Spring 2024

# Seasonal Dynamics of the Introduced Sponge Hymeniacidon Perlevis in the Elkhorn Slough, California, USA

Jackson Hoeke
*San Jose State University*

# SEASONAL DYNAMICS OF THE INTRODUCED SPONGE HYMENIACIDON PERLEVIS IN THE ELKHORN SLOUGH, CALIFORNIA, USA

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Jackson T. Hoeke

May 2024

The Designated Thesis Committee Approves the Thesis Titled

SEASONAL DYNAMICS OF THE INTRODUCED SPONGE HYMENIACIDON PERLEVIS IN THE ELKHORN SLOUGH, CALIFORNIA, USA

by

Jackson T. Hoeke

APPROVED FOR THE DEPARTMENT OF MOSS LANDING MARINE LABORATORIES

SAN JOSÉ STATE UNIVERSITY

May 2024

| | |
|---|---|
| Amanda S. Kahn, Ph.D. | Moss Landing Marine Laboratories |
| Sarah R. Smith, Ph.D. | Moss Landing Marine Laboratories |
| Kerstin Wasson, Ph.D. | Elkhorn Slough National Estuarine Research Reserve |

ABSTRACT

SEASONAL DYNAMICS OF THE INTRODUCED SPONGE HYMENIACIDON PERLEVIS IN THE ELKHORN SLOUGH, CALIFORNIA, USA

by Jackson T. Hoeke

*Hymeniacidon perlevis* is a cosmopolitan sponge with a seasonal life cycle We investigated seasonal and interannual dynamics of *H. perlevis* in Elkhorn Slough estuary, where it is an introduced species, and explored correlations between sponge cover and environmental conditions. We used sponge cover to estimate the potential effects *H. perlevis* on its environment and how those could vary across its seasonal life cycle. We found that successful recruitment is currently restricted to the upper estuary and while it varies annually, the frequency and density of sponge recruits have generally increased from 2007 to 2023. A seasonal life cycle was confirmed for Elkhorn Slough populations, consistent with other temperate populations of the species, with sponge cover peaking in October and declining to a minimum from March to May. Time-lagged Spearman-ranked cross-correlations suggest that sponge cover correlated with warmer temperatures and lower dissolved oxygen at all sites, with a time lag of 2-4 months. Precipitation from severe winter storms in 2023 also coincided with declines in sponge cover. Over the course of a year, we estimated that *H. perlevis* biomass and water filtration are greatest in fall-corresponding with peak cover, and weakest to nonexistent in the spring. Understanding the seasonal and interannual dynamics of this population can inform future approaches to manage or mitigate its ecological impacts.

## ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Amanda Kahn for her support throughout my time at Moss Landing Marine Laboratories. You provided me with fantastic opportunities and guidance that continually kindled my passion for learning. There were many hurdles to overcome during this project, and I could not have completed it without your passion, kindness, and – above all – patience. I could not ask for a better advisor.

To my other committee members, Dr. Sarah Smith and Dr. Kerstin Wasson, thank you for your hours of revisions on my thesis drafts. Sarah, I'm delighted I was able to take your molecular techniques class, and the work ethic and organization you taught me. Kerstin, thank you for sharing your decades of data with me as well as working with me in Elkhorn Slough to survey, collect, and share your expert knowledge of Elkhorn Slough.

I would also like to thank the Elkhorn Slough Foundation (ESF) and Elkhorn Slough National Estuarine Research Reserve (ESNERR) for their support during this project allowing me the opportunity to conduct research in Elkhorn Slough, as well as the California Department of Fish and Wildlife (CDFW) for granting permitting for specimen take.

I would like to thank my funding sources for the research project and my education, including the CSU Council on Ocean Affairs Science and Technology (COAST), the MLML James Nybakken scholarship, the Earl H. and Ethyl M. Meyers Oceanographic and Marine Biology Trust, and the MLML Wave Award.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

## Introduction

Non-native species all have potential to negatively affect their surrounding ecosystems. For example, introduction of the ctenophore *Mnemiopsis leidyi* Agassiz, 1865 in the Mediterranean and Black Seas disrupted fish communities (Fuentes et al., 2010). Non-native suspension feeders also may greatly affect ecosystems by altering nutrient cycling and food webs. For instance, introduction of zebra and quagga mussels *Dreissena polymorpha (Pallas, 1771)* and *Dreissena bugensi*s *(Andrusov, 1897)* to the North American Great Lakes greatly reduced spring blooms and primary productivity (Rowe et al., 2015; Vanderploeg et al., 2010) Understanding spatial and temporal dynamics of non-native species enables more effective management strategies for controlling their spread and potential damage (Giménez et al., 2020; Kamiyama et al., 2021; Klein & Verlaque, 2009; Reznik et al., 2022).

Sponges are filter-feeding aquatic and marine organisms that graze on dissolved organic material (DOM), viruses, bacteria, diatoms, and ciliates (Gili & Coma, 1998; Maldonado et al., 2010). Within benthic communities, sponges can convert material and energy from the water column to structure and habitat on the substrate, a process known as benthic-pelagic coupling (Gili & Coma, 1998). Sponges efficiently take up bacteria and DOM while releasing nitrogenous waste, and dense sponge communities can generate complex habitat in the process (Kahn et al., 2015; Leys et al., 2018). Given their many ecosystem functions, non-native sponges, especially species that succeed and build large or dense populations, have great potential to restructure their new ecosystems.

*Hymeniacidon perlevis (Montagu, 1814)* is a cosmopolitan demosponge (Class Demospongiae) that lives in temperate intertidal and subtidal habitats (de Laubenfels, 1932).

It is thought to be native to Europe, where its presence can be traced to the early 1800s (Montagu, 1814). However, its current range includes Europe, the South American Atlantic coast, the Pacific and Atlantic coasts of North America, South Africa, and East Asia with additional morphological data also suggesting its presence in New Zealand (Samaai et al., 2022; Turner, 2020). It can be found in nearshore subtidal habitats but forms especially dense aggregations in estuaries, where individuals can colonize and nucleate around hard rocks even in soft-sediment habitats.

One estuary that harbors many introduced species (Wasson et al., 2001), including *H. perlevis*, is Elkhorn Slough in central California, a small (1200 ha) estuary situated in the center of Monterey Bay (36.8 N, 121.7 W). The slough has a long history of human use such as converting wetlands into farmland, diverting the Salinas River from the slough, and creating Moss Landing Harbor, connecting the Monterey Bay directly to Elkhorn Slough (Caffrey, Martha, et al., 2002). *H. perlevis* was reported from southern California as early as 1932 (de Laubenfels) but was first detected in Elkhorn Slough in 1998. Surveys of the estuary by MacGinitie (1935), Nybakken et al. (1975), and Carlton (1979) did not mention *H. perlevis*, though they focused in the lower estuary where the sponge is not currently found, so the exact introduction date is unknown. The sponges were likely introduced to the slough via oyster culturing (Wasson et al., 2001). Exotic oyster culturing in the Elkhorn Slough took place between approximately 1900 and 1980, with most efforts in the 1930s and 1940s (Wasson et al., 2001). Oyster culturing is responsible for several other invertebrate introductions to Elkhorn Slough, including the hydroid *Ectopleura crocea (Agassiz, 1862)*, the clam *Gemma gemma (Totten, 1834)*, and the mud snail *Batillaria attramentaria (G. B.*

*Sowerby II, 1855)* (Wasson et al., 2001). The exact route of transport for *H. perlevis* is uncertain because oysters were imported from many locations, but genetic similarities between East Asian and Elkhorn Slough populations (Fuller & Hughey, 2013) suggest that the species was introduced to Japan and subsequently brought to the slough through fouling on Japanese oysters (J. T. Carlton, personal communication, March 8, 2021; Harbo et al., 2021). Since its arrival in Elkhorn Slough, *H. perlevis* has spread and forms wide, often dense aggregations throughout intertidal benthic habitats (Wasson et al., 2001).

*Hymeniacidon perlevis* has a seasonal life cycle that affects its cover throughout the year, although variations in phenology occur across its native range and in introduced regions, with variations presumably driven by environmental conditions and seasons. Populations generally grow during summer, reach peak biomass in early fall, then decline through late fall followed by a period of minimal biomass and/or dormancy in winter through late spring (H. Cao, et al., 2012; X. Cao, et al., 2007; Gaino et al., 2010; Juniper & Steele, 1969; Stone, 1970). The phenology of *H. perlevis* is unknown in Elkhorn Slough but given variations in other regions, it is likely to also have strong seasonal dynamics. As *H. perlevis* expands its now-cosmopolitan range, it is increasingly important to understand the conditions that allow it to thrive or conversely, expire. Since this species can have large-scale changes in its biomass across its life cycle, and given sponges' substantial effects on the water column through filter feeding, seasonal dynamics may radically alter the magnitude of water filtration capacity and accumulated biomass of *H. perlevis* throughout the year.

While an annual life cycle is well established for *H. perlevis*, less clear is how, or which, environmental conditions such as temperature, dissolved oxygen, and precipitation may affect populations. Like most of central California, Elkhorn Slough has a distinct wet season peaking from December to January. During the wet season, freshwater runoff reduces salinity in the slough and increases particulates and nutrients that cause eutrophication and hypoxia, particularly in the upper estuary (Caffrey, Martha, et al., 2002; Caffrey, Neil, & Bess, 2002; Hughes et al., 2011). Whereas many sponges are sensitive to water quality changes such as suspended sediments, *H. perlevis* can survive being partially buried in mud in winter (X. Cao et al., 2007) and thrives in Elkhorn Slough despite muddy substrate and high suspended particulate loads (Caffrey, Martha, et al., 2002). A congener, *H. heliophilia*, can withstand air exposure and episodically muddy waters of the intertidal zone by closing its ostia and oscula in response to stimuli and irritants (Parker, 1910). Additionally, *H. perlevis* may fare particularly well in the relatively warm estuarine intertidal zone. Newly settled juveniles grow faster when incubated in warmer water, up to 23 °C (Xue & Zhang, 2009). To fully understand population dynamics in Elkhorn Slough, it is important to assess how *H. perlevis* populations fluctuate under different environmental conditions. We hypothesized that sponge cover would be positively correlated with increased water temperature, reaching maximum cover during the summer and minimum cover during the winter.

A lack of detailed knowledge about the introduction and spread of *H. perlevis* in Elkhorn Slough and how changes to its environment affect its seasonal life cycle currently limits our ability to assess the magnitude of its impact on the Elkhorn Slough ecosystem. This information is critical to inform effective resource management strategies or any efforts to restore this ecosystem. In order to address this knowledge gap we documented the introduction and spread of *H. perlevis* in Elkhorn Slough, CA over 25 years from 1998 to

2023 through analysis of recruitment across a long-term dataset. In order to assess how temperature, pH, salinity, dissolved oxygen, turbidity, and precipitation correlated with changes in sponge biomass we monitored the monthly cover of *H. perlevis* in Elkhorn Slough across two years from August 2021 to July 2023. Lastly, we estimated the volumetric flow rate of water filtered through *H. perlevis* in the field and the organic weight of *H. perlevis* tissue in the lab to evaluate the impacts of this species as a function of cover over different seasons in Elkhorn Slough. We found that *H. perlevis* populations are gradually recruiting more frequently and in more areas of the upper slough and that this species exhibits strong seasonality, with peak cover in the fall suggesting that it is well established in the ecosystem and can have the strongest impacts to the Elkhorn Slough ecosystem in fall.

