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Reproductive resilience or sweepstakes recruitment? Assessing drivers of lifetime reproductive success in exploited marine fish

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Abstract

Understanding the processes that drive reproductive success in marine fish stocks is critical to effective fisheries management. These processes can be difficult to investigate, especially in age-structured populations, because they occur at transgenerational scales. Reproductive success is often attributed to a small portion of the adult population (<0.01%) and thought to be driven primarily by random external factors, consistent with the concept of sweepstake reproductive success (SRS). A competing concept, the reproductive resilience paradigm, posits that fishes have evolved complex spawner-recruit systems to achieve lifetime reproductive success and maintain population stability within highly variable environments. Here, we examine these two concepts. First, we analyse the popular sport fish red drum (*Sciaenops ocellatus*, Sciaenidae), drawing on genetic and reproductive data to estimate a plausible range for the ratio of effective population size (N_e) to adult abundance (N_A) and to infer variance in lifetime reproductive success (V_k^*). Then, we synthesize available data and infer V_k^* for two other fishes that have N_e / N_A ratios reportedly >0.10, the southern bluefin tuna (*Thunnus maccoyii*, Scombridae) and the silver seabream (*Chrysophrys auratus*, Sparidae). Although commonly regarded as an SRS species, red drum did not meet the SRS criterion. Overdispersed V_k^* values were inferred for all three species, with those for red drum and silver seabream being dependent upon population-closure assumptions. Results are presented within the conceptual framework of reproductive resilience, considering the roles of random extrinsic forces versus evolved traits to achieve lifetime reproductive success and population stability in high and variable mortality environments.

KEYWORDS
effective population size, environmental variability, life history, reproductive success variance, spawning behaviour

1 | INTRODUCTION

Reproductive success is defined as the production of offspring that survive to reproductive age (Clutton-Brock, 1988). It is a biological process that drives population persistence and growth, and its relationship to the heritability of traits is strong (Stearns, 1992). When based on their adult to offspring size, marine species' life history strategies can be classified into two groups: (1) a fixed-ratio strategy, where offspring size is a constant fraction of adult size, similar to many terrestrial animals and associated with parental care, and (2) a small-eggs strategy, where offspring size is independent of adult size (Andersen et al., 2016). The fixed-ratio strategy is associated with Type I and II survivorships and the small-eggs strategy with Type III survivorship. Both strategies have resulted in healthy marine populations. Most marine fishes have the small-eggs strategy, which is hypothesized to have evolved to overcome high and unpredictable mortality rates and/or patchiness of prey resources at relatively large spatial scales (Stearns, 1992; Winemiller & Rose, 1992). The closest terrestrial equivalent to the small-eggs strategy is plants, which produce a large number of seeds, dispersed with the wind (Allen et al., 2017; Lowerre-Barbieri et al., 2017), similar to sessile invertebrates such as broadcasting oysters and coral.

The *sweepstake reproductive success* (SRS) hypothesis proposed that lifetime reproductive success (LRS) in large marine populations operates like a lottery, with a small and largely random chance of 'winning' due to stochastic external forces such as weather and oceanic currents determining offspring survival. It was introduced in 1994 (Hedgecock, 1994) and refined in 2011 (Hedgecock & Pudovkin, 2011). Although not stated explicitly, the SRS hypothesis draws an equivalency between 'large marine populations' and species with a small-eggs strategy. SRS offered a convenient explanation for several genetic patterns observed using the genetic tools of the time; specifically, the very-low ratios of (generation) effective population size, N_e, to adult census abundances, N_A, in populations of Pacific oyster (*Crassostrea gigas*, Ostreidae) and American oyster (*Crassostrea virginica*, Ostreidae), and microgeographic heterogeneity (chaotic patchiness) within populations of the barnacle (*Balanus glandula*, Balanidae) and northern anchovy (*Engraulis mordax*, Engraulidae) (Hedgecock, 1994; Hedgecock et al., 1994; Judge et al., 1988).

The SRS concept drew on a series of hypotheses associated with conditions encountered by larvae at first feeding: Hjort's first feeding hypothesis (Hjort, 1914), extended to the member–vagrant hypothesis (Iles & Sinclair, 1982), later incorporated into the match/mismatch hypothesis (Cushing, 1990), and linked to oceanographic concentration mechanisms by Lasker (1978) and Bakun (1996). However, only through relatively new technological advances can we now test those hypotheses at appropriate temporal scales, with emerging knowledge that larval dispersal and survival can be greatly affected by adult spawning site selection (Ciannelli et al., 2015; Lowerre-Barbieri et al., 2019), larval behaviour (Leis et al., 2015), and many other intrinsic factors, and that marine species often exhibit metapopulation structure, with differing degrees of non-local and natal recruitment among demes (Cadrin, 2020; Cowen et al., 2006; Heath et al., 2008).

The *reproductive resilience paradigm* (RRP, Lowerre-Barbieri et al., 2015, 2017) integrates this emerging knowledge into an eco-evolutionary conceptual model, with a foundational assumption that LRS in marine fish is neither statistically random nor driven primarily by extrinsic factors. The RRP proposes that marine fish have evolved complex, adaptable and, in many cases, phenotypically plastic spawner-recruit systems for which there are no terrestrial equivalents (Lowerre-Barbieri, Brown-Peterson, et al., 2011; Young et al., 2006). These systems have evolved to promote individual fitness (reproductive success) and population persistence within an ecological context that includes environmental heterogeneity and species interactions (Lowerre-Barbieri et al., 2017) and under prevailing mortality regimes (Garrod & Horwood, 1984; Lowerre-Barbieri, 2009; Mangel et al., 2013; Winemiller & Rose, 1992). Although most marine fishes have extreme fecundity, species differ in a host of other traits that affect early survivorship and thus reproductive success, including reproductive lifespan, number of lifetime breeding events, gender and mating systems, spatiotemporal processes associated with spawning and larval dispersal dynamics (Lowerre-Barbieri et al., 2015, 2017; Lowerre-Barbieri, Ganias, et al., 2011; Ospina-Alvarez et al., 2022). The RRP views recruitment variability—that is, year-class strength as well as temporal periodicity between strong year classes—as an adaptive component of spawner-recruit systems, with trade-offs between the above traits and differing (but high) levels of recruitment variability having evolved to provide the reproductive resilience necessary for population stability in a stochastic ocean environment.

1.1 | Reproductive success framework for age-structured fishery stocks

Fisheries ecologists and stock assessment scientists recognize the importance of biologically regulated changes in fecundity and survival, as well as movement and other spatial processes, to reproductive success. Assessment models use 'reproductive potential' to quantify reproductive success within a stock. These models are traditionally based on female spawning stock biomass (SSB) and assume that SSB is proportional to fecundity (Lowerre-Barbieri, Ganias, et al., 2011). However, the 'BOFFFF (big old fat fecund female fish) effect' is increasingly accepted, that is, the importance of old-growth age structure to reproductive success as older females will be more fecund and typically produce eggs of greater quality (Berkeley et al., 2004; Fitzhugh et al., 2012; Hixon et al., 2014; Marshall et al., 2010). Additional work has demonstrated the pattern of hyperallometric scaling—that is, larger individuals tending to produce more eggs by unit body weight than smaller individuals (Barneche et al., 2018; Marshall et al., 2006).

To maintain dynamic population stability, adult females must only produce an average of two offspring during their lifetime that survive to reproductive age. Yet, for fishes with small-eggs strategies, batch fecundity (i.e. fecundity within a given spawning event) typically measures in the thousands of eggs, and often much greater. Lifetime fecundity varies greatly across species, largely as a function of the number of spawning events. Batches may be released once in a lifetime, as in semelparous species (e.g. coho salmon, *Oncorhynchus kisutch*, Salmonidae), or hundreds to thousands of times in iteroparous species having extended spawning seasons and long reproductive lifespans (e.g. red snapper, *Lutjanus campechanus*, Lutjanidae) (Lowerre-Barbieri, Ganias, et al., 2011). RRP predicts that both species can have healthy, stable populations due to tradeoffs between fecundity and evolved behaviours/traits that decrease offspring mortality and/or increase lifetime success.

Spatial processes are also being increasingly recognized as important drivers of reproductive success. Traditionally, stock assessments assume large, well-mixed populations (Cadrin & Secor, 2009; Hawkins et al., 2016). However, more recent studies suggest that spatial structuring occurs at far smaller scales (Goethel et al., 2015; Kerr et al., 2017), requiring that spatial dynamics be better integrated into assessments and management actions to prevent localized depletion or distributional shifts in productivity and resilience (Berger, Goethel, & Lynch, 2017; Berger, Goethel, Lynch, Terrance II, et al., 2017; Ciannelli et al., 2013; Kerr et al., 2010). In terms of investigating LRS dynamics, both spatial and temporal scales are equally important, as will be shown, because it must be assumed that modelled values of N_A are temporally and geographically aligned with the estimate N_e (Shpak, 2005; Waples & Englund, 2011; Palstra & Fraser, 2012; Ryman et al., 2019).

For age-structured populations, important dynamics associated with LRS have been mathematically defined as follows: $N_e \approx 2\overline{k}^* N_\eta T / (V_k^* + 2)$, where $\overline{k}^*$ is the mean lifetime reproductive success of breeders during a generation, N_η is the number of newborn individuals in a given sexually immature year class, T is the generation length in years (y) and V_k^* applies to the N_η newborns (Hill, 1972). Consistent with the RRP, quantitative geneticists focus on the adaptive implications of LRS and gravitate to the metric V_k^* when quantifying population fitness and 'opportunities for selection' (Arnold & Wade, 1984; Brodie et al., 1995; Clutton-Brock, 1988; Crow, 1958). Population geneticists, on the other hand, have relied on N_e and the N_e / N_A ratio as indicators of LRS dynamics due to the usefulness of this ratio in conservation management (Frankham, 1995) and many other applications (Husemann et al., 2016; Ovenden et al., 2016). Despite its broad utility, the N_e / N_A ratio can be subject to confounding properties when certain reproductive traits are considered (Waples, 2016a). For example, mean fecundity at age can be shown to affect N_e / N_A ratios in an offsetting manner: $[(\uparrow N_e / N_A) \leftarrow (\uparrow T) \leftarrow (\uparrow \text{mean fecundity with age}) \rightarrow (\uparrow V_k^*) \rightarrow (\downarrow N_e / N_A)]$. Therefore, by modelling V_k^* and T separately, we create a pathway to tease apart their independent influences on LRS, establishing a more direct linkage with relevant reproductive traits (e.g. maturity schedules, egg and larval quality, timing/duration/location of spawning).

To demonstrate the usefulness of the RRP as a framework for understanding recruitment processes in marine fisheries, we examined the spawner-recruit systems of three large marine populations that possess reproductive traits commonly associated with SRS (extreme fecundity, pelagic larvae and Type III survival). Because we have been studying red drum (*Sciaenops ocellatus*, Sciaenidae) reproductive resilience for the past decade (Figure 1) and because this species has often been cited as an example of SRS (Hauser & Carvalho, 2008; Hedgecock & Pudovkin, 2011; Hedrick, 2005; Hutchins & Reynolds, 2004; Laurent & Planes, 2007; Palstra & Frasier, 2012; Turner et al., 2002), we utilize original data to estimate N_e / N_A and V_k^* for a spawning populations. Relying on published data, we also modelled N_e / N_A and V_k^* for the panmictic southern bluefin tuna (*Thunnus maccoyii*, Scombridae) and silver seabream (*Chrysophrys auratus*, Sparidae) from a reserve population in the Hauraki Gulf of New Zealand. We use these three populations to illustrate potential methodological biases in N_e and N_A estimation and to highlight some of the intrinsic and extrinsic drivers of V_k^* and T in marine fishes having a small-eggs life history strategy. We refute the null hypothesis that they conform to SRS expectations and discuss how their observed LRS dynamics and evolved differences in spawner-recruit systems are instead aligned with tenets of the RRP, which we support as an underlying concept for biological, ecological and evolutionary studies of reproductive success in marine populations.

