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# Host-parasite energy dynamics: The impact of the rhizocephalan parasitic castrator, *Briarosaccus regalis*, on the California king crab and implications for fishery management

A Thesis submitted in partial satisfaction of the
requirements for the degree Master of Science
in Ecology, Evolution, and Marine Biology

by

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# ABSTRACT

## Host-parasite energy dynamics: The impact of the rhizocephalan parasitic castrator, *Briarosaccus regalis*, on the California king crab and implications for fishery management

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Despite the widely acknowledged importance of ecological and biological knowledge for sustainable fishery management, the impact of parasites within fishery systems often goes unrecognized. One such fishery facing this challenge is an experimental deep-sea crab fishery in the Southern California Bight, a primarily size-regulated fishery harvesting the California king crab (*Paralithodes californiensis*). *P. californiensis*, however, is commonly infected by the rhizocephalan parasitic castrator *Briarosaccus regalis*. In the absence of robust longitudinal growth studies and surveys for this host-parasite system, I investigated the impacts of *B. regalis* on the growth of *P. californiensis* using a dynamic energy budget framework. This theoretical framework illustrates how the host's energy resources are distributed to support its maintenance, growth, and reproduction, as well as to meet the parasite's energetic demands. Energy usage was assessed by measuring the reproductive output of rhizocephalans infecting male and female hosts, the reproductive output of uninfected female *P. californiensis*, as well as the growth rate of rhizocephalan externae and infected *P. californiensis*. Results indicated that 100% of the energy typically allocated to host reproduction is diverted to parasite reproduction during castration, requiring the remaining parasite energy demands to be met by other sources of host energy, specifically energy allocated for growth. Consequently, infected crabs exhibit slower growth rates and remain in smaller size classes for a longer time than uninfected crabs. Male hosts appear to experience greater growth suppression, likely due to allocating less energy to reproduction than females. These parasite-induced changes to crab growth and reproduction may have significant implications for fishery management. The current minimum individual size limit on catch implemented by the experimental fishery may be unintentionally sheltering parasitized individuals from fishing pressure, potentially influencing the fishery's sustainability. Integrating these findings into fishery assessment models, such as ecosystem management strategy evaluations (MSEs), could improve understanding of population-level impacts and inform strategies to support the long-term viability of this emerging California fishery.

# I. Host-parasite energy dynamics: The impact of the rhizocephalan parasitic castrator, *Briarosaccus regalis*, on the California king crab and implications for fishery management

## *A. Introduction*

Capture fisheries are vital sources of nutrition across the globe and significantly contribute to the economic stability of coastal communities, producing 91 million tonnes of biomass each year for human consumption and employing over 34 million people (FAO 2024). The sustainable management of capture fisheries is crucial to preserving these vital operations, avoiding overexploitation, and protecting marine biodiversity. However, most global fish stocks lack essential ecological information, such as the reproduction and growth dynamics of the fished species, physiological responses to abiotic and biotic stressors, and predator-prey relationships within the fishery's supporting ecosystem (Costello et al. 2012; Dowling et al. 2015; Nielsen et al. 2018). This information can be central to accurate and effective sustainable management. Notably, one aspect of ecology that could inform fishery management which is typically overlooked is that of host-parasite dynamics. Parasites can have a significant impact on their hosts, especially those that directly impact reproduction and growth, and consequently, the host's population dynamics. When unaccounted for, this ecological interaction can have major consequences for the productivity and sustainability of a fishery (Kuris and Lafferty 1992; Patterson 1996; Levsen et al. 2008; Wood et al. 2010; Morado et al. 2012).

One such fished species faced with the impacts of a parasite is the California king crab, *Paralithodes californiensis*. These are harvested by participants of the experimental deep-sea brown box crab and California king crab fishery operating in the Southern California Bight. Like their Alaskan relatives, *P. camtschaticus* and *P. platypus,* these deep-sea dwelling king crab are commonly infected by the rhizocephalan parasite *Briarosaccus regalis* (Wicksten 2011; Noever et al. 2016). Rhizocephalans are barnacles that are parasitic castrators. As the term implies, they cause the complete elimination of their host's reproductive ability (Kuris 1974; Baudoin 1975). This impact is the result of the rhizocephalan's manipulation of host hormones and damage to host reproductive tissues, including the destruction of the androgenic gland in male crab hosts (Veillet and Graf 1958; Høeg 1995; Sagi et al. 1997). The adult form of the parasite includes an internal and external portion, the interna and the externa. The interna is a root system that infiltrates the host's circulatory, digestive, and nervous systems, absorbing host nutrients and influencing host physiology (Bailey 1975; Miroliubov 2017, 2020; Lianguzova et al. 2023). The externa comprises the reproductive system of the parasite, producing successive broods of eggs which hatch into naupliar larvae. These are released into the water column in cyclical spawning events (Bower and Sloan 1985; Høeg 1995; Kajimoto et al. 2022). Given the intimate nature of this host-parasite relationship, these parasites may have profound implications for the management of the fishery.

As the California king crab fishery is an experimental small-scale operation still early in its development, a valuable opportunity exists to gather and consider essential ecological information to inform the management of the fishery, including potential impacts of this parasite on the crab population. However, the effects of *B. regalis* on its host *P. californiensis*, beyond castration, remain largely unstudied. Unlike other groups of rhizocephalans, *Briarosaccus* spp. do not halt their host's molting cycle (Hawkes 1985;

O'Brien and Van Wyk 1985; Sparks and Morado 1986; Hawkes et al. 1987; Shukalyuk et al. 2005), but changes to host growth rate, which can significantly impact population structure and yield, remain unaddressed. In addition to this, it is unknown whether rhizocephalan infections affect male and female hosts uniformly given sex-specific anatomy and physiology – key information for crab fisheries, which are typically managed by size, sex, and season (the 3-S strategy).

We applied a dynamic energy budget framework to investigate the impacts of *B. regalis* on the growth of *P. californiensis* through the energetic dynamics of this host-parasite relationship (Bailey 1975; Hall et al. 2007). In a dynamic energy budget, an organism has access to a limited amount of energy, which is then used to satisfy the energetic needs of the organism. These energetic costs are typically placed into three categories: maintenance, growth, and reproduction (Figure 1). In *P. californiensis*, we take maintenance to represent the energetic cost of basal bodily functions, often measured as the basal metabolic rate of the organism, as well as any costs associated with foraging and converting food into usable energy. Growth energy satisfies the cost of synthesizing tissues and the molt process. Reproductive energy is the energy used in gamete production and reproductive behaviors, such as mate competition in males and egg brooding in females. Introducing a parasitic castrator into this framework results in the stoppage of host reproduction and offers the availability of that allotment of energy for parasite use (Figure 1). With those shunted host energy resources, the parasite is able to fulfill its own maintenance, growth, and reproductive needs. For *B. regalis*, we define maintenance as the energy needed to absorb nutrients from its host and manipulate its host's physiology. Growth is the energy required to increase in size by creating tissues and molting, and reproductive energy is that which is dedicated to the cyclical production and development of eggs by the externa.

This energetic relationship can be used to illuminate possible impacts on host growth by examining the proportion of host reproductive energy used by the parasite. Because host reproduction is entirely disabled through physiological manipulation and anatomical destruction by the parasitic castrator, if the parasite consumes less than the entirety of the host's reproductive energy, there is energy leftover that could be directed towards other functions within the host. This often manifests as the phenomenon called "parasite-induced gigantism," in which the host grows to a size that is larger than it would have otherwise, had it been not parasitized, as the leftover reproductive energy is channeled towards host growth (Pearre 1976; Gorbushin 1997; Wilson and Denison 1980; Ebert et al. 2004). On the other hand, if the parasitic castrator consumes all the host's reproductive energy and more, it is likely that decreased host growth would be observed, as the parasite consumes energy that would have otherwise been used for host growth (O'Brien and Van Wyk 1985; Takahashi and Matsuura 1994). This can also manifest as a decrease in the longevity of the host if the excess energy consumption draws instead from host maintenance resources (Hall et al. 2007; Pontzer and McGrosky 2022). Finally, if the parasitic castrator consumes only the shunted reproductive energy of its host and no more or less, we would not expect to see any change in the other biological functions of the host (Baudoin 1975; Lafferty and Kuris 2009).