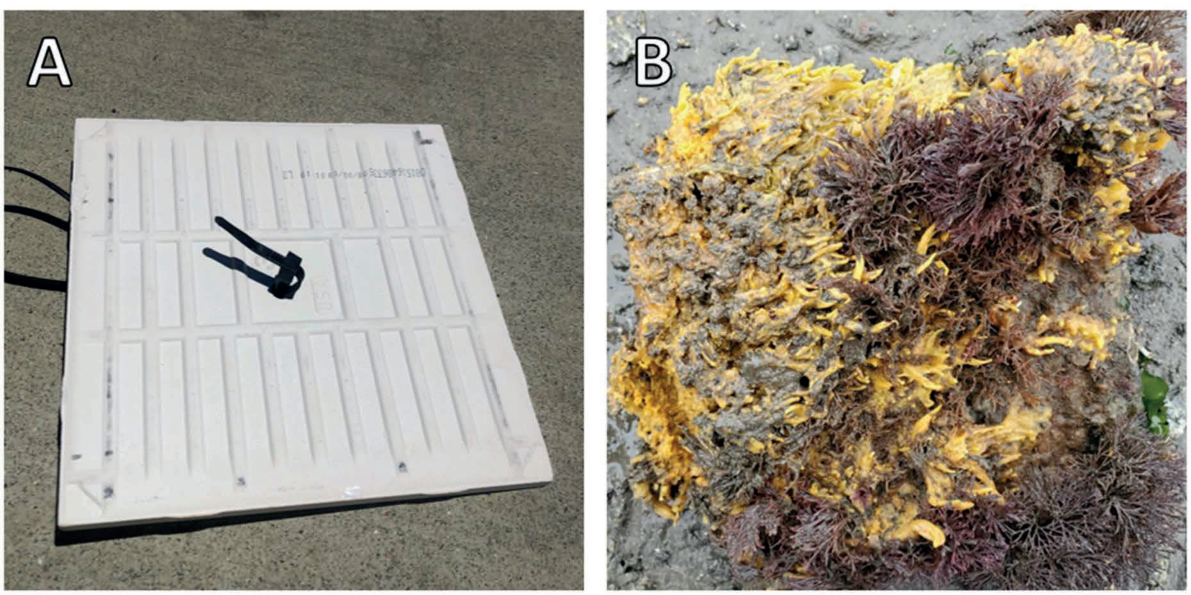
## Methods

### Annual Recruitment Patterns of H. perlevis in Elkhorn Slough

Annual recruitment of *H. perlevis* on fouling plates was monitored across six primary sites from 2007 to 2023, with 4 additional sites surveyed early, from 2010-2014. For complete details of how plates were deployed and processed, see Wasson et al. (2020). In short, five replicate ceramic plates (10 × 10 cm) (Figure 1) were deployed across ten sites and replaced in May or June annually (Figure 1, Table 1), with the primary purpose of detecting native oyster recruitment. Percent cover of *H. perlevis* was recorded on each tile deployed except for 2018-2020, when only presence/absence was recorded. Sponge cover data were averaged across all 5 plates for a site.

**Figure 1**

*Replicate ceramic plates*




(A) A 10 x 10 cm ceramic plate seen bare before deployment. (B) Another plate seen recovered one year after deployment and colonized with H. perlevis.

**Table 1**

*List of Sites with Fouling Plates Deployed.*

| Site (abbreviation) | Coordinates (lat, lon) | Tidal Height (m relative to MLLW) | Years Deployed |
|---|---|---|---|
| Azevedo Pond (APN) | 36.8471, -121.7545 | -0.5 | 2008; 2010-2023 |
| Kirby Park (KP) | 36.8398, -121.7437 | 0 | 2008-2023 |
| North Marsh (NM) | 36.83465, -121.73843 | -0.5 | 2008-2022 |
| Whistlestop Lagoon (WSL) | 36.8240, -121.7400 | -0.5 | 2008-2023 |
| South Marsh – WSL (RSM) | 36.8240, -121.7404 | 0 | 2008; 2010-2023 |
| South Marsh Bridge (RBR) | 36.8199, -121.7371 | 0 | 2009-2023 |
| Vierra Mouth (VM) | 36.8112, -121.7792 | 0 | 2010-2013 |
| Bennett Slough (BSE) | 36.8215, -121.7834 | -0.5 | 2013 |
| Moss Landing Road (MLR) | 36.8000, -121.7844 | 0 | 2012-2013 |
| Jetty Road (JR) | 36.8171, -121.7871 | 0 | 2010-2013 |

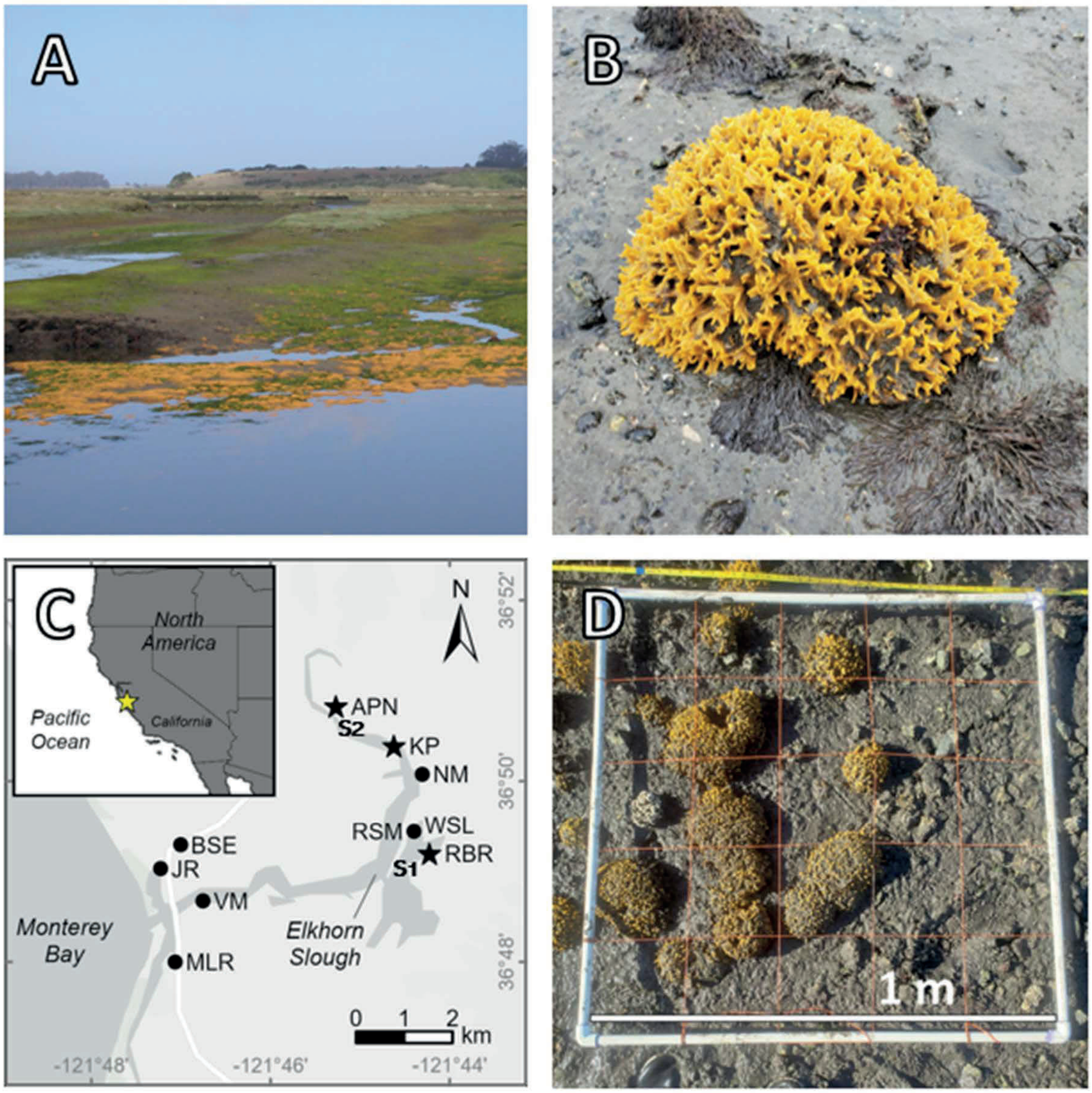
Includes latitude and longitude, Tidal height at which plates were deployed, and years deployed. A thicker line separates upper and lower estuary sites; Sites are ordered from upper to lower estuary. Abbreviations: MLLW – Mean Lower Low Water.

## Seasonally-Resolved Surface Cover Measurements Using Quadrat Surveys

Visual surveys (quadrat) of sponge tissue were recorded at three sites in the upper slough monthly for 2 years from August 2021 to July 2023. Three sites were selected based on their proximity to an NERR water monitoring instrumentation array, accessibility by foot, substrate variability, and previously recorded observations of *H. perlevis* (Figure 2C). Surveys were undertaken by dividing each site into 1 m wide transects, then photographing a 1 x 1 m quadrat at different intervals along each transect. Transect number, length, and quadrat intervals were determined by the shape and accessibility of each site. Photographs of each quadrat were taken with a smartphone and sponge area within each image was measured by tracing polygons using Fiji ImageJ software (Schneider et al., 2012) (Figure 3). Monthly mean sponge cover was calculated by randomly selecting 38 quadrats from each site to

