Appendices

Appendix A

Eel River Restoration and Conservation Plan
Planning Team and Technical Advisory Committee

Eel River Restoration and Conservation Plan Planning Team and Technical Advisory Committee

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APPENDIX B

Channel Archetypes

1 GOALS AND OVERVIEW OF CHANNEL ARCHETYPE ANALYSIS

In developing management and restoration plans, there is a need to conceptualize landscapes into groupings that share similar processes and attributes, to reduce the complexity of understanding and ultimately decision making. These conceptual models, or "archetypes," across a landscape can represent a set of biophysical processes which "control the behavior of the unit, generating and sustaining characteristic features and attributes" (Cullum et al. 2017). Archetypes are "inherently vague and imprecise" because group membership almost always occurs across a spectrum rather than as a binary, but this imprecision does not defy their usefulness in highlighting important processes and features that drive ecological use and management decision.

In developing the framework for prioritizing restoration and conservation actions for the Eel River Restoration and Conservation Plan (the "Plan"), the Planning Team identified a need to identify similar river channel segments across the watershed at the reach-scale. These channel segments (approximately 1 km in length) share primary physical and environmental attributes that reflect physical processes and disturbance mechanisms that work to maintain channel morphology over time. To identify similar channel segments, the Planning Team conducted a channel archetyping analysis, which categorizes reaches following physical attributes that determine (1) how fish use these channel segments and (2) opportunities and constraints for restoration actions. Identifying and mapping these channel archetypes across the Eel River watershed allows streams with similar ecological and physical processes to be quantified at larger spatial scales (e.g., within a sub-watershed or HUC-12 catchment). This information provides a useful framework for visualizing and communicating how different focal fish species, life stages, and life history strategies have the potential to use different parts of the watershed across time and space as part of the species conceptual models (Appendix C). Additionally, these channel archetypes provide a useful reach-scale planning unit for identifying locations that are most appropriate for different restoration actions (Section 4 in the Plan and Appendix E) and expectations for how these actions will evolve given the physical channel processes.

As with any grouping analysis, it was necessary to aggregate some channel segments with unique characteristics to maintain simplicity and a reasonably manageable number of channel categories. A diversity of stream channels exists within most of the archetypes identified, and it will be necessary to conduct additional analyses to identify and describe variation in other key ecological and physical processes to support of various future restoration planning and prioritization steps. For example, within channel archetypes that are suitable for floodplain restoration, further assessments of channel confinement and flow inundation will be needed to identify reaches most suited for floodplain habitat enhancement. Similarly, these channel archetypes can be used as a template to overlay other important datasets for certain species to identify potential unique hotspots on the landscape. Low-gradient channel archetypes that have a relatively unconfined valley and that also have higher summer baseflows with cool temperature, for example, might be areas to prioritize restoration projects that target Coho Salmon rearing.

The data used to construct the channel archetypes are readily available physical variables that provide a template for process controls and species use. The Planning Team expanded on the "Intrinsic Potential" concept, which scores habitat for a species based on drainage area, slope, and channel confinement (Burnett et al. 2007). Our channel archetypes differ from the IP in that they are relevant across salmonid species (rather than having an IP layer for each species) and that they include information about predicted thermal regime. Similar to the IP, the channel archetypes represent potential use/physical conditions, rather than current (impaired) conditions. For example, some of the low-gradient, cold tributary streams may not currently be natal streams for Coho Salmon due to unnaturally high sediment inputs from upslope land use disturbance or lack of channel complexity for over-wintering velocity refugia. The channel archetypes are built with currently available watershed-wide datasets on drainage area, slope, and water temperature, as described below. As a result of the grouping analysis, 14 unique channel archetypes were identified that encompass physical and thermal categories (see Section 3).

2 METHODS

2.1 Datasets

A suite of readily available and watershed wide physical and environmental datasets that potentially influence fish habitat potential were gathered and considered. The initial list was narrowed to drainage area, slope, and water temperature (Table B-1). These variables are primary drivers of fish habitat potential and were available in a consistent channel network. Drainage area and slope data were obtained from FitzGerald et al. (2021), who attributed data to channel segments that were 1 km or shorter from the National Hydrography Dataset Plus (NHDPlus) dataset (10-m resolution) (Moore et al. 2019). Slope measurements were also calculated at this scale, using the change in elevation from the top and bottom of the 1 km segment, so there is likely smaller-scale variability that is not captured, particularly in segments that contain a discrete elevation change (e.g., a waterfall). Predicted mean monthly water temperatures throughout the Eel River watershed were obtained from FitzGerald et al. (2021), who modeled temperatures using a Stream Spatial Network (Ver Hoef & Peterson 2010). Mean monthly August temperatures were used to categorize channels by thermal regimes at a time of year when temperatures can be physiologically stressful for sensitive species. However, water temperatures in the Eel River are often slightly warmer in July (Asarian et al. 2016). Additionally, streams that are seasonally too warm may provide high growth environments, especially if food resources are adequate, at other times of the year (Armstrong et al. 2021, Rossi et al. 2022).

Table B-1. Datasets used for channel archetyping and their source.

Dataset	Source	Scale
Drainage Area	FitzGerald et al. 2021, calculated from NHDPlus (Moore et al. 2019)	1 km or less channel segments
Slope	FitzGerald et al. 2021, calculated from NHDPlus (Moore et al. 2019)	1 km or less channel segments
Mean monthly water temperature	FitzGerald et al 2021, empirical/statistical modeled using a Stream Spatial Network	1 km or less channel segments

In identifying datasets for use in the channel archetypes analysis, additional channel sets were identified that will be useful at later stages of restoration planning and prioritization (Table B-2). These were not used in the channel archetype analysis to reduce complexity at the focal planning units, but they will be important at different stages in the planning. Modelled summer baseflows were downloaded from a statewide functional flow model, the California Natural Flows Database (CEFWG 2021, Grantham et al. 2022). The model estimates functional flows for every 1–3 km channel segment in California. Valley confinement was calculated for the channel segments from valley wall to valley wall, estimated by a 25% slope (Guillon et al. 2019, Byrne et al. 2020). Predicted geomorphic channel types, following Montgomery and Buffington (1997) categories and calculated from methods in Flores et al. (2006) were also provided by FitzGerald et al.

(2021). There are likely other datasets that can be considered as well, but the Planning Team has not identified the best data source yet (e.g., predicted sediment supply), or the which scale to summarize the data (e.g., lithology, riparian forest).

Table B-2. Datasets that will be useful to layer on channel archetypes at later stages of restoration planning and prioritization.

Dataset	Source	Scale	Future use
Dry season baseflow	California Natural Flows Database (Grantham et al. 2022)	3 km or less channel segments	The stability of baseflows and tendency to be intermittent may help with prioritization
Valley Confinement	Byrne et al. 2020	3 km or less channel segments	Identify areas with floodplain potential
Geomorphic Channel Classification	FitzGerald et al. 2021, calculated with methods in Flores et al. 2006	1 km or less channel segments	Estimate predicted geomorphic characteristics within a channel archetype

2.2 Process Overview

The Planning Team first developed biologically and physically relevant categories within each variable in Table B-1 (drainage area, slope, and temperature). To avoid having too many categories within each variable (and amongst all variables), in some cases it was necessary select relatively broad categories (e.g., group all channels with drainage areas from 2–100 km^2). After selecting initial categories for each variable, the distribution of categories within variables was plotted in a hierarchical manner (e.g., the distribution of drainage area categories, distribution of slope categories within each drainage area group, and then temperature distribution within each slope-drainage area group), to understand prevalence of relevant categories within the Eel River watershed. Based on distributions within these hierarchical categories, the smallest number of channel archetypes possible were selected that reasonably represent unique combinations of focal variables. As described above, developing the archetypes in this way meant grouping some potentially unique channel types (e.g., warm, high-gradient tributaries), and a future analysis could highlight these outliers.

2.3 Drainage Area

Drainage area categories were determined by potential fish use, physical processes, professional judgement, and local knowledge of the Eel River (Table B-3, Figure B-1). The Planning Team used a logarithmic scale, with break points at 100 and 1,000 km^2, because this is a scale that governs many physical processes in nature. A logarithmic scale is also consistent with the framework suggested in Higgins et al. (2005) for hierarchically categorizing large watersheds.

Table B-3. Drainage area categories that were considered for channel archetypes.

Drainage area (km^2)	Category	Description
<2	Small Tributary	Very small watersheds, often not perennial fish habitat but some channels may be important for non-natal rearing in the wet season. Relevant for restoration consideration due to sediment and water inputs.
2–100	Tributary	Includes most spawning and natal rearing habitats for Coho Salmon and steelhead and some spawning by Chinook Salmon and Pacific Lamprey. This is generally the channel size at which smaller-scale restoration activities can be effective (e.g., wood addition). This group includes high-energy reaches where allochthonous inputs and riparian shading are important. The largest number of channels fall in this category and it includes the greatest diversity of channel slopes and water temperatures.
100–1,000	Mainstem	Includes channels that are used for seasonal rearing and migration; significant spawning by Chinook Salmon, and Pacific Lamprey, and occasional spawning for Coho Salmon and steelhead. Pikeminnow are common in these channels. Standing crop of benthic algae and cyanobacteria are visible and even dominant in these channels, especially in summer months. Potential for deep pools and connections to larger floodplains. In channel restoration potential is limited relative to tributaries, and restoration activities will typically be larger and process based.
1,000–10,0000	Large Mainstem	Used for seasonal rearing, adult staging. and migration, primary spawning for Green Sturgeon and significant spawning for Chinook Salmon and Pacific Lamprey. Riparian shading is limited or non-existent. In channel restoration potential limited relative to tributaries and mainstems but may be a focus area of reconnecting floodplains.

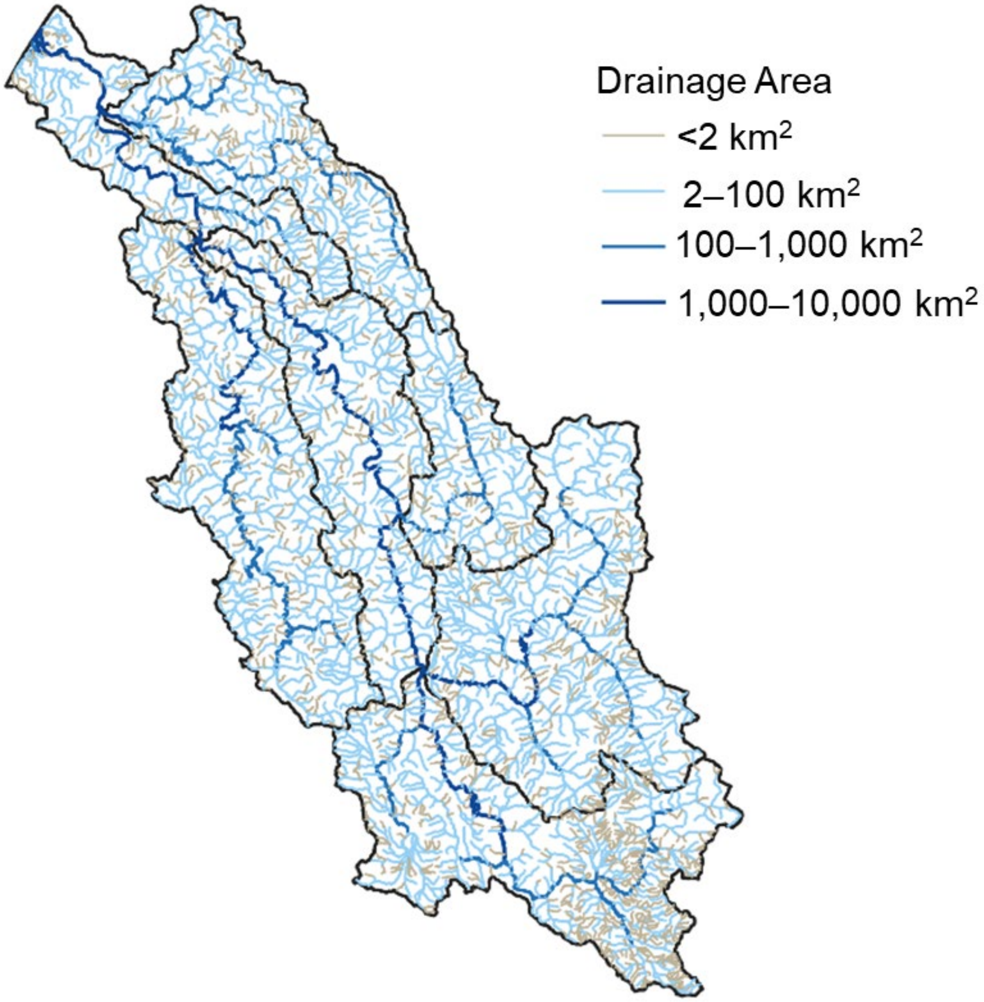

Figure B-1. Streams within each drainage area category in the Eel River watershed (see Table B-3). Drainage areas were obtained from the National Hydrography Database Plus and compiled by FitzGerald et al. (2021).

2.4 Slope

Slope categories were selected primarily based on predicted differences in use by salmonids (Stillwater Sciences 2013, Burnett et al. 2007), and previous studies that have used slope to estimate parr capacity for salmonid species in the Eel River (FitzGerald et al. 2022, Cooper et al. 2020). Selected slope categories are described in Table B-4. The larger drainage areas, Mainstems and Large Mainstems, are dominated by low slopes (<1%), while all the very high-gradient channels (>12%) occur in Tributaries and Small Tributaries (Figure B-2 and Figure B-3). For both Mainstems and Large Mainstems, the vast majority of channel segments fell within the less than 2% category, so these drainage area groups were not divided by slope. While Small Tributaries are important sources of water and sediment, they are expected to provide relatively little fish habitat due to their small size, regardless of slope. For this reason, all slope categories within Small Tributaries were grouped together. The Tributary category was divided into all four slope groups.

Table B-4. Slope breaks that were considered in developing channel archetypes.

Slope break	Category	Description
<2%	Low-gradient	Ideal habitat for Chinook and Coho, potential use by steelhead. Strong Coho streams (Hollow Tree Creek, Indian Creek) are less than 2% gradient
2–7%	Medium-gradient	Potential habitat for Coho, ideal habitat for steelhead. Coho are more common at the lower end of this slope group (i.e., up to 5%; Burnett et al 2007)
7–12%	High-gradient	Likely used by steelhead, possible in-channel restoration actions are limited
>12%	Very high-gradient	Likely not productive fish habitat

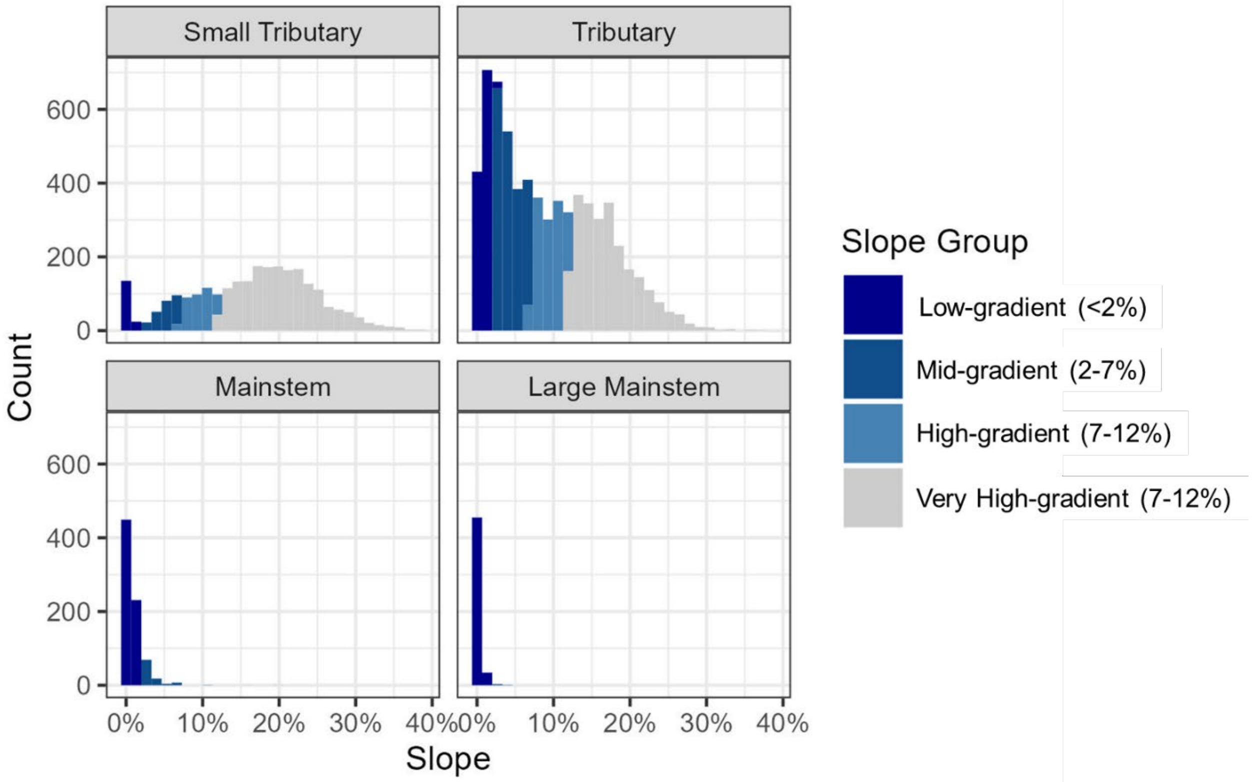

Figure B-2. The distribution of channel segments in each slope category within the drainage area categories, colored by the slope categories considered.

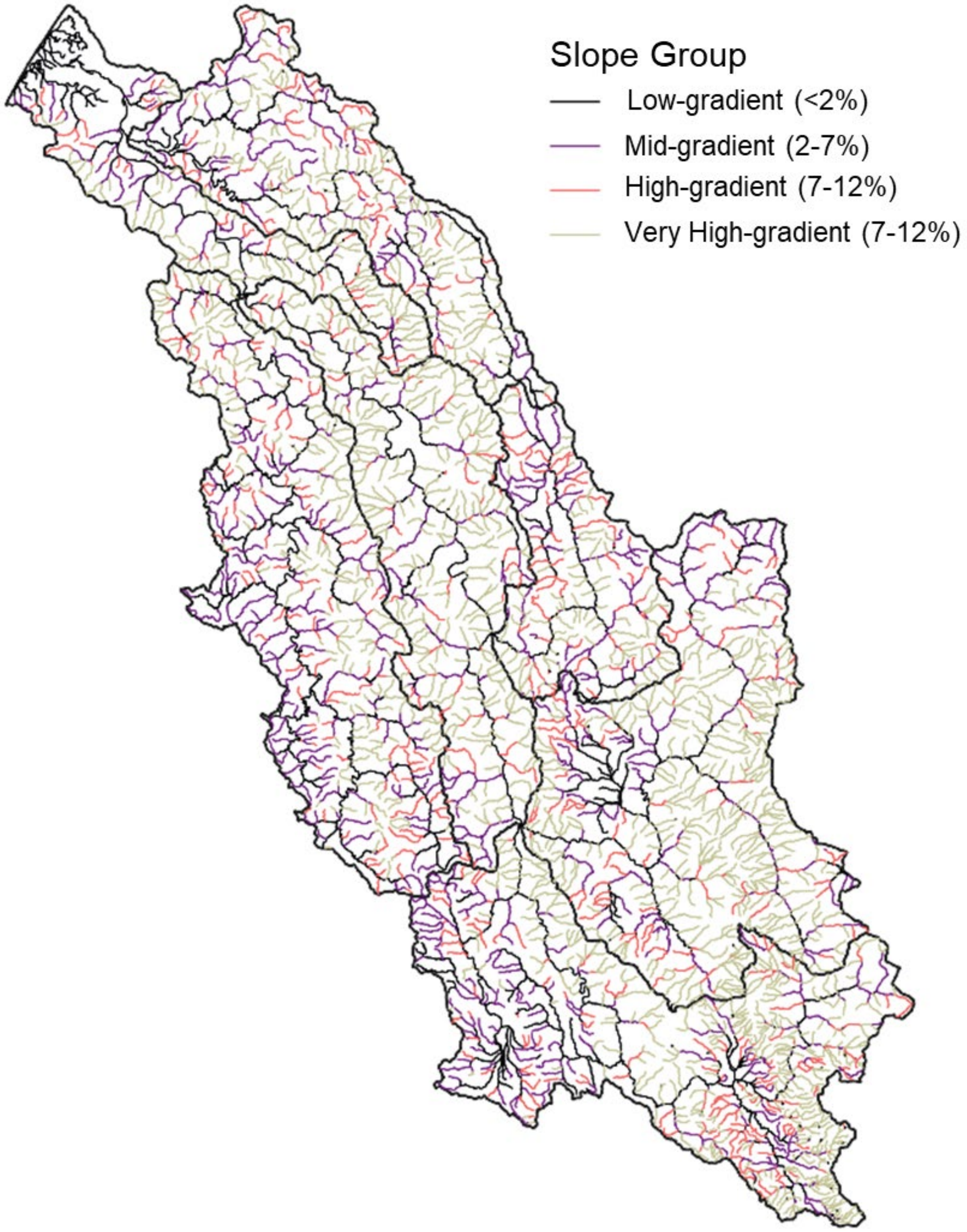

Figure B-3. Map of slope breaks used to define channel archetypes at the stream reach scale in the Eel River watershed.

2.5 Water Temperature

Water temperature categories were developed based on (1) reported thermal tolerances of salmonid species (Myrick and Cech 2000, Sullivan et al 2000, FitzGerald et al. 2021), (2) field observations of when steelhead move into thermal refugia in the Eel River (Wang et al. 2020) and the Klamath River (Sutton et al. 2007, Brewitt and Danner 2014), (3) temperatures at which steelhead are infected with parasites in the Eel River (Schaaf et al. 2017), and (4) temperatures at which nonnative Sacramento Pikeminnow become competitively dominant over steelhead (Reese and Harvey 2002). Selected temperature categories are listed and described in Table B-5. The water temperature dataset that was used in the categorization process includes predicted monthly mean temperature for each channel segment, so, for reference for a more biologically relevant metric, we calculated the corresponding maximum weekly average temperatures (MWAT) (Table B-5). MWAT was calculated from a regression between the two metrics using watershed-wide empirical data (Asarian et al. 2016) ($r^2 = 0.94$, Mean Monthly = 0.864 * MWAT + 1.0035, n = 880 observations).

While August temperatures were used to develop groups of streams with similar dry season thermal characteristics, many of the channels that fall into the “seasonally unsuitable” or “stressful” category may have high value for juvenile salmonid feeding and growth at other times of the year, especially if fish can move or find thermal refugia in the days/times when temperatures are too warm. Both these marginal and seasonally uninhabitable streams likely play a large role in providing high-growth opportunities for salmonids during cooler periods like spring and fall (Armstrong et al. 2021). Furthermore, the source of these data is a large-scale multivariate temperature model, that does not identify and integrate small-scale thermal refugia (e.g., tributary confluences, deep stratified pools).

Table B-5. Temperature categories for mean monthly temperature to group streams of similar thermal conditions.

Category	August Mean Temperature (°C)	Equivalent MWAT (°C)	Description
Cold	<17	<18	Ideal for Coho, steelhead, and Chinook rearing throughout the summer, may be lower growth in winter/spring.
Cool	17–20	18–22	High-growth conditions for steelhead, likely tolerable by Coho earlier in the spring/summer, likely used by Chinook before emigration.
Warm	20–24	22–26	Suitable for steelhead and Chinook rearing, especially with high food and/or access to thermal refugia.
Hot	>24	>26	Possible seasonal rearing for steelhead, higher probability of parasites/diseases and non-native warm water fishes.

The Planning Team next plotted the distribution of mean August temperatures for the drainage area categories (Figure B-4). The majority of Large Mainstems fell within the 20–24°C category, so Large Mainstems was treated as one archetype. The only channel segments that fell within the >24°C category were Large Mainstems, and these can be separately identified. The Mainstems contained channels that were between <20°C and >20°C, and so these channels were divided into Cool and Warm Mainstems, respectively. Small tributaries were dominated by channels that were <17°C and are not critical to fish habitat regardless of thermal conditions, so they are grouped into one archetype.

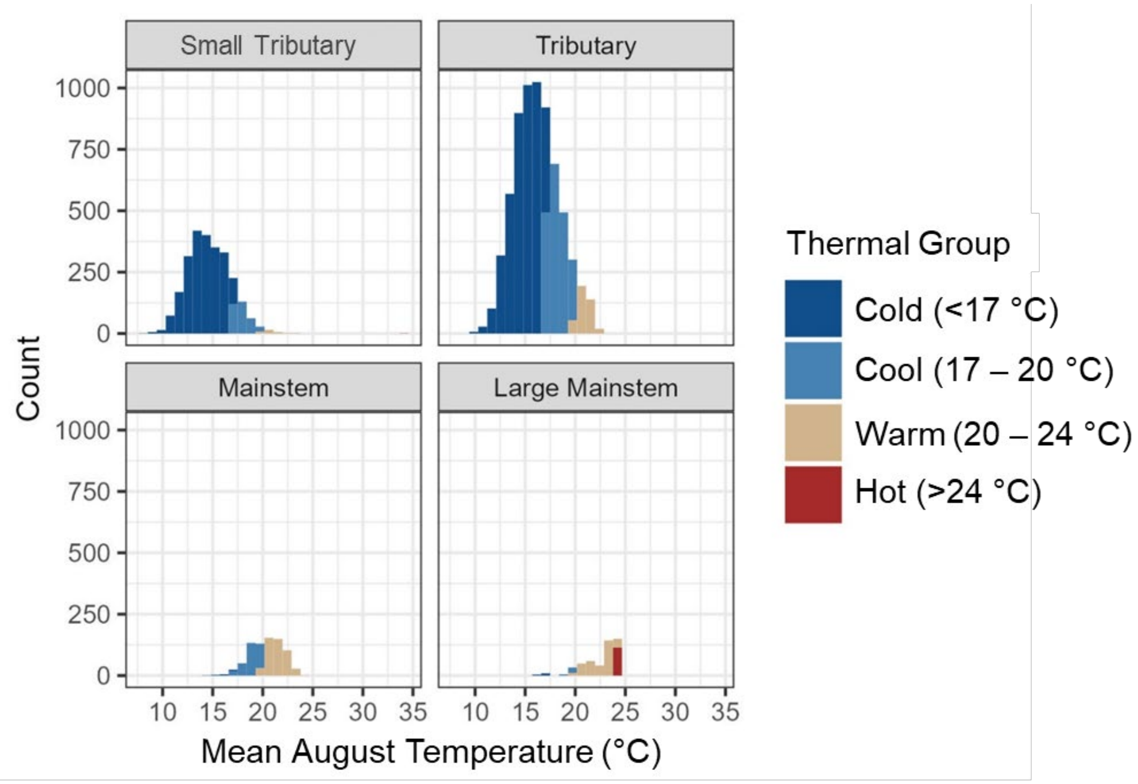

Figure B-4. Distribution of channel segments by mean August water temperature category within the drainage area categories.

For the Tributary groups, the Planning Team predicted that there would be patterns in mean August temperature related to the slope breaks, so the number of channels in each water temperature × slope group was plotted (Figure B-5). The low (<2%) and medium (2–7%) slope groups contained channels from three water temperature groups, <17°C, 17–20°C, and 20–24°C (Figure B-5). For both slope groups, these “Cold,” “Cool,” and “Warm” groupings were maintained. The high (7–12%) slope group was dominated by channels that were either <17°C or 17–20°C, and so these channels were categorized as either “Cold,” or “Cool,” respectively (Figure B-5). The very high slope group (>12%) was dominated by channels that were < 17°C (Figure B-5). Given that these channels will likely only be used by steelhead, and likely not a priority for restoration, these channels were grouped into one channel archetype. The thermal regimes are mapped throughout the Eel River watershed in Figure B-6.

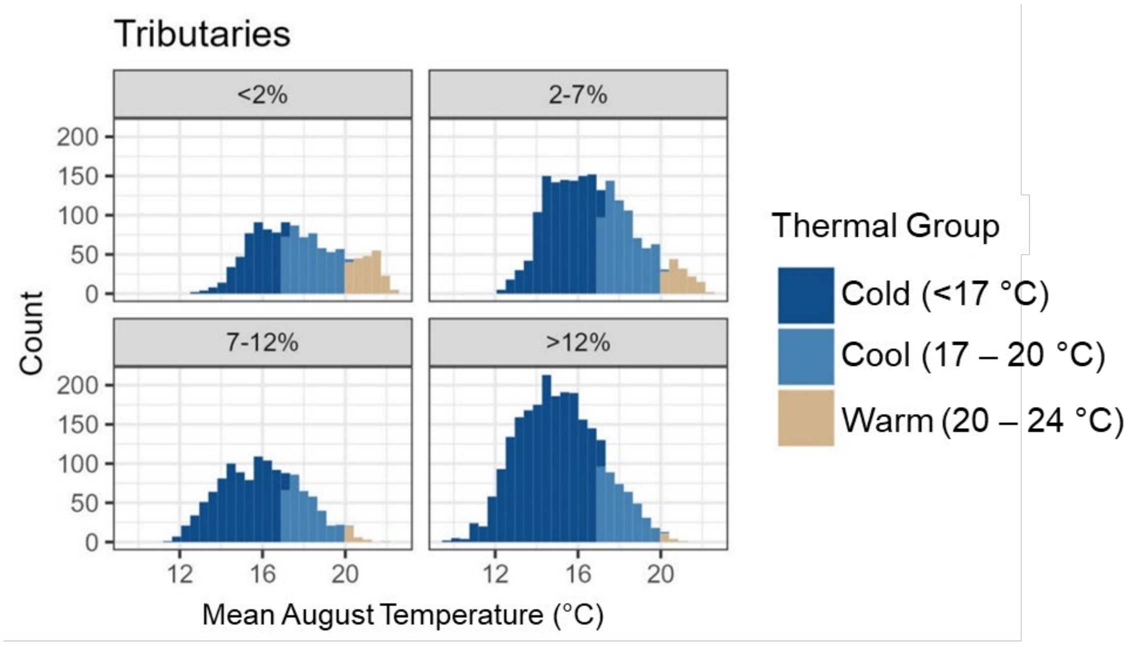

Figure B-5. Distribution of mean August water temperatures within the slope groups of Tributary streams (2–100 km^2).

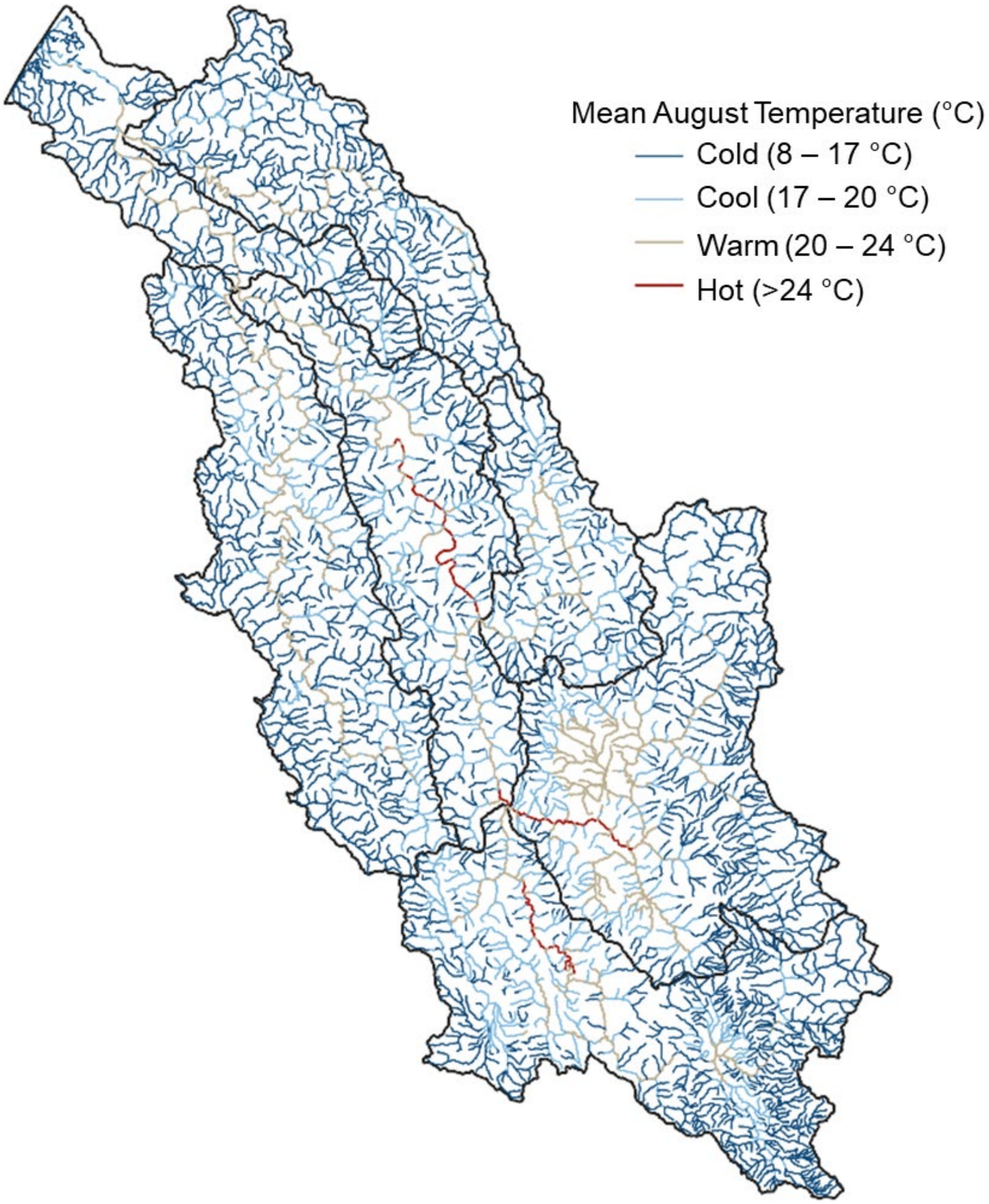

Figure B-6. Mean August water temperatures groups in the Eel River. Data are modeled mean monthly stream temperatures from FitzGerald et al. (2021).

3 RESULTS

The grouping analysis with drainage area, slope, and water temperatures led to 14 channel archetype groups with the addition of the Estuary ecotone (Table B-6 and Figure B-7). Each of these channel archetypes incorporate substantial habitat diversity. They also encompass information on potential use by salmonid species, particularly for natal rearing, non-natal rearing, and migration pathways. Preliminary work estimating the predicted potential use by focal species is outlined in Table B-7. The channel archetypes also link to large categories of restoration actions that might be considered, for example riparian planting, in-channel wood addition, vs. upslope management and large-scale channel restoration (e.g., floodplain reconnection, pool dredging) (see Section 4 in the Plan).

Table B-6. List of channel archetypes and the encompassing drainage area, slope, and thermal groups. The range of mean May and August temperatures is shown to demonstrate that both cool and warm channel archetypes can be seasonally suitable, and even optimal, for focal species.

Channel archetype	Code	Drainage area category	Slope category	Thermal category	Mean August temperature range (°C)	Mean May temperature range (°C)
Small tributary	0	Small tributary (<2 km^2)	All	Cold, Cool, Warm	8.3–23.3	6.5–21.2
Low-gradient, cold tributary	1.1-cold	Tributary (2–100 km^2)	<2%	Cold	11.5–17.0	8.9–15.4
Low-gradient, cool tributary	1.1-cool			Cool	17.0–20.0	9.7–16.4
Low-gradient, warm tributary	1.1-warm			Warm	20.0–23.3	11.4–16.5
Mid-gradient, cold tributary	1.2-cold		2–7%	Cold	11.6–17.0	7.4–15.3
Mid-gradient, cool tributary	1.2-cool			Cool	17.0–20.0	9.3–16.6
Mid-gradient, warm tributary	1.2-warm			Warm	20.0–22.3	12.3–15.3
High-gradient, cold tributary	1.3-cold		7–12%	Cold	10.4–17.0	7.5–15.2
High-gradient, cool tributary	1.3-cool			Cool. Warm,	17.0–21.8	10.5–15.5
Very high-gradient tributary	1.4		>12%	Cold, Cool, Warm	8.3–20.9	6.8–14.9
Cool mainstem	2-cool	Mainstem (100–1,000 km^2)	<2%, 2–7%	Cool	14.7–20	9.7–15.9
Warm mainstem	2-warm		<2%, 2–7%	Warm	20–23.8	10.6–16.6
Large mainstem	3	Large mainstem (>1,000 km^2)	<2%	Cold, Cool, Warm, Hot	16.2–24.6	12.4–16.1
Estuary	4	Estuary	<1%	-	-	-

Table B-7. Preliminary predicted use of channel archetypes by focal species for spawning and natal rearing (NR), non-natal rearing (NNR), rearing (R), and migration (M).

Channel archetype	Chinook				Coho				Steelhead				Green Sturgeon	Pacific Lamprey	Sacramento Pikeminnow
	NR	NNR Wet	NNR Dry	M	NR	NNR Wet	NNR Dry	M	NR	NNR Wet	NNR Dry	M	M & R	M & R	
Small Tributary		P				Y			P	P	P				
Low-gradient, Cold Tributary	Y	Y	Y		Y	Y	Y		Y	Y	Y			Y	P
Low-gradient, Cool Tributary	Y	Y	Y		Y	Y	P		Y	Y	Y			Y	Y
Low-gradient, warm Tributary	Y	P			P	Y			Y	Y	Y			Y	Y
Mid-gradient, Cold Tributary	Y	P	P		Y	P	Y		Y	Y	Y			Y	P
Mid-gradient, Cool Tributary	Y	P			Y	P	P		Y	Y	Y			Y	Y
Mid-gradient, warm Tributary	P	P			Y	P			Y	Y	Y			Y	Y
High-gradient, Cold Tributary									Y	P	Y				
High-gradient, Cool Tributary									Y	P	Y				
Very High-gradient Tributary											P				
Cool Mainstem	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	P	Y	Y
Warm Mainstem	Y	Y		Y	P	P		Y	Y	Y	Y	Y	P	Y	Y
Large Mainstem	Y	Y		Y		P		Y		P	Y	Y	Y	Y	Y
Estuary		Y	Y	Y		Y	Y	Y		Y	Y	Y	Y	Y	Y

[1] Y = yes, commonly used, P = possible, or less-frequently used, and blank = not used.

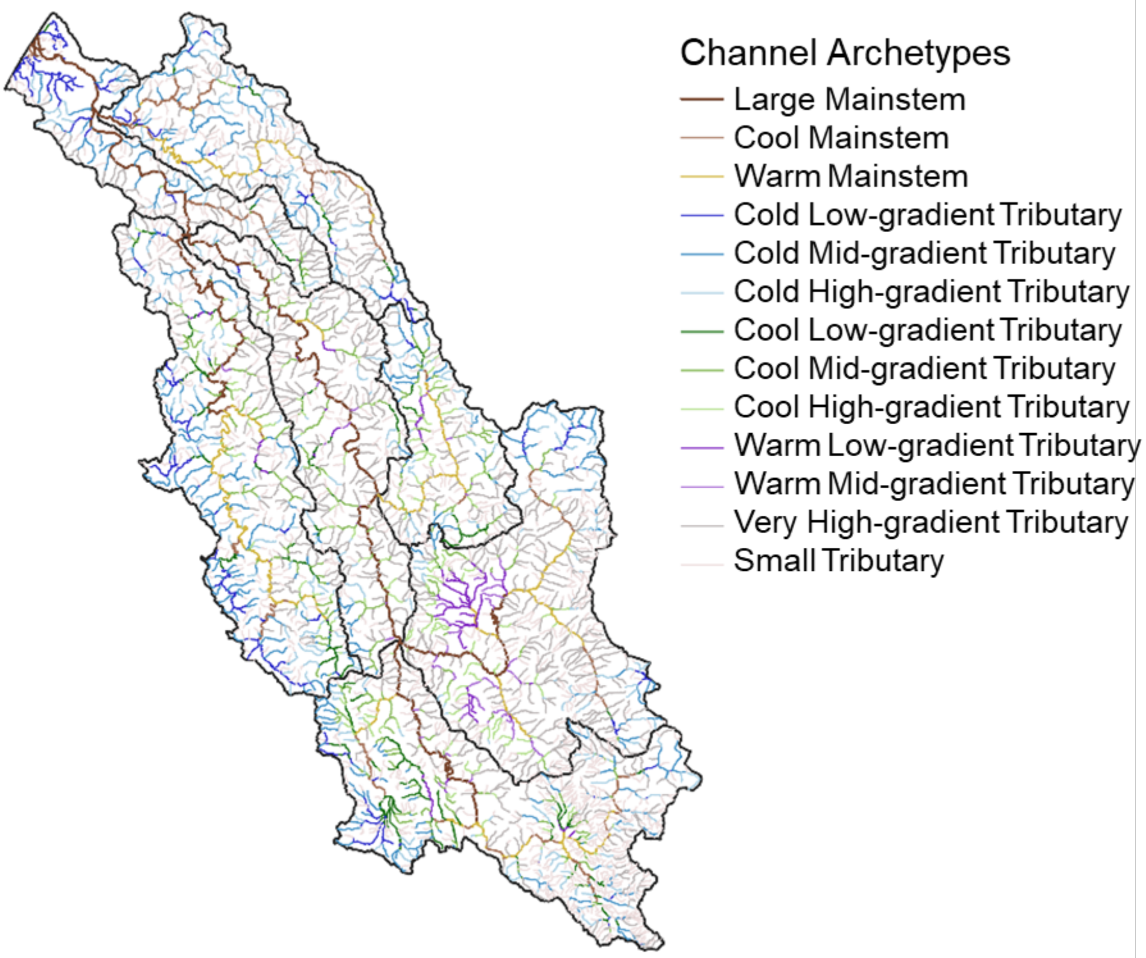

Figure B-7. Channel archetypes in the Eel River that arise from groupings by drainage area, gradient, and thermal regime. The Estuary channel archetype is not shown in the map as a different category from the Large Mainstem.

4 ADDITIONAL DATA OVERLAYS

The channel archetypes provide a template that allows for the addition of other spatial datasets to understand ecological hotspots and unique geomorphic features in the Eel River watershed. For example, valley confinement should be considered in the prioritization framework, especially when identifying habitats that may provide strong over-wintering habitat for focal species. Similarly, trends in baseflows (drier versus wetter) can be considered across the Eel River watershed and within sub-watersheds to highlight tributaries that are more likely to be intermittent or contribute disproportionately high volumes of cool water. Overlaying these additional data sets will allow the channel archetypes to be used in various ways in the Phase 2 prioritization process.

4.1 Baseflows

Baseflows are an important data overlay in understanding the relative discharge in channel segments, which is an important predictor for amount of fish habitat, and potential to maintain cool, connected riverine habitat even through the dry months. Modeled dry season baseflows were downloaded for every channel segment in the Eel River watershed from the California Natural Flows Database (CEFWG 2021, Grantham et al. 2022). Dry season baseflows were scaled by drainage area for every channel segment to standardize the dataset. This scaling allows for the analysis of *relative* baseflows throughout the watershed, acknowledging that there is often error in the estimated magnitude of baseflows in the modelled functional flows. This dataset revealed large spatial patterns in baseflows throughout the watershed (Figure B-8). For example, the South Fork Eel River is dominated by channels that are wetter than average for their drainage area, while the Upper Main Eel and Middle Fork Eel sub-watersheds are drier than average. These patterns align with predictions that arise from the role of subsurface lithology in determining water storage and summer baseflows in the Eel River (Hahm et al. 2019, Dralle et al. 2023). Because the patterns in baseflow are driven by larger-scale geologic features, these groupings were not included in the channel archetypes, but these trends should be considered at a sub-watershed level. For example, warm, low-gradient tributaries in the Middle Fork Eel River are much more likely to be seasonally dry compared to the same archetype in the South Fork Eel River. This information will provide important criteria for ranking restoration and conservation actions in Phase 2 prioritization.

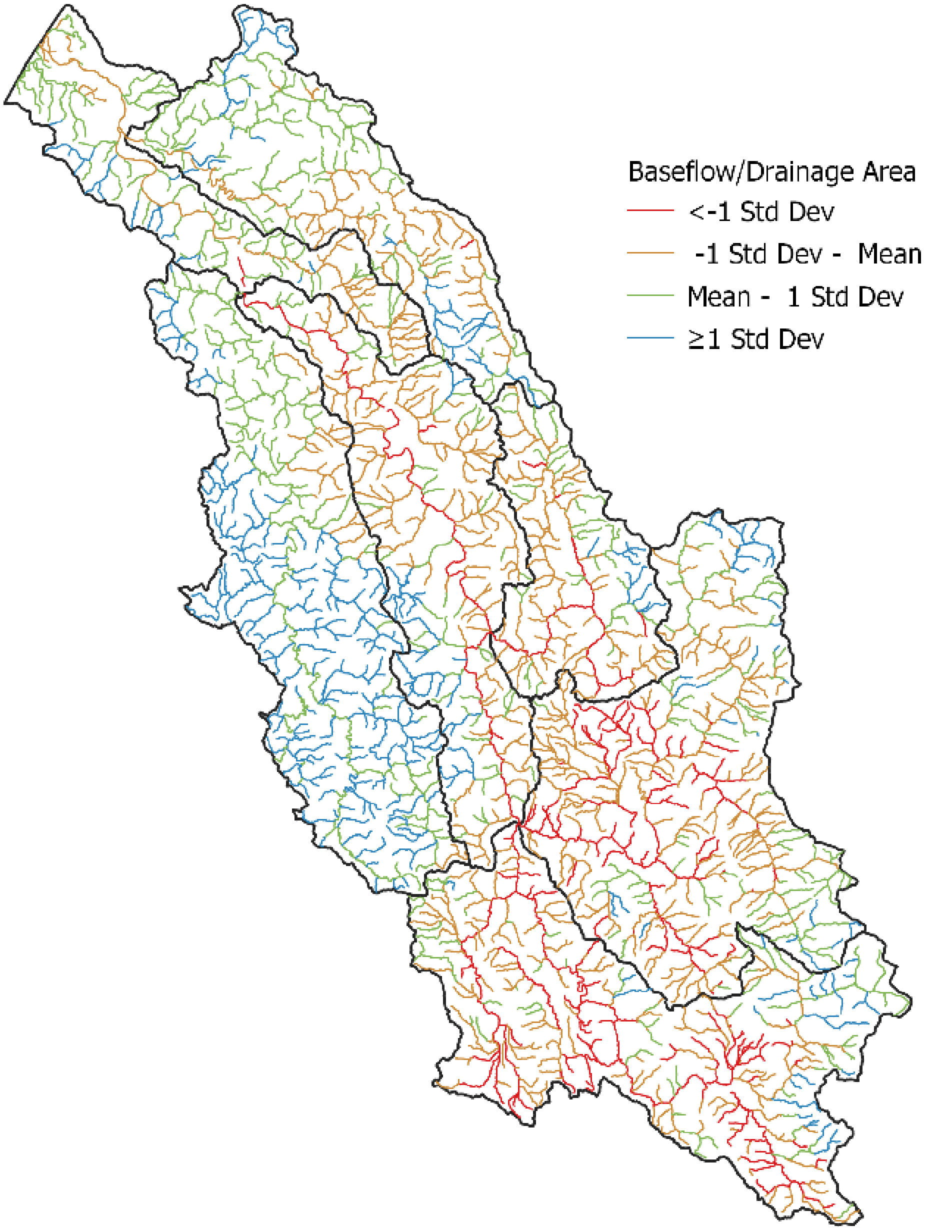

Figure B-8. Modeled dry season baseflows, standardized by drainage area, in the Eel River. Tributaries with a drainage area of <2 km^2 are omitted. Dry season baseflows were estimated by the CEFWG (2021) (Grantham et al. 2022).

4.2 Valley Confinement

Valley confinement describes the width of the valley floor and floodplain, as constrained by hillslopes or other topographic features in a river Nagel et al. (2014). Much of the mountainous Eel River watershed is highly confined, with channels that are surrounded by steep valley walls, a V-shape morphology. There are some notable exceptions, and inland, unconfined valleys were likely historically biological hotspots as the low-gradient, wide valleys create braided channels with high floodplain connectivity. These valleys were likely ecologically productive and complex, high-quality spawning and rearing habitats that contributed to the diversity and resilience of focal species populations. Several notable large, inland valleys include Little Lake Valley (Outlook Creek drainage in the Upper Main Eel sub-watershed), Round Valley (Mill Creek drainage in the Middle Fork Eel sub-watershed), upper Tenmile Creek (near Laytonville in the South Fork Eel sub-watershed), and Gravelly Valley (currently mostly under Lake Pilsbury in the Upper Main Eel sub-watershed). Beyond these large valleys, there locally unconfined reaches that are, or have the potential to be, highly connected to floodplains in otherwise confined reaches. These local anomalies likely provide excellent winter refuge due to their relatively lower velocities during high flow events, good spawning habitat due to the deposition of smaller gravel and sediments, and high-quality summer rearing habitats. For these reasons, there may be analyses in the prioritization framework that include identifying large, unconfined valleys and locally unconfined channel reaches for conservation and for augmentation with restoration actions. Valley confinement here was calculated by Byrne et al. 2020, and scaled by drainage area of each channel segment, to obtain a metric of relative valley confinement. Valley confinement, scaled by drainage area, for each channel segment in the Eel River watershed is shown in Figure B-9.

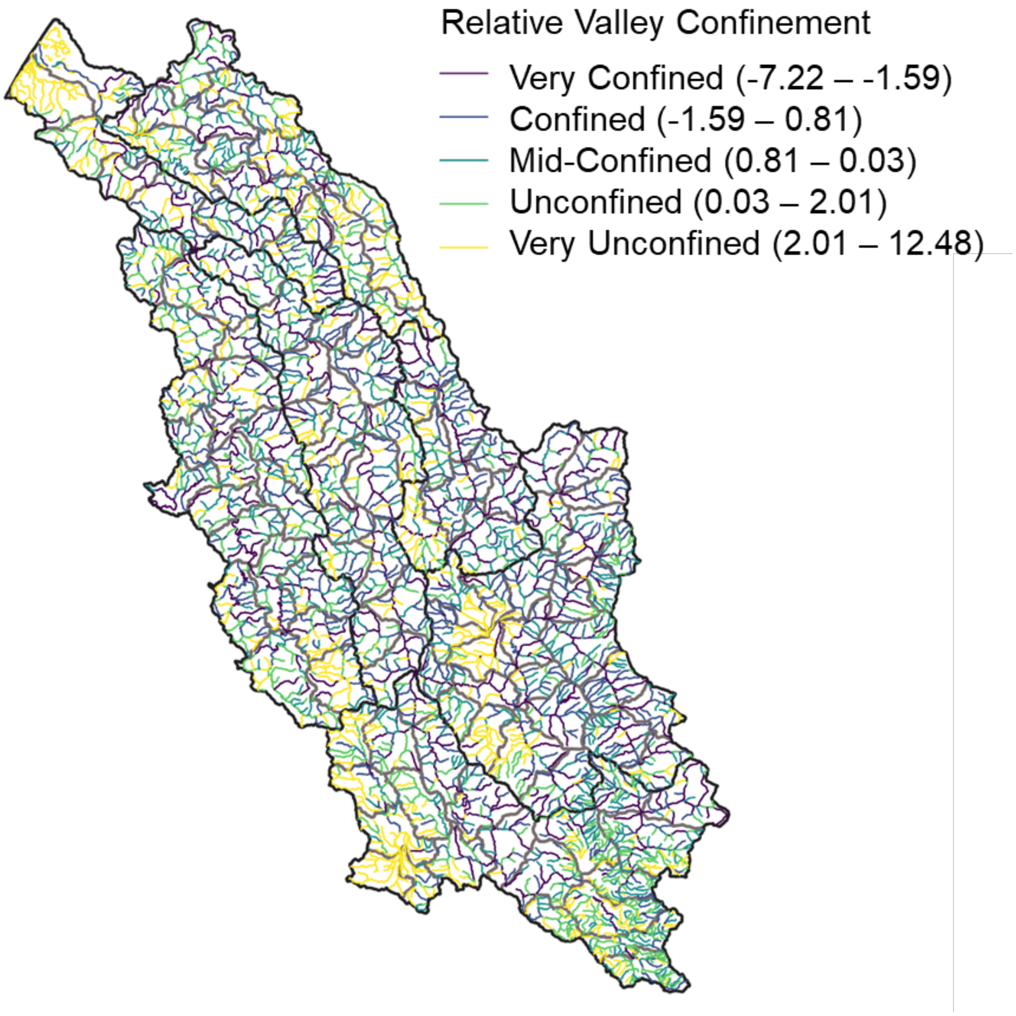

Figure B-9. Relative valley confinement (valley width scaled by drainage area and normalized) along the channel reaches in the Eel River watershed. Valley width was calculated by Byrne et al. 2020, and drainage area estimates are from National Hydrography Database Plus (Moore et al. 2019).

4.3 Geomorphic Channel Types

Geomorphic channel types were estimated from slope and drainage area (FitzGerald et al. 2021), so are redundant with the physical variables that were used to create channel archetypes (Section 2.3 and Section 2.4). The distribution of predicted channel types within drainage area and slope categories supports the grouping analysis based on those variables (Figure B-10). Large mainstems and mainstems are primarily low-gradient and plane-bed channels. Cascades, step-pool habitats are primarily found in Tributaries, with cascades being most common in the >12% slope group. While these geomorphic channel classification predictions were not used in the channel archetype groupings, they may be helpful in identifying habitat features of interest within an archetype during the prioritization and implementation phases of the Program.

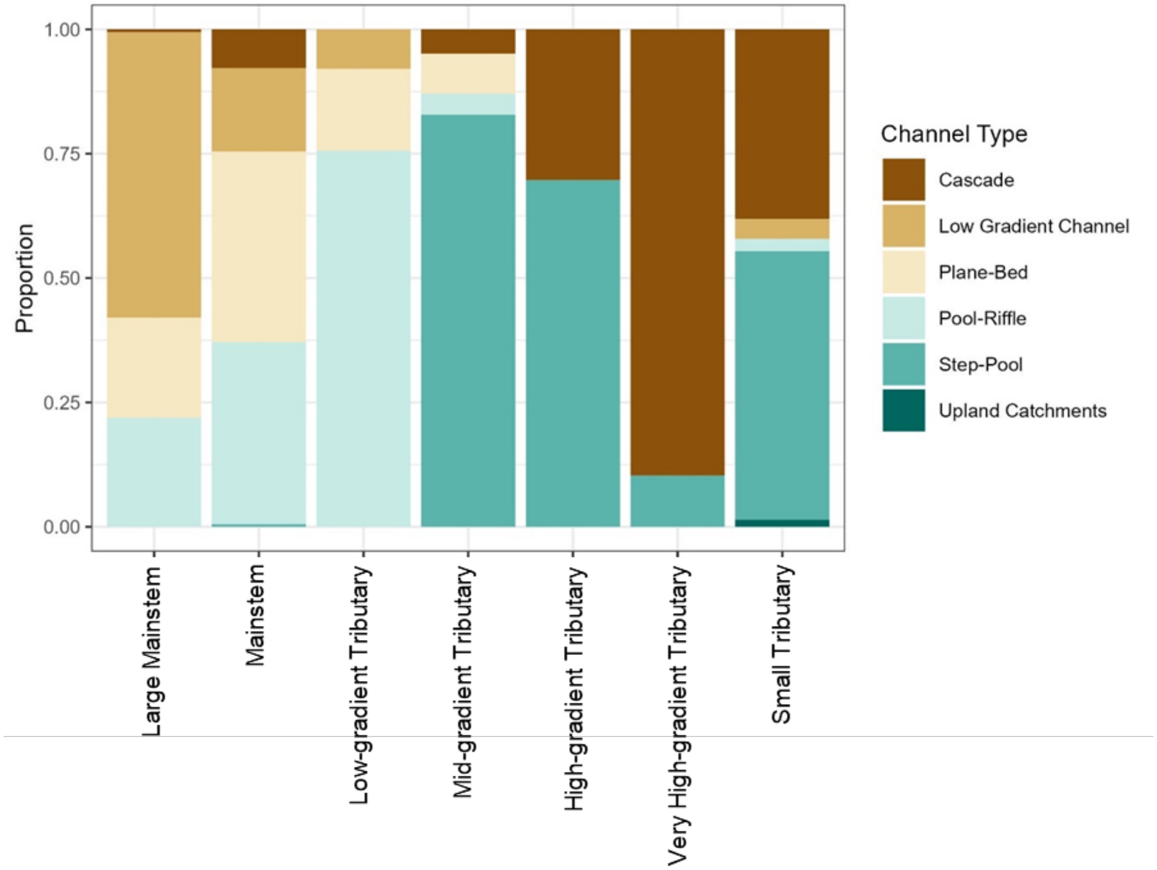

Figure B-10. Predicted geomorphic channel types within the drainage area and slope groupings.

5 NEXT STEPS

One next step in spatial analyses that will guide restoration planning in Phase 2 of the Program is characterization of current channel condition, relative to historic or predicted condition. For example, many large mainstems historically had deep pools that were suitable holding habitat for migrating fish, but these have been filled in from unnaturally high sediment loads. Similarly, tributary habitats are predicted to have riparian areas that contribute allochthonous carbon and buffer stream temperatures. Identifying geographic areas that currently lack a riparian forest, due to forest fires or drought, along with channel types that are most in need of temperature mitigation, will guide prioritization. In summary, an important next step in the Eel River Restoration Program will be to characterize differences between the predicted/historic and current channel condition.

Another next step is to classify the diversity of estuary habitats. The estuary is currently designated as its own channel archetype in this analysis, given its homogeneity in drainage area and slope, and the lack of temperature data at a fine enough resolution to capture thermal diversity used here. When identification of restoration action and fish use *within* the estuary is approached, conducting a classification similar to Simenstad et al. (2011) will be helpful. The Planning Team recommends coordinating with other restoration planning efforts, such as the Lower Eel River SHaRP, in conducting future estuary habitat classifications.

6 FREQUENCY OF CHANNEL ARCHETYPES BY SUBWATERSHEDS AND HUC-12 SUB-BASINS

The channel archetypes are assigned to channel segments throughout the Eel River watershed, which allows for the relative abundance, by channel length, to be summarized at various spatial scales. As channel archetypes are related to predicted use of focal fish species (Table B-7), and to potential restoration actions, summarizing their relative abundance at hierarchical spatial scales can assist with restoration planning in Phase 2 of the Program.

The relative abundance of channel archetypes is summarized for the 7 major sub-watersheds in the Eel River watershed (Figure B-11). Among the sub-watersheds, there are variations in the length of Large Mainstems, Small Tributaries, and thermal regimes of Tributaries. The variation in proportion of Tributaries within each thermal regime is highlighted in Figure B-12, when Small Tributaries and High-gradient Tributaries are excluded.

The relative abundance of channel archetypes can also be summarized for each of the HUC-12 sub-basins in the Eel River watershed. There is variation in the relative lengths within each HUC-12 sub-basin, even within each of the seven sub-watersheds (Figure B-13 through Figure B-19). This variation suggests that there is diversity in habitat types in each HUC-12 sub-basin, and this information will be useful for prioritizing the importance of HUC-12 sub-basins and the suitability of different restoration actions.

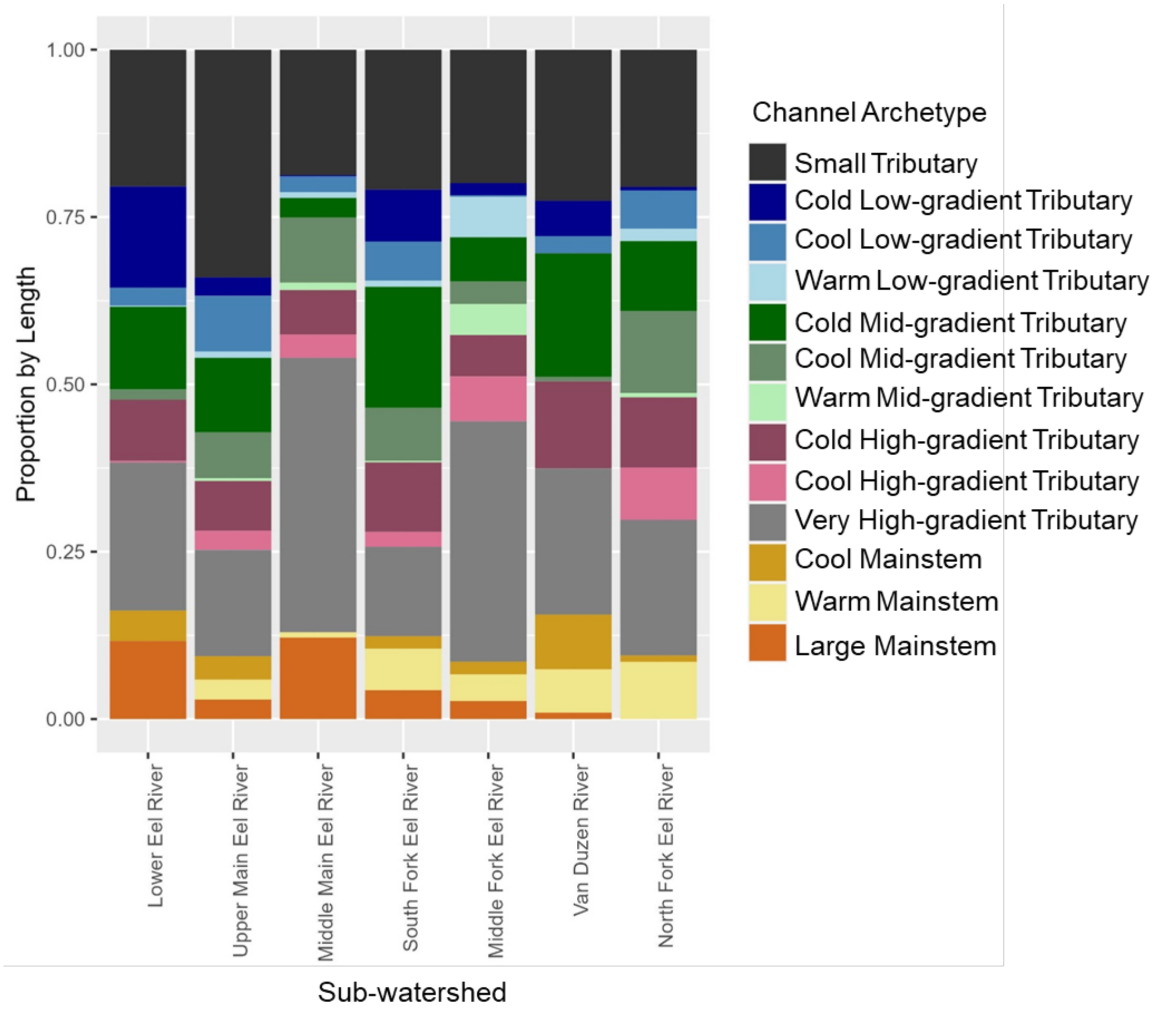

Figure B-11. Proportion of channel length that falls into each channel archetype group within the seven sub-watersheds, excluding the estuary.

