FINE-SCALE DISTRIBUTIONS OF PLANKTONIC FISH EGGS IN THE VICINITIES OF BIG SYCAMORE CANYON AND VANDENBERG ECOLOGICAL RESERVES, AND ANACAPA AND SAN MIGUEL ISLANDS, CALIFORNIA

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ABSTRACT

Nearshore ichthyoplankton surveys were conducted during late winter and early summer 1998, at four sites in southern California: Big Sycamore Canyon and Vandenberg Ecological Reserves, and Anacapa and San Miguel Islands. A continuous underway fish egg sampler (CUFES) was used to sample along each of three or four transect lines oriented alongshore and spaced at about 0.8 km or 1.6 km intervals offshore, and a bongo net was towed vertically through the water column at a series of stations spaced about 0.8 km or 1.6 km apart on each line.

A total of 41 fish egg taxa and an unidentified fish egg category were collected: 30 taxa in winter and 29 in summer. Winter fish egg collections were dominated by northern anchovy; California halibut, speckled sanddab, white croaker, and Pacific hake eggs also were common. Summer egg catches were more evenly distributed over several taxa, primarily senorita, California sheephead, California barracuda plus white seabass, and speckled sanddab, as well as unidentified eggs. Collections of eggs in early developmental stages suggested that many taxa spawned at night. Senorita spawned during the day, California sheephead probably spawned primarily during the day, and California halibut may have begun spawning during the afternoon and continued into the evening.

Both frequency of occurrence and abundance of eggs tended to be higher inshore and were much reduced on the most seaward line for the more common shorefish taxa. White croaker and California sheephead probably spawned primarily shoreward of about the 30 m isobath, and speckled sanddab and senorita shoreward of about the 60 m isobath. California halibut apparently spawned primarily between about the 40 and 60 m isobaths, and California barracuda and white seabass spawned over a broader depth range, about 45–90 m. Abundances of California halibut and white croaker eggs were highest at the Big Sycamore Canyon site, while the islands, especially Anacapa Island, were important sites for California sheephead, senorita, California barracuda, and white seabass spawning.

The CUFES proved to be an effective sampler for fine-scale distributions of planktonic fish eggs, but may

inadequately sample taxa or developmental stages whose vertical distributions are centered above or below its intake depth. Use of another sampler that covers the entire vertical range of the taxa of interest is a necessary adjunct to CUFES sampling.

INTRODUCTION

Four marine ecological reserves were established along the California coast in 1994 as part of the California Marine Resources Protection Act of 1990. In February 1998, a study of the fine-scale distribution of planktonic fish eggs was initiated at two of these reserves on the southern California coast: Vandenberg Ecological Reserve, centered on Point Arguello, and Big Sycamore Canyon Ecological Reserve, just east of Point Mugu (fig. 1). The ultimate goal of this ongoing study is to measure the production of planktonic shorefish eggs from these reserves. Necessary first steps in reaching this goal are the identification of the eggs, and the determination of their temporal and spatial distributions in the vicinities of the reserves.

Among the many functions of a marine reserve (Agardy 1994; Rowley 1994), one of the potentially most important to coastal fisheries is the provision of a protected area for adult fishes whose eggs and larvae can "reseed" fished areas outside the reserve. However, owing to the difficulty of attributing planktonic eggs and larvae to a particular site of origin, the degree to which reserves might fulfill this role is largely unknown. Recently spawned eggs (or the recently released larvae of live-bearing fishes such as rockfishes) are least likely to have dispersed and to have been transported far from spawning sites, and thus are most likely to be attributable to a specific area of origin. Unfortunately, these stages often are among the most difficult to identify to species, and their usually highly aggregated distributions make them the most difficult and costly stages to sample with conventional towed nets.

To overcome this sampling problem, we tried a continuous underway pump system (CUFES: Checkley et al. 1997) as our primary plankton sampler. CUFES has been shown to be an effective tool for sampling largescale planktonic fish egg distributions over deep coastal WATSON ET AL.: DISTRIBUTION OF PLANKTONIC SHOREFISH EGGS CalCOFI Rep., Vol. 40, 1999



Figure 1. Location of the study sites.

and offshore waters (e.g., Checkley et al. 1997; Lynn et al. 1998), and this study is a first attempt to determine whether the methodology is also applicable to the measurement of fine-scale distributions in shallow, nearshore coastal waters.

Our objectives in this first year of the study were to (1) develop techniques to identify the planktonic eggs of the important—i.e., abundant or of value for commercial or sport fisheries—fish species in the area; (2) evaluate the usefulness of the CUFES system for measuring small-scale fish egg distributions in shallow waters; and (3) describe the temporal—primarily day-night—and fine-scale horizontal distributions of the eggs of the important taxa. The primary objective for the second year is to estimate site-specific (or habitat-specific) fish egg production (larval production of the live-bearing genus *Sebastes* will be estimated as well).

In this paper we show that the CUFES system is an effective sampler in shallow coastal water, and we describe the distributional patterns of the eggs of abundant and economically important shorefish taxa, as measured with the CUFES system. Patterns obtained with the CUFES are compared qualitatively with those obtained concurrently with a conventional bongo net.

METHODS

Two surveys were conducted in 1998: one during late winter (survey 9803JD: 19 February-4 March) and another in early summer (9806JD: 12-24 June). Four sites were sampled on each survey: Big Sycamore Canyon (SC) and Vandenberg (VA) Ecological Reserves, and Anacapa (AN) and San Miguel (SM) Islands (fig. 1). SC is a low-relief, soft-bottom site containing little hardbottom and kelp habitat. VA likewise is predominantly a sandy bottom site, but with rocky headlands, some areas of hard bottom, and some patchy surf grass, but little kelp. Coastal currents flow primarily alongshore at both sites, predominantly southerly in spring and summer and northerly in autumn and winter (e.g., Hendershott and Winant 1996). The island sites are predominantly soft-bottom, but with more hard-bottom habitat than the mainland sites and, especially at SM, with more extensive kelp coverage. There has been a no-take reserve along the northeastern end at AN since 1978, in contrast to the recently established (1994) mainland reserves.

