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Title: An updated life history scheme for marine fishes predicts recruitment variability and sensitivity to exploitation

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ABSTRACT

Aim: Patterns of population renewal in marine fishes are often irregular and lead to volatile fluctuations in abundance that challenge management and conservation efforts. Here, we examine the relationship between life history strategies and recruitment variability in exploited marine fish species using a macroecological approach.

Location: Global ocean.

Time period: 1950-2018.

Major taxa studied: Bony and cartilaginous fish.

Methods: Based on trait data for 244 marine fish species, we objectively extend the established Equilibrium-Periodic-Opportunistic (*E-P-O*) life history classification scheme to include two additional emergent life history strategies: "Bet-hedgers" (*B*) and Salmonic (*S*) strategists. *B* strategists include Rockfishes and other species inhabiting patchy benthic habitats with life histories that blend characteristics of *E* and *P* species; they combine very long lifespans with elevated investments in both parental care and fecundity. *S* strategists are comprised of mostly salmonids that share life history characteristics with *E* and *O* species: elevated investments in parental care reminiscent of *E* strategists, but with reduced fecundity and short lifespans characteristic of *O* species. We analyzed how the *E-B-P-O-S* life history classification mapped onto patterns of recruitment variability observed in population time series data (*n* = 156 species).

Results: Generalized linear models suggest that life history strategy explains a modest, yet significant amount of recruitment variability across species. Greater predictive power arose after controlling for increased recruitment variance associated with variable fishing pressure, with *O* strategists showing the strongest sensitivity. *B* strategists were similarly susceptible to exploitation as *P* stocks, but their longer times to maturity make them particularly vulnerable to overfishing.

Main conclusions: A broader recognition of the distinct ecology of Salmonic and Bet-hedger groups is important when studying life history strategies in marine fish. More generally, our results stress the importance of considering life history strategies for understanding patterns of recruitment variability across fish stocks.

KEY WORDS: fecundity, fishing, life history, maturation rate, parental care, recruitment, rockfishes, salmonid

1. INTRODUCTION

Life history strategies are emergent combinations of species functional traits that reflect adaptations to a given set of biotic and abiotic environmental factors (Winemiller, Fitzgerald, Bower, & Pianka, 2015). The most common example is the archetypical *r/K* selection continuum among unpredictable or short-lived environments that favor opportunistic species (*r*-adapted) and the prevalence of good competitors in constant environments (*K*-adapted; MacArthur & Wilson 2001). In fishes, analyses of life history traits usually distinguish three or more strategies (Kawasaki, 1980; McCann & Shuter, 1997; King & McFarlane, 2003; Haltuch et al., 2019). The most broadly applied approach to date is the Equilibrium-Periodic-Opportunistic (*E-P-O*) scheme of Winemiller and Rose (1992) (Figure 1a). The Equilibrium, or *E*, strategy is essentially a *K*-adapted strategy that is most successful in ecosystems operating near their carrying capacity. Examples include live-bearing sharks and brood-bearing reef fishes with low fecundity but high investment per offspring. The Periodic (*P*) strategy is most prevalent when the environmental variability impacting early life stages is periodic and large-scale. Key traits of this strategy are high batch fecundity to take advantage of relatively predictable variations (e.g. seasonal transitions) and long lifespans to hedge against limited sequences of poor recruitment years. The Opportunistic (*O*) strategy is a colonizing strategy dominant in systems experiencing rapid and chaotic disturbances. The early maturity and high overall reproductive investment distributed throughout the year in *O* species ensure successful recruitment should the right conditions arise. The *E-P-O* life history framework is a valuable tool for the monitoring and prediction of environmental impacts on both freshwater and marine fish communities (Winemiller & Rose, 1992; Winemiller, 2005; Mims & Olden, 2012; Pecuchet et al., 2017). In the case of fishing pressure, this life history framework has been proposed as a tool for guiding fisheries management (Winemiller, 2005).

In fisheries science, recruitment is the process of adding new individuals to the fraction of fish vulnerable to harvesting in an exploited population, often attained by reaching a particular size (Ricker, 1954; Beverton & Holt, 1957). Understanding recruitment variability has been a major concern of fisheries scientists and managers for more than a century (c.f. Hjort, 1914). Patterns of population renewal in fisheries are often erratic and lead to unpredictable population dynamics or, at best, highly uncertain predictions (Cushing, Kinne, & Costlow, 1996; Houde, 2008; Longhurst, 2010), often frustrating management plans (Fogarty, Sissenwine, & Cohen, 1991; Winemiller, 2005; Pinsky, Jensen, Ricard, & Palumbi, 2011). Recruitment variability also constrains resilience to fishing (Anderson et al., 2008; Shelton & Mangel, 2011), and the recovery of collapsed stocks (Kuparinen et al., 2014). Efforts to understand recruitment variability have mainly targeted the dynamics of single stocks, focusing on the interplay between noisy "external" variability (e.g. environmental fluctuations or unresolved multi-species interactions) and a presumed relationship between recruitment and spawning stock biomass (Quinn & Deriso, 1999; Fogarty & O'Brien, 2016). Unfortunately, stock-recruitment (S-R) relationships generally have low predictive power (Rose, Cowan, Winemiller, Myers, & Hillborn, 2001; Winemiller, 2005; Szuwalski, Vert-Pre, Punt, Branch, & Hilborn, 2015), resulting in a limited ability to anticipate regime shifts and fisheries collapses (Hutchings & Reynolds, 2004; Vert-pre, Amoroso, Jensen, & Hilborn, 2012).

A major challenge of traditional stock assessment methods is the demand for detailed biological and operational knowledge about the target fisheries (Quinn & Deriso, 1999). This constraint limits the effectiveness of traditional methods in data-poor stocks (King & McFarlane, 2003; Winemiller, 2005; Longhurst, 2010). Predictable variations in recruitment patterns,

however, have emerged from analyses combining multiple species (e.g. Myers, Bowen, & Barrowman, 1999; Myers, 2001). Such studies have explored the mechanisms that lead to increased recruitment variability through fishing (Shepherd, Cushing, & Beverton, 1990; Hsieh et al., 2006), including reduction of the spawning stock biomass (Fogarty et al., 1991; Minto, Myers, & Blanchard, 2008; Andersen & Beyer, 2015), age truncation by removing older fish (Berkeley, Hixon, Larson, & Love, 2004), and altered demographic parameters that amplify nonlinear behavior (Anderson et al., 2008). Other macroecological studies have revealed that demographic traits (e.g., growth rate, size at maturity) confine patterns of population regulation and the pace of recovery following a collapse (Rose et al., 2001; Hutchings & Reynolds, 2004). In particular, Rose et al. (2001) have shown that life history characteristics can predict whether a fish species will experience compensatory increases in recruitment per adult when stock size is reduced. The strength of such compensatory effects determines population resilience to external perturbations (e.g. Lawson, Vindenes, Bailey, & van de Pol, 2015) and provides the basis for setting the reference points guiding fisheries management decisions. Together, these results support the potential for life history traits to provide meaningful constraints on recruitment variability that can be leveraged to improve management. Furthermore, life history theory provides an ideal framework for understanding variability in demographic traits among fish species and for predicting how these traits vary in response to external pressures like fishing or environmental change (Winemiller, 2005; Mangel, Levin, & Patil, 2006).