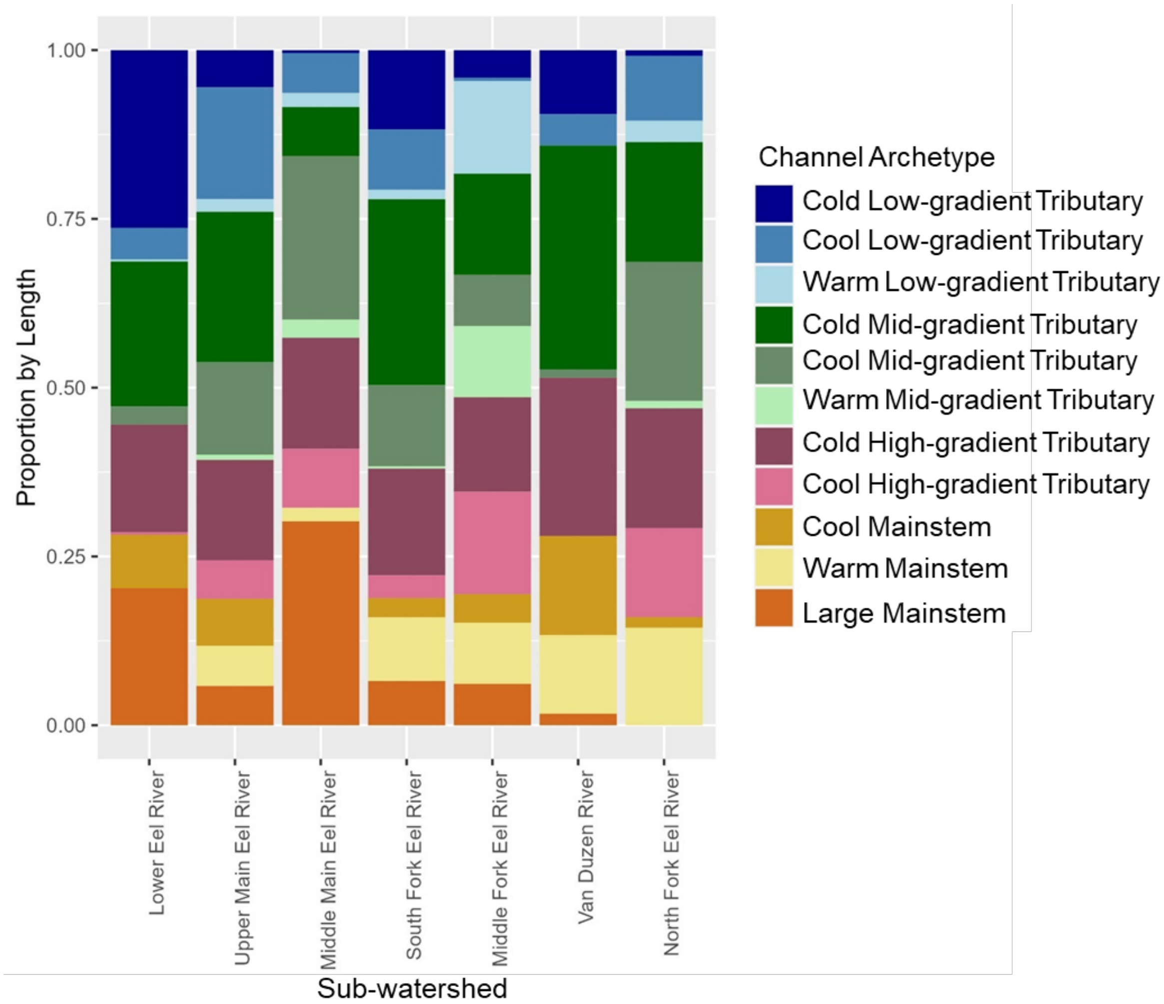

Figure B-12. Proportion of channel length that falls into each channel archetype group within the seven sub-watersheds, excluding Small Tributaries, High-gradeint Tributaries (>12% slope), and the estuary.

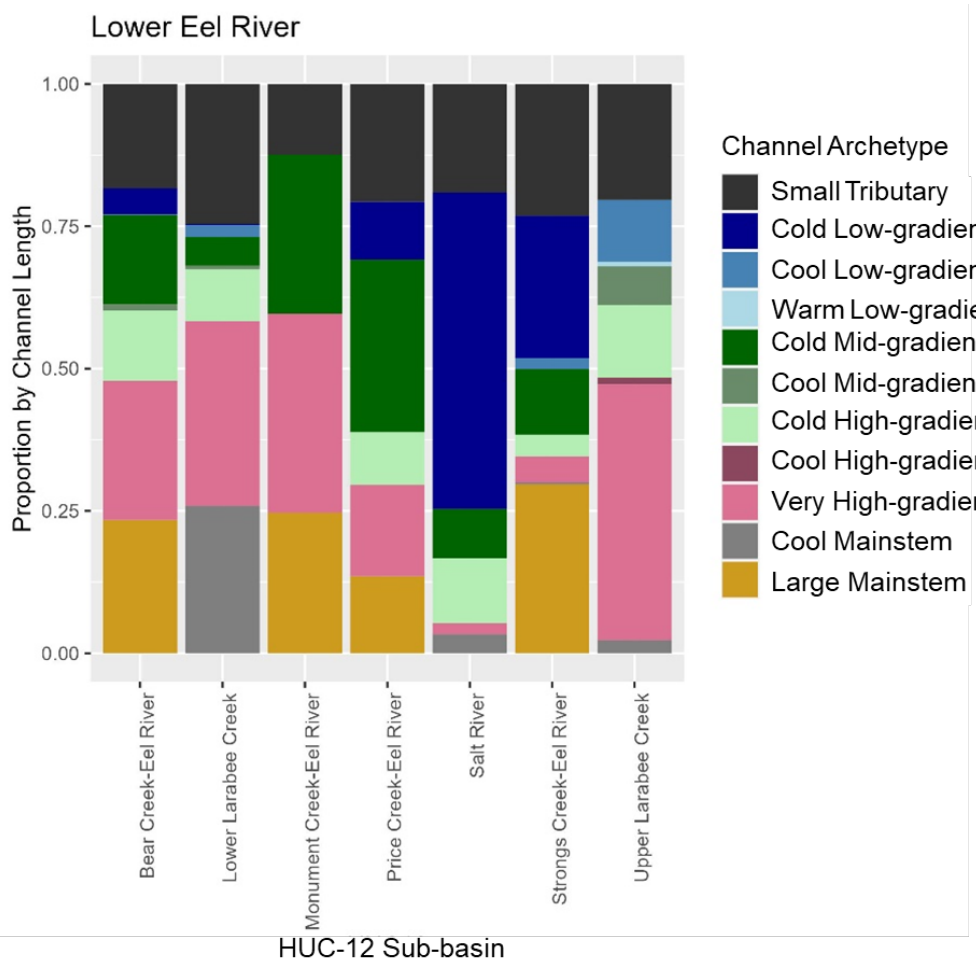

Figure B-13. Proportion of channel archetypes by length within each HUC-12 sub-basin in the Lower Eel River sub-watershed. Note that there are no channel segments in the Warm Mid-gradient Tributary or Warm Mainstem channel archetypes.

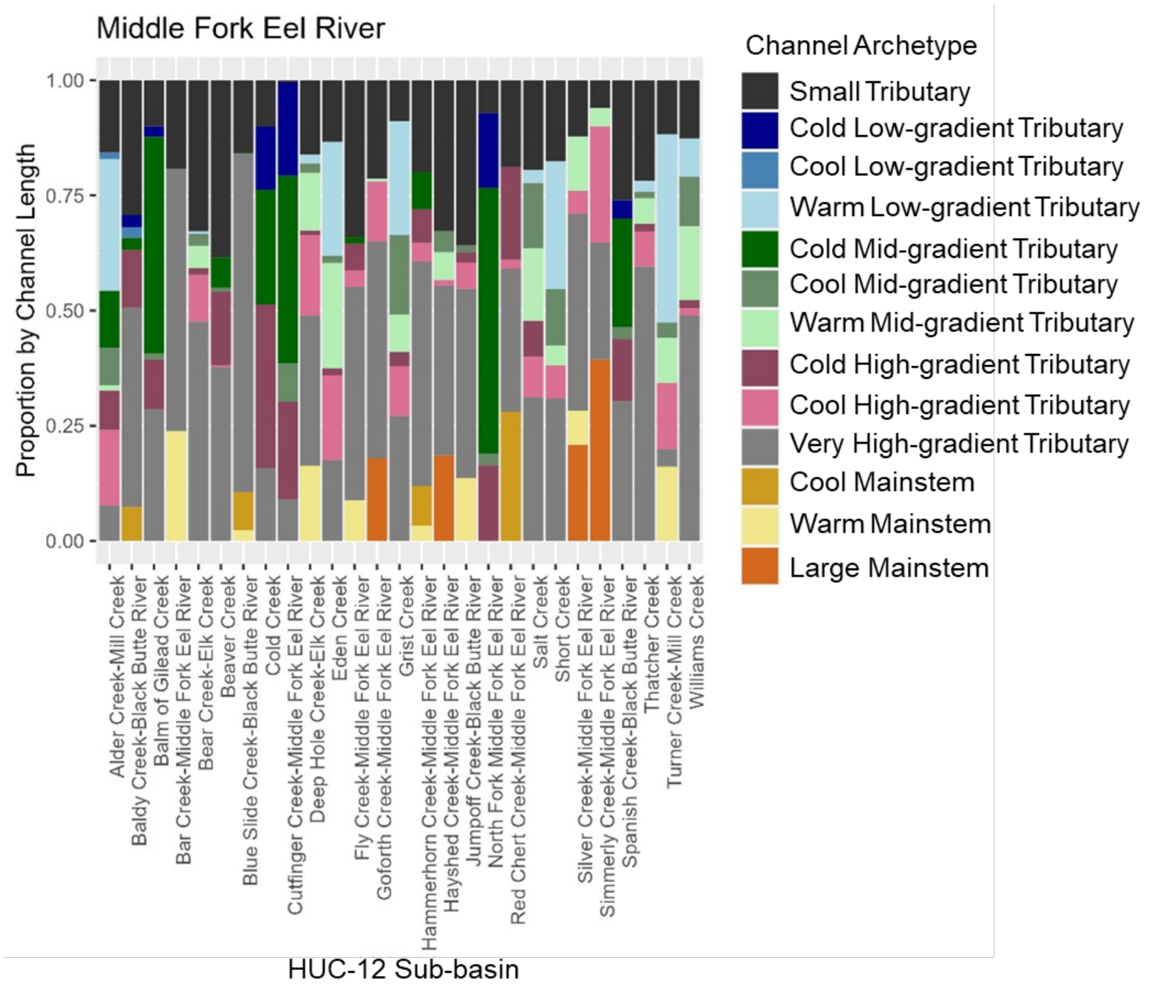

Figure B-14. Proportion of channel archetypes by length within each HUC-12 sub-basin in the Middle Fork Eel River sub-watershed.

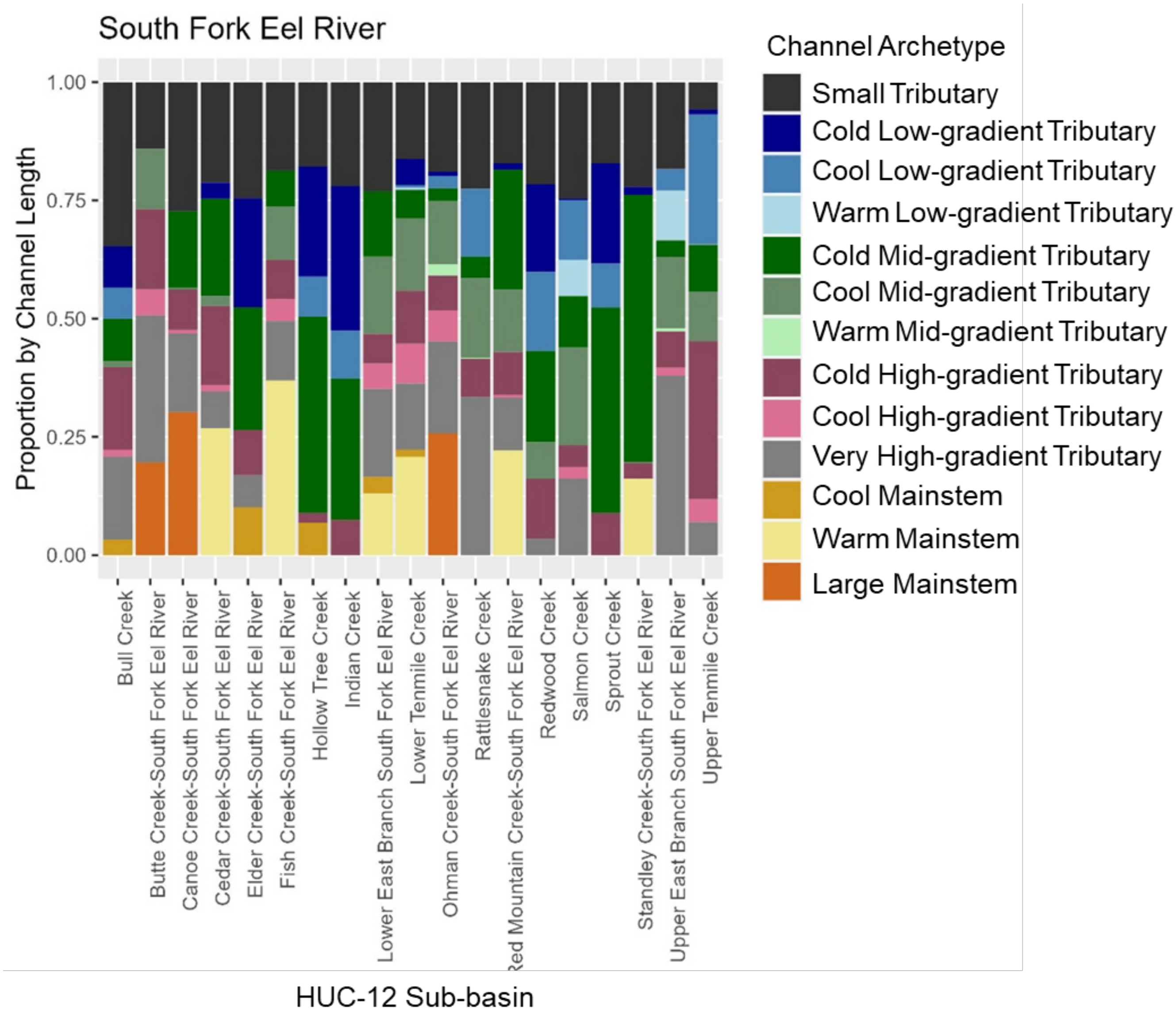

Figure B-15. Proportion of channel archetypes by length within each HUC-12 sub-basin in the South Fork Eel River sub-watershed.

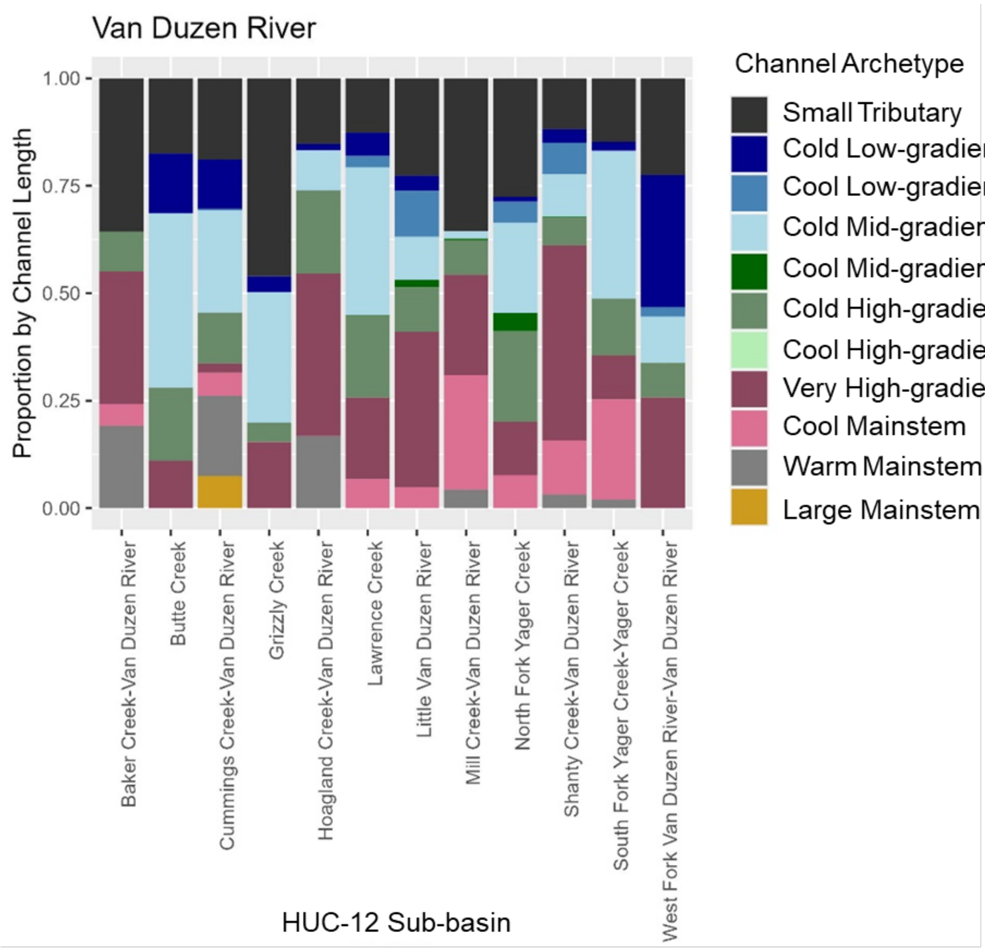

Figure B-16. Proportion of channel archetypes by length within each HUC-12 sub-basin in the Van Duzen River sub-watershed. Note that there are no channel segments in the Warm Low-gradient Tributary or Warm Mid-gradient Tributary channel archetypes in the Van Duzen sub-watershed.

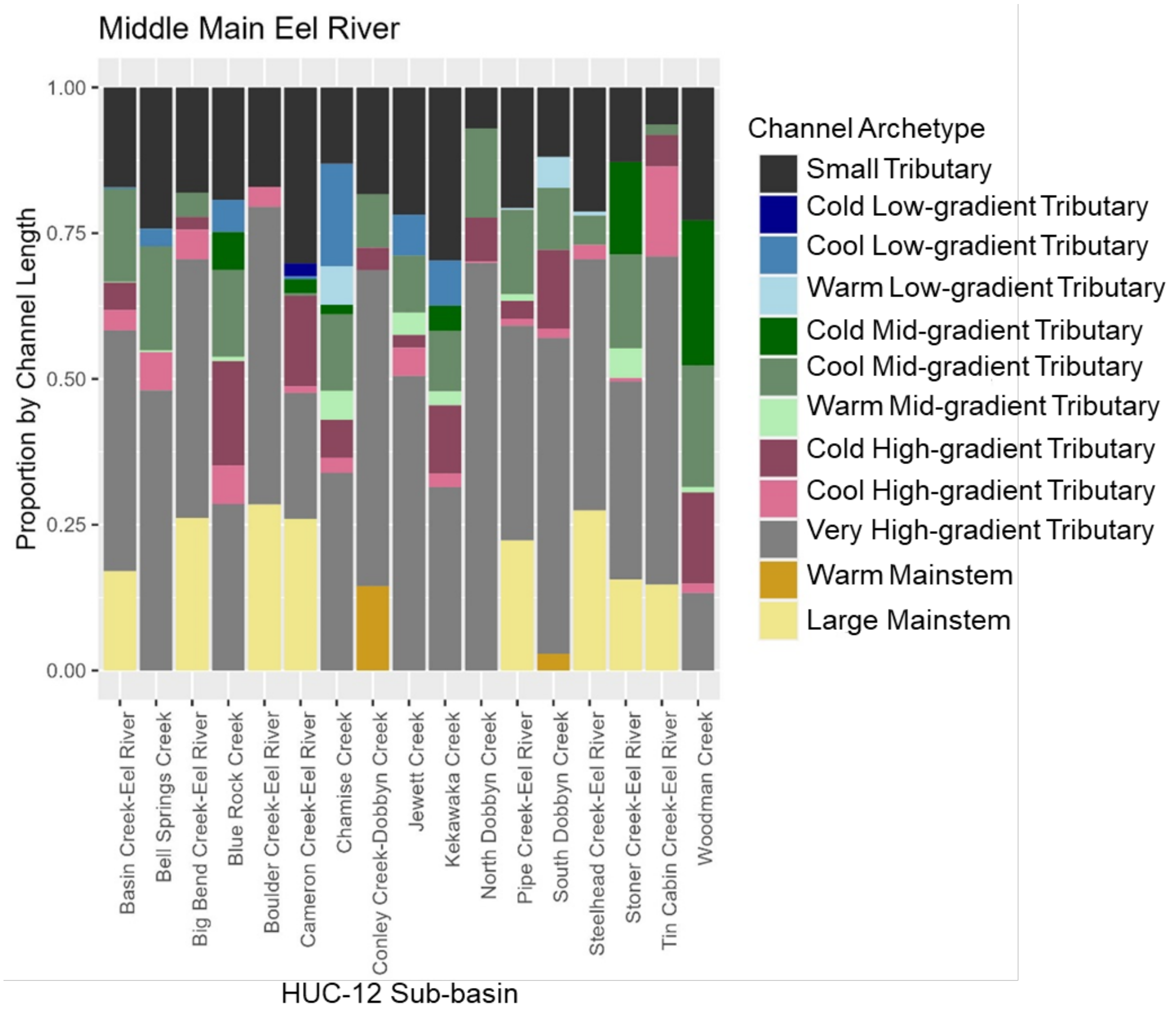

Figure B-17. Proportion of channel archetypes by length within each HUC-12 sub-basin in the Middle Main Eel River sub-watershed. Note there are no channel segments in the Cool Mainstem channel archetype in the Middle Main Eel River sub-watershed.

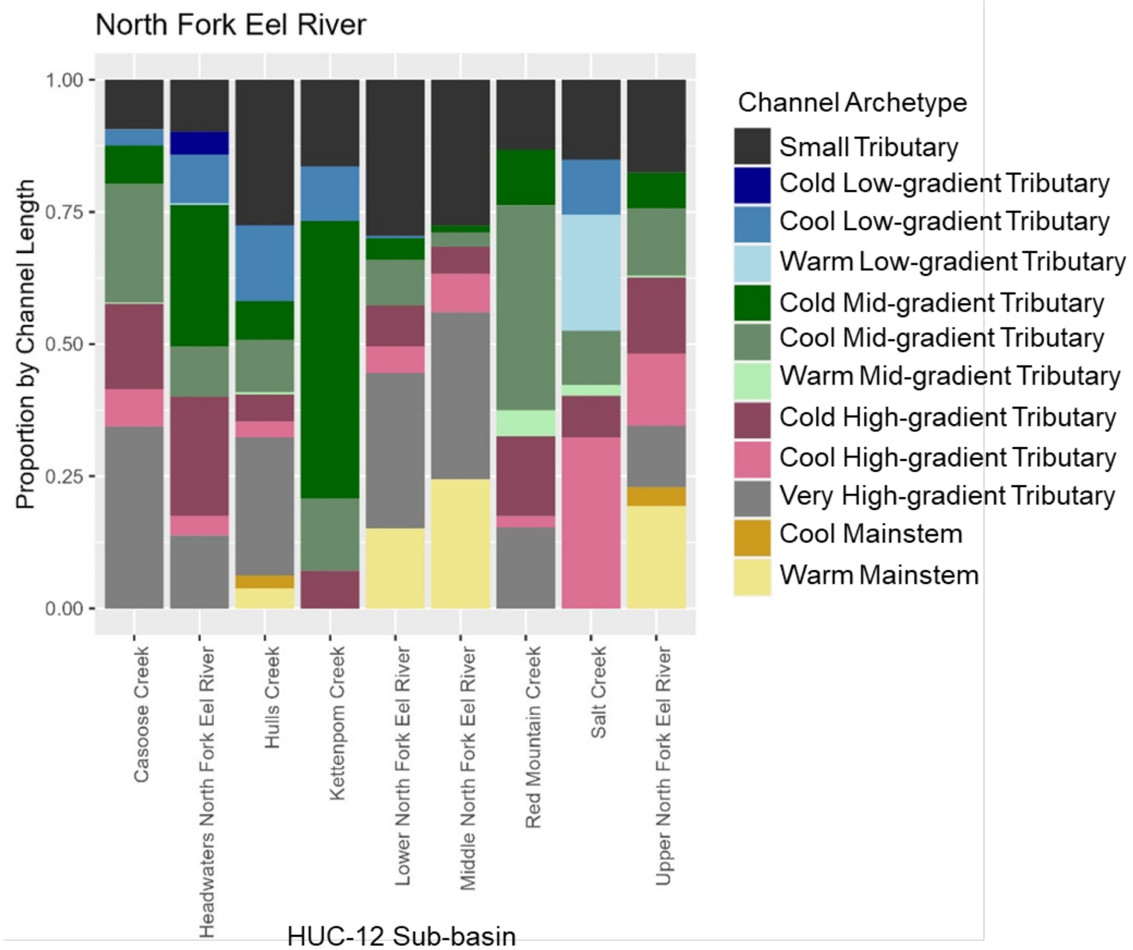

Figure B-18. Proportion of channel archetypes by length within each HUC-12 sub-basin in the North Fork Eel River sub-watershed. Note there are no channel segments in the Large Mainstem channel archetype in the North Fork Eel River sub-watershed.

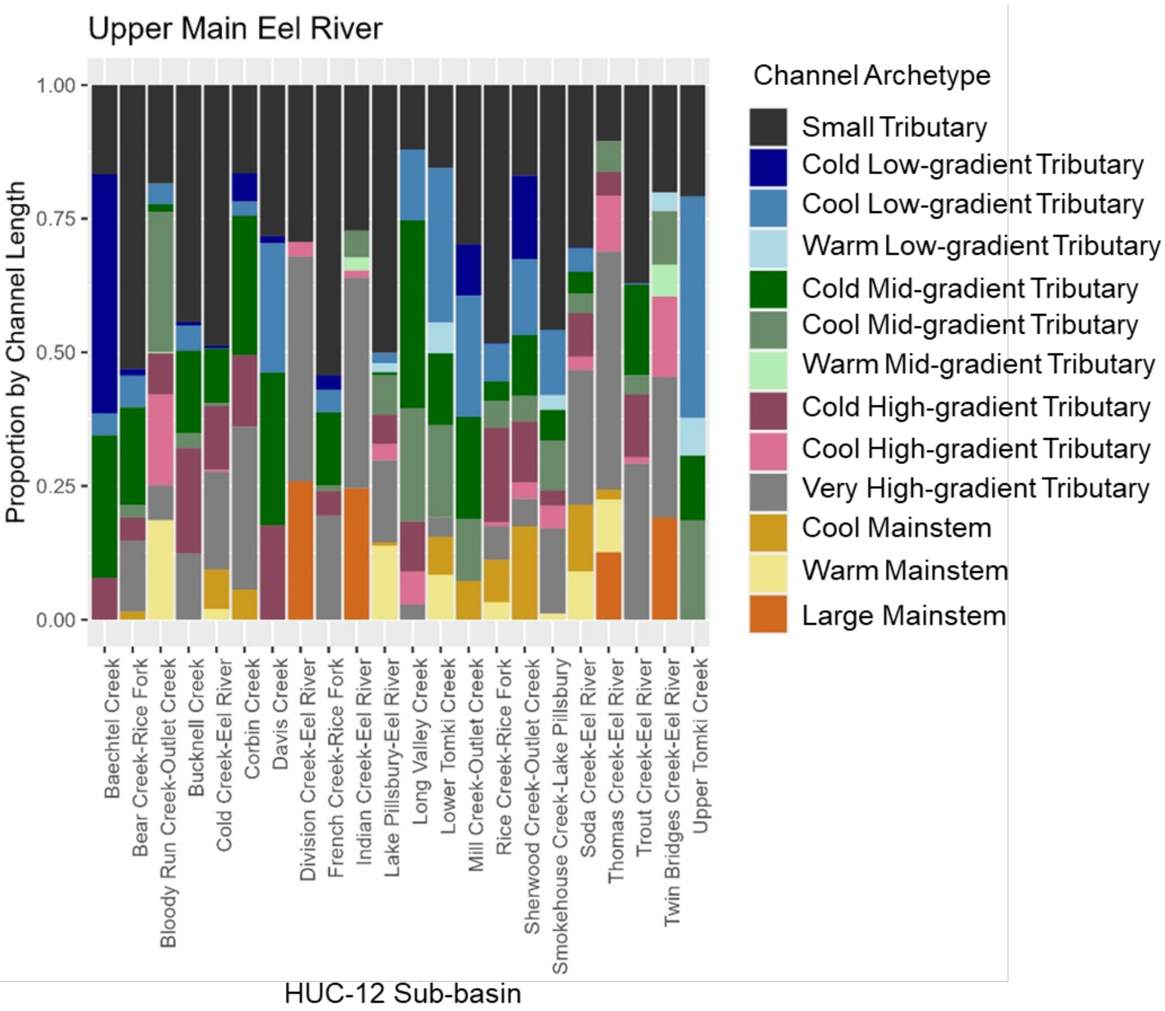

Figure B-19. Proportion of channel archetypes by length within each HUC-12 sub-basin in the Upper Main Eel River sub-watershed.

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Appendix C

Species Descriptions and Life-History Conceptual Models

TABLE OF CONTENTS

INTRODUTION AND PURPOSE

To efficiently recover focal species, it is important to understand their distribution, life-history timing, habitat needs, ecological interactions, and importantly, the factors driving their population dynamics. This understanding will be critical in identifying and prioritizing restoration and conservation actions that address the root causes of population decline. Life-history diversity is a fundamental component of anadromous fish abundance and population resilience to environmental change. The importance of life history diversity is described in Section 3.2.2 of the Eel River Restoration and Conservation Plan (Plan), and briefly discussed below.

In short, life-history diversity can be described as the diverse set of choices that individuals within a population make about how long to spend in certain habitats and when to move between them. Each set of choices, or life-history strategies, is associated with trade-offs related to survival, growth, and reproduction (Stearns 1989). There is increasing recognition that life-history diversity provides stability and resilience in fish populations (Schindler et al. 2010, Greene et al. 2010, Moore et al. 2014). Loss of life-history diversity in a fish population reduces overall abundance and resilience, making the population vulnerable to collapse (Carlson and Satterthwaite 2011, Price et al. 2021, Huber et al. 2024). For this reason, the Eel River Restoration and Conservation Plan places a strong emphasis on understanding, maintaining, and restoring life-history diversity to help recover the five focal species, which are described in this appendix: Chinook Salmon (Section 1), Coho Salmon (Section 2), steelhead/rainbow trout (Section 3), Pacific Lamprey (Section 4), and Green Sturgeon (Section 5).

Understanding the factors that control abundance, persistence, and life-history diversity of anadromous fish populations is an extremely complex undertaking, particularly for a large watershed like the Eel River. Accordingly, the Planning Team developed life-history conceptual models and associated diagrams and narratives that (1) describe the primary juvenile and adult life-history strategies with potential to exist in the Eel River watershed and (2) help identify the factors limiting their prevalence. The process for developing each narrative involved an extensive review of existing literature and other information for each species, including recovery plans (NMFS 2014, NMFS 2016), existing Eel River watershed assessments (Downie et al. 2005; CDFG 2010, 2012; CDFW 2014), and other published papers, historical reports, and unpublished datasets. This review relied on both local information from the Eel River and information from other watersheds where more extensive fish monitoring data are available, especially those that might have similar habitats and life-history strategies (e.g., Klamath River). This body of information was synthesized and developed into narratives for each species that include descriptions of:

- Population status and distribution;
- Life history timing and habitat needs during each life stage; and
- Currently important and potentially historically important life-history strategies for adults and juveniles.

The outcomes of the review of information and synthesis of the conceptual models led to an improved understanding of:

- Primary factors affecting survival and prevalence of each life-history strategy;
- Potentially important stressors for each life stage for each focal species;

- Important themes, opportunities, and actions for conservation and recovery of each species; and
- Key data gaps that should be targeted in monitoring and research efforts in the Eel River watershed.

These species descriptions and life-history conceptual models should be viewed as iterative and will be refined as additional information is compiled during the prioritization process and new data from ongoing and future research and monitoring efforts become available.

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1 CHINOOK SALMON

1.1 Population Status

Chinook Salmon (*Oncorhynchus tshawytscha*) in the Eel River watershed are part of the California Coastal (CC) Chinook Salmon Evolutionary Significant Unit (ESU), which include all naturally spawning populations in coastal watersheds from Redwood Creek in Humboldt County to the Russian River (Sonoma and Mendocino Counties). The CC Chinook ESU constitutes the southernmost coastal portion of the species' range in North America (Spence et al. 2008). In the Eel River, Chinook Salmon are split into two functionally-independent populations; the lower Eel River and upper Eel River populations (NMFS 2016). The lower Eel River population consists of all fish that spawn in the Lower Main Eel River, South Fork Eel River, and Van Duzen River sub-watersheds. The upper Eel River population consists of fish that spawn in the Middle Main Eel River, the Middle Fork Eel River, North Fork Eel River, and Upper Main Eel River sub-watersheds (NMFS 2016).

Chinook Salmon were once the most abundant salmonid in the Eel River watershed, which supported salmon canneries in the late nineteenth and early twentieth centuries (Yoshiyama and Moyle 2010). Yoshiyama and Moyle (2010) used historical reports and archival cannery data to estimate that Chinook Salmon run sizes in the Eel River averaged 100,00–200,000 fish and that peak runs of 700,000-800,000 fish were likely. As cannery production waned in the early twentieth century, the typical range of returns fell to 50,000–100,000 fish until the largescale flooding events of 1955 and 1964 (Yoshiyama and Moyle 2010). Since then, no reliable population estimates of Eel River Chinook Salmon exist due to insufficient monitoring efforts in the basin (Moyle et al. 2017).

Currently, existing populations in the CC Chinook ESU are listed as Threatened under the federal Endangered Species Act (ESA) (NMFS 2016) and are not listed under the California Endangered Species Act (CESA). Moyle et al. (2017) indicates it is reasonable to assume the current population is less than 10% of historical number and categorized the level of concern for the persistence of CC Chinook Salmon as "High" and "vulnerable to extinction in the next 50–100 years if present trends continue and stream conditions deteriorate under climate change." National Marine Fisheries Service's (NMFS) Coastal Multispecies Plan for CC Chinook Salmon list abundance targets for delisting as 7,400 spawners for the Lower Eel River in the North Coastal Diversity Strata (Lower Mainstem and South Fork Eel River), 2,900 spawners for the Lower Eel River in the North Mountain Interior Diversity Strata (Van Duzen River and Larabee Creek), and 10,600 adults for the upper Eel River (NMFS 2016).

Historically, the CC Chinook ESU may have included a spring-run ecotype, in addition to the dominant fall-run ecotype; however, the spring-run has not been observed in recent or historical monitoring and it is unclear whether a viable population ever existed (NMFS 2016). Spring-run are distinct from their fall-run counter parts in that adults enter freshwater in the spring and hold in deep cool pools before spawning in the fall. In the Eel River, the historical occurrence of a viable spring-run population is uncertain. Yoshiyama and Moyle (2010) pointed out: "The apparent historical uncommonness of spring-run Chinook Salmon in the Eel River system is somewhat enigmatic because spring runs historically existed—and in some places presently still exist—in the Klamath River system to the north and throughout the California Central Valley system." Ethnographic data from residents of Round Valley, in the Middle Fork Eel River sub-watershed, compiled by Keter (1995) noted that "Late February or March marks the beginning of the silverside salmon run." Silverside salmon being referred to as the spring Chinook.

Alternatively, Morford (1995) points out that historical records indicate that the “spring-run” phenotype was unlikely to have ever been prevalent in the Eel River watershed.

Fall-run Chinook Salmon enter the river as early as August or September and will make their way up to their spawning habitat with fall storms in October, November and December that bring higher flows and support passage up the watershed. Within the fall-run ecotype, there was historically a secondary “late-run” phenotype of mostly 4–5-year-old “silvery” adults who would enter the river between late December and February. Early European settlers call these fish "silversides”, and they were prized for eating (Morford 1995, Yoshiyama and Moyle 2010). Morford (1995) described them as “…larger than the fall run fish and seem to move up through the system rapidly, still retaining a bright sea-like condition far upstream.” Historical records at the Benbow Dam have adult Chinook Salmon passing the dam in February and sometimes into early March, however these counts are strongly correlated with streamflow and their abundances are too low to surmise if this a distinct “late-run” (Stillwater Sciences 2022). In addition, there is little if any information on the condition of these fish in the Benbow Dam records to determine if they have the silvery color and larger body size described in Morford (1995).

Because of the uncertainty of the historical existence of spring-run Chinook Salmon in the Eel River, this appendix focuses on the fall-run ecotype. However, it is likely that historically there was more diversity in the Chinook Salmon population in the Eel River and the loss of this diversity may not be irrevocable if their genetic variability exists in the extant fall-run population (Spence et al. 2008).

1.2 Distribution

The current distribution of Chinook Salmon in the Eel River extends into at least the mainstems and large tributaries of every major sub-watershed in the basin, with the potential exception of the North Fork Eel sub-watershed (Yoshiyama and Moyle 2010). In the western side of the basin, in the lower gradient sub-watersheds, including the Lower Mainstem Eel, South Fork Eel and tributaries of the lower Van Duzen River, adults can access the majority of mainstem reaches and tributaries that provide Chinook Salmon spawning habitat (NOAA Fisheries 2005). In the eastern side of the basin, adults can access a most of the Middle Fork Eel River, and the undammed portion of the upper Eel River; however, upstream access is naturally limiting in the upper Van Duzen River and North Fork Eel sub-watersheds due to natural high-gradient passage barriers (Figure 1-1). The distribution of adults (and in turn, their juveniles) within these areas can vary considerably between years, depending on the size of the adult spawning population and the timing and magnitude of rain events (MRC 2002, Guczek et al. 2020).

Rivers originating from the eastern Eel River watershed drain some of the most erosive non-glacial terrain in North America, forming rugged stretches of boulder roughs (steep and constrained accumulations of house-sized rocks) (Roering et al. 2015, Kannry et al. 2020). Most barriers to adult Chinook Salmon migration in the eastern streams are assumed to occur within these reaches, which include the roughs just upstream of Bloody Run Creek on the Van Duzen River, the Asbill Roughs near Split Rock near rkm 7 of the North Fork, and the roughs just downstream of Fly Creek on the Middle Fork (Figure 1-1). While significant portions of the Van Duzen and Middle Fork Eel are accessible to Chinook Salmon, Morford (1995) suggests that only the lowest 2 km of the North Fork Eel River were historically important to fall-run Chinook Salmon. The upper mainstem Eel River still provides critical Chinook Salmon spawning habitat in the mainstem and in the Tomki and Outlet Creek drainage; however, an estimated 100 to 150 km of Chinook Salmon spawning and rearing habitat is currently inaccessible due to the presence of Scott Dam (Cooper et al. 2020), which does not provide fish passage, but is slated for decommissioning.

The distribution of Chinook Salmon in the Eel River estuary primarily consists of holding adults in the late-summer and early fall and juveniles that utilize the estuary on the way to the ocean. Little is known about the current prevalence and distribution of juveniles in the estuary, but they were commonly captured during seining conducted there from June to November in 1973-74 (Puckett 1977) and from May to September in 1994-95 (Cannata and Hassler 1995). During these surveys, juvenile Chinook Salmon were also present in tributaries and sloughs connected to the estuary and stream-estuary ecotone. During both sampling periods, Chinook juveniles were encountered throughout the main estuary as well as in the North Bay, McNulty and Hawk sloughs and the Salt River.

Map Sources:
Chinook Salmon Distribution: NOAA
Sub-watershed boundaries: Calwater 2023
Channel network: NHD
Roads, cities: ESRI 2016

Figure 1-1. Approximate current distribution of Chinook Salmon in the Eel River watershed. Data source: NOAA Fisheries (2005) via California Department of Fish and Wildlife's Biogeographic Information and Observation System.

1.3 Ecology, Life-history, and Habitat Needs

1.3.1 Life-history Overview

Chinook Salmon are anadromous, requiring freshwater streams for hatching and rearing, saltwater bays or oceans for growing to adults, and fresh water again where they return as adults to spawn and reproduction. Adult Chinook Salmon in the Eel River currently exhibit a fall-run life-history strategy, entering the watershed in the late summer and fall, before spawning in gravel substrates of mainstem rivers or tributaries shortly after, and dying in fresh water (Table 1-1). After incubating for 1–2 months, eggs hatch as alevins, emerge from the streambed in spring as fry, and typically migrate downstream to salt water as fry or as juveniles in the spring and summer. After entering the ocean, Chinook Salmon spend from 1 to 4 years growing in salt water before returning to the Eel River to spawn and complete their life cycle (Healy 1991, SEC 1998, Quinn 2018).

The generalized life-history timing for each life stage of fall-run Chinook Salmon based on observations from the Eel River watershed is presented in Table 1-1. A more detailed description of each life stage is provided in the following sections.

Table 1-1. Generalized life-history periodicity of fall-run Chinook Salmon in the Eel River watershed.

Life stage	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Adult holding/staging[1-3]								░	░▓	▓	▓░	
Adult migration[4-6, 22]	░	░								░	▓	▓
Spawning[6-8, 22]	▓░	░									▓	▓
Incubation[6, 22]	░	░	░	░							░	░
Age-0 Rearing[9-11,17, 22]		░	▓	▓	▓	░	░	░	░	░	░	
Age-1 Rearing[15-17]	░	░	░	░	░	░	░	░	░	░	░	░
Juvenile emigration / smolt outmigration[1,10-14,17-19, 22]	░	░	░▓	▓	▓	▓	░	░		░	░	░
Estuarine rearing[1,20,21]			░	░	░	▓	▓	▓	▓	░	░	

░ span of activity ▓ peak of activity

[1] Murphy and DeWitt (1951)
[2] Day (1968)
[3] Higgins (2013)
[4] CDFG unpubl. Benbow Dam adult count data, 1938–1976
[5] Kajtaniak and Gruver (2020)
[6] Moyle et al. (2017)
[7] Boozel et al. (2018)
[8] Guczek at al. (2020)
[9] Georgakakos (2020)
[10] MRC (2002)
[11] Vaughn (2005)
[12] CDFG unpubl. Benbow Dam outmigrant trapping data, 1939
[13] VTN (1982)
[14] Roelofs et al. (1993)
[15] Lam and Powers (2016)
[16] CDFW unpubl. South Fork Eel snorkel data, 2022–2023
[17] Sullivan (1989)
[18] USFWS (2001)
[19] Healy (1991)
[20] Puckett (1977)
[21] Cannata and Hassler (1995)
[22] Fitzgerald et al. (2022)

1.3.2 Adult Holding and Migration

Adult fall-run Chinook Salmon return to the Eel River from the ocean beginning in late-August and September and likely continue to enter fresh water as late as January (Murphy and De Witt 1951, Moyle et al. 2017, Kajtaniak and Gruver 2020). The early portion of the run typically holds in the estuary and pools in the lower mainstem Eel River until mid-October or early November when the first rains increase streamflow, allowing passage over shallow riffles and cuing their upstream spawning migration (Kajtaniak and Gruver 2020, Metheny 2020, Kajtaniak and Roberts 2022a, Kajtaniak and Roberts 2022b). Quality of and limited access to holding habitats in the lower Eel River during the late summer is considered an important stressor for the early component of the population since crowding in limited holding habitats with marginal water quality (high water temperature) can result in elevated rates of pre-spawn mortality from disease, predation, or poaching (NMFS 2016; Bowerman et al. 2016, Bowerman et al. 2018). After leaving holding areas in the lower mainstem, Chinook Salmon continue to move upstream to spawning habitats throughout the Eel River sub-watersheds. Adult Chinook Salmon in the Eel River can move upstream at an average rate of approximately 10.2 km per day in mainstem Eel River below the Middle Fork, and approximately 4.4 km per day in the upper mainstem Eel River (Middle Fork to Cape Horn Dam, SEC 1998).

Historical and more recent run timing data in the Eel River have documented adult Chinook Salmon moving upstream to spawn from mid-October all the way into February in some early years, with the peak migration period occurring from mid-October to December. The longest available data set on historical Chinook Salmon run timing in the Eel River (between 1938 and 1976) was collected at the fish counting station at Benbow Dam, located in the South Fork Eel River. Each year, the first Chinook Salmon would typically arrive at the facility between mid-October and early November and the last individuals would arrive between late January and early February (Stillwater Sciences 2022). On the upper mainstem Eel River, run time data at Van Arsdale Fisheries Station (VAFS) located at Cape Horn Dam, have the Chinook Salmon typically reaching the fish ladder between mid-October and January (SEC 1998). Recent fish passage counts from sonar data on the South Fork Eel River and the Middle Mainstem Eel River show Chinook Salmon run timing to be from late-October or mid-November through December with a few fish passing in after January (Kajtaniak and Gruver 2020, Metheny 2020, Kajtaniak and Roberts 2022a, 2022b) and were generally consistent with run times at VAFS and peak run times at Benbow Dam.

Chinook Salmon vary considerably in their age and body size at return, as they can remain in the ocean for 1–4 years before returning to freshwater. Their age at return can range from 2 to 5 years and their body size typically corresponds with age (i.e., larger fish are typically older). In the Eel River, returning adult Chinook Salmon mostly consist of 3- and 4-year-old fish (Healy 1991, SEC 1998) with some proportion returning as 2-year-old precocious males known as jacks. The percentage of jacks among returning adults can vary from year to year ranging from 4% up to 73% between 1979 and 1996 (SEC 1998). Little is known about the trends in age and size of adult Chinook Salmon in the Eel River over time, however it is presumed that current populations have become more homogenous (i.e., contain fewer larger and older individuals than in the past) as with all nearby California Chinook Salmon populations (Spence et al. 2008, Spence et al. 2012).

1.3.3 Spawning and Incubation

Chinook Salmon in the Eel River predominantly spawn between November and December and in some years, as late as early February (SEC 1998). Based on historical passage counts at Benbow

Dam and VAFS, very few fish migrate after mid-January, suggesting that most spawning is complete by the end of January (SEC 1998, Stillwater Sciences 2022), although small numbers of live adults have been documented on spawning grounds as late as late February (Guczek et al. 2020; CDFW unpubl. data, 2010–2021).

In general, Chinook Salmon spawn in the mainstems and larger tributaries (e.g., Tomki Creek) of every major sub-watershed in the basin, with the potential exception of the North Fork Eel River upstream of Split Rock and above Scott Dam in the upper Eel River (Yoshiyama and Moyle 2010). The spatial extent of spawning can vary considerably from year to year due to fluctuations in the population size and the timing and magnitude of rain events (MRC 2002, Guczek et al. 2020). During period of sustained rainfall during the fall and early winter period, spawning can occur in smaller tributaries when flows are high, and tributaries are accessible (Stillwater Sciences 2022).

Fall-run Chinook Salmon spawn immediately once they make it to their spawning grounds, and suitable spawning conditions occur when there is sufficient subsurface flow into coarse material to provide oxygen to eggs. Once eggs are deposited in redds, embryos hatch approximately 40 to 60 days after fertilization and remain in redd gravels as alevins for another 30 to 40 days before emerging as fry (Moyle et al. 2017). Based on spawning timing and capture of newly emerged fry in outmigrant traps in the Eel River, eggs and alevin may be in redd gravels from November through early spring (MRC 2002, Vaughn 2005, Guczek et al. 2020). NMFS (2016) notes that the quantity and distribution of spawning gravels throughout the watershed range from “fair” to “good.” However, after deposition in the gravels, the eggs and alevins may find substandard conditions for survival to emergence. Every major subbasin in the Eel River was mentioned for having “Poor” quality substrate in terms embeddedness in the NMFS Recover Plans (NMFS 2016). Small sediments are known to be detrimental to incubating eggs (Reiser and White 1988, Julien and Bergeron 2006), but it is currently unclear if survival during incubation limits the Chinook Salmon population in the Eel River watershed.

1.3.4 Juvenile Rearing and Emigration

Fall-run Chinook Salmon fry emerge from gravels in the later winter through spring and seek out lower velocity habitats to forage or are displaced downstream until they grow large enough to hold in gentle currents and feed on drift (Healey 1991). It is typical for fry to begin their downstream migration immediately after emergence and will take up residency in estuaries or other non-natal rearing areas to rear until smolt size (Kjelson et al. 1982, Healy 1991). Other juveniles may start downstream migration within a few weeks to a few months after emergence with some individuals staying in the river through summer months before moving to the estuary in the fall or winter (Reimers 1973, Healy 1991, Moyle 2002). Estuaries are an important ecotone for juvenile fall-Chinook, and they can reside there for several months, feeding and growing, before entering the ocean. Juvenile Chinook have been documented to grow 0.4 to 1.2 mm a day in the Sacramento-San Joaquin Estuary, similar to growth rates seen in other Pacific Coast estuaries (Kjelson et al. 1982).

In the Eel River, little is known about the behavior of juvenile Chinook Salmon. Without otolith and scale data or tagging and tracking studies, knowledge of locations and duration of freshwater (natal vs. mainstem) and estuary rearing and timing of ocean entry is limited. Available data from historical and recent outmigrant trapping, seining efforts, and snorkel surveys provide a glimpse into the behavior of captured fish, and viewed collectively, can illustrate general trends in size and location over time.

Juvenile Chinook Salmon in the Eel River predominately emigrate from natal stream reaches at age-0 during their first spring and/or summer (CDFG unpublished Benbow Dam outmigrant data, 1939; MRC 2002, Vaughn 2005). However, small numbers of fish have been documented outmigrating at age-1 during in the early spring from Hollow Tree Creek (MRC 2002) and Sproul Creek (Vaughn 2007), two tributaries of South Fork Eel River, and this life history strategy is likely to occur in other tributaries. Emigration of age-0 fish from spawning areas begins as early as mid-March and continues through June for most of the trapping studies (Puckett 1976, SEC 1998, PCFFA 1988, MRC 2002, Vaughn 2005). It is important to note that detection can be dependent on the trapping period (when traps are installed or "fishing") and in many cases, juvenile Chinook Salmon were detected on the first and/or last day of trapping (SEC 1998, PCFFA 1988, MRC 2002, Vaughn 2005), suggesting individuals may have been moving before or after the trapping period. However, in studies where traps were fishing earlier and/or later in the season, and therefore better able to detect the first and last individuals, most age-0 juvenile Chinook Salmon outmigrated within the same period (Puckett 1976). One emigrant was detected as early as mid-February, although it is unknown whether this individual was age-0 or age-1, and some individuals were detected moving downstream as late as August (Puckett 1976, Puckett 1977, Roeloffs et al. 1993), with one individual detected in the lower mainstem as late as November 5. Puckett (1976) found the earliest catches were generally in tributaries of the South Fork Eel River and the latest catches were in the lower mainstem Eel River.

Juvenile Chinook Salmon outmigrant trapping (from both mainstem and tributary locations) in the Eel River shows that (1) fish size increased over time from March to May and (2) the highest frequency of catch was during April and May (Puckett 1976, Puckett 1977, SEC 1998, PCFFA 1988, MRC 2002, Vaughn 2005). Recent summer snorkel surveys found juvenile Chinook Salmon inhabiting some colder tributaries of the Van Duzen River and Mainstem Eel River (Lam and Powers 2016), as well as tributaries of the South Fork Eel River (CDFW, unpubl. data, 2022–2023). These data suggest that there are at least two general strategies that juveniles use after they emerge from redd gravels. The first involves leaving natal streams as fry or parr in a few weeks to a few months after emergence in spring or early summer and rearing in lower mainstem reaches, the estuary, or other non-natal habitats before entering the ocean. The second strategy involves remaining in natal streams through the summer until they reach smolt size and outmigrating to the ocean with higher flows in the fall (age-0 smolt) or spring (age-1 smolt). As with many anadromous salmonids, there is likely considerable variation within and overlap between these strategies (Quinn 2018, Bourret et al. 2016).

After leaving natal tributaries and mainstem spawning reaches, juvenile Chinook Salmon spend varying amounts of time in the lower mainstem Eel River and estuary, utilizing these locations as transitional habitat between fresh and salt water (Murphy and De Witt 1951, Puckett 1977, Cannata and Hassler 1995). During systematic monthly sampling conducted at sites in the Eel River estuary throughout the 1974 water year, Puckett (1977) captured juvenile Chinook Salmon in all months except December, January, and February, suggesting a diversity in downstream movement timing from natal reaches and duration of estuary utilization. Peak estuary rearing by Chinook Salmon was observed in summer months, which is consistent with estuary seining efforts conducted by Murphy and De Witt (1951) and Cannata and Hassler (1995). Regardless of trends in emigration behavior, all juvenile Chinook Salmon that reach the smolt life stage eventually move through and depend on the lower rivers and/or estuaries. It is common throughout their range for Chinook Salmon to exhibit extensive use of the estuary prior to entering the ocean, where accelerated growth rates increase their size at ocean entry and chance of ocean survival (Reimers 1973, Healy 1983, Sullivan 1989, Bottom et al. 2005, Chen and Henderson 2021).

1.3.5 Ocean Residence

Like other populations of Chinook Salmon in Northern California, adults initiate their spawning migration after spending between 1 and 4 years feeding in the ocean (Healy 1991, SEC 1998). Adults from the Eel River return to spawn as 2-, 3-, 4-, or 5-year-old fish, with 3- and 4-year-old fish likely the most common in the Eel River (Healy 1991, SEC 1998). Historical counts of returning spawners at Benbow Dam indicate that 2-year-old fish (i.e., jacks) on average made up about 25% of the South Fork Eel River Chinook Salmon population, but ranged from 9% to 75% (Stillwater Sciences 2022). However, apart from the unpublished data on fraction of jacks versus adults collected at Benbow Dam, little is known about the current or historical age distribution of Chinook Salmon in the Eel River.

Age structure data collected in river systems from California to Alaska suggests that the age distribution of returning Chinook Salmon is shrinking and returns are increasingly dominated by younger spawners (Ohlberger et al 2018). Several factors including decades of size-selective ocean harvest and homogenous hatchery production are likely to blame. Loss of older and larger individuals can be problematic for Chinook Salmon populations because younger spawners are typically smaller and produce fewer eggs (resulting in lower fecundity; Malick et al. 2023). Additionally, loss of diversity in the age structure of spawners can make populations more vulnerable to climate change and related disturbances such as drought (Carvalho et al. 2023).

1.4 Life-history Diversity Conceptual Model

Of the Pacific Salmon, Chinook Salmon exhibit the greatest diversity of life-history traits (e.g., migration timing, spawning age, and juvenile habitat use) between and within populations throughout their native range. Greater diversity and asynchrony in life-history diversity allows for the occupation of a range of ecological niches and is an important component of population resilience (Healy 1991, Hanski 1998, Sturrock et al. 2015).

The following sections describe the known and potential life-history diversity of fall-run Chinook Salmon in the Eel River, highlighting the spatial and temporal use of habitats throughout the watershed in each life stage. Adult and juvenile life histories are discussed separately; however, both are interdependent and play important roles in the population. For example, the timing and location of spawning influences embryo incubation duration, fry emergence timing, early life-history residency in fresh water, and growth potential, while the size and age of juvenile ocean entry can influence ocean survival and adult maturation timing.

1.4.1 Adult Life-history Strategies

Adult fall-run Chinook Salmon may be present in the Eel River from August to February to live out the reproductive portion of their life cycle. Fish that enter fresh water during the low flow period from about August through mid-October (the early part of the run), stage in the estuary and pools in the lower mainstem until the first fall freshets cue their upstream migration (Figure 1-2). These fall freshets typically occur from mid-October or early November, and adult Chinook Salmon have been documented to begin upstream migration when the onset of rainfall is sufficient to increase stream flows (SEC 1998, Metheny 2020, Kajtaniak and Roberts 2022a and Kajtaniak and Roberts 2022b). Adults continue to move upstream until they reach their natal spawning grounds in mainstem and tributary reaches. Spawning predominately occurs between November and December and in some years, as late as early February. The later portion of the run enters the Eel River after streams flows increase first fall rains, spending less time staging in the lower mainstem before migrating to spawning grounds (Figure 1-2). This portion of the run is not as impacted by the poor habitat conditions that exist in the lower mainstem

Streamflow can influence timing of migration and distribution of spawning throughout the watershed. Sufficient streamflow is needed for Chinook Salmon to pass shallow riffles (i.e., critical riffles), and adults move more frequently during increased flow events (VTN 1982, SEC 1998, Kajtaniak and Roberts 2022a and Kajtaniak and Roberts 2022b). In the lower mainstem Eel River, fall freshets not only increase streamflow but also initiate upstream migration (Murphy and De Witt 1951, Day 1968, SEC 1998, Higgins 2013, Kajtaniak and Gruver 2020). In the upper Eel River, the frequency of adult Chinook passage over critical riffles corresponded with increases in streamflow regardless of magnitude (VTN 1982). Elevated flows can attract adult Chinook Salmon to different spawning grounds in the watershed. In years with sustained rainfall during the fall and early winter, more spawning may occur in many small tributaries and higher in the watershed (SEC 1998, Stillwater Sciences 2022). In contrast, dry fall and winter periods may result in concentrated spawning in mainstems and at lower elevations.

Adult holding habitat in the lower Eel River is integral to fall-run Chinook life cycle. Devastating floods in 1955 and 1964 along with intensive post-World War II timber harvest increased sediment transport in the basin and likely reduced adult holding capacity in the lower Eel River by a significant amount (Morford 1995, Yoshiyama and Moyle 2010). The impacts of limited and poor-quality habitat in the lower Eel River and estuary are compounded by threats of drought and climate change, which could further increase water temperature in holding habitats, and limit passage throughout the mainstems and spawning tributaries. These risks are particularly likely to affect early returners that enter the river at low flows and elevated temperatures (Fitzgerald et al. 2022) and can result in prespawn mortality if warm, dry conditions persist (Bowerman et al. 2016). Habitat restoration in the lower Eel River improves extent and access to deep pool holding habitats, which provide cold water refugia when water temperatures become intolerable (21°C), can help mitigate impacts of climate change.

Historical commercial and sport harvest of salmonids is believed to have contributed to the declines of populations within the region, though little information on harvest rates is provided in status reviews for CC Chinook Salmon. In addition to affecting the number of Chinook Salmon adults that return to their natal streams to spawn, harvest of older individuals can affect the age- and size-structure of returning adults by reducing the proportion of larger, older individuals in a population (Ricker 1981). Changes in the size- and age-at maturity can not only result in immediate demographic consequences (e.g., reductions in spawner abundance, decreased average fecundity of spawners, and increased variability in abundance; Anderson et al. 2008), but may potentially result in genetic selection for early maturation (Hankin et al. 1993). Such changes in population attributes may have longer-term demographic consequences (Spence et al. 2008, Spence et al. 2012).

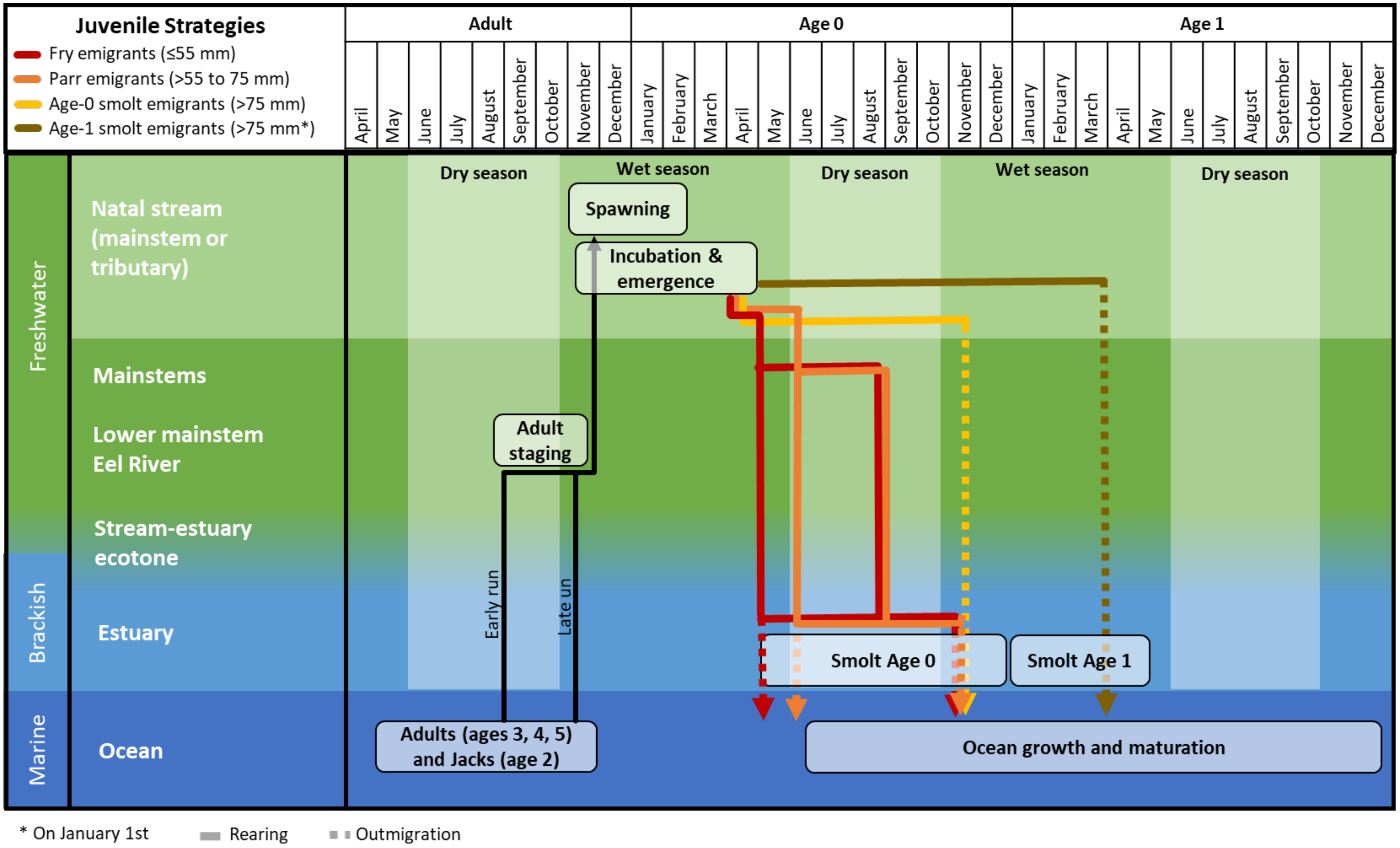

Figure 1-2. Life-history conceptual model for adult Chinook Salmon in the Eel River. Variation in timing and distribution figure shows general trends in behavior of life-cycle strategies. The parr emigration life-history type exhibits a variety of behavior within the conceptual pathways presented in this diagram.

