Aquatic Invasions 2025 Volume 20, Issue 1: 33–51

Research Article

Temporal patterns of the introduced sponge *Hymeniacidon perlevis* (Montagu, 1814) in the Elkhorn Slough, California, USA

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OPEN ACCESS

Academic editor: Thomas Therriault
Received: 13 November 2023
Accepted: 15 November 2024
Published: 15 April 2025

Co-Editors' Note: This study was first presented at the 11th International Conference on Marine Bioinvasions held in Baltimore, Maryland, USA, May 15–19, 2023 (http://www.marinebioinvasions.info). Since their inception in 1999, the ICMB meetings have provided a venue for the exchange of information on various aspects of biological invasions in marine ecosystems, including ecological research, education, management and policies tackling marine bioinvasions.

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Abstract

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 of *H. perlevis* on its environment, and how those could vary across its seasonal life cycle. We found that 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 two years, we estimated that *H. perlevis* biomass and potential for water filtration are greatest in fall—corresponding with peak cover, and weakest to nonexistent in the spring. Understanding the seasonal and interannual dynamics of the *H. perlevis* population in Elkhorn Slough can inform future approaches to manage or mitigate its ecological impacts.

Key words: Porifera, Elkhorn Slough, estuary, non-indigenous species, recruitment, phenology, seasonal dynamics

Introduction

Non-native species all have potential to negatively affect their surrounding ecosystems. For example, introduction of the colonial tunicate *Didemnum vexillum* Kott, 2002 to Europe and North America has disrupted aquaculture efforts through aggressive growth over equipment and sessile stocks such as bivalves (Bullard et al. 2007; Switzer et al. 2011; Çinar and Özgül 2023). Non-native suspension feeders also may greatly affect ecosystems by altering nutrient cycling and food webs.

Citation: Hoeke JT, Wasson K, Kahn AS (2025) Temporal patterns of the introduced sponge *Hymeniacidon perlevis* (Montagu, 1814) in the Elkhorn Slough, California, USA. In: Fowler A, Robinson T, Bortolus A, Canning-Clode J, Therriault T (Eds) Proceedings of the 11th International Conference on Marine Bioinvasions. Aquatic Invasions 20(1): 33–51. https://doi.org/10.3391/ai.2025.20.1.145912

For instance, introduction of zebra and quagga mussels *Dreissena polymorpha* (Pallas, 1771) and *Dreissena bugensis* (Andrusov, 1897) to the North American Great Lakes greatly reduced spring blooms and primary productivity (Vanderploeg et al. 2010; Rowe et al. 2015). Understanding spatial and temporal dynamics of non-native species enables more effective management strategies for controlling their spread and limiting potential damage (Klein and Verlaque 2009; Giménez et al. 2020; Kamiyama et al. 2021; Reznik et al. 2022).

Sponges are filter-feeding aquatic and marine organisms that graze on dissolved organic material (DOM), bacteria, diatoms, and ciliates (Gili and Coma 1998; Maldonado et al. 2010). Within benthic communities, sponges can convert material and energy from the water column into biomass on the substrate, a process known as benthic-pelagic coupling (Gili and 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 sponge (Class Demospongiae) that lives in temperate intertidal and subtidal habitats (de Laubenfels 1932) (although in the Elkhorn Slough it has only been observed in intertidal habitats). 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 (Turner 2020; Samaai et al. 2022). 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 including *Hymeniacidon perlevis* is Elkhorn Slough in central California. Elkhorn Slough is a small 1200 ha estuary, with a maximum depth of 7.5 m at its mouth (beneath the Highway 1 bridge) and an average depth of 1.4 m (Caffrey et al. 2002b). This ecosystem is situated in the center of Monterey Bay (36.8N, 121.7W) and 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, which now connects Monterey Bay directly to Elkhorn Slough (Caffrey et al. 2002b). *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 on 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. Exotic oyster culturing in 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), the mud snail *Batillaria attramentaria* (G. B. Sowerby II, 1855), and three other introduced sponges: *Cliona celata* Grant, 1826, *Halichondria* (*Halichondria*) *bowerbanki* Burton, 1930, and *Chalinula loosanoffi* (Hartman, 1958) (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 and Hughey 2013) suggest the species was introduced to Japan and subsequently

