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POLICY AND PROGRAM ANALYSIS

Where Predators and Prey Meet: Anthropogenic Contact Points Between Fishes in a Freshwater Estuary

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ABSTRACT

The Sacramento–San Joaquin Delta has been invaded by several species of non-native predatory fish that are presumed to be impeding native fish population recovery efforts. Since eradication of predators is unlikely, there is substantial interest in removing or altering manmade structures in the Delta that may exacerbate predation on native fish (contact points). It is presumed that these physical structures influence predator-prey dynamics, but how habitat features influence species interactions is poorly understood, and physical structures in the Delta that could be remediated to benefit native fish have not been inventoried completely. To inform future research efforts, we reviewed literature that focused on determining the effects of predator-prey interactions between fish, based on contact points that are commonly found in the Delta. We also performed a geospatial analysis to determine the extent of potential contact points in the Delta. We found that the effects of submerged aquatic vegetation (SAV) and artificial illumination are well studied and documented to influence predation in other freshwater systems worldwide. Conversely, other common structures in the Delta—such as docks, pilings, woody debris, revetment, and water diversions—did not have the same breadth of research. In the Delta, the spatial extent of the different types of contact points differed considerably. For example, 22% of the Delta water surface area is occupied by SAV, whereas docks only cover 0.44%. Our conclusion, based on both the literature review and spatial analysis, is that the effects of SAV and artificial illumination on predation warrant the most immediate future investigation in the Delta.

KEY WORDS

predator, prey, light, aquatic vegetation, dock, riprap, habitat, river, estuary

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INTRODUCTION

Human development in the 19th and 20th century has significantly altered the landscape in which wild organisms interact with each other (Dudgeon et al. 2006). In particular, freshwater ecosystems have been dramatically altered by anthropogenic activities such as dam construction, water diversions, revetment, shoreline development, and dredging (Meybeck 2003). It is important to understand how these changes affect aquatic predator-prey interactions, especially with the proliferation of invasive species where natives may not be adapted to predation pressures.

Physical habitat alterations can become points of contact between predators and prey that either concentrate fish or influence the outcome of their interactions. These "contact points" can take many shapes and forms: they can be nearly continuously distributed (such as submerged aquatic vegetation [SAV]), discretely spaced (docks), or fall somewhere in-between (artificial lighting). These changes in habitat structure can influence the interaction between organisms in different ways. For example, manmade structures like docks may aggregate predators (Barwick et al. 2004) whereas steep revetments minimize shallow water habitat that smaller fish can use as refuge from large predators (Tiffan et al. 2016). Artificial nighttime lighting may aggregate prey and increase predator efficiency (Becker et al. 2013) while invasive SAV may aggregate both predators and prey into the same areas (Annett 1998).

There is vast potential to remove or modify contact points in freshwater systems to decrease predator-prey interactions and, ultimately, increase survival of imperiled organisms. However, to focus resources most effectively, we must understand (1) the underlying mechanisms that mediate predator-prey interactions, (2) the magnitude to which different contact points affect predation rates, and (3) the abundance and distribution of contact points within areas where native fish prey may be present. This allows the types of contact points that warrant further study—and whose removal or alteration could ultimately yield the highest returns on investment—to be objectively prioritized

The Sacramento-San Joaquin Delta (the Delta) is a heavily modified tidal freshwater estuary in California. It is the nexus of the world's largest water distribution system and has been heavily altered by human activity. The Delta has experienced numerous aquatic species invasions, and several of its native fish populations are in decline (Brown and Michniuk 2007). The survival of juvenile native salmon that migrate through and rear in the Delta is known to be much lower than other major US West Coast river systems (Buchanan et al. 2013; Michel et al. 2015; Perry et al. 2010). High abundance of non-native predatory fish such as Striped Bass (*Morone saxatilis*), Largemouth Bass (*Micropterus salmoides*), and Channel Catfish (*Ictalurus punctatus*) is thought be an important contributor to the low salmon survival (Grossman 2016). Reducing the number of predatory fish has been proposed as a management option to benefit salmon, but to date, there are no proven tools available to control population in the Delta. Furthermore, removal of certain species such as Largemouth Bass or Striped Bass may be untenable because of their economic and cultural value for sport fishing. And the removal of native predatory species, such as Sacramento Pikeminnow (*Ptychocheilus grandis*) would raise an ethical dilemma. Therefore, there is considerable interest in reducing predation on juvenile salmon in the Delta by removing or modifying physical features that increase the localized spatial overlap between predators and prey.

To inform the direction of future research that could lead to new management tools, we reviewed studies in the scientific literature that investigated how different types of contact points influenced fish predation in freshwater and estuarine environments. When possible, we highlight findings that were specifically relevant to the predator or prey species that exist in the Delta. To evaluate the potential for contact point management options in California, we conducted a GIS analysis to calculate the distribution of several types of contact points for which there were publicly available data or that we could assess using satellite imagery. Our assessment indicates which contact points within the Delta may have the highest impact on predator-prey interactions based on the magnitude of their spatial extent, and can be used to guide for future research. Finally, we discuss the nature of established relationships between certain types of contact points and predation and highlight key knowledge gaps.

THE DYNAMICS OF CONTACT POINTS ON PREDATION

Freshwater ecosystems are heterogeneous and face unique and varying degrees of anthropogenic alterations. The purpose of this study was to understand the degree to which certain types of contact points influence fish predation, and the mechanisms driving these influences. The list of contact points we chose to examine is not comprehensive. Instead, we chose to focus on those that are either discrete physical features or disturbances that could be mechanically removed or modified to minimize their effect on fish. This exercise was not intended to provide novel solutions to remediate the unwanted effects of contact points, but to indentify gaps in knowledge that will inform future research efforts relevant to fisheries management in the Delta.

Contact Point Types

We grouped contact points into six categories: armored banks, SAV, artificial lighting, woody debris, scour holes, and water diversions. The Delta, like many watersheds, is channelized to both control floods and convey water. Natural meandering river channels have been straightened with raised earthen levees and reinforced with riprap. These armored banks can decrease the available shallow water refuge habitat for small fish while simultaneously providing a moderately complex habitat that is ideal for ambush predators such as Largemouth Bass (Tabor 2011).

