 doi:10.20944/preprints202002.0177.v1

Simulated fishing to untangle catchability and availability in fish abundance monitoring

Vanessa D. Tobias

US Fish and Wildlife Service, Lodi Fish and Wildlife Office, 850 S. Guild Ave. Suite 105, Lodi, CA 95240; vanessa_tobias@fws.gov;

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 that is 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 due to an effect of changing water clarity on catchability.

KEY WORDS

bias; simulation; long-term monitoring; Delta Smelt; San Francisco Estuary

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 & Punt 2004). 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. 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 monitoring enterprise that is maintained by the Interagency Ecological Program for the San Francisco Estuary (IEP). 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 impact water deliveries for water agencies (USFWS 2008). The declining pattern of abundance of Delta Smelt has been questioned because of the inability of monitoring surveys to distinguish between effects of declining abundance and changes in catchability due to changing environmental conditions and/or habitat use (Feyrer et al. 2007, Latour 2016) and an apparent decline in turbidity measured during surveys such as the Fall Midwater Trawl (FMWT).

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 the effect of turbidity on 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 several factors that are determined by fish physiology (Domenici et al. 2007, 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 dataset to simulate sampling in a location with a fixed number of Delta Smelt available to the gear. To my knowledge, there have yet to be published examples of using individual-based simulation model of behavior to inform effort 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 makes it possible to assess the effect of turbidity on catchability of Delta Smelt, given that visual cues initiate escape behaviors, in a way that is not possible with environmental monitoring data alone.

METHODS

Study System

The SFE is a highly modified estuary, both in terms of land use and hydrology, and several environmental factors have changed over time. One change in water quality in the SFE is turbidity. 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 (*Potamacorbula 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 survey, when Secchi depths are high because of an increased field of visibility compared to when water is more turbid (Latour 2016).

The Delta Smelt (*Hypomesus transpacificus*) is a small (up to 10 cm standard length), planktivorous fish that is endemic to the San Francisco Estuary (SFE; 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 &Mejia 2013, Brown et al. 2014). Delta Smelt were abundant in the SFE 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 Fall Midwater Trawl survey (FMWT) 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 SFE 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 SFE.

Data Simulation

In order 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 1000 tows through a horizontal two-dimensional space which had the width of the midwater trawl net used for the FMWT study (365.8 cm). For each tow, I simulated constant availability of fish by simulating 1000 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), and angle at which to swim (a_f), and a swimming velocity (v_f; Figure 2).

$$d_f \sim uniform(0, 365.8)\ (cm)$$

$$a_f \sim wrapped\ normal(165.8, 3.7)\ (degrees)$$

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

$$v_f \sim normal(27.6, 5.1)\ (cm/s)$$

The critical swimming velocity was defined as the maximum swimming velocity that 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 chance to escape the net that is biologically feasible. 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.

$$w_f \sim binomial(0.4, 1)$$

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 mohua*; Meager et al. 2006). Here, as in Meager et al. (2006), a 0° angle represents swimming towards the stimulus. These values are also consistent with escape angles for herring (*Clupea harengus*; Domenici & Batty 1994, 1997). Here, the fish were assumed that the net approached every fish from behind so that the escape angle calculation would be consistent.

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

$$s_t = uniform(1, 450)\ (cm)$$

$$v_t = normal(72.8, 19.6)\ (cm/s)$$

These values were used 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 make visual contact with the net (i.e. that the distance at which a fish could see the net was the same as the measured Secchi depth). It was also assumed that at the instant a fish made visual contact with the net, it would swim straight toward the edge of the path of the net (Figure 2). This allowed us 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 would escape the path of the net (net time).

$$escape\ distance_f = \tan(a_f) \times d_f$$

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

$$fish\ position_f = s_t + escape\ distance_f$$

$$net\ time_f = \frac{s_t + escape\ distance_f}{v_t}$$

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 that were caught was summed for each tow and recorded as a proportion:

