LIFE HISTORY STRATEGIES, POPULATION DYNAMICS, AND CONSEQUENCES FOR SUPPLEMENTAL STOCKING OF TARPON

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ABSTRACT

Release of hatchery-reared fish is viewed as a potential means to supplement coastal fish stocks, yet the viability of such programs has not been explored either theoretically or empirically. Here we examine implications from life history theory and results from population simulation models to examine the relative impact of alternative ecological and management scenarios on tarpon abundance. Life history theory predicts that "periodic species" (long-lived organisms with high fecundity) should experience large inter-annual variation in recruitment in response to density-independent environmental factors that operate on large scales. Because tarpon possess periodic life-history attributes, population dynamics should reflect strong recruitment episodes that ultimately are driven by climatic/environmental variation. Density-dependent mechanisms probably influence growth and survival of early life stages only during intermittent periods of high recruitment success. To examine these ideas, we configured an age-based matrix model to reflect tarpon life history. We simulated 50-year time series with or without density dependence and with or without supplemental stocking of early or late juvenile fish. Stocking large numbers of age-30 d fish had a negligible effect (1% change) on the abundance of age 20-22 fish, a typical adult cohort, but the addition of density dependence caused a 35% average decline in cohort abundance. Stocking large numbers of age-65 d fish increased the abundance of the age 20-22 cohort by 8%, but this benefit disappeared under an assumption of density dependence. Stochastic inter-annual variation in larval survival had a large negative effect on population abundance. Because life history theory predicts that tarpon should be strongly influenced by large-scale environmental variation, supplemental stocking would be more effective when fish are released at advanced size/age and when environmental conditions dictate low natural recruitment. Even stocking at advanced age could have uncertain and potential marginal benefits. Changes in survival rates of early life stages had a much greater effect on population abundance than either supplemental stocking or density dependence. A 1% increase in survival rate of any given early life stage caused a tenfold increase in adult

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cohort abundance. To increase tarpon stocks, protection of adult breeding stocks and restoration/enhancement of coastal habitats essential for juvenile tarpon provide a more viable strategy than supplemental stocking.

INTRODUCTION

Prior to the 1960s, tarpon were abundant in Texas and supported a thriving sportfishery at Port Aransas and several other coastal locations. The decline and virtual disappearance of tarpon from Texas coastal waters during the 1960-70s was poorly documented and has not been explained, although many theories have been proposed. In recent years, tarpon began to appear in Texas waters during the summer, but catch rates remain far below values reported during the period 1930-1960, and most tarpon are encountered offshore. Much interest now exists for the reestablishment of a tarpon sportfishery in Texas coastal waters. A management option discussed with increasing frequency is population enhancement via supplemental stocking with hatchery-reared fish. Because the fates of hatchery-reared fish and their contributions (relative to natural production) to adult stocks remain undocumented, stocking programs for enhancement of marine fish populations are controversial (Grimes 1998).

Here we examine the potential for supplemental stocking to enhance tarpon populations. We base our analysis on life history theory: the manner in which populations with different reproductive and demographic characteristics respond to environmental variation. We first review fundamental relationships between life history strategies and population dynamics in response to environmental variation. We rely heavily on the triangular model of life history evolution developed by Winemiller and Rose (1992). We then summarize the life history attributes of the tarpon and place it within the framework of the triangular model. Finally, we report results from a series of matrix model simulations that examine the relative effects of supplemental stocking, density dependence, and recruitment variation on population abundance.

Life History Theory and Population Dynamics

Life-history strategies result from correlations among organismal characteristics that affect fitness (reproduction and survival). Comparative studies have produced a robust pattern of life-history strategies observed among fishes, with three primary life-history strategies defining the endpoints of a triangular continuum (Winemiller 1992, Winemiller and Rose 1992). One endpoint, the opportunistic strategy, is defined by early maturation at small sizes, production of small clutches of eggs or embryos at frequent intervals, and long reproductive periods. A second endpoint, the equilibrium strategy, is characterized by production of relatively small clutches of large eggs, extended periods of spawning or gestation, and well-developed parental care. A third endpoint, the periodic strategy, is associated with fishes that delay maturation until achieving intermediate or large size, produce large clutches of small (often pelagic) eggs and larvae, and have high mortality and growth rates during early life stages. Tarpon clearly possess the features of a an extreme periodic strategists (outlined below).

