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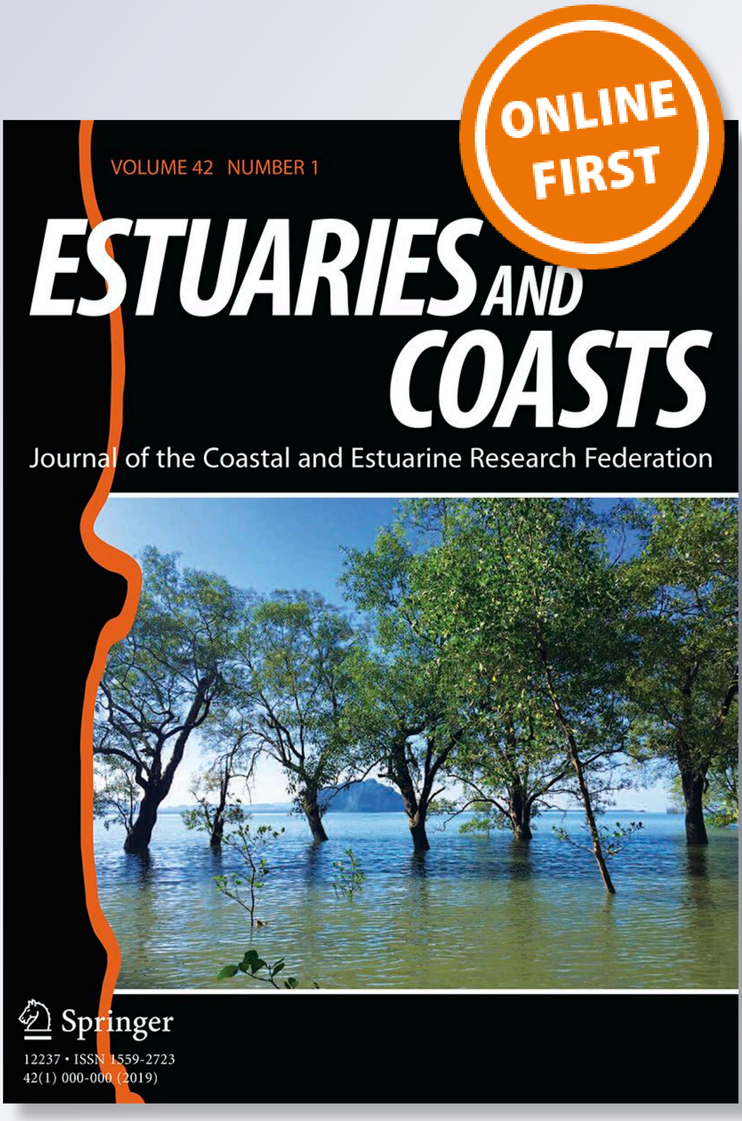

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Larval Transport Modeling Support for Identifying Population Sources of European Green Crab in the Salish Sea

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Abstract

In 2016, the invasive European green crab (*Carcinus maenas*) was observed for the first time east of Vancouver Island in the Salish Sea. Because there are many established green crab populations in the Pacific Northwest region, the invaders' origin was unclear. Understanding likely source populations for the Salish Sea is critical to developing management strategies for the current green crab invasion and future invasion threats. To that end, this study used ocean models to investigate the likelihoods that larvae released from four potential source locations on the West Coast could be successfully transported into the eastern Salish Sea in particle tracking experiments, and then examined the roles of particle release timing and oceanographic processes (i.e., flow reversals in the Strait of Juan de Fuca) in the probability of successful transport. The potential source locations tested were Sooke Basin (British Columbia, Canada), Barkley Sound (British Columbia, Canada), Willapa Bay (Washington, USA), and Coos Bay (Oregon, USA). Model results indicate that during 2014 and 2015 particles released from as far south as Oregon and as far north as the coast of Vancouver Island could have reached the eastern Salish Sea, suggesting that multiple populations on the Pacific coast might be viable sources for the observed eastern Salish Sea invasion in 2016. Flow reversals in the Strait of Juan de Fuca co-occurred with successful invasions from Barkley Sound and Willapa Bay but not from Sooke Basin or Coos Bay. Incursions of particles into the eastern Salish Sea were episodic. Nevertheless, these results suggest that oceanographic patterns and meteorological events could be useful for identifying periods of likely green crab recruitment, particularly during years with high El Niño Southern Oscillation (ENSO) indices.

Keywords Green crab · Invasive species · Particle tracking · Regional ocean modeling

Introduction

The European green crab (*Carcinus maenas*, henceforth green crab) is frequently listed among the most damaging invasive species worldwide (Narberhaus 2019). This species has established populations in several temperate marine habitats including southeastern Australia and Tasmania, Argentina, South Africa, and both coasts of North America (Le Roux et al. 1990; Geller et al. 1997; Carlton and Cohen 2003; Thresher et al. 2003; Ahyong 2005; Hidalgo et al. 2005). In locations where green crabs are abundant, primary direct impacts occur via competition with and predation on native species (Grosholz et al. 2000; Whitlow 2009; de Rivera et al. 2011) and occasionally indirectly via facilitation (Grosholz 2005) or trophic cascades (Kimbro et al. 2009). Increasing evidence also suggests that green crabs can damage seagrass beds and impede their restoration through mechanical disturbance and uprooting while foraging (Malyshev and Quijon 2011; Neckles 2015; Matheson et al. 2016), as well as by consuming both meristem tissue and seeds of the plants

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(Malyshev and Quijon 2011; Infantes et al. 2016). These habitat impacts are associated with significant declines in abundance and biomass of seagrass-associated fish and shifts in community structure (Matheson et al. 2016).