**Figure 2**

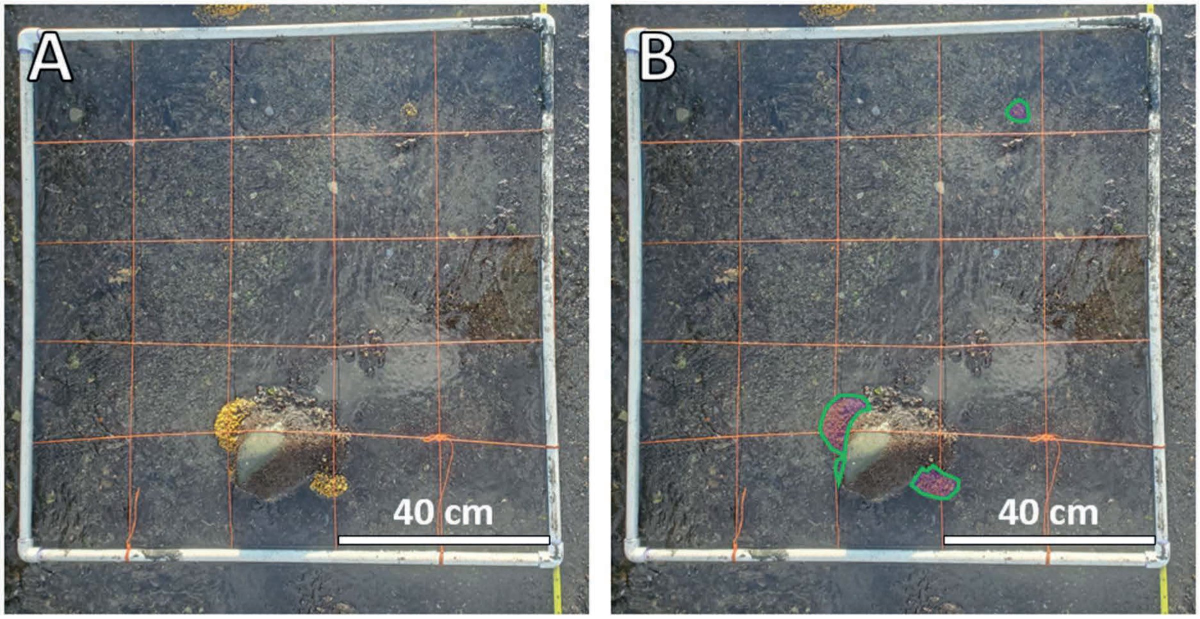
*Scale of H. perlevis introduction in Elkhorn Slough*




(A) A large aggregation of H. perlevis in South Marsh. (B) A large specimen of H. perlevis exposed at low tide. (C) Map of Elkhorn Slough, CA with monthly monitoring sites marked with stars and long-term monitoring sites marked with dots. APN: Azevedo Pond; KP: Kirby Park; NM: North Marsh; WSL: Whistlestop Lagoon; RSM: South Marsh – WSL; RBR: South Marsh Bridge; VM: Vierra Mouth; BSE: Bennett Slough; MLN: Moss Landing Road; JR: Jetty Road S1 and S2 mark the NERR sondes which collected water quality parameter data. (D) Sponge cover was measured using 1x1 meter photoquadrats. Map: Created in ArcGIS Pro; service layer credit Esri, FAO, NOAA, USGS, California State Parks, Esri, HERE, Garmin, SafeGraph, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, USDA.

**Figure 3**

*Traced polygons in ImageJ*




(A) Quadrat before polygon tracing in ImageJ. (B) Quadrat after tracing sponges within. The total area of the sponges highlighted here is 0.01 m2.

standardize results (38 was the minimum number of quadrats measured across all sites and months). To assess whether sponge cover varied over time, a bootstrapped one-way ANOVA was calculated using month as a factor. We also opportunistically collected 10 sponges each month during a period of peak cover from three sites to determine whether sponges were reproductive.

The Azevedo Pond site (APN) is in a channel between a culvert accessing a small, shallow tidal pond and the upper portion of the Elkhorn Slough main channel. The substrate is composed primarily of cobbles but is broken by patches of larger stones or mud. Tidal changes force water swiftly through this channel due to the depth difference between the main channel and the pond. Sponges here were found in dense clusters populating the cobbles and large stones. At APN, eight adjacent transects took up the width of the channel and were deployed out 20 m, at which point the water became too deep as it entered the main channel. 5 quadrats were photographed along each transect at randomly generated points.

The Kirby Park site (KP) lies on a tidal mud flat adjacent to the upper portion of the Elkhorn Slough main channel. The mudflat is broken up with the occasional boulder and the southern edge is bounded by a long horizontal cement piling. Sponges at this site were spaciously spread among the boulders and some small stones across the sediment and had a tendency to be partially buried. At KP, ten transects were randomly placed between 0 and 30 meters north of the cement piling, and deployed out 5 m, at which point the mud became too deep. 5 quadrats were photographed along each transect at randomly generated points.

The South Marsh Bridge site (RBR) lies adjacent to an upraised gravel roadway held in place by wooden walls. One edge of the site is at the mouth of a levee that experiences fast currents when the tide changes. Sponges at this site were found in a narrow band, approximately 3 m wide, as clusters and occasional sheets on the cobbles and adjacent rip-rap. A few individuals colonized the wooden walls of the levy as well. At RBR, thirty adjacent transects were placed between 0 and 30 meters north of the bridge and were deployed to 3 m, at which point the shallow, muddy water made sponge photographs difficult. 3 quadrats were photographed along each transect to compensate for the short transect length.

We assessed whether sponges were reproductive during their period of peak cover by surveying for brooded embryos monthly from September through December 2022. Severe storms in January and February 2023 ended sampling. We sampled from three sites (distinct from the sites where quadrats were surveyed) monthly: one north of the Kirby Park site, and one on each side of the Azevedo Pond culvert (near to but outside of the quadrat sampling area). Ten individuals were dissected in the field and assessed visually to determine if embryos were brooded in the tissues using a 20x loupe.

**Correlation Between Water Quality Parameters and Sponge Cover**

Publicly available National Estuarine Research Reserve (NERR) monitoring data collected from two YSI EXO2 multiparameter instruments (Figure 2) in the Elkhorn Slough were downloaded from the Centralized Data Management Office (https://cdmo.baruch.sc.edu/). Monthly (day 01-31) averages for temperature (°C), acidity (pH), salinity (ppt), dissolved oxygen (mg/L), turbidity (NTU), and precipitation (mm) were calculated from continuous data collected every 15 minutes. Correlations between sponge cover and environmental data were tested using Spearman rank cross-correlations. Since changes in sponge cover may be expected to lag behind environmental changes, time-lagged correlations were also assessed, with monthly sponge cover delayed behind environmental conditions by 1 to 6 months. Monthly averages for environmental variables were calculated using the stats package in R version 4.2.2 (R Core team, 2022). The strongest positive or negative correlation coefficient (rho) for any given environmental parameter (and its time lag) was considered to provide the greatest evidence of correlation with *H. perlevis* cover.

**Measurement of Pumping and Volumetric Flow Rates**

To estimate the total volumetric flow from all sponges at a given site*, H. perlevis* cover was related to pumping rates from individual sponge oscula measured in the field. First, mean osculum density on a sponge was calculated by photographing sponges at APN top-down and counting the number of oscula within a randomly selected cm2 of sponge (n=22). Average osculum size ($cm^2$) was measured by randomly selecting a single osculum from each cm2 and measuring its diameter using Fiji ImageJ (n=22). Half of this average diameter was used to calculate the average osculum area assuming a circular osculum. Error propagation was calculated from products using the formula (Taylor, 1997):

$$If\ x = a \times b, \quad \Delta x = x\sqrt{\left(\frac{\Delta a}{a}\right)^2 + \left(\frac{\Delta b}{b}\right)^2} \tag{2}$$

The velocity of excurrent flow was calculated using the dye front technique following Yahel et al. (2005). In brief, a graduated plastic cylinder was filled with a small amount of fluorescein dye at one end and capped with a finger at the other end while underwater. The cylinder was placed in front of an osculum without touching it and the finger was then removed. The movement of the dye was recorded with a GoPro Hero9 camera and the time for the dye front to reach the end of the cylinder was recorded using Kinovea video annotation software (www.kinovea.org). The velocity of the dye front was averaged across 3 sponges with 1 osculum assessed from one sponge, 2 from the next, and 7 from the third. Each osculum was sampled between 1 and 7 times (n = 10 total oscula). This average was multiplied by the average osculum area to estimate the average volumetric flow assuming plug flow.

**Estimation of H. perlevis Per-Unit Biomass**

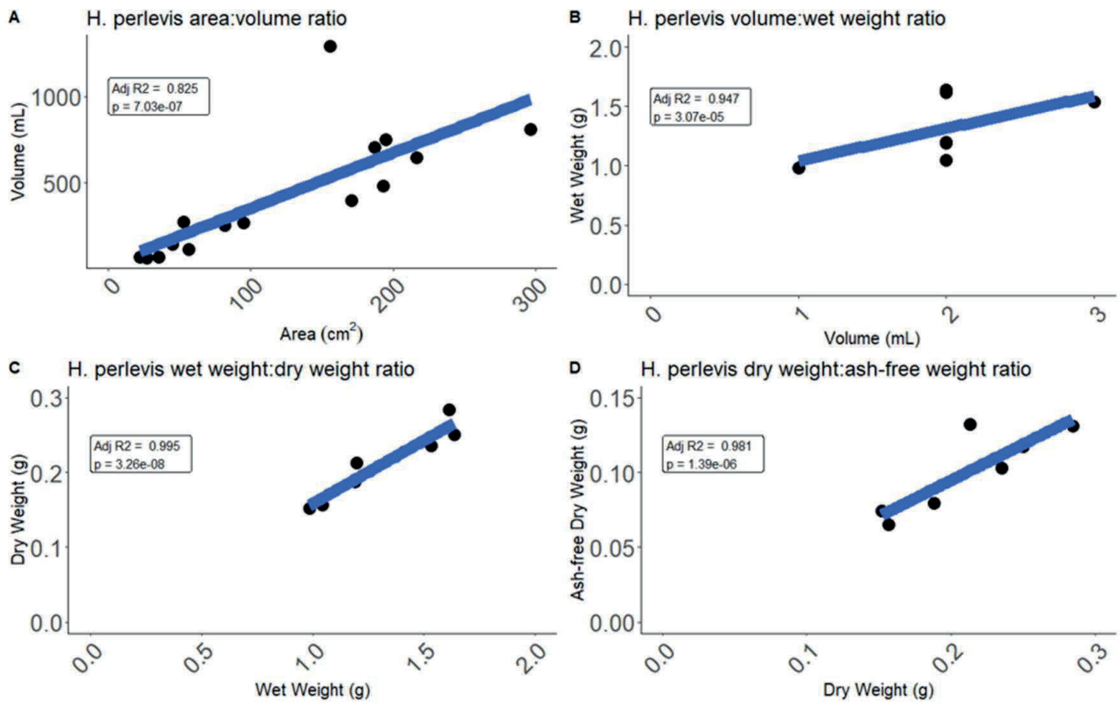
We related two-dimensional sponge cover to estimate biomass using morphometrics on a subset of sponges. First, full individuals were removed from rocks and photographed top-down to calculate their two-dimensional area in ImageJ. Volume of those same individuals was measured using water displacement. A linear regression with an intercept of zero was used to determine the relationship of sponge area:volume using the regression slope (n=15). (Figure 4). A similar relationship was calculated between sponge volume, wet weight, dry weight, and ash-free dry weight. Displacement volumes of wet sponges collected from the field (n=7) were recorded, then sponges were rinsed in fresh water and wet weights were recorded in pre-combusted aluminum trays. Tissue samples were subsequently dried overnight at 55 °C and weighed again to determine dry weight. Finally, the same samples were placed in a muffle furnace for 4 hours at 400 °C to determine ash-free dry weight. Organic weight was calculated by subtracting ash-free dry weight from dry weight. From these relationships, the average biomass per mL of tissue was estimated (Figure 4).

