Thesis Proposal: Modeling Crustacean Morphometric Maturity

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Welcome

Here will be a description of the book.

1 Introduction

1.1 Summary

Accurate estimates of size at maturity are crucial for the effective management of marine crustaceans, which represent the most valuable group of wild-capture fisheries by landed mass. Size at maturity values often influence the establishment of minimum landing sizes and represent crucial inputs in widely-used stock assessment models. For many crustaceans, size at maturity can be observed through changes in the relative size and growth of the chelae (males) or abdomen (females), referred to as a transition to morphometric maturity. Morphometric maturity is often a better indicator of functional maturity (i.e., the ability to successfully mate and produce offspring) than physiological maturity, which generally must be determined through gonad dissection or similarly invasive methods. Over the past century, various methods have been developed to estimate size at morphometric maturity for hundreds of crustacean species across the globe. Despite their widespread use, there has been limited research comparing the accuracy of these methods, and many researchers are unaware of more recently developed approaches to modeling size at maturity using morphometric data. My proposed thesis will address these gaps by comprehensively evaluating all documented approaches to modeling size at morphometric maturity and developing tools to facilitate the adoption of sound quantitative methods by fisheries scientists and managers.

1.2 Proposed Structure

I propose that my dissertation will contain at least five chapters, organized under three main headings: synthesis research (literature reviews and meta-analyses), quantitative methods (simulation testing and R package development), and applications to specific crustacean species (Table 1.1).

My proposed chapters are thematically connected and build upon one another in a natural progression. Chapter 1 will focus on identifying the modeling approaches (e.g., various types of piecewise regression and clustering) used to estimate size at maturity and will examine the context in which they are applied and the conclusions drawn from the given application. Chapter 2 will use the comprehensive dataset compiled in Chapter 1 to identify how changes in morphometry may be correlated with the life history traits, ecological niches, and evolutionary trajectories of different crustacean species. Chapter 3 will use simulation testing to evaluate

Table 1.1: Proposed structure of PhD dissertation

Heading	Chapter	Title
Synthesis	Ch. 1	A systematic review of the use of morphometric data to determine c
Synthesis	Ch. 2	Ecological and evolutionary drivers of changes in crab (Brachyura) a
Quantitative methods	Ch. 3	A guide to determining crustacean size at maturity from morphomet
Quantitative methods	Ch. 4	morphmat: An R package to Model Size at Maturity Using Morphor
Applications	Ch. 5	Modeling spatial variation in Jonah crab size at maturity
Applications	Ch. 6	TBD additional collaborations/applications. May be research output

Table 1.2: Example extensions/applications of the topics discussed in the main chapters.

Topic	Potential collab
Identifying regenerating chelae when analyzing crustacean morphometrics	Jason Goldstei
Climate impacts on size at morphometric maturity for Atlantic crustacean fisheries	Kathy Mills, M
Informing Jonah crab and American lobster population models and stock assessments	Miguel Barajas
Morphometric vs. physiological maturity of the Chesapeake Bay blue crab	Zach Olsen (Te

the performance of the models identified in Chapter 1 when applied to artificial datasets with known size at maturity values. The simulation testing will allow me to determine how accurately each model can recover the true parameters when presented with realistic challenges like small sample sizes, underrepresentation of smaller individuals, and high variability/error in the data.

Chapter 4 describes an open-source R package I am developing that will contain easy-to-implement functions for researchers to implement the modeling approaches identified and tested in the previous chapters. Finally, the Applications section will demonstrate the value of this research by using the best practices I identify in Chapter 3 to model size at maturity for specific crustacean species. At a minimum, this will include a chapter modeling spatial variation in Jonah crab (*Cancer borealis*) size at maturity, illustrating how the workflows discussed under the Quantitative Methods heading can be extended to incorporate spatially-structured or time series data. However, I have identified numerous potential avenues to apply this work in collaboration with external researchers (Table 1.2), and undoubtedly more will arise over the course of my graduate studies.

