Spawning cycles and habitats for ballyhoo (*Hemiramphus brasiliensis*) and balao (*H. balao*) in south Florida

Richard S. McBride
Justin R. Styer
Rob Hudson

Florida Marine Research Institute
Florida Fish and Wildlife Conservation Commission
100 8th Avenue SE
St. Petersburg, Florida 33701-5095
E-mail address (for R. S. McBride): richard.mcbride@fwc.state.fl.us

Abstract—Two halfbeak species, ballyhoo (*Hemiramphus brasiliensis*) and balao (*H. balao*), are harvested as bait in south Florida waters, and recent changes in fishing effort and regulations prompted this investigation of the overlap of halfbeak fishing grounds and spawning grounds. Halfbeaks were sampled aboard commercial fishing vessels, and during fishery-independent trips, to determine spatial and temporal spawning patterns of both species. Cyclic patterns of gonadosomatic indices (GSIs) indicated that both species spawned during spring and summer months. Histological analysis demonstrated that specific stages of oocyte development can be predicted from GSI values; for example, female ballyhoo with GSIs >6.0 had hydrated oocytes that were 2.0–3.5 mm diameter. Diel changes in oocyte diameters and histological criteria demonstrated that final oocyte maturation occurred over a 30- to 36-hour period and that ballyhoo spawned at dusk. Hydration of oocytes began in the morning, and ovulation occurred at sunset of that same day; therefore females with hydrated oocytes were ready to spawn within hours. We compared maps of all locations where fish were collected to maps of locations where spawning females (i.e. females with GSIs >6.0) were collected to determine the degree of overlap of halfbeak fishing and spawning grounds. We also used geographic information system (GIS) data to describe the depth and bottom type of halfbeak spawning grounds. Ballyhoo spawned all along the coral reef tract of the Atlantic Ocean, inshore of the reef tract, and in association with bank habitats within Florida Bay. In the Atlantic Ocean, balao spawned along the reef tract and in deeper, more offshore waters than did ballyhoo; balao were not found inshore of the coral reef tract or in Florida Bay. Both halfbeak species, considered together, spawned throughout the fishing grounds of south Florida.

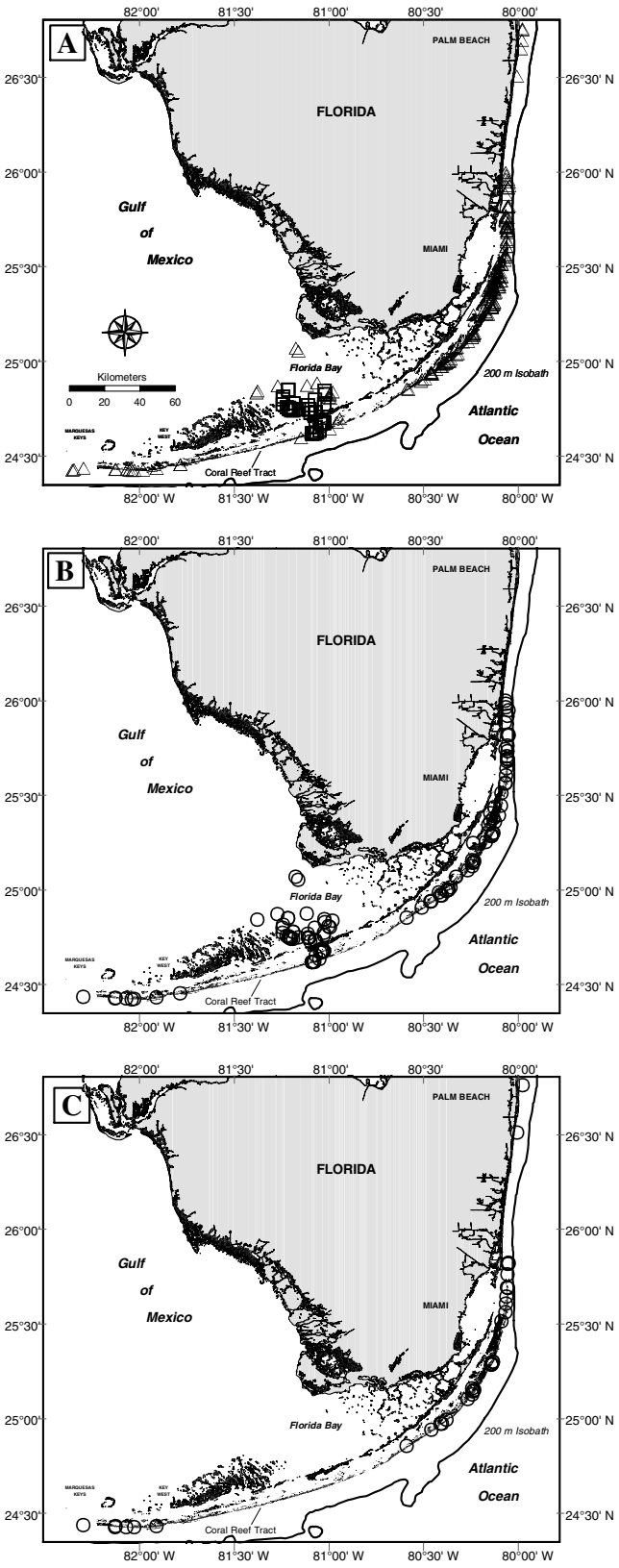
Manuscript approved for publication 30 January 2003 by Scientific Editor.
Manuscript received 4 April 2003 at NMFS Scientific Publications Office.
Fish. Bull 101:583–589 (2003).