**Estimating Volumetric Flow and Biomass by Scaling Morphologic Relationships**

To estimate biomass and volumetric flow for the sponge cover at a given site, the morphometric relationships measured above were scaled with observed cover. Volumetric flow was multiplied by the average number of oscula cm-2 sponge cover, and further multiplied by the estimated average cover at each site each month to approximate the full extent of water processing by sponges at each site assuming continuous flow. Error propagation was calculated using the equation of Taylor (1997) above. Similarly, by multiplying the average volume:area ratio by the estimated average cover, an organic weight for sponges at each site every month was calculated.

## Figure 4

*Morphometric relationships for H. perlevis*




(A) Area-to-volume ratios derived from sponge cover data and body volume [Volume (mL) = 3.39(Area (cm2))] (n=15). (B) Volume to wet weight ratios derived from water displacement of tissue samples and mass values [Wet Weight (g) = 0.632(Volume (mL))] (n=7). (C) Wet weight to dry weight ratios derived from mass of tissue samples before and after oven drying [Dry Weight (g) = 0.161(Wet Weight (mL))] (n=7). (D) Dry weight to ash-free dry weight ratios derived from mass of tissue samples before and after combustion [Ash-free Dry Weight (g) = 0.478(Dry Weight (g))] (n=7).

# Results

## Annual Recruitment Patterns of H. perlevis in Elkhorn Slough

Settlement plates used to track the spread of H. perlevis through Elkhorn Slough showed a generally growing and expanding population over a period of 17 years, but with variation across sites and years. (Figure 5, Figure 6, Table 2) H. perlevis was detected at six sites in the upper estuary and was not detected in any sites in the lower estuary during the sampling period. Though fouling plate deployments were discontinued in the lower estuary after 2014, there have been no anecdotal observations reported since 2014 either, suggesting that recruitment has not occurred in significant numbers (Table 2). Despite high variability in detection and percent cover at various sites, annual surveys confirm successful recruitment every year from 2014 to the present.

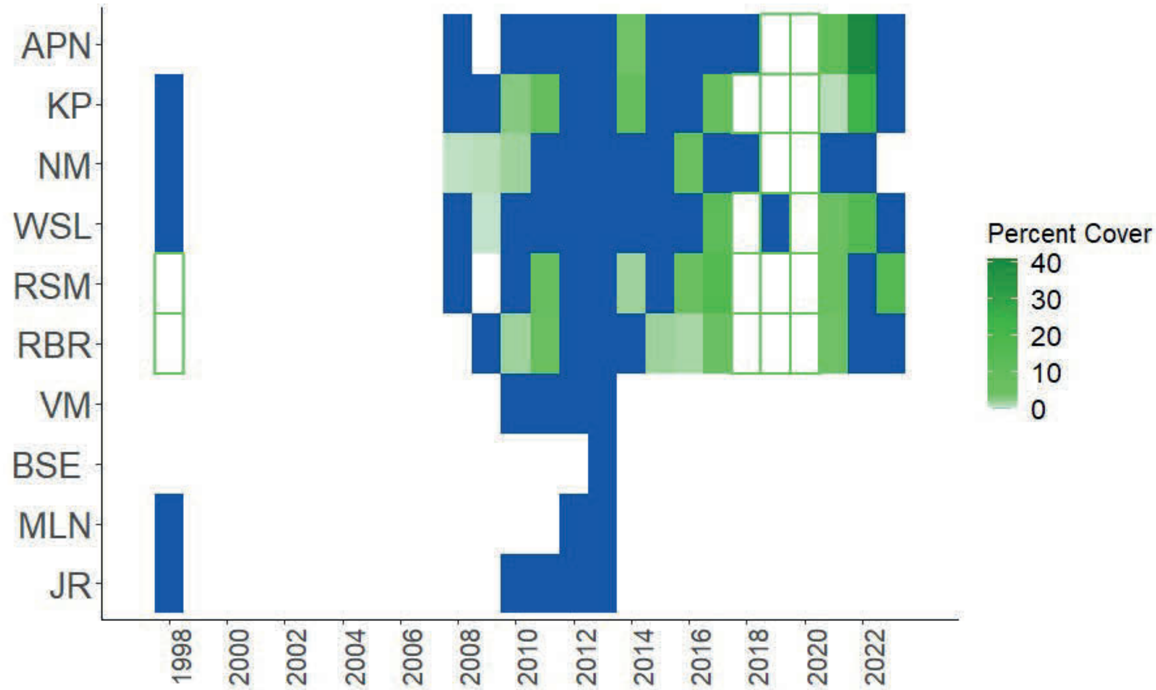
## Seasonally Resolved Sponge Cover

Monthly surveys of sponge cover over two years at three sites in Elkhorn Slough revealed seasonality (Figure 7). Generally, increases in biomass were detected beginning in the summer (August 2021, June 2022), peaked in fall, and then declined in the winter months. From March through May in both years sponges were undetectable (either absent or covered beneath sediments) or at low cover compared to other parts of the year (Figure 7, Table 3). Embryos were detected in sponge tissues during the three months of peak biomass (September – November 2022) at all locations surveyed suggesting seasons of peak biomass correlate with active reproduction, although the full phenology is unknown.

While the overall pattern of sponge cover across the year held true, sponge populations at the three sites varied in cover and timing. Sponge cover at APN (Bootstrapped ANOVA,

**Figure 5**

*Hymeniacidon perlevis detections*

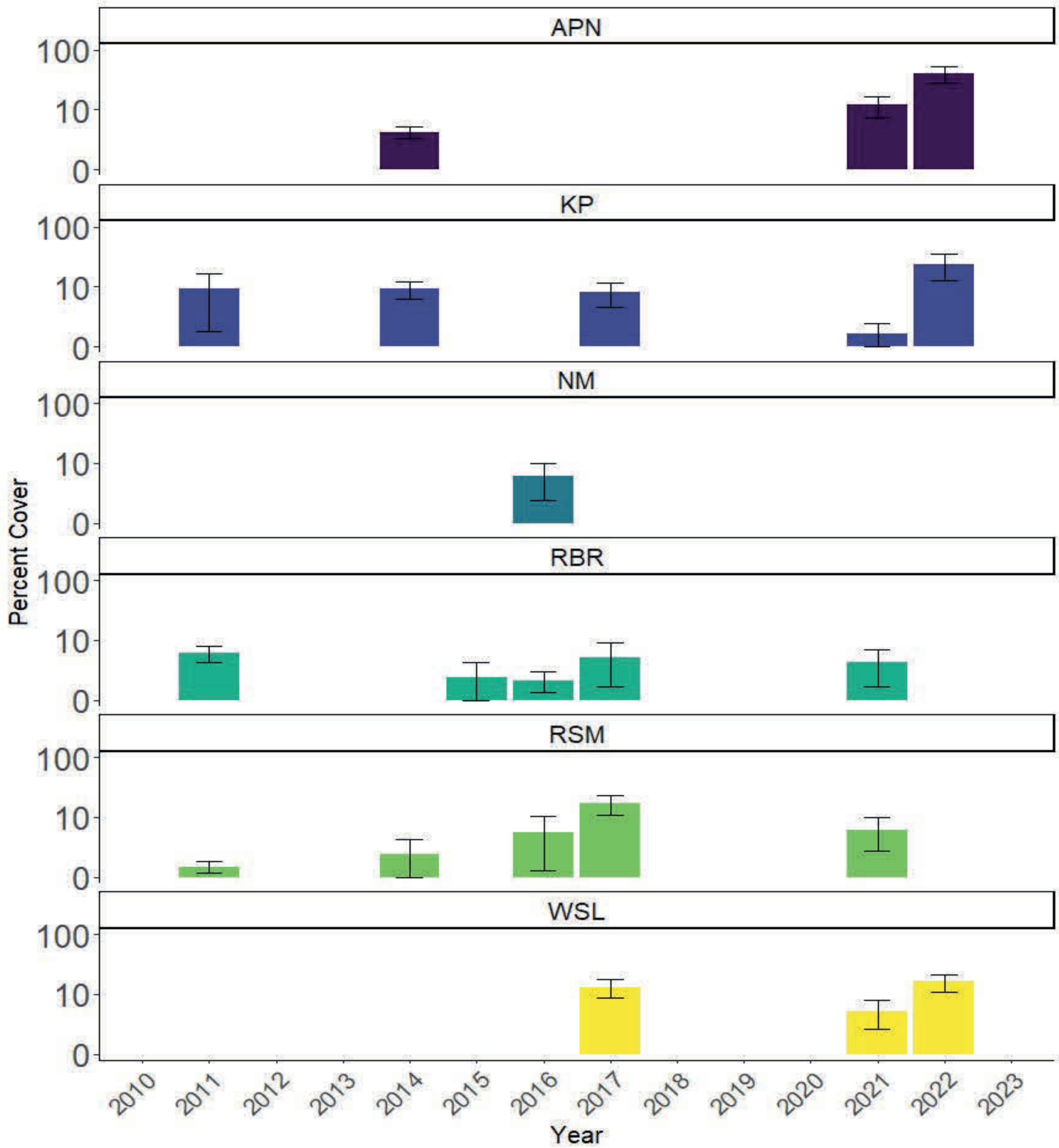



Shown at several sites within Elkhorn Slough over time. The shaded area represents the mean cover of sponges on annual recruitment plates at each site. Blue indicates that no plates deployed at a site were colonized by H. perlevis that year, and green represents that colonization by H. perlevis that year. White represents a period of no sampling at a site, open green boxes represent H. perlevis presence, but no cover data recorded. The dashed line demarcates the upper slough versus lower slough sites.

trials = 1,000, $p < 0.001$) and KP (Bootstrapped ANOVA, trials = 1,000, $p = 0.001$) varied between months, but no significant variation in sponge cover between months was found at RBR (Bootstrapped ANOVA, trials = 1,000, $p = 0.171$). Despite this discrepancy, sponge cover at RBR followed similar trends to cover at APN and KP (Figure 7, Table 3), reaching a maximum in late fall and minimum in the spring.

**Figure 6**

*H. perlevis fouling plate trends*




This figure depicts six fouling plate deployment sites that received any H. perlevis recruits throughout the entire sampling regime. Percent cover describes the annual cover of H. perlevis on the plate area deployed at a given site. Y-axis is on a logarithmic scale. Abbreviations: APN: Azevedo Park North, KP: Kirby Park, NM: North Marsh, RBR: South Marsh Bridge, RSM: South Marsh Reserve, WSL: Whistelstop Lagoon.

