Research Paper

Title

Population dynamics and disease-linked host use of the sea urchin symbiont *Dactylopleustes yoshimurai* (Crustacea: Amphipoda: Pleustidae) on *Strongylocentrotus intermedius*

Running head

Population dynamics of *Dactylopleustes yoshimurai*

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Abstract

Dactylopleustes yoshimurai is an echinoid-associated amphipod that frequently aggregates on disease lesions of the short-spined urchin *Strongylocentrotus intermedius* in Otsuchi Bay, northeastern Japan. However, its life history and use of diseased hosts remain poorly understood. We combined four years of monthly SCUBA surveys (Jan 2020–Jan 2024) with quantitative sampling of diseased and healthy urchins (Jan 2021–Jan 2024) to examine how host disease status structures the population dynamics of *D. yoshimurai*. The amphipod occurred on ~10–80% of urchins and was consistently more frequent and much denser on diseased than on healthy hosts, with winter peaks that broadly coincided with maxima in disease prevalence. Size–frequency distributions on diseased urchins were strongly dominated by juveniles (<2.5 mm), especially in winter to early spring, whereas healthy urchins supported low densities but a relatively higher proportion of adults. Ovigerous females were rare but occurred mainly in late summer and autumn on both host types, and juvenile pulses in winter, together with the year-round presence of small juveniles, indicate an extended reproductive period with a seasonal peak in late summer–autumn and recruitment continuing into winter. These results show that host disease status and amphipod life history jointly shape the population dynamics of *D. yoshimurai*, and highlight lesions on urchins as seasonally dynamic habitat patches that are particularly important for juvenile stages.

Keywords

Dactylopleustes yoshimurai; sea urchin symbiont; bald sea urchin disease; population dynamics; host–symbiont interactions

■ Introduction

The order Amphipoda is one of the largest crustacean orders, comprising more than 10,000 described species (Horton et al. 2025, Lowry & Myers 2017). Symbiotic associations with various other animals have been well documented across the group (e.g., Vader, 1978, 1983; Vader & Tandberg, 2013, 2015; Iwasa-Arai & Serejo, 2018; Tomikawa *et al.*, 2019; Kodama *et al.*, 2022; Hanaoka *et al.*, 2025). However, for many host-specialized amphipods, basic aspects of ecology and life history remain poorly documented.

Amphipods of the genus *Dactylopleustes* Karaman & Barnard, 1979 (Amphipoda: Pleustidae) are known as symbionts of sea urchins and are thought to have evolved adaptations for living on the host's body surface (Vader, 1978; Bousfield & Hendrycks, 1995). Despite this close association, basic information on the ecology and life history of *Dactylopleustes* species is still limited (Vader, 1978), and it remains unclear whether these amphipods affect their host urchins.

Dactylopleustes yoshimurai Tomikawa, Hendrycks & Mawatari, 2004 occurs on the body surface of sea urchins including *Strongylocentrotus intermedius* (Tomikawa *et al.*, 2004; Kodama *et al.*, 2020). Recent field observations further showed that *D. yoshimurai* frequently aggregates on disease lesions of host urchins, while comparable aggregations are not observed on healthy urchins (Kodama *et al.*, 2020). These aggregations are often dominated by small juveniles, whereas juveniles are rarely found on healthy urchins. This pattern has been interpreted as that amphipods feed on exposed host tissues at lesions (Kodama *et al.*, 2020). However, DNA metabarcoding of gut contents suggested that even aggregated individuals contained only a limited proportion of urchin-derived material and instead relied heavily on non-host resources such as sediments (Kodama *et al.*, 2024). Though both the importance of aggregation and the life-stage dependence of host use remain unresolved, aggregations on lesions have been observed repeatedly and with high consistency, suggesting that this behavior may have important implications for the life history of this species. Nevertheless, the basic life history of the species remains unclear, and it is also unknown when and how, within its life cycle, the amphipods used diseased host urchins.

The present study aims to clarify (i) the basic life history and seasonal population dynamics of *D. yoshimurai* on its host urchins and (ii) how host disease status is associated with amphipod density and demographic structure. To address these aims, we conducted monthly SCUBA surveys in order to quantify body length, sex, and maturity stage, as well as the number of amphipods per a diseased and healthy *S. intermedius*. By comparing amphipod population characteristics between diseased and healthy hosts across seasons, we evaluate when (and which life stages of) *D. yoshimurai* are most strongly associated with diseased urchins.

■ Materials and Methods

Field survey and sampling

This study was carried out in a rocky subtidal area at Akahama in Otsuchi Bay, Japan (Figs. 1: 39°21'00" N, 141°56'10" E, 2–3 m deep). Monthly field survey using SCUBA was conducted from Jan 2020 to Jan 2024, except for the following months: Oct 2021; Nov, Dec 2022; Feb, Nov 2023. At each monthly survey, 50 individuals of the short-spined sea urchin *Strongylocentrotus intermedius* were randomly selected. For each urchin, we recorded the test diameter, and visually recorded (i) the presence or absence of visible disease lesions and (ii) the presence or absence of visible *Dactylopleustes yoshimurai.*

To obtain an index of urchin availability/density during each survey, we recorded the elapsed time required to locate and measure 50 individuals and calculated catch per unit effort (CPUE; individuals h^{-1}) as: CPUE = 50 / survey time (h). Because the number of processed individuals was fixed, higher CPUE indicates a shorter search/processing time and thus greater local availability of urchins. CPUE could not be calculated for months in which the end time was not recorded.

The urchin's disease found in Otsuchi Bay appears to be a kind of bacterial disease called 'bald sea urchin disease' (Johnson, 1971, Shaw *et al.*, 2023). However, it is impossible to identify the causes of disease in the field. In this study, therefore, a 'diseased urchin' was defined as an urchin with the following symptoms following Kodama *et al.* (2024): an area of the test without spines and tube feet, exposing the surface tissue discoloured to deep purple or black. These symptoms are typical of bald sea urchin disease.

At the SCUBA surveys from Jan 2021 to Jan 2024 except for Apr 2022, Jun and Aug 2023, six diseased individuals and six healthy individuals of *S. intermedius* were haphazardly collected, respectively, from the area neighboring the area for the above monitoring survey. Each urchin individual was gently placed in plastic bags to prevent escape of symbiotic organisms. The urchins and its symbionts were all anaesthetized with iso-osmotic 7.5% weight% magnesium chloride (MgCl2.6H2O). Then, *D. yoshimurai* detached from the urchins by anesthesia were counted and preserved in 80% ethanol.