The dynamic energy budget framework also allows us to identify possible sex-based variation in the impact of the *B. regalis* infection by illustrating differences in energy usage by the parasite or by the host. For example, it has historically been accepted that male crabs allocate a significantly smaller amount of energy towards reproduction compared to females

(Scharf et al. 2013). However, in recent years, this generalization has been refuted with some authors asserting that gamete development in females and mating behaviors and sperm production in males are roughly equal in energetic cost (Colpo and López-Greco 2018; Pretterebner et al. 2022). In organisms like parasitic castrators, which rely heavily on their host's energy for reproduction, we would expect to see differences in parasite growth or reproduction based on the host's sex, assuming a difference in the reproductive energy available in male and female hosts. Conversely, if no such disparity exists, we would expect no difference in parasite growth or reproduction.

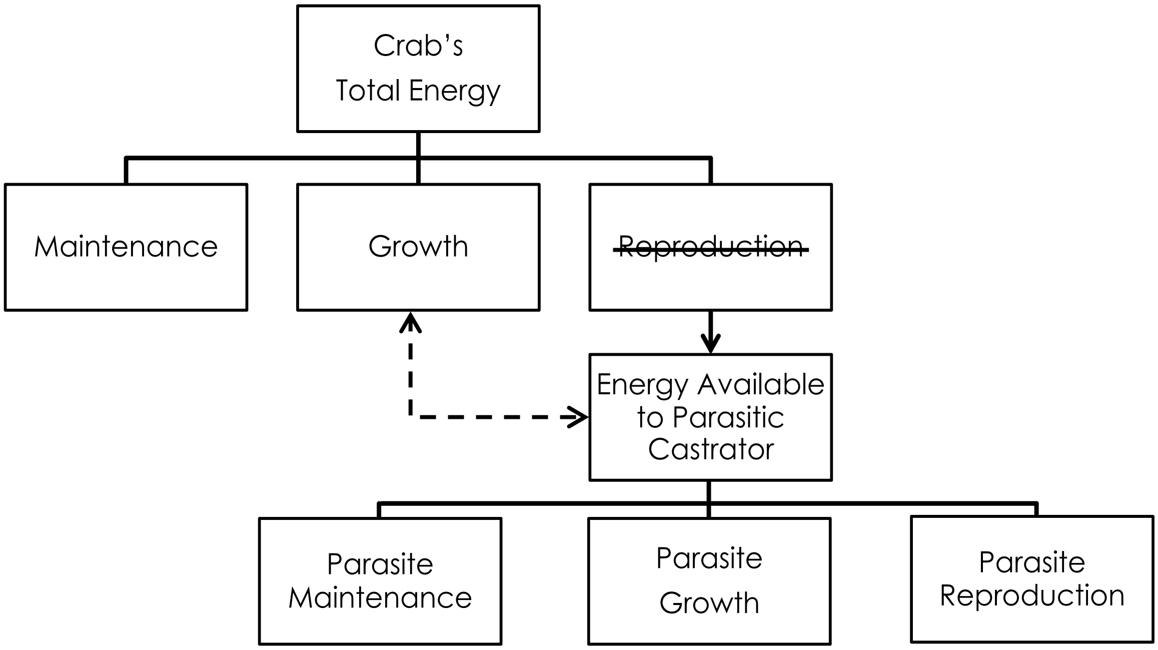

***Figure 1.*** Theoretical framework of the dynamic energy budget between *Paralithodes californiensis* and *Briarosaccus regalis*. Dashed arrows illustrate alternative energy flows: energy originally allocated to host reproduction may be redirected towards host growth if the parasitic castrator consumes less than the entire energy reserve for reproduction, resulting in parasite-induced gigantism, or energy originally allocated to host growth may be consumed by the parasitic castrator if it requires energy in excess to the host reproductive energy reserves, resulting in stunted host growth.

By identifying interspecific and intra-organismal host-parasite dynamics, we seek to define the pattern of energy utilization by *B. regalis* infecting *P. californiensis*. With this, we can project the bodily impact of the infection, in addition to castration, on male versus female hosts. Through this study, we aim to expand our understanding of the impact of *B. regalis* on *P. californiensis* and provide guidance for the management of a sustainable deep-sea crab fishery.

### ***B. Methods***

We approached the energetic relationship between *B. regalis* and *P. californiensis* by quantifying four aspects of the host-parasite energy budget: crab growth, uninfected female crab reproduction, parasite growth, and parasite reproduction as they varied with host body size and sex (Hall et al. 2007; Figure 1). We held maintenance for both the crab and the parasite constant across all groups.

### ***Crab Growth***

*P. californiensis* specimens were collected by commercial fishermen from February to June of 2021. A total of 88 crab were collected, 79 from Santa Barbara and nine from San Diego County. Of these, 17 males and 33 females were infected with *B. regalis* and 12 males and 15 females, not ovigerous, were uninfected. In addition, eleven ovigerous female crabs were collected. Specimens were euthanized and dissected upon arrival in the laboratory, except for seven infected crabs held in a flow through seawater system to document rhizocephalan egg development. Externae and crab egg masses were removed from their hosts and frozen separately for later examination.

Crab body size was represented by a carapace width measurement, not including spines. This measurement was taken to the nearest 0.01 millimeter using a digital caliper. Infection status was confirmed by the presence or absence of the green rhizocephalan interna within the body cavity of the crab (Boschma 1930; Sparks and Morado 1986).

### *Uninfected Female Crab Reproduction*

The broods collected from the eleven ovigerous females were used to assess the yearly reproductive output of uninfected *P. californiensis* females. Per Patrick et al. (2020), eggs were removed from each pleopod, spread evenly into a petri dish, and counted by ImageJ image analysis software. The number of eggs from each pleopod were then added together to determine the total number of eggs present in each crab brood. In addition to enumerating the eggs, ImageJ was used to gather an average egg length and width measurement to the nearest 0.01 micrometer. With these measurements, the average volume of a *P. californiensis* egg was calculated. Because king crab eggs possess a spherical shape, the following equation was used: $\text{Volume}= \frac{4}{3}\pi(\frac{\text{length}}{2})^3$. The average volume of a crab egg was then multiplied by the total number of eggs in the brood to determine the yearly brood volume for the female crab.

### *Parasite Growth*

#### *Externa Age*

Upon thawing during later examination, the chitinized dorsal shield was removed from the mantle cuticle of each externa and examined under a dissecting microscope to assess the number of concentric rings. A ring is created on the dorsal shield each time the externa molts its mantle cuticle which occurs after each spawning event (Lützen 1987). In *Briarosaccus* spp., these rings are roughly an equal distance apart, indicating a consistent time period between each spawning event and molt.

#### *Externa Size*

The morphology of the rhizocephalan externa was assessed through measurements of externa weight, volume, length, width, and height (Bower and Sloan 1985; Figure 2).

Externa length (EL) was measured from the mantle opening to the opposite tip of the structure. Externa height (EH) was taken from the base of the externa where the dorsal shield connects to the interna's stalk to the top of the externa. Externa width (EW) was taken perpendicular to the height measurement, across the body of the externa. Length measurements were taken to the nearest 0.01 mm using a digital caliper. Weight measurements were taken using a digital scale with an accuracy to the nearest 0.0001 grams, and measures of volume were evaluated to the nearest half a milliliter using water-displacement. A correlation plot using Pearson's method was generated for the externa's morphological features and the most representative feature of externa size was selected and used for growth rate analysis. The most representative feature was classified as the measurement with the strongest positive correlation with all other size measurements and the weakest correlations with the reproductive stage of the externa.

