DENSITY AND DISTRIBUTION OF PISCIVOROUS FISHES IN THE SACRAMENTO – SAN JOAQUIN DELTA

By

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ABSTRACT

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Christopher M. Loomis

Predatory fishes, including numerous introduced species, are common to the Sacramento – San Joaquin Delta, but abundance data for most species is insufficient to determine the Delta-wide distribution and ecological impacts of these species. Predatory fishes (e.g. Striped Bass, Largemouth Bass have long been suspected of contributing to the decline of native species, including salmonids, but data has been insufficient to investigate this hypothesis. In this study, I present a novel method to assess predator fish populations across the southern Delta using DIDSON acoustic cameras and analyze the environmental associations that form the landscape and fine-scale distribution of predatory fishes. I found that a mobile application of DIDSON acoustic cameras can be an effective method to enumerate predator fishes in a non-disruptive manner; however, factors affecting detection including environmental conditions and habitat complexity should be evaluated to refine these methods. Additionally, species differentiation of DIDSON footage would benefit from a larger library of acoustic footage of known predator fish species. I found that predator fish distributions were primarily driven by spatial and structural habitat components with little evidence of temporal trends, though high temporal variation was apparent. Landscape-scale distribution was primarily driven by channel sinuosity, variation in depth, and the number of patches of submerged aquatic vegetation (SAV) within reaches. On a fine scale, predators were generally more likely to be found near shallow, littoral habitats, submerged and emergent vegetation, and human-made structures. These results provide both guidance on how to implement a new survey method to assess the abundance of juvenile salmon predators in the Delta and insight into management actions that could affect predator populations in the Delta.

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INTRODUCTION

The Sacramento – San Joaquin Delta (hereafter referred to as the Delta) is one of the most invaded estuaries in the world and has undergone drastic changes in species composition (Cohen and Carlton 1998). Non-native predatory fish in the Delta include largemouth bass (*Micropterus salmoides*), striped bass (*Morone saxatilis*), white catfish (*Ameiurus catus*), channel catfish (*Ictalurus punctatus*), sunfishes (*Lepomis spp*.) and black crappie (*Pomoxis nigromaculatus*); however, basic population information for most of these species is lacking in the Delta (reviewed in Grossman et al. 2013, Nobriga and Feyrer 2007, UC Davis 2017). Although it has long been suspected that these non-native predators are significantly affecting the survival of salmonids and other native species of the Delta, empirical evidence linking salmonid mortality to predation is missing. A recent review of salmonid predation studies in the Delta suggests the effect of piscivorous fishes on salmonid survival is among the most poorly understood factors affecting mortality, due in part to the difficulties in quantifying its effects (reviewed in Grossman et al. 2013). Models based on current population trends, habitat conditions, and diet analyses suggest that striped bass alone could consume up to 29% of the emigrating salmonid population per year and impose a 28% chance of winter-run chinook extinction within 50 years (Lindley and Mohr 2003, Sabal et al 2015).

Recent research has investigated the effects of predators on emigrating juvenile salmon by studying relative predation rates within predator treatment reaches of the San

Joaquin River Delta (Hayes et al. 2017). This research combined acoustic surveys of predator densities with relative predation rates measured by predation event recorders (PER; Demetras et al. 2016). A PER is a free-drifting buoy which can track when and where a live tethered smolt is predated via a magnetic switch, timer, and GPS device. Hayes et al. (2017) found that PERs were effective in measuring fine scale relationships between environmental conditions and predation, but results from predator manipulation studies (i.e., translocation of predators from one reach to another) suggest that relative predation rates were not dependent on local predator abundances. However, the authors note that predator density manipulations may have been insufficient to create a detectable change in predation, and acoustic surveys may not have reflected actual predator abundances present during PER deployment due to temporal asynchrony between PER deployments and acoustic surveys (Hayes et al. 2017).

The acoustic surveys conducted by Hayes et al. (2017) used traditional hydroacoustic methods that are excellent for surveying large areas but have the disadvantage of poor target resolution. Poor resolution results in uncertainty of target size, shape, count and species, particularly near scattering boundaries (e.g. dense vegetation or benthic structures which mask other nearby objects) or in horizontal applications where aspect angle has significant influence on the reflected sound of targets (i.e. the target strength) (Ona 1999, Horne 2000, McQuinn and Winger 2003, Burwen et al 2007, Xie et al. 2007, Martignac et al 2014).

Multibeam imaging sonars, also known as acoustic cameras, such as the Dual-frequency Identification Sonar (DIDSON, Sound Metrics Corp.) have emerged as a useful fisheries tool as a complement or alternative method. DIDSON uses a wide field of view (29 degrees horizontal by 14 degrees vertical) and up to 96 fan-shaped beams to capture sharp spatial resolution. A single frame produces an image of ensonified targets and when combined with a high rate of capture (up to 21 frames per second), near video-quality footage can be recorded. This allows for visually intuitive processing where reviewers can easily distinguish fish from non-fish and observe fish movements, behavior, size, and shape (Martignac et al. 2014, Mora et al. 2015, Kane-Sutton and Gelwick 2013, Xie et al. 2007, Hateley and Gregory 2005). As with tradition hydroacoustic methods, DIDSON also allows users to survey at night or in zero-visibility water, making it a versatile tool for ecological studies of aquatic systems.

Unlike traditional acoustic surveys, DIDSON deployments are typically stationary (i.e. fixed to one position in space with only one field of view), thus, there are no fisheries survey standards for mobile applications of DIDSON (Bonar et al 2009). However, recent experimental applications of DIDSON prove its effectiveness in mobile riverine applications (Able et al. 2014, Mora et al. 2015). The DIDSON has also been shown to be both accurate and precise when compared to traditional riverine survey methods for enumerating fish given a well-aimed camera (Holmes et al 2006, Hightower et al. 2013, Tuser et al. 2014, Mora et al. 2015). Furthermore, the DIDSON has proven an effective tool for estimating abundance and distribution of fishes in estuarine systems (Becker et al. 2011, Becker and Suthers 2014).

The goal of this study was to obtain estimates of predator fish density throughout the Delta using DIDSON acoustic cameras and then build linear models to relate predator densities and predator locations to environmental covariates. Traditional survey methods to assess fish densities in a system like the Delta (e.g. trawl, seine, electroshocking) are highly invasive and too time and labor intensive to be applied over broad regions. DIDSON surveys are non-invasive and allow users to observe fish behavior in relatively undisturbed ecological settings (Xie et al. 2008, Cane-Sutton and Gelwick 2013, Becker et al. 2011, Becker and Suthers 2014, Able et al. 2014, Martignac et al. 2014, Mora et al. 2015). Understanding the relationship between predator fishes and the habitat of the Delta may help identify key management directives to reduce the effects predators have on salmonids. For instance, invasive submerged aquatic plants, which affect recreational and commercial boat access, water conveyance, and natural ecological processes in the Delta, have been linked with the proliferation of invasive predator species (Herbold and Moyle 1989, Freyer and Healey 2003, Nobriga and Feyrer 2007, Ruhstaller and Piepho 2014). Many of these plants are high priority targets of annual weed control efforts and understanding their relationship with predator species may better direct the efforts to abate plant populations. This information may also help researchers to bridge the gaps between salmonid mortality and predation and provide valuable insight into the ecological relationships at play within the Delta. A secondary objective of this research is to provide recommendations for future studies and highlight key findings that could help inform management decisions to control non-native predator populations in the Delta.

METHODS

Site Selection

To achieve a spatially balanced design within the Delta I selected study sites using generalized random tessellation stratified (GRTS) sampling **(**Brown et al. 2015**)**. GRTS sampling allows for evenly distributed sample selection across a broad region while incorporating randomization and spatially explicit probability weighting to account for areas of interest or other metrics to further refine the sampling distribution. In this study, the southern Delta, excluding the Sacramento River, was divided into eight sub-regions based on waterway type and potential route choices a salmonid might make during emigration (Buchanan et al 2013, Figure 1). The GIS shapefile representing these regions was used as the sample frame for an unequal GRTS sample, giving each region equal probability of being sampled independent of area. I randomly generated 74 candidate sites from these regions in order to provide at least 3 candidate sites for each region, which included auxiliary sites in case candidate sites did not fit the criteria for surveying. Of those sites, a subset of 21 were selected for field sampling due to constraints in time, personnel, and funding (Figure 1).

I selected three of the randomly drawn sites for repeat sampling and I visited the remaining 18 sites only a single time throughout the study. The three repeat sites, which were visited each week throughout the study duration, were located in the lower mainstem San Joaquin River (site 01), Turner Cut (site 28), and the upper mainstem San

Joaquin River (site 25). I selected these sites for repeat sampling in order to: 1) capture a broad range of habitat types, 2) continue a dataset from previous predation research efforts (site 25), 3) capture in-season changes in predator densities by re-visiting sites and, 4) address management interests in the salmonid survival of a human-constructed channel that has significant influence on flow in the Delta (Turner Cut, site 28).

I surveyed single-visit sites in the order they were drawn during GRTS selection if they met my criteria for surveying. If I rejected a site during preliminary review of candidate sites the next auxiliary site was selected and evaluated. I rejected sites based on the following criteria:

1. Proximity
    - If a site was within three river kilometers of another site, the first site generated was accepted and the second was rejected.
2. Accessibility
    - Sites were rejected where physical and/or legal barriers prevented reasonable access to a site.
3. Safety
    - Boat traffic and floating or submerged obstacles are significant hazards while working and transiting throughout the Delta. The Delta has many important commercial shipping channels and is also a popular recreational boating destination. Given that much of the surveying would require nighttime boating, I would also consider hazards of nocturnal navigation.

If these circumstances posed a significant threat to people or equipment as a result of accessing or surveying a site, the site was rejected.

- Weather and natural conditions such as flow and waves may also be hazardous to people and equipment. Sites were subject to immediate rejection if conditions became unsafe during a survey.

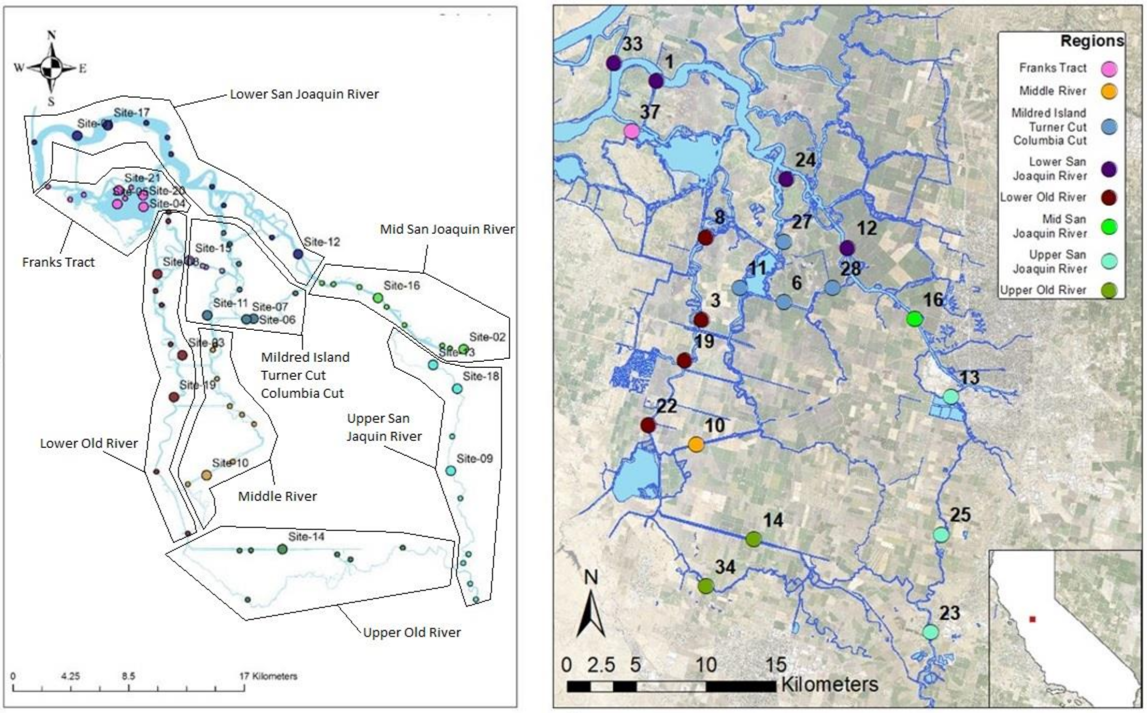


Figure 1. Left panel: Left panel: A map of the locations of the original site selection using GRTS method. Larger circles represent the first 21 main sites drawn and smaller circles represent auxiliary sites, which would have been visited in order of the draw number had a main site been rejected. Right panel: A map of the sites sampled during the field season. Regions used in the GRTS selection are indicated in the left panel and are also color coded.

At each survey site I demarcated a 1 km reach that contained the GRTS-drawn coordinates. Generally, reach endpoints were marked 500 meters upstream and downstream of the GRTS location. If the channel at a site was excessively wide (greater than 120 m) I also demarcated a survey width boundary based on what I could reasonably and safely survey given the limited survey time available, typically less than 180 m. Following the same guidelines for rejection listed above, the 1 km reach was adjusted to accommodate local conditions. For example, if the 500 meter section downstream of a GRTS point included the entrance to a busy marina, I shifted the reach boundaries upstream so that surveys would not impede boat traffic.

Materials and Setup

Two boat-mounted DIDSON units were used to survey potential salmon predators. Prior to conducting field surveys, I obtained approval of these methods to survey for vertebrate animals from the Humboldt State University Institutional Animal Care and Use Committee on 03 March 2017 (IACUC Number 16/17.F.15-A). I used adjustable pole mounts to attach the DIDSONs to opposite sides (port and starboard) of a 6 m aluminum jet boat (Figure 2). Like all acoustic equipment, DIDSONs gather information on the environment by transmitting a sound wave and processing the returning sound, much like a bat using echolocation to navigate. To avoid acoustic noise created by cross-communication between the two DIDSONs, they were aimed in opposite directions (pers. comm. Sound Metrics staff, 2017). Aiming the DIDSONs perpendicular to (and away from) the vessel, which was driven parallel to the length of the channel, allows for a broad field of view focusing on both littoral and mid-channel habitats. This orientation provided the best resolution, and the most accurate morphometric measurements, of fish swimming perpendicular to the DIDSON beam (Hateley and Gregory 2005, Hightower et al 2013, Tuser et al. 2014).

Adjustable pole mounts allowed fine-tuning of the pan, tilt, and height adjustments of the DIDSON units (Cronkite and Enzenhofer, 2005). I set the mounts to a height of 1 m below the gunnel, putting the DIDSON approximately 30 cm below the surface of the water. I set the DIDSONs range to a 10 m window length (the maximum viewing window length in high frequency mode) and started the viewing window 2.08 m from the lens to maximize the viewing range and exclude areas immediately adjacent to the survey vessel since I expected fish to avoid areas within close range of the vessel (Figure 2). To maximize correspondence with PER observations, the DIDSONs were tilted approximately 10 degrees downward from horizontal to capture the upper water column just below the water’s surface with minimal interference from the surface (Figure 2). The panning angle was kept at 90 degrees from the direction of travel.

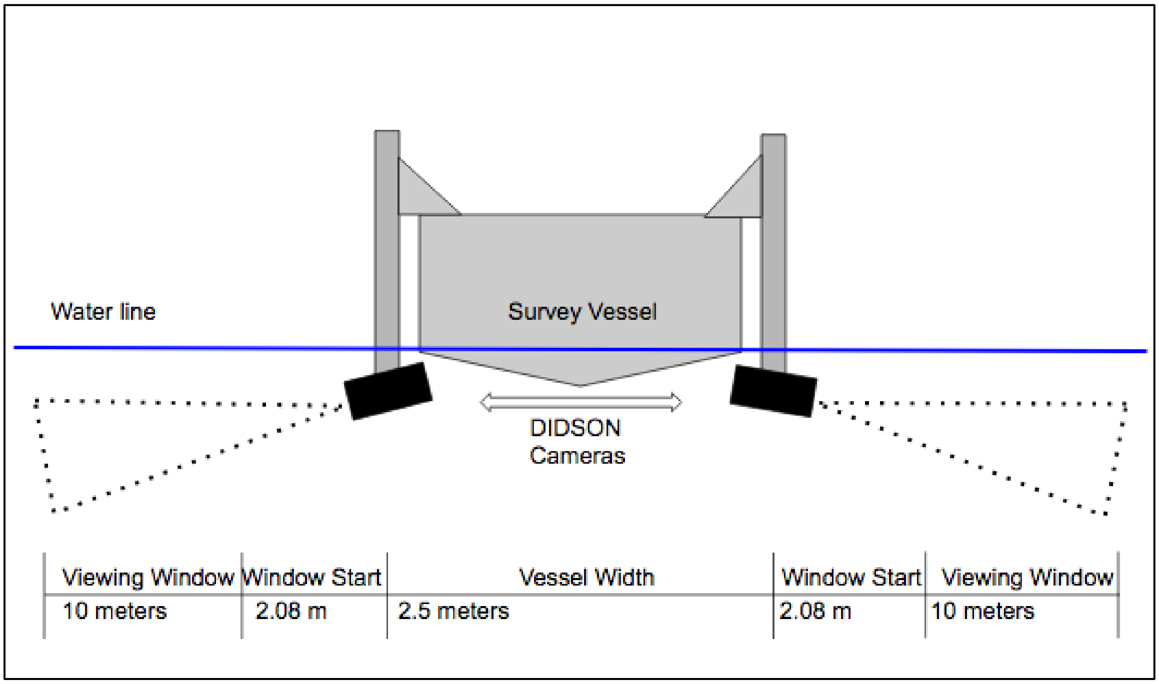


Figure 2. Survey vessel setup. Distances are not drawn to scale.

Survey Methods

Within each 1-km sample reach, I conducted DIDSON acoustic surveys along longitudinal transects. The number and extent of transects conducted was determined by the shape and width of a site in order to maximize the area surveyed and avoid overlapping transects. Given the survey vessel was 2.5 m wide and the DIDSON settings allowed for a 12.08 m viewing range (2.08 m window start + 10 m window length), the vessel had a maximum survey width of 26.66 meters (Figure 2). Transect paths were offset approximately 12 m from the shore or the edge of the survey area to ensure that the full DIDSON beam was contained within the reach. The number of independent transects conducted in a site was determined to maximize the amount of area surveyed while avoiding overlapping transects as dictated by the geometry of a site. For instance, sites that were less than 90 m wide were surveyed by two longitudinal transects parallel to the shoreline to accommodate the 26.66 m wide survey width while avoiding overlap. At sites 90 m wide or greater, additional transects were completed where they would not overlap shoreline transects. At sites with channel widths varying between 60 m and greater than 90 m along the length of the reach, additional transects would only cover the length of stream where overlap of other transects would not occur (Figure 3). Transects would be replicated as time allowed. I surveyed sites during the last two hours of daylight and the first hour after sunset when predator and prey activity are typically high (Demetras et al. 2016). This typically allowed enough time for five to six 1 km length surveys which.

During surveys, an electric trolling motor propelled the boat to avoid disturbing fish along transects (Xie et al 2008, Able et al. 2014) and fine-tune the survey speed. Surveys were completed at approximately 2 km/hr and survey speed was monitored via a Garmin global positioning system (GPS) installed on the survey vessel. This survey speed optimized video resolution and the number of transects that could be completed. At 2 km/hr under normal weather conditions, a single 1 km transect would take approximately 30 minutes to survey, allowing for approximately six 1 km transects within the three-hour survey window; however, poor survey conditions and/or technical difficulties often resulted in fewer transects.

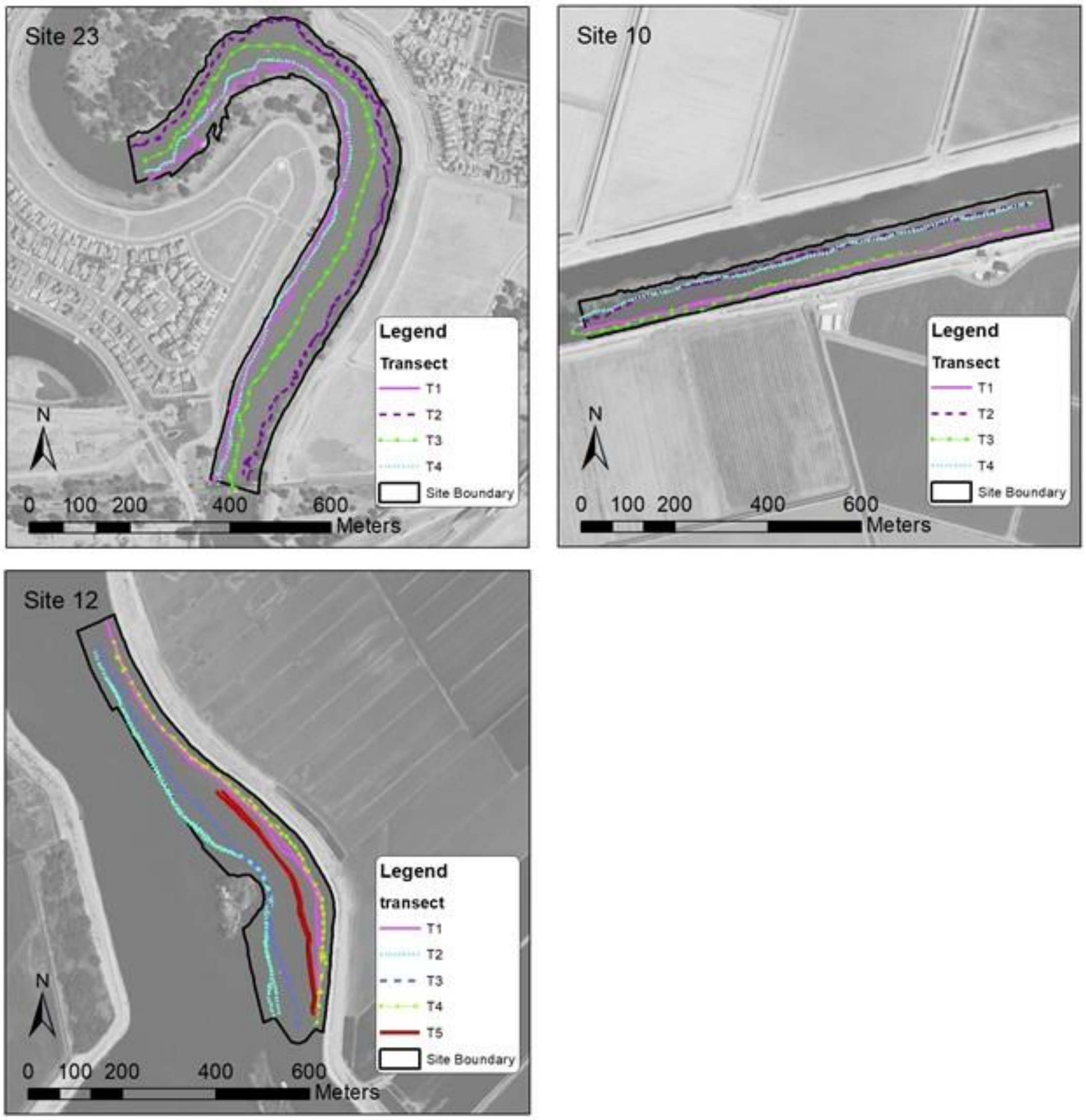


Figure 3. Survey methodology for three typical site structures. Top left panel: Survey design for site 23, a site with channel widths consistently greater than 90 m. Three independent transects were conducted and time allowed for one transect to be replicated. Top right panel: Survey design for site 10, a narrow, uniform channel 75 m wide. Two independent transects were conducted and each was replicated. Bottom left panel: Survey design for site 12, a site with variable width between 80 m and 170 m. Three independent transects were conducts, two were replicated, and one was truncated (center, T7) to avoid overlapping the other two transects in the narrower portion of the survey area.

