Estuaries and Coasts Vol. 29, No. 6B, p. 1172–1184 December 2006

Experimental Evaluation of Biases Associated with Sampling Estuarine Fishes with Seines

MARK A. STEELE*, STEPHEN C. SCHROETER, and HENRY M. PAGE

Marine Science Institute, University of California, Santa Barbara, California 93106

ABSTRACT: Beach seines are widely used to estimate the density and species richness of fishes in estuaries. We evaluated the causes and extent of bias in estimates from seines using a series of field experiments in small estuaries in southern California, USA. Seining in spatially paired areas that were either enclosed by block nets or not, revealed that seines used without block nets underestimated density by more than 4-fold and species richness by more than 2-fold relative to blocked areas. Seining in paired blocked areas with seines of two lengths revealed that net length affected estimates of density, but not species richness; a 7.6-m long seine produced 1.6-fold higher estimates of total density than did a 15.2-m long seine due to increased catches of demersal fishes, but not midwater species. Paired sampling in blocked areas also revealed that many fishes initially evaded capture by the seine. Estimates of density but not species richness were significantly higher in areas through which a seine was swept 5 times compared to once. This was due to higher catches of demersal fishes but not midwater fishes in areas seined 5 times. Repeated seining through blocked areas revealed that the vast majority (90% or more) of species and individuals of midwater fishes were captured within the first 5 sweeps, compared to only about 50% of the individuals of demersal species. A mark-recapture study in blocked areas revealed lower probabilities of capture for demersal species relative to midwater species.

Introduction

A wide variety of both basic and applied research in estuaries relies on estimates of density or species richness of fishes. Seines are one of the most widely used gear types for sampling estuarine fishes (Allen 1982; Allen et al. 1992; Ikejima et al. 2003; Koutrakis et al. 2005; Lukey et al. 2006), because they capture a wide variety of species and are relatively easy to use. But there is often substantial variation in the design and use of beach seines, even within regions (Allen et al. 2002; Desmond et al. 2002), and relatively little is known about how these variations affect their efficiency in sampling estuarine fishes. The lack of standardization combined with a lack of understanding of the biases of the various methods used makes comparison among research projects problematic (Rozas and Minello 1997).

To provide interpretable values, estimates of density and species richness from seines must be unbiased (accurate) or at least representative (i.e., accurately predict true values). We explored how seine length, the use of block nets, and sampling effort within blocked areas affected biases in estimates of density and species richness of fishes. Seine length may influence estimates of density or species richness if capture efficiency is a function of net length. This might occur if it is more difficult to keep the lead line on longer nets in contact with the bottom, allowing increased escapement under the lead line. Precision of the estimate of density may change with seine length if fishes are found in patches, because seines that sample small areas may tend to fall either inside or outside of patches, generating high variability among samples (Wiens 1989). Larger nets that sample larger areas will tend to average out patchiness but will limit replication relative to smaller nets because the greater numbers of fish they capture will increase handling time.

Whether seines are used in conjunction with block nets may also influence catch efficiency and affect estimates of density or species richness. Block nets have been used in some studies on estuarine fishes (Weinstein 1979; Nordby and Zedler 1991; Ambrose and Meffert 1999), but not others (Allen 1982; Yoklavich et al. 1991), complicating comparisons among them. Block nets, which enclose an area to be sampled, can reduce sampling bias of seines by retaining fishes that would otherwise flee the area before they can be captured. Use of block nets in combination with repeated sweeps of a seine through the blocked area allows capture of fish that evade capture by preceding sweeps, further reducing bias.

While block nets have the advantage of providing less biased estimates of fish density and species richness, they require much greater sampling effort than unblocked seines and they complicate logistics. Although it is likely that samples taken without block nets underestimate actual levels of species

* Corresponding author; current address: Department of Biology, California State University, 18111 Nordhoff Street, Northridge, California 91330; tele: 818/677-3340; fax: 818/677-2034; e-mail: steele@lifesci.ucsb.edu

TABLE 1. Summary of studies: sites, habitats, replication, and dates. Study 4 was conducted within the block-netted member of each pair of samples in Study 1. See Study 1 for details.

Estuaries Studied	Habitats Sampled (n of Samples)	Dates of Study
Study 1: Effects of block nets		
Carpinteria Salt Marsh	Main channel (3 pairs), tidal creek (8 pairs)	October 3–4, 2003
Los Peñasquitos Lagoon	Main channel (3 pairs)	October 17, 2003
San Elijo Lagoon	Main channel (2 pairs)	October 16, 2003
Study 2: Effects of seine length		
Carpinteria Salt Marsh	Main channel (1 pair), tidal creek (3 pairs)	May 14–15, 2003
Los Peñasquitos Lagoon	Main channel (1 pair)	May 29, 2003
San Elijo Lagoon	Main channel (1 pair)	June 26, 2003
Study 3A: Single sweep versus 5 sweeps		
Carpinteria Salt Marsh	Main channel (5 pairs), tidal creek (3 pairs)	December 15–16, 2003
Study 3B: Catch versus effort in blocked areas seined 10 times		
Carpinteria Salt Marsh	Main channel (6), tidal creek (6)	April 22–23, 2004
San Dieguito Lagoon	Main channel (5), basin (2)	April 26–27, 2004

richness and density, if these underestimates are consistent and measurable, they could provide representative estimates of the true values at a substantial savings in sampling effort. Such reductions in sampling effort are important because they would allow greater replication of samples and more precise estimates of fish populations. Here we measure the magnitude of the effects of using block nets on estimates of density and species richness and test whether estimates obtained without block nets predict values obtained with block nets. We also explore how repeated sweeps of seines through enclosed sample areas affect estimates of density and species richness in order to determine the relationship between seining effort and accuracy. We measure both relative bias, by comparing estimates of density and species richness from different treatments, and absolute bias, by measuring seine capture efficiency with mark-recapture and depletion estimation techniques (Zippin 1956). We evaluate effects on density of midwater and demersal species separately because evidence from other systems indicates that seines sample these two habitat guilds with very different efficiencies (Lyons 1986; Parsley et al. 1989; Pierce et al. 1990; Allen et al. 1992).

Materials and Methods

System Studied

We studied assemblages of fishes in 4 estuaries in southern California, USA: Los Peñasquitos Lagoon (32°56′N, 117°16′W), San Dieguito Lagoon (32°58′N, 117°16′W), San Elijo Lagoon (33°01′N, 117°17′W), and Carpinteria Salt Marsh (34°23′N, 119°32′W) (Table 1). These small, shallow (<2 m depth at high tide in most places) estuaries are typical of most estuaries in the region (with notable exceptions; see Allen et al. 2006 for an overview of these systems). The estuaries we studied had 1–3 large (>8 m across) channels with branching smaller and shallower channels. We distinguished between these two types of channels (main channels and tidal creeks, respectively) because they differ in physical attributes and there is evidence that fish assemblages differ between them as well (Desmond et al. 2000). Tidal creeks tend to be steeper in cross section than main channels and usually drain completely during extreme low tides, whereas main channels always retain some water. One of our study sites (San Dieguito Lagoon) also contained a large, shallow (<2 m at high tide), man-made basin, in which we conducted limited sampling. Submerged aquatic vegetation was not present in significant densities at our study sites, as is generally the case in estuaries in southern California, so there was little concern that it influenced the efficiency of our seines, as has been noted in other systems (Pierce et al. 1990).

