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Habitat triage for exploited fishes: Can we identify essential "Essential Fish Habitat?"

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Abstract

There is little doubt that estuarine habitat is important for some exploited fish species, at some times, and in some places. However, it is also clear that we do not have enough resources to conserve or restore all estuarine habitat. Consequently, a simple, quantitative and transparent approach to prioritizing estuarine habitat management is required. Here, we present a general framework for identifying critical habitats of exploited fishes. Our approach requires three basic steps: (1) develop stage-structured models and identify sensitive life history stages; (2) determine what habitats, if any, are important to these stages; and (3) identify sites in which high densities of critical life stages occur in important habitat. We will illustrate the utility of this approach using red drum, *Sciaenops ocellatus*. Results of a simulation-based sensitivity analysis of a stage-structured matrix model show that most of the variability in population growth rate (λ) of red drum is explained by larval and juvenile survival rates. Thus, this approach indicates that larval/juvenile red drum habitat should be given higher priority for conservation and/or restoration than habitats used by other life history stages. To illustrate the potential importance of juvenile habitat to red drum, we modeled the growth of a hypothetical red drum population using different population matrices as manifestations of varying habitat conditions. These numerical experiments revealed that restoration of both marsh and seagrass habitats would yield a ca. 24% increase in post-settlement survival and would result in a ca. 2% increase in λ—an increase sufficient to stem a long-term population decline. Our results illustrate that protection of fish habitat depends not only on protecting sites where fish occur but also on protecting the ecological processes that allow populations to expand. Quantitative and synthetic analyses of ecological data are a first step in this direction.
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1. Introduction

The state of the world's marine fisheries has been the subject of much recent attention (Botsford et al., 1997; Pauly et al., 2002; Christensen et al., 2003; Myers and Worm, 2003). In the U.S. more than one-third of fish stocks are overfished (NMFS, 2003), and an additional ca. 50% are considered fully exploited (NMFS, 1999)—a condition that historically precedes overfishing (Garcia and Newton, 1997). While the role of fishing in the demise of fish populations is clear (e.g., Jackson et al., 2001; Pauly and Maclean, 2003), it is also apparent that a number of other human activities have contributed to and may be preventing the recovery of fish stocks (Ruckelshaus et al., 2002; Hilborn et al., 2003). Pollution, for instance, may severely reduce the number of viable offspring fish can produce (Johnson et al., 1998), and thus while harvest may cause an initial decline, a reduction of fishing, alone, would not be sufficient to rebuild depleted populations. Similarly, centuries of fishing in New England have reduced groundfish stocks to a small fraction of their historical abundance, but significant alteration of benthic habitats used by fishes (Levin et al., 2002; Steneck et al., 2002)

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could alter the course of recovery for a number of species (Mangel, 2000).

Fishery problems require us to deal with a network of interactions within dynamic ecosystems. Perhaps, the most basic of these interactions is the relationship between fish and their habitat. High-quality habitat is a fundamental requirement for reproduction, growth, migration and persistence of fish populations. With the passage of the Sustainable Fisheries Act in 1996, significant new opportunities and challenges to protect the habitat of marine and anadromous fish have emerged. Starting in 1998, all federal fishery management councils were charged with the task of modifying their fishery management plans such that the essential fish habitat (EFH) for each managed species is identified. Moreover, threats to EFH and steps necessary to ameliorate those threats now have to be determined by fisheries management councils. The codification of EFH holds the promise to change fishery management by making habitat considerations a key part of management decisions.

The Sustainable Fisheries Act defines EFH as "those waters and substrate necessary to fish for spawning, breeding, feeding and/or growth to maturity." Clearly, the ability of fisheries managers to identify EFH depends on knowledge of what habitats fish use. Researchers typically describe habitats of organisms based on attributes known to be ecologically meaningful. For fishes, such attributes as structure, hydrodynamics and general hydrology usually form the corpus of most fish habitat descriptions (e.g., McCain, 1998). However, since all habitats used by all life history stages are included in EFH descriptions, it is defined very broadly. Pacific salmon freshwater EFH, for example, includes all those streams, lakes, ponds, wetlands, tributaries, and other water bodies currently and historically used by salmon within Washington, Oregon, Idaho, and California (Roni et al., 1999). Similarly, EFH for numerous groundfish species is identified only generally, and consequently, EFH for groundfishes of the U.S. west coast includes all waters of the U.S. Exclusive Economic Zone along the Pacific coast of the U.S. (McCain, 1998).

