1   Title: Simulated fishing to untangle catchability and availability in fish abundance monitoring

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5   **ABSTRACT**

6   In fisheries monitoring, catch is assumed to be a product of fishing intensity, catchability, and

7   availability, where availability is defined as the number or biomass of fish present and

8   catchability refers to the relationship between catch rate and the true population. Ecological

9   monitoring programs use catch per unit of effort (CPUE) to standardize catch and monitor

10   changes in fish populations; however, CPUE is proportional to the portion of the population

11   that is vulnerable to the type of gear that is used in sampling, which is not necessarily the entire

12   population. Programs often deal with this problem by assuming that catchability is constant,

13   but if catchability is not constant, it is not possible to separate the effects of catchability and

14   population size using monitoring data alone. This study uses individual-based simulation to

15   separate the effects of changing environmental conditions on catchability and availability in

16   environmental monitoring data. The simulation combines a module for sampling conditions

17   with a module for individual fish behavior to estimate the proportion of available fish that

18   would escape from the sample. The method is applied to the case study of the well-monitored

19   fish species Delta Smelt (*Hypomesus transpacificus*) in the San Francisco Estuary, where it has

20   been hypothesized that changing water clarity may affect catchability for long-term monitoring

21   studies. Results of this study indicate that given constraints on Delta Smelt swimming ability, it

22   is unlikely that the apparent declines in Delta Smelt abundance are due to an effect of changing

23   water clarity on catchability.

24   **KEY WORDS**

25   bias; simulation; behavior-based model; gear avoidance; monitoring; Delta Smelt

27   **1. INTRODUCTION**

28   For fisheries stock assessments, catch is assumed to be a product of fishing intensity,

29   catchability, and availability, where availability is defined as the number or biomass of fish

30   present at a site and catchability refers to the relationship between the rate at which fish are

31   caught and the true population size (Ricker 1975). Ecological monitoring programs use catch

32   per unit of effort (CPUE) as a way to monitor changes in fish populations and communities;

33   however, CPUE is proportional to the portion of the population that is vulnerable to the type of

34   gear that is used in sampling, which is not necessarily the entire population (Maunder et al.

35   2006). Many methods have been developed to account for variable catchability, including

36   estimating ratios and developing statistical models where environmental conditions and/or

37   time variables can account for changes in catchability (Maunder & Punt 2004). Gear efficiency

38   studies (e.g., Mitchell and Baxter 2021) also seek to account for changes in catchability for

39   different sizes and species of fish.

40   Ecological monitoring programs typically assume that the relationship between catch and

41   biomass or population size is constant, i.e., that catchability is constant. By making this

42   assumption, monitoring programs can compare abundance of organisms relative to abundance

43   in other locations or points in time without having to estimate the proportion of the population

44   that is vulnerable to sampling gear. Essentially, the goal is to standardize catch so that the non-

45   vulnerable portion of the population cancels out of the equation.

46   Whether it is reasonable to assume that catchability is constant depends on the conditions of

47   the monitoring program. It is reasonable to make this assumption when either (1)

48   environmental factors do not influence catchability or (2) the environmental factors that drive

49   catchability are constant. If environmental factors influence catchability and those factors

50   change, catch will reflect changes in both population size and catchability (i.e., population size

51   and catchability are confounded). If catchability is not constant, it is not possible to separate

52   the effects of catchability and population size using monitoring data alone. For example, given a

53   constant population size, if salinity reduces catchability, catch would decrease as salinity

54   increases. If catchability were inaccurately assumed to be constant, the decrease in catch would

55   be interpreted as a decrease in population size, which would introduce a negative bias to the

56   estimates of population size. Where an environmental factor affects both catchability and

57   availability, additional studies are necessary to separate the two effects on catch, but

58   abundance estimates are possible in this situation using N-mixture models (Royle 2004). For

59   ecological monitoring programs, where the primary source of abundance information is derived

60   from field data collections, confounding of the effects of availability and catchability can call

61   into question the validity of observed patterns in species of interest.

62   One example of such a monitoring program is the extensive monitoring enterprise that is

63   maintained by the Interagency Ecological Program for the San Francisco Estuary (IEP). The San

64   Francisco Estuary (SFE) is a highly modified estuary, both in terms of land use and hydrology,

65   and several environmental factors have changed over time. Although turbidity varies

66   considerably by season and weather, an overall pattern of decreasing turbidity has been

67   observed since the introduction of the Asian overbite clam (*Potamacorbula amurensis*) in 1987

68   (Kimmerer et al. 1994, Greene et al. 2011). This trend toward decreasing turbidity and

69   decreasing catch of Delta Smelt over time has led some researchers to speculate whether

70   changes in turbidity might be responsible for a change in catchability. In particular, the question

71   is whether Delta Smelt avoid sampling gear more effectively, particularly that of the Fall

72   Midwater Trawl survey, when Secchi depths are high because of an increased field of visibility

73   compared to when water is more turbid (Latour 2016).