1.4.2 Juvenile Life-history Strategies

Juvenile Chinook Salmon exhibit a wide range of life-history strategies that has been categorized under several different classification structures. The oldest and most widely applied classification is the “ocean” vs. “stream” type. Stream-type juveniles rear in natal streams for extended periods and then migrate downstream as age-1 smolts, whereas ocean-type juveniles rear in fresh water for shorter periods and typically move quickly downstream to enter salt water as age-0 smolts (Gilbert 1912; Healey 1983, Healy 1991). Stream-type juveniles mostly occur in spring-run Chinook Salmon but have been documented in the Eel River (Section 1.3.4) and can occur to a variable degree in other nearby fall-run populations (e.g., Redwood Creek near Orick, Klamath River, and Smith River). Recent evidence suggests that the “ocean” vs. “stream” classification is too general to capture the phenotypic variation that is expressed in Chinook Salmon populations and is not well aligned with ecological processes (Bourret et al. 2016). Efforts to categorize life-history types based on variability within populations have used scales or otoliths, which can help identify the duration of freshwater rearing and time of ocean entry. A study on the Klamath River used scale analysis of returning adult Chinook Salmon to define juvenile life histories into three general types based on how long they reared in freshwater before ocean entry (Sullivan 1989). Type I has the shortest freshwater residency, entering the ocean in the summer months, early enough to experience considerable ocean growth in the first year of life. Type II rear in fresh water longer than Type I, migrating to the ocean in eth fall or early winter. This type is assumed to include both individuals that remain in tributaries until fall rains and those that rearing in mainstem or estuary until ocean entry (Sullivan 1989). Type III have the longest residency in fresh water, rearing throughout the summer, fall, and winter before entering the ocean in the spring as age-1 smolts (also known as yearlings).

The Plan categorizes the primary life-history strategies of juvenile Chinook Salmon expected to occur in the Eel River, based on fork length at time of emigration from natal streams (tributaries or mainstem spawning reaches). This approach—which is based on a classification scheme developed for juvenile CC Chinook Salmon in the Central Valley using otolith and strontium isotope analyses (Miller et al. 2010; Sturrock et al. 2015, 2019)—includes the following life-history strategies: fry emigrant (≤55 mm), parr emigrant (>55 mm to 75 mm), age-0 smolt emigrant (>75 mm), and age-1 smolt emigrant (>75 mm after January 1) (Figure 1-2). Each of these strategies is discussed in the sub-sections that follow. This classification method was selected because size and life stage at time of emigration from natal streams can exert strong influence on ocean survival and likelihood of returning to spawn (Sturrock et al. 2015).

The juvenile life-history strategies shown in the life-history conceptual model (Figure 1-2) should be viewed as generalized groupings, recognizing that a continuum of variability exists within each type. As mentioned in Section 1.3, little information exists to describe the full range of life history patterns exhibited by juvenile Chinook Salmon in the Eel River. However, data from outmigrant trapping, seining efforts, and snorkel surveys provides some insights into the range of life history strategies that may occur. As with other locations where more extensive monitoring has occurred, Juvenile Chinook Salmon in the Eel River are expected to exhibit a wide range movement patterns and timing during emigration from their natal streams to the ocean (e.g., Reimers 1973, Sullivan 1989, Bourret et al. 2016, Figure 1-3). Additionally, phenotypic expression of life-history behaviors can vary between years and locations based on environmental factors and individual fish condition (Bourret et al. 2016).

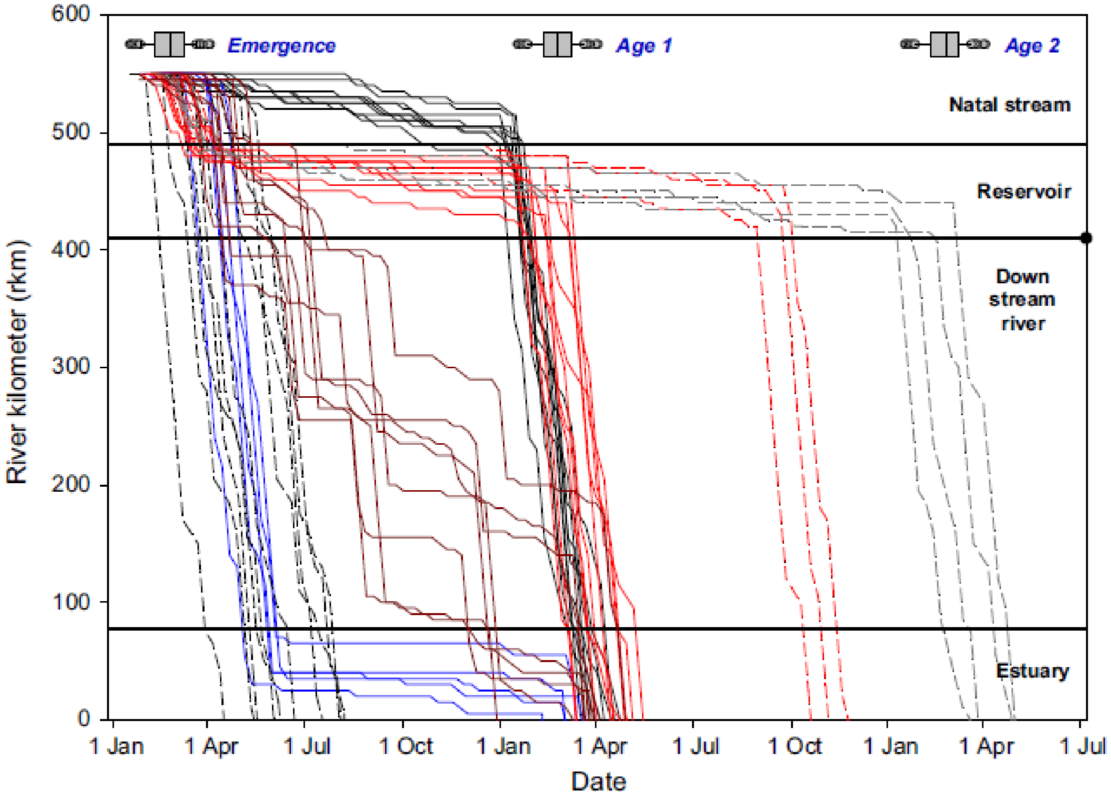

Figure 1-3. Example of hypothetical life-history pathways of juvenile Chinook Salmon in an impounded river system from Bourret et al. 2016. Line colors and styles depict qualitatively recognizable types along a continuum of life-history expressions.

1.4.2.1 Fry emigrant strategy

Fry emigration is the most common juvenile Chinook Salmon life-history type in many watersheds, with most individuals emigrating from natal streams within a week to a month after emergence and entering the ocean at age-0(Moyle et al. 2017). From natal streams, individuals that express the fry emigrant life-history strategy can migrate directly to the estuary or ocean as fry (≤55 mm fork length), or rear as they go, utilizing mainstems or non-natal tributaries for rearing before entering the ocean later in the summer or fall (Moyle et al. 2017, Sturrock et al. 2015, Bourret et al. 2016). It has been hypothesized that juvenile Chinook Salmon exit natal streams as fry because of low stream carrying capacity (caused by low flows or heightened predation; Railsback et al. 2009), displacement due to high flow events, or genetic predisposition for early emigration (Moyle et al. 2017, Sturrock et al. 2015). Because of their small size, fry emigrants have lower survival rates than parr or smolt emigrants but are expected to contribute meaningfully to adult returns (Sturrock et al. 2015). Early emigrants can take advantage of favorable downstream floodplain and estuarine rearing habitats that are maybe be more and productive in wetter water years (Sturrock et al. 2015). Additionally early fry emigrants that move during turbid winter or spring storm events can be less vulnerable to predation (Williams 2006, Yarnell et al. 2015, Sturrock et el. 2019).

In the Eel River, most juveniles are thought to leave natal habitats early as fry, with peak emigration occurring in April or May (Pucket 1976, SEC 1998, PCFFA 1988, MRC 2002, Vaughn 2005). In Tomki Creek, an important Chinook spawning tributary, fry emigrants make up most captures throughout the outmigration trapping period (SEC 1998). The extent to which fry emigrants move directly to the estuary or stop to rear in mainstem or non-natal tributary habitats before entering the estuary is not as clear due to limited monitoring in the Eel River. It is likely that some fry emigrants exhibit both migratory pathways each year, with varying degrees of survival before entering the ocean. Pucket (1976) captured small numbers of juvenile Chinook Salmon at an outmigrant trap in the lower Van Duzen River in April, presumably fry emigrants that then entered the lower mainstem or estuary. Pucket (1976) also documented relatively large numbers of juvenile Chinook emigrating through the mainstem Eel River at McCann during May, and it is likely that some of these individuals entered the estuary as fry. However, large numbers were also observed in June and July, suggesting a longer mainstem rearing period more consistent with the parr emigrant strategy described below. Puckett (1977) captured one fry-sized Chinook Salmon fry in the estuary in May, while all other juveniles captured during the year round er sampling period were >75 mm.

1.4.2.2 Parr emigrant strategy

Parr emigrants (>55 mm to 75 mm) are individuals that typically rear in natal streams for a few months before emigrating, typically in the late spring or summer. These individuals enter the ocean as age-0 smolts, between summer and early fall. As they rear in natal streams, parr emigrants transition from fry to parr, moving from slow and shallower edge water habitat into deeper, swifter water to take advantage of better foraging opportunities. Emigration from natal streams generally starts a few months after the late winter to spring emergence period and continues through the summer. Parr emigrants may have the most variability in rearing behavior and timing as they move to the estuary. In the Sacramento River basin, they can have the highest survival and greatest contribution to adult populations and may be able to take advantage of greater feeding opportunities, have lower vulnerability to predation, and have a greater tolerance of environmental perturbations (Sogard 1997, Sturrock et al. 2015).

Teasing out the rearing behavior of the parr emigrant strategy in the Eel River is challenging without tagging studies or analysis of strontium isotopes from otoliths. Based on the timing of the parr-sized individuals captured at outmigrant traps in the Eel River, parr emigrants generally leave from natal streams beginning in late April or May but timing can vary among trapping sites and years. Emigration from tributary spawning arears appears to continue through about mid-June, with the size of individuals in the parr emigrant size class increasing overtime. The rearing and movement behavior of emigrants once they leave their natal streams is less clear from the available data. Parr-sized individuals have been documented moving through the mainstem Eel River at McCann from April to June (Puckett 1976). It is unclear whether the parr-sized individuals were parr emigrants that recently left natal streams or fry emigrants that reared and grew into parr in mainstem reaches (likely some combination of each strategy). Large numbers of juveniles were also captured moving through the mainstem Eel River at the McCann trapping site through mid-July and at Holmes thought mid-August (Pucket 1976). Limited length frequency data showed fish captured from July onward were >75 mm, but many of these individuals likely emigrated from natal reaches as smaller parr and grew in the mainstem. Length frequency data from estuary seine samples documented juveniles >75 mm entering and utilizing the estuary from June through September (Puckett 1976). Some of these fish were likely parr emigrants that reared and grew in the mainstem corridor, and some were likely age-0 smolt (Section 1.4.2.3) that recently left their natal streams.

Juvenile Chinook Salmon have also been observed rearing in tributaries during recent summer snorkel surveys conducted in the Van Duzen River and Lower Main Eel sub-watersheds (Lam and Powers 2016), and throughout the South Fork Eel River sub-watershed (CDFW, unpubl. data, 2022-2023), indicating that some individuals rear in smaller tributaries before emigrating. Some of these individuals may have been later-moving parr emigrants, but many were likely fish that expressed the age-0 or age-1 smolt emigrant strategies and reared in natal tributaries through the summer before emigrating in the fall, winter, or spring. In the mainstem of Sproul Creek snorkel surveys, most individuals were observed in June. It is unclear if these individuals were fry or parr emigrants from a natal stream upstream (i.e., West Fork Sproul Creek) that were rearing in the mainstem of Sproul Creek before leaving for the estuary. Parr emigration behavior most likely exists on a continuum from migrating straight to the ocean or to the estuary to rear, to rearing as they go, to migrating to mainstem habitat to rear before outmigrating.

Stream flow conditions are expected to influence survival until ocean entry of parr emigrants that rear until reaching smolt size as they move downstream in mainstem reaches. NMFS (2016) lists baseflow conditions and water diversions as population stressors, particularly in the South Fork Eel and Van Duzen rivers. In addition to potentially limiting downstream movement from smaller tributaries, drought and diverted water impacts the spring-summer flow recession, unnaturally accelerating the reduction of drift feeding opportunities, the primary foraging strategy for juvenile Chinook Salmon. Another important risk to juveniles during emigration is predation from non-native species (Brown and Moyle 1997; Nakamoto and Harvey 2003). Non-native Sacramento Pikeminnow are successful predators on juvenile salmonids and that risk is higher during the lower flows and warmer water temperatures that occur in the late-spring and summer when parr emigrant strategy is moving (Nakamoto and Harvey 2003).

1.4.2.3 Age-0 smolt emigrant strategy

Age-0 smolt emigrants rear in natal streams for an extended period, typically through the summer, before outmigrating to the estuary before January 1. These individuals grow to the smolt size (>75 mm) in natal streams, spending little time in non-natal freshwater habitats. Individuals that reach the smolt size class (>75 mm) in natal streams are considered age-0 smolt emigrants, but smoltification can occur at any point before entering the ocean (not necessarily before leaving natal streams). The larger body size at emigration is associated with greater survival, both during emigration and within the ocean (Williams et al. 2016).

In the Eel River, age-0 smolt emigrants leave natal streams in the fall or early winter, as stream flows increase. Juvenile Chinook Salmon have been observed during snorkel surveys in summer months (July to early September) in tributaries of the Van Duzen River and the lower Eel River (Lam and Powers 2016), and throughout the South Fork Eel River (CDFW, unpubl. data, 2022-2023). In Anderson Creek, Sproul Creek, Squaw Creek, Durphy Creek, and Coulborn Creek individuals have been observed in August and September (CDFW, unpubl. data, 2022-2023), suggesting they reared through the summer and may have displayed the age-0 smolt emigrant strategy. Captures of small numbers of juvenile Chinook during the limited outmigrant trapping that has been conducted in the fall and early winter, provide additional evidence for the smolt-0 emigrant strategy. Pucket (1976) captured several juvenile Chinook Salmon in the lower Van Duzen River and a single individual in the mainstem Eel River at Holmes in early November. Notably however, no Chinook Salmon were captured during the limited fall trapping at various other sites across the watershed (Pucket 1976).

Under current conditions, the age-0 smolt life-history strategy is less prevalent in the Eel River than the fry and parr emigrant strategies. Because they spend the summer low flow period in fresh water, they are generally expected to be more common in cools tributaries with persistent stream flow and during wetter water years. Many tributaries in the Middle Fork Eel River and upper Eel Main Eel River sub-watersheds have very low summer flows or even go dry, making it challenging for this life-history strategy to be successful in there. Those tributaries that do support extended rearing into the summer months can allow juvenile Chinook Salmon to grow before undertaking taxing downstream migrations (Garwood and Larson 2014, Parish and Garwood 2015) However, rearing into the summer months, when water temperatures are the greatest, can have negative impacts on juvenile Chinook as well. For example, while warmer conditions can result in faster growth rates, smoltification is significantly impaired at temperatures above 15°C (USEPA 2003, Sturrock et al. 2015), similarly the warmer conditions can also result in increased pikeminnow predation risk (Nakamoto and Harvey 2003).

The timing of ocean entry or if age-0 smolt emigrants utilize the estuary before ocean entry is unclear. Puckett et al. (1977) captured Chinook Salmon juveniles in the estuary into November and described a diversity in downstream movement timing from natal reaches and duration of estuary utilization but there is not data available to specify the timing and duration of estuary use. However, utilization of the Eel River estuary by juvenile Chinook Salmon is likely to be an important life-history regardless of size or timing at natal stream emigration because it supplies rearing and food resources to Chinook Salmon at a critical time before ocean entry. The Eel River estuary was once a highly productive estuarine marsh habitat that was drained and diked for pasture, greatly reducing habitat available for rearing of juveniles. The reduced size of the estuary and loss of complexity, contributing to the decline of salmon populations (NMFS 2016). Habitat restoration in estuaries, that increases complexity and connectivity between stream-estuary ecotones can play a role in potentially increasing juvenile life-history diversity and expression (Wallace et al. 2015).

1.4.2.4 Age-1 smolt emigrant strategy

The age-1 smolt emigrant strategy includes juvenile Chinook Salmon that outmigrate to the ocean after January 1, after spending nearly a full year in freshwater habitat. This strategy includes both age-1 smolts that reared primarily in natal streams and those that reared in non-natal habitats before smolting. The age-1 smolt emigrant strategy typically outmigrates in the spring, alongside much smaller fry emigrants. This strategy is typically associated with spring-run Chinook Salmon populations, but has been documented to varying degrees in the Eel River and other nearby fall-run populations (e.g., Redwood Creek near Orick, Klamath River, Smith River near Crescent City; Moyle et al. 2017).

In the Eel River, a small numbers age-1 smot have been detected outmigrating in the early spring from Hollow Tree Creek (MRC 2002) and Sproul Creek (Vaughn 2007). As described in Section 1.4.2.3, small numbers of juvenile Chinook Samon have been observed over-summering in tributaries to the Van Duzen, lower Eel, and South Fork Eel rivers (Lam and Powers 2016, CDFW During summer snorkel surveys in Shively Creek and Stitz Creek, two tributaries of the lower mainstem Eel River, observed juvenile Chinook Salmon would have to over-summer in the creek, as both creeks were dry at their mouths throughout the summer months (Lam and Powers 2016; CDFW, unpubl. data, 2022-2023). Age-1 smolt emigrants appear to be currently uncommon in the Eel River, but the strategy was likely more prevent before habitat conditions were degraded and may have historically contributed substantially to adult abundance and population resilience. This strategy can make up a relatively large fraction of the juvenile population in other Northern California streams, particularly those with high quality summer habitat conditions (e.g., Smith River; Moyle et al. 2017). For this reason, restoration actions that could increase its presence should be considered. This life-history strategy has potential to expand the portfolio effect in the Eel River, since it outmigrates at a significantly larger size than other strategies and during spring freshets, taking advantage of increased turbidity as cover to avoid predation (Schindler et al. 2010).

1.5 Conceptual Model Outcomes

1.5.1 Stressors

Stressors for Chinook Salmon were identified through the development of the Chinook Salmon conceptual models and by reviewing relevant literature and reports, including NMFS recovery plans (NMFS 2016), restoration plans in the Eel River (Eel River Forum 2016, South Fork Eel River SHaRP Collaborative), and salmonid status assessments (Moyle et al. 2017, Spence et al. 2008). Stressors are presented in Table 1-2 and organized by life stage (adult holding and migration, spawning and incubation, juvenile rearing, smolt outmigration, and ocean residence). Some stressors may impact multiple life stages and are duplicated across the table.

Each stressor includes a mechanism of impact on population productivity, abundance, distribution, and resilience and the driver of the stressor or the underlying cause that can be addressed by restoration. The predicted connection between the stressor and population impacts will be an important reference during the restoration prioritization process, when the predicted efficacy of various restoration actions will be related to how and why they relieve stressors to improve conditions for fish. The driver behind each stressor was used to inform the list of restoration and conservation actions in the Plan (Section 4).

Finally, the relative importance of stressors in the table varies with space and time such as location in the watershed and inter-annual variation in environmental conditions. Some stressors will be more prominent in certain water year types. For example, warming water temperatures due to loss of canopy covers or infilled pools from catastrophic flooding may have a larger impact in drier water year types, when air temperature has a larger effect on water temperatures. The magnitude of stressors also varies between the sub-watersheds and between drainage areas, depending on land use history, underlying geology, and previous restoration actions. As part of prioritization of restoration actions using life-history diversity and conceptual models in Phase 2, these stressors and their associated drivers and opportunities for restoration will be evaluated for their relative importance in space and time.

Table 1-2. Stressors with potential to adversely impact each life stage of Chinook in the Eel River watershed, with life-history strategies that are predicted to be the most impacted.

Life stage	Stressor	Mechanisms of impact on population productivity, abundance, distribution, and resilience	Drivers (underlying causes of stressor to be addressed by restoration)	Life-history strategies impacted
Adult holding and migration	Anthropogenic physical barriers to movement	Reduced spawning distribution, lowered reproductive success, and potential lost juvenile life-history diversity.	Dams, poorly designed or failed road crossings/culverts, other manmade obstructions to movement.	All
	Reduced pool frequency, depth, and channel complexity in the estuary and lower mainstem Eel River	Reduced holding habitats and increased pre-spawning mortality from disease, predation and loss of cool water refugia.	Reduced wood volume due to removal and alteration of riparian forest (reduced supply). Channel aggradation due to increased sediment delivery from historical and current logging, road construction & management, flooding, and fires.	All
	Impaired fall pulse flows	Delayed upstream passage, pre-spawning mortality, and lowered reproductive success, reduced spawning distribution.	Reduced or delayed fall stream flows due to water diversions, dams, or climate change.	Early migrating adults
	Increased prevalence of disease	Pre-spawning mortality	Crowding cause by delayed fall stream flows; increased water temperatures due to diversion or climate change; other unknown drivers of disease prevalence and virulence.	All
	Poaching	Pre-spawning mortality	Inadequate education and enforcement.	All
Spawning and incubation	Redd scour	Reduced egg-to-fry survival	Channelization and reduced substrate sorting; low flows during adult migration & spawning followed by high winter flows.	Early spawning adults
	Fine sediment infiltration of spawning substrates and redds	Reduced egg-to-fry survival	Landslides and erosion of fine sediment due to historical and current logging, road construction and management, flooding, and fires. Reduced sediment sorting due to channelization, floodplain disconnection, and lack of wood.	All
Juvenile rearing	Anthropogenic physical barriers to movement	Reduced rearing habitat capacity	Dams, tide gates, or other manmade obstructions to movement while rearing during downstream migration	Fry and parr emigrants
	Impaired connectivity with and loss of riverine floodplain/off-channel rearing habitats	Reduced winter rearing habitat capacity. Reduced juvenile growth and survival in winter. Reduced high flow refugia.	Channelization, channel incision, levees, bank armoring & roads, wetland draining & agricultural conversion, reduced wood volume, and loss of beaver dams.	Age-1 smolt emigrants
	Reduced estuarine habitat quantity, quality, and complexity, and impaired hydraulic connectivity and drainage patterns.	Reduced growth and survival due to altered estuarine food webs, impaired WQ, lost access to sloughs, tidal wetlands, and salt marsh habitat, and loss of escape cover.	Tide gates and levees, water diversions, wetland drainage and filling for agricultural conversion, agricultural and urban run-off.	Fry and parr emigrants
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Reduced rearing summer and winter habitat capacity, reduced survival to outmigration	Reduced wood volume due to removal & reduced supply. Channel aggradation due to increased sediment delivery from historical land uses & floods.	All
	Impaired dry-season stream flows	Restricted movement & stranding in poor WQ habitat due to sub-surface flows. Direct mortality due to poor WQ, warm water temperatures, and predation. Reduced growth due to higher densities, less invert production and delivery from riffles.	Climate change, water diversion for rural agriculture and domestic use, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Parr, age-0, and age-1 emigrants
	Altered spring recession flows	Reduced rearing habitat, reduced growth through altered food webs and water temperatures, favors fry emigrants type that outmigrate early after emergence.	Climate change, water diversions, dams, hydrological alteration due to draining of wetlands, reduced snowpack, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	All
	Reduced area of and restricted access to thermal refugia	Reduced rearing habitat capacity due to restricted distribution, especially Age-0 and Age-1 smolt emigrants due to loss of over summering habitat. Direct mortality, Chronic stress and reduced growth due to metabolic effects, increased pikeminnow predation and competition.	Filling of thermally-stratified deep pools due to channel aggradation caused by sediment inputs from logging practices, road building and floods. Loss of connectivity with cold tributaries due to channel aggradation. Loss of complex cover at cold tributary confluences.	All
	Elevated turbidity levels beyond reference state levels	Reduced growth through impaired feeding in highly turbid locations during extended high-turbidity periods.	Landslides and erosion of fine sediments due to historical and current logging, road construction & management, and geomorphic impacts of high intensity fires.	Fry emigrants
	Increased prevalence of predation and competition from non-native fishes	Reduced fry to smolt survival and outmigration success, reduced condition	Sacramento Pikeminnow introduction and predation, loss of escape cover from larger wood and deep pools, warmer water temperatures that increase Pikeminnow/Salmonid interactions, limited access to cold water habitat used for predation refugia. Altered salmonid foraging behavior when avoiding Pikeminnow. Competition between food resources between salmonids and Northern Coastal Roach/juvenile Sacramento Pikeminnow	All
	Increased prevalence of disease and decreased condition	Reduced fry to smolt survival and outmigration success.	Reduced stream flows, increased temperatures, less habitat capacity	All
	Thiamine deficiency	Reduced fry to smolt survival	Loss of other prey items due to shifts in marine food webs, leading to increased reliance on anchovies, which are relatively low in Thiamine.	All
	Alterations to the timing, magnitude, and availability of food resources	Reduced juvenile growth and survival	Increased embeddedness, loss of marine-derived nutrients, increased predation risks from Sacramento Pikeminnow, altered riparian forests, altered hydrology.	All

Life stage	Stressor	Mechanisms of impact on population productivity, abundance, distribution, and resilience	Drivers (underlying causes of stressor to be addressed by restoration)	Life-history strategies impacted
Smolt outmigration	Impaired spring recession flows	Reduced smolt to ocean survival.	Climate change, water diversions, hydrological alteration due to draining of wetlands, reduced snow pack, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Fry and parr emigrants
	Delayed spring outmigration below dams (PVP)	Reduced smolt to ocean survival.	Artificially long spring cold-water temperatures delays emigration cues, exposure to summer mainstem temperatures and mainstem non-native predators.	Parr and Smolt Emigrants
	Increased prevalence of predation	Reduced smolt to ocean survival.	Sacramento Pikeminnow predation, loss of escape cover from large wood and deep pools, decreased stream flows and increased water temperatures.	All
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Reduced smolt to ocean survival due to loss of escape cover.	Reduced wood volume due to removal & supply. Channel aggradation due to increased sediment delivery from historical land uses & floods.	All
	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Reduced smolt to ocean survival due to loss of escape cover.	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	All
Ocean residence	Ocean harvest or bycatch	Reduced smolt to adult survival; altered adult age structure and life-history diversity.	Ocean fishing regulations and enforcement	All
	Marine food web alterations	Reduced ocean growth and smolt to adult survival.	Climate change related influences on strength and timing of ocean upwelling, marine productivity, and the salmon prey species.	All

1.5.2 Restoration Take-home Points

The following central themes and focus points related to recovery of Chinook Salmon in the Eel River watershed were identified during the development of the life-history conceptual models and through various internal and TAC discussions.

- Historical life-history diversity that is not currently expressed or is limited in expression may be recoverable through restoration efforts, especially if historical genetic variability still exists.
- Restoring the Eel River estuary and lower river may have the greatest impact on population recovery as an important component of juvenile Chinook freshwater rearing occurs in the estuary.
- Restoring habitat (e.g., deep water pools and large wood) to benefit adult holding and migration, juvenile rearing and smoltification, and outmigration can increase survival and expand life-history diversity.
- Chinook Salmon's propensity for early returners, and cuing migration on flow changes (adult upstream migration, and juvenile downstream migration), make them vulnerable to drought and climate change. Restoration actions (e.g., increased deep pools) that maintain the magnitude of hydrograph components (e.g., fall freshets) and provide cold water refugia during periods of elevate water temperatures could mitigate impacts of drought and climate change.
- Increased capacity and summer rearing conditions in natal streams could increase the expression of the parr, age-1, and age-2 emigration life-history types.
- Reduced predation risks and inter-specific competition in tributaries, mainstems and the estuary on rearing juveniles by non-native fishes can increase survival to ocean residency.
- Remove barriers or provide volitional passage at man-made barriers can expand their current distribution increase population abundance and encourage expression of muted life-history behaviors.

1.5.3 Key Data Gaps

Various gaps in understanding of distribution, life-history, behavior, and habitat use, Chinook Salmon in the Eel River watershed were identified through development of this species review and conceptual model. Since these data gaps may limit effective management and restoration of the species, conducting research and monitoring to fill them is integral to recovery. Key data gaps include:

- Current adult age structure (distribution of age at return) and how it compares to historical age structure.
- Impacts on historical releases of out-of-basin and hatchery reared Chinook Salmon on the genetic structure of native Eel River Chinook Salmon.
- Timing, use, and residence time of juvenile fish in the lower river, estuary, and off channel sloughs.
- Residence time and use of natal streams and mainstem habitat by juvenile fish to better understand the prevalence and behavior of emigration types.
- Spawning distribution and relative utilization of the mainstems versus tributaries.
- Timing, abundance, and use of the Middle Fork Eel and North Fork Eel sub-watersheds by Chinook Salmon.

- Prevalence and impacts of thiamine deficiency complex (TDC) in the Eel River.
- Identification of stressors and limiting factors during ocean residency.

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2 COHO SALMON

2.1 Population Status

Coho Salmon (*Oncorhynchus kisutch*) in the Eel River watershed are listed as threatened under both the CESA and federal ESA (CDFG 2002, NMFS 2014). Populations in the Eel River are part of the federally threatened Southern Oregon/Northern California Coast (SONCC) ESU, which includes all naturally spawning populations between Punta Gorda, California, and Cape Blanco, Oregon (NMFS 2014). Within the Eel River, Williams et al. (2006) identified seven "population units" based on historical distribution, geographic isolation, genetic data, population dynamics, habitat availability, environmental characteristics, and other factors. These population units, which are addressed separately in the species recovery plan (NMFS 2014), include the Lower Eel/Van Duzen (downstream of South Fork Eel confluence), South Fork Eel, Mainstem Eel (South Fork confluence upstream to Middle Fork confluence), North Fork Eel, Middle Fork Eel, Middle Mainstem Eel (Middle Fork confluence up to and including Tomki Creek), and Upper Mainstem Eel River (upstream of Tomki Creek). The South Fork Eel River, Lower Eel and Van Duzen River, and Middle Mainstem Eel River populations are classified as "*Core, Functionally Independent*" populations, which include *"…those with a high likelihood of persisting in isolation over a 100-year time scale and are not substantially altered by exchanges of individuals with other populations*." The Mainstem Eel, North Fork Eel, Middle Fork Eel, and Upper Mainstem Eel populations are all classified as "*Non-Core 2, Potentially Independent*" populations, which are those that "*…have a high likelihood of persisting in isolation over a 100-year time scale, but are too strongly influenced by immigration from other populations to exhibit independent dynamics."* Importantly, these classifications are based on expected historical population structure and characteristics. As described in Section 2.2, Coho Salmon populations are either extirpated or rare in the Eel River watershed outside of the South Fork Eel, Lower Eel, and Van Duzen Rivers.

Available evidence suggests that abundance of Coho Salmon in northern California and the Eel River watershed has declined substantially relative to historical levels (Brown et al. 1994, Yoshiyama and Moyle 2010, CDFW 2014, NMFS 2014, Eel River Forum 2016). Yoshiyama and Moyle (2010) estimated that there were historically between 50,000 and 100,000 spawning adults in the watershed. Today, most spawning occurs in the South Fork Eel River and its tributaries, with relatively small numbers of fish spawning in tributaries to the lower Eel and Van Duzen rivers (NMFS 2014). Remnant numbers of Coho Salmon may occur in cooler tributaries in the watershed upstream of the South Fork in some years (NMFS 2014).

Historical counts of adults passing Benbow Dam on the mainstem South Fork Eel River in the late 1930s and 1940s, when the population was already depressed from overfishing, ranged from about 7,000–25,000 individuals (Stillwater Sciences 2022). These counts did not include fish that returned to the numerous tributaries downstream of the dam site (approximately one-third of the watershed). More recently, the Coho Salmon spawning population in the South Fork Eel River has ranged from about 350–5,000 individuals, based on redd estimates from 2010–2020 (Guczek et al. 2020) and assuming 2.5 adults per redd (South Fork Eel River SHaRP Collaborative 2021).

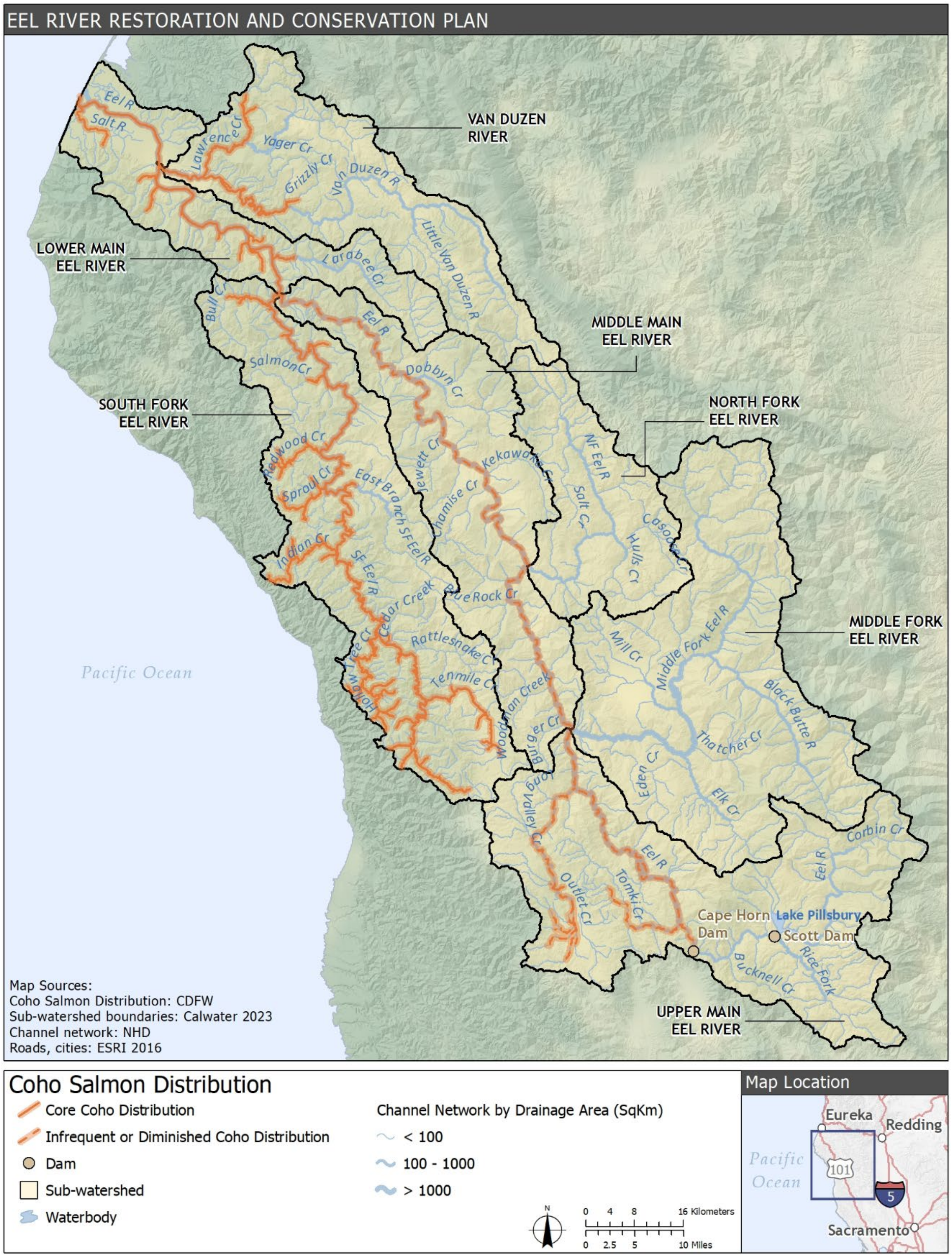
2.2 Distribution

2.2.1 Current

Coho Salmon have a narrower distribution than other salmonids in the Eel River watershed due to their requirement for lower water temperatures and preference for lower gradient, finer substrate natal habitat. The species is generally confined to, coastal-oriented streams that maintain cool water temperatures throughout the year. Summer distribution is typically limited to locations where maximum weekly average temperature (MWAT) is less than about 17–18 degrees Celsius (°C) (63–64°F) (Welsh et al. 2001, USEPA 2003). However, recent research indicates juvenile Coho Salmon can thrive in somewhat higher temperatures when food resources are abundant. Lusardi et al. (2019) found that Coho Salmon growth rates in the food-rich Shasta River peaked at a mean daily average water temperature of 16.6°C and a maximum weekly maximum temperature (MWMT) of 2l.1°C.

The current spawning and summer rearing distributions of Coho Salmon are limited primarily to the cooler and more coastal tributaries to the South Fork Eel, Van Duzen, and lower Eel rivers; however small numbers of individuals may be found in Outlook and Tomki creeks and potentially other tributaries to the upper Eel River (Figure 2-1). Although spawning and summer rearing are concentrated in the colder tributaries, various perennial and intermittent tributaries and mainstem reaches that are too warm or have too little flow to support summer rearing are likely utilized by the species for non-natal rearing during the wet season. The distribution of spawning adults and fry can be strongly influenced by hydrological conditions that occur during the adult migration and spawning periods each year. For example, during winters with sustained flows a greater portion of the population can access smaller streams and headwater reaches compared with dry winters when spawning can be restricted to mainstems and larger tributaries.

Within the South Fork Eel River, the species is widely distributed, but with some exceptions (e.g., cooler tributaries to Ten Mile Creek), spawning and summer rearing are generally concentrated in cooler, tributaries draining the western side of the sub-watershed (Guczek et al. 2020, Stillwater Sciences 2022). In the Van Duzen River sub-watershed, Coho Salmon are found primarily in Lawrence Creek, a tributary to Yager Creek (Lam and Powers 2016). The species has also been recently documented or listed as occurring in several other tributaries to lower Yager Creek or Van Duzen River, including Cooper Mill, Cummings, Root, and Grizzly creeks (Lam and Powers 2016, CDFW 2022).Within lower Eel River below the South Fork confluence, juvenile Coho Salmon have recently been documented in Strongs, Price, Howe, Nanning, Monument, Jordon, Shively, Bear, Chadd, and Bridge creeks (Lam and Powers 2016, CDFW 2022). Juvenile Coho Salmon can also be found in accessible portions of the estuary and its tributaries, including the Salt River and McNulty Slough (Cannata and Hassler 1995, Ross Taylor and Associates 2020).



Map Sources:
Coho Salmon Distribution: CDFW
Sub-watershed boundaries: Calwater 2023
Channel network: NHD
Roads, cities: ESRI 2016

Figure 2-1. Approximate current distribution of Coho Salmon in the Eel River watershed. Data source: California Department of Fish and Wildlife's Biogeographic Information and Observation System. Does not include various small streams that are likely used seasonally for juvenile rearing. The species is currently rare upstream of the South Fork Eel River.

Small, remnant spawning populations of Coho Salmon may persist in more inland portions of the watershed that maintain cool water temperatures, but inadequate monitoring of many of these streams limit documentation (Brown et al. 1994, Garwood 2012, NMFS 2014). Coho Salmon have been documented in Outlet Creek and several of its tributaries as recently as the early 2000s, but population abundance is thought to be very low and possibly missing two year-classes (Garwood 2012, NMFS 2014).

2.2.2 Historical

Historically, Coho Salmon populations were more widely distributed across the Eel River watershed (Brown et al. 1994). In the upper Eel River, viable populations occurred in both the Outlook Creek and Tomki Creek watersheds (Brown et al. 1994, NMFS 2014). The species has not been documented in Tomki Creek since before 1979, except for one observation in 1996 in its tributary, Cave Creek, and are presumed to be extirpated there (Garwood 2012, NMFS 2014). However, records suggest Coho Salmon used to be abundant in Tomki Creek: during a fish "rescue" in 1949, nearly 17,000 individuals were transplanted from drying reaches of Tomki Creek to other locations in the Eel River watershed (CDFG 2010). Coho Salmon were also reportedly documented historically in Indian Creek, a mainstem Eel River tributary upstream of Outlet Creek (Brown et al. 1994). Historical presence of the species in the upper Eel River upstream of Scott Dam is unknown (NMFS 2014); but 47 adult Coho Salmon were documented in the mainstem at the Van Arsdale Fisheries Station (VASF) during the 1946–1947 season (Brown et al. 1994). Since then, the species has been rarely observed (in the early 2000s) at VAFS and in small numbers (NMFS 2014). Historical photographs and descriptions of Gravelly Valley—which is blocked by Scott Dam and largely under Lake Pillsbury—show a broad, unconfined valley and complex channel that would have likely provided high-quality juvenile winter rearing habitat for the species (Figure C-1). Coho Salmon are also thought to have been present in portions of the Middle Fork Eel River sub-watershed, including Rattlesnake, Mill, Girst, and Rock creeks, but have not been recently documented and are thought to be locally extirpated (Brown and Moyle 1991, Garwood 2012). Prior to widespread habitat degradation and hydrological alteration associated with European settlement and resource extraction, the unconfined, low-gradient channels found in Round Valley (Mill Creek in the Middle Fork Eel River sub-watershed), Gravelly Valley (upper Eel River), and Little Lake Valley (Outlook Creek drainage), likely provided complex and high-quality habitats capable of supporting viable and potentially large populations of the species, while further contributing life-history diversity to overall Eel River Coho Salmon population.

2.3 Ecology, Life-history, and Habitat Needs

2.3.1 Life-history Timing Overview

The generalized life-history timing for Coho Salmon life stages in the Eel River watershed is presented in Table 2-1, drawing largely from information in the South Fork Eel River or other northern California populations where more extensive monitoring data are available. Adults typically enter fresh water and migrate upstream to spawning tributaries from November through February (Ricker et al. 2014, Moyle et al. 2017, Guczek et al. 2020). Spawning occurs from November through February, peaking in December and January (Ricker et al. 2014, Guczek et al. 2020). Following deposition in spawning gravels, Coho Salmon eggs incubate for 6–12 weeks before hatching (Murray and McPhail 1988, Moyle et al. 2017) and spend another 4–8 weeks in redd gravels before emerging as fry (Murray and McPhail 1988, Moyle et al. 2017). Following emergence, juvenile Coho Salmon in larger river systems can display a variety of life-history strategies including (1) rearing in natal streams for approximately 1 year before outmigrating to the ocean in the spring; (2) leaving natal streams in the spring soon after emergence and rearing in cool non-natal tributaries or the estuary prior to entering the ocean the following spring or summer; and (3) leaving natal tributaries in the fall or early winter as flows increase and water temperatures decrease and overwintering in suitable low-velocity habitats along in the mainstem corridor, low gradient non-natal tributaries, or in the estuary (Skeesick 1970, Jones et al. 2014, Bennett et al. 2015, Rebenack et al. 2015, Soto et al. 2016). Based on rotary screw trapping data from spawning tributaries in the South Fork Eel River, most individuals emigrate to the ocean as 1-year-old smolt between March and July, with peak emigration in April and May (Mendocino Redwood Company 2002, Vaughn 2005, Ricker et al. 2014).

Table 2-1. Generalized life-history periodicity of Coho Salmon in the Eel River watershed by month. Note that some juveniles may rear in fresh water for 2 years.

Life stage	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Adult migration[1,2,3]	▓░	░	░□							□░	░▓	▓
Spawning[2,3]	▓	▓░	░□								░	▓
Incubation[4,5,6,7]	░	░	░	░	░						░	░
Juvenile rearing[5,6,8]	░	░	░	░	░	░	░	░	░	░	░	░
Juvenile movement to non-natal habitats												
Spring fry redistribution[9,10,11]			░	░	░	░						
Fall juvenile redistribution[9,10,11]									░	░	░	░
Smolt outmigration[6,7,8]			░	▓	▓	░	░□					

░ = Span of activity

▓ = Peak of activity

[1] CDFG unpubl. Benbow Dam count data, 1938–1976
[2] Guczek et al. (2020)
[3] CDFW unpubl. spawning survey data, 2010–2021
[4] Murray and McPhail (1988)
[5] Moyle et al. (2017)
[6] Mendocino Redwood Company (2002)
[7] Vaughn (2005)
[8] CDFG unpubl. Benbow Dam outmigrant trapping data, 1939
[9] Rebenack et al. (2015)
[10] Soto et al. (2016)
[11] Bennett et al. (2015)

2.3.2 Adult Migration

After spending 1 year rearing in fresh water and about 16 months feeding in the ocean, adult Coho Salmon initiate their spawning migration (Sandercock 1991). Early-maturing males known as jacks return to spawn after only 4–6 months in the ocean. Data from historical counts of returning adult salmon conducted at Benbow Dam indicates that jacks typically made up about 23% of the South Fork Eel River Coho Salmon population in most run-years, but ranged from 11% to 55% (CDFG, unpubl. data, 1938–1976; Stillwater Sciences 2022).

Adult Coho Salmon in northern California typically enter fresh water and migrate to spawning tributaries from November through February (Ricker et al. 2014, Moyle et al. 2017, Guczek et al. 2020). Historical counts at Benbow Dam on the South Fork Eel River indicate that the first migrating adult Coho Salmon typically arrived in that reach in early to mid-November and the last individuals typically arrived between late January and early February (Stillwater Sciences

2022). In years with limited fall rains, movement of adults into the South Fork Eel River may be delayed until early to mid-December. Historical counts at Benbow Dam indicate the overall median date of adult Coho Salmon arrival at the site was December 14 (CDFG, unpubl. data, 1938–1976; Stillwater Sciences 2022). Apparent adult migration timing based on observations of live adult Coho Salmon from recent spawning surveys conducted in tributaries to the South Fork Eel River is generally consistent with historical counts at Benbow Dam (Guczek et al. 2020).

2.3.3 Spawning and Incubation

Spawning is typically concentrated in the upper mainstem and tributaries of the South Fork Eel River, tributaries to the lower Van Duzen River, and tributaries to the lower Eel River (NMFS 2014, Guczek et al. 2020). Stream flows during the adult migration and spawning periods can strongly influence distribution of spawning and fry, with more spawning in mainstem reaches and larger tributaries expected during dry winters relative to winters, when sustained flows facilitate migration into smaller channels (Lestelle 2007). Coho Salmon spawning has been documented in the South Fork Eel River watershed between mid-November and mid-March, but peak spawning typically occurs between early December and mid-February (Guczek et al. 2020; CDFW unpubl. data, 2010–2021). A similar timing is expected for the tributaries to the lower Eel and Van Duzen rivers. Like Chinook Salmon, Coho Salmon are semelparous and die after spawning, contributing marine derived nutrients that increase productivity of the stream ecosystem.

Spawning typically occurs loose, silt-free, gravels in pool tailouts, the transitional areas between pools and riffles (Kondolf and Wolman 1993, Moyle et al. 2017). Following deposition in redd gravels, Coho Salmon eggs incubate for 6–12 weeks before hatching, with incubation time being inversely related to water temperature (Murray and McPhail 1998, Moyle et al. 2017). After hatching, alevins remain in the redd gravels while undergoing further development and absorption of the yolk sac for another 4–8 weeks before emerging as fry (Murray and McPhail 1988, Moyle et al. 2017). Based on spawning timing, the incubation period, and timing that newly-emerged fry have been captured during outmigrant trapping, developing Coho Salmon eggs or alevins may be present in spawning gravels from approximately November through May (Murray and McPhail 1988, Mendocino Redwood Company 2002, Vaughn 2005).

2.3.4 Juvenile Rearing

In northern California watersheds, Coho Salmon typically rear in fresh water for 1 year prior to emigrating to the ocean in the spring and summer (Rebenack et al. 2015, Moyle et al. 2017), although some individuals may spend 2 years in fresh water (Bell and Duffy 2007, Wright et al. 2012).Based on length data from outmigrant trapping in South Fork Eel River spawning tributaries (MRC 2002, Vaughn 2005) and nearby watersheds (Maahs 1995, Stillwater Sciences 2023), Coho Salmon fry in the Eel River are expected to begin emerging from redd gravels in late February, with peak emergence from mid-March through mid-May. After emergence, fry seek out low-velocity rearing habitats along the stream margin or in off-channel features. As they grow, juvenile coho, or parr, move to deeper habitats, although they continue to prefer low-velocity habitat throughout the freshwater rearing period (Nickelson et al. 1992). In the summer, Coho Salmon require complex cover and prefer pool habitats (Bisson et al. 1988, Nickelson et al. 1992). Coho Salmon prefer cool water temperatures and are not typically found in the summer in locations with MWAT >17–18°C (63–64°F) (Welsh et al. 2001, USEPA 2003). However, in locations with abundant food resources, they can thrive in higher temperatures, and exhibit growth (Lusardi et al. 2019).

During winter, both instream cover and off-channel areas providing slow water are essential for protecting Coho Salmon from displacement by high flows, and for cover from predation (Bustard and Narver 1975, Hartman et al. 1982, Bell 2001). Deep (>1.5 ft), slow (0.5 ft/s) areas within or near cover of roots, large wood, and flooded off-channel habitats, and beaver ponds constitute preferred habitat, especially during freshets (Tschaplinski and Hartman 1983, Swales et al. 1986, Nickelson et al. 1992, McMahon and Hartman 1989, Pollock et al. 2004). Low gradient and low velocity streams with abundant, cold pool habitat interspersed with woody debris are often highly productive Coho Salmon rearing habitat.

In Northern California, Juvenile Coho Salmon can display a variety of life-history strategies, including (1) natal stream rearing: rearing in natal streams for approximately 1 year before outmigrating in the spring as smolt; (2) spring fry emigrant: dispersing from natal streams in the spring as fry and redistributing to thermally suitable non-natal tributaries or the estuary, where they rear prior to entering the ocean the following spring or summer; and (3) fall parr emigrant: leaving natal tributaries in the fall or early winter with increasing stream flows and decreasing water temperatures and overwintering in low-velocity habitats along in the mainstem corridor, low-gradient non-natal tributaries, or the estuary (Jones et al. 2014, Rebenack et al. 2015, Soto et al. 2016). In northern Washington streams with minimal estuarine habitat, Juvenile Coho Salmon have also been documented entering the marine environment in their first fall or winter (age-0) and returning as adults approximately 2 years later (Bennett et al. 2015).

As discussed above, some individuals can also spend 2 years in fresh water, likely rearing in some combination of natal and non-natal habitats during that time (Bell and Duffy 2007, Wright et al. 2012). The extent to which these life-history strategies are expressed in the Eel River watershed and how their prevalence varies amongst spawning tributaries is uncertain due to limited juvenile monitoring, particularly outside of spring and summer. Their historical incidence is also largely unknown, but based on other healthy Coho metapopulations, life histories that are currently rare in the Eel River were presumably more common under more pristine conditions. This is particularly likely for non-natal life histories and those associated with intermittent streams (Wigington et al. 2006, Koski 2009)

Life-history diversity in Coho Salmon is driven by genetic, environmental, and anthropogenic factors. In some cases, diversity in patterns of juvenile rearing can be associated with food subsidies. For example, in Alaska juvenile Coho Salmon foray into sub-optimally cold (4–8°C) thalweg habitat to feed on abundant salmon eggs (Fitzgerald et al. 2023) or benthic invertebrates (Baldock et al. 2016) and then move to warmer floodplain or beaver-meadow-complex habitat to assimilate their food at faster rates (Rossi et al. 2024).

Section 2.4.1 provides additional description of life-history strategies, including describing variations within each strategy, their expected distributions within the Eel River, factors that influence their relative prevalence, and restoration considerations for each.

2.3.5 Smolt Outmigration

Outmigrant trapping conducted in the spring and early summer in various South Fork Eel River tributaries and nearby watersheds indicates that most Coho Salmon smolt outmigrate from natal streams from early March through late May, but small numbers have been documented moving at late as mid-June in some streams (Puckett 1976, Maahs 1995, PCFFA 1988, MRC 2002, Vaughn 2005). A single year of juvenile outmigrant trapping at Benbow Dam in 1939 suggests that outmigration of juvenile Coho Salmon in the mainstem South Fork Eel River likely occurs soon after outmigration from tributaries: peak capture at Benbow occurred in early to mid-May, with over 75% of annual captures by mid-May (Stillwater Sciences 2022). Juvenile Coho Salmon were first captured on April 3 and last captured on July 27, but very few individuals were caught after late June (Stillwater Sciences 2022).

After leaving the South Fork Eel and Van Duzen Rivers, smolting Coho Salmon utilize the lower Eel River and estuary as transitional habitat between fresh and salt water (Puckett 1977, Cannata and Hassler 1995, Ross Taylor and Associates 2020). Puckett (1977) captured age-1 juvenile Coho Salmon in the Eel River estuary from spring through summer, with most individuals captured in April, May, and June. The typical duration of time spent in the estuary before entering the ocean is unknown, but presence of individuals considerable distances up the McNulty Slough and Salt River drainages suggests that at least some juveniles rear in these areas prior to entering the ocean. In nearby Humboldt Bay, Wallace et al. (2015) found that about 40% of the Coho Salmon smolt production from Freshwater Creek came from individuals rearing in the stream-estuary ecotone, and juveniles rearing there were larger than their cohorts rearing in upstream freshwater habitat. In the Eel River, Puckett (1977) also captured a single juvenile Coho Salmon in late October and Cannata and Hassler (1995) captured several individuals in December and February. More recently, small numbers of juvenile Coho Salmon have been captured in the Salt River from November through May, indicating that some component of the population likely leaves natal tributaries for the estuary prior to spring (when outmigrant trapping efforts were typically initiated).

2.3.6 Ocean Residence

After entering the ocean in the spring or summer, Coho Salmon typically spend about 16 months feeding in the ocean before initiating their spawning migration (Sandercock 1991). Early-maturing males known as jacks return to spawn after only 4–6 months in the ocean. Movement patterns and distribution of Coho Salmon in the ocean are not well described, but individuals from northern California rivers are generally thought to range along the northern California and southern Oregon coasts south of Cape Blanco (Weitkamp and Neely 2002). Ocean conditions, especially during the first few months of ocean residency, have a large influence on smolt-to-adult survival (Bradford 1995, Quinn 2005). Strength and timing of ocean upwelling from the California Current and its influence on marine productivity are key factors affecting marine survival of juvenile salmon (Nickelson 1986, Ruzicka et al. 2011). Interannual differences in ocean conditions and upwelling are driven in part by the Pacific Decadal Oscillation, which can influence the food chain and quantity and quality of food for young salmon (Ruzicka et al. 2011, Peterson et al. 2012). An in-depth review of the influences of interannual variability and changes in ocean conditions in Coho Salmon marine survival can be found in NMFS (2014).

2.4 Life-history Diversity Conceptual Model

This section synthesizes information from the Eel River and elsewhere within the range of Coho Salmon to identify and characterize juvenile and adult life-history strategies with potential to occur in the watershed. Rare or extirpated strategies with potential to contribute to population abundance and resilience in the Eel River are also briefly described. The overall approach, rationale, and uses of these life-history conceptual models in the context of the Restoration Plan are described in Section 3 of the Plan.

2.4.1 Juvenile Life-history Strategies

Juvenile Coho Salmon in the Eel River have potential to display a wide range of life-history pathways, utilizing various habitats across the watershed from the time of emergence from redd gravels until they enter the ocean (Figure 2-2). While the total number of possible pathways that could occur is too many to describe individually, they can be grouped into the following three primary strategies, ordered by decreasing time spent in natal streams (Figure 2-2):

1. **Natal stream rearing**: rear in natal streams for approximately 1 year before outmigrating in the spring as smolt;
2. **Fall parr emigrant**: rear in natal streams from emergence until fall or early winter before overwintering in the mainstem corridor, non-natal streams, or the estuary prior to entering the ocean in the spring or summer;
3. **Spring fry emigrant**: dispersing from natal streams in the spring as fry and redistributing to thermally suitable non-natal tributaries or the estuary, where they rear prior to entering the ocean the following spring or summer

The extent to which these life-history strategies are currently expressed in the South Fork Eel River watershed and how their prevalence varies amongst spawning tributaries is uncertain due to limited juvenile monitoring outside of spring and summer. However, it is likely that each played an important role in the historical meta-population, and recovery of Coho Salmon abundance depends on restoring more than one of these primary life-history strategies.

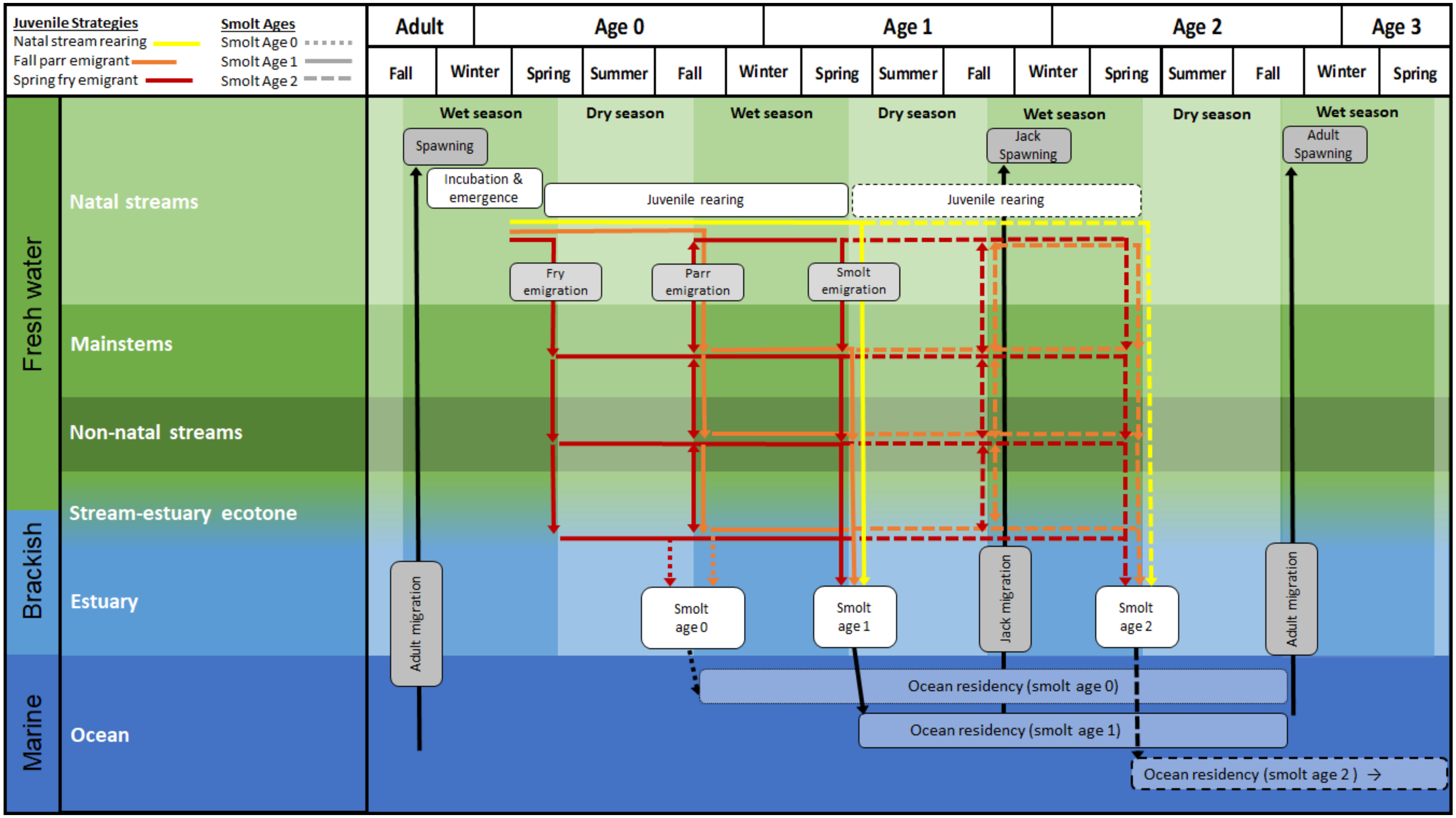


Figure 2-2. Life-history conceptual diagram for Coho Salmon in the Eel River, showing potential pathways across time and space for primary juvenile life-history strategies, which are represented by yellow, orange, and red. Each line represents a potential pathway within a strategy. Arrows direction represents movement direction of movement between primary portions of the watershed.

2.4.1.1 Natal stream rearing strategy

The natal stream rearing strategy includes all life histories where Coho Salmon spend most their 1-to-2-year freshwater residency in the stream where they hatched before emigrating to the ocean in the spring (Figure 2-2; yellow line). This strategy is the most recognized and intensively monitored Coho Salmon juvenile life-history in Northern California today; although it is uncertain whether it was historically the dominant life history. Because this strategy must persist through variable environmental conditions across all four seasons before emigrating to the ocean, it is expected to be more prevalent in streams with high-quality habitat conditions in both the dry and wet seasons. In the dry season, these habitat conditions include perennial flows, cool water temperatures, and complex pool habitats that provide escape cover (Bisson et al. 1988, Nickelson et al. 1992). In the wet season, these conditions include low-velocity winter rearing and high-flow refuge habitats provided by large wood and connected off-channel features, which are more prevalent in low-gradient, unconfined channels (Bustard and Narver 1975, Hartman et al. 1982, Nickelson et al. 1992).

