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Extrusion of fish larvae from SEAMAP plankton sampling nets: a comparison between 0.333-mm and 0.202-mm mesh nets

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Abstract—To assess larval fish and egg extrusion through the standard-size mesh plankton net used during resource surveys of the Southeast Area Monitoring and Assessment Program (SEAMAP), 81 bongo tows with side-by-side nets, each constructed with a different mesh size (0.333 mm and 0.202 mm), were taken during 5 SEAMAP surveys conducted in the Gulf of Mexico during 2005–2007. Retention by length class for the larvae of 6 taxa and an unidentified group was evaluated by using 2 deterministic functions to estimate the number of larvae missed when sampling with the net with standard-size mesh (0.333 mm) compared with sampling with the smaller mesh net (0.202 mm). Smaller larvae, particularly those between 1.5 and 3 mm in body length, were retained in greater numbers in the 0.202-mm-mesh net than in the 0.333-mm-mesh net. Extrusion was most pronounced for small, undeveloped larvae that could be identified only to the suborder Percoidei or that could not be identified. Extrusion was evident also among larvae of taxa in the families Engraulidae, Sciaenidae, and Scombridae, but less so for Clupeidae and Lutjanidae; the latter result was most likely attributable to a mismatch between the timing of sampling and spawning seasons. The functional relationships presented here, based on larval abundance ratios and body lengths, represent the first empirically derived estimates of extrusion and size bias in SEAMAP ichthyoplankton samples.

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Planktonic, early-life-stage fish (ichthyoplankton) have been monitored for over a century worldwide to assess the abundance and distribution of fish stocks (Hjort, 1914; McClatchie et al., 2014). Ichthyoplankton surveys have been used to estimate changes in spawning stock biomass, to identify spawning habitats and seasonality, and to quantify survival through the larval stage (Richardson et al., 2010). Arguably, the greatest value of these surveys is that they provide a method for measuring changes in the trends of larval assemblages over time. Such trends are particularly valuable during a changing climate, since alterations in sea temperature, carbonate chemistry, and ocean circulation influence larval growth, mortality, dispersal, and assemblage connectivity (Llopiz et al., 2014).

In the southeastern United States, larval fish abundances are monitored under the Southeast Area Monitoring and Assessment Program (SEAMAP; Stuntz et al.[1]; Lyczkowski-Shultz and Hanisko, 2007). As part of SEAMAP protocol, plankton samples are collected during annual surveys in the Gulf of Mexico by the National Marine Fisheries Service (NMFS) and agencies of 4 states: Alabama, Florida, Louisiana, and Mississippi. Data from these surveys are used in stock assessments for many managed, commercially significant species, including the bluefin tuna (*Thunnus thynnus*; Scott et al., 1993), king mackerel (*Scomberomorus cavalla*; Gledhill and Lyczkowski-Shultz, 2000), red snapper (*Lutjanus campechanus*;

[1] Stuntz, W. E., C. E. Bryan, K. Savastano, R. S. Waller, and P. A. Thompson. 1983. SEAMAP environmental and biological atlas of the Gulf of Mexico, 1982, 145 p. Gulf States Mar. Fish. Comm., Ocean Springs, MS. [Available from website.]

Hanisko et al., 2007), and vermilion snapper (*Rhomboplites aurorubens*; Hanisko et al.[2]). Ichthyoplankton data from the SEAMAP surveys have also been used to describe larval transport, decadal changes in fish habitat, and annual variations in egg densities in the Gulf of Mexico (Johnson et al., 2009; Marancik et al., 2012; Hernandez et al.[3]; Lyczkowski-Shultz et al., 2013). Additionally, SEAMAP samples have been used to assess the potential impacts of 1) entrainment of larvae in offshore liquefied natural gas facilities (Gallaway et al., 2007) and 2) larval mortality from the 2010 Deepwater Horizon oil spill (Muhling et al., 2012) to Gulf of Mexico fisheries.

Application of such abundance-at-size data is predicated on the assumption that larvae caught and retained in plankton nets consistently and accurately represent the assemblage being sampled (Tranter, 1968; Smith and Richardson, 1977). Inherent catchability issues with plankton nets, however, result in underrepresentation of larger, more developed larvae that are able to detect and avoid the net (Morse, 1989; Somerton and Kobayashi, 1989) and in underrepresentation of the smallest larvae in catches because they are extruded through net meshes (Colton et al., 1980; Lo, 1983; Houde and Lovdal, 1984; Johnson and Morse, 1994). The effect of these sources of bias on larval abundance data have been widely investigated in studies outside the Gulf of Mexico but have never been addressed specifically for data generated from SEAMAP ichthyoplankton surveys. Only 2 previous studies with gear other than SEAMAP plankton nets investigated the extrusion of larval fish from plankton nets in northern Gulf of Mexico waters (Comyns, 1997; Hernandez et al., 2011).

Ideally both of these biases should be evaluated before abundance data are interpreted and used in resource monitoring and environmental and fisheries assessments (Smith and Richardson, 1977). In recent stock assessments, the effect of avoidance was mitigated by including in analyses only the largest size class of larvae that are consistently captured in the net—a decision based on examination of size frequency distributions (Hanisko et al., 2007; Hanisko et al.[2]). Despite the importance of the earliest life stages in estimating absolute abundance or mortality, the underrepresentation of these values due to extrusion of the smallest larvae in SEAMAP samples has not been considered in the development of SEAMAP indices of larval abundance.

Table 1

Cruise number, start and end dates, and number of tows conducted with bongo nets with different mesh sizes during Southeast Area Monitoring and Assessment Program surveys in the northern Gulf of Mexico between October 2005 and August 2007.

Cruise	Start date	End date	No. of tows
04266	22-Oct-2005	01-Nov-2005	45
63062	23-March-2006	29-May-2006	15
63064	31-Aug-2006	27-Sep-2006	7
63075	29-Aug-2007	28-Sep-2007	14

The use of standard gear and towing methods during plankton surveys has ensured consistent sampling within and among SEAMAP cruises and surveys (McClatchie et al., 2014; GSMFC[4]). However, the specific characteristics of the SEAMAP bongo net in relation to loss of eggs and larvae though the meshes of the standard SEAMAP sampling gear have yet to be investigated. Our objective was to evaluate the degree of extrusion of fish eggs and larvae through the standard SEAMAP bongo net, which has a 0.333-mm mesh, by comparing numbers of larvae from that net with larval numbers from a bongo net with a finer, 0.202-mm mesh.

Materials and methods

Field and laboratory methods

Between October 2005 and August 2007, 81 bongo tows with side-by-side nets, each with a different mesh size, were performed during 5 SEAMAP surveys conducted in the Gulf of Mexico (Table 1, Fig. 1). Given the primary objectives for these surveys, samples were taken as time permitted after standard sampling was completed. The 61-cm bongo net frame with a mouth opening of 0.29 m^2 that is used during standard SEAMAP sampling was used in the tows of our study. However, unlike the standard SEAMAP bongo net configuration, which consists of 2 nets with a mesh size of 0.333 mm, the configuration consisted of a net with 0.202-mm mesh on one side of the frame and a net with 0.333-mm mesh on the other side. Although no side-by-side effect was evaluated, it is thought to be minimal because of the short distance between the mouth openings of the 2 nets on the bongo frame. Sampling was conducted

[2] Hanisko, D. S., A. Pollack, and G. Zapfe. 2015. Vermilion snapper (*Rhomboplites aurorubens*) larval indices of relative abundance from SEAMAP Fall Plankton Surveys, 1986 to 2012. Southeast Data, Assessment and Review SEDAR45-WP-05, 34 p. [Available from: website.]

[3] Hernandez, F. J., W. M. Graham, and K. Bayha. 2013. Spatial distribution and abundance of red snapper (*Lutjanus campechanus*), vermilion snapper (*Rhomboplites aurorubens*), and red drum (*Sciaenops ocellatus*) eggs across the northern Gulf of Mexico based on SEAMAP continuous underway fish egg sampler (CUFES) surveys, 52 p. Final Report NOAA/MARFIN Award Number NA09NMF4330153. [Available from Grants Branch, Southeast Reg. Off., Natl. Mar. Fish. Serv., NOAA, 263 13th Ave. S., St. Petersburg, FL 337101.]

[4] GSMFC (Gulf States Marine Fisheries Commission). 2016. SEAMAP operations manual for trawl and plankton surveys, 61 p. GSMFC, Ocean Springs, MS. [Available from website.]