74   The IEP has been monitoring fish and water quality in the estuary for over 50 years. Although

75   the IEP monitors many species, in recent years there has been an increased focus on sampling

76   methods that support the calculation of relative abundance indices for Delta Smelt (*Hypomesus*

77   *transpacificus*). Delta Smelt are of particular interest because of their apparent steep decline in

78   abundance (Figure 1) and because the status and distribution of this endangered species within

79   the estuary can impact water deliveries for water agencies (USFWS 2008). The declining pattern

80   of abundance of Delta Smelt has been questioned because of the inability of monitoring

81   surveys to distinguish between effects of declining abundance and changes in catchability due

82   to changing environmental conditions and/or habitat use (Feyrer et al. 2007, Latour 2016) and

83   an apparent decline in turbidity measured during surveys such as the Fall Midwater Trawl

84   (FMWT).

85   A few studies provide insight into separating catchability from availability for Delta Smelt.

86   Applying zero-inflated negative binomial models to the FWMT to separate true zeros from false

87   zeros, Latour (2016) found that as water clarity increased (larger Secchi depth), catch declined

88   and the probability of false zeros increased. This suggests that decreasing turbidity negatively

89   affects catchability. The mechanism for this change in availability would ostensibly be that Delta

90   Smelt are better able to avoid sampling nets in clearer water. Laboratory experiments also shed

91   some light on the effect of turbidity on availability. For example, experiments with young Delta

92   Smelt indicate that clear water inhibits feeding behaviors (Baskerville-Bridges et al. 2004,

93   Mager et al. 2004). If Delta Smelt prefer turbid waters, turbidity would increase availability. This

94   study takes a different approach to addressing the confounding of catchability and availability.

95   This paper describes an individual-based simulation study that aims to separate the effects of

96   changing environmental conditions on catchability and availability in environmental monitoring

97   data. The simulation combines a module for sampling conditions with a module for individual

98   fish behavior to estimate the proportion of available fish that would escape from the sample.

99   The fish behavior module follows a standard conceptual model of fish behavior in response to a

100 predator or similar threat: when fish are presented with a stimulus, they use environmental

101 cues to determine the type of response and their reaction is governed by several factors that

102 are determined by fish physiology (Domenici et al. 2007, Domenici 2010). As a case study, I use

103 values for swimming speed and escape trajectory from the published literature on fish behavior

104   as well as measurements from the FMWT dataset to simulate sampling in a location with a fixed

105   number of Delta Smelt available to the gear. To my knowledge, there have yet to be published

106   examples of using individual-based simulation model of behavior to inform effort catch

107   standardization efforts. The goals for this simulation are (1) to describe some bounds on the

108   physical ability of Delta Smelt to evade capture in a system where visual cues stimulate

109   avoidance behaviors and (2) to examine the properties that emerge in the sampling process

110   from limitations on individual fish behavior. By holding availability constant for each tow

111   catchability is represented by the proportion of fish caught. This paper demonstrates a

112   modeling approach to evaluating the interaction of environmental factors and fish behavior on

113   monitoring data in a way that is not possible with environmental monitoring data alone.

114   Specifically, this paper evaluates the hypothesis that turbidity affects catchability of Delta

115   Smelt.

116   **2. MATERIALS & METHODS**

117   *2.1 Study Species*

118   The Delta Smelt (*Hypomesus transpacificus*) is a small (up to 10 cm standard length),

119   planktivorous fish that is endemic to the San Francisco Estuary (SFE; the San Francisco Bay and

120   Sacramento-San Joaquin Delta). Delta Smelt spawn in fresh water in spring and spend most of

121   their lives in the mixing zone of the estuary before maturing in the fall (Moyle et al. 1992). They

122   are generally found in turbid water (Bennett 2005, Feyrer et al. 2007, Sommer &Mejia 2013,

123   Brown et al. 2014). Delta Smelt were abundant in the SFE at one time, but they became so rare

124   that they have been listed as threatened by the federal Endangered Species Act since 1993 and

125   as endangered by the California Endangered Species Act since 2010. An index of Delta Smelt

126   abundance based on the Fall Midwater Trawl survey (FMWT) shows that abundance declined to

127   the lowest recorded values in 2018. The decline of Delta Smelt is part of a suite of declining

128   pelagic organism populations in the SFE that occurred in the early 2000s (Sommer et al. 2007).

129   As Delta Smelt have become rarer, interest has grown in evaluating the programs such as the

130   FMWT that are used to monitor their abundance as well as the factors that determine their

131   distribution in the SFE.

132   *2.2 Data Simulation*

133   To investigate the effects of environmental conditions and tow characteristics on the number of

134   fish caught, I first simulated data using a combination of published values and geometric

135   relationships, then I fit a model to the simulated data. I simulated 1000 tows through a

136   horizontal three-dimensional space which had the width and height matching the dimensions of

137   the midwater trawl net used for the FMWT study (365.8 cm). For each tow, I simulated

138   constant availability of fish by simulating 1000 fish in the path of the net. Each fish (f) was

139   assigned a location as the distance from the edge of the path of the net (d_f), a turning angle at

140   which to swim (a_f), a vertical (pitch) angle at which to swim (b_f), a height from the bottom of

141   the net path (h_f) and a swimming velocity (v_f; Figure 2).

