Parasite species identity reshapes geographic patterns of morphology in the hermit crab *Pagurus filholi* across Japan

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Abstract

Geographic variation in morphological traits of marine invertebrates is commonly attributed to local adaptation or phenotypic plasticity, yet such interpretations can be confounded when parasite assemblages — and their morphological effects on hosts — differ systematically among localities. Here, we tested whether the identity of five parasite species—rhizocephalans *Peltogaster postica* and *Peltogasterella gracilis*, and bopyrids *Parathelges enoshimensis*, *Athelges takanoshimensis*, and *Eremitione* sp.—alters the interpretation of geographic morphological variation in the hermit crab *Pagurus filholi* across six Japanese localities (31–42°N), where rhizocephalan barnacles tend to be more common at northern sites and bopyrid isopods at southern ones. We measured six morphological traits in 643 individuals spanning unparasitized *P. filholi* and five parasite-status categories, and applied principal component analysis, allometric regression, ANCOVA, and within-locality effect size analyses (Hedges' *g*) to partition the contributions of body size, locality, sex, and parasite species. Unparasitized individuals showed significant multivariate geographic differentiation (PC1: 86.3% of variance), with allometric slopes heterogeneous among localities. The rhizocephalan *Peltogasterella gracilis*, sampled across multiple localities, reduced right chela length—the primary sexually dimorphic trait in Paguridae—in parasitized males ($g = -0.47$) but increased it in females (+0.72), consistent with parasitic feminization; the bopyrid *Parathelges enoshimensis* reduced multiple size-corrected traits in females (right chela length $g = -1.41$) without affecting body size, consistent with energetic costs. These contrasting, sex-specific effects demonstrate that parasite species identity is an independent and biologically meaningful driver of morphological variation, and that geographic comparisons of hermit crab morphology require explicit identification of parasite species present.

Keywords: Anomura; allometry; parasitic castration; Bopyridae; Rhizocephala; sexual dimorphism; cheliped; Japan

Introduction

Geographic variation in morphological traits is a fundamental pattern in marine ecology, reflecting the combined influence of genetic differentiation, phenotypic plasticity, and local environmental conditions (Conover and Schultz 1995; Sanford and Kelly 2011). In decapod crustaceans, body proportions — particularly the relative size of chelipeds — vary substantially among populations and are subject to strong natural and sexual selection (Mariappan et al. 2000; Sneddon et al. 1997). Identifying the drivers of such variation across a species' range is essential for understanding population-level adaptation and for interpreting morphological data collected at different localities.

Hermit crabs of the genus *Pagurus* are model organisms for studying cheliped morphology and its ecological correlates. The right cheliped, which is typically enlarged relative to the left, is used in intraspecific contests over shell resources and contributes to reproductive success in males (Blackstone 1989; Matsuo et al. 2015). Sexual dimorphism in cheliped size — males generally having proportionally larger chelipeds than females — is well documented in this genus (Matsuo et al. 2015; Iyoda et al. 2025), but the degree of dimorphism varies among populations and species (Blackstone 1989； Young et al. 2002). Geographic comparisons of cheliped morphology in *Pagurus* have highlighted the importance of controlling for body size allometry and environmental covariates, but have rarely accounted for the presence of parasites, rhizocephalans barnacles (Cirripedia: Rhizocephala), or bopyrid isopods (Isopoda: Bopyridae).

Rhizocephalans and bopyrids are notable parasites of other crustaceans, such as crabs (Corral et al. 2019; Toyota et al. 2023), hermit crabs (Kajimoto et al. 2022, 2024a, b; Shinoda et al. 2026), or shrimps (Calado et al. 2006; Lützen et al. 2016). Rhizocephalans form a reproductive organ (externa) outside the host body and a root-like system (interna) within the host (Høeg 1995; Høeg and Lützen 1995). They are parasitic castrators that penetrate the host's body as a root-like system and often induce feminization of male hosts, resulting in altered morphology and reproductive behavior (Høeg 1995; Høeg and Lützen 1995; Toyota et al. 2023; Kajimoto et al. 2025). This feminization is thought to benefit the parasite by inducing a broader abdomen and brood-tending behavior in the host, thereby securing optimal conditions for the attachment and care of their externa. Bopyrid isopods parasitize the gill chambers, body cavity, or abdomen, imposing metabolic costs without necessarily castrating the host (Calado et al. 2006; McDermott et al. 2010; Corral et al. 2021). Because these two parasite groups produce fundamentally different effects on host physiology, their presence confounds morphological comparisons unless parasite species are explicitly identified.

Despite the potential for parasites to obscure geographic patterns in morphology, most studies of geographic variation in decapod morphology have either excluded parasitized individuals or treated them as a single category (Blackstone 1989; Young et al. 2002). When parasite assemblage composition differs among localities — as it does for Paguridae *P. filholi* (De Man 1887), where rhizocephalans tend to be more common at northern localities and bopyrids at southern ones — pooling parasite species or simply excluding them can introduce bias or reduce power. However, the effects of individual parasite species on host morphology, quantified within and across localities, have rarely been reported.

Pagurus filholi is a common intertidal hermit crab widely distributed along the Pacific and the Sea of Japan coasts of the Japanese archipelago. The species harbors at least five parasite species belonging to two taxonomically and functionally distinct groups—rhizocephalans *Peltogaster postica* and *Peltogasterella gracilis*, and bopyrids *Parathelges enoshimensis*, and *Athelges takanoshimensis*. Here, we address this gap by examining morphological variation in *P.*

filholi across six localities spanning 31–42°N along the Japanese coast, using 643 individuals belonging to six parasite-status categories (unparasitized *P. filholi* plus the five parasite species). Specifically, we tested whether parasite species identity changes the interpretation of geographic morphological variation after accounting for body size allometry and sex and estimated the direction and magnitude of species-specific parasite effects using within-locality effect sizes. We demonstrate that parasite species identity is a critical determinant of morphology and that geographic comparisons of *P. filholi* morphology require explicit parasite species information.

Materials and Methods

Study sites and specimen collection

Specimens of *Pagurus filholi* were collected from rocky intertidal habitats at six localities along the Japanese coast: Asari, Otaru, Hokkaido (43.176° N, 141.068° E), Chikura, Minamiboso, Chiba (34.924° N, 139.945° E), Shika, Ishikawa (37.054° N, 136.723° E), Mikuni, Sakai, Fukui (36.251° N, 136.133° E), Baishinji, Matsuyama, Ehime (33.876° N, 132.704° E), and Sakurajima-Yokoyama, Kagoshima, Kagoshima (31.589° N, 130.591° E) (**Fig. 1**). These localities span approximately 1,200 km of coastline and about 11 degrees of latitude, encompassing both the Pacific coast and the Sea of Japan coast of the Japanese archipelago, and include representatives of both Rhizocephala-dominated (Hokkaido, Chiba) and Bopyridae-dominated (Ishikawa, Ehime, Kagoshima) parasite assemblages.

Two different sampling protocols were employed depending on the *P. filholi* status (unparasitized or parasitized). In this study, unparasitized hosts were defined as individuals lacking any attachment scars of previous parasitism resulting from the detachment of an externa or an adult female isopod. Unparasitized individuals were obtained from a single, standardized survey at each locality, in which all individuals encountered within a defined area were collected.

Sampling was conducted in September and November 2025 in Hokkaido, November 2025 in Chiba, September 2025 in Ishikawa, April 2024 in Fukui and Ehime, and March 2026 in Kagoshima. At each locality, approximately 30 unparasitized males and 30 unparasitized females were randomly selected to ensure a wide range of body sizes for morphological measurement; these samples are considered representative of the local unparasitized population at the time of sampling. Parasitized individuals were collected opportunistically across multiple sampling occasions at each locality. Sampling was conducted in September 2024 and September–November 2025 in Hokkaido, March 2023, June and August 2024, and January, March–August, and November 2025 in Chiba, June, September, and October 2025 in Ishikawa, February and April–May 2024 in Ehime, and April–November 2023, January–September and November–December 2024, January–June and August 2025, and March 2026 in Kagoshima. Because parasitized individuals were not sampled in a standardized manner, the relative proportions of parasite species in our dataset do not represent field prevalence, and prevalence was not estimated.

All specimens were preserved in 70–80% ethanol immediately after collection and stored at room temperature until measurement. A total of 643 individuals were included in the final dataset: 339 unparasitized (168 male, 171 female) and 304 parasitized (**Table 1**).

