NURSERY FUNCTIONS OF U.S. WEST COAST ESTUARIES: THE STATE OF KNOWLEDGE FOR JUVENILES OF FOCAL INVERTEBRATE AND FISH SPECIES

Brent B. Hughes[1], Matthew D. Levey[2], Jennifer A. Brown[3], Monique C. Fountain[4], Aaron B. Carlisle[5],
Steven Y. Litvin[5], Correigh M. Greene[6], Walter N. Heady[7] and Mary G. Gleason[7]

1 University of California Santa Cruz; 2 SeaSpatial Consulting; 3 Monterey Bay National Marine Sanctuary;
4 Elkhorn Slough National Estuarine Research Reserve; 5 Hopkins Marine Station, Stanford University;
6 NOAA Northwest Fisheries Science Center; 7 The Nature Conservancy

Prepared by SeaSpatial Consulting LLC: for The Nature Conservancy and
the Pacific Marine and Estuarine Fish Habitat Partnership.

SeaSpatial Consulting

The Nature Conservancy
Protecting nature. Preserving life.®

Pacific Marine & Estuarine Fish Habitat Partnership

Funded by Resources Legacy Fund and the David and Lucile Packard Foundation:

RESOURCES LEGACY FUND
CREATIVE SOLUTIONS. LASTING RESULTS.

the David & Lucile Packard
FOUNDATION

This report, *Nursery Functions of U.S. West Coast Estuaries: The State of Knowledge for Juveniles of Focal Invertebrate and Fish Species*, was commissioned by The Nature Conservancy to support the Pacific Marine and Estuarine Fish Habitat Partnership (PMEP).

PMEP was formed in 2009 to protect, restore and enhance ecological processes and habitats within estuaries and nearshore marine environments to sustain healthy native fish communities and support sustainable human uses that depend on them. PMEP is one of 19 nationally recognized fish habitat partnerships that seeks to advance regional and national goals relating to juvenile fish habitat (http://www.pacificfishhabitat.org). To support its mission, PMEP is working with a broad array of partners (federal, state, tribal, nonprofit, industry and academic) to conduct an assessment of juvenile fish habitat in nearshore and estuarine habitats on the West Coast. The overall goals of the multi-phase assessment are to:

- Better understand the role of estuaries in sustaining native species of fish and shellfish, including those most important to people;
- Identify nursery habitat for fish and shellfish in estuaries, and inform restoration priorities;
- Identify and evaluate key threats to fish habitat in estuaries;
- Demonstrate how conserving and restoring juvenile fish habitat in estuaries contributes to the overall ecological health and economic sustainability of commercial and recreational fisheries;
- Identify gaps in knowledge, science and understanding of the role estuaries play in providing nursery habitats for fish and shellfish of commercial, recreational and cultural importance; and
- Inform conservation and management decisions.

Suggested Citation:
Hughes, B. B., M. D. Levey, J. A. Brown, M. C. Fountain, A. B. Carlisle, S. Y. Litvin, C. M. Greene, W. N. Heady and M. G. Gleason. 2014. Nursery Functions of U.S. West Coast Estuaries: The State of Knowledge for Juveniles of Focal Invertebrate and Fish Species. The Nature Conservancy, Arlington, VA. 168pp.

Cover photos: Clockwise from top left: © Kirsten Ramey/CDFW; © Tom Gaskill; © Andrew Weltz/CDFW

ACKNOWLEDGEMENTS

We would like to thank the many experts and stakeholders who provided data and information, or reviewed a draft of this report. Their contributions ensure that this summary of the present state of scientific knowledge about estuarine use by juveniles of 15 focal species in estuaries of California, Oregon and Washington will be an essential tool for use in designing and planning estuarine restoration and conservation projects to sustain healthy fish and invertebrate populations.

We are especially indebted to Lisa DeBruyckere (PMEP) for compiling peer-review comments on this report, copyediting, and organizing numerous workshops and meetings.

Reviewers included the PMEP Steering Committee—Korie Schaeffer (NOAA Fisheries), John Bragg (South Slough National Estuarine Research Reserve), Jena Carter (The Nature Conservancy), Stan Allen (Pacific States Marine Fisheries Commission), Fran Recht (Pacific States Marine Fisheries Commission), Dan Avery (Oregon Department of Fish and Wildlife), Sarah Beesley (Yurok Tribal Fisheries Program), Randy Carman (Washington Department of Fish and Wildlife), Chuck Combs (Makah Tribe), Joe Petersen (Makah Tribe), Vicki Frey (California Department of Fish and Wildlife, [CDFW]), Kevin Shaffer (CDFW), Jennifer Gilden (Pacific Fishery Management Council), Michael Kellett (US Forest Service), Heather Kapust (Washington Department of Ecology), Dan Shively (US Fish and Wildlife Service), Chris Swenson (US Fish and Wildlife Service), John Stadler (NOAA Fisheries), Kim Kratz (NOAA) and Stan van de Wetering (Confederated Tribes of Siletz Indians).


© Laura S. Brophy

And the PMEP Science and Data Committee—Van Hare (Pacific States Marine Fisheries Commission), Laura Brophy (Estuary Technical Group—Institute for Applied Ecology), Mary Gleason (The Nature Conservancy), Eric Grossman (US Geological Survey), Bill Pinnix (US Fish and Wildlife Service), Steve Rumrill (Oregon Department of Fish and Wildlife), Ken Pierce, Jr. (Washington Department of Fish and Wildlife) and Martha Sutula (Southern California Coastal Water Research Project).

We would like to thank the following experts who provided useful comments on earlier versions of the report: Randy Baxter (CDFW), Paul Reilly (CDFW), Pete Kalvass (CDFW), Ken Oda (CDFW), Christy Juhasz (CDFW), Ryan Bartling (CDFW), Thomas Grenier (CDFW), Joel Fodrie (University of North Carolina at Chapel Hill), Chris Rooper (NOAA Fisheries), Kristen Ramey (NOAA), Jason Toft (University of Washington [UW]) and Jeff Cordell (UW).

Additional contributions to the content were made by The Nature Conservancy Staff—Jena Carter, Matt Merrifield, Dick Vander Schaaf and interns (Kate Labrum, Adrienne Phillips, Bethany Taylor).

We would also like to thank the contractors who developed the West Coast Estuary Inventory, Classification and Geodatabase—Jen Kassakian, Kate Doiron and Daniel Hudgens, of Industrial Economics Incorporated (IEc), and Kevin O'Connor, Charles Endris and Ross Clark with the Central Coast Wetlands Group (CCWG).

EXECUTIVE SUMMARY

© Walter N. Heady/TNC

Estuaries are some of the most productive ecosystems on the planet, and provide many key ecosystem functions, one of which is the provision of juvenile nursery habitat for fishes and invertebrates. Along the West Coast of the United States (California, Oregon and Washington; hereafter, West Coast), estuaries are known to be important nursery grounds for a few ecologically and economically important species, such as Dungeness crab, salmonids and flatfishes. Despite this documented importance for some species, the nursery function of estuaries for a multitude of species along the entire West Coast is poorly understood. This lack of understanding is of concern given that many estuaries are threatened by a suite of anthropogenic stressors and a potential loss of ecosystem function. This report expands upon previous efforts summarizing juvenile use of estuaries and synthesizes the existing geospatial data and information on the nursery role of estuaries for a group of ecologically and economically important fish and invertebrate species.

To define the scope of this report, we first identified all the estuaries along the West Coast that were most likely to provide juvenile habitat, which resulted in an inventory of 303 estuaries and coastal confluences that each has surface areas of more than 0.04 hectares. We synthesized information on juvenile nursery requirements of the 15 focal species and whether juveniles of those species have been documented in these estuaries. Information on juvenile presence in these estuarine systems was compiled in a geodatabase that is associated with this report.

We assembled a list of 15 focal species based on several criteria, which included: a documented use of estuarine habitats during the juvenile life history stage; a broad distribution along the West Coast; a high ecological, cultural, commercial, recreational, or conservation importance; and a diversity of the taxonomic groups and life-history types found in West Coast estuaries. We conducted a literature review and received expert input on the basic biology, feeding habits, life histories, habitat associations and estuarine presence for each of the 15 species. Where more detailed information was available, we developed case studies to illustrate the different nursery functions of estuaries. We also aimed to synthesize: 1) important and emerging threats to the nursery functions of West Coast estuaries, 2) tradeoffs associated with the management of habitats for species-specific nursery function, 3) knowledge gaps and 4) potential management actions to conserve or restore nursery function.

Our review emphasizes the widespread distribution of potential estuarine nurseries across the West Coast. Juveniles of some of the 15 focal species were documented in 113 of the 303 estuaries reviewed. This number included many smaller estuaries (53 at less than 100 ha), which provide juvenile habitat for 11 of the 15 focal species, highlighting the potentially high nursery value of smaller estuaries. This was an important result given that much of the prior focus on the nursery role of West Coast estuaries has centered on large and medium-sized systems (e.g., San Francisco Bay, Columbia River Estuary, Yaquina Bay, Willapa Bay, Puget Sound). These results suggest that future studies should consider a regional approach to evaluate the relative contribution of small and large estuaries for juveniles of species of interest.

Our review also highlighted the importance of different classes of estuaries across the West Coast. We identified four key estuary classes: lagoonal, riverine, embayment and sound, all of which were found to be important systems for juvenile life-history stages of some or all of the 15 focal species. Within estuaries, we identified four important estuarine sub-classes that are used by juveniles of 11 or more of the focal species: estuarine coastal subtidal, tidal channel/creek, slough and lagoon.

At the habitat level, of the 11 estuarine habitat types that we found to be important for juvenile life-history stages, seagrass beds were used by the most species (13 of 15 species). Seagrasses, including *Zostera marina*, which is the primary habitat forming seagrass in West Coast estuaries, are well-known foundation species, that provide important ecosystem services, including nursery habitat for fishes and invertebrates. However, seagrasses are in a state of decline both globally and along the West Coast, and with those losses comes the loss of their important nursery function. Managers should consider areas where seagrass has been lost as priority targets for restoration of important ecosystem functions of estuaries.

The majority of focal species had several documented threats to their juvenile life-history stages in estuaries. Out of the 19 types of threats we reviewed, habitat loss was the common threat to the 15 focal species. Habitat loss was not specific to any one region, but occurred across the entire West Coast. Other important threats we identified include species invasions, hypoxia from eutrophication, the use of pesticides for aquaculture practices and climate change through ocean warming and sea-level rise. The three salmonid species (coho, Chinook and steelhead trout) had the most documented threats, however, this could be the result of greater research effort towards salmonid species.

Our review showed that despite good information demonstrating the importance of estuarine nurseries for some species, significant knowledge gaps remain. First, most of the information on nursery function that does exist is limited to mostly larger, well-studied estuaries. Second, there are several characteristics of the nursery role that have yet to be explored for many species, such as determining relative growth rates in alternative juvenile habitats, exploring ontogenetic shifts in habitat use and determining the important habitats that provide refugia from predation and environmental stress. Third, there is a wealth of information for most of the commercially important species, such as salmonids, crabs and flatfishes, yet there is little information on the nursery role of estuaries for species of lower economic value (e.g., bay shrimp, Pacific staghorn sculpins, bat rays and shiner perch). Although these species have little monetary value, they often provide important linkages in estuarine food webs through their abundance as a food source for predators, or their own role as predators.

© Laura S. Brophy

Together with the estuary inventory and the geodatabase, this report represents the first stage in a larger effort to better understand the nursery functions of West Coast estuaries for fish and invertebrates. Ultimately, a complete analysis of juvenile habitat in all coastal water bodies would add substantially to the state of our knowledge of estuarine nursery function and would be a valuable tool for future conservation, restoration and management of estuaries and the species they support.

TABLE OF CONTENTS

© Mary G. Gleason/TNC

FIGURES

TABLES

BOXES

INTRODUCTION

© Laura S. Brophy

Estuaries, coastal areas where marine, freshwater and terrestrial environments meet, are considered one of the most productive ecosystems on the planet, and provide critical ecological services for a wide array of resident and migratory species. The essential services of estuaries include provision of food, habitat complexity, filtration, buffering from extreme natural forces and refuge from predation, all of which enhance the estuarine nursery function for juvenile life stages of many species (Beck et al. 2001, Beck et al. 2003, Nagelkerken et al. 2013, Sheaves et al. 2014). Estuarine habitats support vital ecosystem functions, such as food production, sediment trapping and predator avoidance, and are known to serve as nursery habitat for many commercially important species along the U.S. West Coast (California, Oregon and Washington; West Coast hereafter), such as Dungeness crabs, Pacific herring, and several species of salmon and flatfish.

Documenting and quantifying the nursery value of juvenile rearing habitat is important in the context of effectively prioritizing efforts to conserve and restore coastal ecosystems and support sustained populations of fish and invertebrates. How nursery value is defined and measured will have a strong influence on how these priorities are set. Beck et al. (2001) formulated a definition of the nursery-role concept that evaluates juvenile habitats based on per-unit-area contribution to the adult population. According to this definition, "[a] habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur."(Beck et al. 2001, see Box 1). Based on this definition, the best way to identify nursery habitat for a given species is to measure the proportion of individuals in the adult population that originated from alternative juvenile habitats. In addition, to gain an understanding of why a particular habitat supports a higher relative contribution of young fish, we must also try to understand why the juvenile fish use that particular location over other acceptable, though less-preferred, habitat types. Measures of relative quality of habitats include density, condition, survivorship and growth rates of individuals and populations residing in alternative habitat types.

Although there are several case studies demonstrating the high nursery value of estuaries on the West Coast, the importance of the nursery function of estuaries along the entire West Coast is poorly understood (Gleason et al. 2011). Our knowledge is generally limited to a few individual species (e.g., steelhead trout, Dungeness crab, English sole), or to the larger estuarine systems (e.g., San Francisco Bay, Yaquina Bay, Puget Sound). There has been little effort to synthesize existing information and data to assess coastwide patterns of nursery function, and threats to species of ecologic and economic importance that use estuaries for juvenile rearing. Because threats have been identified that may affect the entire West Coast (Halpern et al. 2009, Gleason et al. 2011, Merrifield et al. 2011, Greene et al. 2014), this lack of synthesis makes it difficult to identify strategies to strengthen fisheries production, or to alleviate threats to species and habitats of concern.

The information that does exist clearly demonstrates that estuaries have high nursery value for some species and functional groups. Examples of enhanced nursery function along West Coast estuarine habitats have been demonstrated for several species of salmonids, flatfishes, sharks and crabs (e.g., Armstrong et al. 2003, Ebert and Ebert 2005, Bottom et al. 2005a, Brown 2006). One of the richest examples of nursery functioning for estuaries comes from English sole (*Parophrys vetulus*), where in estuaries from California to Washington, it has been found that juveniles from estuarine habitats contribute disproportionately to adult populations compared to other juvenile rearing habitats (Armstrong et al. 2003, Brown 2006). It has also been demonstrated that several imperiled species listed under the Endangered Species Act, such as green sturgeon (*Acipenser medirostris*) and steelhead trout (*Oncorhynchus mykiss*) (Moser and Lindley 2007, Bond et al. 2008), have juvenile or subadult life-history stages dependent on estuaries for growth and survival. Other species, such as smaller forage fish, e.g., Pacific herring (*Clupea pallasii*), have early life-history stages dependent on key estuarine habitats, such as eelgrass beds (*Zostera marina*), which are also habitats that are threatened and sensitive to anthropogenic stressors (Penttila 2007, Waycott et al. 2009).

Estuaries are often heavily impacted by a growing human population along the world's coasts that develops and adds stress to coastal environments and resources (Vitousek et al. 1997). The high percentage loss of coastal habitats along with on-going and future threats, such as sea-level rise, highlights the urgency to understand the nursery role of West Coast estuaries, especially considering their importance in providing a multitude of ecosystem functions and services. Threats to estuaries and the organisms that rely on them come from a variety of sources, and can be either direct, such as excessive fishing (Jackson et al. 2001) and habitat degradation and alteration (Lotze et al. 2006), or indirect, such as climate change (Atrill and Power 2002), eutrophication (Cloern 2001, Rabalais et al. 2002) and changes in community structure (Silliman et al. 2005, Altieri et al. 2012, Hughes et al. 2013). Furthermore, these threats have been demonstrated to be widespread (Halpern et al. 2009, Gleason et al. 2011) and impacting populations of species of economic importance and conservation concern (Jackson et al. 2001, Worm et al. 2006), while simultaneously reducing key functions of estuaries, including their nursery role (Beck et al. 2001, Kennish 2002).

There are many threats to estuarine nursery function along the West Coast. These include urbanization and agriculture along the coast, aquaculture and changes in land use and climate. Examples of climate-driven patterns include large-scale changes in oceanographic conditions, such as the intensification of the California Current, which can lead to increased upwelling intensity and shoaling, bringing low dissolved oxygen water into shallow coastal regions and resulting in the spread of anoxic dead zones over portions of the continental shelf (Grantham et al. 2004, Auad et al. 2006, Booth et al. 2012). This oxygen depleted water can spill over into estuaries, as has been demonstrated in Oregon (Roegner et al. 2011, Hessing-Lewis et al. 2011) and California (Hughes et al. 2012), where it can affect both the availability of acceptable nursery habitat and the recruitment of young fish to populations of economically important species (Cloern et al. 2007, Reum et al. 2011, Hughes et al. 2012).

Additionally, other threats, such as eutrophication and resulting hypoxia from land-based nutrient sources, have been determined to occur along the West Coast in bays and estuaries (Brandenberger et al. 2011, Hughes et al. 2011, McGlaughlin et al. 2013), and threaten their nursery function by reducing biodiversity and available habitat (Carlisle and Starr 2009, Hughes et al. 2012, Hughes et al. 2013). Habitat alteration (e.g., dredging, filling, diking, draining) and eutrophication caused by human activities have also caused widespread loss of essential vegetated estuarine habitats, such as salt marsh (Larson 2001) and seagrass (Waycott et al. 2009, Hughes et al. 2013). These habitats support vital ecosystem functions associated with estuaries and serve as nursery habitat for many commercially important species, such as Dungeness crab, Pacific herring and several species of salmon.

In the last three decades, there were several efforts to synthesize existing information on estuarine use by ecologically and economically important species and establish a baseline for characterizing juvenile life-history stages using West Coast estuaries (e.g., Monaco et al. 1990, Emmett et al. 1991, and Monaco et al. 1992). However, there have been few coastwide reviews in the last quarter century focused on estuarine use by juvenile species of ecological and economic importance and key threats to estuarine functions and processes (Gleason et al. 2011, Merrifield et al. 2011). These previous efforts focused on larger estuaries and thus were limited in their relative coverage of the West Coast and the total number of estuaries included; 32 estuaries in Monaco et al. (1990) and Emmett et al. (1991) and 146 estuaries in Gleason et al. (2011). By compiling information on juvenile presence and habitat use patterns of 15 species for an inventory of 303 estuaries, this review greatly expands our understanding of the coastwide nursery function of West Coast estuaries.

OVERVIEW OF GOALS

This report was commissioned by the Pacific Marine and Estuarine Fish Habitat Partnership (PMEP) to provide a synthesis of the state of scientific knowledge of nursery functions of West Coast estuaries to support a coastwide nursery assessment. We aimed to expand upon prior summaries of juvenile life history use of estuaries (e.g., Monaco et al. 1990, Emmett et al. 1991, Monaco et al. 1992, Gleason et al. 2011) and synthesize the existing geospatial data and information on the nursery role of estuaries for 15 ecologically and economically important species. The 15 focal species were selected to encompass the diversity of life histories, functional groups, habitat-use patterns, and ecological roles of species found in West Coast estuaries. We investigated the potential role of 303 West Coast estuaries as nurseries by compiling, in a geodatabase, information on presence of juveniles from the literature, existing data sources and personal communications with scientists monitoring estuaries. The estuaries included in the geodatabase are from a comprehensive inventory of all estuaries $>$ 0.04 ha in California, Oregon and Washington. Additionally, we generated a review of the nursery requirements for each focal species by reviewing their basic biology, life histories, food habits and life-history stages using estuarine habitats. When more detailed information was available, we developed case studies to illustrate the different nursery functions of estuaries. We also synthesized information on: 1) important and emerging threats to the nursery functions of West Coast estuaries, 2) tradeoffs associated with the management of species and habitats for their nursery function, 3) knowledge gaps, and 4) potential management actions to conserve and restore nursery function.

© Andrew Weltz/CDFW

BOX 1. THE NURSERY CONCEPT OF ESTUARIES

The role of estuaries as valuable rearing habitat for the juvenile stage of fishes and invertebrates has long been appreciated and often used as one of the reasons to conserve and restore estuaries. Estuaries were often found to have high densities of juveniles and were assumed to provide better rearing environments (e.g., more food, lower risk of predation, warmer water) than other juvenile habitats. Understanding which estuaries, and specific estuarine habitats, provide the best rearing environments and contribute disproportionately to the maintenance of adult populations is valuable information to help effectively manage both species and coastal habitats. However, quantifying the nursery value of estuaries, or the specific habitats within estuaries, is a difficult task.

In 2001, Beck and colleagues sought to clarify the meaning of nursery habitat and delineate the types of information needed to quantify nursery value. According to Beck et al. (2001), “A habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur.” This definition applies to species with a complex life cycle, in which larval or juvenile stages enter estuaries, reside in the estuaries for a few months or years, and then move to adult habitats outside the estuary. Under this definition not all habitat used by juveniles are nurseries, only those with the highest per-area contribution. Greater per-area contribution can be attributed to one or more aspects of juvenile habitat quality: higher juvenile density, faster growth rates, higher survival rates and higher recruitment success to adult habitats. Habitats with high per-area contribution will likely be important targets for conservation and management given their high quality as rearing habitat.

However, it is important to note that if those nursery habitats are relatively small in size, then they may contribute only a small proportion of the individuals needed to sustain the overall adult population. An alternative approach for identifying juvenile habitats that could be important conservation and management targets, is to identify juvenile habitats that make the greatest overall contribution of individuals to adult populations irrespective of their unit-area rate. Dahlgren et al. (2006) called these habitats “Effective Juvenile Habitats”. Management efforts targeting effective juvenile habitats would support those habitats that are most important for maintaining the adult population even though their relative value as rearing habitat may be lower.

More recently, the concept of nursery value, whether discussed in terms of “nursery” or “effective juvenile” habitat, has expanded to recognize that most species exhibit multiple habitat shifts during their period of estuarine residency, both within and across life stages. For species that are estuarine residents and those that only spend part of their life history within these systems, a growing body of work calls for the evaluation of nursery value in the context of the habitats that are functionally connected through their movements over the period of estuarine residency (Weinstein et al. 2005, Sheaves et al. 2006, Sheaves 2009, Nagelkerken et al. 2013). In addition, it is clear the growth, condition, survival and ultimately the proportion of individuals that contribute to adult populations of a given species, reflect the physiological suitability, food resources and ecological processes within the mosaic of habitats they have frequented since settlement or birth. Thus, the emerging paradigm is the evaluation of the nursery value of specific estuarine habitats for a given species must be considered in the context of the spatially explicit mosaic encompassed by the estuarine habitats that are functionally connected through their movements over the period of estuarine residency (Weinstein et al. 2014, Sheaves et al. 2014, Litvin et al. 2014).

METHODS

© Adam Frimodig/CDFW

IDENTIFICATION OF FOCAL SPECIES

We worked with regional experts to review a preliminary list of 34 species and select 15 that encompassed a broad range of life histories, functional groups, trophic guilds and ecological roles in estuaries. We used several criteria to select the 15 focal species for this state of the knowledge review. First, as a logical prerequisite of the Beck et al. (2001) definition of estuarine nurseries, focal species should rear extensively in estuaries as juveniles, but not spend their entire life history in estuarine habitats. Likewise, estuary habitats should have higher importance than freshwater floodplain or nearshore marine habitats to the juvenile life history stage. Second, in order for this review to have a broad application across the West Coast, the suite of 15 focal species should include species distributed across Washington, Oregon and California estuarine systems. Third, for this review to have relevance for conservation of estuarine habitats and species, focal species included fish and shellfish with high importance to management due to their ecological and cultural importance, recreational, or commercial harvest, or special regulatory status (e.g., listed under state or federal Endangered Species Acts).

We consulted a number of sources, including Emmett et al. (1991), Monaco et al. (1992), and unpublished lists of observations from state and federal scientists, to assemble species lists and information on estuarine habitat use, geographic range and management importance. Data on habitat use at different life stages and geographic range were derived from Emmett et al. (1991), Allen et al. (2006), and Fishbase (www.fishbase.org) and references therein. Management importance was derived from data on recreational and commercial fishing maintained by the Pacific States Marine Fisheries Commission and consultations with regional biologists. A draft list was reviewed by approximately 100 scientists across the region at a workshop sponsored by PMEP, which focused on designing a nursery assessment for the West Coast. Comments from this expert review were used to further refine the focal species list. The final list (Table 1) focused on balancing geographic range variation and taxonomic diversity with the amount of information available on the degree of estuarine habitat use.

TABLE 1. The 15 focal species for the state of the knowledge report on nursery functions of West Coast estuaries.

Common Name	Scientific Name
Dungeness crab	*Metacarcinus magister*
Bay shrimp	*Crangon franciscorum*
Leopard shark	*Triakis semifasciata*
Bat ray	*Myliobatis californica*
Green sturgeon	*Acipenser medirostris*
Chinook salmon	*Oncorhynchus tshawytscha*
Coho salmon	*Oncorhynchus kisutch*
Steelhead trout	*Oncorhynchus mykiss*
California halibut	*Paralichthys californicus*
English sole	*Parophrys vetulus*
Starry flounder	*Platichthys stellatus*
Brown rockfish	*Sebastes auriculatus*
Staghorn sculpin	*Leptocottus armatus*
Shiner perch	*Cymatogaster aggregata*
Pacific herring	*Clupea pallasii*

LITERATURE REVIEW AND OUTREACH TO EXPERTS

To compile available information on life-history characteristics, estuarine habitat use patterns, threats, and estuarine nursery functions for the 15 focal species, we reviewed the available literature and consulted with experts. For the literature review, we reviewed approximately 1000 peer-review articles and reports on use of West Coast estuaries by juveniles of the 15 focal species. We extracted information on life-history traits (e.g., geographic range, depth range, maximum size and age, age to maturity, spawning season, planktonic duration, size at settlement), and whether a fishery exists for that species. We also compiled information on factors that influence estuary use by the juvenile life-history stage, including geographic range of estuarine use, estuary type, habitat use, temperature range, salinity range, dissolved oxygen range, size range, and predators and prey. Scientific terms, acronyms, and scientific units are defined in Appendix 1.

We assembled information on use of estuaries and estuarine habitats for all life-history stages. We used the Coastal and Marine Ecological Classification Standard (CMECS) to broadly categorize and define classes of estuaries on the West Coast, as well as estuarine sub-classes and habitats within those estuaries (Appendix 2). We only included estuarine sub-classes and habitats for which we could find documentation of juvenile use by at least one of the focal species. We identified four estuarine sub-classes (estuarine coastal subtidal, tidal channel/creek, lagoon and slough) and eleven estuarine habitats (oyster reef, shell debris, seagrass bed, benthic macroalgae, freshwater and brackish tidal aquatic vegetation, tidal flat, very coarse woody debris, emergent tidal marsh, scrub-shrub tidal wetland, tidal forest/woodland and anthropogenic wood).

Finally, we assessed threats to juvenile life history stages in estuaries for the 15 focal species by assembling categories of threats based on studies by Crain et al. 2008, Halpern et al. 2009, Gleason et al. 2011, and Merrifield et al. 2011, and assigning a threat to each species when mentioned in the literature. To avoid duplicating prior efforts, we relied heavily on summary documents of species life histories, habitat use, and threats (e.g., Emmett et al. 1991, Augerot and Foley 2005, Love 2011), and then expanded on them using more up-to-date or missing references associated with the report goals. We then compiled the available information for each species in the 'Focal Species and Known Nursery Requirements' section of this report.

In addition, we created tables summarizing, for each of the focal species, their general life history information (Table 2), juvenile life history characteristics in estuaries (Table 3), juvenile use of estuarine sub-classes and habitats (Table 4) and threats to juveniles in estuaries (Table 5). These summary tables were then presented to approximately 250 experts and stakeholders for review. The experts had backgrounds in estuarine ecology, fish ecology, ecosystem function and nursery habitat. We also contacted regional stakeholders to solicit feedback and input on the information generated from our literature search. Additionally, we hosted three webinars, one for each state (California, Oregon and Washington), to present the summary tables and solicit feedback from regional experts. Invitees who did not attend the seminars were provided with the summary tables and asked to provide input and feedback via an online questionnaire. All information gathered from the webinars and questionnaires were evaluated and incorporated into the summary tables and the text of the report.

GEODATABASE OF JUVENILE PRESENCE

To summarize the available information on the coastwide use of estuaries as juvenile habitat by the focal species, we compiled information on the documented presence of the juvenile life-history stage of each focal species in 303 estuaries along the West Coast (Figure 1). This geodatabase of 303 estuaries, with the potential to be nurseries, was developed by The Nature Conservancy and two contractors—Industrial Economics Incorporated and the Central Coast Wetlands Group (Box 2). Focal species presence data were acquired first from reports dating from about 25 years ago (Monaco et al. 1990, Emmett et al. 1991, and Monaco et al. 1992) and the peer-reviewed literature search described above, then from reports or inventories by local, state and federal agencies, Native American tribes and non-governmental organizations. Personal communications from managers and researchers and unpublished manuscripts were also rich sources of information. When no other sources were found, fishing or nature enthusiast websites were used. From these sources, reports of a focal species with juveniles specifically identified were noted as present (P) and assumed adults. Juvenile rockfish were not recorded as present unless explicitly identified as brown rockfish. Estuary data (rows) and species presence data (columns) were combined and imported into an ArcGIS 10.2 (ESRI 2014) geodatabase for spatial analysis.

© John Bragg/SSNERR

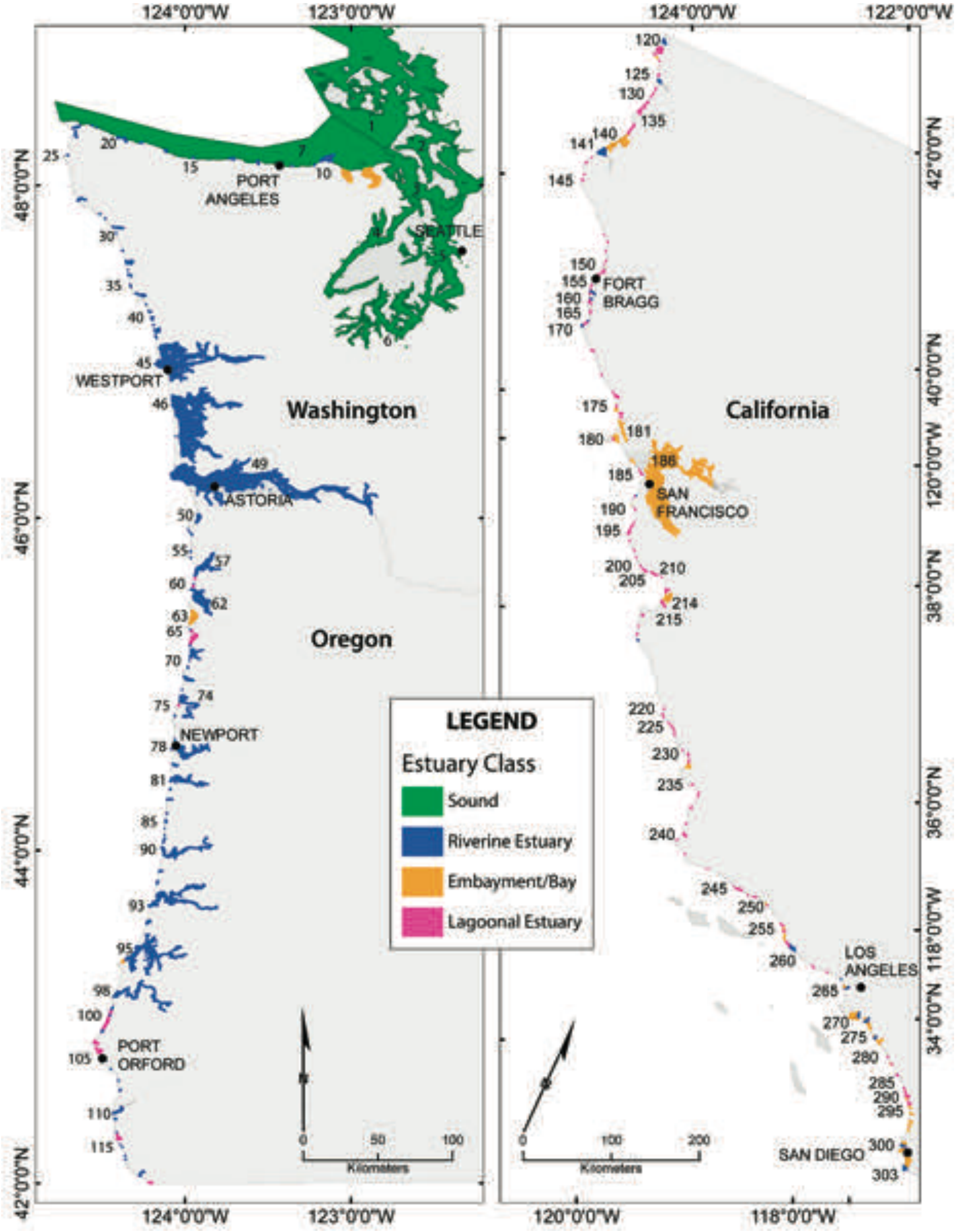
BOX 2. AN INVENTORY AND CLASSIFICATION OF WASHINGTON, OREGON AND CALIFORNIA ESTUARIES

The Nature Conservancy worked with two contractors, Industrial Economics Incorporated (IEc) and the Central Coast Wetlands Group (CCWG), to inventory all estuaries in Washington, Oregon and California, compile polygons outlining each estuary in a GIS geodatabase and classify all estuaries using a single classification scheme (Heady et al. 2014). IEc drew from previous studies (Lee II and Brown 2009, Gleason et al. 2011, Simenstad et al. 2011, Oregon Department of Land Conservation and Development unpublished data) to inventory all coastal confluences (from large estuaries to small ephemeral streams draining into the Pacific Ocean) of Washington and Oregon, and compile all classification schemes applied to these geographies. CCWG also drew from previous efforts (Lee II and Brown 2009, Gleason et al. 2011, Southern California Coastal Water Research Project unpublished data) to inventory all coastal confluences and compile all classification schemes applied to California. CCWG used the National Wetlands Inventory database, the California Coastal Records Project and Google Earth to identify and include any coastal confluences not yet included in this inventory. All data from this effort, including estuary name, state, county, latitude, longitude, size of estuary, estuarine classification data, other available data and data sources for classifications and estuarine outline polygons were compiled in a single excel database. The Coastal and Marine Ecological Classification Standard (FGDC 2012) was applied to all West Coast estuaries and cross-referenced to other estuarine classifications previously applied to each estuary. This resulted in a database containing the above mentioned data for 47 estuaries in Washington, 72 estuaries in Oregon and 572 coastal confluences in California.

As many of the coastal confluences in California were quite small, ephemeral and lacked potential for nursery habitat for the 15 focal species of the nursery review, we limited the nursery review to 188 estuaries in California by excluding urban drains, artificial harbors, lagoons without connectivity to the ocean and estuaries smaller than 0.4 ha. The full inventory of coastal confluences was maintained for other scientific and management uses (e.g., water quality investigations), with those estuaries used in the nursery review clearly identified.

Polygons outlining the extent of estuarine habitat were created and compiled in an ArcGIS geodatabase for each of the 303 West Coast estuaries in the nursery review. Many of the estuary polygons either already existed in other geodatabases (e.g., Gleason et al. 2011, and for California—Southern California Coastal Water Research Project (SCCWRP)) or were created using NWI data (NWI polygons included select marine, all estuarine, all tidal riverine, and lacustrine and palustrine with tidal modifiers). The Puget Sound Nearshore Ecosystem Restoration Project (PSNERP) polygons were used to delineate estuarine sub-basins within Puget Sound. The final estuary inventory geodatabase includes a polygon for each estuary and an attribute table containing locational data, classification and other information. This geodatabase serves as the foundation for this nursery review and other efforts to be further populated with data to inform the nursery requirements, focal species presence data and threats to nursery function and the spatial distribution of each and is maintained by the Pacific States Marine Fisheries Commission (PSMFC; www.psmfc.org).

FIGURE 1. The 303 estuaries in California, Oregon, and Washington that were included in the review of nursery habitat for fish and invertebrates.



Washington

1 SJ Islands and Georgia Strait Basin
2 Whidbey Basin
3 North Central Puget Sound Basin
4 Hood Canal Basin
5 South Central Puget Sound Basin
6 South Puget Sound Basin
7 Strait of Juan de Fuca Basin
8 Discovery Bay
9 Sequim Bay
10 Dungeness Bay
11 McDonald Creek
12 Morse Creek
13 Elwha River
14 Salt Creek
15 East Twin River
16 West Twin River
17 Pysht River
18 Clallam River
19 Hoko River
20 Sekiu River
21 Bullman Creek
22 Sail River
23 Waatch River
24 Sooes River
25 Ozette River
26 Quillayute River
27 Goodman Creek
28 Mosquito Creek
29 Hoh River
30 Cedar Creek
31 Kalaloch Creek
32 Queets River
33 Whale Creek
34 Raft River
35 Camp Creek
36 Duck Creek
37 Quinault River
38 Wreck Creek
39 Moclips River
40 Joe Creek
41 Elk Creek
42 Boone Creek
43 Copalis River
44 Conner Creek
45 Grays Harbor
46 Willapa Bay
47 Loomis Lake Creek

Oregon

48 Clatsop Spit
49 Columbia River
50 Necanicum River
51 Indian Creek
52 Chapman Point
53 Ecola Creek
54 Arch Cape Creek
55 Cove Beach
56 Short Sand Creek
57 Nehalem River
58 Lake Lytle
59 Rockaway Beach Creek
60 Rockaway Clear Lake
61 Smith Lake
62 Tillamook Bay
63 Netarts Bay
64 Rover Creek
65 Chamberlain Lake
66 Sand Lake
67 Sears Lake
68 Miles Creek
69 Nestucca Bay
70 Daley Lake
71 Neskowin Creek
72 Salmon River
73 Devils Lake
74 Siletz Bay
75 Schoolhouse Creek
76 Depoe Bay
77 Little Creek
78 Yaquina Bay
79 Beaver Creek
80 Rock Creek
81 Alsea Bay
82 Big Creek - Lincoln
83 Yachats River
84 Tenmile Creek North
85 Big Creek - Lane
86 China Creek
87 Cape Creek
88 Berry Creek
89 Sutton Creek
90 Siuslaw River
91 Siltcoos River
92 Tahkenitch Creek
93 Umpqua River
94 Tenmile Creek South
95 Coos Bay
96 Miner Creek
97 Sunset Bay
98 Coquille River
99 Twomile Creek South
100 Fourmile Creek
101 New River
102 Floras Creek
103 Sixes River
104 Elk River
105 Port Orford Head
106 Hubbard Creek
107 Brush Creek
108 Mussel Creek
109 Euchre Creek
110 Rogue River
111 Hunter Creek
112 Meyers Creek
113 Pistol River
114 Burnt Hill Creek
115 Cove at Boardman Park
116 Thomas Creek
117 Whaleshead Creek
118 Chetco River
119 Winchuck River

California

120 Smith River
121 Lake Earl
122 Pebble Beach
123 Crescent City Harbor
124 NC9 Crescent Beach
125 Wilson Creek
126 Lagoon Creek
127 Klamath River
128 Johnson Creek
129 Ossagon Creek
130 Fern Canyon
131 Squashan Creek
132 Espa Lag., Gold Bluffs Bch
133 Redwood Creek
134 Stone Lagoon
135 Big Lagoon
136 Little River
137 Clam Beach
138 Widow White Creek
139 Mad River
140 Humboldt Bay
141 Eel River
142 Guthrie Creek
143 Bear River
144 McNutt Gulch
145 Mattole River
146 Jackass Creek
147 Usal Creek
148 Cottaneva Creek
149 Wages Creek
150 Chadbourne Gulch
151 Ten Mile River
152 Sandhill + Inglenook Fen
153 Lake Cleone
154 Virgin Creek
155 Pudding Creek
156 Noyo River
157 Caspar Creek
158 Russian Gulch (Mendo.)
159 Big River Mendocino
160 Little River (Mendo.)
161 Albion River
162 Little Salmon Creek
163 Navarro River
164 Greenwood Creek
165 Elk Creek
166 Irish Gulch
167 Alder Creek
168 Manchester
169 Brush Creek
170 Garcia River
171 Gualala River
172 Stump Beach
173 Russian Gulch (Sonoma)
174 Russian River
175 Salmon Creek
176 Bodega Bay Estuary
177 Estero Americano
178 Estero de San Antonio
179 Tomales Bay
180 Horseshoe Pond
181 Drakes Estero
182 Bolinas Lagoon
183 Redwood Creek/Big Lagoon
184 Tennesee Valley Lagoon
185 Rodeo Valley Lagoon
186 San Francisco Bay
187 Calera Creek
188 San Pedro Creek
189 Half Moon Bay Airport Lagoon
190 Frenchmans Creek
191 Pilarcitos Creek
192 Tunitas Creek
193 San Gregorio Creek
194 Pomponio Creek
195 Pescadero Marsh
196 Lake Lucerne
197 Gazos Creek
198 Waddell Creek
199 Scott Creek Lagoon
200 Laguna Creek
201 Baldwin Creek
202 Lombardi Creek
203 Dairy Gulch
204 Wilder Creek
205 Yonger Lagoon
206 San Lorenzo River
207 Santa Cruz Harbor
208 Schwan Lagoon
209 Corcoran Lagoon
210 Moran Lake
211 Soquel Creek
212 Aptos Creek
213 Pajaro River
214 Elkhorn Slough
215 Salinas River Estuary
216 Carmel River Estuary
217 Joshua Creek (Garapatta)
218 Little Sur River Lagoon
219 Big Sur River Lagoon
220 Carpoforo Creek
221 Arroyo de la Cruz
222 Arroyo del Corral
223 Arroyo Laguna
224 Arroyo del Puerto
225 Little Pico Creek
226 Pico Creek
227 San Simeon Creek Estuary
228 Santa Rosa Creek
229 Villa Creek Lagoon
230 Cayucos Creek Lagoon
231 Old Creek
232 Alva Paul Creek
233 Morro Creek Lagoon
234 Morro Bay Estuary
235 San Luis Obispo Creek Lagoon
236 Pismo Creek Lagoon
237 Arroyo Grande Creek Lagoon
238 Santa Maria River Estuary
239 San Antonio Creek Estuary
240 Santa Ynez River Estuary
241 Honda Creek Lagoon
242 Jalama Creek
243 Canada del la Gaviota Creek
244 Bell Canyon Creek
245 Deveroux Slough
246 Goleta Slough
247 Arroyo Burro Creek Estuary
248 Mission Creek Lagoon
249 Sycamore Creek
250 Andree Clark Bird Refuge
251 Carpenteria Salt Marsh
252 Carpenteria Creek
253 Ventura River Estuary
254 San Buenaventura Beach
255 Ventura Marina
256 Santa Clara River Estuary
257 Channel Islands Harbor
258 Port Hueneme
259 Ormand Beach
260 Mugu Lagoon
261 Trancas
262 Dume Lagoon/Zuma Canyon
263 Malibu Lagoon
264 Santa Monica Canyon
265 Marina del Rey
266 Ballona Creek
267 Cabrillo Marina
268 Long Beach Harbor
269 Los Angeles Harbor
270 Los Angeles River
271 Long Beach Marina
272 Alamitos Bay
273 San Gabriel River
274 Anaheim Bay
275 Muted Bolsa Bay
276 Bolsa Chica Fully Tidal
277 Huntington Channel
278 Santa Ana River
279 Newport Bay
280 Aliso Creek Outlet
281 San Juan Creek
282 Dana Point Harbor
283 San Mateo Lagoon
284 San Onofre Creek
285 Las Pulgas Creek
286 Las Flores Creek
287 Aliso Canyon Creek
288 French Lagoon (Canyon)
289 Cocklebur Canyon
290 Santa Margarita Lagoon
291 Oceanside Harbor
292 San Luis Rey Estuary
293 Loma Alta Slough
294 Buena Vista Lagoon
295 Agua Hedionda
296 Batiquitos Lagoon
297 San Elijo Lagoon
298 San Dieguito Lagoon
299 Los Peñasquitos Lagoon
300 Mission Bay
301 San Diego River
302 San Diego Bay
303 Tijuana River estuary

FOCAL SPECIES AND KNOWN NURSERY REQUIREMENTS

© Jonathan W. Moore/Simon Fraser University

INVERTEBRATES

Invertebrates in West Coast estuaries play key functional roles as both consumers and prey in estuarine food webs. We focused on two species of invertebrates, Dungeness crab (*Metacarcinus magister*) and bay shrimp (*Crangon franciscorum*), which occupy a wide range of estuarine habitats (Table 4) and serve different functional roles in estuarine food webs (Tables 2 and 3). These two species, alone, do not represent the breadth of invertebrate species and functional roles in West Coast estuaries, but they have been shown to use estuaries primarily during their juvenile life-history stages. Additionally, these two species are widespread across most of our study range of California, Oregon and Washington. Dungeness crab and bay shrimp are economically important species along the entire West Coast, with Dungeness crab being one of the more important commercial and recreational fisheries. Bay shrimp is also economically important, but to a much lesser degree, though in previous eras, its commercial value was greater.

Both species use estuaries as juveniles, and for Dungeness crab, estuaries have been demonstrated to serve as important nursery grounds. Both species migrate towards the ocean during late-juvenile and adult stages, further emphasizing the potential nursery function of estuaries for these two species. They serve as prey for numerous species of predatory fish and mammals, and are themselves important predators of smaller consumers, such as amphipods and small bivalves (Table 3). Both crabs and shrimp are considered to be ecosystem engineers through their burrowing activity and resuspension of sediments, which enhances their role in benthic-pelagic coupling.

© Tom Greiner/CDFW

They differ in their use of habitats; juvenile Dungeness crab use diverse estuarine habitats, such as seagrass beds, shell debris, subtidal channels and tidal flats, whereas bay shrimp primarily use subtidal channels and tidal flats (Table 4). Little is known about the nursery role of estuaries for bay shrimp; however, there is a wealth of knowledge for Dungeness crab, which enhances their usefulness as a model species for studying the nursery function of West Coast estuaries.

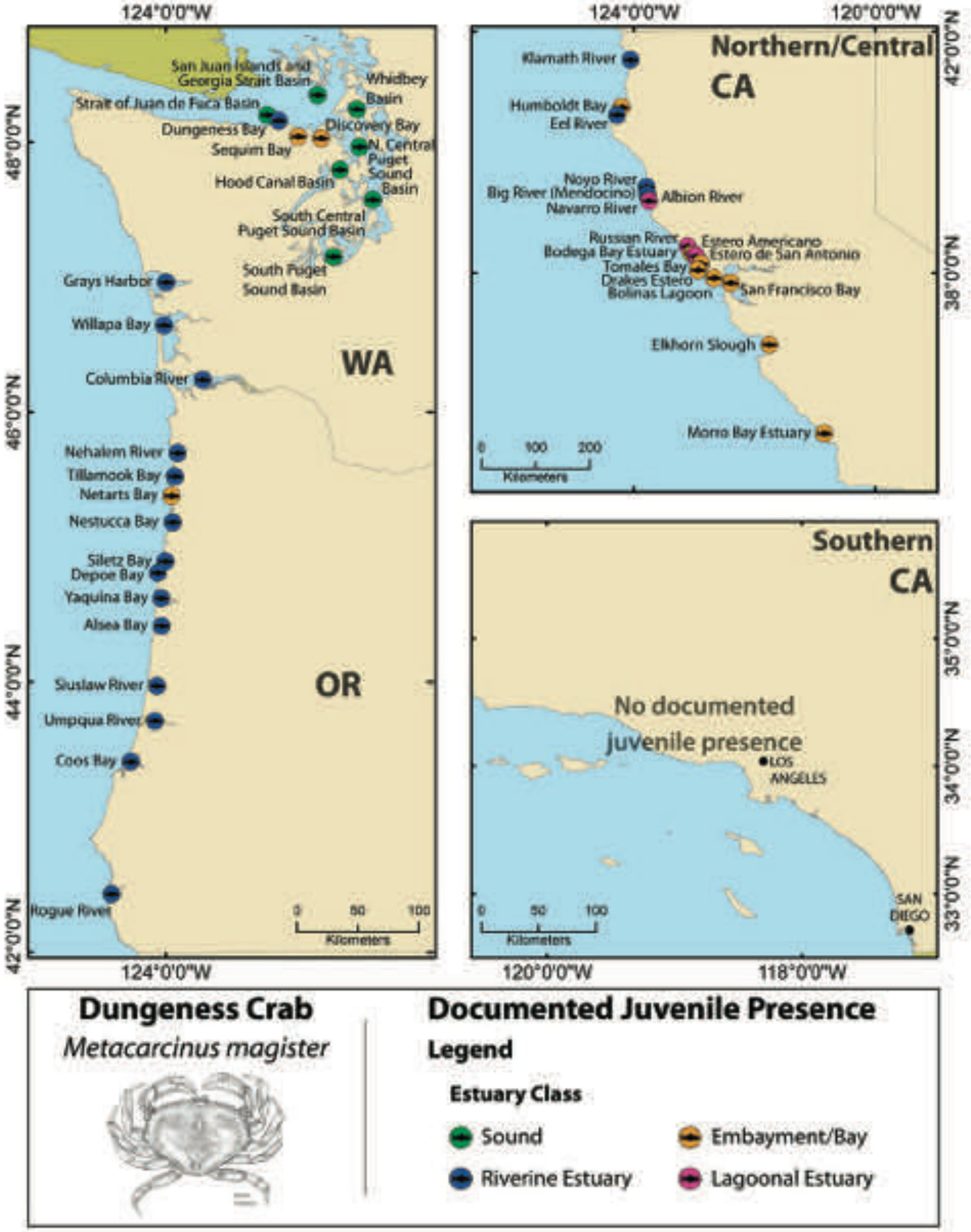


FIGURE 2. DUNGENESS CRAB: Documented juvenile presence in Washington, Oregon and California estuaries.

DUNGENESS CRAB

(*Metacarcinus magister*, formerly *Cancer magister*)

© Adam Frimodig/CDFW

Crabs are ubiquitously found in the majority of estuaries around the world. They play an essential ecological role in coastal food webs as both important predators and prey (e.g., Silliman et al. 2002, Hughes et al. 2013). It has been well established that estuaries are important nursery grounds for several ecologically and economically important species of crabs, such as blue crabs (*Callinectes sapidus*) along the northwest Atlantic and Gulf of Mexico (e.g., Orth and van Montfrans 1990, Perkins-Visser et al. 1996, Beck et al. 2001), blue manna crab (*Portunus pelagicus*) along the Indo-West Pacific Ocean and Mediterranean Sea (e.g., Potter et al. 1983), and Dungeness crab (*Metacarcinus magister*) along the West Coast (e.g., Gunderson et al. 1990). Dungeness crab, to our knowledge, is the only example of an invertebrate species documented as using estuarine habitats as nursery grounds along the West Coast.

Dungeness crab has a broad distribution across the West Coast of North America, ranging from Alaska to southern California; however, they are rarely found south of Point Conception because of thermal stress (Emmett et al. 1991). Adults are distributed from the intertidal to 420 m depth, and inhabit both soft-bottomed and rocky seafloor (Emmett et al. 1991). Dungeness crab composes the largest single commercial fishery in the northeast Pacific (Higgins et al. 1997); average annual landings yield approximately 16 million kg with a value of over $100 million for the tri-state region of California, Oregon and Washington (California Department of Fish and Wildlife, Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife).

It has been well documented that estuaries are areas of recruitment and provide habitats for juvenile Dungeness crab populations across their population range (Gunderson et al. 1990, Armstrong et al. 2003). Gunderson et al. (1990) determined that crabs recruit to both estuaries and nearshore environments, but growth rates of juvenile cohorts are enhanced in estuaries compared to nearshore sibling populations. The overall contribution of estuarine residency to the Dungeness crab fishery has been documented to be approximately 25–30% for Oregon and Washington (Armstrong et al. 2003; see Box 3 for more details). Dungeness crab is an important mesopredator species (i.e., medium-sized predators that often increase in abundance when larger predators are eliminated) in West Coast estuarine ecosystems that is capable of altering population and community dynamics (e.g., Pearson et al. 1981, Stevens et al. 1982, Fernandez et al. 1993).

Life History and Ecology

In general, Dungeness crab adults reproduce offshore during winter, and their larvae migrate to estuarine and coastal areas in late spring and summer (Lough 1976, Stevens et al. 1982, Gunderson et al. 1990). The relative abundance of juvenile Dungeness crab and its role as a secondary consumer within estuaries make it an important member of estuarine food webs. Increased growth rates of juvenile Dungeness crab in estuaries, as compared to nearshore habitats, suggest an abundance of prey items in estuaries (Gunderson et al. 1990). As planktonic larvae, Dungeness crab feed on a mix of phytoplankton and zooplankton (LeBour 1922, Hartman and Letterman 1978). Both young-of-the-year (YOY) and age+1 juveniles and subadult populations forage in intertidal and subtidal habitats (Holsman et al. 2003).

Dungeness crab is a generalist consumer species whose prey items consist of an assortment of crustaceans, bivalves and fish. The feeding habits of juvenile Dungeness crab switches from small bivalves and crustaceans (including cannibalism) for YOY Dungeness crab to *Crangon* spp. shrimp and fish for age+1 juveniles and subadults (Stevens et al. 1982). Additionally, Dungeness crab changes its prey type diurnally—they prefer crustaceans during night when crustacean activity is high, then switch to primarily fish during the day, feeding on an assortment of juvenile fish, such as sandlance (*Ammodytes hexaptera*), Pacific sanddab (*Citharichthys sordidus*), lingcod (*Ophiodon elongatus*) and shiner perch (*Cymatogaster aggregata*, one of the 15 focal species in this report) (Stevens et al. 1982). Their abundance, wide use of habitats and benthic lifestyle make juvenile Dungeness crab susceptible to predation. Predators include crabs (both Dungeness and other species), flatfishes, rockfishes, elasmobranchs, sea otters and octopi (Stevens et al. 1982, Emmett et al. 1991, Fernandez et al. 1993).

© Andrew Weltz/CDFW

Timing and Use of Estuarine Habitats

The nursery value of West Coast estuaries for Dungeness crab is likely to be high given the overall ecological and economic importance of this species (Armstrong et al. 2003), combined with its broad distribution from Alaska to central California (Jensen 2014; Table 2) and its extensive use of estuaries during the juvenile life stage. Although some information is available on factors that influence the timing and use of estuarine habitats by juvenile Dungeness crab, more directed study is needed to better understand the nursery requirements for this species.

Dungeness crab larvae are found in coastal and nearshore environments and usually within 16 km of the shoreline (Emmett et al. 1991, Armstrong et al. 2003). Dungeness crab larvae and adults have an optimal salinity range of 25–30 ppt and 15–36 ppt, respectively (Pauly et al. 1986b, Pauly et al. 1989, Emmett et al. 1991). There is little known about the salinity range requirements for juveniles, however, the range is probably greater for juveniles than adults because juveniles have an affinity for the variable estuarine environment. Juvenile Dungeness crab are sensitive to higher temperatures, with an optimal temperature range of 10–14°C, and mortality occurring at >20°C (Pauly et al. 1986b, Emmett et al. 1991).

Recruitment to estuaries can be highly variable and seems to follow decadal patterns that may be linked to nearshore wind and upwelling processes (Cloern et al. 2007, Grosholz and Ruiz 2009). Larvae settle in estuarine habitats when they are 6–8 mm (Gunderson et al. 1990, Brown and Terwillinger 1992). Growth of YOY Dungeness crab in estuaries can be double the rate in nearshore coastal areas (Gunderson et al. 1990), emphasizing the importance of the estuarine nursery function. Furthermore, YOY Dungeness crab that settle in nearshore habitats often move to estuaries after the first winter, and a large fraction of the population use estuaries at some point during the juvenile stage (Gunderson et al. 1990, Tasto 1983). By the time Dungeness crab juveniles reach age+1, most have moved from the estuary into offshore waters as subadults, and are between 100–130 mm in carapace width (Gunderson et al. 1990, Higgins et al. 1997, Brown and Terwilliger 1992).

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile Dungeness crab have been documented in 42 estuaries from Morro Bay, California to Puget Sound, Washington (Figure 2). They use all four estuary classes found on West Coast: lagoonal, riverine, embayment and sounds. Their ability to use every estuarine class, as well as all the estuarine subclasses (embayments, estuaries, lagoons and sloughs; Table 4) found on the West Coast, probably explains their widespread presence (Figure 2). The diversity of estuarine systems used by juvenile Dungeness crab is high compared to the other focal species.

Additionally, juvenile Dungeness crab use a variety of estuarine habitat types, including seagrass and macroalgal beds, oyster beds, shell and wood debris and bare channels and mudflats (Table 4; Emmett et al. 1991, Fernandez et al. 1993, Rooper et al. 2002, Armstrong et al. 2003). Despite their use of multiple habitat types, juvenile Dungeness crab tend to favor unstructured habitats compared to seagrass beds and oyster reefs (Holsman et al. 2006).

Threats

Dungeness crab are threatened by non-native species, especially ecosystem engineers and competitively dominant species (Table 5). Juvenile Dungeness crab often migrate to intertidal areas to feed; the loss of intertidal foraging habitat has the potential to reduce the growth rate of juvenile stages. In the early 2000s in Willapa Bay, Washington, a decades-long chronic spread of the invasive Atlantic smooth cordgrass (*Spartina alterniflora*) had eliminated nearly one-third of the intertidal foraging habitat that once was available to Dungeness crab, and therefore crab populations had exhibited significantly lower population density (Holsman et al. 2010). Due to its dense shoots, *Spartina* had created sub-optimal foraging habitat for juvenile Dungeness crab that reduced their overall density. However, recent *Spartina* eradication proved to be an effective means of restoring intertidal foraging habitats for juvenile Dungeness crab, and potentially restoring nursery function for crabs in Willapa Bay.

A major invader of West Coast estuaries is the European green crab (*Carcinus maenas*), which uses similar habitats and food sources as juvenile Dungeness crab (Grosholz and Ruiz 2009). The ecological effects of green crabs are highly variable, and can range from positive (Bertness and Coverdale 2013), causing recovery of salt marshes, to negative, causing major changes to estuarine food webs that can lead to the loss of important species, such as oysters (Kimbro et al. 2009). McDonald et al. (2001) found through laboratory and field observations that juvenile green crabs can outcompete equally sized Dungeness crab for prime sheltered habitats and food, thus potentially reducing nursery function for Dungeness crab by reducing the available area of ideal habitat. However, given the varying reported consequences from green crab invasions, further research is needed to fully understand these interactions.

Restoring populations of top predators through trophic upgrading can have negative consequences for their prey community, such as cancrid crabs (species from the Cancridae family, including *Metacarcinus* spp. and *Cancer* spp.), which also serve as important linkages to lower trophic levels and ultimately to marine vegetation. For example, the recovery of sea otters has the potential to reduce cancrid crab populations, and that can lead to cascading effects that benefit marine vegetation (Hughes et al. 2013). Sea otters are analogous to other predators that feed on juvenile and adult stages of cancrid crab, such as elasmobranchs, flatfishes, sturgeon and sculpins (Table 2). All of these predators, individually or in combination, could be important targets for conservation and restoration of ecosystem function. However, the recovery of top predators, such as sea otters, can cause declines in the adult Dungeness crab fishery (Garshelis and Garshelis 1984), and potentially reduce juvenile stages through lower reproductive output.

Beyond species invasions and changes in food webs, another major threat to juvenile Dungeness crab is activities that alter or degrade estuarine habitats (Table 5). For example, Dungeness crab have been shown to be sensitive to the effects of dredging (Dumbauld et al. 1993). Juvenile Dungeness crab settle in subtidal channels in estuaries—if marinas exist and dredging occurs frequently, there could be a risk of harm to juvenile crabs. Impacts would likely be greatest if dredging occurs in spring and summer when juvenile abundance is the greatest (Gunderson et al. 1990, Armstrong et al. 2003). In Grays Harbor, Washington, it was found that placing oyster shells higher in the intertidal zone, above subtidal zones where dredging occurs, yielded high recruitment densities of juvenile Dungeness crab (Dumbauld et al. 1993); thus shell placement may be a potential mitigation strategy.

Widespread nutrient pollution and subsequent eutrophication of coastal environments has motivated researchers to study the consequences of eutrophication for organisms that are vital to ecosystem function and to the livelihoods of humans living in coastal areas (Cloern 2001, Diaz and Rosenberg 2008). Hypoxia has the potential to negatively affect benthic organisms, such as Dungeness crab, that cannot move rapidly enough to escape from areas covered by oxygen-depleted waters. To our knowledge, there has not been a study to investigate the effects of hypoxia on estuarine nursery function for Dungeness crab. However, impacts of hypoxia on adult stages in known nurseries, such as Puget Sound, have been studied. Froehlich et al. (2013) determined that, although hypoxia did not have direct effects on the mortality of adult Dungeness crab, hypoxia did alter crab movement patterns in favor of shallower waters, making them more susceptible to predation.

Another threat to juvenile Dungeness crab populations comes from the application of pesticides, both from agricultural runoff and direct application to eradicate native crustaceans that limit aquaculture production. In Grays Harbor, Washington, carbaryl is commonly used by oyster farmers to eliminate native burrowing shrimp (*Neotrypaea californiensis*; *Upogebia pugettensis*) whose burrowing activity, if left unchecked, resuspends sediment that can have negative effects on introduced, commercially-raised Japanese oysters *(Crassostrea gigas)* (Feldman et al. 2000). The application of carbaryl—a chemical insecticide and the third most widely-used household, agricultural and forest pesticide in the United States—can have negative effects on juvenile Dungeness crab populations through two mechanisms: first, through increased mortality near areas where carbaryl is applied, and second, by killing shrimp, which are important prey items for juvenile Dungeness crab (Feldman et al. 2000). These results indicate that certain aquaculture practices have the potential to negatively affect the nursery function of estuaries through indirect pathways.

© Kirsten Ramey/CDFW

© Andrew Weltz/CDFW

BOX 3. LARGER ESTUARIES SUPPORT HIGHER GROWTH RATES AND CONTRIBUTION FOR DUNGENESS CRAB

It has been well documented that estuaries are areas of recruitment and provide habitats for juvenile Dungeness crab populations along the West Coast (e.g., California: Tasto 1983, Oregon and Washington: Armstrong et al. 2003; Washington: Gunderson et al. 1990). Gunderson et al. (1990) determined that crabs recruited to both estuaries and nearshore environments, but growth rates of juvenile cohorts were enhanced in estuaries compared to those in nearshore environments. The overall estuarine contribution to the Dungeness crab fishery was estimated to be approximately 25–30%, but could be greater after bigger recruitment years in the region (Armstrong et al. 2003). In addition, the importance of estuarine nurseries as contributors to the Dungeness crab fishery increases with the size of the estuary. Armstrong et al. (2003) found that smaller estuaries in Oregon contributed only a fraction to the regional Dungeness crab fishery, compared with the contributions of the larger estuaries of Willapa Bay and Grays Harbor. Results from Gunderson et al. (1990) and Armstrong et al. (2003) suggest that management efforts to maintain or enhance the nursery function of estuaries for Dungeness crab populations should target larger estuarine systems, such as Willapa Bay, Grays Harbor, Humboldt Bay, San Francisco Bay and Puget Sound.

