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RESEARCH

Simulated Fishing to Untangle Catchability and Availability in Fish Abundance Monitoring

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ABSTRACT

In fisheries monitoring, catch is assumed to be a product of fishing intensity, catchability, and availability, where availability is defined as the number or biomass of fish present and catchability refers to the relationship between catch rate and the true population. Ecological monitoring programs use catch per unit of effort (CPUE) to standardize catch and monitor changes in fish populations; however, CPUE is proportional to the portion of the population that is vulnerable to the type of gear used in sampling, which is not necessarily the entire population. Programs often deal with this problem by assuming that catchability is constant, but if catchability is not constant, it is not possible to separate the effects of catchability and population size using monitoring data alone. This study uses individual-based simulation to separate the effects of changing environmental conditions on catchability and availability in environmental monitoring data. The simulation combines a module for sampling conditions with a module for individual fish behavior to estimate the proportion of available fish that would escape from the sample. The method is applied to the case study of the well monitored fish species Delta Smelt (*Hypomesus transpacificus*) in the San Francisco Estuary, where it has been hypothesized that changing water clarity may affect catchability for long-term monitoring studies. Results of this study indicate that given constraints on Delta Smelt swimming ability, it is unlikely that the apparent declines in Delta Smelt abundance are the result of changing water clarity affecting catchability.

KEY WORDS

bias, simulation, behavior-based model, gear avoidance, monitoring, Delta Smelt

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INTRODUCTION

For fisheries stock assessments, catch is assumed to be a product of fishing intensity, catchability, and availability, where availability is defined as the number or biomass of fish present at a site and catchability refers to the relationship between the rate at which fish are caught and the true population size (Ricker 1975). Ecological monitoring programs use catch per unit of effort (CPUE) as a way to monitor changes in fish populations and communities; however, CPUE is proportional to the portion of the population that is vulnerable to the type of gear that is used in sampling, which is not necessarily the entire population (Maunder et al. 2006). Many methods have been developed to account for variable catchability, including estimating ratios and developing statistical models where environmental conditions and/or time variables can account for changes in catchability (Maunder and Punt 2004). Gear efficiency studies (e.g., Mitchell and Baxter 2021) also seek to account for changes in catchability for different sizes and species of fish.

Ecological monitoring programs typically assume that the relationship between catch and biomass or population size is constant, i.e., that catchability is constant. By making this assumption, monitoring programs can compare abundance of organisms relative to abundance in other locations or points in time without having to estimate the proportion of the population that is vulnerable to sampling gear. Essentially, the goal is to standardize catch so that the non-vulnerable portion of the population cancels out of the equation.

Whether it is reasonable to assume that catchability is constant depends on the conditions of the monitoring program. It is reasonable to make this assumption when either (1) environmental factors do not influence catchability or (2) the environmental factors that drive catchability are constant. If environmental factors influence catchability and those factors change, catch will reflect changes in both population size and catchability (i.e., population size and catchability are confounded). If catchability is not constant, it is not possible to separate the effects of catchability and population size using monitoring data alone. For example, given a constant population size, if salinity reduces catchability, catch would decrease as salinity increases. If catchability were inaccurately assumed to be constant, the decrease in catch would be interpreted as a decrease in population size, which would introduce a negative bias to the estimates of population size.

Where an environmental factor affects both catchability and availability, additional studies are necessary to separate the two effects on catch, but abundance estimates are possible in this situation using N-mixture models (Royle 2004). For ecological monitoring programs, where the primary source of abundance information is derived from field data collections, confounding of the effects of availability and catchability can call into question the validity of observed patterns in species of interest.

One example of such a monitoring program is the extensive enterprise maintained by the Interagency Ecological Program for the San Francisco Estuary (IEP). The San Francisco Estuary (the estuary) is a highly modified estuary, both in terms of land use and hydrology, and several environmental factors have changed over time. Although turbidity varies considerably by season and weather, an overall pattern of decreasing turbidity has been observed since the introduction of the Asian overbite clam (*Potamocorbula amurensis*) in 1987 (Kimmerer et al. 1994; Greene et al. 2011). This trend toward decreasing turbidity and decreasing catch of Delta Smelt over time has led some researchers to speculate whether changes in turbidity might be responsible for a change in catchability. In particular, the question is whether Delta Smelt avoid sampling gear more effectively—particularly that of the Fall Midwater Trawl (FMWT) survey—when Secchi depths are high, because of an increased field of visibility compared to when water is more turbid (Latour 2016).

