Title

Stage-dependent host use reveals reproductive and nursery habitats in the sea urchin-associated amphipod *Dactylopleustes yoshimurai*

Running head

Ontogenetic host change in *Dactylopleustes yoshimurai*

Authors and affiliations

Masafumi Kodama[1, *], Ryoga Yamazaki[2], Ko Tomikawa[3], Gen Kume[1], Toru Kobari[1], Jun Hayakawa[4]

[1] Faculty of Fisheries, Kagoshima University, 4–50–20 Shimoarata, Kagoshima 890–0056, Japan

[2] Graduate School of Agriculture, Forestry and Fisheries, Kagoshima University, 4–50–20 Shimoarata, Kagoshima 890–0056, Japan

[3] Graduate School of Humanities and Social Sciences, Hiroshima University, 1–1–1 Kagamiyama, Higashihiroshima, Hiroshima 739–8524, Japan

[4] Center for International and Local Research Cooperation, Atmosphere and Ocean Research Institute, The University of Tokyo, 1–19–8 Akahama, Otsuchi, Iwate 028–1102, Japan

* Corresponding author: mkodama@fish.kagoshima-u.ac.jp

ORCID

Masafumi Kodama: https://orcid.org/0000-0002-0889-5625

Ko Tomikawa: https://orcid.org/0000-0003-1521-9016

Gen Kume: https://orcid.org/0000-0003-2467-175X

Toru Kobari: https://orcid.org/0000-0003-4205-6734

Jun Hayakawa: https://orcid.org/0000-0002-9667-969X

Abstract

Host-associated symbionts are often described by a single host species, yet host use may be partitioned among life stages and host conditions. The sea urchin-associated amphipod *Dactylopleustes yoshimurai* commonly occurs on *Strongylocentrotus intermedius* in Otsuchi Bay, Japan, where juveniles frequently aggregate on disease lesions, whereas ovigerous females are rarely found. This pattern suggests that juvenile recruitment and reproduction may depend on different host resources. We tested whether the larger co-occurring sea urchin *Mesocentrotus nudus* functions as a reproductive host by combining field sampling during the reproductive season with paired-choice host assays. Field samples showed contrasting population structures among host categories: diseased *S. intermedius* was dominated by juveniles, whereas *M. nudus* harboured more large individuals and ovigerous or mature females. These results support a stage-dependent multi-host life-history model in which reproduction and late development occur mainly on *M. nudus*, while recruitment and early growth are concentrated on *S. intermedius*, particularly within lesion microhabitats. In laboratory assays with freely moving hosts, both large and small amphipods settled preferentially on *M. nudus* when offered either healthy or diseased *S. intermedius* as an alternative, although this tendency appeared less pronounced when the alternative host was diseased. Overall, our results show how host specificity in a marine symbiont can emerge from a multi-host life cycle linking reproductive habitat, disease-mediated nursery habitat, and post-settlement retention.

Keywords

Dactylopleustes yoshimurai; sea urchin symbiont; life history; population dynamics; host–symbiont interactions; ontogenetic host change

Introduction

Symbiotic and/or parasitic organisms frequently show strong host-use patterns, but host specificity is not necessarily a fixed property of a species. A single "host species" label may obscure dynamic host use across life stages, host conditions, and habitat contexts. In particular, host use can vary across life stages, such that juveniles and adults experience different constraints and benefits and may therefore occupy different hosts (e.g., Ota et al. 2008; Hadfield et al. 2009; De Bruyn et al. 2010, 2011; Brooker et al. 2013). Detecting such stage-dependent host use is essential for understanding population dynamics, dispersal, and ecological impacts of symbiotic and parasitic organisms.

This issue is particularly relevant in amphipods. The order Amphipoda is among the largest crustacean orders, with more than 10,000 described species (Horton et al. 2026; Lowry and Myers 2017), and symbiotic relationships with a broad range of animal hosts have been reported throughout the group (e.g., Vader 1978, 1983; Vader and Tandberg 2013, 2015; Iwasa-Arai and Serejo 2018; Tomikawa et al. 2019; Kodama et al. 2022; Hanaoka et al. 2025). Nevertheless, many host-associated amphipods are still known primarily from host records, whereas the demographic basis of host use remains poorly understood. In particular, few studies have tested whether different hosts, or different conditions of the same host, support different life-history stages.

Members of the genus *Dactylopleustes* Karaman & Barnard, 1979 live as symbionts on echinoids and are thought to possess adaptations for existence on the host's external body surface, a habitat structured by spines, pedicellariae, and local variation in surface condition (Vader 1978; Bousfield and Hendrycks 1995). Even so, fundamental aspects of *Dactylopleustes* ecology and life history remain poorly resolved (Vader 1978), and whether these amphipods exert measurable effects on their host urchins is still uncertain.

Dactylopleustes yoshimurai Tomikawa, Hendrycks & Mawatari, 2004 is an echinoid-associated symbiont described from Japan (Tomikawa et al. 2004) and commonly found on the surface of *Strongylocentrotus intermedius* in Otsuchi Bay (Kodama et al. 2026a). Recent field observations showed that *D. yoshimurai* can aggregate densely on diseased areas of *S. intermedius*, but occurs only sparsely on healthy hosts (Kodama et al. 2020). Subsequent DNA metabarcoding of gut contents indicated that the amphipod does not rely heavily on host tissues for food, suggesting that disease lesions may function primarily as favourable microhabitats rather than simply food patches (Kodama et al. 2024). Long-term field surveys on *S. intermedius* further demonstrated that host disease status structures the amphipod's population dynamics: diseased urchins support far higher amphipod occurrence and density, and size–frequency distributions on diseased hosts are dominated by juveniles, especially in winter (Kodama et al. 2026a). Reproduction appears to peak from late summer to autumn, yet ovigerous females are seldom encountered on *S. intermedius* (Kodama et al. 2026a). Together, these findings suggest that diseased *S. intermedius* may function as a disease-mediated nursery

microhabitat, whereas reproduction and late development may occur on another host.

These observations raise the broader question of whether *D. yoshimurai* should be regarded as a symbiont associated primarily with *S. intermedius*, or instead as a stage-dependent multi-host symbiont that uses different echinoid hosts or host conditions for different components of its life cycle. In the study area, the larger urchin *Mesocentrotus nudus* co-occurs with *S. intermedius* and may provide different defensive regimes and surface microhabitats. If *M. nudus* functions as a reproductive host, we predict that (i) late-stage individuals and ovigerous females should be disproportionately common on *M. nudus* in the field during the reproductive season, and (ii) amphipods should preferentially occupy *M. nudus* in host-choice assays, potentially even when the alternative *S. intermedius* host is diseased.

Here, we tested these predictions using autumn field sampling and controlled host-choice experiments. By combining field population structure with experimental host choice, we evaluate whether host use in *D. yoshimurai* is best explained by a single-host association or by a stage-dependent, multi-host life history. We then synthesize our findings with the behavioural framework established for lesion-associated aggregation on *S. intermedius* (Kodama et al. 2026b) to propose a life-history model connecting reproduction on a larger echinoid host with disease-mediated nursery habitat on *S. intermedius*.

