Can The Timing And Duration of Planktonic Larval Development Determine 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 North-Eastern 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,* which has existed on the coast since at least the end of the last Ice Age (>10,000 years ago). The initial northern range limit of these species was central California and central 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 inlets on the west coast of Vancouver Island, and possibly also in the Salish Sea, while *P. crassipes,* in thousands of years, never has. 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 ~1-2 months, they can act as an incubator 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.

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, the mole crab, *Emerita analoga*, establishes ephemeral populations on the west coast of Vancouver Island and as far north as Kodiak Island, Alaska when larvae drift north from source populations in California (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 and limited larval recruitment. Populations are re-established during the next incursion of larvae from the south.

Here, we compare range shifts, similar to the mole crab, in the introduced European green crab, *Carcinus maenas*, and the native lined shore crab, *Pachygrapsus crassipes* and advance the hypothesis that life history traits of the adults and larval ecology and behavior play a 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 1) the temperature requirements for mating and egg development, 2) the timing and duration of larval release, 3) the pelagic larval duration (PLD) and 4) 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 investigate the water properties of the larval habitat, including water temperature, alongshore currents and flushing characteristics of the fjords on the west coast of Vancouver Island and the inland Salish Sea (Figs. 1 and 2). From these characteristics, we predict if either, or both, species are likely to establish permanent, self-sustaining populations within these fjords and the Salish Sea.

Range Expansions And Life Histories

Carcinus maenas

While *C. maenas* is a native of the eastern Atlantic coast, from North Africa to northern Norway, it also is a successful global invader. 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 at 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).

In Oregon coastal waters, *C. maenas* are sexually mature at less than a year at around 34 mm in carapace width. 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.). Crabs were observed mating and responding to sex pheromones when the water temperature exceeded 15º C (Nicky Fletcher, pers.com.). Captive females kept in a seawater tank at 12º C carried their eggs for about 2 months from early December to early February (Behrens Yamada 2001). Once the embryos are fully developed, the female agitates the eggs and initiates the hatching process. Hatching occurs soon after a nighttime high tide and the larvae ride an out-going (ebb) tide to the near-shore (Queiroga et al. 1997). There they undertake vertical migration, feed on plankton, and molt through three more zoea stages and into the transitional megalopal stage. Total development time in the plankton is ~ 2 months at 12º C and ~ 1 month at 18º C (Dawirs 1985, deRivera et al. 2007). Late 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). 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). The observation that the Pipestem population 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.

Table 1. Major Range Expansions in *C. maenas* and *P. crassipes* along the west coast of North America. Estimated year of arrival, in many cases, follows strong El Niño events as indicated by asterisks. Latitude of locations (º N Lat) is given. References (Ref) correspond to the following: 1=Cohen et al., 1990; 2=Miller 1996; 3= Neil Richmond & Heath Haempel, pers. com.; 4= Behrens Yamada et al. 2005; 5= Gillespie et al. 2007; 6=Gillespie et al. 2015; 7= Behrens Yamada et al. 2017, Grason et al. 2018; 8= Clint Johnson, pers. com.; 9= Queen 1930; 10= Hiatt 1948, Ricketts, Calvin & Hedgpeth 1968; 11= Dale Snow, pers. com.; 12= Jensen 1995; 13= Ladd Johnson, pers. com.; 14= Jeff Goddard, pers. com.; 15= Boulding et al. 2020; 16= Andrew McCurdy; 17= Royal British Columbia Museum; 18= Armand Kuris, pers. com.

Estimated Year of first arrival	*Carcinus maenas*	º N Lat	Ref	Estimated Year of first arrival	*Pachygrapsus crassipes*	º N Lat	Ref
< 1990	San Francisco Bay, CA	37.8º	1	< 1930	Coos Bay, OR and open coast	43.3º	9
1993	Humboldt Bay, CA	40.7º	2	< 1947	Newport. OR	44.6º	10
1995−1996	Coos Bay, OR	43.4º	3	< 1950	Boiler Bay, OR	44.8º	11
1997−1998*	Oregon, Washington Barkley Sound, BC	48.8º	4,5	1982−1983*	Ecola State Park, OR	45.9º	12
1999	Nootka Sound	49.8º	5	1982−1983*	Tatoosh Island, WA	48.4º	13
2004 or 2005	Quatsino Sound, BC	50.5º	6	1991−1992*	Ozette, WA	48.1º	14
~ 2010	Bella Bella area, BC	52.1º	6	1997−1998*	Barkley Sound, BC	48.8º	15
2015−2016*	Central Salish Sea, WA	48.6º	7	2015−2016*	Ucluelet	48.9	16
2020	Queen Charlotte City, Haida Gwaii, BC	53.2º	8	2015−2016*	Cox Point near Tofino, BC	49.1º	17
				2015−2016*	Nootka Sound, BC	49.8º	15
				2015−2016*	Strait of Juan de Fuca, Neah Bay, and Shipwreck Point, WA	48.4º	18