In order to create a spatial record of the survey effort and geolocate observed fish, surveyed areas were tracked using Global Positionsing Systems (GPS). Two GlobalSat USB GPS receivers linked to each DIDSON camera recorded transect paths. Each DIDSON stored GPS positions for each acoustic frame recorded which allowed for a geolocation for every fish observed. I visually inspected survey tracks for accuracy and the distance between fixes was used to identify potential sources of error. Because seven GPS fixes were recorded for every second of a survey, distances between fixes should always be very small. When consecutive GPS fixes were greater than 10 m apart, a threshold based on the accuracy of the GPS units, I inferred that a position error was present. These types of errors were common, occurring in nearly every transect, but not in abundance (typically much less than 5% of fixes). I replaced the GPS fixes associated with those errors with new sets of coordinates that were interpolated between correct fixes on either side of the error. In the cases where more than 30 consecutive points were inaccurate, an error occurring rarely, the entire segment was replaced by the tracks of the opposite DIDSON and offset to account for the width of the survey vessel. I then used the corrected GPS coordinates to geolocate each identified fish. I used the observed range of the fish and angle of the DIDSON camera measured from the bearing of the survey vessel to project the estimated true location of the observed fish from the DIDSON’s corrected position.

Species Composition Validation

In order to collect samples of fish representative of the local predator community, the California Department of Fish and Wildlife (CDFW) conducted electrofishing surveys at the three repeat sites on two occasions, one at the beginning of the study (11-13 April) and a second near the end of the study (9-11 May). I conducted DIDSON surveys at each site the evening prior to electrofishing and the following morning immediately before electrofishing in order to obtain data that could be compared to the electrofishing surveys. This allowed us to validate the fish community assemblage, compare the catch per unit efforts (CPUE) between electrofishing and DIDSON surveys, and collect predators of known size and species to use in building a DIDSON footage reference library.

Electrofishing surveys consisted of three single pass transects moving from downstream to upstream; one pass on each respective shore (or reach boundary) and one pass up the middle of the reach. Electrofishing was conducted by the CDFW on a boat electrofisher with one boat driver and two netters. Any stunned fish visually estimated to be over 20 cm were netted, retained and processed before release at the end of the survey period.

A subset of captured fishes was retained, and ensonified with the DIDSON, to determine if acoustic data could be used for species differentiation. Research partners from UCSC and NOAA collected several fish of each species representing the range of sizes observed. Collected fishes were identified to species and measurements including fork length, body width, and body depth were recorded. Research partners then attached these fish via a jaw clip to a 1 m tether fixed to a horizontal pulley system deployed near the surface of the water. I then recorded DIDSON footage of these tethered fish for several minutes while increasing the range of the fish in 1 m increments via pulley movements with pauses for natural fish movements between pulley movements. This created reference footage of known fish at several different ranges and orientations with movements like that of a free-swimming fish.

Footage Processing

I reviewed DIDSON survey footage using Sound Metrics DIDSON software (Sound Metrics Corporation 2017). I reviewed footage manually at a rate of 1.5 - 5 times the rate of recording depending on the complexity of the imagery. When I observed a potential fish, I used playback and freeze frame functions to confirm it was a fish based on movement, profile, and image quality. If I determined the object was a fish, I then located the best frame from which to measure the fish. Ideal placement was perpendicular to the camera and within the center of the field of view to limit measurement error and bias (Hightower et al. 2013, Tuser et al. 2014). Length and thickness (the width of a fish from side to side) were both manually measured and recorded for all fish over 20 cm. Based on published diet analysis of Delta predators, I considered fish to be potential predators of salmonid smolts if they were 20 cm long or greater (Nobriga and Feyrer 2007) and I applied additional species differentiation methods after I completed footage processing. Sound Metrics software automatically records data on the position and orientation of the fish after a fish is manually located and measured.

I processed footage of tethered fish captured by electrofishing using Echoview Software because of its ability to extract target strength, the acoustic signature of a fish, from DIDSON footage (Echoview2017). Ensonified fish were first identified and delineated by an automated process. The software identifies objects (fish) based on the acoustic differences between pixels and their backgrounds and creates a layer of polygons delineating those objects. I then reviewed the processed footage for quality assurance; I visually inspected the footage and flagged individual frames in which the delineation accurately represented the true size and shape of the tethered fish. I then exported the tabular data via individual target selection to ensure background objects were excluded and only the ensonified fish's data was exported. I only used the manually flagged data for analysis.

Species Differentiation

I explored identification of individual species from DIDSON footage using discriminant function analysis (DFA) with the primary objective of eliminating non-predator species over 20 cm from the data. A DFA is a multivariate statistical analysis used to determine which variables differentiate naturally occurring groups, such as species. There are two typical methods for conducting a DFA, one differentiates groups based on linear relationships (linear discriminant analysis, LDA) while the other allows for quadratic relationships to differentiate groups (quadratic discriminant analysis, QDA).

Two species of fish common to the Delta, common carp (*Cyrinus carpio*) and Sacramento sucker (*Catostomus occidentalis occidentalis*), are non-piscivorous and can exceed 20 cm. Electrofishing studies conducted in repeat sample reaches were unable to catch Sacramento sucker, thus I assumed their abundances were negligible within the study region. Recent results from another study have suggested that distinguishing common carp from other species of Delta fish is possible with DIDSON footage using length to height ratios (pers comm. Mark Bowen). Additionally, common carp have a distinct swimbladder, which can yield a distinctive acoustic signature (Grom 2015, Hayes et al. 2017).

In systems with high species richness, no single characteristic is likely to distinguish a species, thus I tested multiple characteristics to differentiate species (Horne 2000, Abel et al. 2014). Previous acoustic studies have used body length, height, length to height ratio, orientation and target strength to identify species with varying success (Ona 1999, Horne 2000, Mueller et al. 2010, Kane-Sutton and Gelwick 2013, Martignac et al. 2014, Abel et al. 2014, Mark Bowen, ESA Biological Resources, pers. comm. 01 June 2017). I tested the effectiveness of body length, width, length to width ratio, orientation and target strength for species differentiation using DFA to distinguish the seven most prevalent predators from the electrofishing samples (largemouth bass, striped bass, redear sunfish (*Lepomis microlophus*), white catfish (*Ameiurus catus*), black crappie (*Pomoxis nigromaculatus*), brown bullhead (*Ameiurus nebulosus*), and Sacramento pikeminnow (*Ptychocheilus grandis*)) from the only abundant non-predator over 20 cm (common carp (*Cyprinus carpio*)) (Appendix C). I tested both LDA and QDA using functions in the MASS R package to predict individual species and predators (all predator species combined into one group) from non-predators (*C. carpio*) (Venables and Ripley 2002). A DFA allows a prior probability to be set for each group. For instance, the probability of discriminating a specific group can be based on the frequency that group appears in the population. With little prior knowledge of the community composition in my study region, I set all prior probabilities equal for all species tested. I created a set of candidate models by conducted backwards elimination of predictor variables beginning with both target strength and orientation as those variables require Echoview software to be extracted, a time-consuming process. Model testing and evaluation was conducted using cross validation methods; the available data was divided into a training set (75% of the data) used to create a DFA, and a testing set (the remaining 25% of the data) used to evaluate the performance of the model. I tested each model with 100 replications of randomly selected training and testing data sets and I used the mean of the resulting classification rates (i.e. the percent of fish correctly identified) to compare models.

Predator Density Estimation

To estimate reach predator density from the sample data, I first made several key assumptions. First, I considered each sample reach as a closed population during the three-hour sample period. Second, I assumed that each observed fish is only counted once within a given transect but may be counted again in subsequent transects. Third, I assumed that fish observations are spatially dependent and that transect spacing is sufficient to maintain the independence of non-overlapping transects. Fourth, I assumed that detection probability was constant and varied as a function of distance from the DIDSON cameras. Fifth, I assumed that the survey volume was constant for any given frame. Since the cameras were focused on a fixed volume of the upper water column, I simplified calculations to a two-dimensional surface.

To account for the fifth assumption, each predator observation was weighted as a function of their range from the DIDSON camera. Because the viewing area and arc length of the survey window increase proportionally with range (arc length = 2 π * radius * angle (radians)), there is more area to view fish as range from the DIDSON increases (Figure 4). Conversely, at nearer ranges there is proportionally less area to observe associated predators. Thus, observed predators will be weighted with a scalar calculated from the ratio of maximum survey window range (R_{max}) to the observed predator range (i) to account for the change in viewing area. Since the angle of the viewing window is constant it is not necessary to include in the function. The weighting scalar applied to a predator fish at the observed range (w_i) is calculated as follows:

$$w_i = e^{\left(\frac{R_{max} - R_i}{R_{max}}\right)} \qquad (1)$$

Where R_{max} is the maximum viewing range for the transect and R_i is the range of the observed range of a predator fish. As the observed range approaches the maximum range, the weight approaches 1. A predator fish observed in the near field, e.g. $R_i = 2$ meters when $R_{max} = 12$ meters, would receive a weighting of approximately 2.3. This weighting function was tested with simulations using the WiSP R package (Zucchini et al 2007); it was shown to provide accurate estimates of the true abundance and was robust to a variety of fish distributions and densities (see Survey Simulations).

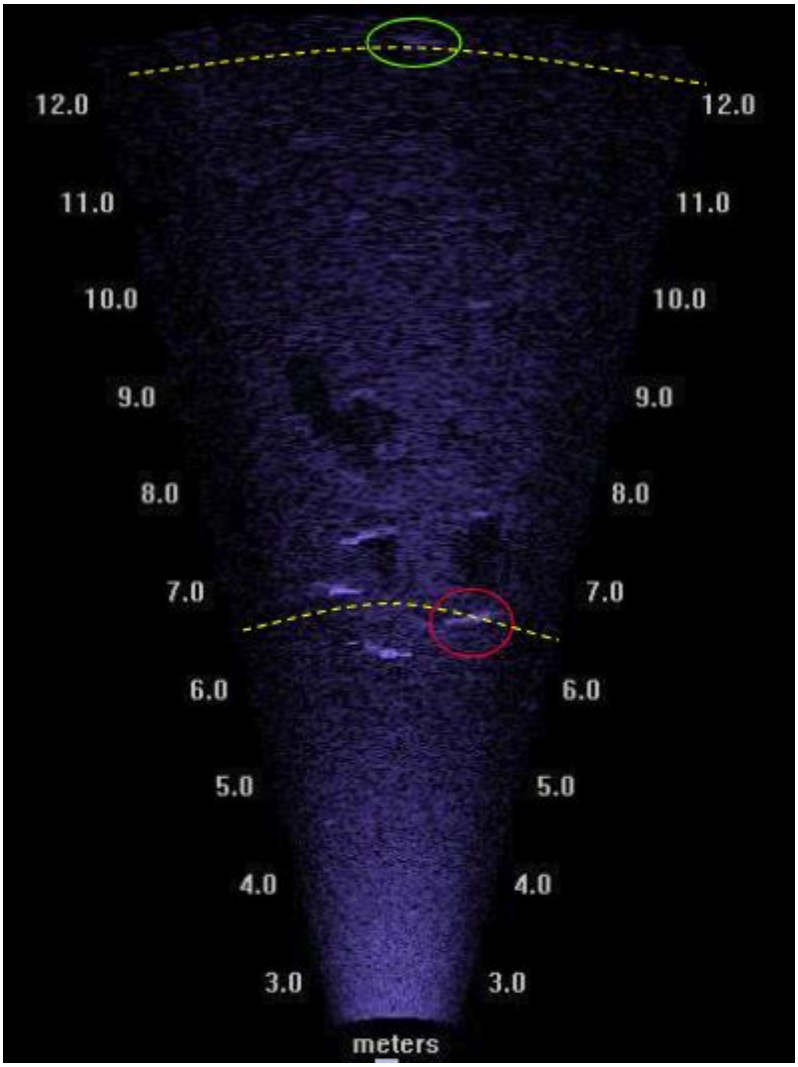


Figure 4. An example of range-based target weighting using the parameters of a DIDSON survey. The fish identified from the DIDSON footage in the red circle at 6.5 m would be given a weight proportional to the maximum range of 12 meters. In this case, the weighting value would be $e^{(5.5\text{m}/12\text{ m})}$, or ~1.6. The fish identified in the green circle at 12 m would be given a weight of $e^{(0\text{m}/12\text{ m})}$, or 1.

The density of predator fish in each reach (D_j) was calculated using independent subsets of transects (i.e. non overlapping survey efforts) with the following equation:

$$D_j = \bar{p}_j / \bar{a}_j \qquad (2)$$

where $\bar{p}_j$ is the mean of the weighted predators observed per transect and $\bar{a}_j$ is the mean area surveyed per transect. Area surveyed per transect was calculated as the sum of the product of window length and transect length for each DIDSON operated.

Because I wanted to utilize all of the available survey data to develop density estimates, I first needed to ensure that estimates were consistent throughout a survey period (i.e. densities were not significantly different if collected at the beginning of the survey period or the end). I first tested for the effect of transect order, the sequence in time in which transects were conducted, with an ANCOVA predicting the number of observed predators per square meter surveyed from the transect order while controlling for the sampling day to account for effects of both site and date. To test if any combinations of transects had significantly different density estimates, I used ANOVAs to predict the density estimates calculated using equation 2 from all possible independent combinations of two or more transects for each site. In this case, I assumed transects were independent if the surveyed areas were not overlapping along the majority of the transect. For example, for site 10 in Figure 3, transects in the following pairs would be considered independent of one another and each used to calculate a density estimate: T1 and T2, T1 and T4, T3 and T2, and T3 and T4. In this example, the transects that overlap spatially

(T1 and T3, T2 and T4) are not independent and were not included as pairs to calculate estimates of predator density. For each ANOVA, a unique identifier of each transect combination was used as the independent variable.

To calculate a final density estimate and quantify the uncertainty surrounding that estimate, I used the predator densities calculated for the ANOVA test described in the previous paragraph. For each site, the mean and variance of the distribution of density estimates was used to describe a final reach density and the uncertainty surrounding that estimate. For the example described above for site 10, the mean of the four independent pairs of transects would be reported as the final density estimate and the standard error of those four estimates would be used to report a 95% confidence interval around the mean. Only fish identified as predators using the length cutoff of 20 cm and the final species differentiation function were used in the tests and calculations described above.

Survey Simulations

I used simulated transect data to test if different fish densities, grouping patterns, exposure to the survey equipment (i.e., how visible a fish is), and physical distribution throughout the survey area resulted in any biases in the predator density estimates. The Wildlife Simulation Package in R (WiSP; Zucchini et al. 2007) allows users to generate environments and closed animal populations with a wealth of parameters to approximate the behavior of an animal population. WiSP also includes functions to simulate some of the more common wildlife survey techniques which can be customized to meet the criteria of a protocol. A key element to WiSP is the random variation it introduces into populations (positioning, grouping, and exposure) and detectability (Table 1). For instance, a population of fish can randomly be assigned range of exposure values which dictate how hidden they are to the observer. These values interact with the distance function to produce different detectability values depending on how far the animal is from the observer. WiSP allows users to test different exposures or any other sources of variation, allowing for a sensitivity analysis of density and abundance estimates under violations of assumptions.

I first created a “null” model that performed well under simple conditions and assumptions. To recreate the environment of the data collection, I generated a 60 by 1000 unit rectangular surface representing a typical 1-km sample reach from the study area. This simulated rectangular grid was used to build density gradients and construct a population. Density gradients can be set from the corners of the region; these were each set to one for a uniform distribution under the null model. Shoals of fish were created with group size controlled by a Poisson distribution with variable mean. The exposure value, or detectability of a fish, is a continuous value from 0-1 whose distribution is defined by a beta distribution. For these simulations, only the value of the mean of the distribution was altered and all other parameters controlling the shape of the distribution were held constant at 1. The mean exposure was set at the default 0.5 for the null model.

For the survey design, I chose the built-in features of the line transect function which models detections based on the principles of distance sampling; detection probability decreases as the distance from the surveyor increases. For the DIDSON acoustic surveys I assume the opposite relationship exists; the observation window area increases in size as it gets farther from the observer and thus there is a greater probability of observing fish in the far field. Since these two relationships are reciprocal and I designed the simulations to avoid any assumptions about the orientation of the observer, I assumed this would not affect the results of the simulations and I proceeded with the built-in line transect methods of WiSP. Based on the field protocol, I set up the survey as two parallel, evenly spaced longitudinal transects, each surveying an area 20 units wide. For simplicity, these transect occurred in the same location and direction for every survey. A single survey consisted of two transects. A replicate is a repeated survey over the same “reach” (i.e. same population, but the sample is redrawn between sampling events). Null model parameters are summarized in Appendix A, Appendix B, and Appendix C.

Using the above models, I ran 100 simulations of four replicate surveys over the reach while varying each parameter that controls either the population characteristics or the detection function separately. Specifically, the parameters tested included the number of groups, group size, the distance sampling detection function, mean exposure, and the distribution of fish. High and low values were chosen to reflect observations made in the field and values from literature (Hayes et al. 2017). A density was calculated using equations 1 and 2 above for each replicate and an abundance is calculated by multiplying the density estimate and the survey area. An average abundance was then calculated for consecutive replicates such that the abundance after three surveys was an average of the three replicate estimates. The parameters tested included the number of groups, group size, the distance sampling detection function, mean exposure, and the distribution of fish. High and low values were chosen to reflect observations made in the field and values from literature (Hayes et al. 2017). Estimates generated under the null model were then compared to estimates generated under an altered model to determine the methods sensitivity to each parameter.

Table 1. Parameters affecting the population and detection of animals in WiSP simulated surveys.

Parameter	Description
Group Number	The number of groups of animals (e.g. schools of fish)
Group Size	The distribution of the number of animals in each group
Distance Function	The relationship between the detectability of an animal (or group of animals) and its distance from a trackline. This function is also mediated by the exposure, aka visibility, of each animal or group.
Exposure	The distribution of exposure values for each group of animals. This value describes how cryptic or visible an animal is.
Distribution	The distribution of animals across the study area. This can define uniform distribution, gradients, hotspots, and areas with no occurrences.

Landscape-Scale Distribution Modeling

To identify the environmental factors influencing the real-world distribution of predator fish across the study region, I modeled predator density on the reach (1-km) scale to address landscape-level habitat selection using linear mixed effects regression. Because many of the environmental variables are only available as a single measure for each site, the objective of this exercise was to determine which of these site-level variables may influence predator habitat selection on a relatively large scale (~1 km). I chose a set of candidate predictor variables from the compiled data for the study region based on their hypothesized influence on predator distribution. For a detailed description of how these data were collected, see Michel et al. (2019). I included average depth, coefficient of variation of depth, flow, turbidity, conductivity (mS/cm), dissolved oxygen (mg/l), temperature (ºC) as these factors either directly affect habitat suitability, metabolism, phenology, or they affect a predator's ability to effectively forage in estuarine and riverine environments (reviewed by Čada et al. 1997, Gregory and Levings 1998, US EPA 2009, Sweka and Hartman 2003, Callihan et al. 2014). I also tested measurements of tule patches and submerged aquatic vegetation (SAV patches including total patch area (m^2) and patch density (patches/m^2)). Predators are often associated with emergent and submerged vegetation and it has been hypothesized that the spread of invasive plants, which dominate the SAV community, has contributed to the success of invasive predator species (Herbold and Moyle 1989, Freyer and Healey 2003, Nobriga and Feyrer 2007). Furthermore, there is growing concern over the effects of anthropogenic alterations such as flow diversions on the interactions of salmonids and predators (Feyrer and Healey 2003, Sabal et al. 2016). The variables representing anthropogenic alterations included in modeling were area (m^2) and count of man-made structures and length of levees along the channel (m). All area-dependent variables were first scaled by the area of their respective study site as proportions. All continuous variables were then scaled and centered by subtracting the means and dividing by the standard deviation. Predator densities were log-transformed to fit a log-normal distribution. Prior to model fitting I conducted pairwise correlations to assess collinearity and removed a single covariate from any pair with a correlation greater than 0.7.

