

Green Crab Larval Retention in Willapa Bay, Washington: An Intensive Lagrangian Modeling Approach

Neil S. Banas · P. Sean McDonald · David A. Armstrong

Received: 19 January 2009 / Revised: 18 April 2009 / Accepted: 25 April 2009 / Published online: 5 June 2009
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Abstract The European green crab (*Carcinus maenas*) is invasive on the U.S. West Coast. This study uses a high-resolution circulation model to determine the likelihood that green crab larvae spawned in Willapa Bay, Washington could be retained by circulation and behavior long enough to reach maturity and resettle within the bay. A particle-tracking method (the “diffusive Lagrangian return map”) is presented that makes it possible to track the dispersion of hundreds of thousands of model larvae—each subject to three-dimensional advection, vertical turbulent diffusion, and imposed vertical migration behavior—over their full 30–50 days development time with modest computational resources. Larvae spawned in summer show significant retention (5–40%) in the southern and western portions of the bay, including the Stackpole shoals near the mouth, the area most likely to be colonized by late-stage megalopae arriving from the coastal ocean. Larvae spawned in spring show much less retention throughout the bay because of (1) increased flushing caused by increased river input relative to summer conditions and (2) longer development times caused by lower water temperatures. The role of larval swimming behavior is secondary to hydrodynamics in setting these spatial and seasonal patterns of retention.

Keywords Green crab · Invasive species · Willapa Bay · Circulation modeling · Biophysical modeling ·

Particle tracking · Dispersion · Larval behavior · Individual-based modeling

Introduction

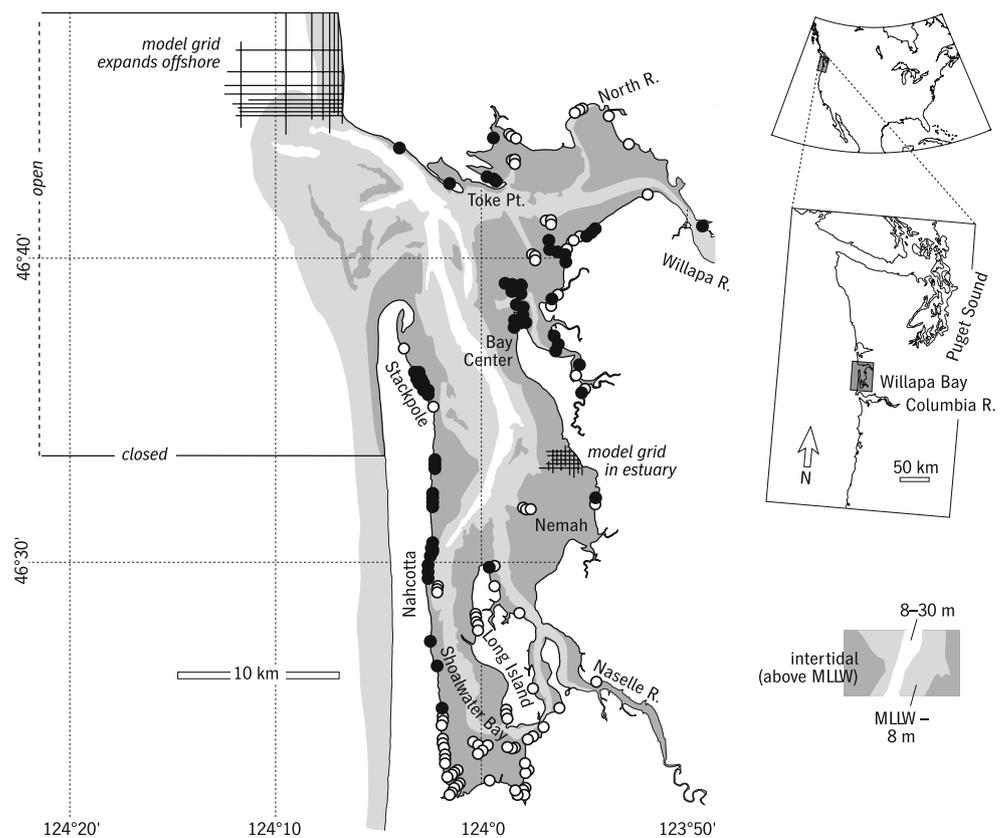
This study considers the potential for self-recruitment by the European green crab, *Carcinus maenas*, in Willapa Bay, Washington, USA, using a high-resolution circulation model and simple models of larval behavior, in the context of trapping data (Fig. 1). *C. maenas* (adults 40–90 mm carapace width [CW]) is a common brachyuran species native to coastal waters of Europe and North Africa (Almacá 1962; Christiansen 1969; Manning and Holthius 1981), where it structures and regulates benthic communities through competition (Eriksson et al. 1975) and predation (Dare and Edwards 1976; Reise 1977; Jensen and Jensen 1985; Sanchez-Salazar et al. 1987; Schratzberger and Warwick 1999; Richards et al. 1999). Aided by human migration and trade, green crab has expanded its worldwide range dramatically over the past two centuries (see review by Carlton and Cohen 2003). Established populations now occur in shallow coastal waters of five continents (LeRoux et al. 1990; Griffiths et al. 1992; Cohen et al. 1995; Grosholz and Ruiz 1995; Hidalgo et al. 2005). Significant ecological effects have been attributed to green crab in many invaded areas, including local declines of economically and ecologically important invertebrates (Glude 1955; Hanks 1961; Grosholz et al. 2000; Grosholz et al. 2001; Floyd and Williams 2004).

