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Ecological consequences of supernumerary arms in eastern Pacific sea stars

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ABSTRACT: Pentameric symmetry characterizes echinoderms and is most readily observed in sea stars. However, some pentamerous sea star individuals deviate from the normal 5-arm pattern, most likely as a result of errors in regeneration, but the frequency of these deviations and their ecological consequences for the individuals are poorly understood. Here, we report the extent of deviations from pentamery in multiple populations of co-occurring sea star species and tested 3 potential advantages of supernumerary arms — increased oral surface area, increased feeding, and faster righting response — in 1 species, the bat star *Patiria miniata*. Using underwater surveys and behavioural experiments at 16 sites in Barkley Sound, British Columbia, Canada, we found individuals with atypical arm numbers in 5 of 9 pentamerous sea star species. There were significant differences among sites and species, with site-specific mean percentages of atypical sea stars ranging from 0.8 to 14.6% and species-specific mean percentages ranging from 0 to 10%. Bat stars had the highest proportion of individuals with atypical numbers of arms, with site-specific frequencies ranging from 0 to 25%. The probability of feeding and righting speed were similar between bat stars with and without supernumerary arms, but bat stars with supernumerary arms had slightly larger oral surface areas for a given arm length, which could confer an advantage in adherence to the substrate. Although the advantages of supernumerary arms for bat stars appear to be negligible, the lack of any clear disadvantage suggests that selection against atypical variants might be weak, leading to limited selection on the accuracy of regeneration in this species.

KEY WORDS: Asteroidea · Starfish · Adaptive function · Development · Pentaradial symmetry

1. INTRODUCTION

Animals in most taxa are bilaterally symmetric as adults. However, exceptions include cnidarians and ctenophores, which have radial or biradial symmetry, and echinoderms, which develop pentameral (i.e. 5-fold or pentaradial) symmetry as adults from bilaterally symmetric larvae (Ji et al. 2012). Pentamery is perhaps most easily observed in the subphylum Asterozoa, which includes brittle stars (class Ophiuroidea) and sea stars (class Asteroidea). Most asteroid families (20 of 34 living families) only have

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5-arm species. However, although most individuals within pentamerous species follow their family-specific pattern, a small proportion of individuals deviate, exhibiting 6 or more arms (Hotchkiss 2000; Table 1). These deviations and their ecological consequences for the atypical individuals are poorly understood.

A number of mechanisms can cause variation in arm number in pentamerous sea stars. Environmental stressors, such as high or low salinity and high temperature, occurring during metamorphosis can disrupt body plan development in sea stars. These stressors have resulted in non-pentamerous symmetry at least in the laboratory (i.e. 6 arms instead of 5; Watts et al. 1983, Marsh et al. 1986, Clark 1988, Balogh & Byrne 2021). Deviations from pentamery could also result from natural genetic variation, with the low prevalence of atypical numbers of arms possibly indicating strong selection for the pentamerous body plan. However, breeding experiments with 4- and 6-arm variants invariably yield 5-arm offspring, suggesting that genetic control of atypical arm number is unlikely (Hotchkiss 2000). More likely, there may be errors in the regeneration process following mechanical damage (Hotchkiss 2000) owing to, for example, partial predation. Indeed, arm loss to crab and fish predation is prevalent in many sea star populations (e.g. Lawrence et al. 1999, Pomory & Lares 2000, Budden et al. 2019).

The process of arm regeneration should be under strong selection in sea stars, as it allows the organism to regain some or all of its foraging ability and reproductive potential after a sublethal injury (Ramsay et al. 2001, Diaz-Guisado et al. 2006, Barrios et al. 2008, Budden et al. 2019). Although regenerating a lost arm often comes at a cost to somatic growth and reproduction, especially when food is limited (Maginnis 2006, Lawrence 2010), regenerating more arms than were lost could still be favoured if there are advantages in doing so. For example, supernumerary arms could accommodate additional gonads and/or pyloric caeca (i.e. lipid storage organs in sea star arms), which might

Table 1. Distribution (%) of naturally occurring arm numbers in pentamerous sea star species; na: not available