We divided the fishes we sampled into two habitat guilds: midwater (fishes normally found in the water column) and demersal (those normally found resting upon the bottom). In our samples the midwater guild included *Atherinops affinis*, *Fundulus parvipinnis*, *Gambusia affinis* (an introduced species), *Cymatogaster aggregata*, *Anchoa compressa*, *Genyonemus lineatus*, and *Mugil cephalus* (listed in approximate order of relative abundance). The demersal guild included the gobies *Clevelandia ios*, *Quietula y-cauda*, *Gillichthys mirabilis*, *Ilypnus gilberti*, and *Acanthogobius flavimanus* (an introduced species); and *Hypsopsetta guttulata*, *Leptocottus armatus*, *Paralichthys californicus*, *Porichthys notatus*, *Syngnathus auliscus*, *S. leptorhynchus*, *Hypsoblennius gentilis*, and *Pleuronichthys ritteri*.

General Methods

We used small seines that were similar or identical in design to many of those used to collect fishes in estuaries around the world. Our seines were either 7.6 or 15.2 m long, and all were 1.8 m deep and built of 3.2-mm mesh knotless nylon netting (delta style). They were heavy leaded (one 75.6 g lead weight every 30 cm on the lead line) and the float line had one float every 30 cm that provided 156 g of buoyancy. The nets were attached to 2-m long wooden poles (brailles) on either end, which a person on either end held while hauling the net. In all but one study, we used seines that were a single panel of netting 7.6-m long. In our study on the effects on seine length, we also used a 15.2-m long bag seine.

In all studies, we set the seines parallel to shore and two persons holding the brailles hauled the seine across the channel by wading through the water and onto the opposite shore. We sampled areas that were no deeper than 1.5 m, and in most cases, we sampled from one bank of a channel to the other bank. In all but one treatment in one experiment (Study 1), we seined in areas enclosed by block nets. The block nets were seines identical in design to the 7.6-m seine described above, except that they varied in length (up to 35 m), allowing us to enclose different sized areas. With block nets, we enclosed rectangular areas that were narrower than the length of the seine used to sample them (details below). Each haul of a seine through the blocked area swept the entire area enclosed (i.e., the seine spanned from one block net to the other). In channels that were <30–35 m wide, the two block nets were set parallel to one another and spanned the entire channel. In areas where the banks were >30–35 m apart, we enclosed a rectangular area bounded on three sides by the two block nets (one set in the shape of an L, the other in a straight line) and on the fourth side by the bank. In these areas we seined from the rear block net panel towards shore. We set the distance between the parallel portions of two block nets at 6 m, and we measured the distance between the two banks or the bank to the rear portion of the blocked area. We calculated the area sampled from these values. Block nets were deployed by two persons who waded them out and into position, where they were then staked down.

We sampled during relatively flat tides of mid to low tidal range, during which times tidal currents were weak. Tidal currents were often strong enough that it was necessary to secure the block nets with wooden stakes that were placed between the netting and the float and lead lines every 1–5 m and driven into the bottom. These stakes kept the nets in place, upright, and the lead line in contact with the bottom. The spacing of stakes varied inversely with current strength.

In addition to counting fishes caught by seining within the blocked area, we also counted fishes caught in the block nets as part of the estimate of density and species diversity for the area sampled. The block nets were retrieved as normal beach seines would be. To accomplish this, the far ends of the two nets were drawn together, then one net was drawn inside the other, and then both far ends were hauled towards the near shore. Once the far ends of both nets had reached the near shore, the inner net was pulled onto the shore. The outer net was hauled in after that. Fishes captured in the seine and the block nets were placed in large (c. $1 \times 0.7 \times 0.4$-m high) bins full of water, identified, counted, and released.

Study 1: Effects of Block Nets

We conducted an experiment to test whether it was necessary to use block nets in conjunction with seines to obtain accurate or representative (predictive) indices of species richness and density of fishes. We took paired samples ($n = 16$ pairs) in immediately adjacent blocked and unblocked areas in 3 estuaries (Table 1). We used a 7.6×1.8 m seine to sample both 6-m-long areas within each pair. The distance between banks ranged from 2.6 to 35 m, so areas sampled ranged from 15.6 to 210 m^2.

In unblocked areas, we captured fishes with one haul of a seine across a 6-m long segment of a tidal creek or main channel. Before sampling, we drove pairs of poles spaced 6 m apart into both banks and used these to guide our progress while hauling the seine across the channel to ensure that our estimates of the area sampled were reasonably accurate. As the unblocked segment was seined, two block nets spaced 6 m apart were simultaneously waded across the blocked segment and then staked in place. The blocked segment was then sampled with one seine haul and by the two block nets as they were retrieved.

We used analysis of variance (ANOVA) to test whether estimates of species richness or density (midwater, demersal, and total) differed between blocked and unblocked areas. The model included the terms Treatment (block nets used or not; a fixed factor), Estuary (random), Station (random, nested within Estuary), and the Treatment × Estuary interaction. Including the term Station accounted for the paired design of the study. In this model, we pooled the two habitats sampled (Table 1), because not all habitats were sampled in all wetlands, making it impossible to separate variability attributable to habitat type from variability among estuaries. Densities were log-transformed $[\ln(x + 0.1)]$ to meet the assumptions of normality and equality of variances, but no transformation of species richness (number of species per sample) was needed. To test whether density or species richness in blocked areas could be predicted from the values of those variables in unblocked areas, we used ordinary least squares (OLS) regression (with densities transformed as above).

Study 2: Effects of Seine Length

To measure the effects of seine length on estimates of density and species richness, we conducted an experiment comparing estimates from a seine that was 7.6 m to those from a seine 15.2 m long. Other than length, the two seines were identical except that the longer seine had a 1.8 × 1.8 × 1.8 m bag in its center, whereas the smaller seine was a single panel of netting. We incorporated a bag into the design of the larger seine because we wanted to replicate exactly a seine design commonly used in studies of southern California estuaries (e.g., Allen et al. 2002; Desmond et al. 2002). The presence of the bag in one seine but not the other confounds our test of the effects of net length, but does so directionally (higher catches are expected with a bag seine) and allows unambiguous interpretation of our results.

We compared estimates of density and species richness obtained in 6 pairs of segments of tidal creeks and main channels that we sampled with the 7.6-m and 15.2-m long seines. Two immediately adjacent segments were enclosed with block nets; one was 6 m long and was sampled with the 7.6-m long seine, and the other 12 m long and sampled with the 15.2-m long seine. The width of the blocked segments (bank to bank) was the same between paired segments, but ranged from 3 to 30 m among pairs, so areas sampled ranged from 18 to 360 m^2.

We sampled each of the 12 enclosed segments by sweeping one of the two seines through it 3–8 times. The number of sweeps varied among but not within pairs so that sampling effort was identical for the two seine lengths. After 3–8 sweeps, the block nets were hauled in and fishes caught in them were also included in the estimates of density and richness for that sample.

We tested whether the two nets of different lengths provided different estimates of density and species richness with ANOVA. For analysis, data were pooled among habitats and estuaries because replication within estuaries was low and not all habitats were sampled in all estuaries. Densities were log-transformed [$\ln(x + 0.1)$] to meet the assumptions of normality and equality of variances, but no transformation of species richness (number of species per sample) was needed.

