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ARTICLE

The Potential for Cryptic Population Structure to Sustain a Heavily Exploited Marine Flatfish Stock

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Abstract

Complex spatial structure is widely viewed as an attribute that can contribute to stability in fish populations. Depending on aspects of stock demography and productivity, the existence of complete or partial spatial refugia can enable population persistence when faced with high rates of exploitation. The Southern Flounder *Paralichthys lethostigma* has been harvested extensively by inshore fisheries in North Carolina for more than three decades, with estimates of fishing mortality (*F*) surpassing 2.0 year^{-1} in several years and systems. Potential hypotheses to explain population persistence under heavy exploitation include high levels of recruitment at low stock sizes (high steepness) and/or the maintenance of adult biomass in offshore habitats that remain cryptic to the fishery. We constructed and applied an age-structured matrix model to evaluate the potential for cryptic stock structure, combined with varying levels of steepness in the stock–recruit relationship, to sustain the Southern Flounder stock across a range of plausible exploitation scenarios. Model simulations predicted that both high steepness in the stock–recruit relationship and large fractions of cryptic biomass were necessary to maintain even modest levels (~25%) of unfished biomass at the high estuarine harvest rates that have likely occurred since the inception of the fishery. When the estuarine fishery exploited the stock at an elevated rate ($F > 1.0$), high steepness in the stock–recruit relationship alone was insufficient to maintain population biomass at sustainable levels. Only maintaining a large fraction of the adult stock within the spatial refuge afforded by offshore habitats could offset high rates of estuarine exploitation and maintain more conservative levels (40% of unfished biomass) of population biomass. Future efforts should be focused on the identification and preservation of spatial structure within the Southern Flounder stock to maintain both age structure and fishery yield.

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There is growing appreciation for the importance of knowledge about the spatial dynamics of fish stocks to both improve understanding of population processes and achieve conservation goals (Kritzer and Sale 2006; Botsford et al. 2009; Secor 2015). As such, the design of optimal fishery harvest policies necessitates some information about spatial stock structure (Begg et al. 1999; Ying et al. 2011). Although it can present a challenge to resource managers, complex spatial structure is widely viewed as an attribute that can contribute to population stability. For example, the portfolio effect (Hilborn et al. 2003; Schindler et al. 2010) and contingent theory (Secor 1999; Kerr et al. 2010) represent examples of how spatial population structure can buffer populations impacted by variable harvest rates or environmental conditions. Similarly, spatially explicit management approaches, such as the establishment of marine protected areas, can satisfy a number of conservation and management objectives (Lester et al. 2009; White et al. 2011; Edgar et al. 2014). However, major impediments to the integration of stock structure in the fishery management process remain, such as the lack of information on connectivity and spatial variation in demographic rates (Sale et al. 2005; Beamish and Rothschild 2009).

The existence of segments of population biomass that remain "cryptic" presents a unique challenge, as key demographic information that impacts the ability to model population dynamics is missing. Broadly, cryptic biomass can be considered any fraction of a stock that is unknown or unavailable to the fishery—usually because the stock occupies habitats that are inaccessible to conventional fishing gears—but that may still contribute to overall stock dynamics in meaningful ways, such as through recruitment (definition modified from Fonteneau 1996). While creating a void in stock demographic information, the existence of cryptic stock segments can also provide a natural refuge from any fishing activities that remove individuals from the remainder of the stock. Walters (1998) argued that having portions of the stock occupying spatial refugia not exposed to fishing pressure enabled harvest on the accessible portion of the stock to continue with less chance of recruitment overfishing. Several historical fish populations that included natural spatial refuges for portions of the stock (e.g., northern Atlantic Cod *Gadus morhua*) experienced rapid declines with expansion of the range of fishing fleets and/or the discovery of the cryptic stock components. Likewise, Caddy (1999) attributed the sustainability of many fisheries in the Mediterranean Sea (particularly when compared to fisheries in the North Sea) to the spatial refuge provided by the rocky bottom topography of the continental slope, which is inaccessible to most fishing gear. Clear examples of cryptic biomass and its role in promoting sustainable fisheries are necessarily rare since often they represent undiscovered stock segments or they are quickly harvested after discovery. However, several modern fisheries do exist in which segments of the stock are unfished or only lightly fished, creating a cryptic biomass that may offset harvest of the fished segments (e.g., West Coast rockfishes *Sebastes* spp.: Yoklavich et al. 2000; various artisanal coral reef fisheries: Tyler et al. 2009; Orange Roughy *Hoplostethus atlanticus*: Dunn and Forman 2011).

Here, we investigate the possibility for cryptic biomass to contribute to the sustainability of the fishery for Southern Flounder *Paralichthys lethostigma* along the U.S. South Atlantic coast. The Southern Flounder occurs in estuarine and continental shelf waters along the southeast U.S. coast from southern Virginia to central Florida and also throughout the northern Gulf of Mexico. Important recreational fisheries are present throughout the species' range, with variable levels of commercial harvest in specific regions (National Oceanic and Atmospheric Administration Fisheries; http://www.st.nmfs.noaa.gov/commercial-fisheries/index). Along the southeastern U.S. coast, commercial harvest of Southern Flounder occurs extensively in North Carolina waters, with most landings from estuarine gill-net and pound-net fisheries. During the 1990s, commercial landings of Southern Flounder in North Carolina routinely approached or exceeded 2,000 metric tons, with landings during the most recent decade averaging closer to 1,000 metric tons. Estimates of the instantaneous rate of fishing mortality (F) on fully recruited ages (2–5 years old) averaged 1.3–2.6 year^{-1} depending on assumptions in the stock assessment models (NCDMF 2005; Takade-Heumacher and Batsavage 2009). As recently as 2006, empirical estimates of F from a tag return study completed in one of the small coastal rivers along the southern coast of North Carolina (New River) exceeded 2.0 year^{-1} during both study years (Smith et al. 2009). These levels of F translate to approximately 70–90% of the stock being removed annually by the fishery. Although commercial landings have declined during the most recent decade, much of the reduction can be attributed to reduced effort (number of trips) driven by management changes, fuel prices, and more recently, specific restrictions to minimize interactions with protected species (NCDMF 2013).