2 | MODEL AND METHODS

Parameter notations for the age-structured LRS model are summarized in Table 1 and age-specific model parameters (s_x, l_x, b_x, b'_x, B_x and N_x) are defined as follows. The user-supplied parameter s_x is the probability of survival from age x to age $x + 1$. The parameter l_x is derived from s_x and represents cumulative survival through age x, where $l_1 = 1$ and $l_x = l_{x-1} s_{x-1}$ for $x > 1$. We define b_x as the birth rates for newborn offspring produced by breeders of age x and scale it to a constant $\sum_1^\omega N_x$ (i.e. where $\overline{k}^* = 2$), the scaled quantity becoming b'_x. We define B_x as the number of newborns produced by breeders of age x, where $B_x = b'_x N_x$ and noting that $N_1 = \sum_\alpha^\omega B_x$. Finally, we define N_x as the expected number of individuals alive within a given age class.

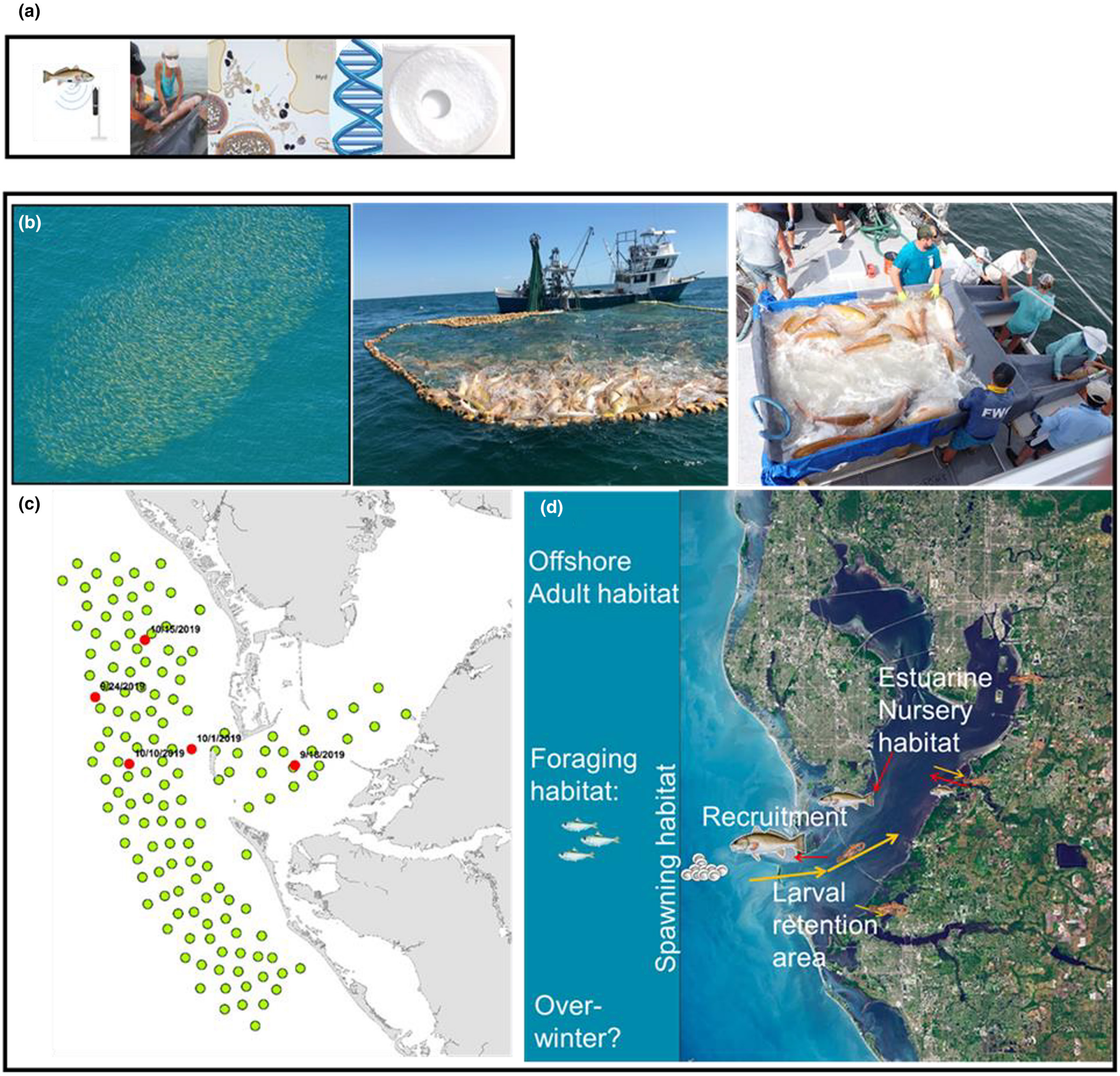

FIGURE 1 The red drum case study uses data from a long-term, multidisciplinary study on a red drum spawning population off Southwest Florida (USA). Methodology includes: (a) aerial surveys (not shown), acoustic tracking, histological evaluation of spawning activity, genetics and egg quality. Non-lethal sampling (b) includes a spotter plane identifying red drum aggregations and guiding a purse seine captain to set on them, after which biologists board the boat and take samples from individuals for sex, reproductive state, size (lengths) and genetics, and then release the fish. The area where purse seine samples occur (sets in 2019 are denoted by red markers) is monitored with acoustic receivers represented by green markers (c) to track red drum from this population which have been acoustically tagged. This multi-method approach is helping us to better understand life cycle space use in this species (d).

Building from the dynamic model framework of Waples et al. (2011), N_e is representative of adult cohort effective sizes over their reproductive lifespans and their newborns survive to a given time period. LRS variance can be measured using any immature age class from $\eta = 1$ to α (Waples, 2016a), depending on investigative aims. The model workflow can be viewed in three steps (Figure 2). First, a partial life table ($s_x|\alpha, \omega$) was scaled to identify values of $\hat{N}_1$ that correspond to empirical estimates of N_A, which in doing provides all values of N_η, including $\hat{N}_\alpha$. Second, a full life-table analysis (s_x, l_x, b_x, $b'_x|\hat{N}_1$, α, ω) was performed to calculate the estimator $\hat{T}$. Values of b_x were scaled to b'_x under the assumption of a stable population abundance (Hill, 1979; Waples et al., 2011) and numbers of newborns (B_x) produced by breeders of age x were estimated as xb'_xN_x. Worksheets for an exemplar partial life table scaling and full

TABLE 1 Parameter notations.

Parameter	Description
N_x	Number of age x (age class) individuals alive at a given time
N_A	Number of potential breeders (adults) in a population, including skip spawners
N_η	Number of individuals in a newborn cohort measured at a given time period
T	Generation length: the expected age of a parent that produced a randomly selected newborn; see mathematical formulation in text
N_e	Per-generation effective population size (for age-structured populations)
n_g	Number of unique genotypes sampled
$\overline{k}^\tau$	Mean lifetime reproductive success of breeders during a generation
V_k^τ	Lifetime variance in reproductive success among breeders in a population
b_x	Birth rates for newborn offspring produced by breeders of age x; for fish, mean fecundities (at age x) may be used as proxies; b_x is scaled to constant $\sum_1^\omega N_x$ (where $\overline{k}^\tau = 2$), the scaled quantity becoming b'_x
B_x	Number of newborns produced by breeders of age x; $B_x = b'_x N_x$; note that $N_1 = \sum_\alpha^\omega B_x$
s_x	Probability of survival from age x to age $x + 1$
l_x	Cumulative survival through age x where $l_1 = 1$ and $l_x = l_{x-1} s_{x-1}$ for $x > 1$
Z_x	Instantaneous natural mortality
d_A	Constant rate of annual mortality for adult ages
α	Age at maturity; the age at which breeders in a population became mature
ω	Longevity (maximum age)
τ	Reproductive lifespan ($\tau = \omega - \alpha + 1$)
V_x	Annual/seasonal variance in the number of newborn births produced by age x
ϕ_x	Overdispersion factor; $\phi_x = V_x / b'_x$, where V_x is annual variance

Note: In the text, '^' denotes estimated or inferred quantity from the model; '˜' denotes a raw (unadjusted) empirical estimate; '´' denotes a bias-adjusted and/or finalized estimate.

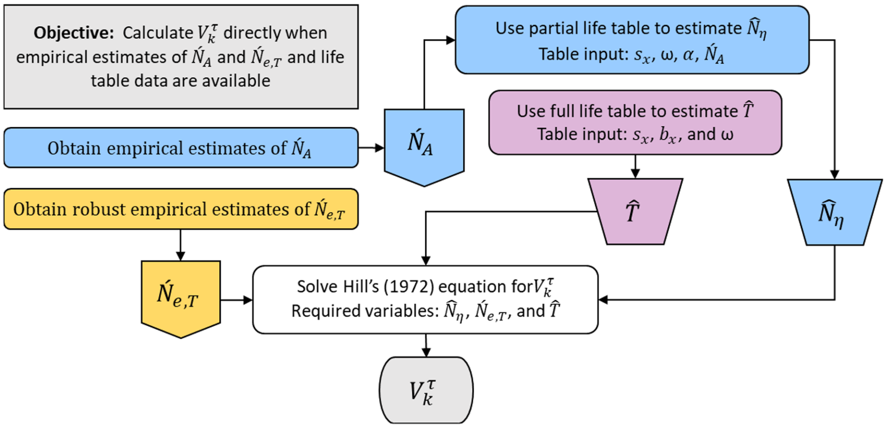

FIGURE 2 Flow chart of procedures used to estimate variance in lifetime reproductive success. Parameter notations are given in Table 1. In the partial life table, α can be inferred from the first non-zero b_x and ω from the last non-zero s_x.

life-table analysis (with equations for the above parameters) are provided in a Supplementary Excel file. Generation lengths were determined using the scaled mean fecundities and $\widehat{N}_1$ via the formula: $\widehat{T} = \left(\sum x l_x b_x \right) / \left(\sum l_x b_x \right) = \sum \left(B_x / \widehat{N}_1 \right)$. Finally, we solved Hill's (1972) equation with V_k^* as the dependent variable, using $\widehat{N}_\eta$, $\widehat{T}$, and an empirical estimate of $\acute{N}_e$ to obtain a deterministic solution. V_k^* was measured at ages $\eta = 1$ and α. See Supporting Information for LRS model assumptions.

2.1 | Case study: Red drum

Red drum is an iteroparous, highly fecund, broadcast spawner (Table 2) that occurs in the US Atlantic Ocean from Massachusetts to Florida and in the Gulf of Mexico (GOM) from Florida to northern Mexico. Adults form large schools that aggregate along the coasts during the fall spawning season (Beckman et al., 1988; Murphy & Taylor, 1990; Pafford et al., 1990; Ross et al., 1995). They spawn pelagic eggs in

TABLE 2 Reproductive life history traits and features for the modelled populations. Literature citations for table cell entries are provided in Table S1a.

Population/Traits and measures	Red drum (Southwest Florida Gulf of Mexico)	Southern bluefin tuna (circumglobal distribution; southern hemisphere)	Silver seabream (Hauraki Gulf)
Spawning habitat/location	Predominantly nearshore areas adjacent to inlets and passes	Open ocean; Indian Ocean South of Java	Within Hauraki Gulf off estuaries and harbours
Spawning season	Mid-August through mid-November; peaking September–October	August through May; peaking September–October and February–March; water temp. >23°C	October through February; water temp. >18°C
Spawning type	Batch, indeterminate fecundity	Batch, indeterminate fecundity	Batch, indeterminate fecundity
Reproductive unit	Aggregate in large schools, surface broadcast in small groups	Aggregate in large schools, surface broadcast in small groups (one female, multiple males)	Aggregate in large schools; surface broadcast in small groups
Pelagic larval duration	~20 days	~20 days	17–33 days
Settlement habitat	Estuarine, sheltered in sea grass, adjacent to marsh edge and oyster reefs	Open ocean	Majority estuarine, sheltered in sea grass, mussel beds; nearshore habitats

nearshore waters off the mouths of estuaries (Figure 1d), where larvae quickly recruit to nearby tidal creeks and rivers, albeit with high mortality (Murphy & Crabtree, 2001; Peters & McMichael, 1987). Red drum along the west coast of central Florida, including Florida's largest estuary, Tampa Bay, support an important recreational fishery for estuarine-dwelling juveniles and subadults (slot size: 457–686 mm total length). As fish age, they leave the tidal creeks and estuaries and move towards the mouth of Tampa Bay (Figure 1d). Maturing fish recruit to full salinity habitat (Lowerre-Barbieri et al., 2016; Walters Burnsed et al., 2020), with many individuals returning to spawn off their natal estuaries (Lowerre-Barbieri et al., 2018).

