



Local adaptation of antipredator behaviors in populations of a temperate reef fish

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Received: 27 June 2019 / Accepted: 9 September 2020
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Abstract

The temperament of animals can vary among individuals and among populations, but it is often unclear whether spatial variation in temperament is the result of acclimation to local environmental conditions or genetic adaptation to spatial differences in natural selection. This study tested whether populations of a marine fish that experience different levels of mortality and fishing exhibited local adaptation in behaviors related to predator avoidance and evasion. First, we measured variation in reactivity to perceived risk in wild populations of black surfperch (*Embiotoca jacksoni*). We compared flight initiation distances (FID) between populations with significantly different mortality rates. After finding that FID values were substantially lower in the low-risk locations, we tested for local adaptation by rearing lab-born offspring from both high- and low-risk populations in a common environment before measuring their behavior. Lab-reared offspring from high- and low-risk populations exhibited significant differences in several behaviors related to reactivity. Between 23 and 43% of the total variation in behaviors we measured could be attributed to source population. These results thus suggest that a substantial amount of spatial variation in behaviors related to predator evasion may represent local adaptation. In addition, behaviors we measured had an average, broad-sense heritability of 0.24, suggesting that the behavioral tendencies of these populations have some capacity to evolve further in response to any changes in selection.

Keywords Animal personality · Behavioral syndromes · Fishery selection · Heritability · Reactivity · Life history · Marine protected areas · Natural selection

Communicated by Aaron J. Wirsing.

Populations of animals that are separated in space often exhibit consistent differences in behavior, but the degree to which these differences represent genetic adaptation to local environments is often unclear. In this study we found locally-adapted temperament that likely resulted from a combination of heritable variation in behaviors and spatial variation in selection via fishing mortality. Our results emphasize that predation, including fishing mortality, can be a strong force shaping the evolution of behavior and that local adaptation in temperament may be prevalent in the wild.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-020-04757-y>) contains supplementary material, which is available to authorized users.

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Introduction

The temperament of an animal may be characterized by a suite of behavioral tendencies that define how they react to environmental stimuli such as perceived risk, situational novelty, and presence of conspecifics (reviewed by Réale et al. 2007). Behavioral tendencies such as boldness, risk aversion, and aggression are generally important for fitness because of their effects on survival probability, resource acquisition, and the subsequent effects on growth and fecundity (Clutton-Brock et al. 1987; Bednekoff 1996; Adriaenssens and Johnsson 2011). Consistent differences in behavior can thus affect individual fitness, and by extension the dynamics of populations and communities (for example, if behavioral tendencies moderate predator–prey relationships; see Stamps 2007; Smith and Blumstein 2008; Duckworth and Aguillon 2015; Hendry 2016). Behaviors comprising temperament may vary markedly among individuals and across populations (see reviews by Foster and Endler 1999; Toms et al. 2010; Mather and Logue 2013), though the

extent to which these variations represent adaptive genetic variation or simply plastic responses to local environments is often unclear.

An animal's tendencies with respect to antipredator behaviors (e.g., tendencies in the degree to which an animal shelters, flees, or groups together with conspecifics when potential threats are detected) are an important component of temperament. These defensive behaviors are influenced by the risk of predation, including predation by humans (Lima and Dill 1990; Lima 1998; Stankowich and Blumstein 2005). There is a clear advantage to behavioral flexibility under varying degrees of risk, and although defensive behaviors typically exhibit a considerable degree of plasticity, consistent differences in temperament are often observed among individuals and populations (Sih et al. 2004; Bell et al. 2009; Dingemanse et al. 2010). Among the clearest examples of spatial variation in temperament are populations of marine fish that experience differences in mortality risk. Fish species that are targeted by humans often display stark differences in behavior inside and out of Marine Protected Areas where fishing by humans is prohibited. Fish within MPAs often exhibit exploratory and bold behaviors whereas fish in high-risk populations often exhibit caution (Gotanda et al. 2009; Strobbe et al. 2011; Januchowski-Hartley et al. 2012; Bergseth et al. 2016; Rhoades et al. 2018). Similar effects have been demonstrated for fish populations that experience a gradient of exposure to natural predators (e.g., Madin et al. 2010; Fu et al. 2015).

Spatial variation in temperament may be considerable. Recent studies suggest that the magnitude of behavioral differences among populations of a single species can rival or even exceed differences in average behavior among species (e.g., Dingemanse et al. 2002; Bolnick et al. 2003; Bell 2005; Januchowski-Hartley et al. 2012; Brodin et al. 2013). Moreover, the importance of among-population variation in temperament may be further underappreciated because of the focus on relatively few dimensions of behavioral variation. Animals are capable of a broad suite of behaviors, but for practical purposes, many studies of temperament have focused on characterizing behaviors along an axis of boldness to shyness (Brown et al. 2007; Frost et al. 2007; Webster et al. 2007; Biro and Post 2008; Wilson and Godin 2009; Harris et al. 2010; Sebastien et al. 2016). This perspective has revealed important variation in behavioral tendencies of individuals and populations, but other defensive behavioral strategies can also alleviate mortality risk. For example, mortality can also be reduced for individuals that react quickly to perceived threats and escape via flight (Walker et al. 2005) and quick start maneuvers (Croes et al. 2007). When considering antipredator responses specifically, it may be illuminating to consider variation along an axis of reactivity. Whether animals are relatively placid or skittish in response to predation risk may reflect alternative strategies

for mitigating risk, and may thus comprise an important dimension of temperament.

A major question accompanying any observation of variation in animal temperament is whether the observed behavioral differences are due to innate, genetic variation or a learned response (Wilson 1998; Gosling 2001; Dall et al. 2004; Dingemanse and Réale 2005). This question may be somewhat complicated to address because genetic variation can exist at multiple levels of biological organization. There may be heritable, genetic variation among individuals within a population (i.e., appreciable heritability of behavior) (Bell 2007; Dochtermann et al. 2019) as well as variation in the average genotypes underlying behavior in different populations (i.e., local adaptation). A powerful test for local adaptation can be made by 'common-garden' experiments in which offspring from adults collected from different populations are reared within a common environment and studied (Kawecki and Ebert 2004). If offspring from different populations continue to exhibit differences in behavior despite developing under similar environmental conditions, this is evidence that these behavioral traits have a component that is inherited, and are not a completely learned response. Within a population, innate differences among individuals can be assayed by measuring behaviors of the same animals multiple times in a controlled environment (e.g., under laboratory conditions). Behavioral tendencies can then be separated from behavioral plasticity (e.g., Nussey et al. 2007) and heritable variation in behavioral tendencies can be quantified by comparing the phenotypic similarities of close relatives (e.g., siblings) vs unrelated individuals (Falconer and MacKay 1996; Lynch and Walsh 1998).

