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Design and Parameterization of a Spatially Explicit Atlantis Ecosystem Model for Puget Sound

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Design and Parameterization of a Spatially Explicit Atlantis Ecosystem Model for Puget Sound

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Abbreviations

%F	percent frequency
%N	percent number
%W	percent weight
ΔGLMM	spatial delta-generalized linear mixed model
AMPS	Atlantis Model for Puget Sound
BB	bacteria, benthic
BC	carnivorous infauna
BD	deposit feeders
BE	raptors
BFF	benthic filter feeders
BG	benthic grazers
BIV	bivalves
BMD	deep macrozoobenthos
BML	crabs
BMS	octopus
CDS	Chinook, Duwamish subyearling
CHC	Chinook, Hood Canal subyearling
CHS	Chinook, hatchery subyearling
CHY	Chinook, hatchery yearling
CKS	Chinook, other subyearling
CMECS	Coastal and Marine Ecological Classification Standard, Version 4
CMF	chum, fall subyearling
CMH	chum, Hood Canal summer-run subyearling
CMS	chum, hatchery subyearling
CNS	Chinook, Nisqually subyearling
CNY	Chinook, Nisqually yearling
COD	coho, deep south yearling
COH	coho, hatchery yearling
COS	coho, Skagit yearling
COY	coho, other yearling
CPUE	catch per unit of effort
CSL	California sea lions
CSN	Chinook, Snohomish subyearling
CSS	Chinook, Skagit subyearling
CSY	Chinook, Skagit yearling
CTD	conductivity, temperature, and depth
CYE	Chinook, other yearling
DC	carrion
DFO	Fisheries and Oceans Canada
DIN	dissolved inorganic nitrogen
DL	labile detritus
DMP	dockside monitoring program
DOG	spiny dogfish

DON	dissolved organic nitrogen
DR	refractory detritus
DUN	Dungeness crabs
DVR	demersal vulnerable rockfish
E	euphotic
EPA	Environmental Protection Agency
ESA	Endangered Species Act
FDF	small-mouthed flatfish
FL	fork length
FMM	Pacific hake and large gadoids
FPS	small planktivorous fish
FRAM	Fishery Regulation Assessment Model
FVS	large demersal predators
GEC	geoduck clams
HAB	harmful algal blooms
HAP	piscivorous flatfish
HEC	Pacific herring, Cherry Point
HEP	Pacific herring, Puget Sound
HSL	harbor seals
HUW	humpback whales
IRI	Index of Relative Importance
LLTK	Long Live the Kings
MA	macroalgae
MERIS	medium-resolution imaging spectrometer
$mg\ N/m^3$	milligrams of nitrogen per cubic meter
mg/L	milligrams per liter
MoSSea	Modeling the Salish Sea
MRO	midwater rockfish
MSY	maximum sustainable yield
MVR	midwater vulnerable rockfish
N	nitrogen
NetCDF	Network Common Data Form
NH_3	ammonia
NH_4	ammonium ion
NMFS	National Marine Fisheries Service
NO_2	nitrous oxide
NO_3	nitrate
NOAA	National Oceanic and Atmospheric Administration
Nr	reserve nitrogen
Ns	structural nitrogen
NWFSC	Northwest Fisheries Science Center
PacFIN	Pacific Fisheries Information Network
PAH	polycyclic aromatic hydrocarbons
PB	pelagic groups
PBDE	polybrominated diphenyl ethers
PCB	polychlorinated biphenyls

PHR	harbor porpoises
PIN	Steller sea lions
PIS	pink salmon
PIT	passive integrated transponder
PL	large phytoplankton
PON	particulate organic nitrogen
POP	surfperches
PP	primary productivity
PS	small phytoplankton
PSAMP	Puget Sound Assessment and Monitoring Program
PSDOM	Puget Sound Dissolved Oxygen Model
PSMFC	Pacific States Marine Fisheries Commission
PSF	Pacific Salmon Foundation
PWN	shrimp
RAT	spotted ratfish
RMIS	Regional Mark Information System
ROC	demersal rockfish
ROMS	Regional Ocean Modeling System
ROR	resident orcas
ROV	remotely operated vehicle
SAF	Strait of Georgia salmonids
SAL	other salmonids
SB	seabirds, piscivorous
SBL	sixgill sharks
SG	seagrass
Si	silica
SMD	small demersal fish
SP	seabirds, non-piscivorous
SQX	squids
SSK	skates
SSM	Salish Sea Model
t	metric tons
TL	total length
TMY3	typical meteorological year
TNC	The Nature Conservancy
TOR	transient orcas
USGS	United States Geological Survey
VAST	Vector-Autoregressive Spatio-Temporal Model (R package)
WDFW	Washington Department of Fish and Wildlife
WSDOE	Washington State Department of Ecology
ZG	gelatinous zooplankton
ZL	large zooplankton
ZM	mesozooplankton
ZS	microzooplankton

Plain Language Summary

Background

The Pacific Northwest is home to many natural wonders, including the iconic Pacific salmon. Historically, economically, culturally, and ecologically, these five species—Chinook, coho, chum, pink, and sockeye salmon—are an essential aspect of this unique region of the United States.

And yet, their numbers are dropping. This is in part due to their complex life history, which sees them migrating hundreds or thousands of miles, from freshwater streams to the deep salty ocean and back again, facing dangers every step of the way. And while some of these are obvious—pollution and predators, for example—others, like climate change, are more subtle, but potentially even deadlier.

The Northwest Fisheries Science Center, in collaboration with partners at the federal, state, and tribal levels, and groups like the Salish Sea Marine Survival Project and the Puget Sound Partnership, is studying how to best help these species recover and thrive. As part of this effort, we have developed an ecosystem model of Puget Sound that will help us examine and answer important questions about Pacific salmon, including:

- How are salmon affected by water quality?
- How sensitive are marine systems that support salmon to human activities?
- How does competition and predation between and among species affect salmon?

Our model is based on the Atlantis framework. It is a three-dimensional model of Puget Sound that simulates every component of the marine ecosystem, from bacteria to killer whales. Atlantis produces forecasts of changes in the system under different scenarios.

This report describes the model and all of its inputs, and provides details on the data that were used to build the model. It also provides the results of our initial calibration efforts, this essential first step being critical to making sure the forecasts produced by the model are reliable for fishery managers and decision-makers.

Key Takeaways

Our work developing this model demonstrates the need for continued surveying, monitoring, and other field and experimental work in Puget Sound. The data those efforts provide are critical to developing models like this.

We found that the model is generally stable over a variety of fishing scenarios and mortalities. Individual diagnostics are well behaved, indicating reasonable values for the subcomponents of the model.

We expect this model to contribute to efforts to protect and restore the Puget Sound ecosystem. Future publications will use the model to investigate hypotheses of juvenile salmon survival, the ecosystem impacts of conservation actions directed to Southern Resident killer whales, and the cumulative impacts of ocean warming, pollution, and nutrient inputs.

Links used in this section:

- Chinook salmon: https://www.fisheries.noaa.gov/species/chinook-salmon
- Coho salmon: https://www.fisheries.noaa.gov/species/coho-salmon
- Chum salmon: https://www.fisheries.noaa.gov/species/chum-salmon
- Pink salmon: https://www.fisheries.noaa.gov/species/pink-salmon
- Sockeye salmon: https://www.fisheries.noaa.gov/species/sockeye-salmon
- Salmon life history: https://www.youtube.com/watch?v=2xG6waimZnI&t=0s
- Pollution: https://media.fisheries.noaa.gov/dam-migration/stormwater_fact_sheet_3222016.pdf
- Climate change: https://www.fisheries.noaa.gov/west-coast/climate/climate-impacts-salmon-pacific-northwest
- Salish Sea Marine Survival Project: https://marinesurvivalproject.com/
- Puget Sound Partnership: https://www.psp.wa.gov/
- Ecosystem modeling: https://www.fisheries.noaa.gov/national/ecosystems/ecosystem-modeling
- Atlantis ecosystem model: https://research.csiro.au/atlantis/home/about-atlantis/
- Calibration: https://www.fisheries.noaa.gov/resource/peer-reviewed-research/calibrating-process-based-marine-ecosystem-models

Executive Summary

Pacific salmon (*Oncorhynchus* spp.) are highly significant in Puget Sound and throughout the Pacific Northwest because of their ecological, economic, social, and cultural importance. Chinook salmon and coho salmon (*O. tshawytscha* and *O. kisutch*) have experienced tenfold declines in survival during the marine phase of their lifecycle, and their total abundance is well below what it was 30 years ago. Here we present technical details of an ecosystem model for Puget Sound. The model can be used to explore whether bottom-up processes—including short- and long-term changes in circulation, water chemistry, and primary productivity—have led to shifts in prey availability, timing, and quality for juvenile Chinook and coho salmon. It also provides insight into the effects of alternate management scenarios and human disturbances over various temporal and spatial scales. The model was built using the Atlantis modeling framework, a simulation modeling approach that integrates physical, chemical, ecological, and anthropogenic processes in a three-dimensional, spatially explicit domain. This framework has been applied to evaluate management scenarios and investigate the effects of climate change in over 30 ecosystems worldwide. In Atlantis, ecosystem dynamics are represented by spatially explicit submodels that simulate oceanographic processes, biogeochemical factors driving primary production, and food web relations among flora and fauna. The model represents species of ecological and conservation concern and key exploited species at the level of detail necessary to evaluate the direct effects of fishing, and it represents other anthropogenic and climate impacts on the ecosystem as a whole. In this report, we describe the geography and components of the Atlantis Model for Puget Sound (AMPS), our assumptions on ecosystem structure and function, our data sources, and the calibration of the model to historical data.

We linked AMPS to a regional ocean modelling system model for Puget Sound, to force temperature and salinity fluxes. We simulated food web dynamics using 73 functional groups, including salmon (21 groups), demersal fish (9), pelagic fish (1), forage fish (3), elasmobranchs (4), seabirds (3), mammals (7), zooplankton (4), primary producers (4), invertebrates (12), bacteria (2), and detritus groups (3). We reconstructed biomass, catch, and effort trends in Puget Sound based on historical abundance and catch data.

We evaluated the ability of the model to represent historical fishing pressure from 2011 to 2017. Our preliminary assessment shows that AMPS can reasonably approximate historical spatial distribution and abundance for most functional groups and fisheries in the region. We believe that AMPS can be applied to test ecological hypotheses, evaluate ecosystem indicators, assess the effects of climate change, and identify the trade-offs associated with alternative management scenarios.

Acknowledgments

Development of the Atlantis Model for Puget Sound was part of the Salish Sea Marine Survival Project, a research consortium of over 60 organizations coordinated by Long Live the Kings (LLTK) and the Pacific Salmon Foundation (PSF), designed to determine the primary factors affecting the survival of juvenile salmon and steelhead in the Salish Sea. Funding for this study came from the Boeing Company and the Southern Endowment Fund that was established by the U.S.–Canada Pacific Salmon Treaty, and is supported by the Pacific Salmon Commission. Cloud computing resources were provided by an AI for Earth Microsoft Azure Research Grant to Long Live the Kings. The views expressed are those of the authors and do not necessarily reflect the views of the supporting organizations.

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This study is part of the Salish Sea Marine Survival Project, an international, collaborative research effort designed to determine the primary factors affecting the survival of juvenile salmon and steelhead survival in the combined waters of Puget Sound and the Strait of Georgia.[1]

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[1] https://marinesurvivalproject.com/

Introduction

Pacific salmon (*Oncorhynchus* spp.) are highly significant in Puget Sound and throughout the Pacific Northwest region because of their ecological, economic, social, and cultural importance (Harvey et al. 2010). Chinook salmon (*O. tshawytscha*) and coho salmon (*O. kisutch*) in Puget Sound have experienced large declines in survival during the marine phase of their lifecycle, and their total abundance is well below what it was 30 years ago (Beamish et al. 2010, Johannessen et al. 2010, Zimmerman et al. 2015a, Ruff et al. 2017). The Puget Sound Chinook salmon Evolutionarily Significant Unit (ESU), which includes naturally spawned Chinook salmon originating from rivers flowing into Puget Sound—including the Elwha River and rivers in Hood Canal, South Sound, North Sound, and the Strait of Georgia—is now listed as threatened under the Endangered Species Act (USOFR 2014). Stocks from coastal Washington and British Columbia, Canada, have not shown similar declines (Kilduff et al. 2015), suggesting that the factors affecting marine survival occur within Puget Sound.

Puget Sound is experiencing rapid human population growth and is affected by a variety of impacts that could account for the negative effects on salmon marine survival, including:

- Shoreline hardening, which affects salmon diets (Munsch et al. 2015) and residence time (Heerhartz and Toft 2015).
- Land development, which contributes to increased loads of nutrients, contaminants, and sediments due to rapid changes in surface runoff and river discharge.
- Increased nutrient loads, which can reduce dissolved oxygen, water clarity, and submerged aquatic vegetation, increase harmful algal blooms, and alter food webs (Cassin et al. 2008, Kornis et al. 2017).

Contaminants present in urban runoff may include hydrocarbons, plasticizers, flame-retardants, pesticides, metals, pharmaceuticals, and other potentially toxic chemicals (Feist et al. 2011). Climate change effects, such as increases in water temperature, changes in precipitation, and increased extent of hypoxia and ocean acidification, threaten to further affect marine resources in coming decades. Given the diversity of pressures that simultaneously influence Puget Sound, it is prudent to implement an “end-to-end” spatio-temporal ecosystem model (Travers et al. 2007, Rose et al. 2010) that is capable of integrating a broad range of drivers to inform the management and recovery of Puget Sound and its salmon. Widespread declines in the status of species and habitats in marine ecosystems have led to calls for ecosystem-scale management as a strategy to restore ocean ecosystems (Pew Oceans Comission 2003, Congress HCS 2004). Ecosystem-based management (EBM) requires an understanding of the complex dynamics of marine ecosystems, as well as an understanding of how humans fit into the system. EBM can assist resource managers in forecasting changes in ecosystem services across different scenarios, often revealing trade-offs among particular services (Hassan et al. 2005).

In this report, we present the basic formulations and parameterization for the biology and physics of an end-to-end ecosystem model of Puget Sound built in the Atlantis ecosystem modelling framework (Fulton et al. 2011, Weijerman et al. 2016). Atlantis simulations are spatially explicit and typically incorporate survey data statistically extrapolated onto the model’s spatial configuration. Atlantis integrates circulation patterns and nutrient cycling, biological feedbacks, food web interactions, fisheries, and management and monitoring efforts (Fulton et al. 2011, Weijerman et al. 2016). For this work, we have built on previous Atlantis models developed for Central California (Brand et al. 2007) and the California Current (Horne et al. 2010, Marshall et al. 2012), and we leverage existing expertise with Atlantis in other regions (Fulton et al. 2011, Grüss et al. 2017, Kaplan et al. 2017, Marshall et al. 2017, Girardin et al. 2018). Our goal is to develop a robust simulation of Puget Sound that will allow us to explore potential effects of natural and human-induced perturbations over a range of spatial and temporal scales. This model was developed as part of the Salish Sea Marine Survival Project (Pearsall et al. 2021), an international effort with more than 60 partner institutions and research groups working to understand drivers of salmon early marine survival, and to find conservation solutions for Chinook and coho salmon.

The Atlantis model will be used initially to examine how human impacts—such as climate change, contaminants, and nutrients from wastewater and runoff—influence declines in salmon populations in Puget Sound. First, we aim to understand the cause, or causes, of declining trends in juvenile marine survival of Chinook and coho salmon over recent decades (Zimmerman et al. 2015a, Ruff et al. 2017). Some of the general questions that will be examined include (Figure 1):

1. How do short- and long-term changes in circulation, water chemistry, and primary productivity affect the salmon and other relevant species in Puget Sound? Specifically, for Chinook and coho salmon, have these bottom-up processes led to shifts in prey availability, timing, and quality? For instance, for the nearby Strait of Georgia, Riche et al. (2014) have identified warming trends and changes in timing of freshwater and zooplankton blooms.
2. How sensitive are the bottom-up processes relevant to salmon to the effects of human activities, such as nutrient input, and contaminants in Puget Sound? In particular, have runoff and other inputs of nitrogen and contaminants—such as polychlorinated biphenyls (PCBs), polybrominated diphenyl ethers (PBDEs), and hydrocarbons—altered the food web or decreased survival of juvenile salmonids (O'Neill and West 2009)?
3. To what extent has competition and predation within the Puget Sound food web led to declines in survival of juvenile salmon? Specifically, while Chinook and coho salmon have experienced declines in juvenile survival, pink salmon, a potential competitor (Ruggerone and Goetz 2004), has increased. In addition, the significant recovery of harbor seals, porpoises, and sea lions since the 1970s has likely affected the food web, as these species prey on juvenile salmon (Adams et al. 2016, Chasco et al. 2017).

We will apply the Atlantis model described here to provide information to natural resource managers regarding: a) which natural and anthropogenic impacts most strongly affect Chinook and coho salmon survival and broader ecosystem health; b) to what extent those impacts must be addressed; and c) whether stringent management actions imply tradeoffs in other sectors or conservation objectives (e.g., the example of tradeoff analysis via Atlantis in Fulton et al. [2014]). Our work may be tied directly into science support for regional decision-making through collaborations with Washington State, federal NOAA and EPA scientists, and the Puget Sound Partnership. The work will also contribute to ecosystem-based management of Puget Sound, and informs the "vital signs" of the system's health maintained by the Puget Sound Partnership.[1]

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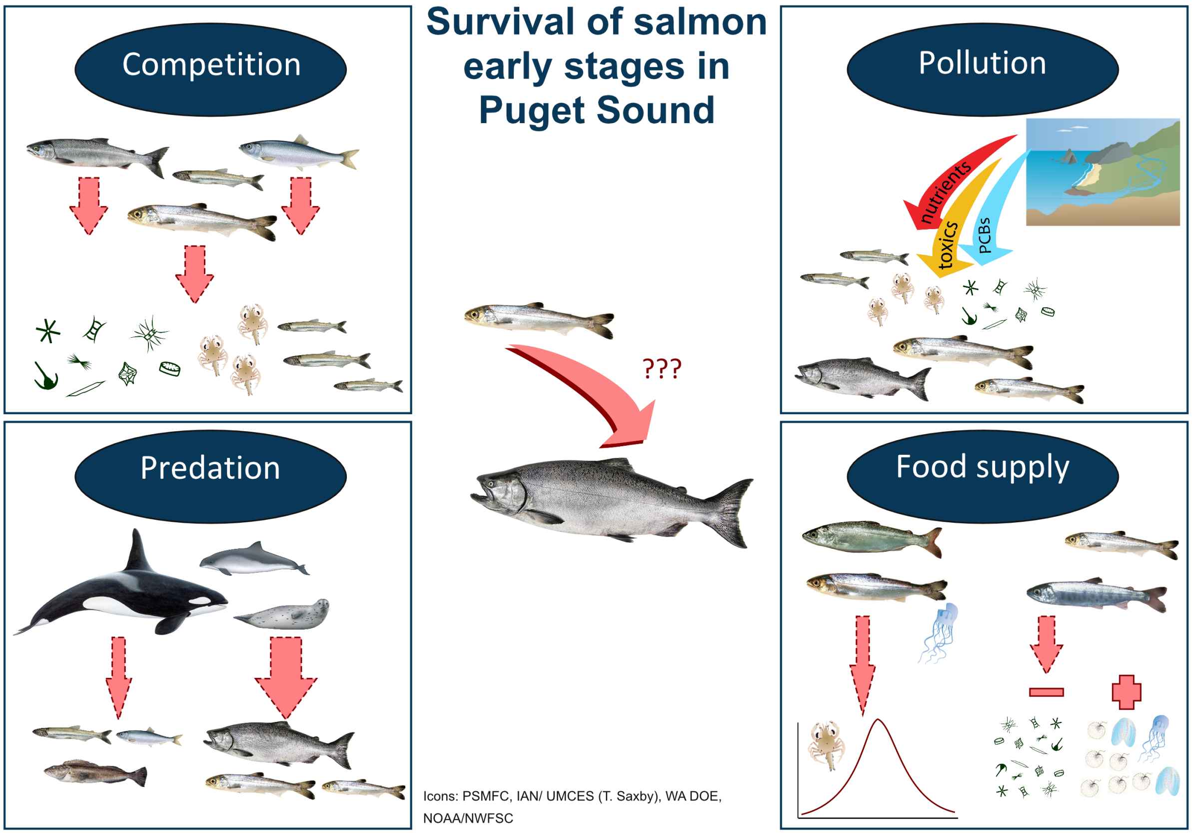
[1] https://vitalsigns.pugetsoundinfo.wa.gov/



Icons: PSMFC, IAN/ UMCES (T. Saxby), WA DOE, NOAA/NWFSC

Figure 1. Hypothesized drivers of juvenile salmon survival in Puget Sound.

Puget Sound

Puget Sound, a multi-basin estuarine ecosystem on the U.S. West Coast, is linked to the rest of the California Current via many processes. Puget Sound receives upwelled water from the California Current, which dramatically affects temperature, salinity, dissolved oxygen, pH, and other water-quality parameters within the sound (Moore et al. 2008); conversely, freshwater outflow from Puget Sound and the neighboring Strait of Georgia contributes to the formation of the Juan de Fuca Eddy, a large, highly productive seasonal feature (MacFadyen et al. 2008). Puget Sound is linked to the California Current through migratory species that spend critical life-history stages or feeding periods in both systems, including federally managed commercial and protected resources such as Pacific salmon (*Oncorhynchus* spp.), marine mammals (e.g., Southern Resident killer whales [*Orcinus orca*]), and seabirds. Some Puget Sound groundfish stocks that have been petitioned for or granted federal protection may be genetically linked to California Current population segments (Gustafson et al. 2000, Drake et al. 2010).

Bathymetry and Geomorphology

Puget Sound is a deep fjord-like estuary that connects to the Pacific Ocean through the Strait of Juan de Fuca (Figure 2). It is composed of four sub-basins: Hood Canal, Whidbey Basin, South Sound, and the Main Basin, which can be subdivided into Admiralty Inlet and the Central Basin (Yang and Wang 2013). The average depth of greater Puget Sound is 62.5 m at mean low tide, while the main channel is 250–280 m at its deepest; the Central Basin and Elliott and Commencement Bays all have depths in excess of 100 m (Andrews and Harvey 2013).

The coastline of Puget Sound is complex, with a large proportion of linear shorelines, embayments of small-to-large size, and several large river deltas (Dethier 2010). Shoreline sediments are dominated by pebbles, sand, and mud; extensive eelgrass (*Zostera marina*) beds are found in sandier areas in the low intertidal zone (Dethier 2010). The organisms and processes on these shoreline environments provide key linkages between terrestrial and marine food webs (Toft et al. 2010). A large proportion of the shoreline of Puget Sound, 25–30%, is armored, with a higher percentage (~63%) in the south-central Sound than further north. On muddy shores, armoring is installed primarily as a landscaping, while in mixed-fine, sand, and cobble beaches, it is used to protect property from erosion or from the perceived risk of erosion (Dethier 2010).

Currents and physical oceanography

The exchange of seawater between Puget Sound and the Pacific Ocean occurs mainly through Admiralty Inlet, at the entrance of Puget Sound (Yang and Wang 2013). The Central Basin is isolated from other sub-basins by relatively shallow sills that can potentially restrict ocean circulation (Ruckelshaus and McClure 2007). In Puget Sound, general circulation patterns are primarily driven by tidal exchange, gravitational forces, and seasonal freshwater input, where outflow moves in the upper layers through Admiralty Inlet and marine waters inflow at depth (Stout 2001). In south Puget Sound, currents generally flow north along the west coast of Vashon Island, and south on the east side near Point Heyer. These oceanographic factors favor larval retention via mechanisms such as vertical migration, hydrographic retention, and habitat selection (Hauser et al. 2007a). River discharge and solar heating lead to stratification in the central basin during the summer, although it is well mixed in the winter; this seasonal pattern leads to phytoplankton and macroalgae peak production during the spring and summer, which influences the abundance of consumers and predators in the pelagic and benthic communities (Andrews and Harvey 2013).

Temperature varies between 8–9°C in the winter and spring and between 10–12°C in the summer and autumn (Andrews and Harvey 2013). The South Sound is moderately stratified compared to most other Puget Sound basins, because no major river systems flow into this basin (Gustafson et al. 2000).

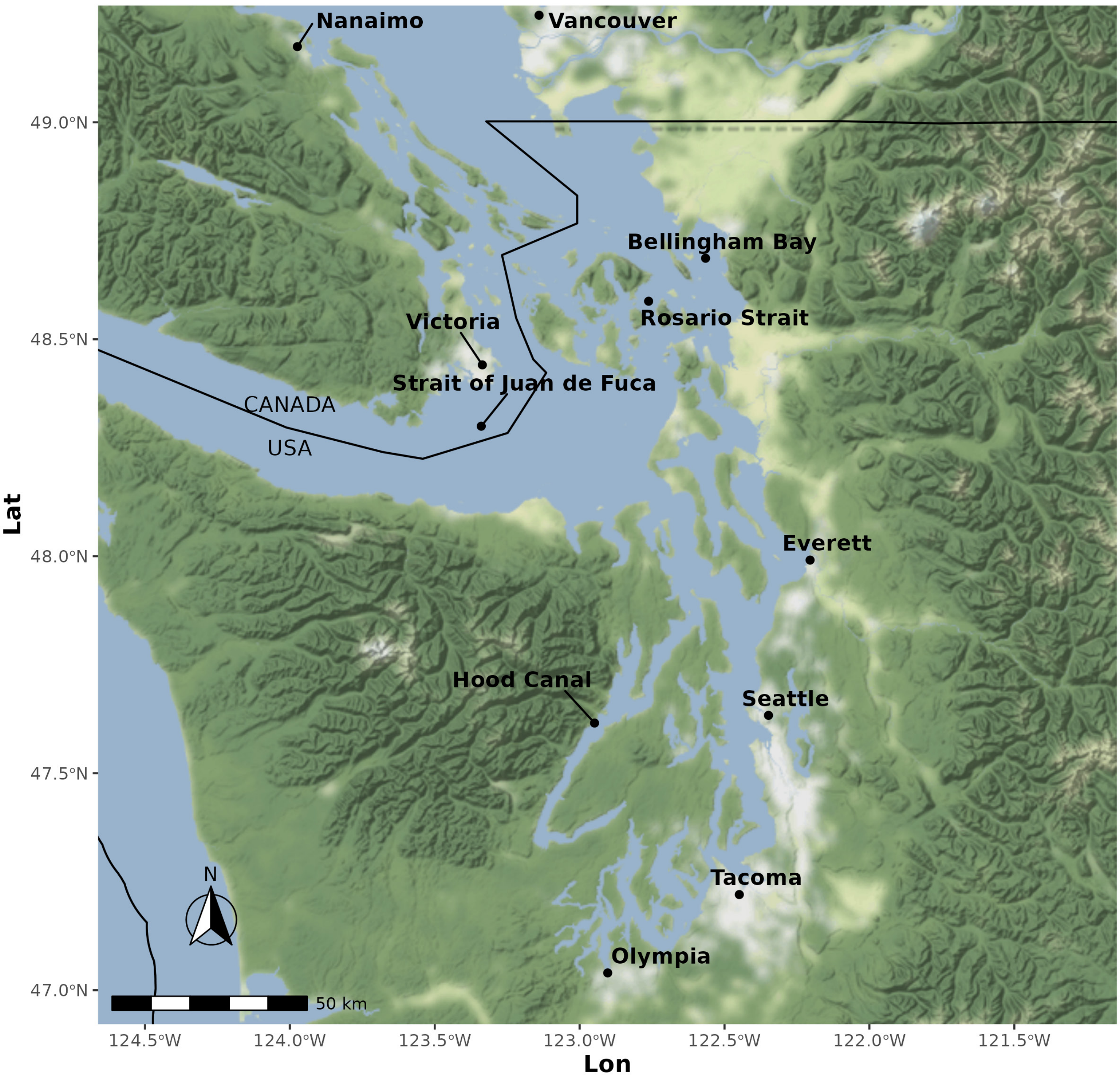


Figure 2. Map of Puget Sound.

Human impacts and conservation

Outfalls that discharge residential, commercial, and industrial wastewater, as well as stormwater runoff, are found across Puget Sound (Gaeckle 2014). Nutrients, including nitrogen and phosphorus, are known to be abundant in the Sound. Several toxic contaminants have been detected at elevated concentrations in water, sediment, and biota within the Puget Sound watershed (James et al. 2017), including trace metals such as copper, zinc, lead, and cadmium, and polycyclic aromatic hydrocarbons (PAHs) that have accumulated in urban sediments, eelgrass, mussels, and oysters found in nearshore areas adjacent to developed landscapes (Gaeckle 2014). Many of these contaminants are bioaccumulated across trophic levels.

There are multiple efforts underway to protect and restore Puget Sound, including reducing input of contaminants into streams, rivers and marine habitats (James et al. 2017); these include the Puget Sound Partnership watershed and salmon recovery plans, the Canadian Federal Contaminated Sites Action Plans at Rock Bay and Esquimault Harbour, and the Salish Sea Marine Survival Project, which this ecosystem modelling effort supports. However, as regional population growth in Puget Sound continues to alter the landscape, contaminant inputs from both point (e.g., oil and chemical spills, industrial and municipal wastewater discharges, etc.) and non-point sources (stormwater runoff, agriculture, atmospheric deposition, etc.) will continue to increase (James et al. 2017).

Fisheries

Fisheries have been a cultural feature in Puget Sound for hundreds of years. Salmon fisheries in particular sustained Native American populations. The tribal fishing rights of thirteen tribes and the U.S. government were reaffirmed through court cases in the 1970s (Spaulding 2008). The treaties ensure that tribes receive 50% of the fish stock in Puget Sound, and allow them to manage their own fisheries.

Puget Sound salmon fisheries have declined dramatically from historical levels; in a report to Congress, NOAA estimated that Puget Sound Chinook salmon levels in ~1900 were around 600,000–800,000 fish per season (Van Cleve 2011). Three species—Puget Sound Chinook salmon, Hood Canal summer-run chum salmon, and Puget Sound steelhead—are now listed under the Endangered Species Act (ESA). The Salmon Recovery Planning Act established a geographic framework for planning activities (Safford and Norman 2011). NOAA Fisheries' West Coast Region manages recovery planning and implementation through its Oregon and Washington Coastal Area Office. Washington State and the Native American tribes also share management of the salmon fishery.

Rockfish, from the genus *Sebastes*, dominate the U.S. Pacific Coast groundfish fishery. Overall rockfish abundance in Puget Sound has decreased 70% since the 1970s; this decline has been attributed to commercial and recreational overfishing and the low intrinsic productivity of rockfish species (Anderson et al. 2013). As a result, canary and yelloweye rockfish were listed as threatened, and bocaccio rockfish are listed as endangered, under the ESA. Currently, Puget Sound yelloweye and bocaccio rockfish are still rebuilding, and are managed under a recovery plan (NMFS 2017). Following the rockfish ESA listing, targeted harvest and retention of rockfish in Puget Sound were prohibited, and fishing for bottomfish was limited to 120 ft or shallower to minimize mortality of incidentally caught rockfish, which are found at similar habitat and depths as lingcod and halibut (Williams et al. 2010b, Beaudreau and Whitney 2016). Recreational anglers have been the dominant fishery sector targeting rockfish and other species in Puget Sound since the 1970s (Williams et al. 2010b).

Atlantis Ecosystem Model

Summary

Atlantis is a deterministic numerical biogeochemical and biophysical modeling framework that simulates the structure and function of marine ecosystems (Figure 3). Further information can be found in the Atlantis User's Guide (Audzijonyte et al. 2017), recently published papers reporting Atlantis applications (Smith et al. 2015, Nyamweya et al. 2016, Olsen et al. 2018), as well as in the Atlantis Wiki.[2] Atlantis represents ecosystems spatially in three dimensions using an irregular polygon structure that saves computation time. The polygons are generally designed to capture important climatic, biophysical, or jurisdictional features. The biotic components of the system are represented as functional groups, i.e., aggregated groups of species according to life history, feeding, or niche similarities. Important species (e.g., managed species, species of conservation interest, or functionally important species) can be included by themselves in a functional group. Vertebrate consumers are age-structured; body weight and numbers are explicitly tracked for each age class. Invertebrates are represented as homogenous biomass pools that are either volumetric (occupying three dimensions) or epifaunal (occupying two dimensions). Subroutines represent nutrient (nitrogen) flows throughout groups, consumption, production, waste production, migration, recruitment, habitat dependency, and mortality, including predation, senescence, and fishery removals. Simulation dynamics follow a 12-hr time step.

The Atlantis ecosystem modeling framework is based on Bay Model 2 (Fulton 2001, Fulton et al. 2004a), which was itself inspired by two other ecosystem models and incorporates some of their successful elements: the Integrated Generic Bay Ecosystem Model (Fulton et al. 2004b) and the Port Phillip Bay Integrated Model (Murray and Parslow 1999). Socioeconomic submodels in Atlantis are described by Fulton et al. (2007). Link et al. (2010) also provide an excellent review of model structure. Therefore, in the following section we provide a summary of critical formulae and refer interested readers to the aforementioned documentation. Reviews of Atlantis and similar marine ecosystem modeling approaches are provided by Plagányi (2007), Cury et al. (2008), and Jørgensen (2008). Discussion on the effects of ecosystem model structure and variable aggregation is available in Fulton et al. (2003), Pinnegar et al. (2005), and Metcalf et al. (2008).

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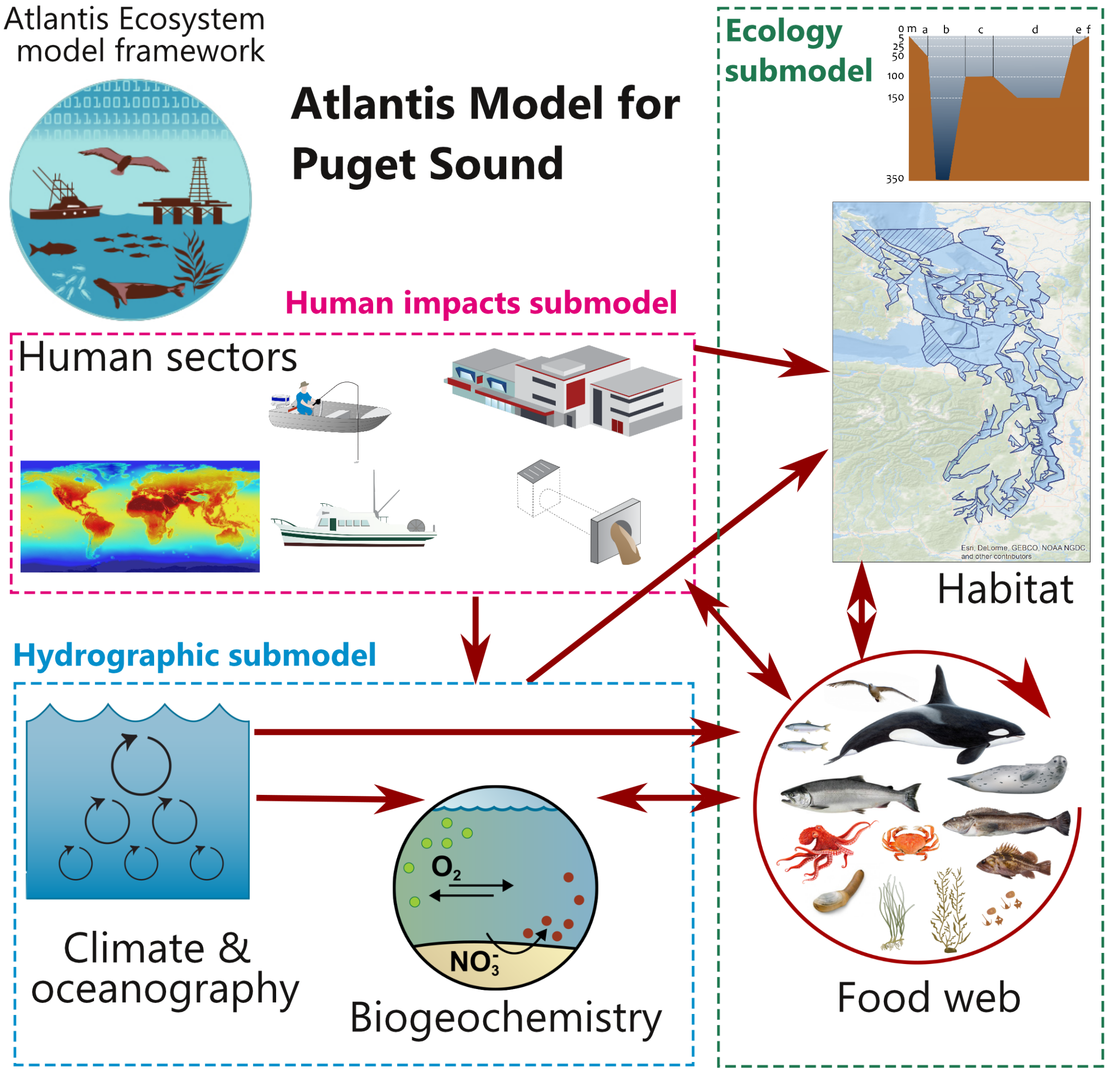
[2] https://research.csiro.au/atlantis/home/links/



Icons: IAN/ UMCES: T. Saxby, D. Kleine, J. Thomas; M. Weijerman; WADNR; Monterrey Bay Aquarium; NOAA

Figure 3. Overview of the structure of the Atlantis Model for Puget Sound.

In 2011, Atlantis underwent a substantial rewrite of the base code that now allows users more control over the functional group structure. Whereas previous models were constrained to operate within a hard-coded group structure (which put strict limits on the number and type of functional groups), Atlantis Version 2 (V2) allows any number of groups and is only limited by computer performance. Similarly, age structure for vertebrate groups was previously limited to ten age classes, but can now accommodate a flexible number of age classes.

Model extent

The Atlantis Model for Puget Sound (AMPS) has 89 polygons that extend over 9,652 km^2; 87 polygons are dynamic boxes flanked by two non-dynamic boundary boxes in the north and west edges (Figure 4, Table 1). These boundary boxes allow for the exchange of water and nutrients to and from the dynamic model domain, but other processes are not explicitly modeled for these areas. There are 60 water column polygons and 29 islands in the model. Water column polygons are further divided into depth layers, from one layer for nearshore boxes to six for offshore boxes (Figure 5). Each polygon also contains one sediment layer.

The model domain boundaries on the landward side lie at the mean high-tide line and below tributary river deltas. Using the high-tide line allowed us to include large bays, such as Padilla Bay, that have major eelgrass beds but that drain to a significant extent during low tides. Keeping the domain below deltas was necessary for simplifying the model food web by excluding the diverse brackish-water fauna in the tidally influenced reaches of tributaries. The domain boundaries on the seaward side are described by the two non-dynamic boundary boxes, one near the eastern entrance to the Strait of Juan de Fuca and the other in the southern Strait of Georgia (hatched boxes in Figure 4). The boundary box at the Strait of Juan de Fuca approximates the location of the relatively shallow Victoria Sill, a major bathymetric feature that heavily influences exchange of water between the Salish Sea and the northeastern Pacific Ocean. Placing a boundary box here also helped simplify the model food web by excluding species more associated with the open ocean to the west. The boundary box in the southern Strait of Georgia was placed somewhat arbitrarily, but its primary purpose is to simplify the model by placing the highly dynamic region of the mouth of the Fraser River outside of the model domain.

Individual polygons within the AMPS domain were defined based on a combination of geographic features, bathymetry, circulation patterns, ecological characteristics, and, to some extent, management boundaries. The number of polygons in any Atlantis model is positively correlated with Atlantis model runtime, however, so we had to compromise on the degree of detail in polygon design. Major sub-basins, bays, and inlets were distinguished by one or more polygons, with edges corresponding to important physical features such as sills (which are at the entrance to many sub-basins and influence circulation and water residence time), bathymetric contours, or islands. Other divisions were added to correspond roughly to coarse-scale spatiotemporal circulation features (N. Banas, University of Strathclyde, personal communication) and statistical reporting areas for key state-managed fisheries (e.g., WDFW 2018,[3] page 12). Polygons were also added to better represent the physical habitat and ecological community structure and dynamics of complex areas such as the San Juan Islands archipelago in the northern portion of Puget Sound.

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[3] https://wdfw.wa.gov/sites/default/files/publications/02002/wdfw02002.pdf

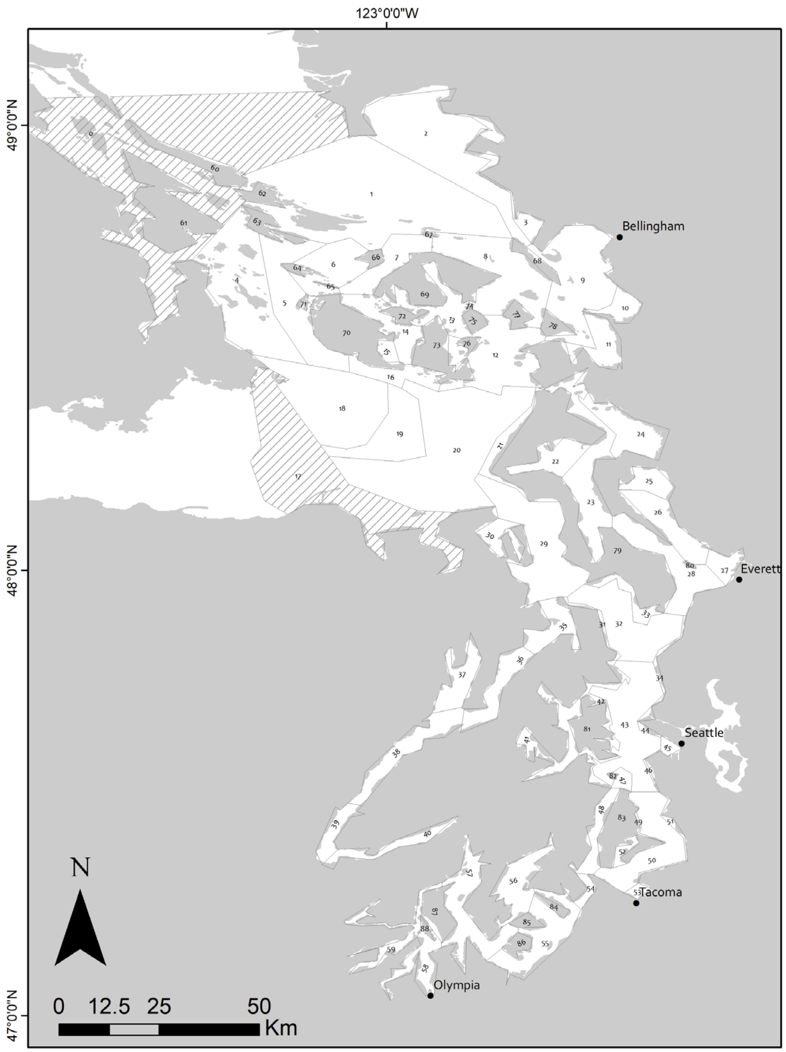

Figure 4. Spatial extent of the Atlantis Model for Puget Sound.

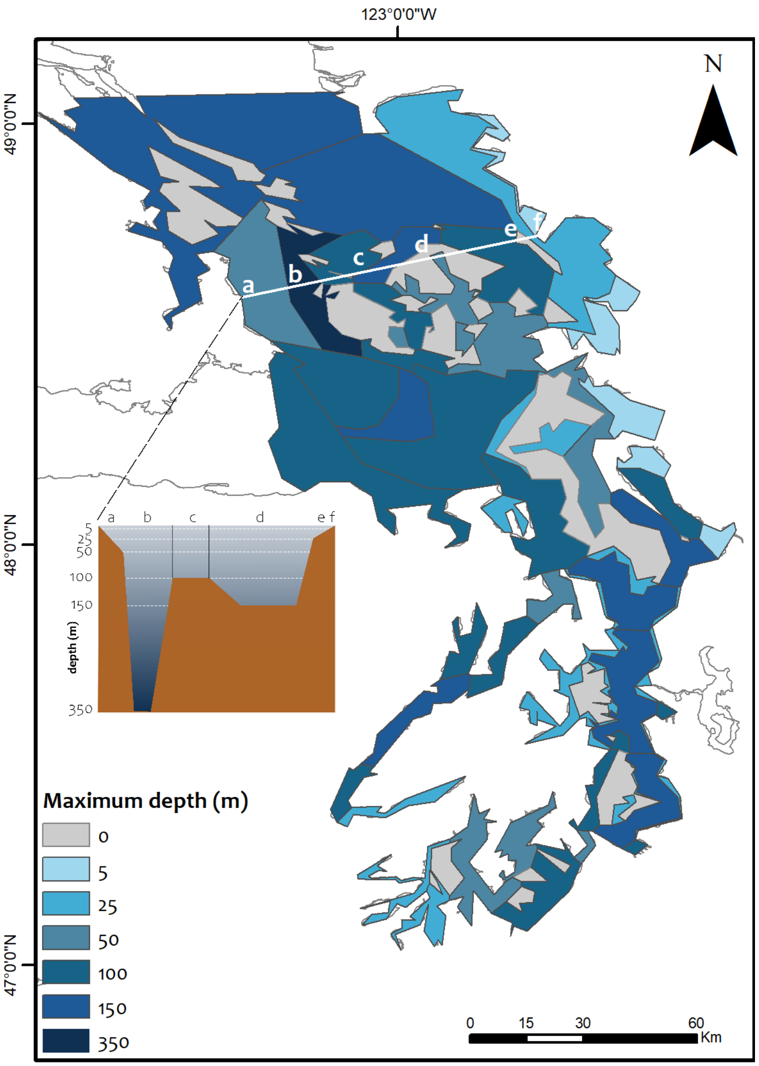

Figure 5. Vertical structure of the Atlantis Model for Puget Sound. Insert shows the cross section.

Seafloor Habitats

Physical habitats

To inform geological habitat type in AMPS, we used a benthic habitat layer produced by The Nature Conservancy (TNC) as part of the Seafloor Mapping Project, developed in collaboration with Tombolo Mapping Lab, the SeaDoc Society, the United States Geological Survey (USGS), and NOAA (Figure 6). This project compiled existing seafloor substrate and sediment data from existing sources (Hewitt and Mosher 2001, Endris et al. 2011, Hemery et al. 2016) and classified the seafloor into categories following the Coastal and Marine Ecological Classification Standard, Version 4 (CMECS; Madden et al. 2009).

Within the AMPS model domain, the substrate is classified within six broad categories: 1) fine unconsolidated substrate: mud and fine sand; 2) rock substrate: rocky shores and bottom; 3) coarse unconsolidated substrate: gravel from small granules to boulders; 4) anthropogenic substrate: artificial reefs; 5) shell substrate: shell reef and sand; and 6) unconsolidated mineral substrate: mix of loose mineral substrate, from clay to boulders (Madden et al. 2009). We associated each substrate type into one of three Atlantis seafloor habitat types: 1) reef, which includes rocky and cobble substrates; 2) soft, composed of sand and mud; and 3) flat, defined by shell and gravel. We overlaid the AMPS polygons over the substrate layer to calculate the proportion of seafloor types that is attributed to each polygon (Figure 7). Coverage of physical habitats sums to one in the model. Atlantis includes two other seafloor types, eddy and canyon, which were not used.

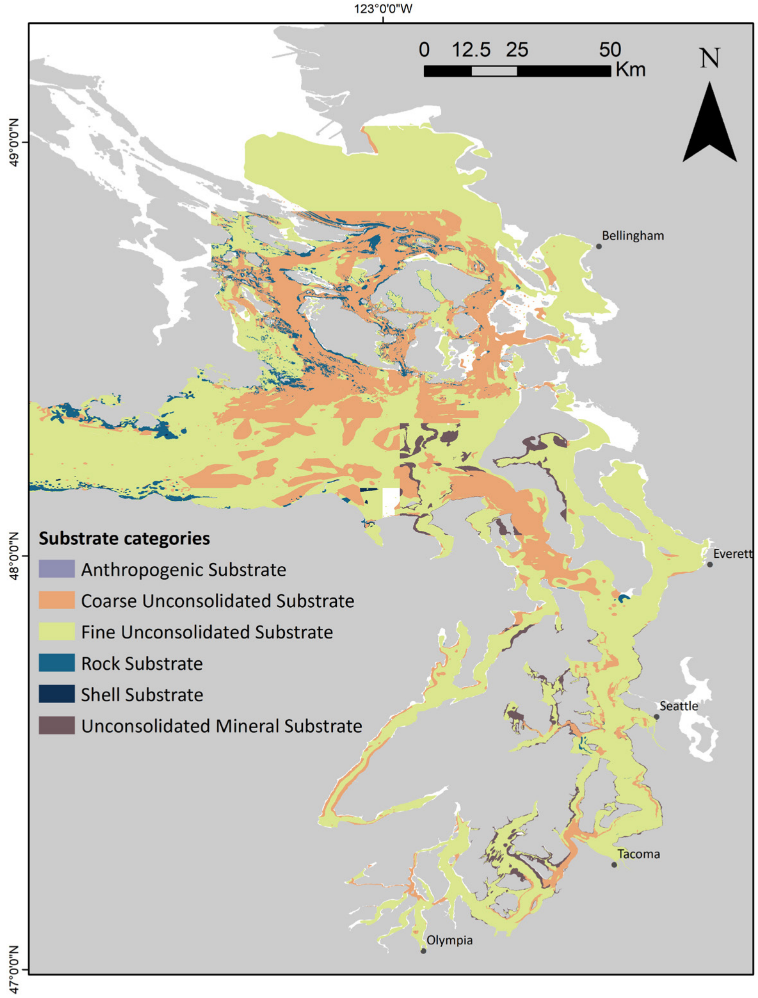

Figure 6. Spatial distribution of substrate types in Puget Sound, produced by The Nature Conservancy (TNC) as part of the Seafloor Mapping Project. Categories follow the Coastal and Marine Ecological Classification Standard, Version 4 (CMECS).

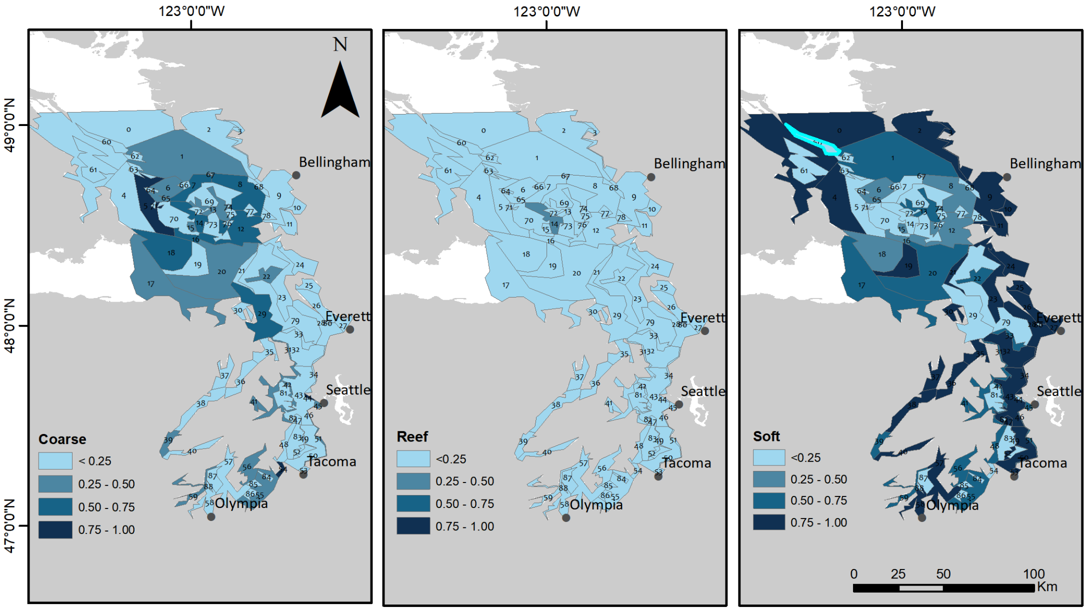

Figure 7. Seafloor type proportion in the AMPS, derived from substrate types in Figure 6. Reef includes rocky and cobble substrates; soft, composed of sand and mud; and coarse, defined by shell and gravel.

Biogenic habitats

Biogenic habitat types in Puget Sound were drawn from data produced by the Nearshore Habitat Program, Washington Department of Natural Resources, Aquatic Resources Division. In Puget Sound, five categories of aquatic vegetation are present: eelgrass, floating kelp, non-floating kelp, sargassum beds, and marsh. Eelgrass occurs along 37% of Puget Sound shorelines, but it is not found in extreme reaches; it grows mostly in sandy and muddy substrates (Berry et al. 2001). We used the Puget Sound Eelgrass Monitoring Main Database 2000–15, which was collected using video surveys as part of a long-term monitoring program tracking eelgrass in greater Puget Sound (Christiaen et al. 2017); the data includes polygons of eelgrass coverage.

Floating kelp (*Macrocystis integrifolia* and *Nereocystis leutkana*) and non-floating kelp (including *Laminaria* spp. and *Egregia menziesii*, among others) show distinct distribution in Puget Sound (Figure 8). Floating kelp is found along 12% of Puget Sound's coast (Van Wagenen and Bowlby 1996). We used data for floating kelp from the Washington State Floating Kelp Inventory of the Strait of Juan de Fuca and Outer Coast. These data report on annual surveys between 1989 and 2016 (except 1993) using photo interpretation of low-tide aerial photography in the late summer, the season of maximum extent; we only used floating kelp areas reported for 2010–16. Polygons represent bed extent or planimeter, which includes the kelp canopy floating on the surface and small gaps between plants, using a 25-m threshold for delineating discrete beds. Non-floating kelp is also common in relatively high-energy rocky shorelines, but it is found throughout Puget Sound; the lowest percentages are found in shorelines with extensive low-angle embayments (Berry et al. 2001). We used the non-floating kelp extent from the Washington State ShoreZone

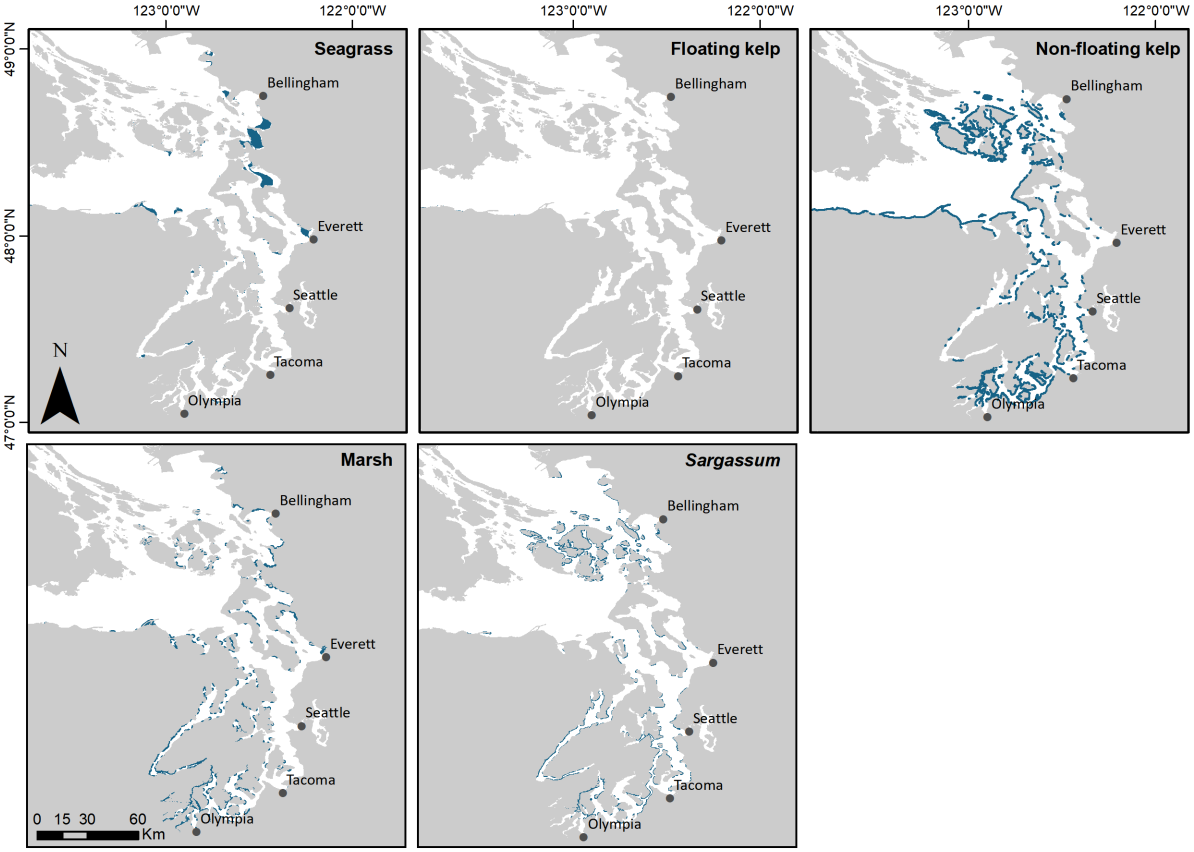

Figure 8. Extent of different categories of biogenic habitats in Puget Sound.

Inventory, which contains data collected between 1994 and 2000 to describe physical and biological characteristics of intertidal and shallow subtidal areas along Washington State's coastal shorelines. This dataset classifies the presence of non-floating kelp along the coastline as continuous, patchy, or absent. We converted the line segments into polygons, set an 18-m buffer around the polygon equivalent to the maximum reported depth of *Laminaria* spp. in Puget Sound (Neushul 1967), and finally overlayed the 18-m isobath over the kelp area using a 30-arc second bathymetry for Puget Sound (Becker et al. 2009).

Marsh and sargassum extent were drawn from the Washington State ShoreZone Inventory, which classifies their presence along the coastline as continuous, patchy, or absent. Marsh includes a variety of emergent vegetation, low marsh, sedge, salt marsh, spartina, and mixed marsh. Sargassum refers to the cover of the non-indigenous brown algae *Sargassum muticum*. For both of these layers, we converted the line segments into polygons, set a buffer around the polygon equivalent to 1 m for marsh and 2 m for *S. muticum* (the reported depth in British Columbia; White 2010), and overlaid the corresponding isobaths over the distribution area using a 30-arc second bathymetry for Puget Sound (Becker et al. 2009).

Habitat associations

Habitat associations for fish functional groups were determined based on observations by Pacunski (Pacunski et al. 2013) using a remotely operated vehicle (ROV) in the San Juan Islands. Distributions for adults and juveniles were recorded separately whenever data existed at that level of precision. Species-level data were then compiled to the level of the functional group.

Invertebrate habitat associations were determined from the California Department of Fish and Game Website.[4] Habitat use was specified on a species-by-species basis and then compiled at the functional group level. For species or groups (invertebrate or vertebrate) that were not included in either of these data sources, we assumed they used all habitat types and were not dependent on benthic habitat.

Projection period

We initialized AMPS to represent 1 January 2011. This start date was selected because it coincides with ambitious sampling efforts (D. Beauchamp, UW/USGS and C. Greene, NWFSC, among others, personal communications), as well as longer-term monitoring programs (e.g., Puget Sound Assessment and Monitoring Program [PSAMP] benthos monitoring, RV *Ricker* pelagic surveys), and is within three years of groundfish monitoring data (see Analyses informing spatial abundance and density). Additionally, this allows a five-year projection period (2012–16) to assess model skill in free-running simulations. Note that oceanographic projections to force Atlantis were not available for 2011; as described in Oceanographic Forcing, oceanography was necessarily taken from 2005 and 2006. Historical simulations during model calibration began on 1 January 1971, to coincide with the data available on salmon hatchery releases (data provided by G. Marston, WDFW, personal communication; data were extracted from the Regional Mark Information System [RMIS] on 20 November 2016).

Nutrient loading

Extensive information on nutrient loading into Puget Sound has been collected and analyzed by the Washington State Department of Ecology (WSDOE)and the Pacific Northwest National Laboratories (Mohamedali et al. 2011, Roberts et al. 2014). These efforts have largely been undertaken to understand dissolved oxygen conditions in Puget Sound in the recent past and under future scenarios of climate and human development. Oxygen concentrations in the Sound are influenced by both ocean-derived nutrients and inputs via local nutrient loading. These local sources of loading include point sources, such as wastewater treatment plants, and non-point sources (in our model these are assigned to river or stream mouths). Mohamedali et al. (2011) and Roberts et al. (2014) discuss detailed data collection, modeling, and scenario projections that aim to quantify nutrient loads that contribute to algal blooms and subsequent decomposition and respiration which depletes oxygen concentrations, particularly on the bottom.

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[4] https://marinespecies.wildlife.ca.gov/

T. Mohamedali (WSDOE, personal communication) provided two sets of model estimates of nutrient loads from point and non-point sources to Puget Sound and the Salish Sea, derived from the Puget Sound Dissolved Oxygen Model (PSDOM). The first set of estimates are described in Mohamedali et al. (2011) and Roberts et al. (2014). We assigned these point and non-point sources to Atlantis polygons (Figure 9). Both sets of estimates are used as inputs to the Salish Sea Model (SSM), which is a 3D hydrodynamic and biogeochemical model developed by Pacific Northwest National Laboratory in collaboration with WSDOE. Non-point source nutrient loads represent estimates of nutrient loading at the mouths of rivers and streams, which are a pathway for both point and non-point watershed sources upstream.

Note that Canadian nutrient sources from the Fraser River and Vancouver wastewater treatment plants fall just outside our model domain, but are critical: the Fraser loads of dissolved inorganic nitrogen (DIN) are the largest for the Salish Sea and are five times larger than for any U.S. river, and three of the top five wastewater treatment plants in terms of DIN are in the Vancouver area (Mohamedali et al. 2011). We therefore added Fraser River and Canadian loadings as nutrient inputs to Atlantis Box 1 (South Georgia Strait). Khangaonkar et al. (2017) suggest that 83% of Fraser River flows pass south through our model domain and ultimately out through the Strait of Juan de Fuca. We therefore scale these additions of nutrients to Box 1 by 0.83.

The first set of nutrient projections from PSDOM was for 1999–2008, provided in terms of flows and concentrations of nutrients. These daily concentrations were based on linear regression predictions from field data (which necessarily included gaps in time and space). We assigned daily ammonium (NH_4) loads from PSDOM to the Atlantis ammonia "NH_3" inputs—nitrate + nitrite ($NO_3 + NO_2$) was assigned to Atlantis "NO_3" inputs—and PSDOM loads of labile particulate organic nitrogen (PON) and labile dissolved organic nitrogen (DON) were assigned to

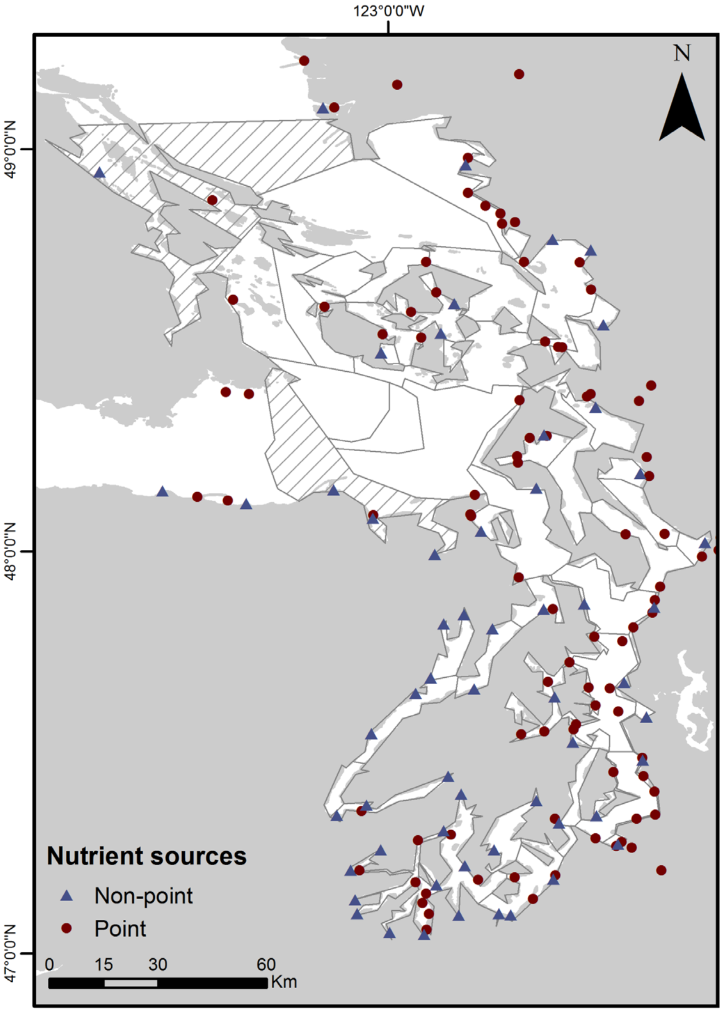

Figure 9. Map of point (e.g., wastewater treatment plants) and non-point (river mouths) nutrient sources where nutrient loading has been estimated by WSDOE. Hatched areas of the Atlantis domain are non-dynamic boundary boxes which cannot receive nutrient inputs.

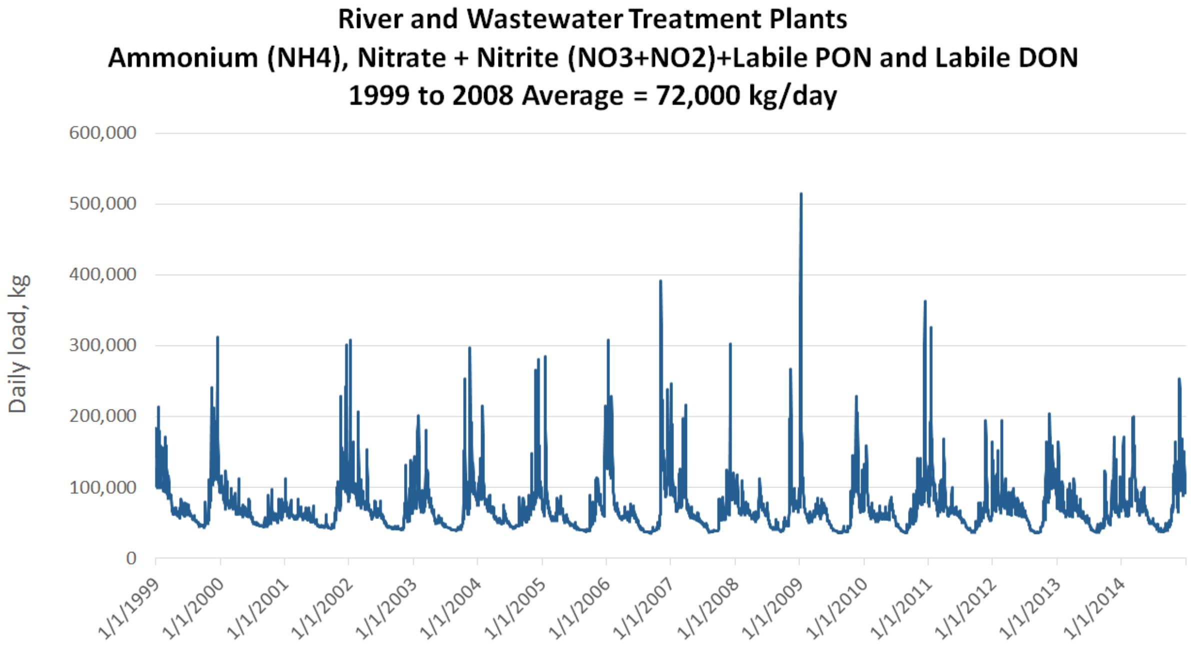

Figure 10. Time series of total daily nutrient loading into Puget Sound and the Salish Sea, 1999–2014. Point and non-point source estimates of nutrient loads were developed using a multiple regression analysis as described in Mohamedali et al. (2011), Roberts et al. (2014), and Ahmed et al. (2019).

the Atlantis “Labile Detritus” group. Units of concentration in PSDOM data were assumed to be in mg/L. No conversions were made from mg of PON or DON to Atlantis Labile Detritus, though, in actuality, Atlantis Labile Detritus should be in units of mg N only.

The second set of nutrient loading estimates from point and non-point sources was for the years 2009–14, and was developed under the assumption that previous statistical relationships held during this latter period. The more recent dataset included some updates to flow and water quality which are described in Ahmed et al. (2019). These data included three additional point sources. Similar to 1999–2008, nutrient estimates were assigned to state variables in Atlantis (NH_3, NO_3, and Labile Detritus). Total daily loads from all point and non-point sources for the full period 1999–2014 are presented in Figure 10.

Silica (Si) loadings were estimated based on reported Si loadings for the Fraser River from Riche et al. (2014), as 40–60 µmol/L. We obtained daily discharge data for the Fraser River at Port Mann Pumping Station in m^3/s from the Government of Canada’s Hydrometric Data Search,[5] scaled based on Khangaonkar et al.’s (2017) suggestion that 83% of Fraser River flows through our model domain.

We note that a third set of future loadings is available for years 2020, 2040, and 2070, taken from Roberts et al. (2014). These projections involve scenarios of future climate and population growth, which are expected to drive changes in both point and non-point sources. The loadings for each of these single years actually represent averages for projection periods of 2015–24, 2035–44, and 2065–69, respectively. We do not apply these loadings presently in Atlantis, but doing so is a clear next step.