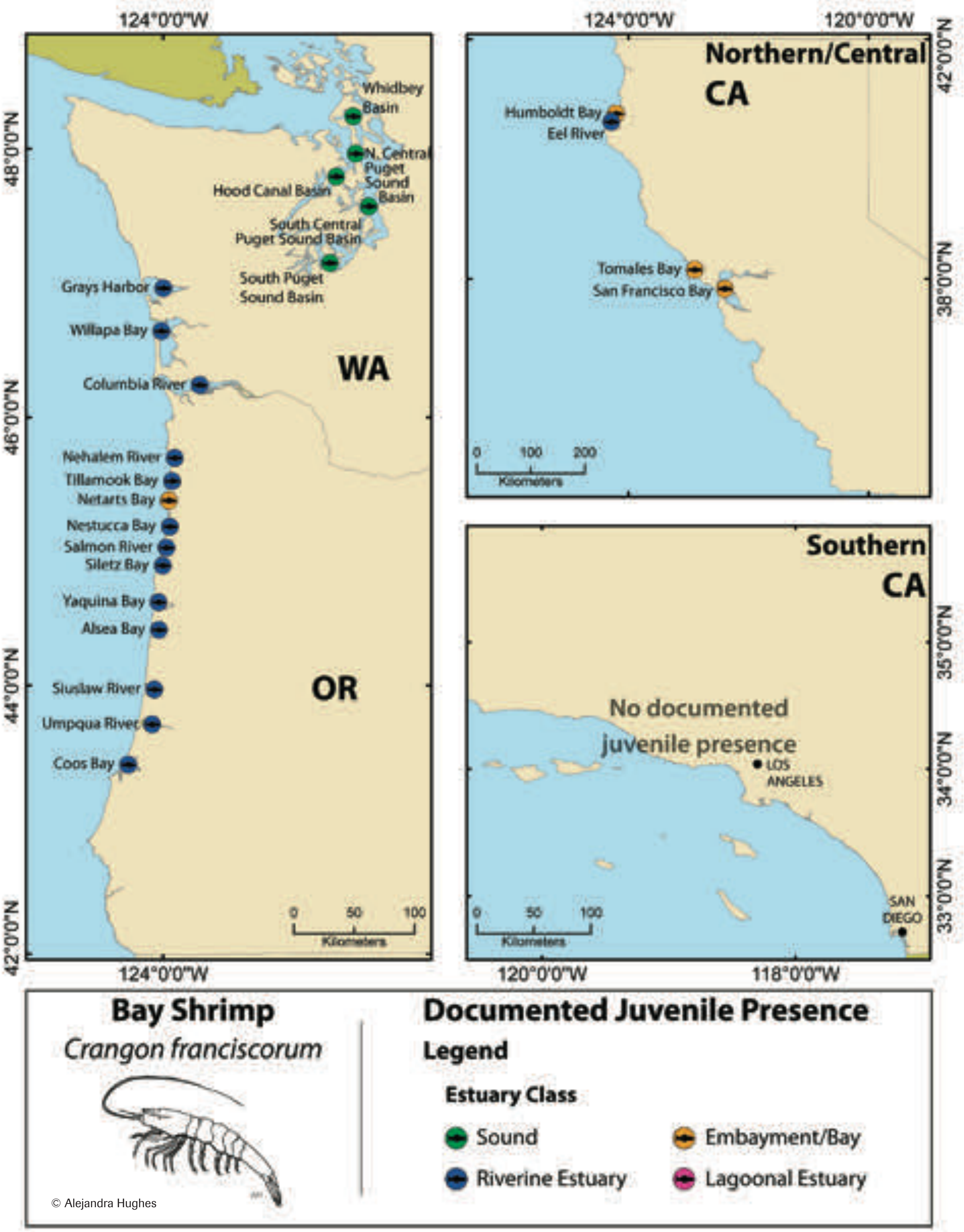


FIGURE 3. BAY SHRIMP: Documented juvenile presence in Washington, Oregon and California estuaries.

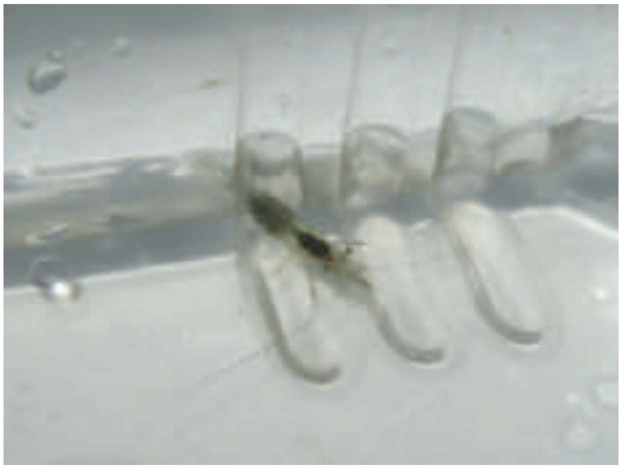
BAY SHRIMP

(*Crangon franciscorum*)

Bay shrimp is a common species of marine and estuarine shrimp that is broadly distributed along the West Coast of North America from Resurrection Bay, Alaska, to San Diego, California (Jensen 2014) (Table 2). Bay shrimp were once an important commercial fishery species for European and Asian immigrants, but the fishery lost popularity in recent years, and currently exists only as a bait fishery (Siegfried 1989). Bay shrimp play an important ecological role as a middle trophic level benthic organism that creates important linkages between benthic and pelagic environments. They are prey for several economically important species of fish and crabs, including many of the other focal species described in this report. Despite occurring as gut contents in almost all predatory estuarine fish and crab species, there is little information available on the general ecology, important habitat associations, threats and nursery function of estuaries for the juvenile life-history stage of this species. Despite this paucity of information on the nursery role of estuaries, it can be assumed that estuaries play an essential nursery function for bay shrimp due to their preference for estuarine habitats as juveniles, and the known nursery function of estuaries for other species of *Crangon* (Cattrijsse et al. 1997).

Life History and Ecology

Bay shrimp are a benthic shrimp that occupy mud and sand flats in estuaries and nearshore marine environments. Bay shrimp are a short-lived species—females generally reach 2.5 years in age; males generally reach 1.5 years in age (Emmett et al. 1991; Table 2). Adults spawn in deeper water and are considered protandric hermaphrodites—males change their sex to female after first mating (Gavio et al. 2006). The spawning season is highly variable, occurring between March and September in San Francisco Bay, and from December to March, and then again between April and August, in Yaquina Bay, Oregon (Emmett et al. 1991). During a 21-day larval period, recruitment occurs by the onshore transport of larvae from deeper waters to the shallow, brackish water of estuaries, where 5–10 mm larvae settle in benthic habitat (Siegfried 1989). Juveniles migrate upstream to near-freshwater habitat, where they remain for about one year until they mature. The migration of juveniles to brackish tidal water suggests that estuarine habitats are key nursery grounds for bay shrimp. Adults migrate to deeper, more saline habitat prior to spawning (Siegfried 1989). Some adults move to marine habitats whereas others remain in the estuary; the relative proportion of marine versus estuarine residents remains unknown, as do the relative contributions of estuaries to adult populations.



© Andrew Weltz/CDFW

High densities of bay shrimp in estuaries, and their preference for open, sandy and muddy habitat that lacks refuge from predators, make them a key link between the benthic and pelagic zones and an essential part of estuarine food webs. Many predators feed on them, including several of the focal species in this report (e.g., bat rays, green sturgeon, staghorn sculpins, flatfishes, Dungeness crab), as well as harbor seals (*Phoca vitulina*), brown smoothhound shark *(Mustellus californicus)* and non-native striped bass (Siegfried 1989, Emmett et al. 1991, Gray et al. 1997). Given the importance of bay shrimp to predatory fish, they might be prey for smolting salmonids in estuaries, but further research is needed.

In addition to being important prey items, juvenile bay shrimp are important mesopredators in estuarine ecosystems, consuming smaller benthic organisms, such as mysids, amphipods, bivalves, foraminifera, isopods, copepods, and ostracods and occasionally plants (Wahle 1985, Siegfried 1989, Emmett et al. 1991). Additionally, their ability to burrow in sediments qualifies them as ecosystem engineers capable of resuspending sediments and nutrients, which is an important estuarine function (Siegfried 1989). The resuspension of sediments enhances benthic-pelagic coupling by making nutrients, once locked in sediments, available for organisms (Levin et al. 1991). Furthermore, the burrowing capabilities of shrimp, such as bay shrimp, can oxygenate sediments that create favorable conditions for other benthic organisms (Levin et al. 1991).

Timing and Use of Estuarine Habitats

Juvenile bay shrimp are present in estuaries throughout the year, but peak in abundance during spring and summer (Emmett et al. 1991; Table 3). Juvenile bay shrimp prefer estuarine habitats, as indicated by their optimal salinity range (0.1–34.2 ppt), and at times will occupy freshwater environments (Siegfried 1989, Emmett et al. 1991). Juvenile bay shrimp also have a broad temperature range (5.1–21.3°C), indicating that they can tolerate a wide range of conditions, but could be sensitive to higher temperatures (Emmett et al. 1991). It has been suggested that bay shrimp use salinity and temperature cues to direct their migration into estuaries as juveniles (for less saline and warmer habitats) and to more marine habitats as adults (for more saline and colder habitats).

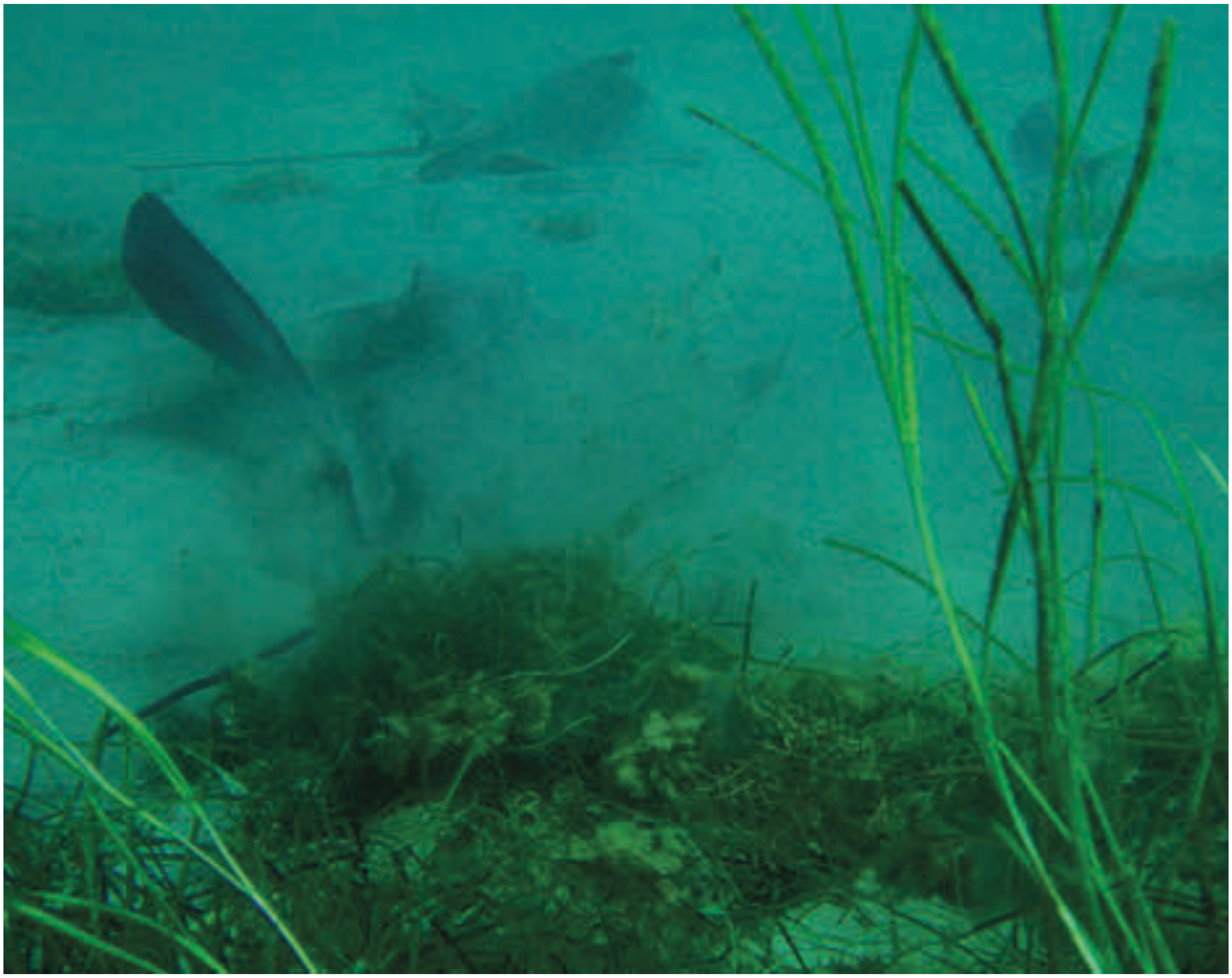
Distribution of Documented Presence of Juveniles in Estuaries

The presence of juvenile bay shrimp is documented in 23 estuaries along the West Coast, ranging from San Francisco Bay, California to Puget Sound, Washington (Figure 3). Bay shrimp use multiple estuarine classes, which include embayments, river mouths and sounds (Figure 3). They have been documented to use three different estuarine sub-classes: sloughs, subtidal areas and tidal creeks (Siegfried 1989; Table 4). Their preferred juvenile habitat consists of channels and muddy and sandy flats, preferably with lower salinities (Siegfried 1989, Emmett et al. 1991; Table 4). All life-history stages use estuaries, however it is the juvenile stage that relies most on estuaries, especially because juveniles use a full range of estuarine salinities and exhibit a migration towards estuarine and brackish water habitats (Siegfried 1989).

Threats

The primary threat to bay shrimp is the alteration of freshwater flow (Siegfried 1989, Jassby et al. 1995, Kimmerer 2002; Table 5). This particular threat has been well documented in San Francisco Bay, where in years of low freshwater flow the upstream migration range of bay shrimp is reduced (Jassby et al. 1995, Kimmerer 2002). This threat may be especially important for bay shrimp populations in California, where droughts are more frequent, and the diversion of fresh water away from estuaries, such as occurs in San Francisco Bay and Delta, is common. If the migrations of bay shrimp are cued by temperature and salinity, then bay shrimp could be sensitive to reductions in freshwater flow, especially in the spring, when both freshwater flow rates and juvenile migrations are at their greatest. A decrease in freshwater flow could have far-reaching consequences considering the important ecological role of bay shrimp in coastal ecosystems as prey for many species of fish, which can also be dependent on freshwater flow, not only as a migratory corridor, but also for important prey items, such as crustaceans (Emmett et al. 1991).

In addition to the main threat of altered freshwater flow, bay shrimp are also threatened by pollution from pesticide runoff and oil spills (Table 5). In particular, bay shrimp are sensitive to insecticides, such as Kelthane, and exposure for long periods can cause mortality (Khorram and Knight 1977). Additionally, carbaryl, a known insecticide that has been used in commercial oyster aquaculture applications in Oregon and Washington, is primarily used to control mud dwelling shrimp, (*Neotrypaea californiensis* and *Upogebia pugettensis*) (Feldman et al. 2000), but could also have negative consequences for bay shrimp. Hypoxia is also of concern for bay shrimp (Siegfried 1989), especially because they occur primarily in shallow benthic habitats where hypoxia is more severe in West Coast estuaries (Hughes et al. 2011).



© Walter N. Heady/TNC

ELASMOBRANCHS

Elasmobranchs are sharks, skates and rays, an ancient and ecologically important group of cartilaginous fishes. Unlike most bony fishes, elasmobranchs are relatively slow-growing, late-maturing, long-lived and reproduce slowly, making them particularly vulnerable to habitat destruction and overexploitation. These species are generally upper trophic level or apex predators in marine ecosystems and, accordingly, are believed to play an important role in structuring food webs.

For the purposes of this report, elasmobranchs include the leopard shark and bat ray, which are two of the most common coastal elasmobranchs along the West Coast. Both species range from Mexico to Oregon or Washington. Both species are of conservation and management interest—habitat alteration and impacts from fishing are issues of concern for both species. Both species are primarily targeted by recreational fisheries. Although neither species is targeted by commercial fishermen, accidental catch in other fisheries is a concern.

Like many coastal elasmobranchs, leopard sharks and bat rays use bays and estuaries extensively throughout their life histories as foraging, pupping and juvenile habitat. Although both species have been described as using bays and estuaries as nurseries, relatively little is known about actual patterns of habitat use, or about the habitat requirements for newborn and juvenile elasmobranchs.

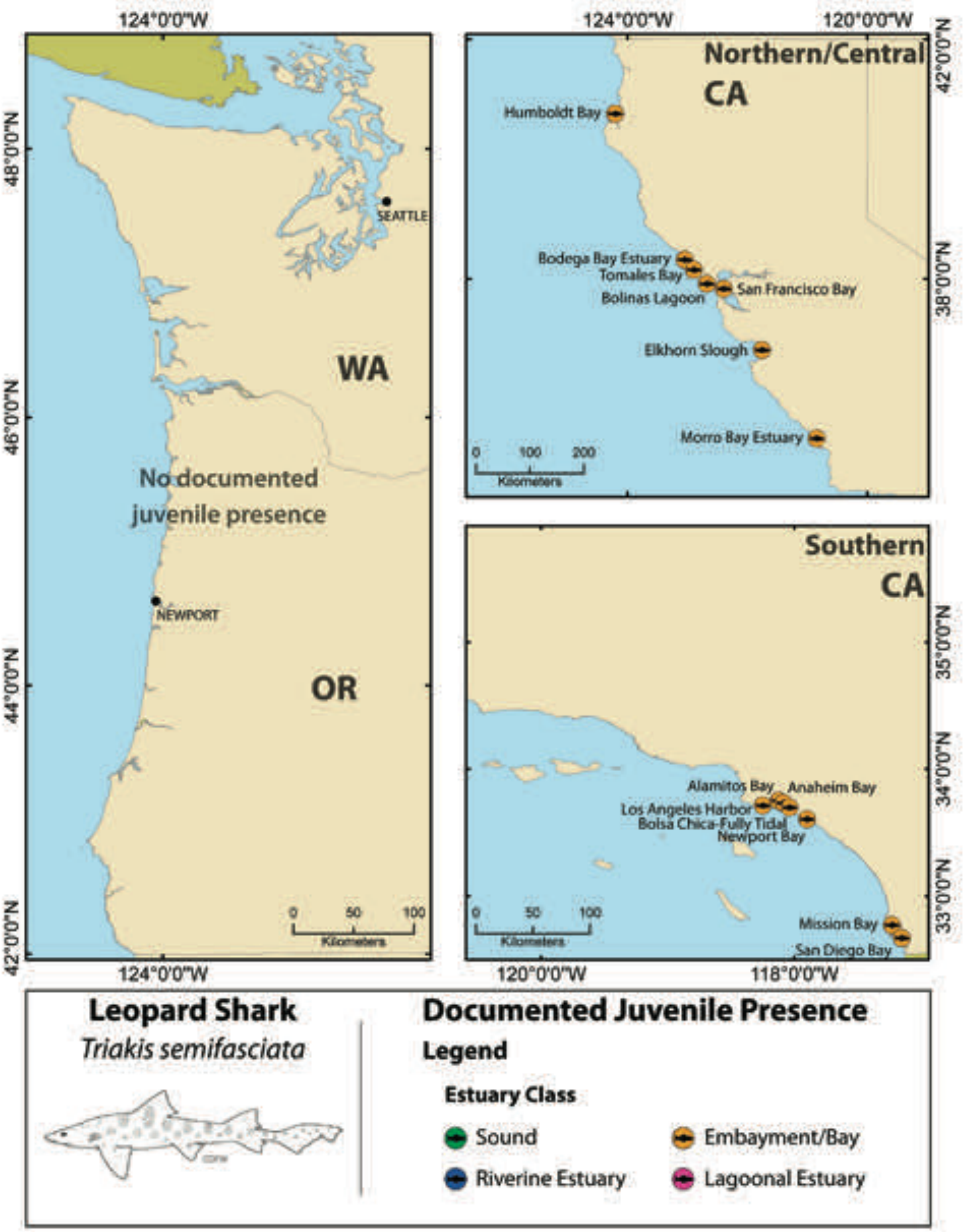


FIGURE 4. LEOPARD SHARK: Documented juvenile presence in Washington, Oregon and California estuaries.

LEOPARD SHARK

(*Triakis semifasciata*)

Leopard sharks are endemic to the Northeast Pacific Ocean and are one of the most common coastal sharks along the West Coast. They occur from Mazatlan, Mexico (including the Gulf of California) to Samish Bay, Washington (Ebert 2003, Love 2011; Table 2). The population of leopard sharks along the West Coast seems to be composed of regionally-specific stocks with limited genetic exchange (Ebert 2003, Lewallen et al. 2007), which may be tied to natal philopatry.

Leopard sharks are primarily found in shallow coastal habitats, generally ranging from the intertidal zone to a depth of 20 m, though they occur to depths of 91 m (Ebert 2003). They occur in a variety of substrates, including soft mud and sandy bottoms, rocky reefs and kelp forests (Barry 1983, Ebert 2003, Carlisle and Starr 2009). Bays and estuaries play an important role as foraging, pupping and juvenile habitats, particularly from central California northwards (Ebert 2003, Ebert and Ebert 2005, Carlisle and Starr 2009). Leopard sharks exhibit a highly tidal pattern of movement when in coastal habitat, moving with the tides to access intertidal habitat to forage (Ackerman et al. 2000, Carlisle and Starr 2009, 2010). Leopard sharks are a relatively eurythermal and euryhaline species, but their distribution is known to be influenced by temperature, salinity and dissolved oxygen levels (Hopkins and Cech Jr. 2003, Carlisle and Starr 2009, Nosal et al. 2014).

Life History and Ecology

The life history characteristics (Table 2) of leopard sharks are typical of elasmobranchs, being relatively long-lived (approximately 30 years), late-maturing (7–13 years for males, 10–15 years for females) and having relatively low fecundity (4–36 pups) and long generation times (22 years) (Ackerman 1971, Cailliet 1992, Kusher et al. 1992, Ebert 2003). They exhibit aplacental viviparity and reproduce annually, with pupping primarily occurring during the spring and summer in shallow, coastal, bay and estuarine habitats (Ackerman 1971, Talent 1985, Smith and Abramson 1990, Ebert 2003). Mating is believed to occur shortly after pupping, and gestation lasts approximately 10–12 months (Ackerman 1971, Talent 1985, Ebert 2003). Similar to many elasmobranchs, leopard sharks exhibit a high degree of sexual segregation, with males and females forming sex-specific schools (Ebert and Ebert 2005, Carlisle et al. 2007).

© Mike Wallace/CDFW

Because of their abundance and relatively high trophic level, leopard sharks likely play an important ecological role in coastal habitats along the West Coast. Leopard sharks are highly opportunistic predators, feeding on a range of benthic invertebrates, fishes and at times, other small sharks and rays. Important prey items include fat innkeeper worms (*Urechis caupo*), crustaceans (crabs and shrimps), clams (in particular clam siphons), small teleosts, polychaetes and fish eggs (Ackerman 1971, Russo 1975, Talent 1976, Barry et al. 1996, Webber and Cech 1998, Kao 2000, Ebert 2003, Ebert and Ebert 2005).

In Elkhorn Slough, California, leopard sharks historically exhibited an ontogenetic shift in diet, with juveniles primarily consuming grapsid crabs and larger sharks consuming a variety of prey, including fat innkeeper worms, teleosts, crabs and clams. This shift is no longer as apparent, as the diet of small and large sharks has converged on fat innkeeper worms and crabs, possibly as a result of habitat alteration or the reintroduction of sea otters (Kao 2000), which might be altering the availability of prey items. In Humboldt Bay, California, adult female leopard sharks shift their diet from fish eggs to crabs coincident with the pupping season, at which time newborn sharks start feeding almost entirely upon the fish eggs (see Box 4). Predators of leopard sharks include larger sharks species, such as the sevengill shark (*Notorynchus cepedianus*), white shark (*Carcharodon carcharias*) and marine mammals (Ebert 2003, Love 2011).

Timing and Use of Estuarine Habitats

Leopard sharks are seasonally abundant in bays and estuaries during the spring, summer and fall (Barry 1983, Yoklavich et al. 1991). Pupping occurs between March and September, peaking during April and May (Ackerman 1971, Talent 1985, Smith and Abramson 1990; Table 2). Newborns and small juveniles primarily use shallow protected habitat, such as tidal creeks, intertidal mudflats and eelgrass beds, as nursery areas (Table 4). For example, in Humboldt Bay, eelgrass beds provide both protection and abundant prey for newborn leopard sharks (Box 4; Ebert and Ebert 2005). Juvenile and adult leopard sharks take advantage of the tide to move into intertidal habitats (Ackerman et al. 2000, Carlisle and Starr 2009).

Leopard sharks are a relatively eurythermal and euryhaline species, but their distribution is known to be influenced by temperature, salinity and dissolved oxygen levels (Hopkins and Cech Jr. 2003, Carlisle and Starr 2009, Nosal et al. 2014). The sensitivity of newborn and juvenile leopard sharks to temperature and dissolved oxygen is unknown. Larger juveniles have been shown to be adversely affected by reduced salinity levels between 20.7 and 27.6 ppt (Dowd et al. 2010; Table 3). As temperatures and salinity levels drop during the winter, leopard sharks move from estuaries to coastal marine habitats (Hopkins and Cech Jr. 2003).

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile leopard sharks have been documented in 14 estuaries along the California coast, all of which are in the embayment/bay class of estuaries (Figure 4). Embayment estuaries seem to play a particularly important role as foraging, pupping and juvenile habitat in the northern part of their range, with San Francisco Bay, Elkhorn Slough, Tomales Bay, Humboldt Bay, Morro Bay and Los Angeles Harbor supporting large populations of leopard sharks of all age classes (Ebert 2003, Ebert and Ebert 2005, Carlisle and Starr 2009). In central and northern California, newborns and small juveniles primarily use shallow protected habitat, such as tidal creeks, intertidal mudflats and eelgrass beds in bays and estuaries (Table 4). In southern California, the surf zone and sheltered coves in more open coast habitats provides habitat for newborn and small juvenile sharks (Barry 1983, Ebert and Ebert 2005, Carlisle 2006, Hight and Lowe 2007, Carlisle and Starr 2009, Nosal et al. 2013, Nosal et al. 2014).

Larger scale patterns of movement and population structure in leopard sharks are poorly understood. Tag-recapture data indicate that they are capable of moving large distances (up to 600 km) (Smith 2001), but these larger scale movements seem to be limited, and are supported by genetic analyses, which indicate that there is genetic structure in the population of leopard sharks (Lewallen et al. 2007). There is some evidence that leopard sharks exhibit natal philopatry (Lewallen et al. 2007), and they are known to show a high degree of site fidelity (Carlisle and Starr 2009, Nosal et al. 2014).

Threats

Demographic analyses have indicated that leopard sharks are vulnerable to fishing pressure (Cailliet 1992, Kusher et al. 1992, Au and Smith 1997; Table 5). They are caught both commercially and recreationally, but recreational anglers are the primary source of mortality for leopard sharks along the West Coast. Regulations (size and catch limits, curtailment of nearshore gillnetting) implemented in the 1990s seem to be effective for this species, and in fact, populations seem to be increasing since the regulations took effect (Pondella and Allen 2008). Leopard sharks are popular in the aquarium trade, and illegal poaching of newborn leopard sharks for the aquarium trade is known to occur (Carlisle and Smith 2009).

Loss and degradation of habitat, especially in coastal bays and estuaries, is of great concern for this species, given the importance of these areas for foraging and as nursery sites (Carlisle and Starr 2009). There is evidence that sharks react to hypoxic conditions, suggesting that dissolved oxygen levels may influence habitat availability of this species (Carlisle and Starr 2009). Leopard sharks have been shown to have significant concentrations of contaminants in their tissues, but the impact of this on their health remains unknown (Schaffer et al. 2006, Carlisle et al. 2007).

BOX 4. SEAGRASS BEDS PROVIDE PROTECTION AND ABUNDANT FOOD FOR NEWBORN LEOPARD SHARKS

Following a pattern common across their range, gravid female leopard sharks move into Humboldt Bay, California, during the spring to give birth. Inside the bay, they forage in the intertidal mudflats and eelgrass beds, and they seem to feed primarily upon fish eggs (jacksmelt, *Atherinopsis californiensis*) that are deposited upon eelgrass leaves at that time of the year. However, once they give birth, the diet of the adult females, despite remaining within Humboldt Bay, shifts almost entirely to crabs, while the newborn sharks seem to feed almost entirely upon the fish eggs within the relative safety of the eelgrass beds. This suggests that adult females shift their diet to avoid competing with newborns. In addition, the timing and location of pupping, which seemed consistent during three years of observation, seems to coincide with the availability of the fish eggs, suggesting that these sharks are pupping in habitats that are protected and have a high availability of prey, underlying why elasmobranchs use these types of habitats as nursery areas (Ebert and Ebert 2005).

© John Bragg/SSNERR

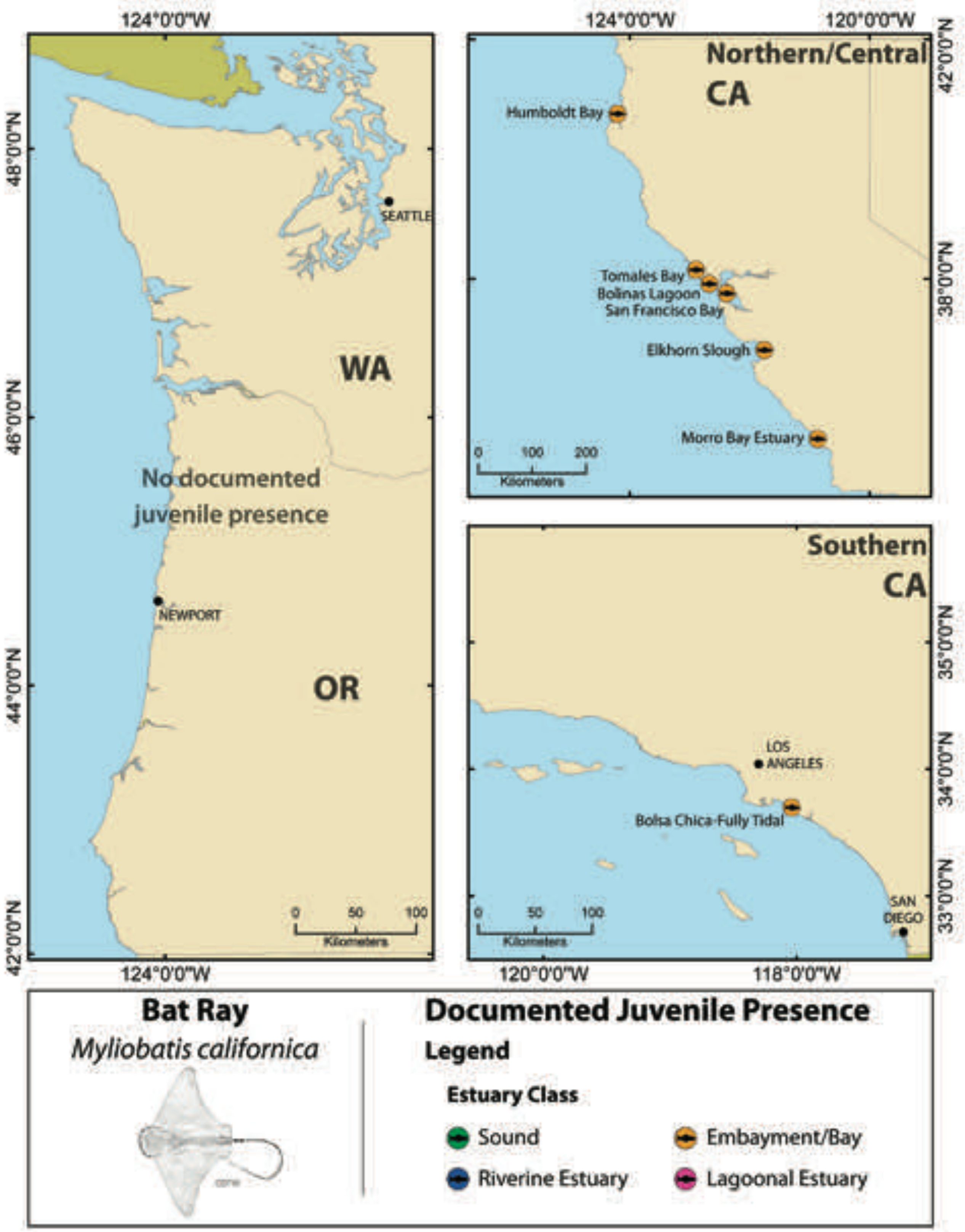


FIGURE 5. BAT RAY: Documented juvenile presence in Washington, Oregon and California estuaries.

BAT RAY

(*Myliobatis californica*)

The bat ray is one of the most common rays along the West Coast. It is endemic from Yaquina Bay, Oregon to the Gulf of California (Table 2). As an abundant, upper, trophic level predator, they are an important component of nearshore ecosystems, and play an important role in structuring soft-bottom benthic communities. Bat rays are generally found in shallow habitats ranging from the intertidal to 50 m, but they can occur as deep as 108 m (Morris et al. 1996, Ebert 2003). They primarily occur on soft sand and mud substrates, but also occur in rocky reef and kelp forest habitats. Bat rays are believed to give birth in protected, shallow waters of bays, estuaries and other shallow coastal habitats (Love 2011). Bays and sloughs are known to play an important role as foraging and nursery areas for this species.

Life History and Ecology

Like other elasmobranchs, bat rays are relatively long-lived (24 years), late-maturing (2–3 years for males, 5 years for females) and have low fecundity (2–12 pups) (Martin and Cailliet 1988a, 1988b; Table 2). Their reproductive mode is aplacental viviparity, and their gestation period lasts approximately 9–12 months. They have an annual reproductive cycle, pupping and mating during the spring and summer in shallow coastal habitats, including bays and estuaries (Talent 1985, Martin and Cailliet 1988a, Gray et al. 1997). Smaller females give birth to fewer young than larger females (Ebert 2003). There can be pronounced sexual segregation in bat rays during the spring and summer pupping period, with ratios of 6:1 (female to male), after which the ratio approaches parity as males move into the area and mating presumably occurs (Ebert 2003). Adult bat rays are generally most abundant in bays and estuaries during the spring and summer, with increasing numbers of newborns and juveniles over the course of summer (Gray et al. 1997).

As upper trophic level predators, bat rays play an important role in coastal ecosystems. Bat rays feed upon a variety of benthic invertebrates, including bivalves, crustaceans, polychaetes, gastropods, echiuran worms and the occasional bony fish (Talent 1982, Barry et al. 1996, Gray et al. 1997, Ebert 2003, Love 2011). The impact of bat rays on soft-bottom ecosystems can be quite pronounced due to their feeding behavior, in which they excavate prey from the bottom by digging their rostrum into the substrate and flapping their wings. This excavates large amounts of sediment from the bottom and has dramatic and cascading effects on soft-bottom communities (Karl and Obrebski 1976). Predators of bat rays include the sevengill shark (*Notorynchus cepedianus*), white shark (*Carcharodon carcharias*) and pinnipeds (e.g., *Zalophus californianus*). Juvenile bat rays have been known to be consumed by leopard sharks (Ebert 1986, 2003).

© Tom Greiner/CDFW

Timing and Use of Estuarine Habitats

Bay rays are seasonally abundant in bays and estuaries, leaving during the winter when temperature and salinity decreases and returning when temperatures increase in the spring (Hopkins and Cech Jr. 2003). Although little is known of the nursery requirements for this species, newborns and juveniles are primarily found in more shallow and protected habitats, such as mudflats, seagrass beds and tidal creeks in central and northern California, and pupping primarily occurs during the spring and summer (Barry and Cailliet 1981, Talent 1985, Martin and Cailliet 1988a, Carlisle et al. 2007; see Box 5).

They are a relatively euryhaline and eurythermal species, occurring in temperatures from 10–26°C (though generally not at the higher range of temperatures) and salinities as low as 14 ppt, though typically above 25 ppt (Love 2011). The importance of temperature, salinity and dissolved oxygen on the nursery use of newborn and juvenile bat rays is unclear, although there is evidence of sensitivity to reduced salinity and increased temperatures (Table 3). The metabolic rate of small bat rays increases with reduced salinity (less than 25 ppt; Meloni et al. 2002). The metabolic rate of large juveniles and small adults is highly sensitive to temperature, increasing rapidly between 14–20°C (Q_{10}=6.8) (Hopkins and Cech Jr.

1994). In Tomales Bay, bat rays exhibit a diel pattern of habitat use that reflects this temperature sensitivity—they forage in the warm waters of the inner bay during the day and move to cooler more oceanic waters during the night to rest and digest their food (Matern et al. 2000).

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile bay rays have been documented in seven estuaries along the California coast, all of which are in the embayment/bay class of estuaries (Figure 5). These bays and sloughs, including Humboldt Bay, San Francisco Bay, Tomales Bay and Elkhorn Slough (Box 5), are known to play an important role as foraging, pupping and juvenile habitat for this species. Newborn and juveniles bat rays are primarily found in the more shallow and protected habitats, such as mudflats, tidal creeks and seagrass beds (Hopkins 1993, Ebert 2003, Love 2011; Table 4).

Some bat rays show a high degree of site fidelity, returning to the same bay or estuary year after year (Hopkins and Cech Jr. 2003, Love 2011). Very little is known about their larger scale migrations and movements, but large schools of bat rays are often observed moving along coastal habitats in California (Ebert 2003).

Threats

Bat rays are caught by recreational anglers and are commonly caught unintentionally in commercial fisheries. The level of unintentional catch is unclear, as most skates and rays are reported as "unspecified skate" or "stingray", but given existing regulations and the low demand for bat rays, there is little evidence suggesting they are being overfished (Table 5). Although the practice stopped in the mid-1990s, bat rays in Humboldt Bay were systematically eliminated based on the belief that they were feeding on commercial, non-native, Japanese oysters *(Crassostrea gigas)*, leading to approximately 43,000 bat rays being killed between 1956 and 1992 (the total does not include an additional 45,000 bat rays that were caught and sold for fertilizer between 1955 and 1960). Research subsequently demonstrated that bat rays do not consume oysters, but are in fact a major consumer of red rock crabs. Red rock crabs, on the other hand, are a significant predator of oysters; recognition of the ecological service that bat rays provide ultimately resulted in cessation of the wholesale destruction of native bat rays (Gray et al. 1997).

Given how sensitive the metabolic rate of bat rays is to increased temperatures, it is possible that habitat alteration in bays and estuaries, resulting in increased temperatures, may reduce the amount of habitat available to bat rays (Hopkins 1993, Hopkins and Cech Jr. 1994). Their seasonal use of bays and estuaries is influenced by temperature and salinity, and decreased salinity levels (<25 ppt) are associated with significant increases in metabolic rate as well, indicating that bat rays may be sensitive to changes in salinity and temperature in important habitats (e.g., nursery) (Meloni et al. 2002, Hopkins and Cech Jr. 2003). Loss and degradation of foraging and nursery habitat in bays and estuaries is of concern for this species (Ebert 2003).

BOX 5. SHALLOW HABITATS ARE SEASONAL NURSERIES FOR BAT RAYS IN ELKHORN SLOUGH

In Elkhorn Slough, California, bat rays enter the slough during the spring and summer to feed, mate and pup. Pupping and mating occurs during the spring and summer, when mature rays are most common and the sex ratio is approximately 1:1. Newborns start to appear during the summer, and mating is believed to occur shortly after pupping. Larger individuals are primarily found in the deeper main channel and lower parts of the slough, whereas neonates and juveniles are primarily found in the more shallow and protected habitats, such as mudflats and tidal creeks. Juveniles are generally more abundant than mature animals, and juveniles of all size classes are abundant during the spring, summer and fall, indicating Elkhorn Slough plays an important nursery role during the early life history of this species (Barry and Cailliet 1981, Talent 1985, Martin and Cailliet 1988, Carlisle et al. 2007).

© Morgan H. Bond

ANADROMOUS FISH

Anadromous fishes include all fishes that hatch from eggs and spend some amount of time rearing in freshwater streams, and then migrate through estuaries to the sea to grow and mature into adults before returning to spawn in their natal streams. These migrations range from being quite short, after which spawning occurs in or just above the estuaries, to spanning thousands of kilometers (Augerot and Foley 2005), and involving dramatic physiological and behavioral changes. Although by definition all anadromous individuals must pass through estuaries, the extent to which juveniles use estuaries as rearing grounds varies both among and within species. For this report, we focused on four anadromous species: green sturgeon, Chinook salmon, coho salmon and steelhead trout. Representatives of these four species are found throughout the entire geographic range covered by this report. Although populations of these four anadromous species are known to use many watersheds throughout this range, we limited presentation on maps and in the text to estuaries where juveniles were documented using estuarine habitat for rearing according to our literature search. Each of these species is of economic and cultural importance, has relatively broad ranges, is relatively well studied and is of conservation concern.

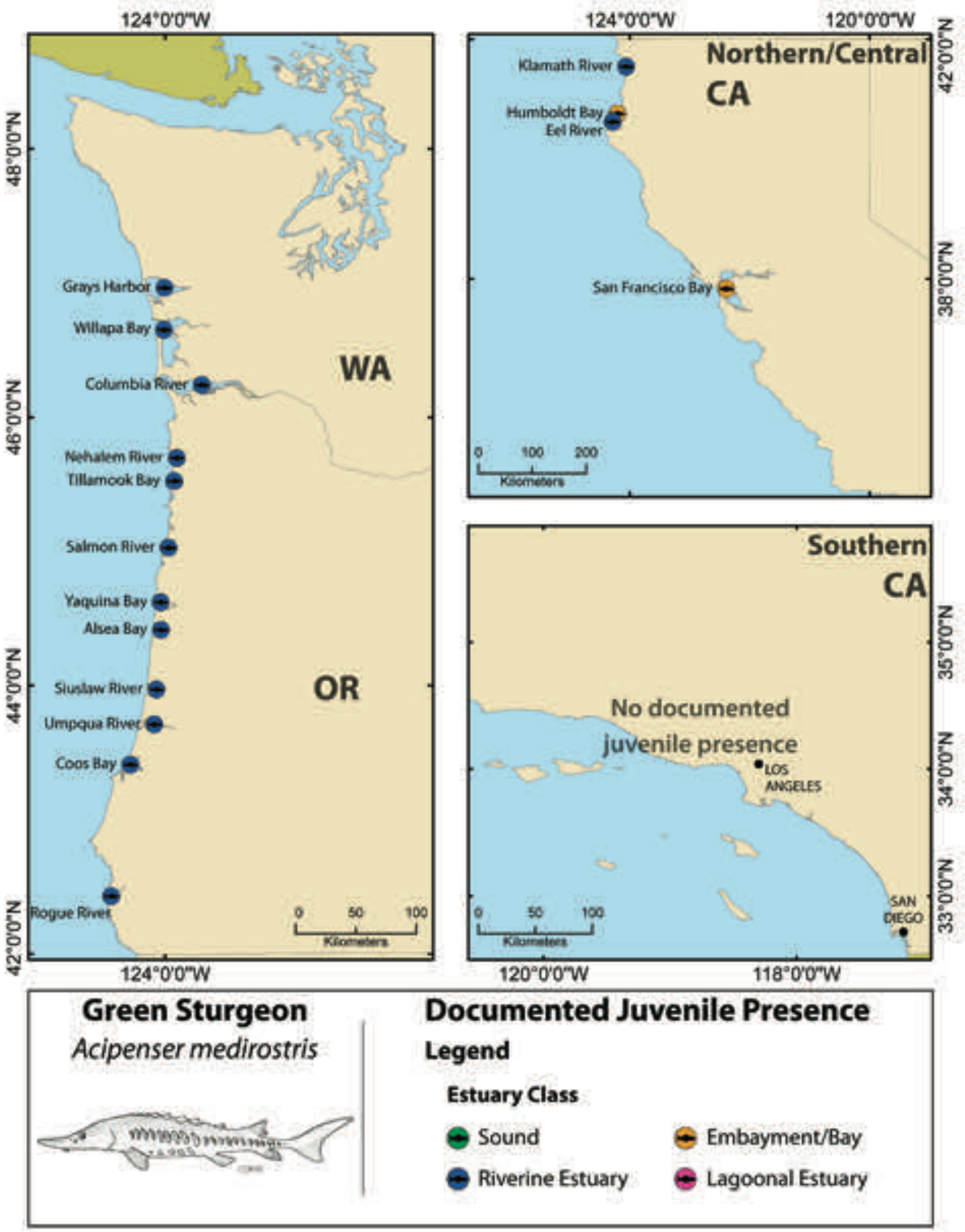


FIGURE 6. GREEN STURGEON: Documented juvenile presence in Washington, Oregon and California estuaries.

GREEN STURGEON

(*Acipenser medirostris*)

The green sturgeon is an anadromous species that, unlike other species of sturgeon, spends the majority of its life in coastal marine and estuarine waters. Green sturgeon occur from Kuskowkim Bay, Alaska (Bering Sea) to Bahía de San Quintín, Mexico (Love 2011; Table 2). Along the Pacific coast of North America, there are two distinct population segments (DPS); a northern population that spawns in rivers from the Eel River, California, to the Rogue River, Oregon, and a southern population that that spawns in the Sacramento River, California (St. Pierre and Campbell 2006).

Life History and Ecology

The green sturgeon is a large (270 cm total length), long-lived (53 years) and late-maturing (16–27 years for females, 13–18 years for males) species with a long generation time (27–33 years) (Davies 2004, Beamesderfer et al. 2007; Table 2). They are believed to spawn only every 2–5 years (Moyle 2002, Davies 2004). Green sturgeon hatch and spend the first few years of their lives in fresh water, but older fish are found primarily in marine waters and estuarine habitats. As adults, they return to fresh water only to spawn, migrating hundreds of kilometers up rivers during the spring and early summer in search of suitable spawning habitat (Beamesderfer et al. 2007, Love 2011).

In the summer or fall, upon leaving rivers after spawning, adult sturgeon generally migrate northwards along the continental shelf to the northern end of Vancouver Island, or occasionally further, where they remain for the winter. Some sturgeon, however, do not migrate and remain in more southern locations throughout the winter (Lindley et al. 2008). When in these neritic environments, they use a relatively narrow range of depths between 40–70 m, although they do use habitats as deep as 110 m and as shallow as the surface. Sturgeon are generally more active and move to shallower depths at night (Erickson and Hightower 2007). In coastal areas, sturgeon seem to preferentially use areas with complex seafloor habitats (Huff et al. 2011). Following this overwintering period, green sturgeon migrate back to southern locations in the spring, and non-spawning fish spend the following summers in bays and estuaries (Moser and Lindley 2007, Lindley et al. 2008, Lindley et al. 2011).

© Toz Soto/Karuk Tribal Fisheries Program

Unlike the early life history, which is relatively well understood, the ecology of older sturgeon in marine and estuarine habitats is poorly known (Beamesderfer et al. 2007). Subadults and non-spawning adults form large aggregations during the summer and fall in various bays and estuaries along the coast (Beamesderfer et al. 2007, Erickson and Hightower 2007, Lindley et al. 2011). Use of these estuaries may be tied to high prey availability and warm water temperatures, which facilitates rapid growth (Moser and Lindley 2007). Sturgeon primarily feed on benthic invertebrates, including crabs, shrimps, amphipods and polychaetes, although they do consume bony fish as well (St. Pierre and Campbell 2006, Love 2011).

Timing and Use of Estuarine Habitats

Newly hatched larvae disperse down river shortly after hatching, and spend the next several years (~1–3 yrs) growing in freshwater or estuarine habitats prior to moving to the marine environment at sizes of 30–80 or 90 cm (Nakamoto and Kisanuki 1995, Beamesderfer et al. 2007). Estuarine habitat use by juveniles is poorly understood. Young sturgeon, particularly those less than six months old, are restricted to fresh and brackish water environments until approximately 1.5 years, at which point they are capable of entering marine environments (Table 3; Allen and Cech 2007). Optimal temperatures for sturgeon less than one year of age are 15–19ºC; higher temperatures result in increased metabolic rate, and swimming performance decreases at temperatures between 19–24ºC (Mayfield and Cech 2004).

The movement patterns of juvenile and subadult green sturgeon have been studied in several large systems. The movements of large juvenile sturgeon (1–1.5 m TL) in San Francisco Bay seem to be influenced by tidal currents, but largely independent of salinity and temperature, and they are capable of moving across strong gradients of salinity (of up to 16.2 ppt) over relatively short periods of time (Kelley et al. 2007, Kelly and Klimley 2012). As they grow larger, they gradually move to deeper and more saline environments (Beamesderfer and Webb 2002). Using acoustic tags, Moser and Lindley (2007) studied the movements of subadult and adult green sturgeon in Washington. They hypothesize that green sturgeon maximize their growth rates in the summer by using estuarine habitats when temperatures were high and prey were abundant (see Box 6).

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile green sturgeon have been documented in 12 riverine estuaries and two embayment estuaries between Grays Harbor, Washington and San Francisco Bay, California (Figure 6). Estuarine habitat use by juvenile green sturgeon is poorly understood. Younger juveniles (less than 18 months) are found in fresh and brackish water habitats (Allen and Cech 2007) after which time they can use more saline habitats (Table 4). Tagging studies have revealed that juvenile and subadult green sturgeon are highly mobile within estuarine systems and may use tidal processes to move into intertidal mudflats as foraging habitat (Box 6; Moser and Lindley 2007).

Threats

The southern population of green sturgeon is listed as threatened, and the northern population as a species of concern, under the under the U.S. Endangered Species Act (ESA) (Roberts and Gingras 2008). The principal threat to the southern population has been identified as the reduction of the spawning area in the Sacramento River. Other factors threaten both populations; many pertain to freshwater habitat, including reduced freshwater flow in spawning areas, contaminants, incidental catch in commercial fisheries, poaching (for caviar), entrainment in water diversions and canals, competition from exotic non-native species, small population sizes, impassable barriers, low dissolved oxygen and elevated water temperatures (Adams et al. 2007). Given the importance of bays to subadult and adult fish as foraging habitats, degradation of habitats and associated decrease in prey availability and habitat may be of concern.

Tagging studies have found that green sturgeon move frequently and rapidly between different bays and estuaries, and fish tagged in different spawning sites used the same bays and estuaries (Moser and Lindley 2007). This tendency to move often and quickly between different locations, and the fact that these areas are being used by sturgeon from both DPSs, suggests that localized fishing efforts could have a disproportionate effect on green sturgeon populations, as they could effectively be fishing the entire population as it transits through a relatively small area.

© Kirsten Ramey/CDFW

BOX 6. SEASONAL USE OF WASHINGTON ESTUARIES MAY SUPPORT FASTER GROWTH RATES IN GREEN STURGEON

Using acoustic tags, Moser and Lindley (2007) demonstrated that subadult and adult green sturgeon primarily use bays and estuaries in Washington during the summer, when water temperatures are at least 2°C warmer than open coastal habitats. Inside these bays and estuaries, green sturgeon are highly mobile and move throughout the systems, likely moving with the tide into intertidal mudflats to feed on burrowing shrimp. They hypothesize, that by using these highly productive habitats during the summer when temperatures were high and prey were abundant, sturgeon maximize their growth rates. Furthermore, given the apparent importance of these habitats to the life history of green sturgeon, they suggest that habitat alteration in bays and estuaries may have serious consequences for green sturgeon populations. As an example, they cited the historic use of carbaryl, a pesticide, on mudflats in Willapa Bay, Washington, to control shrimp populations, which were believed to impact commercially important oyster cultures. This pesticide could have impacts on sturgeon directly, or indirectly, by reducing populations of prey species in mudflat habitats.

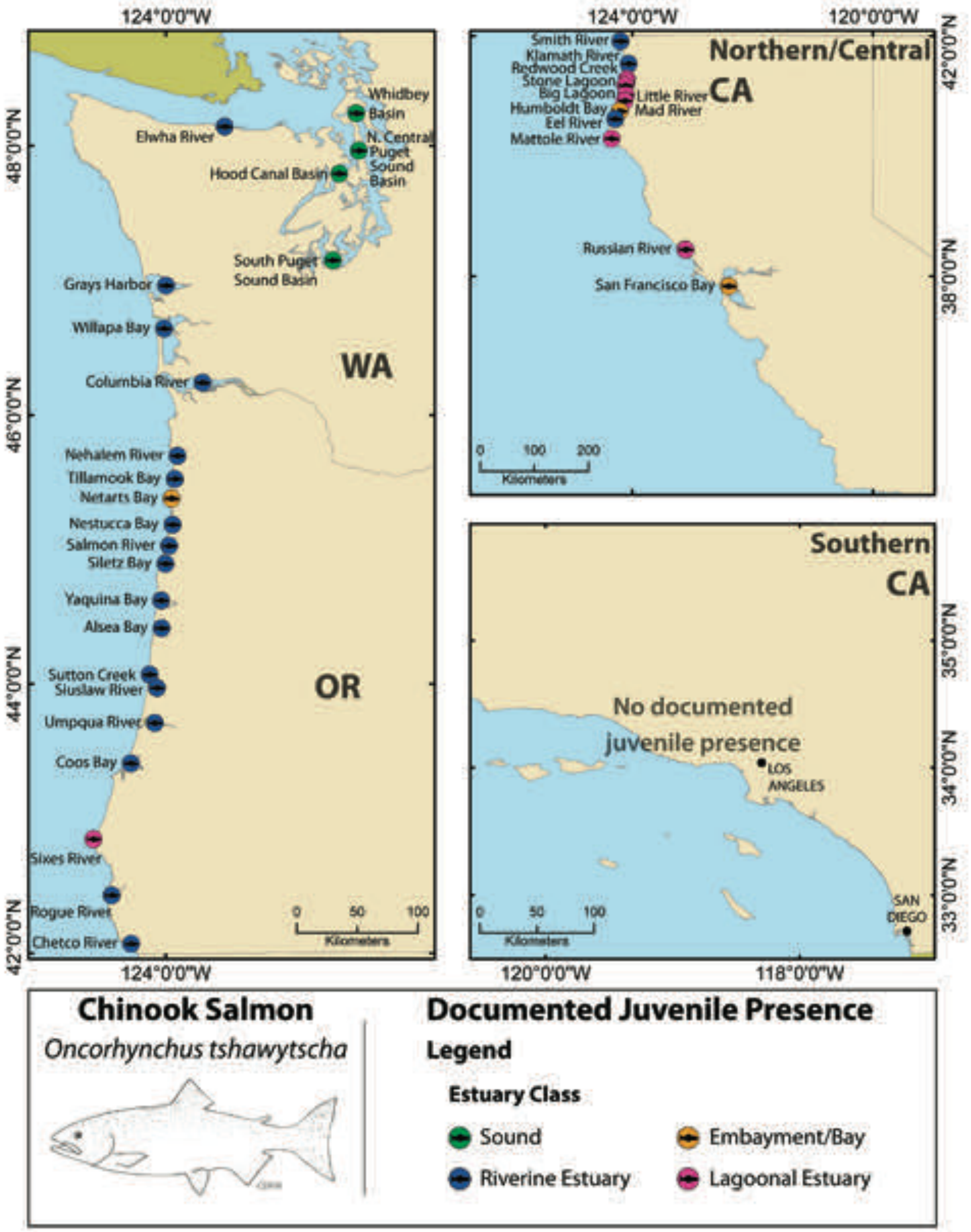


FIGURE 7. CHINOOK SALMON: Documented juvenile presence in Washington, Oregon and California estuaries.

CHINOOK SALMON

(*Oncorhynchus tshawytscha*)

© Morgan H. Bond

Chinook salmon are the largest of the Pacific salmon and thus are also known as king salmon, yet they are the least abundant of Pacific salmon in North America (Behnke 2002). Chinook salmon spawn in rivers of Asia draining into the Sea of Okhotsk, East Siberian Sea and Chuckchi Sea, in rivers of Alaska draining into the Bering Sea and in other rivers of North America draining into the eastern Pacific Ocean as far south as the San Joaquin River and its tributaries in California (Augerot and Foley 2005; Table 2). Chinook salmon forage at sea throughout the northern Pacific Basin above 40° latitude, and as far south as central Baja California (Augerot and Foley 2005, Love 2011). In both Asia and North America, the more northern populations of Chinook salmon (e.g., Alaskan populations) are generally healthy, whereas the more southern populations show increasing risk of extinction (Augerot and Foley 2005). In North America, Chinook salmon historically spawned as far east as Montana and Nevada, deep into small tributaries and headwaters. The Chinook salmon's current spawning distribution has been greatly reduced due to impassable dams and habitat alteration (Behnke 2002, Augerot and Foley 2005).

High spawning site fidelity and distinct timing of spawning gives rise to substantial reproductive isolation among Chinook salmon populations. This reproductive isolation in combination with habitat variability across their range has lead to genetically distinct subunits (runs) within the species. Certain runs have been designated as evolutionary significant units (ESUs), which serve as distinct management units for Washington, Oregon and California (McClure et al. 2008, Williams 2006, USFWS and NMFS 1996). Of the 18 Chinook salmon ESUs, two are listed as endangered, seven are listed as threatened, two are candidates for listing, and two are listed as species of concern (Table 6). The Central Valley spring run in the San Joaquin River is listed as a non-essential, experimental population, as it is composed of fish introduced from elsewhere in northern California (NOAA National Marine Fisheries Service 2014).

Chinook salmon support commercial, recreational and subsistence fisheries. Annual commercial landings in California, Oregon and Washington for 2012 were 2.8 million pounds ($12 million), 1.8 million pounds ($6.7 million) and 4.6 million pounds ($12 million), respectively (NOAA National Marine Fisheries Service 2012). Thousands of salmon are caught in recreational fisheries each year along the coast of all three states. Many indigenous people in the Pacific Northwest rely on Chinook salmon as a mainstay of their diet and a central cultural symbol.

There are several good examples demonstrating the nursery role of estuaries for Chinook salmon (e.g., Quinones and Mulligan 2005, Maier and Simenstad 2009), which are described below.

TABLE 6. Chinook salmon Evolutionary Significant Units (ESUs) and their listing status under the U.S. Endangered Species Act.

ESU	Status
Washington Coast	Not Listed
Puget Sound	Threatened
Upper Columbia River Summer/Fall	Not Listed
Upper Columbia River Spring	Endangered
Middle Columbia River Spring	Not Listed
Lower Columbia River	Threatened
Upper Willamette River	Threatened
Deschutes River Summer/Fall	Not Listed
Snake River Spring/ Summer	Threatened
Snake River Fall	Threatened
Oregon Coast	Not Listed
Southern Oregon and Northern California Coastal	Not Listed
Upper Klamath- Trinity Rivers	Candidate
Sacramento Winter	Endangered
Central Valley Fall and Late Fall	Species of Concern
Central Valley Spring	Threatened
Central Valley Spring—San Joaquin	Non-essential
California Coastal	Threatened

Life-history and ecology

Chinook salmon are anadromous, meaning they hatch from eggs in fresh water streams, migrate to the ocean to attain adult size and return to their natal stream to spawn. However, Chinook salmon are thought to express some of the highest diversity in life history strategies of all salmon species. This diversity includes variation in the timing of adult and juvenile migrations, the timing and duration of all life history stages and the timing, duration and extent of reliance on estuaries as rearing habitats.

Chinook salmon spawn in mainstems of rivers, preferring larger substrate and higher flows than coho salmon and steelhead trout. This means that Chinook salmon generally have further to migrate to spawn, and that juveniles are hatched further away from estuaries. The female makes large pits and mounds within which the eggs are laid and fertilized by the male. The female then guards the nest until she dies. The eggs and alevin (newly hatched with yolksac still attached) remain in these protective nests bathed with clean oxygen-rich water.

Eggs and alevin are riverine, whereas fry (yolk absorbed, total length less than 50 mm) and parr or fingerlings (50 mm–100 mm) can be riverine or estuarine (Augerot and Foley 2005, Bottom et al. 2005b, Fresh 2006). Parr or fingerlings are so named due to vertical striping “parr” marks that provide for camouflage for the young fish and the fact that they are roughly the size of an adult human's finger.

Juvenile Chinook salmon migrating (emigrating) to the sea have varying life history strategies that have evolved across populations and basins (Williams 2006). A variation in life history seen across their geographic range is the presence of stream-type and ocean-type. Stream-type fish can spend a year or more feeding and growing in fresh water before emigrating to the ocean. When stream-type Chinook salmon emigrate to sea, they generally move rapidly, spending less time in the estuary foraging and acclimating (Healey 1991). Ocean-type fish will emigrate to the estuary within the first year, at a smaller size, relying more heavily on the estuary for food and refuge from predators (Bottom et al. 2005b, Williams 2006, Healey 1991). Diel timing of downstream migrations varies between systems. For example, in the Columbia River Estuary, they tend to travel during the day whereas in the Central Valley juveniles tend to migrate during twilight or night with preference decreasing as distance traveled increases (Dawley et al. 1986, Osterback et al. 2013, Chapman et al. 2012).

Chinook salmon move into the ocean after spending variable lengths of time in the estuary (see section below). In the ocean, Chinook salmon can be found from the surface to 344 m deep and are commonly found to 150 m deep (Love 2011; Table 2). Chinook salmon reach maturity anywhere between two and six years of age (Augerot and Foley 2005). Maximum age is reported at more than eight years, and they attain a size of 160 cm total length. After spending an average of three years foraging in the ocean, adult Chinook salmon enter the estuary on their migration back to their natal streams. Chinook salmon may have distinct populations within a given river, separated by the timing of adult migration up river to spawn (Quinn 2004). These phenologically separated adult migrations, or runs, are consistent across their range occurring in the fall, late-fall, winter, spring, or summer (Emmett et al. 1991). Some of these runs, such as the Sacramento River winter run, have been reduced to remnant populations by anthropogenic control of river flow (Williams 2006).

Adults spend little time in the estuary during their return migration. Chinook salmon do not feed during their spawning migration, which can be upwards of thousands of kilometers (Augerot and Foley 2005). Much of their energy is transferred into their gonads in preparation for spawning, and their bodies may start to deteriorate (Love 2011). Chinook salmon are semelparous—they spawn once and then die. Rotting carcasses of Chinook salmon are a source of marine-derived nutrients that nourish various invertebrate species living in the generally low nutrient streams in which Chinook salmon spawn, and which will, eventually, serve as prey for young Chinook salmon (Augerot and Foley 2005).

Timing and Use of Estuarine Habitats

Chinook salmon use estuaries as juveniles during their migration from their natal streams to the ocean and as adults as they return from sea and enter streams during their spawning migration. When Chinook salmon juveniles migrate to sea, an estuary may be important for foraging and refuge as well as a transition zone for the physiological changes that Chinook salmon undergo to survive in the ocean (Aitkin 1998, Boles 1988, Hanson et al. 2012, MacFarlane and Norton 2002, Marine and Cech 2011, Myrick and Cech 1998, Thorpe 1994; Table 3).

Timing of estuarine use by Chinook salmon varies regionally and is dependent on many factors, including duration and intensity of peak riverine flows, population abundance and the physical and chemical characteristics of the estuary (Beauchamp et al. 1983). Smaller juveniles may spend months in the estuary whereas larger juveniles may only spend days. This is related to whether they are stream- or ocean-type and is likely due to the need for smaller fish to grow more to survive once they reach the ocean (Fresh 2006, Woodson et al. 2013). In general, the importance of estuaries is inversely proportional to the size of the fish when it enters the estuary Smaller fry enter earlier in the year and spend more time in the estuary (Fresh 2006, Williams 2006).

In Puget Sound, the first juveniles to enter the estuary are fry (less than 50 mm fork length). Later in the year, from mid-May through June, parr and yearlings begin to enter the estuary. Two scales of variation contribute this to this pattern—population (run) and life history strategy (Fresh 2006). Peak estuarine abundance occurs between December and April. Estuarine residence time averages between 30–60 days, although it may be as much as 120 days (Fresh 2006). In the Columbia River Estuary at the Oregon–Washington border, a relatively small number of fall-run fry move into the estuary in late February, and larger fish move down stream in late spring and early summer (Dawley et al. 1986). Mark and recapture studies led researchers to believe that residence time was relatively short in the estuary; however, a recent otolith study estimated that some fish spend as long as 176 days in the estuary (Campbell 2010). This discrepancy has been attributed to the size of fish needed for mark and recapture studies (over 90 mm total length for acoustic tags and 55–60 mm total length for passive induced transmission tags, which led to an underestimate of residence time).