Combined landings of two halfbeaks species, ballyhoo (*Hemiramphus brasiliensis*) and balao (*H. balao*), constitute a small but valuable bait fishery in south Florida (Berkeley et al., 1975; McBride et al., 1996). Both species occupy coastal pelagic habitat in association with coral reefs (Starck, 1968; Nybakken, 1997). During the 1990s two changes in the halfbeak fishery occurred that caused concerns regarding the exploitation levels in this fishery (McBride, 2001). First, geographic shifts occurred when halfbeak fishing expanded from the Atlantic Ocean into the nearshore waters north of the Florida Keys, an area known as Florida Bay. Second, changes in statewide net fishing regulations[1] created concerns that the net fishermen displaced from other fisheries might preferentially enter the halfbeak fishery, thereby increasing halfbeak fishing effort. These two changes could have specific consequences on halfbeak reproductive output. For example, because some fishermen viewed Florida Bay as a spawning or nursery ground for halfbeaks, it was of interest to learn exactly how concentrated spawning might be in Florida Bay and whether spawning occurred outside Florida Bay. In addition, because halfbeak landings are dominated by a single species, ballyhoo (Berkeley et al., 1975; McBride et al., 1996), it could be argued that these changes in the fishery could disproportionally affect spawning by the less abundant, and potentially more vulnerable target species, balao.

Both ballyhoo and balao are distributed widely in the western and eastern Atlantic Ocean (Collette, 1965), but no study has defined their spawning grounds. Berkeley and Houde (1978) described both species to be small (<32 cm fork length) summer-spawners that rarely live past two years, but in terms of spatial coverage, they collected fish principally from the Miami, Florida, area. We reviewed reports on regional ichthyoplankton collections (e.g. Powell et al., 1989; Limouzy-Paris et al., 1994) and found that the numbers of halfbeak eggs and larvae were too few for characterizing the spawning grounds. Moreover, Berkeley and Houde (1978) suggested that standard ichthyoplankton survey data would underestimate the abundance of halfbeak eggs or larvae for three reasons. First, halfbeak eggs appear to attach to vegetation; therefore oblique tows may not target the appropriate habitats (i.e. benthic or floating vegetation) and halfbeak eggs would be completely lost if pleuston was discarded from ichthyoplankton samples. Second, halfbeak eggs hatch 8–9 days after fertilization and may disperse far away from spawning locations. Third, halfbeak larvae hatch at 5–7 mm and have pigmented eyes; therefore they appear capable of avoiding plankton nets. Various plankton sampling strate-

[1] This referendum (s. 16, Art. X of the Florida Constitution, enacted July 1, 1995) prohibits entangling nets in waters inshore of 3 miles on the Atlantic coast and 9 miles on the Gulf coast of Florida (including Florida Bay). It also prohibits non-entangling nets larger than 500 ft^2 (such as those nets used by commercial halfbeak fishermen), in waters less than 1 mile of Florida's Atlantic coast and 3 miles of the Gulf coast.

gies could be developed to overcome these problems, but we chose an alternative to plankton sampling as a way to define halfbeak spawning grounds.



