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4 Recruitment

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■ 4.1 INTRODUCTION

4.1.1 Recruitment Assessment in Freshwater Fisheries

Recruitment of young fish into catchable, harvestable, or adult size is necessary to sustain any population and fishery. Recruitment failure, due to overfishing, habitat alteration, or abiotic or biotic events, can lead to reduced adult abundance and reduced angler catch rates. If severe, recruitment failure can ultimately result in severe population declines and collapse of a fishery. However, larval, juvenile, and even adult fish can be stocked to augment a fishery or a population if natural recruitment is low or nil. Conversely, if recruitment is high, then catchable-size abundance and fishing success should be greater if density-dependent mortality and growth reduction are not excessive. Recruitment is typically the strongest determinate influencing populations among the three major factors affecting populations, that is, growth, recruitment, and mortality (Carline et al. 1984; Allen and Pine 2000).

Recruitment success typically varies from year to year in most populations due to a number of factors. Some species from certain water bodies may display fairly constant recruitment each year, whereas other species or populations display highly variable recruitment that will cause wide fluctuations in the number of fish reaching a certain age or length. In marine systems, recruitment rates tend to be log-normally distributed with many average and below average years interspersed with periodic strong year-classes (Hennemuth et al. 1980). Although a similar review has not been conducted for North American freshwater fishes, we suspect a similar pattern. Fecundity in fishes is typically high, and recruitment variability is often caused by density-independent factors, but density-dependent regulation can stabilize recruitment (Cowan et al. 2000). The processes and mechanisms that cause recruitment variation have been intensively investigated for many years (reviewed by Cowan et al. 2000). In this chapter, analysis of the effects of environmental factors and parental abundance on recruitment will be explored.

Protection of adult fish stocks from overexploitation to prevent recruitment overfishing has primarily been addressed for commercially important marine fisheries

(Musick 1999). Recruitment overfishing occurs when a fishing rate is maintained over a long time period that results in low yields due to reduced recruitment of fish to adult or catchable size. These concepts of recruitment overfishing can also be important to the conservation of freshwater fishes. Loss of critical habitat and migration barriers in conjunction with overfishing have been cited as the cause for the decline of many Pacific salmon stocks in the northwestern USA (Stouder et al. 1997). Striped bass recovery in the Chesapeake Bay coincided with protection of mature females from exploitation, which increased juvenile abundance and recruitment (Richards and Rago 1999). Conservation of sturgeons has focused on protection of adults (long-lived species with late time to maturity) and habitat due to the low intrinsic rate of population increase via recruitment (Secor and Waldman 1999; Musick et al. 2000).

Fisheries scientists often evaluate the response of a population and fishery to habitat manipulations or regulation changes. However, an accurate result may not be evident due to recruitment variability, particularly if the evaluation time period is short (Allen and Pine 2000). For example, Bettoli et al. (1992) attempted to determine the effects of the complete removal of all submersed aquatic plants by grass carp on harvestable-size (>25 cm in total length [TL]) largemouth bass. Following vegetation removal, density of age-1 largemouth bass declined but growth rates increased. Although 3 years of post-vegetation-removal data were collected, the long-term effects on the adult population were difficult to detect because largemouth bass longevity was greater than 10 years, and obviously recruitment success or failure may take a number of years to detect (Maceina et al. 1994).

Recruitment is typically defined in terms of age or size, and this definition needs to be assigned by the fishery scientist. Terms such as age-0 or age-1 recruits refers to the age at the time of collection. For example, catch rates of age-1 crappies collected with trap nets in fall (fish about 18 months old) were used by Maceina and Stimpert (1998) as an index of recruitment. Hansen et al. (1998) estimated density of age-0 walleye in September over a 39-year period, and thus fish were about 5 months old.

The number of fish reaching a certain length can also be used to define recruitment (e.g., number of fish greater than 100 mm), but length categorization is mostly used either as some minimum length of fish that can be caught by anglers and possibly harvested or as some regulated minimum length. For example, number of recruits entering the fishery at a particular length can be used.

4.1.2 Data Required to Assess Recruitment

Fisheries scientists can collect either long-term monitoring data or specific research data to quantify recruitment in a population or among populations. For a particular species or population, the fisheries scientist must determine what time in the early life of a fish confers recruitment to adult size or the fishery. For example, Sammons and Bettoli (1998) showed that low and high larval abundance of white bass, white crappie, and black crappie were associated with weak and strong year-classes, respectively. Pitlo (1997) reported an increase in the commer-

cial catch of channel catfish in the upper Mississippi River was associated with increased abundance of age-0 fish. [Buynak et al. \(1999\)](#) found the abundance of cohorts (year-classes) of age-5 largemouth bass was correlated to electrofishing catch of these same cohorts at age 1.

Either to document recruitment abundance and variability fully or relate some environmental factor to recruitment variation directly, long-term data collection is necessary. Typically, any sampling method that measures density or catch per effort (C/f) can be used to estimate recruitment (see Chapters 7 and 8). These samples should be taken about the same time each year and ideally under similar environmental conditions. Either fixed or random stations serve as replicates samples taken each year (Chapter 3). Conducting statistical analyses when random sampling is used is easier, but spatial variability in recruits may be greater than year-to-year variation, and low or zero catches can complicate the analysis. Thus, more replicate samples may be needed when random sampling is employed. With fixed-station sampling, repeated-measures analysis of variance (ANOVA) can be used to detect temporal or spatial differences in recruits ([Maceina et al. 1994](#)), but the analysis is more complicated than simple ANOVA.

Evaluation of recruitment enhancement from habitat manipulation or stocking requires a specific study design. Typically, these investigations are shorter in duration and may involve a few years of pre- and postmanipulation data collection. In addition, the frequency of sample collection may be greater than once per year, particularly if the fisheries scientist wants to investigate the effects of manipulation on successful recruitment.

Annual estimates of recruitment can be generated with monitoring data routinely collected by many state, federal, and provincial natural resource agencies in conjunction with population assessments. Many agencies conduct standardized electrofishing, gill netting, trap netting, seining, and sometimes rotenone sampling of age-0 fishes. Sampling bias and differences in catchability either with gear or location can occur and should be assessed (see [Murphy and Willis 1996](#)). Specific investigations to address a priori hypotheses pertaining to recruitment may require more sampling but typically can take place over a shorter period of time.

To determine if a relation exists between recruit and spawner (or parental abundance), long-term data collection of both these variables is necessary. [Madenjian et al. \(1996\)](#) used as little as 13 years of walleye data, whereas [Myers et al. \(1994\)](#) limited their analysis of 72 finfish populations to those with at least 20 years of data. Sources for recruitment-spawner data may include direct estimates from mark-recapture experiments, C/f derived from indices ([Tyler and Crawford 1991](#); [Myers et al. 1997](#)), or estimates from stock assessment modeling derived from some form of sequential population analysis, virtual population assessment, or catch at age. We urge caution in any recruit-spawner analysis with fewer than 20 observations.

4.1.3 Freshwater versus Marine Recruitment Assessment

Similar to freshwater systems, recruitment of marine fishes can be highly variable and is regulated by both density independent and dependent factors. In addition,

low parental abundance due to either overexploitation or natural population cycles can drastically reduce reproductive output, which can ultimately result in a decline of recruits into the population and confound detection of environmental variables related to variable recruitment ([Walters and Collie 1988](#)). The areal extent of marine ecosystems, the sometimes longer interval between juvenile and adult harvestable ages, the difficulty of sampling certain life stages, and the greater difficulty in sampling recruits can confound recruitment assessment in marine environments as compared with freshwater environments.

[Walters and Collie \(1988\)](#) questioned the use of public funds to support correlative approaches to explain recruitment variation due to environmental variables, particularly for variables that cannot be controlled in marine fisheries. Subsequent predictions can fail due to the short-term period or window of data collection “at the frustrating rate of one observation per year” that will not encompass an even prohibitively longer period of recruitment variability ([Walters and Collie 1988](#)). In addition, correlative relations between environment variables and recruitment may be spurious ([Walters and Collie 1988](#); [Myers 1998](#)). [Myers \(1998\)](#) examined numerous studies that had reexamined recruitment patterns primarily of marine fishes and found after retesting that many of the previously derived correlates failed to predict recruitment after additional data had been collected.

An early focus in marine stock assessment focused on recruit–spawner relations. In general, these described the number of recruits as a function of parental spawners either as (1) an asymptotic relation whereby recruitment will not increase once a certain number of spawners occur in the population (Beverton–Holt, with compensation) or (2) a domed-shaped relation (Ricker, with overcompensation) whereby the greatest numbers of recruits will be produced at some intermediate abundance of spawners. With a greater number of spawners, recruits will decline due to density dependence ([Ricker 1975](#)). In freshwater, Ricker recruit–spawner relations have been shown, for example, for walleye ([Madenjian et al. 1996](#); [Hansen et al. 1998](#)) and lake trout ([Hansen et al. 1996](#)).

Typically, attempts to define a critical abundance of spawning adults necessary for adequate recruit production based on Ricker or Beverton–Holt equations have been wrought with high variability, confounding effects of environmental factors that affect recruitment, and the necessity to collect long-term data ([Hilborn and Walters 1992](#); [Goodyear 1993](#); [Hansen et al. 1998](#)). To circumvent the problem of defining recruit–spawner relations, marine fisheries scientists have attempted to address recruitment overfishing quantitatively by means of the spawning potential ratio ([Goodyear 1993](#)). [Slipke et al. \(2002\)](#) introduced the use of the spawning potential ratio to address recruitment overfishing for a freshwater commercial fishery.

■ 4.2 ESTIMATION OF RECRUITMENT

A variety of gears can be used to sample young fish and estimate recruitment. In freshwater, electrofishing gear, gill nets, seines, trap nets, fyke nets, push nets,

bottom and midwater trawls, and rotenone have been used to sample recruits (see Chapters 5–10 in Murphy and Willis 1996). Gear selectivity can cause bias in estimating recruitment ([Jackson and Noble 1995](#)) and should be thoroughly evaluated to ensure representative sizes of all members of a cohort are sampled.

4.2.1 Estimates of Recruitment from Population Estimates

The density and biomass of recruits can be estimated with single or multiple mark-recapture methods, depletion methods, and toxicants (Chapter 8). Serns (1982) used electrofishing to conduct multiple mark-recapture procedures to estimate the population of age-0 smallmouth bass in the fall from 1974 to 1981 in Lake Nebish, Wisconsin, and estimates varied from 1,174 to 7,764 fish. [Rider et al. \(1994\)](#) blocked off 0.1–0.2-ha coves that contained submersed vegetation or open water to estimate the density of age-0 largemouth bass by means of an electrofishing catch depletion technique. Typically, four to seven 10-min passes were required to deplete the number of individuals in order to compute a [Leslie and Davis \(1939\)](#) linear regression line ([Rider et al. 1994](#)).

Long-term (>20 years) annual cove rotenone samples were used to estimate the biomass of age-0 black basses in Bulls Shoals Reservoir, Arkansas ([Ploskey et al. 1996](#)) and age-0 crappie density in four Mississippi reservoirs ([Allen and Miranda 1998](#)). [Hoyer and Canfield \(1996\)](#) used 0.1-ha block nets and rotenone applied in limnetic and littoral regions of Florida lakes to estimate annual density of age-0 largemouth bass. [Allen et al. \(1999\)](#) used a shoreline rotenone technique to relate age-0 largemouth bass density to chlorophyll-*a* concentrations and larval gizzard shad and threadfin shad densities. [Fisher and Zale \(1993\)](#) used a 12.2-m-long by 1.8-m-deep bag seine with 4.8-mm mesh and captured age-0 largemouth bass from quadrants of a known area. Average annual catch rates varied from 0.42 to 3.12 fish/100 m², and density was related to water level fluctuations in conjunction with the implementation of a new water level regulation schedule on Grand Reservoir, Oklahoma ([Fisher and Zale 1993](#)).

4.2.2 Estimates of Recruitment from Indices

In many instances, estimating the density and biomass of recruits (either at age 0 or age 1) is not feasible or too costly. Sampling with electrofishing gear, gill nets, seines, trawls, and trap nets can provide standardized units of effort for either time or distance and can be used to index recruit abundance. [Willis and Stephen \(1987\)](#) and [Sammons and Bettoli \(2000\)](#) used experimental monofilament gill nets to estimate catch per net-night of age-0 walleye and age-1 white bass; recruits of both species varied over two orders of magnitude, and this variation was related to hydrologic variables.

[Maceina and Stimpert \(1998\)](#) used age-1 catch rates (*N*/net-night) of black crappie and white crappie in trap nets as an index of recruitment in Alabama reservoirs and related the variation in recruitment to reservoir hydrologic variables. [Sammons and Bettoli \(2000\)](#) used DC electrofishing in the spring to capture age-1

largemouth bass along 40 randomly chosen 100-m transects throughout Normandy Reservoir, Tennessee, and average annual catch rates varied from about 0.1 to about 1.7 fish/100 m. Jackson and Noble (2000) used a handheld electrofishing apparatus from a boat to collect age-0 largemouth bass during 3-week intervals from June to October from 1988 to 1998; peak average catch rates among years varied from 3.8 to 46.7 age-0 fish/20 min.

Bronte et al. (1993) used a semiballoon bottom trawl with a 11.9-m headrope, a 15.6-m footrope, and a 12.7-mm-mesh cod end to sample all sizes of yellow perch, and the total catch of age-2 fish was used as an index of recruitment and year-class strength. Similarly, [Madenjian et al. \(2000\)](#), using 8-m and 11-m bottom trawls, documented a reduction in catch of age-0 white bass over a 20-year period from Lake Erie that was related to the subsequent decline in the fishery. Coughlin et al. (1999) used a 6.2-m high-rise bottom trawl to assess abundance of age-0 white sturgeons. Highly variable catches were due to patchy distributions and were not normally distributed ([Coughlin et al. 1999](#)). These authors recommended that indices of presence and absence and C/f both be used to assess recruitment levels of age-0 white sturgeons in the Columbia River. Beach seines were used to collect age-0 striped bass from the Chesapeake Bay from 1954 to 1996 to develop a quantitative juvenile index, which was later used to determine that recruitment overfishing caused the collapse of this valuable fishery (Richards and Rago 1999).

4.2.3 Use of Marks and Tags to Assess Recruitment

Coded wire tags, dyes, chemical marking, morphological marks, and genetic tags can be employed to determine the success of stocking and may also be used to examine recruitment processes of wild fish. To evaluate stocking success, otoliths of juvenile fishes can be marked with alizarin complexone, calcein, or oxytetracycline, and these chemicals can be applied by immersion, injection, or orally through prepared foods in a hatchery (Thomas et al. 1995).

[Isermann et al. \(2002\)](#) successfully used oxytetracycline immersion to form marks on young crappie otoliths and suggested this technique can be used effectively to identify stocked crappies up to about 2 years old. [Paragamian et al. \(1992\)](#) established the reliability of stress checks on otoliths of hatchery-reared kokanees to distinguish these fish from wild fish in Lake Pend Oreille, Idaho. Counts of daily increments in relation to stress checks allowed for correct identification of fish from several co-occurring release groups that had been stocked at different times in the same season ([Paragamian et al. 1992](#)).

[Buynak and Mitchell \(1999\)](#) used alternating pectoral fin clips of stocked age-0 largemouth bass (about 11 cm TL) over a 5-year stocking period to evaluate contribution of stocked fish to naturally produced fish in a 1,200-ha Kentucky reservoir. Over time, stocked fish contributed 25% of the total electrofishing catch ([Buynak and Mitchell 1999](#)).

Ryan et al. (1998) used for stocking genetically distinct Florida largemouth bass adults that contained a unique allele (*sIDHP*109*) expressed in the allozyme

locus for isocitrate dehydrogenase (IUBMB [1992] number 1.1.1.42) that was different than the *sIDHP*100* and *sIDHP*122* alleles found, respectively, in the northern largemouth bass and Florida largemouth bass population in Lake Galdwater, Texas. Offspring homozygous for the *sIDHP*109* allele were produced, grown out in nursery ponds, and stocked at rate of 8.8 fish/ha in summer (Ryan et al. 1998). To assess stocking success, age-0 and age-1 largemouth bass were sampled in fall and spring with DC electrofishing, and recruits were identified using electrophoresis (Ryan et al. 1998). [Murphy et al. \(1983\)](#) identified allele frequencies at the malate dehydrogenase locus (*mMDH-2**; IUBMB [1992] number 1.1.1.37) of hatchery-raised walleye, and the success of supplemental stocking was evaluated by quantifying shifts in cohort allele frequencies due to the stocking of juvenile fish with allele frequencies different from resident-hatched fish.

[Ludsin and DeVries \(1997\)](#) used three different color dyes that were injected into small (<100 mm TL), medium (100–150 mm TL), and large (>150 mm TL) age-0 largemouth bass in the fall to assess overwinter size-dependent mortality. In the spring at age 1, a higher proportion of the larger-size individuals were collected, which indicated that size in the fall influenced recruitment to age 1. [Parsons and Pereira \(2001\)](#) used coded wire tags to evaluate walleye stockings and estimated the extent of natural reproduction in three Minnesota lakes. About 95,000 hatchery-reared striped bass were individually marked with coded wire tags and released into Delaware Bay, and a total population estimate of age-0 striped bass was derived from recaptures of both tagged and wild-produced fish ([Burton and Weisberg 1994](#)).