I fit mixed effects linear models to the data and compared models with Akaike's Information Criterion corrected for small sample size (AICc). To account for the repeated measures of sites 01, 25, and 28 throughout the 6 week study period, I included a random intercept for week in all candidate models. I fit the models to the data and performed model selection on all possible subsets of four or less predictor variables, ranking models based on their respective AICc scores. I considered all models with a delta AICc score of two or less for final model selection.

The best model based on both delta AICc and cross-validation was then used to extrapolate measured predator densities within 1 km reaches across the study region. For each 1 km reach, I calculated sinuosity and coefficient of variation of depth using the same methods and data sources as for model construction (Michel et al. 2019). Because I did not have measured extents of SAV outside of the study areas I used remotely sensed SAV data collected by UC Davis (Hestir et al. 2008). Of the available SAV data, the 2015 dataset had the most extensive coverage and was thus used for extrapolation. Due to the low resolution of the survey equipment used in the 2017 environmental data collection, features less than 5 meters across their longest axis were excluded from SAV delineation (Michel et al. 2019). To maintain consistency with this methodology, the 2015 dataset was filtered to exclude SAV polygons whose longest axis was shorter than 5 m. The 2015 data also included SAV polygons occurring in water deeper than SAV is typically found. Based on recommendation from from UC Davis researchers, I clipped the 2015 polygons to exclude SAV in water deeper than 5 m (pers. comm. Shruti Khanna, UC Davis, 2019). Sinuosity and coefficient of variation of depth were then scaled by the mean and standard deviation of the data used in model construction. Because the remotely sensed SAV dataset consistently differed in the number and size of polygons delineating SAV patches within reaches, I scaled those data first by the area of each 1 km reach and then by their own mean and standard deviation. These data were then used to predict predator densities across the study region with the fixed effects of the best model.

Fine-Scale Ecological Niche Modeling

To determine habitat characteristics that predators were selecting on a 1 m scale, I predicted predator occurrence using the observed predator locations compared to the background habitat using Maxent and logistic regression (Phillips 2006, Phillips et al. 2019). Both modeling methods take presence data, in this case spatially explicit observations of predator fish, and compare those observations to background environmental conditions. The output for both models can be interpreted as the relative probability of occurrence for a predator fish at a given point. The main difference between the two methods is that Maxent is based on a machine learning algorithm based on maximum entropy while logistic regression is based on the principals of maximum likelihood. Maxent has much greater freedom and flexibility in its ability to form relationships among and within the variables while logistic regression is confined to the user-specified interactions and uses only linear terms. Because they produce similar products from very different pathways, I chose to compare and contrast both methods to see if the observed distribution was the result of more complex interactions and non-linear relationships or if it could be described in relatively simple terms. For this analysis, I used all data from the single-visit study sites and one week of data from each of the repeat sites. I objectively selected the repeat site visit based on the GRTS selection order. For example, for repeat site 25, I used the sixth visit to this site on May 8th because it was the first visit that occurred after visiting site 24 on May 5th. All predator occurrences from the 20 sites were grouped and 10,000 random points were selected from the surveyed area to represent the background habitat. Background points were selected from a target background area consisting of only the areas surveyed by each 10 m viewing window. All 10,000 background points were used in Maxent modeling and a subset of background points equal to the number of occurrence records (3,588) were used in logistic regression.

Spatially explicit habitat variables believed *a priori* to have an influence of piscivore distribution were used as predictor variables. I created raster layers of distance (1 m resolution) from habitat features including tule patches, SAV patches, and man-made structures over the extent of the study reaches. Additionally, I included distance from shore, pools (depths greater than 2 standard deviations of the mean depth), and channel bathymetry as a proxy for flow velocity as there were no available data on within-reach flow velocity distribution. I calculated distances to each habitat features using the Euclidean distance tool in ArcMap (ESRI 2017). The goal of this analysis is to address fine-scale habitat selection, therefore it is beyond the scope of this analysis to consider habitat features well beyond the boundaries of the study sites. If habitat characteristics were not present at a site or within 1 km of a site boundary, then I assigned each cell of those sites a distance equivalent to the maximum distance to that feature type observed for all occurrence records. For example, there were no patches of tules present at site 16 and the nearest tule patches were much greater than 1 km from the site boundaries. Furthermore, the river distance, i.e. the distance a fish would experience to reach that feature, would be much greater than the Euclidean distance due to the sinuosity of the channels. Thus, I assigned all 1 m cells within site 16 the maximum distance observed distance to tules for all other sites (1,867 m). Substitution of values occurred at only two sites for the pools variable (sites 16 &10) and four sites for the distance to tules variables (sites 16, 14, 23, 25). I tested all variables for collinearity prior to model fitting and excluded one variable from a pair of variables from analysis if the correlation coefficients exceeded 0.7.

I built and evaluated Maxent models using the R package ENMeval (Muscarella et al. 2014). I tested regularization multipliers ranging from 1 to 4 on models utilizing linear, product, and hinge (i.e. stepwise linear) feature classes. Regularization multipliers regulate how closely the data is fit with more constrained models resulting from larger values. Feature classes control the type and shape of response curves. The feature classes selected were believed *a priori* to form biologically relevant responses from the predictor variables. I used random k-folds cross validation using 10 evaluation bins to train and test each model. Models were then ranked by their respective AICc scores and all models with a delta AICc score of two or less were considered for final model selection.

I built mixed-effects logistic regression models using the R package lme4 (Bates et al. 2015). A random intercept based on sample site was selected to control for random site-to-site variation. Fixed effect terms included the main effects of each aforementioned habitat variable, three pairwise interaction terms to test for the interactive effects among three habitat variables (man-made structure, SAV, and tules) that provide cover, and an interaction between depth and distance to shore as a proxy for flow. I chose the habitat interactions since the selection of one cover type may depend on the availability of other types of cover. For example, a predator fish may associate with SAV unless Tules are nearby in which case it may choose to associate with Tules based on some unknown preference. I then performed AIC model selection and all models with a delta AIC score of two or less were considered equivalent to select the most parsimonious model.

RESULTS

Field Surveys

Field sampling occurred on 35 days between April 3rd and May 13th 2017 and throughout those six weeks I visited 20 unique sample sites within the south Delta (Figure 1). After I assessed the selected sites for proximity to other selected sites (using the 3 river km cutoff), 15 sites were dropped and replaced with 15 auxiliary sites. Furthermore, I dropped one site in the middle of Frank's Tract on the day of sampling due to the large wind waves that made surveying unsafe and logistically difficult. This site was replaced on the same day with a nearby oversampled site (Figure 1). One sampling day was also dropped from the schedule after a river otter broke into the live well and ate all the Chinook salmon smolts that were destined to be used for baiting PERs that evening. Due to technical difficulties with a DIDSON camera, I sampled site 22 (April 29) and site 1 (May 1) with a single DIDSON camera mounted to the port side of the survey vessel. Analysis for these sites did not differ as all calculations were based on the area surveyed and were not dependent on the number of DIDSON's in use. Over the six weeks, I recorded over 193 hours of footage from 227 unique transects which yielded a total count of 6638 fish over 20 cm after video processing.

Species Composition Validation

The two electrofishing surveys at the three repeat sites captured a large number of non-native piscivorous fish, and generally contained a large proportion of largemouth bass. CDFW conducted electrofishing at site 1 (April 11 and May 11, 2017), site 25 (April 12 and May 9, 2017), and site 28 (April 13 and May 10, 2017). A total of 624 fish over 20 cm were captured, measured and released (Appendix C). Electrofishing catch compositions were typically dominated by largemouth bass followed by striped bass and sunfishes (Figure 5). Striped bass were notably abundant at site 1 on 11 May 2017 and absent from catches on both sampling occasions at site 28. All other combined species typically composed less than 15% of the total catch. Aside from the large spike in striped bass abundance, catches appear to remain relatively stable between sampling occasions; however, with only two sampling events per site I cannot comment on the statistical significance of catch composition through time.

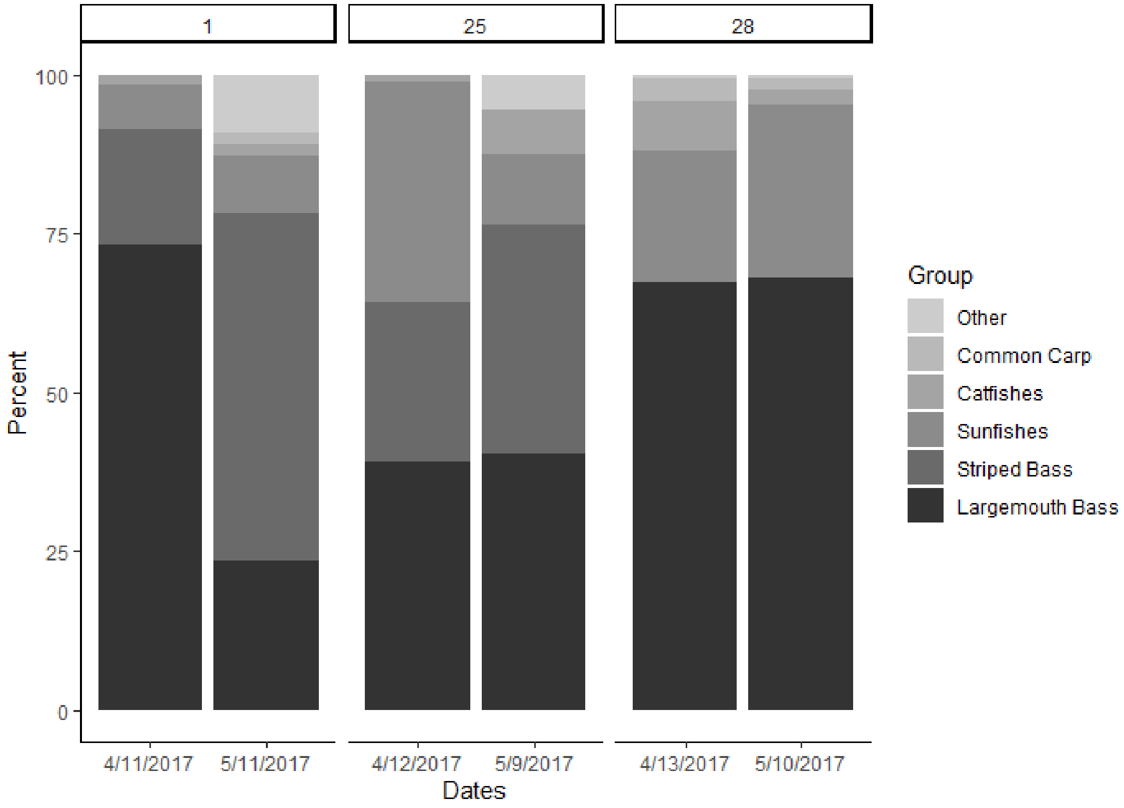


Figure 5. Species composition of electrofishing catches by site and date.

When comparing electrofishing catch data to DIDSON abundance estimates collected on the same mornings from the same transects, I found no evidence of correlation. Linear regression indicated poor correlation between electrofishing catch and DIDSON observations of fish greater than 20 cm in length (r-squared = 0.005, p = 0.888, coefficient = -0.094, se = 0.63, df = 4) (Figure 6). Electrofishing minutes were only recorded during the May sampling events, thus a comparison of catch per unit effort (CPUE) was only possible for those three events, a sample size too small to be useful for analysis. Comparison of catch data alone does not account for the inherent difference in the two methodologies and a more rigorous study would be required to accurately compare these two methods, but these finding suggest that we might reach very different conclusions about fish abundances depending on our method of choice. Because I do not rely on this correlation for any further analysis or conversions of other available data, it has no bearing on the rest of this study; however, it will be a valuable comparison to build upon if my methods are used in future studies.

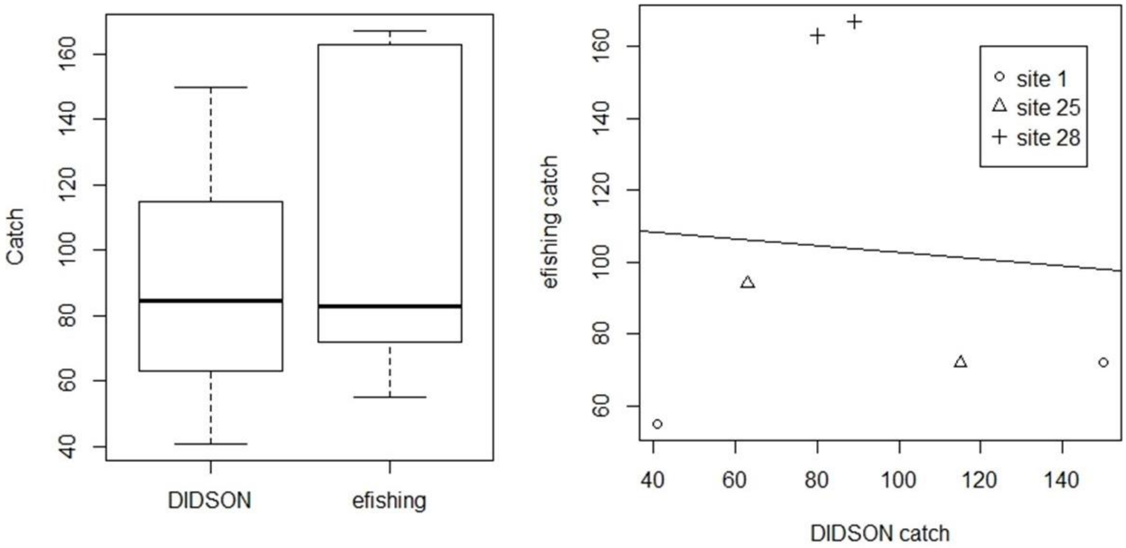


Figure 6. Electrofishing (efishing) catches and fish observed in DIDSON surveys compared in boxplots (left) and a scatterplot with linear regression (right).

Species Differentiation

I tested the accuracy of species discrimination using DFA with 2,248 acoustic measurements from 42 unique fish sampled during electrofishing efforts (Table 3).

Discriminant function analysis was effective in discerning common carp from predator species but provided poor confidence in determining individual predator species (Figure 7). Despite promising preliminary findings (Figure 8), target strength and orientation contributed negligibly to species discrimination. DFA models determining individual species using target strength, orientation, length, width, and length to width ratio had classification accuracy between 51.48% and 62.09%. Determining predator from non-predator with LDA using fish length, width, and length to width ratio resulted in the highest classification accuracy of 98.17% (Table 2). The addition of target strength and orientation improved classification by less than 0.01%. QDA performed similarly as did LDA models using only length and/or width. I chose the LDA function discerning predator from non-predator using fish length, width, and length to width ratio as the final model to distinguish the observed fish due to its accuracy, apparent differences between groups in all the morphometrics used, and previous success with similar models (pers. comm. Mark Bowen 2018). It should be noted that much of the separation achieved by these functions is likely attributed to the differences in the size distribution of the samples used with all of the carp measuring more than 50 cm and most of the predators measuring less than 50 cm in length (Table 3); however, the size distribution is representative of all the fish captured with electrofishing over the six days of sampling. The results of model testing and selection are summarized in Table 2 below. Applying the final function to the observed data resulted in 6,434 observations classified as predators and 186 classified as non-predators.

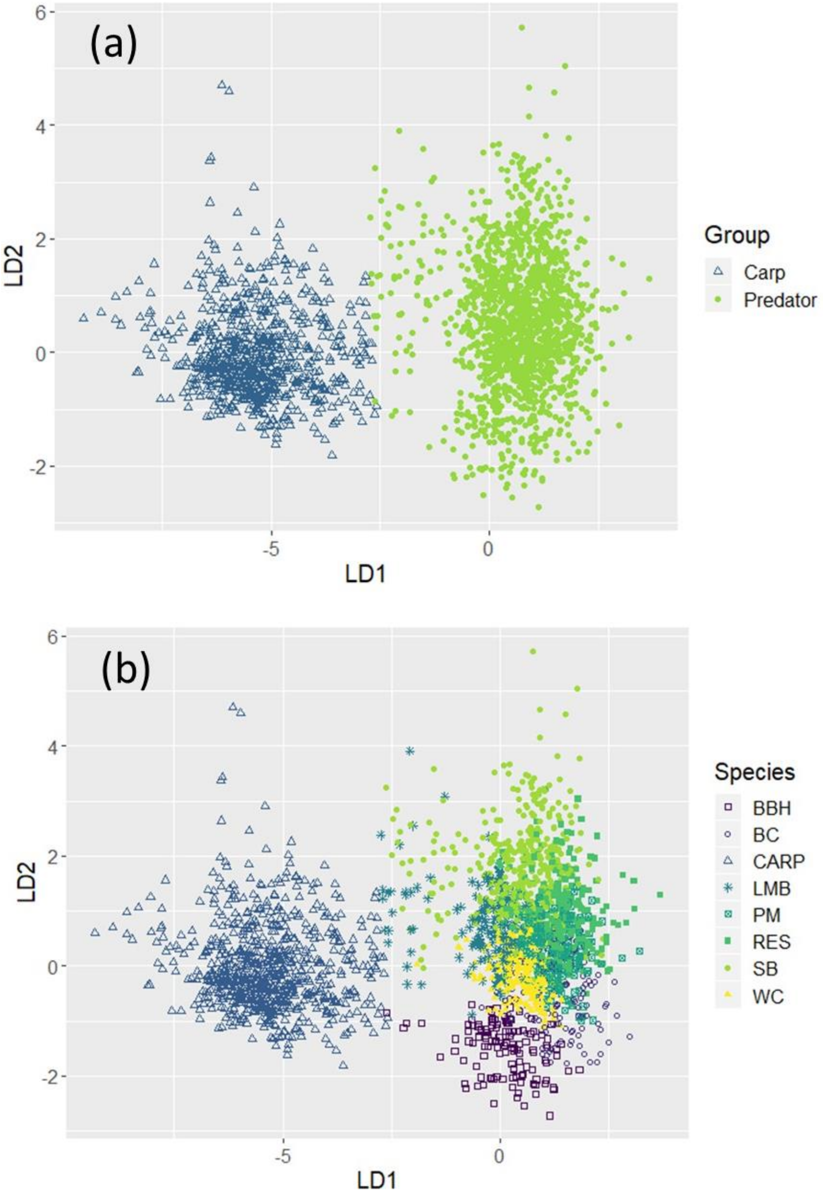


Figure 7. The grouping of fish species resulting from the first two linear discriminants (LD1 and LD2) of linear discriminant analysis using length, width, and length:width ratio to predict species. Plot (a) indicates a clear distinction between common carp (pink) and predator species (light blue). Plot (b) shows the poor separation between individual predator species including brown bullhead (BBH), black crappie (BC), largemouth bass (LMB), Sacramento pikeminnow (PM), redear sunfish (RES), striped bass (SB), and white catfish (WC). LD1 accounts for 92.97 percent of the separation achieved by the function; the separation of common carp from all predator species along the horizontal axis.

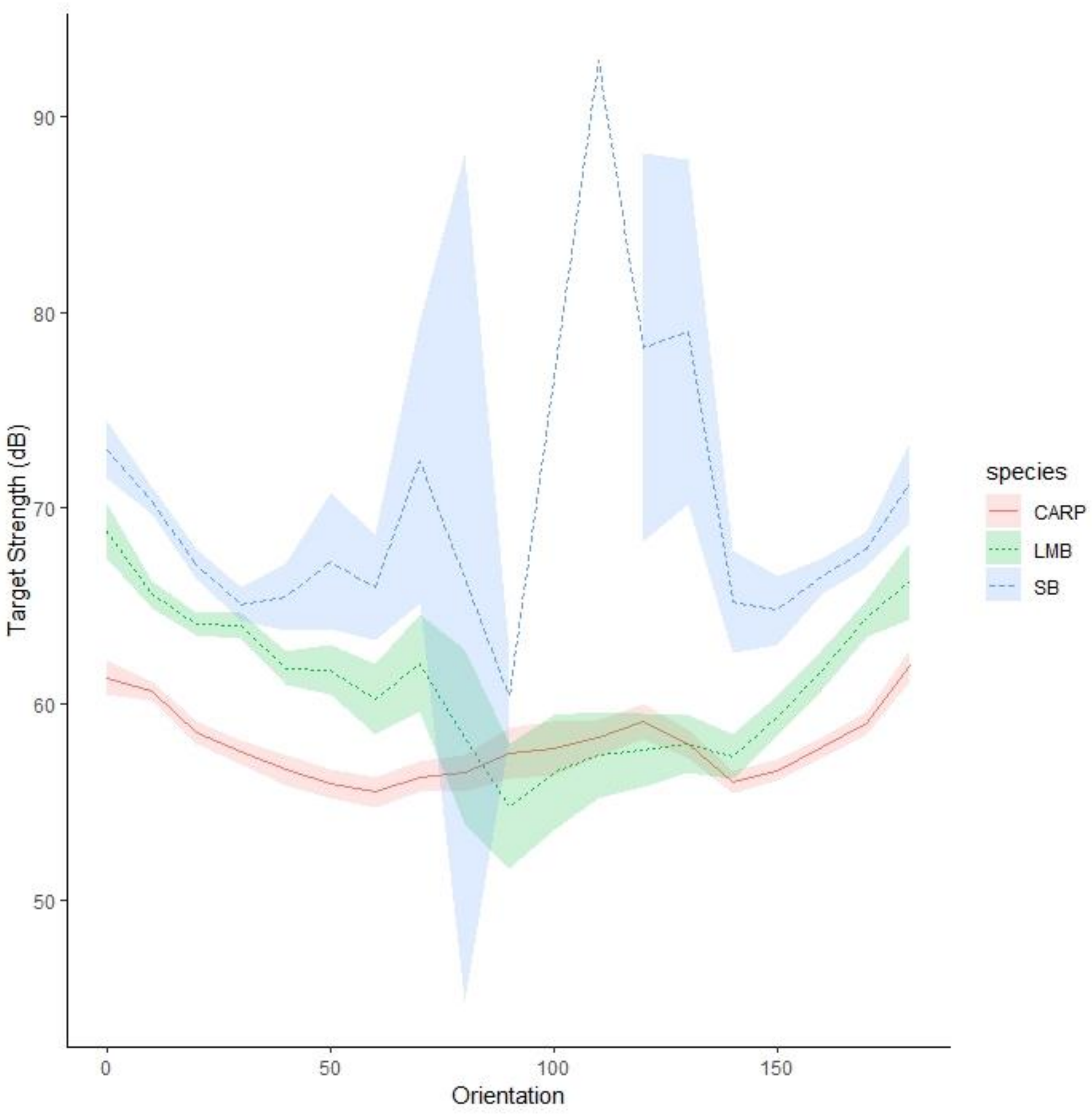


Figure 8. Target strength versus orientation for three species of fish observed in the Delta: common carp, CARP; largemouth bass, LMB; and striped bass, SB. Target Strength is the magnitude of sound reflected by the fish measured in decibels (dB). Orientation is the direction a fish is facing relative to the DIDSON camera. 95% confidence intervals are presented as shaded ribbons around each line.