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[5] https://wateroffice.ec.gc.ca/report/historical_e.html?stn=08MH126

Nutrient initial conditions (NH_4, NO_3, dissolved oxygen, and Si)

Marine water quality sampling was collected by WSDOE's Marine Monitoring Unit from routine water quality monitoring and post-processing in the laboratory, and was provided by T. Mohamedali. Sample years 2006 and 2008 were available, and for Atlantis initial conditions intended to represent 1 January 2011, we focused on winter months in 2008 (January, February, November, and December; Figure 11). Notably, concentrations of dissolved oxygen, silica, and nitrate + nitrite concentrations are uniform across space, especially when considered at the spatial scale of Atlantis polygons. This uniformity, likely due to winter mixing, has been noted by Khangaonkar and colleagues in their nutrient–phytoplankton–zooplankton modeling (Khangaonkar et al. 2012b); those authors applied uniform initial conditions for nutrients to all regions except Hood Canal (see their Table 2.5). Since these are initial conditions that will rapidly evolve during the projection period of the model, we adopted Khangaonkar's uniform values (vertically and horizontally) of 0.43 mg/L for Atlantis NO_3, 8 mg/L for O_2 in most of Puget Sound, 9 mg/L O_2 for Hood Canal (Atlantis polygons 35–40, and all but bottom layer), and 4 mg/L O_2 for the bottom layer of Hood Canal. We also adopted a spatially uniform 3.6 mg/L for Atlantis Si, based on the average across polygons sampled by the water-quality monitoring (Figure 11); no comparable value is documented in Khangaonkar et al. (2012). We also adopted a spatially uniform value of 0.013 mg/L for Atlantis NH_3, based on the average across polygons sampled by the water-quality monitoring in November, December, January, and

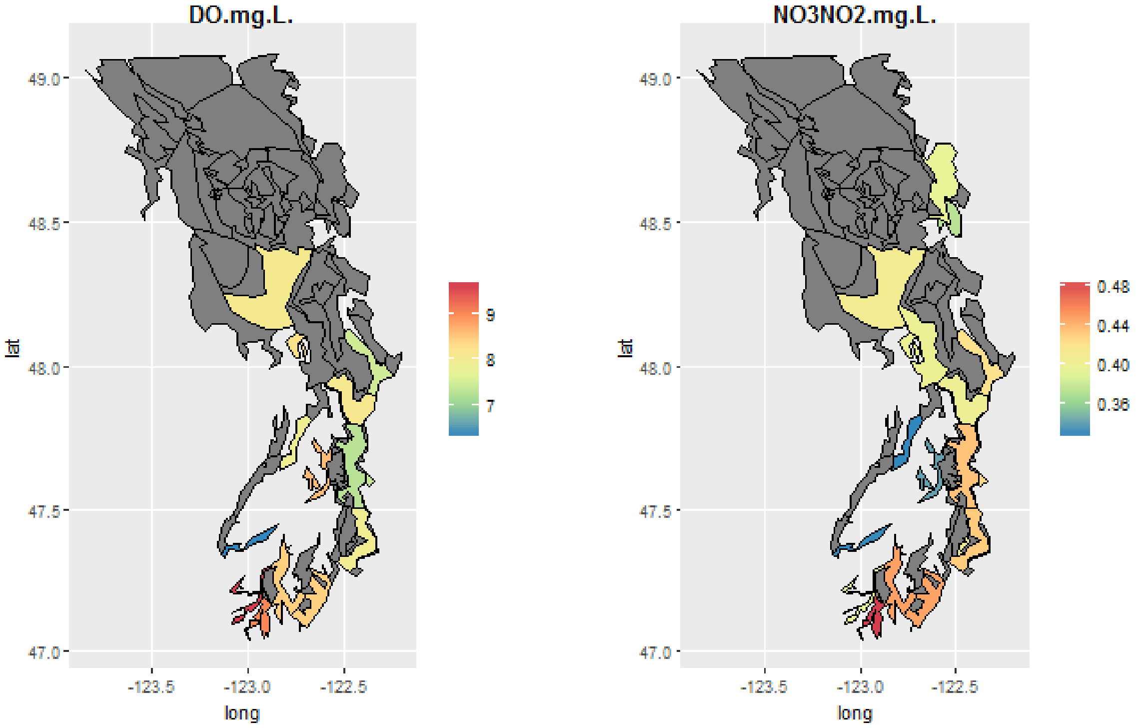

Figure 11. Winter nutrient and dissolved oxygen concentrations, averaged for January, February, November, and December 2008, and allocated to Atlantis polygons where water-quality sampling was available (data courtesy of WSDOE's Marine Monitoring Unit). This page: dissolved oxygen (DO) and nitrate + nitrite ($NO_3 + NO_2$). Next page: ammonia (NH_4) and silica (Si).

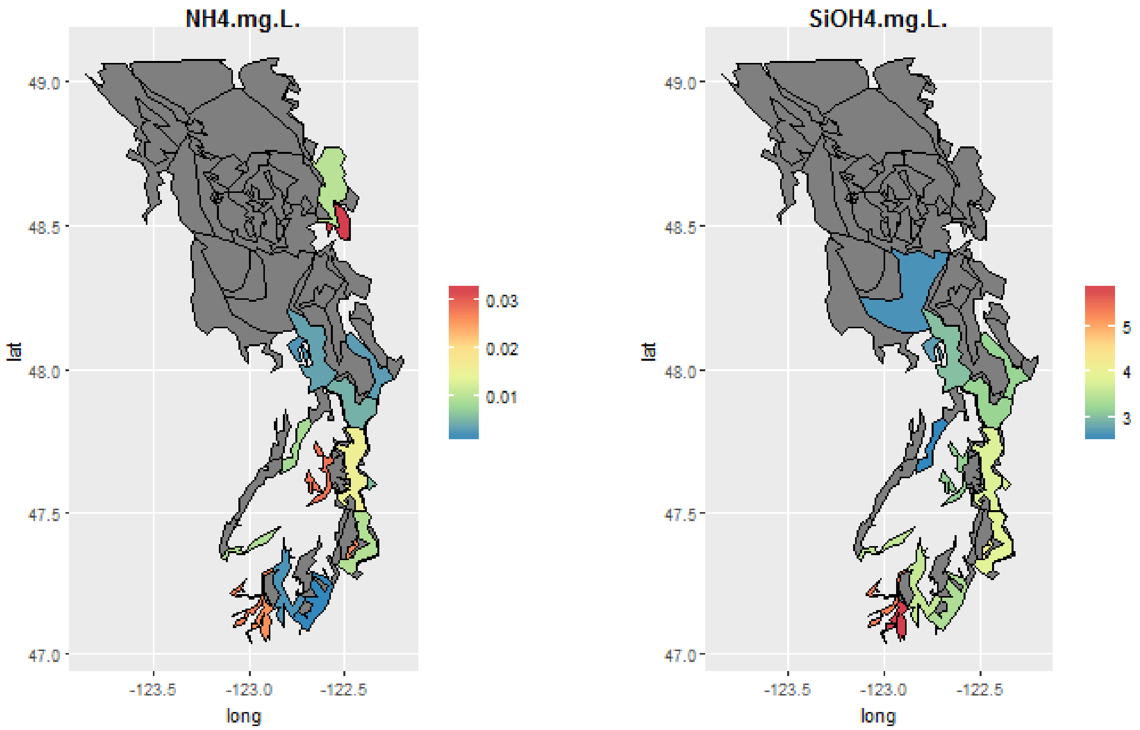

Figure 11 (continued). Winter nutrient and dissolved oxygen concentrations, averaged for January, February, November, and December 2008, and allocated to Atlantis polygons where water-quality sampling was available (data courtesy of WSDOE's Marine Monitoring Unit). This page: ammonia (NH$_4$) and silica (Si). Previous page: dissolved oxygen (DO) and nitrate + nitrite (NO$_3$ + NO$_2$).

February 2008 (Figure 11). This is higher than the initial conditions for NH$_4$ in the nutrient–phytoplankton–zooplankton modeling (Khangaonkar et al. 2012b), which were 0.002. Our higher values appear to be more consistent with winter monitoring values for 1997–2010 (e.g., Figures 22 and 23 in Moore et al. [2016]), and we expect that model dynamics and rate parameters drive results much more than initial conditions.

Oceanographic Forcing

The spatial and temporal fields of circulation, temperature, and salinity used in the food web model were created using output from a high-resolution realistic numerical simulation of the Salish Sea. The model numerical framework is the Regional Ocean Modeling System (ROMS; Haidvogel et al. 2000, Shchepetkin and McWilliams 2005), a community model used in a wide variety of coastal and estuarine applications. The model solves the hydrostatic, incompressible, Reynolds-averaged momentum and tracer conservation equations with a terrain-following vertical coordinate and a free surface.

For this application, the model bathymetry was configured to produce realistic hindcast simulations of the Salish Sea and adjoining coastal waters of the northeastern Pacific Ocean (Figure 1). The horizontal domain is a spherical, stretched Cartesian grid extending from long –127°W to –122°W and from lat 45°N to 50°N. The grid resolution is as fine as 280 m in Puget Sound, and stretches to 3.1 km at the boundaries. There are 20 vertical layers. The model was forced with realistic flow from 16 rivers, as well as tides, atmospheric forcing by wind stress and heat flux, and open ocean boundary conditions. The details of the model setup, forcing, and validation against observations are given in Sutherland et al. (2011). The model was run for the years 2005 and 2006, with the initial fields in Puget Sound for each year derived from conductivity–temperature–depth (CTD) cast observations. These years were chosen because of optimal overlap with observations on the shelf. The model configuration is referred to as MoSSea (Modeling the Salish Sea).

Results were stored as hourly snapshots in Network Common Data Form (NetCDF) files, including 3D fields of temperature, salinity, and the three components of velocity. To create the fields used by AMPS, we had to interpolate from the regular ROMS grid to complex Atlantis polygons. The first step in the processing was to create averaged fields at 12-hr intervals. These were created using the Godin 24-24-25 filter (Emery and Thomson 1998), which averages out the strong tidal variation of currents, leaving the lower-frequency residual currents that are the estuarine exchange flow (MacCready and Geyer 2010). Next, each Atlantis polygon was interpolated to the nearest velocity grid points on the MoSSea grid, taking care that the faces of adjoining polygons were represented by exactly the same model grid points. Model temperature and salinity fields within a polygon were then divided into the depth classes of the Atlantis model, and averaged using a volume-weighted average—because each point in the MoSSea grid represents a different volume of water. The calculation of volume transports through the polygon faces in each depth level was done by similar averaging; however, small adjustments to the transports were required to

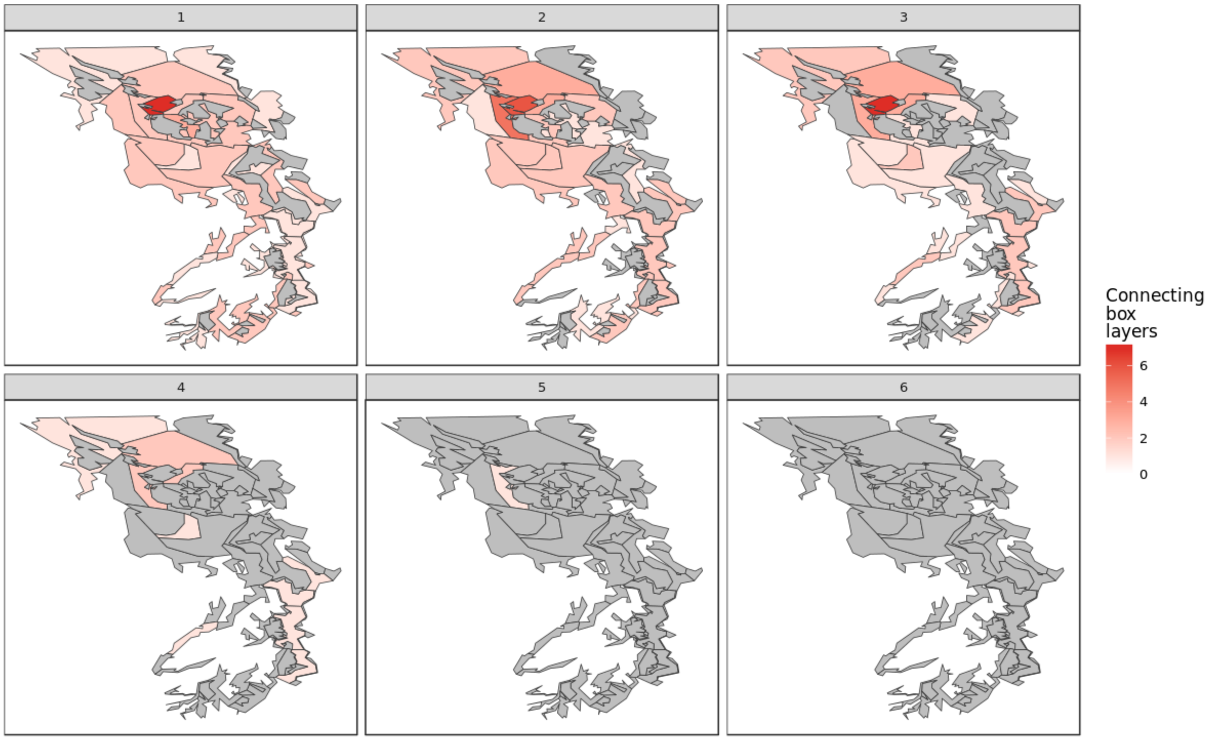

Figure 12. Water exchanges between AMPS polygons, derived from MoSSea model simulations. Each panel represents a vertical depth layer in the model. Red gradation indicates the number of connecting box layers. Polygons in gray do not contain the specified layer.

ensure volume conservation. This was needed because the tidally averaged currents were formed from a weighted average of 71 hourly snapshots, whereas the model calculations are done at a time step of 30 seconds or less, leading to small errors in reconstructed volume flux. A small correction was added to net volume flux into each polygon so the net convergence in a polygon would be zero (an approximation of the very small net convergence due to tidally averaged sea surface change). Then, through an iterative process, the flux through each of the faces was adjusted to be consistent with shared faces of adjoining polygons. Finally, the vertical velocity through layers was calculated to be consistent with the convergence of transport through polygon faces below it. The resulting polygon values were then written to text files and converted to NetCDF input files to drive volume flux, temperature, and salinity in the Atlantis simulations. Forcing files for the years 2005 and 2006 were recycled throughout historical and future model simulations.

Solar Radiation

Solar radiation is one of the drivers of primary production in the model. Solar radiation data were available for SeaTac Airport from the National Solar Radiation Database[6] for "typical meteorological year" (TMY3) data (averaged over 1991–2005). We apply global horizontal irradiance, averaged over each calendar day, for each model year.

Biological Model

The Atlantis Model for Puget Sound uses 73 functional groups to model biological processes (Table 2), including salmon (21 groups), demersal fish (9), pelagic fish (1), forage fish (3), elasmobranchs (4), seabirds (3), mammals (7), zooplankton (4), primary producers (4), invertebrates (12), bacteria (2), and detritus groups (3). Primary producers and invertebrates are modeled as biomass pools (mg N/m^3), while vertebrate groups are divided into age classes each tracked by abundance and weight-at-age. Vertebrates with lifespans less than ten years are modeled as having multiple age classes of one year duration and, if maximum age class was greater than ten, into age classes of equal duration. Weights are measured through both structural and reserve nitrogen (measured in mg N), with structural nitrogen (N_s) representing bones and other hard parts and reserve nitrogen (N_r) representing muscle, fat, reproductive parts, and other soft tissue. The separation of age classes for vertebrates allows for ontogenetic shifts in the parameterization.

We implement a modified version of the Holling Type II functional response designed by Fulton et al. (2003) to model predation (P) by consumers. We used weight estimates from von Bertalanffy curves to obtain maximum consumption for an average individual, and we generalized the constants across functional groups, setting CA equal to 0.3 and CB equal to 0.7; CA and CB are analogous to the a and b of the standard weight-at-length function. We considered growth efficiency to be 10% (Pauly and Christensen 1995). We calculated clearance, which is a measure of feeding efficiency when prey is scarce, as growth rate divided

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[6] https://nsrdb.nrel.gov/data-sets/archives

by ten, noting that this is expected to change during calibration, but that clearance should be expected to be less than growth (Table 3; Audzijonyte et al. 2017). AMPS contains four primary producer groups: seagrass, macroalgae, and large and small phytoplankton. Estimates of large and small phytoplankton abundance come from remotely sensed total chlorophyll. Growth is driven by Michaelis–Menten dynamics and varies with nutrient, light, and space availability. Biomass is lost to predation, lysis, and both linear and quadratic mortality.

AMPS includes 11 invertebrate groups (Table 2), each modeled as biomass pools (mg N/m^3). Densities for invertebrates were derived from WSDOE surveys using benthic grab samples (see Analyses informing spatial abundance and density). Changes in invertebrate biomass are affected by growth, predation, and multiple sources of mortality. In the Atlantis code base, oxygen and space limitation apply only to benthic invertebrates living on or in the sediment layer; however, we do not apply oxygen limitation in this version of AMPS. Space limitation is driven by Michaelis–Menten dynamics. As the density of an invertebrate group increases beyond a lower threshold, the growth of that group is increasingly inhibited until it reaches a maximum allowed density. Lower thresholds, maximum densities, and half saturation constants for invertebrate space limitation were also adapted from Fulton et al. (2004).

AMPS represents vertebrate biomass in 48 functional groups: salmon (21 groups), demersal fish (9), pelagic fish (1), forage fish (3), elasmobranchs (4), seabirds (3), and mammals (7); see Table 2. Each vertebrate group is divided into annual age classes, or equal-width multi-year age classes if maximum lifespan was greater than ten years. For fish groups, we estimated initial abundance at age from estimates of natural mortality and total biomass (Table 4 and Table 2). We applied von Bertalanffy age–length relationships and converted length to weight to generate initial weights. Abundance-at-age is a function of individual movement, predation, fishing mortality, and both linear and quadratic mortality terms. Vertebrate growth follows the same form as for invertebrates, but includes an extra term to allocate growth between structural and reserve nitrogen pools. Spawning and recruitment also affect vertebrate fluxes, and these processes in AMPS are described in Spawning and Recruitment for Fish and Other Vertebrates.

Diet composition

We carried out a thorough review of existing literature to identify studies that have analyzed diet composition of species within Puget Sound. We included 149 published sources of data. In some cases, we obtained the raw data, and in others we could only use the summarized data presented in tables and figures. The published sources of the diet data are provided in Table 5. In addition to the published sources listed in that table, we also obtained additional diet data collected in Hood Canal and provided by H. Daubenberger (Port Gamble S'Klallam Tribe, unpublished data), juvenile salmon diet data collected in the San Juan Islands by Kwiáht (R. Barsh, unpublished data),[7] diet information from Fisheries and Oceans Canada (DFO) groundfish research surveys, diet composition collected as part of the RV Ricker cruises in both Puget Sound and the southern Strait of Georgia, and forage fish diet collected in the San Juan Islands provided by M. Bakker (University of Washington, unpublished data).

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[7] http://www.kwiaht.org/kwiaht.htm

The final aggregated dataset included 438,216 diet samples from data collected between 1927 and 2016. We included data collected only within the Atlantis model extent, excluding data from the Washington coast, Strait of Juan de Fuca, and the Strait of Georgia north of Richmond. We combined data on feeding ecology from the literature and empirical studies. When available, we use diet information in terms of percent weight or percent volume, but for certain cases we also include diet information in terms of frequency of occurrence, counts of individual prey items, or Index of Relative Importance (IRI). For frequency of occurrence, we necessarily converted this to a split sample frequency of occurrence (Olesiuk 1990), crudely assuming the predator consumed one individual of each prey species, and that all prey species weigh the same. We then assumed that the diet proportion was equal to the split sample frequency of occurrence. Where a count of individuals per prey species was provided (but not the weight of those prey species), we assumed all prey species weighed the same. In a few cases, only IRI was reported by study authors, and we assumed that this was equivalent to percent weight. IRI is a compound diet index defined as

$$\mathrm{IRI} = (\%\mathrm{N}i + \%\mathrm{W}i) * \%\mathrm{F}i \tag{1}$$

where %N is percent number, %W is percent weight, and %F is percent frequency of *i* prey.

When possible, we categorized individual diet studies as involving either adult or juvenile predators. When a study did not specify age or maturity of the predator, we assumed that study pertained to adults. When a species had no diet studies of juveniles, we set juvenile diets equal to adult diets. Figures 13, 14, and 15 show the average diet composition for invertebrate and vertebrate juvenile and adult consumers, respectively.

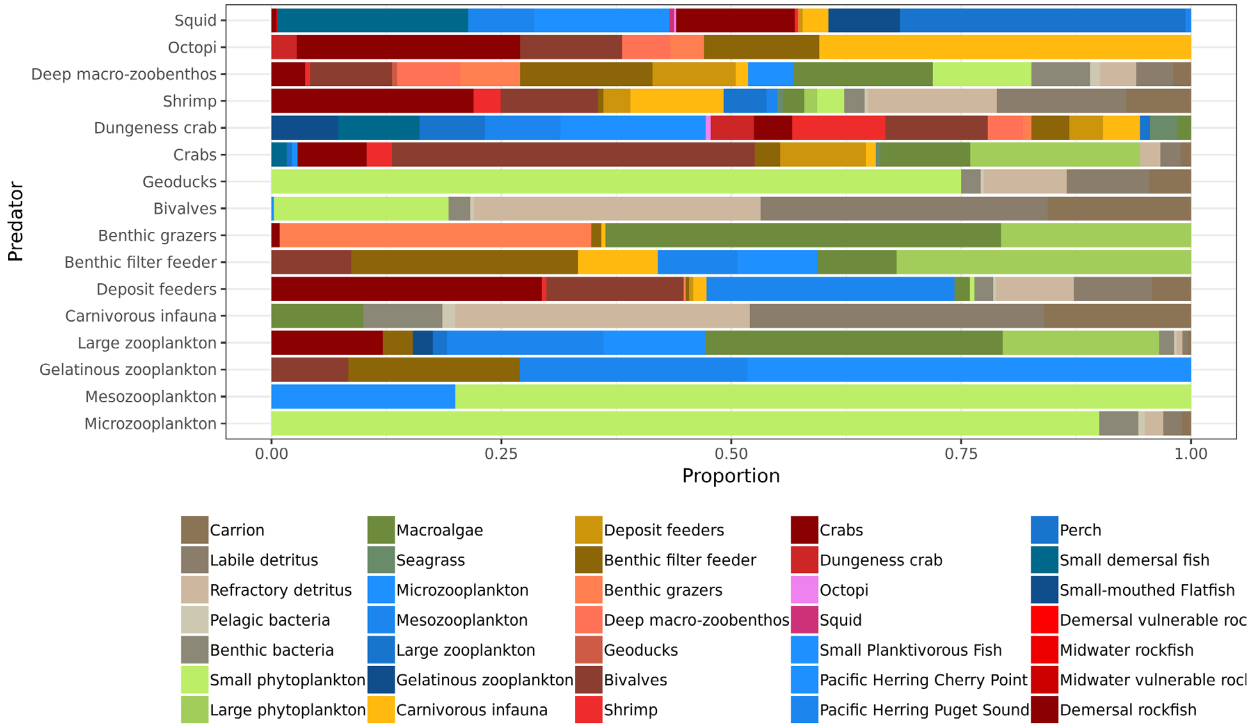

Figure 13. Bar diagram showing mean raw diet compositions for invertebrate predator groups in Atlantis. Functional groups are grouped in guilds.

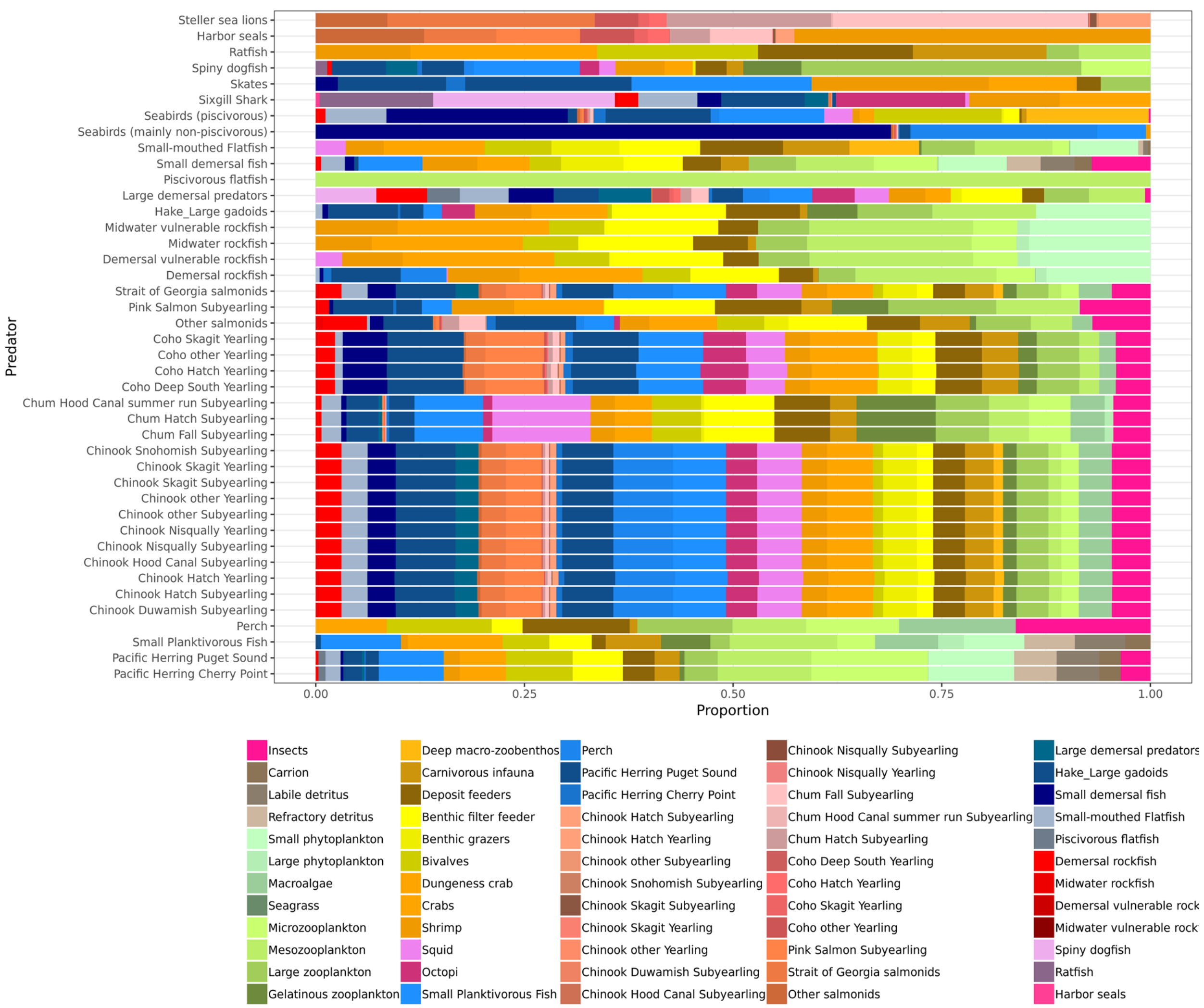

Figure 14. Bar diagram showing mean raw diet compositions for juvenile age-structured predator groups in Atlantis. Functional groups are grouped in guilds.

We obtained robust diet composition estimates and associated uncertainty for the AMPS model by bootstrapping aggregate predator diets from disaggregated samples and published studies. This method accounts for rare predator–prey interactions; these rare interactions can be important when the biomass and consumption rates of the predator are very large and/or the biomass of the prey item is very small (Walters et al. 2008). Atlantis uses “availability” parameters rather than diet proportions; these parameters are scaling values in a Type II predator–prey functional response. Availability reflects predator total consumption potential and diet preference; it is sensitive to functional group aggregation, predator and prey abundances, and spatial co-occurrence (Morzaria-Luna et al. 2018).

Second, we fit a statistical model based on the Dirichlet distribution to the assembled diet data, to quantify the likely contributions of prey to predators’ diet (Ainsworth et al. 2010, Tarnecki et al. 2016). We normalized and organized all the predator diets in a matrix representing all AMPS functional groups. We bootstrapped 10,000 of these samples with replacement and fit the bootstrapped values to the Dirichlet density function, a multivariate

Figure 15. Bar diagram showing mean raw diet compositions for adult age-structured predator groups in Atlantis. Functional groups are grouped in guilds.

generalization of the beta function, using a maximum likelihood fitting procedure (Ainsworth et al. 2010, Masi et al. 2014, Tarnecki et al. 2016). The marginal beta distribution provides a mode representing the most frequently observed diet proportion for a given predator–prey combination, as well as confidence intervals that better account for data quality, diet variability, and the uncertainty surrounding rare feeding events (Ainsworth et al. 2010, Masi et al. 2014, Tarnecki et al. 2016). Diet composition values derived from the beta distribution were divided by 100 to convert them into availability parameters. We used this convention to correct the order of magnitude relative to other linkages, providing a starting point for calibration (Morzaria-Luna et al. 2018).

We used the predator–prey linkages to illustrate the food web in the Atlantis model (Figure 16).

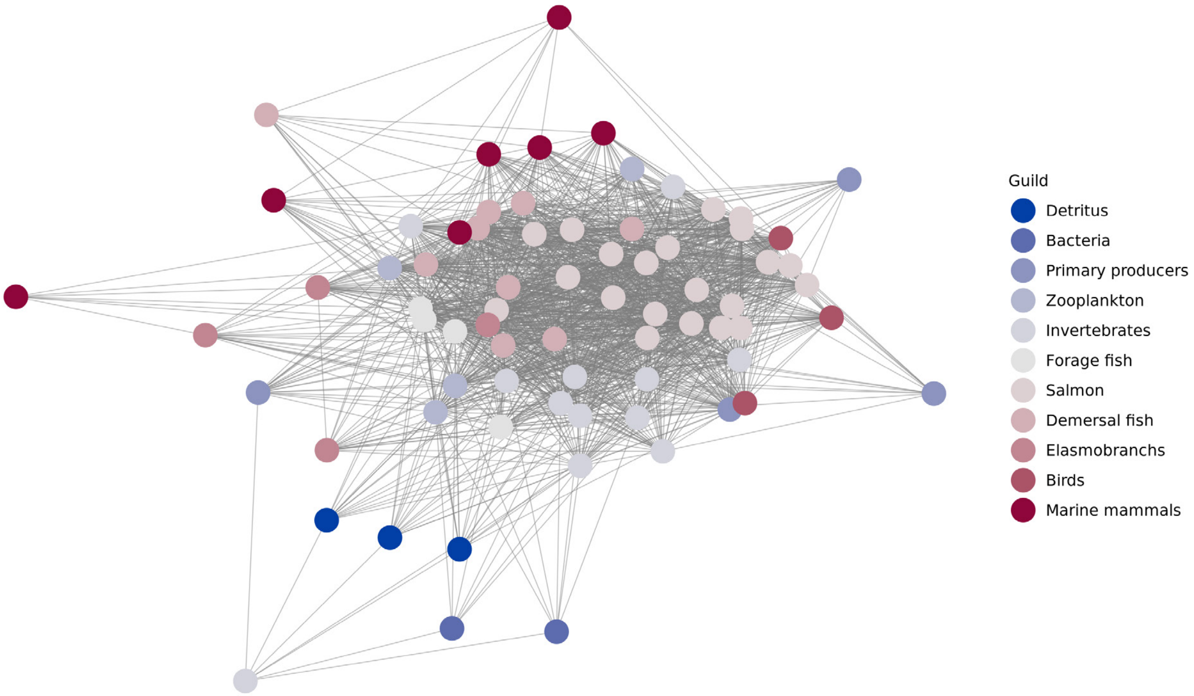

Figure 16. Network diagram illustrating the predator–prey linkages contained in the availability matrix of the Atlantis model for Puget Sound. Functional groups are shown colored by guild.

Analyses informing spatial abundance and density

To derive spatial distribution and initial biomass, we used several datasets, including benthic infauna grab samples collected by PSAMP and WDFW bottom trawl surveys. Table 6 summarizes the data sources used to derive biomass for each functional group. There is additional information in Functional Group Descriptions.

Thirty-nine polygons represent islands. These island polygons include neither depth layers nor biomass, and we excluded them from calculations in the model dynamics. However, important rocky and intertidal habitats occur on the edges of these island polygons. When survey data (or associated imprecisions in survey coordinates) suggested assigning biomass to island polygons, we assigned that biomass equally to adjacent polygons.

Spatio-temporal analysis

To inform spatial distribution and initial biomass, we used the Vector-Autoregressive Spatio-Temporal (VAST) Model, a geostatistical modeling approach in R, to estimate biomass indices and spatial distribution of several Atlantis functional groups based on survey data. VAST applies a spatial delta-generalized linear mixed model (ΔGLMM) for multiple categories (species, size, or age classes) when standardizing survey or fishery-dependent data (Thorson et al. 2015, Thorson and Barnett 2017). This approach was used for each dataset, as described in the following sections. Extrapolated biomass and distribution of functional groups for which the model converged were estimated as described further in this section.

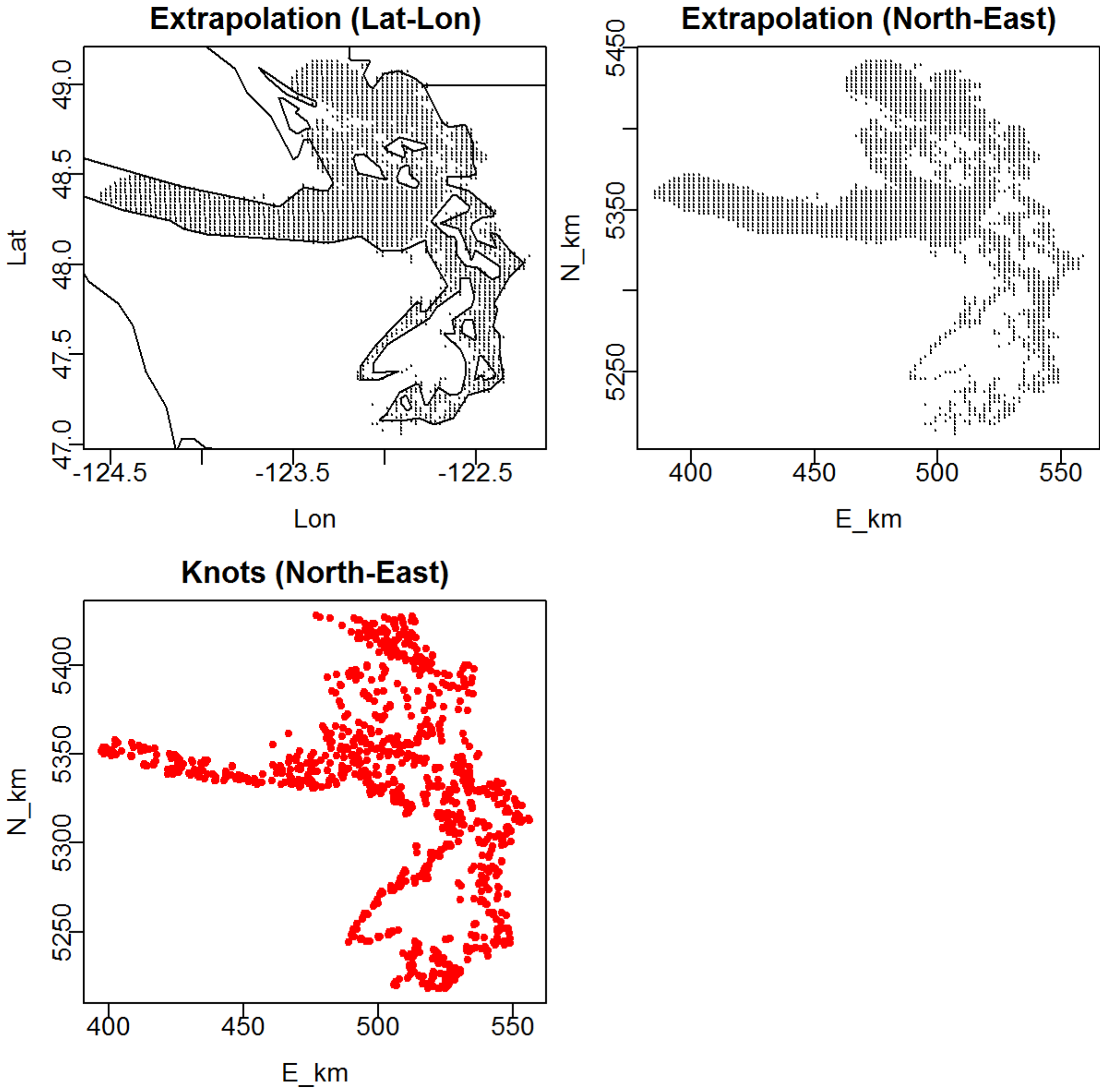

Figure 17. Example of extrapolation grid and knots location (here, 1,000 knots) used by the geostatistical model and applied to WDFW bottom trawl survey data to inform functional group spatial distribution and initial biomass.

In the ΔGLMM, probability of encounter and catch rate for each encounter are modeled separately. The encounter probability is estimated using a logistic model, while the positive catches are approximated using a gamma distribution. The two parts of the model are estimated using Gaussian Markov random fields. We used those random fields to account for spatial and spatio-temporal covariance in both parts of the model; however, they can also be used to introduce environmental covariates or the variability in catch efficiency of different vessels (if more than one vessel were used during the surveys). To reduce the computation time, a "predictive" framework is used to estimate the random fields, based on a number of knots (n_j) used to approximate that field. The value of the random field at a specific sampling location was assumed equal to the value of the random field at the nearest knot. The location of each knot is determined using a cluster algorithm (here, a K-means algorithm; Figure 17).

The final model used for the encounter probability p_i for a sample *i* is:

$$p_i = logit^{-1}(d_{T(i)}^{(p)} + \omega_{J(i)}^{(p)} + \varepsilon_{J(i),T(i)}^{(p)}) \tag{2}$$

and the approximate positive catch λ_i for a sample *i* is:

$$\lambda_i = w_i \,.\, exp(d_{T(i)}^{(\lambda)} + \omega_{J(i)}^{(\lambda)} + \varepsilon_{J(i),T(i)}^{(\lambda)}) \tag{3}$$

where:

w_i = the swept area,[8]
d_T = the average density for a given year period T,
ω_J = the spatially correlated variability at a given knot J persistent among year periods,
$\varepsilon_{J,T}$ = the spatially correlated variability at a given knot J in the year period T,
$T(i)$ = the year period for the sample i, and
$J(i)$ = the nearest knot to sample i.

ω_J and $\varepsilon_{J,T}$ follow two multivariate normal distributions (here both are Matérn distributed with a smoothness of 1). Fixed effects in the model are estimated using maximum marginal likelihood while integrating across all random effects, and the conditional probability of random effects is approximated using a stochastic partial differential equation approach (Thorson et al. 2015). Once the model converges, the catch rate C_i is extrapolated using a 5 km × 5 km grid where *i* is a point on that grid (Figure 17).

$$C_i = p_i \times \lambda_i \tag{4}$$

To inform the distribution and initial biomass of Atlantis functional groups, VAST was applied over the entire datasets, and species were aggregated into functional groups *f* by summing the catch per unit of effort ($CPUE_{S,i}$) from the different surveys for each sample location *i* and each period *T* to obtain the density of the functional group $d_{f,T(i)}$ for the period $T(i)$ and the sample *i*.

$$d_{f,T(i)} = \sum_{S \in f} CPUE_{s,i} \tag{5}$$

Once the model VAST converged using the density of functional groups, the catch rate was estimated at each extrapolation grid point C_i, allocated to each Atlantis polygon, and an average catch rate per polygon was calculated. To obtain the biomass of each functional group in each polygon, the average catch rate per polygon was multiplied by the surface of the polygon. The distribution and the initial biomass were then used to inform model initial conditions. The species and surveys for which VAST was used are detailed in the following sections.

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[8] Here equal to 1, because the survey catches are normalized by the swept area.

Benthic infauna

Benthic fauna surveys were provided by V. Partridge and colleagues at PSAMP (unpublished data). PSAMP monitors sediment quality and contaminants in Puget Sound, and the benthic invertebrate communities associated with these sediments. Dutch et al. (2009) detail the sampling protocol. Sampling used a double 0.1-m^2 stainless-steel modified van Veen grab sampler. The grab sampler collects benthic infauna to 17 cm depth, although the target taxa are in the top 2 cm; samples are collected in depths 2 m (1 fathom) or deeper, in areas with soft sediment. High-current areas were not generally sampled, nor were Canadian waters. Though methodology for taxonomic identification has varied over the years in this extensive and long-term database, WSDOE scientists provided a standardized taxonomy that accounts for this, aggregating to higher taxa when necessary (and still providing adequate taxonomic resolution for Atlantis functional groups). Sediment samples are also collected to assess chemistry, total organic carbon, grain size, and toxicity, but these additional parameters were not used for Atlantis parameterization.

Benthic grab samples were collected from 1997–2015. This sampling program includes 860 unique sites (some sampled repeatedly over the years). The samples were collected over the course of multiple projects: a baseline project (1997–99 and 2002–03), a regional project (2004–14), and an urban bays project (2007–15). Sampling was primarily conducted from April–June, depending upon the project. We based our analysis on 2,954 samples that included 950 taxa and averaged across 1997–2015. These taxa were aggregated into Atlantis functional groups by T. Macdonald and her staff at Biologica Environmental Services Ltd. (Victoria, British Columbia, Canada; personal communication). Additionally, Biologica staff provided conversions from counts (individual organisms) to grams wet weight.

Ten Atlantis functional groups were included in these data, and we use information from six groups: bivalves (BIV), shrimp (PWN), crabs (BML), deep macro-zoobenthos (BMD), benthic filter feeders (BFF), carnivorous infauna (BC), and deposit feeders (BD). We exclude geoduck clams (GEC), Dungeness crab (DUN), and octopus (BMS), all of which can escape the grab sampling gear via size, depth, or mobility. The model for benthic grazers (BG) did not converge in the VAST analysis, and was not used.

Demersal species

The CPUE used derived from WDFW bottom trawl surveys. The surveys were conducted by WDFW between April and June over the period 1989–2007. The year 1987 was not used because the survey occurred in October. The spatial effort changed three times over the period considered (Figure 18). Between 1987 and 1991, annual surveys sampled the entire Puget Sound as well as part of the southern Strait of Georgia. However, between 1994 and 2007, only one of the three sub-areas defined by WDFW was sampled each year. In addition, from 2000 to 2007, the definitions of the sub-areas changed and the survey was extended to the San Juan Islands and the eastern Strait of Juan de Fuca. Data for all years (1989–2007) were combined to estimate indices of biomass and distribution of the different species sampled. The main assumption is that the distribution of species did not change during the four different periods. The total area sampled differed between these four periods (Figure 18).

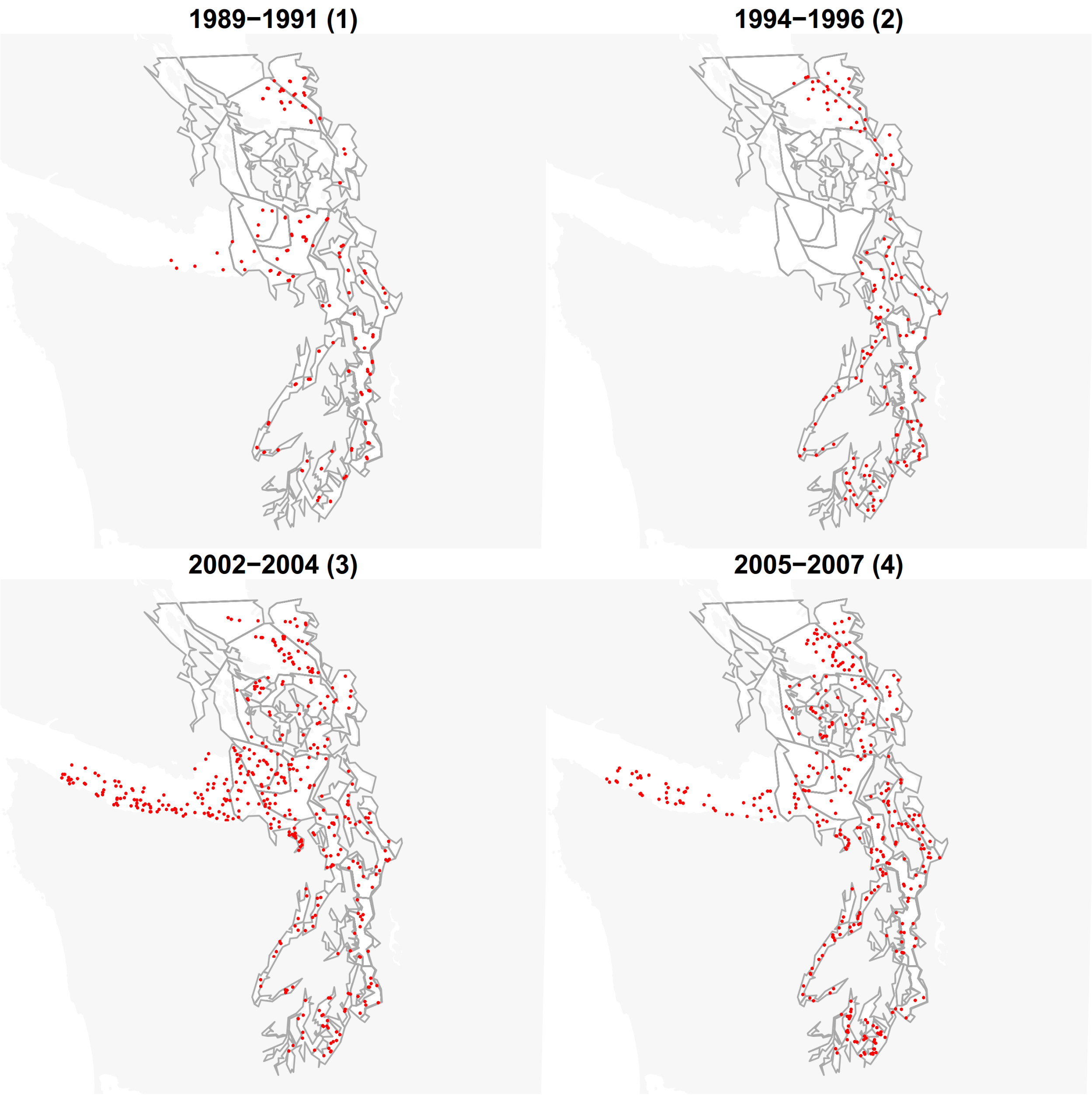

Figure 18. Distribution of WDFW bottom trawl survey data for the four periods considered: 1) 1989–91, 2) 1994–96, 3) 2002–04, and 4) 2005–07.

Pelagic species

We used data from midwater trawl surveys carried out by the RV *Ricker* from 2001–16. The data were obtained from I. Kemp at Long Live the Kings (unpublished data). The survey design is described in Beamish et al. (2000). Briefly, each trawl set encompasses approximately 15 m of depth, with three strata: 0–15 m, 16–30 m, and 31–45 m. The surveys also included one set of deeper strata (31–45 m, 46–60 m, or 61–75 m) and one set >76 m. The fishing gear used is a midwater rope trawl with an opening 21 m deep and 64.5 m wide. When the doors are at the surface, the headrope is between the surface and 3.5 m—thus, the net is fished just below the surface. This survey is distributed across Puget Sound and is conducted during the day, and the design allows for the identification of seasonal and interannual changes in distribution. The surveys included here were carried out in different months each sampled year. We aggregated years and modeled abundance seasonally. Data were only available for summer and fall. In general, we assumed that spring and summer spatial distributions were equivalent, and fall and winter distributions were equal (with exceptions for some functional groups as listed below). Abundance estimates were made by Atlantis functional group, considering data for all the species that the functional group comprised.

Functional Group Descriptions

Detritus and bacteria (DC, DL, DR, BB, PB)

There are three detritus groups included in the Atlantis model. These are carrion (DC, dead matter, large particles), refractory detritus (DR, cohesive, small particles), and labile detritus (DL easily disassociated, small particles). Following Ainsworth et al. (2011) we determined detrital biomass using an empirical relationship that relates to primary productivity and euphotic depth (Pauly et al. 1993).

$$\log10\ \mathrm{D} = -2.41 + 0.954\ \log_{10} PP + 0.863\ \log_{10} E \tag{6}$$

where PP = primary productivity (g C/m^2/y) and E is euphotic depth (m), the depth at which irradiance is 1% of the irradiance at the surface. We apply the maximum euphotic depth for the Strait of Georgia in April, 25.2 m (Loos and Costa 2010). Primary productivity per Atlantis polygon was estimated based on annual average standing stocks of phytoplankton estimated by MEdium Resolution Imaging Spectrometer (MERIS) satellite chlorophyll (see next section), multiplied by annual productivity of 226.3/yr (Harvey et al. 2010). For Atlantis initial conditions, we assumed that labile, refractory, and carrion detritus constitute 40%, 40%, and 20% of the total amount, respectively. All carrion and refractory detritus is assumed to occur in the sediment layer. We assume that 75% of labile detritus is found in the sediment layer, with the remaining 25% distributed in equal concentration throughout the water column. As a comparison, previously Preikshot et al. (2012) assumed a detritus biomass of 10 t wet weight/km^2 for a Strait of Georgia ecosystem model. Converting our Atlantis initial conditions to equivalent units yields approximately 1.15 t/km^2 wet weight.

Bacteria are divided into benthic (BB) and pelagic groups (PB). Nitrogen concentration of pelagic bacteria was assumed uniform at all water column depths and in all polygons, informed by sampling of C. Greene and colleagues at NWFSC (unpublished data). Greene and colleagues sampled bacteria at 6 m depth in April–October 2011. This sampling reports concentrations in numbers of bacteria/mL; median concentration was 1.5 million cells/mL, slightly higher than the 10^5–10^6 cells typically expected in marine systems globally (Schmidt et al. 1998). We convert the bacterial counts of Greene and colleagues to nitrogen by applying the Redfield ratio and an average of 37 femtograms per individual bacterium (Vrede et al. 2002). The resulting pelagic bacteria concentrations averaged per Atlantis polygon ranged from 6–15 mg N/m^3 (Figure 19). For initial conditions, we therefore assume 10 mg N/m^3 for all water column layers in the model domain. For benthic bacteria, we apply a typical global average of 10^9 cells/mL (Schmidt et al. 1998), equivalent to 5,600 mg N/m^3 in the sediment layer.

Large phytoplankton (PL), small phytoplankton (PS)

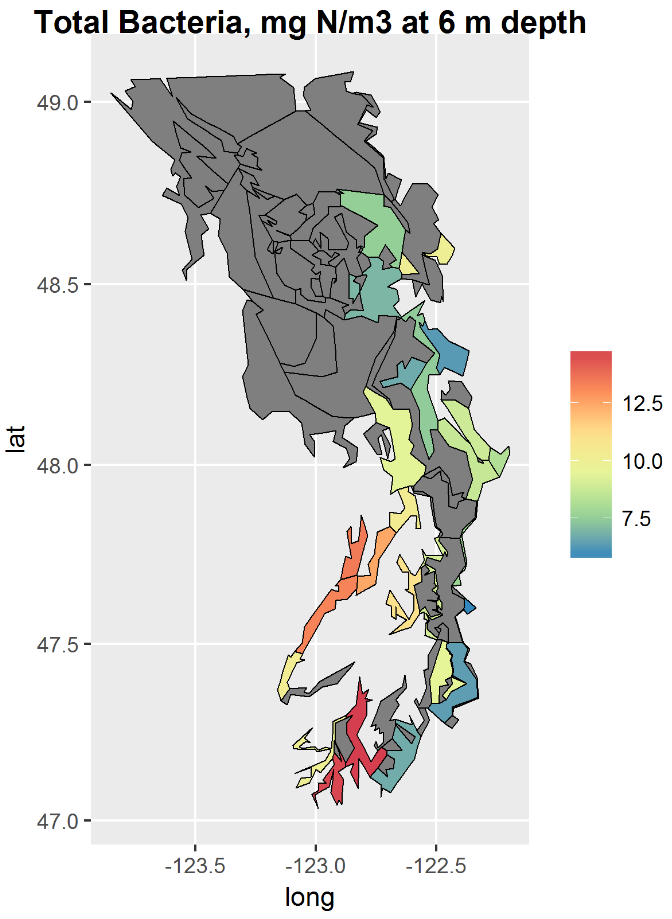

Figure 19. Average concentration of bacteria at 6 m depth in the water column, from sampling by C. Greene and colleagues during Apr–Oct 2011.

There are two phytoplankton groups in the model: large phytoplankton includes diatoms and coccolithophorids, while small phytoplankton includes dinoflagellates and phytoflagellates. Primary producers likely represent the most significant sources of marine autochthonous production in Puget Sound (Harvey et al. 2010). Phytoplankton production in Puget Sound occurs in both nearshore and offshore areas (Ruckelshaus and McClure 2007). Phytoplankton abundance and distribution in Puget Sound are highly heterogeneous or "patchy" both spatially and seasonally, due to variations in circulation, stratification, light availability, turbidity, and nutrient availability (Ruckelshaus and McClure 2007, Khangaonkar et al. 2012a). Puget Sound experiences cyclical episodes of phytoplankton blooms from spring through early autumn (Harvey et al. 2010). Several taxa, including the genera *Alexandrium*, *Pseudo-nitzschia*, *Heterosigma*, and *Chaetoceros*, form harmful algal blooms (HABs) under the right combinations of light, temperature, nutrient levels, and stratification (Ruckelshaus and McClure 2007). Some HAB species contain toxins that can make bivalves unsafe for human consumption, while others produce toxins that can lead to fish kills (Moore et al. 2011).

We used MERIS satellite data from the European Space Agency to estimate total chlorophyll, which we then converted to phytoplankton abundance and then partitioned between small and large phytoplankton. MERIS satellite data were provided by B. Sackman and B. Leonard of Integral Consulting (Olympia, Washington; unpublished data). MERIS data are particularly appropriate for Puget Sound/Salish Sea because they are at a finer resolution (300 m, intended for the coastal ocean) than coarser satellite data intended for offshore applications (see the CoastColour website[9]). We apply estimates of chlorophyll based on neural network algorithms, rather than an alternative method (OC4) which may be more appropriate for offshore regions. For Atlantis initial conditions, we use MERIS data averaged over January 2011, and averaged over pixels within each of the Atlantis model

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[9] https://www.coastcolour.org/about.html

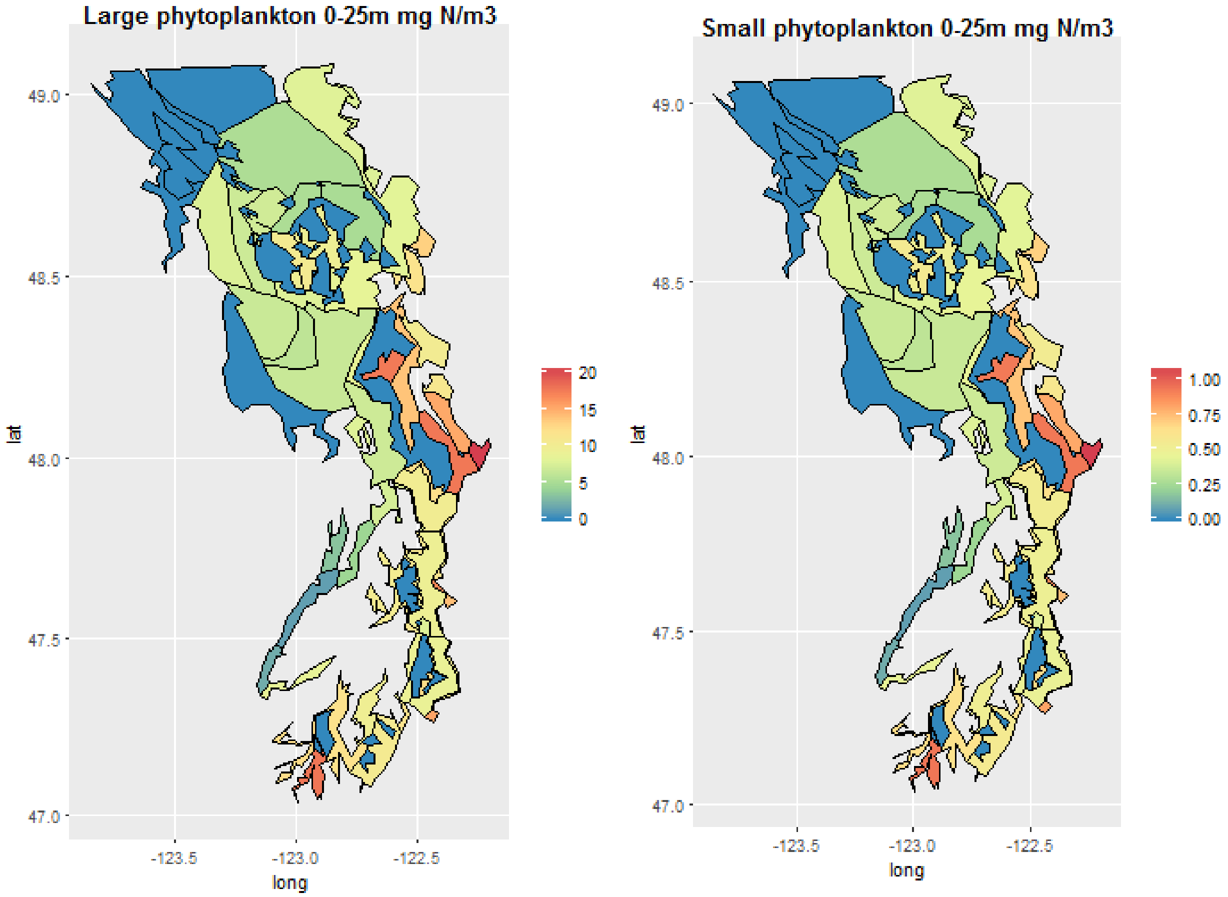

Figure 20. Large and small phytoplankton concentrations (mg N/m^3) applied to the upper 25 m of the water column.

polygons. For each polygon, we also calculated a monthly climatology (seasonal average) over the period for which data are available (2002–12). The climatology allows comparison to seasonal Atlantis projections during model calibration. Data processing to yield chlorophyll-*a* concentration (mg/m^3) was accomplished with minimal modifications to the Matlab functions `roi_summary_months.m` and `roi_summary_monthly.m` (B. Sackman and B. Leonard, personal communication). Concentrations of chlorophyll from MERIS were assumed to apply to photic depths within this Atlantis model, specifically the two upper layers (0–5 m and 5–25 m).

We sought to improve upon our earlier ecosystem modeling, which crudely converted from chlorophyll to abundance of phytoplankton functional groups (Brand et al. 2007, Marshall et al. 2017). In those earlier models, we assigned 75% of chlorophyll-*a* to the large phytoplankton (diatoms) Atlantis functional group, and 25% into a catchall small phytoplankton group (dinoflagellates, phytoflagellates). More refined data are available for Puget Sound, where King County routinely monitors phytoplankton taxa at six monitoring stations in Central Puget Sound. These data (2003, 2016) were provided to us by K. Stark and G. Hannach (King County Department of Natural Resources and Parks, unpublished data). Using biovolume data for diatoms, dinoflagellates, and other phytoplankton, and averaging over monthly samples for the years 2014–17, we calculated that 95% of biovolume is diatoms, assigned to the large phytoplankton group, and 5% is dinoflagellates or other phytoplankton, assigned to the small phytoplankton group. We assumed that biovolume is proportional to carbon content, and estimated total phytoplankton carbon from MERIS satellite data, assuming a ratio of 30 mg C:1 mg chlorophyll-*a* (Strikland 1960) and the assumed Redfield ratio to convert from C to N. We also assumed a ratio of 1:1 for Si:N for large phytoplankton (diatoms), since silica is not considered limiting in Puget Sound (Khangaonkar et al. 2012a). Final concentrations of large and small phytoplankton are shown in Figure 20.

Macroalgae (MA)

This functional group includes kelp and other subtidal and intertidal algae from the phyla Chlorophyta, Rhodophyta, and Phaeophyta. Seaweed assemblages are dominated by the green algae *Ulva,* rockweed (*Fucus* spp.), and massive brown algae (e.g., *Costaria costata*). These seaweeds are abundant on rocky shores throughout Puget Sound where they are a food source for small grazers and their predators (Ruckelshaus and McClure 2007). Kelp are found attached to rocks or cobbles in shallow waters, especially in areas with moderate to high waves or currents; they include floating and non-floating kelp (Mumford 2007). Kelp contributes primary production to Puget Sound, either via direct consumption by sea urchins or as particulate or dissolved organic matter, or detritus as it washes ashore or sinks to deep areas where it decomposes and contributes to carbon production (Feehan et al. 2018). Juvenile rockfish, juvenile salmon, invertebrates, microorganisms, and other algae use kelp as substrate and habitat, taking advantage of its structural complexity (Thom 1984, Haldorson 1987). The abundance of bull kelp (*Nereocystis luetkeana*) decreased 63% in southern Puget Sound between 1878 and 2017, likely due to environmental stressors, and altered shorelines and trophic relationships (Berry et al. 2021). *Sargassum muticum* is an introduced species that may displace native kelp (Thom and Hallum 1990); to our knowledge, there are no assessments of *S. muticum* biomass in Puget Sound. Harvey et al. (2010) developed a biomass estimate for overstory kelp of 291.26 g wet weight (ww) per m^2 of kelp bed habitat, based on both aerial surveys and measures of biomass density in bull kelp beds. Research in Puget Sound suggests *Ulva* produces a dry biomass of 39.9 g dry weight (dw) per m^2 at a depth of 1 m, with substantially less biomass at 0 m

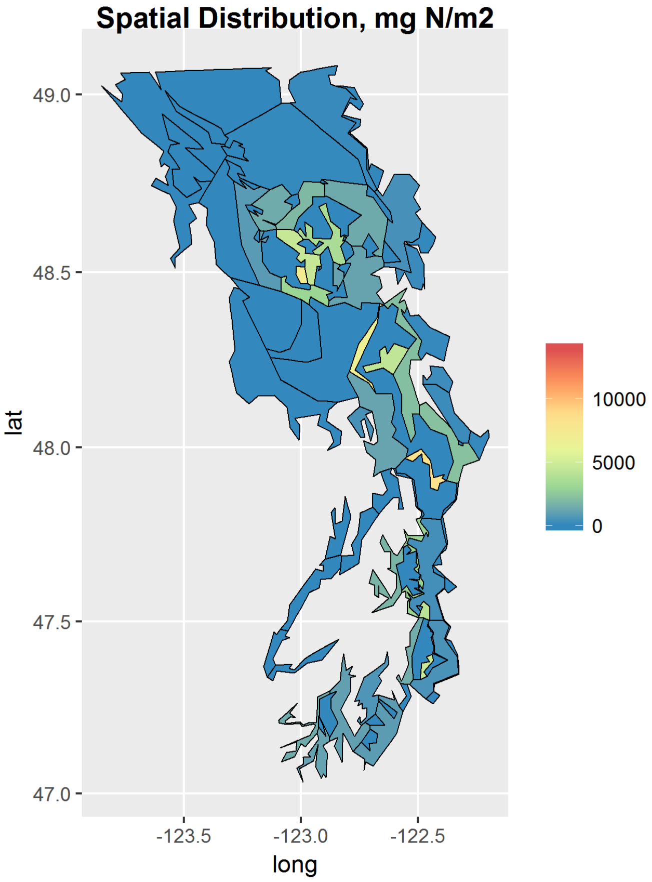

Figure 21. Macroalgae density (mg N/m^2).

and 2 m (22.3 and 19.4 g dw/m^2, respectively; Nelson et al. 2003). Other studies found high average biomass of ~130 g dw/m^2 during the growing season (Thom and Albright 1990). We used this high estimate and converted to wet biomass assuming that dry weight is 14% of wet weight (Gadberry et al. 2018), which, combined with kelp, yields an estimate of 1.220 kg ww/m^2. We obtained biomass per polygon (Figure 21) and across the model by multiplying this estimate by the area occupied by seaweed in Puget Sound (1,280 km^2, or 13% of the model extent); this area was calculated in Biogenic habitats and is based on data produced by the Nearshore Habitat Program, Aquatic Resources Division, Washington Department of Natural Resources (WDNR). We initialize the model at 172.48 mg N/m^2, corresponding to 68,939.95 t. Biomass was converted to N content assuming a mean C:N ratio of 30 of kelp, which can vary from 10 to 40 (Reed et al. 1996).

Seagrass (SG)

Seagrass are flowering plants that grow submerged in marine areas. There are six seagrass species in Washington State: *Zostera marina*, *Z. japonica*, *Phyllospadix serrulatus*, *P. scouleri*, *P. torreyi*, and *Ruppia maritima* (Christiaen et al. 2017). *Zostera marina* (eelgrass) is the most abundant species in Puget Sound, where it provides important ecosystem services as a primary producer, carbon sink, key source of fish and invertebrate habitat, source of detrital organic matter, and as food for grazing invertebrates and many birds, including the brant (*Branta bernicla*; Wilson and Atkinson 1995, Ruckelshaus and McClure 2007, Harvey et al. 2010). Seagrasses reduce erosion and improve water quality by stabilizing sediments with their roots and rhizomes (de Boer 2007). Additionally, eelgrass beds have cultural value for Native Americans and First Nation People in the Pacific Northwest (Christiaen et al. 2017). Recent studies suggest that there have been no recent major declines in the total area of eelgrass in the herring spawn areas between 1970 and 2012 (Shelton et al. 2017), or in Puget Sound as a whole between 2000 and 2015 (Christiaen et al. 2017). Thom et al. (2018) derived an estimate of seagrass biomass of 2.0 mol C/m^2 for a model of eelgrass biomass production in Puget Sound. This amount equals 24 g C/m^2, which we then converted to dry weight assuming that C content is 36.8% of dry weight (*Zostera marina*,

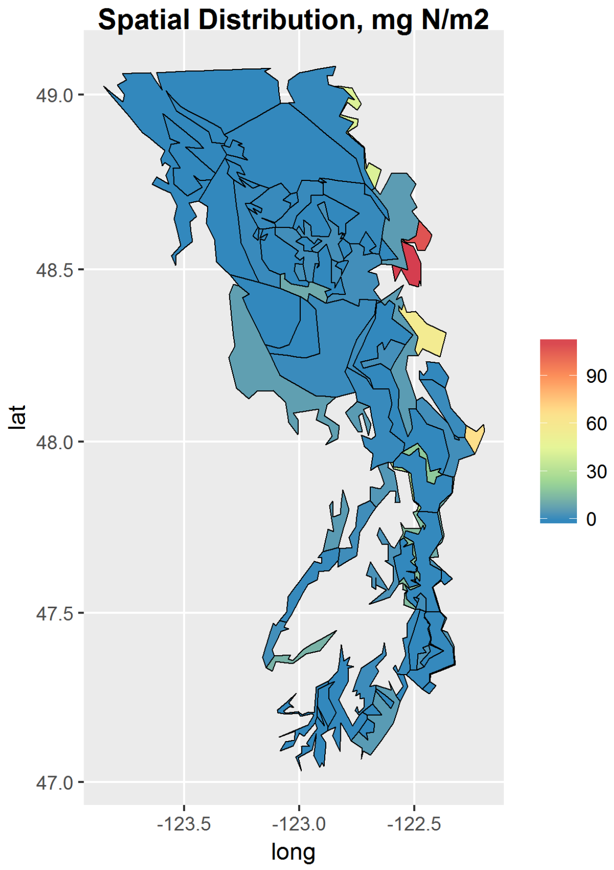

Figure 22. Seagrass density (mg N/m²).

Duarte 1990). This is equal to 65 g dw/m^2, which, when converted from dry weight to wet weight using a conversion multiplier of 8.05 (Keser et al. 2003), results in an estimate of 0.524 kg ww/m^2. We obtained polygon (Figure 22) and model-wide biomass by multiplying this estimate by the area occupied by eelgrass in Puget Sound, 225 km^2 or 0.02% of the model extent; this area was calculated in Biogenic habitats and is based on data produced by WDNR. (It also includes 0.042 km^2 reported for Bowman Bay, British Columbia; Rao et al. [2013].) We initialize the model with 31.66 mg N/m^2, corresponding to a biomass estimate of 12,321.35 t. We converted wet weight to N assuming that the C:N ratio of eelgrass is 11.3, the midpoint of the range 9.35–13.34 (Yang et al. 2013).

Microzooplankton (ZS), mesozooplankton (ZM), large zooplankton (ZL), gelatinous zooplankton (ZG)

Plankton in AMPS are represented as four functional groups: microzooplankton, mesozooplankton, large zooplankton, and gelatinous zooplankton. Examples of microzooplankton observed within Puget Sound include ciliates, dinoflagellates such as *Noctiluca*, foraminiferans, and radiolarians. Mesozooplankton include copepods, specifically *Calanus pacificus*, and the genera *Acartia*, *Pseudocalanus*, *Paracalanus*, and *Eucalanus,* among other species. Large zooplankton include chaetognaths, pelagic shrimp (e.g., the families Sergestidae and Pasiphaeidae), hyperiid amphipods, the pelagic larval stages of benthic macroinvertebrates, and large predatory copepods and euphausiids. Gelatinous zooplankton include small hydromedusae, comb jellies, urochordates, larvaceans, pelagic salps, thecosomes and gymnosomes, crystal jelly (*Aequorea victoria*), moon jelly (*Aurelia labiata*), lion's mane jelly (*Cyanea capillata*), fried egg jelly (*Phacellophora camtschatica*), and sea nettle (*Chrysaora fuscescens*). Note that within the model we represent the species well sampled by monitoring programs, as described below.

