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# A practical identification guide to the zoeae of the invasive European green crab, *Carcinus maenas* (Linnaeus, 1758) (Decapoda: Brachyura: Carcinidae), and to the zoeae of the families of brachyuran crabs in Washington state, USA

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## ABSTRACT

Although the brachyuran crab *Carcinus maenas* (Linnaeus, 1758) is a globally invasive species, early-life history information for its larvae, such as hatch timing, stage duration, dispersal, and behavior, is limited, particularly in newly invaded locations. This is, in part, due to the need for region-specific guides on larval taxonomy that incorporate *C. maenas*. We addressed this issue for Washington state marine waters by developing a dichotomous key for the zoeae of *C. maenas* and a matrix that compares the morphological characters of *C. maenas* zoeae to those of brachyuran crab families reported from the state. To assess whether morphological characters of *C. maenas* from this region reflect taxonomic descriptions from the species' native range, we reared zoeae from females collected in Washington state. We found that zoeae from each crab family reported from Washington state have at least two characters that distinguish them from *C. maenas* zoeae: the presence of lateral carapace spines in most of these families, and for three families lacking lateral carapace spines (Epialtidae, Grapsidae, Pinnotheridae) antennae that are nearly equal to the length of the rostral spine, the presence of posterolateral extensions on any of the somites, or a laterally expanded last somite, respectively. Rearing of larvae showed that the rostral spines of the Washington zoeae I of *C. maenas* were ~ 0.06 mm longer than reported in the literature. We also found that late-stage zoeae may retain more furcal spines than previously reported. The region-specific taxonomic tools we developed allow easier and quicker identification of *C. maenas* zoeae in Washington. These descriptions should facilitate early detection in newly invaded bays, a more rapid understanding of *C. maenas* larval timing and behavior, and better evaluation of larval dispersal that can be used in risk-assessment tools.

**KEY WORDS:** Crustacea, dichotomous keys, plankton

## INTRODUCTION

*Carcinus maenas* (European green crab) is considered one of the worst global invaders, having expanded from its native range in Europe and northern Africa to all other continents except Antarctica (Behrens Yamada, 2001; Carlton & Cohen, 2003; Grosholz *et al*., 2011). Inadvertent introduction through increased human activities and movements (Carlton & Cohen, 2003), as well as climactic events (Behrens Yamada *et al*., 2005) have transported *C. maenas* larvae to new areas. On the west coast of North America, *C. maenas* was first detected in San Fransico Bay, California in 1989, and the species quickly spread northward, reaching Coos Bay, Oregon in 1997 and Willapa Bay and Grays Harbor, Washington (herein WA) in 1998 (Carlton & Cohen, 2003; Weihrauch & McGaw, 2023). The species was found further north in British Columbia, Canada in 1999, but was absent in the Washington portion of the Salish Sea (herein WA Salish Sea) until 2016. While *C. maenas* has been present along Washington's outer coast for almost two decades, the species is still a new invader to the WA Salish Sea (Fig. 1).

In the WA Salish Sea, the specific impacts of *C. maenas* to natural resources such as eelgrass, native crab species, and aquaculture remain unknown. Areas on the west coast of North America that have been invaded by *C. maenas* for a long enough time to have established populations, however, have documented impacts to natural resources. The aggressive behavior of *C. maenas* and its ability to adapt to new environments have greatly impacted native flora and fauna (Grosholz *et al*., 2000; Behrens Yamada, 2001). For example, McDonald *et al*. (2001) showed

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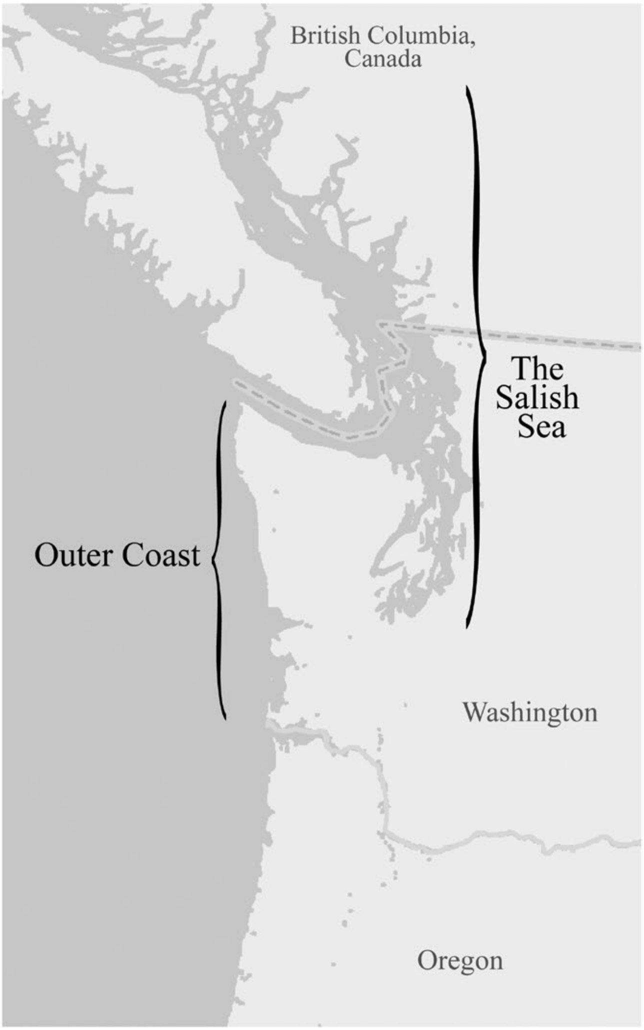

