Can the timing and duration of planktonic larval development contribute to invasion success? A case study comparing range expansion in the European green crab, *Carcinus maenas*, and the native lined shore crab, *Pachygrapsus crassipes*, in the northeast Pacific

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Abstract Major El Niño events and oceanic heat waves are linked to the range expansion of many marine species. For the shores of the northeast Pacific, we compared range expansion in the European green crab, *Carcinus maenas*, which was introduced to San Francisco Bay prior to 1990, to that of the native lined-shore crab, *Pachygrapsus crassipes*. The initial northern range limit of these species was central California and southern Oregon, respectively. Both species increased their northern range along the open coast to northern Oregon, Washington and Vancouver Island after strong El Niño events. *C. maenas*, however, in just a matter of decades, successfully established populations in estuaries from Oregon to inlets on the west coast of Vancouver Island, and possibly also in the Salish Sea, while *P. crassipes*, never has in recorded history. We hypothesize that this difference in invasion success is due to the shorter larval duration of *C. maenas*, < 2 months, compared to that of *P. crassipes*, 3–4 months and timing of larval release, winter for both species. Because the residency times of water in the inlets of the west coast of Vancouver Island are typically 1–2 months, they can act as incubators for the larvae of *C. maenas*, while those of *P. crassipes* are likely flushed out to the open sea before they can complete their development. We propose that the life history of a species coupled with the hydrodynamic setting in which its pelagic larvae develop contribute to the success of range expansion.

Keywords Range expansion · Larval duration · El Niño · Davidson Current · *Pachygrapsus crassipes* · *Carcinus maenas* · Northeast Pacific

Introduction

Inter-annual variations in ocean temperature and circulation have profound effects on the California Current coastal ecosystem. Strong El Niño events are typically coincident with the northern range expansions of invertebrate and fish species (Pearcy and Schoener 1987; Sanford et al. 2019). For example,
during strong El Niño events when larvae drift north from source populations in California, the mole crab, *Emerita analoga*, establishes ephemeral populations on the west coast of Vancouver Island and as far north as Kodiak Island, Alaska (Hart 1982; Pearcy and Schoener 1987; Wonham and Hart 2018). These populations persist for a few years and then die off due to senescence of the adults coupled with limited larval recruitment. Populations are re-established during the next incursion of larvae from the south.

Here, we consult the literature to compare range shifts, similar to that of the mole crab, in the introduced European green crab, *Carcinus maenas*, and the native lined shore crab, *Pachygrapsus crassipes*. We advance the hypothesis that life history traits of the adults, and larval ecology and behavior play a major role in determining the success of establishing self-maintaining populations of these two crab species beyond their previous (*C. maenas*) and historic (*P. crassipes*) limit. We begin by reviewing the literature on the range expansion and life history of these crabs, including the temperature requirements for mating and egg development, the timing and duration of larval release, the pelagic larval duration (PLD) and larval vertical migratory behaviour. The unique set of life history traits determines the waters in which the larvae of a species may survive and develop, and it is these waters that transport them to new locations. We summarize the water properties of the larval habitat, including temperature, prevailing currents along the entire Pacific coast from Southern California to Alaska, and flushing characteristics of the fjords on the west coast of Vancouver Island and the inland Salish Sea (Figs. 1, 2). While many publications focus on regional water properties and currents patterns, this study is the first one to integrate them for the entire coast. From these characteristics, we predict whether either, or both, species are likely to establish permanent, self-sustaining populations within these fjords and the Salish Sea.

**Range expansions**

*Carcinus maenas*, a native of the eastern Atlantic coast, from North Africa to northern Norway, is a successful global invader of temperate shores. Expatriate populations are now established on the east and west coasts of North America, Australia, South Africa, and in Argentina (Say 1817; Fulton and Grant 1900; Le Roux et al. 1990; Grosholz and Ruiz 1995; Hidalgo et al. 2005). Because *C. maenas* is tolerant of air exposure and wide ranges in temperature and salinity, it is able to survive ocean voyages and even plane rides (Cohen et al. 1995). Once released into a new environment, this ecological generalist can subsist on a variety of food organisms, including marsh vegetation, algae, crustaceans, mollusks, worms and fish (Cohen et al. 1995).

*C. maenas* was introduced into San Francisco Bay from the east coast of North America, most likely via seafood products or baitworms (Fig. 1. Cohen et al. 2001). When scientists confirmed the presence of *C. maenas* around 1990, they discovered a self-maintaining population, including gravid females and individuals with a range of sizes, indicating multiple recruitment events. From San Francisco Bay, the species expectedly spread both northward and southward as larvae carried in the prevailing ocean currents (Table 1; Behrens Yamada et al. 2005, 2015; Behrens Yamada and Kosro 2010). Elkhorn Slough, 100 km to the south of San Francisco Bay, is the site of the most southern *C. maenas* population (Grosholz et al. 2011). Major northward range expansions followed strong El Niño events: to Oregon, Washington, and the west coast of Vancouver Island, British Columbia (1997–1998) and through the Strait of Juan de Fuca into the Salish Sea (2015–2016) (Behrens Yamada et al. 2017; Grason et al. 2018; Brasseale et al. 2019). The year-round buoyancy-driven Vancouver Island Coastal Current (Thomson et al. 1989; Hickey et al. 1991; Foreman et al. 2000) likely facilitated the northern range expansion to the inlets on the west coast of Vancouver Island, extending from Barkley Sound (1998) in the south to Quatsino Sound (2004) in the north (Gillespie et al. 2015). The arrival of *C. maenas* to the central mainland coast of British Columbia around Bella Bella (prior to 2010) and Haida Gwaii (2020) was predicted from ocean current models for El Niño and non-El Niño years (Therriault et al. 2008).