Seasonal fluctuation in the number of *D. yoshimurai* on an urchin was assessed and visualized using generalized additive models (GAMs) with the 'mgcv' package in R. The sampling months were treated as explanatory factor. Negative binomial distribution was used in GAM. Sampling month data were transformed into the number of elapsed months from the first sampling and thus treated as a continuous data set (not categorical data).

To examine whether host body size influences the occurrence of lesions and/or amphipod association (i.e., potential size-based host preference), each urchin was assigned to one of four

categories based on the combination of lesion status and amphipod occurrence: (1) healthy urchins without amphipods observed, (2) healthy urchins with amphipods observed, (3) diseased urchins without amphipods observed, and (4) diseased urchins with amphipods observed. Differences in test diameter among the four groups were evaluated using a Kruskal–Wallis rank-sum test. When the overall test was significant, pairwise comparisons were conducted using Dunn's test with Bonferroni adjustment for multiple testing. The analyses were performed using the package "dunn.test" in R.

Sample processing in the laboratory

A total of 1,899 *D. yoshimurai* individuals were collected between January 2021 and January 2024. Eleven individuals were damaged and thus excluded from the measurement, leaving 1,888 individuals for analysis about body length. Body length was measured from the tip of rostrum along the dorsal margin to the posterior margin of telson (measurements were done on the curved body). The determination of sex and developmental stage was based on the presence or absence of oostegites (females) and of genital papillae (males). Females were first classified as ovigerous or non-ovigerous based on the presence or absence of eggs. Non-ovigerous females were then examined for setation on the oostegites: individuals lacking eggs but bearing well-developed and setose oostegites were classified as mature females, whereas those with oostegites that were present but not setose were classified as immature females. Individuals without oostegites or genital papillae were considered juveniles.

■ Results

***Temporal variation in host disease and occurrence of* Dactylopleustes yoshimurai**

Dactylopleustes yoshimurai was frequently found on the short-spined urchin *Strongylocentrotus intermedius* throughout the study period (Fig. 2). The proportion of urchins bearing *D. yoshimurai* ranged from about 10% to about 80% of the 50 individuals examined per month and was usually >20%. Peaks in occurrence (>60% of urchins with amphipods) were typically observed in winter (e.g. late 2020, late 2021–early 2022, late 2022 and late 2023), although elevated values also occurred sporadically in other seasons.

The proportion of urchins showing lesions ("bald sea urchin disease") was generally lower and showed more distinct seasonality than amphipod occurrence, fluctuating between 0 and about 40% (Fig. 2). Disease prevalence tended to increase in late autumn and winter each year, with conspicuous peaks in 2020–2021, 2021–2022 and 2023–2024, whereas it was usually <10% in late spring and

summer. In most years, periods of high disease prevalence overlapped with peaks in the proportion of urchins bearing *D. yoshimurai* (Fig. 2).

Urchin availability, indexed by CPUE, remained broadly stable throughout the monitoring period (Fig. 2). The CPUE were typically around ~100 individuals h^{-1} (median 93.8; mean 95.6), ranging from 46.2 individuals h^{-1} (Apr 2022) to 176.5 individuals h^{-1} (Apr 2021). Although occasional months showed moderately high or low values, CPUE remained broadly stable over time and no clear seasonal pattern in CPUE was apparent.

Test diameter differed among the four groups (Fig. 3; Kruskal–Wallis: $\chi^2 = 17.29$, df = 3, $p < 0.001$; $\varepsilon^2 = 0.006$, indicating a small effect). Post-hoc Dunn's tests with Bonferroni correction detected a significant difference only between healthy urchins without amphipods observed and diseased urchins without amphipods observed (adjusted $p = 0.0024$), whereas all other pairwise comparisons were not significant (adjusted $p > 0.05$). Median test diameter was 43.30 mm in healthy urchins without amphipods and 46.15 mm in diseased urchins without amphipods (median difference = 2.85 mm), with substantial overlap in interquartile ranges. The test diameter distribution consistently peaked at 40–50 mm in all months, and no clear seasonal shift was detected (Fig. 4).

Temporal variation in number of* Dactylopleustes yoshimurai *on diseased and healthy urchins

From January 2021 to January 2024, a total of 348 urchins (six diseased and six healthy urchins per sampling) were collected for quantitative counts of *D. yoshimurai*. A total of 1,899 amphipods were collected, of which 1,696 were from diseased urchins and 203 were from healthy urchins.

The number of *D. yoshimurai* on an urchin differed strikingly between diseased and healthy urchins. Diseased urchins often hosted dense aggregations, with up to about 100 individuals on a single host and many samples exceeding 20 individuals per urchin (Fig. 3). In contrast, healthy urchins typically bore only a few amphipods (0–5 individuals per urchin), and hosts without an amphipod were common. As a result, the fitted GAM for the number of *D. yoshimurai* on an urchin showed consistently higher values for diseased than for healthy urchins throughout the study period (Fig. 3).

The number of *D. yoshimurai* on diseased hosts also exhibited pronounced seasonal variation (Fig. 3). Large numbers of amphipods were observed on diseased urchins in winter of each year. Between these peaks, the number of amphipods on diseased hosts dropped to low values in late spring and summer. By contrast, the fitted GAM for healthy urchins remained close to zero across all months, with only minor seasonal fluctuations and no conspicuous peaks (Fig. 3).

Size structure and demographic composition of* Dactylopleustes yoshimurai *on diseased urchins

Body length of *D. yoshimurai* ranged from ca. 0.5 to 7.0 mm (Figs. 4, 5). On diseased urchins, the assemblage was dominated by juveniles in most months (Fig. 4). Large numbers of small juveniles (body length <2.5 mm) occurred repeatedly in winter to early spring (e.g. January–March 2021, January 2022, January 2023, December 2023–January 2024), forming distinct unimodal peaks at small size classes. Although small juveniles appeared repeatedly in winter to early spring, the subsequent progression of distinct cohorts was not always clear, as size–frequency distributions often overlapped among months and did not consistently show a smooth modal shift.

Adult size classes (mature females, ovigerous females and males, generally > 4.0 mm) were present on diseased urchins in many months but always occupiedsmall proportions of the total assemblage (Fig. 4). Ovigerous females (dark red bars) were detected intermittently, most frequently from late spring to autumn (e.g. May–July 2021, February–June 2022, and sporadically in 2023), and were usually among the largest individuals in the population (5–7 mm; arrows in Fig. 4). Mature but non-ovigerous females and adult males were also concentrated in these larger size classes.

