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An evaluation of acoustic telemetry as a method to study the movements of Asteroidea (*Asterias rubens*)

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Abstract

Background Acoustic telemetry is an important tool to study the movement of aquatic animals. However, studies have focussed on particular groups of easily tagged species. The development of effective tagging methods for ecologically important benthic species, such as sea stars, remains a challenge due to autotomy and their remarkable capacity to expel any foreign material. We tested three methods to surgically attach acoustic transmitters to the common sea star *Asterias rubens*; two methods attached the tag to the aboral side of the central body and the third attached the transmitter to the aboral side of an arm. Laboratory experiments evaluated each method in terms of survivability, tag retention, associated injuries, and changes in feeding behaviour and physical condition.

Results Laboratory results were highly variable; however, all tagging methods caused significant injury to the epidermis and deeper tissue around the attachment site over periods greater than 4 weeks. Attaching a tag by horizontally piercing the central body (method HPC) had minimal effects in the short-term (2–3 weeks) and this method was used for a pilot tagging study in the field, where 10 sea stars were tagged and placed within an existing acoustic telemetry array. Although, the interpretation of field data was challenging due to the characteristic slow movement of sea stars, movements of a similar magnitude to previous studies were identified during the 2–4 weeks after sea stars were tagged and released. However, this apparent period of tagging success was followed by a reduction in movement that, when viewed in conjunction with laboratory results, potentially indicated a deterioration in the sea stars' physical condition.

Conclusions While acoustic telemetry continues to provide novel insights into the ecology of a wide variety of marine species, species-specific effects of tagging should be evaluated before starting field studies. If the autonomous study of benthic movement is to expand beyond hard-bodied macroinvertebrates current methodological and analytical challenges must be addressed.

Keywords Acoustic telemetry, Tagging, Behaviour, Echinoderm, Saint Lawrence, Northwest Atlantic, Subtidal, Macroinvertebrate, Benthic, VEMCO positioning system (VPS), Fine-scale positioning, Common sea star

Background

Acoustic telemetry has become an important tool to better understand the movement ecology of a variety of aquatic organisms [1, 2], including marine mammals [3], herptiles [4, 5], fishes [6, 7], crustaceans [8], and other hard-shelled invertebrates [9–12]. However, the majority of studies have focused on fishes, marine mammals, and

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herptiles as opposed to macroinvertebrates. For example, of the 107,810 individual animals included in the Ocean Tracking Network (<https://oceantrackingnetwork.org/>) database, only 2734 are macroinvertebrates, and most of these (2351) are crabs and lobsters. This is particularly true for studies that use the VEMCO Positioning System (VPS) to quantify fine-scale movements and gain a mechanistic understanding of movement behaviours [13]. In contrast, VPS studies on movements by other types of marine macroinvertebrates, including sea stars, are less common [14].

Sea stars often play important ecological roles as predators and grazers in benthic and intertidal communities [15–17]. As such, there has been an increasing desire to better understand their general ecology [18] and to examine how this may change in the context of global change [19, 20]. Sea star movement ecology has been previously studied using plastic or similar tags to follow animals in situ [21–23], repeated diver observations [24, 25], and laboratory observations [26]. Archival tags have also been used to describe the vertical distribution of sea stars in relation to dynamic environmental covariates that may be drivers of sea star *Coscinasterias muricata* activity [27]. More recently, two studies have pioneered the use of acoustic telemetry to better understand sea star movements in the field (*Protoreaster nodosus*, [28] and *Asterias amurensis*, [29]). These latter efforts have largely concentrated on validating the tagging procedures used for the species of interest and quantifying movement parameters. The scale of adult sea star movement is still considered restricted to their immediate location, with most dispersal happening during the pelagic larval phases [30]. Limited studies have estimated adult monthly displacement ~ 20 m [28] and daily movement speeds of 4.3 ± 9.1 and 18.1 ± 15.2 m/day [29]. However, faster movements assisted by currents could facilitate adult dispersal over greater distances. During these movements, known as “starballing,” sea stars curl back their arms into a spheroid and roll along the seabed during strong tidal flows ~ 0.5 mps; however, it is unclear if this is a true behaviour or a result of becoming dislodged in fast currents [31]. The metres and minutes resolution provided by acoustic telemetry can offer insight into the scale of post-settlement adult movements as well as the possibility of identifying alternate movement states. Currently, the number of sea star studies using acoustic telemetry remains limited, largely due to the generally variable success for tagging sea stars using any method [15, 32]. Tagged animals are known to suffer from autotomy, abscesses, discarding of the tag (with animals, at times, observed to pull at tags until arms are lost or the tag is removed), and cannibalism [32]. At this time, there are only three previous studies

that have successfully attached electronic or acoustic tags to sea stars [27–29] with highly variable tag retention rates that have ranged from less than 2 weeks to more than 12 weeks. These previous acoustic telemetry studies used an external attachment method on the middle arm whereby monofilament line passed along the mid-ridge and aborally through the ambulacral groove [28, 29]. Given the known difficulties associated with tagging sea stars and the variable retention rate, it is prudent to assess species-specific tagging effects on survival and the rate of tag retention before undertaking field studies.

As part of a larger project to better understand the movement ecology of coastal echinoderms in northern latitudes (e.g., [33]), a method was needed to attach acoustic tags to the ecologically important and widely distributed common sea star *Asterias rubens* [34–36]. To obtain representative movement data, it is important to minimise potential handling and tagging effects that may cause stress and injury, and ultimately alter the observed behaviour [37]. This study reports the results of an experiment to evaluate three methods of transmitter attachment, tag retention, and the effects of tagging on sea star health, feeding rate, and condition. We also present preliminary field data on *A. rubens* movement from a pilot study in the Gaspé region of eastern Canada using the best tolerated tagging method.

Methods

Laboratory experiment

Collection and care of sea stars

Around 100 sea stars *A. rubens* (>19.2 – 29.3 cm diameter, i.e., arm tip to arm tip) were collected during the week of December 12, 2021, at Godbout, Quebec, Canada (49.317, -67.583) and transported the same day to the wet lab facilities of the Institut Maurice-Lamontagne (Fisheries and Oceans Canada). Animals were maintained in a large (363×122 cm) tank supplied with continuous ambient seawater (mean temperature ± 1 SE = 3.30 ± 0.14 °C and mean salinity ± 1 SE = 27.0 ± 0.22 ppt during December 2021 Additional file 1: Figs. S1, S2) at a flow rate of about 16 L/min with an air bubbling system and held for an acclimation period of about 1 month.

Three weeks before the beginning of the experiment, 64 individuals were randomly assigned to 1 of 4 groups (3 treatment groups and a control group), each group was replicated 4 times with $n=4$ sea stars per replicate. Each replicate group of sea stars was placed in one of 16 floating baskets (51×35 cm) for the duration of the experiment. During this pre-experimental period and the preceding acclimatisation, all individuals were fed ad libitum with mussels (*Mytilus edulis*).

At the beginning of the experiment (March 7, 2022), all individuals were weighed in-water, measured (diameter, arm to arm), and photographed. Sea stars that were assigned to a treatment group were fitted with a dummy acoustic tag, modelled after Innovasea V9 coded transmitters (0.9 cm × 2.4 cm; 2.0 g in-water) and printed in polylactic acid (PLA) using a 3D printer. Sea stars were tagged in a random order to avoid consecutively tagging all individuals in a single treatment and all tagging was carried out by a single person (J-BN) to avoid variation in handling. The experiment lasted for 119 days. Mean temperature and salinity ± 1 SE during the experiment were 3.94 ± 0.24 °C (range = 0.8–9.7 °C) and 26.1 ± 0.18 ppt (range = 22.2–29.2 ppt; Additional file 1: Figs. S1, S2).

Types of transmitter attachment

Preliminary tests on the attachment of acoustic transmitters to soft-bodied benthic invertebrates allowed us to focus our attachment tests on surgical methods using fishing line (Nadalini, unpublished data). Three types of surgical attachment were evaluated; all used Dyneema (Sufix brand) 0.18 mm diameter ultra-high molecular weight polyethylene (UHMPE) fishing line, but differed by the location of the surgical stitch used to attach the transmitter. Two methods used a horizontally placed surgical attachment (HP, for horizontal piercing), and the third used a vertically placed surgical attachment (VP, for vertical piercing, Fig. 1 and Additional file 1: Fig. S3). The

first attachment method (HPC, for Horizontal Piercing of the Central body) was a horizontally placed surgical attachment, placed above the central body, on the aboral side. The fishing line stitch crossed the central body while taking care not to pierce the stomach. To do this, the needle, once inside the body, followed the inner wall of the aboral part of the central body. The second attachment method also positioned the transmitter horizontally, this time on the aboral side of the arm, with the fishing line stitch placed laterally through the inframarginal plates, about 2.5–5 cm from the central body (HPA, for Horizontal Piercing on the Arm). The third attachment method (VPC, for Vertical Piercing of the Central body), passed the fishing line stitch vertically through the central body, entering on the oral side directly beside the mouth, passing on the inside edge of the ring canal, without piercing the ring canal structure, and then exiting on the aboral side while again taking care not to pierce the stomach, or the radial canals which could damage the hydrovascular system (Fig. 1).