*Pachygrapsus crassipes* is a common native of the upper intertidal zones from southern Oregon to Baja California (Fig. 1). It lives in rock crevices and tidepools on the open coast, under rocks and boulders, and inside marsh bank burrows (Morris et al. 1980). Student reports from Oregon indicate that *P. crassipes* was abundant in both the protected and open coast
around Coos Bay in 1928–1930 and at Boiler Bay in 1950 (Table 1, Queen 1930, Dale Snow, pers. com.). Both Hiatt (1948) and Ricketts et al. (1968) give Newport as its northern distribution (Table 1). Abundance at Newport is linked to El Niño events, suggesting that this population is dependent on a southern
larval source (Boulding et al. 2020). Between 1982 and 1992, *P. crassipes* was discovered by researchers at Ecola State Park in northern Oregon (Jensen 1995) and northern Washington at Tatoosh and Ozette (Ladd Johnson and Jeff Goddard, pers.com.). Subsequent systematic surveys by Boulding et al. (2020) and Armand Kuris (pers.com.), and coincidental observations by Andrew McCurdy, and the Royal British Columbia Museum document the presence of *P. crassipes* in Barkley Sound after the 1997–1998 El Niño and at Ucluelet, Tofino, Nootka Sound and the Washington side of the Strait of Juan de Fuca after the 2015–2016 El Niño (Table 1, Appendix S2).

Life histories

In Oregon, *C. maenas* is sexually mature at less than a year at around 34 mm in carapace width (Table 2).

Longevity is estimated to be 6 years and maximum size is ~100 mm for males and 89 mm for females (Behrens Yamada et al. 2005; Kelley et al. 2015). Ovigerous *C. maenas* in Oregon, Washington and British Columbia are found in structured habitats, primarily during the winter and spring (DiBacco and Therriault 2015; Chelsey Buffington, pers. com.). First instar zoea were sampled in Coos Bay, Oregon in January, February and March 2010 (Shanks et al. 2011), but no later stage zoea were present, suggesting that larvae had been exported to the outer coastal ocean where development took place. In contrast, all zoea stages were present in samples from Pipestem Inlet, in Barkley Sound, on the west coast of Vancouver Island, from March to December 2000 (DiBacco and Therriault 2015). Total development time in the plankton is ~2 months at 12 °C and ~1 month at 18 °C (Dawirs 1985; deRivera et al. 2007). Late
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Megalopae rise to the surface and are carried by an incoming (flood) tide back into an estuary, where they settle and molt into juvenile crabs (Zeng and Naylor 1996). The observation that the Pipestem population of *C. maenas* remained abundant to the present (Graham Gillespie, pers. com.), suggests that the larval pelagic development likely occurs in the waters within the Inlet, or close to its mouth. Between the two major two El Niño events of 1997–1998 and 2015–2016, *C. maenas* populations in Oregon and Washington were extremely rare and could not have acted as larval sources for Pipestem Inlet (Behrens Yamada et al. 2021b).

In California, *P. crassipes* mature within a year with a 12–15 mm carapace width and attain a carapace width of 42 mm for females and 48 mm for males in 3 or 4 years (Hiatt 1948; Jensen 2014). The reproductive season is long. Ovigerous *P. crassipes*

### Table 1

| Estimated Year of first arrival | *Carcinus maenas* | ° N Lat | Ref | Estimated Year of first arrival | *Pachygrapsus crassipes* | ° N Lat | References |
|-------------------------------|------------------|--------|-----|-------------------------------|--------------------------|--------|------------|
| *< 1990* San Francisco Bay, CA | 37.8°             | 1      |     | *< 1930* Coos Bay, OR and open coast | 43.3°                  | [9]    |            |
| 1993 Humboldt Bay, CA         | 40.7°             | 2      |     | *< 1947* Newport, OR           | 44.6°                  | [10]   |            |
| 1995–1996 Coos Bay, OR       | 43.5°             | 3      |     | *< 1950* Boiler Bay, OR        | 44.8°                  | [11]   |            |
| 1997–1998* Oregon, Washington | 48.8°             | 4,5    |     | 1982–1983* Ecola State Park, OR | 45.9°                  | [12]   |            |
| 1999 Nootka Sound, BC        | 49.8°             | 5      |     | 1982–1983* Tatoosh Island, WA  | 48.4°                  | [13]   |            |
| 2004 or 2005 Quatsino Sound, BC | 50.5°           | 6      |     | 1991–1992* Ozette, WA          | 48.1°                  | [14]   |            |
| ~ 2010 Bella Bella area, BC  | 52.1°             | 7      |     | 1997–1998* Barkley Sound, BC  | 48.8°                  | [15]   |            |
| 2015–2016* Central Salish Sea, WA | 48.6°        | 7      |     | 2015–2016* Ucluelet            | 48.9°                  | [16]   |            |
| 2020 Queen Charlotte City, Haida Gwaii, BC | 53.2°         | 8      |     | 2015–2016* Cox Point near Tofino, BC | 49.1°                  | [17]   |            |
| 2015–2016* Nootka Sound, BC | 49.8°             | 7      |     | 2015–2016* Strait of Juan de Fuca, Neah Bay, and Shipwreck Point, WA | 48.4°                  | [18]   |            |

