Applying empirical dynamic modeling to distinguish abiotic and biotic drivers of population fluctuations in sympatric fishes

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Abstract

Fluctuations in the population abundances of interacting species are widespread. Such fluctuations could be a response to abiotic factors, biotic interactions, or a combination of the two. Correctly identifying the drivers is critical for effective population management. However, such effects are not always static in nature. Nonlinear relationships between abiotic factors and biotic interactions make it difficult to parse true effects. We used a type of nonlinear forecasting, empirical dynamic modeling, to investigate the context-dependent species interaction between a common fish (three-spine stickleback) and an endangered one (northern tidewater goby) in a fluctuating environment: a central California bar-built estuary. We found little evidence for competition, instead both species largely responded independently to abiotic conditions. Stickleback were negatively affected by sandbar breaching. The strongest predictor of tidewater goby abundance was stickleback abundance; however, this effect was not a uniform negative effect of stickleback on goby as would be hypothesized under interspecific competition. The effect of stickleback on gobies was positive, though it was temporally restricted. Tidewater goby abundance in the summer was strongly positively correlated to stickleback abundance in the spring, which represents an offset in the reproductive and recruitment peaks in the two species that may help minimize competition and promote coexistence. Our study demonstrates how empirical dynamic modeling can be applied to understand drivers of population abundance in putative competitors and inform management for endangered species.

Both abiotic and biotic factors can drive population fluctuations (Grant et al. 2016; Šipoš et al. 2017; Morris et al. 2020). Understanding which drivers are acting on a given population is important for understanding resilience, estimating population viability, and managing endangered species (Sinclair and Byrom 2006; Traill et al. 2010). Abiotic factors such as climate and habitat degradation may limit population abundance or cause fluctuations in population size (Chavez et al. 2003; Lemoine et al. 2007; Kearney et al. 2010). Alternating population cycles of pairs of species may be taken as evidence for

alternative responses to abiotic forcing variables such as climate (Chavez et al. 2003). Alternating cycles may be due to populations having different optimal values of fluctuating environmental variables, different seasonal patterns, or a combination thereof.

Biotic interactions, such as competition, predation, or parasitism may also influence the abundance of a focal population (Bardsley and Beebee 2001; McGraw and Furedi 2005; Rogowski and Stockwell 2006). However, disentangling abiotic and biotic drivers, especially when those potential drivers fluctuate, can be challenging (Sugihara et al. 2012; Gabaldón et al. 2019). Mirage correlations can occur when the relationship between predictor and population response is state dependent (Deyle et al. 2013). For example, determining whether abiotic conditions or biotic interactions are driving population fluctuations may be difficult if the presence of an interacting species depends on certain abiotic conditions (Rogowski and Stockwell 2006) or if interaction strength changes as a function of those abiotic conditions (Alcaraz et al. 2008; Jiao 2009; Deyle et al. 2016a).

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The magnitude of interaction strengths such as competition coefficients, and even the identity of the dominant competitor can change as a function of the environment (Stewart and Levin 1973; Dunson and Travis 1991; Muench and Elsey-Quirk 2019). Coexistence may depend on changes in the identity of the competitive dominant under fluctuations in environmental conditions (Hutchinson 1961). Typically, understanding such context-dependent species interactions requires conducting manipulative experiments under diverse environmental conditions which may be impractical when threatened and endangered species are concerned (Costanzo et al. 2005; Muench and Elsey-Quirk 2019).

Empirical dynamic modeling, a type of nonlinear state space reconstruction, can be used to overcome these challenges using time series data (Sugihara et al. 2012). Such time series of abundance data is regularly collected for monitoring of some threatened and endangered species. Multivariate s-map projection, a type of empirical dynamic modeling analysis, sequentially estimates the partial derivatives of the response variable with respect to each predictor variable over time. When response and predictors are the abundance of two species, these partial derivatives can be interpreted as a measure of time-varying interaction strength such as competition coefficients (Sugihara 1994; Deyle et al. 2016b). Such measures of interaction strength can be used to assess numerical population responses to competition. For the purposes of this study, competition is defined as a numerical response of one population's growth rate as a function of the other species' density.

The habitat and abiotic conditions in bar-built estuaries in central California undergo dramatic seasonal fluctuations leading to episodic opening and closure (Williams and Stacey 2016). Bar-built estuaries, or lagoons, are intermittently connect to the ocean during the wet seasons but will dry up when the rains stop and the runoff runs out; then a sandbar or berm will form, disconnecting the estuary from the open ocean (Behrens et al. 2009, 2013; Rich and Keller 2013). The bathymetry can change extensively during cycles of breaching and closing (Webb et al. 1991; Elwany et al. 1998; Orescanin and Scooler 2018). These physical changes to the shape of the estuary basin, from flowing and river-like during the winter to still and pond-like during the summer are accompanied by changes in the physicochemical properties of the estuary such as temperature, dissolved oxygen, and temperature and may include changes to stratification (Williams and Stacey 2016). Dissolved oxygen can reach anoxic conditions during the summer dry period. Northern tidewater goby (*Eucyclogobius newberryi*) are a federally threatened species that is a habitat specialist adapted to living in bar-built estuaries (Swenson 1999). Such specialization does not mean they are immune from mortality during extreme environmental conditions such as hypoxia or breaching (Williams and Stacey 2016; Swift et al. 2018). Tidewater goby populations fluctuate dramatically (Swenson 1999).

Three-spine stickleback (TSS; *Gasterosteus aculeatus*) may function as competitors for tidewater gobies. In bar-built estuary habitats both species primarily consume benthic macroinvertebrates (Swenson and McCray 1996; Sánchez-Gonzáles et al. 2001). In laboratory experiments stickleback presence negatively affected tidewater goby survival, but only when food resources were limiting (Chase et al. 2016; Chase and Todgham 2016). TSS are a common and widespread species, not restricted to bar-built estuary habitats (Bell and Foster 1994).

Here we use empirical dynamic modeling to separate the effects of abiotic and biotic drivers on tidewater goby and TSS population abundance. We ask whether stickleback and goby interact (compete) or are independently responding to environmental drivers. Second, we ask whether environmental conditions can cause changes in the interaction strength between stickleback and gobies. For example, the relationship between stickleback and goby abundance may depend on a third value, such as temperature, with competition stronger during warm weather, but weaker during cool weather.

