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[Article]

Estimating Stock Composition of Anadromous Fishes from Mark–Recovery Data: Possible Application to American Shad

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Abstract.—Information on the stock composition of mixed-stock fisheries is often needed to develop management regulations for anadromous fishes. Although several methods can be used to infer stock composition, marking studies have long been identified as a promising approach. Hatchery-reared larval American shad *Alosa sapidissima* are marked with a river-specific mark and released in stock enhancement programs along the U.S. East Coast. We describe and apply a mark–recovery method for inferring the proportion of the catch in a mixed-stock fishery that originates from a particular river. The method is based on comparing the proportion of the mixed-stock catch with marks from the river with the proportion of the fish returning to the river with marks. We explore the utility of using mass marking of hatchery-reared American shad larvae with tetracycline to determine the stock composition of mixed-stock fisheries of American shad in Virginia. Our analysis focuses on the impact of the former Virginia coastal ocean fishery on fish produced in the James and Pamunkey rivers, Virginia, and on the impact of bycatch in Chesapeake Bay pound nets on Susquehanna River American shad. Our results suggest that the coastal ocean fishery harvested relatively small proportions of the James and Pamunkey River stocks and that few American shad captured in pound nets sampled in Chesapeake Bay were from the Susquehanna River system.

Management of mixed-stock fisheries of anadromous fishes is often plagued by a lack of information detailing the contributions of the constituent stocks to the total catch (Cadrin et al. 2005). Several methods can be used to assess stock composition, including genetic analyses (Nolan and Grossfield 1991; Epifanio et al. 1995; Nielsen 1998; Brown et al. 1999; Nolan et al. 2003; Beacham et al. 2004), meristic and morphometric characters (Melvin et al. 1992; Waldman et al. 1997; DeVries et al. 2002), life history characteristics and population parameters (Skillman 1989), natural tags (Thorrold et al. 1998; Campana et al. 1999), and tagging or marking studies (McFarlane et al. 1990; Brodziak 1993). Brodziak (1993) noted that tagging studies may be inadequate for determining the contributions of multiple stocks to total harvest unless the tagging programs are undertaken on a large scale. In this paper, we describe a study design that has proved feasible for determining stock composition of American shad *Alosa sapidissima* in a former offshore mixed-stock fishery and also in the bycatch of pound nets within Chesapeake Bay.

American shad is an anadromous clupeid whose native range extends along the East Coast of North America from the St. Lawrence River, Canada, to the St. Johns River, Florida (Walburg and Nichols 1967). Each spring, mature American shad leave their offshore grounds and migrate to their natal rivers to spawn (Leggett 1973). Juveniles usually exit their natal streams by late fall (Hoffman et al. 2008), and immature fish remain in oceanic environments until sexual maturity. The timing of the spawning migration is related to latitude, the southern stocks commencing their spawning runs earlier than the northern stocks (Leggett and Carscadden 1978).

During the coastal migration and within the natal rivers, American shad historically have supported sizable commercial and recreational fisheries (Walburg and Nichols 1967). Currently, in-river directed harvest of shad stocks continues except in the Chesapeake Bay and its tributaries. In the Maryland and Virginia waters of the bay (including tributaries), fishing moratoria were enacted in 1980 and 1994, respectively. Allowances are made for pound-net and gill-net bycatch in the Potomac River and gill-net bycatch in Virginia rivers. Since 1998, the spawning runs of Virginia stocks of American shad have been evaluated through in-river monitoring programs (Olney and Hoenig 2001a). Despite the closure of these fisheries and stocking programs in some rivers, monitoring data have shown only marginal increases in shad abundance in Virginia rivers (Olney et al. 2003; Olney and Delano 2006).

In 2000, scientists affiliated with the Atlantic States Marine Fisheries Commission (ASMFC) postulated that the coastal ocean mixed-stock fishery was at least potentially responsible for the slow recovery. Annual

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landings in the ocean mixed-stock fishery (including mixed-stock fisheries in large bays) have ranged from 282,000 to 873,000 kg, peaking in the late 1980s (National Marine Fisheries Service and ASMFC data). Hence, the ASMFC considered implementing an offshore tagging program to determine the impact of the fishery on individual river stocks. The question arose as to how the study should be designed and how the data would be interpreted. The ASMFC American Shad and River Herring Technical Committee concluded that tagging fish offshore would not provide the needed information on stock composition and subsequently decided to abandon that idea. Because it was not possible to evaluate the impact of the offshore fishery on individual river stocks, the ASMFC implemented a previously planned phased reduction of effort in the intercept fishery beginning in 2001 with full closure of the fishery in December 2004.