      Here, we revisit life history strategies to assess whether they provide a useful framework for explaining macroecological patterns of recruitment variability across exploited marine fish species at the global scale. To do so, we assembled a dataset of functional traits and fisheries data for 244 species of exploited fishes (Froese & Pauly, 2000; Ricard, Minto, Jensen, & Baum, 2012). We analyzed the database of life history traits to identify emergent strategies that extend the Winemiller and Rose (1992) *E-P-O* scheme to account for variability in the life history strategies of harvested fish species. Secondly, we examined the ability of the updated life history scheme, together with environmental preferences and fishing pressure, to explain recruitment variability patterns. Finally, we examine combinations of functional traits that promote fisheries resilience to human exploitation and, more importantly, those that might help to identify regime shifts and prevent fisheries collapses.

2. MATERIALS AND METHODS
2.1 Defining life history and environment traits
      Life history trait data were collected from FishBase (Supplementary Table S1; Froese & Pauly, 2000) on a stock-specific basis for 244 of the exploited marine fish species included in the RAM Legacy Stock Assessment Database (Ricard et al., 2012; see Section 2.2). We preferred the use of FishBase over FishLife (Thorson, Munch, Cope, & Gao, 2017) because it provided information at the stock rather than the species level and thus reflects regional variation in life history traits within species. FishBase was accessed using the package *rfishbase* (version 3.0.4; Boettiger, Chamberlain, Temple Lang, & Wainwright, 2015) for the software *R* (version 4.0.3; R Development Core Team, 2016). All life history and environment traits used were the mean (if numeric) or most frequent (if categorical) value reported for each stock of each species (see Supplementary Information for further details).

      Winemiller and Rose (1992) defined the *E-P-O* scheme based on the optimization of three demographic parameters: (i) generation time, (ii) fecundity, and (iii) juvenile survivorship. FishBase provides direct information on the first two axes (Table 1); maximum time to maturity

serves as an analog to the generation time axis, while the logarithmic mean of minimum and maximum fecundity, Fec,

$$Fec = \frac{Fec_{max} - Fec_{min}}{ln\,(Fec_{max}) - ln\,(Fec_{min})},$$

aligns directly with the fecundity axis. However, there was little to no direct data on juvenile survivorship. Winemiller and Rose (1992) used a variety of traits and metrics as proxies for juvenile survival. Similarly, we calculated a Parental Care Index (PCI) based on traits related to reproductive investment available in FishBase (Torres, 2000a,b). The PCI weighted quantitative and categorical data on the mode of fertilization, Balon's (1990) reproductive guilds, the presence/absence of any kind of parental care, and the duration of the gestation period. The Supplementary Information (Table S2) provides a detailed account of the weighting scheme. We stress that the PCI differentiates basic contrasts in parental care that are robust to nuanced differences in these weights (see Section 3.1).

Maturity and fecundity data were missing for a small fraction (6% and 19% respectively) of stocks in FishBase (Table S3). Many of these stocks, however, contained information on strongly correlated traits (Figure S1). Thus, missing values of maturity and fecundity for this small fraction of stocks were imputed using closely related traits belonging to that stock and traits from other stocks using additive regression and bootstrapping techniques implemented with the *aregImpute* function in the *Hmisc* package (Harrell et al., 2017) of the software *R*. Separate imputations were performed on different taxonomic groups: Elasmobranchii, Scorpaeniformes, and non-Scorpaeniform teleosts (R^2 = 0.89-1.00; Table S3), resulting in 701 stocks of 244 species with values for all three traits.

This approach concurs with prior studies in the choice of using a few traits to summarize variation in fish life history (Winemiller & Rose, 1992; McCann & Shuter, 1997; Secor, 2015). This choice of three traits was not only pragmatic by allowing the retention of high quality data for the maximum number of stocks, but also supported by multiple analyses that revealed strong correlations and high redundancy in life history characteristics (e.g. Charnov 1993, Figure S3). Life history strategy classification was obtained using the *k*-means clustering algorithm implemented in the base distribution of the *R* software (Hartigan & Wong, 1979). The ideal number of clusters was chosen to minimize the total within-cluster sum of squares, which measures the compactness of the clustering (e.g. Webb & Copsey, 2011).

We controlled for the potential influence of the environment on recruitment variability to better isolate the effect of life history. For information on the biome inhabited by each stock, we retrieved the climate zones defined in FishBase that were derived by matching the distribution of each species to the map in the *Bartholomew Illustrated World Atlas* (Anon., 1991; see also Pauly, 1998). This classification mostly reflects large scale gradients in ocean surface conditions and delineates five major pelagic biomes (boreal, polar, temperate, subtropics, and tropics), and a sixth deep-water biome (Froese, 2000). Due to data sparsity, we merged the boreal (3 stocks) and polar biomes, and the tropical (7 stocks) and subtropical.

2.2 Characterizing recruitment variability and fishing pressure

Variability in fishing rates interact with recruitment to generate fluctuations in fish abundance that further propagate to recruitment variability (e.g. Shelton & Mangel, 2011). Specifically, we characterized recruitment variability among stocks based on time series of recruitment (R) and spawning stock biomass (SSB) retrieved from the RAM Legacy Stock Assessment Data (RAM SAD) version 4.44 assessment data only (http://ramlegacy.org). We retrieved estimates of R and SSB based on a variety of stock assessment methods. We excluded

time series expressed in units that would not be directly proportional to recruitment, spawning stock biomass, or abundance (see the Supplementary Information for details). Estimates based on data gathered prior to 1950, stocks with less than 10 years of data, or with an unknown assessment method were excluded. Each stock was screened individually to exclude recruitment estimates that were not directly informed by data. We targeted variability in normalized recruitment deviations from expectations based on a simple density dependent model, i.e. recruitment is proportional to spawning biomass. Recruits per SSB (R/SSB) is often thought of as a measure of early life stage survival that is independent of changes in SSB when the S-R curve is linear (Myers, 2001; Minto et al., 2008). With the aim of understanding early life stage survival, we estimated the variance of the natural logarithm of the survival index R/SSB to measure recruitment variability, which assumes that variability is constant and does not vary with density (Minto et al. 2008). The logarithmic scaling enables comparing residual variability in the abundance of recruits across stocks with data in differing units (individuals or biomass for different stages). We will refer to this variance as "recruitment variability" throughout the remainder of the text. Alternative measures of recruitment variability based on density-dependent recruitment functions that exhibit normal or over compensation (Beverton-Holt or Ricker models; Yodzis 1989) were explored, but the main results presented are robust to this choice (see the Supplementary Information for further details).

To assess the influence of fishing pressure variability on recruitment variability, we calculated the coefficient of variation of annual fishing rate (F_t, yr^{-1}) retrieved from the RAM SAD. The coefficient of variation of fish mortality is directly related to the variance of population size and thus captures to first order the impact of fishing on recruitment variability (Shelton & Mangel, 2011). The analysis of Shelton and Mangel (2011) and its simple extensions lead to expectations of a linear relationship, at a minimum, between the variance in recruitment and the coefficient of variation of fishing mortality. If fishing rates were missing, they were estimated from annual exploitation rates (ER_t, yr^{-1}), when available, using the Baranov (1918) catch equation,

$$ER_t = \frac{F_t}{F_t + M} \left(1 - exp\left(-(F_t + M)\right)\right),$$

where exploitation rates were retrieved from the RAM SAD and stock-specific natural mortality rates (M, yr^{-1}). Species-specific natural mortality rates were used instead of stock-specific rates for over half of the stocks that lacked information from either FishBase or the RAM SAD. Species-specific estimates were obtained with the *R* package *FishLife* (version 2.0.0; Thorson & Ovando, 2019), which is based on the multivariate model of life history invariants developed by Thorson, Munch, Cope, and Gao (2017). Finally, we calculated the coefficient of variation of the time series of F_t for each stock, cvF, to capture the effect of fishing pressure on population variability.