Table 2. Summary of discriminant functions tested for species differentiation. Groups refers to the number of species groups being predicted; eight groups means the function is predicting the eight individual species and two groups means the function is predicted predator from non-predator. Models are ordered by their classification accuracy. Accuracy is a measure of the rate of correct classification based on k-folds cross validation.

Variables	Groups	Function	Accuracy (%)
Length + Width + L:W	**2**	**LDA**	**98.17**
TS + Orientation + Length + Width + L:W	2	LDA	98.17
TS + Orientation + Length + Width + L:W	2	QDA	98.09
Length + Width	2	LDA	98.06
Length + Width + L:W	2	QDA	97.89
Length	2	LDA	97.31
Width	2	LDA	90.20
TS + Orientation + Length + Width + L:W	8	QDA	62.09
Length + Width + L:W	8	QDA	56.33
TS + Orientation + Length + Width + L:W	8	LDA	54.33
Length + Width + L:W	8	LDA	51.48

TS, target strength; L:W, length to width ratio; LDA, linear discriminant analysis; QDA, quadratic discriminant analysis.

Table 3. Summary of fish recorded in DIDSON footage and used in Discriminant Function Analysis.

Species	Common Name	Unique Fish	Fish length Range (cm)	DIDSON Length Range (cm)	# of DIDSON Frames Used
Ameiurus nebulosus	Brown Bullhead	1	30.5	35.9-23.0	23
Pomoxis nigromaculatus	Black Crappie	1	27.0	29.6-22.6	9
Cyprinus carpio	Common Carp	8	56.0-86.0	94.5-44.2	699
Micropterus salmoides	Largemouth Bass	11	20.9-50.0	60.1-12.7	385
Ptychocheilus grandis	Sacramento Pikeminnow	3	24.5-27.7	36.8-17.9	136
Lepomis microlophus	Redear Sunfish	4	24.0-26.0	36.4-16.3	205
Morone saxatilis	Striped Bass	8	25.4-45.0	53.1-19.8	562
Ameiurus catus	White Catfish	6	21.5-35.0	44.9-15.3	229

Survey Simulations

The density estimation methods performed relatively well under most conditions but demonstrated sensitivity to changes to the distance sampling functions and exposure. In 8 out of the 11 trials, there was a 10% or less difference between the estimated abundance and the true abundance and the true mean was within the 95% confidence interval of the estimated mean (Table 4). However, in 3 of the 4 trials affecting either exposure or the distance function, estimated abundance differed from the true abundance by between 13.9% - 16.25% and the confidence intervals did not contain the true abundance after 4 replicate surveys (Table 4). These results suggest that the methods are robust to changes in abundance, grouping size, and distribution while being relatively sensitive to violations of assumed fish detectability. Because I changed parameters by varying amounts among trials (40-75% difference from null conditions), a value called “Parameter Effect” is presented in Table 4 to show the proportional effect of each parameter (note that value is not available for changes in distribution). Parameter effect values mirror the above conclusions, again confirming that the abundance estimator is typically robust to changes in the surveyed population unless assumptions of fish detectability are violated. In all trials, it is apparent that the number of survey replicates increases the accuracy of the estimates with standard error declining as each additional replicate was added. Even with only 4 replicates conducted there is evidence of an asymptotic relationship; after 3 replicates there is minimal change in the difference between the estimate and the true abundance (Figure 9).

Table 4. Summary of the simulations used to test the sensitivity of the density estimation methods. For simplicity, only the results of the fourth replicates are presented here. “Variable” refers to the parameters which controls the value listed in this column. “Percent Change” described the changes made to each respective variable relative to the null model. “Parameter Effect” is the ratio of the “Percent Difference” to the “Percent Change” in the parameter.

Variable	Percent Change	True Abundance	Change in Abundance	Mean Estimated Abundance	Standard Error	Difference (True – Est.)	Percent Difference	Parameter Effect
Null model	NA	390	0	395.93	17.8	5.93	1.52	NA
group number	-50	203	-187	223.30	15.03	20.30	10.00	-0.20
group number	50	591	201	623.20	25.14	32.20	5.44	0.10
group size	-75	146	-244	144.89	6.6	-1.10	-0.75	0.01
group size	75	629	239	635.98	27.64	6.98	1.11	0.01
distance function	-40	390	0	325.05	15.33	-64.94	-16.65	0.41
distance function	40	390	0	450.17	20.09	60.17	15.43	0.38
mean exposure	-50	381	-9	327.85	16.93	-53.14	-13.94	0.27
mean exposure	50	381	-9	416.08	20.89	35.08	9.20	0.18
distribution (west)	NA	390	0	378.54	18.79	-11.45	-2.93	NA
distribution (south)	NA	390	0	395.40	20.53	5.4	1.38	NA
distribution (thalweg)	NA	390	0	384.72	17.36	-5.27	-1.35	NA

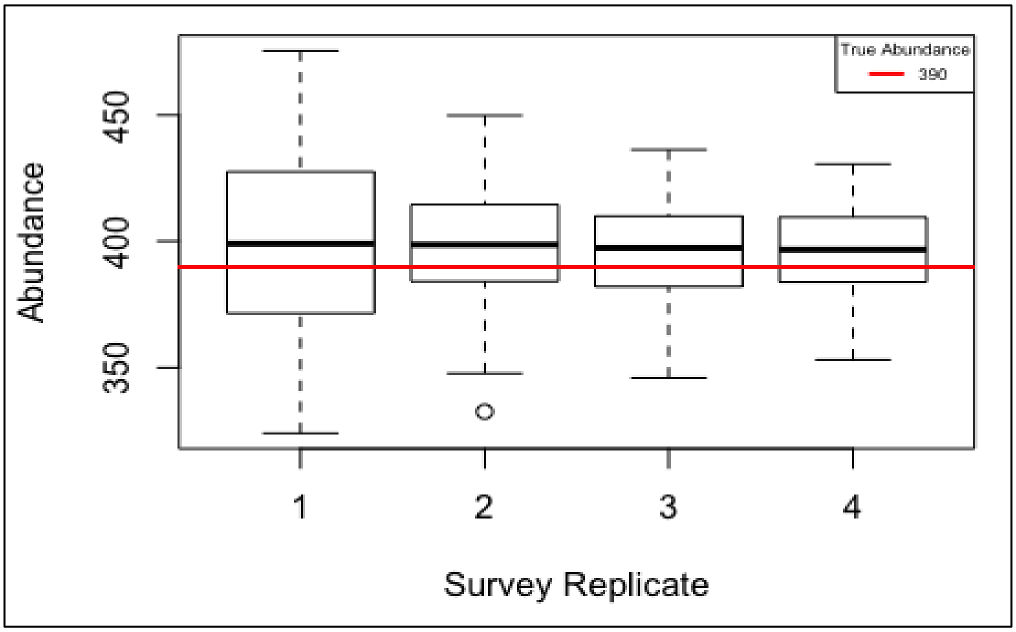


Figure 9. Box plots of abundance estimates generated by simulated repeat sampling under conditions of the null model.

Predator Density

Finding no significant effects of transect order in estimating density, I calculated reach density by bootstrapping density estimates from multiple independent transects. Analysis of covariance showed that transect order had no significant effects on the predator density estimate after controlling for site and date effects ($F_{(19,1)}$ = 0.0122, p = 0.912). Furthermore, I found no significant difference in the predator density estimates for all possible combinations of two or more independent transects using a one-way analysis of variance for each site (minimum p-value = 0.388). Predator densities were thus calculated for all surveyed sites using between 3 and 36 unique combinations of two or more independent transects depending on the number of transects which were completed. I then used the mean and variance of the resulting distributions to describe site density. Mean density estimates from the 35 sampling days ranged from 7.34 to 56.99 predators per 100 m^2 ($mean = 18.9\, predators/100\ m^2,$ $\text{standard deviation} = 10.85\ \text{predators}/100\ m^2$) (Figure 10**).** There were two sites with outlying density estimates greater than two standard deviation above the pooled mean and only a single estimate occurring below one standard deviation of the pooled mean. The highest estimated predator density occurred at site 25 on May 8th, likely the result of an immigration of striped bass to the area (Figure 5). This immigration may also be responsible for the third highest density occurring on May 2nd at site 25. The second highest density outlier occurred on the 21st of April at site 14, a constructed channel designed to allow boat travel through the region. Most of the observed predators occurred along the heavily vegetated southern shoreline of site 14. The lowest predator density estimate occurred at site 19 on April 29th, a site along Old River near the entrance to Discovery Bay, a popular marina and waterfront housing development. The only support I found for a temporal trend in density estimates was a quadratic relationship at site 25 ($R^2 = 0.90, F_{(2,3)} = 13.55, p = 0.032$) and a weak quadratic trend in overall predator density estimates throughout the sampling period ($R^2 = 0.149,\ p =\ 0.076$) (Figure 10).

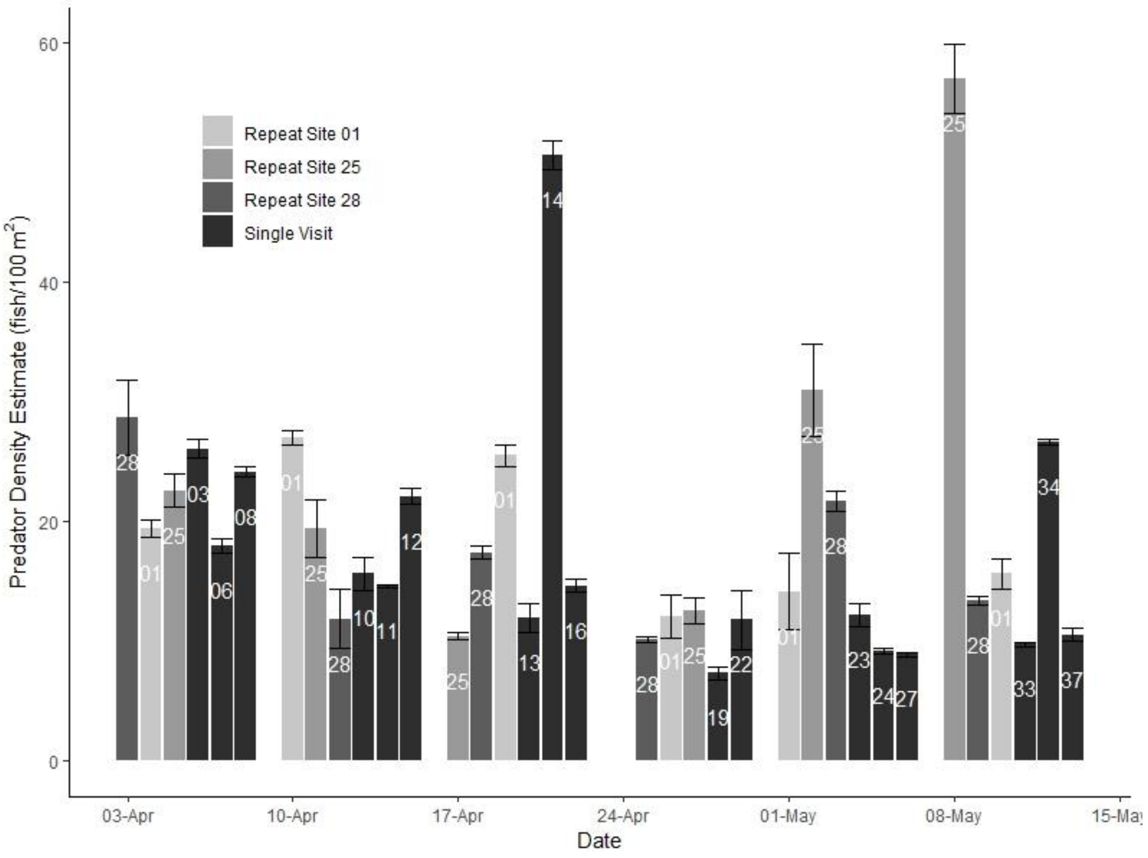


Figure 10. Predator density estimates and 95% confidence intervals for every site sampled during the 2017 field season. Repeat sites 1, 24, and 28 are each represented by a unique shade of grey while single visit sites are all labeled with their respective site number.

Landscape-Scale Distribution Modeling

I used density estimates from all of the repeat sites and 16 of the 17 single visit sites (n = 34) to construct mixed effects linear models to predict predator density from environmental variables summarized per site. I excluded one single visit site (site 12) in the initial model selection due to missing water quality data. The global model included sinuosity, total SAV area, SAV patch count, man-made structure area, total levee length, coefficient of variation of depth, total tule patch area, tule patch count, conductivity, dissolved oxygen, mean temperature, mean flow velocity, and coefficient of variation of depth as fixed effects and week as a random intercept. Model selection resulted in 1470 candidate models, five of which were within a Delta AICc of 2 (Table 5). Because none of the five top models included water quality variables, I excluded these variables from the global model and reran the model selection including data from site 12 (n=35). The model with the most support included Sinuosity (negative effect), SAV patch count (positive effect), and the coefficient of variation of depth (positive; Table 6). This model also had the most predictive power when tested using “leave one out cross validation” (Multiple R-Squared = 0.36) and was thus chosen as the final model for predicting predator density at a landscape scale. This model suggests that I could expect sites that are relatively linear, bathymetrically variable, and with many patches of SAV to have the highest densities of potential salmonid predators (Figure 11). An important distinction is that while both SAV patch count and total SAV area were included in the global model, only SAV patch count appeared in the top models indicating predators may be more likely to select habitats with a patchy distribution of SAV as opposed to large, dense mats. Extrapolation of the landscape-scale model resulted in predicted predator densities ranging from 6.81 – 329.62 predators per 100 m^2 with a mean of 20.79 predators per 100 m^2 100 m^2 (Figure 12, Figure 13, and Figure 14). Noteworthy predictions include many high density reaches along the upper mainstem San Joaquin River, including the highest predicted predator density at the head of Old River, an area of management interest (Monsen et al. 2007, Cavallo et al. 2011, Buchanan et al. 2013)

Table 5. Differences in Akaike's information criterion scores (Delta AICc), AICc weights (Weights), and the degrees of freedom (df) for the top 5 candidate landscape-scale species distribution models. Models were built using all available data from 35 sampling days.

Model	df	Delta AICc	Weight
~ CV Depth + SAV Patches + Sinuosity	6	0	0.04
~ CV Depth + SAV Patches + Sinuosity + Turbidity	7	0.89	0.03
~ CV Depth + SAV Patches + Sinuosity + Mean Depth	7	1.22	0.02
~ CV Depth + Sinuosity + Velocity	6	1.45	0.02
~ CV Depth + SAV Patches + Sinuosity + STR area	7	1.98	0.01

CV Depth, coefficient of variation of depth; SAV Patches, number of patches of submerged aquatic vegetation; STR area, area of human-made structures.

Table 6. Coefficients, standard error (SE), 95 percent confidence intervals of the most supported landscape-scale species distribution model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta. Coefficients and standard errors are based on the single model fit using all site data (n = 35).

Fixed Effects	Coefficient	SE	95% Confidence interval
Intercept	-6.391	0.065	-6.518, -6.264
Sinuosity	-0.248	0.086	-0.417, -0.079
SAV Patches	0.216	0.080	0.059, 0.373
CV Depth	0.209	0.079	0.054, 0.364

Table 7. Random effects of the most supported landscape-scale species distribution model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta. Coefficients and standard errors are based on the single model fit using all site data (n = 35).

Random Effects	Variance	SD
Week (Intercept)	0.00	0.00
Residual	0.150	0.387

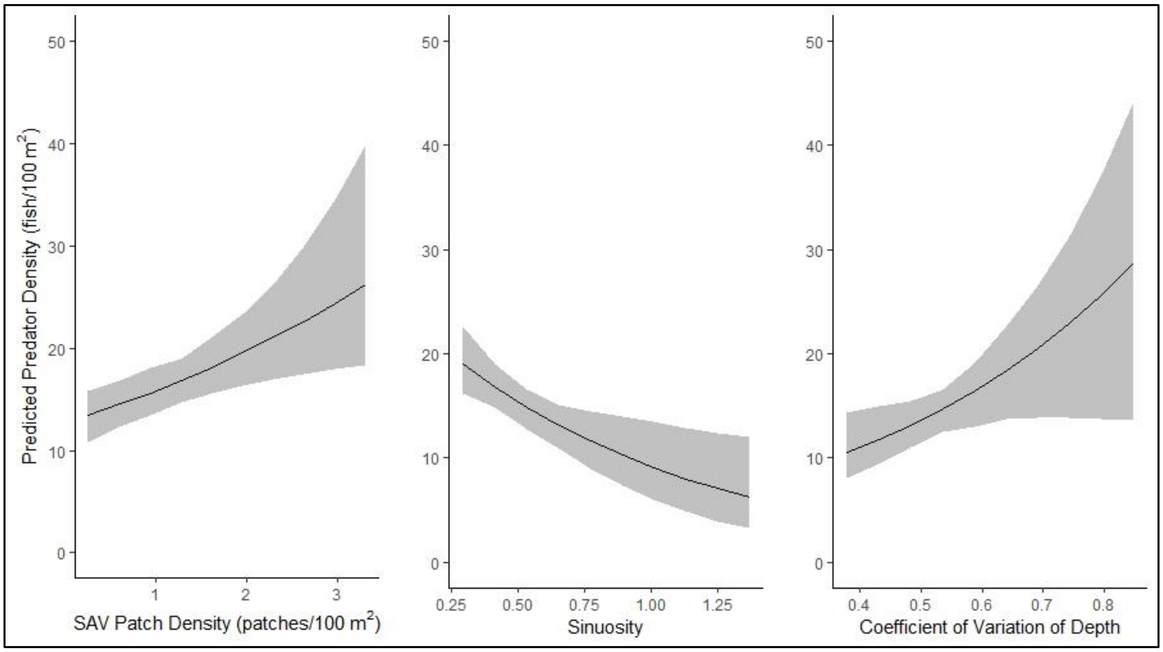


Figure 11. Response curves for the predictor variables of the most supported landscape-scale species distribution model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta. 95% confidence intervals are represented in grey around each line.

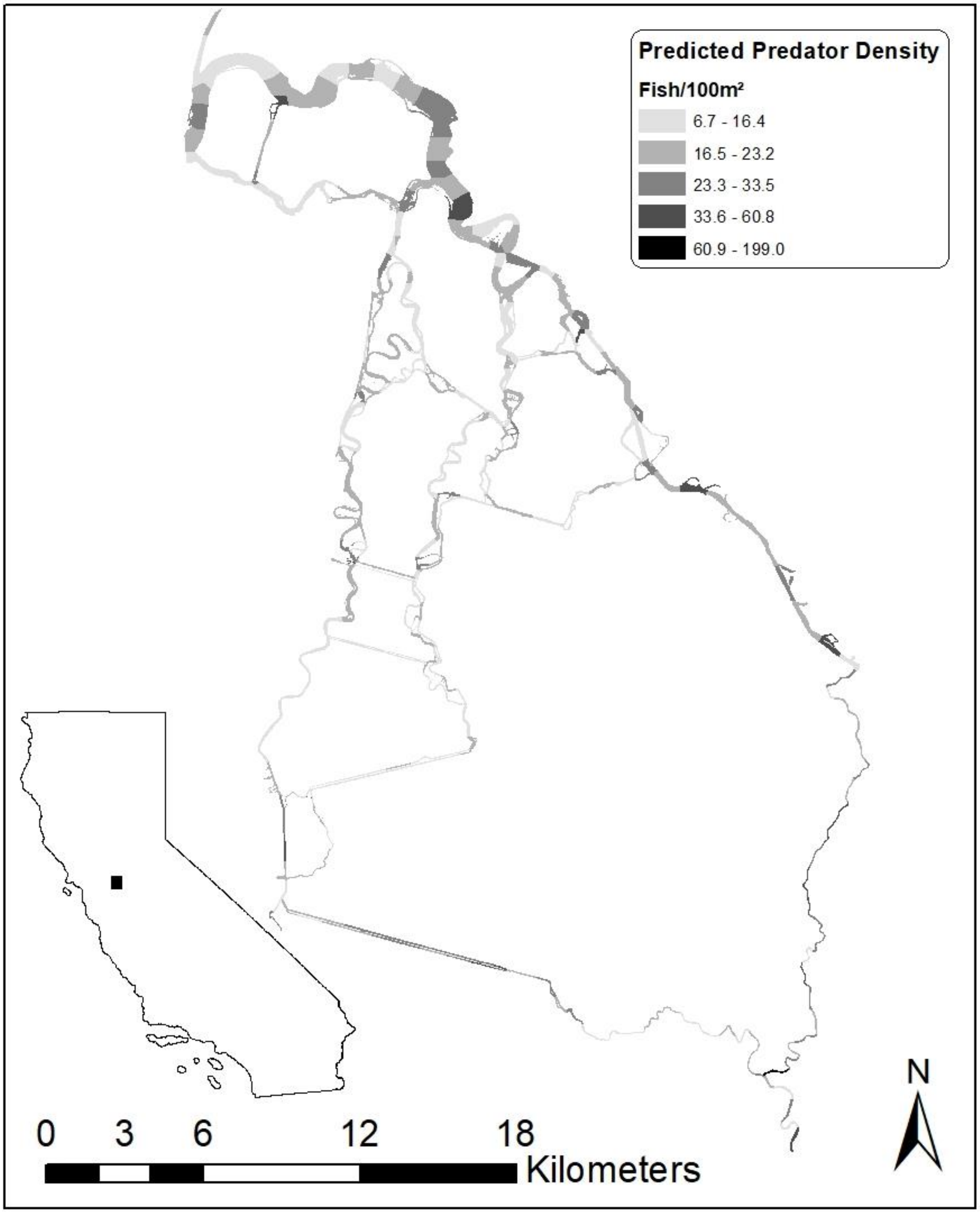


Figure 12. Predicted predator densities across the southern Sacramento - San Joaquin Delta.