The presence of green crabs on the west coast of North America was first detected in 1989–1990 in southern San Francisco Bay (Cohen et al. 1995; Grosholz and Ruiz 1995). Genetic studies subsequently confirmed the source population as the North American east coast (Darling et al. 2008), the species most likely having been introduced unintentionally in shipments of bait or seafood (Carlton and Cohen 2003). Local population growth and larval dispersal permitted spread to nearby embayments to the north and south of San Francisco Bay by 1994 (Grosholz and Ruiz 1995). Range expansion since then has been primarily northward; advection and survival of larvae in this direction is stronger during years with positive Pacific Decadal Oscillation (PDO) and El Niño Southern Oscillation (ENSO) indices (Behrens Yamada and Kosro 2010). Green crabs were first detected in embayments of Oregon and Washington (USA) and British Columbia (Canada) in 1997–1999 (Behrens Yamada 2001; Jamieson et al. 2002), coinciding with years of extremely high ENSO indices. Populations are now established in coastal fjords on the west coast of Vancouver Island and have continued to spread northward episodically (Klassen and Locke 2007; Gillespie et al. 2015; DFO 2018), presumably facilitated by local production and retention of larvae (Banas et al. 2009; Behrens Yamada et al. 2015; DiBacco and Therriault 2015). By contrast, green crabs are only periodically abundant in coastal embayments of Oregon and Washington, appearing to rely on advection of larvae from established populations farther south (Behrens Yamada and Gillespie 2008; Behrens Yamada et al. 2015).

Despite being present in coastal embayments of Oregon, Washington, and British Columbia, no green crabs were observed in the Salish Sea, an inland sea of Washington State (Grason et al. 2018) and southern British Columbia (Fig. 1), throughout the 2000s. Jamieson et al. (2002) attributed the paucity of green crab sightings in the region to hydrogeographic conditions in the Strait of Juan de Fuca that might inhibit incursions of larvae because prevailing surface currents are seaward. In 2012, an established population, consisting of multiple year classes, was discovered in Sooke Basin, 40 km west of Victoria, British Columbia (Curtis et al. 2015) and well within the Strait of Juan de Fuca (Fig. 1). The current strongest hypothesis for the route of introduction for that population was the transfer of contaminated bags of mussels from Clayoquot Sound, an infested embayment on the outer coast of Vancouver Island. We base this inference on two lines of evidence. First, Department of Fisheries and Oceans Canada (DFO) carried out an investigation that surmised this to be the most probable source (T. Therriault, pers. comm). In addition, ongoing genetics work (Tepolt et al. in prep) demonstrates that the population in Sooke Basin does not show connectivity with populations either on the US west coast or from Barkley Sound. Thus, the green crab seemingly overcame the apparent oceanographic barrier via human-mediated transport into the western portion of the Salish Sea.

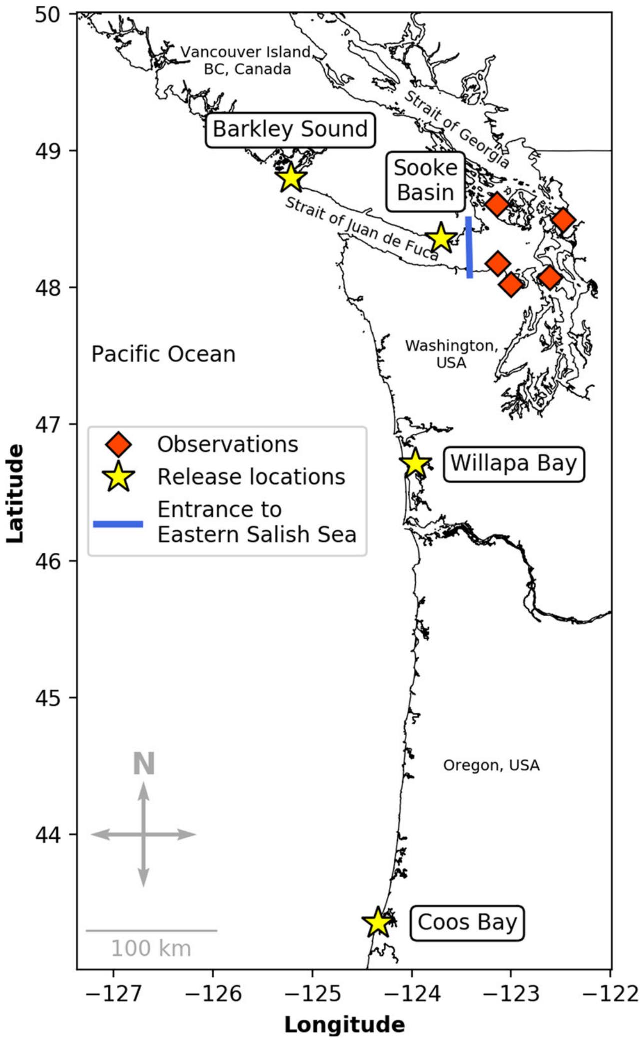


Fig. 1 Map of study area showing Pacific northwest coastal ocean and Salish Sea, which contains Strait of Juan de Fuca, Strait of Georgia, and waters further inland including the Puget Sound. Eastern Salish Sea delineated from Strait of Juan de Fuca by blue line. Orange diamonds = confirmed green crab observations in eastern Salish Sea. Yellow stars = larval release locations

Following discovery of the population in Sooke Basin, early detection monitoring was initiated in Washington State in 2015. A distributed citizen science network of sentinel sites was established, resulting in the first confirmed green crab detections eastward of Vancouver Island in 2016 on San Juan Island and in Padilla Bay (Grason et al. 2018). Since that time, green crabs have been found at very low abundances at four additional locations in the eastern Salish Sea (Fig. 1). Two lines of evidence support the inference that green crabs have only recently (2014 or later) arrived in the eastern Salish

Sea. Firstly, monitoring in this region from 2000 to 2010 found no green crabs (WDFW, unpublished data). Second, sizes of all recent captures indicate these individuals belong to year classes of 2014 or thereafter (Grason et al. 2018). Moreover, it is likely these new detections resulted from "natural" dispersal of larvae rather than by human-mediated transport because crabs of similar size/age were observed in multiple disparate locations not associated with known transport vectors (e.g., ballast water exchange at ports, seafood distribution centers, shellfish aquaculture activities).