Parasite identification

Parasite species were identified based on the morphology of the externa (rhizocephalans) or the adult female isopod (bopyrids) observed on or extracted from each host. Rhizocephalan species were distinguished as *Peltogaster* sp. or *Pge. gracilis* (Boschma, 1928) based on externa shape and attachment site following Shiino (1931) and Kajimoto et al. (2025). Data on the identification of *Peltogaster* sp. as *Peltogaster postica* Sars, 1870 were obtained from Kajimoto et al. (2025). Male hosts of *Pge. gracilis* frequently exhibit a second pleopod on the right pleon (morphological feminization; Kajimoto et al. 2025), recorded as a supplementary identification criterion.

Bopyrid isopods were identified to species based on site of infestation and morphological characters of the adult female following Ishii (1914), Shiino (1950) and Williams et al. (2019). *Parathelges enoshimensis* Shiino, 1950 and *Athelges takanoshimensis* Ishii, 1914 infests the pleon. *Eremitione* sp. was found only in the gill chamber of Hokkaido specimens and represents the first record of this genus parasitizing *P. filholi*; these specimens were included in all analyses. Individuals harboring both rhizocephalan and isopod parasites simultaneously were observed: two individuals parasitized by *Eremitione* sp. and *Peltogaster* sp. from Hokkaido, and one individual parasitized by *Pa. enoshimensis* and bearing an attachment scar of *Peltogaster* sp. from Fukui. These individuals were excluded from all analyses.

Morphological measurements

Six morphological traits were measured for each specimen using digital vernier callipers (resolution 0.01 mm): shield length (SL), shield width (SW), left chela length (LCL), left chela width (LCW), right chela length (RCL), and right chela width (RCW). Shield length was used as the overall body size index. Chelipeds that were regenerating were excluded from measurement, resulting in missing values for RCL and RCW in 16 individuals and for LCL and LCW in four to five individuals. Sex was determined under a stereoscopic dissecting microscope based on the presence (females) or absence (males) of female gonopores on the coxae of the third pereopods. Additionally, the presence (females) or absence (males) of a second pleopod on the left pleon, a female-specific egg-bearing organ, was examined; feminized males were assigned following the criteria of Kajimoto et al. (2025).

Statistical analyses

All morphological measurements were log*e*-transformed prior to analysis. Shield length ranged from 1.6 to 7.5 mm across all specimens (log SL: 0.47 to 2.02). Because the goal of this study was not to estimate parasite prevalence but to quantify the effect of parasite species on host morphology relative to sympatric unparasitized individuals, parasitized individuals were compared within localities against unparasitized conspecifics of the same sex; this within-locality design is implemented through size-corrected residuals and inverse-variance-weighted effect sizes (see below), which account for the opportunistic nature of the parasitized sample.

Principal component analysis.

Multivariate morphological variation among localities was examined using PCA on log-transformed values of all six traits (SL, SW, LCL, LCW, RCL, RCW), standardized to zero mean and unit variance, for unparasitized individuals only. PCA was performed separately for males and females. Ninety-five per cent confidence ellipses were computed per locality based on bivariate normal distributions of PC1 and PC2 scores using the prcomp function in R.

Homogeneity of allometric slopes.

Before fitting ANCOVA models, we tested whether the allometric slope between log(SL) and each response trait was homogeneous among localities using likelihood ratio tests comparing models with and without locality × log(SL) interaction terms.

ANCOVA.

To partition variance in size-corrected morphological traits among locality, sex, and parasite species, we fitted linear models of the form:

$$\log(\text{trait}) \sim \log(\text{SL}) + \text{locality} + \text{sex} + \text{parasite} + \text{locality} \times \text{sex} + \varepsilon$$

We did not include locality × parasite as an interaction term because 19 of 30 locality–parasite combinations contained zero observations, producing aliased (non-estimable) coefficients. Because allometric slopes differed significantly among localities (see above), the global ANCOVA model with a single log(SL) slope does not fully account for these heterogeneities; accordingly, ANCOVA results are interpreted as a summary of factor effects, and inferences regarding biologically meaningful differences are primarily based on locality-specific size-corrected residuals and within-locality effect sizes. Type-II *F*-tests (Anova function, car package; Fox and Weisberg 2019) were used to assess the significance of each effect. Analyses were conducted in R version 4.2.3 (R Core Team 2024).

Within-locality effect sizes.

We calculated Hedges' *g* (Hedges and Olkin 1985) for each combination of parasite species, morphological trait, sex, and locality, using unparasitized individuals of the same locality and sex as the reference group. Individual locality-level estimates were combined using inverse-variance weighting (weight = $1/\text{SE}^2$). Only localities with at least five parasitized individuals per sex were included. Estimates based on a single locality are flagged with †. Two-sided *z*-tests were used to assess significance.

Results

Sample composition

A total of 643 individuals of *P. filholi* were examined, comprising 308 males and 335 females from six localities (Table 1). Unparasitized individuals (339 total; 168 males, 171 females) were obtained from a single survey at each locality, providing 28–63 individuals per sex per locality. Parasitized individuals included 108 *Pg. postica*-parasitized (58 male, 50 female), 83 *Pge. gracilis* (40 male, 43 female), 77 *Pa. enoshimensis* (25 male, 52 female), 21 *At. takanoshimensis* (7 male, 14 female), and 15 *Eremitione* sp. (10 male, 5 female) individuals. Parasite species distributions were strongly locality-specific: rhizocephalan-parasitized individuals were concentrated at Hokkaido and Chiba, whereas *Pa. enoshimensis* predominated at Ishikawa and Kagoshima, and *At. takanoshimensis* occurred mainly at Ehime (**Table 1**). Because parasitized individuals were collected opportunistically, the prevalence of parasitism was not estimated. Descriptive statistics for all morphological measurements by locality, sex, and parasite species are summarized in **Table 2**.

Multivariate morphological variation among localities (PCA)

PCA of unparasitized individuals revealed clear multivariate separation among localities along the first two principal components for both sexes (**Fig. S1**). PC1 accounted for 86.3% of the total variance and was positively loaded by all six traits, representing an overall body size axis. PC2 (5.9% of variance) contrasted shield length (loading positively) against cheliped dimensions (loading negatively in females), reflecting variation in relative cheliped proportions independent of overall size. Ninety-five per cent confidence ellipses were substantially non-overlapping among localities along PC1, confirming significant geographic differentiation in multivariate morphology. Chiba individuals tended to score higher on PC1 (larger overall dimensions), particularly in females, whereas individuals from Ishikawa and Fukui tended to score lower. These patterns are consistent with north-to-south geographic trends in body size and cheliped proportions and motivate the locality-specific analyses that follow.

Allometric relationships and heterogeneity of slopes

Log-transformed shield length (log SL) was strongly correlated with all five response traits across all locality-by-sex combinations (**Fig. 2C, 2D**). Likelihood ratio tests for homogeneity of allometric slopes revealed significant heterogeneity among localities for all five traits ($F = 21.3$–65.8, all $p < 0.001$; **Figs. 2C, 2D**), indicating that the allometric relationship between body size and trait dimensions is not constant across the geographical range of *P. filholi*. Slopes were generally steeper at Chiba than at other localities for shield width and left chela dimensions, whereas those at Hokkaido and Fukui tended to be shallower for right chela length. These differences preclude a single common-slope ANCOVA model and support the use of locality-specific allometric corrections for comparisons of size-corrected morphology.

ANCOVA: effects of locality, sex, and parasite species

ANCOVA with log(SL) as a covariate revealed significant main effects of locality, sex, and parasite species on all five size-corrected morphological traits (all $p < 0.001$; Fig. 3). The covariate log(SL) accounted for the largest proportion of variance in all models ($F = 567.7$–1118.9, all $p < 0.001$; $R^2 = 0.70$–0.82). Locality effects were significant for all traits ($F = 27.8$–47.0), as were sex effects ($F = 10.6$–259.3). The effect of sex was weakest for shield width ($F = 10.6$, $p = 0.001$) and strongest for right chela length ($F = 259.3$, $p < 0.001$), consistent with the right cheliped being the primary sexually dimorphic structure in this species. Parasite species effects were significant for all five traits ($F = 6.9$–13.9, all $p < 0.001$) after controlling for body size, locality, and sex. The locality × sex interaction term was significant for all traits (all $p < 0.001$).