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

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

$$b_f \sim uniform(0, 180) \; (degrees)$$

145
$$h_f \sim uniform(0, 365.8)\ (cm)$$

146

147   Swimming velocity (v_f) was based on measurements of critical swimming velocity for Delta

148   Smelt (Swanson et al. 1998).

149
$$v_f \sim normal(27.6, 5.1)\ (cm/s)$$

150   The critical swimming velocity was defined as the maximum swimming velocity that a fish can

151   maintain for a specific duration (Swanson et al. 1998). Using the critical swimming velocity in

152   this simulation gives the fish the best chance to escape the net that is biologically feasible. In

153   the same Delta Smelt swimming study, approximately 40% of fish experienced some swimming

154   failure that was unrelated to fatigue. This was captured in our simulation by a binomial

155   distribution where fish had a 0.4 probability of experiencing a swimming failure (w_f), resulting in

156   capture.

157
$$w_f \sim binomial(0.4, 1)$$

158   There were no published studies describing the angle of escape for smelt species, so escape

159   angle was based on a study of predator avoidance behavior in juvenile Atlantic Cod where the

160   angle at which the fish swam was calculated based on the angle created by the escape

161   trajectory and the initial position of the fish relative to the predator (*Gadus mohua*; Meager et

162   al. 2006). Here, as in Meager et al. (2006), a 0° angle represents swimming towards the

163   stimulus. These values are also consistent with escape angles for herring (*Clupea harengus*;

164   Domenici & Batty 1994, 1997). This assumes that the simulated net approached every fish from

165   behind so that the escape angle calculation would be consistent.

166   For each tow, Secchi depths were selected from a uniform distribution of the full range of

167   Secchi depths recorded in the FMWT in 1 cm increments (1-450 cm).

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

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

170   These values were used to calculate whether each fish in the population would move out of the

171   path of the net before the net reached the fish. The simulation assumed that Secchi depth was

172   equivalent to the distance at which a fish would make visual contact with the net (i.e. that the

173   distance at which a fish could see the net was the same as the measured Secchi depth). It was

174   also assumed that at the instant a fish made visual contact with the net, it would swim straight

175   toward the edge of the path of the net at the assigned values for turning and pitch angles

176   (Figure 2). This allowed me to calculate the amount of time it would take a fish to escape the

177   path of the net (escape time), the distance the fish would travel away from the net (escape

178   distance), and the amount of time it would take the net to reach the location where the fish

179   would escape the path of the net (net time). The calculations for the escape distance vary

180   depending on whether the fish escapes to the vertical sides (left or right) or the horizontal sides

181   (top or bottom) of the net path (Figure 2; full calculations available at

182   https://github.com/USFWS/Gear-Avoidance-Behavior-Simulation).

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

184
$$fish\ position_f = s_t + escape\ distance_f$$

185
$$net\ time_f = \frac{s_t + escape\ distance_f}{v_t}$$

186   If the fish takes less time to escape the path of the net than it takes the net to reach the final

187   position of the fish (i.e., if the net moves past the fish during the time it takes to escape), the

188   fish is recorded as caught. This is conceptually equivalent to the fish moving too slowly to move

189   out of the path of the net. The number of fish that were caught was summed for each tow and

190   recorded as a proportion:

191
$$caught_f = \begin{cases} 1 \ if\ net\ time_f - escape\ time_f < 0 \\ 0 \ if\ net\ time_f - escape\ time_f > 0 \end{cases}$$

192   Catch proportion was calculated as the simulated catch divided by the number of fish available

193   to the net (in this case, 1000 fish). Catch proportion is the response variable used in the model

194   below.

195
$$p_t = \frac{catch_t}{1000}$$

196   *2.3 Inference*

197   Using the simulated data I fit a regression model using a hierarchical model using Markov chain

198   Monte Carlo (MCMC) simulation in JAGS (Plummer 2003), through R (R Core Team 2014;

199   package R2jags, Su and Yajima 2015) to examine the relationship between Secchi depth and

200   catch proportion in the simulated data. The structure of the model was similar to a generalized

201   linear model in a traditional statistical framework, where the proportion of fish caught depends

202   on the main effects, Secchi depth and net velocity, and the interaction. To improve model

203   fitting, the explanatory variables, Secchi depth and net velocity, were standardized to have a

204   mean of zero and a standard deviation of one. An advantage of the Bayesian approach is that it

205   can include all uncertainty in the posterior distributions, allowing more realistic estimates of

206   model parameters. A truncated normal distribution and identity link were used to model the

207   relationship because visual inspection of binomial models showed an obvious lack of fit.

208   Truncating the normal distribution at 0 and 1 allowed the model to fit the linear shape of the

209   relationship between the variables, without allowing the predicted value to exceed the

210   reasonable bounds for proportions.

211
$$catch\ proportion_t \sim \begin{cases} 0 & (-\infty, 0) \\ normal(\mu_t, \tau) & [0, 1] \\ 0 & (1, \infty) \end{cases}$$

212
$$\mu_t = \alpha + \beta_1 \times secchi_t + \beta_2 \times net\ velocity_t + \beta_3 \times secchi_t \times net\ velocity_t$$

213
$$\tau = \frac{1}{\sigma^2}$$

214   Priors were chosen to be uninformative:

215
$$\alpha, \beta_i \sim normal(0.0, 0.01)$$

216
$$\sigma \sim uniform(0, 100)$$

217   **3. RESULTS**

218   The maximum Secchi depths recorded by the FMWT survey during a year increased over the

219   time series (i.e., the clearest waters became clearer, Figure 3). Mann-Kendall tests for trends

220   indicated that the central tendency of Secchi depth measurements has increased slightly over

221   the years in the complete time series for each month (Kendall's tau: Sept. 0.39, Oct. 0.35, Nov.