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

Observation stochasticity was introduced to the data by modeling total catch as a poisson random variable with the expected value equal to the sum of catch.

$$catch_t = Poisson\left(\lambda = \sum_{f=1}^{1000} caught_f\right)$$

Catch proportion was calculated as the simulated catch divided by the number of fish available to the net (in this case, 1000 fish). Catch proportion is the response variable used in the model below.

$$p_t = \frac{catch_t}{1000}$$

Inference

Using the simulated data I fit a regression model using a hierarchical model using Markov chain Monte Carlo (MCMC) simulation in OpenBUGS (Thomas et al. 2006), through R (R Core Team 2014; package R2OpenBUGS, Sturtz 2005) to examine the effect of Secchi depth on catch proportion,. 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. An advantage of the Bayesian approach is that it can include all uncertainty in the posterior distributions, allowing more realistic estimates of model parameters. A normal distribution and identity link were used to model the relationship because visual inspection of binomial models showed an obvious lack of fit.

$$catch\ proportion_{\,t} \sim normal(\mu_t, \tau)$$

$$\mu_t = \alpha + \beta_1 \times secchi_t + \beta_2 \times net\ velocity_t + \beta_3 \times secchi_t \times net\ velocity_t$$

$$\tau = \frac{1}{\sigma^2}$$

Priors were chosen to be uninformative:

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

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

I centered and standardized the net velocity (on the mean and standard deviation, respectively) to improve estimates and convergence of the model in OpenBUGS.

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 generally slightly 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; $p<0.001$).

In the simulated Delta Smelt capture data, there was a negative relationship between Secchi depth and proportion of fish caught, 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 Bayesian p-value indicated significant effects in the model ($p = 0.502$; values near 0.5 indicate significance for Bayesian p-values). The slope parameter for Secchi depth was small, but negative (Table 1), which indicates that catch proportion declines as Secchi depth increases. The credible interval for the intercept included 1, which indicates that when Secchi depth (and hence reaction time in this model) is zero, it would be expected that all of the fish in the path of the net are captured. 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, as the net is towed faster, an increase in Secchi depth has less of an effect on reducing catch proportion than at lower net velocities. Parameter estimates were similar to those obtained from an ordinary least squares linear regression (see Appendix C).

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 ±0 to 83% ±0.1% (Table 2). For the middle 50% (interquartile range) of Secchi depths measured by the FMWT, catch proportion was between 97 and 99% (Table 2).

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 other values into the calculations. This can be useful for resource managers who need to interpret abundance indices for decision-making purposes. For monitoring in the SFE, this simulation demonstrates that although the water of the SFE has become clearer in recent years, that change in water clarity does not appear to affect the catchability of Delta Smelt. This means 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.

If water clarity influences both availability and catchability of Delta Smelt, using data from field surveys to estimate the effect of water clarity on Delta Smelt catchability is problematic because there appears to be a trend toward clearer water in the SFE. 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 that are 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), there is no difference in catch proportion for different towing speeds. As water becomes more clear (i.e., as Secchi depth increases), the lines for different tow speeds diverge. From a practical standpoint, this means that 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 of the net, making it more difficult for the net to filter the water and for fish to be retained by the net. 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 detection of an acceleration front before visual contact (Clutter & Anraku 1968).

Because the simulation includes a fixed number of fish to potentially be caught, it applies directly only to places where Delta Smelt are present. This means that the results of this simulation can inform the potential for false zeros in a field dataset. Even at the lowest turbidity values recorded in the FMWT, which were rare, the rate of false zeros was 1-2%, which was a substantially lower rate than a previous estimate (Latour 2016). The reason for the difference could be related to the differing timescale used 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. This study also only accounts for two factors that affect the rate of false zeros. 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 very 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). Gartz et al. (1999) found no evidence that fish were more able to avoid nets when water was clearer than when water was more turbid; further, they concluded that visual cues were not an important stimulus for evasion behaviors in larval striped bass because there was no difference between catches in night- and day-time sampling.