**Figure 1.** In the context of the European green crab, the marine waters of Washington state, USA are differentiated as "outer coast" and "WA Salish Sea" since the initial invasions to each area were separated by almost two decades and population dynamics differ between the two areas.

that *C. maenas* outcompeted the brachyuran crab *Metacarcinus magister* (Dana, 1852) of similar size for habitat structure like shell cover. *Metacarcinus magister* is a culturally and commercially important native crab in Washington. Howard *et al.* (2019) confirmed the loss of eelgrass due to mechanical disruption by *C. maenas* in British Columbia, and Grosholz *et al.* (2011) estimated a potential annual loss of commercially harvested bivalves in WA state that equates to US $28,100–$53,400.

*Carcinus maenas,* like all brachyuran crabs, have planktonic larvae, with larval duration lasting 43–83 d (deRivera *et al.*, 2007). The larval development of *C. maenas* consists of one protozoea, four zoeas, and one megalopa, and it is through the zoeal stages that most dispersal takes place. Larval behavior such as vertical migration to exploit tidal exchange in and out of estuaries (Banas *et al.*, 2009; Behrens Yamada & Kosro, 2010; DiBacco & Therriault, 2015) and larval dispersal in general facilitate the establishment of populations in new areas.

Larval behavior has also been found to vary geographically in *C. maenas* (DiBacco & Therriault, 2015). In the species southern native range (Rio de Aveiro, Portugal), larvae use selective tidal stream transport (STST) to develop outside of the bays and estuaries where they hatched (Queiroga *et al.* 1994; DiBacco & Therriault, 2015). Queiroga *et al.* (2002) suggest larvae in Gullmarsfjord, Sweden, a small microtidal fjord, use light intensity as an indicator that currents are changing, allowing them to exploit these currents to exit and enter the fjord. In Pipestem Inlet, British Columbia, part of the non-native range, larvae responded to salinity, which drives circulation in the estuary, allowing them to exit and re-enter the estuary (DiBacco & Therriault, 2015).

While primary invasions have typically been due to human-assisted transport of adults, secondary invasions along the west coast of the United States have often been due to dispersal of larvae via currents and local hydrodynamics, and through human-assisted mechanisms such as transport of larvae or adults in ballast water and packing material (Carlton & Cohen, 2003; Behrens Yamada & Kosro, 2010; McLay, 2015; Weihrauch & McGaw, 2023). Both primary and secondary invasions may go undetected until a significant number of adult crabs are present.

The larvae of *C. maenas* provide another means of detection, particularly if coupled with existing zooplankton sampling efforts. Crab larvae, however, are difficult to identify, requiring expert zooplankton taxonomists. This situation can cause a bottleneck in gathering information needed to understand the life history and dispersal of *C. maenas* during a developing invasion. It is therefore important to have identification resources designed with non-experts in mind. By increasing the number of specialists able to identify *C. maenas* larvae, information about *C. maenas* behavior, timing, and dispersal, can be acquired in a timely manner, which can be important to the management of the species.

Identification guides for the crab larvae of the west coast of North America are not specific to WA and do not include all species found in this area, which may lead to confusion and misidentification (e.g., Puls, 2001; Rice & Tsukimura, 2007). It is therefore necessary to use a combination of the available guides and the original larval descriptions for species not included in these guides for better comparisons. Terminology and inclusion of structures for larval descriptions has historically been inconsistent.

Descriptions of larval morphology for *C. maenas* exist only for larvae of the species' native range (see Rice & Ingle, 1975) despite its expansive spatial and environmental distribution. The existing guides and keys for the identification of larvae from the west coast of North America are based on *C. maenas* from its native range regardless of the potential differences in new environmental conditions, particularly taking into consideration the plasticity of larval morphology. For example, Shirley *et al.* (1987) found that the spine lengths of the zoeae of *Metacarcinus magister* changed with latitude along western North America.

The objectives of our study were to 1) review the literature for the zoeae of brachyuran crab species found in WA's marine waters and synthesize taxonomic information into a practical format for the quick identification of *C. maenas* zoeae, and 2) rear *C. maenas* zoeae from WA and compare their morphology in this non-native range with that from its native range.