Pachygrapsus crassipes

P. crassipes, a common native of the upper intertidal zones from southern Oregon to Baja California (Fig. 1), lives in rock crevices, under rocks and boulders, in tidepools, 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 (Queen 1930, Dale Snow, pers. com., Supplemental table 2) while Hiatt (1948) and Ricketts et al. (1968) give Newport as its northern distribution (Fig. 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, Supplemental Table 2). In California, *P. crassipes* mature within a year with a 12−15 mm carapace width and attain a carapace width of 42 for females and 48 mm for males in 3 or 4 years (Hiatt 1948, Jensen 2014). The reproductive season is long. Ovigerous *P. crassipes* 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, they lasted 115 days at 16ºC and 68−108 days at 20-22ºC (Schlotterbeck 1976, DiBacco 2001). Thus, pelagic larval duration is estimated to be around 3 to 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 perday) 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, Supplemental Table 2). 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.

Table 2
Summary of life history characteristics of *Carcinus maenas* and *Pachygrapsus crassipes* (references for data in text)

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	Male: 48 mm CW
	Female: 89 mm CW	Female: 42 mm CW
Mating temperature	$> 15^O$ C	Unknown
Larval development time at different temperatures	*Ca.* 2 months at 12° C	115 days for zoea stages at 16° C
	Ca. 1 month 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

Boulding el 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 and $>10^o$ C for larval survival and development and $>15^o$ 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). The presence of gravid female *P. crassipes* at Ozette, and in Barkley Sound, suggest that temperatures for reproduction can also be favorable for this species at these northern locations. Since no temperature tolerance data exist for *P crassipes* larvae, it is not known 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, two more conditions are needed for northward range expansion and establishment of self-maintaining populations of the two crab species. The first is favorable currents, such as the Davidson Current, to transport larvae from established breeding populations in California along the California-Oregon-Washington-British Columbia coast, and the second is, mechanisms for the retention of larvae in coastal inlets and the Salish Sea to allow satellite populations to become self-maintaining.

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 et al. 1979, 1989), while the southward flow in summer has been termed the Shelf-Break Current (Thomson et al. 1989; Thomson and Ware 1996). 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 adaptions 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 Supplemental Table 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 et al. 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 (VICC)

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. 1989; Hill et al. 1998), 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 northwestward 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). The estuarine outflow through the Strait is, in turn, driven primarily by the seaward hydraulic head caused by the discharge of the Fraser River (Crean et al. 1988), and to a lesser extent by smaller rivers in the southern Strait of Georgia and within Puget Sound. Due to the Coriolis force, the surface outflow 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).

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 Green crabs, 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

The estuarine circulation that prevails throughout much of the Salish Sea and adjoining waterways is driven by freshwater discharge from major rivers such as the Fraser, Squamish and Skagit. Although the estuarine flow is too complex to describe in detail here, it basically consists of a seaward outflow in the upper 50–75 m and inflow below that depth (e.g., Thomson et al. 2020). The estuarine circulation has two primary components: A barotropic component forced by the seaward-directed hydraulic head arising from freshwater discharge from bordering rivers and streams, and a baroclinic component generated by vigorous tidal mixing of the fresh surface water with salty ocean-derived bottom water (Crean et al. 1988; Sutherland et al. 2011; Khangaonkar et al. 2017; MacCready et al. 2018). The circulation is modified by winds and processes at the oceanic boundaries. Freshwater discharge to the Strait of Georgia ranges from around 10,000 m^3/s in spring (May-June) to around 1,000 m^3/s in winter (February-March) (LeBlond et al. 1984; Pawlowicz et al. 2007; Thomson 2014). Of the annual average discharge of roughly 4,000 m^3/s per day, approximately 68.4% is from the Fraser River. Roughly 83% of the water volume exchange between the strait and the northeast Pacific is through the Strait of Juan de Fuca in the south, with the remaining 17% exchanged through Johnstone Strait in the north (Thomson et al. 2007; Khangaonkar et al. 2011).