While green crab occupy a variety of nearshore habitats within their worldwide range (e.g. Crothers 1968, 1970; Griffiths et al. 1992), in the northeastern Pacific, populations appear limited to low-energy embayments and estuaries (Grosholz and Ruiz 1995, 1996) and

N. S. Banas (✉)
Applied Physics Laboratory, University of Washington,
Campus Box 355640, Seattle, WA 98195, USA
e-mail: neil@apl.washington.edu

P. S. McDonald · D. A. Armstrong
School of Aquatic and Fishery Sciences,
University of Washington,
Campus Box 355020, Seattle, WA 98195, USA

Fig. 1 Map of Willapa Bay, Washington with model grid indicated. *Black circles* mark locations of *C. maenas* captured within Willapa Bay from June 1998 through September 2008. *White circles* mark locations where baited traps were set but no crab were captured. Data are synthesized from the WDFW records and other unpublished sources. These data do not reflect fishing effort



reach highest abundance in isolated intertidal areas and marsh habitats largely devoid of native crab fauna (Hunt and Yamada 2003; McDonald et al. 2006; Jensen et al. 2007). A self-perpetuating population became established in San Francisco Bay prior to 1989 (Cohen et al. 1995; Grosholz and Ruiz 1995). By 1993–1994, the species had colonized five nearby embayments from Monterey Bay (Elkhorn Slough) to Bodega Bay harbor (Cohen et al. 1995; Grosholz and Ruiz 1995), and in 1997, a few individuals were captured in Coos Bay, Oregon, 665 km north of the original population. Anomalously strong oceanic transport in 1997–1998 (Huyer et al. 2002) spread larvae as far north as the west side of Vancouver Island, British Columbia, Canada, the current northern limit of the species' range (Jamieson et al. 2002). Patterns in the range expansion of green crab largely reflect interannual variability in ocean circulation and the El Niño–Southern Oscillation (ENSO; Yamada et al. 2005).

At present, populations of green crab in estuaries and embayments between central California and Vancouver Island are very small, casting doubt on their ability to be self-sustaining (Carlton and Cohen 2003; Yamada et al. 2005). Size frequency and growth data compiled by Yamada et al. (2005) suggest that the large cohort of crabs that settled during 1997/1998 had largely died out by 2004, and there has been little evidence of subsequent significant recruitment events. Without substantial input of larvae from

larger populations in central California, these satellite (sink) populations will only persist at extremely low levels. The frequency of El Niño occurrence (a high-level event sensu Cowen 1985) may be too low relative to the longevity of individual green crab (4–6 years; Yamada et al. 2005) to maintain or grow persistent populations within most small coastal embayments, and “normal” recruitment (low-level events) may not provide enough individuals to sustain population growth in the interim.

Thus, a self-sustaining population in an estuary between central California and Vancouver Island may be a prerequisite for significant spread of green crab within the region and particularly into Puget Sound and Georgia Strait. (The human-mediated vectors likely responsible for the initial spread of the species into San Francisco Bay have largely been eliminated as a result of stricter regulations.) Willapa Bay is the largest coastal-plain estuary north of San Francisco Bay that received significant larval recruitment in 1997/1998. It contains expansive tidal flats and a variety of habitats suitable for green crab (Dumbauld and Kauffman 1998; Yamada 2001). Moreover, past observations and modeling work suggest that conditions are appropriate for self-recruitment of other invertebrate larvae (Chapman and Esveldt 1943; Banas et al. 2007). On the basis of gross estimates of tidal and freshwater residence time (Hickey and Banas 2003), one would expect the other coastal-plain estuaries of Washington and Oregon to have a retention

and self-recruitment potential at most comparable to that of Willapa Bay.

The central question of the present study, then, is to determine whether green crab can form a self-sustaining population in Willapa Bay. A complete answer to this question would require an understanding of both larval retention and population dynamics, but the latter is unfortunately well beyond the scope of available data. Instead, we address two subsidiary questions that are critical to the larger issue:

1. Which areas of Willapa Bay are most likely to receive exogenously produced larvae from the coastal ocean?
2. From which potential spawning locations in the bay could green crab larvae be retained by circulation and behavior long enough to resettle in the bay at the end of their development, instead of being flushed out to sea?

We answer these questions by combining past observations of flushing patterns in Willapa Bay (Banas et al. 2004); a hydrodynamic model that has been shown to reproduce these patterns (Banas and Hickey 2005); our general knowledge of green crab larval behavior in other systems; and green crab presence/absence data from trapping in Willapa Bay.

Model and Methods

The Model

The hydrographic model used in this study has been described in detail by Banas and Hickey (2005, hereafter BH05). The model is an implementation of the general estuarine transport model (<http://getm.eu>), a relatively new hydrodynamic model developed for systems like Willapa Bay where flow over complex topography and flooding and drying of intertidal areas are central (Burchard and Bolding 2002; Stanev et al. 2003; Stanev et al. 2007). The model domain in our implementation for Willapa Bay is shown in Fig. 1. The coastal “ocean” in our model is highly idealized, a semienclosed reservoir, open only to the west, with depth limited to 30 m, and without any along-shelf currents. It is included only so that tidal forcing can be applied to the bay gently and smoothly. The model grid is 175-by-82 in the horizontal with 12 sigma levels in the vertical. The bay itself is covered by uniform squares 255.5 m on a side, although the grid spacing gradually expands to 6 km in the “ocean.” Model bathymetry is adapted from a grid developed by the U.S. Army Corps of Engineers Seattle District, who resurveyed most of the subtidal area of the bay in 1998 (Kraus 2000).

The flushing of Willapa Bay can be thought of as the sum of tidal stirring, which is essentially constant across

seasons, and river-driven exchange, which is highly variable. BH05 validated the models’ representation of both mechanisms. Crucially, the model reproduces the 20-fold along-channel variation in the strength of the horizontal tidal diffusivity, which is known at five locations from analysis of salinity time series (Banas et al. 2004). This is a stringent test that directly confirms the model’s ability to reproduce not just the gross flood–ebb cycle of tidal currents, but the small asymmetries in tidal currents (“tidal residuals”) that drive tidal flushing. The model’s seasonal, river-driven dynamics were validated by comparing a realistic 11-month hindcast with salinity time series along the main channel (BH05). At high riverflow levels, the model underpredicts salinity within 15 km of the bay mouth, but in the central and landward reaches of the bay, the model reproduces the salt intrusion length (and by implication the strength of river-driven flushing) with no measurable bias in any season.

