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A Multi-scale Investigation of Fish Response to Environmental Change

By

ALEXANDRA G. MCINTURF  
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Animal Behavior

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

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Nann A. Fangué, Co-Chair

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Damien Caillaud, Co-Chair

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Heidi Dewar

Committee in Charge

2021

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# Abstract

The impacts of climate change and anthropogenic disturbance are pervasive throughout ecosystems. Yet particularly in aquatic and marine systems, animal responses to the resulting environmental changes can be difficult to determine, which inhibits appropriate management strategies. Conservation efforts are often based on research that examines the effect of stressors or human-induced impacts on a single species and/or scale. However, this approach can be too narrowly focused. Species do not exist in isolation, and there are many potential drivers of their survivorship and behavior that extend beyond the individual or population. Particularly for mobile species, such as many fishes, population dynamics can be strongly influenced by species interactions, individual movements within a habitat, or changes in habitat suitability. As a result, the impacts of environmental change can be highly complex or even counter-intuitive, particularly in locations where these changes are occurring rapidly.

Among these, California hosts a variety of aquatic and marine habitats that have been dramatically modified by human activity over the last century. These ecosystems now face further alteration due to a changing climate. Consequently, there is growing concern about how species will respond to additional stressors, such as increasing water temperatures. Our ability to forecast these effects is becoming increasingly important, because while many endemic fishes are already heavily managed, some populations are continuing to decline. The potential consequences of these declines can be dire, affecting ecological communities as well as human populations that rely on fish for sustenance. However, the mechanisms underlying patterns of fish presence and survival are multifaceted and remain undetermined in many cases, preventing a reevaluation of conservation efforts. To address this, my dissertation demonstrates the value of a more holistic perspective on organismal response to environmental change. Focusing on species



that are threatened or data deficient in California waters, I use select case studies to examine fish responses to environmental changes at multiple scales, including fish physiology, behavior, and habitat use.

Chapter 1 is based in the Sacramento-San Joaquin River Delta of California's Central Valley. Here, increased mortality of outmigrating juvenile salmon has been correlated to warming water temperature. It has been assumed that reduced survivorship is due to salmon thermal physiology. Yet emerging laboratory studies suggest that these salmon populations are relatively thermally robust. Instead, I test the hypothesis that decreases in salmon survivorship are due to increased activity of non-native predators. My results suggest that major predators of salmon in the Delta are more thermally adapted to warmer temperatures, increasing the possibility of their threat to juvenile salmon in light of global warming. This indicates that an understanding of fundamental thermal physiology can be useful in predicting predator-prey dynamics; however, I also show that such an approach is highly dependent on the physiological metric employed, and it is more effective for some species than others. Regardless, given that the Delta is a highly modified ecosystem, managers could hypothetically improve juvenile salmon survivorship by adjusting water flow, and therefore temperature, along primary outmigration routes based on predator thermal preferences.

Chapter 2 scales up to consider fish behavioral response to current flows in the San Francisco Bay Estuary. In estuarine habitats, seasonal and daily hydrological variance is affected by human activity, such as dredging and coastal wetland development, and rising sea levels due to global warming. However, assessing fish responses to hydrological patterns is logistically challenging, limiting our ability to predict how future changes will impact the behavior of local populations. In this chapter, I explore the use of hydrodynamic models for examining the

influence of tidal flow in the San Francisco Bay Estuary on broadnose sevengill sharks (*Notorynchus cepedianus*). Combining acoustic tracking data with these models, I find evidence that sharks swim in and out of the bay with most of the ebb and flood tides, presumably to move in the most energetically efficient manner. However, this movement was not universal, nor was it dependent on the strength of the tide. This suggests that there may be other variables shaping sevengill shark behavior in this habitat, such as prey availability, which offsets the energetic cost of moving against the tide. Taken together, my results demonstrate that tidal movement is not the sole driver of sevengill shark behavior, but this species will likely be susceptible to potential hydrological changes in the future.

Chapter 3 examines environmental impacts at the largest scale, using a spatial modeling approach to determine population-level trends and habitat use in a large, highly migratory species: the basking shark. Historically targeted globally for their liver oil, fins, and meat, basking sharks were classified as globally endangered in 2019. While they seem to be responding well to protective measures in some parts of their range, there appears to be no sign of recovery in the Eastern North Pacific population. However, evaluating the status of this population is hindered by multiple data gaps. It has not been determined whether variation in shark sightings over time is due to changes in population size or the effect of environmental change on basking shark distribution. To fill these gaps, I compile recent and historical data to describe variation in basking shark sightings and school size over time in the California Current Ecosystem (CCE). I also build species distribution models using general additive mixed models to determine the environmental factors that may affect their distribution and sightings probability. My results suggest that the number and probability of sightings declined in the mid-1980s, as did the size of schools reported. Simultaneously, there was a shift in sighting

seasonality, from fall and spring to summer starting in the 2000s. The species distribution models also revealed that sightings probability increased with low sea surface temperature and high chlorophyll *a* concentration, and was correlated with larger-scale climatic oscillations. Based on these analyses and previous studies, I conclude that the decline in sightings after the 1980s most likely emerged because of a decrease in the population following a century of culling and overfishing. This was perhaps exacerbated by an Allee effect based on the simultaneous decrease in group size. Furthermore, there is a high probability that the basking sharks that remain in the CCE will be affected by a combination of changing sea surface temperatures and shifting prey fields in the future, though the degree to which this will shift their spatial or temporal distribution is unknown. To better inform management of the CCE basking shark population, there should be more coordinated documentation of fisheries mortalities and sightings to inform population estimates and track potential changes in habitat use. I also advocate for improved monitoring of shark fin markets to ensure existing conservation regulations are being followed.

In conclusion, climate change and increasing anthropogenic activity are rapidly altering California's aquatic and marine ecosystems, rendering conservation more difficult. My dissertation contributes to a large body of evidence highlighting numerous threats, from warming temperatures to habitat alteration, that are affecting species directly and ecosystem interactions more broadly. Together, these chapters show that species responses to potential threats will vary depending on environmental variables, animal behavior, and community interactions. It is critical to consider each of these levels of influence when predicting how populations will fare with environmental change. In turn, this broader understanding will improve dynamic management strategies for threatened species facing an uncertain future.

## **Chapter 1:**

# **In hot water? Assessing the link between fundamental thermal physiology and predation risk of juvenile salmon in the Sacramento-San Joaquin River Delta**

Alexandra G. McInturf<sup>1,2</sup>, Ken W. Zillig<sup>1,3</sup>, Katherine Cook<sup>1</sup>, Jacqueline Fukumoto<sup>1</sup>, Anna Jones<sup>1</sup>, Emily Patterson<sup>1</sup>, Dennis Cocherell<sup>1</sup>, Cyril Michel<sup>4</sup>, Damien Caillaud<sup>5</sup>, Nann A. Fangué<sup>1</sup>

<sup>1</sup> Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA USA

<sup>2</sup> Animal Behavior Graduate Group, University of California, Davis, CA USA

<sup>3</sup> Graduate Group in Ecology, University of California, Davis, CA USA

<sup>4</sup> NOAA Southwest Fisheries Science Center, Fisheries Ecology Division, Santa Cruz, CA, USA

<sup>5</sup> Department of Anthropology, University of California, Davis, CA, USA

**Abstract:**

In light of ongoing environmental change, understanding the complex impact of interacting stressors on species, communities, and ecosystems is an important challenge. Many studies to date examine the effects of potential stressors (*e.g.*, temperature, toxins, disease) on a single species of concern. Yet these effects often resonate throughout a community and may produce changes in ecosystem dynamics that are equally critical to species resilience. The aim of this study was to develop a mechanistic understanding of how a rapidly changing stressor, temperature, will alter trophic interactions among ectothermic fish species. We focused on the Sacramento-San Joaquin River Delta system, where it has been speculated that the decreased survivorship of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in warming waters may be caused partly by increased predation. Temperature influences metabolic rate functions and the amount of energy available for fitness-relevant parameters (*i.e.*, swim performance and escape response). Consequently, we hypothesized that these patterns of predation emerge due to a physiological advantage of predators over prey at warmer temperatures. To explore this hypothesis, we sought to identify the temperatures at which each species (salmon versus their predators) might have a physiological advantage, and whether fundamental thermal physiology was a good predictor of predator-prey outcomes. Our first objective was to determine the fundamental physiology of juvenile Chinook salmon and their potential predators in the Delta. Three physiological performance traits were measured for each species across a spectrum of temperatures: aerobic scope, burst speed, and the ability to burst repeatedly. For our second objective, we assessed whether the effect of temperature on these performance traits predicted the outcome of predation trials conducted across the same temperature spectrum. We found that temperature effects varied by the species or population of fish. Depending on the performance

trait examined, fundamental thermal physiological performance was not always consistent with predation trial outcomes. However, both absolute burst ability and the relative burst performance between predator and prey were stronger indicators of trophic dynamics than aerobic scope. Our analyses also confirmed that some major predators in the Delta are more thermally adapted to higher temperatures and will likely consume salmon with an increasing frequency as waters warm. Thus, we show that an improved understanding of how fundamental thermal physiology impacts predation risk can provide ecosystem managers with better tools to predictively model predation upon juvenile salmon based on prevailing and future water temperatures.

### **Introduction:**

Among its many known effects, climate change is leading to increases in water temperatures. This trend is forecasted to continue throughout the 21<sup>st</sup> century (Alfonso *et al.*, 2021; IPCC, 2013), and its potential impact on aquatic and marine systems is concerning. Organisms that occupy these habitats, such as ectothermic fishes, have thermal tolerance limits based on the temperature sensitivity of biochemical mechanisms (Pike *et al.*, 2013; Pörtner *et al.*, 2005), which are affected by the surrounding water temperature. Extreme temperatures outside of an organism's tolerance can affect growth and reproductive potential, but also lead to physiological stress and even mortality (Boughton *et al.*, 2007; Crozier *et al.*, 2008; Martins *et al.*, 2012; Hokanson *et al.*, 1977; Pike *et al.*, 2013). In turn, physiological responses to temperature can affect the behavior, population dynamics, and distribution of a given species. For example, known effects of temperature change include range contractions or expansions (Marras *et al.*, 2015; Perry *et al.*, 2005), and in extreme cases, an increase in extinction rate (Ben Rais Lasram *et al.*, 2010; Marras *et al.*, 2015). It has been speculated that the alterations in

physiological performance due to warming conditions is directly correlated with these larger-scale impacts (Marras *et al.*, 2015; Pörtner & Knust, 2007). As a result, many studies are currently designed to understand how temperature affects organisms intrinsically, via their fundamental thermal physiology (*i.e.*, the collection of intrinsic physiological traits that define a species' thermal capacity; Fry, 1947; Zillig *et al.*, 2021). Yet it is unlikely that fundamental physiology alone is a sufficient predictor of a species' response to temperature. Organisms do not exist in isolation, and there is a significant gap in our understanding of how temperature interacts with environmental forces (*e.g.*, predation, competition, disease) to constrain the fundamental thermal physiology of a species, producing its ecological thermal physiology (Brett, 1971; Zillig *et al.*, 2021). Because climate change will undoubtedly affect both fundamental and ecological physiologies, predicting organism response to climate change requires a better understanding of how intrinsic physiology and extrinsic ecosystem dynamics interact to influence population-specific thermal performance.

In California's Central Valley, warming conditions have led to increased focus on the complex effects of temperature on fish physiology and survivorship. This region hosts four runs of Chinook salmon (*Oncorhynchus tshawytscha*; Johnson *et al.* 2017) that are protected under state and federal endangered species acts following severe population declines (Fisher, 1994; Marine & Cech, 2004; Nehlsen *et al.*, 1991; Yoshiyama *et al.*, 1998). These declines have been attributed to low survivorship in outmigrating juveniles at warmer temperatures (Buchanan *et al.*, 2013; Kjelson & Brandes, 1989; Michel *et al.*, 2020; Michel *et al.*, 2015; Perry *et al.*, 2010). Historically, increased juvenile mortality was assumed to result from thermal stress (*e.g.*, Crossin *et al.*, 2015), as water management and extreme variation in precipitation (Dettinger *et al.*, 2011; Johnson *et al.*, 2017; Moyle, 2002) elevated water temperatures during the spawning and rearing

season of the Chinook salmon runs (Marine & Cech, 2004b). Unexpectedly, however, laboratory studies reveal that some runs of Chinook salmon in this region appear thermally robust, capable of physiological growth and performance at the high temperatures often correlated with increased mortality in the wild (Marine & Cech, 2004; Poletto *et al.*, 2017; Verhille *et al.*, 2016; Zillig *et al.*, 2020). It is thus unlikely that lower survival under warm conditions can be solely attributed to the direct effects of temperature on the fundamental physiology of salmon.

Alternatively, recent research on this system (*e.g.*, Nobriga *et al.*, 2021) suggests that warming temperatures may indirectly influence salmon survivorship, specifically via the risk of predation. Central Valley waterways are home to numerous predator species that have demonstrated top-down control on salmon populations (Erhardt *et al.*, 2013; Lindley *et al.*, 2003; Nobriga *et al.*, 2021; Sabal *et al.*, 2016). Acoustic tagging of juvenile Chinook salmon the Sacramento-San Joaquin River Delta has revealed survival rates of <1% (Michel *et al.*, 2018), and it is thought that the Delta is a major survival bottleneck due to the presence of primarily non-native piscivorous predators, such as striped bass (*Morone saxatilis*) and largemouth bass (*Micropterus salmoides*) (Demetras *et al.*, 2016; Michel *et al.*, 2018; Nobriga *et al.*, 2021). In addition, predation in the Delta has been shown to increase with temperatures that correspond to decreased survivorship of outmigrating late-fall run Chinook salmon (Henderson *et al.*, 2019; Johnson *et al.*, 2017; Nobriga *et al.*, 2021). This trend may be due to the physiology of common predators; for example, largemouth bass metabolism is highly sensitive to the range of water temperatures in the Delta, which could accelerate demand for prey as waters warm (Nobriga *et al.*, 2021). However, to date there has been no further exploration of whether predators are physiologically advantaged at warmer temperatures, or whether there is a link between thermal physiology and predation success.



A key next step in determining the patterns of salmon mortality in the Delta is to determine whether species-specific physiology can be used to predict trophic interactions. The fundamental thermal physiology for a given species is measured by a variety of traits: acute and chronic thermal limits (*e.g.*, Myrick & Cech, 2005; Keefer *et al.*, 2018), growth rates (*e.g.*, Cech & Myrick, 1999; Marine & Cech, 2004), and temperature dependent metabolic indices such as aerobic scope (*e.g.*, Eliason *et al.*, 2011; Rummer *et al.*, 2016), cardiac physiology (*e.g.*, Anttila *et al.*, 2018; Eliason *et al.*, 2011), or enzyme activities (*e.g.*, Hochachka & Somero, 1968). These traits are often quantified in a laboratory setting and then extrapolated for management applications; however, they may not all be useful for determining the ecological thermal physiology of an organism in every context. For example, there have been discrepancies in growth rates for juvenile Chinook salmon between laboratory and field experiments (Zillig *et al.*, 2021). These could be attributed to differences in water chemistry or the effects of disease (Myrick & Cech, 2001). Alternatively, as other studies have shown, food availability (Lusardi *et al.*, 2020; Railsback & Rose, 1999) and competition (Reese & Harvey, 2002) may act synergistically with temperature to influence juvenile salmonid growth in the wild. Similarly, much work on salmonids has focused on aerobic scope, or the difference between maximum metabolic rate and resting metabolic rate (*e.g.*, Marine & Cech, 2004; Poletto *et al.*, 2017; Verhille *et al.*, 2016; Zillig *et al.*, 2020). Aerobic scope represents the capacity of aerobic metabolism, in excess of basic maintenance costs, for fitness-enhancing activities, such as feeding and swimming (Rummer *et al.*, 2016). However, studies using aerobic scope can also produce results that do not align with trends observed in the field; for example, aerobic scope values have indicated that salmonid populations are relatively thermally robust, but their survival in the Delta decreases with warmer temperatures.

Collectively, these differences in laboratory- and field-based studies suggest that ecological factors and natural animal behaviors must be considered when designing physiological studies, to produce results that are applicable to natural settings. For predator-prey interactions specifically, other physiological measurements may be important. For instance, bursts are high-energy swimming bouts (<20 seconds; Domenici & Blake, 1997; Domenici & Batty, 1994; Jayne & Lauder, 1993) that are used by most fish when escaping predators or achieving prey capture (Domenici & Blake, 1997). Yet burst swimming in many species of fish, including salmonids, has barely been studied. Furthermore, of the few studies on this topic, burst speed has been commonly reported (reviewed in Domenici & Blake, 1997), but other metrics, such as maneuverability, burst distance or the ability to undertake repeated bursts, also warrant examination based on the behaviors observed during a predator-prey encounter. Given the life-history strategies of different organisms, it is likely that physiological performance across traits will vary not only by temperature, but by species or even populations. Therefore, quantifying a thermal physiological advantage ideally entails assessment of multiple species-specific traits.

In this study, we used a multi-species, multi-trait approach to test the hypothesis that patterns of juvenile salmon mortality in the Delta occur due to a physiological advantage of their predators at warmer temperatures. To do so, our objectives were i) to identify the optimal physiological temperatures for salmon and their common predators based on multiple performance traits; ii) to determine whether these temperatures confer a relative advantage between species in predator-prey interactions. We predicted that predation would be greatest at temperatures where predators possessed a relative physiological advantage, and lowest at temperatures where salmon performed best relative to their predators.

## Methods:

### *Experimental overview*

The aim of this study was to assess how predation outcomes related to physiological performance. We examined two runs of juvenile Chinook salmon (fall-run and late-fall run), which allowed us to explore how salmon populations within the same species vary in their fundamental thermal physiology, if at all. The Chinook salmon is a relatively wide-ranging species and includes several at-risk populations confronting thermal stress (Moyle *et al.*, 2017; Yoshiyama *et al.*, 1998; Zillig *et al.*, 2021), particularly in the Central Valley, which is at the southern end of its range. Our study also examined the two major non-native predators of salmon in this system: largemouth bass and striped bass. Though it only occasionally feeds upon other salmonids, rainbow trout (*Oncorhynchus mykiss*) was included as an additional predator because its physiology may more closely resemble that of salmon. If fundamental thermal physiology were underpinning trophic dynamics, we would expect rainbow trout physiological response and subsequent predation behavior to provide a contrast with that of the other predators, which primarily occupy mid- to high-temperature waters in the Delta.

With these species, we first identified optimal physiological performance temperatures (Objective 1). Three difference performance traits were measured across a temperature spectrum: aerobic scope, burst speed, and the ability to repeatedly burst (Fig. 1.1). Measurements were taken in all species except for striped bass. To then determine if thermal physiological performance influenced the outcome of trophic interactions (Objective 2), we conducted predation trials across the same set of temperatures, using different combinations of salmon and predators (*i.e.*, largemouth bass with late fall-run Chinook salmon; striped bass or rainbow trout

with fall-run Chinook salmon; Fig. 1.1). Details regarding each component of our experiments are outlined below.

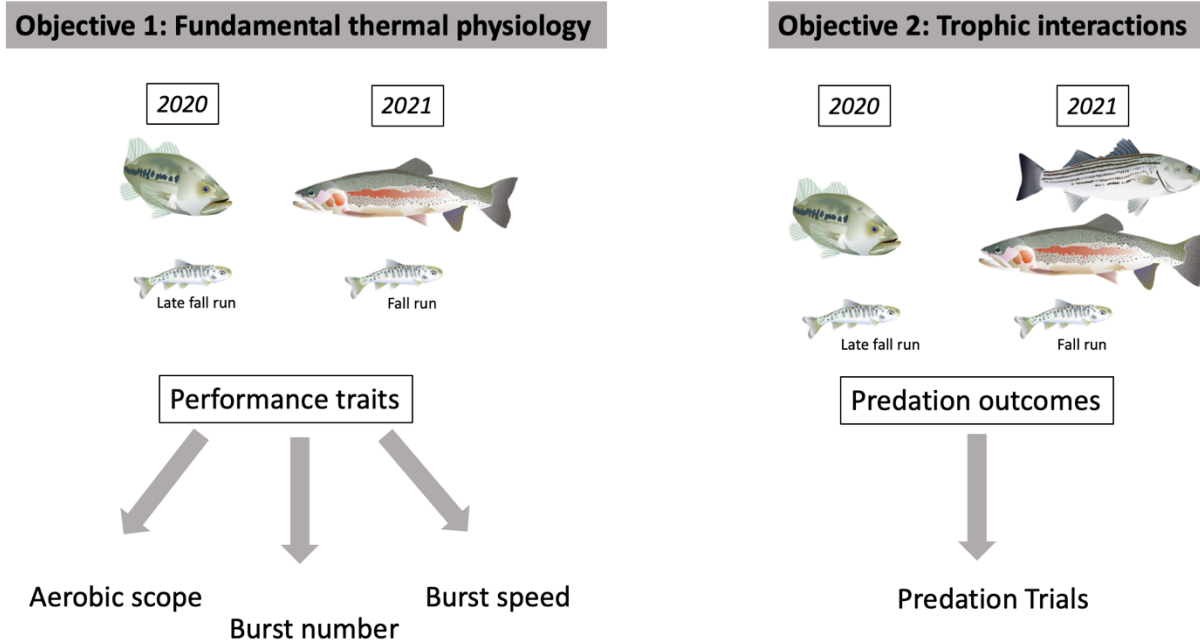


Figure 1.1. A schematic overview of the experimental procedures, which took place in 2020 and 2021. See “Methods” for more details. Illustrations adapted from Amelia Munson, with permission.

### *Fish husbandry and transport*

The experimental procedures for this study took place from January-July, 2020 and January-May, 2021. All fish care and protocols were approved by the University of California Davis (UC Davis) Institutional Animal Care and Use Committee (protocol no. 21468). For the first set of experiments, late fall-run Chinook salmon (n=3,000) were collected from the Coleman National Fish hatchery as eyed eggs (Anderson, CA), and largemouth bass (n=150) were obtained from The Fishery Inc. (Galt, CA). Both species were transported in aerated fresh water to the Center for Aquatic Biology and Aquaculture (CABA) at the University of California, Davis. Largemouth bass were held in a 1.5 m-diameter tank with continuous flows of aerated water from a designated well and fed *ad libitum* with a pelleted diet (Skretting, UT,

USA). Chinook salmon were kept in two 1 m-diameter indoor tanks, again with continuous flows, until they hatched, when they were transferred to a 2 m-diameter outdoor tank. They were transitioned to a semi-moist starter feed (Rangen, Inc., ID, USA) *ad libitum*, and then feed at 4% feed rate (% body weight per fish per day) of commercial pelleted salmon feed (Skretting, UT, USA) *ad libitum* throughout the experimental trials.

During the second set of experiments, fall-run Chinook salmon were collected from the Nimbus River hatchery as eyed eggs (n=6,000), and were reared following the same protocol as the late fall-run Chinook salmon (described above). Wild-caught striped bass (n=77) were gathered via boat electrofishing in the Clifton Court Forebay and held at the Tracy Fish Collection Facility (Contra Costa, CA; permit no. S-19170001-20084-001). They were then transported via a transport tank equipped with oxygen to the Putah Creek Fish Facility of CABA and held in a 2 m-diameter flow-through tank at 11°C (+/- 0.5°C). Here they were fed a diet of live fathead minnows (*Pimephales promelas*) purchased commercially from Anderson Minnows (Lonoke, AR). Roughly 2 weeks before experimental trials, striped bass were transported to the main CABA facility where they were held for experimental trials. In addition, rainbow trout (n=150) were donated for research from the American River Hatchery (Gold River, CA) by California Department of Fish and Wildlife. They were held at the CABA facility in 2 m-diameter tanks with continuous flows of aerated well water and fed a pelleted diet (Skretting, UT, USA) *ad libitum* prior to the experiments.

After transport each year, all predators were given a 7-day acclimation period at their prior holding temperatures (largemouth bass: 16°C; striped bass and rainbow trout: 11°C) before their water temperatures were increased by 2°C per day until they reached 18°C. This was considered the neutral temperature for the study, as it did not represent the extremes of thermal

tolerance for any of the studied species. It has also been reported as a common temperature for the Delta during field-based studies on predation (Michel *et al.*, 2018). We performed the same temperature ramp with the fall- and late fall-run Chinook salmon after they were large enough to consume pelleted feed. All fish were given at least three weeks at 18°C before any experimental measurements were taken. During this time, predators were transferred to a diet of live feed (juvenile Chinook and fathead minnow) to ensure that they would be able to recognize and consume prey during the predation trials.

### *Experimental design*

All fish were assigned to one of 5 different treatment groups, which reflected our test temperatures: 11, 14, 18, 22, 25°C. These temperatures captured the range experienced by Sacramento-San Joaquin River Delta system throughout much of the year (*e.g.*, Marine & Cech, 2004; Pike *et al.*, 2013; Poletto *et al.*, 2017). We aimed to test 6-8 fish per species or population at each temperature for each of the following performance traits: aerobic scope, burst capacity (*i.e.*, speed and number of repeated bursts), and predation trial performance (Table 1.1). In some cases, however, incidental mortality reduced our sample size, particularly among the predators; given a limited supply of fish available, any predator excluded from the experiment due to health or behavioral reasons was not replaced.

Prior to any experimental measurements, fish were transferred to a holding tank for a 24-hour fasting period (see exception in “Predation trials”). They were then ramped to their assigned temperature by 2°C per hour and given 30 minutes to acclimate to that temperature. Following the procedure, the fish were returned to 18°C via the same process. They were given 24 hours to recover and were weighed and measured before being returned to their original tank.

Table 1.1. A summary of the fishes used in each component of this study. Sample size and mean and range of masses are listed. Predation trials took place with late fall-run (LFR) Chinook salmon and largemouth bass in 2020, and fall-run (FR) Chinook salmon and either rainbow trout (RT) or striped bass (SB) in 2021.