The potential for an offshore component of biomass to contribute to sustainability in the face of high exploitation rates in estuarine waters is suggested by aspects of Southern Flounder life history. Mature flounder emigrate from estuaries during fall to participate in offshore winter spawning, estimated to peak between December and February in the U.S. South Atlantic based on ichthyoplankton surveys (Hettler and Chester 1990; Taylor et al. 2009). The exact location of spawning, while presumed to be in outer continental shelf waters, is presently unknown. After spawning, larvae are advected toward the coast and begin to arrive at estuarine inlets at 30–60 d posthatch

(Burke et al. 1991). Southern Flounder then spend the first few years of life in estuarine systems, with subsequent maturation and participation in offshore spawning migrations. Commercial landings are composed primarily of age-1 and age-2 fish, many of which are immature and nearly all of which have not yet spawned (Midway and Scharf 2012). The North Carolina fishery is assumed to comprise a unit stock, and current management (stock assessments) assumes that mature adults return to estuarine waters after the spawning migration (NCDMF 2013). The demography and movements of mature Southern Flounder on the continental shelf are largely unknown, but there are examples of individuals migrating considerable distances (hundreds of kilometers; Craig et al. 2015). No large-scale offshore fishery exists because the locations of spawning aggregations remain undiscovered, and the rugosity of offshore hard-bottom habitats off the southeastern U.S. coast prevents trawling. The low catches of older fish (ages 3 and older [ages 3+]) in the inshore fishery indicate either that only some individuals re-enter estuarine systems after spawning or that adult survival rates in the ocean are extremely low. Therefore, it is possible that sufficient numbers of larger, older Southern Flounder occupy offshore reefs after spawning, where they remain cryptic to the estuarine fishery and supply recruits annually to stabilize the stock.

The possibility of extended offshore residency by post-migratory Southern Flounder was also suggested by Watterson and Alexander (2004) based on observations during a multi-year diving survey conducted off the North Carolina coast. During late spring through early fall, when the estuarine fishery is most active, adult Southern Flounder were located via scuba on nearshore continental shelf artificial reefs in all survey years. Relative to fish landed in the estuarine commercial fisheries during the same time period (mean TL = 382 mm; <10% of the fish were age 3+), the Southern Flounder sampled in continental shelf waters were both larger (mean TL = 469 mm) and older (>50% age-3+ fish). Although the study was limited to safe compressed-air diving depths (≤40 m), the consistent occurrence of adult Southern Flounder in the ocean during the prime estuarine fishing seasons supports the notion that a portion of the mature stock remains outside of estuarine habitats for much of the year and thus is unavailable to harvest.

An alternative possibility for sustained high levels of Southern Flounder harvest is that the stock demonstrates high productivity at low stock sizes (i.e., a high maximum annual reproductive rate; Myers et al. 1999). Between 1979 and 2002, recruitment of Southern Flounder to North Carolina estuaries (as measured by a statewide juvenile trawl survey) regularly experienced variation up to fourfold, but the estimated spawning stock biomass did not appear to explain recruit fluctuations (data presented by Taylor et al. 2010). Indeed, attempts to fit theoretical stock–recruit models to the available data for Southern Flounder have failed to yield reliable parameter estimates, and no dependence on stock size has been assumed for recruitment in recent stock assessments (Takade-Heumacher and Batsavage 2009). It is possible that the true stock–recruit relationship for the Southern Flounder exhibits a high steepness (h) value (>0.8), as has been estimated for other flatfishes (Iles 1994; Myers et al. 1999) and more specifically for its congener, the Summer Flounder *Paralichthys dentatus* (Terceiro 2011; Maunder 2012). A high h-value implies that biological reference points could be set at more aggressive targets to maximize short-term yield in the fishery (Maunder 2012).

In the present study, we use a simple age-structured population model to explore how sustainability of the Southern Flounder fishery in North Carolina waters is related to the potential existence of cryptic adult biomass and elevated recruitment at a low stock size. Our objective was to examine a range of plausible estimates of the fraction of adult biomass that remains cryptic to the fishery, combined with estimates of steepness from a stock–recruit relationship, to identify scenarios that allow persistence of the stock when exposed to high levels of inshore harvest. Rather than producing a strict update to the stock assessment model for the Southern Flounder fishery in North Carolina, our goal was exploratory: to characterize several possible scenarios that could help to explain stock persistence after exposure to a prolonged period of elevated harvest rates. Our findings should guide future research and contribute to the identification of levels of cryptic adult biomass that could be targeted for preservation. The Southern Flounder represents an ideal fishery with which to explore questions related to cryptic stock structure and steepness in the stock–recruit relationship since several lines of evidence support the hypothesis of extended use of unexploited habitats by adults, and they represent a broad phylogenetic group (flatfishes) that is predicted to demonstrate high levels of steepness in their recruitment dynamics.

METHODS

To explore the potential effects on population dynamics of a cryptic component of population biomass located outside of estuarine waters, we developed an age-structured population model in which reproductively mature age-classes that have migrated offshore remain in offshore habitats to varying degrees (Figure 1). Specifically, the parameter ϕ_C represents the fraction of the adult stock that is cryptic (i.e., remains offshore). The fraction of adults returning to estuarine habitats is then $1 - \phi_C$, and this noncryptic portion of the adult stock is exposed to the estuarine fishery (the estuarine harvest rate [F] is applied