Size structure and demographic composition of* Dactylopleustes yoshimurai *on healthy urchins

On healthy urchins, *D. yoshimurai* occurred at much lower numbers, and the size–frequency distributions therefore contained fewer individuals per month (Fig. 5). Juveniles were present in many months but usually only in small numbers (typically fewer than five individuals per size class). Adult males and females, including ovigerous females, were observed intermittently across years. Only five ovigerous females were recorded on healthy urchins, and thus the timing of reproduction cannot be determined conclusively. However, ovigerous females on healthy urchin were most frequently observed in late summer and early autumn (e.g. August–September 2021, September–October 2022, and September 2023; arrows in Fig. 5). This seasonal tendency is broadly consistent with the pattern observed on diseased urchins and supports the inference that reproduction likely peaks from late summer to autumn.

Although the total number of amphipods on healthy urchins was small, the coexistence of juveniles and adults including ovigerous females in some months indicates that all life stages can occur on healthy hosts. Nevertheless, in contrast to diseased urchins where juveniles overwhelmingly dominated, the smaller assemblages on healthy urchins were often comprised of a relatively higher proportion of adults (Fig. 5).

■ Discussion

Our four-year survey revealed that the population dynamics of the urchin symbiont *Dactylopleustes*

yoshimurai differ markedly between diseased and healthy hosts and show a distinct seasonal pattern. On healthy *Strongylocentrotus intermedius*, the amphipod occurred at low densities (number of individuals per an urchin) throughout the year, whereas diseased urchins supported dense aggregations, particularly in winter. These patterns closely paralleled seasonal changes in the prevalence of "bald sea urchin disease", which increased in late autumn and winter and declined in late spring and summer (Fig. 2; see also Johnson, 1971; Shaw *et al.*, 2023; Kodama *et al.*, 2024). These results indicate that *D. yoshimurai* uses host lesions that are most frequent in winter as key habitat patches within its life cycle, while also persisting at low densities on healthy urchins year-round.

The "diseased" urchins in this study were defined by characteristic symptoms (the spines are observed to have fallen off in an area of the test, exposing the tissue, which is black and discolored) that are typical of bald sea urchin disease (Johnson 1971; Shaw *et al.*, 2023; Kodama *et al.*, 2024). The mechanisms of the winter increase in disease prevalence remains unclear and may involve seasonal changes in temperature, bacterial communities, or host condition. Notably, diseased individuals were not restricted to winter; 5–10% of urchins showed a diseased condition even in summer. However, *D. yoshimurai* densities were low in summer on both diseased and healthy urchins, implying that the symbiont's abundance is not simply driven by whether the host is diseased or not. Instead, the seasonal density pattern appears to be shaped by the interaction between host disease dynamics and the amphipod's own reproductive schedule, with high densities in winter arising when newly recruited juveniles encounter abundant diseased hosts.

Based on the CPUE data, urchin availability (as a proxy for local density) was stable both seasonally and interannually (Fig. 2). The size structure of urchins was likewise stable across months and years (Fig. 4). Moreover, test diameter was broadly similar among individuals with and without visible lesions and with and without *D. yoshimurai* (Fig. 3). Although diseased urchins tended to be only marginally larger, there was no consistent tendency for urchins hosting *D. yoshimurai* to be larger or smaller than those without *D. yoshimurai* (Fig. 3). Overall, host density and host size were generally stable across categories and over time, and are therefore unlikely to be major drivers of the seasonal patterns described in this study.

Body-length data of *D. yoshimurai* showed that juveniles (<2.5 mm) occurred on diseased urchins throughout the year but were especially abundant in winter and early spring, forming distinct peaks in the smallest size classes (Fig. 4). Size–frequency distributions often overlapped among months and did not consistently show smooth shifts in mode. Although clear modal progression of cohorts was not always evident, the recurring pulses of small juveniles in winter strongly suggest that recruitment is concentrated in this season. Ovigerous females, in contrast, were rare overall: only

seven were recorded from diseased urchins and five from healthy urchins across the entire study period. They were most frequently observed in late summer and early autumn on both host types. The small number of ovigerous females prevents a definitive determination of the reproductive season, but the temporal combination of (i) ovigerous females and large mature females in late summer–autumn and (ii) juvenile pulses in winter is consistent with reproduction peaking in late summer to autumn and recruitment continuing into winter. At the same time, the detection of small juveniles throughout the year, including summer months when overall densities were low, suggests that some level of reproduction may occur year-round, albeit at much reduced intensity outside this apparent peak.

Marked differences in size structure between diseased and healthy hosts point to strong ontogenetic variation in habitat use. Diseased urchins were overwhelmingly dominated by juveniles in most months, whereas the smaller assemblages on healthy urchins often contained a relatively higher proportion of adults, including ovigerous females (Figs. 4, 5). This pattern suggests that diseased urchins, and their diseased areas in particular, serve as especially important habitat for early life stages. Juvenile recruitment appears to occur mainly in winter, when disease prevalence is high, and juveniles may preferentially occupy lesions rather than the intact surfaces of healthy urchins. In contrast, healthy urchins hosted only small numbers of juveniles, particularly in summer (Figs. 6, 7). This suggests that healthy urchins are likely used only opportunistically, mainly during winter recruitment peaks, when juvenile abundance increases and individuals may spill over from lesions onto alternative substrates.

It is also striking that many diseased urchins hosted numerous juveniles but no large adults, and that ovigerous females were rare on both diseased and healthy hosts despite intensive sampling (348 urchins and 1,899 amphipods in total). One possibility is that *S. intermedius* is not the main reproductive habitat for *D. yoshimurai* and that a substantial fraction of reproduction occurs on other echinoid hosts or alternative substrates in the surrounding habitat (cf. Vader, 1978; Bousfield & Hendrycks, 1995). The frequent occurrence of urchins bearing only juveniles is consistent with substantial host-to-host movement, although our data cannot distinguish between local reproduction on a given host and immigration of juveniles from elsewhere.