## MATERIALS AND METHODS

### Literature review

A review of the description of the larvae was completed for all the brachyuran species (including *C. maenas*) on the Padilla Bay

**Table 1.** Species of brachyuran crabs found in marine waters of Washington state, USA, and references for descriptions of morphological characters of species studied herein. Current and potential invasive species are also included. Species not included due to lack of morphological descriptions: *Chionoecetes angulatus* (Rathbun, 1924)*, Chorilia longipes* (Dana, 1851[Dana, 1851b])*, Oregonia bifurca* (Rathbun, 1902)*, Pinnixa eburna* (Wells, 1928), *Pinnotheres pugettensis* (Holmes, 1900), *Romaleon branneri* (Rathbun, 1926), *R. jordani* (Rathbun, 1900), *Scleroplax littoralis* (Holmes, 1895).

| **Family** | **Species** | **Source** |
|---|---|---|
| Calappidae | *Platymera gaudichaudii* (Milne Edwards, 1837) | Gallardo & Mujica (2010) |
| Cancridae | *Cancer gracilis* (Dana, 1852) | Ally (1975), Lough (1975), Puls (2001), Rice & Tsukimura (2007) |
| | *C. productus* (Randall, 1840) | Rice & Tsukimura (2007), Sorochan *et al.* (2015), Trask (1970) |
| | *Glebocarcinus oregonensis* (Dana, 1852) | Puls (2001), Sorochan *et al.* (2015) |
| | *Metacarcinus magister* (Dana, 1852) | Lee & Ko (2014), Lough (1975), Poole (1966), Puls (2001), Rice & Tsukimura (2007) |
| | *Romaleon antennarium* (Stimpson, 1856) | Rice & Tsukimura (2007), Roesijadi (1976) |
| Carcinidae | *Carcinus maenas* (Linnaeus, 1758) | Rice & Ingle (1975), herein |
| Cheiragonidae | *Telmessus cheiragonus* (Tilesius, 1815) | Ko (2006), Korn *et al.* (2010) |
| Epialtidae | *Pugettia foliata* (Stimpson, 1860) | S.G. Morgan, unpublished data |
| | *P. gracilis* (Dana, 1851 [Dana, 1851b]) | Oh & Ko (2007); S.G. Morgan, unpublished data |
| | *P. producta* (Randall, 1840) | Bashevkin *et al.* (2020); S.G. Morgan, unpublished data |
| | *P. richii* | S.G. Morgan, unpublished data |
| | *Scyra acutifrons* (Dana, 1851[Dana, 1851b]) | Oh & Ko (2010b) |
| Grapsidae | *Planes cyaneus* (Dana, 1851 [Dana, 1851b]) | Konishi & Minagawa (1990) |
| | *P. marinus* (Rathbun, 1914) | Wear (1970) |
| Oregoniidae | *Chionoecetes bairdi* (Rathbun, 1924) | Haynes (1973), Haynes (1981) |
| | *C. tanneri* (Rathbun, 1893) | Hong *et al.* (2009) |
| | *Oregonia gracilis* (Dana, 1851 [Dana, 1851b]) | Lough (1975), Oh & Ko (2010a) |
| Panopeidae | *Lophopanopeus bellus bellus* (Stimpson, 1860) | Hart (1935), Puls (2001) |
| | *L. bellus diegensis* (Stimpson, 1860) | Knudsen (1958), Puls (2001) |
| | *Rhithropanopeus harrisii* (Gould, 1841) | Connolly (1925), Hood (1962) |
| Pinnotheridae | *Fabia subquadrata* (Dana, 1851[Dana, 1851a]) | Lough (1975) |
| | *Pinnotheres taylori* (Rathbun, 1918) | Hart (1935) |
| | *Scleroplax faba* (Dana, 1851 [Dana, 1851a]) | S.G. Morgan, unpublished data |
| | *S. granulata* (Rathbun, 1894) | S.G. Morgan, unpublished data |
| | *S. schmitti* (Rathbun, 1918) | S.G. Morgan, unpublished data |
| | *S. tubicola* (Holmes, 1895) | S.G. Morgan, unpublished data |
| Varunidae | *Eriocheir sinensis* (Milne Edwards, 1853) | Kim & Hwang (1995), Montú *et al.* (1996) |
| | *Hemigrapsus nudus* (Dana, 1851 [Dana, 1851a]) | Hart (1935), Lee & Ko (2008) |
| | *H. oregonensis* (Dana, 1851 [Dana, 1851a]) | Hart (1935), Lee & Ko (2008) |

National Estuarine Research Reserve species list (located in the WA Salish Sea), other species whose zoeae might be swept into the WA Salish Sea, and other invasive species of interest (*Eriocheir sinensis* (Milne Edwards, 1853), *Rhithropanopeus harrisii* (Gould, 1841)) currently found on the western coast of North America but not yet in the WA Salish Sea (Table 1). Species names follow the World Register of Marine Species (WoRMS, 2024) listings. Seven species without published larval descriptions but that could be found in WA Salish Sea were not included in this study (see Table 1).