Species	Arm number				N	Source
	4	5	6	7+		
Family Archasteridae						
Archaster angulatus	1.5	97.1	1.3	0.1	876	Keesing (2017)
Archaster typicus		97			1707	Lawrence & Komatsu (1990)
Family Asteriidae						
Evasterias troschelii	0	100	0	0	106	This study
Orthasterias koehleri	0.2	99.8	0	0	475	This study
Pisaster brevispinus	0	100	0	0	2	This study
Pisaster ochraceus	0	100	0	0	986	Lawrence & Komatsu (1990)
Pisaster ochraceus	0	99.4	0.6	0	175	This study
Stylasterias forreri	0	94.1	5.9	0	11	This study
Family Asterinidae						
Anseropoda placenta	<0.01	97.8	2.1	<0.01	4333	Guillou & Diop (1988)
Aquilonastra minor	0	100	0	0	87	Kawase & Furukawa (2014)
Parvulastra exigua	1	99	0	0	100	Byrne & Anderson (1994)
Patiria miniata	0	96	4	0	na	Pearse (1993)
Patiria miniata	0.8	90	8.2	1	1125	This study
Patiria pectinifera	0.4	96.6	2.7	0.3	4561	Kawase & Furukawa (2014)
Family Asteropseidae						
Dermasterias imbricata	0	99	0.8	0.2	608	This study
Family Astropectinidae						
Astropecten indicus	0.7	97.8	1.5	0	134	Prabhu & Bragadeeswaran (2012)
Family Echinasteridae						
Henricia sp.	0	100	0	0	133	This study
Family Goniasteridae						
Mediaster aequalis	0	100	0	0	9	This study
Family Oreasteridae						
Pentaceraster cumingi	0.8	98.1	1.1	0	837	Galván-Villa et al. (2021)
Family Luidiidae						
Luidia clathrata	0	100	0	0	1143	Lawrence & Komatsu (1990)

increase fecundity and/or accelerate growth after regeneration. Supernumerary arms could also increase oral surface area and tube feet number, potentially increasing an individual's strength of adherence to the substrate or conferring advantages for locomotion and feeding (Lawrence 1988, Wu et al. preprint doi:10.48550/arXiv.1202.2219). There are few tests of these hypotheses, although Pearse (1993) detected no difference in gonadal and pyloric caecal indices between individual bat stars *Patiria miniata* with 5 versus 6 arms after 6 mo of ample feeding. In addition, Montgomery & Palmer (2012) found that additional arms did not significantly affect bat star crawling speed. Thus, any advantages of supernumerary arms for sea stars have yet to be demonstrated.

In this study, we examine the ecological consequences of supernumerary arms in northeastern Pacific sea stars. Our objectives are 2-fold. First, we establish the extent of deviations from pentamery in multiple populations of co-occurring sea star species, providing the largest interspecific and inter-site comparisons to date. Second, focusing on the species with the highest frequency of atypical arm number, we examine the potential advantages of supernumerary arms in terms of oral surface area, feeding (i.e. prey capture), and righting response, i.e. the ability of a sea star to return to a normal orientation after being inverted. Rapid righting following dislodgement by waves or by a predation attempt is critical for sea star feeding and escape from predators (Polls & Gonor 1975, Ardor Bellucci & Smith 2019), and Moore (1941) anecdotally observed slower righting by an 8-arm bat star than by its 5-arm counterparts. We also examine the association between supernumerary arms, colour polymorphism, and habitat features to gain insights into the determinants of the frequency of atypical sea stars.

2. MATERIALS AND METHODS

2.1. Sea star community surveys

To assess the frequency of sea stars with atypical arm numbers (i.e. fewer or more than 5), we performed 30 min roving surveys (1 to 3) using SCUBA at 16 rocky reef sites around Barkley Sound (Huu-ay-aht First Nations territory), on the west coast of Vancouver Island, British Columbia, Canada (Fig. 1, Table 2). Each survey was conducted by 2 divers, who recorded species and arm number for all individuals encountered of 9 typically 5-armed sea star species that occur in the region: bat star *Patiria miniata*, blood star *Henricia* spp., giant pink star *Pisaster brevispinus*,