Dyneema fishing line was threaded through sterile syringes with hollow needles (gauge no. 22 or 0.71 mm O.D). After piercing a sea star with the syringe, the fishing line was held in place and the needle withdrawn, leaving a loop of fishing line threaded through the body of the sea star. The two ends of the line were tied together and the transmitter attached to the resulting loop using a combination of electrical tape and Lepage’s

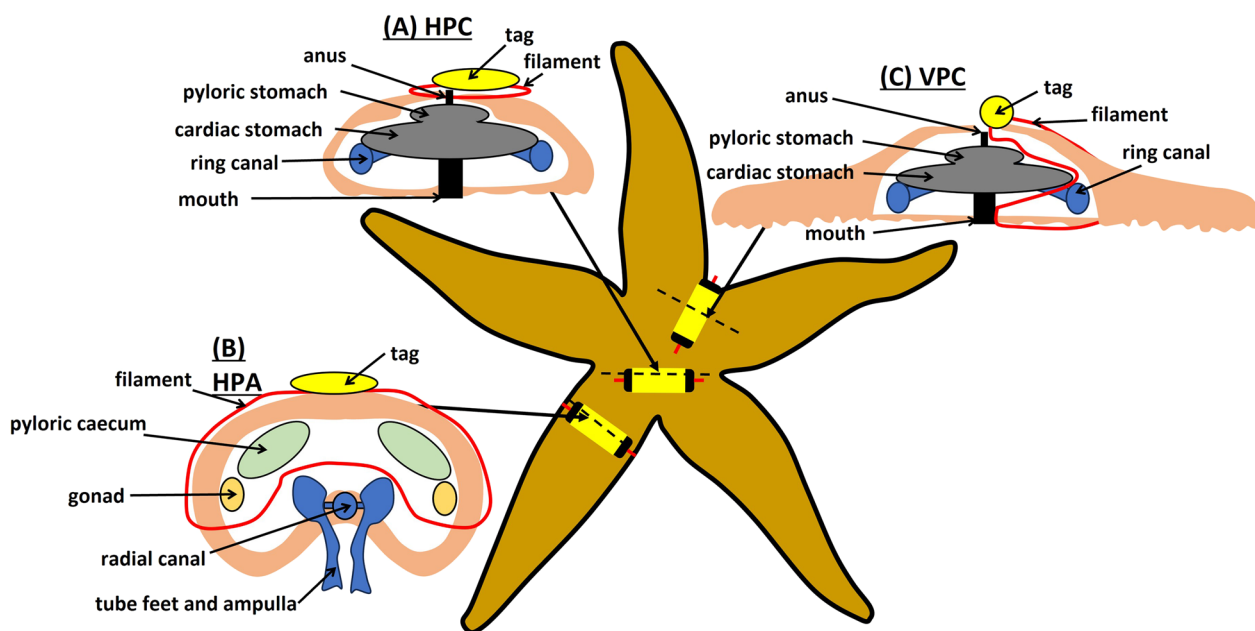


Fig. 1 Simplified schematics of sea star anatomy to highlight the key aspects of each attachment method. **a** HPC—Horizontal Piercing of the Central body, **b** HPA—Horizontal Piercing on the Arm and **(c)** VPC—Vertical Piercing of the Central body. Dashed lines indicate orientation of cross-sections

Ultra Gel glue. A gap of about 2.5 cm was left between the transmitter and the animal's body to ensure that the loop was not too tight. A unique number was assigned to each individual fitted with a transmitter and photos taken to distinguish sea stars in the event of tag loss and to allow identification and surveillance of individuals in the control group.

Response variables

Survival and tag retention

The time of death or day of tag loss (number of days since tagging) were recorded to calculate the probability of survival and tag loss. Dead individuals were removed from the experiment; however, individuals that lost their tag remained in their treatment baskets until the end of the experiment or they died. The status of sea stars was recorded daily except on Saturday and Sunday.

Feeding rate

At the beginning of the experiment, 40 commercial-sized (~5 cm length) mussels were placed in each basket to maintain a density of 10 mussels per individual. Preliminary tests indicated that *A. rubens* maintained in the wet labs consumed mussels at a mean rate of 1.1 ± 0.6 SE mussels/day. Sea stars were fed twice a week (Monday and Friday); the mussels consumed were counted and replaced to maintain the same availability of mussels in each treatment basket to obtain a daily feeding rate per individual per basket. Dead mussels or mussels that did not close on contact were not used and were replaced if encountered during feeding. As dead sea stars were removed from the experiment, the number of mussels provided was adjusted at each feeding to reflect the number of remaining sea stars in each replicate basket. Due to mussel availability, the type of mussels used to feed the sea stars changed during the course of the experiment. Sea stars were initially fed wild mussels during their acclimation period before the start of the experiment; however, between day 0 (the day sea stars were tagged) and day 40 of the experiment sea stars were fed commercial farmed mussels.

Tag-related injuries

An injury scale was used to evaluate the severity of visible injuries for every sea star at the beginning of the experiment (day 0) and then after 7-, 14-, 28-, 56-, 84-, and 147-day post-tagging. Sea star injuries present at the tagging site were classified based on a 6 point scale; 0—no visible injury, 1—discolouration of the epidermis, 2—slight deformation of the epidermis, 3—slight injury (visible lesion ≤ 5 mm), 4—injury (visible lesion > 5 mm), 5—internal organs visible (Fig. 2). The rate of autotomy was

not formally evaluated but, the number of arms lost per individual was recorded.

Sea star health—righting time

The time taken for each individual to right itself after being placed upside down on its aboral side was measured as an index of activity and health [38, 39]. Righting time was carried out on all sea stars before and immediately after tagging (day 0), and then at 7-, 14-, 28-, 56-, 84-, and 147-days post-tagging. The order of individual tests was the same as the randomly determined order of tagging. During the measurements, individuals were placed on the bottom of another large tank, where they were left for 5 min on their oral side, without handling them, to acclimatise. After this time, individuals were turned over and placed on their aboral side, and the time needed for an individual to right itself completely, with all 5 arms on the ground on their oral side, recorded. The maximum time permitted for a sea star to turn over was 1 h.

Data analysis

Survival and tag retention analysis

Survival and tag retention analyses used right censored Kaplan–Meier survival analyses and Cox proportional hazard models that were run using the R packages survival [40] and survminer [41]. Survival curves were generated to compare the probability of an event, in this case death or tag loss, over time and a log rank test used to test the null hypothesis that the probability of an event did not differ between treatment groups at any time point during the study. If there was a significant effect of treatment, this was further investigated using a Cox proportional hazard model with a frailty term to adjust for the grouping effect of treatment replicates (Basket).

Feeding rate analysis

Feeding rate per basket was calculated as the number of mussels consumed per day per sea star to adjust for deaths during the experiment. Feeding rate was modelled as a function of the type of mussel fed (2 level factor wild or farmed), treatment (4 level factor), day (the number of days since tagging, integer), and a two-way interaction between treatment and day. A random effect (Basket) was included due to the repeated measures design. As feeding rate was a continuous variable with a lower bound of 0, an exponentially modified Gaussian error distribution with a log link was used within a Bayesian framework using the R package brms [42]. Priors were placed on the intercept and coefficients of all models, both Normal (0, 5), except the truncated lognormal model for righting time (Sect. "Sea star health—righting time") that used flat prior defaults in brms.