### Table 2

| Trait                      | *Carcinus maenas* | *Pachygrapsus crassipes* |
|----------------------------|------------------|--------------------------|
| Sexual maturity            | < 1 year at 34 mm CW | “within a year” at 12–15 mm CW |
| Longevity                  | 6 years          | 3–4 years                |
| Maximum size               | Male: 100 mm CW  | Female: 89 mm CW         |
|                           | Female: 99 mm CW | Female: 42 mm CW         |
| Mating temperature         | > 15 °C (Nicky Fletcher, unpublished data) | Unknown |
| Larval development time at different temperatures | *Ca* 60 days at 12 °C | 115 days for zoea stages at 16 °C |
|                           | *Ca* 30 days at 18 °C | 68–108 days for zoea stages at 20–22 °C |
| Pelagic larval duration (PLD) | *Ca*. 1–2 months | *Ca*. 3–4 months |
occur from March to November (9 months) and their planktonic larvae are found year-round (Hiatt 1948; Schlotterbeck 1976; Shanks 2006). At the southern end of the California Bight (San Diego, Fig. 1), megalopae were caught nearly year-round, with peak abundance in the fall/winter and very low abundance in the late spring and summer (Shanks 1985). When the five zoea stages were reared in the lab, development time was 115 days at 16 °C and 68–108 days at 20–22 °C (Schlotterbeck 1976; DiBacco 2001). Thus, pelagic larval duration is estimated to be around 3–4 months (Lough 1975). Megalopae have been caught in light traps in Coos Bay, Oregon during winter and up to the time of spring transition. Numbers were highest (70–90 per day) during the 1986/87 and 2015/2016 strong El Niño events, whereas during non-El Niño years few or none were caught (Fig. 3 in Boulding et al. 2020). This pattern suggests that the warmer water temperatures and stronger northward surface currents associated with El Niño events are favorable for the survival and northward alongshore transport of these larvae (Boulding et al. 2020). Each major sighting of *P. crassipes* north of central Oregon has been linked to a major El Niño event (Table 1, Appendix S2). No studies exist on the temperature limitation for reproduction and larval development for *P. crassipes*, but circumstantial evidence suggests that environmental conditions in the Pacific Northwest can be favorable.

Boulding et al. (2020) found ovigerous females after the 1997/98 and the 2015/2016 strong El Niño events in Barkley Sound on southern Vancouver Island and Greg Jensen (pers. com.) found gravid females at Ozette on the northern Washington coast in July 2019. Lough (1975) sampled early instar zoea off Newport, Oregon. He noted that the first appearance of *P. crassipes* zoea followed a rise in surface water temperature to over 10 °C. In 1970 the first larvae appeared in March, but in 1971, when the winter and spring water temperatures were much colder, they appeared in May.

### Oceanographic features favoring Range Expansion and Establishment

#### Temperature

As noted above, *C. maenas* needs critical water temperatures >10° C for larval survival and development and >15° C for mating behavior. Temperatures of 17–18 °C are typically reached in the inlets and fjords on the west coast of Vancouver Island (DiBacco & Therriault 2015), where *C. maenas* has been well established prior to 2008 (Behrens Yamada and Gillespie 2008). No studies have documented the critical water temperatures for *P. crassipes*, but the presence of gravid females at Ozette, and in Barkley Sound, suggest that temperatures for reproduction can be favorable for this species at these northern locations. It is not known, however, if water temperatures in northern Washington and British Columbia are consistently warm enough for the larvae to complete their ~3–4 month-long planktonic development during non-El Niño years.

#### Currents

In addition to favorable temperatures and favorable currents, mechanisms for larval retention in inlets are needed for northward range expansion and establishment of self-maintaining populations of the two crab species. The prevailing currents in the offshore northeast Pacific are dominated by the clockwise rotating Central Pacific Gyre in the south and the counter-clockwise rotating Alaska Gyre in the north (Fig. 1). Both gyres are driven by the curl of the oceanic wind stress, which switches from negative in the south, where the prevailing winds are dominated by the North Pacific High, to positive in the north, where the prevailing winds are dominated by the Aleutian Low (Thomson 1981). The eastward flowing West Wind Drift (also Subarctic Current), which forms the boundary between the two gyres (centered along the line of zero wind stress curl), bifurcates somewhere between the longitude of Ocean Station P (145° W) and the coast to form the equatorward flowing California Current south of roughly 50° N and the poleward flowing Alaska Current to the north of this location. Weakening of the California Current during major El Niño events or a southward shift in the bifurcation zone due to intensification of the Aleutian...
Low increases northward transport in the offshore region.