According to the triangular model, the opportunistic-strategy is associated with high maximum intrinsic rate increase (r_{max}) and rapid population turnover. Populations with early maturation, high reproductive effort, and high r_{max} should be efficient colonizers and thus common in frequently disturbed habitats (e.g., mosquitofish, *Gambusia* spp.). These populations also can compensate for high adult mortality. Thus, these populations are resilient and the opportunistic strategy should be favored in dynamic (especially stochastic) habitats (e.g., coastal marshes) and in the face of high predation risk.

Equilibrium fishes are larger and more advanced at the onset of independent life. Marine ariid catfishes (oral brooding of a few large eggs) and live bearing fishes with long gestation periods and large neonates (e.g., many sharks) exemplify the equilibrium strategy. The equilibrium strategy should be favored in resource-limited, density-dependent settings (e.g., K-selection model of MacArthur and Wilson 1967). Compared with opportunistic and periodic strategists, equilibrium strategists should have lower recruitment variation and conform better to stock-recruit models. Low fecundity in equilibrium strategists is compensated by higher survivorship, especially among early life stages.

Tarpon and other periodic-strategists gain two benefits from delayed maturation and large adult body size: the capacity to spawn large numbers of eggs, and enhanced adult survival (larger fishes escape a wider range of gape-limited predators and can migrate further faster). Periodic fishes respond to large-scale spatial heterogeneity by spawning huge numbers of pelagic eggs, at least some of which thrive once favorable locations or periods are encountered. Even so, survival rates of early life stages are extremely low and variable (Bailey and Houde 1986, Rothschild 1986). The relatively few fortunate larvae that encounter areas of high resource density may achieve rapid growth. Coastal upwellings, gyres, convergence zones, and other oceanographic features create patterns of heterogeneity among physical parameters, primary production, and zooplankton densities. Estuaries used as nurseries by marine species are very heterogeneous. Large clutches of small pelagic eggs probably enhance dispersal capabilities, and increase the probability that at least some larvae will settle into suitable habitats. Over the long-term, mortality due to settlement in hostile habitats (advection) is balanced by survival benefits derived from recruitment of a certain fraction of larval cohorts into suitable regions or habitats (Winemiller and Rose 1993).

Life history tradeoffs associated with the triangular model can be derived from demographic relationships based on *r*, the intrinsic rate of natural increase (Southwood et al. 1974). We can approximate r as ln ($\Sigma l_x m_x$)/T, where l_x is age-specific survivorship, m_x is age-specific fecundity, and T is mean generation time. Thus the growth rate of a population or lineage is directly influenced by tradeoffs among fecundity, survivorship, and the mean generation time. Other life history parameters have positive or negative correlations with these fundamental parameters (e.g., age of maturation is positively correlated with generation time). Averaged over many generations, l_x, m_x, and T must balance, or a population eventually will decline to extinction or grow exponentially.

Following this model, the periodic strategy corresponds to high fecundity, long generation time (delayed maturation), and low juvenile survivorship. Large body size not only enhances adult survivorship, but also allows storage of biomass/energy for future reproduction. Reproduction by periodic strategists often coincides with favorable conditions, when they occur, that facilitate growth and survival of early life stages. Correlations between parental stock densities and densities of recruits have been shown to be minimal in commercial marine stocks (Hilborn and Walters 1992, Rose et al. in press), virtually all of which correspond to the periodic strategy. The periodic strategy typically is associated with high inter-annual recruitment variation in response to large-scale environmental variation, and generations are often recognized as discrete annual cohorts that may dominate populations of these long-live species for many years. Recruitment frequently depends on climatic conditions that influence water movement, egg/larval retention zones, productivity, and other environmental factors that determine early growth and survival (Rothschild 1986, Myers et al. 1990). For periodic fishes, the variance in larval survivorship that serves as input for models projecting population dynamics lies beyond the limits of precision and accuracy of our measurement. Even under the most favorable conditions, the great majority of eggs and larvae fail to survive for even a few days. Because recruitment is largely determined by unpredictable inter-annual and spatial environmental variation, the minimum density needed to ensure strong recruitment is impossible to determine with precision.

