



Long-term observations of a sponge *in situ* reveal a rich repertoire of contractile behaviors, including winter dormancy

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ABSTRACT: Sponges are remarkably active animals with a range of behaviors that are broadly termed sneezes. Little is known about what triggers sneezes or how sneezes propagate in an animal that lacks either muscular or nervous systems. We explored the triggers of sponge behavior *in situ* in the demosponge *Suberites concinnus*. The placement of this tennis ball-sized sponge at the focal point of a camera array on an instrument platform in Barkley Sound, BC, Canada, provided a unique opportunity for our investigation. The observatory has a suite of environmental sensors measuring parameters such as photosynthetically active radiation (PAR), oxygen, turbidity, salinity, pressure, current speed, and temperature. An array of 8 cameras designed for 3D imaging was used to capture hourly images. Our findings revealed both long-term (annual) and short-term (daily) behaviors in *S. concinnus*. The sponge contracted for 2 mo each winter. In February, it gradually expanded and became very active with short-term full-body contractions each lasting 11 h through the summer. A meta-analysis of contraction behaviors in other species of sponge showed that contraction duration is a factor of sponge size and that all sponges contract faster than they expand. Invertebrates and fish were frequently in contact with the sponge, but no single interaction was found to correlate with patterns of sponge behavior. However, significant correlations between sponge behaviors and chlorophyll and turbidity were found using generalized additive mixed models. Our study underscores the dynamic nature of these sessile filter feeders and their responses to their environment.

KEY WORDS: Demosponge · *in situ* time series · Sponge behavior · Winter dormancy · Interspecific benthic communities

1. INTRODUCTION

Sponges are well-known as sedentary filter feeders, but recent work showing that they also have coordinated, whole-body behaviors, such as crawling to areas of better food and sneezing to get rid of wastes, challenges the perception of their immobility (Morganti et al. 2021, Kornder et al. 2022). The extent to which these types of behaviors are exceptional or typical, as well as their functional significance, remains uncertain. Porifera are placed at the base of the

metazoan tree, having evolved approximately 600 to 800 million yr ago (Wörheide et al. 2012, Schultz et al. 2023). The absence of a nervous system and conventional muscles in sponges could be considered either a primitive trait or an early adaptation for energy efficiency in the diverse aquatic environments they inhabit (Leys et al. 2019).

While some sponges are mobile and can move over short distances to enhance feeding or reproduction (Bond & Harris 1988, Maldonado & Uriz 1999, Morganti et al. 2021), most have functionally evolved

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to a sedentary lifestyle of filter feeding and must adapt to their surrounding environmental conditions effectively (Maldonado et al. 2012). This adaptation is evident in both their morphological traits and behavioral responses. For example, empirical observations indicate that the more a sponge filters, the greater the energy it expends (Ludeman et al. 2017), and the amount filtered is directly related to the size of the excurrent chimney, the osculum (Morganti et al. 2019). Presumably then, when a sponge contracts it is reducing its filtration activities, and this may be beneficial when the available food supply is insufficient to sustain the energetic requirements associated with filtering.

Sponges filter large amounts of water, up to 1000 times their volume every hour, removing up to 95% of the bacteria and particulates for food (Reiswig 1974, Yahel et al. 2003, Ludeman et al. 2017, Leys et al. 2018). Such efficient filtration demands a steady water supply to bring new food, either through significant water volume or water currents (Kahn et al. 2015). The presence of other filter feeders can lead to competition for resources (Aerts & van Soest 1997). Sponges cope with this competition by consuming distinct food sources like bacteria, which may not be available to other filter-feeding animals. In certain cases, large sponge aggregations or bigger individual sponges rely on symbiotic relationships to supplement their food intake, such as *Geodia* beds in the North Atlantic or *Xestospongia* in the Caribbean (Maldonado et al. 2016).

Whether sponges also respond behaviorally to changes in their local environment over different seasons has been little studied, largely because of the challenge of working *in situ* during the inclement weather of winter seasons. However, a couple of studies have investigated the mechanics and metabolic rates associated with sponge behavior over time. For example, pioneering work by Reiswig (1971) showed gradual reduction in pumping by several Caribbean sponges as winter approached. A study by Coma et al. (2002) found that respiration rates of a sponge were lower in winter than summer. Both responses were attributed to either reduced food supply or winter storms. Behavioral responses to tidal changes (Parker 1910, 1919), systemic contractions (Weissenfels 1990, Nickel 2004), and responses to direct stimuli (Elliott & Leys 2007, 2010, Kumala et al. 2017, Kumala & Canfield 2018) have long been documented in sponges. However, determining the primary environmental factors that trigger temporal behavior in these sessile and sedentary animals remains an important question.

We aimed to carry out long-term observations on the behavior of sponges by taking advantage of the Ocean Networks Canada (ONC) NEPTUNE Observatory, which established a long-term sub-sea monitoring station at Folger Pinnacle in Barkley Sound, British Columbia, Canada, in October 2012. The observatory is a powered underwater network that allows continual and real-time data collection at specific locations. When the Folger Observatory was established, an experimental 3D camera system was mounted on the main instrument platform and carefully placed on the seafloor adjacent to a tennis ball-sized demosponge, *Suberites concinnus*. This sponge's position enabled us to capture hourly photographs of its behavior and of interactions of other animals with the sponge over a 4 yr period (2012–2015). On the instrument platform, other oceanographic sensors captured the immediate and local-scale environmental variables with a high temporal resolution. In an initial analysis of the image data, we developed an automated semantic segmentation machine learning algorithm to precisely distinguish the sponge from the background, enabling accurate measurement of changes in body size over time (Harrison et al. 2021). That work revealed that this seemingly sessile sponge, which we nicknamed 'Belinda' to prevent confusion with other individuals of the same species found locally in Barkley Sound, exhibited remarkable activity, characterized by rhythmic contractions that appeared to be responding to unidentified triggers.

In the present study, our goal was to understand whether environmental factors are associated with the behavior of the sponge. We used the image data together with the multivariate oceanographic data from the instrument platform to make predictive and explanatory analyses concerning the drivers behind *S. concinnus*' behavior. We hypothesized that long-term behavioral patterns are linked to seasonal triggers, while sporadic short-term behaviors may be responses to the stochastic nature of the marine community immediately surrounding the sponge, such as eliminating accumulated debris on the sponge or movement of neighboring mobile benthic organisms.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted at the Folger Pinnacle, an isolated feature rising from 100 to 25 m depth at the southeast entrance of Barkley Sound, on the west coast of Vancouver Island, Canada (Fig. 1). The loca-



Fig. 1. Folger Pinnacle observatory location on the Pacific coast of Canada as part of the multi-node NEPTUNE fiber optic cabled observatory. Base map shows the study site positioned at the southwest entrance of Barkley Sound, on the west coast of Vancouver Island, Canada. Inset map (top-left) highlights the camera and multi-instrument platform location atop of the pinnacle at 25 m depth (textbox lists the equipment and number of devices on the Folger Pinnacle observatory platform)

tion is 10 km west of the Bamfield Marine Science Center, and has benthic habitats characterized by rocky substrates colonized by a dense and diverse assemblage of macroalgae, hydrozoan corals dominated by *Stylianthea* sp., and other benthic invertebrates (Porfirio et al. 2017). The seafloor substrates and benthic fauna at the pinnacle, despite being more exposed to offshore circulation and wave action, are representative of the relatively well-studied Barkley Sound, which also includes a number of small islands. The area is within the boundaries of the 'Folger Passage Rockfish Conservation Area', one of a network of rockfish conservation areas (Haggarty & Yamana 2018) established by Fisheries and Oceans Canada (Dunham et al. 2020).

The shallow pinnacle is subject to very dynamic oceanographic conditions that vary between seasons

(Pawlowicz 2017). A 10 yr time series of monthly hydrographic stations reveals a standard estuarine circulation in surface and near-surface waters of Barkley Sound, as well as a deep renewal cycle in intermediate and deep waters. The deep basin in the Sound undergoes annual summer renewals in response to wind-driven upwelling on the shelf, separated by stagnation and hypoxia during fall, winter, and spring downwelling periods (Pawlowicz 2017). The onset of deep renewal and subsequent reversal of alongshore winds appear to minimally impact phytoplankton biomass but exhibit responsiveness to local factors, revealing that the uncoupling of inter-annual variations in temperature, density, and dissolved oxygen from the seasonal cycle may be ascribed to longer-term shifts in offshore source water characteristics and/or alterations in shelf processes (Pawlowicz 2017).

2.2. Instrument platform at the Folger Pinnacle, NEPTUNE cabled observatory

On 19 October 2012, an instrument platform with cameras and a suite of oceanographic instruments and sensors were installed at 25 m depth on the Ocean Networks Canada (ONC) Folger Pinnacle monitoring site within the multi-node NEPTUNE fiber optic cabled observatory (Fig. 1). The system was composed of an array of 8 high-definition video cameras (Teledyne Grasshopper GRAS-50S5C model), capable of taking 5 megapixel images. The cameras were evenly distributed around a 30 cm radius semi-circle (180°) allowing 3D image reconstruction; at the time of deployment, a sponge, *Suberites concinnus*, was chosen as the focal point of all 8 cameras (Fig. 2; Yau 2014). Two 30W AGO LED lights with a combined 3960 lumen output provided illumination during image capture.