brought to the slough through fouling on Japanese oysters, a route also suggested for other regions along the west coast of North America (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 (Juniper and Steele 1969; Stone 1970; Cao et al. 2007; Gaino et al. 2010; Cao et al. 2012). Their morphology can change across the year, from massive and encrusting in summer to creating raised oscula and long, thin projections in winter (Cao et al. 2012). The phenology of *H. perlevis* is unknown in Elkhorn Slough but given variations in other regions, including along the west coast of North America in British Columbia (Harbo et al. 2021) 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 *Hymeniacidon perlevis*, less clear is how, or which, environmental conditions 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 et al. 2002a, Caffrey et al. 2002b, 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 (Cao et al. 2007) and thrives in Elkhorn Slough despite muddy substrate and high suspended particulate loads (Caffrey et al. 2002b). A congener, *H. heliophilia* (Wilson, 1911), 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 and 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 warmer 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 *Hymeniacidon 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. To address this knowledge gap, we documented the introduction and spread of *H. perlevis* in the intertidal zone of Elkhorn Slough, CA over 25 years from 1998 to 2023 through analysis of recruitment across a long-term dataset. 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 and can have the strongest impacts to the Elkhorn Slough ecosystem in fall.

Methods

We studied interannual population dynamics and the spread of *Hymeniacidon perlevis* throughout the slough using annual monitoring of fouling plates. We studied seasonal population dynamics by measuring sponge cover monthly across two years. We explored correlations with environmental data from instrument arrays within Elkhorn Slough. Finally, we calculated the range of change in sponge biomass and water processing by relating sponge cover to mass of wet, dry, and combusted tissue, and by measuring sponge pumping rates.

Annual recruitment patterns of *Hymeniacidon perlevis* in Elkhorn Slough

Annual recruitment of *Hymeniacidon perlevis* on fouling plates was monitored across six primary sites from 2007 to 2023, with 4 additional sites surveyed 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) (Suppl. material 1: fig. S1) were deployed across ten sites and replaced in May or June annually (Suppl. material 1: fig. S1, 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.

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. Sites were selected based on their proximity to an NERR water monitoring instrumentation array, accessibility by foot, substrate variability, and previously recorded observations of *Hymeniacidon perlevis* (Fig. 1C). Surveys were undertaken by dividing each site into 1 m wide transects, then photographing a 1 × 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 (Schindelin et al. 2012) (Suppl. material 1: fig. S2). Monthly mean sponge cover was calculated by randomly selecting 38 quadrats from each site to 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.

Table 1. Sites with fouling plate deployments, including latitude and longitude, tidal height at which plates were deployed, and years deployed. Sites are ordered from upper to lower estuary. Abbreviations: MLLW – Mean Lower Low Water.

Site (abbreviation)	Latitude, Longitude	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

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. Five 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 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. Five 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 rapid 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. Three 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 20× loupe.

Correlation between environmental parameters and sponge cover

Publicly available National Estuarine Research Reserve (NERR) monitoring data collected from two YSI EXO2 multiparameter instruments (Fig. 1C) in the Elkhorn Slough were downloaded from the Centralized Data Management Office (https://cdmo.baruch.sc.edu/). Monthly average air temperature (°C) and total monthly precipitation (mm) were recorded from Caspian Weather Station. Monthly (day 01–31) averages for water 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 sponge cover.