If there is an appreciable component of genetic variation underlying variation in temperament, it would suggest that populations have the capacity to evolve relatively quickly in response to shifts in selection. In the wild, changes in the magnitude and even direction of selection may be common as environmental conditions vary (see reviews by Siepielski et al. 2009, 2017), and fishing by humans can be a particularly powerful source of selection that severely alters natural patterns of selection (e.g. Law 2000; Edeline et al. 2007; Allendorf and Hard 2009; Hixon et al. 2014). Given that behavioral characteristics are the traits that are selected most directly by fisheries (Biro and Post 2008; Uusi-Heikkilä et al. 2008; Arlinghaus et al. 2017; Diaz Pauli and Sih 2017), populations with genetic variation in temperament could evolve to become less susceptible to fishing and thus increase their long-term resilience (Magurran 1993; Shumway 1999; Diaz Pauli and Sih 2017; Andersen et al. 2018). Studies that examine defensive behaviors in field populations and the inheritance of these behaviors will therefore be important steps toward understanding the role that genetic variation in temperament will play in the long-term health of populations.

Our study was designed to test for local adaptation in reactivity of a temperate reef fish, the black surfperch (*Embiotoca jacksoni*). There may be variation in selection on this species because mortality rates differ extensively across populations of black surfperch, and mortality rates are positively correlated with measures of spearfishing effort (Johnson et al. 2019). Behaviors, in particular those related to reactivity and wariness, may reduce predation risk and fishing mortality and thus may be subject to selection. The first goal of this study was to measure behaviors of fish in the field and compare reactivity of fish within high- and low-risk environments. The second goal was to conduct a common garden experiment to test whether any differences in behavior between high- and low-risk populations were inherited or learned. A third, ancillary objective was to compare variation in behavior among close relatives (siblings) and estimate broad-sense heritabilities for the behavioral phenotypes we measured in the lab.

Methods

Study system

The black surfperch is a temperate reef fish that is found at depths of 0–46 m and may grow up to 26 cm standard length in coastal regions of Southern California. Adult black surfperch move relatively little (Hixon 1981) and are livebearers whose offspring likely exhibit little dispersal from their natal reefs (Waples 1987; Bernardi 2000). Although direct and comprehensive measures of offspring dispersal are difficult for marine species (Johnson et al. 2018), dispersal can be estimated indirectly using measurements of gene flow. Genetic connectivity of black surfperch populations is low compared to many marine fishes, but values are within the observed range for species that have been studied so far. Isolation by distance slopes (which are negatively related to genetic connectivity) range from range from 2.0×10^{-6} to 1.0×10^{-3} for marine fishes (Nanninga and Manica 2018), and the value for black surfperch is 5.8×10^{-4} [values calculated from Bernardi (2000)]. Thus, populations of black surfperch may be more likely to respond to local selection pressures than populations of species that experience high rates of gene flow across long distances. Black surfperch may live up to 7 years in some locations, and the average generation time is between 2 and 3 years (Baltz 1984). Juvenile surfperch are susceptible to predation by kelp bass (*Paralabrax clathratus*), a large serranid that is common on nearshore reefs of Southern California (Holbrook and Schmitt 1984; Ebeling and Laur 1985; Schmitt and Holbrook 2018). Adult surfperch are taken by spearfishers, and spatial variation in spearfishing activity appears to be a major source of variation in mortality rates (Johnson et al. 2019).

Although other species of surfperch—particularly those found in sandy habitats—are often caught by hook and line, species of surfperch that reside in kelp forests are much less prone to hook and line fishing (Karpov et al. 1995) and thus we focus on spearfishing as a source of selection. Given the combination of strong variation in selection, local retention of offspring, and a short generation time, black surfperch have a high potential for local adaptation.

Assessing reactivity of fish in the field

To test for spatial variation in temperament among black surfperch populations, we measured reactivity of fish within high- and low-risk populations. Our low-risk population included sites along the Palos Verdes Peninsula near Los Angeles, California (hereafter abbreviated as ‘PV’; Appendix S1). Our high-risk population included sites on the northeast side of Santa Catalina Island, California (hereafter abbreviated as ‘CAT’). These populations are approximately 35 km apart and are separated by a deep-water channel. CAT is much more popular with divers and spearfishers (freedivers and scuba) than PV as it generally has greater visibility and better diving conditions (Sheckler and Sheckler 2008). Study populations were chosen because of similarities in depth and structural complexity. Average rugosity of the substrate was very similar (rugosity score for CAT: 0.651 ± 0.027 SE, PV: 0.682 ± 0.038 , Welch t test: $t = -0.680$, $P = 0.508$, $df = 14.0$), and the densities of kelp plants in the area were also similar (CAT: 200.86 ± 73.90 , PV: 203.73 ± 37.10 , $t = 0.035$, $P = 0.973$, $df = 10.4$, Appendix S1). Despite similarities in the structure of the habitat and refuge space for these populations, black surfperch incur greater risk of fishing mortality at CAT and the annual, per-capita mortality rate of black surfperch adults at CAT is estimated to be 2.8 times higher than mortality at PV (Johnson et al. 2019). In addition, surfperch at CAT also experience greater abundances of predatory kelp bass (*Paralabrax clathratus*; Appendix S1) which are more abundant at CAT, likely due to the proximity of nearby marine reserves (one 5 km away and another 22 km away). Kelp bass have dispersive larvae, and an appreciable proportion of offspring are likely to be retained in the local region (Selkoe et al. 2007). The high abundance in our study area of Santa Catalina Island is likely because of local export of larvae from populations within the reserve.