Despite having copper rings around the glass cover of the lenses, in spring and summer months fouling

organisms (e.g. barnacles and bryozoans) covered the field of view and the camera lenses required manual cleaning by SCUBA divers. Since maintenance of the subsea infrastructure was dependent on weather conditions, camera cleaning took place at irregular intervals. Quite noticeably, biofouling occurred faster after cleaning took place in late spring or summer. The above environmental conditions generated 6 periods of variable lengths in which images were of sufficient quality with the least biofouling, which we called 'time-lapse' (TL) periods—TL1 through TL6 (Fig. 2A,B). Variable biofouling among the different cameras also forced the selection of a single camera, which was the least affected by growth and therefore generated the highest number of high-quality images. Images were initially stored on a local sub-sea computer and then transmitted via fiber optic cable to the observatory shore station and finally to ONC's servers at the University of Victoria. Between November 2012 and August 2015, still images were captured at regular hourly intervals.

Oceanographic instruments that were attached to the platform and connected directly to the cabled observatory included 2 Acoustic Doppler Current Profilers, one positioned about a meter above the substrate and facing down over the camera array (Nortek 2MHz) and one facing up to profile the water column (RDI Workhorse Monitor 600kHz), both recording currents near the seafloor and up in the water column; a Conductivity, Temperature, Depth sensor suite (Seabird SBE19plus V2) recording temperature, pressure, and salinity; a Fluorometer (WET Labs ECO FLNTUS) which recorded chlorophyll and turbidity; a dissolved oxygen sensor (SeaBird SBE 63); and a Radiometer (Biospherical Photosynthetic Active Radiation [PAR] Irradiance QSP-2350L) recording daylight.

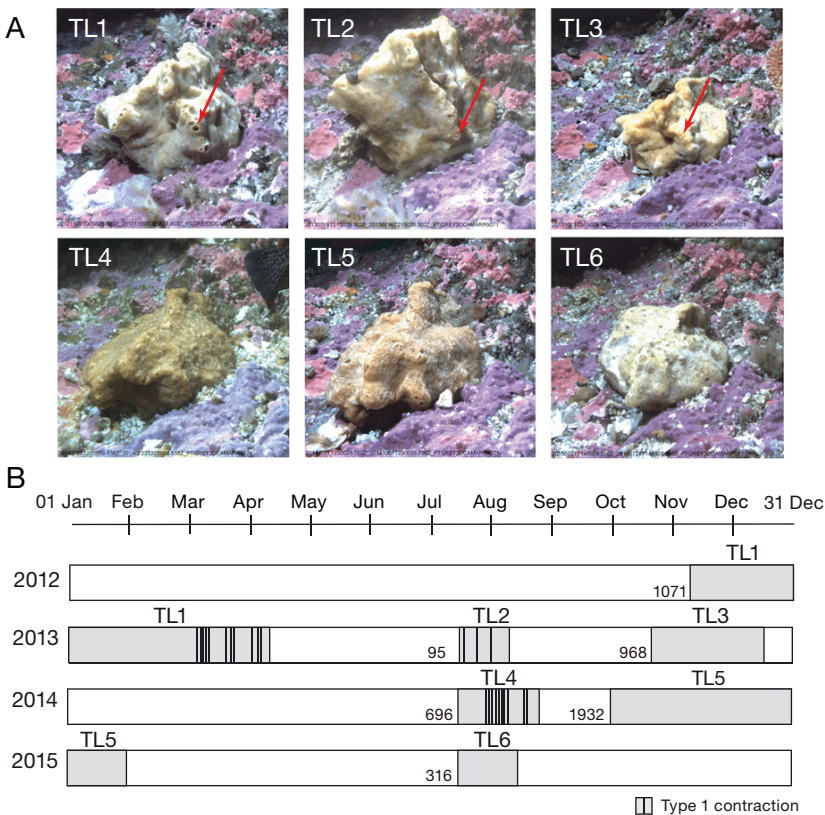


Fig. 2. (A) The view of *Suberites concinnus* captured from the first image of each time-lapse (TL) series. Red arrows indicate examples of open or closed oscula. (B) Periods covered by each TL series. Although images were captured throughout the 4 yr of deployment, images from only one camera remained free of biofouling during the periods indicated in gray, TL1 to TL6. Numbers preceding each gray bar indicate the number of images in each TL series

2.3. Image analysis

To study changes in size of the sponge over time, we used a machine learning algorithm based on convolutional neural networks (CNN) to extract the area of the sponge from the background in each image (Harrison et al. 2021).

To annotate the benthic animals that contacted the sponge during each TL series, the images were cropped from 2448×2048 pixels to 1500×1500 pixels (Harrison et al. 2021), and the image series was compiled into gif files that could be annotated frame by frame in ImageJ (FIJI v.1.53T) (image gifs are available as part of our data set at <https://doi.org/10.7939/r3-z7nh-6193>). The numbers of images in each TL series, TL1 through TL6, were: 1071, 95, 968, 696, 1932, 316 (Fig. 2B). Animals were identified to the lowest taxon possible. The cell counter plugin for ImageJ was used to count and identify every organism that was in direct contact with the sponge in each series. Counts of each type of animal were averaged for each day and week for analysis across season and year.

2.4. Analysis of sponge behavior and environmental variables

All oceanographic sensor data used in this study passed the standard quality assurance and control checks performed by ONC. The preprocessed data, which had removed any quality flags, of temperature, pressure, current velocity and direction, oxygen, salinity, chlorophyll, turbidity, and PAR were analyzed for the 6 designated TL periods (Fig. 2B). A data matrix including all the instrument sensor data, sponge area (in pixels), and the presence of benthic megafauna animals from the images across all 6 TL intervals was generated. To facilitate our investigation of individual data sets, we developed a visualizer tool from 'shinyapps' for some initial data exploration and manipulation (<https://ematveev.shinyapps.io/BelindaVisualizer/>). Quality flags were used to identify outliers that resulted from, for example, a fish moving directly in front of the camera, too much biofouling by barnacles, or on occasion an image that was corrupted due to interlacing issues. Outliers were removed from the final data set (<https://doi.org/10.7939/r3-z7nh-6193>).

The visualizer tool allowed us to view the activity of the sponge in a 2-dimensional format and allowed us to classify different patterns of behavior. Short-term behaviors involved a succession of contractions, each of which lasted several hours; these contractions were divided into categories for the analysis of contraction kinetics (see Section 2.4.1) depending on the rhythm and frequency of the contraction. There were 5 short-term behaviors that met the criteria of successive contractions, 3 in TL1 (TL1.1, TL1.2, TL1.3) and 2 in TL4 (TL4.1, TL4.2). Long-term behaviors lasted weeks to months but were not categorized further because resolution across all time series was patchy.

2.4.1. Sponge contraction kinetics

To quantify rates of contraction by the sponge, we first converted pixel/area to linear dimensions using the calibration scale of a cup coral (*Balanophyllia elegans*), estimated to be 0.5 cm in diameter, that appears in every image. We used 2 approaches to identify the beginning and end of contractions. First, a generalized additive model (GAM) line was fitted through the area data to smooth the overall patterns to remove long-term change effects. Then, points when an area point deviated by >90% from the fitted line were identified, i.e. if the fitted line is at 100 and the actual area is at 10, that would constitute a time when the sponge is in a contracted state (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m748p033_suppl.pdf). While this method was sufficient for identifying contraction events, some contractions were missed, for example, some reductions in the area of the sponge plotted on the visualizer reflected difficulties with the machine-learning algorithm due to fish or sea stars overlying a portion of the sponge. Therefore, in a second approach, we used the data visualization tool (described in the previous section) to identify periods when contractions began and ended, and confirmed the selection with the videos (Video series S1 [available at <https://doi.org/10.7939/r3-z7nh-6193>] & S2 [<https://www.youtube.com/playlist?list=PLIDwRK0-Sr9zBRNpNLR55eWolys-IP5OA>]; descriptions of each series are given in the Supplement). Resulting identifiable contracting behaviors were classified as full body contractions, twitches, and ripples, and were annotated for each time series for *S. concinnus* (Video series S2).

To compare the contraction kinetics of *S. concinnus* with contractions of other sponges, we gathered data on rates of contraction from the literature for *Tethya wilhelma* (Nickel 2004), *Ephydatia fluviatilis* (Weisenfels 1984), *Halichondria panicea* (Kumala et al. 2017), *Hyalonema bianchoratum*, and another unidentified hexactinellid species (Table 1 in Kahn et al. 2020). Data that were not tabulated in the above sources were extracted from graphs using the method described above for *S. concinnus*.

2.4.2. Analysis of environmental variables and sponge behavior

We built generalized additive mixed models (GAMMs) to analyze the temporal patterns of various contractions exhibited by *S. concinnus*, while also investigating potential relationships with environmental variables. The methodology used to build the

Table 1. Akaike's Information Criteria (AIC) table and generalized likelihood ratio test comparing generalized additive models (GAMs) for area of *Suberites concinnus* in each time-lapse (TL) series analyzed, with different temporal and environment covariates. Environment covariates include smooth terms for PAR (photosynthetically active radiation), pressure, oxygen, temperature, chlorophyll, and turbidity. Model number in **bold** represents the final model for each time lapse. (*) indicates significance at $p < 0.05$

Model 1: Area ~ s(Time) + Env. cov.					
Model 2: Area ~ s(Time) + s(Hour) + Env. cov.					
Model 3: Area ~ s(Time) + s(Hour) + ti(Time, Hour) + Env. cov.					
	Model	df	AIC	Test	p
TL1	1	20	7698.6		
	2	21	7695.5	1 vs 2	0.024*
	3	23	7687.4	2 vs 3	<0.002*
TL1 Spring	1	17	4817.9		
	2	18	4809.0	1 vs 2	<0.001*
	3	20	4813.0	2 vs 3	1.000
TL4	1	20	5033.4		
	2	21	4939.7	1 vs 2	<0.001*
	3	23	4940.8	2 vs 3	0.236
TL5	1	17	5126.3		
	2	18	4977.7	1 vs 2	<0.001*
	3	20	4979.8	2 vs 3	0.384

GAMMs models closely followed the guidelines described in Wood (2017). We used the package 'mgcv' v.1.9-1 (Wood 2011) in R v.4.4.1 environment (R Core Team 2023), which provides automated smoothing parameter estimates through built-in algorithms (Wood et al. 2016). Plots were made with 'gratia' R package v.0.9.0 (Simpson 2024) and fitted using the 'mgcv' package. The smoothness parameters were selected using restricted maximum likelihood estimation (REML) and the model was fit to a Gaussian distribution. GAMMs allowed us to explicitly define temporal autocorrelation structures (Lin & Zhang 1999) and offered the advantage of modeling daily and seasonal trends while accounting for residual temporal autocorrelation not captured by the covariates already included in the analysis.