4.2.4 Otolith Microstructure Analysis to Assess Recruitment

The analysis of daily increments on the otoliths of fishes ([Pannella 1971](#)) can provide fisheries scientists with insights on early life history aspects of fish population dynamics, including recruitment. Research has sometimes shown that early hatched cohorts, identified by enumerating daily growth rings, not only have a size advantage compared with later-hatched cohorts but grow faster and are more likely to recruit to the population due to increased survival ([Ludsin and DeVries 1997](#)). Conversely, early hatching in spring could be detrimental to larval fish survival and subsequent recruitment due to unstable climatic conditions such as low water temperatures, high variation in air and water temperatures, or windy conditions ([Kramer and Smith 1962](#); [Summerfelt 1975](#); [Crecco and Savoy 1987](#); [Rice et al. 1987](#)).

[Isely et al. \(1987\)](#) and [Maceina et al. \(1988\)](#) used incremental counts of daily growth rings to assess temporal spawning patterns, growth, and recruitment potential of mixed populations of northern and Florida largemouth bass. [Crecco and Savoy \(1987\)](#) identified 5-d cohorts of American shad, estimated cohort mortality, and found that recruitment was influenced by density-dependent processes and strongly mediated by hydrologic and climatic conditions.

■ 4.3 RECRUITMENT VARIABILITY AND FACTORS RELATED TO YEAR-CLASS STRENGTH

4.3.1 Temporal Variation in Recruitment

Abundance of recruits can be relatively stable or highly variable over time. Fisheries scientists collect long-term monitoring or research data to assess temporal variation in recruitment. Generally, data should be collected at about the same time each year from a random, systematic, or stratified sampling design (Chapter 3).

[Allen and Pine \(2000\)](#) reviewed data on recruitment variability in white crappie and black crappie populations and largemouth bass populations based on age-0 and age-1 abundances, which were assessed using electrofishing, trap nets, and rotenone sampling. Coefficients of variation (CV; $100 \cdot \text{SD}/\text{mean}$) for recruits averaged 82% (55–124%) for crappies and 66% (11–189%) for largemouth bass. In Lake Escanaba, Wisconsin, mark-recapture population estimates based on electrofishing were conducted for age-0 walleye each September–October from 1958 to 1996 ([Hansen et al. 1998](#)). In this lake, age-0 walleye density averaged 99 fish/ha, varied from 5 to 299 fish/ha, and had a CV of 78% ([Hansen et al. 1998](#)). This long-term database is useful for understanding the dynamics of walleye recruitment in Lake Escanaba but represented a tremendous amount of sampling effort over a long time period that obviously cannot be achieved for every system.

High CV values in recruitment will cause population characteristics and associated angler catches to fluctuate. In short-lived populations (i.e., less than 8 years), three to four successive weak year-classes can cause a population to decline drastically. Software programs such as GIFSIM ([Taylor 1981](#)), MOCPOP ([Beamdesfer 1991](#)), and FAST ([Slipke and Maceina 2000](#)) can be used to simulate the response of a fish population over time to stochastic recruitment. Fisheries scientists may be interested in examining some mean or median level of recruitment and associated variance and incorporating this variation (SD, CV, or range) into modeling or other types of analyses.

[Kimura \(1988\)](#) presented a two-way ANOVA technique based on log-linear models that can be applied to catch data of different age fish to test for differences among year-class abundances. In many instances with sampling, collection gears may be positively or negatively biased for a certain age. This bias was evident in the crappie data presented in Table 4.1; age-1 catch was higher than age-0 catch for the 1993 year-class. If fish are collected over time from a number of different age-groups, then potential age-selective bias in the sample can be ameliorated by considering multiple catches of different age fish from the same year-class (Box 4.1).

Over time, recruitment will vary and may show an increasing, decreasing, or stable pattern. Long-term changes in recruitment may be a function of variation in water quality, habitat, or climatic factors, introduction of a competitive species, or excessive exploitation. [Bettoli et al. \(1992\)](#) found a significant correlation ($r = 0.80$; $P < 0.05$) between density of age-1 largemouth bass and macrophyte coverage. A reduction in age-0 channel catfish and striped bass abundance was associated with high exploitation of adults for both of these species, and a subsequent

Table 4.1 Age-0, age-1, and age-2 black crappie and white crappie catch rates (species catch per unit effort, C/f , were pooled) for 11 year-classes collected with trap nets from Weiss Lake, Alabama, from 1989 to 1999. Three reservoir hydrologic variables are also provided (partial data set presented in Maceina and Stimpert 1998). Water levels in Weiss Lake are regulated for flood control and power generation. Mean winter stage was the average daily stage between 1 January and 31 March (prior to crappie spawning). Mean winter retention was derived by dividing average daily volume by discharge, which was computed from average daily readings for Weiss Lake. Full summer pool is normally obtained around 15 April each year at an elevation of 171.95 m above mean sea level (msl). Mean spring stage was computed from average daily stages between 1 April and 31 May and coincided with crappie spawning (Travnichek et al. 1996).

Year-class	Catch per unit effort			Mean winter stage (m mSL)	Mean winter retention (d)	Mean spring stage (m mSL)
	Age-0	Age-1	Age-2			
1989		3.12	0.49	170.85	7.2	171.79
1990	8.03	5.32	2.43	171.76	4.2	171.75
1991	0.47	0.39	0.39	170.73	7.4	171.75
1992	0.61	0.97	0.61	170.67	6.6	171.82
1993	1.38	3.59	1.32	170.99	6.2	171.77
1994	2.73	2.62	0.92	170.93	5.9	171.87
1995	1.66	0.57	0.47	170.88	6.8	171.80
1996	9.89	8.63	2.11	171.39	5.5	171.85
1997	1.86	0.93	0.21	170.83	6.1	171.90
1998	3.72	1.17		171.04	5.6	171.83
1999	2.18			170.77	9.7	171.82

reduction in exploitation resulted in increased recruitment (Pitlo 1997; Richards and Rago 1999). White bass decreased over time in Lake Erie, and this trend was related to a declining temporal trend in the abundance of age-0 fish (Madenjian et al. 2000; Box 4.2).

Fisheries scientists can also examine temporal differences in recruitment from changes in habitat features or by manipulating habitat characteristics. Fisher and Zale (1993) examined abundance of age-0 largemouth bass during a 12-year period for which data were collected prior to and after a change in the reservoir-regulated water levels. In many instances, a manipulation is conducted in a single area or water body and pre- and postmanipulation responses in recruitment are measured. If young fish are collected over time, then one can use one of the ANOVA designs presented by Hubert and Fabrizio (Chapter 7).

4.3.2 Spatial Variation in Recruitment

Fish recruitment can vary among water bodies, within water bodies, and among different habitats within a single water body (Allen and Pine 2000). For example, Wrenn et al. (1996) found that density of age-0 largemouth bass was greater in areas of Lake Guntersville, Alabama, that contained Eurasian water milfoil compared with areas that were devoid of aquatic vegetation. Sammons and Bettoli (2000) collected age-0 largemouth bass for a 6-year period to examine the relation of reservoir hydrology and largemouth bass recruitment. Four distinct areas of the

Box 4.1 Log-Linear Model to Test for Year-Class Abundance Differences

Below we conduct a test for year-class abundance differences among the 1990 to 1997 year-classes (YEARCL) based on catch rates of age-0, age-1, and age-2 crappies (AGE in years) from Weiss Lake (Table 4.1). Trap-net catch rates are transformed to natural log values (LCATCH) to homogenize variances as recommended by Kimura (1988) for log-linear analysis. The data in Table 4.1 were rearranged to conduct the analysis. Year of collection (YEARCOL) was included in the data file, and the following SAS (2001) program was written to conduct the analysis.

Program

```
DATA WECRA;
INPUT YEARCOL YEARCL AGE CATCH;
LCATCH=LOG(CATCH);
LINES;
1990    1990    0    8.03
1991    1990    1    5.32
1992    1990    2    2.43
1991    1991    0    0.47
1992    1991    1    0.39
1993    1991    2    0.39
1992    1992    0    0.61
(continue data input)
;
PROC GLM; CLASS YEARCL AGE;
MODEL LCATCH=YEARCL AGE;
LSMEANS YEARCL/T PDIF STDERR;
MEANS YEARCL/LSD LINES ALPHA=0.001786; RUN;
```

Results

Table Output for two-way analysis of variance (ANOVA) and comparison of least-squares means for catch (dependent variable LCATCH). There were 24 observations in the data set. Abbreviations are given for coefficient of variation (CV), mean square error (MSE), sum of squares (SS), and least-squares mean (LSMEAN).

Class Level Information									
		Class	Levels	Values					
1996 1997		YEARCL	8	1990 1991 1992 1993 1994 1995 1996 1997					
		AGE	3	0 1 2					
Analysis of Variance									
Source	df	SS	Mean square	F-value	P > F				
Model	9	23.11022510	2.56780279	11.67	0.0001				
Error	14	3.07916486	0.21994035						
Corrected total	23	26.18938997							
R ²	0.882427	Root MSE	0.46897798						
CV	138.6533	LCATCH mean	0.33823792						

Source	df	Type III SS	Mean square	F-value	P > F
YEARCL	7	19.01504754	2.71643536	12.35	0.0001
AGE	2	4.09517756	2.04758878	9.31	0.0027

Least-Squares Means for H_0 LSMEAN = 0

YEARCL	LCATCH LSMEAN	SE	P > t	LSMEAN number
1990	1.54751636	0.27076456	0.0001	1
1991	-0.87941322	0.27076456	0.0058	2
1992	-0.33968395	0.27076456	0.2302	3
1993	0.62595581	0.27076456	0.0365	4
1994	0.62803144	0.27076456	0.0360	5
1995	-0.27010797	0.27076456	0.3354	6
1996	1.73115220	0.27076456	0.0001	7
1997	-0.33754732	0.27076456	0.2330	8

Least-Squares Means for H_0 LSMEAN i = LSMEAN j

LSMEAN number (j) t-test, and P^a	LSMEAN number (i)							
	1	2	3	4	5	6	7	8
1								
t-value		6.337973	4.928459	2.406673	2.401252	4.74676	-0.47957	4.922879
P		0.0001	0.0002	0.0305	0.0308	0.0003	0.6389	0.0002
2								
t-value	-6.33797		-1.40951	-3.9313	-3.93672	-1.59121	-6.81754	-1.41509
P	0.0001		0.1805	0.0015	0.0015	0.1339	0.0001	0.1789
3								
t-value	-4.92846	1.409513		-2.52179	-2.52721	-0.1817	-5.40803	-0.00558
P	0.0002	0.1805		0.0244	0.0242	0.8584	0.0001	0.9956
4								
t-value	-2.40667	3.9313	2.521787		-0.00542	2.340088	-2.88624	2.516207
P	0.0305	0.0015	0.0244		0.9958	0.0346	0.0120	0.0247
5								
t-value	-2.40125	3.93672	2.527207	0.005421		2.345508	-2.88082	2.521627
P	0.0308	0.0015	0.0242	0.9958		0.0343	0.0121	0.0244
6								
t-value	-4.74676	1.591212	0.181699	-2.34009	-2.34551		-5.22633	0.176119
P	0.0003	0.1339	0.8584	0.0346	0.0343		0.0001	0.8627
7								
t-value	0.479568	6.817541	5.408028	2.886241	2.880821	5.226329		5.402448
P	0.6389	0.0001	0.0001	0.0120	0.0121	0.0001		0.0001
8								
t-value	-4.92288	1.415093	0.00558	-2.51621	-2.52163	-0.17612	-5.40245	
P	0.0002	0.1789	0.9956	0.0247	0.0244	0.8627	10.0001	

(Box continues)

Box 4.1 (continued)

Least-Significant-Difference Test for Variable LCATCH ^b			
T grouping	Mean	N	YEARCL
A	1.7312	3	1996
A			
A	1.5475	3	1990
A			
B A	0.6280	3	1994
B A			
B A	0.6260	3	1993
B			
B C	-0.2701	3	1995
B C			
B C	-0.3375	3	1997
B C			
B C	-0.3397	3	1992
C			
C	-0.8794	3	1991

^a To ensure overall protection level, only probabilities associated with preplanned comparisons should be used.

^b Means with the same letter are not significantly different. Alpha = 0.001786, $df = 14$, MSE = 0.21994, critical value of $t = 3.84$, and least significant difference = 1.4723. This test controls the type I comparisonwise error rate not the experimentwise error rate.

Interpretation

The two-way ANOVA indicated that both age and year-class were significant ($P < 0.01$) class variables related to crappie C/f . Inspection of the data in Table 4.1 suggested abundance of a year-class decreased at older ages, and this was supported by the analysis ($F = 9.31$; $df = 2, 14$). Accounting for the effects of age, C/f also varied by year-class ($F = 12.35$; $df = 7, 14$).

reservoir were chosen each year, and replicate electrofishing transects were conducted to collect fish in August and September each year. A split-plot repeated-measures design (Maceina et al. 1994) was used to test for spatial differences in C/f among these four areas of the reservoir for data collected in 1992 because the same six electrofishing transects were sampled repeatedly in August and September for that year (Table 4.2; Box 4.3).

4.3.3 Use of Adult Age-Structure Data to Estimate Recruitment Variability

Total annual mortality in a fish population can be obtained from catch-curve regression analysis (see Chapter 6) by which a sample of fish that has recruited to the fishery is collected and aged and the natural log of the number at age (y -variable) is regressed against age (x -variable). When a single sample of fish is collected that represents a number of cohorts or year-classes, highly variable

Below the ANOVA is a table that presents the least-squares means (LSMEANS) for $\log_e(C/f)$, LCATCH, the associated SE, and a probability value from a test that the least-squares mean is not equal to 0 (null hypothesis, H_0 : LSMEAN = 0). A number assigned to each least-squares mean represents each year-class. The LSMEANS procedure in SAS creates least-squares means for the class variables. These are also referred to as adjusted means (SAS 2001). For one-way ANOVA, or in this example, a balanced two-way ANOVA, least-squares means are computed as arithmetic means. In this example, each year-class is weighted by sample size or the number of age-groups ($N = 3$).

Next, a matrix table is presented that shows pairwise t-tests among all eight year-classes and corresponding probability levels. These comparisons allow the fisheries scientists either to accept or reject the H_0 that the least-squares means or year-class abundance estimates are the same for the two year-classes being compared. A caution statement at the end of the table warns the analyst only to make preplanned comparisons (SAS 2001). If many comparisons are being made, some statistical differences may be detected due to random chance and are not true differences.

Because 28 comparisons were made among these eight year-classes ($7 + 6 + 5 + 4 + 3 + 2 + 1$), a Bonferroni correction can be applied to an alpha level to reduce the probability of making a type I error. For this example, if we set alpha at 0.05 and divide by 28, the new alpha level of 0.001786 can be specified in the SAS program to perform Fischer's least-significance-difference multiple-range test, which is analogous to multiple pairwise t-tests. Thus, fewer statistical differences would be evident compared with a standard alpha value of 0.05. The fisheries scientist needs to decide what level of a type I error is acceptable when making multiple comparisons. In this example, the Bonferroni correction is clearly highly conservative and would become more restrictive in rejecting the H_0 as the number of years of data collection increases. If a priori assignment of year-class groups can be assigned, then a Bonferroni correction for preplanned comparisons would be less or contrast statements can be set up to test for preplanned comparisons. From these results, the 1990 and 1996 year-classes were more abundant than were the 1991, 1992, 1995, and 1997 year-classes. Abundance of the 1993 and 1994 year-classes was intermediate and statistically similar to some of these weaker and more abundant year-classes.

recruitment will cause the relation between number at age and age to vary (Ricker 1975; Maceina 1997).

[Guy and Willis \(1995\)](#) introduced and used the recruitment variability index (RVI) to assess black crappie reproductive success in South Dakota. To compute the RVI, the cumulative relative frequency (CRF) distribution (the same as presented for the Kolmogorov–Smirnov one-sample test or PROC CHART in SAS [2001]) is used to describe the magnitude and distribution of the frequency-of-occurrence-at-age data. This index is sensitive to year-classes that are completely missing from the sample. The RVI is computed as

$$RVI = [CRF / (N_m + N_p)] - N_m / N_p, \quad (4.1)$$

where N_m is equal to the number of missing year-classes (no fish were collected), N_p is equal to the number of year-classes present in the sample, and the N_p must

Box 4.2 Evaluation of Time Series Trends in Recruit Abundance

The following program presents a plot and computes the Pearson correlation coefficient between age-0 C/f (AGE0CPE) of white bass and year and the Kendall tau- b nonparametric correlation coefficient for ranks between these two variables (data published in Mandenjian et al. 2000). In addition, the simple linear regression between C/f and year was computed along with the Durbin-Watson statistic (DW) to determine temporal autocorrelation. Finally, the residuals from the regression were plotted against year by means of the following SAS program.