To evaluate the average response of black surfperch to perceived risk in the wild, we measured flight initiation distances (FID) of individual fish at CAT ($n = 59$) and PV ($n = 186$). FID measurements are typically recorded as the distance at which an animal begins to flee from an approaching threat (e.g., Januchowski-Hartley et al. 2011, 2013). The flight response estimated during FID tests is often described as reactivity; one of the behavioral attributes that comprises

temperament (e.g. Gotanda et al. 2009; Januchowski-Hartley et al. 2012; Rhoades et al. 2018). Our measures of FID were conducted on SCUBA at depths of 1–14 m. Divers swam along the reef and began an FID trial once a black surfperch was spotted. During a trial, the starting distance between the diver and surfperch was visually estimated. The diver then approached the surfperch directly until flight behavior was observed. When fish were stationary, flight initiation typically consisted of a rapid turn and acceleration away from the approaching diver. Flight in fish already swimming was recorded when the fish accelerated swimming speed away from the diver. FID was recorded as the visually estimated distance between the diver and the fish when flight behavior first occurred. We also estimated the distance at which the fish was first sighted (encounter distance) and total length of the fish observed. Encounter distance is a measure of the distance at which an animal can detect a potential threat, and thus constrains FID values. Observed FID values could not be larger than the encounter distance, though they were frequently much smaller. Encounter distance is highly correlated with water clarity (e.g., Bozec et al. 2011; MacNeil et al. 2008) and although we did not measure visibility associated with each FID value, visibility certainly differed between and within populations. Recording encounter distance and including this as an explanatory variable allowed us to account for the effects of variable visibility on FID values. Encounter distance was also related to the density of giant kelp, since fish and divers could be concealed from one another in highly vegetated areas. Including encounter distance helped account for this source of variation, and our analyses thus focused on comparing whether FID values differed between our study populations, once the effects of encounter distance and fish size were accounted for.

Before sampling began, divers calibrated their estimates of distance and fish length by visually estimating the distances to, and sizes of, fixed objects underwater (e.g., rocks, kelp blades) then measuring the distances and sizes with a meter tape. Distances were estimated to the nearest 0.25 m and the sizes of fish were estimated to the nearest cm. Visual estimates of distance are common practice in underwater transect surveys (Brock 1954), and although other methods of measurement (e.g., distance markers placed by a second observer) may be more exact, visual estimates are quick, and this approach allowed us to cover more area per unit time and thus sample FIDs for more fish. To minimize the risk of resampling an individual fish, once an FID was recorded, divers swam > 5 m away in a direction opposite from the heading of the previous fish sampled. Minimum, horizontal visibility through the water during our surveys was 6 m.

To analyze variation in FID values, we used a linear model in which mean FID was modeled as a function of encounter distance, fish size, study population, and all possible interactions. In addition to these effects, observer

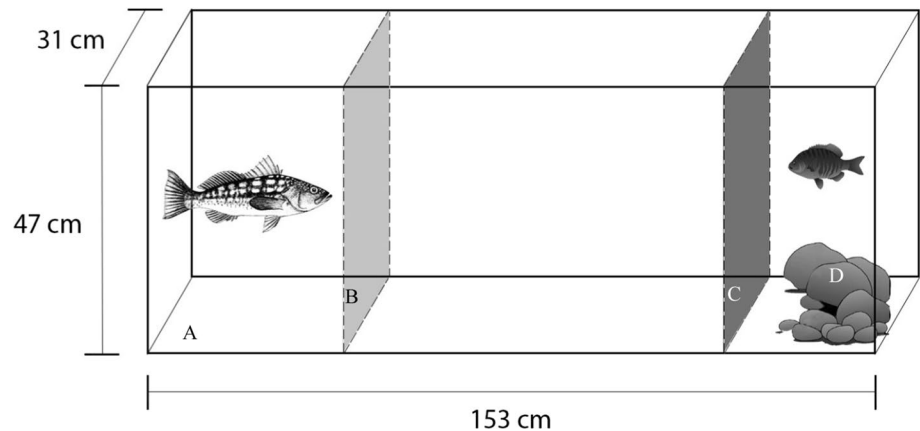
identity was included to test for any systematic variation in how observers estimated FIDs. One of the four observers did not conduct surveys at one of the populations, but there is no evidence to suggest that this confounded the comparison between populations. The three observers that conducted surveys at both populations accounted for 96% of the data collected, and observations made by the fourth observer did not systematically differ from the values recorded by the other observers ($F=0.49$, $df=3$, $P=0.693$). Models were fit using the `aov` and `lm` functions in R (R Development Core Team 2020).

Common garden experiment and behavioral assays

Pregnant surfperch were collected from each site by divers on SCUBA using large hand nets (CAT: $n=6$, PV: $n=8$). Immediately after capture, mothers were transferred to large, insulated and aerated coolers (75 L) and were transported to aquaria at California State University, Long Beach. Mothers were housed individually in identical 55-L tanks separated by opaque dividers. Seawater flowed through the tanks via a 3700-L re-circulating system. The seawater was maintained at 16 °C and a salinity of 34 and tanks were exposed to natural light. Upon parturition, offspring were moved to their own tanks. Brood sizes ranged from 4 to 21 offspring and were divided into groups such that offspring tanks held between 4 and 7 siblings. Offspring were born between 4.1 and 6.2 cm SL. There was a total of 57 lab-born offspring from Catalina, and 71 offspring from Palos Verdes. Juveniles were fed a diet of brine shrimp (*Artemia* sp.) and mysis shrimp (*Mysis* sp.), 5 times daily. Most broods did not begin to feed until the 3rd day after birth, therefore behavioral trials began on the 4th day after birth to allow for recuperation.

