Biol-*

- ogy, management, and protection of catadromous eels. American Fisheries Society, Symposium 33, Bethesda, Maryland.
- Mourning, T. E., K. D. Fausch, and C. Gowan. 1994. Comparison of visible implant tags and Floy anchor tags on hatchery rainbow trout. *North American Journal of Fisheries Management* 14:636–642.
- Muncy, R. J., N. C. Parker, and H. A. Poston. 1990. Inorganic chemical marks induced in fish. Pages 541–546 in N. C. Parker, A. E. Giorgi, R. C. Heidinger, D. B. Jester, Jr., E. D. Prince, and G. A. Winans, editors. *Fish-marking techniques*. American Fisheries Society, Symposium 7, Bethesda, Maryland.
- Murphy, M. D., and R. G. Taylor. 1991. Preliminary study of the effect of reward amount on tag-return rate for red drums in Tampa Bay, Florida. *North American Journal of Fisheries Management* 11:471–474.
- Neilson, J. D., W. T. Stobo, and P. Perley. 2003. Age and growth of Canadian east coast pollock: comparison of results from otolith examination and mark–recapture studies. *Transactions of the American Fisheries Society* 132:536–545.
- Newman, K. B. 1998. State-space modeling of animal movement and mortality with application to salmon. *Biometrics* 54:1290–1314.
- Nielsen, L. A. 1992. *Methods of marking fish and shellfish*. American Fisheries Society, Special Publication 23, Bethesda, Maryland.
- Norris, J. L., and K. H. Pollock. 1995. A capture–recapture model with heterogeneity and behavioural response. *Environmental and Ecological Statistics* 2:305–313.
- Osmundson, D. B., and K. P. Burnham. 1998. Status and trends of the endangered Colorado squawfish in the upper Colorado River. *Transactions of the American Fisheries Society* 127:957–970.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62.
- Paukert, C. P., L. G. Coggins, Jr., and E. E. Flaccus. 2006. Distribution and movement of humpback chub in the Colorado River, Grand Canyon, based on recaptures. *Transactions of the American Fisheries Society* 135:539–544.
- Paukert, C. P., D. L. Ward, P. J. Sonholtz, and K. D. Hilwig. 2005. Effects of repeated hoopnetting and handling on bonytail chub. *Journal of Freshwater Ecology* 20:649–653.
- Phillips, C. T., and J. N. Fries. 2009. An evaluation of visible implant elastomer for marking the federally listed fountain darter and the San Marcos salamander. *North American Journal of Fisheries Management* 29:529–532.
- Pierce R. B. 1997. Variable catchability and bias in population estimates for northern pike. *Transactions of the American Fisheries Society* 126:658–664.
- Pine, W. E., III, M. S. Allen, and V. J. Dreitz. 2001. Population viability of the Gulf of Mexico sturgeon: inferences from capture–recapture and age-structured models. *Transactions of the American Fisheries Society* 130:1164–1174.
- Pine, W. E., K. H. Pollock, J. E. Hightower, and J. A. Rice. 2003. A review of tagging methods to estimate population size and components of mortality. *Fisheries* 28(10):10–23.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture–recapture models using mixtures. *Biometrics* 56:434–442.
- Polacheck, T., J. P. Eveson, and G. M. Laslett. 2006. Estimation of mortality rates from tagging data for pelagic fisheries: analysis and experimental design. Final Report to the Australian Fisheries Research and Development Corporation, Project 2002/015, Deakin West, Canberra.
- Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21:521–532.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2002. Tag reporting rate estimation: 2. Use of high-reward tagging and observers in multiple-component fisheries. *North American Journal of Fisheries Management* 22:727–736.

- Pollock, K. H., H. Jiang, and J. E. Hightower. 2004. Combining radio-telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Transactions of the American Fisheries Society* 133:639–648.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107.
- Pollock, K. H., and W. E. Pine, III. 2007. The design and analysis of field studies to estimate catch-and-release mortality. *Fisheries Ecology and Management* 14:123–130.
- Prince, E. D., M. Ortiz, A. Venizelos, and D. S. Rosenthal. 2002. In-water conventional tagging techniques developed by the Cooperative Tagging Center for large, highly migratory species. Pages 155–171 in J. A. Lucy and A. L. Studholme, editors. *Catch and release in marine recreational fisheries*. American Fisheries Society, Symposium 30, Bethesda, Maryland.