Identifying the pathways by which green crab larvae can penetrate into the eastern Salish Sea and understanding the oceanographic processes responsible for successful recruitment are critical to management of the species in Washington State and British Columbia, as well as ongoing transboundary cooperation to control spread in the region. Here, we considered whether Sooke Basin was the likely larval source for green crabs observed in the eastern Salish Sea or if larvae could have arrived from the Pacific Coast. Grason et al. (2018) suggested a Sooke Basin origin as the most parsimonious explanation if the Strait of Juan de Fuca represents an oceanographic barrier to transport of invasive larvae. However, it was recently postulated that periodic flow reversals caused by storms can transport larvae from coastal sources eastward through the Strait of Juan de Fuca (Behrens Yamada et al. 2017). Under normal conditions, flow in the upper water column is westward within the Strait of Juan de Fuca, preventing eastward transport of coastal larvae inhabiting near-surface waters. During flow reversals, which occur in fall and winter and less frequently in spring and summer (Frisch et al. 1981), near-surface flow changes direction and moves eastward in the Strait of Juan de Fuca, enabling eastward advection of invasive larvae (Thomson et al. 2007; Giddings and MacCready 2017). Thus, the goal of the present study was to evaluate the likely source population for larvae that arrived in the eastern Salish Sea, given what is known about the present distribution of green crabs along the west coast of North America.

We used an oceanographic circulation model to explore likely sources and seasonal timing of larval releases that might have contributed to the observed distribution of green crabs captured within the eastern Salish Sea. In so doing, we evaluated three questions:

1. Given observed ocean conditions, what is the relative probability that larvae released from nearby locations with known populations of green crabs could be transported into the eastern portion of the Salish Sea?
2. Based on current understanding of green crab larval dynamics and seasonality, when is transport of larvae into the eastern Salish Sea likely to be most successful?
3. What oceanographic conditions and mechanisms are likely to support successful transport of green crab larvae into the eastern Salish Sea?

Methods

Green Crab Larval Biology

Although few data exist concerning the general biology, life history, and development of *Carcinus maenas* in the northeastern Pacific, Atlantic populations have been studied extensively. Generally, the timing of reproductive events depends on latitude (Queiroga 1996), and reproduction can occur over only a few months (Berril 1982) or throughout the year (Queiroga 1996), depending on seasonal temperatures. After mating, female crabs can release embryos more than once within a year; the number of broods produced is dependent on the length of the reproductive season and resource availability. Several authors have suggested that shallow mid-latitude estuaries of the northeastern Pacific meet these conditions (Cohen et al. 1995; Behrens Yamada 2001; Jamieson et al. 2002). Banas et al. (2009) report ovigerous females in Willapa Bay, Washington from January through July, while DiBacco and Therriault (2015) observed ovigerous females over a shorter interval (mid-February to June) in British Columbia.

Females carry their broods for several months, and egg development is temperature-dependent. Behrens Yamada (2001) reported females remaining ovigerous for 2–3 months at 12 °C (December–February). Once embryos are fully developed, female crabs may move toward the mouths of estuaries where hatching occurs, typically over successive nighttime high tides or soon thereafter (Queiroga et al. 1994). The timing of release has important implications for the export of larvae since the subsequent ebbing tide will flush them from the estuary (Zeng and Naylor 1996a).

Larvae develop through four zoeal and one megalopa stage before settlement occurs 4–9 weeks after hatching, but again this is dependent on water temperature (Dawirs 1985; Nagaraj 1993; de Rivera et al. 2007). In laboratory experiments, total development time to first benthic instar was 32 and 62 days at 18 °C and 12 °C, respectively (Dawirs 1985); average development at 12.5 °C is 59 days (deRivera et al. 2007). Field results provide similar estimates, and Queiroga (1996) found that development occurred in 56 days at 13.5 °C and at a salinity of 35.

Larval abundance peaks April–July in the northeastern Atlantic and North seas (Lindley 1987), while near the southern geographic limit of the species' native range, larvae are abundant during two periods: February–April and October–December (Sprung 2001). Development takes place on the continental shelf (Lindley 1987; Queiroga 1996). In Portuguese waters, Queiroga (1996) found that larvae were restricted to the inner and middle shelf, with zoeae 1 occurring closest to coastal estuaries and the later zoeae stages furthest offshore (15–20 km). Megalopae were also present nearshore, which indicates onshore transport of that stage. According to Queiroga (1996), all larvae were collected within 45 km of the Portuguese coast.

Experimental Overview

A model was used to recreate ocean conditions from 2014 to 2016 and larval releases were simulated in the source locations (described below) as separate particle tracking experiments. Ten thousand particles were released per experiment in order to provide a statistical distribution of possible transport paths of planktonic crab larvae. Though an individual female green crab can release several hundred thousand larvae in a single brood (Griffen 2014), this number of particles was chosen to provide a relatively high-resolution distribution while balancing computational demands of particle tracking experiments. For each experiment, the particles were released from a single location and tracked for 75 days. Experimental releases were conducted on one day per month during periods when green crabs are known to release larvae (see the "Particle Release Timing" section) in order to sample ocean conditions during different seasons. After the tracks were generated, the success of the invasion was determined by calculating the percentage of the 10,000 released particles transported into the eastern Salish Sea during a competency window (see the "Particle Development" section). This percentage was interpreted as the likelihood that a crab larva would reach the eastern Salish Sea if released from that location at that time.

