Testing the potential for larval dispersal to explain connectivity and population structure of threatened rockfish species in Puget Sound

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ABSTRACT: Yelloweye rockfish *Sebastes ruberrimus* in the Puget Sound/Georgia Basin (PSGB) region are genetically differentiated from those of the outer Pacific coast of North America, while canary rockfish *S. pinniger* show no population structure between these regions. These characteristics helped determine each species' status as a distinct population segment (DPS) under the US Endangered Species Act. Here, we explore larval dispersal patterns and test whether these patterns could explain the differences in population structure. We used a 3-D oceanographic model to simulate dispersal of each species' larvae from sites inside and outside PSGB for up to 120 d. Dispersal patterns were similar across species and site-specific. Most larvae were found in the same DPS region or management basin from which they were released, but dispersal across boundaries was greatest from release sites nearest the DPS boundary for both species. Dispersal of larvae into the DPS from release sites outside the DPS increased and retention of larvae within the DPS increased with increasing pelagic larval duration, but this was also influenced by a simulated ontogenetic shift in larval depth distribution. The proportion of cross boundary dispersal observed for both species was likely high enough by Day 90 to allow gene flow across boundaries, which is consistent with the lack of population structure observed in canary rockfish but conflicts with the differentiated population structure observed in yelloweye rockfish. Understanding the potential larval dispersal pathways within and across management boundaries is an important step in the successful spatial management and recovery of important and protected species.

KEY WORDS: Population connectivity · Puget Sound· Endangered Species Act · Distinct population segment · Oceanographic modeling

1. INTRODUCTION

Connectivity of populations across time and space is fundamental to the processes of evolution and population dynamics, and understanding patterns of population connectivity is essential to natural resource conservation and management (Dunning et al. 1992, Taylor et al. 1993, Cowen et al. 2006, Kool et al. 2013, Selkoe et al. 2016, Morin et al. 2017). Connectivity between populations (or lack thereof) is a critical mechanism for gene flow, genetic differentiation and even speciation (Coulon et al. 2004, Waples & Gaggiotti 2006, Hedgecock et al. 2007). Connectivity within and among populations may also lead to source-sink dynamics (Taylor et al. 1993, Armsworth 2002, Schumaker et al. 2014), which can arise from interactions between life-history characteristics (e.g. dispersal and density-dependent recruitment pro-

cesses), landscape/seascape corridors and barriers (e.g. land masses, rivers, and oceanographic currents) and environmental characteristics (e.g. currents, temperature, prevailing winds, salinity). Understanding the effects of these processes on connectivity in species or populations of concern is an important step for making successful conservation and management decisions (Bennett 1999, Crowder & Norse 2008, Foley et al. 2010).

In the marine environment, the mechanisms for connectivity in animal populations include larval dispersal (Cowen & Sponaugle 2009, Planes et al. 2009, D'Aloia et al. 2015) and nektonic movements of juveniles (Chin et al. 2013, Cardona & Hays 2018) and adults (Rooker et al. 2008, Stelzenmüller et al. 2011, Ciannelli et al. 2013, Frisk et al. 2014, Archambault et al. 2016). Larval dispersal is governed by several life-history characteristics, food-web interactions and oceanographic considerations. Life-history characteristics of particular importance include the timing and depth of larval release, pelagic larval duration, and larval mortality (Treml et al. 2015), which vary by and within species, particularly in species that range across a wide latitudinal gradient. Interacting with each of these life-history characteristics is the influence of oceanographic currents, fronts, eddies and upwelling conditions, which can be highly variable across temporal scales and in 3-dimensional space (Bjorkstedt et al. 2002, Largier 2003, Watson et al. 2010, Woodson et al. 2012, Yu & Kim 2018). The morphological development, behavior (e.g. diel vertical movement, rheotaxis) and swimming ability of planktonic larvae and juveniles subsequently modify the influence of oceanographic conditions (Morgan et al. 2009, Ospina-Alvarez et al. 2018, Blanco et al. 2019).

Following the pelagic dispersal period, the availability and patchiness of suitable settlement and recruitment habitat adds to the complexity of variables and mechanisms responsible for the spatial structure of species and populations (Holbrook et al. 2000). Density-dependent processes, such as post-settlement mortality (e.g. Connell & Jones 1991) and competition with congeners (Schmitt & Holbrook 1999, Poulos & McCormick 2015), further modify these patterns of settlement. Finally, the mobility of adults (Huijbers et al. 2013) and reproductive habits of species (e.g. spawning aggregations, broadcast spawning versus nest brooding) provide yet another layer of complexity that results in the ultimate level of connectivity among populations that we observe in the marine environment (Jones et al. 2005, 2007).

Understanding realized levels of population connectivity (Burgess et al. 2012) is a key step toward achieving conservation and management goals as required under protected species mandates such as the US Endangered Species Act (ESA). One such goal is the recovery of 2 populations of rockfish (*Sebastes* spp) listed under the ESA in the Puget Sound/Georgia Basin (PSGB) region of Washington State, USA, and British Columbia, Canada. In 2010, 3 species of rockfish in the PSGB (Fig. 1) were listed under the ESA: canary rockfish *S. pinniger* and yelloweye rockfish *S. ruberrimus* were declared threatened, and bocaccio *S. paucispinis* was declared endangered (NMFS 2010). Strong evidence existed that rockfish abundances in Puget Sound were declining significantly (Drake et al. 2010, Williams et al. 2010, Tolimieri et al. 2017). Additionally, regional experts concluded that the PSGB populations of the 3 species were distinct from larger populations located along the outer North American West Coast (Drake et al. 2010). These distinct population segment (DPS) designations were based in part on indirect evidence, namely genetic differences that had been found between PSGB and West Coast populations of 3 other *Sebastes* species (Seeb 1998, Buonaccorsi et al. 2002, 2005). Subsequent direct analyses found genetic differentiation between yelloweye rockfish captured in PSGB versus those captured on the outer coast — consistent with the DPS status (Siegle et al. 2013, Andrews et al. 2018). However, canary rockfish captured in PSGB waters were genetically indistinct from canary rockfish captured on the outer coast (Andrews et al. 2018). (No conclusions were reached about bocaccio, due to low sample size.)

