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Seasonal Dynamics of Sex Ratio, Reproduction, and Parasite-specific Feminization in the Hermit Crab *Pagurus filholi* at a Fixed Coastal Site in Chiba, Japan

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Reproductive output in intertidal crustaceans is reshaped by seasonal changes in host demography and its interaction with parasitic castration, yet parasite–species–resolved time series remain scarce for hermit crabs. We conducted year-round monitoring of the hermit crab *Pagurus filholi* at a fixed intertidal site in Chiba Prefecture, Japan, with monthly sampling from January to December 2025. Hosts were sexed and female reproductive status (ovigerous vs. non-ovigerous) was recorded, and rhizocephalan infections were diagnosed by externa morphology and subsequently assigned to *Peltogasterella gracilis* or *Peltogaster postica* using DNA barcoding. Across 12 sampling occasions, 3,134 crabs were recorded (1,586 males; 1,548 females). Sex ratio varied significantly among months, shifting from female-biased in December (early winter)–May (late spring) to strongly male-biased in June (early summer) –November (late autumn). The proportion of ovigerous females also showed strong seasonality, peaking in mid-winter, declining through spring, reaching zero in August–September, and increasing again toward winter. Both parasites exhibited sharply seasonal prevalence with a pronounced June peak: for *Peltogasterella gracilis*, 29/166 in June vs. 8/2,968 in other months, and for *Peltogaster postica*, 19/166 vs. 36/2,968. Male secondary sexual morphology responded in a parasite-specific manner: infected males were more likely to bear a second pleopod, a female-specific egg-brooding structure, than males without externae, driven primarily by *Peltogasterella gracilis* (26/28) rather than *Peltogaster postica* (3/35). Together, these results provide a high-resolution baseline linking reproductive phenology and parasite-specific feminization in a single *P. filholi* population.

Keywords: Reproductive phenology, Sex ratio, Parasitism, Rhizocephala, *Peltogasterella*, *Peltogaster*

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BACKGROUND

Seasonal variation in population structure is a pervasive feature of intertidal crustaceans, reflecting the combined effects of reproduction, recruitment, growth, and mortality under fluctuating environmental conditions. In pagurid hermit crabs, month-to-month shifts in sex ratio and the proportion of ovigerous females provide a compact description of reproductive phenology and demographic turnover and can influence mating dynamics through seasonal changes in the availability of receptive females and the intensity of male–male competition (Wada et al. 2005). The hermit crab *Pagurus filholi* is a well-studied representative species for seasonal reproduction and mating behavior in pagurids, as it is one of the most common hermit crabs inhabiting rocky intertidal areas in Japan and exhibits a broad geographical distribution. The reproductive phenology of this species exhibits marked geographic variation. In Kuroshio-influenced regions along the Pacific coast of Japan, ovigerous females have been reported from October to August, whereas in northern Japan, the main spawning period extends from March to July (Imazu and Asakura 1994; Goshima et al. 1998; Wada et al. 2005). Reproductive activity changes as the season progresses, indicating dynamic scheduling of reproduction in females (Imazu and Asakura 1994; Yoshino et al. 2002). Because male mate choice and precopulatory guarding decisions are closely linked to female reproductive status, demonstrating that temporal variation in female ripeness and fecundity influences mating opportunities and mate guarding intensity (Goshima et al. 1998; Minouchi and Goshima 1998). In addition, *P. filholi* exhibits sex-specific differences in shell use and resource exploitation (Yoshino et al. 2001), suggesting that males and females may differ in their exposure to rhizocephalan parasites due to sex-specific habitat use.

Parasitic castrators, especially rhizocephalan barnacles (Cirripedia: Rhizocephala), are among the strongest biotic drivers capable of reshaping crustacean demography. Rhizocephalans possess an extraordinary life cycle and specialized host invasion stages; females consist of a brooding sac (externa) and a root-like internal system (interna), whereas males are dwarfs that live within the female externa (Glenner and Høeg 1995; Høeg and Lützen 1995). Rhizocephalans absorb nutrients from their hosts through interna and can sterilize hosts, redirect host energy allocation, and induce profound host morphological and behavioral changes (Høeg 1995). Parasitic castration is an extreme strategy of resource redirection from host reproduction to parasite fitness, resulting in significant demographic consequences (Baudoin 1975; Lafferty and Kuris 2009). A hallmark of rhizocephalan infection in decapods is parasite-induced modification of secondary sexual traits in male hosts, often referred to as feminization, whose magnitude can vary among parasite taxa and hosts (Nielsen 1970; Kajimoto et al. 2025).