Modeling Tools

The ocean model was built in the Regional Ocean Modeling System (ROMS) (Shchepetkin and McWilliams 2005), a free surface, hydrostatic, primitive equation model. The model was forced with atmospheric, tide, river, and ocean boundary conditions to simulate the 3D circulation and water properties throughout the domain. It does not include wetting and drying in intertidal zones. The model included 16 river point sources using daily discharge values from the United States Geological Survey (USGS, http://waterdata.usgs.gov/usa/nwis/) and Environment Canada (http://www.wsc.ec.gc.ca/applications/H2O/). These include 14 Puget Sound rivers, the Fraser River, and the Columbia River. Eight tidal constituents derived from the 1/4° TPXO7.2 inverse global tidal model (Egbert and Erofeeva 2002) were forced at the open boundaries. Meteorological forcing of surface pressure, wind, air temperature, relative humidity, shortwave radiation, downward longwave radiation, and rainfall were taken from a Weather Research and Forecasting regional model with 12-km resolution (Mass et al. 2003). Open ocean boundary conditions for daily-averaged velocity, salinity, temperature, and sea surface height came from the HYCOM global model (HYbrid Coordinate Ocean Model, http://hycom.org/). The river, atmosphere, and ocean-forcing models were data-assimilative and so did an excellent job of keeping their forecast fields close to observations. The grid horizontal resolution was 1.5 km on the shelf, and 4.5 km far offshore. There were 40 vertical levels, distributed from the seafloor to the sea surface, giving excellent resolution of both bottom and near-surface processes. The large domain allowed important interactions between the inland and coastal waters, for example, the influence of coastal upwelling and the Columbia River plume on the inflow to the Strait of Juan de Fuca. The ocean circulation model has been extensively validated in terms of currents, temperature, salinity, sea surface height, and biogeochemistry by hindcast experiments from 2004 to 2007 (Davis et al. 2014; Giddings et al. 2014; Siedlecki et al. 2015).

The particle model is a separate program that uses the output of the ocean model. The integration required to get the horizontal positions for the particles from the ocean circulation output was done following methods developed in previous particle tracking projects (Banas et al. 2009; Giddings et al. 2014). Particle tracks were calculated by forward integration in time using bi-linear interpolation of the archived hourly snapshots of 3D velocity fields and 2nd-order Runge-Kutta integration. A 3600-s time step was used which resolved tidal oscillations. Experiments using shorter time steps and 4th-order Runge-Kutta integration gave very similar results.

Particles migrate vertically in the water column since all stages of green crab larvae exhibit diel vertical migration (DVM) (Queiroga et al. 2002), and vertical position significantly impacts horizontal transport (Queiroga et al. 1997). The vertical positions of the particles were programed to move to 3-m depth at sunset and to 15-m depth at sunrise, which is consistent with field observations in British Columbia (DiBacco and Therriault 2015). Although we chose to time the migration of our particles with the photoperiod, other vertical migratory behaviors such as endogenous tidal rhythms have been observed in green crabs in other environments in the field (Zeng and Naylor 1996), so applying this behavior to all green crab larvae stages in all locations introduces uncertainty in our results. These water column positions were based on observations of DVM for zoeae I and megalopa but were used for all zoeal stages despite evidence that DVM varies due to the lack of observations of zoeal stages II–IV (DiBacco and Therriault 2015) and the difficulty of approximating larval development in rapidly changing ocean conditions (as described below in the "Particle Development" section). Swimming rate (0.6 cm s^{-1}; Mileikovsky 1973) was not resolved in this DVM model since we observed that larval swimming rates could overcome displacement from vertical diffusion the vast majority of the time (> 99.9% of model time steps). Most complications in particle tracking arise from difficulties in treatment of vertical diffusion due to turbulence (Visser 1997; Banas et al. 2009); however, by prescribing vertical position as a function of time, that difficulty was avoided.

Particle Release Locations

Four sites where green crabs have been detected were evaluated as possible origins of green crabs in the eastern Salish Sea: Barkley Sound and Sooke Basin (British Columbia, Canada); and Willapa Bay, Washington, and Coos Bay, Oregon (USA). These sites were selected to encompass dispersal patterns that could transport larvae into inland waters from across the range of the green crab on the North American west coast: Morro Bay, California (Carlton and Cohen 2003) to Bella Bella, British Columbia (Gillespie et al. 2015).

Sooke Basin was considered a likely source based on proximity to sites where green crabs were captured in 2016 and 2017 (Grason et al. 2018). Prior to those observations, Sooke harbored the only confirmed population of green crabs in the Salish Sea. When first detected in 2012, the population in Sooke was already sufficiently abundant to be considered established and has remained so since that time (Gillespie et al. 2015; T. Therriault, pers. comm.). Subsequent surveys of embayments on the Strait of Juan de Fuca portion of Vancouver Island and the Southern Gulf Islands in 2013 and 2016 found no green crabs, and a repeat survey in 2017 found only a handful of individuals at one adjacent site, Becher Bay (T. Therriault, pers. comm.), suggesting Sooke Basin was a likely source of propagule origin within the Salish Sea.

Green crabs have been detected, at least periodically, in all three coastal sites (Barkley Sound, Willapa Bay, and Coos Bay) since at least 1999, though abundances across these sites, and over time, have varied by several orders of magnitude (Behrens Yamada et al. 2013; Gillespie et al. 2015). Barkley Sound was selected as representative of northern source populations because of its relative proximity to the Salish Sea and because it has the highest crab abundance of all sites surveyed in British Columbia (Behrens Yamada et al. 2013; Gillespie et al. 2015). The Columbia River plume (on the border between Washington and Oregon) can significantly impact along- and cross-shelf dispersal of plankton because the density difference poses a barrier between the plume and the coastal ocean (Banas et al. 2009; Peterson and Peterson 2009). Plankton outside of the plume can have their alongshelf transport blocked by the plume, and, if entrained into the plume, the plankton will be transported by the plume. We addressed the potential role of the plume by selecting release sites both north and south of the Columbia River. Willapa Bay was chosen as a particle release site to the north of the plume because green crabs have been detected more frequently and at higher abundances in that estuary compared to Grays Harbor. Among the four larval release sites explored in the present study, however, Willapa Bay has the smallest population of adult green crabs, and the species has been undetectable during periods when conditions were unfavorable to northward larval dispersal (Behrens Yamada et al. 2013). Lastly, we chose Coos Bay, Oregon, to represent possible source populations to the south of the Columbia River plume.

The relative freshness of the Columbia River plume poses a problem for green crab larvae during springtime, since laboratory studies have shown that larvae do not survive in a salinity 20 or less (Bravo et al. 2007). The Columbia River plume salinity varies seasonally with the magnitude of river flow. The river flow is highest in the spring, freshening the plume to a salinity of 5–15, below the survivability threshold. In late summer through winter, flow rates are lower and the plume salinity is between 20 and 25, which is sufficiently saline for survival of entrained larvae (Nash et al. 2009).