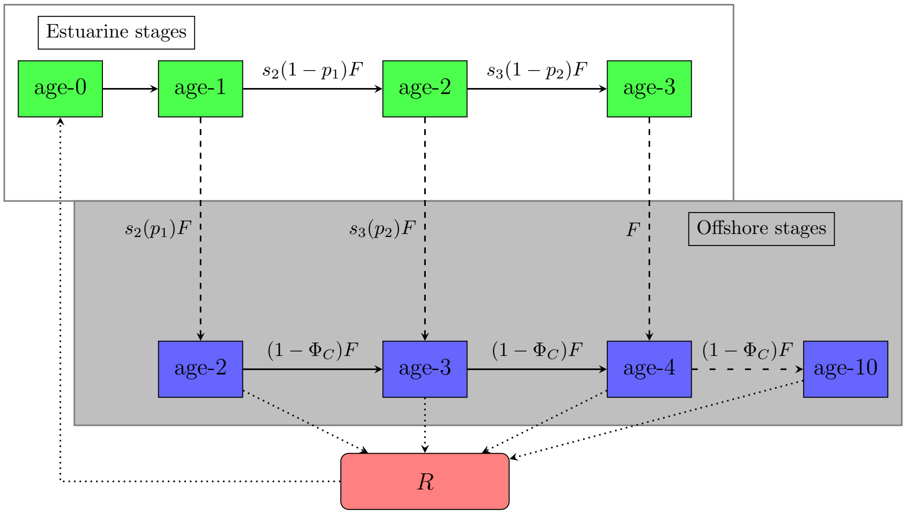

FIGURE 1. Diagram of Southern Flounder population structure as explored in the current study. The green boxes along the top represent estuarine age-groups; all fish enter the model as age-0 fish in the estuary. With each model time step, surviving fish transition to the next age-group and either remain in the estuary (solid horizontal arrows) or emigrate offshore (dashed vertical arrows). Offshore age-groups are shown in blue and begin with age-2 fish, extending through age 10. The symbol ϕ_C represents the fraction of postmigratory adults remaining offshore (unavailable to estuarine harvest F), where $\phi_C = 1$ corresponds to zero harvest of postmigratory adults. The fraction of postmigratory adults vulnerable to harvest is defined as $1 - \phi_C$ and is multiplied by F to determine the adult harvest rate, which is the same for all adult age-groups since fish are fully selected beginning with age 2. Only offshore age-groups can contribute new recruits (represented by the dotted line to the red box) to the age-0 estuarine group. All ages are subject to age-specific natural mortality (M_a), which is not shown explicitly in the diagram. This diagram complements projection matrix **A** in the Methods text; complete explanations of symbols are presented in Table 1.

to all immature individuals and also the fraction of adults that return from offshore). For instance, a purely cryptic biomass scenario ($\phi_C = 1$) would result in no postmigratory adults returning to estuarine habitats; thus, no adults would be exposed to estuarine F. In contrast, under a no cryptic biomass scenario ($\phi_C = 0$), all postmigratory adults would return to estuarine habitats and would be vulnerable to the fishery. This approach to representing adult dynamics corresponds to the hypothesized Southern Flounder life history in which prior to the initial spawning migration, individuals experience fishing rate F in the estuary. After the initial spawning migration (and all subsequent spawning migrations), some fraction of mature individuals then return to estuarine habitats, where they are exposed to F once again. Because the fraction of postmigratory adults remaining in offshore habitats is unknown, current management assumes that all fish return to estuarine habitats and are vulnerable to the fishery (i.e., $\phi_C = 0$). We explored the effects on Southern Flounder population dynamics of the full range of ϕ_C values (0–1), reflecting the uncertainty in the migration dynamics of adult movements.

Estimation of biomass, maturity, and sources of mortality.— We included ages 0–10 in our model, which covers the life span of Southern Flounder (Gilbert 1986; Safrit and Schwartz 1998; Fischer and Thompson 2004). Age-specific natural mortality (M_a) estimates (Table 1) were based on the equation provided by Lorenzen (1996). An age-based maturity vector (**P**) was based on recent findings for female Southern Flounder in North Carolina waters (Midway and Scharf 2012), with 0% of females mature at age 0, 44% mature at age 1, 76% mature at age 2, and 100% mature at ages 3+. To calculate total biomass, we derived length-at-age estimates from the von Bertalanffy growth equation using parameter estimates taken from Takade-Heumacher and Batsavage (2009; Table 1) and then converted length to weight by using an established weight–length relationship.

Stock assessment models have estimated that the Southern Flounder stock in North Carolina has experienced a range of harvest rates since the fishery expanded in the early 1990s. Estimates of F ranged from 1.9 to 3.43 in the original fishery management plan based on the application of the ADAPT virtual population analysis model (NCDMF 2005), while more recent estimates of F from application of the ASAP2 model ranged from 0.75 to 1.65 (Takade-Heumacher and Batsavage 2009). Given the large range in historical estimates of F and the expectation that current (since 2010) harvest levels have declined, we explored F-values on fully recruited fish ranging from 0 to 2.0. Total instantaneous mortality (Z) was then estimated by adding the age-specific estimate of M from the Lorenzen model. Age selectivity (s_a) was asymptotic based on the most recent stock assessment (Takade-Heumacher and

TABLE 1. Symbols and equations used in population modeling of Southern Flounder (Z = total instantaneous mortality; S = female spawning stock biomass; α = slope; β = asymptotic recruitment).

Symbol	Definition	Equation or value	Source
M_a	Age-specific natural mortality	Ages 0–6+: 1.161, 0.569, 0.403, 0.332, 0.294, 0.270, and 0.255	Lorenzen (1996)
p_a	Age-specific maturity	Ages 0–3+: 0, 44, 76, and 100%	Midway and Scharf (2012)
TL_a	Total length at age	$\mathrm{TL} = 699\left\{1 - e^{[-0.284(t+0.761)]}\right\}$	Takade-Heumacher and Batsavage (2009)
W_a	Weight at age	$W = 3e - 9 \times \mathrm{TL}^{3.241}$	Takade-Heumacher and Batsavage (2009)
F	Instantaneous fishing mortality	$Z - M_a$	
s_a	Age-specific selectivity	Ages 0–2+: 0, 0.3, and 1.0	
R	Age-0 larval recruits	$R = \dfrac{\alpha S}{1 + \left(\frac{\alpha}{\beta}\right) S}$	Beverton and Holt (1957)
ϕ_C	Fraction of adult biomass remaining offshore	0–1, where 1 = fully cryptic	

Batsavage 2009) and was modeled as 0 for age 0, 0.3 for age 1, and 1.0 for ages 2+. Our simulations assumed that F remained constant over time, which is common when projecting fishery status by using deterministic biological reference points (e.g., spawning potential ratio [SPR]) to identify sustainable harvest rates (Maxwell et al. 2005).

Recruitment.— We fitted a Beverton and Holt (1957) stock–recruit function to the data on female spawning stock biomass (S) and the subsequent number of age-0 recruits (R) produced. We used the formulation