The IEP has been monitoring fish and water quality in the estuary for over 50 years. Although the IEP monitors many species, in recent years there has been an increased focus on sampling methods that support the calculation of relative abundance indices for Delta Smelt (*Hypomesus transpacificus*). Delta Smelt are of particular interest because of their apparent steep decline in abundance (Figure 1), and because the status and distribution of this endangered species within the estuary can affect water deliveries for water agencies (USFWS 2019). The declining pattern of Delta Smelt abundance has been questioned

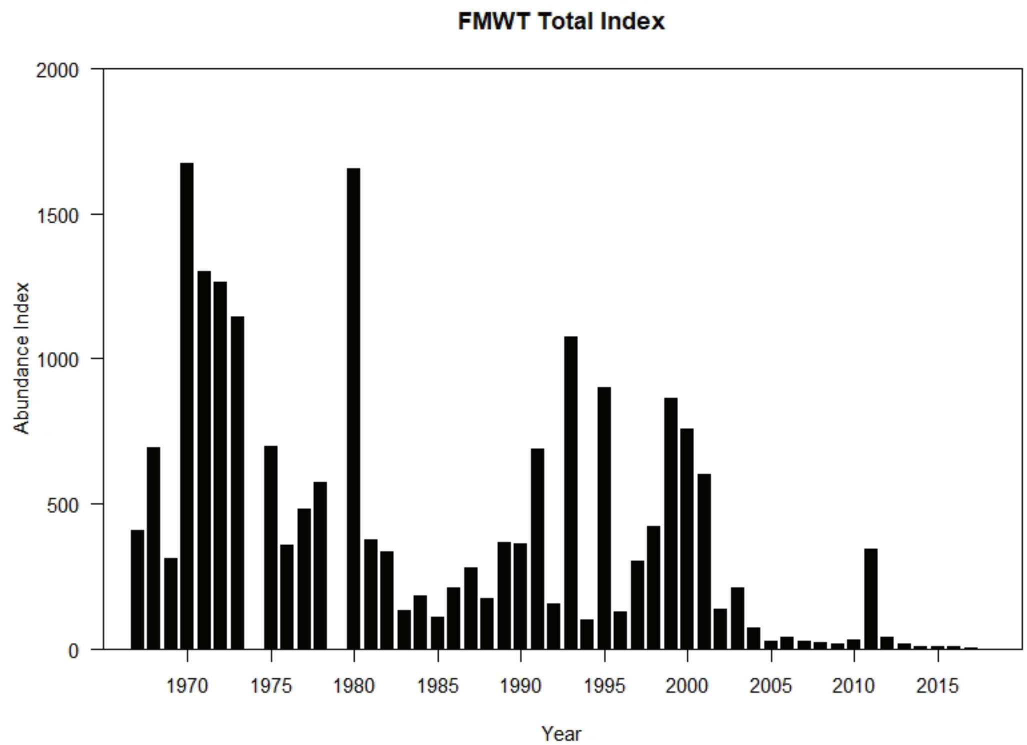

Figure 1 Fall Midwater Trawl abundance index for Delta Smelt. Data source: *https://www.wildlife.ca.gov/Conservation/Delta/Fall-Midwater-Trawl*.

because of (1) the inability of monitoring surveys to distinguish between effects of declining abundance, and (2) changes in catchability from changing environmental conditions and/or habitat use (Feyrer et al. 2007; Latour 2016), often with a specific focus on the apparent decline in turbidity measured during surveys such as the FWMT.

A few studies provide insight into separating catchability from availability for Delta Smelt. Applying zero-inflated negative binomial models to the FWMT to separate true zeros from false zeros, Latour (2016) found that as water clarity increased (larger Secchi depth), catch declined, and the probability of false zeros increased. This suggests that decreasing turbidity negatively affects catchability. The mechanism for this change in availability would ostensibly be that Delta Smelt are better able to avoid sampling nets in clearer water. Laboratory experiments also shed some light on how turbidity affects availability. For example, experiments with young Delta Smelt indicate that clear water inhibits feeding behaviors (Baskerville–Bridges et al. 2004; Mager et al. 2004). If Delta Smelt prefer turbid waters, turbidity would increase availability. This study takes a different approach to addressing the confounding of catchability and availability.

This paper describes an individual-based simulation study that aims to separate the effects of changing environmental conditions on catchability and availability in environmental monitoring data. The simulation combines a module for sampling conditions with a module for individual fish behavior to estimate the proportion of available fish that would escape from the sample. The fish behavior module follows a standard conceptual model of fish behavior in response to a predator or similar threat: when fish are presented with a stimulus, they use environmental cues to determine the type of response, and their reaction is governed by fish physiology (Domenici 2010). As a case study, I use values for swimming speed and escape trajectory from the published literature on fish behavior as well as measurements from the FMWT data set to simulate sampling in a location with a fixed number of Delta Smelt

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available to the gear. To my knowledge, there are no published examples of using individual-based simulation model of behavior to inform catch standardization efforts. The goals for this simulation are (1) to describe some bounds on the physical ability of Delta Smelt to evade capture in a system where visual cues stimulate avoidance behaviors, and (2) to examine the properties that emerge in the sampling process from limitations on individual fish behavior. By holding availability constant for each tow, catchability is represented by the proportion of fish caught. This paper demonstrates a modeling approach to evaluating the interaction of environmental factors and fish behavior on monitoring data in a way that is not possible with environmental monitoring data alone. Specifically, this paper evaluates the hypothesis that turbidity affects catchability of Delta Smelt.

