

An Approach to Estimate Probability of Presence and Richness of Fish Species

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Abstract.—Absence of a species when it is not observed from a given area is ensured only when the probability of observation, when present, is 1. This condition is rarely satisfied in surveys of animals in natural environments, particularly with elusive targets such as fish. Detectability (probability of species encounter) is a function of probability of individual capture, which varies widely with sampling method, fish size, physical habitat, and number of individuals present in a given area. An empirical Bayesian approach was developed for estimating probability of presence for zero-catch samples, in which the number of individuals present for a species is predicted from independent samples and used as an empirical prior. The model was illustrated for 16 species of fish sampled in 121 blocked-off stream reaches in which samples were collected using one of five primary gear methods; treatment with an ichthyocide followed. All species present were caught by the primary gear in only 17 (14%) of the samples. Of the empirical Bayesian predictions of presence or absence from zero-catch samples, 69% were correct. Of these zero-catch samples, 20% of samples in which a species was present and 93% of samples in which a species was absent were correctly predicted. The mean species richness was 10.3, compared with 7.4 for species richness from catch data of (mean bias of -27.4%). The model predicted a mean of 9.6 species (mean bias of -3.3%). Sampling design and subsequent analysis should account for catchability and fish densities (predicted as functions of physical habitat variables) and area sampled in order to reliably estimate probability of presence by species and, subsequently, species richness.

Analyses of the presence and absence of species individually and collectively (e.g., species richness) are increasingly being used by fishery biologists to examine the influence of natural and anthropogenic factors on fish distribution and community structure (e.g., Tonn and Magnuson 1982; Matthews and Robinson 1988; Kruse et al. 1997; Sekine et al. 1997; Dunham and Rieman 1999) and for developing biodiversity conservation strategies (Burley 1988; Lee et al. 1997). Estimates of species presence and species richness are usually only based on catch, but are assumed or implied to be representative of the identity and numbers of species actually present in the sampled area. Unfortunately, complete observation or capture of all species is frequently impossible for mobile, aquatic organisms such as fish (Zalewski and Cowx 1990; Dolloff et al. 1996). Consequently, species presence and species richness estimates from samples underestimate true values to varying degrees.

Approaches to minimize the influence of incomplete observation or capture on estimates of species presence and fish species richness can be roughly categorized as “sampling effort” and “inferential.” Sampling-effort approaches to detect the presence of individual species in a region of interest (sampling frame) rely on a predetermined number of samples and usually are based on an arbitrary threshold density and presumed statistical distribution (Bonar et al. 1997). Hence, inferences regarding species presence are restricted to the region of interest rather than at the site (sampling unit) level. For species richness estimates, the sampling-effort approach depends on cumulative catches indicating an asymptotic value of richness as the sampled area increases (Lyons 1992; Angermeier and Smogor 1995). Subsequently, a sampled area is predetermined for each sample (usually a stream-reach length that is a constant multiple of its mean width) in which the catch is estimated to be a fixed proportion of the asymptotic value. The sampling-effort approach therefore attempts to optimize the individual sample procedure

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rather than the sampling design covering the region of interest.

In contrast, inferential approaches explicitly account for imperfect detectability and can be used with existing data that are consistent with an overall design. Although there are currently no inferential approaches for individual species presence, a variety of species richness estimators have been developed to take into account species that may have been missed during sampling (Sugihara 1980; Smith and Belle 1984; Palmer 1990; Bunge and Fitzpatrick 1993; Solow 1994). These estimators assume that individuals are encountered at random and that probability of detection does not differ among individuals or species (however, see jackknife approach of Burnham and Overton 1979; Boulinier et al. 1998).

However, detectability (the probability of detecting a species), is a function of the number of vulnerable individuals in a given area and the probability of individual capture (i.e., catchability or sampling efficiency), both of which may be influenced by habitat features. Furthermore, differences in catchability due to method (e.g., Figure 1), species, and individual size can also strongly affect detectability. Failure to account for differences in detectability can introduce different biases into estimates of species presence when catchability is strongly influenced by changes in habitat type and scale and the types of species present (Bayley and Dowling 1993). Therefore, a model predicting probability of presence that specifically accounts for empirically derived abundance and catchability estimates of each species is a more desirable approach to estimating species richness and would also provide useful information on distributions of individual species. Here we describe one such approach.

We developed a model that predicts probability of presence by species. Using several sampling methods and a gear-efficiency calibration method, we derived empirical relationships predicting abundance and catchability of 16 fish species in warmwater streams of the midwestern United States. This information was then incorporated in a Bayesian model to estimate probability of species presence for each sample in which a species was not collected (henceforth: "zero-catch sample"). All probabilities of species presence, including those caught, were then used to estimate species richness by sample. We validated the accuracy of model predictions by comparing them with presence determined by a

combination of several gear passes and subsequent rotenone treatment.

Methods

Model Development

When estimating species-specific detection probabilities (detectability), it is important to first consider the process of sampling. Capturing a species in a sampling unit (detection) requires that the species be present and at least one individual be captured. To estimate probability of detection of a species requires two components: an estimate of the number of fish in a sampling site (i.e., the number of chances you get) and an estimate of catchability (i.e., the probability of capturing any individual of the species). Thus, if we consider n_i individuals of species i and individual probability of capture q_i (catchability), then given independence among individuals (an assumption that is relaxed later), the probability of collecting one or more individuals (detectability) is

$$d_i = 1 - (1 - q_i)^{n_i}. \quad (1)$$

If the complement of d_i ($d_i = \text{detect}$) is m_i ($m_i = \text{miss} = 1 - d_i$), then the binomial expansion,

$$\prod_{i=1}^s (d_i + m_i) = 1 \quad (2)$$

describes all possible joint occurrence combinations of s species in the catch. From this the probability distribution function (PDF) of the species richness in the catch (c_j) can be derived algebraically as the probability of all possible combinations of j species, irrespective of their identities. A simulation with six species of contrasting but realistic catchabilities and densities (Figure 2), shows that large biases in catch-based species richness estimates are possible and to be expected given typical differences in catchability and numbers of vulnerable fish.