In this study, we used collections of adult ballyhoo and balao to define each species' spawning grounds in south Florida. Analyses of gonad histological preparations identified a discrete range of gonadosomatic indices (GSI) for females that were ready to spawn within hours, and the locations of these fishes were plotted by using geographic information system (GIS) software (ArcView, version 3.3., Environmental Systems Research Institute, Inc., Redlands, CA). This synthesis of GIS and GSI data was used to map the spawning grounds of ballyhoo and balao.

Materials and methods

Sampling occurred throughout the south Florida commercial halfbeak fishing grounds, from Palm Beach to the Marquesas Keys (Fig. 1A). The area immediately surrounding Vaca Key was well sampled, but other sections of the middle Florida Keys were not because commercial fishermen used only six fishing ports and their day trips were of limited range. Few samples were obtained from the Palm Beach area because net fishing is no longer allowed in much of this area (McBride, 2001). Halfbeak fishing trips by commercial fishermen were monitored from November 1995 to April 1999 by an onboard biologist during as many as four trips per month. A subsample of fish from the first successful net (a lampara net) set, and occasionally from later sets within a day, was obtained by filling a 5-gallon bucket from the catch as it was transferred from the net to holding boxes. This bucket held 100 to 200 halfbeaks, and these fishes were kept on ice and brought back to the laboratory for processing.

Fishery-independent collections were made by using cast nets and small hooks (sabiki rigs) in the middle Florida Keys. This sampling was specifically designed to include inshore areas where lampara net fishermen could not fish because of regulations associated with Florida's net limitation referendum.[1] The target number of these fishery-independent trips from July 1997 to October 1998 was four per month, and the target sample size for each trip was twelve fish. Additional fishery-independent sampling occurred in the springs of 1997, 1998, and 1999.

In the laboratory, whole body weight was recorded to the nearest 0.1 gram, and the gonads were removed and weighed to the nearest 0.01 g. Sex was identified with the aid of a dissecting binocular microscope (25–50×) when nec-

Figure 1

(**A**) Sampling area for halfbeaks (*Hemiramphus* spp.) during 1995–99 in the Atlantic Ocean and in Florida Bay. Each symbol represents an individual sample location where halfbeaks were caught. Fishery-dependent samples (triangles) were taken from commercial lampara net vessels. Fishery-independent samples (squares) were collected in the middle Florida Keys, near Vaca Key (not labeled because of the density of square symbols). Locations of ripe female (**B**) ballyhoo (*Hemiramphus brasiliensis*) and (**C**) balao (*H. balao*) are plotted separately. Ripe females have hydrated eggs, and this condition was determined in B and C by a gonadosomatic index >6.0 (see text for supporting evidence).

essary. Weights of fish collected from July 1997 to October 1998 were measured for up to 30 females per species per trip. Fish body and gonad weights were only occasionally recorded for other trips during 1995–99, but these data were included in the mapping of ripe females (i.e. females with hydrated oocytes in ovigerous lamellae) to increase overall sample size. In total, weight data were collected for 2908 halfbeak females from 79 commercial fishing net sets (63 different fishing days) and 59 fishery-independent sampling events (50 different sampling days). Commercial catches contributed 1649 ballyhoo and 757 balao females, and fishery-independent collections added another 497 ballyhoo and 5 balao females. The gonadosomatic index (GSI) was calculated as

$$GSI=(GW/(BW–GW)) \times 100,$$

where GW = gonad weight; and
BW = body weight.

The processes of final oocyte maturation (FOM) were examined by comparing GSIs with changes in whole oocyte size and histological criteria. Oocyte diameters were measured for 39 ballyhoo collected in April 1998 and March–April 1999. Fixed ovary tissue was washed, teased apart, and placed in a solution of 33% glycerin to 67% water. Measurements of at least 300 oocytes per fish were made to the nearest micron with the aid of a video system and image-analysis software (Optimas, vers. 100, Media Cybernetics, Inc., Silver Spring, MD). A minimum-size cut-off of 0.15 mm was used to exclude debris within the petri dish. Initially, oocyte diameters from six ballyhoo were measured from four separate sections of ovaries (left, right, anterior, posterior), but the modal oocyte diameter within each individual was the same for all four sections; therefore tissue from other fish was extracted without regard to location within the ovary. Berkeley and Houde (1978) performed a similar test and came to a similar conclusion. Ovaries from fish (n=930 females) collected during March and May 1997, July 1997–October 1998, and March–April 1999 were prepared for histological examination. Histological methods are presented in McBride and Thurman (2003). Here, the most advanced oocyte stage was recorded (in increasing order of oocyte maturity) as either perinucleolar, cortical alveolar, vitellogenic, or as either of two stages for oocytes in final maturation: nucleus migration and hydration (West, 1990). McBride and Thurman (2003) have reported the size at 50% maturity to be ≥160 mm FL for female balao and ≥198 mm FL for female ballyhoo (approximately 31.5 g and 60.9 g, respectively, using length-weight relationships from Berkeley and Houde [1978; their Fig. 7]). Mean GSIs and 95% confidence limits were determined for fish with regard to their most advanced stage of oocyte development, and a minimum cut-off value was established for GSI values indicating ripe females.

