Improved viability of populations with diverse life-history portfolios

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A principle shared by both economists and ecologists is that a diversified portfolio spreads risk, but this idea has little empirical support in the field of population biology. We found that population growth rates (recruits per spawner) and life-history diversity as measured by variation in freshwater and ocean residency were negatively correlated across short time periods (one to two generations), but positively correlated at longer time periods, in nine Bristol Bay sockeye salmon populations. Further, the relationship between variation in growth rate and life-history diversity was consistently negative. These findings strongly suggest that life-history diversity can both increase production and buffer population fluctuations, particularly over long time periods. Our findings provide new insights into the importance of biocomplexity beyond spatio-temporal aspects of populations, and suggest that maintaining diverse life-history portfolios of populations may be crucial for their resilience to unfavourable conditions like habitat loss and climate change.

Keywords: biocomplexity; life-history diversity; population dynamics

1. INTRODUCTION

Financial advisors often recommend a diversified stock portfolio in the belief that diversification allows for profits even when some stocks suffer a downturn, because others in the portfolio can still perform well. Ecologists have drawn similar parallels in studies of communities that examine links between ecosystem productivity and species diversity (Lehman & Tilman 2000; Koellner & Schmitz 2006). Likewise, population biologists have predicted that life-history diversity should spread risk across different segments of a population, thereby buffering it from environmental variation over long time periods (Den Boer 1968; Stearns 1992; Fox 2005). At an individual level, theoreticians have also predicted that individuals with complex life histories can outcompete those with simpler life histories under certain circumstances (Stearns 1992). However, unlike the wealth of empirical studies at the community and individual levels, tests of these

predictions at the population level are rare because they require large datasets spanning many generations, and population data exhibiting significant life-history variation.

Sockeye salmon (*Oncorhynchus nerka*) are an ideal study species to address population effects of life-history diversity because they exhibit substantial and measurable life-history variation, and have undergone extreme fluctuations in abundance. Sockeye salmon typically develop in lakes for 1 or 2 years, migrate to the ocean and mature for an additional 2 or 3 years, return to freshwater to spawn, and then die. However, the number of years spent in freshwater and ocean exhibits both genetic variation and plasticity (Quinn *et al.* 2009). Bristol Bay stocks have varied in age composition over time, and have undergone extreme changes in population size over the last half-century (Finney *et al.* 2000). Even so, some populations have replaced others in dominance such that the entire system supports a productive fishery (Hilborn *et al.* 2003). These findings strongly implicate the importance of spatial complexity among stocks for long-term persistence, but do not directly address the influence of life-history diversity. Here we test the hypothesis that life-history variation is related to population growth rate and its variation in nine river systems producing sockeye salmon spawning in Bristol Bay, Alaska.

2. MATERIAL AND METHODS

(a) Population measures

We used run reconstructions of up to 42 cohorts in nine sockeye salmon population complexes (aggregations of discrete breeding groups occupying distinct habitats, summarized for nine river systems) to calculate life-history diversity and recruits per spawner (RPS) after factoring out the influence of density-dependence (see electronic supplementary material). Beginning in 1956, adult sockeye salmon have been counted and sampled from gill-net fisheries and from rivers during upstream migration to reconstruct the entire population's abundance and age composition. Analyses of annuli on scale samples were used to determine duration of freshwater and marine residency for each cohort. We estimated life-history diversity by totalling the reconstructed abundance of each freshwater and marine age combination for the population complex, and then calculating Simpson's index of diversity ($1 - S$) using these totals. Simpson's index of diversity accounts for both presence and abundance of particular types in its calculation (Magurran 1988). Age structure was also used in run reconstructions to calculate RPS for each cohort, factoring in fish lost to harvest. For example, fish of age 5 sampled in 2005 were assigned to the 2000 parental population. Population density was calculated as the estimated number of spawning adults contributing to each cohort, divided by the average area of lakes accessible to sockeye salmon in each watershed. Most sockeye salmon in the Bristol Bay region develop as juveniles in lakes, so this density measure most directly reflects rearing constraints (Rich *et al.* 2009).

(b) Decadal variation in biological data

Changes in the Pacific decadal oscillation (PDO) are strongly linked with variation in the abundance of numerous fish species including sockeye salmon (Finney *et al.* 2000). When PDO is positive, temperature and atmospheric pressure of the northern Pacific Ocean are lower than average, and these effects can dramatically influence juvenile recruitment (Hare *et al.* 1999). Following the hypothesis that PDO influences recruitment during the late spring transition from stream to ocean, we averaged annual PDO values between May and July. We weighted PDO data from multiple years by the proportion of the cohort migrating to sea in each year, as determined by freshwater age (ages 0–3). The resulting values varied between –1 to 1, and were binned into high (≥ 0) and low regime categories.