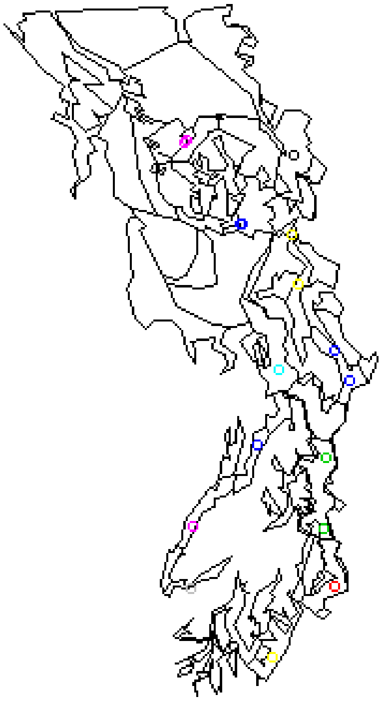

Figure 23. Map of zooplankton sampling locations (Keister and colleagues) throughout Puget Sound, 2014–17. Sites are located in Hood Canal, Whidbey Basin, South Sound, Main Basin (including Admiralty Inlet), Bellingham Bay, and in the San Juan Islands.

Zooplankton initial conditions (for model start at January 2011) were assembled by combining information from two separate sampling programs led by J. Keister (University of Washington) and C. Greene (NWFSC), as detailed below. These results can also be compared qualitatively to samples collected by Canadian researchers, though, for reasons of spatial coverage and methodology, we do not use the Canadian data to initialize the model.

Zooplankton data were available from J. Keister (personal communication) from extensive sampling throughout Puget Sound in 2014–17 (Figure 23). We allocated sample locations to the corresponding Atlantis polygons. Samples were collected by the Keister research group year-round with a vertical ring net (200-µm mesh, sampling the full water column) and oblique bongo net (335-µm mesh, sampling the upper 30 m of the water column). This provided density estimates (mg C/m^3) for the functional groups microzooplankton (matched to Keister data's "dinoflagellates" and "foraminifera"), mesozooplankton (matched to "copepod"), large zooplankton (matched to "krill" and "chaetognaths"), gelatinous zooplankton (matched to "scyphozoans," "larvacea," "siphonophore," and "ctenophore"), and shrimp (matched to "shrimp" and "mysids").

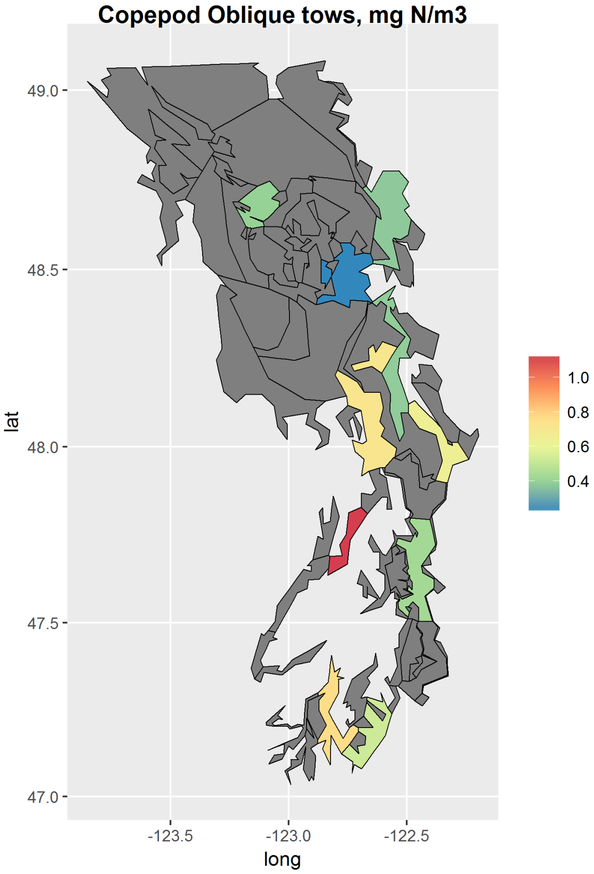

Figure 24. Copepod density derived from oblique plankton tows, as part of zooplankton sampling by Keister and colleagues throughout Puget Sound in 2014–17.

Within the microzooplankton group, *Noctiluca* are the dominant dinoflagellate in the samples, and are known to form large blooms in Puget Sound during summer. We expect microzooplankton sampling efficiency with these nets to be poor, since microzooplankton are typically <200 µm, but we lack any more refined estimates of microzooplankton abundance. Figure 24 shows copepod densities in mg N/m^3. Due to spatial gaps in sampling across the expanse of Puget Sound, we interpolated missing data (per polygon) based on the average of all sampled polygons of similar bottom depth (i.e., with the same number of Atlantis depth layers). Shallow polygons (<5 m depth) were poorly sampled and in most cases are assigned plankton abundances from polygons with 5–25 m bottom depth.

For four plankton groups, vertical ring nets suggest higher densities than oblique bongo tows, and for these groups we therefore rely on vertical densities to avoid underrepresenting zooplankton that might be missed in the oblique bongo tows (perhaps because of coarser bongo mesh or shallower net depths). These four groups were microzooplankton, large zooplankton, gelatinous zooplankton, and shrimp. Though these vertical net tows integrate over the water column, often in deeper basins (median 110 m, maximum 292 m), to simplify model initial conditions we compressed abundance of these groups into the upper 25 m of the water column by multiplying the Keister estimates of density (mg C/m^3) by water column depth, but then allocating this abundance into the upper 25 m. To convert to nitrogen concentrations, we apply a Redfield ratio conversion of 13% N out of total C:N:P. For mesozooplankton only (copepods), oblique bongo tows (surface 30 m) in the Keister data suggest higher abundances than vertical ring nets. Since copepods are a key food source for Puget Sound fish, we therefore rely on the oblique bongo

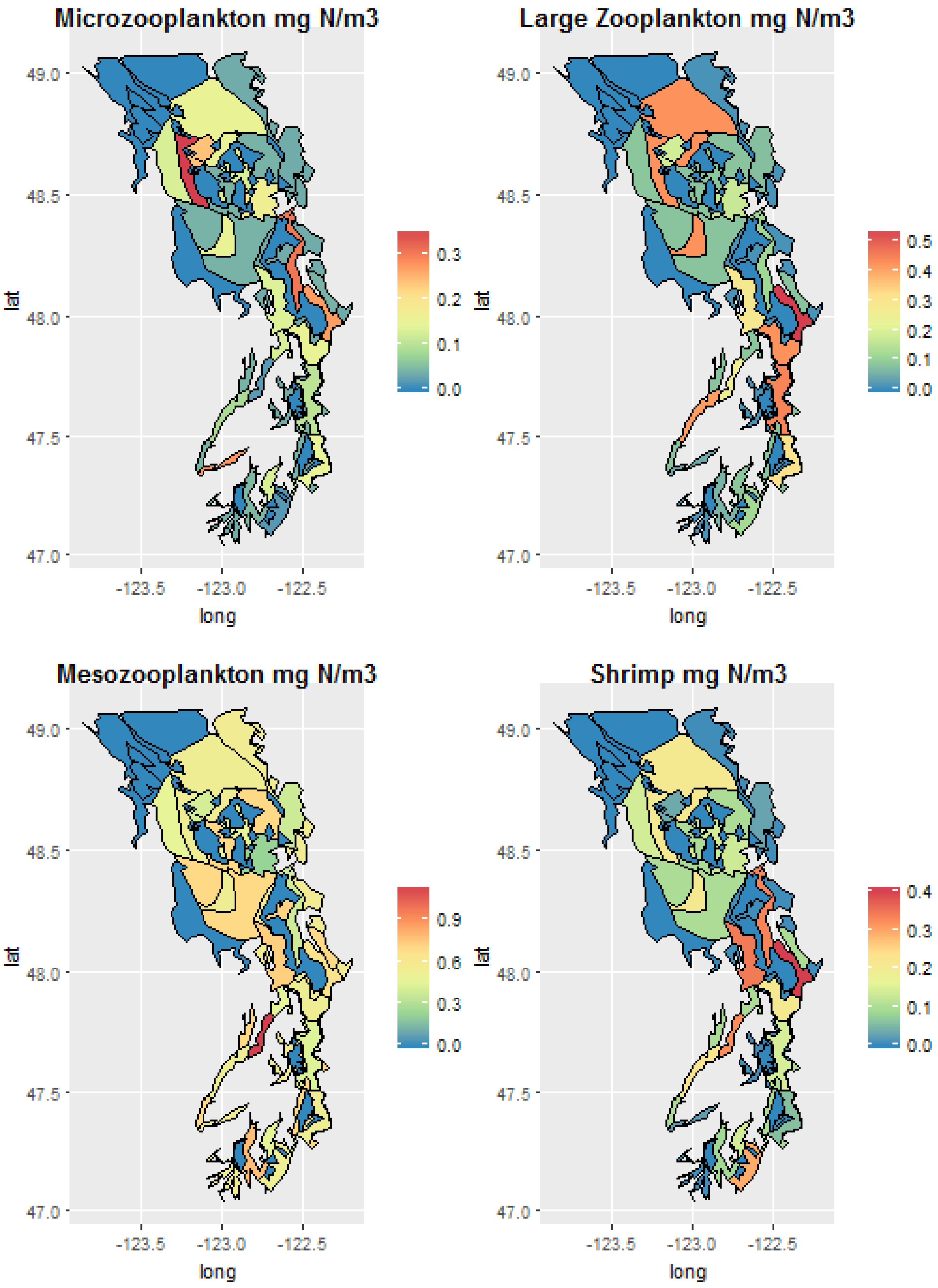

Figure 25. Map of zooplankton concentrations (mg N/m^3), taken from Keister and colleagues and extrapolated to unsampled Atlantis polygons. These concentrations were applied as initial conditions in surface 25 m for 1 Jan 2011.

tows to set initial mesozooplankton abundances. We assign this concentration (mg N/m^3) in the top 25 m (i.e., the top two Atlantis water column layers; Figure 25). The final biomass estimates in wet weight across the model extent were approximately 0.43 t/km^2 for microzooplankton, 2.3 t/km^2 for mesozooplankton, and 0.78 t/km^2 for large zooplankton.

Complementing the Keister et al. data, C. Greene (NWFSC) and colleagues carried out extensive sampling of zooplankton (and fish) in April–October 2011; ultimately, we use this to inform model initial conditions for gelatinous zooplankton but not mesozooplankton, for reasons detailed below. Sampling was conducted in Hood Canal, Whidbey Basin, South Sound, Main Basin (Central Sound and Admiralty Inlet), and Rosario Strait (Figure 26). We allocated sample locations from Greene et al. to Atlantis polygons. Two nets were used to sample zooplankton: a vertical net (250-µm mesh) sampled the entire water column, and a horizontal net (500-µm mesh) sampled the upper 10 m of water column horizontally. This provided density estimates (number/m^3) of copepods (functional group: mesozooplankton, or ZM) and jellyfish (functional group: gelatinous zooplankton, or ZG). 90% of the sites were shallower than 25 m depth, so we apply these zooplankton densities to our top 25 m, meaning the Atlantis depth layers from 0–5 m and 5–25 m. Density estimates from the horizontal tows were applied to the Atlantis 0–5 m layer. Density estimates for the 5–25 m layer (D_{5to25}) were calculated as:

$$D_{5to25} = (25 * D_{vertical} - 5 * D_{horizontal})/(25-5) \tag{7}$$

where $D_{vertical}$ and $D_{horizontal}$ are the densities from the horizontal and vertical nets at the same site.

Densities were converted to mg N/m^3 assuming carbon weights of 0.022 mg/copepod and 0.076 mg/jellyfish (based on carbon weights in the Keister et al. data described above), and a Redfield ratio conversion of 13% N out of total C:N:P. Ultimately we combined the jellyfish data from Greene et al. (Figure 27) with data from Keister et al. to set the Atlantis initial conditions (see next section for details). However, we did not apply the copepod information from Greene et al. because copepod abundance from this sampling was typically >10× higher than from the Keister et al. copepod sampling. We assume this is due to the sampling period in the Greene data, which occurred during periods of high seasonal productivity during spring–fall, while the Keister data also capture lower wintertime productivity, likely better reflecting conditions during the January model initialization. Seasonal signals in the abundance of copepods and all plankton, from both the Greene and Keister data, can be used for model validation in the future.

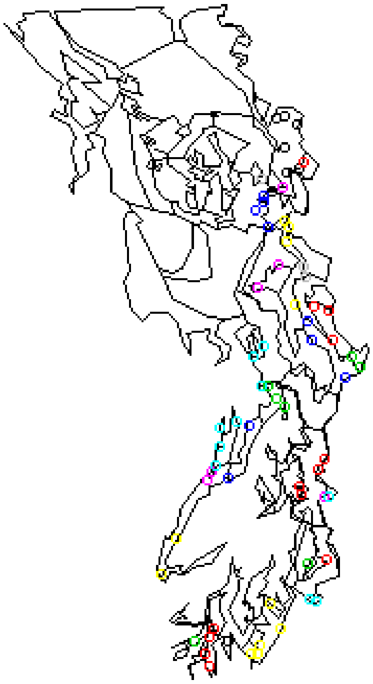

Figure 26. Map of zooplankton sampling locations by Greene et al. throughout Puget Sound, 2011. Sites are located in Hood Canal, Whidbey Basin, South Sound, Main Basin (Admiralty Inlet and Central Basin), and Rosario Strait.

Gelatinous zooplankton (ZG)

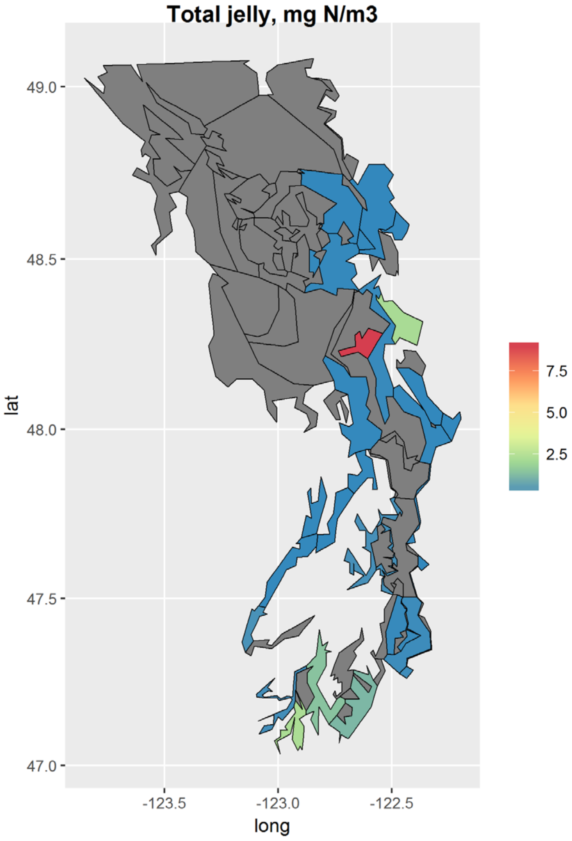

Figure 27. Jellyfish density derived from net sampling by Greene et al., as part of zooplankton sampling throughout Puget Sound, 2011.

Jellyfish have the potential to restructure energy flow through pelagic food webs because of their high rates of growth and reproduction, broad planktivorous diets that show overlap with fish diets, and ability to directly reduce recruitment into fish populations by preying on fish eggs and larvae (Brodeur et al. 2008, Ruzicka et al. 2016). Jellyfish can be major or even dominant components of the pelagic community in Puget Sound during the summer; their abundance varies by location and year, and is strongly influenced by latitude and Julian day (Rice 2007).

As discussed above, abundance of gelatinous zooplankton—especially smaller species—was based on zooplankton data from two sources: 1) J. Keister (personal communication) sampled throughout Puget Sound in 2014–17; the dataset includes gelatinous zooplankton identified under the categories “scyphozoans,” “larvacea,” “siphonophore,” and “ctenophore,” and 2) C. Greene (personal communication) sampled in 2011 using vertical plankton nets (250 µm mesh) and horizontal plankton nets (500 µm mesh). For both the Keister and Greene data sources, we interpolated missing data (per polygon) as described above. Final gelatinous zooplankton concentration (mg N/m^3, Figure 28) per polygon, for the 0–5 m layer, was taken as the average of the Greene et al. value for that polygon’s 0–5 m layer, and the value for that polygon (0–25 m) from Keister data. Similarly, concentration per polygon, for the 5–25 m layer, was taken as the average of the Greene et al. value for that polygon’s 5–25 m layer, and the value for that polygon (0–25 m) from the Keister data.

The zooplankton nets described above are likely to miss larger jellyfish entirely, and we therefore added an additional data source. Extensive surface trawl sampling of larger jellyfish and pelagic fish was undertaken in April–October 2011 by C. Greene and colleagues, concurrent with zooplankton sampling described above. Sampling was conducted in Hood Canal, Whidbey Basin, South Sound, Admiralty Inlet, Central Basin, and Rosario Strait. Tow dimensions were 0.5 km long, 3.1 m deep (from surface), and 6.1 m wide = 9,455 m^3 on average (Rice et al. 2012). We allocated sample locations from Greene and colleagues to Atlantis polygons. Figure 29 shows sampled densities of jellyfish. As for other zooplankton, we interpolated missing data (per polygon) based on the average of all sampled polygons of similar bottom depth (i.e., with the same number of Atlantis depth layers). We used this

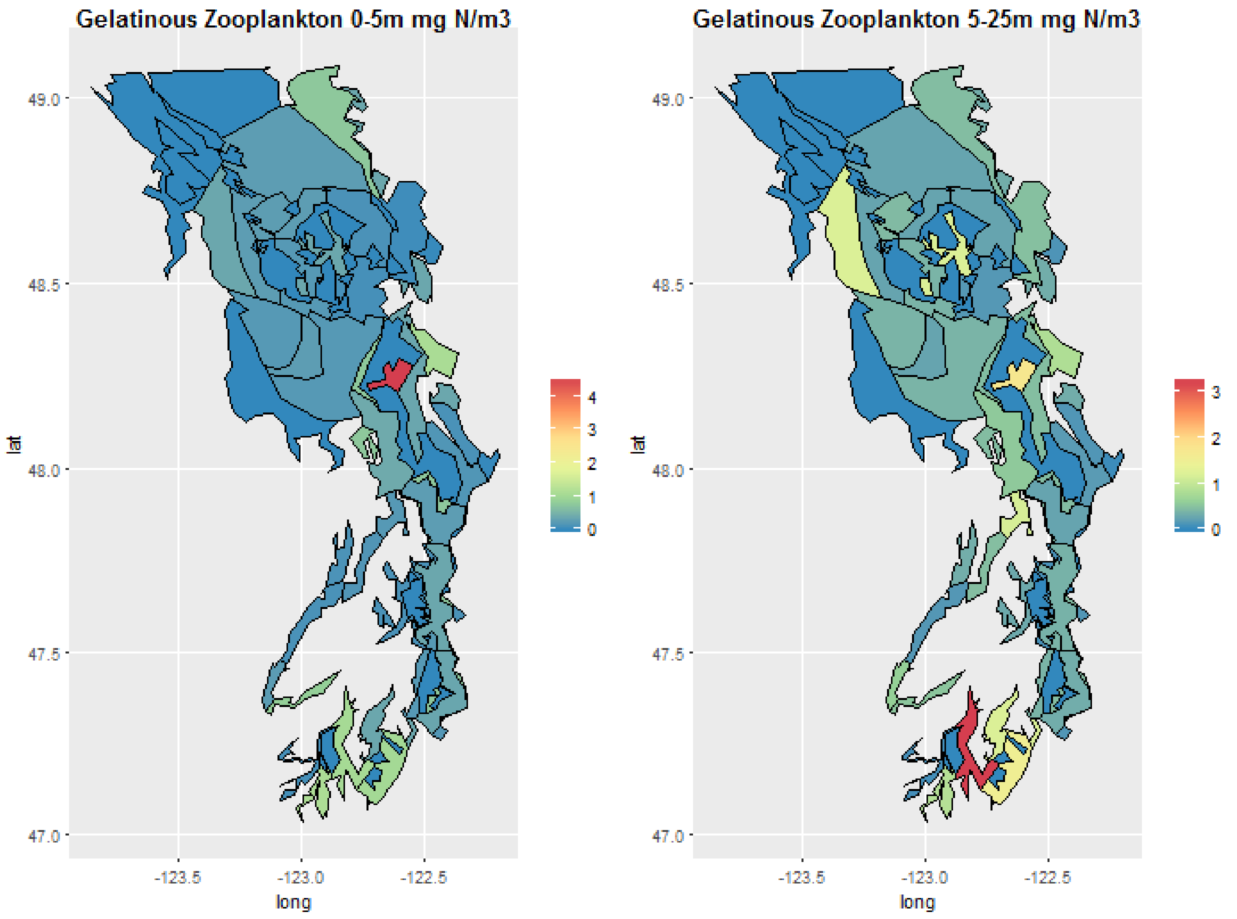

Figure 28. Maps of small gelatinous zooplankton concentrations (mg N/m^3), averaged over data from both Keister and Greene, and extrapolated to unsampled Atlantis polygons. These concentrations applied as initial conditions in surface 0–5 m and 0–25 m layers for 1 Jan 2011. (left) Concentrations in the 0–5 m Atlantis layer. (right) Concentrations in the 5–25 m Atlantis layer.

interpolated field, applied to the surface 25 m (the top two layers of the Atlantis domain), to estimate total biomass and spatial distribution of larger jellyfish. Total abundance of gelatinous zooplankton (per Atlantis polygon) was then taken as the sum of large and small jellyfish abundance. Total biomass is 142,197.7 t.

Zooplankton data from Fisheries and Oceans Canada

As described in Squid (SQX), zooplankton data were available from Canadian researchers (I. Perry, Fisheries and Oceans Canada, unpublished data). Due to the limited amount of spatial overlap with the Atlantis Puget Sound domain and the variety of sampling methodologies, we did not use these data to initialize the model. However, they can be compared to the other zooplankton data sources (Figure 30), and generally suggest zooplankton abundances intermediate between the lower abundances from the Keister et al. sampling and the higher abundance from Greene et al.

Squid (SQX)

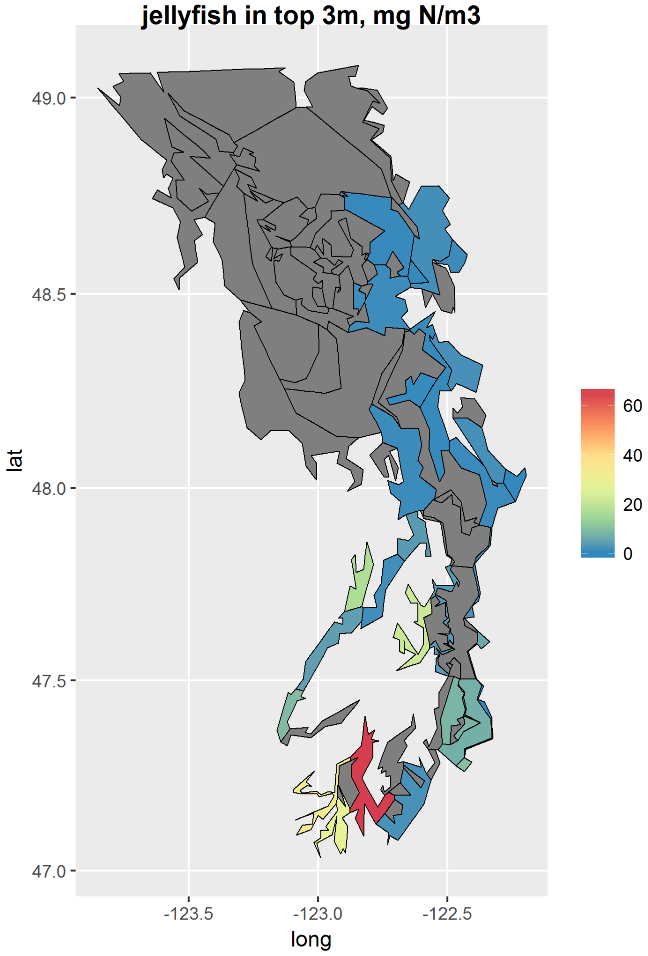

Figure 29. Large jellyfish density derived from surface trawl sampling by Greene et al. as part of fish and jellyfish sampling throughout Puget Sound, 2011.

Squid are a key link between lower trophic levels and vertebrates. The major squid species in Puget Sound is market squid, *Doryteuthis opalescens,* a small cephalopod found in offshore areas that spawns in nearshore areas (Recksiek and Frey 1978). Abundance of squid is poorly quantified in Puget Sound. This is true for market squid, but also for stubby squid (*Rossia pacifica*) and other species. Harvey et al. (2010) estimated 0.902 t/km^2 based on Ecopath balancing. We attempted to compare this Ecopath estimate to estimates of squid abundance in Canadian zooplankton sampling provided by the Institute of Ocean Sciences (M. Galbraith, personal communication); other net surveys mentioned previously in this document do not report squid.

Canadian zooplankton monitoring primarily occurs outside the Atlantis model domain, but 171 of 696 total samples fall within the Atlantis region (excluding “boundary boxes” 0 and 17; Figure 30). Sample locations in the Atlantis domain were primarily from the southern Strait of Georgia, the Gulf Islands area west of the San Juan Islands, and the eastern Strait of Juan de Fuca (especially Atlantis polygons 1, 4, and 5). These zooplankton samples derive from several methodologies and from a wide range of years: seven mesh sizes were used, ranging from 200–350 microns; sample time varied between day and night; and net types include bongo, SCOR, and Norpac. Bottom depths range from 7–334 m, with net tows typically sampling either the surface 20 m or the full water column. Samples were collected across 1980–2017, with more intense sampling in Puget Sound from 2015–17. Sampling took place typically from April–September, but in some cases occurred year-round.

Average density of squid from the Canadian zooplankton survey was only 0.00022 mg N/m^3, equating to only approximately six tons total for the model, likely due to net avoidance. Ultimately, for squid we rely on the Ecopath estimates of Harvey et al. (2010). Based on their estimates of 0.902 t/km^2, we initialize the model at 0.216 mg N/m^3 in the top 25 m, divided uniformly throughout the Atlantis domain; total biomass is 3,885.5 t.

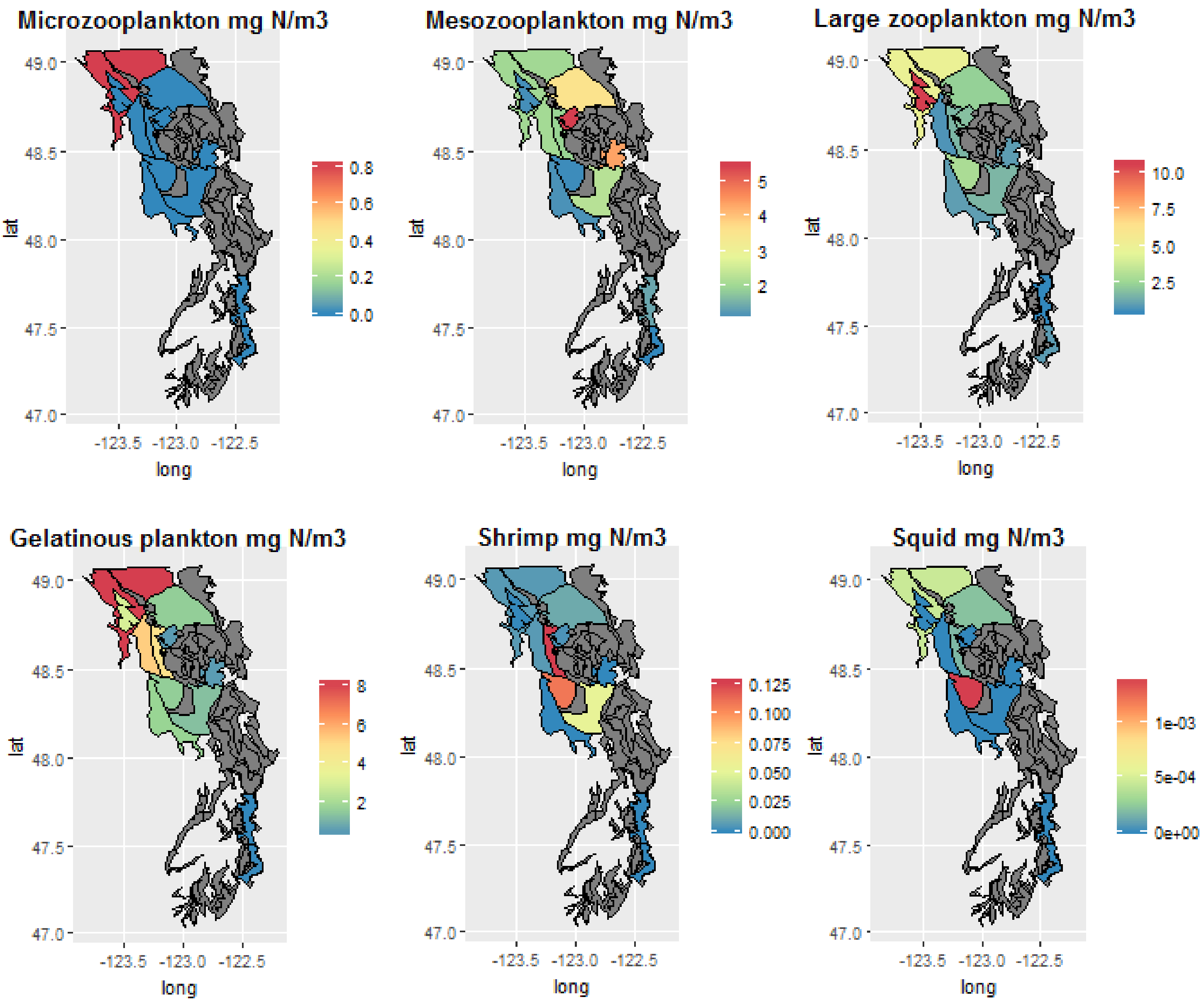

Figure 30. Zooplankton density in Puget Sound, derived from DFO data from 1980–2017.

Deep macrozoobenthos (BMD)

This functional group includes sea stars, predatory snails, and nudibranchs, as well as deposit feeders found in deeper areas, such as Ophiuroids. Some examples include: short-spined pink star (*Pisaster brevispinus*), flat mud star (*Luidia foliolata*), six-rayed star (*Leptasterias hexactis*), rose star (*Crossaster papposus*), sunflower sea star (*Pycnopodia helianthoides*), morning sun star (*Solaster endeca*), hairy Oregon whelk (*Fusitriton oregonensis*), Japanese oyster drill (*Ocinebra japonica*), and moon snail (*Polinices lewisii*). These species are part of benthic assemblages in Puget Sound that have remained stable through time (Nichols 2003). Sea stars include both predatory and scavenging species that can shape community composition through top-down control (Harvey et al. 2010). Starting in 2013, the northeastern Pacific Ocean experienced a mass mortality of sea stars, which led to a trophic cascade involving an increase in sea urchins and a subsequent increase in sea urchin grazing on kelp (Schultz et al. 2016). Biomass of deep macrobenthos was estimated using VAST on data from benthic fauna surveys carried out by PSAMP. For more details, see Analyses informing spatial abundance and density. Based on this model (Figure 31), we initialize the Atlantis model at an average of 73.3 mg N/m^2; total biomass is 69,339.8 t.

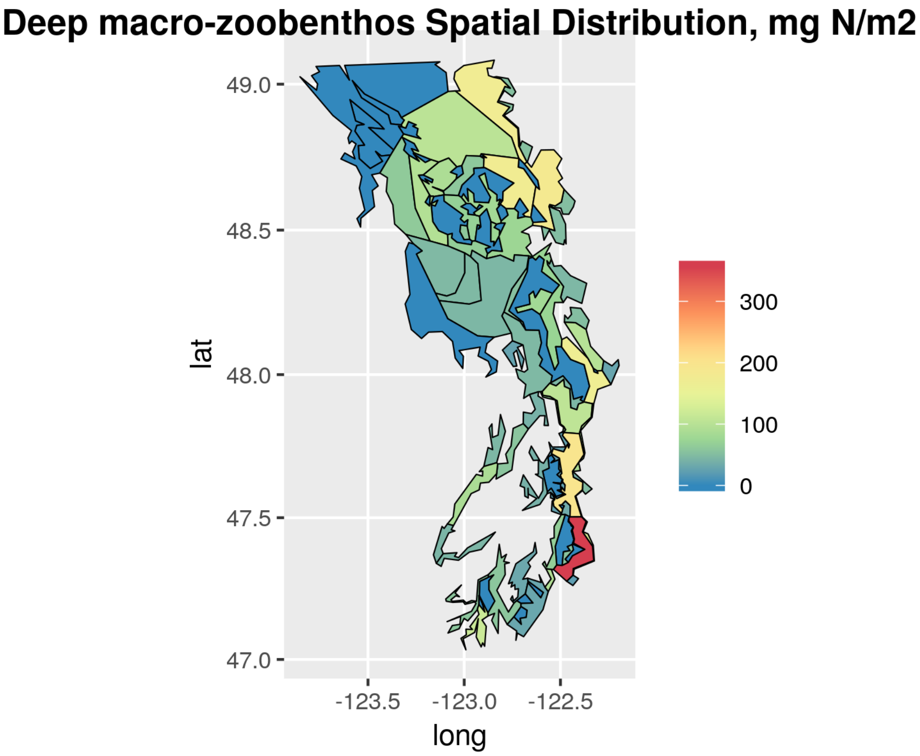

Figure 31. Deep macrozoobenthos density derived from benthic grab sampling, as part of PSAMP.

Deposit feeders (BD)

The deposit feeder functional group includes large sea cucumbers, small crustaceans, and deposit feeders, including the California sea cucumber (*Parastichopus californicus*), cumaceans, benthic-oriented copepods, amphipods, isopods, tanaidaceans, and other sea cucumbers. Sea cucumbers are detritivores that also ingest small infaunal organisms (Morris et al. 1980). The California sea cucumber is the only sea cucumber in Puget Sound that is commercially harvested; it is distinguished by its larger size, up to >40 cm (Harvey et al. 2010). Biomass of deep macrobenthos was estimated using VAST on data from benthic fauna surveys carried out by PSAMP. For more details, see Analyses informing spatial abundance and density. Based on this estimation (Figure 32), we initialize the model at an average of 272.7 mg N/m^2; total biomass is 235,904.4 t.

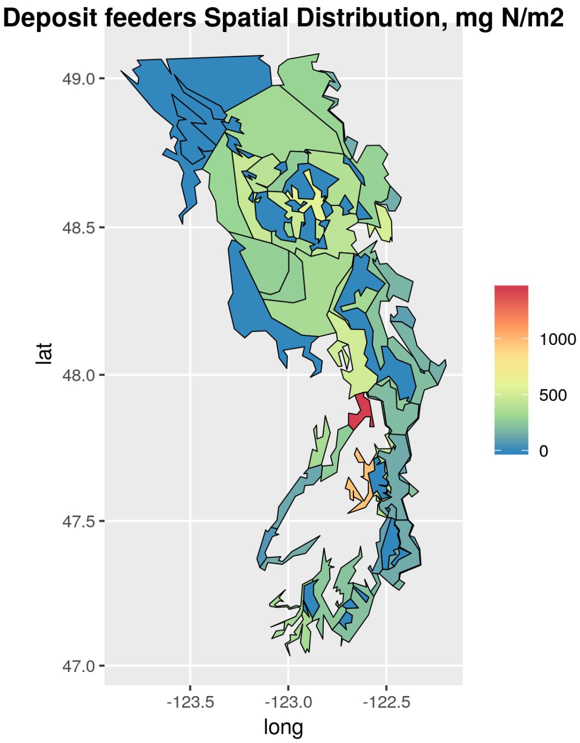

Figure 32. Deposit feeder density derived from geostatistical modeling of benthic grabs collected by PSAMP.

Benthic grazers (BG)

Benthic grazers include sea urchins, other grazers (such as small snails, limpets, and chitons), and other small grazers such as caprellid amphipods. Two of the dominant sea urchins belong to the genus *Strongylocentrotus,* the green sea urchin (*S. droebachiensis*) and the red sea urchin (*S. franciscanus*). Benthic grazers play an important role in determining the dynamics of seaweed and eelgrass communities in Puget Sound (Duggins et al. 2001). Sea urchins in particular act as ecosystem engineers by a) providing biogenic habitat structure and b) altering nutrient dynamics as they graze on seaweeds, detached algal detritus, or crustose coralline algae (Lowe et al. 2015). Biomass of benthic grazers was estimated using VAST on data from WDFW bottom trawl surveys. For more details, see Analyses informing spatial abundance and density. Based on this estimation (Figure 33), we initialize the model at an average of 1.17 mg N/m^2; total biomass is 950.9 t.

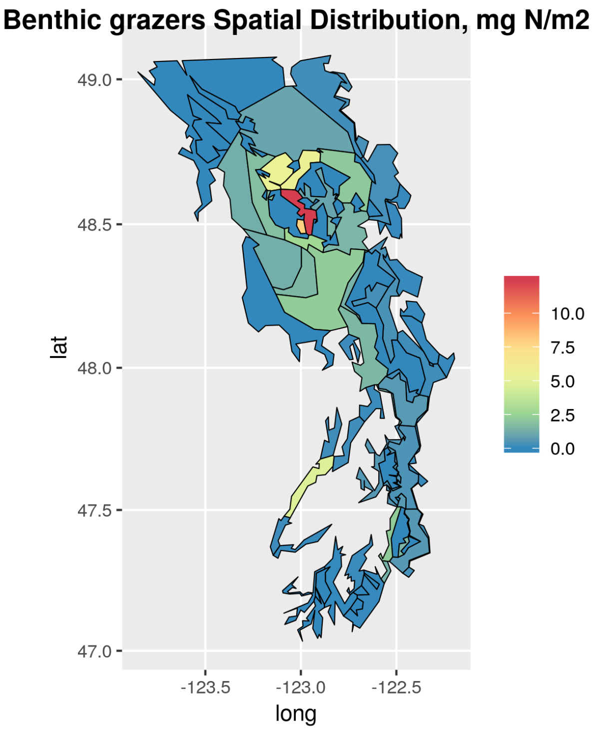

Figure 33. Benthic grazer density estimated using VAST on data from WDFW bottom trawl surveys.

Octopus (BMS)

There are two common species of octopus in Puget Sound: the red octopus (*Octopus rubescens*) and the Pacific giant octopus (*Enteroctopus dofleini*). Octopus have complex predation strategies, including acting as “switching predators” that stabilize prey populations by feeding preferentially on the most abundant species and targeting prey with specific nutrient content (Onthank and Cowles 2011). There are no estimates of octopus biomass in Puget Sound and we could not derive abundance estimates from VAST modeling of benthic grab or bottom trawl data; likely, this species is missed by most sampling methods given its habit of hiding in rocks. Harvey et al. (2010) used the mass balancing routine of Ecopath to estimate the initial octopus biomass in central Puget Sound

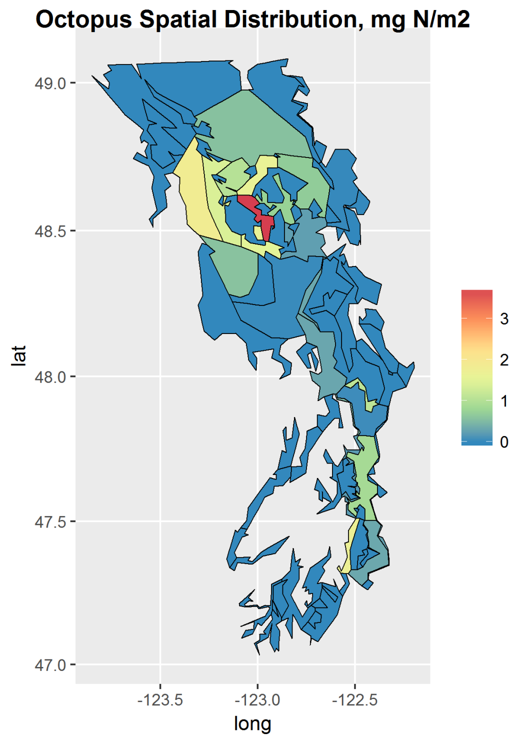

Figure 34. Octopus density derived from the estimate by Harvey et al. (2010), scaled for the proportion of rock habitat in each model polygon.

as 1.158 t /km^2. We used this estimate (Figure 34), scaled for the proportion of rock habitat in each model polygon. This results in a biomass estimate of 328.9 t. We initialized the model at an average 0.36 mg N/m^2.

Dungeness crab (DUN)

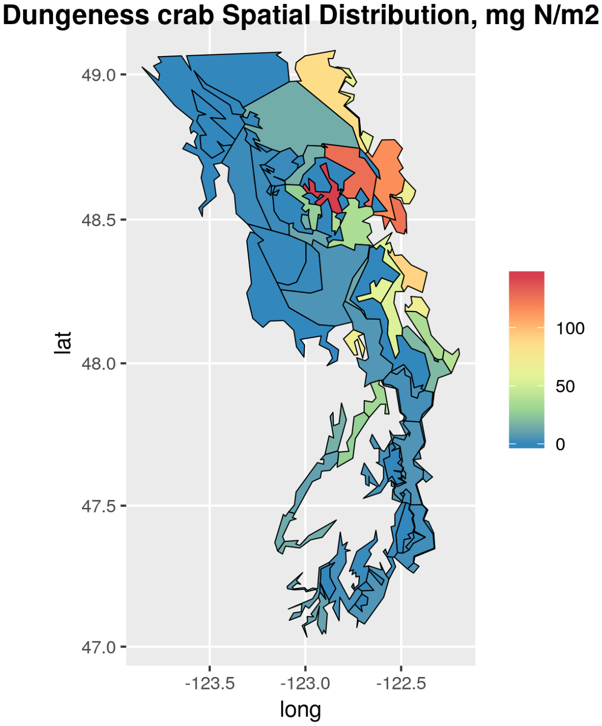

Figure 35. Dungeness crab density estimated using VAST on data from WDFW bottom trawl surveys.

The Dungeness crab (*Cancer magister*) is a culturally and economically important species in Puget Sound. Small juveniles are found in nearshore habitats, including eelgrass, clam, and oyster shell deposits and sand flats, and then move out of intertidal habitats (McMillan et al. 1995); as adults, they are found in sandy or muddy areas deeper than 100 m (Dethier et al. 2006). Ovigerous females return to intertidal habitats to deposit their eggs (Fernandez et al. 1993). Dungeness crab are modeled as a biomass pool, like other invertebrate groups. Life-history parameters were obtained from multiple sources (Armstrong et al. 1981, Collier 1983, Orensanz and Gallucci 1988, Smith and Jamieson 1989, Wainwright et al. 1992, Zhang et al. 2004, Dethier et al. 2006, Toft et al. 2014, Gamblewood et al. 2018). Biomass of Dungeness crab was estimated using VAST on data from WDFW bottom trawl surveys; for more details, see Analyses informing spatial abundance and density. Based on this estimation (Figure 35), we estimate a biomass of 21,915.3 t, or an average of 2.9 t/km^2. As a comparison, Harvey et al. (2010) used Ecopath to estimate a biomass of 0.757 t/km^2 for juvenile *Cancer* crabs and 0.547 t/km^2 for age-1+ crabs. As another comparison, Palsson (Palsson 2003) estimated a Dungeness crab biomass of 5,300 t in the Strait of Georgia and the San Juan archipelago. We expect that the fishery removes a high proportion of adult males (see Catch Reconstruction). During their pelagic larval stage, Dungeness crab feed on phytoplankton and zooplankton and are a key prey source for many fish and seabirds (Harvey et al. 2010). After settlement, the relative importance of sources of mortality, including predation, fishing, and senescence, changes dramatically with increasing size (Harvey et al. 2010). Adult Dungeness crabs are likely opportunistic generalists that feed on fish and invertebrates, including bivalves, crustaceans, forage fish (e.g., osmerids), flatfish (sanddabs), and demersal fish; diet composition was drawn from Butler (1954), Gotshall (1977), and Armstrong et al. (1981).

Crabs (BML)

The crabs functional group includes crabs from the *Cancer* genus—the red rock crab (*Cancer productus*), the graceful crab (*C. gracilis*), and the pygmy rock crab (*C. oregonensis*)—as well as smaller crabs from the family Majidae, the superfamily Paguroidea, and the family Porcellanidae. This group is significant due to the crabs' role as consumers and scavengers in benthic habitats; small crabs are abundant consumers of primary producers and detritus, and a major food source for other invertebrates and fish (Harvey et al. 2010). Biomass of crabs was estimated using VAST on data from benthic fauna surveys carried out by PSAMP. For more details, see Analyses informing spatial abundance and density. Based on this model (Figure 36), we initialize the model at an average of 11.03 mg N/m^2; total biomass is 9,704 t. Diet composition was informed by the descriptions of crab feeding habits in Puget Sound by Knudsen (1964) and Baker (1988), and the diet used by Harvey et al. (2010) for *Cancer* crabs and small crustaceans.

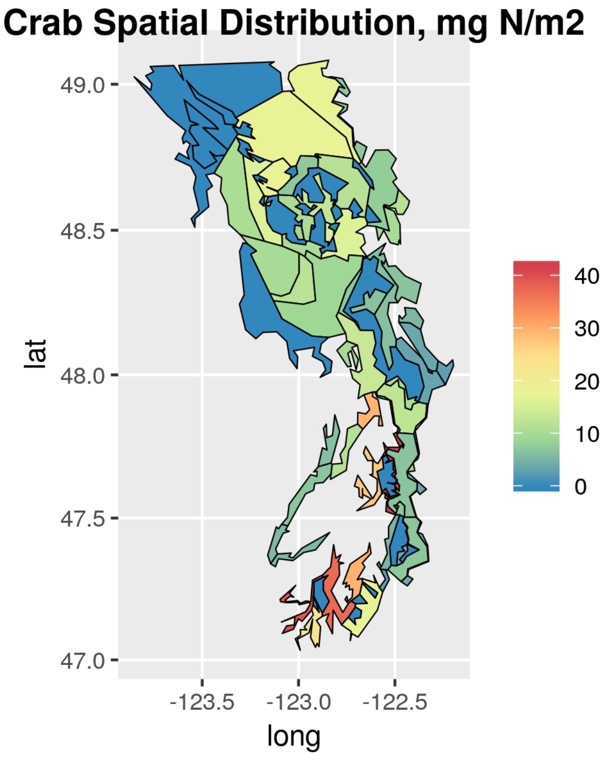

Figure 36. Crab density derived geostatistical modeling of benthic grabs collected by PSAMP.

Shrimp (PWN)

The shrimp group is composed of numerous species, including shrimp that are primarily benthic from the genera *Crangon*, *Pandalus*, and *Pandalopsis*, and pelagic and benthic shrimp in the family Mysidae. Shrimp occupy varied depths on a diel basis, with many species more active or moving up in the water column to forage at night (Harvey et al. 2010); others may move across depth layers as a function of seasonal temperature or reproductive status (Siegfried 1989). Many shrimp species are important prey for higher trophic levels, while *Pandalus* and *Pandalopsis* shrimp support important commercial and recreational fisheries in Puget Sound (Harvey et al. 2010). We base abundance estimates on

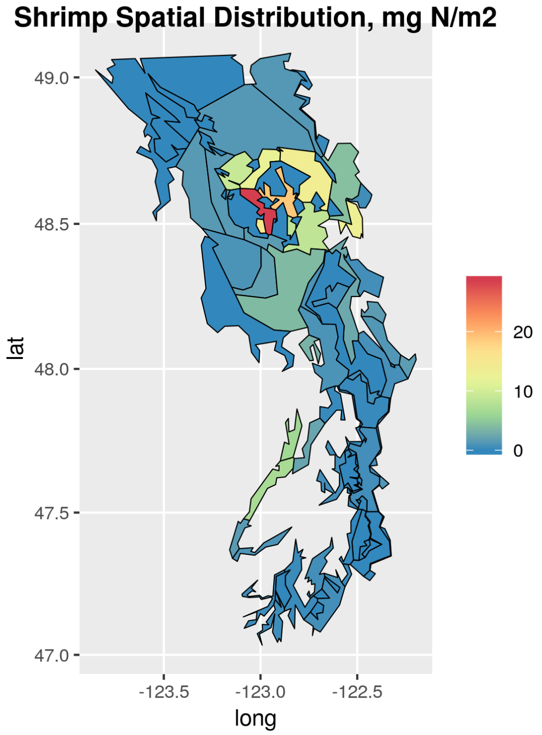

Figure 37. Benthic shrimp density estimated using VAST on data from WDFW bottom trawl surveys.

two different net surveys, one for pelagic and one for benthic shrimp. Abundance of pelagic shrimp was based on zooplankton data from J. Keister (personal communication) sampled throughout Puget Sound in 2014–17. This analysis is described in the zooplankton section. This provided biomass estimates ranging as high as 0.4 mg N/m^3 in some "hotspot" Atlantis polygons; note that this assumes that pelagic shrimp inhabit the surface 25 m. Biomass of benthic shrimp was estimated using VAST on data from WDFW bottom trawl surveys. For more details, see Analyses informing spatial abundance and density. Biomass estimates from the benthic survey range as high as 7.5 mg N/m^2 in some hotspot polygons. We summed the biomass estimates from these surveys and assumed roughly equal vertical distributions split between the bottom layer and the surface 25 m (Figure 37). Total biomass is 2,659.18 t.

Benthic filter feeder (BFF)

This functional group includes barnacles, thatched barnacles, sponges, colonial hydrozoans, sea pens, tube-dwelling worms such as serpulids, horseshoe worms, bryozoans, and tunicates such as the stalked sea squirt and solitary sea squirt. Filter feeders feed on plankton and detritus. They are prey for multiple species, and provide biogenic habitat structure for fish and invertebrates (Harvey et al. 2010). Some species of sponges and bryozoans grow on other organisms, such as seaweed, eelgrass, or on the backs of crabs, or on the shells of scallops (Kozloff 1983). Shallow-water barnacle species such as *Chthalamus dalli*, *Balanus glandula*, and the thatched barnacle, *Semibalanus cariosus*, are found along intertidal areas affixed to natural and artificial hard substrates (Harvey et al. 2010). The subtidal giant barnacle (*Balanus nubilus*) is found in waters up to 90 m deep (Morris et al. 1980), where it may reach a diameter of more than 10 cm and serve as habitat for a variety of other organisms, such as sponges and small fishes (Harvey et al. 2010). This group includes non-indigenous tunicates—such as the stalked sea squirt (*Styela clava*), the solitary sea squirt (*Ciona savignyi*), and *Didemnum* spp.—that were likely introduced to Puget Sound via ballast water transfer or attached to ship hulls (Cordell et al. 2013). Within the Atlantis model, barnacles are considered a habitat cover, as they provide biological substrate. To estimate

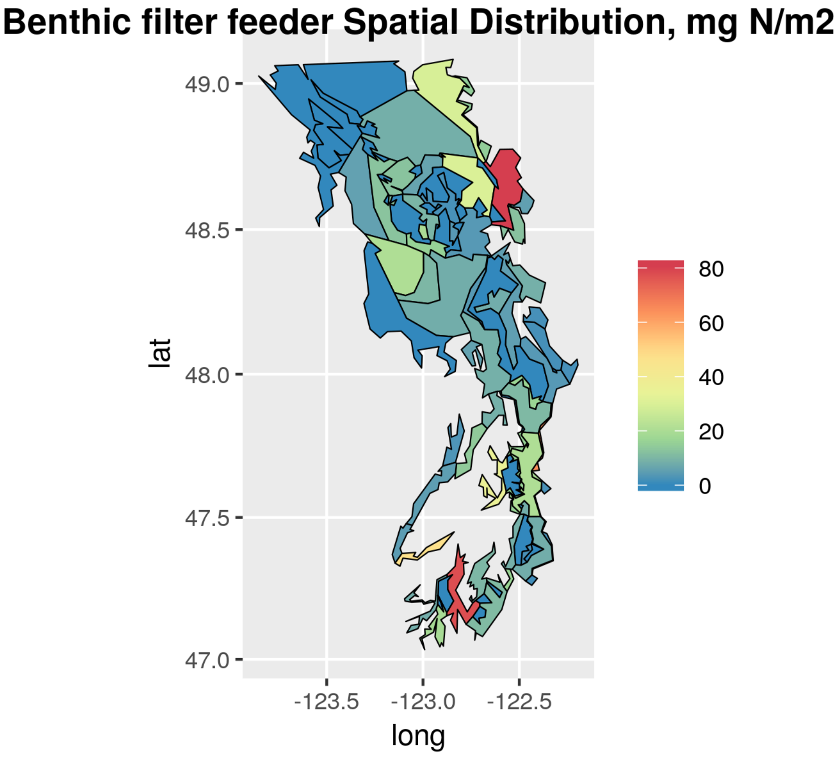

Figure 38. Benthic filter feeder density derived geostatistical modeling of benthic grabs collected by PSAMP.

percent cover for this functional group, we used data from benthic monitoring in the San Juan Islands, which found mean barnacle cover was 0.017% (Dethier and Berry 2008). Biomass of benthic filter feeders was estimated using VAST on data from benthic fauna surveys carried out by PSAMP. For more details, see Analyses informing spatial abundance and density. Based on this model (Figure 38), we initialize the model at an average of 13.35 mg N/m^2; total biomass is 11,969.1 t.

Bivalves (BIV)

This functional group includes bivalve mollusks except for geoducks (next section). The group includes bivalves across a range of sizes from very small clams, such as *Transennella tantilla*, amethyst gemclam (*Gemma gemma*), Charlotte macoma (*Macoma carlottensis*), and Baltic macoma (*M. balthica*), to large clams, such as the horse clam (*Tresus capax*) and the butter clam (*Saxidomus giganteus*), as well as farmed oysters and mussels, including the blue mussel (*Mytilus edulis*), the non-native Pacific oyster (*Crassostrea gigas*), and the native Olympia oyster (*Ostrea conchaphila*). Bivalves are important filter feeders that can reach high densities in Puget Sound (Harvey et al. 2010). Clams are found in soft sediments, while mussels and oysters are found on stable substrates, including anthropogenic structures, between the intertidal zone and up to 36 m deep (Monaco et al. 1991). Oysters form large reefs that are used as habitat by many species, and are a valuable fishery resource for commercial aquaculture and recreational harvesters (Harvey et al. 2010). Biomass of clams was estimated using VAST on data from benthic fauna surveys carried out by PSAMP; for more details, see Analyses informing spatial abundance and density. The estimates based on this model (Figure 39) were further adjusted based on the available soft habitat per polygon (see Physical habitats). We initialize the model at an average of 743.9 mg N/m^2, equivalent to a biomass of 418,439.8 t.

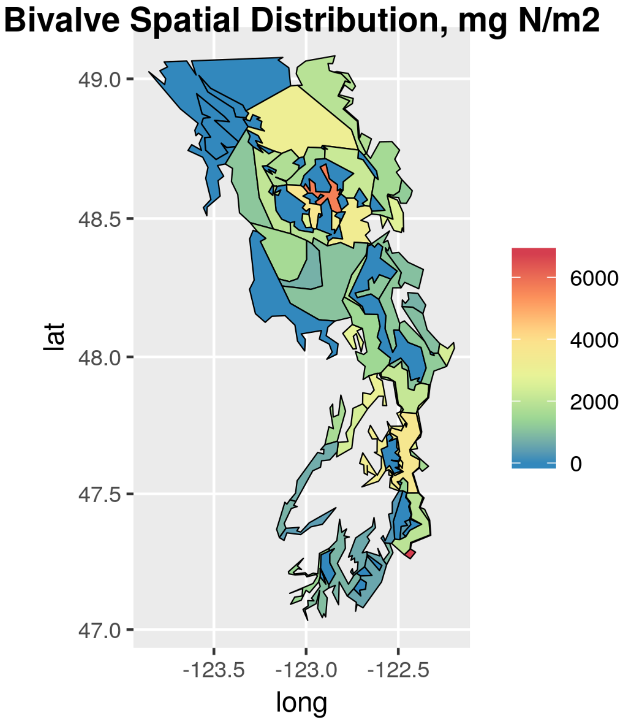

Figure 39. Bivalve density derived using geostatistical modeling of benthic grab data collected by PSAMP.

Geoducks (GEC)

Geoducks (*Panopea generosa*) were placed in a separate functional group due to their unique life history and growth compared to the species grouped in the bivalve functional group (previous section), and because they dominate benthic infaunal communities in many parts of Puget Sound (Andersen 1971). Geoducks are the largest burrowing clams in North America.

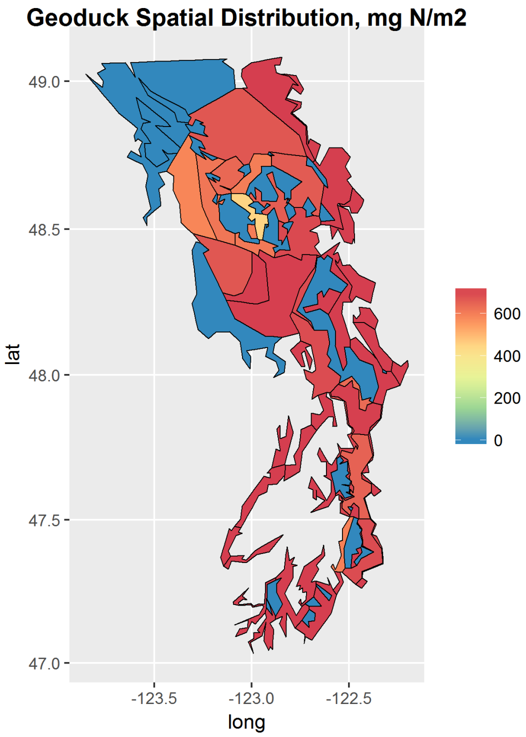

Figure 40. Geoduck density derived from the estimate of Harvey et al. 2010, scaled for the proportion of soft habitat in each model polygon.

They live buried in muddy substrates between coastal areas to over 110 m deep and up to a meter below the sediment surface, where they can avoid most predators (Andersen 1971, Liu et al. 2015). They are an important aquaculture species and support the most valuable dive fishery on the west coast of North America, including Puget Sound (Harvey et al. 2010, Liu et al. 2015). Predation on geoduck larvae and juveniles is likely high (Harvey et al. 2010). After age-2, mortality is low; geoduck can be preyed upon by spiny dogfish (*Squalus suckleyi*), sea stars, and cabezon (*Scorpaenichthys marmoratus*), and moon snails (*Lunatia lewisi*) may prey on juvenile geoducks (Andersen 1971). There is no quantitative data on geoduck diet; both adults and juveniles feed by filtering phytoplankton and detritus (Campbell et al. 2004). Geoducks are modeled as a biomass pool, as with other invertebrate groups. Life history parameters were obtained from multiple sources (Andersen 1971, WoJotira et al. 1989, Bradbury and Tagart 2000, Harvey et al. 2010, Liu et al. 2015). McDonald et al. (2015) estimated geoduck density in Hood Canal as 0.5 individuals/m^2 in sandy bottoms and 0.1 in cobble/sand. We use these estimates and the mean weight for geoducks reported by Liu et al. (2015) of 0.82 kg, scaled for the proportion of soft habitat in each model polygon, accounting only for depths <100 m. This results in a biomass estimate of 206,257.6 t, or an average 261.3 mg N/m^2 (Figure 40).

Carnivorous infauna (BC)

Carnivorous infauna include annelids (polychaetes), sipunculans, nemerteans, and turbellarians. Annelids have been the most abundant taxa of worms captured in benthic grab samples in Puget Sound over the last 30–40 years (Nichols 2003). Biomass of carnivorous infauna was estimated using VAST on data from benthic fauna surveys carried out by PSAMP. For more details, see Analyses informing spatial abundance and density. Based on this model (Figure 41), we initialize the model at an average of 189.91 mg N/m^2, or a total biomass of 154,709 t.

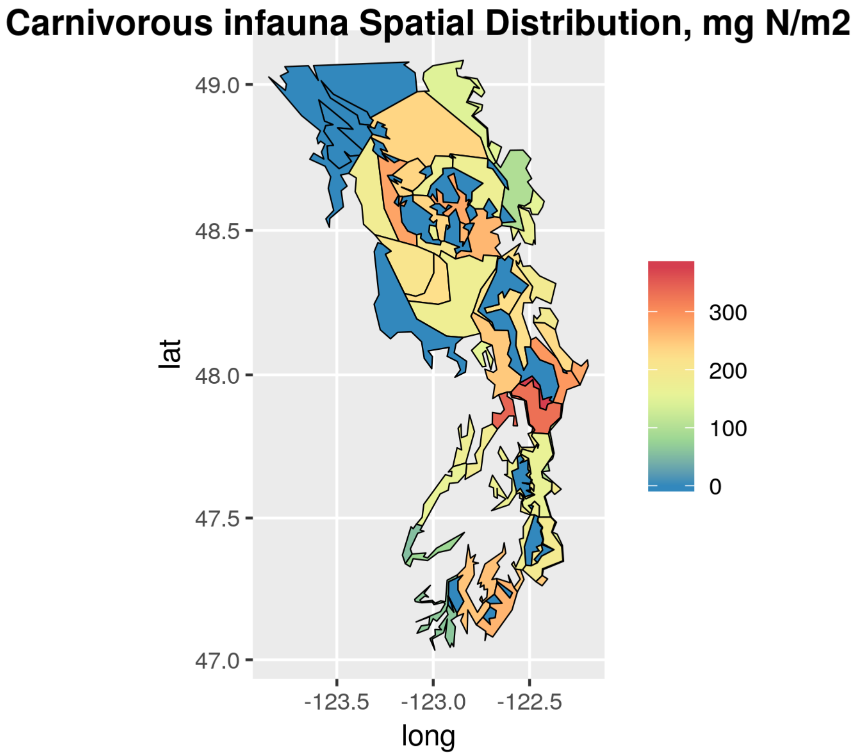

Figure 41. Carnivorous infauna density derived through geostatistical modeling of benthic grab data collected by PSAMP.

Pacific herring

Herring (*Clupea pallasii*) are a major forage fish species in the eastern Pacific Ocean and a vital component of the Puget Sound ecosystem (Siple and Francis 2016, Sandell et al. 2019). The spawning biomass of herring in Puget Sound was selected as a vital sign indicator of the health of the sound by the Puget Sound Partnership in 2010. The Puget Sound herring population contains roughly 20 subpopulations that show differences in spawning timing and behavior, similar growth rates and variability, and overall independent dynamics (Siple and Francis 2016, Sandell et al. 2019). In particular, long-term declines in the once-abundant Cherry Point subpopulation are of particular concern (Figure 42), while, in aggregate, there is relative stability for the other subpopulations. Herring spawn on vegetation within sheltered bays, just below the intertidal zone (Hay 1990).

We parameterized the spatial distribution of herring to capture the broad distribution during the nonspawning period, and fidelity to distinct areas during the spawning period. During the nonspawning period (Figure 43), we parameterized spatial distribution based on VAST analysis (see Analyses informing spatial abundance and density) of pelagic surveys conducted aboard the RV *Ricker*. We also compared this to spatial distributions (Figure 44) from 2011 surface trawls by C. Greene (discussed in Gelatinous zooplankton), but ultimately used the VAST spatial distributions to parameterize Atlantis. During the spawning period (in the model, 15 January–15 April), distribution is parameterized based on locations of documented spawning areas through 1991 (Figure 45), obtained from A. Lindquist (WDFW, unpublished data), and shown on this Forage Fish Spawning Map.[10]

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[10] https://www.arcgis.com/home/item.html?id=19b8f74e2d41470cbd80b1af8dedd6b3

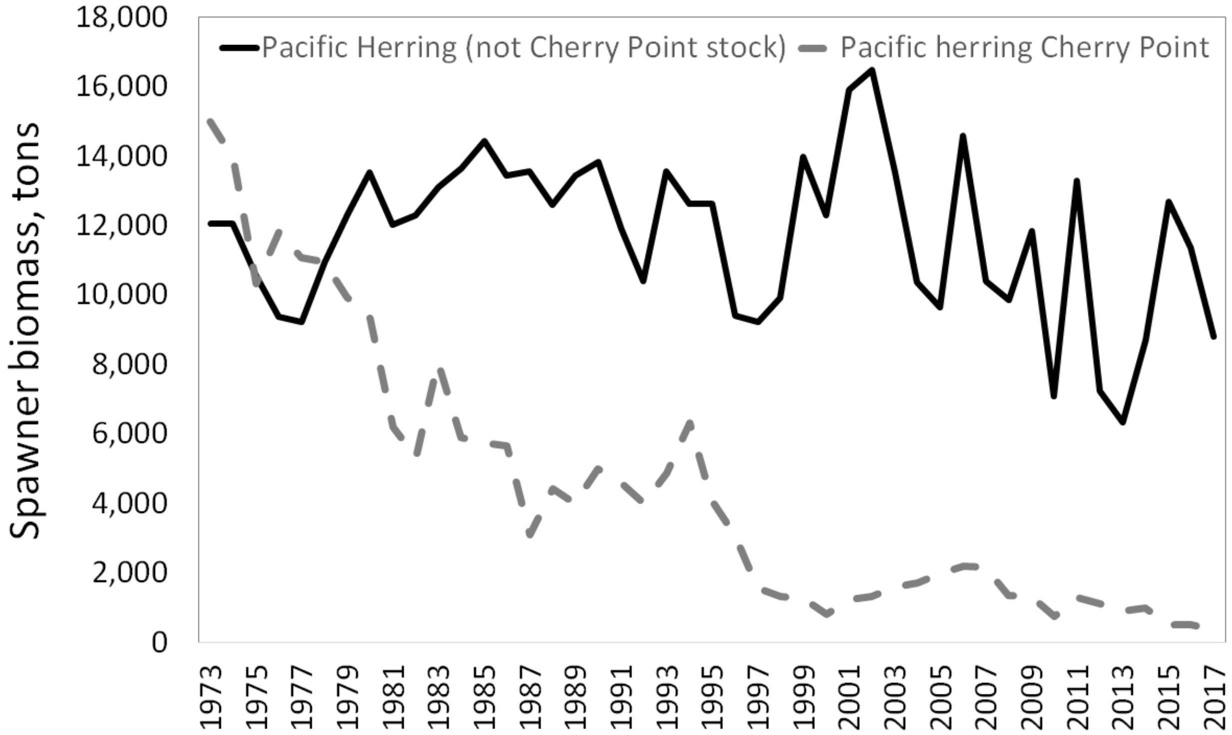

Figure 42. Pacific herring biomass trends for Atlantis Puget Sound domain (T. Sandell, WDFW, personal communication).

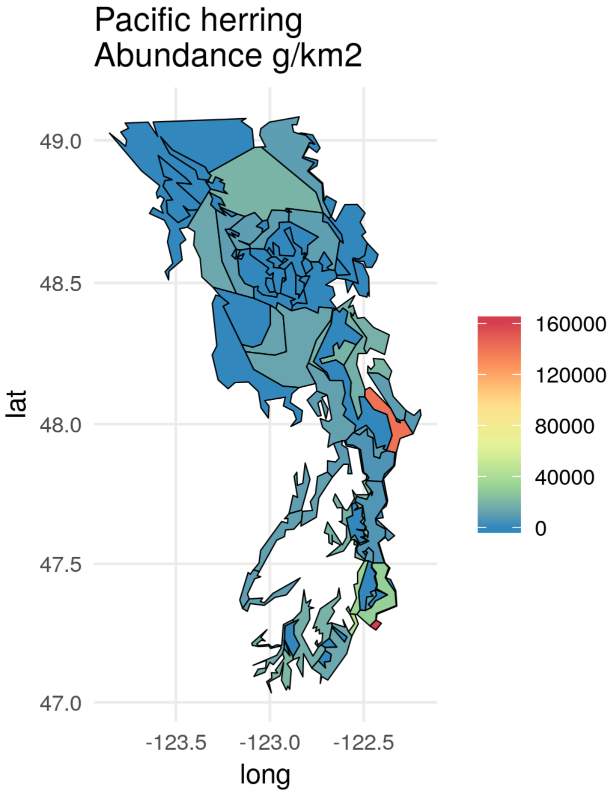

Figure 43. Herring density in summer, from VAST analysis of RV *Ricker* surveys, plotted as g ww/km^2.