1.3 Morphometric Size at Maturity - Background

1.3.1 Types of Maturity

1.3.2 Types of Allometric Growth in Crustaceans

1.4 Importance of size at maturity for management

1.4.1 Minimum harvest size

1.4.2 Stock assessment & model inputs

1.4.3 Accounting for spatial structure

1.4.4 Effects of harvesting

1.4.5 Climate

References

2 Systematic Review

2.1 Introduction

The first step of the project will be to conduct a literature review to identify all modeling approaches used to estimate crustacean size at maturity using morphometric data. Special focus will be placed on understanding the methodologies of studies that have investigated regional/spatial variation in size at maturity. I will aim to follow current best practices for ensuring transparency and reproducibility in ecological systematic reviews and meta-analyses (Foo et al. 2021; O'Dea et al. 2021; Kambouris et al. 2024; Gates 2002).

2.2 Completed work

2.2.1 Formulate initial question and identify inclusion/exclusion criteria

- What methods have previously been used to model crustacean size at maturity based on morphometric data?
- How have previous studies represented spatial variation in size at maturity within a given species?
- How accurate and precise are these methods?

Since the focus of this review does not fit well into the PICO framework, I have used the SPIDER framework to organize the key components of the research question (Methley et al. 2014) (Table 2.1).

Table 2.1: Inclusion criteria in the SPIDER framework.

letter	word	description
S	Sample	Crustacean species
PI	Phenomenon of Interest	Identifying size at sexual maturity based on changes in a morphomet
D	Design	Measured at least two morphological features, then used a computati
E	Evaluation	A numerical estimate of SM50 or conclusion about the utility of morp
R	Research Type	Quantitative

Exclusion criteria:

- Studies that did not attempt to estimate size at maturity or identify maturity-related changes in allometric growth

  - Studies that used existing size cutoffs (e.g., 30mm CW) or discriminant functions for classification

- Studies that only estimate size at gonadal/sexual maturity (no morphometric ratios considered)
- Studies that focused on a non-crustacean species
- Studies written in a language other than English

2.2.2 Execute search

To identify the most appropriate citation databases to use for this review, I consulted several studies comparing the academic search systems commonly used for evidence synthesis (Visser, Eck, and Waltman 2021; Haddaway et al. 2015; Martín-Martín et al. 2021; Gusenbauer 2019; Gusenbauer and Haddaway 2020). Based on the overlap between the databases recommended for use by these studies and the databases to which I have institutional access, I decided to use Scopus, JSTOR, and ProQuest. Although the merits of Google Scholar as a tool for systematic reviews may be somewhat contentious (Boeker, Vach, and Motschall 2013; Giustini and Boulos 2013), it contains many records that are not found in other databases and is a powerful tool to find grey literature and increase the coverage of multi-database searches (Haddaway et al. 2015; Gusenbauer 2019; Martín-Martín et al. 2021). I only included the first 500 results out of 686 returned from Google Scholar (the first 25 pages). This is beyond the threshold of 50-100 results included by many systematic reviewers (Haddaway et al. 2015), and results beyond that appeared to have low relevance to the focal question. I also searched the NOAA Institutional Repository, another excellent source of grey literature, and did preliminary searches of Github and Zenodo to identify code/software developed for size at maturity modeling. Additionally, many additional relevant sources were identified through snowball searching and while reading scientific articles and management documents (e.g., stock assessment reports) (Table 2.2).

For Google Scholar, the search query used was: intitle:(("maturity" AND "size") AND ("crab" OR "Crustacea" OR "Decapoda" OR "Brachyura")). The query used for all other databases was: (morpho* AND "maturity" AND "size") AND ("crab" OR "Crustacea" OR "Decapoda" OR "Brachyura"). The search string was tested with a preliminary Scopus search to ensure that it could find two articles that were highly relevant to the project: Olsen and Stevens (2020) and Lawrence et al. (2021).