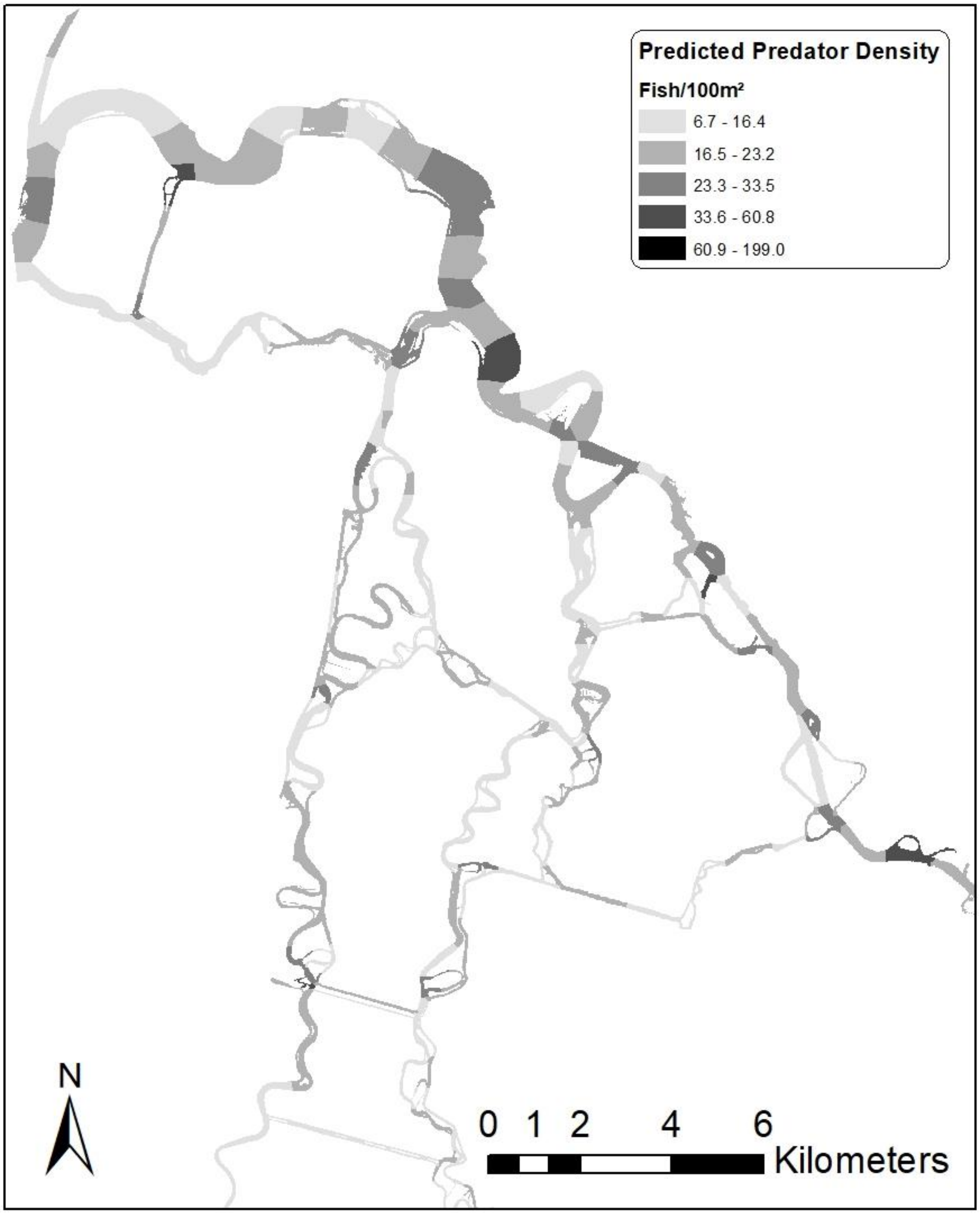


Figure 13. Predicted predator densities in the northern extent of the Delta study region.

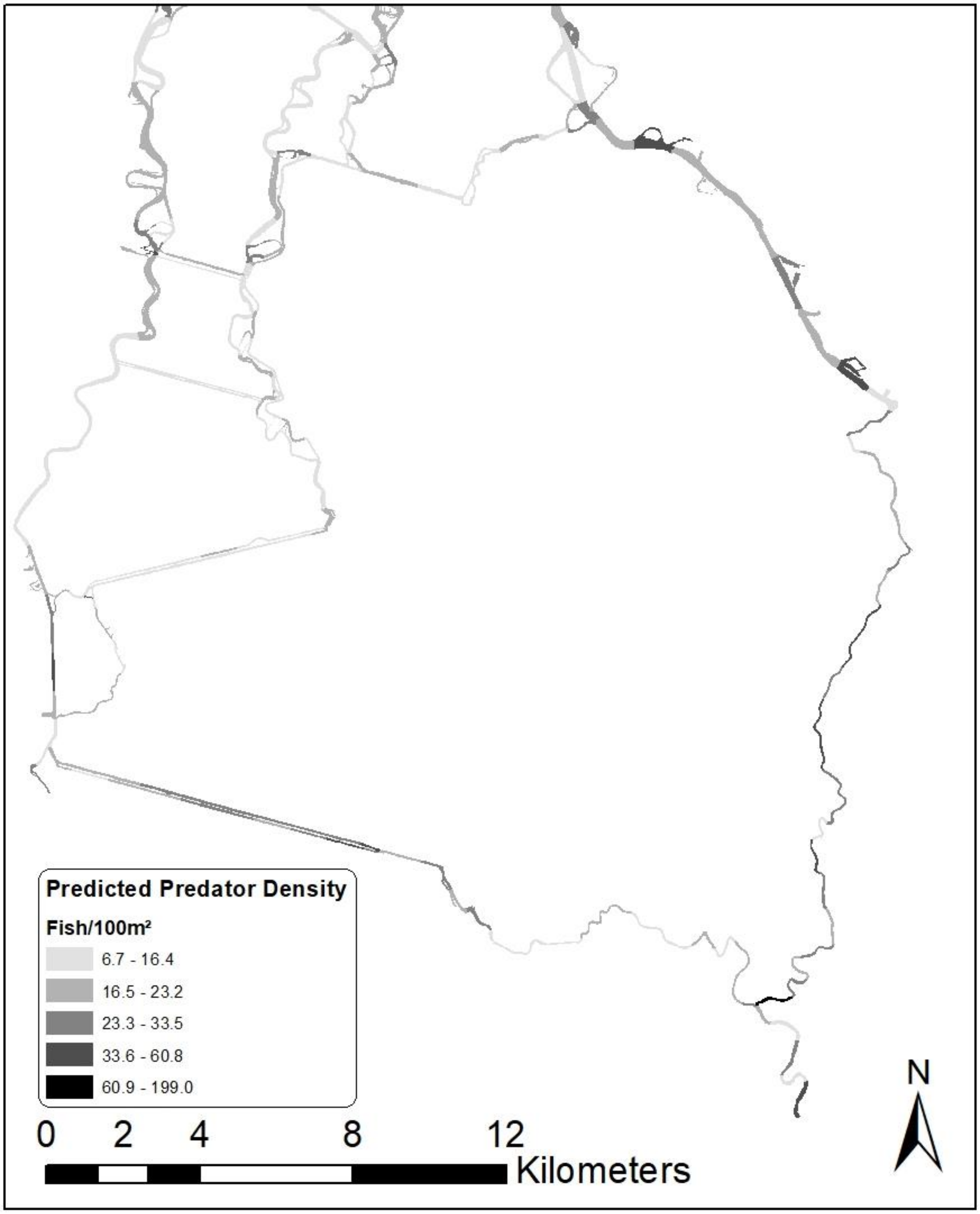


Figure 14. Predicted predator densities in the southern extent of the Delta study region.

Fine-Scale Ecological Niche Modeling

I built models predicting relative probability of occurrence using observed predator locations and background habitat conditions from 20 unique sites. I used a total of 3,448 observed predator locations and 10,000 background points drawn only from surveyed areas and locations which contained data for all variables. Model selection of Maxent models predicting relative probability of predator occurrence on a 1 m scale resulted in 12 candidate models, only one of which had a Delta AICc score less than 10. This model utilized a regularization multiplier of 1 and linear, product and hinge feature classes for all 6 predictor variables resulting in 129 parameters. This model had a mean area under the operator curve (AUC) score of 0.714 (sd = 0.053). Based on the variable metrics “Percent Contribution” and “Permutation Importance”, distance to tules was the most important variable in predicting habitat use followed closely by distance to SAV and distance to shore (Figure 15). Based on the response curves of these variables, predators are generally more likely to be found closer to these habitat features with an approximately exponential decrease in relative suitability with increasing distance (Figure 16). This same response was also evident in depth while distance to structure and pools exhibited somewhat quadratic responses. This is likely a spurious result of correlation with other variables or the bimodal distribution of values resulting from the substitution of maximum observed distance for sites that did not have the variable present. Furthermore, the distance to pools variable contributed negligibly to the model and the linear term for this variable was eliminated by the Maxent algorithm. The sharp hinge near the maximum or minimum observed distances in the response curve of distance to tules is likely due to the same bimodal distribution resulting from occurrence records for four sites having equal distance to tules values (1867 m). While this is a somewhat spurious result (e.g. there is no biological reason to suspect that 1867 m is the ideal distance from tules for Delta predators), it does highlight the observation that while many predators select habitats closely associated with tules, many are also selecting habitats that have no mapped tules within at least one km of the location they were observed in. The mean relatively probability of occurrence predicted for each site had strong correlation with the estimated predator densities (r-squared = 0.63, $p < 0.0001$).

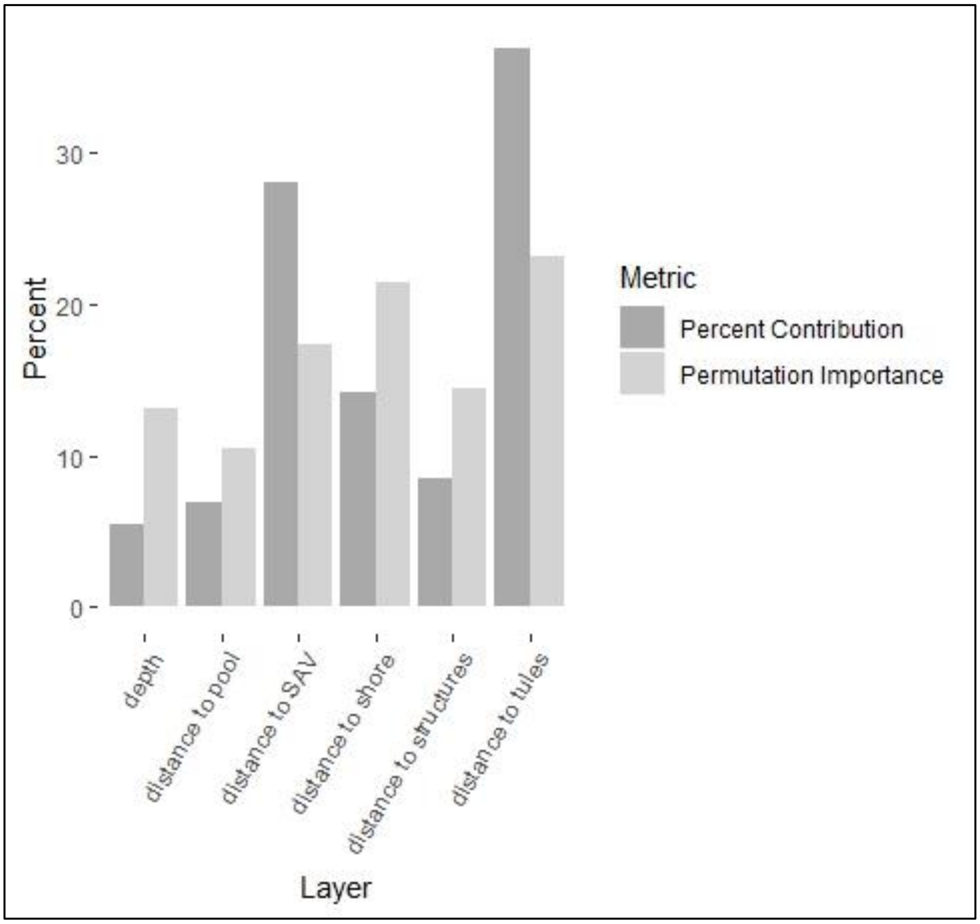
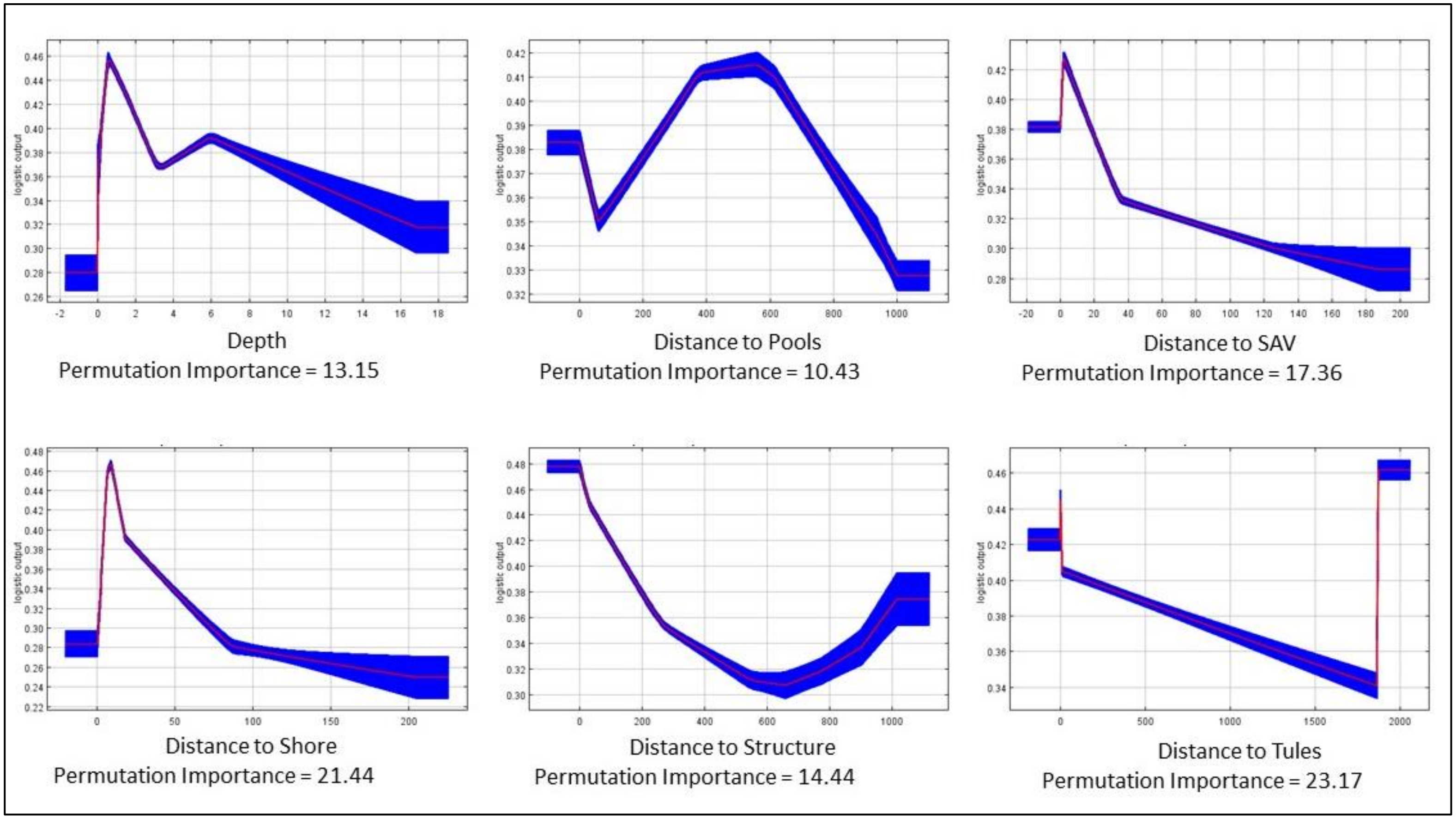


Figure 15. Variable metrics for the most supported Maxent model predicting predator occurrence from habitat characteristics. Percent contribution is a measure of the additive regularized gain from each iteration of the training algorithm. Permutation importance results from the drop in training AUC scores due to randomizing a predictor variable. Values shown are averages over replicate runs.



Depth
Permutation Importance = 13.15

Distance to Pools
Permutation Importance = 10.43

Distance to SAV
Permutation Importance = 17.36

Distance to Shore
Permutation Importance = 21.44

Distance to Structure
Permutation Importance = 14.44

Distance to Tules
Permutation Importance = 23.17

Figure 16. Response curves for the predictor variables contributing to the Maxent ecological niche model predicting relative probability of occurrence of piscivorous fishes in the Sacramento - San Joaquin Delta. The curves depict the mean response from 100 replicate model runs (red) +/- one standard deviation (blue) on a probability scale from zero to one. Distance and depth units across all x-axes are in meters.

Model selection of mixed-effects logistic regression models predicting probability of predator occurrence on a one m scale resulted in 180 candidate models, six of which had a Delta AIC score less than 2 (Table 8). Of the top six models, the most parsimonious model, which included terms for depth, distance to SAV, distance to shore, distance to structure, distance to tules, an interaction term for distance to SAV by distance to tules, and an interaction term for distance to structures by distance to tules, was selected as the best model (Table 9). The best model had an AUC score of 0.72. Based on the response curves of Distance to Shore and Depth predatory fishes are more likely to select habitats closer to shore in shallower water (Figure 17). The main effects of the variables Distance to SAV and Distance to Structures depend on the variable Distance to Tule (Figure 18, Figure 19). At locations that are near tules, the distance to structures has little effect on the probability of occurrence. As the distance from tules increases, the distance to structures has a much more pronounced effect on the probability of occurrence; predators are much more likely to be found nearer to structures in the absence of tules. Conversely, the interaction term between distance to tules and distance to SAV has a fairly weak effect. Predators are most likely to occur at locations near SAV and far from tules. At locations where SAV patches are distant there is little effect of the distance to tules with roughly 50 percent probability of occurrence across the range of observed distances to tules.

Table 8. Differences in Aikaike's information criterion scores (Delta AIC), AIC weights (AIC wght), and the degrees of freedom (df) for the top 5 candidate landscape-scale species distribution models based on logistic regression. The model which was selected as the best model by the principle of parsimony is bolded.

Model	df	Delta AIC	AIC wght
~(Depth * Shore) + (SAV * Tule) + (STR*Tule)	10	0	0.17
~ Depth + Shore + (SAV * Tule) + (STR*Tule)	**9**	**0.11**	**0.16**
~Pool + (Depth * Shore) + (SAV * Tule) + (STR*Tule)	11	0.51	0.13
~Pool + Depth + Shore + (SAV * Tule) + (STR*Tule)	10	0.56	0.13
~(Depth * Shore) + (SAV * Tule) + (STR*Tule) + (SAV * STR)	11	1.53	0.08
~Depth + Shore + (SAV * Tule) + (STR*Tule) + (SAV * STR)	10	1.61	0.08

Shore, distance to shore; SAV, distance to SAV; Tule, distance to tules; STR, distance to structures; Pool, distance to pools.

Table 9. Coefficients, standard error (SE), 95 percent confidence intervals, and random effects of the most supported and most parsimonious fine-scale species logistic regression ecological niche model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta.

Fixed Effects	Coefficient	SE	95% Confidence Interval
(Intercept)	-0.351	0.096	-0.539, -0.163
Distance to Structure	-0.344	0.052	-0.446, -0.242
Distance to Tules	-0.088	0.088	-0.261, 0.084
Distance to SAV	-0.222	0.058	-0.336, -0.109
Distance to Shore	-0.258	0.052	-0.360, -0.156
Depth	-0.171	0.045	-0.083, -0.260
STR:Tule	-0.372	0.068	-0.504, -0.239
Tule:SAV	-0.106	0.043	-0.191, -0.022

Table 10. Random effects of the most supported and most parsimonious fine-scale species logistic regression ecological niche model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta.