$$R = \frac{\alpha S}{1 + \left(\frac{\alpha}{\beta}\right) S},$$

where R represents the number of age-0 female recruits produced; S is the female spawning stock biomass; α is the initial slope (maximum R/S as S approaches 0); and β is the asymptotic or maximum number of recruits produced at a high S. Data used for this relationship (Table 1) were based on model output from the most recent stock assessment (Takade-Heumacher and Batsavage 2009). Although several models have been used to describe the stock–recruit relationships of flatfishes (Iles 1994), there is no clear support for any particular model (e.g., Ricker, Beverton–Holt, or Shepherd). We selected the Beverton–Holt model for use with Southern Flounder because of its general applicability to marine fishes and the lack of evidence that would suggest the presence of intercohort compensatory feedback. We evaluated variable levels of α within the framework of the compensation ratio (CR) originally described by Goodyear (1977) and forming the basis for the current widespread use of SPR as a biological reference point (Goodyear 1993). The CR can be estimated from the stock–recruit relationship as the slope at the origin (α = maximum recruit survival) divided by the slope of the replacement line for an unfished stock (recruit survival at $F = 0$). Commonly, recruitment at low stock sizes is expressed in terms of steepness (h), defined as the fraction of virgin recruitment at which spawner biomass is 20% of virgin spawner biomass (Mace and Doonan 1988), which can be obtained directly from the CR as $h = \mathrm{CR}/(4 + \mathrm{CR})$. Steepness ranges between 0.2 and 1.0 and is widely applied as a dimensionless parameter to define stock productivity at low biomass and thus resilience to fishery exploitation (Conn et al. 2010). To estimate the CR—and hence h—for Southern Flounder, we assumed that F was close to 0 at the observed stock sizes (2.0 million kg [~4.4 million lb]) near the beginning of the time series, and we then estimated the slope of the replacement line (R/S at $F = 0$) to be approximately 2.0. We used weighted least-squares estimation to obtain parameter estimates for the Beverton–Holt model fit to the spawning stock biomass and age-0 recruit data. Although the Southern Flounder data lacked contrast in spawning stock biomass, the model was able to generate an α estimate of 17.6 (SE = 30.8) and a β estimate of 14.3 (SE = 6.2; data presented in Figure 2). The estimated α yielded a CR of 8.8 (17.6/2) and an h-value of 0.69. Given the uncertainty in our estimate of h, we explored a range of h-values from 0.25 to 0.95 at intervals of 0.10, in combination with different values of ϕ_C, for their effects on Southern Flounder population dynamics. We elected to include h-values as high as 0.95 based on past studies indicating that h may routinely exceed 0.80 for flatfishes (Iles 1994; Myers et al. 1999; Maunder 2012), and because high h represents one possible explanation for population

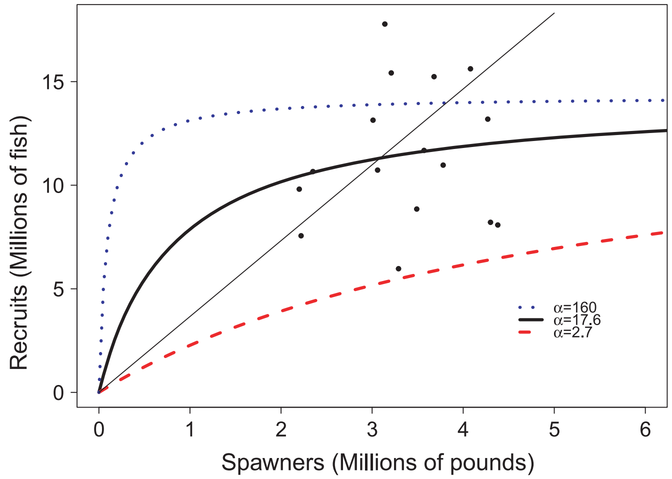

FIGURE 2. Beverton–Holt stock–recruit relationships estimated for Southern Flounder in the current study. Black circles represent the spawner–recruit data from Takade-Heumacher and Batsavage (2009), and the solid black curve shows the model of best fit. The blue dotted and red dashed curves display relationships with the most extreme values for steepness (h = 0.95 and 0.25, respectively) that were explored in this study for their effects on population persistence. In each case, the β parameter in the stock–recruit function (asymptotic recruitment) was fixed at the level estimated by the best-fit line. The thin black diagonal line represents the replacement line.

stability despite elevated harvest rates in the Southern Flounder fishery.

Adult population dynamics.— We combined the age-dependent life history parameters into an 11 × 11 projection matrix **A** (available in the Supplement in the online version of this article). The leading subdiagonal of **A** is a vector of the probabilities of surviving into each successive age. These probabilities depend on the terms M_a (natural mortality at age), s_a (selectivity at age), p_a (maturity at age), F (estuarine harvest rate), and ϕ_C (fraction of postmigratory adults), which are also defined above (Table 1). The subdiagonal has entries e^{-M_0}, $e^{-(M_1+s_1F)}$, $e^{-[M_2+s_2(1-p_1)F+s_2p_1(1-\phi_C)F]}$, $e^{-[M_3+s_3(1-p_2)F+s_3p_2(1-\phi_C)F]}$, and $e^{-(M_4+(1-\phi_C)F)}$ through $e^{-(M_9+(1-\phi_C)F)}$ for ages 4 through 9. All other entries of **A** are zero. Age-0 survival is only determined by M (s = 0); for simplicity, the maturity and selectivity parameters are not included in the equations for the age-4 and older transition probabilities since they are equal to 1. The transition between ages 1 and 2 and between ages 2 and 3 are the most complex because they include both estuarine and offshore substocks. To summarize these transitions, age-3 survival is determined by age-2 fish that do not die of natural mortality (M_2), which are then split into estuarine and offshore ages based on the proportion mature. Those fish (immature individuals) remaining in estuarine waters are then subject to F, while some fraction of the mature offshore fish is subject to F, defined by 1 – ϕ_C. The matrix was then used in the update equation,

$$N_{t+1} = \mathbf{A} \times N_t + \mathbf{R},$$

where **R** is an 11 × 1 column vector with the number of age-0 recruits in the first row followed by 10 zeros; **R** is defined above and included S as the product of fecundity at age and N. Model simulations explored the effects of various levels of F, ϕ_C, and h on the equilibrium population biomass, which was compared to common management reference points of 20% and 40% of unfished biomass.

Model simulations.— Beginning with the unfished stable age distribution, we conducted two sets of simulations. The first set of simulations varied ϕ_C and h at each of three fixed levels of F (0.5, 1.0, and 1.5). This revealed which combinations of cryptic adult biomass and h could maintain sustainable levels of stock biomass (≥40% of unfished adult biomass; Gabriel and Mace 1999; Ralston 2002) when the stock was exposed to a range of F-values. We explored eight values of h (0.25–0.95, in increments of 0.10) combined with 11 values of ϕ_C (0–1.0, in increments of 0.10), and the projection matrix was iterated to the deterministic equilibrium (≤200 model years) with the update equation for each unique combination.