2.3 Relating traits and recruitment variability

Taken together, 427 stocks from 156 species had time series for R, SSB, and F (see the Appendix for time series plots), and values for all three life history traits (time to maturity, fecundity, and PCI). R time series length ranged from 11 to 69 years with a median length of 33 years while F time series ranged from 10 to 68 years with a median of 32 years (Figure S1). For each stock, we calculated recruitment variability and the coefficient of variation of fishing rate as described above. Then, we used generalized linear models (GLMs) to partition the amount of recruitment variability that could be attributed to differences in life history, the environment, and fishing pressure across stocks. GLMs were fit with the *glm* function in *R* assuming a gamma

distribution and a log link function (Venables & Ripley, 2002). We tested every possible model of single and multiple terms, as well as interaction effects. Model selection was based on Aikaike's Information Criterion for small sample sizes (AICc) given that the ratio of observations to degrees of freedom was <40 (Burnham & Anderson, 2002).

3. RESULTS
3.1 Life history classification
The biological constraints underlying the *E-P-O* scheme pose a trilateral continuum space where different fish species could theoretically lie anywhere (Figure 1). After classification, we mapped individual stocks onto this space, represented as a ternary plot with vertices equal to either the highest or lowest observed value of maturation age, fecundity, and PCI according to each strategy.

In support of prior theory, the three Winemiller and Rose (1992) *E-P-O* strategies emerged from partitioning the data into three groups using *k*-means clustering, with characteristic levels of time to maturity, fecundity, and parental investment (Figure 1b, 2a). However, the decrease in the intra-cluster variation supported the choice of five groups (Figure S2). This choice was further supported by significant differences in the fecundity, age of maturity, and parental care of the groups resulting from the unsupervised clustering classification ($F_{5,696} > 875.8$, $p \ll 0.05$, one-way ANOVA; Tables S4-5), which can be seen in the reduction of multiple modalities within each of the three traits with an increasing number of groups (Figs. 2b-c).

The emergent fourth cluster (Figure 1c) is a new group that we term a *B*-strategist because it features mostly benthic species whose distinct fecundity and parental care reflect "bet-hedging" across the standard *E-P-O* life history strategies. *B*-strategists were grouped with the Equilibrium strategists if only three clusters were used. This group includes fishes that, like the *E* group, have high parental investment, but also have high batch fecundity characteristic of *P* fishes (Figure 1c, 2b). The *B* strategy included mainly rockfishes of the genus *Sebastes* spp. and *Sebastolobus* spp., but also other species inhabiting bottom patchy habitats like the wolffish (*Anarhichas lupus* and *A. minor*), black cardinalfish (*Epigonus telescopus*), blackbelly rosefish (*Helicolenus dactylopterus*), shorthorn sculpin (*Myoxocephalus scorpius*), and ocean pout (*Zoarces americanus*).

The fifth cluster introduced a third segregation of fishes along the high fecundity/slow maturation to low fecundity/rapid maturation continuum marking transition from periodic to opportunistic strategies in the interim 3 and 4 cluster schemes (Fig. 1d). The additional segregation occurs at the low fecundity/rapid maturation end point and contains mainly salmonid species. We call this strategy the "salmonic" group after McCann and Shuter (1997). Fishes with the *S* life history strategy, such as the genera *Oncorhynchus* and *Salmo*, are distinguished by low fecundity, early maturation age, and intermediate parental investment (Figure 1d, 2c). In addition to 145 salmonid stocks, this group also included three Rajiformes (*Amblyraja radiata*, *Bathyraja parmifera*, and *Leucoraja erinacea*), four European anchovy (*Engraulis encrasicolus*) stocks, the Brazilian sardinella (*Sardinella brasiliensis*), the Western Atlantic seabream (*Archosargus rhomboidalis*), the slender armorhead (*Pentaceros wheeleri*), and the three-spined stickleback (*Gasterosteus aculeatus*). This new cluster emerged from what was the Opportunistic group in the 4 cluster scheme. The stocks that did not get classified into the Salmonic strategy remained Opportunistic. This new Opportunistic group gained stocks from the lower fecundity/faster maturation portion of the Periodic cluster. Though the separation of these groups along the *P-O-*

S continuum is uncertain (Figure 1c,d), the fecundities and maturation times of the Periodic and Opportunistic strategies under five clusters are statistically different ($F_{5,696} > 875.8$, $p \ll 0.05$, one-way ANOVA; Tables S4-5, Figure 2).

3.2 Single covariate relationships with recruitment variability

Analysis of recruitment variability with respect to individual covariates of the GLM found a significant positive relationship with the coefficient of variation of the fishing rate time series (Figure 3a). Recruitment variability overlapped considerably in relation to environmental biomes (Figure 3b). Temperate and subtropical biomes encompassed wider ranges of recruitment variability (Figure 3b), and the deep-water biome had the lowest median and smallest range of recruitment variability. Together, these results suggest that environments subject to less seasonal variation result in reduced variability, although this does not account for ontogenetic habitat shifts (e.g. Secor 2015). The means for each life history strategy ranked from low variability in Opportunistic stocks to intermediate values for Bet-hedger and Periodic strategists to high variability in Salmonic stocks (Figure 3c). Regrettably, lack of recruitment data prevented the evaluation of recruitment variability for the Equilibrium strategy (2 stocks resulted in the bimodal distribution in Figure 3c).

3.3 Multiple trait models of recruitment variability

Life history strategy was included in all generalized linear models with AICc weights greater than zero (Table 1). The best model of recruitment variability included an interaction between fishing rate variation (cvF) and life history (LH) strategy ($w_{AICc} = 0.62$, Tables 1-2). Though the overall goodness of fit of the model was modest (explained deviance = 26%; Table S6), model selection clearly suggested a distinct interaction between fishing variability and recruitment variability, with a cumulated w_{AICc} of 0.97 for models including such interaction (Table 1, Figure 4). The overall relationship between variability in recruitment and in fishing pressure exhibited a significant positive trend, which then varied by life history strategy (Table 2, Figure 4). Recruitment variability increased the greatest with cvF for Opportunists (Table 2, Figure 4a). Bet-hedgers also had a strong relationship with cvF that was intermediate of Opportunistic and Periodic strategists, though not significantly different from the Periodic (Table 2, Figure 4b-c). In contrast, the interaction unveiled a weak positive relationship between recruitment variability and cvF in Salmonic stocks that was very similar to the interaction of Periodic stocks (Table 2, Figure 4d). The role of the environmental biome was less important than the interaction between life history strategies and fishing or either of these factors individually (Table S7), but was included in the second and third best models (Table 1; cumulated w_{AICc} of 0.36 for models including either biome or the interaction of biome and fishing). GLM results were similar when nonlinear measures of recruitment variability were alternatively considered (Tables S8-10, Figures S4-5).

4. DISCUSSION
4.1 Life history strategies

Our analysis of life history traits in exploited fisheries suggested an extension of the *E-P-O* niche scheme proposed by Winemiller and Rose (1992) to include five life history endpoint strategies (*E-B-P-O-S*). Though not easily depicted in two-dimensional space, these strategies had discernibly different combinations of fecundity, maturity, and parental care life history traits. In the triangular *E-P-O* model, the two new groups had intermediate values of fecundity and

parental care, but set new extreme values for time to maturity.