A station grid was established at each site (fig. 1). The most shoreward line of stations (line 1) was set approximately along the 20 m isobath, and the remaining three lines (two at AN) paralleled this line at fixed distances farther from shore without regard to bottom depth. Lines 2 and 3 were at 0.8 km (0.5 mi) intervals, corresponding very roughly to the 40 and 60 m isobaths, respectively. The most seaward line (line 4) was another 1.6 km (1 mi) farther offshore, or in the vicinity of the 200 m isobath. The reserve at SC extends offshore to the 37 m (20 fm) isobath, and line 1 thus passes through the reserve at this site. The AN and VA reserves extend offshore to approximately the 18 m (10 fm) isobath; concerns for vessel safety precluded sampling within these reserves. Stations were placed at 0.8 km (0.5 mi) intervals (1.6 km at SM) along each line. There were five stations, each corresponding to "downcoast," "reserve," and "upcoast" positions along each line, for a total of 60 stations each at the SC and VA sites. There were 44 stations at SM (11 per line), and 35 at AN (12 each on lines 1 and 2, 11 on line 3).

The CUFES sampling system included three principal components: a submerged pump installed in a box connected to a sea chest in the hull of the RV David Starr Jordan, a concentrator equipped with 0.333 mm mesh, and 0.333 mm mesh collectors (Checkley et al. 1997). The pump, with an 8 cm diameter orifice, drew water from 3 m depth at 640 l/min through a grating in the hull. The CUFES sampled continuously along each line as the vessel proceeded at about 2.6 m/s (5 kts), and the accumulating plankton was collected at 2-10 min intervals, depending on plankton volume (most of these samples were 10 min). A full pattern (all four lines) was sampled twice during the day and twice at night at each site, except during survey 9803JD, when two additional pattern occupancies were obtained at SM during a weather delay in other sampling, and two of the four pattern occupancies were curtailed at VA (line 4 not sampled) because of time limitations. A total of 740 CUFES transect samples was collected on survey 9803JD, and 581 samples on survey 9806JD.

A 71 cm bongo sampler was used to make a vertical plankton tow at each station. The bongo was equipped with 0.333 mm mesh nets and cod ends, and a General Oceanics flowmeter. The nets were attached to a 45 kg weight suspended just below the cod ends. At each station the bongo was lowered to 3 m above the bottom (to a maximum of 210 m at stations deeper than 213 m) and retrieved at 50 m/min. The bongo frame was oriented horizontally with the net mouths opening upward so that the nets did not sample on descent. An attempt was made to maintain a wire angle of $\leq 15^{\circ}$; this generally was the case on descent, but when the wind speed was ≥ca. 10 m/s during retrieval it was not uncommon for the angle to rise above 15° as the net neared the surface. A CUFES sample was collected at each station simultaneously with the bongo sample. Sampling was done

without regard to day or night. A total of 199 bongo and CUFES sample pairs was collected during survey 9803JD; 191 pairs were collected during 9806JD (loss of the bongo precluded collection at VA stations 53–60).

Occasional surface tows were made with a manta net (0.333 mm mesh) to collect live eggs for rearing. Eggs from these samples were sorted into presumed monotypic categories, incubated at constant temperature in 1 l and 4 l beakers placed in Lauda water baths, and sampled at regular intervals through hatching (to yolk exhaustion in some cases). The primary purpose of this exercise was to confirm species identifications of the eggs.

Immediately after collection, each CUFES plankton sample usually was rinsed into a petri dish with seawater, scanned under a binocular dissecting microscope for a preliminary count of fish eggs, then preserved in 5% borate-buffered seawater formalin. Dense samples, and all bongo and CUFES station samples, were preserved directly without being scanned.

In the laboratory, all fish eggs were identified, staged according to the criteria of Moser and Ahlstrom (1985), and counted. All fish larvae were identified, staged as yolk sac, preflexion, flexion, or postflexion (Moser 1996), and counted (because this paper is concerned with fish eggs, larvae will not be discussed). Count data were converted to concentration (number per m³ of water filtered), and the bongo data also were converted to abundance (number under 1 m² of sea surface) prior to analysis. For convenience in data analysis, egg stages were pooled into "early" (stages I–III), "middle" (stages IV–VII), and "late" (stages VIII–XI) categories.

RESULTS

Taxonomic Composition

A total of 41 fish egg taxa and an "unidentified egg" category were recognized in 1998: 30 taxa in winter and 29 in summer (tables 1-4). The "unidentified egg" category contained about 18 distinguishable egg types in winter and about 27 types in summer. Several taxa, primarily flatfishes, occurred in both surveys, but only speckled sanddab (Citharichthys stigmaeus) eggs were relatively common in both. Winter CUFES samples were dominated by eggs of the northern anchovy (Engraulis mordax) at all sites except SC, where California halibut (Paralichthys californicus) eggs were somewhat more common. Winter bongo samples likewise were dominated by northern anchovy eggs except at SM, where eggs of the Pacific hake (Merluccius productus) were most common. During summer, catches were more equitably distributed among several shorefish taxa in both CUFES and bongo samples, and the eggs of coastal pelagic, coastal demersal, and mesopelagic species were uncommon, except for Pacific argentine (Argentina sialis) eggs in the bongo samples.

The more commonly occurring taxa during each survey were essentially the same in both CUFES and bongo samples, but eggs of the Pacific hake and Pacific argentine were much more frequent in the bongo samples, reflecting their deeper vertical distributions. Only the two most commonly occurring taxa, northern anchovy and California halibut, were taken at all sites in winter CUFES samples: four additional taxa-Pacific hake. speckled sanddab, white croaker (Genyonemus lineatus), and California smoothtongue (Leuroglossus stilbius)occurred at all sites in the bongo samples. Five taxa were collected at all sites in the June CUFES samples: senorita (Oxyjulis californica), California sheephead (Semicossyphus pulcher), speckled sanddab, C-O turbot (Pleuronichthys coenosus), and Perciformes-the indistinguishable earlystage eggs of white seabass (Atractoscion nobilis) and California barracuda (Sphyraena argentea). Only speckled sanddab eggs, however, were common to all sites in the bongo samples. The numbers of identifiable taxa collected with the CUFES at the mainland sites were higher in summer than in winter, but differed little between seasons at the island sites (although taxonomic composition differed considerably). More identifiable taxa were collected with the bongo during the winter than in summer at all sites.