**Davidson Current**

The Eastern Boundary Region situated inshore of the southward flowing California Current consists of two seasonally reversing alongshore current systems: (1) The shelf-break flow regime spanning the outer continental shelf and inner slope, and (2) the more regionally determined nearshore flow regime over the inner half of the shelf (Fig. 1.). The prevailing alongshore current that straddles the shelf break (200 m depth contour) from northern California to northern Vancouver Island is poleward in winter, under forcing by the southerly winds of the winter-intensified Aleutian Low in the Gulf of Alaska, and equatorward during summer under forcing by the northerly winds of the strengthened North Pacific High off California. The wintertime northward flow is known as the Davidson Current (Hickey 1979; Hickey et al. 1991), while the southward flow in summer has been termed the Shelf-Break Current (Thomson et al. 1989). The shifts between these two primary seasonal flow patterns are known as the Spring and Fall transitions, respectively. Winds off the west coast between northern California and northern Vancouver Island become upwelling favorable following the Spring transition (roughly mid-April) and downwelling favorable following the Fall transition (roughly mid-October). During major El Niño events, however, the switch from southerly winds in winter to northerly winds in summer is delayed and the northerly winds are generally diminished during the ensuing summer, effectively enhancing northward transport. The enhanced northward flow, reduced upwelling and elevated surface water temperatures during strong El Niño events are principal factors in the northward expansion of both *C. maenas* and *P. crassipes* (Table 1).

**Southern California Bight circulation**

Within the Southern California Bight, a ~700 km long elliptical eddy circulates counter-clockwise between Point Conception and Baja California and is bound by the south-flowing California Current to the west of the Channel Islands and the curved Southern California coastline to the east. Shanks and Eckert (2005) suggest that *P. crassipes*’ long breeding season and larval duration are adaptations for living in this region. Long spawning and long larval durations are shared by a number of fish and benthic crustacean species endemic to the Bight and Baja, but are not typical of benthic crustaceans and fish species endemic to the shelf or nearshore to the north of the California Bight. They suggest that persistent eddies within the Bight and off Baja tend to retain larvae within that system. During winter, the Davidson Current transports some portion of the larvae out of the Bight and north along the coast. During El Niño events, the Davidson Current intensifies and becomes capable of transporting larvae hundreds of kilometers north. For example, after the last three strong El Niño events, *P. crassipes* was found on Tatoosh Island, on the northern open coast of Washington (1982–1983), on Vancouver Island at Bamfield (1997–1998), Ucluelet (2015–2016), Tofino (2015–2016) and Nootka Sound (2015–2016) (Figs. 1 and 2, Table 1, and Appendix S2). While *C. maenas* may be in the process of establishing itself in the Salish Sea (Behrens Yamada et al. 2017; Grason et al. 2018, Grason and Buffington, pers, com.), this is not the case for *P. crassipes*. While this species has been sighted on the open coast of northern Washington since 1983, it has only recently been discovered on the Washington side of the Strait of Juan de Fuca (Fig. 2, Boulding et al. 2020). In May 2018, after the 2015–2016 El Niño, Armand Kuris found *P. crassipes* at two sites: the Neah Bay boat ramp and 10 miles to the east at Shipwreck Point. He noted that *P. crassipes* was common and that more than one year class was present. A variety of fish species typically found associated with kelp beds within the Southern California Bight are also found well north of the Bight during El Niño events as is the mole crab *E. analoga* (Shanks and Eckert 2005; Wonham and Hart 2018). These immigrant populations are ephemeral; the adults survive, but new recruits are too few to maintain these populations and they slowly vanish until the next strong El Niño.

**Vancouver Island Coastal Current**

The prevailing currents along the inner continental shelf off western North America are dominated by coastal alongshore winds and freshwater runoff. Although outflow from the Columbia River can affect the nearshore circulation off Oregon and Washington under southerly wind conditions (Hickey et al.
and also contribute to short-term inflow along the US side of the Strait of Juan de Fuca (Holbrook et al. 1983; Thomson et al. 2007), sustained northward flow does not typically occur during summer months to the south of Vancouver Island. It is off the west coast of Vancouver Island that the hydrodynamic effects of river discharge into the coastal waters may have their greatest impact on northward range expansion of more southern species. Formation of the year-round, buoyancy-driven, surface-intensified northwesterly flowing Vancouver Island Coastal Current (VICC) originates with surface estuarine outflow from the Canadian side of the Strait of Juan de Fuca (Fig. 1; Thomson et al. 1989; Hickey et al. 1991). Due to the Coriolis force, the surface outflow (which is confined to the upper 50–75 m of the water column) is strongest along the Canadian side of Juan de Fuca Strait. Reversals in the estuarine outflow reach maximum speeds on the US side of the strait, again because of Coriolis (the Strait of Juan de Fuca is a "wide strait" in the sense of its internal deformation radius; Thomson et al. 2007). Although the freshwater discharge to the system in spring and summer is typically a factor of 10 times than in fall and winter, the surface outflow from the Strait of Juan de Fuca (and hence the strength of the coastal current) varies by only about 10% over the course of a year (Thomson et al. 2007; Fig. 14). Similarly, interannual changes in the outflow (and coastal current) vary by at most a factor of two and are likely mainly driven by changes in the prevailing winds along the outer coast.