Duplicates were first removed using the duplicate merging feature in the reference manager software Zotero. A second round of duplicate screening was conducted using the online systematic review software Rayyan, which was then used for the initial screening of titles and abstracts. In some cases, the full text was briefly skimmed to resolve uncertainties about

Table 2.2: Databases used for systematic review

Database	# of results	Search field	Notes
JSTOR	33	Abstracts only	
Scopus	332	Abstract, title, keywords	
ProQuest	49	Anywhere but full text	ProQuest One Academic (in
Google Scholar	500	Title	Excluded results that were a
NOAA Institutional Repository	392	Everything	
Snowball & other	139	NA	Sources found in the referen

whether the study should be included that resulted from absent or ambiguous descriptions in the abstract of the method of determining size at maturity. The primary reason for exclusion was that the study determined physiological or functional maturity rather than morphometric maturity (Waiho et al. 2017). Another common category of excluded studies were those using morphometric analysis for a purpose other than determining size at maturity, such as to distinguish two species, compare populations within a species, or identify the biological effects of an external variable like temperature or predation. At least 70 studies were focused on the general morphology and/or size at maturity of a non-crustacean organism, particularly skates, rays, and marine snails.

A small number of studies were excluded because they were written in a language other than English. Although not considering non-English studies can introduce bias into systematic reviews, some authors have found excluding non-English papers has a minimal effect on the overall conclusions of evidence syntheses (Vickers et al. 1998; Nussbaumer-Streit et al. 2020; Jüni et al. 2002). Additionally, one of the major arguments against excluding non-English studies is that it skews the geographical provenance of the body of evidence under consideration towards Europe and North America (Walpole 2019). The >500 English studies retained for future screening represented a wide geographic distribution, and nearly all non-English studies were conducted in a region already represented by multiple English studies.

References

3 Simulation Testing

Testing a proposed model against simulated data generated from a known underlying process is an important but sometimes overlooked step in ecological research (Austin et al. 2006; Lotterhos, Fitzpatrick, and Blackmon 2022). In fisheries science, simulation testing is commonly used to evaluate stock assessment and population dynamic models and assess their robustness to various types of error (Deroba et al. 2015; Piner et al. 2011).

Before applying the size-at-maturity estimation procedures identified through the systematic review to real data, I will create multiple simulated datasets with differing characteristics in order to determine the domains of applicability and inference of each model. The domain of applicability refers to the types of datasets to which a model can reliably be applied, while the domain of inference is defined as the processes or conclusions that can be inferred from the model output (Lotterhos, Fitzpatrick, and Blackmon 2022). The methodology for this chapter will be heavily influenced by the principles for ecological simulation testing outlined by Lotterhos et al. (2022) and the guidelines for computational method benchmarking developed by Weber et al. (2019) (See Box 1).

References

Box 1: Computational benchmarking guidelines

num	guide
1	Define the purpose and the scope of the benchmark.
2	Include all relevant methods.
3	Select (or design) appropriate datasets.
4	Choose appropriate parameter values and software versions.
5	Evaluate methods according to key quantitative performance metrics.
6	Evaluate secondary metrics including computational requirements, user-friendliness, installation
7	Interpret results and provide recommendations from both user and method developer perspectiv
8	Publish results in an accessible format.
9	Design the benchmark to include future extensions.
10	Follow reproducible research best practices, by making code and data publicly available.