We then performed a second set of simulations in which we varied F to determine the range of harvest rates that could be sustained by specific, fixed levels of ϕ_C (0, 0.33, 0.67, and 1.0). These levels were chosen to represent a complete cryptic biomass (ϕ_C = 1), a relatively large cryptic biomass (ϕ_C = 0.67), a moderate level of cryptic biomass (ϕ_C = 0.33), and the absence of cryptic biomass (ϕ_C = 0). We then explored 11 fixed levels of F (0 to 2.0, in increments of 0.2) in combination with the eight levels of h (0.25–0.95, in increments of 0.10). Although low harvest rates (F ≤ 0.2) have not been estimated during the history of the North Carolina Southern Flounder fishery, lower values of F may be observed under future management strategies, and their evaluation permitted us to explore nonlinear changes in equilibrium biomass over a broader range of F.

RESULTS

Using a simple age-structured population model that included specific aspects of Southern Flounder demography and life history informed by recent stock assessments and research findings, we predicted the fraction of postmigratory adults remaining unavailable to the estuarine fishery (i.e., cryptic biomass) that was necessary to maintain sustainable levels of stock biomass under various harvest and steepness scenarios. Under a moderate fixed F of 0.5, model simulations predicted that stock biomass could be maintained at 20–30% of unfished levels even if all adults were exposed to estuarine harvest (ϕ_C = 0) as long as h-values were moderate to high (0.65–0.90; Figure 3A). At this harvest rate (F = 0.5), sustaining greater fractions of unfished stock biomass (40%) required a larger portion of adults ($\phi_C = 0.5$–0.8) to remain cryptic to the fishery, along with higher h-values (0.65–0.95). At a higher harvest rate ($F = 1.0$), maintaining even 20% of unfished stock biomass was not possible unless at least some portion of adults remained cryptic to the fishery, even at the highest level of h (0.95) that we explored (Figure 3B). Even at relatively high levels of steepness ($h = 0.7$–0.9), between 40% and 80% of adults would still need to remain cryptic to the fishery to sustain 20% of unfished stock biomass at an F equal to 1.0. Maintaining 40% of unfished stock biomass at an F of 1.0 required a near-completely cryptic adult stock along with h-values exceeding 0.7 (Figure 3B). When exposed to very high harvest rates ($F = 1.5$), most adults ($\geq$75%) had to remain cryptic to the fishery, and the stock also needed to demonstrate moderate to high levels of h ($\geq$0.6) just to sustain 20% of unfished stock biomass (Figure 3C). Maintaining 40% of unfished stock biomass was not possible under any combination of h and ϕ_C when F was fixed at 1.5.

When the adult stock was fully cryptic to the fishery ($\phi_C = 1$), sustaining stock biomass at conservative levels (40% of unfished biomass) was attainable at harvest rates as high as $F = 1.0$ as long as $h > 0.6$ (Figure 4A). Lower fractions of unfished biomass (20%) could be sustained at much higher harvest rates ($F \geq 1.5$) with moderate steepness levels ($h = 0.55$–0.70) if the adult stock experienced no harvest. If only a small portion of the adult stock (33%; $\phi_C = 0.67$) was exposed to harvest, traditional stock biomass targets (40% of unfished biomass) could be achieved at moderate harvest levels ($F = 0.5$–0.6) as long as h exceeded 0.7 (Figure 4B). At similar steepness levels, the stock could experience much higher rates of harvest ($F \geq 1.0$) and still maintain 20% of unfished stock biomass as long as the majority (67%) of the adult stock remained cryptic to the fishery.

Maintaining conservative stock biomass levels (40% of unfished biomass) when a greater fraction of adults was exposed to the fishery ($\phi_C = 0.33$) required much lower harvest rates ($F \leq 0.5$) in addition to high steepness ($h > 0.9$) in the stock–recruit relationship (Figure 4C). Lower stock biomass levels (20% of unfished biomass) could still be maintained under higher harvest rates ($F = 1.0$) as long as h was sufficiently high ($\geq$0.8) and at least a modest fraction of adults (33%) remained cryptic to the fishery. When adults were fully exposed to harvest (no cryptic adult biomass; $\phi_C = 0$), even the highest levels of steepness in the stock–recruit relationship ($h > 0.9$) could not maintain stock biomass at 40% of unfished biomass levels when F exceeded approximately 0.3 (Figure 4D). Under this scenario of no cryptic adult biomass, lower biomass levels (20% of unfished biomass) could be sustained when the stock was exposed to slightly higher harvest rates ($F = 0.7$–0.9) if steepness was sufficiently high ($h = 0.80$–0.95).

Regardless of the fraction of adult biomass remaining cryptic to the estuarine fishery, the ability of the Southern Flounder stock to achieve stock biomass targets was more sensitive to changes in F than to changes in h. The influence of steepness in the stock–recruit relationship was generally asymptotic at more conservative stock biomass targets (e.g., 40% of unfished biomass) across all fractions of cryptic adult biomass (Figure 4A–D). In comparison, the relative influences of F and h on meeting less-conservative stock biomass targets (e.g., 20% of unfished biomass) were more similar, as evidenced by the near-constant slopes of the 20% stock biomass contour lines in Figure 4.

DISCUSSION

Interactive Effects of Estuarine Harvest Rate, Steepness, and Cryptic Adult Biomass

For the Southern Flounder stock in North Carolina, model simulations predicted that both high steepness in the stock–recruit relationship and large fractions of cryptic biomass were necessary to maintain even modest levels (~25%) of unfished biomass at the high estuarine harvest rates that have likely occurred since the early 1990s (based on multiple stock assessments). When the estuarine fishery exploited the stock at an elevated rate ($F > 1.0$), high steepness in the stock–recruit relationship alone was insufficient to maintain population biomass at sustainable levels. Only maintaining a large fraction of the adult stock within the spatial refuge afforded by offshore habitats could offset high rates of estuarine exploitation and maintain more conservative levels (40% of unfished biomass) of population biomass.