The Sixes River estuary, just north of Cape Blanco, Oregon, supports only a fall Chinook run. Fry and parr start to enter the estuary in spring, and peak abundance occurs in July, possibly in response to increased temperatures upstream (Reimers 1971). Although early growth rates are especially high for fry in the estuary, they decline during peak abundance, likely due to the relatively high population density in the small estuary (Reimers 1971).

Chinook salmon in the Southern Oregon/Northern California Coastal ESU, which extends from Cape Blanco to the Klamath River in California, are primarily late-fall run with an ocean-type life history strategy; migration into the estuary is from March through August and includes fry through fingerling stages (Moyle et al. 2008).

The ESU that includes upper Klamath River and Trinity River Chinook salmon includes both spring and fall runs exhibiting both ocean and stream-type strategies, although most individuals have the characteristics of ocean-type juveniles. Initial timing of juvenile emigration is dependent on physical characteristics, predominantly flow and temperature (Moyle et al. 2008). Peak emigration of juveniles is during the summer. Larger juveniles enter the estuary with the autumn rains, and a small number of yearlings can be found entering the estuary from January through June (Moyle et al. 2008).

The majority of California coastal Chinook salmon ESU exhibit the ocean-type juvenile life stage, with a few stream-types remaining in the coastal watershed over summer (Moyle et al. 2008). Only the fall run remains in this ESU; the spring run has been extirpated. Fry move into the estuaries late winter or spring and remain there until mid- to late summer (Moyle et al. 2008).

The Central Valley ESU fall run fry start to emigrate from January through March. April and May are peak emigration times for parr migrants; yearlings follow in the fall or winter (Williams 2006). The timing of other runs—winter, late fall and spring—is more difficult to determine because expected size-at-date relationships are not consistent. Identification of runs can only be determined through genetic analysis (Hedgecock 2002).

Juvenile Chinook salmon use a variety of estuarine habitats (Table 4). Particular habitat use is generally related to size—smaller fish are found in intertidal areas, and larger fish move to deeper habitat closer to larger prey (Moyle et al. 2008). The ability of any one habitat to support and serve a nursery role for juvenile Chinook salmon depends on how well the habitat provides the three key attributes of the nursery role of estuaries: 1) food, 2) refuge from predation and environmental stress and 3) the physiological transition zone from fresh to salt water (Moyle et al. 2008, Sheaves et al. 2014).

Once in the estuary, prey of juvenile Chinook salmon ranges from benthic invertebrates (i.e., amphipods, copepods, mysids and decapods) and insects to small fish (Emmett et al. 1991, McCabe et al. 1983, Miller and Simenstad 1997, Fresh 2006; Table 3). Small fry and fingerlings are found in shallow intertidal habitats feeding on epibenthic prey.

Growth in the estuary is highly variable and dependent on numerous chemical and biological factors, but individuals with the ocean-type life history strategy will typically double in size (from 50 mm to 100 mm total length) (Healey 1980, McCabe et al. 1983, Burke 2005). In the Columbia estuary, large sub-yearlings and yearlings emigrate directly to the ocean through deep channels (Burke 2005). Ocean-type Chinook salmon spend more time in the estuary and rely more on detrital food webs linked to wetlands. Disruption of this energy flow can have a profound impact on long-term survivorship (Bottom et al. 2005b, McCabe et al. 1983; see Box 7 for more information).

Typical predators of juvenile Chinook salmon are bony fish, sharks, birds and marine mammals (Emmett et al. 1991). The complex habitat structure of the estuarine environment provides abundant refuge from predators and reduced environmental stress (Bottom et al. 2005b). By capitalizing on an increased growth potential within estuaries, juvenile Chinook salmon quickly grow too large for most estuarine and marine predators thereby affording a size-based escape from predation (Healey 1991). Estuaries provide further reductions in environmental stress, including thermal refuge. At high tides some juveniles feed over intertidal mudflats and in salt marshes; at low tides the deeper tidal channels provide refuge from predators and high temperatures that are inherent in tidally-influenced flats (Bottom et al. 2005b). Thermal refugia have become increasingly important as human alteration of thermal regimes, from physical changes to freshwater flow, have become more prevalent (Richter and Kolmes 2005).

The estuarine environment provides a critical transition zone to help juvenile Chinook salmon moving from a freshwater to a saltwater environment and the physiological, morphological and behavioral changes known as smolting. Smolting is cued by environmental factors that include temperature, day length and river flow (Stefansson et al. 2008). In the Pacific Northwest, spring stream temperatures that inhibit smolting are 12–15°C or higher (Richter and Kolmes 2005). An enzyme in the gills (called ATPase) responsible for osmoregulation has reduced activity at this temperature (Richter and Kolmes 2005), and migratory response is inhibited at temperatures above 12.2°C (Boles 1988). Temperatures that inhibit smoltification may be higher for summer migrating fall-run fish. After smoltification, optimal growth in the Pacific Northwest occurs at 12.2–16°C (Richter and Kolmes 2005). Chinook salmon in the Sacramento and San Joaquin River basins regularly smolt at high temperatures (Myrick and Cech 2004). Higher temperatures reduce dissolved oxygen, and juvenile Chinook salmon avoid areas with dissolved oxygen below 4.5 mg per liter (Beauchamp et al. 1983). The estuary provides easier transition to the different chemical, predatory and prey community qualities of the ocean environment, resulting in increased growth and survival of individual Chinook salmon entering the ocean. Smolting primarily occurs upstream of the estuary, but anthropomorphic impacts have altered, and will continue to alter, where smolting is triggered during emigration.

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile Chinook salmon have been documented in estuaries from Puget Sound south to San Francisco Bay. Numerous studies examined the presence of juvenile Chinook salmon in estuaries. We compiled records of juvenile Chinook salmon in 35 different estuaries throughout their range—eight estuaries in Washington, 16 in Oregon and 12 in California (Figure 7). Throughout Washington, Oregon and California, juvenile Chinook salmon use a wide variety of different estuarine classes (sound, embayment/bay, riverine estuary and lagoonal estuary) and estuarine sub-classes found along the West Coast (Table 4). In Washington, they are primarily documented in riverine estuaries along the open coast and within Puget Sound. Moving south into Oregon and California, Chinook salmon are still found predominantly in riverine estuaries, but are also increasingly present in lagoonal and embayment estuaries.

© Laura S. Brophy

Threats

Threats to Chinook salmon populations are broad and include habitat modification and destruction, dams, harvest and hatcheries (Table 5). Habitat loss has been documented to be one of the biggest threats Chinook salmon face throughout the entire study region of Washington, Oregon and California (Augerot and Foley 2005). Historically, poor management of land, forest and water all have contributed significantly to habitat loss in rivers and estuaries along the West Coast; the legacy of poor management still compromises the resilience of Chinook salmon populations (Augerot and Foley 2005, Dawley et al. 1986, Emmett et al. 1991). Hydropower dams and other water diversions have had a significant impact on Chinook salmon stocks, removing 90% of the original habitat in the Sacramento and San Joaquin River basins (Lindley et al. 2007, Schick and Lindley 2007). In addition to habitat loss, a number of studies have pointed to excessive fishing as a leading cause of population declines in Chinook salmon (Bottom et al. 2005a, Moyle et al. 2008, Healey 1991).

As Chinook salmon populations have declined, there has been great effort to rebuild populations, especially those that are considered to be of cultural or economic value. Hatcheries were initially built to provide mitigation for the habitat loss, but have inadvertently impacted naturally spawning stocks (Carlson and Satterthwaite 2011). Chinook salmon reared in hatcheries replace rather than supplement naturally-occurring Chinook when they are introduced to a stream, leading to a loss of genetic diversity and local adaptive fitness leading to reduced survival in the estuary (Unwin and Glova 1997, Johnson et al. 2012). In Oregon and Washington this occurs with an added impact of pollution and disease associated with other finfish aquaculture operations (Naylor et al. 2005). Increasingly, captive salmon breeding programs strive to preserve the genetic diversity and local fitness attributes of native stocks (Arkush and Siri 2001, Anderson et al. 2013), rather than primarily produce fish for catching.

Modifications resulting from the accumulation of poor management decisions have led to the widespread loss of important estuarine habitats, and have contributed to declines of Chinook salmon populations (Bottom et al. 2005a). Widespread loss of wetlands has decreased juvenile habitat and prey availability, which are key functions of estuarine nurseries (Beck et al. 2001, Sheaves et al. 2014). For example, in Oregon's Salmon River estuary, before restoration began in the 1970s, diked areas were shown to be devoid of fry migrants. Following decades of work to restore estuarine habitat and function, both fry and fingerlings returned (Bottom et al. 2005b). The effect of anthropogenic modifications on juvenile Chinook can also be dependent on the type of habitat modification. For example, in Puget Sound, Toft et al. (2007) and Munsch et. al. (2014) found that juvenile Chinook salmon occurred in higher densities along subtidal riprap, compared to overwater structures, such as piers, indicating that types of shoreline modifications can have varying and likely negative effects.

For young fry in the Central Valley, shallow off-channel habitats (floodplains and tidal marshes) are particularly important due to warmer water temperatures and an abundance of food. Extensive loss of that habitat in the Central Valley, and in the San Francisco estuary, has likely contributed to the decline of Central Valley Chinook salmon populations (Moyle et al. 2008). Several studies in this system have shown that residence time and growth in the estuary decreases when juvenile Chinook spend more time in freshwater tidal areas (MacFarlane and Norton 2002, Moyle et al. 2008). It has been hypothesized that historically, California Coastal Chinook salmon summered in coastal lagoons; habitat degradation and poor water quality have presumably eliminated that life history strategy (Moyle et al. 2008) in all but Big Lagoon and Stone Lagoon (Garwood 2012).

Biological invasions of exotic, non-native species have introduced new predators to estuarine waters and changed food web dynamics. For example, striped bass *(Morone saxatilis),* native to the Atlantic, were deliberately introduced into California waters and have been shown to be a key driver in the observed high mortality rates of salmon migrating through the San Francisco Bay-Delta (Cavallo et al. 2012, Moyle et al. 1986). The introduction of the New Zealand mud snail (*Potamopyrgus antipodarum*) to the Columbia River Estuary has the potential to change food web dynamics because they provide a poor food source for juvenile Chinook salmon and reduce other prey availability throughout competing native benthos (Bersine et al. 2008, Naiman et al. 2012).

Within the estuary, water quality issues and disease pose serious threats to juvenile Chinook salmon and the habitat on which they depend. Increased runoff, containing both organic and inorganic substances, poses a considerable risk to young Chinook salmon migrating to sea (Anderson et al. 2014). Meador (2014) showed a 45% decrease in survival rate in contaminated estuaries for hatchery-reared Chinook salmon, which typically spend less time in the estuary than wild fish. Diseases, such as the infectious hematopoietic necrosis virus, also pose a threat to young Chinook salmon (Breyta et al. 2013). Comparisons of current and past Chinook salmon populations of the Columbia River Basin indicate that anthropogenic changes have led to a loss of diversity in life history strategies found in this basin (Burke 2004). Within the estuarine environment, sea-level rise will likely lead to a loss in scale and complexity of estuarine habitat available to young Chinook salmon (Flitcroft et al. 2013), and modeling suggests climate change will lead to reduced growth and subsequent survival rates (Trudel and MacFarlane 2010).

Because they are anadromous, each Chinook salmon passes through a broad range of habitats and encounters many risks. Because all Chinook are dependent, in different ways, on all of the habitats they pass through in their lifetime, any population disruption can have a devastating impact. Estuaries are highly variable, and Chinook salmon are highly plastic, thus their use of estuaries is also highly variable and adaptive. However, the historic extent and duration of changes to estuaries has had a profound impact on the resilience of Chinook salmon (Bottom et al. 2005a, Bottom et al. 2009, Naiman et al. 2012, Fleming et al. 2014).

BOX 7. LIFE HISTORY PATTERNS AND FOODWEB DYNAMICS: IMPORTANT DRIVERS OF ESTUARY USE BY CHINOOK SALMON

© Jean Takekawa/USFWS

Quantifying the value of estuarine habitats to juvenile Chinook salmon requires information on how different life history stages use estuarine habitats and on the food web dynamics of the system. However, this has been challenging due to the plasticity of Chinook salmon life history strategies under varying conditions. Life history strategies for juveniles residing in various habitats of Puget Sound have two important scales of variation to consider—population (run) and life history strategy—and the combination of these will determine habitat use patterns (Fresh 2006). Temperature, flow tolerances and migration distance are determined at the population level, whereas the length of time spent in the natal stream and estuary is influenced by life history strategy.

The details of estuarine food webs dynamics also need to be understood as an important component of nursery function. For example, Magnusson and Hilborn (2003) found a decrease in the ability of the degraded wetlands of the Columbia estuary to support juvenile Chinook salmon, as noted by decreases in survival rates in these areas. Maier and Simenstad (2009) also found that Chinook salmon in the Columbia River use flooded marsh habitat, and that detritus forms the basis of the food web supporting juvenile Chinook salmon. Meyer (1979) speculated that the degradation of wetlands in Puget Sound was leading to decreased Chinook survival rates. Several studies have noted decreased growth rates and altered residence times within San Francisco Bay and Delta (MacFarlane and Norton 2002, Moyle et al. 2008), presumably due to the loss and alteration of habitat and loss of food web dynamics.

As habitat restoration becomes more prevalent, it is encouraging to note that several studies have found that Chinook salmon will use newly-restored estuarine habitat (Miller and Simenstad 1997, Cornwell et al. 2001). For nearly four decades, researchers have been tracking the effectiveness of restoring tidal wetlands that had been diked, drained and isolated from tidal flow (see studies by Cornwell et al. 2001, Bottom et al. 2005b). In the Salmon River estuary, Oregon, juvenile Chinook salmon were found in a restored area within two years of the removal of a dike (Cornwell et al. 2001). Restoration of formally diked wetlands such as these has been shown to have immediate, positive effects on the abundance or availability of species on which juvenile Chinook salmon prey (Bottom et al. 2005b). Fresh (2006) proposed a conceptual framework focused on what will change with a restoration action proposed, to determine the relative role of a particular area as well as to define uncertainties and risks of the restoration effort.

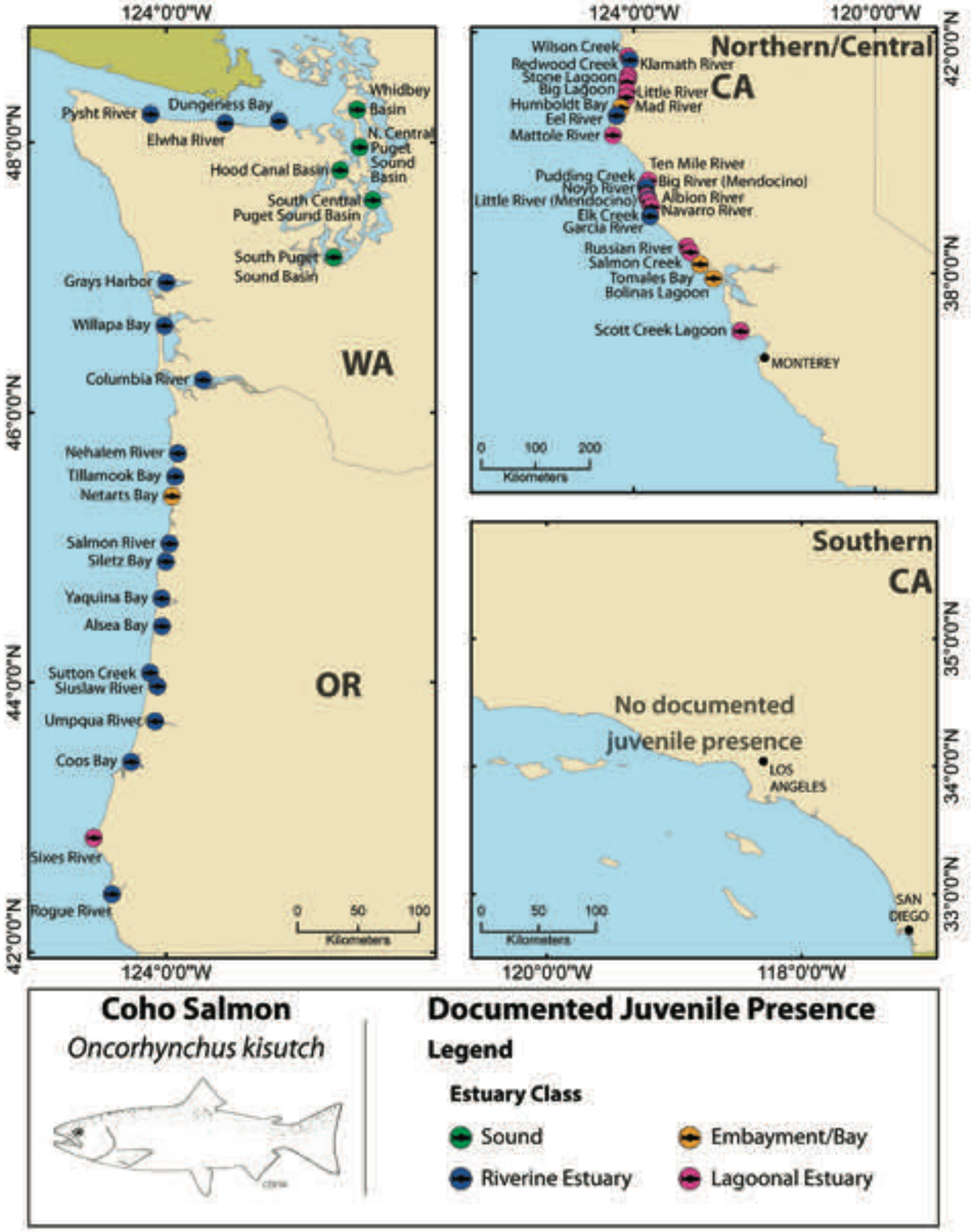


FIGURE 8. COHO SALMON: Documented juvenile presence in Washington, Oregon and California estuaries.

COHO SALMON

(*Oncorhynchus kisutch*)

© Morgan H. Bond

Coho salmon, also known as silver salmon, spawn in rivers of Asia draining into the Sea of Okhotsk, Chuckchi Sea and the Sea of Japan. In North America, coho salmon spawn in rivers draining into the Bering Sea in Alaska (including small streams along the Aleutian Islands chain) and draining to the Pacific Ocean as far south as Scott Creek in central California (Augerot and Foley 2005; Table 2). Coho salmon forage at sea throughout the northern Pacific Basin above 40° latitude, and as far south as northern Baja California, Mexico, but are generally restricted to shelf waters (Augerot and Foley 2005). In Alaska, coho salmon migrate far inland to spawn, however, at lower latitudes, their spawning migrations become shorter (Augerot and Foley 2005). In Alaska, populations of coho salmon are generally healthy. In Washington, coho salmon populations are relatively healthy, however populations have been extirpated in some areas of Puget Sound and the Georgia Basin (Augerot and Foley 2005). Coho salmon have been largely extirpated from the upper Columbia and upper Snake rivers. Populations are increasingly threatened moving south. In California, populations are far below their historical levels trending downward, with a number of populations either already extirpated (e.g., the Sacramento and San Joaquin river basins) or at a moderate to high risk of extinction (Augerot and Foley 2005, Moyle et al. 2008).

Of the seven evolutionary significant units (ESUs) of coho salmon in Washington, Oregon and California, five have been given protection, or are under consideration for protection, under the U.S. Endangered Species Act (ESA) (USFWS and NMFS 1996; Table 7). North of California, coho salmon still support commercial, recreational and subsistence fisheries. Annual commercial landings in 2012 were 103,000 pounds ($168,000), and 3.6 million pounds ($6.5 million) for Oregon and Washington, respectively (NOAA National Marine Fisheries Service 2012). In Oregon, coho salmon also are caught in recreational fisheries, but only hatchery fish can be retained. The 2014 quota for the state was 194,400 coho salmon (Oregon DFW 2014). Culturally, coho salmon have been important in the European smoked fish market and are particularly important ceremonially in the Pacific Northwest (Augerot and Foley 2005).

Life History and Ecology

Coho salmon spawn in tributaries and the mainstem of smaller rivers. Females make nests to hold the fertilized eggs in streambed gravel, and defend these nests until they die. The eggs and alevin (newly hatched with yolksac still attached) remain protected in these gravel nests for 3–6 months (Moyle 2002). In general, juvenile coho salmon rear in streams for one to two years, but may rear in the estuary for part of that time (Augerot and Foley 2005, Bottom et al. 2005a). They spend the remainder of their three-year life cycle at sea before returning to their natal streams to spawn. The eggs and alevin are riverine whereas fry (yolk absorbed, total length less than 50 mm) and parr or fingerlings (50 mm–100 mm) can be riverine or estuarine (Augerot and Foley 2005, Bottom et al. 2005a).

TABLE 7. Coho salmon Evolutionary Significant Units (ESUs) and their status under the U.S. Endangered Species Act.

ESU	Status
Central California	Endangered
Lower Columbia River	Candidate
Olympic Peninsula	Not Listed
Oregon Coast	Threatened
Puget Sound/Strait of Georgia	Species of Concern
Southern Oregon/Northern California Coasts	Threatened
Southwest Washington	Not Listed

Juvenile coho salmon are adaptable and thus have various life history strategies expressed within and across basins (Koski 2009). These life history strategies were, until recently, classified as the same stream- and ocean-type strategies found in Chinook salmon (see the Chinook section, Life History and Ecology for a description of ocean- and stream-type life history strategies) but that description was found to be too constrained, given the amount of variation observed, and a new classification scheme of sub-yearling and yearling out-migrants was proposed (Koski 2009). Most juvenile coho salmon spend the first year rearing in freshwater streams, migrating out to sea as yearlings (similar to Chinook stream-type). Some remain in freshwater an additional winter (Aitkin 1998, Augerot and Foley 2005, Hassler et al. 1987). Some coho salmon migrate to the estuary as sub-yearlings (thought of as nomads until recently) and spend time foraging and growing in the estuary, sometimes using estuaries of non-natal streams (Thorpe 1994, Aitkin 1998, Koski 2009). Recently, a study in the Salmon River estuary, Oregon, indicated that there might be different life history strategies for juvenile coho salmon, each relying on estuaries as rearing habitat to a different degree (Jones et al. 2014, see Box 8 for more information). Male coho salmon that emigrate to the ocean after one winter, mature early and return with adult spawners in the following fall, are called jacks. From year to year, the proportion of jacks to adult fish returning is consistently proportional; thus the number of jacks can be used to predict the size of the following year's run, when the fully mature siblings of the jacks return to spawn (Augerot and Foley 2005).

Once coho salmon enter the ocean, they can be found from the surface to 240 m deep, spending most of their time in 10 m deep water (Love 2011; Table 2). They reach maturity anywhere between four months and three years of age, typically living three years, reaching approximately 95 cm with a maximum size of 108 cm total length (Augerot and Foley 2005, Love 2011). After spending from two to three years foraging in the ocean, coho salmon start the migration back to their natal streams between September and February, making them one of the latest salmon species to migrate upriver (Augerot and Foley 2005). Coho salmon adults use the estuary as a migratory corridor, passing through the estuary quickly and without feeding. Coho salmon spawn from September through March (Hassler 1987, Emmett et al. 1991).

Timing and Use of Estuarine Habitat

Similar to other salmonid species, some coho salmon rely heavily on estuaries as rearing habitat, finding food and refuge from predation, in addition to a migratory corridor and physiological transition zone between freshwater streams and the sea (Thorpe 1994, Aitkin 1998, Clements et al. 2012, Hoem Neher et al. 2013; Table 3). However, there are differences in the timing and use of estuaries for coho salmon compared to other juvenile salmonids.

In most systems, coho salmon spend their first year rearing in freshwater, and as yearlings move quickly to the ocean, spending little time in the estuarine environment (Aitkin 1998, Hassler et al. 1987). Twenty to 30 years ago, researchers thought that juvenile coho salmon that moved downstream during their first year (as sub-yearlings) had been displaced from better rearing habitat upstream by other fry. Only in recent years has it been recognized that instead, some coho salmon were exhibiting an alternative life history strategy that takes advantage of the benefits of rearing in the estuary (Koski 2009). Quinn et al. (2013) found extensive use of the Elwha and Salt Creek estuaries in Washington by coho, prior to smolting, during much of the year, with peak use occurring in September. In Winchester Creek, South Slough, Oregon, Miller and Sadro (2003) found that almost half of a cohort moved into the estuary at less than one year (March–April). Some stayed in the estuary for up to eight months and then migrated back upstream during winter, and sometimes used streams other than their natal stream (Koski 2009). Examples such as these resulted in a paradigm shift in the perception of timing and length of stay in estuaries by salmon, indicating that estuaries were far more important as nurseries for juvenile coho salmon than had previously been realized.

Although some systems have documented long stays of juvenile coho salmon in estuaries, other systems have documented short periods of estuarine use. Thorpe (1994) found that in Yaquina Bay, Oregon, although there may be juvenile fish in the estuary for two to three months, each fish may remain only a few days before entering the ocean. There exists a great amount of variation in estuarine use, often with different overlapping life history strategies. Yearling coho salmon enter the Columbia River Estuary from late April through June or July, peaking in May, and with little indication of growth while moving through the estuary (Dawley et al. 1986, Thorpe 1994). However in Grays River, a tributary to the Columbia River estuary, fry enter in February, and parr are found June through October (Craig 2010, Craig et al. 2014). These sub-yearling fish can spend more than six months in the estuary.

In the Salmon River, Oregon, Jones et al. (2011) found that juvenile coho salmon were observed in the estuary during all months of the year. Yearlings were caught January through June (peaking in April), and residence time in the estuary was on average 13 days (range 2–34 days). Sub-yearlings were caught from February through December primarily in the upper estuary, and residence time ranged between 31 and 147 days (Box 8). Pinnix et al. (2012) found that in the Humboldt Bay estuary, tagged fish entered the estuary in late April through July and stayed well over a month. Wallace and Allen (2009) found yearling coho salmon in the estuary May through July, peaking in May and sub-yearling coho salmon May through October. Yearling coho salmon in the Southern Oregon/Northern California Coast ESU are found in estuaries from late March through June, with numbers peaking in April or May. Residence time can be a few weeks (Moyle et al. 2008). In the Trinity River, California, coho salmon migration downstream is generally at night in the beginning of their journey, with time of day becoming less important as the fish get closer to the estuary (Chase et al. 2012). Seasonal freshwater wetlands have been documented to provide important habitat for young coho salmon (Miller and Sadro 2003, Henning et al. 2007).

Our review of documented habitat use suggests coho salmon use a wide variety of estuarine habitat types (Table 4). In two estuaries of Washington and California, sub-yearling coho salmon were found intertidally early in their life, and as they grew, they moved to more complex substrate with increased cover. Migrating yearlings preferred deep channels with marine influences (Emmett et al. 1991, Hosack et al. 2006, Pinnix et al. 2012). Coho salmon have been shown to use restored estuarine habitat in Chehalis River Estuary, Washington (Miller and Simenstad 1997), such as tidal marsh, indicating that ecological habitat restoration contributes to the recovery of habitat that functions as a nursery.

Prey species of juvenile coho salmon are typical of other salmonid species inhabiting estuaries and include amphipods, mysids, decapod larvae, insects and small fish (McCabe et al. 1983, Fresh and Schroder 1987, Emmett et al. 1991; Table 3). In general, young coho salmon feed on epibenthic prey in shallow intertidal areas and, as they grow, move into pelagic areas with higher salinity (Aitkin 1998). Toft et al. (2007) found that, in Puget Sound, coho salmon feed over cobble and gravel on decapod larvae, amphipods, euphausids and fish larvae throughout the summer. In the Columbia estuary, yearling coho salmon initially feed on insects in the upper estuary and switch to amphipods as they approach the ocean (Thorpe 1994). Sub-yearling coho salmon favor side channels in emergent wetlands and exhibit their highest growth rates in the estuary (Craig et al. 2014), further supporting the nursery role of estuaries for coho salmon.

Predation on juvenile coho salmon is greatest in the lower reaches of the estuary (Clements et al. 2012). Typical predators are bony fish, sharks, birds and marine mammals, with birds accounting for much of the loss (Emmett et al. 1991, Clements et al. 2012, Frechette et al. 2012). In the Columbia estuary, Thorpe (1994) reported heavy predation from Northern squawfish (*Ptychocheilus oregonensis*), and Sebring et al. (2010) reported high rates of predation by cormorants and terns in the same region. Koski (2009) hypothesized that the increased growth rate of coho salmon in the estuary can enable them to quickly

© John Bragg/SSNERR

outgrow their predator's ability to capture them. In Puget Sound, Toft et al. (2007) found that coho salmon use cobble beach, sand beach, riprap, deep riprap and overwater structures, presumably for both finding prey and hiding from predators. In Humboldt Bay, California, Pinnix et al. (2012) found coho salmon smolts used the cover and eddies of deep channels and channel margins more than floating eelgrass mats, or pilings. Estuaries with deep channels, or even smaller thermal refuges, provide relief from heat for juvenile coho salmon, especially during summer months (Richter and Kolmes 2005). Estuaries with a broad and dynamic channel network or large woody debris provide hiding places, as well as reduced flow rates, and create eddies that help retain juvenile coho salmon (Aitkin 1998).

Estuaries also provide a physiological transition zone for juvenile coho salmon during migration: this is a key feature of the nursery function of estuaries (Beck et al. 2001, Sheaves et al. 2014). In Southern Oregon and Northern California, travel through the estuary is slower than through the riverine system, which may give juveniles time to adjust to the changes of smolting and to survive in the ocean (as has been demonstrated in the North Pacific Ocean from studies of coho salmon released from hatcheries (Magnusson and Hilborn 2003)). Juvenile coho salmon can tolerate temperatures from 4–15.2°C and salinities from fresh to euhaline conditions, which are 30–35 ppt (Emmett et al. 1991; Table 3).

Distribution of Documented Presence of Juveniles in Estuaries

Throughout the study area of Washington, Oregon and California, coho salmon have been documented in 49 estuaries (Figure 8), encompassing all four estuarine classes (sound, embayment/bay, riverine estuary and lagoonal estuary) and estuarine sub-classes found along the West Coast (Table 4). In Washington, coho salmon are documented throughout Puget Sound (often in small streams, or even in urban settings) and in six coastal estuaries (Augerot and Foley 2005, Washington DFW 2014). In Oregon, coho salmon have been documented in 14 estuaries, primarily riverine. In California, coho salmon have been documented in 24 estuaries, primarily lagoonal estuaries.

Threats

Although coho salmon are subject to the same threats as Chinook salmon (Table 5), they may be more vulnerable to human perturbation. For example, because of their rigid life cycle (all females spawn in their third year), anthropogenic impacts can extirpate a specific cohort or phenologically distinct population within a stream, as has happened to a number of small coastal California streams (Moyle et al. 2008). In addition, because coho salmon spend an extended period of time in freshwater as juveniles, they are more vulnerable to water quality and quantity perturbations throughout the year, especially in low flow summer periods. Coho salmon also require colder waters, thus may be more susceptible to climate change.

Poor management of land, forest and water all have contributed significantly to habitat loss in rivers along the West Coast (Dawley et al. 1986, Emmett et al. 1991), but likely one of the most crucial and long lasting causes of declining coho salmon populations is the cumulative loss of ecosystem resilience. Bottom et al. (2009) hypothesized that the long, slow decline of wild, native coho salmon was overshadowed by the short-term success of hatcheries that were managed as mass production facilities for salmon harvest during an era of high ocean productivity in the Pacific Northwest. Slow changes to soils and nutrients, loss of biodiversity of prey and loss of freshwater habitat, contributed to the decline of wild coho salmon. As the carcasses of dead salmon provide the primary source of nutrition for the oligotrophic streams in which coho salmon rear, dramatically reduced numbers of returning wild adults no longer provide the amount of nutrients necessary to sustain healthy juvenile populations. Thus, the decline in wild coho salmon populations may be reducing the resiliency of the ecosystem on which these fish depend (Moore et al. 2011). Loss of ecosystem resilience, combined with declines in coho salmon populations, and coupled with changes in ocean conditions, led to the broad, regional collapse of coho salmon fisheries (Bottom et al. 2009).

Within the estuarine environment, sea-level rise will likely lead to a loss of habitat complexity and total habitat available to juvenile coho salmon (Flitcroft et al. 2013). The deterioration of water quality and habitat modification continues to pose threats to coho salmon populations. Increased runoff, containing both organic and inorganic pollutants, also poses a considerable risk to juvenile coho salmon in the estuarine environment (Anderson et al. 2014). Diseases, such as infectious hematopoitic necrosis (IHN), also pose a threat to young coho salmon (Breyta et al. 2013), as do invasive species. Garwood et al. (2010) documented American bullfrog, (*lithobates catesbeianus*) predation on juvenile coho salmon; the one isolated case represents a much larger potential problem, as invasions of American bullfrogs are widespread and overlap the range of coho salmon. Other invasive or subsidized predators (such as the western gull's (*Larus occidentalis*) use of landfills) may also have devastating impacts on imperiled salmon populations (e.g., Osterback et al. 2013).

Shoreline armoring also poses a threat to coho salmon use of estuaries. Recently, a study by Morley et al. (2012) found that armored shorelines tend to have higher substrate temperatures, and the presence of epibenthic invertebrates was ten-fold more abundant on unarmored sites. Other studies have indicated that shoreline modifications that extend into subtidal waters can have significant impacts on the behavior of juvenile coho salmon that is both physically and biologically based (Toft et al. 2007). Coho salmon nomads that spend more time foraging in the estuary are particularly vulnerable to any estuarine changes (Koski 2009).

BOX 8. ESTUARINE REARING IS MORE IMPORTANT FOR COHO SALMON THAN PREVIOUSLY THOUGHT

Historically researchers thought that coho salmon hatched and stayed for one year in their natal streams, and after one year, moved quickly out to sea, with little benefit ensuing from remaining in the estuarine environment. Studies in the past decade have illuminated not only variability in juvenile coho salmon life history, but also the important role that estuaries play for juvenile coho salmon. Jones et al. (2014) identified four juvenile life history strategies that are contributing to the adult population in the Salmon River estuary: 1) One year of rearing in streams before spending a short time in the estuary on their migration to sea; 2) Migrating to the estuary soon after hatching and rearing in the estuary; 3) Migrating to the estuary soon after hatching and then, after several months of estuarine rearing, migrating back to fresh water (not necessarily the natal stream); and 4) Spending the first six months in the natal stream and the next six months rearing in the estuary. Notably, the estuary is important much of the year to juvenile coho salmon of various ages. It should be noted that the Salmon River estuary has undergone extensive habitat restoration within the past 30 years, giving rise to increased availability of wetland habitats, concurrent with the discovery of the diversity of coho salmon life history and estuarine use.

Foraging in the estuary can provide a distinct survival advantage. Hassler (1987) hypothesized that the higher lipid content found in the body fat of coho salmon rearing in the estuary could give them an overwintering advantage compared to stream-reared coho salmon. Jones et al. (2011) found that growth of sub-yearlings in the Salmon River estuary was double that of coho salmon that reared above tidewater.

Estuaries have been documented to provide refuge for coho salmon from predation and environmental stress. Increased growth rates provided by estuarine nurseries have been suggested to decrease predation on coho salmon (Murphy et al. 1988). In Carnation Creek, British Columbia, juvenile coho salmon using the estuary were found to have high survival rates that contributed to the returning adult populations (Hassler 1987), indicating that estuaries potentially provide refuge for coho salmon from predation.

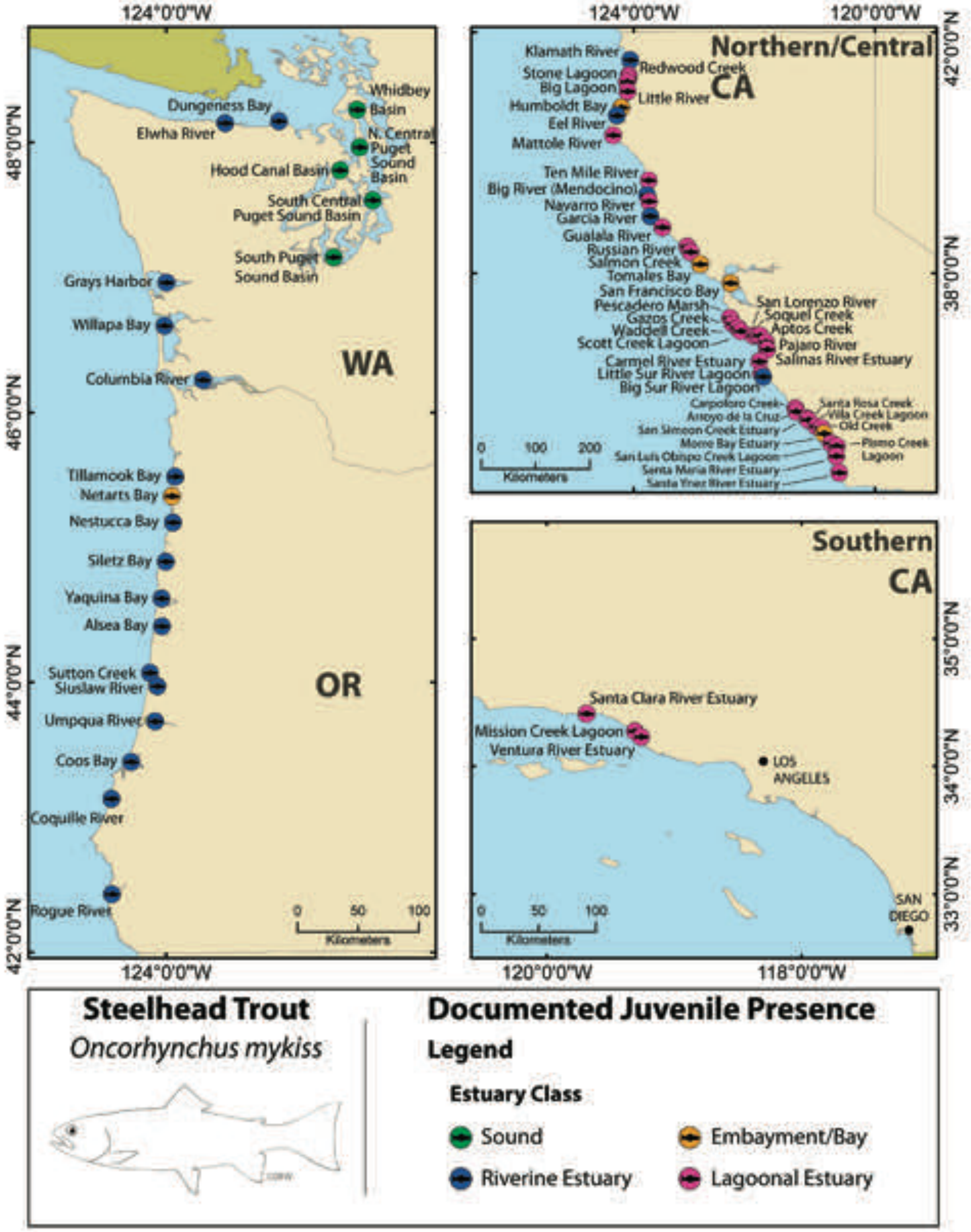


FIGURE 9. STEELHEAD TROUT: Documented juvenile presence in Washington, Oregon and California estuaries.

STEELHEAD TROUT

(*Oncorhynchus mykiss*)

© Morgan H. Bond

Oncorhynchus mykiss express a wide array of life histories ranging from anadromy (i.e., individuals are born in freshwater, migrate to sea to attain adult size, and return to their natal streams to spawn), where they are known as "steelhead", to spending their entire life history within freshwater streams, where they are known as "rainbow trout." Steelhead trout's great life history diversity between these two extremes allows for many different manners of using estuaries. This diversity and plasticity has also presumably allowed the species to persist in natural populations throughout the Northern Pacific Ocean basin. In Asia, steelhead trout spawn in rivers of the Kamchatka peninsula. In North America, steelhead trout spawn in rivers of Alaska in the North to historically as far south as Baja California, Mexico (Moyle 2002, Augerot and Foley 2005; Table 2). Steelhead trout populations in Alaska and northern British Columbia are currently sustainable, as are most populations in Washington (although 19 populations of steelhead trout have been extirpated among the runs of Puget Sound-Georgia Basin, the Upper Columbia River Basin and the coastal populations) (Augerot and Foley 2005). Populations further south are become increasingly threatened. The current range of steelhead trout no longer reaches as far inland on interior river basins, such as the Columbia, Sacramento and San Joaquin, due largely to impassable dams (McEwan 2001, Augerot and Foley 2005). Steelhead trout have suffered many local extirpations south of Point Conception, California and far lower population numbers than historically for the southern end of their range (Moyle 2002). Thirty-nine populations in California either have been extirpated or are at a moderate to high risk of extinction (Augerot and Foley 2005, Moyle et al. 2008). Steelhead trout forage at sea throughout the northern Pacific Ocean Basin predominantly above 40° latitude from North America to Japan (Moyle 2002, Augerot and Foley 2005).

In general, northern populations (e.g., Alaska) of steelhead trout are healthier and southern populations (e.g., Southern California) have suffered more declines and even local extinctions (Augerot and Foley 2005). Thus in Washington, Oregon and California, steelhead trout are managed by NOAA Fisheries under the U.S. Endangered Species Act (ESA) as a collection of Distinct Population Segments (DPS), in which each DPS is discrete and significant to the overall species (USFWS and NMFS 1996). Of the 15 steelhead trout DPSs on the West Coast, one is listed as endangered, nine are listed as threatened and one is listed as a species of concern (Table 8).

TABLE 8. Steelhead trout Distinct Population Segments (DPSs) and their listing status under the U.S. Endangered Species Act.

DPS	Status
Puget Sound	Threatened
Olympic Peninsula	Not Listed
Washington Coast	Not Listed
Upper Willamette River	Threatened
Snake River Basin	Threatened
Upper Columbia River	Threatened
Middle Columbia River	Non-essential
Lower Columbia River	Threatened
Oregon Coast	Species of Concern
Klamath Mountains Province	Not Listed
Northern California	Threatened
Central California Coast	Threatened
California Central Valley	Threatened
South-Central California Coast	Threatened
Southern California	Endangered

In North America, steelhead trout were harvested commercially until the 1930s (Augerot and Foley 2005). Steelhead trout have also long been and still are an important recreational fishery throughout their range, now as catch-and-release in the southern threatened populations (Augerot and Foley 2005). Indigenous tribes also continue to harvest steelhead trout (Augerot and Foley 2005).

Life History and Ecology

Likely due to plasticity in other traits, such as phenology and life history variability, steelhead trout show higher spawning site fidelity than other salmon species. Steelhead trout spawn in smaller stream sections selecting smaller spawning gravel sizes than Chinook salmon. As such, steelhead trout generally spawn in tributaries, but in smaller coastal streams may spawn in the mainstem and potentially near the estuary. Eggs are laid and fertilized, then buried in carefully made nests, which provide protection and oxygen rich water to the eggs and alevin (newly hatched with yolksac still attached). Once steelhead trout emerge from the gravel, they feed and grow in stream habitats, and juveniles may continue to rear in the stream or estuarine habitats for months to several years (Emmett et al. 1991, Moyle 2002, Hayes et al. 2008) and have been documented to move back and forth between the two during this time (Hayes et al. 2011).

Steelhead trout smolts (juvenile downstream migrants preparing for life at sea) that migrate out to sea will do so from age-0 to over three years of age ranging in size from 100–250 mm total length; after 1–4 years at sea, steelhead trout will return to the riverine environment at 350 mm–650 mm total length to their natal stream to spawn (Emmett et al. 1991, Moyle 2002, Bond et al. 2008). There is even variability within the truly anadromous steelhead trout as winter-run steelhead trout migrate upstream in the fall, winter, or early spring, and summer-run steelhead trout migrate upstream early in the spring, summer or early fall, overwinter in deep pools and spawn the following spring or summer (Emmett et al. 1991, Moyle, 2002). Further, some populations (e.g., Klamath River) express a pattern known as “half pounders”, in which juveniles and sub-adults put on most of their growth to adults in estuaries (not necessarily their own) and then overwinter in stream habitats before spawning (Moyle 2002, Moyle et al. 2008). Unlike other Pacific salmon, steelhead trout are iteroparous, meaning they may survive after spawning and return to spawn in as many as five subsequent years, but mortality rates are high such that few fish actually do (Shapovalov and Taft 1954, Moyle 2002). Steelhead trout show remarkable diversity in life history, and post-spawning adults may remain in freshwater, move into the estuary, or migrate back to sea (Augerot and Foley 2005). Adult steelhead trout may express any combination of these repeat spawning migrations over their 8–10-year lifespan (Pauley et al. 1989, Augerot and Foley 2005, Love 2011; Table 2).

Timing and Use of Estuarine Habitat

Throughout their range steelhead trout show a remarkable diversity in the manner and extent of the timing and use of estuarine habitat. In some areas, steelhead trout pass quickly through estuaries into the ocean in a day or so (Clements et al. 2012, Emmett et al. 1991, Dawley et al. 1986, Sandstrom et al. 2012), whereas in other rivers, they migrate to the estuary earlier and stay longer (Wallace and Allen 2012, Hayes et al. 2008). There is even variability within stream systems in the timing and size of entry to the estuary (Shapovalov and Taft 1954), as well as the extent to which individuals use the estuary for rearing (Bond et al. 2008, Hayes et al. 2011). Hayes et al. (2011) documented steelhead trout in Scott Creek, California, migrating back and forth several times between the lagoon and upstream habitat within and among years seemingly in response to either elevated growth rate or sub-optimal water quality conditions within the lagoon relative to upstream habitats.

The timing of estuarine use by steelhead trout varies by latitude and seems dependent on many physical and chemical factors. In the Columbia River Basin, yearling steelhead trout migrate downstream in the spring, primarily April and May (Haeseker et al. 2012). In two coastal Oregon rivers (Nehalem river and Alsea river), Clements et al. (2012) found that steelhead trout moved into the estuary in the beginning of April (peaking in the end of April) and spent less than a day in the estuary. In many estuaries of California, juvenile steelhead trout may be found throughout the year (Moyle 2002), but individuals may vary dramatically in their timing and duration within the estuary (Shapovalov and Taft 1954, Moyle 2002, Hayes et al. 2001). Klamath Mountain Province DPS winter-run juveniles migrate to the estuary starting in April and May and peaking in summer, whereas summer-run steelhead trout from this DPS rear 1–2 years in freshwater and likely move through the estuary quickly (Moyle et al. 2008). Northern California Coastal DPS juvenile winter-run steelhead trout of all sizes will migrate to the estuary during high flows typically peaking in April or May and smaller juveniles follow in the summer (Moyle et al. 2008). In smaller seasonally closed lagoonal estuaries, fish will not migrate to the ocean until the fall, when the sand bar is breached (Moyle et al. 2008). California Central Valley DPS steelhead trout typically spend up to two years rearing in freshwater, with winter- run steelhead trout entering the estuary from December through August (McEwan 2001). In the Russian River, a seasonally closed lagoonal estuary in the California Central Coast DPS, Fuller (2011) found that steelhead trout spent from four to 121 days in the estuary. In Scott Creek, a seasonally closed lagoonal estuary of central California, Hayes et al. (2011) found that steelhead trout larger than 150 mm total length migrated downstream during February and March and entered the ocean without spending time in the estuary, smaller fish migrated from April through June and reared in the estuary, and the largest smolts (greater than 190 mm total length) had reared in the estuary the previous summer.

Estuaries can serve as important foraging areas and refugia, and are importation transition zones for the physiological changes that steelhead trout go through in preparation for ocean survival (Thorpe 1994, Myrick and Cech 1998, Aitkin 1998, Hayes et al. 2011, Clements et al. 2012). Similar to other salmonids, steelhead trout use a variety of habitats within the estuarine environment (Table 4). Juvenile steelhead trout in the estuary can be found using woody debris for cover, if available (Wallace and Allen 2009). Other forms of cover and refuge from predation that steelhead trout use in estuaries include undercut banks, dense submerged and emergent vegetation, overhanging vegetation and water depth (Wallace and Allen 2009). They rely primarily on a detrital food web, feeding on benthic and pelagic organisms, including insects, amphipods, copepods, isopods, decapods, other small crustaceans and small fish (Moyle 2002, Fresh and Schroder 1987, Emmett et al. 1991, Bond et al. 2008). In general, young steelhead trout feed on epibenthic prey in shallow intertidal and as they grow move into pelagic areas with higher salinity (Aitken 1998).

Predation on young steelhead trout is heaviest in the lower reaches of the estuary, sometimes reaching 50% (Romer et al. 2013). Typical predators are bony fish, sharks, birds and marine mammals, with birds accounting for much of the loss (Emmett et al. 1991, Frechette et al. 2012, Osterback et al. 2013). Juvenile steelhead trout can find refuge from predation through cover and accelerated growth in the estuarine environment. Clements et al. (2012) found over 50–60% mortality rates in two coastal Oregon River estuaries and hypothesized this was likely due to predation.

Estuaries have been found to be a more productive environment than upstream in the freshwater rivers that feed into them (Healey 1991, Miller and Sadro 2003, Bond et al. 2008). Accelerated growth rates were found for steelhead trout that spend more time in the estuary in the Russian River (Fuller 2011), as well as in for Scott Creek, with juveniles almost doubling in length (Bond et al. 2008, Hayes et al. 2008; and see Box 9).

As with other anadromous fish, the salinity gradient in the estuarine environment provides an important transition zone in preparation for life at sea. Juvenile steelhead trout can tolerate temperatures from 0–27°C, although very low temperature less than 4°C and very high temperatures greater than 24°C can be lethal if the fish is not acclimated (Moyle 2002, Myrick and Cech 2004) (Summary Table 2). As juvenile steelhead trout grow larger, their tolerance to salinity is increased (Johnsson and Clarke 1988).

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile steelhead trout have been documented in estuaries of the study area from Puget Sound south to the Ventura River estuary. We compiled records of juvenile steelhead trout in 66 different estuaries throughout Washington, Oregon and California—five locations within Puget Sound, five estuaries along the Washington coast, 13 in Oregon, and 43 in California (Figure 9). Throughout their range, juvenile steelhead trout use a wide variety of different estuarine classes (sound, embayment/bay, riverine estuary and lagoonal estuary) found along the West Coast. In Washington and Oregon, they are primarily documented in riverine estuaries of the open coast and within Puget Sound. In California, steelhead trout are found in predominantly lagoonal estuaries.

Threats

As a fish species that spends its life in rivers, estuaries and the ocean, steelhead trout are subject to many human-induced threats (Table 5). Dams, clearcut logging, erosion and human alterations of freshwater flow all have contributed significantly to habitat loss in rivers along the West Coast (Emmett et al. 2011, Bottom et al. 2005a). For example, impassable dams block 80% of the historical spawning habitat that was once available to the California Central Valley DPS, and block all habitat for 38% of populations that spawned historically in the California Central Valley (Lindley et al. 2006). In recent years a number of dam removal projects (Yakima, Elwha and the Carmel rivers) are restoring critical steelhead trout habitat. Throughout the Central Valley, California, the condition of habitat used by steelhead trout is less than ideal, due to water diversion or withdrawal, elimination of riparian habitat, water pollution and disruption of the provision of gravel in spawning areas (Lindley et al. 2006). Fish passage blocked by dams has been shown to alter the expression of life history strategies and reduce genetic variation (McClure et al. 2008).

Hatcheries have produced steelhead trout that mature early with reduced genetic variability (Pauley et al. 1986a, Nielsen et al. 1998). Because they mature early and return from the ocean earlier than wild fish, hatchery-raised steelhead trout can reduce the presence of wild steelhead trout in the same river (Pauley et al. 1986a). Hatchery-raised steelhead trout also interbreed with wild populations, reducing their genetic variability, and with it the local adaptive ability that has evolved among these unique populations (Nielsen et al. 1998).

Increased runoff, containing both organic and inorganic pollutants, poses a considerable risk to young steelhead trout migrating out to sea (Anderson et al. 2014). A recent study investigating the effects of pyrethroid insecticides, such as bifenfrin, from urban runoff, indicate they may reduce fecundity in female steelhead trout (Forsgren et al. 2013). Steelhead trout respond to changes in salinity and temperature in preparation for transitions between fresh and salt water (Hayes et al. 2011), thus reduced flows can often have a significant impact on young steelhead trout transitioning to the ocean, and could lead to delayed mortality (Haeseker et al. 2012). Seasonally closed lagoonal estuaries can undergo dramatic changes in salinity, temperature and dissolve oxygen, making them more susceptible to anthropogenic change (Fuller 2011).

Sea-level rise will continue to reduce estuarine habitat through inundation and displacement, changing the amount and complexity of habitat available in estuaries (Flitcroft et. al. 2013). Diseases, such as the infectious hematopoitic necrosis virus (IHNV), also pose a threat to young steelhead trout, with recorded mortality rates reaching 90% (Breyta et al. 2013). In larger estuarine systems, such as the San Francisco Bay Delta, large interannual variations in steelhead trout populations have been attributed to the complexity of interrelated factors including flow, temperature, turbidity, climate change, diel movements, water withdrawals and predator abundance (Singer et al. 2012).

© Morgan H. Bond

© Matthew S. Merrifield/TNC

BOX 9. INCREASED GROWTH AND SURVIVAL OF STEELHEAD TROUT REARED IN A SEASONALLY CLOSED ESTUARY

Seasonally closed lagoonal estuaries may play an important nursery role for California steelhead trout populations. In smaller, rain-fed watersheds lagoonal estuaries remain open in the winter due to high streamflows and north winter storm swells, but in summer, low base streamflow and smaller south swells may form a sand bar isolating the stream from the ocean. Lagoonal estuaries may close intermittently throughout a year, or even be continually closed for several years. The warm productive waters of closed lagoons may provide high growth potentials to fish. The great diversity and plasticity in life history of steelhead trout allows for populations to persist in the face of potentially dramatic physical and temporal variability (Behnke 2002, Moyle 2002) such as the closure dynamics of lagoonal estuaries.

One excellent case study documented a nursery role in Scott Creek, California, a seasonally closed lagoon that provides elevated growth rates to juvenile steelhead trout relative to freshwater habitats, thereby increasing survival at sea to reproduction (Bond et al. 2008, Hayes et al. 2008). Although the hundreds of other West Coast lagoonal estuaries may also provide nursery habitat, increased growth or higher proportional contribution to returning steelhead trout adults has only been documented in a few (e.g., Atkinson 2010, Zedonis 1992, Fuller 2011). Bond et al. (2008) found that although a small percentage of juvenile steelhead trout reared in the estuary, those that did comprised over 87% of the returning adults, highlighting the critical nursery role the seasonally closed lagoonal estuary plays in the maintenance of the steelhead trout population of Scott Creek. Although the nursery function for steelhead trout has been documented well for Scott Creek, more studies are needed to determine if other seasonally closed lagoonal estuaries throughout the West Coast play the same critical role.

TABLE 2. General life-history characteristics of 15 focal species. Information applies to all life-history stages and all habitats on the U.S. West Coast, including non-estuarine habitats.

	Dungeness crab	Bay shrimp
Range	Pribiloff Islands, AK to Santa Barbara, CA (Jensen 2014)	Resurrection Bay, AK to San Diego, CA (Jensen 2014)
Depth	Intertidal to 420 m (Emmett et al. 1991)	Intertidal to 180 m (Emmett et al. 1991)
Maximum size	190 mm CW (female), 254 mm CW (male) (Jensen 2014)	110 mm (Emmett et al. 1991)
Maximum age	8–10 years (Emmett et al. 1991)	2.5 years (female), 1.5 years (male) (Emmett et al. 1991)
Age/size at maturity	2 years/ 100 mm CW (female), 2 years/ 116 mm CW (male) (Emmett et al. 1991)	1–1.5 years/ 48 mm (female; 55–60 mm in San Francisco Bay), 1–1.5 years/ 34 mm (male) (Emmett et al. 1991)
Spawning season	Eggs extruded Sept–Mar. Varies by region, but generally fall to winter. External incubation lasts 64–128 days, temperature dependent (Gunderson et al. 1990, Emmett et al. 1991)	Variable, dependent on location. Can have two periods: Dec–Mar, Apr–Aug in Yaquina Bay, OR. One long spawning period Mar–Sept in San Francisco Bay (Emmett et al. 1991)
Planktonic duration	90–120 days, December to March, dependent on temperature (Armstrong et al. 2003, Emmett et al. 1991)	21 days (Siegfried 1989, Emmett et al. 1991)
Larval distribution	Both nearshore and coastal regions, within 16 km of shoreline (Armstrong et al. 2003, Emmett et al. 1991)	Surface waters in early stages to bottom in shallow waters toward late development (Siegfried 1989)
Size at settlement	6–8 mm CW (Gunderson et al.1990, Brown and Terwilliger 1992)	5–10 mm (Siegfried 1989)
Commercial fishery	Alaska to central California (Emmett et al. 1991)	Large historical fishery, which has declined significantly because of difficulty in processing and demand (Siegfried 1989)
Recreational fishery	Yes, but data are limited. Substantial tribal fishery	Large recreational bait fishery (Siegfried 1989)

	Leopard shark	Bat Ray	Green sturgeon
Range	Samish Bay, WA to Mazatlan, Mexico (Ebert 2003, Farrer 2009)	Yaquina Bay, OR to Baja California and Gulf of California (Miller and Lea 1972, Love 2011)	Kuskokwiim Bay, Bering Sea to Bahía de San Quintín, Baja California, Mexico (Love 2011)
Depth	Intertidal to 91 m (Ebert 2003)	Intertidal to 108 m (Morris et al. 1996)	Intertidal to 110 m (Erickson and Hightower 2007)
Maximum size	1980–2130 mm TL (Kusher et al. 1992, Miller and Lea 1972)	~1800 mm DW (Eschmeyer et al. 1983)	2700 mm TL (Davies 2004, Beamesderfer et al. 2007)
Maximum age	24–30 years (Miller and Lea 1972)	~24 years (Martin and Cailliet 1988b)	53 years (Farr et al. 2002)
Age/size at maturity	10–15 years/ 1050–1350 mm TL (female), 7–13 years/ 1000–1050 mm TL (male) (Kusher et al. 1992)	~5 years/ ~880 mm DW (female), 2–3 years/ ~600 mm DW (male) (Martin and Cailliet 1988a)	16–27 years/ 1440–2020 mm TL (female) (Beamesderfer et al. 2007), 13–18 years/ 1200–1850 mm TL (male) (Beamesderfer et al. 2007)
Spawning season	Mar–Sept, peaking in Apr and May in Elkhorn Slough and San Francisco Bay, elsewhere Mar–July (Ackerman 1971, Talent 1985, Smith and Abramson 1990)	Mar–June, peaking in Apr and May in San Francisco Bay and Elkhorn Slough, and approximately the same time in other bays and estuaries in California (Miller and Lea 1972, Martin and Cailliet 1988b)	Apr–June, peaking in May (Beamesderfer et al. 2007)
Planktonic suration	Not applicable to this species (live bearing)	Not applicable to this species (live bearing)	Eggs and larvae are all riverine, there is no planktonic phase (Beamesderfer et al. 2007)
Larval distribution	Not applicable to this species (live bearing)	Not applicable to this species (live bearing)	Rivers (Beamesderfer et al. 2007)
Size at settlement	Not applicable to this species (live bearing)	Not applicable to this species (live bearing)	Larvae metamorphose around 45 days and 60–80 mm (Deng et al. 2002)
Commercial fishery	Minimal commercial fishing effort, almost all commercial catch is incidental and in California (Carlisle and Smith 2009)	Bycatch in demersal trawls, longlines, and gillnets in California. Historical fishery in Humboldt Bay to reduce perceived predation pressure of bat rays on oysters, fishery was closed (Gray et al. 1997, Cailliet and Smith 2006)	Bycatch in salmon and white sturgeon fisheries, mainly in Columbia River estuary, Klamath River, Willapa Bay and Grays Harbor, and coastal fisheries in Washington (Love 2011, Beamesderfer et al. 2007, St. Pierre and Campbell 2006)
Recreational fishery	Primary source of fishing mortality, primarily in California (Carlisle and Smith 2009)	Commonly caught by recreational fishermen in California targeting white sturgeon, also a target of sustenance fishery by native tribes (Cailliet and Smith 2006, S. Fluharty pers. comm.)	It is illegal to fish for green sturgeon recreationally (Roberts and Gingras 2008)

TABLE 2. continued: General life-history characteristics for all life-history stages.

	Chinook salmon	Coho salmon	Steelhead trout
Range	Japan north to Chukchi Sea and Alaska south to the San Joaquin River, California (Moyle 2002, Augerot and Foley 2005)	Japan north to Chukchi Sea and Alaska south to the San Lorenzo River, California (Moyle 2002)	Kamchatka north to Chukchi Sea and Alaska south to northern Baja California (Augerot and Foley 2005)
Depth	Intertidal to 344 m, commonly to 150 m (Love 2011)	Intertidal to 240 m, most ~ 10 m (Love 2011)	Intertidal to 20 m (Love 2011)
Maximum size	1500 mm TL (Augerot and Foley 2005)	950 mm TL (Augerot and Foley 2005)	1000 mm TL (Augerot and Foley 2005)
Maximum age	8+ years (Love 2011)	3+ years (Love 2011)	9 years (Emmett et al. 1991)
Age/size at maturity	3–6 years (Augerot and Foley 2005)	2–4 years (Augerot and Foley 2005)	4–7 years (Augerot and Foley 2005)
Spawning season	Any month of the year, depending on life history (Moyle 2002)	Nov to March depending on location (Moyle 2002)	Nov to May (Shapovalov and Taft 1954, Love 2011)
Planktonic duration	Not applicable to this species. Eggs are laid in nests in streams.	Not applicable to this species. Eggs are laid in nests in streams.	Not applicable to this species. Eggs are laid in nests in streams.
Larval distribution	Alevin, or larval salmon reside within nests within streams.	Alevin, or larval salmon reside within nests within streams.	Alevin, or larval salmon reside within nests within streams.
Size at settlement	Not applicable to this species	Not applicable to this species	Not applicable to this species
Commercial fishery	The exclusive economic zone and territorial waters of AK, Canada, WA, OR and CA—subject to harvest management rules and closures	The exclusive economic zone and territorial waters of AK, Canada, WA, and OR to Cape Falcon—subject to harvest management rules and closures	None
Recreational fishery	The exclusive economic zone and territorial waters of AK, Canada, WA, OR and CA, select rivers—subject to hatchery only, harvest management rules and closures. Substantial tribal fishery	The exclusive economic zone and territorial waters of AK, Canada, WA and OR—hatchery only—subject to seasons and specific closures. CA—closed. Substantial tribal fishery	Select streams of AK, Canada, WA and OR; CA—hatchery only and catch and release of wild—subject to hatchery only, seasons and closures. Substantial tribal fishery

	California halibut	English sole	Starry flounder
Range	Quillayute River, northern WA to Almejas Bay, Baja California, Mexico (Tanaka 2013)	Bering Sea and Aleutian Islands, Alaska to Bahia San Cristobal, Baja California Sur (Miller and Lea 1972)	In western Pacific: Bering Sea and Aleutian Islands to Los Angeles, California, although rare south of Point Conception (Orcutt 1950, Cailliet et al. 2000, Ralston 2005, McCain et al. 2005)
Depth	Intertidal to 200 m (Emmett et al. 1991)	Intertidal to 550 m, but primarily in depths <250 m (Emmett et al. 1991)	Intertidal to 375 m although most in waters less than 150 m deep (Cailliet et al. 2000)
Maximum size	1500 mm TL (Miller and Lea 1972)	560 mm TL (Miller and Lea 1972)	910 mm TL (Orcutt 1950)
Maximum age	~30 years (female) (Love 1996)	~22 years (Love 1996)	17 years (female), 24 years (male) (Campana 1984)
Age/size at maturity	2–7 years/ 360–590 mm TL (female), 1–3 years/ 190–320 mm TL (male) (Tanaka 2013)	3–5 years/ 260–350 mm TL (female), 2–3 years/ 210–290 mm TL (male) (Love 1996, McCain et al. 2005)	3–6 years/ 240–440 mm TL (female), 2–4 years/ 220–360 mm TL (male) (Cailliet et al. 2000, McCain et al. 2005)
Spawning season	Year-round w/ peaks mid-winter (Jan/Feb), summer (June/July), fall (Sept/Oct) (Tanaka 2013)	Variable, but most abundant Dec–Apr (McCain et al. 2005)	Nov–Feb in central CA; Feb–Apr off Washington (Cailliet et al. 2000)
Planktonic duration	Temperature dependent: 20–29 days at 18.3–21.9°C and 35–42 days at 16°C (Emmett et al. 1991)	2–4 months (Rosenburg and Laroche 1982, Laroche et al. 1982)	~2 months (Orcutt 1950)
Larval distribution	Upper 30 m of water column and within 6 km of shore (Moser and Watson 1990)	Found primarily in waters less than 200 m deep (Laroche and Richardson 1979)	Epipelagic, found primarily nearshore (within 37 km) and in estuaries (McCain et al. 2005)
Size at settlement	12–15 mm TL (Haaker 1975, Allen 1988)	18–22 mm SL (Misitano 1976, Laroche and Richardson 1979)	Metamorphosis occurs at 10–12 mm TL (McCain et al. 2005)
Commercial fishery	Bodega Bay to Baja California (Maunder et al. 2011)	British Columbia to California (Stewart 2007)	Captured by bottom trawl fishery (Ralston 2005)
Recreational fishery	Bodega Bay to Baja California, small fishery in Humboldt Bay (Bloeser 2000, Maunder et al. 2011)	None	Important recreational species in some areas (Ralston 2005)

TABLE 2. continued: General life-history characteristics for all life-history stages.