Species/Population (year tested)	Aerobic scope	Burst ability	Predation trials	
Largemouth bass (2020)	n=39 mean mass: 227.05 g (range: 146.3 – 298.7 g)	n=39 mean mass: 227.09 g (range: 148.3 – 297.4 g)	n=40 mean mass: 221.29 g (range: 143.6 – 294.6 g)	
LFR Chinook salmon (2020)	n=40 mean mass: 1.86 g (range: 1.17 – 2.57 g)	n=114 mean mass: 1.79 g (range: 0.85 – 2.77 g)	n=480 mean mass: 1.53 g (range: 1.33 - 1.72 g)	
Rainbow trout (2021)	n=24 mean mass: 132.76 g (range: 94.6 – 177.2 g)	n = 25 mean mass: 129.08 g (range: 86.4 – 202.0 g)	n=40 mean mass: 133.93 g (range: 60.0 – 192.0 g)	
Striped bass (2021)	--	--	n=35 mean mass: 348.25 g (range: 210.0 – 482.0 g)	
FR Chinook salmon (2021)	n=38 mean mass: 3.20 g (range: 0.90 – 7.0 g)	n=61 mean mass: 2.23 g (range: 1.05 – 4.62 g)	n=480 (RT) mean mass: 2.21 g (range: 1.53-4.66 g)	n=420 (SB) mean mass: 2.61 g (range: 1.90 - 2.70 g)

Each salmon (fall- and late fall-run) was only used once throughout the experiments. However, each individual rainbow trout and largemouth bass was tested in aerobic scope, burst ability, and predation trial performance (see striped bass exceptions below). Predators were given 7-10 days to recover between their predation trial, aerobic scope, and burst measurements. Juvenile salmon underwent this same sequence of experiments during approximately the same time frame.

### Swim tunnel respirometry

We used swim tunnel respirometry to quantify aerobic scope (AS) for all species across the five test temperatures in our experiment. Because AS is calculated as the difference between maximum metabolic rate (MMR) and resting metabolic rate (RMR), we collected both metabolic

rates (RMR and MMR) based on established methodologies (Poletto *et al.*, 2017; Verhille *et al.*, 2016). More details on the set-up and function of our swim tunnel system are available in Poletto *et al.* (2017). Briefly, each year of the experiment, juvenile Chinook salmon (late fall-run, n=40, mean mass = 1.86 g; fall-run, n=38, mean mass = 3.20 g) were tested in one of two 1.5-liter automated swim tunnel respirometers (Loligo, Denmark), which were controlled using a single-computer system. Our predator species were tested in one of two 30-liter automated swim tunnel respirometers (Loligo, Denmark), which were also controlled using a single computer system. However, striped bass were visibly stressed by any attempted physiological tests. Therefore, we only quantified aerobic scope for largemouth bass (n=39; mean mass = 227.05 g) and rainbow trout (n=24; mean mass = 132.76 g). All tunnels were surrounded by black shade material to reduce external stimuli for the fish, and infrared cameras (QSC1352W; Q-See, China) were mounted overhead each tunnel. These cameras were connected to a computer monitor to observe fish behavior during the trials.

We took metabolic measurements for RMR and MMR using intermittent respirometry (Clark *et al.*, 2013; Poletto *et al.*, 2017). To calculate RMR, fish were acclimated to their test temperature in the swim tunnels. Automatic measurements of oxygen consumption (1200 sec. measurement, 300 sec. flush) then began and were continued overnight by the AutoResp software. For the salmon in the 1.5 L tunnels, the swim tunnel impellor was reduced to its lowest rotational setting to avoid eliciting fish movements while still ensuring adequate water mixing. In the 30L tunnels a second submersible aquarium pump (DC40E-1250, DC12Volt, 500 Lph) was used to mix water without inducing fish movement. Measurements of RMR were typically started between 15:00 and 18:00 h and continued until 07:00 and 09:00 h the next day. Measurement periods were numbered 34 +/- 12, and the resulting data was plotted and visually



analyzed. Though unusual, measurement periods thought to result from a malfunction in the tunnel, unstable temperatures or inexplicably high fish activity at night were discarded. The mean of the lowest three values obtained out of all the measurement periods was then used to estimate RMR.

We measured MMR via a similar approach (1200 sec. measurement, 180-300 sec. flush). In this case, water velocity in the swimming chamber was gradually increased to swim the fish until exhaustion, although that velocity was scaled according to fish size and swimming ability. For both runs of juvenile Chinook salmon, water velocity was increased from 0 to 18 cm/second over a period of ~ 2 minutes prior to the first measurement period. For largemouth bass, water velocity increased to 30 cm/second, and for RT, to 60 cm/s during this same period. For all fish, water velocity then increased by ~10% of the previous test velocity for each subsequent measurement period. The trial was completed when the fish were exhausted and could no longer avoid impingement (see Poletto *et al.*, 2017 for exhaustion threshold). Data was processed visually via the same methods mentioned above for the RMR. However, here the highest metabolic rate, measured over durations of at least 5 minutes in length, was used to determine MMR. For both MMR and RMR, background respiration in the tunnels was accounted for using control values across temperatures.

### Burst tunnel measurements

To quantify burst speed and number (hereafter “burst ability”), we used two custom burst tunnels. These tunnels were built based on a modified design by Nelson *et al.* (2002). Each tunnel was composed of 3/8” Cast Clear Acrylic Plastic, with two chambers at either end that could be opened or closed manually with a door. The salmon tunnel was 122 cm long, 7.5 cm

wide, and 9.8 cm tall with a 5.6 cm fill depth. It was lined with 24 lasers along the outside of the tunnel on one side, the spacing of which ranged from 2 – 5 cm. The other length had corresponding laser detectors. The laser detectors were connected to Raspberry Pi and integrated into a customized code created using Python (Van Rossum & Drake, 1995). As a fish swam through the tunnel and broke a given laser beam, the time was recorded. In post-processing, this time was matched to the distance of the laser from the start of the tunnel, providing a calculation of burst velocity at that point. The larger predator tunnel was nearly identical in function and design, though at a larger scale. It was 200 cm long, 15.2 cm wide, and 25.2 cm tall with a 17.8 cm fill depth. It was also lined with 24 lasers; however, the distance between lasers was adjusted based on the perceived burst ability of the predators. For largemouth bass, laser distance ranged from 1-10 cm, and for rainbow trout, 1-5 cm. High-speed cameras (GoPro Hero 6, 240fps) were placed on either side of both swim tunnels to ground truth the laser readings. Temperature in the tunnels was adjustable, controlled by simultaneously circulating water in the system through a chiller, via thermostat, and using a heat bar, if necessary. Water inflows were placed just above the water line in either chamber and was permitted to flow on both sides at a trickle to stabilize the temperature, oxygen, and volume of the tunnel. Water inflow did not produce a measurable current within the burst tunnel.

Prior to a given trial, individual fish acclimated to their test temperature in separate holding tanks (again, by increasing or decreasing the temperature at a rate of 2°C per hour). The temperature in the burst tunnel was set to match the test temperature. Following the temperature ramp and 30-minute acclimation period in the holding tank, a fish was placed at one of two of the starting chambers and given 5 minutes to acclimate prior to the initial burst. A trial consisted of repeated bursts (<30 seconds apart) across the tunnel until the fish was exhausted or had

reached the maximum number measured (25 bursts), which had been determined as a likely upper bound for performance based on pilot trials conducted with non-experimental largemouth bass (A. McInturf & K. Zillig, unpublished data). We elicited a given burst by tapping the side of the chamber with a small PVC pipe to startle the fish, and then opening the chamber door and pinching the fish tail simultaneously. In cases where fish did not burst the full length of the tunnel, we noted the distance at which it had stopped before startling the fish again with the PVC pipe to swim the remainder of the tunnel. Human error and failures to burst (*i.e.*, refusal to leave the chamber) were also recorded and excluded from the analysis. A fish was considered exhausted when it failed to burst three times.

Bursting methods were identical for rainbow trout (n= 24; mean mass = 129.08 g), fall-run (n= 61; mean mass = 2.23 g) and late fall-run juvenile Chinook salmon (n= 114; mean mass = 1.79 g). However, largemouth bass (n= 39; mean mass = 227.09 g) demonstrated some reluctance to burst. For this species, we established a minimum number of bursts to be reached (10 bursts) before the trial could be completed, and a failure to burst was classified as any movement less than 0.50 m from the starting chamber. As in the swim respirometry, striped bass were easily stressed by this procedure and this species was excluded from burst trials.

After the data was collected, the number of bursts in each trial was confirmed by written records and the corresponding Python code output. To eliminate the possibility of an unnaturally high-speed reading due to premature disturbance of the lasers in the tunnel, we removed the highest speed reading per burst from our calculations and instead used the second highest peak speed recorded per burst. Any remaining physiologically infeasible outliers were also removed (*e.g.*, burst velocity > 400 m/s for rainbow trout (Domenici & Blake, 1997); 50 m/s for Chinook

salmon and largemouth bass). We then took the average of the maximum speed per burst to quantify mean burst speed across the trial for a given individual fish.

### Predation trials

Predation trials took place with largemouth bass and late fall-run Chinook salmon from May-July 2020, and with striped bass, rainbow trout and fall-run Chinook salmon in March-May 2021. Predators were fasted 72 hours before to each trial to avoid satiation during the trial. Juvenile salmon were also fasted for 24 hours. We tested 8 rainbow trout (mean mass = 133.93 g) and 8 largemouth bass (mean mass = 221.29 g) at each temperature across 5 trials (n = 40 for both); due to the ease at which they were stressed, only 35 striped bass (mean mass: 348.25 g) could be handled and were tested across 6 trials. All trials were identical in procedure. On the first day of each trial, we introduced twelve juvenile salmon (2020: late-fall run, mean mass = 1.53 g; 2021: fall run, mean mass = ~2.40 g) into one of eight identical predator tanks. Tanks were 1-m in diameter, and aerated ambient (18°C) water flowed into each tank at a rate of ~1.5 L/min throughout the trials. Water inflows were submerged slightly below the water line, to reduce available shelter for the juvenile salmon and avoid surface water disturbance. Following established protocols (Davis *et al.*, 2019), each predation tank was surrounded by a white shower curtain to eliminate visual stimuli and create consistent lighting. Predators (2020: largemouth bass; 2021: rainbow trout or striped bass) were placed in separate holding tanks, to eliminate the possibility of predation events before the trial began. Holding tanks were identical to the predation tanks in size, water flow, and temperature. All predation and holding tanks were randomly assigned by test temperature (11, 14, 18, 22, 25°C), and salmon and predators had their temperatures ramped simultaneously. After the 30-minute acclimation period following the

temperature ramp, predators were transferred from the holding tank to a predation tank corresponding to their assigned temperatures. Fish were gently netted into buckets underwater and similarly released into their predation tanks to minimize handling stress and eliminate air immersion.

All fish were left with minimal human disturbance for the rest of the trial, which ranged from 48-72 hours depending on the latency of the predator species to consume prey. Largemouth bass and striped bass, which consistently consumed prey in the first 24 hours, had 48-hour trials. Rainbow trout would frequently eat nothing in the first 24 hours, and so were provided 72-hour trials. Regardless of trial length, surviving salmon in each tank were counted independently by two researchers every 24 hours. This provided an indication of how many salmon had been eaten. In cases where the researchers did not agree, the same tank was re-evaluated via the same process until a consensus was reached. These checks were performed silently and with minimal disturbance of the tank, to reduce any impact on the ongoing trials. Temperatures were monitored every three minutes throughout the trial by loggers (Onset HOB0, Bourne, MA) moored in the external tank standpipes, to ensure test temperature stability. At the conclusion of the trial, largemouth bass and rainbow trout were weighed, measured, and returned to their holding tanks. To reduce stress due to any unnecessary handling, striped bass were returned immediately to their holding tanks.

#### Data processing and statistical analysis

We performed our statistical analysis using R Studio version 4.0.2 (R Core Team, 2020) and the lme4 (Bates *et al.*, 2015) and MASS packages (Venables & Ripley, 2002). Plots were generated using the ggplot2 package (Wickham, 2016). We analyzed each set of experiments

(predation trials, aerobic scope, burst ability) using a combination of linear models (LMs) and generalized linear models (GLMs).

For each run or species of fish that was tested for physiological performance traits (late fall-run Chinook salmon, fall-run Chinook salmon, largemouth bass, rainbow trout), we created three models (*i.e.*, aerobic scope, burst speed and burst number) with the same fixed effects predictors: test temperature and fish mass. For aerobic scope, based on previous studies (*i.e.*, Baird *et al.*, 2020; Poletto *et al.*, 2017; Verhille *et al.*, 2016) we used a linear model with both a continuous and quadratic term for temperature as a fixed effect to account for non-linearity between temperature and aerobic scope. We included mass as a continuous fixed effect to account for the possibility that our fish had grown over the course of the experiment. We analyzed burst speed using linear regression with those same predictors, although with temperature as a continuous linear variable (without the quadratic term). We also used a Poisson regression model to determine the effect of temperature and fish mass on burst number.

For our predation trials, we were first interested in examining whether temperature or other factors influenced the number of salmon consumed. Our data for this response variable was overdispersed, and so we analyzed the predation trial results from the largemouth bass, striped bass and rainbow trout trials using a negative binomial GLMM. Because both prey size and water temperature can influence predator consumption rate (Michel *et al.*, 2018), our fixed effect predictors included test temperature as a continuous variable, as well as average salmon mass and the mass of the predator in each tank. Both continuous mass variables were mean-centered and scaled.

We then determined whether predation trial outcome was influenced by relative difference in performance between salmon and their predators. To do so, we calculated the

proportional difference in aerobic scope, burst number, and burst speed for late fall-run and fall-run salmon as compared to largemouth bass and rainbow trout, respectively. Striped bass were excluded from this component of our analysis because we had no data on their aerobic scope and burst ability. To compare differences in performance (*i.e.*, aerobic scope, burst speed, or burst number), we computed the mean performance value at each temperature for all species, and then divided the value for salmon by that of the predator and subtracted by one. We then created three negative binomial GLMs with number of salmon eaten as the response variable. Each model had either the relative difference in aerobic scope, burst speed, or burst number as a fixed effects predictor.

## **Results:**

### Swim tunnel respirometry

As predicted, the effect of temperature on aerobic scope varied by fish species or population (Table S1.1). For juvenile Chinook salmon, there was no significant effect on late fall-run (Table S1.2; Fig. 1.2c), while there was a positive correlation for fall-run (Table S1.3; Fig. 1.2d). Both predator species tested (largemouth bass and rainbow trout) also showed a significant response in aerobic scope to temperature. The effect of temperature on largemouth bass aerobic scope was inverse U-shaped, as indicated by the significant quadratic effect (Table S1.4, Fig. 1.2a), with a peak at the highest test temperatures. For rainbow trout, aerobic scope peaked at ~18 °C (Table S1.5; Fig. 1.2b). Our rainbow trout model also suggested that there was a significant positive effect of mass, which we did not observe in any of the other fish species.

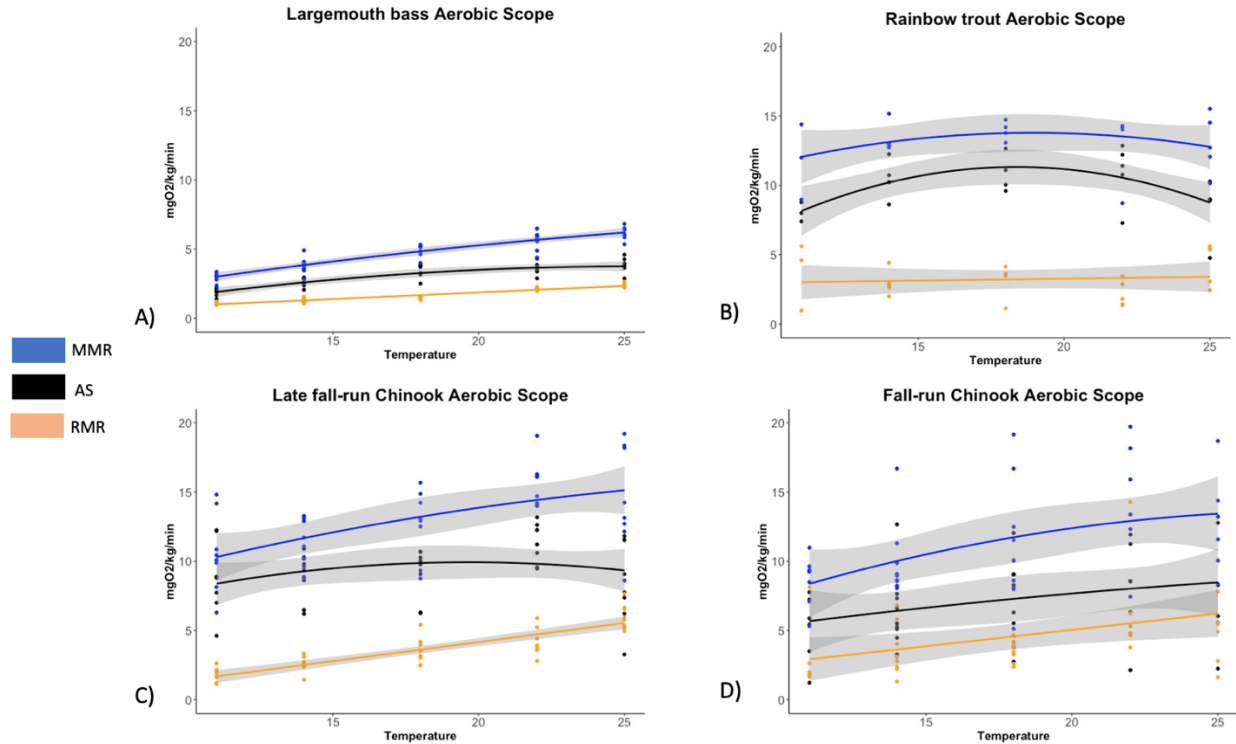


Figure 1.2. Aerobic scope thermal performance curves for A) largemouth bass; B) rainbow trout; C) late fall-run Chinook salmon; D) fall-run Chinook salmon. Aerobic scope is denoted in black, RMR in orange, and MMR in blue.

### Burst tunnel measurements

In contrast to aerobic scope, we observed burst responses to temperature in late fall-run juvenile Chinook salmon (Table S1.6) but not in fall-run (Table S1.7; Fig. 1.3d, Fig. 1.4d). For late fall-run, temperature affected burst speed and number differently; there was a significant positive effect of temperature on burst speed (Fig. 1.4c), but a negative effect on burst number (Fig. 1.3c). Salmon mass was not a significant predictor in either model. Burst speed between the two salmon populations was comparable (range LFR: 18.34792 - 137.73492 cm/s; range FR: 32.62 – 157.58 cm/s). Among our predators, rainbow trout burst ability was not significantly affected by temperature (Table S1.8). However, rainbow trout consistently reached the highest burst speeds among all tested species (range: 142.10 – 350.63 cm/s; Fig. 1.4b), and 75% of individuals undertook at least 20 repeated bursts (Fig. 1.3b). Burst speeds for largemouth bass were more like those of the salmon, ranging from 22.59 to 66.03 cm/s. In parallel with the results



of our predation and aerobic scope models, both burst speed and number were positively correlated with temperature for largemouth bass (Table S1.9; Fig. 1.3a, Fig. 1.4a).

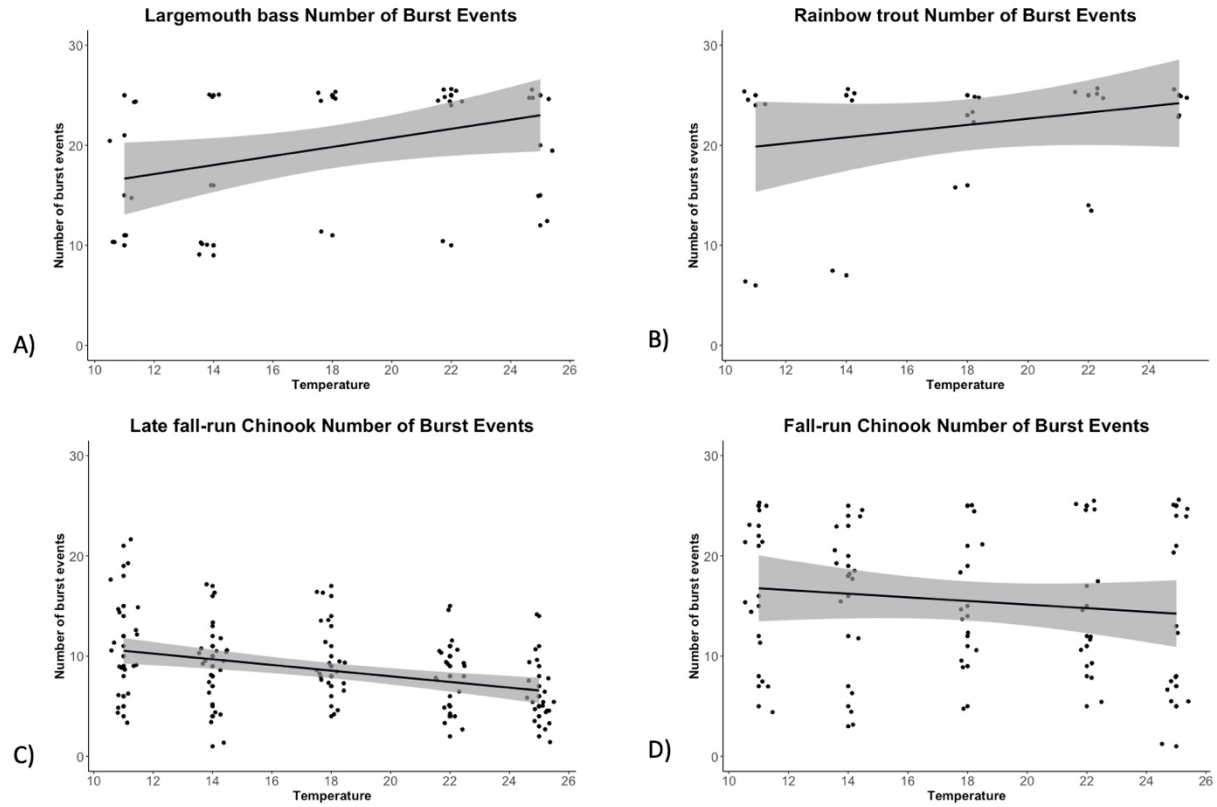


Figure 1.3. The number of repeated bursts performed as a function of test temperature for A) largemouth bass; B) rainbow trout; C) late fall-run Chinook salmon; D) fall-run Chinook salmon.

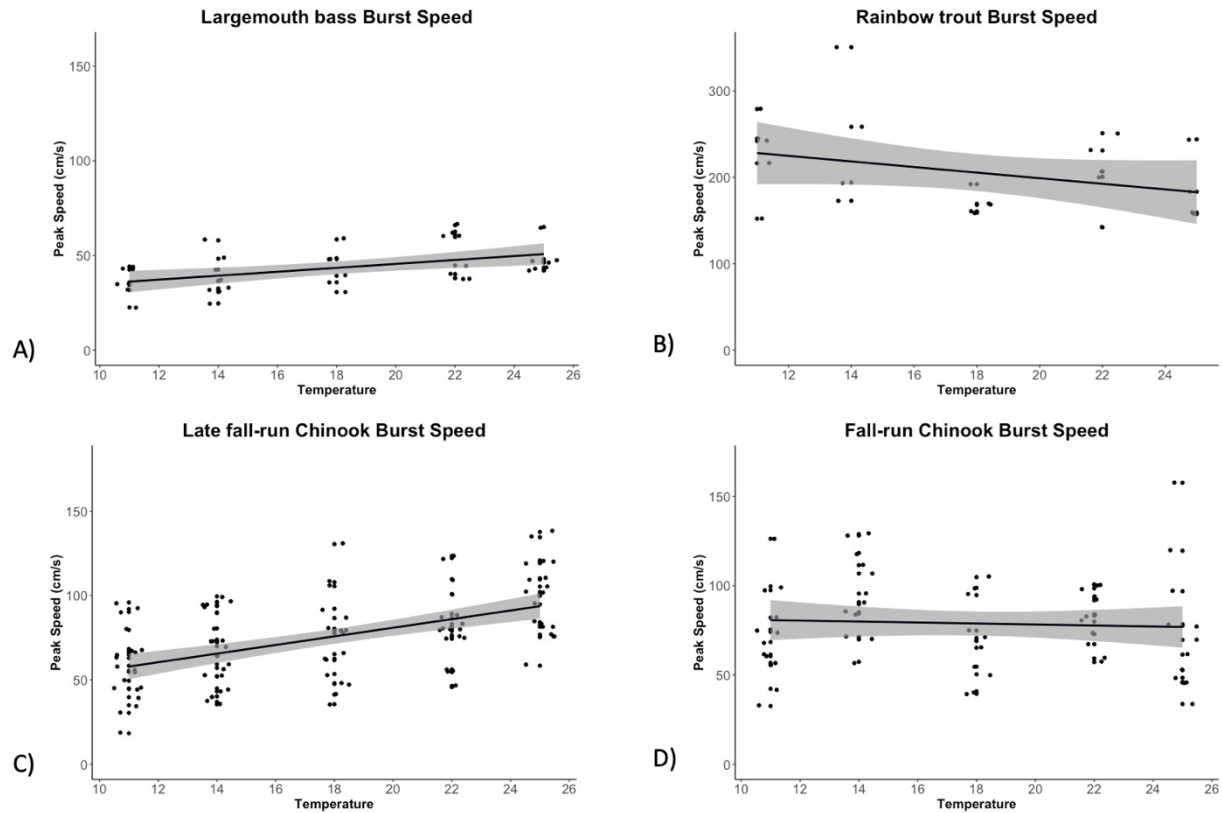


Figure 1.4. Maximum burst speed exhibited as a function of test temperature for A) largemouth bass; B) rainbow trout; C) late fall-run Chinook salmon; D) fall-run Chinook salmon.