Study 3A: Effects of Seining Effort within Blocked Areas—Single Sweep versus 5 Sweeps

Study 1 addressed the effects of block nets on estimates of the density and species richness of estuarine fishes, but provided limited information on how the number of seine sweeps within blocked areas might affect these estimates. To address this question, we conducted an experiment that compared estimates from blocked areas that were seined just once before hauling the block nets with estimates from blocked areas that were swept with a seine 5 times before hauling the two block nets. As with the previous studies, the catch of the block nets was added to that of the seine haul(s). We sampled spatially paired 6-m long segments of tidal creeks and main channels with 7.6 × 1.8 m seines. These segments were 5–28.5 m wide; areas of 30–171 m^2 were sampled. All sampling ($n = 8$ pairs of replicates) was conducted in Carpinteria Salt Marsh (Table 1).

ANOVA was used to test for differences in estimates of species richness and density between the two treatments. The factors Treatment (1 or 5 sweeps), Habitat (tidal creek or main channel), Station (a unique identification for each pair of samples; nested within habitats), and the Treatment × Habitat interaction were included in the model. Log transformations (details in Table 2) of density estimates were required to meet the assumptions of normality and equality of variances; but no transformation was needed for species richness. We used OLS regression to test whether density or species richness in blocked areas seined 5 times could be predicted from values of those variables obtained in blocked areas seined only once, with data transformed as above.

We evaluated the adequacy of the 5 sweeps plus block net sweeps in estimating true densities in the areas sampled by using the Leslie depletion technique (Leslie and Davis 1939; Zippin 1956). We used the 5 beach seine sweeps but not the block net sweeps in these analyses, because we expected the probability of capture to differ between the two types of nets because we anticipated that fish would be chased into the block nets during the initial 5 sweeps. If the probability of capture differed between the two types of nets, this would violate an assumption of the depletion method. It was impossible to estimate densities with the depletion method for some replicates because catches did not decline with additional seine sweeps. So instead, we estimated the overall densities using the means per sweep from all 8 replicates.

Study 3B: Effects of Seining Effort within Blocked Areas—Catch versus Effort in Blocked Areas Seined 10 Times

To determine how many seine sweeps within areas enclosed by block nets is enough to provide accurate estimates of density and species richness in those areas, we intensively sampled 19 areas

TABLE 2. Comparison of estimates of species richness and density obtained with 7.6 × 1.8 m seines swept either 1 or 5 times through paired areas enclosed by block nets. Catches from the block net hauls are included in the estimates. The experiment was conducted in two habitats (tidal creeks and main channels) in Carpinteria Salt Marsh.

	Means and Variation					ANOVA Results[c]							
	1 Seine Sweep		5 Seine Sweeps			Treatment (1 versus 5 Hauls)		Habitat (Creek versus Channel)		Treatment × Habitat		Station (Habitat)	
Variable	Mean (SE)	CV%	Mean (SE)	CV%	n	$F_{1,6}$	p	$F_{1,6}$	p	$F_{1,6}$	p	$F_{6,6}$	p
Number of species	2.88 (0.55)	54	3.25 (0.41)	36	8	0.8	0.41	11.0	0.02	<0.1	0.94	2.0	0.21
Density													
All species[a]	0.68 (0.33)	135	1.01 (0.28)	78	8	7.5	0.03	<0.1	0.98	2.7	0.15	9.2	0.008
Midwater species[b]	0.36 (0.31)	244	0.23 (0.19)	235	8	0.3	0.62	2.5	0.16	0.5	0.50	7.4	0.01
Demersal species[a]	0.32 (0.10)	85	0.78 (0.24)	87	8	34.0	0.001	0.7	0.42	4.1	0.09	17.2	0.002

[a] Transformed to ln(x + 0.1) to satisfy the assumption of normality for ANOVA.
[b] Transformed to ln(x + 0.01) to satisfy the assumption of normality for ANOVA.
[c] Effects of treatment, the interaction of treatment with habitat, and station(habitat) were tested using the residual as the error term; effects of habitat were tested using station(habitat) as the error term.

enclosed within block nets. We swept the entirety of each enclosed area 10 times with a seine before retrieving the two block nets. We used these data to evaluate how estimates of density and species richness changed as a function of the number of times a seine had been swept through the area. We used the Leslie depletion method to estimate true densities in the areas sampled and to determine how effective the 10 sweeps were at estimating those densities. To provide the most robust estimates of the actual densities in the enclosed areas, we used the Leslie depletion technique with means per sweep (1–10) from all 19 replicates, rather than estimating actual densities in each replicate.

The 19 areas sampled were divided between 2 estuaries and among 3 habitats (Table 1). We sampled 6-m long segments of tidal creeks, main channels, and basin shoreline with 7.6 × 1.8 m beach seines. These segments ranged in width from 3.9 to 24.5 m, resulting in sample areas of 23.4–147.0 m^2.

We evaluated graphically how estimates of density and species richness changed as a function of the number of sweeps completed within the blocked areas. This evaluation revealed that ceasing seining after 5 sweeps (plus sweeps by block nets) might represent an acceptable compromise between accuracy and effort; so we used ANOVA to test whether the accuracy of estimates obtained after 5 sweeps (plus block net sweeps) differed among estuaries or habitats. Accuracy of the 5-sweep method was defined as the proportion of the best estimate of density or species richness that it produced. The best estimates were derived from the total catch from 10 sweeps plus two block net sweeps (i.e., not Leslie depletion estimates: see Results). Because we did not sample all of the same habitats in the two estuaries (Table 1), comparisons between estuaries were restricted to samples from the main channel habitat, comparisons between main channel and tidal creek habitats were restricted to Carpinteria Salt Marsh, and comparisons between main channel and basin habitats were restricted to San Dieguito Lagoon. It was necessary to transform the proportion of the total catch obtained with the 5-sweep method to arcsine$\sqrt{X}$ to satisfy the assumption of normality for both total species richness and density of midwater species. No transformation of equivalent data for density of demersal species was needed.

Study 4: Estimating Catch Efficiency of Seines

While conducting Study 1, we also estimated catch efficiency. Specifically, in the blocked member of each pair of samples, we measured recovery efficiency: the proportion of tagged fishes that were recovered by one seine sweep plus two block net sweeps. We released a total of 1,161 tagged fish of 14 species (details in Table 3) into 12 blocked areas in 3 estuaries (Table 1). Fish for the study were captured with seines in nearby areas, tagged with a subcutaneous injection of nontoxic acrylic paint (visible through the skin), and released into the blocked areas. Tagged fish were released throughout each blocked area and allowed to redistribute themselves for at least 10 min before the area was seined.

We used ANOVA to test whether recovery efficiency differed among estuaries or between habitats (tidal creek or main channel). We restricted the tests for differences among estuaries to samples taken in the main channel habitat, because this was the only habitat sampled in all 3 estuaries (Table 1). Likewise, we restricted the tests for differences between habitats to samples taken in Carpinteria Salt Marsh because this was the only

TABLE 3. Recovery efficiency of one sweep of a 7.6 × 1.8 m seine plus the catches from the 2 block nets as estimated by releasing marked fishes into areas enclosed with block nets.