The locations of ripe females were plotted to indicate spawning grounds. Water depth and bottom type of these spawning locations were determined by using the Marine Resources Geographic Information System at the Florida Marine Research Institute (www.floridamarine.org). Point locations were recorded by using a global positioning system hand-held unit. The latitude and longitude of fishery-dependent samples were taken onboard the fishing vessel once the lampara net enclosed the fish. Location data for fishery-independent samples were taken from an anchored position. Depth information was divided into the following categories: area exposed at low tide, 0–1 m, 1–2 m, 2–4 m, 4–6 m, 6–10 m, and 10–20 m; only one of 159 locations was without depth information. Substrate information was divided into one of the following categories: platform margin reefs, patch reefs, other hard bottom, seagrass beds, and bare substrate; 32 of 159 locations did not have substrate information.

Results

Spawning cycles

Ballyhoo and balao had prolonged spawning seasons that peaked in late spring and early summer (Fig. 2). Monthly average GSIs of mature females increased from a low of <0.4 for both species to a high of 6.4 for balao and 6.9 for ballyhoo. The average GSI of individual females with only primary growth oocytes (i.e. their most advanced oocyte stages were perinucleolar or cortical alveolar) fell within a narrow interval of 0.1–0.3 (maximum=0.95, Fig. 3). These females were either small fishes that were immature or they were larger fishes that were regressed (i.e. mature but inactive). Vitellogenesis more than doubled the average GSI values for both species, but all females whose most advanced oocyte stage was vitellogenic had GSIs less than 1.37. Dramatic increases in GSI values also occurred during FOM, and significant differences were evident in the sequential FOM steps of nucleus migration and nucleus breakdown. During nucleus migration, but before hydration, ballyhoo GSIs averaged 3.4 (3.3–3.6; 95% CL) and balao GSIs averaged 5.2 (4.6–5.9). Females with hydrated oocytes had GSIs averaging 7.4 (7.0–7.9; 95% CL) for ballyhoo and 8.7 (6.6–10.8) for balao. Individual female GSIs reached an observed maximum of 13.3 for ballyhoo and 14.2 for balao. By applying these GSI criteria, which indicate that females with a GSI greater than about three had oocytes in FOM, it is evident that the average mature halfbeak female is actively spawning from at least March to August.

Final oocyte maturation also followed a diel cycle. For ballyhoo, FOM began about 30–36 hours before ovulation, hydration of oocytes began about 8–12 hours before ovulation, and ovulation occurred at sunset. Ballyhoo oocytes developed in a group-synchronous pattern, and during FOM, a batch of oocytes increased rapidly in diameter (Fig. 4). Mature female ballyhoo had a bimodal or trimodal distribution of oocyte diameters when spawning. The smallest mode (<1.0 mm oocyte diameter) represented a reservoir of primary growth oocytes and vitellogenic oocytes. Larger modes, between 1 and 3 mm, represented oocytes in FOM. The presence of two larger ooctye modes (~1.0–2.0 and >2.0 mm) in all females sampled during the afternoon period indicated that female ballyhoo typically spawn every day dur-