- Quinn, T. J., II, and R. B. Deriso. 1999. *Quantitative fish dynamics*. Oxford University Press, Oxford, UK.
- Reeves, K. S., and D. L. Buckmeier. 2009. Mortality, predation, and tag visibility of fish marked with visible implant elastomer tags. *North American Journal of Fisheries Management* 29:323–329.
- Replinger, S. E., and J. B. Wood. 2007. A preliminary investigation of the use of subcutaneous tagging in Caribbean reef squid *Sepioteuthis sepioidea* (Cephalopoda: Loliginidae). *Fisheries Research* 84:308–313.
- Richards, R. A., and P. J. Rago. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. *North American Journal of Fisheries Management* 19:356–375.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Robson, D. S., and H. A. Regier. 1964. Sample size in Petersen mark–recapture experiments. *Transactions of the American Fisheries Society* 93:215–226.
- Ross, J. L., T. M. Stevens, and D. S. Vaughan. 1995. Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. *Transactions of the American Fisheries Society* 124:37–54.
- Rountree, R. A., and K. W. Able. 1992. Foraging habits, growth, and temporal patterns of salt-marsh creek habitat use by young-of-year summer flounder in New Jersey. *Transactions of the American Fisheries Society* 121:765–776.
- Sainsbury, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Canadian Journal of Fisheries and Aquatic Sciences* 37:241–247.
- Sandford, B. P., and S. G. Smith. 2002. Estimation of smolt-to-adult return percentages for Snake River Basin anadromous salmonids, 1990–1997. *Journal of Agricultural, Biological & Environmental Statistics* 7:243–263.
- Schmalz, P. J., M. J. Hansen, M. E. Holley, P. C. McKee, and M. L. Toney. 2004. Effect of rewards on lake trout returns in northwestern Lake Michigan. *North American Journal of Fisheries Management* 24:1–6.
- Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* 52:860–873.
- Schwarz, C. J., J. Schweigert, and A. N. Arnason. 1993. Using tag-recovery data to estimate migration rates. *Biometrics* 49:177–194.
- Schweigert, J. F., and C. J. Schwarz. 1993. Estimating migration rates for Pacific herring (*Clupea harengus pallasii*) using tag-recovery data. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1530–1540.
- Seber, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- Seber, G. A. F. 1982. *The estimation of animal abundance and related parameters*, 2nd edition. Griffin, London.
- Siegwarth, G. L., and J. M. Pitlo, Jr. 1999. A modified procedure for surgically implanting radio transmitters in channel catfish. Pages 287–292 in E. R. Irwin, W. A. Hubert, C. F. Rabeni, H. L. Schramm, Jr., and T. Coon, editors. *Catfish 2000: proceedings of the international ictalurid symposium*. American Fisheries Society, Symposium 24, Bethesda, Maryland.
- Smith, B. D., and L. W. Botsford. 1998. Interpretation of growth, mortality, and recruitment patterns in size-at-age, growth increment, and size frequency data. Pages 125–139 in G. S. Jamieson and A.

- Campbell, editors. Proceedings of the North Pacific symposium on stock assessment and management. Canadian Special Publication of Fisheries and Aquatic Sciences 125.
- Smith, B. D., and G. A. McFarlane. 1990. Growth analysis of Strait of Georgia lingcod by use of length-frequency and length-increment data in combination. *Transactions of the American Fisheries Society* 119:802–812.
- Smith, E. B., F. M. Williams, and C. R. Fisher. 1997. Effects of intrapopulation variability on von Bertalanffy growth parameter estimates from equal mark-recapture intervals. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2025–2032.
- Smith, S. E., R. A. Mitchell, and D. Fuller. 2003. Age-validation of a leopard shark (*Triakis semifasciata*) recaptured after 20 years. U.S. National Marine Fisheries Service Fishery Bulletin 101:194–198.
- Smith, W. E., F. S. Scharf, and J. E. Hightower. 2009. Fishing mortality in North Carolina's southern flounder fishery: direct estimates of instantaneous fishing mortality from a tag return experiment. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 1:283–299.
- Sprinkle, K., J. Boreman, and J. B. Hestbeck. 1996. Loss rates for dorsal loop and internal anchor tags applied to striped bass. *North American Journal of Fisheries Management* 16:461–464.