The VICC is confined to the inner shelf at depths of less than about 100 m and, based on decades of current meter observations from sites along the inner shelf (cf. Thomson et al. 2017), the current continues poleward past Brooks Peninsula at the northern end of Vancouver Island at typical speeds of 0.1 to 0.2 m/s. Part of the current appears to recirculate southward within the California Current seaward of the Scott Islands at the northern tip of the island (Fig. 1a), with the remaining remnants of the buoyancy current contributing to northward flow along the mainland (eastern) side of Queen Charlotte Sound. Although the VICC acts as a conduit for nearshore transport, it can also act as a barrier to subsurface cross-shelf transport to the coastal inlets. The VICC may also constrain the cross-shelf dispersal of larvae, such as C. maenas, sourced from the shore. This may tend to retain larvae close to shore and settlement habitats at the coast or within sounds. As shown by Thomson et al. (2020), temporary shutdowns or reversals in the VICC are needed to facilitate subsurface transport of water into the inlets. The speed and direction of the prevailing winds on the outer coast, together with the intensity of the VICC and tidally-induced exchange processes at the mouth of a particular inlet may dictate whether crab larvae enter the inlet or are flushed seaward from the inlet prior to completing their development.

Prevailing circulation within the Salish Sea

Range expansion of crab species into the Salish Sea is restricted by the estuarine flow that normally directs surface waters seaward throughout the year. (Thomson 1981; Sutherland et al. 2011; Khangaonkar et al. 2017; MacCready et al. 2018). Temporary reversals in the estuarine flow in the Strait of Juan de Fuca that connects the outer coast to the Strait of Georgia and Puget Sound typically only occur from late fall to early spring during times of strong southerly winds along the outer coast (Thomson et al. 2007). Thus, warm water intrusions capable of supporting larval development and transport of the two crab species into the inner sectors of the Salish Sea are likely limited to major El Niño events that span the period of fall to spring of the event year (Behrens Yamada et al. 2017). Colder, less hospitable surface waters would be transported toward the inner Salish Sea during non-event years. Within the Strait of Georgia, surface estuarine outflow is especially strong at the southern and northern ends of the strait but estuarine flows are generally weak and confused in the central region. It is in the central region that retention would be more probable, but still highly unlikely.

Within an estuarine environment, the early larval stages of both C. maenas and P. crassipes make tidally timed vertical migrations such that they are transported out of the estuary, that is, they migrate up into surface waters during ebb tide and into deeper water during flood tide (Queiroga et al. 1997; DiBiacco et al. 2001). The Salish Sea is essentially a very large estuary with typical seaward flow at the surface. Hence, the larvae of both species released within the Salish Sea should be transported seaward by the estuarine flow. The long larval PLD of P. crassipes suggests that their larvae would certainly be transported out of the estuary and into the coastal waters where...
coastal currents would transport them potentially for months. In contrast, the much shorter PLD of *C. maenas* means that the larvae may be able to complete their development with the Salish Sea.

**Discussion**

Favorable water temperatures are critical to the northward range expansion and establishment of self-maintaining populations of the two crab species along the west coast of North America. The two additional critical conditions are the formation of the Davidson Current, to transport larvae from established breeding populations in California along the California-Oregon-Washington-British Columbia coast, and mechanisms for the retention of larvae in coastal inlets and the Salish Sea to allow satellite populations to become self-maintaining. During strong El Niño events, *C. maenas* and *P. crassipes* expanded their northern range via larval transport from the south. In their expanded range, crabs survive to adults, produce eggs and release viable zoea larvae. Due to selective tidal stream transport, larvae of both species released within most estuaries are transported to nearshore water for their pelagic development. Megalopae must migrate from coastal waters back to the shore or estuary. Why has *C. maenas* been able to established thriving self-maintaining populations on the west coast of Vancouver Island in just a few decades (Behrens Yamada and Gillespie 2008) after their introduction to San Francisco Bay, while *P. crassipes*, a native species, has not done so? The west coast north of Point Conception and the inland waters of British Columbia and Washington state have been viable habitat for *P. crassipes* since probably the end of the last ice age and we know that permanent populations of this species have not been established since at least the 1930s. We hypothesize that the fact that they have not expanded their range during this time may be related to the timing of their larval release, their long pelagic larval duration, and the circulation system to which the species is adapted.