### Predation trials

We measured the number of juvenile Chinook salmon that were eaten in a total of 115 predation trials. There was a positive correlation between number of salmon eaten and temperature for largemouth bass, which were tested with late fall-run Chinook salmon. Thus, a larger number of salmon were consumed at the upper end of our tested temperature range (22-25°C) than the lower (11-14°C). However, most largemouth bass consumed relatively few salmon (mean: 1.83; range: 0 - 12). There was no effect of predator or juvenile Chinook salmon mass in this model (Table S1.10, Fig. 1.5a).

For our other two predators (rainbow trout and striped bass), we observed no significant predation response to temperature. Both were trialed with fall-run juvenile Chinook salmon. For striped bass, we found a significant negative correlation between the number of salmon eaten and

average salmon mass per tank (Table S1.11, Fig. 1.4b). However, the average number of salmon consumed per trial was higher than with largemouth bass (mean: 2.49; range: 0-10). None of our predictors were significant in explaining variation in rainbow trout predation (Table S1.12, Fig. 1.4c), which may be due in part to the large number of trials in which rainbow trout failed to consume any salmon (mean: .38; range: 0-5). Out of 40 rainbow trout tested, only 8 ate at least one salmon, in contrast to 29/40 largemouth bass and 26/35 striped bass.

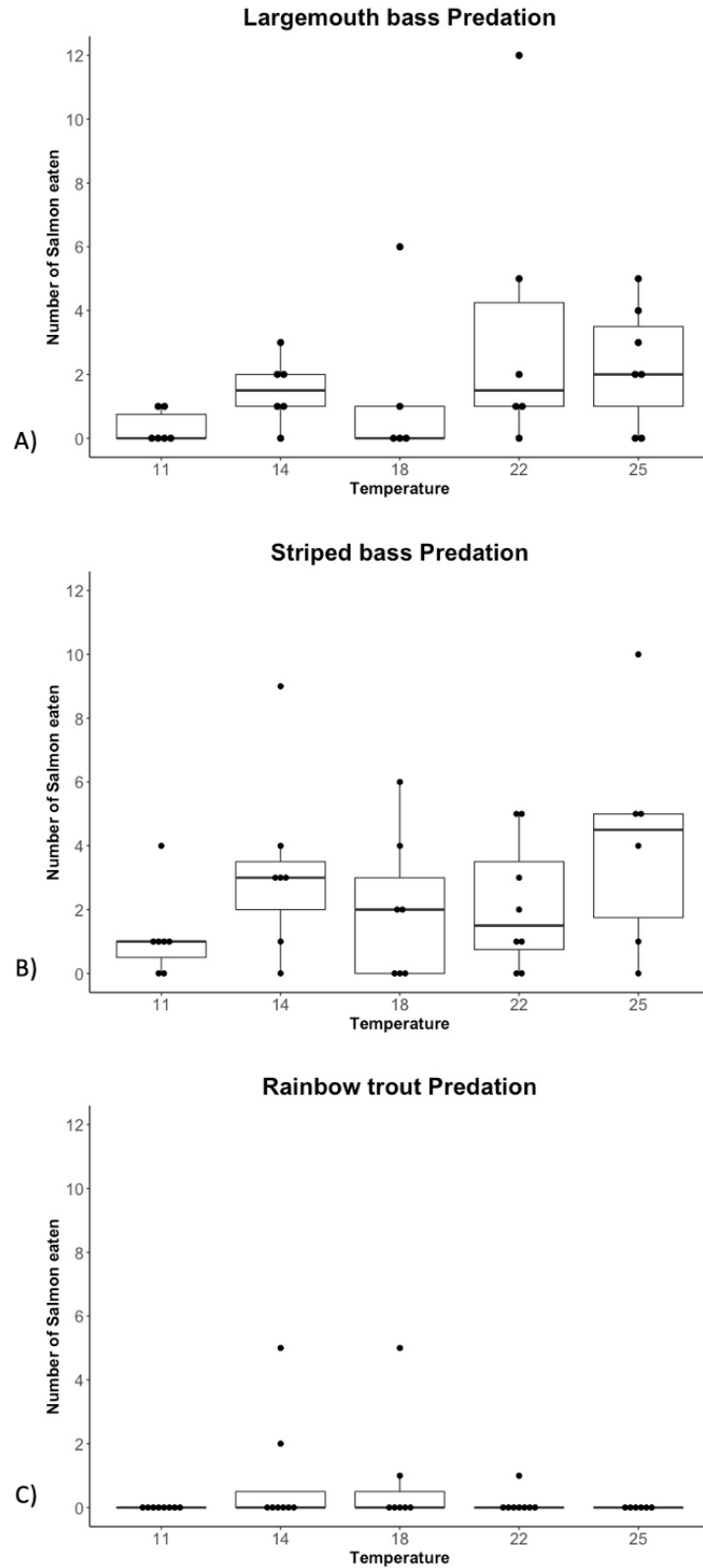


Figure 1.5. Total number of salmon eaten as a function of test temperature during predation trials conducted during 2020 and 2021. Results are shown for A) largemouth bass, which were tested with late fall-run Chinook salmon; B) striped bass, and C) rainbow trout, both of which were tested with fall-run Chinook salmon.

We also analyzed how the mean difference in relative performance between predator and prey affected the outcome of predator-prey interactions. To do so, we compared the physiological performance of each predator-prey pairing in our study for which we had sufficient data. There was no effect in performance difference for any of our physiological performance traits (*i.e.*, aerobic scope, burst number, burst speed) on the predation trials with rainbow trout and fall-run Chinook salmon. For our largemouth bass and late fall-run Chinook salmon trials, the performance difference in burst number was negatively correlated with the outcome of predation trials (Table S1.13). Based on our calculation for performance difference, this indicates that relative increases in bass burst number, compared to those of salmon, were correlated with a larger number of salmon consumed. The other predictors (aerobic scope and burst speed) were not significant in their respective models.

### **Discussion:**

The integration of physiology, behavior, and ecology is becoming increasingly important as we forecast the effects of climate change on fisheries and ecosystems (Horodysky *et al.*, 2015). While warming water temperatures will undoubtedly impact organisms via their fundamental thermal physiology, the resulting impact on extrinsic ecological dynamics, like predator-prey interactions, remains understudied. Yet predator-prey interactions depend on underlying physiological mechanisms, which are likely to be affected by the thermal environment for ectothermic fishes (Grigaltchik *et al.*, 2012). Because species can respond differently to similar temperature changes, disproportionate changes in predator or prey physiological performance can alter predation or evasion success, respectively (Grigaltchik *et al.*, 2012). In the Sacramento-San Joaquin River Delta, current research on juvenile salmon already

suggests that there may be a positive correlation between predation rate and temperature (Johnson *et al.*, 2017; Nobriga *et al.*, 2021). We aimed to determine whether this trend is due to an advantage conferred by the fundamental physiologies of predators versus prey. However, identifying a physiological advantage was challenging and highly dependent on the metric examined. Among our predators, largemouth bass performed best physiologically at the warmest test temperatures, which also corresponded to where the greatest predation occurred. Our results were less conclusive for rainbow trout, which generally appeared more thermally robust. Similarly, there were differences between populations of salmon. Late fall-run Chinook showed no effect of temperature on aerobic scope, but a potential tradeoff between burst speed and number of bursts with temperature. Alternatively, fall-run Chinook showed a significant positive effect of temperature on aerobic scope, but were thermally robust in their burst abilities. Thus, fundamental thermal physiology may not always be the best predictor of trophic interactions in the field, but depending on the species, it can offer insight into where predation may occur.

Salmonids are thought to require cooler waters to survive and grow (<16°C; Marine & Cech, 2004; Yates *et al.*, 2008), and they are often managed accordingly (USEPA (US Environmental Protection Agency), 2003). Consequently, the low survival of juvenile Chinook at warm temperatures in the Delta has been attributed to a lack of thermal tolerance. However, our results join an increasing body of evidence (*e.g.*, Poletto *et al.*, 2017; Zillig *et al.*, in prep) suggesting that the fundamental thermal physiology of salmonids is not the major force driving this trend. While we observed variation between fall-run and late fall-run Chinook among performance metrics, salmon physiological response was often thermally robust. We instead found more support for field-based hypotheses (Nobriga *et al.*, 2021) that survivorship in the Delta depends on a physiological advantage obtained by predators in warming waters. This was

most evident in largemouth bass, of which aerobic scope, burst number, and burst speed significantly increased with temperature. This species also consumed significantly more salmon at our two highest temperatures (22 and 25°C), and our results were consistent with previous work indicating an positive relationship between temperature and food intake in this species (Lemons & Crawshaw, 1985). Similarly, while we were unable to obtain physiological data for striped bass, previous studies suggest that they possess a higher aerobic scope near 20°C (Lapointe *et al.*, 2014), and though more work is required to establish their burst ability, we observed predation more frequently at all but our lowest temperature (<14°C). In contrast, the response to increased acute temperature exposure differed for the rainbow trout. These predators generally tolerated a wide variety of temperatures, which has also been observed in previous research (Chen *et al.*, 2015; Verhille *et al.*, 2016). Only their aerobic scope was significantly affected by temperature and highest at around 18°C, which also corresponded to the middle range of temperatures where they consumed salmon. While a physiological advantage was difficult to determine for this species, our results do match our prediction that they are physiologically similar to the other salmonids in this study based on their broad thermal tolerance.

Taken together, our results suggest that the fundamental physiology of predators can often provide insight into where predation may occur depending on the species. Largemouth bass are structure-oriented, non-native ambush predators (Michel *et al.*, 2018), and our analyses suggest their physiology is well-adapted to exploit prey items at warmer temperatures that occur in the Delta's nearshore habitats. Striped bass also appear more physiologically suited to warmer waters (Lapointe *et al.*, 2014), but their ability to consume salmon across trial temperatures suggests that they can contribute to smolt predation in all but the coldest pelagic habitats where

they are found. Largemouth and striped bass are two of the most impactful piscivorous predators of salmon in the Delta (Michel *et al.*, 2018; Nobriga *et al.*, 2021), and their physiological and ecological performance at warmer temperatures warrants concern for juvenile salmon survival in a changing climate. Conversely, we confirmed that rainbow trout are unlikely to be a major threat to salmon regardless of temperature. It remains unclear whether this can be attributed to similarities between the thermal physiologies of predators and prey, which might reduce any discernable advantage for either species. Rainbow trout demonstrated a reluctance to consume salmon during predation trials, despite their voraciousness for live feed (including salmon) in the holding tank. The lack of predation in our trials may be partially reflective of their ecological role in the wild, where they typically feed on invertebrates (Elliott, 1973; Tippets & Moyle, 1978; C. Michel, pers. comm.). However, they do consume salmon fry in other systems (Beauchamp, 1995; Ginetz & Larkin, 1976) and the laboratory (Mazur & Beauchamp, 2003), and there may have been an effect of our study design preventing them from doing so in our experiments (discussed in more detail below).

While we were able to establish conclusions about predation risk based on general physiological response to temperature, a key challenge we encountered was determining which, if any, physiological performance trait best predicted trophic interactions. The degree to which thermal response differs between traits could affect the use of species-specific fundamental thermal physiology as a tool for predicting ecological outcomes. Of our performance traits, we found one that showed a similar relationship to temperature as the outcome of predation trials for both predators and prey: number of repeated bursts. This was further supported when we calculated the relative difference in performance between largemouth bass and late fall-run Chinook salmon; an increase in relative largemouth bass ability to repeat burst corresponded



with an increase in number of salmon consumed. Yet though it is hypothesized to have a substantial influence on the outcome of predator-prey interactions (Webb, 1986; Domenici & Blake, 1997; Taylor & McPhail, 1985), burst swimming has not been integrated as a routine measurement in physiological research, and there are not yet common protocols across studies. For exploring fundamental thermal physiology, there has been a widespread focus on aerobic scope, which is thought to define the capacities of an organism to undergo fitness-enhancing activities. However, aerobic scope did not appear to correlate with predation trial outcomes based on our results, which may be due to a behavioral trade-off. Whereas aerobic capacity is useful for steady (continuous) swimming (Blake, 1983), fast-starts (<1 second) or bursts (<20 seconds) are often used by predators when attacking prey, or prey when evading predators (Domenici & Blake, 1997). Furthermore, attack or evasion speed may not be the most critical component of a successful capture (Domenici & Blake, 1997); for instance, Webb (1986) found that prey speed was sub-maximal in response to predator attacks that were not followed by a chase. This supports our conclusion that the ability to undertake repeated bursts in pursuit of prey (or during escape from a predator) is likely more deterministic in a predator-prey encounter than burst speed. It was difficult to fully disentangle the mechanisms underpinning the predation trial outcomes; specifically, whether predation at a given temperature emerged due to increased vulnerability of salmon, or a disproportionate increase in performance by predators. Yet it is probable that the ecological outcomes depend in large part on the advantage obtained via burst abilities at a given temperature. Still, as proposed in previous work (Poletto *et al.*, 2017; Verhille *et al.*, 2015; Verhille *et al.*, 2016), our study challenges the use of a single physiological trait for determining the fundamental thermal physiology of a species and predicting ecological outcomes. We recommend future physiological studies expand beyond traditional measurements

and explore other such variables that may have more predictive power for ecosystem interactions.

Given the degree to which response to temperature varied by performance trait within and between species, our results should be considered in the context of our experimental design. While many of our experimental outcomes are also supported by field-based research, we conducted this study in the laboratory using primarily hatchery-raised fishes (except for striped bass) and extrapolating beyond these conditions should be done with caution. For example, our study fishes were acclimated at the same temperature (18°C) before acutely exposing them their test temperatures for each trial. This falls in the range of temperatures where optimal growth for juvenile salmon has been observed in laboratory studies (*i.e.*, Cech and Myrick, 1999; Marine and Cech 2004). Previous research has found that exposure temperature, rather than duration of thermal exposure (acute vs. acclimation), influences swimming performance (Kirby *et al.*, 2020; Poletto *et al.*, 2017). However, we cannot exclude the possibility that this acclimation temperature influenced our results, particularly as temperature is known to affect acute thermal tolerance and growth rate (Zillig *et al.*, 2020). Relatedly, Zillig *et al.* (2020) has also shown that growth and thermal tolerance vary by population in response to the same increases in temperature, which we also observed in our study. Such variation appears strongest in the juvenile life stage (Pörtner & Farrell, 2008; Zillig *et al.*, 2021). Simultaneously, predator assemblages and risks also differ among watersheds, thus producing varying effects on salmonid ecological thermal physiologies (Zillig *et al.*, 2021). Future work is therefore required to examine fundamental and ecological thermal physiology of salmon runs from other locations.

We also controlled for a variety of potentially interactive effects that would be present in a non-captive environment. For instance, existing work on the multiple predator effect (Nobriga

*et al.*, 2021) suggests that habitat may influence the relative impact of predators with different behavioral strategies. Relevant to our study, largemouth bass, which are ambush predators, rely on camouflage from surrounding vegetation during predator-prey interactions, whereas striped bass tend to consume prey in open water. Given the lack of available shelter in the tanks, our predation trials may have been better suited to the natural behaviors of the latter predator. Furthermore, both bottom roughness (Michel *et al.*, 2020) and river inflows (Nobriga *et al.*, 2021) are known to influence predation in the Delta, and how these variables interact with temperature is the focus of ongoing research. We therefore cannot predict how salmon or predators would have responded if we had not controlled for such factors, and future studies should consider their additive effects on ecosystem dynamics. Our predation trials were also conducted with a single predator per tank to remove any conspecific cues. However, in the wild, predation behavior is also influenced by intraspecific dynamics, such as competition. Based on previous studies on other hatchery-raised salmonids (Fenderson *et al.*, 1968), the lack of competition or social cues may explain the differences in rainbow trout feeding behavior during the predation trials versus in the holding tanks, which is related to the captive environment in which the trout were raised. Understanding such intraspecific dynamics, and how they interact with environmental factors like temperature, will be improve our ability to assess predation risk and requires further study.

### *Conclusion*

The Sacramento-San Joaquin River Delta is an ecosystem that faces imminent threat at the forefront of environmental change. Increasing water temperatures and predation by non-native piscivorous predators (Grossman, 2016; Michel *et al.*, 2015) directly correlate to low

survival of outmigrating juveniles, which is a major contributor to the decline of salmon runs in this region (Buchanan *et al.*, 2013; Kjelson & Brandes, 1989; Michel *et al.*, 2020; Michel *et al.*, 2015; Perry *et al.*, 2010). Yet prior to this study, there remained a gap in our knowledge of the mechanisms of this mortality. Our results suggest that fundamental thermal physiologies of predators and prey play a role in shaping trophic dynamics in the Delta. However, care should be taken in using lab-based performance traits to predict ecological outcomes based on species-specific fundamental thermal physiology; ideally, the relative advantage in physiological performance between predators and prey should also be considered. Furthermore, given the consistency with which burst ability specifically predicted the outcome of predation trials, we recommend future physiological studies expand their focus to consider the mechanisms underlying ecologically relevant behaviors. With the continuing miniaturization of tools such as accelerometers, these metrics can also be examined in the field, offering more realistic insight into how fishes will respond to future temperature change. From a management perspective, our results and those of other studies (*i.e.*, Marras *et al.*, 2015) suggest that non-native species such as largemouth bass and striped bass will experience increasing success in the Delta because their thermal window of physiological performance is shifted towards warmer temperatures, as opposed to that of native salmonids. In addition, because temperature can affect fish distribution in response to thermal preferences (Callihan *et al.*, 2014; Díaz *et al.*, 2007; Michel *et al.*, 2020), we have shown that combining physiological and ecological approaches can yield useful insight into where predation hotspots may be occurring based on our understanding of predator and prey physiology. Such predictions can produce actionable results; for example, managers could hypothetically improve the survival of juvenile salmonids by adjusting the magnitude of river flow entering the Delta, which affects water temperature along primary outmigration routes

(Michel *et al.*, 2020; Nobriga *et al.*, 2021). Finally, it has been suggested that salmon in the Delta are at the southern range of the species distribution and may serve as indicator populations for how warming can affect predator-prey interactions (Nobriga *et al.*, 2021; Zillig *et al.*, 2021); however, as we have shown, both fundamental physiology and temperature-driven ecological outcomes are variable and species-specific. We conclude by advocating for more studies linking temperature, physiology, and ecosystem dynamics in other systems, incorporating novel approaches to understand both fundamental and ecological physiologies across a wide variety of species.

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**Author Contributions:**

AGM conceived the study, secured funding, collected data, performed statistical analyses, and wrote the manuscript. KWZ also conceived the study and assisted in collecting data and writing the manuscript. KC, JK, AMJ, and EP assisted in data collection and cleaning and manuscript preparation. DC (Dennis Cocherell) helped organize data collection and advised on husbandry practices. CM contributed to the conception of the study and reviewed the manuscript and statistics. DC (Damien Caillaud) supervised statistical analyses and reviewed the manuscript.

NAF supervised data collection and statistical analysis and reviewed the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Supplementary materials:

S1.1. Summary of mean aerobic scope, RMR, and MMR values (mgO<sub>2</sub>/kg/min) by species/population of fish examined across temperatures.

Species/Population		11°C	14°C	18°C	22°C	25°C
Largemouth bass	AS	1.90	2.55	3.44	3.48	3.84
	RMR	1.10	1.29	1.47	2.11	2.40
	MMR	3.00	3.84	4.91	5.59	6.23
Late fall-run Chinook salmon	AS	8.79	8.80	9.13	11.4	8.57
	RMR	1.80	2.55	3.54	4.17	6.00
	MMR	10.6	11.3	12.7	15.6	14.6
Rainbow trout	AS	8.26	10.4	10.8	11.3	8.62
	RMR	2.63	2.94	3.09	1.53	4.37
	MMR	10.7	13.4	13.2	12.8	13.0
Fall-run Chinook salmon	AS	5.77	6.43	6.82	8.88	8.03
	RMR	2.82	3.50	4.26	7.49	4.69
	MMR	8.59	9.93	11.1	16.4	12.7

S1.2. Model outputs for the linear model used to analyze aerobic scope for late fall-run Chinook salmon. Significant *p*-values are denoted in bold.

Late fall-run Chinook salmon: Aerobic scope			
Predictors	Estimates	std. Error	<i>p</i>
(Intercept)	12.73	2.30	<b>&lt;0.001</b>
Temperature [1st degree]	1.97	2.29	0.396
Temperature [2nd degree]	-2.79	2.29	0.230
Mass	-1.83	1.23	0.145

S1.3. Model outputs for the linear model used to analyze aerobic scope for fall-run Chinook salmon. Significant p-values are denoted in bold.

<b>Fall-run Chinook salmon: Aerobic scope</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	9.09	1.47	<b>&lt;0.001</b>
Temperature [1st degree]	8.94	4.29	<b>0.045</b>
Temperature [2nd degree]	0.05	4.03	0.991
Mass	-0.58	0.43	0.184

S1.4. Model outputs for the linear model used to analyze aerobic scope for largemouth bass. Significant p-values are denoted in bold.

<b>Largemouth bass: Aerobic scope</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	3.53	0.54	<b>&lt;0.001</b>
Temperature [1st degree]	4.22	0.55	<b>&lt;0.001</b>
Temperature [2nd degree]	-1.15	0.55	<b>0.043</b>
Mass	-0.00	0.00	0.350

S1.5. Model outputs for the linear model used to analyze aerobic scope for rainbow trout. Significant p-values are denoted in bold.

<b>Rainbow trout: Aerobic scope</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	15.76	1.74	<b>&lt;0.001</b>
Temperature [1st degree]	0.82	1.53	0.599
Temperature [2nd degree]	-5.75	1.54	<b>0.001</b>
Mass	-0.04	0.01	<b>0.003</b>



S1.6. Model outputs for the GLM used to analyze burst number (top) and the linear model for burst speed (bottom) for late fall-run Chinook salmon. Significant *p*-values are denoted in bold.

Late fall-run Chinook salmon: Burst number			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	2.70	0.21	<b>&lt;0.001</b>
Temperature	-0.03	0.01	<b>&lt;0.001</b>
Mass	0.01	0.09	0.870

Late fall-run Chinook salmon: Burst speed			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	29.05	13.60	<b>0.035</b>
Temperature	2.56	0.44	<b>&lt;0.001</b>
Mass	0.39	5.67	0.945

S1.7. Model outputs for the GLM used to analyze burst number (top) and the linear model for burst speed (bottom) for fall-run Chinook salmon. Significant *p*-values are denoted in bold.

Fall-run Chinook salmon: Burst number			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	15.41	5.32	<b>0.005</b>
Temperature	-0.08	0.20	0.678
Mass	0.62	1.33	0.644

Fall-run Chinook salmon: Burst speed			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	74.73	17.97	<b>&lt;0.001</b>
Temperature	-0.15	0.68	0.830
Mass	3.05	4.48	0.499

S1.8. Model outputs for the GLM used to analyze burst number (top) and the linear model for burst speed (bottom) for rainbow trout. Significant *p*-values are denoted in bold.

<b>Rainbow trout: Burst number</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	2.76	0.31	<b>&lt;0.001</b>
Temperature	0.01	0.01	0.119
Mass	1.00	0.00	0.746

<b>Rainbow trout: Burst speed</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	214.95	70.26	<b>0.006</b>
Temperature	-2.86	2.09	0.187
Mass	0.32	0.39	0.420

S1.9. Model outputs for the GLM used to analyze burst number (top) and the linear model for burst speed (bottom) for largemouth bass. Significant *p*-values are denoted in bold.

<b>Largemouth bass: Burst number</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	2.24	0.28	<b>&lt;0.001</b>
Temperature	0.02	0.01	<b>0.001</b>
Mass	0.00	0.00	0.177

<b>Largemouth bass: Burst speed</b>			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	18.54	12.28	0.141
Temperature	1.05	0.32	<b>0.003</b>
Mass	0.03	0.05	0.561

S1.10. Model outputs for the GLM used to analyze the outcome of predation trials (i.e., number of salmon consumed) with largemouth bass [LMB] and late fall-run Chinook salmon. Significant p-values are denoted in bold.

Predation Trials, 2020: Number of salmon eaten by largemouth bass			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	0.21	0.90	0.083
Temperature	1.12	0.04	<b>0.015</b>
LMB mass	1.24	0.23	0.362
Average salmon mass	1.19	0.25	0.492

S1.11. Model outputs for the GLM used to analyze the outcome of predation trials (i.e., number of salmon consumed) with striped bass [SB] and fall-run Chinook salmon. Significant p-values are denoted in bold.

Predation Trials, 2021: Number of salmon eaten by striped bass			
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	-0.24	0.65	0.710
Temperature	0.06	0.03	0.086
SB mass	-0.14	0.18	0.444
Average salmon mass	-0.46	0.20	<b>0.018</b>

S1.12. Model outputs for the GLM used to analyze the outcome of predation trials (i.e., number of salmon consumed) with rainbow trout [RT] and fall-run Chinook salmon. Significant p-values are denoted in bold.

Predation Trials, 2021: Number of salmon eaten by rainbow trout			
<i>Predictors</i>	<i>Incidence Rate Ratios</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	0.03	2.12	0.988
Temperature	-0.11	0.12	0.345
Average salmon mass	-1.99	1.12	0.075
RT mass	-0.33	0.59	0.571

S1.13. Outputs for the three GLMs to determine the effect of relative performance difference between predator prey on the number of salmon consumed per individual largemouth bass. Performance values examined were aerobic scope (top), burst number (middle), and burst speed (bottom) Significant p-values are denoted in bold.