Tarpon Life History

Despite the fact that tarpon (*Megalops atlanticus*) are one of the most popular sports fish in the world, information on their life history and population dynamics have only been gathered recently (Cyr 1991, Crabtree et al. 1997). Tarpon possess all key characteristics of the periodic life-history strategy. Most Florida and Caribbean tarpon mature by about 10 years (0.8 – 1.2 m fork length, FL) and can survive for over 50 years (> 2.0 m FL), with females larger than males. Batch fecundity ranges from 1 million to over 20 million eggs, with larger females having higher fecundity according to the relationship log(Fecundity) = 5.284 + 1.034 x log(Weight in kg) (Cyr 1991). Spawning is seasonal in Florida (April – July) and essentially year-round in Costa Rica (Crabtree et al. 1997). The number of spawning bouts per year by individuals is not known. Larvae may spend several months in the marine pelagic environment as nonfeeding leptocephali. Based on information for other periodic-type marine fishes, survivorship of larval tarpon is presumed to be extremely low. At about the time of metamorphosis to juvenile morphology, young tarpon drift or migrate into coastal passes (Shenker et al. 1995) and take up residence in coastal marshes where they remain for an unknown period (perhaps 1-3 years) before migrating between coastal inland and offshore waters. Survivorship of subadults and adults has not been estimated, but given the species' longevity is assumed to be high in the absence of fishing mortality.

Simulation Models of Population Dynamics

Population dynamics can be modeled by a variety of conventions, each with its own strengths and limitations. Stock-recruit models are used to interpret recruitment dynamics based on adult stock abundance and assumptions about density dependence. The advantage of this approach is that little information is required about life history and ecology. The obvious disadvantage is that gross assumptions about density dependence are incorporated in a small number of parameters that define the predictive relationship. At the other end of the modeling spectrum are individual-based models, or IBMs. These population models often simulate life history and ecological relationships in great detail. The origins, survival, growth, and fates of individual organisms are modeled with varying degrees of detail. The great advantage of this approach is that numerous assumptions can be stated in detail at fine scales of resolution, which allows greater interpretations about causal mechanisms (DeAngelis and Rose 1992). A major disadvantage of IBMs is the requirement for a great deal of ecological information in support of model development and testing.

An intermediate level of complexity for modeling population dynamics is obtained by age- or stage-based matrix models. Using Leslie Matrix projections, these models simulate population dynamics based on initial abundance, survivorship, and fecundity data for age classes or life stages. The basic Leslie Matrix model contains no elements of density dependence or environmental/demographic stochasticity. We modeled the population dynamics of a tarpon population using RAMAS-Age® (Akçakaya et al. 1999). This model employs several options to impose density dependence, migration, or stochastic influences on Leslie Matrix projections.

For our baseline condition, we first configured a tarpon population without influence from density dependence or significant demographic stochasticity (Table 1). The first age class combined the generalized hatchling and leptocephalus larval stages (1 - 30 days). The second age class combined postlarval and early juvenile early stages (30 - 65days). The third age class was late juveniles (65 days – 1 yr). The next two stages contained immature cohorts (2 - 4 and 5 - 7 yr). Each of the remaining 13 age classes contained units of 3 consecutive cohorts (8 - 10, 11 - 13, 44 - 46). Because mortality and survival rate information is lacking for tarpon, we estimated survival rates based on daily instantaneous mortality rate (M) estimates reported by McGurk (1986) for a variety of fish populations. Survival rate (S_x) = N_t/N_0, and $N_t = N_0e^{-Mt}$, where t is the time interval in days, N_0 is the intitial cohort, and N_t is the number of survivors following interval t. For larval tarpon, we derived a survival rate of 0.000027 from M= 0.35 for *Scomber scombrus* on the Atlantic U.S. coast. For all other stages, we derived values of M from McGurk's dry weight – natural mortality rate regression (McGurk 1986, Figure 1). Following McGurk (1986), we assumed dry weight is 20% of wet weight.