Decreasing catchability with increasing water clarity is not the sole factor influencing increased catch numbers when Secchi depth is low. Although catchability decreased in low turbidity conditions, Delta Smelt are less likely to be found there. There is evidence that turbidity is associated with higher availability of Delta Smelt because at the water diversion pumps, which represent a passive sampling system, the number of adult Delta Smelt observed is correlated with turbidity (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 (~30NTU; Horppila et al. 2004).

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. 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 provides 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 & 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 SFE, 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.

Evaluation of assumptions

The use of Secchi depth as a proxy for the distance at which Delta Smelt visually detect the net likely overestimates 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 & Utne 1997). Visual net detection range for larval striped bass has been estimated at 250-2000mm (Gartz et al. 1999). If escape behavior is initiated when the net comes within this distance range, the proportion of fish that are expected to be captured would be high and nearly constant and more importantly 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 the visual range of fish. 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 underestimates the catch proportion for clearer waters, but one could replace the underestimated portions of Figure 4 with a horizontal line that approximates the predicted catch proportion for a Secchi depth equal to the expected visual range.

The data simulated here use a simplified geometry, placing fish in a two-dimensional, horizontal plane. The FMWT is an oblique tow, meaning that the net is towed at an upward angle, from near the bottom of the bay towards 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 at or 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 I assume in the simulation). This makes estimates of encounter time an over-estimate for fish below the surface, which means that the catch proportion is a lower-bound on the actual catch proportion.

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. If fish swim 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 a visual response to 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 our calculations 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 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 applied to data collected by monitoring surveys, this finding strengthens the ecological interpretation that Delta Smelt catch is higher in turbid waters because Delta Smelt are more likely to be in turbid water than in clear water. Future work will focus on extending this simulation methodology to other species of management concern and other sampling gears.

ACKNOWLEDGEMENTS

The author thanks Emilio Laca for postdoctoral research funding and guidance in the early stages of this work. Thanks also to J. Mclain, L. Mitchell, and W. Smith and the Interagency Ecological Program's Science Management Team for reviewing drafts and assisting with obtaining relevant literature. The findings and conclusions of this article are those of the author and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

REFERENCES

Abrahams M, Kattenfeld M (1997) The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40(3): 169-174.

Aksnes DL, Utne ACW (1997) A revised model of visual range in fish. Saria 82:137-147.

Anthony PD (1981) Visual contact thresholds in the cod *Gadus morhua* L. Journal of Fish Biology 19:87-103.

Baskerville-Bridges B, Lindberg JC, Doroshov SI (2004) The effect of light intensity, alga concentration, and prey density on the feeding behavior of Delta Smelt larvae. In: Feyrer F, Brown LR, Brown RL, Orsi J (eds) Early life history of fishes in the San Francisco Estuary and watershed. Symposium 39. American Fisheries Society, Bethesda, Maryland, USA.

Bennett WA (2005) Critical assessment of the Delta Smelt population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science 3(2). http://escholarship.org/uc/item/0725n5vk.

Bennett WA, Kimmerer WJ, Burau JR (2002) Plasticity in vertical migration by native and exotic estuarine fishes in a dynamic low-salinity zone. Limnological Oceanography 47(5):1496-1502.

Brown LR, Baxter R, Castillo G, Conrad L, Culberson S, Erickson G, Feyrer F, Fong S, Gehrts K, Grimaldo L, Herbold B, Kirsch J, Mueller-Solger A, Slater S, Souza K, and Van Nieuwenhuyse E (2014) Synthesis of studies in the fall low-salinity zone of the San Francisco Estuary, September–December 2011. U.S. Geological Survey Scientific Investigations Report 2014–5041. 136 p.