The Tampa Bay red drum spawning population was sampled in the late 1990s (Murphy & Crabtree, 2001) to evaluate recovery of the adult age structure after the fishery was closed, with a second similar study conducted in 2006–2008, which also collected fecundity data (Winner et al., 2014). Research on the reproductive resilience of this spawning population began in 2012. In 2012–2014 and again in 2019–2021, fish were sampled by purse seine (like the previous studies). However, sampling was non-lethal providing a means to collect data from thousands of fish on sex, size, reproductive state and genetics (Lowerre-Barbieri et al., 2016, 2018; Walters Burnsed et al., 2020; Figure 1). In addition to the biological samples, aerial surveys were used to identify the location and number of spawning aggregations (2012–2014; 2018–2022) and acoustic telemetry to track recruitment to the spawning grounds, consequent behaviour of first-time spawners and adult spawning site fidelity (2012-the present).

These data were used to estimate $\acute{N}_A$, $\acute{N}_e$ and fecundity (see Supporting Information for detailed methods). Individual recapture histories were generated as described in Lowerre-Barbieri et al. (2018) using multilocus genotype profiles consisting of nine highly variable microsatellite loci (Turner et al., 1998). These histories were used in a capture-mark-recapture (CMR) model analysis to estimate annual abundance in 2013, 2014 and 2019 ($n = 12{,}078$ fish sampled, Lowerre-Barbieri et al., 2018; Lowerre-Barbieri et al., 2020). The same genotype data were also used to obtain raw estimates of $\widetilde{N}_e$, using the bias-corrected LD method within the computer program *NeEstimator* V2.1 (Do et al., 2013). Given known issues with $\widetilde{N}_e$ precision, the empirical *CV* was calculated, and the effect of sample size was assessed through a random subsampling of genotypes over progressively smaller subsets of *n*, as described in Supporting Information. To screen for single-locus effects on the estimate of $\widetilde{N}_e$, a jackknifing procedure was also performed, wherein information from each locus was omitted in turn. A red drum life table was compiled using the above data ($\acute{N}_A$ was set as the mean of the above three CMR years) and demographic information from the most recent stock assessment (Addis, 2020). Acoustic tracking indicated low straying to the nearest southern neighbour spawning site (6%–13%) and relatively high repeat spawning between years (48%–91%, Lowerre-Barbieri et al., 2018). However, given the red drum isolation by distance (IBD) population structure and previously reported very low N_e / N_A ratios (Turner et al., 2002) we also estimated N_e / N_A ratios using $\acute{N}_A$ values ~2–3 times larger than the mean (i.e., 400,000, 600,000), with the highest value providing the means to estimate expected ratios at the other end of the extreme, that is, complete mixing with nearest neighbour spawning populations. The program *AgeNe* (Waples et al., 2011; *Ecological Archives E092-126-S1*) was used for the full life table calculation of $\hat{T}$, which was compared to a direct calculation of the average age of adults in the 2006–2008 sample ($n = 702$).

2.2 | Case studies: Southern bluefin tuna and silver seabream

Selected life history traits and features for southern bluefin tuna and silver seabream appear in Table 2. Requisite demographic measures and model parameter values for these two species were synthesized from published works of Waples et al. (2018) and Jones et al. (2019), and from referenced works therein. Full descriptions of these data syntheses are reported in Supporting Information.

3 | RESULTS

3.1 | Red drum spawning and batch fecundity

Most acoustically tagged subadults (88%) from the estuary later detected on the spawning grounds ($n=16$) recruited in the fall after the core spawning season. Of these 16 fish, 11 returned and were detected in the Tampa Bay spawning grounds during consequent spawning seasons (Figure 3). Those detected within the core spawning season were assumed to spawn that year. The age of first-time female spawners agreed well with the reported age at maturity: age 3 ($n=1$) and 4 ($n=2$) but was somewhat younger for males: age 2 ($n=1$), age 3 ($n=5$) and age 4 ($n=2$) fish. One of the 11 fish exhibited a potential skip spawning pattern, as it was detected on the spawning grounds as a three-year-old and a five-year-old but not detected anywhere in the array as a four-year-old.

The studied red drum spawning population exhibited natal homing and multi-year spawning site fidelity, with a highly variable spawning fraction and minimal within-season skipped spawning. Of the females assessed in the spawning aggregations from 2012 to 2014, 97% were spawning capable or actively spawning ($n=2394$), indicating that only 3% of those fish that moved to the spawning site could potentially skip spawn. The spawning fraction (i.e. proportion of sampled females that were active spawners) was highly variable, ranging from 1% on 10 September 2012 ($n=303$) to 100% on 10 July 2013 ($n=155$), highlighting difficulty in obtaining representative spawning fractions to estimate spawning frequency for this species and many other species that aggregate to spawn. Batch fecundity exhibited a weak positive relationship with age (Figure S3). The best-fit line, as indicated by WLS, was $b_x = 80{,}129(10{,}810)x + 1{,}531{,}445(138{,}924)$, where $R^2 = 0.2442$ and the null hypothesis of homogeneity of variance for the relationship was rejected (Breusch-Pagan test; F-statistic: 47.48 on 1 and 166 DF, p-value: $1.101\mathrm{e}^{-10}$).

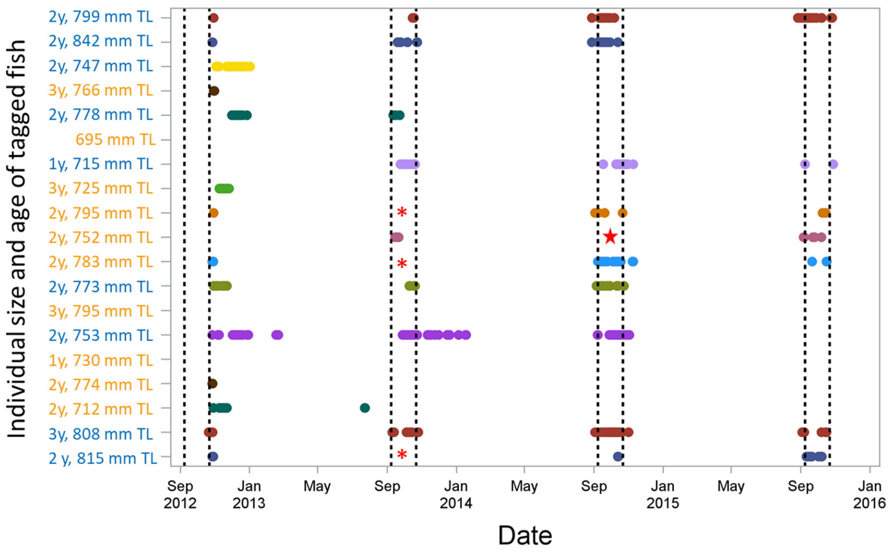

FIGURE 3 Annual detections of subadult red drum on the Tampa Bay nearshore spawning grounds. Fish were originally captured and tagged on the nursery grounds ($n=20$). Age and size at detection is shown on the *y*-axis and ranged from 1 to 3 years old and from 695 to 842 mm TL. Reference lines indicated the core spawning season from 8 September to 22 October. Sixteen of these fish were detected on the Tampa Bay spawning grounds, with 14 recruiting after the core spawning season in the year they were tagged (2012) and another two fish recruiting the following year. Three females, which moved to adult habitat in 2012, were not detected in the 2013 spawning seasons (*). They would have been age 4 ($n=2$) and 3 ($n=1$). Potential skip spawning (★) was observed in a fish which recruited during the 2013 spawning season as a 3 years old, was not detected in the 2014 spawning season but returned again in 2015. First-time spawning males were younger than the females: age 3 ($n=5$) and age 2 ($n=1$). Sex is indicated by *y*-axis text colour, blue = male, orange = female.

3.2 | Red drum adult abundance, effective size, and N_e / N_A ratio

Levels of genetic diversity did not differ among the four spawning seasons sampled (Figure S1) and there was no evidence for temporal genetic differentiation in these years (Figure S2). The estimated mean spawning population abundance was $\acute{N}_A = 199{,}595$ (range: 51,786–347,986). Depending on the sample groupings, bias-adjusted effective population sizes for all loci ranged from 69,129 to 87,671 (Figure 4a; Table S3a). Estimates of CI_{parm} and CI_{jack} were relatively close to the mean value, and finite values for upper *CI*s were observed in all analyses for P_{crit} of 0.01 and 0.005. The coefficient of variation ($CV = 0.303$) for the raw estimate of $\tilde{N}_e$ indicated reasonable precision for the very large estimated effective sizes. The inclusion of the 2019 sample group increased the range of mixed ages in the pooled sample but caused no observable downward bias. Locus Soc204 deviated with respect to HWE. Omitting it resulted in larger confidence intervals but not consistently lower or higher estimates (Table S3a). The bias-adjusted estimate of $\acute{N}_e = 85{,}521$ ($CI_{\text{parm}} = 54{,}002$–$189{,}577$), based on data from all loci and sampling seasons, was thus considered the best estimate for modelling $\hat{V}_k^*$. No unexpected effects on $\tilde{N}_e$ were observed when individual loci were omitted during estimation (Table S3b).

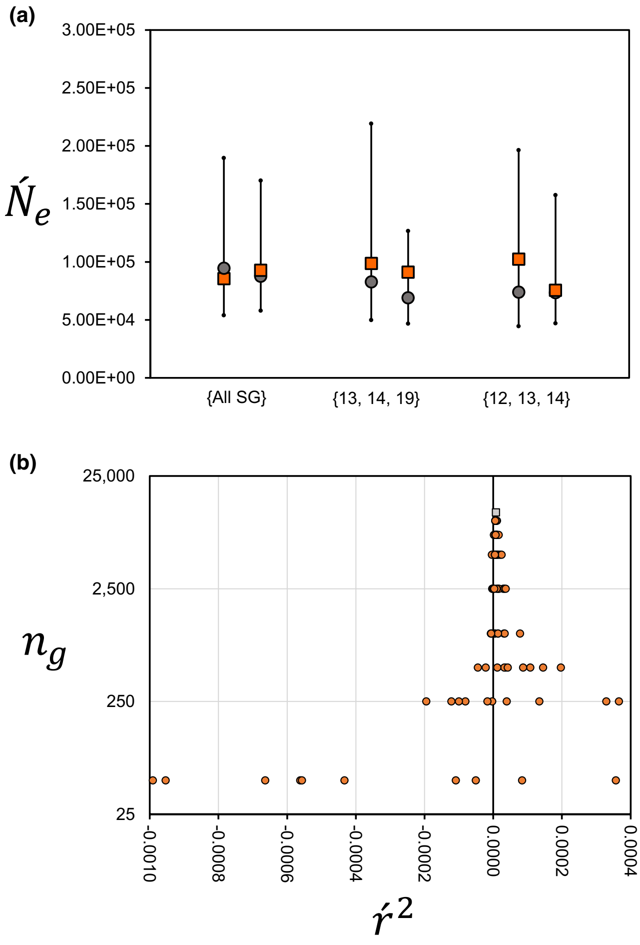

FIGURE 4 (a) Point estimates and 95% parametric confidence intervals (CI_{parm}) for empirically determined per-generation effective population size ($\tilde{N}_e$) for red drum. Estimates are shown for each set of sample groups; for a given set, those based on $P_{\text{crit}} = 0.01$ are depicted in leftmost plots; those based on $P_{\text{crit}} = 0.005$ in rightmost plots. Black circles depict estimates including locus Soc204, which deviated from the Hardy–Weinberg equilibrium expectations; linear *CI*s correspond to those estimates. Orange boxes depict estimates omitting locus Soc204. (b) Plot of sampling-bias-corrected estimates of mean squared correlation of allele frequencies at different gene loci, $\acute{r}^2$, based on replicated random subsampling of the total genotype data set where n_g (depicted on log scale for easier viewing) equates to the number of genotypes selected and analysed. The grey square depicts estimates based on the total data set.