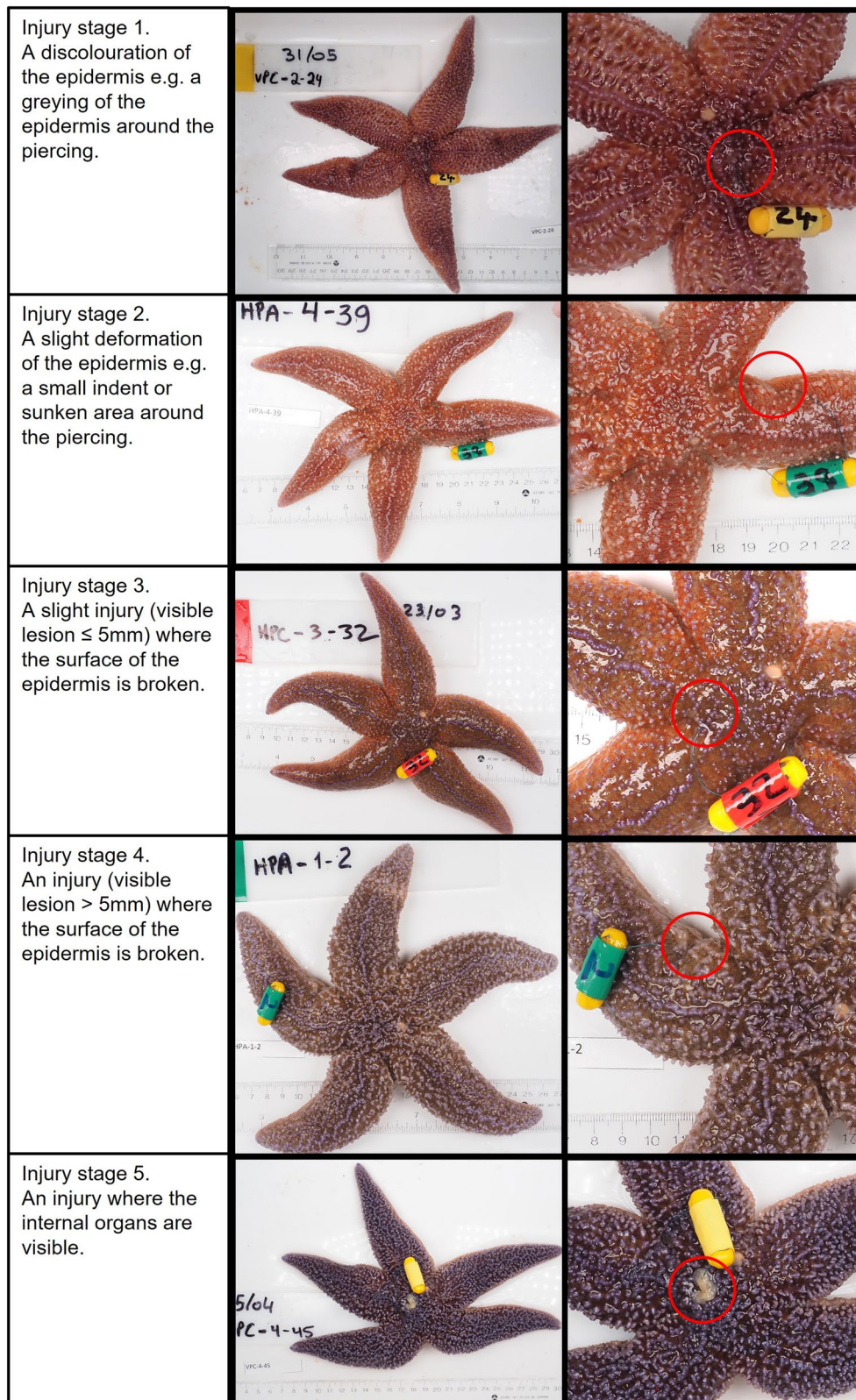


Fig. 2 Typical injuries for injury categories 1–5 on the 6 point injury scale; category 0 was uninjured

All models were run using four parallel MCMC chains, posterior predictive checks (Additional file 1: Fig. S4) and adequate mixing of chains was visually inspected, and all R-hat (Gelman–Rubin statistic) were ≤ 1.00 . R-hat is a model convergence diagnostic that compares chain estimates for model parameters; if chains have not mixed well, R-hat is generally larger than 1 [43]. Models used 6000 iterations with 3000 warm-up interactions. Model results are reported as the mean of the posterior distribution and the associated 95% credible intervals (CIs).

Probability of tag-related injury

Probability of injury was analysed as an ordinal regression using a cumulative distribution with a probit link function (brms, [42]). Probability of injury was modelled as a function of treatment (4 level factor), day (number of days since the sea star was tagged, integer), and the interaction between treatment and day. A random effect Basket/Individual was included to control for the repeated measures experimental design and to control for variation among baskets. The diameter of sea stars was included as a covariate in this model and for the model on righting time (Sect. "Sea star health—righting time") and was assessed using leave-one-out cross-validation [44]. In all cases, sea star diameter did not improve predictive accuracy and was not included in the final models.

Sea star health—righting time

Righting time was analysed using truncated lognormal distribution (brms, [42], 2021; Sect. "Feeding rate analysis") as a function of main effects treatment (4-level factor) and day (Integer) and a two-way interaction between treatment and day, with the random effect Basket/Individual (Sect. "Probability of tag-related injury").

Field experiment

Ten sea stars (mean diameter \pm SE 173 ± 6 mm) were tagged with V9 acoustic transmitters with a nominal delay of 5 min (Innovasea Inc.). Sea stars were tagged using the Horizontal Piercing of the Central Body (HPC) method on June 23, 2021 ($n=7$) and August 28, 2021 ($n=3$) and released within an acoustic receiver array maintained for a large project at Tourelle, Quebec (49.17, – 66.37). Sea stars were collected by divers from within the acoustic array and measured and tagged aboard the research vessel before being returned by divers to their capture locations within the acoustic telemetry array. The tagging procedure took ~ 15 min and individuals were held in 40 L coolers filled with fresh seawater while awaiting processing and subsequent release. As

sea star tracking was part of a large project studying the movements of benthic invertebrates, the array covered an area ~ 3 km \times 4 km and depths between 10 and 170 m. The placement of acoustic receivers was informed via a range test [45]. The frequency of detections logged by each receiver was modelled as a function of distance and the resulting detection function used to optimise the distance between receivers. The distance between receivers varied between 250 and 450 m, depending on depth, to attain a detection probability of ~ 0.8 .

Data pre-processing

Sea star trajectories were visually assessed before pre-processing to assess the presence of positions with a large error to signal ratio [46] and those potentially created by starballing [31]. Positions with a large error to signal ratio typically presented as large apparent step lengths that then immediately returned very close to the previous location, creating an acute turn angle or 'spike' in the trajectory [46]. These positions are usually associated with a large positional error or a movement speed that is beyond the limits of the tagged animal. However, given the possibility of starballing [31] it was important to visually assess trajectories as such movements would exceed the self-propelled speeds of sea stars and legitimate movements could have been removed by simply speed filtering data. Scatterplots of step length (distance travelled per detection period) and speed (distance/time between detections) were used to identify potential outlying positions where a sea star may have moved greater distances at higher speeds. These potential outliers were identified in the sea star's movement track where it was assumed that a starballing movement would result in a large movement, but contrary to positions with a large positional error, the sea star would not immediately return to its original position. Similarly, to assess the possibility of tide-assisted movement, either through starballing or the death of a sea star and subsequent detachment from the substrate, the relation between step length, speed, and time from high tide were investigated using generalised additive mixed models (GAMMs) in R library mgcv [47]. There was no relationship between distance, speed, or the time from high tide (Additional file 1: Tables S2, S3). Therefore, based on visualisations and modelling, it was deemed that there was no tide-assisted movement during the tracking period and data were subsequently filtered for high positional error and high speed positions before further analysis.

The positional error of the acoustic telemetry array was assessed by comparing two measures of error, Horizontal Positioning Error (HPE) and HPEm, that are associated with the synchronisation transmitters using

linear regression [48, 49]. HPE is a relative measure of error sensitivity, whereby a detection associated with a high HPE provides less information on the position of a sea star relative to a detection with a lower HPE. HPE_m is the measured error between a calculated position and its known location (e.g., a GPS position of a transmitter; see [50] for full definition). Subsequently, sea star telemetry data was restricted to detections with an HPE ≤ 6, ensuring a maximum error of 22 m (mean 3 m ± 0.4), and retaining ~ 77% of the field data. Data were then speed filtered to remove positions where the speed was > 15 cm/min [51], which retained 43% of the field data. Based on laboratory results, telemetry data were also restricted to the first 6 weeks after release when the likely effects of tagging (i.e., mortality risk or severe injury) and the probability of tag loss were smallest. This resulted in 6 weeks of data for the sea stars tagged in June and 3 or 4 weeks of data for the sea stars tagged in August due to the receivers being removed temporarily for data downloading at the end of September 2021. The first 24 h of data post-release was removed to limit any impact of handling on sea star behaviour.

Movement and space use of sea stars

Since the likely distance moved by sea stars within the sampling delay (5 min) was smaller than the maximum positional error, movement of sea stars and changes in the distributions of sea star positions were aggregated to produce weekly estimates. The weekly distribution of

sea star positions was quantified using minimum convex polygons [52] within the R library *amt* [53]. Overlap of MCPs and the distance between MCP centroids were calculated between successive weeks to quantify the potential displacement of sea stars. The spatial overlap between sequential MCPs for each sea star was calculated for both the 0.50 and 0.95 MCPs and defined as the proportion of MCP week_{*i*} that overlaps MCP week_{*i*+1} (Eq. 1, sensu [54]):

$$HR_{i,i+1} = \frac{A_{i,i+1}}{A_i}, \tag{1}$$

where HR_{*i*,*i*+1} is the proportion of MCP in week *i* (e.g., week 1) that overlaps the MCP in week *i* + 1 (week 2), *A_i* is the area of MCP week *i* and *A_i,*i*+1* is the area of overlap between both MCPs (e.g., area shared by week 1 and week 2).