Geographic variation in size-corrected morphology

Size-corrected residuals of morphological traits varied significantly among localities for both sexes (**Fig. 4**). Among unparasitized males, right chela length (RCL) residuals were most positive at Fukui, Ehime, and Kagoshima (means +0.27 to +0.30), and near zero at Hokkaido and Chiba (means −0.03 and +0.06, respectively). This pattern — such as relatively larger right chelae in southern localities — was consistent across multiple traits. Females showed a broadly similar pattern of geographic variation, though the locality-specific differences were less pronounced than in males, and residuals were generally negative compared with males, reflecting the sex effect identified in the ANCOVA. Sexual dimorphism in RCL (males larger than females when controlling for body size) was consistent across all six localities.

Parasite species-specific effects on morphology

Within-locality weighted effect sizes (Hedges' *g*) revealed markedly different patterns of morphological change for each parasite species, and these patterns differed between males and females (**Fig. 5**); see also **Fig. S2** for size-corrected residual distributions by parasite species. *Pge. gracilis* produced contrasting effects on right chela length in the two sexes: parasitized males had significantly smaller RCL than unparasitized males at the same localities ($g = -0.47$, 95% CI $[-0.90, -0.04]$; $p = 0.031$; two localities), while parasitized females had larger RCL than unparasitized females ($g = +0.72$ [0.31, 1.13]; $p < 0.001$). This bidirectional, sex-specific pattern — reduction in males, enlargement in females — is consistent with parasite-induced modification of sexually dimorphic traits of hermit crab hosts, particularly reflecting morphological feminization in male hosts. *Peltogaster postica* showed a similar directional pattern for log(SL) (males: $g = +0.68$ [0.27, 1.10]; females: $g = +1.00$ [0.52, 1.49]), but the effect on size-corrected RCL in males was not statistically significant after within-locality correction ($g = -0.25$ [−0.66, 0.15]; $p = 0.21$).

In contrast, the bopyrid *Pa. enoshimensis* showed no significant effect on body size (log SL) but significantly reduced multiple size-corrected traits in females: shield width ($g = -0.82$ [−1.30, −0.34]), left chela length ($g = -0.95$ [−1.43, −0.47]), and right chela length ($g = -1.41$ [−1.93, −0.89]; all $p \leq 0.001$; †single-locality estimates). In males, *Pa. enoshimensis* reduced left chela length ($g = -0.52$ [−1.03, −0.02]) and left chela width ($g = -0.57$ [−1.10, −0.04]).

Effect size estimates for *At. takanoshimensis* and *Eremitione* sp. were based on single-locality samples of small size ($n = 5$–12) and should be interpreted with caution (†). Notable among these was a large positive effect of *At. takanoshimensis* on male left chela width ($g = +2.01$ [1.02, 3.01]; $p < 0.001$; Chiba, $n = 6$) and a large positive effect of *Eremitione* sp. on female right chela width ($g = +4.03$ [2.68, 5.39]; $p < 0.001$; Hokkaido, $n = 5$), both requiring confirmation with larger, multi-locality datasets.

Discussion

This study provides the first multi-locality, parasite-species-resolved analysis of morphological variation in *Pagurus filholi*. Our principal findings are: (1) PCA of unparasitized individuals reveals significant multivariate morphological differentiation among localities, with Chiba consistently showing larger overall dimensions; (2) allometric slopes between shield length and cheliped dimensions are heterogeneous among localities, necessitating locality-specific allometric corrections; (3) locality, sex, and parasite species identity are each significant independent predictors of size-corrected morphological traits; and (4) the direction and magnitude of parasite effects on morphology are strongly species-specific — rhizocephalans reduce male RCL and enlarge female RCL (consistent with feminization in male hosts), whereas the bopyrid *Pa. enoshimensis* reduces multiple traits in females without affecting body size (consistent with metabolic costs). Taken together, these results demonstrate that the identity of parasite species present in a population critically shapes observed morphological variation, and that geographic comparisons of hermit crab morphology that ignore parasite composition risk substantial confounding.

Geographic variation in morphology

The PCA of unparasitized individuals demonstrated clear multivariate separation among localities, with PC1 — an overall size axis — accounting for 86.3% of total variance and showing Chiba individuals to be consistently larger than those at other localities. This is consistent with the ANCOVA results showing significant locality effects on all five size-corrected traits. The finding of heterogeneous allometric slopes — steeper at Chiba than at higher-latitude localities — adds to growing evidence that allometric relationships in crustaceans are not fixed constants but vary among populations (Young et al. 2002; Blackstone 1989). The relatively large right chelae (after size-correction) at Fukui, Ehime, and Kagoshima in males may reflect stronger sexual selection in these populations, though this interpretation requires verification with behavioral data. The pattern parallels latitude-related variation reported for *Pagurus longicarpus* along the North American east coast (Young et al. 2002) and for *P.*

hirsutiusculus on the Pacific coast (Blackstone 1989).

Sexual dimorphism and its geographic variation

Sexual dimorphism in right chela length was the most pronounced sex effect detected, with males having significantly larger size-corrected RCL than females across all localities. This is consistent with the well-established role of the right cheliped in male–male contests and mate guarding in *Pagurus* spp. (Sneddon et al. 1997; Matsuo et al. 2015). The significant locality × sex interaction term in the ANCOVA indicates that the degree of sexual dimorphism varies among localities; however, the direction of dimorphism (males > females for RCL) was consistent across the range studied. Season-related changes in cheliped dimensions, as reported for *P. filholi* at Sagami Bay (Iyoda et al. 2025), could also contribute to apparent geographic variation if sampling was not fully synchronized across localities.

Parasite species-specific effects: rhizocephalans

The contrasting effects of *Pge. gracilis* on the reduction of right chela length in males are consistent with the known biology of rhizocephalan castration parasites: rhizocephalans suppress gonad development and induce feminized phenotypes in male hosts; by converting male hosts into phenotypic females with a broadened pleon and egg-tending behavior, rhizocephalans gain the morphological and behavioral prerequisites necessary for successful externa attachment and embryo survival (Høeg 1995; Kajimoto et al. 2025). Our effect size analyses in male *Pge. gracilis* quantify RCL feminization as moderate in magnitude ($g \approx -0.5$ in males; +0.7 in females) and statistically robust across two localities. The non-significant effect of *Pg. postica* on male RCL after within-locality correction, in contrast to the findings of Kajimoto et al.

(2025). In contrast, strong positive body-size effects suggest preferential parasitism of larger individuals (O'Brien and van Wyk 1985) rather than active size modification. Sloan et al. (2010) proposed that larger hosts, having undergone more molts, may have had greater opportunities for exposure to rhizocephalan parasitism, because they attach to the softened body of decapod hosts after molting. This has broad methodological implications: studies comparing parasitized against unparasitized individuals pooled across localities are likely to overestimate rhizocephalan morphological effects.

Although it has been reported that the right cheliped length does not differ between parasitized and unparasitized female hermit crabs (Kajimoto et al. 2025), our study revealed a completely contrasting pattern of RCL enlargement in both *Pge. gracilis* and *Pg. postica*. The discrepancy between the present and previous results for *Pge. gracilis* likely reflects differences in analytical approaches, as the locality-corrected effect size approach used in this study enhanced sensitivity to detect subtle morphological changes that may have been overlooked in previous analyses. Rhizocephalans target host reproductive energy through advanced hormonal regulation of the host's physiological systems, thereby achieving castration by indirectly manipulating the host's optimal resource allocation strategy (Lafferty and Kuris 2009). Generally, females invest more energy in reproduction, such as egg production, than males (Hayward and Gillooly 2011). In parasitized female hosts in this study, this high reproductive energy may be reallocated, and the surplus energy could contribute to increasing their cheliped length. However, the molecular mechanisms by which rhizocephalans achieve parasitic castration in hermit crab hosts remain largely unknown, warranting further detailed investigation.