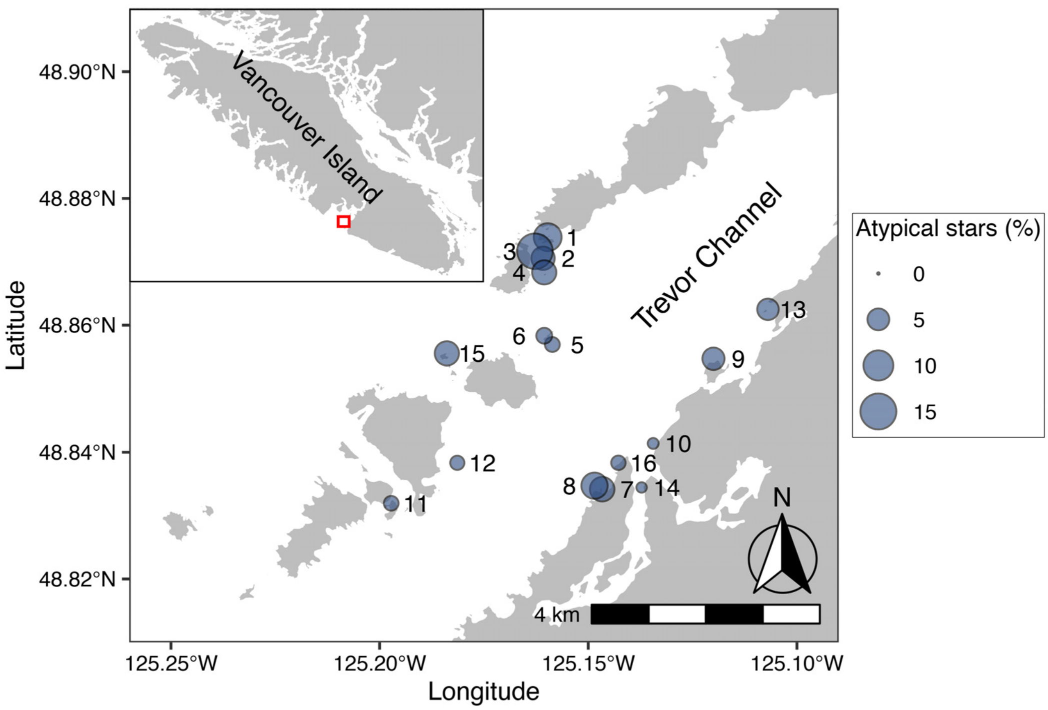

Fig. 1. Location of surveys of sea star assemblages in Trevor Channel, Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada. Point size corresponds to the percentage of sea stars of pentamerous species with atypical arm numbers (i.e. fewer or more than 5) found at each site. The site numbers next to each point correspond to those in Table 2

Table 2. Coordinates and data collected at each site. Site numbers correspond to those shown in Fig. 1. All surveys were conducted in 2022. BMSC: Bamfield Marine Sciences Centre

No.	Name	Latitude	Longitude	Survey date	Other data collected (bat stars only)		
					Morphology	Feeding	Righting
1	Ross Main	48.87389	−125.1597	9 June	×	×	×
2	Ross Slug	48.87056	−125.1608	9 June	×	×	×
3	Ross North	48.87167	−125.1628	13 June		×	×
4	Ross South	48.86833	−125.1606	13 June		×	
5	Wizard South	48.85694	−125.1586	9 June		×	
6	Wizard North	48.85833	−125.1606	9 June	×	×	
7	Scotts In	48.83417	−125.1467	10 June	×	×	×
8	Scotts Out	48.83472	−125.1485	10 June	×	×	
9	Dixon In	48.85472	−125.1200	10 June	×	×	×
10	Goby Town	48.85472	−125.1344	10 June	×		
11	Dodger	48.83194	−125.1972	11 June		×	×
12	Cia Rock	48.83833	−125.1814	11 June		×	
13	Ellis	48.86250	−125.1069	13 June	×	×	
14	BMSC Dock	48.83444	−125.1372	10 June		×	
15	Ohiat	48.85556	−125.1839	14 June	×	×	×
16	Aguilar	48.83833	−125.1428	14 June		×	

leather star *Dermasterias imbricata*, mottled star *Evasterias troschelii*, ochre star *Pisaster ochraceus*, painted star *Orthasterias koehleri*, velcro star *Stylasterias forreri*, and vermillion star *Mediaster aequalis*. Divers began surveys at the sand/rock interface or at 15 m, whichever was deepest, and followed a zig-zag pattern up the rocky slopes to a depth of 4 to 6 m. When multiple diver pairs surveyed a site, they were deployed at least 200 m apart to prevent overlap in survey area.

Preliminary analysis suggested a higher frequency of atypical arm numbers in bat stars than in other species (see Section 3.1). We therefore focused on bat stars for subsequent data collection on the effects of having supernumerary arms.

2.2. Morphology

We compared 3 morphological characteristics of bat stars with 5 arms vs supernumerary arms: colour, average arm length, and oral surface area. We recorded colour for a subset of the individuals during the sea star community surveys at all 16 study sites (Table 2). We scored the colour of the aboral surface of each bat star as 'dark' (blue or grey), 'red', or 'mottled' (more than 1 colour). To assess the other 2 morphological characteristics, we photographed the oral and aboral surfaces of a subset of the bat stars we encountered at 8 of the 16 study sites (Table 2) after community surveys had been completed. Photographs were taken on white underwater slates with a scale bar. We then measured the length of the longest arm (from the centre of the aboral disk) and the oral surface area of each individual using ImageJ.

2.3. Feeding and substrate surveys

We assessed foraging of bat stars with 5 arms and those with supernumerary arms during the community surveys. We did so by inspecting the oral surface of each bat star encountered. We scored bat stars with an everted stomach as 'feeding' (or having recently fed) (Cryan et al. 2022). Those without everted stomachs were scored as 'not feeding'. We also recorded the substrate type (sand, cobble, or rock) under each bat star.

2.4. Righting trials

At 7 of the 16 study sites (Table 2), we measured bat star righting time under field conditions. Using SCUBA and adjacent to the community survey locations, we collected equal numbers of 5-armed bat stars and bat stars with supernumerary arms, matched for size, substrate, and depth over a 30 min period. We then conducted the righting trials *in situ* at each site in a relatively flat area with minimal water motion, typically on fine sediment or sand. Due to substrate limitations, we conducted the righting time trials at Dodger Channel (Site 11) and Ohiat (Site 15; Fig. 1) on cobbled substrate and rock shelf, respectively. We removed any substrate from the oral surface, then placed each star on a plastic slate to promote arm straightening. We then set each bat star onto its aboral surface on the natural substrate and recorded righting time as the time taken by each individual to return to its normal position with the entire oral surface in contact with the substrate. We tested 8 to 14 sea stars at a time, ensuring all were turned over within 10 s of each other and allotted a maximum trial time of 15 min.