**Open Coast**

In the Southern California Bight, the pattern of *P. crassipes* megalopal return to the coast (peak returns Sept/Oct through March) suggests that, given a four-month larval development, larval release begins around May and continues through December, e.g., release starts in late spring, continues through summer and fall and ends at the beginning of winter. Larvae released during the spring and summer by an imaginary population of *P. crassipes* on the Oregon coast would, during the 3 to 4 months of larval development, be carried far to the south by the steady flow of the nearshore Shelf-Current and offshore California Current; larvae would not be returned to this imaginary population. Larvae released around the fall transition (roughly mid-October from southern BC to southern Oregon; Thomson et al. 2014) would be carried far to the north by the Davidson Current and these larvae also would not be returned to the parent population. Larvae released in the winter that remained pelagic through the spring transition and the shift from the Davidson to the Shelf-break Current might be returned to this imaginary population, but they would represent only a small proportion of the total reproductive output of the population. We hypothesize that this mismatch between the timing of larval release coupled with the long PLD and the seasonal hydrodynamics within the California Current prevents the establishment of self-sustaining populations of *P. crassipes* on the Pacific Northwest outer coast.

If in the future, El Niño events become more frequent or the Davidson Current becomes stronger, then recruitment of larvae transported northward out the Bight might occur with enough regularity to sustain populations on the open coast outside the Bight. These would, however, likely not be self-sustaining populations as they still may still be dependent on recruits spawned in the Bight, but they could be much less ephemeral than current populations. The Davidson Current occurs each year, hence, there should be annual transport of larvae from the Bight some distance up the outer coast of California. These recruits may sustain populations on the outer coast some distance north of the Bight, i.e., north of Point Conception.

**Retention on the west coast of Vancouver Island**

We hypothesize that the systems of inlets along the west coast of Vancouver Island, stretching from Barkley Sound in the south to Quatsino Sound in the north, are strong candidates for range expansion
of *C. maenas*, but likely not for *P. crassipes*. Some of the inlets and sounds have water residence times long enough that *C. maenas* larvae may be able to complete their development within the water body, but none of them have long enough residence time to maintain the *P. crassipes* larvae with their much longer PLD. Larvae of either species that are exported out onto the continental shelf will be transported by the northward flowing VICC. The PLD for *C. maenas* is short enough that the larvae may complete their pelagic development and migrate back to shore before they are carried north of Vancouver Island by the VICC. The months longer PLD of *P. crassipes* larvae likely would lead to their transport in the VICC to well north of Vancouver Island.

A comprehensive study of flushing times for inlets on the west coast of Vancouver Island is provided by Pawlowicz (2017) for the main channels in Barkley Sound and adjoining Alberni Inlet. Water property time series collected between 2004 and 2013 show that surface waters down to about 30–40 m depth are renewed by river-driven estuarine exchange processes at periods of about a week. The residence time for the upper layers is especially short in winter due to increased river input from rainfall, and is slightly longer in summer when runoff is markedly reduced. The renewal period for intermediate waters between 70 and 130 m depth in the main portion of Barkley Sound-Alberni Inlet region is less than a month, based on the monthly survey interval of the study. Deep waters below 140 m are also renewed at regular intervals through the summer months due to wind-induced upwelling along the outer coast and, even during the “stagnant” period of six to nine months in winter, Pawlowicz (2017) finds that “… the deep water undergoes significant renewal”. Because similar physical processes apply along most of the west coast of Vancouver Island, the flushing rates for other inlets having freshwater inputs at their heads are expected to follow the patterns derived for the main regions of the Barkley Sound-Alberni Inlet system. The primary exception is the semi-isolated Pipestem Inlet in northern Barkley Sound.

Of the various sites along the west coast of Vancouver Island, Pipestem Inlet is the main water body where sustained populations of *C. maenas* have been observed (Graham Gillespie, pers. com; 2020). What is it about Pipestem Inlet that allows for populations of *C. maenas* but not *P. crassipes*? One immediately obvious reason for the retention of *C. maenas* in the inlet is that there is insufficient freshwater input from the small lake (Skull Lake) at the head of the inlet to generate a positive-type estuarine circulation, i.e., surface brackish outflow and compensating more saline inflow at depth. The Canadian Hydrographic Chart of Pipestem Inlet (No. 3670) shows that the entrance to the inlet (maximum depth of just over 60 m) is almost totally blocked by a series of islands (the Stopper Islands and Hillier and Snowden Islands) and by a shallow (~15 m) sill that impede tidal and estuarine exchange with the sea through Toquat Bay. These barriers will also limit circulation within the inlet. Equally importantly, the main freshwater flows that can affect circulation in the inlet—lake-fed Toquat River and Lucky and Cataract creeks—enter near the mouth of the inlet, rather than at its head. The hydraulic head produced by the freshwater discharge from these sources is directed radially outward from the source, i.e., seaward as well as into the inlet. Thus, the presence of freshwater discharge at the outer boundary of Pipestem Inlet could result in a negative (reverse) estuarine-type two-way circulation, with weak inflow at the surface and even weaker compensating outflow at depth. Locally, at least, there may be a mechanism for retaining larvae in the general vicinity of the inlet. Eastward blowing diurnal seabreezes that develop from late spring to early fall due to the air temperature contrast between the relatively warm land and cold water would help retain brackish water within the inlet, i.e., the seabreeze would push the brackish surface waters back up the inlet. The recirculation around the islands in Toquat Bay leading to Pipestem may help retain organisms just outside the inlet that may then enter/reenter with the “warm” brackish surface water during seabreeze wind conditions in Barkley Sound. Based on the hydrodynamics of Pipestem Inlet, there is a need to examine inlets with possible negative estuarine circulation arising from a combination of negligible runoff at their head and substantial runoff near their mouth.