222   0.52, Dec. 0.42; p < 0.001). Since the invasion of the overbite clam in 1986, the slopes were

223   steeper than slopes for the whole time series, except for December (Kendall's tau: Sept. 0.59,

224   Oct. 0.54, Nov. 0.64, Dec. 0.39; p < 0.001).

225   In the simulated Delta Smelt capture data, there was a negative relationship between Secchi

226   depth and proportion of fish caught in the simulated data, with no obvious curvature (Figure 4).

227   Model diagnostic plots indicated that the model converged (Gelman plots showed that shrink

228   factors approached 1 for all model parameters) and the mean Bayesian p-value indicated that

229   the model fits the data well (p = 0.507; values near 0.5 indicate adequate fit). The intercept

230   parameter estimate represents the expected catch proportion at the mean values of Secchi

231   depth (224.3 cm) and net velocity (73.2 cm/sec) because the predictor variables were centered

232   on zero. The slope parameter for Secchi depth (beta 1) was small, but negative (Table 1), which

233   indicates that catch proportion declined at a shallow angle as Secchi depth increases. Increasing

234   water clarity was also associated with an increase in variability in the proportion of fish caught

235   (Figure 4). This increase in variability was explained by a positive interaction effect of Secchi

236   depth and tow velocity (Table 1). As tow velocity increases, the Secchi slope becomes

237   shallower. In other words, as at faster net velocities, an increase in Secchi depth had less of an

238   effect on reducing catch proportion than at lower net velocities.

239   Over the entire range of Secchi depths ever recorded in the FMWT (0, 450), the estimated catch

240   proportion for average towing speed ranges from 100% to 70% (Table 2). The distribution of

241   Secchi depths in the FMWT dataset is skewed and values over 150 are rare. For the middle 50%

242   (interquartile range) of Secchi depths measured by the FMWT, catch proportion was between

243   94 and 98% (Table 2).

244   **4. DISCUSSION**

245   This simulation demonstrates how information about fish behavior can be combined with

246   information about monitoring protocols to investigate potential sources of bias in monitoring

247   data. The basic framework can be adapted to other species and other sampling gears by

248   substituting representative values into the calculations. This can be useful for resource

249   managers who need to interpret abundance indices for decision-making purposes. This

250   approach is a method for investigating the magnitude of the effects of hypothesized sources of

251   bias where field investigations are impossible or impractical.

252   Although the water of the SFE has become clearer in recent years, this simulation demonstrates

253   that the potential for changes in water clarity to affect the catchability of Delta Smelt through a

254   visual escape mechanism are small. This suggests that the decline in relative abundance of

255   Delta Smelt can be interpreted as a decline in availability as a result of changing habitat or a

256   decline in population size. There have been no direct studies of the effect of visual stimuli on

257   Delta Smelt behavior, but similar conclusions have been drawn for other species. For example,

258   visual cues were not an important stimulus for evasion behaviors in larval striped bass, as they

259   were not more able to evade nets in clearer water than when water was more turbid, and

260   catches were similar in night- and day-time sampling (Gartz et al. 1999).

261   If water clarity influences both availability and catchability of Delta Smelt, using data from field

262   surveys to estimate the effect of water clarity on Delta Smelt catchability is problematic

263   because there appears to be a trend toward clearer water in the SFE. The simulated data in this

264   study separate the effects of catchability from availability by holding availability constant, while

265   allowing catchability to vary with water clarity in specific ways. This simulation provides insight

266   into the proportion of fish caught, given that fish are present. When Delta Smelt availability is

267   held constant, the proportion of Delta Smelt that are caught decreases with increasing Secchi

268   depth (i.e. decreased turbidity or increased water clarity); however within the typical range of

269   Secchi depth values observed in the FMWT, catch proportion is close to 100%.

270   In this simulation, the ability of Delta Smelt to escape the net is determined by the amount of

271   time a fish takes to escape relative to the amount of time it has to react to the visual stimulus

272   of the net. A result of this relationship is that the velocity of the net relative to the water

273   adjusts the effect of Secchi depth (i.e. reaction distance) on the reaction time. At small Secchi

274   depths (turbid water), there is no difference in catch proportion for different towing speeds. As

275   water becomes more clear (i.e., as Secchi depth increases), the lines for different tow speeds

276   diverge (Figure 4). From a practical standpoint, given the assumptions of this simulation, the

277   effects of clearer water can be dampened by increasing the speed at which the net is towed.

278   Increasing the tow velocity might not increase catch proportion in the field, however, because

279   increased speed can make the nets less efficient at capturing fish that encounter the net. This is

280   because towing faster could build up negative pressure inside of the net, making it more

281   difficult for the net to filter the water and for fish to be retained by the net. If the net is pulled

282   too quickly, fish may not be able to enter the net at all and may be alerted to the presence of

283   the net by detection of an acceleration front before visual contact (Clutter & Anraku 1968).