Materials and Methods

Field survey

This study was carried out in a rocky subtidal area at Akahama in Otsuchi Bay, Japan (Fig. 1: 39°21'00" N, 141°56'10" E, 2–3 m deep). Because Kodama et al. (2026a) suggested that late summer to autumn corresponds to the reproductive season of this species, we conducted SCUBA surveys from August to September 2024. In addition, at this study site, monthly surveys of healthy and diseased *S. intermedius* have been conducted since 2021 using the same protocol (see below), although some months are missing (Kodama et al. 2026a). From these previous surveys, we also included available samples of healthy and diseased S. intermedius collected in August and September 2021–2023.

Sea urchins were collected haphazardly, including diseased *Strongylocentrotus intermedius*, healthy *S. intermedius*, and *Mesocentrotus nudus*. The disease symptoms frequently observed in *S. intermedius* in Otsuchi Bay resemble those of lesion-type sea urchin diseases commonly referred to as “bald sea urchin disease”, which involve loss of spines, tube feet, pedicellariae, and epidermal tissues, with exposure and discoloration of the test surface (Johnson 1971; Becker et al. 2008; Shaw et al. 2023 ; Carella et al. 2025). However, the causative agent cannot be identified in the field. In this study, therefore, a “diseased urchin” was defined as an urchin with the following symptoms, as

described by Kodama et al. (2024, 2026a): 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.

Each urchin individual was gently placed in plastic bags to prevent escape of symbiotic organisms. The urchins and their symbionts were all anaesthetized with iso-osmotic 7.5% weight% magnesium chloride ($MgCl_2 \cdot 6H_2O$). Then, *D. yoshimurai* individuals detached from the urchins by anaesthesia were counted and preserved in 80% ethanol. In total, 210 individuals of *D. yoshimurai* were used for analyses (106 individuals from 37 diseased *S. intermedius*, 55 individuals from 51 healthy *S. intermedius*, and 49 individuals from 82 *M. nudus*).

For each individual of *D. yoshimurai*, body length, sex, and developmental stage were determined following Kodama et al. (2026a). 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.

Experiments for host preference

Dactylopleustes yoshimurai and host sea urchins used in the experiments were collected on 11 February 2024, and the experiments were conducted from 13 to 22 February 2024. Using SCUBA, we collected diseased *Strongylocentrotus intermedius* (test diameter: mean ± SD, 45.71 ± 4.82 mm), healthy *S. intermedius* (46.64 ± 5.28 mm), and *Mesocentrotus nudus* (76.58 ± 4.34 mm). Amphipods were collected from host urchins at the same locality and maintained in flow-through seawater tanks until use. To avoid confounding host-of-origin effects, amphipods were pooled regardless of the host type from which they were collected, and individuals were randomly assigned to trials. Immediately before each experiment, sea urchins were rinsed with seawater to remove other symbiotic organisms from their body surfaces.

To examine whether host preference differed between developmental stages, amphipods were separated into two size classes: large individuals (body length: 7.26 ± 1.29 mm) and small individuals (body length: 3.53 ± 0.77 mm). The large size class corresponded to mature stages (see Results, Fig. 2). For the small size class, we used the smallest individuals that could be handled reliably. Individuals

smaller than this size class were too fragile during collection and handling to obtain sufficient numbers of live specimens in good condition for experiments.

Host preference was tested in four paired-choice treatments: (1) large *D. yoshimurai* individuals: healthy *S. intermedius* vs. *M. nudus* (n = 15); (2) large *D. yoshimurai* individuals: diseased *S. intermedius* vs. *M. nudus* (n = 16); (3) small *D. yoshimurai* individuals: healthy *S. intermedius* vs. *M. nudus* (n = 15); and (4) small *D. yoshimurai* individuals: diseased *S. intermedius* vs. *M. nudus* (n = 16). The experimental design followed "Host selection experiment 1: with freely moving sea urchin hosts" in Kodama et al. (2026b). Transparent plastic tanks (425 × 245 × 285 mm) filled with natural seawater to a depth of 15 cm were used. All experimental tanks were placed inside larger flow-through seawater tanks outdoors to maintain ambient seawater temperature. Two host urchins were placed in each tank. After the introduction of the urchins, ten individuals of *D. yoshimurai* were gently introduced into the centre of the tank and left for 24 h to settle freely on the host urchins. After 24 h, each sea urchin was gently enclosed in a plastic net bag with 0.5-mm mesh, together with the *D. yoshimurai* individuals on its surface. The sea urchins were then washed with seawater to detach *D. yoshimurai*, and the number of *D. yoshimurai* individuals on each sea urchin was counted. For each trial, we recorded the numbers of amphipods associated with each urchin, those remaining in the tank, dead individuals, and unrecovered individuals. The Wilcoxon matched-pairs signed-rank test was used to compare the numbers of *D. yoshimurai* individuals between the two host urchins.

Results

Host- and condition-associated differences in population structure

Smaller individuals were more frequently observed on *Strongylocentrotus intermedius*, whereas larger individuals were more frequently observed on *Mesocentrotus nudus* (Fig. 2). Within *S. intermedius*, individuals collected from diseased hosts were predominantly juveniles (84.91%). In contrast, individuals collected from *M. nudus* were mainly advanced developmental stages of both sexes, and juveniles accounted for only 8.16% of the individuals on this host. Ovigerous or mature females were found mainly on *M. nudus* (11/49 individuals: 22.45%) and were less common on healthy *S. intermedius* (6/55 individuals: 10.91%) and diseased *S. intermedius* (4/106 individuals: 3.77%). Within *S. intermedius*, individuals collected from healthy hosts tended to be larger than those collected from diseased hosts.

Experiments for host preference

Across both size classes, amphipods settled predominantly on *M. nudus* even when *S. intermedius* hosts were available (Fig. 3). Large individuals showed higher settlement on *M. nudus* than on either

healthy or diseased *S. intermedius* (both $p < 0.001$; Fig. 3a, b). Small individuals also settled more frequently on *M. nudus* than on healthy *S. intermedius* ($p < 0.001$; Fig. 3c) or diseased *S. intermedius* ($p = 0.010$; Fig. 3d), indicating that the direction of preference was maintained, although the tendency appeared less pronounced when the alternative host was diseased. Across trials, most individuals settled on urchins (9.21 ± 1.12 individuals), whereas fewer remained in the tank (0.45 ± 0.74 individuals). Dead and unrecovered individuals were rare (dead: 0.08 ± 0.27; unrecovered: 0.33 ± 0.57). No mortality was observed in any sea urchin during the experiment.