In general, this model can be forced by realistic tides (imposed as sea-level fluctuations at the open ocean boundary) and variable riverflow. In this study, to aid mechanistic understanding, we use idealized scenarios almost exclusively. Riverflow is held constant at a typical level representing a given season, and the tides are simplified with only the largest constituents included: the lunar semidiurnal (M2, 12.42 h period, 0.98 m half-amplitude) and lunar diurnal (K1, 23.93 h period, 0.43 m half-amplitude). BH05 showed that the M2 constituent alone (with amplitude chosen to match the total root mean square amplitude of the real tide) is sufficient to reproduce the along-channel profile of horizontal tidal diffusivity, as discussed above. We include K1 in this study to allow for the possibility of a net correlation between diurnal tidal currents and diurnal larval behavior. In addition to these idealized-forcing scenarios, we make use of the 11-month realistic hindcast alluded to above in which river and tidal forcing were taken from observations (BH05) for one ancillary result (Fig. 5) and background consistency checks (“larval tracking numerics” below).

Model particles representing green crab larvae were tracked in combinations of three larval behavior model scenarios and two idealized seasonal scenarios. We will describe these scenarios first, and then explain the numerical methods used to implement them.

Larval Behavior Scenarios

Larval behavior is stage-dependent and will also affect model results. Although all but late-stage megalopae are fairly weak swimmers, larvae can maximize or minimize horizontal transport by moving vertically in tidal flows (Hill 1991, 1995). According to Queiroga and Blanton (2005), the behavior is used extensively among decapod crusta-

ceans to facilitate dispersal or retention. Green crab larvae have been observed to vertically migrate with a diurnal period in European estuaries (Queiroga et al. 2002). In addition, first zoeae were seen to vertically migrate in synchrony with the semidiurnal tides—swimming up during ebb and thus facilitating their export from the estuary—in Ria de Aveiro, Portugal (Queiroga et al. 1997) but not in the microtidal Gullmarsfjord, Sweden (Queiroga et al. 2002). Zoeae II through early megalopae display negative phototaxis and are abundant in surface waters at night (Queiroga et al. 2002, Queiroga and Blanton 2005). Accordingly, we tested three behavioral scenarios for our model larvae (Table 1): first, a base case with no behavior included in which larvae are transported by advection and turbulence alone; second, diel migration; and third, tidally timed vertical migration for a brief period representing the first zoeal stage (5–8 days, depending on water temperature) and diel migration thereafter. In the final, megalopal stage, post larvae become competent to settle after a few days but forestall final metamorphosis and actively search for suitable habitat in which to settle (Zeng and Naylor 1996a, b); thus, only the early portion of this stage is included.

Based on laboratory observations (Duchene and Queiroga 2001; Queiroga et al. 2002), we represent vertical migration as active upward swimming for half the cycle followed by neutral behavior for the other half. An upward swimming speed of 0.6 cm s^{-1} was used, following field observations by Mileikovsky (1973).

Seasonal Scenarios

In order to determine likely spawning periods for green crab in Willapa Bay, queries were made of Washington Department of Fish and Wildlife (WDFW) catch records for 1999–2001. Available data consisted of monthly surveys conducted by WDFW personnel using baited and passive traps (for detailed methodology, see McDonald et al. 2006), as well as records of crabs collected opportunistically by hand from rip-rap, aquaculture gear, or shell bags. We

calculated the monthly sex ratio of trapped crabs because previous work has indicated that ovigerous (egg-bearing) crab generally do not enter traps (e.g., Howard 1984; Taggart et al. 2004), and the apparent absence of females may be indicative of mating and spawning activity (personal observations; Fig. 2). Thus, a male-skewed sex ratio reflects periods when females are presumed to be brooding eggs, while a decline in the ratio in consecutive months suggests a return to normal activity following hatching (Fig. 2). We also tallied the number of ovigerous females collected by hand in each month and classified the stage of their eggs (e.g., orange eggs indicate early development, while dark eggs are near hatching), as additional evidence of seasonal spawning behavior. Based on these patterns, we constructed two model scenarios (Table 1) representing two apparent spawning periods: April–May (“spring”) and July–August (“summer”).

There are two key environmental differences between the spring and summer spawning periods. First, water temperatures are higher in summer and thus larval development times are shorter. The mean April–May temperature in Willapa Bay, based on 3 years of near-surface time series at two stations (Fig. 3), is close to 12.5°C , the minimum sustained temperature for proper green crab larval development (de Rivera et al. 2007). This may explain why green crab appears not to spawn earlier in the spring in Willapa Bay, as they do in Oregon estuaries (Yamada et al. 2005). At this temperature, larvae spend on average ~ 8 days in the first zoeal stage and ~ 53 days in all stages combined (Dawirs 1985; Mohamedeen and Hartnoll 1990; Nagaraj 1993; de Rivera et al. 2007). In contrast, typical water temperatures in July and August are $\sim 17^\circ\text{C}$, the optimal temperature for larval growth: ~ 5 days for the first zoeal stage, ~ 31 days for all stages to competency (Dawirs 1985; Mohamedeen and Hartnoll 1990; Nagaraj 1993; de Rivera et al. 2007). This difference in development time by itself creates a large difference in the amount of hydrodynamic dispersion and flushing larvae are subject to. (Note that there may be some years, like El Nino years, in which summer temperatures are several degrees higher: temperatures above $\sim 20^\circ\text{C}$ would

Table 1 Seasonal and behavioral model scenarios

	Tidal forcing	River forcing ($\text{m}^3 \text{ s}^{-1}$)	Typical water temperature ($^\circ\text{C}$)	Development time to competency (days)	Behavioral cases
Spring (April–May)	Idealized mixed-semidiurnal (M2 + K1)	100	12.5	53	No behavior
Summer (July–August)	Idealized mixed-semidiurnal (M2 + K1)	0	17.5	31	No behavior Diel migration Tidally timed migration for 5 d (first zoeal stage) followed by diel migration