Sex-biased parasitism is widely documented across animals and is often attributed to sex-specific exposure, behavior, and life-history trade-offs (Zuk and McKean 1996; Poulin 1996). In arthropods, however, sex bias is not universal and varies among host–parasite combinations, depending on species-specific ecological factors (Sheridan et al. 2000), emphasizing the need for empirical, parasite-resolved analyses. Hermit crabs of the genus *Pagurus* are frequently infected by peltogastrid and peltogasterellid rhizocephalans (Yoshida et al. 2014; Kajimoto et al. 2022, 2025).

In pagurid hermit crabs infested by these rhizocephalans, males show feminization, including the expression of female-specific traits such as the development of the second pleopod, and reduced cheliped propodus length compared with unparasitized males (Nielsen 1970; Kajimoto et al. 2025). In Paguridae, males possess the third to fifth left pleopods, whereas females possess the second to fifth, with the second to fourth pleopods functioning in egg carrying (Yoshino et al. 2002; McLaughlin 2003). Yet species-resolved time series and parasite-specific phenotypic effects remain limited.

Peltogasterellids and peltogastrids are readily distinguishable: peltogasterellids produce multiple elongated externae, whereas most peltogastrids form a single, oval-shaped externa. Along the Pacific coast of Japan, two peltogasterellid species have been reported: *Peltogasterella gracilis* and *Peltogasterella sensuru* (Yoshida et al. 2015). However, *Peltogasterella sensuru* n. sp. has been found only in southern regions such as Okinawa, Japan, whereas *P. gracilis* has been recorded only from northern localities (Yoshida et al. 2015). In contrast, host associations and prevalence of peltogastrids, which have been reported from Okinawa to Hokkaido, Japan, vary among locations, and species identification can be consistent with morphology of externa and molecular identification using mitochondrial loci (Yoshida et al. 2014). Regional comparisons further indicate that prevalence can vary substantially among sites (Yoshida et al. 2012), and barcode resources have expanded the taxonomic resolution for peltogastrids (Yoshida et al. 2011; Jung et al. 2019).

Here, we present year-round monitoring of the population dynamics of *P. filholi* at a fixed coastal site in Chiba Prefecture, Japan, quantifying monthly variation in host sex ratio, the proportion of ovigerous females, and the prevalence of two rhizocephalan barnacles, *Peltogasterella gracilis* and *Peltogaster postica*. Importantly, we quantify the occurrence of a female secondary sexual trait (presence of a second pleopod) in male hosts across infection classes to test whether parasite species differ in the magnitude of feminization-linked morphology (Kajimoto et al. 2025).

MATERIALS AND METHODS

Study site and sampling

All experimental procedures and sampling protocols complied with the guidelines of the Institutional Animal Care and Use Committee of Kanagawa University. All animal experiments were conducted in accordance with the ARRIVE guidelines (Percie du Sert et al. 2020).

A year-round field survey of *P. filholi* was conducted at a fixed intertidal coastal site in Chikura, located in the southeastern part of Minamiboso, Chiba Prefecture, Japan (34°55'27.5"N 139°56'41.4"E). Sampling was performed monthly from January to December 2025 (12 sampling occasions). Hermit crabs encountered within the focal habitat were collected by hand and processed for sex, female reproductive status, rhizocephalan infection status, and (for males) the presence/absence of a second pleopod (P2), a female-specific organ for egg-carrying in hermit crabs (McDermott 1999).