Program

```
DATA WHBASS;
INPUT YEAR AGE0CPE @@;
LINES;
1972 24.38 1973 4.29 1974 10.06 1975 18.16 1976 23.44 1977 20.38 1978 8.06
1979 11.36 1980 25.24 1981 20.49 1982 4.88 1983 2.1 1984 7.68
1985 4.52 1986 3.14 1987 0.57 1988 4.25 1989 1.35 1990 8.42 1991 2.04
1992 3.66 1993 2.84 1994 2.49 1995 0.6 1996 4.85 1997 3.14
;
PROC PLOT; PLOT AGE0CPE*YEAR;
PROC CORR; VAR AGE0CPE YEAR;
PROC CORR KENDALL; VAR AGE0CPE YEAR;
PROC REG; MODEL AGE0CPE=YEAR/DW;
OUTPUT OUT=A R=RES;
PROC PLOT; PLOT RES*YEAR/VFRE=0; RUN;
```

Results

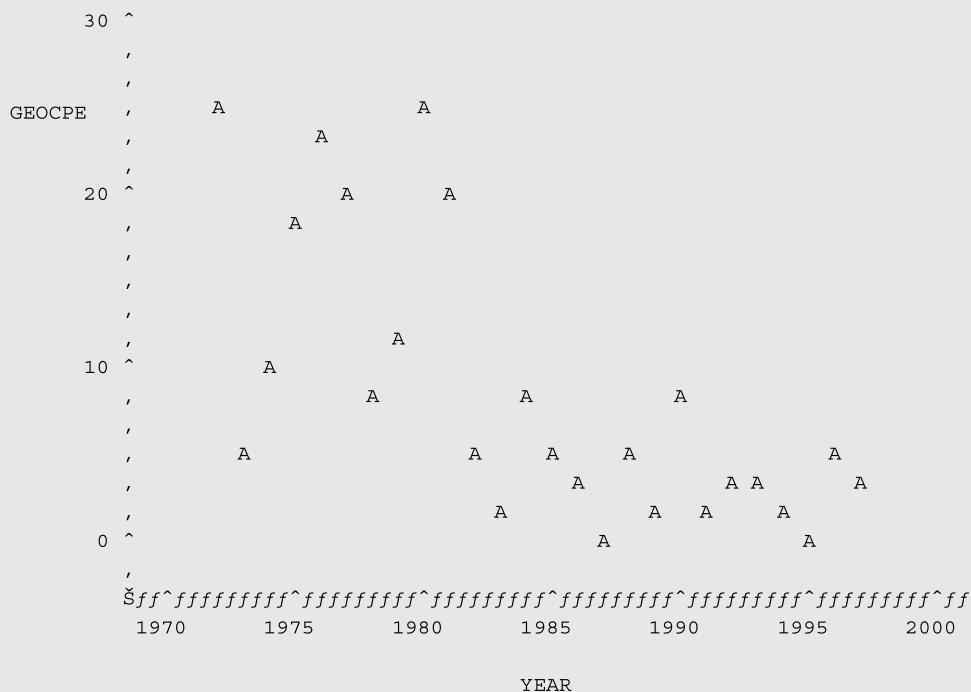


Figure Age-0 C/f (AGE0CPE) of white bass versus year, in which A represents one observation.

Table Output for Pearson and Kendall tau-*b* correlation coefficients. Computed are the Pearson correlation coefficient between AGE0CPE of white bass and year and the Kendall tau-*b* nonparametric correlation coefficient for ranks between these two variables. Both correlation coefficients test for $P > |R|$ under the H_0 that $R(\rho) = 0$ and $N = 26$.

Simple Statistics						
Variable	N	Mean	SD	Sum	Minimum	Maximum
AGE0CPE	26	8.5535	8.0782	222.3900	0.5700	25.2400
YEAR	26	1985	7.6485	51597	1972	1997
Pearson Correlation Coefficients						
	AGE0CPE		YEAR			
AGE0CPE	1.00000		-0.67212			
	0.0		0.0002			
YEAR	-0.67212		1.00000			
	0.0002		0.0			
Kendall's Tau-b Correlation Coefficient						
	AGE0CPE		YEAR			
AGE0CPE	1.00000		-0.48690			
	0.0		0.0005			
YEAR	-0.48690		1.00000			
	0.0005		0.0			
Time Series Regression and Test for Autocorrelation						
Source	df	SS	Mean square	F-value	P > F	
Model	1	736.99067	736.99067	19.775	0.0002	
Error	24	894.43972	37.26832			
Corrected total	25	1631.43039				
R ²	0.4517	Root MSE	6.10478			
Adjusted R ²	0.4289	AGE0CPE mean	8.55346			
CV	71.37202					
Variable	df	Parameter estimate	SE	t-value	P > t	
Intercept	1	1417.304215	316.79344310	4.474	0.0002	
YEAR	1	-0.709877	0.15963274	-4.447	0.0002	
Durbin-Watson statistic (DW)		1.500				
Number of observations		26				
First-order autocorrelation		0.216				

(Box continues)

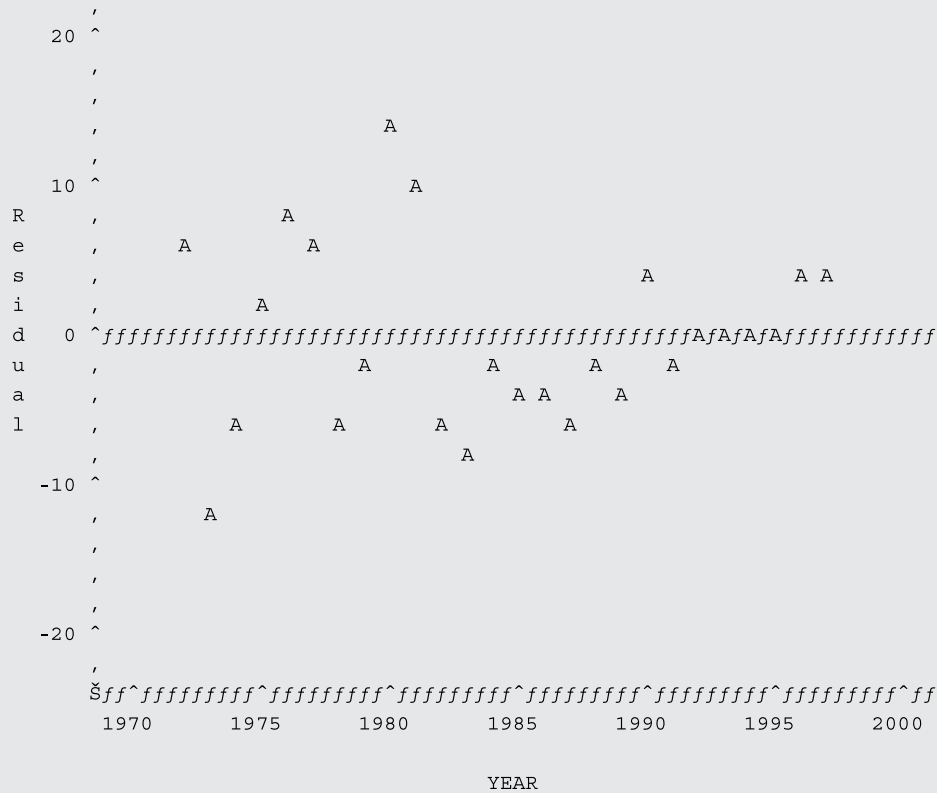
Box 4.2 (continued)

Figure Residuals from the time series regression of age-0 white bass *C/f* versus year, in which A represents one observation.

Interpretation

The SAS plot that examines the relationship between age-0 *C/f* and year clearly showed a decline in white bass recruitment over time. Correlation and regression analyses indicated a significant ($P < 0.01$) decrease in *C/f* of age-0 white bass over time. The Kendall tau-*b* correlation coefficient is a

exceed the N_m . The RVI ranges from -1 to 1, and increases in RVI indicate less recruitment variability. The index assumes that fish are fully recruited to the sampling gear, that catch at age is a valid representation of year-class strength, and that there are not year-classes beyond the last age-group represented in the sample (Guy and Willis 1995). In addition, Guy (1993) recommended that the RVI should not be computed when less than three year-classes are present.

Maceina (1997) built upon the RVI concept and developed a quantitative index of recruitment variability based on the residuals or errors associated with

nonparametric test that numerically ranked the years and age-0 C/f and then computed the association between these two ranks. Similar to Pearson correlation coefficients, Kendall tau- b correlation coefficients can range from -1 to 1 , and these values would be computed if ranks completely matched. The value of Kendall tau- b correlation coefficient was less than that of the Pearson coefficient, but both tests indicated a strong, significant ($P \leq 0.01$) decreasing temporal trend in age-0 C/f . The Kendall tau- b correlation coefficient is useful for time series data because one or a few extremely high or low values can be so influential when using linear methods that the results would be biased.

Autocorrelation can be troublesome with time series analysis because errors or residuals may not be independent. For example, when measuring the response of a variable to some factor, the same factor also influenced that variable of interest some time in the past. The same processes could be evident with recruitment data, for example, due to long-term temporal patterns in climate or recruitment overfishing. If adults have been overexploited to the extent that not enough recruits are being produced to replace adults, then a negative feedback loop occurs; fewer adults confer fewer recruits to become adults, and then there are fewer recruits in the next generation. Although autocorrelation is somewhat troublesome statistically with time series analysis, this should not preclude the inferences drawn from primary trends.

The SAS plot of the residuals from the regression of age-0 C/f versus year showed a somewhat even cyclic pattern of high and low residuals from 1972 to the early 1980s, negative residuals during the rest of the 1980s, followed by residual values around 0 or greater in the 1990s. These residuals did not appear randomly scattered, particularly from 1972 to about 1985, and suggested a weak cyclic pattern in white bass recruitment. The Durbin-Watson statistic (DW) is a test for the existence of a first-order autoregressive process. The personal computer version of SAS (2001) does not provide a statistical probability that tests for a first-order autocorrelation, but probability distribution tables for the DW values can be found in Montgomery and Peck (1982). For this example, the computed DW was 1.5, which exceeded the critical DW value of 1.45 ($P = 0.05$). Thus, errors were autocorrelated based on the DW statistic. The first-order correlation is the actual correlation between adjacent residuals. We computed a first-order autocorrelation of 0.22, which is moderately low, but for time series analysis, the number of years of data was relatively high ($N = 26$). Values approaching -1 or 1 show a high degree of autocorrelation. See Montgomery and Peck (1982) and Freund and Littell (1991) for more information. High values for first-order correlations and significant DW values suggest a cyclic pattern and dictate that the fisheries scientist should investigate this phenomenon in more detail.

catch curves and subsequently verified the index (Maceina 2004). An assumption of this analysis is that positive and negative residuals associated with catch-curve regressions represent strong and weak year-classes. Thus, variation about the catch-curve regression is primarily associated with recruitment variability, though in some instances density-dependent mortality among adult fish may also influence the relation between number at age and age. Maceina (2004) more thoroughly explained the use of this approach for quantifying recruitment, and an example is provided (Box 4.4).

Table 4.2 Catch ($N/100$ m) of age-0 largemouth bass along six 100-m transects (Rep) in four different regions of Lake Normandy for three successive time periods (Time) spaced 2 weeks apart in August (Aug) and September (Sep) 1992 (partial data set from Sammons and Bettoli 2000). The four areas were the Lower Basin (LB), Riley Creek (RC), the Upper Basin (UB), and Carroll Creek (CC).

Month	Area	Rep	Time	Catch	Month	Area	Rep	Time	Catch
Aug	CC	1	1	0	Aug	RC	1	2	2
Aug	CC	2	1	3	Aug	RC	2	2	0
Aug	CC	3	1	0	Aug	RC	3	2	2
Aug	CC	4	1	0	Aug	RC	4	2	1
Aug	CC	5	1	2	Aug	RC	5	2	4
Aug	CC	6	1	1	Aug	RC	6	2	1
Aug	LB	1	1	4	Aug	UB	1	2	0
Aug	LB	2	1	2	Aug	UB	2	2	1
Aug	LB	3	1	11	Aug	UB	3	2	0
Aug	LB	4	1	3	Aug	UB	4	2	0
Aug	LB	5	1	6	Aug	UB	5	2	1
Aug	LB	6	1	3	Aug	UB	6	2	0
Aug	RC	1	1	3	Sep	CC	1	3	0
Aug	RC	2	1	2	Sep	CC	2	3	3
Aug	RC	3	1	0	Sep	CC	3	3	1
Aug	RC	4	1	5	Sep	CC	4	3	0
Aug	RC	5	1	3	Sep	CC	5	3	1
Aug	RC	6	1	0	Sep	CC	6	3	1
Aug	UB	1	1	2	Sep	LB	1	3	2
Aug	UB	2	1	1	Sep	LB	2	3	3
Aug	UB	3	1	4	Sep	LB	3	3	0
Aug	UB	4	1	0	Sep	LB	4	3	2
Aug	UB	5	1	3	Sep	LB	5	3	3
Aug	UB	6	1	0	Sep	LB	6	3	4
Aug	CC	1	2	0	Sep	RC	1	3	0
Aug	CC	2	2	4	Sep	RC	2	3	0
Aug	CC	4	2	1	Sep	RC	4	3	1
Aug	CC	5	2	0	Sep	RC	5	3	0
Aug	CC	6	2	1	Sep	RC	6	3	0
Aug	LB	1	2	4	Sep	UB	1	3	1
Aug	LB	2	2	1	Sep	UB	2	3	0
Aug	LB	3	2	3	Sep	UB	3	3	3
Aug	LB	4	2	1	Sep	UB	4	3	0
Aug	LB	5	2	5	Sep	UB	5	3	0
Aug	LB	6	2	3	Sep	UB	6	3	0

4.3.4 Examination of the Influence of Environmental Factors on Recruitment

Correlation, simple and multiple linear regression, and nonlinear regression techniques are commonly used to explain and predict variation in recruitment because biotic and abiotic variables that influence recruitment typically vary from year to year. For example, Busch et al. (1975), Kallemeyn (1987), and Hansen et al. (1998) found that adverse climatic conditions in spring during walleye spawning

Box 4.3 Evaluation of Spatial Differences in Recruit Abundance

Table 4.2 contains a data set to test for spatial differences in age-0 largemouth bass catch in Lake Normandy, Tennessee (data from Sammons and Bettoli 2000). In this example, four distinct areas of the reservoir (Lower Basin [LB], Riley Creek [RC], Upper Basin [UB], and Carroll Creek [CC]) were chosen to examine spatial variation in abundance of fish along 100-m shoreline electrofishing transects. A handheld DC electrofishing unit was used at night. Six fixed sites, or replicate transects, were chosen within each area and sampled three times at 2-week intervals starting the second week of August 1992 and ending the second week of September 1992. Thus, 24 transects were conducted over three time intervals for a total of 72 transects, or observations.

Because replicate samples were collected at fixed locations over the three time periods within each of the same areas, a split-plot repeated-measures ANOVA was used to test for differences in number of fish among areas (Maceina et al. 1994). In addition, this analysis also tested for differences in catch over time and examined the time \times area interaction. The program and analysis were divided into main-plot A, which included the class variables area, replicates (REP), and the area \times replicate interaction, and subplot B, which contained the time and the time \times area interaction effects. The mean square error (MSE, or type III sums of squares) of the area \times replication term was used as the error term in the denominator and the MSE for area as the numerator of an F -test for statistical differences in the number caught among the four areas in main-plot A. The MSE generated from the entire ANOVA was used in the denominator of the F -test to determine if statistical differences in catch occurred over the three time periods (subplot B), as well as for testing for any interaction between time periods and areas (subplot B).

The following SAS (2001) program provides output to test for differences in catch among areas.

Program

```
DATA NORM_LMB;
INPUT YEAR MONTH AREA $ REP TIME CATCH;
LINES;
92      8      CC      1      1      0
92      8      CC      2      1      3
92      8      CC      3      1      0
(continue data input)
;
PROC GLM; CLASS TIME AREA REP;
MODEL COUNT = AREA REP REP*AREA TIME TIME*AREA;
TEST H = AREA E = REP*AREA;
MEANS AREA/SNK E=REP*AREA;
MEANS TIME/SNK;
RUN;
```

(Box continues)

Box 4.3 (continued)**Results**

Table Output for split-plot repeated-measures ANOVA (type 1 SS omitted) for which the dependent variable is catch. Four areas in analysis are the Lower Basin (LB), Riley Creek (RC), the Upper Basin (UB), and Carroll Creek (CC). The Student–Newman–Keuls' (SNK) multiple-range test compares the variable catch among these sites.

Class Level Information					
Class	Levels	Values			
TIME	3	1 2 3			
AREA	4	CC LB RC UB			
REP	6	1 2 3 4 5 6			

Analysis of Variance					
Source	df	SS	Mean square	F-value	P > F
Model	31	163.2083333	5.2647849	2.05	0.0166
Error	40	102.7777778	2.5694444		
Corrected total	71	265.9861111			
R ²	0.613597	Root MSE	1.602949		
CV	92.32984	COUNT mean	1.736111		

Source	df	Type III SS	Mean square	F-value	P > F
AREA	3	65.26388889	21.75462963	8.47	0.0002
REP	5	21.40277778	4.28055556	1.67	0.1652
AREA*REP	15	43.31944444	2.88796296	1.12	0.3678
TIME	2	18.36111111	9.18055556	3.57	0.0374
TIME*AREA	6	14.86111111	2.47685185	0.96	0.4618

Test of Hypotheses Using Type III MSE for AREA*REP as an Error Term					
Source	df	Type III SS	Mean square	F-value	P > F
AREA	3	65.26388889	21.75462963	7.53	0.0026

Student-Newman-Keuls' Test for CATCH by AREA ^a			
Number of means	2	3	4
Critical range	1.2073957	1.4713811	1.6326421
SNK Grouping	Mean	N	AREA
A	3.3333	18	LB
B	1.5556	18	RC
B	1.1667	18	CC
B	0.8889	18	UB

Student-Newman-Keuls' Test for CATCH by Time ^b			
Number of means	2	3	
Critical range	0.9352266	1.1262514	
SNK Grouping	Mean	N	TIME
A	2.4167	24	1
A			
B A	1.5833	24	2
B			
B	1.2083	24	3

^aThis test controls the type I experimentwise error rate under the complete H_0 but not under partial H_0 s. Alpha = 0.05, $df = 15$, and MSE = 2.887963. Means with the same letter are not significantly different.