284   The simulation applies directly only to places where Delta Smelt are present because it includes

285   a fixed number of fish to potentially be caught; however, results of this simulation can inform

286   understanding of the potential for false zeros in a field dataset. The results of the present study

287   do not generally apply to adjusting catch where presence is uncertain (e.g., when zero fish are

288   caught, but environmental conditions are favorable); however, the simulation predicts that at

289   low values of Secchi depth, nearly 100% of fish that are in the path of the net will be caught.

290   This suggests that if zero fish are caught in very turbid waters, the uncertainty associated with

291   that zero catch should be smaller than previously estimated (e.g., Latour 2016). The reason for

292   the difference could be related to the differing timescale used in these studies; if the

293   probability of presence is more dynamic than is accounted for at the time scales used to

294   summarize the environmental covariates the probability of a false zero could be inflated.

295   Decreasing catchability with increasing water clarity is not the sole factor influencing increased

296   catch numbers in field data when Secchi depth is low. Although in the simulation catchability

297   decreased low turbidity conditions, in the field Delta Smelt are also less likely to be found in

298   clear water. There is evidence that turbidity is associated with higher availability of Delta Smelt

299   because at the water diversion pumps, which represent a passive sampling system, the number

300   of adult Delta Smelt observed is correlated with turbidity (Grimaldo et al. 2009). The biology of

301   Delta Smelt also supports the conclusion that availability increases with decreasing water

302   clarity. A laboratory study of juvenile Delta Smelt (Hasenbein et al. 2013) found optimal feeding

303   conditions and biological markers of stress were consistent with field surveys showing that

304   Delta Smelt prefer somewhat turbid water (NTU 10-50; Feyrer et al. 2007). Another laboratory

305   study showed that Smelt foraging ability peaks at mid-levels of turbidity (~30NTU; Horppila et

306   al. 2004).

307   In field data, wow catch at low turbidity is probably a result of behavioral phenomena that

308   reduce availability to the gear, rather than catchability. In low turbidity conditions, Delta Smelt

309   may not be available to the midwater trawl nets because they are lower in the water column,

310   below the reach of the net. The scale of the fish behavior simulation is on the level of

311   movements made by individual fish in response to local conditions and perceived threats. As

312   described by Bennet and Burau (2015) this scale of movement is distinguished from the

313   population-scale migrations that occur on the population scale in response to seasonal changes

314   in the environment. On an individual level, pelagic estuarine fishes have been known to migrate

315   vertically in the water column in response to light conditions (Bennett et al. 2002). When

316   turbidity is high, they may be near the top of the water column because the turbidity provides

317   both shelter from visual predators and provides good contrast for hunting plankton.

318   Planktivorous fish also tend to use more structured habitats to hide from predators in clear

319   water than in turbid water; prey fish tend to remain in dangerous, open water habitats when

320   turbidity is high (Abrahams and Kattenfeld 1997; Turner & Mittelbach 1990). Turbidity can

321   function as a refuge from predators, expanding the area available for foraging, which can be

322   critical for fish that need to feed continuously (Lehtiniemi et al. 2005). For Delta Smelt in the

323   SFE, this could mean that when turbidity is low fish stay in the shallower margins of the bay,

324   rather than the deep water areas where midwater trawl nets are used. On the scale of

325   migration, Delta Smelt movements have also been documented to coincide with tidal patterns,

326   moving up in the water column during flood tides and down during ebb tides in order to

327   migrate upstream, but these movements also coincided with turbidity patterns created by

328   lagged effects of shifting tidal velocities (Bennet and Burau 2015), thus turbidity seeking may

329   also serve to facilitate migration movements upstream.

330   *4.1 Evaluation of assumptions*

331   The use of Secchi depth as a proxy for the distance at which Delta Smelt visually detect the net

332   likely overestimates the visual range of small fish. Planktivorous fish of a similar size to Delta

333   Smelt (Two-spotted Goby, *Gobiusculus flavescens*) exhibited a visual range of approximately 5

334   cm in low light intensity to 30 cm in high light intensity (Aksnes & Utne 1997). Visual net

335   detection range for larval striped bass has been estimated at 2.50-200 cm (Gartz et al. 1999). If

336   escape behavior is initiated when the net comes within the distance range reported by Gartz et

337   al. (1991), the proportion of fish that are expected to be captured would be high and nearly

338   constant and more importantly in the context of this paper, it would not vary with Secchi

339   depth. The assumption that detection range is proportional to Secchi depth is probably more

340   reasonable for larger predatory fish. For example, Cod (*Gadus morhua;* 30-56 cm length) have a

341   larger visual field, up to about 20 m for high contrast objects in clear water but decreasing as

342   waters become less transparent (Anthony 1981). These studies and others (e.g., Hester 1968)

343   have shown that visual contrast, light intensity, and water clarity all play a role in the visual

344   range of fish. If the range of visibility is more like that of Cod, Secchi depth may be an

345   acceptable indicator of relative differences in visibility because it depends on light intensity as

346   well as scattering and absorption that result from suspended solids and dissolved organic

347   matter (Priesendorfer 1986). If the visual range is limited, as it is for Goby, then this study

348   underestimates the catch proportion for clearer waters, but one could replace the

349   underestimated portions of Figure 4 with a horizontal line that approximates the predicted

350   catch proportion for a Secchi depth equal to the expected visual range. In turbid waters, fish

351   can use non-visual sensory organs for detecting the oncoming net, such as lateral lines. This

352   could dampen any effects of Secchi depth on escape proportion found here.