The interest of the ASMFC in conducting an offshore tagging program for American shad motivated the present analysis in which we consider a way to infer stock composition from tagging or marking data. If an appreciable fraction of the young fish of a particular stock can be marked, then a simple and direct model can be used to estimate composition of the offshore catches, provided both the offshore catch and the subsequent in-river spawning runs are monitored for marked fish. The origin of this method is somewhat obscure. It was apparently described in an unpublished consultant's report in the late 1970s as a means of estimating the stock composition of Pacific salmon *Oncorhynchus* spp. (Carl Walters, University of British Columbia, personal communication). However, we have been unable to procure a copy of this report and thus have developed the method here from first principles. We present the model and then use it to examine the impact of two coastal fisheries on American shad from the James and Pamunkey rivers in Virginia. These two case studies are intended as pilot studies to demonstrate the potential utility of the approach.

Methods

We suppose that each year larval American shad are given a river-specific mark (e.g., by immersion in oxytetracycline [OTC] baths on specific days) and released into the rivers of interest (Hendricks 2003). The surviving juveniles migrate out to sea with their wild counterparts and remain unavailable to the fishery until they are mature. At that time, they can be captured in a mixed-stock fishery either offshore or within large coastal embayments such as Chesapeake Bay or Delaware Bay before returning to their natal streams to spawn. We assume fidelity of American shad to their natal stream (or to the stream where they were stocked).

Samples of the offshore or Chesapeake Bay catch are obtained by an appropriate probability sampling method, which generally involves some type of cluster sampling. The catch samples are examined for hatchery marks, and the proportion of the catch with marks from each river is tabulated. Suppose, for sake of argument, that 2% of the offshore catch has marks from River A. If all of the offshore catch were from River A, then 2% of the adults entering River A to spawn would have hatchery marks. Consequently, if a sample of fish is taken from the spawning run in River A, we should observe that 2% of the fish have marks (except for sampling error). Now suppose that the sample taken in River A reveals that 4% of the fish actually have the hatchery mark. Then, clearly, our premise that all of the offshore catch was from River A is not supported. If half the offshore catch were from River A, then we would expect that 4% of the in-river fish would have the mark because the in-river sample is a "pure" sample of fish from River A, while the offshore sample is a 50% "dilution" of the River A stock.

This concept can be formalized as follows. Let π be the proportion of the offshore catch with hatchery marks for River A, f the fraction of the offshore catch from River A, and p the proportion of the fish sampled in River A that have the mark. Then,

$$\pi = fp \tag{1}$$

and

$$\hat{f} = \frac{\hat{\pi}}{\hat{p}}, \tag{2}$$

where the carets denote estimates. In the previous example, the fraction of the offshore catch that is from River A is estimated to be 0.02/0.04 = 0.50. The variance of the estimate can be approximated by the delta method (see Seber 1982), that is,

$$\mathrm{Var}(\hat{f}) = \left(\frac{1}{p}\right)^2 \mathrm{Var}(\hat{\pi}) + \left(\frac{\pi}{p^2}\right)^2 \mathrm{Var}(\hat{p}). \tag{3}$$

Still to be determined are the variances of $\hat{\pi}$ and $\hat{p}$, which depend on the particular sampling design. If one could obtain a simple random sample of individuals, which implies that each individual could be sampled independently of all others, then $\hat{\pi}$ and $\hat{p}$ would be binomial random variables. However, in general, the sampling unit is a netful of fish (i.e., a cluster) and, to the extent that individuals do not travel independently, the effect is to increase the variance to a value greater than the binomial variance (Cochran 1977).

The covariance of the estimates of the proportions of the offshore catch from two stocks i and j can also be approximated by the delta method. We assume that in-river proportions are estimated independently; thus, the only covariance term involves the proportions of the offshore catch with river-specific marks. The covariance is

$$\mathrm{Cov}(\hat{f}_i, \hat{f}_j) = \frac{\mathrm{cov}(\hat{\pi}_i, \hat{\pi}_j)}{p_i p_j}. \quad (4)$$

The nature of the covariance between $\hat{\pi}_i$ and $\hat{\pi}_j$ depends on the particular sampling design.