^bThis test controls the type I experimentwise error rate under the complete H_0 but not under partial H_0 s. Alpha = 0.05, $df = 40$, and MSE = 2.569444. Means with the same letter are not significantly different.

The main-plot A test detected a significant ($P < 0.01$) difference in catch among areas. Student-Newman-Keuls' (SNK) multiple-range test based on the proper variance term (MSE of the area \times replicate interaction) indicated that catch of fish in the Lower Basin was greater than that in the other three areas, and no differences in catch were evident among Riley Creek, Carroll Creek, and the Upper Basin. The Student-Newman-Keuls' test represents one of many multiple-range tests offered by SAS (2001). Other multiple-ranges tests that statistically separate mean values among treatments can be more or less likely to control the type I error rate.

In addition, the split-plot repeated-measures ANOVA indicated time, a temporal change in catch, was a significant ($P < 0.05$) term in the model. The multiple-range test showed that for all four areas combined, catch was highest during the first sampling time period and declined during the second and third sampling time period. This might be expected as young fish abundance would be expected to decline over time due to natural mortality. An interaction between area and time was not evident ($P = 0.46$) and, thus, did not confound interpretation of temporal effects due to differences in catch among areas for different time periods.

Box 4.4 The Use of Catch-Curve Regression to Identify Weak and Strong Year-Class Formation

This example contains a data set (data published in Maceina and Bettoli 1998) that uses catch-curve regression to detect strong and weak year-class formation in a largemouth bass population. In addition, a reservoir hydrologic variable is included that will be used later (see section 4.3.4) to examine the association between year-class strength and an environmental variable. In spring 1993, 653 age-2 to age-11 largemouth bass were collected using DC electrofishing. Age-length keys (Bettoli and Miranda 2001) were used to estimate the age structure for the entire sample from examination of 190 otoliths.

The SAS program below first computed the regression between the natural log of number at age (LNUM) against age and used the predicted values for the natural log of number at age (PLNUM) as weighting factors when the catch-curve analysis was recomputed. Thus, the second catch-curve regression computed the least-squares fit using the predicted values from the first fit as weights. From this regression, the residuals were computed and printed with the year-class (YEARCL) and age identified. For this analysis, we assumed all fish age 2 and older were fully recruited to the electrofishing gear and the fishery.

Program

```
DATA GUN_LMB;
INPUT YEARCL AGE NUM MEANRET @@;
LNUM=LOG(NUM + 1);
LMEANRET=LOG10(MEANRET);
LINES;
91 2 175 13.7 90 3 273 16.9 89 4 28 9.6 88 5 79 47.7
87 6 18 19.5 86 7 49 49.5 85 8 21 31.0 84 9 8 9.6
83 10 0 10.5 82 11 2 23.2
;
PROC REG NOPRINT; MODEL LNUM=AGE/R; ID YEARCL AGE;
OUTPUT OUT=A P=PLNUM;
DATA B; SET A;
W=PLNUM;
PROC PRINT; VAR YEAR AGE NUM LNUM W;
PROC REG; WEIGHT W; MODEL LNUM= YEARCL AGE/R; RUN;
```

Results

Table Data for 653 age-2 to age-11 largemouth bass collected using DC electrofishing. The number at age (NUM) is given with its associated weighting factor, LNUM ($=\log_e[\text{NUM} + 1]$). Weight is the predicted value for the natural log of number at age.

Observation	YEARCL	AGE	NUM	LNUM	Weight
1	1991	2	175	5.17048	5.48748
2	1990	3	273	5.61313	4.97418
3	1989	4	28	3.36730	4.46088
4	1988	5	79	4.38203	3.94758
5	1987	6	18	2.94444	3.43428
6	1986	7	49	3.91202	2.92098
7	1985	8	21	3.09104	2.40768
8	1984	9	8	2.19722	1.89438
9	1983	10	0	0.00000	1.38108
10	1982	11	2	1.09861	0.86778

Table Catch-curve regression for LNUM versus AGE.

Analysis of Variance					
Source	df	SS	Mean square	F-value	P > F
Model	1	47.50049	47.50049	23.584	0.0013
Error	8	16.11255	2.01407		
Corrected total	9	63.61304			
R ²	0.7467	Root MSE	1.41918		
Adjusted R ²	0.7150	LNUM mean	3.86169		
CV	36.75024				

Parameter Estimates					
Variable	df	Parameter estimate	SE	t-value	P > t
Intercept	1	6.344692	0.56991090	11.133	0.0001
AGE	1	−0.480520	0.09894628	−4.856	0.0013

Predicted LNUM (PLNUM) and Residuals from Weighted Regression							
Observation	AGE	YEARCL	Weight	LNUM	PLNUM	Predicted SE	Residual
1	2	1991	5.4875	5.1705	5.3837	0.402	−0.2132
2	3	1990	4.9742	5.6131	4.9031	0.331	0.7100
3	4	1989	4.4609	3.3673	4.4226	0.277	−1.0553
4	5	1988	3.9476	4.3820	3.9421	0.252	0.4399
5	6	1987	3.4343	2.9444	3.4616	0.265	−0.5171
6	7	1986	2.9210	3.9120	2.9811	0.310	0.9310
7	8	1985	2.4077	3.0910	2.5005	0.377	0.5905
8	9	1984	1.8944	2.1972	2.0200	0.455	0.1772
9	10	1983	1.3811	0	1.5395	0.540	−1.5395
10	11	1982	0.8678	1.0986	1.0590	0.630	0.0396

Residuals and Associated Outlier Statistics from Weighted Regression								
Observation	AGE	YEARCL	SE residual	Student residual	−2−1−012 ^b			Cook's D
1	2	1991	0.453	−0.470				0.087
2	3	1990	0.544	1.306			**	0.316
3	4	1989	0.612	−1.724		***		0.304
4	5	1988	0.668	0.658			*	0.031
5	6	1987	0.719	−0.720		*		0.035
6	7	1986	0.770	1.209			**	0.119
7	8	1985	0.833	0.709			*	0.051
8	9	1984	0.925	0.192				0.004
9	10	1983	1.080	−1.426		**		0.254
10	11	1982	1.387	0.029				0.000

(Box continues)

Box 4.4 (continued)**Residuals and Associated Outlier Statistics from Weighted Regression (continued)**

Sum of residuals ^a	0
Sum of squared residuals ^a	16.1125
Predicted residual SS (Press) ^a	24.7446

^a These statistics use observation weights or frequencies.

^b Graphical representation of Student residuals.

Using weighted regression for catch-curve analysis deflates the importance of rare and older fish when computing regression coefficients by proportioning the contribution to each product and cross product by the corresponding PLNUM–age data point. Thus, residuals for older and rarer cohorts of fish such as the 1983 year-class will be less with weighted than with unweighted regression. Generally, older and rarer year-classes are less likely to be accurately represented if a small to moderate sample of fish is collected, and this weighted regression procedure is recommended. Larger samples of fish will more accurately represent all year-classes, hence residuals from unweighted catch-curves regressions can be used.

From the analysis, the 1985 and 1988 year-classes could be considered moderately strong whereas the 1986 and 1990 year-classes were relatively more abundant and represented greater year-class strength. Conversely, the 1987 and 1991 year-classes were moderately weak, and even poorer year-class formation was evident for the 1983 and 1989 year-classes. The graphic below illustrates the number at age versus year-class (not a plot from SAS). The solid line represents the least-square fit to the data using weighted regression and the dashed lines are the residuals.

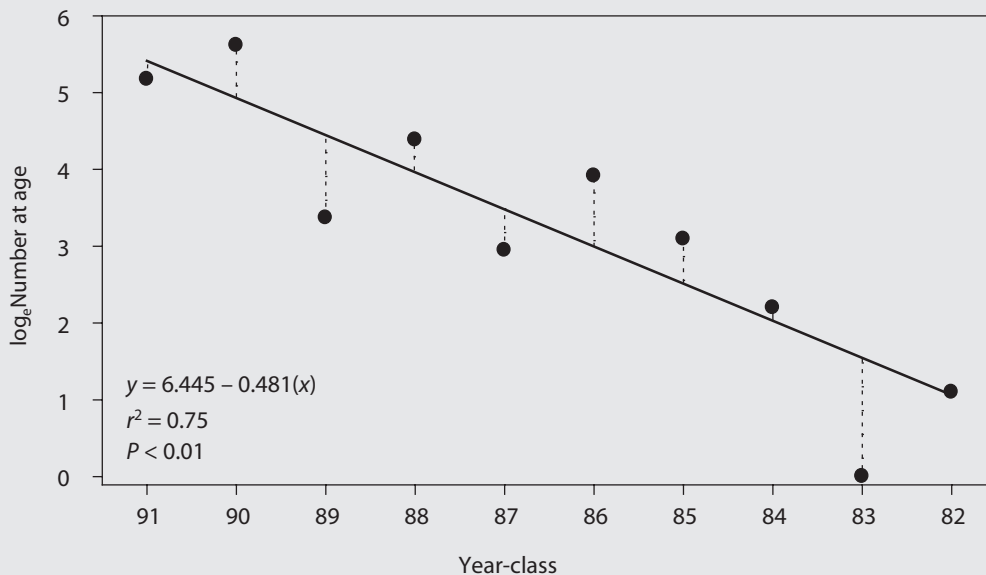


Figure The number at age versus year-class. The solid line represents the least-square fit to the data using weighted regression and the dashed lines are the residuals.

activity inhibited successful recruitment. Allen et al. (1999) found a positive correlation ($r=0.61$) between chlorophyll-*a* concentrations and density of age-0 largemouth bass. Using linear regression, Reinert et al. (1997) used a host of reservoir hydrologic variables to explain 58–99% of the variation in electrofishing catch rates of age-0 and age-1 largemouth bass and spotted bass. Serns (1982) used linear regression and found that mean water temperature from June to August explained 74% of the variation in age-0 smallmouth bass density. Maceina and Stimpert (1998) found winter (January–March) retention in reservoirs prior to spawning and post-winter (April–November) retention were negatively and positively related to, respectively, black crappie and white crappie recruitment ($R^2 = 0.62$). An example of using correlative and regression techniques to explain recruitment variation is given in Box 4.5

The collection of long-term data to document recruitment variation and relate this variation to abiotic and biotic variables is desirable for fisheries scientists attempting to explain fluctuations in recruitment. In the absence of long-term data on recruitment levels, the residuals or errors associated with catch-curve regressions can be used as an index of recruitment variability and compared to biotic and abiotic variables (Maceina 1997). Maceina (1997) expanded the use of simple linear catch-curve regression to incorporate an additional independent environmental variable(s) (ENVIR) that was measured when fish were age 0. The generalized equation is

$$\log_e \text{number} = b_0 - b_1(\text{age}) \pm b_2(\text{ENVIR}). \quad (4.2)$$

For this equation, weighted regression is used to deflate the influence of rarer and older fish in the analysis similar to the procedures in Box 4.5. This technique has been used to explain environmental factors related to variation in fish recruitment for a number of species (Maceina and Bettoli 1998; Slipke et al. 1998; DiCenzo and Duval 2002; Maceina 2003), and an example is shown in Box 4.6. In addition, residuals can be pooled among water bodies and different years of collections and examined in relation to environmental variables to explain recruitment variation (Maceina and Bettoli 1998).

In regression analysis, transforming independent and dependent variables to natural log, common log, or inverse values can improve fit, reduce heteroscedastic variances, and sometimes explain better nonlinear fit between variables. Nonlinear regression can be a useful tool to explain and show graphically, for example, that progressively higher levels of some independent variable will result in an increase (or decrease) in some measure of recruitment before eventually reaching an asymptotic level.

■ 4.4. RECRUIT–SPAWNER RELATIONSHIPS

An important component of fisheries management is to determine if a relationship exists between recruitment and spawner abundance. A quantitative understanding of the amount of recruitment that is necessary to sustain a fishery is

Box 4.5 Use of Correlation, Simple Regression, and Multiple Regression Analyses to Explain Recruitment Variation

From the data presented in Table 4.1, the relations between C/f of age-0 crappies (CPE0) and reservoir hydrologic conditions were determined. The respective year-classes (YEARCL) were also noted. The following SAS (2001) program plots bivariate relations between C/f of age-0 fish and hydrologic variables, computes the Pearson product moment correlation coefficients among age-0 catch and the reservoir hydrologic terms, and finally computes multiple regressions to describe and predict age-0 catch from these hydrologic variables.

Program

```
DATA WECRA;
INPUT YEARCL CPE0 WINSTAGE WINRET SPRSTAGE;
LINES;
1989 . 170.85 7.2 171.79
1990 8.03 171.76 4.2 171.75
(continue data input)
;
PROC PLOT; PLOT CPE0*WINSTAGE; PLOT CPE0*WINRET; PLOT CPE0*SPRSTAGE;
*/ plots not presented but should be examined by the fisheries scientist;
PROC CORR; VAR CPE0 WINSTAGE WINRET SPRSTAGE;
PROC REG; MODEL CPE0=WINSTAGE WINRET SPRSTAGE/SS1 SS2 SCORR1 PCORR2 VIF
COLLINOINT;
PROC REG; MODEL CPE0=WINSTAGE SPRSTAGE/SS1 SS2 SCORR1 PCORR2 VIF
COLLINOINT;
PROC REG; MODEL CPE0=WINSTAGE; RUN;
```

Results

Table Output for correlation analysis among C/f of age-0 crappies (CPE0) and the three hydrologic variables, mean winter stage (WINSTAGE), mean winter retention (WINRET), and mean spring stage (SPRSTAGE) (see Table 4.1). The Pearson correlation coefficient tests for $P > |R|$ under the H_0 that R (rho) = 0.

Simple Statistics						
Variable	N	Mean	SD	Sum	Minimum	Maximum
CPE0	10	3.25300	3.18380	32.53000	0.47000	9.89000
WINSTAGE	11	170.98545	0.32163	1880.84000	170.67000	171.76000
WINRET	11	6.47273	1.39075	71.20000	4.20000	9.70000
SPRSTAGE	11	171.82273	0.05781	1890.05000	171.75000	171.92000

Pearson Correlation Coefficients				
	CPE0	WINSTAGE	WINRET	SPRSTAGE
CPE0				
<i>R</i>	1.00000	0.89313	-0.56302	-0.03217
<i>P</i>	0.0	0.0005	0.0902	0.9297
<i>N</i>	10	10	10	10
WINSTAGE				
<i>R</i>	0.89313	1.00000	-0.71949	-0.29292
<i>P</i>	0.0005	0.0	0.0126	0.3820
<i>N</i>	10	11	11	11
WINRET				
<i>R</i>	-0.56302	-0.71949	1.00000	0.38038
<i>P</i>	0.0902	0.0126	0.0	0.2485
<i>N</i>	10	11	11	11
SPRSTAGE				
<i>R</i>	-0.03217	-0.29292	0.38038	1.00000
<i>P</i>	0.9297	0.3820	0.2485	0.0
<i>N</i>	10	11	11	11

Table Multiple and linear regression analyses for the dependent variable CPE0.

Analysis of Variance with Three Hydrologic Variables					
Source	<i>df</i>	SS	Mean square	<i>F</i> -value	<i>P</i> > <i>F</i>
Model	3	79.79125	26.59708	13.952	0.0041
Error	6	11.43796	1.90633		
Corrected total	9	91.22921			
<i>R</i> ²	0.8746	Root MSE	1.38070		
Adjusted <i>R</i> ²	0.8119	CPE0 mean	3.25300		
CV	42.44383				

Parameter Estimates						
Variable	<i>df</i>	Parameter estimate	SE	<i>t</i> -value	<i>P</i> > <i>t</i>	Type I SS
Intercept	1	-4237.774608	1511.6915952	-2.803	0.0310	105.820090
WINSTAGE	1	9.614666	1.95648369	4.914	0.0027	72.771053
WINRET	1	0.084910	0.47521332	0.179	0.8641	1.008889
SPRSTAGE	1	15.110553	8.50931361	1.776	0.1261	6.011308

(Box continues)

Box 4.5 (continued)

Variable	df	Type II SS	Squared semi-partial correlation	Squared partial correlation	Variance inflation
Intercept	1	14.981201		0.00000000	
WINSTAGE	1	46.037663	0.79767273	0.80099459	2.03665416
WINRET	1	0.060861	0.01105884	0.00529277	2.22235140
SPRSTAGE	1	6.011308	0.06589236	0.34450202	1.22457891

Colinearity Diagnostics (Intercept Adjusted)					
Number	Eigenvalue	Condition index	Variable proportion		
			WINSTAGE	WINRET	SPRSTAGE
1	1.99908	1.00000	0.0912	0.0913	0.0911
2	0.72319	1.66261	0.1262	0.0340	0.8576
3	0.27773	2.68288	0.7826	0.8747	0.0512

Analysis of Variance with Two Hydrologic Variables					
Source	df	SS	Mean square	F-value	P > F
Model	2	79.73039	39.86519	24.268	0.0007
Error	7	11.49882	1.64269		
Corrected total	9	91.22921			
R ²	0.8740	Root MSE	1.28167		
Adjusted R ²	0.8379	CPE0 mean	3.25300		
CV	39.39976				

Parameter Estimates						
Variable	df	Parameter estimate	SE	t-value	P > t	Type I SS
Intercept	1	-4273.240691	1391.1235060	-3.072	0.0180	105.820090
WINSTAGE	1	9.380227	1.34721346	6.963	0.0002	72.771053
SPRSTAGE	1	15.553433	7.55648750	2.058	0.0786	6.959337

Variable	df	Type II SS	Squared semi-partial correlation type I	Squared partial correlation type 2	Variance inflation
Intercept	1	15.500246		0.00000000	
WINSTAGE	1	79.635947	0.79767273	0.87382619	1.12067509
SPRSTAGE	1	6.959337	0.07628408	0.37703313	1.12067509

Colinearity Diagnostics (Intercept Adjusted)				
Number	Eigenvalue	Condition index	Variable proportion	
			WINSTAGE	SPRSTAGE
1	1.32815	1.00000	0.3359	0.3359
2	0.67185	1.40600	0.6641	0.6641

Analysis of Variance with One Hydrologic Variable					
Source	df	SS	Mean square	F-value	P > F
Model	1	72.77105	72.77105	31.540	0.0005
Error	8	18.45816	2.30727		
Corrected total	9	91.22921			
R^2	0.7977	Root MSE	1.51897		
Adjusted R^2	0.7724	CPE0 mean	3.25300		
CV	46.69443				

Variable	df	Parameter estimate	SE	t-value	P > t
Intercept	1	-1445.158045	257.90658352	-5.603	0.0005
WINSTAGE	1	8.470290	1.50823184	5.616	0.0005

Based on C/f of age-0 crappies as a recruitment index, this variable was positively correlated to winter water stage prior to spawning ($R = 0.89$; $P < 0.01$) and weakly, but negatively, correlated to corresponding winter retention ($R = -0.56$; $P = 0.09$). No relation was evident between spring stage ($R = -0.03$; $P = 0.92$) and age-0 C/f . As expected, winter stage and retention were inversely related ($R = -0.72$; $P < 0.05$).