While accurately identifying the habitats used by each life history stage of fish is an essential first step in determining EFH, simply identifying the habitat fish utilize is inadequate. Habitat may not be particularly important during a particular life history stanza of fish (Petrik et al., 1999) and/or existing patterns of distribution may tell us little about what habitats the fish actually prefer (Beck et al., 2001). Certainly, declaring all habitats used by fish as "essential" could be considered a form of precautionary management; however, such a broad approach does not allow for prioritization of habitat conservation or restoration. Instead, prioritization of habitat management requires quantitatively placing habitat effects occurring at specific life history stages in the context of the entire life cycle.

Here, we outline a three-step approach to EFH designation that allows resource managers to prioritize among life history stages and habitats. Using red drum, *Sciaenops ocellatus* (Sciaenidae) as a model species, we (1) develop a stage-structured matrix model (Caswell, 2000a); (2) use the model to identify sensitive life history stages; and (3) determine what habitats, if any, are important to these stages. We then use this model to estimate the potential responses of red drum populations to habitat restoration, using Galveston Bay as an example.

2. Study species

Red drum are an estuarine-dependent fish common to the Gulf of Mexico and southeastern U.S. Historically, red drum were subjected to an intense commercial fishery, and presently this species supports an important recreational fishery. Red drum spawn during late summer and early fall in nearshore waters near tidal passes and inlets. Eggs and planktonic larvae are carried by currents into estuaries (Peters and McMichael, 1987; Holt et al., 1989) where they settle at 6–8 mm SL into seagrass meadows or along the edges of salt marshes (Holt et al., 1983; Rooker et al., 1997; Stunz et al., 2002). They remain in these structured habitats during early juvenile stages (≤40 mm) (Holt et al., 1983; Rooker et al., 1998a,b) and occur commonly in estuaries until they reach age 4 (Pattillo et al., 1997). Red drum appear to have a maximum age of about 39 years (Porch, 2000).

We chose to focus on red drum for two reasons. First, the recreational fishery for red drum is socially and economically important throughout the Gulf of Mexico and red drum is among the most targeted species in the region (Scharf, 2000). Second, a number of researchers have estimated key demographic rates (Rooker et al., 1998a,b, 1999; Scharf, 2000; Stunz and Minello, 2001) and investigated habitat associations (Holt et al., 1983; Rooker and Holt, 1997; Rooker et al., 1998a,b; Stunz et al., 2001, 2002) for red drum making it possible to parameterize a stage-structured model.

3. Model development and implementation

To construct a stage-based matrix model, data on rates of fecundity and survival are required (Caswell, 2000a). Fortunately, much of the data necessary to calculate these vital rates for exploited fishes can be extracted from stock assessments conducted by NOAA Fisheries (National Marine Fisheries Service). To construct the population matrix, we first calculated age-specific survival of fish 0–9 years old and of fish 10+ years old by using estimates of the number of female red drum at ages 1–9 and ≥10 years old from 1979 to 1997 obtained from Porch (2000). We then

calculated the proportion of individuals in each year class in year t that were still alive in year $t + 1$. Survival in each class was considered to be the mean of ages that comprised that class (Table 1).