Case Study 1: American Shad in the James and Pamunkey Rivers, Virginia

Hatchery Production of American Shad Fry

In the spring of 1994, a hatchery-based restoration program for American shad on the James River, Virginia, began through a cooperative agreement between the U.S. Fish and Wildlife Service, the Virginia Department of Game and Inland Fisheries (VDGIF), and the Virginia Marine Resources Commission (VMRC). Each year, VDGIF scientists collect gametes from American shad in the Pamunkey River (a tributary of the York River, Virginia), rear fry in a nearby hatchery, mark their otoliths with an OTC mark specific to the James River, and release 6–9 million fry in a variety of locations in the upper James River (Olney et al. 2003). Although the James River is the primary target for the restoration program, 2–3 million marked American shad fry are also released in the Pamunkey River in an effort to replace those individuals sacrificed for the collection of gametes. The otoliths of these fish are marked with OTC in a manner specific to the Pamunkey River.

Offshore and In-River Sampling

In 2000, a pilot study was conducted to investigate the possibility of assessing the stock composition of American shad in the Virginia coastal fishery (Figure 1). We were aided in this effort by the cooperation of one ocean fisherman, whose total annual catch was 25–30% of the total landings reported to the VMRC in 2000 and 2001 (VMRC data). The fisherman deployed an anchored gill net with 127-mm stretched mesh. Approximately 15–20 randomly selected shad were obtained weekly from mid-February to mid-April. Sagittal otoliths were extracted from each fish and examined by VDGIF scientists for the presence of OTC marks associated with the hatchery releases in the James and Pamunkey rivers, Virginia. Whole otoliths were mounted on glass slides and ground on both sides to produce a thin sagittal section. The sections were examined with an epifluorescent microscope for hatchery marks. In-river samples of migrating American shad from both the James and the York rivers (Figure 1) were collected twice weekly from mid-February to the beginning of May from staked gill nets (124-mm stretched mesh, one in each river; Olney and Hoenig 2001b). Sagittal otoliths from in-river specimens were examined for OTC marks by VDGIF and Virginia Institute of Marine Science (VIMS) scientists.

In 2001, efforts were directed at increasing the sample size of the fish obtained from the offshore fishery. Hence, from the same cooperating fisherman, approximately 30–40 randomly selected American shad were obtained twice weekly from mid-February to mid-April. Likewise, in-river samples from both the James and the York rivers were collected twice weekly from mid-February to the beginning of May from staked gill nets (Olney and Maki 2002). All of the aforementioned biological data were collected from these specimens, and sagittal otoliths from both ocean and in-river specimens were again examined for OTC marks.

Results and Estimates of Stock Composition

In 2000, a total of 192 American shad was collected from the offshore mixed-stock fishery. Of those, two fish possessed OTC marks—one of James River origin and one of Pamunkey River origin. The in-river monitoring programs yielded American shad catches of 434 and 458 fish on the James and York rivers, respectively. Of those fish captured by the James River staked gill net, 387 specimens were successfully scanned, of which 156 fish (40.3%) possessed OTC marks. From the York River staked gill net, a randomly selected subsample of 129 fish was scanned for hatchery marks, and 4 of those fish (3.1%) possessed OTC marks. By equation (2), the estimated proportions of the offshore catch that are of James and Pamunkey river origin, respectively, are

$$\frac{1/192}{156/387} = 1.29\%,$$

$$\frac{1/192}{4/129} = 16.8\%.$$

From these calculations, it appears that the offshore catch of American shad in 2000 consisted of only a small proportion of fish produced in the James River and an appreciable proportion of fish produced in the Pamunkey River.