ing March–April. In total, the trimodal oocyte frequency represents a reservoir of oocytes prior to FOM, one batch of oocytes beginning FOM, and one batch completing FOM. Hydrated oocytes were not observed in balao prior to 1100 h. However, in several ballyhoo collected around dawn (i.e. at approximately 0600–0700 EST), the nucleus in oocytes of the advanced batch was still visible along the chorion but the cytoplasm was lightening in color. This suggested that initiation of hydration at daybreak briefly preceded nucleus breakdown. During the following 12-hour period, oocytes in this maturing clutch advanced from late nucleus migration to nucleus breakdown, and increased in diameter from 1.5–2.0 mm in the morning to 2.0–3.0 mm in the afternoon. Modal egg size for each of three running-ripe ballyhoo (i.e. females with hydrated, ovulated eggs in the ovarian lumen) was 2.35, 2.60, and 2.80 mm diameter. The complete size range of these ovulated eggs was 2.2–3.4 mm diameter. These females were collected at or just before sunset (time: 1810–1855). Most efforts to sample across the full 24-hour cycle failed, apparently because halfbeak do not bite hooks after sundown. A sample of 12 ballyhoo was collected one night, however, by randomly throwing a cast net on dense schools of fish. These fish, collected between 2200 and 2359 hours during March 1997, all appeared to have recently spawned. Histological preparations demonstrated that they had fresh postovulatory follicles, and they contained a distinct clutch of oocytes in early nucleus migration. Whole oocytes from these fish collected at night were not archived in formalin; therefore they were not measured for comparisons to whole oocytes collected at other times during the diel cycle. These patterns of diel reproductive periodicity also appeared to apply to balao, but the available data were not conclusive.

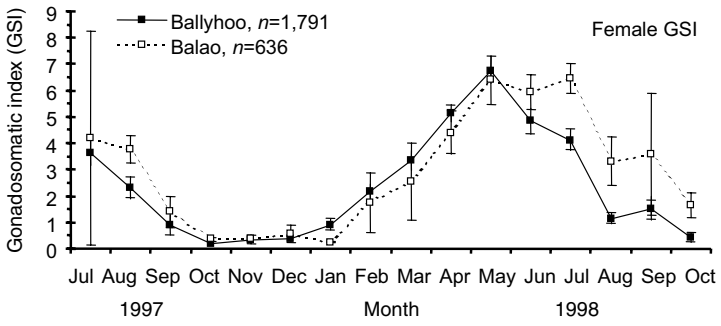


Figure 2

Mean (±95% confidence limits) gonadosomatic indices by month for ballyhoo (*Hemiramphus brasiliensis*) and balao (*H. balao*) females. Values are calculated for fish larger than size at 50% maturity, reported by McBride and Thurman (2003) as ≥198 mm fork length (FL) for ballyhoo and ≥160 mm FL for balao. *n* = number of females.

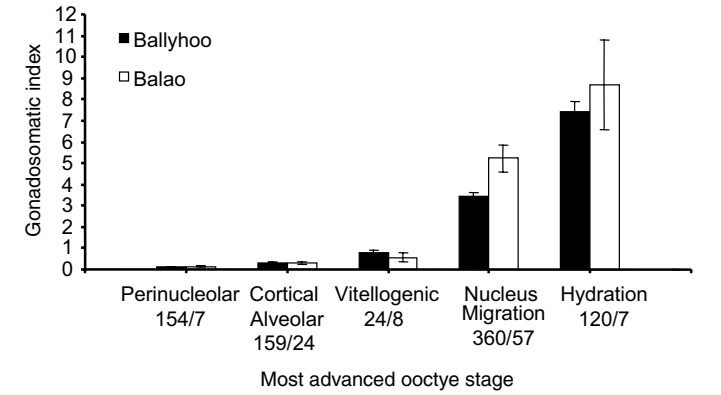


Figure 3

Mean (±95% confidence limits) gonadosomatic indices of female ballyhoo (*Hemiramphus brasiliensis*) and balao (*H. balao*) in various stages of oocyte development. A two-way ANOVA demonstrated a significant effect of both developmental stage and species (P<0.0001) on gonadosomatic index. Numbers indicate the number of fish, by stage, for each species. Hydration = nucleus breakdown.

Spawning habitat

In our study it was shown that hydrated oocytes can be inferred from a threshold criterion of GSI >6.0 (Fig. 3), and ripe females (i.e. with a batch of hydrated oocytes) will spawn within hours. Ripe ballyhoo females were distributed throughout the fishing grounds in both the Atlantic Ocean and Florida Bay (Fig. 1B). In the Atlantic, ripe ballyhoo females were caught in water depths from 1 to 20 m (mode: 6–10 m, 36.3% of the sets containing ripe ballyhoo in the Atlantic Ocean). In Florida Bay, ripe ballyhoo females were caught in areas that were exposed at low tide and out to 6-m deep (mode: 2–4 m; 57.9% of the positive sets in Florida Bay). Ripe ballyhoo females were mainly associated with hard bottom or vegetated habitats in both areas. In the Atlantic Ocean, ripe ballyhoo females were collected above platform reefs in 51.7% of the sets, above seagrass beds in 37.9% of the sets, near patch reefs in 5.2% of the sets, and over bare substrate in 5.2% of the sets. In Florida Bay, these fish were also associated with hard bottom substrates, specifically with vegetated bank habitat, in 44.7% of the sets and with seagrass beds in 55.3% of the sets.