Parasite species-specific effects: bopyrid isopods

The bopyrid *Pa. enoshimensis* showed a pattern fundamentally different from the rhizocephalans: multiple traits were reduced in parasitized females, but body size (SL) was unaffected. This combination — trait reduction without size reduction — is consistent with the parasites diverting energy from reproductive investment in structures such as chelipeds. Bopyrid isopods do not completely castrate their hosts but impose energetic costs by competing for haemolymph nutrients (Beck 1980). The observed parasitic effects may reflect simple nutritional depletion rather than a reallocation of host energy as seen in rhizocephalan parasitism (Lafferty and Kuris 2009). The stronger reduction of RCL in female hosts than males may reflect that the bopyrids exploit all available reproductive resources of female hosts, though the female estimates are based on a single locality (Kagoshima; †) and require confirmation. It has been suggested that host size, female bopyrid size, and bopyrid fecundity are positively correlated (Jay 1989; Romero-Rodríguez and Román-Contreras 2013). However, as the number and size of bopyrid eggs by host sex were not measured in this study, detailed reproductive data are needed. The large but uncertain effect sizes for *At. takanoshimensis* and *Eremitione* sp. should not be taken as reliable species-wide estimates given single-locality samples of fewer than 13 individuals. Although the underlying mechanism remains unclear, this study demonstrates the sex-specific strength of parasitic effects in bopyrid parasites.

Implications for geographic morphological studies

Because parasite species composition differs substantially among localities, any geographic comparison that lumps parasitized individuals into a single "parasitized" category risks systematic bias. In *P. filholi*, the direction of parasite-induced morphological change is opposite between rhizocephalans (RCL reduced in males) and *Pa. enoshimensis* (RCL reduced in females), so that treating all parasitized individuals as equivalent would produce misleading results. Identifying parasite species, or at minimum classifying them by functional group (castrator vs. non-castrator), should be standard practice in geographic morphological studies of species with diverse parasite assemblages. Limitations of the present study include the opportunistic sampling of parasitized individuals (precluding prevalence estimation), unsynchronized collection across localities (potential seasonal confounding), and uncontrolled shell species use (Blackstone 1985). Future studies should address these through standardized simultaneous sampling.

In conclusion, we have shown that *Pagurus filholi* displays significant geographic variation in multivariate and univariate morphological traits across the Japanese archipelago, and that parasite species identity is an independent and biologically meaningful predictor of this variation. The species-specific effects of rhizocephalan feminization and bopyrid metabolic costs produce distinguishable morphological signatures quantifiable by within-locality effect size approaches, underscoring the importance of resolving parasite species identity in geographic morphological comparisons. More broadly, because parasite assemblage composition is itself geographically structured, spatially variable parasite communities can act as a previously underappreciated spatial driver of host morphology in marine decapods — a perspective that should be incorporated into studies of geographic morphological variation across taxa with diverse parasite faunas.

Declarations

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Conflict of Interest

The authors declare that they have no competing interests.

Compliance with Ethical Standards

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).

Data Availability

The datasets generated and analyzed during the current study are not publicly deposited but are available from the corresponding author upon reasonable request.

Author Contributions

Kenji Toyota and AK designed the research. HS, NK, DU, MS and TO conducted the sampling. AK and Kenji Toyota measured the morphological parameters. Kenji Toyota, Keito

Tsunoda, and AK analyzed all data and wrote the first draft, and all authors approved the final version of the manuscript.

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Figure Captions

Fig. 1

Sampling sites of rhizocephalans or bopyrids parasitizing host hermit crab *Pagrus filholi*

Fig. 2

Allometric relationships between log(SL) and each morphological trait — male (C) and female (D). OLS regression lines per locality (colors). Slopes differed significantly among localities for all five traits (likelihood ratio test, all $F \geq 21.3$, all $p < 0.001$).

Fig. 3

ANCOVA results (Type-II F-tests): effects of log(SL), locality, sex, and parasite species on morphological traits of *Pagurus filholi*. Model: log(trait) ~ log(SL) + locality + sex + parasite + locality × sex. Cell color indicates $-\log_{10}(p)$; darker shading denotes stronger significance. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. SW: shield width; LCL: left chela length; LCW: left chela width; RCL: right chela length; RCW: right chela width.

Fig. 4

Size-corrected morphological residuals by locality and sex. Residuals from log(trait) ~ log(SL). Blue boxes: male; pink boxes: female. Dashed line: zero. Circles: outliers. Hok.: Hokkaido; Chi.: Chiba; Ish.: Ishikawa; Fuk.: Fukui; Ehi.: Ehime; Kag.: Kagoshima.

Fig. 5

Effect sizes (Hedges' g) of parasite species on morphological traits of *Pagurus filholi*.

Within-locality inverse-variance-weighted mean Hedges' g (min. $n \geq 5$ per locality). Positive g (red) = larger than unparasitized; negative g (blue) = smaller. †: single-locality estimate; interpret with caution. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ns: not significant. SW–RCW: residuals from log(trait) ~ log(SL).

Supplementary Figure Captions

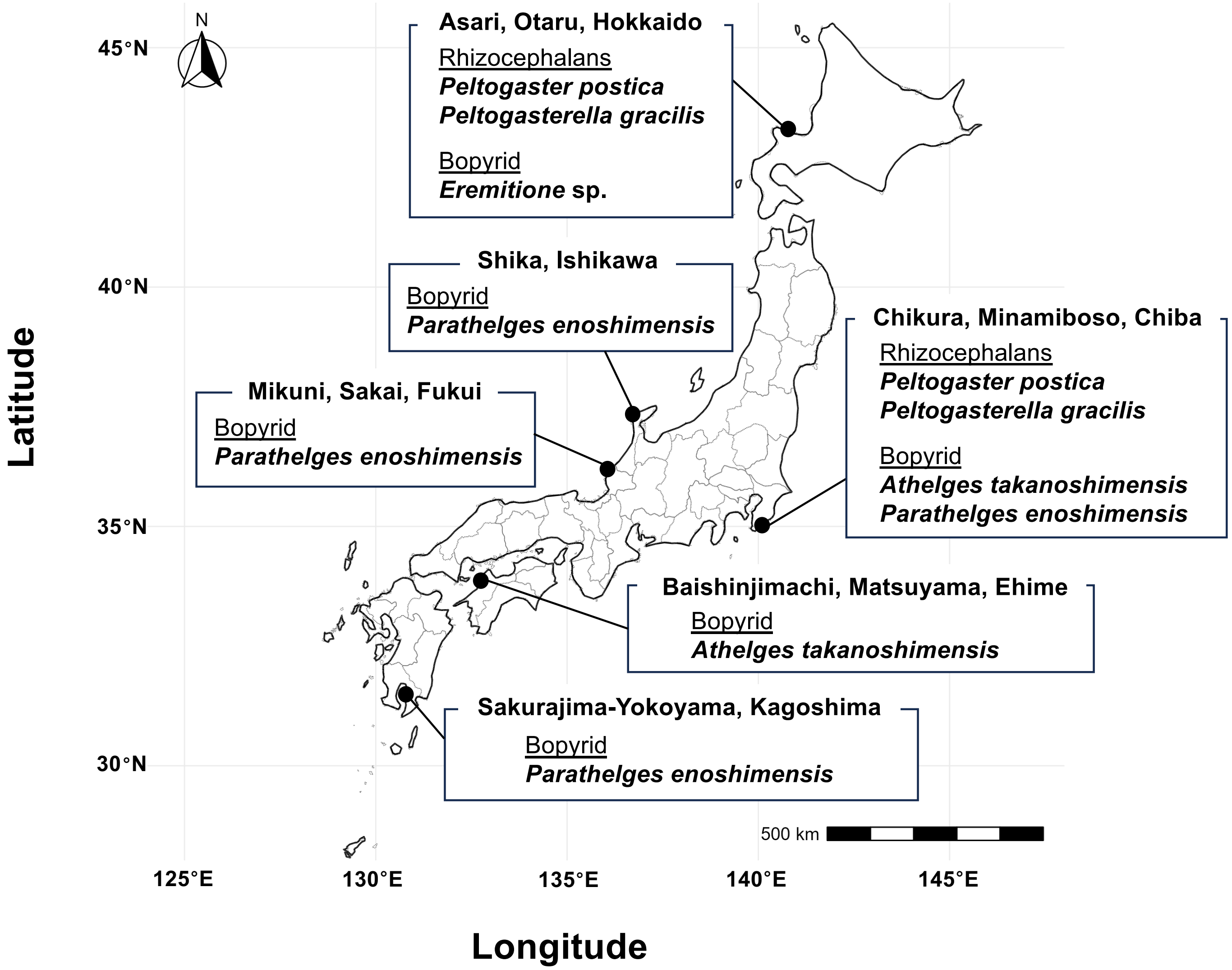
Fig. S1

Principal component analysis (PCA) of six morphological traits in unparasitized *Pagurus filholi* at six Japanese localities. Left panel: male (A); right panel: female (B). Each point represents one individual; colors indicate locality. Ellipses enclose 95% confidence regions. Arrows indicate PC loadings. PC1 (86.3% of variance) represents an overall body size axis; PC2 (5.9%) contrasts body size against cheliped proportions. SL: shield length; SW: shield width; LCL: left chela length; LCW: left chela width; RCL: right chela length; RCW: right chela width.