Of the three hydrologic terms used as regressors in multiple regression analysis of C/f of age-0 crappies, winter retention was the weakest independent variable. The overall model was highly significant ($P < 0.01$), and the three hydrologic terms explained about 87% of the variation in age-0 C/f . However, diagnostics used to detect multicollinearity among independent variables showed winter stage and winter retention covaried. The condition index was elevated (2.683), and the colinearity diagnostics (variable proportion) associated with this condition index was 0.783 and 0.875 for winter stage and retention, respectively, and showed multicollinearity existed in the model. In addition, winter retention was not a significant ($P = 0.86$) regressor in the model. Hence, winter retention was dropped from subsequent analyses, and age-0 C/f was regressed against winter stage and spring stage. We decided for this example to keep spring stage in the analysis even though winter stage was obviously the most influential regressor. In this multiple regression,

(Box continues)

Box 4.5 (continued)

the partial regression coefficient for spring stage was modestly significant ($P = 0.08$) and positive, which suggested after accounting for the effects of winter stage, slightly higher water levels in spring may enhance crappie recruitment. With the use of squared partial correlation coefficients (pr^2 , squared partial correlation type II in table above), winter stage provided the greatest contribution ($pr^2 = 0.87$) to age-0 C/f compared with spring stage ($pr^2 = 0.38$). The squared semi-partial correlations (squared semi-partial correlation type I) were fitted to the independent variables in the order that they were entered into the model and showed that after first accounting for the effects of winter stage (79.8%), spring stage explained an additional 7.6% of the variance for age-0 C/f. The sum of the squared semi-partial correlations will equal the coefficient of determination for the entire model. Finally, a simple linear model was computed that regressed age-0 C/f to winter stage (see figure below; not a plot from SAS 2001).

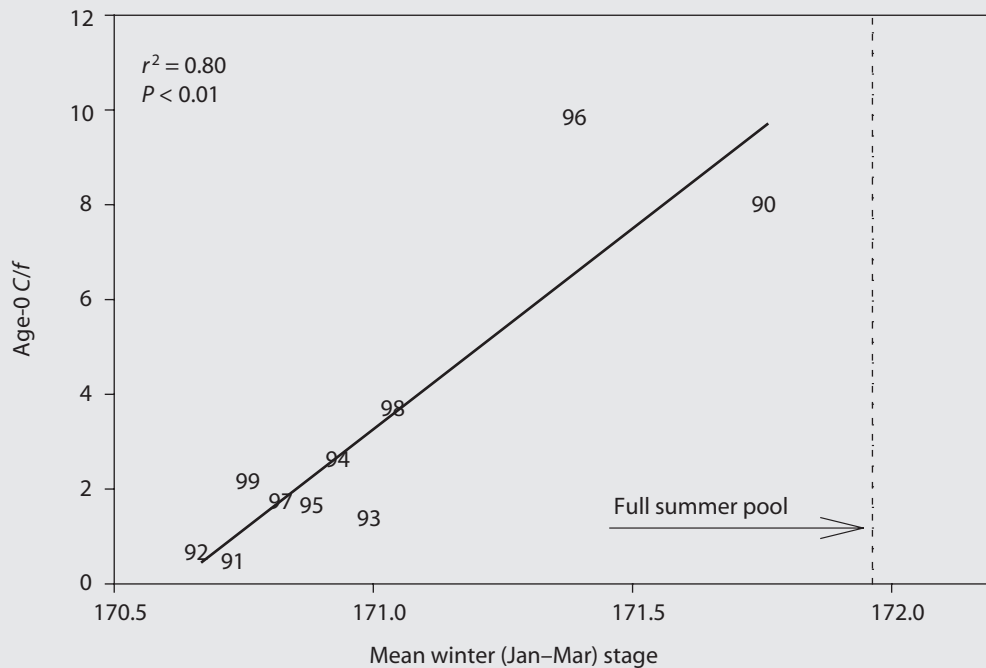


Figure Linear model of C/f of age-0 crappies versus winter stage. Numeric values along regression line refer to year-classes.

extremely useful information. Some fisheries scientists have argued that a quantifiable relation between recruits and spawners does not exist and that abiotic and biotic processes influence recruitment independently of spawner abundance (Van Den Avyle and Hayward 1999). However, Myers and Barrowman (1996) provided clear evidence for a positive relationship between recruits and spawners, though the results were more compelling for marine than for freshwater populations.

Box 4.6 Incorporation of an Environmental Term into a Catch-Curve Regression to Explain Fluctuations in Recruitment

From the data presented in the SAS program in Box 4.4 and the program below, April–July retention will first be plotted against the residuals from the weighted catch-curve regression for largemouth bass. Then, this term will be added to the simple linear catch-curve regression to compute a multiple regression. The mean retention (MEANRET) between April–July corresponds to the hatching and post-hatching time period for each year-class when fish were age 0 (Maceina et al. 1995). The variables YEARCL, AGE, NUM, and LNUM are defined in Box 4.4.

Program

```
DATA GUN_LMB;
INPUT YEARCL AGE NUM MEANRET;
LNUM=LOG(NUM + 1);
LMEANRET=LOG10(MEANRET);
LINES;
91 2 175 13.7 90 3 273 16.9 89 4 28 9.6 88 5 79 47.7
(continue data input)
;
PROC REG NOPRINT; MODEL LNUM=AGE/R; ID YEARCL AGE;
OUTPUT OUT=A P=PLNUM;
DATA B; SET A; W=PLNUM;
PROC REG NOPRINT; WEIGHT W; MODEL LNUM=AGE/R;
OUTPUT OUT=C R=RES;
PROC PLOT; PLOT RES*MEANRET/VREF=0;
PROC CORR; VAR RES MEANRET;
PROC REG; WEIGHT W; MODEL LNUM=AGE LMEANRET/SS1 SS2 PCORR2; RUN;
```

Results

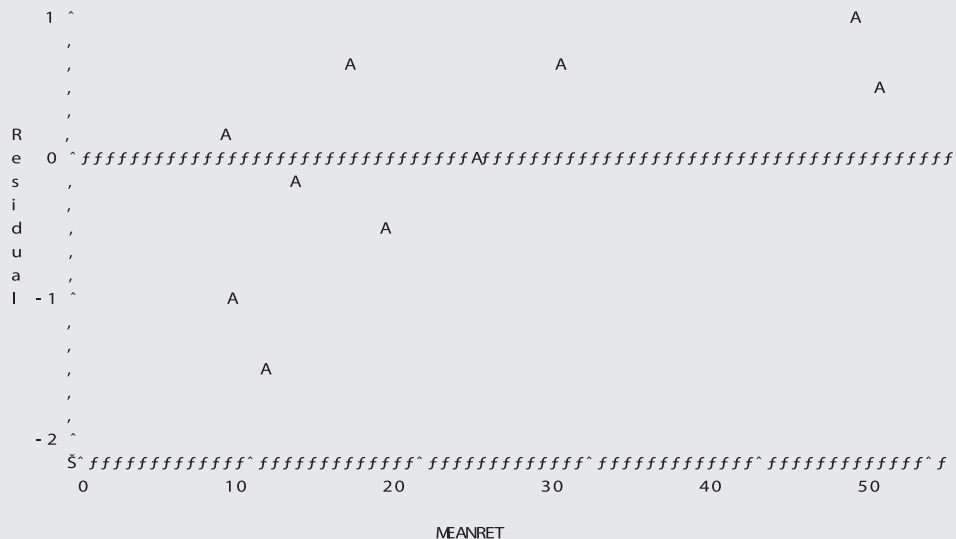


Figure Plot of residuals from the weighted catch-curve regression for largemouth bass versus mean retention, in which A represents one observation.

(Box continues)

Box 4.6 (continued)**Table** Output for correlation analysis between residuals (RES) from the weighted catch-curve regression for largemouth bass and the mean retention (MEANRET) in the reservoir between April–July.

Simple Statistics							
Variable	N	Mean	SD	Sum	Minimum	Maximum	Label
RES	10	−0.0437	0.7975	−0.4368	−1.5395	0.9310	Residual
MEANRET	10	23.1200	15.0095	231.2	9.6000	49.5000	

Pearson Correlation Coefficients		
	RES	MEANRET
RES		
<i>R</i>	1.00000	0.65716
<i>P</i>	0.0	0.0390
MEANRET		
<i>R</i>	0.65716	1.00000
<i>P</i>	0.0390	0.0

Table Multiple regression analysis for the dependent variable LNUM ($\log_e[\text{NUM} + 1]$) of largemouth bass. $\log_{10}(\text{mean retention})$ is given by LMEANRET.

Analysis of Variance					
Source	<i>df</i>	SS	Mean square	<i>F</i> -value	<i>P</i> > <i>F</i>
Model	2	55.57442	27.78721	24.197	0.0007
Error	7	8.03862	1.14837		
Corrected total	9	63.61304			
<i>R</i> ²	0.8736	Root MSE	1.07162		
Adjusted <i>R</i> ²	0.8375	LNUM mean	3.86169		
CV	27.75011				

4.4.1. Types of Recruit–Spawner Relations

Several recruit–spawner models are commonly used, and detecting density dependence, or compensation, is of primary importance in fitting these models. Recruitment in wild populations will be limited by environmental constraints at relatively high densities, and therefore the rate of recruitment (i.e., the number of recruits produced per unit of spawners) may decrease at high levels of spawner abundance. Two common curves have two coefficients with similar functions. One

Parameter Estimates					
Variable	df	Parameter estimate	SE	t-value	$P > t $
Intercept	1	3.950567	1.00022232	3.950	0.0055
AGE	1	-0.526061	0.07666302	-6.862	0.0002
LMEANRET	1	2.048881	0.77270892	2.652	0.0329

Variable	df	Type I SS	Type II SS	Squared partial correlation type II
Intercept	1	473.867469	17.914685	.
AGE	1	47.500491	54.073342	0.87057856
LMEANRET	1	8.073930	8.073930	0.50109573

The SAS plot of residuals of the weighted catch-curve regression against April–July retention (MEANRET) showed higher retention was associated with progressively higher residuals, or stronger year-class formation for largemouth bass, whereas lower retention (<15 d) was associated with lower recruitment for those year-classes, and the relation was not linear. The significant correlation ($R = 0.66$; $P < 0.05$) was computed between catch-curve residuals and April–July retention, and thus the variation about the catch-curve plot in Box 4.4 was related to this hydro-logic term. The plot of catch-curve residuals against April–July appeared nonlinear, hence retention was transformed to \log_{10} values and the multiple regression equation computed. The addition of the retention term explained an additional 13% of the variation in the catch-curve above that explained by the simple catch-curve regression (Box 4.4). Based on the squared partial correlation coefficient ($pr^2 = 0.50$), retention was an important variable in explaining the variation in number at age beyond that explained by age alone (see Maceina and Bettoli 1998 for further analysis).

coefficient (α) represents density-independent recruitment and is often referred to as the productivity coefficient. This is the rate of recruitment in the absence of any environmental constraints, and represents the slope of the stock–recruitment curve at the origin. The second coefficient (β) arises from density-dependent processes. At relatively high spawning stock levels various ecological processes (e.g., rate of predation or habitat or food limitations) will result in compensation in the survival of recruits, and recruitment rate will decline with an increase in spawner abundance.

4.4.1.1 Beverton–Holt Recruit–Spawner Curve

The recruitment curve developed by Beverton and Holt (1957) assumes that competition among early life stages for any limited resource (e.g., food or space) will cause recruits (R) to increase initially, then to decline to an asymptotic value as spawner abundance (S) increases (Figure 4.1). One form of the Beverton–Holt curve is

$$R = \frac{\alpha S}{1 + \beta S}, \quad (4.3)$$

where α is the productivity or density-independent coefficient and is the maximum recruitment rate (R/S) at low spawner abundance (i.e., the initial slope), and β determines the level of density dependence. Maximum recruitment represented by the asymptote is equal to α/β . An example of estimating a Beverton–Holt recruit–spawner curve is given in Box 4.7.

4.4.1.2 Ricker Recruit–Spawner Curve

In some fish populations, the recruit–spawner relation may be dome shaped, with the number of recruits declining at higher levels of spawner abundance due to overcompensation (Ricker 1954). Overcompensation may arise from such obvious processes as cannibalism but more importantly can be induced by predation

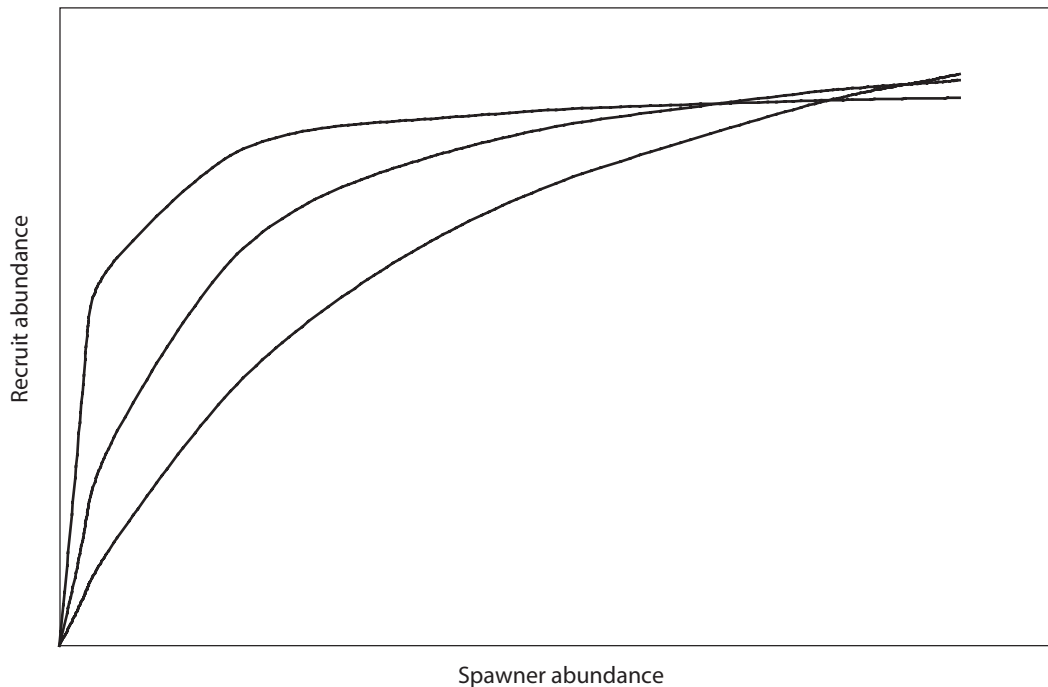


Figure 4.1 Beverton–Holt recruit–spawner curves computed from equation (4.3). The three curves show different productivity coefficients (α) but approximately the same maximum level of density dependence (β), showed by the asymptote.

Box 4.7 Computation of the Beverton–Holt Recruit-Spawner Curve

From 1991 to 1996, crappies were collected from three Alabama reservoirs (LAKE) that displayed similar hydrologic conditions (data from Ozen 1997); 16 to 20 trap nets were used as described in Box 4.1. Fish were collected in the fall of each year, aged, and weighed (1 g). The variable SPAWNER was determined by dividing total weight of all age-2 and older crappies (assumed to be adults) by the number of net-nights of effort and RECRUIT was determined by dividing the total number of age-0 crappies by the number of net-nights of effort. The program below plots the relation between recruits and spawners, then describes the relations between recruits and spawners using nonlinear regression for untransformed and \log_e transformed data (equations [4.3] and [4.5], respectively). From the last nonlinear regression, predicted recruits (PRE_LREC) was regressed against observed recruits to provide additional statistical inference. The predicted number of recruits and associated residuals from the last nonlinear regression were derived and printed. In the nonlinear procedure in SAS (PROC NLIN), the parameters (PARMS) statement refers to approximate coefficients for α (A in SAS) and β (B in SAS) in the nonlinear regression that are provided by the fisheries scientist to initiate the analysis. Hougaard's skewness values for α and β were computed for each nonlinear regression. Finally, residual values from the last nonlinear regression were summed.