<b>Predation Trials, 2020: Number salmon eaten</b>			
<i>Predictors</i>	<i>Log-Mean</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	3.11	1.93	0.108
Relative difference in aerobic scope	3.80	2.90	0.190
<i>Predictors</i>	<i>Estimates</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	-2.10	1.08	0.051
Relative difference in burst number	-4.60	1.78	<b>0.010</b>
<i>Predictors</i>	<i>Log-Mean</i>	<i>std. Error</i>	<i>p</i>
(Intercept)	0.67	0.24	<b>0.006</b>
Relative difference in burst speed	0.35	0.29	0.227

## **Chapter 2:**

### **Use of a hydrodynamic model to examine behavioral response of broadnose sevengill sharks (*Notorynchus cepedianus*) to estuarine tidal flow**

Alexandra G. McInturf<sup>1</sup>, Anna E. Steel<sup>1</sup>, Michele Buckhorn<sup>1</sup>, Philip Sandstrom<sup>1,2</sup>, Christina J. Slager<sup>3</sup>, Nann A. Fangué<sup>1</sup>, A. Peter Klimley<sup>1,4</sup>, Damien Caillaud<sup>5</sup>

<sup>1</sup>Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA USA

<sup>2</sup>Tacoma Public Utilities, 3628 South 35<sup>th</sup> Street, Tacoma, WA USA

<sup>3</sup>Aquarium of the Bay, Biological Programs/Conservation, Exhibits and Educational Engagement, San Francisco, CA USA

<sup>4</sup>Biological consultant, Petaluma, CA USA

<sup>5</sup>Department of Anthropology, University of California, Davis, CA USA

**Abstract:**

Innovative telemetry and biologging technology has increased the amount of available movement data on aquatic species. However, real-time information on the environmental factors influencing animal movements can be logistically challenging to obtain, particularly in habitats where tides and currents vary locally. Hydrodynamic models are capable of simulating complex tidal flow and may thus offer an alternative method of contextualizing animal movement in coastal habitats. Here we use this tool to examine the influence of tide on the movement of broadnose sevengill sharks (*Notorynchus cepedianus*) in the San Francisco Bay estuary. Three sharks were actively tracked using acoustic transmitters for 3 to 4 days. We then generated a hydrodynamic model of the estuary and calculated current vectors along each track. We hypothesized that the sharks would adjust their swimming speed and direction depending on current strength when passing through the channel underneath the Golden Gate Bridge. Our results indicate that sharks did tend to follow the current flow in the channel, but their overall displacement did not significantly correlate with tidal amplitude. We conclude that the sharks may respond to environmental factors other than tidal flow, altering their movement at a finer scale than initially considered. Overall, this suggests that hydrodynamic models can be used to visualize and quantify environmental factors that may affect movement patterns in aquatic organisms. We recommend future studies combine these models with other biologging techniques to measure energy expenditure at a finer spatial scale.

## **Introduction:**

Animal movement is affected by a variety of factors, including the animal's internal state, navigation and motion capacity, and the surrounding biotic and abiotic environment (*Nathan et al.*, 2008). Among these, there has been increasing recognition that external constraints in particular may play a larger role in shaping an organism's movement path than previously considered (*Brownscombe et al.*, 2017; *Gallagher et al.*, 2017; *Shepard et al.*, 2013; *Wilson et al.*, 2012). In estuarine habitats, one such external force is the seasonal and daily hydrological variance, which is generated by complex bathymetry and water flux from various inshore and offshore sources (*Anderson & Beer*, 2009; *Brodersen et al.*, 2008; *Forsythe et al.*, 2012; *Kelly & Klimley*, 2012). Due to the presence and variability of these currents, it is likely that different species that reside in or transit through estuaries will exhibit plasticity in their movement in response to local water flow. In some cases, currents may induce little to no active response from aquatic organisms, while in others they can be an impediment to the organism by deflecting the animal off course (*Chapman et al.*, 2011; *Kelly & Klimley*, 2012). Currents can also be beneficial by reducing an individual's travel time and energetic expenditure (*e.g.*, *Bernatchez & Dodson*, 2008; *Kelly & Klimley*, 2012) or by increasing foraging opportunities (*e.g.*, in upwelling areas; *Benjamins et al.*, 2015).

Assessing the nature of behavioral response requires an understanding of how the animal moves in the context of the major environmental constraint in question. There has been recent attention to this area of research due to interest in dynamic management approaches, which require repeated assessment or measurement of biological and environmental data to update management recommendations. These tools rely on environmental datasets obtained via remote sensing to predict animal location on a daily, regional scale (*e.g.*, *EcoCast*; *Hazen et al.*, 2018).

However, real-time measurements of the more fine-scale environmental variables affecting organism movement patterns, such as current flow, can be logistically challenging to obtain via remote sensing or direct field measurement (Benjamins *et al.*, 2015). Thus, complementary methods may be necessary to contextualize animal movement data and forecast species distribution at a local scale.

Multi-dimensional hydrodynamic models are typically used to investigate water movement, sediment transport, and water quality for estuarine and coastal environments (Elias *et al.*, 2008). These models can also provide information on localized currents in dynamic aquatic habitats. In cases where empirical data from buoys or remote sensors are missing, this tool could therefore be utilized to quantify the environment through which marine organisms move, offering greater insight into the impact of environmental constraints.

Here we explore the use of hydrodynamic models in examining the influence of tide on broadnose sevengill shark (*Notorynchus cepedianus*) movements in the San Francisco Bay estuary. We combine tidal current simulations generated at a ~50m resolution with active tracking data from three sharks. In the estuary, sevengill sharks show a preference for high-flow areas, such as the channel underneath the Golden Gate Bridge (Ketchum *et al.*, 2017). We first hypothesized that sevengill sharks would minimize energy expenditure by consistently moving in the direction of the tide to travel within the high-flow channel. Second, because the San Francisco Bay experiences a mixed semi-diurnal tide, we predicted that this response would vary by current strength; specifically, that i) in slow currents generated by weak tides, sharks would swim more actively in the direction of the current flow in order to move through the channel. In this case, the total displacement of the shark during that tidal segment would be greater than that of the current along the shark's movement path; and ii) in faster currents resulting from stronger



tides, sharks would move passively within the water mass while being transported through the channel in the direction of the tide. The total displacement of the shark would then be equal to or less than that of the current. Our ultimate goal was to explore the use of hydrodynamic models to determine the frequency with which the sharks moved in and out of the estuary with the tide, and whether the environmental tidal conditions altered their mode of transport.

## **Methods:**

### *Study System*

The San Francisco Bay is the most geographically expansive estuary along the California coastline, with a surface area of 1,240 km<sup>2</sup> (Conomos *et al.*, 1985). Tides are mixed and semidiurnal (*i.e.*, two unequal high and low tides per day), with a high-flow channel where currents reach peak velocities (approximately 2.0 m/s; Bennett *et al.*, 2002) through the narrow passage underneath the Golden Gate Bridge (Conomos *et al.*, 1985; Ketchum *et al.*, 2017). The mean tidal range is approximately 1.7 meters (NOAA National Ocean Service), and during the study period, tidal amplitude ranged from 1.5 – 4.0 meters. The mean depth of the entire estuary is less than 10 meters, but the central channels (such as that beneath the Golden Gate Bridge) can reach depths of over 100 meters (US Geological Survey, 2014). The estuary also holds several small islands. Relevant to this study, Alcatraz Island (.09 km<sup>2</sup>) is located approximately 2.9 km east of the Golden Gate Bridge, while Angel Island (3.1 km<sup>2</sup>) is approximately 4 km northeast (Fig. 2.1). It is also important to note that the estuary is highly urbanized and impacted by numerous anthropogenic activities including channel dredging, freshwater diversions, watershed modifications, urban run-off, and ship traffic (Barnard *et al.*, 2013). Due to the complex shape and bathymetry caused by the influence of both these anthropogenic and natural factors, the San

San Francisco Bay estuary is an area in which tidal influence is not only highly variable but also heterogeneously distributed. It is thus an ideal location to examine how organisms respond to dynamic current flow.

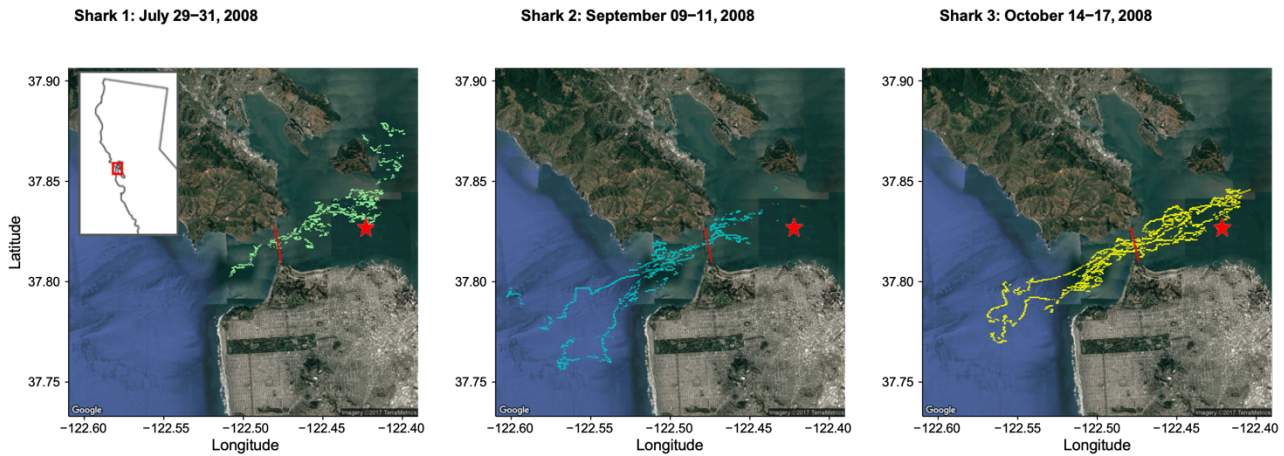


Figure 2.1. Maps of San Francisco Bay Estuary, displaying relocation data for each acoustically tagged sevengill shark. Sharks were captured, tagged, and released northwest of Alcatraz Island (marked with a star), and tracked at three separate time periods in 2008. The red line overlays the Golden Gate Bridge, used in this study as a threshold to mark the transition (i.e., channel) between marine and estuarine habitats. The inset in the upper left shows the location of the study in California, USA.

During the spring and summer, the San Francisco Bay estuary serves as a foraging and pupping ground for one such species, the sevengill shark (*Notorynchus cepedianus*; Barnett *et al.*, 2010a, 2012; Ebert, 1989; Ketchum *et al.*, 2017). Classified as data deficient by the International Union for Conservation of Nature (Compagno, 2009), sevengill sharks are widely distributed in temperate coastal regions, and diet studies have shown that they may play a significant ecological role through regulation of mesopredator populations in these habitats (Barnett *et al.*, 2010b). This species tends to occupy bays and estuaries throughout its range, moving seasonally between inshore and offshore waters (Barnett *et al.*, 2010a, 2012; Ebert, 2003; Ebert & Compagno, 2012; Last & Stevens, 2009). Sevengill sharks also show a preference for high-flow areas (Ketchum *et al.*, 2017), like many other mobile marine predators such as cetaceans, pinnipeds, and seabirds that exploit tidally energetic environments for foraging

opportunities (Benjamins *et al.*, 2015; Lieber *et al.*, 2018). It is therefore likely that their movements are affected by the prevailing tidal flow in the deep narrow channel underneath the Golden Gate Bridge.

### *Active Tracking*

Three sharks were collected on a flood tide near a small reef northwest of Alcatraz Island on 29 July, 9 September, and 14 October 2008. Each was caught using a baited hook and netted to bring aboard the vessel. The shark was then placed in a tank filled with flowing seawater, sexed, and measured for total length (TL, meters), standard length (SL), and girth behind the pectoral fins. The shark was then rotated onto its back to induce tonic immobility. An ultrasonic transmitter (V22TP, 50kHz, 22mm length, Vemco Ltd., Nova Scotia) was inserted into its body cavity through a 2-3 cm incision made off of the midline behind the pelvic fins. The transmitter was sanitized in a 10% solution of chlorhexidine gluconate (Nolvasan) and washed in a bath of deionized water prior to insertion. We also injected a liquid antibiotic into the body cavity following transmitter insertion. The incision was closed with 4-5 absorbable sutures. The shark was then rotated back to an upright position and placed in a stretcher to be lowered into the water, allowing the shark to depart volitionally. Handling time was kept under seven minutes.

Once tagged, each shark was tracked using a portable ultrasonic receiver and directional hydrophone (VR100, Vemco Ltd., Nova Scotia), with boat operators navigating as close as possible to the ultrasonic signal. The electronic tag transmitted pulses at intervals varying from 1-2 seconds. Each transmission received (“fix”) when the shark was within range of the receiver provided a timestamp and signal strength, which were stored along with the boat’s geographic coordinates (latitude, longitude) determined by an external GPS. The boat track thus served as a

proxy for the shark track. The tracking period for each shark lasted for 7-10 semidiurnal tidal cycles. The theoretical range of detectability of the transmitters can be estimated using output power, ambient noise at the transmitter frequency, and the loss of energy due to spherical spreading and absorption in the water (see Klimley *et al.*, 1998; Pincock & Voegeli, 2002). Given an output power of 156 dB measured at a distance of 1 meter, we calculated the range of the transmitter to be approximately 1.0 km given the wave conditions (wave height = 0.33 meters) commonly recorded in the study area. Because the depth of the water at the Golden Gate Bridge (approx. 100 meters) should have allowed for near free-field propagation, the actual range of the transmitter was likely similar to theoretical range. This range of potential error was further supported by range tests conducted in similar habitats (80% detection at 300 meters, Alexandra McInturf, unpublished data; 80% detection at 400 meters, Eric Chapman, unpublished data).

### *Current Simulation*

We modelled tidal flow in the San Francisco Bay estuary by simulating current data for the tracking periods using the Delft3D-FLOW module in the Deltares Open Source Software v. 3.15, Delft3D (Deltares Systems, 2014; Elias *et al.*, 2001; Lesser *et al.*, 2004). The Delft3D suite consists of various process modules that can interact to carry out simulations of flows, sediment transport, waves, water quality, and morphological developments. The hydrodynamic module, Delft3D-FLOW, calculates non-steady flow resulting from tidal and meteorological forcing on a curvilinear, boundary-fitted grid. In the vertical direction, the sigma coordinate system was adopted to represent water layers. Models generated by the Delft3D software have been previously validated by field studies in multiple locations including the San Francisco Bay (Elias

& Hansen, 2013) and have demonstrated accurate reproduction of hydrodynamic measurements even on standard parameter settings (Elias *et al.*, 2001). To test the efficacy of this model in contextualizing movement data, we used the previously compiled and publicly available San Francisco Bay-Delta System Community Model to obtain the Delft3D curvilinear grid (Elias & Hansen, 2013). Produced by environmental data collected by the United States Geological Survey, this DELFT3D-FLOW model consisted of six 2-way coupled curvilinear domains that constituted one 282 x 201 grid (Elias & Hansen, 2013). Though DELFT3D-FLOW models can simulate three-dimensional current flow, we selected a depth-averaged simulation (Delft 2DH) because of the uncertainty in shark position. We thus obtained the estimated average velocities in the general location of the animal, rather than assuming inappropriate precision. Grid resolution varied over the selected habitat but was finest in the vicinity of the Golden Gate Bridge (50 m x 50 m; Elias & Hansen, 2013; US Geological Survey, 2014). The software integrated bathymetry data from the San Francisco Bay (US Geological Survey, 2014), and simulated tides with amplitudes and phases of 12 locally dominant tidal constituents along the open ocean boundary (Elias & Hansen, 2013). During the shark tracking dates, the simulation calculated current direction and strength at each node of the irregular grid (total = 28, 958) covering the estuary. Historical predictions of tidal height (NOAA, National Ocean Service) from the tracking dates were used to verify the patterns observed in the simulated tidal movements. The data generated by the Delft3D model were exported to R v. 3.4 (R Core Team, 2017) using the ncd4 package (Pierce, 2017).

### *Data Processing*

To examine the extent and manner in which the sharks responded to tidal flow, we generated animations of each shark track overlaid on a map of coinciding current vectors in the San Francisco Bay (10.6084/m9.figshare.5791503). While some studies (*e.g.*, Whitney *et al.*, 2017) suggest that it may be appropriate to remove the portion of the track immediately after capture and release to account for the behavioral effects of capture stress, we found that the number of times the sharks moved into and out of the bay in the first twenty hours of tracking (n=6) proportionally reflected what we observed in the following twenty-four hours (n=9). Thus, in order to maximize the movement data available to properly explore the use of hydrodynamic models in this context, we used the entirety of each shark track in the analysis.

To visualize shark movement parameters, the raw GPS tracks for each shark were filtered and smoothed. Missing points (including long periods when transmitter was not in range due to refueling or other instances) were approximated using simple linear interpolation. Because the raw tracks corresponded to the movement of the boat, they included sharp angles and intervals of unnaturally straight bearings. To account for this, we re-sampled and smoothed the resulting positions. We sampled one of every 10 points along the interpolated shark track, then used a cubic spline, fit with the “approxTrack” function from the “trajectories” R package (Pebesma *et al.*, 2015), to smooth the trajectory. After smoothing, all interpolated points were removed from the analysis, and remaining points were spatially rediscritized to create intervals between shark positions of a consistent length (20 m), allowing us to evaluate trends in the track bearings (Turchin, 1998). Large gaps in the track (>2 hours) were excluded from the rediscrization process. Using these post-processed shark tracks, the speed and direction of the shark movements were calculated between sequential fixes and averaged to estimate an overall speed

for each shark. The metrics of current corresponding to each post-processed shark location were extracted from the simulated current dataset.

Finally, we used our animations (10.6084/m9.figshare.5791503) to count the number of times the sharks traveled in and out of the San Francisco Bay, marking the Golden Gate Bridge as the threshold between estuarine and deeper offshore water. With each crossing underneath the Golden Gate Bridge, we noted the timestamp and the approximate phase of the tide based on NOAA records. Each crossing where the shark locations were interpolated was classified as “unknown” and not included in this part of our analysis.

### *Statistical Analysis*

In order to determine how current strength affected shark movement, we explored the relationship between shark movements underneath the Golden Gate Bridge and amplitude of the mixed semidiurnal tide. For each tidal cycle where sharks were observed to cross underneath the bridge and their tracks were relatively complete (missing data < half of tidal phase duration), we calculated the tidal amplitude and duration (Fig. 2.2). Within each tidal cycle, positional fixes for the shark as well as selected current vectors (*i.e.*, current vectors at the shark’s estimated location) were extracted. These vectors were used to calculate the displacement of the shark and the water mass within which it swam. Each shark displacement was defined as the distance between its location at the beginning and end of the cycle, while current displacement was determined by summing the lengths of the current vectors estimated along the shark’s path during the tidal cycle (Table 2.1).

Table 2.1. Summary table of tide, current, and shark movement patterns for selected tidal cycles when sharks were known to move into or out of the estuary, and shark tracks had minimal interpolated data. Amplitude is defined as the absolute value of the difference between the high and low tides for each tidal cycle. Tidal phase reflects the direction of the tide, while duration indicates the amount of time between high and low tides. Displacement differential refers to the difference in shark displacement versus current displacement during a given tide (i.e., positive values indicate greater displacement of the shark than that of the current).

<b>Tidal Segments</b>	<b>Amplitude (m)</b>	<b>Tidal Phase</b>	<b>Duration (hh:mm)</b>	<b>Displacement Differential (km)</b>
2.1	1.53	Ebb	7:22	7.98
2.2	1.23	Flood	7:23	6.02
2.3	0.44	Ebb	4:37	-0.60
2.4	1.59	Ebb	7:03	4.93
3.1	1.94	Ebb	6:18	4.83
3.2	1.64	Flood	6:46	1.35
3.3	1.03	Ebb	4:58	-4.49
3.4	1.42	Flood	6:20	2.41
3.5	2.29	Ebb	6:46	-0.48
3.6	1.76	Flood	7:11	-3.82

We used a linear mixed-effects model to evaluate our hypothesis that current strength would drive shark movement in response to tidal flow. Specifically, our model tested the relationship between shark and current displacement as a function of tidal amplitude, with the expectation that shark displacement would be greater than displacement of the water mass at smaller tidal amplitudes. This model included the difference between shark and current displacement as the response variable, the tidal amplitude and phase as fixed effects, and shark identity as a random effect (Table 2.2).

### **Results:**

Three sharks were caught and tracked from either 29-31 July (Shark 1, tag ID: 8444), 9-12 September (Shark 2, tag ID: 8446), or 14-17 October 2008 (Shark 3, tag ID: 8448; Fig. 2.1). Shark 1 (S1) and shark 3 (S3) were both males of similar size with total lengths of 235 and 246 cm. Shark 2 (S2) was a smaller female with a total length of 135 cm. Between tracking periods,



the range of the mixed semidiurnal tide in the estuary varied slightly. S1 tracking occurred during tides with amplitudes between 0.42-2.52 meters (median: 1.52 m, range: 2.10), S2 tracking occurred during tides with amplitudes between 0.29-1.59 meters (median: 0.72 m, range: 1.30), and S3 tracking occurred during tide with amplitudes between 0.68-2.28 meters (median: 1.64 m, range = 1.60).

As predicted, there was evidence of tidal flow influencing shark movement patterns in our animated model. Sharks displayed directional movements underneath the bridge that were consistent with the tidal flow for approximately 73% of observable tidal segments included in our analysis (n=19; 10.6084/m9.figshare.5791503). S1 demonstrated this behavior the least, during half of all possible flood and ebb tides included in the analysis (2 out of 4 tides, 50%). S2 did so in 62.5% of instances (5 out of 8 tides), while S3 tracked all tidal movements in and out of the estuary during the tracking period (7 out of 7 tides, 100%; Fig. 2.2).

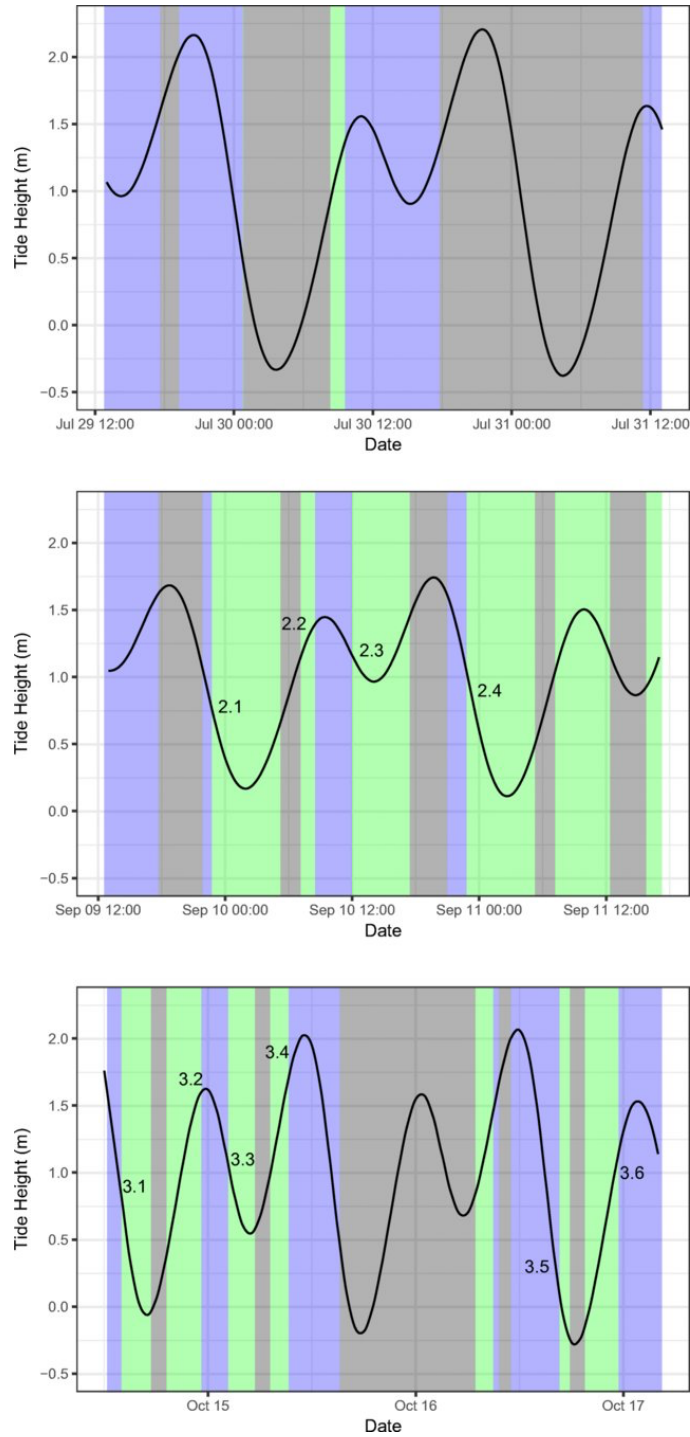


Figure 2.2. Variations in tidal amplitude in the San Francisco Bay (data from the NOAA buoy located at 37.807 N and 122.465 W) during the period of active tracking of each sevengill shark. Shading depicts location of the shark. Blue indicates the shark was in the estuary, green indicates the shark was in the coastal ocean, and grey indicates periods greater than one hour without a shark relocation (often due to refueling the vessel or exchanging crew). Tidal segments used in the statistical analysis are labelled with the tidal segment ID (Table 2.1 for reference).

For those occasions when the sharks did move in or out of the estuary, we analyzed the relationship between their displacement and the current strength (Fig. 2.3). After removing tidal cycles where the shark’s track while moving underneath the bridge was interpolated, we examined 11 tidal phases in total (Fig. 2.2, Table 2.1). Each lasted between approximately 4 and 7 hours, with amplitudes ranging from 0.44 to 2.29 m. During a slim majority of these tidal segments (6 out of 10), we observed shark movements where the shark moved over greater distances than the current displacement. In the remaining segments (4 out of 10), sharks exhibited less displacement than that of the current (Fig. 2.3). However, while we did observe different movement responses to current flow as hypothesized, our linear mixed models found no significant effect of tidal amplitude on difference in displacement (Table 2.2).

Table 2.2. Linear mixed-effects models examining the effect of tidal amplitude (in meters) on the differential between shark and current displacement. Shark identity was treated as a random-effects variable.  $\beta$ : coefficients of the linear predictor of the model. CI: 95% confidence interval of coefficients.