A total of 594 American shad were collected in 2001 from the offshore fishery. Of those, four specimens possessed a James River OTC mark, while only one fish possessed a Pamunkey River OTC mark. The in-river monitoring programs yielded American shad total catches of 267 and 677 fish on the James and York rivers, respectively. Of those fish captured in the James River, 256 specimens were successfully

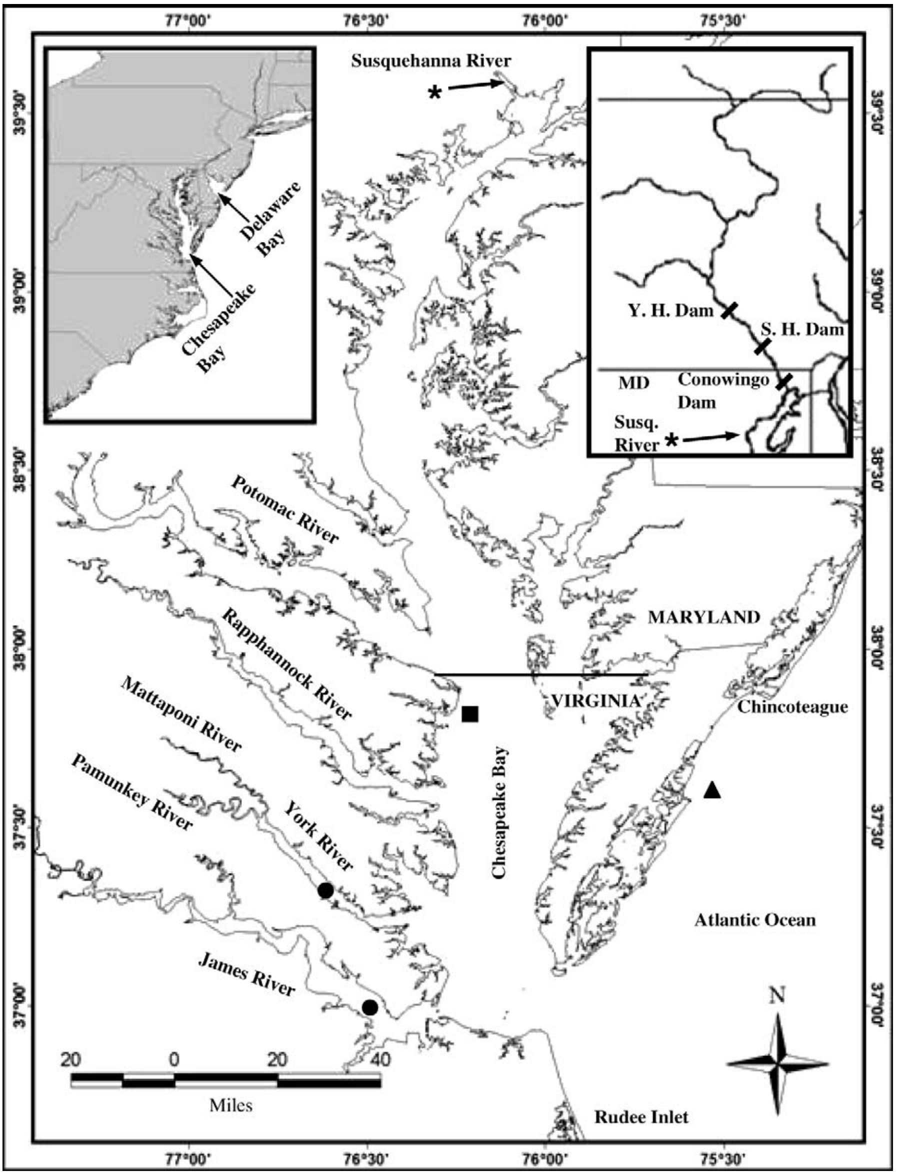

FIGURE 1.—Map of the Chesapeake Bay and coastal Virginia showing the locations of offshore fishing (triangle) and the pound net in the main stem of the Chesapeake Bay (square) from which American shad bycatch samples were obtained. The sampling locations in the James and York rivers are indicated by circles. The inset at top right shows the locations of the Conowingo, Safe Harbor (S. H.), and York Haven (Y. H.) dams on the Susquehanna River.

scanned for hatchery marks, of which 103 (40.2%) possessed those marks. From shad captured in the York River, a randomly selected subsample of 186 fish was scanned for hatchery marks and 9 of those fish (4.8%) possessed OTC marks. Again, by equation (2), the estimated proportions of the offshore catch that are of James and Pamunkey river origin, respectively, are

$$\frac{4/594}{103/256} = 1.67\%,$$

$$\frac{1/594}{9/183} = 3.48\%.$$

In 2001, the offshore harvest of American shad consisted of relatively small proportions of fish produced in both the James and Pamunkey rivers. These low proportions are consistent with the information from 2000, although the results for the Pamunkey River are more variable across years than those for the James River. In both years, the proportion of the offshore catch coming from the Pamunkey River was estimated to be higher than the proportion coming from the James River.