The degree of spatial connectivity among stocks—and among ontogenetic life stages within stocks—is increasingly being used to inform predictions of population response to various harvest scenarios (e.g., Frisk et al. 2008; Kerr et al. 2010; DeCelles and Cadrin 2011; White 2015). The discovery of groups of larger, older individuals within the heavily exploited Southern Bluefin Tuna *Thunnus maccoyii* population led Fonteneau (1996) to suspect the existence of subpopulations of fish that were not susceptible to harvest, which he referred to as "cryptic biomass." Conceptually, having some fraction of a harvested stock that remains cryptic to the fishery may enable the stock to persist despite high rates of exploitation on the remainder of the stock. The historical contribution of spatial refuges to sustainable exploitation has been asserted broadly (Walters 1998; Caddy 1999) and indeed forms the basis behind the implementation of marine reserves or protected areas as a contemporary management tool. Several examples exist that highlight the potential for spatial refugia to protect subsets of individuals from harvest due

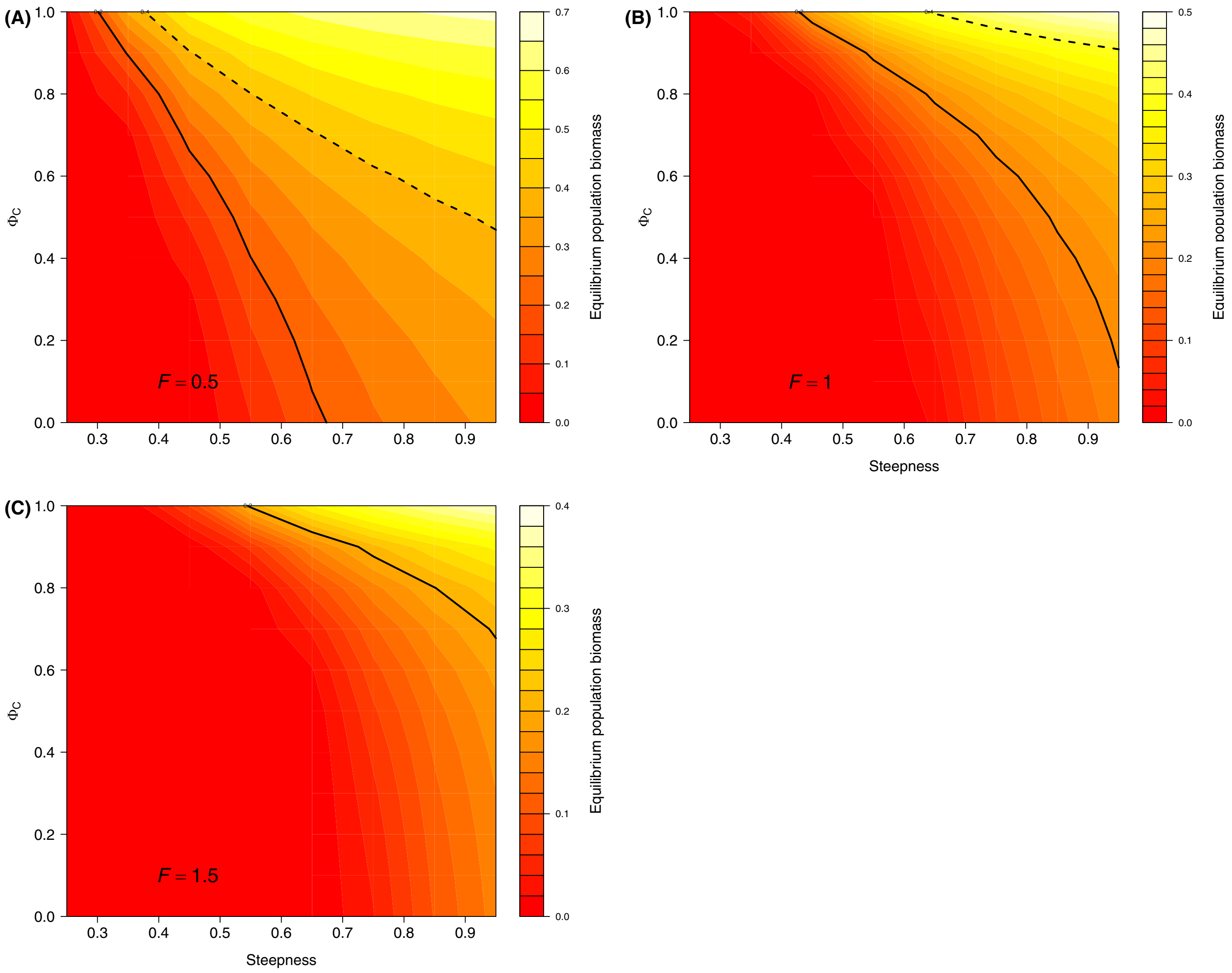

FIGURE 3. Contour plots of equilibrium adult population biomass relative to unfished biomass for Southern Flounder under varying levels of steepness (*h*; *x*-axis) and ϕ_C (fraction of the adult stock remaining offshore, where $\phi_C = 1$ represents a completely cryptic adult biomass and $\phi_C = 0$ represents complete availability to harvest; *y*-axis). The estuarine harvest rate (*F*) is fixed at **(A)** 0.5, **(B)** 1, or **(C)** 1.5. In each panel, the solid black line represents the 0.20 contour (biomass = 20% of unfished biomass), while the dashed line represents the 0.40 contour (biomass = 40% of unfished biomass). Note that the scale of unfished biomass differs among panels.

to their use of inaccessible microhabitats (Yoklavich et al. 2000) or areas that are traditionally subjected to lower rates of exploitation (Dunn and Forman 2011).

For the Southern Flounder fishery in North Carolina waters, our simulations predicted that greater than two-thirds of the adult stock would need to remain cryptic from harvest, regardless of the level of steepness in the stock–recruit relationship, for the population to maintain stock biomass at even 20% of unfished levels when exposed to the high exploitation rates ($F \approx 1.5$) estimated during several years since 1991. There are several pathways through which cryptic adult biomass could be maintained in the Southern Flounder population along the U.S. Atlantic coast. The possibility of postspawn adults remaining in oceanic waters and thus unavailable to estuarine-based fisheries was suggested by the consistent presence of adult Southern Flounder on nearshore reefs during summer diving surveys (Watterson and Alexander 2004). In addition, Southern Flounder are regularly captured from oceanic reefs located off the North Carolina coast during summer by recreational anglers and spearfishermen (NCDMF 2013). Although these observations indicate the strong possibility that a segment of the adult Southern Flounder population is occupying nearshore oceanic habitats during summer, the fraction of biomass remaining cryptic to the inshore fisheries is uncertain.