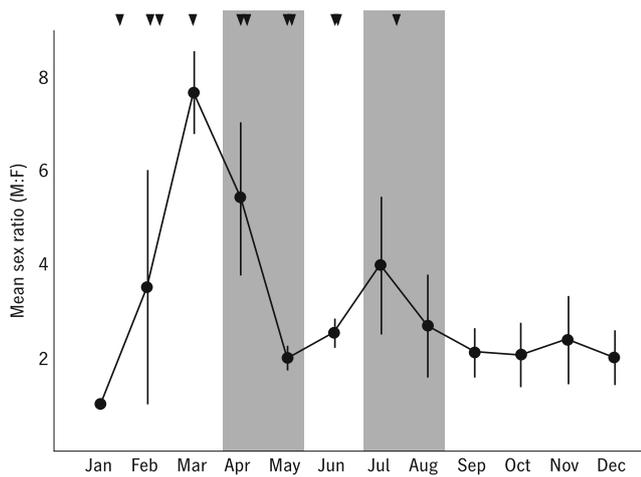


Fig. 2 Mean yearly sex ratio of adult (>30 mm CW) *C. maenas* (male to female ration) in Willapa Bay, 1998–2002, calculated from unpublished WDFW catch records. Error bars are 1 S.E. High ratio values (>4) reflect periods when few female crab enter traps, presumably because they are brooding eggs and thus unresponsive to trapping gear. A decline in the ratio in consecutive months indicates a return to normal activity following spawning. Observations of individual ovigerous (egg-bearing) female crab (*triangles*) are included on a Julian date timeline as additional evidence of seasonal egg-rearing within estuary; these crab were collected opportunistically by hand from aquaculture gear or shell bags. Data suggest two likely periods of larval release (*shaded areas*): April–May and July–August

shorten development time, increasing the possibility of retention, but also significantly decrease larval survival, especially for the first zoeal stage (de Rivera et al. 2007), such that the net effect on recruitment would be hard to predict.)

Second, the circulation of the bay changes between spring and summer. In late summer, riverflow is negligible

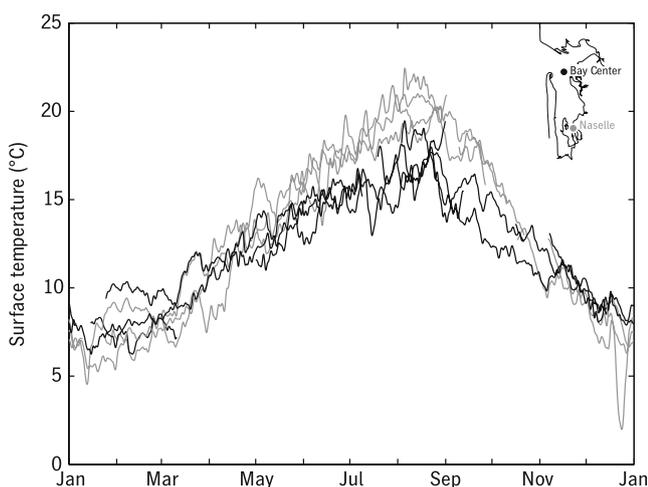


Fig. 3 Seasonal cycle of water temperature at 1 m depth at two stations, Bay Center and Naselle, 1999–2001. Data courtesy of J. A. Newton and the Washington Department of Ecology. Salinity records from this dataset are described in detail by Banas et al. (2004)

($10\text{ m}^3\text{ s}^{-1}$) and so tidal stirring is the predominant flushing mechanism (Banas et al. 2004). In spring, riverflow is close to the long-term median ($100\text{ m}^3\text{ s}^{-1}$) and thus tidal flushing is augmented by a river-driven exchange flow that increases the overall flushing rate ~30% compared with late summer conditions (BH05). This seasonal dynamical difference is represented in our model scenarios (see Table 1) by setting riverflow to a constant level of $100\text{ m}^3\text{ s}^{-1}$ (April–May) or zero (July–August) and running the model to steady state.

Larval Tracking Numerics

Willapa Bay’s dynamics are highly unsteady on every timescale from days to months (Banas et al. 2004). Our approach of representing seasons by steady-state scenarios assumes that the details of this short-timescale variability are relatively unimportant or perhaps even confounding to a general, mechanistic understanding of larval retention. In contrast, for our questions, spatial detail is essential, as is the ability to quantify even low levels of retention from a particular spawning site (without a green crab demographic model and the data to validate it, we cannot properly say whether 5% retention, say, should be thought of as “low” or “high”). In this study, we describe an approach to particle tracking—the “diffusive Lagrangian return map”—designed for such problems where the temporal variability of the flow is less important than detailed spatial coverage and the ability to track large numbers of particles efficiently. In brief, the method is to (1) track particles with high precision from all starting locations in the model domain for one short repeating unit of the simulation—in our case, one tidal day, 24.8 h—and then (2) “loop” this short time period by constructing a convenient lookup table that contains the net motion of particles in step 1. Implementation details and caveats follow.

In step 1, for each of the six circulation–behavior combinations described above (Table 1), particles were released in every grid cell of the model at high slack water and tracked for two ebb–flood cycles. This tracking included advection by all three components of velocity from the model; vertical mixing based on turbulent diffusivities from the model; and the imposed vertical swimming velocities described above. All particle tracking was done in post processing using custom Java code. The timestep of integration was kept very short, 2 s, in order to minimize volume-conservation errors associated with the model’s discretization of steep bathymetry. Vertical mixing was implemented using the random displacement method described by Batchelder et al. (2002) and North et al. (2006): this method is similar to a random walk but includes a correction based on the vertical gradient in model diffusivity. Visser (1997) and others have shown that

a careful implementation of this gradient correction is essential to prevent particles from accumulating artificially in low-diffusivity areas. The randomness introduced by the turbulent mixing calculation means that multiple particles released at the same place and time disperse significantly within a single tidal cycle. Thus, for statistical accuracy, five replicates were released in each horizontal grid cell at each of five depths, for a total of 132,000 particles per model scenario.

One could, in principle, track each larval particle with a 2-s timestep for the full 31–53 days development period, but the computing time required would be unworkable for most users; the Lagrangian return map method allows a 31-fold to 53-fold speed increase. In this method, we keep track of only the starting and ending grid cell locations of these 132,000 particles and rearrange them into a table that gives potential end locations for each start location. This lookup table is similar to a transition matrix, in the language of population modeling. In physical terms, these start–end transitions represent Lagrangian tidal residual velocities. In dynamical systems terms, they constitute a *return map*, a mapping of the model grid onto itself that represents the rearrangement done by a particular combination of circulation and behavior over 24.8 h (see Beerens et al. 1995, BH05). If we assume that every 24.8 h period in our model scenario is well-represented by this first period, then we can integrate particle trajectories over longer periods simply by reapplying the mapping (looking up an end location for a given start location, a nearly instantaneous operation) for each 24.8 h interval. Rounding off particle positions to the nearest grid cell once per lookup introduces a small amount of numerical dispersion (for 255.5 m grid cells and a 24.8-h lookup period, $\sim 0.2 \text{ m}^2 \text{ s}^{-1}$), but this is negligible compared with real hydrodynamic dispersion (BH05).