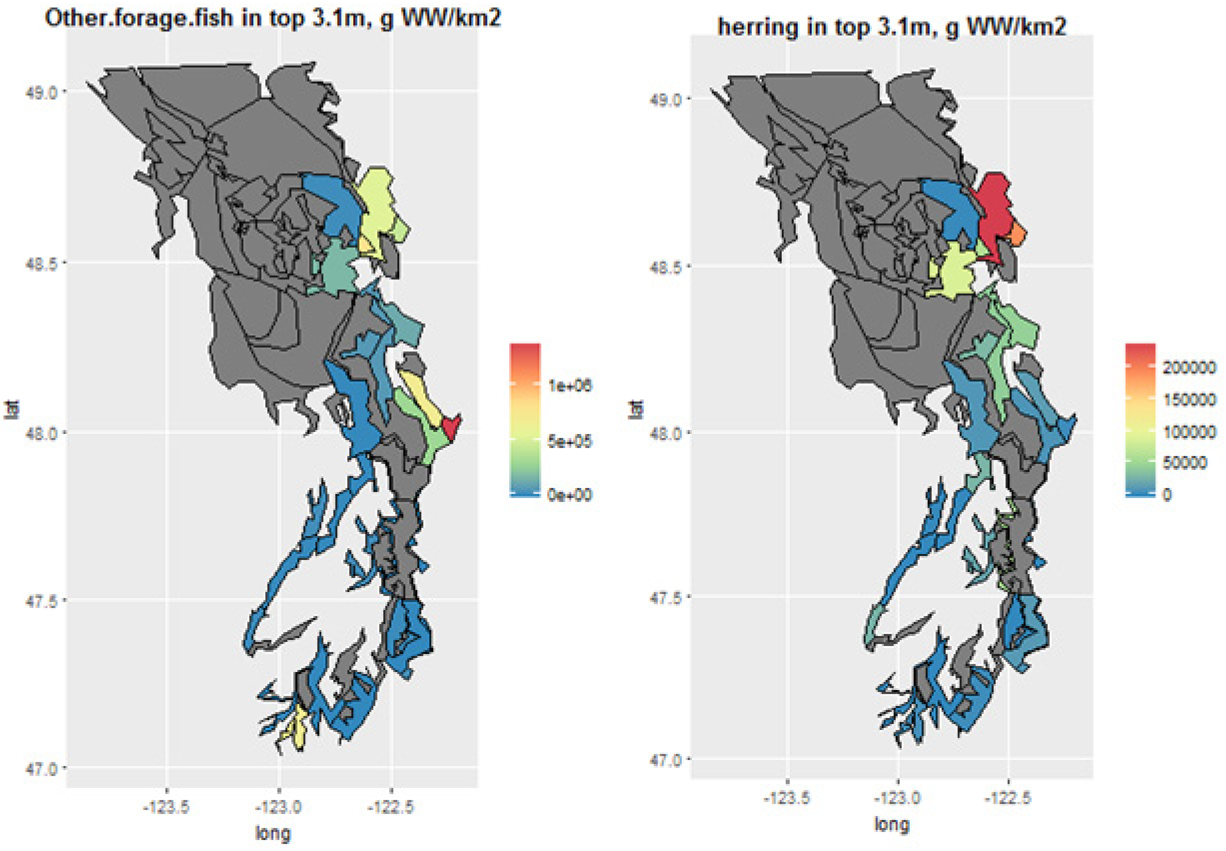

Figure 44. Herring and small pelagic fish ("other forage fish") density in summer, from surface trawl data for 2011 provided by C. Greene (NWFSC), plotted as g ww/km^2.

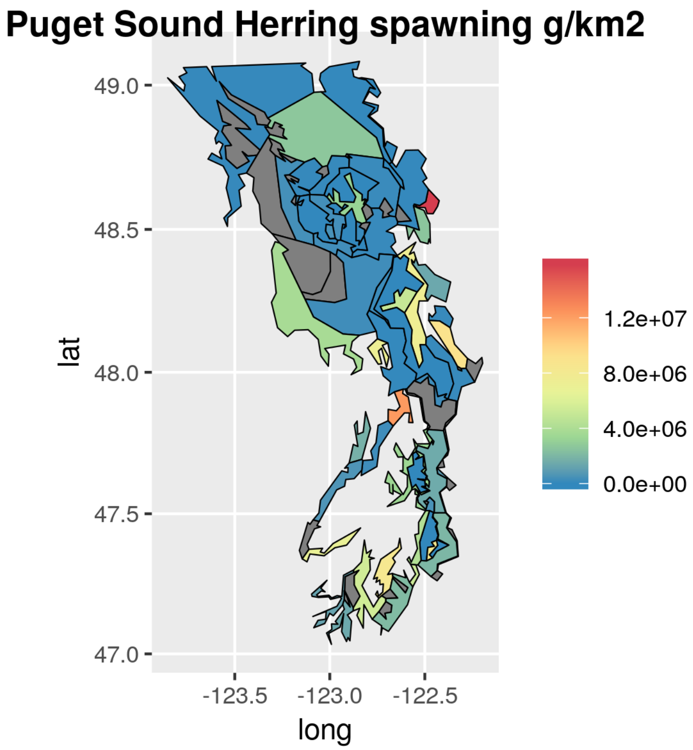

Figure 45. Pacific herring, Puget Sound density during the spawning season, plotted as g ww/km^2.

Pacific herring, Puget Sound (HEP)

This group includes all herring populations in Puget Sound except for the Cherry Point stock. Life-history parameters were obtained from several sources (Bargmann 1998, Harvey et al. 2010, Stick et al. 2014), and we model this group after the Quilcene Bay herring stock, the stock with the highest average spawning biomass from 1973–2017 (Stick et al. 2014, Sandell et al. 2019). Abundance estimates are based on both egg deposition surveys, which take place during the spawning season, and acoustic surveys of pre-spawning aggregations (carried out before 2009), which occur before the onset of spawning at each site (Sandell et al. 2019). We estimated biomass in the model area from the average spawning biomass of all herring populations (except for Cherry Point) between 2009–13 (Stick et al. 2014); this estimate was 8,578 tons, which we increased by 50% to account for nonspawners, for a final biomass estimate of 12,868 tons. Proportion of biomass allocated to each age class was determined by the average proportional 2011 biomass at age of spawner herring by stock, weighted by biomass (Stick et al. 2014). We model migration for this functional group after the Quilcene Bay herring stock. This stock shows seasonal migrations to offshore feeding grounds during the summer (Stick et al. 2014); in the model, herring leave the model starting 1 July and return 15 September (Table 7). Tagging studies suggest that migrating herring from Puget Sound move to feeding grounds off the west coast of Vancouver Island (Stout et al. 2001).

Pacific herring, Cherry Point (HEC)

The Cherry Point herring stock is genetically distinct from Squaxin Pass and the other Puget Sound areas (Beacham et al. 2008); this genetic distinctiveness is likely a result of late spawn timing (Small et al. 2005). This was historically the largest stock in Washington State, but it has suffered a dramatic decline since the 1970s (Gustafson 2005). The annual mortality rate for the Cherry Point stock is estimated at 0.68 (Landis and Bryant 2010). We initialize biomass for this group as the average spawning biomass between 2009–11, taken from Stick et al. (2014). The average, 988 tons, was increased by 50% to account for nonspawners, and the final biomass estimate was 1,482 tons. Biomass distribution by age class was determined by the average proportional 2011 biomass at age of spawner herring by stock, weighted by biomass (Stick et al. 2014). The

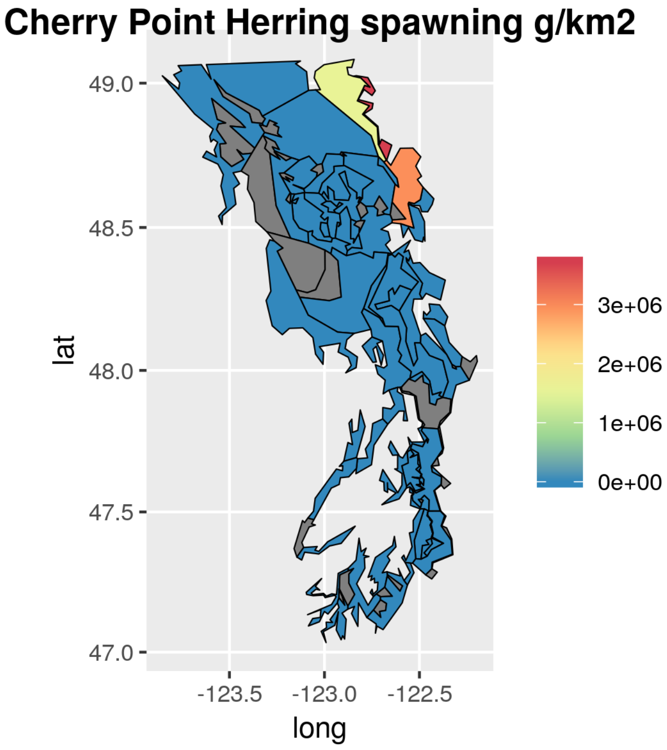

Figure 46. Cherry Point Pacific herring density during the spawning season, plotted as g ww/km^2.

Cherry Point stock spawns between mid-March and June in the intertidal and subtidal nearshore areas between Point Roberts in the north to the base of the Lummi Peninsula in the south (Landis et al. 2004). This migratory stock then moves to feeding grounds on the coastal shelf and Strait of Juan de Fuca during the summer (Gao et al. 2001, Landis and Bryant 2010), returning to Puget Sound in the fall months (Therriault et al. 2009); in the model, herring leave the model starting 1 July and return 15 September (Table 7). We determined fall distribution using VAST on data from RV *Ricker* pelagic surveys (Figure 46). For more details, see Analyses informing spatial abundance and density.

Small planktivorous fish (FPS)

The small planktivorous fish group includes forage fish species—Pacific sandlance (*Ammodytes hexapterus*), surf smelt (*Hypomesus pretiosus*), longfin smelt (*Spirinchus thaleichthys*), eulachon (*Thaleichthys pacificus*), northern anchovy (*Engraulis mordax*), and Pacific sardine (*Sardinops sagax*). Forage fish are crucial conduits of mass and energy between lower and upper trophic levels in Puget Sound, and between habitats, for example moving between marine areas and streams or inshore and offshore areas (Harvey et al. 2010). Forage fish are important prey items for a variety of birds, fish, and mammals (Pinto et al. 1984). Forage fish use intertidal habitats across Puget Sound to spawn (Penttila 2007). This group includes species that occupy different habitats, including: northern anchovy, which is pelagic; surf smelt, which lives in nearshore areas; and sandlance, which burrows into nearshore sediments in diurnal and seasonal cycles (Quinn 1999). The only spawning population of longfin smelt is found in the Nooksack River and adjacent marine waters in Bellingham Bay, Skagit and San Juan Counties (Penttila 2007). Life-history parameters are based on Pacific sandlance (Penttila 1995, 2007, Robards 1999, Selleck et al. 2015, Godersky 2017, Marshall et al. 2017). Surf smelt, sand lance, northern anchovy, and longfin smelt populations have not been assessed in Puget Sound. One obstacle to formal assessment has been the peculiarities of their life histories. We determined abundance and spatial biomass distribution of this group based on the surface trawl sampling undertaken by C. Greene and colleagues (NWFSC) in April–October 2011. As for zooplankton, data were extrapolated to each unsampled polygon based on the average small planktivorous fish abundance in sampled polygons of similar bottom depth. For large zooplankton from this surface trawl, we assumed that densities in the

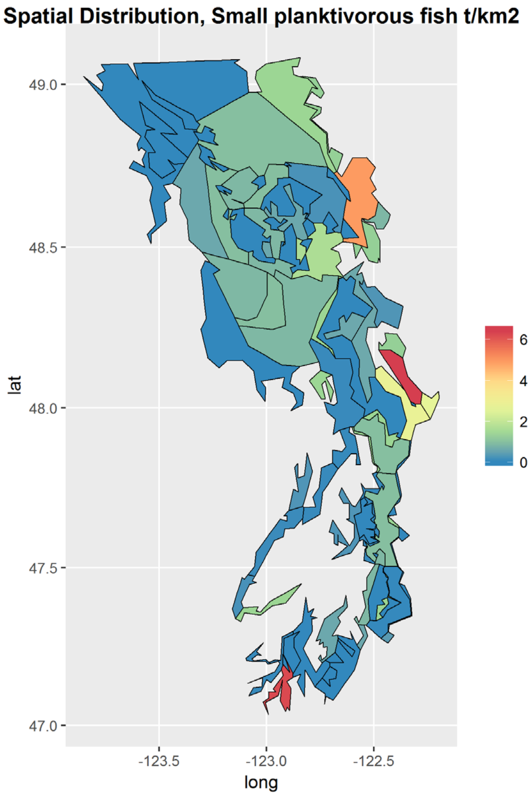

Figure 47. Small planktivorous fish density, from analysis of surface trawls by C. Greene et al., extrapolated to unsampled regions and plotted as tons/km^2.

surface trawl (collected in the top 3.1 m of the water column) were representative of the top two Atlantis depth layers (0–5 m and 5–25 m). Final biomass is 7,022 t, or an average of 1.07 t/km^2 . Spatial distribution (Figure 47) was assumed constant across seasons except during the spawning season, which is set from January to May, reflecting Pacific sandlance spawning. During this time, distribution is based on locations of documented spawning areas through 1991 (Figure 48), obtained from A. Lindquist (unpublished data) and shown on this Forage Fish Spawning Map.[11] We also compared this to densities from the RV *Ricker* survey, but catch rates in that survey were quite low (maximum of 0.075 t/km^2).

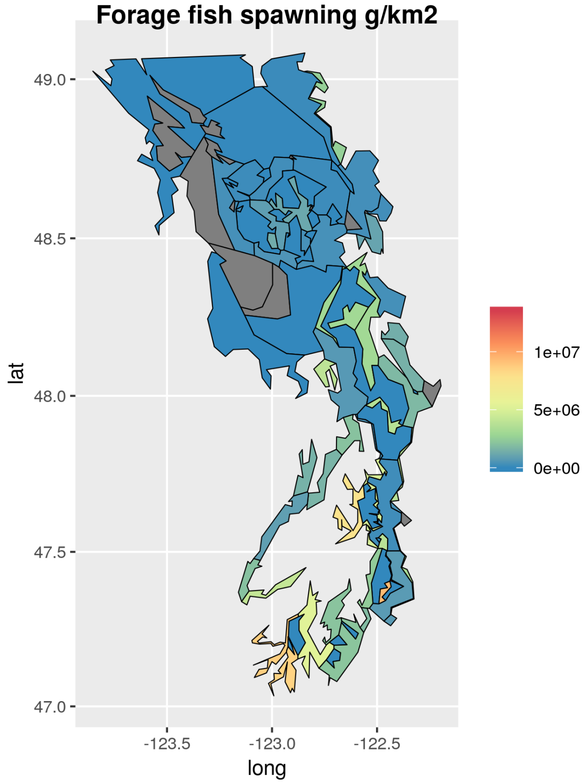

Figure 48. Small planktivorous fish density during the spawning season, plotted as g ww/km^2.

Surfperches (POP)

This functional group includes fish from the family Embiotocidae, such as pile perch (*Rhacochilus vacca*), shiner perch (*Cymatogaster aggregata*), striped perch (*Embiotoca lateralis*), kelp perch (*Brachyisticus frenatus*), surfperch (*Amphistichus rhodoterus*), walleye surfperch (*Hyperprosopon argenteum*), silver surfperch (*H. ellipticum*), and white seaperch (*Phanerodon furcatus*). Surfperches are often targeted by recreational anglers (Lane et al. 2002). These fish form schools of tens to thousands and occupy a variety of habitats, with a preference for areas with high relief, macrophyte cover, and rich invertebrate populations (Fritzsche and Hassler 1989), such as kelp, rocky reefs, eelgrass beds, and artificial structures like pilings and wharves (Harvey et al. 2010). Surfperch are found in 0–24 m depth (Lane et al. 2002), and they exhibit diurnal migrations dictated by light intensity and seasonal migrations determined by water temperature (Fritzsche and Hassler 1989, Love 1996). Shiner perch occupy coastal areas in the spring and summer and move into deeper areas (>50 m depth) in fall and winter. During the spring, shiner perch occupy shallow water during the day and move into deeper water at night. During summer, this pattern reverses and shiner perch are more abundant in shallow water after sunset, and move back into deeper water at dawn (Gordon 1965). Surfperches are viviparous fish that give birth to a few highly developed live young (Lane et al. 2002), with very low fecundity (<100 larvae per female; Love 1996). We used a fixed recruitment relationship in Atlantis for surfperch that assumed 45 young per female per year (Cannon 1987). We drew life-history parameters from previous sampling and ecosystem modeling (Anderson and

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[11] https://www.arcgis.com/home/item.html?id=19b8f74e2d41470cbd80b1af8dedd6b3

Bryan 1970, Fritzsche and Hassler 1989, Lane et al. 2002, Marshall et al. 2017). Biomass of surfperch was estimated as 1,091 t using VAST on data from WDFW bottom trawl surveys. For more details, see Analyses informing spatial abundance and density; however, we acknowledge that this is likely an underestimate of surfperch biomass, since WDFW bottom trawl surveys are not designed to catch surfperch, nor to target their shallow nearshore habitat. Distribution derived from VAST (Figure 49) was assigned to spring and summer; only polygons of >50 m deep are occupied in fall and winter. Surfperch prey include benthic invertebrates (Fritzsche and Hassler 1989). Surfperch feeding niches are restricted by prey size, location, and shell hardness (DeMartini 1969).

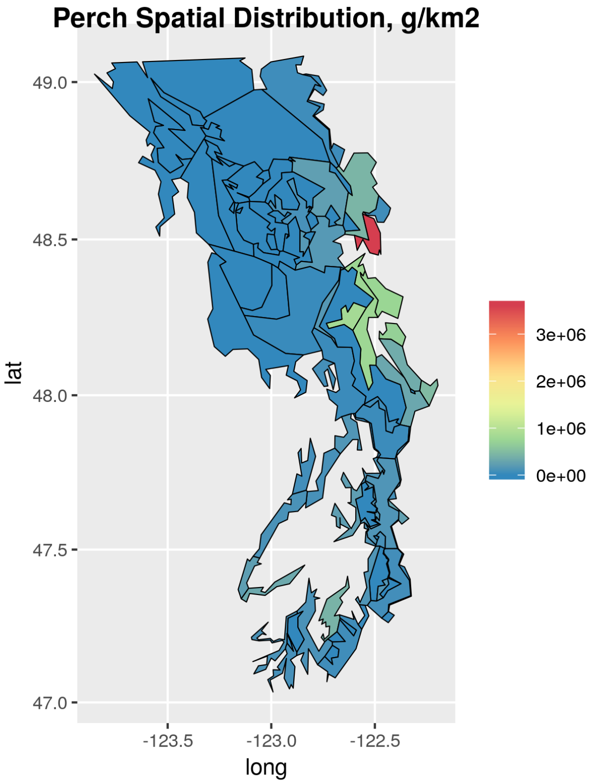

Figure 49. Surfperch density, from analysis of bottom trawl surveys using VAST, plotted as g/km^2.

Salmon functional groups

The functional groups selected per species represent populations with high abundance and adequate availability of key data, while also representing stocks across the full Puget Sound region and across a gradient of urban–rural streams and rivers. The key data needed for modeled stocks include information on adult size and abundance, number of outmigrants, proportion of hatchery-origin:natural-origin, time of smolt entry into Puget Sound, distribution, age structure of returning fish, and date of adult entry into rivers. We do not represent steelhead (*Oncorhynchus mykiss*), due to their relative rarity compared to other salmonids.

Most of the salmon species in the model are divided into multiple functional groups (i.e., populations or groups of populations), based on life history, geography, and origin. For Chinook, coho, and chum salmon, we model hatchery fish as distinct from natural populations, and we also make geographic distinctions among major basins in the north (especially populations returning to the Skagit River), mid-Puget Sound (e.g., stocks returning to the Snohomish or Duwamish River watersheds), Hood Canal, and South Sound (e.g., stocks returning to the Nisqually River). Chinook salmon are divided into the most functional groups, distinguished in part by whether their smolts tend to be yearlings or subyearlings.[12] Coho salmon are composed of yearling runs, with natural coho in the model divided into sub-basins. Natural chum salmon are separated into two different runs, with

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[12] A note on salmon nomenclature. For Puget Sound, we use the term subyearling (a.k.a. fall-run) for salmon that enter saltwater one year after their brood year. Yearlings (a.k.a. spring- or summer-run) enter saltwater two years after their brood year. Note that these refer to the life-history type, and not the age of the fish—i.e., a fish with subyearling life history can be older than one year.

one representing the Hood Canal summer-run population—of particular interest as it is listed as threatened under the Endangered Species Act. An "other salmonids group" is considered to represent sockeye salmon (*O. nerka*). Canadian Fraser River Chinook salmon are represented, primarily because they are a major prey item for Southern Resident killer whales (*Orcinus orca*). Pink salmon (*Oncorhynchus gorbuscha*) are considered a single group.

Salmon abundance, residency, release and return timing, outmigrant size, and hatchery releases are summarized in Table 8. Abundance information for salmon groups was based primarily on spawner counts, as detailed for individual groups in the sections that follow. Model initial conditions require expanding this information to total population sizes, including younger age classes that are in freshwater or the Pacific Ocean and therefore temporarily outside the model domain. To do so, we assume initial age structures based on an exponential decline in abundance with age (see natural mortalities listed in Table 4), and species-specific spawning and return probabilities per age (e.g., Myers et al. 1998, Appendix B). Both spawner biomass and expanded biomass are detailed below.

Spatiotemporal distributions of salmon within the model domain were derived from empirical and modeling information. Juvenile salmon spatial distributions are based on VAST applied to midwater trawl surveys carried out by the RV *Ricker* between 2001–16. A subsample of fish collected in these surveys are weighed, measured, and assessed for the presence of fin clips or passive integrated transponder (PIT) tags. We used these data to derive distribution models for salmon functional groups, which reflect populations originating in different streams or areas of Puget Sound, run type (yearlings or subyearlings), and origin (hatchery vs. natural). We matched available coded wire tag numbers with the RMIS database (Pacific States Marine Fisheries Commission [PSMFC], Regional Mark Processing Center[13]), which includes information on origin by hydrologically defined domains. We matched these domains to the AMPS salmon functional groups (Table 9) and derived spatial distribution models for each group. These models assume that the distribution of natural fish follows that of hatchery fish.

Data from the RV *Ricker* surveys were only available for summer and fall; thus, we could only use them to model spatial distributions for these two seasons. In order to represent the monthly seasonal contributions of juvenile salmon from our functional groups, we complemented the patterns from RV *Ricker* with expert knowledge (J. Chamberlin, NWFSC, personal communication), including general rules of salmon movement: they occupy nearshore habitats after release, then move through Puget Sound as juveniles to feed, before exiting the Sound (corresponding to summer and fall distribution for VAST modeling)—except for some resident fish that remain in local waters and are well distributed across Puget Sound. Variations to this general pattern are specified in the description for each functional group. Based on acoustic tracking, Chamberlin et al. (2011) suggested that juvenile Chinook salmon spend up to three weeks of their early marine phase close to the mouth of their natal stream, typically within 10 km. We therefore base initial spatial distributions of juvenile Chinook salmon on stream locations for one month, and then use survey data from farther offshore (RV *Ricker*) for later months of the life history.

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[13] https://www.rmpc.org/home.html

Data from RMIS were also used to identify outmigrant timing from streams for hatchery fish. This database includes the date of first release. We estimated a weighted average of the initial release month, considering the number of total fish by species, life-history type (yearling and subyearling), and stock location. Salmon migration parameters are detailed in Table 7.

As salmon cohorts mature and return to spawn, they briefly re-enter the model domain and pass through en route to natal streams. For several salmon groups that lacked more specific information, adult spawn time of natural and hatchery fish was inferred from adult trap data (at hatcheries) by C. Mains (WDFW, personal communication). For each group of Chinook, coho, pink, chum, and sockeye salmon, we calculated the window of calendar dates (days 1–365) that account for 75% of adult returns to traps. We assumed that pink and Chinook salmon spawning would occur 14 days after this window, and that coho and chum spawning would occur 30 days later. For sockeye, we assumed that adult spawning would occur coincident with trap dates, because this is approximately 60 days after precise counts of adult sockeye returns to Ballard Locks at the lower edge of the Lake Washington catchment. Note that, when possible, we have used more direct metrics of spawn timing for the salmon groups discussed below.

Chinook salmon

Mature Chinook salmon return to their natal spawning grounds (adult run timing) during fall and spring/summer runs in Puget Sound (Tucker et al. 2011). Although not exclusive, smolts of fall-run Chinook salmon typically migrate as subyearlings, while spring-run Chinook salmon smolts typically migrate as yearlings (Healey 1991, Waples et al. 2004). The geographic distribution of the adult run timing groups generally coincides with the geographic distribution of yearlings and subyearlings. After they leave Puget Sound, Chinook have been found on the west side of Vancouver Island and, to a lesser extent, along the central and northern British Columbia coast, and in southeastern Alaska (Tucker et al. 2011). Chinook diet is based on Simenstad et al. (1977).

General Chinook salmon growth curves are available from the Fishery Regulation Assessment Model (FRAM), for Puget Sound/Hood Canal yearling versus "fingerling" subyearlings (McHugh et al. 2015). The von Bertalanffy parameters for subyearlings and yearlings are *Linf*: 952 and 1,013 mm fork length; *k*: 0.04 and 0.035; and *t0*: 5.3 and 7.4 months (since October of the brood year). We apply these von Bertalanffy parameters to all stocks. Atlantis uses a common value for adults and juveniles while the salmon are outside the model migrating and the external population model is used.

For the Nisqually, Skagit, and Duwamish River populations, initial adult sizes (adult salmon weight-at-age in 2011) were estimated based on sampling of 1,089 adult fish returning in 1992–2007 provided by S. O'Neill (WDFW and NOAA, personal communication). Fish were taken by tribal gear or at hatcheries. Estimates of fork length were available for yearling vs. subyearling stocks (Table 10). For all other stocks, initial adult sizes (adult salmon weight-at-age in 2011) are based on average fork lengths used in the FRAM model to estimate growth parameters (McHugh et al. 2015). Based on sample sizes of 5,119 fish of subyearling and 486 fish of yearling life history, average adult fork lengths for these life histories were 702 and 675 mm, respectively.

For all adult Chinook salmon, conversions from fork length to wet weight (grams) were based on 1,238 fish sampled by O'Neill (personal communication; Table 10). When juvenile outmigrant size was available by length only, juvenile length (in mm) was converted to wet weight (g) by $W = a \times L^b$, with $a = 0.0000237$ and $b = 2.85$, based on average lengths and weights recorded in RMIS (G. Marston, personal communication). Records with juveniles <20 mm and >250 mm were excluded from the length–weight regression. Note that applying this common length–weight conversion still allows Chinook salmon functional groups to differ in the size of outmigrants (Table 11).

Natural mortality rates are used to initialize age structure of the populations in the Atlantis model. For Chinook salmon, survival of smolt-to-ocean age-2 was set to 3%, approximated from Ruff et al. (2017), and total survival of 30% for ages-2–5 was taken from the FRAM model (Workgroup 2008). Over the full lifespan of Chinook salmon, total natural mortality of 0.94/yr yields the expected survival that is the product of Ruff et al. (2017) and the FRAM model, and we therefore applied this natural mortality rate to initialize age compositions in the model. Age at maturity for Chinook salmon stocks was based on information for major stocks as compiled in Myers et al. (1998), Appendix B.

Chinook hatchery yearling (CHY), Chinook hatchery subyearling (CHS)

Total Puget Sound run size of hatchery-origin Chinook salmon was 187,468 adults in 2011 (run reconstruction provided by J. Carey, WDFW, personal communication). We use this estimate of total run size, rather than terminal run size (186,649) or escapement (77,894), since terminal run size and escapement include fisheries and mortality in the freshwater or estuaries that are not captured explicitly in our model domain. These hatchery fish primarily are from Hood Canal, South Sound, and the Nooksack and Samish Rivers. Hatchery release data (G. Marston, personal communication) suggest that 98% of hatchery fish are released as subyearlings. We therefore assume model initial conditions for 183,282 subyearling adult hatchery Chinook salmon and 4,186 yearling adults. Corresponding adult spawner biomass

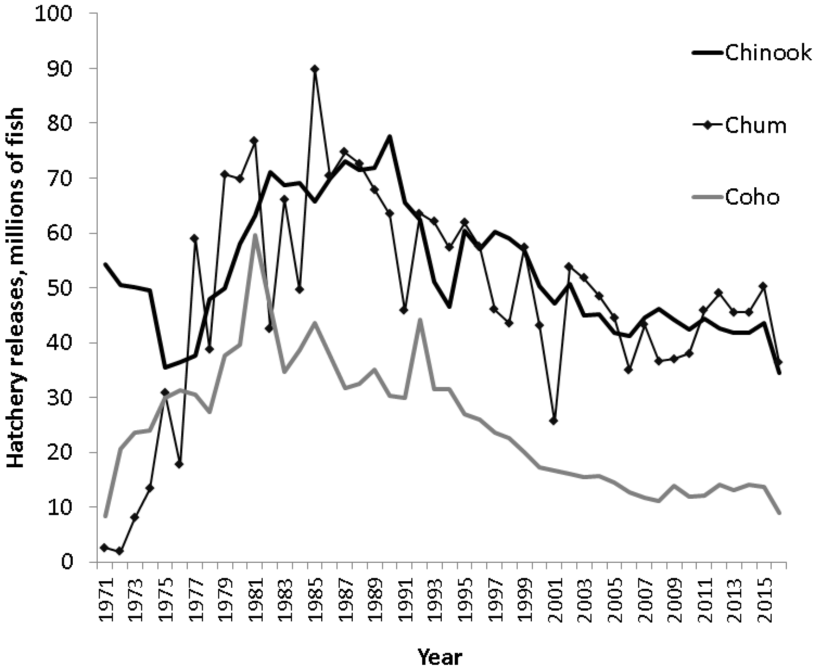

Figure 50. Hatchery releases of juvenile Chinook, chum, and coho salmon in Puget Sound, in millions of fish, 1971–2016. Source: RMIS database.

was 17 tons for yearlings and 839 tons for subyearlings, and expanded biomasses for all age classes were 47 tons and 2,440 tons. We forced the model with hatchery release data for 1971–2016 (G. Marston, personal communication); for instance, these data suggest that in release year 2011, 44 million subyearling juveniles were released, and 890,000 yearling juveniles (Figure 50). We force these release times to occur uniformly over 10 April–14 June (calendar days 100–165), the period which accounts for 75% of RMIS hatchery juveniles released in 2009–13. The size of juveniles released from hatcheries was provided by B. Nelson (NWFSC, personal communication), after he had extracted data from RMIS and imputed missing values. We assumed fish larger than 20 g were yearlings, and fish smaller than 20 g were subyearlings; based on this, hatchery subyearlings averaged 6 g and 81 mm, and hatchery yearlings averaged 52 g and 163 mm.

Adult return time to freshwater was based on Samish River fall-run hatchery Chinook salmon, and was set to early August–mid-October (days 213–288); spawn time was mid-September–late October (days 258–304; B. Barkdull, WDFW, personal communication). Monthly spatial distributions for juveniles and adults are presented for both the Chinook hatchery yearling (Figures 51 and 52) and Chinook hatchery subyearling (Figures 53 and 54) groups.

Chinook Skagit yearling (CSY), Chinook Skagit subyearling (CSS)

Total run size of natural-origin Chinook salmon to the Skagit River basin was 9,211 adults in 2011 (run reconstruction provided by J. Carey (personal communication). Beechie et al. (2006) report 7–16% yearling. We assume 11.5% yearling and 88.5% subyearling. This is roughly consistent with the 17.8% yearling in the 2005 Skagit Recovery Plan.[14] We therefore initialize the model with 1,059 yearlings and 8,152 subyearlings, but note that data from 1999–2008 presented in Zimmerman et al. (2015b) suggest an even higher proportion of subyearlings (>96% for 1993–2008). Corresponding adult spawner biomass was 7 tons for yearlings and 62 tons for subyearlings, and expanded biomasses for all age classes were 32 tons and 305 tons.

Detailed information on migration timing was available from WDFW District 14 (B. Barkdull, personal communication). Spawn time was set to late August through mid-November (days 232–319), based on information for natural fish from WDFW District 14, for the Lower Skagit fall and the Upper Skagit summer runs. Return time for adults to the river from saltwater was set to mid-June through early November (days 166–309), based on information for the Lower Skagit fall and the Upper Skagit summer runs. WDFW District 14 records suggest that outmigrant juveniles occur January through July. However, we base subyearling outmigration on a narrower range of dates, as reported in Zimmerman et al. (2015b): fry 5 February–6 May (days 36–126), parr 6 May–15 July (days 126–196). We assume that yearling outmigrants leave the Skagit River between January and April (days 1–120). Monthly spatial distributions were calculated for juveniles and adults for both the Chinook Skagit yearling (Figures 55 and 56) and Chinook Skagit subyearling (Figures 57 and 58) groups.

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[14] http://psp.wa.gov/salmon-recovery-watersheds.php

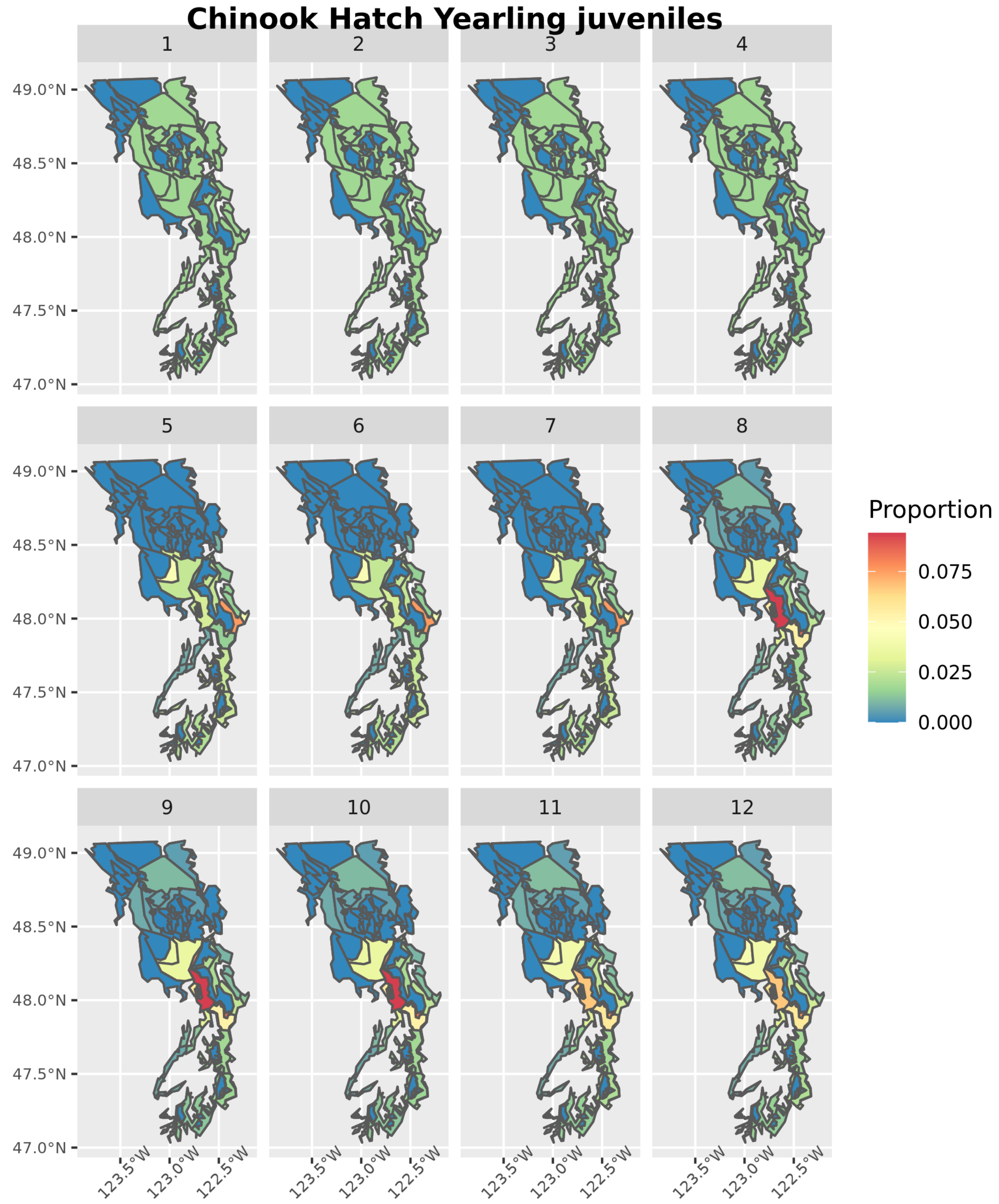

Figure 51. Monthly spatial distribution of juveniles of the Chinook hatchery yearling functional group. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

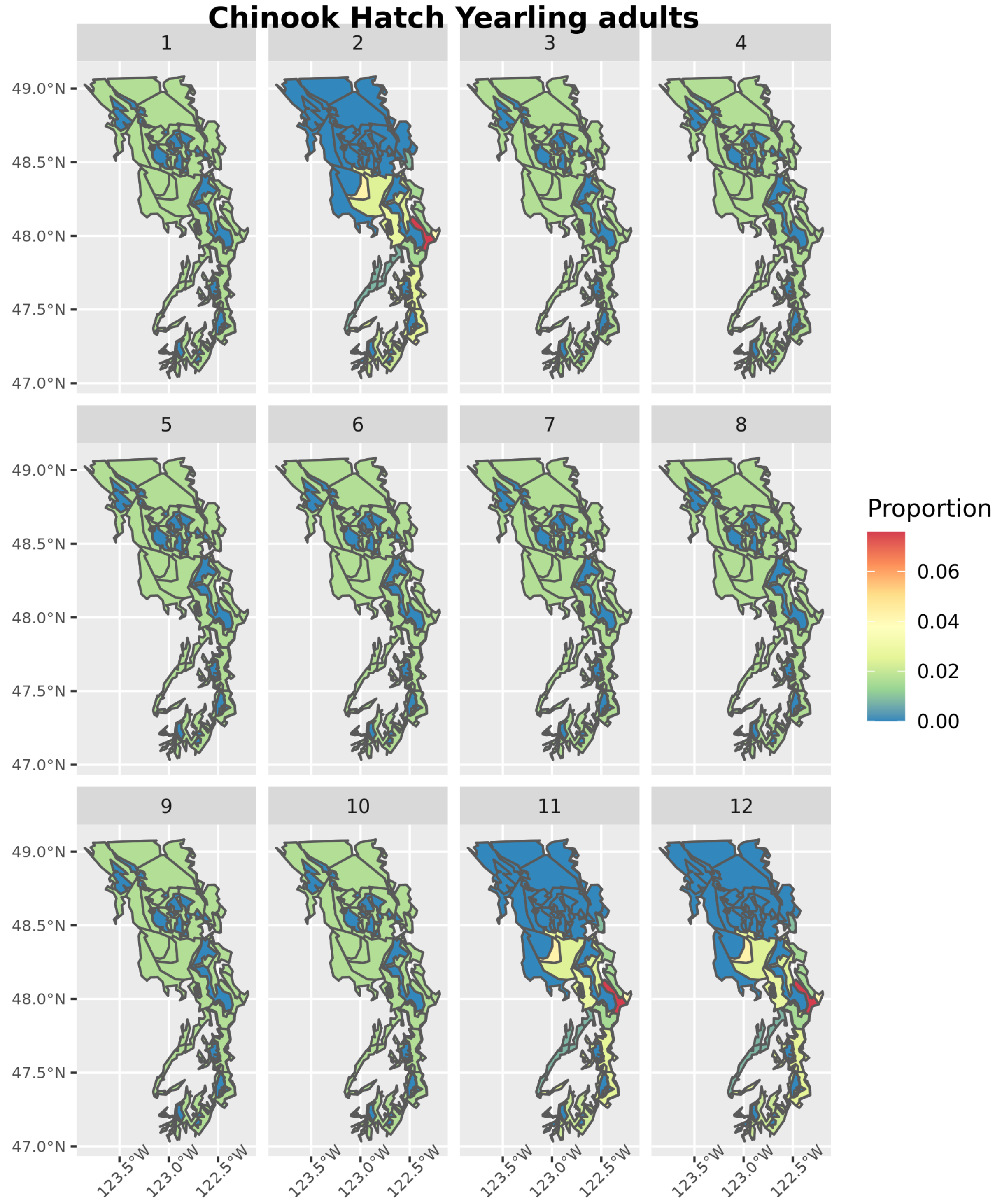

Figure 52. Monthly spatial distribution of adults of the Chinook hatchery yearling functional group. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

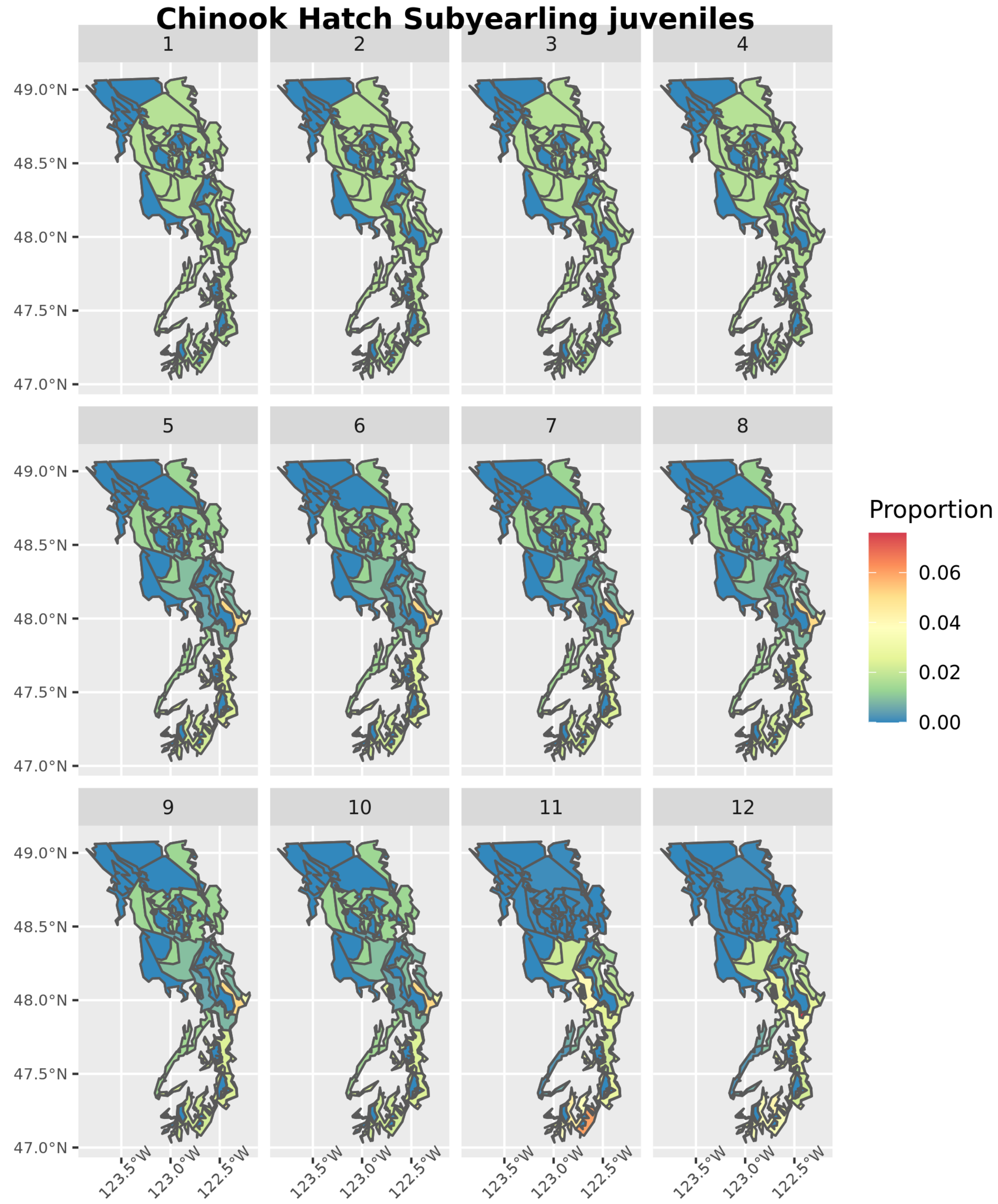

Figure 53. Monthly spatial distribution of juveniles of the Chinook hatchery subyearling functional group. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

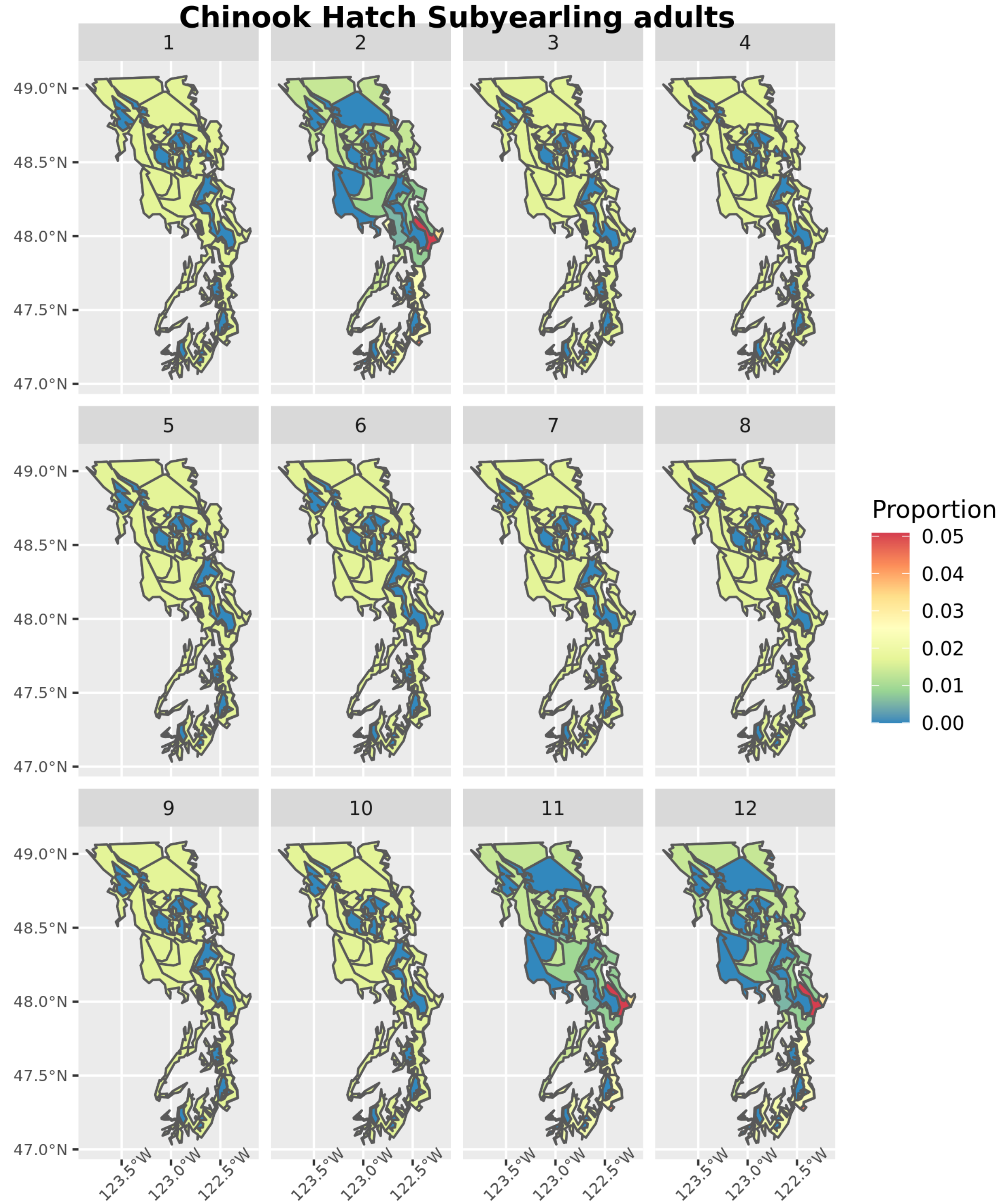

Figure 54. Monthly spatial distribution of adults of the Chinook hatchery subyearling functional group. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

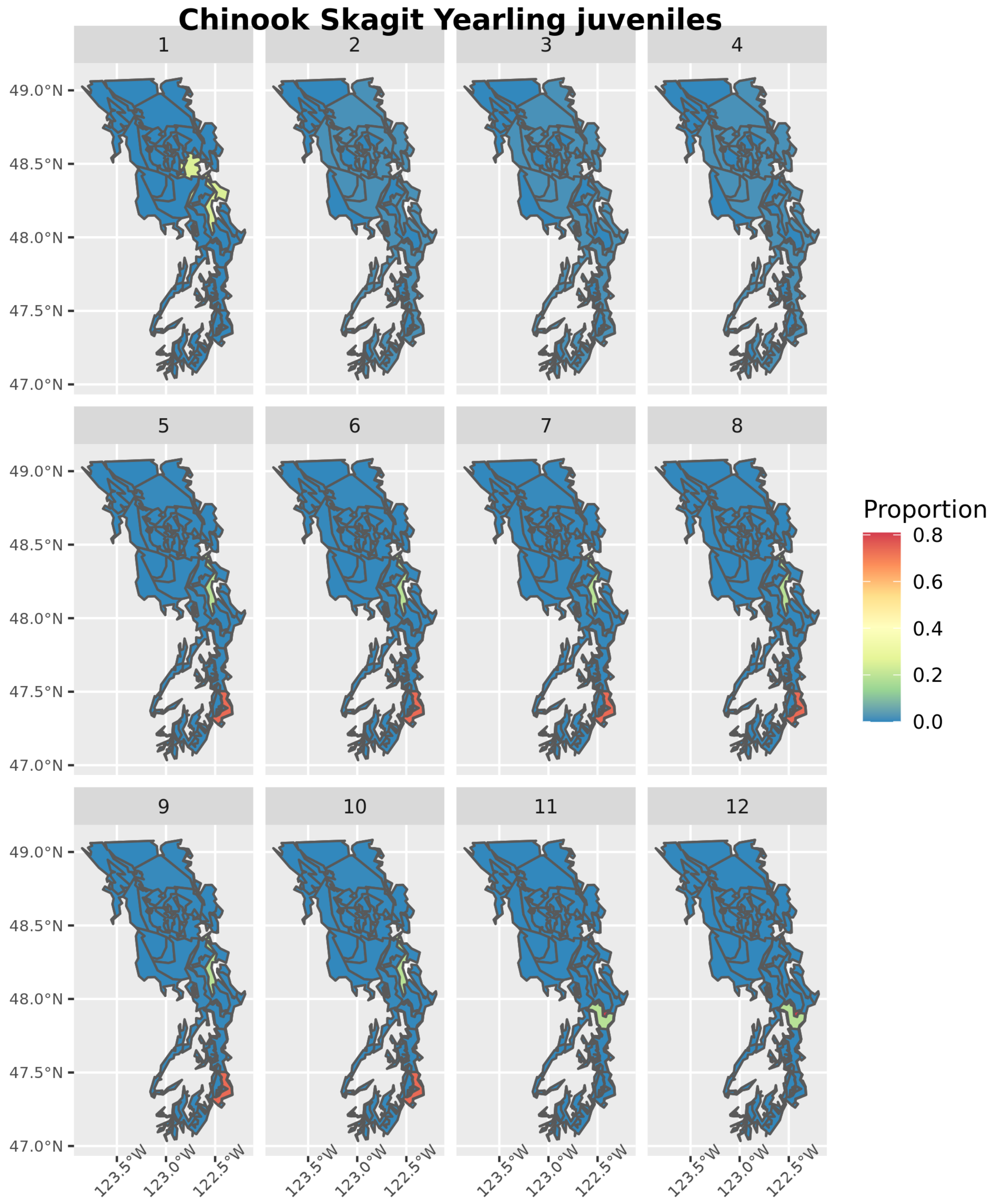

Figure 55. Monthly spatial distribution of Chinook Skagit yearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

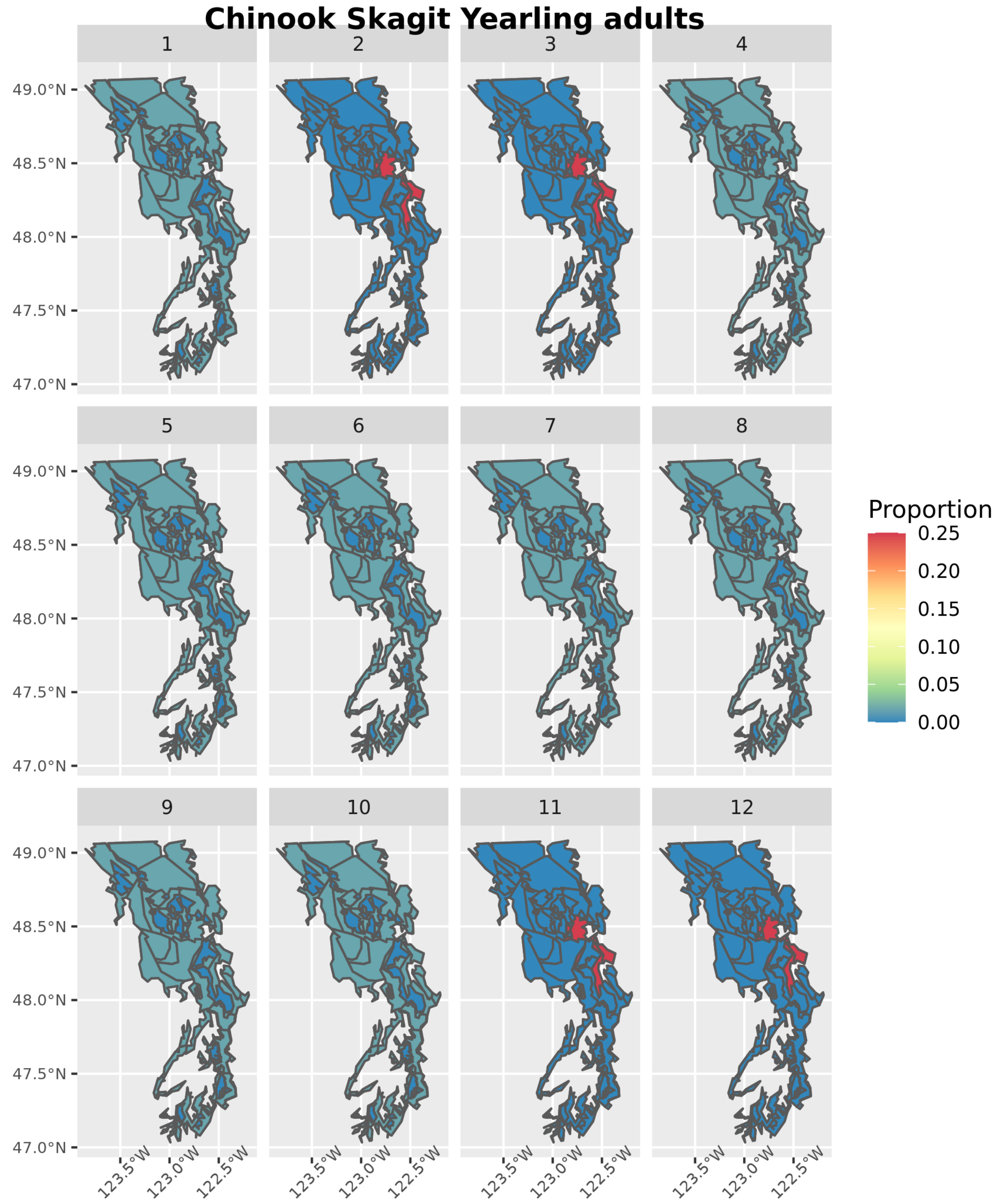

Figure 56. Monthly spatial distribution of spatial distribution of Chinook Skagit yearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

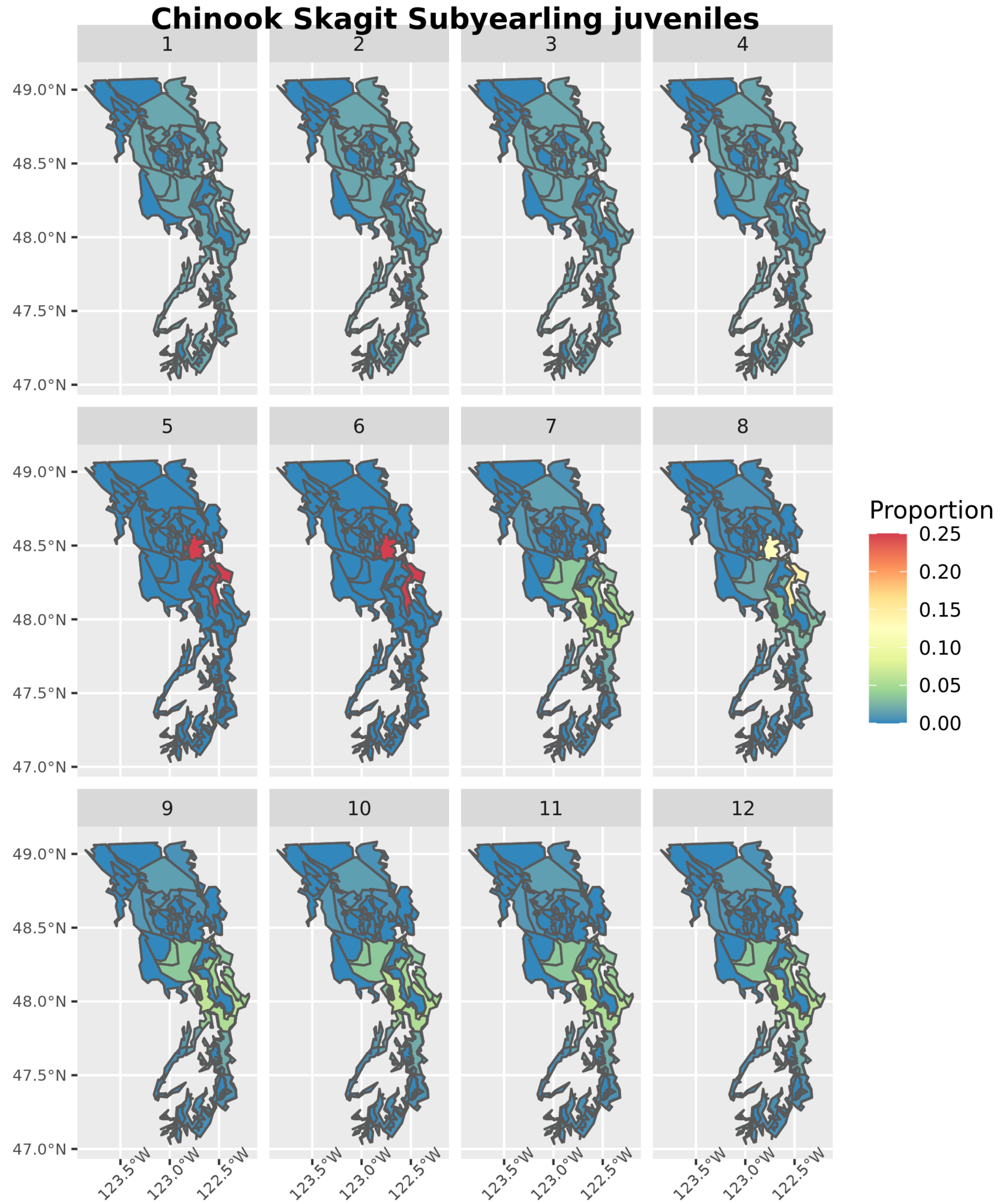

Figure 57. Monthly spatial distribution of Chinook Skagit subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

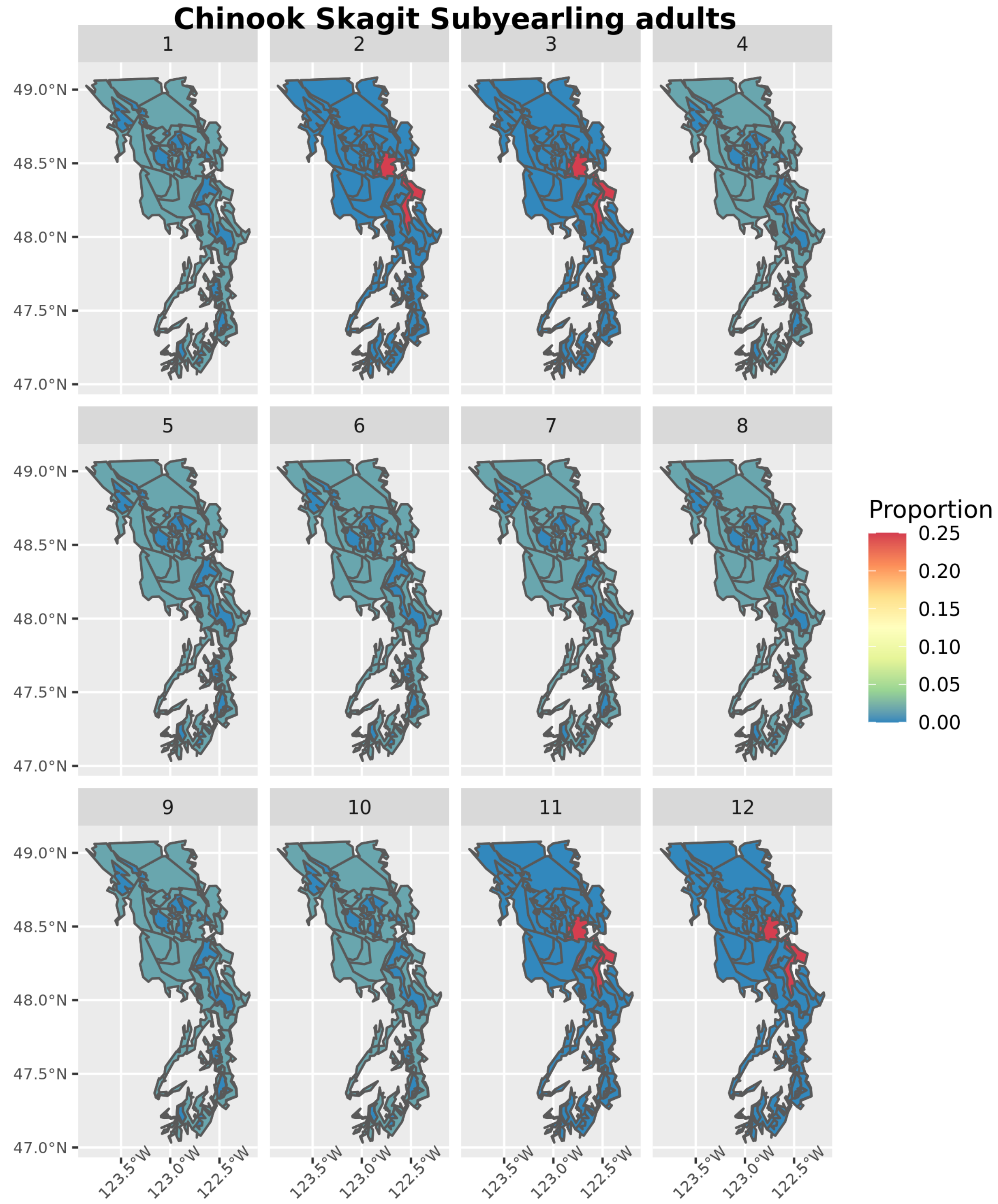

Figure 58. Monthly spatial distribution of Chinook Skagit subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

Chinook Snohomish subyearling (CSN)

Total run size of natural-origin Chinook salmon to the Snohomish River basin was 1,420 adults in 2011 (run reconstruction provided by J. Carey, personal communication). Corresponding adult spawner biomass was 6.5 tons, and expanded biomass for all age classes was 26 tons. We assume all Snohomish River fish are subyearlings. This may be an overestimate since, at least in two tributaries (Snoqualmie and Skykomish Rivers), Beechie et al. (2006) suggest 23% and 36% "stream-type" (yearlings). More recent data also suggest somewhat high yearling frequency: 18% and 24% yearling for 2009–13 for the Snoqualmie and Skykomish Rivers, respectively (M. Crewson, Tulalip Tribes, personal communication). However, because this is a relatively small natural population compared to the Skagit River runs, we opted to make them all "ocean-type" (subyearlings) in order to avoid having additional functional groups that slow model run times. Adult return time (entry to freshwater) was set to occur between 15 May and 15 September (M. Crewson, personal communication). Spawn date was set to 27 August–24 November (days 239–328), based on spawning ground survey data (M. Crewson, personal communication; data from P. Verhey, WDFW). Juvenile outmigration dates for the Snoqualmie and Skykomish Rivers were typically late February through mid-June for fry, and early April through mid-June for parr (data from M. Pouley and M. Crewson, Tulalip Tribes, personal communication). Average fork length of outmigrants was set to 44 mm for fry and 65 mm for parr, based on 2009–14 sampling from the Snohomish River delta (J. Chamberlin and M. Pouley, personal communication), assuming a 50-mm fork length division between fry and parr. Monthly spatial distributions for juveniles and adults are shown in Figures 59 and 60.

Chinook Duwamish subyearling (CDS)

Total run size of natural-origin Chinook salmon in the Duwamish and Green Rivers was 671 adults in 2011 (run reconstruction provided by J. Carey, personal communication). Corresponding adult spawner biomass was 2.5 tons, and expanded biomass for all age classes was 10 tons. We assume all Duwamish and Green River fish are subyearlings. Beechie et al. (2006) report 0% stream type (yearling) fish. Adult return time was set to span August and September (days 213-273). Spawn time was set to 29 September–19 October (days 272–292), based on the adult trap data mentioned above (specifically from trapping of natural and hatchery fish at the Soos Creek hatchery). This is consistent with adult spawner surveys in the Green River for 2009–17, which had high densities from 15 September to 31 October (data provided by N. Overman, WDFW, personal communication). Duwamish River fry and parr size and outmigrant timing were based on observations from 2001–03 sampling in the Duwamish River (Nelson et al. 2004). Fry outmigration was set to 20 February–30 June (days 51–181), and parr outmigration was set to 15 May–30 June (days 135–181), with average fork lengths for fry and parr of 40 and 75 mm, respectively. Monthly spatial distributions for juveniles and adults are shown in Figures 61 and 62.