As a result of the genetic analyses, canary rockfish in the PSGB region were no longer considered a DPS and were delisted under the ESA, while PSGB yelloweye rockfish remain listed as threatened and PSGB bocaccio remain listed as endangered (NMFS 2017a). Conservation of these species has broad implications for fisheries management. All 3 rockfish are targeted by commercial fisheries along the west coasts of the USA (PFMC 2016) and Canada (DFO 2021). Additionally, yelloweye rockfish, canary rockfish and bocaccio occur in deep, rocky habitats in Puget Sound and also co-occur with popular recreational fishing target species such as lingcod *Ophiodon elongatus*; as a result, recreational hook-and-line fishing in Puget Sound for bottomfish has been heavily constrained to reduce the risk of bycatch of ESA-listed rockfish (WDFW 2010). Understanding the mechanisms that promote genetic differentiation among PSGB and outer coast yelloweye rockfish populations, but genetic panmixia in canary rockfish, will be important for implementing suc-
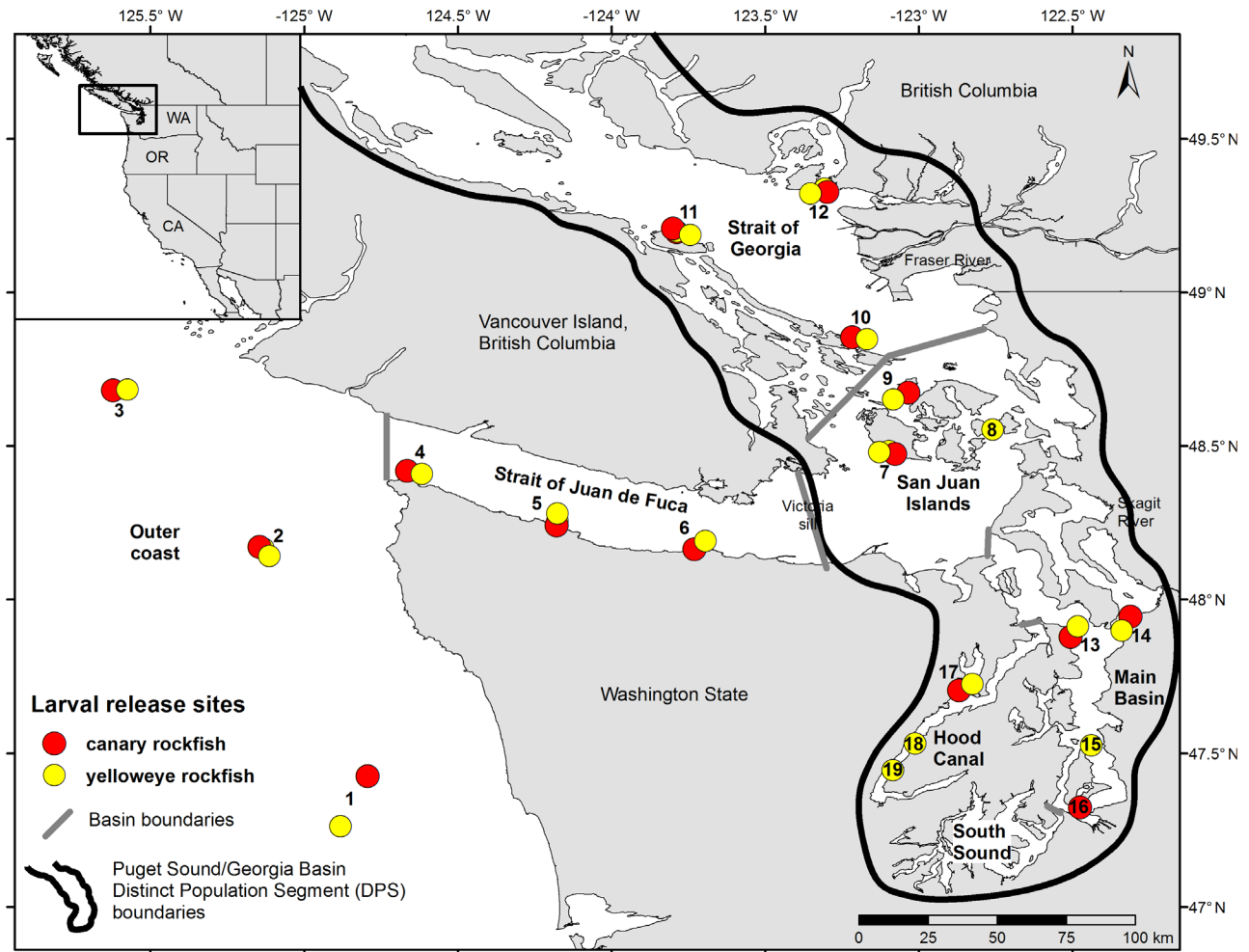
Fig. 1. Larval release sites for each simulation run with canary and/or yelloweye rockfish. Thick black line: Puget Sound/Georgia Basin distinct population segment (DPS) boundary for protected rockfish; gray lines: boundaries for each settlement basin

cessful recovery plans and sustainable management strategies for rockfish in the PSGB region.

In this article, we explore patterns of larval dispersal of yelloweye and canary rockfish in the PSGB and adjacent regions and test whether relevant life-history characteristics can explain the observed differences in their population structures. Specifically, we use a realistic ocean circulation model to simulate larval dispersal from known adult yelloweye and canary rockfish habitats in the PSGB region and the adjacent outer coast. We then quantify the level of connectivity among release and settlement locations across a range of pelagic larval durations for each species. Finally, we use these patterns to hypothesize whether larval dispersal mechanisms are able to explain the observed differences in population structure between these 2 ESA-listed rockfish in the PSGB region.

2. MATERIALS AND METHODS

2.1. Rockfish life history characteristics

Unlike many marine fish species, rockfish are live bearers and extrude 3 to 7 mm larvae (Kendall & Lenarz 1987, Moser 1996). Larvae generally are pelagic for ~1–2 mo and reach a standard length of ~20–30 mm before transforming to a pelagic juvenile stage that lasts weeks to months; they then settle to bottom habitat (Love et al. 2002, Matarese et al. 2003). Many features of the pelagic phase can influence dispersal and are thus relevant to intraspecific population connectivity. These include the following: timing and depth of larval release (Petersen et al. 2010); pelagic larval duration (PLD; Sponaugle et al. 2002, Galarza et al. 2009); larval behavior (Leis 2007, Weersing & Toonen 2009); and swimming ability (Sakuma et al. 1999). Because rockfish larvae are

very difficult to identify to species in the field, much of the data on larval characteristics are at the generic 'rockfish' level. Below, we compare available information on these traits for yelloweye and canary rockfish, typically from studies outside of PSGB.

Little is known about the specific timing or depth of larval release or the PLD for yelloweye or canary rockfish in PSGB waters. However, off the coast of Oregon, larval release (i.e. parturition) for canary rockfish appears to peak from January to February, while parturition for yelloweye rockfish off the coast of British Columbia appears to peak later, from May to June (Love et al. 2002), with some evidence of dual parturition periods in both early spring and mid-late summer in Puget Sound (Washington et al. 1978). Larval and juvenile canary rockfish spend ~3–4 mo in the water column along the outer coast, while there is little information on PLD of yelloweye rockfish from any geographic location (Love et al. 2002).

Similarly, information on larval and pelagic juvenile rockfish behavior tends to be generic rather than species-specific. *Sebastes* larvae tend to be found in the top 100 m of the water column, with evidence suggesting highest densities at depths >20 m (Ahlstrom 1959, Sakuma et al. 1999, Bowlin 2016). Many fish larvae exhibit diel vertical migration, but there has been relatively little support for this behavior for *Sebastes*, particularly along the US West Coast (Barnett et al. 1984, Moser & Boehlert 1991, Sakuma et al. 1999). Some studies have reported more *Sebastes* larvae caught during the night than day, but this was attributed to daytime net avoidance (Sakuma et al. 2007). There is also evidence that younger larval stages (pre-flexion and flexion) of *Sebastes* are found in shallower, more inshore and in lower saline waters than older larval stages (post-flexion; Sakuma et al. 1999, Landaeta & Castro 2006, Bowlin 2016) and that larvae are found deeper in the summer compared to spring (Lenarz et al. 1991). In Puget Sound, limited studies have described the distribution of rockfish larvae in surface waters to vary across seasons, with peaks in early spring and late summer (Greene & Godersky 2012). Together, these characteristics support the assumption that young rockfish larval stages in Puget Sound are likely to occupy shallow, lower-saline waters followed by an ontogenetic shift to deeper water layers.

Though we do not consider it in our analyses, adult movement can also influence *Sebastes* population connectivity (Palumbi 2004, Grüss et al. 2011), and adult movement differs starkly between these 2 species. Adult canary rockfish have been characterized as transient, with wide-ranging spatial movements (Hannah & Rankin 2011) that may cover hundreds of kilometers over the span of multiple years (Lea et al. 1999, Love et al. 2002). In contrast, adult yelloweye rockfish exhibit low rates of migration (Black et al. 2008) and high site fidelity (Coombs 1978) with little month-to-month variability in horizontal and vertical movements (Hannah & Rankin 2011). These respective characteristics may promote population connectivity in canary rockfish and population differentiation in yelloweye rockfish (Andrews et al. 2018).

2.2. Oceanography of Puget Sound/Georgia Basin

The PSGB region is a complex network of inland straits, basins, and estuaries (Fig. 1), including Puget Sound, the Strait of Georgia (SOG) and the eastern Strait of Juan de Fuca (JDF). Circulation in the system is driven by stratified estuarine circulation of the surface layers combined with fortnightly cycles of tidal currents driving the deeper layers. The system experiences annual net outflow of surface waters due to freshwater discharge from 16 major rivers, the most significant of which are the Fraser River in British Columbia and the Skagit River in Puget Sound (Fig. 1; Masson 2002, Babson et al. 2006, Khangaonkar et al. 2011, Banas et al. 2015, MacCready et al. 2021). Freshwater flow rates vary annually and dictate the magnitude of net outward flow (Riche & Pawlowicz 2014, Pawlowicz et al. 2019). Freshwater discharge also varies by season and basin; for example, the Fraser River has one large peak in spring and early summer, while the Skagit River generally experiences multiple peaks of different magnitudes over the course of the year (Fig. 2). Tidal currents introduce denser oceanic waters into the deeper layers of PSGB through the Strait of JDF via neap and spring tide cycles (Alford & MacCready 2014). Salinity and stratification vary seasonally due to changes in river discharges and are spatially based on proximity to straits and to major rivers (Babson et al. 2006, Moore et al. 2008, Khangaonkar et al. 2011). Circulation dynamics within PSGB are constrained by shallow sills at the eastern boundary of the Strait of JDF (Victoria Sill), Boundary Pass (at the northern edge of the San Juan Islands), and at the entrances to Puget Sound proper, Hood Canal, and South Sound, contributing to higher water residence time in some basins (Masson 2002, Sutherland et al. 2011, Deppe et al. 2018, MacCready et al. 2021). These horizontal circulation and vertical mixing

patterns set the stage for complex oceanographic dynamics capable of affecting the dispersal of planktonic organisms (Engie & Klinger 2007), particularly for species that may have ontogenetic shifts in their pelagic depth distribution.