Conditions that support the natal stream rearing strategy are primarily found in the low-gradient cold and cool tributary channel archetypes (Plan Section 2.2 and Appendix C). Within the Coho Salmon distribution in the Eel River, cool streams with persistent summer flows are generally associated with watersheds that have a relatively low fraction of Central Belt mélange geology and a high fraction of Coastal Belt geology, which acts to slow and retain winter run-off and slowly drain groundwater during the summer (Dralle et al. 2023). Conditions that support natal rearing currently occur primarily in the more coastal-oriented spawning tributaries, such as Dutch Charlie and Indian creeks in the South Fork Eel sub-watershed and Lawrence Creek in the Van Duzen sub-watershed. However, natal rearing is expected to have been more prevalent in other parts of the watershed historically, before widespread alteration of channel, riparian, and hydrological conditions.

Within their natal streams, the prevalence of the natal rearing strategy relative to early emigrant strategies is expected to vary between years with different hydrological conditions. For example, in dry water years, both the thermal suitability and physical capacity of summer rearing habitat in these streams may be reduced, resulting in a greater fraction of spring fry emigrants. In wetter years with significant high flow events, the winter rearing habitat capacity of some natal streams may be reduced, resulting in a great fraction of individuals that either volitionally emigrate or are entrained downstream in the fall or winter prior to smolting (fall parr emigrants). As described below, habitat and ecological conditions in non-natal rearing habitats and during movements to reach them are expected to determine the extent to which these early emigrant strategies survive and contribute to adult returns.

Individuals within the natal stream rearing strategy there are expected to display a range of behaviors that contribute additional life-history diversity to the population. For example, some individuals may spend much of their freshwater residency in the same general location, while some individuals are expected to move downstream or upstream within natal streams in response to changing flows, availability of food, and other seasonal ecological changes. Lestelle et al. (2007) observed that survival of juvenile Coho Salmon during summer can be strongly density-dependent in smaller streams. Competition for shrinking space—due to declining flows in late summer—and limited food results can reduce survival at higher juvenile abundance and these factors may drive early emigration of a portion of the rearing population. Additionally, in a typical year, timing of smolt emigration from natal streams ranges from early March until at least mid-June (Puckett 1976, Maahs 1995, PCFFA 1988, MRC 2002, Vaughn 2005), with early emigrants often encountering vastly different environmental and ecological conditions than late emigrants. Likewise, the amount of time natal stream rearing smolts spend in lower mainstem the estuary before entering the ocean is expected to vary. Because this diversity provides additional population resilience it is important to consider ways to protect and enhance it when developing restoration strategies.

2.4.1.2 Fall parr emigrant strategy

Fall parr emigrants spend their first spring and summer rearing in natal streams before emigrating to low-velocity, non-natal winter rearing habitats as temperatures drop and flows rise in the fall. Although fall parr emigrant strategies have not been directly documented in the Eel River through outmigrant trapping or tagging studies, this life history is common in many coho populations (Bennet et al. 2014). The presence of juveniles in the Eel River estuary and its tributaries in the fall and winter (Cannata and Hassler 1995, Ross Taylor and Associates 2020) indicate the strategy is still present and likely an important contributor to the overall Eel River Coho Salmon population. Various studies have shown a large initial pulse of juvenile Coho Salmon movement in response to the first substantial increases in stream flow in the fall (i.e., freshets), and continued pre-smolt movements throughout the fall in winter, typically in response to additional flow increases (Petersen 1982, Scarlett and Cederholm 1984, Miller and Sadro 2003, Stillwater Sciences 2023). Another factor that supports the historical presence of this life history is the large annual decline in mainstem river water temperatures from August to October in the Eel River. Finally, the fall parr emigrant life-history strategy may also have allowed Coho Salmon to capitalize on the historically abundant Chinook Salmon egg subsidy – a strategy observed in other Coho Salmon populations (e.g., Armstrong et al. 2013, Fitzgerald et al. 2023).

Fall-to-winter redistribution by juvenile Coho Salmon has been documented in numerous other river systems, including migrations into small, intermittent tributaries (Ebersole et al. 2006, Wigington et al. 2006), perennial tributaries (Skeesick 1970, Soto et al. 2016, Stillwater Sciences 2023); off-channel ponds, beaver ponds, and wetlands along the mainstem river corridor (Petersen 1982, Miller and Sadro 2003, Soto et al. 2016); and estuarine habitats such as tidal wetlands and sloughs (Miller and Sadro 2003, Koski 2009, Jones et al. 2014, Rebenack et al. 2015, Wallace et al. 2015). Some of these fall movements occur over relatively short distances, while others can involve long distance emigration to overwintering habitats (Petersen 1982, Ebersole et al. 2006, Soto et al. 2016, Stillwater Sciences 2023). For example, studies in the Klamath River have documented fish tagged in the summer in inland spawning tributaries moving over 100 miles downstream to rear in the lower reaches of non-natal tributaries (Adams 2013, Soto et al. 2016). Different individuals tagged leaving the same spawning stream have been documented using non-natal habitats distributed across large distances along the mainstem corridor (Soto et al. 2016).

Many of these non-natal winter rearing habitats are expected to provide high-quality food resources and offer winter growth and survival advantages relative to natal streams. Estuarine habitats in particular can provide abundant food resources and promote high juvenile salmon growth rates (Miller and Sadro 2003, Koski 2009, Wallace et al. 2015). Because of enhanced growth and survival, fall emigrants that rear in the estuary can contribute disproportionately to adult returns (Jones et al. 2014, Bennett et al. 2015).

Small streams, even those that become intermittent in the summer, can also provide high-quality rearing and winter refuge habitat for fall parr emigrants during the wet season (Skeesick 1970, Ebersole et al. 2006, Wigington et al. 2006). Ebersole et al. (2006) found high overwinter survival and growth rates in a small tributary relative to adjacent mainstem reaches. This study also showed that some individuals may enter and leave multiple tributaries and use a wide array of habitats during the winter. These findings highlight the importance of small streams to Coho Salmon populations (and especially early emigrant strategies) and the importance of maintaining and restoring access to these habitats. Low-gradient tributaries that are downstream of a large portion of Coho Salmon spawning locations, such as tributaries entering the lower Eel River are expected to have particularly high potential to provide valuable non-natal rearing habitat for fall parr emigrants, since much of emigrant population has an opportunity to enter them. For this reason, assessing and restoring habitat in and connectivity to these streams is an important strategy for increasing the prevalence of the fall parr emigrant strategy.

In addition to the downstream movements described above, fall parr emigrants can also undertake considerable upstream movements from the lower reaches of larger streams into upper reaches or smaller upstream tributaries. This behavior, often associated with the first freshets of fall, has been described by various studies (Miller and Sadro 2003, Koski 2009, Nordholm 2014, Stillwater Sciences 2023). While some of these fish documented moving upstream in the fall were likely offspring of fish that spawned in lower mainstem reaches, in many cases these fish initially entered the stream-estuary ecotone as fry in the spring or summer before moving back upstream in the fall. The latter life-history pathway has been referred to as “fry-nomad migrants” (Miller and Sadro 2003, Koski 2009) and is described in more detail in Section 2.4.1.3 (*spring fry emigrant*) below.

The prevalence of the fall parr emigrant in the Eel River watershed is expected to vary by both annual differences in hydrological conditions and spawning location. Timing and magnitude of stream flows are expected to influence the fraction of the population in a stream that emigrates in the fall versus in the spring as smolts. In general, high flows that result from wet falls and winters are expected result in more early emigration relative to drought winters, when in-channel water velocities remain lower and fewer fish are entrained downstream.

The fall parr emigrant strategy is expected to be a component of the juvenile population in most, if not all, streams where Coho Salmon spawn, but is hypothesized to be more prevalent in locations that have high-quality summer rearing habitat but lack winter high flow refuge habitat. For example, much of mainstem Hollow Tree Creek—which has high-quality spawning and cool summer rearing habitat but generally lacks high-flow refuge habitat due to its large size and confined channel—is a natal stream that likely promotes a high degree of juvenile emigration in the fall. As flows rise, many individuals that reared in the mainstem of Hollow Tree Creek in the summer are likely forced to enter low-gradient tributaries or leave the watershed and seek overwintering habitats downstream. This fall redistribution could include entering off-channel features along the corridors of the South Fork or mainstem Eel Rivers Eel River, low-gradient tributaries, or estuarine habitats. Importantly, various small tributaries that do not support Coho Salmon spawning or are too hot or dry to support summer rearing have high potential to provide high-quality overwintering habitats. The extent of winter use of such streams by Coho Salmon is largely unknown in the Eel River due to the focus of existing monitoring on cold, perennial streams in the summer.

The fall parr emigrant strategy was likely much more prevalent in the Eel River historically, before the extensive degradation the estuary; large, unconfined valleys that provided extensive winter rearing habitat such as Little Lake Valley (Outlook Creek) and Laytonville Valley (Ten Mile Creek); and other non-natal winter rearing habitats. Nevertheless, the strategy is likely still an important component of the Eel River Coho Salmon population, and one that has great potential to be restored. The various studies described above highlight the importance of connectivity between mainstems and adjacent low-velocity winter rearing habitats such as low-gradient tributaries and off-channel features along mainstem corridors and the estuary. Impassible road culverts and tide gates block juvenile fish access to many of these habitats. Likewise, levees and rip-rapped roads along portions of the South Fork, Van Duzen, and Eel rivers have disconnected many floodplain habitats that likely provided extensive winter rearing habitat historically.

Despite their potential to provide high-quality winter habitat, warmer, drier streams have largely been overlooked in efforts to restore Coho Salmon populations in the Eel River. Along mainstem river corridors, low-velocity winter rearing habitats may occur in floodplain channels with ponded features or off-channel ponds connected to the mainstem by small channels (Soto et al. 2016). Such features are often associated with small tributaries, which can (1) help maintain connectivity with the mainstem; (2) improve water quality in off-channel habitats during drier winter periods; and (3) provide clearwater feeding habitats during high flows when high turbidity levels in adjacent mainstems can cause negative physiological effects, impair feeding, and prompt juvenile salmon to seek refuge habitats (Bisson and Bilby 1982, Sigler et al. 1984, Sedell et al. 1990, Soto et al. 2016).

Alteration of much of the lower mainstems of the South Fork, Van Duzen, and Eel rivers and the lower reaches of their tributaries due to highway and levee construction, as well as sediment deposition from logging and large floods, has likely degraded or disconnected many of the off-channel features that existed historically as well as rearing habitat capacity and quality in the stream estuary ecotone Such changes are expected to have lowered the survival and prevalence of the fall parr emigrant strategy. Likewise, widespread degradation and disconnection of estuarine winter habitats due to diking, tide gates, and agricultural conversion is expected to have has diminished this important component of juvenile Coho Salmon life-history diversity in the Eel River. Loss of mainstem habitat complexity and the introduction of non-native Sacramento Pikeminnow has also likely resulted in decreased survival off fall emigrants during movements from natal to non-natal habitats, further diminishing the prevalence of this strategy.

2.4.1.3 Spring fry emigrant

The spring fry emigrant strategy of juvenile Coho Salmon leaves natal streams in the spring or summer as flows recede and water temperatures warm. Some newly emerged fry may be entrained downstream by higher spring flows (Tschaplinski 1987), while others likely move in response to warming temperatures or shrinking habitat as flows drop in natal streams (Koski 2009). The extent to which fry emigrants are entrained by stream flows, are “surplus” fry that exceed the carrying capacity by summer rearing habitat or are displaying an ingrained life-history strategy that occurs regardless of density-depending mechanisms is unknown. It is likely that each of these factors interact to contribute to fry emigration from a natal stream, and the number of individuals moving on account of each factor varies annually depending on spawning density and hydrological conditions that influence spawning (and emergence) locations, fry entrainment, and summer carrying capacity. Regardless of the reason, evidence from various watersheds indicates that enough early fry emigrants can survive to contribute substantively to the returning adult population (Koski 2009, Jones et al. 2021).

After leaving natal streams, spring fry emigrants can move through and rear in a variety of habitats across time and space before entering the ocean the following spring (Figure 2-2). After moving, some individuals remain in a single location through the summer and winter until smolting. Others may display more of a nomadic life-history pathway, where they move between multiple habitats in response to changing environmental conditions and food resources (Lestelle 2007, Koski 2009, Soto et al. 2016, Jones et al. 2021). While some fry emigrants initially enter non-natal tributaries, many are expected to enter mainstem habitats soon after emergence from natal streams in the spring. Spring movement of Coho Salmon fry from natal streams into the mainstem South Fork Eel River has been documented by outmigrant trapping in various tributaries (Puckett 1976, PCFFA 1988, Maahs 1995, Vaughn 2007). Some of these fry likely continue moving downstream to the stream-estuary ecotone, but, at least historically, others may have reared in productive habitats in and adjacent to the mainstem through the spring and early summer. Based on research in other large river systems, these fry seek out low-velocity habitats, such as backwaters, edge habitats along mainstem floodplain channels including ponds (particularly those fed by small tributaries), and small low-gradient tributaries (Peterson 1982, Beechie et al. 2005, Lestelle 2007, Soto et al. 2016). During the spring and early summer, water temperatures in mainstem reaches of the South Fork Eel, Van Duzen, and lower Eel rivers typically remain suitable for juvenile Coho Salmon (Asarian et al. 2016, Stillwater Sciences and Wiyot Tribe Natural Resources Department 2020). Because these mainstem reaches (and some non-natal tributaries) are warmer and receive more solar exposure, they are expected to be more productive and provide growth advantages for fry in the spring relative to colder natal streams.

Since many mainstem reaches become thermally unsuitable for Coho in the summer (Asarian et al. 2016), remaining fry must either seek out thermal refugia within mainstem reaches or redistribute to cooler habitats in tributaries, the stream-estuary ecotone, or upstream reaches. Such an early summer redistribution has been described in the nearby Klamath River watershed (Adams 2013, Soto et al. 2016). In addition to downstream movements or entering tributaries, upstream movements within mainstem reaches can occur in the summer. For example, in the Shasta River, Adams (2013) documented extensive upstream movements of age-0 Coho Salmon tagged in the late-spring from mainstem locations to cooler reaches in the upper mainstem and adjacent tributaries. Observations by Georgakakos (2020) suggest similar movements may occur into the upper reaches of the South Fork Eel River, where water temperatures can remain suitable throughout the summer rearing period.

The historical and current prevalence of Coho Salmon summer rearing in larger mainstem reaches of the Eel River watershed is generally unknown but would require thermal refugia provided by coldwater plumes at from tributaries, springs or groundwater seeps, or thermally stratified pools. P. Georgakakos (pers. comm., 2024) has observed summer rearing Coho Salmon in the upper mainstem South Fork Eel during August snorkel surveys in every year between 2015 and 2024. Limited monitoring has been conducted to document the distribution and temperature patterns of thermal refugia within the range of Coho Salmon in the Eel River watershed, but such features do occur (e.g., Kubicek 1977, Nielson et al. 1994, Wang et al. 2020) and have potential to support the spring fry emigrant strategy. In the mainstem Klamath River, Deas and Tanaka (2006) documented age-0 Coho Salmon rearing in several thermal refuge sites associated with tributary confluences. Similar refuges are expected to exist at confluences of various cold tributaries to the South Fork Eel, lower Eel, and lower Van Duzen rivers. However, the presence of large numbers of introduced Sacramento Pikeminnow is hypothesized to have greatly limited the ability of juvenile Coho and other salmonids to use these and other productive mainstem habitats, during spring, summer, and fall.

Spring fry migrants that move quickly through mainstem reaches may rear in habitats within the stream-estuary ecotone (e.g., Wallace et al. 2015). One life-history pathway that appears to be common in various river systems is downstream movement into the stream-estuary ecotone in the spring, followed by upstream movement into tributaries or adjacent off-channel habitats as mainstem flows and water velocities increase in the fall (Skeesick 1970, Koski 2009, Miller and Sadro 2003, Stillwater Sciences 2023). In this pathway, individuals feed and grow in productive lower river and brackish estuarine habitats before seeking low-velocity habitats for winter rearing. The current prevalence of this life-history pathway in the Eel River is unknown, but is presumed to be rare relative to historical conditions because of the extensive modification of the lower mainstem corridor and estuary, including rail road, road, and levee construction; reduced supply of large wood; channel aggradation that resulted in filling of deep pools and a reduced tidal prism; and the introduction of predatory Sacramento Pikeminnow, which occur in high densities in lower mainstem habitats that could otherwise support large numbers of salmonids (CDFG 2010).

After summer, depending on the conditions within their summer rearing location, some spring fry emigrants may redistribute again to one of the suitable low-velocity winter habitats described above for the fall parr emigrant strategy (e.g., estuary, small, low-gradient tributaries etc..).The spring fry emigrant strategy is expected to be a component of the juvenile population in all streams where Coho Salmon spawn, but is hypothesized to be more prevalent in natal streams with poor fry habitat (lack of low velocity edgewater habitat) or with summer water temperatures that approach or exceed levels suitable juvenile rearing, such as many of the streams draining the eastern side of the South Fork Eel River watershed (e.g., Dean Creek, East Branch South Fork Eel River, and Ten Mile Creek). As discussed above the annual differences in hydrological conditions is also expected to pay a role in prevalence of fry emigrants. Distribution of spawning and emergent fry can be strongly influenced by stream flows during the adult migration and spawning periods. For example, during winters with sustained flows a greater portion of the spawning population can access smaller streams and headwater reaches that stay cool through the summer. In contrast, during dry winters spawning and fry emergence can be restricted to mainstems and larger tributaries. Following dry winters, a greater fraction of the population is hypothesized to emigrate as fry since (1) larger channels may become thermally unsuitable during the summer and (2) lower summer base flows may constrict summer habitat carrying capacity force more individuals to seek downstream habitats.

2.4.1.4 Other juvenile life-history strategies

Various other less common juvenile Coho Salmon life-history strategies may occur or may have occurred to a greater degree prior to extensive degradation of certain habitats that supported unique life-history strategies. For example, populations that occurred in large, more inland valleys such as Little Lake Valley and Round Valley have been severely reduced or extirpated, but likely used to support juveniles with unique life-history strategies. Some strategies with potential to occur in the Eel River watershed and contribute to the population resilience are briefly described below.

Age-2 smolt

Each of the primary strategies described above typically spends about 1 year in fresh or brackish water before entering the ocean. However, some juvenile Coho Salmon may spend 2 years in fresh water (Holtby 1990, Bell and Duffy 2007, Wright et al. 2012), displaying one or more of the primary strategies during this time. In general, the proportion of 2-year-old smolts in a population increases with increasing latitude, which is thought to be due to slower growth with colder water temperatures (Holtby 1990, Sandercock 1991). However, 2-year freshwater residency has documented to varying degrees in Northern California Coho Salmon populations (Bell and Duffy 2007, Wright et al. 2012, Stillwater Sciences 2023). For example, in Prairie Creek, Bell and Duffy (2007) found that 28% of outmigrants spent 2 years in fresh water and attributed the high prevalence of age-2 smolt to low winter growth rates. In Pudding Creek, Wright et al. (2012) found that, over a 5-year study, 13% of Coho smolt were age-2 smolt, though incidence varied by year. Further, they found that, when initially tagged after about 1 year in fresh water, individuals that went on to smolt at age-2 were smaller (median fork length 76 mm) than those that smolted at age-1 (92 mm). However, measured just entering the ocean, the median length of age-2 smolt was greater (129 mm) than age-1 smolt (104 mm). While this age-2 smolt life-history has not been well described in the Eel River, length data from outmigrant trapping in South Fork Eel River tributaries indicates it occurs to some degree (Pucket 1976, MRC 2002).

The age-2 smolt life-history likely influences population dynamics and contributes to resilience of Coho Salmon populations in several important ways. First, a second year of growth allows smaller individuals to emigrate at a larger size, increasing the likelihood of marine survival. Second, since many age-2 smolt are expected to return to spawn at age-4, a year later than age-1 smolt in their cohort, they promote genetic mixing between spawning cohorts. Finally, if spawning recruitment and juvenile survival are poor for a given cohort, age-2 smolt from the previous cohort can contribute to the returning adult population of that cohort.

Age-0 smolt

Coho Salmon that smolt and enter the ocean at age-0 appear to be rare but have been documented in several instances across the range of the species (Koski 2009, Adams 2013, Shaul et al. 2013, Bennett et al. 2015). In the Klamath basin, considerable numbers of age-0 smolt have been documented leaving the Shasta River, where extremely high spring growth rates can occur in spring and summer (Adams 2013, Lusardi et al. 2019). Coho Salmon have also been observed leaving small Olympic Peninsula streams in Washington and entering the ocean at age-0, primarily during the fall (Roni et al. 2012, Benett et al. 2014). These streams have limited estuaries and discharge directly into the Strait of Juan de Fuca, suggesting that these age-0 fish may have been entrained into the ocean as flows increased in the fall. However, PIT tag data indicated that this fall smolt life-history contributed 37% of the returning adults over an 8-year period, and that half of the individuals spent about 1 year at sea and half spent 2 years at sea (Bennett et al. 2015). Some individuals moved through the marine environment to overwinter in nearby watersheds or reentered their natal watershed (Roni et al. 2012). This phenomenon—which has been termed “habitat shifting through the marine environment” (Lambert and Chamberlin 2023)—has also been documented between tributaries in Southeast Alaska (Shaul et al. 2013), between the Klamath River and Prairie Creek (Faukner et al. 2017), and between Humboldt Bay tributaries (Wallace et al. 2015).

Smoltification and ocean entry at age-0 is expected to be rare under current conditions in the Eel River, but insufficient monitoring has been conducted to understand its true prevalence. It is possible that, when pristine, certain habitats in the Eel River watershed (e.g., the large, connected wetland habitats that used to exist in Little Lake Valley in the Outlet Creek watershed) promoted rapid fry growth and smoltification at age-0. This life-history strategy could influence population dynamics and resiliency since it would allow for genetic mixing between spawning cohorts. Due to rapid growth and the short amount of time spent in fresh water, fry to smolt survival be higher and generation time would be faster.

Relict Inland Populations

Although currently absent or rare, there is some evidence that viable populations of Coho Salmon have historically reared in more inland locations such as Mill Creek in Round Valley, Outlet Creek, and Tomki Creek (Section 2.2.2). Due to the likely higher summer water temperatures, it is possible that spring fry emigrants were prevalent in these populations. Although, under historical conditions with intact hydrology and riparian, over summering may have been more prevalent. Because of their high intrinsic potential to support Coho Salmon and promote further life-history diversity in the Eel River, large valleys such as Little Lake Valley near Willits (Outlet Creek drainage) and Round Valley warrant additional attention.

2.4.2 Adult Life-history Strategies

Adult Coho Salmon in Northern California are generally not known to have substantial variability in adult life strategies relative to steelhead and Chinook Salmon, with most adults coming back to spawn in the fall or early winter at age 3 (Wright et al. 2012, Ricker et al. 2014). The primary life-history variation in adult Coho Salmon is related to (1) age at return to fresh water and (2) variability in run and spawning timing. The potential importance of these sources of variation on population productivity and resilience are briefly discussed below.

2.4.2.1 Age at Spawning

Adult Coho Salmon typically return as either 2-year-old jacks after spending 4–6 months feed in the ocean, or 3-year-old adults after spending about 16 months in the ocean (Sandercock 1991). Data from historical counts of returning adult salmon conducted at Benbow Dam indicates that in typical run-years jacks made up about 23% of the South Fork Eel River Coho Salmon population and ranged from 11% to 55% (Stillwater Sciences 2022). These values are similar to jack percentages documented in southern Oregon coastal streams (Young 2011). Although jacks have been somewhat underemphasized in fisheries research and management, Young (2011) suggests that they could be critically important in maintaining genetic structure of Coho Salmon populations because they provide the only gene flow between otherwise isolated brood years, thereby increasing effective population size and reducing vulnerability to genetic drift and inbreeding depression. Jacks also provide resilience to the population by increasing the likelihood of spawning success for a given cohort, or brood year in the face of environmental stochasticity that might limit spawning success of the 3-year-old component (Young 2011).

2.4.2.2 Run timing variability

Another source of diversity in adult Coho Salmon is variability in run and spawning times. The species has been documented spawning between mid-November and mid-March (Guczek et al. 2020; CDFW unpubl. data, 2010–2021), and developing embryos and offspring of earlier spawning individuals can be exposed to vastly different environmental conditions than later spawning individuals. This diversity increases the likelihood that at least some individuals encounter suitable conditions for incubation, fry rearing, and juvenile recruitment. For example, in a year with a late onset of fall and winter rains, earlier migrating and spawning fish may be forced to build redds in mainstem habitats where redds are more vulnerable to scour by later winter storms, and individuals that do survive to hatch may emerge into less suitable fry rearing habitats. Under the same hydrologic conditions, late migrating and spawning individuals move after stream flows have risen and can access smaller natal tributaries where redds are less likely to scour and rearing conditions are more ideal. In wetter water years, early spawners can access smaller natal streams, and their offspring can emerge from redd gravels several months before those of later spawners, contributing to diversity in juvenile life histories.

2.5 Conceptual Model Outcomes

The information compiled and understanding gained from this species descriptions and life-history conceptual model were used to:

- Identify an initial list of stressors with potential to adversely impact one or more life stages;
- Identify and describe key themes and strategies for restoration and conservation; and

- Catalog important data gaps to help identify research and monitoring activities needed to address them.

2.5.1 Stressors

Table 2-2 provides a list of stressors with potential to adversely impact each life stage of Coho Salmon. This list of stressors was generated from multiple sources, including the above species description and life-history conceptual model and the SONCC Coho Salmon Recovery Plan (NMFS 2014). Importantly, while each stressor listed has the potential to adversely affect one or more life stages, some stressors are expected to be more important than others in terms of limiting population productivity, expression of life-history diversity, and abundance of returning adults. For example, area of low-velocity winter rearing habitat for juveniles is often considered to be a primary factor limiting Coho Salmon smolt production (Tschaplinski and Hartman 1983, Quinn and Peterson 1996, Stillwater Sciences 2011, NMFS 2014, South Fork Eel River SHaRP Collaborative 2021). For the South Fork Eel River population, the SONCC Coho Recovery Plan (NMFS 2014) lists altered hydraulic function and lack of floodplain and channel structure as key limiting stresses for juveniles, which is identified as a "limited life stage." Another example is lost stream-estuary ecotone habitat, which, if restored, would likely benefit all three major life-history strategies; although the largest benefits may be to spring fry and fall parr emigrant strategies.

Spawning habitat quantity is generally not expected to limit the number of fish that can be produced in most streams, since there is often sufficient habitat to support the numbers of spawners returning under current conditions. Additionally, because of degraded rearing habitats, a relatively small number of successful redds are expected to fully seed the available summer and winter rearing habitat with juveniles in many streams. Thus, depending on the stream and hydrological conditions of a given year, the quantity and quality of summer or winter rearing habitat is expected to dictate the number of smolt that leave a natal stream (natal stream rearing life-history strategy). In streams with cold perennial flow that can support large numbers of juveniles through the summer, lack of winter rearing habitat is expected to the primary factor limiting smolt production from natal streams. Importantly, ecological and habitat conditions outside of natal streams, are expected to play a primary role in determining the numbers of early emigrant life-history strategies (fall parr and spring fry migrants) that survive to smolt and enter the ocean.

The impact of a given stressor on habitat capacity, growth, and survival—and ultimately the number of returning adults in a cohort—is also expected to vary by year (due to differences in hydrology and temperature regimes or fry recruitment). For example, the impacts of reduced low-velocity instream winter rearing habitats and impaired connectivity with off-channel habitats are expected to be greater during wet winters relative to dry winters without flood events. The population impacts of increased water temperatures are expected to be greater in drought years relative to wet years.

The population-level impact of certain stressors is also expected to vary between natal streams due to intrinsic differences in temperature and hydrology driven by underlying geology (e.g., Dralle et al. 2023), and also differences in habitat condition from level of past disturbance. For example, a population that spawns in a cold stream with persistent summer stream flow and intact riparian forest (e.g., Elder Creek), is less likely to be limited by increased water temperatures (e.g., Elder Creek) related to a population spawning in a warmer and more degraded stream with intermittent summer flows (e.g., Dean Creek).

Since they inhabit different portions of the watershed at different times, different life-history strategies are also expected to be more or less impacted by various stressors. For example, relative to natal stream rearing juvenile life-history strategy, early emigrant life-history strategies are more likely to be adversely impacted by alteration of and impaired connectivity with estuarine habitats.

Table 2-2. Stressors with potential to adversely impact each life stage of Coho Salmon in the Eel River watershed, with life-history strategies that are predicted to be the most impacted.

Life stage	Stressor	Drivers (underlying causes of stressor to be addressed by restoration)	Mechanisms of impact on population productivity, abundance, distribution, and resilience	Life-history strategies potentially highly impacted
Adult holding and migration	Anthropogenic physical barriers to movement	Dams, poorly-designed or failed road crossings, other manmade obstructions to movement.	Reduced spawning distribution, lowered reproductive success, and potential lost juvenile life-history diversity.	All adult strategies
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Reduced wood volume due to removal and alteration of riparian forest (reduced supply). Channel aggradation due to increased sediment delivery from historical and current logging, road construction & management, and fires.	Impaired staging habitats and increased pre-spawning mortality from predation.	All adult strategies
	Impaired fall pulse flows	Reduced or delayed fall stream flows due to water diversions or climate change.	Reduced spawning distribution and lowered reproductive success. Potential reduced juvenile life-history diversity in cohort.	Early migrating adults
	Increased prevalence of predation	Loss of escape cover and channel complexity due to reduced large wood volume and loss of deep pools.	Pre-spawning mortality	All adult strategies
	Increased prevalence of disease	Crowding cause by delayed fall stream flows; increased water temperatures due to diversion or climate change; other unknown drivers of disease prevalence and virulence.	Pre-spawning mortality	All adult strategies
	Poaching	Inadequate education and enforcement.	Pre-spawning mortality	All adult strategies
Spawning and incubation	Redd scour	Channelization and reduced substrate sorting; low flows during adult migration & spawning followed by high winter flows.	Reduced egg-to-fry survival	Early spawning adults
	Fine sediment infiltration of spawning substrates and redds	Landslides and erosion of fine sediment due to historical and current logging, road construction and management, and fires. Reduced sediment sorting due to channelization, floodplain disconnection, and lack of wood.	Reduced egg-to-fry survival	All adult strategies
	Increased prevalence of predation	Loss of escape cover and channel complexity due to reduced supply of large wood and loss of deep pools.	Pre-spawning mortality	All adult strategies
Juvenile rearing	Anthropogenic physical barriers to movement	Dams, poorly-designed or failed road crossings, tide gates, or other manmade obstructions to movement.	Reduced rearing habitat capacity and lowered survival due to lack of access to cold water refugia.	All juvenile strategies
	Reduced area of low-velocity instream winter rearing habitats in tributaries	Reduced wood volume and channel simplification from road construction. Loss of beaver dams.	Reduced winter rearing habitat capacity.	All juvenile strategies
	Impaired connectivity with and loss of riverine floodplain/off-channel rearing habitats	Channelization, channel incision, levees, bank armoring & roads, wetland draining & agricultural conversion, reduced wood volume, and loss of beaver dams.	Reduced winter rearing habitat capacity. Reduced juvenile growth and survival in winter. Reduced survival/prevalence of fall parr emigrant strategy.	All juvenile strategies
	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	Reduced growth and survival of early emigrant juveniles due to altered estuarine food webs, impaired WQ, lost access to off-channel habitats, and loss of escape cover.	Spring Fry Emigrant and Fall Parr Emigrant
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Reduced wood volume due to removal & supply. Channel aggradation due to increased sediment delivery from historical land uses & floods.	Reduced rearing summer and winter habitat capacity, reduced fry to smolt survival.	All juvenile strategies
	Impaired dry-season stream flows	Climate change, water diversion for rural agriculture and domestic use, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Restricted movement & stranding in poor WQ habitat due to sub-surface flows. Direct mortality due to poor WQ and predation. Reduced growth due to higher densities, less invert production and delivery from riffles.	Natal Stream Rearing, Fall Parr Emigrant
	Increased water temperatures	Loss or alteration of riparian forests, impaired dry-season stream flows (see below for drivers), climate change.	Reduced rearing habitat capacity due to restricted distribution. Chronic stress and reduced growth due to metabolic effects, increased pikeminnow predation and competition.	All juvenile strategies
	Reduced area of and restricted access to thermal refugia	Filling of thermally-stratified deep pools due to channel aggradation caused by sediment inputs from logging practices, road building and floods. Loss of connectivity with cold tributaries due to channel aggradation. Loss of complex cover at cold tributary confluences.	Reduced rearing habitat capacity due to restricted distribution. Direct mortality, Chronic stress and reduced growth due to metabolic effects, increased pikeminnow predation and competition.	Spring Fry Emigrant
	Elevated turbidity levels beyond reference state levels	Landslides and erosion of fine sediments due to historical and current logging, road construction & management, and geomorphic impacts of high intensity fires.	Reduced growth through impaired feeding in highly turbid locations during high-turbidity periods.	All juvenile strategies
	Increased prevalence of predation, especially from non-native predators	Sacramento Pikeminnow predation, loss of escape cover from larger wood and deep pools, decreased stream flows and increased water temperatures.	Reduced fry to smolt survival.	All juvenile strategies
	Introduced competitors and anthropogenic factors that increase vulnerability to them	Northern Coastal Roach and Sacramento Pikeminnow, increased water temperatures	Reduced growth and survival.	Spring Fry Emigrant and Fall Parr Emigrant
	Increased prevalence of disease	Reduced stream flows, increased temperatures, increased prevalence of alternate hosts	Reduced fry to smolt survival.	All
	Alterations to the timing, magnitude, and availability of food resources	Loss of marine-derived nutrients and other beneficial species interactions, presence of non-native pikeminnow in mainstem habitats, degraded riparian forests, and other ecological changes.	Reduced juvenile growth and survival and lost life-history diversity (reduced prevalence of strategies that historically relied on beneficial species interactions that have been lost)	All

Life stage	**Stressor**	**Drivers (underlying causes of stressor to be addressed by restoration)**	**Mechanisms of impact on population productivity, abundance, distribution, and resilience**	**Life-history strategies** potentially highly impacted
Smolt outmigration	Impaired spring recession flows	Climate change, water diversions, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Reduced smolt to ocean survival.	Spring Fry Emigrant and Natal Stream Rearing
	Increased prevalence of predation	Sacramento Pikeminnow predation, loss of escape cover from large wood and deep pools, decreased stream flows and increased water temperatures.	Reduced smolt to ocean survival.	All
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Reduced wood volume due to removal & supply. Channel aggradation due to increased sediment delivery from historical land uses & floods.	Reduced smolt to ocean survival due to loss of escape cover.	All
	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	Reduced smolt to ocean survival due to loss of escape cover.	All
Ocean residence	Ocean harvest or bycatch	Ocean fishing regulations and enforcement	Reduced smolt to adult survival; altered adult age structure and life-history diversity.	All
	Marine food web alterations	Climate change related influences on strength and timing of ocean upwelling, marine productivity, and the salmon prey species.	Reduced ocean growth and smolt to adult survival.	All

2.5.2 Restoration Take-home Points

The following central themes and focus points related to recovery of Coho Salmon in the Eel River watershed were identified during the development of the life-history conceptual models and through various internal and TAC discussions.

- Because of the importance of cold water for the persistence of Coho Salmon, identifying, protecting, restoring, and improving access to coldwater habitats across the watershed is imperative for protecting and restoring the species in the face of climate change. At the watershed-scale, these habitats include important coldwater tributaries, headwater streams, and estuarine habitats that can support the species through the summer during drought years. At smaller, within-reach scales, these habitats include thermal refugia in thermally-stratified pools, coldwater plumes associated with tributaries and springs, coldwater reaches associated with upstream hyporheic or sub-surface flows, and other anomalously cold habitats.
- The extensive and sometimes large-scale movements of juvenile Coho Salmon between varied rearing habitats suggests a system-wide approach to habitat is needed for maximizing production potential over time. While continued focus on protection and restoration of cold-water natal streams is imperative, it will be insufficient to recover Coho Salmon populations. Even when fully restored, the juvenile habitat capacity of natal streams is insufficient to produce the great abundance of returning adults that historically occurred in the Eel River. The life-history conceptual models illuminate the pressing need to expand efforts to protect and restore a mosaic of non-natal rearing habitats that provide variable conditions within and between years for early emigrant life-history strategies. Non-natal habitats with potential to provide seasonally productive rearing conditions and increased carrying capacity for Coho Salmon include (1) mainstem habitats; (2) off-channel ponds, beaver ponds, and wetlands along mainstem corridors (Petersen 1982, Soto et al. 2016); (3) perennial tributaries (Skeesick 1970, Stillwater Sciences 2023); (4) small, intermittent tributaries (Ebersole et al. 2006, Wigington et al. 2006); (5) large unconfined valleys, such as Little Lake Valley, that historically provided extensive winter rearing habitat (NMFS 2014); and (6) estuarine habitats such as tidal wetlands and sloughs (Miller and Sadro 2003, Koski 2009, Jones et al. 2014, Rebenack et al. 2015, Wallace et al. 2015). Not only is restoring these habitats critical – but ensuring that connectivity between these habitats is supported, consistent with the unaltered phenology and seasonality of each habitat, is also necessary.
- Restoration planning efforts should also prioritize restoring habitat at tributary confluences and improving connectivity between mainstems and the lower reaches of tributaries, which provide refugia from both high temperatures in the summer and high stream flows in the winter.
- Stream reaches that are not habitable by Coho Salmon during warmer, drier portions of the year can play significant roles in overall food production, fish growth and life-history diversity during cooler, wetter portions of the year (Armstrong et al. 2021). These reaches have largely been overlooked in efforts to restore Coho Salmon populations in the Eel River but have potential to provide high-quality rearing habitats during the wet season that contribute significantly to overall population abundance and resilience. Even small streams that become intermittent in the summer can provide excellent non-natal rearing and winter refuge habitat during the wet season (Skeesick 1970, Ebersole et al. 2006, Wiginton et al. 2006). For example, Ebersole et al. (2006) found high Coho Salmon overwinter survival and growth rates in a small tributary relative to adjacent mainstem reaches. In addition to providing winter rearing habitats, drier or intermittent streams (associated with Central

Belt mélange) can provide better conditions for rapid fry and juvenile growth during the spring relative to cold perennial streams (associated with Coastal Belt turbidites) because of their quicker rate of flow recession and warmer water temperatures during that season, which are driven by differences in underlying geology (Dralle et al. 2023).

- Restoration of the estuary and the stream-estuary ecotone are essential for restoring life-history diversity and recovering Coho Salmon populations throughout the watershed. These areas play an outsized role in influencing growth, survival, and population dynamics, since entire populations must pass through them, first as juveniles and then as adults. Studies have shown that favorable growth conditions in estuaries can enable juvenile Coho Salmon to recruit disproportionately to the adult population compared with fish that rear in upstream habitats, because larger individuals typically have higher ocean survival rates (Holtby et al. 1990, Miller and Sadro 2003, Bond et al. 2008, Koski 2009, Jones et al. 2014). Moreover, restoration of estuaries has been shown to increase salmonid life-history diversity. For example, extensive restoration of estuarine tidal wetlands in the Salmon River in Oregon increased variation in Coho Salmon juvenile rearing strategies, enhancing the species' overall life-history diversity and resilience in the watershed (Flitcroft et al. 2016).
- Restoring and protecting the lower reaches of the mainstem Eel, South Fork Eel, and Van Duzen rivers—along with adjacent off-channel habitats and the lower reaches of their tributaries—are also critically important for Coho Salmon recovery. In addition to providing important habitat for migrating adults and out-migrating juveniles, these reaches have potential to provide large areas of non-natal rearing habitat. Along mainstem river corridors, low-velocity winter rearing habitats may occur in floodplain channels with ponded features or off-channel ponds connected to the mainstem by small channels (Soto et al. 2016). Low-gradient tributaries entering the lower mainstems of the Eel, South Fork Eel, Van Duzen rivers (e.g., Price, Strongs, and Barber creeks) are expected to have particularly high potential to provide valuable non-natal rearing habitats for early emigrant life-history strategies during both the dry and wet seasons. For this reason, assessing and restoring habitat in and connectivity to these streams is important for increasing the prevalence of early emigrant strategies.
- Large unconfined, inland valleys, which are rare in the watershed and have been severely altered by agricultural and urban development, may have historically provided highly-productive habitat for Coho Salmon and contributed unique life-history strategies to the Eel River watershed. Because of the high potential of these valleys to provide large areas of quality habitat for Coho Salmon and the other focal species, focused planning assessments are needed to identify restoration opportunities and help re-establish robust Coho populations in them. These valleys include Little Lake Valley/Outlet Creek, upper Ten Mile Creek, Round Valley, and Gravelly Valley in the upper Eel River (once the Potter Valley Project is decommissioned).
- Mortality during movements by early emigrant life histories as well as smolts from natal streams is likely an important factor limiting the population and warrants more research and attention. Preliminary results from a 2023 acoustic telemetry study evaluating survival of Coho Salmon smolt emigrating from natal streams through the mainstem South Fork Eel River during the spring found average survival (across tag groups from different streams) was about 20% (G. Rossi, U.C. Berkeley pers. comm., 2024). This high mortality rate may be due largely to predation by non-native Sacramento Pikeminnow and native predatory birds. The impact of predation is likely exacerbated by habitat degradation in of much of the lower mainstems of the Eel, South Fork, and Van Duzen rivers due to highway and levee construction, sediment deposition from logging and large floods, and reduced supply of large wood. Predation and competition from the large numbers of pikeminnow

inhabiting mainstem reaches are also hypothesized to exert strong selective pressures against early emigrating life-history strategies. For these reasons, in addition to restoration actions that improve habitat complexity in mainstems reaches, efforts to suppress the pikeminnow population should be part of a multi-faceted restoration program in the Eel River.

- Beaver dams and associated ponds, bank lodges, side channels, and burrows can create large areas of prime summer and winter rearing habitat for juvenile Coho and other native (Swales et al. 1986, Pollock et al. 2004, Parish 2016). For example, during the winter, juvenile Coho Salmon rearing within side channels created by beaver dams occur at higher densities and have higher growth and survival rates than individuals rearing within side channels without beaver dams (Bustard and Narver 1975, Swales et al. 1986). Beaver dams can also reduce water velocities during high-flow events, providing winter refuge habitat for Coho Salmon and other species (Pollock et al. 2003, Lundquist and Dolman 2020). By slowing and spreading out stream flows, beaver dams also create wetlands and promote groundwater recharge that can enhance summer base flows and fish habitats in downstream reaches (Lundquist and Dolman 2020, Dewey et al. 2022). For these reasons, reintroducing beavers in suitable locations where they have been locally extirpated is a promising strategy for restoring Coho Salmon populations in the Eel River watershed.
- Restoring food subsidies (and the habitat conditions which facilitate them) which supported a diversity of Coho Salmon life histories in the Eel River is also an important restoration goal. Throughout much of their range, juvenile Coho Salmon have been shown to depend on pulsed marine subsidies provided by sympatric populations of Pacific salmon (Fizgerald et al. 2023). These subsidies include nutrients derived from salmon carcasses (Kaylor et al. 2019) and salmon eggs (Armstrong 2010, Armstrong et al. 2016, Scheuerell et al. 2007, Fitzgerald et al. 2023). Egg subsidies, in particular, can account for the majority of summer growth in some populations (Scheuerell et al. 2007. Other critical prey subsidies could include lamprey eggs and carcasses, and larval fish, such as juvenile Pacific Sand Lance, smelt, and Pacific Herring, in estuarine and near shore habitats (Duffy et al. 2010). In some temperature limited systems, these food subsidies may be the basis for the persistence of Coho Salmon (Fitzgerald et al. 2023).

2.5.3 Key Data Gaps

Various gaps in understanding of distribution, life-history, and abundance of Coho Salmon in the Eel River watershed were identified through development of this species review and conceptual model. Since these data gaps may limit effective management and restoration of the species, conducting research and monitoring to fill them is integral to recovery. Key data gaps include:

- Current prevalence and distribution of early emigrant life-history strategies in non-natal rearing habitats within and between years with variable environmental conditions—including in mainstems, adjacent off-channel habitats, warm and cool non-natal tributaries, and the estuary.
- Historical prevalence and distribution of juvenile life-history strategies.
- Distribution and habitat use during the fall, winter, and spring seasons.
- Timing of movements between natal streams and non-natal rearing habitats and survival during these movements.
- Duration of estuarine rearing and movements and habitat use within the estuary.
- Use of thermal refugia in mainstems.
- Seasonal movements within natal streams, including upstream movements.

- Current occurrence and abundance in inland watersheds with high intrinsic potential and cool water, where the species may have been historically present or abundant, but where monitoring is insufficient to document. Specifically, Outlook Creek, Tomki Creek watersheds, and the Mill Creek drainage in the Middle Fork Eel sub-watershed.
- Smolt production from important spawning streams/watersheds.
- Juvenile survival and its variability across time and space. Estimating survival during juvenile summer rearing, winter rearing, and smolt emigration for different life-history strategies and natal watersheds and conducting studies to understand the mechanisms of mortality are critical for identifying and prioritizing effective restoration actions.
- Impacts of pikeminnow predation and presence and how these impacts vary spatially and temporally.
- Spatial, seasonal, and interannual variation in physiological growth potential (bioenergetics) and food resources. Influence of restoration on these factors.
- Ocean survival and influences of ocean conditions, prey composition and abundance, harvest management practices, and bycatch from other fisheries.

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3 STEELHEAD

Oncorhynchus mykiss (*O. mykiss*) are considered the most flexible salmonid species, both behaviorally and physiologically, in the Eel River watershed. *O. mykiss* exhibit a diverse array of juvenile rearing and adult maturation/migration strategies (Shapovalov and Taft 1954, Kendall et al. 2015, Moore et al. 2014). The adult strategies differ in protected status, distribution, and migration timing, so are introduced briefly here. There are three primary strategies for timing and location of maturation in the Eel River: resident Rainbow Trout, winter-run steelhead, and summer-run steelhead. Resident Rainbow Trout complete their entire lifecycle in freshwater, often in or near their natal stream. Winter-run steelhead migrate to the ocean as juveniles, spend one or more years at sea, and then return to freshwater in the winter as reproductively mature adults to spawn. Summer-run steelhead also migrate to the ocean as juveniles but return to freshwater earlier in the year—typically between late spring and summer—as reproductively immature adults (a strategy called "premature migration"). Summer-run adults remain in freshwater while maturing and then spawn in the winter. In addition to these three primary run-timings, the adult steelhead population includes a potentially distinct "fall-run" component (akin to that described in the Klamath River) (Roelofs 1983). Fall-run adults are thought to enter freshwater in late summer or early fall and hold in the lower Eel River until rainstorms facilitate upstream movement into spawning reaches in late fall and winter. Unlike salmon, steelhead are iteroparous; some individuals return to the ocean after spawning as "kelts," and may return to fresh water the following winter to breed again.

3.1 Population Status

Steelhead in the Eel River watershed fall within the Northern California DPS, which is listed as threatened under the federal ESA (NMFS 2006). Steelhead populations in the Lower Main Eel and South Fork Eel sub-watersheds are included in the North Coastal Diversity Stratum, populations in the Middle Main Eel River sub-watershed are included in the Lower Interior Diversity Stratum, and populations in the Van Duzen, North Fork Eel, and Middle Fork Eel sub-watersheds (and accessible portions of the Upper Main Eel sub-watershed) are included in the North Mountain Interior Diversity Stratum. Winter-run and summer-run steelhead are not considered separate listing entities under the federal ESA (NMFS 2020), but summer-run in the Middle Fork Eel River were described as "moderate" risk of extinction, with little known about population numbers in other sub-watersheds in the Eel River (Spence et al. 2008). In contrast, summer-run steelhead in the Northern California DPS are listed as endangered under the CESA, while winter-run steelhead are not listed (CFGC 2022). Fall-run steelhead are not provided separate protection. Non-anadromous Rainbow Trout are not currently considered a separate listing entity, despite freely interbreeding with steelhead in streams where they co-occur (Harvey et al. 2021). However, any *O. mykiss* occurring downstream of impassable barriers in the Eel River have the potential to be anadromous and thus are afforded the associated statutory protections.

3.2 Distribution

The distribution of winter-run steelhead, summer-run steelhead, and resident Rainbow Trout within the Eel River watershed are discussed in detail below.

3.2.1 Winter-run steelhead

Winter-run steelhead have the broadest spatial distribution of any anadromous salmonid in the Eel River. The estimated overall distribution of winter-run steelhead in the Eel River watershed is illustrated in Figure 3-3, based on BIOS spatial data. The dataset, generated in 2012, represents stream reaches that are known or believed to be used by winter-run steelhead, but does not necessarily include all streams or the upper extents of channels where the ecotype may be present. Additionally, the distribution of adult spawning and juvenile rearing within the watershed likely varies between years depending on the timing and magnitude of fall rains, size of the total adult spawning population, and summer stream flows (Kelson et al. 2020).

Observations of live adult steelhead and carcasses from the California Department of Fish and Wildlife's (CDFW) spawning surveys conducted 2010–2021 (Guczek et al. 2020, CDFW unpubl. data, 2010–2021) and various historical observations of juveniles (Becker and Reining 2009, CDFW 2014, CDFW unpubl. data 1939–1941) are generally consistent with the distribution shown in Figure 3-3. However, spawning has been documented in several streams not shown, for example, the South Fork Salmon, Dean, and Cahto creeks in the South Fork Eel sub-watershed.

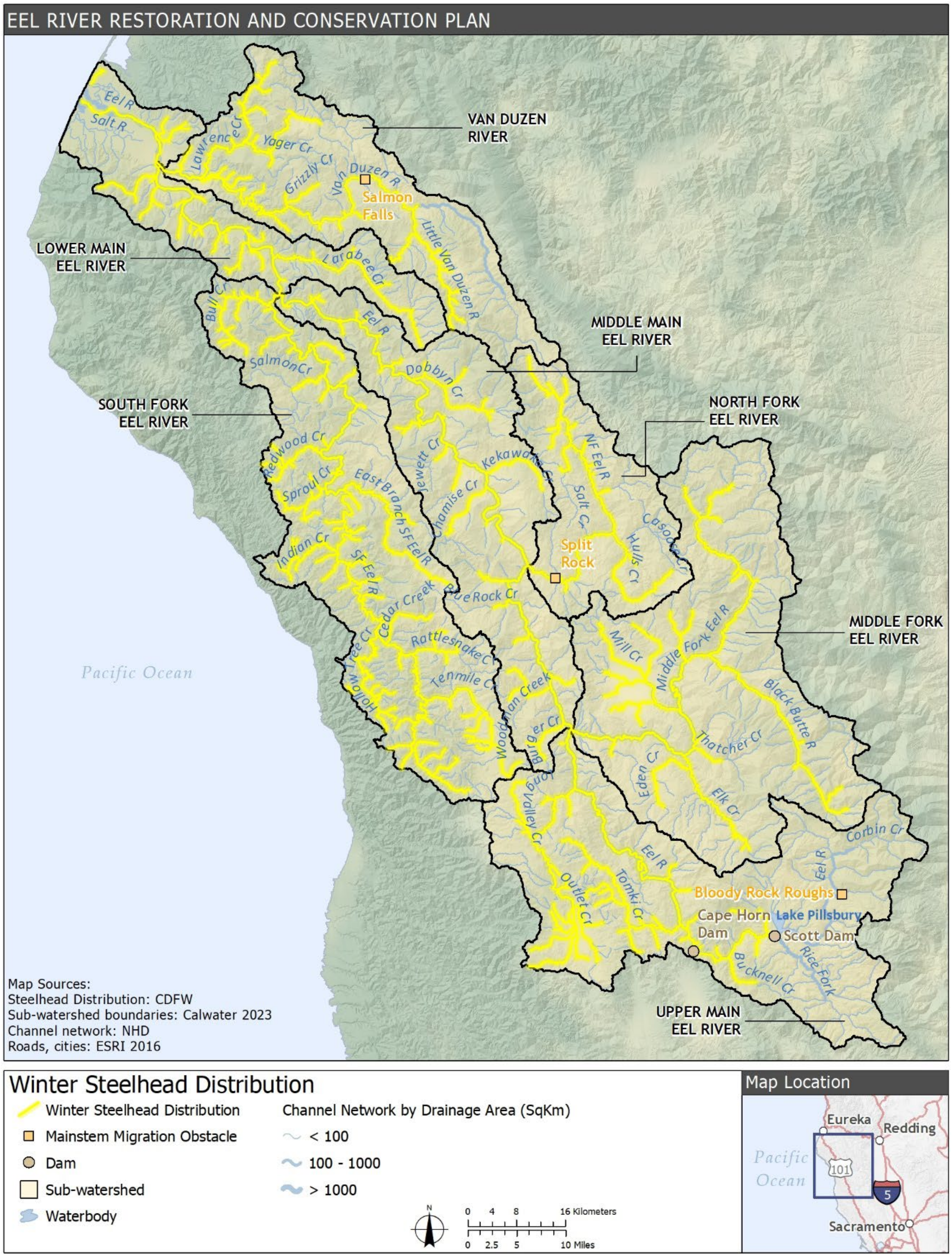

Figure 3-1. Suspected distribution of winter-run steelhead in the Eel River watershed. Data source: California Department of Fish and Wildlife's Biogeographic Information and Observation System.

3.2.2 Summer-run and fall-run steelhead

Summer-run steelhead in the Eel River watershed are primarily found in the Van Duzen River and Middle Fork Eel River (Figure 3-4), which host genetically distinct sub-populations (Kannry et al. 2020). The distribution of the summer-run is restricted relative to the winter-run, largely due to the relative scarcity of habitat needed to support over-summering and holding of premature adults (see Section 3.2). While there is some overlap in the distribution of the summer-run and winter-run steelhead, differences in the stream flows during each ecotype's core migration period generally result in spatial segregation, with summer-run steelhead mostly spawning upstream of flow-dependent barriers are more consistently passage in the snowmelt recession than winter storm flows (Kannry et al. 2020).

Genetic evidence and anecdotal historical accounts suggest the distribution of the summer-run ecotype in the larger watershed has contracted in recent decades (Moyle 2002, Yoshiyama and Moyle 2010, CDFW 2019, Kannry et al. 2020). While summer-run steelhead were observed in the North Fork Eel River downstream of Split Rock in the 1990s, the population may have since been extirpated (Yoshiyama and Moyle 2010, CDFW 2019). Summer-run steelhead also historically spawned in thermally suitable reaches of the upper mainstem Eel River prior to the construction of Scott Dam, and the allele associated with premature migration (called "GREB 1L") is still maintained in the remnant resident Rainbow Trout population. In contrast, while there are some historical accounts of adult steelhead over-summering in the South Fork Eel River prior to major floods in the mid-twentieth century (Jones 1992, Kannry et al. 2020), steelhead in the South Fork Eel River do not currently exhibit premature migration or carry the GREB 1L allele (Kannry et al. 2020). Portions of the upper South Fork Eel River appear to contain suitable adult over-summer holding habitat needed to support the summer-run ecotype but lack the steep, boulder roughs or waterfalls that typically segregate winter-run and summer-run steelhead in the other Eel River sub-watersheds (Trush 1991, Kannry et al. 2020). The headwaters of the South Fork Eel River also have minimal winter snowpack and less-consistent spring flows relative to other streams where summer-run steelhead occur (Kannry et al. 2020). Lack of observation of the summer-run ecotype during historical adult salmonid counts at Benbow Dam (CDFW unpubl. data 1939–1941) further suggests that the ecotype was either not historically present, or at least extremely rare, in the sub-watershed. Summer-run steelhead may have also once spawned in Larabee Creek, Black Butte Creek, and Woodman Creek, but these sub-populations have also likely been extirpated (Jones 1992, Moyle 2002). There are various other tributaries where adult holding and spawning could occur that are not shown in Figure 3-4, such as the North Middle Fork Eel River.

The distribution of fall-run steelhead has not been documented separately from the other run timings. Given that it is not always considered a strategy that is unique from the summer-run ecotype, its historical distribution was likely similar to that of the summer-run (Roelofs 1983).

Figure 3-2. Suspected distribution of summer-run steelhead in the Eel River watershed. Data source: California Department of Fish and Wildlife's Biogeographic Information and Observation System.

3.2.3 Resident Rainbow Trout

Rainbow Trout are likely the most widespread fish in the Eel River but are not always distinguished or noted separately from the other ecotypes. For this reason, there is not a separate distribution map for Rainbow Trout. Patterns in the prevalence of residency varies greatly between watersheds and over time, reflecting complex interactions between genetic and environmental factors that influence whether individuals smolt or remain as residents (Satterthwaite et al. 2009, Sloat and Reeves 2014, Kendall et al. 2015, Kelson et al. 2020). Residency is often presumed to be more prevalent in locations where anadromy is not a viable life-history strategy, such as above impassable barriers to migration (Moyle et al. 2017). Indeed, resident Rainbow Trout populations persist upstream of man-made barriers in the Eel River watershed that restrict access to historical steelhead spawning habitat, such as Scott Dam. However, recent evidence also suggests that resident Rainbow Trout are widely distributed throughout the larger watershed downstream of such barriers (Harvey et al. 2021). Further, resident females appear to make substantial contributions to the persistence of anadromous population components (Harvey et al. 2021).

3.3 Ecology, Life-history, and Habitat Needs

3.3.1 Life-history Timing Overview

Across their numerous life histories, *O. mykiss* spend the most time in freshwater of the anadromous salmonids in the Eel River, with juvenile steelhead rearing year-round and resident Rainbow Trout remaining in freshwater throughout their lives (Table 3-1). Critical periods of movement (i.e., down- and upstream migrations) for steelhead tend to coincide with periods of elevated streamflow, at different times of year depending on ecotype and life stage.

The generalized life-history timing for each steelhead ecotype and life stage in the Eel River watershed is presented in Table 3-1. This information is based primarily on observations from the watershed but also includes references to other watersheds where more extensive monitoring has been conducted. A more detailed description of each life stage and its timing is provided below.

Table 3-1. Generalized life-history timing of steelhead runs in the South Fork Eel River watershed.

Life stage		Month											
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Winter-run	Adult migration[1,2,3]	▓	▓	▓	░	░						░	░
	Spawning[2,3,4]	▓	▓	▓	░	░							░
Summer-run	Adult migration[4,5,6]			░	▓	▓	░						
	Holding[6,7,8]						░	░	░	░	░		
	Spawning[6,7,8]	▓	▓	▓	░								░
Fall-run	Adult entry and holding in lower mainstem[7,9,10]							░	░	░	░		
	Upstream movement & spawning[11]	▓	▓	▓	░						░	░	░
Adult post-spawn outmigration (kelt)[1,12]			░	▓	▓	░	░						
Half-pounder residence[5, 7,13]		░	░	░				▓	▓	▓	▓	░	░
Incubation[8,15,16,17]		░	░	░	░	░	░						░
Juvenile rearing[8,15]		░	░	░	░	░	░	░	░	░	░	░	░
Juvenile redistribution[16,17,18]								▓	░	░	▓	▓	░
Smolt outmigration[16,17,18,19,20]			░	░	▓	▓	▓	░	░				

░ = Span of activity
▓ = Peak of activity

[1] CDFG unpubl. Benbow Dam adult count data, 1938–1976
[2] Guczek et al. (2020); CDFW unpubl. data, 2010–2021
[3] Trush (1991)
[4] Busby et al. (1996)
[5] Everest (1973)
[6] Moyle et al. (2017)
[7] Roelofs (1983)
[8] Barnhart (1991)
[9] Kajtaniak and Gruver (2020)
[10] Hodge et al. (2014)
[11] Roelofs et al. (1993)
[12] Teo et al. (2013)
[13] Kesner and Barnhart (1972)
[14] Murphy and Dewitt (1951)
[15] Shapovalov and Taft (1954)
[16] MRC (2002)
[17] Vaughn (2005)
[18] Kelson and Carlson (2019)
[19] Maahs (1995)
[20] CDFG unpubl. Benbow Dam outmigrant trapping data, 1939

3.3.2 Adult Migration Timing

The timing of adult migration differs among the ecotypes in the Eel River watershed. Winter-run steelhead in the Eel River migrate upstream in the winter and spring during California's wet season (November to April), with migration typically peaking in February.

Summer-run steelhead initially enter freshwater and migrate upstream during the snow melt period between April and late June, as sexually immature adults (Everest 1973, Busby et al. 1996, Moyle et al. 2017) (Table 3-3). Once they arrive to cool headwater reaches, summer-run steelhead spend the summer and early fall holding in deep, thermally suitable pools (Everest 1973, Roelofs 1983, Barnhart 1991, Moyle et al. 2017). Summer-run steelhead migrate further upstream again in late fall and winter rain events into spawning streams (Everest 1973).

Fall-run adults enter the lower mainstem from mid-summer through early fall (Roelofs 1983, Hopelain 1998). These individuals generally stage downstream of the Van Duzen River and move upstream after the arrival of fall freshets. The fall-run is not always considered a separate ecotype from the summer-run strategy, given that its migration timing coincides with the tail of the distribution for summer-run adults.

Kelt, or post-spawned adults, generally tend to migrate downstream to the ocean relatively rapidly after spawning, with peak downstream migration occurring in March and April (Teo et al. 2013, Moyle et al. 2017). In spawning tributaries to the upper South Fork Eel River, Trush (1991) found that individual winter steelhead typically entered, spawned, and moved back downstream within 1–2 weeks, with males remaining longer than females. Historical observations from the Benbow Dam fish counting station indicated kelts moved downstream through the mainstem South Fork Eel River between early February and mid-June, with apparent peak movement in March and April (CDFG unpubl. data, 1938–1976).

3.3.3 Spawning and Incubation

Despite entering freshwater at different times of year and at varying stages of sexual maturity, winter-run, summer-run, and fall-run steelhead all generally spawn between December and May, with peak spawning typically occurring from January through March (Busby et al. 1996; Guczek et al. 2020; CDFW unpubl. data, 2010–2021). In general, steelhead spawn primarily in tributary streams, many of which are perennial, though some of which become intermittent or go dry in the summer (Everest 1973). Mainstem spawning has been observed in years when tributary access is restricted due to lack of winter and spring storm events (Trush 1991). All steelhead ecotypes are capable of spawning multiple times throughout their lives and repeat spawners have been identified in the South Fork Eel, Middle Fork Eel, and Van Duzen River sub-watersheds (Puckett 1975, Trush 1991). However, the precise incidence of repeat spawning varies between watersheds and has not been thoroughly investigated in the Eel River.