(c) Statistical analyses

To statistically control for potential collinearity between life-history diversity and RPS via rearing density, we used the residuals of PDO-specific regressions of both RPS and life-history diversity with spawner density. We found that life-history diversity and RPS

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Table 1. Results of regressions for life history diversity and recruits per spawner (RPS) as functions of spawner density in different regimes of the Pacific decadal oscillation (PDO).

variable	PDO	<i>F</i>	<i>n</i>	<i>p</i>	<i>r</i> ²	coefficients	
						constant	slope
life-history diversity	low	3.89	178	0.05	0.02	0.82	−0.09
	high	1.92	178	0.17	0.01	−0.11	0.07
RPS	low	21.31	178	0.001	0.10	2.58	−0.31
	high	69.85	178	0.001	0.28	4.75	−0.57

both correlated with spawner density, and these relationships differed in warm and cool PDO regimes (table 1). We controlled for this variation by using residuals from these regressions as metrics of life-history diversity and RPS.

We tested whether residual life-history diversity and RPS were correlated at five different time periods: individual brood years, pairs of years, 5 (the average generation length), 10 and 20–40 years. Longer time periods were represented by averages of individual brood years. In the latter four time periods we also tested for a negative correlation between life-history diversity and variation in RPS (as measured by its s.d.), as predicted if life-history diversity buffers populations from environmental variability. To evaluate the effects of life-history diversity on RPS independent of variation across years or individual watersheds, we used sets of mixed models, including life-history diversity and other possible sources of variation, and tested for the best models using Akaike's information criterion (AIC) (Burnham & Anderson 2002). We tested several covariance structures for the mixed models, and used the covariance structure with the lowest AIC.

3. RESULTS

To test for portfolio effects in the nine Bristol Bay stocks, we correlated adult RPS of each cohort with its life-history diversity as measured by Simpson's index of diversity. In all but the 5-year time period, the best predictors of RPS included life-history diversity, although temporal and spatial variation were important for some time periods (figure 1 and table 2). Nonetheless, the combined probability weights of all models that included life-history diversity were greater or equal to 0.95 for all but the 5-year time period, and were greater than the combined weights for spatial and temporal variables at longer time periods (greater than 5 years). These findings indicated that RPS was strongly correlated with life-history diversity across a range of time periods.

Intriguingly, the slope of the relationship between diversity and RPS was not uniformly in the same direction; at annual to 5-year time periods, the slopes of the regressions were negative, but changed to strongly positive at longer time periods (figure 2*a*). This change in the direction of the relationship across time periods resulted in a near-zero slope at the 5-year time period, and is probably why life-history diversity was not included in the best models for this time period. We also saw similar patterns within populations. Seven of nine populations had negative relationships between RPS and life-history diversity at the annual time period, and eight of nine populations had positive slopes at the longest time period.

In contrast to the patterns with RPS, the relationship between life-history diversity and variation in RPS was consistently negative (figure 2*b*), and the slope of the relationship was three times more negative at longer time periods. Spatial and temporal predictors

were not selected in the best model at any time period, suggesting that our measures of spatial and temporal variation played little role in the buffering of population fluctuations. With the exception of the longest time period, the combined probability weight of all models that included life-history diversity exceeded 0.95 (table 2), and was much higher compared with combined weights for spatial and temporal variables.

4. DISCUSSION

These findings provide, to our knowledge, the first direct empirical support of longstanding theoretical predictions that life-history diversity improves productivity over long time scales, and buffers population fluctuations. We also note the strong negative correlation between life-history diversity and RPS at short time scales. These seemingly contradictory results can be resolved if certain life-history types are favoured by natural selection each year, but the types that are favoured change among years (Seamons *et al.* 2007). These selective effects might result from broad-scale physical processes such as changes in precipitation, ice, and lake levels that differentially affect large components of each population complex. Thus, higher population growth rates could occur with low levels of diversity at short time periods, but high diversity would be needed to maintain large growth rates over long time periods. Meanwhile, life-history diversity should always dampen variation in population growth rate owing to the spreading of juveniles across time and space, but this would be particularly important at longer time periods as rarer but more severe impacts on survival occurred.