Species or Group[a]	Total Number Released	Total Number Recaptured	% of Total Recaptured	Average % Recaptured[b] Mean ± SE (n)
Midwater species				
Atherinops affinis	290	222	76.6	75.9 ± 8.3 (8)
Fundulus parvipinnis	496	351	70.8	71.4 ± 5.3 (9)
Other midwater species	1	1	100	(0)
Demersal species				
Clevelandia ios	285	93	32.6	30.3 ± 6.2 (9)
Ilypnus gilberti	35	16	45.7	57.7 (1)
Other demersal species	54	13	24.1	(0)
Midwater species	787	574	72.9	73.9 ± 5.5 (12)
Demersal species	374	122	32.6	30.6 ± 5.2 (11)
All species	1,161	696	59.9	61.3 ± 4.9 (12)

[a] Species for which < 10 tagged individuals were released into any replicate are not listed individually, but are included in calculations for habitat guilds. These species were (midwater guild) *Genyonemus lineatus*; (demersal guild) *Gillichthys mirabilis*, *Hypsoblennius gentilis*, *Hypsopsetta guttulata*, *Leptocottus armatus*, *Paralichthys californicus*, *Pleuronichthys ritteri*, *Porichthys notatus*, *Quietula y-cauda*, and *Syngnathus auliscus*.

[b] Replicates in which < 10 tagged individuals of the species or group were released are excluded from the calculations of average percent recaptured.

estuary in which we sampled more than one habitat. Recovery efficiencies of midwater species were transformed to arcsine$\sqrt{X}$ to satisfy the assumption of normality, but no transformation was needed for recovery efficiencies of demersal species. We tested whether recovery efficiencies differed between midwater and demersal guilds with paired *t*-tests, with pairing by sample (replicate).

Results

Study 1: Effects of Block Nets

A single seine sweep in an unblocked area significantly underestimated species richness and density of fishes relative to the combined catch of a seine sweep and block net sweeps in a paired area enclosed by block nets (Fig. 1 and Table 4). Estimates of density and richness were more than 4-fold (1.09 versus 0.28 fish m^{-2}) and 2-fold (2.94 versus 1.44 species per sample) greater in samples obtained using block nets than in samples obtained without them. Higher overall density estimates in blocked areas relative to unblocked areas were caused by increased catches of both demersal and midwater species, though these estimates differed significantly only for demersal species. The differences in density and species richness between blocked and unblocked samples were relatively consistent among estuaries as shown by nonsignificant block net treatment × estuary interactions in ANOVA. In addition to being higher, estimates of species richness, total density, and density of demersal species were somewhat less variable (8–19% lower CV) in samples from blocked areas than unblocked areas. Estimates of density of midwater species were 80% more variable in samples from blocked areas than unblocked areas. This greater variability was completely attributable to a single exceptional sample in which the density of midwater fishes was more than 6-fold higher than in the next most dense sample.

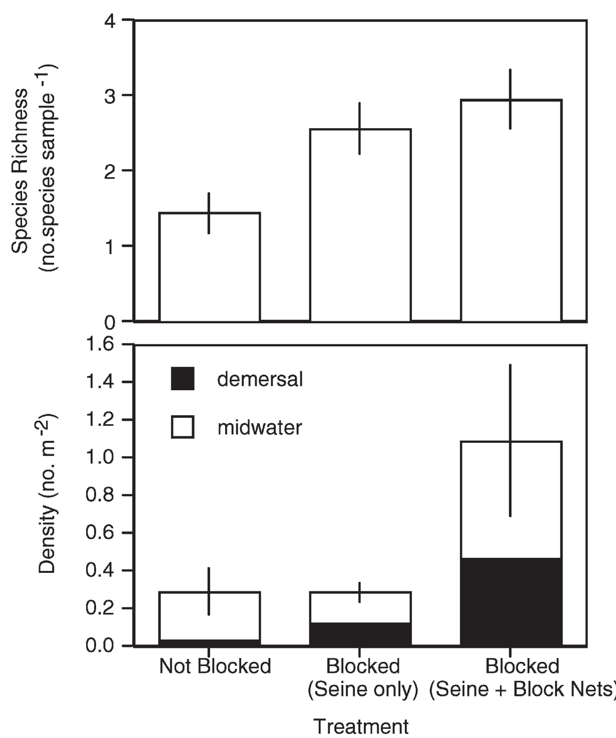

Fig. 1. Comparison of estimates of species richness and mean density of fishes obtained with a 7.6 × 1.8 m seine in paired areas that were either enclosed with block nets or not. Error bars are ± 1 SE (shown for species richness and total density) and n = 16 per bar.

TABLE 4. Results of ANOVA comparing estimates of species richness and density obtained with a beach seine in paired areas (stations) that were either enclosed with 2 block nets or not enclosed.

Variable	Treatment (with or without Block Nets)		Estuary		Treatment × Estuary		Station (Estuary)	
	$F_{1,15}$	p	$F_{2,13}$	p	$F_{2,13}$	p	$F_{6,6}$	p
Number of species	22.50	<0.001	1.60	0.24	0.22	0.80	3.15	0.02
Density								
All species	12.85	0.003	0.24	0.79	0.98	0.40	2.03	0.10
Midwater species	0.35	0.56	2.33	0.14	0.03	0.98	1.00	0.50
Demersal species	47.63	<0.001	1.54	0.25	3.10	0.08	2.43	0.05

*Effects of Treatment, the Treatment × Estuary interaction, and Station (Estuary) were tested using the residual as the error term; whereas effects of Estuary were tested using Station(Estuary) as the error term. The nonsignificant Treatment × Estuary interaction term was pooled in the error term (following Winer et al. 1991) to produce more powerful tests of the block net treatment.

Two factors caused seines used without block nets to underestimate density and species richness of fishes. The beach seine was less efficient at catching demersal fishes in unblocked areas compared to blocked areas. This is shown by comparing estimates of density of demersal fishes and species richness from the single seine sweep in unblocked areas with the single seine sweep in areas enclosed with block nets (i.e., excluding catches from the block nets themselves). A single sweep of a seine in blocked areas produced statistically higher estimates of the density of demersal species (but not midwater species) and species richness than did a single haul of a seine in unblocked areas (Fig. 1; ANOVA, $F_{1,15} = 17.1$, 19.1, and 0.2; $p = 0.001$, 0.001, and 0.6 for species richness, density of demersal fishes, and density of midwater fishes, respectively). The second way that use of block nets increased estimates of density and to a lesser extent species richness was by capturing in block net sweeps many of the fishes that evaded capture by the beach seine, as shown by increases in these estimates when block net catches were added (Fig. 1).

Not only did seines used without block nets underestimate density and species richness, they generally produced poor indices of these variables. Total density in the unblocked member of a pair predicted little of the variation in total density in blocked areas ($r^2 = 0.09$, $p = 0.26$), apparently because the relationship between the two density estimates for midwater species was weak ($r^2 = 0.01$, $p = 0.76$), whereas the relationship between the two density estimates for demersal species was fairly strong ($r^2 = 0.53$, $p = 0.001$). Species richness in the unblocked area also significantly ($p = 0.02$) predicted richness in the blocked area, but the predictive power of this relationship was relatively low ($r^2 = 0.35$).

Study 2: Effects of Seine Length

Seine length did not significantly affect estimates of species richness. Statistically indistinguishable averages of about 6 species per replicate were obtained with either seine (Table 5), and totals of 11 and 10 species were captured by the 7.6 and 15.2 m seines, respectively. The variability (CV) of the estimates of species richness was nearly identical for the two seines.

The shorter seine tended to produce higher estimates of total density and density of demersal species than did the longer seine (Table 5). The statistically significant c. 2-fold higher estimate of density of demersal species from the shorter seine was responsible for the marginally nonsignificant 1.6-fold higher estimate of total density because the density of midwater fishes did not differ between the two seine lengths. Estimates of total density and density of demersal species were somewhat more variable (15–19% higher CV) from the shorter seine

TABLE 5. Comparison of estimates of species richness and density obtained with 7.6-m and 15.2-m beach seines. Both seines were used in paired areas enclosed by block nets and swept through them 3–8 times before hauling the block nets. Catches from the block nets are included in the estimates.