Discussion

Our results show that host use in *Dactylopleustes yoshimurai* is partitioned among host species, host conditions, and life stages. Field samples indicated that large individuals and ovigerous or mature females occurred mainly on *Mesocentrotus nudus*, whereas juveniles were concentrated on *Strongylocentrotus intermedius*, especially diseased individuals. Host-choice assays further showed preferential short-term settlement on the larger *M. nudus* host phenotype across size classes. Together, these findings extend previous work on disease-linked aggregation and population dynamics on *S. intermedius* by indicating that *D. yoshimurai* is not adequately described as a symbiont of a single host species (Kodama et al. 2020, 2024, 2026a, 2026b). Instead, its realized host use appears to involve a stage-dependent, multi-host life history in which reproductive habitat and nursery habitat are separated among host categories and host conditions.

Stage-dependent host use has been documented in other symbiotic crustaceans, but remains poorly known in amphipods. In the commensal porcelain crab *Allopetrolisthes spinifrons*, megalopae and small juveniles use several alternative hosts, whereas mature crabs occur on sea anemones; laboratory experiments further showed that small juveniles can move from limpets to sea anemones, indicating a shift from alternative settlement hosts to sea anemones, the principal adult host (Baeza and Stotz 2001). In the echinoid-associated pea crab *Dissodactylus primitivus*, host use is also asymmetric: the whole post-metamorphic life cycle can occur on *Meoma ventricosa*, whereas *Plagiobrissus grandis* is used mainly by adults and is associated with higher female fecundity (De Bruyn et al. 2010). These studies provide useful precedents for interpreting the host-associated population structure of *Dactylopleustes yoshimurai*. However, the present case differs in that the proposed nursery habitat is not simply a different host species, but a particular host condition: diseased *S. intermedius* with lesion microhabitats.

Stage-dependent host use and reproduction on a larger host

Our field and experimental results jointly support the hypothesis that *M. nudus* functions as a principal

host for late development and reproduction of *Dactylopleustes yoshimurai*. During the inferred reproductive season, ovigerous females and other late-stage individuals were concentrated on *M. nudus*, whereas diseased *S. intermedius* were dominated by juveniles. This pattern addresses a major gap highlighted by long-term surveys on *S. intermedius*, where ovigerous females were rare despite seasonal patterns suggesting reproductive activity before winter recruitment (Kodama et al. 2026a). A parsimonious interpretation is that much of reproduction occurs off *S. intermedius*, and our observations identify *M. nudus* as a plausible reproductive host.

The comparison with *Dissodactylus primitivus* is informative but should not be overstated. In that system, the two echinoid hosts contribute differently to the crab life cycle: *M. ventricosa* supports recruitment, juvenile growth, and reproduction, whereas *P. grandis* is used mainly by adults and may enhance female fecundity (De Bruyn et al. 2010). In *Dactylopleustes yoshimurai*, the separation between juvenile-dominated diseased *S. intermedius* and reproduction-associated *M. nudus* suggests a comparable, although independently evolved, multi-host life-history structure. Unlike *Dissodactylus primitivus*, however, the present study suggests a role for host condition, rather than host species alone, in structuring nursery habitat. This distinction is central to our interpretation: disease lesions on *S. intermedius* appear to generate microhabitats that are functionally different from the intact surface of either healthy *S. intermedius* or *M. nudus*.

The host-choice experiments using large individuals provide independent support for the reproductive-host interpretation. Large amphipods preferentially settled on *M. nudus* even when diseased *S. intermedius* was available as an alternative. This suggests that, when movement and encounter opportunities are unconstrained, *M. nudus* provides cues and/or benefits that outweigh the attraction of disease-associated microhabitats on *S. intermedius*. Importantly, this does not contradict the strong disease association documented on *S. intermedius*; rather, it implies that disease-linked aggregation is embedded within a broader, multi-host life history (Kodama et al. 2020, 2026a, 2026b).

One important caveat is that *M. nudus* was substantially larger than *S. intermedius* in our experiments. Thus, our paired-choice assays cannot fully distinguish species-specific preference from preference for host-size-associated traits, such as greater surface area, spine architecture, pedicellarial defences, or other aspects of the external microhabitat. This caveat is important because host characteristics, including relative host size, abundance, and morphological complexity, can constrain movement among hosts and host-guarding behaviour in symbiotic crustaceans (Baeza and Thiel 2007). Members of *Dactylopleustes* live on the external surface of echinoid hosts, where spines, pedicellariae, and surface topography are likely to affect attachment, movement, and persistence (Vader 1978; Bousfield and Hendrycks 1995). Therefore, the larger body size and surface architecture of *M. nudus* may be part of the host phenotype to which *Dactylopleustes yoshimurai* responds, rather than merely a nuisance factor that can be fully separated from species identity. We therefore interpret

the experimental results as evidence for preferential settlement on the larger *M. nudus* host phenotype, rather than as conclusive evidence for species recognition alone. Future experiments using size-matched host individuals, where available, or artificial substrates that manipulate host surface structure would help disentangle species identity from host-size-associated traits.

A further limitation is that field population structure alone cannot determine whether large individuals on *M. nudus* recruited there directly or moved there after earlier development on *S. intermedius*. However, the convergence between field patterns and host-choice assays strengthens the interpretation that *M. nudus* is an important host for late-stage individuals and reproduction. In this sense, the host shift proposed here should be viewed not as a directly observed individual trajectory, but as the most parsimonious life-history model supported by the combined demographic and behavioural evidence.

Reconciling preference for *M. nudus* with juvenile dominance on diseased *S. intermedius*

A key apparent mismatch is that juveniles dominate on diseased *S. intermedius* in the field, yet even small amphipods preferentially settled on *M. nudus* in host-choice assays. This discrepancy points to the importance of processes beyond initial preference, including post-settlement survival, retention, and host defences. Studies of other symbiotic crustaceans further show that host origin or previous host experience can decouple short-term host choice from field host use. In *Dissodactylus primitivus*, chemical host-detection experiments did not support a simple preference for the host associated with higher fecundity, indicating that field host use is not explained by short-term host choice alone (De Bruyn et al. 2010, 2011). In the pinnotherid crab *Calyptraeotheres garthi*, females attained larger body size and higher fecundity on one limpet host, but host-choice experiments showed attraction to the host species from which individuals had been collected rather than to the host conferring the greatest reproductive benefits (Ocampo et al. 2012). These examples support the view that realized host use cannot be inferred from short-term host-choice assays alone.

This interpretation requires caution because the “small” size class used in our experiments did not include the smallest juveniles observed in the field. For practical reasons, we used the smallest individuals that could be handled reliably, and assays using very small juveniles might have yielded a different result. Thus, whether the earliest juvenile stages show different host preferences remains unresolved. Nevertheless, within the size range examined here, small individuals also preferentially settled on *M. nudus*, suggesting that the juvenile dominance on diseased *S. intermedius* in the field is unlikely to be explained by short-term settlement preference alone.