Measurement of pumping and volumetric flow rates

To estimate the total volumetric flow from all sponges at a given site, cover was related to pumping rates measured from individual sponge oscula 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 cm^2 of sponge (n = 22). Average osculum size (cm^2) was measured by randomly selecting a single osculum from each cm^2 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):

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

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 *Hymeniacidon 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). (Suppl. material 1: fig. S3). A similar relationship was

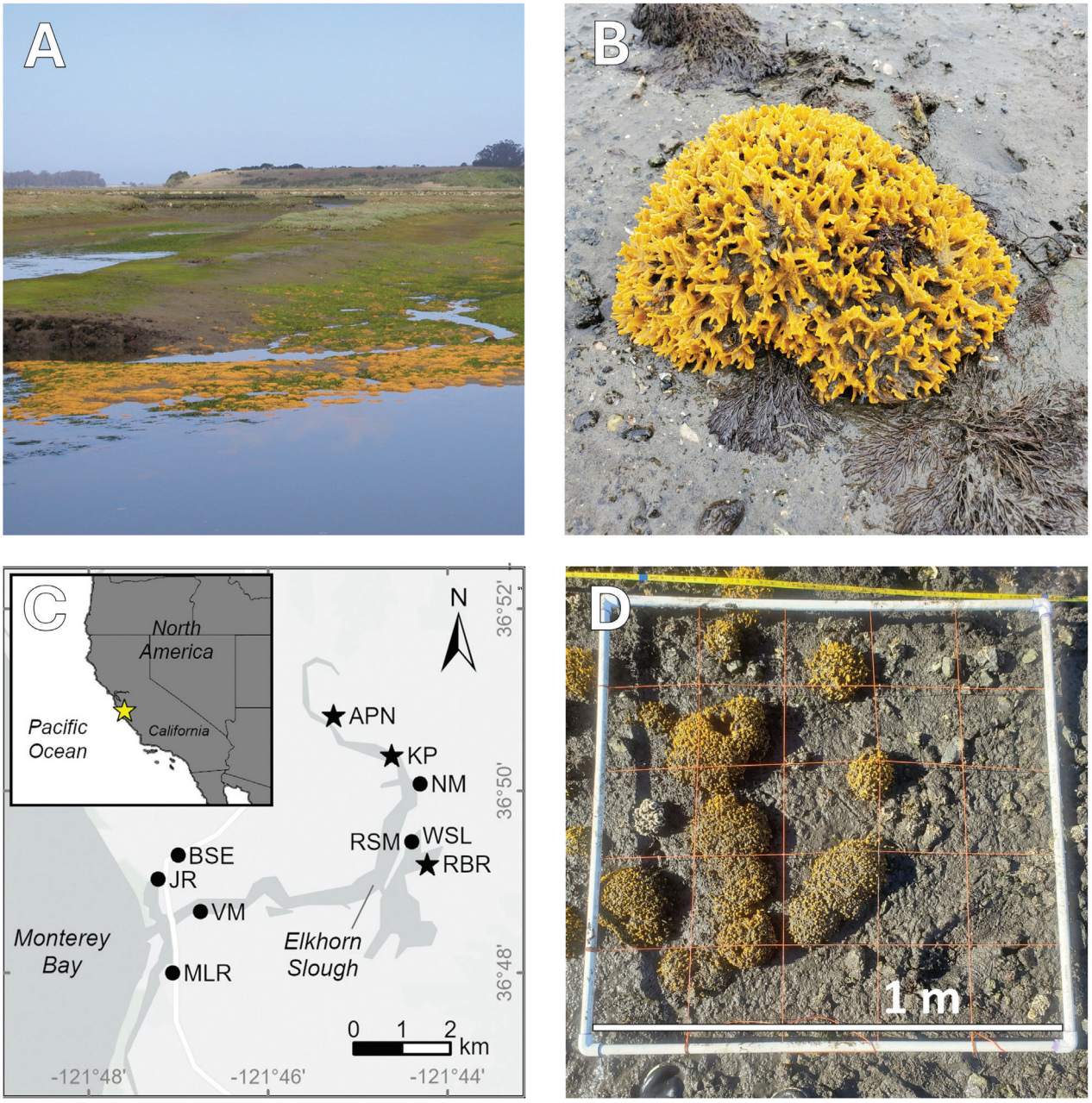

Figure 1. Scale of *H. perlevis* introduction in Elkhorn Slough. **A**. A large aggregation in South Marsh; **B**. A large individual exposed at low tide; **C**. Map of Elkhorn Slough, CA with monthly monitoring sites marked with stars and long-term monitoring sites marked with dots. APN: Azevedo Pond; 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 1 × 1 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.