MATERIALS & METHODS

Study Species

The Delta Smelt (*Hypomesus transpacificus*) is a small (up to 10 cm standard length), planktivorous fish endemic to the estuary (the San Francisco Bay and Sacramento–San Joaquin Delta). Delta Smelt spawn in fresh water in spring, and spend most of their lives in the mixing zone of the estuary before maturing in the fall (Moyle et al. 1992). They are generally found in turbid water (Bennett 2005; Feyrer et al. 2007; Sommer and Mejia 2013; Brown et al. 2014). Delta Smelt were abundant in the estuary at one time, but they became so rare that they have been listed as threatened by the federal Endangered Species Act since 1993, and as endangered by the California Endangered Species Act since 2010. An index of Delta Smelt abundance based on the FMWT survey shows that abundance declined to the lowest recorded values in 2018. The decline of Delta Smelt is part of a suite of declining pelagic organism populations in the estuary that occurred in the early 2000s (Sommer et al. 2007). As Delta Smelt have become rarer, interest has grown in evaluating the programs such as the FMWT that are used to monitor their abundance as well as the factors that determine their distribution in the estuary.

Data Simulation

To investigate the effects of environmental conditions and tow characteristics on the number of fish caught, I first simulated data using a combination of published values and geometric relationships, then I fit a model to the simulated data. I simulated 1,000 tows through a horizontal three-dimensional (3-D) space, which had the width and height that matched the dimensions of the midwater trawl net used for the FMWT study (365.8 cm). For each tow, I simulated constant availability of fish by simulating 1,000 fish in the path of the net. Each fish (f) was assigned a location as the distance from the edge of the path of the net (d_f), a turning angle at which to swim (a_f), a vertical (pitch) angle at which to swim (b_f), a height from the bottom of the net path (h_f) and a swimming velocity (v_f; Figure 2).

$$d_f \sim uniform\ (0, 365.8)\ (cm) \tag{1}$$

$$a_f \sim wrapped\ normal\ (165.8, 3.7)\ (degrees) \tag{2}$$

$$b_f \sim uniform\ (0, 180)\ (degrees) \tag{3}$$

$$h_f \sim uniform\ (0, 365.8)\ (cm) \tag{4}$$

Swimming velocity (v_f) was based on measurements of critical swimming velocity for Delta Smelt (Swanson et al. 1998).

$$v_f \sim normal\ (27.6, 5.1)\ (cm/s) \tag{5}$$

The critical swimming velocity was defined as the maximum swimming velocity a fish can maintain for a specific duration (Swanson et al. 1998). Using the critical swimming velocity in this simulation gives the fish the best biologically feasible chance to escape the net. In the same Delta Smelt swimming study, approximately 40% of fish experienced some swimming failure that was unrelated to fatigue. This was captured in our simulation by a binomial distribution where fish had a 0.4 probability of experiencing a swimming failure (w_f), resulting in capture.

$$w_f \sim binomial\ (0.4, 1) \tag{6}$$

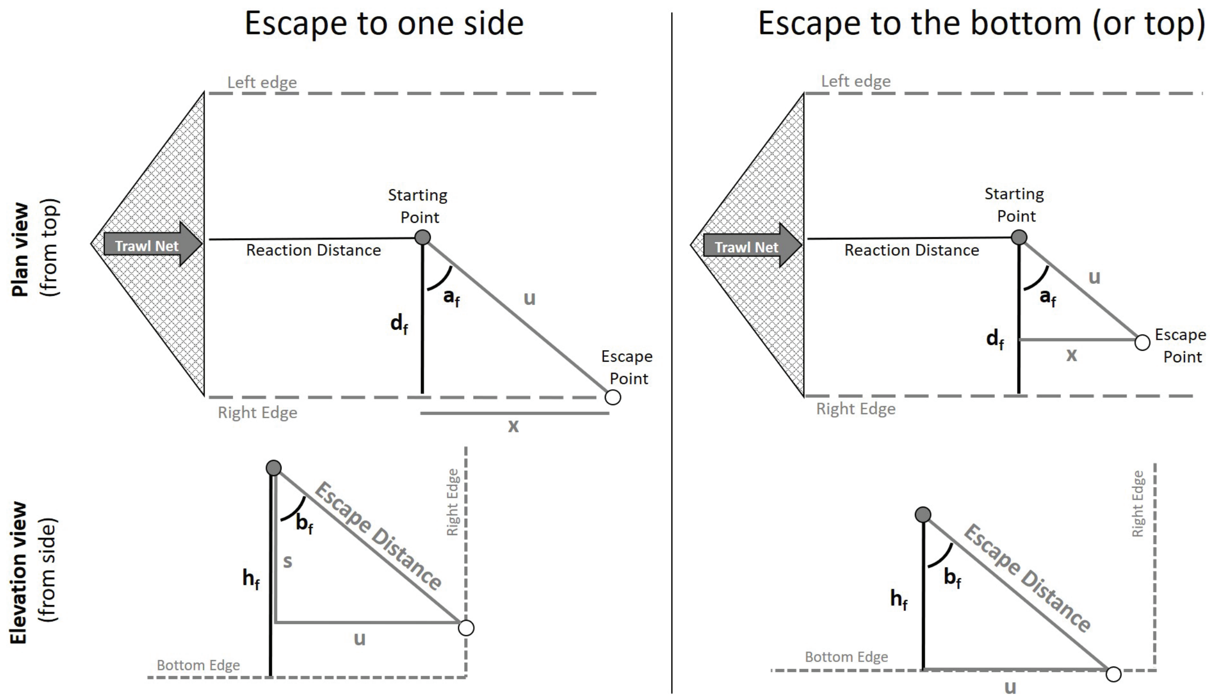

Figure 2 Conceptual diagram of simulated fish (*filled circles*) placement within the three-dimensional path of the net and the geometry of movement to the escape point (*open circles*) from an overhead perspective, looking down on the sampling event (*top row*) and from the side (*bottom row*). Labels in *black with subscripts* correspond to variables described in the text; *grey labels* correspond to intermediate values that must be calculated to determine the escape time and net time.