Ripe balao females were distributed throughout the Atlantic fishing grounds but not in Florida Bay (Fig. 1C). In the Atlantic, they tended to occur in deeper water than did ripe ballyhoo females (range: 2–20 m; mode: 10–20 m, 51.3% of the sets containing ripe balao). The habitat associations of ripe balao females were similar to those of ripe ballyhoo females in the Atlantic Ocean, but typically reflected areas offshore rather than inshore of the reef. In the Atlantic Ocean, ripe balao females were collected above platform reefs in 58.0% of sets, above seagrass beds

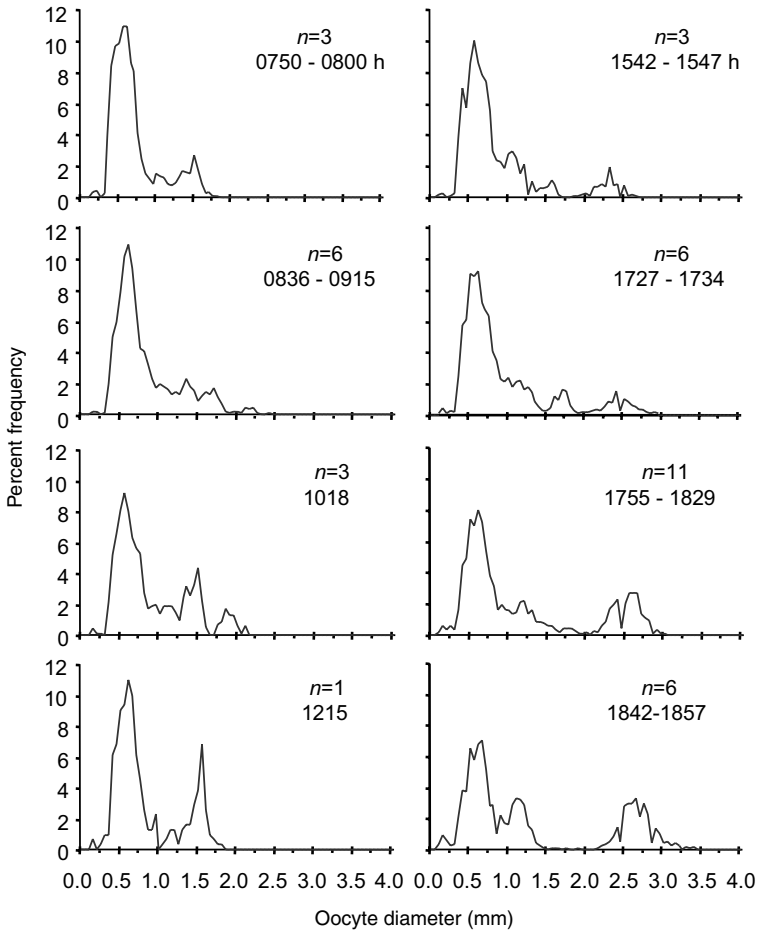


Figure 4

Oocyte diameters for ballyhoo (*Hemiramphus brasiliensis*) collected at different times of the day (EST). At least 300 oocytes were measured per female. Sizes <0.25 mm were not measured representatively because of the minimum size criteria of the image analysis software. Sunset occurred at 1830–1900 EST during this collection period (March–April). *n* = number of females.

in 25.8% of sets, over bare substrate in 9.7% of sets, and above undefined hard bottom in 6.5% of sets.

Discussion

These detailed findings of prolonged summer-spawning seasons, extreme iteroparity, and diel reproductive periodicity are consistent with other studies of halfbeak reproductive biology. Graham (1939), Ling (1958), Talwar (1962, 1967), and Berkeley and Houde (1978) noted a protracted spawning season by hemiramphids during warm months. McBride and Thurman (2003) examined the frequency of postovulatory follicles and reported that both species spawn daily during late spring and early summer, but also that some portion of the ballyhoo population spawns year-round. The present study is the first to follow the diel progression of FOM within the family Hemiramphidae. Lunar periodicity was not evident but it may have been confounded by the highly iteroparous nature of both species.