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 (Suppl. material 1: fig. S3).

Estimating volumetric flow and biomass by scaling morphometric 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.

Results

Annual recruitment patterns of *Hymeniacidon perlevis* in Elkhorn Slough

Settlement plates used to track the spread of *Hymeniacidon perlevis* through Elkhorn Slough showed a generally growing and expanding population over a period of 17 years, but with variation across sites and years (Fig. 2, Suppl. material 1: fig. S4, Suppl. material 2: table S1). When initially discovered in 1998, *H. perlevis* was found across 200 m of shoreline parallel to the main channel. At its greatest extent, from 2019 to 2021, it was found across 3.5 km of shoreline. In 2023, this range reduced to 2.3 km of shoreline. *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 also been no anecdotal observations from any researchers in the Elkhorn Slough reported since 2014 either, suggesting that recruitment has not occurred in significant numbers (Suppl. material 2: table S1). While *H. perlevis* has successfully spread upstream within Elkhorn Slough, there is no evidence it has moved seaward, with its lowermost extent remaining at the RBR site, approximately 4.7 km from the mouth of the slough. 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 (Fig. 3). 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 (Fig. 3, Suppl. material 2: table S2). 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 in Elkhorn Slough 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, 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 (Fig. 3, Suppl. material 2: table S2), reaching a maximum in late fall and minimum in the spring.

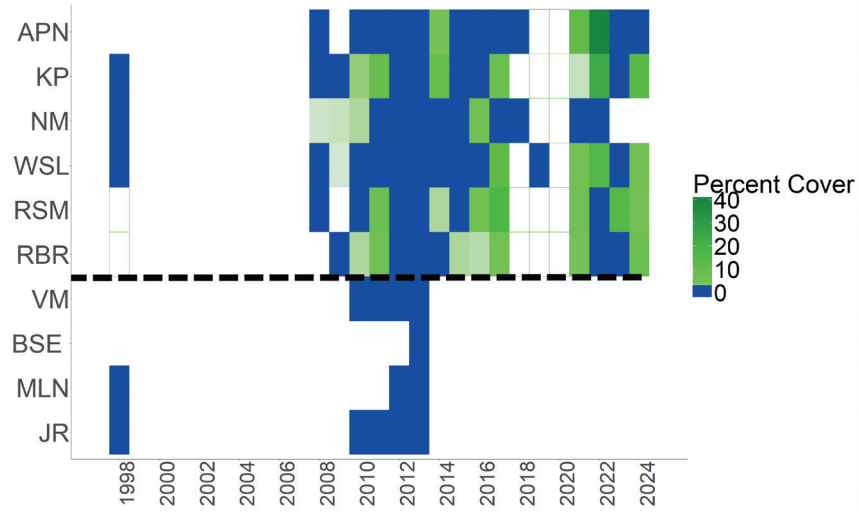

Figure 2. *Hymeniacidon perlevis* detections from settlement plates at several sites within Elkhorn Slough over time. The shaded area represents the mean cover of sponges on annual recruitment plates at each site. Blue indicates that no plates deployed at a site were colonized that year, and green represents colonization occurred that year. White represents a period of no sampling at a site, open green boxes indicate *H. perlevis* presence, but no cover data were recorded. Sites are ordered from upper to lower estuary, with lower slough sites beginning at VM (Vierra Mouth).