### ***Parasite Reproduction***

#### *Spawning Cycle*

To determine the number of broods produced per year by a single externa, we identified the time period occurring between spawning events for parasites attached to the *P. californiensis* specimens held in the laboratory. As per Takahashi and Matsuura (1994), the color of each externa was recorded on a weekly basis over a three-month period. The externa colors were classified into four categories: Red-

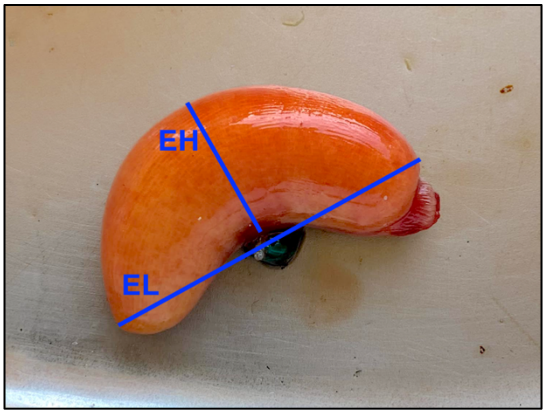

***Figure 2.*** The measurements used for morphometric studies on *B. regalis* (Bower and Sloan 1985): externa length (EL) and externa height (EH). Externa width was measured perpendicular to the plane of the externa height measurement.

Gray, Red, Red-Orange, and Orange. Changes in color signify changes in the reproductive stage of the externa. The number of spawning events completed by a single externa per year was calculated by dividing one year by the period of time between spawning events. The age of the externa in years was also calculated by dividing the number of dorsal shield rings by this value.

*Reproductive Output*

Each externa was then dissected to examine the reproductive output of the parasite. An incision from the aperture across the flank of the externa allowed the mantle cuticle to be peeled back, revealing the ovary and egg mass. The egg mass was removed from the mantle cavity and weighed to the nearest 0.0001 g. To estimate the number of eggs in the egg mass, three subsamples were taken by pinching off a small portion of the egg mass with fine forceps. Each subsample was then weighed to the nearest 0.0001 g, diluted into 1 mL of seawater, and mounted onto a Sedgewick-Rafter slide. Eggs that possessed a clear lipid layer between the developing embryonic cells and the outer cuticle of the egg were classified as male and those lacking this layer of lipids as female (Hawkes et al. 1985; Høeg 1995; Kobayashi et al. 2018). The eggs were then enumerated for each sex. The egg sex ratio, the proportion of male to female eggs within the sample, was calculated using a scale of zero to one, with one being all (100%) male eggs and zero being all (100%) female eggs. The average sex ratio across the three subsamples was calculated and used to represent the sex ratio of the entire brood. The number of eggs counted in each subsample was used to extrapolate the total number of eggs present in the egg mass by multiplying the ratio between the weight of the entire egg mass and the subsample weight with the number of eggs counted in the subsample. The average across the subsamples was calculated and used to represent the number of eggs in the brood.

Volume measurements of rhizocephalan eggs were generated via image analysis of photographs taken of each mounted subsample of eggs using ImageJ image analysis software. The area, length, and width of each egg were recorded to the nearest 0.01 µm, length being measured as the longest distance across the egg and width perpendicular to the length. The shape of a rhizocephalan egg is most akin to an ellipsoid shape with their depth being equal to their height (Lewis 1977). The volume for each egg was calculated according to the following ellipsoid volume equation: $\text{Volume}=\frac{4}{3}\pi(\frac{\text{depth}}{2})(\frac{\text{height}}{2})(\frac{\text{length}}{2})$, where depth and height are both represented by the egg's width measurement. For each brood, the average volume of a male and female egg was recorded.

The total egg volume of the brood was calculated by adding the total volume of male eggs to the total volume of female eggs. Total male egg volume was estimated by multiplying the total number of eggs by the sex ratio of the brood and the average volume of a single male egg. Total female egg volume was determined through the same equation, except that the sex ratio was replaced with one minus the sex ratio to represent the proportion of the brood made up of females.

*Reproductive Output Comparison*

Because king crab eggs and rhizocephalan eggs are comprised of a similar complex of lipid-protein yolk and embryonic cells encased by a protective membrane and cuticle, the volume of eggs produced by *B. regalis* can be directly compared to that of uninfected female *P. californiensis* specimens. However, while female *P. californiensis* presumably produce only one brood of eggs per year like their relative *P. camtschaticus* (Marukawa 1933), *B.*

*regalis* externae produce many broods per year, a disparity that needs to be accounted for when comparing annual egg production. To do so, the total brood volume of each externa was multiplied by the total number of spawning events completed per year, as determined by observing the brooding frequency of parasites on the crabs held in the laboratory. With this calculation, the volume of eggs produced per year ($\mu m^3$) by uninfected female king crab can be directly compared to that of rhizocephalan externae.

### *Statistical Analysis*

To analyze the data, we employed a series of nested linear models. This allowed us to test for group differences after accounting for variability due to crab body size or externa age. Model fit was assessed using the lowest Akaike Information Criterion Correction (AICC). Models were considered significantly different if the delta between the AICC value was greater than two. The statistical significance of the interaction term was then used to identify a significant difference in the slope between groups. The separate models for externa size, age, and total yearly brood volume included host crab body size (CW) as a fixed effect as well as an interaction term between host body size and host sex to assess potential differences in linear relationships across male and female hosts. Models exploring externa age included host crab body size or externa size as fixed effects as well as an interaction term with host sex. The model for yearly total brood volume of uninfected female crab included female body size as the main effect. The total yearly brood volume of uninfected female *P. californiensis* and *B. regalis* externae attached to female hosts and male hosts were also compared through the significance of group interaction terms. For reproductive output analyses, both reproductive volume and crab body size data were log transformed to reveal proportional relationships and satisfy normality assumptions of linear regression analyses.

Analyses were performed in Python Version 3.11.7. Data manipulation and preprocessing methods were carried out using pandas (version 2.1.4). Nested linear models with random intercepts and slopes were fitted using the statsmodels library (version 0.14.0) and scipy (version 1.11.4). Diagnostic plots and visualization of results were created with matplotlib (version 3.8.0) and seaborn (version 0.13.2).

## *C. Results*

### *Crab Growth*

Collected crabs ranged from 28.6 mm in carapace width to 125.8 mm. Females had a mean carapace width of 88.2 mm, and males had a mean of 80.0 mm. In absence of longitudinal growth studies, we assessed the growth rate of parasitized *P. californiensis* specimens by plotting the body size of infected crab against the number of dorsal shield rings counted on the externa collected from the crab. We found a strong positive and linear relationship (Adjusted-$R^2 = 74.1$, $p < 0.001$; Table 1, Figure 3*)*. When an interaction with host sex was included in the model, there was no significant improvement to the model's fit ($\Delta AIC = 0.2$; $p > 0.05$; Table 1). The x-intercept of the regression equation fell at 63.4 mm (Figure 3). The slope of this regression divided by the number of dorsal shield rings created per year indicated a growth rate of 5.21 mm CW per year for both male and female crabs.

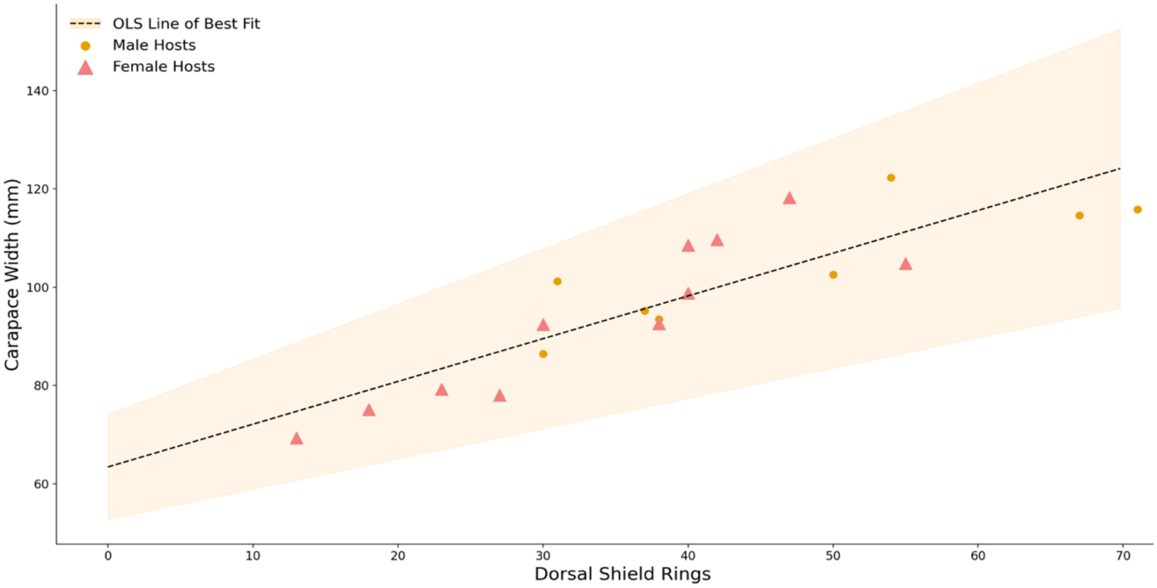

***Figure 3.*** Linear regression of host crab carapace width (mm) by the number of dorsal shield rings counted on the attached rhizocephalan externa. The shaded region denotes the 95% confidence interval of the regression.