Inference from zero catches.—The foregoing illustration does not provide a practical solution because individual samples often do not reveal the presence of a species. Consequently, a means to estimate the probability of presence for a zero catch is needed. Such an estimate requires a consideration of total probability, which simply means that all occurrences that might have caused a zero catch must be considered. During fish sampling, there are two cases that would result in a zero catch (event C_0): (1) a species was present in the sampling unit and missed, or (2) a species

was not in the sampling unit. In standard Bayesian terminology, the total probability of a zero catch occurring, $P(C_0)$, can be expressed as the sum of probabilities of cases 1 and 2:

$$P(C_0) = P(C_0|F) \cdot P(F) + P(C_0|\sim F) \cdot P(\sim F) \quad (3)$$

where the probability of case 1 is estimated as the product of $P(C_0|F)$, the probability of missing a species (C_0) when it is present (event F), and $P(F)$, the prior estimate of probability of species presence (Bayes empirical prior). The probability of case 2 is estimated as the product of $P(C_0|\sim F)$, the probability of not capturing a species when it is absent ($= 1$), and $P(\sim F)$, the probability of species absence (event $\sim F$), where, logically, $P(F) + P(\sim F) = 1$.

By definition (i.e., conditional probability symmetry), the joint probability that a sampling unit contains a species and that it is also missed during sampling is equal to the joint probability that the species is missed (not detected) and that it occurs in the sampling unit (case 1):

$$P(F|C_0) \cdot P(C_0) = P(C_0|F) \cdot P(F) \quad (4)$$

Rearranging (4) and substituting for $P(C_0)$ from equation (3), we obtain the standard Bayes' rule that describes the probability of a species being present (event F) given a zero capture (event C_0):

$$P(F|C_0) = \frac{P(C_0|F) \cdot P(F)}{P(C_0|F) \cdot P(F) + P(C_0|\sim F) \cdot P(\sim F)} \quad (5)$$

Thus, the prior, $P(F)$, is derived independently and adjusted according to the probability of missing the species when present, $P(C_0|F)$. The numerator and denominator of equation (5) can be interpreted respectively as proportional to the number of possibilities of zero catches when present (numerator) and the number of possibilities of zero catches when the species is present or absent (denominator).

Because the probability of missing a species depends on the number of fish present, we express the prior as the PDF for the unconditional probability of n fish being present, $P(F_n)$, and equation (5) is decomposed thus:

$$\hat{P}(F|C_0) = \frac{\sum_1 \hat{P}(C_0|F_n) \cdot \hat{P}(F_n)}{\sum_0 \hat{P}(C_0|F_n) \cdot \hat{P}(F_n)} \quad (6)$$

$P(C_0|F_n)$ is the probability of missing n fish ($= m_i = [1 - q_i]^n$ from equation 1); therefore,

$$\hat{P}(C_0|F_n) = (1 - \hat{q})^n \quad (7)$$

for a given species. Terms in the summations in equation (6) approach zero for increasing n , the rate of approach being greater for higher catchability, q .

The prevalence of overdispersion (variance in excess of that determined by the binomial distribution) in many catchability and mark-recapture models suggests that fish do not respond independently (Bayley 1993). Independence refers to how fish react to the sampling process and its influence on efficiency. For example, during sampling, a group of fish can swim away from the sampler (e.g., electrode), so none are captured (0% efficiency) or it can swim toward the sampler, so all are captured (100% efficiency). In other words, the group or school is acting like a single individual. Overdispersion was consistently observed as extrabinomial variance of catchability, predicted from logistic regressions (Bayley and Dowling 1993), and in the abundance models derived below. Field observations suggested that at least some of this additional variance was due to fish behaving as groups, whereas equation (7) assumes that fish react independently to the capture process.

Accordingly, we adapted the estimator for $P(C_0|F_n)$ to simulate fish responding to gear as random groups rather than as individuals. The mean number of groups corresponds to that which would produce a binomial variance in catchability equal to the observed variance; that is,

$$\hat{P}(C_0|F_n) = (1 - \hat{q})^{\hat{n}_e} \quad (8)$$

where \hat{n}_e , the effective number of groups, is estimated by $n[n \cdot \hat{s}^2 \cdot \hat{q}(1 - \hat{q}) + 1]^{-1}$, and \hat{s}^2 is an estimate of extrabinomial variance in catchability (Bayley and Dowling 1990; Bayley 1993; Bayley and Dowling 1993). Equation (8) was used to provide alternative $P(F|C_0)$ estimators to equation (7) and hereafter is referred to as "overdispersion-corrected."

We did not attempt to derive a theoretical variance estimator for equation (6), but rather depend on an empirical comparison of predictions with high efficiency captures in the example below.

Species richness inference.—Equation (8) provides an estimate of probability of presence of species i ($p_i = \hat{P}(F|C_0)$) when it is not caught. Conversely, $p_i = 1$ when it is caught. For each sample, the expansion

$$\prod_{i=1}^s (p_i + a_i) = 1 \quad (9)$$

produces probabilities of all combinations of occurrences (p_i) and absences ($a_i = 1 - p_i$) for all possible species, s . Although equation (9) appears similar to equation (1), the important distinction is that equation (1) refers to probabilities of appearing in the catch, whereas equation (9) predicts probabilities of co-occurrence of species in the sampling unit on which the p_i are based and is independent of sampling method. Therefore, given estimates of p_i , a distribution of probabilities of co-occurrence of 0, 1, . . . s , species from equation (9) provides an empirical estimate of the actual species richness distribution.

In summary, this process requires a prediction of catchability and distribution of abundance at each sampled site to produce an estimate of probability of presence by species. Such probabilities among species, including those of species known to occur at the site, can be subsequently combined to estimate species richness for each sample. In the following example such estimates are compared with known species presence from a high-efficiency method.