The Salmonic group with the earliest maturation ages was suggested as an outlier by Winemiller and Rose (1992) and has been recognized as an independent life history strategy in other analyses (McCann & Shuter, 1997; King & McFarlane, 2003; Haltuch et al., 2019). Salmonid species formed a strategy in the principal components analysis (PCA) of King and MacFarlane (2003) characterized by shorter lifespans, faster growth rates, and lower fecundities than Opportunists and Equilibrium species, and maturation, body, and egg sizes intermediate of the *O* and *E* strategies. Like King and MacFarlane (2003), we found that the Salmonic strategy had lower fecundity than Opportunists and earlier maturation times than Equilibrium stocks. Our differential placement of the Salmonic strategy in terms of fecundity and maturation is likely related to the smaller loadings of these traits on the King and MacFarlane principal components, whereby the position of a species in PC-space does not map directly to each trait that composes that PC. Additionally, their analysis included maturation size instead of maturation age, egg size instead of parental care, and was performed on a comparatively smaller dataset (up to 42 species). On the other hand, our results agree with the PCA of Secor (2015) where Salmonic species had intermediate fecundities and offspring sizes (proxy for parental investment). The *S* strategy consistently emerges from life history studies as a distinct group, but its position in trait space relative to *E* and *O* is sensitive to the analysis methodology.

McCann and Shuter (1997) studied the allometric relationships of the *E-P-O-S* strategies and found that the Salmonic group set the upper bound of annual investment in reproduction (measured as ovary weight) and lower bound of age at maturity for fishes in their data set with larger sizes at maturity (~55 g – 22 kg). The Salmonic strategy increased its annual fecundity at the expense of adult survivorship and traded increased juvenile survivorship for decreased juvenile growth rate (McCann & Shuter, 1997). Like the Opportunistic strategy, Salmonic strategists are adapted to highly variable, disturbance environments (Crozier et al. 2019). Though the lower fecundities and higher parental investment of the *S* group are often adaptions to specific, predictable environments, such as with Equilibrium fishes, the diversity in timing of spawning, parental care, and juvenile rearing within and across these stocks gives them enhanced flexibility that historically supported greater population stability (Crozier et al. 2019).

In addition to the established Salmonic group, the analysis led to the emergence of a novel life history strategy that we termed "Bet-hedgers" or *B*-strategists. The *B*-strategists have a reproductive scheme that combines fitness-enhancing elements of the classical *E-P-O* strategies. Bet-hedgers were characterized by a late maturity age and moderate to high parental investment and fecundity. High fecundity firmly distinguished them from Equilibrium stocks that exhibited the highest parental investment, while elevated parental investment clearly differentiated Bet-hedgers from Periodic stocks with similarly late maturity ages and the highest batch fecundity. When parental care was ignored, Bet-hedger species were grouped with flatfishes and classified as long-lived, slow growing, and highly fecund Periodic strategists by King and McFarlane (2003), while gadids and scombrids composed an Intermediate strategy. This is contrary to Secor's (2015) analysis where rockfishes (*Sebastes* spp.) were not identified as a unique strategy. Instead, they fell in between Opportunistic and Periodic fishes along the adult size and fecundity (Factor 2) axis, but tended more towards Periodic. Rockfishes could be differentiated from Periodic fishes (flatfishes, gadids, and scombrids) in Secor's analysis by scaling adult length by offspring length, which was not an available trait in our data set. Secor (2015) noted that Periodic and Opportunistic fishes had a continuous distribution along the adult size and fecundity (Factor 2) axis with no clear separation, which agrees with the continuous distributions of these life

history types on our ternary plots.

Fish reproductive strategies cover an entire spectrum from low investment in numerous offspring and no parental care to high investment in few offspring and elaborated protective behaviors (e.g. Balon, 1990). Thus, Bet-hedgers appear as an outlier with moderate-high investment in many offspring. The Sebastidae family truly is highly fecund, with maximum fecundities comparable to those of the Periodic strategists, alluding to their evolution from highly fecund oviparous species (Wourms, 1991). Both Equilibrium and Bet-hedging strategies include live bearers that must provide energy to developing embryos, exchange respiratory gases, and remove waste products. However, the parental investment of Bet-hedgers, while elevated, is not nearly as high as Equilibrium strategists. Viviparous Sebastinae lack specialized provisioning structures (like a placenta) that are well developed in viviparous sharks (Boehlert & Yoklavich, 1984; Wourms, 1991), even if viviparous matrotrophy has been demonstrated in species of the genus *Sebastes* (MacFarlane & Bowers, 1995; MacFarlane & Norton 1995). Pure matrotrophy (i.e. eggs receive energy from the mother during gestation) requires a predictable food supply, whereas lecithotrophy (i.e. all energy derived from the yolk) is selected for in seasonally unpredictable habitats, which correspond well to the different environments of Equilibrium fishes and Bet-hedgers respectively (Wourms, 1991).

Along with lower maternal provisioning, Bet-hedger gestation times are much shorter than that of Chondrichthyes, being on the order of 1-2 months (Wourms, 1991) instead of 4 months to 2 years. These disparities sum to large differences in energy investment between Bet-hedgers and Equilibrium strategies that could not be captured with the simple scoring scheme used to calculate the PCI. It also underlines the fact that, while Bet-hedgers benefit from elevated fecundity and high parental care, energetic compromises still prevent them from achieving the levels of fecundity and parental investment that are reached by fishes that specialize in one or the other.

As internal brooders, the Bet-hedgers group differs from the broadcast-spawning Periodic strategists. Despite size at birth being similar to that of newly hatched oviparous larvae, Bet-hedger larvae have completed organogenesis with well-developed eyes, jaws, guts, and fins that allow them to begin feeding immediately (Boehlert & Yoklavich, 1984; Wourms, 1991). Thus, larvae of these fishes avoid the starvation prone first-feeding stage when larvae switch from yolk resources to plankton. Additionally, they avoid the predation-heavy pelagic egg stage when brooded internally, as in Sebastinae, or deposited pelagically in a distasteful gelatinous matrix, as in *Helicolenus dactylopterus* and the genus *Sebastolobus* (Wourms, 1991). Despite these early life survival advantages, median recruitment variability of Bet-hedgers was greater than that of the oviparous Opportunistic and Periodic fishes (Figure 3c).

4.2 Life history and recruitment variability

Generalized linear modeling revealed that life history strategy is a significant contributor to recruitment variability in marine fishes. We found increasing variability in recruitment from Opportunistic to Periodic to Bet-hedging to Salmonic fish stocks. Equilibrium strategists that were poorly resolved in the recruitment database are expected to have the lowest recruitment variability of all life history strategies (Rose et al., 2001). It is thus striking that neither the Bet-hedgers nor the Salmonic group had lower recruitment variability from occupying life history strategies somewhat intermediate of Equilibrium and Periodic. The high heterogeneity within each life history strategy (Figure 3c) limited the ability of the *E-B-P-O-S* framework alone to describe differences in the variability in early life survival among stocks (Table 1).