### *Uninfected Female Crab Reproduction*

The total number of eggs in a single brood from uninfected female California king crabs ranged from 1,500 to 7,300 eggs with an average egg volume of 2,650.2 $\mu m^3$. The model of total yearly brood volume predicted by female carapace width showed a positive linear relationship (Adjusted-$R^2 = 63.3$, $p < 0.05$; Table 1, Figure 8).

| **Dependent Variable** | **Model Predictors** | **Adjusted-R2** | **Model p-value** | **AIC** | **Interaction p-value** |
|---|---|---|---|---|---|
| **Dorsal Shield Rings** | CW | 74.1 | < 0.005 | 133.9 | - |
| | CW * Sex | 75.5 | < 0.005 | 133.7 | 0.179 |
| **Externa Length** | CW | 65.0 | < 0.005 | 210.9 | - |
| | CW * Sex | 63.9 | < 0.005 | 212.9 | 0.882 |
| | Dorsal Shield Rings | 38.9 | < 0.005 | 127.1 | - |
| | Dorsal Shield Rings * Sex | 35.3 | < 0.05 | 129 | 0.817 |
| **Log Parasite Brood Volume** | Log CW | 38.0 | 0.061 | 22.27 | - |
| | Log CW * Sex | 87.3 | < 0.005 | 10.16 | < 0.005 * |
| **Log Crab Brood Volume** | Log CW | 63.3 | < 0.005 | - | - |

***Table 1.*** Summary statistics of linear models for externa age (dorsal shield rings), size (externa length), and reproductive output (brood volume) predicted by host size (carapace width) and host sex as well as the reproductive output of uninfected female crab regressed against crab size.

## ***Parasite Growth***

### *Externa Size*

Externa length had the highest positive correlation among all other measurements of externa size and the least correlation with the weight of the egg mass, representing the reproductive stage of the externa, which made it the best representative of externa size (Table 2). The largest externa recorded possessed a length of 50.5 mm, and the smallest was 5.81 mm. The size of *B. regalis* externae increased linearly with crab host size (Adjusted-$R^2$ = 65.0, $p < 0.001$; Table 1, Figure 4). There was no significant difference in this relationship in male versus female crab hosts (ΔAIC = 2.0; interaction $p > 0.05$; Table 1).

| | **Externa Length** | **Externa Height** | **Externa Width** | **Externa Volume** | **Externa Weight** | **Egg Mass Weight** |
|---|---|---|---|---|---|---|
| **Externa Length** | 1 | | | | | |
| **Externa Height** | 0.838183 | 1 | | | | |
| **Externa Width** | -0.406925 | -0.481523 | 1 | | | |
| **Externa Volume** | 0.822726 | 0.792516 | -0.420069 | 1 | | |
| **Externa Weight** | 0.733572 | 0.76574 | -0.553331 | 0.96698 | 1 | |
| **Egg Mass Weight** | -0.104632 | -0.376733 | -0.538436 | -0.384445 | -0.443711 | 1 |

***Table 2.*** Correlation matrix of rhizocephalan externa morphological measurements. Externa length is identified as the most representative size metric due to its strong positive correlations with other size measurements and weak correlation with egg mass weight, reflecting the reproductive stage of the externa.

Dorsal shield ring counts, representing externa age, ranged from 13 to 71 with an average of 39.5 rings. The number of dorsal shield rings, however, was not a significant predictor of externa size (Adjusted-$R^2$ = 38.9, $p < 0.05$; Table 1). Based on the regression line described by this model, the predicted size of the externa when it possesses zero dorsal shield rings (a recently infected host), is 19.4 mm. The regression of externa size against carapace width indicates that an externa of this size would occur in a crab measuring 63.2 mm in width (Figure 5).

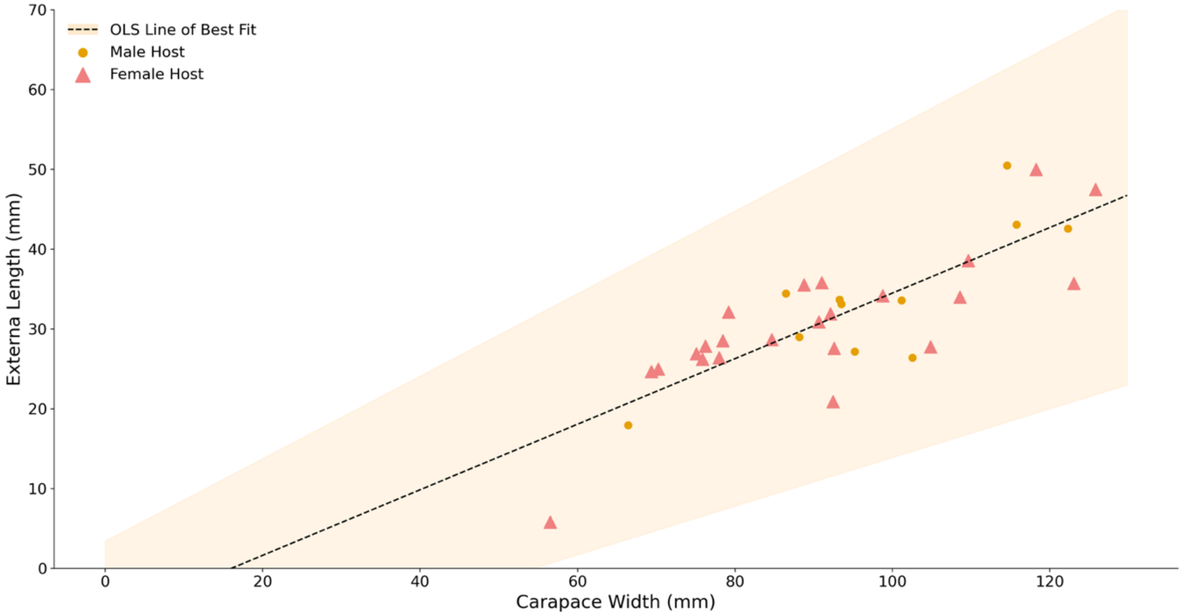

***Figure 4.*** Linear regression of externa length (mm), representing externa body size, by carapace width (mm), representing host body size. The shaded region denotes the 95% confidence interval of the regression.