Experimental work on *S. intermedius* has shown that lesion-associated aggregation can arise through a sequence combining host-level movement and within-host microhabitat retention, and that disturbance-like conditions, such as pedicellariae removal and wounding, can induce local

accumulation even on otherwise healthy hosts (Kodama et al. 2026b). These results emphasize that lesions can act as retention microhabitats, especially during recruitment periods, by reducing costs associated with defensive structures and/or by providing damage-associated cues that concentrate settlers (Kodama et al. 2026a, 2026b). If defence-mediated constraints are stronger on *M. nudus*, small amphipods may experience higher removal or lower persistence there, even if they initially settle on this host. Under this scenario, juveniles that settle on *M. nudus* may subsequently disperse or be excluded, whereas diseased *S. intermedius* provides a more permissive microhabitat, particularly on lesions, leading to the strong juvenile bias observed in the field (Kodama et al. 2020, 2026a, 2026b).

Interhost movement provides another mechanism by which field host use may diverge from short-term preference. In the sand dollar-associated pea crab *Dissodactylus mellitae*, laboratory experiments showed that crowding can induce crabs to leave their host and that transfers to another sand dollar increase when hosts move and come into contact (Bell 1984). This example is not evidence for host switching among different host species, but it demonstrates that echinoid-associated ectosymbionts can move among individual hosts and that host contact can facilitate such movement. Repeated interhost movement is therefore plausible in *Dactylopleustes yoshimurai*, although direct tracking will be needed to test this process.

Dietary evidence also supports a microhabitat-based interpretation. Gut metabarcoding suggests that amphipods on lesions do not depend heavily on host tissues as food, weakening a purely trophic explanation for disease-linked aggregation (Kodama et al. 2024). Instead, disease lesions likely represent a composite of reduced physical defences, altered surface structure, and shifted chemical or microbial environments that collectively enhance settlement and retention. In this framework, diseased *S. intermedius* functions less as a preferred host species and more as a high-value nursery patch produced by seasonal disease dynamics (Kodama et al. 2020, 2024, 2026a, 2026b).

Ecological implications

Our findings contribute to a broader view of host specificity as a demographic outcome rather than a fixed species-level attribute. In *Dactylopleustes yoshimurai*, apparent host use depends strongly on the life stage and host condition being sampled: juveniles are concentrated on diseased *S. intermedius*, whereas large individuals and reproductive females occur mainly on *M. nudus*. Thus, a single-host description would obscure the functional separation between nursery and reproductive habitats.

This stage-dependent multi-host structure may buffer symbiont populations against seasonal limitations of any single host type while coupling amphipod demography to both echinoid community composition and host disease dynamics. By linking juvenile concentration to disease lesions and reproduction to a larger alternative host, *Dactylopleustes yoshimurai* may track temporally variable

habitat quality while maintaining reproductive output. Changes in the relative abundance of *M. nudus* and *S. intermedius*, or in the seasonal prevalence of disease lesions, could therefore alter amphipod population dynamics and the intensity of lesion-associated aggregations. Such changes may also have consequences for disease trajectories and broader epifaunal communities, although these consequences remain to be tested.

More broadly, this study illustrates how apparent host specificity in a marine symbiont can emerge from interactions among host species identity, host phenotype, host condition, and ontogeny. Previous studies have shown that symbiotic crustaceans may shift from alternative settlement hosts to principal adult hosts during ontogeny (Baeza and Stotz 2001), exploit multiple echinoid hosts asymmetrically across life stages (De Bruyn et al. 2010), or show host-choice patterns shaped by host origin rather than current reproductive benefits alone (Ocampo et al. 2012). The present study adds disease-mediated microhabitat availability as another axis along which realized host use can be structured.

Proposed life-history model of *Dactylopleustes yoshimurai*

Our series of studies on *Dactylopleustes yoshimurai* collectively suggests a coherent, but still partly hypothetical, life-history scenario in which host switching and the use of lesions on diseased *Strongylocentrotus intermedius* are integral components (Kodama et al. 2020, 2024, 2026a, 2026b). We propose the following life-history model for *Dactylopleustes yoshimurai*, while recognizing that several steps, particularly dispersal from *M. nudus* to *S. intermedius* and the timing of host switching, require further direct testing.

First, large individuals occur primarily on *M. nudus* in late summer to autumn, when ovigerous females and other late-stage individuals are most common. This pattern, together with the rarity of ovigerous females on *S. intermedius* reported by Kodama et al. (2026a), indicates that *M. nudus* is a major host for reproduction and late development. Second, if most reproduction occurs on *M. nudus*, newly hatched juveniles would need to disperse to other nearby sea urchins to explain the subsequent dominance of juveniles on *S. intermedius*, particularly during winter (Kodama et al. 2026a). Although both large and small individuals showed short-term preference for *M. nudus* in the present study, very small juveniles may be less able to persist there over longer periods, potentially because of host defences such as pedicellariae and spines (Kodama et al. 2026b).

Third, a subset of juveniles likely recruits to *S. intermedius*, particularly during the winter recruitment period documented by Kodama et al. (2026a), and becomes associated mainly with this host during early development. On *S. intermedius*, individuals appear to move across the host surface in ways that reduce exposure to pedicellariae, and they aggregate where pedicellariae are absent or reduced, most notably within lesion areas on diseased urchins (Kodama et al. 2020, 2026a, 2026b).

Such aggregation is unlikely to reflect feeding on diseased tissue, because gut metabarcoding indicates that *Dactylopleustes yoshimurai* does not rely heavily on host tissues as food (Kodama et al. 2024). Instead, lesions are better interpreted as refugia or retention microhabitats that allow juveniles to avoid host defensive responses and persist during early development (Kodama et al. 2026b).

Fourth, while associated with *S. intermedius*, individuals likely move among hosts, although such interhost transfer appears to occur mainly during host contact (Kodama et al. 2026b). Contact-mediated transfer among individual echinoid hosts is plausible because comparable processes have been experimentally demonstrated in *Dissodactylus mellitae*, where host contact increased transfer between sand dollars (Bell 1984). These movements may contribute to the accumulation of juveniles on diseased individuals, whereas healthy *S. intermedius* support only a small number of medium to large individuals, some of which may reproduce there (Kodama et al. 2026a; this study). Finally, as individuals grow, many may shift to *M. nudus* and thereafter use it as their primary host, although a fraction of the population may remain on *S. intermedius* and reproduce there (Kodama et al. 2026a; this study).

In this proposed model, disease does not merely attract amphipods; it structures nursery habitat availability within a stage-dependent host-use strategy spanning multiple echinoid hosts. By separating reproductive and nursery habitats across host species and host conditions, *Dactylopleustes yoshimurai* provides a case in which apparent host specificity emerges from the interaction between life stage, host phenotype, host movement, and disease-mediated microhabitat availability.

Acknowledgements

We gratefully acknowledge Masaaki Hirano, Takanori Suzuki, Naoya Ohtsuchi, and the other members of Otsuchi Coastal Research Center, Atmosphere and Ocean Research Institute, The University of Tokyo for supporting sampling in Otsuchi Bay. We thank Tomohiko Kawamura (The University of Tokyo) for providing helpful comments that improved the study. This study was supported by grants-in-aid from the Mikimoto Fund for Marine Ecology, Japan. This study was also partly supported by the Tohoku Ecosystem-Associated Marine Sciences project, and Cooperative Research (No. 117: Apr 2023-Mar 2024) of Atmosphere and Ocean Research Institute, The University of Tokyo.