We photographed the oral and aboral surfaces of each bat star tested, placing with a scale bar in the field of view. We then used ImageJ to measure the length of the longest arm, as described above, as an index of overall size.

2.5. Analysis

We used R (Version 4.1.2; R Core Team 2019) to analyse and plot our data. We used tidyverse packages to manipulate and visualize data (Wickham et al. 2019), glmmTMB to build models (Brooks et al. 2017), emmeans for pairwise comparisons (Lenth 2022), and DHARMa to check residuals (Hartig 2022).

To examine the interspecific frequencies of atypical stars (i.e. fewer or more than 5 arms) obtained from the community surveys, we constructed a generalized linear model (GLM) with arm number category (5 arms = '0', 4, 6 or 7 arms = '1') as the response variable, and species as the fixed effect with a binomial distribution (link = 'logit'). To explore inter-site frequency of atypical arm numbers in bat stars only, we constructed a second GLM with arm number category as the response variable and site as the fixed effect, with a binomial distribution (link = 'logit'). Next, we ran post-hoc Tukey pairwise comparisons between sites. Both logistic regression models met assumptions upon inspection of the model residuals.

For all subsequent analyses, we considered only bat stars and we did not include sea stars with 4 arms as we focused on the potential effects of supernumerary arms. We conducted a chi-square test to determine whether colour was associated with arm number category (5 arms = '0', 6 or 7 arms = '1'). To determine the effect of arm number on bat star oral surface area, we used a linear mixed-effects model (LMM) with arm number category, length of the longest arm (centred), and an interaction between arm number category and arm length as fixed effects, and site as a random effect.

To determine whether arm number influenced the probability that bat stars were feeding (or had fed recently), we created a generalized linear mixed-effects model (GLMM) with a binomial distribution (link = 'logit') using our feeding score (feeding or not feeding) as the response variable. We included arm number category, substrate type (categorical: sand, cobble, rock), an interaction between arm number category and substrate type, and depth (centred) as fixed effects. We also included site as a random effect and our model met all assumptions.

We modelled bat star righting time using a LMM with arm number category, the length of the longest arm (centred), and their interaction as fixed effects. We also included site as a random effect in our model. To meet model assumptions, we log-transformed the righting time of each bat star in seconds.

3. RESULTS

3.1. Sea star community surveys

We recorded 2650 sea stars in our surveys, of which 122 (4.6%) had atypical arm numbers (Table S1 in the Supplement at www.int-res.com/articles/suppl/m739p147_supp.pdf). Only 5 (bat, leather, ochre, painted, and velcro stars) of the 9 species surveyed had atypical individuals (Table 1). Bat stars were significantly more likely to have atypical arm numbers than leather, ochre, and painted stars (GLM, $p < 0.003$ in all cases), but not velcro stars ($p = 0.57$). We observed 112 atypical bat stars (i.e. 93% of all atypical sea stars), with the majority (82%) having 6 arms. Across all sites, 10% of bat stars had atypical arm numbers (Table 1).

Atypical sea stars (all species combined) and atypical bat stars were not evenly distributed across the 16 sites surveyed (GLM; Table S1). The percentage of atypical sea stars ranged from 0.8% at the Bamfield Marine Sciences Centre (BMSC) dock (Site 14) to 14.6% at Ross North (Site 3; Fig. 1). The probability of finding an atypical sea star was significantly higher at Ross North than at 5 of the 15 other sites (Sites 5, 11, 12, 13, and 16; Tukey contrasts, $p < 0.05$ in all cases). The percentage of atypical bat stars ranged from 0% at Wizard South (Site 5) to 25% at Ross North (Site 3; Fig. 1). The probability of finding an atypical bat star was significantly higher at Ross North (Site 3) and at Ohiat (Site 15) than at Ellis (Site 13; Tukey contrasts, $p < 0.01$ in both cases). All other paired contrasts were not significant.

3.2. Morphology

We scored the colour of 565 bat stars, of which 109 had supernumerary arms. There was no association between bat star colour and arm number category (chi-square test: $\chi^2 = 0.09$, df = 2, p = 0.96). Across all sites, 28% of bat stars with supernumerary arms were red (vs. 29% of 5-armed bat stars), 67% of bat stars with supernumerary arms were dark (vs. 67% of 5-armed bat stars), and 5% of bat stars with supernumerary arms were mottled (vs. 4% of 5-armed bat stars).

We analysed photographs of 210 bat stars, 100 of which had 6 arms and 4 of which had 7 arms. At the mean longest arm length, oral surface area was 5.00 ± 2.18 cm^2 (estimate ± 1 SE), or 6%, larger for sea stars with supernumerary arms than for 5-armed sea stars (LMM, p = 0.02; Fig. 2, Table S2). Oral surface area increased significantly with the length of the longest arm by 16.78 ± 0.95 cm^2 per cm of arm length increase ($p < 0.001$; Table S2). There was a near-significant interaction between the length of the longest arm and arm number category (i.e. typical or atypical), such that oral surface area increased nearly significantly faster with arm length for bat stars with supernumerary arms than for 5-armed bat stars (p = 0.06; Table S2).