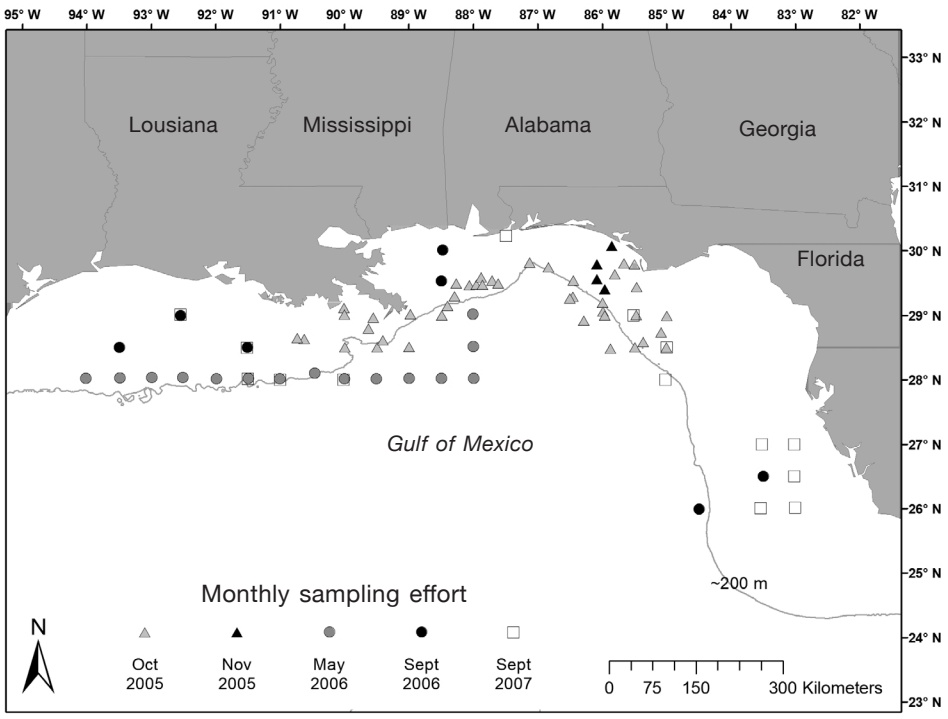

Figure 1

Locations of the 81 tows conducted with bongo nets with different mesh sizes during 5 Southeast Area Monitoring and Assessment Program surveys of ichthyoplankton conducted in the Gulf of Mexico between October 2005 and August 2007. Month and year of sampling are denoted by symbols at each location. The bathymetric contour represents the edge of the continental shelf (~200 m).

irrespective of time of day during 24-h survey operations and resulted in the collection of 35 daytime and 46 nighttime samples with nets of different mesh size. Shipboard handling of the concentration and preservation of samples taken from the nets with different mesh size followed standard SEAMAP protocols (Lyczkowski-Shultz and Hanisko, 2007). Samples were preserved initially in either 5–10% formalin or 95% ethanol. Formalin-fixed samples were later transferred to 95% ethanol after 48 h; samples initially preserved in ethanol were transferred to fresh ethanol after 24–36 h. All tows were made in a double-oblique pattern from the surface to a maximum depth of 200 m (or to within 2 m of the bottom at station depths <200 m) and then back to the surface. Tows were made at ~0.8 m/s (~1.5 kt) and maintained a targeted towing wire angle of ~ 45° (Smith and Richardson, 1977). Tow speeds ranged from 0.64 to 1.47 m/s (1.24–2.85 kt) and an average speed of 0.87 m/s (1.69 kt [standard error 0.03]). Tow durations ranged from 1.7 to 26.3 min depending on station depth and the consequent tow (sampling) depth prescribed by SEAMAP protocols. The volume of water filtered by each net was measured with a flow meter attached within the net mouth.

Larval fish abundances were standardized to account for sampling effort by using volume of filtered sea water and maximum depth at which the nets sampled and were expressed as 'number of larvae under 10 m^2 of sea surface' (Smith and Richardson, 1977; GSMFC[3]). This standardization was accomplished by dividing the number of larvae of each taxon caught in a sample by the volume of water filtered during the tow, and then multiplying the resultant by the maximum depth of the tow in meters and the factor 10. Larval abundances were also standardized by volume of water filtered alone, and are expressed as 'number of larvae per 1000 m^3 of filtered sea water'. This was accomplished simply by dividing the number of larvae of each taxon caught in a sample by the volume of water filtered during the tow, and then multiplying the resultant by the factor of 1000 (number of larvae per 1000 m^3).

Fish larvae from the 162 samples collected during the 81 tows of paired bongo nets were removed and identified to the lowest possible taxon (most often to family) at the Plankton Sorting and Identification Center of the Sea Fisheries Institute in Gdynia and Szczecin, Poland. Fish eggs were also removed and enumerated but were not measured or identified. Wet plankton volumes were measured by displacement ('displacement volume') to estimate net-caught zooplankton biomass (Smith and Richardson, 1977). Following established SEAMAP identification and measurement protocols, body length (BL) was measured as either notochord or standard length depending on caudal fin development of the specimen, to the nearest 0.1 mm. This is the length reported throughout this

article. The actual number of specimens measured depended on the taxonomic group and level of identification. To increase the number of observations available for analysis, up to 50 randomly chosen specimens in the 5 families targeted for analysis (Engraulidae, Clupeidae, Scombridae, Sciaenidae, and Lutjanidae) and unidentified and Percoidei larvae were measured at the NMFS laboratory in Pascagoula, Mississippi. These families were examined because they contain either ecologically or economically important species, many of which are federally managed. Additionally, larvae within these families represent the 2 body shapes of larval fish, clupeiform (slender) and perciform (robust) that have been shown to influence susceptibility to extrusion (Smith and Richardson, 1977). Unidentified larvae (with mixed body shapes) and those identifiable only to the suborder Percoidei (perciform) were measured because larvae in these 2 categories were among the smallest specimens in the samples and were, therefore, most likely to be extruded from the coarser mesh net. Although larval size can shrink as much as 22% to 33% because of tissue damage during capture and preservation (Miller and Sumida, 1974; Theilacker, 1980), this potential damage was not accounted for in our length measurements. This factor may explain why nominal lengths of the smallest larvae in the samples collected with the nets of 2 different mesh sizes were smaller than reported larval sizes at hatching. Larval shrinkage rates, however, were not expected to differ between samples from the nets with fine and coarse mesh sizes.

Species-level identification based on published larval descriptions for the Gulf of Mexico region requires the morphological presence of characters not generally present in larvae <3 mm BL (Richards, 2006). As such, many small specimens in early stages of development from the samples taken with the 2 nets were identifiable only to family. To use data over all sizes represented in the study collections while maintaining taxonomic groups of distinct body shapes, specimens of the 5 targeted families identified to genus or species were combined with specimens at the family level for subsequent analysis (i.e., analysis occurred at the family level).

Statistical analyses

Paired Wilcoxon signed-rank tests were used to determine significant differences in means between samples from nets with the 2 mesh sizes, 0.202 mm and 0.333 mm. Means were examined for the following values: volume filtered, total sample displacement volume, total fish eggs (raw counts), total fish larvae (raw counts), and standardized larval abundance (the number of larvae under 10 m^2 sea surface, and number of larvae per 1000 m^3). To reduce the chance of type-I errors, α values were adjusted by using a sequential Bonferroni adjustment (Rice, 1989). Analyses were not stratified by time of day because the samples from each plankton net attached to the bongo frame were taken at the same time (paired tows) so that any diel influence would be the same for both samples. Plots of volume filtered versus tow depth, by mesh size, were examined to determine whether clogging between the meshes of the 2 nets over the entire range of sampling depths had occurred in our study. Plots of tow duration (related to depth) by larval abundance for each mesh size were also examined to determine whether shorter tows at shallower, inshore stations collected abundances similar to those of longer tows at deeper, offshore stations. Paired *t*-tests were used to test for significant differences in mean larval abundances between the 2 mesh sizes for the groups of interest: unidentified larvae and larvae of Percoidei, Engraulidae, Clupeidae, Scombridae, Sciaenidae, and Lutjanidae. The Kolmogorov–Smirnov test (K–S test) was used to determine whether length-frequency distributions varied significantly for larvae under 10 mm BL for samples from the nets with 0.202-mm and 0.333-mm meshes.