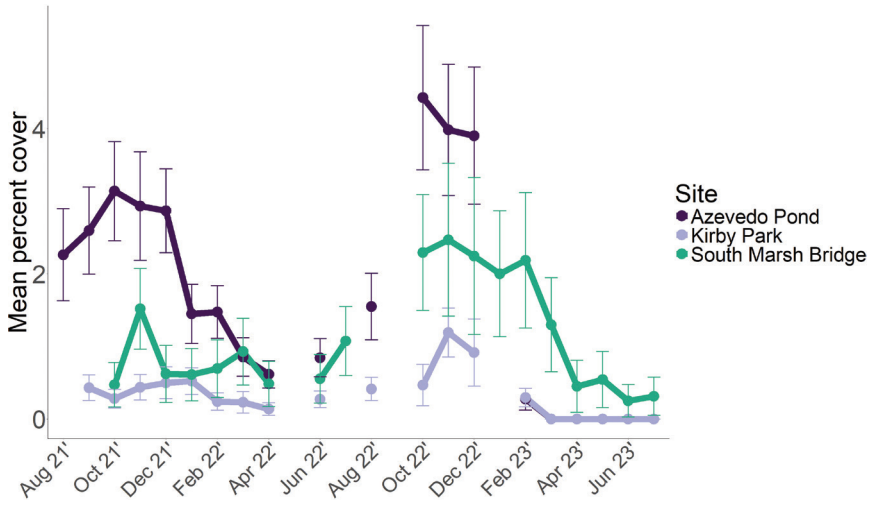

Figure 3. Mean percent cover (± standard error) of *H. perlevis* from three sites over two years of monitoring. Note overlap of Azevedo Pond and Kirby Park sponge cover, as both had 0% cover from March 2023 to July 2023.

Correlation between water quality parameters and sponge cover

Monthly variations in sponge cover were found to lag behind changes in environmental conditions (Table 2). The strongest cross-correlations between several environmental variables and sponge cover at APN, KP, and RBR occurred 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 2). A strong positive correlation was observed between sponge cover and temperature (measured from both water surface and atmosphere) 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 significantly correlated with sponge cover at KP ($p = 0.02$) (Table 2).

Table 2. Correlations between sponge cover and environmental variables. 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/). Spearman-ranked cross-correlations were calculated 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).

Parameter	Azevedo Pond			Kirby Park			South Marsh Bridge		
	Lag (Months)	rho	p	Lag (Months)	rho	p	Lag (Months)	rho	p
Water 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
Atmospheric temperature	**2 and 3 ***	**0.82**	**0.01**	**3 and 4 ***	**0.82**	**0.03**	**3**	**0.83**	**0.02**

* Indicates that a similar correlation coefficient occurred with both a 3- and 4-month time lag.

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 *Hymeniacidon perlevis* cover within each site. The quantity of water processed and sponge biomass changed seasonally (Fig. 4, Suppl. material 2: table S3). *H. perlevis* populations from these three sites in Elkhorn Slough had on average 2.36 ± 0.28 oscula cm^{-2} sponge area when viewed from above (n = 22, mean ± SE). The average size of each osculum was 0.65 ± 0.08 mm^2 (n = 22). The average volume pumped by an active osculum, measured by the dye front method, was 31 ± 3 mL h^{-1} (n = 10).

To estimate potential variation in seasonal biomass and water filtration, we first assessed relationships between several morphometric measurements (Suppl. material 1: fig. S3). A single cm^2 of *Hymeniacidon 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 cover. 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 (0.024 ± 3.5 kg m^{-2} to 0 kg m^{-2}), and RBR sponges pumped 18 ± 8 L h^{-1} m^{-2} in November 2022 to 9 ± 5 L h^{-1} m^{-2} in March 2023 (0.05 ± 7 kg m^{-2} to 0.03 ± 4 kg m^{-2}) (Suppl. material 2: table S3). 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 ± 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