Sex determination and female reproductive status

Sex was determined from external sexual characters following standard pagurid criteria: male has gonopores on the coxae of the fifth pereopods and female has gonopores on the coxae of the third pereopods, respectively. Females were categorized as ovigerous when eggs were present on pleopods and non-ovigerous when eggs were absent. Monthly sex ratio was calculated as the proportion of females among all individuals, and the monthly ovigerous proportion was calculated as ovigerous females among all females.

Rhizocephalan infection screening and male pleopod phenotype

Rhizocephalan infections were screened by external examination for the presence of an externa on the host abdomen. Externae were provisionally assigned to *Peltogasterella gracilis* or *Peltogaster* based on morphology, and all *Peltogaster postica* specimens were previously validated by COI sequencing (accession numbers: LC910526 – LC910626, LC910646 – LC910648) (Kajimoto et al., 2026). For each male, the presence/absence of P2 was recorded. For infected males, P2 presence was tallied separately for *Peltogasterella gracilis* and *Peltogaster postica* infections (Kajimoto et al. 2025).

Statistical analyses

All analyses were performed on monthly aggregated counts. Sex ratio seasonality was analyzed by binomial general linearized model (GLM) with month as a categorical predictor, response = female vs male, and weights = monthly total. Ovigerous proportion seasonality was calculated by binomial GLM with month as a categorical predictor, response = ovigerous vs non-ovigerous among females, and weights = monthly female total. Parasite prevalence was analyzed by monthly prevalence estimates, which were displayed with Wilson 95% confidence intervals. June peak test was performed by Fisher's exact test comparing June vs all other months (infection status: with vs without externae), reporting odds ratios (OR) with 95% confidence intervals. Sex bias was analyzed by Fisher's exact test on annual 2×2 tables (infection status: with vs without externae × sex: male vs female), reporting OR (male vs female infection odds) with 95% confidence intervals. Second pleopod analyses was done and P2 frequencies were calculated for (i) all males, (ii) males without externae, and (iii) infected males separated by parasite species. Infection–P2 association in males was tested using Fisher's exact test, reporting OR with 95% CI. Covariation between monthly male parasite prevalence and P2 frequency was assessed using Spearman's rank correlation.

RESULTS

Sampling composition, seasonal variation in sex ratio, and reproductive phenology

Across 12 sampling occasions in 2025, we recorded 3,134 *P. filholi* individuals (males: 1,586; females including ovigerous: 1,548). Monthly sample sizes varied substantially, and the composition of males without externae, females without externae, ovigerous females, and hosts infested by *Peltogasterella gracilis* or *Peltogaster* is shown in figure 1A and table S1. Monthly sex ratio varied strongly (Fig. 1B). A binomial GLM detected a significant month effect (likelihood-ratio test: χ^2 (11) = 441.77, $p < 0.001$), with female-biased samples in winter–early spring and strongly male-biased samples in late summer–early autumn. Across the year, the overall female proportion was 0.494.

Female reproductive status showed pronounced seasonality (Fig. 1C). A binomial GLM detected a significant month effect on ovigerous proportion among females (χ^2 (11) = 800.15, $p < 0.001$). Ovigerous females were abundant in winter (January–February), declined through spring, were absent in late summer (August–September), and reappeared toward winter. In total, 581 ovigerous females were recorded (ovigerous proportion among females = 0.375).