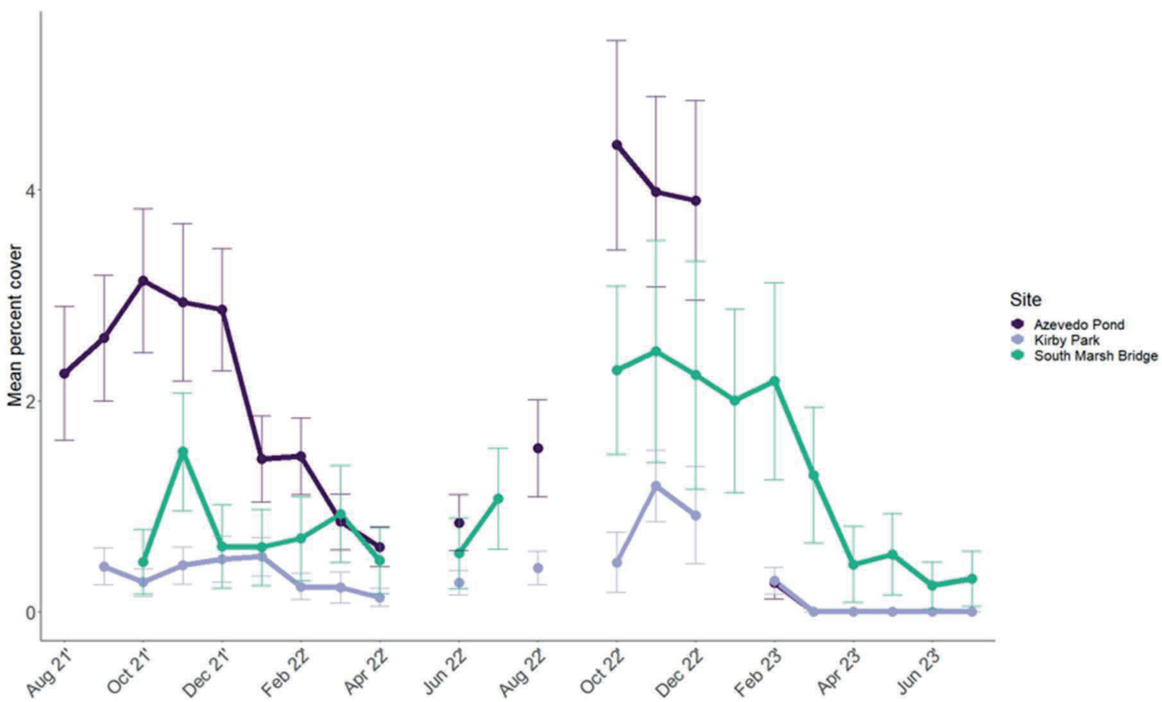
**Table 2**

*List of Years that H. perlevis was Detected or Not at Each Sampling Site.*

| Site (abbreviation) | Years *H. perlevis* detected | Years *H. perlevis* not detected |
|---|---|---|
| Azevedo Pond (APN) | 2014; 2019-2022 | 2008; 2010-2013; 2015-2018; 2023 |
| Kirby Park (KP) | 2010-2011; 2014; 2017-2022 | 2008-2009; 2012-2013; 2015-2016; 2023 |
| North Marsh (NM) | 2008-2010; 2016; 2019-2020 | 2011-2015; 2017-2018; 2021-2022 |
| Whistlestop Lagoon (WSL) | 2009; 2017-2018; 2020-2022 | 2008;  2010-2016; 2019; 2023 |
| South Marsh – WSL (RSM) | 2011; 2014; 2016-2021; 2023 | 2008; 2010; 2012-2013; 2015; 2022 |
| South Marsh Bridge (RBR) | 2010-2011; 2015-2021 | 2009; 2012-2014; 2022-2023 |
| Vierra Mouth (VM) | none | 2010-2013 |
| Bennett Slough (BSE) | none | 2013 |
| Moss Landing Road (MLR) | none | 2012-2013 |
| Jetty Road (JR) | none | 2010-2013 |

**Figure 7**

*Percent cover of H. perlevis*




Shown each sampling site over two years of monitoring. Points are average cover, and error bars represent standard error. Note overlap of Azevedo Pond and Kirby Park sponge cover, as both are at 0% from March 2023 to July 2023.

**Table 3**

*Dates of Peak and Minimum Sponge Cover Shown at Three Sites in Elkhorn Slough, CA.*

| | 2021-2022 season | | | | 2022-2023 season | | | |
|---|---|---|---|---|---|---|---|---|
| | Max | | Min | | Max | | Min | |
| Site | Date | % cover | Date | % cover | Date | % cover | Date | % cover |
| APN | 10/21 | 3.1 ± 0.7 | 4/22 | 0.6 ± 0.2 | 10/22 | 4.4 ± 1.0 | 3/23 | 0 |
| KP | 1/22 | 0.5 ± 0.2 | 4/22 | 0.1 ± 0.1 | 11/22 | 1.2 ± 0.3 | 3/23 | 0 |
| RBR | 11/21 | 1.5 ± 0.6 | 4/22 | 0.5 ± 0.3 | 11/22 | 2.5 ± 1.1 | 6/23 | 0.3 ± 0.2 |

**Correlation Between Water Quality Parameters and Sponge Cover**

Monthly variations in sponge cover were found to lag behind changes in environmental conditions (Table 4). Spearman-ranked cross-correlations between environmental data and sponge cover at APN, KP, and RBR had the strongest correlations (rho values) with a 2-4 month lag, indicating that this is the time until sponge cover visually reflects changes in the environment in Elkhorn Slough (Table 4). A strong positive correlation was observed between sponge cover and temperature and a negative correlation between cover and dissolved oxygen. Sponge cover at APN was significantly correlated ($p < 0.05$) with all parameters except for precipitation ($p = 0.06$). Precipitation was only found to be significant at KP ($p = 0.02$) (Table 4).

**Scaling Potential Impacts Across Seasons**

Relationships between sponge cover, biomass, volume, osculum density $cm^{-2}$ of sponge, and water pumping rate were used to estimate the volume of water filtered and sponge biomass, scaled up to *H. perlevis* cover within each site. The quantity of water processed and sponge biomass changed seasonally (Figure 8, Table 5). *H. perlevis* populations from these three sites in Elkhorn Slough had on average 2.36 ± 0.283 oscula $cm^{-2}$ sponge area when

**Table 4**

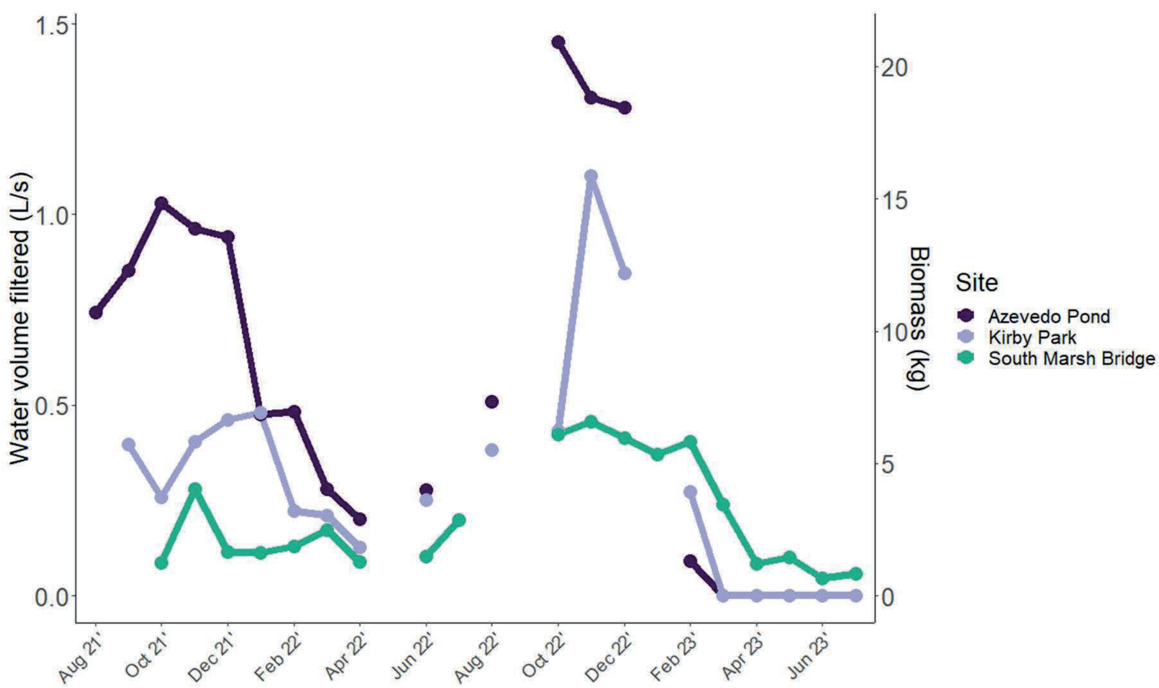
*Correlations between Sponge Cover and Environmental Variables*

| | **Azevedo Pond** | | | **Kirby Park** | | | **South Marsh Bridge** | | |
|---|---|---|---|---|---|---|---|---|---|
| Parameter | Lag (Months) | rho | p | Lag (Months) | rho | p | Lag (Months) | rho | p |
| Temperature | **3** | **0.92** | **<0.01** | **4** | **0.89** | **0.01** | **3** | **0.90** | **<0.01** |
| pH | **2** | **-0.67** | **0.04** | 2 | -0.75 | 0.07 | 1 | -0.62 | 0.11 |
| Salinity | **3** | **0.87** | **<0.01** | **0** | **-0.93** | **<0.01** | 6 | 0.57 | 0.15 |
| Dissolved $O_2$ | **2** | **-0.82** | **<0.01** | **3** | **-0.86** | **0.02** | **3** | **-0.95** | **<0.01** |
| Turbidity | **3 and 4 *** | **-0.74** | **0.01** | **1** | **-0.79** | **0.05** | 5 | -0.31 | 0.46 |
| Precipitation | 3 | -0.61 | 0.06 | 6 | -0.68 | 0.09 | 4 | -0.62 | 0.11 |

Sponge cover was measured monthly at each site and averaged. Environmental factors were averaged per month from continuously monitoring sondes (https://cdmo.baruch.sc.edu/). Rho and p values calculated using Spearman cross correlations for time lags from 0-6 months. Time lags, in number of months, indicate when changes in environmental parameters were most highly correlated with sponge cover. Statistically significant results are indicated in bold (n=24). * Indicates a similar correlation coefficient occurred with both a 3- and 4-Month Time Lag

**Figure 8**

*Estimates of volume of water filtered and biomass.*




Estimated from H. perlevis cover data within each sample site. Points represent the estimated values based on average percent cover. Error bars are not shown due to excessive size.