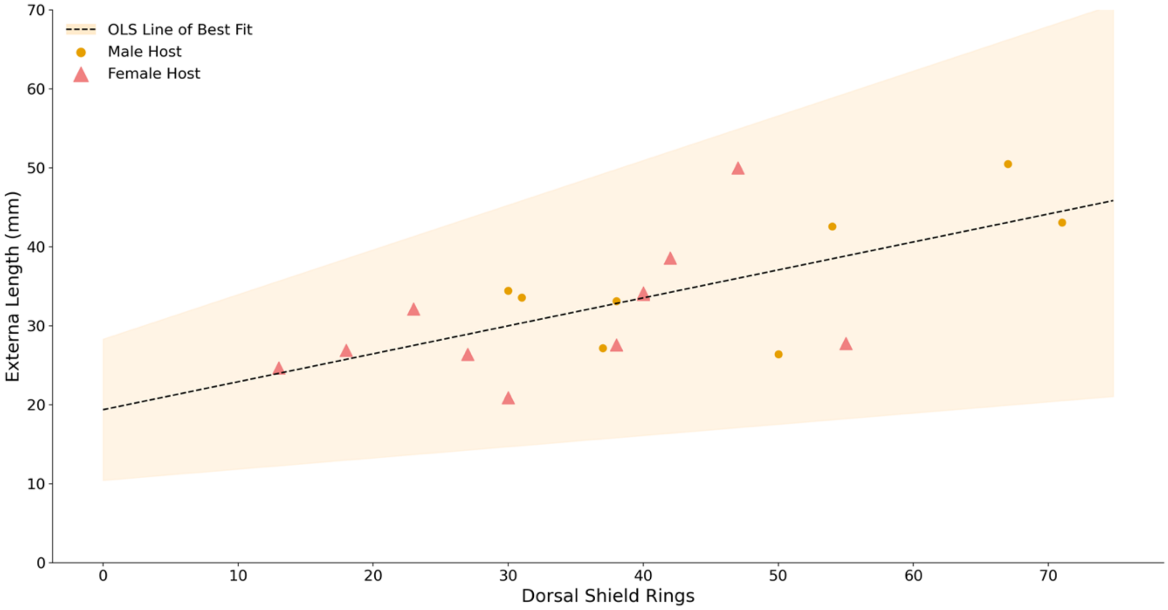

***Figure 5.*** Linear regression of externa length (mm), representing externa body size, by the number of dorsal shield rings possessed by the externa. The shaded region denotes the 95% confidence interval of the regression.

### ***Parasite Reproduction***

#### *Spawning Cycle*

We observed distinctive reproductive stages of *B. regalis* infecting *P. californiensis* based on externa color and texture (Figure 6). An externa that recently produced a brood of eggs was orange, likely because of the color of the egg yolk, and its surface was smooth in texture. When the eggs developed into larvae, the orange color progressively diminished, presumably due to the larvae consuming the yolk. Once the larvae were fully developed and released from the mantle opening as spawn, the color of the externa became pale red-gray, and its texture was wrinkled. As gametogenesis began anew, the color of the externa turned a deep red and the wrinkled texture of the mantle cuticle became smooth once more. Following gametogenesis, the externa returned to an orange color as the mantle cavity filled with newly oviposited eggs. We recorded these color changes over a three-month period, and documented two spawning events with eight weeks, or two months, occurring between them (Figure 7). Based on this time frame, we estimated that each externa was able to complete six spawning cycles per year.

***Figure 6***. Photographic record of the weekly reproductive development of a *B. regalis* externa attached to a *P. californiensis* specimen over a 3-month period. Panels D and L show the externa directly after spawning events with 8 weeks occurring between them.

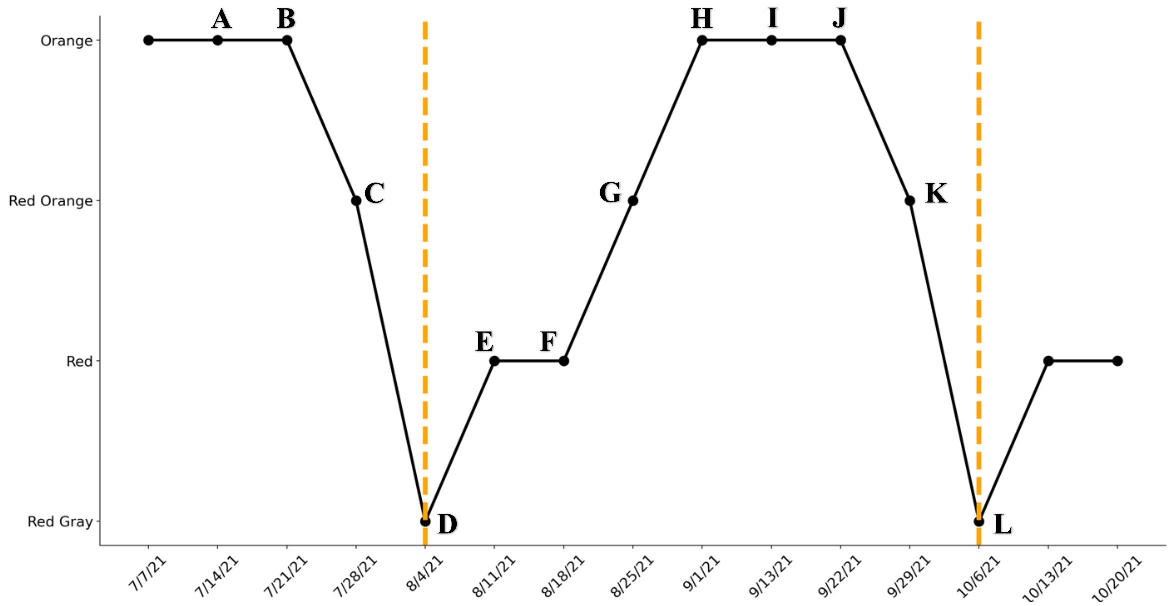

***Figure 7.*** A time-series graph of the change of externa color for one of the *P. californiensis* specimens held in the laboratory for a three-month observation period. The letters assigned to the points from 7/14/2021 to 10/6/2021 correspond with the photograph panels in *Figure 3*. Orange, the upper limit of the y-axis, represents the color at which the externa is full of eggs and/or developing larvae. Red gray, the lower limit of the y-axis, represents the phase of the spawning cycle at which the externa is empty, having spawned all larvae from the mantle cavity. The vertical orange dashed lines mark the time at which the externa underwent a spawning event.

### *Reproductive Output*

Female *B. regalis* eggs had a mean volume of 0.00339 $\mu m^3$, and male eggs were 48% larger than female eggs with a mean volume of 0.00705$\mu m^3$ ($p < 0.005$). The percentage difference between male and female eggs was consistent across all egg measurements. The total number of eggs counted in each brood ranged from 15,000 to 655,000. The calculated volume of eggs produced per year showed a strong positive relationship with host size (Table 1, Figure 8). The addition of an interaction with host sex significantly increased the performance of the model, indicating a difference in rhizocephalan reproductive output between externae of male versus female hosts ($\Delta AIC = 12.1$; $p > 0.05$; Table 1). The slope of the regression for externae attached to male hosts was significantly lower than that of externae attached to female hosts. Externae from male crab showed a consistent drop of roughly 10% reproductive volume across host sizes compared to those from female hosts.

| Dependent Variable | Group Comparison | Adjusted - R2 | Model p - value | Log CW p-value | Group Interaction p-value |
|---|---|---|---|---|---|
| **Yearly Brood Volume** | UIF - IM * | 86.6 | < 0.005 | < 0.005 | < 0.005 * |
| | UIF - IF | 63.6 | < 0.005 | < 0.005 | 0.932 |
| | IM - IF * | 87.3 | < 0.005 | < 0.005 | < 0.005 * |

***Table 3.*** Summary statistics of the linear regression comparisons between the relationships between yearly brood volume and carapace width for uninfected female *P. californiensis* (UIF) and *B. regalis* infecting male hosts (IM) and female hosts (IF).

### *Reproductive Output Comparison*

When the relation between yearly reproductive volume and crab size of uninfected females and the rhizocephalans of infected female hosts was compared, we found no significant difference ($p > 0.05$; Table 3, Figure 8). Subsequently, there was a significant difference between uninfected females and the rhizocephalans infecting male hosts ($p < 0.005$).