Horizontal Distribution

Among the relatively common shorefish eggs (those occurring in $\geq 10\%$ of the CUFES transect samples), patterns of declining concentration with increasing distance from shore were apparent at all sites (e.g., figs. 2–7), but not at every site for every taxon. The cross-shelf pattern most often took the form of generally similar concentrations along the inshore lines, and much reduced concentration on the most offshore line. Similar patterns were apparent in the bongo data, but less clearly so. In contrast, patterns of decreasing concentration as the bottom shoaled, or no pattern relative to distance from shore, depending on site, generally were apparent for the eggs of non-shorefish taxa; for example, the coastal pelagic species, northern anchovy (fig. 8).

Eggs of the California halibut were taken primarily at SC during survey 9803JD. They were rarest offshore and showed some evidence of declining concentration alongshore from generally higher values southeast of the reserve to lower values northwest of the reserve (fig. 2a). Concentrations were lower at the other sites than at SC, and cross-shelf patterns were visible primarily as reduced frequency of occurrence offshore. Alongshore patterns were not apparent at these sites, except at SM (fig. 2d, h) where the highest frequency of occurrence of eggs toward the eastern end of the island, and their virtual absence at the western end, may reflect the strong north-westerly wind (ca. 10-20 m/s) that blew during most of the transect sampling at this site.

Speckled sanddab (fig. 3) and white croaker (fig. 4) eggs showed essentially the same cross-shelf pattern as California halibut, but little evidence of alongshore pattern at SC. Like California halibut, speckled sanddab eggs occurred primarily off the eastern part of the island at SM. At VA, white croaker eggs were more concentrated in CUFES samples collected in a plume of slightly lower-salinity (ca. 32.6 ppt), green water north of Point Arguello than in the slightly saltier (ca. 32.8 ppt), blue water to the south (fig. 4b). No such pattern was apparent in VA bongo data (fig. 4d), suggesting that the "egg-rich" plume was a relatively thin, shallow layer.

During the June survey, senorita eggs were common on the shoreward two lines in CUFES samples at SC and SM, clearly less so farther seaward along line 3 at SC, and nearly absent from the most offshore line at both sites (fig. 5a, c). Alongshore patterns were not evident at either site. Both frequency of occurrence and concentration were highest at AN; here eggs were common on all lines, but the largest CUFES catches were along the most inshore line (fig. 5b). Bongo catches were much smaller at AN, with some indication of decreasing concentration offshore (fig. 5e).

California sheephead eggs were rare at the mainland sites but common at the islands, especially at AN, in June. Large collections were made with the CUFES on all three lines at AN (fig. 6a); at SM frequency of occurrence and numbers in CUFES samples were highest on the most inshore line, and eggs were nearly absent from the most offshore line (fig. 6b). Alongshore patterns were not apparent, except that concentration was lower off the west end of West Anacapa. Like senorita, California sheephead eggs were far less numerous in bongo samples than in CUFES collections; nevertheless, some indication of decreasing concentration offshore could be seen in the bongo data (fig. 6c, d).

White seabass eggs were collected only at the islands, mainly in CUFES samples at AN, at the beginning of the spawning season in late winter (tables 1 and 2), and they remained primarily at AN in summer (tables 3 and 4). During the summer survey, egg distributions were confounded with those of the California barracuda, whose eggs are nearly indistinguishable from white seabass eggs before mid-development (stage VI or VII), when conventional characters are used (e.g., Matarese and Sandknop 1984). Distributions and numbers of the older eggs of both species were similar, except that California barracuda eggs were more common than white seabass eggs at SC. White seabass plus California barracuda eggs (all stages pooled) were far more common at AN than elsewhere; moderate numbers were collected at SC, and



Figure 2. Distribution of California halibut (*Paralichthys californicus*) eggs at the four study sites during survey 9803JD, based on CUFES (a-d) and vertical bongo (e-h) sampling. All egg stages are included.



Figure 3. Distribution of speckled sanddab (*Citharichthys stigmaeus*) eggs at the SC, AN, and SM sites during survey 9803JD, based on CUFES (a-c) and vertical bongo (d-f) sampling. All egg stages are included.



Figure 4. Distribution of white croaker (*Genyonemus lineatus*) eggs at the SC and VA sites during survey 9803JD, based on CUFES (*a*, *b*) and vertical bongo (*c*, *d*) sampling. All egg stages are included.



Figure 5. Distribution of senorita (*Oxyjulis californica*) eggs at the SC, AN, and SM sites during survey 9806JD, based on CUFES (*a–c*) and vertical bongo (*d–f*) sampling. All egg stages are included.



Figure 6. Distribution of California sheephead (*Semicossyphus pulcher*) eggs at the AN and SM sites during survey 9806JD, based on CUFES (*a*, *b*) and vertical bongo (*c*, *d*) sampling. All egg stages are included.



Figure 7. Distribution of white seabass (*Atractoscion nobilis*) plus California barracuda (*Sphyraena argentea*) eggs at the SC and AN sites during survey 9806JD, based on CUFES (*a*, *b*) and vertical bongo (*c*, *d*) sampling. All egg stages are included.



Figure 8. Distribution of northern anchovy (*Engraulis mordax*) eggs at all four study sites during survey 9803JD, based on CUFES (a-d) and vertical bongo (e-h) sampling. All egg stages are included.