Nomenclature for morphological characters suggested by Clark *et al.* (1998) and Clark & Cuesta (2015) were used. The list of morphological characters and measurements was not intended to be a comprehensive list of all characters as it was intended as an identification guide for non-specialists. Not included were features that could not be seen with a dissecting microscope (56× magnification), require dissection, or are not easily discernable (with a few notable exceptions). Some features such as the distribution and arrangement of spinules on spines and the number of furcal spines are included even though they may be hard to observe on small-size species.

The morphological characters for each species in Table 1 were compiled into a detailed matrix table. This full-length matrix was then simplified to focus on distinguishing *C. maenas* zoeae from other brachyuran crab families. Characters that were the same for *C. maenas* and the other families were not used. Although some characters change throughout the successive zoeal stages, the characters that distinguished *C. maenas* from the other species were consistent across all stages with the exception of the number of furcal spines, and length of rostral spine compared to antenna. In addition to lengths, the number of natatory setae, somites, and spines on the inner margin of the furca increase through development, while other characters (like the pleopods and pereiopods) are absent in the first stage but appear in later stages; however, none of these characters were needed for distinguishing *C. maenas* from other WA species. Only measurements of the zoea I (i.e., first zoea or stage 1 zoea) were used to represent the size range for all the species within a family (Table 2) as only this stage was described in many of the species.

A full larval description, including all the characters in Table 2 could not be found in the literature. Full descriptions of the larvae of only *Fabia subquadrata* (Dana, 1851a) and *Pinnotheres taylori* (Rathbun, 1918) (Pinnotheridae) have been published, while partial information for the other species of Pinnotheridae was provided by S. Morgan (personal communication). Conversely, the larvae of some species were described by multiple authors. In this case discrepancies in morphological characters between authors were noted except for *F. subquadrata*, the larvae of which were described by Lough (1975), Irvine & Coffin (1960), and Hong & Park (2017). In this case, only the information provided by Lough (1975) was included in the matrix, because of the potential misidentification of the female reared by the other authors as noted by Lough (1975).

Most characters were conserved across the species within a family, but all options for a character were provided. For example, only some species of Oregoniidae have a spinulate telson. There are, however, several other characters that distinguish Oregoniidae from *C. maenas*. Since there are multiple conservative characters for each family that distinguish it from *C. maenas* at any stage, it was not necessary to include the descriptions of zoeae for each stage.

We developed a dichotomous key to distinguish zoeae of *C. maenas* from zoeae of other families. We first determined the most distinguishing characteristic between *C. maenas* zoeae and those of the other families to eliminate as many families from the key as possible. Further distinguishing characters were added to the key to allow identification of *C. maenas*. The key was only designed to distinguish *C. maenas* from all other brachyuran families, therefore, it is not possible to identify zoeae of other brachyuran families using this key.

### Comparison of the morphology of *C. maenas* zoeae from WA to those in the native range

Two ovigerous *C. maenas* females (49 mm and 53 mm carapace width) collected in baited traps from Bay Center, Willapa Bay, WA (46.629 N, 123.960 W) were held in separate 2.5-l tanks until eggs began hatching. Larvae were collected and reared individually in 20-ml scintillation vials or temporarily held in aerated 1-liter flasks as batch cultures. Filtered seawater (0.2 µm filter) with salinity of 28–29.5 psu and a constant temperature of 15 °C was maintained in both setups. This temperature was used to be consistent with methods in Rice & Ingle (1975), which facilitated comparison of morphological characters described by them. The larvae were fed 24-h old *Artemia* nauplii to excess, and photoperiod (12 h light: 12 h dark) was regulated with automatic timers. Larvae were checked for mortality, exuviae, and moved to vials with clean seawater and food daily. Dead larvae from the individually reared vials were replaced with a larva of the same stage from the batch cultures to ensure enough zoeae from each of the four zoeal stages could be observed and measured. Neither antibiotics nor antifungals were used to treat the water. A total of 10 larvae from each of the four zoeal stages were used for morphological descriptions and measurements. The larvae were preserved in 10% buffered formalin and all descriptions and measurements were made from these preserved specimens.

We measured morphological characters of these *C. maenas* zoeae for comparison with the descriptions by Rice & Ingle (1975). We measured carapace length, tip of rostral spine to tip of dorsal spine, and rostral-spine length with an SZX7 microscope (Olympus, Tokyo) under 8–56× total magnification, 10MP OptixCam camera and Toupeview software (ToupTek Photonics, Zhejiang, China). We also measured the tip of the rostral spine to the tip of the telson, as this is a common measurement found in other zoeal descriptions, although not measured by Rice & Ingle (1975). Because the furcal spines of *C. maenas* are challenging to see with lower magnification, an Accu-scope microscope (ACCU-SCOPE, Commak, NY, USA) with 100–400× magnification, Excelis HD 6 MP camera, and CaptaVision software (ACCU-SCOPE) were used for observation. Comparative measurements were considered different if minimum and maximum values from each zoeal source did not overlap.