Range expansion of crab species into the Salish Sea is restricted by the estuarine flow that normally directs surface waters seaward throughout the year. 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. 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

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 habitats for adult *P. crassipes* at least since the end of the last ice age, yet in these roughly 10,000 years *P. crassipes* has not established self-sustaining populations in these locations. Contributing factors may be related to the timing of larval release, length of pelagic larval duration, and the circulation system to which the species is adapted.

Open Coast

Large populations of the Dungeness crab, *Metacarcinus (Cancer) magister*, are found within the California Current system from British Columbia south to Morro Bay, California. Like *P. crassipes*, *M. magister* has a long larval period (3 to 4 months), yet to date, self-sustaining populations of *P. crassipes* within the range occupied by *M. magister* have not developed. A major difference between the two species is the timing of larval release. Within the California Current, *M. magister* larval release is seasonal, occurring during winter months. The pattern of larvae release by *M. magister* is typical of shelf/slope fish and benthic crustacean species of the California Current system (Shanks and Eckert 2005). Shanks and Eckert hypothesize that this pattern of larval release/spawning coupled with a long PLD has evolved to capture the seasonal north south flow of the waters over the continental shelf as the currents shift from the winter northward flowing Davidson Current to the southward flowing California or Shelf-Break Current. By capturing this season shift in the flow, larvae may ultimately settle back into the extensive adult population of *M. magister*. The results of a coupled bio/physical model of *M. magister* larval dispersal is consistent with this hypothesis (Rasmuson 2013).

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. The extended period of larval release by *P. crassipes* is displayed by many fish and benthic crustacean species in the Southern California Bight (Shanks and Eckert 2005). Flow in the Bight is characterized by large, long-lived eddies; the extended spawning period may be an adaptation to this flow regime. Spawning in a similar pattern within the California Current system may, however, be maladaptive. 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 in the winds (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 spawning 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 retuned 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.

The larvae of a variety of species, mostly fish, typically found in the Southern California Bight are apparently transported northward out of the Bight during El Niño events and, like *P. crassipes*, they settle and establish ephemeral populations on the outer coast to the north of the Bight (Shanks and Eckert, 2005). The adults survive outside the Bight, but, likely because the mismatch of their spawning timing and PLD and the coastal hydrodynamics, self-sustaining populations have also not developed. 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 would be dependent on recruits spawned in the Bight, but they could be much less ephemeral than current populations north of Coos Bay. 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 Vancouver Island.

Of the various sites along the west coast of Vancouver Island, Pipestem Inlet in northern Barkley Sound 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. maenas* populations have been well established for over 10 years (Behrens Yamada and Gillespie 2008), and where *P. crassipes* have been found recently (Boulding et al. 2020). The flushing rate of these inlets and sounds is on the order of 2 months and thus long enough for *C. 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. 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. maenas*, we hypothesize that this is not the case for *P. 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. maenas*. Prior to 2010, a self-maintaining population of *C. 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. 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 Basint 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. maenas* larvae make tidally timed vertical migrations, migrating into surface waters during ebb tide. 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. 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, Brasseale 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). It is only during winter storms that strong southerly winds drive the surface water eastward along the southern shore of the Strait of Juan de Fuca into the Salish Sea. Most years the surface water temperature is below 10° C and not conducive for the development of *C. 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. maenas* has been detected at various other locations on both the US and Canadian side of the Salish Sea (DFO AIS 2020, 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. 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)

As we have pointed out, *P. crassipes* has had the opportunity to colonize the Salish Sea since the end of the last ice age when the glaciers retreated from the area. In other words, they have something like 10,000 years to expand their range yet they have not. If we assume a strong El Niño every decade (roughly the current rate), then there may have been around 500 strong El Niño events during which *P. crassipes* larvae may have been transported into the Pacific Northwest. We hypothesize that the combination of the hydrodynamics of the Salish Sea with the biology of the crab prevents colonization. Flow throughout the Salish Sea is nearly continuously estuarine, i.e., surface flow is out of this large estuary. *P. 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 2012), 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 may provide insight into the requirements for a species to be a successful invader. *C. maenas* is clearly a successful invader. In contrast, 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 & 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 & 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 filled 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 will determine a 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 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 larval release it looks like only a small percentage of larvae will be carried south. A tiny population has established in Elkhorn Slough (Grosholz 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 ($\approx$ 200 km) before they might arrive at another small estuary (Morro Bay). Life history coupled with coastal hydrodynamics appears to be determining range expansion.