When red drum genotypes were randomly subsampled, estimated values of $\tilde{N}_e$ began to show the expected bimodal pattern between $2{,}500 > n_g > 1{,}000$ with some point estimates becoming increasingly small and others becoming infinite (Table 3). Negative estimates of $\acute{r}^2$, which result in infinite $\tilde{N}_e$ estimates and occur when the overall value is less than would be expected from sampling error alone, began to occur with increasing frequency at $n_g \leq 2{,}500$, although a single negative estimate also occurred at $n_g = 5{,}000$ (Figure 4b). Precision was lost at $n_g < 7{,}500$, below which nearly all upper bounds of CI_{parm} became infinite (Table 3).

The empirically derived estimate of $\acute{N}_e$ yielded a ratio value $\acute{N}_e / \acute{N}_A = 0.43$. The lower *CI* estimate of $\acute{N}_{e(lower)} = 54{,}002$ yielded $\acute{N}_{e(lower)} / \acute{N}_A = 0.27$. The upper *CI* was finite for red drum, but its value was greater than half the empirically estimated $\acute{N}_A$ and, as a result, $\acute{N}_e / \acute{N}_A$ exceeded the theoretical norm (0.50) for iteroparous species with long generation times. Using the exploratory value of $N_A = 400{,}000$, $\acute{N}_e / N_A = 0.21\ (0.14 - 0.47)$. Using the exploratory value of $N_A = 600{,}000$, $\acute{N}_e / N_A = 0.14\ (0.09 - 0.32)$. Thus, the lower to upper range of $\acute{N}_e / N_A$ for red drum over the plausible range of N_A was $0.09 - 0.50$ and we posit a most likely $\acute{N}_e / \acute{N}_A$ ratio value of ~0.21, well above the threshold value considered indicative of SRS (0.01).

3.3 | *T* and V_k^* for red drum, southern bluefin tuna, and silver seabream

Life-table values, survival and cumulative survival differed by species (Table S4; Figure 5a,b). Unscaled and scaled batch fecundity-at-age (b_x and b_x') did not increase rapidly for red drum (Figure 5c,d), and the overall fecundity versus age relationship was weak (Figure S3a). Life-table values of $\hat{N}_1$ and $\hat{N}_\alpha$ are provided in Table 4. The life-table-estimated generation length for red drum was $\hat{T} = 11.97$ y, which, although it accounts for fecundity and mortality, was comparable to the direct estimate of 11.88 y, based on age-composition data from randomly surveyed adults (Table S5). Life-table-estimated generation lengths for southern bluefin tuna and silver seabream were $\hat{T} = 13.11$ y and 22.45 y, respectively.

For red drum, estimates of $\hat{V}^*_{k(N_1)}$ ranged from 53.7 to 291.3 (Table 4). The most plausible value, relying on accuracy of the $\acute{N}_e$ point estimate and assuming a modest level of demographic exchange with

TABLE 3 Results of random subsampling red drum genotypes on raw point estimates of N_e.

n_g	$\hat{r}^2$	$\widetilde{N}_e$	Lower *CI*	Upper *CI*
11,781	0.000008	43,939	33,610	62,416
10,000	0.000008	42,907	31,628	65,343
	0.000006	54,377	37,632	95,131
	0.000006	52,975	36,998	90,682
	0.000006	53,492	37,331	91,745
	0.000009	36,083	27,710	50,892
	0.000011	31,115	24,579	41,819
	0.000007	45,379	32,983	71,104
	0.000008	39,862	29,903	58,676
	0.000010	32,965	25,687	45,322
	0.000006	59,283	40,061	110,200
7500	0.000010	33,046	24,197	51,003
	0.000009	34,228	24,926	53,434
	0.000005	58,285	35,523	151,907
	0.000011	30,160	22,401	45,220
	0.000011	29,973	22,401	44,420
	0.000009	35,532	25,355	57,873
	0.000016	19,731	16,058	25,303
	0.000002	143,691	57,172	INF
	0.000006	54,304	33,790	130,424
	0.000007	44,792	29,952	85,590
5000	0.000010	32,990	21,167	71,231
	0.000015	22,348	16,107	35,605
	0.000012	29,591	19,872	55,894
	0.000007	51,951	28,049	287,757
	0.000020	17,187	13,119	24,477
	0.000005	77,543	34,541	INF
	−0.000004	INF	471,121	INF
	0.000024	13,853	11,066	18,276
	0.000005	78,743	34,650	INF
	0.000005	65,740	31,629	INF
2500	0.000029	11,646	8239	19,312
	0.000014	22,990	12,959	89,661
	−0.000003	INF	43,418	INF
	−0.000002	INF	34,052	INF
	0.000017	20,217	11,978	59,594
	0.000010	32,896	15,750	INF
	0.000001	315,548	27,332	INF
	0.000003	112,078	23,652	INF
	0.000032	10,279	7502	15,940
	0.000036	9323	6987	13,731
1000	0.000078	4306	3067	7023
	0.000005	65,972	9570	INF
	0.000005	63,572	9536	INF
	0.000014	23,931	7588	INF
	−0.000007	INF	15,187	INF
	0.000031	10,736	5489	127,790
	−0.000004	INF	13,192	INF
	0.000033	9976	5197	83,159
	0.000014	22,887	7504	INF
	−0.000006	INF	13,908	INF
500	0.000036	9190	3352	INF
	0.000108	3081	1921	7280
	−0.000022	INF	8958	INF
	−0.000045	INF	21,320	INF
	0.000197	1697	1255	2556
	0.000087	3828	2210	12,753
	0.000032	10,423	3406	INF
	0.000145	2289	1586	3977
	0.000012	30,114	4533	INF
	0.000042	8038	3167	INF
250	0.000329	1011	710	1694
	−0.000122	INF	31,143	INF
	−0.000003	INF	2549	INF
	0.000039	8682	1923	INF
	0.000134	2482	1197	INF
	−0.000195	INF	INF	INF
	−0.000081	INF	7168	INF
	−0.000017	INF	2964	INF
	0.000366	908	640	1507
	−0.000100	INF	11,315	INF
50	−0.000433	INF	727	INF
	−0.000109	INF	408	INF
	−0.000954	INF	INF	INF
	0.000084	3978	346	INF
	−0.000664	INF	1552	INF
	0.000357	932	277	INF
	−0.000562	INF	1094	INF
	−0.000557	INF	1083	INF
	−0.000991	INF	INF	INF
	−0.000051	INF	393	INF

Note: INF = infinite. n_g = number of genotypes sampled; where there is no entry for n_g, the preceding row value applies. $\hat{r}^2$ = the mean squared correlation of allele frequencies at different gene loci. Confidence intervals (*CI*) were based on the parametric method. Estimate based on all available genotypes, where n_g = 11,781, is also shown.

neighbouring populations (such that $\hat{N}_1 \approx 220{,}500$), was $\hat{V}^*_{k(N_1)} = 121.5$. For the panmictic southern bluefin tuna, $\hat{V}^*_{k(N_1)}$ estimates ranged from 186.2 to 938.9 (Table 4). The most plausible value, relying largely on the accuracy of $\acute{N}_e$, was $\hat{V}^*_{k(N_1)} = 376.6$. For silver seabream, $\hat{V}^*_{k(N_1)}$ estimates ranged broadly from 45.8 to 2831.6 (Table 4). Considerable uncertainty surrounding the degree of population closure for silver seabream preclude selection of a most plausible $\hat{V}^*_{k(N_1)}$ value. However, information suggestive of a broader geographical scale (see Section 4.1) would render the lowest values of $\hat{V}^*_{k(N_1)}$ implausible. For example, if the true $\hat{N}_1$ is between ~23,000 and 57,000, then the values of $\hat{V}^*_{k(N_1)}$ most likely occur within the range of 302.5–759.3.

Finally, values of $\hat{V}^*_k$ decreased for all three species when calculated using the abundances of α age-classes (Table 4). Since $\acute{N}_e$ and $\hat{T}$ were static, differences in $\hat{N}_\eta$ must be offset by nearly proportional changes in variance; thus, as expected, the percentage decrease in $\hat{V}^*_{k(N_\alpha)}$ relative to $\hat{V}^*_{k(N_1)}$ was approximately equal to $\left(\hat{N}_1 - \hat{N}_\alpha\right) / \hat{N}_1) \times 100$.

4 | DISCUSSION

Historically, the N_e / N_A ratio has been a favoured measure among fishery geneticists and, in the previous two decades, has been widely reported as being 'tiny' ($\ll 0.01$) for marine populations (Hauser & Carvalho, 2008; Waples, 2016b). However, the parameter N_e can be difficult to estimate in nature (Waples et al., 2013). Certain biases—for example, mixed-age sampling, physical linkage among loci—can be anticipated and corrected in silico, as was done herein (see also Waples et al., 2018). Another possible source of bias arises from the complex nature of microsatellite loci. When relatively few microsatellite loci are surveyed, N_e estimates could be unduly influenced by tendencies to mis-score alleles at a particular locus (Davison & Chiba, 2003; Morin et al., 2009; van Oosterhout et al., 2004). For red drum, jackknifing results were not suggestive of bias attributable to individual loci (Table S3b). However, when microsatellite reliability may be a concern, N_e estimates based on thousands of single-nucleotide polymorphism loci represent a powerful alternative, provided they can be bias-adjusted for physical linkage given detailed information on recombination rates (Waples et al., 2016).

Other possible biases involve the robustness of sampling (Marandel et al., 2019; Poulsen et al., 2006) and the appropriateness of spatial scaling (Hare et al., 2011; Nadachowska-Brzysk et al., 2021). Whereas many prior SRS studies involving N_e / N_A ratios were based on 50 or fewer specimens (Hauser & Carvalho, 2008; Poulsen et al., 2006), there is a growing recognition that sampling designs for large marine populations could require multiple thousands of specimens for accuracy and precision (Waples, 2016b), although smaller sample sizes can suffice when the true N_e is small, when enough loci are surveyed. Moreover, the various methods to estimate N_e and N_A can at times yield biased results when applied to populations under migration (Ryman et al., 2019, 2023; Waples & England, 2011). Because genetic and/or demographic connectivity of marine fish populations is often not well known, the spatial scales applied during analyses are also crucial.

4.1 | Importance of sampling design

All three case studies provide insights into how sampling design can affect estimates of N_e and N_e / N_A. Due to the very large sample size for red drum ($n_g = 11{,}871$ genotypes), the adjusted $\acute{N}_e$ estimate was finitely bounded by *CI* values ranging within 45% of the estimated mean. To our knowledge, the red drum data set currently provides the largest linkage-based point estimate of N_e of any animal population (marine or terrestrial) for which a finite value of the upper *CI* has been recovered. Results of the random subsampling analysis with red drum genotypes, which exhibited a strong pattern of bimodality in $\acute{r}^2$ estimates (Table 3 and Figure 4b; see also Figure 5 in Waples, 2016b), reinforced the need for robust sampling. Consistent with prior simulation results (e.g. Waples, 2016b), precision was lost very quickly in red drum N_e estimates as sample size declined from the approximate magnitude of the maximally observed N_e.

While attention to geographical scale is important within fisheries modelling and assessment, the same is true as it applies to modelling LRS dynamics, in large part because V^*_k is proportional to N_η. For southern bluefin tuna, the panmictic population structure simplifies matters, but it remains a consideration for the other two species. Along the eastern Gulf of Mexico, red drum exhibit an IBD pattern of gene flow (Hollenbeck et al., 2019). The majority of exchange, when it occurs, is predicted to happen between adjacent estuaries (Gold et al., 2001). Under IBD, the relationship between geographical and genetic distance should be a function of the single-generation dispersal kernel—that is, the proportional movement of individuals across different distances (D'Aloia et al., 2015; Furstenau & Cartwright, 2016). Most marine species have a vagile phase during some stage of their life history and the dispersal kernel should encompass all stages.