## RESULTS

### Literature review

A total of 36 species of brachyuran crabs could potentially be encountered in plankton tows undertaken in the WA Salish Sea. Two additional non-native species were included because of the potential northward spread to WA (*Eriocheir sinensis, Rhithropanopeus harrisii*). *Carcinus maenas* is the only species in Carcinidae found in WA (Table 2). Calappidae and Cheiragonidae are each represented by only one species in WA, *Playtmera gaudichaudii* (Milne Edwards, 1837) and *Telmessus cheiragonus* (Tilesius, 1815), respectively. All other families have multiple species.

Variations in measurements and other characters were found among species of some of the families (Table 2). For example, the zoeae of *Chionocetes bairdi* (Rathbun, 1924) (Oregoniidae) have a carapace length of 0.54 mm (Haynes, 1973), whereas those of *C. tanneri* (Rathbun, 1893) and *Oregonia gracilis* (Dana, 1851 [Dana, 1851b]) have carapace lengths of 1.29 mm (Hong *et al.* 2009) and 0.95 mm (Oh & Ko, 2010a), respectively. *Scyra acutifrons* (Dana, 1851 [Dana, 1851b]) (Epialtidae) have spinulate dorsal spines but those of *Pugettia* spp. in the same family do not.

The main diagnostic character of *C. maenas* zoeae is the absence of lateral carapace spines (Fig 2A, Table 2). Epialtidae, Grapsidae, and one species of Pinnotheridae, however, also lack lateral carapace spines, these zoeae have other characters that distinguish them from *C. maenas* zoeae. The zoeae of Epialtidae can be distinguished from *C. maenas* because the rostral spines are equal to or shorter than their antennae, but are longer than their antennae in *C. maenas*. The last somite of all Pinnotheridae zoeae is laterally expanded, but are all of the same width in *C. maenas*. The zoeae of Grapsidae have posterolateral extensions on the somites 3–5 but are absent in *C. maenas* (Fig. 2B, bottom arrow).

### KEY TO THE WASHINGTON STATE ZOEA

| | |
|---|---|
| 1a. Lateral carapace spines present | not *C. maenas* |
| 1b. Later carapace spines absent | 2 |
| 2a. Rostral spine length ≤ to antenna length or unknown | not *C. maenas* |
| 2b. Rostral spine length > antenna length | 3 |
| 3a. Last somite laterally expanded | not *C. maenas* |
| 3b. Last somite with same width as other somites | 4 |
| 4a. Posterolateral extensions on somites present | not *C. maenas* |
| 4b. Posterolateral extensions on somites absent | *C. maenas* |

Because specimens and lateral spines may be damaged in collection and processing, additional characters are available to confirm identification. The zoeae belonging to families other than Carcinidae have at least two characters as well as size differences that distinguish them from *C. maenas* zoeae (Table 2).

The zoeae of another invasive species, *R. harrisii* (Panopeidae) are easily distinguished from other zoeae, including those of *C. maenas*, because of their unusually long antennae, which are almost as long as the combined length of their carapace and abdomen (Hood, 1962). Other zoeae, especially in Oregoniidae, also have long antennae, but their antennae are shorter than the combined lengths of the carapace and abdomen. The zoeae of the invasive *E. sinensis* (Varunidae) are small and can be distinguished from and the zoeae of *C. maenas* by the presence of dorsolateral processes on somite 4 (Kim & Hwang, 1995; Montú *et al.*, 1996).

### Morphological comparison of *C. maenas* zoeae from WA to its native range

Rearing confirmed the morphology of *C. maenas* at all zoeal stages as described in Rice & Ingle (1975) with two exceptions. We found that the mean rostral spine length of zoeae I was 0.06 mm (Table 3), longer than reported by Rice & Ingle (1975). A second difference is that Rice & Ingle (1975) described each furca as having a large dorsomedial spine, a small dorsomedial spine, and a thin lateral spine, and that the smaller dorsomedial spine and lateral spine may be reduced or completely absent in zoeae II–IV; however, we observed three spines on at least one furca (Fig. 2C) in numerous zoeae belonging to the three stages. Because the size and number of the furcal spines is not consistent in these later stages, additional distinguishing characters and measurements should be used to confirm the identification of late-stage *C. maenas* zoeae. There were no differences between measurements provided by Rice & Ingle (1975) and ours (Table 3) for carapace length, the distance between the tip of the rostral spine and the dorsal spine, and the length of the dorsal spine.

## DISCUSSION

### Literature review

Morphological traits that distinguished the zoeae of *C. maenas* from those of the 30 species studied were conserved to the family level. It is possible that zoeae of the eight species that lacked descriptions of larvae would also have these features conserved to the family level, resulting in minimal impact on the matrix that we developed.