For each of the particle release sites, the specific location of release was chosen to be as close to the mouth of the bay as possible while still near a location where green crabs have been found. For example, particles in Willapa Bay were released just offshore of Toke Point (Banas, et al. 2009). This is in line with the Queiroga et al. (1994) finding that ovigerous green crabs migrate toward the mouths of estuaries when their larvae are released (described in the "Green Crab Larval Biology" section) while also maximizing the likelihood that the released particles would exit the embayments and reach the coastal ocean. The impact of this choice is that particles leave the embayments sooner than they would if they were released at the head. Particles released at the head might take days or weeks longer to exit the embayment into the coastal ocean, or they might not exit the embayment at all. This impact has only been tested for one of the four source locations used in this study (Willapa Bay in Banas et al. 2009) where self-retention was shown to be possible for particles released away from the mouth, and the magnitude of retention is higher in summer than in spring. However, this result cannot easily be extrapolated to the other source locations because of the differences in size and river flow.

Particle Release Timing

Because the seasonal timing of larval release varies with latitude and there is evidence of multiple release periods in some regions (Banas et al. 2009), particle release dates were selected based primarily on published observations of planktonic larvae. These patterns are a function of the water temperatures required for successful development of eggs and larvae (de Rivera et al. 2007, see the "Green Crab Larval Biology" section). For experiments in Barkley Sound and Willapa Bay, particles were released during spring in April–May and

July–August to match observed reproductive patterns of green crabs from those sites (Banas et al. 2009; DiBacco and Therriault 2015). No data on seasonality of ovigerous females from Sooke Basin are available, but we assumed that because Sooke Basin is between Barkley Sound and Willapa Bay, crabs in this location likely exhibit reproductive seasonality similar to those two sites. Observations from Coos Bay, nearly 500 km south of Willapa Bay, indicate a different reproductive cycle with a spring release that begins in January and continues through April, and a shorter, lower abundance, summer release in August (Shanks et al. 2011), so particle releases were simulated for January–April, and August of each year.

Green crabs preferentially release larvae at high tides and at night which increases dispersal and reduces predation (Zeng and Naylor 2018). We aimed to maximize the likelihood that particles from a monthly release would be successfully transported out of the embayments (and eventually into the eastern Salish Sea) by timing the releases for the nighttime high tide before the lowest low tide of the month. Our results might therefore overestimate the absolute average probability that a larva from a given site could be successfully transported into the eastern Salish Sea.

Particle Development

In the present experiments, particles experience a wide range of temperatures as they move from bays to shorelines and are transported up the coast and might experience a temperature range of 2–3 °C over the course of their DVM. Because it was computationally intractable to model larval development in a rapidly changing environment, all particles were considered potentially able to settle after 30 days and for up to 75 days (roughly the minimum and maximum development times observed in the laboratory). This 45-day range of competency was intended to maximize the modeled opportunity for particles to be successfully transported into the eastern Salish Sea.

A particle was considered to have been successfully transported into the eastern Salish Sea if its position during competency was east of an arbitrarily defined boundary to the eastern Salish Sea: a line extending from Victoria, British Columbia to Port Angeles, Washington (Fig. 1). We evaluated relative support for each of the release locations as potential source populations by comparing the proportions of particles that were successfully transported into the eastern Salish Sea across release dates.

Results

Across all locations and dates (38 simulated releases totaling 380,000 particles), $< 2\%$ of particles were successfully transported into the eastern Salish Sea, supporting the assumption that such advection is likely to be relatively rare. Nevertheless, all four source locations had more than one release date that resulted in successful transport of at least one of the 10,000 particles (Table 1).

Effect of Release Location on Transport Success

Releases from Sooke Basin resulted in successful transport of at least some of the particles on seven of nine release dates, more frequently than any of the other three sites. On the majority of these dates, however, the probability of successful transport was extremely low, and, on average, only 1.73% of all particles released from Sooke Basin were predicted to enter the eastern Salish Sea within their competency period. When each site was averaged across all release dates, particles released from Willapa Bay were more likely to enter the eastern Salish Sea than those from the other sites, at an average of 3.06% transport success. Coos Bay had an average transport success of 1.86% comparable to Sooke Basin, and Barkley Sound was the least likely with only 0.46%.

It was possible for a particle to be present in the eastern Salish Sea and not be counted as successfully transported because it was flushed back out to the coastal ocean before it reached competency at 30 days of age. Most particles that reached the eastern Salish Sea remained there and were not subsequently flushed. Due to proximity, particles released from Sooke Basin often reached the eastern Salish Sea within a week, but the percentage of successfully transported particles could ultimately be low if they were then swept by the tidally averaged westward flow out to the Pacific Ocean before they reached 30 days old.

Effect of Release Timing on Transport Success

Within each site, there was substantial variability in the proportion of particles that were successfully transported into the eastern Salish Sea depending on the date of release. For every release site, the release date with the greatest probability of successful transport occurred in August, though the year differed depending on site. The northern three release sites were most successful in August 2014, while the southernmost site was most successful in August 2016. For Barkley Sound and Willapa Bay, the two sites of intermediate distance to the eastern Salish Sea, August was the only month of release in which any of the particles reached that region during their competency period. Coos Bay differed from this trend only in that the release during August 2015 did not result in any particles reaching the eastern Salish Sea, while one in January 2016 did. But this is a month in which first-stage zoea are not typically observed in the water column at the more northern sites (see “Particle Release Timing” in the “Methods” section), so we did not model particle releases in those locations for that date.