Aside from the direct physical modifications associated with flood control (i.e., dams, levees, and revetment), water management practices that alter flows can have secondary effects, such as the proliferation of non-native SAV and decreases in woody debris. While aquatic vegetation and woody debris are not manmade structures, we chose to include them in this review because their distribution is heavily influenced by human activity. The wholesale elimination of non-native SAV and floating aquatic vegetation (FAV) from the Delta is unrealistic. But there are control programs already in place, tailored primarily to keep waterways open for boating, that vary in intensity and efficacy (Ta et al. 2017).

Fish in the Delta are affected by large state and federal diversions that influence hydrodynamics and are suspected to create predation hot-spots. But these types of diversions were not included in this review because their effects go far beyond their discrete physical presence and are already the subject of much research in the Delta. We focused our review on smaller diversion pipe structures and the influence their presence may have on species interactions. Small, unscreened intake and outfall pipes are ubiquitous throughout the Delta, yet have received limited research attention.

Dredging river channels directly changes the shape of underwater habitat. The modification of river flows associated with dams and diversions can also influence riverbed scouring. Bathymetric features such as scour holes can aggregate fish or alter hydrodynamics in ways that favor predators (Kinzli and Myrick 2010).

Docks, piles, and bridges are discrete structures that influence interactions between predatory fish and their prey. The effects of these structures can be compounding: they can disrupt or delay movements of migratory species such as salmon while simultaneously aggregating predators (Moore et al. 2013).

Finally, man-made nighttime lighting is ubiquitous in many rivers and estuaries as a result of shoreline development, boating navigation, and docks. Although artificial lighting is not a physical object that organisms must navigate, it is a physical habitat disturbance, and the change in natural light cycles within associated aquatic environments is meaningful to fish (Nightingale et al. 2006).

Literature Search

We collected peer-reviewed articles and select gray literature by searching the online databases Web of Science (WOS; *https://www.webofknowledge.com*) and Aquatic Sciences and Fisheries Abstracts (ASFA; *https://proquest.libguides.com/asfa*). Database searches in WOS and ASFA search the title and abstract for search terms. Our search was structured such that results included only publications that have at least one

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word from each set of search terms within the following brackets:

$$\begin{bmatrix} Fish \\ Piscine \end{bmatrix} AND \begin{bmatrix} River* \\ Estuar* \end{bmatrix} AND \begin{bmatrix} Predator \\ Prey \\ Predation \end{bmatrix} AND \begin{bmatrix} Piling \\ Dock \\ Pier \\ Light \\ Illumination \\ Abutment \\ Bridge \\ Revetment \\ Rip\text{–}Rap \\ Diversion \\ Scour \\ Anthropogenic \\ Aquatic\ Vegetation \\ Woody\ debris \end{bmatrix}$$

Where * denotes a wildcard symbol (e.g., "river*" could return results for "riverine" or "river").

This process yielded 1,259 results from WOS and 830 results from ASFA for a combined total of 1,552 unique records. This library was then screened by two independent reviewers to determine if the title and abstract for each record was relevant to the research objective by meeting all three of the following inclusion criteria: The article (1) discussed fish on fish predation in freshwater, estuarine, or coastal marine environments; (2) discussed predation-related topics in relation to physical habitat characteristics; and (3) focused on at least one of the following:

- Predator aggregations
- Prey aggregations
- Predator prey interactions
- Factors that affect predator feeding ability
- Factors that affect prey refuge/evasion capability

Information from articles was classified into categories based on which contact point type(s) the article addressed, and if it provided information on the effect of the contact point type(s) on predator aggregations, prey aggregations, prey vulnerability, predator efficiency, and/or predator/prey interactions. Within each relevant category subgroup (e.g., prey aggregations for contact point type "docks"), the information provided, if any, was classified using the following codes:

- S (Significant relationship based on statistical test)
- NS (Non-Significant relationship based on statistical test)
- Q (Quantitative or Qualitative relationship described using actual measurements, but not tested for statistical significance)
- P (Presumed relationship based on ancillary data, but no appropriate data or statistical test was provided)

The magnitude and direction of the relationship was recorded whenever available. Additionally, if new references found within articles during full-text review met the inclusion criteria, they were added to the list of full-text articles for review. In total, 72 articles met our inclusion criteria and were fully reviewed by one of three independent reviewers.

RESULTS

The initial screening process excluded 1,480 articles from receiving a full review because they did not meet all three of the inclusion criteria. Most of the selected papers ($n = 72$) focused on the influence of SAV (26%, $n = 19$) or artificial light (18%, $n = 13$) on predator-prey dynamics (Table 1). Twenty studies discussed a contact point that we could not categorize into larger distinct groups (e.g. jetties, weirs, shade, etc.) and were therefore excluded from the table. Of the 72 articles we reviewed, only 14 were published before the year 2000.

Submerged Aquatic Vegetation

Although our search was intended to capture studies that described all forms of aquatic vegetation, all of the relevant articles ($n = 19$) we found described the effects of SAV (living or simulated). The general consensus of the reviewed papers indicated that while SAV increased predator and prey aggregations, it generally decreased

Table 1 Predator–prey behavior and interaction by contact point type. Effect is ranked as S – significant relationship based on statistical test, NS – non-significant relationship based on statistical test, Q – relationship described quantitatively or qualitatively using actual measurements, but not tested for statistical significance, P – the authors presumed a relationship based on ancillary data, but no appropriate data or statistical test was provided. Studies including salmonids as prey in *red.*

Contact point	Predator aggregation	Prey aggregation	Predator–Prey interaction	Predator efficiency	Prey vulnerability
Submerged aquatic vegetation	S[4] Q[14] P[5]	S[4,8,36] Q[27] P[5]	S[3,4,8,12,17,18,38,39,40,47] Q[9] P[5]	S[3,17,39,40] P[5,12,15,18,38,41]	S[3,10,17,36,39,40] P[5,12,15,18,38,41]
Artificial light	S[1,7]	S[1,7,11,43,45] P[32]	S[1,11,28,29,34,43] P[23,32]	S[11,20,28,29,49] P[7,32]	S[11] P[7,29,32,35]
Docks and piers	S[1,6,19]	S[1,6,19,30,31,33,42]	P[1,6,19,30]	P[6,19,24,30]	P[6,19,24,30,33]
Riprap	S[46] P[26,44]	S[44,46,48]	P[22,26,46]	P[21,26,44]	P[21,26]
Scour holes	P[2,25]	P[2,25]	P[2,25]	P[25]	
Diversions	S[37] Q[13] P[16]	S[16]	P[37] P[16]	P[16]	P[16]

a. Sources:

1 Able et al. (2013)
2 Allouche (2002)
3 Anderson (1984)
4 Annett (1998)
5 Baras and Nindaba (1999)
6 Barwick et al. (2004)
7 Becker et al. (2013)
8 Bettoli et al. (1992)
9 Buckel and Stoner (2000)
10 Camp et al. (2012)
11 Cerri (1983)
12 Chacin and Stallings (2016)
13 de Mutsert and Cowan (2012)
14 de Mutsert et al. (2017)
15 Ferrari et al. (2014)
16 Floyd et al. (2007)
17 Gotceitas and Colgan (1987)
18 Gregory (1996)
19 Grothues et al. (2016)
20 Hansen et al. (2013)
21 Heerhartz and Toft (2015)
22 Jorgensen et al. (2013)
23 Kehayias et al. (2018)
24 Kemp et al. (2005)
25 Kinzli and Myrick (2010)
26 Kornis et al. (2017)
27 Lazzari (2013)
28 Mazur and Beauchamp (2003)
29 Mazur and Beauchamp (2006)
30 Moore et al. (2013)
31 Munsch et al. (2017)
32 Nightingale et al. (2006)
33 Ono and SimenstadSchool (2014)
34 Petersen and Gadomski (1994)
35 Riley et al. (2015)
36 Rozas and Odum (1988)
37 Sabal et al. (2016)
38 Sammons and Maceina (2006)
39 Savino and Stein (1982)
40 Savino and Stein (1989)
41 Shoup et al. (2003)
42 Southard et al. (2006)
43 Tabor (2001); Tabor et al. (2004)
44 Tabor (2011)
45 Tabor et al. (2017)
46 Tiffan et al. (2016)
47 Tsunoda and Mitsuo (2018)
48 Venter et al. (2008)
49 Vogel and Beauchamp (1999)

predator prey interactions, predator efficiency, and prey vulnerability (Figures 1 and 2). Many of the authors suggested that predators are more efficient in a moderately complex environment (open spaces interspersed with patches of SAV) rather than in a highly complex environment (dense and widespread SAV) (Bettoli et al. 1992; Savino and Stein 1982). This indicates there may be a threshold above which a complex environment imparts decreasing benefits to the predator, likely when the habitat's complexity begins to impede on the predator's visual field and mobility. Additionally, it is important to note that one study did not support this trend: it instead found that all recorded predation events occurred in or near SAV (Annett 1998).

The relationship between SAV density and prey vulnerability is highly species-dependent (Savino and Stein 1989). For example, Ferrari et al. (2014) found that Largemouth Bass feeding efficiency was affected by vegetation density only when prey species associated with SAV were considered. Prey species that associate with open water did not use vegetation as a refuge, even in the presence of predators. They were equally vulnerable to predation whether or not SAV was present in the environment (i.e., behavioral differences between prey species will determine the extent to which SAV provides refuge from predation). The authors did find that turbidity provided cover to these open water species and increased the survival of Delta Smelt (*Hypomesus transpacificus*). Finally, fluctuations in SAV density through both space and time can also significantly affect fish community structure (de Mutsert et al. 2017).

Our literature search term for submerged aquatic vegetation did not return any studies that investigated the relationship between floating aquatic vegetation (FAV) and predator-prey interactions. This may be a crucial data gap, as FAV is widespread in freshwater systems. Species

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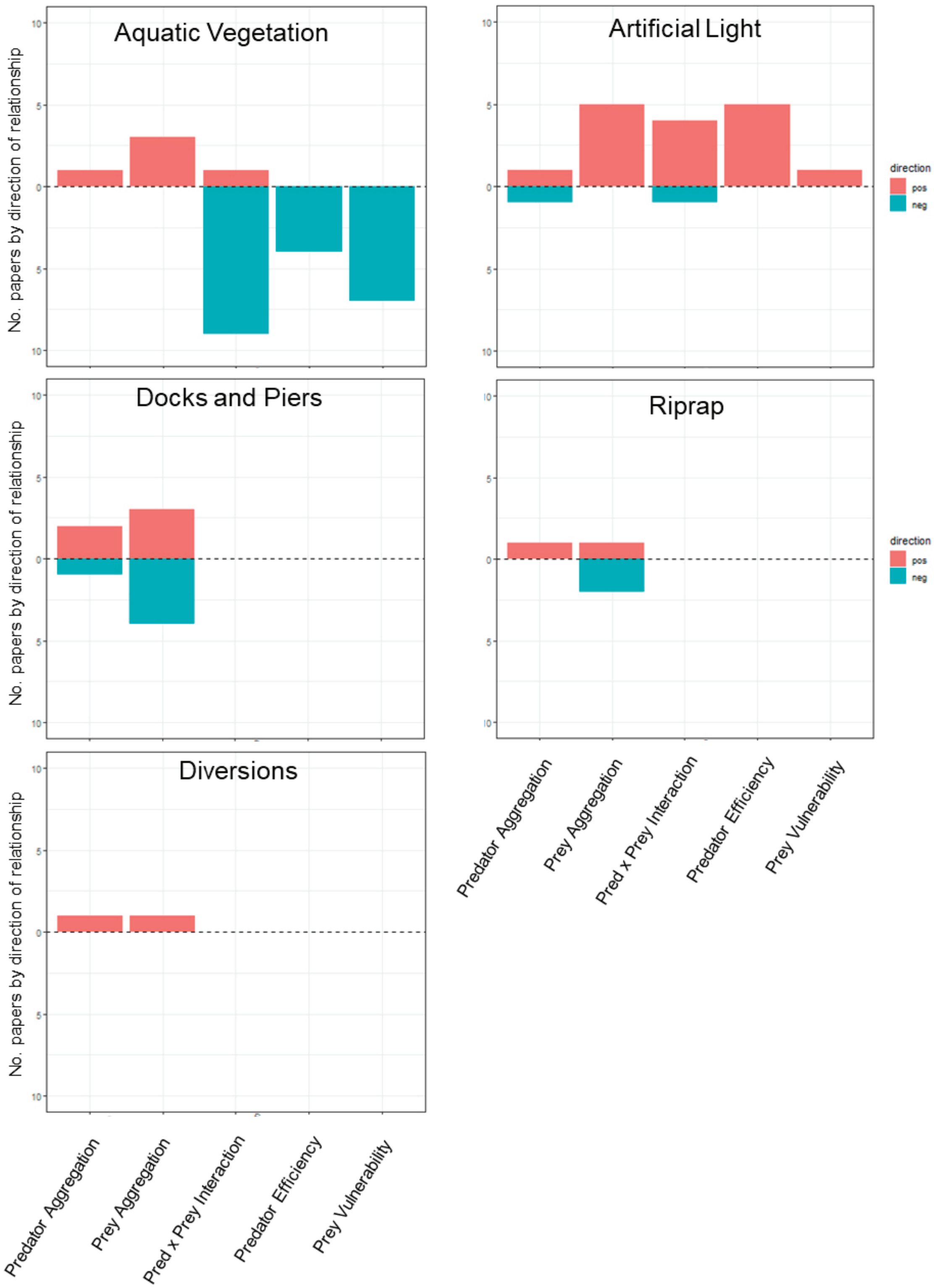