Example and Validation Process

Sampling methods.—For validation we sampled 121 fish communities in second to fourth order streams in Champaign and Vermilion counties, Illinois. Samples were collected during summer from within blocked-off stream sections with one of five primary sampling gears (Table 1). We chose sampling gears that were most frequently used for stream orders 2–5; however, gears were also selected that enabled us to demonstrate a method that could be used to synthesize information from several gears fished separately over a wide range of conditions in a basin of interest. First, the primary sample, one pass of one of the five gears (except that two passes originally had been combined for the net seine), was collected. This single-pass sample procedure was advocated by Lyons (1992) and Angermier and Smoger (1995) and was used by several natural resource agencies (e.g., Meador et al. 1993; Lazorchak et al. 1998). After the primary sample, we collected all fish from additional passes and a subsequently applied treatment of ichthyocide (6 mg/L of a rotenone formulation for a 10-min exposure) followed by a calibrated quantity of detoxicant, KMnO_4 , at the downstream block net (Bayley et al. 1989). Electrically narcotized and rotenoned fish that drifted into

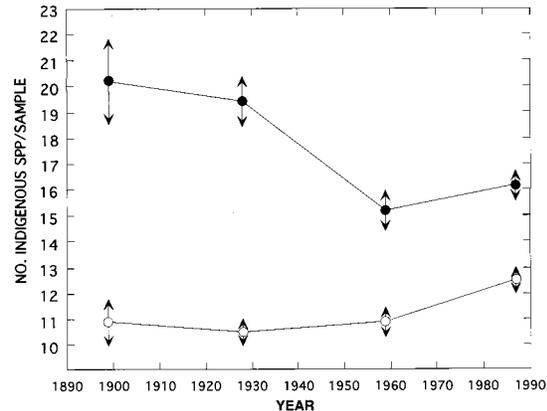


FIGURE 1.—Mean numbers (y-axis) and standard error (arrows) of indigenous fish species per sample from catch data (open circles) and after correction for species richness efficiency (solid circles) for each of four surveys in Champaign County streams (Larimore and Bayley 1996). Corrections to samples were based on gear calibration models (Bayley and Dowling 1990; Bayley and Dowling 1993), in which species richness was determined from the total catch using rotenone plus preceding multiple passes of primary gear between block nets. The first two surveys used a minnow seine; the two later surveys were taken primarily with an electric seine.

the downstream block net were also collected and recorded separately (block-net catch).

Numbers of species caught by the primary sample and Bayesian estimates described below were compared with the known species richness (i.e., the total catch in the blocked-off reach obtained from multiple passes of the primary gear, the block-net catch, and the rotenone treatment). The high catchabilities of rotenone alone, ranging from 0.4 to 0.7, based on mark-recapture experiments, in combination with several additional passes of the primary gear plus block-net captures, indicated that chances of missing small numbers of any of the species considered were extremely small.

Analysis.—Using a leave-one-out approach from prediction models based on independent data, prior estimates of abundance distributions, $P(F_n)$, via equation (6) were obtained for each primary sample in which a species was not caught. We used a subset of 16 species (Table 1) for which robust catchability models have so far been developed, based on a set of field calibrations in the region (Bayley and Dowling 1990; Bayley and Dowling 1993). Abundance, estimated for each species and primary sample (numbers of fish caught/catchability expressed as numbers per 1,000 m^2 of stream surface area), was modeled for each species as a function of ecologically plau-

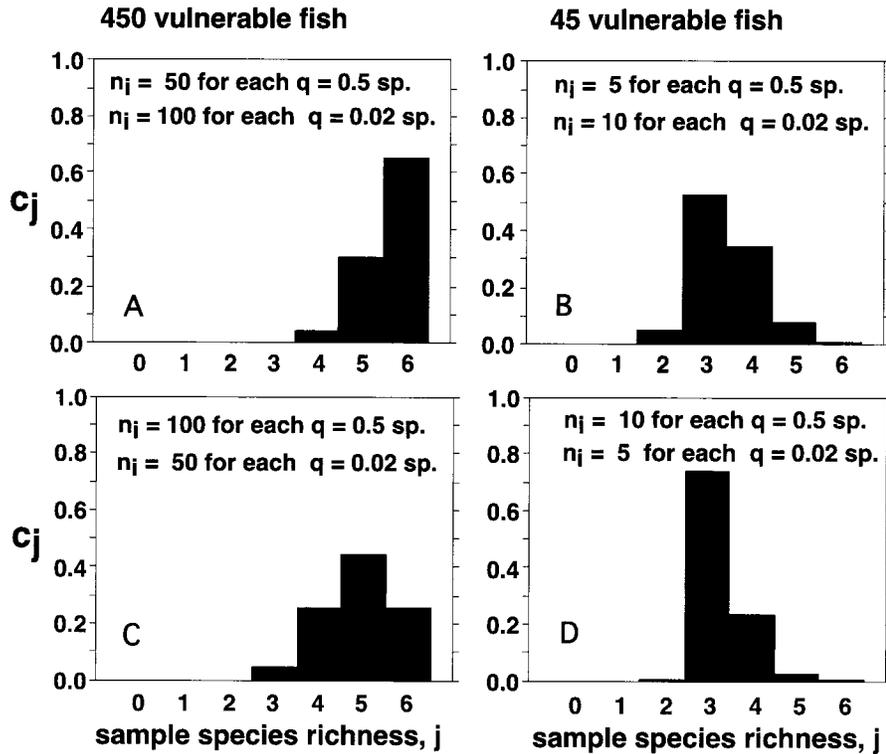


FIGURE 2.—Predicted probability distribution functions (c_j) for species richness of catches (j) for a community of six species with two levels of catchability (probability of individual capture, q), 0.5 and 0.02. Panels (A) and (C) are from two distributions totaling 450 individuals, whereas (B) and (D) are from similar distributions totaling 45 individuals.

sible habitat variables (Table 2). Zero-catch data from primary samples were included.