The reason why *D. yoshimurai* aggregates so clearly on diseased urchins, particularly as juveniles, remains unresolved. Two non-exclusive hypotheses have been proposed to explain this behaviour: (1) amphipods aggregate on diseased areas to feed on exposed host tissues, and (2) diseased areas provide shelter from host defences such as pedicellariae (Kodama *et al.*, 2020, 2024). DNA metabarcoding of gut contents has shown that urchin-derived material constitutes only a minor fraction of the diet of *D. yoshimurai*, even for individuals collected from lesions, whereas sediments

and other non-host resources dominate (Kodama *et al.*, 2024). This evidence partially refutes the idea that feeding on host tissue is the primary driver of aggregation. Considering that juveniles are smaller and likely more vulnerable to physical disturbance and host defensive structures, it seems plausible that lesions function mainly as relatively safe microhabitats where pedicellariae are absent or reduced, and where fine sediments and biofilms accumulate. Under this scenario, diseased urchins provide structurally favourable patches for juveniles, while adults can utilize a broader set of microhabitats on both diseased and healthy hosts.

More broadly, *D. yoshimurai* exemplifies how a symbiotic amphipod can exploit host pathology as a key habitat feature within its life history. Amphipods of the genus *Dactylopleustes* are widely recognised as echinoid symbionts and have evolved morphological traits suited for living on urchin surfaces (Vader, 1978; Bousfield & Hendrycks, 1995; Tomikawa *et al.*, 2004). Our results show that, at least for *D. yoshimurai*, this association is further shaped by the occurrence of disease lesions that appear and disappear seasonally on the host. Such disease- and condition-mediated changes in habitat quality may not be unique to echinoid–amphipod associations. In other echinoids, bald sea urchin disease and related pathologies produce conspicuous test lesions that are colonized by dense and distinctive bacterial communities, distinct from those on surrounding healthy tissues (Becker *et al.*, 2008; Shaw *et al.*, 2023; Carella *et al.*, 2025). These lesions and spineless patches can also be overgrown by macro-epibionts such as encrusting bryozoans (Queiroz *et al.*, 2020). Moreover, epibionts living on echinoid spines and tests act as important biotic substrates that strongly influence the richness and composition of associated sessile assemblages (Hétérier *et al.*, 2008; Linse *et al.*, 2008; Rodríguez-Barreras *et al.*, 2023), and in some cases can even alter host physiological responses (Queiroz *et al.*, 2020). Similar links between host condition and associated fauna are well documented in corals, where disease lesions can be selectively exploited by corallivores and where the diversity and abundance of coral-associated invertebrates depend strongly on the persistence and health of live coral hosts (Stella *et al.*, 2011; Montano 2020, 2022). Taken together, these examples suggest that the strong coupling we observed between host disease status and *D. yoshimurai* abundance is one instance of a broader pattern in which host pathology and condition structure the ecological opportunities available to associated fauna.

CPUE varied little over time (Fig. 2b), suggesting that the disease producing lesions recurs seasonally but is not severe enough to cause a major decline in the local urchin population. This coexistence with a moderate disease burden is likely important for *D. yoshimurai*, since a stable host population can provide a recurrent supply of lesioned microhabitats from year to year. A disease severe enough to substantially reduce host density would be unlikely to sustain a symbiont that depends on lesions as a key habitat, except for short-lived opportunistic use.

From the host's perspective, however, the net effect of *D. yoshimurai* remains uncertain. Although gut-content metabarcoding indicates that the amphipod does not rely heavily on host tissues for food (Kodama *et al.*, 2024) and is therefore unlikely to be a primary cause of lesion formation, dense aggregations on lesions could still influence wound healing and local microbial communities, potentially modifying the trajectory of bald sea urchin disease. Disentangling whether *D. yoshimurai* ultimately mitigates, exacerbates, or is largely neutral with respect to disease progression will require experimental manipulations of amphipod density and lesion presence on infected urchins.

In summary, this study demonstrates that the population dynamics of *D. yoshimurai* on *S. intermedius* are jointly structured by host disease status and the amphipod's life history. Diseased urchins, especially in winter when bald disease is most prevalent, provide critical habitat for juvenile recruitment and growth, whereas healthy urchins support lower densities but are used by all life stages, including ovigerous females. Reproduction appears to peak in late summer to autumn with recruitment continuing into winter, and some level of reproduction likely occurs year-round. These findings highlight the importance of considering host disease status when evaluating the ecology of symbionts and suggest that changes in the frequency or severity of urchin diseases, regardless of whether they are driven by environmental change or by other factors, could have cascading effects on associated amphipod communities. Future work combining experimental manipulations of lesion availability, direct observations of host switching and movement, and further dietary and microbiome analyses will be essential to clarify the functional role of the aggregation of *D. yoshimurai* on the disease lesions of *S. intermedius*.

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■ Statements and Declarations

346 ***Author Contributions statement***

347 MK, RY, and JH conceptualized and designated this study. JH and MK conducted sample collections.
348 KT made a reliable identification of our specimens of *Dactylopleustes yoshimurai*, which had been
349 originally described by KT. MK, RY, and JH carried out all the sample processing. MK and RY carried
350 out data processing and statistical analyses. JH, GK, and TK supervised interpretations for the results.
351 MK wrote the manuscript and made figures with support from RY and JH. KT, GK, and TK critically
352 reviewed the manuscript and provided substantial input. All the authors checked the manuscript and
353 gave their approval for the final version for submission.

354

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359 The University of Tokyo.

360

361 ***Data availability***

362 The data underlying this article will be shared on reasonable request to the corresponding author.

363

364 ***Ethical approval***

365 All applicable international, national and/or institutional guidelines for sampling, care and
366 experimental use of organisms for the study have been followed and all necessary approvals have
367 been obtained. The study did not involve human participants. No animal welfare approval was
368 required as we were working with common invertebrates.

369

370 ***Conflict of interest***

371 The authors declare that they have no competing interests.

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Figure legends

Fig. 1. Map showing the study site in Otsuchi Bay, Japan.

Fig. 2. (a) Seasonal fluctuation in the proportion (%) of *Strongylocentrotus* intermedius individuals bearing *Dactylopleustes yoshimurai* (red) and the proportion (%) showing disease symptoms of "bald urchin disease" (black) at Akahama, Otsuchi Bay, from Jan 2020 to Jan 2024 (n = 50 urchins examined per survey). (b) Seasonal fluctuation in the catch per unit effort (CPUE; individuals h^{-1}) of S. *intermedius* during monthly SCUBA surveys. CPUE was calculated as 50 individuals divided by the elapsed time (h) required to locate and measure 50 urchins; higher values indicate greater local availability of urchins. Plots are missing for months without surveys and for months in which CPUE could not be calculated (e.g., due to missing end-time records). Grey vertical bands indicate winter (Dec–Feb).