Fig. S2

Size-corrected morphological residuals by parasite species and sex. Residuals from log(trait) ~ log(SL). Upper panels: male; lower panels: female. Box colors: blue tones = Rhizocephala (dark blue: Pg.pos.: *Peltogaster postica*; light blue: Pge.gra.: *Peltogasterella gracilis*), red tones = Bopyridae (red: Pa.eno.: *Parathelges enoshimensis*; orange: At.tak.: *Athelges takanoshimensis*), and grey = Unpara.: Unparasitized.

Fig. 1



N
45°N
40°N
35°N
30°N
Latitude
125°E
130°E
135°E
140°E
145°E
Longitude
500 km
Asari, Otaru, Hokkaido
Rhizocephalans
Peltogaster postica
Peltogasterella gracilis
Bopyrid
Eremitione sp.
Shika, Ishikawa
Bopyrid
Parathelges enoshimensis
Mikuni, Sakai, Fukui
Bopyrid
Parathelges enoshimensis
Chikura, Minamiboso, Chiba
Rhizocephalans
Peltogaster postica
Peltogasterella gracilis
Bopyrid
Athelges takanoshimensis
Parathelges enoshimensis
Baishinjimachi, Matsuyama, Ehime
Bopyrid
Athelges takanoshimensis
Sakurajima-Yokoyama, Kagoshima
Bopyrid
Parathelges enoshimensis

Fig. 2

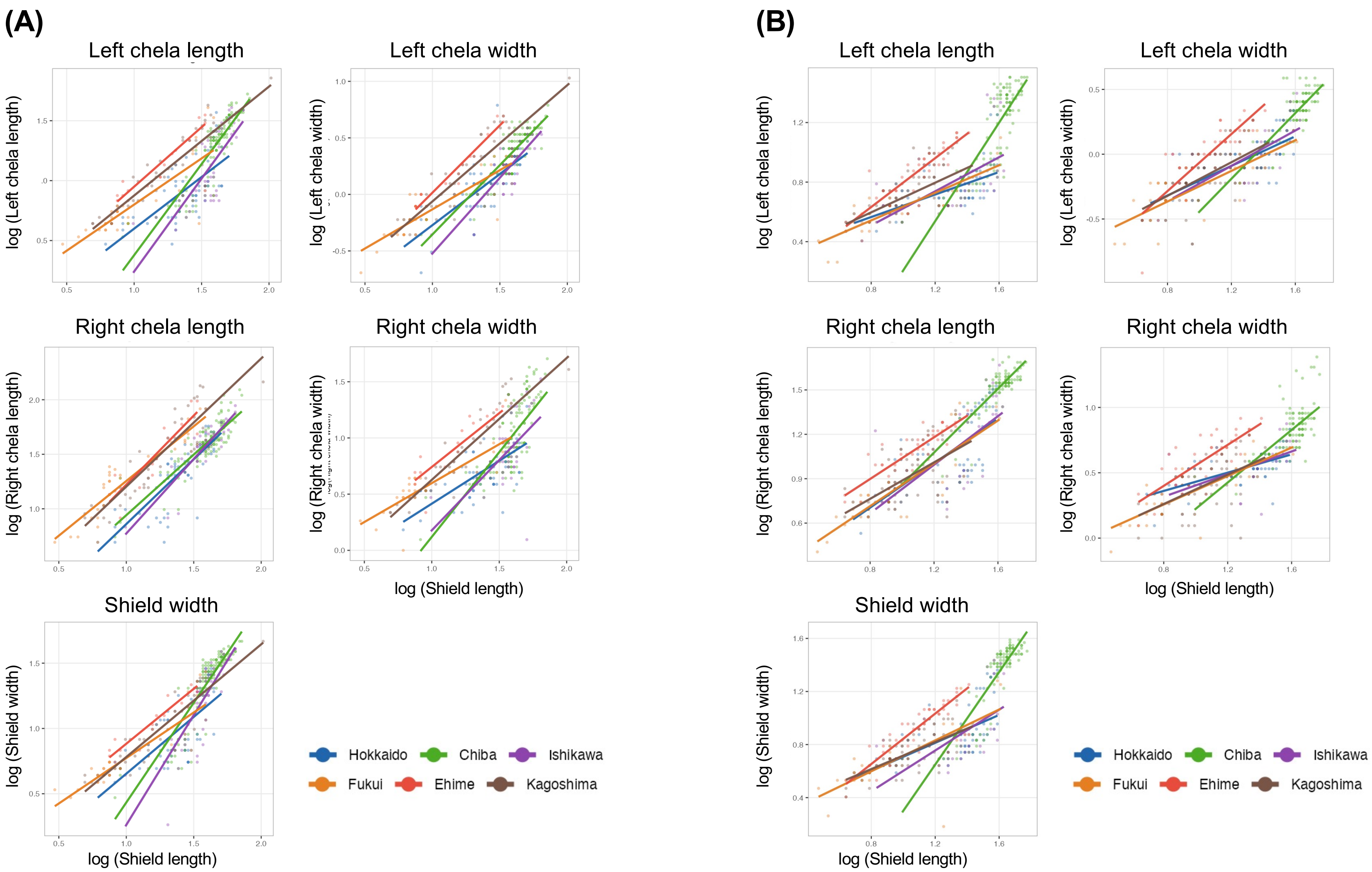
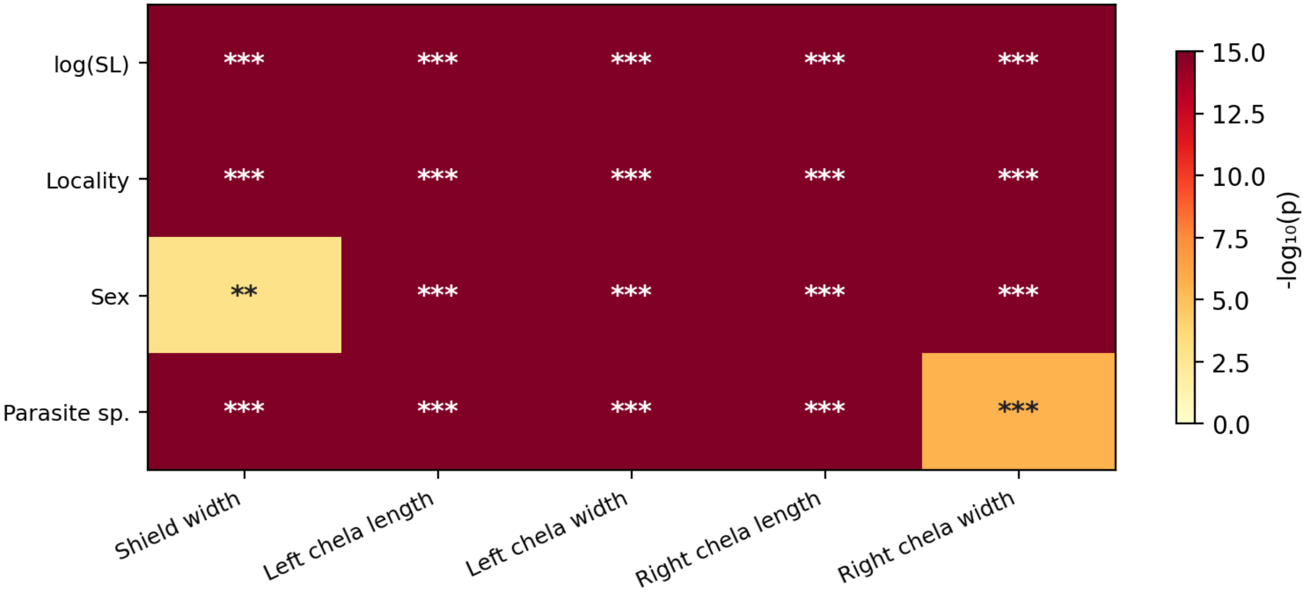