The chosen area standard of 1,000 m² was close to the mean of all water surface areas sampled. Any standard could be chosen for the expression of probability of presence or species richness, but an area within the limited range sampled permits reliable cross-validation using species subsequently caught by rotenone. When total abundance for each species captured was computed for the standardized area, no density estimates less than 0.5 individuals per 1,000 m² were encountered.

Any modeling approach that reliably predicts a discrete distribution of fish numbers, $P(F_n)$, would suffice. A preliminary examination of species-specific regression model fits to abundance data, assuming a Poisson error distribution, consistently showed a greater variance than that predicted by the mean (μ). The negative binomial model (White and Bennets 1996), which accounts for an additional variance term, μ^2/k , provided better predictions with well-behaved residuals. These models were fit using

a quasi-likelihood extension of the iteratively reweighted least-squares algorithm (Wedderburn 1974; McCullagh and Nelder 1989) in GLIM4 (Francis et al. 1993) and a user-supplied macro (available from first author) to enable an iterative fit of the additional parameter, k . There are now several software packages that, with the aid of available macros, can perform fits to this distribution (Francis et al. 1993; Venables and Ripley 1999).

To obtain species-specific abundance models with least unexplained variance (i.e., best fitting), we initially fit negative binomial regression models with a larger data set of 127 samples that included the 121 samples subsequently used for validation. We did this using sets of minimally correlated ($P > 0.05$) explanatory variables describing summer, low-flow habitat conditions (Table 2). Variables were retained if there was a significant ($P < 0.05$) change in deviance when excluded (Aitken et al. 1989; Francis et al. 1993). For each sample in which the species of interest was absent from the primary gear catch, fish abundance was estimated using a similar neg-

TABLE 1.—Mean catchability (based on single pass, except for net seine) and total number of samples in which species was present by primary gear type and the range of abundances for the species analyzed. Catchability = number of fish caught/number of vulnerable fish, where number of vulnerable fish is the sum of catches from all primary gear passes, the block net, and the ichthyocide corrected for rotenone efficiency using mark-recapture (Bayley and Dowling 1993).

Species and sizes of areas sampled	Species code	Electric seine: 30 ft	Electric seine: 50 ft	Backpack electro-fisher	Net seine: 20 ft (2 passes)	Boat-mounted electro-fisher	Abundance range (fish/1,000 m ²)
Grass pickerel <i>Esox americanus vermiculatus</i>	GRP	0.35 (39)	0.380 (7)	0.028 (10)	0.120 (5)	0.1390 (5)	1–229
Common carp <i>Cyprinus carpio</i>	CAP	0.27 (17)	0.480 (8)	0.570 (4)	0.077 (3)	0.1260 (12)	2–682
Creek chub <i>Semotilus atromaculatus</i>	CRC	0.31 (55)	0.130 (6)	0.057 (12)	0.490 (9)	(0)	1–17,382
Silverjaw minnow <i>Notropis buccatus</i>	SJM	0.25 (38)	0.098 (6)	0.044 (5)	0.430 (8)	0.0067 (4)	1–4,856
Sand shiner <i>Notropis stramineus</i>	SAS	0.21 (47)	0.076 (10)	0.044 (7)	0.450 (10)	0.0070 (7)	1–7,301
Redfin shiner <i>Lythrurus umbratilis</i>	RDS	0.19 (46)	0.075 (13)	0.043 (8)	0.420 (10)	0.0067 (11)	2–1,456
Striped shiner <i>Luxilus chrysocephalus</i>	STS	0.36 (66)	0.120 (12)	0.051 (11)	0.480 (10)	0.0075 (11)	4–9,616
Spotfin shiner <i>Cyprinella spiloptera</i>	SFS	0.24 (49)	0.130 (12)	0.045 (6)	0.500 (10)	0.0075 (12)	12–4,262
Steelcolor shiner <i>Cyprinella whipplei</i>	SES	0.28 (12)	0.170 (4)	0.046 (2)	0.410 (3)	0.0079 (7)	2–1,507
Bluntnose minnow <i>Pimephales notatus</i>	BLS	0.21 (63)	0.076 (13)	0.043 (12)	0.048 (12)	0.0069 (12)	3–34,524
Central stoneroller <i>Camptostoma anomalum</i>	COS	0.30 (51)	0.120 (10)	0.046 (7)	0.390 (8)	0.0075 (3)	2–9,329
Creek chubsucker <i>Erimyzon oblongus</i>	CCS	0.78 (23)	0.750 (5)	0.250 (8)	0.096 (7)	(0)	1–2,918
Blackstripe topminnow <i>Fundulus notatus</i>	BLT	0.22 (54)	0.020 (9)	0.110 (11)	0.390 (9)	0.0260 (10)	1–6,100
Smallmouth bass <i>Micropterus dolomieu</i>	SMB	0.36 (35)	0.220 (9)	0.071 (6)	0.160 (6)	0.1140 (9)	2–606
Green sunfish <i>Lepomis cyanellus</i>	GSF	0.30 (51)	0.240 (11)	0.048 (96)	0.081 (10)	0.0270 (12)	1–3,398
Longear sunfish <i>Lepomis megalotis</i>	LOS	0.33 (61)	0.210 (13)	0.049 (12)	0.063 (12)	0.0084 (12)	2–31,897
Total		70	13	13	13	12	1–34,524
Mean stream length sampled (m)		192	168	203	150	210	
Mean quadrat size (m ²)		421	1,063	381	289	1,587	

ative binomial model derived only from abundance estimates from all other samples, including those that had a zero primary catch. Significances of coefficients from each leave-one-out data subset were very similar to those of the corresponding explanatory variables for the full data set models (Table 2). The residuals of each model, ordered according to geographic proximity within years, indicated no autocorrelation (Wald-Wolfwitz test at $P = 0.05$), implying that the abundance prediction of each sample was independent of the other samples used to derive each model.