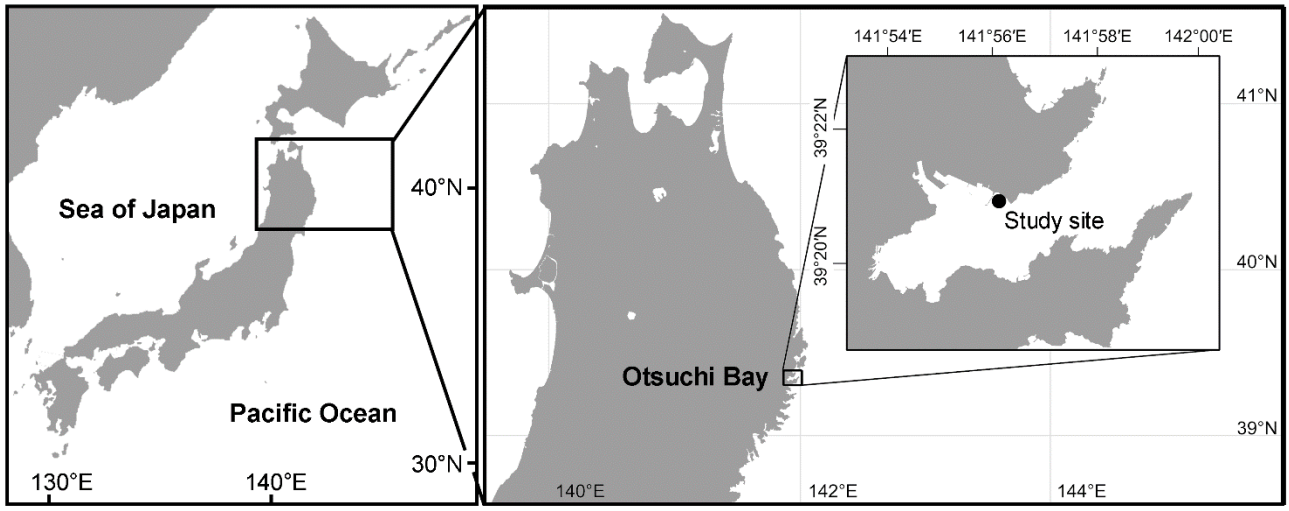
Fig. 3. Test diameter (mm) of Strongylocentrotus intermedius for healthy (no visible lesion) and diseased (with visible lesion) individuals with or without visible *Dactylopleustes yoshimurai*. Boxes represent the lower and upper quartiles. Black bold line in each box indicates the median. Whiskers extend to the most extreme values within 1.5× the interquartile range; values beyond this range are treated as outliers. Grey jittered dots indicate individual urchins. Letters (a, b, and ab) denote significant differences among groups (Dunn's test with Bonferroni correction, $\alpha = 0.05$).

Fig. 4. Monthly size–frequency distributions of Strongylocentrotus intermedius between Jan 2020 and Jan 2024 (50 individuals per survey month). Histograms show test diameter (mm) and are colour-coded by with/without visible lesion and with/without visible *Dactylopleustes yoshimurai*. Panels are absent for unsurveyed months (Jul 2020, Oct 2021; Nov, Dec 2022; Feb, Nov 2023).

Fig. 5. Seasonal fluctuation in the number of *Dactylopleustes yoshimurai* (number of individuals per host urchin) on diseased (red) and healthy (black) *Strongylocentrotus intermedius* from Jan 2021 to Jan 2024. Points indicate observed counts for individual hosts (six diseased and six healthy urchins collected per survey). Solid curves show fitted lines from generalized additive models, with shaded bands indicating 95% confidence intervals. Grey vertical bands indicate winter (Dec–Feb).

Fig. 6. Monthly size–frequency distributions of *Dactylopleustes yoshimura*i collected from diseased *Strongylocentrotus intermedius* between Jan 2021 and Jan 2024 (six hosts per survey month). Histograms show body length (mm) and are colour-coded by sex and developmental stage (juveniles, immature females, mature females, ovigerous females, and males). Arrows indicate ovigerous females. Panels are absent for unsampled months (Oct 2021; Apr, Nov, Dec 2022; Feb, Jun, Aug, Nov 2023), whereas empty panels (Aug 2022, Jul 2023) indicate months that were sampled but yielded no amphipods.

Fig. 7. Monthly size–frequency distributions of *Dactylopleustes yoshimurai* collected from healthy *Strongylocentrotus intermedius* between Jan 2021 and Jan 2024 (six hosts per survey month). Histograms show body length (mm) and are colour-coded by sex and developmental stage (juveniles, immature females, mature females, ovigerous females, and males). Arrows indicate ovigerous females. Panels are absent for unsampled months (Oct 2021; Apr, Nov, Dec 2022; Feb, Jun, Aug, Nov 2023), whereas empty panels (Sep, Oct 2023) indicate months that were sampled but yielded no amphipods.