Because early post-settlement mortality is high, we established an early post-settlement stage. We based our estimate of survival of this stage on the situation in Galveston Bay, TX (see description of Galveston Bay below). The average survival rate of red drum in Galveston Bay requires knowledge of the areal extent of major habitats used by post-settlers, the densities of fish in these habitats, and habitat-specific survival rates. The average of the product of habitat-specific survival rates and the proportion of fish in each habitat is an estimate of overall post-settlement survival for the estuary. We used estimates of density in seagrass, marsh edge and unvegetated habitats (the major habitats used by post-settlement red drum in Galveston Bay) reported by Stunz et al. (2002). Areal extent of each habitat category was extracted from Clark et al. (1999) and White et al. (1993), with the assumption that the marsh edge constituted 15% of the total marsh area and that it was available to red drum 80% of the time (Minello and Rozas, 2002). We also considered only shallow (<1 m) nonvegetated habitat in our estimates. Rooker et al. (1999) estimated mortality rates of newly settled red drum in seagrass as ca. 13% per day. Because Stunz and Minello (2001) did not observe a significant difference in predation rates between marsh and seagrass habitats, we used this same value for marsh edge habitats. Rooker et al. (1998a,b) found mortality was 3.5 times greater in unvegetated than in vegetated habitats, and thus we assumed a mortality of 45.5% per day in unvegetated habitat. Based on the above assumptions, we estimated an average 30-day survival of post-settlement red drum of 0.0024 (Table 1).

We used an instantaneous daily mortality rate of 0.27 for red drum larvae (Bruce Comyns, pers. comm.), yielding an average survival rate of 0.003 for a 30-day larval period. This instantaneous mortality rate is slightly higher than the mean morality rate for marine fish larvae of 0.24 (Houde, 2002), but similar to rates estimated for other species in the northern Gulf of Mexico (Comyns et al., 2003).

We next estimated the annual reproductive output of female red drum. Following Porch (2000), we estimated the frequency of spawning as:

$$\text{frequency} = (1.07 + 0.847 \ln(a)^2) \tag{1}$$

where a is age in years. The number of eggs in each spawning event is given by the following equation:

$$\text{egg number} = e^{14.57 - 19.5/a^2} \tag{2}$$

Porch (2000) estimated the fraction of females that are mature to be 0, 0.05, 0.25, 0.62, 0.9, and 1.0 for ages 0–6+. Average annual fecundity is thus the product of Eqs. (1), (2) and the proportion of females that are mature.

Using age-specific estimates of demographic rates, we created a stage-based matrix consisting of six stages: larvae and pre-settlement post-larvae, early post-settlement (30 days), young-of-the-year (30–365 days), sub-adults (1–2 years), adult 1 (3–9 years), and adult 2 (10+ years) (Table 2). Stage-based matrices require calculation of both the probability of remaining in a stage (P_i) as well as the probability of moving from one stage to the next (G_i). Following Crouse et al. (1987), these probabilities were calculated as follows:

$$P_i = \left(\frac{1 - p_i^{d_i - 1}}{1 - p_i^{d_i}} \right) p_i \tag{3}$$

$$G_i = \frac{p_i^{d_i}(1 - p_i)}{1 - p_i^{d_i}} \tag{4}$$

where p_i is the probability of red drum surviving during stage i and d_i is stage duration. The resulting stage-based matrix is shown in Table 2.

The stage-structured matrix produced by these demographic rates yielded a λ (the dominant eigenvalue of the matrix and the average long-term population growth rate) of 0.989. As a means to determine the degree to which this model captured the actual dynamics of red drum populations, we independently estimated λ from a series of population censuses (Dennis et al., 1991) and compared this estimate to that generated from the matrix model. The procedure involves first selecting pairs of counts $N(i)$ and $N(j)$ from adjacent censuses i and j conducted in years $t(i)$ and $t(j)$. Next, transformed variables, x and y, are estimated as follows:

$$x = \sqrt{t(j) - t(i)} \tag{5}$$

Table 1
Summary of stage classes and demographic rates of red drum

Stage	Age	Stage duration	Mean (SD) survival	Variance survival	Fertility	Variance fertility
Larval	0	20–30 days	0.000304	0.150578	0	–
Post-settlers	0	30 days	0.002391	0.148848	0	–
Young-of-the-year	0	11 months	0.35 (0.026)	0.057609	0	–
Sub-adult	1–2	2 years	0.35 (0.078)	0.062345	10.87729	4.4
Adult 1	3–9	7 years	0.79 (0.074)	0.004663	3 422 000	1 368 800
Adult 2	10+	25 years	0.85	0.002186	15 206 937	6 082 775

Table 2
Stage-class population matrix for red drum based on the vital rates presented in Table 1