For each species and site combination, $P(F_n)$ was estimated as a negative binomial PDF by using abundance estimate (n) and the corresponding dispersion parameter (k) from the leave-one-out procedure; $P(F_n)$ was then multiplied by the $P(C_0|F_n)$ term (equation 6) corresponding to each n , including the term for $n = 0$ for the denominator in equation (6) ($= P[C_0|\sim F] \cdot P[\sim F]$ in equation 5 and $P[C_0|F_0] \cdot P[F_0]$ in equation 6). Summations in equation (6) were continued with increasing n until increments were < 0.0001 .

Probability of presence when absent from the primary sample, $P(F|C_0)$, was estimated for each of 16 species and 121 samples, whether they were ultimately found to occur or not. The $P(C_0|Fn)$ in

equation (6) were estimated for each corresponding n using equation (7) for $P(F|C_0)$ estimates uncorrected for dispersion and using equation (8) for $P(F|C_0)$ estimates corrected for dispersion.

Finally, frequency distributions and mean predictions of species richness were computed from the expansion of equation (9) for each sample, presuming that any of the 16 species could conceivably be present, and 90% confidence limits were computed based on the upper and lower 5% portions of each distribution. Means and confidence limits were computed as real numbers, by including a correction for discontinuity. The confidence range, although computed exactly, was an underestimate because it assumes that the p_i are known exactly, which is only true when the species was encountered in the primary sample ($p_i = 1$).

Results

Two types of error were computed to assess cross-validations by species when it was not caught in the primary sample: if $P(F|Co) < 0.5$ and the species was present (false negative) or if $P(F|Co) \geq 0.5$ and the species was absent from the site (false positive). Results were expressed as percent correct predictions.

Results for overdispersion-adjusted (7) and un-

TABLE 2.—Coefficients (standard errors) and dispersion parameter (k) of empirical negative binomial regression models fit to the abundance estimates (corrected for catchability) from all primary sample data. Actual values used for predicting population size priors, $P(F_n)$, during the cross-validation varied slightly as data from each sample being estimated (i.e., the left-out sample) were excluded to fit each respective negative binomial model. All coefficients were statistically significant ($P < 0.05$) in all models. Each function predicts N as numbers of individuals per 1,000 m² of water surface area (e.g., for the bluntnose minnow $N = \exp(7.64 - 3.95 \cdot \text{depth} - 4.35 \cdot \text{velocity} + 2.64 \cdot \text{macrophytes})$).

Species	Constant	Mean depth (m)	Riffle (proportion of water surface area)	Mean velocity (m/s)	Aquatic macrophytes (proportion of water area)
Grass pickerel	2.32				3.20 (1.16)
Common carp	-1.09				-2.77 (1.66)
Creek chub	9.93	-12.1 (1.3)	-5.95 (2.4)		
Silverjaw minnow	5.42				2.31 (1.25)
Sand shiner	8.77	-6.84 (1.09)	-5.03 (2.17)		-2.91 (1.16)
Redfin shiner	5.91	-5.06 (1.39)	-4.86 (2.70)	-6.03 (3.39)	
Striped shiner	5.95	-2.03 (0.75)			
Spotfin shiner	5.72	-2.99 (0.84)	-3.42 (1.62)	5.73 (2.02)	
Steelcolor shiner	4.52			-13.0 (6.2)	-12.3 (3.7)
Bluntnose minnow	7.64	-3.95 (0.93)		-4.35 (2.33)	2.64 (0.99)
Central stoneroller	10.67	-14.87 (1.51)			
Creek chubsucker	2.60	-5.15 (1.81)			8.42 (1.80)
Blackstripe topminnow	6.77	-8.33 (1.67)	-8.32 (3.18)	-7.32 (3.98)	
Smallmouth bass	3.46		5.4 (2.5)		
Green sunfish	6.25			-8.33 (2.43)	
Longear sunfish	4.32	2.59 (0.84)		-10.1 (2.1)	3.60 (0.88)

^a Nephelometric turbidity units.

adjusted (6) models were similar, but adjusted results were better at predicting presence. From a total of 1039 events when a species was absent from the primary sample, overdispersion-adjusted models correctly predicted 20% of events for species presence and 93% for species absence (Table 3), while for unadjusted models corresponding predictions were 15% and 96%, respectively. All detailed results reported below are for overdispersion-adjusted models; qualitative conclusions would not be different for unadjusted results.

All gear types produced conservative results, in that success rates that correctly predicted absences were higher than those that correctly predicted presence (Table 3) from zero-catch samples. Overall success rates ranged from 56% to 75% among methods (Table 3), and from 42% to 89% among species. Presence of several species occurring at less than 75% of sites tended to be underestimated more than widespread species (Figure 3).

Species richness estimates from the model averaged only 3.3% less than the known species richness from the 121 validation samples (penultimate column in Table 4). Numbers of species from primary samples (=species richness of the catch) averaged 27% below known values, and in only 17 samples (14%) were all the species present caught (Table 4). Species richness was most strongly underestimated (55%) by catches of the boat elec-

trofisher, even though that was the most appropriate primary gear for larger, non-wadeable streams. However, even catches from the most efficient gear in wadeable streams, the 30-ft electric seine, underestimated species richness by an average of 20%. As stated previously, we have not incorporated all species in this example; but preliminary data indicate lower catchabilities for the excluded benthic darters (Percidae) and catfishes (Ictaluridae) (Larimore 1961; Bayley and Dowling 1990) than the species used here, suggesting that biases of catch data compared to total richness may be greater than those estimated here.

The 90% confidence limits computed from the species richness PDFs, included 74% of the known species richness values, compared with 47% of the primary sample species numbers (Figure 4, Table 4). There was a tendency for more samples with high known species richness to be underestimated by the predictions using most primary methods (Figure 4).

Discussion

Species Presence

Probability of species presence estimates, $P(F|Co)$, for individual species can serve as a more accurate, and gear-independent response variable than simple presence/absence in the catch. The

TABLE 2.—Extended.