	<i>Displacement Differential</i>		
	$\beta$	<i>CI</i>	<i>p-value</i>
<b>Intercept</b>	-4.21	-14.24 – 5.83	0.411
<b>Tidal Amplitude</b>	4.24	-3.52 – 5.20	0.706
<b>Phase (flood)</b>	0.84	-0.61 – 9.09	0.087
	<b>R<sup>2</sup> = 0.129</b>		

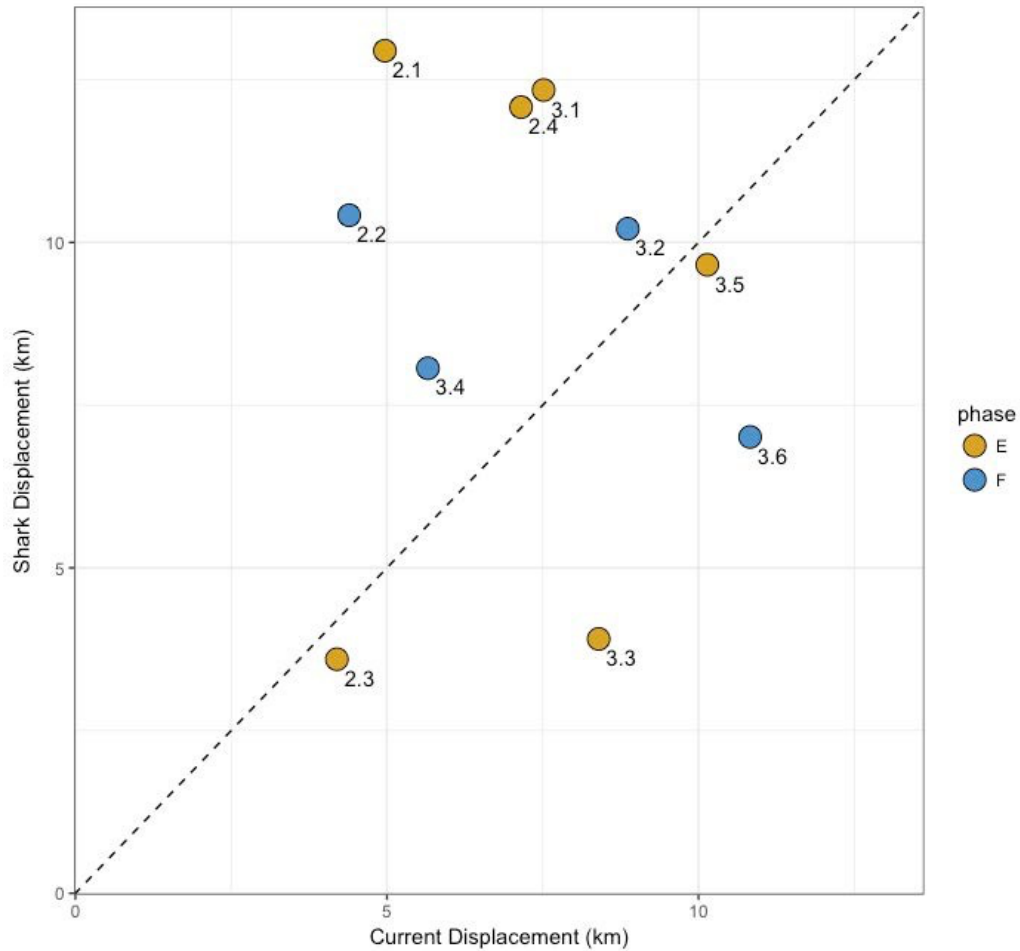


Figure 2.3. Relationship between shark and current displacement for each tidal cycle analyzed in the linear models. Color indicates tidal phase (ebb [E] or flood [F]), and labels correspond to the analyzed tidal segments. The dotted line indicates the 1:1 relationship between the shark and current displacement.

### Discussion:

Over the past century, numerical models of hydrodynamic and sediment processes have evolved from analytical single-dimensional models to multi-dimensional models able to predict more complex tidal flows (Lesser *et al.*, 2004). Though they have been increasingly used for coastal management and engineering (Elias *et al.*, 2001), hydrodynamic models can also be an invaluable tool in addressing the challenge of visualizing dynamic environments through which aquatic organisms move. Here we show that hydrodynamic models can also be used to examine the influence of tide on sevengill shark movement in estuarine systems, particularly in locations

such as high-flow areas characterized by short-term variance due to both natural and anthropogenic factors.

The DELFT3D-FLOW module is powerful in this context because it integrates a large number of processes (*e.g.*, wind shear, tidal and wave forces, density-driven flows, and stratification due to salinity and temperature gradients) to generate hydrodynamic models applicable to a wide range of coastal and estuarine situations (Deltares Systems, 2014). These dynamic environments are often highly productive, supporting a large number of resident species. A unique challenge facing these organisms is the variable flow patterns that characterize these habitats. Species that are selective in habitat choice within these locations have likely evolved means of perceiving and responding to tidal patterns to achieve their movement goals in the most energy-efficient manner (Bernatchez & Dodson, 2008; Kelly & Klimley, 2012). To understand the behavioral responses of estuarine species, however, it is necessary to place their fine-scale movement patterns in an environmental context of similar scale, and a major obstacle in the field of movement ecology is the inability to consistently gather environmental data at the appropriate resolution for the corresponding animal tracks. This study thus presents a unique application of hydrodynamic modeling to contextualize animal movement patterns in a highly dynamic environment.

Many mobile marine predators are known to exhibit evidence of residency within high-flow areas (Benjamins *et al.*, 2015). Among these, sevengill sharks in the San Francisco Bay often selectively occupy the channel underneath the Golden Gate Bridge (Ketchum *et al.*, 2017). Consequently, we hypothesized that the sharks were able to adapt to such a high-energy environment by moving through the channel while adjusting their movement pattern according to the strength of the tidal flow. Our results supported our initial hypothesis that the direction of

sevengill shark movements frequently corresponds with the current direction. Our hydrodynamic model revealed that sharks moved through the channel with the tide during a majority of observed tidal phases (14 out of 19). This was most evident in S3, which traveled through this area with every ebb and flood tide. This pattern may have been due to the fact that the shark was tracked during an equatorial tide when currents were strongest.

However, we did not detect an influence of tidal strength on sevengill shark movement, as initially hypothesized. This may have been because, while the hydrodynamic model demonstrated great potential for examining organism response to tidal flow, we applied this novel method to a fairly small sample size, although our dataset did record high-frequency positions over several days of behavior per individual. Additionally, the measurement error along the sharks' tracks was greater than the scale of the highest resolution grid area (50x50 m) located at the high-flow area near the Golden Gate Bridge. Because our hypotheses were formulated based on movement patterns at a larger spatial scale (*i.e.*, movement through the channel over an entire tidal phase), this was unlikely to bias our results. However, we were not able to distinguish between the possible influence of the scale of data versus the model on our ability to infer movement responses in sevengill sharks in this study. Future studies should address this distinction by considering the use of more precise forms of biologging in addition to acoustic telemetry systems to answer fine-scale behavioral questions more thoroughly. For instance, accelerometers are capable of both identifying complex behaviors and estimating their net energetic cost. When combined with the method presented here, this may offer an avenue for examining fine-scale movement patterns in response to tidal flow in an even greater capacity, such as through mapping energy landscapes to quantify the cost of transport in aquatic taxa.

Our results were also likely affected by behavioral or ecological processes. We assumed that shark movements would be consistent throughout an entire ebb or flood tide and would depend on the amplitude of the tide. However, even during the shortest tidal segment examined (segment ID 2.3; Fig. 2.2, Table 2.1), the current displacement (1.23 km) would have been sufficient to transport the shark through the channel. It is therefore likely that the shark response was more nuanced or may have occurred at a finer temporal scale. For instance, through the generated animations (10.6084/m9.figshare.5791503), we found that some sharks displayed multiple movement patterns within a single tide. In one example, S3 was east of Alcatraz Island at the beginning of the tide (segment ID 3.6), where it was sheltered from strong ebb tides. This animal was only transported through the channel when it swam into currents that were both strong and oriented in that direction later in the tidal phase. Additionally, due to our use of a depth-averaged model, we were unable to account for the potential variation in shark movement due to their position in the water column. It is possible that the sharks experienced changes in the strength of current flow in this dimension, depending on their depth. For instance, sharks swimming near the bottom, where the current is reduced, may not have been exposed to the full strength of the tidal flow.

From an ecological perspective, we focused on the hypothesis that shark response to the variation in tidal current would reduce transport costs. However, it is likely that the sharks respond to other environmental factors as well, specifically those that may offset the cost of moving in a less energetically efficient manner (*i.e.*, energy acquisition; Shepard *et al.*, 2013; Wilson *et al.*, 2012). Some predators, such as those that feed on anadromous fish (*e.g.*, large teleosts, gulls, pinnipeds), have been known to occupy transitional habitats at estuarine or riverine mouths to take advantage of prey moving with the prevailing current flow (Roffe &

Mate, 2007; Wright *et al.*, 2007 and others). However, because the diet of sevengill sharks includes several actively swimming species of fish and marine mammals (Ebert, 1991), it is possible that sharks would exhibit different movement patterns by either tracking prey items as they are transported in the current through the channel or roaming widely to forage outside of the high-flow area. In either case, the motivations for behavioral flexibility may not be mutually exclusive; because sevengill sharks can perceive and respond to changes in tidal flow, they likely take advantage of local currents in addition to the overall tidal flow to forage. If feeding, rather than energy efficient transport, was the primary movement goal, this may have also led to deviations from the expected response to the prevailing tidal movement.

While it is beyond the scope of our study to examine the other factors that may affect the movement of these individuals in particular, the patterns documented using our hydrodynamic model suggest that sharks vary in their responses to dynamic and localized environmental conditions. To determine the extent to which this behavioral flexibility is adaptive will require future work to identify possible benefits of moving with the tides in high-flow areas, including the assessment of foraging opportunities available in different regions of the estuary and under different tidal conditions. Combining the methods used in this study with data from with accelerometers and biologgers could help elucidate the influence of different external factors on fine-scale movement among a variety of taxa within the San Francisco Bay and in other estuaries. This information would provide valuable insight into the effect of local environmental conditions on the distribution and behavior of marine organisms, which could be used to predict how these animals may respond to the multiple anthropogenic threats present in estuarine habitats. For instance, marine renewable energy infrastructure is often concentrated where coastal geometry helps enhance flows, and is thus predicted to alter flow patterns in these



locations (Borthwick, 2016). Consequently, there is a need to improve our understanding of key behaviors and fine-scale movement strategies of animals like sevengill sharks that selectively occupy high-flow regions. Establishing an effective method of doing so, such as through the use of the presented model, is an important step towards this goal.

In this study, we have shown how hydrodynamic models can be used to contextualize aquatic animal movement patterns in response to tidal flow. We believe this method can be powerful in exploring how predatory elasmobranchs and other nektonic organisms in tidal systems respond to currents that vary locally in space and time (Chapman *et al.*, 2011; Stasko, 1975). We encourage future studies to expand the use of hydrodynamic to predict fine-scale species distribution and space use, particularly in areas highly impacted by anthropogenic activities.

**Data accessibility:**

Videos generated from the hydrodynamic model and telemetered data can be found on the FigShare Data repository: DOI 10.6084/m9.figshare.5791503.

**Ethics statement:**

The methods pertaining to shark capture, tagging, and release in this study followed a protocol approved by the University of California, Davis Institutional Animal Care and Use Committee (Protocol 06-12892). Transmitters were inserted by researchers practiced in the appropriate surgical technique, animal stress was monitored throughout the procedure, and handling time from capture to release was minimized.

**Author Contributions:**

AGM wrote the manuscript, created the hydrodynamic model and performed statistical analyses. AES assisted in writing the manuscript, performing statistical analyses and prepared figures. MLB led the tagging and active tracking of sevengill sharks and contributed to the writing of the manuscript. PTS participated in shipboard tracking and reviewed the manuscript. CJS provided funding, assisted in data collection, and reviewed the manuscript. NF assisted in writing and reviewing the manuscript. APK conceived of the project, secured funding, assisted in data collection, and reviewed the manuscript. DC conceived of and supervised statistical analyses, generated the hydrodynamic model, and assisted in writing and reviewing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## **Chapter 3:**

# **Spatial distribution, temporal changes, and knowledge gaps in basking shark (*Cetorhinus maximus*) sightings in the California Current Ecosystem**

Alexandra G. McInturf<sup>1,2</sup>, Barbara Muhling<sup>3,4</sup>, Joseph J. Bizzarro<sup>5,6</sup>, Nann A. Fangue<sup>1</sup>, Damien Caillaud<sup>7</sup>, Heidi Dewar<sup>4</sup>

<sup>1</sup> Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA USA

<sup>2</sup> Animal Behavior Graduate Group, University of California, Davis, CA USA

<sup>3</sup> Institute of Marine Sciences, University of California, Santa Cruz, Santa Cruz, CA, USA

<sup>4</sup> NOAA Southwest Fisheries Science Center, San Diego, CA, USA

<sup>5</sup> Cooperative Institute for Marine Ecosystems and Climate, University of California, Santa Cruz, Santa Cruz, CA, USA

<sup>6</sup> NOAA Southwest Fisheries Science Center, Fisheries Ecology Division, Santa Cruz, CA, USA

<sup>7</sup> Department of Anthropology, University of California, Davis, CA, USA

**Abstract:**

Among the largest fish species, the basking shark (*Cetorhinus maximus*) is found circumglobally in temperate and tropical waters. Though historical documents have recorded their presence in the California Current Ecosystem (CCE), basking sharks are now only rarely observed in this part of their range. We compiled recent and historical data from systematic surveys (1962-1997) and other sources (1973-2018) to i) examine temporal patterns of basking shark sightings in the CCE, and ii) determine the spatial, temporal, and environmental drivers that have affected basking shark presence and distribution here for the last 50 years. We first calculated variation in basking shark sightings and school size over time. We then generated species distribution models using the systematic survey data and evaluated the performance of these models against the more recent non-systematic sightings data. The sightings records indicated that the number of shark sightings was variable across years, but the number and probability of sightings declined in the mid-1980s. The systematic survey data showed up to nearly 4,000 sharks sighted per year until the 1990s, after which there were no sightings reported. In parallel, there was more than a 50% decline in school size from the 1960s to the 1980s (57.2 to 24.0 individuals per group). During the subsequent decades in the non-systematic data (>1990), less than 60 sharks were sighted per year. There were no schools larger than 10 reported, and the mean school size in the last decade (2010s) was 3.53 individuals per group. Low sea surface temperature and high chlorophyll *a* concentration increased sightings probability, and prevailing climatic oscillations (ENSO, NPGO, PDO) were also correlated with basking shark presence. Lastly, we observed a significant shift in the seasonality of sightings, from the fall and spring during the systematic survey period to the summer months after the 2000s. We conclude by offering suggestions for future research and conservation efforts;



specifically, coordinating the documentation of fisheries mortalities and sightings throughout the Pacific basin would facilitate more robust population estimates and identify sources of mortality. Additionally, monitoring shark fin markets and developing region-specific genetic markers would help ensure that CITES regulations are being followed.

### **Introduction:**

Natural ecosystems are increasingly impacted by human activity, leading to losses in biodiversity and population declines of many species worldwide. Of particular concern is the decline of marine top predators, including a number of shark species (Estes *et al.*, 2011; Pacoureau *et al.*, 2021). The projected impacts of predator loss are numerous and diverse, and many are species-specific. Ecological consequences include trophic cascades, mesopredator release, and potential declines in commercially important teleost species and their prey (Heithaus *et al.*, 2008; Polovina & Woodworth-Jefcoats, 2013). Unfortunately, identifying potential trends in shark population size can be challenging, as studies that quantify these trends are often restricted to localized fisheries-independent surveys, or more commonly, broader fishery-dependent analyses of catch per unit effort (*e.g.*, Simpfendorfer *et al.*, 2002; Lucifora, Menni and Escalante, 2005; Drymon *et al.*, 2011; Polovina and Woodworth-Jefcoats, 2013; Peterson *et al.*, 2017). For large mobile species that have limited interactions with fisheries, frequently occupy offshore areas, and are difficult to survey, there is a lack of data that renders the underlying mechanisms and magnitude of potential declines challenging to determine.

The basking shark (*Cetorhinus maximus*) is among the species for which data gaps limit analysis of population trends. It is the world's second largest fish and one of three filter-feeding shark species. Though many aspects of its biology remain unknown, it is thought to be a long-

lived organism with a low rate of population growth (*i.e.*, generation time of ~20-30 years; McFarlane *et al.*, 2009). Circumglobally distributed in temperate and tropical regions, basking sharks are capable of large-scale migrations, traversing entire ocean basins beyond the legal protection of one single country (Gore *et al.*, 2008; Braun *et al.*, 2018; Dewar *et al.*, 2018). During certain months, individuals aggregate in shallow coastal hotspots, many of which are characterized by high frontal activity or merging water masses (*e.g.*, Sims and Quayle, 1998; Skomal, Wood and Caloyianis, 2004; Miller *et al.*, 2015; Crowe *et al.*, 2018). In these locations, sharks can be observed feeding at the surface, often on calanoid copepods (*Calanus* spp.), along visible tidal lines that mark the front boundary (Baduini, 1995; Sims and Quayle, 1998; Miller *et al.*, 2015). Basking shark coastal hotspots have been recorded primarily in the northern hemisphere and in New Zealand (Finucci *et al.*, 2021; Francis & Duffy, 2002), though their seasonality varies by location. In regions in the Northern Atlantic, the Eastern Coast of North America, and in New Zealand, hotspots consistently form in late April through early September (*i.e.*, Sims *et al.*, 2003; Speedie, Johnson and Witt, 2009; Lieber *et al.*, 2013, 2019; Hoogenboom *et al.*, 2015; Gore *et al.*, 2018; Finucci *et al.*, 2021). Conversely, in the Eastern North Pacific (ENP), hotspots were observed in the mid-20<sup>th</sup> century during summer months along the southern coast of British Columbia in Canada, but during winter months in California's Morro and Monterey Bays (Squire, 1967; Squire, 1990; McFarlane *et al.*, 2009). As a result, sharks in this region were thought to represent single ENP population that ranged from Alaska between March and October, as far south as Baja California from October through May (Squire, 1990; McFarlane *et al.*, 2009; Dewar *et al.*, 2018). However, historical and recent observations suggest that this seasonality may have changed. Fishermen in the early 1900s noted shark presence in central California year-round (Squire, 1967), yet starting in the 1990s, basking sharks have been

primarily observed in June, July and August (Baduini, 1995; Dewar *et al.*, 2018). Factors driving shifts in occurrence have not been determined.

Historically, their seasonal aggregation behavior made basking sharks a periodic target for direct commercial fisheries in temperate waters. Particularly in the early 20<sup>th</sup> century, they were fished for their liver oil, fins, and meat. In the Atlantic, Ireland's Achill Island fishery alone captured over 1,000 basking sharks annually from 1951 to 1955 and continued to operate through 1965 (Went and Súilleabháin, 1967). Minor sport and commercial fisheries in central California also emerged to target basking sharks in the early twentieth century. Starting in 1924, an average of 25 sharks were landed each season (September – May), with a maximum of 100 sharks landed in a single year until the fishery ended in 1938 (Phillips, 1948), partly because of a decline in shark availability. The fishery re-emerged in 1946, with roughly 300 sharks landed in the first year (Phillips, 1948; Roedel and Ripley, 1950; Thomas, 2004; McFarlane *et al.*, 2009). Approximately 200 sharks were landed in each subsequent year until fishing activity was suspended in 1950, again due in part to a decrease in shark numbers (CITES, 2002; McFarlane *et al.*, 2009; Squire, 1967). In Canada, the basking shark was considered a nuisance and subjected to a culling effort by government agencies due to its frequent entanglement in fishing nets (McFarlane *et al.*, 2009). Approximately 1,000 sharks were killed by eradication, entanglement, and sport fishing in Canadian waters between 1945 and 1970 (McFarlane *et al.*, 2009). The overexploitation of basking sharks likely contributed to population declines in multiple locations by the mid- to late-1900s (*e.g.*, Squire, 1990; Sims *et al.*, 2005; Southall *et al.*, 2005; McFarlane *et al.*, 2009; Witt *et al.*, 2012). In the ENP specifically, systematic surveys, sightings reports, and catch data all indicate that since the mid-1900s, observations have decreased from thousands of

individuals per year to few, if any (Baduini, 1995; Dewar *et al.*, 2018; McFarlane *et al.*, 2009; Squire, 1990; Squire, 1967).

Targeted fishing for basking sharks in the ENP ended decades ago (Dewar *et al.*, 2018; McFarlane *et al.*, 2009), and protective measures for the species were established locally and globally starting in the 1990s. Among these, the basking shark is now listed under Appendix II under the Convention on International Trade in Endangered Species (CITES, 2002). In addition, basking sharks are listed as endangered globally (International Union for the Conservation of Nature [IUCN], Rigby *et al.*, 2019) and, for the ENP population, endangered in Pacific Canadian waters (COSEWIC, 2007). In the United States, the National Oceanic and Atmospheric Administration (NOAA) designated the basking shark as a Species of Concern in 2010, although the program has since been discontinued. Basking sharks are also a prohibited species in the Pacific Fisheries Management Council (PFMC) Highly Migratory Species Fisheries Management Plan (PFMC, 2018).

In some areas throughout their range, basking sharks appear to be responding well to protective measures. For example, basking sharks are still sighted regularly in the North Atlantic (*e.g.*, Witt *et al.*, 2012; Miller *et al.*, 2015; Gore *et al.*, 2016). Though sharks occur in fewer numbers than had been observed prior to the establishment of targeted fisheries (Southall *et al.*, 2005), some studies (*i.e.*, Witt *et al.* 2012) suggest a potential population recovery in this region. In contrast, there is no documented increase in sightings in the ENP, although analyses are limited by the lack of systematic data collection.

Evaluating the status of the basking shark population in the North Pacific is difficult due to multiple data gaps. While modeled estimates of the population size suggest that less than 1,000 individuals may remain in the ENP (McFarlane *et al.*, 2009), stock structure has not been

determined (Dewar *et al.*, 2018; McFarlane *et al.*, 2009), rendering stock assessments impossible. Potential sources of mortality are also unquantified. Though some threats have been mitigated, basking sharks are vulnerable to a range of gear types, particularly gillnets, and they have been incidentally taken in coastal and high-seas fisheries (Bonfil, 1994; Darling & Keogh, 1994; Dewar *et al.*, 2018; Larese & Coan, 2008; McFarlane *et al.*, 2009; McKinnell & Seki, 1998; Sandoval-Castillo *et al.*, 2008). Additionally, given the high cost of their fins (Magnussen *et al.*, 2007), there is strong motivation to retain any landed sharks. Finally, long-term, systematically collected datasets are not available for recent decades. These considerable data gaps also preclude formal stock assessments (Mieras *et al.*, 2017).

An additional challenge to the management of basking sharks is the lack of knowledge on habitat use. Basking sharks are known to exhibit high interannual variability in occurrence, but the forcing mechanisms behind this are not known (Jordan, 1887; Dewar *et al.*, 2018). Such information is critical to differentiate whether variation in sightings occur due to changes in population size or in movement patterns and distribution because of environmental change. Understanding habitat is also necessary to develop methods (*e.g.*, dynamic ocean management; Hazen *et al.*, 2018; Abrahms *et al.*, 2019; Blondin *et al.*, 2020) to avoid ship strikes and incidental capture by reducing overlap between vessels and basking sharks. Furthermore, identifying the environmental drivers of basking shark movement patterns can help forecast potential changes in habitat quality and hotspot location associated with climate change. There is a considerable amount of data in the Northeast Atlantic indicating that both biotic and abiotic factors (*e.g.*, sea surface temperature, plankton density, frontal activity) affect basking shark presence and behavior (Austin *et al.*, 2019; Berrow & Heardman, 1994; Cotton *et al.*, 2005; Hoogenboom *et al.*, 2015; Miller *et al.*, 2015; Sims & Quayle, 1998; Witt *et al.*, 2012). However,

few studies on this topic (*e.g.*, Squire, 1990; Baduini, 1995; Dewar *et al.*, 2018) exist in the Pacific.

The aim of this study is two-fold: i) to compile recent and historical data to re-examine temporal trends in basking shark sightings and school size over time using the most up-to-date information, and ii) to determine the environmental factors that affect basking shark abundance and distribution in the ENP. We primarily focus on the California Current Ecosystem (CCE), which runs from the southernmost point of Baja California, Mexico to Washington, USA. With sightings data collected from 1962-2018, our analysis uses species distribution models to assess the impact of environmental factors hypothesized to predict basking shark presence (sea surface temperature, climactic oscillations, and chlorophyll abundance), in addition to spatial (latitude and longitude) and temporal (month and year) trends in occurrence. Species distribution models can also offer insight into whether the decline in sightings in the CCE could be driven by declining suitability in environmental conditions. Additionally, because important behaviors like feeding, mating and social interaction have been proposed as other mechanisms driving coastal basking shark aggregations, we examine variation in aggregation size over time. We conclude by highlighting ongoing gaps in our knowledge of the ENP population (*i.e.*, population demographics and behavioral information) and offer suggestions to address these areas.

## **Methods:**

### *Sightings data*

Basking shark sighting information along the west coast of the United States was compiled by NOAA from a variety of sources, including NOAA aerial surveys, fisheries data, tagging and research efforts, and public observations. It is important to note that for all data

sources, sharks were only sighted when near the surface. Sightings were defined as a single report of any number of sharks observed in given location and time point. We divided the dataset into two categories: sightings obtained via NOAA systematic aerial surveys (hereafter “systematic survey data”), and those that were reported opportunistically (hereafter “non-systematic data”) by other means (Fig. S3.1).