	Larval	Post-settlers	Young-of-the-year	Sub-adult	Adult 1	Adult 2
Larval	0	0	0	10.8	3 421 999	15 206 936
Post-settlers	0.000304	0	0	0	0	0
Young-of-the-year	0	0.002391	0	0	0	0
Sub-adult	0	0	0.35	0.2595740	0	0
Adult 1	0	0	0	0.0909998	0.739643	0
Adult 2	0	0	0	0	0.049715	0.847375

$$y = \frac{\ln\left(\frac{N(j)}{N(i)}\right)}{x} \qquad (6)$$

Pairs of x and y are then used to perform a linear regression of y on x while forcing the regression line through the origin. The slope of the regression is an estimate of μ, a descriptor of the mean change in population size. The mean squared residual of the regression is an estimate of σ^2, which governs how the variance of the distribution changes over time. Once μ and σ^2 have been estimated the average population growth rate, λ, can be estimated as follows:

$$\bar{\lambda} = e^{\mu + (1/2)\sigma^2} \qquad (7)$$

Using annual population counts of adult red drum from 1979 to 1997 (Fig. 1), we estimated an average λ of 0.991. Because this value and the estimate of λ from the matrix model (0.989) are comparable, it seems likely that the matrix model provides a reasonable conceptual framework from which to conduct our analyses.

4. Sensitivity analysis

We conducted a sensitivity analysis in which biological limits are placed on variable demographic rates

following the procedures outlined by Morris and Doak (2002). This approach involves randomly generating a large set of matrices ($N = 500$) each using different values for the demographic rates drawn from within reasonable limits for the rates. We then estimated a population growth rate (λ) for each matrix. Next, we performed regressions in which λ was the response variable and each vital rate was a single independent variable. The percentage of the variation in λ explained by each vital rate is an estimate of the relative importance of vital rates in causing variation in population growth (Morris and Doak, 2002).

We chose to simply draw from a normal distribution with a mean equal to the rate specified in the matrix models. Variance of survival rates was specified by:

$$\sigma^2(\mu) = \exp[2.231 \ln(\mu) - 1.893] \qquad (8)$$

Bradford (1992) developed Eq. (8) by examining the relationship between average mortality and variance of 97 fish species, and this approach has been used in other fishery applications of matrix models (e.g., Quinlan and Crowder, 1999). Estimates of variance in fecundity were derived from Wilson and Nieland (1994).

This analysis revealed that larval survival explained 42.9% of the variation in λ, and post-settlement survival explained 39% of the variation in λ (Fig. 2). This was 1 order of magnitude greater than the variation in λ explained by young-of-the-year survival, 2 orders of

Fig. 1. Estimated abundance of red drum from 1979 to 1997 in the Gulf of Mexico. Data extracted from Porch (2000).
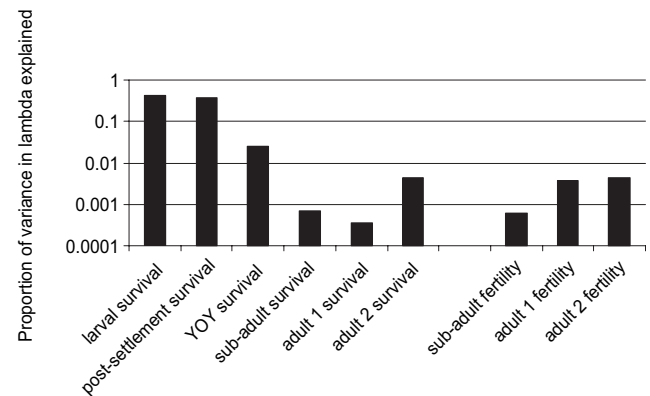

Fig. 2. Results of a life-stage simulation analysis showing the proportion of variation in λ explained by stage-specific survival rates.

magnitude greater than adult 2 survival, and 3 orders of magnitude greater than the variation in λ explained by sub-adult or adult 1 survival (Fig. 2). The sensitivities of fecundity parameters were low, explaining from 0.06% to 0.4% of the variance in λ (Fig. 2).