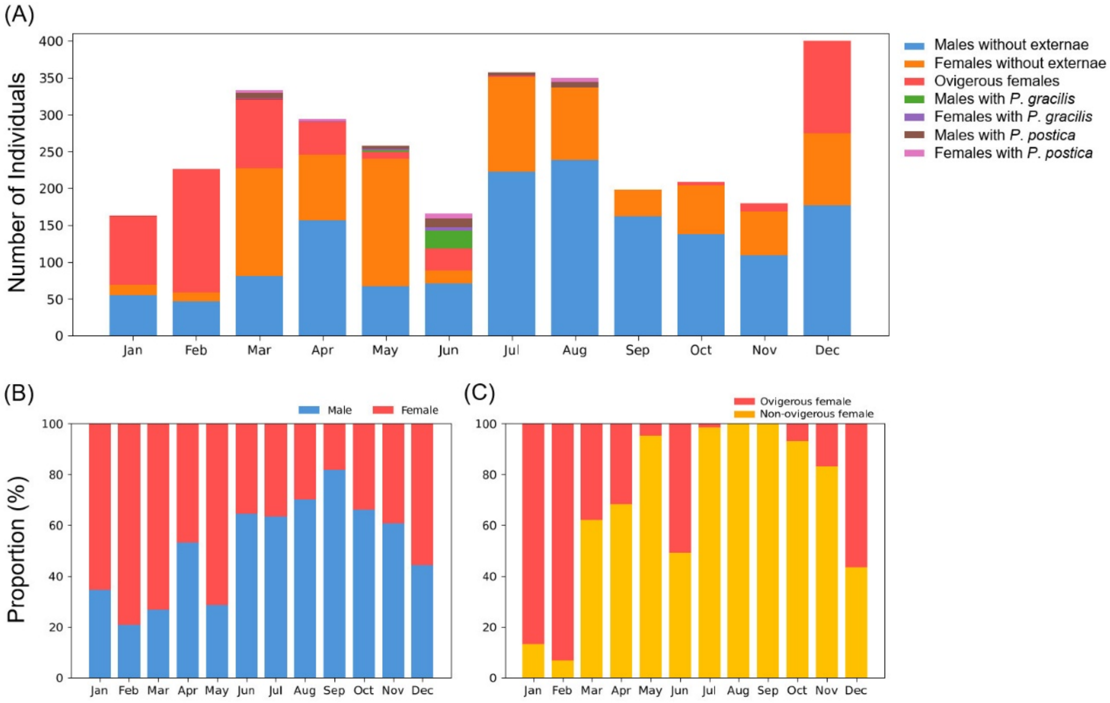

Fig. 1. Monthly sampling composition of *Pagurus filholi* at a fixed coastal site in Chiba, Japan (January–December 2025). Stacked bars show the number of males without externae, females without externae, ovigerous females, and hosts infected by the rhizocephalans *Peltogasterella gracilis* and *Peltogaster postica* (counts separated by host sex) (A). Seasonal variation in host sex ratio and female reproductive status. Monthly sex ratio shown as 100% stacked bars (male = blue; female = red) (B). Monthly female reproductive status shown as 100% stacked bars within females (non-ovigerous = red; ovigerous = orange) (C).

Seasonal prevalence and sex bias of *P. gracilis* and *P. postica*

Both rhizocephalans exhibited sharply seasonal prevalence with a strong early-summer peak (Fig. 2A and 2B). Fisher's exact tests contrasting June with all other months confirmed that June prevalence was significantly elevated for both parasites: *Peltogasterella gracilis* was June 29/166 vs other months 8/2968; OR = 78.32, 95% CI (35.15, 174.52), $p < 0.001$, while *Peltogaster postica* was June 19/166 vs other months 36/2968; OR = 10.53, 95% CI (5.89, 18.80), $p < 0.001$. Additionally, annual infection frequencies differed between host sexes: *P. gracilis* was males 28/1586 vs females 9/1548; OR = 3.07, 95% CI (1.45, 6.53), $p = 0.003$ (Fig. 2C), while *Peltogaster postica* were males 35/1586 vs females 20/1548; OR = 1.72, 95% CI (0.99, 3.00), $p = 0.057$ (Fig. 2D).