Resident Rainbow Trout in coastal California streams also spawn in the spring, between February and June (Moyle 20002). Resident adults will readily interbreed with anadromous adults and can produce both anadromous and resident offspring (Harvey et al. 2021). The age and corresponding size at which resident Rainbow Trout spawn depends on local growth potential (Moyle 2002) and has not been described for populations in the Eel River. In general, coastal Rainbow Trout mature by age two or three and may spawn multiple times throughout their lives (Moyle 2002).

Steelhead eggs incubate in redds for 3–14 weeks after fertilization, depending on water temperatures (Shapovalov and Taft 1954, Barnhart 1986, Barnhart 1991). Steelhead eggs can likely tolerate a wide range of temperatures (0–24°C), with the optimum temperatures close to 10°C (Bovee 1978). After hatching, alevins remain in the gravel for an additional 2–5 weeks while absorbing their yolk sacs, and then emerge in spring or early summer (Barnhart 1991). Based on the timing of spawning, the typical incubation period, and when newly emerged fry have been captured during outmigrant trapping, developing steelhead eggs or alevin may be present in spawning gravels from approximately December through June (MRC 2002, Vaughn 2005).

3.3.4 Juvenile Rearing

Juvenile steelhead in the Eel River watershed display a diversity of life-history strategies and movement patterns, with multiple age classes utilizing a variety of habitats in cool headwater spawning tributaries, non-natal tributaries, mainstem corridors, and the estuary (Puckett 1977, Nielson et al. 1994, Kelson and Carlson 2019, Kelson et al. 2020, Georgakakos 2020, Wang et al. 2020). The full array of juvenile steelhead life-history strategies and their relative prevalence across space and time has not been empirically described. Several strategies that have been observed in the Eel River are described in detail below (Section 3.5.2).

After emerging from spawning gravels, steelhead fry generally occupy shallow, low-velocity habitats such as stream margins or off-channel habitats (Hartman 1965). As fry grow and improve their swimming ability throughout the summer and fall, they are increasingly associated with faster water velocities and deeper habitats that contain cover such as cobble and boulders (Hartman 1965, Everest and Chapman 1972).

Juvenile steelhead require cool water temperatures to grow and survive. Acceptable temperatures for growth are typically between 11-22°C (Myrick and Cech 2001, Richter and Kolmes 2005), with optimal growth occurring from 19-20.5 °C (Zillig et al. 2018). At temperatures above 22°C steelhead typically move into coldwater refugia (Sutton et al. 2007, Brewitt and Danner 2014, Wang et al. 2020). Mean weekly average temperatures below 24°C provide growth within 20% of maximum, and maximum instantaneous lethal exposure temperature is estimated at 26°C (Carter 2005).

Juvenile rearing occurs throughout the range of drainage areas in the Eel River. In the summer, water temperatures are an important quality for suitable rearing habitat. Many perennial tributaries provide thermally suitable habitat for juvenile rearing in the summer, and juvenile steelhead also make use of intermittent tributaries in the inland sub-watersheds (e.g., Middle Fork Eel). Tributaries also likely provide shelter from high flow events in the winter throughout the watershed. The mainstem Eel River and other major forks regularly exceed temperature thresholds associated with reduced growth, fitness, or mortality (Kubicek 1977). Thus, summer rearing in large mainstems is most common where cold-water inputs create thermal microrefugia, such as stratified pools (Nielson et al. 1994), tributary confluences (Wang et al. 2020), or habitats with cold hyporheic upwelling flows.

Juvenile steelhead have also been captured in the lower mainstem and upper estuary during most months of the year (Murphy and De Witt 1951, Puckett 1977, Cannata and Hassler 1995), suggesting that the estuary-ecotone is an important rearing habitat. Historical sampling indicates that juvenile steelhead were abundant in the Eel River estuary from mid-May through mid-July (Murphy and De Witt 1951). During sampling conducted at sites in the Eel River estuary throughout the 1974 water year, Puckett (1977) captured juvenile steelhead during all months and at numerous sites across the estuary. Subsequent sampling by Cannata and Hassler (1995) indicated greatest utilization of the estuary by juvenile steelhead during the summer and early fall months. Multiple age classes (age-0, age-1, and age-2) of juvenile steelhead were documented utilizing portions of the estuary for rearing, but age-0 and age-1 were present during the most months (Puckett 1977). Duration and spatial distribution of estuary utilization by juvenile steelhead requires additional research due to the importance of this part of the watershed for the South Fork Eel River steelhead population.

Juvenile steelhead in northern California spend 1–3 years rearing in freshwater before emigrating to the ocean. Age at emigration varies by location and is largely driven by environmental conditions that influence growth rate in early life (Brown 1990, Hopelain 1998, Kendall et al. 2015, Moyle et al. 2017). For example, in the upper mainstem sub-watershed, individuals can rear in tributaries for 2 or 3 years before emigrating, whereas individuals rearing in the mainstem Eel River below Scott Dam may emigrate after a single year due to enhanced growth conditions (SEC 1998). Similarly, analyses of scales collected from adult summer-run steelhead suggests most individuals in the Van Duzen emigrated after rearing for single year, whereas juveniles in the Middle Fork Eel River reared for 1 to 3 years before emigrating (Puckett 1975), and juvenile winter-run steelhead in the South Fork Eel River typically reared in freshwater for 2 years (Trush 1991).

3.3.5 Juvenile Downstream Movement

Juvenile downstream movement of *O. mykiss* includes juvenile re-distribution within freshwater and smolts on their way to the ocean. Outmigrant monitoring conducted in the spring and early summer in tributaries to the South Fork Eel River has documented downstream movement of both age-0 (YOY) and age-1+ steelhead (Puckett 1976, Maahs 1995, PCFFA 1988, MRC 2002, Vaughn 2005, Kelson and Carlson 2019). Based on available length data, many of the age-0 individuals are likely moving downstream soon after emerging from redd gravels and are likely redistributing from upstream spawning areas to larger tributary channels, mainstem habitats, and/or the estuary. These age-0 migrants were historically the most numerous size/age class to be moving in the spring (Puckett 1976). Age-1 and older juveniles can also move moving downstream, potentially to rear in the mainstem, non-natal tributaries, or the estuary, and larger age-2 juveniles are likely beginning to smolt and migrate to the ocean. Salmonid smolt outmigrant trapping data from the upper Eel River indicate that steelhead smolt outmigration generally occurs from March through mid-June and peaks in April and May (VTN 1982, Beak Consultants Inc. 1986, SEC 1998).

While most downstream movement of juvenile steelhead appears to occur in the spring and summer, they may move throughout the year (Puckett 1976, Brown 1990, Roelofs et al. 1993). In 1 year, Kelson and Carlson (2019) documented smaller numbers of juvenile steelhead moving downstream in Elder Creek (tributary to the South Fork Eel River) after pulse-flow events in the fall, a period not typically included in other outmigrant monitoring efforts. Non-spring movements of juvenile steelhead in the watershed warrant additional research due to the potential role of these life-history variants in increasing population resiliency.

Available evidence suggests that juvenile steelhead downstream movements through the mainstem South Fork Eel River (CDFG unpubl. data, 1938-1976; Roelofs et al. 1993; Stillwater Sciences 2022;) likely peak approximately 1–3 months after emigration from tributaries (Maahs 1995, MRC 2002, Vaughn 2005, Kelson and Carlson 2019), indicating that a portion of the juvenile population likely spends up to several months rearing in the mainstem after leaving tributaries. Limited mainstem trapping from Benbow Dam in 1939 documented downstream movement of juvenile steelhead (primary age-1 and older) in the mainstem South Fork Eel River from the initiation of trapping in early April through mid-August (CDFG unpubl. data, 1938-1976; Stillwater Sciences 2022). Peak capture at Benbow was in June, with over 75% of annual captures by late-June and 90% by mid-July. Notably, however, there was a significant gap in trapping from May 18–25. A subset of juvenile steelhead captured at Benbow Dam were measured in late April and again in late July (CDFG unpubl. data, 1938-1976; Stillwater Sciences 2022). Late April lengths ranged from approximately 75–185 mm and most individuals were >120 mm, indicating the early component of the trapped population were primarily age-1 or older. Late July lengths ranged from 50–250 mm, indicating the likely presence of age-0, age-1, and age-2 individuals in the catch. More recent mainstem outmigrant trapping conducted at multiple sites in the vicinity of Benbow in 1993 (a year with relatively high flows and low water temperatures) found considerable movement of age-0 steelhead in the mainstem through July and age-1 and older steelhead through August (Roelofs et al. 1993).

3.3.6 Ocean Residence

Steelhead in Northern California typically spend 1 to 3 years in the ocean before spawning for the first time (Moyle 2002), with most individuals first spawning after 2 years in salt water. This pattern appears to hold true in the Eel River watershed; scale samples collected from adult winter-run steelhead in the South Fork Eel River (Beach 1972 as cited in Trush 1991) and summer-run steelhead in the Van Duzen and Middle Fork Eel rivers (Puckett 1975) suggest most individuals spent 1 or 2 years in the ocean before spawning, while very few spent 3 years in the ocean. Several of the fish sampled in each population were repeat spawners, having spent one or more additional years in the ocean between spawning migrations.

3.4 Life-history Diversity Conceptual Models

O. mykiss display extensive diversity in movement timing and habitat use as both juveniles and adults. Here, we describe the diversity of juvenile and adult strategies separately, to highlight diversity in spatial and temporal use of habitats throughout the watershed in each life stage. Even though they are separated here, we acknowledge that adult strategies influence juvenile strategies, as the timing and location of spawning influences incubation length, emergence timing, and early life-history growth potential.

3.4.1 Steelhead Adult Life-history Strategies

Adult steelhead in the Eel River watershed exhibit several distinct life-history strategies (also referred to as ecotypes or run-times) that vary in the seasonal timing of arrival to freshwater and state of maturity. These adult life-history strategies and their movement and timing throughout the watershed are visualized below in Figure 3-3 and are catalogued in Table 3-2. Additionally, documentation and prevalence of these strategies in the Eel River watershed are described in further detail below (Sections 3.5.1.1–3.5.1.3). Within these fundamental strategies there is considerable variation between individuals in age at return to freshwater and propensity to out-migrate and spawn again in subsequent years. In general, genetically ingrained predispositions for run-timing interact with interannual hydrologic variation, and possibly other environmental factors, to influence the distribution of holding and spawning locations utilized by individuals each year, which in turn impacts fry emergence location and may influence juvenile growth, survival, and the expression of early life-history strategies.

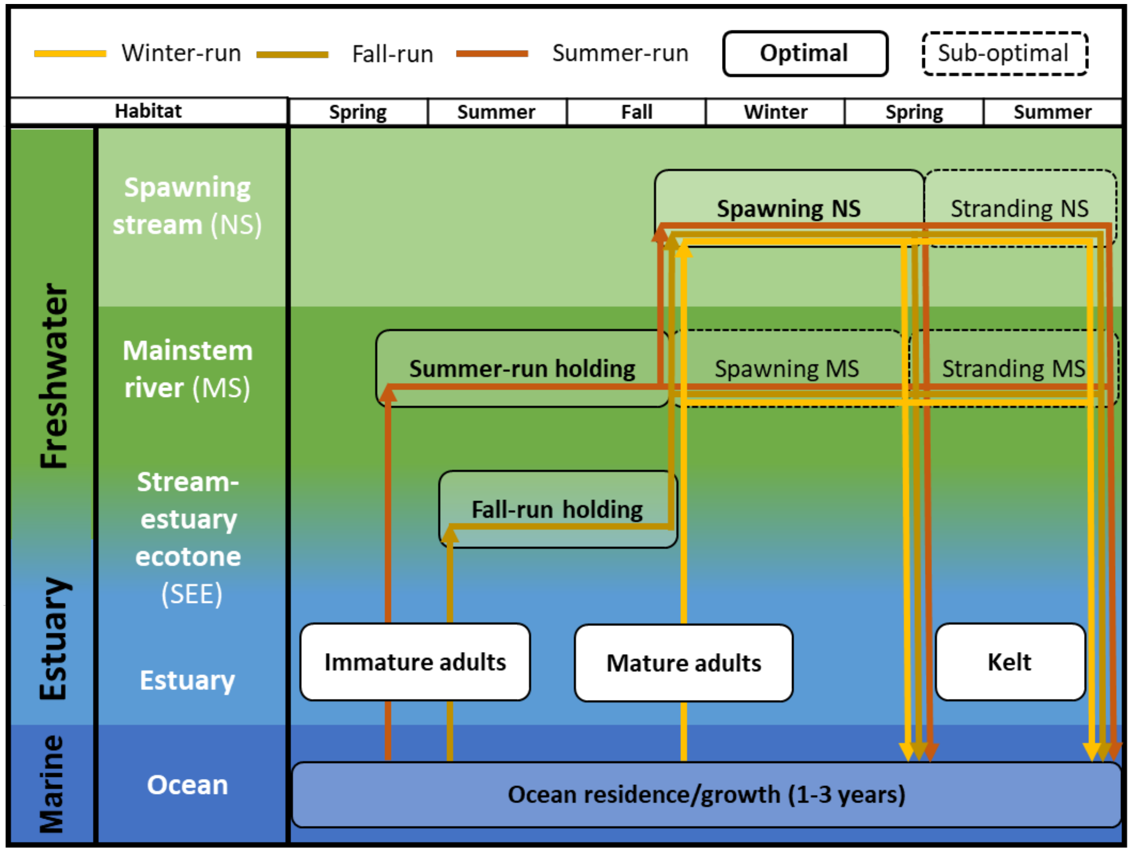

Figure 3-3. Diversity in adult life-history strategies and run timing in *O. mykiss*.

Table 3-2. Adult life-history strategies in *O. mykiss* organized by timing of entry into freshwater and state of maturity.

Strategy	Variant	Description of behavior	Variation within strategy	Occurs in Eel River	Trade-offs and stressors	Citations
Resident	N/A	Remains in freshwater, rearing and reaching sexual maturity between ages 2 and 3. Spawns in late winter and spring. May interbreed with anadromous steelhead. May spawn multiple times throughout lifespan before dying	Movement within and between freshwater and estuarine habitats	Yes	Lower risk of predation and reduced growth potential/fecundity (especially for females) in freshwater compared to the marine environment. Require high quality freshwater rearing habitats for several consecutive years.	Harvey et al. 2021, Moyle 2002
Summer-run	One year ocean growth	Begins first spawning migration at age 2–4 after 1 year of feeding and growth in the ocean. Enters freshwater in late spring in sexually immature state, holds in thermally suitable habitat in upper reaches until elevated streamflows allow access to spawning habitat in late fall or winter. May out-migrate and spawn again.	Age at first spawn varies based on smolt age and duration of ocean residence. Spawning location varies based on natal origin and the timing and magnitude of wet season precipitation relative to timing of arrival to freshwater. Fecundity presumed to increase with age and size. Some individuals may outmigrate to the ocean (kelt) and return in subsequent year(s) to spawn, while others may die after spawning once	Yes	Premature migration allows adults to exploit spawning habitats that are inaccessible during the winter (i.e., above flow-dependent barriers), but this strategy needs elevated streamflows two times in the year (snowmelt runoff and winter peaks) to reach ideal spawning grounds. Over-summer holding is energetically costly, and stressors include lack of holding habitats with suitable water quality. Fecundity generally increases with size, but individuals face higher risk of predation in the marine environment.	Puckett 1975, Roelofs 1983, Yoshiyama and Moyle 2010, Moyle et al. 2017
	Two years ocean growth	Begins first spawning migration at age 3–5 after 2 years of feeding and growth in the ocean. Enters freshwater in late spring in sexually immature state, holds in thermally suitable habitat in upper reaches until elevated streamflows allow access to spawning habitat in late fall or winter. May out-migrate and spawn again.		Yes		Puckett 1975, Roelofs 1983, Yoshiyama and Moyle 2010, Moyle et al. 2017
	Three years ocean growth	Begins first spawning migration at age 4–6 after 3 years of feeding and growth in the ocean. Enters freshwater in late spring in sexually immature state, holds in thermally suitable habitat in upper reaches until elevated streamflows allow access to spawning habitat in late fall or winter. May out-migrate and spawn again.		Unknown		Puckett 1975, Roelofs 1983, Yoshiyama and Moyle 2010, Moyle et al. 2017
Winter-run	One year ocean growth	Begins first spawning migration at age 2–4 after 1 year of feeding and growth in the ocean. Enters freshwater in fall or winter in sexually mature state, travels directly to accessible spawning habitat. May out-migrate and spawn again.	Age at first spawn varies based on smolt age and duration of ocean residence. Spawning location varies based on natal origin and the timing and magnitude of wet season precipitation relative to timing of arrival to freshwater. Fecundity presumed to increase with age and size. Some individuals may outmigrate to the ocean (kelt) and return in subsequent year(s) to spawn, while others may die after spawning once	Yes	Fecundity generally increases with size, but individuals face higher risk of predation in the marine environment. Require sufficient streamflows to move into and use suitable spawning habitat in the winter.	CDFG 1976, VTN 1982, SEC 1998
	Two years ocean growth	Begins first spawning migration at age 3–5 after 2 years of feeding and growth in the ocean. Enters freshwater in fall or winter in sexually mature state, travels directly to accessible spawning habitat. May out-migrate and spawn again.		Yes		CDFG 1976, VTN 1982, SEC 1998
	Three years ocean growth	Begins first spawning migration at age 4–6 after 3 years of feeding and growth in the ocean. Enters freshwater in fall or winter in sexually mature state, travels directly to accessible spawning habitat. May out-migrate and spawn again.		Yes		CDFG 1976,, VTN 1982, SEC 1998
Fall-run	One year ocean growth	Begins first spawning migration at age 2–4 after 1 year of feeding and growth in the ocean. Enters freshwater in late summer or early fall in sexually immature state. Holds in the estuary/lower mainstem until elevated stream flows in late fall/winter allow passage over critical riffles in the lower mainstem. May out-migrate and spawn again.	Age at first spawn varies based on smolt age and duration of ocean residence. Spawning location varies based on the timing and magnitude of wet season precipitation relative to timing of arrival to freshwater. Fecundity in older, larger females presumed to be higher than younger, smaller females. Some individuals may outmigrate to the ocean (kelt) and return in subsequent year(s) to spawn, while others may die after spawning once	Mixed	Fecundity generally increases with size, but individuals face higher risk of predation in the marine environment. Require thermally suitable holding habitat in the mainstem/estuary, and require high flow events in the winter to reach ideal spawning grounds.	Roelofs 1983, Moyle et al. 2017, Yoshiyama and Moyle 2010
	Two years ocean growth	Begins first spawning migration at age 3–5 after 2 years of feeding and growth in the ocean. Holds in the estuary/lower mainstem until elevated stream flows in late fall/winter allow passage over critical riffles in the lower mainstem. May out-migrate and spawn again.		Mixed		
	Three years ocean growth	Begins first spawning migration at age 4–6 after 3 years of feeding and growth in the ocean. Enters freshwater in late summer or early fall in sexually immature state. Holds in the estuary/lower mainstem until elevated stream flows in late fall/winter allow passage over critical riffles in the lower mainstem. May out-migrate and spawn again.		Mixed		
Kelt	One repeat spawn	Begins outmigration to the ocean after first spawn in late winter, spring, or early summer. Returns to freshwater the following year to spawn for a second time. May out-migrate and spawn again.	Timing of outmigration depends on spawn timing, location, and coincident streamflows. Males likely remain in spawning areas longer than females. Age at repeat spawn varies based age at first spawn. Fecundity presumed to be higher than during prior spawn years. Fecundity in older, larger females presumed to be higher than younger, smaller females. Some individuals may die after repeat spawn	Yes	Repeat spawning increases lifetime fecundity, but iteroperous individuals may devote proportionally fewer energetic resources towards the first reproductive event. If kelt do not survive their second period of marine residency, fitness benefits will not be realized. Require elevated spring flows to facilitate downstream migration, with the risk of becoming stranded inland.	Puckett 1975, Trush 1991
	Two repeat spawns	Begins outmigration to the ocean after second spawn in late winter, spring, or early summer. Returns to freshwater the following year to spawn for a third time. May out-migrate and spawn again.		Yes		Puckett 1975, Trush 1991

3.4.1.1 Winter-run

Adult winter-run steelhead migrate upstream during the wet season, when storm flows tend to facilitate upstream movement. Historical fish counts at Benbow Dam on the South Fork Eel River indicate that the first migrating adult steelhead typically arrived at that location from mid- to late November while the last individuals typically arrived between late April and early May (CDFW unpubl. data 1939–1941). Historical fish counts conducted at the Cape Horn Dam fish latter at the Van Arsdale Fisheries Station (VAFS) reveal a similar pattern in the upper mainstem Eel River, with the first adult steelhead arriving in November, the last arriving in May, and peak movement occurring between January and March (VTN 1982). More recent sonar counts of adult salmonids in the lower South Fork Eel River are generally consistent with movement patterns observed at Benbow Dam and VAFS (Metheny 2020).

Interannual variation in hydrologic conditions influences the ability of adult winter-run steelhead to access and utilize spawning habitat in some tributaries. Access to these spawning locations may be restricted in low-water years as described by Trush (1991), and adults may spawn in the mainstems of the major forks or higher-order tributaries under such conditions, where suitable spawning habitat exists. Spawning distribution extent, reproductive success, and the probability of successful kelt outmigration are also likely maximized in wet years.

The winter-run strategy is the most broadly distributed adult ecotype throughout the Eel River (Figure 3-3). The winter-run strategy is likely advantageous because the primary migration window coincides with high flows, allowing relatively consistent access to suitable spawning grounds. Winter-run steelhead also spend more time in the ocean and may have a longer time window for growth there. Additionally, the lack of a holding stage reduces mortality during the freshwater spawning migration.

3.4.1.2 Summer-run

Adult summer-run steelhead migrate upstream in the Eel River watershed during spring and early summer. These individuals depend on moderate spring flows—often driven by snowmelt runoff—to navigate past flow-dependent barriers and reach over-summer holding habitat. This strategy allows adults to move even further upstream in the watershed during winter flows, allowing them to spawn further upstream than winter-run adults (Kannry et al. 2020). In springs following winters with low snowpack, summer-run steelhead may not be able to successfully reach holding areas. If no suitable holding habitat exists downstream of flow-dependent barriers, it is not clear whether some summer-run adults forego spawning and return to the ocean, or if they perish before spawning. In years when they can reach holding areas but following fall/winter flows are low, adults may spawn in sub-optimal locations.

As described in Section 3.1.2, summer-run steelhead rely on stream systems with regularly accessible habitats that support over-summer holding, such as pools that remain thermally suitable through the dry season. Extreme deviations from typical summer water conditions (i.e., very low streamflow and resultant hydrologic disconnection that degrades water quality, or alterations to typical patterns of thermal stratification in bedrock pools) may render such habitats unsuitable and could threaten the viability of summer-run populations in the long term.

Adults typically move from holding areas into spawning reaches upon the arrival of rainstorms during the wet season. Delayed onset of the wet season may prolong the duration of the over-summer holding period or force steelhead to utilize sub-optimal spawning habitat closer to holding areas (i.e., in mainstems), which could increase pre-spawn mortality or reduce reproductive success. California's wet season is predicted to "sharpen" in coming decades, with proportionally less rain falling in fall and spring (Swain et al. 2018). Such changes could reduce the spatial extent of habitats that support summer-run populations, further restricting the distribution of the ecotype.

The summer-run ecotype has some advantages over the winter-run, which has likely maintained the strategy through evolutionary time. First, the summer-run can access habitats that are higher in the watershed, including smaller, low-order and intermittent tributaries since they undertake the migration in two movements. These lower order streams may be advantageous due to lower risk of scour from winter storms and lower risk of predation during the vulnerable alevin and fry stages by other salmonids (Roelofs 1983). Because spawning can occur in smaller intermittent tributaries, juveniles may emigrate earlier than winter-run steelhead, moving downstream soon after emergence or as small fry (Roelofs 1983).

3.4.1.3 Fall-run

The fall-run is sometimes described separately from the summer-run steelhead, but it is not clear if this is a truly distinct strategy, with genetic underpinnings, or a hybrid of the winter and summer-run adults. Fall-run individuals typically enter the river later than the peak of the hydrograph associated with snowmelt run-off, but before winter storms. As a result, fall-run adults can have trouble with upstream passage.

Because the mouth of the mainstem Eel River remains open year-round, adult fall-run steelhead can enter the estuary and lower Eel River when relatively low baseflows in the mainstem may restrict further upstream movement. Certain riffles in the lower Eel River may be too shallow for adults to successfully navigate at typical dry season baseflows, a phenomenon that has described in the watershed for adult fall-run Chinook Salmon (CDFG, unpubl. data, 1938–1976). Similar interruptions to upstream movement by steelhead have also been documented at riffles in the upper Eel River (VTN 1982, SEC 1998). As described above, more recent sonar-based estimates of migration timing in the South Fork Eel River are generally consistent with this pattern (Metheny 2020).

When riffle crest depths in the lower mainstem are sufficient to permit passage, adult fall-run steelhead may continue migrating upstream into the Upper Main Eel and other sub-watersheds. However, because brief fall freshets may produce such conditions before the onset of the true wet season, fall-run adults may encounter additional flow-dependent impediments to movement further upstream, for example in the South Fork Eel River above Rattlesnake Creek (Trush 1991) or in the upper Eel River at Hearst Riffle (VTN 1982). As a result, in low-water years, adults may not be able to access upper spawning tributaries. Under such circumstances, adults may spawn in less optimal locations—such as the mainstems of larger tributaries or the major forks—where suitable spawning habitat exists. Such locations may not be as conducive to egg incubation or development of alevin, thus hydrologic conditions have the potential to influence reproductive success. The timing, duration, and ultimate success of each migration and spawning effort is therefore influenced by the coincident hydrological conditions each year. Reproductive success is likely maximized in wet years when elevated streamflow facilitates movement past critical riffles in the lower mainstem and entry into spawning tributaries for extended periods, increasing the area of suitable spawning habitat available to spawning adults.

It is not clear whether fall-run steelhead enter freshwater in a state of sexual maturity, or whether they must undergo some reproductive development while holding in the lower river or potentially further upstream. Because the fall-run adult migration period partially overlaps with the summer-run and winter-run migration period, it is difficult to draw precise conclusions about spawning ecology. For example, it is unclear whether spawning adult fall-run or winter-run intermix or remain spatially or temporally segregated.

3.4.2 Juvenile Life-history Strategies

Juvenile *O. mykiss* display a dizzying number of life-history strategies, and pathways within each strategy, with the ability to move between natal and non-natal rearing habitats in freshwater and spend varying amounts of time in freshwater before smolting or maturing in freshwater (residency). We organized the juvenile life-history strategies into groups with increasing amount of time spent in freshwater: residency, age-2 smolt, and age-1 smolt (Table 3-2, Figure 3-4), and time spent in different freshwater rearing habitats. The age at out-migration can depend on growth rates and local environmental conditions (Brown 1990, Kendall et al. 2015). For example, in the upper Eel River, trout may rear for 2 years before out-migrating, while enhanced growth conditions below Scott Dam may encourage out-migration after only 1 year in freshwater (SEC 1998). Other ages at smoltification are possible, but rarely documented, historically, or currently, in *O. mykiss,* including age-0 smolts and age-3 smolts. Age-0 smolts would be most likely to occur in extremely high growth years, while age-3 smolts would be most likely to occur in a series of low-growth years. Age-3 smolts would face the same decision matrix in their final year in freshwater as in the first two, so we excluded them from the diagram for simplicity.

Regardless of age at out-migration, juvenile *O. mykiss* may move into non-natal habitats, and back into natal streams, in the freshwater rearing stage. The time points at which redistribution is most common are the spring, accompanying the flow recession, and the fall, following the first rains (Pucket 1976, Kelson and Carlson 2019). As such, our second level of organization is *where* juveniles spend the dry vs. wet season, with options including the natal stream, a mainstem, a non-natal stream, or the estuary (Figure 3-4, Table 3-3).

Finally, the half-pounder strategy, where ocean out-migrants move back into freshwater for several months, was historically common (Snyder 1925) and is still present in smaller numbers in the Eel River. This unique strategy is described below as a juvenile life-history strategy (Figure 3-4 and Figure 3-8).

The total number of possible strategies, with *O. mykiss* moving between habitats throughout the year and varying in age at entry to the ocean (Pucket 1976), is too many to discuss individually. Our overview table (Table 3-3) and conceptual model figure (Figure 3-4) show some of the diversity that likely occurred in the Eel River. Below we discuss in detail a few of the strategies that likely occur, or occurred historically, in the Eel River. We recommend that future monitoring better capture the diversity of juvenile strategies and their potential to contribute to adult runs throughout changing environmental conditions (Section 3.5.3).

Table 3-3. Juvenile life-history strategies in *O. mykiss* organized by time in freshwater and variants that describe locations of rearing. Locations are abbreviated as NS = natal stream, NNS = Nonnatal stream, MS = mainstem, and SEE = stream estuary ecotone.

Strategy	Variant	Description of behavior	Dry season location	Wet season location	Variation within strategy	Documented occurrence in the Eel River	Predicted prevalence in dry water years	Predicted prevalence in wet water years	Trade-offs for strategy
Age-1 smolt	Age-1 smolt, natal rearing	Remains in natal stream for first year, migrates as an age-1 smolt directly to the ocean	NS	NS	Movement within the natal stream	Yes, Kelson et al. 2019, Puckett 1975, Maahs 1995, Vaughn 2007 (age 1 downstream migrants)	May be important in dry years in natal tributaries that are cold and have high baseflows, but less common in warm, intermittent tributaries	Likely to occur in wet years, especially if adults were able to access a diversity of spawning habitats, leading to lower densities of juveniles the following summer	Age-1 smoltification typically occurs if growth is rapid in the first year (Satterthwaite et al. 2009), they spend more time in the high-growth marine environment and may be able to spawn earlier/more times, at the risk of higher mortality rates given more time in the ocean.
	Age-1 smolt, non-natal mainstem rearing	Remains in natal stream as a fry, moves to mainstem for rearing in first summer, migrates to ocean as age-1 smolt	NS, MS	NS, NNS, MS	Mainstem rearing is most likely to occur in the summer months, over-wintering can occur in mainstems with habitat complexity or in nearby natal or non-natal streams	Yes, Kelson et al. 2019, Puckett 1975, Maahs 1995, Vaughn 2007 (age 1 downstream migrants), Wang et al. 2020, Kannry et al. 2020 (mainstem rearing)	May be more likely to occur in dry years if natal tributaries warm or become intermittent, but mainstem rearing may be less profitable in reaches that are thermally marginal	May be less likely to occur in wet years when conditions in natal streams are profitable, but the juveniles that do rear in the mainstem may find profitable conditions	
	Age-1 smolt, non-natal tributary rearing	Remains in natal stream as a fry, moves to non-natal tributary for rearing in first summer, migrates to ocean as age-1 smolt	NS, NNS	NS, NNS,MS	Movement to a different over-wintering location, from the summer non-natal tributary, is possible	Yes, Kelson et al. 2019, Puckett 1975, Maahs 1995, Vaughn 2007 (age 1 downstream migrants),	May be more likely to occur in dry years if natal tributaries warm or become intermittent	May be less likely to occur in wet years when conditions in natal streams are profitable	
	Age-1 smolt, estuary rearing	Remains in natal stream as a fry, moves to estuary for rearing in first summer, migrates to ocean as age-1 smolt	NS, SEE	NS, NNS, MS,SEE	Over-wintering habitats are likely streams near the estuary, but could also be within the estuary in velocity refugia, or possible return to upper river locations	Yes, Kelson et al. 2019, Puckett 1975, Maahs 1995 (age 1 downstream migrants), Puckett 1976, Cannata and Hassler 1995 (estuary rearing)	May be more likely to occur in dry years when conditions in the natal streams and nearby streams and mainstems become thermally marginal	May be less likely to occur in wet years when conditions in natal streams are profitable	

Strategy	Variant	Description of behavior	Dry season location	Wet season location	Variation within strategy	Documented occurrence in the Eel River	Predicted prevalence in dry water years	Predicted prevalence in wet water years	Trade-offs for strategy
Age-2 smolt	Age-2 smolt, natal rearing	Remains in natal stream for 2 years, migrates to the ocean as a smolt at age 2	NS	NS	Movement within the natal stream	Yes, Kelson et al. 2019, Puckett 1975, Vaughn 2007 (age 2 smolts)	May be important in dry years in natal tributaries that are cold and have high baseflows, but less common in warm, intermittent tributaries	Likely to occur in wet years, especially if adults were able to access a diversity of spawning habitats, leading to lower densities of juveniles the following summer	Age-2 smolts likely experienced lower risk of predation before smoltification in freshwater, increased size at ocean entry compared to age-1 smolts which may lead to higher marine survival. In Washington, age-2 smolts were the highest proportion of adult returns (Hall et al. 2016).
	Age-2 smolt, non-natal mainstem rearing	Remains in natal stream first year, moves downstream to larger mainstem rivers for another year, migrates to the ocean as a smolt at age 2	NS, MS	NS, NNS, MS	Possible that juveniles move into mainstem for summer rearing at age-0 rather than age-1. Mainstem rearing is most likely to occur in the summer months, over-wintering can occur in mainstems with habitat complexity or in nearby natal or non-natal streams.	Yes, Kelson et al. 2019, Puckett 1975, Vaughn 2007 (age 2 smolts), Wang et al 2020, Kanrry et al. 2020 (mainstem rearing)	May be more likely to occur in dry years if natal tributaries warm or become intermittent, but mainstem rearing may be less profitable in reaches that are thermally marginal	May be less likely to occur in wet years when conditions in natal streams are profitable, but the juveniles that do rear in the mainstem may find profitable conditions	
	Age-2 smolt, non-natal tributary rearing	Remains in natal stream first year, moves downstream to a non-natal tributary for another year, migrates to the ocean as a smolt at age 2	NS, NNS	NS, NNS	Possible that juveniles move into non-natal tributary for summer rearing at age-0 rather than age-1. Movement from summer rearing location to a different winter rearing location (return to natal stream, or move to mainstem), is possible	Yes, Kelson et al. 2019, Puckett 1975, Vaughn 2007 (age 2 smolts)	May be more likely to occur in dry years if natal tributaries warm or become intermittent	May be less likely to occur in wet years when conditions in natal streams are profitable	
	Age-2 smolt, estuary rearing	Remains in natal stream first year, moves downstream to the estuary for their second summer, over-winters in nearby refugia, migrates to the ocean as a smolt at age 2	NS, SEE	NS, NNS, MS, SEE	Possible that juveniles move into estuary for summer rearing at age-0 rather than age-1. Over-wintering habitats are likely streams near the estuary, but could also be within the estuary in velocity refugia, or possible return to upper river locations	Yes, Kelson et al. 2019, Puckett 1975, Vaughn 2007 (age 2 smolts), Puckett 1976, Cannata and Hassler 1995 (estuary rearing)	May be more likely to occur in dry years when conditions in the natal streams and nearby streams and mainstems become thermally marginal	May be less likely to occur in wet years when conditions in natal streams are profitable	
Age-3 smolt	Age-3 smolt	Remains in freshwater for 3 years prior to ocean migration	NS, NNS, MS, SEE	NS, NNS, MS, SEE	Combination of possible movements between NS, NNS, MS, and SEE are the same as age-1 and age-2 smolts	Yes, Puckett 1975	May be more likely to occur in series of dry years when freshwater growth is slow	May be less likely to occur in wet years when freshwater growth is fast	Slower growth rate in freshwater leads to smaller size at age compared to age-1 and age-2 out-migrants, but potentially higher survival rates in freshwater and at ocean entry.

Strategy	Variant	Description of behavior	Dry season location	Wet season location	Variation within strategy	Documented occurrence in the Eel River	Predicted prevalence in dry water years	Predicted prevalence in wet water years	Trade-offs for strategy
Resident	Resident, natal rearing	Remains in natal stream for life cycle, matures and breeds in natal stream at age 2-4, typically breeds multiple times	NS	NS	Movement within the natal stream	Yes, widespread (Harvey et al. 2021, Kelson et al. 2020)	Remain in tributaries in dry years, can maintain populations when anadromous adults can't access habitats (Kelson et al 2020)	Rapid growth in wet years may either (1) encourage residency and early maturation if growth is very high (McMillan et al. 2012), or (2) encourage smoltification (Beaks et al. 2010)	Typically lower mortality rates due to no migration or ocean rearing stage, but obtain a smaller adult body size compared to ocean-migrating strategies. For females this directly leads to lower fecundity, for males this means they typically sneak spawn with larger females. Residency is male-dominated given this lower loss in fecundity compared to females
	Resident, non-natal mainstem and tributary rearing	Remains in natal stream for first year, spends time rearing in nearby tributaries or mainstems, breeds in freshwater without migrating to the ocean	NNS	NNS	Possible that juveniles move to nearby non-natal rearing habitat at age-0 rather than age-1. Movement between natal tributary, mainstem, and non-natal tributary are most likely to occur in first 1 to 2 years, before establishing a territory. Spawning occurs in suitable tributary or mainstems	Yes, widespread (Harvey et al. 2021, Kelson et al. 2020)		Mainstem rearing may be more profitable in wet years when water temperatures are cooler and pikeminnow remain in lower river (Georgakakos 2020)	
Half pounder	Smolt age-1 half pounder	Re-enter freshwater (estuary/lower river) as age-2 smolt after 3-5 months in the ocean, remain in freshwater until the following spring	Ocean	SEE, MS	Over-wintering can occur in estuary or lower river, some sightings of half-pounders further upstream (e.g., Middle Fork Eel River). Half-pounder tactic is correlated with the summer-run adult strategy	Yes, Snyder (1925)	Unknown	Unknown	Steelhead that undertake the half-pounder migration typically have lower growth rates than their counterparts who remain in the ocean, but higher survival rates. This strategy may provide resilience for the population in years when ocean conditions are poor.
	Smolt age-2 half pounder	Re-enter freshwater (estuary/lower river) as age-1 smolt after 3–5 months in the ocean, remain in freshwater until the following spring	Ocean	SEE, MS		Yes, Snyder (1925)			

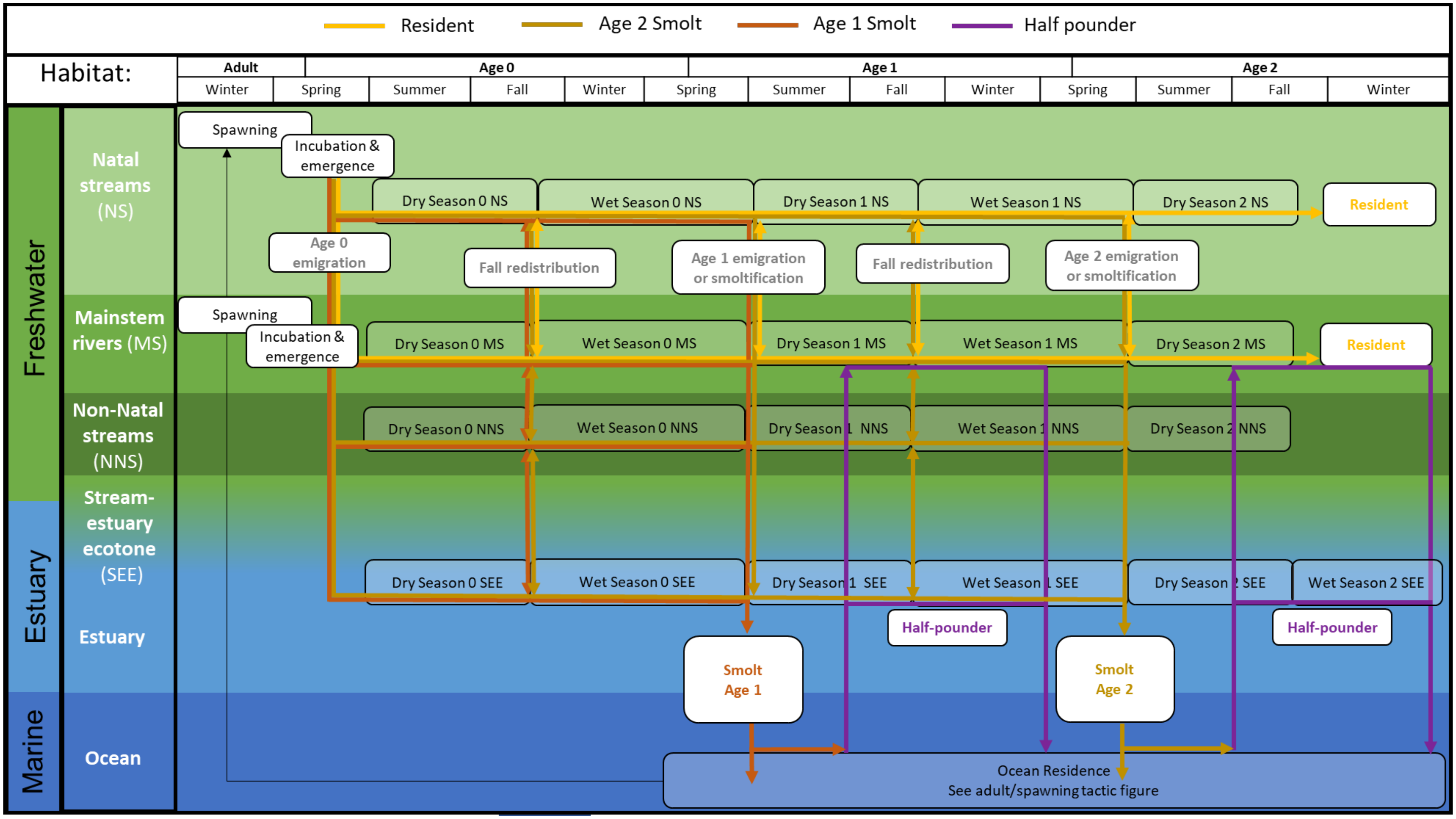

Figure 3-4. Diagram demonstrating the spatial and temporal use of different habitats by juvenile *O. mykiss* in the Eel River, organized by age at smoltification and location in the dry vs. wet season.

3.4.2.1 Spotlight strategy: Resident

The resident life-history strategy is characterized by freshwater rearing and maturation, without a migration to the ocean. Resident *O. mykiss* often remain in their natal stream for their entire life cycle, as shown in Figure 3-5 but rearing and maturing in nearby larger mainstem rivers is also likely a common variant. Resident juveniles are rarely distinguished from migratory juveniles in populations where both strategies occur.

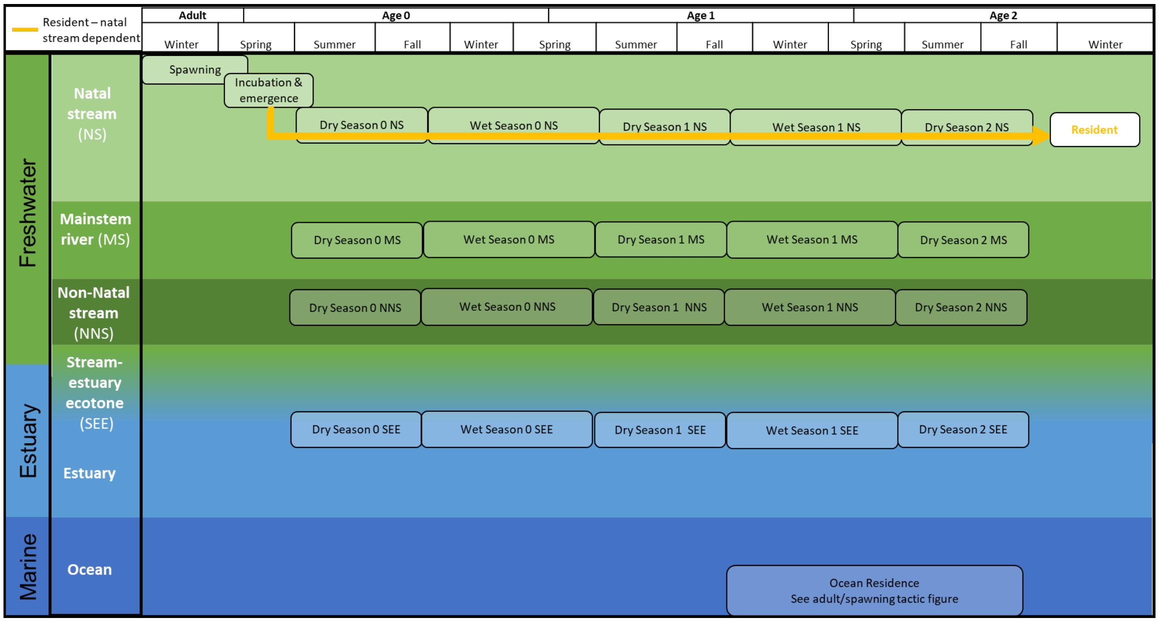

Figure 3-5. Diagram showing the pathway of resident, natal-rearing juvenile *O. mykiss*.

Residency is common in coastal streams throughout California, and the Eel River is no exception (Shapovalov and Taft 1954, Harvey et al. 2021, Kelson et al. 2020). In a study using otolith microchemistry, Harvey et al. (2021) found that juveniles who had resident mothers were broadly distributed, and there was no difference in their distribution across stream size (from 0.1–7.7 m^3 mean annual discharge) or distance from the ocean (from 23–219 km). At a finer spatial scale, the proportion of juveniles within a single tributary stream who are likely from anadromous parents can vary through time. Kelson et al. (2020) found that migratory-genotype juveniles were present in lower frequencies above partial barriers in dry years, when there were fewer opportunities for passage of anadromous adults, in tributaries to the South Fork Eel River.

Advantages of the resident life history include that individuals do not undertake the risky and energetically expensive migration to the ocean and can reproduce more times. Disadvantages of residency include that individuals forego high growth environments and as a result are much smaller at maturation. For females, this smaller size is directly linked to fecundity, as they produce fewer eggs. This connection is less direct with males, who can still experience high reproductive success rates through the "sneaker" spawner strategy of fertilizing redds (Jonsson and Jonsson 1993).

There are several aspects that contribute to the "decision" of individual fish to adopt a resident vs. migratory life-history strategy in *O. mykiss,* including individual body condition, environmental conditions, sex, and genetics, sex. There is generally a positive correlation between lipid content and maximum achievable body size in freshwater and residency (Kendall et al. 2015). Sex is a strong predicter of migratory behavior, with females being more likely to out-migrate than males, in the Eel River (Kelson et al. 2019) and throughout their broader Pacific Northwest (Ohms et al. 2014). Anadromy in *O. mykiss* is also strongly associated with *Omy5,* a large genomic inversion (Pearse et al. 2014). This genomic region likely indirectly influences migratory behavior via effects on other traits (Kelson et al. 2021). For example, the alleles associated with residency are also associated with faster early life-history growth, in hatchery clonal lines and in wild fish (Kelson et al. 2021). Additionally, there are likely interactions between genetics and all other aspects that ultimately determine an individual's migratory behavior. For example, in tributaries to the Eel River, male juveniles with the resident alleles almost always expressed residency, while female juveniles with the migratory alleles almost always expressed migration (Kelson et al. 2019). All these various factors likely work to preserve genetic and life-history diversity within a watershed, as the likelihood of anadromy at an individual level can vary through space and time.

The resident life-history strategy of *O. mykiss* likely provides an important population buffer for migratory trout throughout the Eel River, as they can maintain population numbers in streams above barriers or high in the watershed in years when access is difficult for anadromous fish (Kelson et al. 2020). Additionally, because resident fish are not susceptible to estuary or ocean conditions, they likely provide an important buffer when mortality rates in the ocean or migration phase are high (Sloat et al. 2014).

3.4.2.2 Spotlight strategy: Mainstem rearing

Many juvenile *O. mykiss* likely rear in mainstem rivers at some point in their freshwater rearing stage prior to ocean entry. One common life-history strategy for *O. mykiss* in the Eel River may be to emerge in natal, lower-order headwater streams, then quickly move to larger mainstem rivers where food is more abundant (Figure 3-6). Another variation of this strategy may be to rear in the relatively safe, predator-free, but lower-growth environment of the tributaries for 1 full year, before moving to larger mainstem rivers (Figure 3-6).

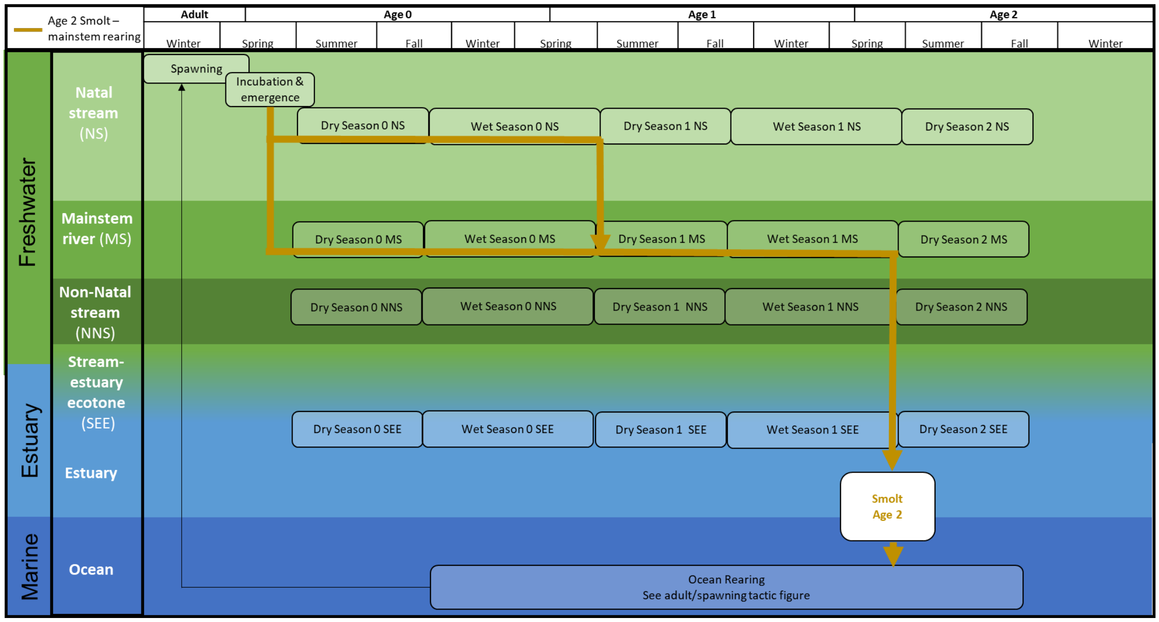

Figure 3-6. Diagram showing the pathway of age-2 smolt, mainstem-rearing *O. mykiss*.

The strategy of mainstem rearing has been supported by many observations of both young of year and age-1 trout rearing in the mainstem rivers (Wang et al. 2020, Georgakakos 2020), even in years when spawning in tributaries was likely to occur. Observations of downstream movement also suggest the prevalence of re-distributing as age-0 and age-1 fish into larger mainstem habitats. Pucket (1976) found that both YOY trout and age-1 trout move downstream from larger tributaries and mainstems throughout the Eel River, especially in the spring. Of these two age classes, the YOY trout were more numerous. Age-0 trout have also been observed moving downstream from tributaries in the South Fork Eel River, including Hollow Tree Creek and Redwood Creek (PCFFA 1988, Maahs 1995) in the spring and early summer (April-June). Many of these fish moving downstream were likely re-distributing within freshwater before moving all the way to the estuary (See Section 3.5.2.4). The age at which trout move from their natal stream to the mainstem rivers within their freshwater stage likely varies among years and among sub-watersheds in the Eel River, depending on the relative profitability of nearby habitats and prevalence of predators, especially pikeminnow, in the mainstem.

The timing of when the downstream migration from natal streams into mainstem rivers occurs in the spring and early summer likely differs among the sub-watersheds. These differences were noted by the extensive downstream trapping in the 1960s (Pucket 1976). In the Van Duzen River and the Middle Fork Eel River, the peak of downstream migration was in mid-June. In the South Fork Eel River, Redwood Creek, and the mainstem Eel River near Dos Rios, downstream migration was a little earlier, in mid-late May. Additionally, Kelson and Carlson (2019) noted that some juvenile fish move downstream with a fall pulse flow, suggesting that some movements into the mainstem for over-wintering is also possible.

Mainstem rearing is likely a profitable strategy over tributary-only rearing due to the potential for higher growth rates with more food resources (Armstrong et al. 2021). However, in some years and locations, mainstem rivers may become too warm to support juvenile *O. mykiss* rearing and may instead support non-native predatory fishes such as pikeminnow (Georgakakos et al. 2023). The thermal stress of mainstem rivers may be offset by tributary confluences provide cold water plumes and local refugia (Wang et al. 2020), or into foggy, cooler non-natal tributaries near the mouth of the Eel River (CDFG 2010). Regardless, mainstem rearing may be a higher-reward but higher-risk habitat than cold, groundwater-fed tributaries, which can have stable flows and growth opportunities across dry and wet years (Kelson and Carlson 2019). An additional stressor for mainstem rearing may be the lack of high velocity refugia during the winter (NMFS 2016). This stressor may be alleviated in locations that have floodplain access or channel complexity to provide shelter from high velocities.

3.4.2.3 Spotlight strategy: Estuary rearing

Similar to the previous mainstem-rearing strategy, a portion of *O. mykiss* leave their natal stream for the stream-estuary ecotone to take advantage of ecologically productive rearing habitats. It is likely that some portion of the age-0 and age-1 *O. mykiss* that have been observed moving downstream (Pucket 1976) are headed to the stream-estuary ecotone for rearing. For age-0 fish, we predict that this movement may be a little later in the year, in the end of their first dry season, leaving time to grow and reduce predation risk in transit downstream (Figure 3-7). For age-1 fish, this movement might occur earlier in the spring/summer to avoid migrating through a warm, inhospitable mainstem (Figure 3-7). The commonality of estuary-rearing strategy is supported by year-round observations of juvenile *O. mykiss* in the Eel River estuary (Murphy and DeWitt 1951, Pucket 1976, 1977, Cannata and Hassler 1995, CDFW 2010). This strategy is also logical in the Eel River, where downstream-moving *O. mykiss* encounter harsh conditions in lower, inland mainstem rivers (warm and/or full of non-native pikeminnow predators), and keep dispersing downstream to the stream-estuary ecotone, which is in the fog belt and remains cooler throughout the dry season.

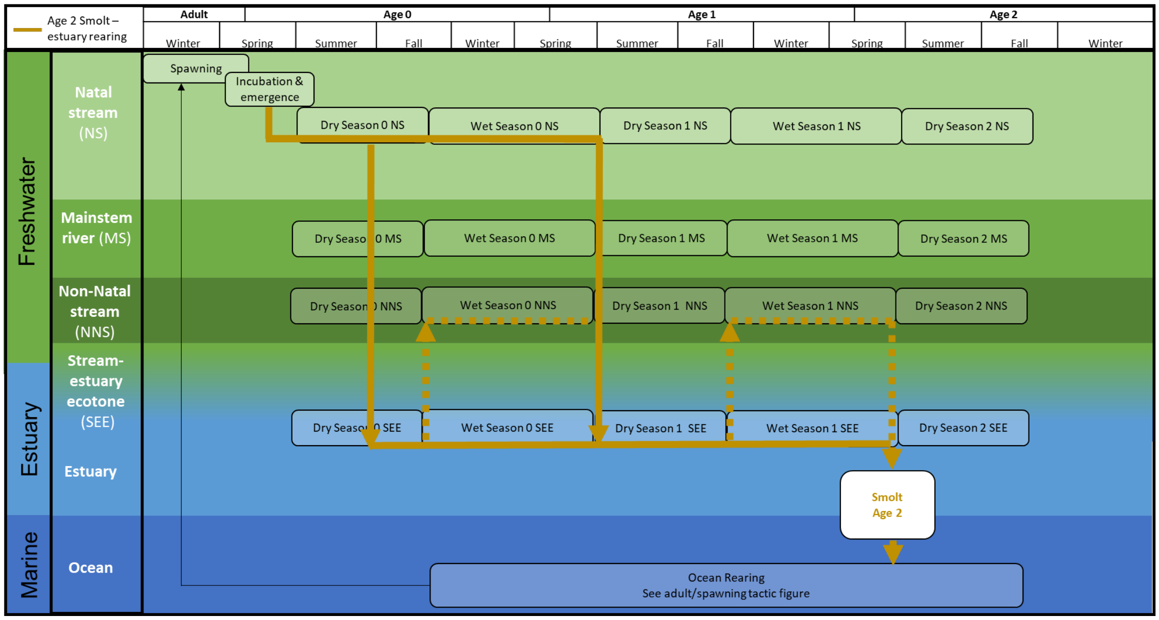

Figure 3-7. Diagram showing likely pathways of age-2 smolt, estuary-rearing *O. mykiss*.

In Mediterranean-climate rivers, summer-fall estuary rearing has the potential to be an extremely high growth habitat (0.2–0.8% of growth per day), compared to up-river growth (0.1% per day), when stream flows are at their annual low (Hayes et al. 2008). In Scott Creek in southern California, the majority of returning adults spent some time rearing in the estuary (Hayes et al. 2008), and the largest smolts are ones that spent some time estuary rearing (Hayes et al. 2011), suggesting that this strategy may contribute disproportionately to adult returns if the estuary is in good condition. However, in estuaries further north, such as the Columbia River estuary, juvenile steelhead tend to pass quickly through the estuary, without rearing for as long as other salmonid species (Weitkamp et al 2012), moving quickly to nearshore coastal areas (Daly et al. 2014). Given that juvenile steelhead still use the estuary year-round in the modern era despite extensive impacts from diking and levees (CDFW 2010), it is likely that the estuary was historically an important rearing habitat. Understanding factors that currently limit estuary-rearing will help revive a high-growth habitat that contributes greatly to population recovery and resilience.

While the estuary may be a high growth environment in the summer, it can become a seasonally harsh environment due to higher velocities in the winter. In Scott Creek, many juvenile steelhead retreat upstream into freshwater for the winter as the estuary becomes too warm (Hayes et al. 2011). In the Eel River, it is likely that juvenile steelhead may seek out nearby velocity refugia in the winter. They may move into non-natal streams that are near the estuary, such as the Salt River, or further upstream, until migrating through the estuary again the following spring. This potential seasonal upstream movement is noted with dashed lines in Figure 3-7.

3.4.2.4 Spotlight Strategy: Half-pounder

The half-pounder migration is a unique strategy where immature *O. mykiss* re-enter freshwater in the late summer/fall (August–November), after only 3–5 months in the ocean, then return to the ocean the following spring (Figure 3-8) (Kesner and Barnhart 1972). The half-pounder migration is different from an upstream breeding migration, and steelhead are foraging while in freshwater, unlike mature adults (Kesner and Barnhart 1972). This life-history strategy occurs primarily in streams in southern Oregon and northern California coastal, including the Eel, Klamath and Rogue Rivers (Everest 1973). Half-pounders are typically 25–45 cm in fork length and remain in the lower reaches of the river (Murphy and De Witt 1951, Kesner and Barnhart 1972), but there are observations of half-pounders as far upriver as the South Fork Eel River and at the Van Arsdale trap (Stillwater Sciences 2022). Both sexes have been observed equally in half-pounder migrations.

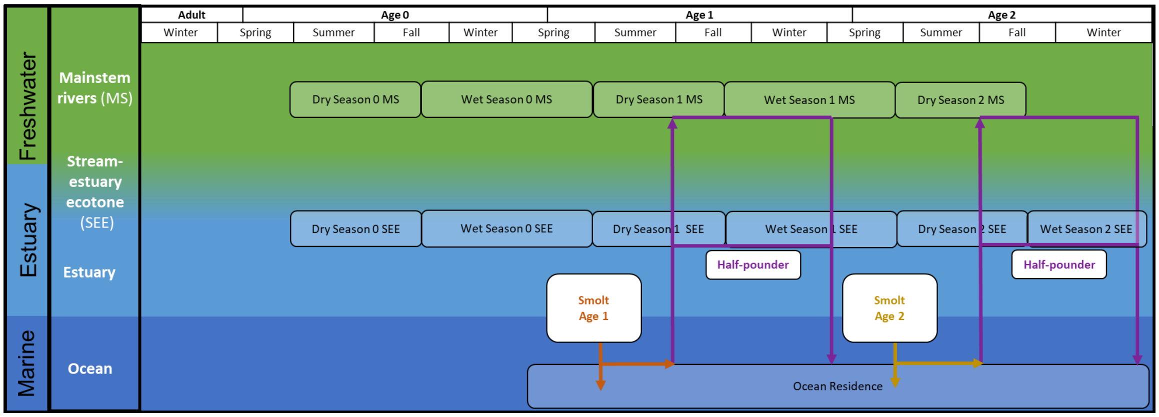

Figure 3-8. Diagram showing the pathway of age-2 smolt, estuary-rearing *O. mykiss*.

The association between the half-pounder migration and age at smoltification/ocean entry is mixed. In the Trinity River, Peterson (2011) found that the half-pounder strategy was more common for smolts that entered the ocean at age-1, but also occurred for age-2 and age-3 fish. However, Kesner and Barnhart (1972) found that most half-pounders had entered the ocean at age 2. The age-at-smoltification that is most likely to undergo a half-pounder migration may vary through time and depend on size at out-migration and current ocean conditions. In both studies, steelhead only spend a few months in the ocean before entering freshwater again.

One benefit of the half-pounder migration may be relatively high survival rates (Satterthwaite 1988). Peterson (2011) noted that juveniles that were smaller for their age when exiting the estuary where more likely to undergo a half-pounder migration, and these are fish that may otherwise have had a higher ocean mortality rate. Hodge et al. (2014) estimated through life-cycle models that that first-year ocean survival is 21-40% higher for half-pounder phenotypes.

The trade-off for high survival rate in the winter may be a loss of growth opportunities in the ocean. Half-pounders may grow half as much as their counterparts in the ocean during their winter in freshwater. Hodge et al. (2014) reported that steelhead in their first winter in the ocean grew an average of 29 cm (range of 9–40 cm), while half-pounders grew 14.5 cm (range of 7–26 cm) in the same time window. However, it is possible that growth rates were higher when Chinook eggs were available as a food source, given that the run timing mirrors that of historical Chinook runs. In the current state of the estuary, the reduced body size and associated loss of fecundity of half-pounders leads to a 17–28% loss of fitness (Hodge et al. 2014).