Figure 1 The number of peer-reviewed articles summarized by direction of the relationship between submerged contact points and five different biotic functions: predator aggregations, prey aggregations, frequency of predator and prey interactions, predator hunting efficiency, and prey vulnerability. Only studies that found significant results were included in the analysis.

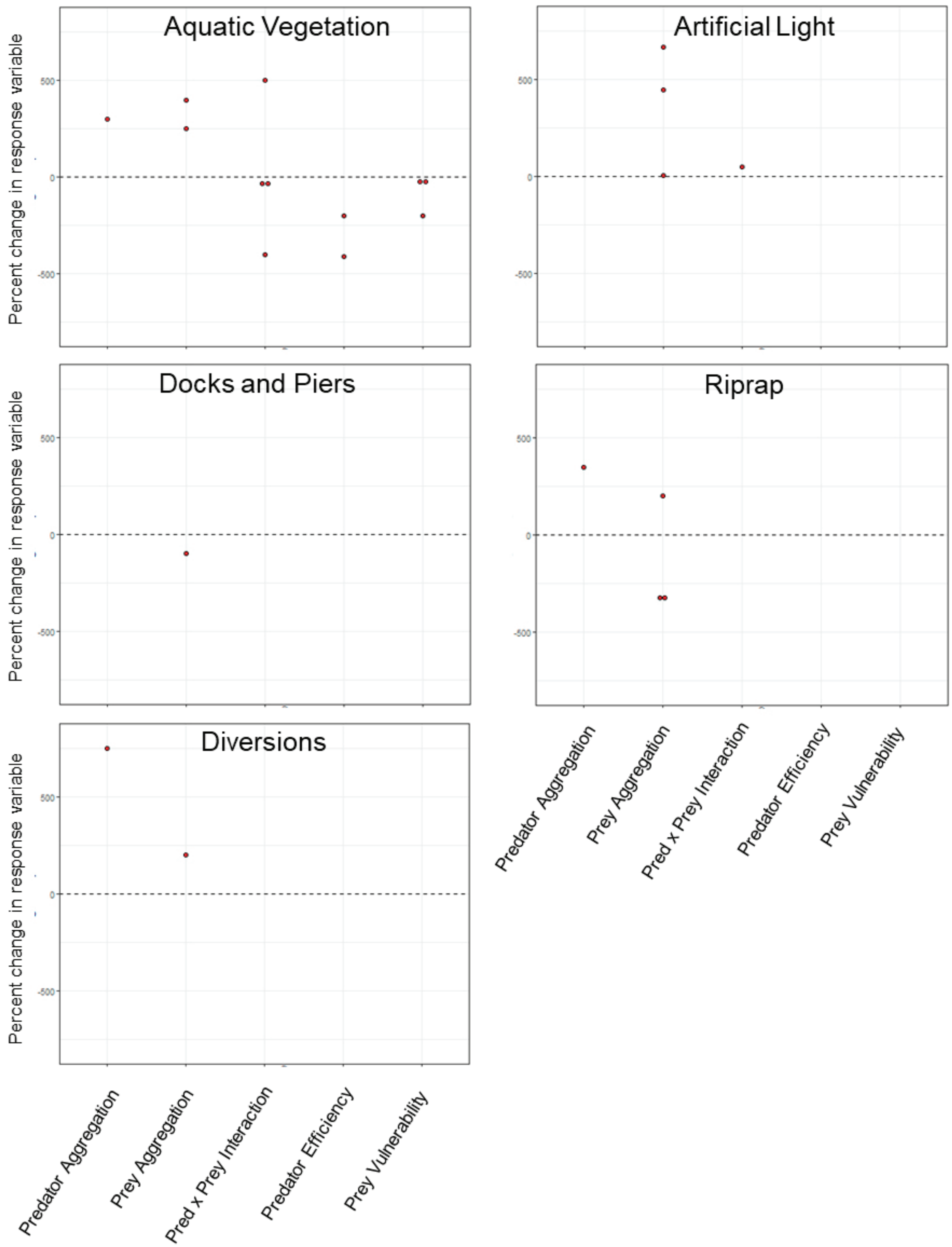

Figure 2 The magnitude of change (%) caused by contact points on five different biotic functions: predator aggregations, prey aggregations, frequency of predator and prey interactions, predator hunting efficiency, and prey vulnerability. Each point represents results from one statistical test within a given study. Only studies that found significant results that included magnitude of change were included in the analysis.

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such as water hyacinth (*Eichhornia crassipes*) are a prominent feature in the Delta and may be influencing fish behavior.

Artificial Light

All quantitative and qualitative measurements indicated that artificial lights increased the likelihood of predator success. Light attracted predator and prey aggregations, increased predator and prey interactions, increased predator efficiency and increased prey vulnerability (Figure 1). However, out of the 13 reviewed studies, only four reported the magnitude of the change (Figure 2).