Of particular relevance to this study are any differences in circulation patterns in 2006 compared to other years (the focal year for the oceanographic circulation model; see Section 2.3) that might suggest our results are not indicative of 'average' oceanographic conditions. The primary driver of the stratified estuarine circulation of the PSGB region is freshwater input, while the deep-layer tidal currents will be relatively consistent across years. Daily flow rates from 1980 to 2020 from the Skagit and Fraser rivers suggest that 2006 was a relatively average year during the first ~180−200 d of the year, which encompasses the entire dispersal period for canary rockfish and the first 60−80 d for yelloweye rockfish, after which below-average flow conditions occurred (Fig. 2).
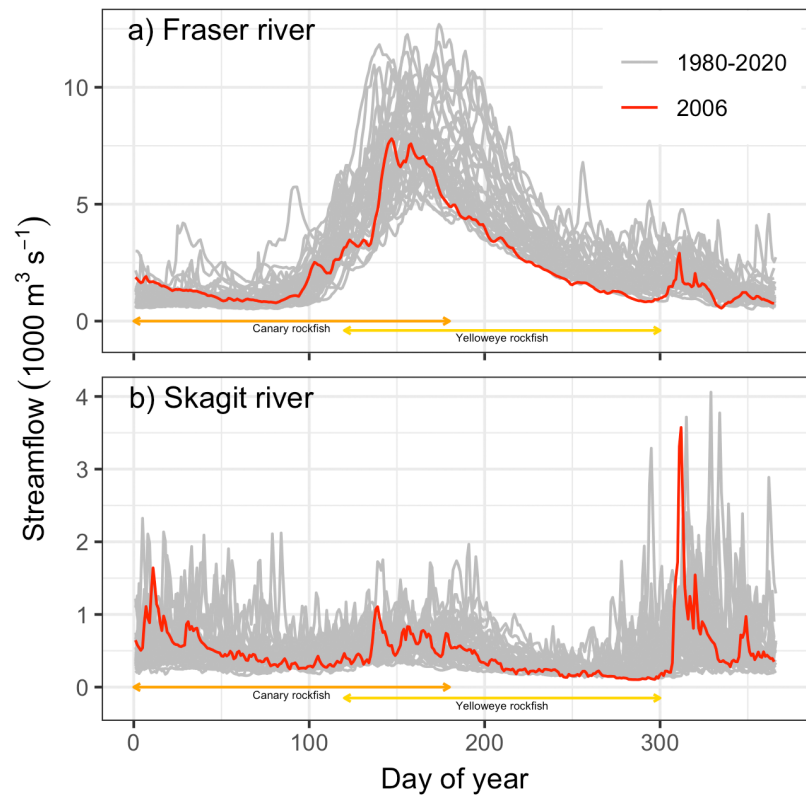

Fig. 2. Daily freshwater streamflow volume from (a) Fraser River in the Strait of Georgia Basin and (b) Skagit River in the Main Basin of Puget Sound from 1980 to 2020. Dispersal modeling occurred across Days 0−180 for canary rockfish (orange arrow) and across Days 120−300 for yelloweye rockfish (yellow arrow)

2.3. Larval dispersal modeling

The dispersal patterns for larval rockfish were simulated using particle tracking in velocity fields from a numerical model. The spatial and temporal fields of circulation used in the particle tracking were derived from MoSSea (modeling the Salish Sea), a high-resolution realistic numerical simulation of the Salish Sea (includes PSGB) and adjacent coastal waters (Fig. 1). MoSSea has been extensively validated by comparison with data from tide gauges, CTD casts, and a variety of moorings (Sutherland et al. 2011). The model was run for the year 2006, with the initial fields in Puget Sound derived from CTD cast observations. This year was chosen because of optimal overlap with observations on the shelf.

The numerical framework of MoSSea is the regional ocean modeling system (ROMS), a community model used in a wide variety of coastal and estuarine applications (Haidvogel et al. 2000, Shchepetkin & McWilliams 2005). ROMS solves the hydrostatic, incompressible, Reynolds-averaged momentum and tracer conservation equations with a terrain-following vertical coordinate and a free surface. For this application, the model bathymetry was configured to produce realistic hindcast simulations of the Salish Sea and adjoining coastal waters. The horizontal domain is a spherical, stretched Cartesian grid extending from longitude 127° to 122° W, and latitude 45° to 50° N. The grid resolution is as fine as 280 m in Puget Sound and stretches to 3.1 km at the boundaries. The model uses a vertical grid in which there are always 20 active layers between the sea floor and the tidally varying free surface (Sutherland et al. 2011). The layer spacing is somewhat tighter near the free surface and bottom to allow better resolution of the surface and bottom boundary layers. The model was forced with realistic flow from 16 rivers, tides, atmospheric forcing by wind stress and heat flux, and open ocean boundary conditions. Complete details of MoSSea setup, forcing, boundary conditions and validation are in Sutherland et al. (2011). Results were recorded in hourly time steps, including 3-D fields of temperature, salinity, horizontal and vertical components of velocity, and turbulent eddy diffusivity (example data from a single time-step

are in Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m677p095_supp1.pdf).

For the particle tracking experiments, we used the full 3-D velocity fields, as well as the vertical turbulent eddy diffusivity. A total of 33 experiments were performed: 15 for canary rockfish and 18 for yelloweye rockfish. An experiment consisted of releasing a total of 100 000 particles (= rockfish larvae) from the seafloor bottom depth at a given release site. Release sites (Fig. 1) were selected based on locations where adults of each species had been collected in previous research (Andrews et al. 2018). Particles were released sequentially over a period of 59 d (2 lunar cycles) and allowed to disperse for up to 120 d. The timing and distribution of releases were based on the duration of peak parturition periods for coastal populations of these species (Love et al. 2002) and the distribution of parturition across the lunar cycle of a congener rockfish species (Fig. S2 in Supplement 1; Pastén et al. 2003). Larvae were released beginning with the first new moon in January for canary rockfish and in May for yelloweye rockfish.

Particles were advected in space using established methods of 4th-order Runge-Kutta integration from the 3-D velocity field (Banas et al. 2009, Giddings et al. 2014, Banas et al. 2015). Dispersive effects of turbulence were included using a random walk based on the local modeled eddy diffusivity and its vertical gradient (Visser 1997, Banas et al. 2009). An advective time step of 1 h was chosen to match the temporal resolution of the MoSSea model fields. This works well in most of the domain, but in extreme spots such as Tacoma Narrows (near release site Site 16 in Fig. 1), where there are strong currents and narrow channels, it led to artificial loss of some particles to land. Particles were allowed to resolve their trajectories over time, but particles that were lost to land by the dispersal day of interest (i.e. 20, 40, 90 or 120 d) were removed from the analysis. Due to limitations in post-processing, we subsampled the 100 000 particle pathways created by selecting every tenth particle from each release day, for a total of 10 000 particle pathways to use in subsequent analyses.

Recent research along the US West Coast suggests that rockfish larvae are more likely to inhabit the upper 20–50 m for the first 40 d (pre-flexion and flexion larval stages), then move deeper (range 50–100 m; post-flexion larval stage) for the remainder of the pelagic stage (Bowlin 2016). To reflect this behavior, particles were given these age-dependent depth behaviors (Fig. S3 in Supplement 1), and any particles that exceeded these limits for a given time step were moved back to the appropriate depth range.

We tracked particle locations relative to 2 management-based spatial scales. First, we divided the model domain into waters that were 'inside' or 'outside' the PSGB DPS boundaries (Fig. 1, Table 1). Second, we divided the model domain into polygons based on the major oceanographic basins of the PSGB region, which coincide with the spatial management units in the Puget Sound Rockfish Recovery Plan (NMFS 2017b). The coordinates, depth, management unit basin and inside/outside DPS categorization were recorded for the location of each particle on Days 1–120 post-release. Particles that dispersed out of the model's domain on the outer coast were included in the 'Outside DPS' and 'Outer Coast' DPS and management basin categories, respectively.