	Brown rockfish	Staghorn sculpin
Range	Northern Gulf of Alaska (Prince William Sound) to central Baja California (Bahia San Hipolito) (Miller and Lea 1972, Love et al. 2002)	South Bearing Sea to San Quintin Bay, Baja California (Miller and Lea 1972, Eschmeyer et al. 1983.)
Depth	<1 to 135 m (Love et al. 2002)	Intertidal to 275 m (Miller and Lea 1972, Love 2011), common to ~9 m (Love 2011)
Maximum size	560 mm TL (Love et al. 2002)	480 mm TL (Love 2011) 305 mm TL (Miller and Lea 1972) 460 mm TL (Hart 1973)
Maximum age	~34 years (Love et al. 2002)	10+ years (Weiss 1969, Love 2011)
Age/size at maturity	First maturity between 190–160 mm TL (2–3 years) with 50% maturity at 250–310 mm TL (4–5 years) and all fish mature by 380 mm TL (10 years) (Wyllie-Echeverria 1987, Reilly et al. 1994, Cailliet et al. 2000, Love et al. 2002)	End of first year (Love 2011) 110 mm SL–122 mm TL (male; Jones 1962, Love 2011) 120–153 mm TL (female, Jones 1962)
Spawning season	Dec–Aug with peak spawning varying with latitude (Cailliet et al. 2000, Love et al. 2002)	May occur throughout the year, with peak timing varying across the range (Love 2011). In San Francisco Bay, peak spawning occurs in Jan and Feb (Jones 1962, DeVlaming et al. 1984).
Planktonic duration	2–3 months (Cailliet et al. 2000, Love et al. 2002)	Up to ~ 8 weeks (Matarese et al. 1989)
Larval distribution	planktonic (Moser 1996, Baxter et al. 1999, Cailliet et al. 2000, Love et al. 2002)	Freshwater through near offshore (Jones 1962, Tatso 1975, Moyle 2002)
Size at settlement	18–25 mm TL (West et al. 1994)	15–20 mm TL (Matarese et al. 1989)
Commercial fishery	Important hook-and-line species for the commercial live-fish fishery in California (Stein and Hassler 1989, Love et al. 2002)	Minor bait fishery (Love 2011)
Recreational fishery	Puget Sound and Bodega Bay to Northern Baja California (Love et al. 2002)	Taken for bait (Love 2011)

	Shiner surfperch	Pacific herring
Range	Port Wrangell, southeast Alaska to Bahía de San Quentín, Baja California Norte, Mexico (Eschmeyer and Herald 1983)	North Pacific/Arctic-circumboreal. Eastern Pacific: Cape Bathurst, Beaufort Sea to Ensenada, Mexico. Arctic: Coronation Gulf, Canada to Chukchi Sea to Russia. Western Pacific: Toyama Bay, Japan to Yellow Sea (Emmett et al. 1991)
Depth	Surface to 140 m (Miller and Lea 1972)	High intertidal to 150 m (Emmett et al. 1991)
Maximum size	203 mm TL (Baltz 1984)	460 mm TL (Love 2011)
Maximum age	7 years (Baltz 1984)–9 years (unconfirmed)	19 years (Emmett et al. 1991)
Age/size at maturity	1 year/ 82 mm TL (female) (Baltz 1984)	130–260 mm LT, 2–3 years California, 3–4 years Washington (Emmett et al. 1991)
Spawning season	Varies with latitude; Apr–July (Odenweller 1975, Bayer 1985)	Variable, Nov in southern range, Aug in northern range. CA: Peaks in Dec and Jan (Emmett et al. 1991)
Planktonic duration	Not applicable to this species (live bearing)	2 to 3 months (Emmett e al. 1991)
Larval distribution	Not applicable to this species (live bearing)	Tend to stay in shallow embayments in estuaries where hatched (Emmett et al. 1991)
Size at settlement	34–43.7 mm TL (Wilson and Millemann 1969, Wang 1986, via Emmett et al. 1991)	35–150 mm TL (Emmett et al. 1991)
Commercial fishery	Minor bait fishery (Emmett et al. 1991)	Fished within its entire range, comprises a major fishery for roe and adults (Emmett et al. 1991)
Recreational fishery	Incidental and bait fishery (Eschmeyer and Herald 1983)	Primarily caught for using as a bait fish for salmon (Emmett et al. 1991)

TABLE 3. Juvenile life-history characteristics of 15 focal species in West Coast estuaries.

	Dungeness crab	Bay shrimp
Geographic range of estuarine residence	Aleutians, Alaska to Santa Barbara, California (Jensen 1995, Armstrong et al. 2003)	Entire range (Siegfried 1989)
Temperature range	Optimal: 10–14°C, Mortality occurs >20°C (Pauley et al. 1986b, Emmett et al. 1991)	5.1–21.3°C (Emmett et al. 1991)
Salinity range	Larvae: 25–30 ppt, Adults 15–36 ppt, Juveniles: N/A (Pauley et al. 1986b, Pauley et al. 1989, Emmett et al. 1991)	0.1–34.2 ppt (Siegfried 1989, Emmett et al. 1991)
Dissolved oxygen	No information	No information
Estuarine types used	Coastal embayments, estuaries, lagoons, sloughs (Emmett et al. 1991)	Coastal embayments, estuaries, lagoons, sloughs, near rivers (Siegfried 1989)
Preferred estuarine habitat(s)	Subtidal channels, intertidal mudflats are preferred, also use *Zostera* beds, oyster beds, and macroalgal beds (Rooper et al. 2002, Holsman et al. 2006)	Prefer low salinity, channels and mudflats muddy to sandy (Emmett et al. 1991, Siegfried 1989)
Timing of estuarine residence	Apr to June (Gunderson et al. 1990, Armstrong et al. 2003). But can be as early as mid-Mar in central CA (CDFW pers.obs.), or as late as Sept in OR (Roegner et al. 2007)	Primarily spring and summer, but can be all year (Emmett et al. 1991)
Duration of estuarine residence	2–3 years (Gunderson et al. 1990, Higgins et al. 1997)	>1 year (Emmet et al. 1991)
Size range estuarine residence	6–100 mm CW (females), 6–130 mm CW (males) (Gunderson et al. 1990, Higgins et al. 1997, Brown and Terwilliger 1992). CW—carapace width	All sizes (Emmett et al. 1991)
Prey of juveniles	Fish (sandlance, sanddab, lingcod, shinerperch), shrimp (*Crangon*, *Callianasa*), Bivalves (*Mya*, *Macoma*), barnacles, smaller crustaceans (Stevens et al. 1982)	Mysids, amphipods, bivalves, foramanifera, isopods, copepods, ostracods, plants (Wahle 1985, Emmett et al. 1991)
Predators on juveniles	Crabs (cannibalistic), fish (sculpins, starry flounder, English sole, rock sole, lingcod, cabezon, wolf-eel, rockfish, sturgeon, sharks, skates, sea otters, and octopus (Stevens et al. 1982, Emmett et al. 1991, Fernandez et al. 1993, Armstrong et al. 1995)	Shrimp (cannibalistic), fish (striped bass, brown smoothound, bat ray, sturgeons, sculpins, sand sole), harbor seal, and Dungeness crab (Emmett et al. 1991, Gray et al. 1997)

	Leopard shark	Bat Ray	Green sturgeon
Geographic range of estuarine residence	Humboldt Bay, CA to San Diego, CA (Talent 1985)	Humboldt Bay, CA—San Pedro Bay, CA (Talent 1985, Ebert 2003, Gray et al. 1997)	British Columbia (Skeena River)—San Francisco Bay, CA (Beamesderfer et al. 2007)
Temperature range	No information	Larger juveniles sensitive to higher temperatures (14–20°C) (Hopkins and Cech 1994)	Optimal temperatures for sturgeon <1 year are 15–19°C (Mayfield and Cech 2004)
Salinity range	Larger juveniles adversely affected by reduced salinity levels (20.7–27.6 ppt) (Dowd et al. 2010)	Sensitive to reduced salinity (<25 ppt) (Meloni et al. 2002)	No information
Dissolved oxygen	No information	No information	No information
Estuarine types used	Coastal embayments, estuaries, lagoons, sloughs (Carlisle and Smith 2006)	Bays and sloughs (Cailliet and Smith 2006 (IUCN))	Bays, estuaries (Beamesderfer et al. 2007, Moser and Lindley 2007, Lindley et al. 2008)
Preferred estuarine habitat(s)	Intertidal mudflats, tidal creeks, eelgrass beds in central and Northern California, shallow surf zone in southern California (Carlisle and Starr 2009, Barry and Cailliet 1981, Smith 2001)	No information	No information
Timing of estuarine residence	Seasonally during the spring and summer, departing for coastal habitats during the late fall and winter (Carlisle and Smith 2009, Smith 2001, Hopkins and Cech 1993, Ebert 2003)	Spring, summer and fall (Talent 1985)	1–4 years in estuaries/lower rivers as juveniles, during summer and fall as adults (Beamesderfer et al. 2007, Moser and Lindley 2007, Lindley et al. 2008)
Duration of estuarine residence	Unknown, but most leopard sharks are seasonally abundant during spring and summer (Ebert 2003)	No information	1–4 years in estuaries/lower rivers as juveniles, during summer and fall as adults (Beamesderfer et al. 2007, Moser and Lindley 2007, Lindley et al. 2008)
Size range estuarine residence	Newborn to adults reside in estuaries for several months to years (Carlisle and Smith 2006, Carlisle and Starr 2009, Ebert 2003)	Newborn to adults use estuaries for an unknown period of time	Juveniles leave freshwater/estuarine habitats for marine habitats at 30–80 cm TL (Beamesderfer et al. 2007)
Prey of juveniles	Fat innkeeper worms, crabs, polychaetes (Kao 2000)	Crustaceans, molluscs, polychaete (Gray et al. 1997, Barry et al. 1996, Talent 1982)	Opportunistic benthic feeders. Diet includes various invertebrates and fish (St. Pierre and Campbell 2006, Dumbauld et al. 2008)
Predators on juveniles	Elasmobranchs (Smith 2001, Miller and Lea 1972)	Elasmobranchs, pinnipeds (Ebert 1989, Ebert 2003)	No information

TABLE 3. continued: Juvenile life-history characteristics in West Coast estuaries.

	Chinook salmon	Coho salmon	Steelhead
Geographic range of estuarine residence	Asia and AK, south to San Francisco Bay, CA (Augerot and Foley 2005)	Asia and AK, south to Scott Creek, CA (Moyle 2002, Shapovalov and Taft 1954)	Kamchatka and Alaska, south Ventura River, CA (Augerot and Foley 2005)
Temperature range	5–22°C (Moyle 2002)	4.0–15.2°C (Emmett et al. 1991)	0–27°C (Moyle 2002)
Salinity range	Not found explicitly for estuary, presumably freshwater to euhaline	Freshwater to euhaline (Emmett et al. 1991)	Juvenile salinity tolerance is determined by size and water temp. Tolerance increases with size (Johnsson and Clark 1988)
Dissolved oxygen	Dissolved oxygen levels below 4 mg/L are avoided (Emmett et al. 1991)	Dissolved oxygen levels below 4mg/l reduce food consumption, conversion and growth (Emmett et al. 1991, Ruggerone 2000, Wallace and Allen 2009)	Species susceptible to changes in temperature, dissolved oxygen, and turbidity (Emmett et al. 1991)
Estuarine types used	All types with a fresh water stream at the head	All types with a fresh water stream at the head	All types with a fresh water stream at the head
Preferred estuarine habitat(s)	Intertidal to pelagic, tidal flats, emergent vegetation, flooded fields, eelgrass, deep channels, sloughs overhanging cover, undercut banks (Emmett et al.1991, Beauchamp et al. 1983, Moyle et. al. 2008)	Intertidal to pelagic (Emmett et al. 1991) eelgrass, oyster beds (Hosack et al. 2006), large wood, off channel habitats, sloughs (Koski 2009, Miller and Sadro 2003, Wallace and Allen 2009)	Intertidal to pelagic, emergent vegetation, overhanging cover, undercut banks, large wood (Wallace and Allen 2009)
Timing of estuarine residence	Varies by region, peaking in spring and summer (Emmett et al.1991, Beauchamp et al.1983, Dawley et al. 1986)	Throughout the year depending on latitude and life history, generally peaking in Spring (Emmett et al. 1991, Koski 2009, Miller and Sadro 2003, Wallace and Allen 2009)	Throughout the year, peaking in spring (Love 2011)
Duration of estuarine residence	Days to months depending on location and life history (Dawley et al. 1986, Healey 1991)	From 1 day to 1 year depending on location and life history (Emmett et al. 1991, Hoem Neher et al. 2013, Pinnex et al. 2012, Clements et al. 2012)	From 1 day to multiple years (potentially intermittently) depending on location and life history (Dawley et al. 1986, Hayes et al. 2008, Wallace and Allen 2009, Fuller 2011, Clements et al. 2012, Romer et al. 2013)
Size range estuarine residence	40–140 mm TL (Bottom et al. 2005b)	55–170 mm FL (Wallace and Allen 2009)	40–300 mm TL (Shapovalov and Taft 1954)
Prey of juveniles	Amphipods, copepods, mysids, insects, decapod larvae and fish (Emmett 1991)	Amphipods, copepods, mysids, insects, decapod larvae, larvae and juveniles fish (Emmett et al. 1991, Fresh and Schroder 1987)	Amphipods, copepods, mysids, insects, decapod larvae and fish (Moyle 1976, Fresh and Schroder 1987)
Predators on juveniles	Fishes, birds and marine mammals (Emmett 1991)	Fishes, birds and marine mammals (Emmett et al. 1991, Clements et al. 2012, Frechette et al. 2012, Osterback et al. 2013)	Fishes, birds and marine mammals (Emmett et al. 1991, Frechette et al. 2012, Osterback et al. 2013)

	California halibut	English sole	Starry flounder
Geographic range of estuarine residence	Humboldt Bay, CA (Barnhart et al. 1992) to southern Baja California (Love 1996), but, rare or absent from estuaries north of Bodega Bay	Gulf of Alaska to San Pedro Bay, CA (Monaco et al. 1990), but rare in estuaries south of Pt. Conception	Aleutians, AK (Love 1996) to San Antonio Creek Estuary, CA (AEG 2006)
Temperature range	Smaller juveniles tolerated a wider temperature range (16–28°C) than larger juveniles (~18–22°C), higher growth rates for small juveniles reared at 20–28°C than at 16°C (Gadomski and Caddell 1991, Madon 2002)	Wide temperature tolerance of 9–21°C (Rooper et al. 2003). Significant reduction in growth rate at 17.5°C (Yoklavich 1982). Upper lethal limit of 26.1°C (Ames et al. 1978)	Wide thermal tolerance (Emmett et al. 1991), but seem to prefer warmer waters. In San Francisco Bay, age–0 fish were collected from waters ranging from 8–23°C (Baxter et al. 1999)
Salinity range	Polyhaline to euhaline waters (Emmett et al. 1991). Smaller juveniles tolerated a wider range of salinities (8–34 ppt) than larger juveniles (especially diluted salinities) (Madon 2002)	Mesohaline to euhaline waters (Emmett et al. 1991), density decreased with decreasing salinity especially for salinity less than 18 ppt (Rooper et al. 2003)	Euryhaline—juveniles found in all salinities from fresh to seawater (de Ben et al. 1990), generally found in mesohaline to fresh water (Cailliet et al. 2000)
Dissolved oxygen	Relatively tolerant of reduced dissolved oxygen (Emmett et al. 1991)	Density of adults decreased when DO dropped below 3 mg/L and no adults remained in the area when DO dropped to 1 mg/lL (Levings 1980 as reported in Toole et al. 1987)	No information
Estuarine types used	Coastal embayments, estuaries, lagoons, sloughs (also see Table 4)	Coastal embayments, estuaries, lagoons, sloughs (also see Table 4)	Estuaries, lagoons, and lower reaches of major coastal rivers (Cailliet et al. 2000), may be estuarine-dependent (Emmett et al. 1991)
Preferred estuarine habitat(s)	Juveniles more abundant in, and seem to prefer, unvegetated areas with sandy to muddy substrates (Drawbridge 1990, Valle et al. 1999, Fodrie and Mendoza 2006)	Commonly found on mudflat and sandflats and in areas with eelgrass and oyster beds (Toole et al. 1987, Hosack et al. 2006)	Juveniles prefer sandy to muddy substrates (Moles and Norcross 1995, Cailliet et al. 2000)
Timing of estuarine residence	Primary settlement period Feb–Aug (Kramer 1990)	Primary settlement period Dec–May (Baxter et al. 1999)	Primary settlement period Mar–May (Baxter et al. 1999), most age–0 and age–1 fish are found in estuaries (Orcutt 1950, Baxter et al. 1999)
Duration of estuarine residence	Up to 2 years (Haaker 1975, Allen 1988)	6–18 months (Cailliet et al. 2000)	1–2 years (Cailliet et al. 2000, Baxter et al. 1999), most age-2 fish migrate into ocean habitats adjacent to estuaries (Orcutt 1950)
Size range estuarine residence	20–200 mm TL (Haaker 1975)	25–150 mm TL, however some age-1 fish are found in estuary, especially large estuaries (Krygier and Pearcy 1986)	Smallest recruits 10–12 mm TL to 240–280 mm TL (de Ben et al. 1990, McCain et al. 2005)
Prey of juveniles	Larval and small fish, small crustaceans (e.g., gammarid amphipods, mysids, harpacticoid copepods) (Cailliet et al. 2000)	Small crustaceans (e.g., harpacticoid copepods, gammarid amphipods, mysids), cumaceans, small polychaetes, small bivalves and bivalve siphons, and other benthic invertebrates (Cailliet et al. 2000)	Small crustaceans (copepods, mysids, amphipods), annelid worms, nemerteans, priapulids, tanaids (Cailliet et al. 2000)
Predators on juveniles	Fishes, shore birds, water fowl, seals and sea lions (Cailliet et al. 2000, Love 1996)	Large fishes (lingcod, greenlings, rockfish, sharks, croakers), piscivorous birds and mammals (Cailliet et al. 2000)	Larger fishes, sharks, herons, cormorants, seabirds, pinnipeds and other marine mammals (Cailliet et al. 2000)

TABLE 3. continued: Juvenile life-history characteristics in West Coast estuaries.

	Brown rockfish	Staghorn sculpin
Geographic range of estuarine residence	Puget Sound, San Francisco Bay, Elkhorn Slough (Baxter et al. 1999b, Stein and Hassler 1989, Brown 2002, Matthews 1990ab)	South Bering Sea to San Quintin Bay, Baja California (Miller and Lea 1972, Eschmeyer and Herald 1983)
Temperature range	9.5–19.5°C in the San Francisco Estuary (Baxter et al. 1999)	No information
Salinity range	>20 ppt (Baxter et al. 1999, Love et al. 2002)	Euryhaline (0–34 ppt+, Moyle 2002)
Dissolved oxygen	No information	No information
Estuarine types used	Estuaries, coastal embayments (Stein and Hassler 1989)	All types including fresh water creeks (Emmett et al. 1991)
Preferred estuarine habitat(s)	No information	Muddy or sandy bottoms which include eelgrass or other vegetation (Love 2011)
Timing of estuarine residence	Year round in San Francisco Bay, age-0 present April–Dec (Baxter et al. 1999)	Anytime (Jones 1962, Tatso 1975)
Duration of estuarine residence	Age–0 brown rockfish immigrate into the San Francisco Bay Estuary and then utilize this system between 1 and 2 years before migrating to the open coast (Baxter et al. 1999)	Juveniles generally present year round with the occurrence of adults increasing during peak spawning periods, which varies with latitude (Jones 1962, Tatso 1975, Moyle 2002, Love 2011)
Size range estuarine residence	31–340 mm TL in San Francisco Bay (Baxter et al. 1999)	5–220 mm TL (Tatso 1975, Moyle 2002)
Prey of juveniles	Small crustaceans, amphipods, copepods and > 130 mm small fish and crabs (Gaines and Roughgarden 1987, Stein and Hassler 1989, Love et al. 2002)	Opportunistic benthic feeder with a heavy reliance on decapods, amphipods and fishes, predominantly Gobiidae spp. (Jones 1962, Tatso 1975, Armstrong et al. 1995)
Predators on juveniles	Fishes, birds, marine mammals (Stein and Hassler 1989, Cailliet et al. 2000)	Birds including gulls, cormorants, great blue heron (Cailliet et al. 2000)

	Shiner surfperch	Pacific herring
Geographic range of estuarine residence	Puget Sound, WA to Bahía de San Quentín, Mexico (Emmett et al. 1991)	Within the entire range of the North Pacific (Emmett et al. 1991)
Temperature range	Up to 25°C (Allen and Horn 1975), newborns prefer cooler temperatures than juveniles and adults (Shrode et al. 1983)	12 °C is the optimal temperature for growth (Haist and Stocker 1985, Lassuy 1989b)
Salinity range	Euryhaline though they were observed to move when salinity dropped due to increased freshwater input (Chamberlain and Barnhart 1993). Found at 0–35 ppt but prefer at least 10 ppt (California Fish Website)	Eggs and larvae are tolerant of salinities 3–28 ppt, and their optimal range is 12–19 ppt (Emmett et al. 1991), no info on juvenile salinity ranges
Dissolved oxygen	May be tolerant to low dissolved oxygen as fetus and as newborns (Ingermann and Terwilliger 1982)	No information
Estuarine types used	Nearshore shallow marine, bay, and estuaries (Eschmeyer and Herald 1983)	All types with a freshwater influence (Love 2011)
Preferred estuarine habitat(s)	Shallow, calm, complex habitats, eelgrass beds, pilings (Eschmeyer and Herald 1983, Horn and Allen 1981)	Eggs are dependent on either vegetated or hard substrate. Juveniles and adults use the entire water column (Emmett et al. 1991)
Timing of estuarine residence	South: April–Aug, North: May–Nov (Odenweller 1975, Horn and Allen 1981, Shrode et al. 1983, Bayer 1985)	All times of year (Emmett et al. 1991)
Duration of estuarine residence	Varies with latitude, three months to year-round (Odenweller 1975, Horn and Allen 1981, Shrode et al. 1983, Bayer 1985)	2–3 years, and can remain in estuaries into adulthood (Emmett et al. 1991)
Size range estuarine residence	34–55 mm TL (Odenweller 1975, Horn and Allen 1981, Bayer 1985)	All sizes (Emmett et al. 1991)
Prey of juveniles	Omnivorous, copepods, amphipods, algae, mysids, polychaetes, crab larvae (Odenweller 1975, Martin 1995)	Larval plankton and copepods, amphipods, and barnacle larvae in eelgrass beds (Emmett et al. 1991, Lassuy 1989b)
Predators on juveniles	Fishes, birds (Thompson et al. 2002), marine mammals (Orr et al. 2004)	Squid, sharks, salmonids, gadids, sculpins, lingcod, sand sole, and other fishes, many species of birds, and seals, (Emmett et al. 1991)

TABLE 4: Documented use of estuarine sub-classes and habitats for all life history stages of 15 focal species in West Coast estuaries. Estuarine sub-classes and habitats were selected by identifying key habitats from the literature review, and were categorized based on CMECS classifications (see Appendix 1 for more information). Habitats were separated by type (Biogenic, Geologic and Anthropogenic).

	CMECS classification	Dungeness crab	Bay shrimp	Leopard shark	Bat Ray
Estuarine sub-class	***Estuarine Coastal Subtidal***	L, J, A (Emmett et al. 1991, Rooper et al. 2002)	L, J, A (Emmett et al. 1991)	J, A (Ebert 2003, Love 2011)	J, A (Ebert 2003, Love 2011)
	Tidal Channel/ Creek	L, J, A (Emmett et al. 1991, Rooper et al. 2002)	L, J, A (Emmett et al. 1991)	J, A (Ebert 2003, Carlisle and Starr 2009)	J, A (Barry and Cailliet 1981, Ebert 2003, Love 2011)
	Slough	L, J, A (Emmett et al. 1991, Rooper et al. 2002)	L, J, A (Emmett et al. 1991)	J, A (Ebert 2003, Carlisle and Starr 2009)	J, A (Barry and Cailliet 1981, Ebert 2003, Love 2011)
	Lagoon	J (present study)			
Biogenic habitats	**Oyster Reef**	J (Fernandez et al. 1993)			
	Shell rubble	J (Emmett et al. 1991, Rooper et al. 2002)			
	Seagrass Bed	J (Emmett et al. 1991, Rooper et al. 2002)		J, A (Ebert and Ebert 2005)	J, A (Love 2011)
	Benthic Macroalgae	J (Rooper et al. 2002)			
	Freshwater and Brackish Tidal Aquatic Vegetation				
	Emergent Tidal Marsh				
	Tidal Scrub-Shrub Wetland				
	Tidal Forest/ Woodland				
	Very Coarse Woody Debris	J (Armstrong et al. 2003)			
Geologic habitat	**Tidal Flat**	A, J (Emmett et al. 1991, Rooper et al. 2002)	L, J, A (Emmett et al. 1991)	J, A (Ebert 2003, Carlisle and Starr 2009)	J, A (Barry and Cailliet 1981)
	Anthropogenic habitat				
	Anthropogenic Wood				

🟧 = used by larval and juvenile stage, 🟨 = used by juvenile stage, 🟩 = used by juvenile and adult stages, 🟫 = used by adult stage, 🟦 = used by larval, juvenile, and adult stages, 🟪 = used by larval stage
L = larval stage, J = juvenile stage, A = adult stage

L = larval stage
J = juvenile stage
A = adult stage

🟧 = used by larval and juvenile stage
🟨 = used by juvenile stage
🟩 = used by juvenile and adult stages

🟫 = used by adult stage
🟦 = used by larval, juvenile, and adult stages
🟪 = used by larval stage

	CMECS classification	Green sturgeon	Chinook salmon	Coho salmon	Steelhead trout
Estuarine sub-class	***Estuarine Coastal Subtidal***	J, A (Emmett et al. 1991, Beamesderfer et al. 2007, Moser and Lindley 2007)	J, A (Emmett et al. 1991)	J, A (Emmett et al. 1991)	J, A (Emmett et al. 1991)
	Tidal Channel/ Creek		J (Hood 2002)	J (Hood 2002, Wallace and Allen 2009)	
	Slough		J (Hood 2002)	J (Hood 2002, Wallace and Allen 2009)	
	Lagoon		J (B. Pinnix pers. comm.)	J, A (Shapovalov and Taft 1954, Garwood 2012)	J, A (Shapovalov and Taft 1954, Bond et al. 2008, Hayes et al. 2008)
Biogenic habitats	**Oyster Reef**		J not found (Semmens 2008)		
	Shell rubble				
	Seagrass Bed		J (Semmens 2008)	J (Pinnix et al. 2012)	
	Benthic Macroalgae		J (Emmett et al. 1991)	J (Emmett et al. 1991)	
	Freshwater and Brackish Tidal Aquatic Vegetation	L, J, A (Beamesderfer et al. 2007)	J, A (Emmett et al. 1991, Henning et al. 2007)	J, A (Emmett et al. 1991, Henning et al. 2007. Wallace and Allen 2009)	J (Wallace and Allen 2009)
	Emergent Tidal Marsh		J (Bottom et al. 2005b)		J (Wallace and Allen 2009)
	Tidal Scrub-Shrub Wetland		J (Miller and Simenstad 1997)	J (Miller and Simenstad 1997)	J (Wallace and Allen 2009)
	Tidal Forest/ Woodland		J (Emmett et al. 1991)	J (Emmett et al. 1991)	
	Very Coarse Woody Debris		J (Miller and Simenstad 1997)	J (Miller and Simenstad 1997, Aitkin 1998)	J (Wallace and Allen 2009
Geologic habitat	**Tidal Flat**	J, A (Moser and Lindley 2007, Dumbauld et al. 2008)	J (Emmett et al. 1991)	J (Emmett et al. 1991)	J,A (Wallace and Allen 2009)
	Anthropogenic habitat				
	Anthropogenic Wood			J (Pinnix et al. 2012)	

TABLE 4. continued: Documented use of estuarine sub-classes and habitats

	CMECS classification	California halibut	English sole	Starry flounder
Estuarine sub-class	***Estuarine Coastal Subtidal***	L, J, A (Emmett et al. 1991)	L, J, A (Emmett et al. 1991)	L, J, A (Emmett et al. 1991)
	Tidal Channel/ Creek	J (Kramer 1990, Baxter et al. 1999, Madon 2008)	L, J (Toole 1980, Emmett et al. 1991, Yoklavich et al. 1991, Baxter et al. 1999)	J, A (Emmett et al. 1991, Yoklavich et al. 1991, Baxter et al. 1999)
	Slough	J (Yoklavich et al. 1991)	J (Yoklavich et al. 1991, Brown 2002)	J (Yoklavich et al. 1991)
	Lagoon	J (Fodrie and Mendoza 2006)	J (PWA and WRA 2006)	J (PWA and WRA 2006)
Biogenic habitats	**Oyster Reef**		J (Hosack et al. 2006)	J (Hosack et al. 2006)
	Shell rubble		J (Rogers 1985)	
	Seagrass Bed	J (Valle et al. 1999, Reeve 2013)	J (Hosack et al. 2006)	J (Hosack et al. 2006)
	Benthic Macroalgae			
	Freshwater and Brackish Tidal Aquatic Vegetation			
	Emergent Tidal Marsh			J (Moyle et al. 1986)
	Tidal Scrub-Shrub Wetland			
	Tidal Forest/ Woodland			
	Very Coarse Woody Debris			
Geologic habitat	**Tidal Flat**	J (Kramer 1990, Baxter et al. 1999, Fodrie and Mendoza 2006)	J (Emmett et al. 1991, Baxter et al. 1999, Hosack et al. 2006)	J (Emmett et al. 1991, Baxter et al. 1999, Hosack et al. 2006)
	Anthropogenic habitat			
	Anthropogenic Wood			

🟧 = used by larval and juvenile stage, 🟨 = used by juvenile stage, 🟩 = used by juvenile and adult stages, 🟫 = used by adult stage, 🟦 = used by larval, juvenile, and adult stages, 🟪 = used by larval stage
L = larval stage, J = juvenile stage, A = adult stage

L = larval stage
J = juvenile stage
A = adult stage

🟧 = used by larval and juvenile stage
🟨 = used by juvenile stage
🟩 = used by juvenile and adult stages

🟫 = used by adult stage
🟦 = used by larval, juvenile, and adult stages
🟪 = used by larval stage

	CMECS classification	Brown rockfish	Staghorn sculpin	Shiner perch	Pacific herring
Estuarine sub-class	***Estuarine Coastal Subtidal***	J, A (Baxter et al. 1999, Matthews 1990)	L, J, A (Emmett et al. 1991)	J, A (Emmett et al. 1991)	L, J, A (Lassuy 1989b, Emmett et al. 1991)
	Tidal Channel/ Creek	J (Baxter et al.1999)	L, J, A (Emmett et al. 1991, Simenstad et al. 2000)	J, A (Horn and Allen 1981)	L, J, A (Lassuy 1989b, Emmett et al. 1991)
	Slough	J (Yoklavich et al. 1991)	L, J, A (Emmett et al. 1991)	J, A (Horn and Allen 1981)	L, J, A (Lassuy 1989b, Emmett et al. 1991)
	Lagoon	J (present study)	J (present study)	A (Eschmeyer et al. 1983)	J (present study)
Biogenic habitats	**Oyster Reef**		J, A (Hosack et al. 2006)	J (Wechsler 1996)	L (Emmett et al. 1991)
	Shell rubble				
	Seagrass Bed	J (West et al. 1994)	J, A (Emmett et al. 1991, Hosack et al. 2006)	J, A (Bayer 1985)	L, J, A (Lassuy 1989b, Emmett et al. 1991)
	Benthic Macroalgae	J (West et al. 1994)	J (Grant 2009)	J, A (Eschmeyer et al. 1983)	L, J, A (Lassuy 1989b, Emmett et al. 1991)
	Freshwater and Brackish Tidal Aquatic Vegetation				
	Emergent Tidal Marsh		A (Higley and Holton 1981, Simenstad et al. 2000)	A (Eschmeyer et al. 1983)	
	Tidal Scrub-Shrub Wetland				
	Tidal Forest/ Woodland				
	Very Coarse Woody Debris				L (Emmett et al. 1991)
Geologic habitat	**Tidal Flat**		J, A (Emmett et al. 1991, Hosack et al. 2006)	A (Eschmeyer et al. 1983)	
	Anthropogenic habitat				
	Anthropogenic Wood			A ([pier pilings] Eschmeyer et al. 1983)	L ([pier pilings] Emmett et al. 1991)

TABLE 5. Documented threats to juvenile life history stages of 12 species in West Coast estuaries. Note: brown rockfish, staghorn sculpin, and shiner perch were not included because our review did not find documentation of threats to juvenile life-history stages in estuaries.

		Dungeness crab	Bay shrimp	Leopard shark	Bat Ray	Green sturgeon	Steelhead
Pollution	**Nutrient inputs**						Naiman et al. 2012, Bilby et al. 1998
	Organic pollution	Armstrong et al. 1976, Buchanan et al. 1970, Feldman et al. 2000	Khorram and Knight 1977, Siegfried 1989	Russo 1975, Emmett et al. 1991		Emmett et al. 1991, Adams et al. 2002, Boreman 1997, St. Pierre and Campbell 2006	Anderson et al. 2014
	Inorganic pollution	Martin et al. 1981, Emmett et al. 1991		Russo 1975, Emmett et al. 1991		Emmett et al. 1991, Adams et al. 2002, Boreman 1997, St. Pierre and Campbell 2006	Emmett et al. 1991
Habitat modifications	**Habitat loss**	McGraw et al. 1988, Wainwright et al. 1992, Dumbauld et al. 1993	Siegfried 1989, Jassby et al. 1995, Kimmerer 2002	Carlisle and Starr 2009	Carlisle et al. 2007	Emmett et al. 1991, St. Pierre and Campbell 2006	Emmett et al. 1991
	Freshwater flow/salinity		Siegfried 1989, Jassby et al. 1995, Kimmerer 2002	Ebert 1986	Hopkins and Cech Jr. 2003	Emmett et al. 1991, Adams et al. 2002, Boreman 1997, St. Pierre and Campbell 2006	Emmett et al. 1991
	Armoring/ hardened shoreline					Emmett et al. 1991, Adams et al. 2002, Boreman 1997, St. Pierre and Campbell 2006	
	Dredging	McGraw et al. 1988, Wainwright et al. 1992, Dumbauld et al. 1993					Collis et al. 2001
	Altered tidal regime						
	Dams					Emmet et al. 1991, St. Pierre and Campbell 2006	Emmett et al. 1991
	Clearcutting						Emmett et al. 1991

TABLE 5. continued: Documented threats to juvenile life history stages in West Coast estuaries.

		Dungeness crab	Bay shrimp	Leopard shark	Bat Ray	Green sturgeon	Steelhead
Habitat modifications *(continued)*	**Marinas/ harbors**	McGraw et al. 1988, Wainwright et al. 1992, Dumbauld et al. 1993					
	Sediment increase					St. Pierre and Campbell 2006	Emmett et al. 1991
Biological	**Invasive species**	McDonald et al. 2001, Holsman et al. 2010	Siegfried 1989				Moyle 2002
	Aquaculture	Feldman et al. 2000					Emmett et al. 1991
	Recreational fishing	Dahlstrom and Wild 1983		Carlisle et al. 2007			
	Commercial fishing						Emmett et al. 1991
Climate	**Temperature**			Ebert 1986	Matern et al. 2000, Hopkins and Cech Jr. 2003	Adams et al. 2002	Emmett et al. 1991
	Sea level rise						Flitcroft et al. 2013
	Hypoxia	Bernatis et al. 2007, Froelich et al. 2014	Siegfried 1989	Carlisle and Starr 2009			

TABLE 5. continued: Documented threats to juvenile life history stages in West Coast estuaries.

		Coho salmon	Chinook salmon	California halibut	English sole	Starry flounder	Pacific herring
Pollution	**Nutrient inputs**	Naiman et al. 2012, Bilby et al. 1998	Naiman et al. 2012	Hughes et al. 2012	Hughes et al. 2012		
	Organic pollution	Anderson et al. 2014	Anderson et al. 2014		Feldman et al. 2000, Johnson et al. 1998, Myers et al. 1998, da DaSilva et al. 2013	Stehr et al. 1997; Moles 1998; Myers et al. 1998; Smalling et al. 2013	Carls et al. 1999, Kennedy and Farrell 2005, Incardona et al. 2012
	Inorganic pollution	Emmett et al. 1991	Emmett et al. 1991				
Habitat modifications	**Habitat loss**	Emmett et al. 1991	Emmett et al. 1991	Tanaka 2013	Emmett et al. 1991	Emmett et al. 1991	Kimmerer 2002
	Freshwater flow/salinity	Emmett et al. 1991	Emmett et al. 1991	Madon 2008; Ritter et al. 2008	Baxter et al. 1999; Rooper et al. 2003	Baxter et al. 1999, Kimmerer 2002, Ritter et al. 2008	
	Armoring/ hardened shoreline	Toft et al. 2013	Toft et al. 2013		Toft et al. 2007	Morley et al. 2012	
	Dredging		Ryan et al. 2003				Suedel et al. 2008
	Altered tidal regime			Madon 2008; Ritter et al. 2008		Ritter et al. 2008	
	Dams	Emmett et al. 1991	Emmett et al. 1991				
	Clearcutting	Emmett et al. 1991	Emmett et al. 1991				

TABLE 5. continued: Documented threats to juvenile life history stages in West Coast estuaries.

		Coho salmon	Chinook salmon	California halibut	English sole	Starry flounder	Pacific herring
Habitat modifications ***(continued)***	**Marinas/ harbors**						
	Sediment increase	Emmett et al. 1991	Emmett et al. 1991	PWA and WRA 2006	PWA and WRA 2006	PWA and WRA 2006	Griffin et al. 2009
Biological	**Invasive species**	Moyle 2002, Garwood et al. 2010	Moyle 2002			Feyrer et al. 2003	
	Aquaculture	Emmett et al. 1991	Emmett et al. 1991, Semmens 2008, Dumbauld et al. 2009		Feldman et al. 2000	Feldman et al. 2000	Kimmerer 2002
	Recreational fishing			Tanaka 2013			
	Commercial fishing	Emmett et al. 1991	Emmett et al. 1991	Tanaka 2013	Stewart 2007	Ralston 2005	Musick et al. 2000
Climate	**Temperature**	Emmett et al. 1991	Emmett et al. 1991	Madon 2008; thermal discharges may attract juvenile halibut as long as it does not exceed thermal tolerance (>28°C (Innis 1990)	Lassuy 1989a; Baxter et al. 1999; Rooper et al. 2003		Tanasichuk 1997
	Sea level rise	Flitcroft et al. 2013	Flitcroft et al. 2013	Nelson et al. 2010	Nelson et al. 2010	Nelson et al. 2010	
	Hypoxia			Hughes et al. 2012	Hughes et al. 2012		

© Joe Hatfield


© Ed Bierman/Creative Commons

FLATFISH

Flatfishes are unique in that they have both eyes positioned on the same side of the head. Species with both eyes on the right side of the head are called right-eyed. Left-eyed flatfish have both eyes on the left side. In some species (e.g., California halibut, starry flounder) populations contain both right-eyed and left-eyed individuals. Flatfishes are common components of the soft-bottom fish assemblage ranging from shallow coastal habitats seaward to more than 1,500 m in depth. Often flatfishes live in shallower habitats—juveniles move into progressively deeper waters as they mature. The eyed side of the fish is pigmented and serves to camouflage the fish as it lies on the bottom, helping it to avoid predation and also to ambush its own prey. Many species are popular as food for people, and thus they are important components of recreational and commercial fisheries, especially commercial bottom-trawl fisheries.

The value of estuarine habitats as nursery grounds for flatfish has been the subject of extensive study in a number of coastal regions throughout the world. In this report, we focus on three species of flatfish: California halibut, English sole and starry flounder. Collectively, these species inhabit estuaries that span the geographic range of this report. English sole and California halibut use both estuaries and the shallow open coast for juvenile rearing. The relative importance of these alternative rearing environments, and the nursery value of estuaries, has been extensively studied for California halibut in the southern California region, and for English sole from central California north to Puget Sound. For both species, there is substantial evidence that estuaries contribute a significant proportion of recruits to the offshore adult population. Juvenile starry flounders are rarely found along the open coast, suggesting that this species may be estuary-dependent. The nursery value of the different types of estuarine systems and specific estuarine habitats to starry flounder is not well understood, and further research is needed to fully understand the nursery role of estuarine habitats for this species.

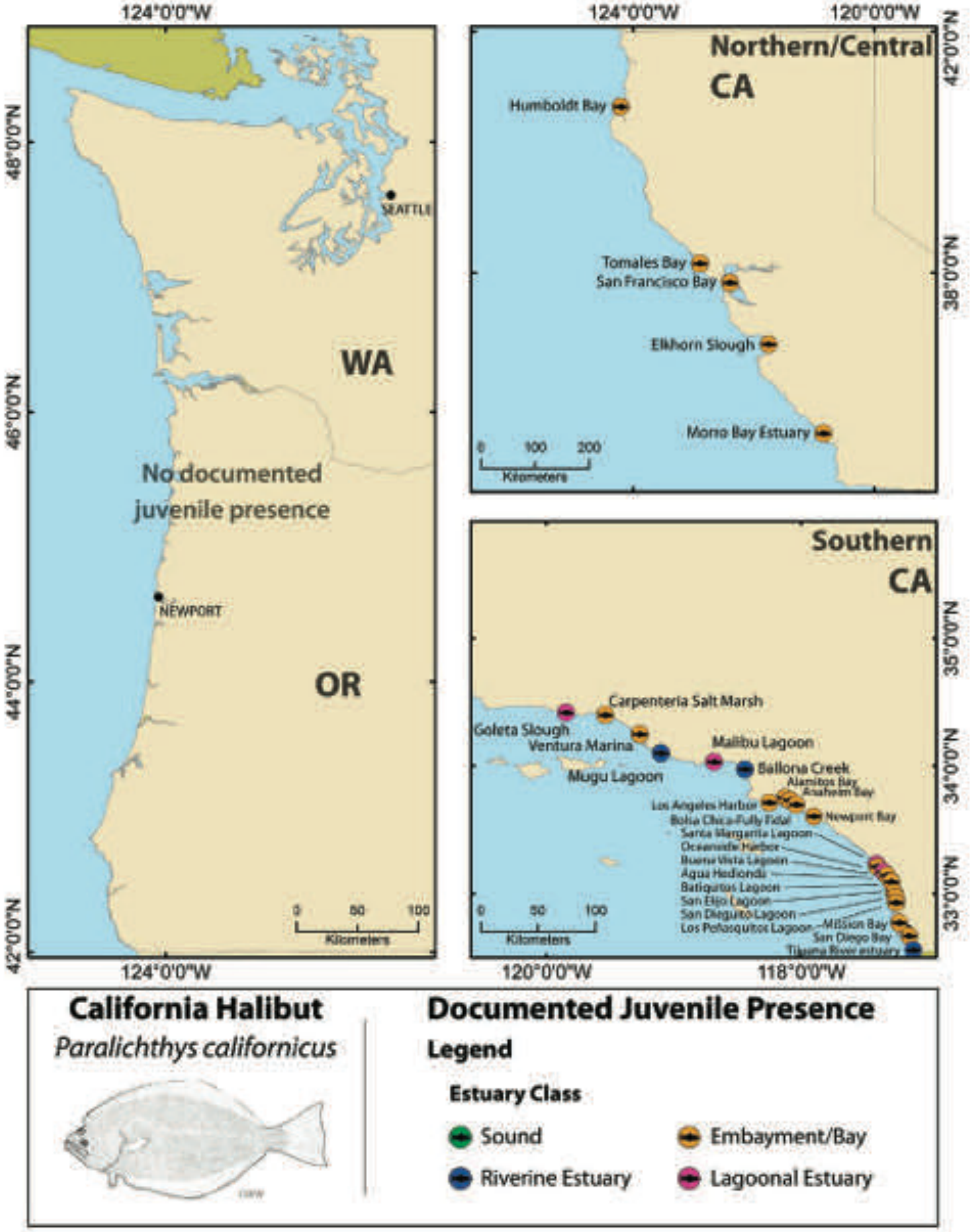


FIGURE 10. CALIFORNIA HALIBUT: Documented juvenile presence in Washington, Oregon and California estuaries.

CALIFORNIA HALIBUT

(*Paralichthys californicus*)

© Lenny Flank/Creative Commons

The California halibut (*Paralichthys californicus*) inhabits shallow (less than 200 m), soft-bottom coastal habitats along the west coast of North America ranging from Quillayute River, Washington, south to Almejas Bay, Baja California, Mexico (Tanaka 2013). The species is most common south of Bodega Bay, California, and in depths less than 30 m (Tanaka 2013). California halibut is an important component of the recreational and commercial fisheries in central and southern California. Historically, the commercial fishery was centered in southern California, and the population off central California was about one-third of that off southern California (Leet et al. 2001). Along the southern California coast and in embayments, Kramer (1990) found that California halibut was the predominant flatfish by weight and the second most abundant species (Kramer 1990). More recently, commercial landings have shifted to central California, particularly the San Francisco port area (Tanaka 2013).

Life History and Ecology

The California halibut is a long-lived species (up to 30 years) with females reaching sizes up to 150 cm (Miller and Lea 1972, Love 1996, Tanaka 2013; see Table 2). Although most adult California halibut occur in soft-bottom habitats along the open coast, adults may also be found in large bays, such as San Francisco Bay (Fish et al. 2013). Spawning can occur year round, but most spawning occurs in mid-winter (January-February), summer (June-July) and fall (September-October) (Tanaka 2013).

Larvae are found typically in the upper 30 m of the water column and within 6 km of shore (Moser and Watson 1990). Based on larval distribution, most spawning seems to occur from central California southward (Moser and Watson 1990). However, Bloeser (2000) detected spawning females in a population of California halibut in Humboldt Bay, northern California. The northern spawning range limit is likely influenced by water temperature (Baxter et al. 1999). Water temperature influences survival and growth of larvae, and duration of the larval phase, with cooler waters resulting in lower survival, slower growth and longer larval duration (Gadomski et al. 1990, Gadomski and Caddell 1991). Given the demographics of the population in Humboldt Bay and the lack of larvae and young juveniles in the estuary, Bloeser (2000) concluded that this population likely arose from migration of older individuals into Humboldt Bay as a result of an El Niño event in the late 1980s rather than local reproduction.

Larvae settle out in shallow, soft-bottom habitats along the open coast and in bays and estuaries at a size of approximately 12 mm (based on studies in southern California; Allen 1988, Allen and Herbison 1990, Kramer 1990). Within estuaries, smaller halibut use shallower habitats and then move progressively into deeper channels closer to the estuary mouth as they grow. Eventually, juveniles migrate from the estuary to the shallow open coast. Recent migrants from estuaries (150–200 mm) are most concentrated in the coastal habitats adjacent to bays and estuaries (Kramer 1990).

Halibut are ambush predators that seem to feed more during daylight hours (visual predator) (Haaker 1975, Barry and Cailliet 1981). Preferred prey shifts as fish grow and mature. The diet of small California halibut (less than 55 mm) is dominated by small crustaceans (e.g., gammarid amphipods, mysids, harpacticoid copepods) and small fish, such as gobies (Haaker 1975, Allen 1988, Barry and Cailliet 1981). Larger juveniles (55–230 mm) feed on mysids, bay shrimp, ghost shrimp, topsmelt, California killifish and gobies (Haaker 1975, Plummer et al. 1983). Subadult and adult California halibut (larger than 230 mm) are almost totally piscivorous (Haaker 1975). Prey species include topsmelt, Pacific sardine, northern anchovy, small flatfish, white croaker, California grunion, Pacific saury, market squid, octopus, gobies and surfperches (Allen 1990).

Timing and Use of Estuaries

In southern California, newly settled California halibut (12–15 mm total length) are found primarily in shallow water soft-bottom marine habitats, including the open coast, semi-protected embayments and estuaries (Allen 1988, Allen and Herbinson 1990, Kramer 1990, Kramer 1991, Fodrie and Mendoza 2006; Table 3). A large proportion of larval California halibut settle (i.e., transition from the pelagic larval phase to the benthic juvenile phase) along the open coast or near the mouth of bays before migrating into estuaries at a slightly larger size (Kramer 1990, Fodrie and Herzka 2013).

© Laura S. Brophy

The majority of California halibut 20–150 mm (standard length) is found in bays and estuaries (Allen and Herbinson 1990, Kramer 1990, Fodrie and Mendoza 2006) with far fewer individuals in the 40–140 mm size range found along the exposed open coast (Allen and Herbinson 1990, Kramer 1990). Fodrie and Herzka (2013) found that approximately 25% of age-0 California halibut collected from Punta Banda estuary (Baja Mexico) had migrated into the estuary as larvae, and the rest entered the estuary after settlement. Settlement along the exposed coast and migration into estuaries as slightly larger, benthic individuals could have several benefits for juvenile California halibut, including reducing the risk of predation and increasing the time window for finding the most productive juvenile habitat.

Timing and intensity of recruitment of juvenile California halibut in a particular embayment varies from year to year. Allen (1988) found that in southern California, recruitment was strong and relatively continuous in 1983, more sporadic in 1984, and very light and sporadic in 1985. Kramer (1990) captured newly settled California halibut primarily in the first and second quarter of 1987, although in 1988 the greatest settlement occurred in the second and third quarter. In San Francisco Bay, strong recruitment years seem to be associated with exceptionally warm coastal ocean temperatures (Baxter et al. 1999, Fish et al. 2013). There is also high year-to-year variability in the proportion of the age-0 California halibut populations that remain in exposed coastal habitats (i.e., do not seem to enter estuaries) (Plummer et al. 1983, Allen 1988, Allen and Herbinson 1990, Allen 1990, Kramer 1990, Kramer 1991, Fodrie and Mendoza 2006). Given the variety of classes of estuaries along the central and southern California coast, and the year-to-year variability in both conditions inside the estuary (e.g., freshwater flows) and access (e.g., periodic inlet closure), small California halibut may be generalists in their use of available juvenile habitats as a bet-hedging strategy (Kramer 1991, Fodrie and Herzka 2013).

Despite this variability, an overall pattern in relative densities of age-0 California halibut among alternative habitat types has been found: the highest densities are generally found in bays and estuaries, lower densities in semi-protected habitats (harbors and leeward sides of points and islands) and the lowest densities at exposed sites (Allen 1988, Allen and Herbison 1990). Given this pattern in relative densities, and the total available area of the alternative habitat types, it seems that estuaries and other protected coastal embayments likely contribute a significant proportion of juveniles that recruit to the subadult, coastal population (e.g., Fodrie and Levin 2008; see Box 10). However, because of the substantial interannual variability in California halibut densities in embayments, the relative importance of a given embayment as a source of recruits to the adult population changes from year to year (Allen and Herbison 1990).

Tidal flats and shoreline habitat (Table 4) seem to be important both as initial settling areas and as rearing habitat for small juveniles, based on relative densities of size classes (Kramer 1990, Baxter et al. 1999, Fodrie and Mendoza 2006). This preference for shallow habitats may be due to young fish seeking warmer temperatures (Allen et al. 1990, Baxter et al. 1999, Fodrie and Mendoza 2006). Gadomski and Caddell (1991) found that juvenile California halibut growth rates at 20, 24 and 28°C were directly proportional to temperature, leading them to suggest that juveniles in shallow areas of bays and estuaries may have the advantage of rapid growth and survival because of warmer waters. Shallow, mudflat and side-channel habitats may also be preferred because of greater availability of small-sized prey eaten by juvenile California halibut (Madon 2008).

As juveniles grow, their estuarine habitat preferences shift to deeper, more centrally located channel and bay habitats (Kramer 1990, Baxter et al. 1999, Madon 2008). The exact timing and size class of this shift varies among studies and may be influenced by ontogenic changes in tolerances to temperature and salinity and interannual variability in freshwater input and water temperature. In laboratory experiments, small California halibut (118–172 mm TL) tolerated a wide range of salinities (8–34 ppt), and experienced high osmoregulatory stress only when exposed to low salinity at low temperature (i.e., 8 ppt and 14°C; Madon 2002). In San Francisco Bay, low salinity seemed to limit upstream distribution of juvenile California halibut; California halibut did not seem to select sites with salinities less than 20 ppt (Baxter et al. 1999).

As California halibut grow, they become less tolerant of variable water temperature and salinity (Madon 2002). Larger California halibut (greater than 200 mm TL) likely move to deeper portions of the estuary for thermal refuge (Madon 2008). Ultimately, many large juvenile California halibut migrate from lagoons and other smaller, shallow estuaries into open-coast environments, where salinities and temperatures are more stable and where larger prey are more abundant (Madon 2002). However, California halibut larger than 200 mm are often found in larger, deeper estuaries. For example, Baxter et al. (1990) found that more than half of the California halibut collected in otter trawls in San Francisco Bay are larger than 200 mm, including some sexually mature fish.

Although juvenile California halibut are collected from seagrass beds (Table 4), most studies have found that California halibut are more abundant and seem to prefer unvegetated, fine sandy bottom (Drawbridge 1990, Valle et al. 1999, Fodrie and Mendoza 2006). However, a manipulative experiment involving caging and tethering suggests that there may be tradeoffs between vegetated and unvegetated habitats—halibut were less vulnerable to predation in unvegetated habitats due to better camouflage, but availability of prey for halibut was higher in mixed or vegetated habitats (Reeve 2013).

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile California halibut have been documented in 22 estuaries in southern California and five estuaries in central and northern California (Figure 10). We found evidence of juvenile presence in only one estuary north of Tomales Bay. Juvenile California halibut were documented in Humboldt Bay by both Barnhart et al. (1992) and Pinnix et al. (2005). However, juvenile use of

Humboldt Bay seems to be variable given that studies by Bloeser (2000) and Garwood et al. (2013) failed to detect any age-0 California halibut in the estuary.

In southern California, juvenile California halibut use all three of the estuary classes that occur in California (embayment/bay, riverine estuary and lagoonal estuary). In northern and central California they have only been documented in the embayment/bay class of estuaries. It is unclear if this pattern reflects an actual change in estuarine use patterns by juvenile California halibut, or is an artifact of differences in sampling effort, or reporting in these regions.

Most of the published studies examining the patterns of use of West Coast estuarine habitats and the relative importance of alternative habitat types as nursery habitat for juvenile California halibut have occurred along the southern California coast, where juvenile California halibut are a regular and abundant component of the estuarine assemblage (Monaco et al. 1990). Repeated sampling of a variety of estuary classes in this region provides a wealth of information on the spatial distribution of juvenile California halibut in southern California estuaries.

The lack of similar published studies in central California is likely due in part to the very high interannual variability in abundance of age-0 California halibut in estuaries north of Point Conception, California. Juvenile California halibut become more abundant in central California estuaries (such as Elkhorn Slough and San Francisco Estuary) during warm water events (Yoklavich et al. 1991, Baxter et al. 1999, Fish et al. 2013), but it is not unusual for age-0 California halibut to be undetected in central California estuaries for one or more years in a row (e.g., Baxter et al. 1999, Fish et al. 2013). In addition, distribution and abundance data for juvenile California halibut is generally lacking along the open coast in central California, further diminishing our ability to understand the relative importance of these alternate juvenile habitat types as nursery habitat for this species.

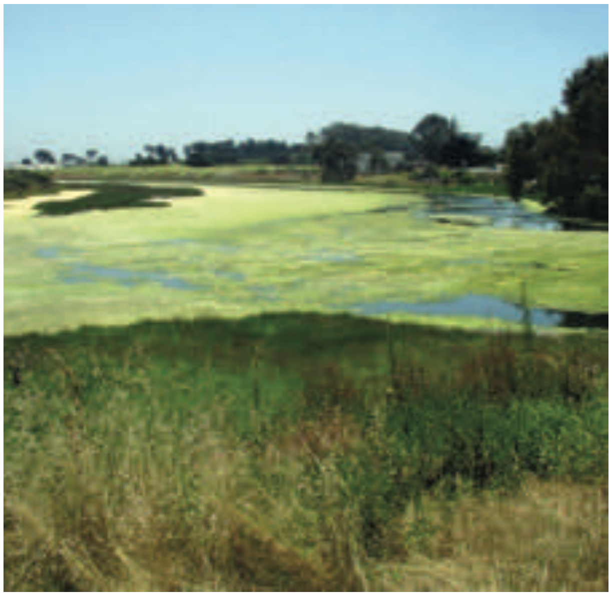
Threats

Historically, the California halibut population has shown oscillations in abundance that seem to be influenced by a combination of factors, including large-scale oceanic regimes (e.g., Pacific Decadal Oscillation, El Niño-Southern Oscillation), regional or seasonal shifts in currents and sea-surface temperature, availability of suitable juvenile habitat and fishing (Allen 1990, Baxter et al. 1999, Maunder et al. 2011, Tanaka 2013). Juvenile recruitment tends to be higher during El Niño events, which may provide better conditions for recruitment by promoting conditions that retain eggs and larvae closer to shore (Tanaka 2013). These conditions, or other occurrences of warm water, create conditions more favorable for larval and juvenile growth and survival, especially at the northern end of their spawning range (Baxter et al. 1999, Hughes et al. 2012, Fish et al. 2013).

Although the California halibut population in central California is composed of fish from all year classes (P. Reilly, CDFW, pers. comm.), the fishery is heavily reliant on strong year classes associated with warm water. In the 1980s and 1990s, a series of warm water events helped to build the adult population and supported several years of very good fishing in the 1990s and 2000s (Baxter et al. 1999, Tanaka 2013). However, lack of substantial juvenile recruitment since 2005, coupled with increased levels of fishing, have likely been important factors contributing to the decline in the recreational catch since 2008 (Fish et al. 2013, Tanaka 2013).

In southern California, there has been a downward trend in the abundance of California halibut, which seems related to high levels of fishing coupled with poor recruitment (Tanaka 2013). Successful recruitment in southern California is linked to environmental conditions as well as the condition and availability of suitable bay and estuary habitat (Tanaka 2013). In southern California, approximately 90% of historic bay and estuarine habitat has been severely altered or destroyed by human activities, which has likely had a significant impact on the California halibut population (Allen 1990). Continued improvements to water quality and restoration of habitat, such as have been occurring during the last four decades, are important to ensure that estuaries are viable and productive systems for juvenile California halibut (Tanaka 2013).

Habitat destruction and alteration is one of a variety of potential threats to juvenile California halibut in estuaries in central and southern California (Table 5). Habitat modification that results in the restriction of tidal exchange in estuaries, such as addition of dikes and other water control structures, reduces available habitat for juvenile California halibut (Nelson et al. 2010). In Elkhorn Slough, California halibut were most abundant at sites with full tidal exchange, less common in sites with moderate exchange through water control structures, and absent from tidally restricted sites (Ritter et al. 2008). Sediment accumulation in Bolinas Lagoon (California), is reducing subtidal shallow and channel habitat areas and is likely linked to observations that populations of several species of flatfish seem to have decreased over the past decade (PWA et al. 2006).


© Brent Hughes

Madon (2008) found that tidal inlet closures induce variations in water temperature and salinity and negatively affect growth of juvenile California halibut. Closure of river mouths likely poses the greatest risk to large juvenile California halibut, should they become trapped in cold, hyposaline coastal wetlands. Maintaining an open tidal inlet, implementing sediment management programs, and designing coastal wetlands with tidal creek networks consisting of channels and creeks of various orders are key to providing the access and habitat diversity required by different size classes of juvenile California halibut (Madon 2008).

Nutrient loading may reduce habitat suitability for California halibut by reducing dissolved oxygen. In Elkhorn Slough, hypoxic conditions were found to have negative effects on three flatfish species (California halibut, English sole and speckled sanddabs). Predicted presence of these species significantly declined as a function of decreasing dissolved oxygen. Declines in presence occurred at dissolved oxygen levels between eight and four mg per liter, and four mg per liter was the threshold for complete absence (Hughes et al. 2012).

Oil spills, especially in southern California, where there are substantial extraction, transportation and refinement activities, are another threat to this species. Exposure to crude oil has been shown to reduce hatching success and size of larvae at hatching, produce morphological and anatomical abnormalities and reduce feeding and growth rates of California halibut (MBC Applied Environmental Science 1987 cited in Emmett et al. 1991).

Sea-level rise will likely influence the availability of preferred habitats for this species. However, the overall impact of sea-level rise on the population is difficult to predict because, based on local topography and hydrology, it is likely to increase the availability of suitable habitat in some estuaries while diminishing it in others.

BOX 10. DETERMINING NURSERY VALUE OF ALTERNATIVE HABITATS FOR CALIFORNIA HALIBUT

Quantifying the value of nursery habitat is important in the context of effectively managing coastal ecosystems for fish production and determining priorities for conservation and restoration. However, there are various approaches for quantifying the nursery value of alternative juvenile habitats, and the selected approach can strongly influence conservation and management priority setting.

In southern California, a number of studies have compared the relative densities of age-0 California halibut among alternative habitats to determine the relative value of those habitat types to the California halibut population (assuming density is a suitable measure of habitat value). When these alternative habitats are grouped by habitat class or level of exposure to offshore swells (Table 9), the general pattern observed is that juvenile density increases with decreasing exposure to the offshore environment. Based on relative density measures of nursery value, estuaries would be considered the most valuable type of nursery habitat for this species and open coast would be considered the least valuable.

More recently, two studies used otolith microchemistry to identify which type of juvenile habitat was used by subadult and adult California halibut and to quantify the overall contribution of embayments (as a group), versus the open coast, to the southern California halibut population. Both studies found that a little more than 50% of the subadults and adults sampled had used protected embayments during the juvenile phase, even though a much smaller percentage of the available juvenile habitat area is located within embayments (Forrester and Swearer 2002, Fodrie and Levin 2008). Thus, embayments had a much higher per-area contribution than open coast habitats, making embayments the most valuable nursery habitat under the Beck et al. (2001) definition of nursery habitat. Fodrie and Levin (2008) found that their estimates of the relative contributions of different habitat types, based on otolith chemical signatures, agreed very well with their own estimates of habitat contribution, based on field surveys of relative densities in embayments and open coast habitats in those same years.