For red drum, larval dispersal along Florida's southwest estuaries is largely a localized process (Figure 1d), but the migration of mature individuals between adjacent spawning grounds, unless it occurs at negligible levels, requires that we consider larger values of N_1 and N_α in the model. Assuming localized larval retention and a limited amount of adult connectivity with the nearest northern and southern estuaries, we identified the most plausible geographically scaled adult abundance as one that was approximately twice the empirical mean estimate (i.e. $N_A = 400{,}000$). Because linkage-based estimates of N_e have been shown to be unbiased at low levels of migration (Waples & England, 2011), the favoured scenario resulted in an N_e / N_A of ~0.21. This ratio value is strongly at odds with conventional thought that red drum has SRS. Even the most conservative analytical result based on a presumptive $N_A = 600{,}000$ yielded an N_e / N_A ratio of ~0.14, which is still highly inconsistent with the SRS criterion.

Our findings differ from those of Turner et al. (2002), which sampled red drum over a larger spatial scale and reported an N_e / N_A ratio of ~0.001. For that study, young-of-the-year specimens were collected in small batches at seven widely separated locations over four consecutive years ($n_g \approx 20$/location ≈ 250/year class), panmixia at the GOM scale was assumed, and N_e estimation was based

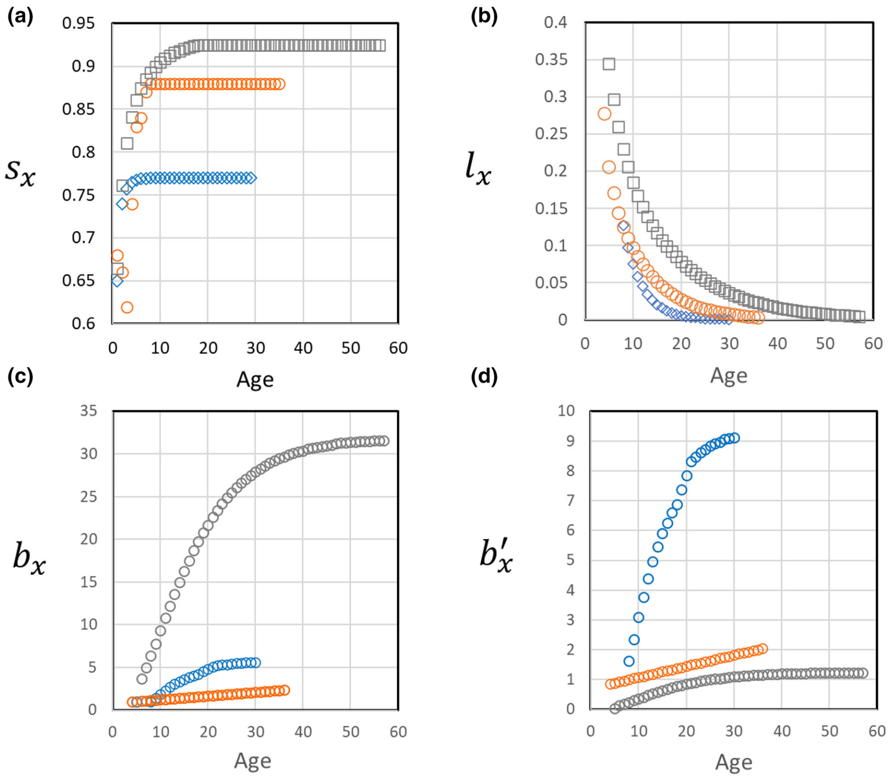

FIGURE 5 Life table rates and measures for southern bluefin tuna (blue), red drum (orange) and silver seabream (grey). (a) Survivorship at age. (b) Cumulative survivorship at age. (c) Unscaled mean fecundity-at-age. (d) Mean fecundity-at-age scaled to $\bar{k}^* = 2$. Note the dynamic shifts in unscaled versus scaled mean fecundities due to the differences in survivorship.

on a maximum likelihood evaluation of temporal variance in allele frequency (Wang, 2001). The resulting estimate of 3516 (95% CI: 1785 to 18,148) was approximately an order of magnitude below our lower*CI* values (Table S3). Temporal estimators, like linkage-based estimators, are highly imprecise when sample sizes are too small (e.g. Waples, 2016b), and also when the temporal spacing between collections is too brief (Waples, 1989). They are also sensitive to spatial differences in productivity when sampling occurs across structured subpopulations (Ryman et al., 2023).

The earlier N_e / N_A ratio was also calculated at a much larger geographical scale. However, due to the physical distances and energetic costs that would be involved, as well as observed patterns of site fidelity and limited larval dispersal, it would seem exceedingly unlikely that adult red drum from the east Texas coast and west Florida coast routinely mate with each other and contribute more or less randomly (if at all) to the same newborn cohorts. Red drum tracked in this study have been detected in only one other adjacent spawning site (in low numbers), even though the iTAG network allows fish to be tracked throughout the GOM (Friess et al., 2020). Therefore, it is our belief that the numerator in the previously reported N_e / N_A ratio was likely too low, and its denominator ($\sim 3 \times 10^6$) was almost certainly too high, resulting in an underestimated ratio falsely suggestive of SRS.

Silver seabream have also had conflicting N_e / N_A ratios reported from sampling in the same general area. In a study of silver seabream from the fished population in the Hauraki Gulf (Hauser et al., 2002), N_e was found to be in the range of 100–1000. That study was based on six microsatellite DNA loci (after excluding a seventh, linked locus), for which the average number of alleles per locus was ~10.5. The N_e / N_A ratio was estimated using a spawning stock abundance representing the entire gulf ($N_A \sim 55$ million adults) and, thus, fell easily well within the range of the SRS criterion. However, given the sizes reported for each generation sample of n_g~50, which was common at the time for marine species, the signal from sampling error in the temporal and heterozygosity-based estimators used would be expected to overwhelm the relevant signal of genetic drift unless true N_e was very small (~100 or smaller; Nunney, 2006). When estimated by Jones et al. (2019) using a single sample of ~1000 adult genotypes from the unfished MPA and the sample-bias-adjusted LD method, both the point estimate and lower *CI* of N_e were considerably larger. Similar to red drum, that study was based on nine microsatellite loci and the average number of alleles per locus was ~18. As shown in simulations by Waples (2016b) and consistent with the red drum random-subsampling results, an n_g of 1000 genotypes would have been insufficient to estimate the true N_e with the needed precision if it was larger.

The critical issue from Jones et al. (2019) pertains to the geographical home range of the parents that produced the ~1000 adults genotyped for that study. Silver seabream in the reserve have a predominantly bipartite life cycle characterized by a dispersive larval phase and a relatively sedentary adult phase. Thus, larval dispersal drives the exchange of individuals (and alleles) among populations. The Hauraki Gulf has a surface area of ~4000 km^2 and the Leigh reserve (5.6 km^2) is ~1% of the gulf. There is no evidence of genetic differentiation within the gulf, and tagging studies suggest at least some demographic exchange within a range of ~100 km (Crossland, 1982; Gilbert & McKenzie, 1999; Parsons et al., 2014; Paul, 1967). Silver seabream larvae are reported to disperse along

TABLE 4 Hill's equation estimates for variance in lifetime reproductive success.

Species	$\acute{N}_e$	N_A	$\hat{N}_1$	$\hat{N}_\alpha$	$\hat{V}^*_{k(N_1)}$	$\hat{V}^*_{k(N_\alpha)}$
Southern bluefin tuna	200,000	1,970,000	3,588,041	454,214[b]	938.9	117.1
	500,000				**374.3**	**45.6**
	1000,000				186.2	21.8
Red drum	54,002	199,595	110,037	30,618	95.6	25.1
	85,521				59.6	15.1
	99,798[a]				50.8	12.7
	54,002	400,000	220,521	61,362	193.5	54.4
	85,521				**121.5**	**32.4**
	189,577				53.7	13.5
	54,002	600,000	330,781	92,042	291.3	79.6
	85,521				183.2	49.5
	189,577				81.5	21.2
Silver seabream	4403	31,393	8723	3010	175.9	59.4
	16,388				45.8	14.5
	INF				INDET	INDET
	4403	200,000	55,574	19,182	1131.4	389.2
	16,388				***302.5***[c]	***103.1***[c]
	100,000[a]				47.9	15.2
	4403	500,000	138,935	47,956	2831.6	976.1
	16,388				759.3	260.8
	250,000[a]				47.9	15.2

Note: Sequential values of $\acute{N}_e$ reflect lower confidence intervals (*CI*s), point estimates and upper *CI*s, respectively. INF = infinite; INDET = indeterminate. Most plausible values of $\hat{V}^*_{k(N_1)}$ and $\hat{V}^*_{k(N_\alpha)}$ for southern bluefin tuna and red drum are shown in bold type; minimum plausible values for silver seabream are shown in bold italics; minimum and maximum values for all species are highlighted in grey. Blank entries equate to those in the preceding rows.

[a] Values assume theoretical maximum of $\frac{N_A}{0.5}$.

[b] The modelled value is nearly identical to that independently estimated for N_α in Waples et al., 2018

[c] Minimum plausible values are based on the assumption of an expanded geographical scale.

the coast at an average distance of ~30 km in both northerly and southerly directions from the reserve, with <1.5% exhibiting self-recruitment (Le Port et al., 2017). In contrast, red drum larvae are spatially constrained by the estuary off of which they spawn. Although it is possible that silver seabream offspring from the reserve exhibit natal homing as adults, the genetic structure does not support this, suggesting the MPA adult residents are members of a larger demographically connected (reproductively interdependent) unit. Our results using N_A congruent with greater mixing suggests the need for additional work to estimate N_e in this region and to assess the spatial processes driving mixing, as well as consideration of impacts on $s_x$and T from harvest on the non-MPA portion of the adult stock (see below).

4.2 | Limitations of deterministic modelling

A common limitation of deterministic modelling is capturing the relevant underlying complexity of biological systems. Several aspects of life history and spawning behaviour, such as stochasticism in spawning stock abundance and year-class strength, intermittency in individual spawning and various forms of persistent individual differences were not addressed in our genetic-demographic model. For red drum, we obtained estimates of seasonal adult abundance that differed significantly each measured year, varying by as much as sevenfold between 2014 ($N_A \approx 50{,}000$) and 2019 ($N_A \approx 350{,}000$). Because sampling occurred during spawning seasons on grounds where adults are not year-long residents, the large observed inter-seasonal variability could be attributed to fluctuations either in the number of returning spawners or in the number of recruiting first-time spawners (Lowerre-Barbieri et al., 2015; Walters-Burnsed et al., 2020). Tracking results did not suggest most first-time spawners recruit directly from the estuary, but sample sizes were very small. Certainly, given the large numbers of younger adults (Table S5) and evidence of strong, persistent year classes (Murphy & Crabtree, 2001; Winner et al., 2014), variable recruitment of maturing fish to the spawning grounds is a plausible hypothesis for the annual variability in N_A.

Spawning stock abundance is known to be poorly related to recruitment in most marine populations (Munch et al., 2018), often showing chaotic, nonstationary or non-linear dynamics (Sharma et al., 2019). In this study due to data limitations, we estimated N_1 and N_α for each species by scaling them to values of N_A using a discrete-time partial life table. This appears to have had little impact, as our scaled estimates of N_1 and N_α for southern bluefin tuna were quite similar to those based independent methods (Preece et al., 2019; Waples et al., 2018). As exemplified by red drum, spawning stock abundance cannot be assumed to be static over time, leading to a non-stable adult age distribution, and variable reproductive output. Although recruitment is well known to be a result of biotic and abiotic factors (Cardinale & Arrhenius, 2000), variability in source dynamics is rarely considered and there is a need to better assess uncertainty associated with modelled values of N_1 and N_α.

In iteroparous species, it is common for some members of a cohort to be consistently more productive than others. Whereas 'persistent individual differences' are not explicitly addressed in our model, they are expected to increase V_k^* and reduce N_e when they occur (Lee et al., 2011, 2020; Nunney, 1996). Assuming lifelong continuity in size advantages, size-at-age variation is one of several factors that can lead to persistent individual differences in reproductive success. Persistent individual differences in egg and larvae size and quality might also be a factor (Kjørsvik et al., 1990) and the phenomenon extends to behavioural traits as well (Hertel et al., 2020). These differences could have an underlying heritable basis. However, they could also be products of maternal effects (Kjesbu et al., 1996; Marshall et al., 1998; Marteinsdottir & Thorarinsson, 1998), epigenetically controlled development (Herrera & Bazaga, 2011) or simply reflect early but lasting environmental (silver spoon) effects (Tuljapurkar et al., 2021), which arise stochastically.