Another way to examine the importance of life history stages is to simply ask what value of λ could be generated with increases in each vital rate (with all other rates unchanged). Because traditional fisheries management focuses on reducing (adult) mortality, we asked what λ would be generated by our density-independent matrix model when mortality is reduced by 10%. Such changes in mortality rates show that substantial increases in λ could hypothetically be achieved by reducing mortality of larval and post-settlement red drum, while only modest improvements could be achieved by reducing mortality of older stages (Fig. 3).

5. Potential responses of red drum to habitat restoration

To heuristically examine the importance of habitat restoration for red drum, we modeled the growth of a hypothetical red drum population using different population matrices as manifestations of varying habitat conditions. For simplicity, we opted to focus on the post-settlement stage since our sensitivity analysis indicated it was an important life history stage and because habitat-specific mortality rates are available for post-settlement red drum. The approach that we use is highly stylistic and simplified (see assumptions below), but motivated by the situation in Galveston Bay, TX. The Galveston Bay complex is about 2020 km^2 and is the seventh largest estuary in the U.S. It is mostly shallow with some oyster reefs, dredge material areas, river channels and dredged navigation channels (Clark et al., 1999). *Spartina alterniflora* (smooth cord grass) is

the dominant shoreline vegetation and because of extensive tidal inundation, the marsh is available for use by nekton about 78% of the time (Minello and Webb, 1997). Coverage of marshes in Galveston Bay has declined by about 20% since the 1950s (White et al., 1993). Seagrasses, dominated by *Halodule wrightii* (shoal grass), historically occurred throughout Galveston Bay, but seagrass coverage has declined by 80% leaving seagrass only in the southwestern portion of the estuary (Pulich and White, 1991; Adair et al., 1994; Sheridan et al., 1998).

Seagrass and the edges of marshes appear to be important habitats for post-settlement red drum (Holt et al., 1983; Rooker et al., 1998b; Stunz et al., 2001, 2002), and thus we asked how population growth rate (i.e. λ) would change if marsh edge and/or seagrass habitats were increased to their coverage of the 1950s. To accomplish this, we re-estimated the bay-wide post-settlement survival we estimated for our matrix model (Table 1) with increased coverage of seagrass and/or marsh habitats. For the seagrass restoration scenario, we increased the coverage of seagrass 7.14-fold (White et al., 1993), with the corresponding decrease of unvegetated habitat. Similarly, for the marsh restoration scenario we increased marsh coverage by 22% and reduced unvegetated habitat by the same amount.

For the sake of simplicity, we assumed that red drum populations are not recruitment limited (sensu Roughgarden et al., 1988), and thus that an increase in seagrass coverage would result in an increase in fish density. We also did not include density dependence in this model, nor do we consider the effects of habitat restoration on any other life history stages. We also assume a closed population. While this assumption is almost surely violated, substantial genetic divergence among red drum populations suggests that demographic links among populations separated by 100s of kilometers may be minimal (Gold et al., 2001). Our model is meant to be conceptual rather than an application tool (Mangel et al., 2001). While our assumptions in combination with very crude estimates of average post-settlement survival limit the use of this model, our numerical experiments do serve to sharpen our thinking about the importance of restoration of essential fish habitat. Moreover, as data become available, it is a simple matter to modify this model to address specific management questions (Morris and Doak, 2002).