An alternative to directly measuring the contribution of different habitat types is to calculate an expected contribution model, which multiplies the relative densities in each habitat type by the total area of available habitat. For example, Fodrie and Mendoza (2006) found that although estuaries had the highest juvenile densities, this habitat had the lowest nursery value based on expected contribution. Bays had the highest expected contribution. They estimated that San Diego Bay alone could account for over half of the juvenile California halibut available to recruit annually to the adult population in San Diego County while the contribution of exposed habitats and estuaries was 31–42% and 5–10%, respectively. Under the Dahlgren et al. (2006) definition of effective juvenile habitat, bays would be identified a high priority nursery habitat as they have the potential for greater than average overall contribution to the adult population, and may be essential for sustaining the California habitat population off San Diego County (Fodrie and Mendoza 2006).

Most recently, Fodrie et al. (2009) proposed an additional approach for ranking nursery habitat, which uses habitat-specific vital rates (e.g., growth, survival) to calculate population fitness. They used four years of vital-rate data from nearshore habitats off San Diego County to simulate population fitness. Their simulation models found that estuaries had the highest population fitness, followed by bays, lagoon and exposed coast. Exposed coast habitat ranked the lowest because, in three of the four years studied, juveniles from this habitat type contributed to negative population growth, and this habitat may be a demographic sink in some years. The authors concluded that to maintain a stable or growing California halibut population in San Diego County, at least 40% of all juveniles needed to have used embayments (estuaries, lagoons and bays) as rearing habitats versus exposed coast habitat.

How one defines and quantifies nursery value will have a strong influence on the relative values assigned to alternative habitats types and to specific sites. The specific conservation goals of resource managers can be used to help determine which approach for estimating relative value—direct measurement, expected contribution, or vital rates—is most appropriate. Conservation plans that maintain habitat diversity may be the best approach for managing California halibut, given this species' bet-hedging strategy (Fodrie et al. 2009).

Although coastal embayments seem to be productivity hot spots for this species, exposed habitat should also be valued both for contributing a significant number of recruits in some years, and for its relatively high availability and low level of human impacts (Fodrie and Levin 2008). In addition, a population with juveniles inhabiting multiple habitat types may have a higher diversity of environmental tolerances and adaptations, which could promote resistance and resilience to a variety of current and emerging threats. Thus, conserving a variety of juvenile habitat options—not only the nursery habitats—may be an important management goal for this species.

TABLE 9: The relative density of juvenile California halibut observed in alternative habitat types that vary in the level of protection for open ocean conditions.

Study	Location	'Exposed' open coast	'semi-protected' harbors	'Protected' bays	'Protected' estuary
Allen 1988	Los Alamitos Bay-Long Beach Harbor	Virtually absent	¼ - ½ less common	Most common	Most common
Allen and Herbinson 1990	Hermosa Beach-Carlsbad	Lowest	Intermediate	Highest	Low
Kramer 1990	San Diego County	Low		Intermediate	Highest
Fodrie and Mendoza 2006	San Diego County	Lowest		5-10 times higher	20-30 times higher

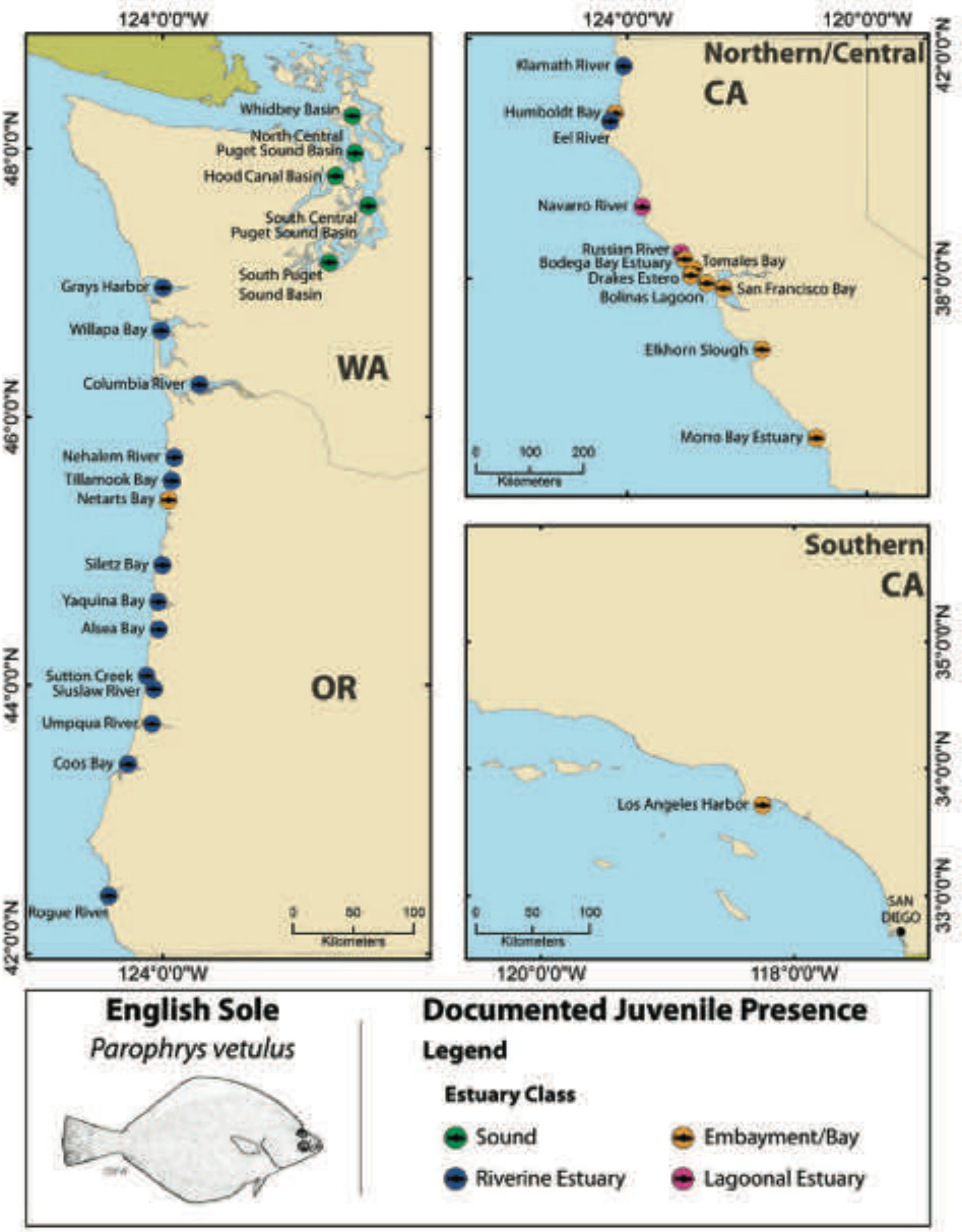
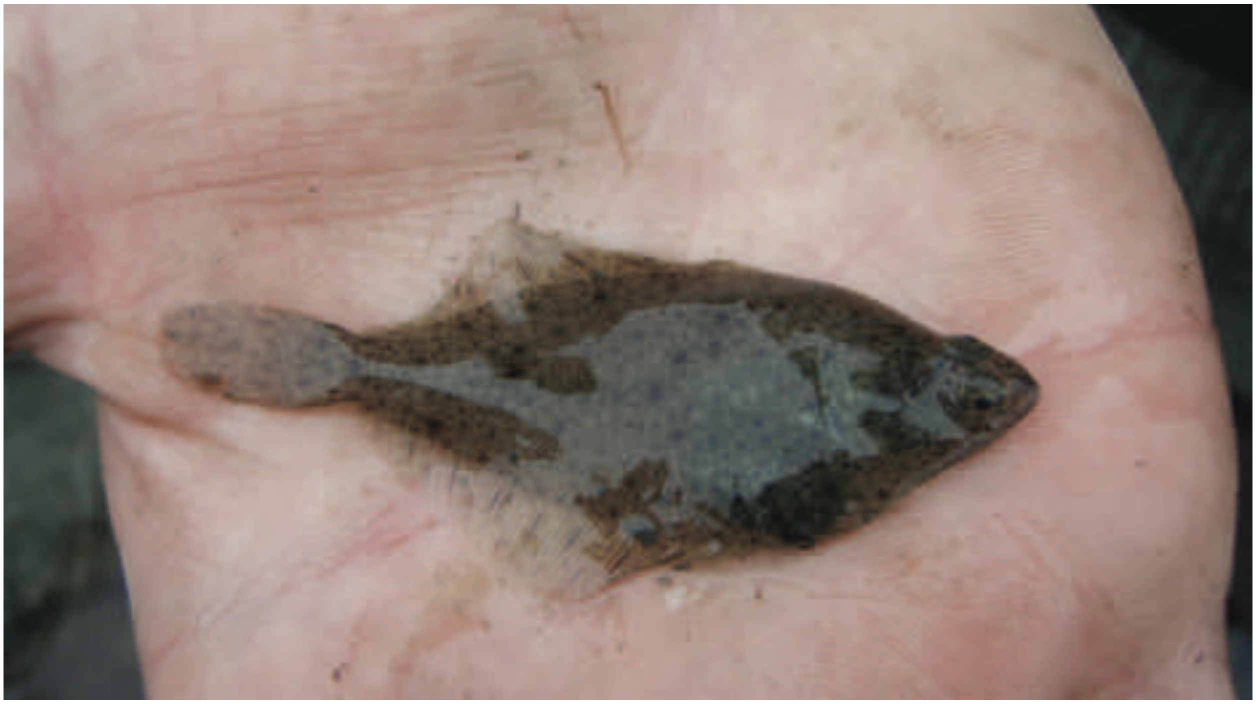


FIGURE 11. ENGLISH SOLE: Documented juvenile presence in Washington, Oregon and California estuaries.

ENGLISH SOLE

(*Parophrys vetulus*)



© Kirsten Ramey/CDFW

The English sole, *Parophrys* (formerly *Pleuronectes) vetulus,* is a right-eyed flatfish with a distinctively pointed head. It is a common species ranging from northwest Alaska (Bering Sea) to Bahia San Cristobal, central Baja California, Mexico (Miller and Lea 1972). Adults are typically found on soft sediments between 35 and 250 m depth, but have been captured to a depth of 550 m (Emmett et al. 1991). English sole are not commonly caught in the recreational fishery, but for more than a century, they have been an important component of the bottom trawl fishery operating along the West Coast (Stewart 2007). English sole is one of the few species along the West Coast to have been the subject of many studies (beginning in the 1970s) examining the relative contribution of alternative juvenile habitats to the offshore adult populations and the value of estuaries as nursery habitat. There is substantial evidence to support the contention that, over a large portion of the West Coast, estuaries are valuable nursery habitat for this species (see Box 11).

Life History and Ecology

The largest recorded English sole was 56 cm (Miller and Lea 1972), and the maximum estimated age for this species is 22 years (Love 1996). Adult English sole do not have specific migration patterns, but small seasonal movements along the coast are probably common, and some tagged fish have moved more than 320 km (Jow 1969). Seasonally, adults move between deeper water in winter and shallower water in summer (Leet et al. 2001).

The spawning period for English sole on the West Coast is long and variable. Most spawning occurs between September and April, often with multiple peaks (Laroche and Richardson 1979, Lassuy 1989a, Leet et al. 2001, Rooper et al. 2006a; Table 2). Eggs hatch four to 12 days after spawning, and the larvae are pelagic for two to four months (Rosenburg and Laroche 1982, Laroche et al. 1982). In a 4-year study off the coast of Oregon, larval English sole occurred primarily in waters less than 200 m deep (Laroche and Richardson 1979). Pelagic larvae sink as they grow,

© John Bragg/SSNERR

and then settle to the seafloor at a size of 18–22 mm (Misitano 1976, Rosenberg and Laroche 1982).

Recently-settled English sole occur on shallow sand and mud bottoms in nearshore coastal habitats (usually less than 16 m depth) and in estuaries (Laroche and Holton 1979, Rosenberg 1982, Krygier and Pearcy 1986). The combination of multiple spawning episodes and variability in ocean conditions can create multiple cohorts of age-0 juveniles in estuaries (Krygier and Pearcy 1986). The youngest juveniles often use tidal flats and shallow shoals (Baxter et al. 1999). Juveniles gradually move to deeper water as they grow, and most age-0 fish have left juvenile rearing habitats once they reach a size of 130–160 mm TL (Misitano 1976, Yoklavich 1982, Krygier and Pearcy 1986). Some juveniles seem to remain in shallow nearshore areas, or return to these habitats during the second year of their life, when reduced temperatures allow (Gunderson et al. 1990, Baxter et al. 1999).

As juveniles grow, the size of prey items increases and the types of prey they select change (Toole 1980). The smallest juveniles feed primarily on epibenthic crustaceans (e.g., harpacticoid copepods, cumaceans) and later add polychaetes and other infauna to the diet (Toole 1980, Hogue and Carey 1982). Larger juveniles found in subtidal channels consume bivalves, amphipods and a variety of other invertebrates (Toole et al. 1987). Adults are opportunistic feeders eating surface-active and shallowly burrowed prey, such as worms, small crustaceans, clams and occasionally small fish, crabs and shrimp (Cailliet et al. 2000). The main predators of juveniles are probably piscivorous birds, larger fishes (e.g., lingcod, rock sole, spiny dogfish) and marine mammals. Adults may be eaten by marine mammals, sharks and other large fishes (Emmett et al. 1991, Cailliet et al. 2000).

Timing and Use of Estuaries

Juvenile habitat for English sole is shallow, soft-bottom, open coastal habitat and estuaries of various types, including embayments, lagoons and sloughs (Table 3; Laroche and Holton 1979, Krygier and Pearcy 1986, Rogers et al. 1988). The number of juveniles at open coast sites has been observed to decrease sharply after initial settlement, concurrent with an increase in small juveniles in adjacent estuarine habitats. For example, in Oregon, densities of transforming larvae were sometimes higher at Moolack Beach than in Yaquina Bay, but densities of juvenile fish larger than 30 mm were usually more than an order of magnitude higher in Yaquina Bay (Krygier and Pearcy 1986). Migration into Yaquina Bay occurred over a size range of 25–40 mm (Krygier and Pearcy 1986). Similarly, recently-settled juveniles off the Washington coast were common both on the open coast and in estuaries, but most medium-sized juveniles (approximately 55 mm) were found in estuaries (Gunderson et al. 1990). Much of this pattern is likely due to migration into estuaries, but differential survival may be a contributing factor.

Transport of larvae into nearshore habitats is not well understood, but it has been suggested that oceanic onshore transport processes may help bring late-stage larvae into nearshore areas (Boehlert and Mundy 1987, Toole et al. 1987, Parnel et al. 2008). Selective tidal transport—the movement of post-settlement flatfish off the bottom during flood tides—may facilitate transport into estuaries (Toole et al. 1987). Boehlert and Mundy (1987) found that transforming English sole larvae were usually most abundant during flood tides at night near the seafloor in the lower portion of the Yaquina Bay estuary, and that recruitment to the bay was correlated with on-shore Ekman transport during the period of larval recruitment from mid-February to May. However, in May and June, when surface water transport was offshore, they observed that new recruits were typically of later juvenile stages that may have come from adjacent coastal habitats.

The timing of juvenile migration into estuaries is very protracted because of the long spawning period and the large size range over which migration occurs. Migration of late-stage larvae or early-stage juveniles has been observed to begin in winter months in Yaquina Bay, San Francisco Bay and Elkhorn Slough (California), with peak numbers occurring between April and June (Pearcy and Myers 1974, Ambrose 1976 as cited in Yoklavich 1982, Baxter et al. 1999). In Willapa Bay and Grays Harbor, Washington, age-0 sole seem to move into estuaries after settlement, and most of them eventually migrate into an estuary by 55 mm (Gunderson et al. 1990).

Throughout their range, juveniles move to deeper water as they grow and continue to do so after they migrate to the open coast (Toole 1980, Krygier and Pearcy 1986). In San Francisco Bay there is a general pattern of new recruits using intertidal areas in spring, subtidal shoals in summer and channel habitat for the rest of the year (Baxter et al. 1999). Toole (1980) also found that English sole moved from intertidal areas to subtidal channels in Humboldt Bay. They disappeared from intertidal areas in early fall at an average size of 82 mm.

The rapid decrease in densities of age-0 English sole in estuaries during the fall and winter months is evidence of migration to offshore areas. In Washington, English sole begin migrating from the estuaries at about 75 mm, and few remain in estuaries during their second year of life (Gunderson et al. 1990). In Yaquina Bay, the average density and size of age-0 fish decreased in the late fall, suggesting larger-sized juveniles had left the estuary, and most fish had migrated out of the estuary by 150 mm (Westrheim 1955, Olson and Pratt 1973, Krygier and Pearcy 1986, de Ben et al. 1990). Similar patterns have been observed in Tillamook Bay and Humboldt Bay (Forsberg et al. 1977 cited in Krygier and Pearcy 1986, Toole 1980). However, some age-0 and age-1 fish were present in Yaquina Bay in the winter, but the age-1 fish disappeared the following spring (Krygier and Pearcy 1986). In San Francisco Bay, juvenile English sole may reside in the estuary for six to 18 months before migrating to the coast to mature (Baxter et al. 1999). Limited otter-trawl sampling in open coast habitat adjacent to the mouth of San Francisco Bay caught age-0 fish in each month sampled, but most were caught in October, as would be the case if estuary-reared fish exited the estuary in fall (Baxter et al. 1999). Thus, similar to other studies, this estuary seems to be an important, but not an exclusive, rearing area.

Substrate type may influence English sole distribution in estuaries, but the overall importance of substrate as a determining factor is unclear. English sole are commonly found on submerged mudflat and sandy intertidal areas (Toole et al. 1987, Cailliet et al. 2000), but they are also collected in areas with submerged vegetation (Table 4). Juvenile English sole are found in shallow marshes, tidal creeks and eelgrass beds, habitats that may provide advantages of cover and increased prey densities (Barry and Cailliet 1981, Barry 1983, Phillips 1984, Yoklavich et al. 1991). In Humboldt Bay, Misitano (1970, as cited in Toole et al. 1987) compared intertidal habitats, and found that areas with mud and sparse seagrass had the highest densities of English sole.

However, studies in many other estuaries did not find English sole abundance to be higher in seagrass beds than on mud or sand flats (Bayer 1981, Borton 1982 as cited in Toole et al. 1987). In Willapa Bay, Washington, Hosack et al. (2006) found no statistical differences in catch rates among seagrass, non-native oyster beds and mudflats. Rogers (1985 as cited in Toole et al. 1987) surveyed areas with sand, silty sand and mud—either bare, or with varying types of biogenic materials (e.g., shell hash, seagrass)—and found no obvious differences in abundance of juvenile English sole attributable to substrate type or bottom cover.

Upper thermal tolerance likely limits use of shallow water habitats by English sole, particularly in estuaries near the southern edge of their range (Yoklavich 1982, Yoklavich et al. 1991, Baxter et al. 1999). Laboratory experiments have found a significant reduction in growth rate of juveniles reared at 17–18ºC compared to 13–15ºC (Williams and Caldwell 1978, Yoklavich 1982). The mean upper lethal temperature was found to be between 25.7 and 27.0°C for juvenile and adult English sole subjected to a gradual rise in temperature (Ames et al. 1978). Baxter et al. (1999) reported for San Francisco Bay, that age-0 fish initially migrated to intertidal and subtidal areas, but as intertidal temperatures approached and exceeded 20°C in late spring, the fish moved to deeper and cooler shoal and then channel habitats.

Juvenile English sole tolerate a wide range of salinities (Table 3), but it is the lower limit that influences their distribution in estuaries. In Pacific Northwest estuaries, Rooper et al. (2003) found that the average density of juvenile English sole decreased with decreasing salinity, especially for salinities less than 18 ppt. Olson and Pratt (1973) considered salinity in the upper estuary of Yaquina Bay, specifically the wide range (0–34 ppt) and extreme variability, to be the most important factor causing low density of English sole. The extent of upper estuarine area that is used by juveniles in San Francisco Bay seems to be influenced by the flow of fresh water (Baxter et al. 1999). In years when freshwater flows are low, English sole were more abundant in San Pablo Bay and even Suisun Bay. Conversely, in years with extremely high freshwater flows, low salinities (less than 12 ppt) in the upper estuary eliminated or reduced juvenile English sole use of Suisun and San Pablo bays. However, in estuaries in which salinity generally remains above 21 ppt year-round (e.g., Humboldt Bay, Elkhorn Slough), salinity did not seem to have a strong influence on abundance (Toole et al. 1987).

The depth, salinity and temperature associations of age-0 English sole may result in habitat partitioning and a reduction in inter- and intra-specific competition among flatfish using estuaries. For example, in San Francisco Bay, newly recruited English sole are separated from similarly-sized speckled sanddabs and starry flounders, because sanddabs prefer cooler channel habitats, and starry flounders prefer fresher and warmer waters (Baxter et al. 1999). Similarly, Rooper et al. (2006b) found that, because Pacific sanddabs are not as tolerant as English sole of the relatively warm water (13–17.5°C) found in side channels, competition between these two species is reduced.

Gunderson et al. (1990) suggested that estuaries offer English sole a refuge from competition with buttersole, whose diet overlaps considerably with that of English sole on the open coast. Toole (1980) suggests that the ontogenic movement of juvenile English sole from intertidal areas to subtidal channels was driven by changes in feeding habits and possibly resulted in a reduction in intraspecific competition among younger and older 0-age cohorts. Rooper et al. (2003) also suggested that changing habitat use patterns of small and large juveniles reduce intraspecific competition in estuaries, but they attributed it to smaller size classes having more restrictive habitat requirements in depth and temperature than larger size classes.

© MBNMS

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile English sole have been documented in estuaries from Puget Sound to Los Angeles Harbor, California (Figure 11), but they are rarely found in estuaries south of Point Conception (Monaco et al. 1990, Allen et al. 2006). Juveniles use a wide variety of the estuary classes (sound, embayment/bay, riverine estuary and lagoonal estuary) and estuarine sub-classes found along the West Coast (Figure 11, Table 4). Only a few studies have documented juvenile English sole in lagoonal estuaries, despite the abundance of this estuary class in central and northern California (Figure 1). It is not clear if this pattern is due to lower use of this estuary class by juvenile English sole, or to less sampling effort in these relatively small, and often remote, estuarine systems.

Abundance of larval and juvenile English sole seems to increase during cold-water regimes, especially in the southern portion of their range. Abundance of juvenile English sole in San Francisco Bay was very high during a cold-water regime that lasted from 1999–2011 (Fish et al. 2013). Fish et al. (2013) suggested that during the cold-water regime, the distribution of coastal adults shifted southward, increasing the abundance of spawning stock off central California.

Threats

Harvest of English sole by the commercial bottom trawl fishery reduces overall population abundance and has the potential for strong negative impacts if not properly managed. Harvest of English sole along the West Coast is managed by the Pacific Fishery Management Council, whose most recent stock assessment was completed in 2007 (Stewart 2007). In 1953 and 1992, the English sole population was estimated to be at 20% and 23%, respectively, of the population size that would exist in the absence of fishing (Stewart 2007). Since 1992, the population has increased rapidly to approximately 116% of the unfished population size by early 2007.

© Brent Hughes

Rooper et al. (2004) hypothesized that recruitment from estuaries to the adult population outside the estuaries is relatively constant, due to a density-dependent carrying capacity of estuary rearing areas. This stability in recruitment to the post-juvenile population seemed to be robust, even in response to changes in environmental conditions (e.g., upwelling, sea surface temperature, El Niños). Activities that negatively impact the nursery function of estuarine habitats, or reduce the carrying capacity of estuaries for English sole, could ultimately reduce the size of the adult population.

There are a variety of potential threats to juvenile English sole in estuarine habitats along the West Coast (Table 5). Thermal pollution has the potential to alter the suitability of existing estuarine nursery areas, particularly near the southern end of their distribution (Lassuy 1989a, Yoklavich et al. 1991, Baxter et al. 1999). For example, distribution in shallow habitats and length of stay of English sole in Elkhorn Slough could be limited by their thermal tolerance; migration of juveniles out of the slough in late summer and early fall coincides with slough water temperatures approaching 17–20˚C (Yoklavich 1982).

High water temperatures have also been associated with increased mortality due to parasitism by the microsporidean protozoan, *Glugea stephani*. In Yaquina Bay, juveniles become infected in the upper estuary, the only part of the estuary where water temperature far exceeds that of the coastal ocean (Olson 1976 and 1981 as cited in Toole et al. 1987). In addition to *G. stephani*, several other parasites infect English sole in the Yaquina Bay estuary, and the composition of the parasite fauna was found to have changed substantially between 1971 and 2000 (Olson et al. 2004). Climate-associated phenomena and changes in the estuary ichthyofauna were identified as the two most likely factors influencing the host-parasite relationship. Olson et al. (2004) hypothesized that changes in the ichthyofauna since 1971 could be caused by increases in the number of California sea lions in Yaquina Bay since their protection under the Marine Mammal Protection Act in 1972.

Chemical contaminants in sediments pose a significant threat to English sole given that this species dwells on the bottom, feeds on organisms living in the sediments and inhabits embayments polluted by runoff from municipal, industrial and agricultural activities. Myers et al. (1998) found that exposure to polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), dichlorodiphenyltrichloroethane (DDT), organochlorine insecticides (chlordanes) and polychlorinated hydrocarbons (dieldrin) were significant risk factors for toxicopathic liver lesions in English sole. Relative risks for most lesions were significantly higher in fish from contaminated sites in Puget Sound and San Francisco Bay.

Studies on English Sole in Puget Sound on the effects of exposure to contaminants show that the fish are experiencing a range of biological effects, including reproductive dysfunction and altered immune competence (Johnson et al. 1998). There is some evidence of reduced survival in fish from urban areas of Puget Sound due to increased disease (Johnson et al. 1998). An analysis of endocrine disrupting compounds (EDCs) in bile of male English Sole in Puget Sound (da Silva et al. 2013) found that fish were exposed to these anthropogenic EDCs, especially at the most urban of the sites.

Intentional application of pesticides for aquaculture is another source of chemical exposure. In Willapa Bay and Grays Harbor, commercial growers of non-native Japanese oysters sometimes apply carbaryl (an organocarbamate pesticide) to control populations of native burrowing shrimp on mudflats. Surveys after the carbaryl application have shown that fish of many species are killed along with the burrowing shrimp that the insecticide is intended to eliminate (Hueckel et al. 1988 cited in Feldman et al. 2000). In one survey of treated oyster beds, English sole comprised 27% of the fish that were killed (Tufts 1989 and 1990 as cited in Feldman et al. 2000).

Habitat modifications that reduce or degrade the available area of soft-bottom intertidal and subtidal habitat impact this species. For example, sediment accumulation in Bolinas Lagoon, California, is reducing subtidal shallow and channel habitat areas and is likely linked to observations that populations of several species of flatfish, including English sole, seem to have decreased over the past decades (PWA et al. 2006). Intertidal juvenile flatfish habitat is also lost when this zone is hardened with riprap or other hard structure. In Puget Sound, juvenile flatfish (mostly English sole) were more abundant at sand beaches than in areas where riprap extended into the upper intertidal zone (Toft et al. 2007).

English sole seem to tolerate moderately hypoxic conditions (Boese 1988), but very low dissolved oxygen can affect the distribution of this species. Surveys of English sole along a hypoxic gradient on the Oregon coast found no significant hypoxic effects on fish distribution (Keller et al. 2010). However, Levings (1980) found that the distribution of adult English sole was influenced by hypoxic conditions—fish density declined when dissolved oxygen dropped below three mg per liter, and there were no adults when dissolved oxygen reached one mg per liter. Tagged English sole in Hood Canal, Washington, showed little evidence of large-scale directed movement out of hypoxic regions (Froehlich et al. 2013). However, it is possible that they used smaller-scale movements to take advantage of local variability in dissolved oxygen levels to find refuge from hypoxic conditions.

Nutrient loading may reduce habitat suitability for English sole by reducing dissolved oxygen. In Elkhorn Slough, hypoxic conditions were found to have negative effects on three flatfish species (California halibut, English sole and speckled sanddabs). There were significant declines in predicted presence of these species as a function of decreasing dissolved oxygen. The threshold for complete absence was 4 mg per liter (Hughes et al. 2012). Hypoxic conditions in Elkhorn Slough were found to be influenced by El Niño intensity, with improved dissolved oxygen conditions likely due to increased flushing during rainy years and suppression of upwelling that lowers the depth of the deep sea oxygen minimum layers (Hughes et al. 2012).

Sea-level rise will have a significant influence on the availability of preferred habitats for this species. However, the overall impact of sea-level rise on the population is difficult to predict because, based on local topography and hydrology, it is likely to increase the availability of suitable habitat in some estuaries while diminishing it in others.

© Kirsten Ramey/CDFW

BOX 11. WEST COAST ESTUARIES ARE KEY NURSERY GROUNDS FOR ENGLISH SOLE

English sole is one of the few species along the West Coast for which studies have directly measured the relative contribution of alternative juvenile habitats. In addition, there are a number of studies that have explored different aspects of nursery function, in particular, relative growth and survivorship. There is substantial evidence to support the contention that estuaries are key nursery grounds for English sole.

Do estuaries contribute more juveniles to offshore adult populations?

The relative contribution of alternative estuarine habitat has been examined in many studies ranging from central California to Puget Sound. Most studies have compared relative contribution of estuaries and adjacent open coast habitat, though a few have considered alternative habitats within estuaries. Most studies have not directly measured contribution, but instead inferred it using a variety of methods. For example, based on the presence of estuarine-acquired parasites as indicators of former estuarine residence of older English sole collected offshore, Olson and Pratt (1973) concluded that estuaries may be the exclusive nursery ground for English sole on the Oregon coast. Similarly, Rooper et al. (2004) suggest that, based on the average August density of age-0 English sole in four estuaries spanning Oregon and Washington, the English sole population on the Oregon–Washington shelf could potentially be supported solely by estuarine production.

Other studies have found that although densities of age-0 English sole are usually much greater in summer in estuarine habitats, a portion of the age-0 fish remains in open coast habitats and never enters estuaries. The estimated relative contribution of estuary versus open coast juveniles has varied depending on the study. Rogers et al. (1988) found that at least half of 0-age sole in the Grays Harbor nearshore area were likely to have inhabited the estuary during the first year of life despite the 18 times greater geographic extent of the offshore area. In Oregon, Krygier and Pearcy (1986) used relative catch per square meter and total area of suitable habitat to calculate a total abundance of age-0 juveniles in open coast habitat of 643×10^5 (in May–June) and 70×10^5 (in June) compared to 140×10^5 (May–June) for the five estuaries. These estimates suggest that the open coast is an important initial settling area for English sole and that both estuaries and the open coast are important habitat for fully transformed age-0 English sole.

Two recent studies directly measured relative contribution of alternative juvenile habitats to the subadult population of English sole. Using chemical habitat fingerprints recorded in otoliths, Brown (2006) found that estuarine habitats in central California provide significant nursery habitat for English sole. In a sample of 67 subadults and adults collected in the commercial fishery in Monterey Bay, 45% to 57% were identified as having used estuarine habitats even though estuaries comprise much less than 50% of the available juvenile habitat in central California.

Chittaro et al. (2009) used otolith chemistry to examine the relative contribution of estuarine habitat located in different regions within Puget Sound to the subadult English sole population in the Sound. Over the two years of the study, completely different spatial patterns of regional contribution were observed; three regions were identified as important nursery habitat one year whereas only one region was identified as significant nursery habitat the following year. This study suggests that the relative value of alternative juvenile habitats may vary from year to year and that the availability of a variety of nursery habitats may increase chances for good survival of young fish from at least one habitat, when adverse conditions affect the other juvenile habitat(s).

Do estuaries support higher density?

In most studies, the unstated premise has been that, all else being equal, habitats with higher densities of juveniles are likely to make greater contributions to the production of adults than habitats with lower densities of juveniles. In the majority of studies examined (see section above), estuarine habitats are found to support higher densities of juveniles relative to open coast habitat. Assuming these individuals are successful in recruiting to the adult population, then estuaries seem to be very productive nurseries.

Do fish grow faster in estuaries?

Higher growth rates during the juvenile phase can have a marked influence on an individual's success in both the juvenile and subsequent adult phases. For example, rapidly growing juveniles will be less vulnerable to size-selective mortality and will attain a larger size at the end of the juvenile period, which may improve recruitment success to the adult habitat. Below we provide some evidence that estuaries can support increased growth rates, but by no means is the evidence uniform or conclusive.

A few studies have used size progression in length-frequency histograms to compare 'apparent' growth rates in estuarine and coastal habitats. Off Washington, Shi et al. (1997) calculated growth rates of 0.33–0.49 mm per day for the period from May to September. Growth rates were not found to be significantly different among fish living in Grays Harbor, Willapa Bay and the adjacent nearshore coast. Off Oregon, apparent growth rates of age-0 English sole in the spring-fall period were generally higher and less variable (0.46–0.49 mm per day) for fish collected from Yaquina Bay than those off Moolack Beach (0.28–0.42 mm per day) (Krygier and Pearcy 1986).

Other studies have measured growth rates of estuarine and coastal fish more directly. Based on both the width of daily increments in otoliths of wild fish and growth rates measured in caging experiments, Brown (2003) found that estuaries supported faster growth rates in age-0 English sole than adjacent coastal habitats in central California. Specifically, caged juveniles grew an average of 0.18 mm per day in Elkhorn Slough and 0.04 mm per day in Monterey Bay. In contrast, growth rates calculated from increments in otoliths were not significantly different for juveniles collected from Yaquina Bay (0.33 mm per day) and Moolack Beach (0.34 mm per day) (Rosenberg 1982).

In laboratory experiments, mean growth rate of juvenile English sole increased with increased food ration (Yoklavich 1982), thus habitats with higher prey abundance may support increased growth rates. Yoklavich et al. (1991) suggest that warm temperature and elevated nutrient content in some estuarine habitats may enhance production of prey items during spring and early summer. There is some evidence that more prey items are available in estuaries, particularly in the summer months. In the Monterey Bay area, densities of infaunal and epifaunal invertebrates can reach 10,000 per square meter on the coast (Oliver et al. 1980) and 50,000 per square meter in Elkhorn Slough (Nybakken et al. 1982). Gunderson et al. (1990) reported similar differences in prey densities between Grays Harbor estuary and the coastal habitats in Washington. These higher densities of prey items in estuaries may support higher growth rates in juvenile flatfish living in estuaries compared to those living on the coast. Faster growth rates may not be realized by all age-0 English sole in estuaries, but enhanced growth rates may be achieved by some based on availability of preferred habitat conditions in some locations or in some years.

Evidence of increased survival in estuaries?

It is often stated that estuaries are a preferred habitat because juvenile fish experience higher survival rates than in open coast habitats. However, only a few studies have attempted to compare survival rates of age-0 English sole in alternative juvenile habitats. Krygier and Pearcy (1986) found no evidence for grossly higher mortality rates at Moolack Beach than in Yaquina Bay. Shi et al. (1997) found that mortality of juvenile flatfish is highest during and immediately after settlement, irrespective of the habitat type. Toole (1980) hypothesized that intertidal areas give recently metamorphosed English sole protection from predation as well as decreased competition for food from larger flatfish in channels, however, he did not directly test this hypothesis.

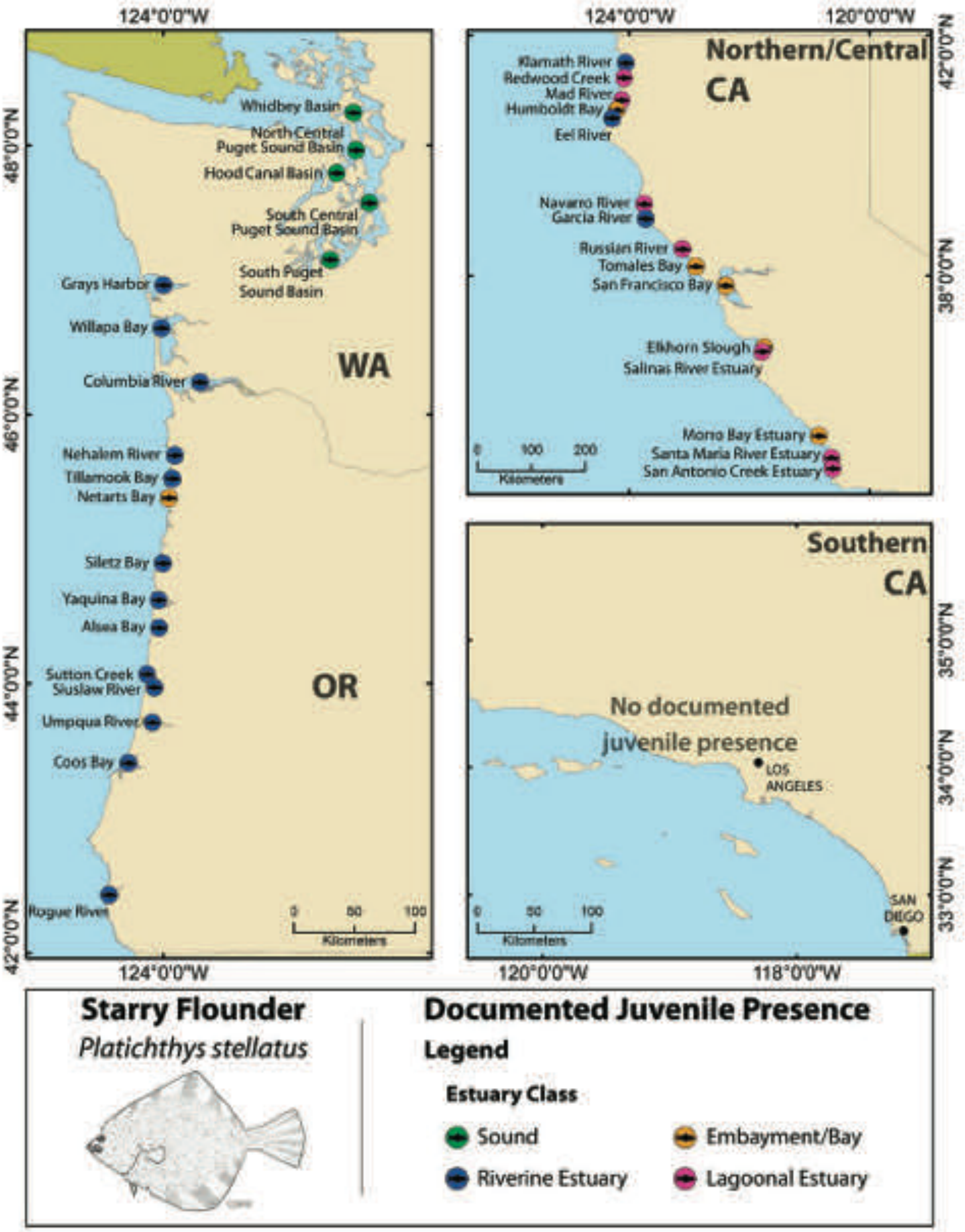


FIGURE 12. STARRY FLOUNDER: Documented juvenile presence in Washington, Oregon and California estuaries.

STARRY FLOUNDER

(*Platichthys stellatus*)

© Mike Wallace/CDFW

Of all the flatfish, the starry flounder (*Platichthys stellatus*) is probably the most easily identified because of the alternating light and dark bars that occur on both the dorsal and anal fins. Although it is a member of the right-eyed flounders, a large proportion of individuals are left-eyed (Orcutt 1950). Starry flounder have a very broad geographic distribution along the rim of the North Pacific Ocean. In the Eastern Pacific Ocean, they occur from the Bering Sea and Aleutian Islands south to Los Angeles, California, although they are rare south of Point Conception, California (Figure 12; Orcutt 1950, Emmett et al. 1991, Ralston 2005, McCain et al. 2005). Adult starry flounder inhabit shallow coastal marine waters, often near estuaries, and juveniles occur in estuaries. This species may be estuarine dependent given the strong preference of juveniles for shallow, warm, low salinity habitats and the relative lack of age-0 to age-2 fish observed in coastal marine areas (Emmett et al. 1991, Baxter et al. 1999, McCain et al. 2005). The starry flounder is a species of moderate importance in the commercial bottom-trawl fishery, from Washington to Point Conception, and is an important component of the recreational fishery in some areas (Ralston 2005).

Life History and Ecology

Starry flounder can reach a size of 91 cm (Orcutt 1950) and have been aged up to 17 years for males and 24 years for females (Campana 1984; Table 2). Most occur in waters less than 150 m deep, but occasionally they are collected off the continental shelf in excess of 350 m (Cailliet et al. 2000). Adults move inshore in late winter and early spring and then move offshore into deeper water in the summer and fall (Ralston 2005), but these coastal movements are generally less than 5 km (McCain et al. 2005). Spawning occurs primarily during the winter months; November–February in central California and February–April off Washington (Garrison and Miller 1982, Cailliet et al. 2000).

Larvae are epipelagic and found primarily near shore (within 37 km) and in estuaries (McCain et al. 2005). Larval duration is approximately two months (Orcutt 1950), at the end of which time transforming larvae (10–12 mm) or newly settled juveniles migrate into brackish or freshwater habitats. Settled age-0 starry flounder are found almost exclusively in estuaries, as are age-1 fish (Orcutt 1950, Baxter et al. 1999, Kimmerer 2002). As they grow, juveniles progressively move to water of higher salinity until they migrate to open coastal habitats. By age-2, many fish have migrated to ocean habitats adjacent to the estuary in which they reared (Ralston 2005).

Starry flounder larvae are planktivorous, whereas juveniles and adults are carnivorous. Small juveniles feed on small crustaceans (e.g., copepods, mysids, amphipods), annelid worms, nemerteans, priapulids and tanaids (Cailliet et al. 2000). As fish grow, they feed on a wider variety of items, including crabs, bivalves, echinoderms and other more mobile prey (Orcutt 1950). Predators include larger fishes, sharks, herons, cormorants, seabirds, pinnipeds and other marine mammals (Cailliet et al. 2000).

Timing and Use of Estuaries

Age-0 starry flounder seem to seek shallow, warm, low salinity rearing habitats where they stay for two years or more (Baxter et al. 1999; Table 3). Juveniles are commonly found in a variety of shallow estuarine habitats, including shoals, intertidal mudflats, tidal marshes, tidal creeks, lagoons and sloughs (Table 4; Orcutt 1950, Moyle et al. 1986, Yoklavich et al. 1991, Baxter et al. 1999). In addition, juveniles are collected from the mouths and tidally influenced sections of streams, creeks and rivers (Orcutt 1950, Kukowski 1972, Baxter et al. 1999).

Migration into the estuary may occur as late-stage larvae, recently settled juveniles, or as slightly larger juveniles. Pre-settlement larvae were collected in San Francisco Bay only from March to June (Baxter et al. 1999). Orcutt (1950) collected numerous 10–29 mm juveniles from March–May in the Salinas River, California. Juveniles (30–70 mm) were caught most frequently from May–July in San Francisco Bay (Baxter et al. 1999). Migration in late May or June of starry flounder larger than 30 mm also has been observed in Elkhorn Slough, California (Yoklavich et al. 1991) and in the Columbia River Estuary at upper estuary sites (Haertel and Osterberg 1967, McCabe et al. 1983).

Patterns in the distribution of different size classes along the axis of the Yaquina Bay estuary indicated that the smallest starry flounder frequented the less saline upper portion of the estuary all year (de Ben et al. 1990). The 60–180 mm size range was most abundant in February, the 180–200 mm size range was most abundant in late spring and early summer, and the 240–280 mm size range used the lower estuary during the winter months.

A comparison of the relative abundance of starry flounder in mudflat and biogenic habitats in Willapa Bay, Washington, found no apparent preference among mud, oyster and seagrass habitats, however sample sizes were low (Hosack et al. 2006). Relative abundance in beach seine collections from nearshore waters of the Bering Sea suggest that starry flounder prefer sand to cobble, and cobble to bedrock (Thedinga et al. 2008). In laboratory trials, juvenile starry flounder preferred fine-grained sediments and never selected round granules, coarse sand, or pebble (Moles and Norcross 1995). Juveniles seemed to select larger particles with increasing fish size, which may indicate that the ability to use coarser sediments increases with body size (Moles and Norcross 1995).

The starry flounder is a euryhaline species that is capable of tolerating a wide range of salinities, especially during the juvenile phase. The majority (66%) of the starry flounder collected from Yaquina Bay were in waters ranging from 16–34 ppt, whereas 18% (primarily in the 30–120 mm size class) were collected in waters with salinities of 0–2 ppt (de Ben et al. 1990). In controlled experiments, growth and survival rates did not differ for juveniles reared under salinities ranging from 5–33 ppt, and there were no signs of osmoregulatory disturbance or stress across this salinity range (Lim et al. 2013). Wada et al. (2007) found that during metamorphosis, starry flounder developed strong low-salinity tolerance, and juveniles were able to survive in 0 ppt.

In the San Francisco Bay, Hieb and Baxter (1993) determined specific habitat criteria for starry flounder less than 70 mm in length: 90% were collected from habitat having bottom depth less than 7 m and salinity less than 22 ppt. Additional survey data from San Francisco Bay suggests a negative correlation between abundance of age-0 starry flounder and salinity (Baxter et al. 1999, Kimmerer 2002). Baxter et al. (1999) suggest that, during the winter, low salinity habitats may provide a refuge from predators with less tolerance for low salinity.

Juvenile starry flounder also have a wide thermal tolerance (Emmett et al. 1991), but seem to prefer warmer waters. In San Francisco Bay, age-0 fish were collected from waters ranging from 8–23°C, but seemed to select warmer waters within the range available (Baxter et al. 1999). From June to October, age-0 fish were found in waters 16.4–23.8°C, and in winter they were collected in waters from 8–12°C. In Yaquina Bay, most juveniles (88% of those collected) were in waters 8–18°C (de Ben et al. 1990).

Recently settled juveniles along the coast may use outflow of warmer, low salinity water in the spring as cues to help them find estuaries (Baxter et al. 1999). In addition, juvenile starry flounder may seek habitats within estuaries with higher temperatures and lower salinity than are preferred by other flatfish species. Rooper et al. (2006) found evidence that variation in temperature and salinity tolerances result in habitat partitioning among co-occurring flatfish species in Pacific Northwest estuaries, with starry flounder preferring upper estuarine sites. In addition to allowing for reduced competition, Wada et al. (2007) suggested that the ability of starry flounder to settle into low salinity riverine estuaries at a young age and small size may be an adaptation to enhance survival after settlement by rapidly entering and settling into areas with lower predator densities.

Distribution of Documented Presence of Juveniles in Estuaries

Along the West Coast, juvenile starry flounder have been documented in estuaries from Puget Sound to the San Antonio Creek Estuary, California (Figure 12). Juveniles seem to use a wide variety of the estuary classes (sound, embayment/bay, riverine estuary and lagoonal estuary) and estuarine sub-classes found along the West Coast (Table 4). Unlike California halibut and English sole, juvenile starry flounder commonly occur in the mouths and tidally influenced sections of streams, creeks and rivers, including the Columbia River, Sacramento and San Joaquin Rivers in the San Francisco Bay area and the Salinas River in the Monterey Bay area (Orcutt 1950, Kukowski 1972, Bottom et al. 1984, Baxter et al. 1999). Occasionally, small juveniles have been collected 70 km or more upstream, such as in the Columbia River (Orcutt 1950) and the Fraser River, British Columbia (Richardson et al. 2000). Although estuaries are primarily used by juveniles age-2 and younger, large starry flounder are caught in the more saline deeper portions of larger estuaries, such as Puget Sound and San Francisco Bay (Haertel and Osterberg 1967, de Ben et al. 1990, Baxter et al. 1999).

Threats

The combined harvest of starry flounder in the commercial and recreational fishery reduces population abundance and has the potential for negative impacts if not properly managed. The Pacific Fishery Management Council is responsible for managing harvest of starry flounder on the West Coast. The fished stocks were assessed for the first time in 2005 (Ralston 2005). The assessment estimated a population size of 44% of unfished level for the stock off Washington-Oregon and 62% of unfished levels for the stock off California. Both these estimates were above the precautionary threshold (i.e., 40% of unfished levels). The assessment noted some important data gaps, including size and age composition of the landed fish and independent estimates of fish abundance. Ralston (2005) suggests that closed areas adopted by Washington and California in state waters have likely reduced trawl fishing impacts on starry flounder populations, which may result in an increase in abundance of this species along the West Coast.

Given its dependence on estuaries, the starry flounder population along the West Coast is threatened by activities that degrade estuarine habitat quality, or reduce the amount of available estuarine and riverine habitat (Table 5). Shoreline modification, such as armoring, has been shown to influence the distribution of flatfish, such as starry flounder. In the Duwamish River estuary, in Puget Sound, benthic species, such as starry flounder and staghorn sculpin, were captured more frequently and in higher numbers at unarmored sites compared to armored sites (Morley et al. 2012). Using enclosure nets and snorkel surveys along the shorelines of Seattle, Toft et al. (2007) found fewer flatfish associated with areas with intertidal riprap.

Alterations to tidal regimes and other changes in freshwater flow within estuaries have the potential to impact this species. Kimmerer (2002) suggests that species that hatch in or near the ocean prior to moving up the estuary, such as bay shrimp, starry flounder and Pacific herring, could be affected by changes in gravitational circulation in the seaward reaches of the San Francisco Bay estuary. Presumably these species use bottom currents to move into and up the estuary, thus alterations to the estuary that could interfere with this flow pattern could disrupt this mode of recruitment.

Reduction or diversion of fresh water flowing into estuaries has the potential to negatively impact juvenile starry flounder, given this species' preference for low salinity rearing habitat and the hypothesized advantages of reduced competition and predation rates in these habitats (Baxter et al. 1999, Rooper et al. 2006, Wada et al. 2007). Baxter et al. (1999) suggest that a reduction in freshwater outflow associated with the drought in California (1987–1992) was one factor associated with the decline in starry flounder observed in San Francisco Bay after the mid-1980s.

Habitat modifications that result in the restriction of tidal exchange in estuaries reduce available habitat for juvenile starry flounder. For example, the addition of dikes and other water control structures has significantly reduced flatfish habitat in Elkhorn Slough (Nelson et al. 2010). In Bolinas Lagoon, sediment accumulation is reducing subtidal shallow and channel habitat areas and is likely linked to observations that populations of several species of flatfish have decreased over the past decades (PWA et al. 2006).

Human use of estuarine habitat for aquaculture has the potential to negatively impact this species if that use alters available habitat or impacts water quality. For example, in Willapa Bay and Grays Harbor, commercial growers of non-native Japanese oysters sometimes apply carbaryl (an organocarbamate pesticide) to control populations of native burrowing shrimp on mudflats. Surveys of oyster beds after carbaryl application have shown that many fish species, including starry flounder, are killed in addition to the native species of shrimp that are targeted by these applications (Hueckel et al. 1988 cited in Feldman et al. 2000).

Chemical contaminants in sediments pose a significant threat to starry flounder given that this species is bottom dwelling, feeds on organisms that live in the sediment, and inhabits embayments polluted by runoff from urban and agricultural lands and discharge of municipal and industrial waste. Myers et al. (1998) found that exposure to polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), dichlorodiphenyltrichloroethane (DDT), organochlorine insecticides (chlordanes), and polychlorinated hydrocarbons (dieldrin) were significant risk factors for toxicopathic liver lesions in starry flounder. Relative risks for most lesions were significantly greater in flounder collected from contaminated sites in Puget Sound, San Francisco and San Diego bays and the Los Angeles area. In addition, studies on the effects of contaminants on starry flounder in San Francisco Bay suggest that reproduction is adversely affected in fish inhabiting sites with high levels of sediment contaminants (Spies and Rice 1988).

A recent study detected 13 currently-used pesticides in starry flounder collected from Santa Maria estuary, California (Smalling et al. 2013). This was the first study to document the occurrence of these pesticides in tissues of resident fishes, and there is limited information on the effects these chemicals could have on fish. Additional studies are needed to understand the impacts of pesticides on fishes in estuaries, especially small estuaries surrounded by agricultural lands. Juvenile starry flounder have also been shown to be sensitive to exposure to hydrocarbons. Moles (1998) found that flounder showed greater sensitivity to chronic exposure (28 days) to hydrocarbons than to acute exposure (4 days); the concentration of hydrocarbon that killed half the starry flounder in the chronic exposure trials was significantly lower than in the acute exposure trials.

Changes in species composition in a juvenile habitat, such as abundance of predator or prey species, can influence the abundance of starry flounder and the suitability of available habitat. Olson et al. (2004) noted that the growing numbers of California sea lions and harbor seals in Yaquina Bay between 1971 and 1997–2000 may have contributed to declining catch rates of adult starry flounder over the same period. In Suisun Marsh (San Francisco Bay), the invasion of a non-native bivalve, the overbite clam (*Potamocorbula amurensis*), has caused a major decline in mysid shrimp abundance (Feyrer et al. 2003). Prior to invasion, starry flounder relied heavily on mysids as prey items. After the invasion, mysids were a negligible contribution to the starry flounder diet, and this species had to switch to a much greater proportion of annelids.

Sea-level rise will have a significant influence on the availability of preferred habitat for this species. However, the overall impact of sea-level rise on the population is difficult to predict because, based on local topography and hydrology, sea-level rise is likely to increase the availability of suitable habitat in some estuaries while diminishing it in others.

© Walter N. Heady/TNC

SCORPAENIFORMES

Scorpaeniformes represent an incredibly diverse as well as ecologically and economically important order of bony fishes. For the purposes of this report, Scorpaenniformes include a sculpin (*Leptocottus armatus*, the Pacific staghorn sculpin) and a rockfish (*Sebastes auriculatus*, brown rockfish). These species represent the diverse array of life histories found in this order, with differing rates of maturity, longevities, maximum sizes, trophic levels and abundances in shallow coastal and estuarine waters. Both species are found along the West Coast of North America, ranging from Baja, Mexico north to the Gulf of Alaska (brown rockfish) and Bering Sea (staghorn sculpin). Both species are a concern for management, with brown rockfish targeted in commercial fisheries and both species sought by recreational anglers. Both species have been documented as using bays, sounds and estuaries throughout their life histories, with Pacific staghorn sculpin considered common in these systems. Little is known about the extent to which either of these species relies on estuaries during their juvenile stages.

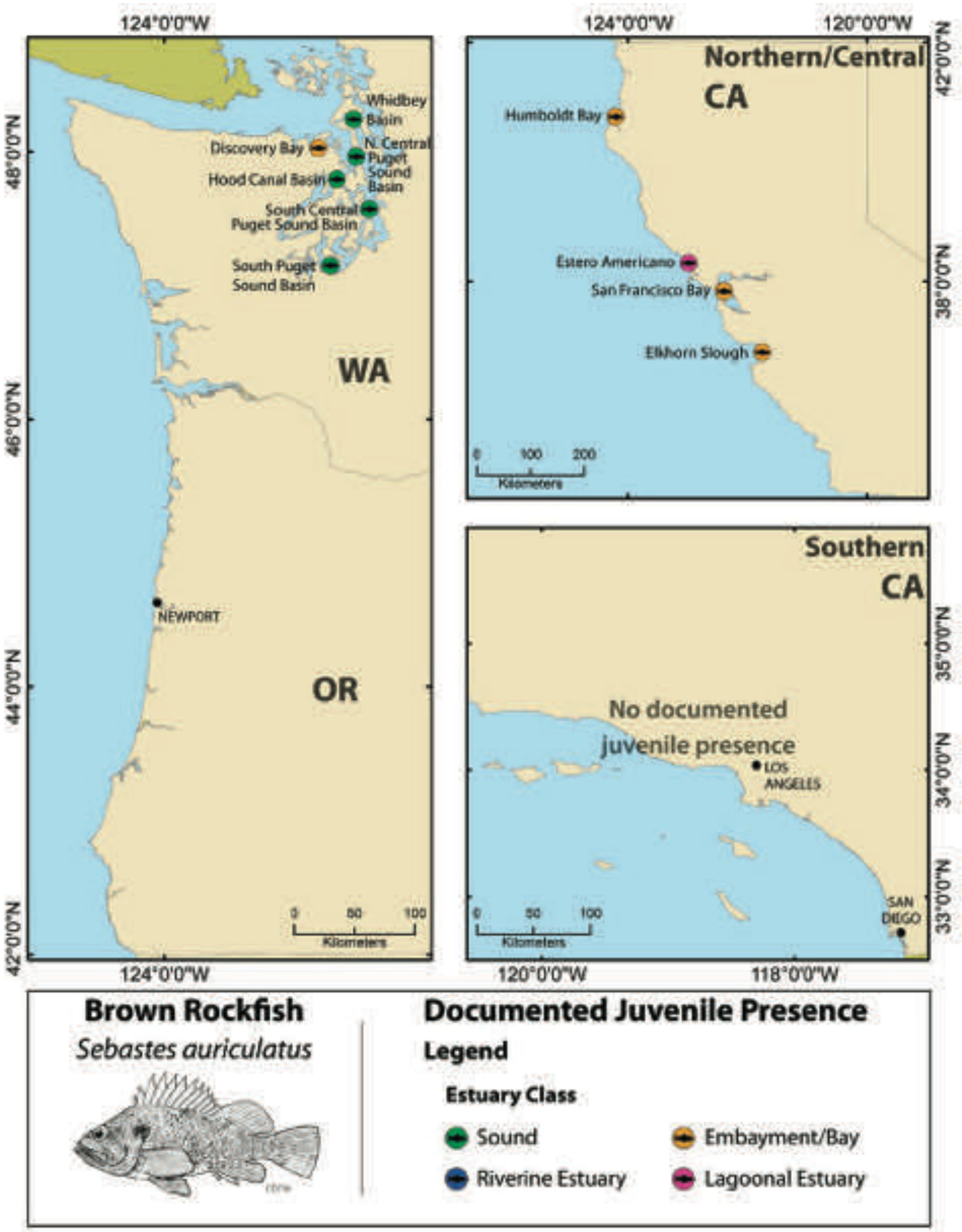


FIGURE 13. BROWN ROCKFISH: Documented juvenile presence in Washington, Oregon and California estuaries.

BROWN ROCKFISH

(*Sebastes auriculatus*)

© Dana Roeber Murray/Creative Commons

Brown rockfish occur from Prince William Sound, Alaska, to southern Baja California (Bahia San Hiploito), and are abundant in central and southern Puget Sound, and from Bodega Bay, California, to near the southern end of their range (Miller and Lea 1972, Love et al. 2002, Palsson et al. 2009). Brown rockfish use a variety of shallow water habitats, including coastal embayments and estuaries, and are found in Puget Sound, San Francisco Bay, Elkhorn Slough and Santa Monica Bay (Stein and Hassler 1989, Matthews 1990a, Baxter 1999, Brown 2002, Palsson et al. 2009).

Life History and Ecology

Brown rockfish are a moderately sized (580 mm maximum total length), long-lived (about 34 years) and slowly maturing species, with first maturity at two to three years of age and 160–190 mm, and 50% maturity at four to five years, 250–310 mm, and 100% maturity at 10 years, 380 mm (Table 2; Echeverria 1987, Cailliet et al. 2000, Love et al. 2002). Females may spawn more than once per year, between December and August, with the timing of peak spawning varying with latitude (Cailliet et al. 2000, Love et al. 2002). Larvae are planktonic (Baxter 1999), with early juveniles remaining in the coastal water column for two to three months before settling at a size range of 18–25 mm (West et al. 1994, Cailliet et al. 2000, Love et al. 2002).

Juvenile brown rockfish settle on a variety of relatively shallow (less than 36 m) coastal habitats, primarily over low and high rocky relief, but also to a lesser degree in seagrass, over sand, among drift algae and on canyon walls (Matthews 1990a, Baxter 1999, Love et al. 2002, Palsson et al. 2009). Brown rockfish are found year round in larger estuaries, such as Puget Sound and San Francisco Bay (Matthews 1990a, Baxter 1999, Palsson et al. 2009). In San Francisco Bay, age-0 brown rockfish immigrate into shallow open waters, remaining between one and two years (up to 240 mm) before migrating to the open coast (Baxter 1999). Juveniles eat a variety of small crustaceans, amphipods, copepods and shrimp with small fish and crabs constituting an important part of the diet of individuals greater than 130mm TL (Gains and Roughgarden 1987, Stein and Hassler 1989, Love et al. 2002). Brown rockfish are preyed upon by a variety of birds, marine mammals and fishes (Stein and Hassler 1989, Cailliet et al. 2000), with younger individuals particularly targeted by king salmon and harbor seals (Love et al. 2002).

Timing and Use of Estuaries

In Puget Sound, rocky relief is the primary habitat used by juvenile brown rockfish (Matthews 1990a, Baxter 1999, Palsson et al. 2009), while in San Francisco Bay juveniles use shallow open water habitats (Baxter 1999; Tables 3 and 4). In addition, juvenile brown rockfish may use sand, drift algae and seagrass, which may be an important settlement habitat in estuaries (Matthews 1990a and b, West et al. 1994, Love et al. 2002, Palsson et al. 2009). In larger estuaries, juvenile rockfish are found year round, though age-0 abundance is generally higher from early summer through December. Juvenile brown rockfish may remain in larger estuaries as they reach adulthood, while in other systems they may move to coastal systems after one to two years of estuarine residency (Matthews 1990a, Baxter 1999, Palsson et al. 2009). In estuarine, sound and coastal habitats, adults are associated with deeper depths than young-of-the-year (YOY) and juveniles (Stein and Hassler 1989, Matthews 1990a, West et al. 1994, Baxter 1999, Love et al. 2002, Palsson et al. 2009).

In southern Puget Sound, Matthews (1990a) used repeated visual diving surveys conducted over a 23-month period to investigate changes in habitat utilization between YOY, sub-adults and adults of four rockfish species, including brown rockfish. Habitats studied included low (less than 10 m depth) and high relief (12–20m depth) natural reef sites with high seasonal (spring–fall) bull kelp and perennial understory algal coverage, high-relief artificial reef sites (15–20 m depth) with little kelp coverage, and shallow sand sites with seasonal (spring–fall) seagrass coverage. Young-of-the-year, including brown rockfish, used all habitat sites, though they were only found in seagrass habitats for a short period in the summer, during which low densities of adult brown rockfish were also present. High-relief natural reefs support the highest consistent densities of brown rockfish of all life stages, with size classes greater than 200 mm numerically dominant while YOY and adult brown rockfish were found on low-relief natural reefs primarily in the summer, when they were covered in seasonal algae. Matthews concluded that although all four habitat types were used, natural reefs, particularly with high relief, may represent source habitats for brown rockfish in Puget Sound, an assertion supported by the relatively smaller home ranges of this species on high relief natural reef habitats (Matthews 1990b).

Distribution of Documented Presence of Juveniles in Estuaries

Throughout the study area of Washington, Oregon and California, juvenile brown rockfish have been documented in 10 estuarine systems (Figure 13). This relatively low level of documented presence in West Coast estuaries is likely caused by problems with species-specific reporting rather than true absence from some of these estuarine systems. Field identification of the juvenile stage of many rockfish species on the West Coast is difficult, and there were a number of estuaries for which documentation was only of 'juvenile *Sebastes* spp'. Thus, brown rockfish may occur in many more estuaries than we were able to document here.

Despite these data limitations, we did find evidence that juvenile brown rockfish can use a wide variety of the types of estuaries found along the West Coast, including three of the four estuary classes (sound, embayment/bay and lagoonal estuaries; Figure 13) and all four estuarine subclasses (Table 4). Within estuarine systems, juvenile brown rockfish are found over open bottoms and in association with rocky outcrops, other hard substrates (including artificial reefs) and vegetation, including seagrass beds and benthic macroalgae (Table 4).