Results

Laboratory experiments

Survival and tag retention analyses

The probability of survival for the different treatment groups did not vary significantly over time, therefore there was no effect of tagging on survival (log rank test, *p* = 0.190, Fig. 3a). Tag retention probability differed significantly between treatments (log rank test, *p* = 0.012, Fig. 3b). The probability of tag retention remained above 90% for the HPC treatment, however, both HPA and VPC tagging methods resulted in about 50% tag loss after 90 days and 119 days, respectively (Fig. 3b). There was no

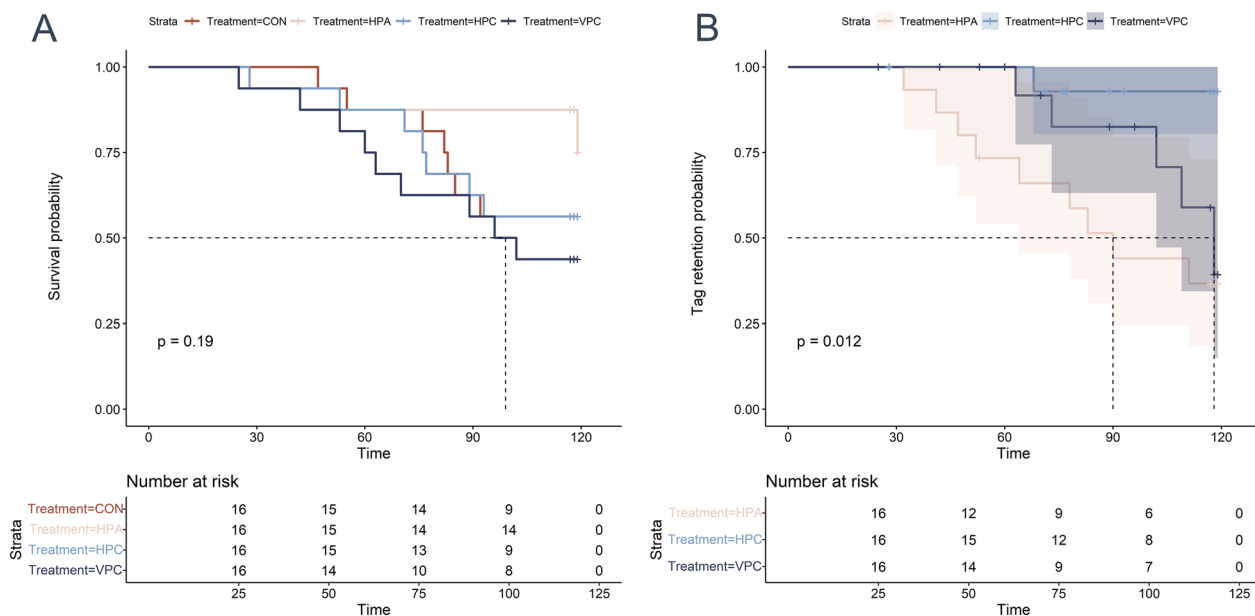


Fig. 3 Probability of (a) survival and (b) tag retention across treatments based on Kaplan–Meier estimates and log rank test *p* values. Black dashed line = median survival or tag retention (i.e., when 50% of sea stars had died or lost their tag)

overlap in the CIs of HPA and HPC after day 90 of the experiment. Results from the Cox proportional model for the probability of tag loss indicated that tag loss was significantly less likely for the HPC method compared to the HPA method ($\beta = -2.79$, $p < 0.05$, $HR = 0.062$ [0.005–0.71 95% CI]). HPA and VPC treatments did not differ significantly ($\beta = -1.019$, $p = 0.230$) and there was a significant effect of sea star diameter on tag retention, whereby larger sea stars were less likely to have lost their tags ($\beta = -0.395$, $p = 0.032$, $HR = 0.674$ [0.470–0.966]). There was no significant interaction between treatment and sea star diameter (likelihood ratio test, $p = 0.648$).

Feeding rate analysis

The feeding rate of all tagged sea stars decreased throughout the study period relative to the control group (Fig. 4). The rate of decrease was similar for all treatments with considerable overlap of the CIs ($\beta_{HPA:Day} = -0.03$ [-0.03, -0.02]; $\beta_{HPC:Day} = -0.04$ [-0.05, -0.03], $\beta_{VPC:Day} = -0.04$ [-0.05, -0.04]; Fig. 4). There was a negative effect of farmed mussels on the feeding rate of sea stars compared to wild caught mussels (Farmed mussels = -1.22 [-1.42, -1.04]).

Probability of tag-related injury

The probability of injury differed between HPC and the other treatments ($\beta_{HPA} = 0.74$ [0.08, 1.43] and $\beta_{VPC} = -1.41$ [-2.48, -0.50]) and there was a small increase in the probability of injury over time for VPC relative to HPC ($\beta_{HPA:Day} = 0.01$ [-0.01, 0.02] and $\beta_{VPC:Day} = 0.03$ [0.01, 0.05]; Fig. 5). Fourteen days after tagging, the probability of injury remained small for HPC and VPC, however, the probability of remaining uninjured for the HPA treatment group had declined to ~50%. After 28 days, the probability of a small injury (≤ 5 mm, category 3) was similar to being uninjured (category 0) for the HPA treatment. After 56 days, the probability of injury had increased further, and CIs of the uninjured and injured categories overlapped; this was particularly marked for the HPA treatment (Fig. 5). The rate of autonomy was not explicitly investigated; however, 9 sea stars lost arms during the experiment; 6 of these were associated with category 5 injuries (VPC $n = 4$, HPC $n = 1$, Control $n = 1$), for which between 1 and 3 arms were lost. In the final weeks of the experiment, a control sea star lost 3 arms between 31 May and 5 July. The remaining

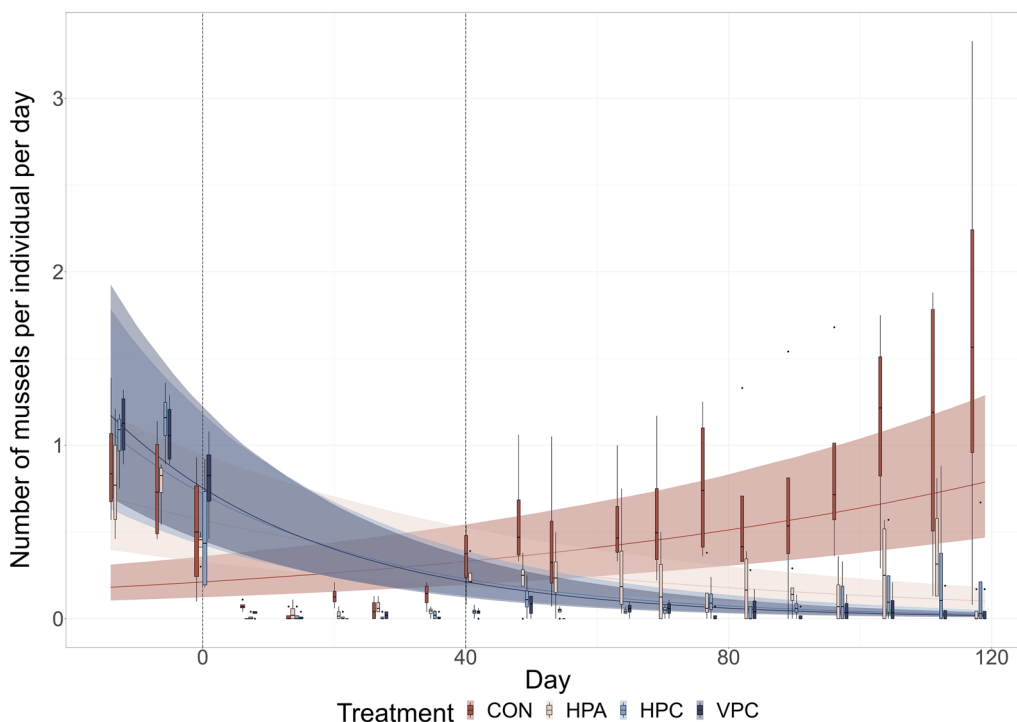


Fig. 4 Conditional effects and 95% CI of a two-way interaction between treatment and number of days since tagging on sea star feeding rate. Day 0 = day of tagging, preceded by 2 weeks of acclimatisation. Dashed lines mark the start (day 0) and the end of the farmed mussel diet (day 40). The superimposed boxplot is the number of mussels per individual per day for each treatment at each time step. The horizontal line indicates the median, lower, and upper hinges corresponding to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the hinge to no further than 1.5x the inter-quartile range

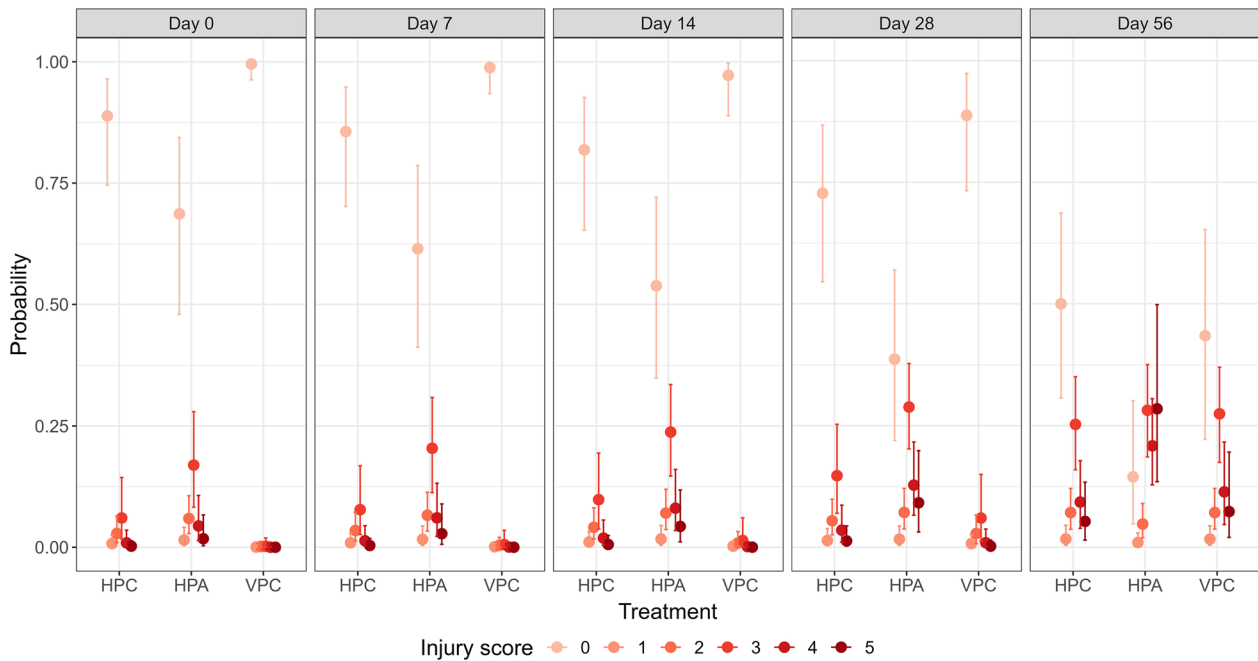


Fig. 5 Conditional effects and 95% credible intervals for the probability of injury as a function of the interaction between treatment and days since tagging. Injury scored on a 6 point index: 0—no visible injury, 1—discolouration of the epidermis, 2—slight deformity, 3—slight injury \leq 5mm, 4—injury $>$ 5 mm, 5—internal organs visible