Variable	7.6-m Seine		15.2-m Seine			Results of ANOVA*	
	Mean (SE)	CV	Mean (SE)	CV	n	$F_{1,5}$	p
Number of species	6.00 (0.63)	26	6.33 (0.72)	28	6	0.35	0.58
Density							
All species	4.81 (1.79)	91	2.96 (0.87)	72	6	6.00	0.06
Midwater species	0.69 (0.37)	131	0.85 (0.46)	132	6	0.20	0.67
Demersal species	4.12 (1.45)	86	2.12 (0.53)	61	6	8.07	0.04

*ANOVA included the factors net length and station. Stations differed significantly in species richness, total density, and density of demersal species ($F_{5,5} > 4.9$, $p < 0.05$), but not quite significantly in density of midwater species ($F_{5,5} = 4.6$, $p = 0.06$).

than the longer seine, but were nearly the same for the density of midwater species.

Study 3A: Effects of Seining Effort within Blocked Areas—Single Sweep versus 5 Sweeps

Five sweeps of a seine through a blocked area produced significantly higher estimates of total density and density of demersal species but not species richness or density of midwater species than did a single sweep. A total of 7 versus 8 species and averages of 2.88 versus 3.25 species replicate^{-1} were captured with 1 versus 5 sweeps (plus the catches of both block nets for both treatments), respectively (Table 2). Estimates of the density of midwater species did not differ significantly between the two treatments (0.36 versus 0.23 fish m^{-2} for 1 versus 5 hauls, respectively; $p = 0.6$). There were large and statistically significant differences between the two treatments in estimates of density of demersal species and of all species combined. Five sweeps plus the catch of both block nets produced a 1.5-fold greater estimate of total density (1.01 versus 0.68 fish m^{-2}; $p = 0.03$) and a 2-fold greater estimate of density of demersal species (0.78 versus 0.32 fish m^{-2}; $p = 0.001$) than did 1 sweep plus the catches of both block nets. Precision of the estimates of richness and density ranged from similar to somewhat better for the 5-sweep than 1-sweep treatment (CVs within 2% to as much as 57% lower for 5 sweeps than 1 sweep). There was no indication that the relative efficiency of the two sampling treatments differed between tidal creeks and main channels, as Treatment × Habitat interactions in ANOVA were not statistically significant.

Estimates of species richness and density obtained with the 1-sweep treatment were significantly correlated with the values obtained in the 5-sweep treatment. The predictive power of this relationship was moderate for species richness ($r^2 = 0.46$, $p = 0.04$) and total density ($r^2 = 0.46$, $p = 0.04$), and somewhat higher for midwater ($r^2 = 0.61$, $p = 0.01$) and demersal species density ($r^2 = 0.71$, $p = 0.006$) when analyzed separately.

The Leslie depletion technique indicated that the 5-sweep treatment provided a good estimate of the actual density of midwater fishes in the areas enclosed by block nets, but the same level of seining effort slightly underestimated density of demersal species. The depletion estimate of midwater species density was 0.18 fish m^{-2}, somewhat less (~ 21%) than the estimate of 0.23 fish m^{-2} that we actually obtained. The depletion estimate of demersal species density of 0.85 fish m^{-2} was slightly greater (c. 9%) than the 0.78 fish m^{-2} we obtained with the 5-sweep treatment.

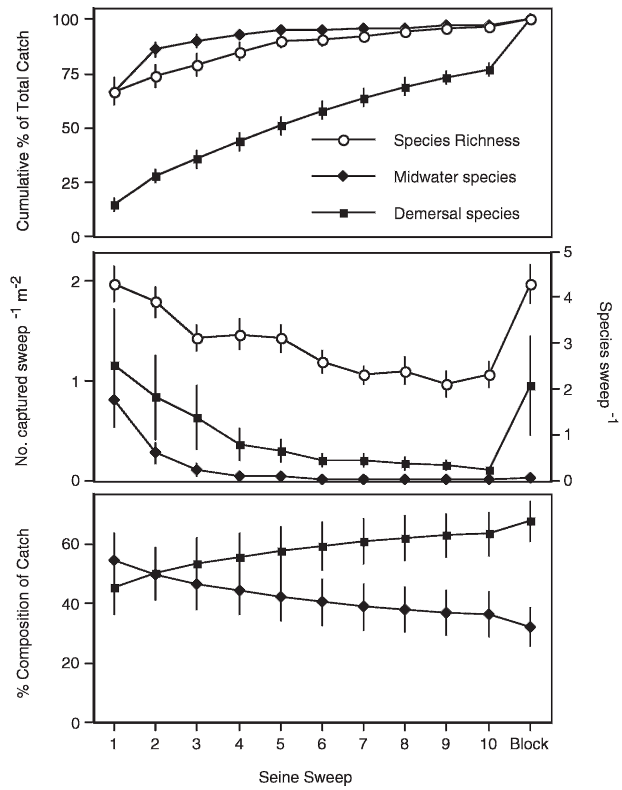

Fig. 2. Catch versus the number of seine sweeps through areas enclosed by block nets that were seined 10 times with a 7.6-m long beach seine before retrieving (and seining with) the 2 block nets. Values are means ± 1 SE and n = 19. For midwater and demersal fishes, the mean % captured was only calculated from replicates in which at least 10 individuals total were captured.

Study 3B: Effects of Seining Effort within Blocked Areas—Catch versus Effort in Blocked Areas Seined 10 Times

Ten sweeps of a seine through an area enclosed by block nets appeared to be quite effective at depleting the vast majority of fish that could be caught with our seines (Fig. 2). Leslie depletion estimates of density of all species combined, and midwater and demersal species separately, were all somewhat less than the densities we actually captured: 5.40 versus 6.46, 1.31 versus 1.37, and 4.27 versus 5.09 fish m^{-2} for depletion estimates versus actual catches for total, midwater, and demersal species, respectively. Examination of the catch per haul versus cumulative catch curves (not shown) using the Leslie method revealed that the reason this method underestimated actual densities was that the per capita probability of capture declined noticeably after 5–6 sweeps. The results of the depletion analysis combined with the observed pattern of depletion indicate that 10 sweeps plus the catch of the two block nets provide a good basis for estimating the efficiency of

TABLE 6. Catch efficiency (percent[a] of total estimate from 10 seine sweeps plus block net sweeps) of 5 seine sweeps within areas enclosed by block nets. Fish captured in sweeps of the block nets were included in the estimates of efficiency. The study was conducted in two estuaries and three habitats.