The half-pounder migration is thought to be most closely associated with the summer-run and/or fall-run ecotype, but also occurs in the winter-run (Everest 1973, Hodge et al. 2014, Peterson et al. 2017). In the Rogue River, Everest (1973) found that 97% of summer-run adults completed a half-pounder migration before their spawning migration, whereas only 21% of winter run adults make a half-pounder migration (McPherson and Cramer 1982). Hopelain (1988) also noted that the half-pounder migration was more common in the summer run in the Klamath River and its tributaries. The connection between half-pounders and the summer vs. fall-run is not always distinguished, given inconsistencies in terminology and separation between the summer and fall-run. Summarizing from multiple sources, Peterson et al. (2017) describes that the fall-run is often made of >90% of individuals that expressed the half-pounder strategy. One possibility is that the fall-run is comprised of half-pounders from the summer-run who needed to put on more weight in the ocean in the spring and early summer, and as a consequence enter freshwater later than most summer-run adults.

The half-pounder strategy likely evolved due to relatively higher success in years with poor ocean conditions and may provide important population resilience in those years. Ocean survival for steelhead in the Pacific Northwest has been declining since 1980 (Kendall et al. 2016). Climate change may continue to provide bioenergetically challenging conditions for ocean survival as anomalously warm years become more normal. For example, the warm "Blob" in 2015-2016 altered prey resources for ocean steelhead and contributed to lower body condition (Thalmann et al. 2020). Restoring a half-pounder migration would restore one strategy that relies less heavily on ocean conditions. Notably, restoring the half-pounder phenotype may require restoring conditions that allow for persistence of summer-run steelhead given the correlation between the two.

3.5 Conceptual Model Outcomes

3.5.1 Stressors

Stressors for steelhead were compiled through the development of the conceptual models and by reviewing relevant literature and reports, including NMFS and CDFW recovery plans (NMFS 2016, CDFG 1997), restoration plans in the Eel River (Eel River Forum 2016, South Fork Eel River SHaRP Collaborative 2021), and watershed assessments (Downie et al. 2005, Becker and Smetak 2010, Becker and Reining 2009, CDFG 2010, 2012; CDFW 2014).

Stressors are organized by life stage (adult, spawning and incubation, juvenile rearing, ocean migration, and ocean residence). Some stressors may impact multiple life stages, and are duplicated. For example, a stressor that occurs lower in the watershed or in the estuary may impact multiple life stages (juvenile rearing, out-migrating, and adult migration), and thus may have large impacts on population recovery. Additionally, some stressors may be more associated with certain life-history strategies, and these are noted in Table 3-4.

The mechanisms behind each stressor that could ultimately alter population productivity, abundance, distribution, and resilience are described in Table 3-4. This predicted connection between the stressor and population impacts will be an important reference during the restoration prioritization process, when the predicted efficacy of various restoration actions will be related to how and why they relieve stressors to improve conditions for fish. The driver behind each stressors is also described in Table 3-4, and this was used to inform the list of restoration and conservation actions in the Plan (Section 4).

Finally, the relative importance of stressors in the table varies with space and time such as location in the watershed and inter-annual variation in environmental conditions. Some stressors will be more prominent in certain water year types. For example, warming water temperatures due to loss of canopy covers or infilled pools may have a larger impact in drier water year types, when air temperature has a larger effect on water temperatures. The magnitude of stressors also varies between the sub-watersheds and between drainage areas, depending on land use history, underlying geology, and previous restoration actions. As part of prioritization of restoration actions using life-history diversity and conceptual models in Phase 2, these stressors and their associated drivers and opportunities for restoration will be evaluated for their relative importance in space and time.

Table 3-4. Stressors with potential to adversely impact each life stage of *O. mykiss* in the Eel River watershed, with life-history strategies that are predicted to be the most impacted.

Life stage	Stressor	Mechanisms of impact on population productivity, abundance, distribution, and resilience	Drivers (underlying causes of stressor to be addressed by restoration)	Life-history strategies potentially highly impacted
Ocean residence	Ocean harvest or bycatch	Reduced smolt to adult survival; altered adult age structure and life-history diversity.	Ocean fishing regulations and enforcement	All strategies
	Marine food web alterations	Reduced ocean growth and smolt to adult survival.	Climate change related influences on strength and timing of ocean upwelling, marine productivity, and the salmon prey species.	All strategies
Adult holding and migration	Anthropogenic physical barriers to movement	Reduced spawning distribution, lowered reproductive success, and potential lost juvenile life-history diversity.	Dams, poorly designed or failed road crossings, other manmade obstructions to movement.	All adult strategies
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Impaired staging habitats and increased pre-spawning mortality from predation.	Reduced wood volume due to removal and alteration of riparian forest (reduced supply). Channel aggradation due to increased sediment delivery from historical and current logging, road construction & management, and fires.	Summer-run, fall-run
	Impaired fall pulse flows	Reduced ability to reach upper-watershed spawning habitats and potentially increase overlap in distribution with other run-timings.	Reduced or delayed fall stream flows due to water diversions or climate change.	Fall-run
	Impaired winter flow events	Reduced ability to reach diverse spawning grounds, increased likelihood of mainstem spawning, leading to redd scour and/or reduced juvenile life-history strategies	Reduced or delayed winter storm events from climate change, water diversions	Winter-run
	Impaired spring recession	Reduced ability to reach suitable over-summer holding habitat, increase overlap in spatial distribution of spawning with other run-timings	Loss of snowpack from climate change	Summer-rung
	Increased prevalence of predation	Pre-spawning mortality	Loss of escape cover and channel complexity due to reduced large wood volume and loss of deep pools.	Winter-run, summer-run, fall-run
	Poaching	Pre-spawning mortality	Inadequate education and enforcement.	Winter-run, summer-run, fall-run
Spawning and incubation	Redd scour	Reduced egg-to-fry survival	Channelization and reduced substrate sorting; low flows during adult migration & spawning followed by high winter flows.	Winter-run
	Fine sediment infiltration of spawning substrates and redds	Reduced egg-to-fry survival	Landslides and erosion of fine sediment due to historical and current logging, road construction and management, and fires. Reduced sediment sorting due to channelization, floodplain disconnection, and lack of wood.	All adult strategies
	Increased prevalence of predation	Pre-spawning mortality	Loss of escape cover and channel complexity due to reduced supply of large wood and loss of deep pools.	All adult strategies

Life stage	Stressor	Mechanisms of impact on population productivity, abundance, distribution, and resilience	Drivers (underlying causes of stressor to be addressed by restoration)	Life-history strategies potentially highly impacted
Juvenile rearing	Anthropogenic physical barriers to movement	Reduced rearing habitat capacity and lowered survival due to lack of access to cold water refugia, loss of connectivity between habitats.	Dams, poorly-designed or failed road crossings, tide gates, or other manmade obstructions to movement.	All juvenile strategies
	Reduced area of low-velocity instream winter rearing habitats	Reduced winter rearing habitat capacity.	Reduced wood volume and channel simplification from legacy impacts of logging and road construction. Loss of beaver dams.	All juvenile strategies
	Impaired connectivity with and loss of riverine floodplain/off-channel rearing habitats	Reduced winter rearing habitat capacity. Reduced juvenile growth and survival in winter. Reduced survival/prevalence of fall parr emigrant strategy.	Channelization, channel incision, levees, bank armoring & roads, wetland draining & agricultural conversion, reduced wood volume, and loss of beaver dams.	All juvenile strategies
	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Reduced growth and survival of estuary-rearing juveniles due to altered estuarine food webs, impaired WQ, lost access to off-channel habitats, and loss of escape cover.	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	Estuary-rearing juveniles
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Reduced rearing summer and winter habitat capacity, reduced fry to smolt survival.	Reduced wood volume due to removal & supply. Channel aggradation due to increased sediment delivery from historical land uses & floods.	All juvenile strategies
	Impaired dry-season stream flows	Restricted movement & stranding in poor habitat due to sub-surface flows. Direct mortality due to poor water quality and predation. Reduced growth due to higher densities, less invert production and delivery from riffles.	Climate change, water diversion for rural agriculture and domestic use, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	All juvenile strategies
	Increased water temperatures	Reduced rearing habitat capacity due to restricted distribution. Direct mortality, chronic stress and reduced growth due to metabolic effects, increased pikeminnow predation and competition. Reduced ability to disperse through warm mainstem rivers to cooler tributaries or estuary.	Loss or alteration of riparian forests, impaired dry-season stream flows (see below for drivers), climate change.	Mainstem rearing juveniles
	Reduced area of or access to thermal refugia	Reduced rearing habitat capacity due to restricted distribution. Direct mortality, chronic stress and reduced growth due to metabolic effects, increased pikeminnow predation and competition.	Filling of thermally-stratified deep pools due to channel aggradation caused by sediment inputs from logging practices, road building and floods. Loss of connectivity with cold tributaries due to channel aggradation. Loss of complex cover at cold tributary confluences.	Mainstem and estuary rearing juveniles
	Elevated turbidity levels beyond reference state levels	Reduced growth through impaired feeding in highly turbid locations during high-turbidity periods.	Landslides and erosion of fine sediments due to historical and current logging, road construction & management, and geomorphic impacts of high intensity fires.	Mainstem rearing juveniles
	Increased prevalence of predation, especially from non-native predators	Reduced growth and survival in warm-water habitats, especially lower Eel River and larger mainstems. Loss of ability to disperse through mainstems to seasonally suitable habitats in the summer.	Sacramento Pikeminnow predation, loss of escape cover from larger wood and deep pools, decreased stream flows and increased water temperatures.	Mainstem rearing juveniles, estuary rearing juveniles
	Introduced competitors and anthropogenic factors that increase vulnerability to them	Reduced growth and survival due to interspecific competition, loss of profitability of mainstem-rearing strategy.	Northern Coastal Roach and juvenile Sacramento Pikeminnow, increased water temperatures	Mainstem rearing juveniles, estuary rearing juveniles
	Increased prevalence of disease	Reduced growth and survival, especially in warmer water habitats, loss of profitability of mainstem-rearing strategy.	Reduced stream flows, increased temperatures	Mainstem rearing juveniles, estuary rearing juveniles
	Alterations to the timing, magnitude, and availability of food resources	Reduced juvenile growth and survival and lost life-history diversity (reduced prevalence of strategies that historically relied on beneficial species interactions that have been lost)	Loss of marine-derived subsidies and nutrients and other beneficial species interactions, presence of non-native pikeminnow in mainstem habitats, degraded riparian forests, simplification of channel, embeddedness of substrate from sediment inputs, altered flow regimes.	All juvenile strategies
Smolt outmigration	Impaired spring recession flows	Reduced success on outmigration to ocean.	Climate change, water diversions, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	All juvenile strategies
	Increased prevalence of predation	Reduced smolt to ocean survival due to prevalence, primarily in mainstem corridors.	Sacramento Pikeminnow predation, loss of escape cover from large wood and deep pools, decreased stream flows and increased water temperatures.	All juvenile strategies
	Reduced pool frequency, depth, and channel complexity in mainstems and tributaries	Reduced smolt to ocean survival due to loss of escape cover.	Reduced wood volume due to removal & supply. Channel aggradation due to increased sediment delivery from historical land uses & floods.	All juvenile strategies
	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Reduced smolt to ocean survival due to loss of escape cover.	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	All juvenile strategies

3.5.2 Restoration Take-home Points

The following central themes and focus points related to recovery of *O. mykiss* in the Eel River watershed were identified during the development of the life-history conceptual models and through various internal and TAC discussions.

- The possible diversity of juvenile life-history strategies in *O. mykiss* demonstrates that rearing juveniles will use the whole watershed if they can. While it is not possible to restore all habitats in the watershed, ensuring connectivity between seasonally suitable habitats with stop-over habitats, or temporary refuges, as needed is likely very important in allowing diverse juvenile rearing strategies.
- The ability of mainstem habitats to function as rearing habitats and dispersal for juveniles has been severely impaired due to introduced pikeminnow, compounded by channel homogenization and warming stream temperatures. Almost every life-history juvenile rearing strategy might have used the mainstem at some point in their freshwater stage, and the loss of the mainstem function may currently be a limiting factor for increasing abundance and recovering diverse life-history strategies.
- Estuary-rearing was potentially a highly profitable juvenile rearing strategy, especially given that the estuary, in the "fog belt," can remain thermally suitable and ecologically productive in the summer and fall, when nearby, inland, lower rivers are warming. Increasing the capacity and quality of estuary habitat could greatly improve the diversity of life-history strategies, including the prevalence of the half-pounders.
- Restoration in seasonally "marginal" habitats will allow steelhead to make use of diverse habitats, such as mainstem rivers and intermittent tributaries. These habitats may be suitable for steelhead but not for Coho, which could allow growth in a habitat with less intraspecific competition. These seasonally marginal habitats may provide high growth environments and may contribute disproportionately to annual growth of juvenile trout. Additionally, in some sub-watersheds such as the Middle Fork Eel, many to most habitats may be considered "marginal," and improving these habitats could greatly increase the total habitat capacity for steelhead throughout the watershed.
- The half-pounder migration is a unique life-history strategy found in only a few watersheds along the Pacific Rim, and understanding limiting factors and current relative contributions to adult returns could unlock a potentially important life-history strategy that provides resilience to fluctuating ocean conditions.
- The summer run of steelhead is a unique adult strategy that is only found in a few sub-watersheds of the Eel River due to its reliance on the snowmelt component of the hydrograph, actions to conserve and improve holding conditions for the summer-run should be a high priority to conserve the genetic diversity.
- Resident *O. mykiss*/rainbow trout are not afforded the same legal protections and collective attention as steelhead trout, but are likely ubiquitous throughout the watershed, interbreeding with steelhead, and providing resilience to the population as it lacks an ocean/estuary/lower river component of the life cycle.

3.5.3 Key Data Gaps

Various gaps in understanding of distribution, life-history, and abundance of steelhead in the Eel River watershed were identified through development of this species review and conceptual model. Since these data gaps may limit effective management and restoration of the species, conducting research and monitoring to fill them is integral to recovery. Key data gaps for adult and juvenile life stages are listed below.

Adult run-timing and spawning ecology:

- Connection between half-pounder strategy and summer-run/fall-run steelhead
- Extent of divergence between fall-run and other run-timings, including differences in run timing and spatial location of spawning
- Explore genetic makers for fall-run steelhead, possibility of heterozygosity for run-timing gene or unique genetic background
- Ability for the half-pounder migration to support successful repeat spawning
- Understanding the role of residency in maintaining population stability throughout the basin, including in areas with easy access to the ocean
- Understanding age structure of adult spawners, including time spent in freshwater and in the ocean

Juvenile ecology:

- Diversity in age at dispersal from natal streams between the sub-watersheds and in relation to environmental conditions
- Contribution of estuary and mainstem-rearing strategy to adult returns, and variability of that contribution through time and space
- Contribution of age at smoltification to adult returns, and variability of that contribution through time and space
- Ecology of half-pounders: state of sexual maturity, prevalence, timing, and upper extent of migration
- Prevalence of downstream movement and migration in the fall, age composition and fate of the fish who re-distribute at this time of year
- Current abundance of age-0 juveniles moving downstream to rear outside of natal tributaries, and their fates
- Impacts of pikeminnow on the growth, survival, and prevalence of mainstem-rearing juveniles

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4 PACIFIC LAMPREY

The Pacific Lamprey (*Entosphenus tridentatus*)—which is one of the most widely distributed fish species along the Pacific Rim—is found across the northern margin of the Pacific Ocean, from central Baja California north along the west coast of North America to the Bering Sea in Alaska (Ruiz-Campos and Gonzales-Guzman 1996, Lin et al. 2008, USFWS 2019). This anadromous species rears in fresh water before outmigrating to the ocean, where it grows to full size (approximately 400–700 mm [16–28in]) prior to returning to freshwater to spawn and ultimately die. Adults migrate into and spawn in a wide range of river systems, from short coastal streams to interior tributaries of the Snake River in Idaho, where they may migrate over 1,450 km (900 mi) to reach (Claire 2004). Within the Eel River watershed, Pacific Lamprey are found in all major sub-basins and in relatively small and large streams (Stillwater Sciences 2010, Stillwater Sciences and Wiyot Tribe Natural Resources Department [WNRD] 2016; Section 4.3).

In the Eel River watershed and across its range, the Pacific Lamprey is both a key component of the aquatic ecosystem and a culturally important food source for Native American Tribes (Close et al. 2002, Petersen-Lewis 2009, Stillwater Sciences 2010, WNRD and Stillwater Sciences 2016). Historically, the species was so abundant in the Eel River that the river was named “Eel River” by European settlers, who mistook Pacific Lamprey for eels (Elliott 1881). However, the Pacific Lamprey population has declined substantially in response to widespread habitat degradation, barriers to fish passage, invasive predators, and water diversions (Stillwater Sciences 2010, Boyce et al. 2022). Due to its cultural and ecological importance and in response to its rapid decline, the Pacific Lamprey has recently gained more recognition as a priority species for conservation and restoration, both in the Eel River and across its native range (Goodman and Reid 2012, WNRD and Stillwater Sciences 2016). For this reason, and because it is listed as a California Species of Special Concern, Pacific Lamprey is included as a focal species of the Eel River Restoration and Conservation Plan.

The Section describes the current state of knowledge of the species in the Eel River and presents a conceptual model to (1) organize the available information, (2) identify data gaps, (3) identify potential stressors and limiting factors, (4) inform efforts to identify and prioritize restoration strategies that are most likely to increase population size and resilience. This Section draws heavily from and builds on a conceptual framework for understanding factors limiting Pacific Lamprey production in the Eel River developed by Stillwater Sciences (2014). That effort was conducted for the Wiyot Tribe Natural Resources Department with funding from a U.S. Fish and Wildlife Service (USFWS) Tribal Wildlife Grant.

4.1 Genetic Population Structure

Unlike Pacific salmon and steelhead, Pacific Lamprey do not necessarily return (“home”) to natal spawning streams (Moyle et al. 2009, Spice et al. 2012). Instead, migrating adults appear to select spawning streams, at least in part, based on bile acid compounds secreted by larvae (also known as ammocoetes) that act as migratory pheromones (Robinson et al. 2009, Yun et al. 2011). This mode of selecting spawning streams induces migratory adults to select locations where larval rearing has been successful due to suitable habitat. Lack of homing means that extensive gene-flow likely occurs between watersheds and regions, and thus Pacific Lamprey populations generally do not exhibit the fine-scale stock-structure seen in migratory salmonids (Goodman et al. 2008, Lin et al. 2008, Spice et al 2012).

Unlike Pacific salmon and steelhead, Pacific Lamprey do not exhibit precise homing to natal spawning streams (Moyle et al. 2009, Spice et al. 2012, Hess et al. 2023). However, a recent study that used parentage genetics to track the of the return of adult offspring of parents from known spawning locations in the interior Columbia River basin suggests a coarse scale of homing (i.e., at the larger basin scale rather than at the stream reach scale) (Hess et al. 2023). This study found that Pacific Lamprey originating in the Snake River as adults to the Columbia River in substantial numbers and were largely absent from adult collections distributed across the range outside of the Columbia River basin. Additionally, after returning to the Columbia River, most Snake River Pacific Lamprey continue upstream past Bonneville Dam into the interior Columbia River, rather than entering the Willamette River subbasin in the lower Columbia River (Hess at al. 2022, 2023).

Migrating adult lampreys are thought to select specific spawning streams, at least in part, based on presence of bile acid compounds secreted by larvae that act as migratory pheromones (Robinson et al. 2009, Yun et al. 2011). This mode of selecting spawning streams induces migratory adults to select locations where larval rearing has been successful due to suitable habitat, and therefore has been called the “suitable river strategy” (Waldman et al. 2008).

Lack of precise homing means that extensive gene-flow likely occurs between spawning streams and to some extent larger regions, and thus Pacific Lamprey populations generally do not exhibit the fine-scale genetic stock-structure seen in migratory salmonids (Goodman et al. 2008, Lin et al. 2008, Spice et al 2012). Results of genetics studies generally support this assertion. In a study of Pacific Lamprey population structure using mitochondrial DNA markers, Goodman et al. (2008) found little genetic differences among individuals sampled at widely dispersed sites across the species’ range, indicating substantial genetic exchange among populations from different streams. Results of a study that applied amplified fragment length polymorphisms (AFLPs) to assess genetic population structure of Pacific Lamprey also indicated considerable historical gene flow across the range of the species, but found significant genetic divergence among samples collected in the Pacific Northwest, Alaska, and Japan, suggesting some regional-scale genetic structure (Lin et al. 2008). Results also indicated a weak trend of decreasing gene flow with increased geographical distance, suggesting a pattern of genetic isolation by distance. Lin et al. (2008) also found significant genetic differences among Pacific Lamprey samples from different locations within the Pacific Northwest, but these differences did not follow an obvious geographical pattern. Analyses of microsatellite and mitochondrial DNA from Pacific Lamprey collected from 20 sites in British Columbia, Washington, Oregon, and California also indicated low but significant genetic differentiation among sites and weak but significant genetic isolation by coastal distance (i.e., marine dispersal distance between watersheds), based on analysis of the influence of distance between estuaries on genetic variation (Spice et. al 2012). This study supports the premise that Pacific Lamprey do not necessarily home to their natal streams, but indicates that relatively limited dispersal at sea may contribute to the weak, larger-scale genetic structure observed. These findings appear to be consistent with a parasitic feeding mode and relatively poor swimming performance (i.e., some fraction are carried away a long distance by migratory hosts, while some fraction likely remain relatively close, returning to their natal watershed or adjacent watersheds).

Despite the generally weak fine-scale population genetic structure and lack of homing indicated by these studies, there is some evidence for significant adaptive genetic divergence related to migration timing and body size among some Pacific Lamprey collections, which suggests natural selection is acting on migrating adult lamprey (Hess et al. 2013).

Results of the studies summarized above help illustrate the evolutionary context of lamprey population dynamics and reveal some important principles for identifying key limiting factors in managing and restoring populations—most notably the need to develop regionally-coordinated management, restoration, and monitoring strategies.

4.2 Population Status and Abundance

Pacific Lamprey are not formally protected under the federal ESA. In 2003, USFWS received a petition to list Pacific Lamprey under the ESA (Nawa 2003), but species status review was halted after a "90-day-finding" stating that information available at that time did not warrant full consideration for ESA listing of the species (USFWS 2004). The status of Pacific Lamprey has remained a concern to Native American Tribes, conservation organizations, agencies, and biologists across their range. To encourage regional implementation of research and conservation actions aimed at restoring and protecting Pacific Lamprey populations and avoiding the need for ESA listing, in 2008, USFWS initiated the Pacific Lamprey Conservation Initiative (https://www.pacificlamprey.org/). This collaborative initiative has resulted in structured efforts to help guide planning and conservation efforts throughout the species' range, including the formation of Regional Management Units aimed at identifying, prioritizing, and implementing conservation actions across the range of the species. Regional Implementation Plans—which outline status and distribution, threats and limiting factors, and recommended conservation actions for Pacific Lamprey—have been developed for each Regional Management Unit, including the California North Coast Regional Management Unit, which includes the Eel River watershed (Boyce et al. 2022).

The Bureau of Land Management (BLM) maintains a list of sensitive species that are not listed under the ESA but require special management consideration to reduce the need for listing. In addition to being included on this list, the Pacific Lamprey is listed as a sensitive species by USFS in Region 5, which includes the Eel River watershed.

Finally, the Pacific Lamprey is listed by the state of California as a Species of Special Concern, with a status rating of "Moderate Concern" (Moyle et al. 2015). This rating denotes the species was "*considered to be under no immediate threat of extinction but were in long-term decline or had naturally small, isolated populations which warrant frequent status reassessment….*"

No historical or recent watershed-wide estimates of Pacific Lamprey abundance exist for the Eel River watershed. However, there are widespread and consistent reports of a considerable decline in abundance of migrating and spawning adults and carcasses in the basin. Interviews with biologists, Wiyot Tribal eelers and elders, and other stakeholders living or working in the basin, all indicate a decline in the Eel River Pacific Lamprey beginning around the 1950s (Stillwater Sciences 2010). This decline generally mirrors an apparent range-wide decline in abundance of the species that has been widely reported (Nawa 2003, Moyle et al. 2009, CRITFIC 2011, Goodman and Reid 2015, Boyce et al. 2022). The species still occupies much of its accessible native range in California, but no longer has access to numerous upstream habitats blocked by large dams or other impassable structures (Moyle et al. 2009, Goodman and Reid 2015, Boyce et al. 2022).

Several recent efforts to monitor the adult population in portions of the watershed have been initiated, including adult spawning surveys conducted by the Wiyot Tribe Natural Resources Department in 2014 in index reaches of the lower Eel River and South Fork Eel River (Stillwater Sciences and WNRD 2016), annual counts conducted in the upper South Fork Eel River from

2016 through present (Georgakakos 2020), and counts of adults passing Cape Horn Dam in the upper mainstem Eel River since 2016 (Boyce et al. 2022). These counts, along with recent anecdotal observations from biologists working in the watershed, suggest the size of adult population can vary substantially between years. Counts of individuals at Cape Horn Dam have ranged from a low of 4 in 2021 to 11,506 in 2017 (Figure 4-1). Some of this variation is likely due to annual differences in stream flow and water temperature that influence the number of adults entering the upper Eel River and attempting to pass the dam, and some is due to the actual size of the watershed's population each year.

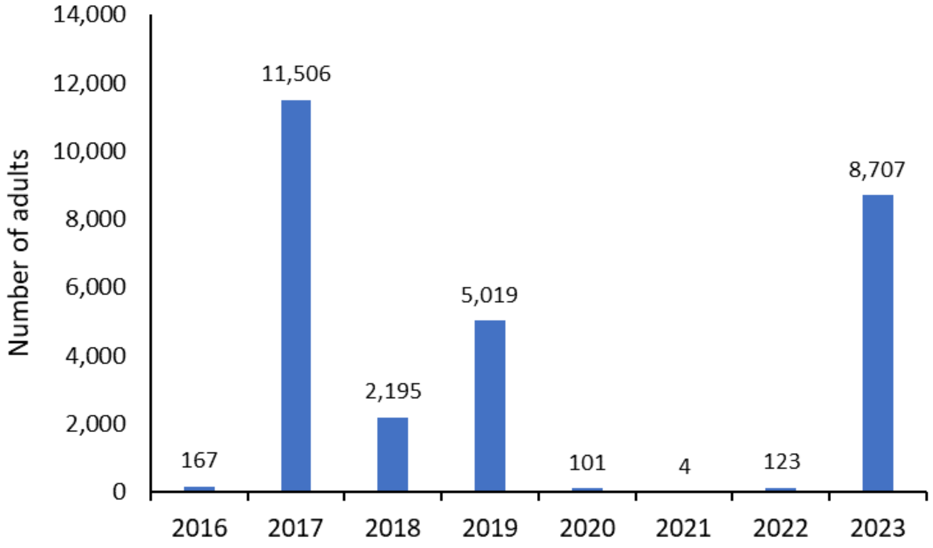

Figure 4-1. Number of adult Pacific Lamprey counted passing Cape Horn Dam from 2016–2023. Data from 2016–2021 were provided by U.S. Fish and Wildlife Service. Data from 2022 and 2023 were provided by PG&E and Kleinfelder. Data represent either individuals moving upstream through the lamprey passage structure installed at the dam in 2016 (recorded with a video monitoring system) or through the fish ladder. 2016 represents a partial year of monitoring, with counts beginning on June 30. Monitoring in other years typically occurred year-around, except for August through October and brief periods when counting operations were interrupted by high flows.

4.3 Distribution

Comprehensive distribution data are not available for the Pacific Lamprey in Eel River due to limited monitoring, but available data and observations suggest they are widespread. Within the Eel River watershed, Pacific Lamprey are found in all major sub-basins and in both relatively small channels and large mainstem reaches (Stillwater Sciences 2010, 2014, Stillwater Sciences and WNRD 2016). In general, the species has the potential to be present in any accessible stream reach within the distribution of anadromous salmonids. Because they can ascend some natural barriers (e.g., waterfalls) by climbing with their suctorial discs (Zhu et al. 2011), they also have potential to be present in reaches that are not accessible to anadromous salmonids. Differences between historical and current distribution in the are unknown due to lack of monitoring, but the species was historically present upstream of Scott Dam, which currently blocks its migration in the upper Eel River.

Pacific Lamprey spawning has been observed in a wide range of stream sizes but is more prevalent in larger (active channel widths >15 m [49 ft]), lower-gradient streams than in smaller streams (Stone 2006, Gunckel et al. 2009). In the Eel River watershed, the species has been documented spawning in channels draining areas ranging from approximately 6 km^2 (Ryan Creek in the Outlook Creek drainage) to greater than 9,000 km^2 (lower mainstem Eel River; Stillwater Sciences and WNRD 2016). Pre-spawning adult Pacific Lamprey have been documented holding during the summer in small, relatively high-gradient tributaries such as Fox Creek in the upper South Fork Eel River, which has a contributing drainage area of 3 km^2 (B. Trush, pers. comm., May 20, 2010). Larval Pacific Lamprey are also expected to be widely distributed throughout the watershed, occurring in relatively small headwater spawning streams downstream to the estuary (Stillwater Sciences 2010, 2014). Overall, because they require fine sediment burrowing habitats for rearing, larval lampreys are generally found in higher densities in less-confined, lower gradient (<3%) stream reaches that contain low-velocity, depositional areas such as pools, alcoves, and side channels (Torgersen and Close 2004, Nystrom 2020, Jones et al. 2020).

Since a comprehensive distribution dataset for Pacific Lamprey in the Eel River watershed does not exist, potential distribution for the species was predicted for this conceptual model to aid in restoration planning. This was done by applying minimum contributing drainage area and maximum channel gradient thresholds for each freshwater life stage (Figure 4-2). These thresholds were developed based on observations of the species from the Eel River watershed and other northwestern streams (Stone 2006, Gunckel et al. 2009, Starcevich and Clements 2013, Dunham 2013, Jones et al. 2020). A minimum drainage area criterion of 2 km^2 was initially applied to restrict the upper limit of distribution to larger streams. Within channels with a drainage area greater than 2 km^2, the upstream-most stream reach with gradient less than 4% was considered the upper limit of potential Pacific Lamprey distribution. All channels less than 2.5% gradient were considered potential larval rearing habitat, and all channels less than 4% were considered potential spawning habitat. Channels greater than 4% gradient that were downstream of lower gradient reaches were considered potential migratory or holding habitat only. These predictions of potential distribution should be considered a coarse representation of actual distribution and were designed to err on the side of including smaller channels with a relatively low likelihood of occurrence under current conditions (and depressed population size). Additionally, the predicted distribution shown in Figure 4-2 does not account for potential manmade or natural barriers to Pacific Lamprey migration, except for Scott Dam.

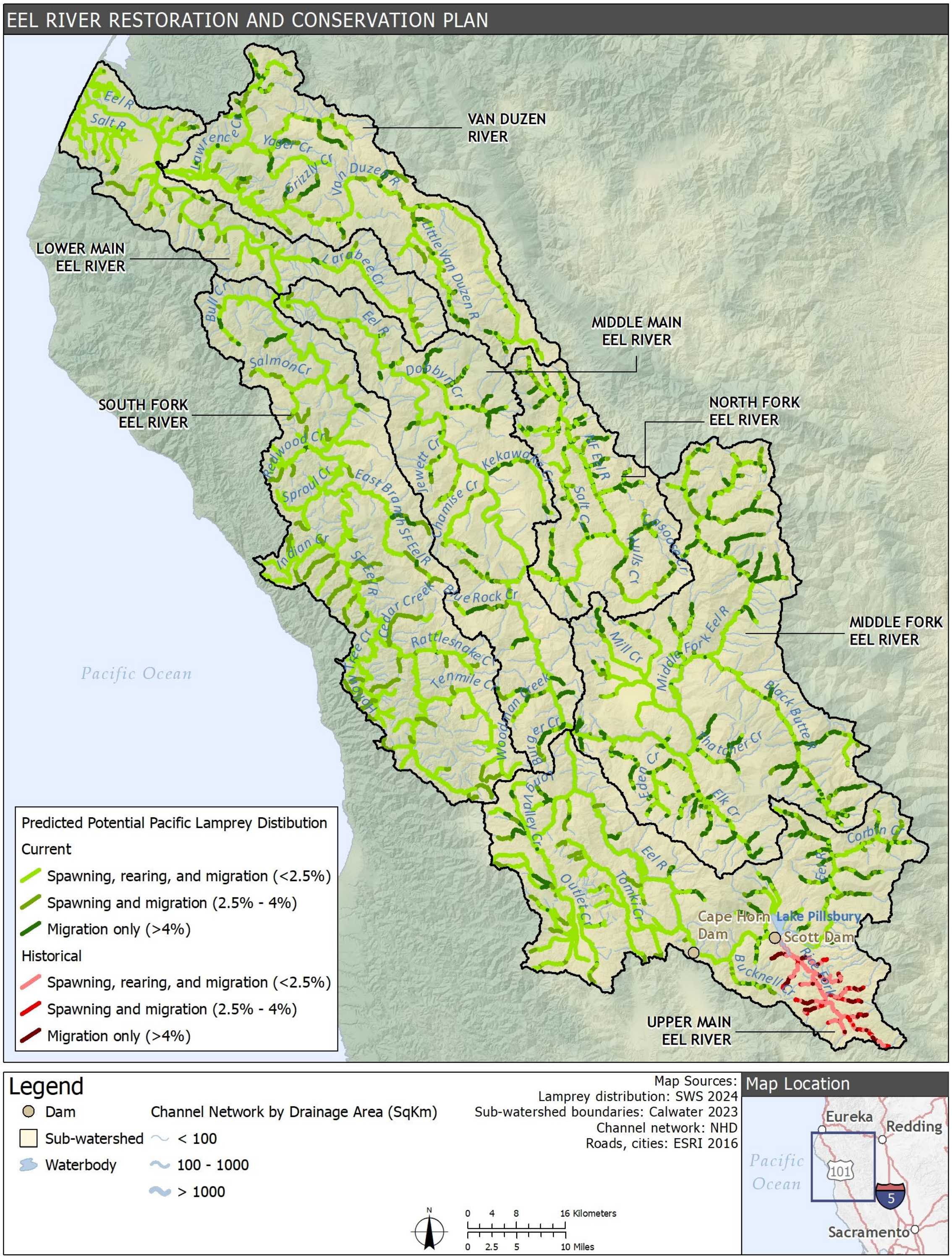

Figure 4-2. Predicted potential distribution of freshwater life stages of Pacific Lamprey in the Eel River watershed. These predicted distributions, based on channel gradient and contributing drainage area thresholds, are conservatively inclusive and do not account for potential manmade or natural barriers to adult migration, except for Scott Dam. Additionally, tidally-influenced reaches do not support spawning, and larval rearing distribution in those reaches may be restricted by salinity.

4.4 Ecology, Life History, and Habitat Needs

This section begins with a high-level overview of Pacific Lamprey life-history timing (Section 4.4.1) and is followed by more detailed information on timing, spatial distribution, movement, habitat requirements, and factors potentially affecting survival of each life stage in the Eel River (Sections 4.4.2–4.4.7).

4.4.1 Life-history timing overview

Figure 4-3 depicts the life cycle of Pacific Lamprey and Table 4-1 presents the generalized life-history timing for each life stage. The timing shown here is based largely on information from other watersheds where more extensive monitoring has been conducted, but where available, Eel River observations are included.

Pacific Lamprey typically spawn from March through July depending on water temperatures and local conditions such as seasonal flow regimes (Kan 1975, Brumo et al. 2009, Gunckel et al. 2009, Stillwater Sciences and WNRD 2016). More inland, high-elevation, and northerly populations generally initiate spawning considerably later than southerly populations (Kan 1975, Beamish 1980, Farlinger and Beamish 1984, Chase 2001, Brumo et al. 2009), presumably due to cooler water temperatures. Spawning generally takes place at daily mean water temperatures from 10–18°C (50–64°F), with peak spawning around 14–15°C (57–59°F) (Stone 2006, Brumo 2006). Redds are typically constructed by both males and females in gravel and cobble substrates within pool and run tailouts and low gradient riffles (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009). During spawning, eggs are deposited into the redd and hatch after approximately 15 days, depending on water temperatures (Meeuwig et al. 2005, Brumo 2006). Pacific Lamprey are highly fecund: depending on their size, females lay between 30,000 and 240,000 eggs (Kan 1975). In comparison, Chinook Salmon generally lay approximately 4,000 to 12,000 eggs (e.g., Jasper and Evensen 2006). Pacific Lamprey typically die within a few days to 2 weeks after spawning (Pletcher 1963, Kan 1975, Brumo 2006). The egg-sac larval stage, known as prolarvae, spend another 15 days in the redd gravels, during which time they absorb the remaining egg sac, until they emerge at night and drift downstream (Brumo 2006).

After drifting downstream, the eyeless larvae, known as ammocoetes, settle out of the water column and burrow into fine silt and sand substrates that often contain organic matter. Within the stream network they are generally found in low-velocity, depositional areas such as pools, alcoves, and side channels (Torgensen and Close 2004). Depending on factors influencing growth rates, they rear in these habitats from 2.5 to 11 years (Pletcher 1963, Goodman and Reid 2022, Hess et al. 2022), filter-feeding on algae and detrital matter prior to metamorphosing into the adult form (Moore and Mallatt 1980, van de Wetering 1998). During metamorphosis, Pacific Lamprey develop eyes, a suctoral disc, sharp teeth, and more-defined fins (McGree et al. 2008). After metamorphosis, smolt-like individuals, known as macropthalmia, migrate to the ocean, typically in conjunction with high-flow events between fall and spring (van de Wetering 1998, Goodman et al. 2015).

In the ocean, Pacific Lamprey feed parasitically on a variety of marine fishes (Richards and Beamish 1981, Beamish and Levings 1991, Murauskas et al. 2013). They remain in the ocean for approximately 2 to 7 years (Kan 1975, Beamish 1980, Hess et al. 2022) before returning to fresh water as sexually immature adults, typically from winter to early summer (Starcevich et al. 2014, Stillwater Sciences and WNRD 2016). In the Klamath and Columbia rivers, they have been reported to enter fresh water year-round (Kan 1975, Petersen Lewis 2009, Parker 2018). Notably, recent research suggests that two distinct life-history strategies (also called ecotypes), somewhat analogous to summer- and winter-run steelhead, occur in some river systems: one, an “ocean maturing” life history that spawns several weeks after entering fresh water, and two, a “stream-maturing” life history—the more commonly recognized strategy of spending 1 year in fresh water prior to spawning (Clemens et al. 2013, Parker et al. 2019). This research supports longstanding recognition of distinct adult life history strategies by Native American Tribal members (e.g., Close et al. 2004, Petersen Lewis 2009)

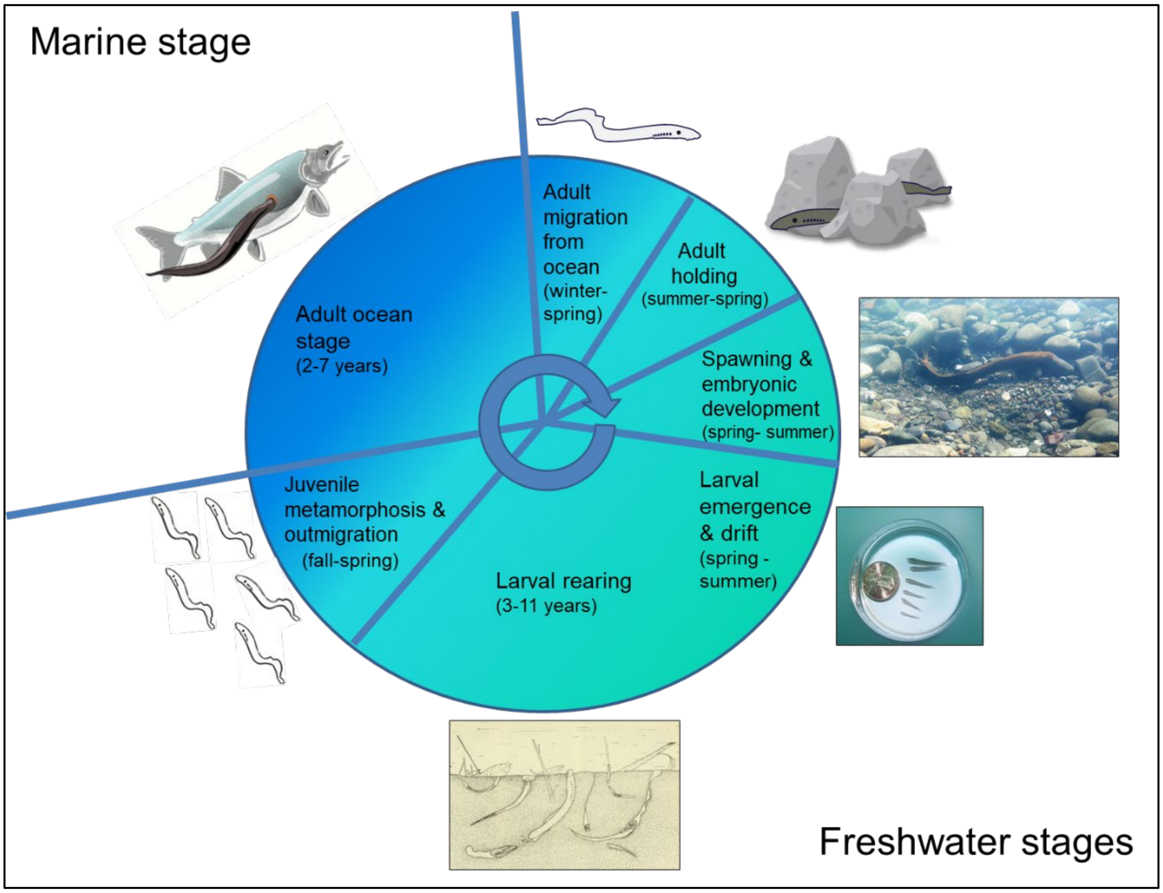

Figure 4-3. Pacific Lamprey life-cycle overview.

Table 4-1. Generalized life-history periodicity of Pacific Lamprey in the Eel River watershed.

Life stage	Month											
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Adult migration[1,2,3,4,5]	▒	▓	▓	▓	▓	▒	▒	▒		▒	▒	▒
Pre-spawning holding[6,7,8] (river-maturing ecotype)	▒	▒	▒			▒	▒	▒	▒	▒	▒	▒
Spawning[1,2,9]		▒	▒	▓	▓	▒	▒					
Incubation[10,11]			▒	▒	▒	▒	▒					
Larval emergence and drift[11,12,13]				▒	▒	▒	▒	▒				
Larval rearing[2] (ammocoete)	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
Juvenile outmigration[14,15] (macrophthalmia)	▓	▓	▓	▓	▒	▒				▒	▓	▓

▒ = Span of activity
▓ = Peak of activity

[1] Stillwater Sciences (2010)
[2] Stillwater Sciences and WNRD (2016)
[3] CDFG, unpubl. Benbow Dam count data (1938–1976)
[4] Parker (2018)
[5] PG&E and USFWS, unpubl. data from Van Arsdale Fisheries Station (2016–2023)
[6] Robinson and Bayer (2005)
[7] Clemens et al. (2012)
[8] Starcevich et al. (2014)
[9] Groff and Renger (2016)
[10] Meeuwig et al. (2005)
[11] Brumo (2006)
[12] Harvey et al. (2002)
[13] White and Harvey (2003)
[14] van de Wetering (1998)
[15] Goodman et al. (2015)

4.4.2 Adult Migration from the Ocean

After spending between 2 and 7 years in the ocean (see Section 4.4.7), adult Pacific Lamprey reenter freshwater at a potential age range of 4 to 18 years (Hess et al. 2022). As described above, Pacific Lamprey can display at least two distinct adult life-history strategies: (1) an "ocean maturing" ecotype that likely spawns several weeks after entering fresh water, and (2) a "stream-maturing" ecotype, that spends 1 year in fresh water prior to spawning (Clemens et al. 2013, Parker et al. 2019). The relative prevalence of these strategies in the Eel River watershed is unknown. These strategies are discussed in mor detail in Section 4.5.1.

The adult freshwater residence period for the apparently more common stream-maturing ecotype can be divided into three distinct stages: (1) initial migration from the ocean to holding areas, (2) pre-spawning holding, and (3) secondary migration to spawning sites (Robinson and Bayer 2005, Clemens et al. 2010, Starcevich et al. 2014). These stages are described below.

Sexually immature adult Pacific Lamprey have been documented entering the Eel River and migrating upstream to holding and spawning habitats between October and mid-August, with peak period of freshwater entry likely occurring from January to May (Table 4-1). Based on reported harvest by Tribal fishers ("eelers") at the mouth of the Eel River, adult Pacific Lamprey typically enter fresh water in catchable numbers from January until at least June (Stillwater

Sciences 2010). Creel surveys conducted at the Eel River mouth in 2014 found peak harvest, and presumably migration, occurred in late February (Stillwater Sciences and WNRD 2016).

Available information suggests that the initial upstream migration from the ocean can continue for a month or more after freshwater entry. Historically, eelers continued to capture adult lamprey further upstream in the mainstem Eel and South Fork Eel rivers later in the summer than at the mouth (Stillwater Sciences 2010). Periodic historical observations of adult Pacific Lamprey by fish counters at Benbow Dam provide a coarse indication of adult run timing in the mainstem South Fork Eel River (CDFG unpubl. data, 1938–1976), that is consistent with more recent observations. Pacific Lamprey attempting to pass the dam were noted in every month from October through June, with apparent peak movement in winter and early spring (CDFG unpubl. data, 1938–1976). Recent video monitoring of adult Pacific Lamprey at Cape Horn Dam in the upper mainstem Eel River has shown individuals moving upstream as early as March 31 and as late as August 10 (PG&E and USFWS, unpubl. data, 2016–2023). Peak movement varied by year, but typically occurred from May through June (Figure 4-4).

Differences in timing migration timing between the ocean-maturing and stream-maturing ecotypes have not been described for the Eel River, but in the Klamath River, Parker (2018) found significant differences between the two types: the onset of freshwater migration for ocean-maturing occurred mostly in the winter, whereas the river-maturing ecotype entered freshwater throughout the winter, spring, and summer.

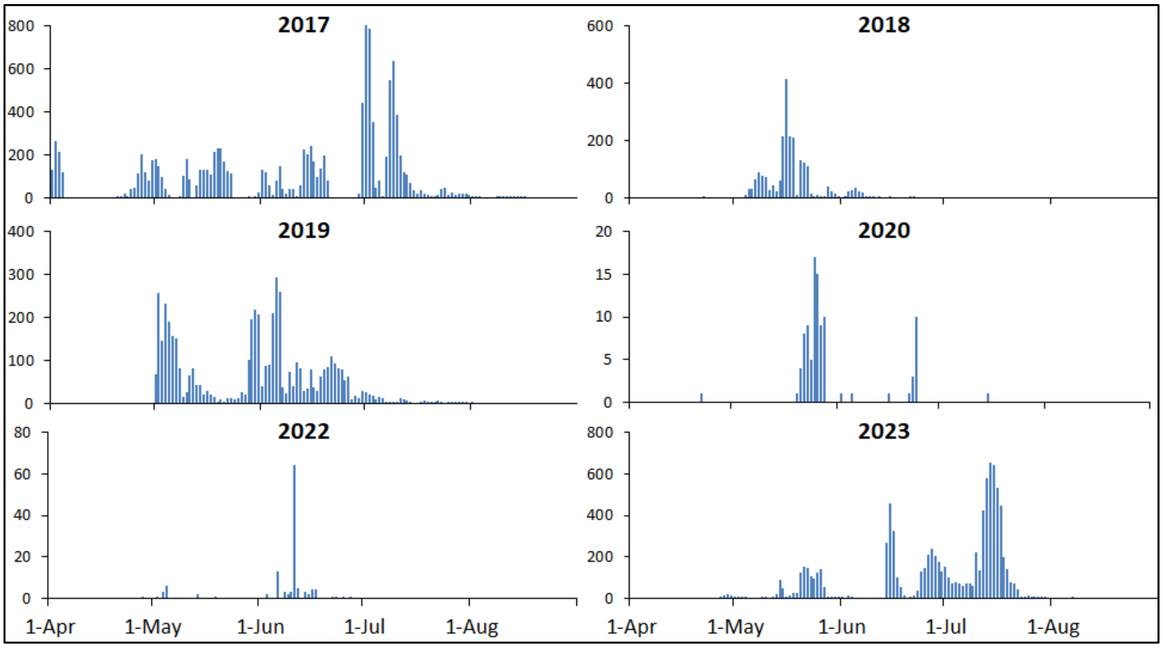

Figure 4-4. Daily counts of adult Pacific Lamprey moving upstream at Cape Horn Dam in the upper Eel River. Daily data from 2016–2019 provided by the U.S. Fish and Wildlife Service. Daily data from 2020–2023 provided by PG&E and Kleinfelder. Data for 2021 were excluded because only four Pacific Lamprey were observed that year.

4.4.3 Pre-spawning Holding

The stream-maturing adult ecotype engages in pre-spawning holding behavior, which begins when individuals cease upstream movement, generally in the summer, and continues until they begin their secondary migration to spawning areas the following spring (Robinson and Bayer 2005, McCovey 2011, Starcevich et al. 2014). Radio telemetry studies suggest adult lamprey prefer holding in protected areas associated with large cobble or boulder substrates, bedrock crevices, large wood, or man-made structures such as bridge abutments and preferentially select glide or run habitat types (Robinson and Bayer 2005, Lampman 2011, Starcevich et al. 2014). Most holding individuals remain stationary throughout the late summer, fall, and winter, but some may undergo additional movements in the winter following high-flow events (McCovey 2011, Starcevich et al. 2014).

The exact water temperature requirements for holding adult Pacific Lamprey have not been identified, but several studies have documented thermal conditions during the holding period and at specific holding locations. Starcevich et al. (2014) found that mean daily water temperatures at holding locations in the Smith River, Oregon during the summer holding period ranged from approximately 16°C to 20°C, with daily maxima from 26°C to 29°C. In the John Day River, Oregon, most holding did not begin until after summer water temperatures peaked, and water temperatures ranged from approximately 3°C to 20°C during the fall through winter holding period. Lampman (2011) reported that lamprey holding in the warmer reaches of the lower North Umpqua River sought out microhabitats with cooler water temperatures during holding and hypothesized that hyporheic exchange may be an important factor in selection of holding areas. Clemens et al. (2009) found that water temperature during the summer holding period plays a key role in regulating maturation timing. Adult Pacific Lamprey held in laboratory tanks at fluctuating temperatures that mimicked ambient river temperatures during the summer (20–24°C) had lower body weights and were significantly more likely to become sexually mature and die the following spring than those held in constant cool water treatments (13.6°C). Although fish in the warm water group matured within the typical spawning period and showed no significant difference in summer survival than the cool water group, the authors of this study suggest that excessively high water temperatures during holding could result in early maturation, which could result in a mismatch between spawning time and optimal habitat characteristics for spawning, embryonic development and larval emergence.

Very few holding locations have been documented in the Eel River watershed, and preferred holding locations are unknown (Stillwater Sciences 2010). Based on studies in other watersheds, most Pacific Lamprey remain in mainstem rivers and larger tributaries during the pre-spawning holding stage (Robinson and Bayer 2005, Clemens et al. 2009, Fox et al. 2010, McCovey 2011, Starcevich et al. 2014), but some individuals hold in mid-size and smaller tributaries (Fox et al. 2010, Stillwater Sciences 2010). For example, in the Eel River watershed, adults have been documented holding in the summer in relatively small streams, including Fox and Rock creeks in the South Fork Eel sub-basin (B. Trush, McBain & Trush, pers. comm. 2 May 2010), Ryan Creek, a tributary to Outlet Creek (S. Harris, CDFW, pers. comm., 21 May 2010), and Cahto Creek, a tributary to Tenmile Creek in the upper South Fork Eel sub-basin (D. Goodman, USFWS, pers. comm., 2012). The extent to which adult Pacific Lamprey may utilize small streams for over-summer holding remains an uncertainty. It is possible that some small headwater streams provide superior water quality or other conditions preferred for holding compared with larger, lower-gradient reaches. In portions of the Eel River watershed where summer stream flows and water temperature are impaired, small headwater streams may play an increasingly important role for Pacific Lamprey over-summer holding.

4.4.4 Spawning and Incubation

Following the pre-spawning holding period, Pacific Lamprey undertake a secondary migration from holding areas to spawning areas. This movement generally begins in March and continues through July, by which time most individuals have spawned and died (Robinson and Bayer 2005, Starcevich et al. 2014). During this secondary migration, movement from holding areas to spawning areas can be upstream or downstream (Robinson and Bayer 2005, Lampman 2011, Starcevich et al. 2014). Individual Pacific Lamprey have been documented spawning in multiple locations, moving substantial distances (up to 16 km) in the spring between spawning areas (Starcevich et al. 2014).

Pacific Lamprey typically spawn between March and July, depending on water temperatures and seasonal flow regimes (Kan 1975, Brumo et al. 2009, Gunckel et al. 2009, Stillwater Sciences and WNRD 2016). In the Eel River watershed, spawning has been documented as early as late February (in Indian Creek; Groff and Renger 2016) and as late as early June (in Bull Creek and the mainstem; Stillwater Sciences and WNRD 2016). Peak spawning time for Pacific Lamprey in the Eel River watershed and other northern California streams typically occurs in April and May (Stillwater Sciences and WNRD 2016, Stillwater Sciences et al. 2016).

As described in section 4.3, Pacific Lamprey spawning has been observed in a wide range of stream sizes, but is more prevalent in larger, high-order streams than smaller, low-order streams. They are expected to spawn in accessible stream reaches throughout much of the Eel River watershed and have been documented spawning in channels draining areas ranging in size from approximately 6 km^2 (e.g., Ryan Creek) >9,000 km^2 (lower mainstem Eel River; Stillwater Sciences 2010, Stillwater Sciences and WNRD 2016). Relatively high redd densities have been documented both in large tributaries such as Bull Creek and Lawrence Creek, and in reaches of the lower mainstem Eel, South Fork Eel, and Van Duzen rivers (Stillwater Sciences and WNRD 2016).

Spawning habitat requirements for Pacific Lamprey are relatively well understood compared with other life stages. Spawning generally takes place at daily mean water temperatures from 10–18°C (50–64°F), with peak spawning around 14–15°C (57–59°F) (Stone 2006, Brumo 2006). Redds can be constructed by both males and females, typically in gravel and cobble substrates within pool and run tailouts and low-gradient riffles (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009). Pacific Lamprey can utilize a wide range of substrate sizes for building redds, ranging from fine gravel to large cobble. Most spawning occurs in substrate patches with dominant particle sizes ranging from approximately 10–100 mm (0.4–3.9 in) (Howard and Close 2004, Stone et al. 2006, Gunckel et al. 2009).

During spawning, eggs are deposited into the redd and hatch after approximately 15 days, depending on water temperatures (Meeuwig et al. 2005, Brumo 2006). Pacific Lamprey are highly fecund: depending on their size, females lay between 30,000 and 240,000 eggs (Kan 1975). Pacific Lamprey typically die within a few days to 2 weeks after spawning (Pletcher 1963, Kan 1975, Brumo 2006). Developing embryos are known to require water temperatures below approximately 20°C (Meeuwig et al. 2005). The egg-sac larval stage, known as prolarvae, spend another 15 days in the redd gravels, during which time they absorb the remaining egg sac, until they emerge at night and drift downstream in search of suitable habitat (Meeuwig et al. 2005, White and Harvey 2003, Brumo 2006).

4.4.5 Larval (Ammocoete) Rearing

After drifting downstream, the eyeless larvae (or ammocoetes) settle out of the water column and burrow into fine silt and sand substrates that often contain organic matter (Torgersen and Close 2004, Stone and Barndt 2005, Shultz et al. 2016). Within the stream network they are generally found in low-velocity, depositional areas such as pools, alcoves, and side channels (Torgersen and Close 2004, Shultz et al. 2016). Notably, these are the same habitats preferred by juvenile Coho Salmon (Section 2). Depending on factors influencing growth rates, larval lamprey may rear in these habitats for 2.5 to 11 years (van de Wetering 1998, Goodman and Reid 2022, Hess et al. 2022), filter-feeding on algae and detrital matter prior to metamorphosing into the adult form (Pletcher 1963, Moore and Mallatt 1980, van de Wetering 1998). While the duration of larval rearing has not been described for the Eel River, it is expected that that maximum duration is typically considerably less than 11 years, since water temperatures in the watershed are generally warmer that more northerly populations and predicted to promote relatively rapid growth and metamorphosis.

Downstream movement by approximately 8 to 9 mm long newly-emerged larvae may continue into late summer, and YOY larvae continue to move downstream in relatively large numbers throughout their first summer (White and Harvey 2003, Brumo 2006). YOY larvae are expected to be widely distributed throughout the Eel River watershed, occurring from spawning locations downstream considerable distances to rearing locations. Studies of drifting larval fishes in the Van Duzen, lower mainstem Eel, and South Fork Eel sub-basins indicated YOY larval lamprey (of unknown species) were present in both the mainstems and in most major tributaries (Harvey et al. 2002, White and Harvey 2003). White and Harvey (2003) indicated that relatively few young-of the year larvae drift into the Eel River estuary based on low catches in their most downstream sites.

Larvae are generally thought to be relatively sedentary once they locate a suitable rearing location, but there are very few studies examining small- or large-scale movements. Age-1 and older larvae have been documented moving downstream, predominately at night, in the winter, spring, and summer, often in association with increases in stream flow (van de Wetering 1998, White and Harvey 2003, Brumo 2006).

Available data indicates that larval Pacific Lamprey are relatively widespread in the Eel River watershed (Stillwater Sciences 2010, Stillwater Sciences 2014, Stillwater Sciences and WNRD 2016). Electrofishing presence/absence surveys of several small to mid-sized tributaries (drainage areas of approximately 2–50 km2) found larval Pacific Lamprey only in stream reaches with drainage areas larger than approximately 15 km2, and the species was absent from sampled reaches of numerous smaller streams (and some larger streams)—many of which had suitable larval habitat (Stillwater Sciences 2014, Stillwater Sciences and WNRD 2016). Larvae in the genus *Lampetra* (western brook or river lampreys) were detected in several streams, where Pacific Lamprey were not present. Significant numbers of larval lamprey, presumably Pacific Lamprey, have been observed as far downstream as Fernbridge (Stillwater Sciences 2010) and relatively high densities of larvae (both Pacific Lamprey and *Lampetra spp.*) have been documented at a site sampled in the lower mainstem Eel River near Fortuna. The extent to which larvae utilize the expansive areas of fine sediment in the stream-estuary ecotone and estuary (downstream of Fernbridge) remains an important data gap. A laboratory study found 100% survival of larval lamprey exposed to a constant salinity of 10 ppt after 96 hours, but 0% survival at 12 ppt (after 48 hours) (Silver 2015). After 6 days of exposure to a constant salinity of 10 ppt, all larvae left their burrows and exhibit signs of stress, but all larvae exposed to 8 ppt salinity survived and behaved normally for 14 days (Silver et al. 2015). The same study found 100%

survival when salinity was oscillated between 0 ppt and 12 ppt (approximating a tidal cycle). Larval lamprey were documented persisting the lower Columbia River estuary at locations where maximum tidal cycle salinity exceeded 15 ppt, suggesting potential for them to utilize certain estuarine habitats (Silver 2015).

Availability of suitable burrowing substrates is widely recognized as one of the most important factors limiting the distribution of larval lampreys (Applegate 1950, Kan 1975, Torgersen and Close 2004, Stone and Barndt 2005, Graham and Brun 2007). In general, larvae prefer benthic habitats (typically along channel margins) characterized by silt and fine sand dominated substrates, often containing organic matter such as decaying plant material. Although larvae have been found in substrates ranging in size from fine silts to gravels, they are consistently more abundant in areas dominated by fine substrates and organic matter compared with larger sand and gravel substrates (e.g., Kainuna and Valtonen 1980, Stone and Barndt 2005, CTWSRO 2012). However, larval lamprey may avoid substrates with too high a fraction of fine silt and clay, which may inhibit oxygen uptake by clogging the gills and also obstruct burrowing due to compaction (Beamish and Lowartz 1996, Smith 2009).

Other chemical and ecological variables such as chlorophyll levels, dissolved oxygen presence, preferred food items, or organic content may also influence the extent to which a patch of fine sediment is used for rearing (Sutton and Bowen 1994, Stone and Barndt 2005, Moser et al. 2007). In addition to suitable substrate size, larval lamprey require sufficient sediment depth for successful burrowing and cover from predators. The minimum substrate depth required for rearing is unknown, but likely varies with size, with larger individuals requiring more depth. Graham and Brun (2007) found that mean depth of fine substrates was highly correlated with presence of larval lamprey in the lower Deschutes River, Oregon.

Water temperature requirements and preferences for larval Pacific Lamprey received little research, but a recent laboratory study estimated upper incipient lethal temperature (UILT; or temperature at which individual have been observed to die) to be in the range of 27.5°C to 30.2°C (Whitesel and Uh 2023), which suggests they can withstand considerably higher temperatures than juvenile salmon and steelhead. This finding is similar to ULIT estimates for four lamprey species from eastern North America, which were found to have ULITs ranging from 28°C to 30.5°C after being acclimated at 15°C (Potter and Beamish 1975). Larval lampreys can experience sublethal physiological or behavioral impacts at lower water temperatures (Clemens et al. 2016; Whitesel and Uh 2023), and how results of laboratory experiments translate to the stream environment is unknown. In an Idaho stream, Claire (2004) found Pacific Lamprey larvae in water temperatures up to 26.7°C, but reported that substrate temperatures averaged 2.2°C less than stream temperatures in the summer. This observation suggests that, in some locations, larvae may be able behaviorally thermoregulate by burrowing deeper during periods of high stream temperature.

4.4.6 Metamorphosis and Juvenile Outmigration

During metamorphosis from the larval to juvenile form, Pacific Lamprey undergo morphological and physiological changes to prepare for outmigration and parasitic feeding in salt water, including development of eyes, a suctorial disc, sharp teeth, and well-defined fins (McGree et al. 2008). Metamorphosis of Pacific Lamprey has been reported to occur from July through November in British Columbia and the Columbia River basin (Pletcher 1963, Richards and Beamish 1981, McGree et al. 2008), but timing in the Eel River is unknown. A small number of partially metamorphosed individuals (also known as transformers) were captured in Eel River watershed tributaries during the late summer and early fall (Wiyot Tribe Natural Resources

Department, unpubl. data, 2013), which is consistent with the idea that metamorphosis takes place prior to the typical fall-to-spring outmigration period. Water temperature has been shown to play a key role in initiating and controlling the rate of metamorphosis in Sea Lamprey (Holmes and Youson 1997), but water temperature requirements for Pacific Lamprey during metamorphosis and outmigration are not known.