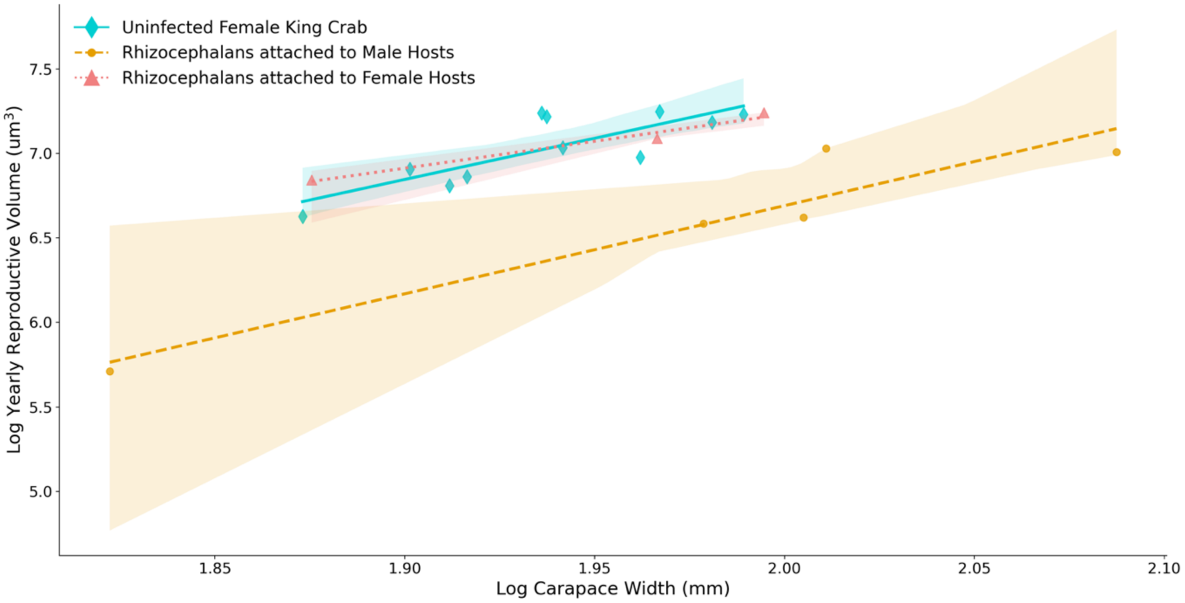

***Figure 8.*** Linear regression of log yearly reproductive volume ($\mu m^3$) of *B. regalis* infecting male and female hosts as well as uninfected female *P. californiensis* with crab (host) body size (mm). The shaded regions denote the 95% confidence interval of each regression.

### *D. Discussion*

Rhizocephalans are highly host-specific parasites, evolving and speciating along with their decapod hosts. This constrained coevolutionary relationship leads to significant variation in the impacts and dynamics of their host-parasite interactions, making host-specific assessments of rhizocephalan infections necessary (O'Brien and Van Wyk 1985; Noever 2016). *B. regalis* was previously thought to be limited to hosts in the northern Pacific, such as *P. camtschaticus* and *P. platypus*, but this study extends that range to include *B. regalis* infecting *P. californiensis* as far south as the Mexican border. Although *P. californiensis* is well-documented as a lithodid species in Southern California, its biological and ecological characteristics have not been previously assessed (Wicksten 2011). Our investigation sheds light on *P. californiensis* and the host-parasite interaction between it and *B. regalis*, providing new insights into the importance of dynamic energy budgets within host-parasite systems, as well as the influence of male and female host biology on the impacts of the infection.

Others have hypothesized that members of the family *Peltogastriidae*, such as *Briarosaccus* spp., follow a relatively K-selected reproductive strategy compared to other rhizocephalans, investing more energy per offspring to increase their survival probability (Parry 1981; Nagler et al. 2017). This strategy is often characterized by large body size, longer lifespans, and small brood size relative to body size. Our data supports this hypothesis for *B. regalis*. In accordance with the expectations, our sample of *B. regalis* externae reached a much larger maximum size (50.5 mm) than other documented species of rhizocephalan, such as *Sacculina carcini* with a maximum recorded externa length of 17.5 mm and *Sylon hippolytes* with a maximum of 15.2 mm (Lützen 1981, 1984; Poulin and

Hamilton 1997). The lifespan of *B. regalis* externae, as evidenced by the number of rings present on the dorsal shield, also exceeds that of other rhizocephalan species, which typically live for only one to five years (Lützen 1987). In contrast, the oldest *B. regalis* externa in our collections was almost twelve years old. Furthermore, the brood size of *B. regalis* is roughly equal to that of smaller rhizocephalan species, despite its significantly larger body size (Lützen 1981; Nagler et al. 2017). However, the eggs produced in the brood are larger than that of other rhizocephalan species, measuring an average of 245 µm in diameter while other rhizocephalans produce eggs between 70 and 160 µm, indicating larger parental investment per offspring by *B. regalis* (Poulin and Hamilton 1997). Importantly for *B. regalis*, the long lifespan of its externae also supports a potential lifetime reproductive output that far exceeds that of other species.

The findings of this study deviate from prior reports about peltogastrid rhizocephalan body size and age in relation to host size. Host crab body size was a significant determinant of *B. regalis* externa size, with no observed variation in growth rate based on host sex. In contrast, *Peltogaster paguri*, for example, displays a faster growth rate when attached to female hosts than when infecting male hosts (Reinhard 1942). Further, it has been suggested that the size of the externa in *Briarosaccus* spp. is the best representation of the age of the parasite because of their linear growth rate over their long lifespan (Bower and Sloan 1985). Our finding that host size outperforms externa age as a predictor of externa size instead supports the hypothesis that larger hosts provide a greater supply of resources (Reinhard 1942). They are thus capable of supporting larger parasites, and the correlation between parasite age and parasite size is a consequence of the concomitant linear relationship between parasite age and host body size.

Additionally, insights into the probable life history of *B. regalis* gleaned from our investigations reveal cryptic patterns in its growth and reproductive cycle. The linear relationship between host body size and externa age suggests that all parasitized *P. californiensis* specimens are infected by *B. regalis* at the same life cycle stage. None of the large, and therefore older, crab had "young" externae i.e., externae with few dorsal shield rings. The linear relationship between parasite size and host body size indicates that the externa emerges when its host possesses a carapace width of ~16 mm. At that size, the crab host is a juvenile, likely about one to two years old (Dvoretsky and Dvoretsky 2014; Artemenkov et al. 2022). In the king crab life cycle, juvenile crabs of this size participate in a behavior called "podding" where tens to thousands of crab gather in a large group on the sea floor, until they reach the size-at-maturity and disperse into deeper waters (Stevens and Jewett 2014). We suggest that this is the time at which the king crab encounters the infective larval form of the rhizocephalan parasite. The parasite then develops within the host as the crab continues to grow. Reproduction of *B. regalis* is then initiated when virgin externae emerge, are mated by male rhizocephalan larvae, and start producing consecutive broods of eggs, marked by the creation of dorsal shield rings. The regression of dorsal shield rings against host body size implies that this process commences once the host has reached a carapace width of ~ 63 mm. This host size is close to the size-at-maturity for other king crab species, such as *P. camtschaticus* and *P. platypus* (Di Salvatore et al. 2021; Artemenkov et al. 2022). We infer from this that the reproductive maturity of the externa is synchronized with that of its host.

Our investigation challenges the widely held assumption that parasitic castrators consistently 'out-reproduce' their hosts by surpassing their fecundity (Ding and Morand

1998; Timi et al. 2005; Grunberg and Anderson 2022). Historically, rhizocephalans have been included in this assumption due to the thousands of eggs produced by the parasite which outpaces the fecundity of their crustacean hosts. *Sylon hippolytes*, for example, produces a single brood of 20,000 to one million eggs, compared to its host *Pandalus platyceros*, which produces only 2,628 to 4,669 eggs per brood (Kelly et al. 1977; Lützen 1981; Bower and Boutillier 1990). However, this comparison does not account for the energetic trade-off between egg size and egg number. There is a considerable size difference between the eggs of the parasites and their hosts. Further, the energetic cost of producing the eggs, specifically the chemical composition (protein, lipids, carbohydrates, fatty acids), is often overlooked. The reproductive effort of the two crustacean species we studied produce eggs of similar chemical composition, justifying our comparison of reproductive output between an uninfected female California king crab and a rhizocephalan barnacle parasite (Lewis 1977; Holland 1987;  Dvoretsky et al. 2024). This, taken together with the consideration of energetic costs, likely explains our finding of equal reproductive output of uninfected female *P. californiensis* crabs and that of rhizocephalan parasites infecting parasitically castrated female crabs. Quantification of the reproductive output of uninfected male crabs is still needed to address the energetic costs of reproduction in males.