We estimated that an increase in marsh coverage to that of the 1950s would increase average post-settlement survival in Galveston Bay by about 6%, while an increase in seagrass coverage would increase average survival by nearly 20%. Restoration of both marsh and seagrass habitats would yield a ca. 24% increase in post-settlement survival (Fig. 4). The 6% increase in post-settlement survival associated with marsh restoration would result in a modest increase in λ from a current
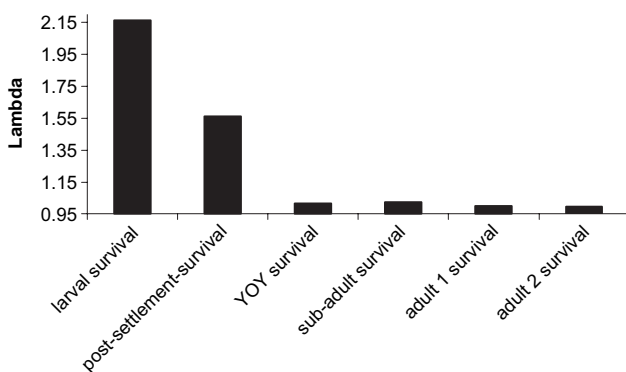
Fig. 3. The potential λ achieved when mortality of each life history stage is reduced by 10% (while others are held constant). Current λ is 0.989.
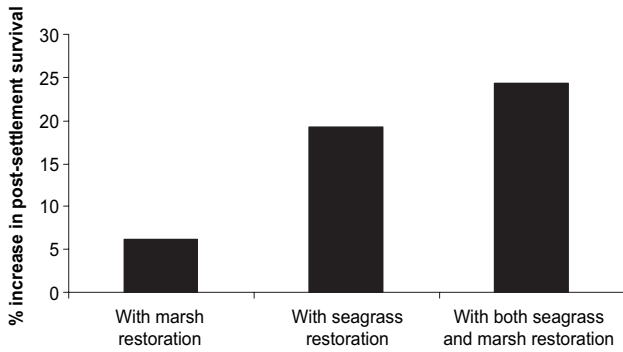
Fig. 4. The estimated percent increase in post-settlement survival of red drum in Galveston Bay, TX under various habitat restoration scenarios.

value of 0.989 to 0.9966 (Fig. 5). Restoration of seagrass would increase λ to >1, and re-establishment of both marsh and seagrass habitats would result in a ca. 2% increase in λ (Fig. 5).

6. Discussion

Conserving and/or restoring habitats are unquestionably important to the successful management of exploited fish stocks (Schmitten, 1999). Identifying what habitats each life stage of fish use is crucial as managers begin to employ ecosystem-based approached to fisheries management. However, an approach in which essential fish habitat is considered to be the sum of all habitats fish use during the course of their lives results in very broad EFH designations covering large swathes of estuarine and marine waters. For instance, in the Gulf of Mexico, EFH for red drum includes all estuaries and all marine habitats where red drum are known to occur (GMFMC, 1998). This issue is compounded because EFH is described not by species, but by fishery management plan. Since fishery management plans often contain more than one species, EFH, broadly defined, quickly becomes the entire U.S. exclusive
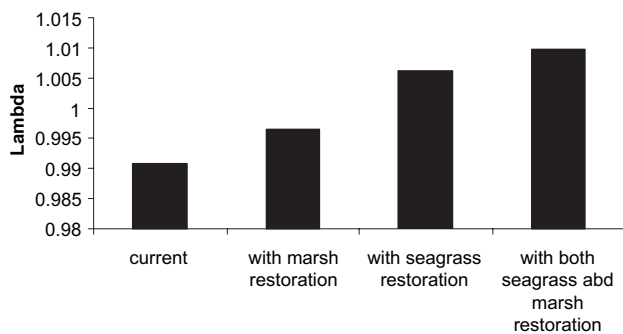
economic zone (McCain, 1998). Designating a habitat as essential simply because a fish occurs there belies the observation that some habitats may be more important to fish than others (e.g., Tupper and Boutilier, 1995), or that fish may not respond strongly to habitat (Petrik et al., 1999). Given the finite resources of management agencies, effective management of fish habitat requires prioritization, but a framework in which all habitats fish use are considered equivalent does not allow a science-based ranking of habitats.

In this paper, we present an approach for identifying habitats of high conservation priority for fishes of conservation and management concern. The approach we propose is conceptually simple, transparent and flexible enough to accommodate diverse life histories (Caswell, 2000a). The matrix model-based methodology we employed here is a now standard technique in conservation biology; however, any age- or stage-based model could be used as the basis for habitat prioritization. We contend that whatever approach is used, it is crucial to quantitatively place habitat effects occurring at specific life history stages in the context of the entire life cycle. We propose that essential EFH is habitat that has significant impacts on vital rates of sensitive life history stages. Defined in this manner, small changes in the quantity or quality of essential fish habitat will have large impacts on population dynamics.