Habitat	Species Richness Mean% ± SE (n)	Midwater Species (Density) Mean% ± SE (n)	Demersal Species (Density) Mean% ± SE (n)
Carpinteria Salt Marsh			
Tidal creek	97 ± 3 (6)	96 ± 3 (4)	56 ± 4 (6)
Main channel	90 ± 3 (6)	99 ± 1 (5)	40 ± 2 (6)
San Dieguito Lagoon			
Main channel	81 ± 10 (5)	96 ± 1 (4)	50 ± 10 (5)
Basin	94 ± 6 (2)	80 ± 11 (2)	75 ± 10 (2)
Results of ANOVA			
Differences between estuaries[b]	$F_{1,9} = 0.24$, $p = 0.63$	$F_{1,7} = 4.61$, $p = 0.07$	$F_{1,9} = 1.03$, $p = 0.34$
Tidal creek versus main channel[c]	$F_{1,10} = 3.22$, $p = 0.10$	$F_{1,7} = 1.08$, $p = 0.33$	$F_{1,10} = 12.3$, $p < 0.01$
Main channel versus basin[d]	$F_{1,5} = 0.40$, $p = 0.56$	$F_{1,4} = 5.61$, $p = 0.08$	$F_{1,5} = 1.96$, $p = 0.22$

[a] Percentages of total numbers of fishes captured (midwater and demersal) were only calculated for samples in which a total of at least 10 individuals of that group were captured to avoid having percentages based on small numbers unduly influence estimates.
[b] Comparison restricted to samples taken in the main channel habitat.
[c] Comparison restricted to samples taken in Carpinteria Salt Marsh.
[d] Comparison restricted to samples taken in San Dieguito Lagoon.

reduced-effort sampling schemes (i.e., fewer than 10 beach seine sweeps within blocked areas).

We found that estimates of midwater species density changed little after 2 seine sweeps; whereas estimates of demersal species density continued to climb over all 10 sweeps, and catches from the block net sweeps significantly increased this estimate (Fig. 2). The pattern of accumulation of the estimate of species richness was intermediate between the two density estimates, climbing rapidly up to 5 sweeps and changing little after that. After 5 sweeps, species richness estimates were 90 ± 3% (mean ± 1 standard error) of the total captures. Capture efficiency varied markedly between midwater and demersal species. Whereas two sweeps resulted in density estimates for midwater species that were 86 ± 3% of the total captured (with 10 sweeps and both block nets), even after 10 sweeps, demersal species densities were only 77 ± 3% of the total captured. As a result of the different patterns of depletion of midwater and demersal species, the estimated proportion of demersal species increased as a function of the number of sweeps.

Given that estimates of species richness and density of midwater species changed relatively little after 5 sweeps, limiting seining to 5 sweeps and then hauling the block nets might represent an acceptable compromise between accuracy and effort. The block net catches added 4%, 3%, and 23% to the total estimates for species richness and midwater and demersal densities, respectively, to the catches after 5 seine sweeps. Five seine sweeps plus the block net catches resulted in estimates of species richness and density of midwater and demersal species that were 94%, 98%, and 75%, respectively, of those obtained with all 10 sweeps of the beach seine plus block net sweeps. These estimates assume that similar proportions of the total catch would be obtained from the two block nets when they are hauled in after only 5 rather than 10 sweeps of the primary beach seine. This assumption is conservative because a larger proportion of fishes would be expected to remain uncaptured in blocked areas after 5 sweeps than after 10. This assumption is supported by the fact that block nets retrieved after 5 sweeps in Study 3A did contribute somewhat greater proportions of the total estimate of density of demersal species (28% versus 24%) and species richness (6% versus 4%) than did block nets retrieved after 10 sweeps, though these differences were not statistically significant (one-tailed *t*-tests, $t < 0.5$, $p > 0.3$). (Too few midwater fishes were captured in Study 3A to make a reliable comparison for this group.)

Reducing the number of seine sweeps from 10 to 5 would save considerable time and effort; we estimate about a 30–40% savings in total time and effort per sample. Such savings in effort would be most valuable if the reduced-effort method was equally effective in different estuaries. ANOVA results indicated that catch efficiency (% of total catch) of 5 seine sweeps plus block net sweeps did not differ significantly among estuaries, but it did differ significantly between tidal creek and main channel habitats for demersal species (Table 6).

Study 4: Estimating Catch Efficiency of Seines

Consistent with the findings of the preceding studies, our mark-recapture study found relatively high recovery efficiency for midwater fishes and relatively low recovery efficiency for demersal fishes. We found that one sweep of a beach seine plus the

TABLE 7. Catch efficiency of one seine sweep plus sweeps of two block nets in 8 areas enclosed by block nets in 3 estuaries[a] and 2 habitats[b] based on recovery of tagged fishes.

	Catch Efficiency (% recapture rate)	
	Midwater Species Mean ± SE (n)	Demersal Species Mean ± SE (n)
Estuary		
Carpinteria Salt Marsh	80.7 ± 0.8 (3)	47.7 ± 7.7 (3)
San Elijo Lagoon	98.0 ± 2.0 (2)	30.0 ± 17.0 (2)
Los Peñasquitos Lagoon	67.7 ± 16.4 (3)	26.0 ± 7.8 (3)
ANOVA results: differences among estuaries	$F_{2,5} = 3.21$, $p = 0.13$	$F_{2,5} = 1.49$, $p = 0.31$
Habitat		
Main channel	80.7 ± 0.8 (3)	47.7 ± 7.7 (3)
Tidal creek	61.5 ± 5.6 (4)	18.3 ± 7.3 (3)
ANOVA results: differences between habitats	$F_{1,5} = 8.61$, $p = 0.03$	$F_{1,4} = 7.64$, $p = 0.05$

[a] Comparison among estuaries restricted to main channel habitat as tidal creeks were only sampled in Carpinteria Salt Marsh.
[b] Comparison between habitats restricted to Carpinteria Salt Marsh, see note above.

catches of two block nets recaptured 74% of tagged midwater fishes and only 31% demersal fishes (Table 3). There were relatively large differences in recovery efficiency among estuaries (68–98% and 26–48% for midwater and demersal species, respectively), but these differences were not statistically significant due to high variance and low replication (Table 7). Recovery efficiency was significantly higher in the main channel habitat than the tidal creek habitat for both midwater and demersal fishes (81% versus 62% and 48% versus 18% for main channel versus tidal creek for midwater and demersal fishes, respectively).

Discussion

We found that estimates of density and species richness were significantly affected by three differences in beach seine configuration and methods: seine length, the use of block nets, and the number of hauls made within blocked areas. These findings highlight the need to either standardize seine design and methodology or measure catch efficiency of each design and method if a goal is to make comparisons among studies or sites (Rozas and Minello 1997). It is currently difficult to make comparisons among studies even within regions because of the variety of seine designs and methods used and a lack of information on catch efficiencies. In studies of estuarine fishes in southern California, there are differences in seine length, mesh size, the use of block nets, and the number of hauls within blocked areas (Horn and Allen 1985; Nordby and Zedler 1991; Saiki 1997; Ambrose and Meffert 1999; Brooks 1999).

Our findings indicate that block nets must be used in conjunction with seines to obtain either accurate density estimates or indices that are reasonably well correlated to actual density or species richness. We found that use of block nets increased estimates of density and species richness in two ways: by increasing the efficiency of a beach seine used within the area enclosed and by capturing in the block nets fish that evaded capture by the beach seine. The increased efficiency of the beach seine was presumably due to block nets retaining fish within the enclosed area that would otherwise swim out as the seine was hauled across the channel (Peterson et al. 2005). Increased effort, in the form of repeated seine sweeps either by block nets as they are retrieved or by a beach seine before the block nets are retrieved, captured fish that initially evaded capture (e.g., by swimming under the lead line). Additional sweeps increased estimates of density and species richness, providing more accurate estimates of these variables, a finding consistent with those from other studies (Weinstein 1979; Nordby and Zedler 1991).