Clutter RI, Anraku M (1968) Avoidance of samplers. In: Tranter DJ (ed) Part 1. Reviews on Zooplankton Sampling Methods. UNESCO Monographs on Oceanographic Methodology 2. Zooplankton Sampling. UNESCO, Paris, France, pp. 57-76.

Domenici, P (2010) Escape Responses in fish: kinematics, performance, and behavior. In: Domenici P, B Kapoor (Eds) Fish Locomotion: An Eco-Ethological Perspective. CRC Press, Enfield. ISBN: 9781439843123

Domenici P, Batty RS (1994) Escape manoeuvres of schooling *Clupea harengus*. Journal of Fish Biology 45(Supplement A): 97-110.

Domenici P, Batty RS (1997) Escape behavior of solitary herring (*Clupea harengus*) and comparisons with schooling individuals. Marine Biology 128: 29-38.

Domenici P, Lefrancois C, Levine RP (2004) The effect of hypoxia on the antipredator behavioir or fish. Philosophical Transactions of the Royal Society B. 362:2105-2121.

Feyrer F, Nobriga ML, Sommer TR (2007) Multidecadal trends for three declining fish species: habitat patterns and mechanisms in the San Francisco Estuary, California, USA. Can J Fish Aquat Sci 64:723–34.

Gartz RG, Miller LW, Fujimura RW, Smith PE (1999) Measurements of larval striped bass (*Morone saxatilis*) net avoidance using evasion radius estimation to improve estimates of abundance and mortality. Journal of Plankton Research 21(3):561-580.

Greene VE, Sullivan LJ, Thompson JK, Kimmerer WJ (2011) Grazing impact of the invasive clam Corbula amurensis on the microplankton assemblage of the northern San Francisco Estuary. Marine Ecology Progress Series 431:183-193

Grimaldo LF, Sommer T, Van Ark N, Jones G, Holland E, Moyle PB, Herbold B, Smith P (2009) Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary: Can fish losses be managed. North American Journal of Fisheries Management 29(5):1253-1270.

Hasenbein M, Komoroske LM, Connon RE, Geist J, Fangue NA (2013) Turbidity and salinity affect feeding performance and physiological stress in the endangered Delta Smelt. Integrative and Comparative Biology 53(4):620-634.

Hester FJ (1968). Visual contrast thresholds of the goldfish (Carassius auratus). Vision Res. 8, 1315-1335. doi:10.1016/0042-6989(68)90053-9

Horppila J, Liljendahl-Nurminen A, Malinen T (2004) Effects of clay turbidity and light on the predator-prey interaction between smelts and chaoborids. Canadian Journal of fish and Aquatic Science 61:1862-1870.

Kimmerer WJ, Gartside E, Orsi JJ (1994) Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. Marine Ecology Progress Series 13: 81-93.

Latour RJ (2016) Explaining patterns of pelagic fish abundance in the Sacramento-San Joaquin Delta. Estuaries and Coasts 39:233-247. DOI: 10.1007/s12237-015-9968-9

Lehtiniemi M, Engström-Öst J, Viitasalo M (2005) Turbidity decreases anti-predator behavior in pike larvae, Esox lucius. Environmental Biology of Fishes 73: 1-8.

Mager R, Doroshov SI, Van Eenennaam JP, Brown RL (2004) Early life stages of Delta Smelt. In: Feyrer F, Brown LR, Brown RL, Orsi J (eds) Early life history of fishes in the San Francisco Estuary and watershed. Symposium 39. American Fisheries Society, Bethesda, Maryland, USA.

Meager JJ, Domenici P, Shingles A, Utne-Palm AC (2006) Escape responses in juvenile Atlantic cod *Gadus morhua L*.: the effects of turbidity and predator speed. The journal of Experimental Biology 209:4171-4184. DOI: 10.1242/jeb.02489.

Moyle PB, Herbold B, Stevens DE, Miller LW (1992) Life history and status of Delta Smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121: 67-77.