Methods

We surveyed fish in Younger Lagoon monthly from February 2014 through September 2020. Younger Lagoon is a 10-ha bar-built estuary, which is noteworthy in being unimpeded by habitat alteration such as channelization or anthropogenic breaching (Clark and O'Connor 2019). Younger Lagoon experiences annual breaching cycles as described above. In addition, during the dry, warm summer conditions, the lagoon is often densely populated by a primary producer. In many years, that is the submerged vegetation *Ruppia*, but other years a phytoplankton bloom occurs. Anoxic conditions may occur in the late summer as the producer biomass begins to senesce and decay, especially overnight.

We placed 12 unbaited minnow traps (40.5 cm long, 22.9 cm diameter at the center, with 3 mm mesh, and openings with a diameter of 22 mm) along the eastern shore of the lagoon in the evening and retrieved them the next morning. Minnow traps were allowed to sink to the substrate. We did not place minnow traps in fixed locations. Instead, location was allowed to vary along the shoreline to prevent fish mortality since fluctuating water levels led to seasonal changes in habitat and anoxia risk. The front of the lagoon (the channel on the beach) was generally the deepest, the large central basin was less shallow, and the two upstream arms were the most shallow. When conditions warranted (warm temperatures and the potential for low oxygen), we varied the depth of water we set out traps in. As such we often moved them away from shore into deeper water. In the extreme, during hot summers and fall months, our traps in the central basin were placed along the thalweg (the deepest channel), and few if any traps were placed in the upstream arms because they were too shallow for the traps to even remain submerged. We

counted the number of each species of fish encountered in each trap and report the average catch per unit effort for each survey.

Starting in September 2014, we measured the surface water temperature, salinity, and dissolved oxygen (percent saturation) using a YSI Pro2030 at a subset of the trap locations, usually every other trap. We used linear interpolation to fill in missing data due to equipment failure (1 salinity measurement and 2 dissolved oxygen measurements).

Rainfall data were provided by the University of California Natural Reserve System (https://ucnrs.dendra.science/). Rainfall was summarized for the water years 1991–2020 (water year starts on 01 October of the preceding calendar year, https://water.usgs.gov/nwc/explain_data.html). Data on estuary breaching were taken from an automated camera that photographed the lagoon mouth every 15 min during daylight hours. Photos were available for water years 2014–2020. We manually searched all photos available during the wet season to identify breaches. The lagoon does not breach during the dry season. Overnight breaches were detected by observing differences in mouth morphology from evening until morning photos. We augmented missing data with personal observations taken during the surveys and other visits to the lagoon. To determine whether breaching dynamics are primarily driven by within-year variation in rainfall, or cumulative effects of rainfall (such as multiyear droughts) we used an ANOVAANOVA to test for the effect of total rainfall and Accumulated Drought Severity and Coverage Index (https://droughtmonitor.unl.edu/) on the log-transformed total number of days open in a given water year; because the interaction term was not significant we removed it.

Drivers of fish abundance

To understand which environmental drivers influence stickleback and goby abundances, we used empirical dynamic modeling, a set of tools for understanding nonlinear processes from time series data (Sugihara and May 1990; Sugihara 1994; Sugihara et al. 2012; Ye and Sugihara 2016). Empirical dynamic modeling uses time-lagged values of the measured variables to reconstruct the attractor of the underlying dynamic system based on generalized Taken's theorem (Sugihara and May 1990; Deyle and Sugihara 2011). We can then use this graphical model to make predictions and use measures of cross-validated prediction accuracy (rho, R^2) to compare alternative models (Deyle et al. 2013). For empirical dynamic modeling analysis we used a time series from September 2014 to September 2020. Our focal variables were the mean number of stickleback and tidewater goby caught per trap. Potential environmental drivers included the total amount of precipitation that had fallen (rain), the total number of days the lagoon was documented as open (breach) since the last survey, and the mean of temperature, dissolved oxygen, and salinity weighted by the number of traps associated with each measurement. We normalized all variables to mean

0 and standard deviation 1 to compare the relative importance of drivers measured on very different scales.

We used convergent cross-mapping to identify which, if any, of the environmental variables, including the abundance of the other species, influence the abundance of the two focal species (Sugihara et al. 2012). In convergent cross-mapping, lags of the focal variable are used to make predictions about the state of a hypothesized driver (target variable) via simplex projection. If that target variable's states can be predicted by using lags of the focal variable then we say the focal variable cross-maps onto the target and that is evidence that the target variable exerts causal influence on the focal variable (Sugihara et al. 2012). We used this procedure to evaluate which target variables causally influence the abundance of each fish species. The embedding dimension (number of lags we used) for each species was the optimal embedding dimension for predicting the abundance of that species using a univariate simplex projection model (Sugihara and May 1990). To test whether the cross-mapping was significant, we compared the forecast accuracy for the target variable (cross-map skill, measured as *rho*, the Pearson correlation between predicted and observed values) from the model to cross-map skills derived from a null distribution (Deyle et al. 2016a). We created the null distribution of cross-map skills from 1000 surrogate time series by extracting a mean seasonal trend with a smoothing spline and then shuffling the residuals.

If the abundance of a focal species (e.g., gobies) is driven primarily by abiotic factors, then we would expect it to only cross-map onto abiotic factors (e.g., temperature or dissolved oxygen). Alternatively, if competition is important in driving focal species abundance, then we would expect it to significantly cross-map onto the abundance of the other species (e.g., stickleback). If the focal species abundance significantly cross-maps to both abiotic factors and biotic factors then both are important for driving the abundance of the focal species and we can use s-map regression to determine whether those effects are merely additive, or whether they are interactive (i.e., context-dependent competition) (Deyle et al. 2016b).

Drivers of interaction strength

To test whether interaction strength between the two fish species varies with environmental conditions, we used another empirical dynamic modeling technique, s-map regression (Sugihara 1994). Multivariate s-map projection sequentially estimates the Jacobian matrix of partial derivatives of the response variable with respect to each predictor variable over time and can be interpreted as a measure of time-varying interaction strength (May 1973; Deyle et al. 2016b). For each species we ran a number of multivariate s-map projections to predict species abundance at time $t + 1$. All models included two "seasonal predictors": s_t and s_{t-3}, to account for seasonal variation (Rogers et al. 2020). The seasonal predictors were two sine functions (mean 0, variance 1) offset by 3 months,

with a period of 1 yr and a timestep of 1 d, which used the sample date and the sample date from three samples earlier as input variables (e.g., if s_t was the date of the April sample, then s_{t-3} was the date of the January sample). We then searched through a set of candidate models that included all possible combinations of those two seasonal predictors, lags of the two species abundance, and lags of any other predictors