BH05 describe a simpler, less accurate version of this method in which vertical mixing, the diurnal tide, and behavior are ignored and depth-averaged currents are used in place of the three-dimensional velocity fields we have used in this study. Two complications arise in the present version. First, because of vertical mixing and vertical velocity variation, particles released in one grid cell may end in many: the return map is multiply valued. To track a single larva, we choose an end location at random from the list of (weighed) possibilities at each iteration of the return map. Second, there is a mismatch between the 24.8-h return map period and the ~ 24 -h period of the K1 tide and diel migration. Since the return map is calculated from trajectories that begin and end at high slack, this mismatch—which can be thought of as a kind of round-off error—amounts to 0.8 h of weak advection and mixing near slack water. We confirmed that this round-off error is relatively small ($\sim 4\%$ of net daily transport) by comparing

24 and 24.8 h averages in 30 days of realistically varying currents at test locations in the 1999–2000 hindcast mentioned above. (If the diurnal tide did not have such a negligible role in our results [see below], then it might be necessary, at great computational cost, to use a full spring–neap cycle rather than 24.8 h as the base unit of the return map calculation, and even this would be imprecise.)

The principal benefit of the diffusive Lagrangian return map method is the huge increase in computational efficiency, which allows much better spatial and statistical coverage for a given investment of computer time. This efficiency also allows one to track large numbers of particles interactively: a Java-based tool demonstrating this for summer conditions in Willapa Bay can be found at <http://coast.ocean.washington.edu/willapa/tidemodel/>. Finally, note that one can invert the return map (linking each end location to the start locations that lead to it, rather than the other way around) and thus track particles backwards in time (Batchelder 2006) with equal ease.

Results

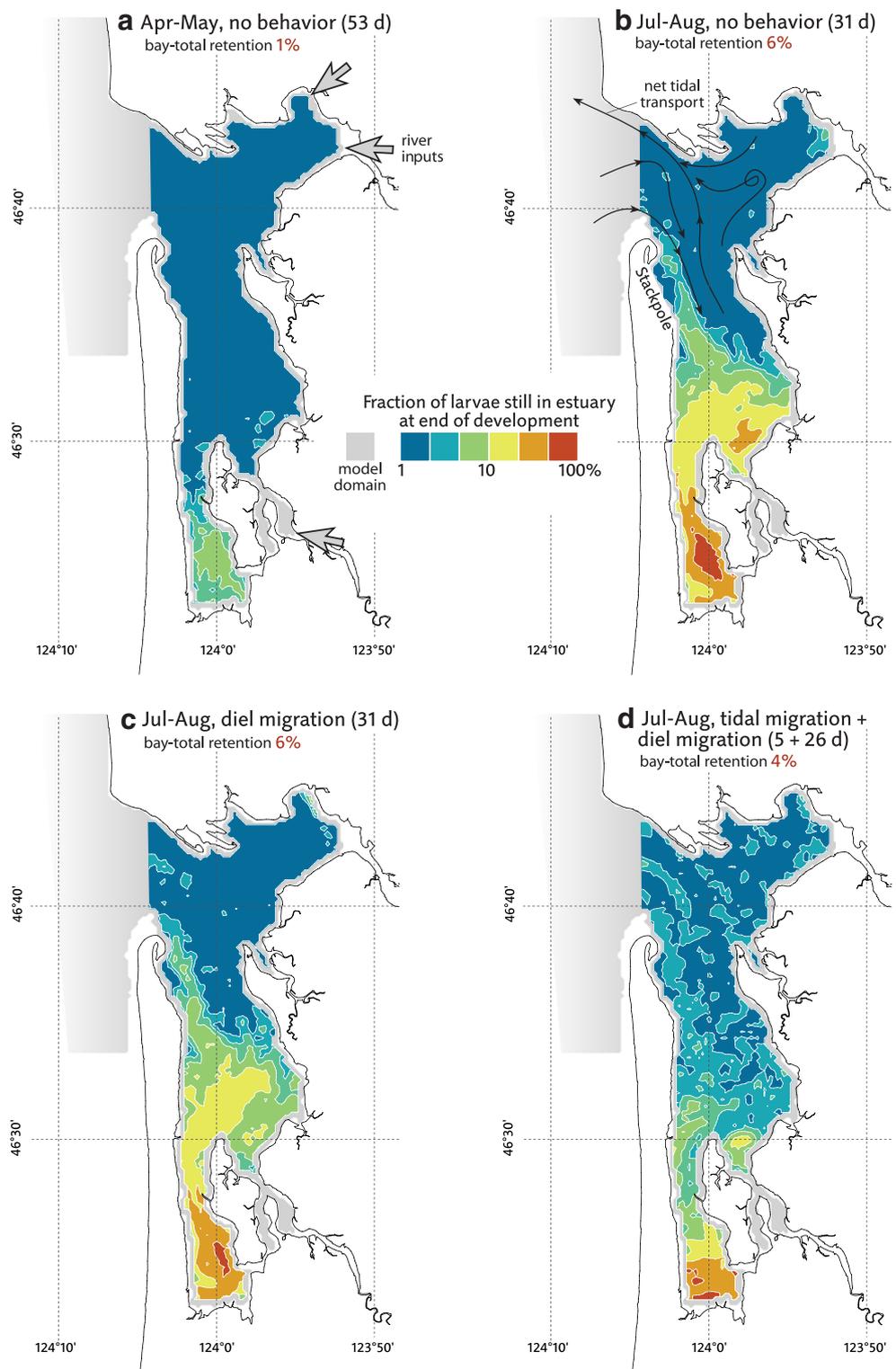
Seasonal Variation in Larval Retention

Results from the intensive particle tracking described above are summarized as maps of likelihood of larval retention in Fig. 4. In each horizontal grid cell in each scenario, 100 particles were tracked using the return map method; likelihood of retention is defined as the fraction of the 100 still found in the estuary at the end of their development. The lowest resolvable value is therefore 1 out of 100=1%. The full model domain is shaded to indicate the high intertidal areas and narrow channels where even with a timestep of 2 s volume-conservation errors are too large (i.e., the depth variation between adjacent grid cells too steep) for meaningful statistics.