Program

```
DATA REC_SPA;
INPUT LAKE $ YEAR SPAWNER RECRUIT @@;
/* SPAWNER = INDEX OF ADULT BIOMASS OF AGE-2 AND OLDER CRAPPIE;
*/RECRUIT = TRAP NET CATCH RATE OF AGE-0 CRAPPIE;
LRECRUIT=LOG(RECRUIT);
LINES;
AL 91 340 5.41 AL 92 907 3.00 AL 93 171 2.41 AL 94 1040 2.25
AL 95 55 0.41 AL 96 524 8.71
DE 92 213 1.13 DE 93 1034 4.66 DE 94 457 1.94 DE 95 200 7.28
DE 96 669 10.56
JB 90 372 9.33 JB 91 386 2.19 JB 92 585 6.75 JB 93 660 13.85
JB 94 337 3.58 JB 95 396 3.48 JB 96 620 23.70
;
PROC PLOT; PLOT RECRUIT*SPAWNER; /* plot not shown;
PROC NLIN HOUGAARD; PARMS A=0.03 B=0.002;
MODEL RECRUIT=(A*SPAWNER)/(1 + B*SPAWNER);
PROC NLIN HOUGAARD; PARMS A=0.01 B=0.002;
MODEL LRECRUIT=LOG((A*SPAWNER)/(1 + B*SPAWNER));
OUTPUT OUT=A P=PRE_LREC R=RES;
PROC REG; MODEL PRE_LREC=LRECRUIT;
DATA B; SET A;
PRE_REC=EXP(PRE_LREC);
PROC PRINT; VAR LAKE YEAR RECRUIT SPAWNER PRE_LREC RES;
PROC MEANS NOPRINT; VAR RES;
OUTPUT OUT=B SUM=SUMRES;
PROC PRINT; VAR SUMRES; RUN;
```

(Box continues)

Box 4.7 (continued)**Results**

Table Nonlinear regression (NLIN) of RECRUIT (total number of age-0 crappies divided by number of net-nights of effort) versus SPAWNER (total weight of age-2 and older crappies divided by number of net-nights of effort). In the estimation summary, R , PPC(B), and RPC(B) are measures and diagnostics of the degree of convergence of the model; smaller values represent better model fit. An intercept was not specified for this model.

Iterative Phase					
Iteration	A	B	SS		
0	0.0300	0.00200	502.9		
1	0.0418	0.00388	486.2		
.					
.					
17	0.0386	0.00369	484.5		
18	0.0386	0.00369	484.5		

Estimation Summary	
Method	Gauss-Newton
Iterations	18
R	9.328×10^{-6}
PPC(B)	0.000068
RPC(B)	0.000103
Object	6.74×10^{-11}
Objective	484.4791
Observations read	18
Observations used	18
Observations missing	0

Analysis of Variance					
Source	df	SS	Mean square	F -value	Approximate $P > F$
Regression	2	747.8	373.9	12.35	0.0006
Residual	16	484.5	30.2799		
Uncorrected total	18	1232.3			
Corrected total	17	552.2			

Parameter Estimates					
Parameter	Estimate	Approximate SE	Approximate 95% confidence limits		Hougaard's skewness
A	0.0386	0.0474	-0.0619	0.1391	5.6771
B	0.00369	0.00675	-0.0106	0.0180	6.1140

Approximate Correlation Matrix		
	A	B
A	1.0000000	0.9864924
B	0.9864924	1.0000000

Table Nonlinear regression of \log_e RECRUIT (LRECRUIT) versus SPAWNER, with right side of equation (4.5) transformed using a natural log. This is followed by a linear regression between predicted (PRE_LREC) and observed recruits. Nonlinear regression model details as above.

Iterative Phase			
Iteration	A	B	SS
0	0.0100	0.00200	18.3365
1	0.0147	0.00110	10.2141
.			
.			
9	0.0170	0.00142	10.1303
10	0.0170	0.00142	10.1303

Analysis of Variance					
Source	df	SS	Mean square	F-value	Approximate P > F
Regression	2	42.5153	21.2576	9.38	0.0074
Residual	16	10.1303	0.6331		
Uncorrected total	18	52.6455			
Corrected total	17	16.0679			

Parameter Estimates					
Parameter	Estimate	Approximate SE	Approximate 95% confidence limits		Hougaard's skewness
A	0.0170	0.00934	-0.00282	0.0368	2.6078
B	0.00142	0.00192	-0.00264	0.00549	2.9081

Linear Regression of Predicted versus Observed Recruits					
Source	df	SS	Mean square	F-value	P > F
Model	1	1.66803	1.66803	9.71	0.0067
Error	16	2.74841	0.17178		
Corrected total	17	4.41644			
R ²	0.3777	Root MSE	0.41446		
Adjusted R ²	0.3388	PRE_LREC mean	1.42551		
CV	29.07430				

(Box continues)

Box 4.7 (continued)**Table** Predicted number of recruits (PRE_LREC) and associated residuals (RES) and the sum of the residuals (SUMRES). Also given are the variables SPAWNER, RECRUIT, LAKE (from Ozen 1997), and YEARCL.

Observation and sum	LAKE	YEARCL	RECRUIT	SPAWNER	PRE_LREC	RES
1	AL	1991	5.41	340	3.89039	0.32974
2	AL	1992	3.00	907	6.72230	-0.80682
3	AL	1993	2.41	171	2.33517	0.03154
4	AL	1994	2.25	1040	7.11974	-1.15194
5	AL	1995	0.41	55	0.86608	-0.74782
6	AL	1996	8.71	524	5.09635	0.53595
7	DE	1992	1.13	213	2.77528	-0.89854
8	DE	1993	4.66	1034	7.10312	-0.42152
9	DE	1994	1.94	457	4.70153	-0.88520
10	DE	1995	7.28	200	2.64343	1.01305
11	DE	1996	10.56	669	5.81874	0.59599
12	JB	1990	9.33	372	4.12979	0.81501
13	JB	1991	2.19	386	4.23010	-0.65832
14	JB	1992	6.75	585	5.42008	0.21943
15	JB	1993	13.85	660	5.77837	0.87416
16	JB	1994	3.58	337	3.86719	-0.07717
17	JB	1995	3.48	396	4.30019	-0.21163
18	JB	1996	23.70	620	5.59234	1.44408
SUMRES						-2.02×10^{-9}

Interpretation

For 18 iterations, an optimal solution (convergence criteria met) was found that minimized the residual error for this recruit-spawner data. The analysis indicated that the nonlinear regression was highly significant ($F = 12.35$; $df = 2, 16$; $P < 0.01$), but this test is highly suspect (see section 4.4.3). The nonlinear regression procedure in SAS (2001) does not compute a coefficient of determination, but this can be approximated by subtracting the residual SS from the corrected total SS and then dividing this by the corrected SS. For this example, $r^2 = (552.2 - 484.5)/552.2 = 0.12$. The spawner abundance did not explain a high proportion in variation in crappie recruits, although statistically significant. The coefficients for α (0.0386) and β (0.00369) are given along with approximate SEs and 95% confidence limits for these coefficients. Thus from equation (4.3),

$$R = 0.0386 \times S / (1 + 0.00369 \times S) .$$

Hougaard's skewness values for α and β were 5.7 and 6.1, respectively, which were high and indicated these parameters were not normally distributed and were potentially biased. Thus, the equation may be inaccurate. Finally a correlation matrix was presented that estimates the relation between α and β ; correlations typically will also be high as these coefficients will covary when the least-squares solution is computed through iteration.

The second model includes lognormal error structure by taking the natural logarithms of both sides of the nonlinear Beverton–Holt recruit–spawner equation. An optimal solution was found (convergence criteria met), and the output suggested that the regression was significant ($P < 0.01$). The approximate r^2 value was 0.37 ($[16.07 - 10.13]/16.07$). Next, the coefficients are given for α (0.0170) and β (0.00142) with approximate SEs and confidence intervals. Hougaard's skewness values were still high for α and β (2.6 and 2.9) but lower than those computed for normal error structure. The next analysis presents the linear regression between predicted and observed recruits (\log_e transformed). The F -statistic (9.71) and r^2 value (0.38) were very similar to those derived from the previous nonlinear regression.

The last table contains a print of predicted crappie recruits (PRE_LREC) and residuals (RES) for a given level of crappie spawners computed from the last nonlinear regression equation. Observed and predicted recruits and spawners can be used to construct a bivariate plot, and the nonlinear regression line (not a plot from SAS) of the relation between crappie recruits and spawners is shown below. The sum of the residuals (SUMRES) was approximately 0, which suggested an optimal least-squares fit to the data.

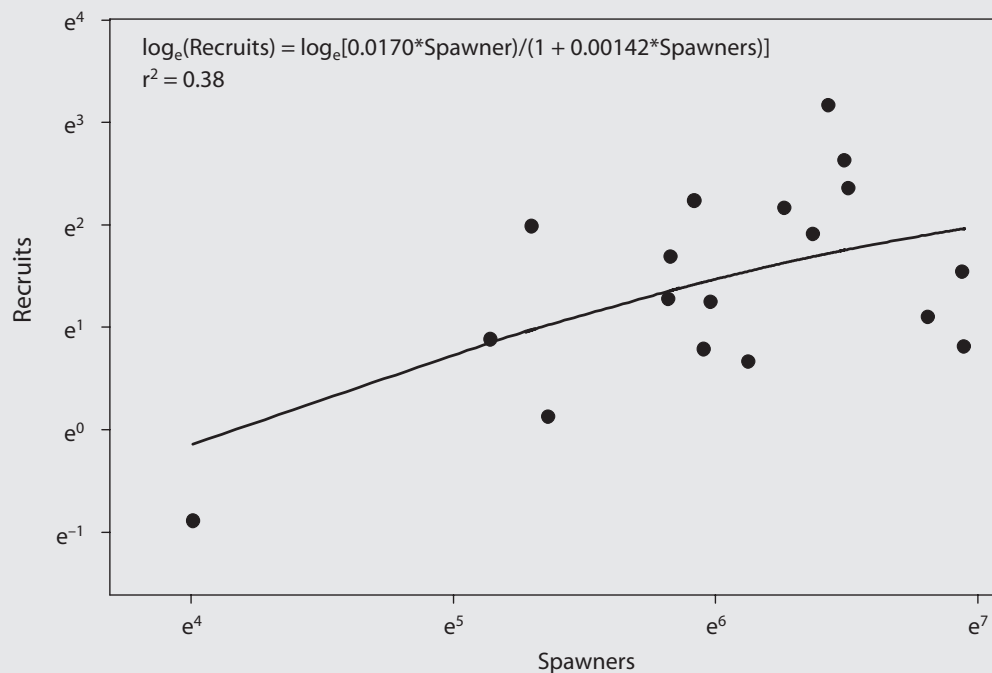


Figure Plot of the raw data (\log_e scale) and the nonlinear regression of the relation between crappie recruits and spawners.

on prerecruits, including predation by other species. Specifically, if a predator responds to increased prey (i.e., the potential recruits in our stock–recruit relationship) either by increasing its own abundance or predatory effectiveness, then overcompensation may occur. Thus, while cannibalism may be an attractive explanation for overcompensation, predation by a variety of species may also result in a domed recruit–spawner curve. Ricker (1954) also suggested that overcompensation may be a prevalent condition in lake ecosystems that are more confining and potentially habitat limited in comparison to large marine systems. Hilborn and Walters (1992) reported that overcompensation will also arise when growth of young fish is density dependent and predation is size dependent. Therefore, fisheries scientists should examine their data for a dome shaped recruitment curve even for species that are not expected to be cannibalistic. In semelparous salmon species, overcompensation may arise from superpositioning of spawning redds and disease outbreaks affecting egg mortality at high spawner densities (Ricker 1954).

The Ricker curve is defined by

$$R = Se^{\alpha - \beta S}, \quad (4.4)$$

where α is the density-independent or productivity coefficient, representing the rate of recruitment at low spawner abundance (i.e., the slope at the origin), and β is the density-dependent coefficient, with the curve reaching a maximum at β^{-1} units of spawners before declining (Figure 4.2). An example of computing a Ricker recruit–spawner curve is given in Box 4.8.

4.4.1.3 *Additional Recruit–Spawner Curves*

Fisheries scientists may attempt to construct an alternative recruit–spawner curve that differs from the Beverton–Holt and Ricker forms. Alternate curves may integrate other processes that affect the early life history of a species. The Beverton–Holt and Ricker recruit–spawner curves typically will accommodate most of these conditions. However, a variety of other mathematical models for describing these relationships can be found in Cushing (1971, 1973), Deriso (1980), and Shepherd (1982), with further elaboration by Schnute (1985), and Reish et al. (1985).

4.4.2 **Estimation of Recruit–Spawner Coefficients**

There are several methods available to fisheries scientists for fitting models to recruit–spawner data, and these include both linear and nonlinear regression procedures. Extreme data points, especially those associated with abnormally high number of recruits, will influence the curve, and thus robust-fitting algorithms may also be appropriate. An important initial consideration in fitting recruit–spawner curves is the error distribution for the model. Many parameter estimation methods have the common assumption that the model residuals are normally distributed, but Peterman (1981) showed that models with lognormal errors were more appropriate to recruit–spawner data. Two common observations of recruit–spawner data are that (1) distributions are skewed to the left and display a

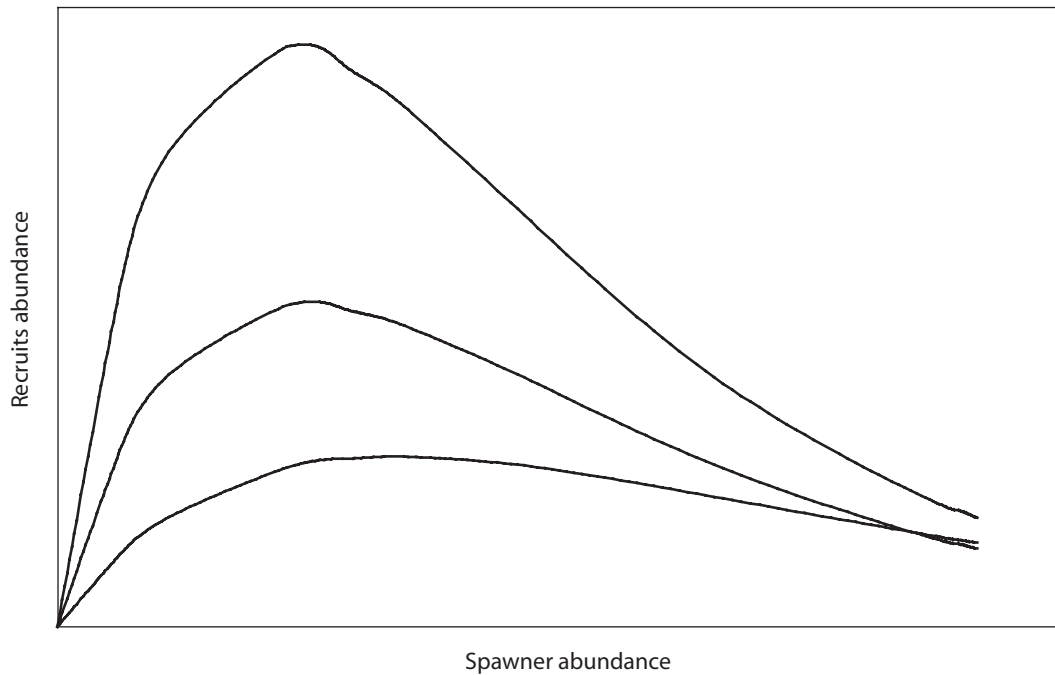


Figure 4.2 Ricker recruit–spawner curves computed using equation (4.4). The three curves have different values for the density-independent coefficient (α) but display approximately the same values for the density-dependent coefficient (β). This results in variation in the maximum recruitment, but the maximum occurs at approximately the same abundance of spawners.

long right tail, and (2) the amount of variation will be proportional to the average recruitment expected at a given spawner abundance, and recruitment will appear more variable at high spawner abundance when compared with low abundance. Thus, lognormal errors typically are apparent, and data transformation is usually necessary.