variables that the focal species was found to significantly cross-map to. We ran all possible combinations of lags for each predictor up to E, the univariate embedding dimension for the focal species (e.g., with two variables, we could have $2 + 3E$ predictors: 2 seasonal variables, and E lags of two variables $+ E$ lags of the species itself). S-map projection requires a nonlinear tuning parameter, θ, which indicates the
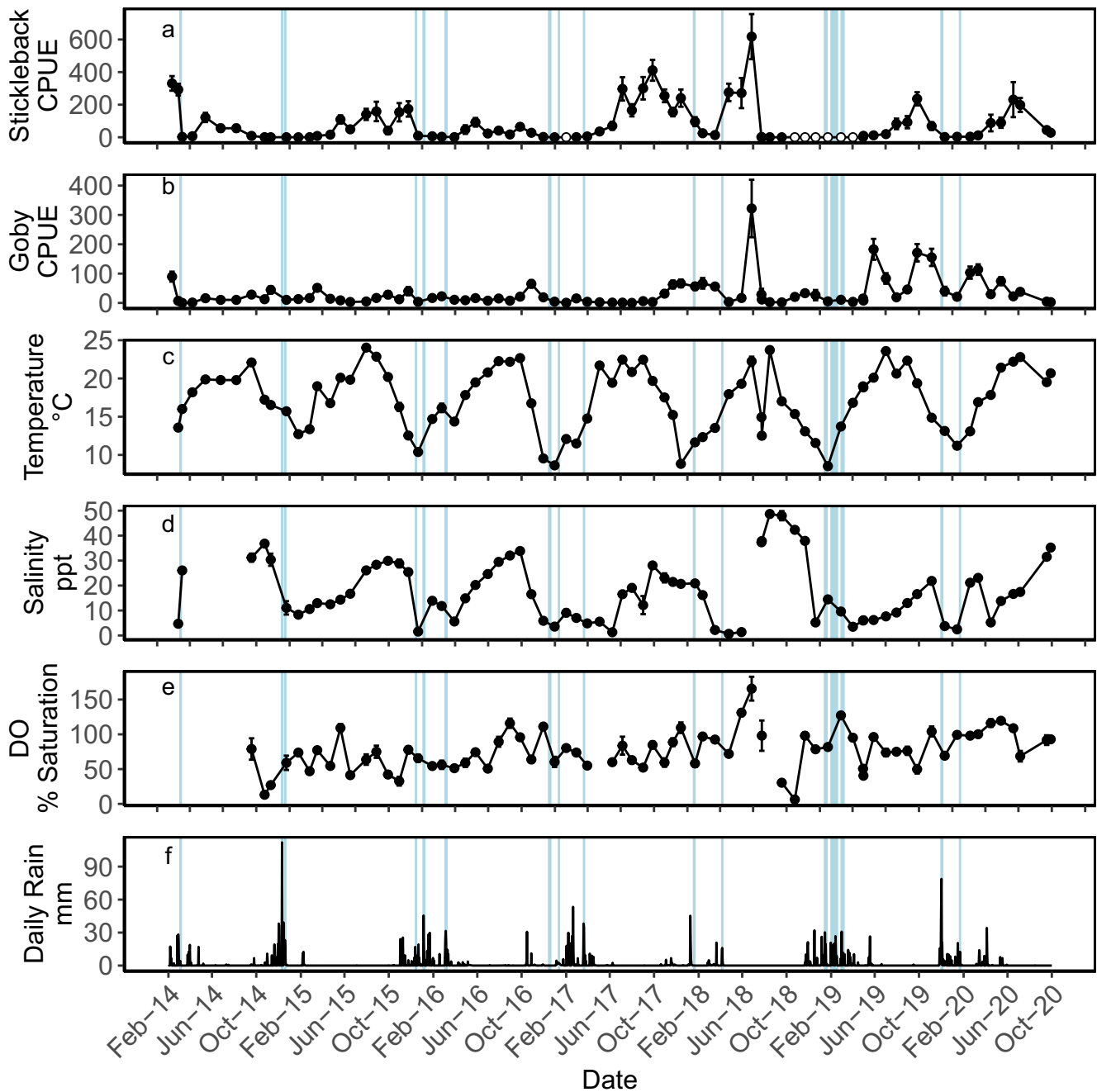
Fig. 1. Time series from monthly fish surveys and water quality monitoring. Blue shading indicates days for which known breaches occurred. Points show mean values, error bars depict one standard error. (**a**) Stickleback catch per unit effort (CPUE), (**b**) tidewater goby CPUE, (**c**) temperature (°C), (**d**) salinity (parts per thousand), (**e**) dissolved oxygen (percent saturation), (**f**) daily rainfall (mm).

Table 1. ANOVA table for log-transformed number of days open per water year against predictors: Accumulated Drought Severity and Coverage Index (ADSCI) and annual rainfall (mm).

Predictor	SS	Df	F	p
ADSCI	0.30411	1	1.9031	0.2398
Annual rainfall	1.15491	1	7.2273	0.0548*
Residuals	0.63919	4		

*alpha = 0.10.

relative weighting of points nearby in predictor space (Sugihara 1994). A value of $\theta = 0$ represents an unweighted global model where all points contribute equally to predictions, whereas a larger value of θ means points nearby in predictor space are more heavily weighted. For each model (set of predictor lags) we chose the best value of θ between 0 and 20 based on prediction accuracy (R^2). We then picked the best

model for predicting the focal species by choosing the one with the highest prediction accuracy (R^2).