We assumed an average wet weight of 5 g for early juveniles (yielding M = 0.0075) and 50 g for late juveniles (yielding M = 0.005). We estimated average wet weights of larger tarpon in various age classes from the relationship derived by Cyr (1991, Figure III-12). Average fecundity of each age class was derived from the empirical relationship reported by Cyr (1991): Fecundity = 372,540(Age in years).

To draw inferences about the potential influence of various ecological factors and stocking practices, we compared a series of simulated scenarios: 1) weak density dependence, 2) stochastic survival rate for the larval stage, 3) supplemental stocking of early juvenile or late juvenile fish, and 4) enhanced survival of larval, early juvenile, and late juvenile cohorts. The baseline condition together with various combinations of these four components yielded 18 simulated scenarios (Table 2).

Density dependence was simulated using the Beverton-Holt stock-recruit (or diminishing returns) function in RAMAS-Age ($Z= 1/(\rho + k/E)$, in which Z is number of recruits, ρ is the reciprocal of the number of age-0 individuals produced, and k is a dimensionless parameter that determines the steepness of the function's ascent). Density dependence was simulated by setting $\rho = 1 \times 10^{-14}$ and k= 1.90.

A large stochastic influence on recruitment was simulated by setting the coefficient of variation (CV) for larval survival rate at 2.5 based on a normal distribution. Thus, in each time step of each simulation, larval survival changed to a new value randomly drawn from a normal distribution with a mean equal to the fixed value in the baseline scenario and CV = 2.5. This was the only stochastic feature of RAMAS manipulated for our simulations.

Table 1. Parameters used in the baseline matrix model simulation for tarpon population dynamics and variations used in 17 additional simulations. Survival rate estimates are

based on data reported by McGurk (1986); fecundity data are based on data reported by Cyr (1991).

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1. Baseline: no density dependence, no stochastic forcing, no stocking

Age class	Initial abundance	Survival rate	Fecundity
0 - 30 d	5×10^{12}	0.000027	0
30 - 65 d	1×10^{6}	0.065	0
65 d - 1 yr	65,000	0.160	0
2 - 4 yr	10,000	0.400	0
5 - 7 yr	4,000	0.680	0
8 - 10 yr	2,500	0.690	4,843,000
11 - 13 yr	1000	0.700	5,960,000
14 - 16 yr	700	0.710	7,078,000
17 - 19 yr	600	0.720	8,195,000
20 - 22 yr	500	0.730	9,313,000
23 - 25 yr	450	0.740	10,431,000
26 - 28 yr	400	0.745	11,548,000
29 - 31 yr	350	0.750	12,666,000
32 - 34 yr	300	0.755	13,783,000
35 - 37 yr	250	0.760	14,901,000
38 - 40 yr	200	0.765	16,019,000
41 - 43 yr	100	0.770	17,136,000
44 - 46 yr	50	0	18,254.000

2. Baseline + density dependence (Beverton-Holt, rho= 1×10^{-14}, k= 1.9)
3. Baseline + stock 250,000 “early” juvenile (30 - 65 d) fish
4. Baseline + density dependence + stock 250,000 early juveniles
5. Baseline + stock 25,000 “late” juvenile (65d - 1 yr) fish
6. Baseline + density dependence + stock 25,000 late juveniles
7. Baseline + double larval (0-30 d) survival rate
8. Baseline + double early juvenile survival rate
9. Baseline + double late juvenile survival rate

10 -18. Each of the above repeated + demographic stochasticity for larval survival rate (CV= 2.5, normal distribution)

Table 2. Summary of the response of the total population (including all age classes except larvae) from 16 simulated scenarios. Mean abundance is based on 100 simulations and a time span of 50 years.