2.4. Analyses

We focused our analyses on the spatial distribution of larvae across 2 spatial management scales and the effect of PLD on those dispersal patterns for both species. We calculated the proportion of particles re-

Table 1. Geographical and management organization of larval release sites and basins. DPS: Puget Sound/Georgia Basin distinct population segment; JDF: Strait of Juan de Fuca

Site no. in Fig. 1	Release site	DPS region	Basin	Release species
1	Quinault Canyon	Outside DPS	Outer Coast	Both
2	JDF Canyon	Outside DPS	Outer Coast	Both
3	Ucluelet offshore	Outside DPS	Outer Coast	Both
4	Neah Bay	Outside DPS	Strait of JDF	Both
5	Sekiu	Outside DPS	Strait of JDF	Both
6	Crescent Bay	Outside DPS	Strait of JDF	Both
7	SW San Juan Island	Inside DPS	San Juan Islands	Both
8	Black Rock	Inside DPS	San Juan Islands	Yelloweye
9	Point Disney	Inside DPS	San Juan Islands	Both
10	Salt Spring Island	Inside DPS	Strait of Georgia	Both
11	Nanaimo	Inside DPS	Strait of Georgia	Both
12	Bowen Island	Inside DPS	Strait of Georgia	Both
13	Point No Point	Inside DPS	Main Basin	Both
14	Mukilteo	Inside DPS	Main Basin	Both
15	Blake Island	Inside DPS	Main Basin	Both
16	Vashon Island	Inside DPS	Main Basin	Canary
17	Dabob Bay	Inside DPS	Hood Canal	Both
18	Chinom Point	Inside DPS	Hood Canal	Yelloweye
19	Dewatto Bay	Inside DPS	Hood Canal	Yelloweye

leased from each site across all release days that were found (1) in each geographic DPS designation (i.e. 'inside' or 'outside') and (2) in each management unit basin for 20, 40, 90 and 120 d PLDs. We chose these PLDs to examine 2 periods of dispersal that focused on dispersal patterns of young larval stages that occupied shallow depths (20–50 m) during the first 40 d and dispersal patterns that integrated the change in larval depth distributions (depths from 50–100 m) and bracketed the ~3–4-mo PLD for canary rockfish on the outer coast of US waters (Love et al. 2002). We used these results to compare spatio–temporal patterns of dispersal for each species and to compare the dispersal patterns between the 2 species. All proportions were used in a connectivity matrix framework to evaluate differences in species-specific dispersal patterns and the connectivity between release sites and destination locations (Mitarai et al. 2009). We used R version 4.0.1 (R Core Team 2020) for all calculations and matrix mapping.

3. RESULTS

3.1. Larval dispersal tracks

Dispersal tracks varied by individual particle, by species, and by release site. Fig. 3 shows examples of dispersal tracks and destination locations from 4 simulations after a 120 d PLD (n = 100 randomly chosen from 100 000 tracks). Panels (a) and (b) in Fig. 3 illustrate divergences in dispersal patterns for the 2 species for larvae released from Salt Spring Island in the SOG basin. In general, yelloweye rockfish larvae released from this site were heavily concentrated in the same basin as they were released (Fig. 3a), while canary rockfish larvae dispersed across several basins within the DPS plus some dispersal outside the DPS (Fig. 3b). Fig. 3c provides an example of cross-boundary dispersal that was observed for canary rockfish larvae released at SW San Juan Island, while Fig. 3d provides an example where 100% of simulated yelloweye rockfish larvae released in Hood Canal remained within the release basin. The variation in depths inhabited over the 120 d simulation of canary rockfish larvae released from Salt Spring Island (Fig. 3b) is shown in Fig. S3.

3.2. Spatial and temporal patterns of dispersal

At the broadest spatial scale, we found high proportions of both species' larvae in the same DPS region ('inside' or 'outside') as they were released, independent of PLD (e.g. red shading generally corresponds with the dotted diagonal lines in Fig. 4). This was most consistent for larvae released from sites within the Hood Canal, Main Basin and SOG basins, in which >71% of canary rockfish larvae and >90% of yelloweye rockfish larvae were found inside the DPS across all PLDs, with the lowest proportions for both species being released from the southernmost SOG site (Site 10) (see Table S1 in Supplement 2 for matrix values; www.int-res.com/articles/suppl/m677p095_supp2.xlsx). Larvae of both species released from Outer Coast sites (Sites 1–3) were 100% retained outside the DPS at Day 20 and 40, but progressively dispersed into the DPS by Day 90 and 120 (up to 7% for canary and 16% for yelloweye rockfish). This pattern was even more pronounced for yelloweye rockfish larvae released from sites in the Strait of JDF (Sites 4–6).

Dispersal across the DPS boundary was greatest for larvae released from sites nearest the DPS boundary. This was particularly evident for both species released from Site 7 at Days 20 and 40 (Fig. 4). The largest changes in cross-DPS boundary dispersal occurred between Days 40 and 90 (Fig. 5). Larvae from Outer Coast and Strait of JDF sites progressively increased in proportions found inside the DPS from approximately Day 40 to the end of the simulation. Larvae released from inside the DPS, particularly from the San Juan Islands (SJI) sites for both species, showed high levels of dispersal outside the DPS through Day 40 but then reversed that trend and increased in proportions retained inside the DPS through the end of the simulation (Fig. 5). These changes and reversals in dispersal patterns coincide with the ontogenetic change in depth distribution imposed on larval behavior at Day 40 in the simulation.