Spring and summer retention and flushing patterns driven by circulation alone, with no larval behavior included, are shown in Fig. 4a, b. In spring, retention is indistinguishable from zero everywhere except the far south end of the bay. In summer, the tidal circulation flushes the northern bay efficiently, but retention is much higher in the midestuary, in the Nemah area, and the Stackpole area on the west side of the bay near the mouth.

The weaker retention in spring is consistent with both the faster spring circulation and the longer development times. A hybrid model case (not shown) in which larvae were tracked for a spring development period (53 days), but in the slower summer circulation, suggests that the two effects play comparable roles in establishing the spring–summer contrast shown in Fig. 4a, b.

Fig. 4 Likelihood of retention of model larvae spawned throughout Willapa Bay, in four model scenarios: **a** spring spawning period, no larval behavior; **b** summer spawning, no larval behavior; **c** summer spawning, larvae vertically migrate with a 24-h period; **d** summer spawning, larvae vertically migrate with a 12.42-h period for 5 days (the zoea 1 stage) and with a 24-h period thereafter. The net (tidally averaged or “residual”) tidal circulation in the outer estuary as schematized by Banas and Hickey 2005 is also shown in **b**



The Role of Larval Behavior

The variants on the summer base case in which larval behavior is included are shown in Fig. 4c, d. Inclusion of diel migration makes very little difference in the pattern of retention (Fig. 4c). We tested four relative phasings

between the modeled day–night cycle (and hence diel migration) and the modeled mixed-semidiurnal (M2 + K1) tide; none of these cases showed qualitative differences from the retention likelihood map shown in Fig. 4c, which is an average of the four (cell by cell, correlation between the individual phasings, and the average has $r^2=0.7$; for

four-by-four cell averages, $r^2 > 0.9$). The average of multiple phasings is most appropriate here, since our analysis period is much longer than the 15-day beating between M2 and K1 frequencies.

Note that, although the integrated effect of diel migration on retention is weak, these model larvae are in fact strong enough swimmers to control their vertical position in most (but not all) conditions. The diel migration of 50 larval particles, tracked for 5 days in a one-dimensional (vertical) flow field taken from April 2000 in the 11-month hindcast described by BH05, are shown in Fig. 5. During the day, when no behavior is imposed, turbulent mixing rapidly disperses the larvae through the entire water column. During the night, when larvae are swimming upwards, they are frequently found at the surface boundary (e.g., day 4), indicating that their swimming is much stronger than turbulent dispersion. Only on some flood tides is this not the case (in general, turbulence in a stratified estuary is stronger on flood than on ebb; e.g., Stacey et al. 1999). For example, ~1 day into the simulation, larvae are dispersed downwards for most of a nighttime flood, although this effect diminishes on subsequent nights as tidal amplitude decreases slightly.

Thus, the similarity of the no-behavior case and the diel-migration case (Fig. 4b, c) does not indicate that larval swimming can be thought of as weak. Instead, it indicates that the depth variation of the K1 tidal constituent—the only part of the model velocity field that diel, behavioral changes in vertical position could correlate with—is not important compared with other hydrodynamic transport and dispersion.

In contrast, tidally timed vertical migration (which can correlate with depth variation in the dominant M2 tidal constituent) does have a measurable effect on larval retention (Fig. 4d). Adding a brief period of ebb-timed

vertical migration to the summer model case increases the spatial scatter in the retention likelihood map and partially flattens the along-estuary gradient (Fig. 4d vs. b). The basic pattern seen in the no-behavior case persists, but retention in the Stackpole area now appears more similar to that in the rest of the northern bay. Bay total retention is weaker (4% vs. 6%; Fig. 4), as one would expect for the addition of swimming behavior timed to facilitate export.

Spatial Connectivity

In this presentation of results, we have described retention in point-by-point terms, mapping the retention and flushing process by spawning location (Fig. 4). It is important to note, however, that on the 1- to 2-month timescale of green crab larval development, retention of any particle is essentially a bay-wide process. As an example of this, the spatial connectivity of the Stackpole area with the rest of the bay in the summer, no-behavior case is illustrated in Fig. 6. The spawning locations of all model larvae found at Stackpole at the end of their 31-day development are shown in black; the end locations of all larvae spawned at Stackpole and retained within the bay are shown in gray. Both sets of points essentially fill the entire estuary, particularly the more retentive portion of the bay to the south. (A large number of end locations [gray] are also found in the main channel near the mouth: most of these larvae are likely to be flushed out soon by the net tidal circulation, although some will be dispersed back into the central bay (BH05).)

This bay-wide connectivity indicates that there is a substantial quantitative difference between “retention” as we have defined it (larvae ending their development anywhere within Willapa Bay) and a stricter, local, “self-