Priesendorfer RW (1986) Secchi disk science: visual optics of natural waters. Limnological Oceanography 31(5): 909-926.

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Sommer T, Armor C, Baxter R, Breuer R, Brown L, Chotkowski M, Culberson S, Feyrer F, Gingras M, Herbold B, Kimmerer W, Mueller-Solger A, Nobriga M, Souza K (2007) The collapse of pelagic fishes in the upper San Francisco estuary. Fisheries 32:270–7.

Sommer T, Mejia F (2013) A place to call home: a synthesis of Delta Smelt habitat in the upper San Francisco Estuary. San Francisco Estuary and Watershed Science 11(2). http://www.escholarship.org/uc/item/32c8t244.

Sturtz S, Ligges U, Gelman A (2005) R2WinBUGS: A Package for Running WinBUGS from R. Journal of Statistical Software, 12(3), 1-16.

Swanson C, Young PS, Cech JJ (1998) Swimming performance of Delta Smelt: maximum performance and behavioral and kinematic limitations on swimming at submaximal velocities. The Journal of Experimental Biology. 201:333-354.

Thomas A, Hara BO, Ligges U, Sturtz S (2006.)Making BUGS Open. R News 6: 12-17. http://www.rni.helsinki.fi/~boh/publications/Rnews2006-1.pdf

Turner AM, Mittelbach GG (1990) Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. Ecology 71(6): 2241-2254.

USFWS (United States Fish and Wildlife Service) (2008) Formal Endangered Species Act consultation on the proposed coordinated operations of the Central Valley Project (CVP) and State Water Project (SWP). U.S. Fish and Wildlife Service, Sacramento, CA.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 14 February 2020 doi:10.20944/preprints202002.0177.v1

TABLES

Table 1: Parameter estimates with a summaries of spread and posterior distributions.

Parameter	Mean	SD	SE	2.50%	25%	50%	75%	97.50%
alpha	1.001	0.002	0.000	0.997	0.999	1.001	1.002	1.004
beta1	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
beta12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
beta2	-0.001	0.002	0.000	-0.005	-0.002	-0.001	0.000	0.003
sigma	0.031	0.001	0.000	0.030	0.030	0.031	0.031	0.032

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	0.99	0.99
median	59	0.97	0.98	0.98
mean	68	0.97	0.97	0.98
3rd quartile	85	0.96	0.97	0.97
maximum	457	0.82	0.83	0.84

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 14 February 2020 doi:10.20944/preprints202002.0177.v1