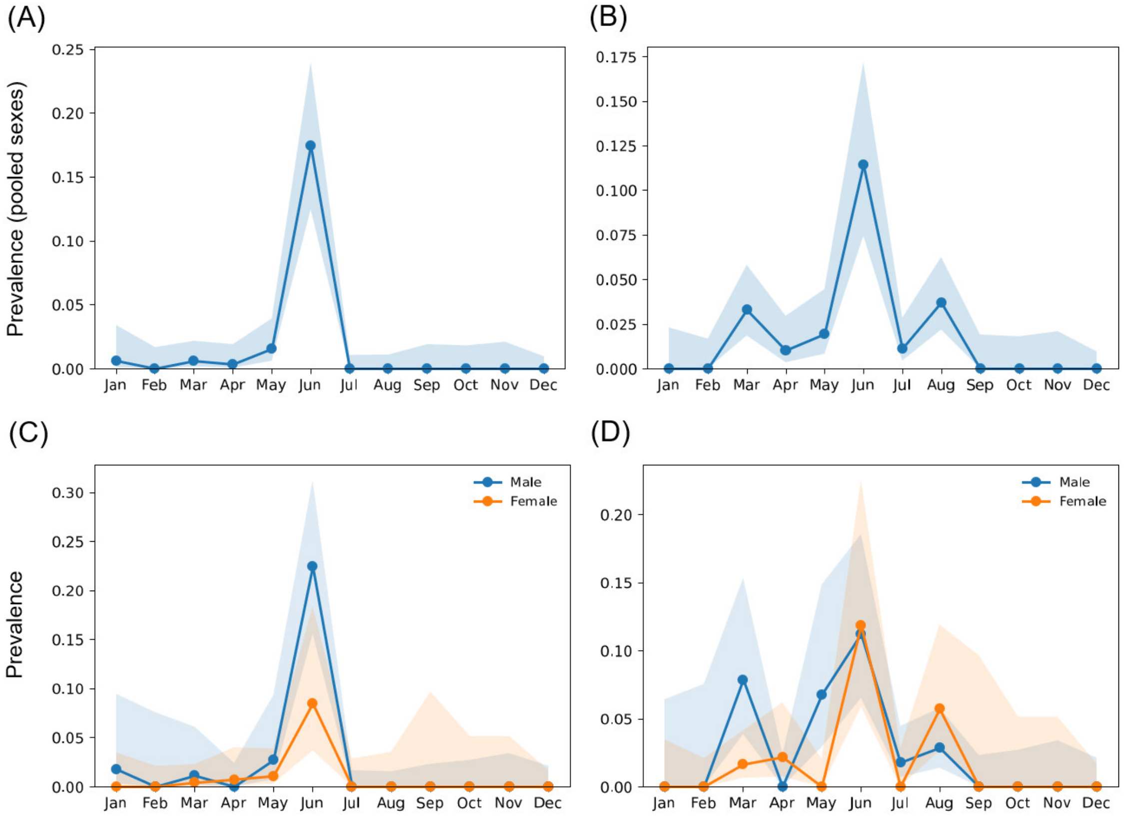

Fig. 2. Seasonal prevalence of two rhizocephalan parasites and sex-specific patterns in *Pagurus filholi*. Monthly prevalence (infected/total) pooled across host sexes is shown for (A) *Peltogasterella gracilis* and (B) *Peltogaster postica*. Sex-specific monthly prevalence is shown for (C) *Peltogasterella gracilis* and (D) *Peltogaster postica* (*male vs. female hosts*). Shaded bands indicate Wilson 95% confidence intervals.

Parasite-triggered occurrence of a second pleopod in males

P2 occurrence in males differed strongly among infection classes (Fig. 3). Across the year, P2 was observed in 98/1523 males without externae (6.43%) but in 29/63 males without externae (46.0%). Infection status and P2 presence were strongly associated (Fisher's exact test, $p < 0.001$), with infected males showing elevated odds of bearing P2 (OR = 12.37, 95% CI (7.27, 21.07)). Crucially, the magnitude of P2 expression differed between the two parasites: males infected by *Peltogasterella gracilis* almost uniformly exhibited P2 (26/28 = 92.9%), whereas males infected by *Peltogaster postica* were rarely with P2 (3/35 = 8.6%) (Fig. 3). Monthly P2 frequencies varied seasonally (Fig. 4A and 4B). P2 frequency among males without externae covaried positively with monthly male parasite prevalence (Spearman $\rho = 0.616$, p = 0.033; Fig. 4C), and a similar positive covariation was observed for P2 frequency calculated across all males (Spearman $\rho = 0.649$, $p = 0.022$; Fig. 4D).