353   The data simulated here use a simplified geometry, placing fish in a three-dimensional space to

354   represent the path of a net through the water. The placement of fish within the path of the net

355   does not consider water depth. Little research has been done on the vertical distribution of

356   Delta Smelt in the water column, but there is some evidence to suggest that youngest life

357   stages are evenly distributed throughout the water column (Rockriver 2004) and juvenile to

358   adult life stages are more surface oriented (Souza 2002, Hobbs et al. 2006, Mitchell et al. 2017).

359   Based on some of these studies, Polansky et al. (2019) estimated that life stages captured by

360   the FMWT occupied depths of 0.5m to 4.5m.

361   The FMWT is an oblique tow, meaning that the net is towed at an upward angle, from near the

362   bottom of the bay towards the surface of the water. This simulation ignores depth effects,

363   which affects the assumption that the visual contact distance for the net is equivalent to Secchi

364   depth. While this assumption is more easily true near the surface, reduced light availability at

365   depth would effectively reduce the visual contact distance to less than Secchi depth (i.e. fish

366   would see the net later, or when it is closer to them than this simulation assumes). This makes

367   estimates of encounter time an over-estimate for fish deeper in the water column, which

368   means that the catch proportion estimated here is a lower-bound on the actual catch

369   proportion of the FMWT. Future work could incorporate light attenuation and absorption

370   functions into the calculation of the reaction distance, given Secchi depth and the depth

371   occupied by the fish.

372   The uniform distribution of fish was chosen to simulate fish distribution at a fine scale.

373   Although at a bay-wide scale, small pelagic fish would presumably be clustered into schools,

374   rules that govern this simulation assume that if fish are present, the net passes through a

375   school and that the school is larger than the path of the net. This simulation also includes

376   simplified fish behavior, where fish would swim straight in response to a stimulus and that

377   swimming speed would be constant over the escape path. These assumptions might not be

378   realistic over longer escape paths. The use of critical swimming speeds as a constant swim

379   speed likely overestimates speed over the entire escape trajectory. If fish slow down after an

380   initial burst, they would take longer to escape the path of the net. This would tend to cause the

381   calculated catch proportions to be underestimates. If fish swim and take a circuitous route to

382   escape the net, the escape time calculated here would be an under-estimate of actual escape

383   times. This would result in a higher catch proportion than was calculated. In this simulation, the

384   only cue that stimulates a fish to move out of the path of the net is a visual response to the net.

385   It does not allow for interactions among fish. In reality, fish that are closer to the net probably

386   induce some degree of startle response from fish farther from the net. In terms of this

387   simulation, the encounter time would be longer than calculated here based on net velocity and

388   Secchi depth. This would reduce the proportion of fish caught relative to calculations made

389   here because fish would have longer to escape the path of the net than I calculated.

390   *4.2 Conclusion*

391   Although the effect of environmental conditions on availability and catchability of fish is

392   confounded in data from field sampling, this paper demonstrates how these parameters can be

393   decoupled using individual-based behavior simulations. For Delta Smelt, the species simulated

394   here, the simulation shows that the effect of turbidity on catchability is small when availability

395   is held constant. This suggests that influence of water clarity on reaction distance is not likely to

396   be the cause of the relationship between Secchi depth and Delta Smelt catch that has been

397   observed in monitoring data. Future work will focus on extending this simulation methodology

398   to other species of management concern and other sampling gears. It may be beneficial to

399   explore the dynamic effects of turbidity, depth, and net velocity on catch proportion, especially

400   for faster-swimming fish species.