Initially we modeled for sponge area (number of pixels) as a proxy for size, by incorporating all relevant environmental variables and time elapsed (or total time), daily hour, and their interaction as temporal terms. To verify autocorrelations, we examined the autocorrelation function (ACF) and partial ACF (PACF) plots on the residuals. As autocorrelations were present, we introduced an autoregressive (AR) correlation structure (Fig. S3). The order of the correlation structure and, subsequently, the temporal

terms were chosen by comparing models using Akaike's Information Criteria (AIC; Burnham & Anderson 2002) and analysis of deviance (Table 1).

GAMMs were only performed on TL1, TL4, and TL5 because for the other TL series, there were significant gaps in many of the environmental data or some of the periods were simply too short to capture any patterns of behavior. Each TL series above (TL1, TL4, and TL5) was modeled individually due to the lack of hourly data in-between these periods. For our analysis, the environmental variables were averaged in 1 h bins to match the same temporal resolution of the sponge images. The TL1 GAMM covered multiple seasons (fall through spring); however, to explore the increased activity after winter dormancy, we performed a GAMM on a subset of TL1 that included only spring (from 8 February 2013 to 13 April 2013). Additionally, to assess the relationships with the environmental variables, we performed Kendall's τ correlation analyses with the adjusted p-values using the Holm–Bonferroni method on the 5 short-term behaviors (TL1.1, TL1.2, TL1.3, TL4.1, and TL4.2) (Fig. S7).

3. RESULTS

3.1. General description of the behavior of the sponge *Suberites concinnus*

Suberites concinnus is an orange-red sponge, approximately the size of a tennis ball, but with an irregular shape. The species is common in Barkley Sound, British Columbia, where it lives in wave-swept rocky environments at depths as shallow as 5 m. The sponge is attached at its base, with a firm body and surface that is smooth to the touch. When relaxed, the sponge has lobes with ridges that have a string of small holes along the top, which are the exhalant openings (oscula) for water that is filtered by the sponge. The oscula are open when the sponge is fully expanded (e.g. Fig. 2A, red arrows in TL1 and TL2), and closed and invisible when the sponge is partially or fully contracted (e.g. Fig. 2A, red arrow in TL3).

Images captured by the camera array on the platform show that the sponge undergoes dynamic changes in size and shape on a daily, monthly, and seasonal basis, with some movements taking place over only a part of the body, and others involving the entire sponge. Short-term behaviors involved successive whole-body contractions during spring and summer (Fig. 3A–C), resulting in a reduction of the sponge to half its size each time it contracted. In contrast, long-term behaviors entailed a seasonal reduc-

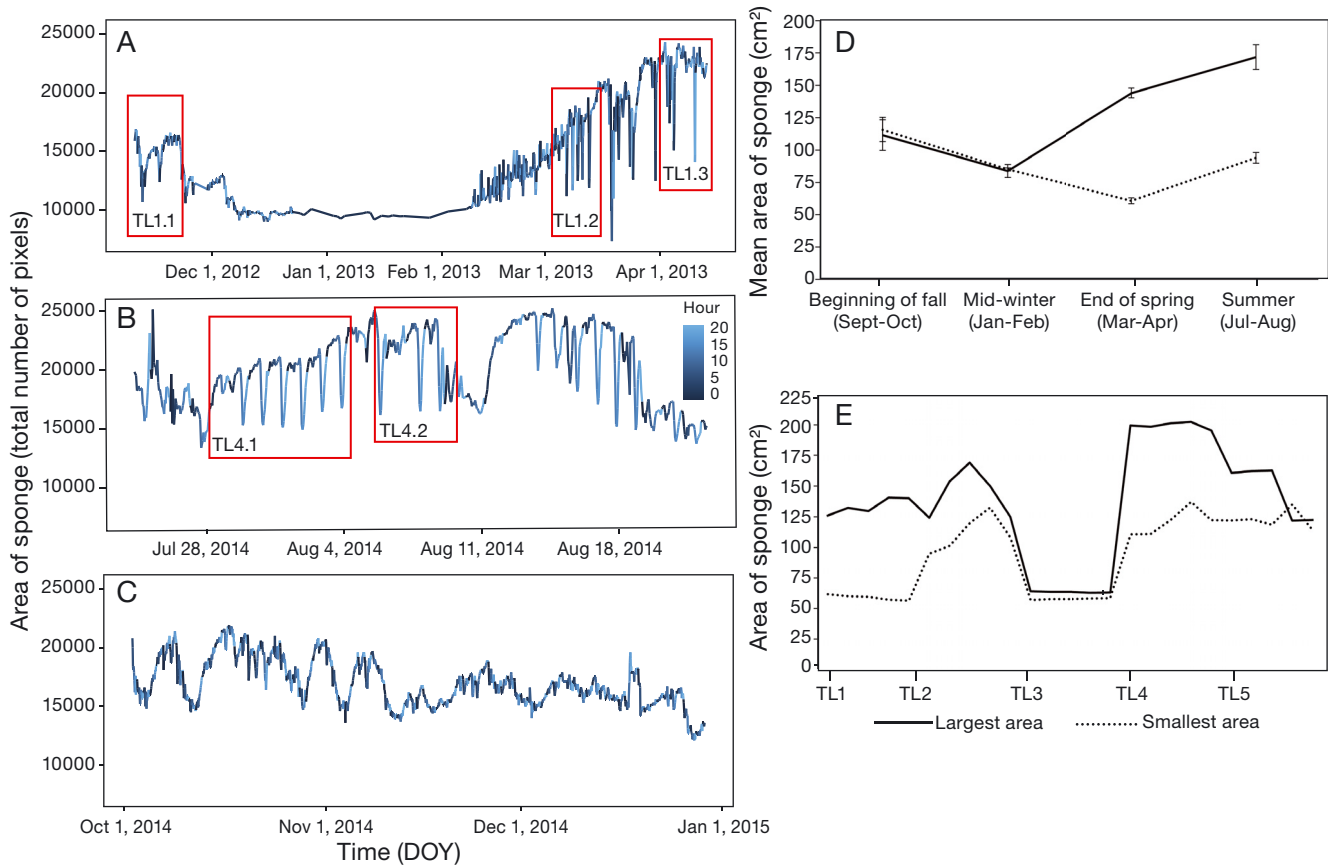


Fig. 3. Changes in *S. concinnus* area in (A) TL1, (B) TL4, and (C) TL5. Red boxes indicate the periods when the sponge carried out a series of Type 1 contractions. TL1.1 was between 9 and 16 November 2012, TL1.2 was between 4 and 14 March 2013, and TL1.3 was between 2 and 12 April 2013. TL4.1 was between 28 July and 8 August 2014 and T4.2 was between 8 August and 8 October 2014. The duration of each contraction is indicated using a blue-scale gradient color hue. (D) Seasonal comparison between *S. concinnus*' largest (solid line) and smallest (dotted line) size, illustrating the increased activity in the spring and summer months. Error bars: \pm SE. The mean for each season is as follows: beginning of fall, largest area = 223, smallest area = 188; mid-winter, largest area = 168, smallest area = 123; end of spring, largest area = 288, smallest area = 170; summer, largest area = 344, smallest area = 232. (E) Comparison of the largest (solid line) and smallest (dotted line) areas of the sponge, suggesting that the sponge becomes larger generally, over time

tion in sponge size beginning in late October or November, with the sponge remaining contracted throughout the winter months until it gradually expanded again in late February (Fig. 3D).

Over the 4 yr, when the cameras were installed on the platform, the sponge was smallest at the end of winter and largest in mid-summer (Fig. 3D; Table 2). The sponge also grew in size over time, as determined from its smallest contracted and largest expanded sizes (Fig. 3E; Table 2). Between 2012 and 2015, the sponge's color changed significantly from a pale orange-yellow with a smooth surface in August 2013 (TL2) to a dark orange and lumpy surface in August 2014 (TL4), and returned to a paler color, although still quite

lumpy, in August 2015 (TL6) (Fig. 2A). In addition, in August 2014, the sponge was transiently covered by a large amount of shelly debris that was removed from the surface within days. Although the camera system was removed from the platform at the end of 2015, images captured in 2022 during routine maintenance of the observatory platform by divers show the sponge

Table 2. *S. concinnus* sizes (area, cm²) over the seasons of each year

Season (N)	Dates	Largest mean	Largest SE	Smallest mean	Smallest SE
Start of fall (10)	Sep–Oct	111.48	11.75	93.96	9.37
Mid-winter (10)	Jan–Feb	83.81	5.03	60.91	1.24
End of spring (5)	Mar–Apr	144.11	3.71	85.12	2.26
Summer (10)	Jul–Aug	171.88	9.54	115.87	3.99

very much as it appeared in 2012/2013—pale yellow with a smooth surface—suggesting that while there are yearly changes to the sponge, it is resilient to change, and that in 2022, it was at least 10 yr old.