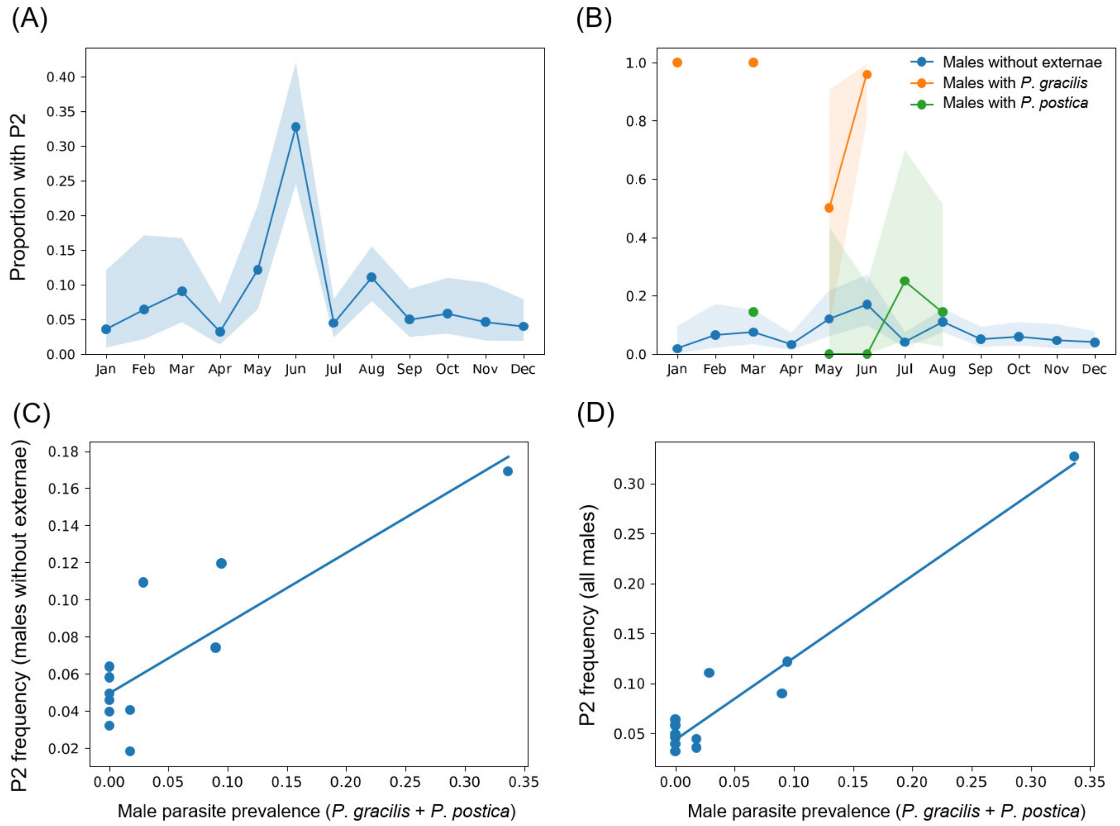

Fig. 4. Seasonal frequency of males bearing a second pleopod (P2). Monthly proportion of all males bearing P2 (infection status: with + without externae) (A). Monthly P2 frequency in males by infection class (without externae, *Peltogasterella gracilis*-infected, *Peltogaster postica*-infected) (B). Shaded bands indicate Wilson 95% confidence intervals. Covariation between male parasite prevalence and P2 frequency. Relationship between monthly male parasite prevalence (combined *Peltogasterella gracilis* + *Peltogaster postica*) and P2 frequency among males without externae (C).

Same relationship using P2 frequency among all males (D). Lines show least-squares fits for visual guidance.