3.3. Bat star feeding

We collected feeding data for 455 bat stars, 101 of which had supernumerary arms. Having additional arms did not significantly affect the probability that a bat star was feeding or had recently fed (GLMM, p = 0.33; Fig. 3, Table S3). However, bat stars were significantly more likely to be feeding if they were found on cobble (p = 0.01) or rock (p = 0.007) than if they were found on sand (Fig. 3, Table S3). Bat stars were less likely to be feeding as depth increased (p = 0.003). There were no significant interactions between substrate type and arm number category ($p > 0.4$ in both cases, Table S3).

3.4. Righting time

We tested the righting time of 135 bat stars, including 68 individuals with 5 arms, 59 individuals with 6 arms, and 8 individuals with 7 arms. One of the 7-armed individuals did not right itself within the 15 min time limit, so was excluded from the analysis. Righting times did not vary between bat stars with 5 arms and bat stars with supernumerary arms (LMM, p = 0.52; Fig. 4, Table S4). Bat star size (i.e. length of the longest arm) also had no effect on righting time (p = 0.16), and there was no interaction between length of the longest arm and arm number category (p = 0.87; Fig. 4, Table S4).

4. DISCUSSION

The proportion of normally pentamerous northeastern Pacific sea stars with atypical arm numbers was highly variable both among sites and among sea star species. In Barkley Sound, we found more bat stars *Patiria miniata* with atypical arm numbers than any other co-occurring pentamerous sea star species, with 10% of bat stars, on average, having more or fewer than 5 arms. This proportion reached 25% at 1 site. In bat stars, we found no association between colour and arm number. Neither the probability of feeding nor righting speed was affected by the presence of supernumerary arms, but bat stars with supernumerary arms had a larger oral surface area at mean longest arm length, which might provide an advantage to deviating from pentamery.

The frequency of bat stars with supernumerary arm numbers varied spatially. While previous studies have reported up to 4% atypical individuals for bat star populations near Central California (Table 1), the frequency of bat stars with supernumerary arms in Barkley Sound varied from 0 to as much 25%, the highest proportion reported to date (Table 1). Environmental factors can drive deviations from pentamery, at least in the laboratory (Watts et al. 1983, Marsh et al. 1986, Clark 1988, Balogh & Byrne 2021). Such developmental effects occur at extreme values of salinity (e.g. ±3 ppm over ambient) and temperature (e.g. +2 to 4°C over ambient; Balogh & Byrne 2021) that are sometimes reached in Barkley Sound. For example, between 2014 and 2016, the northeast Pacific region, including Barkley Sound, experienced a long period of anomalously warm water when surface waters were up to 4°C warmer than normal (DiLorenzo & Mantua

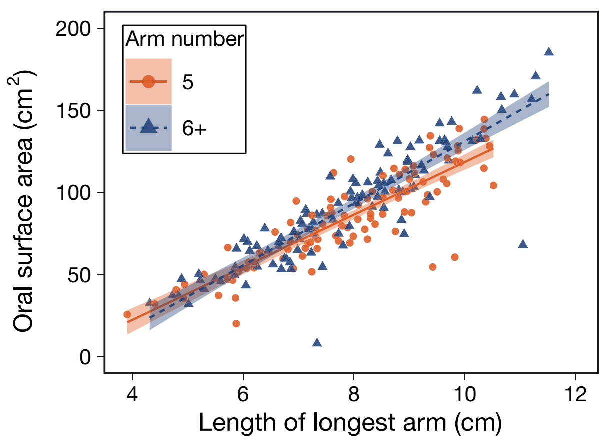

Fig. 2. Relationship between oral surface area and length of the longest arm for bat stars with 5 arms and supernumerary arms (6 or more arms). Shaded areas: 95% confidence intervals around the lines of best fit