**Table 5**

*Peak and Minimum Pumping Rates and Biomass at Three Sites in Elkhorn Slough, CA.*

| | Max | | | Min | | | Site Area $m^2$ |
|---|---|---|---|---|---|---|---|
| Site | Date | Volumetric Flow $L\ h^{-1}\ m^{-2}$ | Organic Weight kg $m^{-2}$ | Date | Volumetric Flow $L\ h^{-1}\ m^{-2}$ | Organic Weight kg $m^{-2}$ | |
| APN | 10/21 | 33 ± 8.9 | 0.091 ± 13 | 10/22 | 4.4 ± 1.0 | 0 | 160 |
| KP | 1/22 | 8.8 ± 2.8 | 0.024 ± 3.5 | 11/22 | 1.2 ± 0.3 | 0 | 450 |
| RBR | 11/21 | 18 ± 8.3 | 0.051 ± 6.5 | 11/22 | 2.5 ± 1.1 | 0.3 ± 0.2 | 90 |

viewed from above (n = 22, mean ± SE). The average size of each osculum was 0.65 ± 008 $mm^2$ (n = 22, mean ± SE). The average volume pumped by an active osculum, measured by the dye front method, was 31 ± 3 mL $h^{-1}$ (n = 10, mean ± SE) through each active osculum.

To estimate potential variation in seasonal biomass and water filtration, we first assessed relationships between several morphometric measurements. (Figure 4). A single $cm^2$ of *H. perlevis* when measured from above had a volume of 3.4 ± 230 mL (n=15). For 1 mL of *H. perlevis* tissue, the average wet weight was 0.63 ± 0.31 g (n = 7), dry weight was 0.10 ± 0.056 g (n=7), ash-free dry weight was 0.048 ± 0.033 g (n=7), and organic biomass was 0.054 ± 0.029 g (n=7). Using these relationships, we estimate that sponges at APN had the greatest biomass and water filtration, based on their density. APN sponges pumped 36 ± 9 L h-1 m-2 in November 2022 and 0 L h-1 m-2 in March 2023 (0.09 ± 13 kg m-2 to 0 kg m-2), KP sponges pumped 8.6 ± 2.8 L h-1 m-2 in November 2022 and 0 L s-1 m-2 in March 2023 (0.0244 ± 3.47 kg m-2 to 0 kg m-2), and RBR sponges pumped 18.4 ± 8.3 L h-1 m-2 in November 2022 to 9.4 ± 5.0 L h-1 m-2 in March 2023 (0.0507 ± 7.18 kg m-2 to 0.0266 ± 3.78 kg m-2) (Table 5). (Note the large standard error, which was driven by the very patchy distribution of sponges in their habitat, variation in area:volume ratios, and propagation of that error into these calculations).

By scaling estimates from a square meter up to the full extent of intertidal zone occupied by sponges at each of the three sites, we estimate that the volume pumped by APN sponges had the greatest change across the year, from 1.6 ± 0.40 L s-1 at peak sponge cover in October 2022 to 0 L s-1 when sponges were absent, in March 2023. The corresponding change in sponge biomass was from 14.5 ± 2060 kg to 0 kg. By comparison, all KP sponges filtered a peak rate of 1.1 ± 0.35 L s-1 at peak sponge biomass of 11.0 ± 1560 kg in November 2022, and 0 L s-1 at minimum sponge biomass of 0 kg by March 2023. Sponges at the RBR site pumped a peak of 0.46 ± 0.21 L s-1 with 4.56 ± 646 kg biomass during November 2022 and in contrast with the other two sites, sponges persisted through March 2023, which meant a calculated rate of 0.240 ± 0.124 L s-1 pumped and 2.39 ± 340 kg of sponge biomass (Table 5).

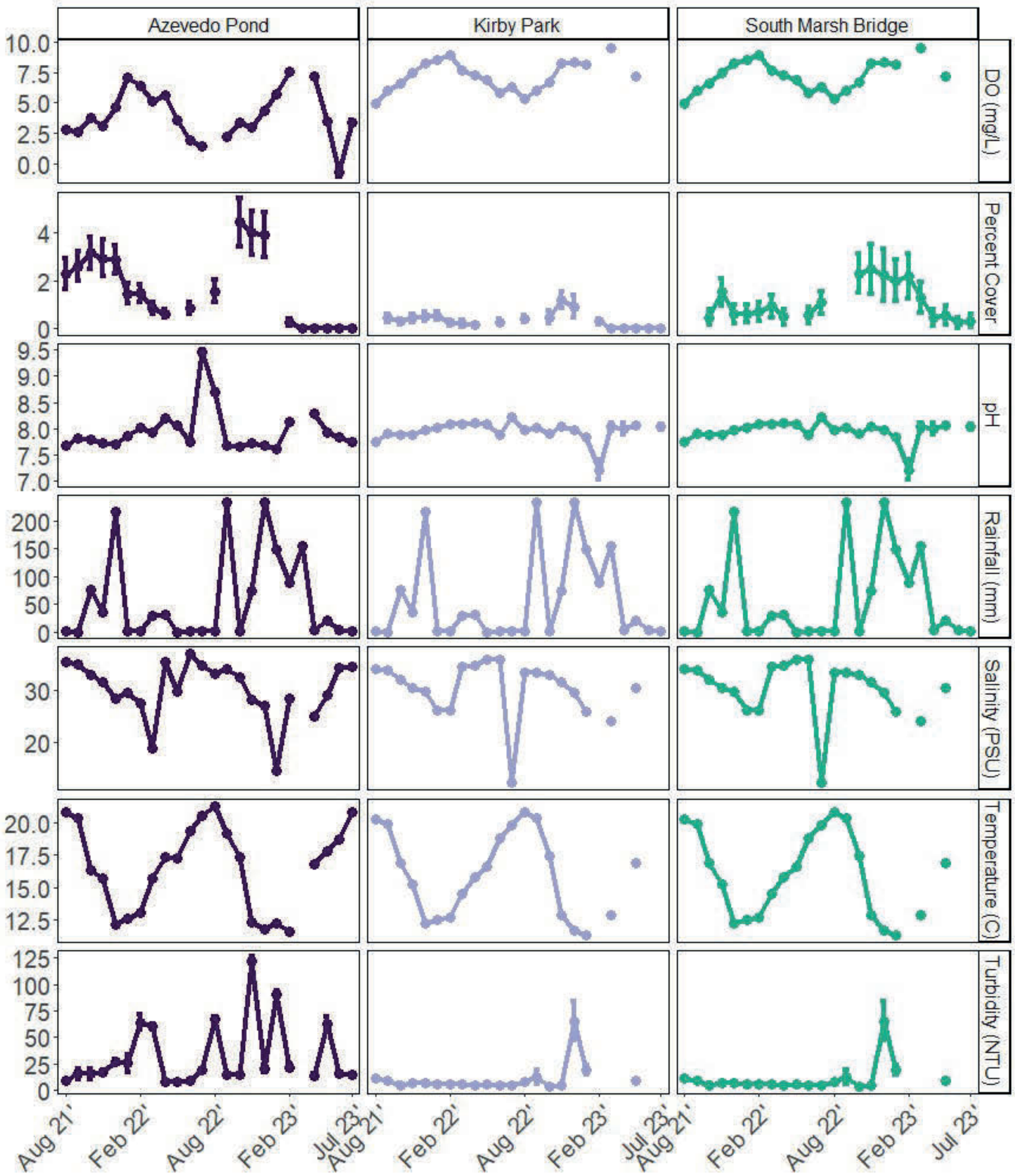
## Discussion

### Annual Recruitment Patterns of H. perlevis in Elkhorn Slough

From 2008 to 2022, recruitment varied as typical for many species (Connell, 1985; Menge & Sutherland, 1987), but there was a general increase in the number of sites, frequency, and density of *H. perlevis* recruits on settlement plates. However, recruitment was only observed in upper estuary sites. Adults of this species are also only found in the upper estuary. This distribution follows a general pattern in Elkhorn Slough, with introduced species being more diverse and more abundant in the upper estuary (Wasson et al., 2005). The upper estuary is more eutrophic than the lower estuary, with higher chlorophyll and temperature and longer residence time (Figure 9); APN is even considered "hypereutrophic" (Hughes et al., 2011), and also has the greatest levels of *H. perlevis* cover. In a 2023 study, *H. perlevis* grew faster and more densely in the eutrophic outflow water of an inland fish farm compared to neighboring areas (Mercurio et al., 2023). *H. perlevis* may grow in greater densities in the upper estuary due to increased food availability from eutrophication, particularly in sites such as APN where eutrophic water is provided via daily tidal flow through narrow channels. However, abiotic, density-independent factors such as severe weather incurred broad effects across all sites. For example, after several years of consistent recruitment, sponges only recruited to a single site in 2023 (Figure 5). This was in the wake of frequent storms with heavy rainfall in central California from November 2022 to April 2023, which generated the heaviest precipitation observed during the study period. We infer that this intense precipitation period may have in part created unsuitable conditions for *H. perlevis* reproduction or recruitment.

**Figure 9**

*Environmental data*




Mean (± SD, error bars) monthly dissolved oxygen, pH, precipitation, salinity, temperature, and turbidity from NERR data monitoring stations, and high-resolution H. perlevis cover collected during this study from the Azevedo Pond, Kirby Park, and South Marsh Bridge sites. The Azevedo Pond data monitoring station provided data for Azevedo Pond, while the South Marsh station provided data for both Kirby Park and South Marsh Bridge.

**Population Dynamics and Phenology**

Although the populations in Elkhorn Slough follow annual cycles like other populations, the Elkhorn Slough populations reached peak above-ground biomass in mid-October and minimum biomass by February or March. In the Yellow Sea and United Kingdom, *H. perlevis* populations reach peak biomass earlier, in September (H. Cao et al., 2012; X. Cao, et al., 2007; Juniper & Steele, 1969; Stone, 1970). The timing of minimal biomass and/or dormancy varies even more. In the Yellow Sea, sponges regressed completely from December through February; in the United Kingdom sponges declined through late spring until May but did not reach complete dormancy. In the Ionian Sea, sponges became dormant in September, which is during or even before peaks for populations in other areas of the world (Gaino et al., 2010). Within Elkhorn Slough, populations at APN and KP reached extremely low cover during late winter and spring, with most individuals becoming undetectable from above-ground and presumably regressing either completely or so that the only tissue that remained was covered by sediments. RBR populations did not disappear completely but also shrank to their smallest cover in March. In future it will be important to assess the full above- and below-ground biomass of sponges, and to determine whether this species can remain functional as a psammobiontic species or has other adaptations to a semi-infaunal lifestyle (Ilan & Abelson, 1995; Rützler, 1997; Schönberg, 2015; Werding & Sanchez, 1991).

Temperature may in part explain differences in *H. perlevis* population dynamics across various regions., Water temperatures in the English Channel (within *H. perlevis'* presumed native range) only dropped to 5 °C during the winters of 1967 and 1968 when sponge cover was measured (Stone, 1970), while in the Yellow Sea where sponges regress completely, the water temperature was as low as -1.1 °C in the winter (H. Cao et al., 2012). However, sudden population declines such as those observed in the Ionian Sea (just after temperatures peaked at 26.8 °C) (Gaino et al., 2010) indicate factors such as salinity, food availability, and dissolved oxygen influence *H. perlevis*' phenology. The minimum temperature in Elkhorn Slough across this study period was 4.5 °C, much closer to the recorded temperatures in the English Channel. From the 2-4 month time lags we found between sponge cover and environmental variables, we hypothesize that peak sponge cover occurred 2-4 months after conditions were typical of summer periods in Elkhorn Slough: warmer, saltier, more acidic, with lower turbidity and lower dissolved oxygen concentrations (Caffrey, Martha, et al., 2002). While the conditions at the end of winter may trigger new growth, we hypothesize that the conditions required to reach maximum biomass occur during summer.