DISCUSSION

Seasonal covariation of host demography and reproduction

At a fixed coastal site, *P. filholi* showed strong seasonal structure in sex ratio and ovigerous frequency (Fig. 1), consistent with prior studies demonstrating temporally structured reproduction and mating behavior. The ovigerous period of *Pagurus filholi* observed in the present study is largely consistent with that reported for the Boso Peninsula by Imazu and Asakura (1994), who documented an extended reproductive period from October to August. The female-biased sex ratio in winter and ovigerous peak in mid-winter align with the size-structured temporal pattern of reproduction described in *P. filholi* by Yoshino et al. (2002), in which larger females breed earlier within the season. The close dependency of male mate choice and precopulatory guarding on female ripeness and reproductive value (Goshima et al. 1998; Minouchi and Goshima 1998) further explains the tight coupling between ovigerous frequency and mating activity observed in our data. Reproductive phenology in *P. filholi* varies geographically. In the Kuroshio-influenced region, ovigerous females occur from October to August on the Boso Peninsula (Imazu and Asakura 1994), and females carry clutches mainly during winter in Tosa Bay (Wada et al. 2005). In contrast, in Hakodate Bay, Hokkaido, northern Japan, which is subject to occasional intrusions of Coastal Oyashio water during the cold season, ovigerous females are observed throughout the year, although the main spawning period extends from March to July (Goshima et al. 1998). However, the environmental factors and mechanisms underlying this geographic variation in reproductive phenology remain unresolved (Wada 2000).

Distinct phenology and sex bias of two rhizocephalan parasites

Both *Peltogasterella gracilis* and *Peltogaster postica* peaked in early summer with a pronounced June maximum (Figures 2A and 2B), consistent with the expectation that rhizocephalan transmission and development can be seasonally structured (Glenner and Høeg 1995; Høeg 1995). Because rhizocephalans are parasitic castrators, seasonal changes in their infection prevalence may strongly affect host population demography (Baudoin 1975; Lafferty and Kuris 2009). Rhizocephalans parasitizing hermit crabs in Japan reproduce mainly from spring to autumn, during which infective larvae are released to infect hermit crab hosts. This seasonal reproduction likely reflects the availability of hermit crabs that serve as settlement substrates for the larvae (Kajimoto et al. 2022). However, the present study was not able to examine the relationship between larval release timing and parasite prevalence. Investigating the time interval between larval settlement and the emergence of the externa from the host would provide a more detailed understanding of the seasonal dynamics of rhizocephalans. The parasite-specific differences in sex bias observed in figure 2C and 2D suggest that exposure and/or susceptibility may differ between male and female hosts depending on parasite taxa. This pattern is consistent with general frameworks of sex-biased parasitism (Zuk and McKean 1996; Poulin 1996) and with evidence that sex bias in arthropods can vary among host–parasite systems (Sheridan et al. 2000). Regional peltogastrid studies indicate substantial geographic variation in host use and prevalence (Yoshida et al. 2012 2014), emphasizing that phenological patterns observed at a single site should be evaluated in a broader regional context.

Parasite-specific feminization signal: *P. gracilis* vs *P. postica*

A major new result is that parasite species differed strikingly in their association with an increased frequency in males of the second pleopod (P2), a female-specific secondary sexual trait used for egg brooding. While infected males overall were much more likely to bear P2 than males without externae, this signal was driven almost entirely by *Peltogasterella gracilis*: males infected by *P. gracilis* nearly always exhibited P2, whereas *Peltogaster postica*-infected males were rarely with P2 (Fig. 3). The reason why some hermit crabs without externae in this study possess P2 remains unknown, although this may be explained by the presence of potential interna already developed within the host. However, this parasite-specific divergence suggests that "feminization" is not a uniform outcome of rhizocephalan infection in *P. filholi*, but instead depends strongly on parasite identity. Such parasite-specificity is consistent with the broader concept that castrators can vary in the extent to which they redirect host developmental and endocrine pathways, producing different magnitudes of secondary sexual trait modification (Høeg 1995; Lafferty and Kuris 2009). Kajimoto et al. (2025 2026) suggest that differences in P2 occurrence between rhizocephalan species reflect the extent to which each parasite requires host grooming and egg-care behavior for the maintenance of its externae; thus, *Peltogasterella gracilis*, which produces multiple externae, may need the help of the host's P2. Recent work on rhizocephalan-induced feminization in hermit crabs provides direct precedent for using pleopod traits as quantitative markers of infection-associated morphological change and for testing these effects statistically (Kajimoto et al. 2025, 2026). The strong contrast between *Peltogasterella gracilis* and *Peltogaster postica* in our dataset, therefore, highlights the need to resolve parasite identity when linking rhizocephalan infection to host phenotype.