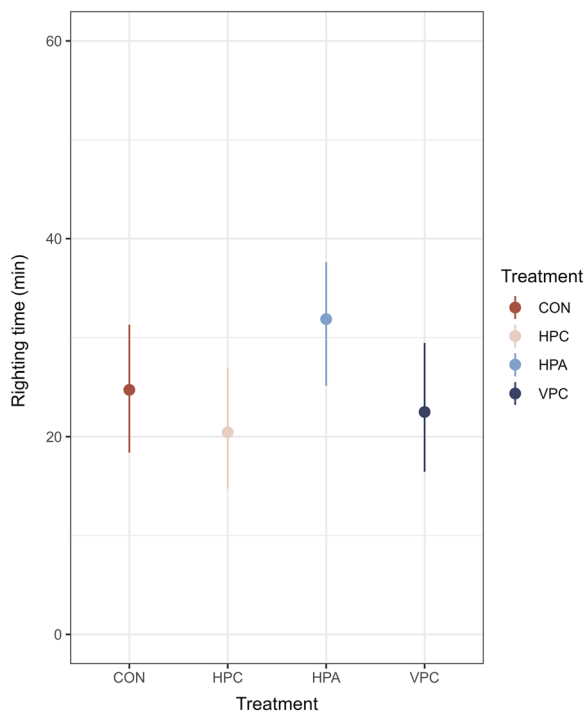


Fig. 6 Conditional effects and 95% CI of tagging treatment on righting time

instances were of single arm losses; 1 in HPA treatment (an untagged arm), and 1 in the VPC treatment.

Righting times

Several sea stars in each group, including the control, failed to completely right themselves within 60 min for all groups including the control (Additional file 1: Fig. S5). There was considerable overlap of the CIs between treatments (Fig. 6; $\beta_{HPC} = -0.24 [-0.65, 0.16]$; $\beta_{HPA} = 0.41 [-0.01, 0.84]$; $\beta_{VPC} = 0.12 [-0.54, 0.29]$), suggesting righting times varied, were similar between treatment groups, and did not differ from the Control (Fig. 6). Posterior predictive checks suggested a slight lack of model fit (Additional file 1: Fig. S4C). The predictive accuracy of models was not improved by including day or an interaction between day and treatment.

Field experiment

Tagged sea stars were released at depths of 10m and 15 m and remained between 10 and 20 m during tracking. After pre-processing, there were 8275 sea star detections (range n detections per sea star, 112–1242), and between 5 and 296 positions per week (mean n detections per

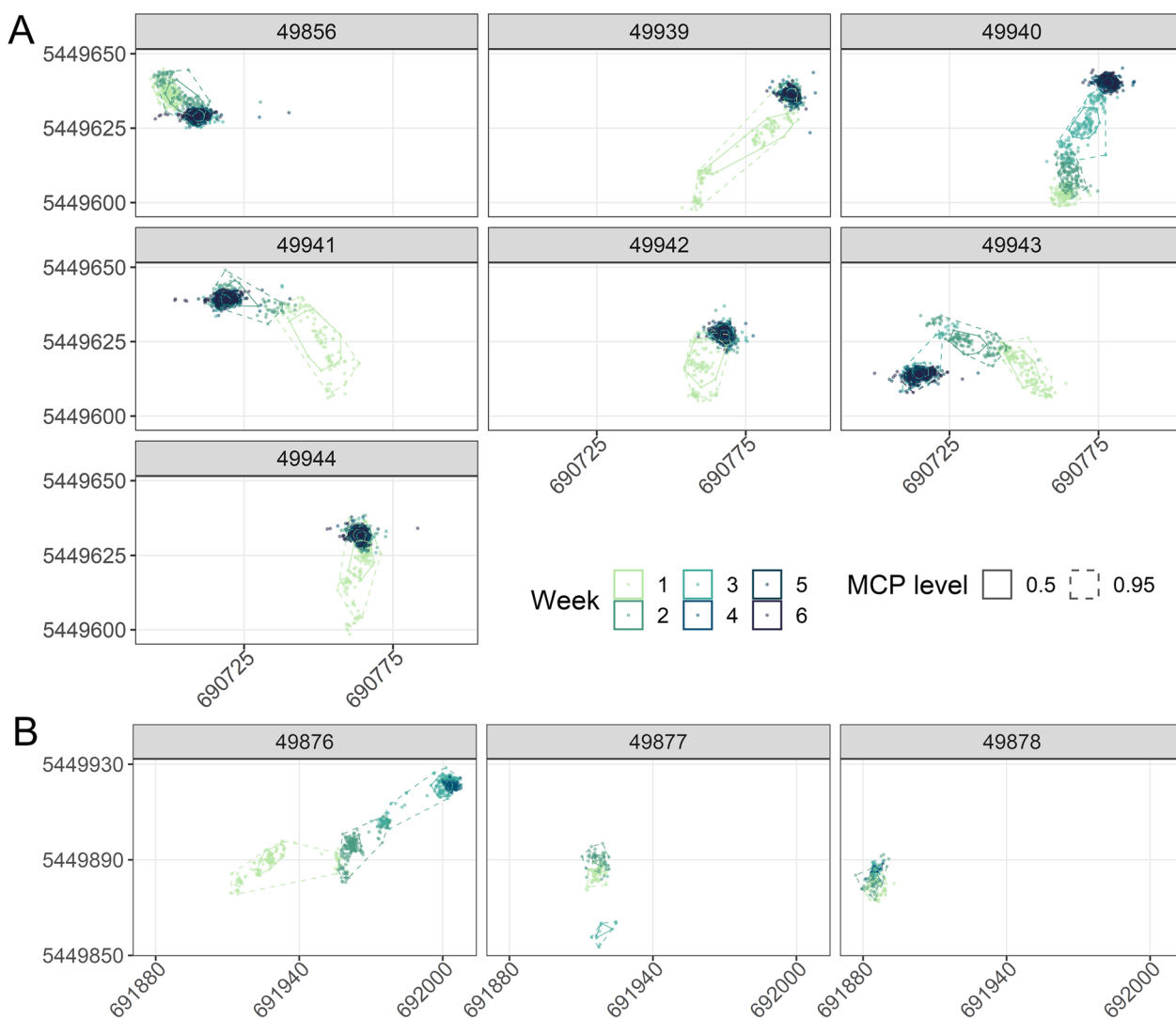


Fig. 7 Weekly minimum convex polygons. **a** Sea stars tagged and released on 23 June 2021 and **(b)** those released on 28 August 2021. Coordinates are in metres (UTM zone 19N)

week \pm 1SE, 156 ± 9). The mean speed for sea stars was $8 \text{ cm/min} \pm 0.1$ (mean weekly speed per sea star \pm 1SE, range $7 \text{ cm/min} \pm 0.4$ to $9 \text{ cm/min} \pm 1$). The size of both 95% and 50% MCPs continued to decrease over the first 3 or 4 weeks of tracking for both individuals tagged in June and those tagged in August (Fig. 7; Additional file 1: Fig. S6). The degree of overlap between sequential MCPs varied between individuals and between weeks (Additional file 1: Fig. S7). Similarly, the distance moved, defined here as the distance between the centroids of sequential MCPs, also decreased in 2–3 weeks after release as the overlap between MCPs continued to increase. All MCPs overlapped by 50% by the 5th week of the study (Fig. 8).