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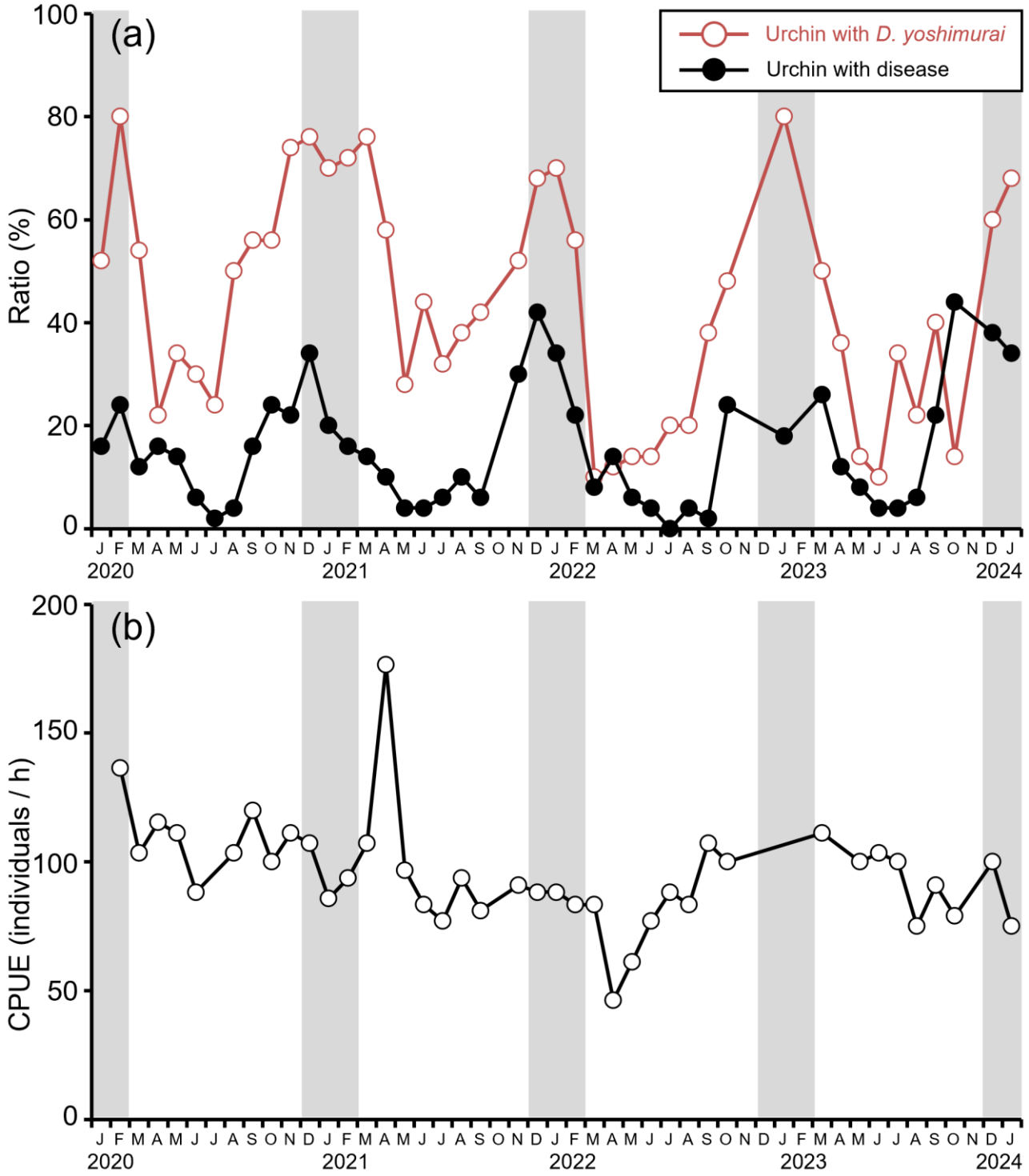

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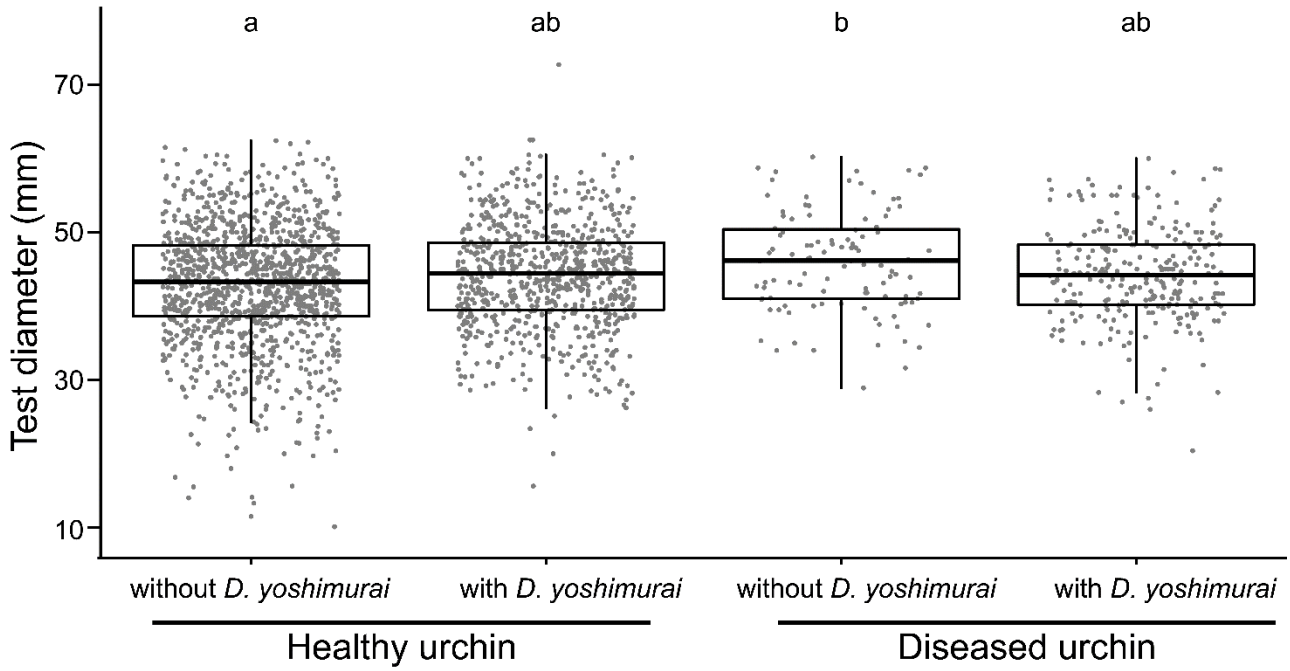