After metamorphosis, smolt-like juveniles sometime referred to "macropthalmia" migrate to the ocean, typically in conjunction with high-flow events between fall and spring (van de Wetering 1998, Goodman et al. 2015). Limited information is available on juvenile outmigration timing in the Eel River watershed (Stillwater Sciences 2010). Juvenile Pacific Lamprey were periodically captured, sometimes in large pulses, during outmigrant trapping conducted on Redwood and Sproul creeks during April and May (S. Downie, CDFW, pers. comm., 2010). However, few conclusions about outmigration timing can be drawn from these data since traps were only operated for a part of the potential outmigration period. During year-round trapping in the upper mainstem of the Eel River, juvenile lamprey were captured in small numbers in all months; however, movement was concentrated in late winter and spring (Ebert 2008). Pulses of movement were almost always coincident with large increases in flow (Ebert 2008), which is consistent with juvenile outmigration documented in the Sacramento River (Goodman et al. 2015).

Habitat requirements of this transitory life stage are generally not well known. During metamorphosis, Pacific Lamprey typically move from fine substrate in low-velocity areas to coarser gravel and cobble substrates with moderate current and higher dissolved oxygen content (Richards and Beamish 1981). This change in habitat preference is thought to be related to changes in respiration occurring during metamorphosis that result in the need for higher dissolved oxygen levels. When metamorphosis is complete, they move to gravel or boulder substrate with high velocity currents (Beamish 1980, Richards and Beamish 1981). Salinity tolerance increases markedly as metamorphosis nears completion (Richards and Beamish 1981) and therefore estuarine habitats are likely important during this life stage. Time spent and habitat use in the Eel River estuary is an important data gap.

4.4.7 Ocean Residence

Despite the potential importance of the adult ocean stage in lamprey population dynamics, information on this stage is limited, with most research coming from the Columbia River Bain, Canada and Russia (Beamish 1980, Orlov et al. 2009, Murauskas et al. 2013, Clemens et al. 2019, Weitkamp et al. 2023). Since there are no known data on use of marine habitats by Pacific Lamprey originating in the Eel River watershed, information from these and other studies is summarized herein.

After metamorphosis, juvenile Pacific Lamprey migrate to the ocean between fall and spring where they feed parasitically on a variety of marine fishes (Richards and Beamish 1981, Beamish and Levings 1991, Orlov et al. 2009, Murauskas et al. 2013, Clemens et al. 2019). They remain in the ocean for approximately 2 to 7 years before returning to fresh water to spawn (Kan 1975, Beamish 1980, Hess et al. 2022). Factors influencing duration of ocean residency are unknown but may reflect different growth rates related to diverse feeding behaviors and prey species. Pacific Lamprey are parasitic, feeding on the blood, body fluids, and flesh of a wide range of host species (Beamish 1980, Murauskas et al. 2013, Clemens et al. 2019, Weitkamp et al. 2023). At least thirty-two different species of fish and mammals have been documented as hosts for Pacific Lamprey, suggesting opportunistic feeding behavior (Clemens et al. 2019).

Captures during trawl surveys and presence of lamprey wounds on diverse prey species from various habitats indicate Pacific Lamprey are widely distributed across much the Pacific Ocean (Beamish 1980, Orlov et al. 2009, Clemens et al. 2019, Murauskas et al. 2019, Weitkamp et al. 2023). Pacific Lamprey are widespread off the west coast of Canada and across the North Pacific Ocean and have been found as far south as Southern California (Beamish 1980, Clemens et al. 2019, Weitkamp et al. 2023). Most catches are from waters over the shelf and continental slope (Beamish 1980, Orlov et al. 2008 as cited by Luzier et al. 2011, Weitkamp et al. 2023).

Pacific Lamprey are thought to generally move to water deeper than 70 m soon after reaching the ocean (Beamish 1980), and most ocean collections of the species have been from either midwater trawls targeting Pacific Hake or bottom trawls targeting groundfish or shrimp, with very few collected in surface trawls targeting juvenile salmon (Weitkamp et al. 2023). Most captures have been in depths less than 500 m and bottom depths less than 800 m (Orlov et al. 2008 as cited by Luzier et al. 2011, Clemens et al. 2019, Weitkamp et al. 2023).

Magnitude and patterns of movement in the ocean have not been well-described. Results from recent genetics studies suggest relatively limited marine dispersal (Spice et al. 2012); however, it many of the Pacific Lamprey documented off Russian and Alaskan coasts may originate in contiguous U.S. and Canadian waters (Murauskas et al. 2013). An adult Pacific Lamprey tagged in the western Bering Sea was detected in the Columbia River, indicating that the species is capable of lengthy transoceanic migrations from feeding areas to spawning areas (Murauskas et al. 2019). Movement within the ocean is likely dictated in large part by movements of the host species (Beamish 1980, Murauskas et al. 2013).

Recent analyses indicate significant positive correlations between the abundance of a number of common host species (including Pacific hake *Merluccius productus*, walleye pollock *Theragra chalcogramma,* Pacific cod *Gadus macrocephalus*, Chinook Salmon *Oncorhynchus tshawytscha*, and Pacific herring *Clupea pallasii*) and returns of adult Pacific Lamprey to the Columbia River basin between 1997 and 2010 (Murauskas et al. 2013). Results of these analyses indicated that regional indices of oceanic productivity (Pacific Decadal Oscillation and coastal upwelling anomalies) help explain variation in Pacific Lamprey adult returns. Based on these correlations, the authors suggest that conditions during the adult feeding phase may be the primary factor determining spawning escapement to the Columbia River. The roles of host availability and ocean productivity and their relative importance to Pacific Lamprey populations relative to freshwater conditions warrant additional research.

4.5 Life-history Diversity and Limiting Factors Conceptual Models

This section synthesizes information from the Eel River and elsewhere within the range of Pacific Lamprey to identify and characterize life-history strategies with potential to occur in the watershed. The overall approach, rationale, and uses of these life-history conceptual models in the context of the Restoration Plan are described in Section 3 of the Plan.

Across their range, and presumably within the Eel River watershed, Pacific Lamprey can display a wide range of life-history strategies. This diversity includes, but is likely not limited to the following:

- Stream-maturing and ocean-maturing adult ecotypes that may enter freshwater at the same time, but spawn 1 year apart;
- Variation in location and timing of spawning within and between years (within adult ecotypes);

- Variation in larval rearing locations and time spent in freshwater before outmigrating to the ocean
- Variation in time spent in the ocean and,
- Variation in age at spawning due to a potentially wide range of freshwater and ocean rearing times.

Figure 4-5 provides a simplistic overview of adult life-history strategies, which are discussed in Section 4.5.1. Section 4.5.2 discusses life-history diversity in the larval and juvenile life stages.

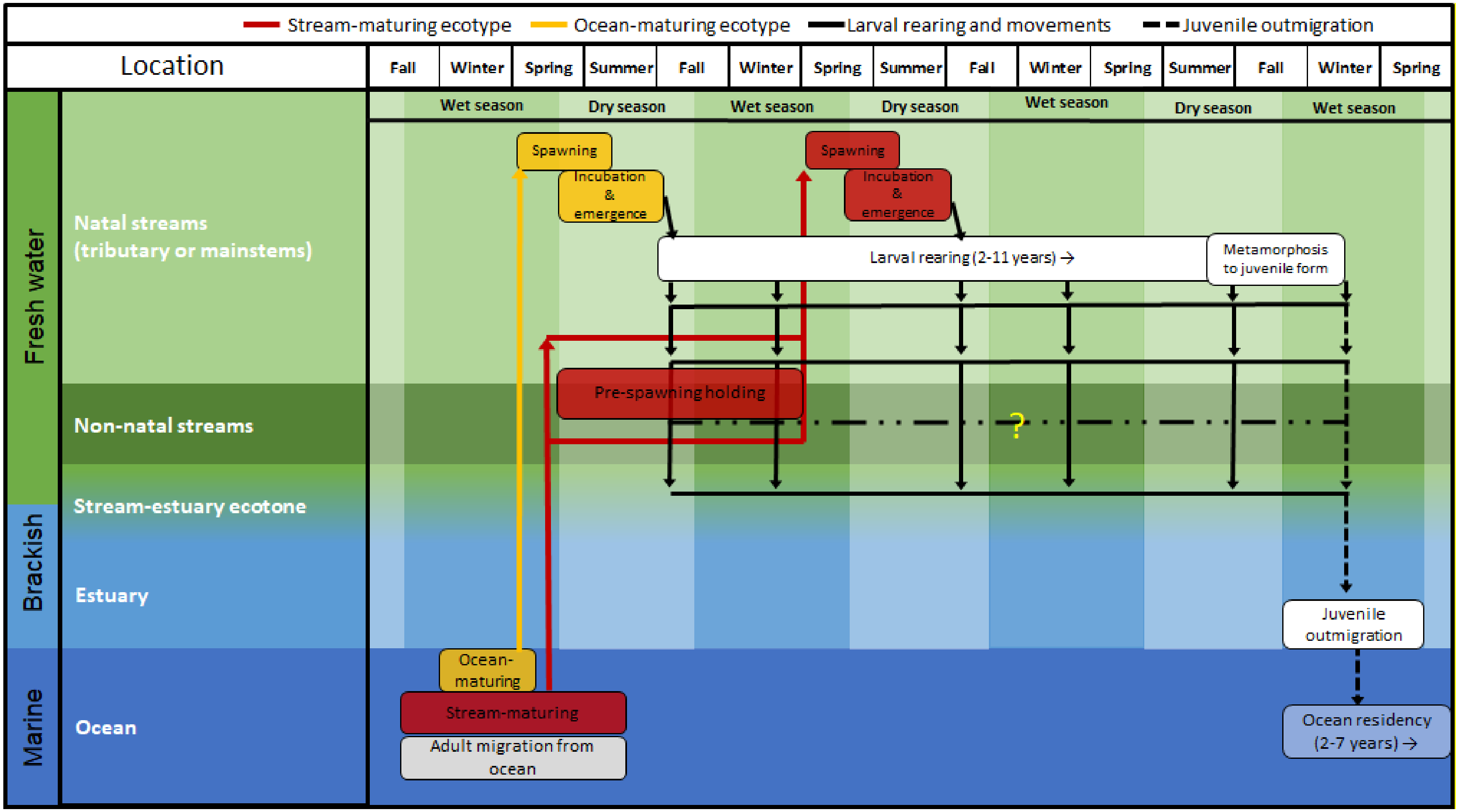

Figure 4-5. Life-history conceptual diagram for Pacific Lamprey in the Eel River, showing pathways across time and space for primary adult life-history strategies, or ecotypes, which are represented by yellow and red lines. Arrows direction represents movements between primary portions of the watershed. In each year, river-maturing individuals that entered freshwater the previous year spawn during the same period as ocean-maturing individuals from the current year. Since adult migration from the ocean is only shown for 1 year, this overlapping spawning by the two ecotypes is not depicted here. Note: extent of use of non-natal streams for larval rearing is designated with "?" since it is a key uncertainty.

4.5.1 Adult Migration, Holding, and Spawning

Various scientists and Native American Tribal members have documented or hypothesized about diversity in Pacific Lamprey adult life-history strategies across the species' range, primarily related to differences in timing of freshwater entry, sexual maturation, spawning timing, and migratory patterns (Close et al. 2004, Petersen Lewis 2009, Moyle et al. 2009, Clemens et al. 2013, Hess et al. 2014, Parker et al. 2019, Hess et al. 2020). Primary adult life-history strategies (Section 4.5.1.1) and other adult life-history diversity with potential to occur in the Eel River (Section 4.5.1.2) are described below.

4.5.1.1 Ocean-maturing and stream-maturing ecotypes

Clemens et al. (2013) documented two distinct adult life-history strategies in the Klamath River based on differences in morphology and sexual maturity (as measured by egg mass size and histology) at time of freshwater entry: ocean-maturing and stream-maturing ecotypes. Evidence for a genetic basis for these two ecotypes was found in the Klamath River (Parker et al. 2019) and Columbia River Basin (Hess et al. 2020). Although these life-history strategies have not been clearly described in the Eel River, their presence in the Klamath and Columbia basins suggest they are likely expressed through the range of Pacific Lamprey.

As described in Section 4.4, the ocean-maturing ecotype is thought to spawn several weeks after entering fresh water, whereas the stream-maturing ecotype spends about 1 year in freshwater prior to spawning (Clemens et al. 2013, Parker et al. 2019). Egg mass of the river-maturing ecotype is typically less than half of the ocean-maturing ecotype at freshwater entry (Clemens et al. 2013). Parker (2018) found significant differences in the onset of freshwater migration between the two life-history strategies in the Klamath River: the ocean-maturing ecotype entered fresh water primarily in the winter; whereas the river-maturing ecotype entered fresh water throughout the winter, spring, and summer (Parker 2018; Parker et al. 2019). Despite differences in peak river entry timing and time spent holding in freshwater before spawning, river-maturing individuals spawn during the same period and are expected to interbreed with ocean-maturing individuals (Parker et al. 2019).

Clemens et al. (2016) developed a conceptual model of how differences in water temperature and stream flow may differentially select for the two Pacific Lamprey adult life-history strategies. This model predicts that warm summertime temperatures and low river flows select against the stream-maturing ecotype (and for the ocean-maturing ecotype) due to increased maturation rate, slowed migration rates, increased mortality in females, and increased gonadal damage in males. In contrast, locations with relatively cool temperatures and high river flows are predicted to select for the stream-maturing ecotype, due to slower maturation, faster migration, and decreased temperature-related mortality (Clemens et al. 2016). Based on this model, Clemens et al. (2016) hypothesized that, within the range of Pacific Lamprey, there may be a higher proportion of ocean-maturing individuals further south and a lower proportion further north. Recent genetic analyses from Hess et al. (2020), generally supports this hypothesis, predicting a higher proportion of the stream-maturing ecotype in British Columbia, and a mixture of stream- and ocean-maturing ecotypes in more southern portions of the species' range. The same study suggests that the ocean-maturing ecotype is distributed mainly in coastal regions and the river-maturing ecotype becomes more prevalent further inland—presumably due to differences in temperature regimes and migration distances to spawning areas.

Relative prevalence of these two adult life-history strategies and their distributions in the Eel River is unknown, but research on this topic is warranted given the important role they are expected to play in resilience and abundance of the watershed's Pacific Lamprey population. The diversity of stream flow and temperature regimes in habitats across the large and diverse Eel River watershed suggests both ecotypes present but likely vary in prevalence in different locations across the watershed. Based on the results and hypotheses from Clemens et al. (2016) and Hess et al. (2020), spawning by the ocean-maturing strategy is hypothesized to be more prevalent in streams closer to the coast, especially those that are warmer and drier in the summer (i.e., watersheds that have a relatively high fraction of Central Belt mélange geology; Dralle et al. 2023). The stream-maturing strategy is expected to be more prevalent in cooler coastal streams with perennial flows (i.e., watersheds with a high fraction of Coastal Belt geology, which acts to retain winter run-off and slowly drain groundwater during the summer (Dralle et al. 2023), as well as more inland and higher-elevation streams that require a long migration distance and maintain cool summer water temperatures.

4.5.1.2 Other adult life-history diversity

In addition to the two primary adult life-history strategies discussed above, several other sources of adult life-history diversity that likely increase resilience of the Pacific Lamprey population may exist. For example, the species spawns over a period of 3 to 4 months and offspring of earlier spawning individuals can be exposed to vastly different environmental conditions than later spawning individuals because stream flows are dropping and water temperatures are increasing during the late-spring and summer embryonic development period (Gunckel et al. 2009, Brumo et al. 2009, Stillwater Sciences and WNRD 2016).

Another potential source of life-history diversity is variation in age at spawning, which is related to both duration of larval freshwater residence (2.5 to 11 years) and duration of adult ocean residence (2 to 7 years). Assuming most larvae in the relatively warm Eel River watershed undergo metamorphosis and emigrate to the ocean by at least age 6, in any given spawning year, there could be adults ranging in age from approximately 4.5 to 13 years old that are interbreeding. This genetic intermixing between multiple brood years (offspring born in different years), likely helps maintain genetic diversity imparts resilience to the population.

Other potentially distinct adult life histories likely exist but require further study. For example, based on limited count data, Moyle et al. (2009) report that there may be two distinct "runs" of adult Pacific Lamprey in the Russian River, where a larger spring run and smaller fall run has been observed. Various Native American Tribal members have documented distinct adult morphotypes, including a larger, gray-blue type known as "night eels" and a smaller, brown type called "day eels" (Close et al. 2004). It is unclear whether these types are distinct life history strategies, or just two different overlapping adult run cohorts of the stream-maturing ecotype: (1) immature adults that recently migrated from the ocean (night eels) and (2) spawning stage adults that have held in freshwater for a year (day eels). Finally, Hess et al. (2014, 2020) found a genetic basis for phenotypes related to body size, migration distance, and level of sexual maturation and suggest that these traits may be expressed as different life-history strategies adapted to unique ecological conditions throughout the species' range. Research is needed to understand the prevalence and distribution of these traits in the Eel River and how they may interrelate with ocean- and stream-maturing ecotypes described above.

4.5.2 Larval Rearing

Due to their multi-year freshwater residency and wide distribution in the Eel River watershed, Pacific Lamprey larvae are exposed to a wide range of environmental conditions, from summer low flows and high temperatures to scouring winter flows and low temperatures. Like salmonids, the species is expected to have evolved a diversity of larval and juvenile life-history strategies in response to these environmental fluctuations. Distinct larval and juvenile life-history strategies have not been described for Pacific Lamprey in the Eel River, but during its protracted freshwater residency, the species is expected to exhibit significant variation in movement patterns, growth rates, and habitat use throughout its range in the watershed. Characterizing this diversity and understanding the mechanisms that create it are important for restoring this important species.

4.5.2.1 Diversity in larval rearing locations and movement patterns

As with juvenile salmonids, larval Pacific Lamprey are expected to spend variable amounts of time rearing in their natal streams and non-natal habitats before emigrating to the ocean. Typical patterns of larval movement and rearing across time and space have not been described, but potential patterns are depicted in Figure 4-5. Following emergence from redd gravels, if they can find stable, fine-sediment rearing habitats nearby, some individuals may undergo relatively short downstream movements and then rear in their natal streams throughout their multi-year freshwater residency. Other newly-emerged larvae may drift downstream for considerable distances, leaving natal streams, before settling in suitable rearing habitat in the lower mainstem. Another subset of larvae may make multiple movements throughout their time in fresh water in response to shifting habitat conditions or density-dependent habitat limitations, rearing in several locations (natal stream, larger river, stream-estuary ecotone) before entering the ocean.

In general, movements by larvae are expected to occur either (1) during the late spring and summer, when the receding hydrograph shrinks the area of wetted rearing habitats along the stream margins, or (2) in the winter during periods of high flow that can scour fine sediment habitats (Brumo 2006, van de Wetering 1998, Harvey et al. 2002, White and Harvey 2003). Stream flows drop substantially during the transition from the wet season to the dry season, causing much of the available larval habitat along stream margins to go dry, presumably forcing larvae into higher densities or causing them to move in search of new habitat. Lamprey larvae rearing at high densities may exhibit slower growth, lower survival, later metamorphosis, and a higher frequency of males compared with those rearing at low densities (Mallatt 1983; Rodriguez-Muñoz et al. 2003, Zerrenner and Marsden 2005). These density-effects may have population-level impacts due to decreased survival and lost reproductive potential. During extreme drought years, impacts of both density-dependent and density-independent sources of summer larval mortality are expected to higher, especially in smaller streams and locations with limited rearing habitat area. Larvae that are displaced downstream by receding flows are likely vulnerable to predation, starvation, and exposure if they cannot find suitable habitat. Limited observations indicate considerable areas of fine sediment rearing habitat persists throughout the summer in lower-gradient reaches of larger tributaries, along with the South Fork Eel, Van Duzen, and mainstem Eel rivers (Stillwater Sciences 2014). These locations are expected to support larval lamprey originating from numerous spawning streams.

During typical winter flows, substantially more fine sediment rearing habitat (the majority of which is found along stream margins) is expected to be inundated, thus summer rearing habitat may be more limiting to larval survival and abundance than winter habitat in many streams. However, larvae are susceptible to high scouring flows and thus need habitat that is relatively stable and protected from high flows or connected with the flood plain. Larval lamprey have been documented moving downstream during high flows, which may be due in part to scouring of fine sediments or other changes in habitat suitability (van de Wetering 1998, Harvey et al. 2002, White and Harvey 2003).

During both summer and winter these movements, finding new downstream rearing is critical for survival of larval lamprey. Limited observations indicate that larval fine-sediment rearing habitat is relatively scarce in many areas of the watershed, suggesting that rearing habitat availability could limit the Pacific Lamprey population under current conditions. There appears to be ample suitable spawning habitat to support relatively high numbers of spawning adults across much of the Eel River watershed (Stillwater Sciences 2014). For this reason, availability of spawning habitat is not expected to limit the population in most years relative to larval rearing habitat.

Because larvae typically spend several years rearing prior to metamorphosis, each year-class potentially competes for space with several other year-classes (in addition to larvae from *Lampetra spp.* in many streams), increasing the likelihood that carrying capacity of rearing habitat would be exceeded. Even in higher gradient reaches where spawning habitat is less abundant, availability of fine substrate rearing habitat is expected to limit the size of the larval population. Overall, availability of suitable rearing habitat may be a central factor governing the number of larval and juveniles produced from the Eel River watershed. A better understanding of rearing habitat availability throughout watershed is needed to test this hypothesis.

4.5.2.2 Variation in age-at-metamorphosis

Another source of diversity within the Pacific Lamprey larval population is age-at-metamorphosis to the juvenile form. In a study of larvae originating from various natal streams in the Columbia River Basin, Hess et al. (2022) found that the age of outmigrating juveniles ranged from 4 to 11 years, with a mean of 6.7 years. They found that age of these juveniles varied between years and locations, which may be driven by differences in larval growth rate related to temperature differences. In the same study, Hess et al. (2022) found considerable variation in size-at-age (larval growth rate) for 5-year-old and 6-year-old larvae between three sites with variable summer stream temperatures and watershed area. The largest sized 5-year-old and 6-year-old larvae were captured in the largest and warmest stream (mean at age 5 = 151 mm; age 6 = 157 mm). The smallest larvae at the same ages were in the smallest and coolest stream (age 5: 109 mm; age 6: 115 mm). This finding suggests that a combination of warm temperature and larger stream size may lead to faster growth and earlier metamorphosis in Pacific Lamprey, similar to Great Lakes Sea Lamprey (Dawson et al. 2015). Since Pacific Lamprey in the Eel River spawn and rear in a wide range of stream sizes, with varying water temperatures, considerable variability in growth rates and age at outmigration is expected across the watershed. The fewer years that larvae spend in fresh water, the lower the risk of freshwater mortality due to predation, stranding, disease, or other factors and thus the more individuals that survive to reach the juvenile stage. Larval growth rate may also influence size at outmigration, which is expected to influence estuary and ocean survival, as is the case with salmonids. Because of their potential large impact on population dynamics, the mechanisms that regulate larval growth potential and food resources across the watershed warrant research.

4.5.3 Juvenile Emigration

Juvenile production, loosely defined here as the number of individuals that enter the ocean, is expected to be a central determinant of the number of adult Pacific Lamprey that return to a large watershed such as the Eel River (Stillwater Sciences 2014). For this reason, understanding life-history diversity and the primary factors limiting abundance of this stage is critical for species recovery.

In addition to the variation in age at outmigration described above, the primary types of diversity in the juvenile life stage are (1) time of outmigration and (2) size at outmigration. Juveniles have potential to outmigrate throughout the entire wet season, from November through May, but pulses of movement typically occur with increases in flow (Ebert 2008, Goodman et al. 2015). This variable timing means that different individuals may encounter variable ecological conditions both during their emigration through the river and when they reach the ocean, presumably serving as a bet hedging strategy for the population that ensures at least some individuals encounter suitable estuarine and ocean conditions. Juvenile lamprey moving downstream during high, turbid flows are expected to have higher survival compared with those moving during low clear water, when they are more vulnerable to predation. Additionally, key predators such as Sacramento Pikeminnow are more metabolically active when water temperatures begin to increase the spring, likely resulting in higher predation on juvenile lamprey moving during the spring compared with the late fall and winter when temperatures are cooler. Time of outmigration also determines what ocean conditions are encountered by young adult lampreys. Entering the ocean at a time when important host species are abundant off the coast of the Eel River may be critical for survival, since lampreys must begin feeding and growing soon after entering the ocean to avoid starvation or predation.

Size at outmigration to the ocean, which is influenced by habitat quality and growth during the larval phase, is also expected to influence both riverine and ocean survival. Larger individuals have higher swimming speeds and thus a greater likelihood of escaping both riverine and ocean predators and catching hosts.

4.6 Conceptual Model Outcomes

4.6.1 Stressors

The root causes of lamprey population decline are unknown but are likely multifaceted. Due to similarity in habitat requirements and life histories between the Pacific Lamprey and anadromous salmonids, as well as some parallels in the timing of their population collapse (i.e., following the 1955 and 1964 floods), it is likely that many of the same factors led to their decline. Dams, diversions, grazing, urban development, mining, estuary modification, decline in prey abundance, and non-native species have all been postulated as factors limiting Pacific Lamprey abundance across their range (Moyle et al. 2009, Luzier et al. 2011). Little direct evidence of factors limiting overall population size of Pacific Lamprey in the Eel River watershed exists. However, likely factors include the Potter Valley Project dams and water withdrawals, migration obstructions affecting upstream passage to historical spawning areas, the effects of the large floods of 1955 and 1964, forest management and roads, and introduction of non-native species—as well as cumulative and synergistic impacts from these factors.

Table 4-2 lists stressors with potential to adversely impact each life stage of Pacific Lamprey. This list was generated primarily from the above species description and conceptual model, Boyce et al. (2022), and Stillwater Sciences (2014), which includes more in-depth discussion of key factors with potential to affect survival of each life stage. Importantly, while each stressor listed has the potential to adversely affect one or more life stages, some may be more important than others in terms of limiting population productivity, expression of life-history diversity, and abundance of returning adults. In some cases, factors affecting survival of specific life stages may or may not affect numbers of returning adult lampreys. For example, under current conditions, the area of suitable spawning habitat is generally not expected to limit population size of Pacific Lamprey in the Eel River watershed (Stillwater Sciences 2014).

The impact of a given stressor on habitat capacity, growth, and survival—and ultimately the number of returning adults in a cohort—is also expected to vary by year (due to differences in hydrology and temperature regimes or larval densities). For example, the impacts of elevated water temperature on larval survival and juvenile production are expected to be greater during periods of drought relative to wetter periods. The population-level impact of certain stressors is also expected to vary between natal streams due to intrinsic differences in temperature and hydrology driven by underlying geology (e.g., Dralle et al. 2023).

Finally, since they inhabit different portions of the watershed at different times, different life-history strategies are also expected to be differentially impacted by various stressors. For example, because it holds in fresh water through the summer, the stream-maturing adult ecotype is more likely to be adversely affected by elevated water temperatures relative to the ocean-maturing ecotype.

Based on Section 4.5 above and the limiting factors conceptual model prepared by Stillwater Sciences (2014)—which integrates information on life-stage-specific habitat carrying capacities and density-independent mortality to identify key population bottlenecks hypothesized to limit the number adults returning to the Eel River—the following are considered important factors with high potential to limit Pacific Lamprey population size and life-history diversity:

- Passage barriers that obstruct adult access to spawning habitat;
- Reduced availability and quality of main channel and off-channel larval rearing habitats due to channel simplification and degraded water quality, leading to lowered growth and survival;
- Reduced survival of juveniles during outmigration due to increased predation from non-native pikeminnow, channel simplification, and degradation of the estuary;
- Lowered ocean survival due to alterations to host availability, ocean productivity, or bioaccumulation of contaminants; and
- Diminished quality of over summer holding habitat due to channel simplification and increased water temperatures, decreasing survival and prevalence of the stream-maturing life-history strategy.

Importantly, as described in Section 4.6.3, there are many gaps in our understanding of Pacific Lamprey in the Eel River and additional studies are needed to better understand the extent to which these key factors limit the population and the underlying environmental and ecological factors causing these limitations.

Table 4-2. Stressors with potential to adversely impact each life stage of Pacific Lamprey in the Eel River watershed, with life-history strategies that are predicted to be the most impacted.

Life stage	Stressor	Drivers (underlying causes of stressor to be addressed by restoration)	Mechanisms of impact on population productivity, abundance, distribution, and resilience	Life-history strategies potentially highly impacted
Adult holding and migration	Anthropogenic physical barriers to movement	Dams, poorly-designed or failed road crossings, other manmade obstructions to movement.	Reduced spawning distribution, lowered reproductive success, and potential lost larval life-history diversity.	All adult strategies
	Degraded large cobble and boulder holding habitats	Channel aggradation and fine sediment infiltration of interstitial spaces due to increased sediment delivery from historical and current logging, road construction & management, and fires.	Increased pre-spawning mortality from predation.	Stream-maturing ecotype
	Increased summer water temperatures	Loss or alteration of riparian forests, impaired dry-season stream flows (see below for drivers), climate change.	Reduced extent of suitable holding habitat. Increased mortality and gonadal damage. Increased prevalence of disease (Clemens et al. 2016).	Stream-maturing ecotype
	Increased prevalence of predation by pinnipeds, otters, and other predators	Loss of escape cover and channel complexity due to reduced channel aggradation and fine sediment infiltration of holding and staging habitats.	Pre-spawning mortality	All adult strategies
	Increased prevalence of disease	Crowding cause by delayed fall stream flows; increased water temperatures due to diversion or climate change; other unknown drivers of disease prevalence and virulence.	Pre-spawning mortality	Stream-maturing ecotype
	Poaching (for consumption or bait)	Inadequate education and enforcement.	Pre-spawning mortality	All adult strategies
Spawning and incubation	Fine sediment infiltration of spawning substrates and redds	Landslides and erosion of fine sediment due to historical and current logging, road construction and management, and fires. Reduced sediment sorting due to channelization, floodplain disconnection, and lack of wood.	Reduced egg-to-fry survival	All adult strategies
	Increased water temperatures	Loss or alteration of riparian forests, impaired dry-season stream flows (see below for drivers), climate change.	Lowered embryo survival and increased developmental abnormalities at temperatures greater than approximately 20°C during incubation (Meeuwig et al. 2005).	All adult strategies
	Impaired spring recession flows	Climate change, water diversions, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Increased incidence of redd desiccation and lowered embryo survival.	All adult strategies
	Increased prevalence of predation	Introduction of non-native cyprinids that can prey on spawning-stage adults and their eggs. Increased water temperatures and reduced channel complexity.	Pre-spawning mortality and lowered embryo survival.	All adult strategies

Larval rearing	Entrainment and stranding by diversions	Unscreened or poorly-designed water diversions, including the Van Arsdale Diversion, can entrain and strand larval lamprey, particularly smaller size classes.	Reduced larval survival.	All larval strategies
	Reduced area of low-velocity, fine sediment instream rearing habitat	Reduced wood volume due to removal & supply. Channel simplification from road construction. Loss of beaver dams.	Reduced larval rearing habitat capacity.	All larval strategies
	Impaired connectivity with and loss of floodplain/off-channel rearing habitats	Channelization, channel incision, levees, bank armoring & roads, wetland draining & agricultural conversion, reduced wood volume, and loss of beaver dams.	Reduced larval rearing habitat capacity in the wet season. Potentially reduced larval growth.	All larval strategies
	Alteration of habitat quantity and quality in the stream-estuary ecotone.	Channel simplification due to levees, aggradation and pool filling, wetland drainage for agricultural conversion, agricultural and urban run-off.	Reduced growth and survival of early emigrant juveniles due to altered estuarine food webs, impaired water quality, lost access to off-channel habitats, and loss of escape cover.	All larval strategies
	Impaired dry-season stream flows	Climate change, water diversion for rural agriculture and domestic use, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Reduced area of larval rearing habitat capacity. Mortality due to poor water quality and increased predation risk for fish forced to move by receding flows. Reduced growth due to higher densities.	All larval strategies
	Increased water temperatures	Loss or alteration of riparian forests, impaired dry-season stream flows due to diversions, climate change.	Reduced extent of suitable rearing habitat. Direct mortality. Sublethal effects such as reduced growth. Potential for increased susceptibility to disease or predation.	All larval strategies
	Reduced area of and restricted access to thermal refugia	Filling of thermally-stratified deep pools due to channel aggradation caused by sediment inputs from logging practices, road building and floods. Degraded habitat at cold tributary confluences due to channel aggradation and reduced supply of large wood.	Reduced extent of suitable rearing habitat. Direct mortality. Sublethal effects such as reduced growth. Potential for increased susceptibility to disease or predation.	All larval strategies
	Increased prevalence of predation, especially from non-native predators	Introduction and expansion of Sacramento Pikeminnow and other non-native predators. Decreased stream flows and increased water temperatures.	Reduced larval survival.	All larval strategies
	Increased prevalence of disease	Reduced stream flows, increased temperatures, increased prevalence of alternate hosts	Reduced larval growth and survival.	All larval strategies
	Alterations to the timing, magnitude, and availability of food resources	Loss of marine-derived nutrients and other beneficial species interactions such as freshwater mussels, alterations to the algal community due to elevated nutrient inputs from agricultural run-off, degraded riparian forests, and other ecological changes affecting food resources.	Reduced larval growth and survival and potential lost life-history diversity (reduced prevalence of strategies that historically relied on food resources and beneficial species interactions that have been lost)	All larval strategies
	Elevated levels of chemical contaminants / toxins in rearing habitats	Mercury inputs from historically mined areas; agricultural and industrial toxins such as polychlorinated biphenyls (PCBs), dioxins, atrazine, flame-retardants, and various pesticides; flame-retardants from fire suppression.	Potential for acute mortality or chronic impacts on growth or fitness.	All larval strategies
Juvenile metamorphosis and outmigration	Increased water temperatures	Loss or alteration of riparian forests, impaired stream flows due to diversion, climate change.	Potential for reduced growth, delayed metamorphosis, and decreased juvenile survival.	All
	Impaired fall pulse flows and spring recession flows	Climate change, water diversions, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Reduced juvenile to ocean survival.	All
	Increased prevalence of predation	Introduction and expansion of Sacramento Pikeminnow and other non-native predators. Loss of escape cover due to decreases in large wood volume and area of unimbedded cobble-boulder substrates; decreased stream flows and increased water temperatures.	Reduced juvenile to ocean survival.	All
	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	Reduced juvenile to ocean survival.	All
Ocean residence	Alterations to host availability and ocean productivity	Climate change related influences on strength and timing of ocean upwelling, marine productivity, and populations of host species. Commercial fishing impacts on host species populations.	Reduced growth and ocean survival.	All
	Host contaminant loads and bioaccumulation	Emissions and bioaccumulation of mercury and other pervasive contaminants	Reduced ocean survival or altered reproductive development and fitness.	All
	Increased incidence of predation and fisheries by-catch	Changes in predator abundance due to climate change or ecological changes related to commercial fishing.	Reduced ocean survival.	All

4.6.2 Restoration Take-home Points

Because of the numerous parallels and shared habitats between Pacific Lamprey and anadromous salmonids (Lamprey Technical Workgroup 2023), many of the restoration strategies and actions aimed at recovering salmonids in the Eel River (especially for Coho Salmon due to shared need for low-velocity habitats; Section 2.5.2) are expected to benefit Pacific Lamprey. However, there are numerous differences between the species that point to the need for targeted restoration actions for Pacific Lamprey (Lamprey Technical Workgroup 2023). For example, because of considerable differences in swimming and jumping abilities between lamprey and salmonids, actions designed to improve fish passage require species considerations for lamprey. Based on the above review, conceptual models, and identified stressors, the following central themes and focus points related to recovery of Pacific Lamprey in the Eel River watershed:

- Evaluating and improving adult passage at road crossings and other migration obstacles should be a priority, since it has potential to open up large areas of habitat not currently accessible.
- Maintaining and restoring cool river temperatures and stream flows and creating complex habitats that support over-summer holding is critical for promoting adult life-history diversity and preventing loss of the stream-maturing adult life history.
- Maintaining and restoring dry season flows to prevent desiccation and loss of larval habitat is critical.
- Restoration of off-channel features and creating in-channel low-velocity habitats with fine sediment through construction of large wood features are important actions, since larval rearing habitat quantity and quality may limit juvenile production in many areas.
- Taking actions to improve juvenile survival during outmigration are important, since low juvenile survival may limit the overall population. These actions include suppression of non-native pikeminnow and adding channel complexity within mainstems and the estuary.
- Educating the public, as well as the scientific and restoration communities, about the ecological value and restoration needs of Pacific Lamprey is paramount due to lack of understanding of and widespread misperceptions about the species (Clemens and Wang 2021).
- During design and implementation of habitat restoration actions targeting salmonids, steps should be taken to (1) protect Pacific Lamprey from unintended consequences of those actions (e.g., dewatering impacts on the larval life stage) and (2) consider lamprey habitat needs when evaluating design alternatives.
- Filling key data gaps is needed to conduct informed prioritization and implementation of restoration actions for Pacific Lamprey (Section 4.6.3).
- Improving coordination amongst lamprey research and monitoring efforts within the Eel River watershed and across the larger region is needed to (1) fill key data gaps that impeded efficient species recovery and (2) leverage limited funding that is available to support lamprey research, monitoring, and restoration.

4.6.3 Key Data Gaps

Relative to salmon and steelhead, very little research and monitoring has been conducted to describe Pacific Lamprey distribution, life-history timing, or population status in the Eel River watershed. Key data gaps for the species include:

- Distribution of each freshwater life stage in the watershed;

- Factors influence larval habitat quality and suitability (beyond sediment size) such as water temperature, dissolved oxygen, chemical composition, and food resources;
- Presence and severity of barriers to adult passage;
- Relative prevalence of the ocean-maturing and stream-maturing adult ecotypes in the watershed as a whole and within different sub-watersheds;
- Range and peak timing of adult migrations for the ocean of stream-maturing vs. ocean-maturing ecotoypes;
- Important holding locations for adult Pacific Lamprey;
- Role of thermal refugia in supporting both rearing larvae and over-summering adults;
- Seasonal movement patterns and duration of freshwater residence of larval lamprey watershed and factors controlling them;
- Timing of juvenile outmigration and level of juvenile production at the watershed and tributary scale;
- Abundance and density of spawning adults and larvae at the watershed and tributary scale;
- Extent to which juveniles born in the Eel River watershed return to the watershed (vs. straying to other river systems);
- Population origin and relative abundance of adults originating from other watersheds (juveniles born outside the Eel);
- Use of non-natal streams for adult holding and larval rearing;
- Use of the estuary and stream-estuary ecotone, both adult holding, larval rearing, and juvenile outmigration;
- Foodscape for larval rearing and growth potential in different habitats; and
- Ocean distribution, residence time, and primary host species of juveniles from the Eel River and factors influencing them

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5 GREEN STURGEON

5.1 Species Overview

5.1.1 Population Status and Structure

North American Green Sturgeon (hereafter Green Sturgeon) are a widely distributed anadromous and marine-oriented species found in nearshore waters from Baja California to the Bering Sea (Adams et al. 2007, NMFS 2009a, Lindley et al. 2011). There are two genetically DPSs of Green Sturgeon: (1) a Northern DPS consisting of populations originating from coastal watersheds northward of (and including) the Eel River in California, with documented spawning populations in the Klamath, Rogue, and Eel rivers; and (2) a Southern DPS consisting of populations originating from coastal watersheds south of the Eel River, with the only known spawning population occurring in the Sacramento River Basin (NMFS 2006, Seesholtz et al. 2015, Stillwater and Wiyot Tribe Natural Resources Department [WNRD] 2017). The distributions of both the Northern and Southern DPSs overlap outside of their natal rivers where they congregate to feed in coastal estuaries and bays (Lindley et al. 2011). Notable feeding areas include Humboldt Bay, Columbia River estuary, Umpqua River estuary, Willapa Bay, and Grays Harbor (Heublein et al. 2009, Lindley et al. 2011).

While the Northern DPS is not listed under the federal ESA or the CESA, it is considered a Species of Concern by NMFS (NMFS 2006) and a Species of Special Concern by the California Department of Fish and Wildlife (CDFW) (CNDBB 2024). Unlike the federally threatened southern DPS, Northern DPS Green Sturgeon are not considered to be at risk of range-wide extinction, or of becoming endangered in the foreseeable future (NMFS 2006, Adams 2007). However, Northern DPS Green Sturgeon in the Eel and elsewhere have been adversely affected by numerous human activities (i.e., loss and degradation of spawning habitat from development and dam construction, mortality from poaching, etc.) and substantial knowledge gaps regarding population dynamics and overall abundance make it difficult to accurately assess long term trends.

In the Eel River watershed, the Green Sturgeon population appears to have undergone a substantial decline in abundance compared with historical levels (Adams et al. 2007). Anecdotal reports of adults in the Eel River go back as far as 1877, with articles published in the Ferndale Express reporting fishermen catching “large numbers of sturgeon” in 1899 and the lower Eel River near Scotia being “well filled with sturgeon of gigantic size” (Van Kirk 1996). Moyle (2002) and Moyle et al. (2015) suggest that aggradation of holding and spawning habitats caused by major flooding in 1964—which exacerbated the effects of extensive logging in the intrinsically erosive watershed—extirpated the spawning. However, Puckett (1976) captured numerous juvenile Green Sturgeon in the mainstem Eel River between 1967 and 1970, suggesting that spawning occurred only a few years following the aforementioned floods. Recently, widespread incidental observations of relatively small numbers of adult Green Sturgeon have been documented in the lower Eel River near Fortuna, with adults holding in the mainstem approximately 140 (river kilometers (87 miles) from the ocean indicate spawning still occurs in the watershed (Stillwater Sciences and WNRD 2017).

5.1.2 Distribution

Adult Green Sturgeon have been observed in mainstem Eel River from the estuary upstream to Island Mountain, approximately 140 river kilometers (87 miles) from the ocean (Murphy and Dewitt 1951, Puckett 1977, Stillwater Sciences and WNRD 2017). Few accounts exist of the species occurring in the other major tributaries, but CDFG staff reported observing a sturgeon in the South Fork Eel River at the base of the Benbow dam in January 1943 (CDFW, unpubl. data, 1943). Historical newspaper articles from the Rohnerville Herald reported observations of large sturgeon in the South Fork Eel River near Garberville (in 1878) and in the lower Van Duzen River in 1883 (Van Kirk 1998).

No recent observations of sturgeon in South Fork Eel River, Van Duzen River, or other large tributaries to the Eel River have been reported. Based on historical observations and the contributing drainage area (proxy for channel size and pool depth) of locations where the species has been documented, they have potential to occur in any channel with a drainage area >1,000 km^2 (large mainstem channel archetypes; see Appendix B) and possibly in smaller channels. Assuming adequate conditions for upstream passage, the potential upper distribution includes: (1) the Van Duzen River upstream to Yager Creek, (2) the South Fork Eel River upstream to the East Branch, (3) the Middle Fork Eel River upstream to Williams Creek (nearly to Black Butter River), and (4) the upper mainstem Eel River to Tomki Creek (Figure 5-1).

Spawning adults are expected to occur in the mainstem Eel River in spring and early summer. High-quality spawning substrate in deep pools appears to be most available in mainstem reaches between the South Fork and Middle Fork Eel River (Stillwater Sciences and WNRD 2017). Young-of-year juveniles (<140 mm) and larvae (<75 mm) captured near McCann and Fort Seward suggest spawning may occur in nearby mainstem reaches (Puckett 1976). In dry years when low flows inhibit upstream movement, holding and spawning adults may congregate further downstream. Some adults may outmigrate soon after spawning in late spring or summer, whereas others may remain near spawning locations before outmigrating in fall or winter.

Larval sturgeon remain in the vicinity of spawning locations for several weeks, at which point they distribute to downstream habitats where they will remain until metamorphosing to the juvenile stage. Juveniles may rear in the middle or lower mainstem reaches of the Eel River or estuary throughout the year. Young-of-year juvenile Green Sturgeon have been documented during limited historical trapping in the mainstem Eel River as far upstream as Fort Seward (rkm 100) and as far downstream as the mouth of the Van Duzen River (Murphy and Dewit 1951 and Puckett 1976). Relatively small juveniles captured moving downstream near the mouth of the Van Duzen suggest that they may rear in the estuary for extended periods, a behavior observed in the Klamath River and San Francisco Bay Estuary (Murphy and Dewitt 1951).

Non-spawning adult and sub-adult Green Sturgeon (from both the northern and southern DPS) occupy coastal estuaries and bays along the Pacific Coast of North America between spawning migrations (Section 5.2.8). However, no sturgeon tagged with acoustic transmitters in other basins have been detected entering the Eel River watershed, suggesting that the watershed may not be an important non-spawning aggregation area (Stillwater Sciences and WNRD 2017).

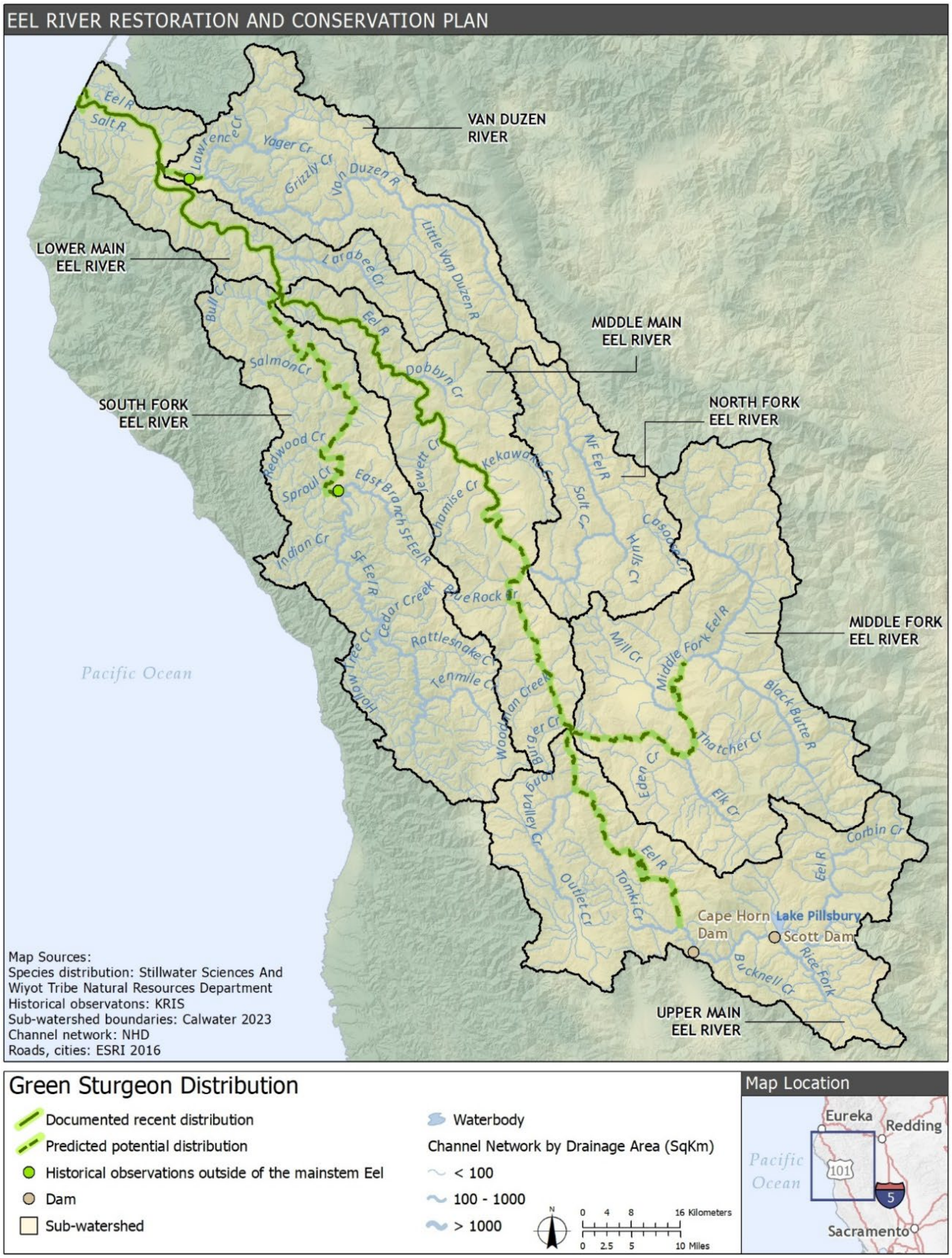

Figure 5-1. Approximate current distribution of Green Sturgeon in the Eel River watershed. Documented recent distribution is based on Stillwater Sciences and WNRD (2017) and predicted potential distribution is based on historical accounts and channel size as described in the text.

5.2 Ecology, Life History, and Habitat Needs

5.2.1 Life-history Timing Overview

Non-spawning adult and sub-adult Green Sturgeon typically occupy the nearshore marine environment, coastal bays, and estuaries along the Pacific Coast (NMFS 2009a, Lindley et al. 2011). Every few years, reproductively mature adults enter freshwater in spring and early summer and quickly move upstream to reaches that contain suitable spawning habitat (Moyle 2002). Spawning occurs in early to mid-summer. Some adults may outmigrate shortly after spawning, while others likely remain in freshwater until fall or winter (Benson et al. 2007). Eggs hatch approximately one week after fertilization, and larvae feed on endogenous yolk sacs for several days before dispersing downstream (NMFS 2010). Metamorphosis to the juvenile stage occurs approximately 1.5 months after hatching (Moyle 2002). Juveniles rear in fresh water or brackish estuaries for between 1 and 3 years, at which point they outmigrate and enter the marine environment and are considered sub-adults. Sub-adults remain in saltwater until they reach reproductive maturity around age 15 (NMFS 2018).

The generalized life-history timing for each life stage is presented in Table 5-1. Research on Green Sturgeon is relatively limited compared to other anadromous fish species in coastal Northern California, and substantial knowledge gaps regarding the species' ecology and phenology remain (Section 5.4.3). Further, the unlisted northern DPS has received considerably less attention than the federally threatened southern DPS. Only a single study of the Eel River spawning population has been conducted to-date. As a result, the information presented in Table 5-1 (and in subsequent sections) includes inferences drawn from other watersheds, with particular emphasis on spawning populations in the Klamath and Trinity Rivers. Information gleaned from the southern DPS is also included when necessary. A more detailed description of each life stage and its timing is provided below.

Table 5-1. Generalized life-history periodicity of Green Sturgeon in the Eel River watershed.

Life stage	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Adult upstream migration[1,2,3]			▒	▒	▒	▒						
Spawning[4]				▒	▒	▒	▒					
Adult outmigration[,2,5]	▒	▒	▒	▒	▒	▒			▒	▓	▓	▓
Adult post-spawn holding[1]						▒	▒	▒	▒	▒		
Egg incubation and larval development[6]				▒	▒	▒	▒					
Larval dispersal[7]					▒	▒	▒	▒				
Metamorphosis to juvenile[6]					▒	▒	▒	▒	▒			
Juvenile rearing[4]	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒
Juvenile outmigration[7,10]	▒	▒								▒	▒	▒
Coastal estuary residency[4,8]						▒	▒	▒	▒	▒		
Marine residency (sub-adults and non-spawning adults) [4,8,9]	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒	▒

▒ = Span of activity
▓ = Peak of activity

[1] Benson et al. 2007
[2] Colborne et al. 2022
[3] Poytress et al. 2015
[4] Israel et al. 2008
[5] Stillwater Sciences and WNRD 2017
[6] Based on life-history information reported in Deng et al. 2002
[7] Gaines and Martin 2002 and CDFG 2002, as cited in USDI 2008
[8] Moser and Lindley 2007
[9] Erickson and Hightower 2007
[10] Poytress et al. 2024

5.2.2 Adult Freshwater Migration

Adult Green sturgeon make freshwater spawning migrations every 2 to 6 years, with spawning intervals of 3 to 4 years being the most common (Moyle 2002, Adams et al. 2002, NMFS 2010, Doukakis 2014). Adults typically enter rivers in spring and early summer (Table 5-1; Benson et al. 2007) and move rapidly upstream to spawning areas (Heublein et al. 2009). Adult Green Sturgeon have been documented actively migrating upstream (i.e., swimming through riffles) or displaying apparent migratory behavior (i.e., holding in habitats too shallow for spawning) in the Eel River watershed from March through May (Van Kirk 1996, Stillwater Sciences and WNRD 2017, Kajtaniak and Roberts 2022). Upstream movement in the mainstem may be constrained by low flows at certain shallow riffles. Stillwater Sciences and WNRD (2017) suggested movement over critical riffles may be restricted at discharges below about 1,500–2,000 cubic feet per second (cfs). Adults may spawn in the lower mainstem Eel River in very dry years when low flows restrict access to spawning habitat further upstream (Stillwater Sciences and WNRD 2017). Adult sturgeon are regularly observed in the mainstem Eel river downstream of the South Fork in summer and fall during periods of low flow (Stillwater Sciences and WNRD 2017, Kajtaniak and Roberts 2022). Given the timing of these observations, these are likely post-spawn individuals.

After spawning in spring or early summer, some adults quickly move back downstream to the estuary and ocean when stream flows are still elevated by snowmelt, while others may remain near spawning areas until the fall (Section 5.2.4) (Benson et al. 2007, Heublein et al. 2009, NMFS 2009b, Colborne et al. 2022). In the Sacramento River, Heublein et al. (2009) reported that Green

Sturgeon lingered at the apex of their riverine migrations for 15 to 41 days, presumably engaging in spawning behavior and subsequently holding prior to moving back downstream. In the Eel River, outmigrating adults have been detected moving downstream through the estuary in December (Stillwater Sciences and WNRD 2017). Additionally, in February 2022, one sturgeon was documented moving downstream past a stationary sonar unit located in the mainstem just upstream of the South Fork Eel River confluence (Kajtaniak and Roberts 2022). While spring and summer outmigration (just after spawning) have not been documented in the Eel River, populations in both the northern and southern DPS exhibit the behavior and it likely occurs there.

There is little information on the feeding habitats and diet of adult Green Sturgeon during their freshwater residency. NMFS (2009b) noted that adult Green Sturgeon may not feed during warm summer months based on the reportedly low hook-and-line fishing success rates. Capture rates increase in the early fall when water temperatures decrease, which may indicate onset of feeding behavior. An adult Green Sturgeon captured in the Rogue River was found to have an exoskeleton of a crayfish (*Pacifasticus* spp.) and algae in its digestive tract, but there was no indication of when it was taken (Farr and Kern 2005). Digestive tracts from 46 adult Green Sturgeon commercially caught during 2000–2004 in the Columbia River contained only algae (Farr and Kern 2005).

5.2.3 Spawning

Adult Green Sturgeon generally spawn shortly after arriving at spawning areas in spring and early summer (Israel et al. 2008). The Eel River population is no exception; ripe adults have been captured in the watershed in spring, and apparent post-spawn individuals have been captured in late summer (Stillwater Sciences and WNRD 2017). Green Sturgeon typically spawn in pools with complex hydraulic features, upwelling flows, bedrock shelves, and cobble/boulder substrate (Moyle 2002, Adams et al. 2002, NMFS 2005, Heublein et al. 2009). Substrates suitable for egg deposition and development include bedrock sills and shelves, boulders, or cobbles and gravel with silt-free interstices or irregular surfaces that “collect” eggs and to provide protection from predators (NMFS 2005, Poytress et al. 2011).

Based on documented spawning locations, spawning behavior, and habitat requirements for embryonic development, reproductive females likely select spawning areas with turbulent, high velocities near low velocity resting areas (Israel and Klimley 2008). Poytress et al. (2011) conducted underwater videography in three confirmed Green Sturgeon spawning pools in the Sacramento River and found that these pools generally had highly turbulent flow in the upstream area that flowed over bedrock or hardpan, with downstream areas having lower velocities and substrates composed of cobble, gravel, and sand. Eggs are broadcast and externally fertilized in relatively fast water, typically at depths greater than 10 ft (3 m) (Moyle 2002). However, in the Sacramento River, Poytress et al. (2015) documented variability in microhabitat characteristics at seven spawning sites the Sacramento River, where spawning depths ranged from 0.6–11.3 m and water velocity averaged 0.8 m/s.

Both the lower mainstem Eel River (below the South Fork) and middle mainstem Eel River (from the South Fork to the Middle Fork) contain sufficiently deep pools with suitable spawning substrates (Stillwater Sciences and WNRD 2017). However, potential spawning habitat in the lower mainstem Eel River has been more substantially impacted by aggradation than upstream habitats. Pools in downstream reaches tend to be shallower with smaller diameter substrate and greater fine sediment loads (Stillwater Sciences and WNRD 2017). As a result, spawning success may be higher in the middle mainstem Eel River.

5.2.4 Post-spawn Adult Holding and Outmigration

After spawning, some adults remain in freshwater reaches of spawning rivers, holding in deep pools until the fall or winter of following their spawning run (NMFS 2009b). Holding for extended periods after spawning has been observed in all spawning populations of Green Sturgeon (Israel 2008). Summer holding was documented in the Trinity and Klamath rivers, with suspected periods of restricted movement and inactivity occurring primarily in deep pools (Benson et al. 2007). In the Rogue River, during summer and fall months when water temperatures were 15–23°C (59–73°F), Green Sturgeon were found to reside in deep (>5 m) pools with little current (Erickson et al. 2002). Holding by Green Sturgeon in these pools is suspected to provide thermal refugia in some watersheds, and to conserve energy in low velocity areas before exiting the system (Benson et al. 2008).

Fall outmigration timing in the Klamath River and San Francisco Bay Estuary appears to be positively related to discharge (Benson et al. 2007, McCovey 2011, Colborne et al. 2022). Colborne et al. (2022) found that individual sturgeon generally exhibited similar outmigration timing across years, suggesting timing may be influenced by genetic factors. Significant increases in flows related to fall/winter rains and water temperatures of 10–12°C were the strongest indicators of downstream migration in the Klamath River (Benson et al. 2007).

5.2.5 Egg Incubation

Female Green Sturgeon produce 59,000 to 242,000 eggs that are about 0.17 inches (4.3 millimeters [mm]) in diameter (Van Eenennaam et al. 2004). Green sturgeon eggs are highly adhesive, limiting their downstream movement from spawning areas (Van Eenennaam et al. 2008). Eggs hatch 6 to 8 days after fertilization (Deng et al. 2002). Optimal water temperatures for the development, growth, and survival of Green Sturgeon eggs and larvae are between 15–19°C (59–66°F) (Mayfield and Cech 2004). Van Eenennaam et al. (2004) reported water temperatures between 17–18°C (63–64°F) to be the upper limit of thermal optima for Green Sturgeon embryos, with greater temperatures affecting development and hatching success. Similarly, Doroshov et al. (2004) found high survival rates for a temperature range of 16–19°C (61–66°F), but abnormalities increased significantly above 19°C (66°F). Water temperatures greater than 23°C (73°F) have been shown to cause complete mortality before hatch (Van Eenennaam et al. 2004). Because the flow regime is closely related to stream water temperature (Power et al. 2015, Dralle et al. 2023), interannual variation in flow may impact egg incubation and hatch success. Additionally, survival during incubation may be impacted by excessive silt in spawning substrates, which can smother eggs (NMFS 2018).

5.2.6 Larval Development

Upon hatching, most body systems of larval Green Sturgeon are incomplete. Consequently, substantial organogenesis and acquisition of organ functions occur during the larval development stage (Deng et al. 2002). Newly hatched larvae have poor swimming ability and tend to stay in contact with structure/cover in low-light habitats as opposed to open-river bottoms (Kynard et al. 2005). Larvae begin to display a nocturnal swim-up behavior at 6 days post-hatch, when the rudiments of the pectoral and ventral fins become developed, dorsal and anal fin rays are apparent, yolk of the mid-intestine is depleted, and the mandible begins rhythmic movement (Deng et al. 2002, Kynard et al. 2005). This swim-up behavior may assist in downstream dispersal to nursery areas (Deng et al. 2002). Larvae begin feeding exogenously approximately 10 days after hatching when they are approximately 1 inch (25 mm) in length (Deng et al. 2002).

Green Sturgeon larvae initiate a nocturnal downstream dispersal that begins when they are about 6 to 9 days old and lasts about 12 days (USDI 2008). Trap samples at Red Bluff Diversion Dam and the Glenn-Colusa Irrigation District (GCID) Diversion showed the downstream dispersal of larval Green Sturgeon in the upper Sacramento River to occur from May through August at sizes ranging from 0.8 to 2.4 inches (20 to 60 mm) (Gaines and Martin 2002, CDFG 2002, both as cited in USDI 2008). Larvae occupy bottom habitat with cover during daylight periods, and thus downstream dispersal typically occurs at night (USDI 2008). Poytress et al. (2010) conducted an experimental benthic D-net survey in water that was 8.9 to 10.8 feet (2.7 to 3.3 m) deep that had a surface velocity of 2.0 feet per second (ft/s) and observed a peak in larval captures between 10:00 p.m. and 11:00 p.m., when the water temperature was approximately 15.5°C (60°F).

Larval Green Sturgeon are regularly captured during the dispersal stage at about two weeks of age at the Red Bluff Diversion Dam (CDFG 2002, as cited in USDI 2008) and are three weeks of age when captured further downstream at the GCID Diversion (USDI 2008). The distance between these two facilities is approximately 34 river miles (55 km). The average rate of downstream dispersal by larval Green Sturgeon between those two points was approximately 4.9 miles (7.9 km) per day (or more specifically, per night). Assuming that the downstream larval Green Sturgeon migration reported in USDI (2008) occurs only at night and that there are 9 hours of darkness during the late spring and summer months, then the dispersal rate would be approximately 0.24 m/s (0.8 ft/s).

Water temperatures below 11°C (52°F) and above 19°C (66°F) are detrimental for larval Green Sturgeon development (Doroshov et al. 2004, Van Eenennaam et al. 2004). Doroshov et al. (2004) also determined that water temperatures between 22 and 26°C (72 and 79°F) resulted in notochord deformities in larval Green Sturgeon. Metamorphosis from the larval to juvenile stage is completed at approximately 45 days post-hatch, when fish range in size from 2.5 to 4.0 inches (6.3 to 9.9 cm) (Deng et al. 2002).