Discussion

Tagging soft-bodied echinoderms, such as *A. rubens*, remains challenging with injury and significant alterations of behaviour and condition evident across all tagging treatments tested. While acoustic telemetry offers the possibility of autonomous data collection on echinoderm movement, none of the tagging methods tested could provide longer term (> 4 weeks) attachment without deleterious effects on sea star condition under laboratory conditions due to injury and reduced feeding rate. Laboratory and field data suggest that 2–4 weeks is the maximum period within which conclusions about *A. rubens* behaviour could be drawn with reasonable certainty. Although tagging was not well tolerated in the later stages of the study,

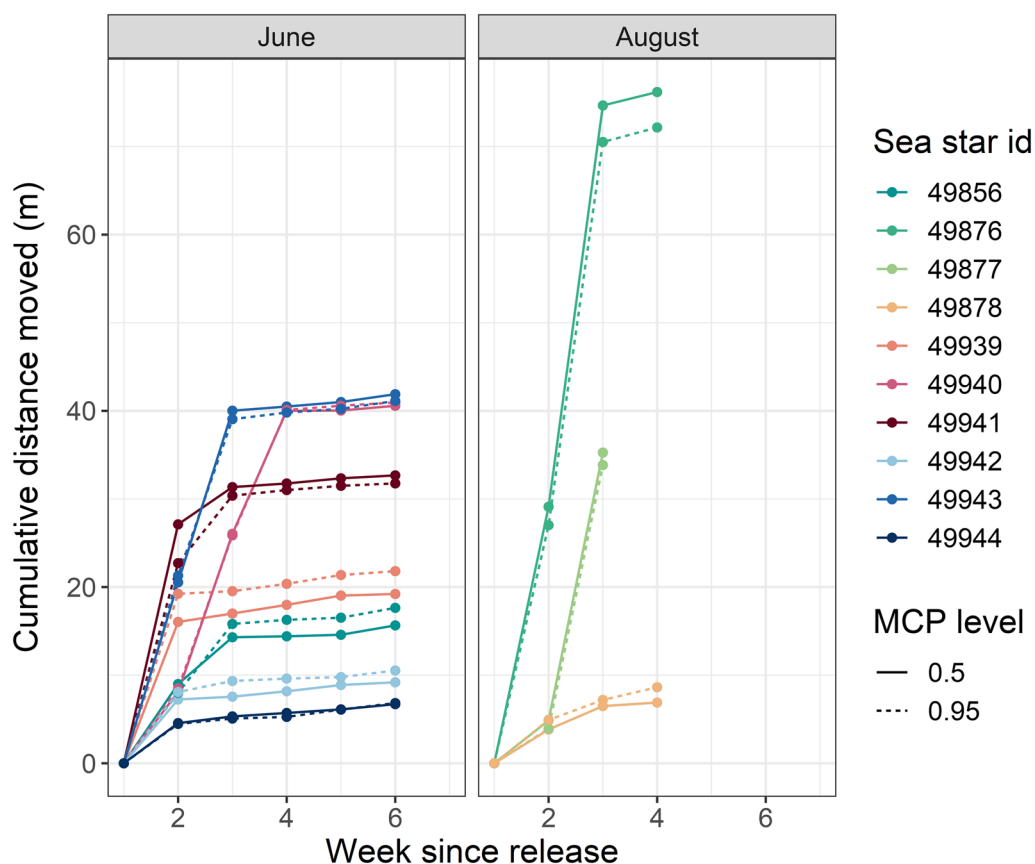


Fig. 8 Cumulative distance moved per week, calculated as the cumulative distance between the centroids of weekly minimum convex polygons

tag retention rate for the worst performing method (HPA) was ~50% after 90-day post-tagging. This is comparable to other studies; for example, Miyoshi et al. [29] observed that 50% of tags were lost by 90 days and Chim and Tan [28] observed that 50% of tags were lost by 60 days. Evidence of high tag retention, despite low feeding rates and visible injury, should caution against evaluating tagging success simply in terms of tag retention; gathering detailed movement data from individuals under significant physical stress and in degraded condition may result in inaccurate estimates of movement metrics and behaviours.

Laboratory experiments

Survival probability remained above 50% for all groups during the first 90 days of the experiment and there was no difference in the probability of survival between groups, suggesting a limited effects of tagging on survival. However, there was a low number of events during both the survival experiment and the tag retention experiment that could have resulted in a lack of statistical power to detect differences between groups. Tag retention was higher for HPC compared to the HPA treatment and did

not differ between HPC and VPC. HPA tag placement was perhaps the treatment where it was easiest for the sea stars to touch the tag with their other arms and this may have contributed to greater injury and earlier tag loss. There was overlap in tag retention between HPC and VPC, suggesting that a central tag placement that avoids the arms potentially reduces tag loss via rejection of foreign material, such as the nylon string (e.g., [55]). Despite the consistent tag retention rate observed for HPC, to have confidence that natural behaviours are observed in the field and that tagging will not result in excess mortality, all possible measures of tagging impacts should be considered.

Feeding rate was low for all treatments. Sea stars were fed approximately weekly so there were only two feeding occasions that occurred during the period before tagging. Unfortunately, tagging also coincided with a change to farmed mussels, which were larger than the wild mussels that had been collected by divers which may have contributed to the precipitous fall in the feeding rate immediately after tagging. It was not possible to disentangle the change in mussel diet from the effect of tagging due to the small number of data

points per treatment before tagging ($n=2$). However, feeding rate in the control group did improve after day 40 of the experiment when wild mussels were available again, but the feeding rate did not improve for the treatment groups, remaining close to zero until the end of the experiment. This suggests that tagging treatments impacted sea star foraging behaviour either directly via difficulty in processing prey or indirectly via a loss in physical condition that prevented sea stars from profiting from the change back to wild mussels as seen in the control group feeding rate. Sea stars were fed farmed mussels for 40 days, which is not long enough to trigger autolysis or autotomy, although they may have experienced a depletion of their energy reserves [56]. Tagging likely affected the ability to feed in different ways, with the possible effect of the VPC treatment, which pierced the sea star through the mouth, being perhaps the most self-evident; however, HPA and HPC sea stars fared just as badly. Piercing the arm (HPA) not only limited movement, but also likely interfered with the sea stars' ability to handle mussels. While the HPC treatment did not affect the mouth parts or result in an increased probability of injury as observed for the HPA treatment, internal organs may have been accidentally damaged during tagging that were not immediately apparent. By 7- or 8-weeks post-tagging, all sea stars were just as likely to have some kind of an injury as to be uninjured (Fig. 5). These cumulative effects of reduced feeding, reduced energy reserves, and injury contributed to overall low sea star survival. The presence of injuries was not monitored for the control group as the detection of injuries within the treatment groups focussed solely on the area of the sea star in the vicinity of the tag. Nonetheless, a small number of injuries (3 'category 1' injuries and 1 'category 5' injury) were opportunistically recorded for the control group; unfortunately, it was not possible to elaborate on the cause of these injuries. Most instances of autotomy were associated with category 5 injuries and were likely a secondary response to physical injury and associated physiological effects (e.g., infection and reduced feeding). Although sea stars were removed carefully from their tanks during righting experiments, it is possible that disturbance from repeated handling could have contributed to arm losses, particularly if sea stars were severely injured or in poor condition, such as those with category 4 or 5 injuries. Autotomy has been linked to increased prey handling time and reduced feeding rates (e.g., [57]), which in turn could have exacerbated injury or poor condition of affected sea stars.

Righting times were highly variable across all groups, including the control, and at all stages of the experiment

with ~ 1 in 10 righting attempts taking more than the allowed 60 min. Although the righting time model indicates that tagging did not affect righting time, the posterior predictive check suggests a slight lack of model fit. An alternative model was explored where righting time was a function of injury type, however this model was too complex and could not converge. As there was a high level of individual-variability in righting times across all groups, including the control, it also could indicate there was some unidentified stressor within the experimental set-up that obscured differences between groups. The multiple stresses of reduced feeding and injury in the later stages of the experiment likely increased individual-level variability further.

Field studies

When considering a tagging method, the goal should be to maximise tag retention while minimising deleterious effects associated with tagging. Although some ambiguity remains around the effects of tagging due to small sample sizes and individual variability, the choice of HPC seems to have maximised tag retention and minimised injury, at least in the short-term. Due to logistical constraints, field work began before the laboratory study was completed, and therefore the decision to use HPC for the field trials was based on short-term tank observations and the assumption that, compared to the two other proposed methods, difficulties feeding and the probability of autotomy would be lower with HPC. While incidences of autotomy during the laboratory experiment were low across the HPA and HPC treatments, longer term changes (>4 weeks) in feeding behaviour and an increase in the prevalence of injuries were observed in all groups. All three measures used to quantify the distribution of weekly detections, area (m^2) of MCPs, overlap of sequential MCPs, and the movement of MCP centroids, suggest increased movement in the 2–3 weeks after release followed by a gradual reduction in the spatial spread of detections, which could suggest a reduction in sea star movement. Due to the limited time frame of the study, it is difficult to interpret this initial period of movement and subsequent period of reduced space use. Initial movement could be a prolonged disturbance effect or a genuine period of activity unrelated to the tag and driven by other internal or external stimuli, although it was observed in almost all tagged sea stars. *A. rubens* has previously been observed to generally move between 1 and 7 m (net displacement) every 12 h and to alternate between stationary, moving, and digesting states, spending 1–2 days in each phase [25]. Given this pattern of observed behaviours, our observations likely indicate 2–3 weeks of normal movement, which would include periods of stationary and digesting behaviours as

indicated by areas of concentrated detections identified by the 50% MCPs. The apparent reduction in space use in the 4–5-week post-tagging would then indicate that the condition of the tagged sea stars was beginning to decline, or even that tags may have been lost.

A large amount of data was lost in pre-processing due to speeds that were beyond what would be physically possible for a sea star [51]. While speeds considered beyond the maximum possible by a tagged animal can occur whenever there is a measure of uncertainty associated with a position, the error to signal ratio can dominate the data when tracking slow-moving animals such as sea stars, e.g., if the majority of step lengths are <2 m then a measurement error of just 1 m is considerable and will have a profound effect on the resultant movement path. To compensate for this effect, we focussed on describing the weekly distributions of points as an indicator of sea star displacement. Another option would have been to use a tag with a much longer nominal delay, and or to consider a priori the acceptable level of HPE relative to the distance moved per transmission delay, e.g., the size of the HPE error should be half the size of the distance moved during the transmission delay [29].