Our analysis revealed a positive relationship between fishing and recruitment variability that varies in strength by life history strategy. Though this interaction was the greatest contributor to the goodness of fit with recruitment variability, our analysis cannot disentangle correlation from causation. Below we examine a few mechanisms by which fishing pressure could affect recruitment variability. These mechanisms include the effect that variability in fishing pressure has on changing (1) the total size and (2) the age structure of the spawning stock (Shepherd et al., 1990; Hsieh et al., 2006; Anderson et al., 2008), both of which may interact with environmental conditions that also influence recruitment.

An increase in recruitment variability at low spawning stock biomass (SSB) is consistent both with theory and observations suggesting that density dependence operates mainly on the early life stages of marine fishes (Fogarty et al., 1991; Minto et al., 2008). Opportunistic fishes had a strong positive relationship between variation in fishing rate (cvF) and recruitment variability despite rapid maturation rates and high turnover rates that are less influenced by compensatory density dependent processes. The increase in recruitment variability with fishing rate variability may reflect a direct negative impact of fishing on recruitment when new recruits make up a large proportion of the spawning population. In this case, a high fishing rate one year would lower SSB and recruitment, but subsequent reductions in fishing rate would increase SSB and recruitment success faster than in stocks with later maturation ages. Variation in fishing rates were also positively related to recruitment variability for Bet-hedging and Periodic strategists. High exploitation rates can push fish populations to low SSB levels and lead to a decrease in the buffering effect of density dependent regulation against external environmental perturbations (Andersen & Beyer, 2015). The buffer effect is predicted to be more important in species with a large asymptotic size, which is positively related to maximum fecundity in our analysis.

The interaction between recruitment variability and fishing rate variation did not have a linear relationship with any of the three life history metrics. Both Opportunistic stocks with the strongest interaction and Salmonic stocks with the weakest interaction have early maturation ages and low fecundity, which may suggest that their higher parental investment buffers the effect of fishing. However, the Bet-hedgers have much greater parental investment than the Periodic stocks, but had a stronger rather than weaker interaction between recruitment and fishing variability. In the case of these two strategies, time to maturity may be a more important factor in regards to fishing through the impact of age truncation effects (Longhurst, 2002; Berkeley et al., 2004).

Age truncation linked to fishing reduces the natural buffering against environmental fluctuations provided by older age classes and may also enhance the intrinsic nonlinear behavior of exploited populations (Higgins et al., 1997; Anderson et al., 2008; Shelton & Mangel, 2011). Available evidence suggests that age-truncation tends to increase recruitment variability in fish and to decrease population resilience under harvest (Longhurst, 2002; Rouyer et al., 2012). A well-known mechanism involves the increase in recruitment variability due to age-dependent maternal effects (Green, 2008; Marshall & White, 2018). In other cases, internal fluctuations associated with an altered age structure align with environmental noise to amplify natural fluctuations in the population dynamics, although these responses are more difficult to ascertain (i.e. resonance effects; Botsford et al., 2011, 2014). In the context of life-history strategies, truncation has a limited impact on species with a short lifespan like Opportunistic or Salmonic strategists, but it can be critical for long-lived Periodic and Bet-hedging species (Botsford et al., 2014). For instance, older female rockfishes produce more larvae with increased growth rates and starvation tolerance, and they tend to spawn earlier in the season (Berkeley et al., 2004). In a

population with an intact age structure, these females spread the risk over a greater period of time to maximize the chance that larvae match the ideal oceanographic conditions for survival (Cushing, 1984; Hedgecock, 1994). This match-mismatch window may have a spatial component as well (Iles & Sinclair, 1982; Hedgecock, 1994), such that local extinctions by fishing would have a similar effect as removing one part of the spawning season. This could particularly affect rockfishes and other deep-water fishes that are associated with complex substrate (i.e. rocks, reefs, kelp, seamounts, etc.; Love, Yoklavich, & Thorsteinson, 2002) and have patchy distributions. This has been recognized by fisheries managers who manage many rockfish stocks to maintain population age-structure through area closures (King & MacFarlane, 2003).

Even though the Salmonic strategy had a weaker interaction with fishing variance, it had the largest median recruitment variability of all the life history types. This variability is derived from the unique life cycle of salmonid species that includes both freshwater and marine stages, and can be complicated by competitive interactions between wild and hatchery fishes. Bottlenecks in the life cycle that experience strong environmental pressure, of which salmonids have multiple, can lead to high variability in recruitment. For many eastern Pacific stocks, the dominant contributor to recruitment success has been marine conditions during the first few months of ocean entry (Haltuch et al., 2019). However, precipitation, temperature, and anthropogenic land and water use influence the size and availability of freshwater nest sites and favorable nursery habitat, adding two more bottlenecks that may become increasingly important to recruitment under changing climate conditions (Crozier et al., 2019). Because these bottlenecks occur over short periods of time, they may actually promote the success of predicting recruitment for fisheries management (Haltuch et al., 2019).

4.3 Environment and recruitment variability

Environmental variability has traditionally been invoked to explain fluctuations in the early life survival of fishes (Cushing et al., 1996; Houde, 2008; Fogarty & O'Brien, 2016). However, we found that large scale gradients of environmental variability, represented by ocean biomes, was of lesser importance in describing recruitment variability than life history strategy, exploitation rate, and their interaction. Fishes have complex life cycles with spawning migrations and ontogenetic habitat shifts that can significantly interact (Secor 2015). The biomes used in this analysis were adult habitats, which may not reflect the stability/seasonality of the conditions that early life stages experience. The importance of the timing and location of ontogenetic habitat shifts for early life survival deserves future study in the life history framework.

4.4 Considerations and perspectives

It should be emphasized that a reduction in recruitment variability is not always beneficial. High recruitment variability at low stock sizes accelerates and increases the probability of stock collapse (Kuparinen, Keith, & Hutchings, 2014), but low recruitment variability, under high fishing pressures, can prevent rebuilding and lead to collapse (Shepherd et al., 1990; Hutchings & Reynolds, 2004). This is especially true in short-lived species that cannot outlive an extended period of poor conditions. At such low biomasses, recruitment compensation may be more important than its variability.

Another caveat of our approach is its reliance on the output of stock assessments to characterize recruitment variability. Despite our efforts to avoid recruitment estimates uninformed by observations, it is well-known that model-based estimates tend to smooth out

variability in observations, to the extent of introducing in occasions artifacts that can affect later analyses (Walters & Ludwig 1981, Dickey-Colas et al. 2014, Brooks & Deroba 2015). Differences in recruitment variability across strategies were fairly robust to the subset of stocks included in our analyses, but we acknowledge the need to explore the potential impact and improve the approach by directly using abundance estimates (Brooks & Deroba 2015). Additionally, these analyses use mean life history traits for each stock and are based on a moderately small sample of stocks and species, especially with respect to patterns of variability in Bet-hedgers and the Salmonic strategy. Databases like FishLife set the path by providing robust estimates of fish traits and may support more extensive analysis of fish life history at the species level and across supraspecific taxonomic levels (e.g. Thorson et al., 2017; Thorson, 2020). However, life history traits are plastic and a range of phenotypes may be present within each fish stock. Also, changes in life history traits can be induced through fishing pressure (e.g. age at maturity; Heino, Díaz Pauli, & Dieckmann, 2015) and climate change (e.g. changes in size; Daufresne, Lengfellner, & Sommer, 2009). Similarly, fishing and climate change may increase or decrease individual stocks, thereby altering the distribution of life history strategies in a given environment (e.g. depletion of long-lived, large, higher trophic level fishes and replacement by faster growing, earlier maturing species of lesser trophic level; Myers & Worm, 2003).