(A)
Left chela length
log (Left chela length)
Left chela width
log (Left chela width)
Right chela length
log (Right chela length)
Right chela width
log (Right chela width)
Shield width
log (Shield width)
log (Shield length)
0.5
1.0
1.5
2.0
Hokkaido
Chiba
Ishikawa
Fukui
Ehime
Kagoshima
(B)
Left chela length
log (Left chela length)
Left chela width
log (Left chela width)
Right chela length
log (Right chela length)
Right chela width
log (Right chela width)
Shield width
log (Shield width)
log (Shield length)
0.8
1.2
1.6
Hokkaido
Chiba
Ishikawa
Fukui
Ehime
Kagoshima

Fig. 3


log(SL)
Locality
Sex
Parasite sp.
***
**
Shield width
Left chela length
Left chela width
Right chela length
Right chela width
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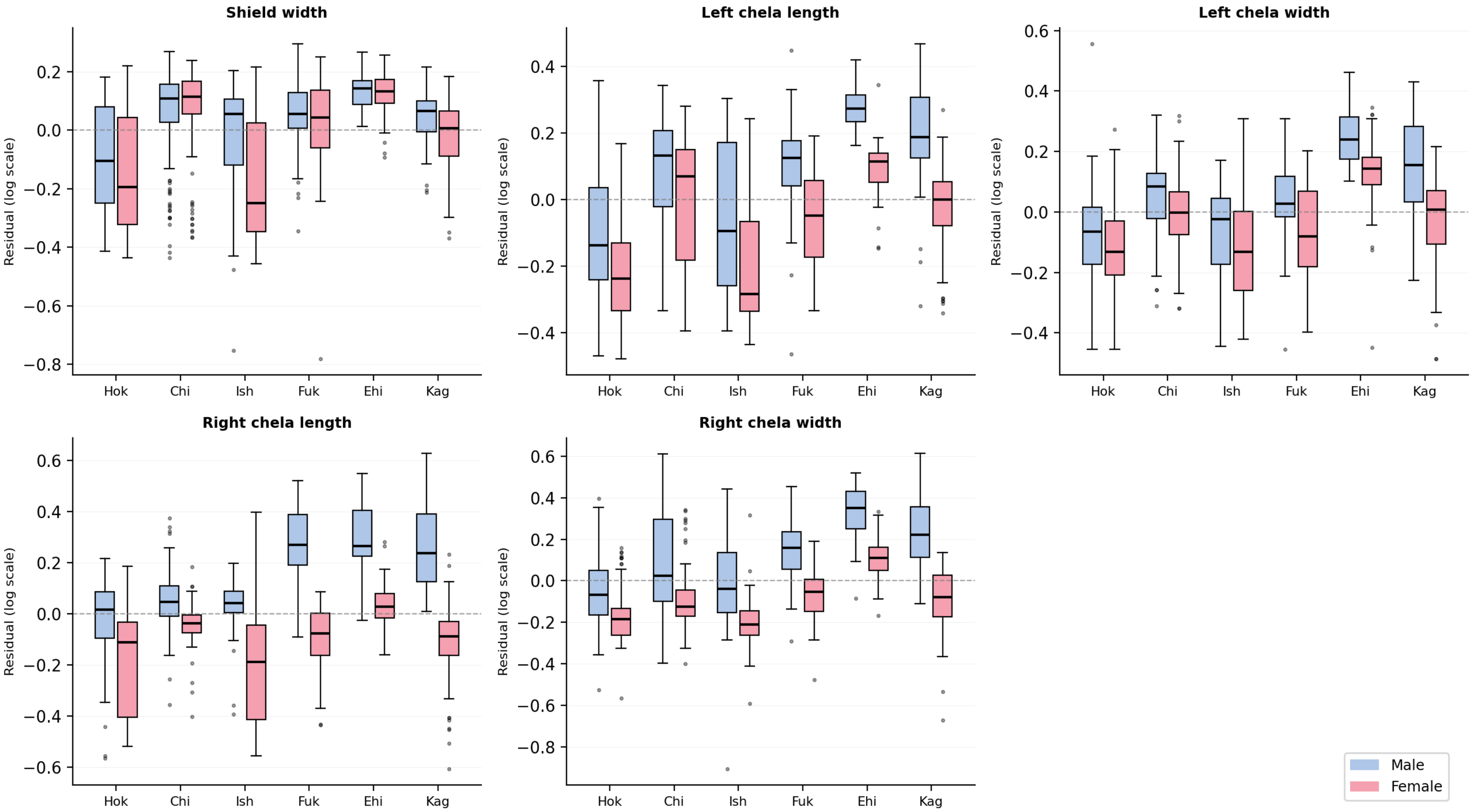
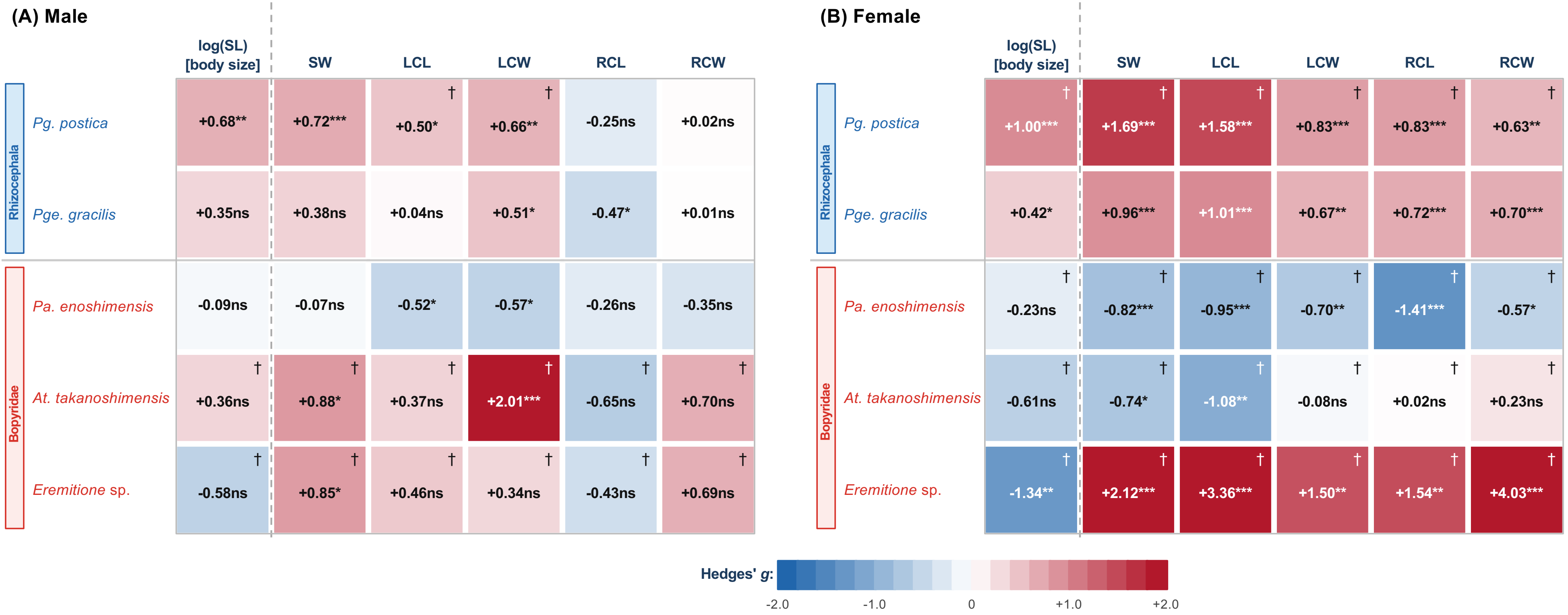
12.5
10.0
7.5
5.0
2.5
0.0
-log₁₀(p)

Fig. 4



Shield width
Left chela length
Left chela width
Right chela length
Right chela width
Residual (log scale)
Hok
Chi
Ish
Fuk
Ehi
Kag
0.6
0.4
0.2
0.0
−0.2
−0.4
−0.6
−0.8
Male
Female

Fig. 5



(A) Male

		log(SL) [body size]	SW	LCL	LCW	RCL	RCW
Rhizocephala	*Pg. postica*	+0.68**	+0.72***	† +0.50*	† +0.66**	-0.25ns	+0.02ns
	Pge. gracilis	+0.35ns	+0.38ns	+0.04ns	+0.51*	-0.47*	+0.01ns
Bopyridae	*Pa. enoshimensis*	-0.09ns	-0.07ns	-0.52*	-0.57*	-0.26ns	-0.35ns
	At. takanoshimensis	† +0.36ns	† +0.88*	† +0.37ns	† +2.01***	† -0.65ns	† +0.70ns
	Eremitione sp.	† -0.58ns	† +0.85*	† +0.46ns	† +0.34ns	† -0.43ns	† +0.69ns