Most shark sightings (402/624) were reported during the NOAA systematic surveys, which took place from 1962-2004 (Fig. 3.1). During this time, commercial aerial fish spotters flew along the southern and central California coast to estimate tonnage of coastal pelagic fish species such as sardine (*Sardinops sagax*). Surveys were conducted in a block design, each block covering a 10-arcminute squared area, or 8x10 nautical miles (Caruso, Meyer, and Iacometti 1983). There were over 20,000 flights conducted; however, not all pilots reported basking sharks. It was unknown whether this was intentional on behalf of those pilots or due to basking shark absence during their flights. Consequently, we only included data from pilots who had reported a basking shark at least once and accounted for potential variation between pilots in our models (see analyses below). Due to pilot turnover, our dataset was limited to years prior to 1997. The systematic survey sampling method also provided information on school size and basking shark absence, from blocks in each flight that were surveyed in which no sharks were recorded (26,655 absences).

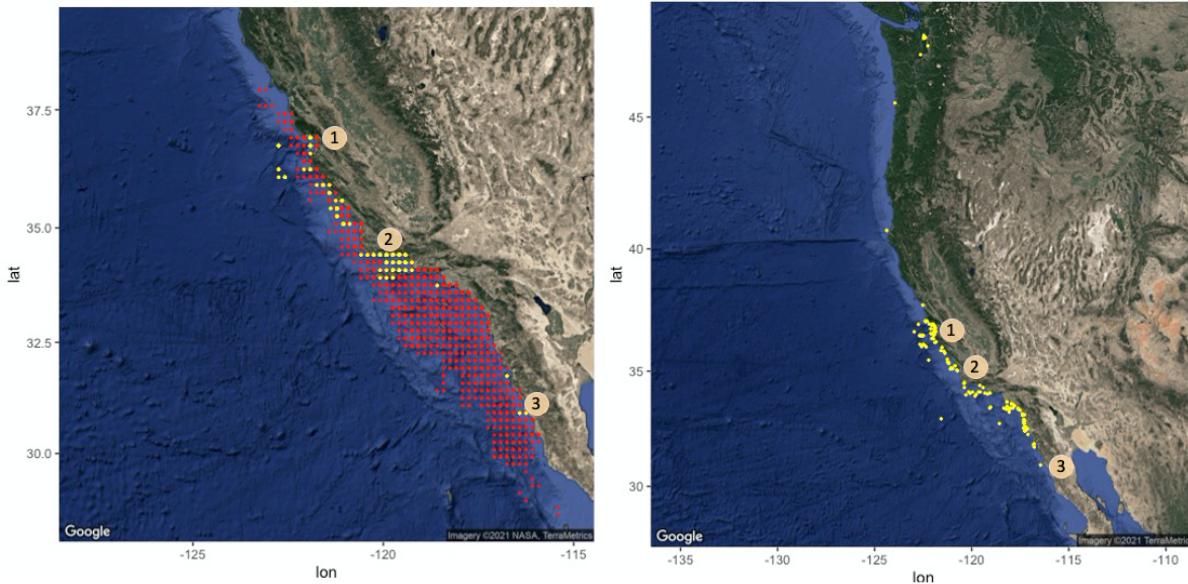


Figure 3.1. Maps of sightings data collected from 1962-2018, from systematic surveys (left; 1962-1997) and non-systematic data (right; 1973-2018) along the western coast of the United States and Mexico. Presences are denoted in yellow. Those above 46° latitude were observed in the bay near Seattle, Washington (USA). Sightings from drift gillnet records have been excluded in this figure because of NOAA confidentiality policies. Centroids of blocks where sharks were not found, based on systematic surveys by pilots who had reported a basking shark at least once, are marked in red. Numbers indicate shark hotspots identified in both this and previous studies, in 1) Monterey Bay, 2) Santa Barbara, and 3) Baja California.

In addition to systematic survey data, other instances of basking shark sightings (222/624) were collated by NOAA from 1973-2018 (Fig. 3.1; S3.1). These were reported from tagging efforts (n=20), gillnet observer records (n=51), leatherback sea turtle (n=8) and porpoise aerial surveys (n=15; Forney *et al.*, 2014), public sightings records (*e.g.*, the Spot-A-Basking Shark program by the Pacific Shark Research Center; n=58) and other NOAA reports (n=70). The aerial surveys in particular (Forney *et al.*, 2014) offer the most direct comparison to the systematic survey data given the similarity of methods. These sea turtle and porpoise surveys reported basking shark presence and school size from 1990-2013, beyond the systematic survey period. Notably, corresponding absence data were not available for any non-systematic observations. For our analysis we generated pseudo-absences in R for each presence in this subset of the data in a 10:1 ratio, using the `randomPoints` function in the *dismo* package to conduct random background sampling of the spatial extent (Hijmans *et al.*, 2017; R version



4.0.2; R Core Team, 2020). However, given the wide variation in sampling techniques, this subset of the data was primarily used for model evaluation (see below) and to allow for further exploration of temporal trends in sightings.

Most sightings in the systematic and non-systematic data ( $n = 621/624$ ) included information on number of sharks observed, which were binned into categories (solitary, 2-10, 11-50, 51-100, and 101-500 sharks) to quantify changes in aggregation size. For reports with multiple individuals sighted, we then calculated the mean group size per decade. We compared the values for the first and last decades of the systematic survey data in which sharks were sighted (1960 and 1980) and the last decade of the non-aerial survey data (2010).

#### *Predictor variables*

Fine- and broad-scale environmental predictors selected for our analysis were chosen based on previous studies. At a fine-scale, predictors included sea surface temperature (SST) and surface chlorophyll *a* (chl-*a*) concentration (Squire, 1990; Cotton *et al.*, 2005; Witt *et al.*, 2012). Water temperature is known to drive patterns in abundance and distribution (Brown *et al.*, 2004; Payne *et al.*, 2016). Chl- *a* is often used as a proxy for ocean productivity and thus feeding conditions, which basking sharks and other planktivorous species are shown to track (Austin *et al.*, 2019; Miller *et al.*, 2015). As many of our observations pre-date the satellite era, we used the Hadley Centre Sea Ice and Sea Surface Temperature data set (Rayner *et al.*, 2003) to estimate SST at sampled locations, calculated monthly at 1-degree spatial scale from 1870 to near present. Additionally, because consistent ocean color observations are only available starting in the late 1990s, we created a climatology of chl-*a* for each month at each spatial coordinate from 1997 through 2019. Monthly values were calculated from re-analyses developed through the Ocean-

Colour Climate Change Initiative (OC-CCI) using multiple ocean color sensors (Sathyendranath *et al.*, 2019). We were therefore able to determine whether sightings were related to specific locations and season(s) where chl-*a* has been high on average during the ocean color satellite era, although we could not assess surface chlorophyll conditions for most basking shark sightings (as they were from years prior to 1997). Both environmental variables were obtained from NOAA's ERDDAP server (Simons, 2020), and extracted using the `rerddapXtracto` package (Mendelssohn, 2020).

Broad-scale cues included predictors for prevailing climatic oscillations in this region: the El Niño-Southern Oscillation index (ENSO), North Pacific Gyre Oscillation (NPGO: Di Lorenzo *et al.*, 2008) and Pacific Decadal Oscillation (PDO: Mantua and Hare, 2002). All were reported by month and year.

To account for other spatiotemporal processes not captured by the selected environmental data, we included spatial (latitude, longitude) and temporal (month, year) predictors. In addition, because existing literature is currently contradictory with respect to the seasonality of basking shark sightings (Squire, 1967; Dewar *et al.*, 2018), we added an interaction term to account for variation in monthly sightings by decade within our dataset. Given the possibility that localized cues (*e.g.*, SST or chl-*a*) drove changes in sightings over time, we also calculated the mean SST by decade at all sighting locations to supplement the results of our models (Fig. S3.2). We were unable to calculate mean chl-*a* by decade prior to 2000 given that its values were calculated from a climatology.

## *Analysis*

We created three species distribution models using general additive mixed models (GAMMs) to determine the effect of our selected predictors on basking shark presence, using the *mgcv* package (Wood, 2017). We used a cross-validation approach to assess the performance of each GAMM (Table 3.1a). Because the systematic survey data constituted most of our data and included both presences and true absences, this subset of the sightings data was used for cross-validation. Comparing model performance allowed us to determine whether our selected environmental predictors alone were sufficient to predict basking shark presence, or whether unmeasured spatiotemporal processes were also important (Brodie *et al.*, 2020). In all models, 1) environmental variables (fixed effects) and Pilot identity (random effect) were included as predictors, 2) chl- *a* was fourth-root transformed before analysis to reduce skewness, and 3) all variables were smoothed using a thin-plate regression spline, except for month where a cyclic cubic regression spline was used. Model 1 also included year, latitude and longitude as an interaction term, and month as a fixed-effects variable, which was allowed to vary by decade to assess changes in seasonality over time (Table 3.1a). Model 2 only included year as an additional predictor.

For cross-validation, the systematic survey data was divided into an 80% training/20% testing split. To account for the strong class imbalance due to the large proportion of absences, we up-sampled the training data such that presences represented 8% of the dataset (versus ~1.5% before up-sampling). We assessed model skill using the Area Under the Receiver Operating Characteristic (ROC) curve: (AUC) (Runcie *et al.*, 2019; Hanley and McNeil, 1982). The AUC metric varies between 0 and 1, with a value of 0.5 indicating that the model predictions were no better than random, and a value of 1 indicating that the model is capable of distinguishing

presences and absences perfectly (Runcie *et al.*, 2019; Elith *et al.*, 2006; Parisien and Moritz, 2009).

We calculated the mean AUC on the withheld 20% of data across five different, random testing/training splits to determine model performance for each GAMM (Table 3.1a). For each split, we also evaluated Model 3 on the non-systematic data, which included presences and pseudo-absences. Because Models 1 and 2 contained year and decade terms, they were unable to predict beyond the temporal constraints of the systematic survey data to which they were fitted (1962-1997); Model 3 excluded these terms and consequently could evaluate the non-systematic data through 2018. We accounted for the Pilot predictor by assigning a single pilot ID to the entirety of the non-systematic data, selected from a pilot who had a relatively high positive observation rate and an average number of records throughout the systematic survey period.

Table 3.1. a) Summary table of general additive mixed models [GAMMs] used in testing and training. b) Output summary of GAMMs, including p-values and chi-square values. Summaries represent an example from one round of testing and training; outputs from all five rounds were similar.

		Mean AUC (training)	Mean AUC (testing)	Mean AUC (non-aerial data)
<b>a)</b>	<b>Predictor variables</b>			
Model 1	SST + CHL + ENSO + PDO + NPGO + pilot (re) + year + lon:lat + month, by decade	0.93	0.92	---
Model 2	SST + CHL + ENSO + PDO + NPGO + pilot (re) + year	0.90	0.88	---
Model 3	SST + CHL + ENSO + PDO + NPGO + pilot (re)	0.88	0.87	0.74

<b>b)</b>	<b>Predictor variables</b>	<b>Model 1</b>		<b>Model 2</b>		<b>Model 3</b>	
		<i>Chi Sq.</i>	<i>p</i>	<i>Chi Sq.</i>	<i>p</i>	<i>Chi Sq.</i>	<i>p</i>
	s(MeanHadleySST)	124.94	<0.05	169.55	<0.05	310.97	<0.05
	s(Lon,Lat)	509.0	<0.05				
	s(Month):Decade1960	188.43	<0.05				
	s(Month):Decade1970	284.47	<0.05				
	s(Month):Decade1980	16.66	<0.05				
	s(Month):Decade1990	3.26E-08	1				
	s(Year)	1175.32	<0.05	3455.56	<0.05		
	s(PDO)	83.87	<0.05	66.12	<0.05	116.93	<0.05
	s(ENSO)	118.37	<0.05	171.62	<0.05	194.70	<0.05
	s(NPGO)	22.64	<0.05	76.06	<0.05	441.51	<0.05
	s(CHL)	108.03	<0.05	667.23	<0.05	1021.41	<0.05
	s(Pilot)	282.65	<0.05	525.62	<0.05	731.88	<0.05

## Results:

### *Basking shark records*

The complete dataset included 624 shark sightings. Sightings were reported throughout the year, from 27.75° N to 49.82° N and -125.66° W to -115.42° W, and spanned more than five decades (1962-2018). There were 8 pilots in our systematic survey data who reported basking sharks. They varied in the number of flights conducted by month and year, which we accounted for using the Pilot identity term in our GAMMs. Collectively, flights from these pilots covered every year from 1962-1995, and again in 1997 (Fig. S3.3). Flights also generally took place from

February to November, with a greater number during the fall months (August to November). Out of the 7,076 flights conducted, 262 of these reported basking sharks, with the last presence observed in 1988. There was a peak in the total number of sharks sighted per year and the mean number per flight between 1960-1970, as well as a second smaller peak around 1980. Shark sightings were comparatively low in the 1970s and the mid to late 1980s (Fig. 3.2). Over this time, sightings were reported primarily in the late fall through early spring (September through June; Fig. S3.4). The maximum total number of sharks sighted in a year was nearly 4,000 individuals, in 1966. From 1962 – 1988, there were only 5 years of zero shark sightings. However, after 1988, none were reported for the duration of the systematic surveys (through 1997). In comparison, in the non-systematic survey data, there was only 1 report prior to 1988 (in 1973). After 1988, there were 10 years in which no sharks were reported (Fig. 3.3).

Most non-systematic sightings were reported during the 2010s (n=114), and the relatively high number of sharks observed during this time provides some opportunity for comparison with the systematic survey data. The maximum number of sharks reported each year was 57 individuals in 2011, from a combination of public sightings schemes, NOAA reports, and tagging efforts (Fig. 3.3; Fig. S3.1). Non-systematic sightings were distributed throughout the CCE, clustered near Monterey Bay, Santa Barbara, and Baja California (Fig. S3.5). Interestingly, there were 8 sightings (7%) off Oregon and Washington as well. Sightings took place primarily in summer months (April through October), with a few sightings in the late fall and early winter (Fig. S3.4). For example, in the 2010s, 94% of sightings were from April-September with a peak of 25% in May. Though the non-systematic data was not used to build the GAMMs, the mean SST in shark sighting locations remained relatively consistent across decades in this data from 1990 to 2018 (mean SST: 14-16°C; Fig. S3.2), although temperatures overall ranged from 11.4 –

19.8°C. We were only able to calculate chl-*a* values at shark sighting locations starting in the 2000s, but mean chl-*a* was relatively consistent between the 2000s and 2010s (mean: 1.55 and 1.27, respectively) with a wide range across individual sightings, from 0.27 – 4.84.

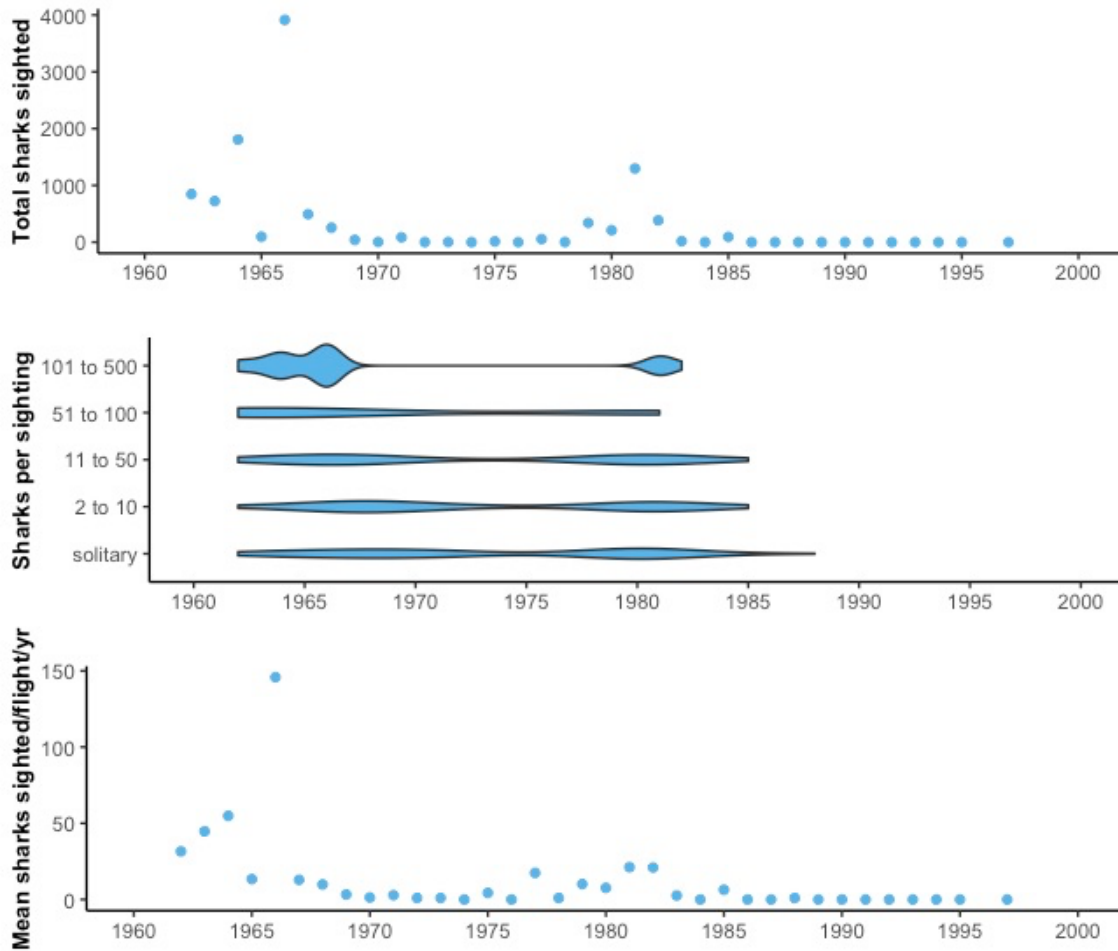


Figure 2.2. Top: The total number of sharks sighted based on flights conducted each year in the systematic survey. Peaks in sightings are evident from 1962-1985, with few sightings after that time. Middle: Number of sharks per sighting in the systematic survey data, with each sightings report binned according to the size of the aggregation (solitary individuals, 2-10, 11-50, 51-100, and 101-500). Larger aggregations are present primarily prior to 1983, with smaller groups of sharks reported after that year. Bottom: Mean number of sharks sighted per flight per year during the systematic survey period, showing similar trends to the total number of sharks sighted each year but accounting for variation in the number of flights conducted.

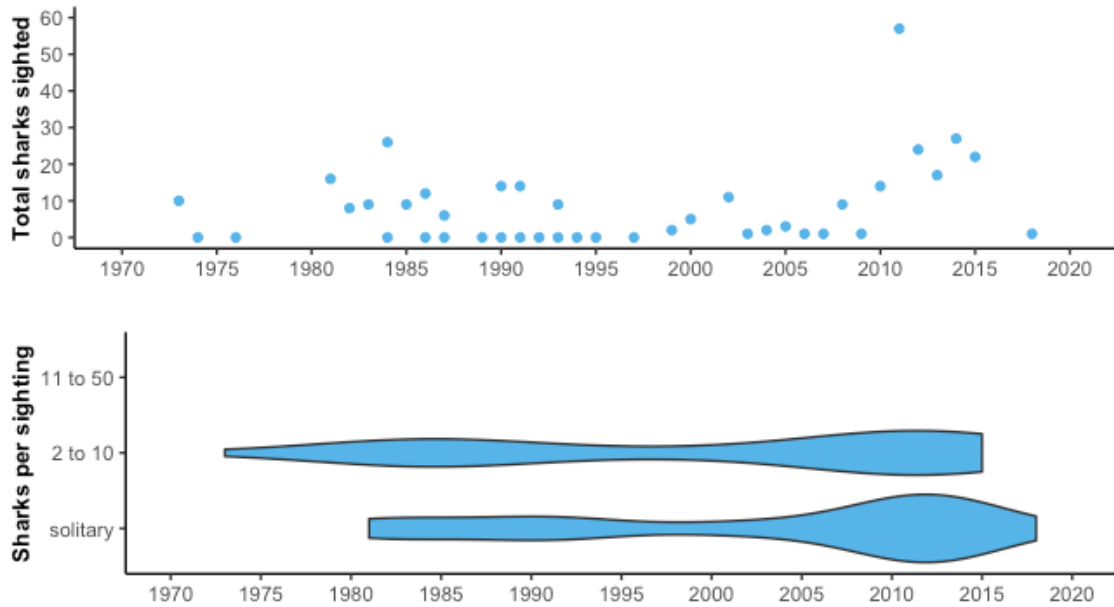


Figure 3.3. Top: The total number of sharks sighted opportunistically each year in the non-systematic survey data. Slight peaks in sightings occur between 1980 and 1990, and between 2011 and 2018. Bottom: Number of sharks per sighting, binned as in Figure 3.2. All records report less than 10 individuals per sighting.

Of the 624 records, 621 reported school size (402 for the systematic data and 219 for the non-systematic data). Our systematic surveys reported a variety of aggregation sizes, from two individuals to up to 500. However, sightings in the high-number bins (11-50+ sharks) decreased dramatically in the late 1980s (Fig. 3.2). Between the 1960s and 1980s, there was a ~58% decline in the mean size of basking shark aggregations in the systematic survey data (57.2 to 24.0 individuals). In the non-systematic data we examined, there were no shark aggregations larger than 10 (Fig. 3.3). This includes the leatherback sea turtle and porpoise surveys for which, of 20 sightings from 1990-2013, only two reported more than one shark with aggregations of 2 and 3 individuals. For comparison, only 33% of reports in the systematic survey data were of solitary sightings.

### *Species distribution models*



Our models performed well on both testing and training datasets derived from the systematic data, with AUC values ranging from 0.87 to 0.93 (Table 3.1a). The model containing the largest number of potentially relevant predictors (Model 1) emerged as the top model in terms of average skill (AUC training = 0.93, AUC testing = 0.92). This suggests that our predictions were improved slightly by accounting for unknown spatiotemporal processes. When Model 3 was applied to the non-systematic data, it performed moderately well with a predictive power of 0.74.

All three models contained Pilot as a random-effects variable and the same environmental variables. The effects of nearly all variables (other than month-decade) were statistically significant ( $p < 0.05$ ; Table 3.1b). However, the relative influence of these predictors differed based on the model AIC's sensitivity to the loss of each term (Fig. S3.6). The Pilot variable was consistently highly influential, suggesting that observer bias influenced some of the patterns in our data. Each model also generally predicted a higher probability of basking shark presence with increased chl-*a* concentration and cooler temperatures ( $< 14\text{-}15\text{ }^{\circ}\text{C}$ ; Fig. 3.4), although chl-*a* appeared to be a stronger predictor in Models 2 and 3, while SST was a weak predictor in all models. When we also examined the mean SST values by decade at shark sighting locations, there was significant variation among sightings ( $11.4\text{-}19.8\text{ }^{\circ}\text{C}$ ). However, we found relatively little difference between the mean SST values across decades (range mean SST:  $14.3\text{ - }15.8\text{ }^{\circ}\text{C}$ ; Fig. S3.2) and no trend over time. Notably, this is similar to temperatures observed in the non-systematic data (2010-2018; mean SST:  $15.8\text{ }^{\circ}\text{C}$ , Fig. S3.2).

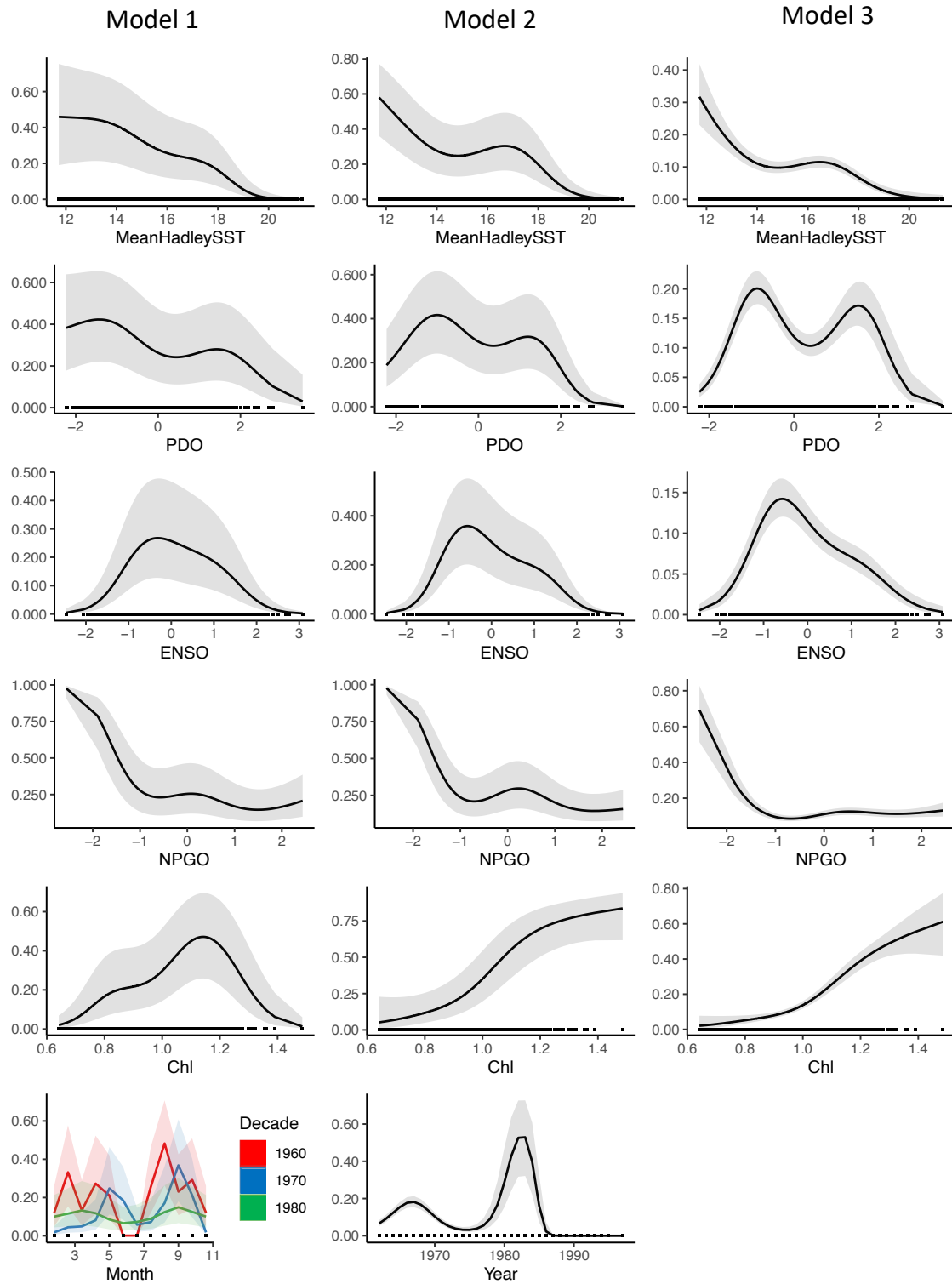


Figure 3.4. Partial response plots for the temporal and environmental predictors from each of the three models, fitted to the systematic survey data (parameters for each model are fully outlined in Table 3.1). The y-axis represents predicted probabilities of basking shark sightings. There was little variation in each of the five iterations of model testing and training. This is a representative example of one iteration.