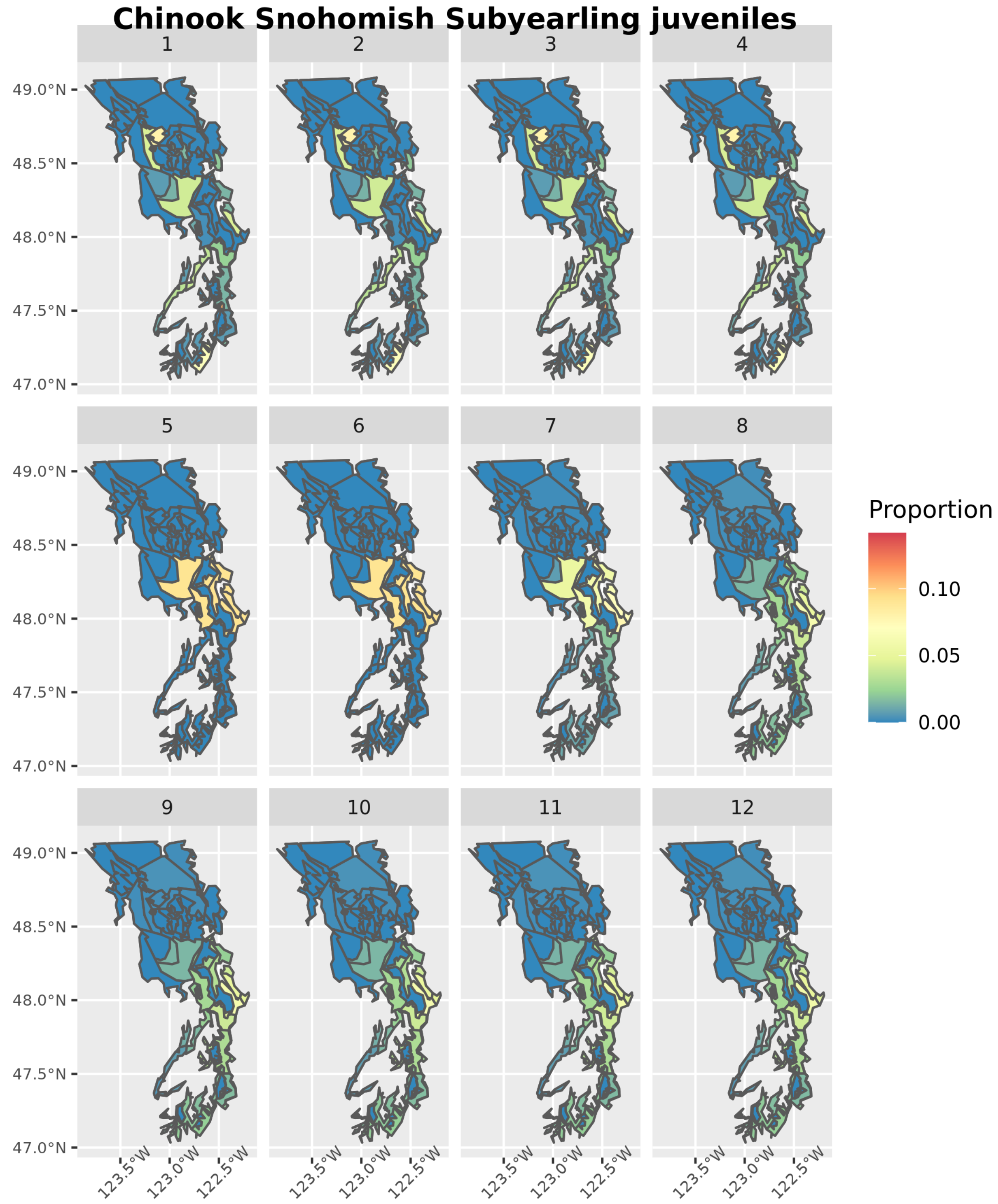

Figure 59. Monthly spatial distribution of Chinook Snohomish subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

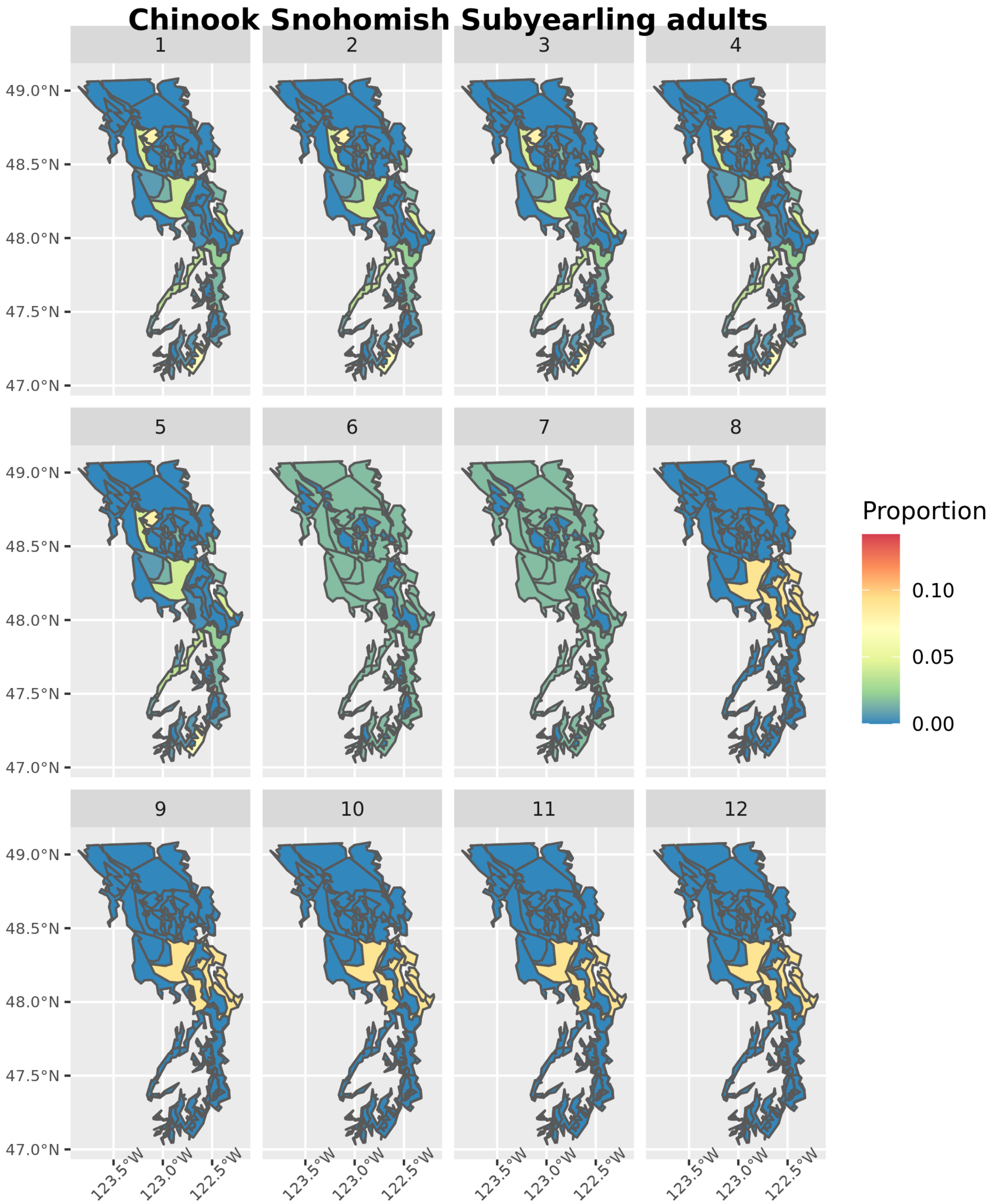

Figure 60. Monthly spatial distribution of Chinook Snohomish subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

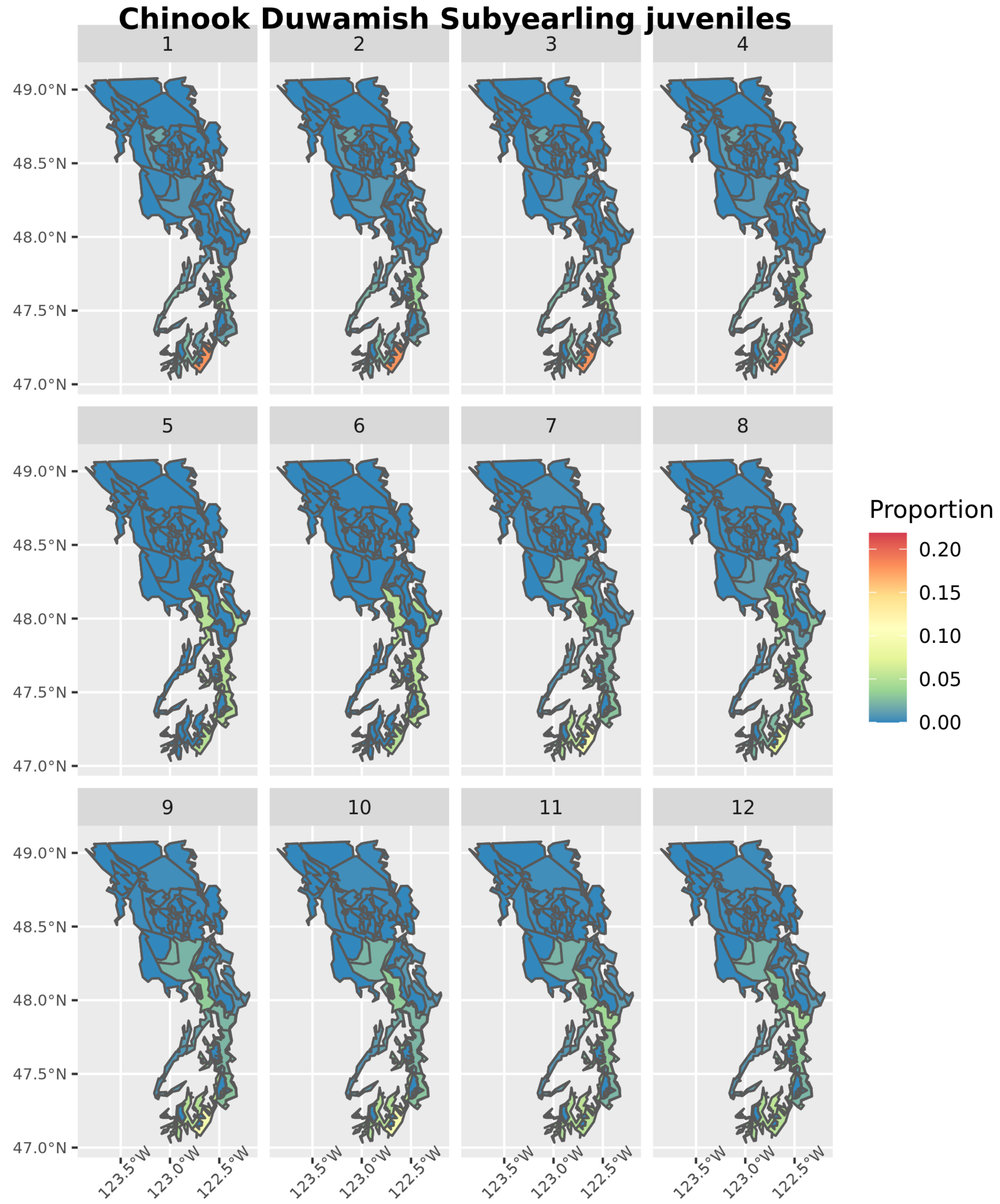

Figure 61. Monthly spatial distribution of the Chinook Duwamish subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

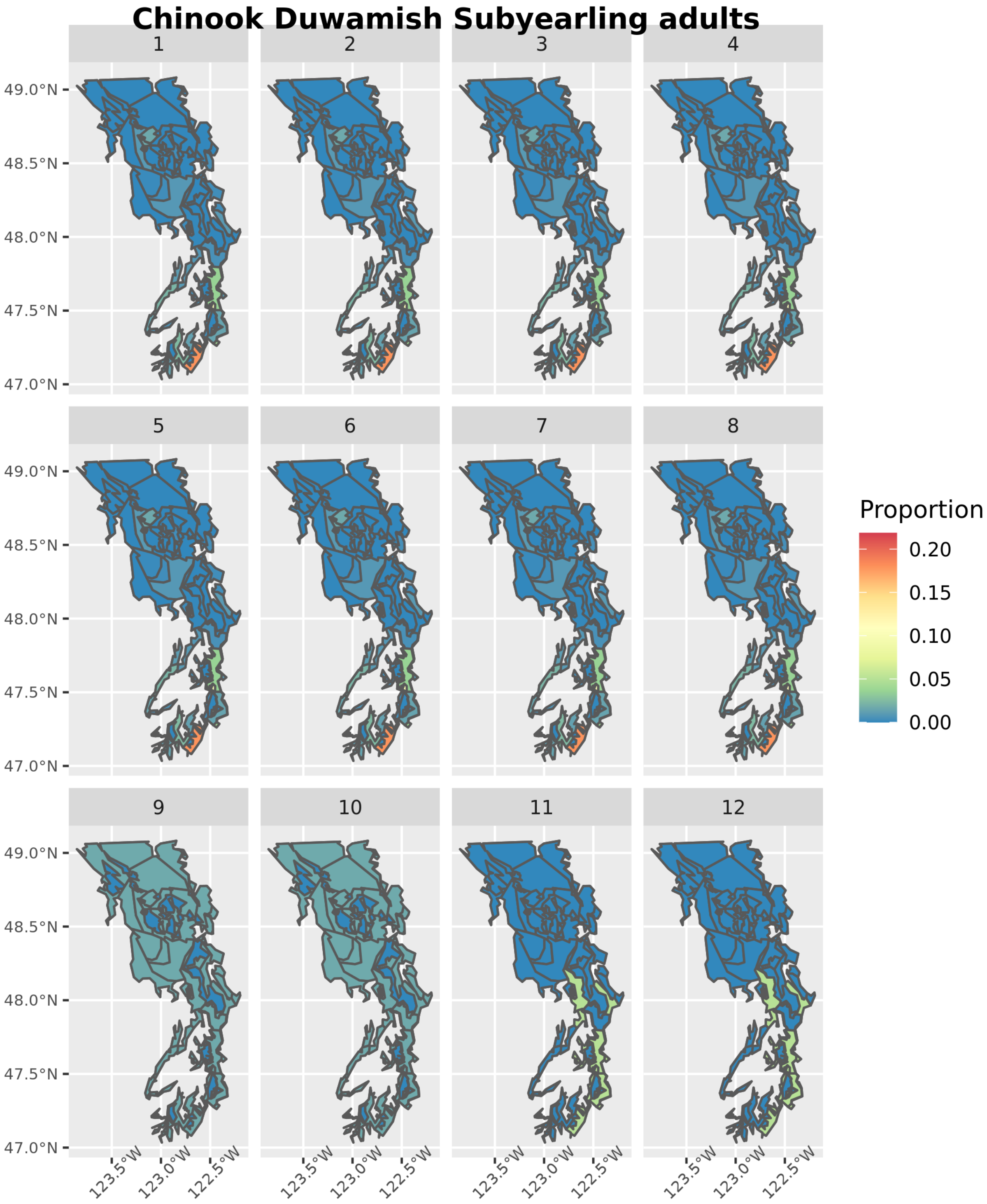

Figure 62. Monthly spatial distribution of the Chinook Duwamish subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

Chinook Nisqually yearling (CNY), Chinook Nisqually subyearling (CNS)

Total run size of natural-origin Chinook salmon to the Nisqually River basin was 541 adults in 2011 (run reconstruction provided by J. Carey, personal communication). Beechie et al. (2006) report 1% stream type (yearling) fish. The Nisqually Recovery Plan (2005) also suggests a small population of yearling fish. We assume 536 subyearling fish and 5 yearling fish in 2011. Corresponding adult spawner biomass was 2.8 tons for subyearlings and 0.03 tons for yearlings, and expanded biomasses for all age classes were 6.1 tons and 0.048 kg.

Adult run timing data provided by J. Losee (WDFW, personal communication) for 2009–16 suggest the start day of the run to range from 1 July to 11 August, the peak day of adult returns each year to occur between 31 August and 19 September, and the final day of the run to range from 26 September to 2 November. For Nisqually River subyearlings, we therefore assume the runs begin 11 August and end 26 September (days 223–269). We apply this for both yearling and subyearling groups. Based on the adult trap data mentioned above, spawn time would likely be 20 August–26 September (days 232–269). This is specifically from trapping natural and hatchery fish at Minter Creek (also in South Sound, but approximately 30 km away), since adult trap data were not available from the Nisqually River. However, J. Moore (Nisqually Tribe, personal communication) suggested a slight modification, which we implemented in the model, to spawn days of 20 August–3 October (days 232–276). Monthly spatial distributions are shown for juveniles and adults for both the Chinook Nisqually yearling (Figures 63 and 64) and Chinook Nisqually subyearling (Figures 65 and 66) groups.

Chinook Hood Canal subyearling (CHC)

Total run size of natural-origin Chinook salmon to the Hood Canal basin was 2,631 adults in 2011 (run reconstruction from J. Carey, personal communication). We assume all fish are subyearlings, consistent with the 2010 Skokomish River (Hood Canal) Recovery Plan.[15] Corresponding adult spawner biomass was 12 tons; expanded biomass for all age classes was 38 tons.

Adult return time to freshwater was set to 15 July–31 August (days 196–243) based on tribal gillnet catches on the Skokomish River (Tribe 2017). Spawn time was set to 24 August–5 October (days 236–278) based on redd counts, reported in the recovery plan by Skokomish Indian Tribe and WDFW (Tribe 2017). This is similar to 21 August–29 September (days 233–272), estimated based on the adult trap data mentioned above (specifically from trapping of natural and hatchery fish at the Adams and Hoodsport hatcheries); however, we base our timing directly on the redd counts rather than trap data. Subyearling size and timing were informed by beach seine sampling in 2011–14 provided by the Port Gamble S'Klallam Tribe Natural Resources Department. Sampling occurred in March–October. We assume juvenile Chinook salmon <100 mm were subyearlings beginning outmigration. These fish were typically observed in June (days 152–181), with mean fork length of 83 mm (E. Bishop and H. Daubenberger, Port Gamble S'Klallam Tribe Natural Resources Department, personal communication). Monthly spatial distributions for juveniles and adults are shown in Figures 67 and 68.

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[15] https://pspwa.app.box.com/s/uvyhcxu9nhpmng1l47kt0knadcx31jew/file/276630847962

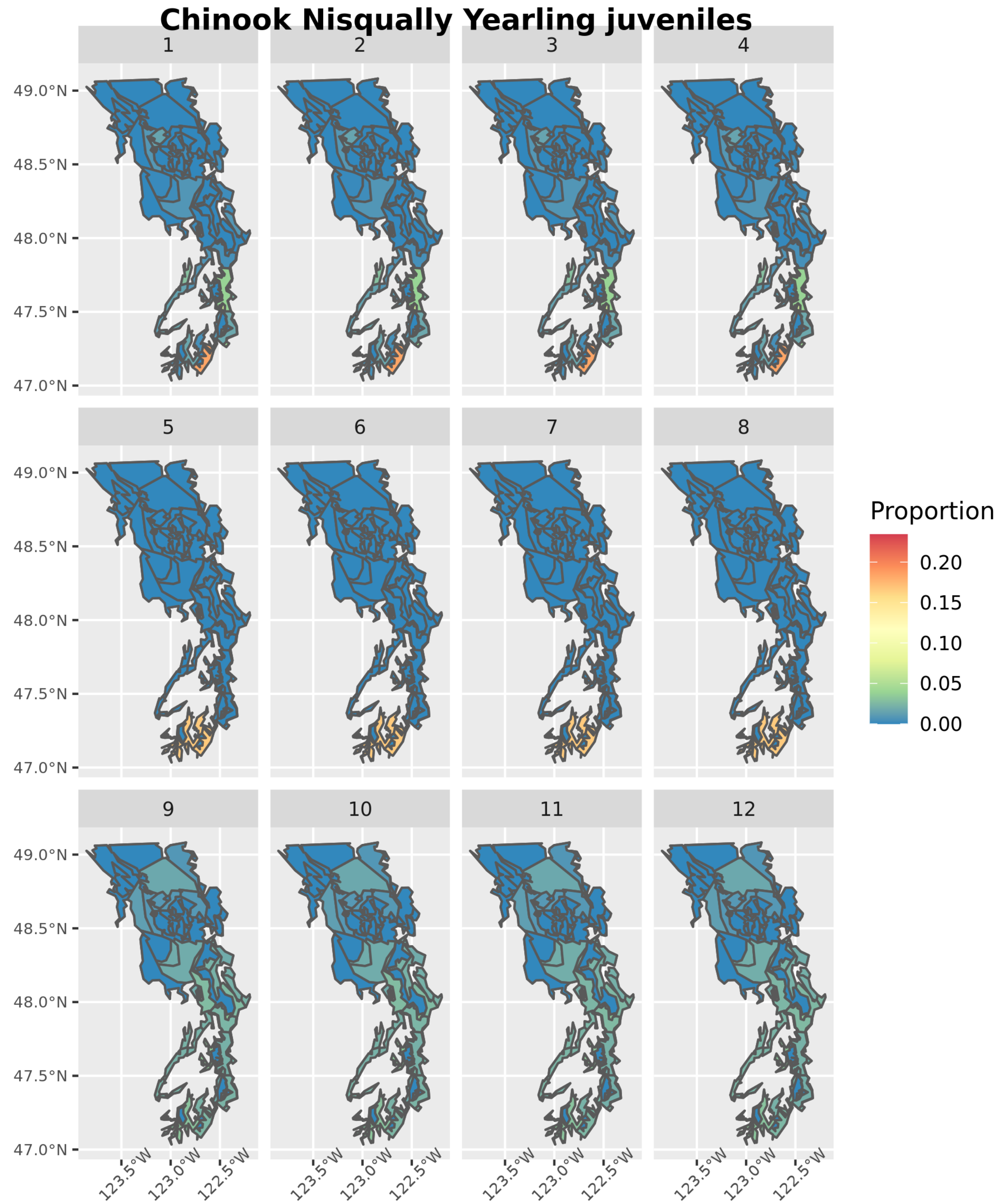

Figure 63. Monthly spatial distribution of Chinook Nisqually yearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

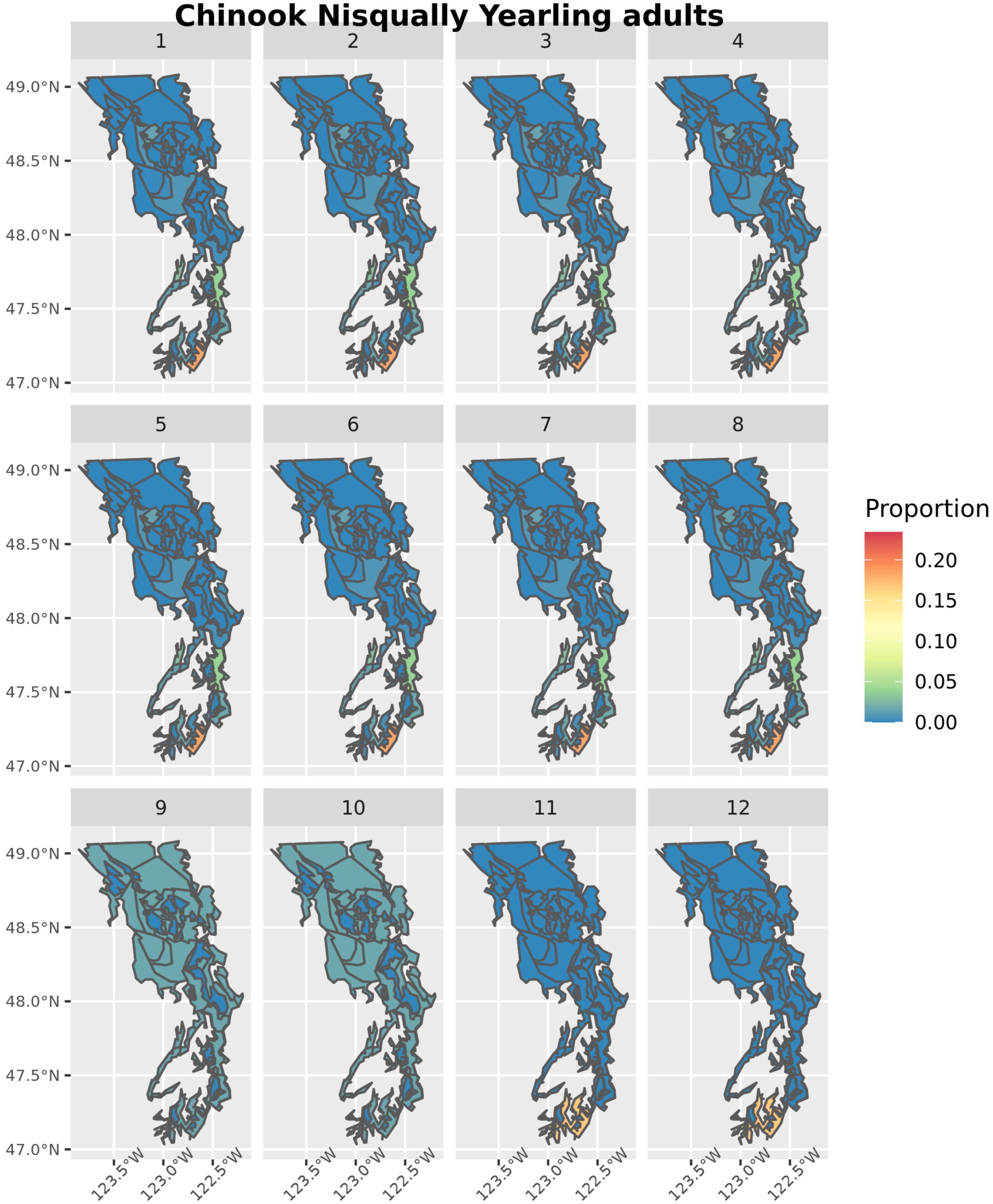

Figure 64. Monthly spatial distribution of Chinook Nisqually yearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

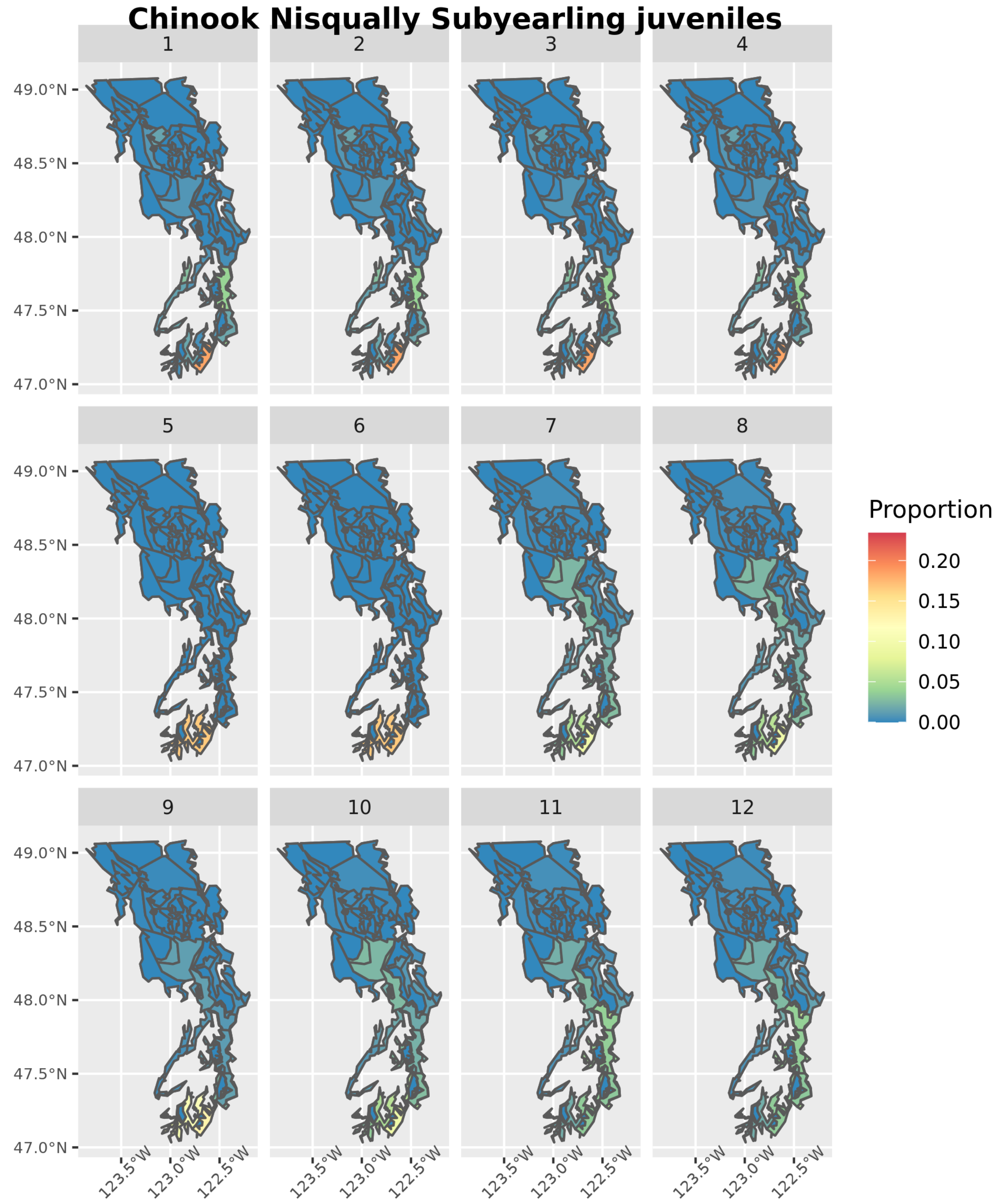

Figure 65. Monthly spatial distribution of Chinook Nisqually subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

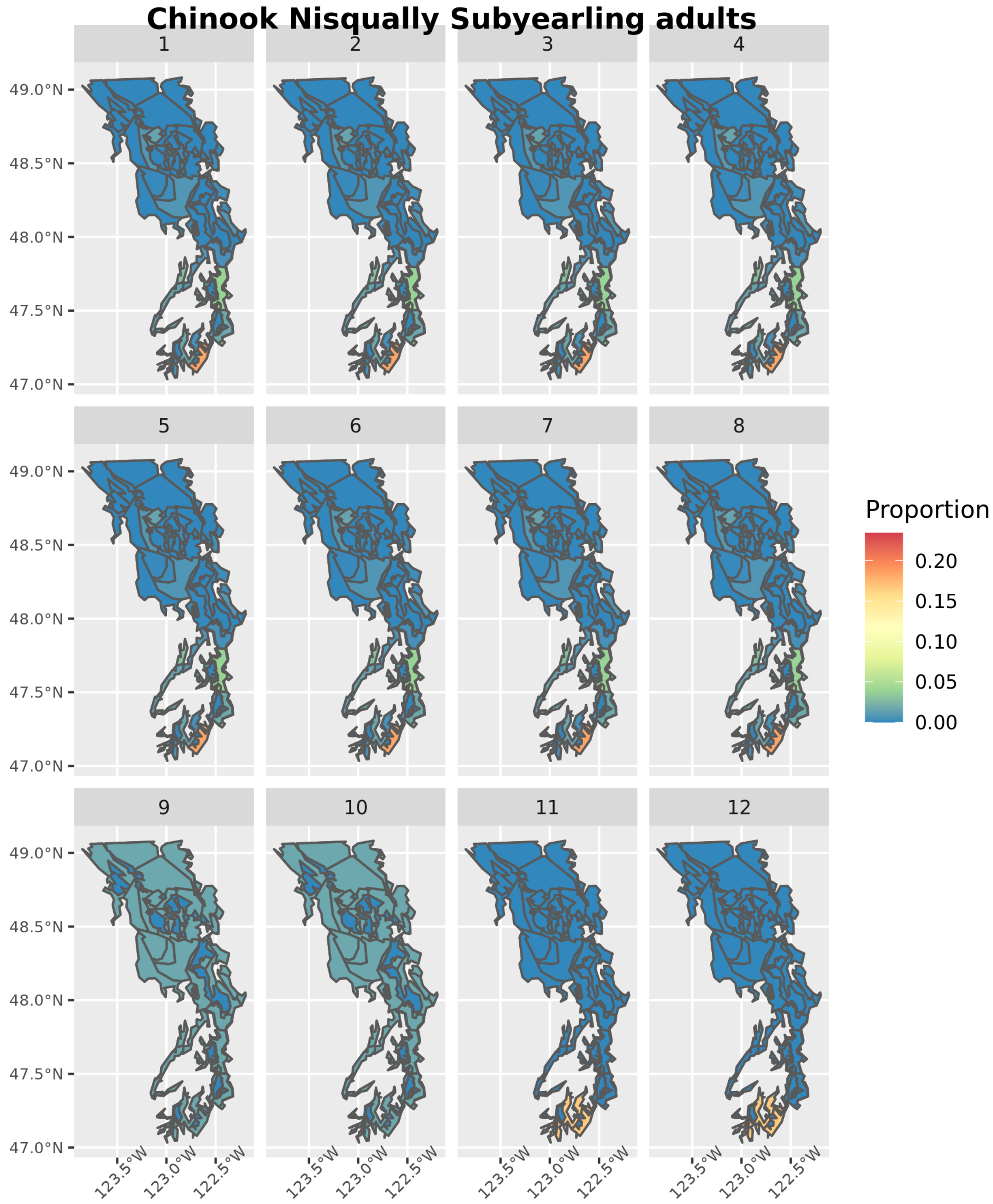

Figure 66. Monthly spatial distribution of Chinook Nisqually subyearling adults. Based on data from the RV Ricker surveys, Chamberlin et al. (2011) and expert knowledge.

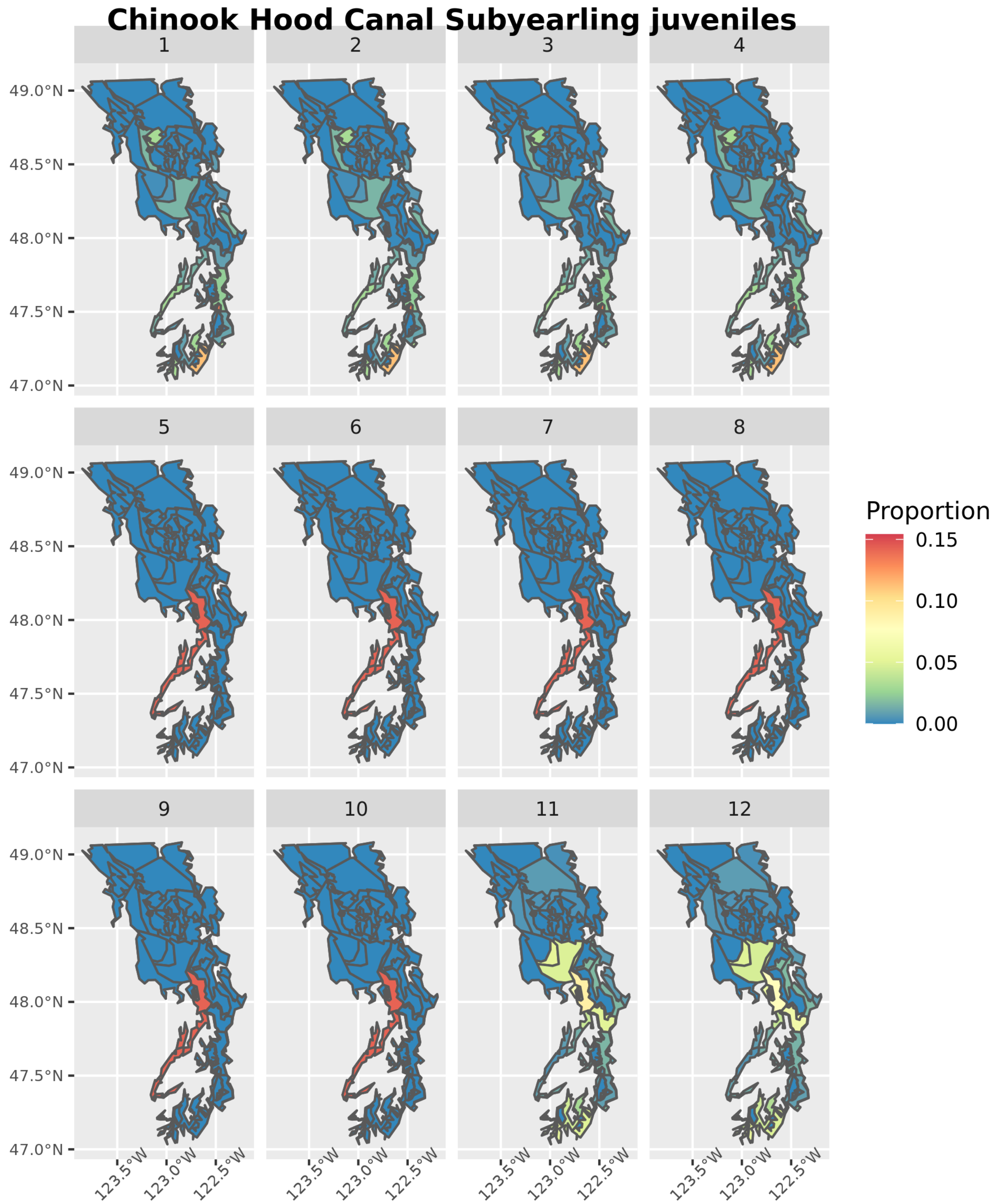

Figure 67. Monthly spatial distribution of Chinook Hood Canal subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

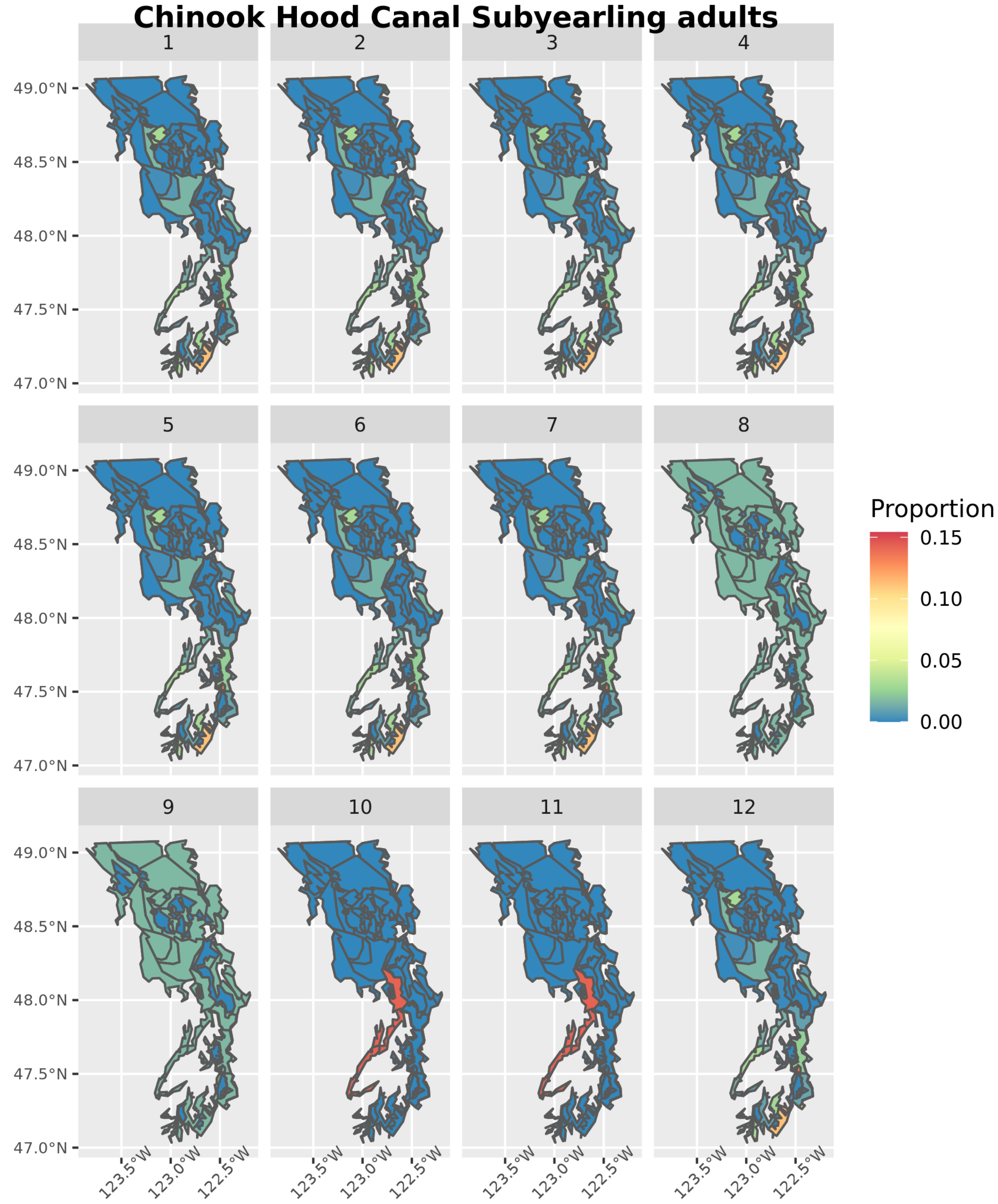

Figure 68. Monthly spatial distribution of Chinook Hood Canal subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

Chinook other yearling (CYE), Chinook other subyearling (CKS)

Total Puget Sound run size of these natural-origin fish was 3,531 Chinook salmon in 2011 (run reconstruction provided by J. Carey, personal communication). Primarily, these fish are from the Puyallup River, Stillaguamish River, and Lake Washington. Beechie et al. (2006) report 1–5% yearling fish for the Puyallup River, the North and South Forks of the Stillaguamish River, and North Lake Washington. We assume 3% yearlings, or 106 yearling fish and 3,425 subyearling fish. Corresponding adult spawner biomass was 0.43 tons for yearlings and 15.7 tons for subyearlings, and expanded biomasses for all age classes were 2.3 and 89.2 tons. Adult return time for Lake Washington Chinook salmon is primarily 15 July–15 September (days 196–258), based on counts at the Ballard Locks from 2009–17 (J. Thompson, WDFW, personal communication). We assume this applies for both CYE and CKS. Spawn time was set to 22 September–25 October (days 265–298), based on the adult trap data mentioned above (specifically from trapping of natural and hatchery fish at the Voights Creek and Issaquah hatcheries, for the Puyallup River and Lake Washington populations respectively). We base juvenile outmigrant size and timing on data from the Stillaguamish River. Stillaguamish smolt traps suggest fry (<50 mm) outmigration over 24 February–20 April (days 55–110) and parr (>50 mm) outmigration over 20 April–9 June (days 110–160), with average fork lengths of 43 and 63 mm, respectively (data from C. Scofield, Stillaguamish Tribe of Indians, unpublished data). Monthly spatial distributions are shown for juveniles and adults for both the Chinook other yearling (Figures 69 and 70) and Chinook other subyearling (Figures 71 and 72) groups.

Coho salmon

For all coho salmon, conversions from adult fork length to wet weight (grams) were based on 2,926 fish sampled by S. O'Neill (personal communication; Table 11). For the majority of coho salmon groups (and unless noted below), adult spawn times of natural and hatchery fish were inferred from adult trap data (at hatcheries) by C. Mains (personal communication). We calculated the window of calendar dates that account for 75% of adult returns to traps. We assumed that coho spawning would occur 30 days later. We provide details for particular stocks below.

When juvenile outmigrant size was available by length only, juvenile length (in mm) was converted to wet weight (g) by $W = a \times L^b$, with $a = 0.000151$ and $b = 2.46$, based on average length and weights recorded in the RMIS database (G. Marston, personal communication). Records with juveniles greater than 200 mm were excluded from the length–weight regression.

Coho hatchery yearling (COH)

For initial conditions, this group includes 76,209 adult returns to hatcheries in 2011 (C. Mains, personal communication). We also include 2,283 adult hatchery coho that strayed to natural spawning grounds (WDFW SaSI 2018): 1,891 spawners to East Kitsap, 101 spawners to Northeast Hood Canal, and 291 spawners to Quilcene/Dabob Bay. "Composite" stocks with natural production are included in other coho groups described below. Note that all of these

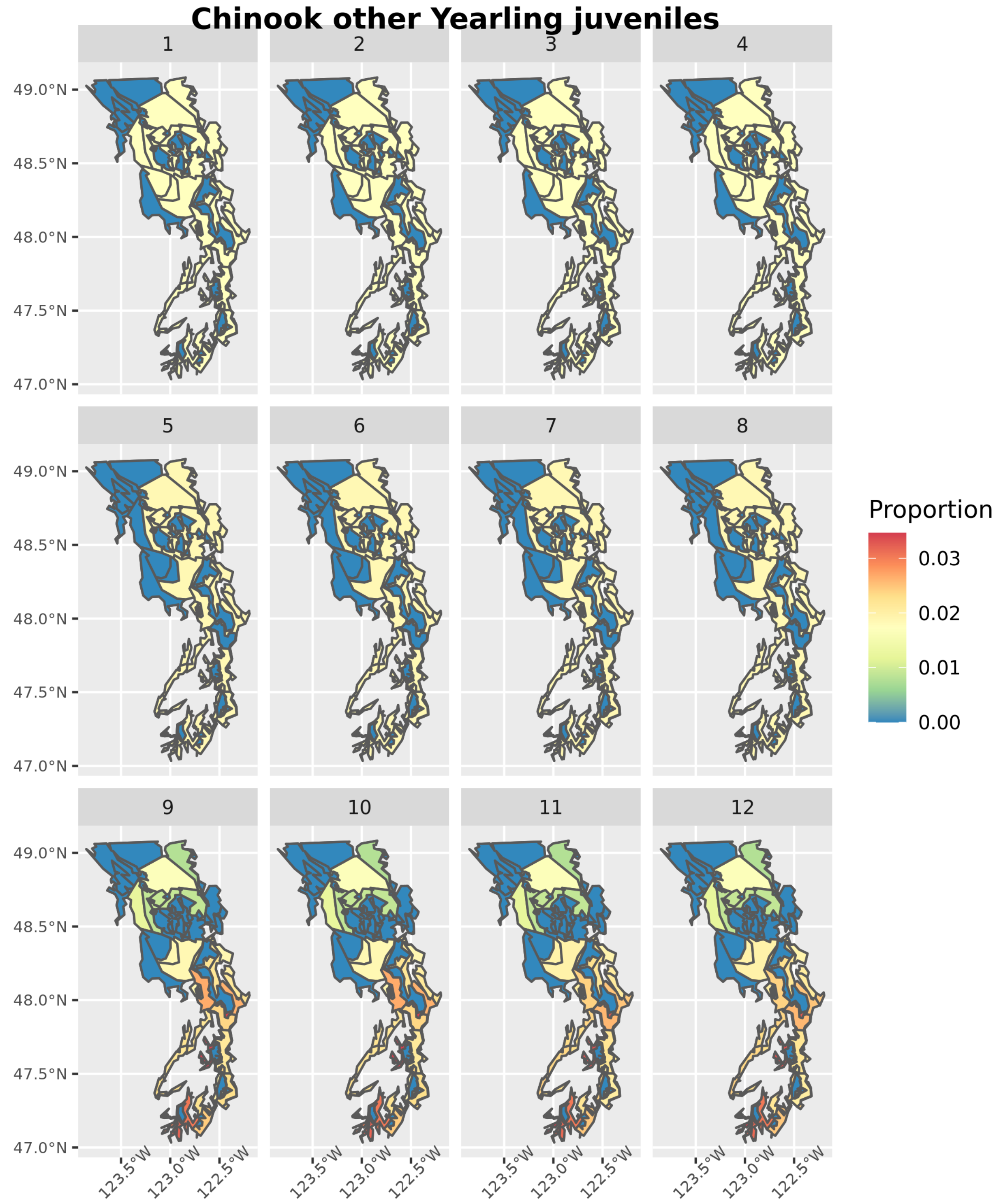

Figure 69. Monthly spatial distribution of Chinook other yearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

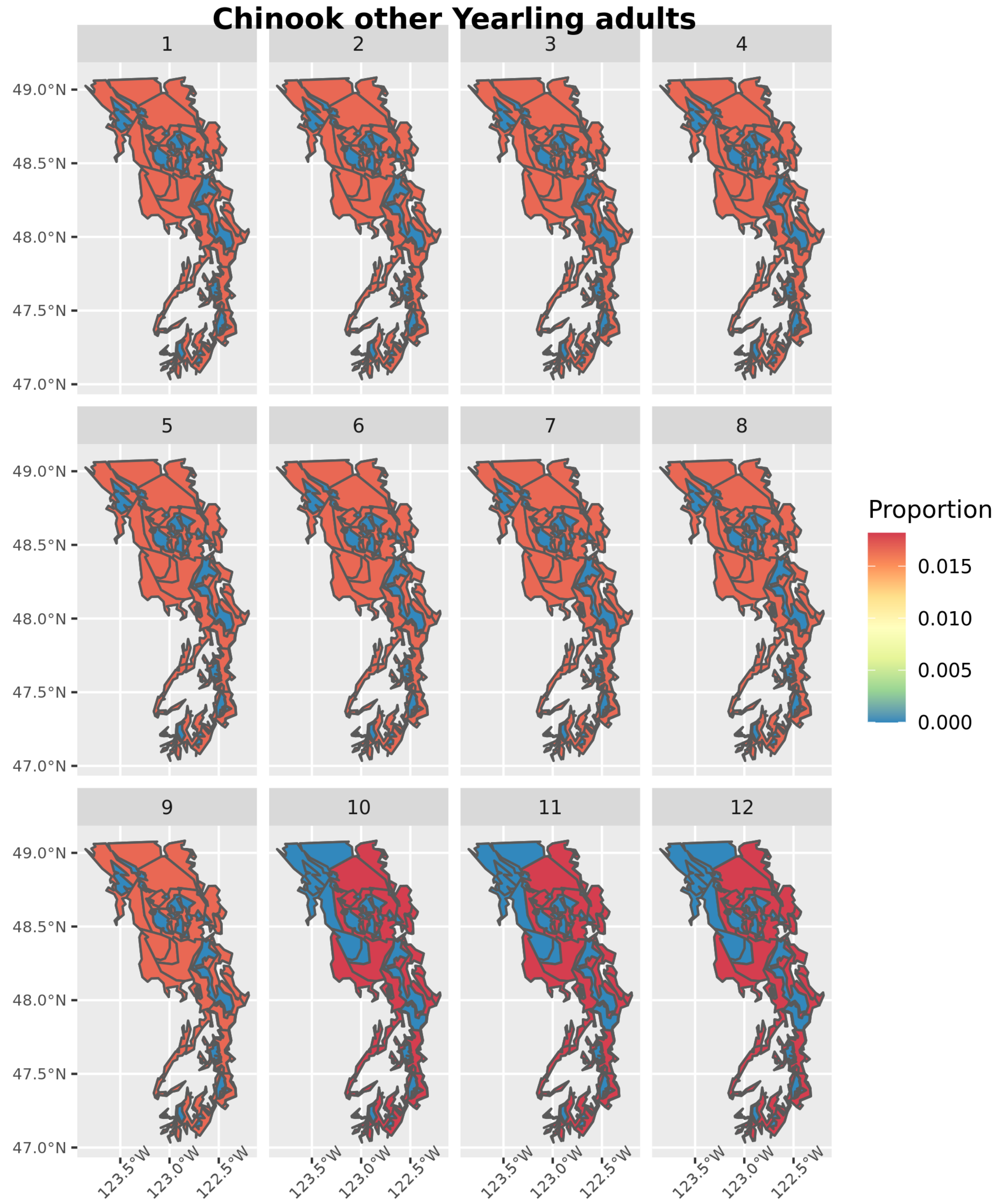

Figure 70. Monthly spatial distribution of Chinook other yearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

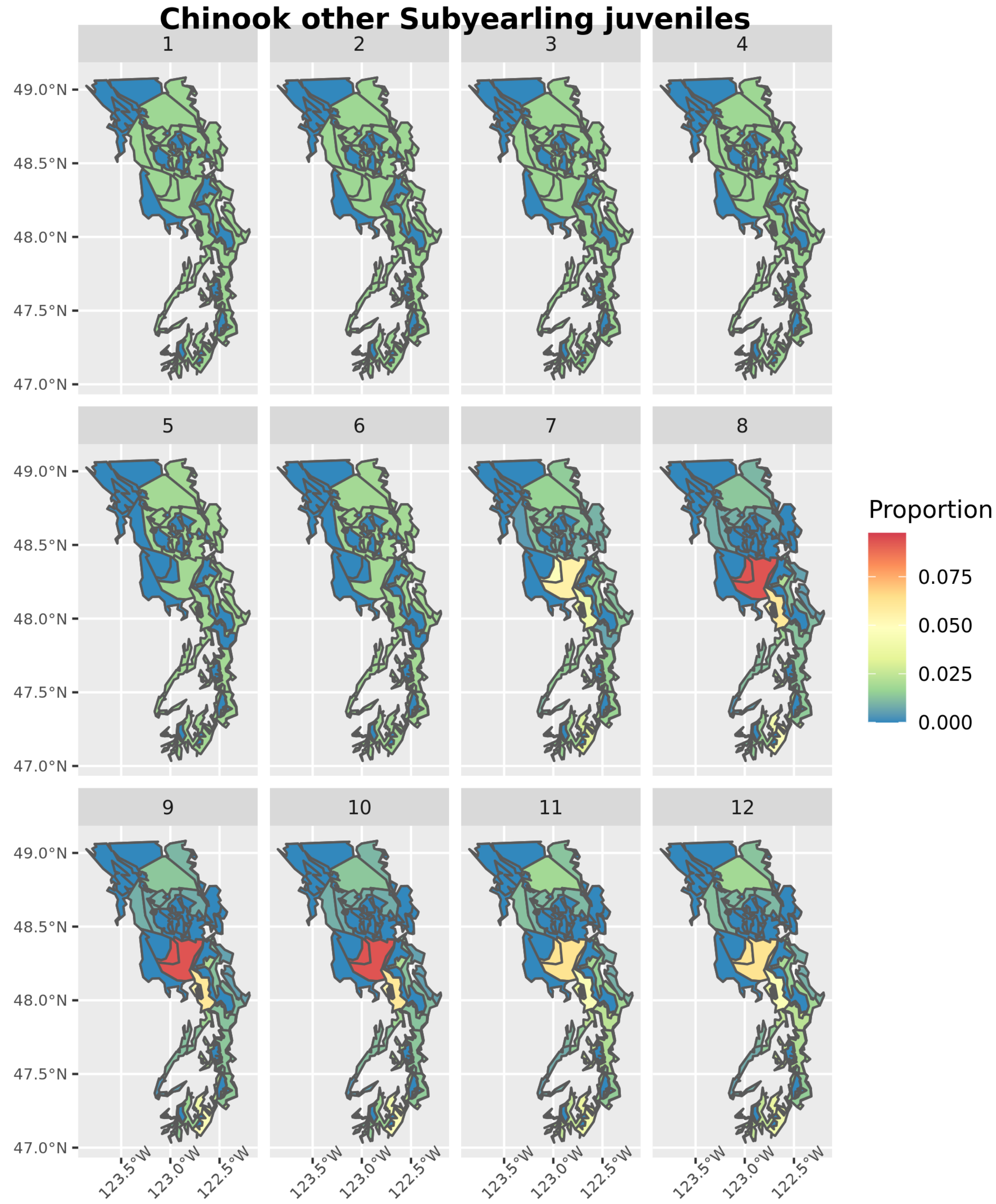

Figure 71. Monthly spatial distribution of Chinook other subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

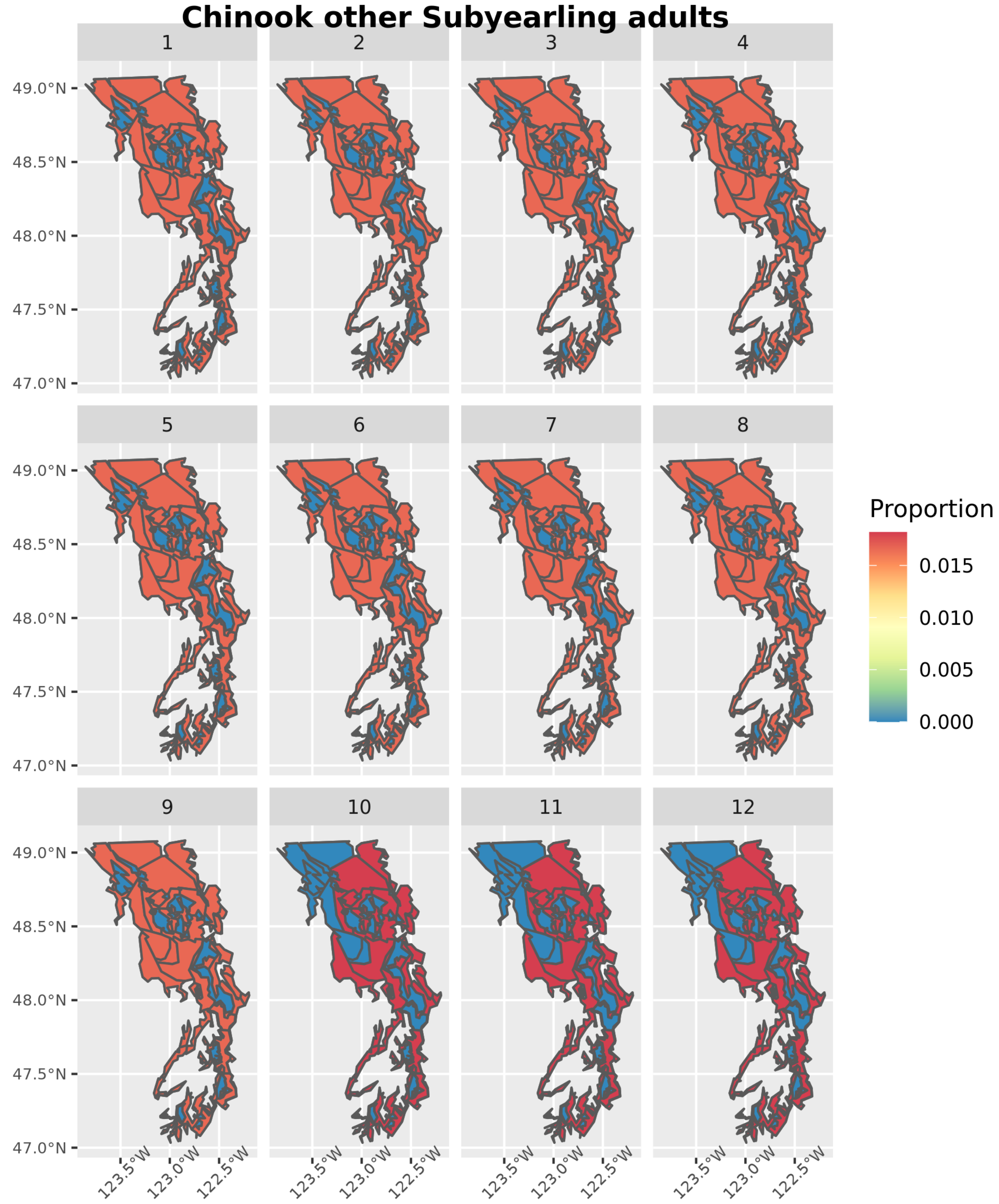

Figure 72. Monthly spatial distribution of Chinook other subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

populations have natural stocks that are grouped separately under “coho other yearling.” Based on these returns, adult spawner biomass was 196 tons, and expanded biomass for all age classes was 1,643 tons. Hatchery release data for coho were provided by Benjamin Nelson (NOAA NWFSC, pers. comm). Total releases in Puget Sound were 5,096,000 juveniles in 2011, averaging 136 mm and 28 g per individual. We force these release times to occur uniformly over 2 March–23 May (days 61–143), the period which accounts for 75% of RMIS hatchery juveniles released in 2009–13 (G. Marston, personal communication).

Adult size was based on data provided by S. O’Neill (personal communication), with fish taken by tribal gear or at hatcheries. After separating out data for the Skagit and “deep south” (Nisqually and Deschutes Rivers) populations, we had 1,852 observations of adult sizes taken from 1992–2008, from the Duwamish, Minter, Nooksack, and Snohomish River populations. Average adult fork length was 577 mm. Adult return time to rivers was assumed to be late September through October (days 263–304), based on Weitkamp et al. (1995). Adult spawn time was calculated as 1 November–6 December (days 305–340), based on the adult trap data for Soos Creek on the Green River, as described above. Soos Creek was selected as representative of run timing because it had the largest number of returns of marked fish to hatcheries in 2011, with over 19,000 returns (C. Mains, personal communication). Monthly spatial distributions for juveniles and adults are shown in Figures 73 and 74.

Coho Skagit yearling (COS)

For initial conditions in 2011, we set Skagit coho abundance at 41,061 spawners (WDFW SaSI 2018). Adult size was based on data provided by S. O’Neill (personal communication). For the Skagit, this involved 472 observations of adult size taken by tribal fisheries from 1992–2008. Average adult fork length was 611 mm. Corresponding adult spawner biomass was 123 tons, and expanded biomass for all age classes was 1,031 tons. Adult return time to freshwater was set to late June to early December (days 171–344), and spawn time was set to early October to late March (days 274–90), based on data from WDFW District 14 for the Skagit River (B. Barkdull, personal communication). We note that this is a wider range of dates than adult return times to traps at the Marblemount Hatchery (trap dates of days 288–325 typical in data from C. Mains). Juvenile outmigrant time was set to March–June (days 60–181; B. Barkdull, personal communication). Monthly spatial distributions for juveniles and adults are shown in Figures 75 and 76.

Coho deep south yearling (COD)

Populations in the coho deep south functional group include salmon in the Nisqually River, Deschutes River, and Chambers Creek. Smaller “deep south” tributaries (WDFW SCoRE 2018) include known coho habitat (WDFW Salmonscape 2018), but abundance estimates are not available (WDFW SaSI 2018). These “composite” populations in the Nisqually and Deschutes Rivers and Chambers Creek include natural and hatchery fish, but we treat them in Atlantis as a single natural stock. Population size for this Atlantis functional group in 2011 was therefore the sum of 220 spawners in the Nisqually River, escapement of 98 salmon in the Deschutes River, and escapement of 94 salmon in Chambers Creek. Corresponding adult spawner biomass was 1.1 tons, and expanded biomass for all age classes was 9.1 tons.

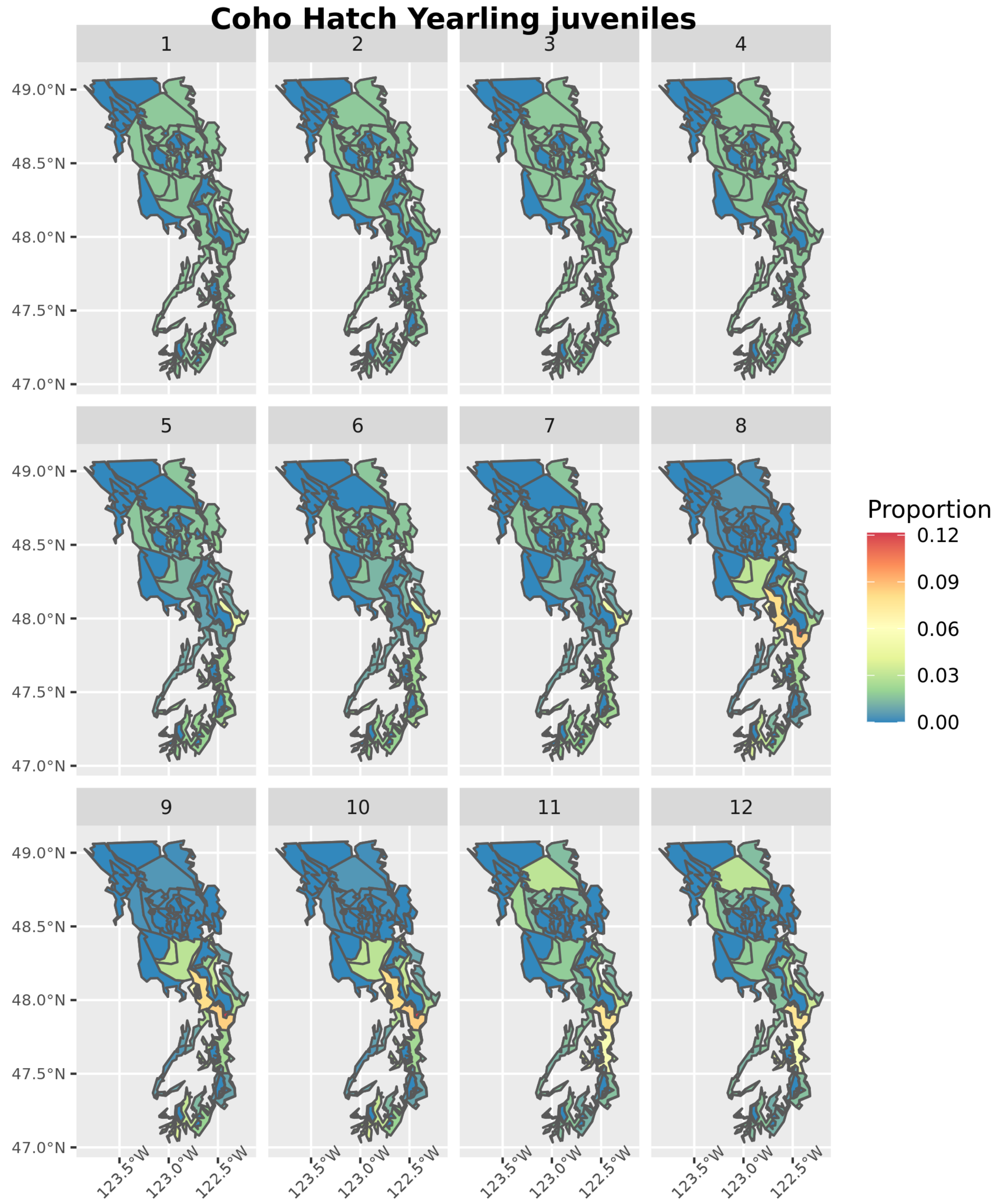

Figure 73. Monthly spatial distribution of coho hatchery yearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

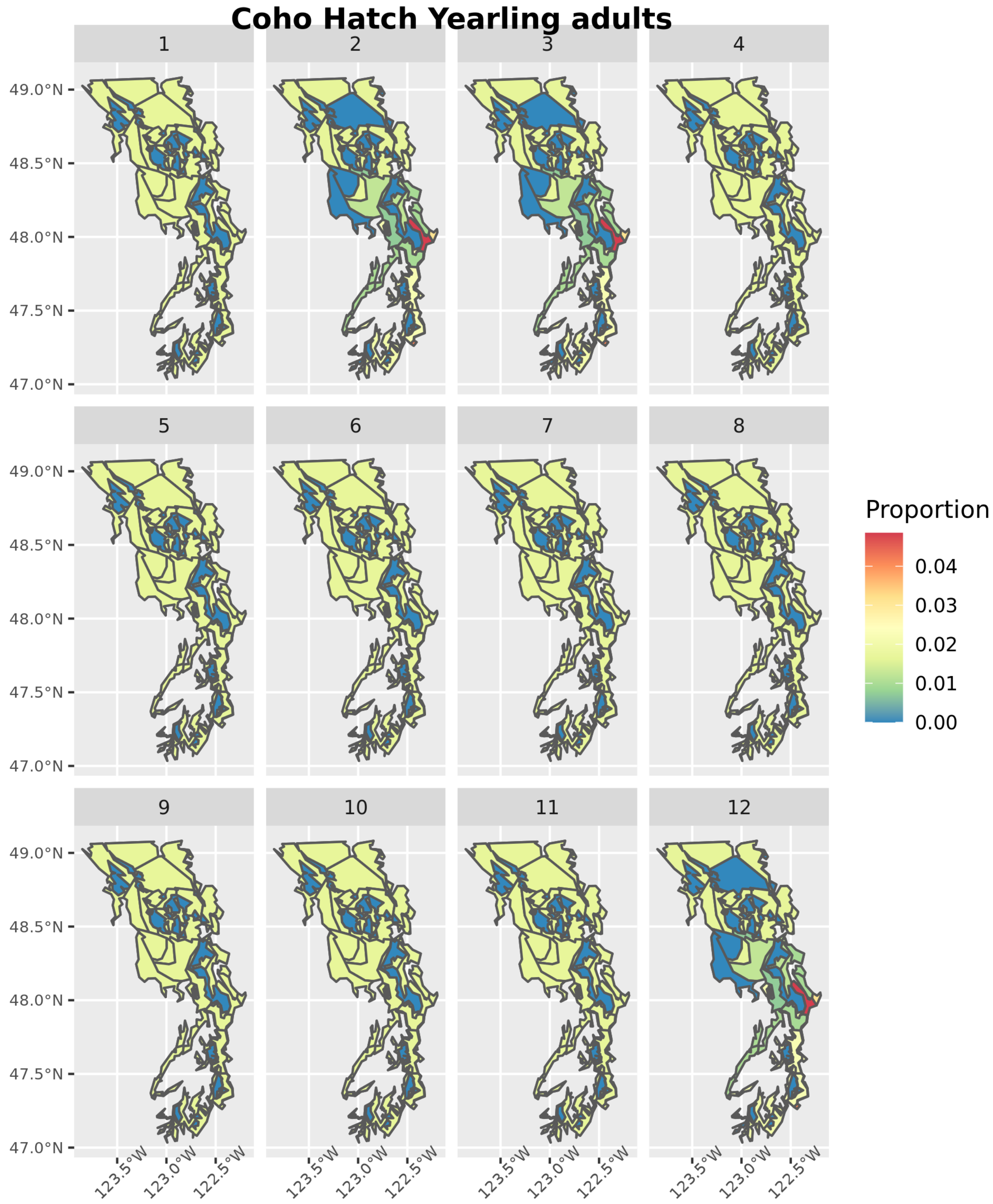

Figure 74. Monthly spatial distribution of coho hatchery yearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

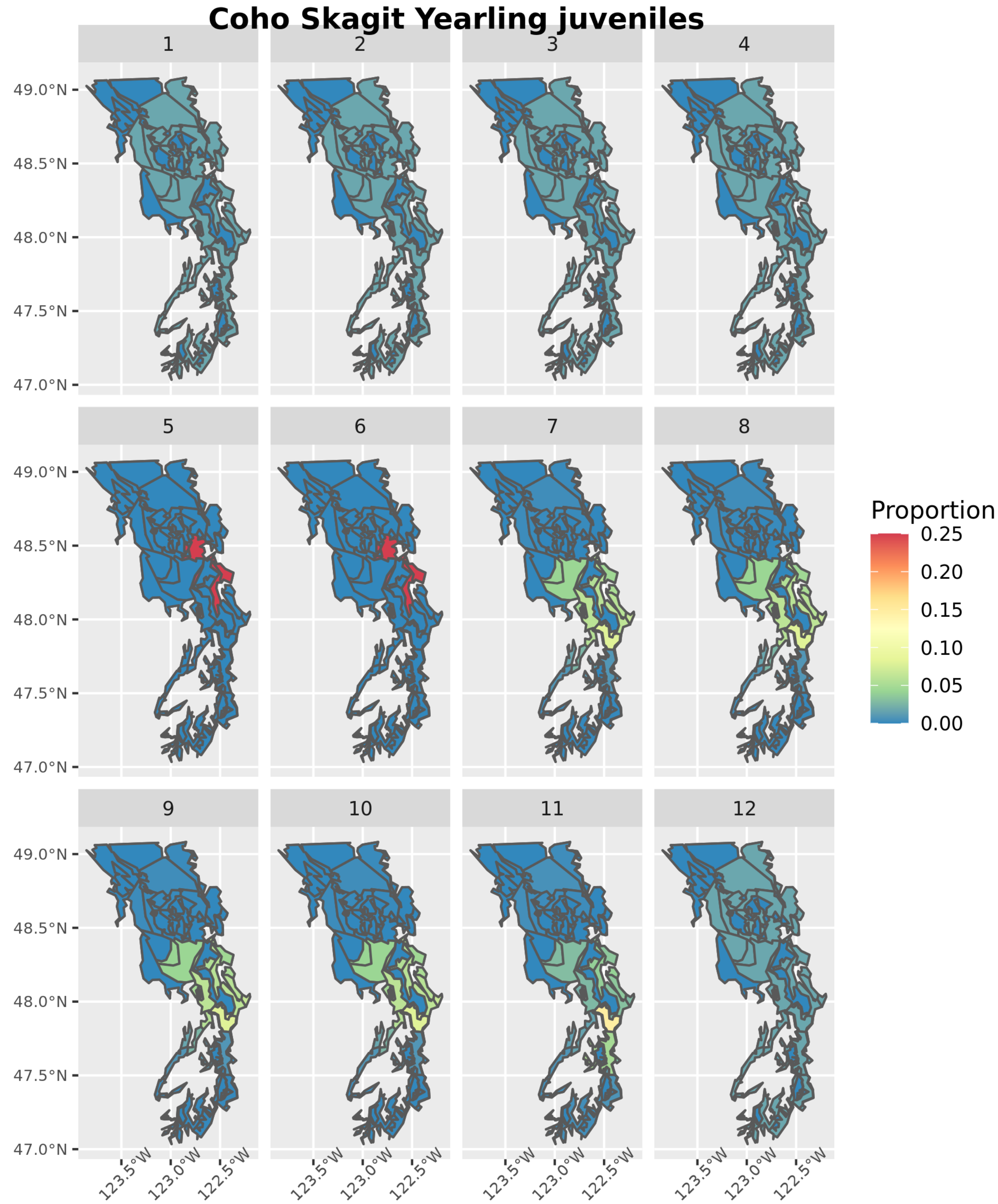

Figure 75. Monthly spatial distribution of coho Skagit yearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

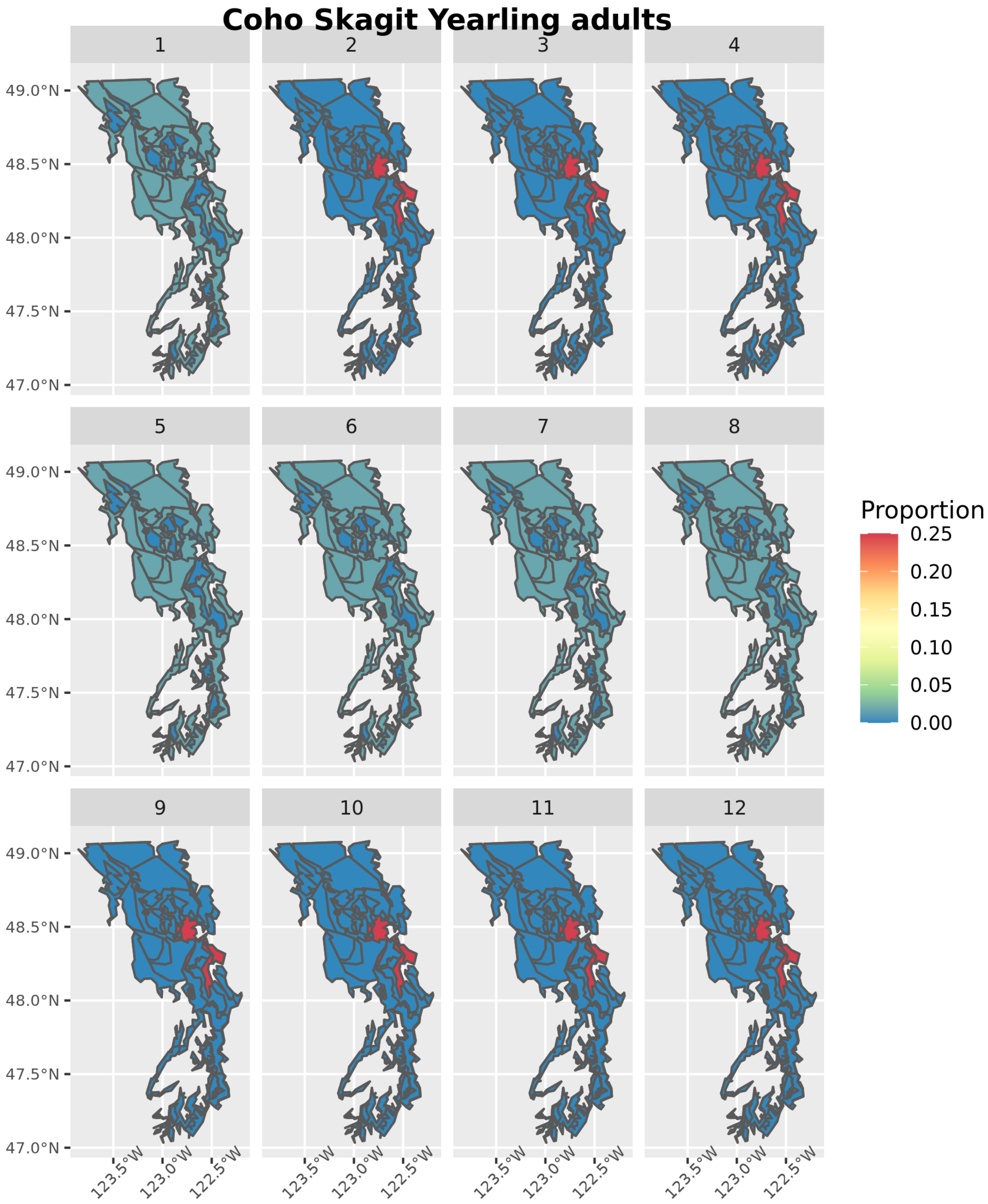

Figure 76. Monthly spatial distribution of coho Skagit yearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

Adult size was based on data provided by S. O'Neill (personal communication). For the deep south, this involved 172 observations of Deschutes River adult coho taken at the hatchery from 1993–2006, and 402 observations of Nisqually River coho taken by tribal fisheries from 1993–2008. Average size was 587 mm fork length. Adult run timing data from the Nisqually River for 2009–16 (J. Losee, personal communication) suggest the start day of the run to range from 21 August–10 September, the peak day of adult returns per year to occur between 10 September and 10 October, and the final day of the run to range from 29 September–13 November. We therefore assume the runs begin 10 September and end 10 October (days 253–283). Spawn time was set to 1 November–23 November (days 305–327) based on the adult trap data mentioned above (specifically from trapping natural and hatchery fish at Garrison Hatchery on Chambers Creek). Outmigrant timing is taken from data provided by S. Steltzner (Squaxin Tribe, personal communication) for Cranberry, Skookum, and Goldsborough Creeks, where coho show highest densities in traps from 30 March–30 June (days 89–181). This also spans the bulk of coho outmigrant timing in the Nisqually River, which appears to be approximately 1 May–21 June (Klungle et al. 2017). Monthly spatial distributions for juveniles and adults are shown in Figures 77 and 78.