Model	Mean abundance	Percent change
1. Baseline	1.50 x 10^{7}	
2. Density dependence	7.73 x 10^{6}	–48%
3. Stock early juveniles	1.88 x 10^{7}	+25%
4. Density-dep. + stock early juvs.	5.70 x 10^{6}	–62%
5. Stock late juveniles	1.77 x 10^{7}	+18%
6. Density-dep. + stock late juvs.	8.29 x 10^{6}	–44%
7. 2X larval survival rate	3.63 x 10^{9}	+24,100%
8. 2X early juvenile survival rate	2.15 x 10^{9}	+1,420,000%
9. 2X late juvenile survival rate	2.13 x 10^{11}	+1,419,900%
10. Baseline + stochastic larval survival	1.18 x 10^{4}	–99%
11. Stochastic + density dependence	6.51 x 10^{3}	–99%
12. Stochastic + stock early juveniles	2.60 x 10^{4}	–98%
13. Stoch. + den. dep. + stock early juvs.	1.60 x 10^{4}	–98%
14. Stochastic + stock late juveniles	1.30 x 10^{6}	–99%
15. Stoch. + den. dep. + stock late juvs.	1.30 x 10^{6}	–99%
16. Stochastic + 2X larval survival	3.91 x 10^{4}	–99%
17. Stochastic + 2X early juv. survival	1.55 x 10^{4}	–99%
18. Stochastic + 2X late juv. survival	1.41 x 10^{4}	–99%

Supplemental stocking of early and late juveniles was simulated using the migration option of RAMAS-Age. We performed two manipulations: addition of 2.5 x 10^{5} early juveniles (a quarter of the initial baseline abundance of this cohort), and addition of 2.5 x 10^{4} late juveniles (greater than a third of the initial baseline abundance of the cohort). By default RAMAS creates a minor random component during each time step, which yields variation around the mean of multiple runs with identical input data. We ran each simulated scenario 100 times for a period of 50 years. We then examined the mean abundance of the total population (minus the larval stage) after the final time step. To indicate responses by a typical adult cohort, we also examined mean abundance of the 20-22 yr class (near the middle of the range of age intervals). Mean abundance from each scenario was compared with the mean abundance from the baseline configuration. The magnitude of difference was expressed in terms of both absolute abundance and relative abundance (% change).

Simulation Results

The baseline configuration yielded a slight decline in population abundance after 50 years (lambda = 1.0009). Imposition of density dependence decreased both the total population and the age 20-22 class (referred to hereafter as “age-20 fish”) by 48% (Table 3).

Table 3. Summary of the response of the 20 - 22 yr age class from 16 simulated scenarios. Mean abundance is based on 100 simulations and a time span of 50 years.

Model	Mean abundance	Percent change
1. Baseline	8.95×10^3	
2. Density dependence	4.64×10^3	–48%
3. Stock early juveniles	9.05×10^3	+1%
4. Density-dep. + stock early juvs.	5.84×10^3	–35%
5. Stock late juveniles	9.63×10^3	+8%
6. Density-dep. + stock late juvs.	8.70×10^3	–3%
7. 2X larval survival rate	5.83×10^5	+6,414%
8. 2X early juvenile survival rate	5.84×10^5	+6,425%
9. 2X late juvenile survival rate	7.70×10^7	+860,235%
10. Baseline + stochastic larval survival	8.66×10^0	–99%
11. Stochastic + density dependence	3.92×10^0	–99%
12. Stochastic + stock early juveniles	1.75×10^2	–98%
13. Stoch. + den. dep. + stock early juvs.	1.74×10^2	–98%
14. Stochastic + stock late juveniles	2.70×10^2	–97%
15. Stoch. + den. dep. + stock late juvs.	2.68×10^2	–97%
16. Stochastic + 2X larval survival	1.31×10^1	–99%
17. Stochastic + 2X early juv. survival	2.04×10^1	–99%
18. Stochastic + 2X late juv. survival	1.78×10^1	–99%

Density dependence tended to have a stronger influence on population dynamics than massive supplemental stocking of early juveniles (1 - 30 d). Supplemental stocking of early juveniles without density dependence resulted in a 25% increase in total abundance and a 1% increase in age-20 fish relative to baseline. The combination of density dependence and stocking of early juveniles yielded a 62% decrease in the total population and a 35% decrease in the abundance of age 20 fish relative to baseline. Relative to density dependence without stocking, stocking of early juveniles with density dependence decreased the total population by 26% and increased age-20 abundance by 25%.