Spawning halfbeaks were distributed so widely throughout the fishing grounds that no specific areas were identified for the protection of spawning individuals. We noted interspecific differences in spawning areas, but these are not necessarily related to preferences by spawning females *per se*. Instead these differences appeared to be the result of interspecific distribution patterns of adult halfbeaks in general (i.e. adult ballyhoo are a more inshore species compared to adult balao [McBride, pers. obs.]). Because balao were not found in Florida Bay, fishing in Florida Bay does not affect this species. Spawning by ballyhoo was evident in Florida Bay, as predicted by fishing industry participants, but spawning ballyhoo were also widespread along south Florida's coral reef tract. Existing, albeit recent,

regulations[1] should provide some measure of protection for spawning ballyhoo in inshore waters.

Our study design was limited to the presence and absence of spawning females and did not identify concentrations of spawning activity associated with specific habitats. Presumably submerged vegetation is an important microhabitat. Several authors have noted that hemiramphid eggs, including those of ballyhoo, attach by filaments (of the chorion) to vegetation such as *Syringodium filiforme* and *Sargassum* sp. in waters less than approximately 6 m deep (Graham, 1939; Ling, 1958; Talwar, 1962, 1967; Berkeley and Houde, 1978). However, Berkeley and Houde (1978) collected eggs in plankton tows. The specific importance for halfbeak reproductive success of attached versus floating vegetation, or no vegetation, has not been identified.

The methods of this study define the macroscale spawning habitat of halfbeaks based on the distribution of spawning females. We demonstrate here that GSI values, even for highly iteroparous species, can distinguish females with hydrated oocytes from females in a less advanced stage of oocyte development. The GSI value is simple and inexpensive to measure, and by including individual halfbeaks for which we had GSI values but no histological data, we more than tripled our sample size with little additional laboratory cost. We could have instead characterized oocyte development macroscopically and such a modification is well suited when conditions affect weighing devices. But macroscopic characterization of oocyte development usually follows an ordinal scale that may vary between observers.

The distribution of females with hydrated eggs may be a better indication of spawning habitat than the distribution of eggs because hydration occurs for only a few hours (DeMartini and Fountain, 1981; Hunter and Macewicz, 1985; Brown-Peterson et al., 1988; McBride et al., 2002), whereas egg dispersal may occur over several days. In this study we assumed that spawning females move only limited distances within the few hours of the hydration process, and although limited movement has not been documented for either ballyhoo or balao, we believe that our interpretation of the data supports this assumption. The size of the study area was approximately 200 km by 250 km, and it seems reasonable that spawning halfbeaks were not moving extensively within this spatial boundary on an hourly basis. The approach discussed in the present study may meet the needs of other investigators wanting to generate a first approximation of spawning habitats for management purposes, which was the goal of this study. Also, this approach has good potential for use in areas were species identification of halfbeak eggs or larvae is problematic (Noell et al., 2001). Analyses requiring a smaller area or finer spatial resolution will depend on verification of a hydration period that is short in relation to expected fish movements.

The specific example presented in our study was limited because we collected the fish using commercial fishing vessels on routine fishing operations. This was cost-effective, but we were not able to identify spawning habitat preference or to define the complete geographic extent of the spawning grounds within south Florida. Gaps in the distribution of ripe females, which were particularly evident in the middle Florida Keys, were typically related to gaps in sampling coverage. In addition, both species presumably spawn outside the area we sampled. Still, much of the reported geographic range of ballyhoo and balao in the western Atlantic Ocean has been covered in the present study. The remaining shortcomings of this specific example could be resolved by using this approach within a statistically valid sampling design and estimating size-specific batch fecundity to map reproductive rates within a spatial and temporal context. The data resulting from such a comprehensive sampling design would be well-suited for identifying essential spawning habitat, for siting habitat-specific investigations of spawning dynamics, or for validating dispersal models for early life stages of marine fish.

Acknowledgments

We are grateful to many individuals for assistance in this research. First, to the fishermen and processors in the halfbeak fishery, all of whom participated in this survey. T. Brown, J. Hunt, and R. Moretti provided logistical support in Marathon. R. Beaver, K. Krumm, E. Robillard, D. Snodgrass, and J. Whittington assisted in fish collection and processing. G. Gerdeman, P. Nagle, F. Stengard, C. Stevens, and P. Thurman assisted with tissue processing and reproductive staging. C. Anderson assisted in preparing Figure 1 and GIS habitat analyses. B. Mahmoudi, R. Taylor, M. Zimmermann, and two anonymous reviewers provided constructive comments. Editorial assistance was provided by J. Leiby and J. Quinn. This research was funded in part by a grant from the National Oceanic and Atmospheric Administration (NOAA) to the Florida Fish and Wildlife Conservation Commission (Saltonstall-Kennedy Program, NOAA award no. NA77FD0069).