Declarations

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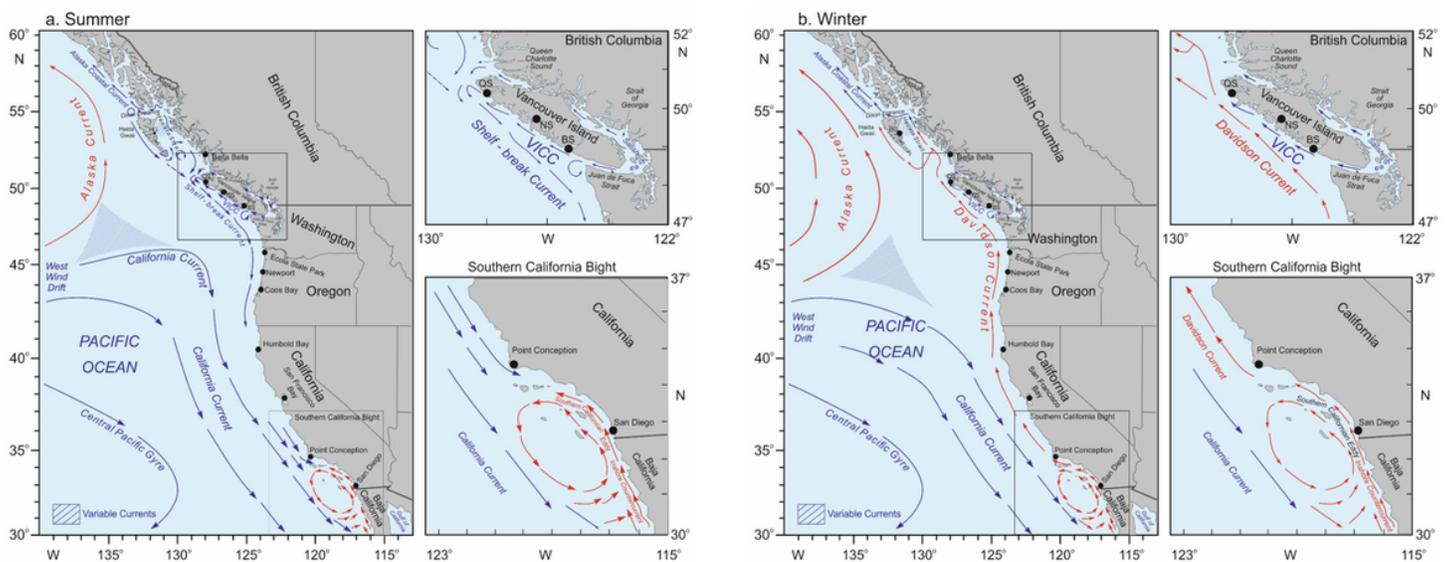
Figures

Figure 1

Map of the west coast of North America showing current patterns during: 1a. summer and 1b. winter. Location abbreviations are: VICC= Vancouver Island Coastal Current, BS= Barkley Sound, NS= Nootka Sound, QS= Quatsino Sound. Currents indicated in red are relatively warm, those in blue, cold. Note that the north-flowing Davidson Current in winter. During a strong a strong El Niño this current can exceed 50 km per day and last from September to April (Barth & Smith 1998, Huyer et al. 1998). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

First sightings of Carcinus maenas (green circles), and Pachygrapsus crassipes (purple triangles) in the Salish Sea and adjacent open coast as of Fall 2020. A single C. maenas from Price Bay (PB) settled during the 1997/98 El Niño and while the Sooke Basin population (SB) originated from the introduction of live C. maenas prior to 2010. Five sites were seeded during the 2015/16 El Niño: WB= Westcott Bay (2015), PB= Padilla Bay (2016), DS=Dungeness National Wildlife Refuge (2015 & 2016), SqB=Sequim Bay (2016) and PTB=Port Townsend Bay (2016). For subsequent sighting see Behrens Yamada et al. 201X and www.tinyurl.com/wagreencrab). First sightings of P. crassipes followed strong El Niño events: OZ = Ozette (2091/92 and 2015/16), TI = Tatoosh Island (1982/83), NB = Neah Bay (2015/16), SW = Shipwreck Point (2015/16), BA = Bamfield in Barkley Sound (1994/95, 1997/98, 2015/16), UC-Ucluelet (2015/16), TO=Tofino (2015/16), Nootka Sound (2015/16). Canadian sightings for P. crassipes are from Fig. 1a and Table S1 in Boulding et al. 2020. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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