Our prescription for identifying valuable habitats requires some form of sensitivity analysis to identify important life history stages. We used a simulation-based approach that expressed variation in λ as a function of variation in vital rates. Our analysis shows clearly that a great deal of the variation in population growth rate of red drum can be explained by variation in both larval and post-settlement survival. Assigning "importance" to a life stage using this approach assumes that past patterns of variance will continue into the future, and that some management intervention could change the mean value of the vital rate (Caswell, 2000b). In the case of red drum, post-settlement survival appears to consistently vary by an order of magnitude among habitats of varying structure (Stunz and Minello, 2001). Thus, in this instance, the simulation approach appears to identify a life stage where habitat actions should yield substantial conservation benefits. In contrast, even though larval survival made a large contribution to variability in λ, it may be an unattractive target for management. Larval survival is potentially the function of stochastic environmental forcing (Fromentin et al., 2001), and thus management intervention aimed at this life history phase may be swamped by environmental noise.

Importantly, a number of approaches to sensitivity analysis exist (Morris and Doak, 2002), and there is some disagreement about what approach is best (Mills et al., 1999; Caswell, 2000b; Wisdom et al., 2000). For instance Caswell (2000b) advocates elasticity analysis which

Fig. 5. The estimated λ of red drum under various habitat restoration scenarios in Galveston Bay, TX.

examines the functional relationship between λ and vital rates—a relationship that is a fundamental property of the life history of the organism, independent of the variance in the vital rates. However, elasticity analysis identifies life history stages as potential management targets without regard to how feasible it is to make changes in a vital rate. For example, in red drum, survival of adults offshore is relatively high, and because fishing mortality offshore is very low (Porch, 2000), there is little potential to improve λ by increasing its value. It is not our goal in this paper to advocate one type of sensitivity analysis over another; however, we do emphasize the importance of carefully using sensitivity analysis to identify life history stages as potential management targets.

Moving beyond the status quo of EFH to an effective framework for prioritizing habitat protection/restoration requires data to parameterize life cycle models. While a life cycle modeling approach is data intensive, for exploited fish species, estimates of fecundity and adult survival are available in most stock assessments. Unfortunately, for most species, data on juvenile survival are lacking, and habitat-specific survival and estimates of the variability of these rates are even more rare. Thus, part of the benefit of attempting to parameterize a life cycle model is that it identifies key data gaps and should help guide future research. While data may be lacking, using only rough estimates of vital rates, it should be possible to improve habitat protection under EFH. In the worst case, knowing only average adult survival, age at maturity, and an estimate of λ, it is possible to calculate elasticities of adult and juvenile stages (Heppell et al., 2000). Since these basic estimates can be obtained for nearly all exploited species, a broad prioritization of habitat conservation among life history stages is possible with existing information.

Interest in conserving and managing the world's fisheries is intense and widespread, but limited time and money require the judicious use of these resources. Simple assessments that produce broad EFH designations may have heuristic appeal, but do not aide, and may actually hinder, the work that needs to occur (Beck et al., 2001). By understanding what habitats fish use, the demographic rates associated with these habitats, and the factors that make some habitats more valuable than others, it will be possible to make more efficient use of limited resources. On the other hand, when all habitats are considered as EFH, prioritization becomes a purely political, rather than scientific, process. Without the appropriate science, a purely political process is unlikely to be efficient (i.e. produce the greatest increase in λ per expended resource), and may not be effective (i.e. protect the truly critical habitats). Importantly, we are not suggesting that we need to wait until more data become available before we designate EFH. Clearly, such a course would be imprudent. Instead, we suggest that the prudent course is to make use of current knowledge, put in the framework of a life cycle model. While initially such an approach may be rough, it acknowledges that conservation of exploited fishes depends not only on protecting sites where fish occur, but also on protecting the ecological processes that allow populations to expand (or at least persist). Quantitative and synthetic analyses of ecological data are a first step in this direction, and ultimately, conservation of exploited fishes will rest upon our ability to understand how changes in habitat and harvest interact with each other and natural ecological processes affect fish populations.

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