Statements and Declarations

Author Contributions statement

MK, RY, and JH conceptualized and designed the study. JH and MK conducted sample collections. KT confirmed the identification of *D. yoshimurai* specimens. MK, RY, and JH carried out all the sample processing and experiments. MK and RY carried out data processing and statistical analyses. JH, GK, and TK contributed to the interpretation of the results. MK wrote the manuscript and made figures with support from RY and JH. KT, GK, and TK critically reviewed the manuscript and provided substantial input. All the authors read and approved the final manuscript.

Funding

This study was supported by grants-in-aid from the Mikimoto Fund for Marine Ecology, Japan. This study was also partly supported by the Tohoku Ecosystem-Associated Marine Sciences project, and Cooperative Research (No. 117: Apr 2023-Mar 2024) of Atmosphere and Ocean Research Institute, The University of Tokyo.

Data availability

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

Ethical approval

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

Conflict of interest

The authors declare that they have no competing interests.

References

Baeza JA, Stotz WB (2001) Host-use pattern and host-selection during ontogeny of the commensal crab *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) (Decapoda: Anomura: Porcellanidae). J Nat Hist 35:341–355. https://doi.org/10.1080/002229301300009586

Baeza JA, Thiel M (2007) The mating system of symbiotic crustaceans: a conceptual model based on optimality and ecological constraints. In: Duffy JE, Thiel M (eds) Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms. Oxford University Press, Oxford, pp 249–268.

https://doi.org/10.1093/acprof:oso/9780195179927.003.0012
Becker PT, Egea E, Eeckhaut I (2008) Characterization of the bacterial communities associated with the bald sea urchin disease of the echinoid *Paracentrotus lividus*. J Invertebr Pathol 98:136–147.
Bell JL (1984) Changing residence: dynamics of the symbiotic relationship between *Dissodactylus mellitae* Rathbun (Pinnotheridae) and Mellita quinquiesperforata (Leske) (Echinodermata). J Exp Mar Biol Ecol 82:101–115.
https://doi.org/10.1016/0022-0981(84)90097-2
Bousfield EL, Hendrycks EA (1995) The amphipod family Pleustidae on the Pacific Coast of North America. Part III. Subfamilies Parapleustinae, Dactylopleustinae, and Pleusirinae: Systematics and distributional ecology. Amphipacifica 2:65–133.
Brooker AJ, Shinn AP, Souissi S, Bron JE (2013) Role of kairomones in host location of the pennellid copepod parasite, *Lernaeocera branchialis* (L. 1767). Parasitology 140:756–770.
https://doi.org/10.1017/S0031182012002119
Carella F, Correggia M, Cordone A, Iacovino O, Maresca F, Villari G, Roque A, De Vico G. (2025) Bald disease in a natural population of the purple sea urchin *Paracentrotus lividus* of the Mediterranean Sea: from spines to tissues. J Invertebr Pathol 213:108415.
https://doi.org/10.1016/j.jip.2025.108415
De Bruyn C, David B, De Ridder C, Rigaud T (2010) Asymmetric exploitation of two echinoid host species by a parasitic pea crab and its consequences for the parasitic life cycle. Mar Ecol Prog Ser 398:183–191.
https://doi.org/10.3354/meps08315
De Bruyn C, De Ridder C, Rigaud T, David B (2011) Chemical host detection and differential attraction in a parasitic pea crab infecting two echinoids. J Exp Mar Biol Ecol 397:173–178.
https://doi.org/10.1016/j.jembe.2010.12.005
Hadfield KA, Smit NJ, Avenant-Oldewage A (2009) Life cycle of the temporary fish parasite, *Gnathia pilosus* (Crustacea: Isopoda: Gnathiidae) from the east coast of South Africa. J Mar Biol Assoc UK 89:1331–1339.
https://doi.org/10.1017/S0025315409000587
Hanaoka T, Goto R, Nakajima H, Kodama M (2025) A new species of the genus *Leucothoe* Leach, 1814 (Crustacea: Amphipoda: Leucothoidae) associated with a limid bivalve from Sugashima Island, Japan. Zootaxa 5696:567–589.
https://doi.org/10.11646/zootaxa.5696.4.6
Horton T, Lowry JK, De Broyer C, Bellan-Santini D, Copilaș-Ciocianu D, Corbari L, Costello MJ, Daneliya ME, Dauvin JC, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks EA, Hughes LE, Jaume D, Jazdzewski K, Kim YH, King R, Krapp-Schickel T, LeCroy SE, Lörz AN.,

Mamos T, Senna AR, Serejo CS, Souza-Filho JF, Tandberg AHS, Thomas JD, Thurston M, Vader W, Väinölä R, Valls Domedel G, Vonk R, White KN, Zeidler W (2026) World Amphipoda Database. (URL: https://www.marinespecies.org/amphipoda) Accessed on 12 Feb 2026. https://doi.org/10.14284/368

Iwasa-Arai T, Serejo CS (2018) Phylogenetic analysis of the family Cyamidae (Crustacea: Amphipoda): a review based on morphological characters. Zool J Linn Soc 184:66–94. https://doi.org/10.1093/zoolinnean/zlx101

Johnson PT (1971) Studies on diseased urchins from Point Loma. In: W. J. North, (ed.), Kelp habitat improvement project, annual report, 1970–1971, California Institute of Technology, Pasadena, pp. 82–90.

Kodama M, Hayakawa J, Kawamura T (2020) Aggregations of *Dactyloplestes* (Amphipoda: Pleustidae) on the diseased areas of the host sea-urchin, *Strongylocentrotus intermedius*. Mar Biodiv 50:62. https://doi.org/10.1007/s12526-020-01100-9

Kodama M, White KN, Hosoki TK, Yoshida R (2022) Leucothoid amphipod and terebellid polychaete symbiosis with description of a new species of *Leucothoe* Leach, 1814 (Crustacea: Amphipoda: Leucothoidae). Syst Biodivers 20:2118389. https://doi.org/10.1080/14772000.2022.2118389

Kodama M, Yamazaki R, Hayakawa J, Murata G, Tomikawa K, Kawamura T, Kume G, Kobari T (2024) Feeding ecology of the urchin symbiont *Dactylopleustes yoshimurai* (Amphipoda) revealed by DNA metabarcoding. Mar Biol 171:190. https://doi.org/10.1007/s00227-024-04507-1

Kodama M, Yamazaki R, Tomikawa K, Kume G, Kobari T, Hayakawa J (2026a) Population dynamics and disease-linked host use of the sea urchin symbiont *Dactylopleustes yoshimurai* (Crustacea: Amphipoda: Pleustidae) on *Strongylocentrotus intermedius*. Crustac Res 55:45–60. https://doi.org/10.18353/crustacea.55.0_45