Threats

In coastal waters the brown rockfish is a moderately targeted species in the commercial fresh-fish fishery and of greater importance in the commercial live-fish fishery. Their use of relatively shallow water habitats has made them an important species for recreational fishing, particularly in Puget Sound and from San Francisco Bay southward. In addition, at the southern end of their range (Baja California), large numbers of brown rockfish are taken in artisanal fisheries (Stein and Hassler 1989, Love et al. 2002).

© John Bragg/SSNERR

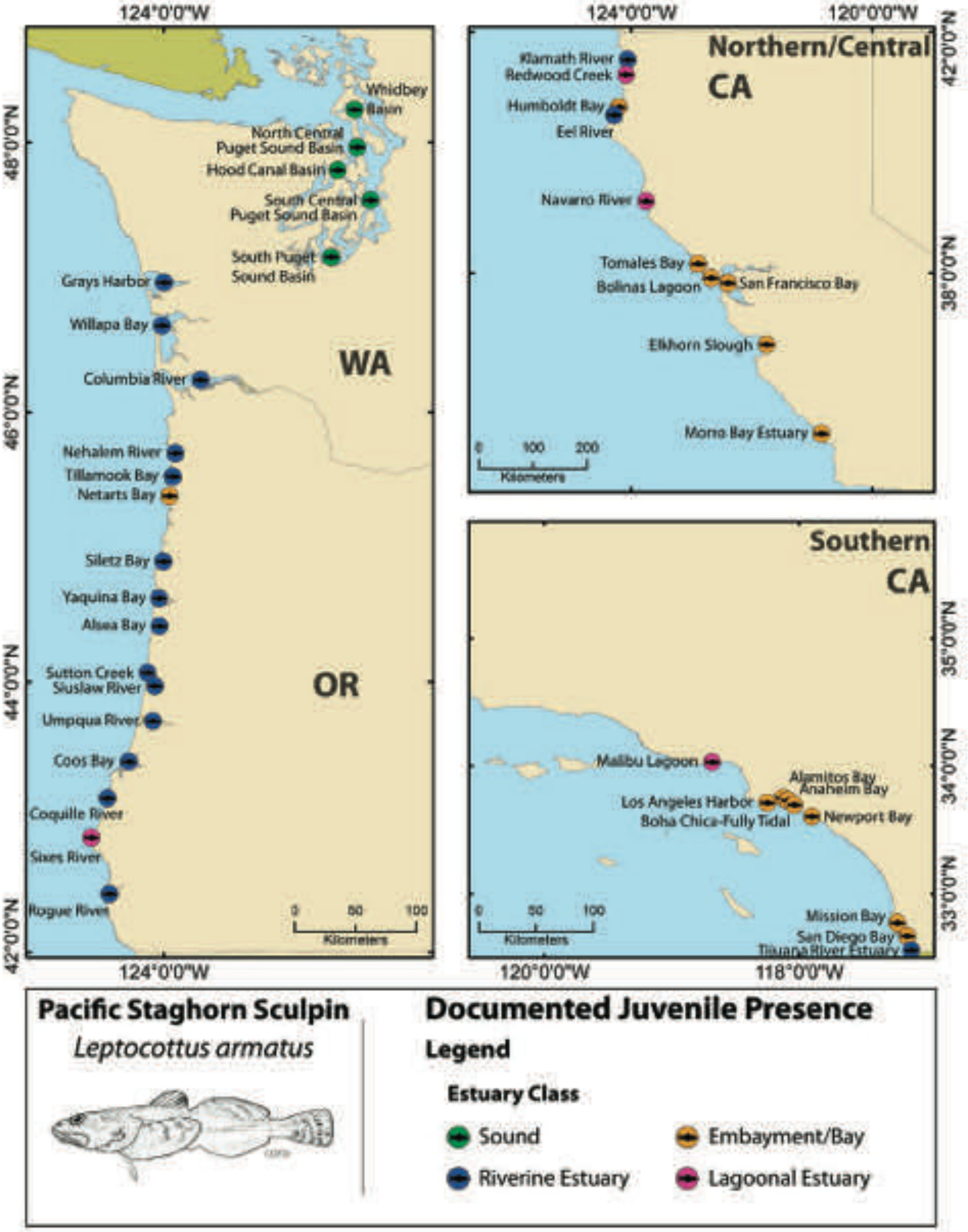


FIGURE 14. PACIFIC STAGHORN SCULPIN: Documented juvenile presence in Washington, Oregon and California estuaries.

PACIFIC STAGHORN SCULPIN

(*Leptocottus armatus*)

© Kirsten Ramey/CDFW

Pacific staghorn sculpin occur from the South Bering Sea through San Quintin Bay, Baja California (Miller and Lea 1972, Eschmeyer et al. 1983, Love 2011) and are known to be abundant between Puget Sound and San Francisco Bay (Emmett et al. 1991). Although they are commonly found in estuaries, they also use a variety of marine and freshwater habitats throughout their range. Estuaries are generally not considered critical for completion of their life cycle (Tatso 1975, Moyle 2002, Love 2011).

Life History and Ecology

Pacific staghorn sculpin are a small (305–480 mm max) and moderately lived (10+ years) fish that matures at the end of the first year of life at 120–153 mm and 110–122 mm, for females and males respectively (Jones 1962, Weiss 1969, Hart 1973, Miller and Lea 1972, Love 2011; Table 2). As adults, Pacific staghorn sculpin spawn once per year, which can occur anytime throughout the year, with peak spawning varying geographically and among years (Jones 1962, DeVlaming et al. 1984, Love 2011). Eggs hatch in approximately 10 days, producing larvae (Jones 1962) that swim to the surface and remain planktonic for up to eight weeks before settling at a size range of 15–20 mm (Matarese et al. 1989).

Juvenile Pacific staghorn sculpin settle throughout a wide variety of shallow inshore marine habitats and estuaries and may move into freshwater habitats for brief periods (up to three months) before returning to more saline environments (Moyle 2002) (Table 2). The sizes of Pacific staghorn sculpin found within estuaries encompass almost their complete size range (5–220 mm, Tatso 1975, Moyle 2002). Juveniles are generally present throughout the year within estuaries—the occurrence of adults increases during peak spawning periods (Jones 1962, Moyle 2002, Love 2011), after which adults tend to move to deeper waters (Tasto 1975).

The greater abundance of both juvenile and adult Pacific staghorn sculpin in estuarine habitats make them important secondary consumers, particularly within summer months when warm temperatures may drive high food requirements (Armstrong et al. 1995). Both age-0 and age-1 sculpin are visually opportunistic, generalist predators, and have a diet that includes a range of decapod crustaceans, amphipods, isopods, shrimps, polychaetes and fishes, predominately *Gobiidae* species (Jones 1962, Tatso 1975, Armstrong et al. 1995, Love 2011). In Padilla Bay, Washington, there was a shift in diet with size—the smallest juveniles (less than 79mm) consumed amphipods and isopods, large juveniles (80–119 mm) increased their consumption of juvenile crabs, while the adults (greater than 120 mm) consumed primarily crabs and fish (Dinnel et al. 1990). Because Pacific staghorn sculpin reside in the settlement habitats of other species, they may consume a significant amount of newly settled individuals, including commercially important species, such as Dungeness crab (Armstrong et al. 1995). The wide use of habitats, including shallow estuarine areas, make Pacific staghorn sculpin susceptible to predation by birds, including gulls, cormorants and great blue herons, making them important prey items (Cailliet et al. 2000).

Timing and Use of Estuaries

Throughout their range, juvenile Pacific staghorn sculpin may use habitats across the entire marine-freshwater salinity gradient within estuaries, though higher salinity estuarine waters become preferred within a few months of settlement. Juveniles show no known preference for habitat or estuarine class, which can include mudflats, sandy bottoms, eelgrass beds, macroalgae beds and oyster beds across embayments, lagoons, sloughs and tidal estuaries (Tatso 1975, Emmett et al. 1991, Moyle 2002; Table 4). Spawning and juvenile Pacific staghorn sculpin settlement and residence in estuaries occurs year round, though peak spawning and juvenile abundance varies across locations and years (Jones 1962, DeVlaming et al. 1984, Moyle 2002, Love 2011).

In Willapa Bay, Washington, Hosack et al. (2006) investigated how the distribution of mobile fish and decapods, including Pacific staghorn sculpin across a range of size classes, was related to the epifauna and benthic invertebrate communities. The study examined the known prey of fish and decapod crustaceans in seagrass, in non-native, cultured oyster beds and on unvegetated mudflats. The authors hypothesized that introduction of non-native oysters, which are cultured on bare mudflats, may compete with native habitats, such as eelgrass, that provide both refugia and resources for the mobile fish and decapod species. Although epifauna and benthic invertebrate communities were found to vary in composition and density across the habitat types, the distribution of mobile fish and decapod species, including sculpins, was more strongly correlated with position in the estuary than with habitat type. The authors suggested that the spatial configuration of habitat patches at a larger scale, rather than at the small scale they sampled (individual patch), could be important for maintaining the diversity and abundance of mobile estuarine species, such as Pacific staghorn sculpins.

Distribution of Documented Presence of Juveniles in Estuaries

The range of habitat types used by Pacific staghorn sculpins is extensive, including intertidal to deep subtidal depths (up to 275 m) and muddy and sandy bottoms that may contain eelgrass, macroalgae or other coverage (Table 4). This relative flexibility in habitat use, and its relatively high tolerance for a range of environmental conditions, results in juvenile Pacific staghorn sculpins being found across the West Coast and in every estuarine class and subclass, including embayments, sounds, riverine estuaries, lagoons and sloughs (Figure 14 and Table 4; Emmett et al. 1991, Moyle 2002).

Although we were able to document juvenile staghorn sculpin in 40 estuarine systems (Figure 14), it is likely that they occur in more West Coast estuaries. Lack of documented presence is likely due to lack of sampling or reporting, rather than actual absence from many of the estuaries in the inventory. For example, many of the smaller, seasonal riverine or lagoonal estuaries common in central and southern California (Figure 1) have not been assessed for non-salmonid fishes, or in some systems that have been sampled, the presence of the juvenile life stage was not explicitly stated, or those data are not readily available. We would predict that future sampling of some of these smaller estuarine systems would reveal that they are used by juvenile staghorn sculpin.

Threats

Historically, sculpins have been targeted as both a commercial and recreational bait fish (Love 2011). Shoreline development and armoring may impact the quality of their shallow estuarine habitats (Morley et al. 2012).

© Jonathan W. Moore/Simon Fraser University

PERCIFORMES

Perciformes is a very large and very diverse order containing more than 10,000 fish species (Moyle and Cech 2004; Nelson 2006). The order is controversial among taxonomists and has been described as a catch-all for fishes that do not fall neatly into other categories, as no one characteristic clearly distinguishes them. However, most have common physical qualities, such as similar pelvic fin location and spine to soft-ray ratio (Paxton and Eschmeyer 1998).

Though most are shallow marine species, Perciformes are found globally from mountain streams to deep ocean bottoms. Some are important commercially (tunas and snappers), recreationally (billfish) and ecologically (parrotfish). Perhaps because of their ubiquity, there are 146 species of Perciformes listed as critically endangered, 114 species listed as endangered and 358 species listed as vulnerable on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List (http://discover.iucnredlist.org).

Perciform fishes are found in estuaries throughout the world. Along the West Coast, they are represented by families with one or more species, including croakers (Scianidae), gobies (Gobiidae) and surfperches (Embiotocidae). An embiotocid, the shiner perch (*Cymatogaster aggregata*), has been chosen here as a representative of perciform fishes occurring in West Coast estuaries. Embiotocids are noted for being viviparous—bearing fully developed young. The family consists of 13 genera and 23 species distributed in the coastal northern Pacific Ocean from Mexico to Korea, with one species exclusive to freshwater streams of California (Nelson 2006).

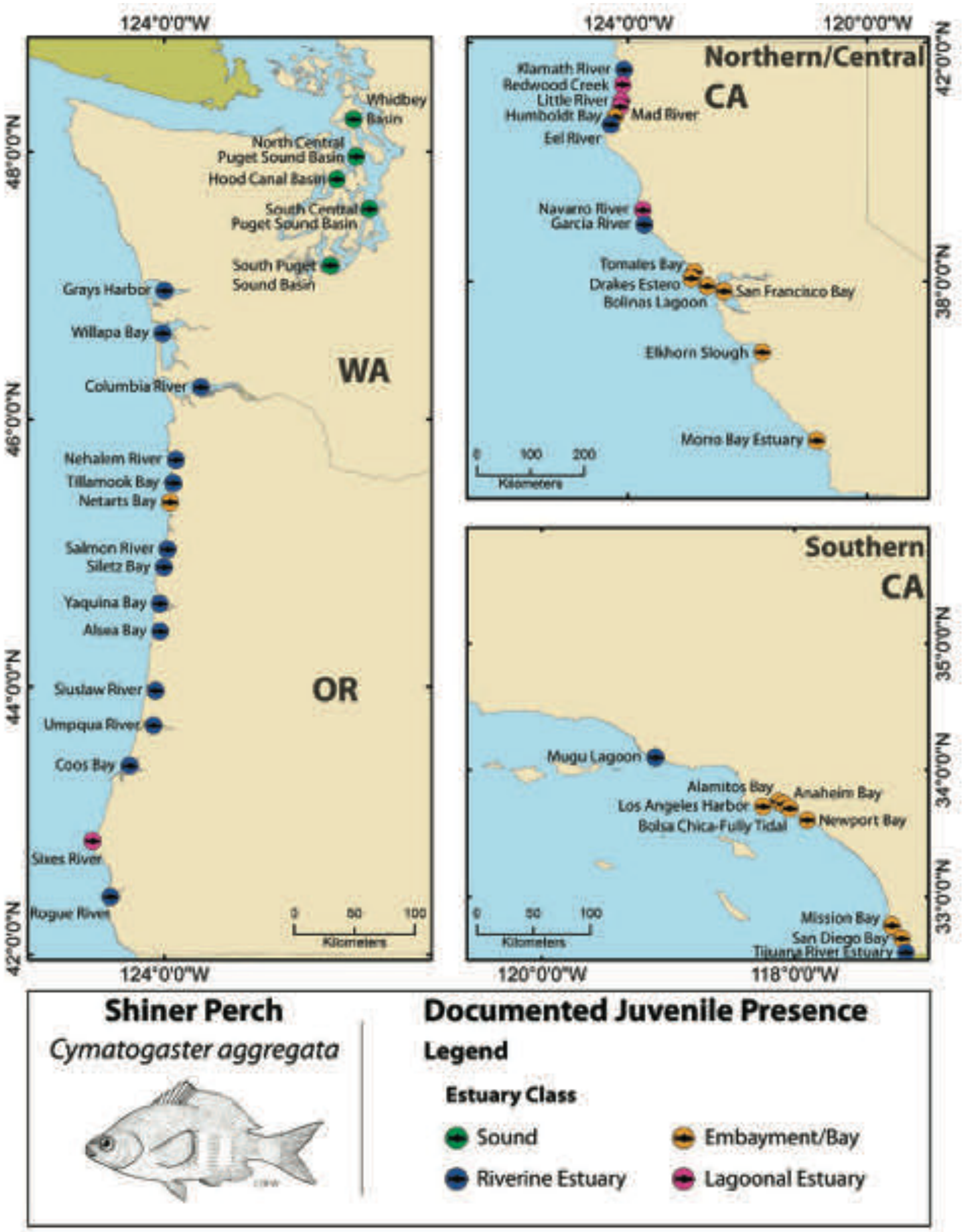


FIGURE 15. SHINER PERCH: Documented juvenile presence in Washington, Oregon and California estuaries.

SHINER PERCH
(*Cymatogaster aggregata*)

© Tom Greiner/CDFW

Shiner perch (or shiner surfperch or shiners) are commonly occurring temperate marine fishes that inhabit the subtidal zone, embayments and estuaries from Mexico to Alaska. A significant forage species (Allen et al. 2002), shiner perch are loosely schooling fish characterized by deep, compressed bodies and large silvery scales. Adult shiner perch are sexually dimorphic with females often having three pale yellow vertical bands and breeding males being almost entirely black (Morrow 1980). Though considered a nondependent marine fish—fishes that are found toward the mouths of estuaries that do not need them to complete their lifecycles (Moyle and Cech 2004)—adult and juvenile shiner perch are often one of the most abundant species captured within estuaries. They are omnivorous, euryhaline and temperature tolerant, and are believed to be seasonally present in nearly every major and minor estuary along the West Coast (P. Moyle pers. comm.), using these estuaries to give birth and as nursery grounds for newborns and juvenile fish.

Life History and Ecology

The geographic distribution of shiner perch is from Bahía de San Quentín, Mexico, to Port Wrangell in southeastern Alaska (Table 2). The center of their range, where they are most abundant, is from San Diego, California to Ketchikan, Alaska (Morrow 1980). They are most common in calm nearshore waters, in bays and estuaries and in quiet backwaters, inhabiting marine, brackish and even fresh waterbodies (Eschmeyer et al. 1983). Shiner perch are most often found at shallow depths, though they have been taken as deep as 146 meters (Miller and Lea 1972).

In spring, mature male and gravid female shiner perch migrate into estuaries, or other shallow, calm waters, prior to giving birth and then mating. The warmer temperatures and longer days in the spring promote embryo growth and oocyte formation (Wiebe 1968). Age at 50% maturity is unreported, but in the Strait of Georgia, 99% of females age-2+ were mature and carrying embryos (Gordon 1965). Shiner perch have relatively low fecundity compared to other embiotocids, with age-6 fish averaging 20 embryos

(Baltz 1984). Shortly after migrating into estuaries, shiner perch give birth to live, fully functional offspring. As newborn shiner perch grow larger, they join adult schools and eventually migrate out of the estuary and overwinter offshore in deeper water (Gordon 1965, Horn and Allen 1981). Here the cooler water and shorter days stimulate oocyte development, and then fertilization from stored sperm.

Shiner perch are among the smaller of the embiotocids with a mean standard length (SL) at age-7 of 122.2 mm (Baltz 1984). The largest individual shiner perch on record was taken in Alaska and measured 203 mm (Morrow 1980). Latitude influences their physiology—shiner perch grow slower, achieve a larger size, have higher fecundity and live longer in higher latitudes (DeMartini et al. 1983). Shiner perch are euryhaline and can withstand very low salinities. Shiner perch are genetically very similar to the only freshwater perch, the tule perch (*Hysterocarpus traskii)*, which may explain their tolerance for low salinity (Bernardi and Bucciarelli 1999).

Shiner perch are omnivorous opportunistic feeders (Odenweller 1975, Barry 1983, Martin 1995). The preferred diet of juvenile and adult shiner perch are zooplankton picked out of the water column. However, during periods of low zooplankton abundance, adults will feed off of the bottom, eating epibenthic crustacean, plant material and even topsmelt (*Atherinops affinis*) eggs deposited there (Allen and Horn 1975, Barry 1983). In the Pescadero Creek estuary in central California, adult shiner perch diet was altered depending on the condition of the estuary opening (Martin 1995). When the mouth of the estuary was open, adults fed on amphipods and isopods, but when the mouth was closed, the adult fish diet shifted exclusively to snails.

Timing and use of Estuarine Habitats

There is no known latitudinal migration of shiner perch along the coast, but rather a seasonal movement from nearshore habitats into estuaries. In spring and summer prior to spawning and mating, yearlings, followed by adult males, then adult females, move into estuaries or other sheltered waters (Gordon 1965). The precise timing of this event is generally latitude dependent. In Anaheim Bay, Alamitos Bay, Newport Bay and San Diego Bay in southern California, adults migrate March–April (Odenweller 1975, Allen and Horn 1975, Horn and Allen 1981, Allen et al. 2002). In Elkhorn Slough in central California, adults migrate in June (Barry 1983) and in Humboldt Bay (Chamberlain and Barnhart 1993) and in Yaquina Bay, Oregon (Bayer 1985), they begin to appear in May. During their time within estuaries, males and non-gravid female adult shiner perch are found in the deeper main channels closer to the estuary mouth (McConnaughey 1971, Horn and Allen 1981, Barry 1983, Valle et al. 1999). At parturition, males and gravid females undergo diurnal migrations, moving into tidal creeks, pannes and other shallow areas during daylight where the females give birth and then returning to the deeper channels at night. Young-of-the-year shiner perch begin to appear in May and June in southern California and in July in Oregon. Juveniles remain in these shallow areas for several months before eventually migrating into the deeper main channels and joining the adults. By November, nearly all juveniles and adults leave the estuaries, although in some estuaries, such as the nearly enclosed Colorado Lagoon in Alamitos Bay, shiner perch are year-round residents.

Similar to other small embioticids, shiner perch are often associated with habitats that provide complex cover. They are often found in calm water near eelgrass beds, oyster beds, piers and pilings (Table 4; Horn and Allen 1981, Eschmeyer et al. 1983, Baltz 1984, Bayer 1985, Valle et al. 1999, Hosack et al. 2006). Shiner perch distribution at all life stages is affected by water temperature within an estuary (Table 3). In laboratory conditions, newborn shiner perch preferred cooler water than juveniles, which preferred cooler water than adults (Shrode et al. 1983). Newborns moved toward water with a median temperature of 9°C, 14°–15°C for juveniles, and 17°C for the largest adults. This coincides with a thermal limit of 18.5°C reported by Odenweller (1975) for shiner perch in Anaheim Bay. Though these fish will move to cooler water when available, they have a high thermal tolerance, which allows them to occupy areas of higher than preferred temperatures. This ability is apparent in the shallow and tidally restricted Colorado Lagoon, where the thermal tolerance of adults has been reported to be as high as 25°C (Allen and Horn 1975).

Distribution of Documented Presence of Juveniles in West Coast Estuaries

Juvenile shiner perch are a very common member of the estuarine fish fauna along the West Coast. They have been recorded in every large estuary (Monaco et al. 1990) and in many of the smaller estuaries (Figure 15). Lack of documented presence in more estuaries is likely due to sampling effort or sampling methods rather than actual absence from many of the estuaries. Many of the smaller, seasonal riverine or lagoonal estuaries common in central and southern California (Figure 1) have not been assessed for non-salmonid fishes, or if they have been sampled, presence of the juvenile life stage is not explicitly stated, or those data are not readily available. Apparent absence of juvenile shiner perch in some studies could be the result of sampling design, such as a study in Los Peñasquitos Lagoon in San Diego County, California, that did not report shiner perch in an estuary within the center of their range (Nordby and Zedler 1991). In this case, sampling targeted the upper estuary whereas shiner perch tend to be found near the mouths of estuaries.

Shiner perch do seem to be absent from some estuaries where sampling has been conducted. In previously degraded estuaries in southern California, such as Malibu Lagoon and Ballona Creek, and Estero de San Antonio in northern California, shiner perch were not recorded in multiple years of survey data (Dagit and Swift 2005, Johnston et al. 2012, Commins et al. 1996). Their absence could be due to timing of mouth openings preventing entry, a lack of suitable habitat within an estuary, or perhaps an abundance of alternative areas for shiner perch to give birth and mate. Riverine estuaries, which are the most common class of estuaries in Washington and Oregon (Figure 1), are fast moving with little sedimentation and may not provide the calm, sheltered habitat most often used by shiner perch. This, and the abundance of high-quality habitat in the larger bay-like riverine estuaries in the Pacific Northwest, could explain the lack of shiner perch in many of the smaller estuaries.

Threats

Shiner perch are motile, euryhaline, eurythermal and omnivorous. As generalists, they are well equipped for variability within their environment. Even so they are still susceptible to direct and indirect natural and man-made threats. Due to their ubiquity and abundance, shiner perch are common forage for fish, birds and marine mammals (Thompson et al. 2002, Orr et al. 2004). A minor commercial fishery for shiner perch as bait exists in California, and they are taken incidentally or for bait in the recreational fishery (Larinto 2013).

The main direct threat to shiner perch is loss of calm, shallow habitat with dense eelgrass beds or other complex structures. Loss of this type of habitat can come directly from dredging or construction, or from intense storms (Onuf and Quammen 1983). Indirect threats are changes to tidal flow, which deepens tidal creeks favored by juveniles, or from siltation, which buries eelgrass. Increased storm activity and sea-level rise is predicted as global climate change continues. In addition to habitat loss, shiner perch are susceptible to low oxygen and have been affected by mass die-offs due to hypoxia (Palsson et al. 2008). They are often used as indicators of estuary health due to their trophic level, and are commonly tested for pesticides or other toxins (Thompson and Gunther 2004).

© Kirsten Ramey/CDFW

© Bill Abbott/Creative Commons

CLUPEIFORMES

Clupeiformes is an order of fish that includes the herring, anchovy, sardine, menhaden, alewife and shad. They are one of the most common and abundant order of fishes on the planet, and cover tropical, temperate and arctic waters, although the majority of species occur in the northern hemisphere. Most species within this order are marine and, to a lesser degree, anadromous or freshwater. Most species of *Clupeiformes* are small (less than 30 cm total length). Despite their small size, they are a commercially important order and play an essential ecological role. Because of their relatively high abundance and schooling nature, they are common prey for larger fish. Their predators include whales, seals, sea lions and many species of birds and predatory fish.

There are no general life-history characteristics of species within the *Clupeiformes*, as they vary across species and regions. However, most *Clupeiformes* lay their eggs in nearshore waters. There are no general patterns in post-embryonic stages—some move to open ocean and others stay near the coast. The majority of species within the *Clupeiformes* are pelagic and planktivorous during juvenile and adult stages.

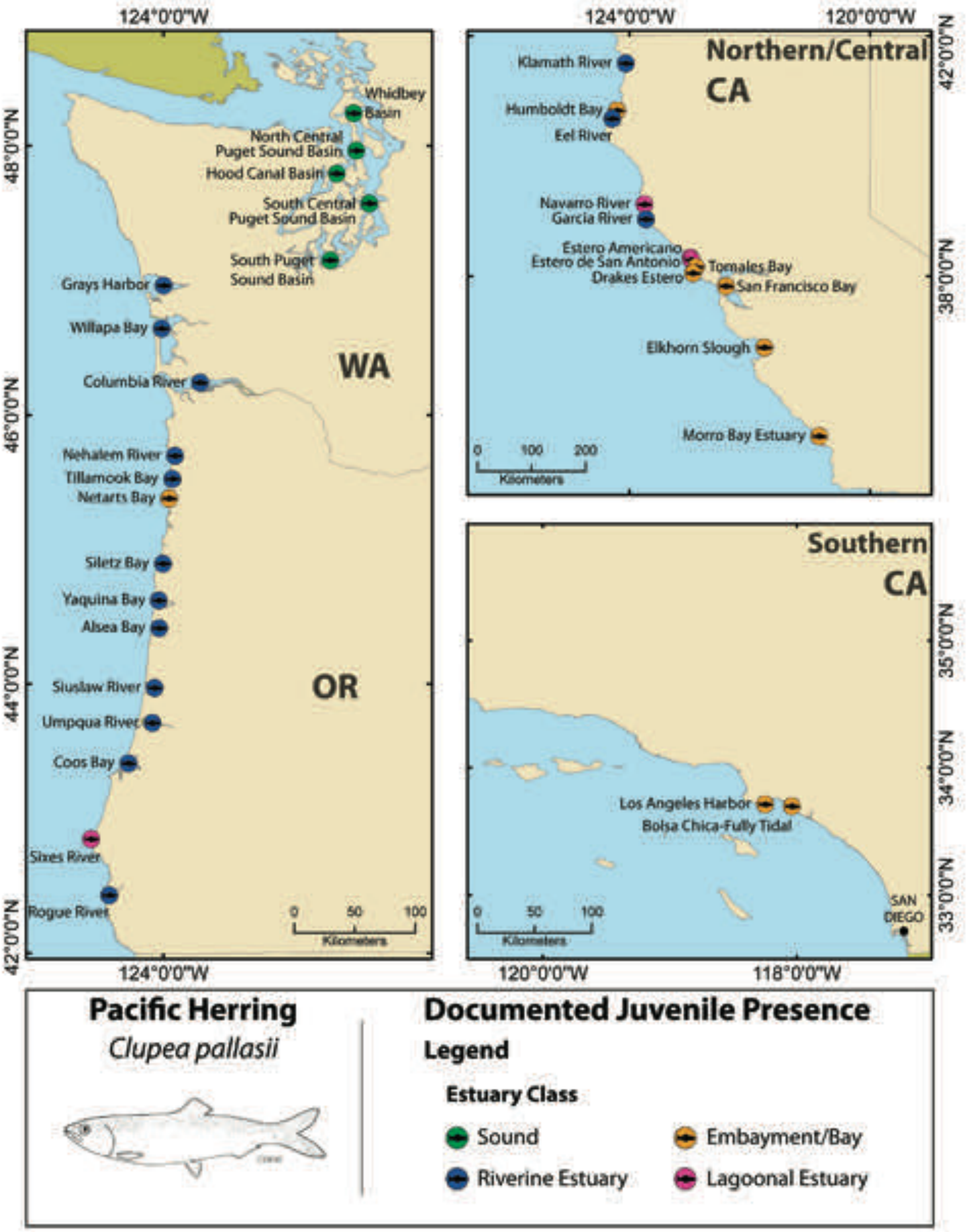


FIGURE 16. PACIFIC HERRING: Documented juvenile presence in Washington, Oregon and California estuaries.

PACIFIC HERRING

(*Clupea pallasii*)

© Mike Wallace/CDFW

Pacific herring are a highly abundant coastal and estuarine species with a broad distribution along the northern Pacific Rim, which extends from Cape Bathurst in the Beaufort Sea to Ensenada, Baja California, Mexico (Emmett et al. 1991; Table 2). They play a significant ecological role due to their high densities in estuaries. In trophic food webs, they are both important prey and mesopredators. Pacific herring provide important trophic linkages between their planktonic prey and pelagic predators, such as salmon, sharks, birds and seals. Pacific herring are also key indicators of ecosystem health in estuaries because their larval stages are closely associated with important and vulnerable estuarine habitats, such as seagrass meadows, macroalgal beds and oyster reefs.

Pacific herring have a long history of exploitation. Prior to the 1970s, Pacific herring fisheries were thriving, and abundance was demand-related. A major decline occurred in the 1970s, which was probably the result of excessive fishing during a period of poor recruitment in the northern fisheries (Ware 1985). Since that time, fishing effort has shifted to roe fisheries, primarily for export to Japanese markets.

Life History and Ecology

Their dependency on a broad range of estuarine habitats over the course of their life make Pacific herring an important species for this review. Adults use open ocean, nearshore and estuarine habitats (Emmett et al. 1991), and can live to 19 years and reach a size of 460 mm (Love 2011; Table 2). Pacific herring reach reproductive size at 130–260 mm when they are two to three years old in California and three to four years old in Washington (Emmett et al. 1991).

Adults move into estuaries to spawn, where environmental cues trigger mass spawning events initiated by release of milt by male herring. Females deposit eggs on a variety of substrates, which include eelgrass (*Zostera marina*), macroalgal beds, oyster beds (*Crassostrea* spp.), salt marsh vegetation, driftwood, pilings and rocks (Lassuy 1989b, Emmett et al. 1991, Pentilla 2007, Paul Reilly and Ryan

Bartling—California Dept. of Fish Wildlife—*pers. comm.*). In general, spawning can occur throughout the year, but peaks occur in early winter in California and late winter to early spring in the Puget Sound region (Emmett et al. 1991, Penttila 2007). Larvae have a planktonic duration of two to three months, and tend to stay in estuaries until they settle as juveniles having a size range of 35–150 mm (Emmett et al. 1991).

Timing and Use of Estuarine Habitats

All Pacific herring life history stages use estuaries, but the egg stages receive the most attention because of the economically valuable roe fishery. Eggs and larvae are found in all estuarine classes with freshwater flow (Love 2011), and have a broad salinity range (3–28 ppt), and an optimal salinity range of 12–19 ppt (Emmett et al. 1991). The optimal temperature for growth is 12°C (Emmett et al. 1991), but given their large geographic range (Baja Mexico to Alaska), they must exhibit a broad range in temperature tolerance. Juveniles are primarily pelagic and can stay in estuaries until they reach adulthood, at which point they either migrate to the ocean or remain in the estuary for the remainder of their lives (Emmett et al. 1991). Because they have a pelagic lifestyle, the main prey for juveniles is zooplankton, however, they will feed on benthic prey in eelgrass beds, such as copepods and gammarid amphipods (Lassuy 1989). The predators of juvenile Pacific herring are diverse, indicating that herring are an important trophic link in estuarine food webs. Predators include sharks, salmonids, sculpins, lingcod, flatfishes, birds and seals (Emmett et al. 1991).

Distribution of Documented Presence of Juveniles in Estuaries

Juvenile Pacific herring have been documented in a total of 33 West Coast estuaries from Bolsa Chica, southern California to Puget Sound, Washington. Juvenile Pacific herring have been documented to use a range of estuary sizes and classes, including all four classes on the West Coast (lagoonal, riverine, embayment and sound; Figure 16). However, they use the larger estuaries as their primary spawning grounds (e.g., Puget Sound, Grays Harbor and Willapa Bay in Washington; Columbia River Estuary, Winchester Bay and Coos Bay in Oregon; Humboldt Bay, Tomales Bay, and San Francisco Bay in California).

On smaller spatial scales, juvenile Pacific herring undergo daily vertical migrations; they migrate toward the surface at night to feed (Lassuy 1989) and use habitats ranging from the high intertidal down to 150 m (Emmett et al. 1991). Within estuaries they use a variety of estuarine sub-classes, which include subtidal, tidal channels and creeks and sloughs (Table 4). Within estuaries, juvenile Pacific herring occur primarily in the water column, but they can use some benthic habitats, such as eelgrass and macroalgal beds (Table 4).

Threats

Pacific herring face many threats (Table 5) that range from natural predation (Schweigert et al. 2010), excessive fishing (McKechnie et al. 2014), disease (Marty et al. 2003), habitat loss (Kimmerer 2002, Penttila 2007) and pollution effects (West et al. 2008, Incardona et al. 2012). Much research on threats to Pacific herring focuses on their egg and larval stages because these early life history stages are currently the most exploited and have strong associations with specific benthic habitats.

© Dirk Rosen/MARE

Pacific herring have experienced a long history of exploitation, beginning with the native Americans (McKechnie et al. 2014) and through the early twentieth century, when primarily adults were harvested, processed, and sold as dry salted herring, oil and fish meal (Lassuy 1989, Love 2011). More recently, in Puget Sound, where highly sensitive spawning stocks were fished to excess, herring experienced slow recovery, even after receiving legal protection (Musick et al. 2000). The protection of some marine mammals that are predators of adult herring (Schweigert et al. 2010) could further slow stock recovery when combined with excessive fishing. There has been a documented increase in mortality from 20–80% from increased predation by pinnipeds (i.e., seals and sea lions) since passage of various conservation measures, such as the North Pacific Fur Seal Treaty of 1911, the Fur Seal Act of 1966 and the Marine Mammal Protection Act of 1972 (Musick et al. 2000).

In Puget Sound, some populations of Pacific herring are considered vulnerable due to population reductions of 90–95% that have resulted either from excessive fishing (Musick et al. 2000), or from unknown causes (Penttila 2007). Degradation of spawning habitats, primarily critical macrophyte habitats, such as eelgrass (*Z. marina*), should be considered a threat to Pacific herring. Anecdotal evidence indicates that the loss of eelgrass can lead to declines in Pacific herring (Penttila 2007). Because of its habitat value, both California and Washington have identified eelgrass as critical nursery habitat for Pacific herring. Both states have established no net loss policies for eelgrass (Penttila 2007, NMFS 2011). Despite a lack of information on the potential nursery function of vegetated habitats for juvenile Pacific herring, there is a clear link between the health and abundance of spawning habitats and both juvenile and adult Pacific herring abundance. Most research is focused on the embryonic life-history stage; therefore, the relationship of aquatic vegetation to the nursery function of estuaries represents the most readily identifiable target for fruitful research about the habitat needs of juvenile Pacific herring.

Pacific herring seem to be highly selective of spawning habitat. For example, within Puget Sound, approximately 10% of shorelines are selected for spawning grounds, highlighting the importance of management and protection of those specific areas (Penttila 2007). In certain cases, such as San Francisco Bay, the loss of natural vegetated habitat has shifted emphasis to providing artificial spawning areas, such as docks and pilings (Spratt 1992). However, the use of lumber-based substrates can threaten the early developmental stages because of toxicity from the application of wood preservatives, such as creosote (Vines et al. 2000).

In California, Pacific herring are not threatened by exploitation because they are carefully managed to prevent overfishing. However, Pacific herring populations in California are affected by poor environmental conditions and pollution. For example, the 1982–83 and 1997–98 El Niños resulted in major declines in Pacific herring spawning in San Francisco Bay (Bartling 2006). Additionally, a severe drought from 1987 to 1992 resulted in significant declines to the Tomales Bay population and closure of the fishery (Bartling 2006). This decline could have been the result of low freshwater flow conditions as a similar, albeit weak, negative effect of reduced freshwater flow has been detected for San Francisco Bay (Kimmerer 2002). Alternatively, sediments resuspended either through increased freshwater flow or through dredging activity have been demonstrated to cause increased mortality to Pacific herring embryos (Griffin et al. 2009).

Oil spills also threaten the capacity of estuaries to provide habitat for juvenile Pacific herring. Crude oil has been experimentally shown to cause increased stress to juvenile Pacific herring (Kennedy and Farrell 2005). The 2007 *Cosco Busan* oil spill in 2007 caused a major decline in San Francisco Bay's Pacific herring population, the largest population within the California, Oregon and Washington study region (Incardona et al. 2012). The adult population in San Francisco Bay was already in a period of decline in years prior to the oil spill (R. Bartling, *pers. comm.*), and the oil spill likely exacerbated the decline through a massive die off of embryos. Consistent with other oil spills, such as the 1989 *Exxon Valdez* oil spill in Alaska (Kocan et al. 1996), the *Cosco Busan* oil spill in San Francisco Bay yielded two important insights: oil spills can result in mortality of Pacific herring embryos, and the tidal height of the trapped oil can exacerbate its harmful effects in shallow intertidal areas by interacting with sunlight, causing increased mortality of Pacific herring embryos (Incardona et al. 2012). This highlights the sensitivity of shallow habitat used by herring, such as eelgrass and macroalgal beds, to the harmful effects of oil spills.

DISCUSSION

© Walter N. Heady/TNC

Our review of the available information on estuarine nursery functions and synthesis of the documented presence of juveniles of the 15 focal species indicates that the actual role of West Coast estuaries as nurseries for juvenile fish could be of greater importance and extent than previously thought. The synthesis of knowledge for these 15 species across such a comprehensive inventory of West Coast estuaries illuminates the general nursery potential across a wide geography. However, we also found a wide range of threats that potentially reduce the nursery function of these estuaries. In addition, even given the extensive efforts of our review, we found that much is still unknown about estuarine juvenile life-history stages for many of the 15 focal species. The collective state of the knowledge on the nursery function provided by West Coast estuaries for 15 focal species, the threats to this nursery function and the knowledge gaps identified in this report demonstrate many areas for future research and conservation efforts. We highlight the emerging patterns of the nursery role of West Coast estuaries, and discuss knowledge gaps, threats and tradeoffs associated with managing multiple species.

EXPANDING OUR UNDERSTANDING OF JUVENILE PRESENCE IN ESTUARIES

An important first step in understanding the potential nursery role of West Coast estuaries is to understand patterns of juvenile presence within those estuarine systems. In this review, we have expanded on past efforts to obtain a fuller understanding of estuarine use by the 15 focal species.

Previous coastwide reviews of estuarine use by juvenile fish and invertebrate species have focused on a subset of the larger estuaries along the coast. Monaco et al. (1990) focused on 47 species in 32 of the larger estuaries on the West Coast (Figure 17). Monaco et al. (1990) found that all 32 estuaries had the potential to provide nursery function for the fish and invertebrate species included in our review (Table 10). For example, juvenile Pacific staghorn sculpin and shiner surfperch, species that are distributed throughout the study region, were found to be present in 32 and 31 of the estuaries, respectively. This number is lower for other species, but that is partially an artifact of the geographic distribution of the species across the study region.

More recently, Gleason et al. (2011) conducted a literature review of juvenile presence of 12 species in 146 West Coast estuaries, including some medium and small-sized estuaries; they documented presence of juveniles of one or more of our focal species in 96 estuaries, 66% of the 146 estuaries examined (Figure 17; Table 10). In the current study, we have greatly expanded the estuarine inventory to 303 estuaries (see Box 2) through inclusion of many more of the smaller estuaries common along the West Coast (Figure 1). Based on our review of the peer-reviewed literature, unpublished reports, online databases and input from regional experts, we have documented presence of juveniles of one or more of the focal species in 113 estuaries, 37% of the estuaries in the inventory. This substantially increases the total number of potential estuarine nurseries along the West Coast from the initial review of 32 estuaries by Monaco et al. (1990), but a more moderate increase from the 96 estuaries by Gleason et al. (2011). However, despite the moderate increase in the number of estuaries with documented juvenile presence, the total number of estuaries with potential nursery value for the focal species increases with each new review.

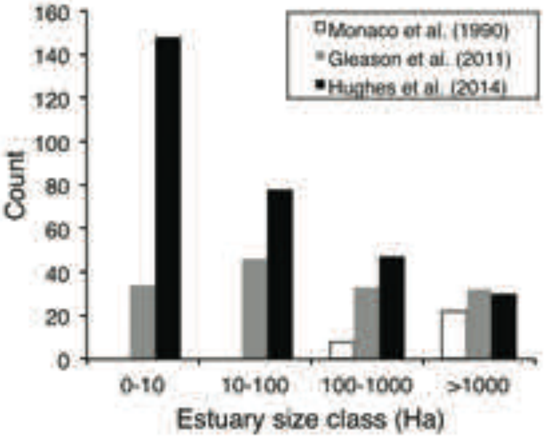
The estuaries with the greatest number of species with documented juvenile presence were the larger, more well-studied systems, such as Humboldt Bay (15 species), San Francisco Bay (14 species), Tomales Bay (12 species) and 13 other estuaries from northern California, Oregon and Washington with a relatively high proportion of the focal species (11 species). Though we were able to compile additional information on the timing and use of these estuaries by the focal species, the earlier efforts by Monaco et al. (1990) and Gleason et al. (2011) had already documented the importance of these systems for juveniles of a variety of fish and invertebrate species.

It is important to recognize that even with our extensive efforts to identify new information sources on fish and invertebrate occurrence in all West Coast estuarine systems, we have expanded the total number of systems with documented juvenile presence of the focal species by less than 20 systems. Lack of documented presence of the focal species in 63% of the estuarine systems may be indicative that these 15 focal species do not use many of these systems as juvenile habitat. However, at this time, it is difficult to evaluate this hypothesis given that there is little to no information available on the fish and invertebrate assemblage in many of the smaller estuarine systems along the West Coast. Future efforts to sample these smaller systems for these 15 focal species may reveal that these species actually occur in a higher percentage of the estuaries, and our current estimates are an artifact of sampling effort to date.

Although details of the potential nursery function of small estuaries (i.e., less than 100 ha) compared to large estuaries is not completely understood, the sheer number of smaller estuarine systems on the West Coast (226 out of our inventory of 303) indicates a potentially significant role in both regional population maintenance and coastwide production of juveniles for species that commonly use smaller estuarine systems. We found that 53 small estuaries, primarily lagoons and river mouths, have documented presence of juveniles for several focal species. For example, Navarro Creek in northern California is a relatively small estuary (36 ha), yet had documented juvenile presence of eight of the 15 focal species. Juvenile life stages of the focal salmonid species were documented in 30 small estuaries, and salmonids had the greatest presence in smaller estuaries compared with the other taxonomic groups reviewed.

These smaller estuarine systems have a documented nursery role for species, such as steelhead trout (Bond et al. 2008, Hayes et al. 2011), English sole (Brown 2006) and California halibut (Forrester and Swearer 2002). Of the focal species, flatfishes and salmonids have generally been the subject of more studies on estuarine habitat use and nursery function, which

Figure 17. The number of estuaries by size class included in three West coastwide reviews of estuaries as habitat for juvenile fishes and invertebrates.



may account for the higher documented presence in smaller systems. Additional research is needed to evaluate the importance of the smaller estuarine systems to the juvenile life stages of less well-studied species. The documented case studies of the importance of smaller estuaries for the maintenance of regional populations of some species brings a new perspective to the relative conservation importance of smaller estuaries, given the continued and emerging threats, such as anthropogenic disturbance and climate change.

GEOGRAPHIC DISTRIBUTION OF FOCAL SPECIES IN ESTUARIES

The number and types of species using West Coast estuaries as juveniles varies geographically as a function of the species' ranges within the study area and estuary classes found in different regions (Figure 1). Four of the focal species have a range of estuarine use that overlaps the entire study area and thus have the potential to occur in the most systems in this study. Juvenile steelhead trout have been documented in 63 West Coast estuaries, more systems than for any

TABLE 10. Three coastwide reviews documenting the number of estuaries with juvenile presence for 15 focal species. NA indicates that a species was not used for the given review.

	Monaco et al. (1990)	Gleason et al. (2011)	Hughes et al. (2014)
Estuary inventory	**32**	**146**	**303**
Dungeness crab	24	37	39
Bay shrimp	20	NA	23
Leopard shark	13	NA	14
Bat ray	NA	NA	7
Green sturgeon	12	15	14
Chinook salmon	21	34	31
Coho salmon	20	43	46
Steelhead trout	21	41	60
California halibut	14	27	28
English sole	26	39	32
Starry flounder	24	31	33
Brown rockfish	NA	NA	10
Staghorn sculpin	32	NA	41
Shiner surfperch	31	NA	40
Pacific herring	26	34	33

* Higher numbers in Gleason et al. (2011) than Hughes et al. (2014) reflect subdivision of estuaries, e.g., San Francisco Bay, by Gleason et al. (2011).

other species in this study (Figure 9). Juveniles of the three other coastwide species, Pacific herring, Pacific staghorn sculpin and shiner perch, were also distributed widely throughout the study area, having been documented in 33, 41 and 42 estuaries, respectively (Figures 14–16). These patterns of relative high presence for these species are consistent with results from prior reviews (Monaco et al. 1990, Gleason et al. 2011). Though a broad geographic range is a likely contributor to the high occurrence rates for these species, the fact that these species are able to use a diversity of estuaries, including all four estuary classes on the West Coast, is also an important factor.

Eight of the focal species were rarely or never documented in estuaries from the southern portion of the study area. Of these more northern ranging species, English sole, starry flounder and Dungeness crab were documented in 32, 34 and 42 systems, respectively, between Puget Sound and Point Conception, California, including many examples of all four estuary classes (Figures 2, 11–12). Coho and Chinook salmon were documented in 48 and 35 systems, respectively, from Puget Sound south to Scott Creek and San Francisco Bay, respectively (Figures 7–8). The remaining three northern species—green sturgeon, bay shrimp and brown rockfish—were documented in far fewer estuarine systems (15, 23 and 10 systems, respectively). This lower level of occurrence may be due in part to more specificity in the types of systems used. Juvenile green sturgeon seem to have a preference for riverine and embayment estuaries, whereas juvenile brown rockfish and bay shrimp were found in all estuarine classes except riverine estuaries and lagoonal estuaries, respectively (Figures 3, 5, 13). However, given the low occurrence rates for these three northern species, it is difficult to be certain if these patterns reflect actual habitat preferences, or are influenced by the level of sampling effort.

Three focal species showed a southern distribution in the study area; they were not reported from estuaries north of Humboldt Bay. Despite this limited range, juvenile California halibut were reported from 28 systems that vary in type and size (Figure 10). This species has been the focus of extensive research to determine distribution and abundance in large and small estuarine systems, particularly in southern California, thus it is likely that most systems in which it commonly occurs have been reported here. Leopard shark and bat ray show much more limited use of the estuaries off central and southern California, being documented in 14 and 7 systems, respectively, of which all are embayment/bay estuaries (Figures 4 and 5).

Our review revealed that several focal species had relatively low documented juvenile presence in West Coast estuaries; however, this may reflect a lack of study rather than an absence in many estuaries. For certain taxa, field identification of species at juvenile stages is difficult, making assessment of juvenile use of estuarine habitats challenging. In addition, many existing datasets fail to identify individuals to the species level. For example, many of the estuaries documented ‘juvenile *Sebastes* spp’ because juveniles in this genus are difficult to identify to species in the field. Thus, brown rockfish may occur in many more estuaries than we have documented here. In addition, there could be many more rockfish species (e.g., black rockfish—*Sebastes melanops*) that use estuaries as nurseries, but have not been identified. Fortunately, there are new genetic techniques in development, such as environmental DNA (eDNA), that will allow researchers to detect presence of even the most cryptic species (Kelly et al. 2014).

With expanded effort, the documented presence of juvenile life stages in estuaries increases with each review, indicating that the potential nursery role of West Coast estuaries is greater than previously known. We believe the lack of documented juvenile presence for any given species should not be equated with their absence in those estuaries, but potentially arising from a lack of monitoring. For example, our review documented juvenile presence for both flatfishes and salmonids in many small estuaries (less than 100 ha), especially in California. In addition, it is likely that additional information exists for some of these species and estuarine systems that was not available for this review, either because the data has not been published or made available. Also, for some species, estuarine use is not spatially/temporally consistent. Due to biological limits or physical patterns and processes, juveniles may only use some estuaries in some years, thus absence in one small study (e.g., California halibut in Humboldt Bay; Garwood et al. 2013) does not mean juveniles of a species never use the estuary. Similarly, the preferred habitat type may not have been sampled in a given study. We suggest that future monitoring efforts should explore smaller estuarine systems to verify juvenile presence or absence of key species.

PATTERNS IN ESTUARINE HABITAT USE BY JUVENILES

The 15 focal species selected span a wide range of sizes, trophic levels and ecological roles found in estuaries. Our review identified key West Coast estuarine habitats associated with juvenile life histories, including four estuarine sub-classes and 11 habitats within estuaries that are potentially important for the nursery function of estuaries (Table 4, Appendix 2).

Estuarine Sub-classes

Every species except green sturgeon was documented to use the Estuarine Coastal Subtidal sub-class (Table 4), which is not surprising given that this is probably the most widely distributed estuarine subclass along the West Coast. Tidal channels and creeks, as well as sloughs, were also documented as important estuarine sub-classes for juveniles for all 15 focal species except for green sturgeon and steelhead trout.

We reviewed many studies from lagoons; however, in many cases sufficient detail was not provided to differentiate between the species' use of the lagoonal estuary or the lagoon estuarine subclass (definitions available in Appendix 2). However, all the focal species with documented presence in lagoonal estuaries were also documented as using the lagoon subclass and thus can be considered to use lagoonal systems in general. Lagoonal estuaries are the numerically dominant estuarine class comprising 47% of 303 systems in the inventory, and 71% of the systems in California (Figure 1). Despite their abundance, many of the lagoonal systems are small systems that comprise less than 1% of the available area in estuarine systems coastal-wide. Although the lagoonal systems do not comprise much total area, juveniles from 11 of the 15 species were documented to use these systems (Table 4). Lagoons are very unique in that a sand bar may form in the summer when stream flows are diminished, which seasonally isolates the river from the sea. Only species that are highly plastic and adaptable to environmental variability, or that have life histories tuned to this seasonality and dramatic physical changes, would be able to use lagoons and potentially derive nursery benefit.

© Walter N. Heady/TNC

Steelhead trout and starry flounder meet these characteristics, therefore it is not surprising that these species were found to use lagoons. However, our more detailed review of existing data sources, combined with the expanded estuarine inventory (Box 2), suggests that the use of lagoon systems is more widespread than previously thought, as other species—such as Dungeness crab, shiner perch, staghorn sculpins, Pacific herring, brown rockfish, coho and Chinook salmon—were all documented using lagoonal systems as well (Table 4 and Figures 2-16). The majority of these lagoonal estuaries occurred in California, with a few in Oregon and none in Washington (Figure 1). Thus lagoonal habitat is less available to the northern species, which likely accounts for some of the lower reported occurrence for some northern ranging species.

Estuarine Habitats

Along the West Coast, seagrass and tidal flats are the estuarine habitat used by juveniles of almost all of the focal species, 12 and 13 species, respectively (Table 4). Our results support previous findings that seagrasses are an important foundation species that play a critical nursery function for a variety of fish and invertebrate species (e.g., Beck et al. 2001, Heck et al. 2003, Pihl et al. 2006). The primary seagrass species in estuaries along the West Coast is eelgrass (*Zostera marina*). When present, it forms dense stands that provide numerous ecological functions beyond serving as juvenile habitat, such as protecting shorelines from wave disturbance, sequestering carbon and enhancing secondary production (Bruno et al. 2003, Duarte et al. 2005, Waycott et al. 2009).

The high association of tidal flats with juvenile size classes is not surprising given that tidal flats are a common feature of West Coast estuaries (Emmett et al. 2000). Juveniles in shallow mudflat and sandflat habitats may have the advantage of rapid growth and survival due to warmer waters as well as greater availability of the small-sized prey eaten by newly settled juveniles (Gadomski and Caddell 1991, Madon 2008). All three flatfish species use shallow tidal flat habitats, particularly in the first few months of the juvenile phase when they seem to have wider tolerances for temperature and salinity. Bay shrimp also use tidal flats as their preferred habitat, likely due to increased food availability as well as their burrowing behavior is more suitable in unvegetated habitats (Siegfried 1989, Emmett et al. 1991).

Other biogenic habitats, such as macroalgae and oyster reefs, had documented use by Dungeness crab, staghorn sculpins and shiner perch. That suggests that these habitats might be good alternative nursery habitats to seagrass beds for these species and emphasizes the general importance of biogenic or habitat-forming species. Furthermore, other biogenic habitats, such as emergent tidal marshes, tidal scrub-shrub wetlands and tidal forests/woodlands, were frequently documented habitat for juvenile salmonids. There could be reasons for the less documented use of these other biogenic habitats (macroalgae, oyster reefs and marsh) beyond species habitat preferences, such as lower sampling effort compared to seagrass and tidal flats. Therefore, some caution should be used when interpreting our results as other habitat types might have more importance than indicated by the summary tables.

Future efforts should concentrate on quantifying the relative distribution and area of diverse habitats to better understand their nursery value relative to the well-documented habitats, such as seagrass and tidal flats. For example, juvenile coho and Chinook salmon, two well-studied species, use habitats other than seagrass, such as macroalgae, emergent marsh, scrub-shrub tidal wetland, tidal forest/woodland and large woody debris (Emmett et al. 1991, Miller and Simenstad 1997, Henning et al. 2007), which may also serve an important nursery function for the other less studied species. Furthermore, alternate habitats should be explored for nursery function given the coastwide decline of seagrass.

© Kirsten Ramey/CDFW

NURSERY FUNCTIONS OF WEST COAST ESTUARIES

Despite the potential widespread estuarine nursery habitat, the state of knowledge on the potential nursery function of estuarine habitats is generally lacking on the West Coast. The documented juvenile presence for 15 focal species does not necessarily translate to a documented *nursery role* for all 113 estuaries where juveniles were found. Despite the lack of knowledge for the majority of estuaries on the West Coast, our review highlights three important aspects of nursery function provided by some West Coast estuaries: 1) provision of food leading to enhanced growth rates, 2) provision of refuge from environmental stress and predation and 3) provision of migratory corridors that enhances population connectivity. In combination, these three factors can greatly contribute to enhanced adult populations outside the estuary. The effectiveness of these factors on the nursery role of estuaries are enhanced when these systems provide a mosaic of habitats, which are functionally connected through the diel and ontogenetic movements of species during critical juvenile stages (Nagelkerken et al. 2013, Sheaves et al. 2014).

Evidence of enhanced growth and survival in estuarine habitats

High productivity provided by estuaries has been documented to increase growth rates of salmonids and enhance subsequent life-history stages entering the ocean (Aitkin 1998, Bond et al. 2008, Maier and Simenstad 2009). Furthermore, estuarine habitats can simultaneously provide food for juvenile salmonids while also providing refugia from predators and environmental stress, such as waves (Bottom et al. 2005a, Fresh 2006), suggesting that enhanced growth rates and refuge from predation are interacting factors that influence the nursery function of estuaries. The three factors influencing the nursery quality of estuaries are certainly not limited to salmonids, as increased growth rates have been demonstrated for English sole (Brown 2003). Also, estuarine habitats have been demonstrated to provide refugia from competition, predation and stress for Dungeness crabs (Fernandez et al. 1993), English sole (Gunderson et al. 1990) and starry flounder (Baxter et al. 1999).

Evidence for the role of estuarine habitats to sustaining adult population

For several of the focal species, it has been demonstrated that nursery function provided by estuaries leads to an enhanced contribution to adult populations. For invertebrate species, enhanced growth rates in estuaries for Dungeness crab leads to the production of a stable source to the coastal adult population, which may be particularly important to fisheries in years where coastal production is low (Armstrong et al. 2003). For finfish, flatfish provide the strongest direct example of the nursery function of West Coast estuaries. For English sole, although methodologies and estimates vary, studies suggest estuaries likely disproportionally contribute to coastal adult populations (Olson and Pratt 1973, Rogers 1998, Rooper et al. 2004, Brown 2006), though the contribution may vary among years (Chittaro et al. 2009).

ASSESSING THREATS TO FOCAL SPECIES AND NURSERY FUNCTION

We identified 19 specific threats to the focal species and the nursery function of West Coast estuaries that were documented in the available literature (Table 5). Multiple threats are troubling for managers, who often can only target a few specific threats, or threatened species, when many more may exist. Of the 19 threats to juvenile life history stages in West Coast estuaries, habitat loss was the most common threat across the 15 species. The number of threats could be much greater than what is presented because we only identified a threat for a certain species if it was documented in the literature.

Most species were documented to be affected by habitat loss, with the exception of brown rockfish, Pacific staghorn sculpin and shiner perch (possibly a result of these species being less studied). However, given widespread habitat loss, pollution and climate change along the West Coast, potential threats could very well exist for these species. Not surprisingly, the three well-studied salmonid species had the most identified threats (15–16 threats for each species). Threats to salmonids included pollution, altered freshwater flow, habitat loss, disease, invasive species, excessive fishing and climate change, and have been well documented in the literature (e.g., Emmett et al. 1991, Moyle 2002, Gleason et al. 2011, Naiman et al. 2012, Flitcroft et al. 2013, Toft et al. 2013).

© John Bragg/SSNERR

By focusing on one key function, the nursery role of estuaries, we were able to expand on previous efforts (e.g., Halpern et al. 2009, Gleason et al. 2011, Merrifield et al. 2011, Greene et al. 2014), summarizing more general threats to West Coast estuaries. One threat in particular, habitat loss and modification, is a common threat that occurs along the entire West Coast and is not specific to any one region. However, studies from Gleason et al. (2011) and Merrifield et al. (2011) highlighted that other threats vary by region. In general, estuaries in southern and central California are threatened primarily from urban development, climate change and agriculture, whereas estuaries in northern California, Oregon and Washington are threatened by forestry practices and aquaculture, and many estuaries throughout the entire region face multiple threats (Gleason et al. 2011, Merrifield et al. 2011).

Our review highlighted trends similar to those of other regional threat assessments. For example, in southern and central California, agriculture has been shown to lower the nursery function for some of our focal species, such as leopard sharks, California halibut and English sole, by increasing eutrophication and the harmful effects of hypoxia (Carlisle and Starr 2009, Hughes et al. 2012). Additionally, pesticides and other agricultural contaminants have been documented to affect nearly all of the focal species (Table 5); at times, these pollutants have been shown to cause mortality, such as in bay shrimp (Khorram and Knight 1977), and to have deleterious effects on other native fishes not included in our review. The aquaculture industry has used carbaryl as a pesticide that can have negative effects on juvenile stages of Dungeness crab, bay shrimp, starry flounder and English sole (Feldman et al. 2000). Currently, other pesticides considered to be less toxic to endemic species, such as imidacloprid, are under review for use in Willapa Bay and Grays Harbor. Another threat to the southern region and Puget Sound is urban development, and shoreline armoring and diking, which have been documented to threaten juvenile salmonids (Morley et al. 2012) and flatfishes (Ritter et al. 2008, Nelson et al. 2010). Lastly, climate change, through increased temperature and sea-level rise, is a threat to the nursery function of estuaries. Many species dependent on lagoonal habitats, such as salmonids and flatfishes, are threatened by sea-level rise and the subsequent loss of lagoons and other important estuarine habitats (Flitcroft et. al. 2013). Furthermore, thermal stress through ocean warming could have negative effects on estuarine nursery functioning for the southerly range of English sole (Lassuy 1989a, Yoklavich et al. 1991, Baxter 1999).


© John Bragg/SSNERR

Beyond direct threats to the species we reviewed are the threats to the key habitats they depend on, such as seagrasses, tidal flats, emergent tidal marshes, tidal scrub-shrub wetlands and tidal forests/woodlands. Habitat alteration has resulted in major losses to seagrass beds, in addition to major losses to other nursery habitats, such as salt marshes and soft sediments, through urban expansion and shoreline armoring (Nichols et al. 1986, Zedler 1996, Larson 2001, Van Dyke and Wasson 2005, Silliman et al. 2009, Waycott et al. 2009). For example, in California, approximately 90% of salt marshes have been lost due to human population expansion and associated land reclamation (Nichols et al. 1986, Dahl 1990).

This habitat loss comes with a heavy price in the simultaneous loss of key ecosystem functions and services, such as resilience and nursery functioning. Seagrasses are under threat world-wide, including the West Coast, from eutrophication, sedimentation and habitat alteration (Waycott et al. 2009, Hughes et al. 2013). The overall ecological importance of biogenic habitats (seagrasses, emergent tidal marshes, scrub-shrub tidal wetlands, tidal forests/woodlands and oyster reefs) to the enhancement of the nursery function of estuaries, their widespread distribution along the West Coast, along with their vulnerability, should motivate future research and conservation efforts on these important foundation species. Tidal flats, another important habitat of juvenile life history stages (Table 4), are also compromised by coastal development and shoreline alteration.

Beyond the well-documented threats, there also exists less documented but emerging threats. These threats are the result of human-caused climate change and hypoxia (Table 5). Ocean warming, for example, is one mechanism that could alter the nursery function of estuaries. Certain species may benefit from ocean warming, such as California halibut at the northern end of their range, due to their affinity for higher temperatures, while increased temperatures could result in a net loss of estuarine nurseries for other species, such as English sole at the southern end of their range. Identifying estuaries in which these shifts in nursery function may occur will be important for informing future management strategies.

Sea-level rise could also pose severe threats to anadromous and other species dependent on freshwater habitats adjacent to estuaries. Predictions from modeling efforts have indicated that increasing sea-level rise could reduce available nursery habitats for steelhead trout, Chinook and coho salmon and starry flounder (Flitcroft et al. 2013). Interestingly, ocean acidification has not been documented as a threat to estuarine nursery function, however careful consideration should be given to ocean acidification in the future, as it is known to cause deleterious effects to calcifying animals (Kroeker et al. 2013), such as bivalves, that are important estuarine prey items for many of the focal species selected for this analysis.

Finally, hypoxia is another emerging threat coming from two sources: enhanced upwelling driven by changes to the California Current (Grantham et al. 2004, Booth et al. 2012, Hughes et al. 2012, Hessing-Lewis and Hacker 2013), and land-based nutrient inputs causing eutrophication (Cloern 2001, Hughes et al. 2011, McLaughlin et al. 2013). These nutrient enriched waters can trigger algal blooms and increase organic deposition that depletes oxygen from the water column, leading to the decline of water quality in juvenile fish and shellfish habitat (Hughes et al. 2012). Management of climate change and sea-level rise is highly complicated and usually involves management on scales much greater than that of the estuary. However certain mitigation actions, such as the identification of important migratory corridors, or reductions in anthropogenic nutrients, could help buffer the harmful effects of climate change and eutrophication-induced hypoxia.