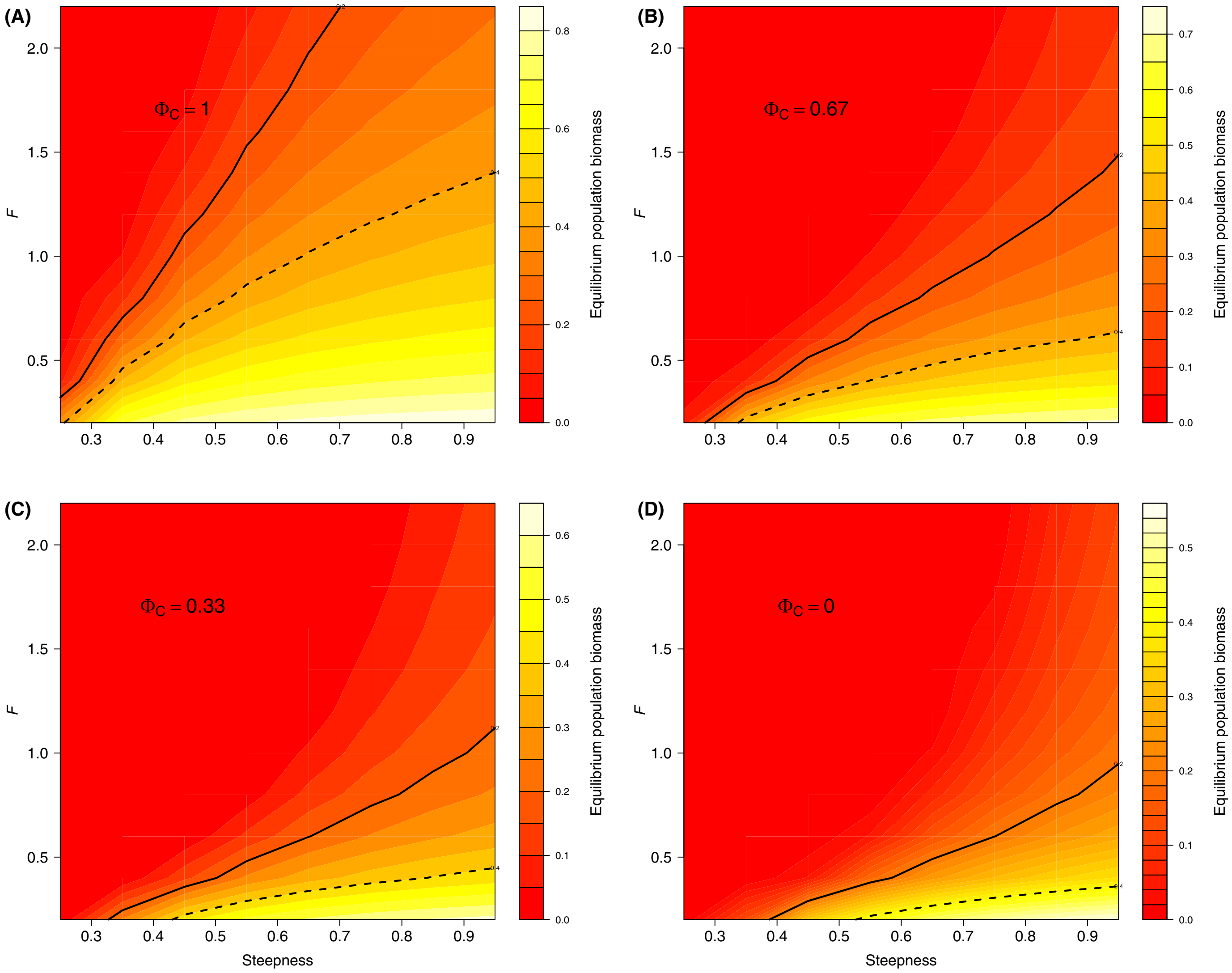

FIGURE 4. Contour plots of equilibrium adult population biomass relative to unfished biomass for Southern Flounder under varying levels of steepness (*h*; *x*-axis) and estuarine harvest rate (*F*; *y*-axis). Each panel illustrates model predictions for a specific fraction of adult biomass remaining offshore (ϕ_C = 1.0, 0.67, 0.33, and 0, in panels **A–D**, respectively). In each panel, the solid black line represents the 0.20 contour (biomass = 20% of unfished biomass), while the dashed line represents the 0.40 contour (biomass = 40% of unfished biomass). Note that the scale of unfished biomass differs among panels.

Large-scale movement by adult flounder represents another potential pathway leading to cryptic biomass. Similar to observed patterns in the Gulf of Mexico (Anderson et al. 2012), recent studies of Southern Flounder otolith morphometrics (Midway et al. 2014) and population genetics (Wang et al. 2015) each revealed evidence for limited population structure within the U.S. South Atlantic. High rates of mixing among substocks may be achieved through large-scale movements by adult Southern Flounder during fall and winter. Craig et al. (2015) synthesized multiple conventional tag return data sets, which illustrated consistent large-scale (hundreds of kilometers) directional movements to the south by Southern Flounder tagged in North Carolina waters. The patterns observed in North Carolina align closely with historical patterns of tag returns in South Carolina (Wenner et al. 1990) and Georgia (Music and Pafford 1984), which demonstrated the recovery of fish large distances to the south of their release locations. Frisk et al. (2014) proposed that population connectivity in marine fishes may be mediated largely by adult movements, especially spawning-related migration by adults that contributes to extensive mixing during mating. In the case of Southern Flounder, emigrating adults that depart North Carolina waters may re-enter estuarine systems in southern states (South Carolina, Georgia, and Florida) where *F* is considerably lower. If oceanic transport mechanisms return larvae to North Carolina estuaries, recruitment in North

Carolina may benefit from translocated adults that are subsequently exposed to lower rates of exploitation in other states, contributing to population persistence despite high estuarine fishing rates in North Carolina.

With regard to recruitment potential, our efforts reflect the considerable level of uncertainty in the stock–recruit relationship for Southern Flounder in North Carolina, whether derived from the stock assessment process (Takade-Heumacher and Batsavage 2009) or from direct field observations (Taylor et al. 2010). Given this uncertainty, the exploration of a wide range of values for *h* was justified. When exploitation rates in the estuarine fishery were very high ($F \approx 1.5$), even *h*-values that exceeded 0.9 could only sustain roughly 10% of unfished biomass if the stock was fully exposed to harvest through the adult age-groups (i.e., no cryptic biomass). In general and across different fractions of cryptic biomass, we found that the effects of steepness in the stock–recruit relationship were greater at more liberal management reference points (illustrated by the difference in slope between the 20% and 40% unfished biomass contours in Figure 4). The ability of the Southern Flounder stock to achieve more conservative reference points (e.g., 40% of unfished biomass) was more sensitive to variation in *F* compared to the effects of changing steepness, as biomass targets could only be met when *F* was narrowly constrained (0.5–0.6) across a broader range of *h* (0.6–0.9).