Sea star movements were of a similar magnitude to those observed in previous studies; for example, *Coscinasterias muricata* tagged with data loggers that record depth and temperature sensors moved a total vertical distance of between 53.3 and 178.7 m over a 2-week period [27]. *Asterias amurensis* tagged with acoustic tags (Vemco V9 dimensions) attached to the arm using nylon fishing line had a mean movement during summer of 25.1 ± 18.9 m and a speed of 4.3 ± 9.1 m/day [29]; these V9 tags were placed on the arm of the sea star and were retained for 71 days. HPA tag placement had a retention probability of ~70% by day 70, however, HPA-tagged sea stars were as likely to be injured as uninjured by day ~56 post-tagging. It is therefore likely that tagging effects are species-specific, and that retention of foreign bodies, such as nylon string, can be affected by environmental conditions that can further contribute to physiological stress (e.g., temperature, [55]).

Conclusion

The experimental and field aspects of this study highlight the two principal problems when tracking soft-bodied benthic invertebrates, firstly the impacts of tagging on the health and behaviour of soft-bodied invertebrates, and second the ability of current acoustic telemetry systems to collect data at a biologically informative resolution. Considerable impacts on the condition and behaviour of tagged individuals were observed for all 3 attachment methods, which,

if laboratory results are representative of their success in the field, would limit their use to short-term observations (<4 weeks). However, this is still a much longer period than can be achieved using other available methods such as video or in situ diver observations. When comparing this study to others, it is clear that the impacts of tagging can differ considerably between species, suggesting that an attachment method that worked for one species should not, without thorough testing, be generalised to another. Thus, although acoustic telemetry presents an opportunity to record novel data with finer and finer resolution, it is necessary to remain aware that finer resolution does not necessarily convey more biological information. Sea stars and other similar benthic organisms likely respond to spatial and temporal processes that occur at centimetre and second resolution, and while we can use acoustic telemetry to describe generalised movements as part of an observational study, it is not currently possible to accurately quantify movement in response to dynamic spatial or temporal environmental processes in the field. This area remains a considerable challenge for the study of slow-moving benthic organisms. However, responses to external stimuli can still be conducted in laboratory settings and integrated with observational field data within simulation models that can aid in the development and testing of new hypotheses.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-024-00362-5>.

Additional file 1: Figure S1. Ambient water temperature during acclimatisation and the experimental period. The start of the experiment is marked by a vertical dashed line. **Figure S2.** Salinity ppt during acclimatisation and the experimental period. The start of the experiment is marked by a vertical dashed line. **Figure S3.** Sea star attachment methods a) Horizontal Piercing of the Central body, b) Horizontal Piercing on the Arm, and c) Vertical Piercing of the Central body. **Figure S4.** Posterior predictive checks that compare the observed variable y to 100 simulated datasets y_{rep} for a) feeding rate, b) probability of injury, and c) righting time models. **Figure S5.** Righting times in minutes per righting attempt for each of the four Treatment levels and Basket replicates (1–4). The thickness of boxes represents the number of sea stars per righting attempt. The horizontal line indicates the median, lower, and upper hinges corresponding to the first and third quartiles (the 25th and 75th percentiles). Whiskers extend from the hinge to no further than $1.5 \times$ the inter-quartile range. **Table S1.** Summary table of weekly minimum convex polygon data. n = number of detections per week. **Figure S6.** Area m^2 of weekly sea star minimum convex polygons. **Figure S7.** Proportion of MCP overlap between successive weeks since release. **Figure S8.** Distribution of sea star detections per month for entire tracking period A) June 2021 to December 2021 or B) August 2021 to February 2022. **Table S2.** Parametric coefficients for model 1 (response variable step length) and model 2 (response variable speed). **Table S3.** Approximate significance of smooth terms for model 1 (response variable step length) and model 2 (response variable speed).

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Author contributions

CWM conceived the study. J-BN and KAM designed the experiment. J-BN developed the experimental methods, and led the experimental phase. J-BN and M-FL led the field phases of the study. KJL led the analysis and writing of the manuscript. J-BN wrote the experimental methods. All authors contributed to the writing of the manuscript and the interpretation of the results.

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Availability of data and materials

Additional Supporting Information may be found in the online version of this article. The datasets generated and/or analysed during the current study will be available in the Open Data repository, the Government of Canada Open Data portal (<http://open.canada.ca>).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

- Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE, Whoriskey FG. Aquatic animal telemetry: a panoramic window into the underwater world. *Science*. 2015;348:1255642. <https://doi.org/10.1126/science.1255642>.
- Matley JK, Klinard NV, Barbosa Martins AP, Aarestrup K, Aspillaga E, Cooke SJ, Cowley PD, Heupel MR, Lowe CG, Lowerre-Barbieri SK, Mitamura H, Moore JS, Simpfendorfer CA, Stokesbury MJW, Taylor MD, Thorstad EB, Vandergoot CS, Fisk AT. Global trends in aquatic animal tracking with acoustic telemetry. *Trends Ecol Evol*. 2022;37:79–94. <https://doi.org/10.1016/j.tree.2021.09.001>.
- Wright BE, Riemer SD, Brown RF, Ougzin AM, Bucklin KA. Assessment of harbor seal predation on adult salmonids in a Pacific Northwest estuary. *Ecol Appl*. 2007;17:338–51. <https://doi.org/10.1890/05-1941>.
- Letnic M, Webb JK, Jessop TS, Florance D, Dempster T, Rhodes J. Artificial water points facilitate the spread of an invasive vertebrate in arid Australia. *J Appl Ecol*. 2014;51:795–803. <https://doi.org/10.1111/1365-2664.12232>.
- Chambault P, Dalleau M, Nicet JB, Mouquet P, Ballorain K, Jean C, Ciccione S, Bourjea J. Contrasted habitats and individual plasticity drive the fine scale movements of juvenile green turtles in coastal ecosystems. *Mov Ecol*. 2020;8:1. <https://doi.org/10.1186/s40462-019-0184-2>.
- Marsden JE, Blanchfield PJ, Brooks JL, Fernandes T, Fisk AT, Futia MH, Hlina BL, Ivanova SV, Johnson TB, Klinard NV, Krueger CC, Larocque SM, Matley JK, McMeans B, O'Connor LM, Raby GD, Cooke SJ. Using untapped telemetry data to explore the winter biology of freshwater fish. *Rev Fish Biol Fish*. 2021;31:115–34. <https://doi.org/10.1007/s11160-021-09634-2>.
- Verhelst P, Brys R, Cooke SJ, Pauwels I, Rohtla M, Reubens J. Enhancing our understanding of fish movement ecology through interdisciplinary and cross-boundary research. *Rev Fish Biol Fish*. 2022;33:111–35. <https://doi.org/10.1007/s11160-022-09741-8>.
- Florko KRN, Davidson ER, Lees KJ, Hammer LJ, Lavoie M-F, Lennox R, Simard É, Archambault P, Auger-Méthé M, McKindsey CW, Whoriskey FG, Furey NB. Tracking movements of decapod crustaceans: a review of a half-century of telemetry-based studies. *Mar Ecol Prog Ser*. 2021;679:219–39. <https://doi.org/10.3354/meps13904>.
- Glazer RA, Delgado GA, Kidney JA. Estimating queen conch (*Strombus gigas*) home ranges using acoustic telemetry: implications for the design of marine fishery reserves. *Gulf Caribb Res*. 2003;14:79–89. <https://doi.org/10.18785/gcr.1402.06>.
- Schlaff A, Menéndez P, Hall M, Heupel M, Armstrong T, Motti C. Acoustic tracking of a large predatory marine gastropod, *Charonia tritonis*, on the Great Barrier Reef. *Mar Ecol Prog Ser*. 2020;642:147–61. <https://doi.org/10.3354/meps13291>.
- Matsumoto Y, Takami H. The effect of brown kelp phenology on abalone locomotion and spatial distribution: acoustic telemetry and spatially explicit individual-based model approach. *Fish Sci*. 2022;88:693–701. <https://doi.org/10.1007/s12562-022-01640-y>.
- Sclafani M, Bopp J, Havelin J, Humphrey C, Hughes SWT, Eddings J, Tettelbach ST. Predation on planted and wild bay scallops (*Argopecten irradians irradians*) by busyconine whelks: studies of behavior incorporating acoustic telemetry. *Mar Biol*. 2022;169:66. <https://doi.org/10.1007/s00227-022-04033-y>.
- Orrell DL, Hussey NE. Using the VEMCO Positioning System (VPS) to explore fine-scale movements of aquatic species: applications, analytical approaches and future directions. *Mar Ecol Prog Ser*. 2022;687:195–216. <https://doi.org/10.3354/meps14003>.
- Long M, Jordaan A, Castro-Santos T. Environmental factors influencing detection efficiency of an acoustic telemetry array and consequences for data interpretation. *Anim Biotelemetry*. 2023;11:18. <https://doi.org/10.1186/s40317-023-00317-2>.
- Paine RT. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology*. 1976;57:858–73. <https://doi.org/10.2307/1941053>.
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT. Challenges in the quest for keystones: identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *Bioscience*. 1996;46:609–20. <https://doi.org/10.2307/1312990>.
- Menge BA, Sanford E. Ecological role of sea stars from populations to meta-ecosystems. In: Lawrence J, editor. *Starfish: biology and ecology of the Asteroidea*. Baltimore: Johns Hopkins University Press; 2013. p. 67–80.
- Caballes CF, Byrne M. Demography, ecology, and management of sea star populations: introduction to a special issue in *The Biological Bulletin*. *Biol Bull*. 2021;241:217–8. <https://doi.org/10.1086/718198>.
- Ruiz-Ramos DV, Schiebelhut LM, Hoff KJ, Wares JP, Dawson MN. An initial comparative genomic autopsy of wasting disease in sea stars. *Mol Ecol*. 2020;29:1087–102. <https://doi.org/10.1111/mec.15386>.
- Wolf F, Seebass K, Pansch C. The role of recovery phases in mitigating the negative impacts of marine heatwaves on the sea star *Asterias rubens*. *Front Mar Sci*. 2022;8:790241. <https://doi.org/10.3389/fmars.2021.790241>.
- Branham JM, Reed SA, Bailey JH, Caperon J. Coral-eating sea stars *Acanthaster planci* in Hawaii. *Science*. 1971;172:1155–7. <https://doi.org/10.1126/science.172.3988.1155>.
- Savy S. Activity pattern of the sea-star, *Marthasterias glacialis*, in Port-Cros Bay (France, Mediterranean Coast). *Mar Ecol*. 1987;8:97–106. <https://doi.org/10.1111/j.1439-0485.1987.tb00177.x>.
- Kim SL, Thurber A, Hammerstrom K, Conlan K. Seastar response to organic enrichment in an oligotrophic polar habitat. *J Exp Mar Biol Ecol*. 2007;346:66–75. <https://doi.org/10.1016/j.jembe.2007.03.004>.
- Gaymer CF, Dutil C, Himmelman JH. Prey selection and predatory impact of four major sea stars on a soft bottom subtidal community. *J Exp Mar Biol Ecol*. 2004;313:353–74. <https://doi.org/10.1016/j.jembe.2004.08.022>.
- Himmelman JH, Dutil C, Gaymer CF. Foraging behavior and activity budgets of sea stars on a subtidal sediment bottom community. *J Exp Mar Biol Ecol*. 2005;322:153–65. <https://doi.org/10.1016/j.jembe.2005.02.014>.