Functional relationships were constructed by comparing the ratio of the numbers of larvae collected with the 0.202 mesh net to the numbers of larvae collected with the standard 0.333 mesh net to assess the numbers of larvae extruded through the coarser mesh. Models were constructed for unidentified larvae, percoidei larvae, and larvae from the 5 targeted families. Ratios of mean standardized abundance (number under 10 m^2 sea surface) from the nets with 0.202-mm mesh to the mean standardized abundance from the nets with 0.333-mm meshes were calculated for each taxon by 0.1-mm size classes. Only size classes where both nets had positive catches of the target taxa were used as data for fitting the models. All functions were fitted with maximum likelihood estimation and log-normally distributed error structures by using the 'bbmle' package in the software R, vers. 3.3.1 (Bolker, 2008; R Core Team, 2016). Power (Eq. 1) and exponential (Eq. 2) models were used to describe the relationship between the larval abundance ratios:

$$P_r = aL^b \text{ and} \quad (1)$$

$$P_r = de^{-Lf}, \quad (2)$$

where P_r = the predicted ratio of abundances in samples collected with nets of the 2 mesh sizes (0.202-mm:0.333-mm); and
L = the size class (in millimeters).
Parameters a, b, d, and f are constants estimated during the fitting process.

Akaike information criterion (AIC) was used to determine which model was the best fit for a given taxon (Burnham and Anderson, 2002). In this study, ΔAIC scores are presented as the relative difference between the AIC score of each model from that of the best fitting model within a taxonomic group.

Results

Fish eggs and larvae were collected in all 162 samples from 81 tows of paired bongo nets. Samples included

Table 2

Mean values, with standard errors (SEs), for sample displacement volume (mL), total number of larvae caught (raw counts), standardized larval abundances, volume filtered (m^3), and total number of eggs (raw counts) of samples collected with bongo nets that had different mesh sizes, 0.202 mm (n=81) and 0.333 mm (n=81), during Southeast Area Monitoring and Assessment Program surveys in the northern Gulf of Mexico during 2005–2007. The standardized larval abundances were calculated as the number of larvae per 1000 m^3 of filtered sea water and as the number of larvae caught in a sample by the volume of water filtered during the tow, multiplied by the maximum depth of the tow in meters and the factor 10 (abundance under 10 m^2 of sea surface). P-values and adjusted α levels are listed for paired Wilcoxon signed-rank tests. Asterisks denote significant differences between samples from the nets with the 2 mesh sizes.

	Mean (SE)			
	0.202 mm	0.333 mm	P-value	Adj. α
Displacement volume	32 (2.7)	19 (1.3)	<0.0001	0.0083*
Total number of larvae	465 (102.1)	299 (73.5)	<0.0001	0.01*
Abundance per 1000 m^3	4665 (1340.7)	2660 (797.3)	<0.0001	0.0125*
Abundance under 10 m^2	2455 (557.3)	1537 (342)	<0.0001	0.0167*
Volume filtered	171 (9.3)	170 (9.5)	0.1888	0.025
Total number of eggs	778 (591.6)	596 (390.4)	0.9498	–

Table 3

Summary of total number of larvae caught and standardized total and mean larval abundances in samples collected with nets of 2 different mesh sizes in the northern Gulf of Mexico during 2005–2007. Values are given for unidentified larvae and larvae of 6 taxa of interest: Percoidei, Engraulidae, Clupeidae, Scombridae, Sciaenidae, and Lutjanidae. Asterisks represent significant statistical differences in mean larval abundances (paired t-tests) and length-frequency distributions (K–S test) between paired samples from the nets with 2 different mesh sizes, 0.202 mm and 0.333 mm. Larval abundance was calculated as the number of larvae caught in a sample per the volume of water filtered during the tow multiplied by the maximum depth of the tow in meters and the factor 10 (number under 10 m^2 of sea surface).

		Total larvae		Total abundance		Mean abundance (SE)			
Taxa	Body shape	0.202 mm	0.333 mm	0.202 mm	0.333 mm	0.202 mm	0.333 mm	P-value	K–S test
Unidentified	Undetermined	3808	430	22,141	2335	273 (125)	29 (9)	0.02*	*
Percoidei	Perciform	1227	180	4614	699	58 (28)	9 (3)	0.03*	*
Engraulidae	Clupeiform	1261	1306	5246	5642	65 (22)	69 (26)	0.31	*
Clupeidae	Clupeiform	8283	7102	36,207	31,290	447 (373)	386 (330)	0.09	*
Scombridae	Perciform	432	256	2447	1404	30 (10)	17 (4)	0.06	*
Sciaenidae	Perciform	4674	1901	32,874	10,582	406 (297)	131 (66)	0.18	*
Lutjanidae	Perciform	307	292	1525	1448	19 (4)	19 (4)	0.33	*

a total of 111,283 eggs and 61,950 fish larvae representing 252 taxa. Samples collected from nets with the finer mesh (0.202 mm) contained more larvae than samples from nets with the larger mesh (0.333 mm)—37,696 versus 24,254 larvae—an increase of 55.4%. For all tows combined by mesh size, samples from nets with a 0.202-mm mesh had significantly higher mean displacement volumes (68.4% difference), number of larvae (55.5%), larvae per 1000 m^3 (75.4%), and larvae under 10 m^2 (59.7%) than samples from nets with a 0.333-mm mesh (Table 2). Mean number of eggs did not vary significantly between mesh sizes (0.6% difference). Volume of water filtered, by mesh size, ranged from 27 to 382 m^3 for the samples from nets with a 0.202-mm mesh and from 40 to 380 m^3 for the samples from nets with a 0.333-mm mesh. Mean volume filtered did not vary significantly between the mesh sizes (30.5% difference; Table 2). Additionally, regressions of volume filtered by tow depth revealed similar filtering efficiencies for both mesh sizes over the range of sampling depths, tow durations, and the broad spatial extent of our study (y=1.1003x+55.036, coefficient of determina-

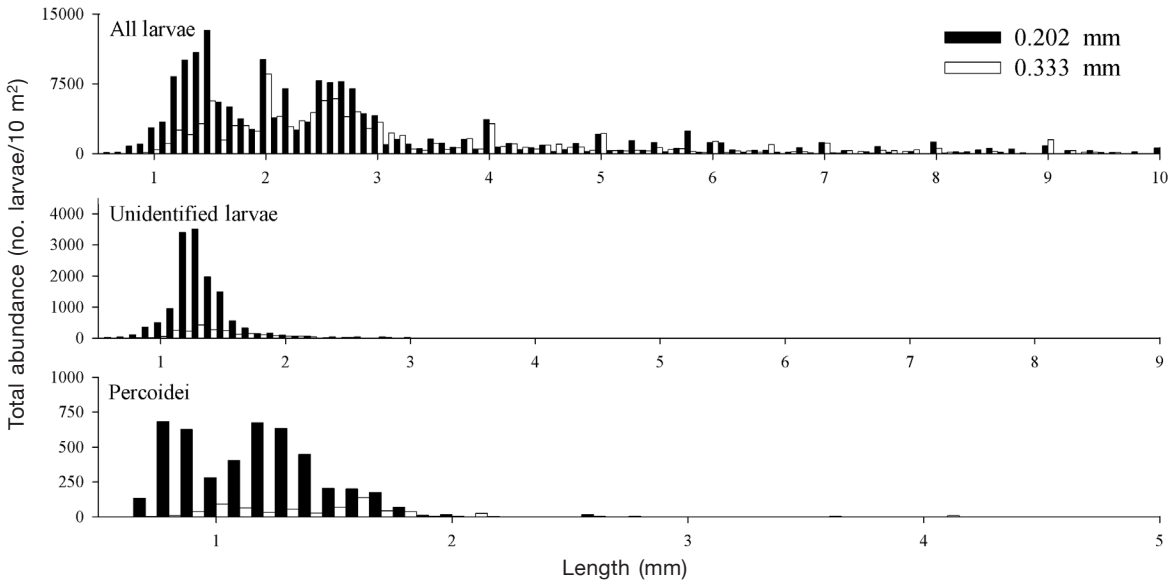

Figure 2

Length-frequency histograms of body length by total larval abundance in samples collected in the Gulf of Mexico during 2005–2007 with nets of 2 different mesh sizes (0.202 and 0.333 mm) for all larvae, unidentified larvae, and larvae of the suborder Percoidei. Larval abundance was measured as the total number of larvae caught in a sample per the volume of water filtered during the tow multiplied by the maximum depth of the tow in meters and the factor 10 (total number of larvae under 10 m^2 of sea surface). Only body lengths up to 10 mm are displayed in this figure. Note the different range in body length for each category of larvae.

tion (r^2)=0.841; y=1.0615x+57.643, r^2=0.8076, for the samples collected with nets with 0.202-mm and those collected with 0.333-mm mesh, respectively). Plots of tow duration by larval abundance for each mesh size revealed that higher levels of abundance occurred in shorter tows at shallower, inshore stations where larvae are more concentrated than in longer tows at deeper, offshore stations.