Among several factors, the lack of contrast in spawning stock biomass is most problematic in resolving stock–recruit relationships and obtaining reliable estimates of recruitment potential at low stock sizes (Hilborn and Walters 1992). Although often uncertain, *h* is a critical parameter in predicting stock dynamics when confronted with exploitation, as high steepness can enable stock persistence at higher rates of fishing and can shorten rebuilding times for overexploited stocks. The difficulty in obtaining accurate and precise estimates of *h* has been addressed in several recent studies (Conn et al. 2010; Lee et al. 2012; Shertzer and Conn 2012). The available data for Southern Flounder probably suffer from many of the issues described in these studies, most notably a lack of contrast in adult biomass during the time series, resulting in a high level of uncertainty in parameter estimates for the stock–recruit relationship. That said, flatfishes in particular are suspected to demonstrate high steepness ($h > 0.8$; Iles 1994; Myers et al. 1999) relative to most other marine fishes (mean $h \approx 0.7$; Forrest et al. 2010; Shertzer and Conn 2012). Indeed, Maunder (2012) estimated *h*-values close to 1.0 for the closely related Summer Flounder and suggested that if higher values of *h* could be confirmed, management reference points could use lower biomass targets to avoid the potential loss of fishery yield. Estimates of *h* for Southern Flounder could potentially benefit from the development of prior distributions constructed from meta-analyses (Myers et al. 1999; Forrest et al. 2010), life history frameworks (Mangel et al. 2010; Shertzer and Conn 2012), or evolutionary theory (He et al. 2006).

Assumptions and Limitations

With any model, the selection of parameters can dictate the output while also requiring additional assumptions. Our objective in this modeling exercise was to keep the model simple enough that the level of uncertainty in model input parameters did not account for large deviations in the outcomes. For example, although a stock–recruit relationship is not well defined for many fishes, including many flatfishes (Iles 1994), it is assumed that there is some dependence of recruitment on adult stock size for all stocks (Ricker 1954; Beverton and Holt 1957; Tyler 1992). Our use of the Beverton and Holt (1957) function permitted us to focus on the slope parameter (α) with only one other parameter (β; asymptotic recruitment) to estimate, which was likely approximated well based on the available data for Southern Flounder, including several estimates of age-0 recruitment that were similar in magnitude across the range of adult biomass. Although alternative stock–recruit relationships (e.g., Ricker and Shepherd) may be applicable to Southern Flounder, there is no evidence for overcompensation or other dynamics that would necessitate a more complex model. The large variance around our estimate of α facilitated the exploration of several plausible *h*-values to determine the effect of steepness on achieving reference stock levels under different harvest scenarios that were specific to assumed aspects of Southern Flounder life history and demography.

We modeled Southern Flounder growth, natural mortality, and fishery selectivity as functions of age/size following relationships used in the most recent stock assessment in North Carolina (Takade-Heumacher and Batsavage 2009). Although we did not explicitly evaluate their impact on sustaining target biomass levels, we acknowledge that deviations from assumed growth and natural mortality relationships would likely modify the effects of steepness and cryptic biomass that our model revealed. Similarly, shifts in fishery selectivity toward younger or older ages could amplify or diminish the influence of cryptic biomass on stock persistence. While our assumptions about Southern Flounder growth dynamics and fishery selectivity have empirical support, the timing and magnitude of natural mortality are poorly understood. As part of a comprehensive stock assessment, exploration of the sensitivity of Southern Flounder stock dynamics to variation in vital rates and size/age selectivity during harvest would be valuable.

Management Implications

There are several possible benefits of a cryptic biomass of adults that are mostly unavailable to harvest. Egg production in fish increases exponentially with body length, so larger adults contribute disproportionately greater numbers of offspring. A growing body of evidence also indicates that repeat spawners (second and third spawning events) generate greater larval production (Trippel 1998), which could be partly related to the potential for production of more viable offspring by larger and older females as has been shown in the genus *Sebastes* (Berkeley et al. 2004; Birkeland and Dayton 2005; Hixon et al. 2014; but see Marshall et al. 2010). Thus, a similar amount of biomass of larger, older female Southern Flounder could conceivably make disproportionately greater contributions to recruitment than younger, smaller mature females. Protecting some portion of adult biomass from harvest also avoids the destabilizing effects of age truncation that can occur through removal of unique genetic and behavioral components of the stock (e.g., Hauser et al. 2002) and provides for temporal buffering to variable environmental conditions (Botsford et al. 2014). Given that Southern Flounder collected in offshore habitats are, on average, larger and older than fish in the estuary, a cryptic offshore stock component could provide many of these benefits.

If the existence of a stock component that remains in offshore habitats can be confirmed for Southern Flounder, the fishery management plan should include strategies to (1) manage harvest rates in the estuarine fishery to achieve target levels of escapement and (2) ensure minimal harvest of adults from offshore habitats, allowing these areas to essentially function as a marine reserve. Most fisheries have historically concentrated effort on removing the largest individuals from a stock; however, there is a growing number of contemporary fisheries that harvest immature life stages and protect larger, mature individuals. For example, several sciaenid species (e.g., Red Drum *Sciaenops ocellatus*) along the U.S. Gulf of Mexico and South Atlantic coasts are managed using slot limits that restrict both minimum and maximum sizes of fish that can be landed. Harvest rates (*F*) on younger, smaller individuals are managed to achieve specific escapement targets, allowing fish to advance to sizes at which they are afforded protection (see SEDAR 2015 for details on Atlantic Red Drum management). Resurgent interest in rebuilding and conserving population age structure has led to calls for more widespread application of slot limits as a fishery management tool to take advantage of high levels of reproductive output from older, multi-year spawners and to protect against recruitment failure (Gwinn et al. 2015).

At present, empirical evidence is lacking to confirm the fraction of adult Southern Flounder that may remain cryptic to harvest. The fact that the North Carolina fishery has avoided collapse despite estimates of exceedingly high rates of removal ($F > 1.5$) by the estuarine sector since the early 1990s suggests that some form of larval subsidy from a stock component exposed to low or no harvest is likely. The model results presented here predict that high estuarine harvest rates can be sustained by a combination of high steepness in the stock–recruit relationship and a moderate amount of adult biomass that is not subject to fishery exploitation. Likewise, White (2015) used a generic age-structured model to predict that, for fish with an ontogenetic migration pattern similar to that of Southern Flounder, high exploitation rates on juveniles in nursery habitats could be sustained if adults receive protection from a spatial reserve. In light of the complex life histories and patterns of spatial connectivity observed in other flatfishes (e.g., Metcalfe 2006), Southern Flounder would benefit from focused efforts to determine adult residency in offshore habitats and their potential function as spatial reserves.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.