At the scale of oceanographic/management basins, we found similar patterns of within- and cross-boundary dispersal as found at the DPS scale — larvae were generally found in higher proportions within the same management basin as they were released, independent of PLD (Fig. 6). This was again most consistently observed for larvae released from the Hood Canal and Puget Sound's Main Basin for both species (most pronounced for yelloweye rockfish), and these proportions remained at similar levels across each of the PLDs. However, at this scale, a relatively large proportion of dispersal was observed for larvae released from the SOG sites (Sites 10–12) into the SJI basin, particularly for canary rockfish, and this dispersal was highest by Day 20 and was retained at slightly lower levels at Days 90 and 120. Of particular note was that both species' larvae released from Strait of
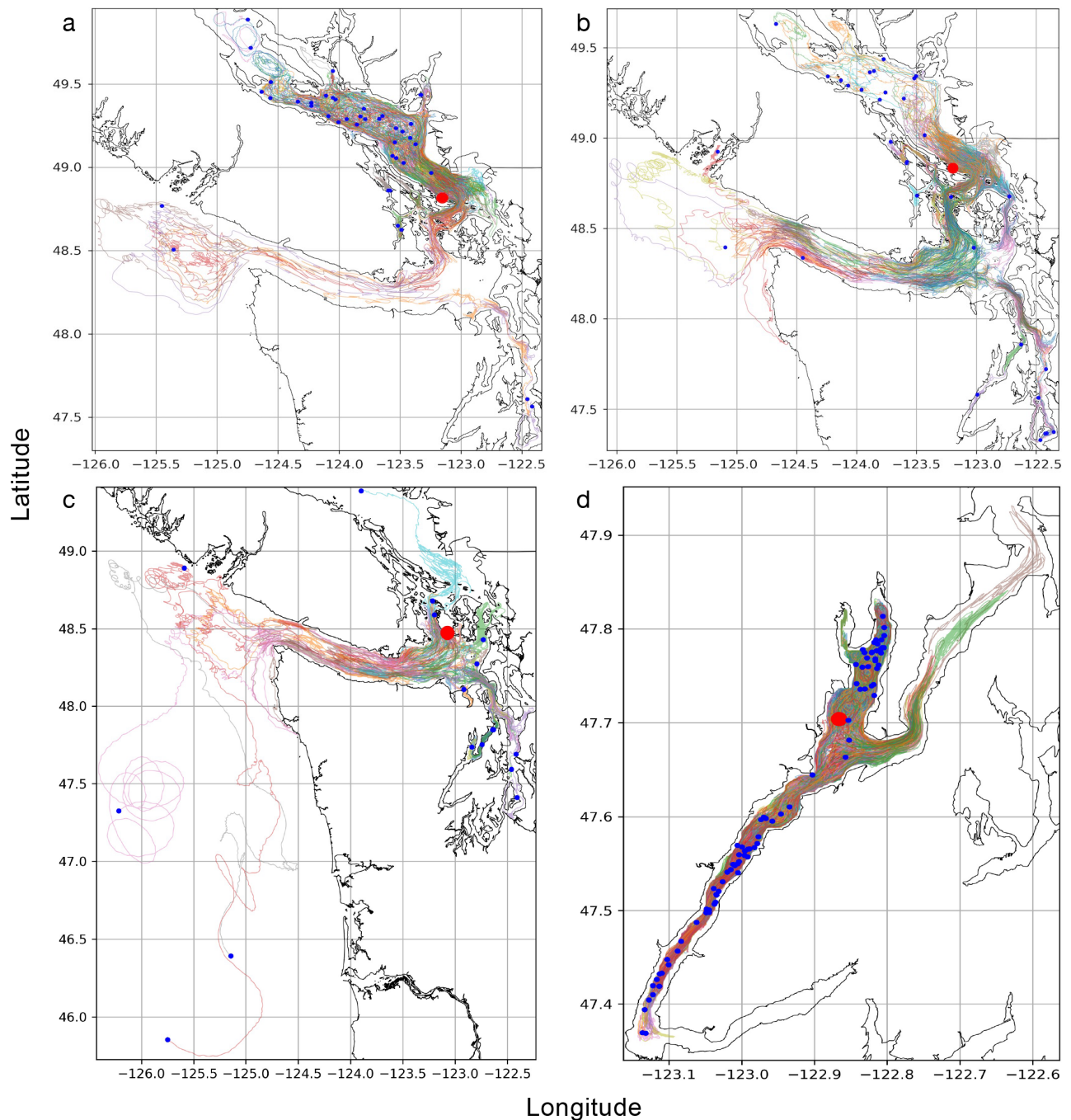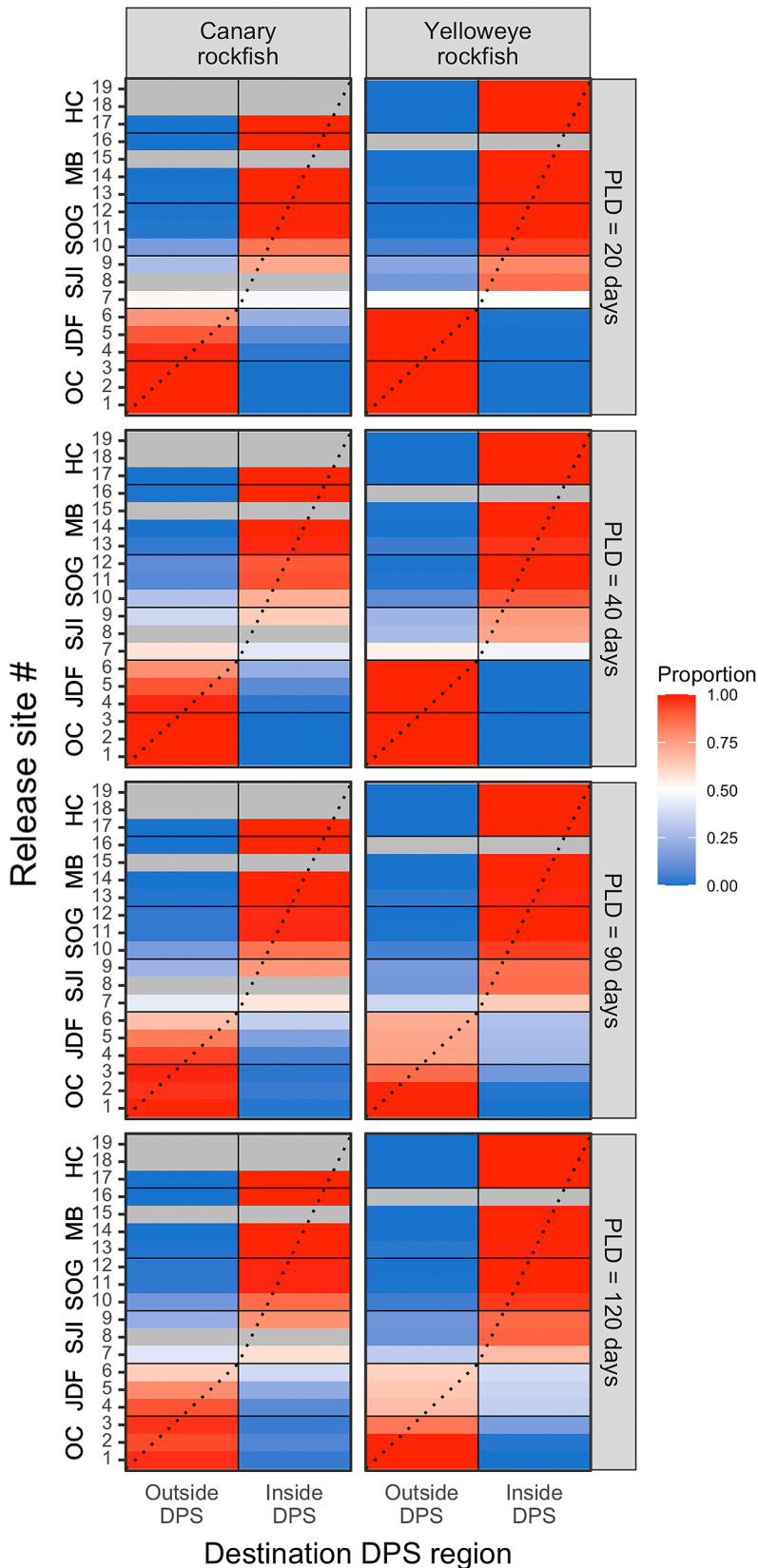
Fig. 3. Larvae dispersal patterns across the model's domain from 4 simulations showing 100 out of 100 000 possible tracks. Release site (large red circles), dispersal pathways (colored lines) and ending locations (small blue circles) after a 120 d pelagic larval duration are shown for (a) yelloweye rockfish and (b) canary rockfish released from Salt Spring Island in the Strait of Georgia Basin, (c) canary rockfish released from SW San Juan Island in the San Juan Islands basin and for (d) yelloweye rockfish released from Dabob Bay in the Hood Canal basin

JDF sites (Sites 4–6) dispersed quickly (< 20 d) to the Outer Coast, and the only other significant proportions of larvae found in the Strait of JDF over the entire modeling period were 20 d old larvae from both species that were released from sites in the SJI (see Table S2 in Supplement 2 for matrix values).

The most variable dispersal at the scale of management basins was observed for larvae released from sites in the SJI (Sites 7–9; Fig. 6). Canary rockfish larvae released from the northern site (Site 9) were retained within the SJI at levels of ~40–50% across each PLD and the remaining larvae dispersed to the

Fig. 4. Proportion of simulated canary and yelloweye rockfish larvae found inside or outside the boundaries of the Puget Sound/Georgia Basin distinct population segment (DPS) when released from each site after a pelagic larval duration (PLD) of 20, 40, 90 and 120 d. Release sites are listed in order of site numbers in Fig. 1 and grouped with horizontal lines into their respective management basin. OC: Outer Coast; JDF: Strait of Juan de Fuca; SJI: San Juan Islands; SOG: Strait of Georgia; MB: Main Basin of Puget Sound; HC: Hood Canal. Diagonal dotted lines: regions of self-connectivity (i.e. the release site and destination location are within the same DPS region). Gray rows: release sites not simulated for one species