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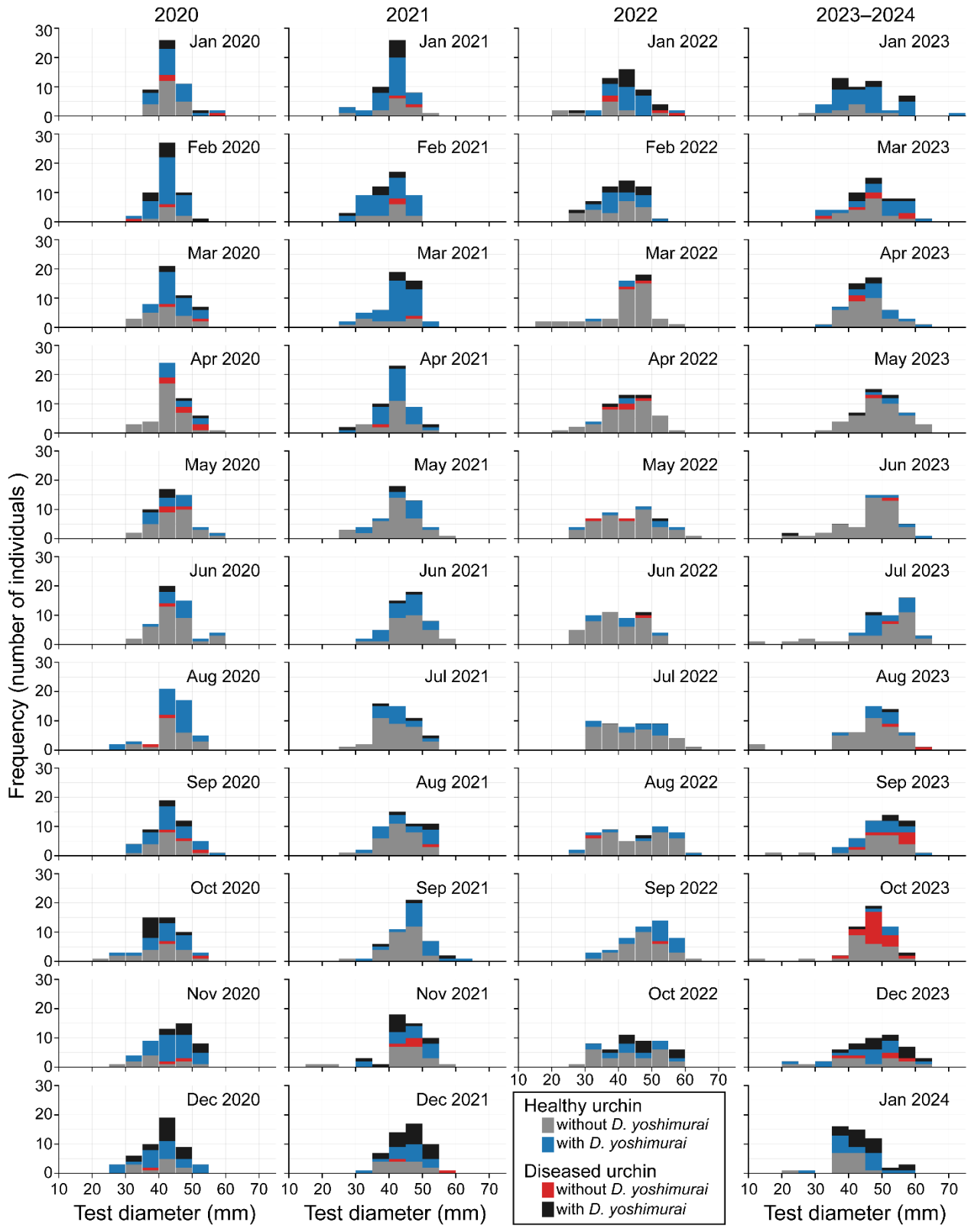

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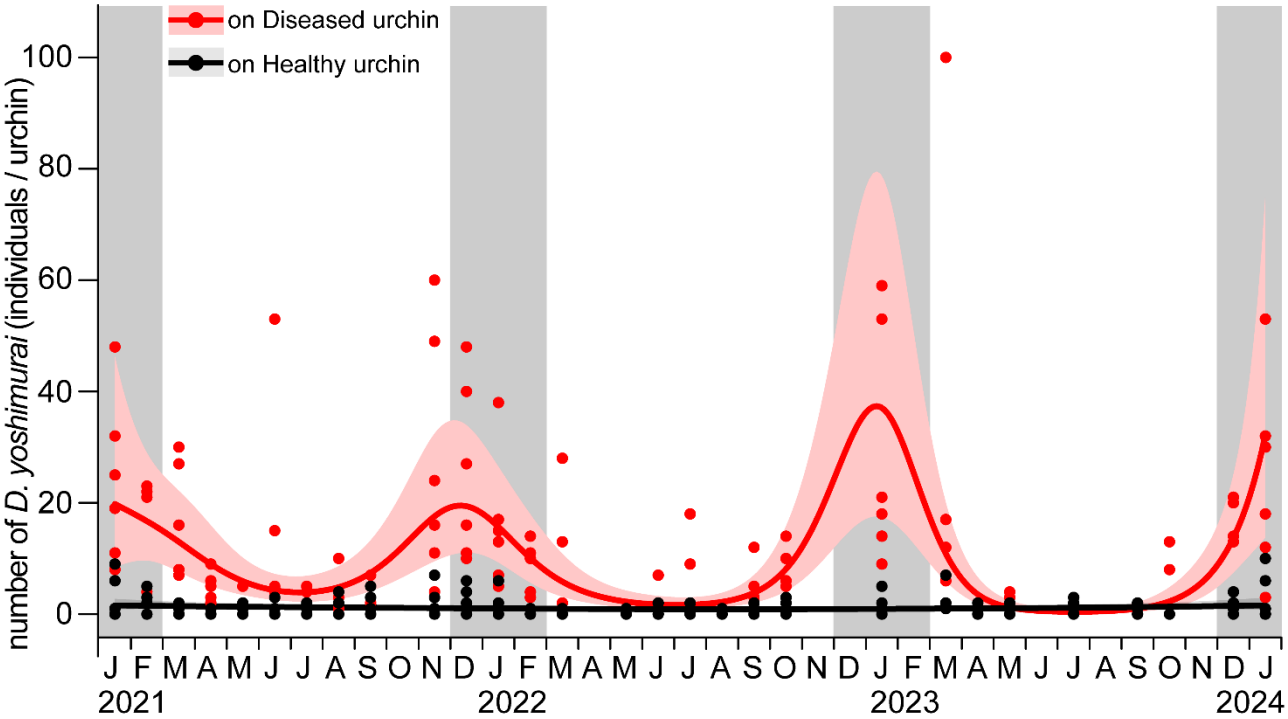