In the end, fishes are one of the most successful taxa, inhabiting multiple habitats and exhibiting an amazing diversity originated by the largest radiation among vertebrates. The evolutionary success of marine fishes translates in a huge variety of life history schemes. With the identification of two additional endpoint strategies, our analysis extends the successful *E-P-O* niche scheme, but still provides a first order approximation within a continuum of adaptations (Secor 2015). This aspect remains especially important along the slow/fast continuum involving Periodic, Opportunistic and Salmonid strategies. Our relatively simple clustering approach, which relied on a model-free, heuristic algorithm like *k*-means, delimited groups with distinct life history traits and distinct patterns of recruitment variability in response to fishing pressure. However, the specific limits of these strategies in the niche space defined by life history traits remains highly uncertain and, together with the drivers favoring each strategy under different conditions, a target for future work is employing a more mechanistic approach.

This analysis is a broad synthesis that suggests how to structure more mechanistic approaches to predicting recruitment variability or recruitment of fish stocks, species, or functional types. In this way, our life history classifications can guide the design of ecological models incorporating adaptive dynamics (e.g. McGill & Brown, 2007). Our results demonstrate that not all life history aspects or recruitment characteristics are size-based and provide a natural starting point for adding traits to global size-based models. In these models, fecundity and time to maturity scale with size in the way seen in Opportunistic and Periodic fishes, but the Equilibrium, Salmonic, and Bet-hedger groups do not follow these patterns. The addition of a Bet-hedging strategy with late maturity age, moderate to high parental investment, and high fecundity would be particularly important for studies on the effects of fishing on different stock complexes. The formalization of these five life history strategies provides a foundation for designing management frameworks for fishes without adequate data (King & MacFarlane, 2003) and for identifying stocks that would benefit from inclusion of environmental forecasts for setting fisheries reference points (Haltuch et al., 2019).

5. CONCLUSIONS

Parental investment, time to maturity, and fecundity capture major aspects of the functional ecology of marine fishes and provide the basis of the classification of life history strategies in fish, including the *E-P-O* scheme proposed by Winemiller and Rose (1992). Our analysis, however, extends previous niche schemes by featuring two new strategies; a group of "Salmonic" species characterized by large investments in parental care but reduced fecundity and short lifespans, and a distinct and previously neglected "Bet-hedging" strategy that groups species with very long lifespans and elevated investments in parental care and fecundity. The new life history scheme proved valuable in explaining differences in early life survival variability amongst harvested marine fish stocks. Indeed, recruitment variability was driven nearly equally by life history strategy, variability in fishing pressure, and their interaction. Our results suggest that functional traits provide a framework for understanding how life history strategies determine the resilience of different fish species to exploitation, and a way forward to defy prevailing challenges in fisheries management.

DATA AVAILABILITY STATEMENT
All data and additional supporting information may be found online in the Supplementary Information and Appendix. The RAM fisheries time series data are publicly available at https://www.ramlegacy.org/. The FishBase trait data are publicly available at https://www.fishbase.org/ and can be accessed via the R package *rfishbase*.

BIOSKETCH
The research team is interested in marine ecosystem dynamics and physical-biological interactions over a broad range of space and time scales. Together and separately they have studied the global carbon cycle, the use of chemical tracers to study ocean circulation, and the impact of climate change on ocean biology, biogeochemistry, ocean productivity, and fisheries.

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TABLES

Table 1. Summary of the generalized linear model selection procedure. Each row is an individual model of recruitment variability as a function of life history strategy (LH), environmental biome (Bm), and/or the coefficient of variation of fishing rate (cvF).

model	df	logLik	AICc	ΔAICc	wAICc
LH + cvF + LH × cvF	9	-266.47	551.38	0.00	0.62
LH + Bm + LH × cvF + Bm × cvF	15	-261.29	553.73	2.35	0.19
LH + Bm + LH × cvF	12	-264.68	554.11	2.74	0.16
LH + cvF	6	-272.95	558.09	6.72	0.02
LH + Bm × cvF	9	-270.44	559.30	7.93	0.01
LH + Bm + Bm × cvF	12	-269.61	563.95	12.58	0.00
Bm + LH × cvF	9	-282.87	584.16	32.78	0.00
Bm + cvF	6	-290.13	592.47	41.09	0.00
cvF	3	-293.70	593.46	42.09	0.00
Bm + cvF + Bm × cvF	9	-288.61	595.65	44.28	0.00
LH + Bm + Bm × LH	15	-288.67	608.50	57.13	0.00
LH + Bm	8	-300.36	617.06	65.68	0.00
LH	5	-303.51	617.16	65.79	0.00
Bm	5	-330.27	670.68	119.30	0.00
Null (intercept)	2	-338.98	681.98	130.61	0.00

Note. ×: interaction; df: number of parameters; logLik: log likelihood; AICc: Akaike Information Criterion for small sample sizes (Burnham & Anderson, 2004).

Table 2. Parameter estimates of the generalized linear model for recruitment variability with the lowest AIC (Table 1). The model included life history strategy (LH) and the coefficient of variation of fishing rate (cvF) of each stock as covariates. Model dispersion was estimated following the recommendations in Venables and Ripley (2004). All covariates were scaled before the analysis following Gelman (2008) to ease the comparison among effects: numeric variables that take on more than two values are each rescaled to have a mean of 0 and a sd of 0.5; binary variables are rescaled to have a mean of 0 and a difference of 1 between their two categories; single-valued variables and non-numeric variables that take on more than two values are unchanged.

	Estimate	Std. Error	z value	Pr(>|z|)
LH Per	-0.30	0.07	-4.17	0.00
LH Bet	-0.52	0.15	-3.44	0.00
LH Opp	-0.62	0.09	-7.08	0.00
LH Salm	0.00	0.07	0.03	0.97
LH Per × cvF	0.59	0.18	3.32	0.00
LH Bet × cvF	1.03	0.47	2.20	0.03
LH Opp × cvF	1.87	0.29	6.43	0.00
LH Salm × cvF	0.59	0.10	5.72	0.00