SOG and the Outer Coast, with a small fraction dispersing into the Main Basin and Hood Canal by Day 90 and 120. However, canary rockfish released from the western site (Site 7) dispersed rather quickly to the Strait of JDF and Outer Coast basins by Day 20 and 40 with ~30% retained in the SJI. By Days 90 and 120, these larvae were nearly equally distributed between the SJI and the Outer Coast (~30% each) with the remaining larvae dispersing in equal proportions (~10%) to the SOG, Main Basin and Hood Canal basins. Dispersal from the SJI was also site-specific for yelloweye rockfish. Yelloweye larvae released from the northern-most SJI site (Site 9) were found in high proportions in the SOG basin (~50% for each PLD); 30% were retained in the SJI, and the majority of the remaining larvae dispersed to the Outer Coast. Yelloweye larvae released from the eastern SJI site (Site 8) were primarily retained in the SJI (~45–65% across PLDs) with ~20% dispersing to the Main Basin and ~10% to each of the SOG and the Outer Coast by Days 90 and 120. Finally, yelloweye larvae released from the western SJI site (Site 7) initially dispersed in high proportions to the Outer Coast basin (~50% by Day 40) with relatively equal retention/dispersal of the remaining larvae in the SJI and the SOG, but by Days 90 and 120 dispersal was approxi-
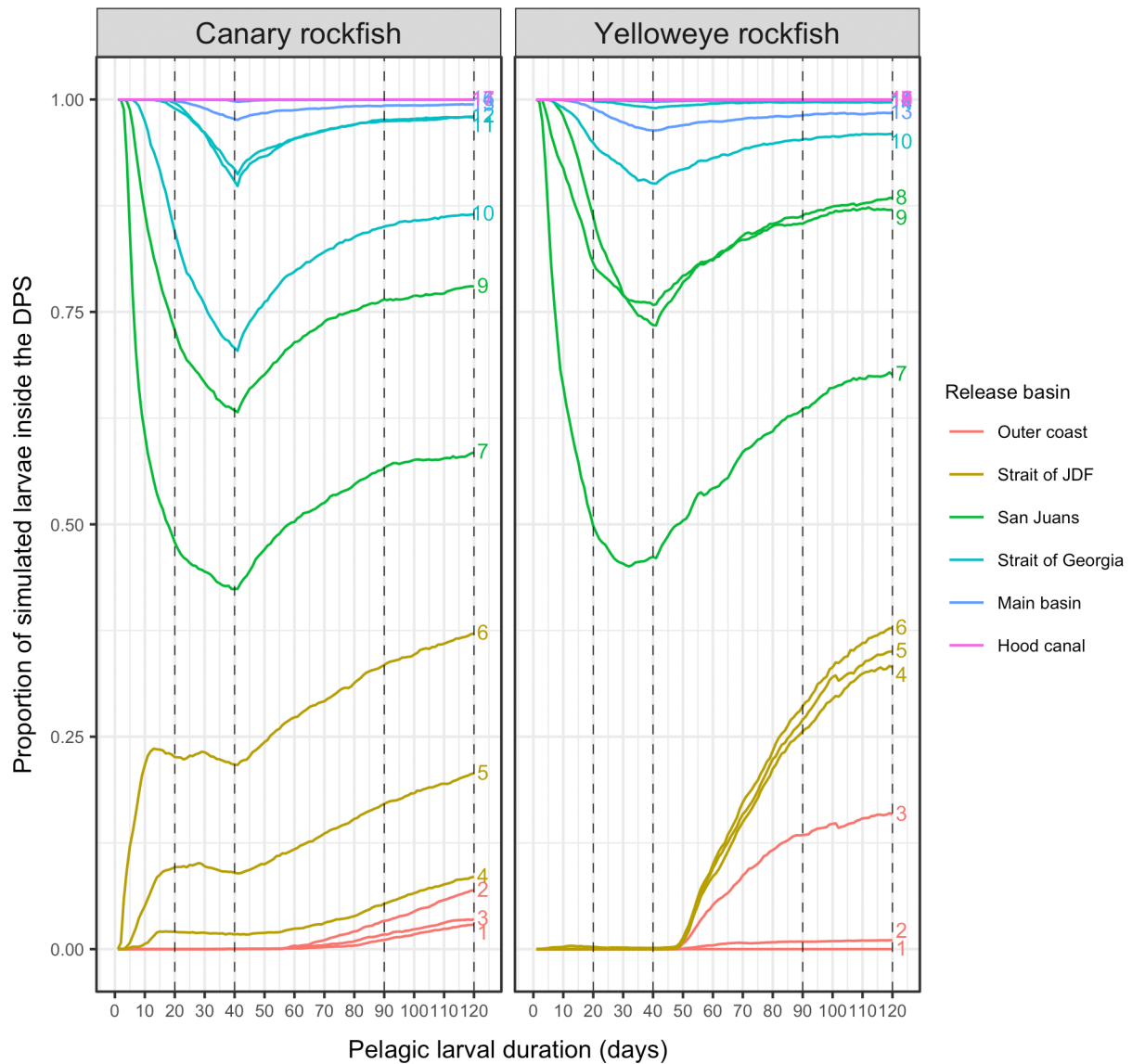
Fig. 5. Proportion of simulated larvae found inside the geographical boundaries of the Puget Sound/Georgia Basin distinct population segment (DPS) for each day of pelagic dispersal. Numbers are the release site numbers as in Fig. 1. Dashed vertical lines: pelagic larval duration (PLDs) presented in Fig. 4. JDF: Juan de Fuca

mately equally divided across the SJI, SOG and Outer Coast basins (~30% each).

3.3. Differences in dispersal between species

At the scale of DPS regions, differences in the proportion of each species found inside the DPS were generally small (<0.10) across most release sites (leftmost column of Fig. 7). For example, there were no differences observed between species for releases from the Hood Canal or Main Basin across any of the 4 PLDs. The only substantial differences at this scale

were that canary rockfish had higher proportions of larvae found inside the DPS boundaries than yelloweye rockfish at 20 and 40 d PLDs when released from the Strait of JDF (particularly Site 6), but that pattern disappeared by Day 90, and we found yelloweye rockfish in higher proportions inside the DPS when released from the Strait of JDF (particularly Site 4).

The largest differences between the 2 species were observed at the scale of management basins (righthand columns of Fig. 7) with the most notable difference being that yelloweye rockfish larvae were initially found in much higher proportions in the Outer Coast basin when released from the Strait of JDF
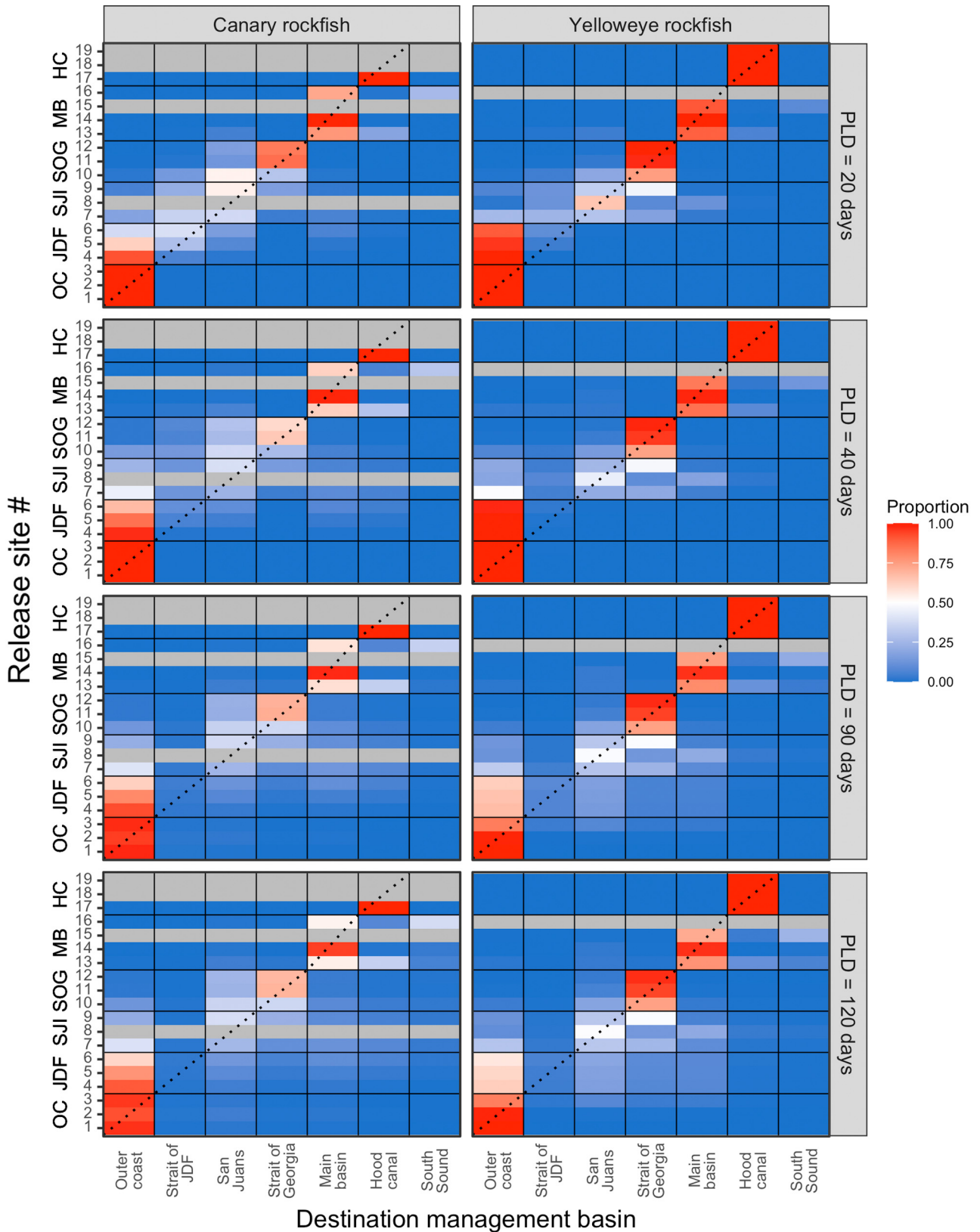
Fig. 6. Proportion of simulated canary and yelloweye rockfish larvae found within each management basin when released from each site after a pelagic larval duration (PLD) of 20, 40, 90 and 120 d. Release sites are listed in order of site numbers in Fig. 1 and grouped with horizontal lines into their respective management basin. Basin abbreviations as in Fig. 4. Diagonal dotted lines: regions of self-connectivity (i.e. the release site and destination location are within the same management basin). Gray rows: release sites not simulated for a species