Table 1 Percent of 10,000 released particles successfully transported into eastern Salish Sea organized by date of release (row) and release location (column). Particles were counted as successful if present in eastern Salish Sea when 30–75 days old. Gray shading = no release. White shading = no successfully transported particles. Light yellow shading = 0–1% success. Yellow shading = 1–10% success. Dark yellow shading = > 10% success

Date	Sooke Basin	Barkley Sound	Willapa Bay	Coos Bay
10 Aug 2014	11.38	4.10	27.46	0.22
27 Jan 2015				0
22 Feb 2015				0
22 Mar 2015				0
19 Apr 2015	0.81	0	0	0
18 May 2015	0.03	0	0	
3 July 2015	0	0	0	
1 Aug 2015	0.09	0.03	0.02	0
17 Jan 2016				0.08
13 Feb 2016				0
12 Mar 2016				0
9 Apr 2016	1.90	0	0	0
8 May 2016	0.68	0	0	
2 July 2016	0	0	0	
2 Aug 2016	0.64	0.01	0.05	20.16
AVERAGE	1.73	0.46	3.06	1.86

Oceanographic Conditions Favoring Transport Success

To see how dependent particle transport success was on flow reversals, a timeline was made overlaying transport successes from each release experiment with whether the Strait of Juan de Fuca had reversed flow or normal flow at the surface during the dates the particles were active (Fig. 2). These results supported the hypothesis that flow reversals could contribute to successful transport of larvae into the eastern Salish Sea from the outer coast. That is, for the three coastal source locations, successful transport only occurred following flow reversals, but such reversals were not required for particles released from the sole inland source location, Sooke (Fig. 2). During some April and May releases, particles released in Sooke Basin were successfully retained in the eastern Salish Sea, albeit at low probabilities, without any coincident flow reversal during the dispersal window. Releases from the other locations during those months did not result in any successful transport of particles to the eastern Salish Sea. Reversal events did not always result in successful transport of particles, however. Even though those released from Coos Bay in January, February, and March overlapped with flow reversals, they nevertheless had very low probability of being transported into the eastern Salish Sea, and in some release months, no particles from Coos Bay were transported to that region.

Discussion

Overall, the probability of larvae reaching the eastern Salish Sea from any site appears to have been quite low, even though our experiments were run during years with strong ENSO conditions, which have been observed to be favorable for larval transport and survival (Behrens Yamada and Kosro 2010). We also observed that successful transport of particles into the eastern Salish Sea could be geographically and seasonally variable.

Effect of Release Location on Transport Success

Sooke Basin was a potential source of crab larvae for other areas of the Salish Sea, but larvae from Sooke were not as persistent and ubiquitous in the eastern Salish Sea as might be expected based on geographic proximity. Indeed, as discussed above, distance of the source to the eastern Salish

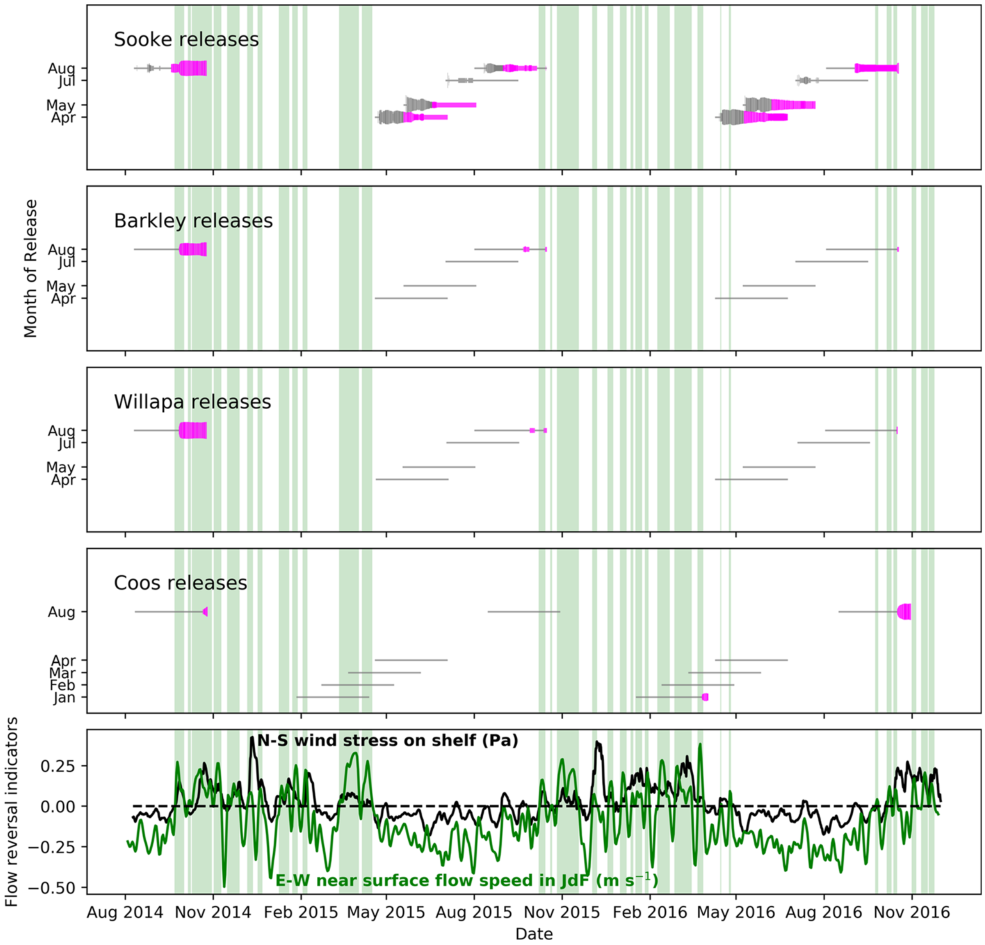


Fig. 2 Timeline indicating successful transport of larvae into eastern Salish Sea per release overlaid with occurrence of flow reversals (green shading). Bottom subplot shows presence of two flow reversal indicators: wind direction over coastal ocean (black) and flow direction in Strait of Juan de Fuca (green). Release locations separated into subplots. Horizontal lines represent release dates. Number of larvae transported into eastern Salish Sea indicated by line thickness. Line is magenta when larvae meet two conditions: present in eastern Salish Sea and 30–75 days old. Otherwise, line is gray

Sea by itself was not a strong predictor of probability of transport success. One release event (August 2016) from Coos Bay had a higher rate of transport success than any release from Sooke Basin, contrary to the hypothesis that the closest source is necessarily the most likely source. Sooke Basin is unique among release sites in that particles debouche into the Strait of Juan de Fuca rather than the Pacific Ocean. The Strait of Juan de Fuca has two features that enhance the likelihood of transport success relative to the coastal ocean: a restrictive coastline and high flow variability (Sponaugle et al. 2002). Particles released from Sooke exit into the Strait of Juan de Fuca and are restricted topographically to travel either to the eastern Salish Sea or to the Pacific Ocean. The high flow variability from the tidal currents in the Strait of Juan de Fuca enhances horizontal dispersion of particles so that even when tidally averaged flows would transport particles to the Pacific Ocean (as during a non-reversed flow regime), some particles can be transported into the eastern Salish Sea.