Larval abundance in samples collected with the different mesh sizes varied widely among the 6 taxa and the unidentified group chosen for analysis (Table 3). Overall, clupeid larvae were captured in the greatest numbers followed by sciaenids and the category for unidentified larvae. Lutjanid larvae were the least numerous taxon collected. Disparities between samples from nets with the 2 mesh sizes were greatest for sciaenid, unidentified, and percoid larvae, and least for lutjanid, engraulid, and clupeid larvae. These disparities were especially evident for unidentified and percoid larvae for which total larval abundance in samples from nets with 0.202-mm mesh was an order of magnitude greater than in samples from nets with 0.333-mm mesh (Table 3). Although mean abundance varied significantly only for 2 of the groups examined (unidentified larvae and Percoidei), K–S tests revealed significant differences in length-frequency distribution for larvae under 10 mm for all taxa examined (Table 3).

Larvae of taxa that spawn during late summer and early fall predominated in collections from the nets of different mesh size because of the preponderance of sampling in the months of September and October (Table 4). This temporal coverage resulted in greater availability of the smallest, least developed sciaenid larvae in samples taken with both mesh sizes. Scombrid larvae were equally prevalent in spring (May) and late summer (September) samples. The presence of both spring-spawning taxa (*Auxis* spp. and *Thunnus* spp.) and protracted-spawning taxa, including the little tunny (*Euthynnus alletteratus*), king mackerel, and Spanish mackerel (*S. maculatus*), increased the availability of the smallest size category of scombrid larvae.

Standardized abundances (number of larvae under 10 m^2) of all fish larvae taken in the nets with 2 different mesh sizes during this study, combined and grouped by 0.1-mm size classes, indicate that larvae ≤3 mm were consistently found in greater numbers in the nets with 0.202-mm mesh than in the nets with 0.333-mm mesh (Fig. 2). This was also the case for the categories of unidentified larvae and larvae identified to the suborder Percoidei, for which most specimens were <2 mm in length (Fig. 2). Among the smallest larvae identifiable to 1 of the 5 target families, all but clupeid larvae were abundant at sizes ≤2 mm, and larvae in that size category were found in greater numbers in the finer-mesh net than in the coarser-mesh net (Fig. 3). The smallest, most abundant size classes of clupeid larvae present in study samples ranged from 2 to 3 mm, and those larvae were also found in greater num-

Table 4

Summary of mean body length (mm), number of larvae measured, and total number of samples by month for taxa within the 5 target families as originally identified in samples collected with 0.202-mm and 0.333-mm-mesh nets in the northern Gulf of Mexico during 2005–2007. The total number of samples is the total number of samples in which a taxon was collected. The total number of samples collected in a month is provided in parenthesis next to name of the month. Months of peak spawning as inferred from larval abundance or occurrence were obtained primarily from Hernandez et al.[1] and the following additional studies: Ditty et al.[2]; Scott et al. (1993)[3]; Lyczkowski-Shultz and Hanisko (2007)[4]; Domeier et al.[5]; Lyczkowski-Shultz and Hanisko.[6]

		Mean length (mm)		Number measured		Total no. of samples	May (n=15)		Sept (n=21)		Oct (n=41)		Nov (n=4)		Peak spawning
Family	Taxon	0.202	0.333	0.202	0.333		0.202	0.333	0.202	0.333	0.202	0.333	0.202	0.333	
Engraulidae	Engraulidae	4.6	5.0	227	206	57	2	2	7	6	19	18	1	2	-
Clupeidae	*Brevoortia patronus*	3.6	3.9	125	98	30	1	1	-	-	14	13	1	-	[1] Nov/Jan
Clupeidae	Clupeidae	2.4	1.9	64	52	11	-	-	3	3	3	1	-	1	-
Clupeidae	*Etrumeus teres*	3.4	4.4	10	10	9	2	3	-	-	2	-	1	1	[1]Mar
Clupeidae	*Harengula jaguana*	-	5.6	-	12	7	-	-	-	7	-	-	-	-	[1] June/Aug
Clupeidae	*Opisthonema oglinum*	4.6	4.0	120	126	16	1	-	9	6	-	-	-	-	[1]May
Clupeidae	*Sardinella aurita*	4.6	6.1	21	22	6	-	-	3	3	-	-	-	-	[1] June/Aug/Oct
Scombridae	*Acanthocybium solandri*	-	5.1	-	1	1	-	-	-	1	-	-	-	-	?
Scombridae	*Auxis* spp.	3.1	3.6	47	51	33	8	11	3	6	2	2	-	1	-
Scombridae	*Euthynnus alletteratus*	3.6	3.6	69	86	19	1	-	9	9	-	-	-	-	[1] June/Aug
Scombridae	*Katsuwonus pelamis*	3.2	3.0	12	8	14	3	2	4	2	2	1	-	-	?
Scombridae	*Sarda sarda*	-	6.1	-	1	1	-	-	-	1	-	-	-	-	?
Scombridae	*Scomber scombrus*	-	2.2	-	1	1	-	-	-	-	-	1	-	-	?
Scombridae	*Scomberomorus* spp.	2.0	-	5	-	3	1	-	2	-	-	-	-	-	-
Scombridae	*Scomberomorus cavalla*	3.0	2.7	19	25	18	-	-	7	9	2	-	-	-	[2] Aug/Sept
Scombridae	*Scomberomorus maculatus*	1.9	3.4	7	8	7	-	-	3	4	-	-	-	-	[2] Aug/Sept
Scombridae	Scombridae	1.9	2.2	136	12	30	8	-	9	11	2	-	-	-	-
Scombridae	*Thunnus* spp.	2.6	3.0	59	46	33	10	9	6	8	-	-	-	-	-
Scombridae	*Thunnus thynnus*	4.5	5.9	3	3	5	3	2	-	-	-	-	-	-	[3] May
Sciaenidae	*Bairdiella chrysoura*	1.6	-	1	-	1	-	-	1	-	-	-	-	-	[2] Apr-Aug
Sciaenidae	*Cynoscion* spp.	2.2	3.0	2	15	6	-	-	-	2	1	2	-	1	-
Sciaenidae	*Cynoscion arenarius*	1.9	3.6	34	19	17	-	-	4	4	5	3	-	1	[1] Aug
Sciaenidae	*Cynoscion nothus*	3.7	5.3	39	26	26	-	-	4	4	10	6	1	1	[1] Sept/Oct
Sciaenidae	*Larimus fasciatus*	2.5	2.6	52	41	38	1	-	4	4	15	12	2	-	[1]Oct
Sciaenidae	*Leiostomus xanthurus*	1.7	1.8	172	147	44	-	-	-	2	19	15	4	4	[1]Nov
Sciaenidae	*Menticirrhus* spp.	2.8	2.4	12	19	20	-	-	3	6	4	6	1	-	-
Sciaenidae	*Micropogonias undulatus*	2.6	2.7	365	368	68	-	-	-	1	29	31	3	4	[1] Oct-Dec
Sciaenidae	*Pareques* spp.	-	2.2	-	1	1	-	1	-	-	-	-	-	-	-
Sciaenidae	*Pogonias cromis*	1.9	-	3	-	2	2	-	-	-	-	-	-	-	[2] Feb-Apr
Sciaenidae	Sciaenidae	1.7	2.3	36	17	25	-	-	4	-	11	7	-	3	-
Sciaenidae	*Sciaenops ocellatus*	1.7	2.5	9	14	7	-	-	2	2	2	1	-	-	[2] Sept/Oct
Sciaenidae	*Stellifer lanceolatus*	3.6	3.7	11	14	6	-	-	1	1	1	2	-	1	?
Lutjanidae	Lutjanidae	2.3	2.2	144	151	57	9	6	19	14	1	7	1	-	-
Lutjanidae	*Lutjanus* spp.	3.2	3.0	28	24	17	1	1	7	8	-	-	-	-	-
Lutjanidae	*Lutjanus campechanus*	3.7	4.3	10	20	18	1	2	6	6	-	3	-	-	[4] July/Sept
Lutjanidae	*Lutjanus griseus*	3.5	4.4	4	8	8	-	1	2	5	-	-	-	-	[5] July/Aug
Lutjanidae	*Pristipomoides aquilonaris*	2.6	2.9	50	37	31	4	7	6	6	3	5	-	-	?
Lutjanidae	*Rhomboplites aurorubens*	4.5	4.8	29	35	32	-	3	7	10	7	2	1	2	[6] Aug/Sept