Literature cited

Berkeley, S. A. and E. D. Houde.
1978. Biology of two exploited species of halfbeaks, *Hemiramphus brasiliensis* and *H. balao* from southeast Florida. Bull. Mar. Sci. 28:624–644.

Berkeley, S. A., E. D. Houde, and F. Williams.
1975. Fishery and biology of ballyhoo on the southeast Florida coast. *In* Sea Grant Special Report 4, 1–15 p. Univ. Miami Sea Grant Program, Coral Gables, FL.

Brown-Peterson, N., P. Thomas, and C. R. Arnold.
1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in south Texas. Fish. Bull. 86:373–88.

Collette, B. B.
1965. Hemiramphidae (Pisces, Synentognathi) from tropical west Africa. Atlantide Report 8:217–235.

DeMartini, E. E., and R. K. Fountain.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fish. Fish. Bull. 79:547–60.

Graham, D. H.
1939. Breeding habits of the fishes of Otago Harbour and adjacent seas. Trans. Proc. Royal Soc. New Zealand 69:361–372.

Hunter, J. R. and B. J. Macewicz.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*) (R. Lasker, ed.), 79–94 p. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Limouzy-Paris, C. B., M. F. McGowan, W. J. Richards, J. P. Umaran, and S. S. Cha.
1994. Diversity of fish larvae in the Florida Keys: results from SEFCAR. Bull. Mar. Sci. 54:857–870.

Ling, J. K.
1958. The sea garfish, *Reporhamphus melanochir* (Cuvier & Valenciennes) (Hemiramphidae), in South Australia: breeding, age determination, and growth rate. Aust. J. Mar. Fresh. Res. 9:60–110.

McBride, R. S.
2001. Landings, value, and fishing effort for halfbeaks, *Hemiramphus* spp., in the south Florida lampara net fishery. Proc. Gulf Carib. Fish. Inst. 52nd Ann. Meeting, Key West, FL.

McBride, R. S., L. Foushee, and B. Mahmoudi.
1996. Florida's halfbeak, *Hemiramphus* spp., bait fishery. Mar. Fish. Rev. 58:29–38.

McBride, R. S., F. J. Stengard, and B. Mahmoudi.
2002. Maturation and diel reproductive periodicity of round scad (Carangidae: *Decapterus punctatus*). Mar. Biol. 140: 713–722.

McBride, R. S., and P. E. Thurman.
2003. Reproductive biology of *Hemiramphus brasiliensis* and *H. balao* (Hemiramphidae): maturation, spawning frequency, and fecundity. Biol. Bull. 204:57–67.

Noell, C. J., S. Donnellan, R. Foster, and L. Haigh.
2001. Molecular discrimination of garfish *Hyporhamphus* (Beloniformes) larvae in southern Austrailian waters. Mar. Biotechnol 3: 509–514.

Nybakken, J. W.
1997. Marine biology: an ecological approach, 4th ed., 481 p. Addison Wesley Longman, Inc., Menlo Park, CA.

Powell, A. B., D. E. Hoss, W. F. Hettler, D. S. Peters, and S. Wagner.
1989. Abundance and distribution of ichthyoplankton in Florida Bay and adjacent waters. Bull. Mar. Sci. 44: 35–48.

Starck, W. A., Jr.
1968. A list of fishes of Alligator Reef, Florida, with comments on the nature of the Florida reef fish fauna. Undersea Biol. 1:4–40.

Talwar, P. K.
1962. A contribution to the biology of the halfbeak, *Hyporhamphus georgii* (Cuv. & Val.) (Hemirhamphidae) [*sic*]. Indian J. Fish. 9:168–196.
1967. Studies on the biology of *Hemirhamphus* [*sic*] *marginatus* (Forsskål) (Hemirhamphidae-Pisces). J. Mar. Biol. Assoc. India 9:61–69.

West, G.
1990. Methods of assessing ovarian development in fishes: a review. Aust. J. Mar. Freshwater Res. 41:199–222.