3.2. Contraction kinetics

The short-term behaviors described in the previous section consisted of different types of whole-body contractions. To allow comparisons of these short-term behaviors in *S. concinnus* with those described in other sponges, we termed the most common full body

contraction 'Type 1'. Each contraction took approximately 11 h and reduced the sponge's size by 50%, with the sponge returning to its previous size at the end of the contraction cycle (Fig. 4A). Often Type 1 contractions occurred in a succession of 4–6 contractions, one contraction each day, and most of them occurred during daylight hours. The second type, 'Type 2', involved a series of contractions that reduced the size of the sponge more each time (Fig. 4B). Types 1 & 2 contractions were repeated during spring and summer months over 3 yr. A third type of contraction, 'Type 3', was seen only in one year of our observations (TL5) and was similar to Type 1 contractions

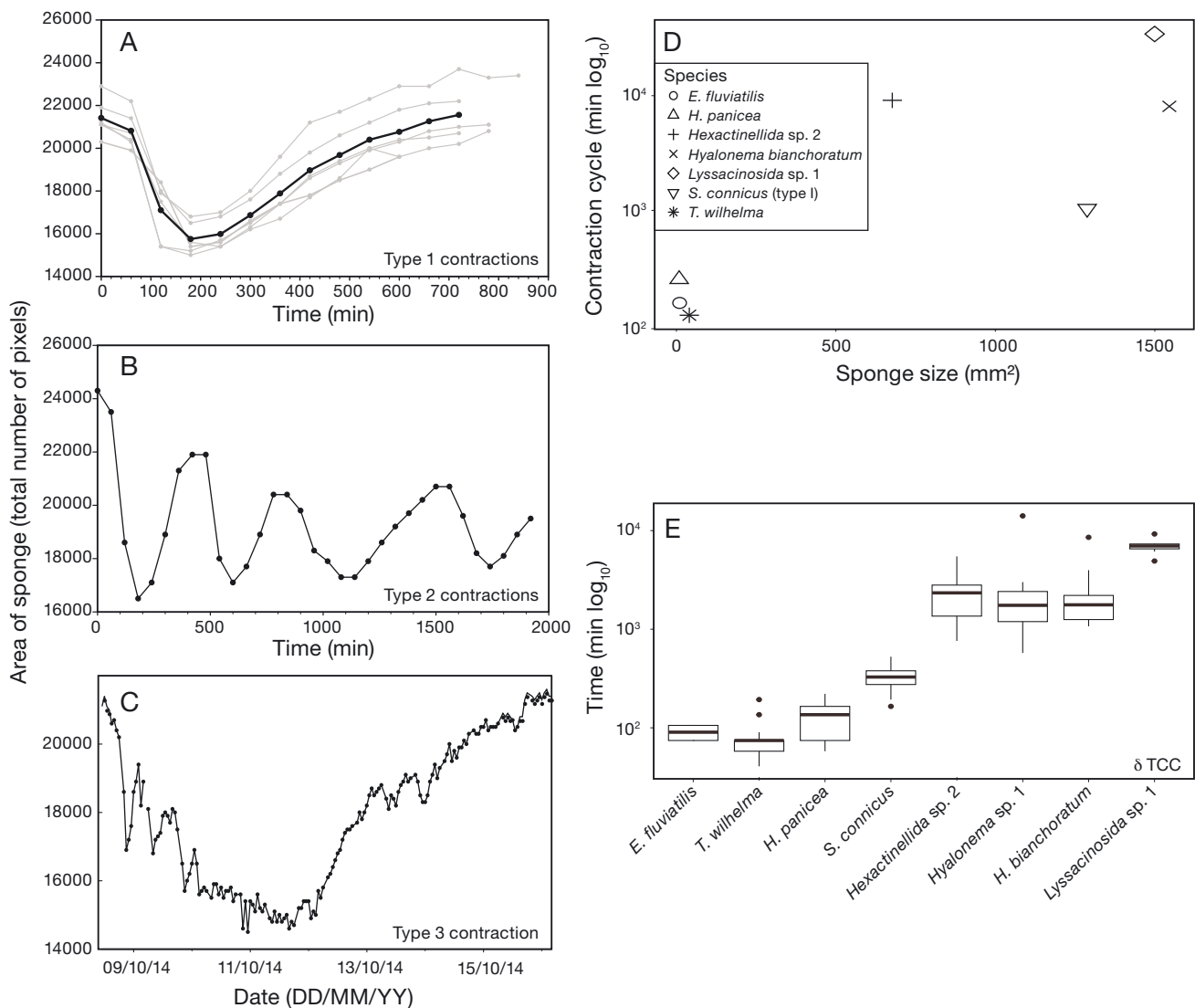


Fig. 4. Three types of contractions in *S. concinnus* were identified: (A) Type 1 took approximately 11 h and reduced the sponge size by half; the sponge then returned to its full size at the end of the contraction cycle. Individual contractions are plotted in grey with mean shown in black; (B) Type 2 reduced the sponge size more with each contraction; (C) Type 3 (only seen once in the entire time series) were prolonged single reductions in size. (D) Contraction cycle time of 7 sponge species of varying sizes. (E) Contraction duration (δT_{CC}) across different species. Horizontal line: median; upper and lower edges of the box: first and third quartiles, respectively. Whiskers: extended range of data, no further than $1.5 \times$ interquartile range (IQR); dots: outliers.

Note for panels D–E, y-axis is the \log_{10} scale of time

but it took several days for the sponge to reduce its size and several days more to expand back to its original size (Fig. 4C).

In addition to the observed whole-body contractions, waves of ripples spread over portions of the sponge's surface in the summer months of all years, and in winter, when the sponge was mostly fully contracted, small twitches occurred on different parts of the body (Video series S2).

3.3. Contraction kinetics: comparisons with other sponges

The duration of the whole-body contraction cycle for *S. concinnus* falls in the mid-range of contraction cycles documented for other sponges with some contraction cycles as short as 30–50 min and others several hours long (Fig. 4D; Tables 2 & 3). In some deep-sea hexactinellid sponges, the contraction cycle can take weeks (Kahn et al. 2020), which may be a factor of their expansive canal system and syncytial tissues. However, overall, smaller sponges have a shorter contraction cycle than larger sponges. As in other demosponges, the rate of contraction in *S. concinnus* was shorter than the rate of expansion (Table 3).

3.4. Contact with other animals

We found a diverse benthic community on and around the sponge; examples of each animal are shown in Fig. 5A. Most animals contacting the sponge were snails and hermit crabs (Fig. 5A, Fig. S2). Sea stars and anemones were active visitors, and occasionally fish rested near but not on the sponge. Sea stars *Solaster dawsoni* and *S. stimpsoni* often lay with arms over a large part of the sponge. In the winter of 2013, when the sponge was contracted for over a month, a blood star *Henricia leviuscula* moved over

the sponge for some time, appearing to feed on its surface. As most of our images were captured every hour it was not possible to determine exactly what the animals were doing, but in a few instances, it was possible to see that the proboscis of the snail *Calliostoma ligatum* was in contact with the sponge as it moved over the surface for many hours. In winter 2015 (TL6), a dorid nudibranch *Doris montereyensis* moved onto the sponge and grazed the surface over many weeks. Also, in TL6 (August 2015), a brooding anemone *Epiactis prolifera* moved up to and climbed on top of the sponge for 12 h. During all years, a crab (possibly a spider crab) lived tucked under the edge of the sponge (best viewed in the fall of 2014, TL5; Video series S1). There was a seasonal trend in benthic faunal abundance on the sponge with more invertebrates and fish on and around the sponge during spring and summer months and fewer during fall and winter months (Fig. 5B).

There was no evidence that contractions by the sponge were related in any way to the presence of animals because the sponge contracted even when no animals were present, and did not respond when fish, sea stars or small snails and crabs were in contact with it for either short or long periods (Fig. 5C).

3.5. Analysis of the interaction of environmental variables with sponge behavior

The GAMMs reveal that there are significant correlations between the change in area of the sponge with time (temporal covariates) for the 3 TL series, TL1, TL4 and TL5, with AR3, AR2, and AR1 models for residuals, respectively (effective degrees of freedom [edf]: 150.12, 17.65, and 67.93, respectively, and all $p < 0.001$; Table 4, Fig. 6). All models had time elapsed and daily hour as significant temporal covariates, and only TL1 had a significant interaction (edf: 1.94, $p < 0.001$). First, the best-fit model for TL1 was significantly associated with chlorophyll and turbidity (edf: 4.63 and 5.42,

Table 3. Comparison of contraction kinetics (mean \pm SD, min) of 7 sponge species. T_{CC} : duration of contraction cycle; T_C : duration of contraction phase; T_E : duration of expansion phase

Species (N)	Area (cm ²)	T_{CC}	T_C	T_E
<i>Ephydatia fluviatilis</i> (9)	9	150 \pm 8.5	83.3 \pm 10.3	70 \pm 5.7
<i>Tethya wilhelma</i> (42)	39.1	119 \pm 7.7	128.82 \pm 17.4	104.12 \pm 13.6
<i>Halichondria panicea</i> (17)	7.7	232.9 \pm 24.8	41 \pm 2.9	77.86 \pm 7.7
<i>Suberites concinnus</i> (25)	127.2	866.4 \pm 64.1	278 \pm 28.1	602.4 \pm 66.4
<i>Hexactinellida</i> sp. 2 (46)	667.8	6502 \pm 508	1671 \pm 136	2493 \pm 147
<i>Hyalonema bianchoratum</i> (30)	1526.1	5814 \pm 875	2018 \pm 277	2542 \pm 829
<i>Lyssacosida</i> sp. 1 (7)	1480.6	22346 \pm 1824	11143 \pm 2155	8194 \pm 829