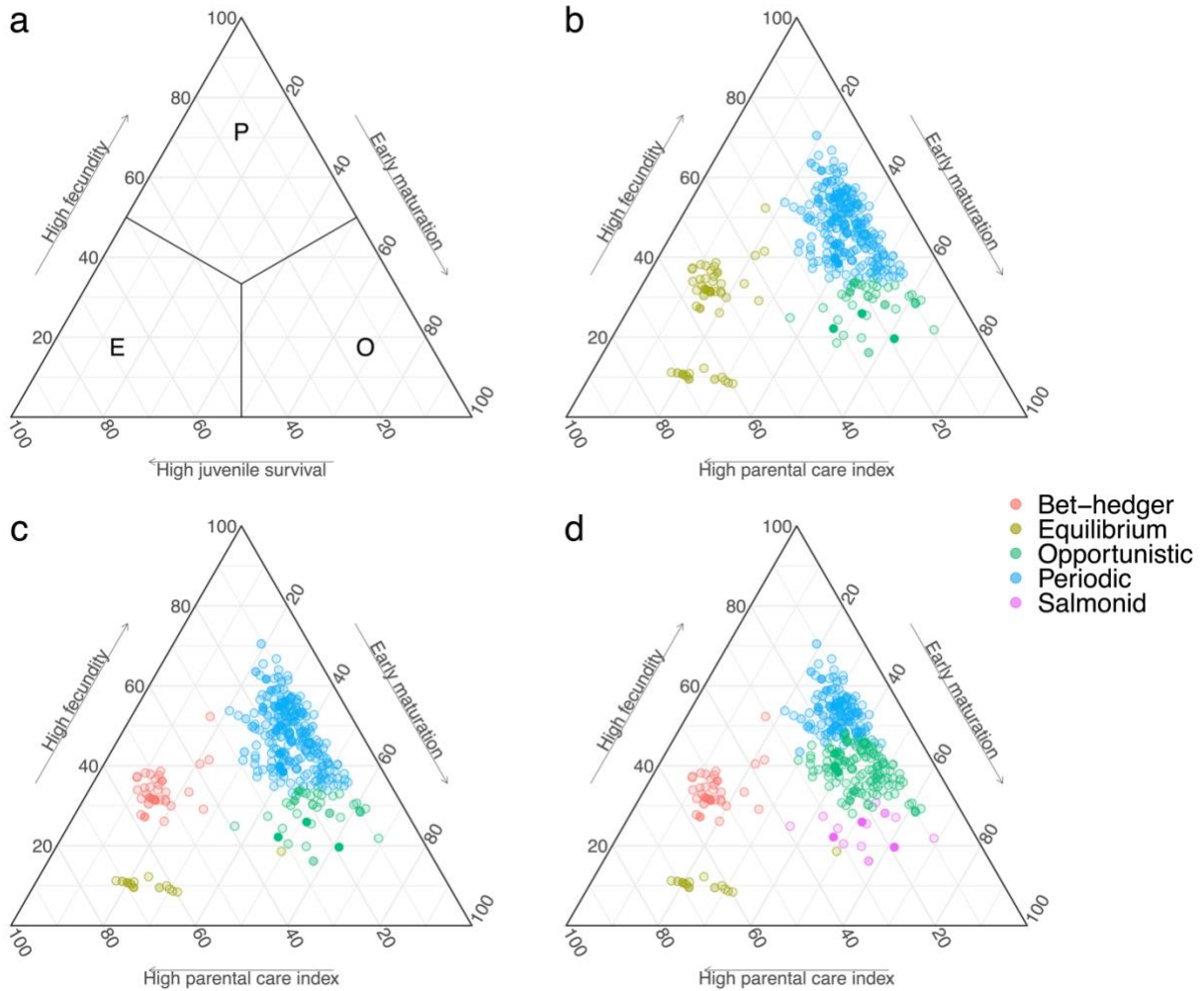Note. Per: Periodic; Bet: Bet-hedgers; Opp: Opportunistic; Salm: Salmonic; ×: interaction.