No published studies describe the angle of escape for smelt species, so escape angle was based on a study of predator avoidance behavior in juvenile Atlantic Cod, where the angle at which the fish swam was calculated based on the angle created by the escape trajectory and the initial position of the fish relative to the predator (*Gadus morhua*; Meager et al. 2006). Here, as in Meager et al. (2006), a 0° angle represents swimming toward the stimulus. These values are also consistent with escape angles for herring (Clupea harengus; Domenici and Batty 1994, 1997). This assumes that the simulated net approached every fish from behind, so the escape angle calculation would be consistent.

For each tow, I selected Secchi depths from a uniform distribution of the full range of Secchi depths recorded in the FMWT in 1-cm increments (1–450 cm).

$$s_t = \mathit{uniform}\ (1, 450)\ (\mathit{cm}) \tag{7}$$

$$v_t \sim \mathit{normal}\ (72.8, 19.6)\ (\mathit{cm/s}) \tag{8}$$

I used these values to calculate whether each fish in the population would move out of the path of the net before the net reached the fish. The simulation assumed that Secchi depth was equivalent to the distance at which a fish would see the net (i.e., that the distance at which a fish could see the net was the same as the measured Secchi depth). I also assumed that the instant a fish saw the net, it would swim straight toward the edge of the path of the net at the assigned values for turning and pitch angles (Figure 2). This allowed me to calculate the amount of time it would take a fish to escape the path of the net (escape time), the distance the fish would travel away from the net (escape distance), and the amount of time it would take the net to reach the location where the fish

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would escape the path of the net (net time). The calculations for the escape distance vary depending on whether the fish escapes to the vertical sides (left or right) or the horizontal sides (top or bottom) of the net path (Figure 2; full calculations available at *https://github.com/USFWS/Gear-Avoidance-Behavior-Simulation*).

$$escape\ time_f = \frac{d_f}{\cos(a_f)} \times 1/v_f \qquad (9)$$

$$fish\ position_f = s_t + escape\ distance_f \qquad (10)$$

$$net\ time_f = \frac{s_t + escape\ distance_f}{v_t} \qquad (11)$$

If the fish takes less time to escape the path of the net than it takes the net to reach the final position of the fish (i.e., if the net moves past the fish during the time it takes to escape), the fish is recorded as caught. This is conceptually equivalent to the fish moving too slowly to move out of the path of the net. The number of fish caught was summed for each tow and recorded as a proportion:

$$caught_f = \begin{Bmatrix} 1\ if\ net\ time_f - escape\ time_f < 0 \\ 0\ if\ net\ time_f - escape\ time_f > 0 \end{Bmatrix} \qquad (12)$$

I calculated catch proportion as the simulated catch divided by the number of fish available to the net (in this case, 1,000 fish). Catch proportion is the response variable used in the model below.

$$p_t = \frac{catch_t}{1000} \qquad (13)$$

Inference

Using the simulated data, I fit a regression model using a hierarchical model to examine the relationship between Secchi depth and catch proportion in the simulated data. The hierarchical model used Markov chain Monte Carlo (MCMC) simulation in JAGS (Plummer 2003), through R (R Core Team 2014; package R2jags; Su and Yajima 2015). The structure of the model was similar to a generalized linear model in a traditional statistical framework, where the proportion of fish caught depends on the main effects—Secchi depth and net velocity—and the interaction. To improve model fit, the explanatory variables—Secchi depth and net velocity—were standardized to have a mean of zero and a standard deviation of one. An advantage of the Bayesian approach is that it can include all uncertainty in the posterior distributions, allowing more realistic estimates of model parameters. I used a truncated normal distribution and identity link to model the relationship because binomial models showed an obvious lack of fit. Truncating the normal distribution at 0 and 1 allowed the model to fit the linear shape of the relationship between the variables, without allowing the predicted value to exceed the reasonable bounds for proportions.