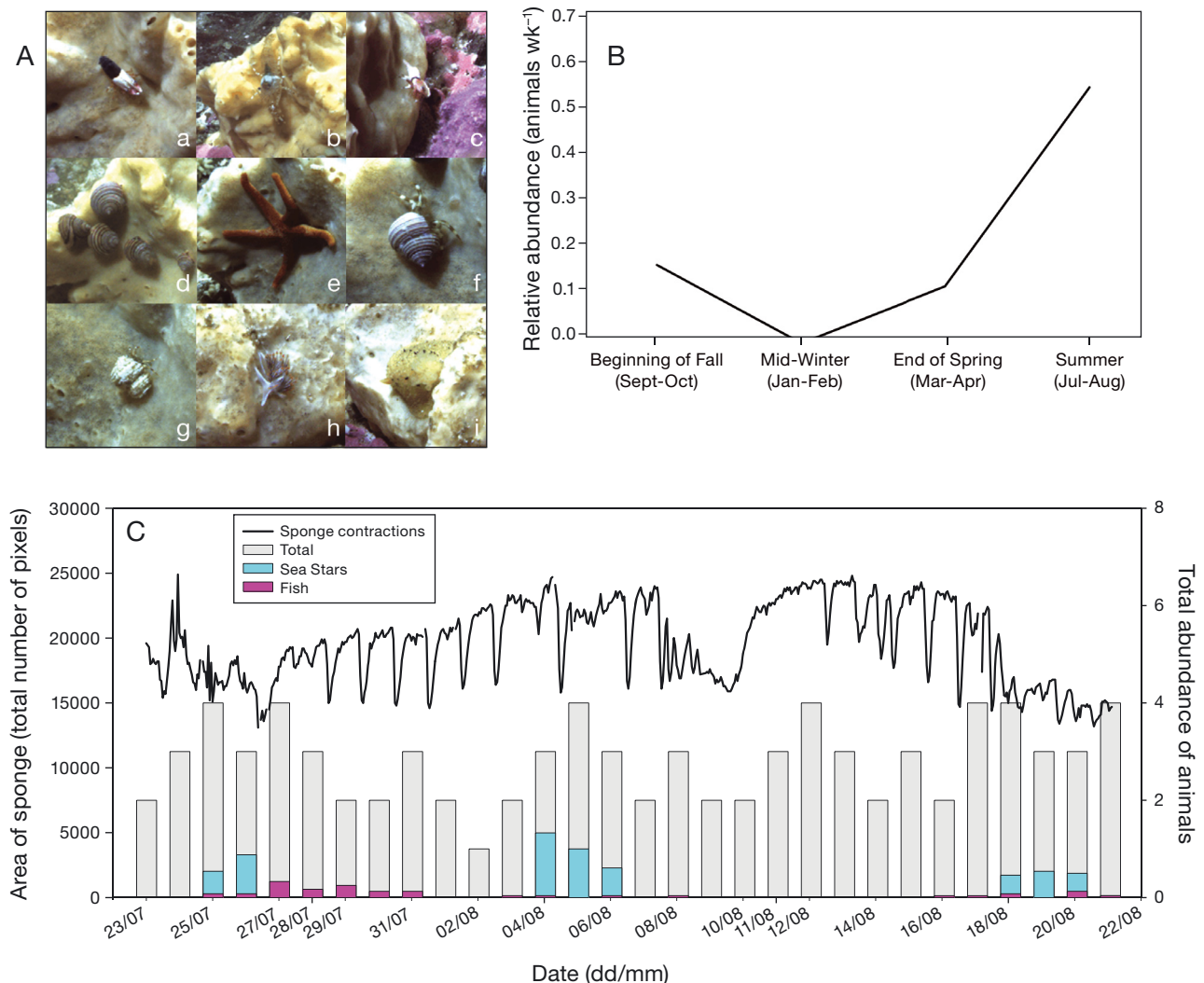


Fig. 5. Interactions of other benthic animals with *S. concinnus*. (A) Examples of animals identified are (a,c) *Spriontocharis* sp. (shrimp), (b) spider crab, (d) *Caliostoma ligatum* (snails), (e) *Henricia* sp. (blood star), (f,g) *Pagurus* sp. (hermit crab), (h) *Hermisenda crassicornis* (nudibranch), (i) *Doris montereyensis* (nudibranch). (B) Relative abundance of animals on the sponge; it was greater in spring and summer than in the fall and winter months. (C) Sponge behavior plotted as change in area (black solid line) and abundance of all animals on the sponge (grey bars)

Table 4. Effective degrees of freedom (edf) and p-value of each covariate of the final generalized additive mixed models (GAMMs) for *S. concinnus* area in each time lapse. (*) indicates significance at $p < 0.05$. PAR: photosynthetically active radiation

Covariate (unit)	TL1		TL1 Spring		TL4		TL5	
	edf	p	edf	p	edf	p	edf	p
Time	150.12	<0.001*	1.94	<0.001*	17.65	<0.001*	67.93	<0.001*
Hour	8.87	0.007*	4.77	<0.001*	7.40	<0.001*	6.23	<0.001*
PAR ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	1.00	0.80	1.00	0.005*	1.76	0.304	1.33	0.859
Pressure (dbar)	1.00	0.016*	1.00	0.005*	2.44	0.154	1.00	0.671
Oxygen (ml l^{-1})	1.20	0.94	1.00	0.795	1.00	0.853	2.06	0.404
Temperature ($^{\circ}\text{C}$)	4.84	0.23	4.50	0.083	1.00	0.552	1.82	0.108
Chlorophyll ($\mu\text{g l}^{-1}$)	4.36	0.002*	3.80	0.002*	4.78	<0.001*	1.00	0.793
Turbidity (NTU)	5.42	<0.001*	4.17	0.001*	1.67	0.465	1.26	0.748

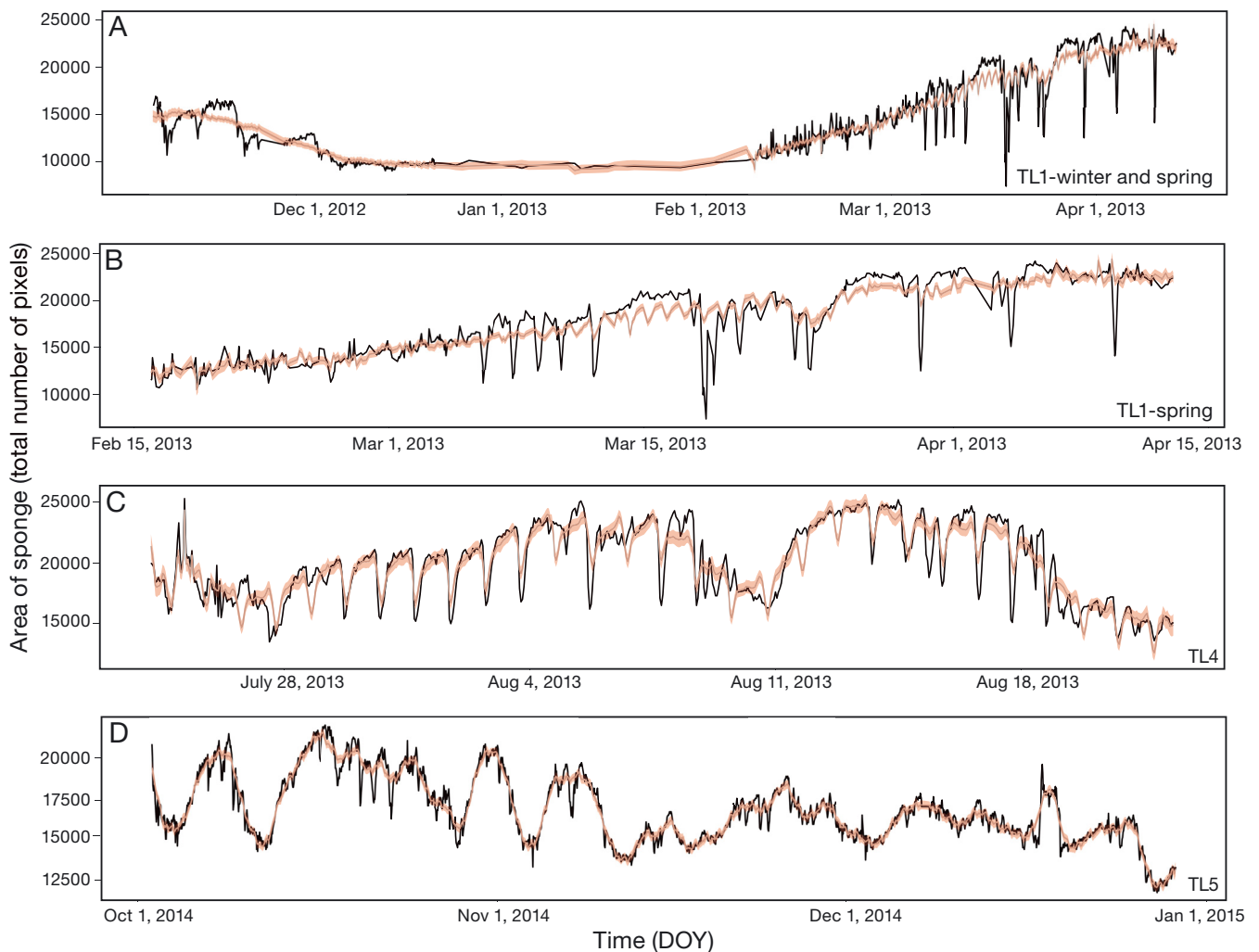


Fig. 6. Generalized additive mixed models (GAMMs) of *S. concinnus* behavior across time. Solid black lines represent changes in sponge area (behavior) in (A) TL1 winter and spring, (B) TL1 spring, (C) TL4, and (D) TL5. Orange lines superimposed along the observed time series data are the predicted sponge behaviors from the GAMMs, and the ribbons are \pm pointwise 95% confidence intervals