4 `morphmat`

R has become a foundational tool for quantitative fisheries research, with specialized packages such as `FSA`, `ggFishPlots`, and `ss3sim` enhancing the functionality of base R and more generalized packages to provide fisheries scientists with an ever-growing toolbox for data analysis and visualization. I will create an open-source R package, `morphmat`, which will allow fisheries scientists and managers to implement the multitude of modeling approaches identified through my synthesis research. The package will include user-friendly functions for estimating size at morphometric maturity, along with guidelines for choosing the optimal method for a given dataset and correctly interpreting results. Both novel and historically popular (e.g., broken-stick regression) methods will be included, and users will be able to obtain SM50 estimates from over a dozen different approaches with a single function call. Crucially, by combining code for the various models within a single package, `morphmat` will represent the first software tool enabling the application of multi-model inference to SM50 estimation, avoiding the arbitrary selection of a single "best" model (Katsanevakis 2006; Grueber et al. 2011) By increasing the accessibility of modern statistical methods for estimating SM50, I hope to facilitate the widespread adoption of improved SM50 modeling procedures.

I will follow the best practices for package development described by Wickham and Bryan (2023), including comprehensive function documentation with illustrative examples, informative package metadata, and automated (unit) testing (Wickham 2011). I will also refer to the FAIR Principles for Research Software (FAIR4RS Principles) when developing and sharing `morphmat`. In addition to submitting `morphmat` to the Comprehensive R Archive Network (CRAN), I will ensure that `morphmat` meets the rOpenSci guidelines for inclusion in their suite of packages. I plan on submitting morphmat to rOpenSci for software peer review, during which two reviewers will provide feedback on the quality, documentation, and clarity of the package.
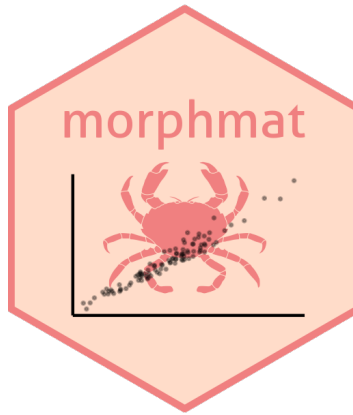
Figure 4.1: Hex sticker logo for the R package "morphmat"

In addition to receiving useful feedback from experienced developers, submitting a package to rOpenSci will allow me to receive support with ongoing maintenance issues such as those associated with updates to R, dependencies, and CRAN policies, as well as promotion of the package on various social media platforms (Anderson et al. 2024). Finally, acceptance into the rOpenSci repository generally results in a fast-tracked review process for accompanying manuscripts submitted to the *Journal of Open Source Software.*

In conjunction with vignettes included in the package and articles hosted on the `morphmat` website (built using `pkgdown`), having a published manuscript describing `morphmat` will maximize the potential for widespread adoption by fisheries scientists and other biologists interested in size at maturity determination. I also hope that `morphmat` could be included in more domain-specific repositories, such as the NOAA Fisheries Integrated Toolbox or the fishR collection of packages, which would provide additional exposure to potential users who could benefit from these tools.

References

5 Ecological & Evolutionary Applications

Using changes in the relative growth of the claws or abdomen as a sign of the onset of sexual maturity is complicated by the multitude of ecological and evolutionary factors that work together to shape crustacean claw and abdomen morphology. This section will focus on the ecological and evolutionary context of crustacean morphometric maturity.

5.1 Morphometric Maturity: When and Why?

Although changes in morphometry have been successfully linked to sexual maturity and used to estimate SM50 in many crustacean species, other studies have found no distinct changes in claw or abdomen growth rates at maturity.

- Does the importance of morphometric maturity follow taxonomic patterns (i.e., is it true that morphometric maturity is not useful for the genus *Chaceon*)?
- Why is allometric growth a useful indicator of maturity for some crustacean taxa but not others? Are there crustacean taxa where these types of morphometric maturity analyses are not justified as a way to estimate functional maturity for management purposes?
- Are there correlations between the life history traits of a species and the presence or magnitude of changes in the relative growth of secondary sexual characteristics? Similarly, how much can be assumed about a species' size at morphometric maturity based on the patterns observed in species that are closely related, fill similar ecological niches, or have similar life history characteristics/functional traits?