sites (PLD = 20), but that pattern faded as PLD increased to 90 and 120 d. In addition, yelloweye rockfish were retained within the SOG basin at much

higher proportions (>0.40) than canary rockfish at each PLD, which instead dispersed at higher rates into the SJI basin.
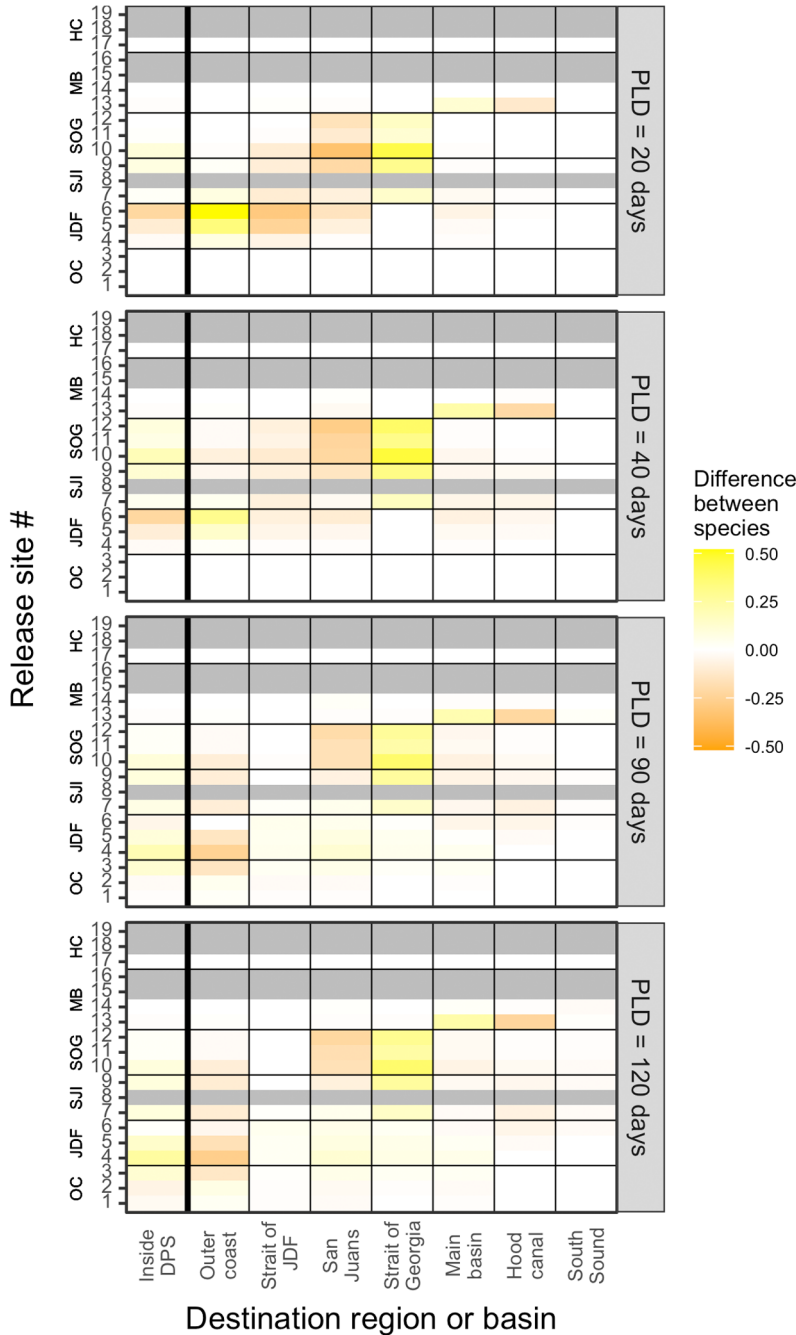

Fig. 7. Difference between species' proportion of larvae found inside the boundaries of the destination region after a pelagic larval duration (PLD) of 20, 40, 90 and 120 d. Positive (yellow) values: release sites which had yelloweye rockfish found inside the destination region at higher proportions. Negative (orange) values: release sites which had canary rockfish found inside the destination region at higher proportions. Release sites are numbered as in Fig. 1 and respective basin abbreviations as in Fig. 4. Gray rows had only one species released. 'Outside DPS' (distinct population segment) is not shown on the left-hand side because the values are simply the negative value of 'Inside DPS'

4. DISCUSSION

For 2 highly valued rockfish species in the Puget Sound/Georgia Basin region, we found 3 generalizable patterns of larval dispersal: (1) levels of larval retention and cross-boundary dispersal at both spatial scales were highly dependent on the location of the release site, (2) pelagic larval duration interacted with larval depth distribution to determine the likelihood of larvae dispersing into or being retained within the DPS, and (3) there were few differences in the overall patterns of dispersal between the 2 species despite the seasonal differences in release periods. The overall levels of cross-DPS boundary dispersal by Day 90 suggest both species should have similar levels of connectivity across the DPS boundary, and we would not expect strong population structure, provided that our assumptions about species-specific PLD, larval depth, and behavior are reasonable and our circulation model is generally representative of long-term physical conditions. This outcome is in contrast to genetic results for yelloweye rockfish showing distinct differences across the DPS boundary (Andrews et al. 2018).

4.1. Site-specific patterns of larval retention and dispersal

The retention and cross-boundary dispersal of larvae for both species depended heavily on the geographic location of the release site. Larvae released from sites far inside the DPS were retained inside the DPS and inside their respective management basins at the highest rates across all sites and across all PLDs. In contrast, larvae released from sites nearest the DPS boundary had the lowest levels of

retention and the highest levels of dispersal across DPS and management basin boundaries.

These rates of dispersal correspond to interactions between PLD, larval depth distribution, and the influence of ocean circulation patterns at each release site. This is evident in 2 illustrative ways. First, larvae released from the Strait of JDF and the SJI quickly dispersed through the Strait of JDF and out to the Outer Coast when they were distributed at shallower depths in the first 40 d. This is consistent with net outward flow of surface waters and recent studies of surface drifters from the PSGB region (Pawlowicz et al. 2019). When these larvae re-distributed to deeper depths after Day 40, we observed a 'U-turn' behavior in which the proportion of these larvae found inside the DPS progressively increased with PLD. This is consistent with the deep-layer tidal current circulation of the region (Alford & MacCready 2014) and hypotheses of onshore transport of planktonic organisms being driven by internal waves that vary with the tidal cycle (Shanks et al. 2014, Shanks & Morgan 2018). The ontogenetic change in larval depth distribution is consistent with limited studies in the PSGB region that have shown densities of rockfish larvae in the upper 2–3 m of surface waters peak in early spring and late summer (Greene & Godersky 2012), coinciding with larval release periods across multiple rockfish species.

Second, larvae released in the SJI basin showed highly variable within-basin patterns and dispersed across DPS boundaries and across more destination basins than larvae released from any other basin. The SJI basin is an area of local upwelling due to 2 sills and deeper channels to the north (Boundary Pass and SOG) and west (Victoria Sill and Strait of JDF), along with high currents, year-round vertical mixing, and constrictions of water movement amongst the islands. These factors contribute to relatively short water residence times that average ~5 d over the entire year (Babson et al. 2006, Pawlowicz et al. 2019). In contrast, water residence time in the basins where we saw high levels of larval retention are ~40 and ~80 d in the summer and winter in the SOG, respectively; ~30–45 d in surface layers and ~90 d in deeper layers for most of the year in the Main Basin of Puget Sound; and ~60–120 d in Hood Canal (Babson et al. 2006, Sutherland et al. 2011, Pawlowicz et al. 2019). These conditions create a mosaic of highly dynamic and dispersive locations interspersed with highly predictable and retentive areas; such heterogenenous conditions have been found to promote site-specific larval dispersal patterns in other systems (Karnauskas et al. 2011, Nickols et al. 2012).

4.2. Effects of pelagic larval duration

The effects of PLD on the dispersal patterns of each species can be viewed in 2 primary ways. First, we observed an overall pattern of increased dispersal into the DPS and an increase in the retention of larvae inside the DPS as PLD increased for both species. These changes were most prominent for canary rockfish as the result of larvae from the Strait of JDF (particularly Site 6) dispersing into 4 of the 5 DPS basins by Days 90 and 120, and larvae from the Outer Coast dispersing into the SJI by Day 120. For yelloweye rockfish, this pattern was mostly due to larvae from the Strait of JDF dispersing into the SJI by Day 90 and even more so by Day 120. Thus, increases in PLD appear to increase the probability of larval spillover from outside the DPS to inside the DPS.