Although we were not able to quantify the reproductive output of male crabs, the consistent decrease in the reproductive volume produced by *B. regalis* externae attached to male hosts compared to female hosts represents, to our knowledge, the first record of variation in rhizocephalan reproductive output due to the sex of the host. This difference strongly suggests that the physiological differences between male and female hosts may influence the availability of energy for parasite reproduction, possibly due to a lower amount of energy dedicated to reproduction in male versus female crabs. Others have posited that reproductive energy allocation in crabs is balanced between the sexes, with the high energetic cost of male reproductive behaviors offsetting the lower cost of sperm production as compared to female gamete production (Colpo and López-Greco 2018; Pretterebner et al. 2022). This does not, however, explain the difference in *B. regalis* reproduction because rhizocephalans inhibit gamete production and modify the behavior of male and female hosts to reflect the same level of aggression, migration patterns, and absence of mating behavior (Boschma 1930; Rasmussen 1959; Bower and Sloan 1985; Sparks and Morado 1986; Hoggarth 1990; Huber et al. 1997; Shukalyuk et al. 2005; Miroliubov et al. 2020; Lianguzova et al. 2023). This may effectively standardize behavioral energetic costs across the sexes. Instead, this observation suggests that male *P. californiensis* appear to devote significantly less energy to reproduction compared to females. This may consequently lead to the lower reproductive output of *B. regalis* infecting male hosts.

Our growth comparisons also provide evidence that *B. regalis* may significantly impair the growth of *P. californiensis*, with male crabs being particularly affected. Although growth rates have not been documented for *P. californiensis*, related species of lithodid (king) crabs indicate that males grow at a rate roughly double that of their female counterparts. Based on similarly sized crabs to our study (50 to 100 mm), we calculated that female *P. platypus* exhibit an average yearly growth rate of 5.75 mm in carapace width (CW) and males an increase of 10.7 mm CW (Hawkes et al. 1987; Artemenkov et al. 2022). Similarly, *L. aequispinus* were reported to have annual growth rates averaging 4.25 mm CW for females and 8.15 mm CW for males (Koeneman and Buchanan 1985; Watson et al. 2002). This higher growth rate for male king crabs, as compared to females, is in direct contrast to our findings that infected male *P. californiensis* grow at a rate equal to that of infected females. Furthermore, that rate, 5.2 mm CW per year, is close to that of uninfected female *P. platypus* and *L. aequispinus*. Nonetheless, because growth and age-size studies have not been conducted for *P. californiensis*, we are not able to unequivocally conclude that there is a negative impact on growth due to the energetic toll of *B. regalis*.

### *Energy Dynamics*

Direct measurements of energy usage were beyond the scope of this study, but contextualization within a dynamic energy budget model reveals the significant impact that the profound energetic demands imposed by the parasitic castrator have on male and female host growth (Figure 9). Our model makes the assumptions that maintenance energy requirements for king crabs remain constant regardless of sex or infection status (Figure 9A, B), while rhizocephalan parasites exhibit consistent maintenance demands irrespective of host sex (Figure 9C). Additionally, uninfected male king crab are assumed to allocate significantly more energy to growth compared to uninfected females (Figure 9A), consistent with findings in other king crab species. Because we found that the externae attached to male and female hosts increased in size at equivalent rates, the proportion of energy devoted to growth by the parasites was considered independent of host sex, and, therefore, equivalent (Figure 9C). Similarly, infected male and female crabs exhibited equal growth rates, indicating that their energy reserves allocated for growth are also the same (Figure 9B). With the reproductive effort of parasites attached to male hosts consistently lower than that of parasites on female hosts, we conservatively interpreted this as a 10% lower amount of energy dedicated to reproduction for the parasites attached to male hosts compared to those attached to females (Figure 9B). Further, we considered the energy allocated to reproduction in female crabs and the parasites infecting female hosts to be equal because uninfected female crabs and rhizocephalan externae from female hosts demonstrated equivalent annual reproductive output.

Based on our assumptions, female host growth must be negatively impacted when infected in order to meet the energy requirements of the parasite. The entirety of host reproductive energy is consumed by the parasite and redirected to satisfy its reproductive needs in a female host. Growth and maintenance needs of the parasite must be met using energy in excess of the host’s reproductive energy allotment (Figure 9). This would result in a stunted growth pattern for such a host, as energy that would have otherwise been spent on growth is now consumed by the parasite to satisfy its other metabolic needs. This is consistent with a previous study of the impact of *B. callosus* on *P. platypus* in which a small decrease in growth was observed in infected female hosts (Hawkes et al. 1987).

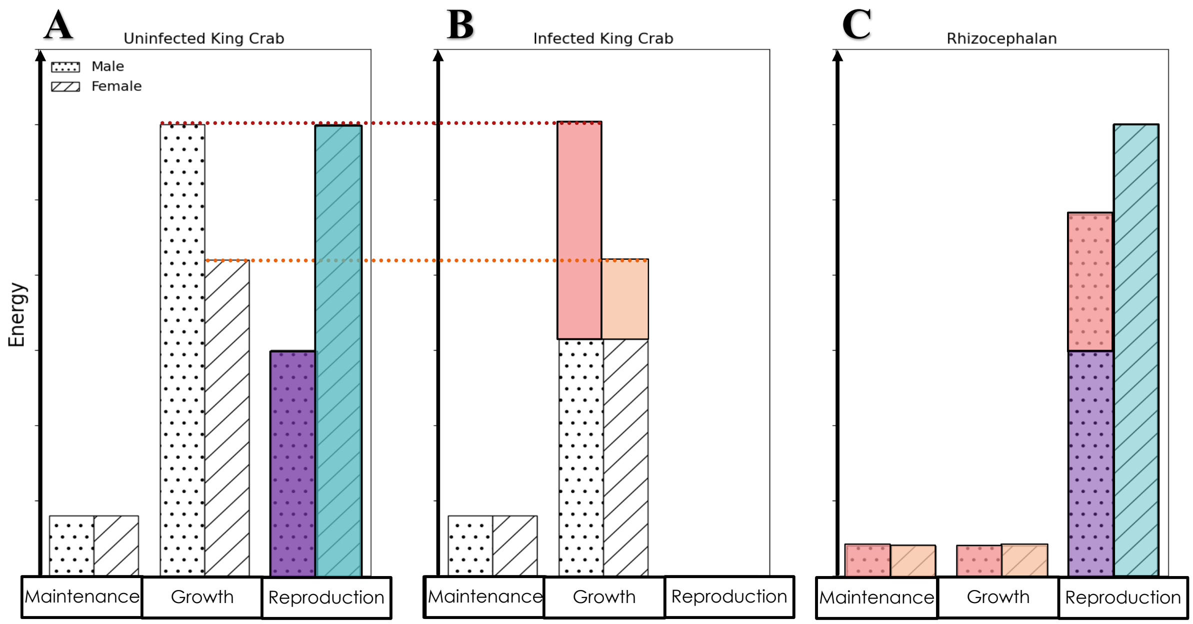

***Figure 9.*** Hypothetical depiction of the dynamic energy budget between uninfected (A) and infected (B) male and female *P. californiensis* and the rhizocephalan parasite *B. regalis* (C). Energy availability (y-axis) is arbitrarily represented based on observed ratios. Dotted and striped bars denote male and female crabs, respectively. Purple and blue boxes (uninfected crabs) represent reproductive energy consumed by the parasite, corresponding to the same colors in the parasite's energy budget. Red and orange boxes (infected crabs) indicate growth energy deficits compared to uninfected crabs with redirection of that energy represented in the parasite's energy budget.

A similar, but much more severe, impact on growth is expected and apparent for male *P. californiensis* infected by *B. regalis*. For male hosts, a substantial decrease in growth would be evident if their growth rate matched that of a stunted female host. In this scenario, the rhizocephalan consumes a much larger share of the male host's growth energy to meet its energetic needs (Figure 9). Hawkes et al. (1987) reported that male *P. platypus*, infected with *B. callosus,* grew at a significantly slower rate than did uninfected males. This rate was equivalent to that of infected female crabs. Sloan (1984) also observed this pattern in male *L. aequispinus* infected with *B. callosus*.