The main component of life-history diversity in this analysis—variable duration of freshwater and ocean residency—is based on a complex set of interactions of organisms with their environment. At evolutionary time scales, bet-hedging strategies that support phenotypic plasticity have probably been favoured by fluctuating natural selection (Seamons *et al.* 2007; Simons 2009). For example, population-specific norms of reaction have evolved, such that similar growth rates result in different durations of freshwater residence, and similar sizes at sea water entry and growth rates at sea result in different ages at maturity among populations (Quinn *et al.* 2009). At more immediate time scales, the environment in each lake (temperature, zooplankton production, competition) affects growth (Edmundson & Mazumder 2001), and hence age and size at sea water entry. The outcome of these processes produces some patterns of residency that are not necessarily favourable

Figure 1. Relationships between life-history diversity and recruits per spawner (RPS), and life-history diversity and the s.d. in RPS at five time periods in nine watersheds of Bristol Bay, Alaska. Measures of both life-history diversity and RPS are residuals from regressions that accounted for variation in spawner density in different regimes of the PDO. Lines indicate slopes of the relationship of life-history diversity and RPS. Open circle, Alagnak; open square, Egegik; small filled circle, Igushik; large filled circle, Kvichak; large filled triangle, Naknek; plus, Nushagak; filled square, Togiak; small filled triangle, Ugashik; open triangle, Wood.

Table 2. ΔAICc values (best model $\Delta\text{AICc} = 0$) for seven models of recruits per spawner (RPS) and variation (s.d.) in RPS at five time periods. (Probability weights of the best models and the combined probability weights of models that included life-history diversity, watershed or time are provided in *italics*.)

model	time period (no. of brood years)				
	1	2	5	10	20–40
RPS					
diversity	78.2	52.1	17.16	0	2.03
watershed	116.53	56.05	21.95	7.66	5.41
time	40.68	9.79	0.59	14.23	11.53
diversity, time	10.49	7.01	1.36	9.21	7.89
diversity, watershed	74.41	45.93	23.32	2.56	0
watershed, time	36.29	6.81	0	12.18	7.28
diversity, watershed, time	0	0	1.2	6.98	1.26
<i>probability weight of best model</i>	<i>0.99</i>	<i>0.93</i>	<i>0.36</i>	<i>0.74</i>	<i>0.50</i>
<i>probability of all models that include</i>					
<i>diversity</i>	<i>1.00</i>	<i>0.96</i>	<i>0.38</i>	<i>0.98</i>	<i>0.95</i>
<i>watershed</i>	<i>0.99</i>	<i>0.96</i>	<i>0.55</i>	<i>0.25</i>	<i>0.81</i>
<i>time</i>	<i>1.00</i>	<i>1.00</i>	<i>1.00</i>	<i>0.03</i>	<i>0.29</i>
s.d. RPS					
diversity		0	0	0	0
watershed		15.94	8.5	8.83	2.56
time		24.94	10.23	15.28	6.31
diversity, time		26.02	8.72	8.8	4.24
diversity, watershed		16.78	8.65	3.22	3.03
watershed, time		39.51	17.35	16.25	7.03
diversity, watershed, time		42.41	16.64	12.51	7.97
<i>probability weight of best model</i>		<i>1.00</i>	<i>0.96</i>	<i>0.82</i>	<i>0.58</i>
<i>probability of all models that include</i>					
<i>diversity</i>		<i>1.00</i>	<i>0.98</i>	<i>0.99</i>	<i>0.80</i>
<i>watershed</i>		<i>0</i>	<i>0.03</i>	<i>0.17</i>	<i>0.32</i>
<i>time</i>		<i>0</i>	<i>0.02</i>	<i>0.01</i>	<i>0.12</i>

every year, but are effective at buffering environmental variation at longer time scales.

The sockeye salmon populations we studied are large (10^4 – 10^7 adults) and live in almost pristine freshwater habitat, but they help inform recovery efforts for populations at risk of anthropogenic disturbance. Our study indicates that long-term monitoring of life-history variation is needed to reveal its positive population consequences. Further, our findings suggest that simplifying a population's life-history portfolio through artificial propagation (Araki *et al.* 2007), habitat alteration (Watters *et al.* 2003) and size- or age-selective harvest (Berkeley *et al.* 2004) will have negative consequences on long-term population viability. Conversely, practices that help diversify population structure, such as maintaining large population sizes, and habitat protection and

Figure 2. Slope of the relationship between residual life-history diversity and (a) residual RPS at five time periods and (b) s.d. in residual RPS at four time periods. Slopes were generated by the best mixed model (table 1) that included life-history diversity.

restoration, may help populations flourish. Such efforts may be critical for populations subject to disturbance regimes altered by habitat modification, harvest and long-term climate change (Finney *et al.* 2000; Battin *et al.* 2007).

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