Random Effects	Variance	SD
Site (intercept)	0.153	0.391

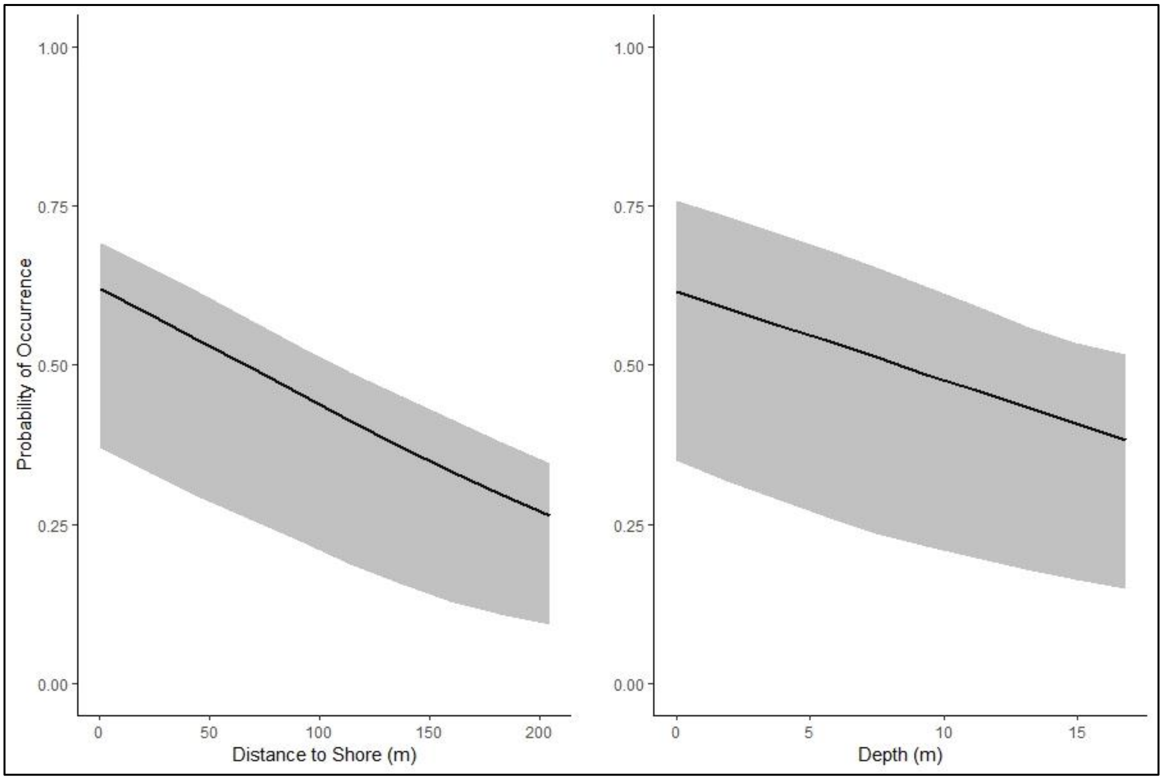


Figure 17. Response curves for the main effects of predictor variables Distance to Shore and Depth of the most supported fine-scale logistic regression model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta. Each panel depicts the response curve of each respective variable (black) with 95 percent confidence intervals (grey) while all other variables are held at their mean value.

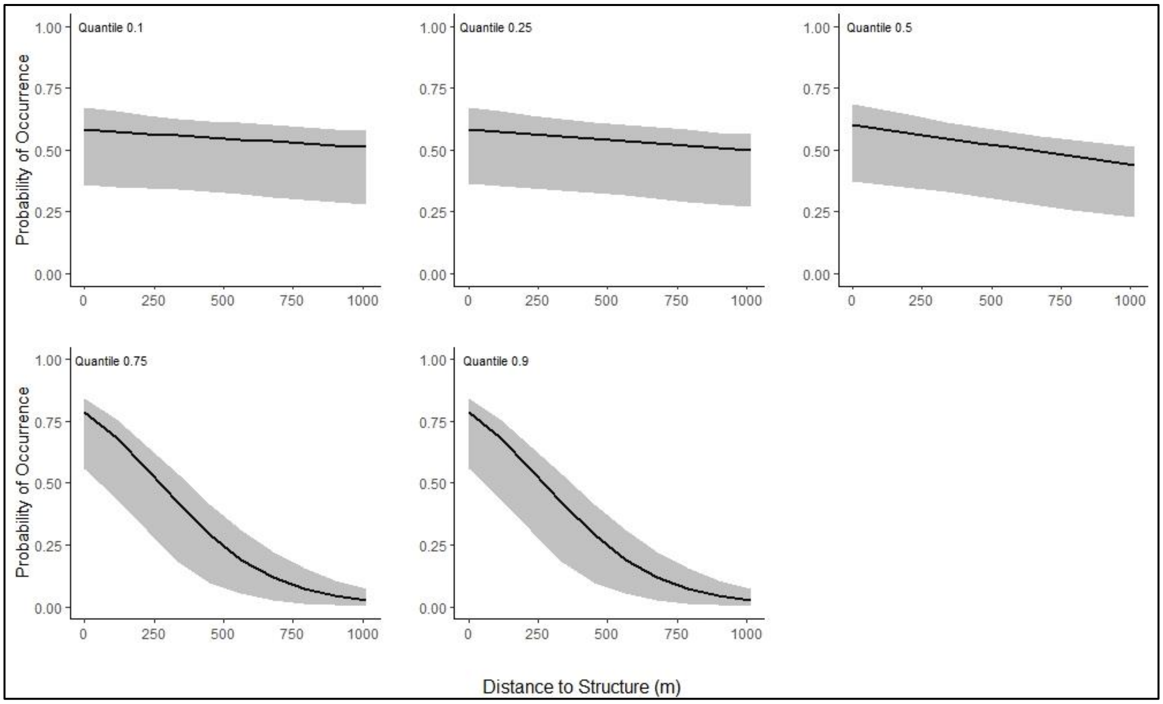


Figure 18. Response curves for the interaction between predictor variables Distance to Structure and Distance to Tules from the most supported fine-scale logistic regression model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta. Each panel depicts the response curve of Distance to Structure at different quantiles of the variable Distance to Tules (black) with 95 percent confidence intervals (grey) while all other variables are held at their mean value.

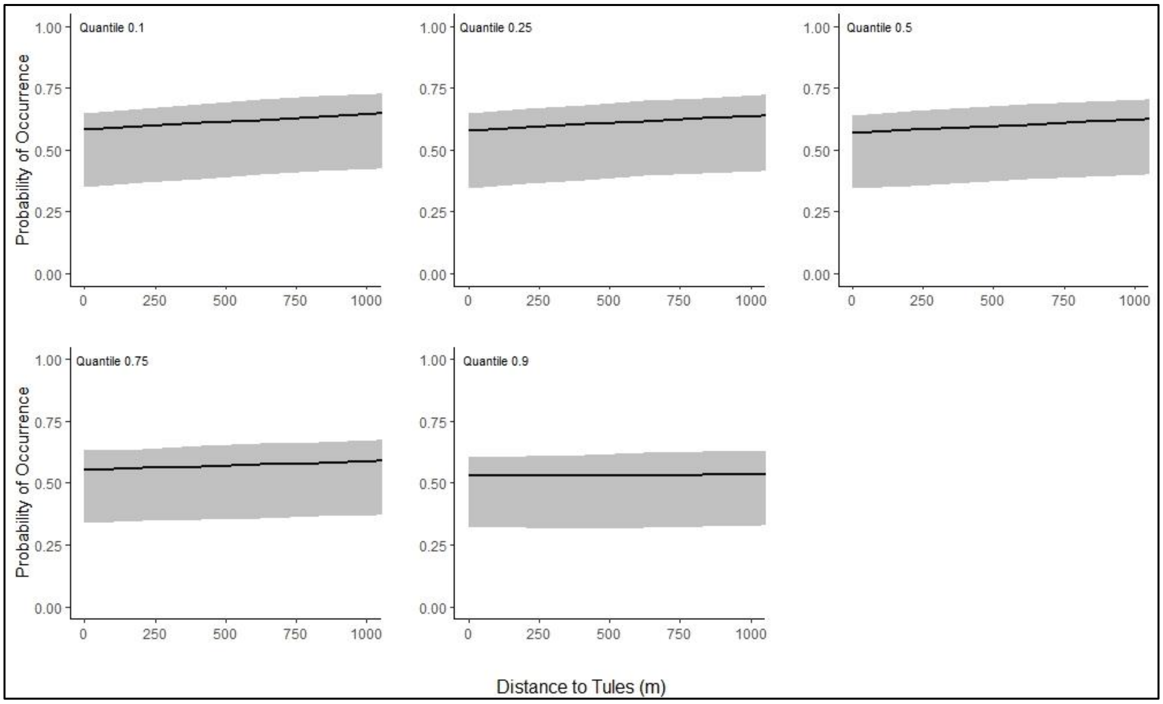


Figure 19. Response curves for the interaction between predictor variables Distance to Submerged Aquatic Vegetation and Distance to Tules from the most supported fine-scale logistic regression model of habitat selection by piscivorous fish in the Sacramento - San Joaquin Delta.

Logistic regression and Maxent modeling had similar predictions for the probability of predator occurrence in areas throughout the different surveyed reaches. Predictive power of both models is only moderate on a 1 m scale; however, both models are able to capture large-scale trends. The mean relative probability of occurrence predicted by both logistic regression and Maxent had strong correlation with the estimated predator density for each site surveyed (logistic regression prediction~ density estimate: $R^2 = 0.69, p = 5.83 * 10^{-6}$; Maxent prediction ~ density estimate: $R^2 = 0.63, p = 2.78 * 10^{-5}$) (Figure 20). Furthermore, qualitative comparison of predator occurrence predicted across each study area indicated that both models tended to agree on the relative suitability of habitat patches within sites (Figure 21).

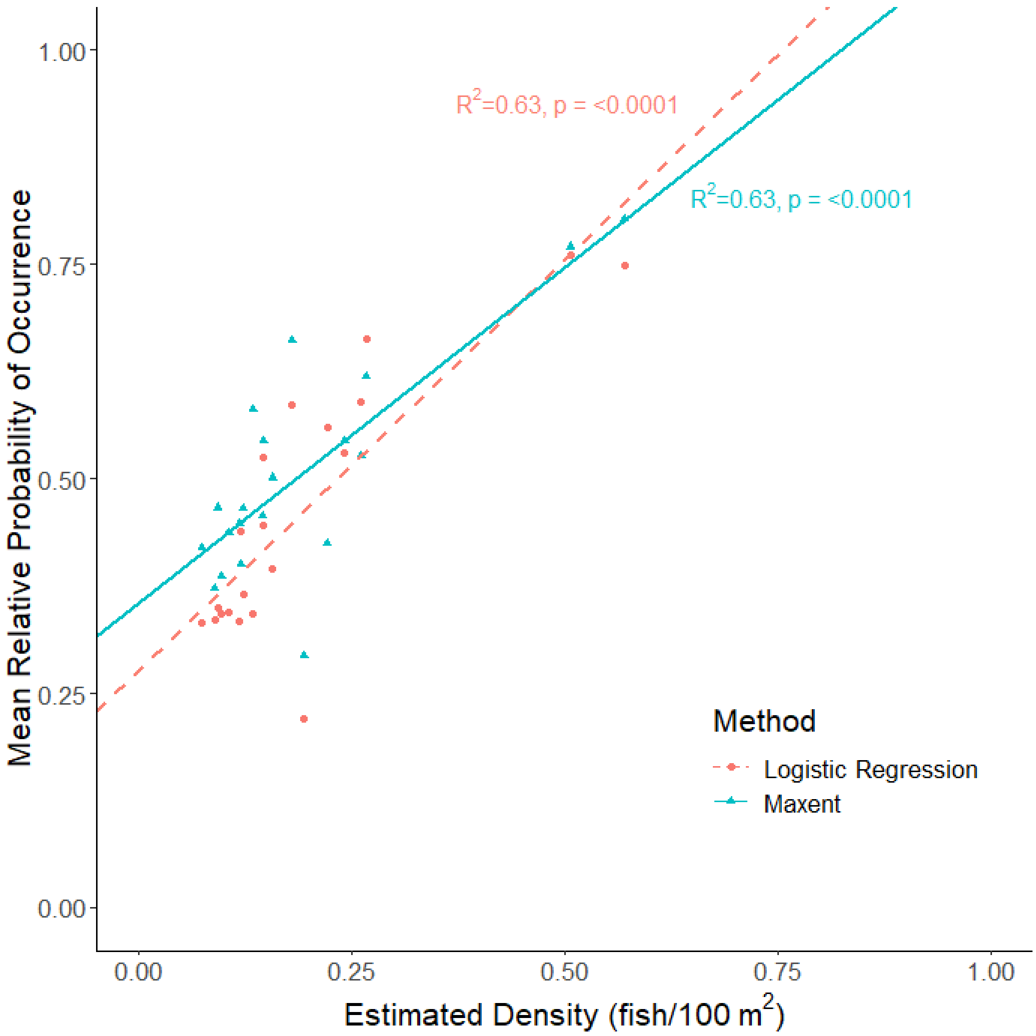


Figure 20. Comparison of mean relative probability of occurrence predicted from logistic regression and Maxent ecological niche models to estimates of predator densities derived from field surveys. Regression lines relate each model's predicted mean site suitability to estimated predator densities.

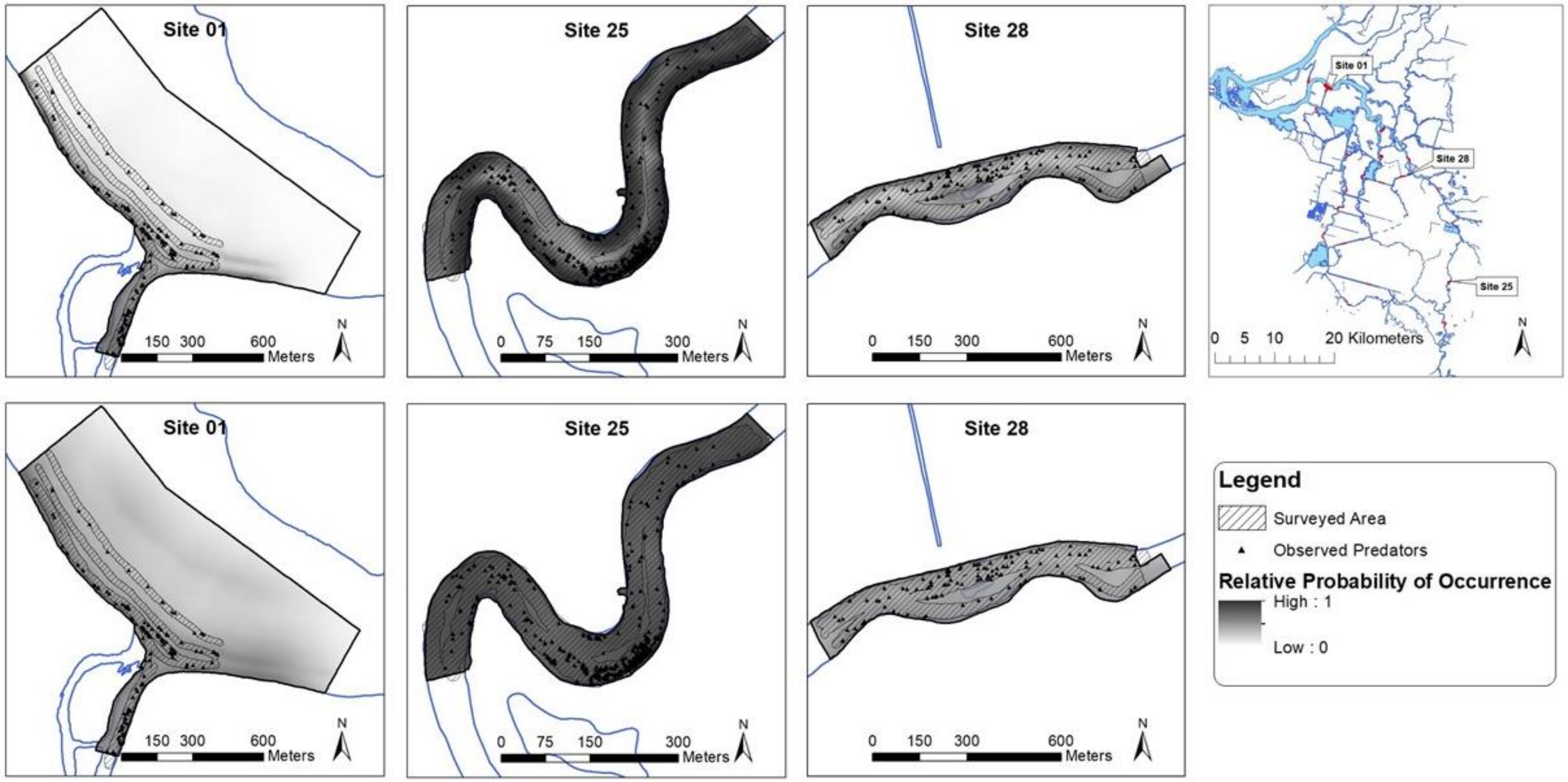


Figure 21. Predicted relative probability of occurrence of piscivorous fishes at sites 1, 25 and 28 using Maxent (upper panels) and logistic regression (lower panels).

DISCUSSION

Landscape-Scale Predator Distribution

I found that landscape-scale predator distributions were predominantly driven by spatial and structural habitat characteristics and not temporal variables. While there is apparent variation in abundance through time and space, there does not seem to be any consistent temporal trends across sites and the variance is not well explained by any of the time-dependent covariates tested. The variance is best explained in space; habitat characteristics that do not change throughout the sample season were the most significant predictors of reach density. The best model suggests that on both a landscape scale and a fine scale, predators were selecting habitats near SAV or habitats with many patches of SAV. Largemouth bass, the most abundant predator captured during electrofishing efforts, are known to reside and forage within areas of dense vegetation (Savino and Stein 1989). Largemouth bass are also known to seek submerged cover, including SAV, to search out prey that may be taking refuge, but also use the structure as cover for ambush predation (Wanjala et al. 1985, Savino and Stein 1989). Furthermore, the proliferation of invasive SAV in the Delta has been linked to the expansion of largemouth bass habitat (Brown and Michniuk 2007, Conrad et al. 2016).

The establishment of invasive species of SAV, such as Brazilian waterweed (*Egaria densa*), has created novel habitats suitable to invasive piscivores, which may affect native fishes by altering the habitats they evolved with, and in the case of salmonids, by promoting their predators. Naïve salmonids, which have not evolved in a landscape where ambush predators lurk amongst the vegetation, are likely moving through these habitats unaware that predators likely reside within. These results also suggest that the patch count of SAV was a much stronger predictor of predator density than total SAV area. It is likely that habitats with many patches of SAV are less dense and therefore less complex than habitats with large total areas of SAV by traditional measures of structural complexity (e.g. vegetation stems/m^2). In habitats with patchy SAV, ambush predators may be able to more effectively utilize the patchy cover for predation than prey can utilize it for evasion. Studies of predator-prey interactions have suggested that largemouth bass foraging success may decrease as habitat complexity increases beyond a threshold, especially when prey seek refuge in dense cover (Savino and Stein 1982, 1989, Takamura 2007). A study of another ambush predator, the spotted gar (*Lepisosteus oculatus*), has also shown that predation can be mediated by the complexity of vegetative structure (Ostrand et al. 2004). Crowder and Cooper (1982) found that in an experimental setting Bluegill sunfish had better growth and consumed more prey at intermediate densities of aquatic vegetation. If Delta habitats with numerous SAV patches are truly of moderate complexity relative to their surroundings, this could suggest that predator fishes in the Delta may be selecting habitats with a patchy distribution of SAV because it provides the most optimal foraging conditions.

Landscape-scale distributions of predators were also mediated by sinuosity and coefficient of variation of depth. I observed a positive relationship between predator density and the coefficient of variation of depth, suggesting that predators are selecting habitats with more abiotically complex structure, likely for the same reasons they are selecting areas with complex SAV structure. Contradictory to this notion, the negative relationship observed with sinuosity suggests that predators are selecting more linear sites which one would expect to have low structural complexity or habitat heterogeneity. It is possible that sinuosity is collinear with unmeasured habitat variables such as substrate type. Many linear channels of the Delta are the result of levee construction which are often built from or armored with riprap. Sport fisherman often target these riprapped embankments due to frequent encounters with largemouth bass and other centrarchid fishes (Dance 2014). Brown and Michniuk (2007) also speculated that the replacement of natural banks with riprap material could explain the dominance of non-native fish in littoral habitats of the Delta. Unfortunately, little data is available on the extent and location of riprap in the Delta so this relationship remains speculation.

I found that predator fishes were widely distributed across the entire study area, with potential predators occurring at every site sampled. This was similar to results of previous studies in the Delta (Feyrer and Healey 2003, Nobriga and Feyrer 2007, reviewed in Grossman et al 2013). While most sites were within one standard deviation of the mean estimated predator density, I observed several distinct high-density outliers. At site 25, I observed the immigration of an apparently large school of striped bass during the last two weeks of sampling which was likely responsible for producing the highest density estimate on May 8th and the third highest density on May 2nd. Although this immigration coincided with a rise in temperatures, it is difficult to separate this coincidence from their normal phenology; striped bass typically migrate up the San Joaquin River in spring (Calhoun 1952). This phenomenon demonstrates that highly migratory, schooling predators such as striped bass can cause drastic, though temporary, fluctuations in local predator density, which may help explain the variance in density estimates across time. The second highest density estimate, occurring at site 14 on April 21st is not as easily attributed to an influx of striped bass as I have no supplemental data to suggest what the species composition might have been at this site and thus I can only speculate on the reasons why this site might have such a high density of predators. It is noteworthy that the majority of predators observed at site 14 occurred along the southern bank, an extensively vegetated shoreline in an otherwise uniform constructed navigational waterway (Grant Line Canal). The landscape-scale model predicts multiple reaches through this same canal as well as the parallel Fabian and Bell Canal with relatively high predator densities driven by low sinuosity and high SAV patch counts. It is possible that the structure of this canal encourages growth of high quality SAV habitat. Additionally, large abundances of American shad (*Alosa sapidissima*), a forage fish which can attract concentrations of predators, have been documented in this region from May to April (Stevens 1966). The lowest density estimate occurred within 2 km of Discovery Bay, a very popular destination for fisher people due to its large population of largemouth bass. If local predators are drawn to Discovery Bay for the high density of structures, riprap, and low velocity habitat occurring there, it could be acting as a predator “sink” and drawing predators away from comparatively less desirable locations such as site 19. This broad distribution of predators means that emigrating salmonids will face predators throughout their journey regardless of route choice. Furthermore, they will likely encounter high densities of predators at some point in space and/or time due to the migratory predators.