Coho other yearling (COY)

This group includes coho from Chimacum Creek, Discovery Bay, East KitsapRiver , Green River/Soos Creek, Northeast Hood Canal, Quilcene/Dabob Bay, and the Nooksack, Snohomish, Stillaguamish, and White/Puyallup Rivers. Total adults (measured in either spawners or escapement) in 2011 was 195,888 individuals (WDFW SaSI 2018), with the majority in the Snohomish (111,524 spawners), Stillaguamish (49,991 spawners), and White/Puyallup Rivers (escapement of 23,770). Corresponding adult spawner biomass was 490 tons, and expanded biomass for all age classes was 4,101 tons.

Adult return time (entry to freshwater) was set to occur between 15 July and 15 November, based on data from the Snohomish River (M. Crewson, personal communication). Estimates of first and last redd dates in 2009–13 for coho salmon in the Snohomish River suggest spawning from 25 October–21 January (M. Crewson, personal communication, based on spawning ground survey data from P. Verhey). Within the model, we truncated this to 25 October–31 December (days 298–365). Though we did not use adult trap data to parameterize spawn timing, we note that adult trap data are roughly coincident with the spawning ground survey data from the Snohomish River. For instance, dates spanning 75% of adult trap data on the Skykomish/Snohomish Rivers were 276–318 (Sunset Falls) and 290–322 (Wallace River), and on the Puyallup 75% of adults were trapped between days 282–322 (Voights Creek). Adult size was set equal to the size of coho hatchery yearling, 577 mm fork length. As described above, this was based on data provided by S. O'Neill (personal communication). Juvenile outmigration dates for the Snohomish River tributaries (Snoqualmie and Skykomish Rivers) were typically late February through late June for fry, and late March through mid-June for parr (data from M. Pouley and M. Crewson, personal communication). Monthly spatial distributions for juveniles and adults are shown in Figures 79 and 80.

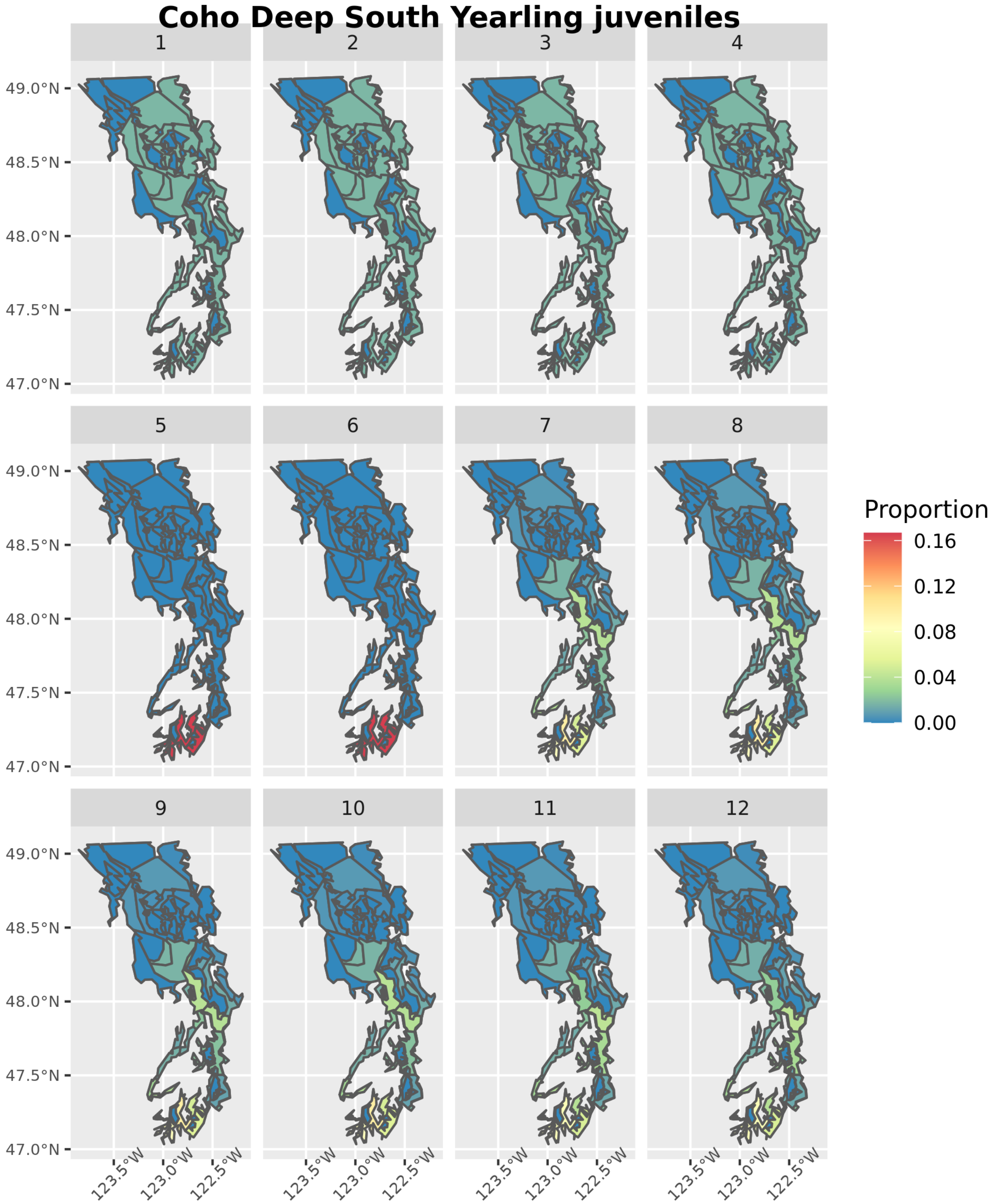

Figure 77. Monthly spatial distribution of coho deep south yearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

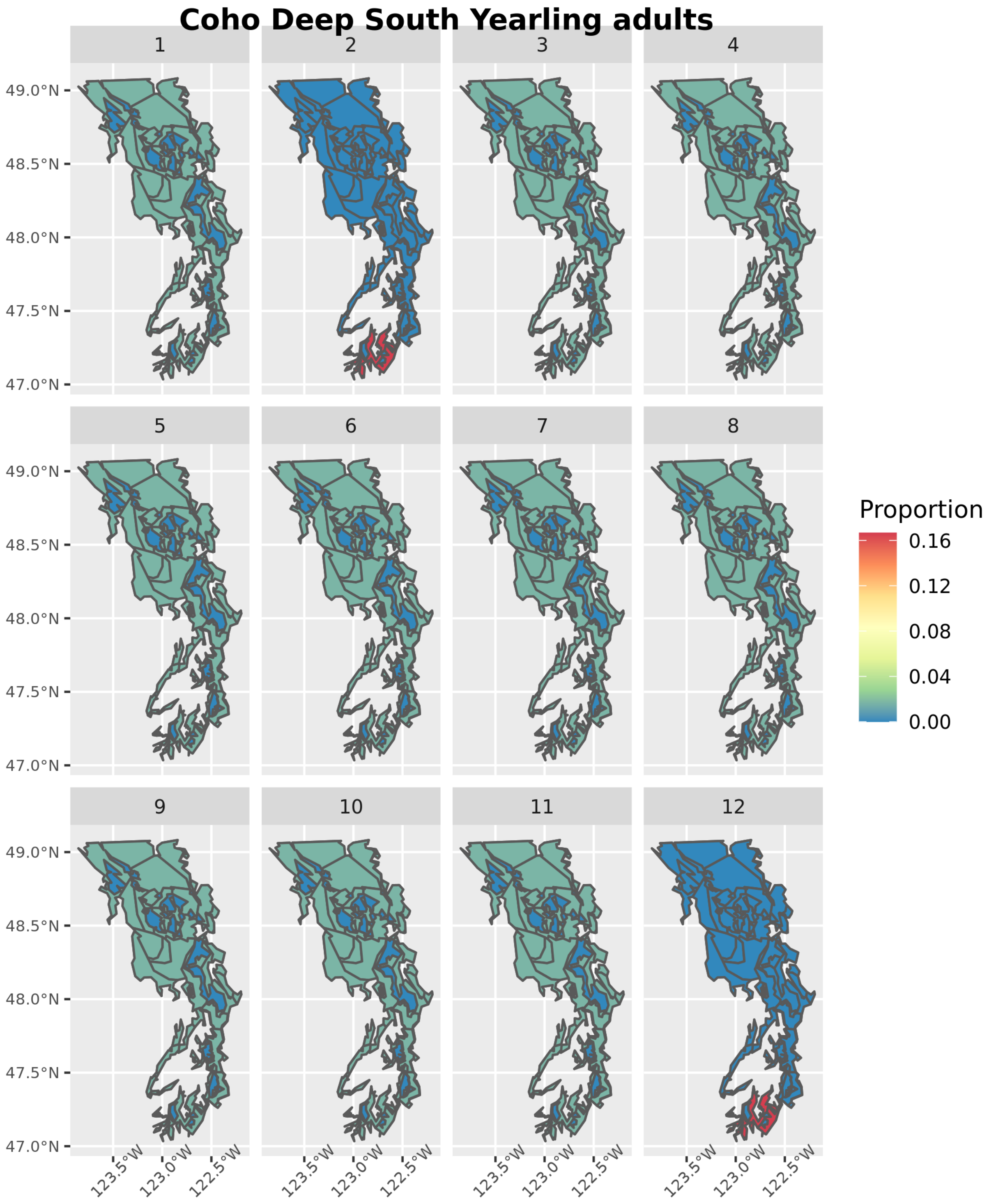

Figure 78. Monthly spatial distribution of coho deep south yearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

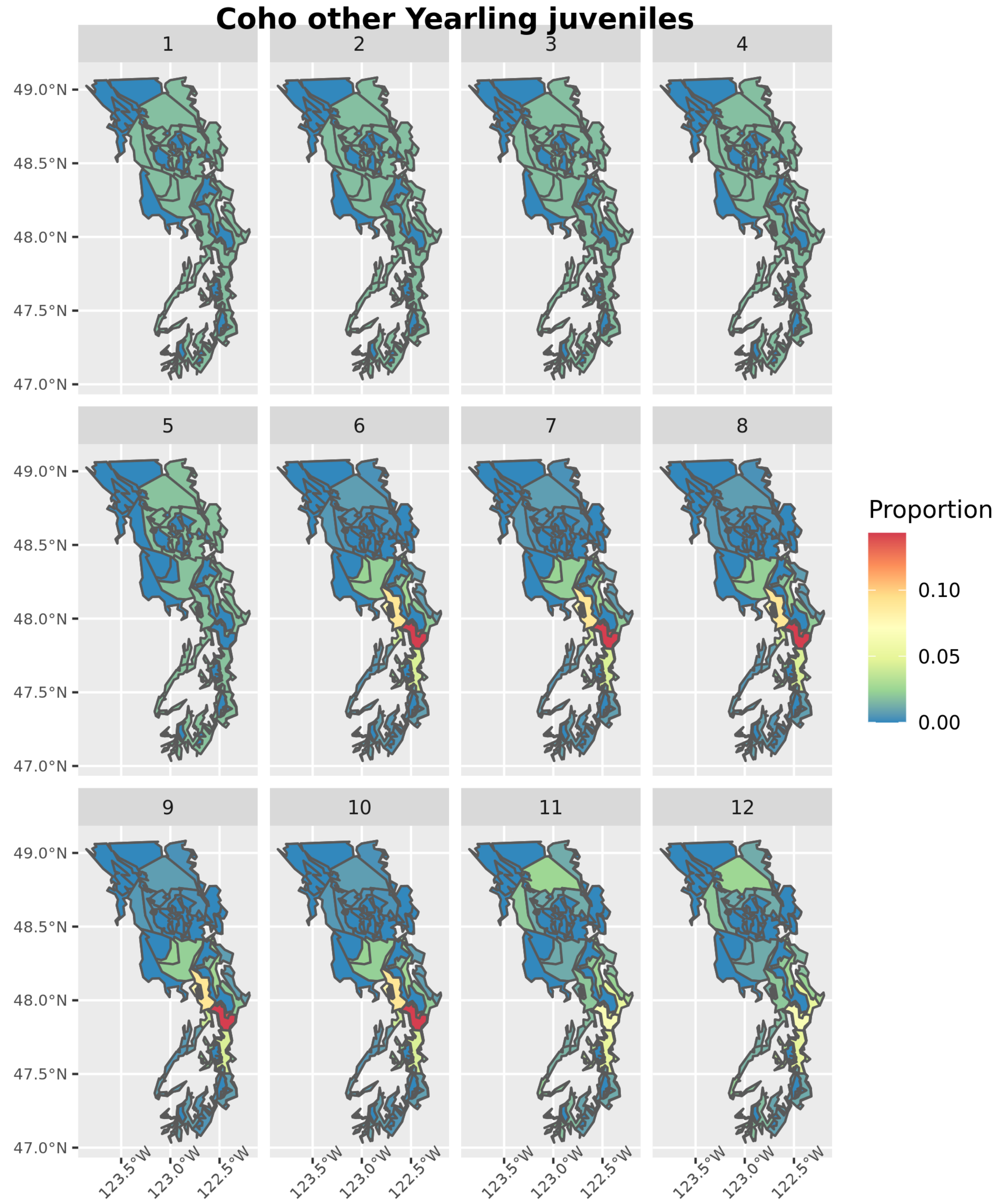

Figure 79. Monthly spatial distribution of coho other yearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

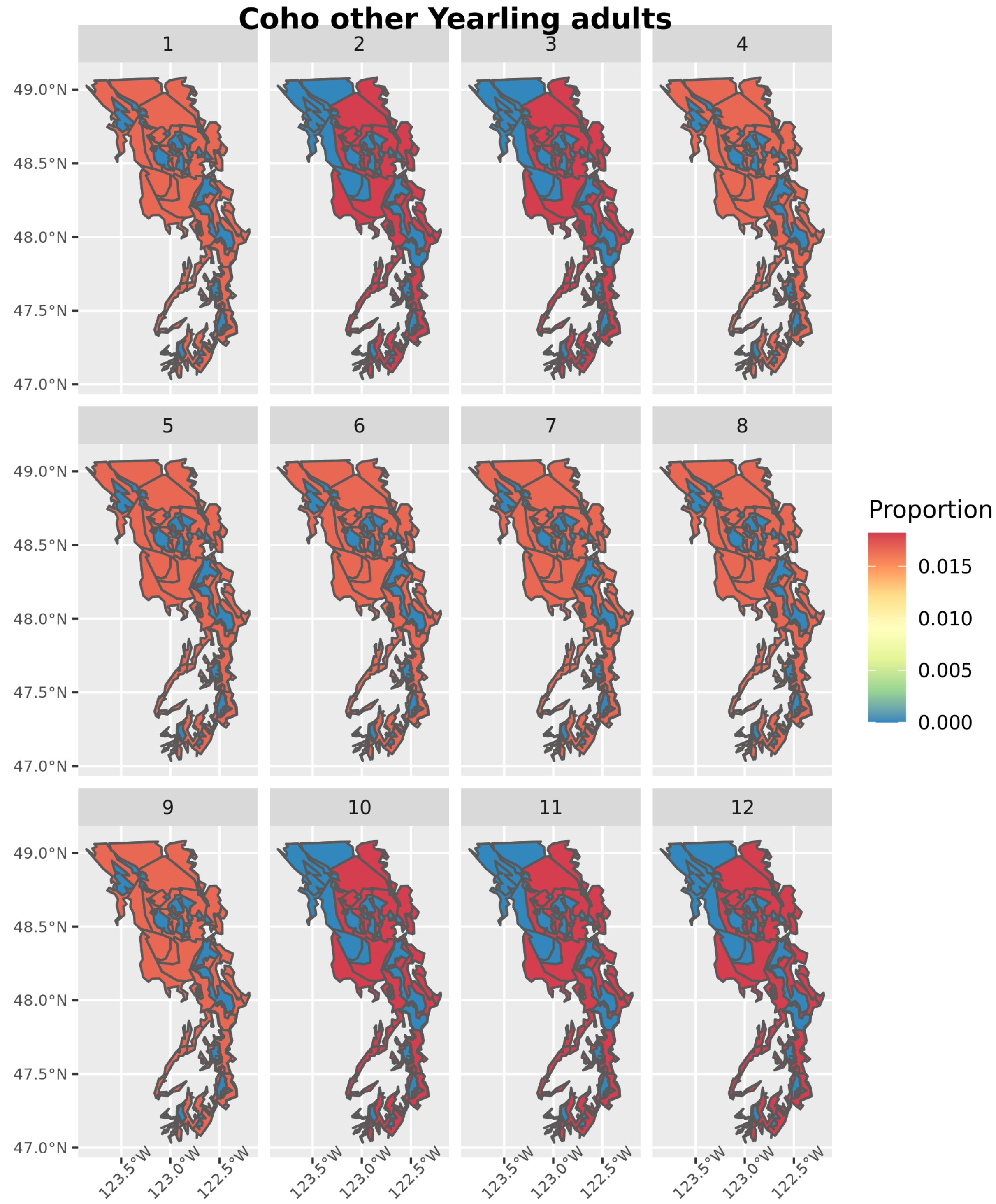

Figure 80. Monthly spatial distribution of coho other yearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

Chum salmon

We assume chum salmon residence within the model domain throughout their marine phase is rare enough that all modeled individuals can be treated as leaving Puget Sound during outmigration.

Chum hatchery subyearling (CMS)

Hatchery-origin chum salmon abundance for 1992–2015 was provided by A. Dufault (WDFW, personal communication). For our initial conditions (year 2011), total run size (escapement + harvest) of hatchery-origin chum salmon was 538,000 individual salmon. We assume 4.47 kg/spawner (Groot and Margolis 1991, p. 275), for a total spawner biomass of 2,405 tons, but note that there is uncertainty in spawner weights: Quinn (2005, p. 277) suggests 3.73 kg as typical adult weight. Corresponding expanded biomass for all age classes was 9,434 tons. We forced the model with hatchery releases of juveniles for 1971–2016; for instance, these data suggest 46 million hatchery releases in 2011, with over half in Hood Canal (G. Marston, personal communication). We force these release times to occur uniformly over 1 March–1 May (days 60–121), the period which accounts for 75% of RMIS hatchery juveniles released in 2009–13 (G. Marston, personal communication).

Juvenile outmigrant timing was set to 1 April (day 91), with average size of 45 mm and 0.8 g, based on RMIS and values reported in Johnson et al. (1997). We assume that some chum salmon mature at age-3, but that the majority return at age-4. For model initial age structure, we assume a 1% survival rate from fry to adult, based on references in Groot and Margolis (1991, Table 10, p. 282). This equates to a natural mortality (N) rate of 1.15/yr (where M = natural mortality rate and $N_{Year\_t+1} = N_{Year\_t} \times e^{-M}$). Adult return time, prior to spawning, is typically mid-November to mid-January (days 319–15) for fall-run chum salmon in Hood Canal (Johnson et al. 1997). Adult trap data for natural and hatchery chum (at hatcheries) were provided by C. Mains (personal communication), and we use these to set the spawn date. The largest numbers of returning adults in traps for 2009–13 were from McKernan Hatchery in Hood Canal and Minter Creek Hatchery in South Sound. At those sites, 75% of adult returns occurred between calendar day windows of 308–325 and 320–340, respectively. The other major sites in Hood Canal (George Adams and Hoodsport), as well as Whatcom Creek (near Bellingham), had dates similar to McKernan Hatchery. We therefore set chum salmon spawn day to 30 days after the average of these calendar day windows, with final spawning dates parameterized as days 344–363. Adult return time to freshwater was also therefore truncated to day 363 (rather than day 15). Monthly spatial distributions for juveniles and adults are shown in Figures 81 and 82.

Chum fall subyearling (CMF)

Chum abundance for 1992–2015 was provided by A. Dufault (personal communication). For our initial conditions (year 2011), total run size (escapement + harvest) of natural fall-run chum was 835,000 individual salmon. We assume 4.47 kg/spawner (Groot and Margolis 1991, p. 275), for a total spawner biomass of 3,732 tons. Corresponding expanded biomass for all age classes was 14,639 tons.

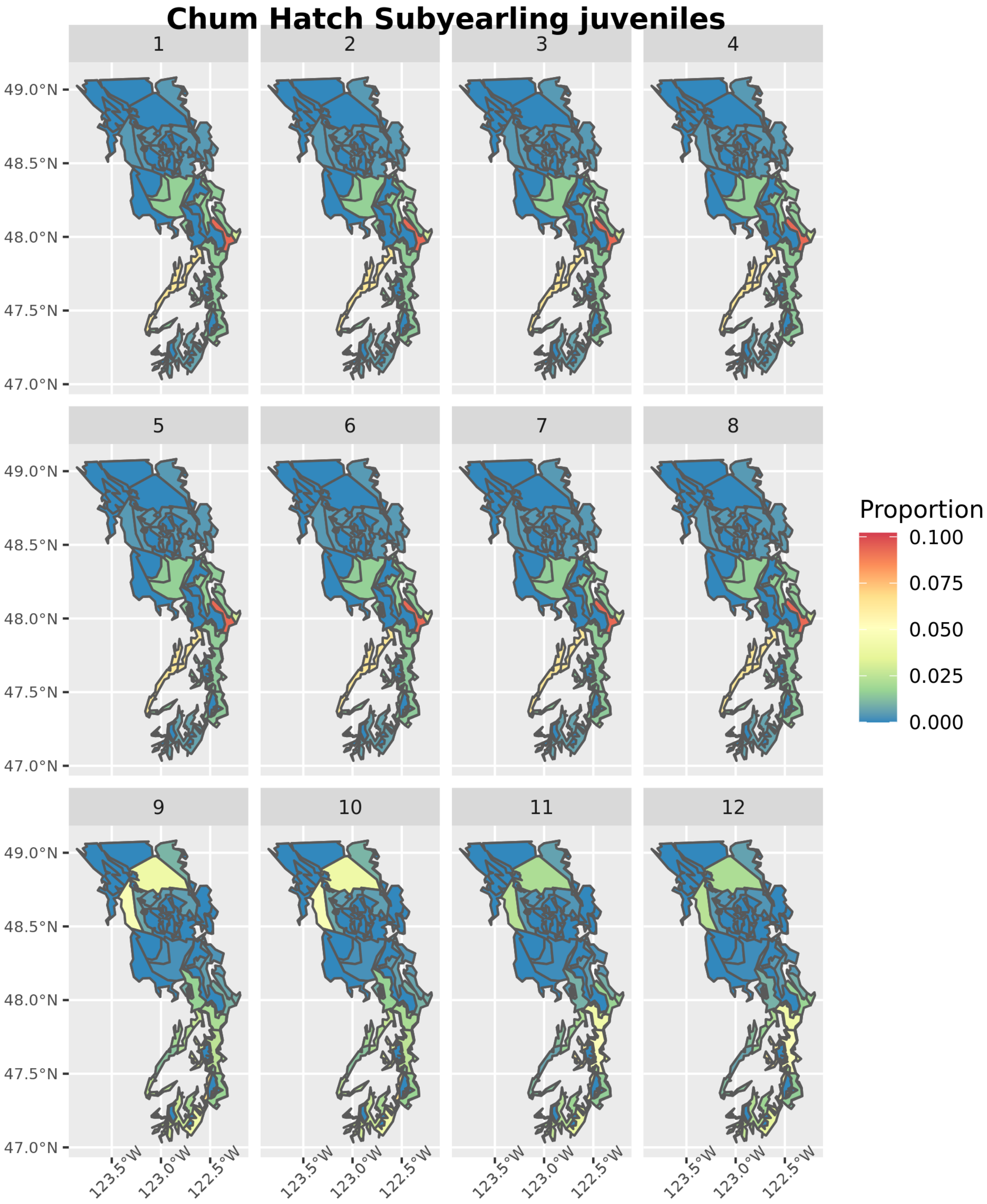

Figure 81. Monthly spatial distribution of chum hatchery subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

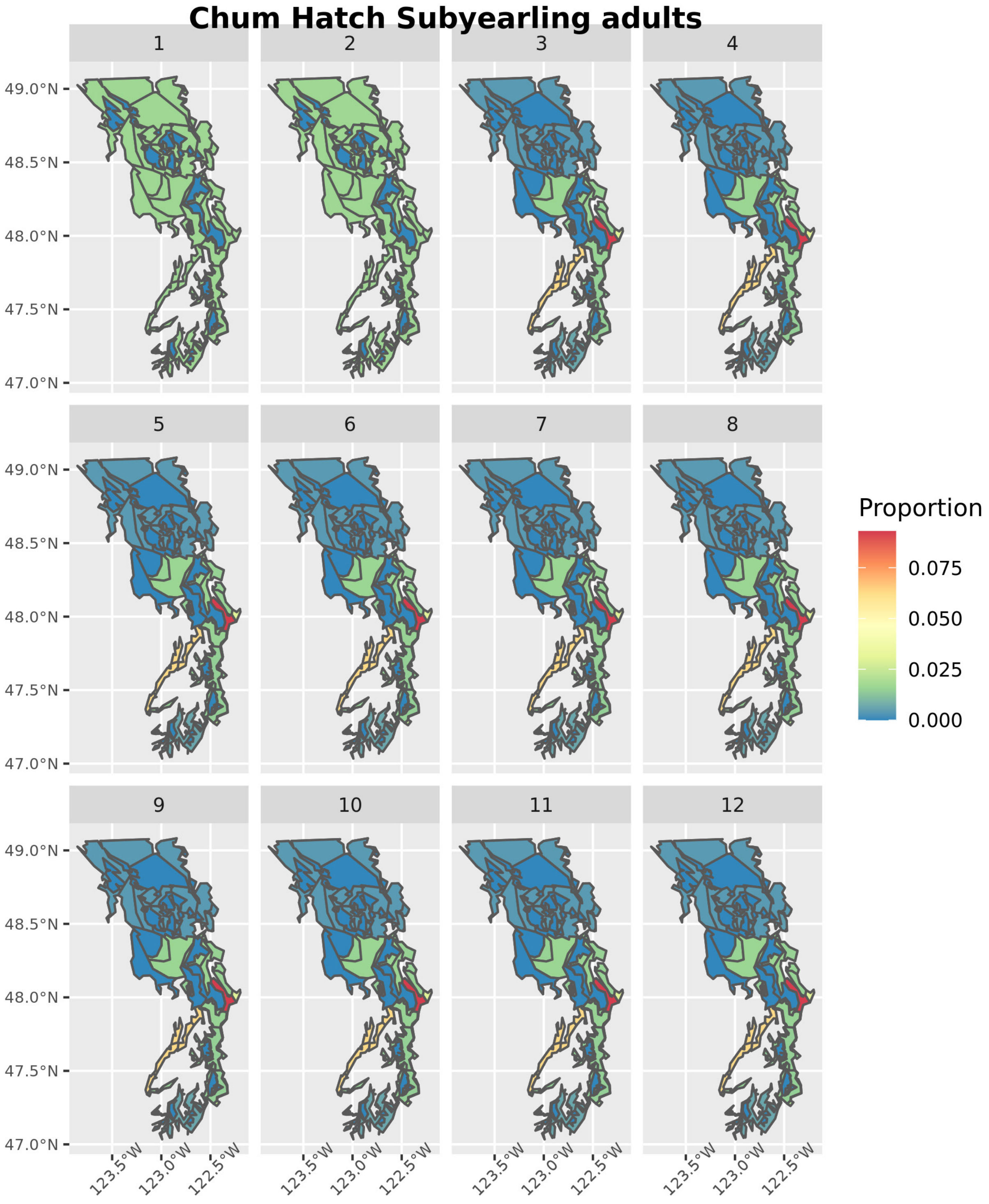

Figure 82. Monthly spatial distribution of chum hatchery subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

We assume outmigration from freshwater during February to May, but with a peak in March–April (Johnson et al. 1997). Adult return time was available from adult trap data (at hatcheries) by C. Mains (personal communication), as described above for hatchery chum. Monthly spatial distributions for juveniles and adults are shown in Figures 83 and 84.

Chum Hood Canal summer-run subyearling (CMH)

Summer-run chum salmon were listed as threatened under the ESA in 1999, and under a recovery plan have shown some signs of improved abundance in recent years (Johnson et al. 2008). We base the return time of adults on Tynan (1997), who suggested return times to Hood Canal from late August to late October (days 240–300). Returns have recently been quite variable, but total run size was ~7,200 spawners in 2011 (Lestelle et al. 2014), or total escapement of 6,968 (M. Downen, WDFW, personal communication), excluding the summer-run chum salmon populations in the Strait of Juan de Fuca that are outside our model domain. These 7,200 spawners are likely all natural-origin fish, and hatchery contributions in other recent years are minimal (Lestelle et al. 2014). Hatchery releases of juvenile summer-run chum salmon were relatively low (140,000 juveniles in 2011; G. Marston, personal communication). We therefore assume this functional group is entirely of natural origin. We assume 4.47 kg/spawner (Groot and Margolis 1991, p. 275), for a total spawner biomass of 32.2 tons. Corresponding expanded biomass for all age classes was 126.3 tons. Average fork length of spawners was 654 mm in 2011 (M. Downen, personal communication). Spawn time was set to 15 September to late October (Johnson et al. 1997), or days 258–300, and juvenile outmigrant time and size were set to February–March (days 32–90) and 39 mm (Tynan 1997). Monthly spatial distributions for juveniles and adults are shown in Figures 85 and 86.

Pink salmon (PIS)

Pink salmon have a simple, specialized life history with a fixed, two-year span (Heard 1991). Fry emerge from redds and then move quickly into estuarine or nearshore marine environments where they remain for a week to months, then quickly move through coastal systems to the open ocean. After approximately 18 months at sea, they return to their original streams in the fall, spawn, and die. In Puget Sound, virtually all pink salmon are of natural origin and are odd-year stocks, meaning that adults spawn in the fall in odd calendar years and fry enter Puget Sound the following spring in even years (Heard 1991). We include a single group representing the population in Puget Sound. We assume pink salmon residence is rare enough that the modeled groups can be treated as leaving Puget Sound during outmigration.

Pink salmon abundance for 1959–2015 was provided by A. Dufault (personal communication). For our initial conditions (year 2011), total run size (escapement + harvest) was 5,329,014 individual salmon. To approximate the age structure for initial conditions, we assume survival rates (fry-to-adult return) of 3%, based on an average from Table 21 in Groot and Margolis (1991). We assume that a spawning population (escapement) of 3,629,000 adults (A. Dufault, personal communication) with a 1:1 sex ratio, a fecundity of 2,000 eggs per female, and an egg-to-fry mortality rate of 87.3% (Parker 1968) would yield approximately 464 million fry that survive to enter the marine environment the following spring. We

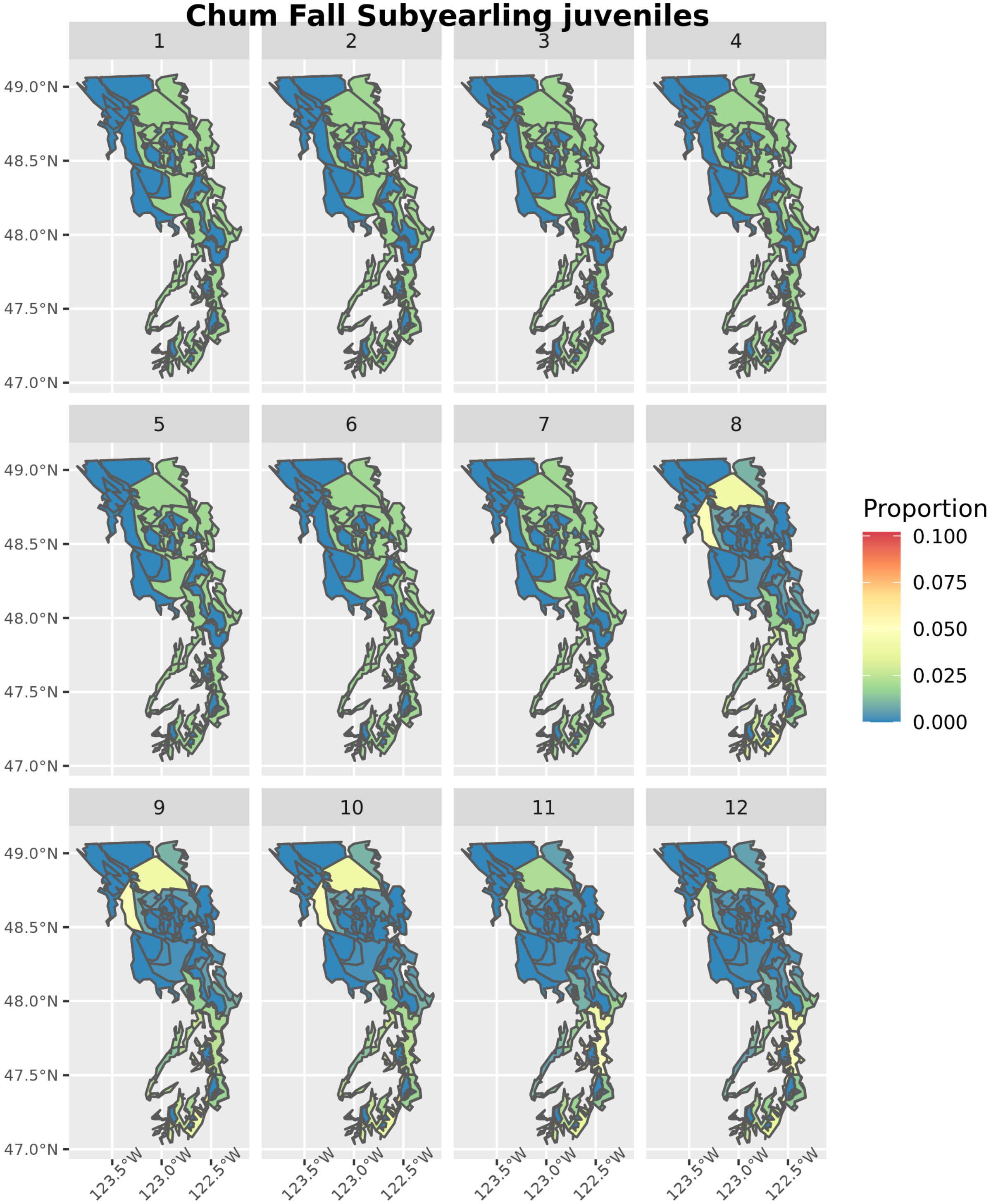

Figure 83. Monthly spatial distribution of chum fall subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

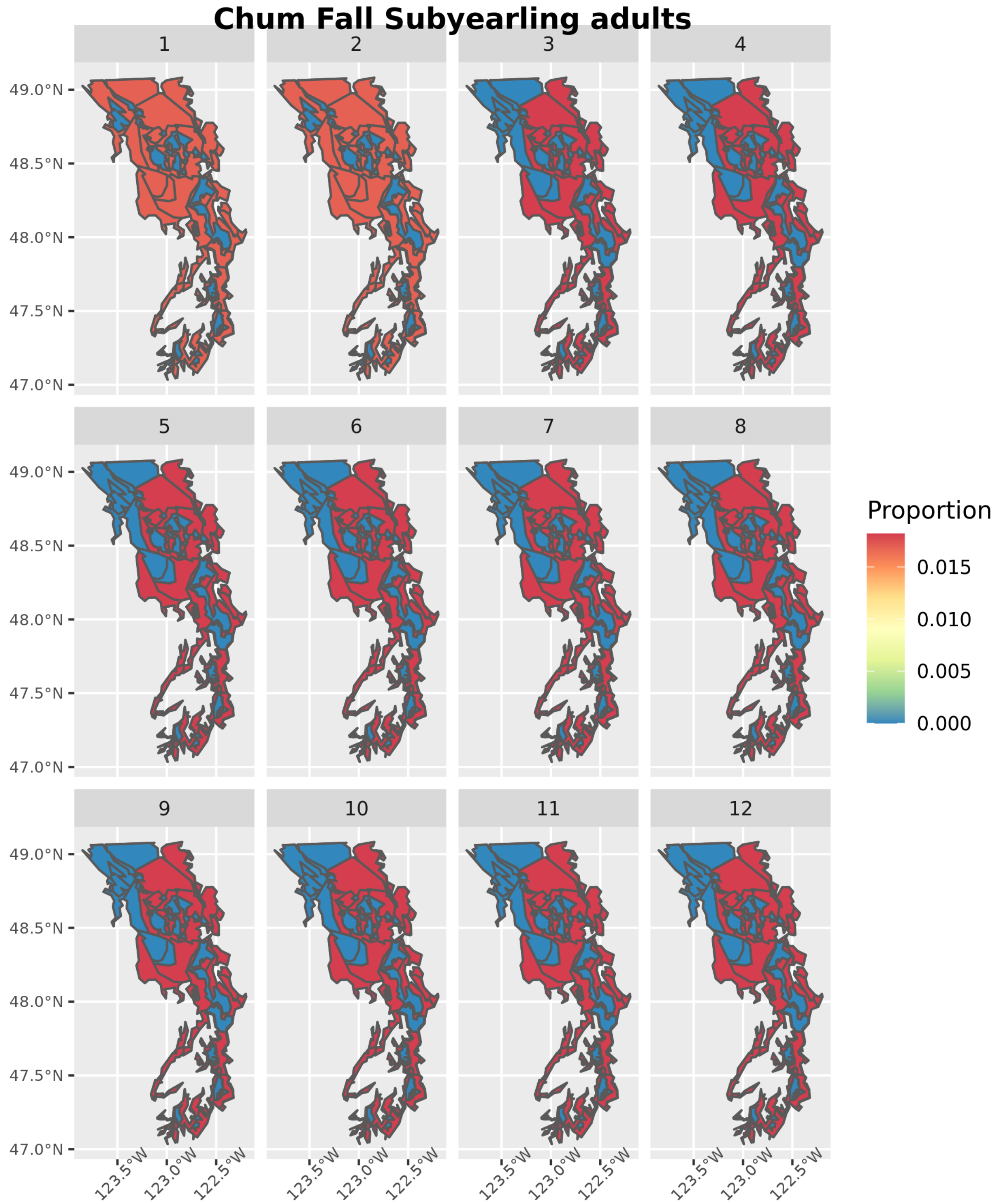

Figure 84. Monthly spatial distribution of chum fall subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

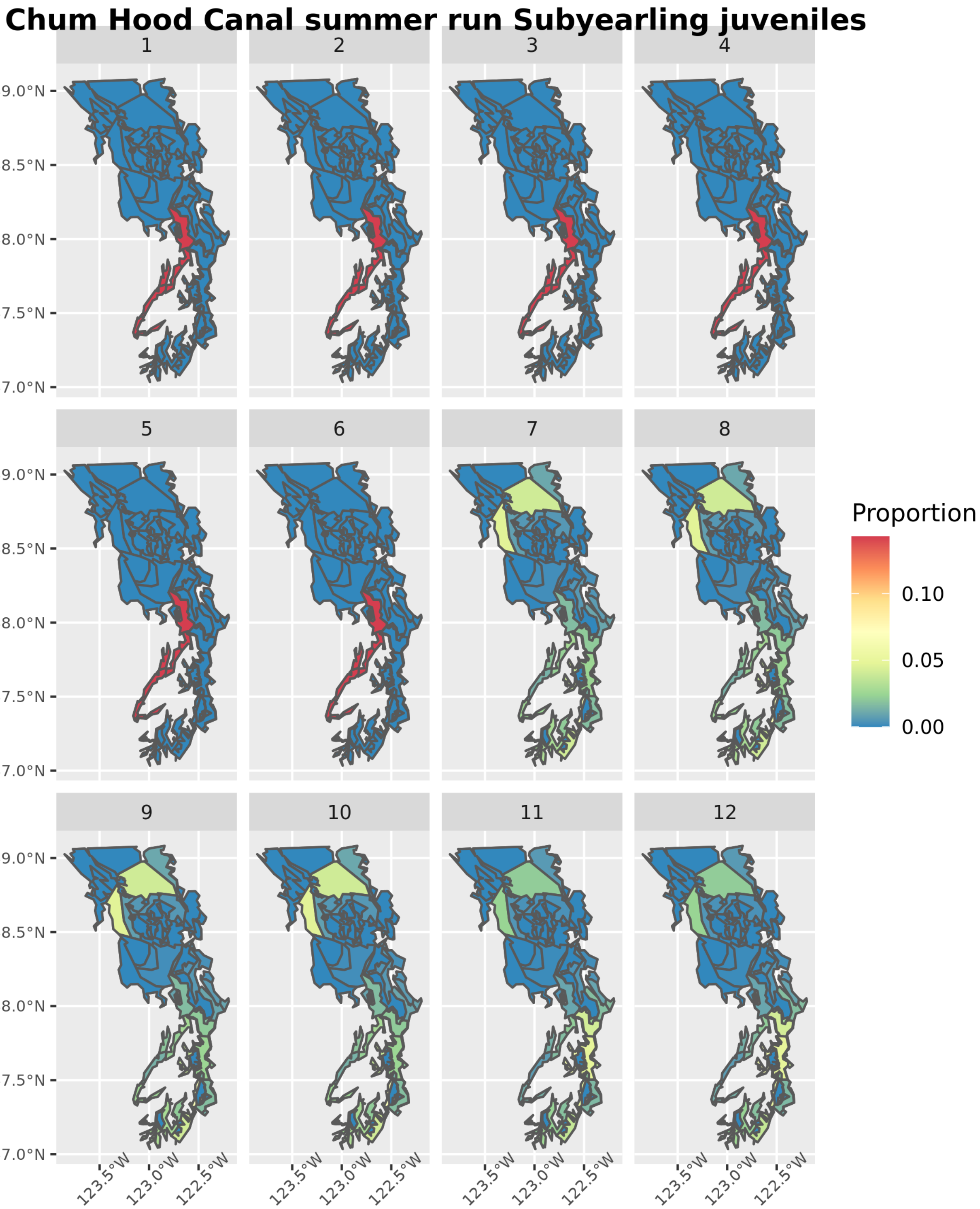

Figure 85. Monthly spatial distribution of chum Hood Canal summer-run subyearling juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

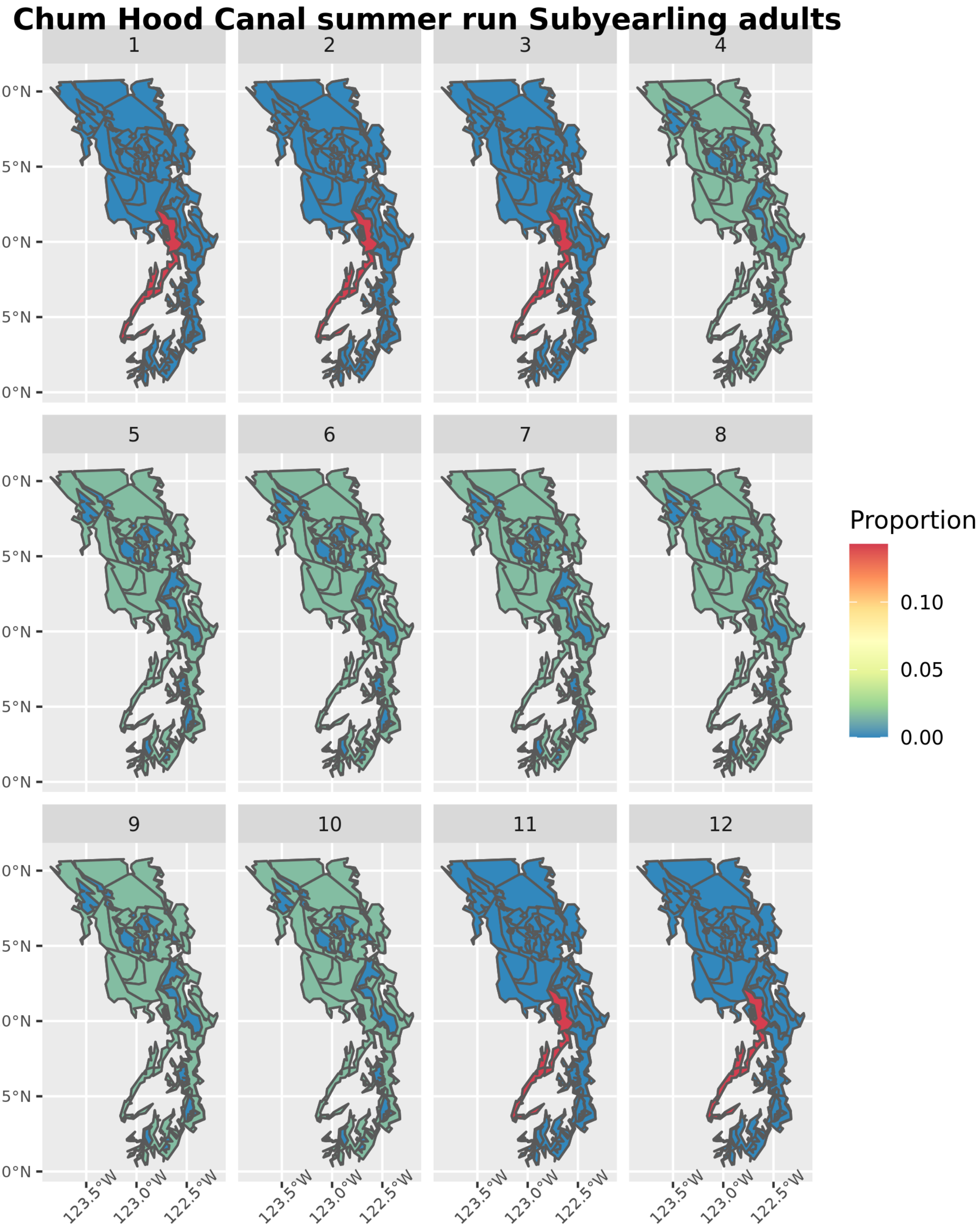

Figure 86. Monthly spatial distribution of chum Hood Canal summer-run subyearling adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

do not drive the model with hatchery releases of pink salmon, which are substantially lower than natural production: 673,000 juveniles released on average for 2010 and 2012, primarily in Hood Canal (G. Marston, personal communication). Multiplying fry abundance of 464 million by a weight of 0.24 g/fry (Heard 1991) results in a juvenile biomass of 111 t. Assuming 1.8 kg/adult × 5,329,014 individuals suggest 9,592 tons of adult pink salmon biomass and fry. Corresponding expanded biomass for all age classes was 44,190 tons.

For model initial age structure, we assume a 3% survival rate from fry to age-2 adults, on the basis of Fraser River estimates in Groot and Margolis (1991, Table 21). This equates to a natural mortality rate of 1.74/yr. Return times of adult pink salmon were set to 17 September–7 October (days 260–280) based on Hood Canal values in the status review (Hard et al. 1996). Spawn times for Hood Canal are approximately 1 September–25 October (days 244–298; Hard et al. 1996), but here we truncated this to days 260–298 in the model so that no spawning would occur before the upriver migration begins. We note that there is some evidence for slightly earlier adult migrations in recent years, but it is not clear whether this should affect model parameterization for adult return time and spawning. Adult trap data (at hatcheries; C. Mains, personal communication) suggests that the majority of returns for 2009–13 were from Hoodsport (Hood Canal) and Sunset Falls (Skykomish River). For Hoodsport and Sunset Falls, respectively, 75% of adult returns to traps occurred between days 206–219 and 234–269, corresponding to an average calendar-day window of 220–244. This might suggest a spawning period about one month earlier than the dates we have parameterized here.

Juvenile outmigrant size and timing were informed by Hood Canal beach seine sampling in 2011–14 provided by the Port Gamble S'Klallam Tribe Natural Resources Department. Sampling occurred in March–October. These fish were typically observed in April–June (days 91–181). Mean fork length of fish in April was 38 mm (E. Bishop and H. Daubenberger, personal communication). When converting to weight, these outmigrants would be 0.3 g. Monthly spatial distributions for juveniles and adults are shown in Figures 87 and 88.

Other salmonids (SAL)

Other salmonids represent only sockeye salmon (*Oncorhynchus nerka*). Cutthroat trout (*O. clarkii*) were also of interest, but ultimately we did not include them in this group. Based on cutthroat trout diet compositions and bioenergetics, they may be important predators on juvenile salmonids (Duffy and Beauchamp 2008). However, reliable estimates for their abundance appear lacking, except for some spawner counts in the western South Sound (WDFW SaSI 2018) though there are 12 other spawning streams or areas. We therefore do not include cutthroat trout in this model group.

Sockeye salmon populations in Puget Sound represent both natural and hatchery fish from Baker River, Cedar River, the Lake Washington beach-spawning population, and the Lake Washington and Sammamish Tributaries population (WDFW SCoRE 2018). Total escapement in 2011 was 59,000 fish (WDFW SaSI 2018), with an additional 11,781 returns to hatcheries (C. Mains, personal communication), primarily to Baker Lake and Cedar River. Corresponding spawner biomass is 190 tons, and expanded biomass for all age classes was 315 tons.

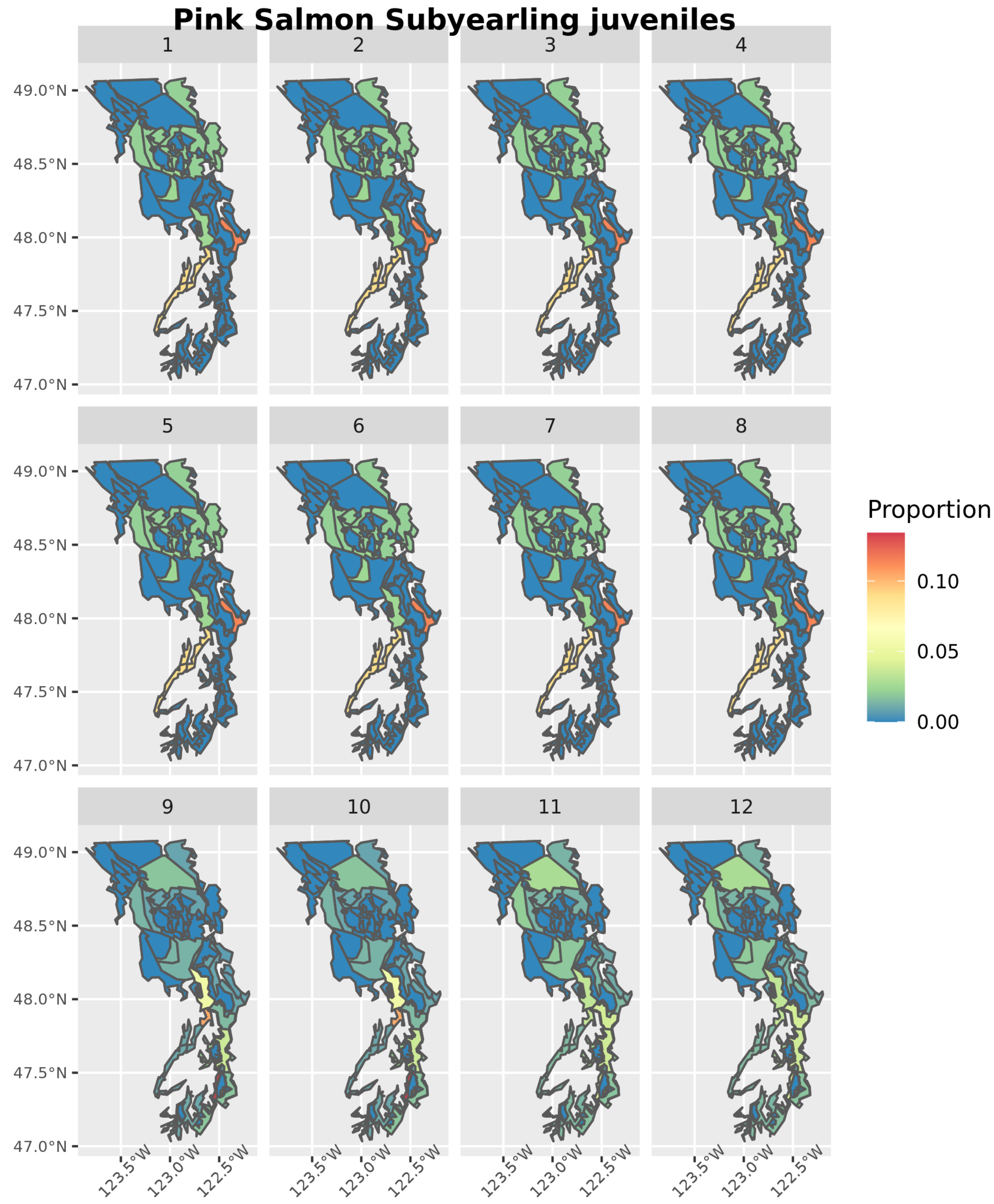

Figure 87. Monthly spatial distribution of pink salmon juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

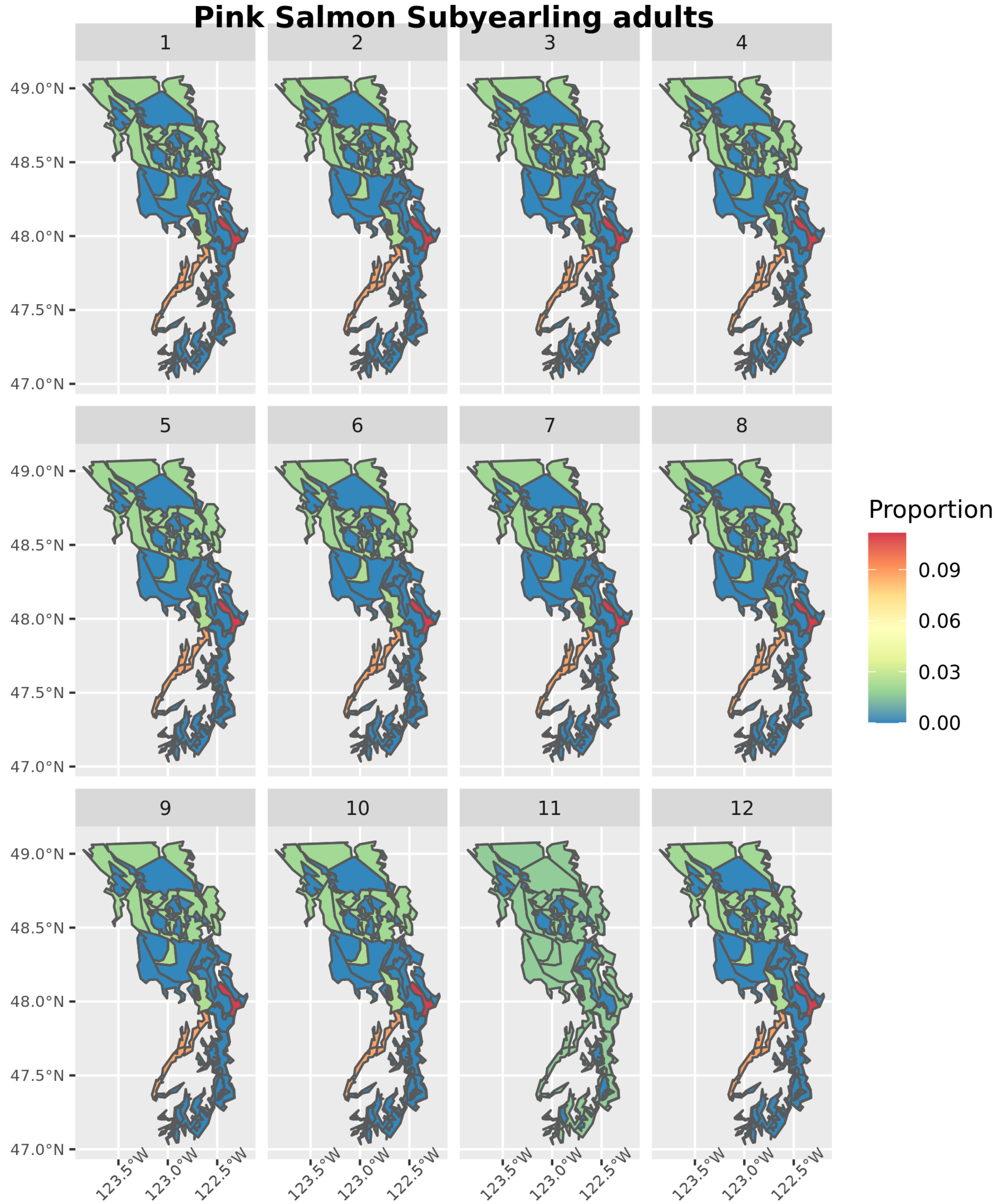

Figure 88. Monthly spatial distribution of pink salmon adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

We do not drive the model with hatchery releases of sockeye salmon, since adult hatchery returns appear to be a small fraction of the total population. Note, however, that hatchery releases of juveniles in 2011 included 5.5 million from the Skagit River region hatcheries, and 8.8 million from mid-Puget Sound hatcheries (G. Marston, personal communication). Quinn (2005, p. 277) suggests an average individual adult weight of 2.69 kg. Expanding to the population level, this results in an estimate of 190.1 tons total biomass. We based sockeye salmon adult return timing on counts at Ballard Locks for 2009–16, when 75% of returning adults were counted between 21 June–17 July (days 172–198; N. Overman, personal communication). Spawning time was therefore based on adult trap data from the Cedar River Hatchery (C. Mains, personal communication), since these fish would have passed through the Ballard Locks. 75% of adults at Cedar River Hatchery traps for 2009–13 were counted between calendar days 263 and 295, which we set as the sockeye spawn dates. Sockeye smolt size of 135 mm and outmigrant timing on days 115–135 are based on observations from Lake Washington and Baker Lake (Gustafson et al. 1997). Monthly spatial distributions for juveniles and adults are shown in Figures 89 and 90.

Strait of Georgia salmonids (SAF)

This functional group represents Fraser River Chinook salmon, primarily to capture their role as forage for Southern Resident killer whales. Hanson et al. (2010) found that of the Chinook salmon consumed by Southern Resident killer whales, genetic methods suggested that 80 to 90% were from the Fraser River. These included the Upper Fraser, Middle Fraser, South Thompson, and Lower Fraser River stocks. Within Atlantis, for initial conditions in 2011, we include estimates of adult Chinook salmon from Fraser River spring/summer (terminal run size of 215,636 fish), Harrison River (escapement of 123,647), and Lower Shuswap (escapement of 18,895; Joint Chinook Technical Committee 2018). We assume average weight (4.58 kg) and life-history parameters identical to the Puget Sound Chinook other subyearling group, but with run timing and spawn timing of 1 September–31 December (days 244–365; DFO 1999). Corresponding spawner biomass is 1,641 tons, and expanded biomass for all age classes was 9,979 tons. Other salmonids, including chum salmon, are abundant in the Fraser River (escapement of 1.6 million in 2015 per the Joint Chum Technical Committee [2018]), but we do not include these in the model; we expect limited interactions with Puget Sound Chinook and coho salmon. Monthly spatial distributions for juveniles and adults are shown in Figures 91 and 92.