Artificial light is difficult to quantify; it can be high-intensity and focused, such as floodlights on a dock, or it can be muted and dispersed across a large area, as from nearby urbanized areas. One study concluded that predators are more likely to be successful at an illumination threshold of 0.5-1 lux (Mazur and Beauchamp 2003; 2006), which is not much higher than illumination from a full moon. This may suggest that low-intensity, widespread illumination of the night sky could be sufficient to substantially alter the dynamics between visual predators and prey by disrupting natural dark cycles that offer refuge to prey. Indeed, the lunar cycle is understood to structure the migratory, foraging, spawning, and recruitment timing and behavior of many fishes (Nightingale et al. 2006). But the natural nighttime illumination from the moon is diffuse and consistent throughout space, though it varies in intensity on multiple temporal scales. Artificial nighttime lighting interrupts these natural cycles and deprives fish from naturally occurring periods of darkness.

Lights that shine directly on the water can aggregate prey by offering increased foraging opportunities (Becker et al. 2013; Tabor 2001). This may, in turn, attract predators cueing in to higher densities of prey fish. It is unclear if the color of the light influences predation success—only one study in our review examined light color, and it was found to be an insignificant factor (Kehayias et al. 2018).

Docks and Piers

There is conflicting evidence on how docks and piers influence predator and prey aggregations (Figure 1). One possibility is that the predator aggregation depends largely on the particular predator species. Specifically, ambush predators may benefit from the decreased light and shelter under docks, while roving predators do not. Some studies found that fishes aggregated near docks but not under them (Moore et al. 2013). However, docks may also be attractive to predator and prey species alike because they increase habitat complexity and provide shelter. Overall, the influence of docks and piers is still unclear and likely to be strongly influenced by the local predator community composition, thereby warranting further research.

Many of the studies on docks and piers focused on juvenile salmonids. Five papers found that large overhead structures impaired the movement of salmonids, either by delaying the timing of their movement until nightfall when shadows cast by the structure were less relevant (Ono and Simenstad 2014) or by causing them to swim around the structure (Kemp et al. 2005; Moore et al. 2013; Munsch et al. 2017; Southard et al. 2006). Although none of these studies directly measured changes in predator interactions associated with disruptions to movement associated with docks, several presume that being pushed into deeper habitat may expose juvenile salmon (and other small, soft-bodied fishes) to increased predation risk.

Riprap

Our review attempted to assess the effects of riprap specifically in the context of armored shorelines. We found only six studies that discussed our criteria in relation to coarse rocky revetment on the banks of rivers or estuaries. This may be, in part, because of the difficulty of defining concise search terms that describe this feature, or that more information on this subject is contained in reports or technical memos that were not found in our review. Of these six studies, four were focused on juvenile salmonids as prey species. Both (Tabor et al. 2017; Tiffan et al. 2016) found about a 3-fold decrease in the abundance of juvenile salmon along armored shorelines