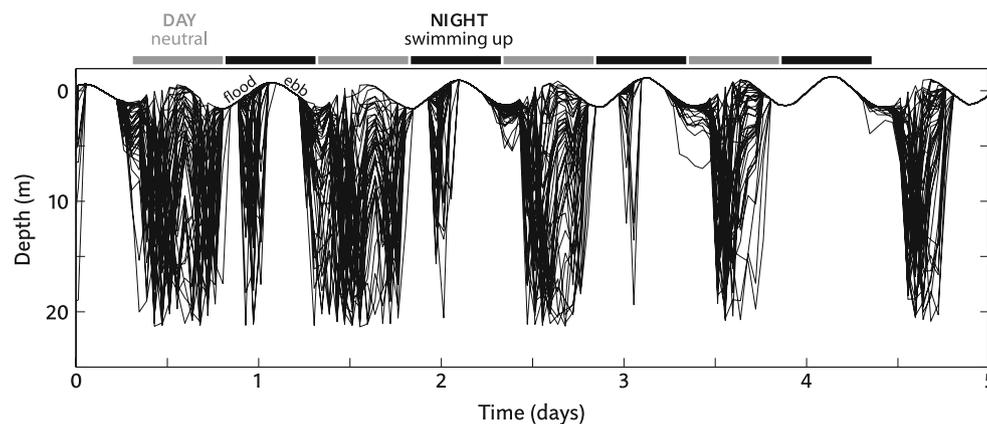
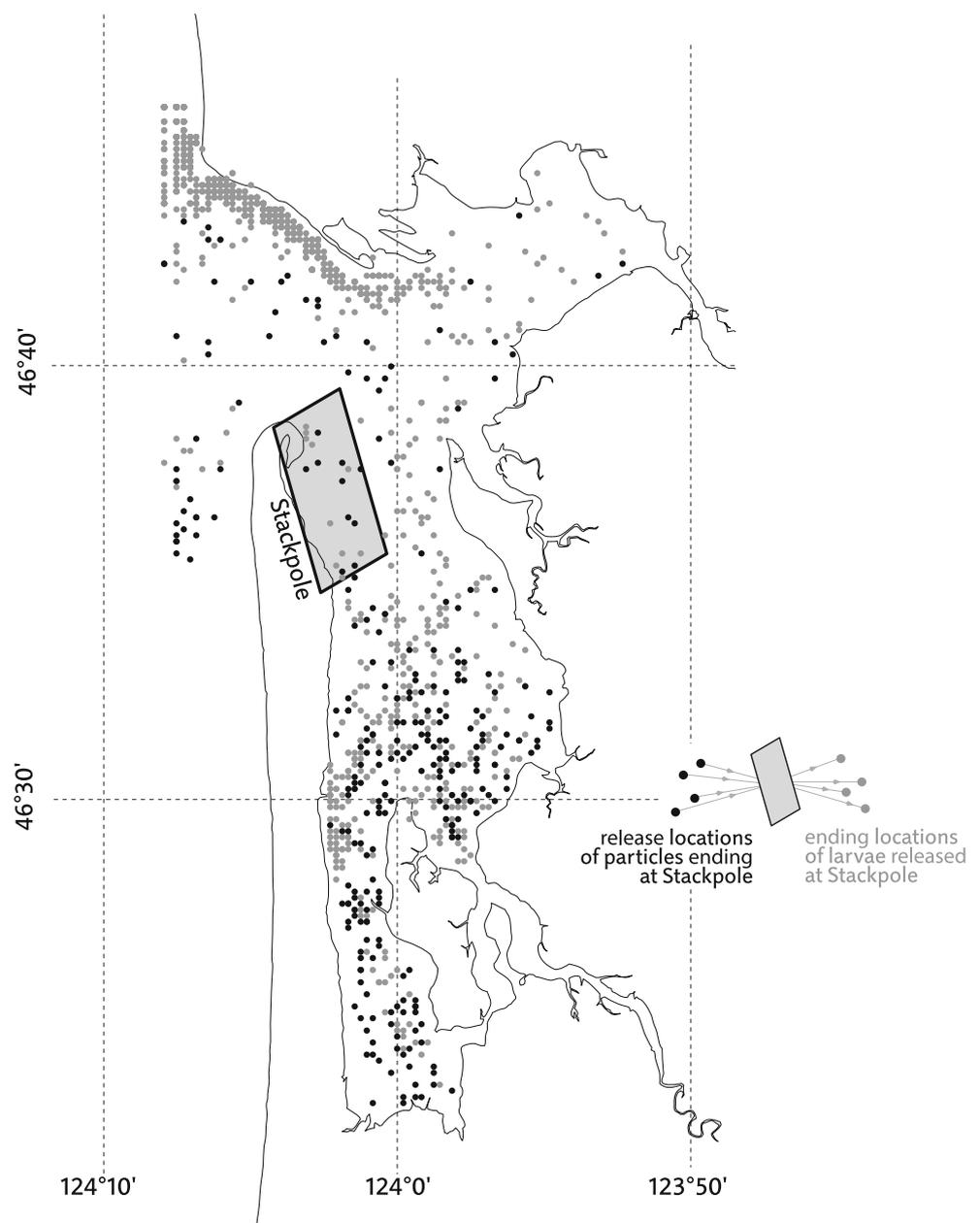


Fig. 5 Vertical position of 50 larvae engaged in diel migration over 5 days in a one-dimensional (vertical) flow field. The flow field (which contains vertical velocity and turbulent diffusivity) is extracted from mid-April 2000 at a main channel location near Bay Center

(Fig. 1) in the realistic 1999–2000 hindcast described by Banas and Hickey 2005. The alternating 12-h periods of upward swimming (night) and neutral behavior (day) are marked

Fig. 6 Spatial connectivity between the Stackpole area and the rest of Willapa Bay, over 31 days of tidal transport (the summer, no-behavior model scenario, compare Fig. 4b). The spawning locations of all model larvae found at Stackpole at the end of their development are shown in *black*; the end locations of all larvae spawned at Stackpole and retained within the bay are shown in *gray*



seeding” definition (the return of larvae to the particular place they were spawned). The fraction of larvae spawned at Stackpole returning to Stackpole in time to settle (dots within shaded area; Fig. 6) is $\sim 0.06\%$, compared with the 6% that settle within the bay as a whole.

Discussion

A Targeted Search for Self-sustaining Green Crab Populations

We began with the question: *Can green crab form a self-sustaining population in Willapa Bay?* Answering this

question has two parts: larval retention, which we have modeled in this study, and population dynamics and habitat suitability, which we have not. Combining what we know of spawning timing, larval swimming behavior, and the flushing patterns of the bay, the answer to the larval-retention half of the question appears to be *yes*. In summer, larvae spawned in southern and western areas of Willapa Bay can be retained by the tidal circulation long enough to reach maturity within the bay and potentially resettle. Point by point, the retention rate varies from 5% to 40% in the southern and western bays.