$$catch\ proportion_t \sim \begin{cases} 0 & (-\infty, 0) \\ normal(\mu_t, \tau) & [0,1] \\ 0 & (1, \infty) \end{cases} \qquad (14)$$

$$\mu_t = \alpha + \beta_1 \times secchi_t + \beta_2 \times net\ velocity_t + \beta_3\ x\ secchi_t \times net\ velocity_t \qquad (15)$$

$$\tau = \frac{1}{\sigma^2} \qquad (16)$$

Priors were chosen to be uninformative:

$$\alpha, \beta_i \sim normal\ (0.0, 0.01) \qquad (17)$$

$$\sigma \sim uniform\ (0, 100) \qquad (18)$$

RESULTS

The maximum Secchi depths recorded by the FMWT survey during a year increased over the time-series (i.e., the clearest waters became clearer, Figure 3). Mann–Kendall tests for trends indicated that the central tendency of Secchi depth measurements has increased slightly over the years in the complete time-series for each month (Kendall's tau: Sept. 0.39, Oct. 0.35, Nov. 0.52, Dec. 0.42; $p < 0.001$). Since the invasion of the overbite clam in 1986, the slopes were steeper than slopes for the whole time-series, except for December (Kendall's tau: Sept. 0.59, Oct. 0.54, Nov. 0.64, Dec. 0.39; $p < 0.001$).

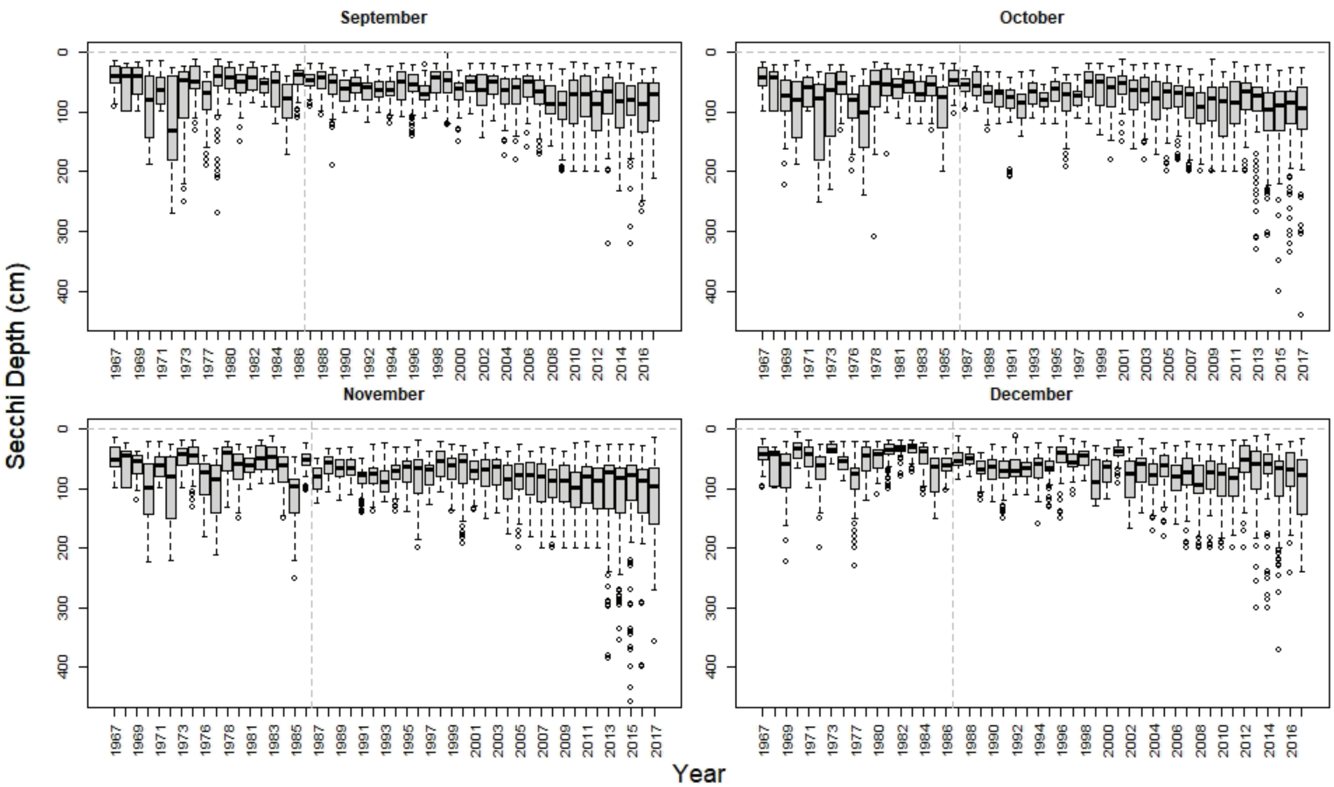

Figure 3 Boxplots of Secchi depth by month and year from September through December. A *vertical dashed line* shows the summer of 1987, when clams invaded. The *horizontal line* at depth = 0 cm represents the surface of the water.

In the simulated Delta Smelt capture data, there was a negative relationship between Secchi depth and proportion of fish caught in the simulated data, with no obvious curvature (Figure 4). Model diagnostic plots indicated that the model converged (Gelman plots showed that shrink factors approached 1 for all model parameters), and the mean Bayesian *p*-value indicated that the model fit the data well ($p = 0.507$; values near 0.5 indicate adequate fit). The intercept parameter estimate represents the expected catch proportion at the mean values of Secchi depth (224.3 cm) and net velocity (73.2 cm/sec) because the predictor variables were centered on zero. The slope parameter for Secchi depth (beta 1) was small, but negative (Table 1), which indicates that catch proportion declines at a shallow angle as Secchi depth increases. Increasing water clarity was also associated with an increase in variability in the proportion of fish caught (Figure 4). This increase in variability was explained by a positive interaction effect of Secchi depth and tow velocity (Table 1). As tow velocity increases, the Secchi slope becomes shallower. In other words, an increase in Secchi depth reduced catch proportion less at faster net velocities than at lower net velocities.