### Morphological comparison of *C. maenas* zoeae from WA to those in its native range

The morphological characters and measurements of the WA *C. maenas* zoeae were consistent with those reported in zoeae I–IV by Rice & Ingle (1975) with two exceptions (see above). Although these differences do not interfere with the identification of the zoeae I, other characters may be used to distinguish late stage zoeae. It is important to notice that differences may be due to artifacts of the microscopic examination (see Clark *et al.*, 1998; Clark & Cuesta, 2015), morphological plasticity expressed with environmental shifts (Shirley *et al.*, 1987), or changes in morphology due to shifts in population genetics. Natural variation of specimens is more likely to lead to discrepancies between authors and even different zoeae observed by one author. For example, Sorochan *et al.* (2015) noted that a single zoea III of *Glebocarcinus oregonensis* (Dana, 1852) had two lateral furcal spines on one side instead of one, a variation observed in zoeae I collected in the field (NB, personal observation).

Environmental conditions such as temperature can cause phenotypic shifts such as the spine and body lengths of decapod larvae. Shirley *et al.* (1987) reported that the length of the rostral, dorsal, and lateral carapace spine of *Metacarcinus magister* increased with decreasing temperature. These differences in spine length in addition to body lengths were found in field-collected zoeae as well as in those reared in the laboratory at different temperatures. Shirley *et al.* (1987) suggests this might be due to temperature-regulated allometric growth and may aid in predation avoidance. The temperatures experienced by the gravid females collected by Rice & Ingle (1975), and those we collected in Willapa Bay, WA are unknown. Methods for rearing the larvae in both studies, however, used 15 °C. Further studies need to be done to determine if different temperatures during rearing could contribute to phenotypic differences in rostral spine length and retention of furca spines or if there is another cause for the morphological variation.

Changing population genetics may be another source of observed morphological differences in larvae. Darling *et al.* (2008)

**Table 2.** Morphological characteristics of the zoeae of *Carcinus maenas* and for families of species listed in Table 1. Characters are consistent throughout zoeal stages except those noted (*) and lengths are ranges for zoea I. Bold indicates a character that differs from *C. maenas*. Morphological features not described in the literature were recorded as "unknown;" †, conflicting references.

| | ***Carcinus maenas*** | **Calappidae** | **Cancridae** | **Cheiragonidae** | **Epialtidae** | **Grapsidae** | **Oregoniidae** | **Panopeidae** | **Pinnotheridae** | **Varunidae** |
|---|---|---|---|---|---|---|---|---|---|---|
| Carapace length (mm) | 0.55$^*$ | unk | unknown | 0.84$^*$ | 0.71–0.9$^*$ | 0.54*, unknown | 0.54–1.29$^*$ | 0.49, unknown | 0.45–0.72$^*$ | 0.43–0.64$^*$ |
| Tip of rostral spines to tip of telson distance (mm) | 2.07$^*$ | unknown | 1.8–2.64$^*$ | unknown | unknown | 1.14–1.25* | 4.0–5.15$^*$ | unknown | unknown | unknown |
| Tip of rostral spines to tip of dorsal spine distance (mm) | 1.52$^*$ | 1.7* | 1.12–2.1$^*$ | 2.44$^*$ | 1.48–2.0$^*$ | 0.87, unknown | 3.5–5.73$^*$ | 1.5–2.2$^*$ | 1.0–1.5$^*$ | 1.02–1.3$^*$ |
| Rostral spine spinulate | No | **Yes** | No | **Yes** | No | No | **Yes** | No | unknown | **Yes** |
| Dorsal spine spinulate | No | No | No | **Yes** | No, **Yes** | No | **Yes** | No | unknown | **Yes** |
| Antennae spinulate | Yes | Yes | Yes | Yes | Yes | Yes | Yes | **No** | Yes, unknown | Yes |
| Rostral spine length compared to antenna | > | ≥ | > | ≥ | <, = | =, unknown | ≥ | ≤$^*$, = | unknown | > |
| Lateral spines on carapace | No | **Yes** | **Yes** | **Yes** | No | No | **Yes** | **Yes** | **Yes**, No | **Yes** |
| Somites with dorsolateral processes (somite no.) | 2 | **2, 3** | 2 | 2 | 2 | **2, 3; 2–4** | **2, 3** | 2; **2, 3** | **2, 3; 2–4**, unknown | **2; 2, 3; 2–4** |
| Somites with posterolateral extensions (somite no.) | 0 | **3–5** | **1–5; 2–5; 3–5**$^\dagger$ | **3–5** | **3–5** | **3–5** | **3–5** | 0 | 0, unknown | 0, **2–5th** |
| Number of dorsal spines on each furca | 2$^*$ | **0** | **1** | **1** | **0**, unknown | 2 | 1, 2$^\dagger$ | **1** | unknown | **0** |
| Number of lateral spines on each furca | 1$^*$ | **2** | 1 | **2** | 1 | **0** | 1 | **0, 2**$^*$ | unknown | **0** |
| Spines on furca spinulate | No | No | No | unknown | **Yes**, No †, unknown | No | **Yes**, No | unknown | unknown | unknown |
| Telson spinulate | No | No | No | unknown | **Yes**, unknown | Yes, No | **Yes**, No | No, unknown | **Yes**, unknown | **Yes** |
| Lateral expansion of last somite | No | No | No | No | No | No | No | No | **Yes** | No |