(B) Female

		log(SL) [body size]	SW	LCL	LCW	RCL	RCW
Rhizocephala	*Pg. postica*	† +1.00***	† +1.69***	† +1.58***	† +0.83***	† +0.83***	† +0.63**
	Pge. gracilis	+0.42*	+0.96***	+1.01***	+0.67**	+0.72***	+0.70***
Bopyridae	*Pa. enoshimensis*	† -0.23ns	† -0.82***	† -0.95***	† -0.70**	† -1.41***	† -0.57*
	At. takanoshimensis	† -0.61ns	† -0.74*	† -1.08**	† -0.08ns	† +0.02ns	† +0.23ns
	Eremitione sp.	† -1.34**	† +2.12***	† +3.36***	† +1.50**	† +1.54**	† +4.03***

Fig. S1

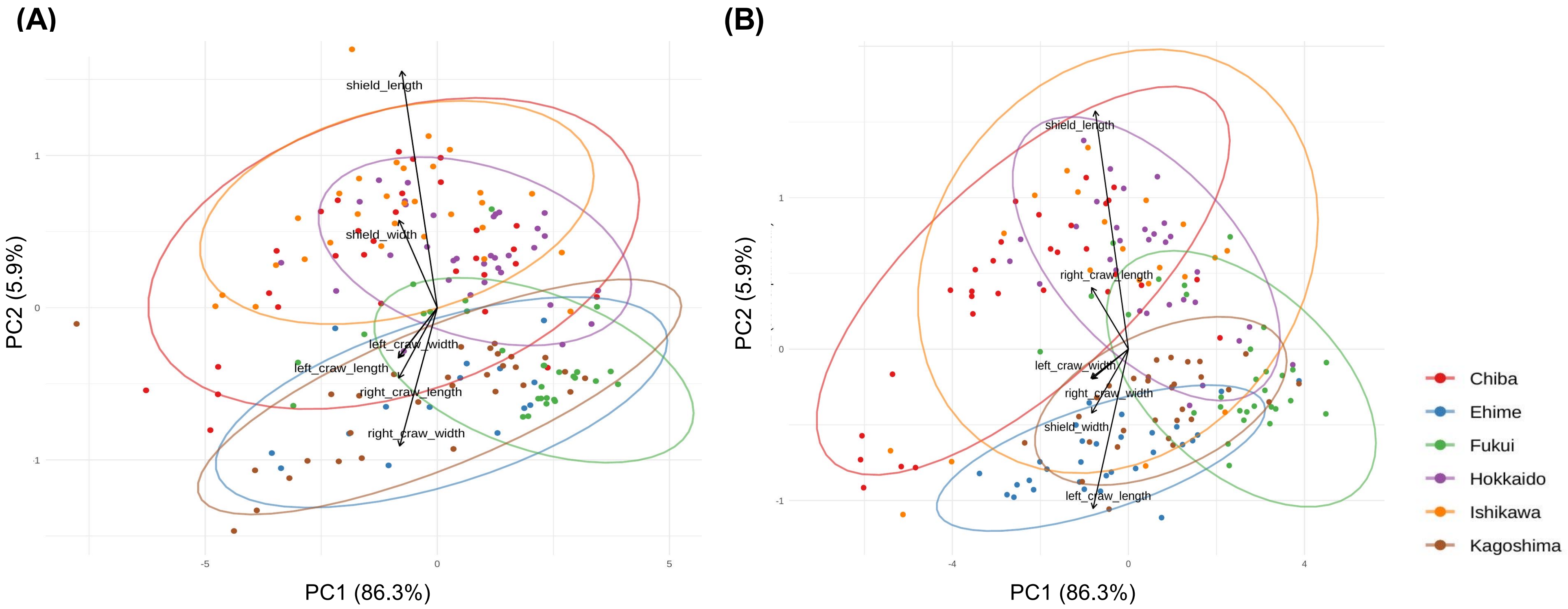

(A)
shield_length
shield_width
left_craw_width
left_craw_length
right_craw_length
right_craw_width
PC2 (5.9%)
PC1 (86.3%)
1
0
-1
-5
0
5
(B)
shield_length
right_craw_length
left_craw_width
right_craw_width
shield_width
left_craw_length
PC2 (5.9%)
PC1 (86.3%)
1
0
-1
-4
0
4
Chiba
Ehime
Fukui
Hokkaido
Ishikawa
Kagoshima

Fig. S2

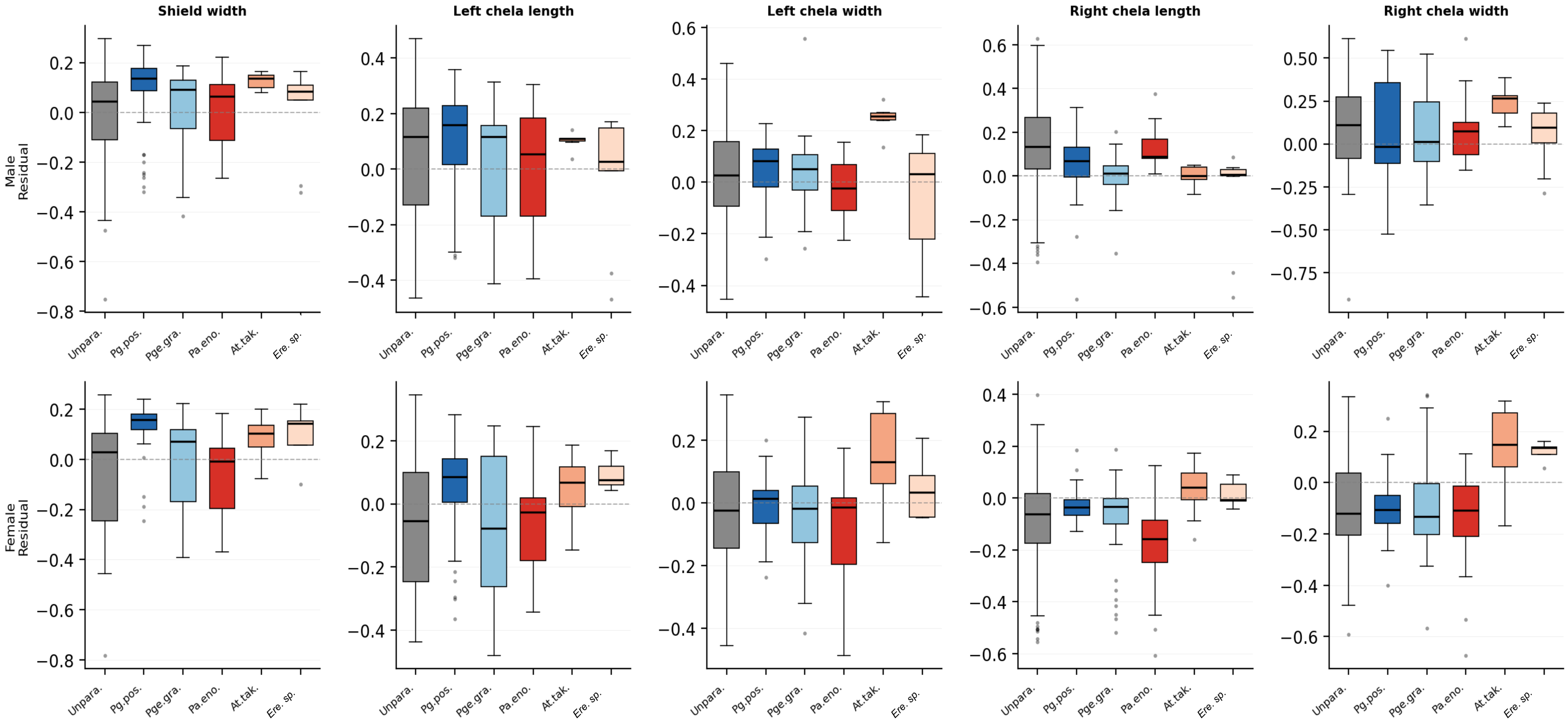

Shield width
Left chela length
Left chela width
Right chela length
Right chela width
Male Residual
Female Residual
0.2
0.0
−0.2
−0.4
−0.6
−0.8
0.4
0.6
0.50
0.25
0.00
−0.25
−0.50
−0.75
Unpara.
Pg.pos.
Pge.gra.
Pa.eno.
At.tak.
Ere. sp.