Over the entire range of Secchi depths ever recorded in the FMWT (0, 450), the estimated catch proportion for average towing speed ranges from 100% to 70% (Table 2). The distribution of Secchi depths in the FMWT data set is skewed, and values over 150 are rare. For the middle 50% (interquartile range) of Secchi depths measured by the FMWT, catch proportion was between 94 and 98% (Table 2).

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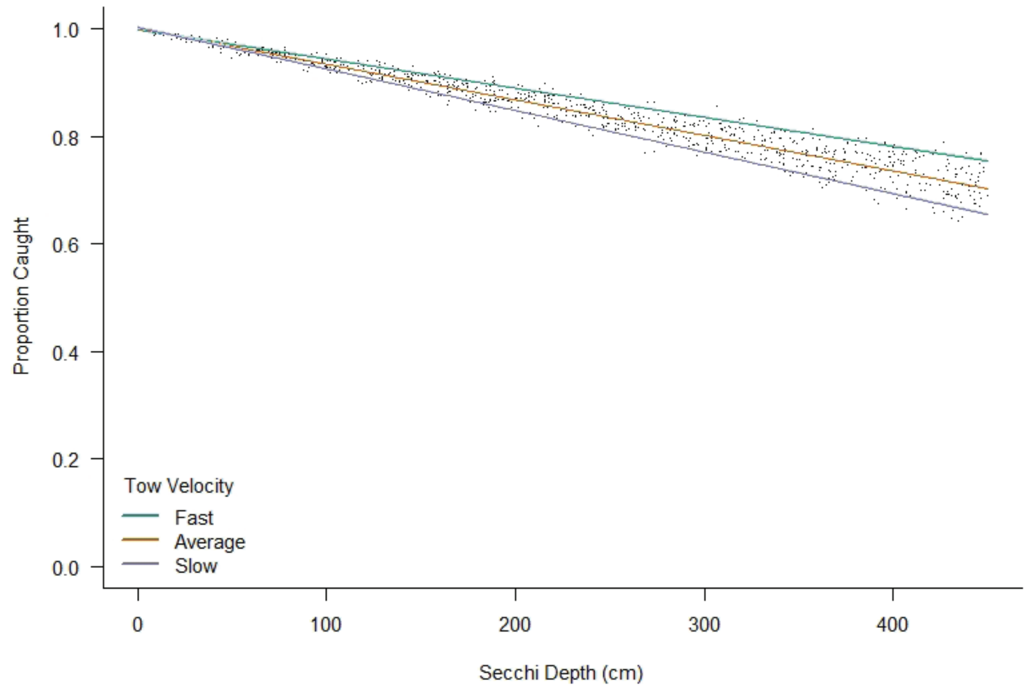

Figure 4 Predictions and 95% credible intervals of proportion of fish caught by Secchi depth and fast, average, and slow tow velocities (85, 73, and 62 cm s^{-1}, respectively). *Black dots* are simulated data points.

Table 1 Parameter estimates with summaries of spread and posterior distributions

Parameter	Mean	SD	SE	2.5%	25%	50%	75%	97.5%
alpha	0.853	3.48E-04	5.13E-06	0.852	0.853	0.853	0.853	0.854
beta1	– 0.085	3.62E-04	4.67E-06	– 0.086	– 0.085	– 0.085	– 0.085	– 0.084
beta12	0.009	3.48E-04	4.49E-06	0.008	0.008	0.009	0.009	0.009
beta2	0.014	3.48E-04	4.49E-06	0.013	0.013	0.014	0.014	0.014
sigma	0.011	2.41E-04	4.33E-06	0.010	0.011	0.011	0.011	0.011

Table 2 Predicted (mean) proportion of Delta Smelt caught for summary values of Secchi depth (cm) in the FMWT surveys with 95% credible intervals for average tow velocity

Secchi depth (cm)		Predicted catch proportion		
		Lower	Mean	Upper
Minimum	**0**	1.00	1.00	1.00
1st quartile	**39**	0.98	0.98	0.97
Median	**59**	0.96	0.96	0.96
Mean	**68**	0.96	0.96	0.96
3rd quartile	**85**	0.94	0.94	0.94
Maximum	**457**	0.70	0.70	0.70

DISCUSSION

This simulation demonstrates how information about fish behavior can be combined with information about monitoring protocols to investigate potential sources of bias in monitoring data. The basic framework can be adapted to other species and other sampling gears by substituting representative values into the calculations. This can be useful for resource managers who need to interpret abundance indices to make decisions This method is a way to investigate the magnitude of the effects of hypothesized sources of bias where field investigations are impossible or impractical.