Nonlinear regression algorithms can be used to fit the Beverton–Holt (equation [4.3]) and Ricker (equation [4.4]) models that will provide for lognormal errors by taking the logarithm of both sides of these equations. Expressed in this manner, the Beverton–Holt (equation [4.5]) and Ricker (equation [4.6]) models are

$$\log_e(R) = \log_e[\alpha S / (1 + \beta S)], \quad (4.5)$$

and

$$\log_e(R) = \log_e(S^{\alpha - \beta S}). \quad (4.6)$$

These equations can be fitted using nonlinear procedures in SAS (2001; see Boxes 4.7 and 4.8). Equation (4.6) can also be expressed in a linear form as

$$\log_e(R/S) = \alpha - \beta S, \quad (4.7)$$

Box 4.8 Computation of Ricker Recruit–Spawner Curves with the Inclusion of an Environmental Term to Explain Recruit Variation

Population estimates for age-5 and older adult walleye (SPAWNER) and age-0 walleye (RECRUIT) were made in Escanaba Lake, Wisconsin, from 1958 to 1991 (data presented in Hansen et al. 1998; see Table 4.3). The following SAS (2001) program computes a nonlinear regression to describe the relation between recruits and spawners assuming lognormal error structure (equation [4.6]). From this regression, predicted recruits are regressed against observed recruits to provide additional statistical inference. Next the program computes the Ricker recruit–spawner relation (equation [4.7]) using linear regression. The corrected coefficient of determination and associated *F*-statistic was given by regressing predicted recruits against observed recruits. Finally, the program also computes the nonlinear regression with lognormal error structure in the recruit–spawner relation to include the variation in May air temperature (MTEMPCV) as an additional regressor of walleye recruits (equation [4.9] modified to include lognormal error structure).

Program

```
DATA WALLEYE;
  INPUT YEAR RECRUIT SPAWNER MTEMPCV;
  /*AGE0 AND AGE5 IS THE NUMBER OF WALLEYE IN ESCANABA LAKE, WI;
  /* MAYTEMP IS THE CV FOR MAY AIR TEMPERATURES;
  RATIO=RECRUIT/SPAWNER;
  LRATIO=LOG(RATIO);
  LRECRUIT=LOG(RECRUIT);
  LINES;
  1958      4532      775      0.24125
  1959      22996     2310     0.16319
  .
  .
  .
  1990      35607     735      0.19356
  1991      4876      1261     0.32032
  ;
  PROC NLIN DATA=WALLEYE HOUGAARD; PARS A=4 B=0;
  MODEL LRECRUIT=LOG(SPAWNER*EXP(A + B*SPAWNER));
  OUTPUT OUT=A P=PRE;
  PROC REG; MODEL PRE=LRECRUIT;
  PROC REG DATA=WALLEYE; MODEL LRATIO=SPAWNER;
  OUTPUT OUT=B P=P R=RESIDUAL;
  DATA C; SET B;
  PRATIO= EXP(P);
  PRECRUIT=PRATIO*SPAWNER;
  LPREC=LOG(PRECRUIT);
  PROC REG; MODEL LPREC=LRECRUIT;
  PROC NLIN DATA=WALLEYE HOUGAARD; PARS A=4 B=0 C=-7.0;
  MODEL LRECRUIT=LOG(SPAWNER*EXP(A + B*SPAWNER + C*MTEMPCV));
  RUN;
```

Results

Table Ricker recruit–spawner curve using nonlinear regression and accounting for lognormal error structure. The Gauss-Newton method is employed and convergence criterion was met.

Iterative Phase					
Iteration	A	B	SS		
0	4.0000	0	194.0		
1	3.3916	−0.00118	33.7931		

Analysis of Variance					
Source	df	SS	Mean square	F-value	Approximate P > F
Regression	2	2724.0	1362.0	2.13	0.1540
Residual	32	33.7931	1.0560		
Uncorrected total	34	2757.8			
Corrected total	33	36.0449			

Parameter Estimates					
Parameter	Estimate	Approximate SE	Approximate 95% confidence limits		Hougaard's skewness
A	3.3916	0.4118	2.5529	4.2303	-771×10^{-20}
B	−0.00118	0.000302	−0.00179	−0.00056	-292×10^{-19}

Table Linear regression between predicted \log_e RECRUIT (PRE; from the previous nonlinear regression) and observed recruits (\log_e transformed).

Analysis of Variance					
Source	df	SS	Mean square	F-value	P > F
Model	1	0.15590	0.15590	2.14	0.1534
Error	32	2.33335	0.07292		
Corrected total	33	2.48925			
R^2	0.0626	Root MSE	0.27003		
Adjusted R^2	0.0333	PRE mean	8.94712		
CV	3.01809				

(Box continues)

Box 4.8 (continued)**Table** Linear regression between $\log_e(\text{RECRUIT}/\text{SPAWNER})$ (LRATIO) versus SPAWNER and linear regression between re-predicted (LPREC) and observed recruits.

Analysis of Variance of LRATIO versus SPAWNER					
Source	df	SS	Mean square	F-value	P > F
Model	1	16.04272	16.04272	15.19	0.0005
Error	32	33.79315	1.05604		
Corrected total	33	49.83587			
R^2	0.3219	Root MSE	1.02764		
Adjusted R^2	0.3007	LRATIO mean	1.94113		
CV	52.93998				

Parameter Estimates					
Variable	df	Parameter estimate	SE	t-value	P > t
Intercept	1	3.39157	0.41176	8.24	<0.0001
SPAWNER	1	-0.00118	0.00030179	-3.90	0.0005

Analysis of Variance of LPREC versus Observed Recruits					
Source	df	SS	Mean square	F-value	P > F
Model	1	0.15590	0.15590	2.14	0.1534
Error	32	2.33335	0.07292		
Corrected total	33	2.48925			
R^2	0.0626	Root MSE	0.27003		
Adjusted R^2	0.0333	LPREC mean	8.94712		
CV	3.01809				

Table Ricker recruit-spawner curve from nonlinear regression using lognormal error structure and including the variation in May air temperature as an environmental predictor (coefficient C) of recruitment variation (LRECRUIT). The Gauss-Newton method is employed and convergence criterion was met.

Iterative Phase				
Iter	A	B	C	SS
0	4.0000	0	-7.0000	32.5687
1	4.7915	-0.00073	-7.8388	21.9990

Analysis of Variance					
Source	df	SS	Mean square	F-value	P > F
Regression	3	2735.8	911.9	9.90	0.0005
Residual	31	21.9990	0.7096		
Uncorrected total	34	2757.8			
Corrected total	33	36.0449			

Parameter Estimates					
Parameter	Estimate	Approximate SE	Approximate 95% confidence limits		Hougaard's skewness
A	4.7915	0.4815	3.8095	5.7736	2.23×10^{-16}
B	-0.00073	0.000271	-0.00128	-0.00018	1.06×10^{-16}
C	-7.8388	1.9228	-11.7604	-3.9173	-485×10^{-19}

Interpretation

The nonlinear regression for the Ricker recruit-spawner relation assuming lognormal error structure converged quickly to find an optimal least-squares fit to the data. However, based on this nonlinear regression and the linear regression between predicted and observed recruits, the relation was not significant ($F = 2.13 - 2.14$; $P = 0.15$), and spawners only explained about 6% of the variation in recruits. The confidence intervals for α and β were positive and negative, respectively, and did not overlap with 0, which suggested that adult walleye abundance explained only a small percentage of the total variation in walleye recruits. Hougaard's skewness values approximated 0 and showed the parameter coefficients were normally distributed and potentially not biased. Walleye recruitment in Escanaba Lake was weakly explained as

$$\log_e R = \log_e (Se^{3.392 - 0.00188S}).$$

Similar to the Beverton-Holt recruit-spawner relation, α and β were just approximated in the PARMS statement, and SAS (2001) estimates the optimal solution for these two coefficients.

For the liner regression method (equation [4.7]) between the \log_e of the ratio of recruit to spawner (LRATIO) against spawner, identical values for α (3.3916) and β (-0.00118) were derived by this method as compared with the nonlinear regression, but the computed coefficient of determination and F-statistic were much higher. Note that the errors, or residual SS, were identical (33.79) for both the linear and nonlinear regression, but the corrected total SS varied. However, the linear regression of predicted versus observed recruits for the linear method (equation [4.7]) computed nearly an identical coefficient of determination (0.06) and F-statistic ($F = 2.14$) to that derived in the previous analysis using nonlinear regression.

(Box continues)

Box 4.8 (continued)

Finally, the variation in May air temperature (MTEMP) that occurred during walleye hatch in Escanaba Lake was obviously a highly significant regressor of recruits when included in the recruit-spawner curve and improved the approximate coefficient of determination from 0.062 to 0.390. The equation was

$$\log_e R = \log_e [Se^{4.792 - 0.007305 - 7.839(MTEMP)}].$$

The slope coefficient for the variation in May air temperature was negative and indicated that greater fluctuations in air temperatures in May was related to reduced production of walleye recruits. Hougard's skewness values approximated 0 and indicated the three parameters included in the nonlinear regression were normally distributed. Inclusion of additional regressors can be tested using full and reduced model techniques presented in Montgomery and Peck (1982), which test for the reduction in the residual SS or error in the full model. Fisheries scientists should be cautious and conservative when adding additional predictors to stock-recruitment models. A plot (not a SAS 2001 plot) of the recruit-spawner relation and the nonlinear regressions for normal and lognormal error structure is presented below for walleye from Lake Escanaba.

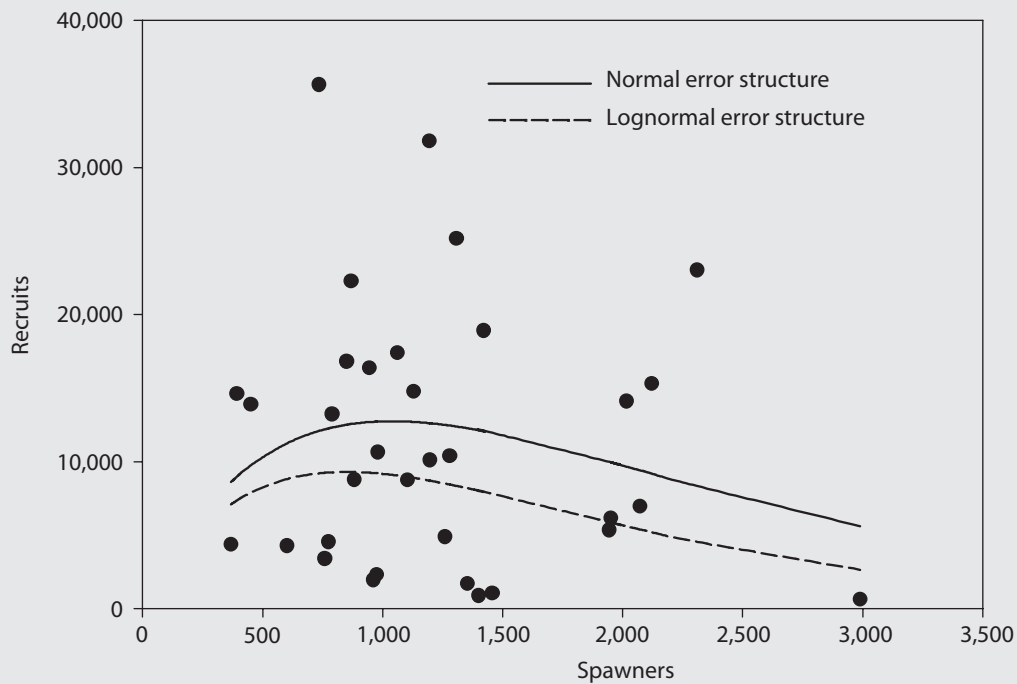


Figure Recruit-spawner relation and the nonlinear regressions for normal and lognormal error structure is presented below for walleye from Lake Escanaba, Wisconsin.

which retains the lognormal equation structure contained in equation (4.6) (see Box 4.8). Thus, the intercept will provide an estimate of productivity parameter, α , with the density-dependent term, β , estimated by the slope of equation (4.7). Equations (4.6) and (4.7) provide identical estimates of α and β (see Box 4.8), but statistical properties and associated inferences usually vary between these two equations (see section 4.4.3).

4.4.3 Statistical Properties and Inferences Associated with Recruit–Spawner Models

Recruit–spawner models can be computed using nonlinear regression techniques, but some of the properties that exist for linear regression do not apply for nonlinear least-squares estimates (Neter et al. 1996). For nonlinear regression, the sum of the residuals may not equal 0 and nonlinear models have no intercept, hence the corrected sum of squares (SS) may have no meaning (Freund and Littell 1991). The error or residual SS and the regression SS may not necessarily sum to the total SS for nonlinear models (Neter et al. 1996). Thus, the computation of the coefficient of determination and associated mean squares used in F -tests will likely be incorrect. Finally, the linear method (equation [4.7]) to estimate coefficients of α and β for the Ricker recruit–spawner model has spawner abundance on both sides of the equation, and a spurious test for β (density-dependent term) will typically arise. The error or residual SS are identical when computing the nonlinear (equation [4.6]) and linear (equation [4.7]) equations, but the model and total SS vary. Thus, coefficient of determination and corresponding F -statistic computed from the mean squares will typically be different between nonlinear and linear computations.

In our review of published papers, most fisheries scientists report the coefficient of determination and sometimes the probabilities associated with F -statistics for recruit–spawner relations. We recommend fisheries scientists use caution and careful evaluation when making statistical inferences pertaining to recruit–spawner relations. To assist fisheries scientists in interpreting the statistical strength of the recruit–spawner relations and other nonlinear regressions, we recommend the following procedures be used. Some of these were recommended by Neter et al. (1996).

1. Although not statistical, a plot of the normal and lognormal error structure of the recruit–spawner relation should always be conducted to help interpret the shape (Ricker, Beverton–Holt, or other) and relative fit or strength of the relation.
2. For nonlinear regression, the closer the sum of the residuals is to 0, the more likely a better fit to the model has occurred (see Box 4.7).
3. For most computational programs such as SAS (2001), numerous iterations are conducted that minimize the residual SS to produce a least-square fit to the data,

hence producing the “optimal” model and associated parameters coefficients. If the number of iterations to solve the equation is high (>10 – 20), then the results may be suspect. In SAS, users are required to provide an initial estimate of the specified regression coefficients, such as α and β for the Beverton–Holt and Ricker recruit–spawner relations (see Boxes 4.7 and 4.8). If the number of iterations is high, then the fisheries scientist can adjust the initial estimate of the regression coefficients to reduce the number of iterations required to obtain the optimal least-squares fit.

4. Hougaard (1985) presented a method to measure the skewness of each of the parameter coefficients generated from nonlinear regression. Coefficient estimates that are more normally distributed, hence are less biased, display absolute skewness values close to 0 (see Boxes 4.7 and Box 4.8).
5. Bootstrap parameter estimation can provide a method to examine if the estimates of the parameter coefficients are approximately normal and whether the bias in each of the parameter coefficients is relatively small (see section 4.4.5 and Box 4.9).
6. Fisheries scientists can predict the number of recruits from nonlinear regression (normal or lognormal error structure) and regress this value against the observed number of recruits (see Boxes 4.7 and 4.8). The coefficient of determination and associated F -statistic to test that a recruit–spawner relation exists using this method can provide more accurate and correct statistical inference information. In some instances, both the nonlinear and the linear regression between predicted and observed recruits will compute nearly identical coefficients of determination and F -statistics, and conducting both analyses can provide a level of confidence to the statistical properties of the recruit–spawner relation. The degrees of freedom for the linear model associated with the predicted versus observed recruits is equal to 1 (spawners are the only independent variable), which is correct, compared with 2 df for the Beverton–Holt and Ricker recruit–spawner models, where the α and β coefficients are generated for nonlinear regression.
7. For equation (4.7), the linear regression between predicted and observed recruits will compute a nearly identical coefficient of determination and F -statistic as equation (4.6) for the lognormal error structure for the Ricker recruit–spawner relation (see Box 4.8). Slight differences are due to computational differences between linear and nonlinear methods. If equation (4.7) is used to estimate a and b , then the linear regression of predicted versus observed recruits is recommended to make statistical inferences.

4.4.4 Incorporation of Environmental Terms to Explain Additional Variation in Recruit–Spawner Models

A broad suite of both abiotic and biotic factors such as climate and prey abundance may explain recruitment variation above that explained by spawners. Additional explanatory variables can easily be added to the traditional recruit–spawner models. The Beverton–Holt model (equation [4.3]) can be modified as

$$R = \frac{\alpha S}{1 + \beta S} (e^{c_1 x_1 + \dots + c_n x_n}), \quad (4.8)$$

where x_1 to x_n are n additional independent variables, and c_1 to c_n are the respective estimated coefficients. Hilborn and Walters (1992) suggested expressing the x -values as deviations from a mean value. A similar modification can be applied to the Ricker model for equation (4.4) as

$$R = S e^{\alpha - \beta S + c_1 x_1 + \dots + c_n x_n}, \quad (4.9)$$

where the additional terms are defined as in equation (4.8). An example of adding an environmental term to a Ricker recruit-spawner curve with lognormal error structure is shown in Box 4.8.

The addition of external variables to recruit-spawner models has been extensively debated and should be used with caution (Walters and Collie 1988). Robust analysis of environmental factors should include testing the integrity of any relations over a relatively long period of time. Myers (1998) reanalyzed a large number of previous studies of recruitment-environmental correlates and found that few relations persisted over time. Tyler (1992) argued in support of research on environmental factors while acknowledging the criticisms of such work and specifically cautioned against “data dredging,” whereby a fisheries scientist assembles an extensive list of environmental factors and tests for correlation with a recruitment time series. This analytical approach can be highly vulnerable to spurious correlation that may arise simply at random or may be due to the selection of an improper error rate for hypothesis testing. Tyler (1992) suggested that data suitable for correlative studies should include several time periods of both increasing and decreasing trends in recruitment. An iterative, operational approach that combines mechanistic simulation with additional analyses from natural experiments will help reject some of the alternate hypotheses developed from the conceptual phase of the study. Finally, we urge caution in the interpretation of statistical output based on either linear or nonlinear methods when environmental variables are added to recruit-spawner models (see section 4.4.3).