Supplemental stocking of late juveniles (30 - 65 d) caused an 18% increase in the total population an 8% increase in age-20 fish relative to baseline. In contrast, stocking of late juvenile fish with density dependence resulted in a 45% decrease in total abundance and a 3% decrease in abundance of age-20 fish relative to baseline. Relative to density dependence without stocking, stocking of late juveniles with density dependence increased the total population by 7% and increased age-20 abundance by 87%.

The forcing of stochastic dynamics on larval survivorship on the baseline scenario caused a 99% decline in the total population and abundance of age-20 fish. Similar results were obtained when the stochastic feature was combined with density dependence, stocking without density dependence, and stocking with density dependence (Table 2, 3). Apparently, our seemingly modest stochastic adjustments of the baseline larval survival rate resulted in numerous simulations in which early recruitment was insufficient to sustain the population (population crashes) and infrequent cases in which early recruitment was enhanced to a degree sufficient to sustain or enhance the overall population.

To estimate the potential effects of early life stage recruitment under favorable environmental conditions or habitat restoration, we simulated the effect of enhanced survival rates for larval, early juvenile, and late juvenile fishes. The effect of doubling our empirical estimates of survival rates on population abundance was several orders of magnitude larger than any of the other simulated components (Table 2, 3). Given the very large numbers of eggs produced by the adult population each year, seemingly minor increases in survival rates or early life stages can have profound positive influence on tarpon populations.

DISCUSSION

Detailed descriptions of tarpon population structure are lacking, but ample evidence indicates that fishes with periodic-type life histories (delayed maturation, high fecundity, long lifespan) experience large inter-annual variation in recruitment. During most years, survivorship of early life stages probably approaches zero in these populations. Only under particular environmental circumstances is above-average recruitment realized. These boom and bust recruitment dynamics imply high population variance in the reproductive success within and between years. Density-dependent factors probably affect the survival and growth of early life stages only during infrequent years with exceptionally high recruitment. During normal years with poor to average recruitment, density dependence is probably very weak or absent. Depending on key abiotic driving variables and species interactions, strong year classes could be affected by density-dependent processes over variable periods and regions. What are the implications of this life history strategy and mode of population regulation for the success of supplemental stocking programs for tarpon and other periodic-type fishes?

According to our tarpon model simulations, density dependence and stochastic variation in early recruitment have much greater influence on population abundance than massive supplemental stockings of juvenile fishes. As expected, stocking older fish had a greater per-capita effect on the population (the number of late juveniles stocked was 1/10 the number of early juveniles). However, the costs associated with rearing and releasing the massive numbers of late juvenile fishes required to enhance the population would likely be prohibitive. Large gains from stocking under the density-independent scenario were eliminated by the addition of weak density dependence. The addition of stochastic larval survivorship (simulating stochastic recruitment to age-1) completely eliminated the positive influence of age-1 stocking. Climatic and oceanographic conditions are probably the most important driving variables for early life stage success. Because environmental conditions responsible for poor or good early life stage survival are essentially unpredictable, there is little chance that the overriding influence of environmental stochasticity on the magnitude of stocking effect can be ameliorated.

Of course, simulation models cannot be expected to provide accurate and precise predictions of population dynamics. Instead, models allow us to examine relationships among key variables that influence dynamics. Our discussion of life history theory and our model simulations reveal some critical aspects of tarpon ecology that require careful consideration before initiating a supplemental stocking program in Texas or other locations. Clearly, the degree to which natural recruitment to juvenile age classes is influenced by stochastic factors needs to be evaluated carefully. If stochastic abiotic factors indeed strongly influence recruitment, then supplemental stocking should have negligible influence on long-term population trends. Likewise, density dependence has the potential to negate any positive influence of supplemental stocking. We simulated strong density dependence and large supplementations of young fish to the natural population. For most periodic fish species, including tarpon, we have little or no knowledge of the degree that density-dependent mechanisms, such as food limitation or predation, influence recruitment dynamics (Rose et al. in press). Clearly, if density dependence is significant, it is highly variable in time and space. To detect and quantify this variation remains one of the greatest challenges of fisheries management.