Species	Overhanging shoreline vegetation (proportion of banks)	Turbidity (NTU) ^a	Water temperature (°C)	<i>k</i>
Grass pickerel				0.174
Common carp			0.172 (0.081)	0.090
Creek chub		-0.041 (0.019)		0.157
Silverjaw minnow		-0.036 (0.010)		0.153
Sand shiner		-0.035 (0.010)		0.190
Redfin shiner		0.036 (0.012)		0.115
Striped shiner	0.0188 (0.004)	-0.012 (0.006)		0.405
Spotfin shiner	-1.69 (0.45)	0.022 (0.008)		0.321
Steelcolor shiner				0.037
Bluntnose minnow				0.239
Central stoneroller		-0.058 (0.013)		0.147
Creek chubsucker				0.073
Blackstripe topminnow	3.73 (0.85)			0.086
Smallmouth bass	-3.3 (0.71)	-0.018 (0.011)		0.136
Green sunfish	1.24 (0.52)	0.021 (0.008)	-0.114 (0.051)	0.233
Longear sunfish		0.063 (0.007)		0.315

prediction success rate of 20% for presence (Table 3) is a considerable improvement on 0% from the raw catch data, while the 93% success rate for correctly predicting absence limits false positive signals when $P(F|Co) > 0.5$.

Because $P(F|Co)$ incorporates catchability it is independent of habitat features that may influence catchability and species presence. Often better habitats that are attractive to the species concerned, such as those with deeper water, result in lower catchability (Zalewski and Cowx 1990; Bayley and Dowling 1993). The resulting increase in probability of zero catch would be exacerbated for

rarer species whose numbers are low even in their favored habitats. Even if some are caught, assuming 'relative abundance' on the basis of catches only will often underestimate the better habitats. Misguided and costly restoration attempts can result from erroneous ranking of preferred habitats when such biases remain uncorrected.

$P(F|Co)$ is an absolute measure and thus differs from current approaches (e.g., Hillman and Platts 1993; Bonar et al. 1997) that estimate the probability of species occurrence with a density above an arbitrary threshold. Estimates of $P(F|Co)$ do not require the assumption of some arbitrary threshold

TABLE 3.—Summary of zero-capture events and predicted presences and absences from cross-validation of empirical Bayesian models, by primary sampling method. Empirical Bayesian models were adjusted for overdispersion.

Primary sampling method	Number of events in which one of 16 species was not caught	Percent of correctly predicted events in which species was present and missed ^a	Percent of correctly predicted events in which species was absent ^a	Percent of events correctly predicted for presence or absence when species not caught ^a
Electric seine: 30 ft	555	8	98	75
Electric seine: 50 ft	112	10	97	56
Backpack electrofisher	126	42	73	62
Net seine: 20 ft	110	18	97	73
Boat electrofisher	136	38	83	60
Combined results	1,039	20	93	69

^a Based on known presence from combined catch from rotenone, all passes with primary gear, and block net.

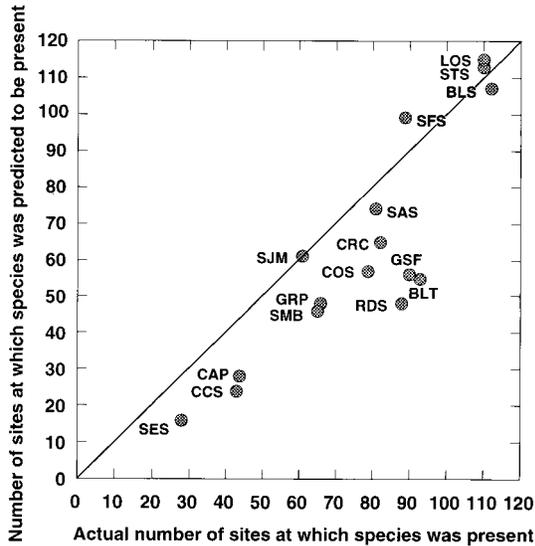


FIGURE 3.—Number of sites at which each of 16 species was predicted to be present by an empirical Bayesian model with contagion adjustment for zero catches plus those present in primary samples versus the number of sites each species was known to be present (see Table 1 for three-letter codes for the species). The diagonal line represents perfect agreement between predicted and actual presence.

and hence, are fully compatible with Endangered Species Act regulations, which only consider species presence (as opposed to density above a certain threshold).

Additionally, $P(F|Co)$ estimates can be used to develop predictive models of the effects of land-use or stream habitat and could be incorporated into formal decision analysis and risk assessment (sensu Clemen 1996). A graphical portrayal of probabilities of presence, such as in GIS systems, could also be used to derive contours of probability of presence.

$P(F|Co)$ estimates, combined with information of known presence when the species is caught, is also useful in expressing probability of joint presence, from which the species richness estimates derived here is one example. Other combinations could help answer common ecological questions that require a multispecies response for each sample, such as the probability of co-occurrence of two or more species representing a fish guild or a predator-prey combination.

Any comparable set of $P(F|Co)$ probability estimates must, logically, be referenced to a constant habitat area, which in our example was 1000 m² of stream surface area. The issue of an area ref-

erence standard is also germane to species richness estimates, as discussed below.

Sampling Protocol and Design

The example of an inferential approach to estimating species richness outlined here contrasts with the sampling effort approach mentioned in the Introduction. The latter presumes that a predictable proportion of species present will be caught by sampling a predetermined sample area. Cumulative numbers of species caught suggest that wider streams require a longer stream length to be sampled representatively (Lyons 1992; Angermeier and Smogor 1995). Even though none of these authors recommend a specific ratio of length to width to estimate a given proportion of species present, constant-ratio sampling protocols are becoming widespread in the belief that a consistent proportion of species will be captured. Although the method we describe here can accommodate data from that protocol, we are concerned about this trend for several reasons.