We found that the catch per sweep declined as extra seine sweeps depleted fishes in areas enclosed by block nets. This pattern sets up a tradeoff between accuracy and effort; gains in accuracy per seine sweep decline with additional sweeps, whereas effort per sweep stays relatively constant. The question then is at what point is additional effort better spent by sampling new areas (i.e., increasing replication of samples) rather than repeatedly seining the same area to improve the accuracy of estimates of density and species richness? The answer to this question will depend in part on whether the goal of the research program is to obtain accurate rather than representative (predictive) estimates, and whether the goal is to accurately characterize community composition or just obtain good estimates for a single species or habitat guild. Taken together, our findings indicate that a single sweep in a blocked area plus sweeps by the block nets provides fairly accurate estimates of species richness and density of midwater species. This sampling method is expected to underestimate density of demersal species by at least 3-fold, although this estimate should be representative, i.e., correlated with actual densities. For a research program that needs relatively accurate estimates of species richness but only representative estimates of density of estuarine fishes, this relatively low effort sampling approach may be sufficient.

Research aimed at characterizing estuarine fish community composition will require accurate estimates of relative abundance. Our results indicate that because of the differential catchability of demersal and midwater fishes, beach seining alone cannot provide such accurate estimates in general, and that the degree of bias is inversely related to sampling effort (i.e., number of seine sweeps). Though seine sampling within blocked areas has often been used for this type of work, there has been no standardization of the number of seine sweeps within blocked areas. Ambrose and Meffert (1999) used 5 sweeps, Weinstein (1979) recommended 8, Weinstein and Davis (1980) used 11, and Nordby and Zedler (1991) ceased sampling when catches declined to near zero, usually 4–5 sweeps. When accurate estimates of density and species richness are needed, seining in enclosed areas beyond the point at which the estimates cease to change much with each additional sweep is a waste of effort. We found that this point came after different numbers of sweeps for different variables: after only 2 sweeps for density of midwater species and after 5 sweeps for species richness. In our study, which was limited to 10 seine sweeps, this point was never reached for estimates of density of demersal species (Fig. 2). Use of the Leslie depletion method (Leslie and Davis 1939; Zippin 1956) for estimating population size revealed that the reason that estimates of density of demersal species never leveled off was that the probability of capture per sweep declined as more sweeps through the blocked area were made. This pattern violates an underlying assumption of the depletion estimation method and explains why the depletion estimates of density were lower than our actual catches. We think the decline in probability of capture occurred because progressively larger fractions of the remaining uncaught population of fishes moved into or against the block nets and became less accessible to the beach seine. The most effective way to capture these fishes is to haul the block nets, rather than making more sweeps of the beach seine through the blocked area.

We found that 5 seine sweeps within blocked areas plus the catches of block net sweeps provided quite accurate (>90% of what was attainable with more sampling effort) estimates of density of midwater fishes and species richness. Greater numbers of sweeps may be required to achieve the same level of accuracy for estimates of species diversity in systems with more species (e.g., Weinstein 1979; Weinstein and Davis 1980). In our study, 5 sweeps plus block net sweeps underestimated the density of demersal species by c. 25%, but we find it hard to justify a >30% increase in effort for a ≤25% increase in the density estimate. In most cases, that effort would be better spent increasing replication by sampling more areas. Our work indicates that the 5-sweep rule is a good one for balancing accuracy and effort in the systems we studied if seine sampling is confined to estimating species richness or the densities of midwater fishes. It is not suitable for accurately estimating the densities of demersal fishes or relative abundances (and species diversity indices) for estuarine fish assemblages as a whole, unless the bias in density estimates of demersal fishes is measured and corrected.

Our findings also indicate that seine length can bias estimates of density of fishes and community structure, so care should be taken when comparing findings of studies that used seines of different lengths (e.g., Saiki 1997 versus Desmond et al. 2002). In our study, a longer seine underestimated densities of demersal species relative to a shorter net. We suspect this bias was caused by greater difficulty keeping the lead line of the longer net in contact with the bottom in areas where the topography was not smooth. Estimates of density of demersal fishes from the smaller net were also somewhat more variable than those from the larger net. We suspect this difference in variability reflects natural patch structure, with the smaller net tending to fall either inside or outside of patches of demersal fishes, whereas the larger net tended to average out patches of high and low density (Wiens 1989).

It is possible that the differences we attribute to effects of seine length were actually caused by the different designs of the two nets we used—the longer seine also had a central bag in it that the smaller net lacked. Though we cannot rule out this possibility, we think it is unlikely. Bag seines should outperform beach seines without bags because the bag is meant to serve as a holding area for captured fish as the net is drawn through the water (Hayes et al. 1996), reducing escapement under the lead line or avoidance beyond the sides of the net. If the bag functioned in this way in our study, any reduced escapement or avoidance was outweighed by the inefficiency of the larger net relative to the smaller net.

Much of the preceding discussion is concerned with how accuracy of estimates of density and species richness is affected by seine design and usage. Several points must be made regarding our estimates of accuracy. We estimated accuracy in two general ways: a relative measure that compared treatments and assumed that the treatment providing higher estimates was more accurate, and direct measures that estimated the proportion of fishes in a sampled area that were captured (also termed catch efficiency). We estimated catch efficiency with mark-recapture and depletion techniques. Though it is somewhat difficult to compare the two types of estimates because they were derived from different studies with different methods (Study 4 versus 3B), the general similarities between the two kinds of estimates inspire some confidence in their reliability. Both approaches measure only recovery efficiency, the proportion of fishes retained within an enclosed area after the block nets were deployed. We have no data on avoidance of block nets and it is possible that some fish were chased from the blocked area when block nets were being deployed, resulting in an underestimate of the true abundances. Field observations lead us to believe that any such bias would be small. We did observe fish avoiding persons wading the block nets across channels, but these fish seemed as likely to swim into the area being blocked as out of it. It would be informative to test whether avoidance of block nets biases estimates of density and species richness obtained by seining in blocked areas.

A further limitation of our estimates of seine catch efficiency is that they apply only to fish that can be captured with seines. All fish used in our mark-recapture study were initially captured with seines before being tagged, and our depletion estimates apply only to fish that were captured (and depleted) with seines. Fishes small enough to pass through the 3-mm mesh of our seines or that were otherwise unavailable to seines (e.g., by hiding in burrows) are not included in our estimates of seine efficiency. Other sampling methods (e.g., enclosure traps: Rozas and Minello 1997) could produce higher estimates of density than we obtained with seines. Our work with enclosure traps in the same estuaries (Steele et al. 2006) has produced density estimates that are more than an order of magnitude higher than those in this paper, due to higher rates of capture of small gobies.

A common theme in our findings was that seine efficiency and factors influencing efficiency (seine length, use of block nets, number of sweeps within enclosed areas) differed between midwater and demersal fishes. Seine efficiency was lower for demersal species than midwater species, a common finding in other systems (Lyons 1986; Parsley et al. 1989; Pierce et al. 1990), and factors that affected estimates of density and species richness did so mostly by altering the efficiency of capture of demersal species, with smaller if any effects on midwater species. These findings indicate that it will be necessary to expend more effort (e.g., use multiple seine sweeps through enclosed areas) to sample demersal species accurately than to obtain accurate estimates of midwater species. It may be necessary to use other methods to accurately sample demersal fishes, particularly species of gobies that are an important component of the demersal fish guild in the estuaries we studied.