Table 4 notes on following page

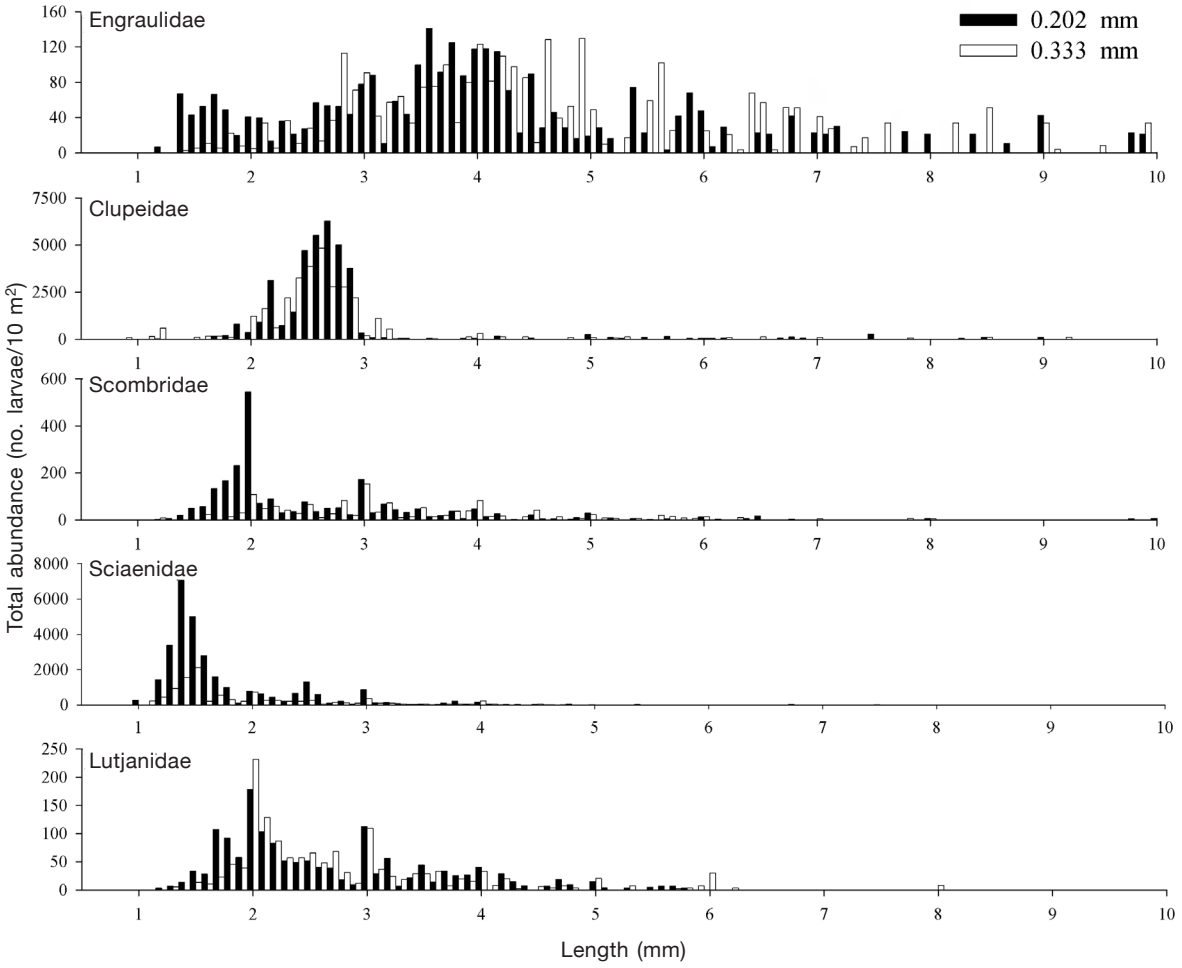

Figure 3

Length-frequency histograms of body length by total larval abundance in samples collected in the Gulf of Mexico during 2005–2007 with nets of 2 different mesh sizes (0.202 and 0.333 mm) for larvae of the 5 families targeted in this study: Engraulidae, Clupeidae, Scombridae, Sciaenidae, and Lutjanidae. Larval abundance was measured as the total number of larvae caught in a sample per the volume of water filtered during the tow multiplied by the maximum depth of the tow in meters and the factor 10 (total number of larvae under 10 m^2 of sea surface). Only larval lengths up to 10 mm are displayed in this figure.

Table 4 notes

[1] Hernandez, F. J., Jr., S. P. Powers, and W. M. Graham. 2010. Detailed examination of ichthyoplankton seasonality from a high-resolution time series in the northern Gulf of Mexico during 2004–2006. Trans. Am. Fish. Soc. 139:1511–1525. [Available from website.]

[2] Ditty, J. G., G. G. Zieske, and R. F. Shaw. 1988. Seasonality and depth distribution of larval fishes in the northern Gulf of Mexico above latitude 26°00′N. Fish. Bull. 86:811–823.

[3] Scott, G. P., S. C. Turner, B. Grimes, W. J. Richards, and E. B. Brothers. 1993. Indices of larval bluefin tuna, *Thunnus thynnus* , abundance in the Gulf of Mexico: modelling variability in growth, mortality, and gear selectivity. Bull. Mar. Sci. 53:912–929.

[4] Lyczkowski-Shultz, J., and D. S. Hanisko. 2007. A time series of observations on red snapper larvae from SEAMAP surveys 1982–2003: seasonal occurrence, distribution, abundance, and size. Am. Fish. Soc. Symp. 60:3–23.

[5] Domeier, M. L., C. Koenig, and F. Coleman. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other Western Atlantic snapper (Lutjanidae). *In* Biology, fisheries and culture of tropical groupers and snappers (F. Arreguín-Sánchez, J. L. Munro, M. C. Balgos, and D. Pauly, eds.), p. 189–201. ICLARM Conf. Proc. 48. [Available from website.]

[6] Lyczkowski-Shultz, J., and D. S. Hanisko. 2005. Review of the early life history of vermilion snapper, *Rhomboplites aurorubens*, with a summary of data from SEAMAP plankton surveys in the Gulf of Mexico: 1982–2002. Southeast Data, Assessment and Review SEDAR9-DW24, 42 p. [Available from website.]

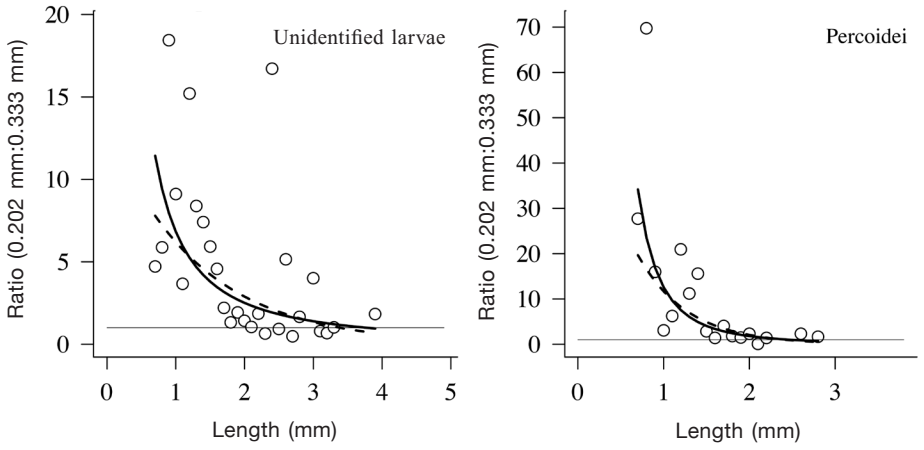

Figure 4

Ratios of larval abundance observed in nets with 0.202-mm mesh to larval abundance observed in nets with 0.333-mm mesh, by body length, for unidentified larvae and larvae of the suborder Percoidei. The solid and dashed lines represent modeled ratios of larval abundance that represent how many larvae were extruded from the coarser-mesh net (power and exponential functional relationships, respectively). The thin, horizontal line represents 1:1 ratios of total larval abundance or the point at which the finer- and coarser-mesh nets retained the same number of larvae at subsequent size classes.

bers in the net with 0.202-mm mesh than in the net with 0.333-mm mesh (Fig. 3).