Angermeier and Smogor (1995) summarized the available cumulative catch data in streams and concluded that sampling of reaches from 5 to 105 stream widths was necessary to catch 95% of estimated species present and that a sampling-effort design was not cost-effective across different streams. Lyons (1992) found that the sampled distance required to catch 95% of the estimated species richness asymptote was positive but variable and poorly related to stream width ($P = 0.21$; over a 3.5-fold range of widths among 10 streams). He cautioned that different capture efficiencies must account for part of the variation.

We agree that the spatial distribution (Angermeier and Smogor 1995) and scale of habitats influence species distributions, but we emphasize that the large variation in detectability warrants its inclusion. The longer reaches that typically need to be sampled for a 95% catch of species richness in larger streams can be explained by decreasing catchabilities that have been observed as stream depth and width increase (Bayley and Dowling 1993). The larger an area sampled, the greater the number of vulnerable individuals (n in equation 1), which partially compensates for decreasing individual probability of capture, q . However, for detectability to be constant, these two factors would need to change in concert for every species as a function of stream width. Angermeier and Smogor (1995) observed that to accurately characterize fish community structure, increased effort (as area sampled) is needed as relative density of

TABLE 4.—Summary of known species richness estimates from 121 sites compared with primary sample data only and with estimates from cross-validation of empirical Bayesian models applied to primary sample data. Empirical Bayesian models were adjusted for overdispersion (CI = confidence interval).

Primary sampling method	Number of samples	Mean of known species richness ^a	Primary sample catches			Samples (%) in which number species from primary sample was within predicted 90% CI	Empirical Bayesian model estimates		
			Percent of samples in which all species present were caught	Mean number of species	Percent bias ^b		Mean species richness	Percent bias ^b	Samples (%) in which known species richness was within predicted 90% CI
Electric seine: 30 ft	70	10.1	20	8.1	-19.9	62	9.6	-1.8	79
Electric seine: 50 ft	13	11.4	0	7.4	-35.1	38	9.6	-13.8	62
Backpack electrofisher	13	9.8	8	6.3	-35.7	8	10.2	9.1	85
Net seine: 20 ft	13	10.1	15	7.5	-25.6	54	9.4	-3.3	62
Boat electrofisher	12	10.6	0	4.7	-55.4	0	9.0	-13.9	67
Combined results	121	10.3	14	7.4	-27.4	47	9.6	-3.3	74

^a Known species richness was based on combined catch from rotenone, all passes with primary gear, and block net and was limited to the 16 species considered.

^b Percent bias was estimated as 100-(observed or estimated number of species - known species richness)/(known species richness) for each sample; means of these values are reported.

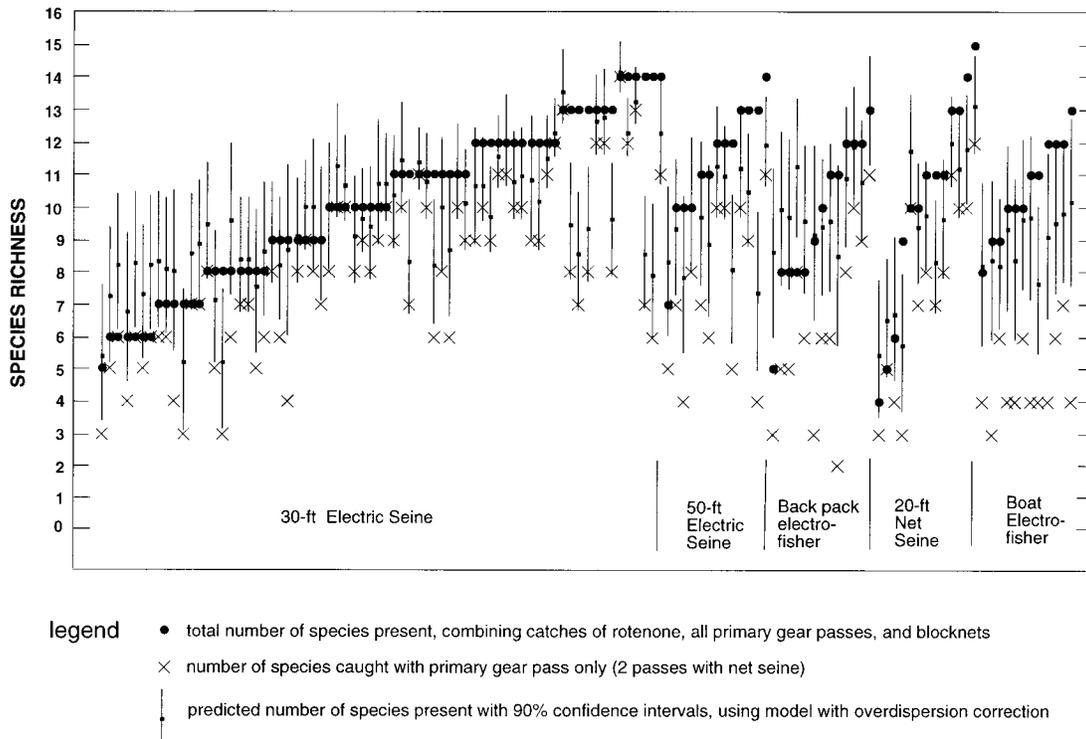


FIGURE 4.—Numbers of species present and 90% confidence intervals as determined by combined catches with rotenone, primary gear, and block net (large solid circles); by primary gear catches (x); and by the Bayesian model (small solid squares). The 121 samples were ordered by primary gear and numbers present.

fish declined. This is expected to be at least partly the affect of a small n on detectability.

Interpretation of uncorrected catches from a wide range of sampled areas is problematical. A typical watershed, through fourth-order streams, could have fish-bearing reaches with mean summer widths ranging from 1 m to 30 m (e.g., Bayley and Dowling 1993). Applying the sampling effort protocol as a constant-ratio would mean that the areas sampled covered a 900-fold range (the square of the ratio of maximum to minimum mean width). The non-linear, power relationship $S = aA^b$ (species number, S , as a function of area, A , with a and b fitted constants) encountered in many such systems and samples (Preston 1962) demonstrates that a simple correction, proportional to sampled area, would be invalid because b is less than 1. Applying a typical value of $b = 0.3$ to the numerical example above would result in an eight-fold range in species richness due to sampled area alone. Without an independent means to estimate the supposed constants a and b , potential ecological or management effects on species richness would be confounded, due to stream size and position in the watershed, by the unknown effect of sampled area that frequently covaries with such effects.