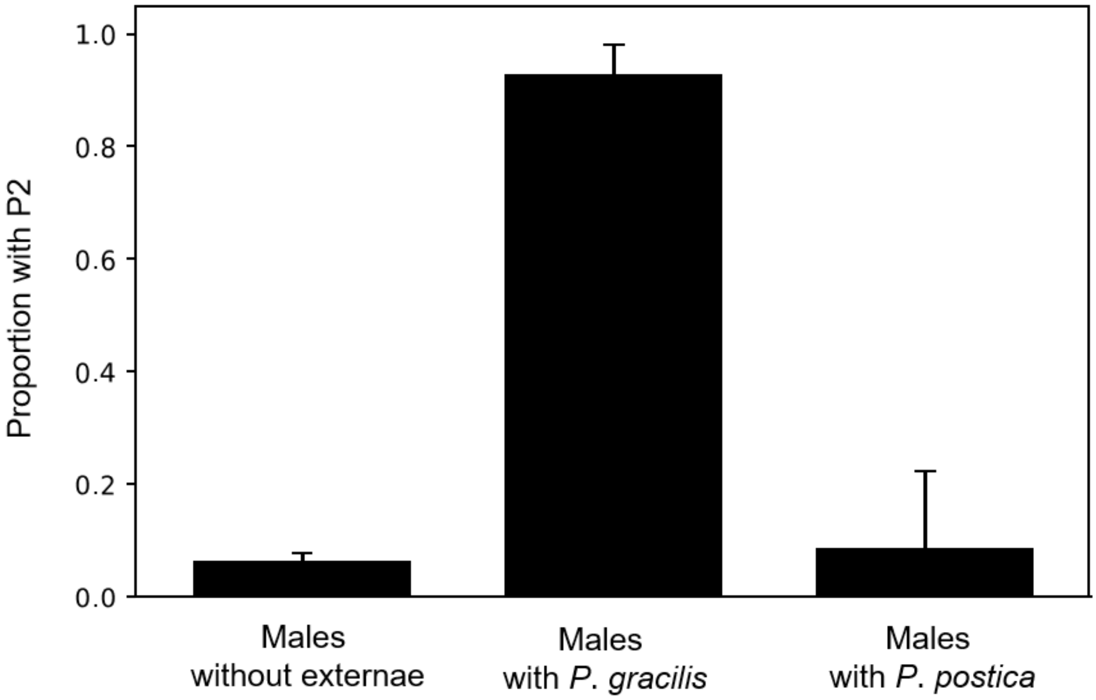

Fig. 3. Annual proportion of males bearing a second pleopod (P2) by infection category. Bars show the proportion of males with P2 among males without externae, males infected with *Peltogasterella gracilis*, males infected with *Peltogaster postica*, and all infected males combined. Error bars denote Wilson 95% confidence intervals.

CONCLUSIONS

Because our dataset is based on a single site and a single year, interannual replication will be required to test the generality of the early-summer prevalence peaks and parasite-specific P2 patterns. Moreover, externa-based prevalence necessarily reflects infections that have progressed to externally visible stages; molecular screening of externa-negative males would help determine whether the seasonal covariation between male parasite prevalence and P2 frequency among males without externae (Fig. 4C and 4D) reflects early infections not yet producing externae versus other seasonal processes. Nonetheless, our parasite-resolved time series provides a robust baseline demonstrating that two co-occurring rhizocephalans (*Peltogasterella gracilis* and *Peltogaster postica*) differ not only in phenology and sex bias, but also in the magnitude of infection-associated modification of male secondary characters.

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Authors’ contribution: AK, TO, and KT designed the research. AK and AT conducted the sampling and measured the morphological parameters. AK and KT analyzed all data and wrote the first draft, and all authors approved the final version of the manuscript.

Conflict of interests: The authors declare that they have no competing interests.

Availability of data and materials: All data collected in this study have been included in this manuscript.

Consent for publication: -.

Ethics approval consent to participate: Not applicable. This study did not involve vertebrate animals or human participants. Invertebrate organisms (anomuran hermit crabs and rhizocephalan barnacles) were handled in accordance with institutional and national regulations.

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Supplementary materials

Table S1. All individual data used in this study. (download)