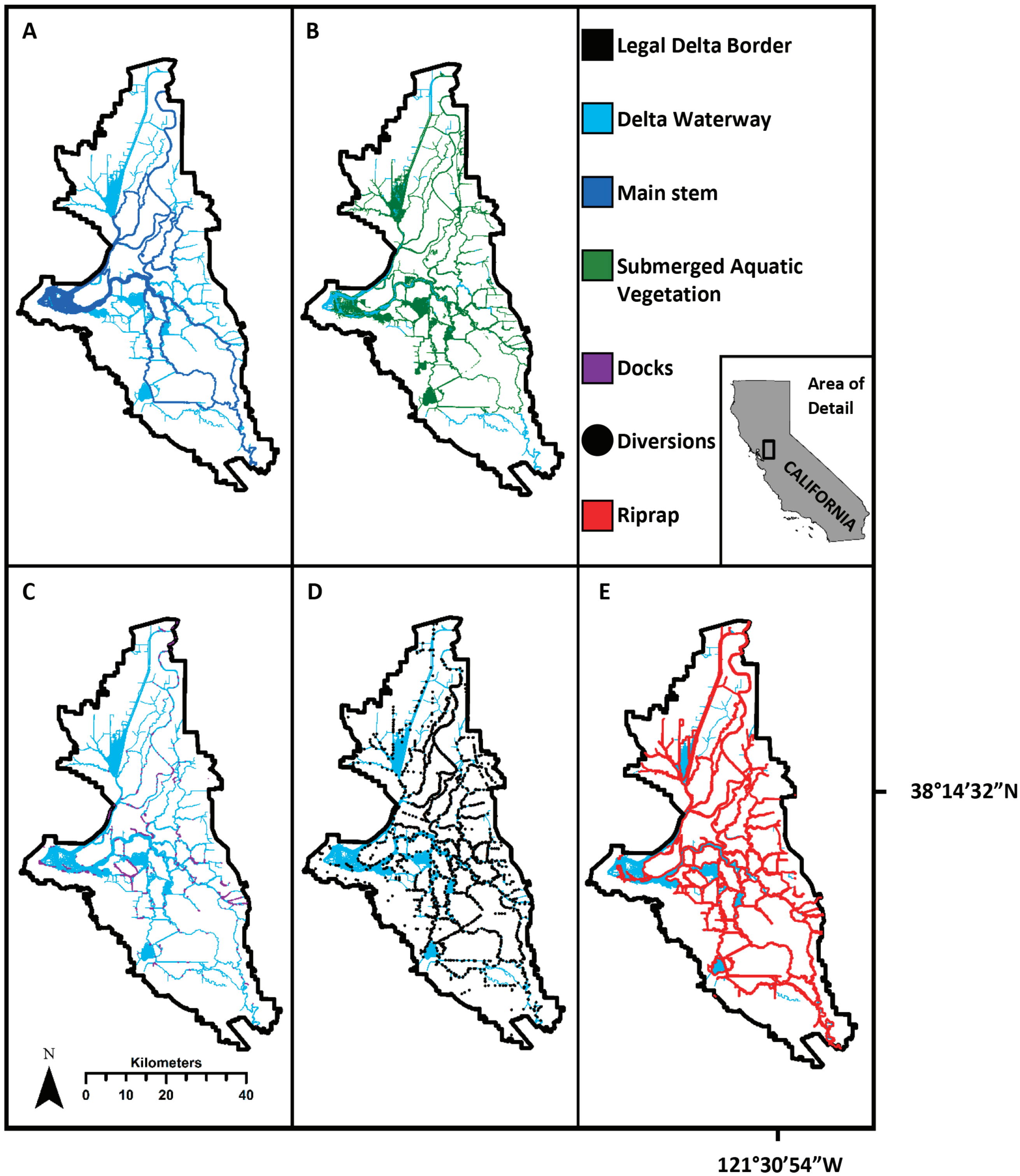

Figure 3 Maps of known contact points within the legal Sacramento–San Joaquin Delta. Map **A** depicts the waterways and mainstem waterways within the Delta. Map **B** shows submerged aquatic vegetation (SAV) distribution. Map **C** displays visible docks and floating houses, and map **D** shows the diversions throughout the Delta. Map **E** displays riprap throughout the Delta.

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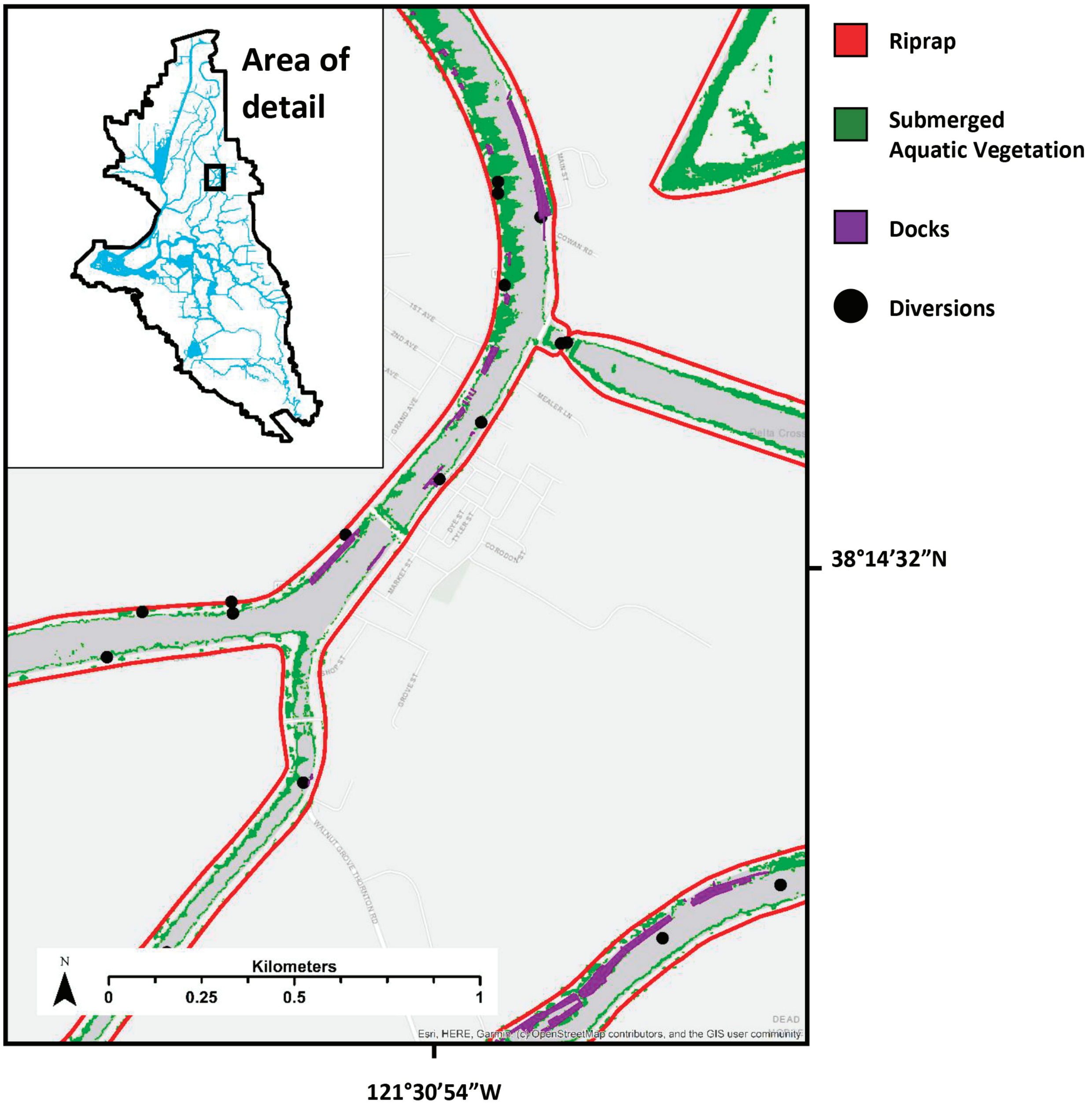

Figure 4 Close-up depicting the different types of potential contact points within the Sacramento–San Joaquin Delta: riprap, submerged aquatic vegetation (SAV), docks, and diversions

compared with naturalized banks with shallower slopes. No studies have directly quantified the difference in predation rates between these habitat types, yet several authors presume that shoreline armoring increases predation of salmonids, either by excluding them from shallow water habitat (Heerhartz and Toft 2015; Tabor et al. 2011) or by increasing abundances of predatory fish such as Smallmouth Bass (Tiffan et al. 2016).

Coarse Woody Debris

Only four papers examined the effects of woody debris on predation, and presented weak and conflicting results. Studies suggest that the relationship between woody debris and piscivory is non-linear, where depending on the size and distribution of wood, it may create refuge for prey (Enefalk et al. 2017) or it may create overlapping habitat with ambush predators (Helmus 2008).

None of the four papers in our set discussed woody debris in the context of larger watersheds and estuaries such as the Delta. Since woody debris are a major physical component in many natural freshwater systems, this subject warrants more investigation.

Scour Holes

It is widely assumed that bathymetric features affect fish behavior. However, our review found scant information on the effects of scour holes on predation. One paper (Kinzli and Myrick 2010) presumed that scour holes created by bendway weirs in the Rio Grande may create aggregations of fish that predate on the Silvery Minnow (*Hybognathus amarus*). The limited results from our search for the effects of scour holes on predator-prey interactions or aggregation could be the result of a lack of research on this topic, or an artifact of the difficulty in defining concise search terms that cover large bathymetric features in rivers and estuaries.