Although the water of the estuary has become clearer in recent years, this simulation demonstrates that the potential for changes in water clarity to affect the catchability of Delta Smelt through their seeing the net are small. This suggests that the decline in relative abundance of Delta Smelt can be interpreted as a decline in availability as a result of changing habitat or a decline in population size. There have been no direct studies of how visual stimuli affects Delta Smelt behavior, but similar conclusions have been drawn for other species. For example, visual cues were not an important stimulus for evasion behaviors in larval striped bass, because they were not more able to evade nets in clearer water than when water was more turbid, and catches were similar in night- and day-time sampling (Gartz et al. 1999).

If water clarity influences both availability and catchability of Delta Smelt, using data from field surveys to estimate how water clarity affects Delta Smelt catchability is problematic because there appears to be a trend toward clearer water in the estuary. The simulated data in this study separate the effects of catchability from availability by holding availability constant, while allowing catchability to vary with water clarity in specific ways. This simulation provides insight into the proportion of fish caught, given that fish are present. When Delta Smelt availability is held constant, the proportion of Delta Smelt caught decreases with increasing Secchi depth (i.e., decreased turbidity or increased water clarity); however, within the typical range of Secchi depth values observed in the FMWT, catch proportion is close to 100%.

In this simulation, the ability of Delta Smelt to escape the net is determined by the amount of time a fish takes to escape, relative to the amount of time it has to react to the visual stimulus of the net. A result of this relationship is that the velocity of the net relative to the water adjusts the effect of Secchi depth (i.e., reaction distance) on the reaction time. At small Secchi depths (turbid water), different towing speeds do not affect catch proportion. As water becomes clearer (i.e., as Secchi depth increases), the lines for different tow speeds diverge (Figure 4). From a practical standpoint, given the assumptions of this simulation, the effects of clearer water can be dampened by increasing the speed at which the net is towed. Increasing the tow velocity might not increase catch proportion in the field, however, because increased speed can make the nets less efficient at capturing fish that encounter the net. This is because towing faster could build up negative pressure inside the net, making it more difficult for the net to both filter water and retain fish. If the net is pulled too quickly, fish may not be able to enter the net at all, and may be alerted to the presence of the net by detecting an acceleration front before they see it (Clutter and Anraku 1968).

The simulation applies directly only to places where Delta Smelt are present because it includes a fixed number of fish to potentially be caught; however, results of this simulation can inform understanding of the potential for false zeros in a field data set. The results of the present study do not generally apply to adjusting catch where presence is uncertain (e.g., when zero fish are caught, but environmental conditions are favorable); however, the simulation predicts that at low values of Secchi depth, nearly 100% of fish that are in the path of the net will be caught. This suggests that if zero fish are caught in very turbid waters, the uncertainty associated with that zero catch should be smaller than previously estimated (e.g., Latour 2016). The reason for the difference could be related to the differing time-scale used

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in these studies; if the probability of presence is more dynamic than is accounted for at the time-scales used to summarize the environmental covariates, the probability of a false zero could be inflated.

Decreasing catchability with increasing water clarity is not the sole factor that influences increased catch numbers in field data when Secchi depth is low. Although in the simulation catchability decreased under low-turbidity conditions, in the field Delta Smelt are also less likely to be found in clear water. For example, passive sampling at the water export facilities shows a pattern of greater catch of adult Delta Smelt under highter turbidity conditions (Grimaldo et al. 2009). The biology of Delta Smelt also supports the conclusion that availability increases with decreasing water clarity. A laboratory study of juvenile Delta Smelt (Hasenbein et al. 2013) found optimal feeding conditions and biological markers of stress were consistent with field surveys showing that Delta Smelt prefer somewhat turbid water (NTU 10–50; Feyrer et al. 2007). Another laboratory study showed that Smelt foraging ability peaks at mid-levels of turbidity (~30 NTU; Horppila et al. 2004).

In field data, low catch at low turbidity is probably a result of behavioral phenomena that reduce availability to the gear, rather than catchability. In low-turbidity conditions, Delta Smelt may not be available to the midwater trawl nets because they are lower in the water column, below the reach of the net. The scale of the fish behavior simulation is on the level of movements made by individual fish in response to local conditions and perceived threats. As described by Bennet and Burau (2015), this scale of movement is distinguished from the population-scale migrations that occur in response to seasonal changes in the environment. On an individual level, pelagic estuarine fishes have been known to migrate vertically in the water column in response to light conditions (Bennett et al. 2002). When turbidity is high, they may be near the top of the water column because the turbidity provides both shelter from visual predators and good contrast for hunting plankton. Planktivorous fish also tend to use more structured habitats to hide from predators in clear water than in turbid water; prey fish tend to remain in dangerous, open-water habitats when turbidity is high (Abrahams and Kattenfeld 1997; Turner and Mittelbach 1990). Turbidity can function as a refuge from predators, expanding the area available for foraging, which can be critical for fish that need to feed continuously (Lehtiniemi et al. 2005). For Delta Smelt in the estuary, this could mean that when turbidity is low fish stay in the shallower margins of the bay, rather than the deep water areas where midwater trawl nets are used. On the scale of migration, Delta Smelt movements have also been documented to coincide with tidal patterns, moving up in the water column during flood tides and down during ebb tides to migrate upstream. But these movements also coincided with turbidity patterns created by lagged effects of shifting tidal velocities (Bennet and Burau 2015), thus turbidity-seeking may also serve to facilitate migration movements upstream.