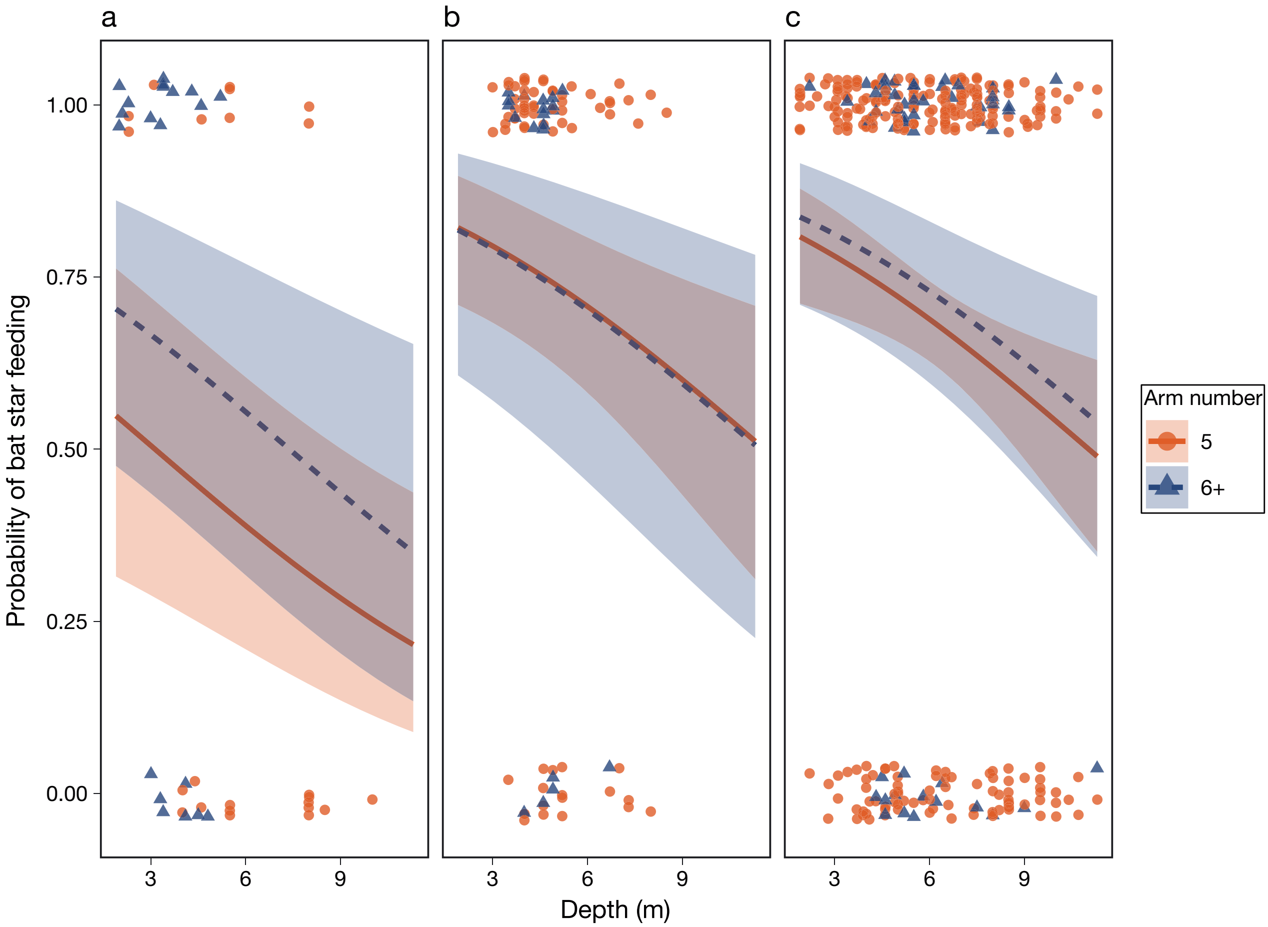

Fig. 3. Probability of bat stars with 5 arms and supernumerary arms (6 or more arms) being found with everted cardiac stomachs, a proxy for feeding, on (a) sand, (b) cobble, and (c) rock across a depth range. The shaded areas are the 95% confidence intervals around the model-generated predictions. The observed data are jittered for clarity at values of 0 (i.e. not feeding) and 1 (i.e. feeding) on the *y*-axis. Stars were observed across 16 sites in Barkley Sound, British Columbia, Canada

2016). Then, in 2021, another heatwave (the 'heat dome') resulted in the highest subtidal temperatures ever recorded in the Barkley Sound region (Climate Canada 2022). These unprecedented recent large-scale thermal anomalies could be partly responsible for driving supernumerary arm development in larval bat stars resulting in the high frequency of supernumerary arms in adult bat stars recorded here, but they do not explain the interspecific or smaller-scale, inter-site differences we observed. Disease incidence could vary on a small scale (e.g. Eisenlord et al. 2016) linked, for example, with variation in population density (Lafferty et al. 2004), and wasting disease events that affected many large sea star species have occurred recently in the region (Montecino-Latorre et al. 2016). However, bat stars were largely unaffected by wasting disease in our study area (authors' unpubl. data) and beyond (Cryan et al. 2022). Variation in predation pressure may be a more likely explanation for site-level differences in atypical sea stars, where bat stars at sites with higher levels of predation experience arm loss more often and have more frequent chances of developing supernumerary arms during regeneration. We do not have information on the

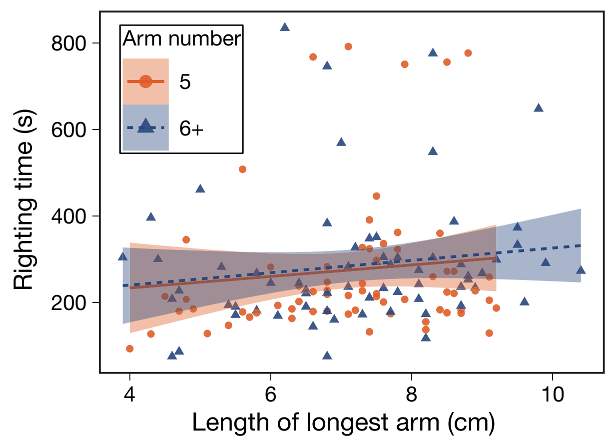

Fig. 4. Relationship between righting time and the length of the longest arm for bat stars with 5 arms and supernumerary arms (6 or more arms). Shaded areas: 95% confidence intervals around the lines of best fit

abundance of sea star predators at our study sites. However, the extremely low frequency of individuals with fewer than 5 arms (Table 1) suggests that predation pressure might not be the whole answer.