Hake and large gadoids (FMM)

This group includes Pacific hake (*Merluccius productus*), Pacific cod (*Gadus macrocephalus*), and walleye pollock (*Gadus chalcogramma*). All three species were once found at high abundances in Puget Sound, but have been depleted either by fisheries or trophic effects (Harvey et al. 2010). Pacific cod and walleye pollock in Puget Sound are found at the southern margin of their geographical range, while Pacific hake are at the northern part of theirs. There are two genetically distinct Pacific hake stocks in Puget Sound, a northern spawning aggregation in the Bellingham area and a southern stock with spawning

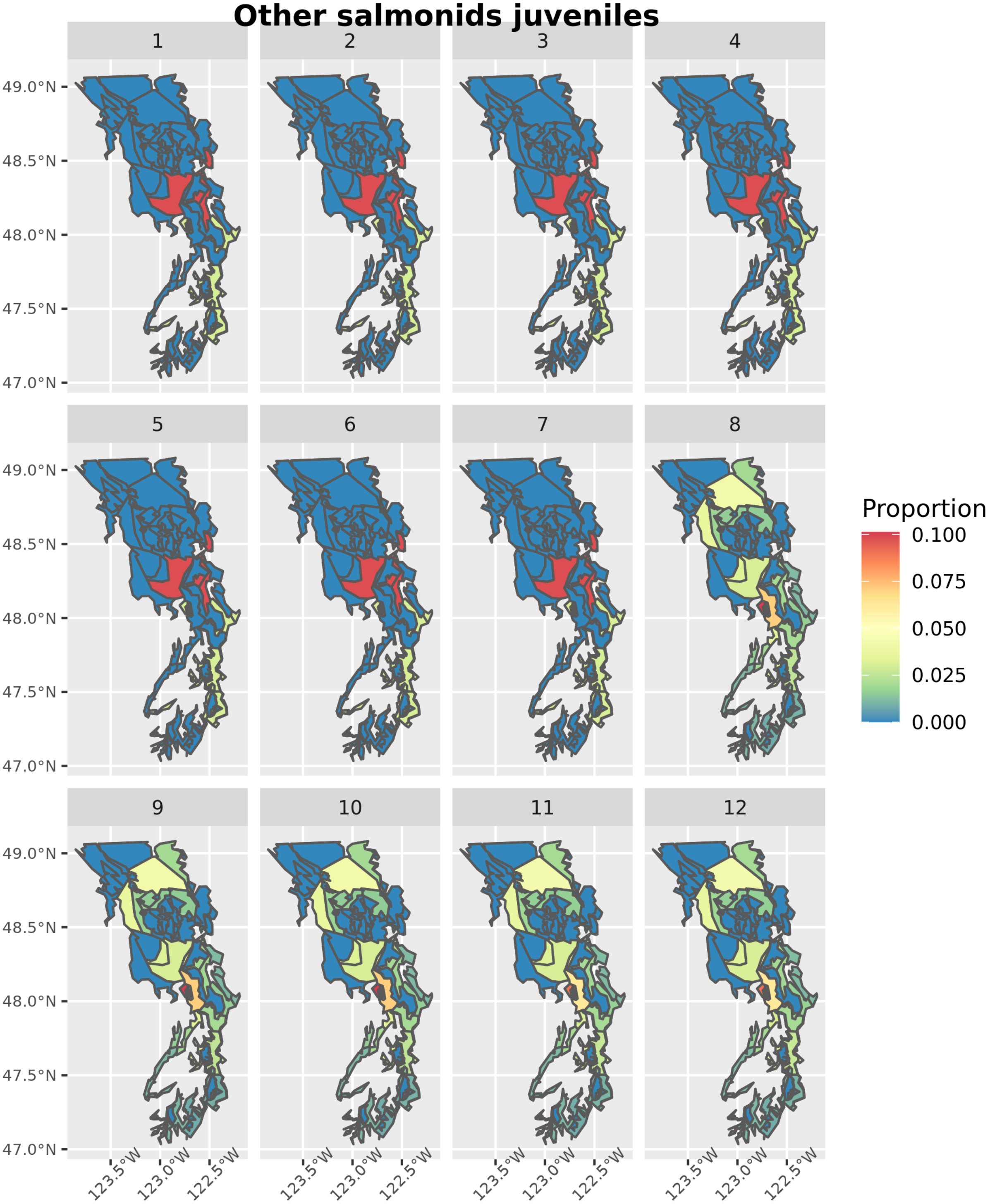

Figure 89. Monthly spatial distribution of juvenile other salmonids. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

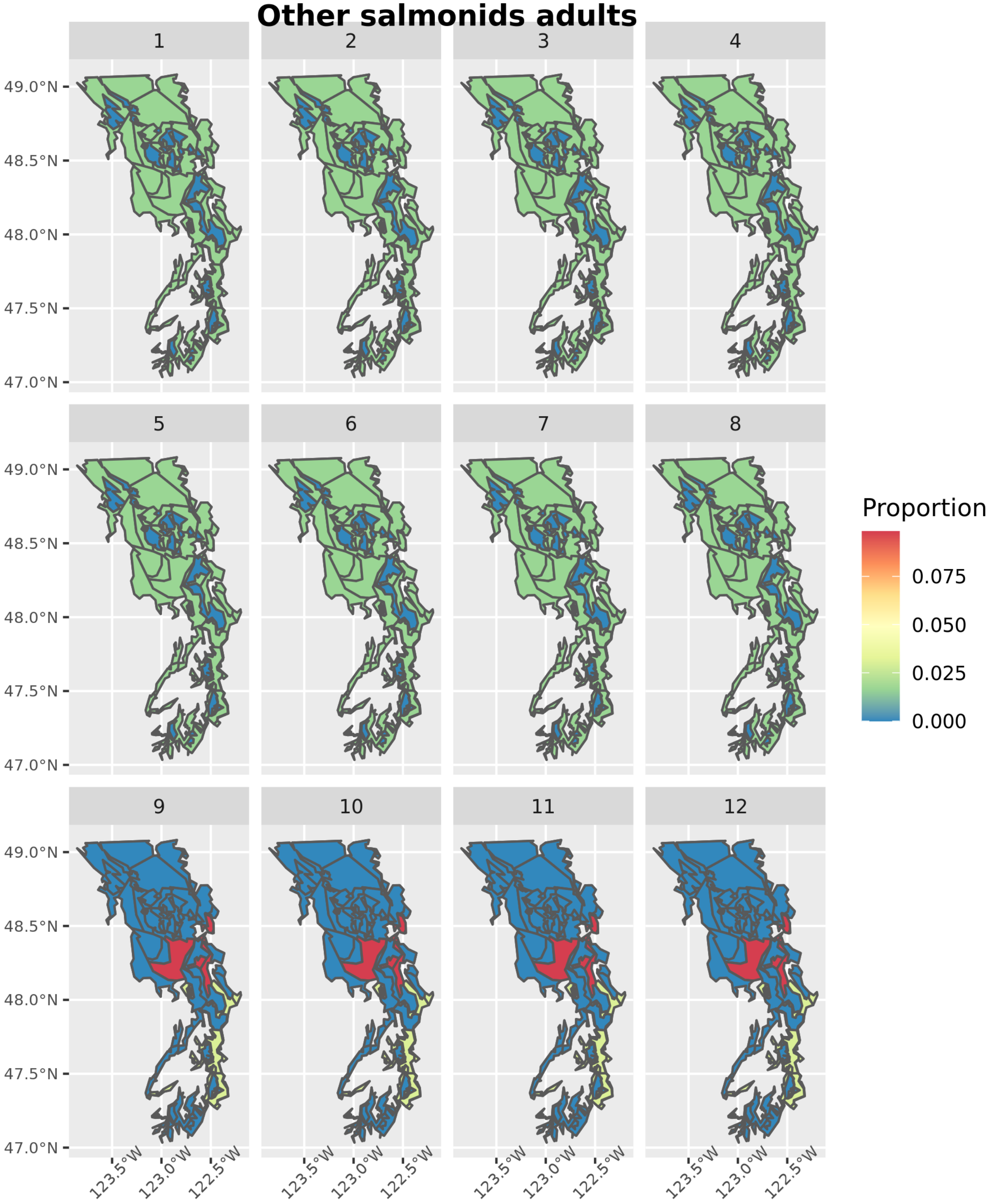

Figure 90. Monthly spatial distribution of other salmonids adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

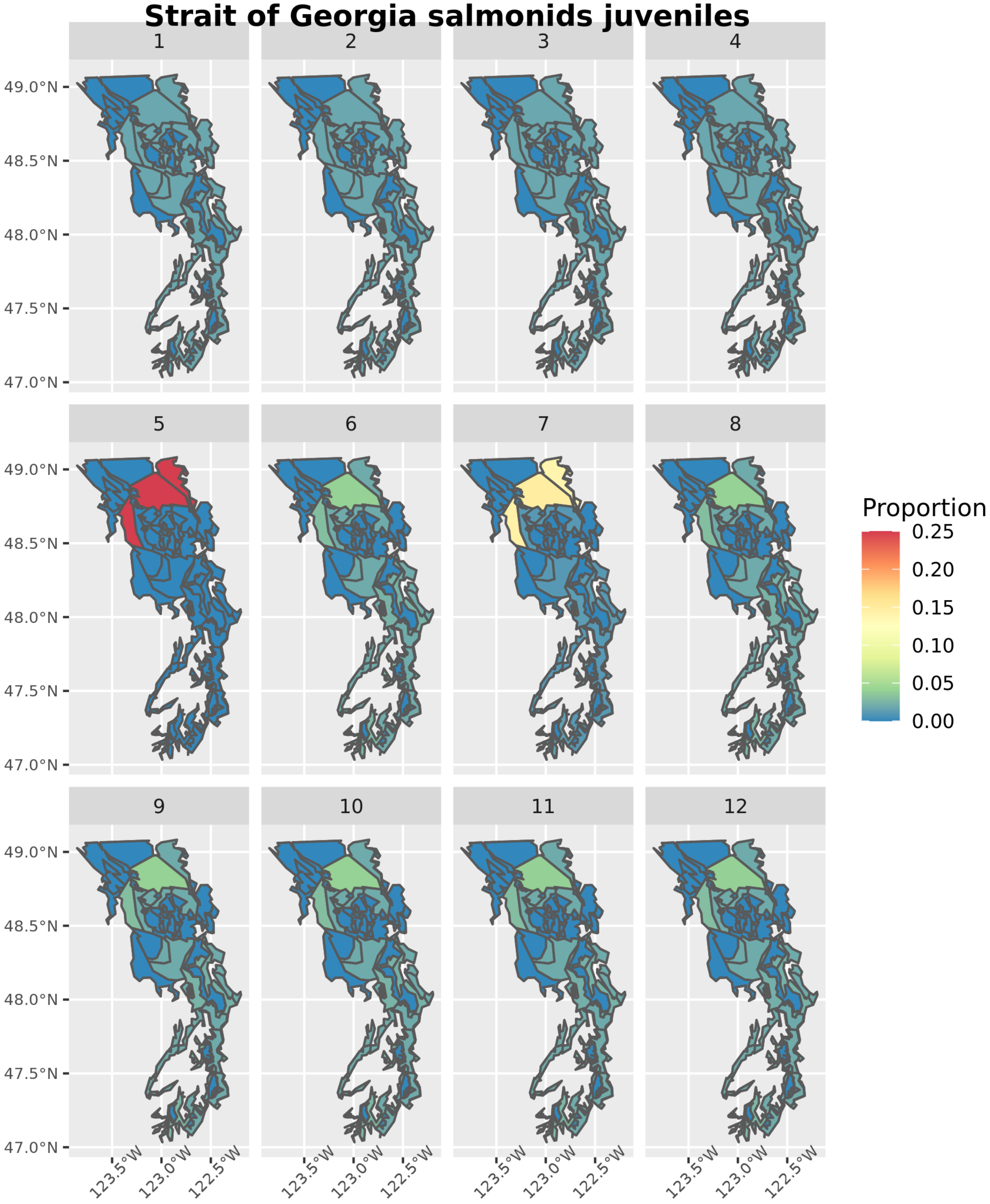

Figure 91. Monthly spatial distribution of Strait of Georgia salmonids juveniles. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

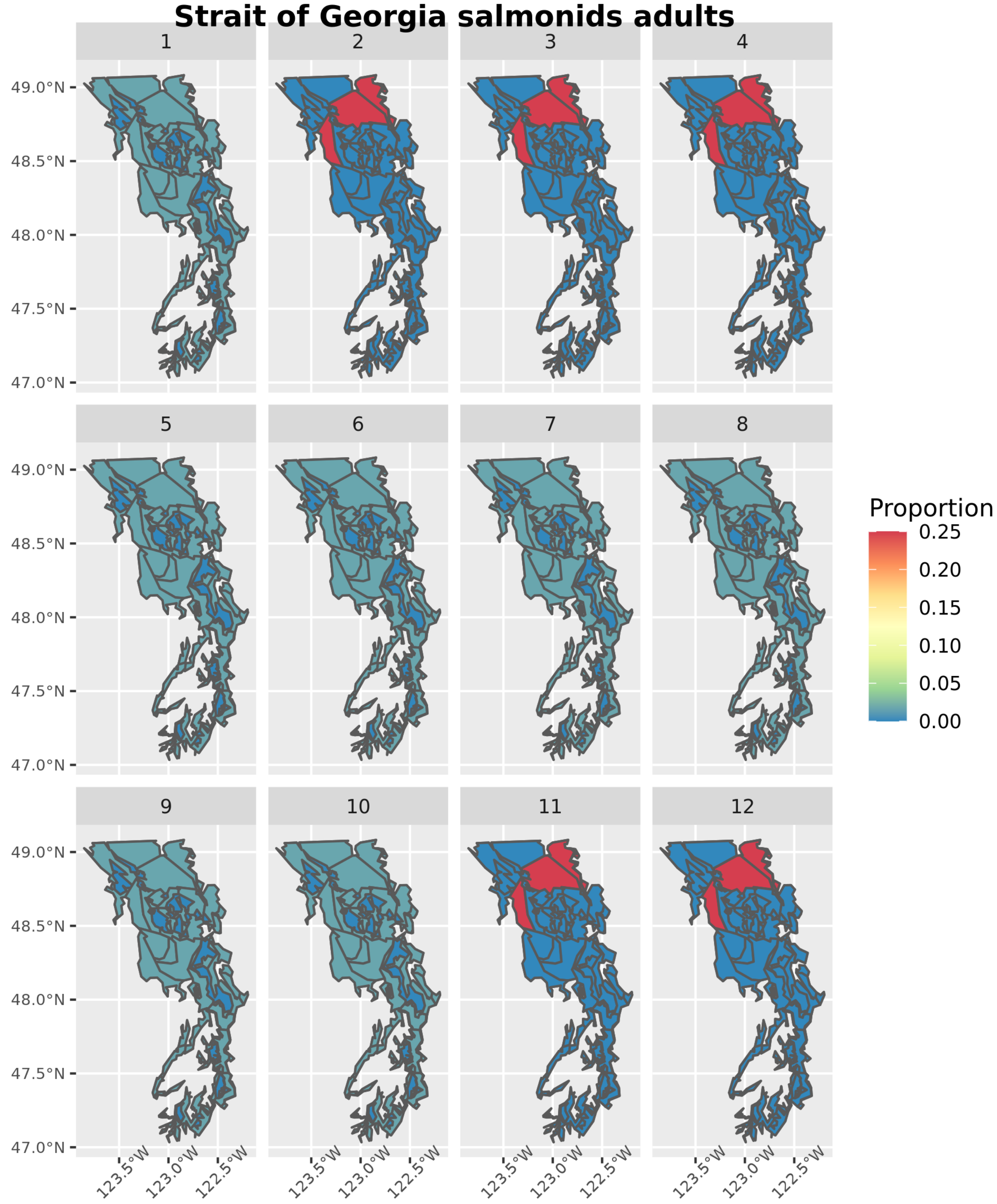

Figure 92. Monthly spatial distribution of Strait of Georgia salmonids adults. Based on data from the RV *Ricker* surveys, Chamberlin et al. (2011), and expert knowledge.

aggregations in Port Susan, and one stock in the Strait of Georgia (Gustafson et al. 2000). Hake and cod are found at highest densities between 50 and 500 m, but adults may occur as deep as 920 m and spawn between 130 and 500 m (Bailey 1982). Walleye pollock occur between 100 and 300 m. Pacific cod form small subpopulations with a high degree of isolation. Pacific hake spawn near major sources of freshwater inflow, such as near the Skagit and Snohomish Rivers in Port Susan (Gustafson et al. 2000). Life-history parameters were drawn from several sources (Forrester 1964, Miller et al. 1978, Stauffer 1985). Pacific hake school at depth during the day, then move to the surface and disperse at night for feeding (Gustafson et al. 2000). We estimated biomass and distribution of this group using VAST on data from WDFW bottom trawl surveys. For more details, see Analyses informing spatial abundance and density; however, we acknowledge that these biomass estimates are likely an underestimate, since hake and pollock are midwater rather than demersal species. Estimated biomass (Figure 93) from the VAST analysis of the bottom trawl survey was 4,875.5 t, or 0.534 t/km^2. For reasons discussed below, in the Atlantis model we use the spatial distribution from VAST, but use an alternative for biomass.

Recent commercial catches and historical data suggest substantially higher biomass. These species have experienced decline in abundance and in fisheries catch in Puget Sound and the Strait of Georgia (Gustafson et al. 2000), also exemplified in historical catch time series (see Catch Reconstruction). As a comparison, Palsson (2003) estimated biomass of Pacific cod at 322.5 t and of walleye pollock at 1,541.4 t in the Strait of Georgia and San Juan Islands archipelago using trawl survey data. However, the reported average catch between 2009 and 2013, which was used to estimate the fishing mortality rate for Atlantis forward simulations, was 4,909.53 t, most reported by Canadian fisheries. Harvey et al. (2010) also estimated higher biomass in the Central Basin (3.405 t/km^2 for Pacific hake, 0.200 t/km^2 for Pacific cod, and 3.704 t/km^2 for walleye pollock) using a mass balance routine for Ecopath. At the scale of the Atlantis model, this Ecopath estimate equates to approximately 73,000 t. For Atlantis initial conditions, considering these multiple lines of evidence for higher biomass, we approximate biomass by assuming that the average catch for 2009–18 was sustainable, i.e., equal to that biomass multiplied by the population growth rate. The average minimum population doubling time (t) of Pacific hake, Pacific cod, and walleye pollock is 3.47 years (Froese and Pauly 2014), equivalent to a population growth rate (r) of 0.1999, $2 = e^{r \times t}$. We update the biomass value as catch/r, equal to 24,554 t.

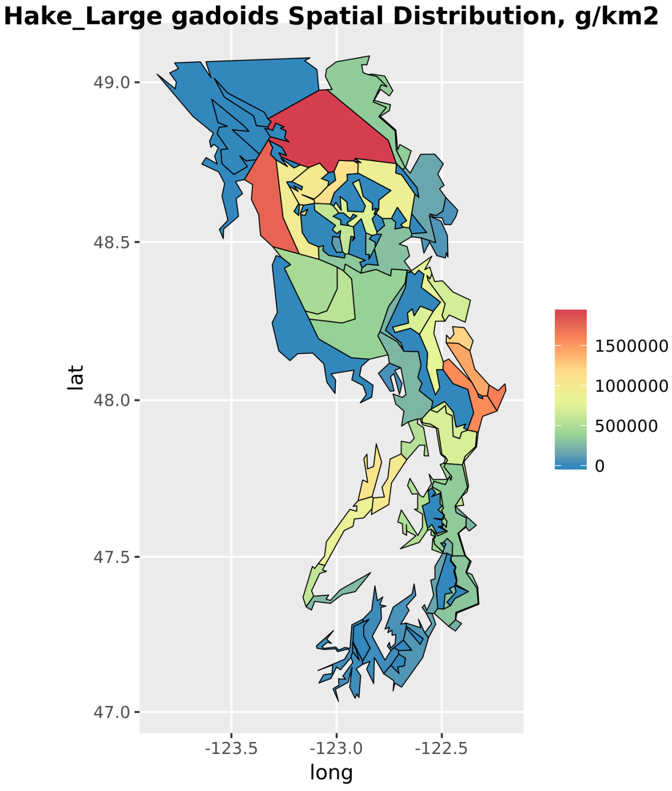

Figure 93. Hake and gadoid summer density, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

Large demersal predators (FVS)

This functional group includes lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys marmoratus*), and wolf eel (*Anarrhichthys ocellatus*). These species are top predators in Puget Sound and are most often associated with complex habitats such as the rocky reefs and outcroppings typical of northern Puget Sound (Harvey et al. 2010). Lingcod are generally solitary demersal predators, most abundant in waters less than 200 m deep, while cabezon are found from tidepools to 76 m (Lauth 1988, Tolimieri et al. 2009). Genetic evidence suggests that lingcod in Puget Sound are partially isolated from those along the open coast; they have home ranges of several hundred square meters (Jagielo et al. 1997, Tolimieri et al. 2009). Female lingcod likely leave deeper areas and move inshore prior to spawning (Jagielo et al. 1997). Recreational hook-and-line anglers and spearfishers target lingcod, while commercial or recreational fishers catch wolf eel occasionally (Harvey et al. 2010). Lingcod feed voraciously on other fishes and macroinvertebrates, including rockfish (Beaudreau and Essington 2007). Spatial distribution is based on the VAST model for the non-spawning period (Figure 94); during January–April, large demersal predators are found in the nearshore (≤50 m). Life-history parameters for this group were taken from multiple sources, including studies from within the Salish Sea (Lauth 1988, Pikitch and Rogers 1989, Smith and McFarlane 1990, Martell 1999, Harvey et al. 2010, Horne et al. 2010, Marshall et al. 2017).

Biomass of large demersal predators was estimated as 0.05 t/km^2 (total 321 t in the model extent), based on VAST on data from WDFW bottom trawl surveys. However, recent catch data used to estimate fishing mortality showed 416.9 t. As a comparison, Palsson (2003) estimated lingcod biomass at 46.9 t in the Strait of Georgia and San Juan Islands archipelago using trawl survey data. Martell (1999) estimated lingcod population biomass in the Strait of Georgia at 1.3 t/km^2 in 1999, and noted a steadily increasing biomass trajectory. Harvey et al. (2010) estimated lingcod biomass at 0.3 t/km^2. There is no biomass estimate of wolf eel in Puget Sound (Harvey et al. 2010). Therefore, we assume that biomass must be higher than 321 t. As an alternative, we approximate biomass by assuming that the average catch for

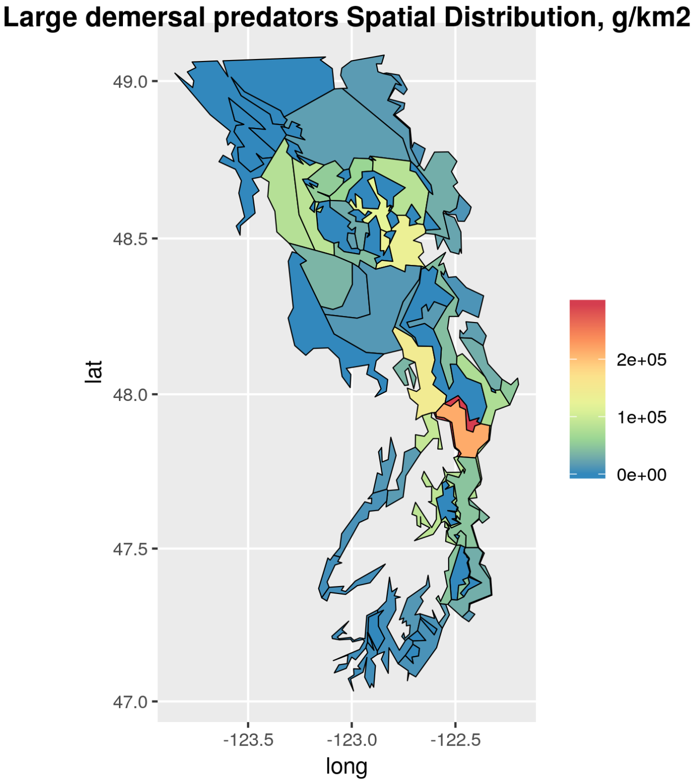

Figure 94. Large demersal predator density, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

2009–18 was sustainable, i.e., equal to that biomass multiplied by the population growth rate. The minimum average population doubling time (t) of fish in this group is 2.4 years (Froese and Pauly 2014), equivalent to a population growth rate (r) of 0.2848, $2 = e^{r \times t}$. This suggests a biomass of 1,463.55 t (calculated as catch/r).

Rockfish species

Rockfish in Puget Sound are of conservation concern, as they are vulnerable to fishing pressure given their long life and slow growth (Mathews and Barker 1983). Several rockfish species, including relatively common species such as copper and quillback rockfish, are species of concern at the state and federal levels (Harvey et al. 2010, WDFW 2015). Rockfish (genus *Sebastes*) comprise over 100 species, most of which occur in the northeastern Pacific Ocean; twenty-one species were reported in Puget Sound in the 1970s (Washington et al. 1978,[16] Love et al. 2002), and were traditionally important commercial and recreational fishery species (Murie 1991). Many rockfish are long-lived (30–100+ years), and their populations suffered severe declines in the 1980s from overfishing, which led to the commercial rockfish closure in 1999 (Lotterhos et al. 2014). Currently, retaining any rockfish is prohibited in Puget Sound and in the San Juan Islands east of Port Angeles (Sawchuk 2012, NMFS 2017). Rockfish species in Puget Sound segregate bathymetrically, but are otherwise ecologically similar; they occupy multiple habitats in the sound, ranging from the pelagic environment and the nearshore to deepwater habitats (Sawchuk 2012). Demersal rockfish are found in close association with rocky areas or other complex habitat types (i.e., kelp). We divided the rockfish into four functional groups based on their habitat preference and vulnerability. Most Pacific rockfish are live-bearers. Rockfish diets were based on multiple sources (Simenstad et al. 1977, Murie 1991, Turner 2016).

Spatial distribution of demersal vulnerable rockfish was based on the habitat suitability model developed by Aschoff and Greene (2017), which assumed yelloweye rockfish as a target species, but also considered bocaccio, canary, brown, copper, greenstriped, quillback, tiger, and vermilion rockfish. This model is based on bathymetric, LiDAR, terrestrial geology, and fish survey data.

Demersal rockfish (ROC)

This group includes copper rockfish (*Sebastes caurinus*), brown rockfish (*S. auriculatus*), redstripe rockfish (*S. proriger*), quillback rockfish (*S. maliger*), greenstriped rockfish (*S. elongatus*), Puget Sound rockfish (*S. empheus*), splitnose rockfish (*S. diploroa*), China rockfish (*S. nebulosus*), tiger rockfish (*S. nigrocinctus*), redbanded rockfish (*S. babcocki*), brown Irish lord (*Hemilepidotus spinosus*), brown Irish lord (*H. hemilepidotus*), great sculpin (*Myoxocephalus polyacanthocephalus*), and shortspine thornyhead (*Sebastolobus alascanus*). Note that the Irish lords and great sculpin are not rockfish, but are included due to their ecological similarity with other species in this group. Copper, quillback, and brown rockfish are self-sustaining populations within Puget Sound (Drake et al. 2010). Quillback are a common species; they are found between 21–115 m depth (Murie 1991). Tiger rockfish

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[16] Washington, P. M., R. Gowan, and D. H. Ito. 1978. A Biological Report on Eight Species of Rockfish (*Sebastes* spp.) from Puget Sound, Washington. U.S. Department of Commerce, NOAA Processed Report.

are rare and found between 41–60 m depth. Copper and quillback rockfish are usually found in shallow inlets associated with nearshore reefs (Mathews and Barker 1983), and in areas of high relief, broken rock, and high percentage cover of kelp (Richards 1987). Brown rockfish have small, insular populations in Puget Sound with small home ranges (<3 km; Hauser et al. 2007b). The model's spawning period for this group was set from March to June, which reflects parturition of copper rockfish which are abundant in Puget Sound. This also includes the parturition period for quillback rockfish, April–May. Shortspine thornyhead are oviparous, and release egg masses into the water column (Love et al. 2002). Copper rockfish are opportunistic carnivores that feed mainly on pelagic fish, and pelagic and demersal crustaceans, while quillback rockfish have a more generalist diet than other rockfish (Stout et al. 2001). Biomass of demersal rockfish was estimated as 2,378 t using VAST on data from WDFW bottom trawl surveys (Figure 95). For more details, see Analyses informing spatial abundance and density; note that we expect this to be an underestimate, since the bottom trawl survey can't target the rocky habitat preferred by these species. As a comparison, in northern and southern Puget Sound, Palsson et al. (2009) reports biomass of copper (307.2 t), quillback (229.3 t), and Puget Sound rockfish (163.4 t) based on quantitative video abundance. Life-history parameters for demersal rockfish were based on Patten (1973), Washington et al. (1978), Gowan (1983), Murie (1991), Love et al. (2002), Coates et al. (2007), and Laidig (2010).

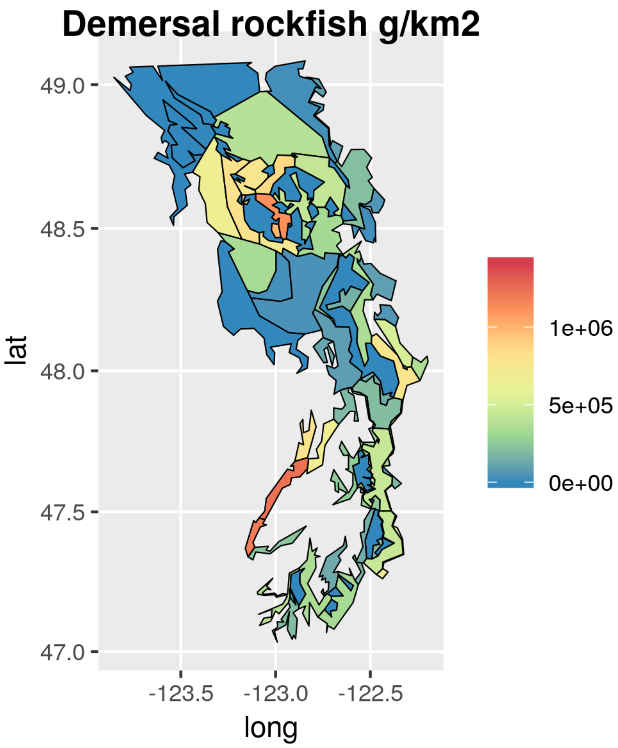

Figure 95. Demersal rockfish density based on the biomass estimated from the analysis of bottom trawl surveys using VAST, then allocated using the habitat suitability model developed by Aschoff and Greene (2017). Plotted as g/km^2.

Midwater rockfish (MRO)

This group includes black rockfish (*Sebastes melanops*), vermilion rockfish (*S. miniatus*), yellowtail rockfish (*S. flavidus*), widow rockfish (*S. entomelas*), and blue/deacon rockfish (*S. mystinus/diaconus*). Black and yellowtail rockfish are abundant offshore to 400 m depth, but found in shorelines and shallow rocky areas in Puget Sound (Mathews and Barker 1983). Both black and yellowtail rockfish are semi-pelagic, schooling fish (Love et al. 2002). Black rockfish are usually found in high-exposure areas and commonly form schools associated with kelp, or in high-relief habitats (Lotterhos et al. 2014); this species is found at low abundances in Puget Sound (Williams et al. 2010b) and is genetically different from coastal populations, indicating differences in dispersal patterns (Lotterhos et al. 2014).

Black rockfish depth preference ranges between 1–48 m, but they may be found up to 55 m deep (Love et al. 2002); the adults have small home ranges (Parker et al. 2007). Black and yellowtail rockfish appear to recruit to Puget Sound as yearlings from northern waters (Drake et al. 2010). Yellowtail rockfish are only found as juveniles in the San Juan Islands, then they migrate to the ocean once they reach sexual maturity at age-5–7 (Drake et al. 2010). Life-history parameters for midwater rockfish were based on sources including studies from within Puget Sound (Washington et al. 1978, Gunderson et al. 1980, Pikitch and Rogers 1989, Love et al. 2002, Sawchuk 2012).

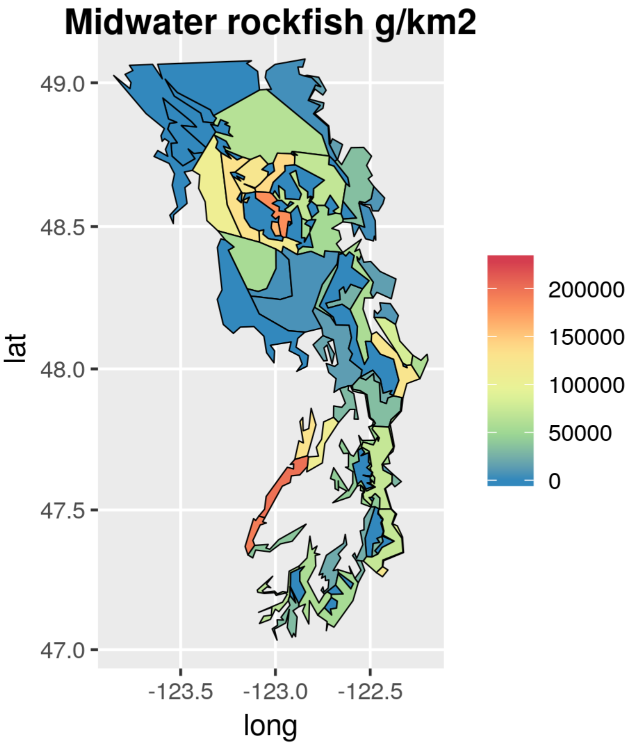

Figure 96. Midwater rockfish density based on the biomass reported by Palsson et al. (2009) from quantitative video abundance, then allocated using the habitat suitability model developed by Aschoff and Greene (2017). Plotted as g/km².

The biomass estimates from VAST of WDFW bottom trawl survey data were very low (13 t across the whole model extent). Meanwhile, Palsson et al. (2009) estimated abundance as 384.8 t based on quantitative video abundance (Figure 96), including yellowtail (18.7 t), black (203.7 t), and vermilion rockfish (162.4 t). However, the reported average catch between 2009 and 2018, which was used to estimate the fishing mortality rate for forward simulations, was 702.94 t, most reported by Canadian fisheries. Given the difficulty in surveying rocky areas, we approximate biomass by assuming that the average catch for 2009–18 was sustainable, i.e., equal to that biomass multiplied by the population growth rate. The minimum population doubling time (t) of midwater rockfish is 6.4 years (Froese and Pauly 2014), equivalent to a population growth rate (r) of 0.1083, $2 = e^{r \times t}$. This suggests a biomass of 6,490.44 t (calculated as catch/r).

Demersal vulnerable rockfish (DVR)

This group includes only yelloweye rockfish (*Sebastes ruberrimus*). Yelloweye rockfish are large, with a distinct bright yellow and red color. They are a demersal species as adults (Love et al. 2002). This species is rare in Puget Sound, and can be characterized as low-abundance, long-lived, late-maturing, slow-growing, and susceptible to overfishing (Wallace 2001). Yelloweye rockfish populations in Puget Sound have declined and the species is listed under the ESA (Palsson et al. 2009). It is one of the most long-lived rockfish species, and growth slows after 30 years. Life-history parameters for demersal vulnerable rockfish were based on sources including studies from Puget Sound (Washington et al. 1978, Drake et al. 2010, Sawchuk 2012). The most recent yelloweye biomass estimate, 1.2 t (Figure 97), is based on trawl data for 2004–05 (Palsson et al. 2009). However, the reported average catch between 2009 and 2018, which was used to estimate the fishing mortality rate for forward simulations, was 169.97 t, most reported by Canadian fisheries. Given the difficulty in surveying rocky areas, we assume that biomass must be higher than 1.2 t, especially in northern regions. As an alternative, we therefore approximate biomass by assuming that the average catch for 2009–18 was sustainable, i.e., equal to that biomass multiplied by the population growth rate. The minimum population doubling time (*t*) of yelloweye rockfish is more than 14 years (Froese and Pauly 2014), equivalent to a population growth rate (*r*) of 0.0495, $2 = e^{r \times t}$. This suggests a biomass of 234.15 t (calculated as catch/*r*).

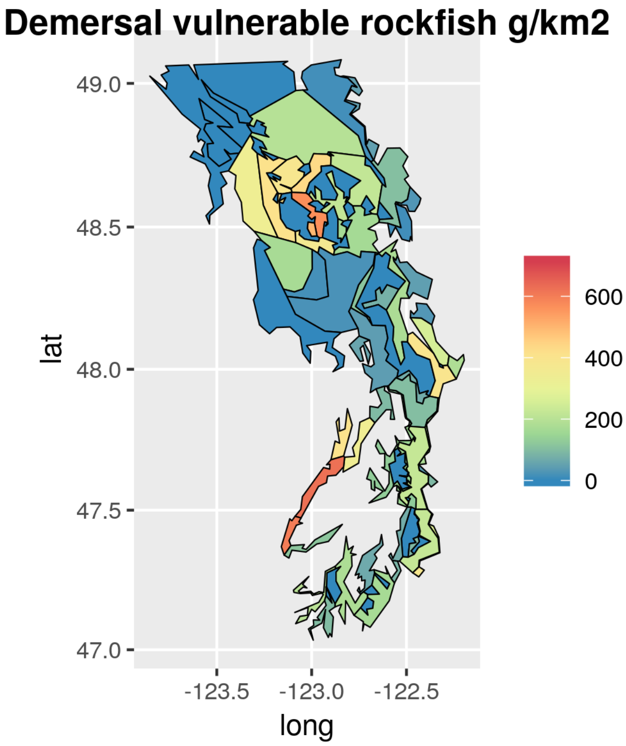

Figure 97. Demersal vulnerable rockfish density based on the biomass reported by Palsson et al. (2009) from trawl data, then allocated using the habitat suitability model developed by Aschoff and Greene (2017). Plotted as g/km^2.

Midwater vulnerable rockfish (MVR)

This group includes bocaccio (*Sebastes paucispinis*) and canary rockfish (*S. pinniger*). These two species have large populations in offshore waters, and Puget Sound is likely a sink for larvae that drift in (Drake et al. 2010). The early life stages of bocaccio and canary rockfish have not been confirmed in Puget Sound, and their documented occurrence is restricted to less than 24 locations (Garrison and Miller 1982, Drake et al. 2010). Life-history parameters for midwater vulnerable rockfish were based on Puget Sound and California Current sources (Washington et al. 1978, Pikitch and Rogers 1989, Love et al. 2002, Drake et al. 2010, Sawchuk 2012). The most recent biomass estimate (Figure 98) for canary rockfish is 4.4 t based on quantitative video abundance; the stock status of bocaccio is unknown (Palsson et al. 2009). However, the reported average catch between 2009 and 2018, which was used to estimate the fishing mortality rate for forward simulations, was 15.65 t. Given the difficulty in surveying rockfish habitats, we assume that the video analysis underestimated the biomass of midwater vulnerable rockfish. As an alternative, we therefore approximate biomass by assuming that the average catch for 2009–18 was sustainable, i.e., equal to that biomass multiplied by the population growth rate. The minimum population doubling time (*t*) of both bocaccio and canary rockfish is 4.5–14 years (Froese and Pauly 2014). We used the midpoint, 9.25, to estimate a population growth rate (*r*) of 0.0749, $2 = e^{r \times t}$. We update the biomass value as catch/*r*, equal to 208.94 t.

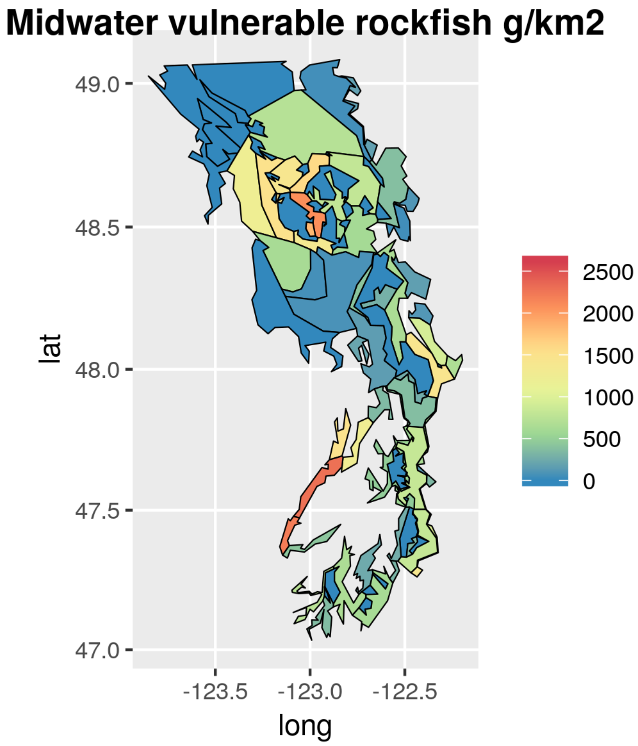

Figure 98. Midwater vulnerable rockfish density based on the biomass reported by Palsson et al. (2009) from quantitative video abundance, then allocated using the habitat suitability model developed by Aschoff and Greene (2017). Plotted as g/km^2.

Small demersal fish (SMD)

This group represents small fish that are found associated with benthic habitats. It includes eelpouts and sculpins, in the families Zoarcidae and Cottidae, greenlings (Hexagrammidae), poachers (Agonidea), gunnels (Pholidae), pricklebacks (Stichaeidae), plainfin midshipmen (*Porichthys notatus*), northern ronquil (*Ronquilus jordani*), Pacific tomcod (*Microgadus proximus*), blackeye goby (*Rhinogobiops nicholsii*), bay pipefish (*Syngnathus leptorhynchus*), tube snout (*Aulorhynchus flavidus*), northern smoothtongue (*Leuroglossus schmidtii*), and sablefish (*Anoplopoma fimbria*). Many of these species have not been assessed for biomass and many have been poorly studied, which made characterizing their life histories challenging. Life-history parameters are based on northern smoothtongue (Mason and Phillips 1985), painted greenling (DeMartini and Anderson 1980), and on the

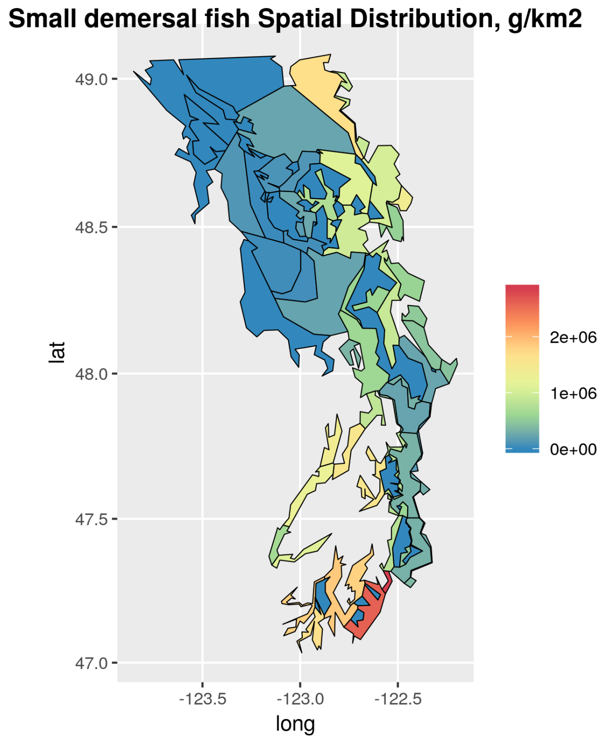

Figure 99. Small-mouthed flatfish abundance, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

parameters used for the California Current Atlantis Model for plain midshipmen (Marshall et al. 2017). Painted greenling is a small hexagrammid fish found in shallow, rocky bottoms up to 20 m; juveniles have small home ranges, and adults are intraspecifically territorial (DeMartini and Anderson 1980). The northern smoothtongue is a deep-sea smelt that is found up to 700 m (Mason and Phillips 1985). Biomass and distribution of small demersal fish were estimated using VAST on data from WDFW bottom trawl surveys. For more details, see Analyses informing spatial abundance and density. Estimated biomass is 4,335 t (Figure 99).

Small-mouthed flatfish (FDF)

This group includes smaller flatfish, including Dover sole (*Microstomus pacificus*), Pacific sanddab (*Citharichthys sordidus*), sand sole (*Psettichthys melanostictus*), English sole (*Parophrys vetulus*), C-O sole (*Pleuronichthys coenosus*), starry flounder (*Platichthys stellatus*), speckled sanddab (*Citharichthys stigmaeus*), rock sole (*Lepidopsetta bilineata*), rex sole (*Glyptocephalus zachirus*), flathead sole (*Hippoglossoides elassodon*), butter sole (*Isopsetta isolepis*), and slender sole (*Lyopsetta exilis*). This group is highly abundant and forms (together with ratfish and spiny dogfish) the bulk of demersal fish biomass in Puget Sound (Harvey et al. 2010). English sole are common in Puget Sound (Nash and Geffen 2005); there are also substantial numbers of rock sole and C-O sole present (Reum 2006). Starry flounder are relatively abundant in shallow waters, while Dover and rex sole are found in deeper waters of Puget Sound (Harvey et al. 2010). Biomass and distribution of small-mouthed flatfish were estimated using VAST on data from WDFW bottom trawl surveys; for more details, see Analyses informing spatial abundance and density. We estimated 27,729 t in the model extent (Figure 100). In comparison, Palsson (2003) estimated biomass of English sole (3,561.2 t), rock sole (968.1 t), starry flounder (832.7 t), sand sole (186.6 t), and Dover sole (298.3 t) in the Strait of Georgia and San Juan Islands archipelago using 2001 trawl survey data. Life-history parameters are based on sources from Puget Sound and the California Current (Pierce et al. 1977, Washington 1977,[17] Pikitch and Rogers 1989, He et al. 2013, Godersky 2017).

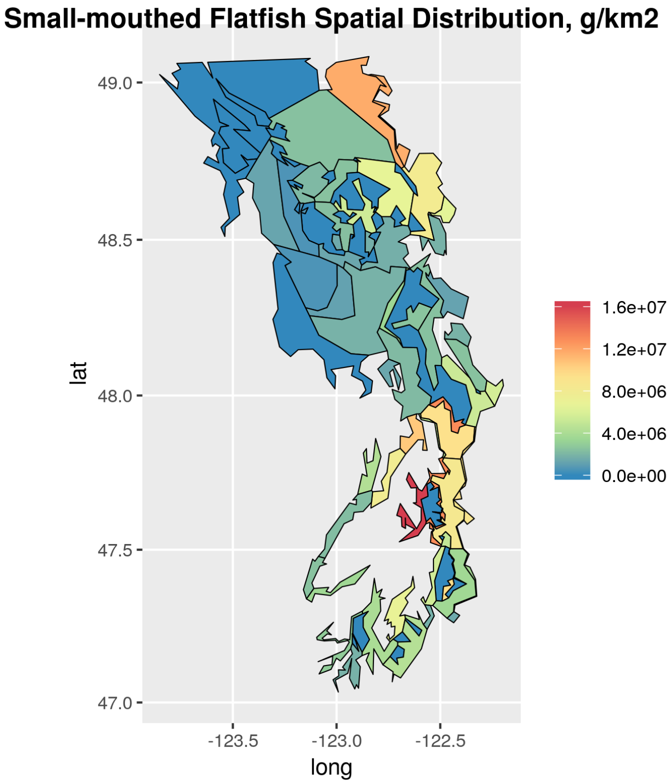

Figure 100. Small-mouthed flatfish abundance, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

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[17] Washington, P. M. 1977. Recreationally Important Marine Fishes of Puget Sound, Washington. U.S. Department of Commerce, NOAA Processed Report.

Piscivorous flatfish (HAP)

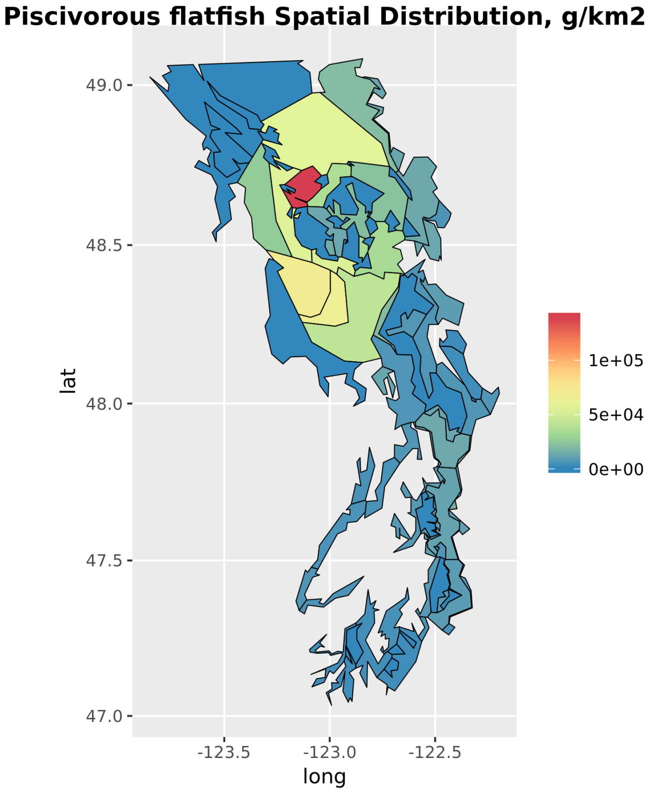

Figure 101. Piscivorous flatfish abundance, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

This group includes Pacific halibut (*Hippoglossus stenolepsis*) and arrowtooth flounder (*Atheresthes stomias*). Pacific halibut are the largest flatfish found in Puget Sound, and can weigh more than 100 kg. They are highly predatory and prized by sport anglers (Harvey et al. 2010). Pacific halibut is also one of the most valuable commercial species of groundfish in the northeastern Pacific Ocean. Puget Sound Pacific halibut may belong to a stock distinct from Washington coast halibut, based on body size and otolith morphology; they are mostly found in northern Puget Sound (Harvey et al. 2010). Arrowtooth flounders are batch spawners and spawn from fall to winter at depths of >366 m (Kaplan and Helser 2007). Adults migrate seasonally, from shallower waters in the summer to deeper areas in the winter (Rickey 1995). Life-history parameters are based on multiple sources (Du et al. 1991, Clark et al. 1999, Perkins 2015, Then et al. 2014). Biomass and distribution of piscivorous flatfish were estimated using VAST on data from WDFW bottom trawl surveys. For more details, see Analyses informing spatial abundance and density. Biomass was estimated as 176.67 t for the Atlantis model domain (Figure 101). In comparison, Palsson (2003) estimated 19.7 t in the Strait of Georgia and San Juan Islands archipelago. However, average catch 2009–18 of piscivorous flatfish, used to estimate fishing mortality, was 1,488.01 t, higher than the VAST estimate. As an alternative, we therefore approximate biomass by assuming that the average catch for 2009–18 was sustainable, i.e., equal to that biomass multiplied by the population growth rate. The minimum average population doubling time (t) of piscivorous flatfish in this group is 4.5 years (Froese and Pauly 2014), equivalent to a population growth rate (r) of 0.154, $2 = e^{r \times t}$. This suggests a biomass of 9,660.36 t (calculated as catch/r).

Spiny dogfish (DOG)

This functional group includes spiny dogfish (*Squalus suckleyii*), because it is the most abundant demersal piscivore in Puget Sound and an upper trophic level predator (Andrews and Harvey 2013). Dogfish represent over 5% of the total fish biomass and >80% of the total consumer biomass of trophic level >4.0 in the central Puget Sound basin (Harvey et al. 2012b). Spiny dogfish are common throughout Puget Sound and are part of a transboundary stock shared with British Columbia, and often school near the surface when pursuing forage fish (Palsson et al. 1995). Pacific spiny dogfish are small and semipelagic; they prefer water temperatures between 7–15°C, and will migrate latitudinally and vertically to follow this temperature preference. Spiny dogfish are long-lived and show late maturity (Saunders and McFarlane 1993), and have internal fertilization and are ovoviviparous (Holden 1977). We used a fixed recruitment relationship in Atlantis for spiny dogfish that assumed 6.9 young per female per year, equivalent to the average litter size (Tribuzio 2004). In Puget Sound, a large proportion of the Pacific spiny dogfish population is nearly absent in the winter and spring, when they travel through the Strait of Juan de Fuca to the outer coast; they return to Puget Sound in summer and autumn (Reum and Essington 2011, Andrews and Harvey 2013). Ninety percent of spiny dogfish migrate out of the model domain on 1 January and return on 1 May. Dogfish also undergo seasonal changes in depth distribution in response to temperature and salinity patterns. They occupy shallower waters in summer, while in winter they are most abundant in deepwater habitat (250–500 m; Ketchen 1986, King et al. 2013). Biomass and distribution of spiny dogfish were estimated using VAST on data from WDFW bottom trawl surveys; for more details, see Analyses informing spatial abundance and density. We expect biomass of the species to be well sampled based on the trawl gear and because sampling occurs during peak seasonal abundance. Biomass was estimated as 8,984 t (Figure 102). As a comparison, using trawl survey data, Palsson (2003) estimated a spiny dogfish biomass of 3,609.8 t in the Strait of Georgia and San Juan Islands archipelago. Biomass estimated through VAST modeling and based on midwater trawling, which samples deeper than 75 m, found 2.5 times more biomass in the summer than in the fall. Life-history parameters were based primarily on two sources (Wood et al. 1979, Andrews and Harvey 2013). Dogfish prey opportunistically on pelagic and benthic prey and many of their prey are also generalists (Reum and Essington 2008). Dogfish also have high direct and indirect trophic impacts (Harvey et al. 2012b).

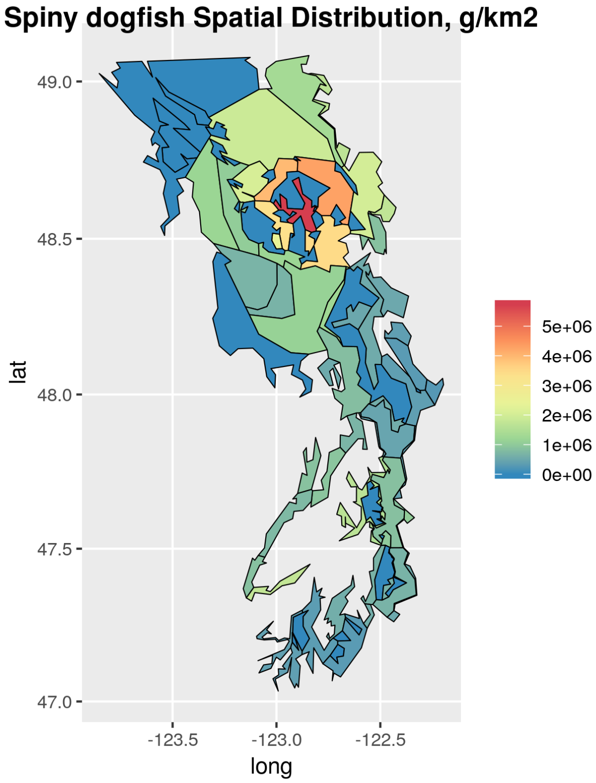

Figure 102. Spiny dogfish abundance, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

Sixgill sharks (SBL)

The bluntnose sixgill shark (*Hexanchus griseus*) is a large demersal predatory shark with a wide geographic range. Sixgill sharks are found in deep water (>100 m) along the continental shelf and upper slope, and into Puget Sound. In Elliot Bay (next to downtown Seattle), abundance estimated through a mark–resight model ranged from 27 individuals in March 2004 (95% CI: 11–68) to 98 in July 2004 (95% CI: 65–146; Griffing et al. 2014). Sixgill sharks are oviparous; we used a fixed recruitment relationship in Atlantis for sixgill that assumed 77 young per female per year, the mean of the reported range for litter size, 47–108 pups (Williams et al. 2010a). There is limited information on growth rates; in Puget Sound, one recaptured subadult grew at a rate of 12 cm/yr (Andrews et al. 2009), while captive young-of-year nearly doubled in size during their first year (Ebert 2003). Sixgill sharks spend several years in Puget Sound, and eventually leave for the outer coast; they may return as adults following prey resources, or related to reproductive cycles or mating behavior (Andrews et al. 2010). Within the Central Basin of Puget Sound, sixgill sharks move seasonally to the north from winter to spring, and to the south from summer to fall, typically on the scale of 10–25 kilometers. Many larger individuals appear to migrate out of Puget Sound in spring (Andrews et al. 2010). Sixgill sharks use shallower habitats during summer and at night; their movement is likely driven by foraging opportunities (Andrews et al. 2009, King and Surry 2017). We assume that juveniles remain within Puget Sound, and adults migrate out of the model domain on 1 April and return on 1 November (Table 7). Sixgill shark abundance appears to have decreased in recent years in Puget Sound (K. Andrews, NWFSC, personal communication), though pockets of high abundance are still reported in locations including off Maury Island and Anderson Island (D. Lowry, WDFW, personal communication). For Atlantis initial conditions, we assume a Sound-wide population of 98 individuals, at 75 kg each (typical weights from Andrews et al. [2010]). We assume equal density of sixgill in model polygons 100 m or deeper; we do not attempt to capture the small-scale (10–25 km) seasonal movements reported by Andrews et al. (2010). Life-history parameters for sixgill sharks are based on Puget Sound and California Current studies (Ebert 1986a,b, Williams et al. 2010a, Marshall et al. 2017, Matta et al. 2017).

Skates (SSK)

This group includes two species of skate common in Puget Sound: the longnose skate (*Raja rhina*) and the big skate (*Beringraja binoculata*). There is little information on the ecological role of skates in Puget Sound, and they are not significantly targeted by fisheries in this region (Harvey et al. 2010). The big skate is common on sandy and muddy areas at depths ranging from the low intertidal zone to 800 m, but usually at less than 200 m. Individual big skates can exceed 45 kg (Kincaid 1919, King et al. 2015). The longnose skate is found on mud-cobble bottoms, often near boulders and rocky ledges, and at depths of usually <350 m, but can range between 20–1,000 m (Ebert 2003). Skates have internal fertilization, and females are oviparous, depositing eggs in purse-like egg cases on the bottom (King et al. 2015). We used a fixed recruitment relationship based on big skate that assumes two egg cases, each containing four pups, for every breeding event, and a 1:1 sex ratio; the incubation period is unknown but may last 1–2 years (Ebert 2003). Big skate have no defined breeding season—their egg cases are deposited year-round. Longnose skates have an extended reproductive season ranging from six months to year-round (Ebert et al. 2008). Big and longnose skates dominate the skate catches of northern Puget Sound and are the most common skates throughout the area (Palsson et al. 1995). No fishery age-composition data are available (Gertseva and Schirripa 2008). Life-history parameters are based on multiple sources (Jordan and Starks 1895, King et al. 2015, Matta et al. 2017). Biomass and distribution of skates were estimated using VAST on data from WDFW bottom trawl surveys; for more details, see Analyses informing spatial abundance and density. From this VAST approach (Figure 103), the Atlantis model is initialized with 3,199 t. In comparison, Palsson (2003) estimated skate biomass as 1,196.5 t in the Strait of Georgia and San Juan Islands archipelago from trawl survey data.

Spotted ratfish (RAT)

Spotted ratfish (*Hydrolagus colliei*) is a chimeroid fish closely related to sharks, skates, and rays, and differentiated from elasmobranchs by numerous morphological characters. Ratfish are likely the most abundant demersal fish species in Puget Sound in biomass per unit area (Palsson 1997, Harvey et al. 2010). They are found in bycatch captured and discarded by recreational fishermen, as well as from commercial bottom trawl and longline fisheries (Palsson et al. 1995). Spotted ratfish have k-selected life-history characteristics, including low growth rate, high longevity, and later age at first maturation. Chimaeroids are serial indeterminant spawners, making it difficult to determine the duration of spawning season; we set parturition in July–August when egg cases are common in Washington (Sathyanesan 1966). In Puget Sound, smaller ratfish use deep water by day and move to shallower areas at night (Quinn et al. 1980).

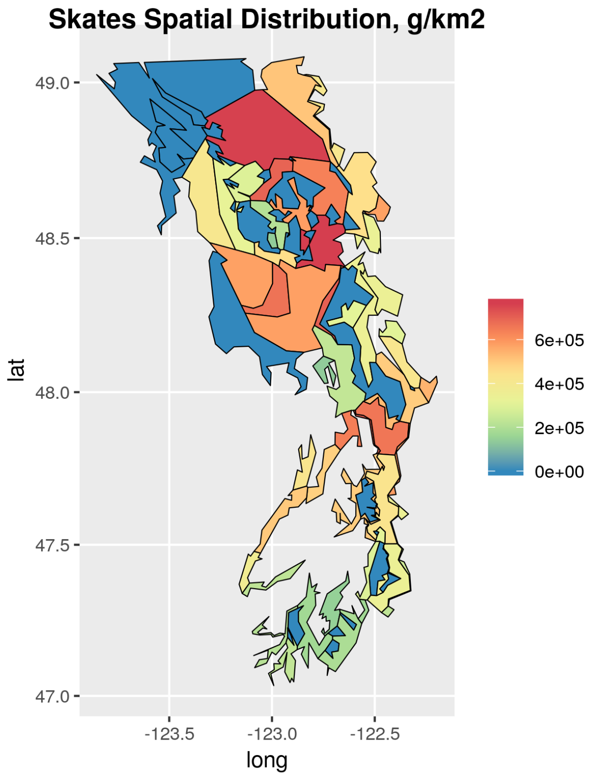

Figure 103. Skate abundance, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

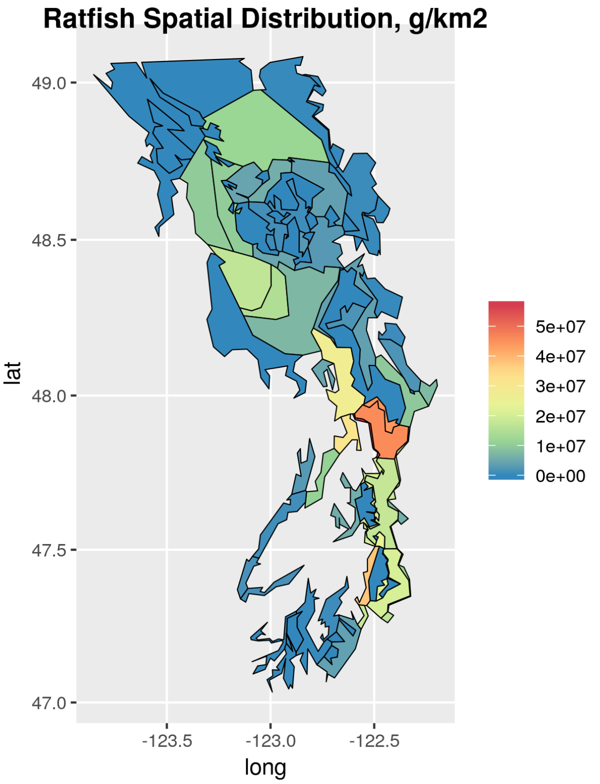

Figure 104. Spotted ratfish abundance, from the analysis of bottom trawl surveys using VAST. Plotted as g/km^2.

Life-history parameters were drawn from multiple sources (Johnson 1967, Barnett 2008, Barnett et al. 2008, King and McPhie 2015). We used a fixed recruitment relationship in Atlantis for spotted ratfish that assumed 24.2 young per female per year, based on annual fecundity of captive ratfish from Puget Sound, 19.5–28.9 (Barnett et al. 2008). Biomass and distribution of spotted ratfish were estimated using VAST on data from WDFW bottom trawl surveys (Figure 104); for more details, see Analyses informing spatial abundance and density. Biomass is 63,219 t. As a comparison, Palsson (2003) estimated skate biomass as 12,610 t in the Strait of Georgia and San Juan Islands archipelago using trawl survey data.

Piscivorous seabirds (SB) and mainly non-piscivorous seabirds (SP)

These two groups include the complete water bird, shorebird, and marine bird communities in Puget Sound (except for raptors found in the nearshore). These seabird groups are found in many habitats, ranging from the nearshore to pelagic zones. The Puget Sound area is an important nesting and feeding ground for marine birds, many of which appear to have experienced marked declines in recent decades (Nysewander et al. 2005). Marine birds in this area include the rhinoceros auklet (*Cerorhinca monocerata*), glaucous-winged gull (*Larus glaucescens*), pigeon guillemot (*Cepphus columba*), cormorants (*Phalacrocorax* spp.), marbled murrelet (*Brachyramphus marmoratus*), and brant (*Branta bernicla*). Although they are a small component of community biomass, their high activity levels and endothermic metabolisms result in very high consumption rates, and thus they have a high ecological footprint (Harvey et al. 2010). Many bird species are protected by general legislation and treaties (e.g., the Migratory Bird Treaty Act[18]), and a smaller number are included in state or federal endangered species legislation. They are also regarded as leading indicators of marine ecosystem change (e.g., Cairns 1987, Piatt et al. 2007, Mallory et al. 2010). They can be regarded as apex predators, as very few species (apart from other birds or terrestrial nest predators) feed on them.

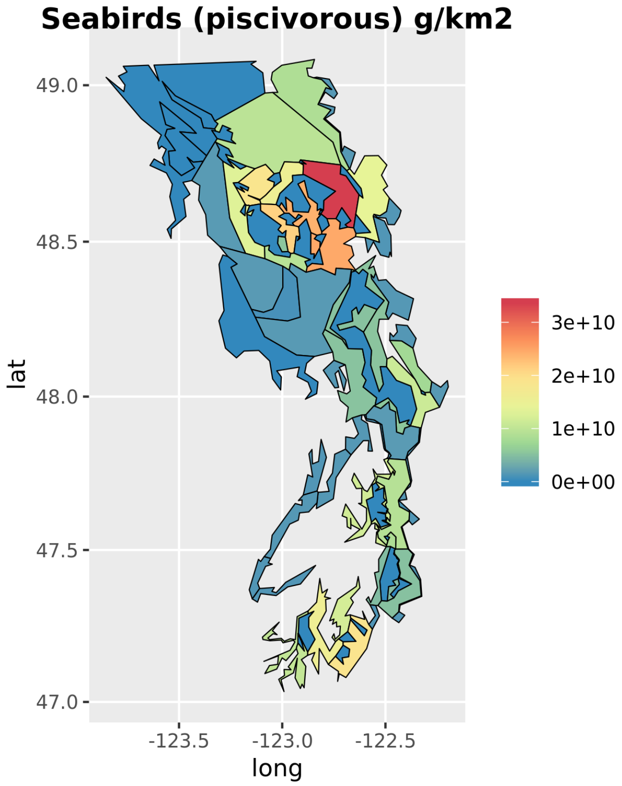

Figure 105. Seabirds (piscivorous) density, from PSAMP aerial surveys. Plotted as g/km^2.

Abundance and distribution of these two seabird groups were taken from PSAMP surveys (Nysewander et al. 2005). Data were available for 1992–2004 (Evenson and Kraege 2013) from OBIS-Seamap (Halpin et al. 2009). Aerial surveys covered our entire Puget Sound model domain in winter, when peak bird abundances are three times summer abundances (Nysewander et al. 2005). We did not analyze summer survey data, since model initial conditions represent

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[18] https://www.fws.gov/law/migratory-bird-treaty-act-1918

January 2011. For the winter surveys, two observers identified birds from an airplane flying at 80–90 knots (148–167 km/h) at an elevation of approximately 65 m. Visual “transect width” was approximately 100 m. Sampling covered two strata, a nearshore stratum from approximately 0–20 m that covered ~13–15% of Puget Sound annually, and an offshore stratum that covered ~3–5% of Puget Sound annually. To account for the high density of birds and sampling effort in the nearshore area, we first analyzed the data at a fine spatial resolution of 0.01 degrees. For each 0.01-degree grid cell, we calculated average density (birds/km^2) by dividing species counts (summed over all transects and years) by sampling effort (per km^2, summed over all transects in that grid cell and all years). We multiplied this average density per species by wet weight per individual (grams) from Hunt et al. (2000) or the Cornell Lab of Ornithology.[19] We then summed over all species in each functional group, as listed in Table 2. Finally, we allocated individual 0.01-degree grid cells to Atlantis polygons, averaging over grid cells to yield wet weight/km^2 per Atlantis polygon (Figures 105 and 106). This determined both model initial conditions and relative spatial distribution of abundance. We view these as minimum abundance estimates for birds, since some birds are likely undetectable to observers due to diving or other avoidance behaviors. Nysewander et al. (2005) suggest that for some species of grebes and guillemots, surveys from boats may detect two to six times more individuals than are detected by aerial surveys, but we do not have a method to extrapolate this broadly to all species in this survey.

Based on the winter PSAMP aerial surveys, major components of the piscivorous seabird (SB) group included glaucous-winged gull, common murre, western grebe, double-crested cormorant, and red-breasted merganser. These five species accounted for 75% of individuals in the functional group, if we assume that individuals identified only to coarser taxonomic resolution can be assigned to these species.[20] Life-history parameters are taken primarily from the Cornell Lab of Ornithology, and based on this we assume maximum clutch size of four eggs (based specifically on glaucous-winged gulls). Breeding season was set to begin on 1 May, based on observations from Triangle Island in British Columbia (Hipfner and Greenwood 2008). We do not include seasonal migrations

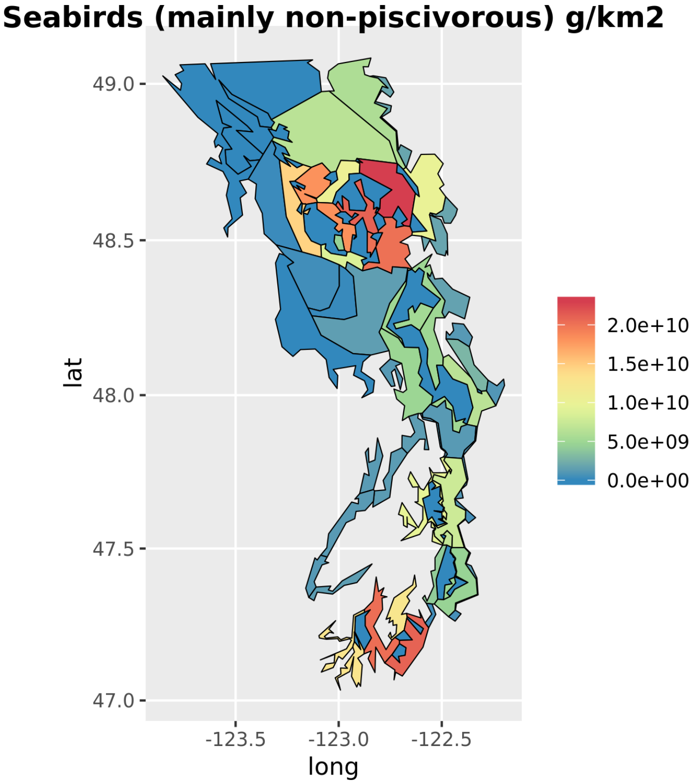

Figure 106. Seabirds (non-piscivorous) density, from PSAMP aerial surveys. Plotted as g/km^2.

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[19] https://www.allaboutbirds.org/guide/, accessed in 2018.

[20] These coarser taxa in the PSAMP database are Unidentified Gull, Unidentified Black-Wing Tip Gull, Unidentified Cormorant, and Unidentified Merganser.

for this group, since the majority (~60%) of individuals are permanent residents such as glaucous-winged gulls; however, we note that some less-common species such as common murres are winter visitors.

Similarly, major components of the non-piscivorous seabird group (SP) include bufflehead, surf scoter, and common goldeneye. These three species accounted for 75% of individuals in the functional group, if we assume that individuals identified only to coarser taxonomic resolution can be assigned to these species.[21] Life-history parameters are also taken primarily from the Cornell Lab of Ornithology, and based on this we assume a maximum clutch size of eight eggs. We assume eggs are laid in late April, based on bufflehead nesting season. Bufflehead, surf scoter, and common goldeneye are winter visitors to Puget Sound, common or frequent from October–May (Seattle Audubon Society 2018).

Raptors (BE)

We have limited the raptors group to bald eagles (*Haliaeetus leucocephalus*), the most abundant marine-feeding bird of prey in the Puget Sound basin. Bald eagles in the system are made up of two populations: a "resident" group that spends most of the year, builds nests, and rears its young in the region; and a "migratory" group that overwinters in the Salish Sea area and spends the balance of the year, including the breeding season, in other regions of western North America, primarily Alaska and Canada.

The resident population consists of breeding pairs, as well as "floating" resident adults that are non-breeding. The number of breeding pairs is derived from surveys of viable bald eagle nests conducted by WDFW; the most recent comprehensive nest survey was in 2005, but the data have been updated opportunistically as recently as 2017 (G. Blatz, WDFW, personal communication). We used nest count data compiled through 2015 (Kalasz and Buchanan 2016, Figure 2). Among resident adults, the home range size during breeding season for bald eagles that nest along the shores of Puget Sound likely ranges from 3.3–6.4 km^2, with the upper limit occurring in bays with extensive tide flats (Watson 2002). The core feeding areas ranged from 0.8–1.7 km^2 and averaged 1.2 km^2 (Watson 2002). Less information is available for the size and distribution of feeding territories during winter, although Stinson et al. (2001) concluded that the feeding locations were similar to summer feeding areas but more concentrated around salmon spawning streams and waterfowl wintering habitats. It is likely that overwinter feeding, particularly on spawning chum salmon, occurs well upstream in tributaries of Puget Sound (e.g., Stinson et al. 2001, Watson and Pierce 2001, Elliott et al. 2011) and thus, after the adult chum salmon have left the model domain. Based on this information, we filtered the nest locations to only include nests within a 1.43-km buffer around our Atlantis polygons.