Kodama M, Yamazaki R, Tomikawa K, Kume G, Kobari T, Hayakawa J (2026c) Population dynamics and disease-linked host use of the sea urchin symbiont *Dactylopleustes yoshimurai* (Crustacea: Amphipoda: Pleustidae) on *Strongylocentrotus intermedius*. EcoEvoRxiv [preprint] https://doi.org/10.32942/X2Z07Z

Kodama M, Yamazaki R, Tomikawa K, Kume G, Kobari T, Hayakawa J (2026b) Disease-associated aggregation of *Dactylopleustes yoshimurai* on sea urchins: host-level and lesion-level processes. J Exp Mar Biol Ecol 603:152212. https://doi.org/10.1016/j.jembe.2026.152212

Lowry JK, Myers AA (2017) A phylogeny and classification of the Amphipoda with the establishment

504 of the new order Ingolfiellida (Crustacea: Peracarida). Zootaxa 4265:1–89.
505 https://doi.org/10.11646/zootaxa.4265.1.1
506 Ocampo EH, Nuñez JD, Cledón M, Baeza JA (2012) Host-specific reproductive benefits, host
507 selection behavior and host use pattern of the pinnotherid crab *Calyptraeotheres garthi*. J Exp
508 Mar Biol Ecol 429:36–46.
509 https://doi.org/10.1016/j.jembe.2012.06.009
510 Ota Y, Tanaka K, Hirose E (2008) Seasonal fluctuations of the sponge-dwelling gnathiid isopod
511 *Elaphognathia aff. cornigera*. Crustac Res 37:14–25.
512 https://doi.org/10.18353/crustacea.37.0_14.
513 Shaw CG, Pavloudi C, Barela Hudgell MA, Crow RS, Saw JH, Pyron RA, Smith LC (2023) Bald sea
514 urchin disease shifts the surface microbiome on purple sea urchins in an aquarium. Pathog Dis
515 81:ftad025.
516 https://doi.org/10.1093/femspd/ftad025
517 Tomikawa K, Hendrycks EA, Mawatari SF (2004) A new species of the genus *Dactylopleustes*
518 (Crustacea: Amphipoda: Pleustidae) from Japan, with a partial redescription of *D. Echinoides*
519 Bousfield and Hendrycks, 1995. Zootaxa 674:1–14.
520 https://doi.org/10.11646/zootaxa.674.1.1
521 Tomikawa K, Yanagisawa M, Higashiji T, Yano N, Vader W (2019) A new species of *Podocerus*
522 (Crustacea: Amphipoda: Podoceridae) associated with the whale shark *Rhincodon typus*. Species
523 Divers 24:209–216.
524 https://doi.org/10.12782/specdiv.24.209
525 Vader W (1978) Associations between amphipods and echinoderms. Astarte 11:123–134.
526 Vader W (1983) Associations between amphipods (Crustacea) and sea anemones (Anthozoa,
527 Actiniaria). Aust Mus Mem 18:141–153.
528 http://doi.org/10.3853/j.0067-1967.18.1984.380
529 Vader W, Tandberg AHS (2013) A survey of amphipods associated with molluscs. Crustaceana
530 86:1038–1049.
531 https://doi.org/10.1163/15685403-00003210
532 Vader W, Tandberg AHS (2015) Amphipods as associates of other Crustacea: a survey. J Crustac Biol
533 35:522–532.
534 https://doi.org/10.1163/1937240X-00002343
535
536
537

Figure legends

Fig. 1. Map showing the study site in Otsuchi Bay, Japan. This figure is reproduced from Kodama et al. (2026c) under the Creative Commons Attribution 4.0 International license (CC BY 4.0); this reuse does not infringe copyright.

Fig. 2. Body-length frequency distributions of *Dactylopleustes yoshimurai* collected from three host categories: (a) *Mesocentrotus nudus*, (b) healthy *Strongylocentrotus intermedius*, and (c) diseased *S. intermedius* at Akahama, Otsuchi Bay, Japan. Bars are stacked by sex and developmental stage: juveniles (grey), immature females (light pink), mature females (red), ovigerous females (dark red), and males (blue). Sample sizes: *M. nudus* (n = 49), healthy *S. intermedius* (n = 55), and diseased *S. intermedius* (n = 106).

Fig. 3. Results of host preference of *Dactylopleustes yoshimurai* in paired-choice assays with freely moving sea urchin hosts: (a) large *D. yoshimurai* individuals: healthy *S. intermedius* vs. *M. nudus*; (b) large *D. yoshimurai* individuals: diseased *S. intermedius* vs. *M. nudus*; (c) small *D. yoshimurai* individuals: healthy *S. intermedius* vs. *M. nudus*; (d) small *D. yoshimurai* individuals: diseased *S. intermedius* vs. *M. nudus*. Each box indicates the upper and lower quartiles. Black bold line in each box indicates the median. Whiskers indicate minimum and maximum values excluding outliers. Grey dots represent all the raw data. Values outside 1.5 times the interquartile range above the upper quartile and below the lower quartile are treated as outliers. The *p* value was calculated by the paired Wilcoxon signed-rank test.

Fig. 4. Schematic summary of the proposed life history of *Dactylopleustes yoshimurai* and its ontogenetic host shift between *Mesocentrotus nudus* and *Strongylocentrotus intermedius* in Otsuchi Bay, Japan.