We examined 3 potential advantages of having supernumerary arms but found some support for only 1. Compared to pentamerous bat stars, those with more than 5 arms had a larger oral surface area (at mean longest arm length). There was also a near-significant interaction between arm number and longest arm length, with oral surface area being increasingly larger for atypical than for typical bat stars as body size, or longest arm length, increased. Such an interaction was expected given that it concerns a relationship between a linear metric and an areal metric. Nevertheless, a larger oral surface area is often used as a proxy for tube feet number, which is assumed to result in a greater capacity to adhere to the substrate and/or to capture prey (Lawrence 1988, Wu et al. preprint doi:10.48550/arXiv.1202.2219). We did not test adherence strength to the substrate, but our results suggest that prey capture by bat stars might not be enhanced by the presence of supernumerary arms. A lack of advantage in prey capture was confirmed by the similarity of feeding probability of bat stars with 5 arms and those with supernumerary arms. The only determinants of feeding probability were depth and substrate type, with bat stars on cobble and rocky substrate being more likely to be found feeding, or to have fed recently, than individuals on sand, which reflects the association of the species with kelp forests and its predilection for feeding on detritus and carrion (Cryan et al. 2022). It remains possible that supernumerary arms increase foraging success in ways that our feeding metric could not detect, such as by shortening prey handling times. Finally, we found no difference in righting time between typical and atypical bat stars, and no relationship between body size and righting time. Extra arms therefore neither help nor hinder this critical behaviour.

It remains unclear why bat stars deviate from pentamery more often than other co-occurring sea star species in Barkley Sound. If supernumerary arms develop most often from the process of regeneration, then bat stars would be expected to be more susceptible to mechanical damage, from predation or dislodgement, than other pentamerous species. Their smaller body size compared to co-occurring sea star species could underpin such a trend, but this remains undocumented. By the same reasoning, we might expect more bat star predators at the Ross North site than elsewhere, though it seems likely that other factors are at play. Although we detected only a slight advantage of supernumerary arms in terms of larger oral surface area for atypical bat stars, we also did not find any clear disadvantage. This suggests that selection against atypical variants may be weak in bat stars, relaxing the strength of selection on the accuracy of arm regeneration.

Data availability. All data generated from the present study, and associated analyses are available in the repository: https://github.com/em-lim13/Bat_star_arms.

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LITERATURE CITED

Ardor Bellucci LM, Smith NF (2019) Crawling and righting behavior of the subtropical sea star *Echinaster* (*Othilia*) *graminicola*: effects of elevated temperature. Mar Biol 166:138

Balogh R, Byrne M (2021) Developing in the intertidal: effects of salinity and temperature on development to the pentameral juvenile seastar, *Parvulastra exigua.* Mar Biol 168:99

Barrios JV, Gaymer C, Vásquez JA, Brokordt KB (2008) Effect of the degree of autotomy on feeding, growth, and reproductive capacity in the multi-armed sea star *Heliaster helianthus.* J Exp Mar Biol Ecol 361:21–27

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A and others (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400

Budden C, Butler I, Wolfe K, Deaker D, Sweatman H, Byrne M (2019) Effect of sublethal predation on reproductive output of the crown-of-thorns starfish *Acanthaster* sp., with an overview of arm damage. Mar Ecol Prog Ser 629: 103–116

Byrne M, Anderson MJ (1994) Hybridization of sympatric *Patiriella* species (Echinodermata: Asteroidea) in New South Wales. Evolution 48:564–576

Clark KE (1988) The roles of heredity, osmotic stress, and regeneration in non-pentamerous symmetry in *Patiria miniata* (Asteroidea). In: Burke RB, Mladenov PV, Lambert P, Parsley RL (eds) Echinoderm biology. Proc 6th Int Echinoderm Conf, Victoria, BC, 23–28 August 1987. Balkema, Rotterdam, p 792