In addition to seasonal variations, sponges were affected by severe episodic events. The series of strong storms that struck central California from November 2022 to April 2023 coincided with a far more dramatic decrease in sponge cover than the previous year in both intensity and duration. While the decline of sponge cover began after mid-October in both years, the decline in the winter of 2022-2023 was far faster than the previous (2021-2022) winter and led to the complete disappearance of above-ground *H. perlevis* at APN and KP up through the end of sampling, July 2023. Sponge populations at RBR did not completely disappear and some above-ground biomass remained before growth resumed in May 2023. One possible explanation is that the storms covered such a long period that while sponges were able to close their ostia to survive increased turbidity and/or low salinity temporarily

(Parker, 1910), they were unable to feed. However, the only significant statistical correlation with precipitation was at KP, where sponge cover lagged 1 month behind precipitation. Other parameters, most notably temperature, have been implicated in driving *H. perlevis'* phenology due to correlation with cover (H. Cao et al., 2012; Gaino et al., 2010; Stone, 1970), but the specific mechanism triggering sponge regression remains an open question for further study. Considering the number of regions *H. perlevis* now inhabits (Samaai et al., 2022), understanding these reactions to severe weather is important in the context of ongoing climate change.

While a seasonal life cycle is common in populations of *H. perlevis* around the world, there can be exceptions. *H. perlevis* grew rapidly and continuously with no seasonal pattern in areas near to a nutrient-rich wastewater outflow from a fish farm while sponge populations further from the inlet showed greater variability (Mercurio et al., 2023). These observations support a plastic seasonality that is variable and may not occur under stable conditions. Within Elkhorn Slough, the population dynamics of *H. perlevis* across years and between sites demonstrates the importance of microhabitats, perhaps related to food availability and water flow as noted by Mercurio et al. (2023). These relationships are crucial to predicting the abundance and timing of *H. perlevis* in all habitats, artificial and natural.

**Estimating the Scale of Environmental Impact**

Given seasonal changes in sponge cover, the impacts of *H. perlevis* on Elkhorn Slough are unlikely to be uniform over the year. Pumping and biomass may not scale as tightly with cover as we have shown here in our simple model (Figure 8, Table 4), since sponges may vary in shape or in proportion of biomass that is buried in the mud. However, in the absence of more detailed measurements, it seems reasonable to assume that pumping rates and biomass increase with cover. Thus, the environmental impacts of *H. perlevis*, on water filtration and biomass, are likely greatest during mid-October in this estuary, when cover is highest, and smallest to nonexistent during March to May, when cover is lowest.

The impacts of filtration by *H. perlevis* on Elkhorn Slough water are not known. In laboratory experiments, *H. perlevis* consumed bacteria, reducing concentrations by 38-90% in laboratory conditions (Longo et al., 2010; Longo et al., 2022; Maldonado et al., 2010; Zhang et al., 2010), making it a potent feeder on bacterioplankton. Elkhorn Slough is characterized by eutrophication and nutrient runoff from agriculture throughout the watershed that lowers water quality (Caffrey, Martha, et al., 2002; Caffrey, Neil, & Bess, 2002; Hughes et al., 2011). At the densities *H. perlevis* achieves, especially at peak biomass in the fall, this grazing capability may affect bacterial densities in Elkhorn Slough. If *H. perlevis* is in a site with abundant bacteria as food, it may persist and affect water conditions year-round. Feeding rates vary with water temperature, with peak removal rates at 15 °C and less removal at higher and lower temperatures (Zhang et al., 2010). In those same mesocosm experiments, elevated water temperatures also resulted in greater ammonia released into the water by the sponges, suggesting *H. perlevis* may play a role in both carbon and nitrogen cycling within the Elkhorn Slough and other coastal habitats.

**Ecological Interactions with H. perlevis**

*H. perlevis* may provide novel habitat as it grows, or in contrast be a competitor for space. This species can grow rapidly in a period of months, which along with its resilience likely enables it to outcompete native species for space. Large aggregations alter a boundary layer that provides unique habitat overlying the sponges (Gili & Coma, 1998). The sponges may also serve as novel habitat: amphipods and polychaetes were seen within the tissues of *H. perlevis*. Both temperate and tropical sponges have long been recognized as habitat for a variety of fish and invertebrate species (Wulff, 2006), with relationships ranging from mutualistic (Siemann & Turco, 2023) to predatory/parasitic (Magnino & Gaino, 1998). However, many of these endobionts are specialists that seek out a particular host species (Rützler, 2012) as opposed to the presumably opportunistic invertebrates making use of an introduced sponge in Elkhorn Slough. While this novel, seasonally available habitat may shelter invertebrate species, the improvised nature of these relationships suggests they may be subject to rapid change.

The spectrum of impacts described above complicate an assessment of whether *H. perlevis* should be considered invasive, or if its seasonal and interannual dynamics make its impacts too variable over time. Estimating the seasonal abundance of *H. perlevis* in a specific site can be a useful first step in adaptive management for this species. If removal or reduction of *H. perlevis* populations is required, then timing culling efforts to periods when *H. perlevis* is visually present but not yet reproductive (i.e. June-August for population dynamics such as observed at Elkhorn Slough) may provide the most efficient removal method. This is not possible once the species is widely established, such as at Elkhorn Slough, but could be possible soon after detection in a new area. Additionally, understanding seasonal cycles may facilitate efforts to model the spread of *H. perlevis* to new regions. Such season-informed models have been generated using phenology data of non-native species before, such as the brown marmorated stink bug, *Halyomorpha halys (Stål, 1855)*

(Kamiyama et al., 2021; Reznik et al., 2022) and the Asian shore crab *Hemigrapsus sanguineus (De Haan, 1835)* (Giménez et al., 2020). These phenological models are particularly important to understand how non-native species may alter their ecosystems in the face of climate change (Colautti et al., 2017) or anomalous climate events, such as the severe storms that affected *H. perlevis'* phenology during this study.

## Conclusion

This is the first study to systematically document the abundance and distribution of *H. perlevis* in Elkhorn Slough, and conclusively identifies the species is firmly established in the system. We found that *H. perlevis* populations in Elkhorn Slough are recruiting annually with generally increasing regularity and spread throughout the estuary. *H. perlevis* populations in Elkhorn Slough followed a novel seasonal cycle distinct in timing from observations elsewhere around the world, reaching peak biomass in October and minimal biomass or complete dormancy in February or March. Increases in sponge cover followed 2-4 months after seasonal changes in water temperature, dissolved oxygen, and salinity. However, intense storms from November 2022 to April 2023 changed sponge cover rapidly and likely disrupted/supplanted typical seasonal patterns. These combined results suggest *H. perlevis* is a highly adaptable, plastic species that responds to environmental conditions. Ecological impacts of this non-native species vary over the year, with maximum cover, biomass, and peak water processing occurring in the fall in Elkhorn Slough. Though the precise effects of *H. perlevis* are still unknown, the dramatic changes in sponge cover over time suggests a growing importance for understanding its ecological role under varying conditions in a global context.

## References


Caffrey, J. M., Martha, B., Tyler, W., & Silberstein, M. (Eds.). (2002). *Changes in a California Estuary: A profile of Elkhorn Slough*. Elkhorn Slough Foundation.

Caffrey, J. M., Neil, H., & Bess, W. (2002). Biogeochemical processes in a small California estuary. 1. Benthic fluxes and pore water constituents reflect high nutrient freshwater imputs. *Marine Ecology Progress Series, 233*, 39-53. https://www.jstor.org/stable/10.2307/24865177

Cao, H., Cao, X., Guan, X., Xue, S., & Zhang, W. (2012). High temporal variability in bacterial community, silicatein and hsp70 expression during the annual life cycle of Hymeniacidon sinapium (Demospongiae) in China's Yellow Sea. *Aquaculture, 358–359*, 262–273. https://doi.org/10.1016/j.aquaculture.2012.06.005

Cao, X., Fu, W., Yu, X., & Zhang, W. (2007). Dynamics of spicule production in the marine sponge *Hymeniacidon perlevis* during in vitro cell culture and seasonal development in the field. *Cell Tissue Research, 329*, 595-608. https://doi.org/10.1007/s00441-007-0443-1

Carlton, J. T. (1979). *History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the pacific coast of North America*. [Doctoral dissertation, University of California, Davis]. UC Davis Library.

Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology, 93*, 11-45.

Colautti, R. I., Ågren, J., & Anderson, J. T. (2017). Phenological shifts of native and invasive species under climate change: insights from the *Boechera-Lythrum* model. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*, 20160032. http://dx.doi.org/10.1098/rstb.2016.0032

Fuentes, V. L., Angel, D. L., Bayha, K. M., Atienza, D., Edelist, D., Bordehore, C., Gili, J., & Purcell, J. E. (2010). Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiologia, 645*, 23-37, https://doi.org/10.1007/s10750-010-0205-z

Fuller, T. L., & Hughey, J. R. (2013). Molecular investigation of the invasive sponge Hymeniacidon sinapium (de Laubenfels, 1930) in Elkhorn Slough, California. *Aquatic Invasions, 8*, 59–66. http://dx.doi.org/10.3391/ai.2013.8.1.07

Gaino, E., Cardone, F., & Corriero, G. (2010). Reproduction of the intertidal sponge *Hymeniacidon perlevis* (Montagu) along a bathymetric gradient. *The Open Marine Biology Journal, 4*, 47-56. https://doi.org/10.2174/1874450801004010047

Giménez, L., Exton, M., Spitzner, F., Meth, R., Ecker, U., Jungblut, S., Harzsch, S., Saborowski, R., & Torres, G. (2020). Exploring larval phenology as predictor for range expansion in an invasive species. *Ecography, 43*, 1423-1434. https://doi.org/10.1111/ecog.04725

Gili, J., & Coma, R. (1998). Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Evolution and Ecology, 13*(8), 316-321.