Taxon ^a	All sites	Big Sycamore Reserve	Vandenberg Reserve	Anacapa Island	San Miguel Island
Engraulis mordax	63.9	78.1	65.8	70.9	54.5
Paralichthys californicus	28.3	88.3	12.8	10.5	13.9
Genyonemus lineatus	20.6	56.9	35.6	9.3	
Citharichthys stigmaeus	14.4	35.0		17.4	11.2
Merluccius productus	8.6		5.4	3.5	15.5
Sardinops sagax	5.5			37.2	1.7
Atractoscion nobilis	3.9			25.6	1.3
Unidentified eggs	2.7	1.5	0.7	7.0	3.0
Pleuronichthys coenosus	1.9	0.7		5.8	2.3
Pleuronichthys verticalis	1.2	2.9	2.0	1.2	
Parophrys vetulus	0.7		3.4		
Pleuronichthys ritteri	0.7	2.9			0.3
Ophidiidae	0.6				1.3
Hypsopsetta guttulata	0.4			3.5	
Argentina sialis	0.3	0.7	0.7		
Citharichthys sp(p).	0.3	1.5			
Xystreurys liolepis	0.3	1.5			
Leuroglossus stilbius	0.1				0.3
Lyopsetta exilis	0.1			1.2	
Pleuronectidae	0.1		0.7		
Pleuronichthys decurrens	0.1			1.2	
Scomber japonicus	0.1		0.7		
Sebastolobus sp(p).	0.1				0.3

TABLE 1

Percent Positive Collections of Fish Eggs in CUFES Transect Samples during Survey 9803JD, 19 February-4 March 1998

^aTaxa are ordered from highest to lowest overall frequency of occurrence.

Taxon ^a	All sites	Big Sycamore Reserve	Vandenberg Reserve	Anacapa Island	San Miguel Island
Engraulis mordax	75.9	68.3	76.7	97.1	68.2
Merluccius productus	53.3	43.3	48.3	22.9	97.7
Genyonemus lineatus	50.3	85.0	66.7	22.9	2.3
Paralichthys californicus	50.3	98.3	23.3	42.9	27.3
Argentina sialis	23.1	40.0	25.0		15.9
Citharichthys stigmaeus	22.1	30.0	1.7	40.0	25.0
Leuroglossus stilbius	13.1	13.3	11.7	25.7	4.5
Pleuronichthys verticalis	11.6	26.7	5.0	11.4	
Unidentified eggs	11.6	6.7	18.3	20.0	2.3
Atractoscion nobilis	7.5		1.7	34.3	4.5
Pleuronichthys coenosus	7.5			31.4	9.1
Sardinops sagax	7.5		1.7	40.0	
Hippoglossina stomata	4.0	1.7		2.9	13.6
Parophrys vetulus	4.0	8.3	3.3	2.9	
Lyopsetta exilis	3.5	3.3	6.7		2.3
Citharichthys sp(p).	1.5		3.3	2.9	
Trachurus symmetricus	1.5	1.7	1.7		2.3
Embassichthys bathybius	1.0				4.5
Pleuronichthys ritteri	1.0	3.3			
Eopsetta jordani	0.5	1.7			
Glyptocephalus zachirus	0.5		1.7		
Ophidiidae	0.5		1.7		
Symphurus atricauda	0.5			2.9	
Tetragonurus cuvieri	0.5	1.7			

TABLE 2		
Percent Positive Collections of Fish Eggs in Vertical Bongo Samples during Survey 9803ID	19 February-4 I	March 1998

^aTaxa are ordered from highest to lowest overall frequency of occurrence.

Taxon ^a	All sites	Big Sycamore	Vandenberg	Anacapa	San Miguel
	All sites	Keserve	Reserve	Island	Island
Oxyjulis californica	35.1	19.6	2.9	100.0	48.7
Citharichthys stigmaeus	27.8	49.0	14.0	61.0	8.6
Semicossyphus pulcher	23.6	1.3	1.8	93.6	29.9
Perciformes ^b	22.9	32.7	0.6	100.0	1.1
Unidentified eggs	20.7	35.3	7.6	40.2	12.3
Sphyraena argentea	7.9	6.5		43.9	0.5
Atractoscion nobilis	6.6	2.0		43.9	
Pleuronichthys coenosus	4.7	1.3	0.6	25.6	2.1
Citharichthys sp(p).	4.6	9.2	7.6		
Paralichthys californicus	3.0	7.8	2.9	1.2	
Ophidiidae	1.3	0.7	1.2	6.1	
Pleuronichthys verticalis	1.3		2.3	4.9	
Trachurus symmetricus	0.7		2.3		
Pleuronichthys decurrens	0.5		1.8		
Labridae	0.3			2.4	
Lyopsetta exilis	0.2		0.6		
Mugil cephalus	0.2	0.7			
Parophrys vetulus	0.2	0.7			
Peprilus simillimus	0.2				0.5
Pleuronectiformes	0.2	0.7			
Pleuronichthys ritteri	0.2	0.7			
Sardinops sagax	0.2				0.5
Sciaenidae	0.2	0.7			
Scomber japonicus	0.2		0.6		
Symphurus atricauda	0.2	0.7			

TABLE 3	
Percent Positive Collections of Fish Eggs in CUFES Transect Samples during Survey 9806ID, 17	2–24 June 1998

^aTaxa are ordered from highest to lowest overall frequency of occurrence.

^bIndistinguishable eggs of Atractoscion nobilis and Sphyraena argentea; almost all are stage I-VI eggs that have not yet developed diagnostic embryonic pigmentation.

Taxon ^a	All sites	Big Sycamore Reserve	Vandenberg Reserve	Anacapa Island	San Miguel Island
Oxyjulis californica	27.7	3.3		88.6	45.5
Perciformes ^b	22.0	21.7		82.9	
Citharichthys stigmaeus	18.8	31.7	17.3	17.1	4.5
Unidentified eggs	18.3	16.7	1.9	51.4	13.6
Paralichthys californicus	16.2	46.7	5.8		
Semicossyphus pulcher	15.2	1.7		45.7	27.3
Argentina sialis	9.4	13.3		20.0	6.8
Sphyraena argentea	9.4	18.3	1.9	17.1	
Trachurus symmetricus	5.8			31.4	
Pleuronichthys coenosus	4.2		3.8	14.3	2.3
Pleuronichthys verticalis	3.7	1.7	3.8	11.4	
Seriphus politus	2.6	8.3			
Citharichthys sp(p).	2.1	6.7			
Hippoglossina stomata	2.1	6.7			
Ophidiidae	2.1	3.3			4.5
Lyopsetta exilis	1.6	3.3			2.3
Atractoscion nobilis	1.0			5.7	
Peprilus simillimus	1.0			5.7	
Pleuronichthys decurrens	1.0		1.9	2.9	
Engraulis mordax	0.5		1.9		
Hypsopsetta guttulata	0.5	3.3			

TABLE 4		
Percent Positive Collections of Fish Eggs in Vertical Bongo Samples during Survey 9806ID	12-24 June 19	105

^aTaxa are ordered from highest to lowest overall frequency of occurrence. ^bIndistinguishable eggs of *Atractoscion nobilis* and *Sphyraena argentea*; almost all are stage I–VI eggs that have not yet developed diagnostic embryonic pigmentation.