$p = 0.002$ and < 0.001 , respectively; Tables 1 and 4, Fig. 6A). We then ran a separate model for TL1 spring to isolate the spring activity from the winter dormancy (AR4 model for residuals; Fig. 6B). We found TL1 spring was significantly associated with PAR, chlorophyll, and turbidity (edf: 1.00, 3.80, and 4.17, $p = 0.005$, 0.002, 0.001, respectively; Table 4). TL4 was significantly associated with chlorophyll (edf: 4.78, $p < 0.001$; Table 4, Fig. 6C), and TL5 was not significantly associated with the environmental covariates (Table 4, Fig. 6D). The partial effects demonstrated the individual contributions (directions or patterns of the relationships) of the significant covariates of the models—namely, time, chlorophyll, pressure, PAR, oxygen, and turbidity. All significant covariates had non-linear contributions with a few exceptions (Figs. 7 & 8). There

were linear relationships between TL1 spring and PAR and pressure, i.e. change in sponge area is positively correlated with PAR and pressure. The partial effects also showed the significant daily trends of change in area, and they were all non-linear (Figs. 7F & 8B,E). ACF and PACF plots of the 4 best-fit models for each time lapse are available in Fig. S3. Fig. 6 showed the predicted sponge behaviors from the GAMMs in comparison with the observed time series data.

To assess the short-term behavior patterns, we used Kendall's τ correlation (Fig. S4), which revealed only a few significant associations between environmental variables and the specific contraction series under investigation, namely, TL4.1 and TL4.2 with oxygen and TL4.2 with chlorophyll (all adjusted p -values were < 0.001 ; Fig. S4).

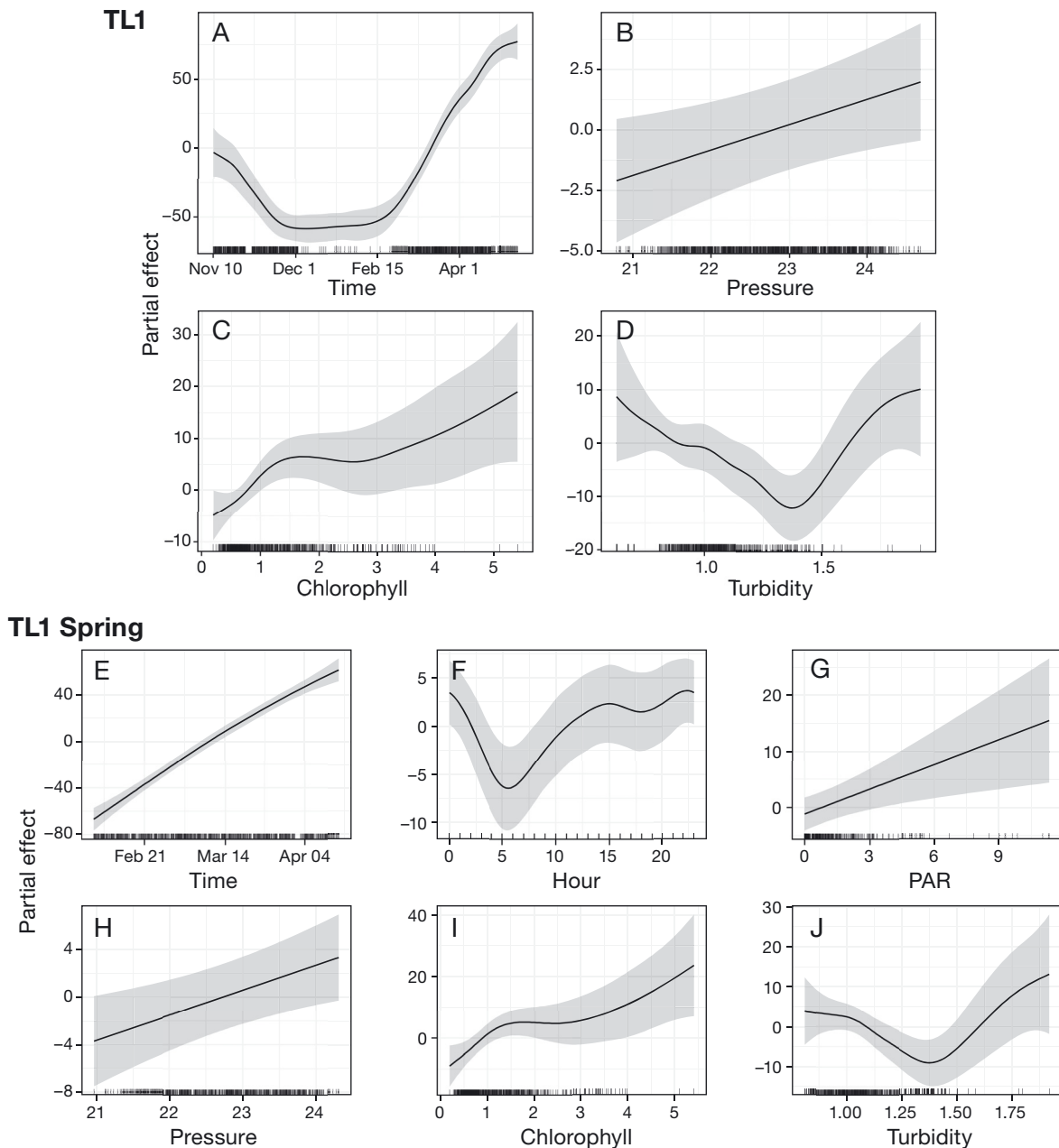


Fig. 7. Partial effects of the GAMM for sponge area in (A–D) TL1 and (E–J) TL1 during spring. Significant partial effects of TL1 covariates for (A) time, (B) pressure, (C) chlorophyll, and (D) turbidity and of TL1 spring covariates for (E) time, (F) hour, (G) photosynthetically active radiation (PAR), (H) pressure, (I) chlorophyll, and (J) turbidity on sponge area, grey ribbon represents $\pm 95\%$ confidence intervals. Solid black lines represent the effect of the covariate on sponge area, rug marks on the x-axis are observed data points

4. DISCUSSION

The unique placement of this *Suberites concinnus* individual in front of an array of cameras on an instrument platform connected to the Ocean Networks Canada Observatories offered a rare opportunity to study the behaviors of a sessile animal over several years.

The sponge carried out a range of behaviors, some spanning hours and weeks, others months. Throughout the 4 yr of observations, various benthic organisms interacted with the sponge, such as fish, sea stars, snails, and hermit crabs, but none of these interactions, including predation, cleaning, or cohabitation, were correlated with contractions by the sponge. Instead,

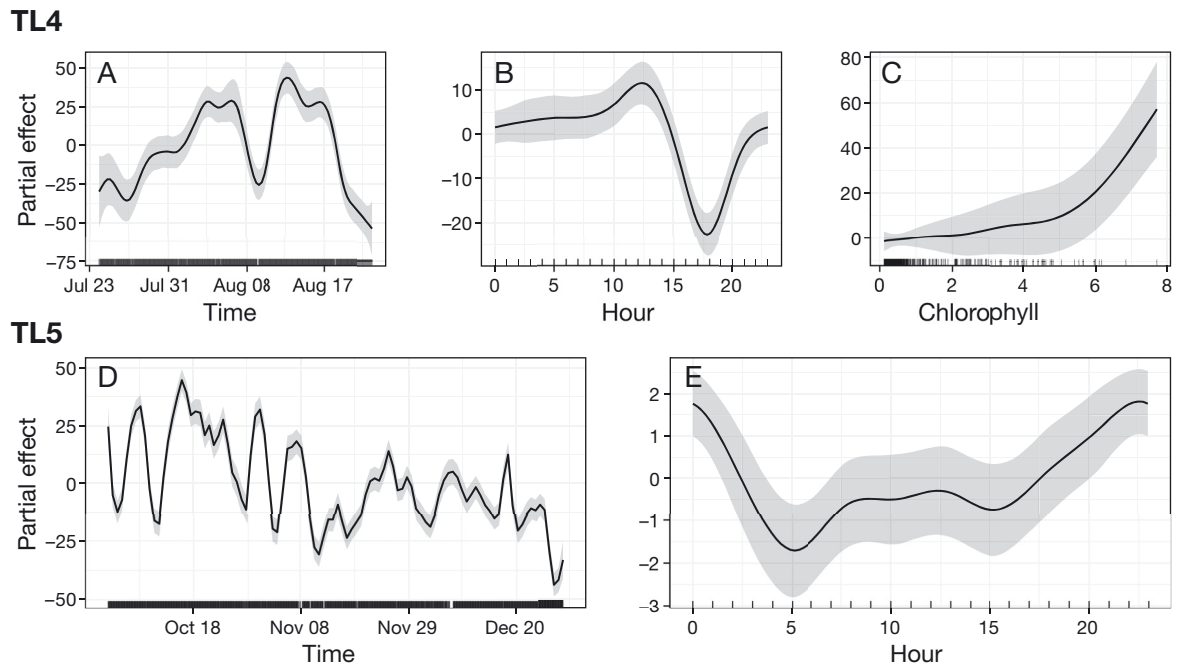


Fig. 8. Partial effects of the GAMM for sponge area in (A–C) TL4 and (D,E) TL5 (AR4 and AR1, respectively). Significant partial effects of TL4 covariates for (A) time, (B) hour, and (C) chlorophyll and of TL5 spring covariates for (D) time and (E) hour on sponge area. Solid black lines represent the effect of the covariate on sponge area, grey ribbon represents $\pm 95\%$ confidence intervals. Rug marks on the x-axis are observed data points

long-term contractions over winter months were most strongly correlated with chlorophyll and turbidity, while short-term contractions were significantly associated with chlorophyll, turbidity and temporal covariates, suggesting that both extrinsic (environmental) and intrinsic (metabolic) factors play a role in causing contraction behavior in this sponge.