Harbo, R. M., Ott, B., Reiswig, H. M., & Mcdaniel, N. (2021). First Canadian record (Ladysmith Harbour, British Columbia) of the non-native European sponge Hymeniacidon perlevis (Montagu, 1814) (Porifera, Demospongiae). *BioInvasions Rec., 10*(2), 277-286, https://doi.org/10.3391/bir.2021.10.2.05

Hughes, B. B., Hasins, J. C., Wasson, K., & Watson, E. (2011). Identifying factors that influence eutrophication in a central California estuary. *Marine Ecology Progress Series, 439*, 31-43. https://doi.org/10.3354/meps09295

Ilan, M., & Abelson, A. (1995). The life of a sponge in a sandy lagoon. *The Biological Bulletin, 189*, 363-369. https://doi.org/10.2307/1542154

Juniper, A. J., & Steele, R.D. (1969). Intertidal sponges of the Portsmouth area. *Journal of Natural History, 3*(2), 153-163, https://doi.org/10.1080/00222936900770161

Kamiyama, M. T., Matsuura, K., Yoshimura, T., & Yang, C.S. (2021). Improving invasive species management using predictive phenology models: an example from brown marmorated stink bug (*Halyomorpha halys*) in Japan. *Pest Management Science, 77*, 5489-5497. https://doi.org/10.1002/ps.6589

Kahn, A. S., Yahel, G., Chu, J. W. F., Tunnicliffe, V., & Leys, S. P. (2015). Benthic grazing and carbon sequestration by deep-water glass sponge reefs. *Limnology and Oceanography*, *60*, 78-88. https://doi.org/10.1002/lno.10002

Klein, J. C., & Verlaque, M. (2009). Macrophyte assemblage associated with an invasive species exhibiting temporal variability in its development pattern. *Hydrobiologia, 636*, 369-378. https://doi.org/10.1007/s10750-009-9966-7

de Laubenfels, M. W. (1932). The marine and fresh-water sponges of California. *Proceedings of the United States National Museum, 81*, 1–140.

Leys, S. P., Kahn, A. S., Fang, J. K. H., Kutti, T., & Bannister, R. J. (2018). Phagocytosis of microbial symbionts balances the carbon and nitrogen budget for the deep-water boreal sponge Geodia barretti. *Limnology and Oceanography, 63*, 187-202. https://doi.org/10.1002/lno.10623

Longo, C., Corriero, G., Licciano, M., & Stabili, L. (2010). Bacterial accumulation by the

Demosponge Hymeniacidon perlevis: A tool for the bioremediation of polluted seawater. *Marine Pollution Bulletin, 60*, 1182-1187. https://doi.org/10.1016/j.marpolbul.2010.03.035

Longo, C., Pierri, C., Mercurio, M., Trani, R., Cardone, F., Carbonara, P., Alfonso, S., & Stabili, L. (2022). Bioremediation capabilites of Hymeniacidon perlevis (Porifera, Demospongiae) in a Land-Based Experimental Fish Farm. *Journal of Marine Science and Engineering, 10*, 874. https://doi.org/10.3390/jmse10070874

MacGinitie, G. E. (1935). Ecological Aspects of a California Marine Estuary. *The American Midland Naturalist, 16*, 629.

Magnino, G., & Gaino, E. (1998). *Haplosyllis spongicola* (Grube) (Polychaeta, Syllidae) associated with two species of sponges from east Africa (Tanzania, Indian Ocean). *Marine Ecology, 19*(2), 77-87. https://doi.org/10.1111/j.1439-0485.1998.tb00455.x

Maldonado, M., & Young, C. (1996). Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. *Marine Ecology Progress Series, 138*, 169-180, https://doi.org/10.3354/meps138169

Maldonado, M., Zhang, X., Cao, X., Xue, L., Cao, H., & Zhang, W. (2010). Selective feeding by sponges on pathogenic microbes: A reassessment of potential for abatement of microbial pollution. *Marine Ecology Progress Series, 403*, 75–89. https://doi.org/10.3354/meps08411

Menge, B. A., & Sutherland, J. P. (1987). Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist, 130*(5), 730-757. https://www.jstor.org/stable/2461716

Mercurio, M., Longo, C., Pierri, C., Cardone, F., Corriero, G., Lazic, T., Zupa, W., & Carbonara, P. (2023). Life-cycle traits in the demosponge *Hymeniacidon perlevis* in a land-based fish farm. *PeerJ, 11,* e14685. https://doi.org/10.7717/peerj.14685

Montagu, G. (1814). An Essay on Sponges, with Descriptions of all the Species that have been discovered on the Coast of Great Britain. *Memoirs of the Wernerian Natural History Society, 2*, 67–122.

Nichols, S. A., & Barnes, P. A. G. (2005). A molecular phylogeny and historical biogeography of the marine sponge genus Placospongia (Phylum Porifera) indicate low dispersal capabilities and widespread crypsis. *Journal of Experimental Marine Biology and Ecology, 323*(1), 1–15. https://doi.org/10.1016/j.jembe.2005.02.012

Nybakken, J. W., Cailliet, G. M., & Broenkow, W. W. (1975). *A Baseline Study of the Moss Landing/Elkhorn Slough Environment*. Moss Landing Marine Laboratories.

Parker, G. H. (1910). The reactions of sponges with a consideration of the origin of the nervous system. *Journal of Experimental Zoology,* 8, 1–41.

Parker, G. H. (1919). *The Elementary Nervous System*. JB Lippincott Company.

Preisler, R. K., Wasson, K., Wolff, W. J., & Tyrrell, M. C. (2009). Invasions of Estuaries vs the Adjacent Open Coast: A Global Perspective. In G. Rilov & J. Crooks (Eds.), *Biological Invasions in Marine Ecosystems* (pp. 587-617). Springer. *Ecological Studies, 204*. https://doi.org/10.1007/978-3-540-79236-9_33

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reznik, S. Y., Karpun, N. N., Zakharchenko, V. Y., Shoshina, Y. I., Dolgovskaya, M. Y., Saulich, A. K., & Musolin, D. L. (2022). To every thing there is a season: Phenology and photoperiodic control of seasonal development in the invasive Caucasian population of the brown marmorated stink bug, Halyomorpha halys (Hemiptera: Heteroptera: Pentatomidae). *Insects, 13*, 580. https://doi.org/10.3390/insects13070580

Rowe, M. D., Anderson, E. J., Wang, J., & Vanderploeg, H. A. (2015). Modeling the effect of invasive quagga mussels on the spring phytoplankton bloom in Lake Michigan. *Journal of Great Lakes Research, 41*, 49–65. https://doi.org/10.1016/j.jglr.2014.12.018

Ruiz, G. M., Carlton, J. T., Grosholz, E. D., & Hines, A. H. (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist, 37*, 621–632. https://doi.org/10.1093/icb/37.6.621

Rützler, K., (1997). The role of psammobiontic sponges in the reef community. *Proceedings of the 8th International Coral Reef Symposium, 2*, 1393-1398. https://repository.si.edu/handle/10088/7843

Rützler, K. (2012). The role of sponges in the Mesoamerican barrier-Reef ecosystem, Belize. In M. A. Becerro, M. J. Uriz, M. Maldonado, & X. Turon (Eds.), *Advances in Sponge Science: Phylogeny, Systematics, Ecology* (pp. 211-271). Academic Press. *Advances in Marine Biology, 61*. https://doi.org/10.1016/B978-0-12-387787-1.00002-7

Samaai, T., Turner, T. L., Kara, J., Yemane, D., Ngwakum, B. B., Payne, R. P., & Kerwath, S. (2022). Confirmation of the southern African distribution of the marine sponge Hymeniacidon perlevis (Montagu, 1814) in the context of its global dispersal. *PeerJ*, *10*, e14388. https://doi.org/10.7717/peerj.14388

Schneider, C.A., Rasband W.S., & Eliceiri, K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods, 9*(7), 671-675. https://doi.org/10.1038/nmeth.2089

Schönberg, C. H. L. (2015). Happy relationships between marine sponges and sediments – a review and some observations from Australia. *Journal of the Marine Biological Association of the United Kingdom, 96*(2), 493-514, https://doi.org/10.1017/S0025315415001411

Siemann. M. J., & Turco, A. (2023). The influence of sponge-dwelling gobies (Elactinus horsti) on pumping rates of Caribbean sponge hosts, Aplysina lacunosa and Aplysina archeri. *Coral Reefs, 42*, 513-517. https://doi.org/10.1007/s0038-023-02362-y

Stone, A. R. (1970). Growth and reproduction of Hymeniacidon perleve (Montagu) (Porifera) in Langstone Harbour, Hampshire. *Journal of Zoology, London, 161*, 443-459, https://doi.org/10.1111/j.1469-7998.1970.tb02048.x

Taylor, J. R. (1997). *An Introduction to Error Analysis: The Study of Uncertainties in Physical Measurements*, (2nd ed.). University Science Books.

Turner, T. L. (2020) The Marine Sponge Hymeniacidon perlevis is a globally-distributed exotic species. *Aquatic Invasions, 15*(4), 541-561, https://doi.org/10.3391/ai.2020.15.4.01

Vanderploeg, H. A., Liebig, J. R., Nalepa, T.F., Fahnenstiel, G. L., & Pothoven, S. A. (2010). Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. *Journal of Great Lakes Research, 36*, 50–59. https://doi.org/10.1016/j.jglr.2010.04.005

Van Dyke, E., & Wasson, K. (2005). Historical ecology of a Central California estuary: 150 years of habitat change. *Estuaries, 28*(2), 173-189. https://doi.org/10.1007/BF02732853

Wasson, K., Gossard, D.J., Gardner, L., Hain, P. R., Zabin, C. J., Fork, S., Ridlon, A. D., Bible, J. M., Deck, A. K., & Hughes, B. B. (2020). A scientific framework for conservation aquaculture: A case study of oyster restoration in central California. *Biological Conservation, 250*, 108745. https://doi.org/10.1016/j.biocon.2020.108745

Wasson, K., Fenn, K., & Pearse, J. S. (2005). Habitat differences in marine invasions of central California. *Biological Invasions, 7*, 935-948, https://doi.org/10.1007/s10530-004-2995-2

Wasson, K., Zabin, C. J., Bedinger, L., Diaz, M. C., & Pearse, J. S. (2001). Biological invasions of estuaries without international shipping: The importance of intraregional transport. *Biological Conservation, 102*, 143–153. https://doi.org/10.1016/S0006-3207(01)00098-2

Werding, B., & Sanchez, H. (1991). Life habits and functional morphology of the sediment infaunal sponges Oceanapia oleracea and Oceanapia peltana (Porifera, Haplosclerida). *Zoomorphology, 110*, 203-208. https://doi.org/10.1007/BF01633004

Wulff, J. L. (2006). Ecological interaction of marine sponges. *Canadian Journal of Zoology,* *84*, 146-166. https://doi.org/10.1139/z06-019

Xue, L., Zhang, W. (2009). Growth and survival of early juveniles of the marine sponge Hymeniacidon perlevis (Demospongiae) under controlled conditions. *Marine Biotechnology, 11*, 640–649. https://doi.org/10.1007/s10126-009-9180-7

Yahel, G., Marie, D., & Genin, A. (2005). InEx — a direct in situ method to measure filtration rates, nutrition. *Limnology and Oceanography: Methods., 3*, 46–58. https://doi.org/10.4319/lom.2005.3.46

Zhang, X., Zhang, W., Xue, L., Zhang, B., Jim, M., & Fu, W. (2010). Bioremediation of bacteria pollution using the marine sponge Hymeniacidon perlevis in the intensive mariculture water system of turbot Scophthalmus maximus. *Biotechnology and Bioengineering, 105*(1), 59-68. https://doi.org/10.1002/bit.22522