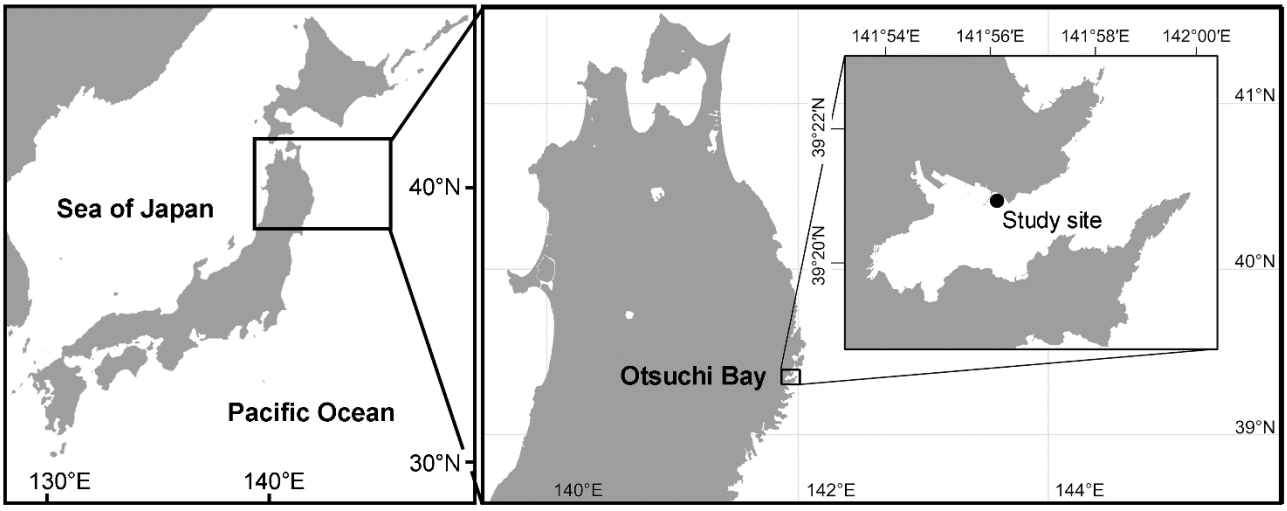
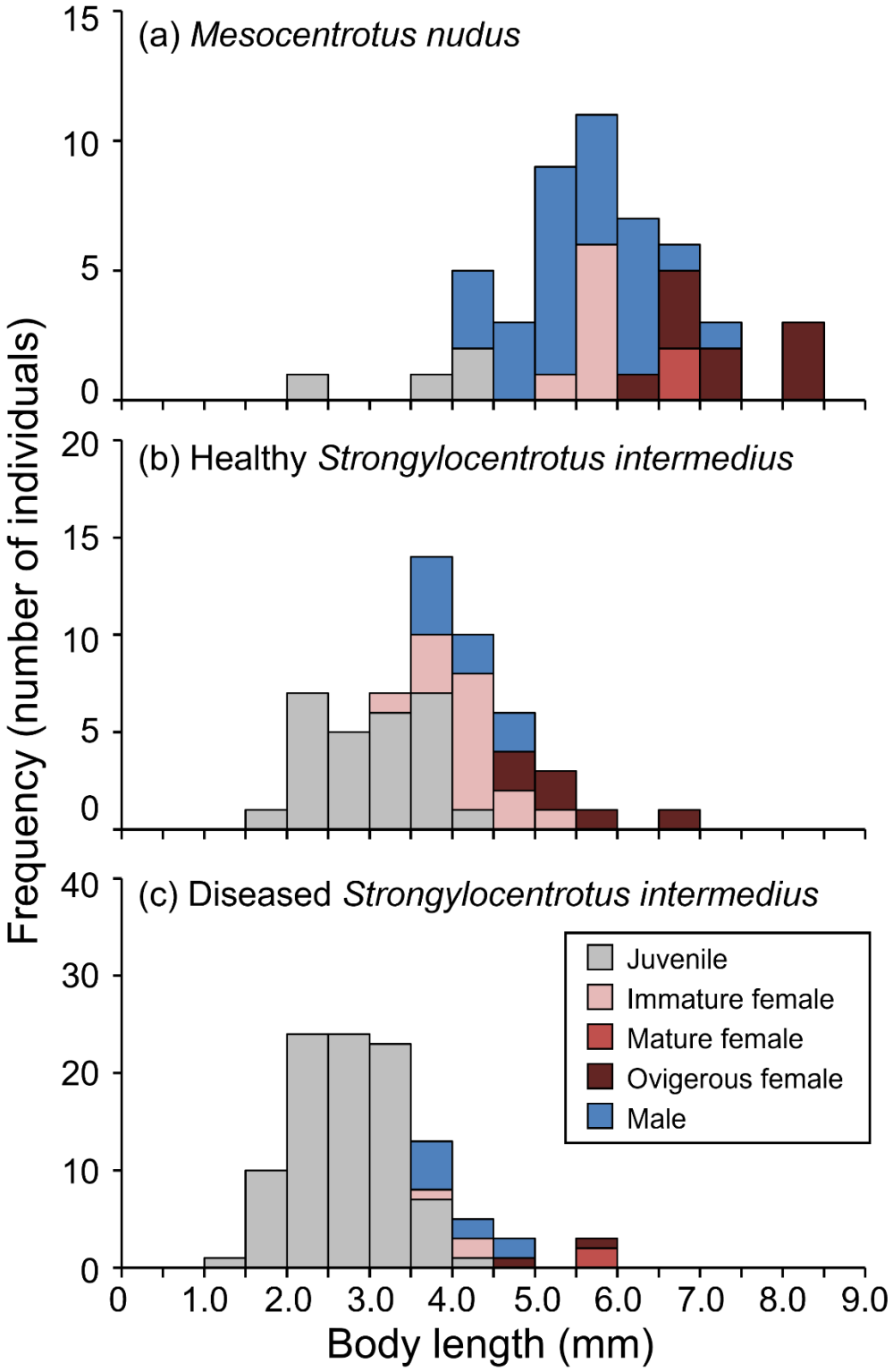


Fig. 1. Map showing the study site in Otsuchi Bay, Japan. This figure is reproduced from Kodama et al. (2026c) under the Creative Commons Attribution 4.0 International license (CC BY 4.0); this reuse does not infringe copyright.



570

571 Fig. 2. Body-length frequency distributions of *Dactylopleustes yoshimurai* collected from three host
572 categories: (a) *Mesocentrotus nudus*, (b) healthy *Strongylocentrotus intermedius*, and (c)
573 diseased *S. intermedius* at Akahama, Otsuchi Bay, Japan. Bars are stacked by sex and
574 developmental stage: juveniles (grey), immature females (light pink), mature females (red),
575 ovigerous females (dark red), and males (blue). Sample sizes: *M. nudus* (n = 49), healthy *S.*
576 *intermedius* (n = 55), and diseased *S. intermedius* (n = 106).