showed that adult *C. maenas* from the west coast of North America are genetically similar to those on the east coast populations, both of which have genetically diverged from the initial native source populations in Europe. Isolated populations of *C. maenas* on the west coast of North American may, however, become genetically distinct over time. Further studies to describe the larval morphologies of genetically distinct adult populations should be pursued to understand the implications for larval identification.

## Future research and management applications

Current management efforts of *C. maenas* focus on the adult phase of the crab's life history. It is important, however, to include the larval stages in management efforts. Objective 2.2 of the management plan for the European green crab in the US (Grosholz & Thom, 2023) states the need to "expand the development and use of new tools for early detection and population monitoring," which includes early larval stages. The plan notes the challenge of such investigations because of the difficulty in identifying these stages among other species of crabs.

The management of *C. maenas* can benefit from further research to understand 1) larval hatch timing, stage duration, and behavior to inform larval dispersal models; 2) the relationship between larval abundance and adult population dynamics such as the amount of time from larval stages to young-of-the-year sizes and the relationship between larval abundance and adult abundance, and 3) timing and settlement behaviors of

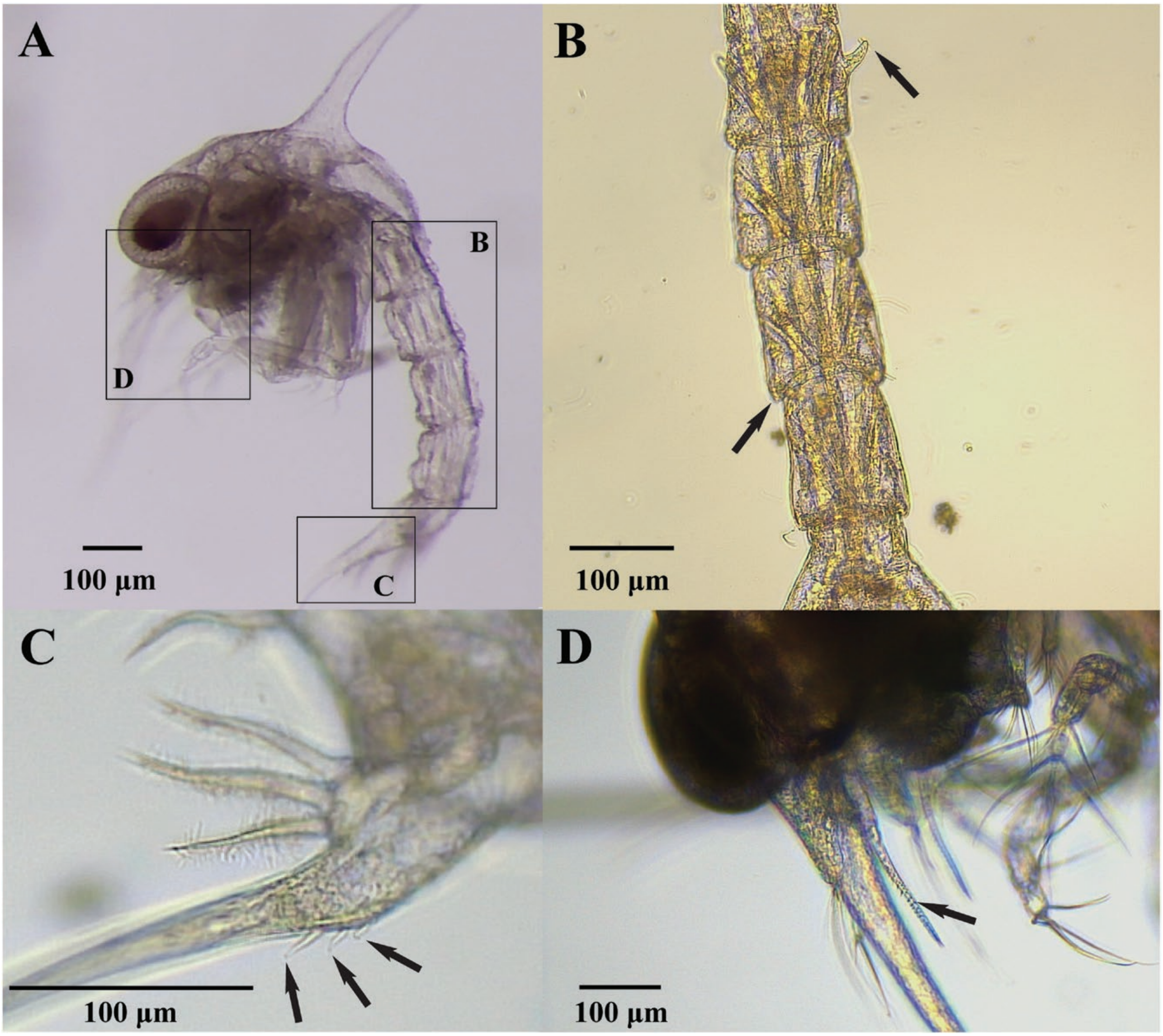

**Figure 2.** Lateral view of the zoea I of *Carcinus maenas* (**A**) reared from females collected in Willapa Bay, WA, with panels B–D showing the dorsolateral processes on the second somite (top arrow, dorsal view), rounded posterolateral margins (bottom arrow, not posterolateral extensions) (**B**), all three furcal spines (**C**), smooth rostral spine, and spinulate antenna (**D**). Magnification: under 40× (A) and 100× (B-D).

megalopae. Such studies could be used to parameterize larval dispersal models for WA and the Salish Sea (Banas *et al.*, 2009; Brasseale *et al.*, 2019; Du *et al.* 2024), which currently rely on best-available information from other locations.

Larval abundances have the potential of indicating adult population dynamics once quantitative relationships between larval and adult abundances are investigated. The identification resources developed in our study are for the zoeal stages, but the megalopa stage is a crucial stage as well. Dispersal is mainly attributed to the zoeal stages while the megalopa is an indicator of settlement. The ability to quickly identify *C. maenas* megalopae would aid in the understanding of larval mortality, final destinations of dispersal, and provide another link in the connection between zoeal and adult abundances.