We extracted the coefficients from this best model for each species, which represents a time series of partial derivatives for the focal species with respect to each predictor. Coefficients describing the relationship between species represent time-varying interaction strengths between them (Deyle et al. 2016b). However, since the variables were normalized to compare the relative importance of drivers measured on very different scales, they are not exactly interchangeable with per-capita interaction strengths determined experimentally, rather they are more analogous to standardized regression coefficients and are useful in determining the relative importance of predictors (Paine 1992; Laska and Wootton 1998). We used an ANOVA to determine if either of the season variables or any of the environmental variables we measured were associated with the interaction strengths between the two species. Significant effects of
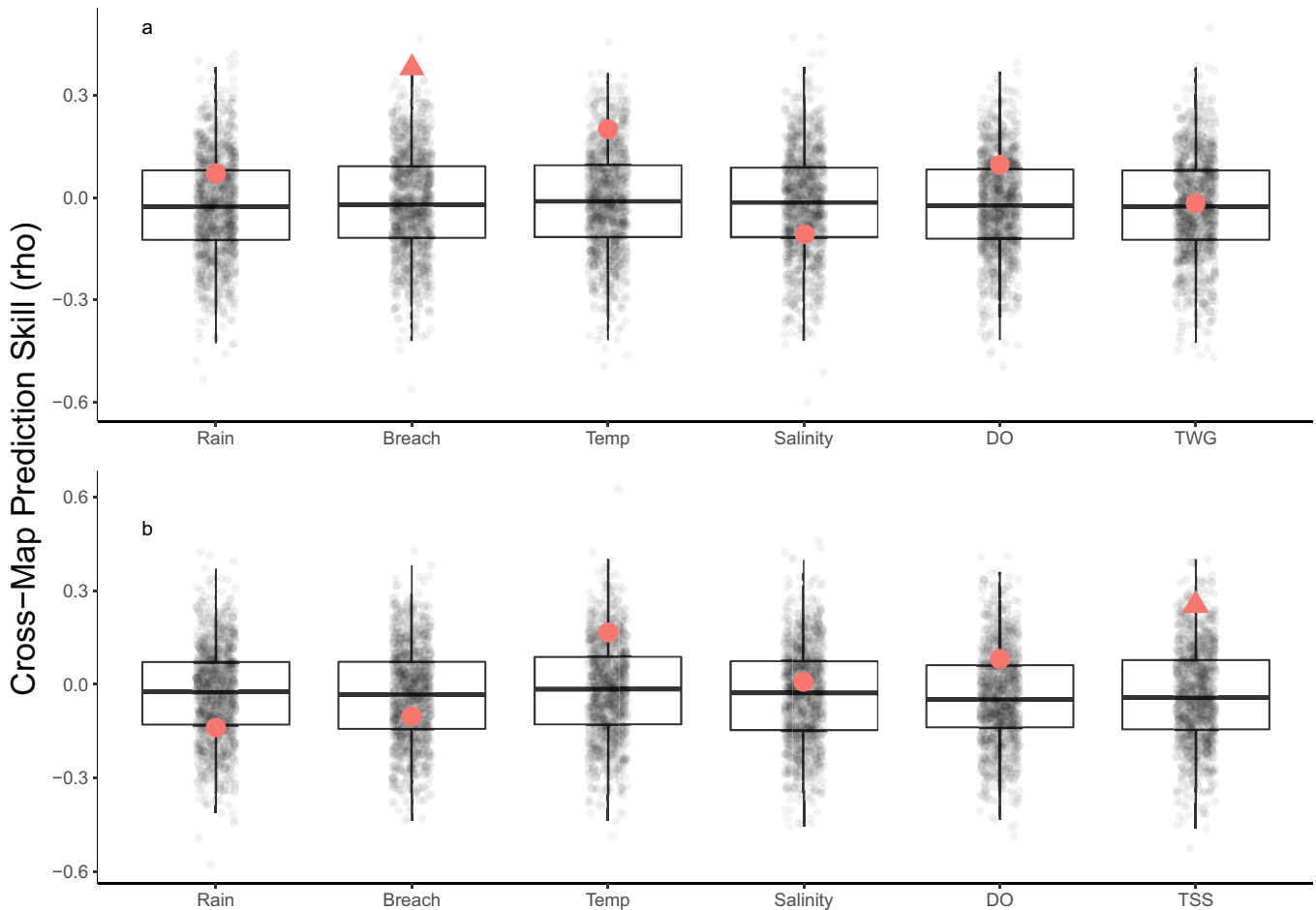

Fig. 2. Convergent cross-map forecast skill (*rho*), red symbols, circles are not significant and triangles are significant ($p < 0.05$) when compared to seasonally-matched null distributions (black boxes and scatterplots) for (**a**) threespine stickleback (TSS), and (**b**) tidewater goby (TWG). Predictors include monthly rainfall, number of days open (Breach), temperature, salinity, dissolved oxygen (DO), and the abundance of the other species of fish.

environmental variables on interaction strengths would be considered evidence of context-dependent competition. We checked for multicollinearity using variance inflation factors, all were less than 5.

Results

Stickleback and tidewater goby catch per unit effort fluctuated by three orders of magnitude (Fig. 1a,b), generally increasing in the spring and summer and crashing in the late summer, fall, or winter. No stickleback were encountered for 6 months from September 2018 through March 2019. It is not possible to distinguish whether the population persisted at low levels or whether it truly went extinct in fall of 2018 and was recolonized during the open phase of winter 2018–2019. In the spring of 2019, after several months with no stickleback captures, tadpoles of two species of amphibians, Pacific Chorus Frogs (*Pseudacris regilla*) and California Red-legged Frogs (*Rana draytonii*) were captured and swarming cladocerans (*Daphnia magna*) were observed in the shallows but were not observed at any other time during this survey.