FIGURES

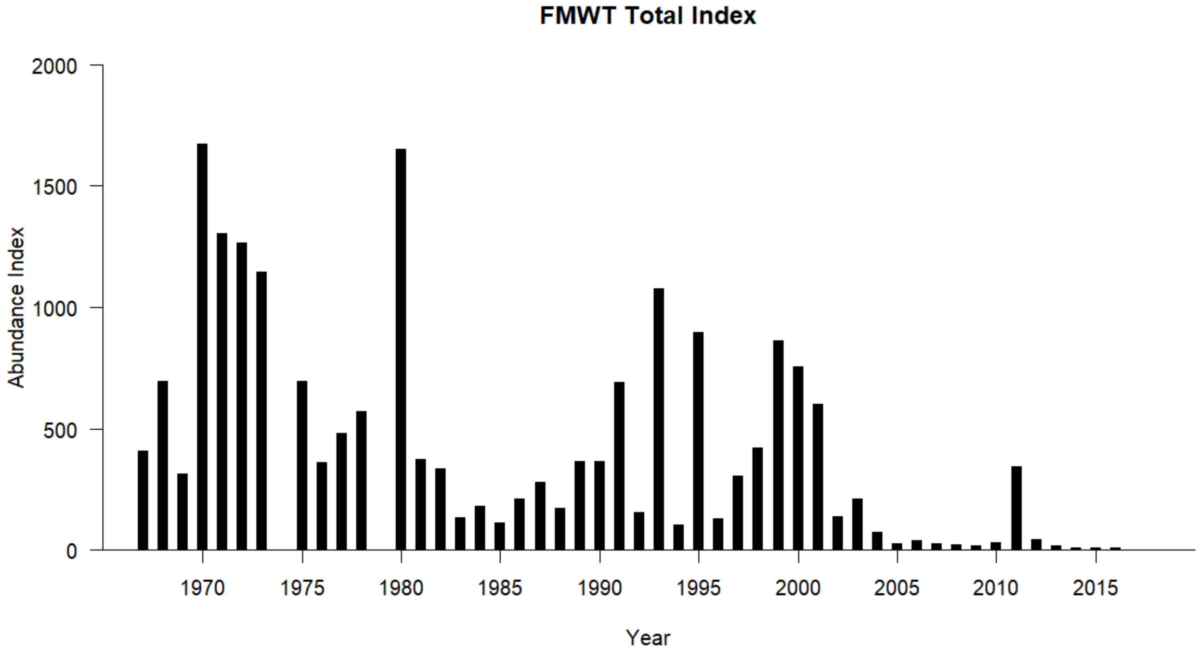

Figure 1: Fall Midwater Trawl abundance index for Delta Smelt. (Data are from https://www.wildlife.ca.gov/Conservation/Delta/Fall-Midwater-Trawl.)

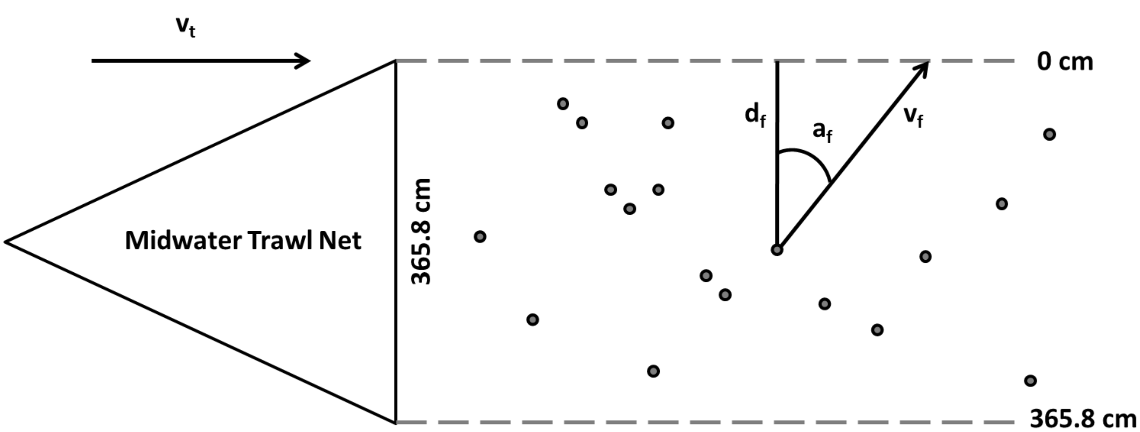

Figure 2: Conceptual diagram of simulated fish (circles) placement within the path of the net from an overhead perspective, looking down on the sampling event. Labels correspond to equations given in the text.