Together, these findings support our conclusion that male *P. californiensis* allocate a significantly lower amount of energy towards reproduction than do female crabs. The energy needs of the parasite are largely met by the reproductive energy of female hosts, with minimal reduction in growth. For male hosts, our results suggest there is a substantially greater impact on growth because the parasites are not able to satisfy their energetic needs solely from the reproductive energy of castrated male crabs. The reduced reproductive output of parasites infecting male hosts further suggests that male hosts provide significantly less energy for parasite use from male reproduction stores. Moreover, the difference in crab reproductive energy between the sexes is undoubtedly greater than the 10% difference we assigned to the rhizocephalans in our hypothetical model. Excess growth energy consumed in male hosts likely subsidizes the reproductive effort of the parasite, and this unknown amount may be attributed to reproduction stores, depressing the estimated difference in reproductive energy available from female versus male hosts (Figure 9).

Alternatively, the discrepancy in parasite reproductive output could be explained by dynamic energy budget components that we were not able to measure. These include the energetic costs of host manipulation and castration processes. Perhaps the reduction in reproductive output of parasites infecting male hosts is due to a larger energetic requirement for host manipulation in males compared to females. The production and secretion of hormones and structures involved in manipulating and castrating a host can be energetically expensive (Baudoin 1975). Some effects of castration on male host crabs include a widening of the abdomen and behavioral changes that mock breeding behaviors of females, i.e., feminization (Ritchie and Høeg 1981; Innocenti et al. 2003; Toyota et al. 2023). These impacts are likely energetically expensive manipulations. Furthermore, in crustaceans, the base hormonal state is that of female, and male traits require this base state be altered through the addition of male hormones (Charniaux-Cotton 1962; Hasegawa et al. 1993; Sagi et al. 1997). Because rhizocephalans in male hosts must terminate male hormone production, in addition to other hormonal manipulations which also take place in female hosts, there is likely an increased energetic cost to a castrating parasite in a male host. This could result in a decrease in reproductive output. This assumed increase in energetic cost could be satisfied by the greater consumption of host growth energy in male hosts or the energy saved by ceasing male hormone production. Further study of comparative energetic costs of growth, reproduction, and host manipulation are needed to fully elucidate the energy dynamics of this host-parasite system.

### ***Implications for Fishery Management***

The profound impacts of *B. regalis* on the growth and reproduction of *P. californiensis* emphasize the need for targeted strategies to safeguard the ecological sustainability of a *P. californiensis* fishery in Southern California. Rhizocephalans block reproduction of both male and female hosts, rendering them unable to contribute offspring to the population. Fished populations of other *Paralithodes* and *Lithodes* spp. have experienced major reductions in fishery productivity due, in part, to high prevalence of *B. callosus* (Sloan 1984, 1985). Reduced rate of crab replacement would presumably lead to a buildup of infected crabs in the population, as fewer uninfected juvenile crabs would be produced per year. In turn, the number of uninfected susceptible crabs would diminish, resulting in a subsequent decrease in the parasite population. This, in tandem with the high levels of reproduction achieved by *B. regalis*, could result in a boom-bust dynamic in both the crab and parasite population (Blower and Roughgarden 1987). Evidence for such a pattern comes from reports of king crab populations infected by rhizocephalans, where prevalence ranges from 1% to 76% (McMullen and Yoshihara 1970; Sloan 1984; Hawkes et al. 1986; Selin

1998). At times when there is a high parasite prevalence, the added mortality to the breeding population from fishery harvest – even at low levels – could be detrimental, leading to a crash in the *P. californiensis* population. Monitoring parasite prevalence thus is warranted to inform development of suitable management strategies.

In addition to the effects of castration, the stunted growth of *P. californiensis* caused by *B. regalis* infection suggests that the overall biomass and age-size structure of the crab population may also be affected. As a result of the parasitic castrator's presence, the energetic burden affects not only the individual hosts that support the parasite but also extends to the entire host population. Castrated individuals continue to consume valuable resources to meet both their own and the parasite's energetic needs—resources that, in a resource-limited environment, would otherwise contribute to crab reproduction or growth (Lafferty 1991; Lafferty and Kuris 2009). In populations with high parasite prevalence, resource consumption by castrated crabs may significantly reduce the availability of resources for uninfected crabs, potentially decreasing growth and reproduction in the uninfected population as well. In a fishery, such decreased growth and reproduction would translate to decreased fishery yield. Furthermore, because infected crabs grow at a slower rate than do uninfected individuals, they transition from lower to upper size classes at a slower rate, resulting in a buildup of infected crabs in the lower size classes of the population. This shift in population age-size structure would be challenging for stock managers to predict, absent data on parasite prevalence and growth impacts.

To mitigate the negative effects posed by *B. regalis*, biologically and ecologically informed fishery management strategies are critically needed to ensure population and fishery stability. In some places, commercial crab harvesting practices include returning parasitized specimens to the sea, considering them commercially unsuitable. This practice shelters the population of infected crabs from fishing mortality, while consequently further burdening the uninfected breeding population (Kuris and Lafferty 1992; Shukalyuk et al. 2005). Others have suggested that a practical effective approach may be to harvest infected crabs and then destroy or sell them where marketable, given there is no human health concern posed by the rhizocephalan (Sloan 1984, 1985; Kuris and Lafferty 1992; Shukalyuk et al. 2005). The current experimental *P. californiensis* fishery is primarily regulated through a minimum size limit, requiring crabs smaller than 127 mm CW to be returned to the sea regardless of infection status. As a result, infected crabs below this size limit avoid fishing mortality. Due to their reduced growth rates, they also remain unharvestable for a longer period than do uninfected crab. During this time, as the infected crabs remain in the population and slowly grow to legal harvestable size, the rhizocephalan externa is able to spawn about 65 times, producing nearly 800 million larval offspring on a female host (or about 300 million, if attached to a male host). Facilitating retention of infected and castrated crabs through a minimum size limit management strategy inadvertently perpetuates infections and depletes resources for the uninfected population. Continuing use of a size limit is needed to protect the upcoming class of breeding crab but adjusting it to exclude infected juveniles may prove beneficial for reducing and maintaining a low prevalence of rhizocephalan infections in the crab population.

Hoggarth (1990) describes how the rhizocephalan externa could also be removed from infected juveniles when encountered, thereby terminating the infection, with the altered crabs being returned to the sea. Upon investigating this strategy in *P. granulosa* infected by *B. callosus*, Hoggarth (1990) observed that following externa removal, female *P. granulosa* remained unable to reproduce but exhibited accelerated growth rates, surpassing those of uninfected females. This phenomenon likely occurs because the host energy previously used by the parasite is redirected into host growth, as reproduction cannot be restored. This is akin to the effects of parasite-induced gigantism (Pearre 1976; Gorbushin 1997; Ebert et al. 2004; Hall et al. 2007). Male *P. granulosa* resumed normal male growth rates after termination of the infection. Although the altered crabs cannot contribute reproductively to the population, they are able to grow to legal size and become part of the fishable biomass. As is the case for removing undersized parasitized crabs, this practice would likely reduce the prevalence of the parasite by limiting its reproductive capacity. Both strategies, however, rely on the ability to identify parasitized crabs while offshore and, in one instance, requires the additional step of removing the externa. This raises concerns about feasibility due to the extra effort and time required to do so under the often challenging shipboard conditions.

This study sheds light on the host-parasite relationship through a dynamic energy budget framework, but the underlying mechanisms of the energetic relationship remain undefined. Future research exploring the comparative energetic costs of maintenance, growth, and reproduction would improve understanding about the flow of energy from host to parasite. Additionally, long-term tagging and recapture studies of both infected and uninfected *P. californiensis* are needed to confirm our conclusions about stunted growth of infected crab in nature and provide valuable insights into potential impacts on host longevity, a factor that has not been thoroughly explored in lithodid crabs. Further, the heightened reproductive success of *B. regalis* infecting female hosts suggests an evolutionary advantage to preferentially infecting female crabs. Investigating rhizocephalan prevalence and pheromonal attraction across host sexes may reveal a preference for female hosts among rhizocephalan larvae. If confirmed, management strategies encouraging the harvest of parasitized females below harvest size could offer additional benefits. Beyond this, the findings of this study could inform commercial fishery assessment models, such as ecosystem management strategy evaluations (MSEs), to assess the impact of this host-parasite relationship on a population-level and evaluate the effectiveness of the proposed management strategies (Punt 2017).

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