Fine-Scale Predator Distribution

On a fine scale, habitat depth and proximity to shorelines, aquatic vegetation (SAV and tules), and human-made structures all played a role in determining a predator’s habitat selection. Distance to shore and depth consistently had a negative relationship with relative probability of occurrence suggesting that predators are more likely to be found in shallow, littoral habitats (Figure 16, Figure 17). This is consistent with habitat selection typical of largemouth bass and other centrarchid fishes which dominated electrofishing samples on five of the six sampling days (Feyrer and Healey 2003, Brown and Michniuk 2007, Conrad et al. 2016, Michel et al. 2018). Similarly, the negative relationships I observed between predator occurrence and distance to SAV and distance to tules reinforces the previously observed associations centrarchid fishes have with complex vegetative structure (Crowder and Cooper 1982, Savino and Stein 1989, Feyrer and Healey 2003, Brown and Michniuk 2007, Conrad et al. 2016). These results also suggest that these relationships may be interdependent; the selection of one vegetation type may depend on the proximity of the other and the proximity to human-made structures. While there is abundant literature to support selection of moderately complex habitats for foraging, little is known about the preferences of predator species for different vegetation types. In an experimental removal of SAV, researchers observed largemouth bass migrating to, and forming associations with, artificial structures, mirroring the interactions I observed between the distance to tules and the distance to structures (Colle et al. 1989). However, I cannot conclude habitat preference or requirements from this data and to distill a predator's preference or requirement for a vegetation or cover type would require controlled experiments (Rosenfeld 2003). Furthermore, the relationships observed on both a fine scale and landscape scale result from the cumulative responses of at least 12 different predators. While many of the centrarchids exhibit similar habitat selection of littoral habitats, striped bass and white catfish typically select mid-channel, open water habitats (Feyrer and Healey 2003, Michel et al. 2018). Because centrarchids numerically dominated the catch composition during electrofishing efforts, the observed relationships are likely more representative of the choices these species make and the uncertainty of these models is due in part to the observations of the typically less abundant mid-channel dwelling species. Species differentiation to a finer resolution than what I have achieved would likely drastically improve the predictive power of these models.

Emigrating salmonids may form some of the same habitat associations as predators in the Delta which may increase their encounters with predators, though that is not a common pattern observed. Zajanc et al. (2013) found that the presence of structural habitat features which provide both velocity refuge and shade increase the probability of holding and holding duration of Chinook salmon smolt during emigration through the Sacramento River. Structures such as docks and pilings may provide these types of refugia and my models indicate that predators may also utilize those habitats. Simple structures such as docks and pilings typically don’t provide the habitat complexity which can moderate predation success as described earlier. Thus, if a smolt seeks refuge near anthropogenic structure that predators are associating with, this may increase the likelihood that it will be consumed. Structures that pass juvenile salmonids, such a diversion dams, have also been known to aggregate predators which then consume disproportionately large numbers of salmonids (Sabal et al. 2016). Smolts are typically not found in nearshore habitats of the Delta and may not encounter the numerous littoral-dwelling predators I observed unless seeking refuge. Michel et al. conducted a salmonid predation study concurrent with my study, sharing both the same study sites and habitat data used in my study (2019). Their preliminary results indicated that none of the fine-scale habitat variables discussed here have a significant effect on salmonid predation but the mean distance to a predator (derived from my data) is a significant predictor. This would suggest that habitat characteristic do not significantly affect predation rate; however, because my models suggest predator density and position are strongly associated with spatial habitat characteristics, including a metric for predator density in a predation model may account for some of the variability due to spatial characteristics. Furthermore, predators are likely selecting habitats that are productive in terms of foraging success so I would expect higher predator densities and higher predation rates to occur in similar habitats. Thus, in an ecological setting it may be too difficult to distinguish the effects of habitat and predators on predation without experimental controls.

Survey Methods and Species Differentiation

With this study I have shown that DIDSON acoustic cameras can be used to quantify predator fish abundance in a broad scale, mobile application but these methods would benefit from additional research. With a relatively simple survey design, footage processing protocol, and density estimator, I calculated predator densities on a reach scale that have significant correlation with concurrent predation studies (Michel et al. 2019). DIDSON's high resolution, ease of use, and low disturbance made it ideal for use in ecological study; however, there are some key considerations for expanding on this methodology.

First, my species differentiation function is likely biased and would benefit greatly from a larger sample size. The best LDA model separating common carp from predators had an accuracy of up to 98.18 % when applied to the training footage; however, this rate is likely biased by the size distribution of fish sampled. All of the *C. carpio* recorded in reference footage were over 56 cm while all predator species used were less than 50 cm (Table 3). LDA models trained using only fish length from "predator" and "carp" groups resulted in classification rates greater than 97 % suggesting that the other measured morphometric values are contributing insubstantially to the discrimination function (Table 2). Predator fish in the Delta do reach sizes over 50 cm and *C. carpio* also occurs in smaller sizes, but in all six days of electrofishing, no fish in these size classes were captured. Without access to an additional data base of morphometrics and acoustic measurements for these species, I am unable to refine the functions further and I must assume that the sampled fish are representative of the fish population present in the study area during the survey period.

Though my species differentiation methods resulted in coarse discrimination of common carp from predators, I observed the potential for higher resolution species differentiation. Given a larger sample size of reference footage, or if studies were conducted in systems with limited numbers of species, differentiation beyond functional groups may be possible. Because width and the length:width ratio seemed to have inherent morphological differences and previous studies have used these metrics succesfully, I believe these methods would still be effective at distinguishing common carp from predator species(Appendix D, Mark Bowen 2018). In addition, I believe there is strong potential for target strength to play a role in differentiating species, but in this study the effects of target strength were likely overshadowed by the comparatively strong effects of length. I observed strong patterns of distinct target strengths for several of the well represented species in the study (Figure 8) and target strength has a successful history of implementation in traditional fisheries acoustics (Martignac et al. 2014, Ona 1999, Horne 2000, McQuinn and Winger 2003).

Secondly, a key finding of the simulations I conducted is that these methods were most susceptible to violations of a constant detection probability. I grouped variables which may affect detection of predators into two categories: 1) variables which affect fish behavior and 2) variables that affect DIDSON footage. Variables in group 1 include, but are not limited to, temperature, light, cover, depth, species interactions, and human disturbances. For example, as water temperatures increase and predatory fish become more active, we may be more likely to observe actively foraging species and count them towards our estimate. If the goal is to estimate the active predator population during the time of the study, then this variability in detection is likely proportional to the estimate of interest. Conversely, if the goal is to estimate the absolute population of predatory fish, then understanding the influence of group 1 variables is essential to correct population estimates. Variables in group 2 include underwater structure, drifting particulate, weather, turbulence, boat wakes and other waves. Typically these variables would either cause excessive platform motion that makes it very difficult to review footage or they may directly obstruct the view of potential predators and will effect population estimates regardless of the unit of interest. Understanding the influence of both of these sets of variables would require controlled experiments on a closed population; an effort that was beyond the scope of this study. I recommend that future use of this methodology take these variables into consideration and perhaps plan controlled experiment to evaluate their influence.

Management Implications

The information conveyed in this study can be useful to managers of the Delta ecosystem, but appropriate caution is needed when utilizing these results. The data collected and analyzed in this study is representative of only a single, unusually wet spring (CDWR 2017). Therefore, the relationships I observed may be unique to the unusually high flows and cool temperatures observed in spring of 2017. Furthermore, the models I present are relatively simple with only moderate predictive power and thus I recommend that the predictions presented in this study be used to inspire further scientific explorations. For instance, these model predictions indicate that predator densities in the upper San Joaquin River between the Stockton ship yard and the Head of Old River are consistently high (mean, 32.04 predators/m^2) which could help explain why survival estimates are typically very low through this region (Buchanan et al. 2018). If management actions to reduce the predator population are considered, I recommend focusing on habitat manipulations, such as reducing the extent of invasive SAV, along salmonid emigration routes with high predator densities. Because broad scale predator removals have been largely ineffective in the Delta, efforts to manipulate habitat to discourage non-native predator recruitment and favor native species recruitment may be more effective (reviewed in Bowen 2018, Wikert 2018). Efforts to reduce invasive SAV could also reduce habitat suitability for predator species; model predictions using the landscape model developed in this study indicate that a reduction of SAV patches along the upper San Joaquin River between the Head of Old River and Stockton by only 50% could reduce predator densities by approximately 18% while a complete eradication of SAV in this region could reduce predator densities by approximately 32%. Invasive SAV, including *Egeria densa*, have been identified as problematic throughout large portions of the San Joaquin River and Delta, due to interference with water conveyance, recreational and commercial boat passage, and threats natural ecological processes (Ruhstaller and Peipho 2014). Annual weed control efforts are undertaken to mitigate these effects, but are limited by high costs, lack of funding, a complex regulatory structure, and a lack of consistent monitoring (Ta et al. 2017). Consistent implementation of invasive SAV control measure will require that managers find consistent routes to navigate these barriers. Furthermore, the effectiveness of using weed control to reduce local predator populations will require testing and evaluation. Given the extent of fish invasions in the Delta, the species community will likely remain altered regardless of management actions taken, but restoring conditions to favor native species will increase the probability that they will persists alongside their alien neighbors.

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Appendix A

Appendix A. Summary of simulated line transect parameter specifications under null conditions.

Line Transect Survey Parameters	
Truncation distance	10
Number of lines	2
Total line length in survey region	2000
Survey area	60000
Covered area	40000
Percentage of survey area covered	66.67%

Appendix B

Appendix B. Summary of the detection function parameter specification for survey simulations under null conditions.

Detection function for the half-normal model	
Model	$p(detection) = e^{(\frac{-0.5*distance^2}{e^{(\theta_0+\theta_1*exposure)}})^2}$
Parameters	$\theta_0 = 1.45$; $\theta_1 = 0.69$
Effective strip width at minimum exposure	5.22
Effective strip width at maximum exposure	8.10
Mean effective strip width	6.76

Appendix C

Appendix C. Summary of the population and survey area parameters specified for survey simulations under null conditions.

Simulated Population and Survey Area	
Region (length x width)	60 x 1000
Number of groups	100
Number of individuals	390
Group sizes	1 : 9
Mean group size	3.9
Exposure boundaries	[0,1]
Mean exposure	0.51

Appendix D

Appendix D. Summary of sites visited during the 2017 field season.

Site	Region	Sampling Date(s)	Channel Type	Site Area (km^2)	Mean Depth (m)	Sinuosity	Channel width (m)
1	Lower San Joaquin	4/4/2017 4/10/2017 4/19/2017 5/1/2017 4/26/2017 5/10/2017	Mainstem	0.33	9.11	1.24	730
3	Lower Old River	4/6/2017	Mainstem	0.12	3.15	1.12	98
6	Mildred Island and Cuts	4/7/2017	Distributary	0.12	4.22	1.00	105
8	Lower Old River	4/8/2017	Distributary	0.18	3.93	1.33	160
10	Middle River and Cuts	4/13/2017	Distributary	0.83	3.29	1.00	76

Site	Region	Sampling Date(s)	Channel Type	Site Area (km^2)	Mean Depth (m)	Sinuosity	Channel width (m)
11	Mildred Island and Cuts	4/14/2017	Mainstem	0.19	5.02	1.52	126
12	Lower San Joaquin	4/15/2017	Mainstem	0.13	3.97	1.07	260
13	Upper San Joaquin	4/20/2017	Mainstem	0.83	2.90	1.65	75
14	Upper Old River and Cuts	4/21/2017	Distributary	0.70	2.26	1.00	71
16	Mid San Joaquin	4/22/2017	Mainstem	0.70	6.16	1.01	168
19	Lower Old River	4/28/2017	Mainstem	0.19	3.13	1.29	146
22	Lower Old River	4/29/2017	Mainstem	0.14	3.81	1.35	106
23	Upper San Joaquin	5/4/2017	Mainstem	0.15	2.13	2.08	130
24	Lower San Joaquin	5/5/2017	Mainstem	0.22	2.36	1.02	238
25	Upper San Joaquin	4/5/2017 4/11/2017 4/17/2017 4/27/2017 5/2/2017	Mainstem	0.71	2.01	1.49	82

Site	Region	Sampling Date(s)	Channel Type	Site Area (km^2)	Mean Depth (m)	Sinuosity	Channel width (m)
		5/8/2017					
27	Mildred Island and Cuts	5/6/2017	Mainstem	0.17	5.68	1.43	185
28	Mildred Island and Cuts	4/3/2017 4/12/2017 4/18/2017 4/25/2017 5/3/2017 5/9/2017	Distributary	0.15	3.78	1.06	98
33	Lower San Joaquin	5/11/2017	Distributary	0.21	4.74	1.00	189
34	Upper Old River and Cuts	5/12/2017	Mainstem	0.87	1.24	1.38	72
37	Franks Tract	5/13/2017	Distributary	0.11	4.30	1.23	91

Appendix E

Appendix E. Species captured during electrofishing sampling events.

Site	Date	Species	Common Name	Count
1	11 April 2017	*Micropterus salmoides*	Largemouth Bass	52
		Morone saxatilis	Striped Bass	13
		Ameiurus catus	White Catfish	1
		Lepomis microlophus	Redear Sunfish	4
		Lepomis gulosus	Warmouth	1
1	11 May 2017	*Lepomis macrochirus*	Bluegill Sunfish	1
		Cyprinus carpio	Common Carp	1
		Micropterus salmoides	Largemouth Bass	13
		Ptychocheilus grandis	Sacramento Pikeminnow	1
		Lepomis microlophus	Redear Sunfish	4
		Notemigonus crysoleucas	Golden Shiner	3
		Morone saxatilis	Striped Bass	30
		Hysterocarpus traskii	Tule Perch	1
		Ameiurus catus	White Catfish	1
25	12 April 2017	*Lepomis macrochirus*	Bluegill Sunfish	9
		Micropterus salmoides	Largemouth Bass	36

Site	Date	Species	Common Name	Count
		Lepomis microlophus	Redear Sunfish	23
		Morone saxatilis	Striped Bass	23
		Ameiurus catus	White Catfish	1
25	9 May 2017	*Micropterus salmoides*	Largemouth Bass	29
		Ptychocheilus grandis	Sacramento Pikeminnow	1
		Lepomis microlophus	Redear Sunfish	3
		Morone saxatilis	Striped Bass	26
		Lepomis macrochirus	Bluegill Sunfish	1
		Carassius auratus	Goldfish	1
		Ptychocheilus grandis	Sacramento Pikeminnow	2
		Lepomis microlophus	Redear Sunfish	4
		Ameiurus catus	White Catfish	5
28	13 April 2017	*Ameiurus nebulosus*	Brown Bullhead	3
		Lepomis macrochirus	Bluegill Sunfish	6
		Carassius auratus	Goldfish	1
		Micropterus salmoides	Largemouth Bass	111
		Lepomis microlophus	Redear Sunfish	27
		Ameiurus catus	White Catfish	10
		Lepomis gulosus	Warmouth	1
		Cyprinus carpio	Common Carp	6

Site	Date	Species	Common Name	Count
28	10 May 2017	*Lepomis macrochirus*	Bluegill Sunfish	11
		Pomoxis nigromaculatus	Black Crappie	1
		Cyprinus carpio	Common Carp	3
		Lepomis cyanellus	Green Sunfish	1
		Micropterus salmoides	Largemouth Bass	115
		Lepomis microlophus	Redear Sunfish	29
		Ameiurus catus	White Catfish	4
		Lepomis gulosus	Warmouth	5

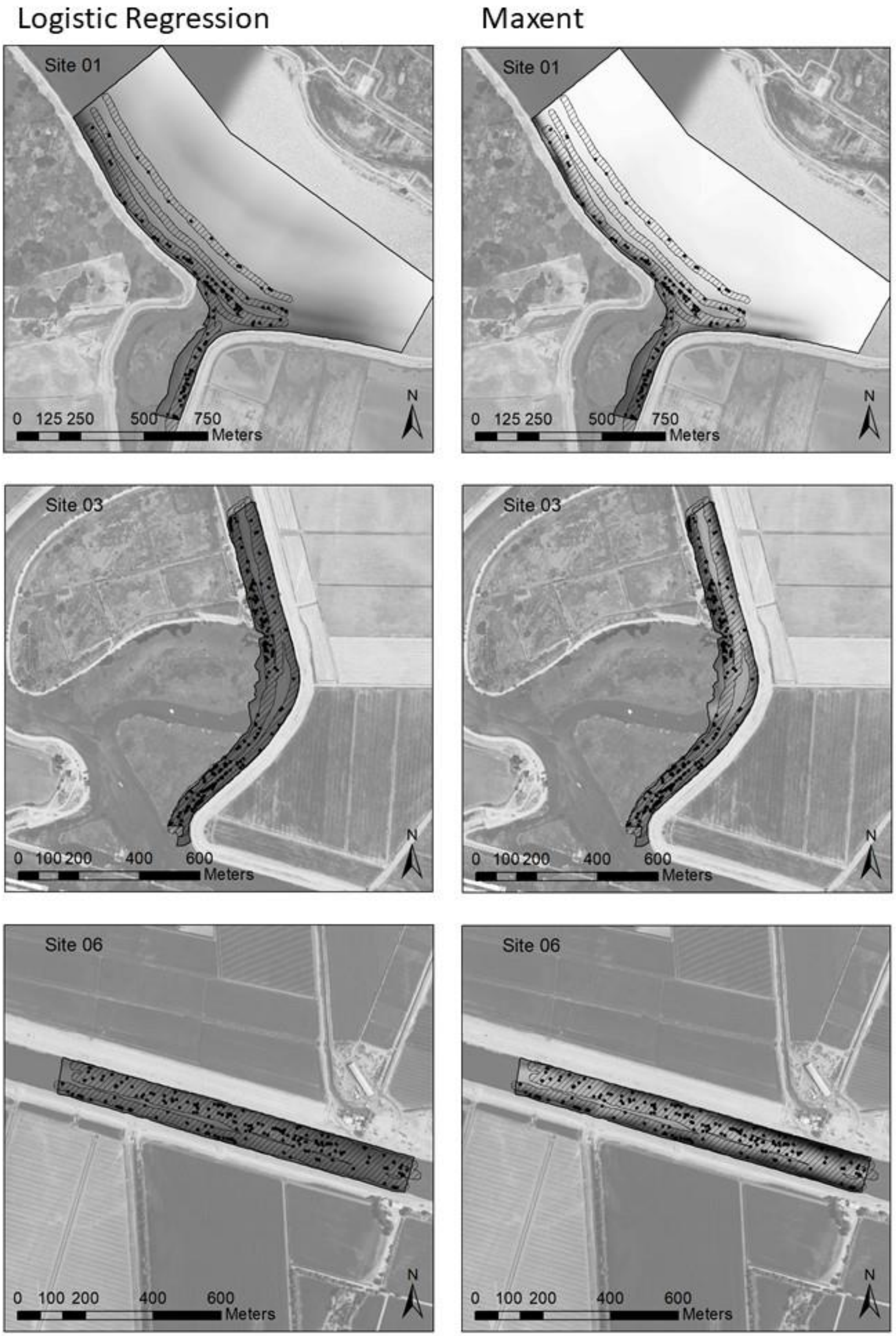
Appendix F

Appendix F. Coefficient of linear discriminants and group means for the best linear discriminant function discerning common carp from predator fishes.

Variable	Coefficient of Linear Discriminant	Carp Group Mean	Predator Group Means
Length	-0.134	67.61	31.07
Width	-0.023	33.14	10.48
Length:Width	0.197	2.46	3.32

Appendix G

Appendix G. Predicted relative probability of occurrence of predator species using the best logistic regression model (left column) and the best Maxent model (right column) for all sites surveyed. Observed predators are indicated by dots and the surveyed regions are marked with hash lines.