5.2.7 Juvenile Rearing and Outmigration

After metamorphosing from the larval stage, juvenile Green Sturgeon spend between 1 to 3 years (NMFS 2009a) rearing in freshwater and estuarine habitats in their natal river system. Generally, for the first 10 months of life, Green Sturgeon are primarily nocturnal: in addition to larval migration occurring at night, foraging by post-migrant larvae and early juveniles has been shown to peak at night, late summer and fall juveniles migrate downstream and forage nocturnally, and early juvenile winter movements are nocturnal (Kynard et al. 2005).

As described in Section 5.1.2, YOY and 1-year-old juveniles have been captured in the middle mainstem Eel River between McCann and Eel Rock (Puckett 1976), and in the lower Eel River near the mouth of the Van Duzen River (Murphy and Dewitt 1951). Captures of YOY and 1-year olds in the middle mainstem Eel River were primarily during spring to late summer, during low streamflows and water temperatures exceeding 20°C (68°F) (Pucket 1976). While juveniles have not been caught in the Eel River estuary, this may be the result of the small overall population size, relatively inconsistent sampling effort compared to other river systems where juveniles are regularly detected, and the difficulty effectively sampling large areas of estuarine habitat. Based on information gleaned from other watersheds, it is likely that most juveniles spend some amount of time rearing in the Eel River estuary before outmigrating to the ocean. Allen et al. (2011b) suggested saltwater tolerance gradually increases with body length, but that osmoregulatory ability could be influenced by both internal (i.e., somatic growth, hormones) and external factors. An earlier study by Allen et al. (2005) found that juveniles as young as 100 days old (with an average length of approximately 18 cm) could consistently tolerate brackish water (10 parts per thousand [ppt]), and that juveniles are generally capable of entering saltwater (33 ppt) at body lengths typically achieved by age 1.5 (75 cm). Indeed, in a laboratory setting, juvenile Green Sturgeon (220 to 220 days old) acclimated to both freshwater and saltwater showed a preference for saline environments (Poletto et al. 2013).

However, the exact duration of freshwater versus estuarine residency in the Eel River watershed is not well understood and likely varies between individuals based on emergence location, larval dispersal dynamics, coincident physical and biotic habitat conditions in settling locations, and ontogenetic variability. Juveniles exhibit similar variation in other watersheds; some southern DPS juveniles in the San Francisco Bay estuary rear entirely in the Delta while others make repeated forays into the more saline waters of San Francisco Bay (Thomas et al. 2022). In the Klamath River, trace element analysis in the pectoral fins of adult sturgeon suggested that juveniles first entered brackish water between ages 0.5 and 1.5 and first entered the ocean between ages 3.5 and 4.5 (Allen et al. 2011a). Juveniles between ages 1–4 have also been captured in the Klamath River estuary (Nakamoto et al. 1995).

Juveniles grow rapidly, reaching 12 inches (30 cm) in 1 year and over 24 inches (60 cm) in 2 to 3 years (Nakamoto et al. 1995). Very little information is available on the food and nutrient requirements of different life stages of Green Sturgeon (Klimley et al. 2006). Mayfield and Cech (2004) found that juvenile Green Sturgeon bioenergetic performance was optimal at water temperatures of 15–19°C (59–66 °F) and that swimming performance decreased beyond 19°C (66°F). Allen et al. (2002) reported that river temperatures should not increase beyond 15–19°C (59–66°F) for optimal juvenile Green Sturgeon growth rates. Mayfield and Cech (2004) found that juvenile Green Sturgeon acclimated to temperatures of 11°C (52°F) and 19°C (66°F) did not differ significantly in their thermal preferences (15.9±1.7°C [60.6±3.1°F] and 15.7±2.9°C [60.3±5.2°F], respectively); however, fish acclimated to 24°C (74°F) exhibited a significantly higher preferred temperature (20.4 ±3.1°C [68.7±5.6°F]). Exposure to temperatures above 24°C may be lethal to juvenile Green Sturgeon (Mayfield and Cech 2004). However, a study conducted by Allen et al. (2006) suggests that growth rates can increase at temperatures >24°C and adverse effects of elevated temperatures are lessened when food is abundant and dissolved oxygen is sufficient.

Timing and cues of outmigrating juveniles are not well understood, and have been based primarily on lab studies of osmoregulatory ability, size, and incidental captures. Recent evidence from the Sacramento River suggests that outmigration cues for juveniles was significantly linked to increases in discharge and turbidity (Poytress et al. 2024). During fall and winter months, tagged juvenile Green Sturgeon moved in either a stepped or continuous downstream migration pattern, with larger individuals more prone to a continuous migration (Poytress et al. 2024).

Although specific diet data are lacking for juvenile Green Sturgeon, nutritional studies on the closely related White Sturgeon within riverine systems indicate fed on amphipods, bivalves, and fly larvae (NMFS 2009b). These food resources are important for juvenile foraging, growth, and development during their downstream migration to the Delta and bays (NMFS 2009b).

5.2.8 Sub-adult and Adult Ocean Residency

The sub-adult life stage lasts from juvenile entry into the marine environment until the onset of sexual maturity (NMFS 2018), which typically occurs around age-15 (NMFS 2018). Recent analysis from coded tags, acoustic tags, and Oregon bottom trawl logbook records indicate that Green Sturgeon are widely distributed in the nearshore ocean at depths up to 360 ft (110 m), with most use occurring at depths between 130 and 230 ft (40 and 70 m) (Erickson and Hightower

2007). However, the distribution of sturgeon in the nearshore environment does not appear to be random, and fish may aggregate in particular areas (Lindley et al. 2011). Huff et al. (2011) reported that Green Sturgeon prefer to occupy highly complex seafloor habitats where the substrate contains a large proportion of boulders.

Members of both the Northern and Southern DPSs travel widely up and down the Pacific Coast, with acoustically-tagged individuals detected along the continental shelf, the Columbia and Umpqua river estuaries, the Strait of Juan de Fuca and Puget Sound, Humboldt Bay, Willapa Bay, and Grays Harbor in Washington (Erickson et al. 2007, Heublein et al. 2009, Lindley et al. 2011, Moser et al. 2020). It is believed that Green Sturgeon from disparate spawning populations aggregate in bays and estuaries to feed throughout the summer during years in which they are not making spawning migrations (Moser and Lindley 2007, Lindley et al. 2011, Moser et al. 2020). Three acoustic receivers deployed by the Yurok Tribal Fisheries Department in the ocean offshore of the Klamath River reportedly detected 19 tagged Green Sturgeon in 2007 (McCovey 2008), with 10 of these detections being originally tagged in San Pablo Bay. Of these 10 fish, none entered the Klamath River. The rest of the detections were from fish tagged in Willapa Bay, Grays Harbor, and the Rogue and Klamath rivers. Tagged adults originating in other watersheds have not been detected entering the Eel River watershed, despite 21 individuals (tagged in the Sacramento River, San Pablo Bay, Willapa Bay, Rogue River, and the Columbia River) being detected within 2 miles of the mouth during 1 year of monitoring (Stillwater Sciences and WNRD 2017).This finding suggests the Eel River estuary may not be an important aggregation site for estuarine feeding by non-natal individuals.

5.3 Life-history Diversity Conceptual Model

Like other anadromous fish species in the Eel River watershed, Green Sturgeon display diverse patterns of migratory movement and habitat use across their life cycle. The life-history strategy expressed by each individual represents interactions between genetically-influenced behavioral predispositions and spatiotemporal variability in environmental conditions.

This section synthesizes information from the Eel River and elsewhere within the range of Green Sturgeon to identify and characterize adult and juvenile life-history strategies with potential to occur in the watershed. Figure 5.2 presents a conceptual diagram for Green Sturgeon in the watershed, showing potential pathways across time and space for the primary adult and juvenile life-history strategies, which are described in Section 5.3.1 and Section 5.3.2, respectively. The overall approach, rationale, and uses of these life-history conceptual models in the context of the Restoration Plan are described in Section 3 of the Plan.

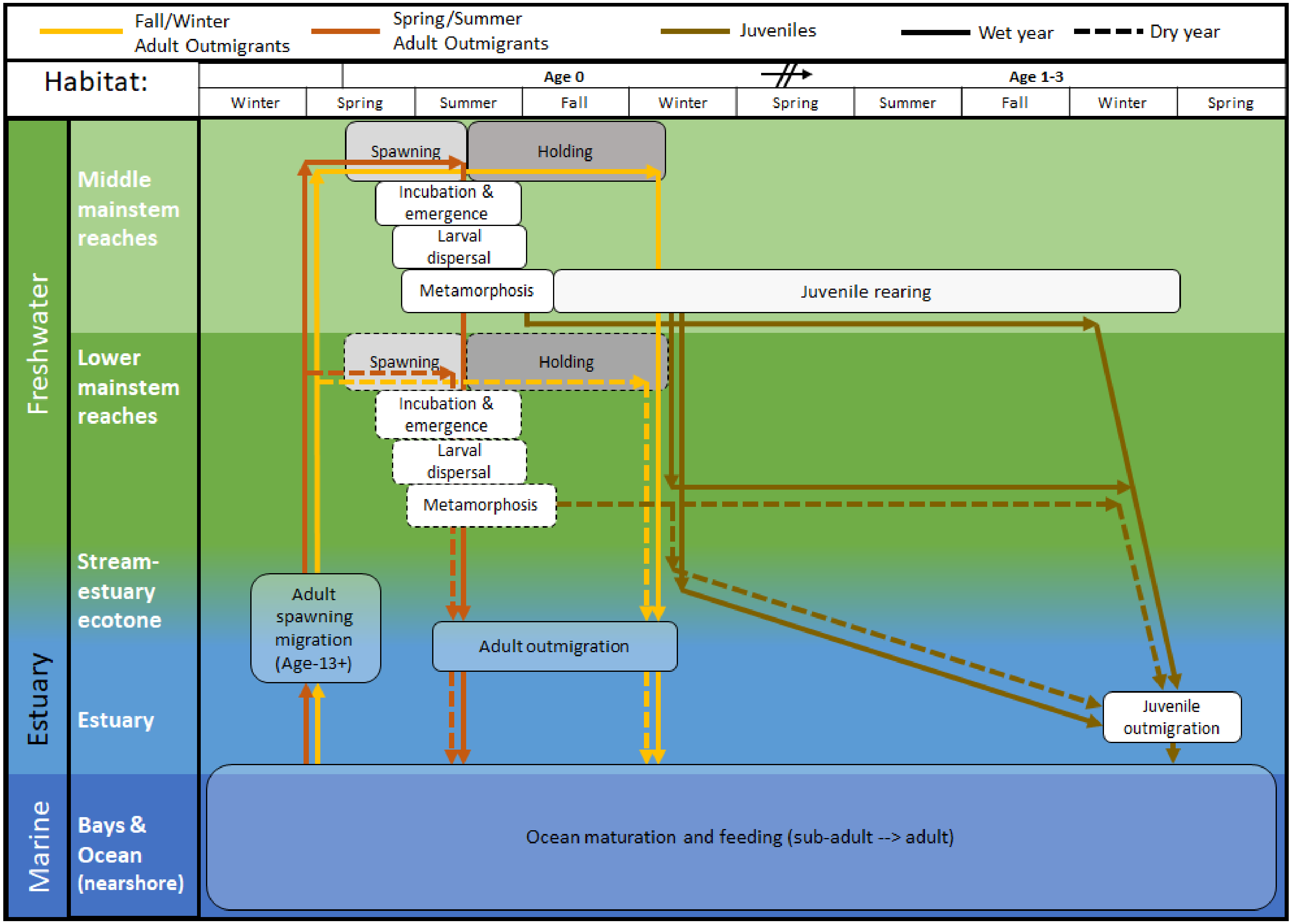

Figure 5-2. Life-history conceptual diagram for Green Sturgeon in the Eel River watershed, showing potential pathways across time and space for life stages and primary life-history strategies. Each line represents a potential pathway within a strategy. Arrows direction represents movement direction of movement between primary portions of the watershed.

5.3.1 Adult Life-History Strategies

Adult Green Sturgeon populations can exhibit diversity in migration timing to spawning areas, spawning locations used, and duration of holding in fresh water prior to outmigrating back to the ocean (Figure 5-2). As described in Section 5.2, after spawning, some adults outmigrate during the wet season flow recession in spring or early summer, while others hold through the summer and outmigrate during the onset of the wet season in fall or winter. These primary adult life-history strategies are described in Section 5.3.1.1 and 5.3.1.2, respectively. Notably, adult outmigration timing appears to be under partial genetic control, as individual sturgeon tend to exhibit consistent outmigration timing across spawning events (Colborne et al. 2022). Because Green Sturgeon are periodic spawners, individuals may vary in spawning interval; however, no studies assessing variability in this regard have been conducted to-date. Additionally, interannual hydrologic variability during the spawning migration influences where adults can access suitable spawning habitat each year (Section 5.3.2). Interannual variability in spawning locations likely leads to variability in spawning success and juvenile recruitment due to differences in (1) habitat quality between lower mainstem and middle mainstem spawning locations, and (2) variable conditions experienced by larval and juvenile sturgeon that hatch in these different locations.

5.3.1.1 Spring/summer adult outmigrant

A proportion of the Green Sturgeon adult spawning population in the Eel River likely outmigrates shortly after spawning in the spring or early summer, as has been described for populations in the San Francisco Bay Estuary and Klamath River. However, due to limited monitoring, this behavior has not been documented in the Eel River watershed and the exact proportion of the population that exhibits the behavior is not clear. Telemetry studies conducted in the Klamath and Rogue rivers suggest that the spring/summer outmigrant life-history strategy is less prevalent than the fall/winter strategy (Erickson et al. 2002, Benson et al. 2007).

Adult sturgeon that outmigrate in the spring or summer shortly after spawning experience a different suite of environmental and ecological conditions than those that hold through the summer before outmigrating in the fall or winter. Spring/summer outmigrants avoid potential exposure to high summer water temperatures that may impact growth and fitness, and returning to food rich estuarine or marine habitats earlier may impart growth advantages relative to fall/winter outmigrants. More research on seasonal food resources and diet differences between adult life-history strategies is needed.

Outmigration in spring or early summer could theoretically occur in both wet and dry years. In wet years, high spring flows driven by late rains or snowmelt could facilitate downstream movement past hydraulic features in the middle and lower mainstem that impede or discourage movement. In dry years, since adults may be forced to spawn in the lower mainstem, they may need to navigate past fewer such obstacles during outmigration and may reach the estuary before flows drop to impassable levels. However, adults that might otherwise outmigrate during the spring or summer could become trapped by low flows in certain years and be forced to holdover until the wet season.

5.3.1.2 Fall/winter adult outmigrant

As described above, a portion of the adult spawning population remains in fresh water after spawning and outmigrates in the fall or winter. Indeed, adult outmigration has only been documented in the Eel River in December (Stillwater Sciences and WNRD 2017). The duration of the over-summer holding period by the fall/winter adult outmigrant strategy is influenced by the timing of the wet season onset, and delayed arrival of rainstorms may result in a longer holding period (Benson et al. 2007, Israel et al. 2008). In other watersheds, adults have been observed holding for up to 300 days in dry years (Colburn et al. 2022). Because adults may feed minimally during parts of the holding period (Section 5.2.4), an extended holding period could have fitness consequences. The plasticity of outmigration timing observed in post-spawn adults has likely evolved in response to long-term variation in climatic conditions in Northern California, though recent increases in the incidence of drought conditions from climate change and anthropogenic water use may increase the prevalence of the fall/winter outmigrant strategy.

5.3.1.3 Influence of hydrologic variability on spawning location and movement timing

As mentioned above, annual variation in rainfall patterns and hydrology can exert a strong influence on spawning location and movement timing, contributing to observed variation in life-history strategies. In wet years, elevated streamflow in the lower Eel River allows adults to reach suitable spawning habitat in the middle mainstem Eel River (Figure 5-2, solid line; Stillwater Sciences and WNRD 2017). Under such circumstances, adults appear to congregate and spawn primarily in the middle mainstem, passing by suitable spawning habitat in the lower Eel River.

Low flows in the lower Eel River may prevent adults from reaching preferred spawning areas in the middle Eel River (Figure 5-2, dashed line; Stillwater Sciences and WNRD 2017). Low flows during the adult spawning migration may result from reduced spring snowmelt fewer late-winter and spring rainstorms. Adults do not appear to adjust migration timing in response to stream flow (Stillwater Sciences and WNRD 2017); that is, in low-flow years, they do not attempt to move upstream earlier in the year to reach spawning areas in the middle mainstem and instead spawn in suitable habitat in the lower mainstem Eel River. Because pools in the lower mainstem generally contain more fine sediment, and embedded, smaller diameter substrate compared to pools in the middle mainstem, spawning success may be reduced in dry years (Stillwater Sciences and WNRD 2017).

5.3.2 Juvenile Life-History Strategies

As described in Section 5.2.7, juvenile Green Sturgeon rear for variable amounts of time in freshwater and estuarine habitats before outmigrating between ages 1 and 3. Because there appears to be a size-related lower threshold for saltwater tolerance (Allen et al. 2005, Allen et al. 2011b, Poletto et al. 2013), age at outmigration is influenced by early life growth rate. Consequently, the growth potential of juveniles in a given emergence location—which is partly driven by hydrologic conditions during the spawning migration (Section 5.3.1.3)—likely plays an important role in determining an individual's propensity to express a particular juvenile rearing strategy. Sections 5.3.2.1 and 5.3.2.2 describe the potential role that hydrology during adult spawning migration plays in influencing expression and relative prevalence of different juvenile life-history strategies in a given water year and make hypotheses related to the growth and survival trade-offs of each.

5.3.2.1 Dry year strategies

In dry years, low flows during the adult migration period may prevent Green Sturgeon from reaching spawning areas in the middle mainstem of the Eel River. Consequently, more individuals spawn in the lower Eel River and more larvae are hatched there. Since developing larvae that emerge in the lower Eel River are closer to the estuary, downstream larval drift may result in exposure to higher salinities, leading to reduced recruitment or higher energetic costs due to reduced salinity tolerance at smaller body sizes (Allen et al. 2006). Conversely, rearing in highly productive estuarine feeding habitats could offset energy costs related to osmoregulatory changes upon early entry into salt water. Juveniles that rear in the lower mainstem and estuary may also achieve higher growth rates, resulting in earlier outmigration to the ocean and feeding in productive nearshore and bay habitats at a younger age (Israel et al. 2008). Shorter migration distance to the estuary and higher growth rates may also result in lower risk of predation by riverine predators such as pikeminnow and higher survival to the sub-adult stage. Conversely, entry into the estuary at a smaller size could make these individual more vulnerable to estuarine predators.

5.3.2.2 Wet year strategies

In wet years, since most adults spawn in reaches of the middle mainstem Eel River, more juveniles are expected to hatch in reaches in that location. These juveniles must travel (both via larval drift and juvenile downstream movements) a substantially longer distance to reach the estuary than a juvenile spawned in the lower mainstem Eel River. For this reason, these individuals are more vulnerable to riverine predators, but they have the opportunity to exploit different habitats than individuals spawned in dry years in lower mainstem reaches. Furthermore, since salinity tolerance appears to be correlated with body size, growth rate—which is influenced by both intrinsic metabolic differences and growth potential (dictated by local quantity, quality, and availability of food resources)—likely plays an important role in determining age and size at transition to the sub-adult phase. This likely contributes to a longer growth period, and with higher fitness when entering saline environments.

5.4 Conceptual Model Outcomes

5.4.1 Stressors

Since Green Sturgeon are a long-lived, late-maturing anadromous fish species they are vulnerable to freshwater and estuarine habitat loss and exploitation, and population recovery has the potential to be slow (Moyle 2002, Adams et al. 2002, NMFS 2010). Conversely, being long-lived and having an extended and variable spawning periodicity of 2 to 6 years allows sturgeon to be more resilient in the face of variably suitable environmental conditions and periods with poor river conditions.

Table 5-2 lists stressors with potential to adversely impact each life stage of Green Sturgeon in the Eel River. This list was generated primarily from the above species description and conceptual model and NMFS (2018), which includes more in-depth discussion of key factors with potential to affect survival of each life stage. Importantly, while each stressor listed has the potential to adversely affect one or more life stages, some may be more important than others in terms of limiting overall population productivity, expression of life-history diversity, and abundance of returning adults. Due to lack of research and monitoring, the primary factors limiting abundance and resilience of Green Sturgeon in the Eel River watershed are not known. Addressing the key data gaps listed in Section 5.4.3 will improve understanding of the most important stressors and allow for more targeted restoration and conservations actions to address them.

The impact of a given stressor on habitat capacity, growth, and survival—and ultimately the number of returning adults in a cohort—is also expected to vary by year (due to differences in hydrology and temperature regimes). For example, the impacts of elevated water temperatures are expected to be greater during periods of drought relative to wetter periods. Finally, since different life-history strategies inhabit different portions of the watershed at different times, they are expected to be more or less impacted by various stressors. For example, juveniles that predominately rear and grow in estuarine reaches may be less impacted by elevated water temperatures relative to those that rear in more inland reaches in the middle mainstem Eel River.

Table 5-2. Stressors with potential to adversely impact each life stage of Green Sturgeon in the Eel River watershed.

Life stage	Stressor	Drivers (underlying causes of stressor to be addressed by restoration)	Mechanisms of impact on population productivity, abundance, distribution, and resilience
Adult freshwater migration	Physical barriers to movement	Shallow riffles that limit adult passage due to impaired stream flows caused by drought, climate change, and water withdrawals.	Reduced spawning distribution, lowered reproductive success, and potential lost juvenile life-history diversity.
	Reduced pool frequency, depth, and channel complexity in mainstems	Channel aggradation due to increased sediment delivery from historical and current logging, road construction & management, and fires. Reduced wood volume due to removal and alteration of riparian forest (reduced supply).	Impaired staging habitats, increased intraspecific competition, and lost thermal refugia.
	Impaired flows	Reduced or delayed stream flows due to water diversions or climate change (drought or reduced snow pack).	Reduced spawning distribution and increased proximity to estuary. Potential reduced juvenile life-history diversity in cohort. Impaired migratory cues.
	Poaching	Inadequate education and enforcement.	Pre-spawning mortality
Spawning and incubation	Increased water temperatures	Low flows during incubation periods, drought and warming due to climate change.	Reduced egg-to-larvae survival
	Fine sediment infiltration of spawning substrates	Landslides and erosion of fine sediment due to historical and current logging, road construction and management, and fires. Reduced sediment sorting due to channelization, floodplain disconnection, and lack of wood.	Reduced area of suitable spawning habitat and lowered egg-to-larvae survival
	Reduced pool frequency and depth	Channel aggradation due to increased sediment delivery from historical and current logging, road construction and management, fires, and historical flooding.	Reduced area of suitable staging and spawning habitats
	Contaminants/bioaccumulation	Exposure to mercury, selenium, pesticides and other persistent environmental contaminants	Reduced reproductive fitness due to skeletal deformities and mortality of early life stages due to maternal exposure; direct mortality or reduced growth rates of juveniles;
Adult post-spawn holding	Reduced pool frequency, depth, and channel complexity in mainstems	Channel aggradation due to increased sediment delivery from historical and current logging, road construction & management, and fires. Reduced wood volume due to removal and alteration of riparian forest (reduced supply).	Impaired holding habitats, increased intraspecific competition, and lost thermal refugia.
	Contaminants/bioaccumulation	Exposure to mercury, selenium, pesticides and other persistent environmental contaminants	Bioaccumulation of toxins during extended holding, reduced fitness.
	Increased water temperatures	Loss or alteration of riparian forests, impaired dry-season stream flows, climate change.	Sub-lethal to lethal cumulative effects during extended holding.
	Impaired flows	Reduced or delayed stream flows due to water diversions or climate change (drought or reduced snow pack).	Limiting thermal refugia during summer months, lost cues for out-migration.
Larval growth and juvenile rearing	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	Reduced growth and survival of juveniles due to altered estuarine food webs, impaired WQ.
	Reduced pool frequency, depth, and channel complexity in mainstems	Channel aggradation due to increased sediment delivery from historical land uses & floods.	Reduced rearing summer and winter habitat capacity, reduced larvae to juvenile survival.
	Increased water temperatures	Loss or alteration of riparian forests, impaired dry-season stream flows, climate change.	Reduced rearing habitat capacity due to restricted distribution. Direct mortality, sub-lethal stress and reduced growth due to metabolic effects.
	Reduced area of and restricted access to thermal refugia	Filling of thermally-stratified deep pools due to channel aggradation caused by sediment inputs from logging practices, road building and floods. Loss of complex cover at cold tributary confluences.	Reduced rearing habitat capacity due to restricted distribution. Direct mortality, sub-lethal stress and reduced growth due to metabolic effects.
	Elevated turbidity levels beyond reference state levels	Landslides and erosion of fine sediments due to historical and current logging, road construction & management, and geomorphic impacts of high intensity fires.	Reduced growth through energetic costs associated with increased suspended sediment during high-turbidity periods.
	Increased prevalence of predation, especially from non-native predators	Sacramento Pikeminnow predation, loss of escape cover from larger wood and deep pools, decreased stream flows and increased water temperatures.	Reduced larval and juvenile survival.
	Alterations to the timing, magnitude, and availability of food resources	Loss of marine-derived nutrients and other beneficial species interactions.	Reduced juvenile growth and survival, intraspecific competition

Life stage	Stressor	Drivers (underlying causes of stressor to be addressed by restoration)	Mechanisms of impact on population productivity, abundance, distribution, and resilience
Juvenile outmigration	Impaired flows	Climate change, water diversions, hydrological alteration due to draining of wetlands, loss of beaver dams, channel aggradation, alteration of forest & riparian structure.	Reduced juvenile to estuary/ocean survival
	Increased prevalence of predation	Introduction and expansion of Sacramento Pikeminnow and other non-native predators. Loss of escape cover due to decreases in large wood volume and area of unimbedded cobble-boulder substrates; decreased stream flows.	Reduced juvenile to estuary/ocean survival
	Alteration of estuarine habitat quantity and quality and impaired connectivity with estuarine habitats	Tide gates, levees, wetland drainage for agricultural conversion, agricultural and urban run-off.	Reduced juvenile to ocean survival due to loss of rearing habitat
Ocean residence	Ocean bycatch	Ocean fishing regulations and enforcement	Reduced sub-adult to adult survival; altered adult age structure and life-history diversity.
	Marine food web alterations	Climate change related influences on strength and timing of ocean upwelling, marine productivity, and sturgeon prey species.	Reduced ocean growth and sub-adult to adult survival.

5.4.2 Restoration Take-home Points

The population abundance of Green Sturgeon was greatly reduced from flooding events in past decades that reduced suitable spawning habitat in the Eel River. This loss of critical habitat for reproduction, coupled with anthropogenic impacts such as ocean bycatch/harvest, reduced or modified flows, and migration barriers, have led to a depressed population likely losing some genetic diversity and cohort structure. As a long lived, late-maturing species, Green Sturgeon recovery would likely not be detectable even over decadal time scales. As described in Section 5.4.1, there is considerable uncertainty in the most important factors liming recovery of Eel River Green Sturgeon populations, limiting implementation of the most impactful restoration actions. However, in general, actions that (1) help restore quality of and access to historical adult spawning, holding, and rearing habitats in the mainstem reaches of the Lower Main Eel River and Middle Main Eel River sub-watersheds, and (2) improve habitat and water quality in the stream-estuary ecotone and estuary are expected to help alleviate potential bottlenecks and increase population resiliency. Because of the large overlap in habitat requirements and distribution in the Eel River (i.e., mainstem channels and estuary) between Green Sturgeon life stages and Chinook Salmon adults and juveniles, many of the restoration strategies and actions aimed at recovering them are expected to benefit Green Sturgeon.

5.4.3 Key Data Gaps

- Current population size of sturgeon in the Eel River watershed
- Contribution of adults from other DPS watersheds to the Eel River spawning population
- Presence and duration of freshwater versus estuarine residency of juveniles in the Eel River
- Riverine diet of post egg-sac larvae (switch from exogenous to endogenous)
- Riverine diet of juvenile and adult sturgeon in the Eel River
- Food resource composition and distribution for juveniles and adults in riverine and estuarine habitats in the Eel River.
- Vulnerability of juveniles to high water temperatures and how this is influenced by food availability.
- Cues for outmigration and proportion of adults that use spring/summer versus fall/winter
- Marine habitat use and migratory corridors/aggregation areas by Eel River Green Sturgeon
- Extent of Eel River Green Sturgeon bycatch in various commercial fisheries
- Extent of sedimentation from flooding on historical spawning habitat
- Prevalence of various toxins/contaminants in Eel River and nearshore feeding habitats and the impacts of toxin exposure/bioaccumulation influence on Green Sturgeon individual fitness and population size

5.5 References

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Appendix D

Tiered Goals and Objectives

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Table D-1. Tiered goals and objectives for fish population category of influence.

	Goals	Sub-Goals	Objectives: *action statement*	Sub-Objectives
Fish Populations	Achieve naturally self-sustaining and harvestable native fish populations	Increase species population sizes	Adult abundance*: Increase the number of successfully spawning adults that return to freshwater*	Increase number of returning adults
				Reduce pre-spawn mortality
				Increase smolt-to-adult survival
			Juvenile abundance*: Increase the number of juveniles that successfully outmigrate to the ocean*	Increase juvenile rearing habitat carrying capacity
				Increase juvenile survival (summer low-flow and winter high-flow)
				Reduce smolt outmigration mortality due to predation
		Increase freshwater productivity of anadromous fish species (e.g., population growth rate, smolts per adult, adults per adult)	Egg-to-fry survival*: Increase embryo and larvae survival rates from their deposition to emergence*	Increase egg-to-fry survival
				Reduce elevated levels of fine sediment in spawning beds
			Fry-to-smolt survival*: Increase survival rates through juvenile life stages*	Increase survival of fry and rearing juveniles in freshwater stage
				Reduce fish mortality due to stranding or entrainment
				Reduce fish mortality due to predation
			Juvenile growth*: Increase the size and health of juveniles that successfully outmigrate to the ocean*	Increase growth of fry and juveniles by inducing favorable changes to food resources.
				Improve rearing habitat and reduce competition
		Restore species distributions to historical extents	Barriers to juvenile and adult migration*: Expand potential for adult and juvenile species distributions*	Restore or mitigate passage at large barriers that block access to historic habitat
				Improve passage conditions, physical and flow, at small barriers or obstacles that discourage movement
				Remove or improve fish passage that prevent access to historically occupied habitats
			Competition and predation: *Suppress or eradicate non-native predatory species and reduce impacts of unnatural interspecies competition*	Increase length of time native fish can use mainstem habitats in summer
				Reduce presence of pikeminnow in summer

	Goals	**Sub-Goals**	**Objectives:** ***action statement***	**Sub-Objectives**
Fish Populations (cont.)	Achieve naturally self-sustaining and harvestable native fish populations (cont.)	Maintain and increase diversity of life history tactics	Diversity in juvenile tactics: *Support diversity of juvenile life history tactics by encouraging fish use of diverse habitats throughout the watershed*	Increase spatial distribution of juveniles and diversity of habitat use
				Restore the estuary and nearby habitats for refuge for juvenile rearing and adult holding
				Improve conditions in the mainstem for juvenile rearing
				Improve spawning habitat in streams with diverse over-summering conditions, including mainstems and/or habitats that are more accessible in dry years
				Restore habitats that may be necessary for spawning/rearing in dry years, including lower quality habitat
			Variability in migration timing*: Encourage natural variability in juvenile and adult life history tactics through time*	Extend the time window when juveniles can migrate downstream by creating predator-free mainstems for longer in the spring
				Restore natural flow regimes to allow fish passage
				Extend time window when adults can successfully migrate by removing barriers in the estuary and lower river
			Population gene flow and genetic diversity*: Maintain or restore genetic diversity by encouraging gene flow among sub-populations*	Maintain genetic diversity at neutral alleles for all species
				Increase spatial distribution of early-migration genetic diversity in salmonids (Greb1L/ROCK)
				Maintain diversity at OMY5 in O. mykiss
				Increase spatial distribution of migratory alleles at OMY5 in O. mykiss
				Maintain early vs late maturation genetic diversity in lamprey

Table D-2. Tiered goals and objectives for habitat category of influence.

	Goals	Sub-Goals	Objectives: action	Sub-Objectives
Habitat	Improve quantity, complexity and diversity of habitats within the stream corridor	Increase quantity of suitable habitat for focal species and life stages	Adult holding habitat: *Increase the number and size of early fall holding habitats that have been depleted for returning salmon adults in the lower Eel River and estuary reaches*	Increase deep pools in the lower mainstem Eel River for all species
				Increase deep pools and cover in snowmelt streams for spring-run Chinook and summer-run steelhead
				Increase deep pools and other holding habitat in mainstem reaches
			Spawning habitat quantity: *Increase spawning gravel area by restoring to optimal spawning substrate assortments*	Increase suitable spawning substrate patches and substrate diversity in mainstems
				Increase substrate diversity in sediment-loaded tributaries
				Reduce fine sediment inputs to improve quantity of high-quality spawning habitat
				Increase large flow obstructions to promote substrate sorting and patch diversity
				Increase access to tributaries for spawning
			Wet season rearing habitat: *Increase quantity and diversity of wet season rearing habitats*	Increase off-channel habitats such as alcove/backwaters and off-channel ponds
				Increase floodplain connectivity
				Increase area of in-channel low velocity refuge habitat through large wood augmentation
				Increase clear-water habitats to provide winter and spring foraging opportunities
			Dry season rearing habitat: *Increase extent of cool perennial streams*	Improve currently unsuitable habitats with temperature mitigation, in-channel restoration
				Maintain suitable baseflows to support dry season rearing habitats

	Goals	Sub-Goals	Objectives: action	Sub-Objectives
Habitat (cont.)	Improve quantity, complexity and diversity of habitats within the stream corridor (cont.)	Increase complexity and quality of key habitats	In-channel habitat complexity*: Increase complexity of in-channel habitat features*	Add large wood, boulders, and/or other channel roughening features to increase instream cover and complexity for juvenile summer rearing habitat
				Add large wood and vegetation features to provide cover and shelter during spring-summer recession and base flow periods
				Add large wood, boulders, and/or other channel roughening features to create high flow refuge habitat
				Increase pool depths where pools have filled in, such as on the mainstem
				Restore and increase riparian vegetation to provide cover and wood recruitment
			Habitat sequence diversity*: Restore natural riffle-pool sequencing where conditions have been altered*	Restore and maintain natural balance of riffles and pools
			Thermally suitable conditions and refugia*: Create, expand and enhance cold-water refuge areas and increase accessibility to incorporate current and projected flow regimes*	Increase and protect thermal refugia, especially in warmer tributaries and mainstem rivers
				Increase accessibility to current thermal refugia
			Turbidity: *Restore natural levels of turbidity to improve foraging opportunities for visual feeders and growth for primary production*	Increase access to and amount of clear-water habitats to provide winter and spring foraging opportunities for fish
				Address sources of fine-sediment input

	Goals	**Sub-Goals**	**Objectives: action**	**Sub-Objectives**
Habitat (cont.)	Improve quantity, complexity and diversity of habitats within the stream corridor (cont.)	Restore connectivity between habitats	Lateral Connectivity—connectivity to off-channel and floodplain habitat*: Improve migration pathways for rearing juveniles to access productive winter refuge habitats via tributaries, side-channels and low-lying floodplains*	Remove or lower physical barriers blocking access to off-channel habitats
				Restore sediment and flow regimes to prevent channel incision
				Restore flow regimes to maintain seasonal connectivity to off-channel habitats
			Longitudinal connectivity: *Improve connectivity between tributaries and mainstems, between sub-watersheds and estuary*	Remove barriers (flow and physical) to allow upstream passage of adult migratory species
				Increase access to and passage between diverse rearing habitats, including mainstem and tributaries
				Remove barriers (flow and physical) to allow downstream passage of ocean-migrating juveniles
		Foster productive riverine food webs that support growth of native fishes	Primary productivity: *Create habitats that encourage growth of nutrient-dense and edible epilithic and epiphytic diatoms and natural filamentous algae, and discourage toxic cyanobacteria*	Promote natural growth of nutrient dense filamentous algae, and epilithic and epiphytic diatoms
				Reduce growth of toxic cyanobacteria
			Macroinvertebrates: *Create diversity of habitats through space and time for proliferation of diverse and edible macroinvertebrates*	Support persistence of diverse of benthic macroinvterbrates through habitat, substrate, and flow diversity
				Support persistence of sensitive macroinvertebrates (EPT) through high water quality
				Restore riparian zones to increase input of terrestrial invertebrates
			Non-native aquatic species: *Create habitats that favor native over non-native fishes, active removal when necessary*	Reduce abundance and spatial distribution of pikeminnow
				Reduce other non-native fishes (e.g., catfish, bass) and predators (bullfrog)

	Goals	Sub-Goals	Objectives: action	Sub-Objectives
Habitat (cont.)	Improve quantity, complexity and diversity of habitats within the stream corridor (cont.)	Increase and improve estuarine habitat	Tidal slough network accessibility*: Expand and enhance the inter-tidal slough network to increase capacity across all trophic levels*	Expand and reconnect inter-tidal slough network
				Restore/increase spatial extent of the estuary
				Restore connections to nearby refugia such as small tributaries
			Estuarine and slough channel habitat complexity*: Enhance habitat complexity in slough channels to provide shelter, cover for rearing and foraging juveniles*	Restore salinity regimes in estuary
				Increase habitat complexity through large wood structures or other features
				Restore thermal refugia within estuary
			Estuarine food webs*: Increase estuarine primary production that supports healthy and diverse food web dynamics*	Increase primary production and support diverse macroinvertebrate populations in the estuary
				Increase inundation area/tidal prism to increase primary producers

Table D-3. Tiered goals and objectives for Landscapes category of influence.

	Goals	Sub-Goals	Objectives: action	Sub-Objectives
Landscapes	Protect, enhance, and restore intrinsic physical watershed processes (e.g., hydrologic, geomorphic, and riparian) that create and maintain complex channel morphology and regulate habitat connectivity.	Protect, enhance, and restore functional flow components	Baseflow components: *Protect, maintain, and/or enhance dry-season and wet-season baseflows.*	Reduce dry-season diversions
				Maintain habitat connectivity to allow movement
			Transitional flow: *Maintain functional flow components during spring and fall transitional periods.*	Maintain natural recession hydrograph during spring to promote productivity
				Maintain hydrologic response to fall freshets
		Protect, enhance, and restore geomorphic processes to healthy ranges	Sediment production and delivery: *Reduce fine sediment supply and suspended sediment concentrations*	Reduce fine sediment supply to channel
				Reduce suspended sediment concentrations
				Reduce open slope surface erosion and mass wasting
			Channel transport and storage: *Encourage dynamic sediment mobility and transport processes.*	Constant bed mobility, bed scour and sediment transport
				Transport sediment downstream at equilibrium with delivery rate
				Observe channel lateral migration over multiple years
				Reduced fine sediment deposition in channel
				Allow sediment deposition on floodplains
				Reduce riparian encroachment
				Increase/maintain substrate diversity
			Channel form and complexity: *Create and enhance complex channel forms (e.g., diversity in geomorphic units and substrate) that are the basis for high quality aquatic and riparian habitat.*	Increase the size, frequency, and topographic relief of bar/pool sequences
				Increase/maintain substrate diversity
				Increase channel sinuosity

	Goals	**Sub-Goals**	**Objectives: action**	**Sub-Objectives**
Landscapes (cont.)	Protect, enhance, and restore intrinsic physical watershed processes (e.g., hydrologic, geomorphic, and riparian) that create and maintain complex channel morphology and regulate habitat connectivity. (cont.)	Promote riparian corridor processes that support and sustain complex aquatic habitats	Riparian Zone Protection: *Limit activities that impact riparian vegetation and associated soils, geomorphology, and hydrology.*	Increase riparian buffer areas
				Allow terrestrial inputs (leaf matter and invertebrates) into channel
				Increase shading over river channel
				Increase recruitment of wood into channel
				Identify key locations and landowners to integrate working lands and promote shared goals
			Riparian Vegetation Dynamics: *Encourage geomorphic, sedimentological, and hydraulic processes that promote riparian seed dispersal, establishment, and growth in appropriate locations.*	Reduce riparian encroachment
				Maintain regular seed dispersal by riparian vegetation
				Maintain age diversity of riparian trees and vegetation
			Riparian Vegetation Diversity: *Encourage native riparian species diversity and structure that supports habitat and invertebrate food production.*	Maintain species diversity of riparian species
				Reduce non-native or nuisance riparian plants
				Maintain diversity of riparian phenology, leaf out/leaf drop timing
		Improve water quantity and quality	Water temperature: *Reduce water temperatures where the thermal regime has or will warm, and increase cold water refugia areas*	Maintain water temperatures in suitable range for focal species
				Restore thermal refugia and connectivity between them
			Nutrients and pollutants: *Minimize introduction of pollutants to the watershed from agricultural practices (e.g., herbicides, pesticides & fertilizers), roads (e.g., gas, diesel & oil) and return nutrient loads to natural levels to prevent overgrowth of cyanobacteria and toxic algae*	Minimize input of pesticides and anthropogenic toxins
				Maintain nutrient levels to support biological production but not overgrowth
				Restore turbidity to natural levels
			Dissolved oxygen: *Increase dissolved oxygen to healthy levels where appropriate to reduce lethal and sublethal effects on fish in egg, larval and juvenile life stages*	Maintain dissolved oxygen in water column to be suitable for focal species
				Maintain dissolved oxygen at high levels in interstitial spaces for fish egg and larval incubation

	Goals	Sub-Goals	Objectives: action	Sub-Objectives
Landscape (cont.)	Protect, enhance, and restore intrinsic physical watershed processes (e.g., hydrologic, geomorphic, and riparian) that create and maintain complex channel morphology and regulate habitat connectivity. (cont.)	Improve water quantity and quality (cont.)	Water volume (ground water and surface water): *Improve conditions to maintain groundwater and surface water in key locations*	Identify groundwater basins within the Eel River watershed that may be threatened by overextraction and/or require study to determine the interaction of groundwater and surface water flows (e.g., Covelo Valley, Willits Valley, Laytonville Valley, Lower Eel River at Ferndale, etc.)
				Identify key locations and landowners for summer flow augmentation

Table D-4. Tiered goals and objectives for conservation and watershed resiliency.

	Goals	Sub-Goals	Objectives	Sub-Objectives
Conservation	Protect the Eel River's natural resources through land conservation actions that promote habitat connectivity and resiliency	Increase amount of conserved and protected land	Conservation areas new and extended	Increase the size of existing protected areas, adding new protected areas and buffer areas to protect core habitat.
			Land acquisition and management by government land management agencies, local conservancies, and Native American Tribes	Seek a state or federal land designation for long-term Eel River watershed-wide conservation; this designation would serve as a mechanism for identifying priority acquisitions and acquiring private properties into public ownership and management. For example, elevate key riparian corridors to Eel River Greenways to be recommended as part of the Wildlife Corridors Conservation Act.
				Facilitate good management of existing Wild and Scenic River segments. Coordinate the creation of management plans for and communication between state and federal parties for Wild and Scenic River areas.
				Shift balance of property ownership toward more public ownership into land conservation designations; emphasize Eel River opportunities to contribute to 30x30 goals. Especially estuarine / salt marsh transition areas.

	Goals	Sub-Goals	Objectives	Sub-Objectives
Conservation (cont.)	Protect the Eel River's natural resources through land conservation actions that promote habitat connectivity and resiliency (cont.)	Increase amount of conserved and protected land (cont.)	Land acquisition and management by government land management agencies, local conservancies, and Native American Tribes (cont.)	Define and map existing Wild and Scenic Corridors to the standard 0.25-mile buffer in public lands. Coordinate with agencies to develop management for the standard buffer.
				Make recommendations to advance the management and extension of Wild and Scenic Rivers. Rank potential riparian resilience within the Wild and Scenic River areas of the watershed to promote the protection of those areas. Work with management agencies to develop management plans for the Wild and Scenic River areas of the Eel River.
		Establish and maintain connectivity and heterogeneity of conserved areas	Secure protection status for parcels that could bridge currently conserved or protected areas	Prioritize connectivity to existing protected areas. Link protected areas with riparian corridors or other natural areas where landscape impacts are low. (Collingham and Huntley 2000, Donald and Evens 2006, Synes et al. 2015).
				Establish working groups with local land management agencies to bridge resource management plans where rivers run through multiple agency holdings: National Park Service (Wild and Scenic Rivers management), U.S. Bureau of Land Management, U.S. Forest Service, and Round Valle Indian Tribes
				Use strategic planning to manage an effective protected riparian corridor system or greenway: Create and protect upland forest corridors between wetlands and uplands.

	Goals	Sub-Goals	Objectives	Sub-Objectives
Conservation (cont.)	Protect the Eel River's natural resources through land conservation actions that promote habitat connectivity and resiliency (cont.)		Secure protection status for parcels that could bridge currently conserved or protected areas (cont).	Representation: Protect representative habitats across the landscape (Keeley et al. 2018). Include areas within urban boundaries, upland and lowland areas in the represented habitats. Identify green belts that can contribute connective pieces to a larger climate resilient network.
		Use climate refugia strategy for planning conservation areas	Apply climate refugia criteria to priority rankings for protected area recommendations	Prioritize reconnecting tributaries and mainstems to floodplains and protecting those connections.
			Define and map climate corridors	Focus on physical landscape level ecological processes that will support resilience to temperature change. For example, upland to lowland corridors that follow temperature and precipitation gradients will support species movement irrespective of climate impacts (Pearson and Dawson 2005).
			Riparian forest connection to landscape	In land adjacent to and or impacting riparian corridors, avoid conversion and advance durable protection measures, such as acquisition, voluntary easements, and less sprawl in potential development near forested areas. Retain forests to preserve carbon storage value, reduce sediment loads in rivers, cool air temperatures, and retain climate resilience.

	Goals	Sub-Goals	Objectives	Sub-Objectives
Conservation (cont.)	Protect the Eel River's natural resources through land conservation actions that promote habitat connectivity and resiliency (cont.)	Use climate refugia strategy for planning conservation areas (cont.)	Riparian connection to wetlands	Connect wetlands to riparian areas, prioritize those with dense vegetation values. Where vegetation values are low, prioritize revegetation, restoration, and connect to riparian corridors between existing protected areas and other core habitat.
			Climate mitigation strategy	Focus prioritizations to protect remnant and/or connecting parcels with low solar radiation, lower temperatures, and heat mitigating landscape features on interior sub-regions of the Eel, especially Tribal lands and Disadvantaged Community Areas within the Middle Fork, North Fork, Van Duzen, and Upper Eel watersheds.
			Improve fire protections	Strategize and connect with local forestry managers to support restoration action in vulnerable areas. Recommend revegetation where upland habitat connects to riparian corridors, incorporate U.S. Forest Service data from recently burned areas, updated vegetation maps post-fire impacts.
		Protect ecosystem services	Protect multi-benefit landscapes	which deliver multiple ecosystem services, are resilient and likely to persist under future climate conditions.
			Lesson impacts from drought land for revegetation, where those restoration actions could connect to riparian corridors.	Connect wetlands to riparian areas, prioritize those with dense vegetation values. Prioritize connective upland areas with low vegetation values or bare
			Protect and promote agriculture best management practices	Identify parcels of agriculture options for grazing management and tidal interface conservation easements

	Goals	Sub-Goals	Objectives	Sub-Objectives
Conservation (cont.)	Protect the Eel River's natural resources through land conservation actions that promote habitat connectivity and resiliency (cont.)	Protect ecosystem services (cont.)	Flood impact mitigation	The southern extent of the North Coast is more vulnerable to sea level rise than the north. Partner with community and agency groups to recommend parcels for flood mitigation acquisition.
		Priority habitat data integration	Connect conservation values to restoration planning with analysis overlay	Crosswalk salmonid life-history needs by integrating other restoration plans and aquatic spatial data in the region (e.g., SHaRP, Eel River Action Plan).
		Protect species diversity and persistence	Prioritize protection of high biodiversity areas, and areas with high terrestrial and aquatic species richness	Establish conservation targets for state listed species of concern and other important habitats by integrating available data into biodiversity metrics.
				Identify “critical salmonid refugia”
				Mitigate impacts of anadromous fish scarcity from Pikeminnow food web competition.
				Develop Early Detection and Rapid Response long-term monitoring for invasive species at the sub region scale and eradicate invasive species.
		Develop regional partnerships	Form regional conservation partnerships with Tribal land trusts, community land trusts, and other regional planning groups	Identify locations where conservation actions can achieve common goals that promote habitat connectivity and resiliency.

Appendix E

Restoration and Conservation Actions

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Table E-1. Actions table for fish passage improvements.

Fish passage improvements: *Actions that improve aquatic habitat connectivity by improving volitional upstream and/or downstream movement of fish and aquatic species, particularly at man-made or otherwise anthropogenic barriers and obstacles such as road-stream crossings.*

Actions	Description	Channel archetype or location[1]
Large dam modification or removal	Remove Scott Dam to allow fish access to historically available habitat in the Upper Eel River watershed	2 (cool mainstem), Coho (Mainstem Eel River, Middle Mainstem Eel River, Upper Mainstem Eel River) Steelhead (Middle Mainstem Eel River, Upper Mainstem Eel River)
	Remove or modify Cape Horn Dam to improve upstream and downstream fish passage by reducing potential for injury and delay	2 (cool mainstem), Coho (Mainstem Eel River, Middle Mainstem Eel River, Upper Mainstem Eel River)
Small dam modification or removal	Remove or improve passage at small dams	all
Road-stream crossing improvements	Upgrade culverts that impair fish passage, ideally with bridges or stream simulation designs	0 and 1.1, 1.2, 1.3
	Build bridges or install culverts to prevent driving over shallow riffles	all
Tide gate removal or modification	Remove or modify tide gates to improve fish passage opportunities	4 (estuary)
Tributary access improvements	Remove or modify sediment deposits at tributary confluences to improve juvenile and adult access into high quality tributary habitats and thermal refuges by excavate channels or install wood features that concentrate flow into channels	1.1, 1.2, 1.3 (cold and cool focus)
Mainstem passage at shallow riffles	Manage flow diversions at Potter Valley Project to support low flow fish passage through the mainstem Eel River and reduce potential for false attraction leading to partial migration.	2, 3

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Table E-2. Actions table for instream habitat enhancements.

Instream habitat restoration: *Actions that increase or improve physical habitat conditions within the active stream channel and adjacent floodplain to support greater abundance and/or life history diversity for focal fish species.*

Actions	Description	Channel archetype or location[1]
Large wood addition	Includes single and multiple large wood placements and engineered logjams. Addition of large wood to increase habitat complexity and cover for fish in channel, and promote local bed scour and sediment sorting, and provide high flow velocity refuge.	1.1, 1.2 Steelhead (South Fork Eel River, Middle Fork Eel River)
Large rock/channel roughening additions	Addition of large boulders or other features to increase in-channel habitat complexity and cover for fish, promote local bed scour and sediment sorting. Can be combined with large wood structures.	1.1, 1.2
Active channel reconfiguration	Mechanical/active reconfiguration of reaches to restore riffle-pool sequences, increase channel sinuosity, create side channels, increase pool frequency and depth, and other habitat complexity elements.	1.1, 1.2, 2 Steelhead (South Fork Eel River)
Beaver dams analogs	Addition of beaver dam analogs to increase habitat complexity, flow retention, sediment storage, and create low-velocity habitats to support rearing and high flow refuge.	1.1, 1.2
Bridge/overpass modifications	Modify bridges and road overpasses to reduce effects on channel form and process	all
Bank protection modification or removal	Modify or remove bank protection (e.g., riprap) to allow channel migration and formation of under-cut banks. Frequently preformed in combination with land conservation action to allow for channel expansion.	all

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Table E-3. Actions table for off-channel habitat restoration and connectivity.

Off-channel habitat restoration and connectivity: *Actions that increase or improve physical habitat conditions outside the active stream channel but within the riparian/floodplain corridor that have at least seasonal connectivity (e.g., during high flow periods) to support greater abundance and/or life history diversity.*

Actions	**Description**	**Channel archetype or location**
Floodplain reconnection	Mechanical reconfiguration to improve hydraulic connection between active channel and floodplain, particularly in reaches where channel incision has occurred, and stream is disconnected from floodplain and/or side channels	1.1, 1.2, 2,3
Bank protection modification or removal	Removal or modification of levees or other bank protection (e.g., riprap) to allow channel migration and floodplain reconnection. Frequently done in combination with land conservation action to allow for channel expansion.	all
High-flow side channel construction or reconnection	Construct complex high-flow side-channel to increase habitat complexity and provide high flow velocity refuge	1.1, 2, 3
Off-channel pond construction or reconnection	Construct off-channel pond or alcove to provide high flow refuge habitat	1.1, 2, 3
Focused restoration planning in rare, large valleys where off-channel habitat restoration is expected to have greater opportunity and value	Need to highlight need for focused restoration planning in rare, large valleys where off-channel habitat restoration is expected to have greater opportunity and value	(Round Valley, Little Lake Valley, Laytonville/Ten Mile Valley)

Table E-4. Actions table for estuary habitat restoration.

Estuary Habitat Restoration: *Actions that increase or improve physical habitat conditions or habitat connectivity within the estuary, floodplain, and stream-estuary ecotone*		
Actions	**Description**	**Channel archetype or location**
Levee set-back or removal	Removal or modification of levees or other bank protection to allow tidal channels to form and floodplain areas to reconnect	4 (estuary) Steelhead
Tide gate upgrade or removal	Restore tidal prism and provide fish passage	4 (estuary)
Re-establish historical slough channels	Reconnect and restore historical slough channels	4 (estuary)
Reconnect freshwater tributaries to estuary	Restore connectivity between estuary and tributaries that have been disconnected	4 (estuary)
Install livestock fences	Install exclusion fencing to protect channels and banks from trampling	4 (estuary)

Table E-5. Actions table for Instream flow protection and enhancement.

Instream flow protection and enhancement: *Actions that increase, improve, or protect water supply and aquifers or conditions that maintain surface and groundwater that contribute to supporting instream flows for fish and other aquatic species and the ecosystems they depend on (e.g., riparian corridor ecosystem)*

Actions	Description	Channel archetype or location[1]
Regulate/reduce summer water diversions	Reduce water diversions and groundwater extraction/pumping during summer that reduces summer flow volume	0, 1, 2, Coho (South Fork Eel River); Chinook (South Fork Eel River, lower Mainstem Eel River, Upper Eel River, Van Duzen River) Steelhead (South Fork Eel River, Middle Fork Eel River, Middle Mainstem Eel River, Upper Mainstem Eel River, Van Duzen River)
Establish diversion guidelines/rules for Potter Valley Project that protect fish and ecosystem processes	PVP water management and diversions can affect fish passage and movement as well as fish life history, growth, and production. Water diversions should be protective of these considerations and other ecosystem processes.	2 (cool mainstem)
Develop off-channel water storage programs	Encourage and facilitate winter high-flow diversions that store water in stable (lined) ponds for summer flow augmentation	0, 1, 2
Beaver dam analogs	Install beaver dam analogs to provide flow retention, groundwater recharge, and locally increase the water table.	1.1, 1.2, 2
Beaver reintroduction	Reintroduce beaver to provide flow retention, groundwater recharge, and locally increase the water table	1.1, 1.2, 2
Stream flow gaging	Monitor streamflow at critical points in the watershed to establish and frequently evaluate instream flow needs	2

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Table E-6. Actions table for Water Quality Improvement.

Water quality improvement (including water temperature): *Actions that improve water quality conditions for fish and other aquatic species and support the ecosystem on which they depend including water temperature, water chemistry, fine sediment, and pollution.*

Actions	Description	Channel archetype or location[1]
Identify, protect, enhance, and provide access to thermal refugia	Thermal refugia may include lower reaches of cool tributaries and their coldwater plumes in adjacent mainstems, thermally-stratified deep pools, wetted reaches below dry/sub-surface reaches, estuarine/coastal oriented habitats, headwater streams.	1.1-W, 1.2-W, 2-W, 3, 4
Reduce summer water temperature in key rearing habitats	Identify locations where summer water temperatures are near the threshold for suitability and develop strategies for improvement	1, 2 Steelhead (South Fork Eel River)
Reduce nutrient loading	Identify and reduce point- and non-point source nutrients where high nutrient supply determined to be an issue	all
Reduce fine sediment loading (also see upslope sediment control)	Reduce fine sediment supply to watercourses and streams from streambank and upslope sources	1, 2, 3
Riparian re-vegetation	Improve riparian vegetation conditions	0, 1, 2

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Table E-7. Actions table for Riparian and wetland habitat restoration.

Riparian and wetland habitat restoration: *Actions that increase, improve, or protect riparian and wetland habitat conditions that influence channel form and geomorphic processes (e.g., large wood supply), aquatic habitat conditions (e.g., stream shading, water quality), and ecology (e.g., allochthonous inputs).*

Actions	Description	Channel archetype or location[1]
Riparian vegetation management	Improve riparian habitat function and composition through thinning and planting. Plant riparian trees and shrubs where historic clearing or large fires have impacted riparian cover/shade	0, 1, 2 Chinook (Larabee Creek)
Riparian fencing or livestock management	Protect riparian areas from livestock, particularly where summer water temperatures are high and shade has been reduced, and where bank stability and sedimentation are issues of concern.	all
Riparian buffers and protection	Protect riparian habitat within stream meander belt/riparian corridor to allow natural channel process and local wood supply	0, 1, 2, 3
Wetland habitat protection and restoration	Protect and/or restore wetland areas within the riparian corridor to provide seasonal habitat and/or contribute	all

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Table E-8. Actions table for streambank and upslope sediment control/management.

Streambank and Upslope sediment control/management: *Actions that decrease sediment delivery rates to streams particularly increased sediment supply caused by man-made infrastructure (e.g., roads), land management activities (e.g., timber harvest), or other anthropogenic disturbance (recreation, increased wildfire activity).*

Actions	Description	Channel archetype or location[1]
Reduce sediment delivery from roads	Perform road maintenance where sediment issues have been identified	**Coho** (North Fork Eel, South Fork Eel, Middle Fork Eel, Middle Mainstem Eel River, Upper Mainstem Eel River); **Chinook** (South Fork Eel River, lower Mainstem Eel River, Upper Eel River, Larabee Creek, Van Duzen River) **Steelhead** (South Fork Eel River, Middle Fork Eel River, North Fork Eel River, Middle Mainstem Eel River, Upper Mainstem Eel River, Van Duzen River)
	Remove or replace undersized and failing culverts	
	Decommission roads that are no longer needed	
Reduce sediment delivery from severely eroding banks	Install features to prevent mass wasting (e.g., willow walls)	0, 1, 2, 3
	Line ponds to prevent mass wasting	0, 1, 2
Wildfire management	Fire management to reduce fuels. Support cool, controlled burning over fast, uncontrolled, destructive burning	Coho (North Fork Eel River), Chinook (Upper Eel River) Steelhead (Middle Fork Eel River, North Fork Eel River)
Vegetation management	Manage upslope vegetation to avoid young, dense forests that are prone to high severity wildfire	Coho (North Fork Eel River), Chinook (Upper Eel River)

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Table E-9. Actions table for invasive species and disease management.

Invasive species and disease management: *Actions that reduce the impact of invasive species on focal fish species, particularly predation by non-native fish (e.g., Sacramento pikeminnow).*

Actions	Description	Channel archetype or location[1]
Removal, control/suppression, and/or monitoring of non-native fishes	Reduce abundance of Sacramento pikeminnow	Coho (Mainstem Eel River), Chinook (Upper Eel River, Van Duzen River) Steelhead (South Fork Eel River, Middle Fork Eel River, Middle Mainstem Eel River, Upper Mainstem Eel River, Van Duzen River)
	Physical removal (e.g., through targeted angling, e-fishing, weirs) or genetic extinction (e.g., Trojan Y)	1, 2, 3
Monitoring/prevention/early detection of aquatic invasive species	Invasive aquatic species including fish and other taxa. Smallmouth bass is a significant concern because of their potential to establish. Mussels and snails are a concern because of their potential to change ecological processes and food web dynamics.	all
Removal, management, and/or monitoring of non-native terrestrial wildlife	Invasive terrestrial species including wild boar and feral pig are a concern because of their potential to disturb riparian vegetation and soil.	0, 1, 2
Removal, management, and/or monitoring of invasive plant species within riparian corridor	Invasive terrestrial species including Arundo etc. are a concern because of their potential to displace native species.	all
Fish disease monitoring	A monitoring program is needed to understand / monitor prevalence of fish diseases in the Eel River (similar to Klamath)	2, 3

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Table E-10. Actions table for active species management.

Active species management: *Actions that improve habitat conditions or productivity of focal fish species through active species management (e.g., beaver re-introductions; hatchery or hatch box program).*

Actions	Description	Channel archetype or location
Beaver reintroduction, management, and/or relocation	Beaver dams and activities can increase habitat complexity, improve growth and survival, regulate flow and sediment, and increase water table.	1.1
Develop conservation hatchery or hatch box program	Enhance production of focal species through conservation hatchery or hatch box program.	1.1-cold, 1.2 cold, 2-cool

Table E-11. Actions table for land conservation.

Land conservation: *Actions that protect or conserve lands with unique, important, and/or intact habitats to maintain or improve river corridor habitat, preserve natural processes, and/or improve habitat connectivity over 10s to 100s year time scale.*

Actions	Description	Channel archetype or location
Promote and expand conservation easements	Protect and connect high-quality habitats	all
Establish streamside protected areas to encourage riparian growth in heavily populated/visited areas		all
Expand Wild and Scenic River designation and protections	Coordinate management among agencies—NPS, State, BLM, USFS	
	Write management plan for areas outside of Federal management	

Table E-12. Actions table other potential strategies.

Other potential strategies		
Actions	**Description**	**Channel archetype or** location[1]
Community outreach and watershed education	Continue Eel River Forum meetings	n/a
	Support youth education programs	n/a
	Support community science participation	n/a
Improve biotic conditions to increase food supply and juvenile growth	Supplement nutrients through fish carcass/egg additions or other strategies	1
Regulatory	Wild and Scenic River designation	See Plan section 1.3.5.
	Fishing regulations and fisheries management	2, 3, Steelhead (South Fork Eel River, Middle Fork Eel River, Van Duzen River)

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