To test whether offspring from different source populations exhibited innate differences in behavior, we conducted behavioral trials that measured exploration of a novel environment: a long, rectangular tank that contained both a shelter (LWH=31, 24, and 24 cm) and a predator (*Paralabrax clathratus*) that was visible, but separated by a clear plastic divider (Fig. 1). Fish were introduced to the end of the tank with the shelter, and after a period of acclimation, subject fish could move freely about the tank. Behaviors tracked during each trial included total duration of time spent in the shelter zone, time to leave shelter area after start of the trial (latency), average swimming speed, and average distance to the predator divider. A single *P. clathratus* was used during the span of this experiment, though the order of trials was randomized such that no one brood was tested on a single day and that fish from CAT and PV were included on each test day. Trials were 15-min long, and trials were repeated three times, one to two weeks apart for each fish. For additional details, see Appendix S2. To assess of whether size and growth were correlated with behavior, we measured

Fig. 1 Behavioral trial tank. **a** Predator holding area containing kelp bass (*Paralabrax clathratus*); **b** clear divider separating predator from the remainder of the trial tank; **c** opaque acclimation divider, removed before start of trials; **d** rocky shelter area



standard length (to the nearest 0.1 cm) and weight (to the nearest 0.01 g) of each fish after each trial (Appendix S2). We found no significant relationships between behaviors and measures of size or growth of lab-born fish (Appendix S2).

Statistical analyses of behaviors within the lab

To test whether behaviors of lab-born offspring differed among mothers from high-risk locations (CAT) and low-risk locations (PV), we used linear mixed effect models to compare results from our behavioral trials (R package lme4; Bates et al. 2015). In these analyses, population was included as a fixed factor, since this was our main comparison of interest. If there were behavioral differences between offspring from the two source populations, then it would support the idea that the behavioral differences are inherited. Given that offspring are not independent samples (siblings shared mothers, and some siblings shared tanks in our study) we included the identity of the mother and the tank group nested within mother as random effects. Offspring identity was also included as a random effect to account for non-independence in measurements from the same fish. Each fish was subjected to three trials that were separated by 15 days on average, but were otherwise identical. Because it was possible that behaviors of fish could change over time as fish became habituated to the testing procedure, and because it was possible that any habituation or learning differed by source population, we included fixed effects for both trial number (treated as numeric and centered) and trial by population interaction. To obtain *P* values for the fixed effects (including behavioral differences among the populations), we used a *t* test approximation. Specifically, we calculated the *P* values using the *t* value from the linear mixed effects model and the most conservative degrees of freedom for our study design (*df* = 12, as there were 14 mothers and means were estimated from two populations). We used a similar analytical approach to test whether the size and growth rates of lab-born offspring differed between the two source

populations. Additionally, we examined correlations among morphological characteristics and behaviors measured.

Our mixed effects analyses tested for inherited differences in behavior among populations and also allowed us to separate phenotypic variation into four components: variance among mothers (within populations), variance among tanks (within mothers), variance among individuals (within tanks), and residual variation (variation among trials, after accounting for any general patterns in habituation). In essence, this was a full-sib analysis: a standard procedure in the field of quantitative genetics that is used to estimate heritability of traits (Falconer and Mackay 1996; Lynch and Walsh 1998). We estimated the broad-sense heritability (h^2) of behavioral traits by comparing variation among mothers to the overall phenotypic variation (Appendix S3). Collecting gravid adults was a very labor-intensive process, and our collections are the result of over 100 person-hours of diving. Although the sample sizes of mothers was relatively small, this procedure also derives statistical power from replication at the level of offspring (Lynch and Walsh 1998) and our study included 57 offspring from CAT, and 71 from PV. The goal of heritability analysis is estimation, rather than hypothesis testing, and although the logistics of working in a particular study system can sometimes restrict sample sizes (e.g. Bakker 1986; Garenc et al. 1998; Bell et al. 2018), estimates of heritability (accompanied by appropriate measures of uncertainty) provide useful information. This is particularly true for characteristics such as behaviors of marine fishes—an area where there is little information about heritable variation (reviewed by Bell et al. 2009).

Results

Assessing reactivity of fish in the field

The response of black surfperch to perceived risk (approaches of SCUBA divers in the field) differed

substantially between our study locations (Fig. 2, Table 1). Overall, fish in the high-risk population (CAT) displayed a higher degree of vigilance and fled at distances that were significantly longer than fish in the low-risk population (Fig. 2a, Table 1). However, FID values were also affected by the size of the fish and the distance at which the fish was

first encountered (Table 1). All higher order interactions were significant, indicating not only that the slopes of FID with length of fish and FID with encounter distance differed between the study populations, but that mean FID depended on the combination of fish size and encounter distance differently at each of the study populations (Table 1). Figure 2c,