Rainfall varied seasonally as expected (Fig. 1f). Winters were characterized by rainfall that led to decreased salinity, and temperature, and eventually led to one or more breaching events (Fig. 1). Dry summer seasons were characterized by increased temperature, increased salinity as water evaporated from the isolated lagoon, and, in some cases, anoxia (Fig. 1c–f). Our fish surveys span most of the range of variation in annual rainfall at Younger Lagoon; they ranged from the 4th wettest to the very driest years in the 25 years with sufficient data (Fig. S1a). In addition, drought monitor data reveal that of the 20 water years since 2001, our fish surveys ranged from the 1st to the 16th drouthiest years on record (Fig. S1b). The lagoon was open between 2 and 14 d per water year (mean = 5.3, SD = 4.2). We observed 32 d total where the lagoon was open. During the winters of 2015–2017, there were a total of 133 d during the wet season, split across several distinct periods, for which no photo data were available; however, our direct observations identified at least one breaching event during each of those periods. It is therefore possible (but not certain) that the counts of days open in the winters of 2015–2017 are slightly underestimated. The log-transformed
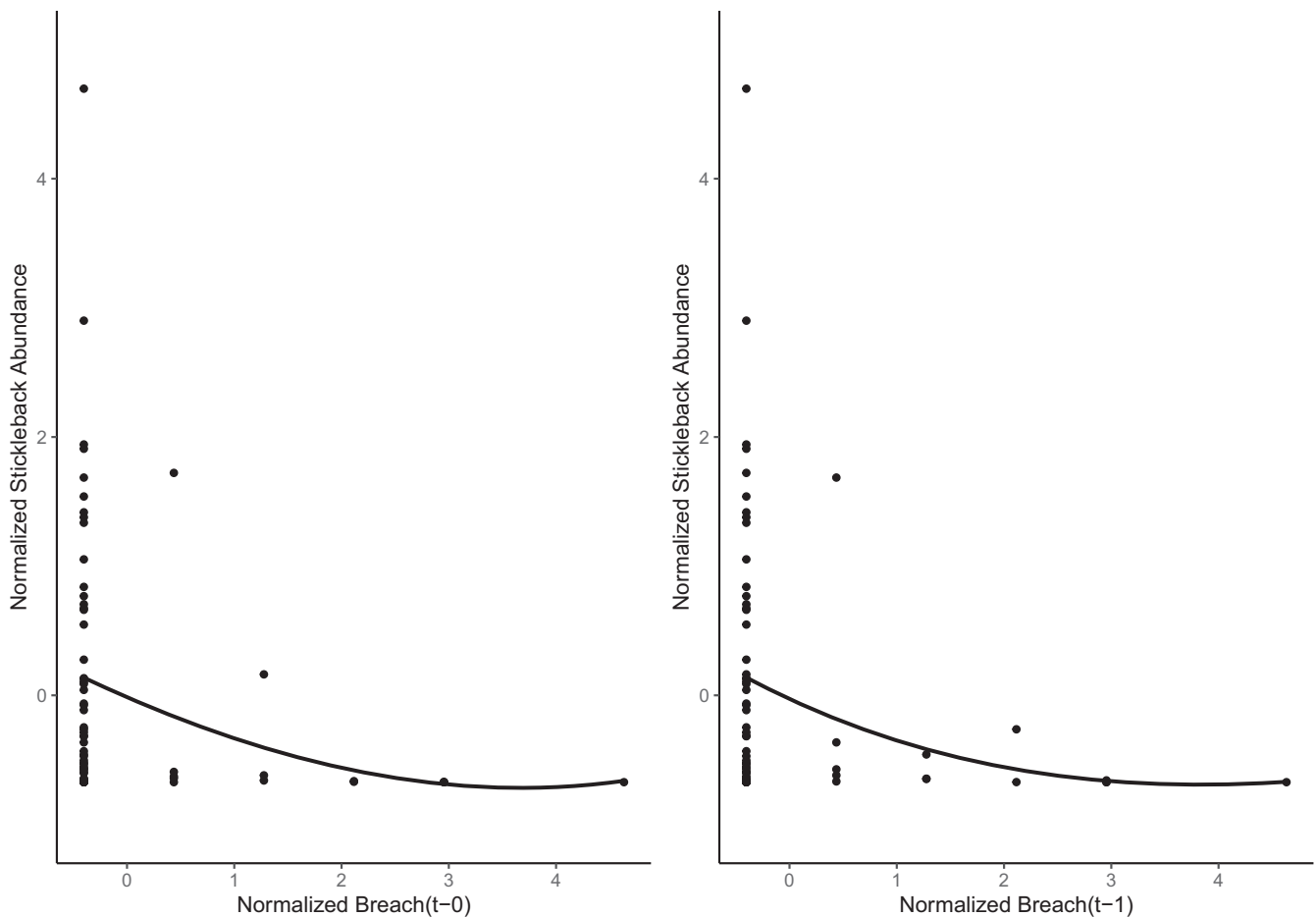

Fig. 3. Normalized stickleback catch per unit effort vs. normalized number of days open (Breach) (**a**) at the same time step, and (**b**) at the previous time step. Lines are LOESS smoothing curves to help visualization, they are not outputs of the convergent cross-mapping model.

Table 2. Time-averaged s-map coefficients for the best model for (a) stickleback (TSS), and (b) Tidewater goby (TWG).

(a) TSS		(b) TWG	
Predictor	Coefficient	Predictor	Coefficient
s_t	0.16	s_t	1.83
s_{t-3}	0.30	s_{t-3}	2.33
$Breach_t$	−0.06	TSS_{t-2}	−0.12
TSS_t	0.86	TSS_{t-3}	4.86
TWG_t	−0.08	TWG_{t-3}	−0.07

total numbers of days the lagoon breached in a water year was more closely related to rainfall within a year than to Accumulated Drought Severity and Coverage Index which measures cumulative drought conditions (Table 1, Fig. S2). Therefore, breaching is largely a function of within-year conditions rather than multiyear droughts.

Drivers of fish abundance

In general, stickleback were more predictable than gobies. The optimal simplex univariate embedding dimension for stickleback was 2, with $R^2 = 0.21$, while the optimal embedding dimension for tidewater gobies was 4, with $R^2 = 0.03$. We found one significant predictor for each species using convergent cross mapping (CCM). Breaching was the only significant predictor of stickleback abundance (CCM, $p = 0.002$) (Fig. 2a). Stickleback abundance was negatively related to the first two lags of breaching (Fig. 3). Stickleback abundance was the only significant predictor of tidewater goby abundance (CCM, $p = 0.025$) (Fig. 2b). Tidewater goby abundance was positively correlated with stickleback abundance.

Drivers of interaction strength
Effects on stickleback

The best model for predicting the abundance of stickleback at time $t + 1$ included the seasonal predictors and the current time points of stickleback (TSS_t), tidewater goby (TWG_t), and breach ($Breach_t$), but no time lags from further back. This model had an R^2 of 0.28, slightly better than the univariate stickleback model. The optimal value for θ, the nonlinear tuning parameter, in this model was 0.1 and this means that the model was weakly nonlinear, that is, interaction strengths did not change much as a function of ecosystem state. The mean magnitudes of the coefficient for the effect of tidewater goby abundance and breaching on stickleback abundance were similar and slightly negative; they were smaller than the coefficients for either seasonal predictor or stickleback abundance itself (Table 2).

Even though seasonal variables were included as predictors in the s-map projections, the coefficient for the effect of gobies on stickleback was primarily associated with season, s_t,

(ANOVA, $F_{1,59} = 12.75$, $p = 0.001$), and tidewater goby abundance (ANOVA, $F_{1,59} = 6.22$, $p < 0.016$) (Table 3). The interaction strength of tidewater gobies on stickleback was highest

Table 3. ANOVA tables testing for the effects of environmental predictors on the interaction strengths recovered from the multivariate s-map projections. Predictors include seasonal sine functions, monthly rainfall, number of days open (Breach), temperature, salinity, dissolved oxygen (DO), and the abundance of threespine stickleback (TSS), and tidewater goby (TWG).