Evaluation of Assumptions

The use of Secchi depth as a proxy for the distance at which Delta Smelt see the net likely over-estimates the visual range of small fish. Planktivorous fish of a similar size to Delta Smelt (Two-spotted Goby, *Gobiusculus flavescens*) exhibited a visual range of approximately 5 cm in low light intensity to 30 cm in high light intensity (Aksnes and Utne 1997). Larval Striped Bass have been estimated to see the net at 2.50 to 200 cm (Gartz et al. 1999). If escape behavior is initiated when the net comes within the distance range reported by Gartz et al. (1999), the proportion of fish expected to be captured would be high and nearly constant, and more important in the context of this paper, it would not vary with Secchi depth. The assumption that detection range is proportional to Secchi depth is probably more reasonable for larger predatory fish. For example, Cod (*Gadus morhua*; 30–56-cm length) have a larger visual field, up to about 20 m for high-contrast objects in clear water, but decreasing as waters become less transparent (Anthony 1981). These studies and others (e.g., Hester 1968) have shown that visual contrast, light intensity, and water clarity all play a role in how far fish can see. If the range of visibility is more like that of Cod, Secchi depth may be an acceptable indicator of relative differences in visibility, because it depends on light intensity as well as scattering and absorption that result from suspended solids and dissolved organic matter (Priesendorfer 1986). If the visual range is limited, as it is for Goby, then this study under-estimates the catch proportion for clearer waters, but one could replace the under-estimated portions of Figure 4 with a horizontal line that approximates the predicted catch proportion for a Secchi depth equal to the expected visual range. In turbid waters, fish can use non-visual sensory organs—such as lateral lines—to detect the oncoming net. This could dampen any effects of Secchi depth on escape proportion found here.

The data simulated here use a simplified geometry, placing fish in a 3-D space to represent the path of a net through the water. The placement of fish within the path of the net does not consider water depth. Little research has been done on the vertical distribution of Delta Smelt in the water column, but there is some evidence to suggest that youngest life stages are evenly distributed throughout the water column (Rockriver 2004) and juvenile to adult life stages are more surface oriented (Souza 2002; Hobbs et al. 2006; Mitchell et al. 2017). Based on some of these studies, Polansky et al. (2019) estimated that life stages captured by the FMWT occupied depths of 0.5 m to 4.5 m.

The FMWT is an oblique tow, meaning that the net is towed at an upward angle, from near the bottom of the bay toward the surface of the water. This simulation ignores depth effects, which affects the assumption that the visual contact distance for the net is equivalent to Secchi depth. While this assumption is more easily true near the surface, reduced light availability at depth would effectively reduce the visual contact distance to less than Secchi depth (i.e., fish would see the net later, or when it is closer to them than this simulation assumes). This makes estimates of encounter time an over-estimate for fish deeper in the water column, which means that the catch proportion estimated here is a lower-bound on the actual catch proportion of the FMWT. Future work could incorporate light attenuation and absorption functions into the calculation of the reaction distance, given Secchi depth and the depth occupied by the fish.

The uniform distribution of fish was chosen to simulate fish distribution at a fine scale. Although at a bay-wide scale, small pelagic fish would presumably be clustered into schools, rules that govern this simulation assume that if fish are present, the net passes through a school and that the school is larger than the path of the net. This simulation also includes simplified fish behavior, where fish would swim straight in response to a stimulus and that swimming speed would be constant over the escape path. These assumptions might not be realistic over longer escape paths. The use of critical swimming speeds as a constant swim speed likely over-estimates speed over the entire escape trajectory. If fish slow down after an initial burst, they would take longer to escape the path of the net. This would tend to cause the calculated catch proportions to be under-estimates. If fish swim and take a circuitous route to escape the net, the escape time calculated here would be an under-estimate of actual escape times. This would result in a higher catch proportion than was calculated. In this simulation, the only cue that stimulates a fish to move out of the path of the net is seeing the net. It does not allow for interactions among fish. In reality, fish that are closer to the net probably induce some degree of startle response from fish farther from the net. In terms of this simulation, the encounter time would be longer than calculated here based on net velocity and Secchi depth. This would reduce the proportion of fish caught relative to calculations made here because fish would have longer to escape the path of the net than I calculated.

CONCLUSION

Although the effect of environmental conditions on availability and catchability of fish is confounded in data from field sampling, this

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paper demonstrates how these parameters can be decoupled using individual-based behavior simulations. For Delta Smelt, the species simulated here, the simulation shows that the effect of turbidity on catchability is small when availability is held constant. This suggests that water clarity's influence on reaction distance is not likely to be the cause of the relationship between Secchi depth and Delta Smelt catch reflected in the monitoring data. Future work will focus on extending this simulation methodology to other species of management concern and other sampling gears. It may be beneficial to explore the dynamic effects of turbidity, depth, and net velocity on catch proportion, especially for faster-swimming fish species.

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