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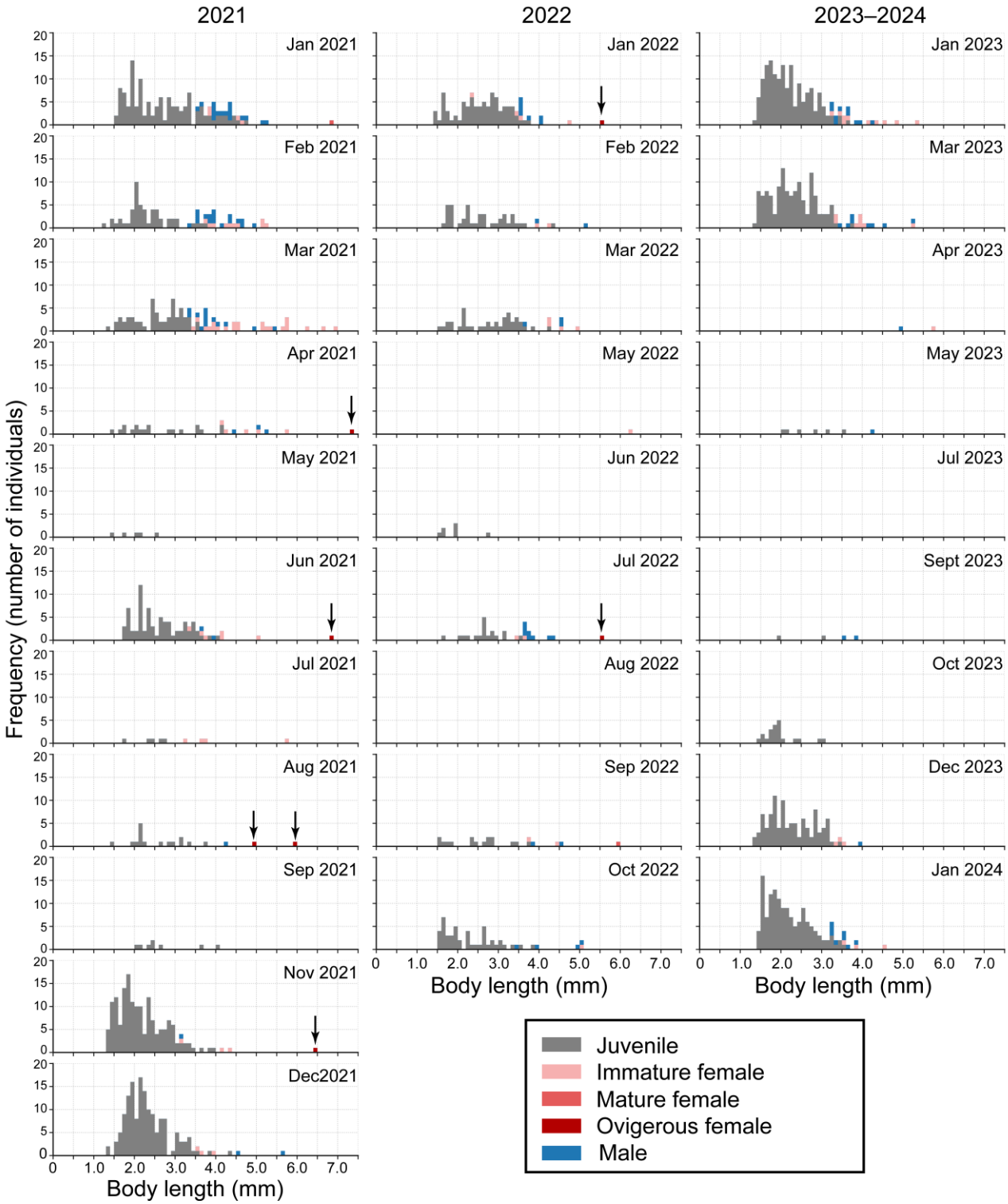

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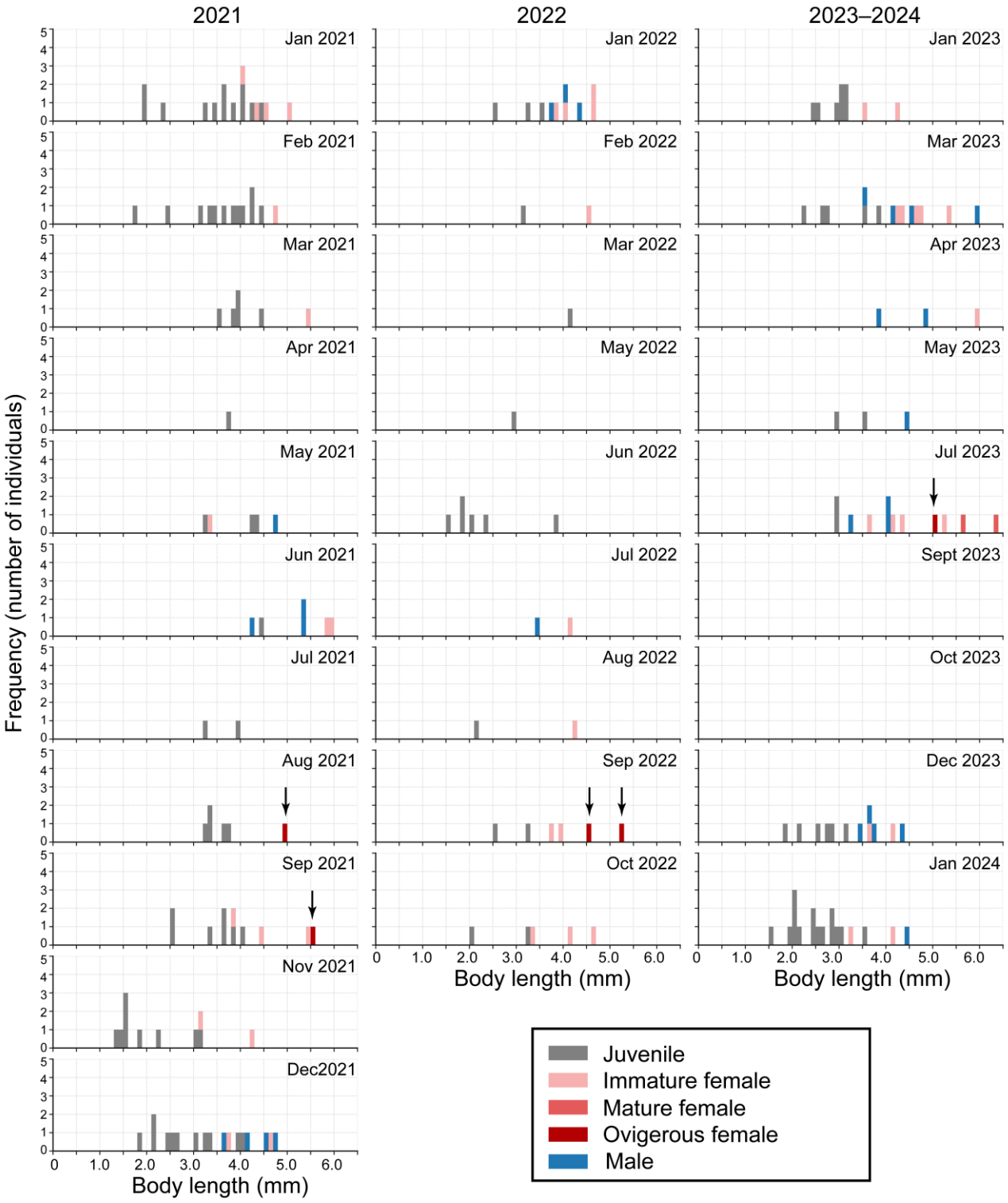

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