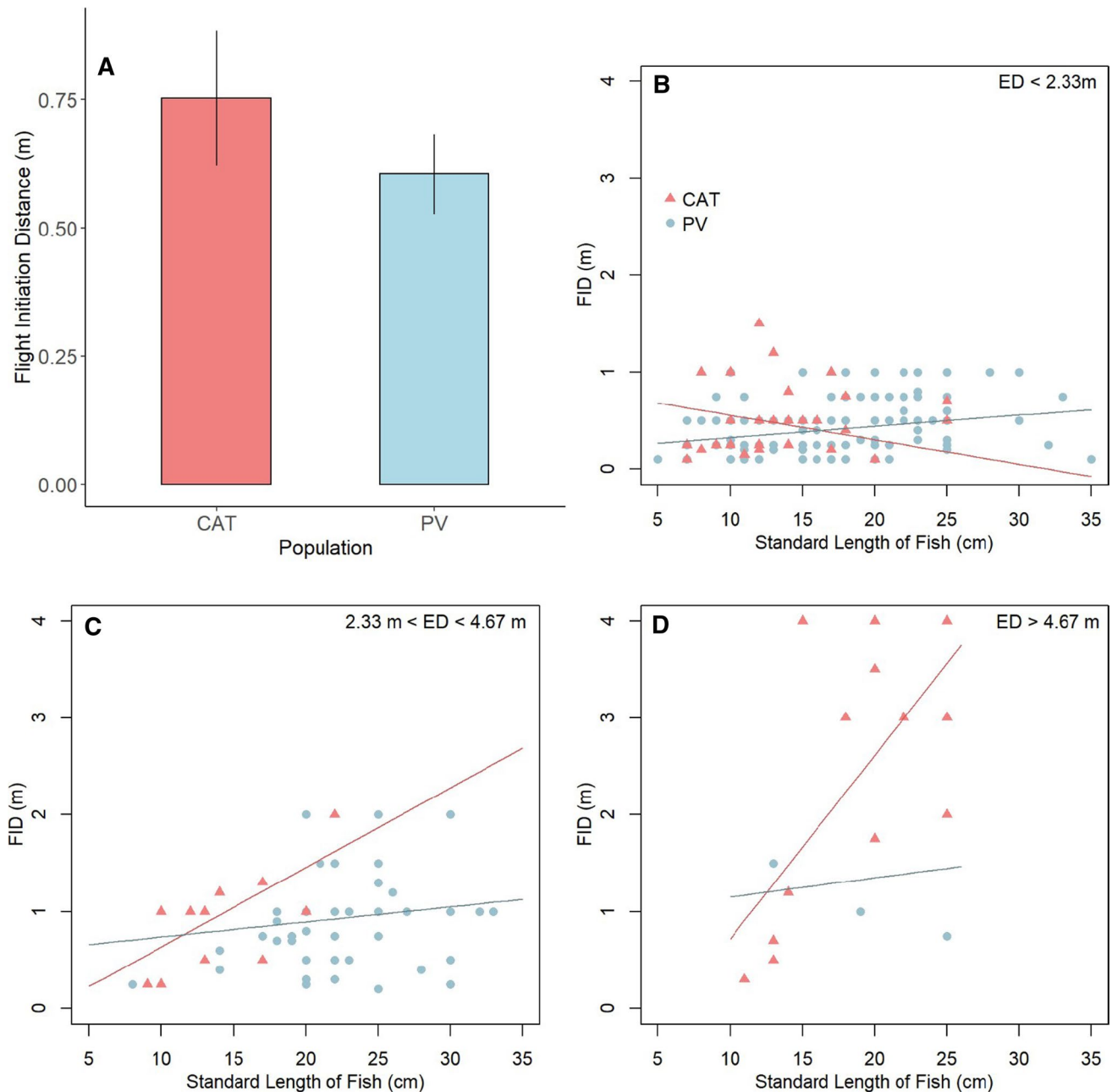


Fig. 2 Variation in flight initiation distance (FID) of black surfperch (*Embiotoca jacksoni*) measured in the field at Santa Catalina Island, the high-risk population (CAT; red triangles, $n=59$) and Palos Verdes Peninsula, the low-risk population (PV; blue circles, $n=186$). **a** Illustrates overall differences in mean FID between the study populations. Bars represent the marginal means ($\pm 95\%$ confidence intervals), evaluated at the average values of body size and encounter

distance. **b–d** Illustrate the three-way interaction among encounter distance, body size, and study population. Each panel shows observations binned by encounter distance (ED), and lines illustrate the mean FID values estimated by the overall model with encounter distance evaluated at the midpoint of the observations within each bin. See main text and Table 1 for additional details

Table 1 The results of the linear model analysis in which flight initiation distance (FID) of black surfperch in the field was modeled as a function of encounter distance, fish size, study population, and all possible interactions

Source	df	SS	F	P
Population	1	7.36	49.11	<2E-16
Length of fish	1	18.09	120.65	2.51E-11
Distance at first sighting	1	25.99	173.33	<2E-16
Observer	3	0.22	0.49	6.93E-01
Population \times length	1	4.68	31.21	6.37E-08
Length \times distance	1	1.72	11.46	1.00E-03
Population \times distance	1	2.58	17.19	4.72E-05
Population \times length \times distance	1	5.09	33.97	1.82E-08
Residual	236	35.39		

Observer identity was included to test for any systematic differences in FID estimates among observers

d illustrate the three-way interaction in detail. In particular, when encounter distance was short and there was less scope for variation in FID, there was little-to-no relationship between fish size and FID, and the differences in average FID between the high- and low-risk populations were less pronounced (Fig. 2b). However, at medium encounter distances, there was a clearer increase in FID with fish size, and it was clear that these relationships differed between the study populations and that fish in the high-risk population had higher FID values (Fig. 2c). Finally, at the largest encounter distances, there was an even stronger overall increase in FID with fish size, and when comparing the study populations, fish of a given size had much higher FID values in the high-risk population (CAT; Fig. 2d).

Common garden experiment and behavioral assays

Significant differences were found between fish from the two study populations for all four of the behavioral responses we measured. On average, offspring from CAT spent approximately half as much time ($0.53\times$) in the shelter zone than offspring from PV did ($t=2.993$, $df=12$, $P=0.011$, Fig. 3a). Additionally, offspring from CAT emerged from shelter faster; on average in 0.60 times the amount of time it took offspring from PV to emerge ($t=3.149$, $df=12$, $P=0.008$, Fig. 3b). Average swimming speed for PV offspring was 0.54 times slower than for offspring from CAT ($t=3.620$, $df=12$, $P=0.004$, Fig. 3c). Lastly, offspring from PV maintained an average distance from the predator that was 1.67 times the distance of offspring from CAT ($t=4.040$, $df=12$, $P=0.002$, Fig. 3d). No significant differences were found among populations for the standard length ($t=0.012$, $df=12$, $P=0.991$) and weight ($t=0.358$, $df=12$, $P=0.727$), or average growth rate in length ($t=0.470$, $df=12$, $P=0.647$), or in weight ($t=0.012$, $df=12$, $P=0.991$) of lab born offspring.

Similarly, variation in size and growth rate of individual fish in this study did not explain a significant amount of the variation in behavior (Appendix S2).

In addition to the significant, between-population differences in overall activity, lab-born offspring did exhibit a degree of habituation to the behavioral trials, though the response was much more pronounced for fish whose parents came from the high-risk population (CAT). In later trials, fish from parents collected at CAT swam at slightly slower speeds, spent more time sheltering, and less time in open areas of the tank near the predator. In contrast, fish from parents collected at PV showed little-to-no change in average swimming speed, sheltering time, and time near the predator. The trial by population interactions were significant for all three of these metrics ($P=0.002$, 3.3×10^{-6} and 3.04×10^{-5} respectively), but not for latency to leave shelter ($P=0.12$). Model coefficients for the fixed effects of trial and population are summarized in Table 2.