Climate Canada (2022) Historical data. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Cryan DM, Low NHN, Litvin SY, Osenberg CW, Micheli F (2022) Trophic ecology of an abundant kelp forest echi-

noderm, the bat star *Patiria miniata.* Mar Ecol Prog Ser 696:57–68
Di Lorenzo E, Mantua N (2016) Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat Clim Chang 6:1042–1047
Diaz-Guisado D, Gaymer CF, Brokordt KB, Lawrence JM (2006) Autotomy reduces feeding, energy storage and growth of the sea star *Stichaster striatus.* J Exp Mar Biol Ecol 338:73–80
Eisenlord ME, Groner ML, Yoshioka RM, Elliott J and others (2016) Ochre star mortality during the 2014 wasting disease epizootic: role of population size structure and temperature. Philos Trans R Soc B 371:20150212
Galván-Villa CM, Solís-Marín FA (2021) Population size structure and abnormalities in the number of rays of the sea star *Pentaceraster cumingi* (Valvatida: Oreasteridae) in Bahia Chamela, Mexican Pacific. Rev Biol Trop 69:262–273
Guillou M, Diop M (1988) Ecology and demography of a population of *Anseropoda placenta* (Echinodermata: Asteroidea) in the Bay of Brest, Brittany. J Mar Biol Assoc UK 68:41–54
Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6. https://cran.r-project.org/web/packages/DHARMa/index.html
Hotchkiss FHC (2000) On the number of rays in starfish. Am Zool 40:340–354
Ji C, Wu L, Zhao W, Wang S, Lv J (2012) Echinoderms have bilateral tendencies. PLOS ONE 7:e28978
Kawase O, Furukawa R (2014) Regional difference of ray number variation in a starfish, *Patiria pectinifera.* Annu Rep Premed Sci Dokkyo Med Univ 3:49–52
Keesing JK (2017) Population size structure, growth, arm number and damage in the sea star *Archaster angulatus* Müller and Troschel, 1842 (Echinodermata: Asteroidea). Invertebr Reprod Dev 61:119–127
Lafferty KD, Porter JW, Ford SE (2004) Are diseases increasing in the ocean? Annu Rev Ecol Evol Syst 35:31–54
Lawrence JM (1988) Functional consequences of the multi-armed condition in Asteroids. In: Burke RB, Mladenov PV, Lambert P, Parsley RL (eds) Echinoderm biology. Proc 6th Int Echinoderm Conf, Victoria, BC, 23–28 August 1987. Balkema, Rotterdam, p 597–602
Lawrence JM (2010) Energetic costs of loss and regeneration of arms in stellate echinoderms. Integr Comp Biol 50: 506–514
Lawrence JM, Komatsu M (1990) Mode of arm development in multiradiate species of asteroids. In: Jangoux M (ed) Echinoderm research. CRC Press, London, p 269–275
Lawrence JM, Byrne M, Harris L, Keegan B, Freeman S, Cowell BC (1999) Sublethal arm loss in *Asterias amurensis*, *A. rubens*, *A. vulgaris*, and *A. forbesi* (Echinodermata: Asteroidea). Vie Milieu 49:69–73
Lenth RV (2022) emmeans: estimated marginal means, aka least-squares means. R package version 1.8.2. https://cran.r-project.org/package=emmeans
Maginnis TL (2006) The costs of autotomy and regeneration in animals: a review and framework for future research. Behav Ecol 17:857–872
Marsh AG, Watts SA, Chen C, McClintock JB (1986) The effect of high salinity on development, mortality and ray number of *Echinaster spinulosus* (Echinodermata: Asteroidea) at different developmental stages. Comp Biochem Physiol A 83:229–232
Montecino-Latorre D, Eisenlord ME, Turner M, Yoshioka R and others (2016) Devastating transboundary impacts of sea star wasting disease on subtidal asteroids. PLOS ONE 11:e0163190
Montgomery EM, Palmer AR (2012) Effects of body size and shape on locomotion in the bat star (*Patiria miniata*). Biol Bull 222:222–232
Moore AR (1941) Dysfunction in righting and locomotion in a starfish (*Patiria*) with supernumerary rays. J Comp Psychol 32:483–487
Pearse JS (1993) Five rays or six: does it make any difference in potential fecundity of sea stars? Abstracts 33rd Ann Meet Amer Soc Zool, Los Angeles, 26–30 December 1993. Amer Zool 33:72A
Polls I, Gonor J (1975) Behavioral aspects of righting in two asteroids from the Pacific coast of North America. Biol Bull 148:68–84
Pomory CM, Lares MT (2000) Rate of regeneration of two arms in the field and its effect on body components in *Luidia clathrate* (Echinodermata: Asteroidea). J Exp Mar Biol Ecol 254:211–220
Prabhu K, Bragadeeswaran S (2012) Occurrence of abnormal starfish *Astropecten indicus* (Doderlein, 1888) (Echinodermata: Astroidea) along southeast coast of India. Biotemas 25:293–296
R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
Ramsay K, Kaiser MJ, Richardson CA (2001) Invest in arms: behavioural and energetic implications of multiple autotomy in starfish (*Asterias rubens*). Behav Ecol Sociobiol 50:360–365
Watts SA, Scheibling RE, Marsh AG, McClintock JB (1983) Induction of aberrant ray numbers in *Echinaster* sp. (Echinodermata: Asteroidea) by high salinity. Fla Sci 46: 125–128
Wickham H, Averick M, Bryan J, Chang W and others (2019) Welcome to the tidyverse. J Open Source Softw 4:1686

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