Figure 1. (a) Life history niche model of Winemiller and Rose (1992) depicting three fish life history endpoint strategies as a function of maturation time, fecundity, and juvenile survival. Mapping of FishBase exploited marine fish stocks with data for all three life history traits (701 stocks, 244 species) colored by life history classifications arising from *k*-means of (b) 3 clusters, (c) 4 clusters, and (d) 5 clusters. The *E-P-O* trilateral continuum is represented by a ternary plot with vertices equal to either the highest or lowest observed value of time to maturation (tmax), mean fecundity (*Fec*), and Parental Care Index as indicated by the arrows on the faces. The coordinates of each stock were found by scaling each trait between 0 and 1, and then normalizing the Manhattan distance between each triplet and the vertices of the graph in trait space using the normalized exponential function. Fecundity is measured with respect to the horizontal lines, maturation with the vertical lines running NE-SW, and PCI with the vertical lines running NW-SE. E: Equilibrium; P: Periodic; O: Opportunistic.
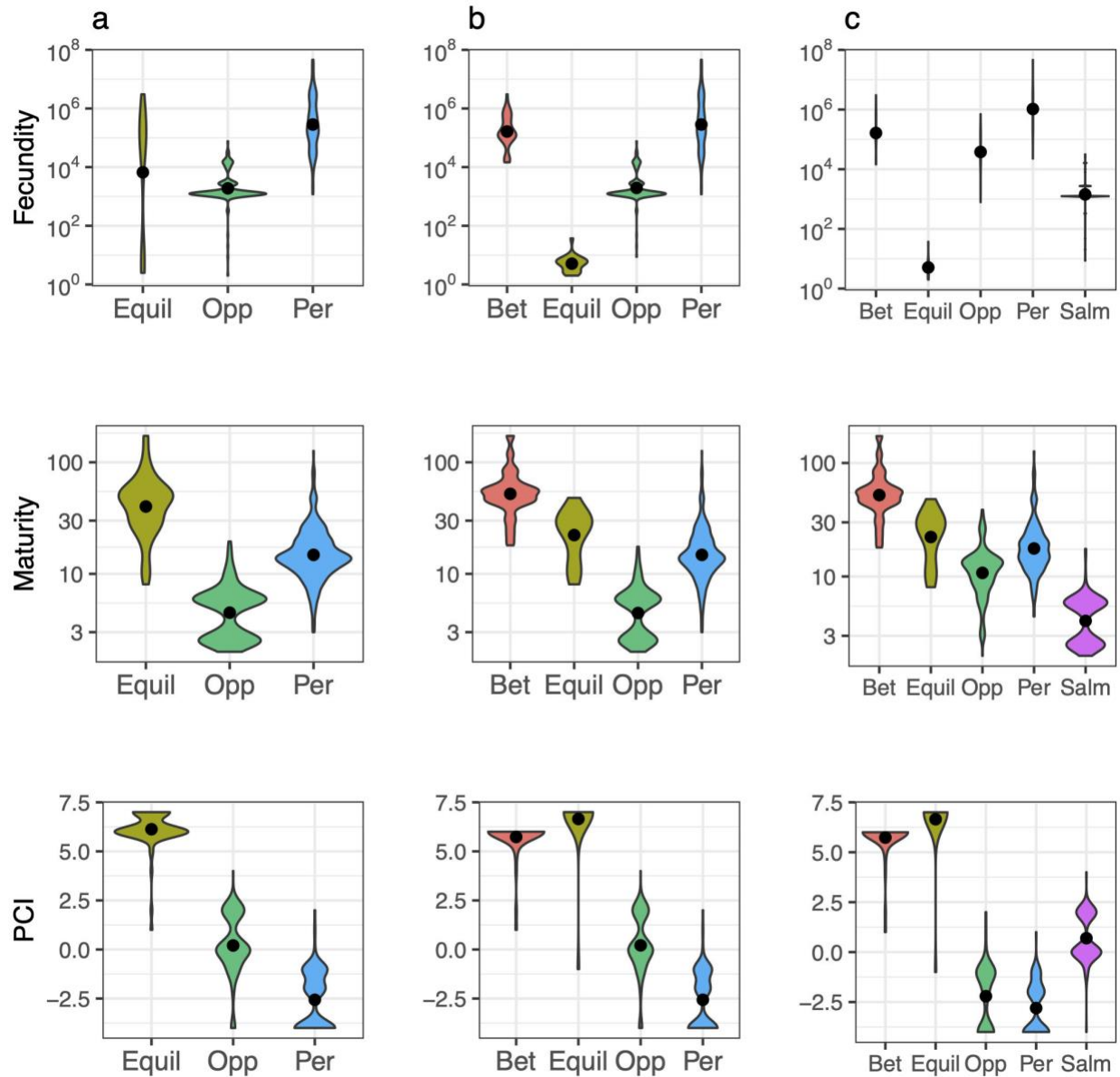
Figure 2. Distributions of the life history traits used to classify each life history strategy. Results from *k*-means of (a) 3 clusters, (b) 4 clusters, and (c) 5 clusters. Fecundity: logarithmic mean fecundity (*Fec*); Maturity: maximum time to maturity (tmax); PCI: Parental Care Index; Bet: Bet-hedgers; Equil: Equilibrium; Opp: Opportunistic; Per: Periodic; Salm: Salmonic.
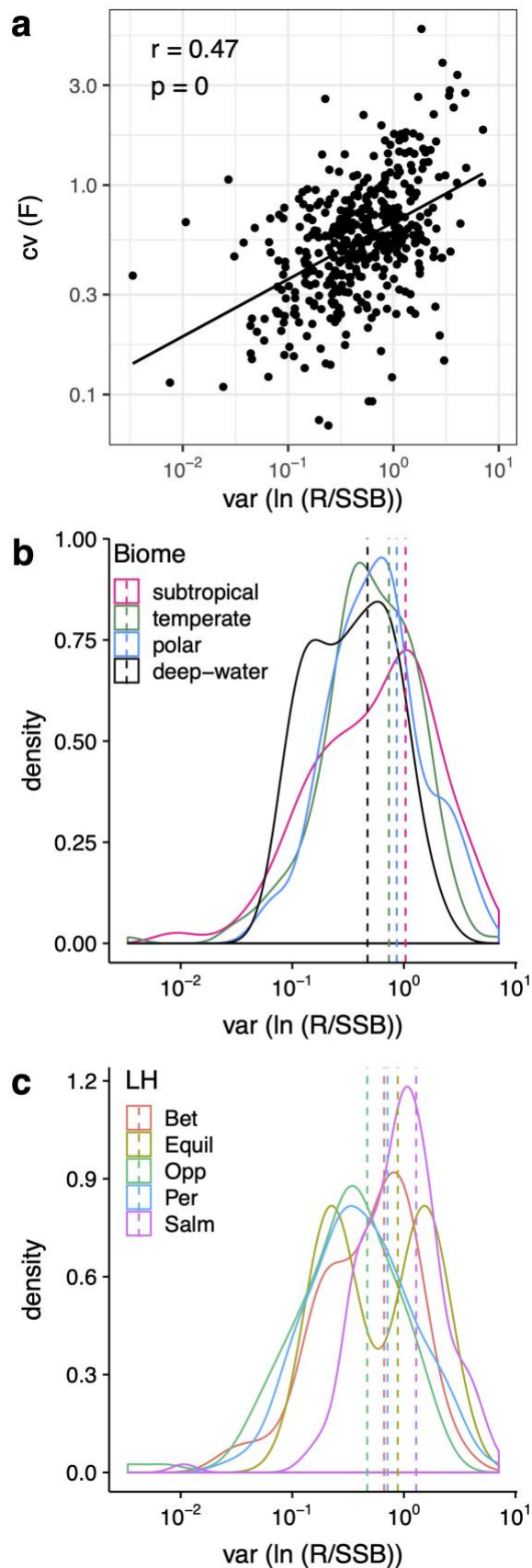
Figure 3. Distribution of recruitment variability (variance of ln(R/SSB)) of (a) the coefficient of variation of fishing rate (cvF), (b) environmental biome, Biome, and (c) life history strategy, LH. Bet: Bet-hedgers, Equil: Equilibrium, Opp: Opportunistic, Per: Periodic, Salm: Salmonic. Dashed lines are mean values.
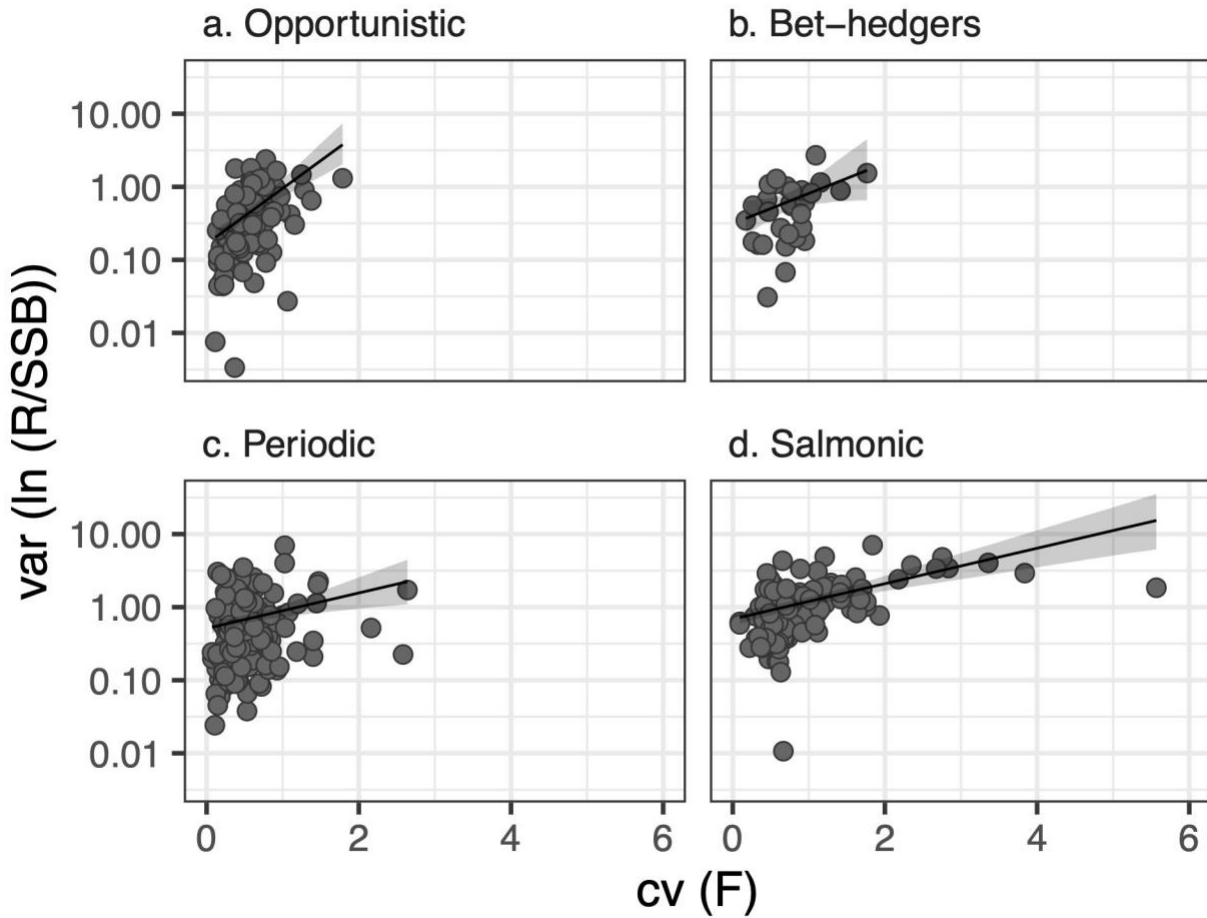
Figure 4. Relationship between variability in fishing pressure (cvF) and variability in recruitment (variance of (ln(R/SSB))). The line on each graph corresponds to the prediction of the best generalized linear model (Table 2), which includes an interaction between the coefficient of variation of the fishing rate and life history strategies (LH): (a) Opportunistic LH, (b) Bet-hedgers LH, (c) Periodic LH, (d) Salmonic LH. The shading is the 90% confidence interval of each model.