A final caveat—our model assumes a dynamically stable population with random demographic stochasticity over longer periods such that, on the whole, members replace themselves within their lifespans. However, drivers of spawning stock abundance may change over time (Kell et al., 2016), further complicating estimation. Stocks might display large, temporally correlated changes in recruitment that are seemingly unrelated to N_A, perhaps reflecting regime-shifts in productivity (Hare et al., 1999; Mantua et al., 1997). Ultimately, values of N_e are dependent on the abundances of newborn or recruiting cohorts, not N_A. However, certain model parameters and procedures (e.g. values of s_x, the scaling of b'_x) could be affected if these correlated changes in N_A arise and persist in a magnitude and periodicity that disrupts population stability within the modelled generations (Waples et al., 2014). In summary, parameter specification and the treatment of stochasticity could be expanded and improved for the genetic model used herein (see Supporting Information for specific means of improvement).

4.3 | Lessons from the three modelled populations

The primary lesson is this—these three populations maintain their effective population sizes through quite different sets of intrinsic traits and behaviours. Yet over time, all have demonstrated population-level reproductive resilience to the random extrinsic processes that forcefully drive mortality. As such, they represent model populations for the RRP. Despite having variances in LRS that are unquestionably overdispersed, each population yielded values of N_e / N_A that were highly inconsistent with SRS. There are important adaptive differences in the life histories of these species that likely impact their effective population sizes through individual or combined influences on T and V_k^* (Table 5). For example, each population differs with respect to maturation timing and generation length. When all else is equal, delaying maturity increases generation length and, because N_e is proportional to T, should lead to a higher N_e (Lee et al., 2011). However, not all increases in T result in increases in N_e due to competing effects between V_k^* and T on N_e (see Section 1.1). In terms of BOFFFF effects, there is a direct pathway between B_x and V_k^*. That is, when the reproductive contributions of the oldest females to annual cohorts are considerably higher than those of younger females due to BOFFFF effects on B_x, V_k^* is expected to increase. It should be noted that this pathway also depends to a degree on levels of ϕ_x (Waples, 2016a; see also Nunney, 1996). Ultimately, the best approach to specifically examine BOFFFF effects on V_k^* will be through individual-based modeling (*see* Supporting Information), due to flexibility in incorporating a range of factors (beyond batch fecundity) that drive age-specific reproductive success, while removing the need to scale b'_x to $2\bar{k}^*$.

4.4 | Reproductive resilience as a conceptual model for marine populations

As conceptual models, the RRP and SRS address similar natural processes and systems but are constructed with quite different assumptions and expectations. Both acknowledge the fact that LRS occurs at the individual biological scale and that a close relationship between adult abundance and population productivity may not exist. Both agree that understanding of reproductive success in marine fish requires knowledge of the processes that influence egg production and fertilization, as well as survivorship of those eggs to maturity and eventual recruitment to the spawning population (Hedgecock & Pudovkin, 2011; Lowerre-Barbieri et al., 2009, 2015, 2017). Both also highlight the fact that LRS dynamics in marine populations differ from those observed in most terrestrial species (Hedgecock, 1994: Lowerre-Barbieri et al., 2017).

The SRS proposes that random extrinsic forces are the main drivers of marine fish offspring survival and recruitment. This suggests, by extension, that large marine populations are poorly adapted to their environments. In a broad sense, the evidence does not support this 'corollary'. As long as critical habitat remains free of anthropogenic destruction, heavily exploited marine populations rarely reach abundances sufficiently small for concerns about population viability (Poulsen, 2010), and they seldom reach effective population sizes that result in inbreeding, rapid genetic change, overwhelmed selective forces or loss of genetic diversity (Hauser & Carvalho, 2008;

TABLE 5 Intrinsic influences on effective population size in contexts of generation length or lifetime variance in reproductive success. Literature citations for table cell entries are provided in Table S1b.

Population/traits and measures	Red drum	Southern bluefin tuna	Silver seabream	Parameter influenced
Age at maturity	4 (50%); 5 (100%)	8 (50%)	5(39%); 6 (100%)	
Longevity	36–40 years	30–40 years	50–60 years	
Reproductive lifespan	~32–36 years	~22–32 years	~45–55 years	
Important difference	Southern bluefin tuna has delayed maturity while silver seabream has the longest generation length.			T
Maximum body weight	45 kg	260 kg	20 kg	
Maximum body length	974 mm FL	1813 mm FL	588 mm FL	
Mean batch fecundity	2,548,137	6.5 million	45,785	
Important difference	Degree of hyperallometric scaling is low in red drum, high in southern bluefin tuna and silver seabream (Figure 5c, d).			V_k^*
B_x of oldest females compared to youngest	2.4 times higher	5.6 times higher	8.6 times higher	
Important difference	Oldest female age classes produce more offspring in a given cohort than youngest age classes in silver seabream compared to red drum and southern bluefin tuna			V_k^*
Lower than expected annual success in fish spawning in their first few seasons	Spawning season of first-year spawners truncated by ~50%	Unknown	Unknown	
Important result	In red drum, early reproductive age classes may contribute less than expected to particular cohorts.			T and V_k^*
Spawning interval	3.7 days	Mean 1.4 d (↑ with size)	Posited daily	
Estimated no. of annual spawning events (female)	~11	~19 (based on Atlantic bluefin tuna)	~55 (based southern Australian stock)	
Maximum no. of lifetime spawning opportunities	~396	~418	~2860	
Important difference	Silver seabream breeders have many more lifetime opportunities for reproductive success than red drum or southern bluefin tuna breeders, albeit at much lower batch fecundities			V_k^*

Ryman et al., 1995). Most importantly, the great diversity and enormous complexities of their reproductive strategies indicate that natural selection plays a key role in the viability and persistence of marine populations.

In contrast to the SRS, the RRP proposes that marine species have evolved their small-eggs strategies to achieve LRS within their ecological context—that is, that natural selection continually creates and filters suites of species-specific traits that enable marine fish (including those that are harvested) to be reproductively successful in a wide range of mortality environments (Lowerre-Barbieri et al., 2015, 2017). Further, the RRP hypothesizes that persistent populations have evolved both density-dependent and fitness feedback loops made up of fixed, behavioural and ecologically variable traits (see Figure 3 in Lowerre-Barbieri et al., 2017) and that these feedback loops, as drivers of LRS, are critical determinants of V_k^* and N_e / N_A.

The RRP requires a 'shift' from the idea that LRS is driven solely or predominantly by a lottery system that treats natural selection as a bystander. As noted by Waples and Reed (2023), opportunities for selection do not represent selection itself. Thus, biologically relevant genetic mechanisms must be identified demonstrating that small-eggs reproductive strategies can be adaptive in marine populations even when reproductive success is strongly skewed towards a relatively small fraction of potential breeders. For example, in a recent comparison by Árnason et al. (2023), a model based mechanistically on recurrent and pervasive selective sweeps of abundant beneficial mutations arising from enormous lifelong fecundities was shown to provide the best explanation for observed patterns of genetic variation in whole-genome sequences of Atlantic cod, *Gadus morhua*, outperforming a 'random sweepstake' (i.e. SRS) model. Whereas a 'recurrent selective sweepstakes' (RSS) hypothesis will not apply ubiquitously to marine populations, unlike SRS, its nexus with the broader concept of the RRP is obvious. Continued exploration of this and other genetic mechanisms, with inclusion of the role of phenotypic plasticity (Lowerre-Barbieri et al., 2016), is strongly encouraged.

5 | CONCLUSIONS

Ecological paradigms in fisheries science are rapidly changing with the advent of new technologies, not the least of which are new genetic and genomic approaches. Greater collaboration across fields within fisheries science, integrating research from genetics, reproductive dynamics and early life history is needed to better understand the dynamic processes driving reproductive resilience and how they are impacted by fishing. With improvements in empirical genetic methodology and non-lethal sampling, as well as a wider range of tagging/tracking methods, we are developing a more comprehensive toolbox. However, a better understanding will also require embracing new ways of thinking about reproductive success in marine fish, acknowledging that a broad array of biological, ecological and evolutionary interactions drives population resilience and growth, not just the total number of eggs produced by females and not just luck.

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DATA AVAILABILITY STATEMENT

Data and information needed to evaluate the conclusions in the paper are present within the paper, cited literature, and/or Supporting Information. Genotype data sets used in this study for N_e estimation in red drum, including randomly sampled subsets, as well as primary batch fecundity data are available from the Dryad data repository at doi:10.5061/dryad.3j9kd51pd.

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REFERENCES

Addis, D. (2020). The 2020 stock assessment of Red Drum, Scieanops ocellatus, in Florida. Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute. 100 8th Ave SE, Saint Petersburg, Florida 33701. December 2020. In-House Report: IHR 2020–002.

Allen, R. M., Metaxas, A., & Snelgrove, P. V. R. (2017). Applying movement ecology to marine animals with complex life cycles. *Annual Review of Marine Science*, *10*, 19–42. https://doi.org/10.1146/annurev-marine-121916-063134

Andersen, K. H., Berge, T., Gonçalves, R. J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N. S., Lindemann, C., Martens, E. A., Neuheimer, A. B., Olsson, K., Palacz, A., Prowe, A. E. F., Sainmont, J., Traving, S. J., Visser, A. W., Wadhwa, N., & Kiørboe, T. (2016). Characteristic sizes of life in the oceans, from bacteria to whales. *Annual Review of Marine Science*, *8*, 217–241.

Árnason, E., Koskela, J., Halldórsdóttir, K., & Eldon, B. (2023). Sweepstakes reproductive success via pervasive and recurrent selective sweeps. *eLife*, *12*, e80781. https://doi.org/10.7554/eLife.80781

Arnold, S. J., & Wade, M. J. (1984). On the measurement of natural and sexual selection: Applications. *Evolution*, *38*, 720–734.

Bakun, A. (1996). Patterns in the ocean: Ocean processes and marine population dynamics. Univ. California Sea Grant, San Diego, CA (in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, BCS, Mexico), 323 pp.

Barneche, D. R., Ross Robertson, D., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science*, *360*(6389), 642–645. https://doi.org/10.1126/science.aao6868

Beckman, D. W., Fitzhugh, G. R., & Wilson, C. A. (1988). Growth rates and validation of age estimates of red drum, *Sciaenops ocellatus*, in a Louisiana salt marsh impoundment. *Contributions in Marine Science*, *30*, S93–S98.

Berger, A. M., Goethel, D. R., & Lynch, P. D. (2017). Introduction to "space oddity: Recent advances incorporating spatial processes in the fishery stock assessment and management interface". *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 1693–1697.

Berger, A. M., Goethel, D. R., Lynch, P. D., Terrance, Q., II, Mormede, S., McKenzie, J., & Dunn, A. (2017). Space oddity: The mission for spatial integration. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(11), 1698–1716. https://doi.org/10.1139/cjfas-2017-0150

Berkeley, S. A., Hixon, M. A., Larson, R. J., & Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, *29*, 23–32.

Brodie, E. D., III, Moore, A. J., & Janzen, F. J. (1995). Visualizing and quantifying natural selection. *Trends in Ecology & Evolution*, *10*(8), 313–318.

Cadrin, S. X. (2020). Defining spatial structure for fishery stock assessment. *Fisheries Research*, *221*, 105397.

Cadrin, S. X., & Secor, D. H. (2009). Accounting for spatial population structure in stock assessment: Past, present, and future. In R. J. Beamish & B. J. Rothschild (Eds.), *The future of fisheries science in North America. Fish & fisheries series* (Vol. *31*). Springer. https://doi.org/10.1007/978-1-4020-9210-7_22

Cardinale, M., & Arrhenius, F. (2000). The influence of stock structure and environmental conditions on the recruitment process of Baltic cod estimated using a generalized additive model. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(12), 2402–2409. https://doi.org/10.1139/f00-221

Ciannelli, L., Bailey, K., & Olsen, E. M. (2015). Evolutionary and ecological constraints of fish spawning habitats. *ICES Journal of Marine Science*, *72*(2), 285–296. https://doi.org/10.1093/icesjms/fsu145

Ciannelli, L., Fisher, J. A. D., Skern-Mauritzen, M., Hunsicker, M. E., Hidalgo, M., Frank, K. T., & Bailey, K. M. (2013). Theory, consequences, and evidence of eroding population spatial structure in harvested marine fishes: A review. *Marine Ecology Progress Series*, *480*, 227–243.