 doi:10.20944/preprints202002.0177.v1

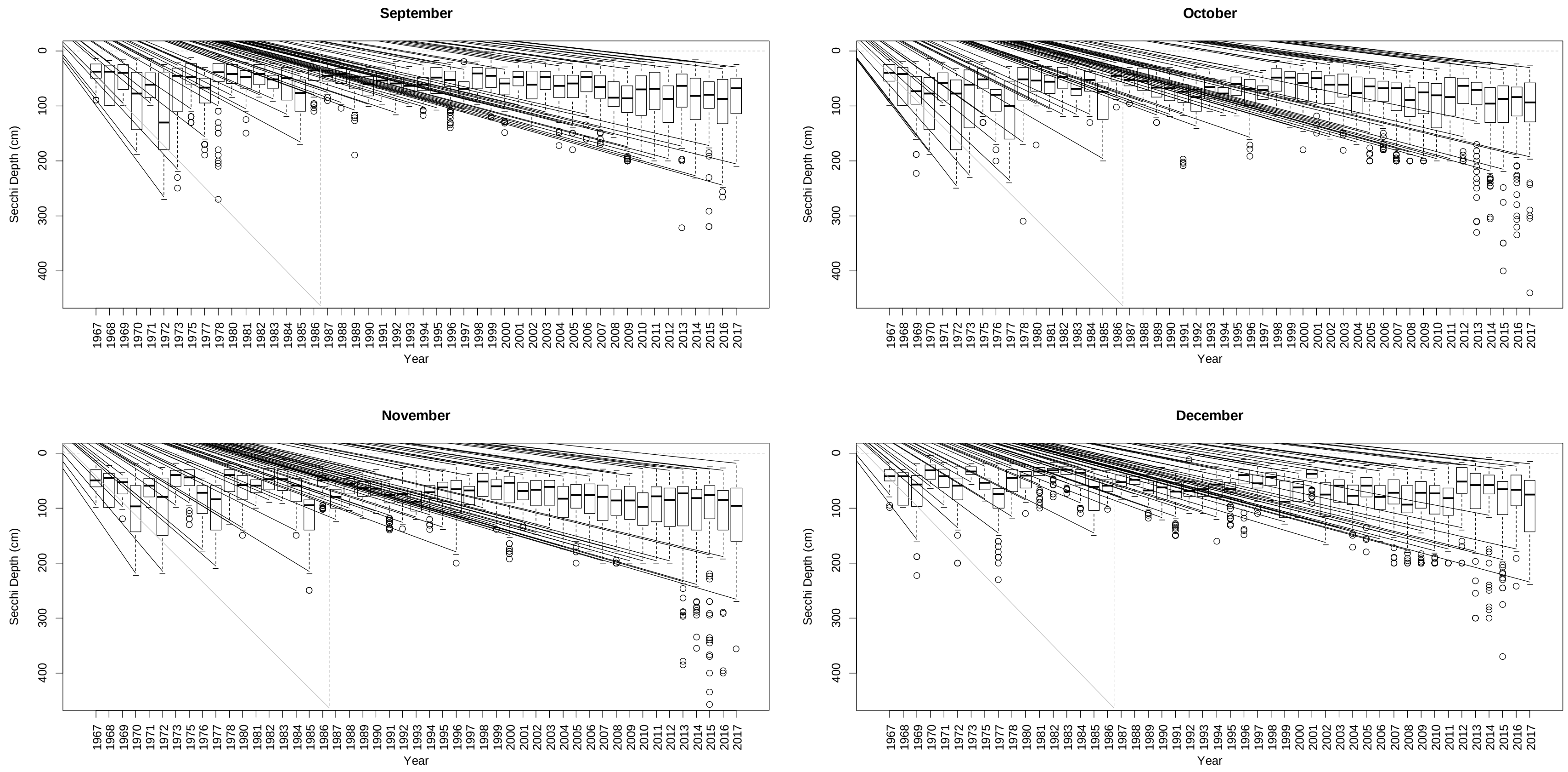

Figure 3: Boxplots of Secchi depth by month and year in (a-d) September-December. A vertical dashed line shows the summer of 1987, when clams invaded. The horizontal line at depth = 0 cm represents the surface of the water.