- Summers, D. W., D. E. Roberts, N. Giles, and D. N. Stubbing. 2006. Retention of visible implant and visible implant elastomer tags in brown trout in an English chalk stream. *Journal of Fish Biology* 68:622–627.
- Talbot, G. B., and J. E. Sykes. 1958. Atlantic coast migrations of American shad. U.S. Fish and Wildlife Service Fishery Bulletin 58:473–490.
- Taylor, R. G., J. A. Whittington, W. E. Pine, III, and K. H. Pollock. 2006. Effect of different reward levels on tag reporting rates and angler behavior for common snook in southeast Florida. *North American Journal of Fisheries Management* 26:645–651.
- Thorrold, S. R., C. M. Jones, S. E. Campana, J. W. McLaren, and J. W. H. Lam. 1998. Trace element signatures in otoliths record natal river of juvenile American shad (*Alosa sapidissima*). *Limnology and Oceanography* 43:1826–1835.
- Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. *Science* 291:297–299.
- Thurrow, R. F., J. T. Peterson, and J. W. Guzevich. 2001. Development of bull trout sampling protocols. Final report to U.S. Fish and Wildlife Service, Aquatic Resources Division, Lacey, Washington.
- Turan, C. 2004. Stock identification of Mediterranean horse mackerel (*Trachurus mediterraneus*) using morphometric and meristic characters. *ICES Journal of Marine Sciences* 61:774–781.
- Waits, L. P. 2004. Using noninvasive genetic sampling to detect and estimate abundance of rare wildlife species. Pages 211–228 in W. L. Thompson, editor. *Sampling rare or elusive species*. Island Press, Washington, D.C.
- Waldman, J. R., D. J. Dunning, and M. T. Mattson. 1990. A morphological explanation for size-dependent anchor tag loss from striped bass. *Transactions of the American Fisheries Society* 119:920–923.
- Walters, C. J., and T. Essington. 2010. Recovery of bioenergetics parameters from information on growth: overview of an approach based on statistical analysis of tagging and size-at-age data. *The Open Fish Science Journal* 3:52–68.
- Wang, Y. G. 1998. An improved Fabens method for estimation of growth parameters in the von Bertalanffy model with individual asymptotes. *Canadian Journal of Fisheries and Aquatic Sciences* 55:397–400.
- Welch, D. W., G. W. Boehlert, and B. R. Ward. 2003. POST—The Pacific Ocean salmon tracking project. *Oceanologica Acta* 25:243–253.
- Welch, D. W., B. R. Ward, and S. D. Batten. 2004. Early ocean survival and marine movements of hatchery and wild steelhead trout (*Oncorhynchus mykiss*) determined by an acoustic array: Queen Charlotte Strait, British Columbia. *Deep Sea Research II* 51:897–909.
- White, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* 47:716–728.

- White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Publication LA-8787-NERP, Los Alamos, New Mexico.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement):120–138.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.
- Whitehead, H. 2001. Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology* 82:1417–1432.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California.
- Wilson, B., P. S. Hammond, and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications* 9:288–300.
- Wilson, S. G., M. E. Lutcavage, R. W. Brill, M. P. Genovese, A. B. Cooper, and A. W. Everly. 2005. Movements of bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. *Marine Biology* 146:409–423.
- Yoshizaki, J., C. Brownie, K. H. Pollock, and W. A. Link. 2011. Modeling errors that result from use of genetic tags in capture–recapture studies. *Environmental and Ecological Statistics* 18:27–55.
- Yoshizaki, J., K. H. Pollock, C. Brownie, and R. A. Webster. 2009. Modeling misidentification errors in capture–recapture studies using photographic identification of evolving marks. *Ecology* 90:3–9.
- Youngs, W. D., and D. S. Robson. 1975. Estimating survival rate from tag returns: model tests and sample size determination. *Journal of the Fisheries Research Board of Canada* 32:2365–2371.
- Zehfuss, K. P., J. E. Hightower, and K. H. Pollock. 1999. Abundance of Gulf sturgeon in the Apalachicola River, Florida. *Transactions of the American Fisheries Society* 128:130–143.
- Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* 12:163–189.
- Zlokovitz, E. R., D. H. Secor, and P. M. Piccoli. 2003. Patterns of migration in Hudson River striped bass as determined by otolith microchemistry. *Fisheries Research* 63:245–259.
- Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. *Fisheries* 31:492–502.