Clutton-Brock, T. (1988). *Reproductive success* (3rd ed.). University of Chicago Press.

Cowen, R. K., Paris, C. B., & Srinivasan, A. (2006). Scaling of connectivity in marine populations. *Science*, *311*, 522–527.

Crossland, J. (1982). *Movements of tagged snapper in the Hauraki gulf*. Occasional publication no. 35, Fisheries Research Division, New Zealand Ministry of Agriculture and Fisheries, Wellington.

Crow, J. F. (1958). Some possibilities for measuring selection intensities in man. *Human Biology*, *30*, 1–13.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. In J. H. S. Blaxter & A. J. Southward (Eds.), *Advances in marine biology* (pp. 250–313). Academic Press Limited.

D'Aloia, C. C., Bogdanowicz, S. M., Francis, R. K., Majoris, J. E., Harrison, R. G., & Buston, P. M. (2015). Patterns, causes, and consequences of marine larval dispersal. *Proceedings of the National Academy of Sciences*, *112*(45), 13940–13945. https://doi.org/10.1073/pnas.1513754112

Davison, A., & Chiba, S. (2003). Laboratory temperature variation is a previously unrecognized source of genotyping error during capillary electrophoresis. *Molecular Ecology Notes*, *3*, 321–323.

Do, C., Waples, R. S., Peel, D., Macbeth, G. M., Tillett, B. J., & Ovenden, J. R. (2013). NeEstimatorv2: re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. *Molecular Ecology Resources*, *14*(1), 209–214. https://doi.org/10.1111/1755-0998.12157

Fitzhugh, G. R., Shertzer, K. W., Kellison, G. T., & Wyanski, D. M. (2012). Review of size- and age-dependence in batch spawning: Implications for stock assessment of fish species exhibiting indeterminate fecundity. *Fishery Bulletin*, *110*, 413–425.

Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: A review. *Genetical Research*, *66*(2), 95–107. https://doi.org/10.1017/S0016672300034455

Friess, C., Lowerre-Barbieri, S., Poulakis, G., Hammerschlag, N., Gardiner, J., Kroet, Z. A., Bassos-Hull, K., Bickford, J., Bohaboy, E., Ellis, R., Menendez, H., Patterson, W., Price, M. E., Rehage, J. S., Shea, C. P., Smukall, M. J., Walters-Burnsed, S., Wilkinson, K. A., Young, J., … Griffen, L. (2020). Regional scale variability in the movement ecology of marine fishes revealed by an integrative acoustic tracking network. *Marine Ecology Progress Series*, *663*, 157–177. https://doi.org/10.3354/meps13637

Furstenau, T. N., & Cartwright, R. A. (2016). The effect of the dispersal kernel on isolation-by-distance in a continuous population. *PeerJ*, *29*(4), e1848. https://doi.org/10.7717/peerj.1848

Garrod, D. J., & Horwood, J. W. (1984). Reproductive strategies and the response to exploitation. In G. W. Potts & R. J. Wootton (Eds.), *Fish reproduction: Strategies and tactics* (pp. 367–384). Academic Press.

Gilbert, D. J., & McKenzie, J. R. (1999). Sources of bias in biomass estimates from tagging programmes in the SNA 1 snapper (*Pagrus auratus*) stock. In *New Zealand fisheries assessment research document 99/16*. NIWA Library.

Goethel, D. R., Legault, C. M., & Cadrin, S. X. (2015). Testing the performance of a spatially explicit tag-integrated model of yellowtail flounder (Limanda ferruginea) through simulation analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 582–601.

Gold, J. R., Burridge, C. P., & Turner, T. F. (2001). A modified steppingstone model of population structure in red drum, Sciaenops ocellatus (*Sciaenidae*), from the northern Gulf of Mexico. *Genetica*, *111*(1–3), 305–317. https://doi.org/10.1023/a:1013705230346

Hare, J. A., Quinlan, J. A., Werner, F. E., Blanton, B. O., Govoni, J. J., Forward, R. B., Settle, L. R., & Hoss, D. E. (1999). Larval transport during winter in the SABRE study area: Results of a coupled vertical larval behaviour–three-dimensional circulation model. *Fisheries Oceanography*, *8*, 57–76.

Hare, M. P., Nunney, L., Schwartz, M. K., Ruzzante, D. E., Burford, M., Waples, R. S., Ruegg, K., & Palstra, F. (2011). Understanding and estimating effective population size for practical application in marine species management. *Conservation Biology*, *25*(3), 438–449.

Hauser, L., Adcock, G. J., Smith, P. J., Bernal Ramírez, J. H., & Carvalho, G. H. (2002). Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (*Pagrus auratus*). *Proceedings of the National Academy of Sciences*, *99*(18), 11742–11747. https://doi.org/10.1073/pnas.172242899

Hauser, L., & Carvalho, G. R. (2008). Paradigm shifts in marine fisheries genetics: Ugly hypotheses slain by beautiful facts. *Fish and Fisheries*, *9*, 333–362.

Hawkins, S. J., Bohn, K., Sims, D. W., Ribeiro, P., Faria, J., Presa, P., Pita, A., Martins, G. M., Neto, A. I., Burrows, M. T., & Genner, M. J. (2016). Fisheries stocks from an ecological perspective: Disentangling ecological connectivity from genetic interchange. *Fisheries Research*, *179*, 333–341.

Heath, M. R., Kunzlik, P. A., Gallego, A., Holmes, S. J., & Wright, P. J. (2008). A model of meta-population dynamics for North Sea and West of Scotland cod—The dynamic consequences of natal fidelity. *Fisheries Research*, *93*, 92–116.

Hedgecock, D. (1994). Does variance in reproductive success limit effective population sizes of marine organisms? In A. Beaumont (Ed.), *Genetic and evolution of aquatic organisms* (pp. 122–134). Chapman and Hall.

Hedgecock, D., Hutchinson, E. S., Li, G., Sly, F. L., & Nelson, K. (1994). The central stock of northern anchovy (*Engraulis mordax*) is not a randomly mating population. *Reports of California Cooperative Oceanic Fisheries Investigations*, *35*, 121–136.

Hedgecock, D., & Pudovkin, A. I. (2011). Sweepstakes reproductive success in highly fecund marine fish and shellfish: A review and commentary. *Bulletin of Marine Science*, *87*, 971–1002.

Hedrick, P. (2005). Large variance in reproductive success and the Ne/N ratio. *Evolution*, *59*, 1596–1599.

Herrera, C. M., & Bazaga, P. (2011). Untangling individual variation in natural populations: Ecological, genetic and epigenetic correlates of long-term inequality in herbivory. *Molecular Ecology*, *20*, 1675–1688. https://doi.org/10.1111/j.1365-294X

Hertel, A. G., Niemelä, P. T., Dingemanse, N. J., & Mueller, T. (2020). A guide for studying among-individual behavioral variation from movement data in the wild. *Movement Ecology*, *8*, 30. https://doi.org/10.1186/s40462-020-00216-8

Hill, W. G. (1972). Effective size of population with overlapping generations. *Theoretical Population Biology*, *3*, 278–289.

Hill, W. G. (1979). A note on effective population size with overlapping generations. *Genetics*, *92*(1), 317–322.

Hixon, M. A., Johnson, D. W., & Sogard, S. M. (2014). BOFFFFs: On the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, *71*, 2171–2185.

Hjort, J. (1914). Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Conseil Permanent International Pour l'Exploration de la Mer*, *20*, 1–228.

Hollenbeck, C. M., Portnoy, D. S., & Gold, J. R. (2019). Evolution of population structure in an estuarine-dependent marine fish. *Ecology and Evolution*, *9*(6), 3141–3152.

Husemann, M., Zachos, F., Paxton, R., & Habel, J. C. (2016). Effective population size in ecology and evolution. *Heredity*, *117*, 191–192. https://doi.org/10.1038/hdy.2016.75

Hutchings, J. A., & Reynolds, J. D. (2004). Marine fish population collapses: Consequences for recovery and extinction risk. *Bioscience*, *54*(4), 297–309.

Iles, T. D., & Sinclair, M. (1982). Atlantic herring: Stock discreteness and abundance. *Science*, *215*(4533), 627–633. https://doi.org/10.1126/science.215.4533.627

Jones, A., Lavery, S., Le Port, A., Wang, Y.-G., Blower, D., & Ovenden, J. (2019). Sweepstakes reproductive success is absent in a New Zealand snapper (*Chrysophrus auratus*) population protected from fishing despite 'tiny' Ne/N ratios elsewhere. *Molecular Ecology*, *28*(12), 2986–2995.

Judge, M. L., Quinn, J. F., & Wolin, C. L. (1988). Variability in recruitment of *Balanus glandula* (Darwin, 1854) along the Central California coast. *Journal of Experimental Marine Biology and Ecology*, *119*(3), 235–251. https://doi.org/10.1016/0022-0981(88)90195-5

Kell, L. T., Nash, R. D. M., Dickey-Collas, M., Mosqueira, I., & Szuwalski, C. (2016). Is spawning stock biomass a robust proxy for reproductive potential? *Fish and Fisheries*, *17*, 596–616. https://doi.org/10.1111/faf.12131

Kerr, L. A., Cadrin, S. X., & Secor, D. H. (2010). The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. *Ecological Applications*, *20*, 497–507.

Kerr, L. A., Niels, T., Hintzen, S. X., Cadrin, L. C., Dickey-Collas, M., Goethel, D. R., Hatfield, E. M. C., Kritzer, J. P., & Nash, R. D. M. (2017). Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES Journal of Marine Science*, *74*(6), 1708–1722. https://doi.org/10.1093/icesjms/fsw188

Kjesbu, O. S., Solemdal, P., Bratlan, P., & Fonn, M. (1996). Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 610–620.

Kjörsvik, E., Mangor-Jensen, A., & Homefjord, I. (1990). Egg quality in marine fishes. *Advances in Marine Biology*, *26*, 71–113.

Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in the California current: Identification of factors contributing to recruitment failure. *Rapports et Procès Verbaux Des Réunions—Conseil International Pour L'exploration de la Mer*, *173*, 212–230.

Laurent, V., & Planes, S. (2007). Effective population size estimation on *Sardina pilchardus* in the Bay of Biscay using a temporal genetic approach. *Biological Journal of the Linnean Society*, *90*, 591–602.

Le Port, A., Montgomery, J. C., Smith, A. N. H., Croucher, A. E., McLeod, I. M., & Lavery, S. D. (2017). Temperate marine protected area provides recruitment subsidies to local fisheries. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1865), 20171300. https://doi.org/10.1098/rspb.2017.1300

Lee, A. M., Engen, S., & Sæther, B.-E. (2011). The influence of persistent individual differences and age at maturity on effective population size. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *278*, 3303–3312.

Lee, A. M., Myhre, A. M., Markussen, S. S., Engen, S., Solberg, E. J., Haanes, H., Røed, K., Herfindal, I., Heim, M., & Sæther, B.-E. (2020). Decomposing demographic contributions to the effective population size with moose as a case study. *Molecular Ecology*, *29*, 56–70.

Leis, J. M., Siebeck, U. E., Hay, A. C., Paris, C. B., Chateau, O., & Wantiez, L. (2015). In situ orientation of fish larvae can vary among regions. *Marine Ecology Progress Series*, *537*, 191–203. https://doi.org/10.3354/meps11446

Lowerre-Barbieri, S., Brown-Peterson, N., Murua, H., Tomkiewicz, J., Wyanski, D., & Saborido-Rey, F. (2011). Emerging issues and methodological advances in fisheries reproductive biology. *Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science [Online Serial]*, *3*, 32–51.

Lowerre-Barbieri, S., Crabtree, L., Switzer, T., Walters Burnsed, S., & Guenther, C. (2015). Assessing reproductive resilience: An example with South Atlantic red snapper *Lutjanus campechanus*. *Marine Ecology Progress Series*, *526*, 125–141.

Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catala'n, I. A., Muhling, B., Erisman, B., Cadrin, S. X., Alos, J., Ospina-Alvarez, A., Stachura, M. M., Tringali, M. D., Walters Burnsed, S., & Paris, C. B. (2017). Reproductive resilience: A paradigm shift in understanding spawner-recruit systems in exploited marine fish. *Fish and Fisheries*, *18*, 285–312.

Lowerre-Barbieri, S., Ganias, K., Saborido-Rey, F., Murua, H., & Hunter, J. (2011). Reproductive timing in marine fishes: Variability, temporal scales, and methods. *Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science [Online Serial]*, *3*, 71–91.

Lowerre-Barbieri, S., Menendez, H., Bickford, J., Switzer, T. S., Barbieri, L., & Koenig, C. (2020). Testing assumptions about sex change and spatial management in the protogynous gag grouper, *Mycteroperca microlepis*. *Marine Ecology Progress Series*, *639*, 199–214.

Lowerre-Barbieri, S. K. (2009). Reproduction in relation to conservation and exploitation of marine fishes. In B. G. M. Jamieson (Ed.), *Reproductive biology and phylogeny of fishes (agnathans and bony fishes), volume 8B* (pp. 371–394). Science Publishers. Enfield.

Lowerre-Barbieri, S. K., Kays, R., Thorson, J. T., & Wikelski, M. (2019). The ocean's movescape: Fisheries management in the bio-logging decade (2018–2028). *ICES Journal of Marine Science*, *76*, 477–488.

Lowerre-Barbieri, S. K., Tringali, M. D., Shea, C. P., Walters Burnsed, S., Bickford, J., Murphy, M., & Porch, C. (2018). Assessing red drum spawning aggregations and abundance in the eastern Gulf of Mexico: A multidisciplinary approach. *ICES Journal of Marine Science*, *76*(2), 516–529.

Lowerre-Barbieri, S. K., Walters Burnsed, S. L., & Bickford, J. W. (2016). Assessing reproductive behavior important to fisheries management: A case study with red drum, *Sciaenops ocellatus*. *Ecological Applications*, *26*, 979–995.

Mangel, M., MacCall, A. D., Brodziak, J., Dick, E. J., Forrest, R. E., Pourzand, R., & Ralston, S. (2013). A perspective on steepness, reference points, and stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*, 930–940.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, *78*, 1069–1079.

Marandel, F., Lorance, P., Berthelé, O., Trenkel, V. M., Waples, R. S., & Lamy, J. B. (2019). Estimating effective population size of large marine populations, is it feasible? *Fish and Fisheries*, *20*, 189–198.

Marshall, C. T., Needle, C. L., Thorsen, A., Kjesbu, O. S., & Yaragina, N. A. (2006). Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: Implications for stock-recruit theory and management. *Canadian Journal of Fisheries and Aquatics Sciences*, *63*, 980–994.

Marshall, D. J., Heppell, S. S., Munch, S. B., & Warner, R. R. (2010). The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring? *Ecology*, *91*, 2862–2873.

Marshall, T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P., & Ulltang, Ø. (1998). Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1766–1783.

Marteinsdottir, G., & Thorarinsson, K. (1998). Improving the stock–recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*, 1372–1377.

Morin, P. A., Manaster, C., Mesnick, S. L., & Holland, R. (2009). Normalization and binning of historical and multi-source microsatellite data: Overcoming the problems of allele size shift with ALLELOGRAM. *Molecular Ecology Resources*, *9*, 1451–1455.

Munch, S. B., Giron-Nava, A., & Sugihara, G. (2018). Nonlinear dynamics and noise in fisheries recruitment: A global meta-analysis. *Fish and Fisheries*, *19*, 964–973. https://doi.org/10.1111/faf.12304

Murphy, M. D., & Crabtree, R. E. (2001). Changes in the age structure of nearshore adult red drum off west-Central Florida related to recruitment and fishing mortality. *North American Journal of Fisheries Management*, *21*, 671–678.

Murphy, M. D., & Taylor, R. G. (1990). Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. *Fishery Bulletin*, *88*, 531–542.

Nadachowska-Brzyska, K., Dutoit, L., Smeds, L., Kardos, M., Gustafsson, L., & Ellegren, H. (2021). Genomic inference of contemporary effective population size in a large Island population of collared flycatchers (*Ficedula albicollis*). *Molecular Ecology*, *30*, 3965–3973. https://doi.org/10.1111/mec.16025

Nunney, L. (1996). The influence of variation in female fecundity on effective population size. *Biological Journal of the Linnean Society*, *59*, 411–425.

Nunney, L. (2006). The effect of neighborhood size on effective population size in theory and in practice. *Heredity (Edinb)*, *117*(4), 224–232. https://doi.org/10.1038/hdy.2016.76

Ospina-Alvarez, A., Vásquez, S. I., Catalán, I. A., Lowerre-Barbieri, S., Arteaga, M., & Juan, S. D. (2022). A reproductive resilience index for pelagic fish in the southern Humboldt current large marine ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, *79*, 2138–2159.

Ovenden, J. R., Leigh, G. M., Blower, D. C., Jones, A. T., Moore, A., Bustamante, C., Buckworth, R. C., Bennett, M. B., & Dudgeon, C. L. (2016). Can estimates of genetic effective population size contribute to fisheries stock assessments? *Journal of Fish Biology*, *89*, 2505–2518.

Pafford, J. M., Woodward, A. G., & Nicholson, N. (1990). *Mortality, movement, and growth of red drum in Georgia*. Georgia Department of Natural Resources.

Palstra, F. P., & Fraser, D. J. (2012). Effective/census population size ratio estimation: A compendium and appraisal. *Ecology and Evolution*, *2*, 2357–2365.

Parsons, D. M., Sim-Smith, C. J., Cryer, M., Francis, M. P., Hartill, B., Jones, E. G., le Port, A., Lowe, M., McKenzie, J., Morrison, M., Paul, L. J., Radford, C., Ross, P. M., Spong, K. T., Trnski, T., Usmar, N., Walsh, C., & Zeldis, J. (2014). Snapper *Chrysophrys auratus*: A review of life history and key vulnerabilities in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *48*(2), 256–283. https://doi.org/10.1080/00288330.2014.892013

Paul, L. J. (1967). An evaluation of tagging experiments on the New Zealand snapper *Chrysophrys auratus* (Forster), during the period 1952 to 1963. *New Zealand Journal of Marine and Freshwater Research*, *1*, 455–463.

Peters, K. M., & McMichael, R. (1987). Early life history of the red drum *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries*, *10*, 92–107.

Poulsen, B. (2010). The variability of fisheries and fish populations prior to industrialized fishing: An appraisal of the historical evidence. *Journal of Marine Systems*, *79*(3–4), 327–332. https://doi.org/10.1016/j.jmarsys.2008.12.011

Poulsen, N. A., Nielsen, E. E., Shierup, M. H., Loeschcke, V., & Grønkjær, P. (2006). Long-term stability and effective population size in North Sea and Baltic Sea cod (*Gadus morhua*). *Molecular Ecology*, *15*, 321–331.

Preece, A. L., Eveson, J. P., Bradford, R. W., Grewe, P. M., Aulich, J., Clear, N. P., Lansdell, M., Cooper, S., & Hartog, J. (2019). Report on the gene-tagging juvenile abundance monitoring program: 2016-2019. CSIRO, Australia. CCSBT-ESC/1909/10.

Ross, J. L., Stevens, T. M., & Vaughan, D. S. (1995). Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. *Transactions of the American Fisheries Society*, *124*, 37–54.

Ryman, N., Laikre, L., & Hössjer, O. (2019). Do estimates of contemporary effective population size tell us what we want to know? *Molecular Ecology*, *28*, 1904–1918. https://doi.org/10.1111/mec.15027

Ryman, N., Laikre, L., & Hössjer, O. (2023). Variance effective population size is affected by census size in sub-structured populations. *Molecular Ecology Resources*, *00*, 1–14. https://doi.org/10.1111/1755-0998.13804

Ryman, N., Utter, F., & Laikre, L. (1995). Protection of intraspecific biodiversity of exploited fishes. *Reviews in Fish Biology and Fisheries*, *5*(4), 417–446.

Sharma, R., Porch, C. E., Babcock, E. A., Maunder, M. N., & Punt, A. E. (2019). Recruitment: Theory, estimation, and application in fishery stock assessment models. *Fisheries Research*, *217*, 1–4. https://doi.org/10.1016/j.fishres.2019.03.015

Shpak, M. (2005). Evolution of variance in offspring number: The effects of population size and migration. *Theory in Biosciences*, *124*(1), 65–85. https://doi.org/10.1016/j.thbio.2005.05.003

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Tuljapurkar, S., Zuo, W., Coulson, T., Horvitz, C., & Gaillard, J.-M. (2021). Distributions of LRS in varying environments. *Ecology Letters*, *24*(7), 1328–1340. https://doi.org/10.1111/ele.13745

Turner, T. E., Richardson, L. R., & Gold, J. R. (1998). Polymorphic microsatellite DNA markers in red drum (*Sciaenops ocellatus*). *Molecular Ecology*, *7*, 1771–1788.

Turner, T. F., Wares, J. P., & Gold, J. R. (2002). Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). *Genetics*, *162*(3), 1329–1339.

van Oosterhout, C., Hutchinson, W. F., Wills, D. P. M., & Shipley, P. (2004). MICRO-CHECKER: Software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, *4*, 535–538.

Walters Burnsed, S., Lowerre-Barbieri, S., Bickford, J., & Hoerl Leone, E. (2020). Recruitment and movement ecology of red drum *Sciaenops ocellatus* differs by natal estuary. *Marine Ecology Progress Series*, *633*, 181–196.

Wang, J. L. (2001). A pseudo-likelihood method for estimating effective population size from temporally spaced samples. *Genetics Research*, *78*, 243–257.

Waples, R. K., Larson, W. A., & Waples, R. S. (2016). Estimating contemporary effective population size in non-model species using linkage disequilibrium across thousands of loci. *Heredity*, *117*, 233–240.

Waples, R. S. (1989). A generalized-approach for estimating effective population-size from temporal changes in allele frequency. *Genetics*, *121*, 379–391.

Waples, R. S. (2016a). Life-history traits and effective population size in species with overlapping generations revisited: The importance of adult mortality. *Heredity*, *117*, 241–250.

Waples, R. S. (2016b). Tiny estimates of the Ne /N ratio in marine fishes: Are they real? *Journal of Fish Biology*, *89*, 2479–2504.

Waples, R. S., Antao, T., & Luikart, G. (2014). Effects of overlapping generations on linkage disequilibrium estimates of effective population size. *Genetics*, *197*, 769–780.

Waples, R. S., Do, C., & Chopelet, J. (2011). CalculatingNeandNe/Nin age-structured populations: A hybrid Felsenstein-Hill approach. *Ecology*, *92*, 1513–1522.

Waples, R. S., & England, P. R. (2011). Estimating contemporary effective population size on the basis of linkage disequilibrium in the face of migration. *Genetics*, *189*(2), 633–644. https://doi.org/10.1534/genetics.111.132233

Waples, R. S., Grewe, P. M., Bravington, M. W., Hillary, R., & Feutry, P. (2018). Robust estimates of a high Ne/N ratio in a top marine predator, southern bluefin tuna. *Science Advances*, *4*, eaar7759.

Waples, R. S., Luikart, G., Faulkner, J. R., & Tallmon, D. A. (2013). Simple life history traits explain key effective population size ratios across diverse taxa. *Proceedings of the Royal Society B*, *280*, 20131339.

Waples, R. S., & Reed, T. E. (2023). Null models for the opportunity for selection. *The American Naturalist*, *201*(6), 779–793.

Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in north American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 2196–2218.

Winner, B. L., Flaherty-Walia, K. E., Switzer, T. S., & Vecchio, J. L. (2014). Multidecadal evidence of recovery of nearshore red drum stocks off west-Central Florida and connectivity with inshore nurseries. *North American Journal of Fisheries Management*, *34*, 780–794.

Young, J. L., Bornik, Z. B., Marcotte, M. L., Charlie, K. N., Wagner, G. N., Hinch, S. G., & Cooke, S. J. (2006). Integrating physiology and life history to improve fisheries management and conservation. *Fish and Fisheries*, *7*, 262–283.

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