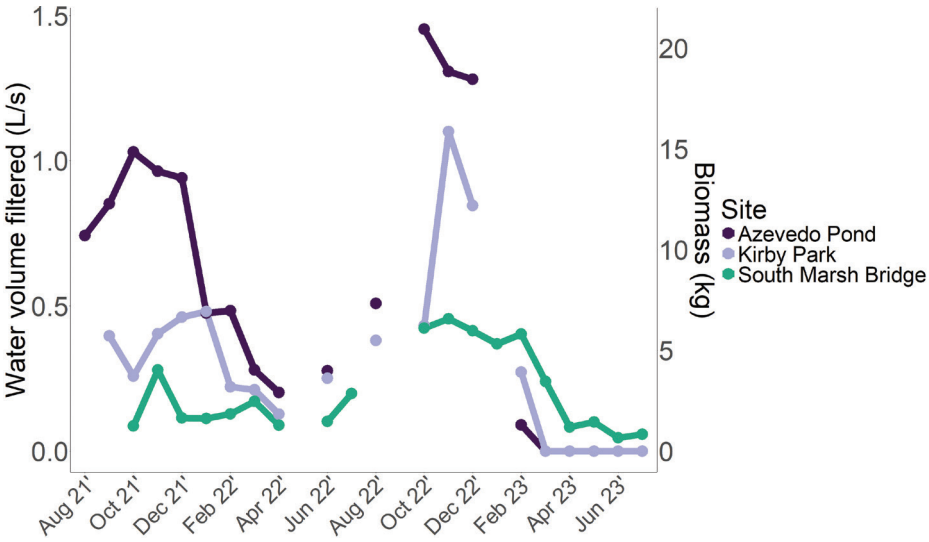

Figure 4. Estimates of volume of water filtered and biomass,calculated using *H. perlevis* cover data within each sample site. Error bars are not shown due to excessive size.

of 0.46 ± 0.21 L s^{-1} with 4.6 ± 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 0.24 ± 0.12 L s^{-1} pumped and 2.4 ± 340 kg of sponge biomass (Suppl. material 2: table S3).

Discussion

As a cosmopolitan species, *Hymeniacidon perlevis* is abundant in areas throughout the world. Its spread in areas like Elkhorn Slough, and the seasonal changes we observed in its cover, biomass, and filtration, may inform future strategies to mitigate its impacts.

Annual recruitment patterns of *Hymeniacidon perlevis* in Elkhorn Slough

From 2008 to 2022, recruitment varied, as is typical for many species (Connell 1985; Menge and Sutherland 1987), but there was a general increase in the number of sites, frequency, and cover of *Hymeniacidon 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 (Suppl. material 1: fig. S5); APN is even considered "hypereutrophic" (Hughes et al. 2011), and also has the greatest levels of *H. perlevis* cover. In a study near an inland fish farm, *H. perlevis* grew faster and more densely in the eutrophic outflow water of the 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 (Fig. 2). 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.

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 contrast, populations in the Yellow Sea and United Kingdom reach peak biomass earlier, in September (Juniper and Steele 1969; Stone 1970; Cao et al. 2007; Cao et al. 2012). 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 (Werding and Sanchez 1991; Ilan and Abelson 1995; Rützler 1997; Schönberg 2015).

Temperature may in part explain differences in *Hymeniacidon 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 (Cao et al. 2012). The minimum water surface temperature in Elkhorn Slough across this study period was 4.5 °C, much closer to the recorded temperatures in the English Channel. Air temperature at Elkhorn Slough was generally temperate but occasionally reached freezing in February and April of 2022, with -0.5 °C the lowest recorded temperature during April 2022. 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. 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 et al. 2002b). 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 *Hymeniacidon 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 or survive prolonged exposure. However, the only significant statistical correlation with precipitation was at KP, where sponge cover lagged 1 month behind. Other parameters, most notably temperature, have been implicated in driving *H. perlevis*' phenology due to correlation with cover (Stone 1970; Gaino et al. 2010; Cao et al. 2012), 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 *Hymeniacidon 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 *Hymeniacidon 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 (Fig. 4, Suppl. material 2: table S3), 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 *Hymeniacidon 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; Maldonado et al. 2010; Zhang et al. 2010; Longo et al. 2022), 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 et al. 2002a, Caffrey et al. 2002b, 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 other species