Tarpon spawn offshore and, following variable periods in marine pelagic waters, metamorphosing larvae migrate or are transported through coastal passes and reside in coastal marshes (Crabtree et al. 1992, Crabtee 1995). Shenker et al. (1995, this volume) documented episodic strong recruitment into the Indian River Lagoon, Florida in association with a tropical depression. Apparently, the storm altered coastal currents in a manner that increased entry of larval tarpon into this coastal system. These kinds of unpredictable, large-scale events are believed to influence early life stage recruitment in marine fish populations (Rothschild 1986). In addition, stochastic abiotic factors can interact with biotic factors (e.g., food supply and predator densities) to influence recruitment dynamics of early life stages (Bailey and Houde 1989). Recently, Fromentin et al. (2001) analyzed 136 long-term time series of juvenile cod (11 populations) and found that population variability was a function of both density-dependent processes and the interaction between density-dependent processes and stochastic factors.

Scharf (2000) determined that periodic appearances of strong year classes of red drum (*Sciaenops ocellatus*) were positively correlated across estuaries in Texas, which suggested that factors determining distribution and abundance in this species vary on large spatial scales. Correlative evidence suggested density-dependent mechanisms influenced age-0 survival of red drum, and juvenile survival appeared to influence year-class strength. These patterns are consistent with predications about population regulation in periodic strategists, and the red drum certainly possesses all of the attributes of the periodic strategy. Scharf was unable to detect any effects from a decade of supplemental stocking of hatchery-reared juveniles on the abundance of age-0 and age-1 red drum in Texas. This finding is consistent with our theoretical arguments and predictions based on results from our model simulations.

By far, the greatest effect on our simulated population dynamics (100 to10,000-fold increase relative to baseline) was created by doubling the survival rates of early life stages. Smaller increases in survival rates of naturally produced larvae yielded similar positive effects. For example, a chronic increase in larval survival of just 1% increases age-20 abundance by 1,000% (tenfold) over baseline. Fisheries management is largely powerless to influence larval survival rates. However, a variety of management actions can potentially influence survival rates of juvenile life stages of tarpon. Juvenile tarpon inhabit freshwater and brackish coastal marshes. On Florida's east coast, water control structures often block the entrance of fishes and macroinvertebrates into coastal marshes and disrupt normal hydrodynamics (Lin and Beal 1995). These wetlands are essential habitat for young tarpon (Crabtree et al. 1997, Shenker et al 1995). Reduction of freshwater discharge to coastal habitats alters hydrology, salinity regimes, and system productivity, all to the detriment of juvenile fishes that exploit secondary production in these productive ecosystems. Actions that enhance or restore access to and the quantity and quality of essential juvenile habitat have far greater potential to enhance tarpon populations than supplemental stocking programs. A mere1% increase in late juvenile survival increases age-20 abundance by 2,224% (more than tenfold) over baseline.

We conclude that supplemental stocking, even on a massive scale, is unlikely to have a major effect on tarpon and other coastal marine fish populations with periodic life history strategies. Tarpon year classes are expected to be highly variable and strongly influenced by stochastic factors operating on broad spatial scales. Density-dependent processes probably influence early growth and survival under appropriate conditions during unusual years. Periodic strategists also are vulnerable to overfishing from which their populations recover slowly due their advanced maturation age and unpredictable recruitment dynamics (Adams 1980). Given the great natural potential for high recruitment under appropriate conditions, it seems unlikely that supplemental stocking with hatchery-reared fish can significantly impact tarpon stocks. The great mobility of tarpon (with potential for Gulf-wide movement) and regionally variable fishing mortality also make stocking programs risky investments. More ecological research and demographic analysis is needed before large investments are made in support of research on captive rearing and hatchery production. A more viable strategy for tarpon population enhancement would be to protect wild breeding stocks (as is being done currently in Florida and Texas) coupled with watershed and coastal habitat management to improve juvenile tarpon access to productive marsh habitats essential for their feeding, growth, and survival.

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