Response	Predictor	Sum Sq	Df	F-value	p
$dTSS_t/dTWG_t$	$SeasonalSine_t$	0.040	1	12.753	0.001*
	$SeasonalSine_{t-3}$	0.001	1	0.267	0.607
	$Rain_t$	0.007	1	2.074	0.155
	$Breach_t$	<0.001	1	0.07	0.792
	$Temp_t$	0.005	1	1.617	0.208
	$Salinity_t$	0.005	1	1.466	0.231
	DO_t	0.001	1	0.252	0.617
	TSS_t	0.001	1	0.237	0.628
	TWG_t	0.019	1	6.217	0.016*
	Residuals	0.184	59		
$dTSS_t/$ $dBreach_t$	$SeasonalSine_t$	0.003	1	7.479	0.008*
	$SeasonalSine_{t-3}$	0.001	1	3.633	0.062
	$Rain_t$	<0.001	1	0.868	0.355
	$Breach_t$	<0.001	1	0.030	0.864
	$Temp_t$	<0.001	1	0.007	0.934
	$Salinity_t$	0.001	1	2.541	0.116
	DO_t	<0.001	1	0.628	0.431
	TSS_t	0.002	1	4.141	0.046*
	TWG_t	0.001	1	3.381	0.071
	Residuals	0.023	59		
$dTWG_t/$ $dTSS_{t-2}$	$SeasonalSine_t$	41.8	1	0.312	0.578
	$SeasonalSine_{t-3}$	118.7	1	0.886	0.350
	$Rain_t$	22.9	1	0.171	0.681
	$Breach_t$	10.9	1	0.081	0.777
	$Temp_t$	110.4	1	0.825	0.367
	$Salinity_t$	0.9	1	0.007	0.936
	DO_t	9.7	1	0.073	0.789
	Residuals	8169.3	61		
$dTWG_t/$ $dTSS_{t-3}$	$SeasonalSine_t$	0.6	1	0.005	0.947
	$SeasonalSine_{t-3}$	822.5	1	6.679	0.012*
	$Rain_t$	6.2	1	0.05	0.824
	$Breach_t$	<0.1	1	<0.001	0.988
	$Temp_t$	1	1	0.008	0.929
	$Salinity_t$	8.1	1	0.066	0.798
	DO_t	0.7	1	0.006	0.939
	Residuals	7511.6	61		

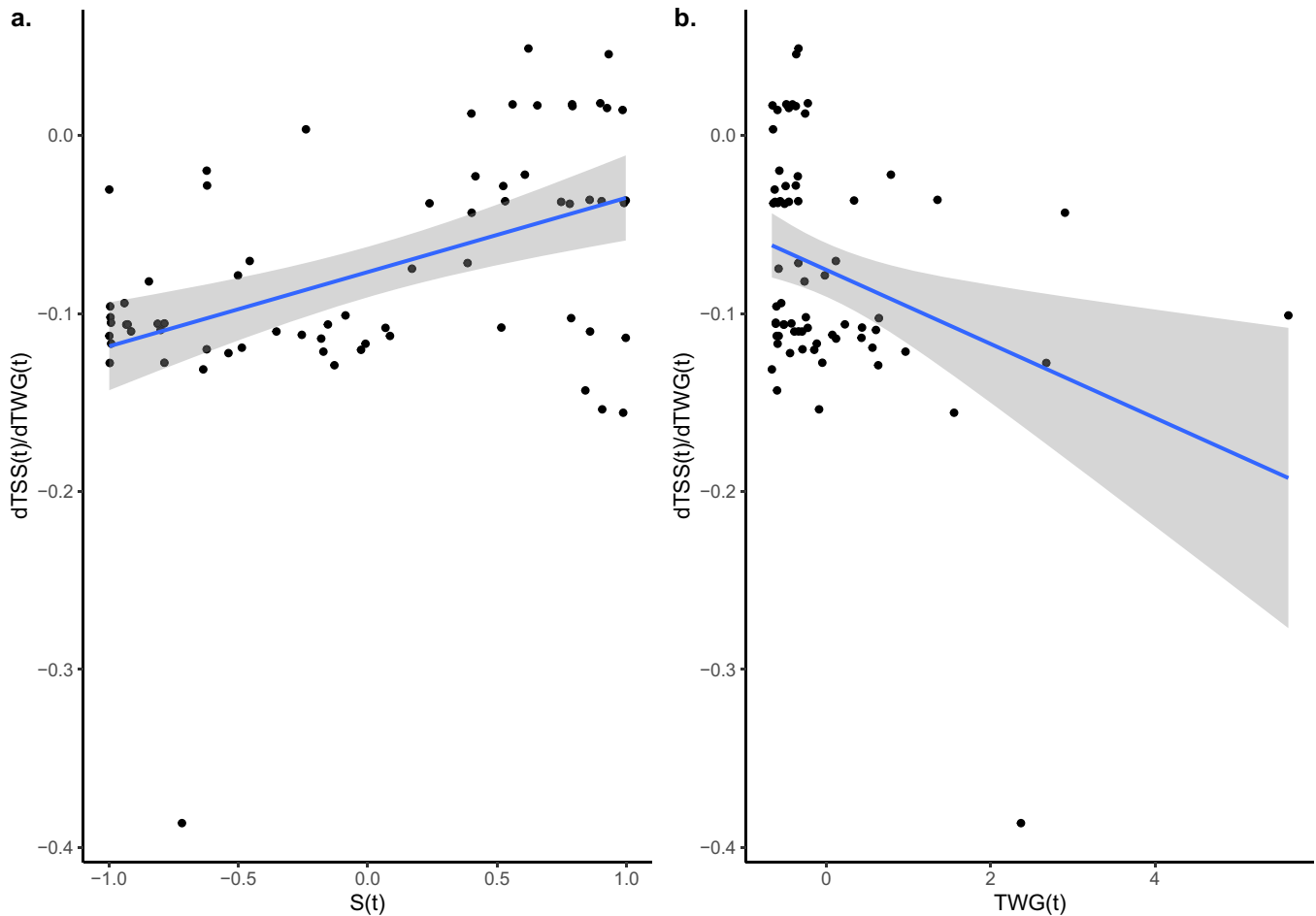*Statistical significance ($p < 0.05$).

Fig. 4. Effect of tidewater gobies on stickleback ($d\text{TSS}_t/d\text{TWG}_t$) as a function of (**a**) season s_t (minimized in mid-September and maximized in mid-March), and (**b**) tidewater goby density (TWG_t).

(least negative) in March and when tidewater goby abundance was highest (Fig. 4).