Quayle (1988) lists inlets in British Columbia, where introduced Japanese oysters (*Magallana gigas*) reproduce naturally, and where shellfish growers can collect seed oysters. These inlets typically reach water temperatures > 18 °C in the summer, allowing this warm temperate oyster species to mature, spawn, complete its planktonic development in ~1 month, and settle as seed oysters. On the west coast of
Vancouver Island, these inlets include Pipestem Inlet in Barkley Sound and Tlupana Inlet in Nootka Sound. These are sites where $C.\text{maenas}$ populations have been well established for over 10 years (Behrens Yamada and Gillespie 2008), and where $P.\text{crassipes}$ have been found recently (Boulding et al. 2020). The flushing rate of these inlets and sounds is typically on the order of 2 months and thus long enough for $C.\text{maenas}$ larvae to complete their development within the inlets and sounds. At water temperatures $>$ 18 °C the larval PLD is even shorter making retention more probable. The larvae of $P.\text{crassipes}$, however, would not be retained in these inlets because their planktonic development is 3–4 months and they would, thus, likely be flushed out to the open coast and not return to sustain the parental population. While these inlets served as incubators for $C.\text{maenas}$, we hypothesize that this is not the case for $P.\text{crassipes}$.

Retention in the Salish Sea

Gillespie et al. (2001) noted that many non-native mollusk species that are introduced into the Salish Sea take only a decade or so to spread throughout the Sea because their larvae are retained. This process may already be happening with $C.\text{maenas}$. Prior to 2010, a self-maintaining population of $C.\text{maenas}$ was unintentionally introduced as hitch-hikers on mussels to Sooke Basin, northwest of Victoria. These mussels were collected from the west coast of Vancouver Island and stored in the inlet for biotoxin studies (Curtis et al. 2015). Densities of $C.\text{maenas}$ built up quickly within Sooke Basin, but larvae from this population did not immediately start satellite populations in the Salish Sea. Due to the Coriolis force, the surface outflow from the Salish Sea is strongest along the Canadian side of Juan de Fuca Strait, in other words, right where the waters of Sooke Basin connect with the Straits of Juan de Fuca. This estuarine outflow of lower salinity water, fed by the Fraser and Skagit Rivers, flows out the Strait of Juan de Fuca most of the time (Thomson et al. 2017). $C.\text{maenas}$ larvae make tidally timed vertical migrations, migrating into surface waters during ebb tide (Queiroga et al. 1997). This behaviour would tend to transport larvae out of the inland waters such as Sooke Basin and into the plume of estuarine waters flowing onto the continental shelf where the water mass turns northward becoming the VICC.

It was not until after the 2015–2016 El Niño and Pacific Heat Wave of 2014–2015 (The Blob Heat Wave) that $C.\text{maenas}$ was discovered on the US side of the Salish Sea by members of Washington Sea Grant Crab Team, a consortium of volunteers, agency, tribal, University of Washington biologists and shellfish growers. Early sightings included Westcott Bay on San Juan Island, Padilla Bay, Dungeness Spit National Wildlife Refuge, Sequim Bay and Port Townsend Bay (Fig. 2; Grason et al. 2018; Brassele et al. 2019). The proposed mechanism is the transport of larvae from the open coast into the Salish via the Olympic Peninsular Counter Current (Behrens Yamada et al. 2017). The Counter Current only occurs during winter storms when strong southerly winds drive the surface water eastward along the southern shore of the Strait of Juan de Fuca and into the Salish Sea. Most years the surface water temperature is below 10 °C and not conducive to the development of $C.\text{maenas}$ larvae. But during the winters of 2014–2015 and 2015–2016, water temperatures were warm enough (Behrens Yamada et al. 2017). Since then, $C.\text{maenas}$ has been detected at various other locations on both the US and Canadian side of the Salish Sea (European Green Crab (dfo-mpo.gc.ca), www.tinyurl.com/wagreencrab). The discovery of young-of-the-year crabs in high retention bays and lagoons (Buffington 2019; Mueller & Jefferson 2019) indicates local reproduction. Intense trapping efforts by Washington Sea Grant Crab Team, including Washington Department of Fish and Wildlife, the United States Fish and Wildlife Service, Padilla Bay National Estuarine Research Reserve, the Lummi Nation, the S'Klallam tribe, Taylor Shellfish and others are continuing. The goal is to reduce the breeding population in an attempt to prevent $C.\text{maenas}$ from permanently establishing itself in the inland sea. For recent updates for Washington State sightings see: (https://wsg.washington.edu/crabteam/about/blog/ and www.tinyurl.com/wagreencrab).