The retention for larvae spawned in the Stackpole region is especially notable because the secondary channel

adjacent to the Stackpole shoals is the most direct pathway by which new ocean water enters the bay on flood tide. BH05 find that Willapa's net tidal circulation, in addition to being highly dispersive in all directions (Fig. 6), has a net counterclockwise tendency, such that new ocean water enters on the south side of the mouth, continues up-estuary, and exits on the north side of the mouth (Fig. 4b). Thus, Stackpole is both the most likely shoal region where late-stage megalopae entering from the coastal ocean might settle and also the beginning of a persistent (if leaky) hydrodynamic pipeline that would move any larvae spawned there deeper into the bay. Because of this intersection of colonization likelihood and larval-retention likelihood, Stackpole is a key area of concern. Secondary areas of concern include Nemah, Nahcotta, and Shoalwater Bay (Figs. 1 and 4) because of their retention times. The Bay Center and Toke Point areas stand out in the trapping data (Fig. 1), but these areas of the bay are well-flushed (Fig. 4; BH05) and are unlikely to be self-recruiting.

Controls on Retention

The patterns of larval retention and flushing we have described are largely hydrodynamic effects modulated secondarily by larval biology. First, the contrast between high summer larval retention rates and the much lower rates in spring (Fig. 4a, b) largely mirrors the seasonal contrast in water residence time reported by BH05. The underlying mechanism is the increase in riverflow and hence river-driven exchange in spring. This seasonal difference in water residence time is amplified in the case of green crab larvae, however, by the difference in water temperatures and hence larval development time.

Likewise, the strong spatial gradients in retention in summer (Fig. 4b) are primarily hydrodynamic—created by the interaction of the tides with the bay's complex, curving channels (BH05)—but these gradients may be modulated by larval swimming behavior. Diel migration appears to have a negligible effect, as might be expected in an estuary with weak diurnal tides, but even just a short period of tidally timed vertical migration reduces retention by one third and noticeably flattens the along-estuary gradient in retention (Fig. 4d). This flattening effect probably occurs because this behavior amplifies the effect of localized variations in vertical velocity shear in the tidal flow, adding small-scale complexity to an already spatially complex process. Since it is unclear whether green crab on the U.S. West Coast engages in tidally timed migration or not, we believe that the clearer spatial patterns in the no-behavior model case (Fig. 4b) are a better guide for decision-making, with the caveat that larval biology may dilute or disrupt these spatial patterns.

Conclusions

The model study described in this study suggests that larvae of green crab spawned within the southern and western portions of Willapa Bay may be retained throughout development. Thus, establishment of a substantial breeding population could result in self-recruitment and the long-term persistence of a local population in Willapa Bay largely independent of previously established source populations in central California. The Stackpole Shoals area is particularly important for the continued growth of the green crab population since it is the most likely (but not the only) location where late-stage megalopae entering the estuary from the coastal ocean might settle and also the beginning of a "pipeline" that moves larvae spawned there deeper into the bay (see Fig. 6). Abundance of mature green crab has been consistently higher at Stackpole Shoals than any other location in Willapa Bay according to WDFW trapping records, and many ovigerous crab have been collected in the area. Resource managers and citizen conservation organizations should utilize these results by focusing monitoring and control efforts at Stackpole Shoals, thereby maximizing limited financial and personnel resources. Moreover, concerted effort to remove ovigerous green crab at Stackpole Shoals may forestall the establishment of a self-perpetuating population.

Currently, green crab are not abundant in the southern, or upper, portion of the estuary (Shoalwater Bay), but potential recruitment to this area as predicted by our model is of grave concern. Shoalwater Bay does not support abundant native cancrid crabs, such as *C. magister* and *C. productus* (Rooper et al. 2002; Holsman et al. 2003), which have been shown to limit the distribution and abundance of green crab elsewhere (Hunt and Yamada 2003; McDonald 2006; Jensen et al. 2007). Without substantive biotic resistance, growth of the green crab population might go largely unchecked. Previous work in central California has shown that local populations of green crab can reach exceedingly high densities in isolated areas free of native competitors and predators (McDonald 2006; Jensen et al. 2007).

A large population in Willapa Bay would also eventually contribute to the species' spread through the Pacific Northwest. Even during the most retentive period of the year (July–August), the majority of green crab larvae spawned in Willapa Bay will be exported to the coastal ocean during their development period (Fig. 4). Larvae would be likely to disperse both north and south, in accordance with seasonal and shorter-scale reversals in coastal ocean currents (Hickey and Banas 2003), although the predominant oceanic transport of larvae spawned in spring would be northward. Analysis of the potential for green crab range expansion into the Gulf of Alaska should consider both a potential source in Willapa Bay and

populations in the coastal embayments of Vancouver Island, which Yamada and Gillespie (2008) suggest are supported by local recruitment. Some of these areas experience little flushing and warm summertime surface temperatures that would favor rapid larval development (Yamada and Gillespie 2008).

It is far from obvious that Willapa Bay would likewise have the potential for developing a self-sustaining green crab population, as we have found. Willapa Bay's tidal prism is >50% of the bay's volume (Hickey and Banas 2003), meaning that, in the absence of detailed observations and modeling, one might easily assume a residence time of ~2 tidal cycles or perhaps a few days, far shorter than the green crab development period. Thus, our result that a significant fraction of particles or larvae released close to the mouth of Willapa Bay could be retained for more than 1 month is striking. This result may indicate that the other small Pacific Northwest coastal-plain estuaries also have greater retention potential than gross estimates of residence time would suggest. Future studies of biological invasions in Pacific Northwest coastal-plain estuaries should continue to include high spatial resolution and careful treatment of hydrodynamics, in addition to better incorporating population dynamics and habitat variability.

Acknowledgements We thank R. A. Figlar-Barnes, A. Randall, E. M. Carr, B. E. Kauffman, and other Washington Department of Fish and Wildlife personnel who collected field data in Willapa Bay. J. Haug provided logistical support for trapping efforts in the upper estuary. Our appreciation goes out to K. Holsman, P. Barreyro, M. Smith, and H. Stapleton for the assistance with the collection of field data. We are grateful to D. Wilson and other Willapa Bay shellfish growers for providing access to tidelands and for imparting insight concerning abundance of green crab in Willapa Bay. This paper is a result of research funded by the Oceanic and Atmospheric Administration Coastal Ocean Program under award number NA06OAR4170165 to the University of Washington. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. Research conducted for this study was done in accordance with institutional, national, and international guidelines concerning the use of animals in research and the sampling of endangered species.

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