The ratios of larval abundance collected with the finer net to larval abundance collected with the coarser net varied among the 6 taxa and unidentified group that were analyzed (Figs. 4 and 5). Although no pattern was seen regarding extrusion rates and body shape (perciform versus clupeiform), greater extrusion was suggested by the somewhat higher predicted abundance ratio of engraulid (clupeiform) larvae 1–2 mm in length compared with that of similar-size scombrid (perciform) and sciaenid (perciform) larvae. Extrusion for the categories of unidentified larvae and Percoidei was greater than for larvae identified to the family level. All abundance ratios for unidentified larvae, both observed and modeled, were greater than 1, indicating greater retention in the samples from the nets with a 0.202-mm mesh (Fig. 4). The greatest modeled abundance ratio for unidentified larvae was 11.4 for the 0.7-mm size class with the use of the power function. Modeled abundance ratios for the suborder Percoidei were above 1.0 for all sizes under 2.4 mm, and abundance ratios were as high as 34.0 and 17.0 for 0.7-mm larvae, with the power and exponential functions, respectively (Fig. 4). Modeled engraulid abundances were 4.0 and 1.9 times greater (power and exponential models, respectively) in samples from nets with 0.202-mm mesh than in samples from nets with 0.333-mm mesh for larvae at 1.2 mm (Fig. 5). Abundances of engraulid larvae in samples from nets with the different mesh sizes were equal for larvae at 4.7 mm for the power model and at 6.1 mm for the exponential model. Contrary to expectations, both the power and exponential models for Clupeidae indicated slight increases in abundance ratios with increasing size (Fig. 5). Abundance ratios were greatest at 10 mm, reaching 1.2 and 1.1 for the power and exponential models, respectively. Scombrid larvae at 1.2 mm were retained 3.1 (power model) to 2.2 (exponential model) times more in the samples from nets with a 0.202-mm mesh than in the samples from nets with a 0.333-mm mesh (Fig. 5). Larval abundances in both mesh sizes were higher at sizes between 4.1 and 4.5 mm. Sciaenid larvae appear to be extruded from 0.333-mm-mesh nets at sizes less than 5.5 mm (power model) and 5.1 mm (exponential model; Fig. 5). Sciaenid extrusion was greatest at the 1.0-mm size, and power and exponential models indicated that abundances were 3.1 and 2.5 greater in samples from nets with 0.202-mm mesh were than in samples from nets with 0.333-mm mesh, respectively (Fig. 5). Despite the high variability of abundance ratios for Lutjanidae (Fig. 5), both models projected greater abundances of larvae in the samples from nets with 0.202-mm mesh over all lengths. The power model for Lutjanidae reflected little overall change in abundance ratios by lengths, whereas the exponential model indicated slightly greater abundances in finer-mesh nets as larval lengths increased.

Coefficients derived from the models for both power and exponential functions are presented for use in future comparisons of sampling with bongo nets of differ-

Table 5

Parameters and the relative difference between the Akaike information criterion (ΔAIC) score from each model and that of the best fitting model within a group for unidentified larvae and larvae of 6 taxa: Percoidei, Engraulidae, Clupeidae, Scombridae, Sciaenidae, and Lutjanidae. The 2 models used were the power (a, b) and exponential (d, f) model.

	Parameters					
	Power		Exponential		ΔAIC	
Taxa	a	b	d	f	Power	Exponential
Unidentified	6.83	–1.44	13.29	–0.76	0	1
Percoidei	12.59	–2.80	66.26	–1.74	0	2.46
Engraulidae	4.79	–1.00	2.21	–0.13	0	8.04
Clupeidae	0.75	0.21	0.92	0.02	0	0.3
Scombridae	3.64	–0.90	2.96	–0.24	0	1.51
Sciaenidae	3.10	–0.66	3.15	–0.22	0	0.22
Lutjanidae	1.27	0.00	1.13	0.03	0.13	0

ent mesh sizes, 0.202 and 0.333 mm (Table 5). Among the 6 taxa and the unidentified group, extrusion was better described by using the power rather than the exponential model (Table 5). The difference between power and exponential model performance was greatest for Engraulidae, with the power model having the best fit. Differences in AIC scores obtained from the models, however, were relatively small for the unidentified group and all other taxa that were analyzed (ΔAIC<2.5), indicating that both functions are suitable for predicting extrusion rates for those taxa (Burnham and Anderson, 2002).

Discussion

Despite the wide range in observed larval abundance ratios among samples collected with the nets of different mesh sizes, functional relationships between predicted larval abundance and size indicated that small larvae were underrepresented in samples collected with a standard SEAMAP survey bongo net (0.333 mm). For smaller body lengths, predicted abundance ratios indicated that samples from the finer-mesh net contained up to 3–4 times the numbers of larval fish for 3 of 5 Gulf of Mexico fish families than samples from the coarser-mesh net. Observed abundance ratios indicated extrusion could be even higher, depending on the taxa. Underestimation of the smallest size category of sampled larvae was greatest for larvae that could not be identified to any taxonomic level or could be identified only to a suborder because the smallest larvae in the samples had not yet developed enough morphological characteristics that could be used for identifications to family level. Fish egg densities, however, did not differ significantly between the nets with 2 mesh types, suggesting that the standard SEAMAP survey net adequately samples fish eggs. This finding is not surprising because egg sizes of the analyzed taxa all exceeded the mesh size of the standard SEAMAP plankton net.

Differences in larval fish retention between 0.333-mm-mesh and 0.202-mm-mesh plankton nets were previously investigated in northern Gulf of Mexico waters by Comyns (1997) and Hernandez et al. (2011). Comyns (1997) found that red drum larvae in the smallest size group, 1.5–1.9 mm, were 5 to 8 times more abundant in the finer than in coarser mesh samples. Hernandez et al. (2011) found few to no significant differences among the taxa between the samples from nets with the 2 mesh sizes in either larval abundances or length frequencies. Mean size of larvae, however, was smaller in samples from the finer-mesh nets than in samples from the coarser-mesh nets for 4 groups: total fish larvae (all taxa combined, excluding unidentified larvae), Leptocephali and Syngnathidae (combined), Sciaenidae (the family that includes the red drum), and unidentified larvae. In the current study, mean standardized abundances varied significantly between samples from nets with the different mesh sizes for only 2 groups examined (unidentified larvae and Percoidei), whereas length-frequency distributions for all 6 taxa and the unidentified group that were examined were significantly different in samples taken with nets of the 2 mesh sizes.

Study design, sampling gear, and collection protocols used in these prior studies differed from each other and from the current study, as did results, making direct comparisons of the 3 studies problematic. Despite these differences, some useful inferences can be drawn regarding the influence of study design, sampling gear, and protocols on larval fish retention in comparisons of mesh sizes of nets. In the Comyns study, sampling was conducted only during the peak month of red drum spawning and consisted of collections taken in association with a subsurface current drogue, which