Although our analyses concern only one individual of *S. concinnus*, given the universality of sponge contraction as a stereotypical behavior of a species, we are confident the findings here help explain the factors that trigger the distinct patterns of behavior in this nearshore Northeast Pacific coast species. To the best of our knowledge, this is the only data set describing sponge behavior that has both high temporal resolution and covers such a long period together with so many local environmental sensors (<https://doi.org/10.7939/r3-z7nh-6193>). The data set also documents, for the first time in a demosponge *in situ*, repeated, seasonal changes in behavior, which we refer to as 'dormancy'. In the following sections, we address how the contractions of this sponge compare to those reported in other sponges, what the drivers of short- and long-term contraction behaviors are, and finally, we examine the phenomenon of dormancy and discuss how it compares to other types of reduced activity, which include quiescence and hibernation. We

suggest our results can help shed light on the causes of sponge behavior in general and, as a proxy for other sessile filter-feeding animals, the effects of changes in the environment on sessile filter feeders. In addition, it highlights the use of marine cabled observatories as effective tools for monitoring species' behavior over long time periods and under changing environmental conditions.

4.1. Sponge activity: comparison with other sponges

Sponges have a wide range of behaviors, which are often undervalued because they are slow and difficult to capture in real-time. Even so, such active behavior in the absence of muscle and nervous systems has intrigued researchers who have documented sponge activities since the early 1900s (Parker 1910, 1914, McNair 1923, Prosser et al. 1962, Emson 1966, Weisenfels 1990, Nickel 2006, Kumala & Canfield 2018, reviewed in Leys et al. 2024).

The range of behaviors that have been well-documented in adult sponges is quite diverse. For example, some early investigations found sponge oscula contracted in response to different stimuli, such as lowering water levels with outgoing tides or mechan-

ical stimulation, while other sponges contracted oscula in response to more rapid water movement around the osculum (Parker 1910, McNair 1923, reviewed in Leys et al. 2024). In all instances, researchers have documented the aspect of contraction as most tractable to measure (whether osculum, ostia, or whole body). Our observations are of whole-body contractions because the oscula are open only intermittently, making measurements of them less informative. Whole-body contractions are also easier to measure in other sponges, which allows us to compare the activities of this sponge with those in other species.

Modern investigations on shallow-water and deep-sea sponges show different periodicity in contraction cycles, with small sponges often contracting several times in a day, and a deep-sea sponge contracting once over a period of 5 mo (Fig. 4D). The periodicity of the *S. concinnus* contraction cycle falls in the middle of those reported for other sponges, and at approximately 300–500 ml in volume, this sponge was mid-size compared to others studied. Comparisons across the phylum show that the rate of contraction is completely size-dependent (Fig. 4D), suggesting that the volume of water to be expelled from the sponge determines the rate at which it can contract.

Like other demosponges, *S. concinnus* is able to contract by about 50% of its size. For our study, we called a unit of behavior one whole-body contraction, and we classified more complex responses by the types of contractions (Types 1, 2 or 3). Individual contractions followed a stereotypical pattern with a faster contraction phase and slower expansion phase. The more rapid contraction phase suggests active contraction by epithelia while the slower expansion phase suggests a relaxation of that epithelium and passive expansion of the elastic collagenous mesohyl that lies between all of the minute canal spaces and increasing 'hydrostatic pressure' within the canal system as a result as described by Nickel (2004).

A recent study (Rupert et al. 2024) suggests a different view, that reduction in sponge size results from the collapse of incurrent spaces due to loss of tension in surface tissues, leading to a loss of system pressure. However, it is difficult to see how this might be the case for *S. concinnus*. First, the pressure difference (head loss) across the sponge pump is minimal (0.67–3.4 mmH₂O) (Parker 1910, 1914, 1919, Riisgård et al. 1993, Larsen & Riisgård 1994), and 3 to 10 times lower than what the surface tissues can withstand (measured at 11–15 mmH₂O) (Parker 1910). Second, in thin-walled freshwater sponges, contractions continue to move slowly across the tissues despite the

surface tissues and canals being torn open, implying that there is a paracrine-type signal which involves cell-to-cell communication via calcium (Elliott & Leys 2010, Nickel 2010, Ludeman et al. 2014, Colgren & Nichols 2022). Finally, the change in size observed in the sponge *in situ* at Folger Pinnacle takes 11 h, while contractions in even larger deep-sea glass sponges take longer (Kahn et al. 2020). It seems unlikely that such a slow process could be caused by 'deflation'.

4.2. Drivers of sponge activity: short-term behaviors

Of the few *in situ* studies of sponge behavior, ours is the only one to follow a single sponge through all 3 seasons over 4 yr. Our time series showed that there was a significant temporal disparity between the behavior types, i.e. Type 1 was found 90% of the time (clearly seen in Fig. 3B), Type 2 about 10% of the time (blue boxes in Fig. 3A,B), and Type 3 only once during the 4 yr of our study (Fig. 4B,C). This differential ratio of behavior types suggests that behavior can either be regular physiological maintenance or environmentally plastic and adaptive.

We found that sponge contractions *in situ* showed both cyclical and reactive patterns. The *in situ* contractions had 3 distinct patterns: (1) a single full-body contraction (Type 1; 10–12 h long; Fig. 4A), (2) a series of full-body contractions with decreasing size before winter (Type 2; each ~10 h long; Fig. 4B), and (3) a prolonged contraction and expansion (Type 3; several days; Fig. 4C) in summer months seen in TL5. During our 4 yr study, Type 3 contraction occurred once, representing an unusual finding. While the cause of Type 3 behavior remains unclear, the lack of consistency in this behavior suggests the sponge can respond to stochastic disturbances. For example, Hill & Hill (2002) found that reduced spicule production in response to increased predation led to changes in sponge behavior. In a previous study, we found some evidence that this sponge decreased in size and rates of activity ahead of a large storm (Leys et al. 2019). Interestingly, none of the models showed significance with changes in current speed or salinity, both of which are usually related to random disturbances such as a storm or large freshwater runoff. Some behaviors may be a response to random events, which most likely would not be captured in our models but may explain the large variability in sponge behavior.

The models of Type 1 behavior in TL4 were significantly and positively associated with chlorophyll. The Folger Pinnacle, due to its location at the outer edge

of Barkley Sound, experiences few sediments from any terrestrial input, but turbidity measured by the fluorometer/turbidity sensor represents particles in the seawater and these could be plankton or resuspended detritus and other material from below the pinnacle. Resuspended sediments have been shown to irritate and cause arrests of filtration in glass sponges (Hexactinellida) *in situ* (Grant et al. 2018, 2019). Because the daily contractions of the sponge were not associated with storm events that would resuspend sediments from below the pinnacle, and because the sponge remained contracted through the turbulent winter months, it seems more likely that both chlorophyll and turbidity could therefore be associated with food availability. If so, this suggests that sponge activity increases in the spring in response to the available particulate food (phytoplankton) and to the increase in particulates (here recorded by chlorophyll and turbidity). The contractions themselves may be due to particle accumulation in the sponge choanocyte chambers and expulsion of wastes, such as the 'sneeze' behavior documented in other sponges when they filter out charcoal or ink particles they are fed, or when they accumulate too much debris in their natural environment (Elliott & Leys 2007, Kornder et al. 2022), and this behavior might be enhanced as a result of increased plankton taken in by the sponge.

The exact mechanism that triggers contraction of epithelia in this sponge remains unknown, but as glutamate and ATP are both potent triggers of sponge sneezing in *in vitro* experiments, they may also function here (Ellwanger & Nickel 2006, Ellwanger et al. 2007, Elliott & Leys 2010). Accumulation of detritus or phytoplankton either by clogging the sponge canals or as waste could cause an increase in either glutamate or ATP locally and trigger a contraction that would rid the canal system of particles. The fact that Type 1 contractions generally occurred during the day for TL1 and TL4, and the strong correlation with temporal covariates (day/hour), suggests that some diurnal biological factor such as the diurnal migration of plankton and their excretion may play a role in triggering these whole-body contractions.

4.3. Seasonal behavior: winter dormancy

Many studies have found that sponges are highly seasonal and respond to changes in temperature or food availability by reducing filtration activity. For example, some studies have found that *Halichondria panicea* shows seasonal changes in biomass, gly-

cogen, and lipid stores (Barthel 1988, 1989, Luskow et al. 2019a,b), while others found that temperate sponges have lower choanocyte turnover rates in fall and winter (Kahn & Leys 2016), the respiration rates and filtration activity of sponges increase during summer (Coma et al. 2002), and sponges slough seasonally (Leys & Lauzon 1998). These examples also imply that in all such cases, the sponges are feeding much less during winter months, and as such their biomass and 'condition' are likely to diminish during these periods, as described above for the temperate demosponge *Halichondria panicea* (Barthel 1986, 1989). For *H. panicea*, seasonal collections of tissues from different individuals showed reduced biomass during winter months, with sponges in deeper water being affected for longer periods than those in shallow water (Barthel 1986). Given the exposed location of the Folger Pinnacle, we were unable to collect water samples during all seasons, and because only one sponge was at the location of the cameras, we also did not sample tissues more than episodically when the cameras were being cleaned by divers during calm periods (usually spring, summer and early fall).