The behaviors we measured exhibited a moderate range of broad-sense heritabilities. For total duration spent in shelter, the proportion of genetic variance over total phenotypic variance was 0.496 (95% CI 0.079–0.843). However, for latency to leave shelter following the start of a trial, heritability was estimated to be 0.029 (95% CI 0–0.349). Heritability was 0.345 (95% CI 0.023–0.657) for average swimming speed and 0.097 (95% CI 0.001–0.446) for average distance to predator.

Discussion

Our results demonstrated significant variability in temperament between populations of black surfperch that inhabit high- and low-risk environments. In our field evaluations of behavior, fish from the high-risk population (CAT) exhibited a much greater degree of reactivity and fled soon after encountering an approaching diver. In contrast, fish from our low-risk population (PV) allowed divers to approach relatively close before moving away. These results are consistent with the often-observed pattern of increased wariness when animals are routinely exposed to greater mortality risk (reviewed by Lima and Dill 1990; Stankowich and Blumstein 2005) and are similar to the behavioral trends exhibited by other fishes in high- and low-mortality environments, especially inside and out of Marine Protected Areas (Gotanda et al. 2009; Januchowski-Hartley et al. 2012; Rhoades et al. 2018). Importantly, the results of our common garden experiment suggest that such differences in temperament are in part due to inherited differences, and are not entirely a learned response to the level of risk in the environment the fish developed in.

We found strong evidence for inherited differences in behavior that were distinct between fish from different

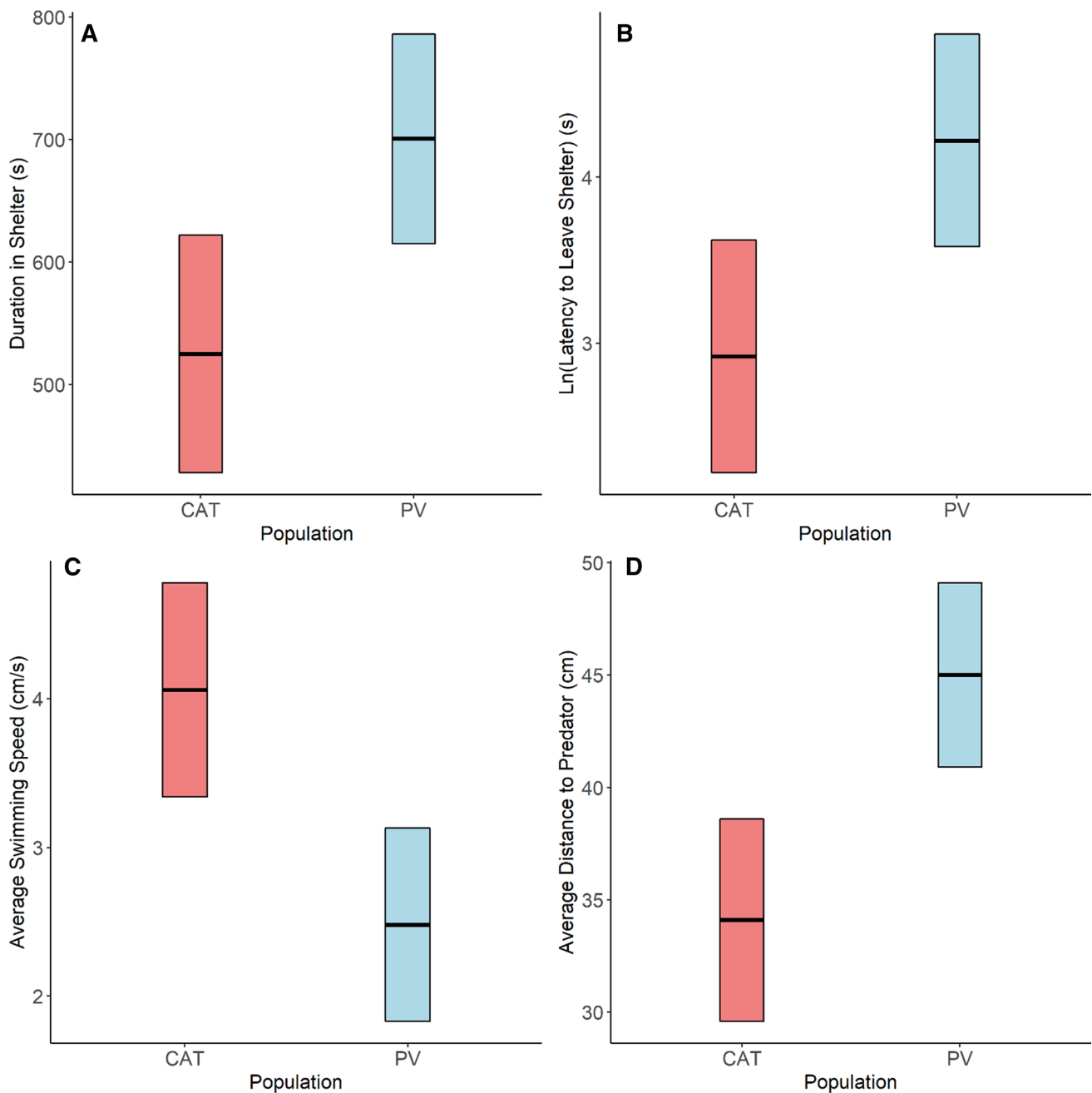


Fig. 3 Behavioral differences in lab-born black surfperch (*Embiotoca jacksoni*) offspring from Santa Catalina Island (CAT; in red, $n=57$) and Palos Verdes Peninsula (PV; in blue, $n=71$). Graphs indicate the estimated marginal means (solid line) and 95% confidence intervals (colored box). Marginal means were calculated for the second of three repeated trials and account for both the hierarchical nature

of the study, and differences in sample sizes between source populations. **a** The total duration of time spent in shelter out of the 15-min trial. **b** Latency to leave shelter upon removal of the acclimation divider, the beginning of the trial. **c** The average swimming speed. **d** The average distance of the subject black surfperch to the predator divider during the 15-min trial

populations, although the behavioral differences were not as we initially expected. Because fish from the low-risk population exhibited greater boldness in the field (in the sense that they let divers approach closer, on average), we expected offspring from this population to exhibit greater boldness in the lab (if variation in temperament had an inherited

component). For instance, latency to emerge from shelter is commonly interpreted as a measure of boldness (e.g., Brown et al. 2007; Harris et al. 2010), but in our study offspring from the low-risk population took longer to emerge from shelter than their counterparts from high-risk populations. Studies that measure variation in temperament in both field