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522

523

524   **TABLES**

525   Table 1: Parameter estimates with a 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

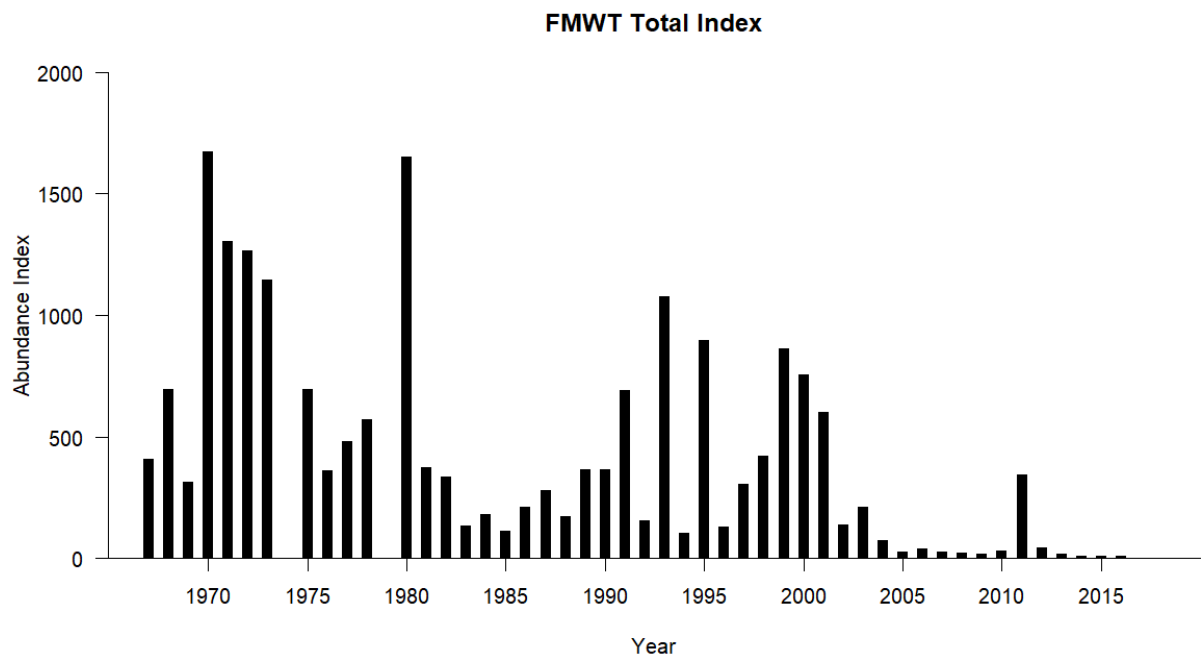
526

527   Table 2: Predicted (mean) proportion of Delta Smelt caught for summary values of Secchi depth

528   (cm) in the FMWT surveys with 95% credible intervals for average tow velocity.

		Predicted Catch Proportion		
Secchi Depth (cm)		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

529

530   **FIGURES**

531

532   Figure 1: Fall Midwater Trawl abundance index for Delta Smelt. (Data are from

533   https://www.wildlife.ca.gov/Conservation/Delta/Fall-Midwater-Trawl.)

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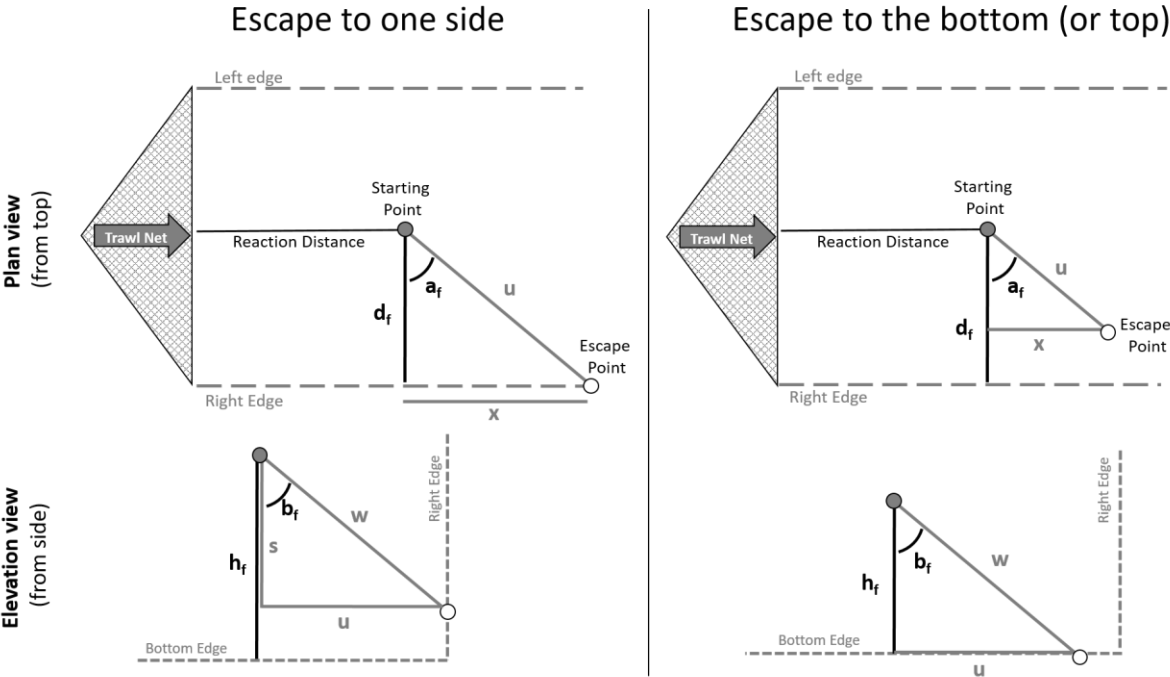
536

537   Figure 2: Conceptual diagram of simulated fish (filled circles) placement within the three-

538   dimensional path of the net and the geometry of movement to the escape point (open circlces)