Transport success from Willapa Bay and Barkley Sound coincided temporally, despite being on opposite sides of the Strait of Juan de Fuca. During typical flow regimes, the Strait of Juan de Fuca is upstream of Barkley Sound. While there is evidence that some upstream larval dispersal is not uncommon (Gharouni et al. 2017; Pringle et al. 2011; Sponaugle et al. 2012), it was expected that transport success from Barkley Sound would be low and out of phase with transport success from Willapa Bay. This hypothesis was supported in part by the result that transport success from Willapa Bay was consistently greater than transport success from Barkley Sound, but the hypothesis was challenged by the synchrony of success from the two locations.

Transport success from Coos Bay was inconsistent. This could be due to the influence of the Columbia River plume, which (as hypothesized in the "Particle Release Locations" section) can block upshelf transport from sites south of the plume if particles are not entrained in the plume (Peterson and Peterson 2009). Whether particles being transported from the south are blocked by the Columbia River plume or entrained in it may depend on the direction of the plume at the time that particles arrive. Another hypothesis is that since the distance between Coos Bay and the eastern Salish Sea was greater than for the other sites, the stochastic nature of larval dispersal makes successful transport inherently less likely. Regarding the latter, it appeared that time was not the limiting factor, and particles from Coos Bay that did reach the Strait of Juan de Fuca were transported there on timescales similar to particles from the other two coastal sites.

Effect of Release Time on Transport Success

Seasonal patterns emerged from the results. Broadly speaking, the eastern Salish Sea might be most easily reached by larvae that are present in the water during early fall. August particle releases were the most consistently successful, with transport success into the eastern Salish Sea from every location for every year (except for from Coos Bay in August 2015). Furthermore, the releases that had the greatest fraction of successfully transported particles were August releases. On the other hand, summer was the least likely season for transport success. Particles released in July were never successfully transported into the eastern Salish Sea. Since the wind direction was persistently southward during the releases in April 2015, May 2015–2016, and July 2015–2016, transport success was expected to be consistently low or impossible for those release experiments. This hypothesis was supported by the result that no particles released in April, May, or July in Coos, Willapa, and Barkley were successfully transported into the eastern Salish Sea, but challenged by the springtime transport successes from Sooke Basin. This could be explained by the seasonal variation in tidal amplitude in the Strait of Juan de Fuca from a greater tidal range in early summer near the summer solstice to a smaller tidal range in late summer (Mofjeld and Larsen 1984). A greater tidal range would come with stronger tidal currents, extending the tidal excursion and increasing the horizontal dispersion of particles in the Strait of Juan de Fuca, allowing more particles to be advected into the eastern Salish Sea during westward subtidal flow in the Strait of Juan de Fuca. For the coastal release locations, the improbability of larvae reaching the eastern Salish Sea during spring would be compounded by the spring freshet of the Columbia River plume, a seasonal event that freshens the plume below the salinity threshold for larval survival (as described in the "Particle Release Locations" section). During the fall and winter, the only seasons with transport success of particles from coastal release locations, the Columbia River plume salinity is high enough for larvae to survive (Nash et al. 2009; Bravo et al. 2007).

It had been hypothesized that winter would be a likely season for advection of larvae into the eastern Salish Sea because of southerly winds and the likelihood of flow reversals in the Strait of Juan de Fuca (Behrens Yamada et al. 2017). However, the winter particle releases in Coos Bay during January and February were not successful except for the release in January 2016, suggesting winter is not as likely as previously expected to coincide with arrival of larvae into the eastern Salish Sea.

Effect of Oceanographic Conditions on Transport Success

Fall and winter particle releases co-occurred with flow reversals, but only one spring release, April 2016, co-occurred with a brief flow reversal (which is typical, as meteorological conditions during spring and summer are less conducive to flow reversals). Within the fall and winter, flow is reversed approximately half the time, with reversals as brief as a few days and as long as a few weeks (Thomson et al. 2007). For green crabs, spring spawns produce more larvae than fall spawns (as described in the "Particle Release Timing" section), so there is a mismatch between spawn size and the likelihood of co-occurrence with flow reversals and transport success. This mismatch contributes to the overall low probability of green crabs reaching the eastern Salish Sea.