We refer to the seasonal reduction in sponge activity as 'dormancy' due to the prolonged contraction and reduced activity of the sponge that we observed during winter. Dormancy, quiescence, senescence, and hibernation describe stages of reduced activity in organisms, parts of organisms, or cells; all these stages involve reduced feeding, but they are temporary states rather than starvation. Dormancy and quiescence are terms used for overwintering gemmules of freshwater sponges (Ostrom & Simpson 1978, Harrison et al. 1981, Schill et al. 2006). Quiescence is reversible, while senescence usually refers to an irreversible decline in a part of a plant or cells, with nutrition moving to other regions (Tuomi et al. 2013, Fujimaki & Yao 2020). Dormancy includes these states, indicating a period of lower metabolic activity from which the organism can revive. Thus, we call the winter contraction state of *S. concinnus* dormancy, as the sponge revives each spring, grows larger yearly, and likely uses reserves from summer feeding to survive periods with less food.

Reiswig (1971) showed that *Verongula gigantea* (published as *Verongia gigantea*) contracted the atrial cavity during reduced pumping, and implied that this was how sponges reduced pumping as winter approached. However, exactly how sponges reduce their activity levels in winter months had not yet been observed at a high temporal resolution. Our documentation of winter dormancy by seasonal contraction, closing almost all, if not all, ostia and con-

stricting the aquiferous system, shows how demosponges can reduce their filtration. We found significant size reduction and minimal activity of this sponge during the winter during each year. This reduction in size was seen clearly in TL1, where there was a gradual, month-long, reduction in size from November through December of 2012. During this period, the oscula closed and the tissue took on a darker shade of orange. We found the long contraction from fall to spring in TL1 to be significantly associated with chlorophyll, turbidity and pressure. While chlorophyll and turbidity point to seasonal changes suggesting seasonal contraction may be associated with lower food availability, the association with pressure points to the potential effect of changes in weather such as storms (Fig. 7B–D). The expansion of the sponge in the spring of TL1 showed similar associations with pressure, chlorophyll, and turbidity but also a significant and positive correlation with PAR, suggesting the change in light availability may play a role in increased activity but not decreased activity (Fig. 7G–J).

The reduced size in the winter means reduced ability to filter feed, which is an interesting indicator of the limited food available in temperate regions during winter months. Other benthic animals with limited mobility also show seasonal changes in response to low food. Sea cucumbers lose their guts by evisceration during winter months as an economic solution to low food availability (e.g. Byrne 1985), deep-sea sponges show changes in recruitment and reduction in size in some individuals (Kahn et al. 2012), and a range of filter feeders show effects of a winter low food diet in Antarctica (Clarke & Peat 2022).

Food availability in the form of particulate or dissolved organic carbon is often highlighted as a factor controlling abundance of benthic animals in the deep sea and coastal regions (Billett et al. 1983, Rice et al. 1986, Levin & Dayton 2009). Factors such as the flux of macro-algae, phytoplankton, and detritus that reaches the sea floor determine the density and abundance of diverse benthic animals (e.g. echinoderms, foraminifera and amphipods) (Billett et al. 2010, Jones & Murray 2017, Horton et al. 2020, Command et al. 2023). Sponges are unusual among 'grazers' in being able to feed on the picoplankton in the water, but this is highly seasonal in the North East Pacific, with blooms in Barkley Sound starting in May and ending in September (Taylor & Haigh 1996, Boyd & Harrison 1999). We suspect the reduced activity of *S. concinnus* during winter is likely a response to low food, serving as a mechanism to minimize metabolic costs.

4.4. Responses to change in oxygen

A completely contracted sponge suggests it is not filtering for many weeks on end, and this raises a number of interesting questions. When sponges are contracted, their tissues quickly go hypoxic (Hoffmann et al. 2005, 2008, Schläppy et al. 2010), but many experiments now show that sponges, like many invertebrates and some vertebrates, have a high tolerance of low oxygen either due to low energetic expenditure or by use of different pathways (Mentel et al. 2014, Mills et al. 2014, 2018, Leys & Kahn 2018). Our analyses did not find significant relationships between changes in oxygen levels and changes in size (contraction) for Belinda, except for in the winter of TL1 when there was very little activity and oxygen levels were at their highest. Sponges inhabiting fjords that are seasonally anoxic have been found to host different microbial communities than those living in fully oxygenated areas (Schuster et al. 2021). The fjord sponges in hypoxic conditions were found to be pumping (Schuster et al. 2021), and individuals of the deep-sea sponge *Geodia barretti*, experimentally treated to hypoxic conditions of <4% present atmospheric levels, still continued to pump (Leys & Kahn 2018). It is, however, unknown if sponges in anoxia actually pump. We noticed that during the winter 'dormancy' of *S. concinnus*, although most of the sponge was contracted, a small region at its base occasionally expanded to reveal paler tissues as evidence that it was filtering (e.g. TL1; Video series S1), suggesting that aeration of tissues is spatially controlled through the winter months.

4.5. Invertebrate community

As only few *in situ* observations of interactions of motile invertebrates with sessile animals like sponges have been published, our observations provide useful insight into long-term activity of sessile animals in a very stochastic environment. First, despite the great range of animals found crawling over the sponge over the 4 yr of our observations, no one set of contacts by animals could be clearly correlated with any of the sponge's contraction behaviors we documented. Individual rockfish appeared to rest very occasionally beside the sponge. After the fish moved away, the sponge did not contract; however, too few instances of fish were seen near the sponge to be able to confirm whether they did or did not produce a behavioral response in the sponge. Similarly, both *Solaster stimpsoni* and *S. dawsoni*, large carnivorous sea stars

in the Pacific northeast, visited the sponge in several different periods, lying with arms draped over its surface, but neither sea star left any mark of grazing the tissues after they moved away. Many aeolid nudibranchs seen moving over the surface of the sponge also left no traces of their presence. Despite dorid nudibranchs often being found on *S. concinnus* in other locations, we only found one instance of grazing causing physical damage to the sponge tissue during the 4 yr time series. Interestingly, the dorid grazed the surface of the sponge for several weeks but only grazed discolored tissue, and recent images captured from 2023 show there is no evidence of scarring or lasting damage from this predation event.

Given the demonstration that invertebrates feed on mucus-laden excreted wastes from sponges (Kornder et al. 2022), the increase in the number of invertebrates we documented on the surface of *S. concinnus* during the summer months, together with both the sponge's heightened activity and increased chlorophyll (a measure of phytoplankton) in the water column, could be attributed to increased particulates on the sponge and to excretion by the sponge. The organisms interacting with the sponge may feed on sponge mucus-containing waste, as suggested by one instance where a proboscis could be seen sweeping the surface of the sponge. The decreased activity of the sponge during winter could lead to reduced availability of such waste, potentially explaining the decrease in associated organisms.

It occurred to us that some of our image data on animals and shelly objects on the sponge over time, as well as the response of the sponge to these, highlighted a more complex change in the environment that was not captured in our GAMMs analyses. For example, in 2013, a heatwave that began in the Gulf of Alaska spread towards the northern Pacific coasts and became more intense throughout 2014–2015 (Bond et al. 2015). Massive die-offs of organisms such as whales, seabirds, and cod occurred. It is probable that this event, dubbed 'The Blob', was also recorded and felt throughout the benthos (Pineda et al. 2018). In 2013, images from TL1 to TL3 show a sudden input of shelly debris. In TL1, the rock around Belinda was relatively free of loose shells whereas in TL3 the rock surface around the sponge was covered with shell fragments. A detailed study on the benthic community responses under pre- and post-marine heat wave conditions is still underway, with only preliminary results available (Porfírio et al. 2017). The change in color of Belinda during that period may also reflect changes in the water properties, such as increased temperature, decreased oxygen, and increased par-

ticulates due to die-offs in the water around and above the pinnacle. Both the shape and the surface of the sponge changed during this period, and it might have appeared that the sponge itself was not healthy, except that in 2022 and 2023 images captured by divers cleaning the instrument platform showed the sponge had a healthy surface with a bright orange colour, and appeared to be the same as it was 10 yr previously when the platform was installed (Fig. S5).

5. CONCLUSIONS

Sponges show extensive behavior that is difficult to observe except in time-lapse, so most data come from laboratory experiments. To the best of our knowledge, our data are the highest resolution and most comprehensive in terms of associated parameters collected for monitoring *in situ* sponge behavior, and the first documented case of winter dormancy in a demersal sponge. The patterns of contraction by the sponge observed in this study align with those carried out by other sponges, especially the way they contract and expand, and confirm that the timing of contractions is dependent on the size of the sponge. The cyclic winter and summer activity were significantly correlated with pressure, turbidity, chlorophyll, and PAR, which suggests that the reduced size of the sponge during the winter period represents a dormancy phase and is triggered by a lack of food, decreased sunlight, and potentially also by storms, and that the reverse is true for the increased summer activity.

The community and interspecific interactions seemingly have no negative impact on sponge growth and survival, and over the course of our 4 yr study, we only found a few small instances of predation. Still, 10 yr later the sponge has not been consumed. There are many assumptions that sponges are sessile and stagnant; however, our data illustrate that there is significant variability in behaviors across time and behaviors that are correlated with the immediate surroundings of the sponge. Although this study focuses on a single individual, the aforementioned assumptions have led to a lack of understanding about how sponges behave. Our findings demonstrate that sponge behavior can be reactive or innate, responding to local and global environmental stimuli. Future research should focus on increasing the diversity of inter- and intra-specific sample sizes to capture the true variation in sponge behavior across ecological populations and communities, as well as testing the discrete variables we have identified in mesocosm settings.

Data availability. Supplementary data set containing long-term observations of *Suberites concinnus in situ* is available at <https://doi.org/10.7939/r3-z7nh-6193>. The interactive data visualizer is located at <https://ematveev.shinyapps.io/BelindaVisualizer/>.

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