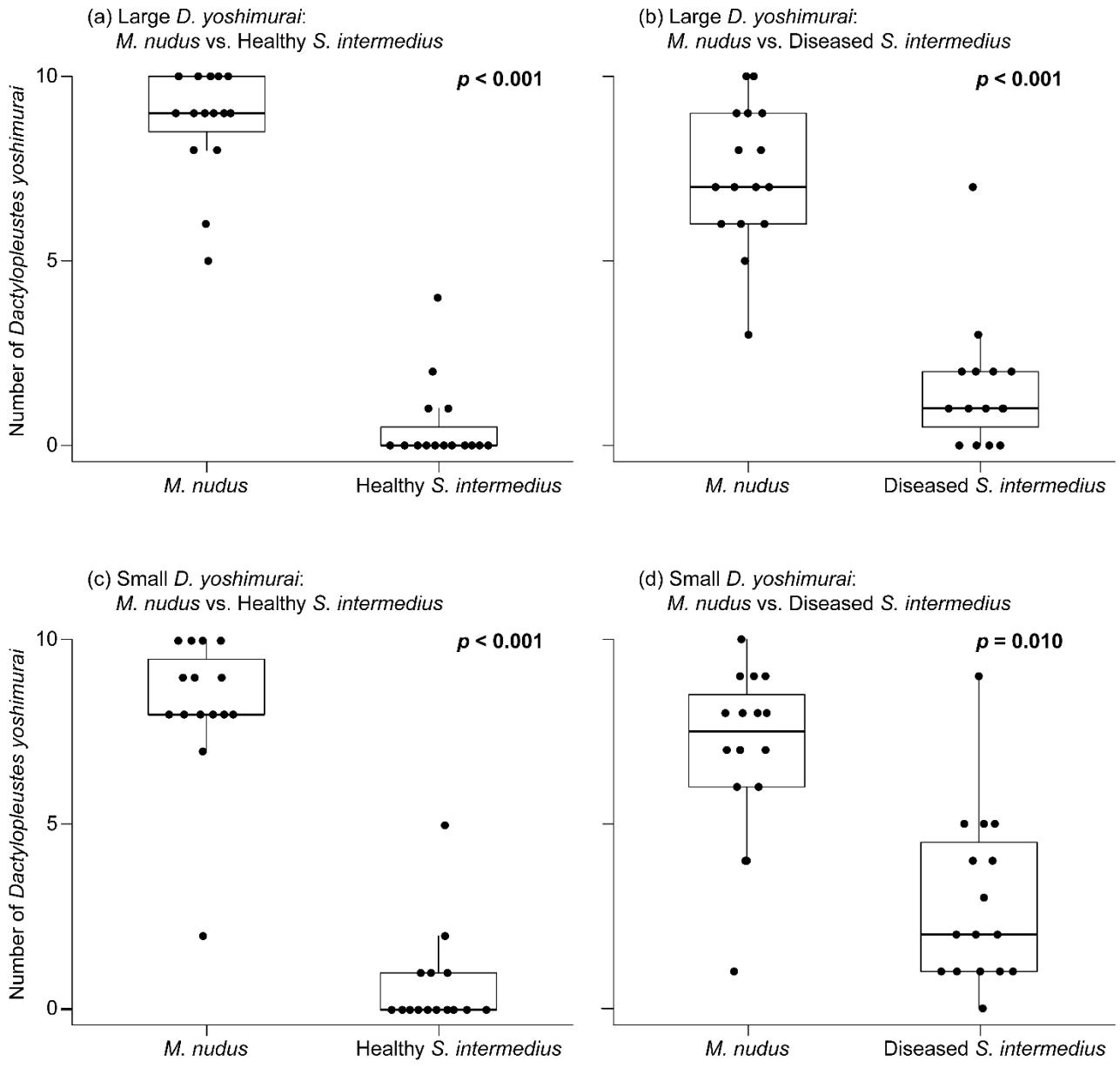


Fig. 3. Results of host preference of *Dactylopleustes yoshimurai* in paired-choice assays with freely moving sea urchin hosts: (a) large *D. yoshimurai* individuals: healthy *S. intermedius* vs. *M. nudus*; (b) large *D. yoshimurai* individuals: diseased *S. intermedius* vs. *M. nudus*; (c) small *D. yoshimurai* individuals: healthy *S. intermedius* vs. *M. nudus*; (d) small *D. yoshimurai* individuals: diseased *S. intermedius* vs. *M. nudus*. Each box indicates the upper and lower quartiles. Black bold line in each box indicates the median. Whiskers indicate minimum and maximum values excluding outliers. Grey dots represent all the raw data. Values outside 1.5 times the interquartile range above the upper quartile and below the lower quartile are treated as outliers. The *p* value was calculated by the paired Wilcoxon signed-rank test.

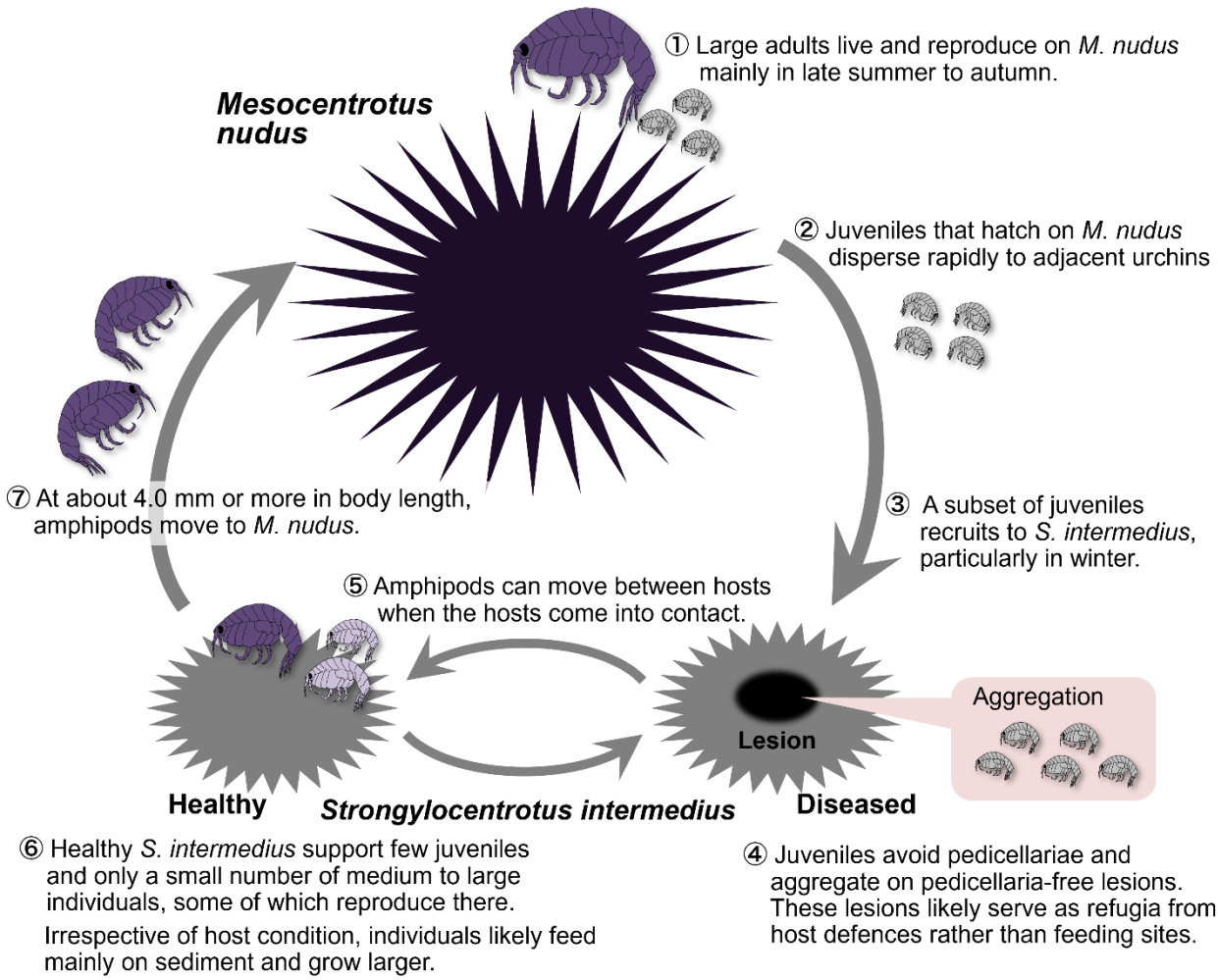


Fig. 4. Schematic summary of the proposed life history of *Dactylopleustes yoshimurai* and its ontogenetic host shift between *Mesocentrotus nudus* and *Strongylocentrotus intermedius* in Otsuchi Bay, Japan.