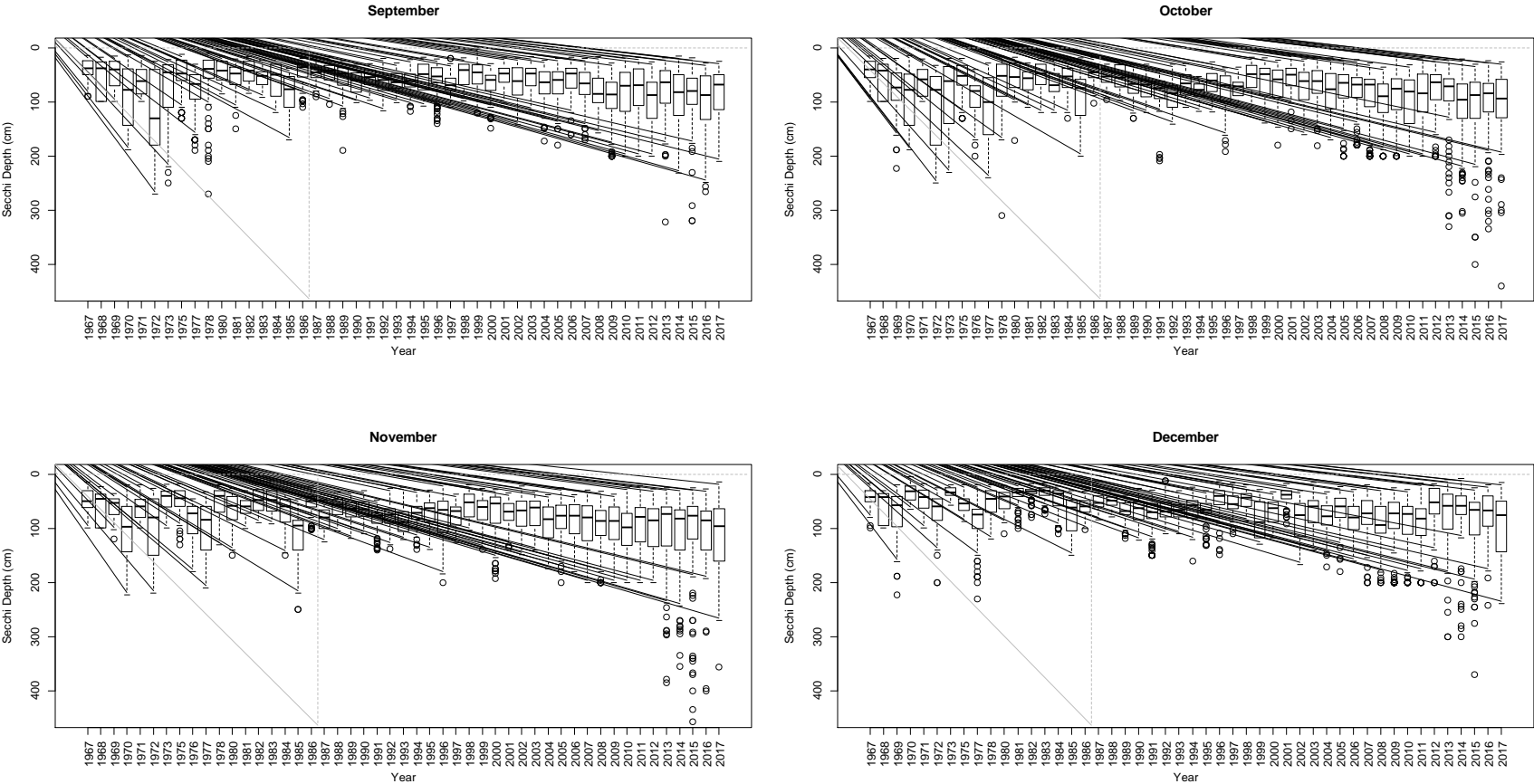
539   from an overhead perspective, looking down on the sampling event (top row) and from the side

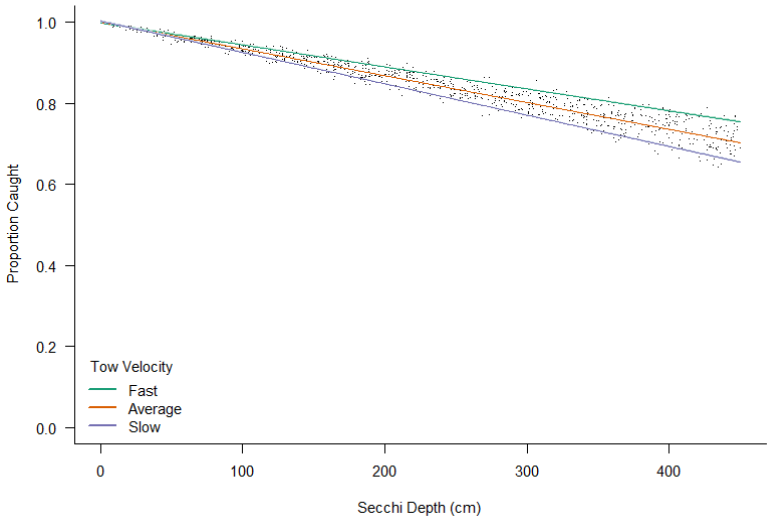
540   (bottom row). Labels in black with subscripts correspond to variables described in the text; grey

541   labels correspond to intermediate values that must be calculated to determine the escape time

542   and net time.

543

544

545   Figure 3: Boxplots of Secchi depth by month and year in (a-d) September-December. A vertical dashed line shows the summer of

546   1987, when clams invaded. The horizontal line at depth = 0 cm represents the surface of the water.

547

548   Figure 4: Predictions and 95% credible intervals of proportion of fish caught by Secchi depth

549   and fast, average, and slow tow velocities (85, 73, and 62 cm/sec, respectively). Black dots are

550   simulated data points.