We hypothesize that the combination of the hydrodynamics of the Salish Sea with the biology of the crab affects colonization success. Flow throughout the Salish Sea is nearly continuously estuarine, i.e., surface flow is out of this large estuary. $P.\text{crassipes}$ larvae within an estuary vertically migrate to exploit the seaward estuarine flow such that the larvae are transported onto the continental shelf. The long PLD provides enough time for the larvae to transit out of...
even this large estuary to the coast. This combination of hydrodynamics and larval biology may prevent *P. crassipes* from colonizing the Salish Sea via natural larval transport. However, if *C. crassipes* were to be transplanted into Hood Canal, a basin at the southern end of the Salish Sea (Fig. 2) with a water retention time of half to one year (Khangaonkar et al. 2011), then a satellite population might establish. To test this prediction, we alert biologists to look for *P. crassipes* at other sites in the Salish Sea, and if they do, to document their sighting as range expansions.

Invasive potential

A comparison of the range expansion of these two crab species suggests that a shorter PLD and retention of larvae close to their origin are requirements for a species to be a successful invader. The brackish water crab, *Rhithropanopeus harrissii*, is such a species. It is native to the Atlantic coast of North American but has established populations around the world, including estuaries in the Baltic and Mediterranean, the Caspian Sea, lagoons in the Panama Canal and lakes in Texas (Roche and Torchin 2007). Its success is linked to its short larvae stage (7–35 days to megalopal stage) and the ability of the larvae to stay close to the parental population (Gonçalves et al. 1995; Cronin 1982). It was introduced into San Francisco Bay prior to 1937, most likely along with east coast oysters (Cohen and Carlton 1995). Populations were discovered in four Oregon estuaries, including Coos and Yaquina Bay. Genetic analysis by Peterson (2006) suggest that these were not separate introductions but must have been derived from larval transport during strong El Nino events.

While *C. maenas* is clearly a successful invader, we are unaware of any reports of *P. crassipes* introductions and, as pointed out above, they have been unable to establish self-maintaining populations, even on the outer coast of Washington and northern Oregon, despite having literally thousands of years (if not much longer) in which to accomplish this. A disjunct Asian population of *P. crassipes* is found in Korea and Japan (Morris et al. 1980; Canepa and Terhorst 2019). Genetic analysis concluded that crabs from a Korean population were not introduced with shipping from the eastern Pacific, but that the two populations, on either side of the Pacific, diverged around one million years ago (Cassone and Boulding 2006). Furthermore, genetic analysis of populations sampled in California, Oregon, Washington and Bamfield, BC showed that these populations were not genetically distinct and that the Bamfield population did not exhibit reduced genetic diversity. These observations suggest that the gene pool of *P. crassipes* in the eastern Pacific is well mixed. We suspect that the difference in the invasion success between *C. maenas* and *P. crassipes* has to do with the pattern of coastal hydrodynamics to which their spawning and larval pelagic phase has evolved. Adult *C. maenas* is primarily estuarine-dependent, larvae are released within estuaries, but are exported to the coastal ocean where they go through their development. The megalopae migrate back to the shore and enter estuaries to complete their development. The hydrodynamics to which they have evolved are generic for many coasts; flow within estuaries and in the nearshore coastal ocean (i.e., within the coastal boundary layer) is very similar the world over. Hence, as the hydrodynamics to which they have evolved is common, we can think of their life history as being pre-adapted to many coastal settings. In contrast, we suspect that *P. crassipes* has evolved their spawning and larval pelagic phase to a unique hydrodynamics setting, the eddy dominant Southern California Bight. The type of hydrodynamics present in the Bight is not common and this we suggest means that *P. crassipes* is pre-maladapted as an invader species nearly everywhere. They seem incapable of even establishing self-maintaining populations just to the north of the Southern California Bight.

What we are proposing is that the life history of a species, coupled with the hydrodynamic setting in which their pelagic larvae develop, plays a very significant role in the process of their range expansion. If we compare the northward and southward range expansion of *C. maenas* out of San Francisco Bay we can actually see an example of this. During the El Niños, the range of *C. maenas* expanded rapidly northward such that they are present in Canada; a range expansion of about 1,500 km. Over the same period, they have expanded to the south only as far as Elkhorn Slough in Monterey Bay; a range expansion of only 150 km. Why do we see a factor of 10 difference in their range expansion? A likely explanation is the timing of larvae release (Jan–March in Coos Bay, Oregon) coupled with the hydrodynamics of the coastal ocean during that period; flow is primarily to
the north as the Davidson Current. The southward flowing California Current does not ‘return’ to the shelf waters until after the shift from the winter northward winds to the spring summer southward winds, the spring transition, which on average occurs in mid April. Nearly all of the Carcinus larvae leaving San Francisco Bay travel north in the Davidson Current. Larvae released after the spring transition will travel to the south in the California Current, but given the available data on the timing of larval release it looks like only a small percentage of larvae are available to be carried south. A tiny population has established in Elkhorn Slough (Grosholz et al. 2011). What happens to their larvae? Given the timing of larvae release nearly all will go north and the very few larvae from this tiny population that are released after the spring transition must be carried past the coast of Big Sur (≈ 200 km) before they might arrive at another small estuary (Morro Bay). Life history coupled with coastal hydrodynamics appears to contribute to range expansion.

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