Diversions

We found only one study that discussed how water diversion structures affected fish predation. Sabal et al. (2016) found that a low-overhead dam to divert irrigation water aggregated high densities of predatory Striped Bass. The authors presume that the predators cue in on juvenile salmonids that become disoriented after passing through the dam spillway. They measured predation to be higher around this structure than anywhere else within several kilometers. However, these structures are relatively rare compared to bankside diversions or outfall pipes that are ubiquitous in lower-gradient rivers and estuaries such as the Delta. Our intention was to focus on the physical presence of bankside intake pipes that are common in the Delta and how their presence may alter predator-prey interactions. We found no peer-reviewed publications that discussed the influence of these pipes, but there may be more information available in gray literature.

CONTACT POINTS IN THE DELTA

To determine the spatial extent of four types of contact points throughout the Sacramento-San Joaquin Delta, we conducted a spatial analysis to determine the frequency and area of each contact point type using GIS (ESRI ArcGIS 10.4.1). We limited our spatial analysis to SAV, docks, riprap, and diversion (and outfall) pipes because there was no available information on artificial light, coarse woody debris, and scour holes on a Delta-wide scale. To complete this analysis, we compiled GIS layers that were either created for this study or that were assembled by other organizations. The geo-referenced information was then summarized by area and by count for the totality of Delta waterways (*https://www.wildlife.ca.gov/Data/GIS*), as well as for a subset of mainstem waterways (Figures 3 and 4). We defined mainstem waterways as channels that are frequently used by migrating juvenile Chinook Salmon (Perry et al. 2010): the Sacramento River; Sutter, Steamboat, and Miner sloughs in the North Delta; the North and South forks of the Mokelumne River and Georgiana Slough in the Central Delta; and the San Joaquin River, as well as Old and Middle rivers, in the South Delta.

Information on the extent of SAV in the Delta was acquired from University of California-Davis' 2015 remote-sensed SAV data set (Hestir et al. 2008). Submerged aquatic vegetation covers a substantial portion (~22%) of the Sacramento-San Joaquin Delta as measured by surface area (Table 2) and is present along ~20% of the shoreline (Table 3). The most abundant species are non-native and include *Egeria densa*, *Hydrilla verticillata*, and *Ludwigia spp.* (Ta et al. 2017). These form dense mats that likely impede fish movement and restrict open-water-associated species, such as salmon and Delta Smelt (*Hypomesus transpacificus*), to the mid-channel. The presence of SAV may have a large-scale effect on other native fishes in cases where it influences predator-prey dynamics. Relatively recent increases of SAV are presumed to be responsible for increases in Black Bass population such as Largemouth Bass (Conrad et al. 2016). In addition to increasing the frequency of predator-prey interactions, increases in SAV coverage in the Delta may be driving a large-scale change in

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Table 2 The frequency and area of submerged aquatic vegetation (SAV), docks, and diversions within the Sacramento–San Joaquin Delta. Blacked-out boxes indicate calculations are not possible due to type of data.

Contact point	Total count	Total density per linear km	Total area (km^2)	% Total area	Main stem count	Main stem density per linear km	Main stem area (km^2)	% Main stem area
SAV[a]	135042	82.50	50.94	22.24%	46845	82.57	18.20	15.77%
Docks[b]	2430	1.48	1.00	0.44%	752	1.33	0.41	0.36%
Diversions[c]	2497	1.53			1241	2.19		
Waterway[d]			229.10				115.42	

a. University of California–Davis, created from 2015 remote-sensed SAV data set.
b. University of California–Santa Cruz, created in 2019.
c. California Department of Fish and Wildlife created from Passage Assessment Database (PAD) in 2015.
d. California Department of Fish and Wildlife created from vegetation layer in Geographic Information Center and Chico Research Foundation.

Table 3 The length of shoreline that contains riprap and submerged aquatic vegetation throughout the Sacramento–San Joaquin Delta. Blacked-out boxes indicate calculations are not possible due type of data.

Contact point	Total shoreline extent (km)	% Total shoreline	Main stem shoreline extent (km)	% Main stem	Distributary shoreline extent (km)	% Distributary
Riprap[a]	1876.84	57.52%	914.17	72.63%	962.67	48.03%
SAV[b]	658.76	20.19%	235.64	18.72%	423.12	21.11%
Shoreline[c]	3262.85		1258.73		2004.12	

a. US Army Corps of Engineers, National Levee Database.
b. University of California–Davis, created from 2015 remote-sensed SAV data set.
c. California Department of Fish and Wildlife created from vegetation layer in Geographic Information Center and Chico Research Foundation.

the food web that supports a growing population of this non-native predatory fish (Brown and Michniuk 2007; Conrad et al. 2016).

Using satellite images from ArcGIS 2016-2017, we created the layer for dock contact points by hand-digitizing polygons around every visible dock and floating house. Many derelict pilings and submerged boats are not visible from satellite images, but may have similar effects. Therefore, our total area estimate is likely a conservative estimate of the extent of these types of structures. Docks cover a smaller portion of the Delta by surface area (0.44% total area) and an even smaller portion of the mainstem channels (0.36%; Table 2). The density of docks per river kilometer is similar between waterway types, but dock size was both larger and more variable in the mainstem channels ($M = 609\,m^2$, $SD = 1446\,m^2$) than in the distributaries ($M = 320\ m^2$, $SD = 97\,m^2$). This is most likely results from the varied uses of docks in the mainstem (both residential and commercial), while the docks in the distributaries were smaller, most likely for residential uses. It is possible that docks are affecting the migration of juvenile salmon in their migratory corridors and exposing them to increased predation risk. Southard et al. (2006) found that large ferry terminals impaired juvenile salmon movement along shorelines in Puget Sound because of the light contrast caused by the edge of the dock. Most large docks have bright lights that cast an underwater shadow at night, which may also affect fish activity. Docks are common and distributed throughout the Delta, but any efforts to understand their effect on fish predation should also focus on modifications that could be made to reduce their effect. Most docks and piers are either privately owned, or used for important human activities, so their removal in most cases would be contentious.