Any shift in SST should also capture some of the influence of broader scale cues, such as PDO, ENSO, and NPGO. For PDO, our models showed a bimodal pattern with an increased probability of occurrence at slightly negative and positive values. The probability of basking shark occurrence was also higher at neutral to negative ENSO values, and at negative NPGO values (Fig. 3.4). Yet as with SST, these climatic oscillations were had moderate to weak influence on our models compared to other predictors (Table 3.1b; Fig. S3.6).

Model 1 allowed for the examination of year, decade, month, and latitude/longitude. All were highly influential predictors in this model compared to the environmental variables (Fig. 3.4; Table 3.1b; Fig. S3.6). There was a significant seasonal and monthly change in sightings probability, and patterns of seasonal variation changed between decades. Specifically, in the 1960s, Model 1 predicted a higher probability of basking shark sightings in mid-spring and late summer. This shifted to early summer and late fall in the 1970s. In the 1980s there was lower variability between months, though a slight increase in probability in early spring and late fall (Fig. 3.4). Across all decades, there was a lower probability in the summer months.

In addition to environmental variables, Model 2 also examined the effect of year on basking shark sightings and found that it affected sightings probability significantly (Table 3.1b) and was a moderately influential predictor (Fig. S3.6). There was a high probability of occurrence from the late 1970s to the early 1980s. From 1975 to 1983 the probability increased from an average of 0.31 to 0.68. After that time, probability decreased to 0 for the rest of the systematic survey period (Fig. 3.4). These results, combined with those from Model 1, indicate that there were additional spatial and temporal processes affecting sightings probability that were unaccounted for by the other environmental predictors. Chl-*a* was also a strong predictor in Model 2 (Table 3.1b; Fig. S3.6).

In terms of spatial distribution, across the entire aggregated systematic survey period (1962-1997), all models also predicted a higher probability of shark sightings directly along the coastline from Monterey Bay down to Santa Barbara, as well as off northern Baja California (Fig. 3.1; S3.7; S3.8). When we mapped the model predictions by decade, we found that this distribution varied over time. Specifically, all our models predicted a higher probability of basking shark sightings in the Monterey Bay area during the 1960s (Fig. 3.5a; S3.8a). During the 1970s, basking sharks were predicted to be sighted further south, near Santa Barbara and Baja California (Fig. 3.5b; S3.8b), although there were still a few observations north of Santa Barbara. In the 1980s, the last decade in which a basking shark was sighted in the systematic surveys, the probability of basking sharks sighting increased primarily near the Santa Barbara area (Fig. 3.5c; S3.8c).

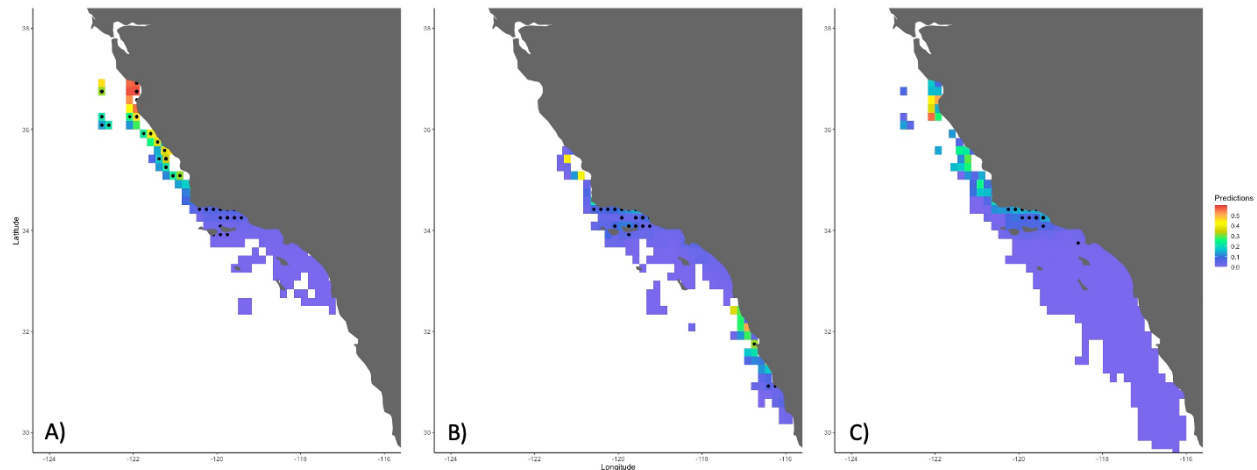


Figure 3.5. Maps of the western United States and Mexico extending from San Francisco (top of map) to Baja California (bottom of map), showing predicted shark sightings probability from our best-fit model (Model 1) for each decade for which there were presences throughout the systematic survey period (A-C: 1960s, 1970s, 1980s). Black dots represent basking shark presences recorded during the systematic surveys. White represents areas for which there is no model prediction. Maps from Models 2 and 3 can be found in the supplementary materials.

## **Discussion:**

Published information on the behavior, movement patterns, distribution, and abundance of basking sharks in the CCE is sparse. Using a cumulative analysis of historic and contemporary sightings datasets, we conducted a detailed examination of basking sharks in the CCE. We assessed sightings numbers and school size to determine patterns in basking shark behavior and distribution over time. We also generated the first habitat models for this species in the ENP, exploring the influence of environmental and other spatiotemporal variables on sightings probability.

This research builds on the few studies that have been conducted previously, many of which have also reported a decline in observations. Squire (1967) analyzed log records of aerial surveys conducted in from 1948-1950, noting the number of basking sharks and seasonality of sightings in the Monterey area. During this time, basking sharks arrived here in large numbers, with one instance of a reported shoal reaching over 1,000 individuals. In a later paper, Squire (1990) assessed a different set of aerial survey records in the CCE from 1962-1985 and found a notable decrease in abundance of sharks observed after 1970. Similarly, based on opportunistic sightings and aerial survey data, Baduini (1995) determined that abundance of basking sharks after 1967 was much less than that observed by fish spotters from 1948-1951. In a 2009 report, McFarlane *et al.* provided a comprehensive report of sightings trends and historic threats to basking sharks in Canada and California, compiling data available up until 2007. These authors also found evidence of a dramatic decline in sightings over time and advocated for further research on the ENP basking shark population.

In addition to examining trends in basking shark sightings, previous studies have also explored potential drivers of seasonal habitat use, though with mixed results. Squire (1967)

recorded peaks of apparent abundance in March and October and noted that shark sightings occurred most frequently when temperatures were below 14°C. In a subsequent paper, Squire (1990) reported the same seasonal peaks in sightings during spring and fall in Monterey and Morro Bays. Interestingly, this study also observed that occurrence of sharks was low during periods of high phytoplankton abundance, concluding that residence in the CCE is likely not for feeding. Conversely, Baduini (1995), in a study of foraging ecology, later found that in Monterey Bay, peak shark abundance corresponded to greater zooplankton abundance. Yet here groups of sharks were reported in July and August rather than spring and fall. Similarly, in 2010-2011, Dewar *et al.* (2018) observed that satellite-tagged sharks left coastal regions in the summer and fall. They also suggested that changes in movement patterns and habitat use were linked to prey availability and oceanography (Dewar *et al.*, 2018). Generally, however, it is important to note that no habitat modeling has been conducted prior to our study. Without information on the environmental drivers of basking shark distribution, it has been difficult to determine the degree to which yearly variation in sightings is due to environmental changes or population-level trends.

### *Spatial and temporal trends*

Expanding the temporal scale of previous studies, our analyses confirmed that over the course of less than 50 years (1962-2018), there was substantial change in the number, timing, and spatial distribution of CCE sightings. Consistent with the published reports indicating declines in local basking shark abundance throughout the ENP (Baduini, 1995; McFarlane *et al.*, 2009; Squire, 1990), we found that the number of sharks sighted yearly declined by the 1980s and remained low in subsequent years. Moreover, our systematic survey data showed a corresponding decrease in the size of basking shark aggregations from 1962-1997. This trend

apparently continued in the non-systematic data through 2018, which included 23 observations from aerial surveys for leatherback sea turtles and porpoises that were comparable methodologically to our systematic survey data (Forney *et al.*, 2014). Between 1990 and 2013, these surveys recorded sightings of mostly solitary individuals.

We also found that seasonality shifted over time. Our model predictions indicate that sightings were generally bimodal in the 1960s to the 1980s with the timing of these peaks varying each decade, although primarily in the spring and fall in the CCE. Given that the peak of sightings in Canada historically occurred during the summer, it was hypothesized that the ENP population spent May through September further north. However, this pattern has evidently changed. Based on our non-systematic data and other studies, basking shark sightings occurred primarily during summer months starting in the 1990s (Baduini, 1995; Dewar *et al.*, 2018) with the majority of records from the late spring through early fall. This is also the season they are sighted in the temperate waters of the North Atlantic (*e.g.*, Sims *et al.*, 2003; Doherty *et al.*, 2017; Johnston *et al.*, 2019; Dolton *et al.*, 2020). It is possible that these recent changes were biased to some degree by season; for example, more people may undertake recreational activities on the water during the summer. Regardless, such a marked seasonal difference in CCE sightings is noteworthy.

The spatial patterns of sightings in our data suggest that coastal areas from Monterey Bay to Baja California remain important habitat for basking sharks in the CCE (Baduini, 1995; Dewar *et al.*, 2018; Squire, 1990). Our models predicted a slight change in spatial distribution from 1960 to the 1990s. Sighting probability was higher near the Monterey Bay area in the 1960s and shifted further south to Baja California and Santa Barbara by the 1980s. However, non-systematic sightings in the 2000s, as well as tagging data, were distributed throughout the study

region, from just north of Monterey to Baja California, with some hotspots near Monterey Bay, Santa Barbara, and off the coast of San Diego (Fig. S3.5). Interestingly, there did not appear to be a corresponding change in temperature associated with this shift; though SST was highly variable, the mean temperature across decades remained relatively consistent in both datasets (Fig. S3.2). Based on hotspot formation along the shelf and slope in the Atlantic (*e.g.*, Southall *et al.*, 2005; Gore *et al.*, 2016; Lieber *et al.*, 2019), basking shark habitat appears similar across ocean basins and is likely linked to forcing mechanisms that concentrate prey, which is known to be critical to successful foraging in filter feeders (Sims and Quayle, 1998; Croll *et al.*, 2005; Doniol-Valcroze *et al.*, 2007; Block *et al.*, 2011; Miller *et al.*, 2015).

### *Environmental drivers*

The influence of the environment on the distribution and seasonality is challenging to determine, particularly as survey coverage was uneven through time. The consistent significance of our Pilot variable in each model suggests that observer bias played a strong role in influencing the patterns observed in this study. Yet while it is important to consider the impact of observer bias in the interpretation of our results, our analysis nonetheless offers some important environmental insights.

Consistent with our study, some research has concluded that chl-*a*, an indicator of plankton density, positively correlates with basking shark presence in the CCE as well as the North Atlantic (*e.g.*, Austin *et al.*, 2019; Baduini, 1995; Doherty *et al.*, 2017; Witt *et al.*, 2012). However, as noted above, other studies have found no such effect (Austin *et al.*, 2019; Dewar *et al.*, 2018; Squire, 1990). For example, in addition to Squire (1990), Dewar *et al.* (2018) noted that one tagged individual moved offshore in the CCE even while the plankton concentration



remained high, while another did so as chl-*a* and SST began to decline. There is thus clear variability in the influence of chl-*a* on basking shark distributions within the CCE.

In addition to chl-*a*, SST was also a significant variable in all our models and is likely another key driver of large-scale movement patterns. Basking sharks have been found across a broad range of SST, from 8 to 24°C, with differences in their apparent thermal preference. For example, in Newfoundland, Lien and Fawcett (1986) reported most basking sharks when waters were 8-12°C while other studies have reported sightings at higher temperatures (*e.g.*, 15 – 17.5°C; Skomal, Wood and Caloyianis, 2004; Cotton *et al.*, 2005), reaching up to 24°C (Dewar *et al.*, 2018; Owen, 1984). The influence of SST on abundance is also variable, with some studies finding a high correlation (Cotton *et al.*, 2005) and others finding little to none (Finucci *et al.*, 2021 and Hoogenboom *et al.*, 2015, respectively). For sightings in the CCE, SST has been relatively low and consistent over time (Fig. S3.2), despite shifts in seasonality. Squire (1967) also reported low basking shark abundances above 14°C in 1951, and our model results suggested a higher probability of sightings when the SST was less than 14-15°C. This temperature is slightly lower than the mean SST across decades in the systematic survey data (Fig. S3.2), likely because randomly generated pseudo-absences were frequently correlated with higher temperatures. However, it aligns with the non-systematic survey data, in which SST fell within a very narrow range (mean SST: ~15.5°C). Thus, our collective results suggest a higher probability of shark presences at temperatures <16°C. Yet while SST was a significant predictor of sightings probability in this study, its influence was relatively low (Fig. S3.6). The broad range of SST and differences across regions suggest that SST itself may have a lower overall importance than other environmental parameters that covary with SST, such as seasonal plankton abundance.

Finally, we found that the three climate indices (ENSO, NPGO, PDO) were significant environmental predictors in all models though with relatively low predictive value. Other studies (*i.e.*, Witt *et al.*, 2012; Hoogenboom *et al.*, 2015) have shown that climatic oscillations in the North Atlantic (*i.e.*, North Atlantic Oscillation) predict interannual sightings variability of basking sharks, probably due to the effect of NAO on the abundance of dominant prey species. In the CCE, ENSO has been attributed to changes in basking shark sightings, as the peaks in sightings from 1975-1981 were reduced after the 1982-1983 El Niño perturbations (Squire, 1990). This is consistent with model results showing a higher sightings probability at negative ENSO values, when temperatures are cooler and productivity in the CCE is higher. In contrast, our model results for NPGO predicted a higher probability of basking shark presence at negative NPGO, which is associated with lower productivity (Harvey *et al.*, 2020). The relationship between PDO and basking shark sightings was challenging to interpret given its bimodal nature. More work is needed to understand the effect of these large-scale phenomena on basking shark abundance in the CCE.

The significance of these collective environmental predictors in our models and studies in other locations portend further change in basking shark space use due to climate change. Given the broad range of SST, the specific temperature may be less important below and above certain thresholds, particularly as basking sharks appear to avoid higher SST by diving to deeper cooler waters (Braun *et al.*, 2018; Dewar *et al.*, 2018; Skomal *et al.*, 2009). Additionally, as with previous studies in the region, we found high interannual variability in the apparent abundance of basking sharks that is independent of environmental conditions in the CCE. Consequently, the distribution of this population is likely influenced heavily by spatiotemporal processes not accounted for in this study, although it is possible that the sightings patterns observed were also

influenced by declines in basking shark abundance (discussed in more detail below). Future efforts defining the essential habitat for basking sharks in the CCE will need to consider additional, more dynamic variables (Table 3.2) that better measure factors influencing prey abundance in three dimensions (Baduini, 1995; Dewar *et al.*, 2018). Additional work is also needed to characterize the entire range of this population.

Table 3.2. Recommendations for future research on and conservation of basking sharks in the CCE and broader Eastern North Pacific (ENP).

Research priorities	Purpose	Suggested action items
Systematic monitoring effort	Improve understanding of distribution, abundance, and movement patterns of sharks throughout the ENP	<ul style="list-style-type: none"> <li>• Create a sightings network through ongoing commercial, research and recreational surveys (<i>i.e.</i>, whale-watching vessels)</li> <li>• Include demographic and behavioral information in survey forms (<i>i.e.</i>, size, sex, number of sharks observed; common behaviors exhibited [swimming in formation, feeding, breaching etc.])</li> <li>• Establish a user-friendly database online to collate international sightings throughout the ENP</li> <li>• Opportunistically tag basking sharks when observed in the CCE, via satellite or visual identification tags</li> </ul>
Genetic sampling	Contribute to understanding of population structure <sup>1</sup> and composition of basking shark aggregations	<ul style="list-style-type: none"> <li>• Collect slime when feasible<sup>2</sup></li> <li>• Collect e-DNA when feasible</li> <li>• Use existing samples for forensic identification of fins on the market (see “Conservation measures”)</li> </ul>
Improved data collection for dynamic predictors ( <i>i.e.</i> prey field, areas of physical forcing, frontal activity)	Allow for better modeling of essential habitat for basking sharks in the CCE	<ul style="list-style-type: none"> <li>• Undertake systematic surveys of plankton abundance at large spatial and temporal scales, and collect monthly samples of plankton composition and abundance at consistent regions throughout hotspot regions in the CCE (<i>i.e.</i>, Monterey Bay, Morro Bay, Santa Barbara, Baja California)</li> <li>• Contextualize current sightings and tagging data using more recently developed remote-sensing and field-based tools to quantify frontal activity and bathymetry</li> </ul>

<sup>1</sup> Lieber *et al.*, 2020

<sup>2</sup> Lieber *et al.*, 2013

<sup>3</sup> McFarlane *et al.*, 2009

Conservation measures		
Prevent harassment and boat strikes	Mitigate ongoing local threats, and increase knowledge of such threats for boaters	<ul style="list-style-type: none"> <li>• Distribute best-practice guidelines for vessels in the proximity of basking sharks to marinas, boat launches, aquariums, etc.</li> <li>• Work with and incentivize recreational vessels to limit potential boat strikes</li> </ul>
Identify locations of ongoing incidental or targeted fisheries mortality	Quantify sources of mortality for the ENP stock to assess potential for population recovery and identify regions where efforts could reduce mortality.	<ul style="list-style-type: none"> <li>• Encourage reporting of bycatch and discards<sup>3</sup></li> <li>• Engage RFMOs and countries throughout the Pacific</li> <li>• Monitor markets selling shark fin throughout the Pacific</li> </ul>
Research presence and source of basking shark fins in markets and match to CITES records	Ensure that CITES regulations are being followed by member nations.	<ul style="list-style-type: none"> <li>• Increase international public awareness and advocacy for basking shark protection</li> <li>• Encourage policy-makers and non-governmental organizations to coordinate internationally and reinvigorate basking shark monitoring and protection</li> <li>• Consider if additional protections are warranted (<i>e.g.</i>, uplisted to CITES Appendix I), and if so, engage with appropriate delegates</li> </ul>

### *Decline in basking shark sightings*

Our findings offer key insights into local basking shark abundance trends in the CCE, with implications for the broader ENP population. Most striking is the decrease in CCE sightings after the 1970s and 1980s, the drivers of which remain unclear. The decline cannot be attributed to sample design. While our most recent data was not systematically collected, the decline was first evident in systematic survey data. Squire (1967) reported sightings on 51.5% of flights during aerial surveys conducted from 1948-1950, whereas our systematic survey reported sightings on only 3.7% of flights from 1962-1988, after which no sharks were reported. Aerial surveys from 1962-1985 also showed a decline in abundance levels (Squire, 1990).

Alternatively, this decline could be caused by a shift in the vertical distribution of sharks, since these data are contingent on sharks being at the surface. Yet though basking sharks do exhibit

high variability in diving behavior, the predominant pattern in coastal regions globally is that sharks are at or near the surface feeding on convergence zones (Sims *et al.*, 2005; Gore *et al.*, 2008; Skomal *et al.*, 2009; Miller *et al.*, 2015; Dewar *et al.*, 2018), and there is no evidence to suggest that vertical movement patterns changed (McFarlane *et al.*, 2009).

Another potential hypothesis to explain reductions in basking shark sightings is that the sharks have migrated from the CCE due to changes in habitat suitability (*i.e.*, high chl-*a* concentrations and cooler SST). Sims and Reid (2002) found that the decrease in basking shark catches in Irish fisheries from 1948-1975 correlated with a long-term zooplankton decline in the region and suggested that basking sharks had moved to more productive areas. However, McFarlane *et al.* (2009) argue that habitat availability for this species in the CCE is unlikely to have changed, given that basking sharks are often associated with humpback whale (*Megaptera novaegliae*) distribution (Wallace & Gisborne, 2006) and humpback whale populations have actually increased over the same time period (COSEWIC, 2003). Furthermore, our analysis indicates that year was the strongest predictor of basking shark sightings, especially compared to the environmental predictors, with a significant decline in both sightings and group size.

The most parsimonious explanation for the reduction in basking shark sightings in the CCE and ENP is a decline in the population. McFarlane *et al.* (2009) came to the same conclusion based on sightings patterns in Pacific Canada from the same population. A likely contributor to the declining population is fisheries mortality. As mentioned above, basking sharks were historically targeted in fisheries, taken incidentally as bycatch and killed in Canada's eradication program (Dewar *et al.*, 2018; McFarlane *et al.*, 2009). While the full range of the population is not known, basin-scale migrations are possible and additional sources of fisheries mortality likely came on the high-seas as well as off Japan, where there was a targeted fishery

that stopped due to reduced occurrence of sharks (Bonfil, 1994; CITES, 2002; McKinnell & Seki, 1998). There is also precedence for reduced population size due to fisheries mortality for basking sharks in other regions; for example, in the United Kingdom (*e.g.*, Sims *et al.*, 2005).

Consistent with a decline in population is a reduction in aggregation size in known hotspots (Chute, 1930; Roedel and Ripley, 1950; McFarlane *et al.*, 2009). While there was variation in group size across all datasets, the 1948-1950 aerial survey reported occasional schools of hundreds to thousands of sharks (Squire, 1967) and the 1962-1985 aerial survey reported some schools of hundreds up to the early 1980s with an average of 21.8 sharks per sighting (Squire, 1990). In contrast, in the non-systematic data there were no groups of more than 10 individuals, including the aerial surveys for turtles and porpoises that ran until 2013 and reported primarily solitary individuals (Forney *et al.*, 2014). While group size is inconsistently reported, studies suggest that other regions have had significantly larger aggregations over these same time periods. For example, Crowe *et al.* (2018) reported 10 large aggregations of 30 to 1,398 individuals from 1980-2013 in the Northeast Atlantic. Gore *et al.* (2018) observed 25 instances of >11 individuals off the coast of Scotland in 2016, and Wilson (2004) reported schools of up to 50 sharks in the Gulf of Maine in 2002.

The reduction in aggregation sizes in the CCE could have broader implications for basking shark recovery throughout the ENP. Recent studies in the Northeast Atlantic have found that basking sharks surfacing together are on average more genetically related than expected by chance (Lieber *et al.*, 2019). It is therefore possible that aggregations, particularly among related individuals, may facilitate social information transfer, optimal foraging, and assortative mating (Lieber *et al.*, 2019). For example, Baduini (1995) found that zooplankton density in the ENP was greater inside feeding areas when groups of 4+ sharks were observed, in comparison to areas

with single animals. Consequently, aggregations may enhance foraging. Additionally, if aggregations are important for mating, a reduced group size could limit the population's rebound potential. This is known as the Allee effect, when a population at low densities suffers a decrease in growth rate and consequently faces an increase likelihood of extinction (Courchamp *et al.*, 1999). Comprehensive genetic, behavioral, and demographic research will be required to explore hypotheses for the suspected decline of the basking shark population in the ENP (Table 3.2).

### *Conservation implications*

Many of the historical threats to this population (*i.e.*, targeted fisheries and incidental takes) have ceased in the CCE, with the last reported take in 2004 (McFarlane *et al.*, 2009). However, threats outside of the CCE need to be considered. There are a variety of potential sources of mortality and sublethal effects throughout their range, of which the CCE and Canada represents only a portion. Based on electronic tagging data (Dewar *et al.*, 2018; Gore *et al.*, 2008; Johnston *et al.*, 2019), basking sharks that occur in the ENP enter international waters and may traverse the Pacific ocean basin. Hazards in coastal areas include development, habitat alteration, harassment, and ship strikes given their habit of moving slowly at the surface (McFarlane *et al.*, 2009; Speedie *et al.*, 2009). Another concern is incidental take in fisheries, especially in nets. In the Pacific, basking sharks have been documented both in coastal waters and on the high-seas in large-mesh drift gillnets, artisanal gear and in trawls (Berrow & Heardman, 1994; COSEWIC, 2007; Larese & Coan, 2008; McFarlane *et al.*, 2009; Sandoval-Castillo *et al.*, 2008). In addition, other directed fisheries appear to have recently emerged. Given that the number of marketed fins is more than accounted for in the CITES trade documents (Magnussen *et al.*, 2007), fisheries mortality persists, although where those sharks originated is

not always known given the lack of adequate species-specific data (Dewar *et al.*, 2018; Magnussen *et al.*, 2007).