We do not present estimates of the variances because the samples were collected opportunistically rather than according to a particular probability-based sampling scheme, and therefore it is not possible to assess the precision of the estimates.

Case Study 2: Pound-Net Catches of Susquehanna River System American Shad

Hatchery Production of American Shad Fry

Natural reproduction of American shad is limited in the Susquehanna River, occurring only in riverine habitats above Safe Harbor and York Haven dams. The spawning run is currently dominated by hatchery fish, as judged by sampling of mature shad in the fish lift at Conowingo Dam. Shad spawn in the lower 10 miles of the Susquehanna River below the first dam and in the upper Chesapeake Bay, and the surviving progeny are unmarked. We assume that all fish stocked as fry above Conowingo Dam are trying to ascend the dams to reach their natal streams. Consequently, we are attempting to infer the proportion of fish in the pound nets that originate from above Conowingo Dam. We will return to this point in the Discussion section.

American shad larvae that are used to stock the upper Susquehanna River are cultured by methods developed at the Pennsylvania Fish and Boat Commission's Van Dyke Hatchery beginning in 1985 (Hendricks 2003). From 1990 to 1999, an average of 3 million fry was released each year (McBride et al. 2005). In most years, released larvae possess a river-specific mark. However, marks applied in other Chesapeake Bay hatcheries are similar in some cases and could be confused with those of Susquehanna River fish (see Results and estimates of stock composition).

Pound-Net Bycatch and In-River Sampling

American shad enter the mouth of the Chesapeake Bay in late winter and spring annually and migrate to the spawning grounds of their natal rivers in Virginia, Maryland, Delaware, and Pennsylvania. It is generally believed (but not well documented) that fish destined for northerly systems (principally the Rappahannock, Potomac, and Susquehanna rivers and the upper bay region) migrate along the western shore of the bay, being attracted by the freshwater outflows of the tributaries (Stevenson 1899). Along this migratory corridor, fish encounter commercial fishing gear, including pound nets, haul seines, and gill nets. Throughout the open waters of the Chesapeake Bay, it is unlawful to possess American shad. Removals of fish as bycatch in commercial fishing gear are known to occur, but information on these interactions is limited because there are no requirements to report discards. Managers and scientists are concerned that these mixed-stock catches might slow or reverse the recovery of the individual stocks throughout the region. To address this need for information, VIMS scientists secured the cooperation of a single fisherman and began monitoring his pound nets located in the upper, western portion of Chesapeake Bay just south of the Potomac River (Figure 1). Samples were obtained in 2004 ($n = 24$ on 8 April; $n = 26$ on 6 May) and 2005 ($n = 39$ on 28 March; $n = 50$ on 2 May; and $n = 38$ on 14 April). Sagittal otoliths from these fish were examined for OTC marks by scientists at the Pennsylvania Fish and Boat Commission. The same procedures were used as in case study 1.

Results and Estimates of Stock Composition

In 2004, 50 American shad were collected from the pound nets. Of those, 49 had readable otoliths and 5 possessed OTC marks. Two of the OTC marks were clearly Susquehanna marks and, although there was some ambiguity in determining whether the remaining three were of Susquehanna River or James River origin, we assigned them to Susquehanna River origin because the location of capture of these fish was well north of the entrance to the James River. This assignment may overstate the impact of the pound nets on the Susquehanna stock. The in-river monitoring program at Conowingo Dam yielded 158 American shad, of which 113 (72%) of those were of Susquehanna hatchery origin. By equation (2), the estimated proportion of the pound net catch that is of Susquehanna River origin is

$$\frac{5/49}{113/158} = 14.3\%.$$

In 2005, otoliths from 127 fish from the pound nets were examined, 116 having usable otoliths; of these, 12 had OTC marks. Again, there was some ambiguity in the origin of 9 of these 12 fish, and for the reason given above we assigned them to Susquehanna origin along with the 3 with unambiguous Susquehanna marks. Otoliths from 274 fish from Conowingo Dam were examined, of which 178 (65%) had Susquehanna hatchery marks. By equation (2), the estimated proportion of the pound-net catch of Susquehanna River origin is

$$\frac{12/116}{178/274} = 15.9\%.$$

From these calculations, it appears that about 15% of the pound-net bycatch of American shad in 2004 and 2005 consisted of fish produced in the Susquehanna River system.