Hymeniacidon 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 of sponges can alter a boundary layer that provides unique overlying habitat (Gili and Coma 1998). The sponges may also serve as novel habitat: amphipods and polychaetes were seen within the tissues. 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 and Turco 2023) to predatory/parasitic (Magnino and 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. Recent experimental evidence suggests that brittle stars, polychaete worms, crabs, and fish all act as spongivore predators on *H. perlevis* in Argentinian Patagonia where it has also been introduced (Buch et al. 2024). Species that might consume *H. perlevis* in Elkhorn Slough are unknown, though observations from British Columbia suggest that the native nudibranch *Doris montereyensis* Cooper, 1863 grazes on *H. perlevis* (Harbo RM, *personal communication*). While the sponges, as novel, seasonally available habitat and prey may shelter and/or provide food for invertebrate and fish species, the improvised nature of these relationships suggests they may be subject to rapid change. *H. perlevis* may provide distinct food and habitat compared to other Elkhorn Slough sponges, including the introduced *Cliona celata* Grant, 1826, *Halichondria* (*Halichondria*) *bowerbanki* Burton, 1930, and *Chalinula loosanoffi* (Hartman, 1958), the cryptogenic *Haliclona* (*Reneira*) *cinerea* (Grant, 1826), and unidentified *Topsentia* sp. Berg, 1899, as well as the native *Halisarca sacra* de Laubenfels, 1930 and *Mycale* (*Mycale*) *macginitiei* de Laubenfels, 1930 (Wasson et al. 2001; Caffrey et al. 2002b).

The spectrum of impacts described above complicate an assessment of whether *Hymeniacidon 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 sponges are 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 for predicting 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.

Conclusions

This is the first study to systematically document the abundance and distribution of *Hymeniacidon 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 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 air and water temperature, dissolved oxygen, and salinity. However episodic events like the 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.

Funding Declaration

This research was supported by the 2021 CSU Council on Ocean Affairs, Science, and Technology Graduate Student Research Award (# CSUCOAST-HOEJAC-SJSU-AY2021), the Dr. Earl H. Meyers and Ethyl M. Meyers Oceanographic & Marine Biology Trust, the 2023 James Nybakken Scholarship, the 2023 MLML Wave Award, and a CSUBIOTECH research development grant to ASK. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Author Contributions

JTH: field study, conceptualization, sample design, methodology, investigation and data collection, data analysis and interpretation, writing and editing the manuscript; KW: field study, data collection, sample design, editing the manuscript; ASK: conceptualization, sample design, methodology, data interpretation, editing the manuscript.

Ethics and Permits

Samples were collected under California Department of Fish and Wildlife permit #S-210260011-21049-001.

Acknowledgements

We thank K. Duncan for her support with data collection, K. Guillas for contributing data of sponge pumping rates, and we thank S. Smith and two anonymous reviewers for suggestions and constructive feedback that improved the manuscript.

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Supplementary material 1

Additional images

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Data type: docx

Explanation note: **fig. S1.** Replicate ceramic plates. **fig. S2.** Traced polygons in ImageJ. **fig. S3.** Morphometric relationships for *H. perlevis*. **fig. S4.** *H. perlevis* fouling plate trends. Percent cover of the six fouling plate deployment sites that received any *H. perlevis* recruits throughout the entire sampling regime. **fig. S5.** Environmental data of monthly dissolved oxygen, pH, precipitation, salinity, temperature, and turbidity from NERR data monitoring stations, and high-resolution *H. perlevis* cover.

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Link: https://doi.org/10.3391/ai.2025.20.1.145912.suppl1

Supplementary material 2

Additional tables

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Data type: docx

Explanation note: **table S1.** List of years that *H. perlevis* was detected or not at each sampling site. **table S2.** Dates of peak and minimum sponge cover shown at three sites in Elkhorn Slough, CA. **table S3.** Peak and minimum pumping rates and biomass at three sites in Elkhorn Slough, CA.

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