Sampling protocols based on the sampling effort approach can also be cost-prohibitive or impossible because of access limitations. Maintaining an effort level for consistent detectability of rare or difficult-to-sample fish species can result in large numbers of required samples. For example, 120 samples would be required to maintain a 95% probability of detecting the presence of rare fish species (mean density <0.10) under an assumed average sampling efficiency of 25% (Bonar et al. 1997). Similarly, applying the sampling effort protocol to wide streams results in very large sampled areas. For example, a 30-m-wide stream would require a sampling quadrat about 1,100 m long to obtain a reliable estimate of species richness (Lyons 1992).

Conversely, limiting the range of stream widths sampled in a basin would undersample the natural range of many riverine species and communities. We therefore consider it advantageous to be able to make inferences on species richness and presence on a standard area basis. Sampled areas do not have to be constant in order to apply our approach, but the inference from an observed presence ($p_i = 1$), if one or two individuals of a rare species are caught in a sampled area much larger than the standard area, would have to be adjusted so that presence is not a function of area sampled.

Restricting the area sampled to as narrow a range as is practically possible also has positive implications for habitat and scale, as discussed below.

When there is a need to design surveys that relate habitat to fish species, a wide range of sampled areas is problematical. An inferential model could be applied to survey results with a constant-ratio protocol to estimate species richness and probability of presence. However, the data collected by that protocol would be less powerful in interpreting species-habitat relationships because (1) the geometric increase of area sampled in wider streams would typically include more habitat types, (2) the species-area effect noted above would confound interpretation, and (3) sample variance is influenced by sample unit size (Wiens 1989). A conventional survey operating within practical constraints, such as one sampling from a narrow range of reach lengths or a riffle-pool sequence, cannot be perfect in terms of associating species with specific habitat types for each sample. However, spending effort on fewer but larger samples on wider rivers would provide much less information than taking more but smaller samples, providing that a practical minimum reach length that ensures predictable catchability is maintained. Splitting large samples into subunits will not help because spatial autocorrelation will reduce statistical power and complicate analyses. A valid design maintaining site areas close to a standardized area can include larger streams, even if the habitat sizes exceed the sampled area.

Using a narrow range of sampled areas also permits valid ecological inferences when dealing with larger scales within or across habitats. When spatial scale increases beyond that of the individual sample it is obvious that probability of presence and richness will tend to increase, but estimating values at larger scales is not trivial, unless a single estimate for a large, intensively sampled basin is desired. When the sample unit is consistent on a spatial basis, estimates of $P(F|C_0)$ from two or more samples can be combined to estimate joint probabilities and species richness across larger units, such as defined reach lengths or habitat types.

An argument for consistently large sampled areas or more intensively sampled areas can be made for less common species because large numbers of zero catches can decrease the power of statistical inference. However, accuracy of inferences is generally more influenced by low numbers of samples that capture each species than by the number or proportion of zero catches. Changing the design

to one comprising a smaller number of larger samples may not be an improvement, and an optimum tradeoff should be estimated by incorporating catchability and a sample variance from preliminary samples.

Finally, the sampling-effort approach does not allow for incorporating existing data collected with different methods or effort levels, such as from historical fish collection data (Figure 1) or from current surveys that include different gear that are more appropriate for different habitats. Probably the most crucial factor in answering management or ecological problems related to stream fishes is the number of quantifiable samples over the temporal and spatial universe required. We use the term quantifiable because existing data should have sufficient protocol and habitat description to permit estimates of catchability to be applied based on subsequent calibrations.

In conclusion, using uncorrected catch data from a constant-ratio protocol to estimate richness incorporates biases due to species with variable abundances, catchabilities, and habitat preferences that affect catchability. In addition, there are significant problems interpreting data based on widely varying sampled areas. Species detectability must be accounted for before considering ecological effects. Any design approach that attempts to optimize by sample, rather than through the design of a set of comparable samples, will have similar problems. Our arguments for developing inferential approaches apply to any composite measure that depends on species detectability, such as the Shannon–Wiener diversity measure or the Index of Biotic Integrity and its metrics.

Further developments.—Although the method described here is logical and supported by validation tests, it requires significant computation and some experience with statistics. Alternative statistical approaches, such as the use of conjugate distributions (Carlin and Louis 1996), would simplify computation and produce variance predictors for probability of species presence.

Because of the limited but essential information provided by the zero-catch observation, the prior estimate inevitably has a strong effect on the Bayesian adjusted estimates. Several potential improvements may be feasible, such as including a larger set of existing samples from similar communities in ecologically applicable systems in the region. Any single predictive model of abundance will inevitably be incomplete and will tend to overestimate abundance in low-density areas. A two-part, conditional model (e.g., Welsh et al. 1996),

in which one part defines conditions for absence, may be worth the cost of additional parameters but may require a larger set of samples for prior estimation than we used in our example. Such a process is certainly advisable when additional ecological or physiological information precludes any reasonable likelihood of species presence from particular sites or regions.

These and other improvements need to be tested for sensitivity of the predicted values and accuracy, given variance estimates for catchability and abundance. We anticipate that this process may also lead to simplified computation.

Finally, optimum sampling design of surveys, as hinted above, needs to explicitly account for detectability. To assess candidate designs requires simulation of sampling processes. Catchability estimates should be combined with information on preliminary or historical samples representing spatial and temporal distributions relevant to the questions being asked. The tradeoff between the cost of individual sampling intensity (area sampled, methods used, number of passes) and the costs associated with sampling frequency is critical and needs to be assessed in the context of current questions, as well as those likely to be asked from surveys in the future.

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