Most of the Delta channels are leveed and armored with large riprap. On the National

Levee Database from the US Army Corps of Engineers (*https://levees.sec.usace.army.mil/#/*), we found a comprehensive data set of leveed banks throughout the entire legal Delta. Riprap covered at least 57% of channel edges in the Delta (Table 3). With 73% of the mainstem channels leveed, there are very few places within the mainstem channels where the bank is not heavily modified to prevent scouring or flooding. Delta waterways have a cross-sectional "U" shape, with steep slopes and a uniform bottom. This severely limits the amount of shallow water habitat that small fish can access as refuge from predators. High densities of SAV along the banks may exacerbate the exclusion of species such as salmon from the limited shallow-bank margin habitat and increase their exposure to predatory fish such as Striped Bass, which are predominantly in the center of the river channel (Michel et al. 2018).

The water diversion data set was acquired from the Passage Assessment Database (PAD; *https://nrm.dfg.ca.gov/PAD/Default.aspx*) compiled by the California Department of Fish and Wildlife. There are nearly 2,500 bankside diversion structures, over 90% of which have unscreened pipe intakes (Table 2). Local resource managers are concerned that these may increase predation opportunities for large fish by entraining small prey that aren't strong enough to swim against the flow (Grossman et al. 2013). Because the pipes are typically distinct features from otherwise-homogenous riprap bank habitat, even when they are not operational they may also aggregate predators or prey. However, our literature review found few studies that assessed the effect of water diversions on fish predation, so these relationships are largely theorized.

There are currently no reliable geo-referenced data of artificial illumination in the Delta. However, shoreline development is common along the mainstem of the Sacramento and San Joaquin rivers. The Delta is likely to be negatively affected by disruptions to natural light cycles and warrants surveys to inventory the number and intensity of lights along its banks.

CONCLUSIONS

Predator-prey dynamics are mediated by physical, chemical, and biological factors. The relationship between habitat features and predation interactions is complex and species-ecological system specific. Thus, restoration actions aimed at improving native fish populations by altering the physical habitat of rivers and estuaries must consider the existing literature and local habitat and species compositions. This literature review can guide future areas of research and attention, and, ultimately, potential remediation options.

Our literature review indicates that SAV and artificial illumination greatly influence fish predation in freshwater ecosystems worldwide. The effect of these habitat features is species- and context-dependent, and given the vast spatial extent of SAV and artificial illumination in the Central Valley, they are both important future avenues of research. Currently, there is no inventory of areas subject to artificial illumination in the Delta, let alone any regulations in place to minimize the effect of artificial illumination on wildlife. And, at present, most efforts to control SAV are focused on clearing channels for boat navigation. There may be opportunities to discover new tools for fisheries management through developing methods to reduce or alter SAV distribution.

Urban and shoreline development will inexorably lead to further increases in nighttime lighting. And, as sea levels rise, shifting climatic conditions and new invasions will likely result in changes to the distribution and density of SAV (McKee et al. 2012). Even if controlling SAV and reducing lighting are intractable issues, quantifying their effect on species of management concern will be valuable for forecasting future population trends.

The absence of studies that describe the effects of other types of contact points on fish predation does not necessarily indicate that they are not important. For example, we found no studies that discussed the effects of FAV on predator-prey dynamics. However, given the relationship between similar habitat features such as SAV and large woody debris (LWD), future efforts to

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understand how FAV influences the interaction of fishes in the Delta are warranted. Quantifying how physical features influence the contact between two organisms is difficult because effects may be indirect and have multiple components (e.g., a dock may affect underwater lighting as well as local hydrodynamics). Similarly, a lack of significant results in studies does not necessarily mean that a contact point is not an important factor on predation dynamics. Effects on fish behavior may be difficult to measure directly because they are not discrete points in space, and may or may not have a linear effect on behavior (e.g., riprap often extends along shorelines for miles and is confounded by other bathymetric features such as slope steepness and depth). Additionally, research on the subject may have been ancillary to a different question and therefore may not have been designed to isolate the effect. Directed studies will provide more nuanced insight on the effect that different contact points have on predator-prey dynamics.

Furthermore, while it is important to understand the individual influence of each type of contact point on predator-prey interactions, fish may often interact with multiple contact points in a small area (Figure 4). Thus, it is important to also understand the compounding and interacting effects of multiple contact points (e.g., aquatic vegetation surrounding a dock with a light).

Management actions that modify physical features to improve native fish populations in the Delta must consider both the magnitude of influence of any given contact point, and potential reduction in predation associated with the action. For example, although several studies have shown that docks and piers significantly affect juvenile salmon migration (Moore et al. 2013; Southard et al. 2006), these structures are relatively sparse within the main migratory pathways in the Delta, and we hypothesize that their removal might have limited effect on salmonid populations. Because salmon migrate primarily at night (Chapman et al. 2013), we believe that an assessment of nighttime lighting in the Delta would be a worthwhile avenue for future research. Submerged aquatic vegetation and associated predatory centrarchid populations (Conrad et al. 2016) are prevalent throughout hundreds of kilometers of salmon migration corridors. Salmon are more likely to be found in margin habitats without SAV than in those with sparse or dense SAV (Simenstad et al. 1999). If the widespread proliferation of SAV is excluding them from littoral margins of waterways, it may be indirectly subjecting them to increased predation pressure by pelagic predators such as Striped Bass (Grimaldo et al. 2000). There is limited information available to estimate how SAV removal would affect salmon predation in the Delta. And without those estimates, it's impossible to determine if SAV removals will have a population-level effect. Thus, given the large spatial extent of SAV, the subject deserves future research.

The Central Valley rivers and the Delta have been irreversibly modified to serve human needs such as land reclamation and water distribution. However, there is considerable interest in funding habitat restoration projects that will improve native fish populations within the confines of a highly altered landscape. The relationships between human habitat alterations and wild organisms are still mostly unknown. Pairing literature reviews with spatial data sets can be an objective way to prioritize research in areas that are currently data-poor. In collaboration with government agencies and stakeholder groups, the authors are currently designing studies to further our understanding of how contact points affect interactions between salmon and their predators in the Central Valley.

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