© Walter N Heady/TNC

MANAGEMENT OF NURSERY FUNCTION AND POTENTIAL TRADEOFFS

Habitat restoration is an important strategy for conservation and enhancement of the nursery function of West Coast estuaries. Though there have been many restoration actions, few studies have specifically documented if restoration activities can improve or restore nursery function. However, a few studies have shown that habitat restoration has the potential to restore estuarine nursery function in powerful ways. For example, Miller and Simenstad (1997) demonstrated that restored slough habitat in the Chehalis River, Washington, produced equal growth rates of juvenile Chinook and coho salmon compared to naturally occurring sloughs. Future restoration activities should incorporate nursery function as one of the key outcomes in the design to provide evidence and quantification of the benefits from restoration to the nursery function of estuaries.

Restoring habitat alone may not fully restore the nursery function of estuaries. Our review highlights many other factors that can interact with habitat change, such as the effects from pollution, disease, species invasions and climate change, impacting the nursery role beyond the habitat value itself (Table 5). These potential interactive effects could be very harmful for certain species, and multiple stressors acting on a system could yield difficult challenges for managers, who may have to consider tradeoffs. A good example of this comes from Elkhorn Slough, California, which has experienced the simultaneous loss of salt marshes through erosion caused by habitat alteration (Van Dyke and Wasson 2005), and the ill effects of eutrophication and hypoxia resulting from agricultural land development in the surrounding watershed (Hughes et al. 2011). During the last century, the estuary has changed from a lagoonal bar built system to a coastal embayment (Van Dyke and Wasson 2005, Broenkow and Breaker 2005). These changes have impacted the nursery function of this estuary for English sole, California halibut and starry flounder, the latter of which are no longer abundant in the estuary (Hughes et al. 2012). Restoring salt marsh habitat is a management objective in Elkhorn Slough, yet presents a tradeoff as its restoration could lead to increased severity of eutrophication and hypoxia (through the creation of dikes) and decreased habitat quality for species using the estuary as nursery grounds, such as English sole and leopard sharks (Brown 2006, Carlisle and Starr 2009).

Management conflicts require consideration of impacts to the nursery function in estuaries caused by changes in top predator populations. For example, moving a nesting colony of Caspian terns (*Hydroprogene caspia*), which prey on juvenile salmonids, to another estuary or location within an estuary could cause shifts in benefits and impacts (Adrean et al. 2012). Caspian terns currently nest at great abundances in the Columbia River Estuary, consuming juvenile salmon in the system. As part of a mitigation strategy to minimize the impact to Columbia River salmon, managers have proposed moving part of the Caspian tern colony to San Francisco Bay where the risk to endangered juvenile salmon mortality could be enhanced by tern predation. This example highlights certain tradeoffs, which are often specific to a single estuary or in this case two, and its unique species assemblage and combination of threats.

Many restoration activities have net positive or neutral effects to estuarine nursery function. For example, it has been shown that when eelgrass is reduced from its original distribution and abundance, negative consequences accrue to species and functions (Bruno et al. 2003, Waycott et al. 2009). Restoring eelgrass may have mostly positive effects on nursery function. Simulations of eelgrass restoration on ecosystem services in Puget Sound by Plummer et al. (2013) yielded positive effects for juvenile salmonids, Pacific herring, rockfishes, elasmobranchs and Dungeness crabs, and minor negative effects on other forage fish. Therefore, eelgrass expansion could result in restoration of coastal food webs that benefit multiple species.

The eradication of invasive species could also benefit a suite of species by simultaneously removing negative species interactions, while restoring important ecosystem functions. For example, Holsman et al. (2010) demonstrated that removal of invasive Atlantic smooth cordgrass (*Spartina alterniflora*) in Willapa Bay increased the abundance of Dungeness crab, which are dependent on intertidal habitats as foraging grounds. Furthermore, invasive green crabs, *Carcinus maenas,* were found to reduce habitat availability for juvenile Dungeness crabs in Bodega Bay, CA (McDonald et al. 2001), suggesting that eradication of invasive green crabs could restore the estuarine nursery function for native crabs. These examples all indicate that restoration of specific habitats and removal of invasive species could have net positive effects for a suite of species dependent on estuaries for their nursery function.

IDENTIFICATION OF KNOWLEDGE GAPS

There is still much we do not know about the nursery role of estuaries for species of commercial, recreational, cultural, or conservation importance. The critical information gaps that remain include further characterization and quantification of juvenile life history stages and their key habitats in estuaries throughout the West Coast of the United States. This will be an important first step for identifying priority nurseries for conservation and restoration efforts. Although prior efforts focused on larger estuarine systems, this review indicates that smaller estuaries may also be very important for their nursery role. Further research into the nursery function and threats to these smaller systems is needed.

This review of 15 focal species demonstrated that although juvenile life stages occur in many West Coast estuaries, little is known about whether these populations are enhanced by estuarine habitats (i.e., whether these estuaries are truly performing as “nurseries” relative to other nearshore habitats).

The species with the most information on estuarine nursery role are primarily species of economic importance (crabs, salmonids and flatfishes). For these species, there is strong evidence that estuaries serve as important nurseries. For certain species, such as Dungeness crab, there is good indication that the larger well-studied estuarine systems (e.g., San Francisco Bay, Grays Harbor, Puget Sound) are more important nurseries compared to smaller systems (Armstrong et al. 2003). Salmonids, on the other hand, have been documented to derive nursery benefits from both large (e.g., Maier and Simenstad 2009, Jones et al. 2011) and small (e.g., Hayes et al. 2008, Moyle et al. 2008) estuaries. How ubiquitous the nursery function of smaller systems for salmon is among the larger West Coast estuaries is not known. Future research should not only investigate the geographic extent of the importance of smaller estuaries as nursery habitat for salmonids, but also elucidate the importance of smaller estuaries relative to larger estuaries for different populations throughout the geography.

Finally, the limited information on the nursery function of estuaries and on important threats to the less economically important and lower trophic species creates another important knowledge gap, as many of these species play key ecological roles. Lower trophic species, such as bay shrimp, shiner perch and Pacific staghorn sculpin have little economic value, but due to their abundance and key ecological roles in estuarine food webs, they should also be considered for future studies to understand their use of estuarine nursery habitats. These studies on lower trophic level species should complement further studies on the nursery function for higher trophic level predators, such as Dungeness crab, salmonids, elasmobranchs and flatfishes.

There remains a lack of understanding of the overall importance of estuarine dependent fish and shellfish from lower trophic levels on one key element of estuarine nurseries, which is the provision of prey items for their predators. These lower trophic level species could face similar threats as higher trophic levels through habitat loss, altered freshwater flow, hypoxia and climate change (Siegfried 1989, Kimmerer 2002). For example, it has been shown that habitat modifications to estuarine habitats through construction of water control structures can fundamentally change the community structure at all trophic levels, with simultaneous declines to native crabs, sculpins, Pacific herring and flatfishes (Ritter et al. 2008). There could be strong associations with the nursery function for lower and upper trophic levels, indicating a need to incorporate community ecology and food webs into the design of future studies on estuarine nursery functions, and into the design of estuarine habitat restoration projects.

CONCLUSION

In this report, we have summarized the ecology, spatial distribution, habitat use and threats for juvenile life-history stages of 15 focal species in estuaries along the West Coast of the United States. We have documented juvenile presence in estuaries, identified cases of demonstrated nursery function and identified the important knowledge gaps that should serve as a guide for future research on the ecology and nursery role of estuarine systems.

Although specific examples of nursery functions of West Coast estuaries are relatively limited when compared to other parts of the United States, there are examples of the important nursery function of estuaries for California halibut in southern California estuaries; English sole, leopard sharks, coho salmon, Chinook salmon and steelhead trout in central California; and Dungeness crab, English sole, coho salmon, Chinook salmon and steelhead trout in Oregon and Washington. Most of these case studies are limited to larger well-studied estuaries, except for a few smaller estuaries that serve as important nurseries for several species of salmonids and flatfishes. Given that our review of existing information has highlighted the potential role of smaller estuaries for many of the focal species, this finding should motivate future research into exploring the relative contribution of smaller versus larger estuaries, and taking regional approaches when identifying critical nurseries for fish and invertebrate species of importance.

© Walter N. Heady/TNC

REFERENCES

© Walter N. Heady/TNC

Ackerman, L. T. 1971. Contributions to the biology of the leopard shark, *Triakis semifasciata* (Girard), in Elkhorn Slough, Monterey Bay, California. M.A. Thesis. Sacramento State College, Sacramento, CA.

Ackerman, J. T., M. C. Kondratieff, S. A. Matern, and J. J. Cech. 2000. Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. *Environmental Biology of Fishes* 58:33–43.

Adams, P. B., C. B. Grimes, S. T. Lindley, and M. L. Moser. 2002. Status review for North American green sturgeon, *Acipenser medirostris*. National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, CA.

Adams, P., C. Grimes, J. Hightower, S. Lindley, M. Moser, and M. Parsley. 2007. Population status of North American green sturgeon, *Acipenser medirostris*. *Environmental Biology of Fishes* 79:339–356.

Adrean, L. J, D. D. Roby, D. E. Lyons, K. Collis, and A. F. Evans. 2012. Potential effects of management of Caspian tern *Hydroprogne caspia* predation on juvenile salmonids at a colony in San Francisco Bay, California. *Transactions of the American Fish Society* 141:1682–1696.

Aitkin, J. K. 1998. The importance of estuarine habitats to anadromous salmonids of the Pacific Northwest: A literature review. Lacey, Washington. US Fish and Wildlife Service. 29pp.

Allen, L. G. 1988. Recruitment, distribution, and feeding habits of young-of-the-year California halibut, (*Paralichthys californicus*) in the vicinity of Alamitos Bay-Long Beach Harbor, California, 1983–1985. Bulletin of the Southern California Academy of Science 87:19–30.

Allen, L. G., and M. H. Horn. 1975. Abundance, diversity and seasonality of fishes in Colorado Lagoon, Alamitos Bay, California. *Estuarine Coastal Marine Science* 3:371–380.

Allen, L. G., R. E. Jensen, and J. R. Sears. 1990. Open coast settlement and distribution of young-of-the-year California halibut, *Paralichthys californicus*, along the southern California coast between Point Conception and San Mateo Point, June-October, 1988. Pages 145–152 *in* C. W. Haugen, editor. The California Halibut, *Paralichthys californicus*, Resource and Fisheries. Calif. Dep. Fish Game, Fish. Bull. 174.

Allen, L. G, A. M. Findlay, and C. M. Phalen. 2002. Structure and standing stock of the fish assemblages of San Diego Bay, California from 1994 to 1999. Bulletin Southern California Academy of Sciences 101:49–85.

Allen, L. G., M. M. Yoklavich, G. M. Cailliet, and M. H. Horn. 2006. Bays and estuaries. In *The Ecology of Marine Fishes: California and Adjacent Waters*, eds. L. G. Allen, D. J. Pondella II, and M. H. Horn, 119–148. Berkeley, California: University of California Press.

Allen, M. J. 1990. The biological environment of the California halibut, *Paralichthys californicus*. In *The California halibut*, Paralichthys californicus, *resource and fisheries*, ed. C.W. Haugen, 7–29. California Department of Fish and Game, Fisheries Bulletin 174.

Allen, M. J., and K. T. Herbinson. 1990. Settlement of juvenile California halibut, *Paralichthys californicus*, along the coasts of Los Angeles, Orange, and San Diego counties in 1989. California Cooperative Oceanic Fisheries Investigations Report 31:84–96.

Allen, P. J., and J. J. Cech. 2007. Age/size effects on juvenile green sturgeon, *Acipenser medirostris*, oxygen consumption, growth, and osmoregulation in saline environments. *Environmental Biology of Fishes* 79:211–229.

Altieri, A. H., M. D. Bertness, T. C. Coverdale, N. C. Herrmann, and C. Angelini. 2012. A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. *Ecology* 93:1402–1410.

Ambrose, D. A. 1976. The distribution, abundance, and feeding ecology of four species of flatfish in the vicinity of Elkhorn Slough, California. San Jose State University.

Ames, W. E., J. R. Hughes, and G. F. Slusser. 1978. Upper lethal water temperature levels for English sole (*Parophrys vetulus*) and rock sole (*Lepidopsetta bilineata*) subjected to gradual thermal increases. *Northwest Science* 52:285–291.

Anderson, B., B. Phillips, J. Hunt, K. Siegler, J. Voorhees, K. Smalling, K. Kuivila, M. Hamilton, J. A. Ranasinghe, and R. Tjeerdema. 2014. Impacts of pesticides in a Central California estuary. *Environmental Monitoring and Assessment* 186:1801–1814.

Anderson, J. H., P. L. Faulds, W. I. Atlas, and T. P. Quinn. 2013. Reproductive success of captively bred and naturally spawned Chinook salmon colonizing newly accessible habitat. *Evolutionary Applications* 6:165–79.

Arkush, K. D., and P. A. Siri. 2001. Exploring the role of captive broodstock programs in salmon restoration Captive breeding as a response to declining salmon stocks. Fishery Bulletin 2: 319–330.

Armstrong, D. A., D. V. Buchanan, M. H. Mallon, R. S. Caldwell, and R. E. Millemann. 1976. Toxicity of the insecticide methoxychlor to the Dungeness crab *Cancer magister*. *Marine Biology* 38:239–252.

Armstrong, J. L., D. A. Armstrong, and S. B. Mathews. 1995. Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister*. *Fishery Bulletin* 93:456–470.

Armstrong, D., C. Rooper, and D. Gunderson. 2003. Estuarine production of juvenile Dungeness crab (*Cancer magister*) and contribution to the Oregon-Washington coastal fishery. *Estuaries* 26:1174–1188.

Aspen Environmental Group (AEG). 2006. Tranquillon Ridge Oil and Gas Development Project. County EIR # 06-EIR-000000-00005. Santa Barbara, CA: County of Santa Barbara Planning and Development.

Atkinson, K. A. 2010. Habitat conditions and steelhead abundance and growth in a California lagoon. M.S. Thesis. San Jose State University. 118pp.

Atrill, M. J., and M. Power. 2002. Climatic influence on a marine fish assemblage. *Nature* 417:275–278.

Au, D. W. and S. E. Smith. 1997. A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:415–420.

Auad, G., A. Miller, and E. Di Lorenzo. 2006. Long-term forecast of oceanic conditions off California and their biological implications. *Journal of Geophysical Research* 111:1–14.

Augerot, X., and D. N. Foley. 2005. Atlas of Pacific salmon: The first map-based status assessment of salmon in the North Pacific. University of California Press. 125pp.

Baltz, D. M. 1984. Life history variation among female surfperches (Perciformes: Embiotocidae). *Environmental Biology of Fishes* 10(3):159–171.

Barnhart, R. A, M. J. Boyd, and J. E. Pequegnat. 1992. The ecology of Humboldt Bay, California: An estuarine profile. U.S. Dept. of the Interior, Fish and Wildlife Service. Washington, D.C.

Barry, J. P. 1983. Utilization of shallow marsh habitats by fishes in Elkhorn Slough, California. M.S. San Jose State University, San Jose, CA.

Barry, J. P., and G. M. Cailliet. 1981. The utilization of shallow marsh habitats by commercially important fishes in Elkhorn Slough, California. *Cal-Neva Wildlife Transactions* 38–47.

Barry, J. P., M. M. Yoklavich, G. M. Cailliet, D. A. Ambrose, and B. S. Antrim. 1996. Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974-1980. *Estuaries* 19:115–138.

Bartling R. 2006. Status of the fishery report, 11: Pacific Herring. California Department of Fish and Game.

Baxter, R. 1999. Brown Rockfish. In *Report on the 1980-1995 Fish, Shrimp, and Crab Sampling in the San Francisco Estuary, California*, ed. J. Orsi, 443–476. California Department of Fish and Game, Technical Report No. 63.

Baxter, R., K. Hieb, S. DeLeon, K. Fleming, and J. Orsi. (editor). 1999. Report on the 1980–1995 Fish, Shrimp, and Crab Sampling in the San Francisco Bay Estuary, California. California Department of Fish and Game, The Interagency Ecological Program for the Sacramento-San Joaquin Estuary.

Bayer, R. 1981. Shallow water intertidal ichthyofauna of the Yaquina Estuary, Oregon. *Northwest Science* 55(3):182–193.

Bayer, R. D. 1985. Shiner perch and Pacific staghorn sculpins in Yaquina Estuary, Oregon, 59(3):230–240.

Beamesderfer, R. C. P., and M. A. H. Webb. 2002. Green sturgeon status review information. Report to S.P. Cramer and Associates to State Water Contractors, Sacramento, CA.

Beamesderfer, R. C. P., M. Simpson, and G. Kopp. 2007. Use of life history information in a population model for Sacramento green sturgeon. *Environmental Biology of Fishes* 79:315–337.

Beauchamp, D. A., M. F. Shepard, and G. B. Pauley. 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest) Chinook salmon. U.S. Fish and Wildlife Service, Division of Biological Services, FWS/OBS-82/11.6. U.S. Army Corps of Engineers, TREL-82-4.15pp.

Beck, M. W, K. L. Heck, Jr., K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, T. J. Minello, R. J. Orth, P. F. Sheridan, and M. P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51:633–641.

Beck, M. W., K. Heck, K. Able, D. L. Childers, D. B. Eggleston, B. Gillanders, and M. P. Weinstein. 2003. The role of nearshore ecosystems as fish and shellfish nurseries. *Issues in Ecology* 2003:1–12.

Behnke, R. J. 2002. Trout and salmon of North America. New York: The Free Press.

Bernardi, G., and G Bucciarelli. 1999. Molecular phylogeny and speciation of the surfperches (Embiotocidae, Perciformes). *Molecular Phylogenetics and Evolution* 13(1):77–81.

Bernatis, J. L., S. L. Gerstenberger, and I. J. McGaw. 2007. Behavioural responses of the Dungeness crab, Cancer magister, during feeding and digestion in hypoxic conditions. *Mar Biol* 150:941–951.

Bersine, K., V. E. F. Brenneis, R. C. Draheim, A. M. W. Rub, J. E. Zamon, R. K. Litton, S. A. Hinton, M. D. Sytsma, J. R. Cordell, and J. W. Chapman. 2008. Distribution of the invasive New Zealand mudsnail (*Potamopyrgus antipodarum*) in the Columbia River Estuary and its first recorded occurrence in the diet of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Biological Invasions* 10:1381–1388.

Bertness, M. D., and T. C. Coverdale. 2013. An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. *Ecology* 94:1937–1943.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and J. K. Walter. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1909–1918.

Bloeser, J. A. 2000. Biology and population structure of California halibut, *Paralichthys californicus*, in Humboldt Bay, California. M.S. Thesis, Humboldt State University.

Boehlert, G. W., and B. C. Mundy. 1987. Recruitment dynamics of metamorphosing English sole, *Parophrys vetulus*, to Yaquina Bay, Oregon. *Estuarine, Coastal and Shelf Science* 25:261–281.

Boese, B. L. 1988. Hypoxia-induced respiratory changes in English sole (*Parophrys vetulus* girard). Comparative Biochemistry and Physiology Part A: Physiology 89:257–260.

Boles, G. 1988. Water temperature effects on Chinook salmon (*Oncorhynchus tshawytscha*) with emphasis on the Sacramento River. California Department of Water Resources, Sacramento, CA.

Bond, M. H., S. A. Hayes, C. V. Hanson, and R. B. MacFarlane. 2008. Marine survival of steelhead (*Oncorhynchus mykiss*) enhanced by a seasonally closed estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 65(10):2242–2252.

Booth, J. A., E. E. McPhee-Shaw, P. Chua, E. Kingsley, M. Denny, R. Phillips, S. J. Bograd, L. D. Zeidberg, and W. F. Gilly. 2012. Natural intrusions of hypoxic, low pH water into nearshore marine environments on the California coast. *Continental Shelf Research* 45:108–115.

Boreman, J. 1997. Sensitivity of North American sturgeons and paddlefish to fishing mortality. *Environmental Biology of Fishes* 48:399–405.

Borton, S. F. 1982. A structural comparison of fish assemblages from eelgrass and sand habitats at Alki Point, Washington. M.S. Thesis, University of Washington, Seattle.

Bottom, D. L., K. K. Jones, and M. L. Herring. 1984. Fishes of the Columbia River estuary. Columbia River Data Development Program, 113 p. CREST, 750 Commercial St. Rm. 205, Astoria, OR 97103.

Bottom, D. L., C. A. Simenstad, J. Burke, A. M. Baptista, D. A. Jay, K. K. Jones, E. Casillas, and M. H. Schiewe. 2005a. Salmon at river's end: The role of the estuary in the decline and recovery of Columbia River salmon. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS-NWFSC-68, 246 p.

Bottom, D. L., K. K. Jones, T. J. Cornwell, A. Gray, and C. A. Simenstad. 2005b. Patterns of Chinook salmon migration and residency in the Salmon River estuary (Oregon). *Estuarine, Coastal and Shelf Science* 64:79–93.

Bottom, D. L., K. K. Jones, C. A. Simenstad, and C. L. Smith. 2009. Reconnecting social and ecological resilience in salmon ecosystems. *Ecology and Society* 14:5.

Brandenberger, J. M., P. Louchouarn, and E. A. Crecelius. 2011. Natural and post-urbanization signatures of hypoxia in two basins of Puget Sound: Historical reconstruction of redox sensitive metals and organic matter inputs. *Aquatic Geochemistry* 17:645–670.

Breyta, R., A. Jones, B. Stewart, R. Brunson, J. Thomas, J. Kerwin, J. Bertolini, S. Mumford, C. Patterson, and G. Kurath. 2013. Emergence of MD type infectious hematopoietic necrosis virus in Washington State coastal steelhead trout. *Diseases of Aquatic Organisms* 104:179–95.

Broenkow, W. W., and L. C. Breaker. 2005. A 30-year history of tide and current measurements in Elkhorn Slough, California. Moss Landing Marine Laboratories Technical Report, Moss Landing, CA.

Brown, A. C., and N. B. Terwilliger. 1992. Developmental changes in ionic and osmotic regulation in the Dungeness crab, *Cancer magister. Biological Bulletin* 182:270.

Brown, J. A. 2002. A plan for monitoring the fish assemblage in Elkhorn Slough. Elkhorn Slough Technical Report Series 2002:1. 25pp.

Brown, J. A. 2003. An evaluation of the nursery role of estuaries for flatfish populations in central California. PhD Dissertation, University of California, Santa Cruz.

Brown, J. A. 2006. Using the chemical composition of otoliths to evaluate the nursery role of estuaries for English sole *Pleuronectes vetulus* populations. *Marine Ecology Progress Series* 306:269–281.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18:119–125.

Buchanan, D., R. Millemann, and N. Stewart. 1970. Effects of the insecticide Sevin on various stages of the Dungeness crab, *Cancer magister. J. Fish. Board Canada* 27:93–104.

Burke, J. L. 2004. Life histories of juvenile Chinook salmon in the Columbia River estuary, 1916 to present. Oregon State University.

Cailliet, G. M. 1992. Demography of the Central California population of the leopard shark (*Triakis semifasciata*). *Australian Journal of Marine and Freshwater Research* 43:183–193.

Cailliet, G. M., E. J. Burton, J. M. Cope, and L. A. Kerr. 2000. Biological characteristics of nearshore fishes of California: A review of existing knowledge and proposed additional studies for the Pacific Ocean inter-jurisdictional fisheries management plan coordination and development. Report submitted to the Pacific State Marine Fisheries Commission.

Cailliet, G. M. and W. D. Smith. 2006. *Myliobatis californicus*. The IUCN Red List of Threatened Species. Version 2014.2. <www.iucnredlist.org>. Downloaded on July 2014.

California Fish Website—http://calfish.ucdavis.edu

Campana, S. E. 1984. Comparison of age determination methods for the starry flounder. *Transactions of the American Fisheries Society* 113:365–369.

Campbell, L. A. 2010. Life histories of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River Estuary as inferred from scale and otolith microchemistry. M.S. Thesis. Oregon State University.

Carlisle, A. B. 2006. Movements and habitat use of female leopard sharks in Elkhorn Slough, California. M.S. Thesis. San Jose State University, San Jose, CA.

Carlisle, A., and S. E. Smith. 2009. *Triakis semifasciata*. In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. <www.iucnredlist.org>. Downloaded on 17 February 2014.

Carlisle, A. B., and R. M. Starr. 2009. Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Marine Ecology Progress Series* 380:213–228.

Carlisle, A. B., and R. M. Starr. 2010. Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. *Environmental Biology of Fishes* 89:31–45.

Carlisle, A. B., A. King, G. M. Cailliet, and J. S. Brennan. 2007. Long-term trends in catch composition from elasmobranch derbies in Elkhorn Slough, California. *Marine Fisheries Review* 69:25–45.

Carls, M. G., S. D. Rice, and J. E. Hose. 1999. Sensitivity of fish embryos to weathered crude oil: Part I. Low level exposure during incubation causes malformations, genetic damage, and mortality in larval pacific herring (*Clupea pallasii*). Environmental Toxicology and Chemistry, 18:481–493.

Carlson, S. M., and W. H. Satterthwaite. 2011. Weakened portfolio effect in a collapsed salmon population complex. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1579–1589.

Cattrijsse, A., H. R. Dankwa, and J. Mees. 1997. Nursery function of an estuarine tidal marsh for the brown shrimp *Crangon crangon*. *Journal of Sea Research* 38:109–121.

Cavallo, B., J. E. Merz, and J. Setka. 2012. Effects of predator and flow manipulation on Chinook salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary. *Environmental Biology of Fishes* 96:393–403.

Chamberlain, R. H., and R. A. Barnhart. 1993. Early use by fish of a mitigation salt marsh, Humboldt Bay, California. *Estuaries* 16(4):769–783.

Chapman, E. D., A. R. Hearn, C. J. Michel, A. J. Ammann, S. T. Lindley, M. J. Thomas, and P. Klimley. 2012. Diel movements of out-migrating Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) smolts in the Sacramento/San Joaquin watershed. *Environmental Biology of Fishes* 96:273–286.

Chase, R., N. Hemphill, J. Beeman, S. Juhnke, J. Hannon, and A. M. Jenkins. 2012. Assessment of juvenile coho salmon movement and behavior in relation to rehabilitation efforts in the Trinity River, California, using PIT tags and radiotelemetry. *Environmental Biology of Fishes* 96:303–314.

Chittaro, P. M., R. J. Finley, and P. S. Levin. 2009. Spatial and temporal patterns in the contribution of fish from their nursery habitats. *Oecologia* 160(1):49–61.

Clements, S., T. Stahl, and C. Schreck. 2012. A comparison of the behavior and survival of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) in a small estuary system. *Aquaculture* 362–363:148–157.

Cloern, J. E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210:223–253.

Cloern, J. E., A. D. Jassby, J. K. Thompson, and K. A. Hieb. 2007. A cold phase of the East Pacific triggers new phytoplankton blooms in San Francisco Bay. *Proceedings of the National Academy of Sciences* 104:18561–18565.

Collis, K., D. D. Roby, D. P. Craig, B. A. Ryan, and R. D. Ledgerwood. 2001. Colonial waterbird predation on juvenile salmonids tagged with Passive Integrated Transponders in the Columbia River Estuary: Vulnerability of different salmonid species, stocks, and rearing types. *Transactions of the American Fisheries Society* 130:385–396.

Commins, M. L., M. H. Fawcett, and J. C. Roth. 1996. Environmental Conditions in West County Waterways. Santa Rosa, CA.

Cornwell, T. J., D. L. Bottom, and K. K. Jones. 2001. Rearing of juvenile salmon in recovering wetlands of the Salmon River Estuary. Oregon Department of Fish and Wildlife, Information Reports 2001-05, Portland.

Craig, B. E. 2010. Life history patterns and ecology of juvenile coho salmon (*Oncorhynchus kisutch*) within a tidal freshwater estuary. Master's Thesis. School of Aquatic and Fishery Sciences, University of Washington. 95 pages.

Craig, B. E., C.A. Simenstad, and D. L. Bottom. 2014. Rearing in natural and recovering tidal wetlands enhances growth and life-history diversity of Columbia Estuary tributary coho salmon *Oncorhynchus kisutch* population. Journal of Fish Biology 85: 31-51.

Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11:1304–1315.

da Silva, D. A. M., J. Buzitis, and W. L. Reichert. 2013. Endocrine disrupting chemicals in fish bile: A rapid method of analysis using English sole (*Parophrys vetulus*) from Puget Sound, WA, USA. *Chemosphere* 92:1550–1556.

Dagit, R., and C. Swift. 2005. Malibu Lagoon Fish Survey June 2005. Malibu, CA.

Dahl, T. E. 1990. Wetlands losses in the United States 1780's to 1980's. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., 13pp.

Dahlgren, C. P., G. T. Kellison, A. J. Adams, B. M. Gillanders, M. S. Kendall, C. A. Layman, J. A. Ley, I. Nagelkerken, and J. E. Serafy. 2006. Marine nurseries and effective juvenile habitats: Concepts and applications. *Marine Ecology Progress Series* 312:291–295.

Dahlstrom, W., R. Wild. 1983. A history of Dungeness crab fisheries in California, p. 7-28. Ira R Wild and R. Tasto (eds.), Life History, Environment, and Mariculture Studies of the Dungeness Crab, Cancer rnagister, with Emphasis on the Central California Resource. California Department of Fish and Game Bulletin 172.

Davies, T. D. 2004. Update COSEWIC status report on green sturgeon (*Acipenser medirostris*). Committee on the Status of Endangered Wildlife in Canada (COSEIC). CWS, Ottawa, ON, CA.

Dawley, E. M., R. D. Ledgerwood, T. H. Blahm, C. W. Sims, J. T. Durkin, R. A. Kirn, A. E. Rankis, G. E. Monan, and F. J. Ossiander. 1986. Migrational characteristics, biological interactions, and relative survival of juvenile salmonids entering the Columbia River estuary, 1966–1983. Final Rep. to Bonneville Power Adm., Contract DE-A 179-84BP39652, 256 p. Available Northwest and Alaska Fish. Center, 2725 Montlake Blvd. E., Seattle, WA.

de Ben, W. A., W. D. Clothier, G. R. Ditsworth, and D. J. Baumgartner. 1990. Spatio-temporal fluctuations in the distribution and abundance of demersal fish and epibenthic crustaceans in Yaquina Bay, Oregon. *Estuaries* 13(4):469–478.

DeMartini, E., T. O. Moore, and K. M. Plummer. 1983. Reproductive and growth dynamics of *Hyperprosopon argenteum* (Embiotocidae) near San Diego, California. *Environmental Biology of Fishes* 8: 29–38.

Deng, X., J. P. Van Eenennaan, and S. I. Doroshov. 2002. In *Biology, management, and protection of North American sturgeon*, eds., W. Van Winkle, P. J. Anders, D. H. Secor, and D. A. Dixon, 237–248. American Fisheries Society, Symposium 28, Bethesda, MD.

DeVlaming, V., R. Fitzgerald, G. Delahunty, J. J. Cech, Jr., K. Selman, and M. Barkley. 1984. Dynamics of oocyte development and related changes in serum estradiol-17, yolk precursor, and lipid levels in the teleostean fish, *Leptocottus armatus*. *Comparative Biochemistry and Physiology* Part A: Physiology 77:599–610.

Diaz, R. J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–929.

Dinnel, P. A., J. A. Armstrong, R. R. Lauth, K. Larsen, D. A. Armstrong, and S. Sulkin. 1990. Fish predation on Dungeness crab in Padilla Bay, Washington. Seattle, WA. Padilla Bay National Estuarine Research Reserve Reprint Series No. 14. 69pp.

Dowd, W. W., B. N. Harris, J. J. Cech Jr., and D. Kültz. 2010. Proteomic and physiological responses of leopard sharks (*Triakis semifasciata*) to salinity change. *The Journal of Experimental Biology* 213:210–224.

Drawbridge, M. A. 1990. Feeding relationships, feeding activity and substrate preferences of juvenile California halibut, *Paralichthys californicus*, in coastal and bay habitats. M.S. Thesis, San Diego State University.

Duarte, C. M., J. J. Middelburg, and N. Caraco. 2005. Major role of vegetation on the oceanic carbon cycle. *Biogeosciences* 2:1–8.

Dumbauld, B., D. Armstrong, and T. McDonald. 1993. Use of oyster shell to enhance intertidal habitat and mitigate loss of Dungeness crab (*Cancer magister*) caused by dredging. *Canadian Journal of Fisheries and Aquatic Science*s 50:381–390.

Dumbauld, B. R., Holden, D. L., and O. P. Langness. 2008. Do sturgeon limit burrowing shrimp populations in Pacific Northwest estuaries? *Environmental Biology of Fishes* 83:283–296.

Dumbauld, B. R., J. L. Ruesink, and S. S. Rumrill. 2009. The ecological role of bivalve shellfish aquaculture in the estuarine environment: A review with application to oyster and clam culture in West Coast (USA) estuaries. *Aquaculture* 290:196–223.

Ebert, D. A. 1986. Observations on the Elasmobranch assemblage of San-Francisco Bay. *California Fish and Game* 72:244–249.

Ebert, D. A. 2003. Sharks, rays and chimaeras of California. University of California Press, Berkeley, CA.

Ebert, D. A., and T. B. Ebert. 2005. Reproduction, diet and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California, USA. *Marine and Freshwater Research* 56:1089–1098.

Emmett, R. L., S. L. Stone, S. A. Hinton, and M. E. Monaco. 1991. Distribution and abundance of fishes and invertebrates in West Coast estuaries, Volume II: species life history summaries. ELMR Rep. No. 8. NOAA/NOS Strategic Environmental Assessments Division, Rockville, MD, 329pp.

Emmett, R., R. Llanso, J. Newton, and R. Thom. 2000. Geographic signatures of North American West Coast estuaries. *Estuaries* 23:765–792.

Erickson, D. L., and J. E. Hightower. 2007. Oceanic distribution and behavior of green sturgeon (*Acipenser medirostris*). In *Anadromous Sturgeons: Habitats, Threats, and Management*, eds. J. Munro, J. E. Hightower, K. McKown, K. J. Sulak, A. W. Kahnle, and F. Caron, 197–211. Bethesda, MD: American Fisheries Society, Symposium 56.

Eschmeyer, W. N., E. S. Herald, and H. Hammon. 1983. A field guide to Pacific Coast fishes. Peterson Field Guide Series. Houghton and Mifflin Co., Boston. 336pp.

Farr, R. A., M. L. Hughes, and T. A. Rien. 2002. Green sturgeon population characteristics in Oregon. Annual progress report to sport fish restoration project F-178-R.

Farrer, D. A. 2009. Northern range extension of the leopard shark, *Triakis semifasciata*. *California Fish and Game* 95:62–64.

Federal Geographic Data Committee. 2012. Coastal and Marine Ecological Classification Standard. Marine and Coastal Spatial Data Subcommittee. FGDC-STD-018-2012. June.

Feldman, K., D. Armstrong, and B. Dumbauld. 2000. Oysters, crabs, and burrowing shrimp: Review of an environmental conflict over aquatic resources and pesticide use in Washington State's (USA) coastal estuaries. *Estuaries* 23:141–176.

Fernandez, M., O. Iribarne, and D. Armstrong. 1993. Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Marine Ecology Progress Series* 92:171–177.

Feyrer, F., B. Herbold, S. A. Matern, and P. B. Moyle. 2003. Dietary shifts in a stressed fish assemblage: Consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67:277–288.

Fish, M., J. Messineo, and K. Hieb. 2013. 2011 Bay study fishes annual status and trends report for the San Francisco estuary. In Interagency Ecological Program for the San Francisco Estuary, eds. L. Conrad, G. Castillo, R. D. Baxter, S. Slater, K. Gehrts, and F. Keeley, 30–44. IEP Newsletter, Sacramento, CA.

Fleming, I. A., D. L. Bottom, K. K. Jones, C. A. Simenstad, and J. F. Craig. 2014. Resilience of anadromous and resident salmonid populations. *Journal of Fish Biology* 85:1–7.

Flitcroft, R., K. Burnett, and K. Christiansen. 2013. A simple model that identifies potential effects of sea-level rise on estuarine and estuary-ecotone habitat locations for salmonids in Oregon, USA. *Environmental Management* 52:196–208.

Fodrie, F. J., and G. Mendoza. 2006. Availability, usage and expected contribution of potential nursery habitats for the California halibut. *Estuarine Coastal and Shelf Science* 68(1–2):149–164.

Fodrie, F. J., and L. A. Levin. 2008. Linking juvenile habitat utilization to population dynamics of California halibut. *Limnology and Oceanography* 53(2):799–812.

Fodrie, F. J., and S. Z. Herzka. 2013. A comparison of otolith geochemistry and stable isotope markers to track fish movement: Describing estuarine ingress by larval and post-larval halibut. *Estuaries and Coasts* 36(5):906–917.

Fodrie, F. J., L. A. Levin, and A. J. Lucas. 2009. Use of population fitness to evaluate the nursery function of juvenile habitats. *Marine Ecology Progress Series* 385:39–49.

Forrester, G. E., and S. E. Swearer. 2002. Trace elements in otoliths indicate the use of open-coast versus bay nursery habitats by juvenile California halibut. *Marine Ecology Progress Series* 241:201–213.

Forsberg, B. O., J. A. Johnson, and S. M. Klug. 1977. Identification, distribution and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. 117pp.

Forsgren, K. L., N. Riar, and D. Schlenk. 2013. The effects of the pyrethroid insecticide, bifenthrin, on steroid hormone levels and gonadal development of steelhead (*Oncorhynchus mykiss*) under hypersaline conditions. *General and Comparative Endocrinology* 186:101–107.

Frechette, D., A.-M. K. Osterback, S. A. Hayes, M. H. Bond, J. W. Moore, S. A. Shaffer, and J. T. Harvey. 2012. Assessing avian predation on juvenile salmonids using passive integrated transponder tag recoveries and mark–recapture methods. *North American Journal of Fisheries Management* 32:1237–1250.

Fresh, K. L. 2006. Juvenile Pacific salmon in Puget Sound. Technical Report 2006-06 prepared in support of the Puget Sound Nearshore Partnership. 22pp.

Fresh, K. L., and S. L. Schroder. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences* 44:236–243.

Froehlich, H. E., T. E. Essington, A. H. Beaudreau, and P. S. Levin. 2013. Movement patterns and distributional shifts of Dungeness crab (*Metacarcinus magister*) and English sole (*Parophrys vetulus*) during seasonal hypoxia. *Estuaries and Coasts* 37:449–460.

Fuller, J. A. 2011. Extended residency and movement behavior of juvenile steelhead (*Oncorhynchus mykiss*) in the Russian River Estuary, CA. Thesis. Humboldt State University.

Gadomski, D. M., and S. M. Caddell. 1991. Effects of temperature on early-life history stages of California halibut *Paralichthys californicus*. *Fishery Bulletin* 89:567–576.

Gadomski, D. M., S. M. Caddell, L. R. Abbott, and T. C. Caro. 1990. Growth and development of larval and juvenile California halibut, *Paralichthys californicus*, reared in the laboratory. In *The California Halibut,* Paralichthys californicus*, Resource and Fisheries*, ed. C. W. Haugen, 85–98. Calif. Dep. Fish Game, Fish. Bull. 174.

Gaines, S., and J. Roughgarden. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science* 235:479–481.

Garrison, K. J., and B. S. Miller. 1982. Review of the early life history of Puget Sound fishes. Seattle, WA. 759pp.

Garshelis, D. L., and J. A. Garshelis. 1984. Movements and management of sea otters in Alaska. *Journal of Wildlife Management* 48:665–678.

Garwood, J. 2012. Historic and recent occurrence of Coho salmon (*Oncorhynchus kisutch*) in Califorrnia streams within the Southern Oregon/Northern California Evolutionarily Significant Unit. CDFG, Fisheries Branch Administrative Report, 2012–03.

Garwood, J., S. Ricker, and C. Anderson. 2010. Bullfrog predation on a juvenile coho salmon in Humboldt County, California. *Northwestern Naturalist* 99–101.

Garwood, R. S., T. J. Mulligan, and E. P. Bjorkstedt. 2013. Ichthyological assemblage and variation in a Northern California *Zostera marina* eelgrass bed. *Northwestern Naturalist* 94(1):35–50.

Gavio, M. A., D. Armstrong, and J. M. (Lobo) Orensanz. 2006. Evaluation of alternative life history hypotheses for the sand shrimp *Crangon franciscorum* (Decapoda: Caridea). *Journal of Crustacean Biology* 26:295–307.

Gleason, M. G., S. Newkirk, M. S. Merrifield, J. Howard, R. Cox, M. Webb, J. Koepcke, B. Stranko, B. Taylor, M. W. Beck, R. Fuller, P. Dye, D. Vander Schaaf, and J. Carter. 2011. A conservation assessment of West Coast (USA) estuaries. The Nature Conservancy, Arlington VA. 65pp.

Gordon, C. D. 1965. Aspects of the life-history of *Cymatogaster aggregata* Gibbons. University of British Columbia.

Grant, N. E. 2009. Changes in cover and use of *Zostera marina* habitats in Elkhorn Slough, California. MS Thesis, California State University, Monterey Bay.

Grantham, B., F. Chan, K. J. Nielsen, D. S. Fox, J. A. Barth, A. Huyer, J. Lubchenco, and B. A. Menge. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429:749–754.

Gray, A. E., T. J. Mulligan, and R. W. Hannah. 1997. Food habits, occurrence, and population structure of the bat ray, *Myliobatis californica*, in Humboldt bay, California. *Environmental Biology of Fishes* 49:227–238.

Greene, C. M., K. Blackhart, J. Nohner, A. Candelmo, and D. M. Nelson. 2014. A national assessment of stressors to estuarine fish habitats in the contiguous USA. *Estuaries and Coasts*, in press.

Griffin, F. J., E. H. Smith, C. A. Vines, and G. N. Cherr. 2009. Impacts of suspended sediments on fertilization, embryonic development, and early larval life stages of the pacific herring, *Clupea pallasii*. *Biological Bulletin* 216:175–87.

Grosholz, E. D., and G. M. Ruiz. 2009. Multitrophic effects of invasions in marine and estuarine systems. *Biological Invasions in Marine Ecosystems* 204:305-324.

Gunderson, D. R., D. A. Armstrong, Y-B Shi, and R. A. McConnaughey. 1990. Patterns of estuarine use by juvenile English sole (*Parophrys vetulus*) and Dungeness crab (*Cancer magister*). *Estuaries* 13:59.

Haaker, P. L. 1975. The biology of the California halibut, *Paralichthys californicus* (Ayres) in Anaheim Bay. In *The Marine Resources of Anaheim Bay*, eds. E. D. Lane and C. W. Hill, 137–151. Calif. Dept. Fish Game.

Haertel, L., and C. Osterberg. 1967. Ecology of zooplankton, benthos and fishes in the Columbia River estuary. *Ecology* 48(3):459–472.

Haeseker, S. L., J. A. McCann, J. Tuomikoski, and B. Chockley. 2012. Assessing freshwater and marine environmental influences on life-stage-specific survival rates of Snake River Spring–Summer Chinook salmon and steelhead. *Transactions of the American Fisheries Society* 141:121–138.

Haist, V., and M. Stocker. 1985. Growth and maturation of Pacific herring (*Clupea harengus*) in the Strait of Georgia. *Canadian Journal of Fisheries and Aquatic Sciences* 42:138–146.

Halpern, B. S., C. V. Kappel, K. A. Selkoe, F. Micheli, C. M. Ebert, C. Kontgis, C. M. Crain, R. G. Martone, C. Shearer, and S. J. Teck. 2009. Mapping cumulative human impacts to California Current marine ecosystems. *Conservation Letters* 2:138–148.

Hanson, K. C., K. G. Ostrand, and R. A. Glenn. 2012. Physiological characterization of juvenile Chinook salmon utilizing different habitats during migration through the Columbia River Estuary. Comparative Biochemistry and Physiology. Part A, *Molecular and Integrative Physiology* 163:343–9.

Hart, J. L. 1973. Pacific fishes of Canada. Fisheries Research Board of Canada Bulletin 180:1–740.

Hartman, M. C., and G. R. Letterman. 1978. An evaluation of three species of diatoms as food for *Cancer magister* larvae. Proceedings of the Annual Meeting—World Mariculture Society, 9:271–276.

Hassler, T. J., E. Pendleton, and D. Moran. 1987. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest) biological report. California Cooperative Fishery Research Unit, Humboldt State University, Arcata, CA. Vol. 82, pp. 1–28.

Hayes, S. A., M. H. Bond, C. V. Hanson, E. V. Freund, J. J. Smith, E. C. Anderson, A. J. Ammann, and B. R. MacFarlane. 2008. Steelhead growth in a small Central California watershed: Upstream and estuarine rearing patterns. *Transactions of the American Fisheries Society* 137(1):114–128.

Hayes, S. A., M. H. Bond, C. V. Hanson, A. W. Jones, A. J. Ammann, J. A. Harding, A. L. Collins, J. Perez, and R. B. MacFarlane. 2011. Down, up, down and smolting twice? Seasonal movement patterns by juvenile steelhead (*Oncorhynchus mykiss*) in a coastal watershed with a bar closing estuary. *Canadian Journal of Fish Aquatic Sciences* 1350:1341–1350.

Heady, W. N., J, Kassakian, K. Doiron, D. Hudgens, K. O'Connor, R. P. Clark, C. Endris, J. Carter, and M. G. Gleason. 2014. An inventory and classification of U.S. west coast estuaries. The Nature Conservancy, Arlington, VA.

Healey, M. C. 1980. Utilization of the Nanaimo River estuary by juvenile Chinook salmon, *Onchorynchus tshawytscha*. *Fishery Bulletin* 77:653–668.

Healey, M. C. 1991. Life history of Chinook salmon. In *Pacific Salmon Life Histories*, eds. C. Groot and L. Margolis, 311–394. Vancouver: University of British Columbia Press.

Heck, K., C. G. Hays, and R. Orth. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253:123–136.

Hedgecock, D. 2002. Microsatellite DNA for the management and protection of California's Central Valley Chinook salmon (*Oncorhynchus tshawytscha*) Final Report for the Amendment to Agreement No. B-59638, University of California, D (Vol. 0247, p. 25). Bodega Bay, California.

Henning, J. A., R. E. Gresswell, and I. A. Fleming. 2007. Use of seasonal freshwater wetlands by fishes in a temperate river floodplain. *Journal of Fish Biology* 71:476–492.

Hessing-Lewis, M., S. D. Hacker, B. A. Menge, and S. Rumrill. 2011. Context-dependent eelgrass-macroalgae interactions along an estuarine gradient in the Pacific Northwest, USA. *Estuaries and Coasts* 34:1169–1181.

Hessing-Lewis, M. L., and S. D. Hacker. 2013. Upwelling-influence, macroalgal blooms, and seagrass production; temporal trends from latitudinal and local scales in northeast Pacific estuaries. *Limnology and Oceanography* 58:1103–1112.

Hieb, K., and R. Baxter. 1993. Delta Outflow/San Francisco Bay. In 1991 Annual Report: Interagency Ecological Studies Program for the Sacramento-San Joaquin Estuary. Sacramento, CA: Department of Water Resources, pp.101–116.

Higgins, K., A. Hastings, J. Sarvela, and L. Botsford. 1997. Stochastic dynamics and deterministic skeletons: Population behavior of Dungeness crab. *Science* 276:1431–1435.

Hight, B. V. and C. G. Lowe. 2007. Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: Evidence for behavioral thermoregulation? *Journal of Experimental Marine Biology and Ecology* 352:114–128.

Higley, D. L., and R. L. Holton. 1981. *A study of the invertebrates and fishes of salt marshes in two Oregon estuaries* (U.S. Army Corps of Engineers, Fort Belvoir, VA).

Hoem Neher, T. D., A. E. Rosenberger, C. E. Zimmerman, C. M. Walker, and S. J. Baird. 2013. Estuarine environments as rearing habitats for juvenile coho salmon in contrasting south-central Alaska watersheds. *Transactions of the American Fisheries Society* 142:1481–1494.

Hogue, E. W., and A. G. Carey. 1982. Feeding ecology of 0-age flatfishes at a nursery ground on the Oregon coast. *Fishery Bulletin* 80:555–565.

Holsman, K. K., D. A. Armstrong, D. A. Beauchamp, and J. L. Ruesink. 2003. The necessity for intertidal foraging by estuarine populations of subadult Dungeness crab, *Cancer magister*: evidence from a bioenergetics model. *Estuaries* 26:1155–1173.

Holsman, K., P. McDonald, and D. Armstrong. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Marine Ecology Progress Series* 308:183–195.

Holsman, K. K., P. S. McDonald, P. A. Barreyro, and D. A. Armstrong. 2010. Restoration through eradication? Removal of an invasive bioengineer restores some habitat function for a native predator. *Ecological Applications*, 20:2249–62.

Hood, W. G. 2002. Landscape allometry: from tidal channel hydraulic geometry to benthic ecology. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1418–1427. doi:10.1139/F02-109.

Hopkins, T. E. 1993. The physiological ecology of bat rays, *Myliobatis californica*, in Tomales Bay, California. Ph.D. University of California Davis.

Hopkins, T. E., and J. J. Cech Jr. 1994. Effect of temperature on oxygen consumption of the bat ray, *Myliobatis california*. *Copeia* 1994:529–532.

Hopkins, T. E., and J. J. Cech Jr. 2003. The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. *Environmental Biology of Fishes* 66:279–291.

Horn, M. H., and L.G. Allen. 1981. Ecology of fishes in upper Newport Bay, California: Seasonal dynamics and community structure. California Dept. Fish & Game Technical Report No. 45. 102pp.

Hosack, G. R., B. R. Dumbauldt, J. L. Ruesink, and D. A. Armstrong. 2006. Habitat associations of estuarine species: Comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. *Estuaries and Coasts* 29:1150.

Hueckel, G., B. Benson, D. Pentilla, A. Reaman, K. Li, and R. Buckley. 1988. Pilot studies on Sevin impacts to marine fish in Willapa Bay and Grays Harbor in 1987–1988. Washington State Department of Fisheries, Marine Fish Program, Habitat Investigations Unit. Olympia, WA.

Huff, D. D., S. T. Lindley, P. S. Rankin, and E. A. Mora. 2011. Green sturgeon physical habitat use in the coastal Pacific Ocean. *PLoS ONE* 6:e25156.

Hughes, B. B., J. Haskins, K. Wasson, and E. Watson. 2011. Identifying factors that influence expression of eutrophication in a central California estuary. *Marine Ecology Progress Series* 439:31–43.

Hughes, B. B., M. Fountain, A. Carlisle, M. Levey, and M. Gleason. 2012. The impacts of nutrient loading and environmental conditions on the fish assemblage and available nursery habitat in Elkhorn Slough. The Nature Conservancy.

Hughes, B. B., R. Eby, E. van Dyke, M. T. Tinker, C. I. Marks, K. S. Johnson, and K. Wasson. 2013. Recovery of a top predator mediates negative eutrophic effects on seagrass. *Proceedings of the National Academy of Sciences, USA* 110:1513–1518.

Incardona, J. P., C. A. Vines, B. F. Anulacion, D. H. Baldwin, H. L. Day, B. L. French, J. S. Labenia, T. L. Linbo, M. S. Meyers, O. P. Olson, C. A. Sloan, S. Sol, F. J. Griffin, K. Menard, S. G. Morgan, J. E. West, T. K. Collier, G. M. Ylitalo, G. N. Cherr, and N. L. Scholz. 2012. Unexpectedly high mortality in Pacific herring embryos exposed to the 2007 Cosco Busan oil spill in San Francisco Bay. *Proceedings of the National Academy of Sciences, USA* 109:E51–8.

Ingermann, R. L., and R. C. Terwilliger. 1982. Blood parameters and facilitation of maternal-fetal oxygen transfer in a viviparous fish (*Embiotoca lateralis*), Comparative Biochemistry and Physiology Part A: Physiology. *Comparative Biochemistry and Physiolog*y 73(3):497–501.

Innis, D. B. 1990. Juvenile California halibut, *Paralichthys californicus*, growth in relation to thermal effluent. In *The California Halibut,* Paralichthys californicus*, Resource and Fisheries*, ed. C. W. Haugen, 153–165. Calif. Dep. Fish Game, Fishery Bulletin 174.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradfury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.

Jassby, A. D., W. J. Kimmerer, S. G. Monismith, C. Armor, J. E. Cloern, T. M. Powell, J. R. Schubel, and T. J. Vendlinski. 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* 5:272–289.

Jensen, G. C. 1995. Pacific coast crabs and shrimp (Sea Challengers, Monterey, CA).

Jensen, G. C. 2014. Crabs and shrimps of the Pacific coast: A guide to shallow-water decapods from southeastern Alaska to the Mexican border, 1st edition. Seattle: MolaMarine. 240pp.

Johnson, L. L., J. T. Landahl, L. A. Kubin, B. H. Horness, M. S. Myers, T. K. Collier, and J. E. Stein. 1998. Assessing the effects of anthropogenic stressors on Puget Sound flatfish populations. *Journal of Sea Research* 39(1–2):125–137.

Johnson, R. C., Weber, P. K., Wikert, J. D., Workman, M. L., MacFarlane, R. B., Grove, M. J., and Schmitt, A. K. 2012. Managed metapopulations: do salmon hatchery sources lead to in-river sinks in conservation? *PloS One* 7:1–11.

Johnsson, J., and W. C. Clarke. 1988. Development of seawater adaptation in juvenile steelhead trout (*Salmo gairdnen*) and domesticated rainbow trout (*Salmo gairdnen*)—Effects of size, temperature and photoperiod. *Aquaculture* 71:247–263.

Johnston, K. K., E. DelGiudice-Tuttle, I. D. Medel, C. J. Piechowski, D. S. Cooper, J. Dorsey, and S. Anderson. 2012. The Ballona Wetlands Ecological Reserve Baseline Assessment Program 2010-2011 Final Report. Los Angeles, CA.

Jones, A. C. 1962. The biology of the euryhaline fish *Leptocottus armatus armatus* Girard. University of California Publications in Zoology 67:321–367.

Jones, K. K., T. J. Cornwell, D. L. Bottom, S. Stein, H. W. Kelly, and L. A. Campbell. 2011. Recovery of wild coho salmon in Salmon River basin, 2008–2010 Oregon Plan for Salmon and Watersheds Annual Monitoring Report No. OPSW-ODFW-2011-10 (p. 62).

Jones K. K., T. J. Cornwell, D. L. Bottom, L. A. Campbell, and S. Stein. 2014. The contribution of estuary-resident life histories to the return of adult *Oncorhynchus kisutch*. *Journal of Fish Biology* 85:52–80.

Jow, T. 1969. Results of English sole tagging off California. *Pacific Marine Fisheries Commission Bulletin* 7:16–33.

Kao, J. S. 2000. Diet, daily ration and gastric evacuation of the leopard shark (*Triakis semifasciata*). Dissertation (California State University, Hayward).

Karl, S. and S. Obrebski. 1976. The feeding biology of the bat ray, *Mylioatis californica*, in Tomales Bay, California.in C. A. Simenstad and S. J. Lipovski, editors. Fish Food Habit Studies. Washington Sea Grant, Seattle.

Keller, A. A., V. Simon, F. Chan, W. W. Wakefield, M. E. Clarke, J. A. Barth, and E. L. Fruh. 2010. Demersal fish and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. *Fisheries Oceanograph* 19:76–87.

Kelley, J. T., A. P. Klimley, and C. E. Crocker. 2007. Movements of green sturgeon, *Acipenser medirostris*, in the San Francisco Bay estuary, California. *Environmental Biology of Fishes* 79:281–295.

Kelly, J. T. and A. P. Klimley. 2012. Relating the swimming movements of green sturgeon to the movement of water currents. *Environmental Biology of Fishes* 93:151–167.

Kelly, R. P., J. A. Port, M. Yamahara, R. G. Martone, N. Lowell, P. F. Thomsen, M. E. Mach, M. Bennett, E. Prahler, M. R. Caldwell, and L. B. Crowder. 2014. Harnessing DNA to improve environmental management. *Science* 344:1455–1456.

Kennedy, C. J., and A. P. Farrell. 2005. Ion homeostasis and inter-renal stress responses in juvenile Pacific herring, *Clupea pallasii*, exposed to the water-soluble fraction of crude oil. *Journal of Experimental Marine Biology and Ecology* 323:43–56.

Kennish, M. J. 2002. Environmental threats and environmental future of estuaries. *Environmental Conservation* 29:78–107.

Khorram, S., and A. W. Knight. 1977. The toxicity of kelthane to the grass shrimp (*Crangon franciscorum*). *Bulletin of Environmetnal Contamination and Toxicology* 18:674–82.

Kimbro, D. L., E. D. Grosholz, A. J. Baukus, N. J. Nesbitt, N. M. Travis, S. Attoe, and C. Coleman-Hulbert. 2009. Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. *Oecologia* 160:563–575.

Kimmerer, W. J. 2002. Effects of freshwater flow on abundance of estuarine organisms: Physical effects or trophic linkages? *Marine Ecology Progress Series* 243:39–55.

Kocan, R. M., J. E. Hose, E. D. Brown, and T. T. Baker. 1996. Pacific herring (*Clupea pallasii*) embryo sensitivity to Prudhoe Bay petroleum hydrocarbons: Laboratory evaluation and in situ exposure at oiled and unoiled sites in Prince William Sound. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2366–2387.

Koski, K. V. 2009. The fate of coho salmon nomads: The story of an estuarine-rearing. *Ecology and Society* 14(1).

Kramer, S. H. 1990. Distribution and abundance of juvenile California halibut, *Paralichthys californicus*, in shallow waters of San Diego County. In *The California Halibut,* Paralichthys californicus*, Resource and Fisheries*, ed. C. W. Haugen, editor, 99–126. Calif. Dep. Fish Game, Fish. Bull. 174.

Kramer, S. H. 1991. Growth, mortality, and movements of juvenile California halibut *Paralichthys californicus* in shallow coastal and bay habitats of San Diego County, California. *Fishery Bulletin* 89:195–207.

Kroeker, K. J., R. L. Kordas, R. Crim, I. E. Hendriks, L. Ramajo, G. S. Singh, C. M. Duarte, and J. P. Gattuso. 2013. Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming. *Global Change Biology* 19:1884–1896.

Krygier, E. E., and W. G. Pearcy. 1986. The role of estuarine and offshore nursery areas for young English sole, *Parophrys vetulus* Girard, of Oregon. *Fishery Bulletin* 84(1):119–132.

Kukowski, G. E. 1972. A checklist of the fishes of the Monterey Bay area including Elkhorn Slough, the San Lorenzo, Pajaro and Salinas rivers (Vol. Technical, p. 69). Moss Landing Marine Laboratories.

Kusher, D. I., S. E. Smith, and G. M. Cailliet. 1992. Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. *Environmental Biology of Fishes* 35:187–203.

Larinto, Traci (Ed.). 2013. Status of the Fisheries Report: An Update through 2011. Sacramento, CA.

Laroche, J. L., and S. L. Richardson. 1979. Winter-spring abundance of larval English sole, *Parophrys vetulus*, between the Columbia River and Cape Blanco, Oregon, during 1972–75 with notes on occurrences of 3 other pleuronectids. *Estuarine, Coastal, and Marine Science* 8(5):455–476.

Laroche, J. L., S. L. Richardson, and A. Rosenberg. 1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fishery Bulletin, 80:93–104.

Laroche, W. A., and R. L. Holton. 1979. Occurrence of 0-age English sole, *Parophrys vetulus*, along the Oregon coast: An open coast nursery area? *Northwest Science* 53:94–96.

Larson, E. J. 2001. Coastal wetlands-emergent marshes.. In *California's Living Marine Resources: A Status Report*, eds. W. S. Leet, C. M. Dewees, R. Klingbeil, and E. J. Larson, 483–486. California and California Department of Fish and Game, Sacramento, California.

Lassuy, D. R. 1989a. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): English sole. U.S. Fish and Wildlife Service Biological Report 82(11.101). U.S. Army Corps of Engineers, TR EL-82-4. 17pp.

Lassuy, D. R. 1989b. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): Pacific herring. U.S. Fish and Wildlife Service Biological Report 82(11.126). U.S. Army Corps of Engineers, TR EL-82-4. 18 pp

LeBour, M. V. 1922. The food of plantonic organisms. *Journal of the Marine Biological Association of the UK* 12:644–677.

Lee, II H., and C. A. Brown. 2009. Classification of regional patterns of environmental drivers and benthic habitats in Pacific Northwest estuaries. U.S. EPA, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division. EPA/600/R-09/140.

Leet, W. S., C. M. Dewees, R. Klingbeil, and E. J. Larson. 2001. California's living marine resources: A status report. California Department of Fish and Game.

Levin, L. A., D. F. Boesch, A. Covich, C. Dahm, C. Erséus, K. C. Ewel, R. T. Kneib, A. Moldenke, M. A. Palmer, P. Snelgrove, D. Strayer, and J. M. Weslawski. 1991. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4:430–451.

Levings, C. D. 1980. Demersal and benthic communities in Howe Sound basin and their responses to dissolved oxygen deficiency. Canadian technical report of fisheries and aquatic sciences; no. 951. Government of Canada, Fisheries and Oceans. West Vancouver, B.C.

Lewallen, E. A., T. W. Anderson, and A. J. Bohonak. 2007. Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. *Marine Biology* 152:599–609.

Lim, H. K., B. H. Min, and M. G. Kwon. 2013. Blood physiological responses and growth of juvenile starry flounder, *Platichthys stellatus,* exposed to different salinities. *Journal of Environmental Biology* 34(5):885–890.

Lindley, S. T., R. S. Schick, A. Agrawal, M. Goslin, T. E. Pearson, E. Mora, and J. G. Williams. 2006. Historical population structure of Central Valley steelhead and its alteration by dams. *San Francisco Estuary & Watershed Science* 4:1–19.

Lindley, S. T., E. Mora, P. B., Adams, J. J. Anderson, S. Green, J. G. Williams. 2007. Framework for assessing viability of threatened and endangered Chinook salmon and steelhead in the Sacramento-San Joaquin Basin. *San Francisco Estuary and Watershed Science* 5:1–26.

Lindley, S. T., M. L. Moser, D. L. Erickson, M. Belchik, D. W. Welch, E. L. Rechisky, J. T. Kelly, J. Heublein, and A. Klimley. 2008. Marine migration of North American green sturgeon. *Transactions of the American Fisheries Society* 137:182–194.

Lindley, S. T., D. L. Erickson, M. L. Moser, G. Williams, O. P. Langness, B. W. McCovey, M. Belchik, D. Vogel, W. Pinnix, J. T. Kelly, J. C. Heublein, and A. P. Klimley. 2011. Electronic tagging of green sturgeon reveals population structure and movement among estuaries. *Transactions of the American Fisheries Society* 140:108–122.

Litvin, S., M. Weinstein, and V. Guida. 2014. Habitat utilization patterns determine the physiological condition of *Cynoscion regalis* during estuarine residency. *Marine Ecology Progress Series* 510:87–99.

Lotze, H. K., H. S. Lenihan, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809.

Lough, R. G. 1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71. *Fishery Bulletin* 74:353–376.

Love, M. S. 1996. Probably more than you want to know about the fishes of the Pacific Coast. Santa Barbara, CA: Really Big Press. 381pp.

Love, M. S. 2011. Certainly more than you want to know about the fishes of the Pacific Coast, a postmodern experience. Really Big Press, Santa Barbara, CA. 672p.

Love, M. S, M. M. Yoklavich, and L. Thorsteinson. 2002. The Rockfishes of the Northeast Pacific. Berkeley, CA: University of California Press.

MacFarlane, R. B., and E. C. Norton. 2002. Physiological ecology of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) at the southern end of their distribution, the San Francisco Estuary and Gulf of the Farallones, California. 100:244–257.

Madon, S. P. 2002. Ecophysiology of juvenile California halibut *Paralichthys californicus* in relation to body size, water temperature and salinity. *Marine Ecology Progress Series* 243:235–249.

Madon, S. P. 2008. Fish community responses to ecosystem stressors in coastal estuarine wetlands: a functional basis for wetlands management and restoration. *Wetlands Ecology and Management* 16(3):219–236.

Magnusson, A., and R. Hilborn. 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the U.S. Pacific coast. *Estuaries and Coasts* 26:1094–1103.