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			Day			Night			
Taxon	Survey	N	Mean	S.D.	N	Mean	S.D.		
CUFES									
Genyonemus lineatus	9803	291	0.03	0.13	449	0.08	0.62		
Atractoscion nobilis + Sphyraena argentea	9806	294	0.58	1.66	287	2.08	8.51		
Oxyjulis californica	9806	294	1.23	7.87	287	0.22	0.82		
Semicossyphus pulcher	9806	294	0.30	1.20	287	1.18	6.91		
Citharichthys stigmaeus	9803	291	0.02	0.20	449	0.12	0.52		
Paralichthys californicus	9803	291	0.09	0.39	449	0.15	0.52		
Bongo									
Genyonemus lineatus	9803	87	0.01	0.06	112	0.04	0.11		
Atractoscion nobilis + Sphyraena argentea	9806	133	0.02	0.06	58	0.03	0.12		
Oxyjulis californica	9806	133	0.06	0.19	58	0.01	0.03		
Semicossyphus pulcher	9806	133	0.03	0.25	58	0.001	0.005		
Citharichthys stigmaeus	9803	87	0.01	0.02	112	0.01	0.03		
Paralichthys californicus	9803	87	0.01	0.04	112	0.15	0.27		

 TABLE 5

 Mean Concentrations of Early-Stage (I-III) Eggs of Selected Shorefish Taxa in Day and Night CUFES and Vertical Bongo Collections

Concentrations (number/ m^3) were averaged over all samples collected during the day, and all those collected at night, on survey 9803JD or 9806JD. Day was defined as 7 a.m. to 6 p.m. (sunrise to sunset) for survey 9803JD, and 5 a.m. to 8 p.m. for survey 9806JD. N = number of samples; S.D. = standard deviation.

few at the other sites. At SC, the highest concentrations of eggs were in CUFES samples at intermediate distance from shore (lines 2 and 3); there were fewer eggs along the most seaward line, and they were rare on the most shoreward line (fig. 7a). No alongshore pattern was apparent in the CUFES collections, and the smaller bongo catches showed neither cross-shelf nor alongshore patterns (fig. 7c). The large CUFES and small bongo catches at AN likewise showed no clear cross-shelf or alongshore patterns, except that perhaps there was some tendency for catches to be larger along Middle Anacapa and to decline off the west end of West Anacapa (fig. 7b, d). The later-stage eggs (stages VII-XI) of both species were absent from the west end of West Anacapa, and were present in somewhat lower concentration along line 3 than along the more shoreward lines.

Time and Cross-Shelf Location of Spawning

A preliminary comparison of mean concentrations of early-stage eggs in day and night (sunset to sunrise) samples (table 5) suggested that the majority of the common shorefish taxa may spawn at night. Senorita apparently spawned during the day, and California halibut may have begun spawning during the day and continued into the night. During the winter survey, CUFES and bongo catches of early-stage California halibut eggs suggested nocturnal spawning, with numbers increasing after sunset (especially in the bongo collections), peaking before midnight, and then declining concurrently with an increase in the number of middle-stage eggs (fig. 9). The concentration of middle-stage eggs peaked during the afternoon, was quite variable, and CUFES estimates tended to be higher than bongo estimates. Late-



Figure 9. California halibut (*Paralichthys californicus*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 10. California halibut (*Paralichthys californicus*) eggs: concentration (a-d) and abundance (e-h) vs. distance from shore at the four study sites during survey 9803JD, using transect line as a proxy for distance. Data from CUFES (a-d) and vertical bongo (e-h) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 11. Speckled sanddab (*Citharichthys stigmaeus*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

stage eggs were rarer, and catches were variable with both samplers. Plots of cross-shelf concentrations and abundances of the composite stages suggested that spawning was centered primarily at intermediate distance from shore (fig. 10). At SC, where California halibut eggs were most common, early-stage eggs occurred in highest concentration (fig. 10a) and abundance (fig. 10e) on line 2 and decreased both shoreward and seaward.

Despite rather variable catches, early-stage speckled sanddab eggs showed some evidence of nocturnal spawning, probably beginning near sunset and perhaps continuing until near dawn, in the winter CUFES samples (fig. 11a). The largest bongo collections of early-stage eggs also were at night (fig. 11b), but because catches in the bongo samples were even more variable than in the CUFES samples, nighttime spawning was not clearly shown. Catches of middle- and late-stage eggs were quite variable with both samplers. Both concentration (fig. 12a-c) and abundance (fig. 12d-f) of early-stage eggs usually was highest toward shore, on line 1 or 2. In the CUFES samples, early stages were slightly more concentrated on line 2 than farther inshore; in the bongo samples they were most abundant on line 1, except at AN.

Nocturnal spawning of white croaker, probably beginning just after sunset, was suggested by catches with both samplers during the winter survey. The concentration of early-stage eggs measured with the CUFES rapidly increased beginning at about 8 p.m., peaked at about 11 p.m.-midnight, then declined to a generally low level by about dawn (fig. 13a). A similar pattern, with higher nighttime concentration but lacking the clear middle-of-the-night peak, was apparent in the bongo data (fig. 13b). Both CUFES and bongo provided more or less similar estimates of concentrations of middle-stage eggs, but for late-stage eggs bongo estimates tended to be slightly larger than CUFES estimates. Earlystage eggs were most concentrated on the inshore line at SC, and decreased monotonically with increasing distance from shore in both CUFES and bongo samples (e.g., fig. 14a), but abundance as indicated by the bongo samples was highest on line 2 (fig. 14c). At VA the few early-stage eggs collected with the bongo were taken primarily near shore on line 1, but the CUFES catches, dominated by the collections north of Point Arguello (fig. 4b), were slightly larger on line 2 than on the adjacent lines (fig. 14b).