Effects on tidewater goby

The best model for predicting the abundance of tidewater goby at time $t + 1$ included the seasonal predictors, the second and third lags of stickleback (TSS_{t-2} and TSS_{t-3}), and the first lag of tidewater goby (TWG_{t-1}). This model had an R^2 of 0.13, considerably better than the univariate model for tidewater goby. The tidewater goby model was highly nonlinear, optimal $\theta = 13.8$, meaning that interaction strengths change as a function of system state.

The largest mean coefficient in the model was for the third lag of stickleback abundance (Table 2). The only significant predictor of this coefficient was season, s_{t-3} (ANOVA, $F_{1,61} = 6.68$, $p = 0.012$). During June and July $d\text{TWG}_t/d\text{TSS}_{t-3}$ had a large positive value, whereas during other times of the year the value was close to zero, usually slightly negative (Fig. 5). There were no significant predictors for the coefficient

for the second lag of stickleback abundance ($d\text{TWG}_t/d\text{TSS}_{t-2}$) (Table 3).

Discussion

Our results support the hypothesis that fluctuations in stickleback and endangered tidewater goby abundance reflect independent responses to environmental fluctuations rather than the effects of interspecific competition. Stickleback abundance was negatively affected by sandbar breaching. Tidewater goby abundance was affected by TSS abundance. However, when we used s-map regression to investigate the nature of that relationship, we found that the pattern was primarily driven by a large positive coefficient for the effect of stickleback abundance in the spring on tidewater goby abundance in the summer, rather than by fluctuations in the magnitude of negative interaction strengths that we would expect if state-dependent competition was occurring.

Although prior experiments have indicated the potential for competition (Chase et al. 2016; Chase and Todgham 2016)

and the dynamics of population fluctuations in our study system seem to imply competition, our analyses revealed little evidence of competition. In our best model for explaining variation in goby abundance, positive effects of the third lag of stickleback ($dTWG_t/TSS_{t-3}$) outweighed the negative effect of the second lag of stickleback ($dTWG_t/dTSS_{t-2}$), and so the overall mean effect of stickleback on goby was positive (Table 2). Conversely, the mean effect of gobies on stickleback ($dTSS_t/dTWG_t$) was negative, but had a very small magnitude, smaller than either seasonal effects or the effects of lagged stickleback abundance. Therefore, tidewater goby abundance did not have a major impact on stickleback abundance (also see Fig. 2). Taken at face value, this suggests a commensalism whereby stickleback have a positive effect on gobies, but we do not know of a plausible mechanism by which this would occur.

Using s-map regression we investigated the temporal variation in interaction strength to better understand the relationship between the two species. Compared to the small effect of gobies on stickleback, stickleback were the primary driver of goby abundance in our models. For most of the year the

magnitude of the effect was quite small. However, counter to our expectations, during the time periods when that effect was large, the effect was positive: in June and July, the lagged effect of stickleback on gobies was positive and very large ($dTWG_t/dTSS_{t-3}$) (Fig. 5). Therefore, for most of the year, there is not much meaningful effect of stickleback on gobies in either direction, but in these 2 months there is a distinct, but lagged, positive effect of stickleback. The lagged effect corresponds to a positive correlation between the abundance of stickleback in March and April with the abundance of gobies in June and July. When stickleback have a good spring, gobies are predicted to have a good summer.

Most likely, this reflects the season when juveniles of each species recruit to a size large enough to be caught in our traps and it may point toward the mechanisms for coexistence of these two species that share a resource base. Perhaps then, stickleback and gobies are responding similarly to an unmeasured environmental driver, such as the onset of spring productivity and availability of shared macroinvertebrate prey, but stickleback respond earlier or more quickly. The major reproductive period of the two species appear to be offset, so
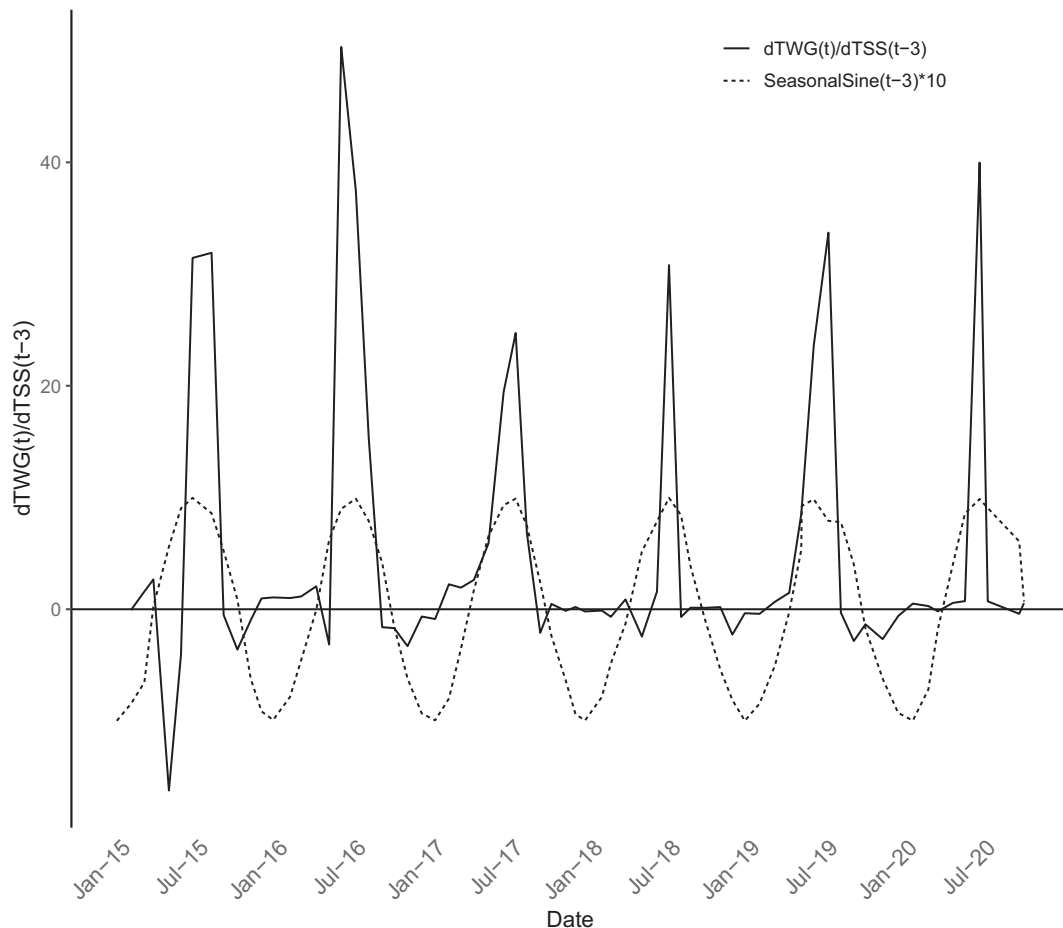