### *Future directions*

The data available for our analyses had limitations that should be considered and improved for ongoing studies (Table 3.2). For example, we did not have enough data to account for changes in seasonality by year rather than decade, limiting our inferences regarding the drivers of shark sighting seasonality. We were also restricted in our selection of predictors for our species distribution models. For instance, we excluded high-resolution SST and data from plankton sampling surveys, which were missing information on the full temporal and spatial scale, respectively. Yet such information may provide important insights regarding prey abundance, as surface chl-*a* is not necessarily a good proxy for lipid-rich boreal copepods (Brodeur *et al.*, 2003). More dynamic variables that predict convergence zones would likely also better reflect the spatial distribution of basking shark prey (see Finucci *et al.*, 2021). Similarly, our model did not account for offshore or non-environmental cues that may drive basking sharks to coastal waters. For example, work on blue whales in the CCE has suggested that both long-term memory and resource tracking drive the migratory movements of some marine megafauna (Abrahms *et al.*, 2019). Larger-scale studies of basking sharks would better be able to identify whether similar drivers of distribution exist within this species. In addition, the aerial survey is no longer in operation, ending the best available time-series. Finally, the population structure and extent of the basking shark range is unknown but critical for any future stock assessment. Characterizing population structure will require additional research, monitoring, tagging and genetic analyses, as well as international coordination across studies (Table 3.2).



In parallel, it will be important to coordinate conservation measures across international boundaries to protect basking sharks from ongoing threats (Table 3.2). In the EEZ of the U.S., Mexico and Canada, basking sharks are protected and few, if any, incidental takes have been documented since the early 2000s (COSEWIC, 2007; Dewar *et al.*, 2018; McFarlane *et al.*, 2009). Here, actions to protect basking sharks could be expanded to reduce ships strikes by educating boaters on best practices. Outside of these three EEZs, markets selling shark fins should be closely monitored and efforts to develop forensic genetic methods should be undertaken. In addition to enforcing current local and international regulations, such as CITES, one option to consider would be to upgrade the CITES listing to I, which would restrict international trade. Given the highly migratory nature of basking sharks, efforts at population recovery, particularly in the ENP, will require international cooperation for both research and management.

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**Author Contributions:**

AGM wrote the manuscript and performed the modeling and statistical analyses. BM assisted in writing the manuscript and performing the modeling and statistical analyses. HD, JJB, NAF and DC assisted in writing and reviewing the manuscript. HD, BM and JJB collated the sightings data. All authors contributed critically to the drafts and gave final approval for publication.

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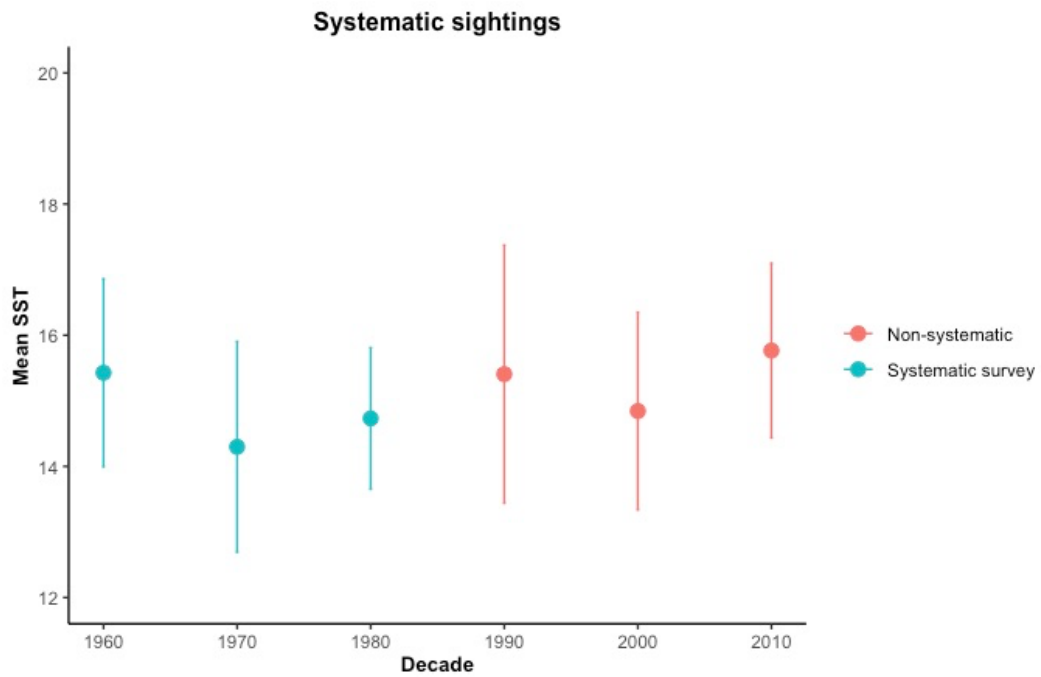
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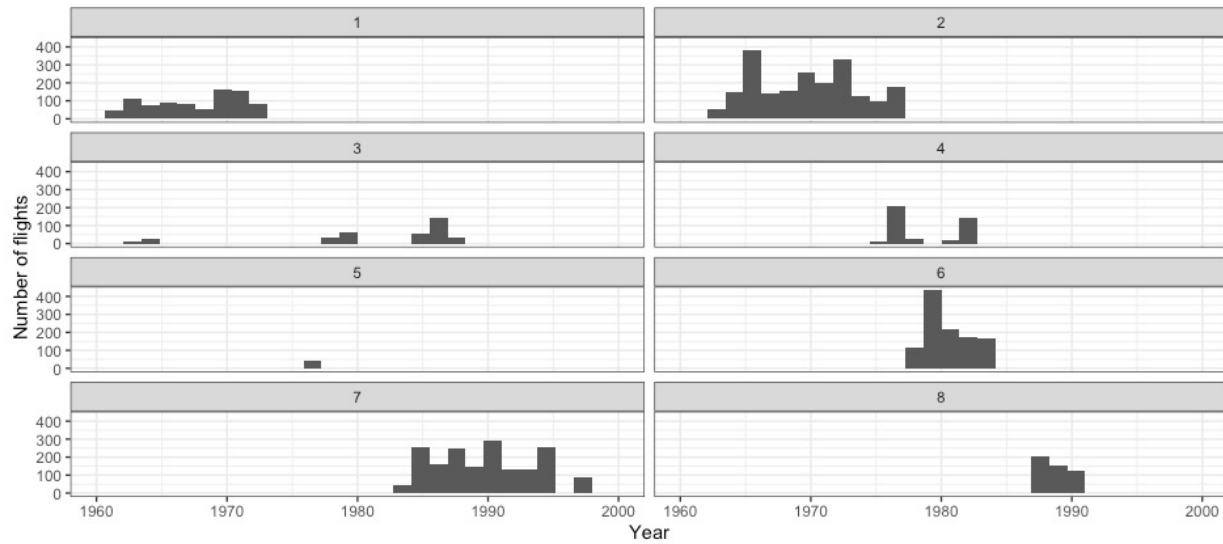
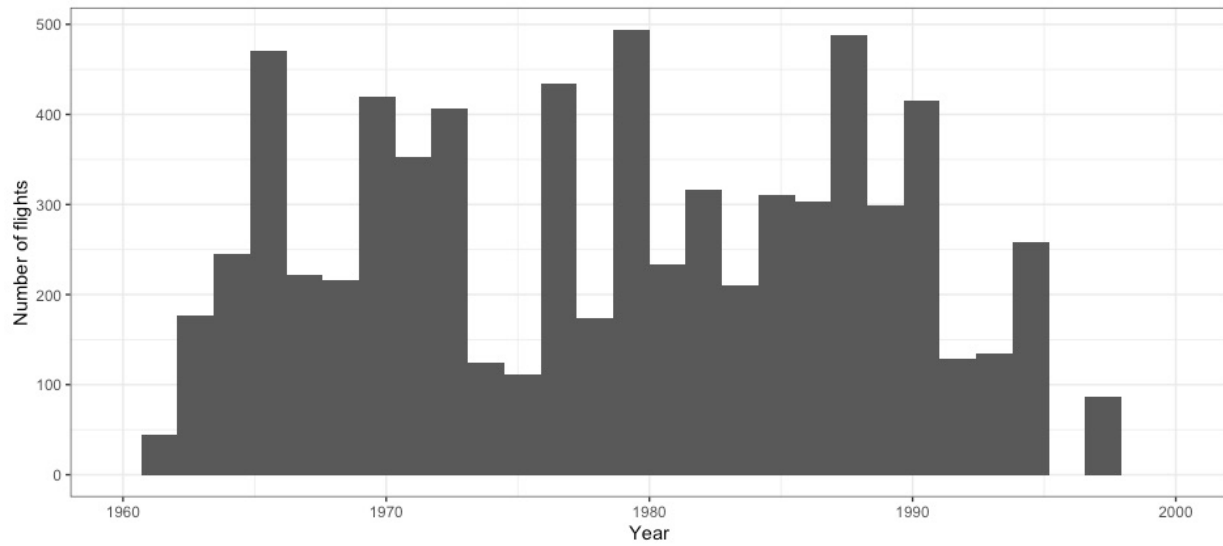
**Supplementary materials:**

*S3.1. Summary of sources from which data was compiled.*

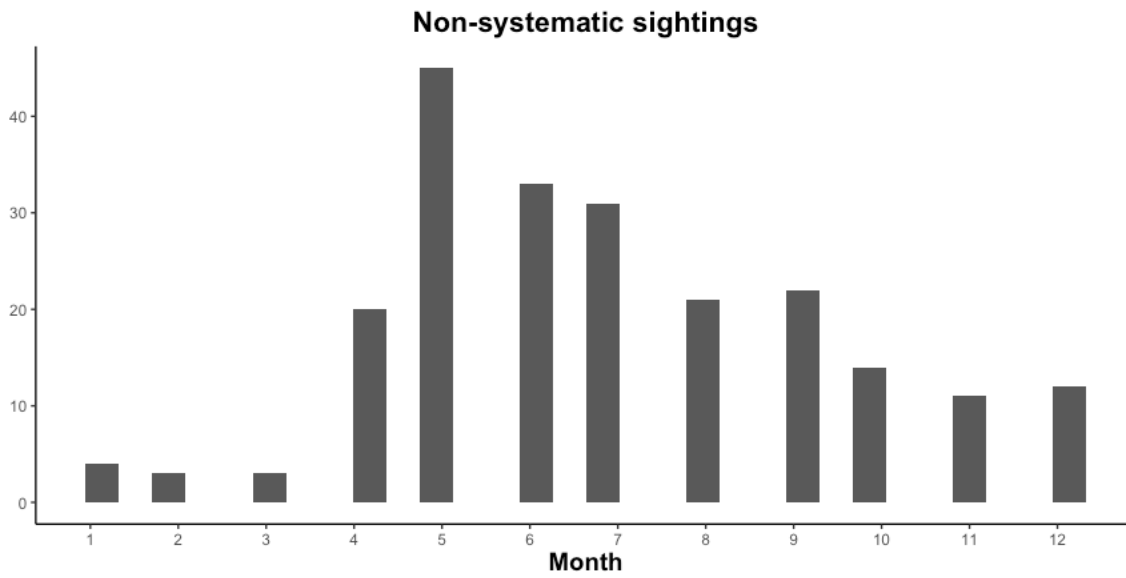
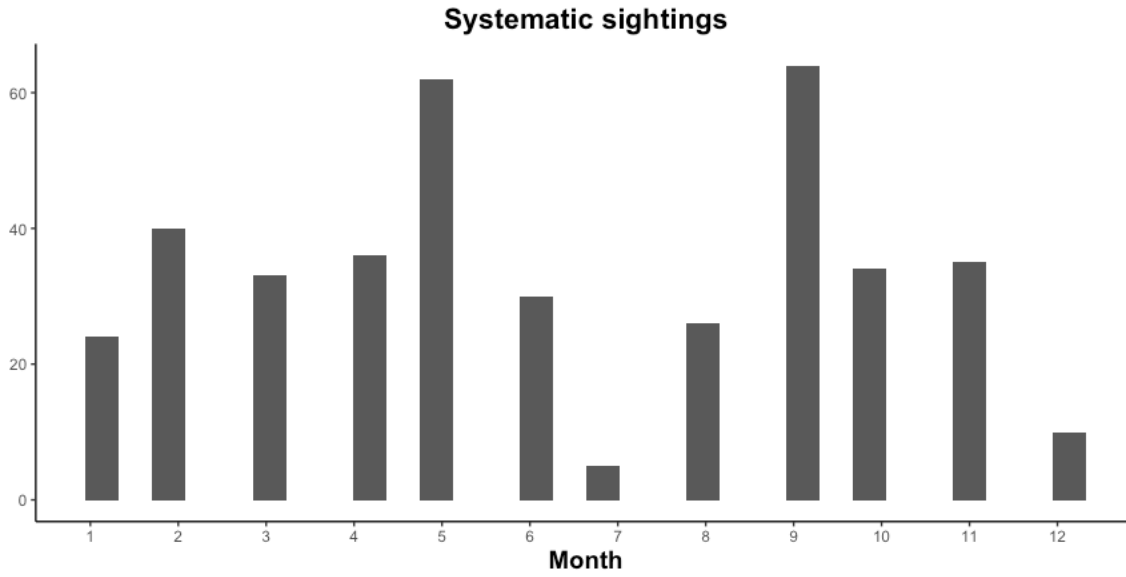
Source	Number of sightings reported	Years reported
Systematic aerial surveys	402	1962-1988
Satellite tagging	5	2010-2014
Conventional tagging	15	1990-2000
Gillnet observer records	51	1981-2006
Leatherback surveys	8	1990-2013
Porpoise surveys	15	1990-2013
Pacific Shark Research Center Spot-A-Basking Shark	58	1973-2018
NOAA reports	70	2010-2015



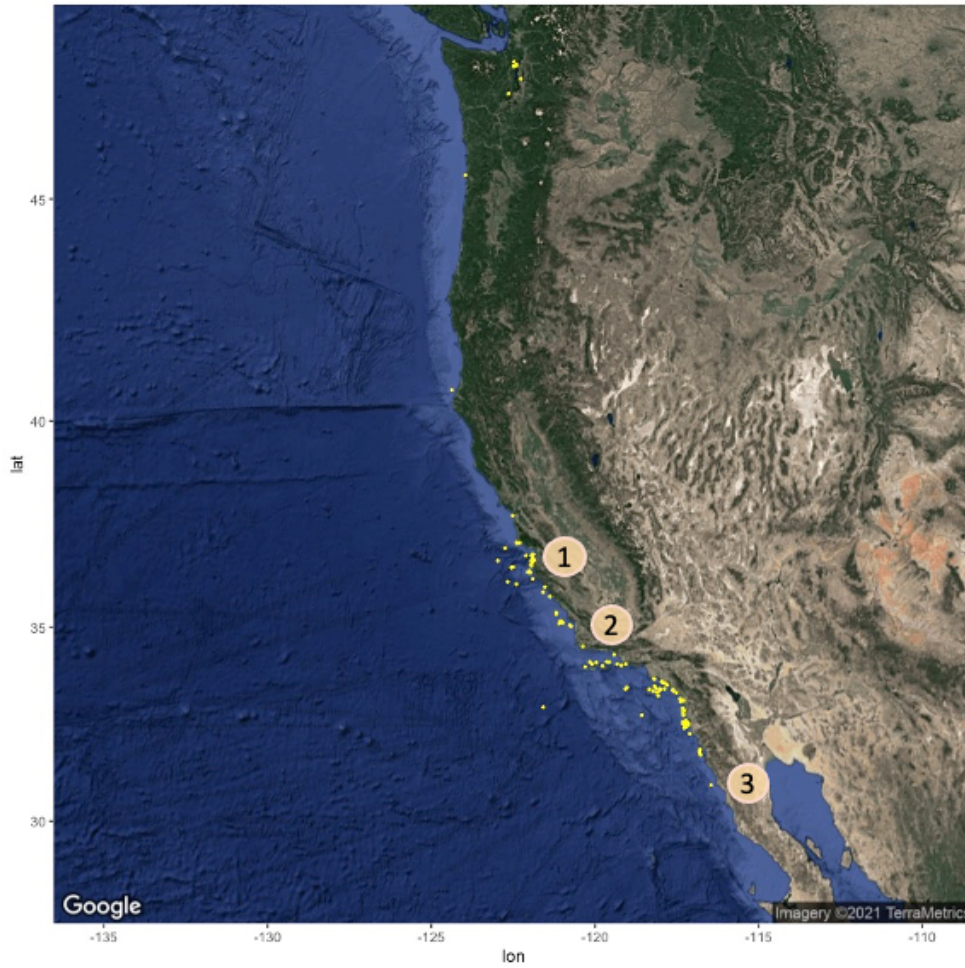
*S3.2. Mean SST calculated by decade for our systematic survey (1960s-1980s) and non-systematic sightings (1990s-2010s).*



S3.3. Histograms of the number of flights by year conducted by the pilots in our systematic survey data who observed basking sharks at least once. Collectively, flights took place nearly every year from 1962 – 1997 (top), although there was individual variation in number of flights and year flown between the eight pilots (bottom).



S3.4. Histograms of the number of shark sightings by month, according to our systematic survey data from the 1960s through the 1980s (top) and the non-systematic survey data from the 1970s through the 2010s (bottom).

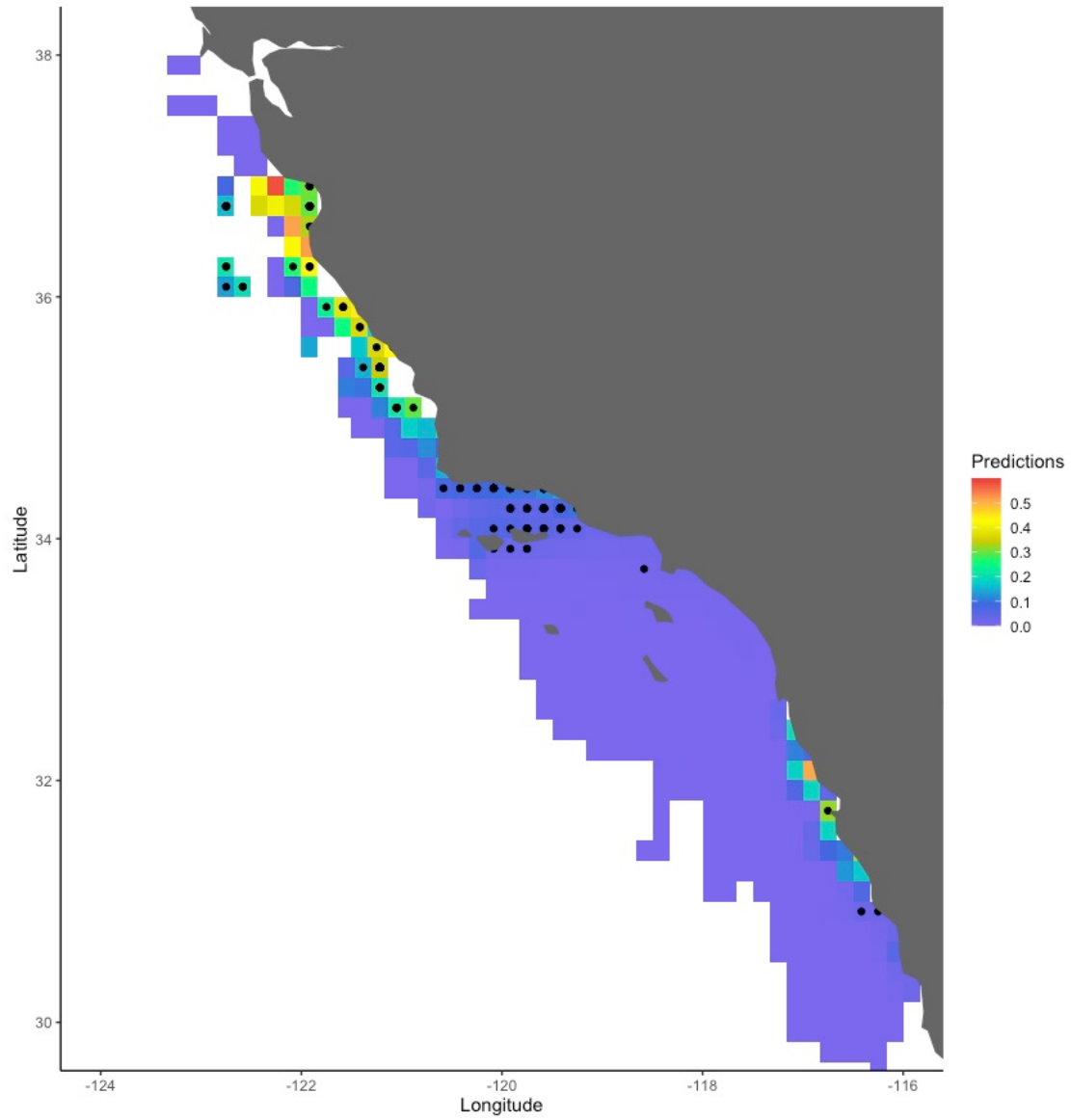


S3.5. Map of the western United States and Mexico showing non-systematic survey sightings since 2000. In the CCE, sharks are distributed from Monterey Bay (1) down to Santa Barbara (2) and Baja California (3).

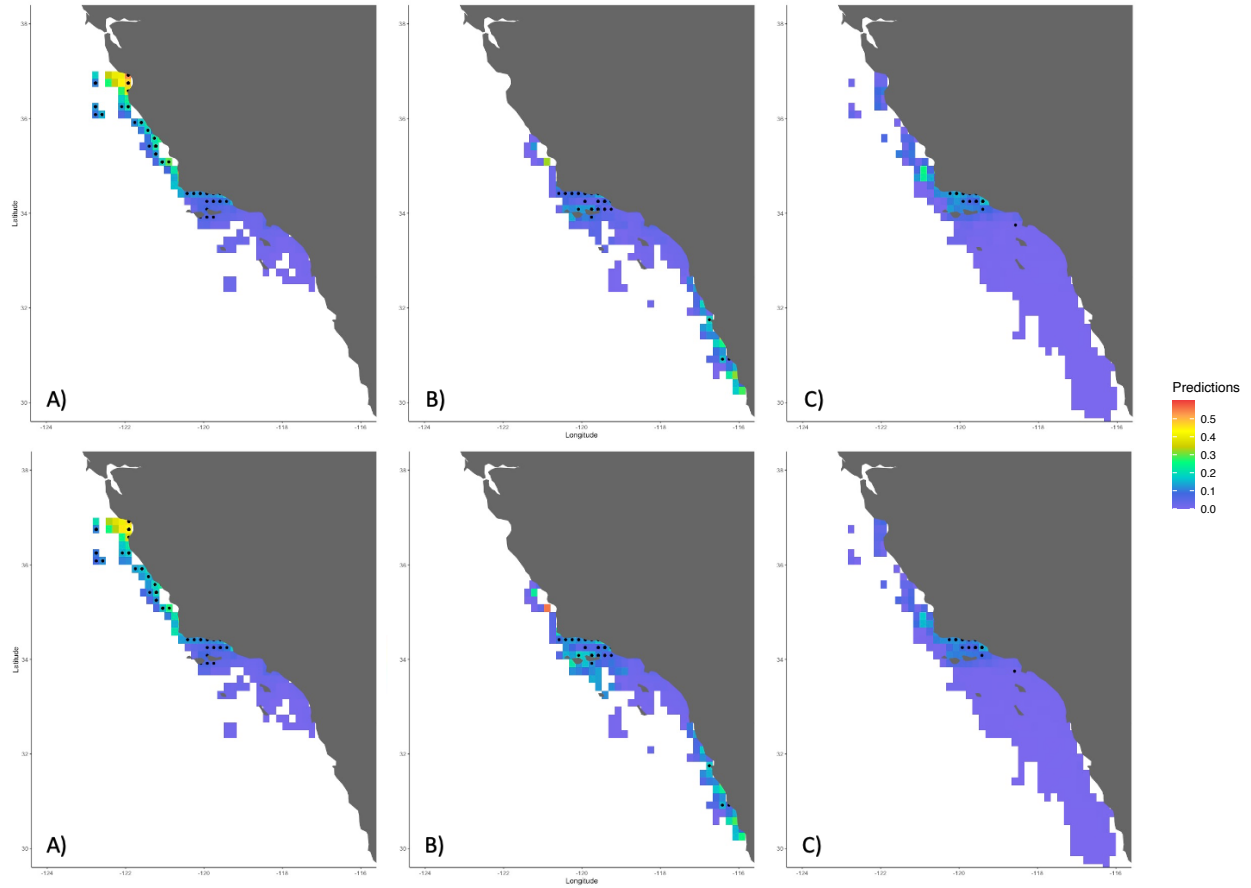
S3.6. Table indicating the AIC's sensitivity to the loss of every smoothed term in all three models. Labels indicate the dropped term in each model version. There was little variation in relative AIC across five iterations of model testing and training.

<b>Model 1</b>	<b>Degrees of freedom</b>	<b>AIC</b>
Full model (no dropped terms)	57.12	8048.18
NPGO	54.05	7958.79
CHL	50.32	8010.01
PDO	51.54	8011.45
SST	51.92	8044.67
ENSO	52.46	8111.29
Pilot	48.57	8225.45
Lat:Lon	51.33	8242.39
Year	54.32	8260.43
Month	33.10	8600.08
<b>Model 2</b>		
Full model (no dropped terms)	29.73	9013.87
NPGO	25.33	9165.65
SST	26.00	9221.67
Year	26.94	9234.71
ENSO	26.59	9255.10
PDO	25.96	9268.18
Pilot	22.87	9492.00
CHL	26.88	9543.13
<b>Model 3</b>		
Full model (no dropped terms)	26.95	9343.20
PDO	22.90	9421.29
ENSO	22.89	9566.89
NPGO	21.93	9574.51
SST	23.35	9598.72
CHL	21.93	9837.13
Pilot	20.45	10288.50





*S3.7. Map of predicted shark sightings probability over the aggregated systematic survey period (1962-1997) from our best-fit model (Model 1). Black dots represent basking shark presences recorded during the systematic surveys. White represents areas for which there is no model prediction.*



S3.8. Maps of predicted shark sightings probability from Models 2 (top row) and 3 (bottom row) for which there were presences throughout the systematic survey period (A-C: 1960s, 1970s, 1980s). Black dots represent basking shark presences recorded during the systematic surveys. White represents areas for which there is no model prediction.