In late winter, early-stage white seabass eggs usually were more numerous in the CUFES samples at night and early in the morning than later during the day, while in the bongo samples larger catches were made only at night (fig. 15a, b). At AN the concentration of earlystage eggs steadily increased with increasing distance from shore, based on the CUFES data (fig. 15c), while their abundance based on bongo data was slightly higher on line 2 than elsewhere (fig. 15d). During the summer survey, early-stage eggs of white seabass plus California barracuda peaked at night: before midnight in bongo samples and after midnight in CUFES samples (fig. 16). Concentration measured with the CUFES at SC was highest on line 3 (fig. 17a), although abundance based on the bongo samples was highest on line 4 (fig. 17c). At AN, where the eggs were far more common, both concentration (fig. 17b) and abundance (fig. 17d) were highest on the offshore line.

Early-stage eggs of California sheephead were most numerous at night, peaking near midnight and decreasing well before dawn, in summer CUFES samples (fig. 18a). Eggs were collected in bongo samples only between about 10 a.m. and 10 p.m. (fig. 18b), and concentrations of all stages except very recently spawned (stage I) eggs were lower on the basis of bongo samples than on the basis of CUFES samples. Nearly all of the stage I eggs collected were taken in the bongo samples all during the day. At AN the highest concentrations of



Figure 12. Speckled sanddab (*Citharichthys stigmaeus*) eggs: concentration (a-c) and abundance (d-f) vs. distance from shore at the SC, AN, and SM sites during survey 9803JD, using transect line as a proxy for distance. Data from CUFES (a-c) and vertical bongo (d-f) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

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Figure 13. White croaker (*Genyonemus lineatus*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 14. White croaker (*Genyonemus lineatus*) eggs: concentration (*a*, *b*) and abundance (*c*, *d*) vs. distance from shore at the SC and VA sites during survey 9803JD, using transect line as a proxy for distance. Data from CUFES (*a*, *b*) and vertical bongo (*c*, *d*) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

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Figure 15. White seabass (*Atractoscion nobilis*) eggs: concentration vs. time of day (a, b), and concentration (c) and abundance (d) vs. distance from shore at the AN site, based on CUFES (a, c) and vertical bongo (b, d) sampling, during survey 9803JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 16. California barracuda (*Sphyraena argentea*) plus white seabass (*Atractoscion nobilis*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9806JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 17. California barracuda (*Sphyraena argentea*) plus white seabass (*Atractoscion nobilis*) eggs: concentration (a, b) and abundance (c, d) vs. distance from shore at the SC and AN sites during survey 9806JD, using transect line as a proxy for distance. Data from CUFES (a, b) and vertical bongo (c, d) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 18. California sheephead (*Semicossyphus pulcher*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9806JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 19. California sheephead (*Semicossyphus pulcher*) eggs: concentration (a, b) and abundance (c, d) vs. distance from shore at the AN and SM sites during survey 9806JD, using transect line as a proxy for distance. Data from CUFES (a, b) and vertical bongo (c, d) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 20. Senorita (*Oxyjulis californica*) eggs: concentration vs. time of day based on CUFES (*a*) and vertical bongo (*b*) sampling during survey 9806JD. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.



Figure 21. Senorita (*Oxyjulis californica*) eggs: concentration (a-c) and abundance (d-f) vs. distance from shore at the SC, AN, and SM sites during survey 9806JD, using transect line as a proxy for distance. Data from CUFES (a-c) and vertical bongo (d-f) samples. Early = stages I–III; middle = stages IV–VII; late = stages VIII–XI.

early-stage eggs were offshore on line 3 as indicated by CUFES samples (fig. 19a) and inshore on line 1 as indicated by bongo samples, although abundance was highest on line 2 (fig. 19c). The high concentration offshore measured with the CUFES was attributable almost entirely (97%) to stage III eggs, while nearly 60% on line

1 were earlier (younger) stage II eggs. A few newly spawned eggs were collected at AN; most were taken on line 1. Both the concentration (fig. 19b) and abundance (fig. 19d) of early-stage eggs were highest on the most shoreward line at SM. Middle- and late-stage eggs tended to be more numerous toward shore at both sites. Early-stage senorita eggs occurred primarily during the day in both CUFES and bongo samples (table 5), perhaps with morning, midday, and afternoon peaks (fig. 20). Concentrations measured with both samplers were more or less comparable for each of the composite egg stages. Concentrations of early-stage eggs were highest on line 1 or 2 (fig. 21a–c), and abundance was highest on line 1 (fig. 21d–f). No early-stage eggs were collected offshore, except at AN, where some were taken on line 3 with both samplers.

DISCUSSION

Most fish egg types collected in winter, but fewer in summer, were identifiable to some taxonomic level, usually to species. The taxonomic composition generally is consistent with results of other studies of nearshore ichthyoplankton (most were concerned primarily with fish larvae and gave little or no information on fish eggs) off southern California (e.g., Gruber et al. 1982; Lavenberg et al. 1986; Walker et al. 1987; McGowen 1993). For example, Walker et al. (1987) and McGowen (1993) identified winter-spring assemblages that included among their major components northern anchovy, white croaker, and California halibut-the three most common taxa in our winter survey. Summer-fall assemblages included queenfish (Seriphus politus) and the kelp and sand basses (Paralabrax spp.) among their major components, as well as labrids (including California sheephead and senorita), California barracuda, and white seabass. A few, mostly middle-stage, queenfish eggs were identified during our summer survey (table 4), but most early-stage queenfish eggs, as well as all stages of Paralabrax spp., were probably included in the "unidentified egg" category. Labrid, California barracuda, and white seabass eggs all were important components of our summer collections. Speckled sanddab eggs were common in the winter survey and present in lower numbers during summer; McGowen (1993) identified Citharichthys spp. eggs as part of a winterspring assemblage, whereas Walker et al. (1987) characterized larval Citharichthys spp. as a primarily winter-spring taxon that remains moderately abundant throughout the remainder of the year.