Table 1 Number of Pagurus filholi specimens examined, by locality, sex, and parasite species

Locality	Unparasitized		*Pg. postica*		*Pge. gracilis*		*Pa. enoshimensis*		*At. takanoshimensis*		*Eremitione* sp.		Total	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Hokkaido	33	30	5	2	8	24	0	0	0	0	10	5	56	61
Chiba	30	30	53	48	32	19	1	0	7	2	0	0	123	99
Ishikawa	30	21	0	0	0	0	12	2	0	0	0	0	42	23
Fukui	30	30	0	0	0	0	1	3	0	0	0	0	31	33
Ehime	15	30	0	0	0	0	0	0	0	12	0	0	15	42
Kagoshima	30	30	0	0	0	0	11	47	0	0	0	0	41	77
Total	**168**	**171**	**58**	**50**	**40**	**43**	**25**	**52**	**7**	**14**	**10**	**5**	**308**	**335**

M: male; F: female. Rhizocephala (blue): *Peltogaster postica*, *Peltogasterella gracilis*. Bopyridae (pink): *Parathelges enoshimensis*, *Athelges takanoshimensis*, *Eremitione* sp.

Note: Parasitized individuals were collected opportunistically across multiple sampling occasions; unparasitized individuals were collected in a single survey per locality. Prevalence of parasitism was therefore not estimated.

Table 2 Morphological measurements (mean ± SD, mm) of Pagurus filholi by locality, sex, and parasite species

Locality	Sex	Parasite	n	SL	SW	LCL	LCW	RCL	RCW
				mean ± SD (mm)					
Hokkaido	Male	Unparasitized	33	4.06 ± 0.79	2.66 ± 0.78	2.60 ± 0.75	1.08 ± 0.24	3.98 ± 1.12	2.07 ± 0.55
Hokkaido	Male	*Pg. postica*	5	4.48 ± 0.72	2.94 ± 0.91	2.97 ± 1.23	1.23 ± 0.28	3.86 ± 1.43	2.06 ± 0.90
Hokkaido	Male	*Pge. gracilis*	8	4.43 ± 0.85	3.19 ± 0.87	2.60 ± 0.72	1.30 ± 0.43	4.25 ± 0.80	2.21 ± 0.64
Hokkaido	Male	*Eremitione sp.*	10	3.56 ± 0.34	2.73 ± 0.48	2.54 ± 0.57	1.04 ± 0.26	3.24 ± 0.67	2.08 ± 0.40
Hokkaido	Female	Unparasitized	30	3.87 ± 0.69	2.29 ± 0.45	2.06 ± 0.22	0.97 ± 0.17	2.94 ± 0.80	1.68 ± 0.21
Hokkaido	Female	*Pg. postica*	2	3.35 ± 0.78	2.35 ± 0.07	2.00 ± 0.14	0.90 ± 0.00	2.60	1.80
Hokkaido	Female	*Pge. gracilis*	24	3.98 ± 0.83	2.65 ± 0.65	2.26 ± 0.47	1.03 ± 0.20	3.34 ± 0.82	1.78 ± 0.24
Hokkaido	Female	*Eremitione sp.*	5	2.92 ± 0.26	2.46 ± 0.44	2.36 ± 0.21	0.94 ± 0.09	2.90 ± 0.12	1.88 ± 0.16
Chiba	Male	Unparasitized	30	4.67 ± 0.90	3.46 ± 1.08	3.39 ± 1.11	1.33 ± 0.36	4.96 ± 1.31	2.72 ± 1.15
Chiba	Male	*Pg. postica*	53	5.14 ± 0.49	4.23 ± 0.69	3.94 ± 0.78	1.54 ± 0.23	5.29 ± 0.82	3.02 ± 0.95
Chiba	Male	*Pge. gracilis*	32	4.96 ± 0.76	3.82 ± 0.95	3.63 ± 0.93	1.46 ± 0.29	4.79 ± 0.91	2.79 ± 0.84
Chiba	Male	*Pa. enoshimensis*	1	4.00	3.70	2.80	1.30	4.20	2.00
Chiba	Male	*At. takanoshimensis*	7	4.93 ± 0.30	4.09 ± 0.26	3.68 ± 0.19	1.78 ± 0.16	4.70 ± 0.28	3.19 ± 0.27
Chiba	Female	Unparasitized	30	4.66 ± 0.64	3.21 ± 0.88	2.71 ± 0.68	1.23 ± 0.25	4.10 ± 0.71	2.04 ± 0.29
Chiba	Female	*Pg. postica*	48	5.15 ± 0.31	4.32 ± 0.45	3.68 ± 0.55	1.44 ± 0.15	4.74 ± 0.28	2.34 ± 0.27
Chiba	Female	*Pge. gracilis*	19	5.18 ± 0.48	4.22 ± 0.43	3.93 ± 0.65	1.52 ± 0.20	4.88 ± 0.41	2.69 ± 0.66
Chiba	Female	*At. takanoshimensis*	2	4.65 ± 0.07	4.05 ± 0.07	3.60 ± 0.28	1.80 ± 0.00	4.70 ± 0.14	3.05 ± 0.21
Ishikawa	Male	Unparasitized	30	4.90 ± 0.72	3.47 ± 1.01	3.21 ± 0.99	1.30 ± 0.32	4.80 ± 1.06	2.54 ± 0.87
Ishikawa	Male	*Pa. enoshimensis*	12	4.79 ± 0.46	3.73 ± 0.72	3.28 ± 0.92	1.34 ± 0.20	5.01 ± 0.54	2.64 ± 0.65
Ishikawa	Female	Unparasitized	21	4.16 ± 0.78	2.55 ± 0.75	2.38 ± 0.62	1.08 ± 0.24	3.29 ± 0.97	1.80 ± 0.32
Ishikawa	Female	*Pa. enoshimensis*	2	4.15 ± 0.64	3.00 ± 1.41	2.95 ± 1.48	1.05 ± 0.35	4.80	2.30
Fukui	Male	Unparasitized	30	2.90 ± 0.99	2.25 ± 0.67	2.39 ± 0.88	0.92 ± 0.25	3.81 ± 1.37	1.91 ± 0.60
Fukui	Male	*Pa. enoshimensis*	1	4.60	3.50	2.50	1.20	4.90	2.40
Fukui	Female	Unparasitized	30	2.56 ± 0.74	1.95 ± 0.42	1.81 ± 0.24	0.76 ± 0.17	2.28 ± 0.63	1.40 ± 0.29
Fukui	Female	*Pa. enoshimensis*	3	4.63 ± 0.55	3.17 ± 0.67	2.57 ± 0.51	1.07 ± 0.15	3.40 ± 0.79	1.83 ± 0.21
Ehime	Male	Unparasitized	15	3.36 ± 0.80	2.89 ± 0.61	3.20 ± 0.83	1.32 ± 0.40	4.52 ± 1.53	2.59 ± 0.67
Ehime	Female	Unparasitized	30	3.11 ± 0.56	2.68 ± 0.47	2.53 ± 0.37	1.09 ± 0.21	3.12 ± 0.42	1.93 ± 0.33
Ehime	Female	*At. takanoshimensis*	12	2.76 ± 0.46	2.27 ± 0.41	2.12 ± 0.37	0.97 ± 0.21	2.82 ± 0.51	1.82 ± 0.36
Kagoshima	Male	Unparasitized	30	3.59 ± 1.08	2.84 ± 0.80	3.29 ± 1.05	1.37 ± 0.48	4.95 ± 1.90	2.67 ± 0.93
Kagoshima	Male	*Pa. enoshimensis*	11	3.55 ± 1.18	2.59 ± 0.82	2.64 ± 0.83	0.99 ± 0.28	4.11 ± 1.55	2.32 ± 1.03
Kagoshima	Female	Unparasitized	30	2.95 ± 0.45	2.31 ± 0.35	2.27 ± 0.35	0.94 ± 0.16	2.89 ± 0.44	1.62 ± 0.27
Kagoshima	Female	*Pa. enoshimensis*	47	2.84 ± 0.56	1.99 ± 0.20	1.95 ± 0.20	0.82 ± 0.14	2.30 ± 0.36	1.44 ± 0.24

SL: shield length; SW: shield width; LCL: left chela length; LCW: left chela width; RCL: right chela length; RCW: right chela width.

"–": single specimen (SD not calculable). See Table 1 note regarding sampling of parasitized individuals.