Logistic Regression
Maxent
Site 01
0 125 250 500 750 Meters
N
Site 01
0 125 250 500 750 Meters
N
Site 03
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N
Site 03
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N
Site 06
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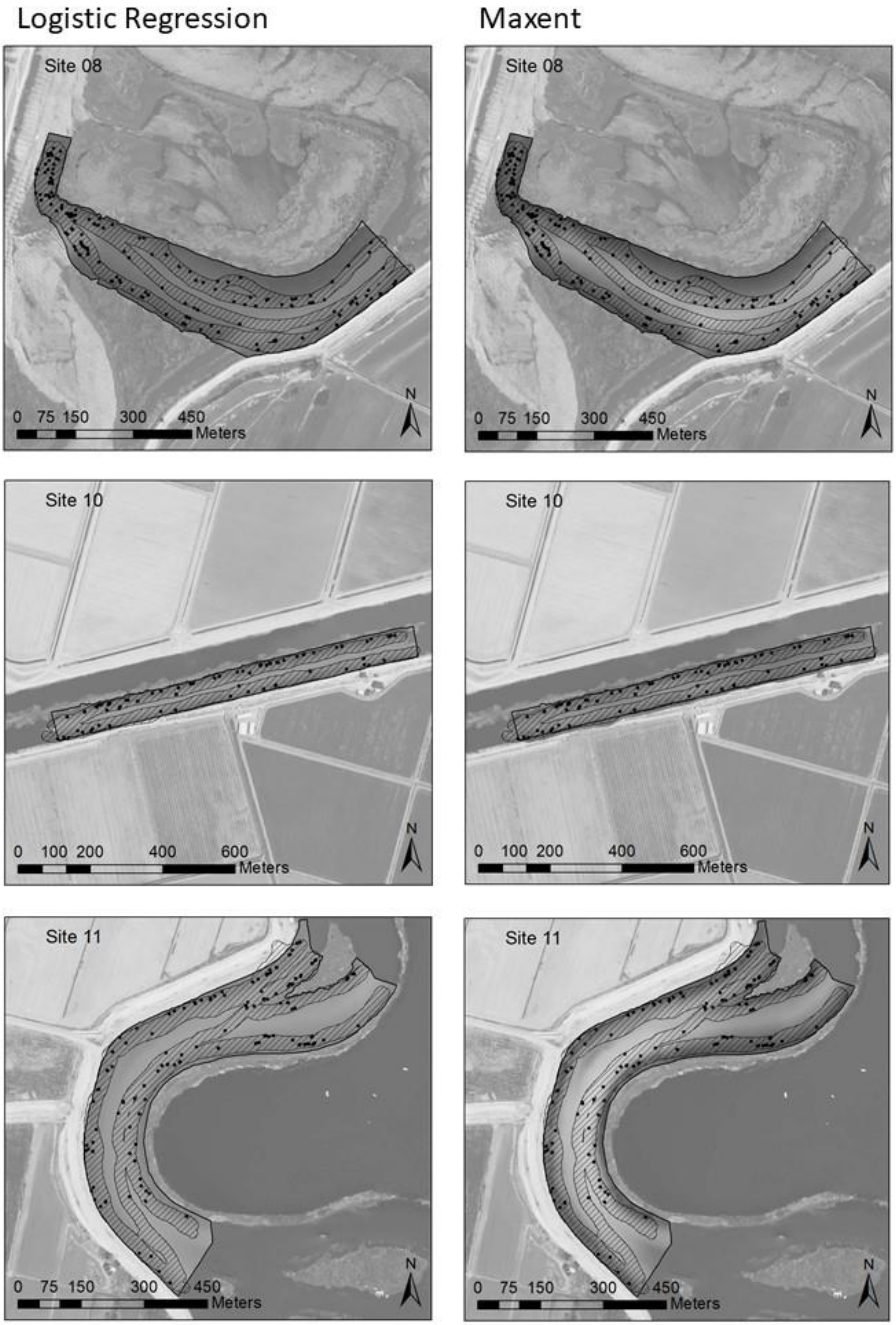
Site 06
0 100 200 400 600 Meters
N


Logistic Regression
Maxent
Site 08
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Meters
N
Site 08
0 75 150 300 450
Meters
N
Site 10
0 100 200 400 600
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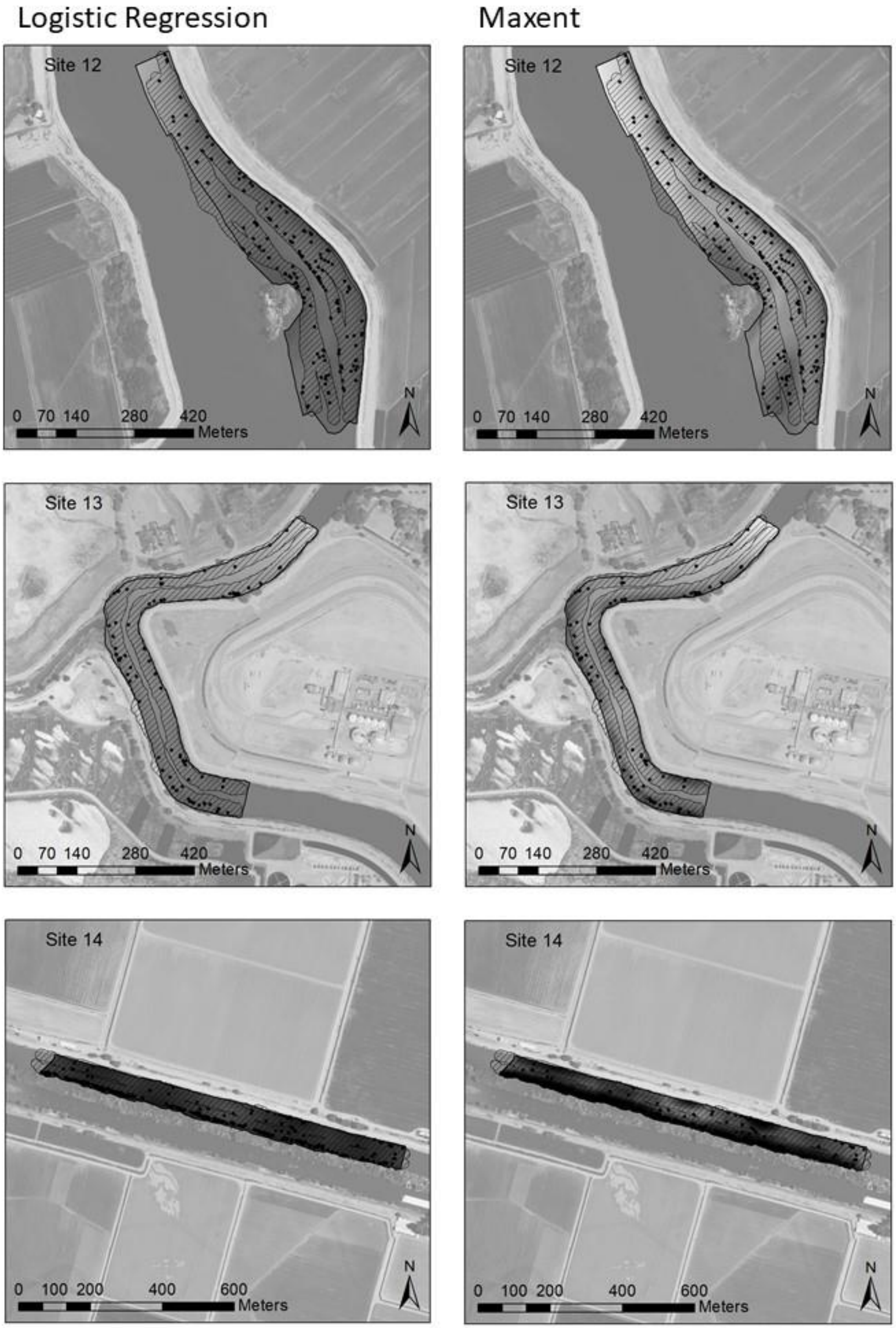
Meters
N


Logistic Regression
Maxent
Site 12
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Meters
N
Site 12
0 70 140 280 420
Meters
N
Site 13
0 70 140 280 420
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Site 14
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Meters
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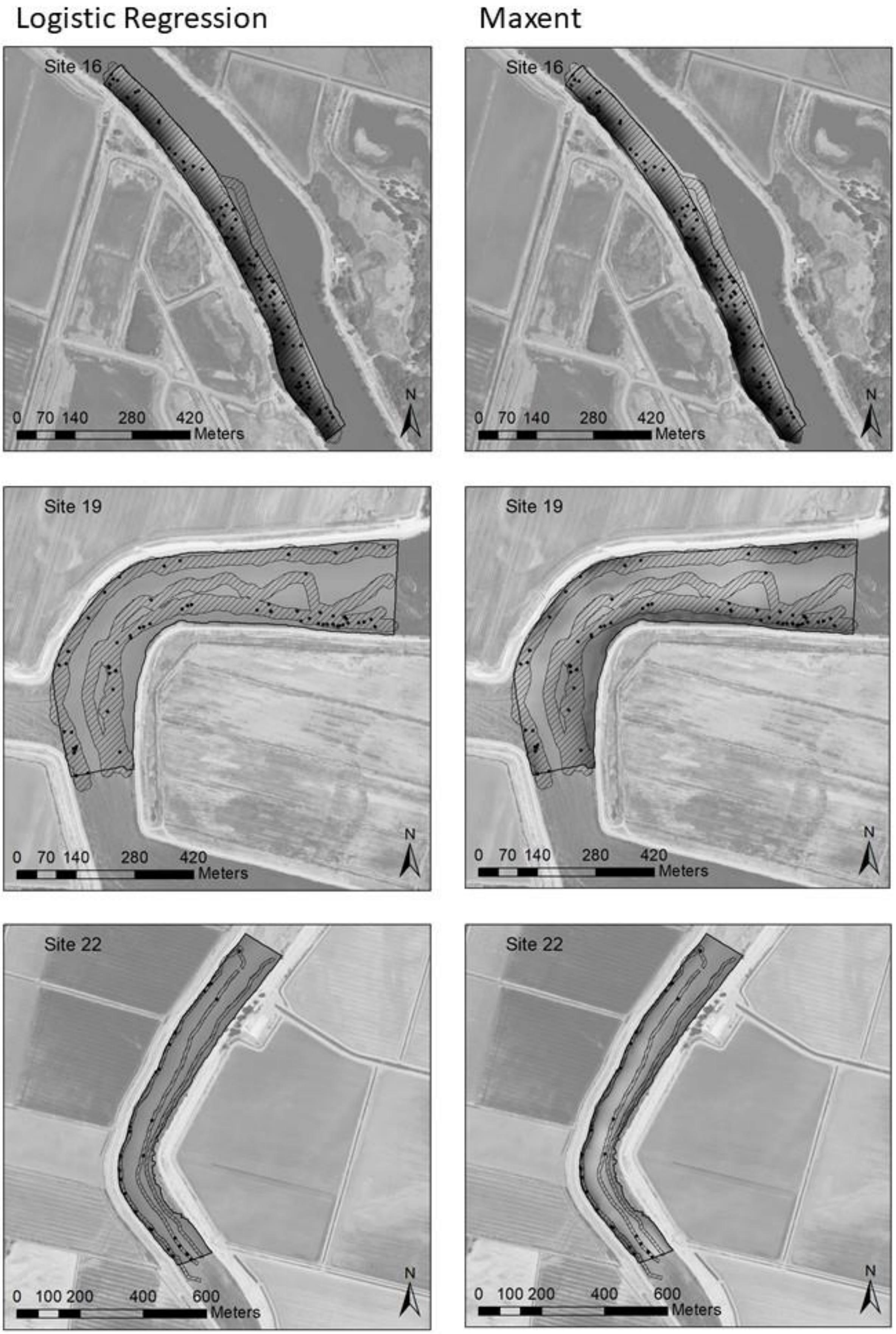
Logistic Regression
Maxent
Site 16
0 70 140 280 420 Meters
N
Site 16
0 70 140 280 420 Meters
N
Site 19
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Site 22
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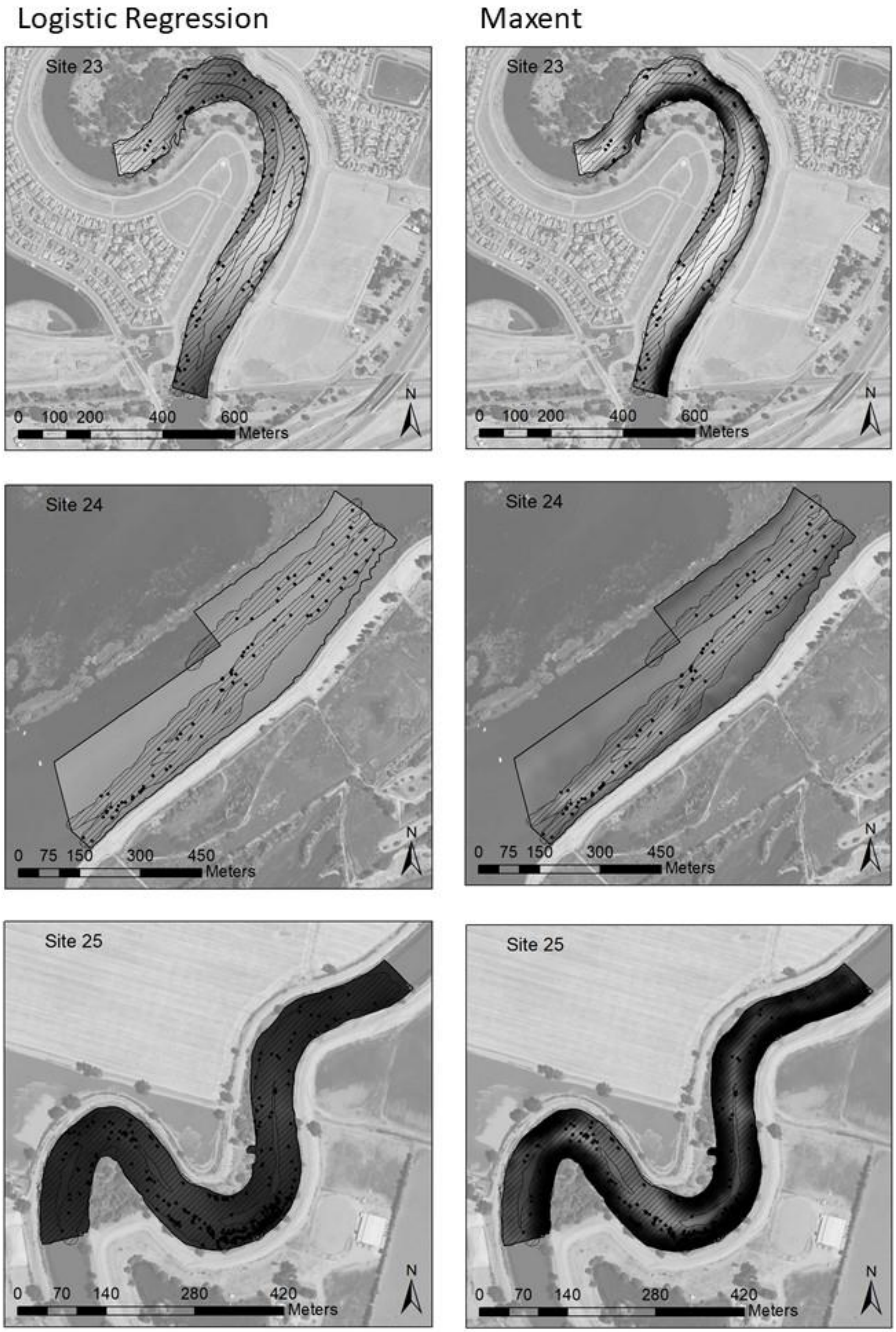
N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Site 23
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Site 25
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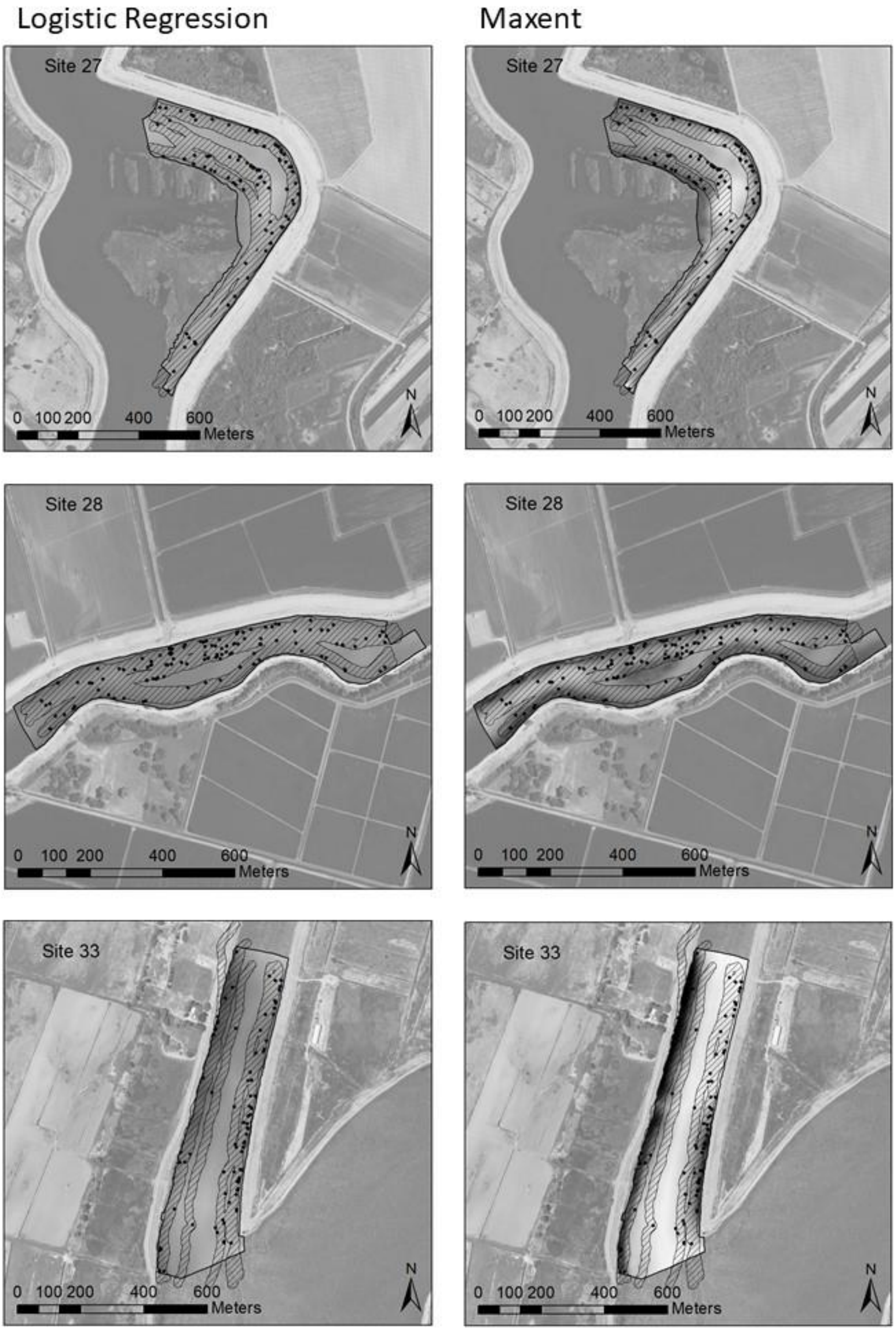
N


Logistic Regression
Maxent
Site 27
Site 27
Site 28
Site 28
Site 33
Site 33
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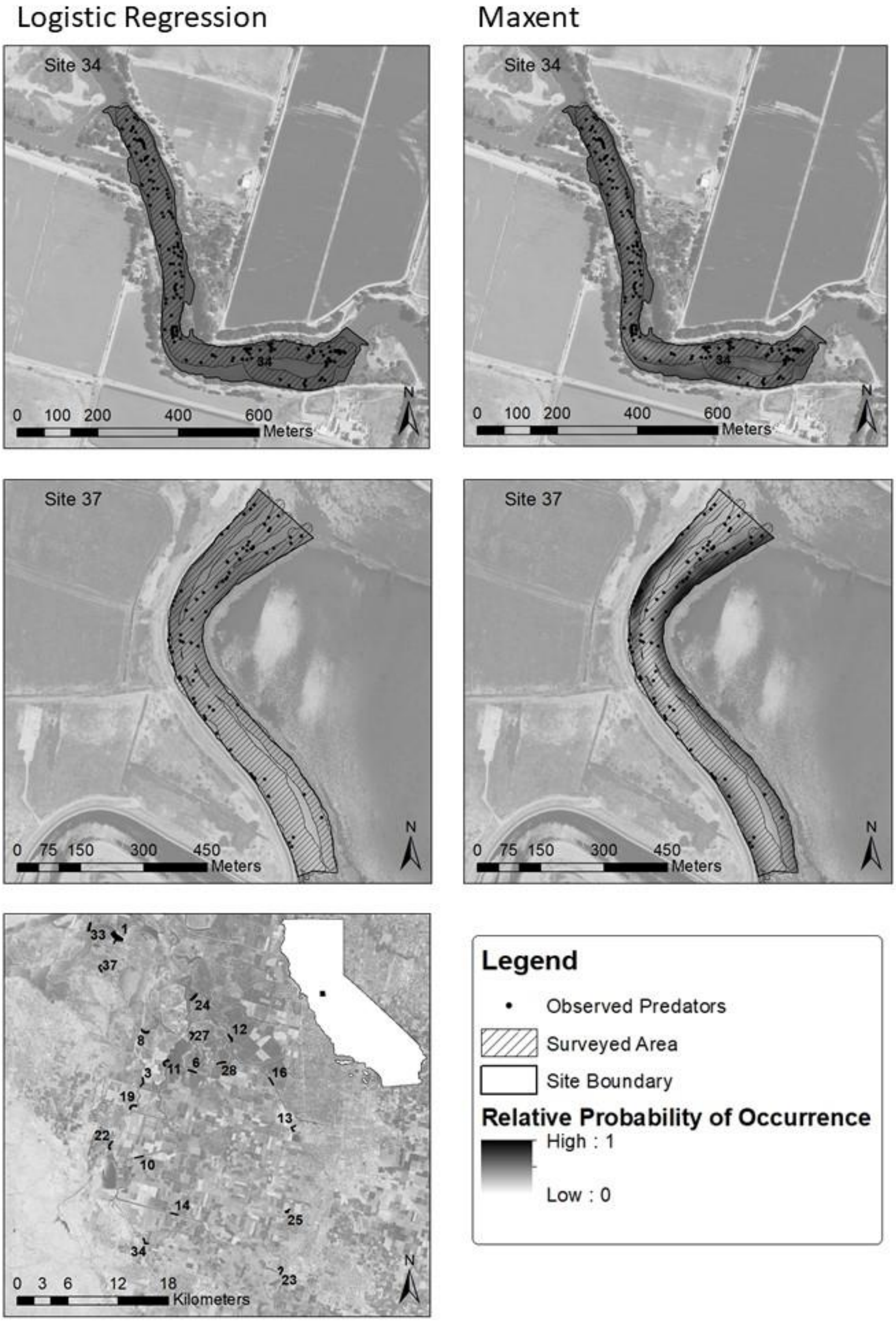
Meters
N


Logistic Regression
Maxent
Site 34
34
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Meters
N
Site 37
0 75 150 300 450
Meters
N
33
1
37
24
27
12
8
3
11
6
28
16
19
13
22
10
14
25
34
23
0 3 6 12 18
Kilometers
N
Legend
Observed Predators
Surveyed Area
Site Boundary
Relative Probability of Occurrence
High : 1
Low : 0