26. Drolet D, Himmelman JH. Role of current and prey odour in the displacement behaviour of the sea star *Asterias vulgaris*. *Can J Zool.* 2004;82:1547–53. <https://doi.org/10.1139/z04-135>.
27. Lamare MD, Channon T, Cornelisen C, Clarke M. Archival electronic tagging of a predatory sea star—testing a new technique to study movement at the individual level. *J Exp Mar Biol Ecol.* 2009;373:1–10. <https://doi.org/10.1016/j.jembe.2009.02.010>.
28. Chim CK, Tan KS. A method for the external attachment of acoustic tags on sea stars. *J Mar Biol Assoc UK.* 2013;93:267–72. <https://doi.org/10.1017/S0025315411002128>.
29. Miyoshi K, Kuwahara Y, Miyashita K. Tracking the northern Pacific sea star *Asterias amurensis* with acoustic transmitters in the scallop mariculture field of Hokkaido. *Japan Fish Sci.* 2018;84:349–55. <https://doi.org/10.1007/s12562-017-1162-5>.
30. Barker MF, Nichols D. Reproduction, recruitment and juvenile ecology of the starfish, *Asterias rubens* and *Marthasterias glacialis*. *J Mar Biol Assoc UK.* 1983;63(4):745–65. <https://doi.org/10.1017/S0025315400071198>.
31. Sheehan EV, Cousens SL. “Starballing”: a potential explanation for mass stranding. *Mar Biodiv.* 2017;47:617–8. <https://doi.org/10.1007/s12526-016-0504-3>.
32. Kvalvågnaes K. Tagging of the starfish, *Asterias rubens* L. *Sarsia.* 1972;49:81–8. <https://doi.org/10.1080/00364827.1972.10411210>.
33. MacGregor KA, Lavoie M-F, Robinson SMC, Simard É, McKindsey CW. Lab and field evaluation of tagging methods for the use of acoustic telemetry to observe sea urchin movement behaviour at ecologically relevant spatio-temporal scales. *Anim Biotelemetry.* 2023;11:3. <https://doi.org/10.1186/s40317-022-00309-8>.
34. Himmelman JH, Dutil C. Distribution, population structure and feeding of subtidal seastars in the northern Gulf of St. Lawrence. *Mar Ecol Prog Ser.* 1991;76:61–72.
35. Keppel EA, Scrosati RA, Courtenay SC. Interactive effects of ocean acidification and warming on subtidal mussels and sea stars from Atlantic Canada. *Mar Biol Res.* 2014;11:337–48. <https://doi.org/10.1080/17451000.2014.932914>.
36. Capelle JJ, van Stralen MR, Wijsman JWM, Herman PMJ, Smaal AC. Population dynamics of subtidal blue mussels *Mytilus edulis* and the impact of cultivation. *Aquacult Environ Interact.* 2017;9:155–68. <https://doi.org/10.3354/aei00221>.
37. Jepsen N, Mikkelsen JS, Koed A. Effects of tag and suture type on survival and growth of brown trout with surgically implanted telemetry tags in the wild. *J Fish Biol.* 2008;72:594–602. <https://doi.org/10.1111/j.1095-8649.2007.01724.x>.
38. Ardor Bellucci LM, Smith NF. Crawling and righting behavior of the subtropical sea star *Echinaster (Othilia) graminicola*: effects of elevated temperature. *Mar Biol.* 2019;166:138. <https://doi.org/10.1007/s00227-019-3591-4>.
39. Watts SA, Lawrence JM. The effect of temperature and salinity interactions on righting, feeding and growth in the sea star *Luidia clathrata* (Say). *Mar Freshw Behav Physiol.* 1990;17:159–65. <https://doi.org/10.1080/10236249009378765>.
40. Therneau TM. A package for survival analysis in R. R package version 3.1–12; 2020. <https://cran.r-project.org/package=survival>.
41. Kassambara A, Kosinski M, Biecek P. survminer: Drawing Survival Curves using ‘ggplot2’. R package version 0.4.9. 2021.
42. Bürkner P. Bayesian item response modeling in R with brms and Stan. *J Stat Softw.* 2021;100:1–54.
43. Vehtari A, Gelman A, Simpson D, Carpenter B, Bürkner P-C. Rank-normalization, folding, and localization: an improved R-hat for assessing convergence of MCMC (with Discussion). *Bayesian Anal.* 2021;16:667–718. <https://doi.org/10.1214/20-BA1221>.
44. Vehtari A, Gelman A, Gabry J. Practical Bayesian model evaluation using leave-one-out cross validation and WAIC. *Stat Comput.* 2017;27:1413–32. <https://doi.org/10.1007/s11222-016-9696-4>.
45. Vemco. Vemco Range Test Software Manual. p 43. 2015. <https://support.vemco.com/s/downloads>.
46. Hurford A. GPS measurement error gives rise to spurious 180 turning angles and strong directional biases in animal movement data. *PLoS ONE.* 2009;4: e5632. <https://doi.org/10.1371/journal.pone.0005632>.
47. Wood SN. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J Roy Stat Soc (B).* 2011;73(1):3–36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>.
48. Skerritt DJ, Robertson PA, Mill AC, Polunin NVC, Fitzsimmons C. Fine-scale movement, activity patterns and home-ranges of European lobster *Homarus gammarus*. *Mar Ecol Prog Ser.* 2015;536:203–19. <https://doi.org/10.3354/meps11374>.
49. Coates JH, Hovel KA, Butler JL, Klimley AP, Morgan SG. Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery. *Mar Ecol Prog Ser.* 2013;486:189–201. <https://doi.org/10.3354/meps10365>.
50. Smith F. Understanding HPE in the VEMCO positioning system (VPS). 2013. Available: <https://go.innovasea.com/understanding-hpe-vps.pdf>.
51. Castilla JC, Crisp DJ. Responses of *Asterias rubens* to olfactory stimuli. *J Mar Biol Assoc UK.* 1970;50(03):829–47. <https://doi.org/10.1017/S0025315400005075>.
52. Johnson DH. The comparison of usage and availability measurements for evaluating resource preference. *Ecology.* 1980;61:65–71.
53. Signer J, Fieberg J, Avgar T. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol Evol.* 2019;9:880–90. <https://doi.org/10.1002/ece3.4823>.
54. Kernohan BJ, Gitzen RA, Millspaugh JJ. Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM, editors. *Radio tracking and animal populations.* Cambridge: Academic Press; 2001. p. 125–66.
55. Olsen TB, Christensen FEG, Lundgreen K, Dunn PH, Levitis DA. Coelomic transport and clearance of durable foreign bodies by starfish (*Asterias rubens*). *Biol Bull.* 2015;228:156–62. <https://doi.org/10.1086/BBLv228n2p156>.
56. St Pierre AP, Gagnon P. Effects of temperature, body size, and starvation on feeding in a major echinoderm predator. *Mar Biol.* 2015;162:1125–35. <https://doi.org/10.1007/s00227-015-2655-3>.
57. Ramsay K, Kaiser M, Richardson C. Invest in arms: behavioural and energetic implications of multiple autotomy in starfish (*Asterias rubens*). *Behav Ecol Sociobiol.* 2001;2001(50):360–5. <https://doi.org/10.1007/s002650100372>.

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