We do not present estimates of the variances because the samples were collected opportunistically rather than according to a particular probability-based sampling scheme and therefore it is not possible to assess the precision of the estimates.

Discussion

Methodology

It is not our intent to suggest that this is the best method for inferring stock composition in all cases. Rather, we believe it is a viable possibility with some important advantages. First, when larvae are transported from one river to another for stock enhancement programs, the genetic distinctiveness of stocks is reduced, making it difficult or impossible to infer river origins of fish from genetic analyses. Transriver transport of larvae does not affect our method, which is based on tagging results. Second, interest tends to be focused on populations at risk, which are the populations most likely to be supplemented with stocked larvae. Thus, a major component necessary for application of the tag-based method may already be in place. The marginal cost of applying the tag-based method may simply be that of procuring and processing the otoliths from the mixed-stock fishery.

Our approach assumes high fidelity of American shad to their natal streams. This seems justified because we found only 4 fish in the James River out of 419 examined over a 5-year period that had been stocked in the Pamunkey River. Additionally, McBride et al. (2005) found extremely few strays in Delaware River of fish stocked in the Susquehanna River. From equation (2) it can be seen that the effect of straying is to increase the estimate of p, resulting in overestimation of the proportion f of the offshore catch from the river.

Another assumption of the model is that the detection of marks in otoliths is complete and accurate. From equation (2) it can be seen that, if only x% of the marked fish are detected when the otoliths are examined, then both the numerator and denominator are multiplied by x and the estimator is unaffected. When there is misidentification (hatchery marks attributed to the wrong river), the situation is more complicated. If James River fish with marks were more common in the offshore catch than marked fish from the other rivers, then the attribution of a few non-James marks to the James stock would not affect the estimator much. On the other hand, if James River marks are rare relative to other marks in the offshore catch, then the estimator may be sensitive to misidentifications. In our study, there was some uncertainty in the identification of some hatchery marks. However, the results still indicate low percentages of Susquehanna fish in the mixed-stock fishery even when the uncertain identifications are accepted as Susquehanna fish.

Investigators contemplating using the method described in this paper need to consider the level of precision desired and the necessary sample sizes. This can be approached by performing sample calculations with equations (2) and (3). For example, it appears that $f = 5\%$ of the offshore catch was from the James River. The proportion marked in the river is under the control of the investigator. We can investigate the consequences of releasing enough larvae such that $100p = 10$, 20, or 30% of the returning adults have marks. In such cases the fraction of the offshore catch with marks will be 0.005, 0.010, or 0.015, respectively. If we could obtain simple random samples of 100 fish from the offshore catch and from the in-river sampling, the variances of the estimated proportions could be calculated according to the formula for binomially distributed random variables. Given this information, the proportional standard error (= standard error/parameter value) can be calculated. The results for $p = 10$, 20, and 30% of the James River adults having marks are proportional standard errors of 144, 101, and 83%, respectively. That is, we might expect the upper limit of the confidence band to range from $2 \times 0.83 \times 0.05 = 0.083$ to $2 \times 1.44 \times 0.05 = 0.144$ when $f = 0.05$. Of course, in practice, the binomial variance will be overly optimistic and a somewhat larger sample size will be needed to have an effective sample size of 100.

We applied the method described in this paper to data on American shad in Virginia waters. Unfortunately, the American shad catches were sampled on an opportunistic basis rather than according to a prescribed probability-based sampling design. Consequently, the results are of unknown reliability in terms of both bias and precision, and calculations of variance are inappropriate. We believe the results are of interest, nonetheless, for three reasons. First, they serve to illustrate the potential use of the method. Second, the estimates of stock proportions are the best information available and thus merit inspection. Readers can exercise whatever caution in the interpretation of the results as they see fit. Third, we believe the examples serve to illustrate how future studies may be conducted and thus serve as an aid for planning future assessment and management programs. For these reasons, we consider the possible implications of the examples in some detail.