Unidentified fish eggs were a minor component of our winter samples but an important part of the summer collections. At least four of the winter unidentified types might be mesopelagic ("stomiiform-like") taxa, and two might be shelf flatfishes. Many of the summer unidentified types might be shorefish species; however, nearly all were early- and middle-stage eggs that fell within the 0.7–1.0 mm size range, and had a single oil globule 0.1–0.2 mm in diameter—i.e., they were "typical" planktonic marine fish eggs (e.g., Ahlstrom and Moser 1980). It seems unlikely that most will be identifiable with conventional morphological characters (Ahlstrom and Moser 1980; Matarese and Sandknop 1984). Thus our first objective—identification of the planktonic fish eggs—was largely met in winter but less successfully met in summer.

Nocturnal spawning seems to be common among fishes with planktonic eggs (e.g., Johannes 1978) and may be common here as well: most of the shorefish taxa, with the notable exception of senorita, showed at least some indication of nighttime spawning, based on the occurrence of early-stage (stages I-III) eggs. Stage I eggs should provide the best estimate of spawning time, but for most taxa these very recently spawned eggs were collected only occasionally, or not at all. When stage I eggs were collected, estimated spawning times usually agreed reasonably well with those inferred from the broader "early-stage" category, except for California sheephead. The only taxon for which stage I eggs were collected with some regularity and in moderate abundance was the pooled taxon, California barracuda plus white seabass. Of the 35 stage I occurrences of this taxon, 30 were at night, between about 8 p.m. and 3 a.m. (about twothirds of these between 8 p.m. and midnight), in accord with the nocturnal spawning inferred from the "early-stage" category. Two of the stage I collections were attributable with some degree of certainty to California barracuda (yolk segmentation, absent in white seabass and present in California barracuda-but often not visible in field-collected eggs-was visible in these eggs); both were collected between about 8 and 9 p.m. Thus California barracuda apparently spawns at night, probably beginning soon after sunset and continuing to about midnight or a little later. None of the stage I eggs was definitely attributable to white seabass during the summer survey, and none of their stage I or early stage II eggs were collected in the winter survey. Nevertheless, it seems likely that white seabass spawn at essentially the same time as California barracuda.

The single occurrence of a stage I speckled sanddab egg was just before midnight, and the few occurrences of first- and second-cleavage stage II white croaker eggs (stage I eggs were not collected) were at night before midnight. These are generally consistent with the nocturnal spawning times inferred for those species.

Concentrations of early-stage California halibut eggs were highest at night, peaking near midnight, with catches before the peak being predominantly stage II, shifting to predominantly stage III after the peak. Caddell et al. (1990) reported that California halibut cultured under natural light and water conditions spawn primarily during mid- to late afternoon early in the spawning season, shifting to evening spawning, or not, later in the season. Spawning beginning in the afternoon is not inconsistent with our results; indeed, occurrences of a few stage II eggs undergoing first blastomere cleavage in late afternoon samples suggested some afternoon spawning. However, a few first- and second-cleavage stage II eggs also were collected well into the evening, and all catches of stage I eggs were between 8 p.m. and 5 a.m. (three of the four occurrences were between 2 and 5 a.m.), suggesting that spawning may be protracted.

Eight of the ten occurrences of stage I California sheephead eggs were during daylight hours; six of these were between about 1:30 and 6:30 p.m., but the largest collection (94 eggs) was made just before noon. This clearly suggests spawning primarily during the day. The increasing numbers of stages II and III during the evening probably reflect both the rate of embryonic development and dispersal of the initially highly aggregated eggs following spawning.

Nine of the ten collections of stage I senorita eggs were in the morning; eight between 8 and 10 a.m. The remaining stage I egg was collected in midafternoon. Midday and late afternoon peaks of more advanced earlystage eggs probably reflect normal development and dispersal following morning spawning, although some spawning might have continued into the afternoon. Daytime spawning is well known in tropical labrids (e.g., Colin and Bell 1991) and appears to be the case for the local species as well.

Higher abundance and frequency of occurrence of some taxa at certain sites suggested that these sites are important spawning habitats for those taxa. For example, the low-relief, low wave energy, soft-bottom coastline of the Big Sycamore Canyon Ecological Reserve vicinity is a typical adult habitat for white croaker, California halibut, and speckled sanddab, and these species clearly favored it for spawning. All three species spawned primarily shoreward of the 60 m isobath. The highest abundance of early-stage California halibut eggs was on line 2, and the few stage I eggs collected were taken along line 2, between the 40 and 60 m isobaths (bottom depth ca. 45–57 m along most of this line). Allen (1990) noted that adult California halibut are most common inshore at depths $\leq 20-30$ m, and Frey (1971) stated that they spawn near shore in about the 6-20 m depth range. Distributions of early-stage eggs in our study clearly suggest that spawning in the vicinity of Big Sycamore Canyon was centered farther from shore in deeper water in 1998. Abundances of early-stage eggs were highest, and most of the youngest (stage II) speckled sanddab eggs collected at this site were on lines 1 and 2 (ca. 20-60 m). Most of the youngest white croaker eggs (stage II) were collected on line 1 (ca. 20-30 m), although the abundance of the composite early-stage category was highest on line 2. During summer, white seabass and California barracuda spawned to some extent along the Big Sycamore Canyon coastline, where most of the youngest eggs (stage II, probably predominantly barracuda) were collected on lines 2 and 3 (ca. 45-90 m). Big Sycamore Canyon Ecological Reserve extends seaward to the 37 m isobath and thus probably includes a large part of the primary depth range for white croaker and speckled sanddab spawning, but it is possible that it includes little of the principal California halibut and California barracuda spawning habitat. Our surveys yielded no evidence of higher egg production at the reserve relative to nearby areas outside the reserve for any taxon. The only suggestions of alongshore patterns in the vicinity of the reserve were the tendencies for the concentration of California halibut eggs to decrease toward Mugu Submarine Canyon and for northern anchovy eggs to remain high on the shoreward lines in the vicinity of the canyon during the winter survey, and in summer for senorita eggs to occur more frequently, in slightly higher concentration on average, in samples east of the reserve, perhaps reflecting spawning near the small area of hard bottom and kelp habitat east of the reserve.