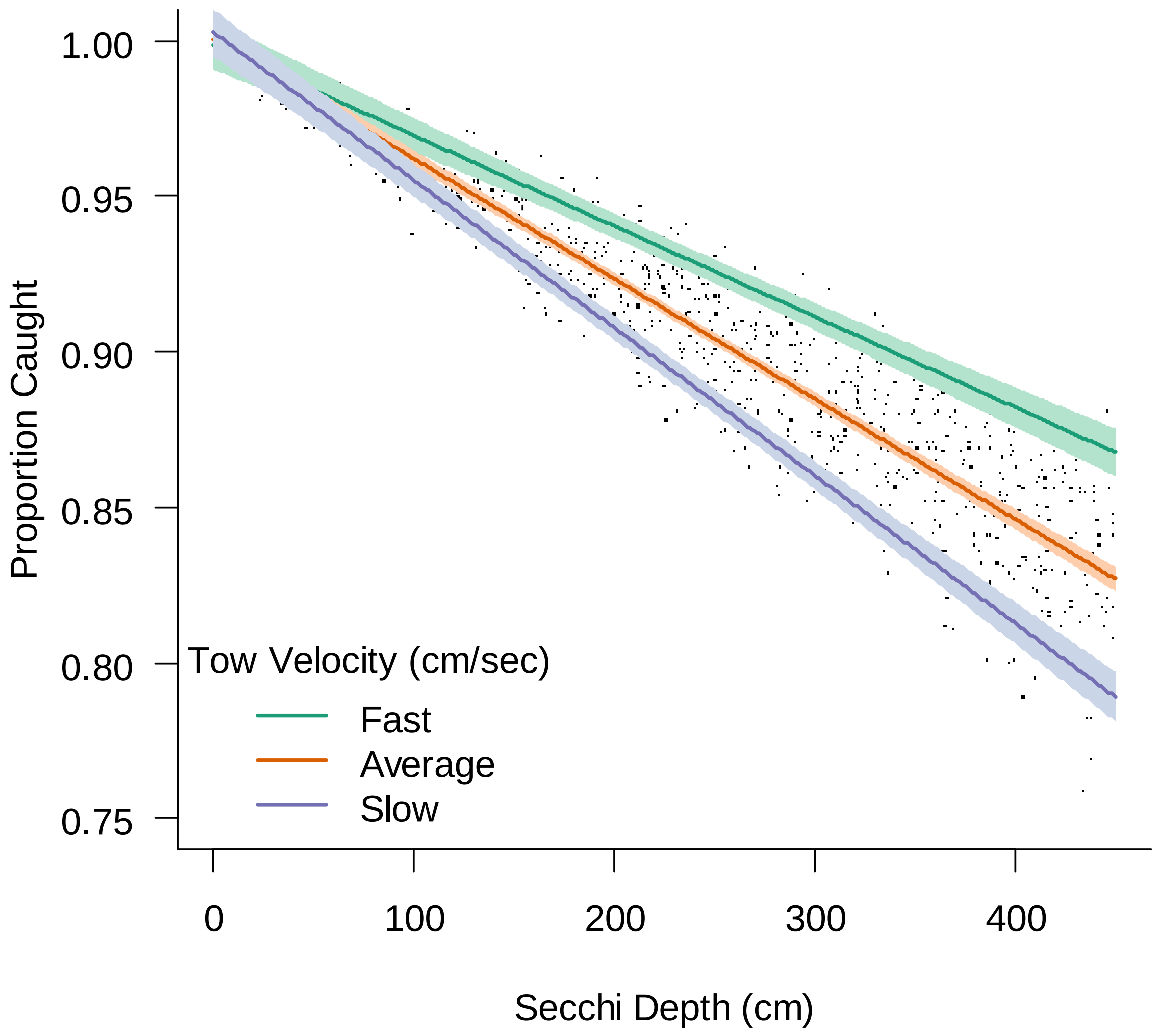

Figure 4: Predictions and 95% credible intervals of proportion of fish caught by Secchi depth and fast, average, and slow tow velocities (85, 73, and 62 cm/sec, respectively). Black dots are simulated data points.