We found no compelling evidence that the efficiency of beach seining varied among estuaries (e.g., Tables 5, 6, and 7), but there was evidence that efficiency varied among habitats (Tables 6 and 7). These findings imply that comparisons of density and species richness among estuaries will be valid if the same methods are used in all estuaries, but comparisons among habitats should be made with caution. The evidence for differences among habitats is difficult to interpret, because it varied between methods used to estimate recovery efficiency. The mark-recapture study indicated that recovery efficiency for both midwater and demersal species was lower in tidal creeks than in main channels; whereas depletion estimates indicated that recovery efficiency of demersal species was lower in main channels than tidal creeks and similar in the two habitats for midwater species. We have no logical explanation for these conflicting results.

We found that variation in seine length and seining techniques significantly altered estimates of density and species richness of estuarine fishes. If the goal of sampling is to obtain accurate or representative estimates of density and species richness, it will be important to measure the biases associated with the particular seine configuration used for sampling. These estimates of bias, provided they are consistent among places and times to be compared (and they may not be: see e.g., Allen et al. 1992), can then be used to correct the raw data so they better reflect true values. Measures of the magnitude of biases associated with different gear configurations will be particularly valuable in facilitating comparisons among studies using different gear configurations (e.g., Allen et al. 2006). If accurate estimates are less important than reliable indices, standardizing the methods used to obtain these indices among projects will facilitate comparisons among projects. We hope that the work presented in this paper will help other researchers decide on appropriate seining configurations and techniques, and provide some guidance on how to measure biases in estimates of density and species richness of fishes obtained with seines.

Acknowledgments

We thank L. Allen, R. Ambrose, A. Brooks, J. Dixon, P. Raimondi, D. Reed, and R. Schmitt for advice and suggestions on this work. We thank all those who helped us in the field, especially

J. Wolf, M. Kirkland, K. Johnston, and J. Bram. The manuscript was improved by the comments of three anonymous reviewers. Funding for this study was provided by Southern California Edison as required by the California Coastal Commission under SCE's coastal development permit (No. 6-81-330-A, formerly 183-73) for Units 2 and 3 of the San Onofre Nuclear Generating Station.

Literature Cited

ALLEN, D. M., S. K. SERVICE, AND M. V. OGBURN-MATTHEWS. 1992. Factors influencing the collection efficiency of estuarine fishes. *Transactions of the American Fisheries Society* 121:234–244.

ALLEN, L. G. 1982. Seasonal abundance, composition, and productivity of the littoral fish assemblage in upper Newport Bay, California. *Fishery Bulletin* 80:769–790.

ALLEN, L. G., A. M. FINDLAY, AND C. M. PHALEN. 2002. The fish assemblages of San Diego Bay in the five-year period of July 1994 to April 1999. *Bulletin of the Southern California Academy of Sciences* 101:49–85.

ALLEN, L. G., M. M. YOKLAVICH, G. M. CAILLIET, AND M. H. HORN. 2006. Bays and estuaries, p. 119–148. *In* L. G. Allen, D. J. Pondella, and M. H. Horn (eds.), The Ecology of Marine Fishes: California and Adjacent Waters. University of California Press, Berkeley and Los Angeles, California.

AMBROSE, R. F. AND D. J. MEFFERT. 1999. Fish-assemblage dynamics in Malibu Lagoon, a small, hydrologically altered estuary in southern California. *Wetlands* 19:327–340.

BROOKS, A. J. 1999. Factors influencing the structure of an estuarine fish community: The role of interspecific competition. Ph.D. Dissertation, University of California, Santa Barbara, California.

DESMOND, J. S., D. H. DEUTSCHMAN, AND J. B. ZEDLER. 2002. Spatial and temporal variation in estuarine fish and invertebrate assemblages: Analysis of an 11-year data set. *Estuaries* 25:552–569.

DESMOND, J. S., J. B. ZEDLER, AND G. D. WILLIAMS. 2000. Fish use of tidal creek habitats in two southern California salt marshes. *Ecological Engineering* 14:233–252.

HAYES, D. B., C. PAOLA FERRERI, AND W. W. TAYLOR. 1996. Active fish capture methods, p. 193–220. *In* B. R. Murphy and D. W. Willis (eds.), Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

HORN, M. H. AND L. G. ALLEN. 1985. Fish community ecology in southern California bays and estuaries, p. 169–190. *In* A. Yañez-Arancibia (ed.), Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration. DR (R) UNAM Press, México City, México.

IKEJIMA, K., P. TONGNUNUI, T. MEDEV, AND T. TANIUCHI. 2003. Juvenile and small fishes in a mangrove estuary in Trang province, Thailand: Seasonal and habitat differences. *Estuarine Coastal and Shelf Science* 56:447–457.

KOUTRAKIS, E. T., A. C. TSIKLIRAS, AND A. I. SINIS. 2005. Temporal variability of the ichthyofauna in a northern Aegean coastal lagoon (Greece). Influence of environmental factors. *Hydrobiologia* 543:245–257.

LESLIE, P. H. AND D. H. S. DAVIS. 1939. An attempt to determine the absolute number of rats on a given area. *Journal of Animal Ecology* 8:94–113.

LUKEY, J. R., A. J. BOOTH, AND R. FRONEMAN. 2006. Fish population size and movement patterns in a small intermittently open South African estuary. *Estuarine Coastal and Shelf Science* 67:10–20.

LYONS, J. 1986. Capture efficiency of a beach seine for seven freshwater fishes in a north-temperate lake. *North American Journal of Fisheries Management* 6:288–289.

NORDBY, C. S. AND J. B. ZEDLER. 1991. Responses of fish and macrobenthic assemblages to hydrologic disturbances in Tijuana Estuary and Los Peñasquitos Lagoon, California. *Estuaries* 14:80–93.

PARSLEY, M. J., D. E. PALMER, AND R. W. BURKHARDT. 1989. Variation in capture efficiency of a beach seine for small fishes. *North American Journal of Fisheries Management* 9:239–244.

PETERSON, J. T., N. P. BANISH, AND R. F. THUROW. 2005. Are block net necessary?: Movement of stream-dwelling salmonids in response to three common survey methods. *North American Journal of Fisheries Management* 25:732–743.

PIERCE, C. L., J. B. RASMUSSEN, AND W. C. LEGGETT. 1990. Sampling littoral fish with a seine: Corrections for variable capture efficiency. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1004–1010.

ROZAS, L. P. AND T. J. MINELLO. 1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: A review of sampling design with focus on gear selection. *Estuaries* 20:199–213.

SAIKI, M. K. 1997. Survey of small fishes and environmental conditions in Mugu Lagoon, California, and tidally influenced reaches of its tributaries. *California Fish and Game* 83:153–167.

STEELE, M. A., S. C. SCHROETER, AND H. M. PAGE. 2006. Sampling characteristics and biases of enclosure traps for sampling fishes in estuaries. *Estuaries and Coasts* 29:630–638.

WEINSTEIN, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fishery Bulletin* 77:339–357.

WEINSTEIN, M. P. AND R. W. DAVIS. 1980. Collection efficiency of seine and rotenone samples from tidal creeks, Cape Fear River, North Carolina. *Estuaries* 3:98–105.

WIENS, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.

WINER, B. J., D. R. BROWN, AND K. M. MICHELS. 1991. Statistical Principles in Experimental Design, 2nd edition. McGraw-Hill, New York.

YOKLAVICH, M. M., G. M. CAILLIET, J. P. BARRY, D. A. AMBROSE, AND B. S. ANTRIM. 1991. Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. *Estuaries* 14:465–480.

ZIPPIN, C. 1956. An evaluation of the removal method of estimating animal populations. *Biometrics* 12:163–189.

Received, October 25, 2005
Revised, April 17, 2006
Accepted, June 14, 2006