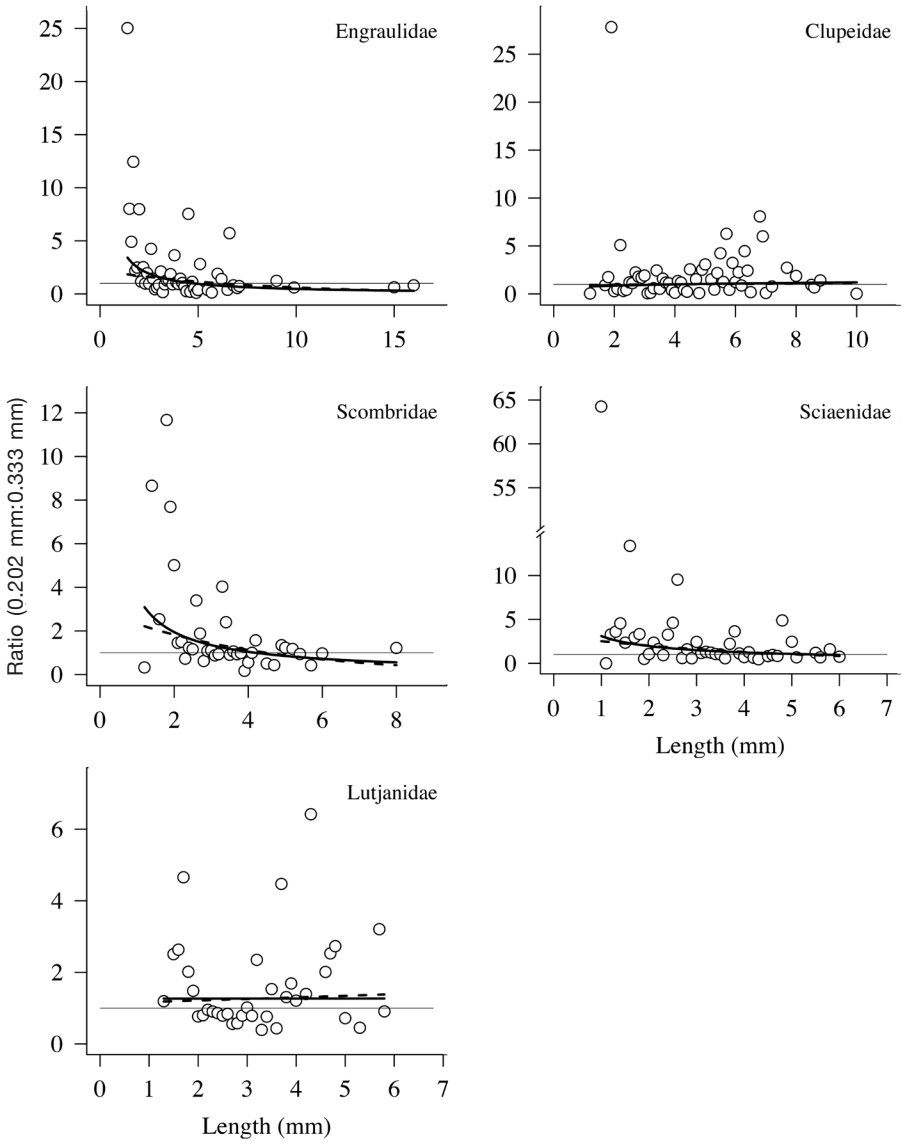

Figure 5

Ratios of larval abundance observed in nets with 0.202-mm mesh to larval abundance observed in nets with 0.333-mm mesh, by body length, for larvae of Engraulidae, Clupeidae, Scombridae, Sciaenidae, and Lutjanidae. The solid and dashed lines represent modeled ratios of larval abundance that represent how many larvae were extruded from the coarser-mesh net (power and exponential functional relationships, respectively). The thin, horizontal line represents 1:1 ratios of total larval abundance or the point at which the finer- and coarser-mesh nets retained the same number of larvae at subsequent size classes.

maximized sampling in the same patch of larvae over a period of hours (Lyczkowski-Shultz et al.[5]). However, in the Hernandez et al. (2011) and the current study, samples were collected without consideration of taxon-specific spawning seasons, and no attempt was made to remain in a defined water mass. The discrepancy in the findings for Sciaenidae between Comyns (1997) and Hernandez et al. (2011) was attributed by Hernandez et al. (2011) to gear differences—the larger mouth

[5] Lyczkowski-Shultz, J., J. P. Steen Jr., and B. H. Comyns. 1988. Early life history of red drum (*Sciaenops ocellatus*) in the northcentral Gulf of Mexico. Miss.-Ala. Sea Grant Consort., Tech. Rep. MASGP-88-013, 126 p. [Available from website.]

opening of the net and longer tow durations used by Comyns (1997) resulted in higher volumes of water filtered and subsequent greater numbers of larvae captured than in the Hernandez et al. (2011) study. Similarly, mean volume filtered in our study was less than that in the Comyns (1997) study, 170 m^3 and 256 m^3, respectively. Additionally, of the different gear used in the 3 studies, only the SEAMAP bongo frame allowed side-by-side towing and paired sample collection. These 'true' paired tows ensured that the nets sampled at the same location in the water column, at the same tow speed and ambient light level, and would, presumably, encounter the same assemblage of larvae. The arrangement of the nets used to gather plankton samples by Comyns (1997) and Hernandez et al. (2011) did not allow simultaneous sampling with different mesh sizes.

Although the opportunistic nature of this study allowed the sampling of various regions and species in the Gulf of Mexico, directed sampling in months and locations of peak spawning for species of interest would have improved the probabilities of capturing greater numbers of smaller larvae, and increased the number of taxa within the target families that would have been 'available' for evaluating mesh retention. The importance of sampling with nets of different size during times of peak spawning when earliest stage larvae are most abundant was exemplified by the observed size distributions among sciaenid and scombrid larvae. Sampling with different mesh sizes coincided with reported months of peak spawning for 4 species of Sciaenidae and 5 species of Scombridae. A clear relationship between abundance ratios of the smallest sampled larvae and the mesh size of sampling nets was evident for those 2 families. This was the case even though scombrid larvae were the second least abundant of the target families. Although retention of small clupeid and lutjanid larvae was observed to differ between the paired samples collected with the nets with both mesh sizes and was supported by the significant difference in the length-frequency distributions of the 2 taxa, the modeled results for those taxa failed to indicate a substantial difference in abundance-at-size between the samples collected with the finer- and coarser-mesh nets. The lack of apparent difference between the nets with the 2 mesh sizes in size-related retention for those 2 families most likely resulted from the smallest larvae being unavailable to our plankton samplers because of a mismatch between sampling with these nets and the times, locations, and seasons of clupeid and lutjanid spawning (Fitzhugh et al.,[6]; Ditty et al., 2005; Hanisko et al., 2007).

Species-specific correction factors for larval abundance by body length in coarser mesh nets, generated from comparison studies of net meshes have been used to adjust larval abundances in order to mitigate bias caused by extrusion of the smallest size category of larvae in sampled assemblages (Lo, 1983; Houde and Lovdal, 1984; Somerton and Kobayashi, 1989). However, our study did not result in species-level comparisons of retention between the nets with different mesh sizes because of the problematic nature of morphology-based identification of fish larvae in waters of the U.S. Southeast (Richards, 2006; Fahay, 2007). Large abundance ratios for unidentified and percoid larvae in our samples highlight the effect of extrusion at the smallest sizes. Those 2 categories can represent a large portion of ichthyoplankton survey catches. In our study alone, the unidentified and percoid categories accounted for 9.1% of all specimens. Improved identification of smaller larvae with genetic procedures (Marancik et al., 2010) would provide more accurate estimates of total abundances of both eggs and larvae and aid in identifying true larval retention patterns by species. Although not at species-level, these models represent the first empirically derived approach to evaluating the degree of extrusion in SEAMAP ichthyoplankton samples.

Currently, SEAMAP larval indices are used as indicators of spawning stock biomass, not as direct estimates of biomass. Furthermore, these indices are calculated from the abundance of larger larvae that can be reliably identified to species by using established morphological features and that are of a size indicating full recruitment to the sampling gear. Including the size fraction of larvae that are underrepresented in SEAMAP samples collected in bongo nets with a 0.333-mm mesh could eventually lead to more realistic estimates of larval mortality and therefore more precise larval indices than those currently in use. Such an improvement in the reliability of a SEAMAP larval index was recently demonstrated when data on the abundance of small, genetically identified, early stage red snapper larvae were, for the first time, incorporated into the SEAMAP index (Pollack[7]).

Corrections for larval extrusion will also aid in better estimation of larval fish injuries and mortalities in future Gulf of Mexico damage assessments. Previously larval fish mortalities and subsequent production have been estimated in preparation of offshore liquefied natural gas developments (Gallaway et al., 2007) and as a result of the 2010 Deep Water Horizon oil spill (Muhling et al., 2012). Such estimates have been based on SEAMAP data for constructing baseline larval conditions for injury calculations (French McCay et al.[8]), however net efficiency issues with larval retention in the standard SEAMAP nets were simply noted.

[6] Fitzhugh, G. R., M. S. Duncan, L. A. Collins, W. T. Walling, and D. W. Oliver. 2004. Characterization of red snapper (*Lutjanus campechanus*) reproduction: for the 2004 Gulf of Mexico SEDAR. Southeast Data, Assessment and Review SEDAR7-DW-35, 27 p. [Available from website.]

[7] Pollack, A. G. 2015. Personal commun. Riverside Technology, Inc. Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 3209 Frederic St., Pascagoula, MS 39568.

[8] French McCay, D., M. C. McManus, R. Balouskus, J. J. Rowe, M. Schroeder, A. Morandi, E. Bohaboy, and E. Graham. 2015. Technical Reports for Deepwater Horizon Water Column Injury Assessment—WC_TR.10: Evaluation of baseline densities for calculating direct injuries of aquatic biota dur-

The lack of taxa-specific information on extrusion has inhibited correcting larval abundances for previous damage claims (French McCay et al.[6]). Other injury assessments have assumed a single multiplier for all fish larvae abundances to correct for extrusion (Nielsen et al.[9])—an approach that our results indicate is an inadequate simplification.