Table 2 The results of a mixed-effects model used to evaluate variation in behaviors of juvenile black surfperch in the laboratory

Model: lmer (Behavior~trial×population+(1 mother/tank/fish))					Random effects	Variance
Behaviors	Fixed effects	Coefficient	Std. error	<i>P</i>		
Speed	Trial	−0.719	0.118	5.41×10^{-5}	Mother	3.09×10^{-1}
	Population	−1.577	0.436	4.00×10^{-3}	Tank	3.43×10^{-1}
	Trial×population	0.734	0.187	2.00×10^{-3}	Fish	1.60×10^{-1}
	Intercept	4.058	0.324	2.99×10^{-8}	Residual	1.61×10^0
Shelter duration	Trial	146.800	15.830	8.05×10^{-7}	Mother	7.58×10^3
	Population	175.790	58.740	1.12×10^{-3}	Tank	4.13×10^3
	Trial×population	−190.300	23.490	3.31×10^{-6}	Fish	0.00×10^0
	Intercept	524.910	44.000	5.17×10^{-8}	Residual	2.95×10^4
Latency to emerge	Trial	−0.287	0.311	1.08×10^{-1}	Mother	4.20×10^{-2}
	Population	1.301	0.413	8.39×10^{-3}	Tank	6.37×10^{-1}
	Trial×population	−0.405	0.244	1.23×10^{-1}	Fish	0.00×10^0
	Intercept	2.921	0.311	6.96×10^{-7}	Residual	3.21×10^0
Distance to predator	Trial	6.466	1.067	5.69×10^{-5}	Mother	5.83×10^0
	Population	10.908	2.698	1.63×10^{-3}	Tank	1.94×10^1
	Trial×population	−10.239	1.581	3.04×10^{-5}	Fish	2.51×10^0
	Intercept	34.128	2.010	9.36×10^{-10}	Residual	1.34×10^2

Comparisons of study populations and repeated trials were treated as fixed effects. *P* values in bold font are significant. Fixed effects accounted for any systematic differences among populations and trials; random effects described how much of the remaining variance in behavior was associated with the various groups in our study

and lab populations are rare (but see Kobler et al. 2009; Pellegrini et al. 2010), and at first, our results may seem somewhat contradictory. However, we must recognize that temperament is a complex, higher-order property, and there are obvious constraints when measuring behavior in the lab. Other studies have found that fish from low-risk populations tend to emerge later from shelter and thus exhibit less boldness in the lab (Brown et al. 2007; Harris et al. 2010), but even a characteristic like boldness can be subdivided into components including reaction to novel stimuli and tendency towards risk-taking (Toms et al. 2010). These components may not always be positively correlated (e.g., Wilson et al. 2010) and the degree to which these components are correlated can depend strongly on environmental context (e.g., Coleman and Wilson 1998; Webster et al. 2007), and whether selection acts on these traits independently (Conrad et al. 2011). We believe that behavioral variation we measured is best characterized as variation in reactivity—an attribute that is related to, but not synonymous with boldness. Fish from the low-risk population were relatively placid, which manifested as low FID values in the field, less movement in the lab, and because they started the behavioral trials in shelter, greater shelter use. In contrast, fish from the high-risk population were more skittish, which manifested as high FIDs in the field, greater swimming activity and less shelter use in the lab. We note that a general tendency toward reactivity and flight in fish from the high-risk population resulted in more time out in the open, and thus more time

spent near the predator. Based on the orientation and posture of the fish, we believe that time spent near the predator was more closely related to overall activity within the confines of the aquarium, rather than a true tendency toward predator inspection or approach. Despite the complexities associated with measuring behavioral phenotypes in laboratory assays, our results highlight reactivity as an important aspect of temperament that can influence an individual's risk of mortality, and thus may be subject to selection.

We hypothesize that frequent encounters with spearfishermen and/or predatory fishes have disproportionately removed slow and less reactive individuals within the Catalina population, such that adults surviving to reproduce are those with a tendency to react sooner, move quickly, and cover greater distance. In addition, black surfperch with elevated reactivity may incur an opportunity cost in low-risk environments if overreacting to perceived risk results in greater energy expenditure and/or fewer feeding opportunities (Ydenberg and Dill 1986). Our results are generally congruent with evidence suggesting that active fishing techniques (such as spearfishing) can selectively remove the most passive individuals such that more reactive individuals survive to reproduce (Diaz Pauli and Sih 2017; Andersen et al. 2018). We believe that reactivity is a generalized response expressed at all ages, and even though small juveniles are not subject to spearfishing mortality, selection on adults can result in changes in behavior that are also expressed during the juvenile phase. Sheltering can reduce both detection and

capture when fish face natural predators (e.g., Tupper and Boutilier 1997; Steele 1999; Johnson 2006), but sheltering is a less effective defense when facing spearfishers because fish within natural refuges (in this case within kelp or under rocks) can still be captured by spear. Our findings are thus consistent with the results reported by Guidetti et al. (2008) which also found that in areas where spearfishing is common, fish flee in open water to evade mortality, whereas in protected areas lacking spearfishing pressure, fish use shelter to mediate natural predation risk.

Local adaptation in behavior has been reported for several other species of fish, but most of these fishes exist in populations that are isolated to a greater degree than black surfperch (Bell 2005; Dingemanse et al. 2009). Our common garden experiment revealed that differences in behavior between source populations were passed down to their offspring in the lab. However, the actual mechanisms of this inheritance are not entirely clear. We were able to measure heritability in the broad sense, and given the reproductive biology of black surfperch, we were unable to separate genetic effects from effects that are maternally transmitted. Fish from the high-risk population may simply include more genotypes that code for a greater degree of reactivity, but it is also possible that conditions experienced by mothers affect the behavior of offspring by other means (e.g., epigenetic effects or maternal inheritance; Jensen 2013). In this study, it was possible that mothers living in a high-risk environment influenced behavior of offspring through mechanisms such as the transfer of stress hormones during early development. Experimental studies on other species have demonstrated the possibility of such effects (e.g. Eriksen et al. 2011; Best et al. 2017), but it is unclear whether the treatments used in those studies (direct injection of concentrated stress hormones) are comparable to the less concentrated, but chronic stresses fish are likely to experience in high-risk populations. In addition, the behavior of offspring in this study was not correlated with maternal attributes such as time spent in the lab before giving birth or maternal size (Appendix S3). In any case, exploration of maternal inheritance in this species is an avenue for future study. In the current study, we consider inheritance and heritability in the broad sense.