Fig. 5. Effect of stickleback on tidewater gobies ($dTWG_t/dTSS_{t-3}$ solid line) over time compared to the seasonal variable (s_{t-3}, dashed line) over time for the best multivariate s-map model of tidewater goby. Note the magnitude of the seasonal variable is increased 10-fold to aid in ease of interpretation.

niche partitioning may be achieved across seasons (for data on annual cohort timing in nearby lagoons, *see* Swenson 1999 for gobies and Wasserman et al. 2021 for stickleback). Such allochrony has been shown to help limit the potential for competition by offsetting peak resource use (Trivelpiece et al. 1987; Spilseth and Simenstad 2011; Clewlow et al. 2019). Another study of a bar-built estuary food web suggests a similar mechanism at play. Young et al. (2022) found stickleback and prickly sculpin to have a greater overlap in diet and stable isotope niche during the summer than the spring; tidewater goby were also similar during the summer but no goby data were available from the spring. Spatial segregation of resource use could also lead to a lack of negative impacts of the two species, but that does not explain the temporal pattern of positive interactions we detected.

There was a great deal of spatial variation in conditions in Younger Lagoon, just as there was a great deal of temporal variation. We chose to focus on the temporal variation averaged over the spatial variation in this study. This allows us to focus on population- and system-wide data and processes. Our method of attractor reconstruction assumes that measured fish abundance acts as an observation function of the true state of abundance in the population; as long as catch (averaged over all 12 traps) is a monotonically increasing function of true abundance, our attractor reconstructions should give accurate results (Takens 1981). Still, it is possible that the two species might use the habitat differently during different periods of the year when those environmental conditions change (Moyle 2002). For example, we moved our traps around the lagoon to avoid locations where diel oxygen swings may cause fish mortality, but this may have changed the relative accessibility of our traps to stickleback and more anoxia-tolerant gobies (Swift et al. 2018). Unfortunately, this confounding effect could drive some of the relationships we see in the data. Further research could compare trapping studies to other methods, such as contemporaneous seine surveys or trap placement controls to further investigate this source of bias.

An important direct effect of the environment we detected was a negative effect of breaching on stickleback abundance. Breaching appears to be a major mortality event for stickleback, with 90% or more reduction in abundance following the first breach in most years (Figs. 1a, 3). Goby abundance was not impacted by breaching in the same way (Fig. 1b). Although goby mortality in response to artificial, out-of-season breaches has been documented, our data reaffirm that natural breaching is not a major source of mortality for gobies and that they are well adapted to this feature of the environment (Swift et al. 2018). When we observed fish mortality following breaches, the majority of fish stranded on dewatered mud or sand flats were stickleback, and the few tidewater goby observed were alive, and many were on a section of mudflat that would likely rewater at the next high tide (B. A. Wasserman pers. obs.).

All of our models did a better job of predicting stickleback abundance than they did tidewater goby abundance including univariate Simplex, bivariate convergent cross-mapping, and multivariate S-Map. Our analyses are robust to measurement error because time-delay embedding allows us to use data from multiple time points (Munch et al. 2020). However, measurement error or process error (stochasticity) may provide an upper limit on prediction accuracy in empirical dynamic modeling. It is therefore possible that tidewater goby abundance is marked by more stochasticity than stickleback abundance in this system. In addition, there may be other, rarer effects that we were unable to detect because they did not happen during our time series, or only happened on a single occasion. Empirical dynamic modeling generally require a time series that includes enough data to cover several times the characteristic return time for the system to resolve the attractor in that area of parameter space (Munch et al. 2020). For example, in 2018 we witnessed the largest abundances of both stickleback and gobies, followed by a population crash and an apparent wave overtopping event with unseasonable temperature and salinity measurements. The following spring tidewater goby abundances were higher than in other years. One might conclude this was due to lack of stickleback presence. While the Smap coefficients were slightly more negative in that year than others, our ANOVA did not identify any proximate driver of that difference, instead it only detected the overwhelming effect of season on the Smap coefficient of stickleback on gobies.

The conclusion that stickleback and goby are not influencing each other's population abundance, but rather responding separately to environmental fluctuations will be important for the management of these species. However, they co-occur in a variety of environments and these results will be most applicable to similar ecosystems. Small bar-built estuaries draining intermittent streams in central California share a number of features that may influence this interaction. In such small sites that are rarely flowing, the submerged aquatic plant *Ruppia* is common in some summers. Predatory fishes are not present in Younger Lagoon and similar sites, but are found in many other estuaries draining larger watersheds where stickleback and goby co-occur (Wasserman et al. 2020). Many other elements of the ecosystem and community change along the north–south axis of the tidewater goby's range that might impact this interaction, such as climate and the presence of other species (des Roches et al. 2020).

Empirical dynamic modeling has been used to make predictions and infer causality, and it is now starting to be used to improve forecasting of commercially valuable fish stocks (Anderson et al. 2008; Ye et al. 2015; Giron-Nava et al. 2020) and to answer questions in community ecology such as determining the effect of biodiversity on stability and the drivers of bottom-up and top-down effects (Sugihara et al. 2012; Ushio et al. 2018; Rogers et al. 2020). As opposed to computing such community-wide metrics, our goal was to understand the

environmental factors that affect a particular species of conservation concern and its interspecific interactions (Deyle et al. 2016a). We think there is a real opportunity in using these methods for such studies when monitoring data are available but manipulative experiments are impractical, whether that be for cost, logistical, or ethical reasons.

We used empirical dynamic modeling to understand the interaction between two putative competitors in a seasonally fluctuating environment. We showed fluctuations in interaction strength but rarely showed competition. Instead, our data revealed that seasonal cycles of both species reflect their unique responses to environmental conditions including annual pulses of recruitment that were offset by approximately 3 months. Empirical dynamic modeling can be used to understand the context dependence in interactions, especially in cases like ours utilizing endangered species, when the usual methods (manipulative experiments) are not an option. Our method allows us to understand the drivers of variation in abundance of the endangered goby and strongly suggests against competition from TSS as a threat to goby population numbers. This information can be used to make decisions about the management of the focal species. We suggest that restoration of bar-built estuaries should take precedence over efforts to eliminate the interaction with stickleback (Zedler 1996; Clark and O'Connor 2019). Similarly, empirical dynamic modeling can be used to decide between alternative conservation actions in other cases.

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Conflict of interest
None declared.