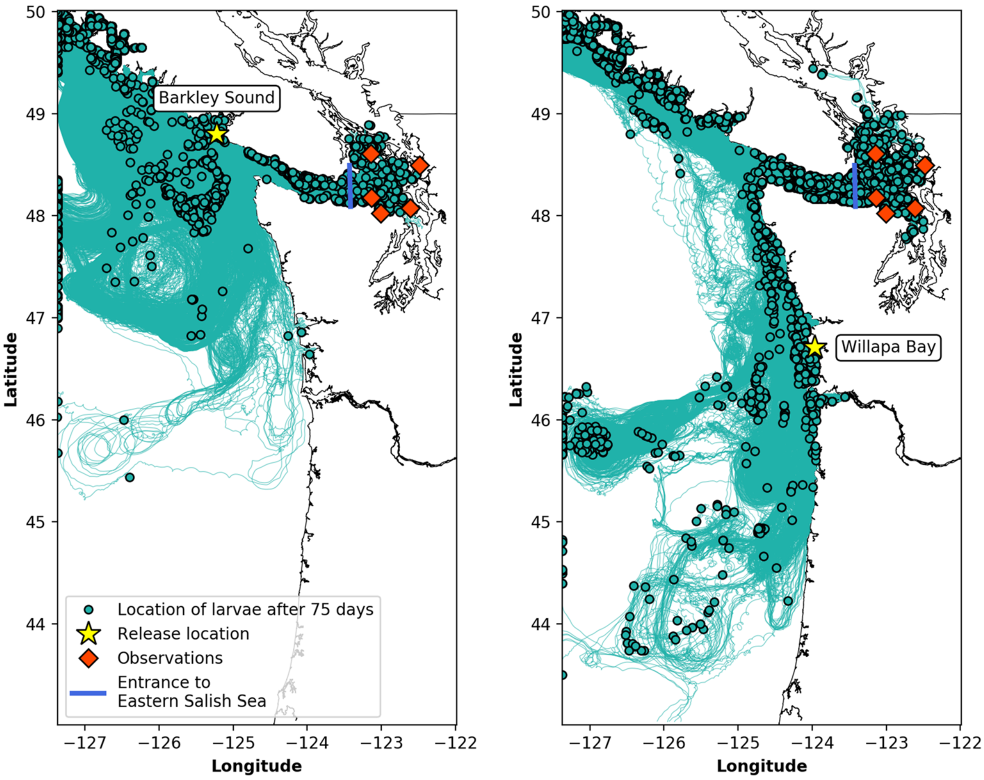
Flow reversals contributed to transport success differently for each of the release sites. Successful transport from Sooke Basin into the eastern Salish Sea was possible without flow reversals, although flow reversals enhanced transport success. Particles released from Willapa and Barkley were successfully transported into the eastern Salish Sea during flow reversals, but only when the timing of the flow reversal corresponded to the presence of particles in adjacent waters. By examining particle tracks (Fig. 3), the synchrony of Willapa Bay and Barkley Sound appears to reflect a lag between the flow reversals and particle releases. When particles were released from Barkley Sound during a southward flow regime, they had a chance to disperse southward before the flow reversed northward. Therefore, it may still be true that coastal larvae enter the Strait of Juan de Fuca from the south during a flow reversal, and it is more likely that larvae entering the Strait of Juan de Fuca from the south were released in the south, but it is not impossible for larvae released in the north to enter from the south.

For Coos Bay, the relationship between flow reversals and transport success was weaker. Even though Coos Bay green crabs spawn later in the year when flow reversals are more common, transport success from Coos Bay was not more likely than from the other sources. This might be because of the great distance between Coos Bay and the eastern Salish Sea, as noted above.

Future Directions

Although results of these particle release experiments revealed viable transport pathways between established green crab populations and the eastern Salish Sea, additional information could further improve our understanding of potential green crab spread in this this region. In particular, the absolute probability of larvae reaching the eastern Salish Sea from any one of the four sites tested here will also be strongly influenced by the size of the adult crab population at the release site. That is, the probability that a given site is a source for green crab larvae entering the eastern Salish Sea is a product both of the likelihood that any individual larva released from that site could be transported there, and of the actual number of larvae released from that site. Data to assess relative population densities are not consistently available for the times and locations assayed here, but we can draw some general conclusions. For one, Willapa Bay, despite showing a relatively high potential for transport success for larval releases from 2014 to 2016, had extremely low densities of adult green crabs during those years, indeed below detection limits in 2014 (Behrens Yamada et al. 2013). Thus, the overall chance that Willapa Bay was a

Fig. 3 August 10, 2014 larval release experiments from Willapa Bay and Barkley Sound. Larvae were successfully transported into the eastern Salish Sea from both release locations



source population is quite low. By contrast, periodic monitoring in Sooke Basin and Barkley Sound indicates that those populations are typically much larger than either Coos or Willapa Bays, presumably increasing the likelihood that those sites, rather than the southern sites, could act as a source relative to model results. Similarly, there is uncertainty in the modeled probabilities of successful recruitment from all four sources because only a handful of potential release periods were evaluated.

There are also a few open questions that arise from restrictions in the model domain that could be addressed in future investigations. The model domain prevented us examining the possibility that green crab larvae can be advected into the eastern Salish Sea from the north, through Johnstone Strait, or from populations in California. The first scenario is considered unlikely because transport through Johnstone Strait is 1/15 of the magnitude of transport through the Strait of Juan de Fuca (Thomson 1981). We attempted to account for the possibility of larvae arriving from California by modeling particle release from Coos Bay, the closest population to the southern model extent.

Another source of uncertainty inherent in the model is that it does not resolve exchange flow in sites where female green crabs release larvae. Because smaller rivers were not included in the model, particles were transported out of embayments by tidal currents alone and not exchange flow. The impact of exchange dynamics within embayments on large scale connectivity is an open question and would also be a good topic for future study.

Conclusions

The main conclusion is that green crab larvae released in any of the source locations tested in this study could be transported into the eastern Salish Sea, but only infrequently. This connectivity influences the potential for unassisted (by humans) regional spread of green crabs (Pineda et al. 2007). In addition, larvae from Sooke Basin are apparently not substantially more likely to be advected into the eastern Salish Sea than larvae from populations on the Pacific Coast, possibly affording some protection for inland shorelines from further range expansion by this relatively dense population. Understanding sources, connectivity, and pathways of spread (Hulme 2009) can inform ongoing trans-boundary management efforts between the USA and Canada. Two potential strategies include targeting likely source populations for eradication and control and focusing early detection and control efforts during years with oceanographic conditions favorable to dispersal. These findings also help explain why green crabs apparently did not expand their range into the Salish Sea (excepting Sooke) prior to 2016: the overall low probability of transport into the Salish Sea from any of the potential sources observed here, combined with the fact that ENSO events, and associated warm waters, were much weaker between 1999 and 2014, likely did not provide sufficient opportunity for advection of larvae. Lastly, global climate change is predicted to increase the frequency and intensity of ENSO events (Cai et al. 2015) which, based on prior research (Behrens Yamada and Kosro 2010) and the present model results, indicates greater likelihood of successful transport of green crab larvae into the eastern Salish Sea. In the face of more frequent or more intense ENSO events, the Strait of Juan de Fuca might pose less of a barrier to further introductions of green crabs or other non-indigenous species.

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