Our estimates of broad-sense heritability values for behaviors were in the low to moderate range. Values for total time spent in shelter (0.496), average swimming speed (0.345), and average distance to the predator (0.097) were comparable to heritability estimates for behavior in populations of other fish species (Bell 2005, 2009; Dingemanse et al. 2009; Van Oers and Sinn 2011; Ariyomo et al. 2013). It is worth noting that previous studies in this area have concentrated on smaller fishes that inhabit freshwater or estuarine environments (e.g., sticklebacks, zebrafish, and poeciliids), and despite the larger size of black surfperch and differences in life history and dispersal potential, estimates of

heritability for behavioral tendencies are comparable. Our observed heritabilities suggest behavioral responses to risk may adapt to local shifts in selection at an appreciable rate, and our results are consistent with artificial selection experiments on Atlantic silversides and zebrafish demonstrating that significant differences in behavior can evolve over 4–5 generations of selection (Walsh et al. 2006; Uusi-Heikkilä et al. 2015).

Because of the logistic challenges of capturing gravid females of fish this size and housing many of their offspring in the laboratory, our common environment experiment focused on comparing fish from two source populations. It is possible that inherited differences in behavior are due to other factors, but we believe that mortality risk is the most likely explanation. The structural complexity of the habitat and the availability of refuge space for black surfperch is similar for these populations. Water clarity is typically higher at Santa Catalina Island, but it is unlikely that visibility itself is a selective agent. Rather, visibility likely moderates selection via predation and fishing mortality. In a prior study (Johnson et al. 2019), we compared demography of black perch within nine populations distributed across ~350 km of coastline. We found that mortality risk varied substantially among populations, and mortality was significantly correlated with spearfishing activity, but not significantly correlated with densities of *P. clathratus*. This suggests that spearfishing pressure is a stronger source of risk than natural predation, though analysis of other natural predations could be informative. Additionally, patterns of behavior observed in our prior study mirrored those observed in this study: fish in populations with high spearfishing activity were more difficult to approach, regardless of other habitat attributes such as water clarity or substrate rugosity (Johnson et al. 2019). Santa Catalina Island has been a popular spearfishing destination for at least three decades, and given evidence of heritable variation in behavior, selective mortality and evolved responses of behavior provide a parsimonious explanation for the inherited differences in behavior we observed.

Certainly there is a plastic element to behaviors such that flexibility in behavioral responses to perceived risk is common (reviewed by Lima and Dill 1990; Stamps and Biro 2016). However, our results emphasize that differences in overall reactivity among populations may represent inherited adaptations to local variation in natural mortality risk and fishing. Although local adaptation is easier to demonstrate empirically within controlled, laboratory environments (Kawecki and Ebert 2004), there is some indirect evidence from wild fish populations to suggest that behavioral variation in response to variable predation risk may be due to adaptation. For example, Rhoades et al. (2018) compared flight responses in seven species occurring in old and new no-take marine reserves with those

in unprotected areas. Her results revealed similar FIDs among fish in new reserves and unprotected areas, while FIDs were significantly smaller in old reserves where fish had been protected for multiple generations. Similarly, Januchowski-Hartley et al. (2013) observed reduced FIDs for two groups of reef fishes (Acanthuridae and Scaridae) residing in a twenty-nine-year-old marine reserve compared to fishes in newer reserves (5 and 6 years old). These studies suggest greater changes in reactivity occur when populations have been protected long enough for adaptation to occur. Our study demonstrates that some of the spatial differences in reactivity to predation risk are because of inherited differences, and we suspect this phenomenon may be common in the wild.

Genetic variation in temperament among individuals and among populations highlights the potential for populations to evolve in response to fisheries selection. If certain aspects of temperament (e.g., greater reactivity, reduced willingness to bite a lure, etc.) can make individuals less likely to be captured in a fishery, populations may subsequently evolve to be less vulnerable to fishing. Conclusively demonstrating fisheries-induced evolution in field populations is a major challenge, and although direct demonstrations are rare (Philipp et al. 2009), evidence consistent with evolutionary changes in behavior is accumulating across multiple species and environments (e.g., Alós et al. 2015; Tsuboi et al. 2016; Louison et al. 2018). Evolutionary changes in behavior that make individuals less susceptible to capture will increase average survival and will, to some extent, offset the effects that fishing has on populations. However, the reduction in catchability may be small in magnitude when compared to the overall effect of fishing mortality on populations, and the evolved changes in temperament may not necessarily increase fitness if changes in behavior are negatively correlated with other components of fitness (e.g., parental care, reproductive success, growth; see Sutter et al. 2012; Biro and Sampson 2015). Given the accumulation of evidence that fisheries can select on temperament, and that temperament is a heritable characteristic, it will be important for future studies to evaluate both the direct effects of fishing mortality and the concomitant effects that evolutionary change in temperament (and related components of fitness) can have on the dynamics of populations. Such studies will be critical for understanding the selective effects of fishing and anticipating the long-term consequences for the health of fished populations.

Acknowledgements We thank the many people who helped in the field and lab, especially Brian Stirling, Yvette Ralph, Janelle Paz and Bailey McCann. We are grateful for the reviews and comments from Chris Lowe, Mark Steele, and Peter Wainwright. This research was conducted with support from the California State University Council on Ocean Affairs, Science and Technology (award # COAST-GDP-2017-004),

the Southern California Academy of Sciences, and the Department of Biological Sciences and the Office of Research and Sponsored Programs, California State University, Long Beach.

Author contribution statement DRS and DWJ conceived and designed this study. DRS and DWJ were responsible for field collection, statistical analysis, and writing of the manuscript. DRS was responsible for data collection, animal husbandry, and design of figures.

Compliance with ethical standards

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed.

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