This interpretation, however, must take into account the change in larval depth distribution that we imposed on larvae in the simulation at Day 40. The largest differences in proportions of larvae found inside the DPS or among management basins were observed between the 40 and 90 d PLD results. After Day 40, we observed a dramatic reversal in the proportion of larvae found inside the DPS when released from sites in the SJI and SOG and a progressive increase in larvae dispersing into the DPS from release sites outside the DPS. To separate the effects of PLD and the depth distribution shift, we can compare between the 20 and 40 d PLDs and between the 90 and 120 d PLD results. The 20 to 40 d comparison showed small differences at the scale of dispersal across DPS regions, but several larger differences at the management-basin scale with dispersal primarily occurring from more 'inshore' to more 'offshore' locations (top row in Fig. S4 in Supplement 1). These results correspond with the net outward estuarine flow of surface waters in the region. The 90 to 120 d comparison showed fewer and smaller changes for both species than observed across the 20 to 40 d comparison (bottom row in Fig. S4), suggesting that the final extent of dispersal for both species had mostly been realized by Day 90. Dispersal of other rockfish species has been shown to be unrelated to PLD along the Oregon and Washington coasts, where alongshore currents would otherwise predict wider dispersal ranges and more intermixing of larvae than observed from microchemistry analyses (Miller & Shanks 2004). The strong interaction between PLD and changes in larval depth distribution could help explain recent studies showing higher prevalence of self-recruitment for marine fish populations than previously thought (Jones et al. 1999, Planes et al. 2009,

Christie et al. 2010, Berumen et al. 2012, Hameed et al. 2016, Baetscher et al. 2019), particularly when complex oceanography is accounted for in the model (Nickols et al. 2012).

4.3. Are dispersal patterns consistent with genetic structure?

The 2 focal rockfish species were previously shown to have different population structures: canary rockfish collected within the DPS were genetically similar to canary rockfish collected outside the DPS boundaries, while yelloweye rockfish collected within the DPS were genetically distinct from yelloweye rockfish collected outside the DPS (Siegle et al. 2013, Andrews et al. 2018). If larval dispersal was the primary mechanism responsible for the interspecific differences in population structure, then we would have expected high rates of canary rockfish dispersal across DPS boundaries, but almost no dispersal of yelloweye rockfish larvae across DPS boundaries. However, by Day 90 we found that both species showed cross-boundary dispersal rates of similar magnitude, which should allow for the necessary gene flow to homogenize genetic variation across regions for both species (Slatkin 1987, Palumbi 2003, Waples & Gaggiotti 2006).

There are many possible reasons why the dispersal patterns generated by our model are inconsistent with the genetic structure found for yelloweye rockfish across the DPS regions. The simplest explanation is that the PLD of yelloweye rockfish in this region is shorter than the 90–120 d assumed for our model simulations. If PLD is ~50–60 d, then our results would be consistent with the genetic results — no dispersal from outside the DPS into the DPS and limited dispersal from inside the DPS (particularly from SJI) to locations outside the DPS (Andrews et al. 2018). However, as discussed above, accurately modeling the interaction between shifts in larval depth distribution and PLD will be critical to estimating cross-boundary connectivity in this system. Empirical studies to identify species-specific larval rockfish depth distributions would help parameterize further dispersal modeling.

A second source of inconsistency between the larval dispersal and genetics results relates to spatially discrete survival rates of larvae and newly settled recruits. Larvae that travel through or are entrained in highly productive oceanographic features such as fronts and eddies have been shown to have higher survival than larvae that do not encounter these pro-

ductive features (Bakun 2006, Woodson et al. 2012, Shulzitski et al. 2016). The Strait of JDF connects the 2 DPS regions and is remarkably uniform in its seaward surface-layer flow and shoreward deep-layer flow, limiting the development of these productive features, which may reduce the growth and survival of young larvae traveling through this basin. Similarly, finding suitable habitat upon the transition from pelagic to benthic environments will modify the ultimate survival of larvae. Benthic habitat in the Strait of JDF consists mostly of soft, sandy, muddy bottom with the exception of narrow bands of shallow settlement habitat along the northern and southern shorelines (e.g. eelgrass beds, kelp forests and rocky reefs). Anecdotal evidence from SCUBA-based monitoring (REEF 2019, R. Pacunski, Washington Department of Fish & Wildlife, pers. comm., K. Andrews unpubl. data), and remotely operated vehicle surveys (Pacunski et al. 2013) suggests post-settled young-of-year yelloweye rockfish are found in deep (>20 m), unvegetated rocky reefs, while other rockfish species, including canary rockfish, are commonly found in shallow (<10 m) kelp forests and eelgrass beds. This potential phenotype-environment mismatch could limit the amount of suitable settlement habitat and survival of settlers throughout the Strait of JDF, thus altering the realized levels of connectivity across management boundaries of yelloweye rockfish (Marshall et al. 2010). Additionally, our results may differ from *in situ* patterns due to site-specific differences between losses of particles due to model boundary conditions compared to actual rates of larval mortality under these conditions (Fig. S5 in Supplement 1).

It is also possible that the dispersal patterns we observed only represent the specific oceanographic conditions in 2006 and thus do not capture interannual variation in larval dispersal that may be important over time (e.g. Watson et al. 2010). Subsequent research across multiple years using newly developed numerical models (MacCready et al. 2021) will provide a better sense of whether these results are robust across years. This would be of particular interest for simulated larval releases at sites near the DPS boundary, which showed high levels of cross-boundary dispersal. Our results may be conservative estimates of dispersal from PSGB waters to the outer coast, given the average to below-average freshwater flow of 2006 and its potential effect on dispersal rates of the youngest larval stages, but given the persistent nature of the incoming deep-layer tidal currents, interannual variability in dispersal from the outer coast to waters inside the DPS due to oceanographic conditions is likely to be minimal.

4.4. Application to management

Understanding the connectivity of yelloweye and canary rockfish populations among basins and across the DPS boundary will play a large role in determining whether conservation and management goals are being met. Perhaps the most important finding of this study related to population recovery goals for ESA-listed yelloweye rockfish is the site-specific variation in dispersal rates. There were only a few release sites that appeared to substantially contribute larvae to other DPS basins and are thus likely to play an outsized role in replenishing depleted yelloweye numbers in the connected basins. For example, larvae released from the western and northern SJI sites (Sites 7 and 9) dispersed into the SOG basin at relatively high rates (~24 and 49%, respectively), while the eastern SJI site (Site 8) was the only significant source of dispersal into the Main Basin of Puget Sound. Moreover, the only substantial dispersal of larvae into Hood Canal and the South Sound came from the central Main Basin (Sites 13 and 15, respectively). The potential value of these release sites as larval sources may be analogous to the role of a small number of coral reefs in supplying coral larvae across much of the Great Barrier Reef (Hock et al. 2017).

The importance of these sites to the recovery of yelloweye rockfish abundance, however, will depend heavily on where high densities of adult yelloweye rockfish occur. For example, if biomass is concentrated throughout the SJI or the southern portions of the SOG, then it is likely these locations could serve as a source of larvae to increase recruitment to other basins within the DPS, thus decreasing the time necessary for recovery. However, if biomass is concentrated in northern SOG or within Hood Canal, then recovery across the DPS may take much longer due to the high rates of larval retention in these locations.

Understanding the dynamics between larval dispersal, adult movement among the basins, and the location of high densities of yelloweye rockfish will also help inform potential spatial management strategies of recreational fisheries and/or other ocean-use activities that may contribute to direct or indirect mortality of ESA-listed rockfish species. Sites with high adult densities that are also potential sources of larvae for other basins could provide a framework for identifying critical habitat for PSGB yelloweye rockfish, in the same way that marine protected areas (MPAs) are designed to protect population sources, provide connectivity among populations and to provide spillover of individuals to populate habitats outside the MPAs (Crowder et al. 2000, Burgess et al. 2014, Di Lorenzo et al. 2016).

5. CONCLUSIONS

Larval dispersal and adult/juvenile movement are the 2 primary mechanisms that explain both evolutionary and ecological connectivity among marine fish populations. Larval dispersal integrates a complex set of oceanographic, ecological, physiological and behavioral variables that ultimately contribute to the genetic structure, connectivity and spatiotemporal patterns of abundance that we observe in nature. Simulating the dispersal of larvae from 2 rockfish species of high management and conservation value showed similar patterns of dispersal and connectivity among geographic and management units that are not entirely consistent with the patterns of population structure observed in the genetic code. Further research should explore these inconsistencies and span a broader range of oceanographic conditions to increase our understanding of connectivity across management boundaries and improve the likelihood of sustainable management of these species.

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