4.4.5 Estimates of Uncertainty in Recruit-Spawner Curves

To obtain reliable estimates of uncertainty for recruit-spawner coefficients is difficult for a variety of reasons (Hilborn and Walters 1992). One problem with recruit-spawner data is that model errors are often autocorrelated and thus result in time series bias of parameter estimates. Thus, the assumption of independent errors that is necessary for standard parametric statistical inference is violated. Equations (4.5) and (4.6) provide relatively reliable estimates of the recruit-spawner model parameters, as these equations incorporate lognormal errors (Hilborn and Walters 1992).

Hilborn and Walters (1992) recommended jack-knife and bootstrap methods for producing reliable confidence intervals about recruit-spawner coefficients.

Although the bootstrap method is computationally more intensive than is the jack-knife method, the former will provide frequency distributions of parameter estimates, and reasonable confidence intervals can be extracted even when the distribution is asymmetrical. The bootstrap involves resampling with replacement either the original data pairs or residuals from the model fit. For regression models, Efron and Tibshirani (1998) recommend bootstrapping residuals due to strong assumptions that must be made regarding linear models when bootstrapping data pairs. One iteration would involve drawing n random residuals with replacement and adding these to the original observations of the y -variable. The parameters are reestimated from this resampled data set. This process is repeated from 100 to 1,000 times to obtain a frequency distribution of the estimated parameters from which we can then estimate the variance of this distribution and bias corrected and accelerated confidence intervals (Efron and Tibshirani 1998). An example of utilizing bootstrapped methods for a Ricker recruit-spawner curve is presented in Box 4.9.

4.4.6 Sources of Bias in Recruit–Spawner Relations

Two primary sources of bias in estimating recruit–spawner coefficients are time series bias and measurement error bias. In wild populations, spawner abundance fluctuates and quite often, mortality from juvenile life stages to the time of maturation (i.e., recruitment to the spawning population) may or may not be relatively constant over time. Thus, variation in spawner abundance will not be independent of the process errors that impart variation in recruitment. Large recruitment events will therefore lead to increased spawner abundance in the future, and vice versa. Under this condition, the errors in recruit–spawner models are not independent but are autocorrelated (i.e., a good year is likely to be followed by a good year, and vice versa), and we therefore violate a key assumption of parametric statistics resulting in potential bias of parameter estimates.

For walleye from Escanaba Lake (Hansen et al. 1998; see Table 4.3), the largest observed spawner abundance (2,990) was about eight times greater than the smallest (369). Hilborn and Walters (1992) suggested that biases can be ignored if the smallest stocks are less than 10% the size of the largest; in Escanaba Lake this ratio was about 12%. Walters and Ludwig (1981) suggested that if spawners are estimated with $\pm 30\%$ error or better, then bias from measurement errors is probably not severe. In Escanaba Lake, spawner abundance was estimated with mark-recapture methods, and standard deviations of these estimates ranged from 5.1% to 19.2% and averaged 10% of the mean from 1959 to 1991 (Carpenter et al. 1994). Thus, measurement error of spawner abundance may not impose serious bias on the estimated recruit–spawner coefficients for walleye in Escanaba Lake.

■ 4.5 USE OF ADULT SPAWNER DATA TO ASSESS RECRUITMENT OVERFISHING

In some instances in freshwater fisheries, recreational or commercial exploitation (or both) can so severely deplete the number of adults in the population at such

Box 4.9 Computation of Bootstrapped Parameter Estimates for the Ricker Recruit–Spawner Curve

The SAS program below conducts bootstrapped parameter estimation for walleye recruit–spawner data (recruits given as R , spawners given as S) listed in Table 4.3. The program uses the nonlinear form of the Ricker recruit–spawner relation and incorporates lognormal error structure (equation [4.6]). In total, 500 estimates were generated. The program includes information that provides an explanation of the computations that each statement is doing (noted by **/*).

Program

```

*/INPUT DATA;
DATA ALLDATA;
INPUT J YEARCLASS R S @@;
CARDS;
1 1958 4532 775
2 1959 22996 2310
(continue data input)
33 1990 35607 735
34 1991 48761261
;
*/transform data;
DATA TRANSDATA;
SET ALLDATA;
LOGR=LOG(R);
LOGS=LOG(S);
RUN;

*/ FIT CURVE TO ORIGINAL DATA SET USING EQN. 4.6;
PROC NLIN DATA=TRANSDATA MAXITER=60 METHOD=MARQUARDT;
PARMS ALPHA=1 BETA=.001;
MODEL LOGR=LOGS+ ALPHA - BETA*S;
OUTPUT OUT=PREDOUT PREDICTED=PRCT;
RUN;

*/creates data set that contains 34 residuals for logR;
DATA NEWDATA;
SET PREDOUT;
RESRCT=LOGR-PRCT;
DROP J YEARCLASS R S LOGR LOGS PRCT;
RUN;

*/define bootstrap macro;
%MACRO BOOT;
%DO I=1 %TO 500;

*/create bootstrap data set;
*/creates data set of 34 random residuals;
DATA TEMP;
CHOICE=INT(RANUNI(23456+&I)*N)+1;
SET NEWDATA POINT=CHOICE NOBS=N;
J+1;
IF J>N THEN STOP;
RUN;

```

(Box continues)

Box 4.9 *(continued)*

```
    /*creates data set containing logS, logR, predicted logR and predicted logR
+ random residual;
    data analysis;
    SET PREDOUT;
    SET TEMP;
    /*ADDS RANDOM RESIDUAL TO PREDICTED LOGR;
    BSRCT=PRCT+RESRCT;
    RUN;

    /*fit curve to bootstrap data set;
    PROC NLIN DATA=ANALYSIS MAXITER=60 METHOD=MARQUARDT NOPRINT;
    PARMS ALPHA=1 BETA=.001;
    MODEL BSRCT=LOGS+ ALPHA - BETA*S;
    IF _ITER_=60 THEN CONVERGE=0;
    IF _ITER_<60 THEN CONVERGE=1;
    ID CONVERGE;
    OUTPUT OUT=BOOTOUT PARMS=ALPHA BETA CONVERGE;
    RUN;

    /* delete unnecessary data;
    DATA TEMPBOOT;
    SET BOOTOUT;
    IF J<34 THEN DELETE;
    RUN;

    /*save parameter estimates from each bootstrap run;
    PROC APPEND BASE=ALLBOOT DATA=TEMPBOOT;
    RUN;

    %END;
    %MEND;
    /*end macro define;

    /*run bootstrap macro;
    %BOOT;

    /*summarize bootstrap results;
    PROC UNIVARIATE DATA=ALLBOOT;
    VAR ALPHA BETA;
    OUTPUT OUT=BOOTSUM P10=P10 P90=P90;
    RUN;
    QUIT;
```

Results**Table** Output for bootstrapped estimation of Ricker recruit–spawner curve assuming lognormal error structure. The Marquardt method is employed. The dependent variable is $\log_e R$ (logR).

Iterative Phase					
Iteration	A		B		SS
0	1.0000		0.00100		194.9
1	3.3916		0.00118		33.7931

Analysis of Variance					
Source	df	SS	Mean square	F-value	Approximate P > F
Regression	2	2724.0	1362.0	2.13	0.1540
Residual	32	33.7931	1.0560		
Uncorrected total	34	2757.8			
Corrected total	33	36.0449			

Approximate Correlation Matrix		
	A	B
A	1.0000000	−0.9037713
B	−0.9037713	1.0000000

Table Distribution patterns of α for the Ricker recruit–spawner curve as described by the UNIVARIATE procedure.

Moments			
N	500	Sum weights	500
Mean	3.38337872	Sum observations	1691.68936
SD	0.40222105	Variance	0.16178178
Skewness	−0.2077502	Kurtosis	−0.0742384
Uncorrected SS	5804.35489	Corrected SS	80.7291065
CV	11.8881475	SE Mean	0.01798787

Basic Statistical Measures			
Location		Variability	
Mean	3.383379	SD	0.40222
Median	3.390297	Variance	0.16178
Mode		Range	2.17523
		Interquartile range	0.53847

(Box continues)

Box 4.9 (continued)

Tests for Location: $\mu_0 = 0$				
Test	Statistic symbol	Statistic value	Comparison	P-value
Student's <i>t</i>	<i>t</i>	188.0922	$P > t $	<0.0001
Sign	<i>M</i>	250	$P \geq M $	<0.0001
Signed rank	<i>S</i>	62625	$P \geq S $	<0.0001

Quantiles	
Quantile	Estimate
100% Maximum	4.30214
99%	4.22918
95%	4.04890
90%	3.91125
75% Q3	3.66141
50% Median	3.39030
25% Q1	3.12294
10%	2.88759
5%	2.68240
1%	2.36726
0% Minimum	2.12691

Table Distribution patterns of β for the Ricker recruit-spawner curve as described by the UNIVARIATE procedure.

Moments			
<i>N</i>	500	Sum weights	500
Mean	0.00117151	Sum observations	0.58575379
SD	0.00029632	Variance	8.78072×10^{-8}
Skewness	-0.0636916	Kurtosis	-0.0124084
Uncorrected SS	0.00073003	Corrected SS	0.00004382
CV	25.2941464	SE mean	0.00001325

Basic Statistical Measures			
Location		Variability	
Mean	0.001172	SD	0.0002963
Median	0.001169	Variance	8.78072×10^{-8}
Mode		Range	0.00168
		Interquartile range	0.0003932

Tests for Location: $\mu_0 = 0$				
Test	Statistic symbol	Statistic value	Comparison	P-value
Student's <i>t</i>	<i>t</i>	88.40259	$P > t $	<0.0001
Sign	<i>M</i>	250	$P \geq M $	<0.0001
Signed rank	<i>S</i>	62625	$P \geq S $	<0.0001

Quantiles	
Quantile	Estimate
100% Maximum	0.002026458
99%	0.001804193
95%	0.001680089
90%	0.001553971
75% Q3	0.001367037
50% Median	0.001169344
25% Q1	0.000973827
10%	0.000807687
5%	0.000676374
1%	0.000422876
0% Minimum	0.000343403

From the 500 estimates of the Ricker recruit-spawner, α and β were positively correlated ($r = 0.91$), similar to the r -value of -0.90 from the approximate correlation matrix from the single nonlinear equation computed at the beginning of the SAS output. High correlation between nonlinear parameters typically occurs as these coefficients are simultaneously determined and are not independent regressors of the dependent variable.

The output for 500 randomized Ricker recruit-spawner curves and coefficients showed that the mean and median values for α and β were very similar to the empirical estimates generated from the nonlinear equation ($\beta = 3.392$ and $\beta = -0.00188$). Student t -tests, sign, and sign ranks tests for both α and β indicated these coefficients were not equal to 0 for these 500 estimates. The minimum value for β was not less than 0, and thus this bootstrap method provided evidence that weak density dependence occurred in the recruit-spawner relation for walleye in Escanaba Lake. Finally, the UNIVARIATE procedure in SAS showed α and β were approximately normally distributed, similar to the results from Hougaard's skewness values computed in Box 4.8.

Table 4.3 Recruit (age-0) and spawner (age-5 and older) walleye data for Escanaba Lake, Wisconsin (from Hansen et al. 1998). Abundances of recruits and spawners were determined from mark–recapture population estimates, and May temp CV is the coefficient of variation in May air temperature, which is when walleye were spawning.

Year-class	Number		May temp CV
	Age-0	Age-5 and older	
1958	4,532	775	0.24125
1959	22,996	2,310	0.16319
1960	628	2,990	0.46056
1961	879	1,400	0.33028
1962	14,747	1,130	0.22618
1963	13,205	790	0.20596
1964	31,793	1,195	0.19229
1965	10,621	981	0.20363
1966	22,271	870	0.3452
1967	8,736	1,104	0.27511
1968	8,761	883	0.10884
1969	18,885	1,421	0.17799
1970	10,098	1,198	0.2106
1971	3,394	760	0.22098
1972	1,697	1,354	0.39461
1973	25,159	1,308	0.19696
1974	14,093	2,016	0.20992
1975	1,932	962	0.33459
1976	2,292	976	0.24803
1977	17,386	1,062	0.19815
1978	5,334	1,945	0.32837
1979	6,957	2,073	0.4162
1980	1,036	1,458	0.26409
1981	16,345	946	0.25728
1982	6,149	1,952	0.27111
1983	10,366	1,280	0.18882
1984	16,795	851	0.28661
1985	14,599	394	0.12269
1986	15,299	2,121	0.18605
1987	13,882	452	0.14723
1988	4,351	369	0.18968
1989	4,262	603	0.34298
1990	35,607	735	0.19356
1991	4,876	1,261	0.32032

a high rate that recruitment is reduced. Evidence presented by Davidoff et al. (1973) and Walker et al. (1993) for lake whitefish, Chevalier (1977) and Anthony and Jorgensen (1977) for walleye, and Eshenroder (1977) for yellow perch strongly suggested that recruitment overfishing was associated with a decline in catch and yield in these freshwater fisheries. Rieman and Beamesderfer (1990) found the recruit–spawner relation exerted the greatest influence on the dynamics of a white sturgeon population, which indicated these long-lived, slow-growing fish were

vulnerable to recruitment overfishing. Secor and Waldman (1999) found that high exploitation caused the Atlantic sturgeon population in Delaware Bay to collapse in the early 1900s due to recruitment overfishing. Slipke et al. (2002) predicted the reduction in young channel catfish was associated with overharvest of adults in the upper Mississippi River.

In the 1980s, marine fisheries scientists attempted to address the problem of recruitment overfishing quantitatively and developed a simple index termed the spawning potential ratio (SPR; Goodyear 1993). Typically, attempts to use Ricker or Beverton–Holt equations of recruit–spawner relations to define a critical abundance of spawning adults (Hilborn and Walters 1992) have been wrought with high variability, confounding effects of environmental factors that affect recruitment, and the lack of long-term data collection (Goodyear 1993; Hansen et al. 1998).

The SPR is the number of mature eggs produced at a certain level of exploitation for a given population divided by total number of eggs produced in the population if no fish were exploited. Goodyear (1993) defined potential recruit fecundity (P) as the number of mature eggs that could be produced by an average recruit in a population where density-dependent growth and survival did not occur. This represents the actual average lifetime production of mature eggs per recruit at equilibrium population densities in the absence of any density-dependent suppression of maturation or fecundity at age. Potential recruit fecundity (P) is determined (Goodyear 1993) from

$$P = \sum_{i=1}^n E_i \prod_{j=0}^{i-1} S_{ij} \quad (4.10)$$

where

n = number of ages in the population;

E_i = mean fecundity of females of age i in the absence of density-dependent growth;

$S_{ij} = e^{-(F_{ij} + M_{ij})}$, the density-independent annual survival probabilities of females of age i when age j ;

F_{ij} = the fishing mortality rate of females of age i when age j ; and

M_{ij} = the natural mortality rate of females of age i when age j .

Exponential functions for fishing mortality (F) and natural mortality (M) are incorporated into this integral equation similar to predicting cohort abundance.

The SPR is defined as

$$\text{SPR} = P_{\text{fished}} / P_{\text{unfished}} \quad (4.11)$$

The SPR has a maximum value of 1.00 (unity) and declines toward 0 as fishing mortality increases. The software developed by Slipke and Maceina (2000) can compute SPR values for fish displaying a wide variety of different life history traits and different rates of fishing and natural mortality.

Goodyear (1993) recommends SPR targets of no less than 20–30% based on observations of pelagic marine species. Slipke et al. (2002) estimated the critical

SPR to maintain adequate recruitment of channel catfish in the upper Mississippi River was 10% based on the response of C/f of age-0 fish and subsequent harvest of adult fish. Quist et al. (2002) recommended a maximum conservative SPR target of 40–50% to protect overexploitation of shovelnose sturgeon in the Missouri River. Other than the work of Slipke et al. (2002), critical values for SPR have not been defined nor used to evaluate freshwater sport or commercial fisheries, but exploring the utility of SPR for these fisheries warrants investigation. Target SPRs are achieved by protecting mature females by means of harvest regulations. The SPR is used as a management criterion to maintain adequate females in the population to prevent recruitment overfishing. Typically, mature ova production increases exponentially with fish length or linearly with weight. In some instances, larger females can produce one to two orders of magnitude more eggs than can smaller sexually mature fish. For example, management strategies to maintain white sturgeon in the Columbia River include protecting older mature females that can be caught and released using hook-and-line gear but allowing harvest of a slot length (92–183 cm TL) of smaller fish (Rieman and Beamesderfer 1990). The use of SPR critical values should be analyzed with caution as a direct relationship between fecundity and subsequent recruits may not occur, and from year to year environmental variables can also influence reproductive success.

■ 4.6 SUMMARY

A wide variety of parametric statistical procedures can be used by fisheries scientists to examine spatial and temporal fluctuations in recruit abundance. These tools can also be used to examine the effects of manipulations or biotic and abiotic impacts on recruitment success. The relation between recruits and spawners can be investigated, but typically these relations require long-term data collection, accurate estimates of spawner abundance are difficult to obtain, and recruitment variation is likely to be more influenced by environmental conditions. For most freshwater fishes, fluctuations in recruitment exert a very strong influence on population dynamics, and obtaining information on recruitment variation is paramount to understanding and managing fisheries. Typically, most recreational and commercial fisheries display wide variation in recruits, and this variation should be considered when sampling designs are considered, planned, and executed. Although recruit variation can be high, adequate replicates can be taken to provide the fisheries scientist with enough statistical power to examine and test hypotheses related to fish recruitment.

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