    - "It was concluded that there was little correlation between growth format and phylogenetic level… Gross ecological habit similarly failed to produce any general correlation with growth format" (Hartnoll 2001). Will this hold for the much larger body of research included in my systematic review?

This line of inquiry has management implications because it can inform how resources are allocated when researchers are attempting to estimate SM50 for a new species. If it seems unlikely that the onset of maturity for males of the species will exhibit discontinuous growth of the chelae, it may not be an efficient use of time and money to measure the chelae of thousands of individuals.

Other questions and hypotheses that may be addressed include:

- Which factors influence the timing of the transition to morphometric maturity relative to the transition to physiological maturity?
- Under what circumstances can morphometric maturity be considered to be equivalent to functional maturity?
- Investigate possible correlations between the presence of (1) heterochely and (2) a terminal molt and the timing and severity of changes in allometric growth that occur at morphometric maturity.
- Are Portunid crabs less likely to show significant positive allometry for chela growth because of the potential for interfering with swimming ability/is there evidence for an evolutionary constraint on chela size in Portunid crabs? (Daniels 2001; Abelló, Pertierra, and Reid 1990)
- Effects of rhizocephalan parasitization on morphometric size at maturity (Narvarte et al. 2007)

There are many interesting opportunities for comparative phylogenetics surrounding this topic. For example, carapace morphometrics have been used to identify morphological convergence events within the family of primarily symbiotic pea crabs (Pinnotheridae) (Hultgren, Foxx, and Palacios Theil 2022; Gier et al. 2023). Initial analyses of carapace aspect ratio (AR, the ratio of carapace width to carapace length) found that correlations between carapace AR and host identity remained even after statistically accounting for phylogeny, indicating repeated evolution to specific host associations across the extensive pea crab phylogenetic tree(Hultgren, Foxx, and Palacios Theil 2022). This idea has been corroborated by later research linking phylogenetic position and preferred host phyla to landmark-based carapace morphology (Gier et al. 2023) Along with earlier work on pea crab ecomorphology (Gier and Becker 2020), these studies illustrate how integrating morphological, ecological, and molecular data can reveal strong evolutionary patterns within a subset of Crustacea.

5.2 Claws

5.2.1 Feeding & movement

Diet-induced plasticity

There is a large body of evidence that differences in diet-related exercise can affect claw size and shape within the lifespan of an individual crab as well as between individuals and populations. Changes in claw morphology are associated with ontogenetic shifts in diet for both marine and freshwater crabs (Lim, Yong, and Christy 2016; Viozzi et al. 2021). Smith and Palmer (1994) found significant differences in claw size and performance between *C. productus* individuals raised on experimental diets of varying levels of toughness, concluding that claw morphology is affected by differential use. Analogous results have been found for green crabs (*C. maenas*) raised on a diet of winkles (hard prey) compared to a diet of soft fish flesh (Abby-Kalio and Warner 1984).

Reasons for differences between species/population chela size or shape

- Diet consists of different prey species: crabs with larger chelae can consume a wider size range of hard-bodied prey items and can thus exploit a wider spectrum of prey species (Lee and Seed 1992)

- Diet consists of the same prey species, but there are population differences in prey morphology (e.g., a high correlation between *C. maenas* crusher claw size and *L. obtusata* shell mass) (Edgell and Rochette 2008)

- Geographic differentiation was only observable in the *C. maenas* crusher claw, not the cutter claw, and occurred in both sexes, indicating a trophic function (Smith 2004)

- Differences in food availability (e.g., food resource concentrations, foraging opportunities) influence the energy available for claw growth (McLain and Pratt 2010)