Maier, G. O., and C. A. Simenstad. 2009. The role of marsh-derived macrodetritus to the food webs of juvenile Chinook salmon in a large altered estuary. *Estuaries and Coasts* 32(5):984–998.

Marine, K. R., and J. J. Cech. 2011. Effects of high water temperature on growth, smoltification, and predator avoidance in juvenile Sacramento River Chinook salmon. *North American Journal of Fisheries Management* 37–41.

Martin, J. A. 1995. Food habits of some estuarine fishes in a small, seasonal Central California Lagoon. M.S. Thesis, San Jose State.

Martin, L. K., and G. M. Cailliet. 1988a. Aspects of the reproduction of the Bat ray, *Myliobatis californica*, in Central California. *Copeia* 754–762.

Martin, L. K., and G. M. Cailliet. 1988b. Age and growth determination of the Bat ray, *Myliobatis californica* Gill, in Central California. *Copeia* 762–773.

Martin, M., K. Osborn, P. Billig, and N. Glickstein. 1981. Toxicities of ten metals to *Crassostrea gigas* and *Mytilus edulis* embryos and *Cancer magister* larvae. *Marine Pollution Bulletin* 12:305–308.

Marty, G., T. Quinn II, G. Carpenter, T. Meyers, and N. Willits. 2003. Role of disease in abundance of a Pacific herring (*Clupea pallasii*) population. *Canadian Journal of Fisheries and Aquatic Sciences* 1265:1258–1265.

Matarese, A., A. Kendall, D. Blood, and B. Vinter. 1989. Laboratory guide to early life history stages of northeast Pacific fishes. NOAA Tech Rep 80:652.

Matern, S. A., J. J. Cech, and T. E. Hopkins. 2000. Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: Evidence for behavioral thermoregulation? *Environmental Biology of Fishes* 58:173–182.

Matthews, K. R. 1990a. A comparative study of habitat use by young-of-the-year, subadult, and adult rockfishes on four habitat types in central Puget Sound. *Fishery Bulletin* 80(4):223–239.

Matthews, K.R. 1990b. An experimental study of the habitat preferences and movement patterns of copper, quillback, and brown rockfishes (*Sebastes* Spp.). *Environmental Biology of Fishes* 29(3):161–178.

Maunder, M., P. Reilly, T. Tanaka, G. Schmidt, and K. Penttila. 2011. California Halibut Stock Assessment.

Mayfield, R. B. and J. J. Cech. 2004. Temperature effects on green sturgeon bioenergetics. *Transactions of the American Fisheries Society* 133:961–970.

MBC Applied Environmental Sciences. 1987. Ecology of important fisheries species offshore California. Rep. to Min. Manag. Serv., U.S. Dept. Int., Washington, D.C., 251pp. (Contract No. MMS 14-12-0001-30294).

McCabe, G. T. J., W. D. Muir, R. L. Emmett, and J. T. Durkin. 1983. Interrelationships between juvenile salmonids and nonsalmonid fish in the Columbia River Estuary. *Fishery Bulletin* 81(4):815–826.

McCain, B. B., S. D. Miller, and W. W. Wakefield. 2005. Life history, geographical distribution, and habitat associations of 82 West Coast groundfish: A literature review. In Appendix H in Pacific Coast Groundfish Fisheries Management Plan, Essential Fish Habitat Designation and Minimization of Adverse Impact, Draft Environmental Impact Statement. Portland, OR: Pacific Fisheries Management Council.

McClure, M. M., S. M. Carlson, T. J. Beechie, G. R. Pess, J. C. Jorgensen, S. M. Sogard, and R. W. Carmichael. 2008. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. *Evolutionary Applications* 1:300–318.

McConnaughey, EA. 1971. Coos Bay Study: An Interdisciplinary Study of Man and the Estuary.

McDonald, P. S., G. C. Jensen, and D. A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. Journal of Experimental Marine Biology and Ecology 258:39–54.

McEwan, D. R. 2001. Central Valley steelhead. In *Contributions to the Biology of Central Valley Salmonids,* ed. R. L. Brown, 179(1):1–44. San Diego, CA: Scripps Institutions of Oceanography Library.

McGraw, K., L. Conquest, J. Waller, P. Dinnel, and D. Armstrong. 1988. Entrainment of Dungeness crabs, *Cancer magister* Dana, by hopper dredge in Grays Harbor, Washington. *Journal of Shellfish Research* 7:219–231.

McKechnie, I., D. Lepofsky, M. L. Moss, V. L. Butler, T. J. Orchard, G. Coupland, F. Foster, M. Caldwell, and K. Lertzman. 2014. Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. *Proceedings of the National Academy of Sciences, USA* 111:E807–16.

McLaughlin, K., M. Sutula, L. Busse, S. Anderson, J. Crooks, R. Dagit, D. Gibson, K. Johnston, and L. Stratton. 2013. A regional survey of the extent and magnitude of eutrophication in Mediterranean estuaries of southern California, USA. *Estuaries and Coasts* 37:259-278.

Meador, J. P. 2014. Do chemically contaminated river estuaries in Puget Sound (Washington, USA) affect the survival rate of hatchery-reared Chinook salmon? *Canadian Journal of Fisheries and Aquatic Sciences* 180:162–180.

Meloni, C. J., J. J. Cech Jr., and S. M. Katzman. 2002. Effect of brackish salinities on oxygen consumption of bat rays (*Myliobatis californica*). *Copeia* 2:462-465.

Merrifield, M. S., E. Hines, X. Liu, and M. W. Beck. 2011. Building regional threat-based networks for estuaries in the Western United States. *PLoS One* 6:e17407.

Meyer, J. H. 1979. A review of the literature on the value of estuarine and shoreline areas to juvenile salmonids in Puget Sound, Washington. US Fish and Wildlife Service, Olympia, WA. 25pp.

Miller, B. S., and S. Sadro. 2003. Residence time and seasonal movements of juvenile coho salmon in the ecotone and lower estuary of Winchester Creek, South Slough, Oregon. *Transactions of the American Fisheries Society* 132:546–559.

Miller, D. J. and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. Fish Game, Fish. Bull. 157. 249pp.

Miller, G. 2010. Fisheries. In central California, coho salmon are on the brink. *Science* 327:512–513.

Miller, J. M., and C. A. Simenstad. 1997. A comparative assessment of a natural and created estuarine slough as rearing habitat for juvenile Chinook and coho salmon. *Estuaries* 20(4):792–806.

Misitano, D. A. 1970. Aspects of the early life history of English sole (*Parophrys vetulus*) in Humboldt Bay, California. M.S. Thesis, Humboldt State College.

Misitano, D. A. 1976. Size and stage of development of larval English sole, *Parophrys vetulus*, at time of entry into Humboldt Bay. *California Fish and Game* 62(1):93–98.

Moles, A. 1998. Sensitivity of ten aquatic species to long-term crude oil exposure. *Bulletin of Environmental Contamination and Toxicology* 61(1):102–107.

Moles, A., and Norcross, B. L. 1995. Sediment preference in juvenile Pacific flatfishes. *Netherlands Journal of Sea Research* 34:177–182.

Monaco, M. E., R. L. Emmett, D. M. Nelson, and S. A. Hinton. 1990. Distribution and abundance of fishes and invertebrates in West Coast estuaries, Volume I: Data summaries. ELMR Rep. No. 4. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD, 232 pp.

Monaco, M. E., T. A. Lowry, and R. L. Emmett. 1992. Assemblages of U. S. West Coast estuaries based on the distribution of fishes. *Journal of Biogeography* 19:251–267.

Moore, J. W., S. A. Hayes, W. Duffy, S. Gallagher, C. J. Michel, D. Wright, and B. Jonsson. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1161–1170.

Morley, S. A., J. D. Toft, and K. M. Hanson. 2012. Ecological effects of shoreline armoring on intertidal habitats of a Puget Sound urban estuary. *Estuaries and Coasts* 35:774–784.

Morris, P. A., M. Domeier, and J. Stephens. 1996. Notes on the occurrence and depth distribution of the bat ray in the Southern California Bight, with comments on the effect of trawl size on estimates of abundance. *California Fish and Game* 82:48–53.

Morrow, J.E. 1980. The Freshwater Fishes of Alaska. Anchorage, Alaska: Alaska Northwest Publishing Co.

Moser, H. G. 1996. Introduction. In *The early stages of fishes in the California Current region*, ed. H. G. Moser, 1–72. CalCOFI Atlas 33.

Moser, H. G., and W. Watson. 1990. Distribution and abundance of early life history stages of the California halibut, *Paralichthys californicus*, and comparisons with the fantail sole, *Xystreurys liolepis*. In *The California Halibut,* Paralichthys californicus*, Resource and Fisheries*, ed. C. W. Haugen, 31–84.Calif. Dep. Fish Game, Fish. Bull. 174.

Moser, M. L., and S. T. Lindley. 2007. Use of Washington estuaries by subadult and adult green sturgeon. *Environmental Biology of Fishes* 79:243–253.

Moyle, P. B. 2002. Inland Fishes of California. Second Edition. University of California Press, Berkeley, CA.

Moyle, P. B. and J. J. Cech, Jr. 2004. Fishes: An Introduction to Ichthyology. Fifth Ed. Upper Saddle River, NJ: Prentice Hall.

Moyle, P. B., R. A. Daniels, B. Herbold, and D. M. Baltz. 1986. Patterns in distribution and abundance of a non-coevolved assemblage of estuarine fishes in California. *Fishery Bulletin* 84(1):105–118.

Moyle, P. B., J. A. Israel, and S. E. Purdy. 2008. Salmon, steelhead and trout in California. Technical Report Commissioned by California Trout, Davis, California. 316 pp.

Munsch, S. H., J. R. Cordell, J. D. Toft, and E. E. Morgan. 2014. Effects of seawalls and piers on fish assemblages and juvenile salmon feeding behavior. *North American Journal of Fisheries Management* 814–827.

Murphy, M. L., J. F. Thedinga, and K. V. Koski. 1988. Size and diet of juvenile Pacific salmon during seaward migration through a small estuary in Southeastern Alaska. *Fishery Bulletin* 86: 213–222.

Musick, J. A., M. M. Harbin, S. A. Berkeley, G. H. Burgess, A. M. Eklund, L. Findley, R. G. Gilmore, J. T. Golden, D. S. Ha, G. R. Huntsman, J. C. McGovern, G. R. Sedberry, S. J. Parker, S. G. Poss, E. Sala, T. W. Schmidt, H. Weeks, and S. G. Wright. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (Exclusive of Pacific Salmonids). *Fisheries* 25:6–30.

Myers, M. S., L. L. Johnson, O. P. Olson, C. M. Stehr, B. H. Horness, T. K. Collier, and B. B. McCain. 1998. Toxicopathic hepatic lesions as biomarkers of chemical contaminant exposure and effects in marine bottomfish species from the Northeast and Pacific Coasts, USA. *Marine Pollution Bulletin* 37(1-2):92–113.

Myrick, C. A., and J. J. Cech. 1998. Temperature effects on Chinook salmon and steelhead: A review focusing on California's Central Valley Populations. In Bay-Delta Modeling Forum Technical Publication 01-1.

Myrick, C. A., and J. J. Cech. 2004. Temperature effects on juvenile anadromous salmonids in California's Central Valley: What don't we know? *Reviews in Fish Biology and Fisheries* 14:113–123.

Nagelkerken, I., M. Sheaves, R. Baker, and R. M. Connolly. 2013. The seascape nursery: A novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries* 47:23–38.

Naiman, R. J., J. R. Alldredge, D. A. Beauchamp, P. A. Bisson, J. Congleton, C. J. Henny, N. Huntly, R. Lamberson, C. Levings, E. N. Merrill, W. G. Pearcy, B. E. Rieman, G. T. Ruggerone, D. Scarnecchia, P. E. Smouse, and C. C. Wood. 2012. Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences USA* 109:21201–7.

Nakamoto, R. J., and T. T. Kisanuki. 1995. Age and growth of Klamath River green sturgeon (*Acipenser medirostris*). U.S. Fish and Wildlife Service Report 93-FP-13, Yreka, CA.

National Marine Fisheries Service (NMFS). 2011. CA Eelgrass Mitigation Policy.

Naylor, R., K. Hindar, I. A. Fleming, S. Williams, J. Volpe, F. Whoriskey, and M. Mangel. 2005. Fugitive salmon: Assessing the risks of escaped fish from net-pen aquaculture. *BioOne* 55(5):427–437.

Nielsen, J. L., M. C. Fountain, J. C. Favela, K. Cobble, and B. L. Jensen. 1998. *Oncorhynchus* at the southern extent of their range: a study of mtDNA control–region sequence with special reference to an undescribed subspecies of *O. mykiss* from Mexico. *Environmental Biology of Fishes* 51:7–23.

Nelson, J. S. 2006. Fishes of the World. Bulletin of Marine Science. Fourth. Vol. 3rd edition. New York: John Wiley & Sons, Inc.

Nelson, P. A., S. Kramer, and J. A. Brown. 2010. Selected flatfish: Factors that control distribution and abundance in Pacific Coast estuaries and a case study of Elkhorn Slough, California. Elkhorn Slough Technical Report Series 2010:6.

Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. *Science* 231:567–573.

NOAA National Marine Fisheries Service, Office of Science and Technology. 2012. Commercial Landings. http://www.st.nmfs.noaa.gov/commercial-fisheries/fus/fus12/index

NOAA National Marine Fisheries Service, Office of Protected Resources. July 2014. http://www.nmfs.noaa.gov/pr/species/fish/

Nordby, C. S, and J. B. Zedler. 1991. Responses of fish and macrobenthic assemblages to hydrologic disturbances in Tijuana estuary and Los Penasquitos Lagoon , California. *Estuaries* 14(1):80–93.

Nosal, A. P., D. P. Cartamil, J. W. Long, M. Luhrmann, N. C. Wegner, and J. B. Graham. 2013. Demography and movement patterns of leopard sharks (*Triakis semifasciatat*) aggregating near the head of a submarine canyon along the open coast of southern California, USA. *Environmental Biology of Fishes* 96:865–878.

Nosal, A. P., A. Caillat, E. K. Kisfaludy, M. A. Royer, and N. C. Wegner. 2014. Aggregation behavior and seasonal philopatry in male and female leopard sharks *Triakis semifasciata* along the open coast of southern California, USA. *Marine Ecology Progress Series* 499:157–175.

Nybakken, J. W., J. S. Oliver, and C. Jong. 1982. The ecology of intertidal flats of Central California: A community profile. Report The National Coastal Ecosystem Team, U.S. Fish and Wildlife Service. Slidell, Louisiana.

Odenweller, D. B. 1975. Aspects of the biology of the shiner perch in a southern California estuary. *Cal-Neva Wildlife Transactions* 93–101.

Oliver, J. S., P. N. Slattery, L. W. Hulberg, and J. W. Nybakken. 1980. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. *Fishery Bulletin* 78:437–454.

Olson, R. E. 1976. Laboratory and field studies on *Glugea stephani* (Hagenmuller), a microsporidian parasite of pleuronectid flatfishes. *Journal of Protozoology* 23:158–164.

Olson, R. E. 1981. Effects of low temperature on the development of the microsporidan *Glugea stephani* in English sole (*Parophrys vetulus*). *Journal of Wildlife Diseases* 17:559–562.

Olson, R. E., and I. Pratt. 1973. Parasites as indicators of English sole (*Parophrys vetulus*) nursery grounds. *Transactions of the American Fisheries Society* 102:405–411.

Olson, R. E., J. R. Pierce, K. C. Jacobson, and E. M. Burreson. 2004. Temporal changes in the prevalence of parasites in two Oregon estuary-dwelling fishes. *The Journal of Parasitology* 90(3):564–571.

Onuf, C. P, and M. L. Quammen. 1983. Effects of major storms on distribution and abundance. *Marine Ecology Progress Series* 12: 1–14.

Orcutt, H. G. 1950. The life history of the starry flounder *Platichthys stellatus (*Pallas). Department of Fish and Game Fish Bulletin 78. 101pp.

Oregon Department of Fish and Wildlife. 2014. Recreational Fishing Report. http://www.dfw.state.or.us/rr/marine/

Orr, A. J., A. S. Banks, S. Mellman, H. R. Huber, R. L. DeLong, and R. F. Brown. 2004. Examination of the foraging habits of Pacific harbor seal (*Phoca vitulina richardsi*) to describe their use of the Umpqua River, Oregon, and their predation on salmonids. *Fishery Bulletin* 102(1):108–117.

Orth, R. J., and J. van Montfrans. 1990. Utilization of marsh and seagrass habitats by early stages of *Callinectes sapidus*: A latitudinal perspective. *Bulletin of Marine Science* 46:126–144.

Osterback, A.-M., D. M. Frechette, A. S. Shelton, S. Hayes, M. H. Bond, S. A. Shaffer, and J. W. Moore. 2013. High predation on small populations: Avian predation on imperiled salmonids. *Ecosphere* 4(September):1–21.

Palsson, W. A., R. E. Pacunski, T. R. Parra, and J. Beam. 2008. The effects of hypoxia on marine fish populations in southern Hood Canal, Washington. In American Fisheries Society Symposium 64:000-000, 26. American Fisheries Society.

Palsson, W. A., T. S. Tsou, and G. G. Bargmann. 2009. The Biology and Assessment of Rockfishes in Puget Sound. Washington Department of Fish and Wildlife. 208p.

Parnel, M. M., R. L. Emmett, and R. D. Brodeur. 2008. Ichthyoplankton community in the Columbia River plume off Oregon: effects of fluctuating oceanographic conditions. *Fishery Bulletin* 106(2):161–173.

Pauley, G. B., B. M. Bortz, and M. F. Shepard. 1986a. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest) -- steelhead trout. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.62). U.S. Army Corps of Engineers, TR EL-82-4. 24 pp.

Pauley, G. B., D. A. Armstrong, and T. W. Heun. 1986b. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)--Dungeness crab. U. S. Fish Wildl. Serv. Biol. Rep. 82(11.63). U. S. Army Corps of Engineers, TR EL-82-4. 20 pp

Pauley, G. B., D. A. Armstrong, R. Van Citter, and G. L. Thomas. 1989. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest)—Dungeness crab. U.S. Fish Wildl. Sew. Biol. Rep. 82(11.121). U.S. Army Corps of Engineers, TR EL-82-4. 20 pp.

Paxton, J. R., and W. N. Eschmeyer. 1998. Encyclopedia of Fishes, a Comprehensive Illustrated Guide by International Experts. Edited by J.R. Paxton and W.N. Eschmeyer. Second. San Diego, CA: Academic Press.

Pearcy, W. G., and S. S. Myers. 1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? *Fishery Bulletin* 72(1):201–213.

Pearson, W. H., D. L. Woodruff, P. C. Sugarman, and B. L. Olla. 1981. Effects of oiled sediment on predation on the littleneck clam, *Protothaca staminea*, by the Dungeness crab, *Cancer magister*. *Estuarine, Coastal and Shelf Science* 13:445–454.

Penttila, D. 2007. Marine forage fishes in Puget Sound. Puget Sound Nearshore Partnership Report No. 2007-03. Published by Seattle District, U.S. Army Corps of Engineers, Seattle, Washington.

Perkins-Visser, E., T. G. Wolcotth, and D. L. Wolcotth. 1996. Nursery role of seagrass beds: enhanced growth of juvenile blue crabs (*Callinectes sapidus* Rathbun). *Journal of Experimental Marine Biology and Ecology* 198:155–173.

Philip Williams and Associates (PWA), and Wetland Research Associates. 2006. Projecting the future of Bolinas Lagoon. Final Public Draft. Prepared for Marin County Open Space District.

Phillips, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: A community profile. U.S. Fish and Wildlife Service FWS/OBS-84/24 (p. 85).

Pihl, L., S. P. Baden, N. Kautsky, P. Rönnback, T. Söderqvist, M. Troell, and H. Wennhage. 2006. Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. *Estuarine, Coastal, and Shelf Science* 67:123–132.

Pinnix, W. D., T. A. Shaw, K. C. Acker, and N. J. Hetrick. 2005. Fish communities in eelgrass, oyster culture, and mudflat habitats of North Humboldt Bay, California, Final Report. US Fish and Wildlife Service, Arcata Fisheries Technical Report TR2005-02, Arcata, CA.

Pinnix, W. D., P. A. Nelson, G. Stutzer, and K. A. Wright. 2012. Residence time and habitat use of coho salmon in Humboldt Bay, California: an acoustic telemetry study. *Environmental Biology of Fishes* 96:315–323.

Plummer, K. M., E. E. Demartini, and D. A. Roberts. 1983. The feeding habits and distribution of juvenile-small adult California halibut, (*Paralichthys californicus*) in coastal waters off northern San Diego County. California Cooperative Oceanic Fisheries Investigations Report, 24:194–201.

Plummer, M. L., C. J. Harvey, L. E. Anderson, A. D. Guerry, and M. H. Ruckelshaus. 2013. The role of eelgrass in marine community interactions and ecosystem services: Results from ecosystem-scale food web models. *Ecosystems* 16:237–251.

Pondella, D. J. and L. G. Allen. 2008. The decline and recovery of four predatory fishes from the Southern California Bight. *Marine Biology* 154:307–313.

Potter, I., P. Chrystal, and N. Loneragan. 1983. The biology of the blue manna crab *Portunus pelagicus* in an Australian estuary. *Marine Biology* 85:75–85.

Quinn, T. P. 2004. The behavior and ecology of Pacific salmon and trout. Seattle: University of Washington Press.Reimers, P. E. 1971. The length of resdence of juvenile fall Chinook salmon in Sixes River, Oregon. Doctoral Thesis. Oregon State University. 320pp.

Quinn, T. P., N. Harris, J. A. Shaffer, C. Byrnes, and P. Crain. 2013. Juvenile coho salmon in the Elwha River estuary prior to dam removal: Seasonal occupancy, size distribution, and comparison to nearby Salt Creek. *Transactions of the American Fisheries Society* 142(4):1058–1066.

Quinones, R. M., and T. J. Mulligan. 2005. Habitat use by juvenile salmonids in the Smith River estuary, California. *Transactions of the American Fisheries Society* 134:1147–1158.

Rabalais, N. N., R. E. Turner, and W. J. Wiseman. 2002. Gulf of Mexico hypoxia, aka The dead zone. *Annual Review of Ecology and Systematics* 33:235–263.

Ralston, S. 2005. An assessment of starry flounder off California, Oregon, and Washington. NOAA, NMFS, Southwest Fisheries Science Center, Santa Cruz, CA.

Reeve, L. D. 2013. Can eelgrass (*Zostera marina*) serve as a nursery habitat for California halibut (*Paralichthys californicus*)? M.S. Thesis. San Diego State University.

Reilly, P. N., D. Wilson-Vandenberg, R. N. Lea, C. Wilson, and M. Sullivan. 1994. Recreational angler's guide to the common nearshore fishes of Northern and Central California. California Department of Fish and Game, Marine Resources Leaflet.

Reimers, P. E. 1971. The length of residence of juvenile fall Chinook salmon in Sixes River Oregon. Oregon State University.

Reum, J., T. Essington, C. Greene, C. Rice, and K. Fresh. 2011. Multiscale influence of climate on estuarine populations of forage fish: The role of coastal upwelling, freshwater flow and temperature. *Marine Ecology Progress Series* 425:203–215.

Richardson, J. S., T. J. Lissimore, M. C. Healey, and T. G. Northcote. 2000. Fish communities of the lower Fraser River (Canada) and a 21-year contrast. *Environmental Biology of Fishes* 59(2):125–140.

Richter, A., and S. A. Kolmes 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. *Reviews in Fisheries Science* 13:23–49.

Ritter, A. F., K. Wasson, S. I. Lonhart, R. K. Preisler, A. Woolfolk, K. A. Griffith, S. Connors, and K. W. Heiman. 2008. Ecological signatures of anthropogenically altered tidal exchange in estuarine ecosystems. *Estuaries and Coasts* 31:554–571.

Roberts, E. and M. Gingras. 2008. Sturgeons, *Acipenser* spp. In Status of the fisheries report: an update through 2008, ed. K. California Department of Fish and Game Marine Region, Monterey, CA, USA.

Roegner, G., D. Armstrong, and A. Shanks. 2007. Wind and tidal influences on larval crab recruitment to an Oregon estuary. *Marine Ecology Progress Series* 351:177–188.

Roegner, G. C., J. A. Needoba, and A. M. Baptista. 2011. Coastal upwelling supplies oxygen-depleted water to the Columbia River Estuary. *PLoS ONE* 6(4):e18672.

Rogers, C. 1985. Population dynamics of juvenile flatfish in the Grays Harbor estuary and adjacent nearshore area. M.S. Thesis. University of Washington, Seattle.

Rogers, C. W., D. R. Gunderson, and D. A. Armstrong. 1988. Utilization of a Washington estuary by juvenile English sole, *Parophrys vetulus*. *Fishery Bulletin* 86:823–831.

Romer, J. D., C. A. Leblanc, S. Clements, J. A. Ferguson, M. L. Kent, D. Noakes, and C. B. Schreck. 2013. Survival and behavior of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in Oregon, USA. *Environmental Biology of Fishes* 96:849–863.

Rooper, C. N., D. A. Armstrong, and D. R. Gunderson. 2002. In *Crabs in Cold Water Regions: Biology, Management, and Economics*, 608–629. Alaska Sea Grant, University of Alaska Fairbanks.

Rooper, C. N., D. R. Gunderson, and D. A. Armstrong. 2003. Patterns in use of estuarine habitat by juvenile English sole (*Pleuronectes vetulus*) in four Eastern North Pacific estuaries. *Estuaries* 26:1142–1154.

Rooper, C. N., D. R. Gunderson, and D. A. Armstrong. 2004. Application of the concentration hypothesis to English sole in nursery estuaries and potential contribution to coastal fisheries. *Estuaries*, 27(1):102–111.

Rooper, C. N., D. R. Gunderson, and B. M. Hickey. 2006a. An examination of the feasibility of passive transport from coastal spawning grounds to estuarine nursery areas for English sole. *Estuarine Coastal and Shelf Science* 68(3-4):609–618.

Rooper, C. N., D. R. Gunderson, and D. A. Armstrong. 2006b. Evidence for resource partitioning and competition in nursery estuaries by juvenile flatfish in Oregon and Washington. *Fishery Bulletin* 104:616–622.

Rosenberg, A. A. 1982. Growth of juvenile English sole, *Parophrys vetulus*, in estuarine and open coastal nursery grounds. *Fishery Bulletin* 80(2):245–252.

Rosenberg, A. A., and J. L. Laroche. 1982. Growth during metamorphosis of English sole, *Parophrys vetulus*. *Fishery Bulletin* 80(1):152–155.

Ruggerone, G. 2000. Differential survival of juvenile sockeye and coho salmon exposed to low dissolved oxygen during winter. *Journal of Fish Biology* 56(4) (April):1013–1016.

Russo, R. A. 1975. Observations on food habits of leopard sharks (*Triakis semifasciata*) and brown smoothhounds (Mustelus henlei). *California Fish and Game* 61:95–103.

Ryan, B. A., S. G. Smith, J. M. Butzerin, and J. W. Ferguson. 2003. Relative vulnerability to avian predation of PIT-tagged juvenile salmonids in the Columbia River estuary, 1998–2000. *Transactions of the American Fisheries Society* 132:275–288.

Sandstrom, P. T., T. Keegan, and G. Singer. 2012. Survival and movement patterns of central California coast native steelhead trout (*Oncorhynchus mykiss*) in the Napa River. *Environmental Biology of Fishes* 96(2–3):287–302.

Schaffer, P., C. Reeves, D. R. Casper, and C. R. Davis. 2006. Absence of neurotoxic effects in leopard sharks, *Triakis semifasciata*, following domoic acid exposure. *Toxicon* 47:747–752.

Schick, R. S., and S.T. Lindley. 2007. Directed connectivity among fish populations in a riverine network. *Journal of Applied Ecology* 44(6):1116–1126.

Schweigert, J. F., J. L. Boldt, L. Flostrand, L., and J. S. Cleary. 2010. A review of factors limiting recovery of Pacific herring stocks in Canada. *ICES Journal of Marine Science* 67:1903–1913.

Sebring, S., M. Morrow, R. Ledgerwood, B. Sandford, A. Evans, and G. Matthews. 2010. Detection of passive integrated transponder (PIT) tags on piscivorous avian colonies in the Columbia River Basin, 2009. Report of the National Marine Fisheries Service, Northwest Fisheries Science Center, NOAA:43.

Semmens, B. X. 2008. Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary. *Canadian Journal of Fisheries and Aquatic Sciences* 65(9):2053–2062.

Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California and recommendations regarding their management. *Fish Bulletin* 98.

Sheaves, M. 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. *Marine Ecology Progress Series* 391:107–115.

Sheaves, M., R. Baker, and R. Johnston. 2006. Marine nurseries and effective juvenile habitats: an alternative view. *Marine Ecology Progress Series* 318:303–306.

Sheaves, M., R. Baker, I. Nagelkerken, and R. M. Connolly. 2014. True value of estuarine and coastal nurseries for fish: incorporating complexity and dynamics. *Estuaries and Coasts* (in press).

Shi, Y., D. R. Gunderson, and P. J. Sullivan. 1997. Growth and survival of 0+ English sole, *Pleuronectes vetulus*, in estuaries and adjacent near-shore waters off Washington. *Fishery Bulletin* 95:161–173.

Shrode, J. B., L. J. Purcell, and J. S. Stephens, Jr. 1983. Ontogeny of thermal preference in four species of viviparous fishes (Embiotocidae). *Environmental Biology of Fishes* 9(1):71–76.

Siegfried, C. 1989. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest) Crangonid shrimp. US Fish and Wildlife Service Biological Report, 82(11.125):18.

Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences* 99:10500–5.

Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelssohn. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310:1803–1806.

Silliman, B. R., T. Grosholz, and M. D. Bertness, eds. 2009. Human impacts on salt marshes: A global perspective (Univ California Press, Berkeley, CA).

Simenstad, C., W. Hood, and R. Thom. 2000. In Concepts and Controversies in Tidal Marsh Ecology, Weinstein, M. P., and D. Kreeger, eds. (Springer Netherlands), pp 597–630.

Simenstad, C. A., J. L. Burke, J. E. O'Connor, C. Cannon, D. W. Heatwole, M. F. Ramirez, I. R. Waite, T. D. Counihan, and K. L. Jones. 2011. Columbia River estuary ecosystem classification - concept and application. U.S. Geological Survey Open-File Report 2011–1228. 54p.

Singer, G. P., A. R. Hearn, E. D. Chapman, M. L. Peterson, P. E. LaCivita, W. N. Brostoff, and A. P. Klimley. 2012. Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Environmental Biology of Fishes* 96(2–3):363–379.

Smalling, K. L., K. M. Kuivila, J. L. Orlando, B. M. Phillips, B. S. Anderson, K. Siegler, J. W. Hunt, and M. Hamilton. 2013. Environmental fate of fungicides and other current-use pesticides in a central California estuary. *Marine Pollution Bulletin* 73(1):144–153.

Smith, S. E. 2001. Leopard sharks. In *California's living marine resources: A status report*, eds. W. S. Leet, C. M. Dewees, R. Klingbeil, and E. J. Larson, 252–254. California Department of Fish and Game Publication SG01-11.

Smith, S. E., and N. J. Abramson. 1990. Leopard shark *Triakis semifasciata* distribution, mortality rate, yield, and stock replenishment estimates based on a tagging study in San Francisco Bay. *Fishery Bulletin* 88:371–381.

Spies, R. B., and D. W. J. Rice. 1988. Effects of organic contaminants on reproduction of the starry flounder *Platichthys stellatus* in San Francisco Bay. II. Reproductive success of fish captured in San Francisco Bay and spawned in the laboratory. *Marine Biology* 98(2):191–200.

Spratt, J. D. 1992. The evolution of California's herring roe fishery: Catch allocation, limited entry, and conflict resolution. *California Department of Fish and Game* 1:20–44.

St. Pierre, R., and R. R. Campbell. 2006. *Acipenser medirostris*. IUCN Red List of Threatened Species Version 2013.2. http://www.iucnredlist.org. Accessed July 2014. IUCN, Cambridge, UK.

Stefansson, S. O., Björnsson, B. T., L.O. Ebbesson, and S. D. McCormick. 2008. Smoltification. In *Fish Larval Physiology*, eds. R. N. Finn and B. G. Kapoor, 639–681.

Stehr, C. M., M. S. Meyers, D. G. Burrown, M. M. Krahn, J. P. Meador, B. B. McCain, and U. Varansi. 1997. Chemical contamination and associated liver diseases in two species of fish from San Francisco Bay and Bodega Bay. *Ecotoxicology* 6:36–65.

Stein, D., and T. J. Hassler. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Southwest). Brown rockfish, copper rockfish; and black rockfish. U S Fish Wildl Serv Rep TR EL-82-4:15.

Stevens, B., D. Armstrong, and R. Cusimano. 1982. Feeding habits of the Dungeness crab *Cancer magister* as determined by the Index of Relative Importance. *Marine Biology* 145:135–145.

Stewart, I. J. 2007. Updated U.S. English sole stock assessment: Status of the resource in 2007 (p. 213). National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA.

Suedel, B. C., J. Kim, D. G. Clarke, and I. Linkov. 2008. A risk-informed decision framework for setting environmental windows for dredging projects. *Science of the Total Environment* 403:1–11.

Talent, L. G. 1976. Food habits of leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. *California Fish and Game* 62:286–298.

Talent, L. G. 1982. Food habits of the gray smoothhound, *Mustelus californicus*, the brown smoothhound, *Mustelus henlei*, the shovelnose guitarfish, *Rhinobatos productus*, and the bat ray, *Myliobatis californic*a, in Elkhorn Slough, California. *California Fish and Game* 68:224–234.

Talent, L. G. 1985. The occurrence, seasonal distribution, and reproductive condition of elasmobranch fishes in Elkhorn Slough, California. *California Fish and Game* 71:210–219.

Tanaka, T. 2013. California halibut, *Paralichthys californicus*. In *Status of the Fisheries Report: An Update through 2011*, ed. T. Larinto. Report to the Fish and Game Commission prepared by California Department of Fish and Wildlife, Marine Region.

Tanasichuk, R. 1997. Influence of biomass and ocean climate on the growth of Pacific herring (*Clupea pallasii*) from the southwest coast of Vancouver Island. *Canadian Journal of Fisheries and Aquatic Sciences* 2788:2782–2788.

Tasto, R. N. 1975. Aspects of the biology of Pacific Staghorn sculpin, *Leptocottus armatus* Girard, in Anaheim Bay. California Department of Fish and Game, Fish Bulletin 165:123–195.

Tasto, R. N. 1983. Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the Central California fishery resource. *Fish Bulletin* 172:352pp.

Thedinga, J. F., S. W. Johnson, A. D. Neff, and M. L. Lindeberg. 2008. Fish assemblages in shallow, nearshore habitats of the Bering Sea. *Transactions of the American Fisheries Society* 137:1157–1164.

Thompson, B., and A. Gunther. 2004. Development of environmental indicators of the condition of San Francisco Estuary. A Report to the San Francisco Estuary Project. Oakland, California.

Thompson, C. W., E. R. Donelan, M. M. Lance, and A. E. Edwards. 2002. Diet of Caspian terns in Commencement Bay, Washington. *Waterbird*s 25(1):28–85.

Thorpe, J. E. 1994. Salmonid fishes and the estuarine environment. *Estuaries* 17(1):19.

Toft, J. D., J. R. Cordell, C. A. Simenstad, and L. A. Stamatiou. 2007. Fish distribution, abundance, and behavior along city shoreline types in Puget Sound. *North American Journal of Fisheries Management* 27(2):465–480.

Toft, J. D., A. S. Ogston, S. M. Heerhartz, J. R. Cordell, and E. E. Flemer. 2013. Ecological response and physical stability of habitat enhancements along an urban armored shoreline. *Ecological Engineering* 57:97–108.

Toole, C. L. 1980. Intertidal recruitment and feeding in relation to optimal utilization of nursery areas by juvenile English sole (*Parophrys vetulus*: Pleuronectidae). *Environmental Biology of Fishes* 5:383–390.

Toole, C. L., R. A. Barnhart, and C. P. Onuf. 1987. Habitat suitability index models: juvenile English sole (p. 27) U.S Fish and Wildlife Service Biological Report 82 (10.133).

Trudel, M., and R. B. MacFarlane. 2010. Energy dynamics and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from the Central Valley of California during the estuarine phase and first ocean year. *Canadian Journal of Fisheries and Aquatic Sciences* 67(10):1549–1565.

Tufts, D. E. 1989. The use of the insecticide carbaryl to control burrowing shrimp in Willapa Bay and Grays Harbor, Washington, in 1986. Washington State Department of Fisheries, Special Shellfish Report 4. Olympia, Washington.

Tufts, D. E. 1990. The use of the insecticide carbaryl to control burrowing shrimp in Willapa Bay and Grays Harbor in 1987. Washington State Department of Fisheries, Special Shellfish Report 5. Olympia, Washington.

Unwin, M. J., and G. J. Glova. 1997. Changes in life history parameters in a naturally spawning population of Chinook salmon (*Oncorhynchus tshawytscha*) associated with releases of hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences* 54(6):1235–1245.

USFWS, and NMFS. 1996. Policy Regarding the Recognition of Distinct Vertebrate Population Segments under the Endangered Species Act. Federal Register (7 February 1996) 61(26):4722-4725.

Valle, C. F., J. W. O'Brien, and K. B. Wiese. 1999. Differential habitat use by California halibut, *Paralichthys californicus*, barred sand bass, *Paralabrax nebulifer*, and other juvenile fishes in Alamitos Bay, California. *Fishery Bulletin* 97:646–660.

Van Dyke, E., and K. Wasson. 2005. Historical ecology of a central California estuary: 150 years of habitat change. *Estuaries* 28:173–189.

Vines, C. A., T. Robbins, F. J. Griffin, and G. N. Cherr. 2000. The effects of diffusible creosote-derived compounds on development in Pacific herring (*Clupea pallasii*). *Aquatic Toxicology* 51:225–39.

Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Application*s 7:737–750.

Wada, T., M. Aritaki, Y. Yamashita, and M. Tanaka. 2007. Comparison of low-salinity adaptability and morphological development during the early life history of five pleuronectid flatfishes, and implications for migration and recruitment to their nurseries. *Journal of Sea Research* 58(3):241–254.

Wahle, R. 1985. The feeding ecology of *Crangon franciscorum* and *Crangon nigricauda* in San Francisco Bay, California. *Journal of Crustacean Biology* 5:311–326.

Wainwright, T., D. Armstrong, P. Dinnel, J. Orensanz, and K. McGraw. 1992. Predicting effects of dredging on a crab population: An equivalent adult loss approach. *United States Marine Fisheries Service Bulletin* 90:171–182.

Wallace, M., and S. Allen. 2009. Juvenile salmonid use of the tidal portions of selected tributaries to Humbolt Bay, CA 2007–2009, (August). Technical Report to the Pacific States Marine Fisheries Commission. 32 pp.

Wang, J. C. S. 1986. Fishes of the Sacramento–San Joaquin Estuary and adjacent waters, California: A guide to the early life histories. Interag Ecol Program Tech Rep 9.

Ware, D. M. 1985. Life history characteristics, reproductive value, and resilience of Pacific herring (*Clupea harengus pallasii*). *Canadian Journal of Fisheries and Aquatic Sciences* 42(1):127–137.

Washington Department of Fish and Wildlife. 2014. http://wdfw.wa.gov/fishing/salmon/coho.html

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck, Jr., A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. T. Short, and S. L. Williams. 2009. Accelerating loss of seagrass across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences, USA* 106:12377--12381.

Webber, J. D. and J. J. Cech. 1998. Nondestructive diet analysis of the leopard shark from two sites in Tomales Bay, California. *California Fish and Game* 84:18–24.

Wechsler, J. F. 1996. Assessing the relationship between the ichthyofauna and oyster mariculture in a shallow coastal embayment, Drakes Estero, Point Reyes National Seashore. Dissertation (University of California, Davis).

Weinstein, M. P., S. Y. Litvin, and V. G. Guida. 2005. Wetland restoration design of habitat linkages, and the trophic estuarine landscapes, spectrum in wetland restoration design considerations. *Journal of Coastal Research* SI:51–63.

Weinstein, M. P., S. Y. Litvin, and J. M. Krebs. 2014. Restoration ecology: Ecological fidelity, restoration metrics, and a systems perspective. *Ecological Engineering* 65:71–87.

Weiss, P.W. 1969. The Age and Growth of the Marine Cottid *Leptocottus armatus*. *Proceedings of the Montana Academy of Sciences* 29: 63–71.

West, J. E., R. M. Buckley, and D. C. Doty. 1994. Ecology and habitat use of juvenile rockfishes (*Sebastes* spp.) associated with artificial reefs in Puget Sound, Washington. *Bulletin of Marine Science* 55:344–350.

West, J. E., S. M. O'Neill, and G. M. Ylitalo. 2008. Spatial extent, magnitude, and patterns of persistent organochlorine pollutants in Pacific herring (*Clupea pallasii*) populations in the Puget Sound (USA) and Strait of Georgia (Canada). *Science of the Total Environment* 394:369–78.

Westrheim, S. J. 1955. Size composition, growth, and seasonal abundance of juvenile English sole (*Parophrys vetulus*) in Yaquina Bay. *Fish Commission of Oregon, Research Briefs* 6(2):4–9.

Wiebe, J. P. 1968. The reproductive cycle of the viviparous seaperch, *Cymatogaster aggregata* Gibbons. M.S. Thesis, University of British Columbia.

Williams, J. G. 2006. Central Valley salmon: A perspective on Chinook and steelhead in the Central Valley of California. *San Francisco Estuary and Watershed Science* 4(3):1–393.

Williams, S. F., and R. S .Caldwell. 1978. Growth, food conversion and survival of 0-group English sole (*Parophrys vetulus* Girard) at five temperatures and five rations. *Aquaculture* 15(2):129–139.

Wilson, D. C., and R. E. Millemann. 1969. Relationships of female age and size to embryo number and size of the shiner perch, *Cymatogaster aggregata*. *Journal of the Fisheries Research Board of Canada* 26:2339–2344.

Woodson, L., B. Wells, P. Weber, R. MacFarlane, G. Whitman, and R. Johnson. 2013. Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. *Marine Ecology Progress Series*, 487:163–175.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson, H. K. Lotze, F. Micheli, S. R. Palumbi, E. Sala, K. A. Selkoe, J. J. Stachowicz, and R. Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–90.

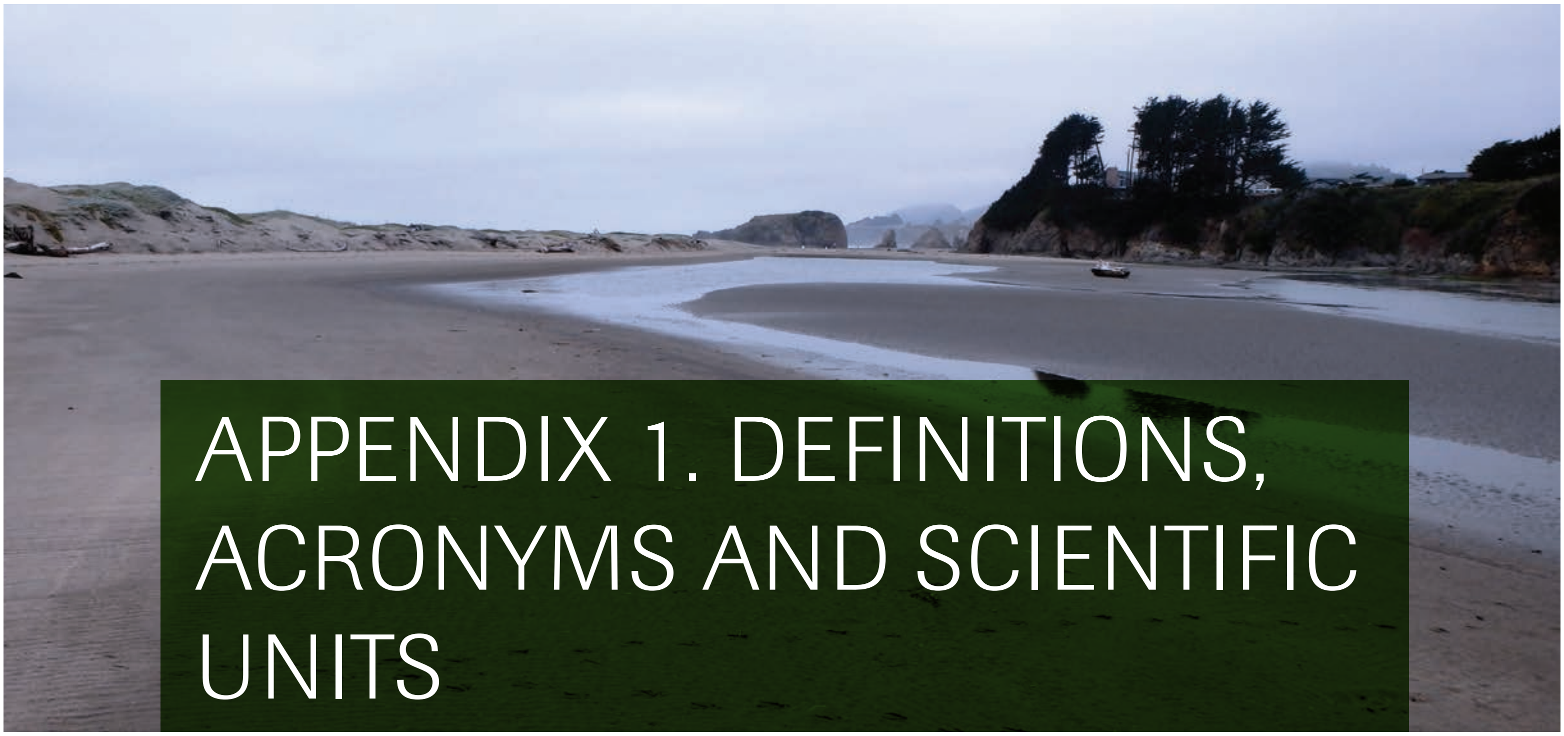
Wyllie-Echeverria, T. 1987. Thirty-four species of California rockfishes: Maturity and seasonality of reproduction. *Fishery Bulletin* 85(2):229–250.

Yoklavich, M. M. 1982. Growth, food consumption, and conversion efficiency of juvenile English sole (*Parophrys vetulus*). In *Gutshop '81: Fish Food Habits Studies,* eds. G. M. Cailliet and C. A. Simenstad, 97–105. Seattle, WA: Washington Sea Grant Publication.

Yoklavich, M. M., G. M. Cailliet, J. P. Barry, D. A. Ambrose, and B. S. Antrim. 1991. Temporal and spatial patterns in abundance and diversity of fish assemblages in Elkhorn Slough, California. *Estuaries* 14(4):465–480.

Zedler, J. B. 1996. Coastal mitigation in southern California: The need for a regional restoration strategy. *Ecological Applications* 6:84–93.

Zedonis, P. 1992. The biology of juvenile steelhead (*Onchorynchus mykiss*) in the Mattole River Estuary/Lagoon. Master's thesis, Humboldt State University. 88pp.



APPENDIX 1. DEFINITIONS, ACRONYMS AND SCIENTIFIC UNITS

© Walter N. Heady/TNC

Definitions and Acronyms

adult: a life stage characterized by the ability to reproduce.

age-0: animal in the first year of it life; less than one year old.

alevin: a newly hatched salmonid with the external yolk-sac still attached; generally residing within the safe gravels of nests created by the mother.

Anadromous: a life-history in which individuals hatch from eggs and spend some amount of time rearing in freshwater habitats, and then migrate through estuaries to the sea to grow and mature into adults before returning to spawn in their natal freshwater habitats.

aplacental viviparity: embryos do not have a placental connection with mother and are born live.

carnivorous: feeds on animals.

DPS: distinct population segment—a management unit under the Endangered Species Act recognizing a population or group of populations as being discrete from other conspecific DPS and significant to the entire species; used for the management of sturgeon and steelhead trout in this report .

elasmobranch: cartilaginous fishes, in particular the sharks, skates and rays.

estuarine-dependent: species which usually require the estuarine habitat for some stage of the life history.

estuary: a partially enclosed coastal body of water that is either permanently or periodically open to the sea and which receives at least periodic discharge from a river(s), and thus, while its salinity is typically less than that of natural sea water and varies temporally and along its length, it can become hypersaline in regions when evaporative water loss is high and freshwater and tidal inputs are negligible (from Potter et al. 2010).

ESU: evolutionary significant unit—a salmonid management unit under the Endangered Species Act consisting of a group of populations that are reproductively isolated from other conspecific ESUs and that represent an important component of the evolutionary legacy for the species.

fry: early juvenile life-history stage for salmonids.

fingerling: later and larger salmonid life-history stage than fry.

generation time: estimate of amount of time it takes one cohort to grow up and replace another.

gravid: pregnant; carrying eggs or young.

hypoxia: oxygen deficiency in a biotic environment.

juvenile: a life stage of fish and invertebrates that starts when an organisms completes metamorphosis from larvae? and ends with onset of sexual maturity (any reference to sub-adult).

larvae: a distinct life stage, common in fish and invertebrates, that starts when the organism hatches from an egg and ends upon metamorphosis into the juvenile form.

length-frequency: a summary of the frequency of observations of different length classes.

macrophyte: an aquatic plant that grows in or near water and is either emergent, submergent, or floating such as kelp and seagrass.

natal philopatry: a tendency to breed at or near their place of birth.

nearshore: the region of the sea or seafloor relatively close to the shoreline.

nursery: a juvenile habitat that provides enhanced rearing conditions—often measured through factors such as growth, condition, survival—and disproportionately higher contribution of individuals to the adult populations.

parr: juvenile salmonid showing black vertical “parr marks” along each side that act as camouflage within the stream environment.

pelagic: relating to or living in open oceans or seas rather than waters adjacent to land or the seafloor.

phytoplankton: plankton that makes energy through photosynthesis and inhabits the upper sunlit layer of a body of water.

planktivorous: feeds on plankton.

plankton: the passively floating or weakly swimming animal and plant life in a body of water.

settlement: the transition from the pelagic larval phase to the benthic juvenile phase.

smolt: juvenile salmonid undergoing physiological, morphological, and behavioral changes in transition from life in freshwater to life at sea, including a thinner more streamlined morphology, silver coloration, changes in osmoregulation, and downstream migration.

YOY: young-of-the-year—a term describing juveniles born within the most recent year.

Zooplankton: plankton that gets energy through consumption of other organisms; includes both mature (e.g., copepods, krill) and immature stages of larger animals (e.g., crab and fish larvae).

Scientific Units

%: percentage

°C: degrees centigrade or Celsius

CM: centimeter

CW: carapace width

DW: disc width

FL: fork length

HA: hectare

KG: kilogram

KM: kilometer

M: meter

MM: millimeter

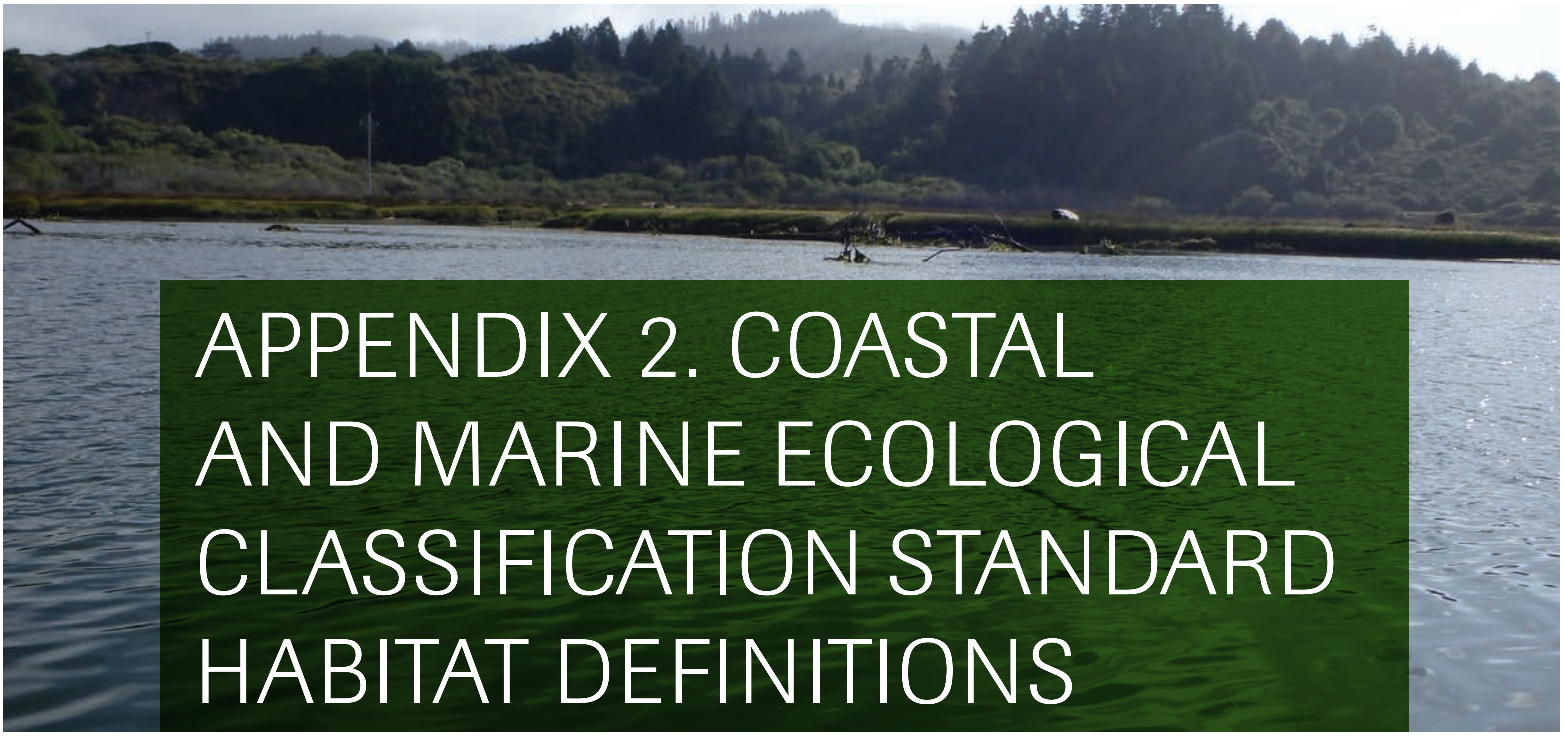
N: sample size

PPT: parts-per-thousand (re: salinity)

Q_{10}: measure of temperature sensitivity of physiological processes due to an increase of 10ºC.

SL: standard length

TL: total length



APPENDIX 2. COASTAL AND MARINE ECOLOGICAL CLASSIFICATION STANDARD HABITAT DEFINITIONS

© Walter N. Heady/TNC

The Coastal and Marine Ecological Classification Standard (CMECS; FGDC 2012; see http://coast.noaa.gov/digitalcoast/publications/cmecs) was applied to all West Coast estuaries and cross-referenced to other estuarine classifications applied to each estuary. As a comprehensive national framework, CMECS can be used to classify the environment and to organize information and data about coasts and oceans and their living systems. CMECS is designed for use within all waters ranging from the head of tide to the limits of the exclusive economic zone, and from the spray zone to the deep ocean.

CMECS best met the criteria for an estuarine classification scheme that could be standardized across Washington, Oregon, and California and was applied to all the estuaries in the West Coast inventory. This standardized scheme is a federally-accepted format that uses common terminology with global applicability. The modular nature of CMECS allows for coarser or finer resolution of classification, as needed, to support a wide range of future research and management among the estuaries of Washington, Oregon, and California.

We used CMECS to broadly categorize and define classes of estuaries on the West Coast, as well as estuarine sub-classes and habitats within those estuaries.

Classes of Estuaries (Geomorphic classes)

The physiographic setting subcomponent of CMECS describes landscape-level geomorphological features from the coast to the deep-water marine environment. The subcomponent contains 21 feature types, seven of which are applicable to the estuarine environment. Of these seven estuarine features, four (Embayment/Bay, Lagoonal Estuary, Riverine Estuary, and Sound) are found on the West coast of the continental United States and were used broadly to classify types of estuaries.

- **Embayment/Bay**—A water body with some level of enclosure by land at different spatial scales. These can be wide, curving indentations in the coast, arms of the sea, or bodies of water almost surrounded by land. These features can be small—with considerable freshwater and terrestrial influence—or large and generally oceanic in character.

- **Sound**—(a) A relatively long, narrow waterway connecting two larger bodies of water (or two parts of the same water body), or an arm of the sea forming a channel between the mainland and an island (e.g., Puget Sound, WA). A sound is generally wider and more extensive than a strait. (b) A long, large, rather broad inlet of the ocean, which generally extends parallel to the coast (e.g., Long Island Sound, NY).

- **Lagoonal Estuary**—This class of estuary tends to be shallow, highly enclosed, and have reduced exchange with the ocean. They often experience high evaporation, and they tend to be quiescent in terms of wind, current, and wave energy. Lagoonal estuaries usually have a very high surface-to-volume ratio, a low-to-moderate watershed-to-water-area ratio, and can have a high wetland-to-water ratio. The flushing times tend to be long relative to riverine estuaries and embayments because the restricted exchange with the marine-end member and the reduced river input lengthen residence times. As such, there tends to be more benthic-pelagic interaction, enhanced by generally shallow bathymetry. Additionally, exchange with surrounding landscapes (often riparian wetland and palustrine systems) tends to be enhanced and more highly coupled than in other types of estuaries. Occasionally, a lagoon may be produced by the temporary sealing of a river estuary by a barrier. Such lagoons are usually seasonal and exist until the river breaches the barrier; these lagoons occur in regions of low or sporadic rainfall.

- **Riverine Estuary**—This class of estuary tends to be linear and seasonally turbid (especially in upper reaches), and it can be subjected to high current speeds. These estuaries are sedimentary and depositional, so they may be associated with a delta, bar, barrier island, and other depositional features. These estuaries also tend to be highly flushed (with a wide and variable salinity range) and seasonally stratified. Riverine estuaries have moderate surface-to-volume ratios with a high watershed-to-water-area ratio—and they can have very high wetland-to-water-area ratios as well. These estuaries are often characterized by a V-shaped channel configuration and a salt wedge. High inputs of land drainage can promote increased primary productivity, which may be confined to the water column in the upper reach, due to low transparency in the water column. Surrounding wetlands may be extensive and healthy, given the sediment supply and nutrient input. This marsh perimeter may be important in taking up the excess nutrients that are introduced to the system. Physically, the system may tend to be stratified during periods of high riverine input, and the input of marine waters may be enhanced by countercurrent flow.

Sub-classes and Habitats within Estuaries

We used the CMECS classification scheme to identify and define a broad array of estuarine subsystems and habitat types that were important for the nursery assessment. The following definitions of estuarine subclasses and habitats were drawn from various CMECS hierarchical levels including tidal zones, geoforms, biogenic substrates, and biotic subclasses (FGDC 2012).

Estuarine sub-classes:

- **Estuarine Coastal Subtidal**—The substrate is generally continuously submerged in this zone and includes those areas below Mean Low Low Water.

- **Tidal Channel/Creek**—Linear or sinuous body of water through which ebb-and-flood tidal movement takes place. Smaller tidal creeks often branch off of these features. Portions of tidal channels may be intertidal or completely subtidal.

- **Slough**— (a) A sluggish body of water in a tidal flat, bottomland, or coastal marshland; may also be called bayous or oxbows. (b) A sluggish channel of water (such as a side channel of a river) in which water flows slowly through either low, swampy ground (such as along the Columbia River) or a section of an abandoned river channel (which may contain stagnant water) that occurs

- **Lagoon**—Lagoons tend to be shallow, highly enclosed, with reduced exchange with the ocean, often experiencing high evaporation, and quiescent in terms of wind, current, and wave energy. They tend to have a very high surface to volume ratio, low to moderate watershed to water area ratio and can have a high wetland to water ratio. The flushing times tend to be long relative to riverine estuaries and even embayments, as the restricted exchange with the marine end member and reduced river input lengthen residence times.

Biogenic habitats:

- **Oyster Reef**—Areas dominated by the ridge- or mound-like structures formed by the colonization and growth of oysters that are attached (cemented) to a substrate of live and dead conspecifics. Oyster reefs provide excellent structural habitat as well as effective water filtration. For the purposes of this report oyster reefs also include oyster aquaculture areas.

- **Seagrass Bed**—Tidal aquatic vegetation beds dominated by any number of seagrass or eelgrass species, including *Ruppia* sp., *Phyllospadix* sp., and *Zostera* sp. Seagrass beds may occur in true marine salinities, and they may extend into the lower salinity zones of estuaries. Seagrass beds are complex structural habitats that provide refuge and foraging opportunities for abundant and diverse faunal communities in shallow waters. Seagrass beds require a specific set of ecological conditions for success, and they are generally perceived as areas of high environmental quality.

- **Benthic Macroalgae**—Aquatic beds dominated by macroalgae attached to the substrate, such as kelp, intertidal fucoids, and calcareous algae. Macroalgal communities can exist at all depths within the photic zone, on diverse substrates, and across a range of energy and water chemistry regimes. In the CMECS framework, macroalgae that dominate the benthic environment and form a vegetated cover fall within this subclass.

- **Freshwater and Brackish Tidal Aquatic Vegetation**—Tidal aquatic vegetation beds dominated by submerged, rooted, vascular species that have limited (or no) salt tolerance. Some species, such as *Ruppia maritima*, can have a wide range of salt tolerance, and are included in this group when occurring in low salt environments or with other salt intolerant species that indicate low salt environments.

- **Emergent Tidal Marsh**—Communities dominated by emergent, halophytic, herbaceous vegetation (with occasional woody forbs or shrubs) along low-wave-energy, intertidal areas of estuaries and rivers. Vegetation in this subclass is composed of emergent aquatic macrophytes, especially halophytic species—chiefly graminoids (such as rushes, reeds, grasses and sedges), shrubs, and other herbaceous species (such as broad-leaved emergent macrophytes, rooted floating-leaved and submergent species [aquatic vegetation], and macroscopic algae). The vegetation is usually arranged in distinct zones of parallel patterns, which occur in response to gradients of tidal flooding frequency and duration, water chemistry, or other disturbances. Tides may expose mudflats that contain a sparse mix of pioneering forb and graminoid species. Salinity levels (which control many aspects of salt-marsh chemistry) vary depending on a complexity of factors, including frequency of inundation, rainfall, soil texture, freshwater influence, fossil salt deposits, and more. Salt marshes often grade into (or are intermixed with) scrub-shrub wetlands in higher areas.

- **Tidal Scrub-Shrub Wetlands**—Estuarine or tidal riverine areas dominated by shrub vegetation that has less than 10% tree cover.

- **Tidal Forest/Woodland**—Estuarine or tidal riverine areas with greater than 10% tree cover.

- **Shell Rubble**—Shell Rubble (with a median particle size of 64 millimeters to < 4,096 millimeters) that is primarily composed of cemented or conglomerated oyster shells.

- **Very Coarse Woody Debris**—Woody Debris with a median particle size from 256 millimeters to < 4,096 millimeters.

Geologic habitat:

- **Tidal Flat**—An extensive, nearly horizontal, barren (or sparsely vegetated) tract of land that is alternately covered and uncovered by the tide. Tidal flats consist of unconsolidated sediment (mostly clays, silts and/or sand, and organic materials).

Anthropogenic habitat:

- **Anthropogenic Wood**—Substrate that is primarily composed of woody materials that were processed or assembled by humans (e.g., jetty, pilings).

Data used to generate this report can be accessed through the Pacific States Marine Fisheries Commission (www.psmfc.org), or by contacting the lead authors: Brent Hughes (bbhughes@ucsc.edu) and Matthew Levey (mlevey@seaspatial.com).

Back cover photos: Clockwise from top left: © John Bragg/SSNERR, © John Bragg/SSNERR, © John Bragg/SSNERR, © Laura S. Brophy