With improved models and an understanding of how larval abundances impact adult populations, managers can plan for capacity and resources needed for adult trapping efforts (i.e. increase the number of traps, target young-of-the-year crabs, direct resources to specific areas). The practical identification guide produced by our study aims to provide a foundation for pursuing such investigations.

Identification of zooplankton is traditionally reserved to specialized investigators because of the time, effort, and complications of identifying crab zoeae to species. Increasing the number of researchers who can identify *C. maenas* zoeae in field samples could provide important information on this invasive species in newly invaded areas. Early detection efforts, risk assessment, and broadening our understanding of *C. maenas* with local larval information will provide more tools that can aid in the management of this invasive species.

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**Table 3.** Measurements (in mm) of zoeae of *Carcinus maenas* reared from females obtained from Willapa Bay, Washington state (WA) and as reported in Rice & Ingle (1975).

| | | **Zoea I** | | **Zoea II** | | **Zoea III** | | **Zoea IV** | |
|---|---|---|---|---|---|---|---|---|---|
| | | **WA** | **Rice & Ingle** | **WA** | **Rice & Ingle** | **WA** | **Rice & Ingle** | **WA** | **Rice & Ingle** |
| Carapace length | Mean | 0.53 | 0.50 | 0.63 | 0.67 | 0.76 | 0.82 | 0.94 | 1.06 |
| | Range | 0.49–0.57 | 0.47–0.53 | 0.55–0.75 | 0.60–0.70 | 0.71–0.88 | 0.79–0.85 | 0.83–1.08 | 1.02–1.06 |
| Tip of rostral spine to tip of dorsal spine distance | Mean | 1.52 | 1.38 | 1.72 | 1.75 | 2.07 | 2.14 | 2.56 | 2.37 |
| | Range | 1.44–1.61 | 1.36–1.44 | 1.60–1.95 | 1.58–1.85 | 1.93–2.35 | 2.13–2.15 | 2.20–2.77 | 2.20–2.50 |
| Rostral spine length | Mean | 0.55 | 0.49 | 0.59 | 0.58 | 0.74 | 0.73 | 0.92 | 0.77 |
| | Range | 0.52–0.58 | 0.46–0.51 | 0.47–0.67 | 0.52–0.65 | 0.65–0.79 | 0.70–0.80 | 0.81–0.99 | 0.74–0.83 |
| Dorsal spine length | Mean | 0.55 | 0.55 | 0.61 | 0.67 | 0.77 | 0.82 | 0.90 | 0.86 |
| | Range | 0.46–0.62 | 0.53–0.57 | 0.43–0.66 | 0.55–0.70 | 0.70–0.87 | 0.80–0.85 | 0.77–1.00 | 0.81–0.91 |
| Tip of rostral spine to tip of telson distance | Mean | 2.07 | NA | 2.39 | NA | 2.99 | NA | 3.70 | NA |
| | Range | 1.98–2.16 | NA | 2.13–2.66 | NA | 2.56–3.40 | NA | 2.95–4.27 | NA |
| | *N* | 10 | 10 | 10 | 8 | 10 | 3 | 10 | 5 |

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