5.2.2 Sexual selection

Aggression/intrasexual competition

In some species, it appears that claw morphology has evolved for effectiveness in male-male competition rather than selection by female mating preferences (Callander et al. 2013). Responses of male *C. maenas* to conspecific male competitors were strongly influenced by relative chela size, while body size had a comparatively weak effect (Lee and Seed 1992). The role of cheliped size in decisions to initiate contests and in determining the outcome of those contests has also been demonstrated across a number of hermit crab species (Yasuda and Koga 2016; Yoshino, Koga, and Oki 2011). In fact, examples of the importance of claw morphology in intrasexual competition can be found in essentially all branches of the crustacean phylogenetic tree. The arched morphology of squat lobster chelae appears to have evolved to inflict puncture wounds on opponents during agonistic interactions (Claverie and Smith 2007). Crayfish with experimentally impaired chelae were displaced from optimal shelter locations by unimpaired conspecifics (Levenbach and Hazlett 1996). Chela development and differentiation has been especially well-studied for the American lobster (*Homarus americanus*). As early as 1935, Templeman noted that the outcome of a physical contest between two male lobsters of similar shell hardness was generally determined by the size of their large chelae (Templeman 1935).

However, this phenomenon is by no means universal: for example, the dotillid crab *Scopimera globosa* does not use its chelae to grasp or strike during male-male combat, instead predominantly using its walking legs during wrestling matches (Ida and Wada 2017). Accordingly, Ida and Wada (2017) found that leg length had a significant impact on *S. globosa* fighting success, but carapace width and chela length did not.

Mating/copulation/signaling to females

- Males in mating pairs of *C. maenas* had significantly larger chelae than the total male population (Lee and Seed 1992).

5.2.3 Physiological constraints

- Mechanical advantage does not always decline with increasing claw length (Taylor 2001; Dennenmoser and Christy 2013). The optimal claw shape for signaling females is in opposition to the optimal shape for fighting, like the sexual selection vs. locomotion conflict, but Dennenmoser and Christy (2013) found that claw physiology and male fighting tactics compensate for the selective pressure for effective signals such that the claw remains a potent weapon (Allen and Levinton 2007; Dennenmoser and Christy 2013). However, muscle stress (force per unit area) generally declines with increasing claw size, leading Taylor (2001) to suggest that the positive allometric shifts in claw size observed in male decapod crustaceans may be needed to compensate for the declining muscle stress in order to maintain a constant force output per unit body size.

- **Energetic and lomotion-related costs + increased predation risk:** for example, treadmill endurance capacity was significantly lower for fiddler crabs with intact claws compared to those without (Allen and Levinton 2007). Fiddler crab sprint velocity was shown to increase following autonomy when running on a flat surface (Martin 2019). Coevolution of leg morphology may help mitigate such locomotor and energetic costs of bearing enlarged chelae, as demonstrated by Bywater et al. (2018) in a genus-wide study of fiddler crabs. In other crustaceans, lactate levels (an indicator of fatigue) were positively related to cheliped size in the hermit crab *Pagurus bernhardus* (Doake, Scantlebury, and Elwood 2010). Swimming speed was negatively correlated with chela size for the crayfish *Cherax dispar* (Wilson et al. 2009).

5.2.4 Abiotic & other

- Habitat/substrate type (Marochi, Masunari, and Schubart 2017; McLain and Pratt 2010)

- Temperature differences

  - There is evidence that the major claw serves a thermoregulatory function for the fiddler crab and may allow them to occupy a broader range of thermal niches (Darnell, Munguia, and Benkman 2011; De Grande, Fogo, and Costa 2021).

- Cannibalism (Dutil et al. 2000)

- Harvest-induced evolution was observed in the European lobster (*Homarus gammarus*) as a result of the selective pressure against large chelae exerted by the fishery (Tonje K. Sørdalen et al. 2018). However, in a follow-up study, Sørdalen et al. (2020) showed that marine protected areas (MPAs) may partially restore trait loss, with males inside MPAs possessing larger claws than similarly-sized males in nearby fished areas.

- Seasonal variation (Yasuda et al. 2017)

6 Species Applications

Jonah crab, lobster, etc.

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