Implications for American Shad Assessment and Management

In January 2005, the coastal intercept fisheries for American shad in the waters of Rhode Island, New Jersey, Delaware, Maryland, Virginia, North Carolina, and South Carolina were closed. The rationale for closing these fisheries was the lack of information about their relative impact on the mixed-stock assemblage along the eastern seaboard, with specific concern that fish from depleted stocks under restoration (e.g., those stocks from Chesapeake Bay) were being harvested before spawning. Our analysis indicates that the Virginia offshore harvest of American shad consisted of relatively small proportions of fish produced in both the James and Pamunkey rivers in two years of sampling. However, we recognize that the data supporting our investigation are limited, in that we worked with only a single commercial fisherman. At the time of our sampling, 53–54 licensed fishers reported catches from several locations along the Virginia coast from Rudee Inlet (Virginia Beach, Virginia) north to Chincoteague, Virginia. The landings reported to VMRC in 2002 and 2001 were 73,482 and 109,769 kg, respectively; of the licensed fishers, however, fewer than 20 individuals reported catches greater than 454 kg (VMRC data). In the event that shad managers give consideration to reopening mixed-stock fisheries for American shad, we strongly advocate simultaneously monitoring the stock composition of the commercial catch. This should be relatively easy for systems where there are in-river monitoring programs and hatchery operations that use river-specific OTC marks on fry. However, for systems without such monitoring programs or hatchery operations, we recognize that inferring the stock composition of the offshore catch may be more difficult. Along the East Coast, 21 rivers are currently stocked with hatchery-raised fry, most of these in the Chesapeake region (Hendricks 2003).

Currently, about 25 pound-net operators are permitted in Virginia (VMRC data); they fish approximately 60 nets during the spring spawning run of American shad. In 2006, these fishers recorded 439 trips through 30 April to the VMRC. The total bycatch of American shad is unknown. Given the manner of fishing (the catch is usually bailed into the boat first and later sorted by species), the bycatch mortality of shad is probably high. Although the potential for Virginia pound nets to capture American shad migrating to the Susquehanna River exists, our preliminary data suggest that the impacts may be small. However, unmarked fish in the Virginia pound-net samples may be Maryland fish because our method is limited in its detection of other stocks. Regardless, we document for the first time that the bycatch of American shad in Virginia pound nets is mixed stock.

Despite our not being able to identify with certainty all of the Susquehanna hatchery marked fish recaptured, our procedure is still valuable because it tends to overstate the impact of the pound nets; that is, if the proportion estimated to come from the Susquehanna is low, then it is probably even lower in reality.

As stated earlier, we assume that all fish stocked as fry above Conowingo Dam are trying to ascend the dams to reach their natal streams. Consequently, we are attempting to infer the proportion of fish in the pound nets that originate from above Conowingo Dam. We acknowledge that, if some fish originating above Conowingo spawn below the dam and hence are not susceptible to sampling at the dam, we will have a confused situation where it is not clear what population we are studying. Unfortunately, it is not easy to determine whether adult American shad below Conowingo Dam will spawn below the dam or continue their efforts to reach the upper reaches of the river.

Tag–recovery studies are considered to be one of several methods that can be used to infer the stock composition, provided the scale of the tag–recovery study is sufficiently large that small sample sizes are avoided. However, in cases where stock composition information is needed for the management of mixed-stock fisheries (particularly for anadromous species), the usefulness of a tag–recovery study is a direct function of its design. We contend that tagging should take place in the natal streams and rivers rather than on the mixed-stock fishing grounds. If in-river monitoring programs are in place, then stock composition can be easily inferred by simply sampling the offshore commercial catch and comparing the proportion of marked fish in the catch with that in the in-river monitoring program. This assumes that adults from a particular river are well mixed regardless of whether they are of wild origin or were stocked as larvae. Thus, the approach does not require fisheries-independent sampling for adults on the mixed-stock fishing grounds. Moreover, this approach can also support other stock-specific life history investigations. For example, if the locations of the commercial catches are known with reliable precision, it may be possible to infer relative migration pathways of interacting stocks or possibly within-stock ontogenetic migration corridors.

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