Despite its shortcomings, our comparison study with nets of different mesh size provides the first estimates of size bias in SEAMAP ichthyoplankton sampling. Where previously the effect of extrusion on the smallest larvae in sampled assemblages was either ignored or approximated, the functional models presented here can be used to provide more accurate estimates of true larval fish abundances, and assessments of biological injuries due to industrial disasters. Extrusion-corrected larval abundance estimates could be used to improve the reliability of SEAMAP indices only after species-specific identification of the earliest and smallest larvae of species are attained. These species-level identifications could be achieved with more complete, traditional morphological descriptions of larval development and/or by incorporation of genetic identification methods in SEAMAP protocols that explicitly target problematic species.

Acknowledgments

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Literature cited

Bolker, B. M.
2008. Ecological models and data in R, 396 p. Princeton Univ. Press, Princeton, NJ.

Burnham, K. P., and D. R. Anderson.
2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed., 488 p. Springer-Verlag, New York.

ing the Deepwater Horizon oil spill, 122 p. RPS ASA, South Kingstown, RI.

[9] Nielsen, R. D., T. C. Ginn, L. M. Ziccardi, and P. D. Boehm. 2005. An evaluation of the approaches used to predict potential impacts of open loop LNG vaporization systems on fishery resources of the Gulf of Mexico, 62 p. Report prepared for The Center for Liquefied Natural Gas Seawater Usage Technology Committee. Exponent, Menlo Park, CA. [Available from website.]

Colton, J. B., Jr., J. R. Green, R. R. Byron, and J. L. Frisella.
1980. Bongo net retention rates as effected by towing speed and mesh size. Can. J. Fish. Aquat. Sci. 37:606–623. Article

Comyns, B. H.
1997. Growth and mortality of fish larvae in the north-central Gulf of Mexico and implications to recruitment. Ph.D. diss., 150 p. Louisiana State Univ., Baton Rouge, LA.

Ditty, J. G., T. W. Farooqi, and R. F. Shaw.
2005. Clupeidae: sardines and herrings. *In* Early stages of Atlantic fishes: an identification guide for the western central Atlantic, vol. 1 (W. J. Richards, ed.), p. 73–99. Taylor & Francis Group, Boca Raton, FL.

Fahay, M. P.
2007. Early stages of fishes in the western north Atlantic Ocean (Davis Strait, southern Greenland and Flemish Cap to Cape Hatteras), vol. 1, 931 p. Northwest Atlantic Fish. Org., Dartmouth, Canada.

Gallaway, B. J., W. J. Gazey, J. G. Cole, and R. G. Fechhelm.
2007. Estimation of potential impacts from offshore liquefied natural gas terminals on red snapper and red drum fisheries in the Gulf of Mexico: an alternative approach. Trans. Am. Fish. Soc. 137:655–677. Article

Gledhill, C. T., and J. Lyczkowski-Shultz.
2000. Indices of larval kind mackerel (*Scomberomorus cavalla*) abundance in the Gulf of Mexico for use in population assessments. Fish. Bull. 98:684–691.

Hanisko, D. S., J. Lyczkowski-Shultz, and G. W. Ingram.
2007. Indices of larval red snapper occurrence and abundance for use in stock assessment. Am. Fish. Soc. Symp. 60:285–300.

Hernandez, F. J., Jr., L. Carassou, S. Muffleman, S. P. Powers, and W. M. Graham.
2011. Comparison of two plankton net mesh sizes for ichthyoplankton collection in the northern Gulf of Mexico. Fish. Res. 108:327–335. Article

Hjort, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. p.-v. Reun. 20:1–228.

Houde, E. D., and J. A. Lovdal.
1984. Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Est. Coast. Shelf Sci. 18:403–419. Article

Johnson, D. L., and W. W. Morse.
1994. Net extrusion of larval fish: correction factors for 0.333 mm versus 0.505 mm mesh bongo nets. NAFO Sci. Coun. Stud. 20:85–92.

Johnson, D. R., H. M. Perry, J. Lyczkowski-Shultz, and D. Hanisko.
2009. Red snapper larval transport in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 138:458–470. Article

Llopiz, J. K., R. K. Cowen, M. J. Hauff, R. Ji, P. L. Munday, B. A. Muhling, M. A. Peck, D. E. Richardson, S. Sogard, and S. Sponaugle.
2014. Early life history and fisheries oceanography: new questions in a changing world. Oceanography 27(4):26–41. Article

Lo, N. C. H.
1983. Re-estimation of three parameters associated with anchovy egg and larval abundance: temperature dependent incubation time, yolk-sac growth rate and egg and larval retention in mesh nets. NOAA Tech. Memo. NMFS-TM-SWFC-31, 33 p.

Lyczkowski-Shultz, J., and D. S. Hanisko.
2007. A time series of observations on red snapper larvae from SEAMAP surveys 1982–2003: seasonal occurrence, distribution, abundance, and size. Am. Fish. Soc. Symp. 60:3–23.

Lyczkowski-Shultz, J., D. S. Hanisko, K. J. Sulak, M. Konieczna, and P. J. Bond.
2013. Characterization of ichthyoplankton in the northeastern Gulf of Mexico from SEAMAP plankton surveys, 1982–1999. Gulf Caribb. Res. 25:43–98. Article

Marancik, K. E., D. E. Richardson, J. Lyczkowski-Shultz, M. Konieczna, and R. K. Cowen.
2010. Evaluation of morphological characters to identify grouper (Serrandiae: Epinephelini) larvae in the Gulf of Mexico using genetically identified specimens. Bull. Mar. Sci. 86:571–624.

Marancik, K. E., D. E. Richardson, J. Lyczkowski-Shultz, R. K. Cowen, and M. Konieczna.
2012. Spatial and temporal distribution of grouper larvae (Serranidae: Epinephelinae: Epinephelini) in the Gulf of Mexico and Straits of Florida. Fish. Bull. 110:1–20.

McClatchie, S., J. Duffy-Anderson, J. C. Field, R. Goericke, D. Griffith, D. S. Hanisko, J. A. Hare, J. Lyczkowski-Shultz, W. T. Peterson, W. Watson, et al.
2014. Long time series in US fisheries oceanography. Oceanography 27(4):48–67. Article

Miller, J. M., and B. Y. Sumida.
1974. Development of eggs and larvae of *Caranx mate* (Carangidae). Fish. Bull. 72:497–514.

Morse, W. W.
1989. Catchability, growth, and mortality of larval fishes. Fish Bull. 87:417–446.

Muhling, B. A., M. A. Roffer, J. T. Lamkin, G. W. Ingram, Jr., M. A. Upton, G. Gawlikowski, F. Muller-Karger, S. Habtes, and W. J. Richards.
2012. Overlap between Atlantic bluefin tuna spawning grounds and observed Deepwater Horizon surface oil in the northern Gulf of Mexico. Mar. Pollut. Bull. 64:679–687. Article

R Core Team.
2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from website, accessed July 2016.]

Rice, W. R.
1989. Analyzing tables of statistical tests. Evolution 43:223–225. Article

Richards, W. J. (ed.).
2006. Early stages of Atlantic fishes: an identification guide for the western central Atlantic, 2 vols. (set), 2591 p. Taylor & Francis Group, Boca Raton, FL.

Richardson, D. E., J. A. Hare, W. J. Overholtz, and D. L. Johnson.
2010. Development of long-term larval indices for Atlantic herring (*Clupea harengus*) on the northeast US continental shelf. ICES J. Mar. Sci. 67:617–627. Article

Scott, G. P., S. C. Turner, B. Grimes, W. J. Richards, and E. B. Brothers.
1993. Indices of larval bluefin tuna, *Thunnus thynnus*, abundance in the Gulf of Mexico; modelling variability in growth, mortality, and gear selectivity. Bull. Mar. Sci. 53:912–929.

Smith, P. E., and S. L. Richardson.
1977. Standard techniques for pelagic fish egg and larval surveys. FAO Fish. Tech. Pap. 175, 100 p. FAO, Rome.

Somerton, D. A., and D. R. Kobayashi.
1989. A method for correcting catches of fish larvae for the size selection of plankton nets. Fish. Bull. 87:447–455.

Theilacker, G. H.
1980. Changes in body measurements of larval northern anchovy, *Engraulis mordax*, and other fishes due to handling and preservation. Fish. Bull. 78:685–692.

Tranter, D. J. (ed.).
1968. Zooplankton sampling. Monogr. Oceanogr. Method. 2, 174 p. UNESCO, Paris.