Like the Big Sycamore Canyon site, the Vandenberg area also is a mostly low-relief, soft-bottom site, but wave energy typically is much higher, and currents and upwelling are stronger than at SC. Vandenberg apparently was not particularly favored as a spawning site by any planktonic spawner during the 1998 surveys. The broad area of moderate white croaker egg abundance to the north of Point Arguello during the winter survey may have resulted from southwesterly advection in a shallow plume of eggs spawned inshore along the coast. During the summer survey, surface water temperature was quite low $(13^{\circ}-14^{\circ}C)$ at the site, and temperature and salinity gradients north of Point Arguello suggested upwelling. These might account, at least in part, for the apparent low level of spawning in the area at that time. The reserve at the Vandenberg site extends seaward only to the 18 m isobath, and it may not encompass the principal spawning depth of any of the local planktonically spawning fish species.

The more extensive hard bottom and kelp coverage at the islands provide better labrid habitat than is available at the mainland sites, and the islands clearly were far more important than the mainland sites for California sheephead and senorita spawning in 1998. Lower concentration and frequency of occurrence of eggs at San Miguel Island suggests reduced spawning there relative to Anacapa Island, possibly associated with the lower water temperature (surface temperature ca. 13.5°-14.5°C vs. ca. 16° – 18°) at San Miguel during the summer survey. The few newly spawned California sheephead eggs collected at Anacapa Island were mostly inshore, and the remainder were on the next line seaward. Most were taken off East Anacapa and the eastern half of Middle Anacapa. The very large collection of stage I eggs at San Miguel Island was made inshore, and two small collections there were farther seaward on line 3. Thus California sheephead appear to have spawned primarily, but perhaps not exclusively, inshore at the islands. There was a hint in the distribution of stage I eggs (but not in the distributions of stages II and III) that spawning at Anacapa Island might have been predominantly at the eastern half of the site. Stage I senorita eggs were collected mainly at San Miguel Island, with all but one occurrence on lines 1 and 2 (the majority on line 2). The single occurrence at Anacapa Island was on the inshore line at East Anacapa. Thus senorita also appear to have spawned primarily near shore, but perhaps over a broader depth range than California sheephead.

The northern Channel Islands are near the northern range limit of California sheephead, and recruitment there occurs only sporadically (Cowen 1985). During strong El Niño events recruitment to the northern islands should be especially good, and these events may largely account for recruitment north of Point Conception (Cowen 1985). If the high egg abundance at Anacapa and San Miguel Islands in June 1998, near the end of the 1997-98 El Niño, was typical of that event, then strong recruitment of California sheephead might be expected. However, zooplankton biomass was especially low through spring of 1998 (e.g., Lynn et al. 1998), and larval survival in 1997 might have been poor (very few larval California sheephead were collected during the 1997 CalCOFI cruises). Plankton volume generally was much higher in samples collected during survey 9806JD than during 9803JD, suggesting a return to higher zooplankton biomass; thus larval survival and subsequent recruitment of California sheephead to the northern Channel Islands, and perhaps north of Point Conception, might have been enhanced in 1998. The summer 1999 survey will allow a comparison of California sheephead spawning during the past El Niño and currently normal, or perhaps La Niña, conditions and afford an opportunity to determine whether spawning is enhanced in the northern part of the range during warming events.

Newly spawned eggs of California barracuda plus white seabass were collected almost exclusively at Anacapa Island. Stage I eggs were taken on all three lines, with slightly higher occurrences on the inshore line but with the larger catches mostly on the next two lines. The only other stage I occurrences were at San Miguel Island: one egg each on lines 2 and 3. Thus California barracuda and white seabass spawned over a broad depth range at the islands, shoreward of about the 100 m isobath but probably mainly seaward of about the 20 m isobath.

Fine-scale distributions detected with the CUFES system were generally concordant between sites for the more common taxa, and for the most part were consistent with what is known of the biology of those taxa, suggesting that the patterns were real. Similar patterns obtained with the vertical bongo sampling support this assessment of the CUFES data. Thus the CUFES system does appear to be suitable for measuring fine-scale distributions of planktonic fish eggs in shallow coastal waters, and the higher sampling intensity available with CUFES provides a clear advantage over conventional towed nets in this application.

On the other hand, the CUFES system has a potentially significant limitation in that it samples at a fixed depth. Eggs of some taxa were far more common in vertical bongo samples than in the CUFES samples-e.g., Pacific hake; hornyhead turbot (*Pleuronichthys verticalis*); bigmouth sole (Hippoglossina stomata)—suggesting that their distributions in the water column are centered well away from the CUFES intake depth. Comparisons of the CUFES and vertical bongo catches of early egg stages suggest that for some taxa (e.g., California sheephead, California halibut, white croaker) eggs are spawned below the CUFES intake depth and ascend during their first few hours of development, so that the youngest eggs are underrepresented in CUFES samples. For other taxa (e.g., senorita, California barracuda + white seabass) this may be less of a problem (although results of the shipboard rearing suggested that white seabass eggs may begin to sink shortly before hatching).

Estimates of the concentration of planktonic eggs collected with CUFES have been shown to be well correlated with abundance estimates based on vertically integrated net tows for some coastal pelagic fishes (e.g., Checkley et al. 1997), but it is unknown whether a similar relation holds for planktonic shorefish eggs. Linear regressions of concentration on abundance from our CUFES-bongo sample pairs generally yielded statistically nonsignificant results, with coefficients of determination ranging from -0.39 to 0.07 for the shorefish taxa. In contrast, the relationship (regression coefficient 0.028, $R^2 = 0.33$, $P \ll 0.01$ between samplers was significant for northern anchovy eggs during the winter survey, when they were far more abundant than any other taxon. Among the shorefish eggs, one of the "stronger" relationships was obtained for California halibut (regression coefficient 0.023, $R^2 = 0.03$, P = 0.10), one of the most common taxa in the winter survey.

These analyses suggest that CUFES may be inappropriate for obtaining abundance indices for planktonic shorefish eggs. Alternatively, they may indicate only that too few samples were available for analysis; reanalysis of the full two-year data set may clarify this. In any case, it is clear that the CUFES system cannot be relied upon as the sole sampler for all taxa; it must be calibrated against (and perhaps, for the less abundant taxa, always used in conjunction with) a sampler that includes the full vertical range of the taxa of interest.

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