To estimate biomass, we assumed that the individual biomass of an adult or post-fledged juvenile was 4.5 kg (Stalmaster and Gessaman 1984). We further assumed that only 80% of the nests were actively used by breeding pairs (Figure 107), based on observations of the proportion of active bald eagle nests in Washington state between 1980 and 2005 compiled

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[21] These coarser taxa in the PSAMP database are Unidentified Scoter, Unidentified Goldeneye, and Unidentified Diving Duck.

by Stinson et al. (2007). For the expansion of the resident population to account for floating adults, we assumed 1.13 floating adults per breeding adult, following assumptions of Millsap et al. (2016). The migratory population was thought to outnumber the resident population by 2.5:1 during the overwintering period (Stinson et al. 2007). The rate of increase of the resident bald eagle population in Washington state through 2015 appears to have slowed slightly (Kalasz and Buchanan 2016, Figure 3; see also Millsap et al. 2016), and the rate of increase of overwintering bald eagles is also thought to be slowing regionally and throughout the 48 contiguous United States (Eakle et al. 2015). We conservatively assume that the ratio of overwintering to resident bald eagles remains 2.5:1; we assume overwintering eagles are found in the same areas as resident eagles. Based on these assumptions, we initialize the model with a total biomass of 24.67 t (Figure 108).

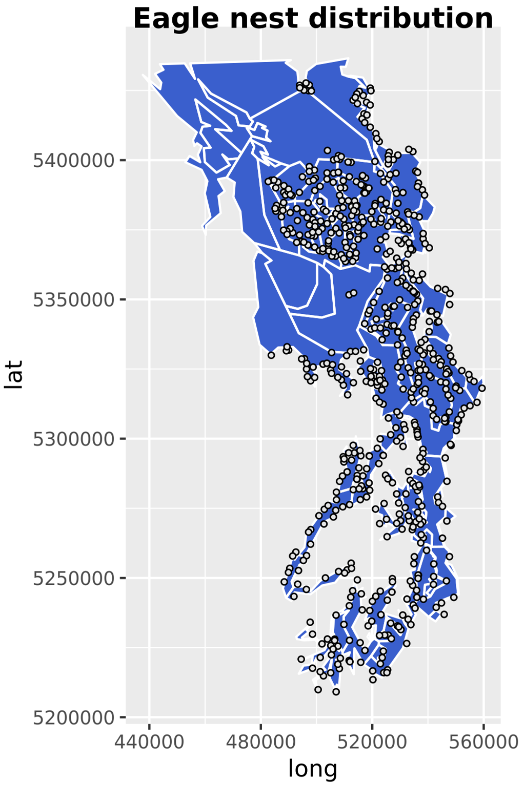

Figure 107. Overlap between eagle nests and Atlantis model domain. Based on WDFW surveys.

Estimates of maximum age and age-specific survival rates in the wild vary widely by region and study (e.g., Stinson et al. 2007). We assumed a maximum age of 25 years, based on anecdotal maximum age reports mostly ranging from 20–30 years, and an instantaneous annual mortality coefficient of –0.338/yr based on Stinson et al. (2007), Table 1; this is notably greater mortality than the North American average estimated by Millsap et al. (2016). Eggs are generally laid in the third week of March and hatch in late April, followed by a brooding period and fledging after roughly 12 weeks (i.e., early to mid-July; Stinson et al. 2007). While a nesting pair of bald eagles typically produces two eggs in a breeding season (Stalmaster 1987), mean production in the most recent regional survey (1980–98) was 0.95 successful young per breeding pair per year (Stinson et al. 2007); a more recent national survey of bald eagles yielded a net productivity of 1.12 successful young per pair per year (Millsap et al. 2016).

Resident bald eagles occupy nesting territories from roughly January through early fall, when they depart the region for up to six weeks to feed on early salmon runs in Alaska and British Columbia (Stinson et al. 2007). They then return to Puget Sound to feed on fall and winter salmon runs before returning to their breeding territories in January. Migratory bald eagles, originating from Alaska and Canada, typically migrate into Puget Sound beginning in October, with most adults arriving in November and December and juveniles arriving in January (Stinson et al. 2001, Watson and Pierce 2001). Migratory eagles depart the Puget Sound area from roughly 30 January to 20 April 20, averaging 9 March (as summarized by Stinson et al. 2001).

We used the bald eagle diet summary from Harvey et al. (2010). Bald eagle diets in the Puget Sound basin are broad and represent a range of feeding behaviors, from hunting to kleptoparasitism to scavenging, and are highly seasonal (Stinson et al. 2007). Key prey groups include fish and seabirds, though invertebrates and mammals are also consumed. Food habits studies derived from direct overwater observation suggest the greatest dependence on small fish, while sampling in or around nests implies greater reliance on birds, large fish, and mammals (Watson 2002); the diets derived from nest-based sampling likely overestimate bald eagle dependence and impact upon seabirds (Harvey et al. 2012a). Watson (2002) estimated that resident adult bald eagles foraging along Puget Sound shorelines during the January–July breeding season ate mostly unidentified fish (77–84% of items consumed), followed by seabirds (13–22%) and mammals (1–3%). Fish prey during breeding season likely include pelagic and demersal species found near the surface during daylight in waters within the radius of the home range, as well as occasional discards from fisheries. Seabird prey include various ducks and scoters, gulls, alcids, grebes, loons, and herons (Watson 2002). Adult salmon, particularly post-spawned chum salmon carcasses, are a major source of food in fall and winter (Stinson et al. 2007).

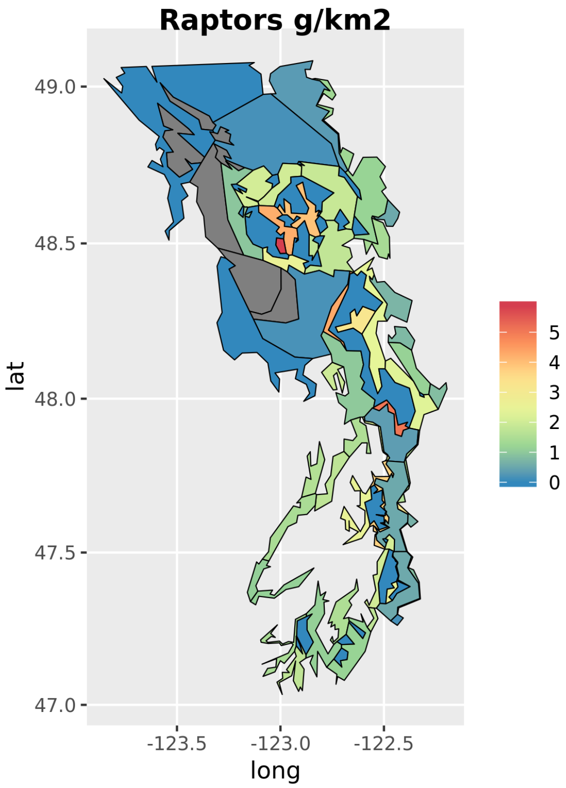

Figure 108. Raptor abundance based on nest locations. Plotted as g/km^2.

Harbor seals (HSL)

Harbor seals are the most abundant pinniped in Puget Sound. The population in inland Washington waters is considered a distinct stock, which includes more than 13,000 individuals (Jeffries et al. 2003). We used harbor seal abundance information assembled by Chasco et al. (2017) from Jeffries et al. (2003), based on haulout data, expanded by a factor of 1.52 to account for seals in the water. In terms of biomass, total seasonal peak abundance based on these sources is estimated to be 510 metric tons. Additional sources for bioenergetics, life history, and diet information are listed in Chasco et al. (2017), Table 1. Growth parameters were complemented with Fu et al. (2012). Note that Atlantis does not differentiate between sexes, so weight-at-age at initial conditions was set at the average value for males and females. The model was initialized with an age structure exhibiting an exponential decline (e^{-M}, with M based on the assumption that 99% of individuals die by age-10). For harbor seals and all other vertebrates, we assume there is no "plus group" (i.e., no accumulation of very old individuals in the oldest age class).

The Jeffries et al. (2003) and Chasco et al. (2017) summaries of harbor seal abundance assign this species with coarse spatial resolution. Those papers consider abundance in terms of five areas: the Strait of Juan de Fuca, the San Juan Islands, the Eastern Bays, Puget Sound, and Hood Canal. Approximately only six of 33 haulout sites in the Strait of Juan de Fuca area (Jeffries et al. 2003) are within our model domain (specifically only within Atlantis Box 30, Port Townsend Bay), and we therefore scale harbor seal abundance for this area by 6/33. For the Puget Sound area of Jeffries et al. (2003), we retain the abundance estimates from Jeffries et al. (2003) and Chasco et al. (2017), but refine the relative spatial distribution based on recent aerial surveys (Smultea et al. 2016) . This Puget Sound area is from southern Whidbey Island south. Within this Puget Sound area, Smultea et al. (2016) report harbor seal abundance for the following zones: South Whidbey, Seattle, Bainbridge, Vashon, and South Sound. We partition the abundance of harbor seals to these zones. Once abundance was partitioned to the finest spatial resolution in the data—either the aerial survey zones for Puget Sound or the four coarser areas from Jeffries et al. (2003) within each zone or area—we assumed uniform density of harbor seals (number/km$^{2;}$ Figure 109). We assume harbor seals are resident in Puget Sound, and that pupping season is June–September, based on the descriptions in an atlas of haulout sites by Jeffries et al. (2000).

California sea lions (CSL)

Parameterization of California sea lions in the Atlantis model was informed by the recent study of Chasco et al. (2017). California sea lion abundance was taken from Jeffries et al. (2014), NMFS (2015), and R. DeLong (National Marine Mammal Laboratory, personal communication), and is based on pup count surveys using an expansion factor to convert from pups to total abundance, including adults. In terms of biomass, total seasonal peak abundance was based on the sources listed above and was estimated to be 408 metric tons. Additional sources for bioenergetics, life history, and diet information are listed in Chasco et al. (2017), Table 1. Growth parameters were complemented with additional studies (Greig et al. 2005). Only male California sea lions utilize Puget Sound, so weight-at-age for initial conditions for this species is set to values for males only. The model was initialized with an age structure exhibiting an exponential decline, e^{-M}, with M based on the assumption that 99% of individuals die by age-20).

Though we use abundance estimates for California sea lions as compiled by Chasco et al. (2017), relative spatial distributions (Figure 110) of California sea lions are informed by aerial surveys of haulout sites by Jeffries et al. (2014). These 24 aerial surveys covered the Strait of Juan de Fuca, Hood Canal and Dabob Bay, the Eastern Bays, and Puget Sound, between March 2013 and February 2014, with summer-only surveys of the San Juan Islands. We assumed that the raw count per site was a proxy for relative abundance. Jeffries et al. (2014) reports counts of individuals (per site) within larger areas 7–14 as defined in the atlas of seal and sea lion haulouts by Jeffries et al. (2000). We assumed that counts per area were proportional to abundance, assigned Atlantis polygons to these areas 7–14, and then assumed uniform density of sea lions (number/km^2) in the Atlantis polygons within those areas. Peak abundances are in fall and late spring (Jeffries et al. 2000). We approximate the detailed migration timing in Chasco et al. (2017) by allowing California sea lions to enter Puget Sound over a 30-day period beginning on 1 September (day 244), and to depart over a 30-day period beginning on 10 March (day 69).

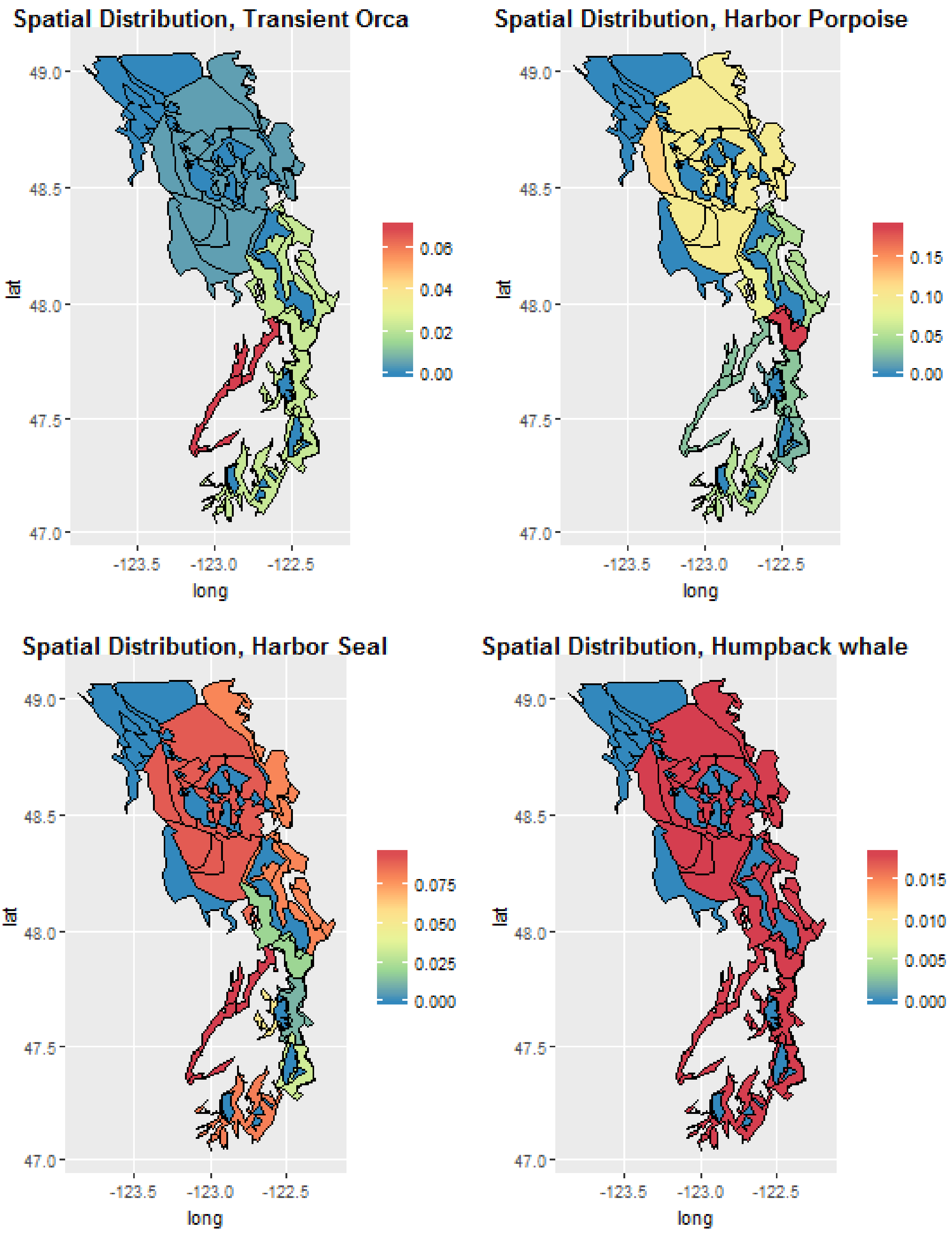

Figure 109. Spatial distribution of transient killer whales, harbor porpoise, harbor seals, and humpback whales. Plotted as g/km^2. See text for data sources.

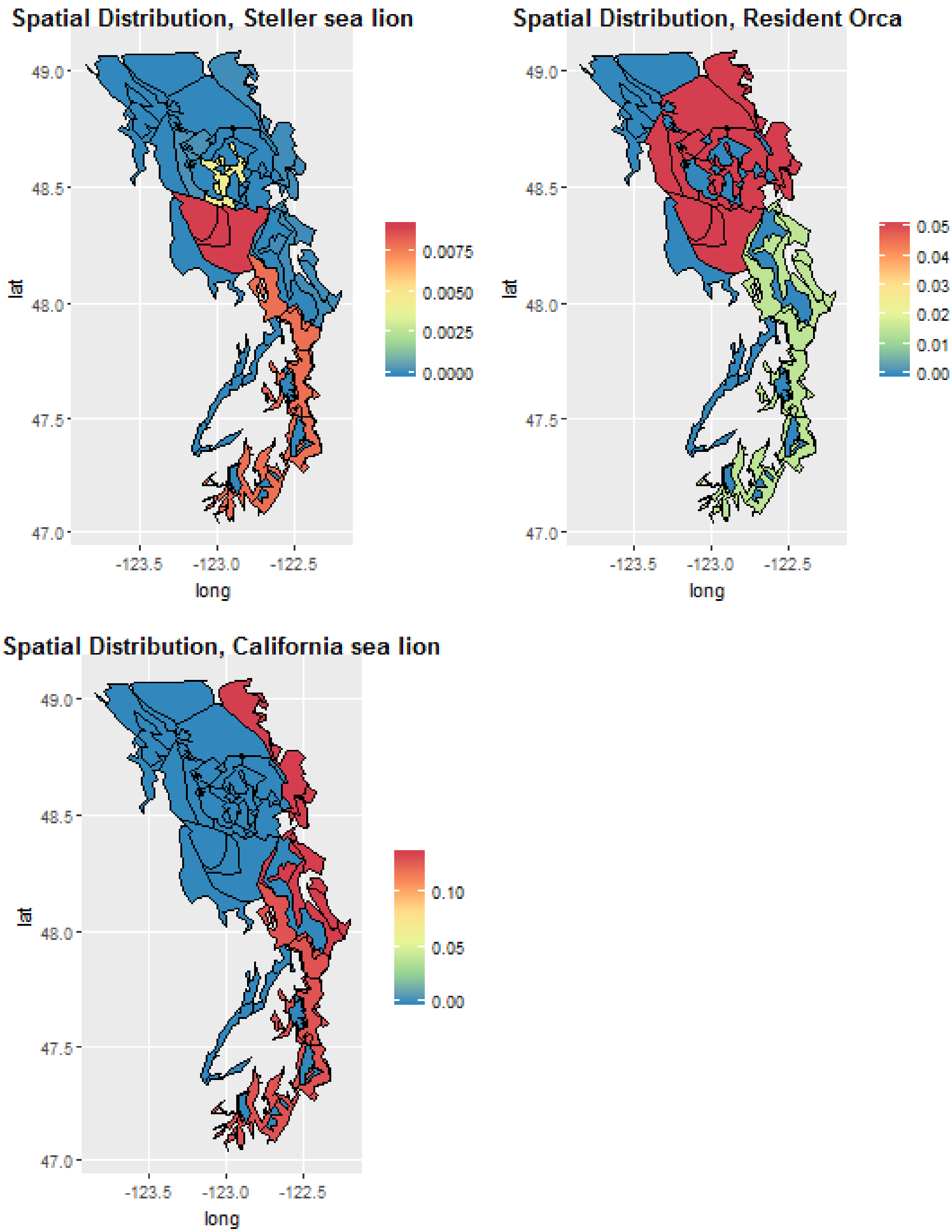

Figure 110. Spatial distribution of Steller sea lion, resident orca, and California sea lion. Plotted as g/km^2.

Steller sea lions (PIN)

Steller sea lion abundance was taken from Chasco et al. (2017), based on Jeffries et al. (2014); additional sources for bioenergetics, life history, and diet information are listed in Chasco et al. (2017), Table 1. In terms of biomass, we estimated total seasonal peak abundance as 23 metric tons, based on Chasco et al. (2017). Note that Atlantis does not differentiate between sexes, so weight-at-age at initial conditions was set at the average value for males and females. Though we use abundance estimates for Steller sea lions as compiled by Chasco et al. (2017), relative spatial distributions (Figure 110) of Steller sea lions were informed by aerial surveys of haulout sites by Jeffries et al. (2014), as described above for California sea lions. The population of Salish Sea Steller sea lions is mostly transient males that migrate from British Columbia and the Washington coast during fall, winter, and spring. There are 12 Puget Sound and Georgia basin haulout sites within the Atlantis model domain (Wiles 2014). Migrations for Steller sea lions involve peak Puget Sound abundance in fall and winter (Jeffries et al. 2000). We approximated the seasonal migrations for Steller sea lions, as parameterized by Chasco et al. (2017), by allowing 35% of the Steller sea lion population to remain within Puget Sound year-round, and 65% of the population to enter Puget Sound during an autumn migration beginning on 1 September (day 244) and continuing over a 30-day period. This is followed by high winter abundance, and a rapid migration out of the sound beginning on 1 February (day 32) and continuing over a 30-day period.

Harbor porpoise (PHR)

Abundance and spatial distribution of harbor porpoise were calculated from aerial surveys (Smultea et al. 2016, Jefferson et al. 2016). Those authors report density (individuals/km^2) per sub-basin. Assigning Atlantis polygons to these sub-basins suggests 11,551 individuals (Jefferson et al. 2016), with highest density in the South Whidbey area and the San Juan Islands. Growth parameters (L_{inf}, k) and length–weight parameters (a, b) were taken from SeaLifeBase,[22] resulting in a maximum weight per individual of 70 kg, with an average individual of 47 kg. Total biomass is therefore 542 metric tons in the model domain. The model was initialized with an age structure exhibiting an exponential decline, e^{-M}, with M based on the assumption that 99% of individuals die by age-24, with the expectation that the realized age structure in simulation would exhibit higher survival of most adults, prior to senescence.

Spatial distributions for harbor porpoise (Figure 109) are informed by aerial surveys by Smultea et al. (2016). These surveys covered Puget Sound, the southern Strait of Georgia, and the Strait of Juan de Fuca in 2013–15, with density estimates calculated from sightings via Distance software.[23] Sampling occurred in July, September, January, and April, covering in total 20,554 km on 61 flights over 35 days. Smultea et al. (2016) report marine mammal abundance for the following zones within the Atlantis domain: Bainbridge, East Whidbey, Hood Canal, Seattle, South Whidbey, South Sound, Vashon, Area J (the San Juan Islands), and Area JC (the Gulf Islands). Once we partitioned abundance to these aerial survey zones, we

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[22] https://www.sealifebase.ca/

[23] https://distancesampling.org/

assumed uniform density of harbor porpoise (number/km^2) within each zone. We assume that one-third of abundance in Area JC (the Gulf Islands) falls within our model domain, and that two-thirds of abundance in Area J (the San Juan Islands, including the eastern Strait of Juan de Fuca) falls within the Atlantis domain. These surveys did not focus on haulout areas, and detected 386 harbor porpoise and 2,170 harbor seals, but only 66 sea lions. We assume harbor porpoises are residents and do not have seasonal migrations outside Puget Sound. Breeding season of July–October and gestation of 10–11 months are based on Hall (2011). We assume a maximum fecundity per female per year of 0.3, based on the maximum pregnancy rate of adult females for the Salish Sea (Norman et al. 2018).

Resident orcas (ROR)

Killer whales (also known as orcas) have two sympatric ecotypes in the eastern North Pacific, the fish-eating residents and the mammal-eating transients (Hauser et al. 2007a). Resident killer whales (*Orcinus orca*) are found year-round in coastal waters of Washington and British Columbia. Resident killer whales have distinct behavior and genetics from transients, including seasonal occurrence, social organization, acoustic signals, diet, and foraging. Residents feed almost entirely on fish and squid, mainly salmonids; the majority of non-salmonid fish species are demersal or epibenthic species (Ford et al. 1998). The predominant salmon species in the diet is Chinook salmon (Ford et al. 1998). The population is listed as endangered under the ESA (Hanson et al. 2010).

Chasco et al. (2017) constructed population trends and bioenergetics models for marine mammals in Washington State inland waters, including resident killer whales, to quantify the consumption of Chinook salmon. Resident killer whale abundance from Chasco et al. (2017) was based on mark–recapture data taken from Center for Whale Research (2016) and informed by Jeffries et al. (2014) and Hauser et al. (2007). Additional sources for bioenergetics, life history, and diet information are listed in Chasco et al. (2017), Table 1. Note that Atlantis does not differentiate between sexes, so weight-at-age at initial conditions was set at the average value for males and females. In terms of biomass, total seasonal peak abundance is estimated to be 233 metric tons. Spatial distributions (Figure 110) are based on NMFS (2006), which designated three critical habitat areas: Area 1 in the San Juan Islands, Area 2 in Puget Sound (excluding Hood Canal), and Area 3 (the Strait of Juan de Fuca). Based on 11,876 sightings from the Whale Museum database from 1990–2003, NMFS (2006) estimated that 72% of sightings of resident killer whales were in U.S. waters, and 85% of U.S. sightings of residents were in Area 1 ("Core Summer Area" in the San Juan Islands). We assign 85% of resident killer whale spatial distribution to the San Juan Islandss (Atlantis polygons 1–20), with 15% distributed evenly throughout the rest of the model domain, excluding Hood Canal. We assigned model polygons 1, 4, and 18 to the "Core Summer Area" despite including Canadian waters (outside the NMFS critical habitat area), on the basis of Hauser et al. (2007a), who reported common space use by all pods in Canadian waters.

In the Atlantis model, Southern Resident killer whales are not differentiated into J, K, and L pods, and therefore some detailed aspects of the pods' movement and migration are not captured in the model. These pods are matrilineally related subgroups (Hauser et al. 2007a). Southern Residents live along the western shore of San Juan Island and Puget

Sound in summer months, May–November (Hanson et al. 2010), when they congregate in inshore areas where they can access Chinook salmon, their preferred prey (Ford et al. 1998). Though we do not include this level of detail in the model, during summer the Southern Resident whales spend ~20% of their time outside Puget Sound, taking frequent trips lasting a few days to the outer Washington coast and southern Vancouver Island (Hauser et al. 2007a, Hanson et al. 2010). During winter, the J pod, which represents ~30% of the population, spends about 25% of its time in the Salish Sea, and the rest of its time in Central California, Northern California, Oregon, and the outer Washington coast (Chasco et al. 2017). The K and L pods do not spend any time in Salish Sea waters during winter.

We base migration dates for the aggregated Atlantis resident killer whale group on the parameterization from Chasco et al. (2017). Killer whales migrate out of the model over a 45-day period beginning on 1 October (day 274). They return over a 45-day period beginning 1 May (day 121). Breeding occurs in April through October (NMFS 2008).

Transient orcas (TOR)

Transient killer whales (*Orcinus orca*) are a distinct population that move throughout Washington and British Columbia. Abundance consists of 15 pods of about 47 whales each (Heimlich-Boran 1988). Transient killer whales have different behavior and genetics from residents, including seasonal occurrence, social organization, acoustic signals, diet, and foraging (Ford et al. 1998). Transients feed in shallow, nearshore areas that correspond to seal haulout areas (Heimlich-Boran 1988). Harbor seals are their main prey item, but transients will likely feed on any small marine mammal and seabird (Ford et al. 1998).

Total abundance of "inner coast" transient killer whales in northern Washington, British Columbia, and southeastern Alaska was estimated to be 304 by Ford et al. (2013), identified during 2,988 encounters between 1990 and 2011. We do not attempt to include a separate population of offshore transients, which visit the Salish Sea less frequently (Ford et al. 2014). The inner coast transient killer whales range over an area much larger than our model domain, and though Ford et al. (2013) suggest that 74% of individuals have at least occasional use of the Salish Sea, there is also heavy habitat use in six other regions ranging from southwestern Vancouver Island to southeastern Alaska. For model initial conditions, we assume peak annual abundance of 50 individuals within the Atlantis domain, or a total of 100 metric tons of biomass.

Transient killer whales move from Central California to southern Alaska (Ford et al. 1998), including Puget Sound and the Strait of Georgia. In these inland waters, their distribution is concentrated in the southern Strait of Georgia (Heimlich-Boran 1988), in the northern end of the Atlantis model domain. Seasonal distribution shows two peaks in observation from March–May and August–October (Heimlich-Boran 1988, Ford et al. 2013). Baird and Dill (1995) attributed the autumn peak in abundance off southeastern Vancouver Island to availability of harbor seal pups as prey during the weaning season.

Spatial (Figure 109) and temporal distribution within the model domain were based on cumulative annual occurrence in the Salish Sea by subarea from 2004–10 (Houghton et al. 2015). Atlantis spatial polygons fall within Houghton's Puget Sound, San Juans, and

Hood Canal areas. We assumed abundance was distributed between areas as specified in Houghton et al. (2015), but that, within any single area from Houghton et al. (2015), the density of transient killer whales was uniform. Based on these data from Houghton, we then parameterized relative spatial distributions. The same data suggest seasonal migrations into Puget Sound, with peaks in May and August (Table 7).

Within Atlantis, we approximated this as: 1) a brief June partial migration out of the Sound with an August return, and 2) a migration of the full population starting in September, with a return in March. The first of these migrations involves 75% of the population and begins 1 June (day 152); outmigration continues for 15 days with a rapid return over 15 days beginning 1 July (day 182). The second migration involves the full population and begins 1 September (day 244); outmigration continues over 60 days, with return over a 60-day period beginning 1 March (day 60).

Humpback whale (HUW)

Humpback whales were abundant along the coast of Washington State, particularly in inside waters, at the start of the 20th century (Falcone et al. 2005). Following decades of commercial whaling, the humpback group in Washington and British Columbia is now approximately 189 individuals, but increasing (Carretta et al. 2017). Humpbacks are found frequently in the Juan de Fuca canyon, just west of our model domain (Calambokidis et al. 2004). Humpback whales occur sporadically in our Puget Sound model domain, including for instance a sighting in Hood Canal in 2012 (Smultea et al. 2016). Prior to 2003, only three individuals had been identified in Puget Sound; in spring and fall of 2003 and 2004, 13 unique individuals were identified in the Strait of Georgia, the Strait of Juan de Fuca, and South Sound (Falcone et al. 2005). Further evidence that this large whale uses much of Puget Sound is offered by Calambokidis and Steiger (1990), who reported two humpbacks in South Sound and Hood Canal. As a starting point, we assume peak annual abundance in the Atlantis model of six individuals, or a total of 120 tons assuming mean body mass of 20 tons per individual. We assume equal densities throughout Puget Sound (Figure 109). The primary prey source for humpback whales in inside waters is herring (Stout et al. 2001). Females give birth to one calf every one to four years; calves stay with their mother at least nine months after birth (Stendahl 2014). Growth parameters were taken from Chittleborough (1965).

Humpback whales typically spend the summer feeding in productive, high-latitude waters, then migrate to low-latitude areas in winter to breed (Falcone et al. 2005). Whales along the Washington coast appear to migrate mainly to the Mexican mainland (Calambokidis et al. 2001). Humpback whales are found in higher abundance between May–November, but can be found as late as December (Stendahl 2014). Humpback whales migrate out of the model domain over a 30-day period beginning on 1 December (day 335) and return over a 30-day period beginning 1 May (day 121). Migration dates for humpback whales and other migratory marine mammals are shown in Table 7.

Spawning and Recruitment for Fish and Other Vertebrates

Reproduction of vertebrates is modeled in two distinct phases in AMPS. First, spawning occurs over a time window specified for each functional group, and the material (nitrogen) required for reproduction is removed from reserve nitrogen pools, which includes both gonadal and somatic tissue, such that parental weight-at-age declines. After spawning, each age class is incremented by one year, and the oldest class leaves the model domain. Recruitment into the population follows at a specified time after spawning, and new recruits are then assigned to the first age class. The lag time between spawning and recruitment represents larval settlement time for fish, incubation period for birds, and gestation period for mammals.

We modeled recruitment for fish groups using Beverton–Holt dynamics:

$$R = \frac{\alpha\, S}{(\beta + S)} \tag{8}$$

where R is recruits (numbers of age-0 individuals) and S is stock size (adult biomass in mg N), α is the maximum number of recruits produced at high stock size, and β is the stock size at which recruitment is ½ α. As a starting point for calibration, we parameterize α and β based on three assumptions:

1. That steepness is 0.6 for salmon, 0.5 for rockfish, and 0.8 for all other fish. By definition, steepness is the proportion of maximum recruitment that is produced when spawning biomass is 20% of unfished spawning biomass (Mace and Doonan 1988).
2. That unfished spawning biomass is 5× current spawning biomass for all fish.
3. That the maximum number of recruits is 3.75× current recruitment for all fish.

We estimated bird and mammal recruitment using a fixed number of offspring produced per adult. For birds, recruit per adult is the product of hatch success, broods per year, and clutch size; for mammals, it is the product of the number of calves per female, pregnancy rate, proportion of females in population, and pregnancy interval.

Salmon Life Cycle

During the development of AMPS, new routines were developed for Atlantis that simulate different aspects of the salmon life cycle. Implementation in Atlantis is described in detail in technical documentation (Girardin et al. 2017). Atlantis simulates different salmon life stages (Figure 111), including the river stage. The river stage covers the period from hatching through to first entry into the saltwater environment in Puget Sound; this stage is best represented implicitly in Atlantis. Survival is represented using a standard stock recruit relationship, generating a base number of new recruits dependent on the adult spawning stock within the model, and then scaling that using a multiplier derived from a time-series file.

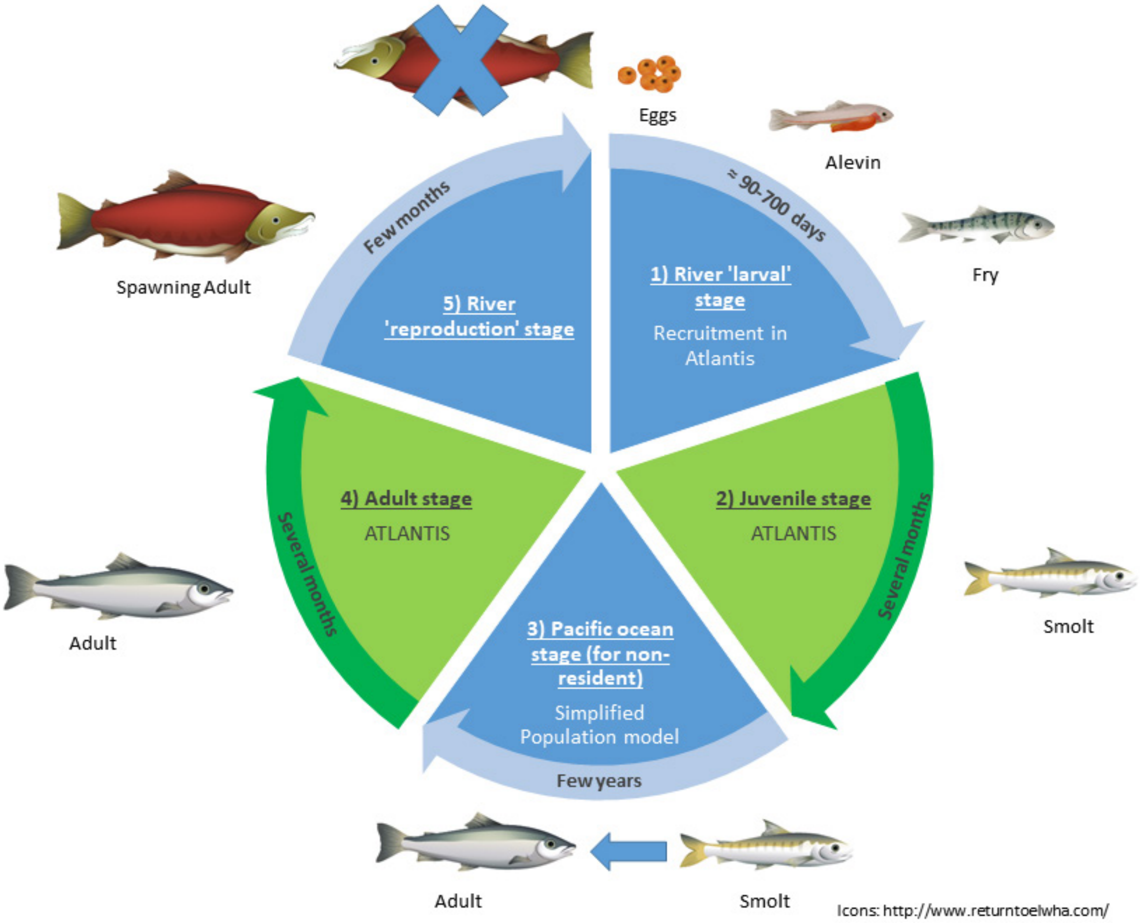

Figure 111. Salmon life cycle. Figure shows how Atlantis simulates the different life stages.

Juvenile stage (inside model domain)

Two key processes must be considered for the juvenile phase once the fish have entered the model domain: movement and feeding. Juveniles move rapidly within the model domain; to incorporate this, AMPS was modified to allow monthly (rather than quarterly) distributional shifts. During the first months in saltwater, salmon remain nearshore and feed on terrestrial insects. Additional Atlantis code in AMPS allows external input of food into the salmon diet, assuming proportional access across all age classes and only in surface waters.

Multiyear migration outside of model domain

Code added to Atlantis for salmon in AMPS accounts for the fact that: 1) salmon are outside the model for more than a year, and 2) salmon mature outside the model (change stage from juvenile to adult) and do not return to the model domain as juveniles. To represent the juvenile (at-sea) period, a population model is triggered to handle growth and mortality during this period outside the model domain. Growth during this period follows the von Bertalanffy growth equation. Maturation occurs outside the model domain, but spawning is delayed until adults arrive in the natal rivers. Adult salmon are allowed back into the model domain and follow monthly spatial distributions. Adult salmon in AMPS spawn and die (once again outside of the model). Atlantis also allows for scaling values for linear mortality (*mL*), growth rates (*mum*), and recruitment, which can be used to simulate time-varying scenarios.

Turbidity and survival rate

A logistic curve is applied to represent the escapement of salmon from predation due to turbidity (Ward et al. 2016):

$$f(x) = 1 - \frac{L}{1 + e^{-a(x-b)}} \tag{9}$$

where (1 – L) is the fraction escaping from predation when turbidity is very high, L is the predation fraction when turbidity is very high, a is a rate parameter dictating how strongly escape responds to turbidity, x is the turbidity value, and b is an offset that determines the minimum turbidity at which escape begins to increase with increasing turbidity.

The value of the escapement is a proportion (i.e., between 0 and 1). At present, this escapement only modifies the availability of the prey to its predator during feeding. It does not alter the prey's movement (i.e., the prey species move to their preferred habitat and ignore any turbidity effects).

Contaminant tracers

Contaminant tracers, when present, are traced through the food web to allow for assessment of the accumulation of contaminants in the food chain. The level of accumulated contaminants in an individual can impact its growth. This is also implemented using a logistic curve that is applied as a scalar to the growth rate:

$$f(x) = 1 - \frac{L}{1+e^{-a(x-b)}} \tag{10}$$

where (1 – L) is the fraction experiencing growth effects when contaminants are very high, a is a rate parameter dictating how strongly the growth rate responds to contaminants, x is the contaminant value, and b is an offset that determines the minimum contaminants at which the growth rate effects begin to occur with increasing contaminants.

At present, the contaminant may be "metabolized" by setting the decay terms. Growth effects due to contamination can also be represented using a simple scalar.

Contaminant uptake

The groups within Atlantis take up contaminants either through contact, general uptake, or through consumption. There are currently two options for uptake:

a. Linear uptake (parts/sec):

$$C_{uptake} = \tau \cdot C \tag{11}$$

where τ is the uptake rate and *C* is the ambient contaminant level in the environment.

b. Sigmoidal uptake, which is ideal for representing interactions with a toxin that has no effect until a critical concentration is reached:

$$C_{uptake} = \frac{1}{dt} \cdot \left(\frac{C}{C_{in} + (C - C_{in}) \cdot e^{-\tau \cdot dt}} - C_{in}\right) \tag{12}$$

where C_{in} is the contaminant level within the functional group (i.e., the internal level), τ the uptake rate, *d*τ is the change over time in uptake rate, and *C* is the ambient contaminant level in the environment.

Catch Reconstruction

Historical Landings

We compiled available historical time series of fisheries landings across Puget Sound and the southern Strait of Georgia from 1970 to 2017. The time series were grouped based on Atlantis functional group definitions (Table 2) and then distributed across time and space for the AMPS model domain. We considered commercial and recreational fisheries catch, including treaty fisheries. Landings included species produced in aquaculture, but not freshwater species. United States data from 1981–2017 were obtained from the Pacific Fisheries Information Network (PacFIN). We retrieved monthly landing data, specifying gear, gear group, area recorded, port, and whether the origin was commercial or Native American treaty (Figure 112). Monthly data were used to derive the seasonal proportions needed to drive fisheries in Atlantis.

Canadian catch data (Figure 113) were obtained from Fisheries and Oceans Canada (I. Pearsall, Pacific Salmon Foundation, unpublished data) and from summary statistics on Fisheries and Oceans Canada in the Pacific Region.[24] Data are reported by Groundfish Management Area. Data used include aboriginal catch 1970–2013, recreational catch 1970–2012, and commercial groundfish data. Aboriginal and recreational catch are reported by number of fish; we used reported weight by fish species in commercial line gears to convert this number to catch in kilograms. Mean average weight for prawns was obtained from Whyte and Craswell (1982). Canadian commercial data come from five sources:

1. Trawl and trap (1970–95)—a merge of fisher logbooks, which provide a set-by-set enumeration of location details and the amounts of each species caught, and sales slip data, which provide the actual weight of each species landed. The amounts from sales slips are prorated to fishing locations based on the proportions recorded at sea.
2. Trawl (1996–2007)—a merge of at-sea observer logbooks, which provide set-by-set enumeration of location details and the amounts of each species caught, and dockside monitoring program (DMP) data, which provide the actual weight of each species landed. The amounts from DMP are proportional to fishing sets based on the proportions recorded at sea.
3. Line gears except traps (1986–2006)—a merge of fisher logs, which provide set-by-set enumeration of location details and piece counts of each species caught, and DMP data, which provide the actual weight of each species landed. Weight values have been derived using weights applied to piece counts.
4. Trawl (2007–16)—a merge of at-sea observer logbooks, which provide set-by-set enumeration of location details and the amounts of each species caught, and DMP data, which provide the actual weight of each species landed. The amounts from DMP are prorated to fishing sets based on the proportions recorded at sea.
5. Line gears (2006–16)—a merge of fisher logbooks, which provide set-by-set enumeration of location details and the amounts of each species caught (mix of pieces and weights, depending on species), and DMP data, which provide the actual weight of each species landed. The amounts from DMP are proportional to fishing sets based on the proportions recorded at sea.

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[24] https://www.pac.dfo-mpo.gc.ca/stats/index-eng.html

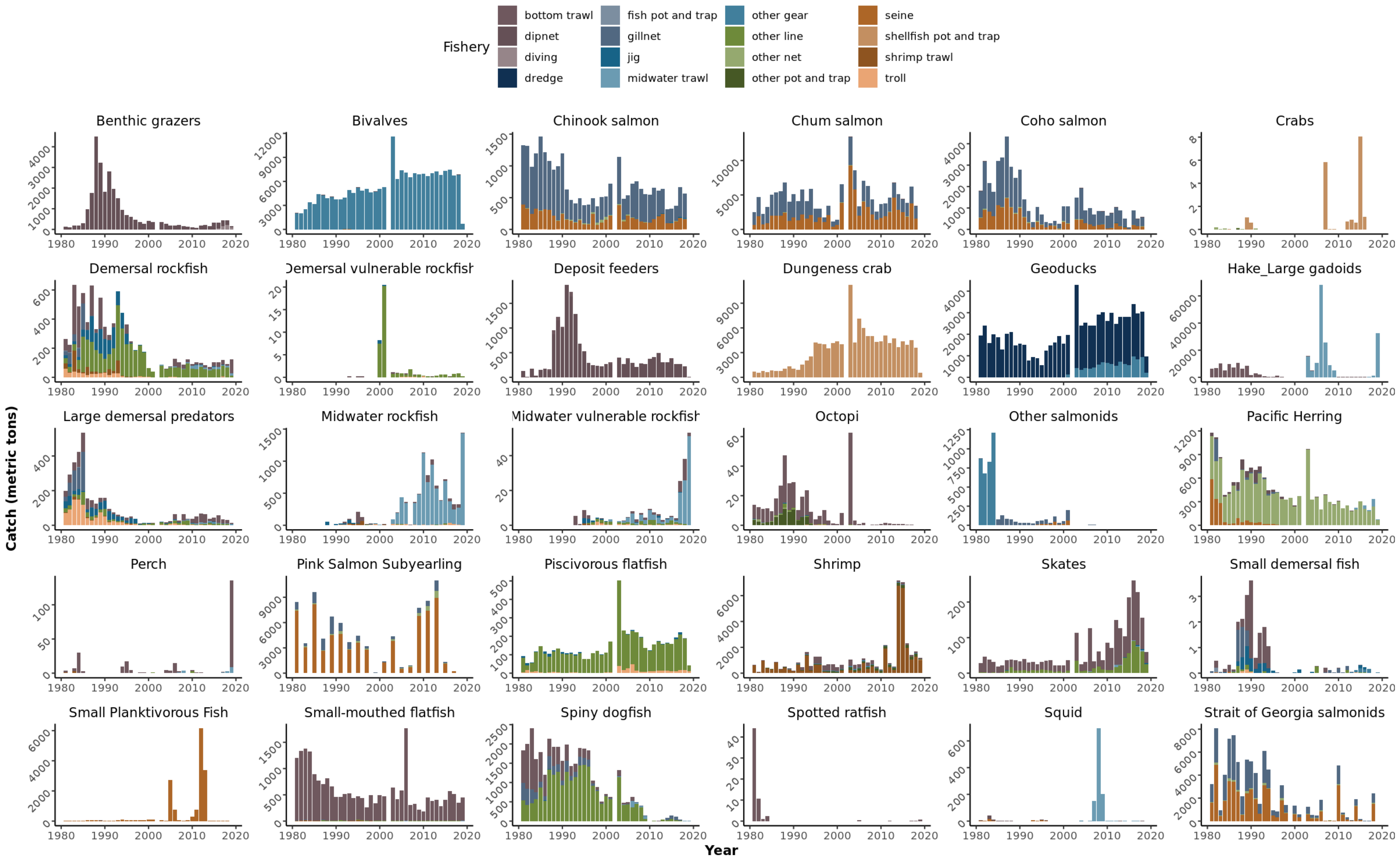

Figure 112. Commercial catch data (metric tons) from Puget Sound by Atlantis functional group and gear group, 1981–2017, from PacFIN.

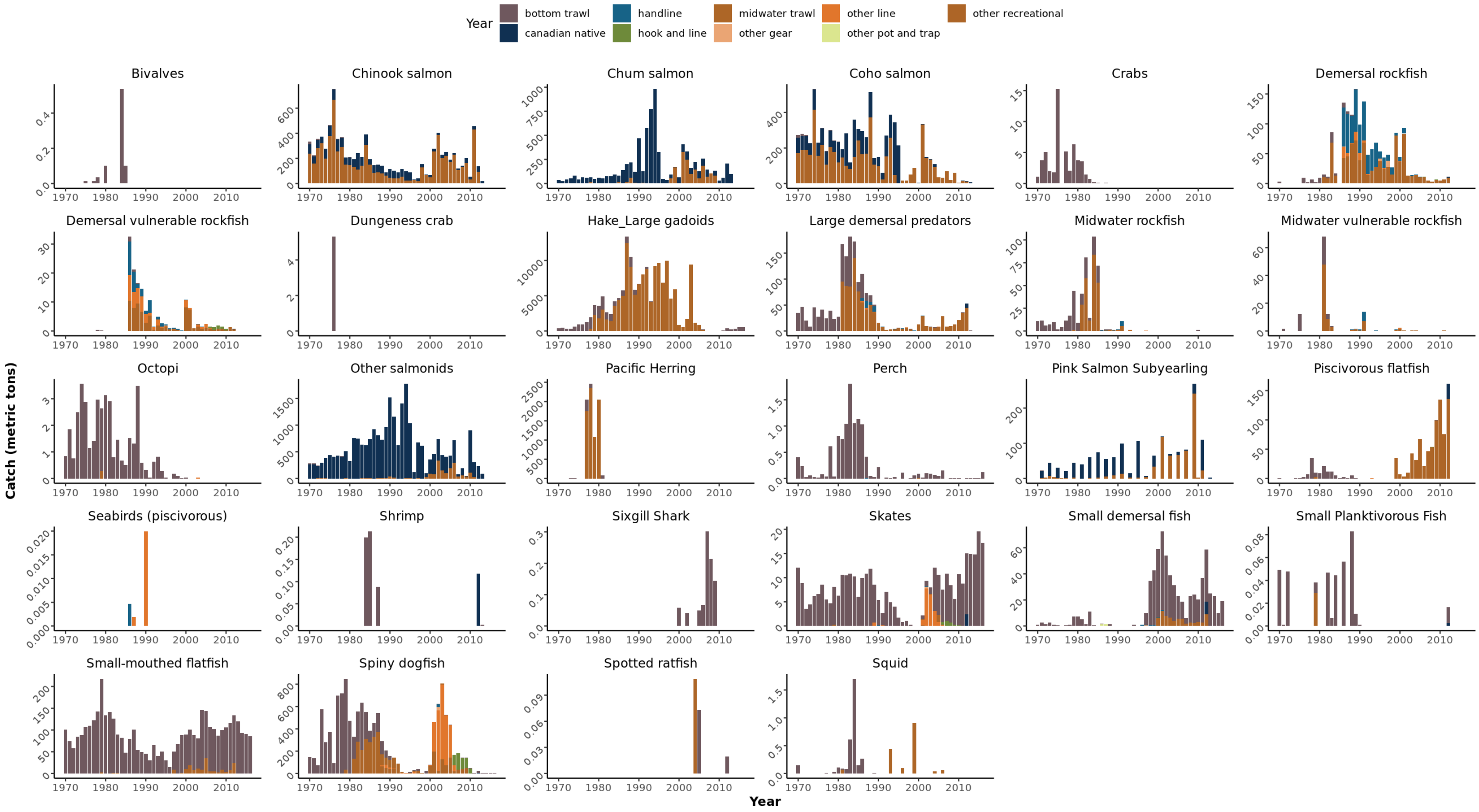

Figure 113. Commercial catch data (metric tons) caught by Canadian fishers for Atlantis functional groups and gear groups, 1970–2016.

Groundfish data between 1970 and 1988 (Figure 114) were obtained from Schmitt et al. (1991). That report provides standardized commercial groundfish statistics from Puget Sound based on data gathered by WDFW on catch, effort, and value from commercial groundfish landings from Washington's marine waters. Those data were collected from commercial fish buyers, fishers' logbooks, and department sampling programs. We used data tables of catch per management area and year, digitized directly from the printed report and checked manually.

Data prior to 1981 for species other than groundfish were obtained at the state level (Washington) from NOAA's Office of Science and Technology Commercial Fisheries Statistics database (NMFS 2011; Figure 115). Commercial landings in this source are specified by common name. The Integrated Taxonomic Information System (ITIS 2012) and FishBase (Froese and Pauly 2014) were used to associate species names to common names. The species-specific time series were then grouped based on the Atlantis functional group definitions (Table 2). We assumed that the Puget Sound fraction of Washington State catch prior to 1981 was equal to the Puget Sound fraction of the catch recorded in PacFIN during 1981–83. This ratio was used to estimate catch for Puget Sound.

Recreational landings time series (Figure 116) were compiled from the Washington State Sport Catch Reports, which are available from 1967–2016.[25] These reports estimate harvests from catch record cards for salmon, sturgeon, steelhead, Dungeness crab, and halibut. The card data are supplemented with field or creel survey data, or telephone surveys where available, to improve recreational harvest estimate accuracy. Marine fish and intertidal shellfish sport harvest estimates are based on field and creel surveys. Harvested oysters are predominately the non-native Pacific oyster and are reported in terms of numbers harvested. There are no data on the size structure of oysters harvested, although the minimum harvest size is 6.35 cm. We converted oyster numbers to weight using an average 96.4 g per oyster, as reported by Lang et al. (2010), which provides oyster weights from individuals in intertidal and subtidal areas of the Yaquina River estuary in Newport, Oregon. Fish are also reported in numbers; we used length–weight data from WDFW port sampling and surveys of sportfishers (K. Andrews, unpublished data) to derive average weight per fish and used these weights as conversion factors to transform fish numbers to biomass. For species where no length–weight data were available from WDFW port sampling, we either used average weight from a bottomfish survey in northern Puget Sound (Lauth et al. 1988) or we estimated weight from common length using length–weight relationships available in Fishbase (Froese and Pauly 2014). The average fish weights used as correction factors are in Table 12.

The comprehensive catch reconstruction of historical landings (Figure 117) was then used to develop catch time-series files that describe the landings of each functional group (in mg/sec) from 1970 to 2011 within each polygon that reflect the spatiotemporal patterns in biomass distribution. We then used the catch time-series files to force historical simulations of AMPS and test the model's ability to replicate historical catch trends under historical fishing pressure, as described in Model Performance.

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[25] https://wdfw.wa.gov/publications?title=sport&category=All&author=

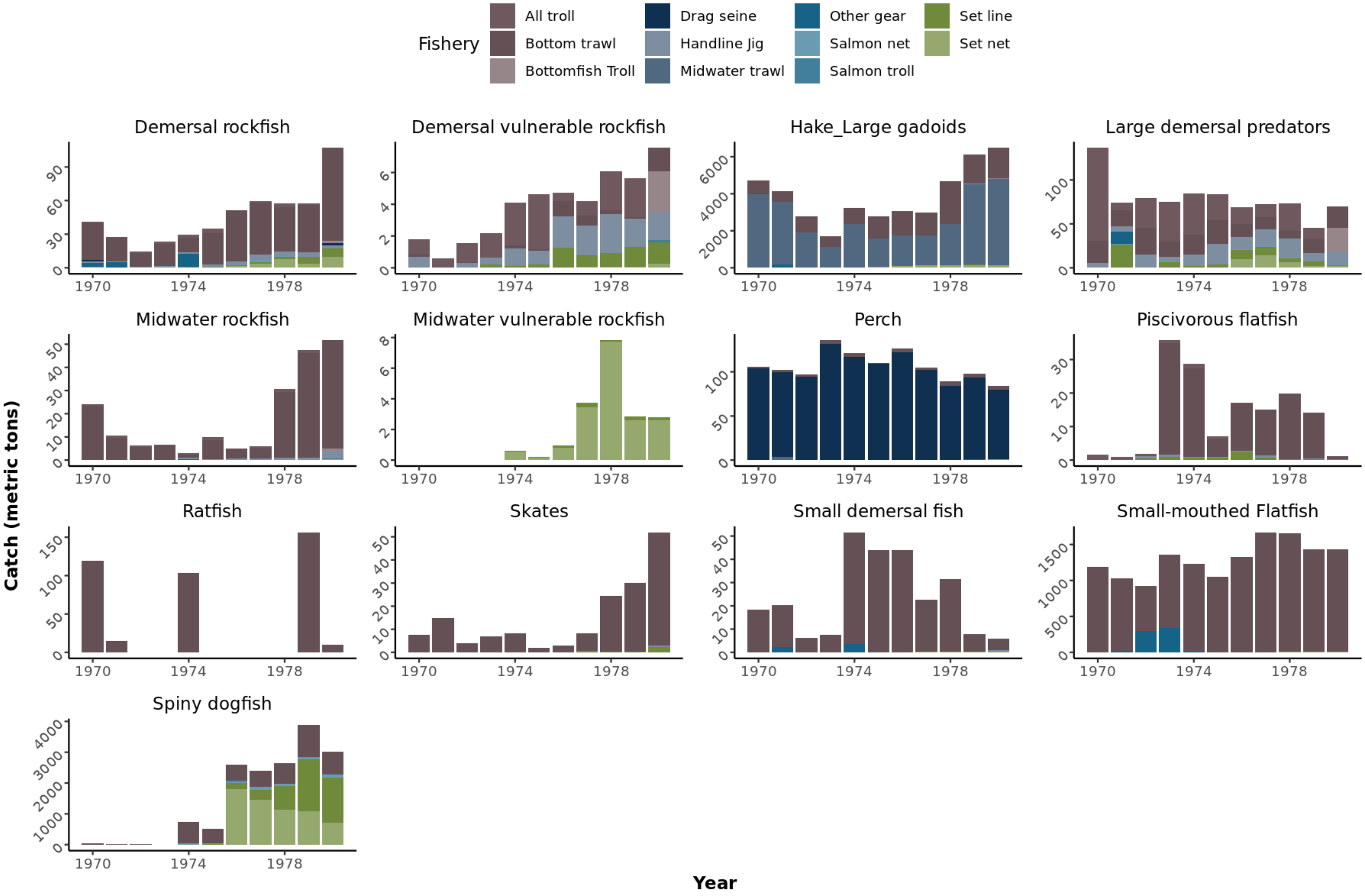

Figure 114. Groundfish commercial catch data (metric tons) from Puget Sound by Atlantis functional group and fishery, 1970–80, from Schmitt et al. (1991).

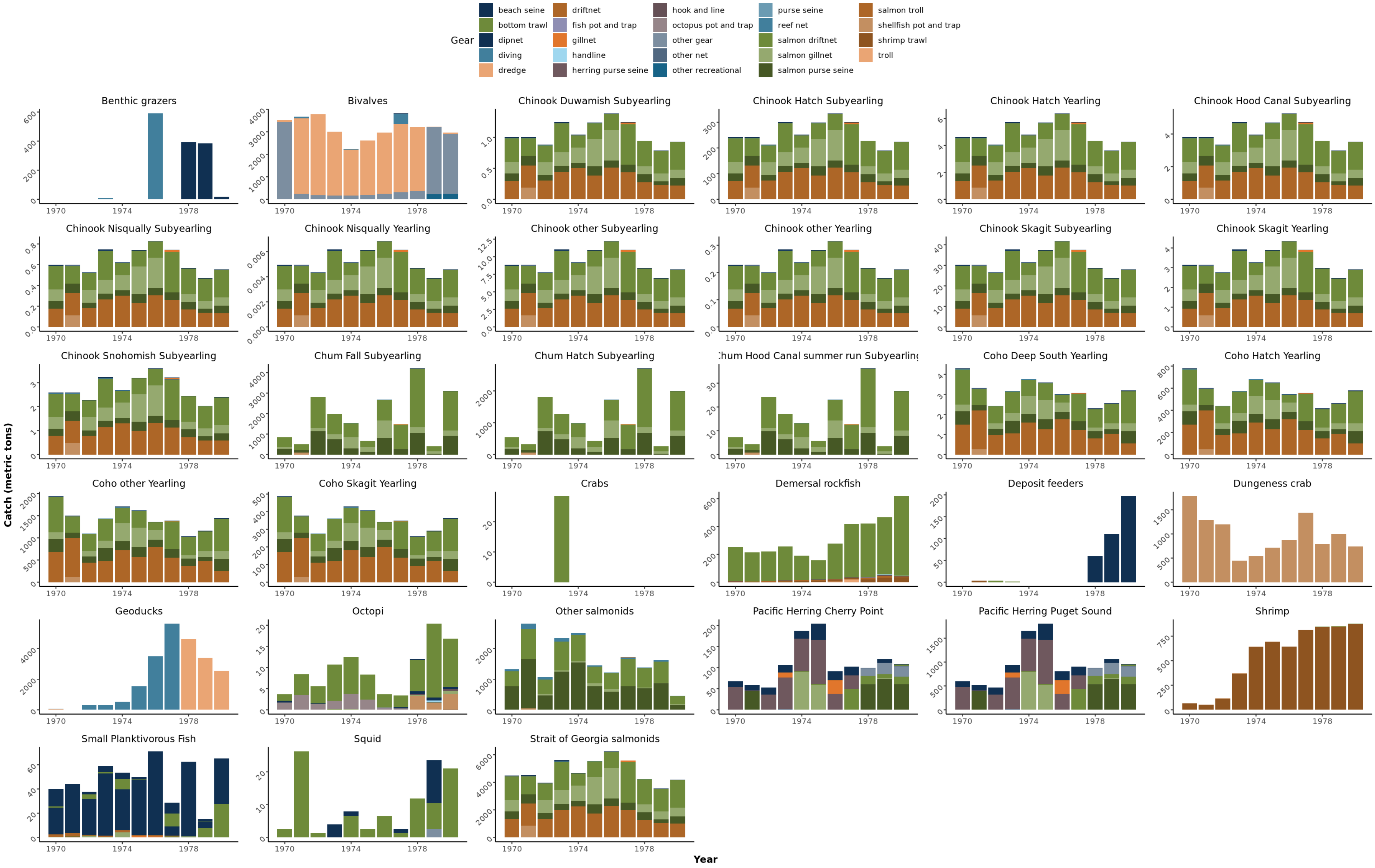

Figure 115. Commercial catch data (metric tons) from Puget Sound by Atlantis functional group and gear, 1970–80, estimated from NOAA's Office of Science and Technology Commercial Fisheries Statistics database.

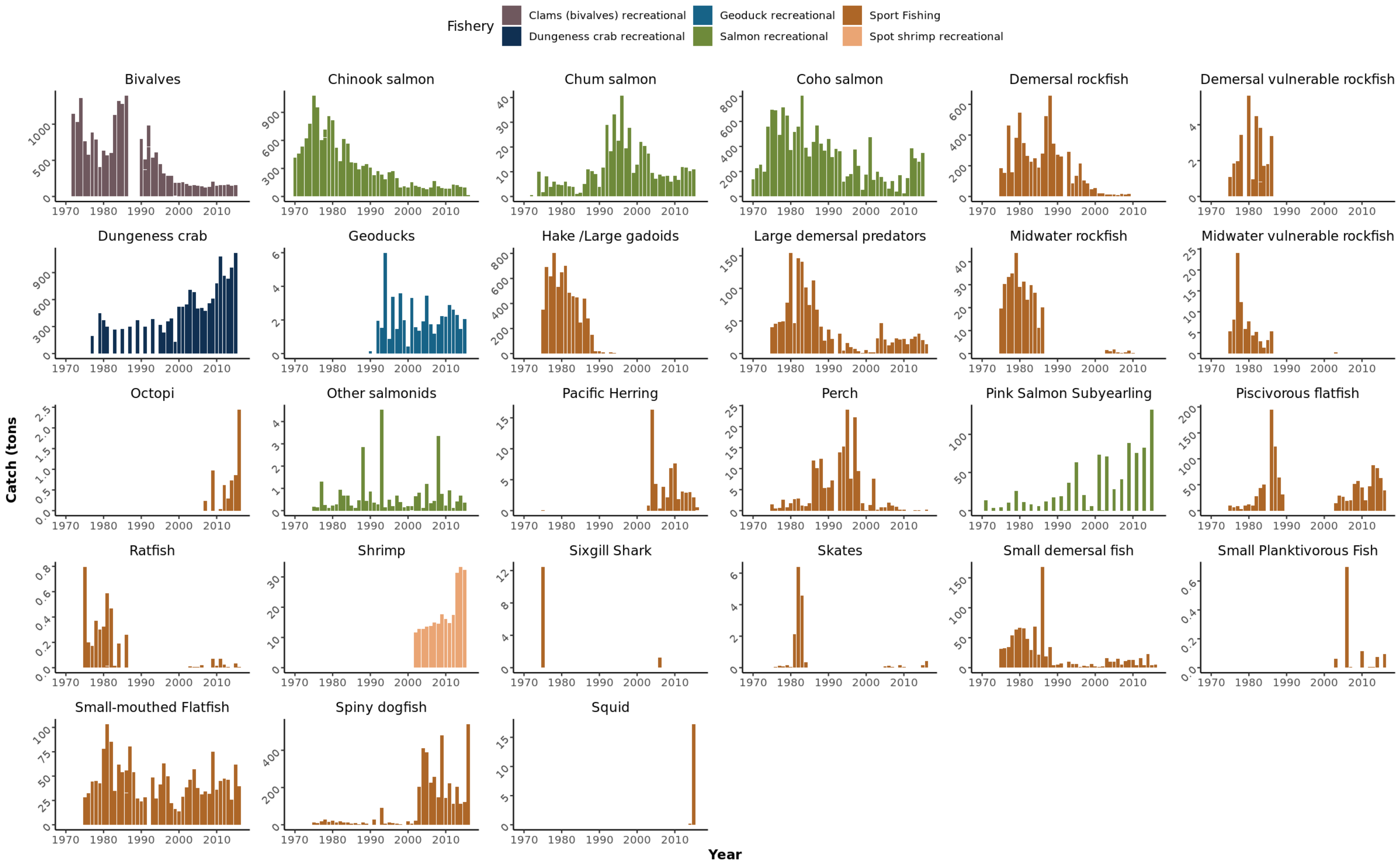

Figure 116. Recreational catch data (metric tons) for Puget Sound by Atlantis functional group and fishery, 1970–2015, estimated from WDFW data.

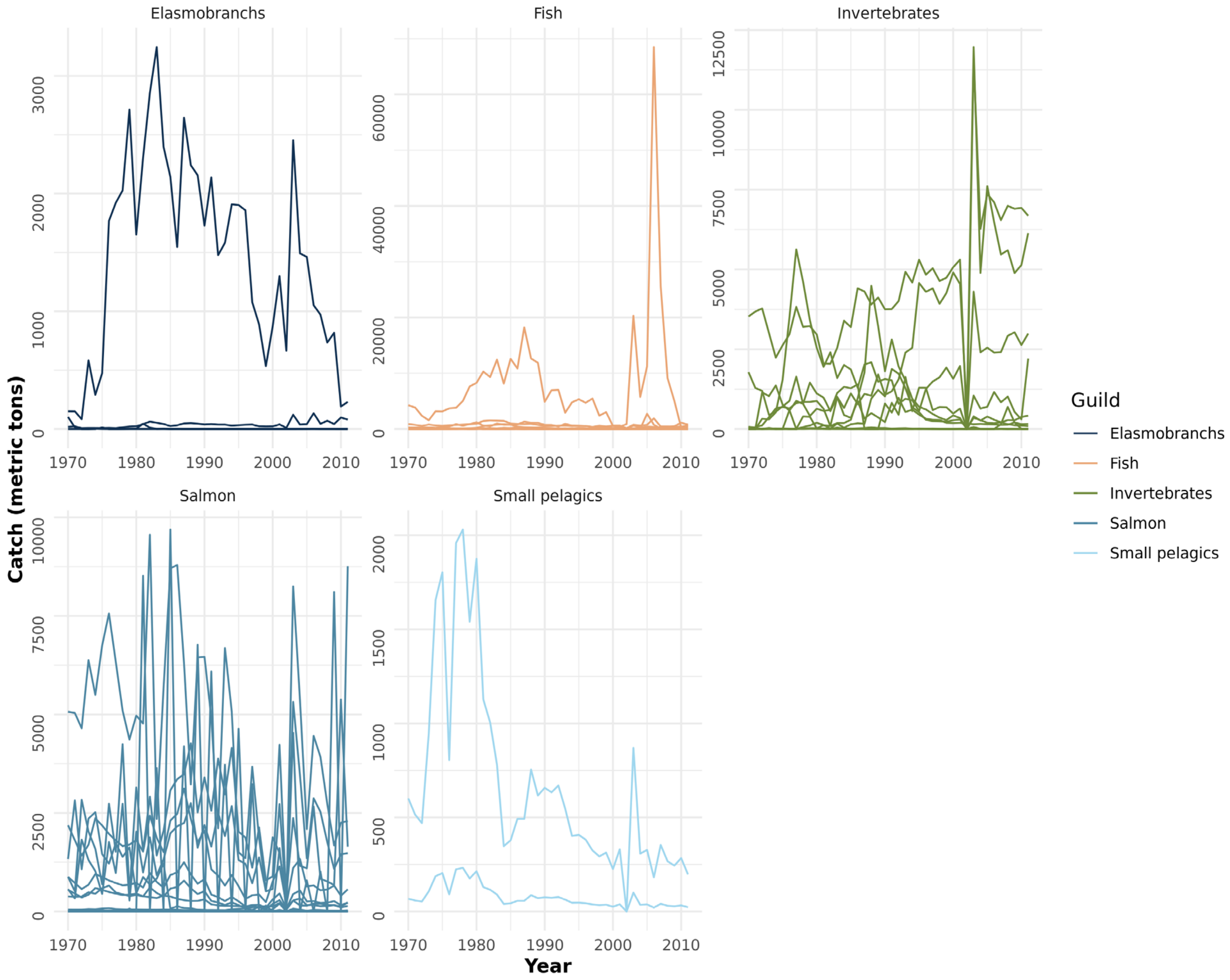

Figure 117. Reconstructed historical catch time series (metric tons) for Puget Sound by species guild, 1970–2011.

Spatial and Fleet Distribution of Landings

We produced an annual time series describing the seasonal landings from each model polygon. These data were used to create catch time-series files to force historical simulations in AMPS. We selected the fishing fleets represented in the model based on gears used. In total, we identified 59 fishing fleets (Table 13). We used the proportional allocations of PacFIN catch data for salmon, which are reported according to WDFW salmon management and catch reporting areas (Figure 118), to assign salmon catch throughout our model extent based on the overlap between AMPS polygons and WDFW areas. Catch reported in boundary polygons 0 and 17 was assigned to adjacent polygons 1 and 20, respectively. Records of catch data for species other than salmon in Puget Sound do not include the specific area; thus, for these species we spatially apportioned catch proportional to biomass (see Functional Group Descriptions). We used the temporal distribution of catch data in the PacFIN database, which is reported monthly, to assign data for the rest of the data sources.

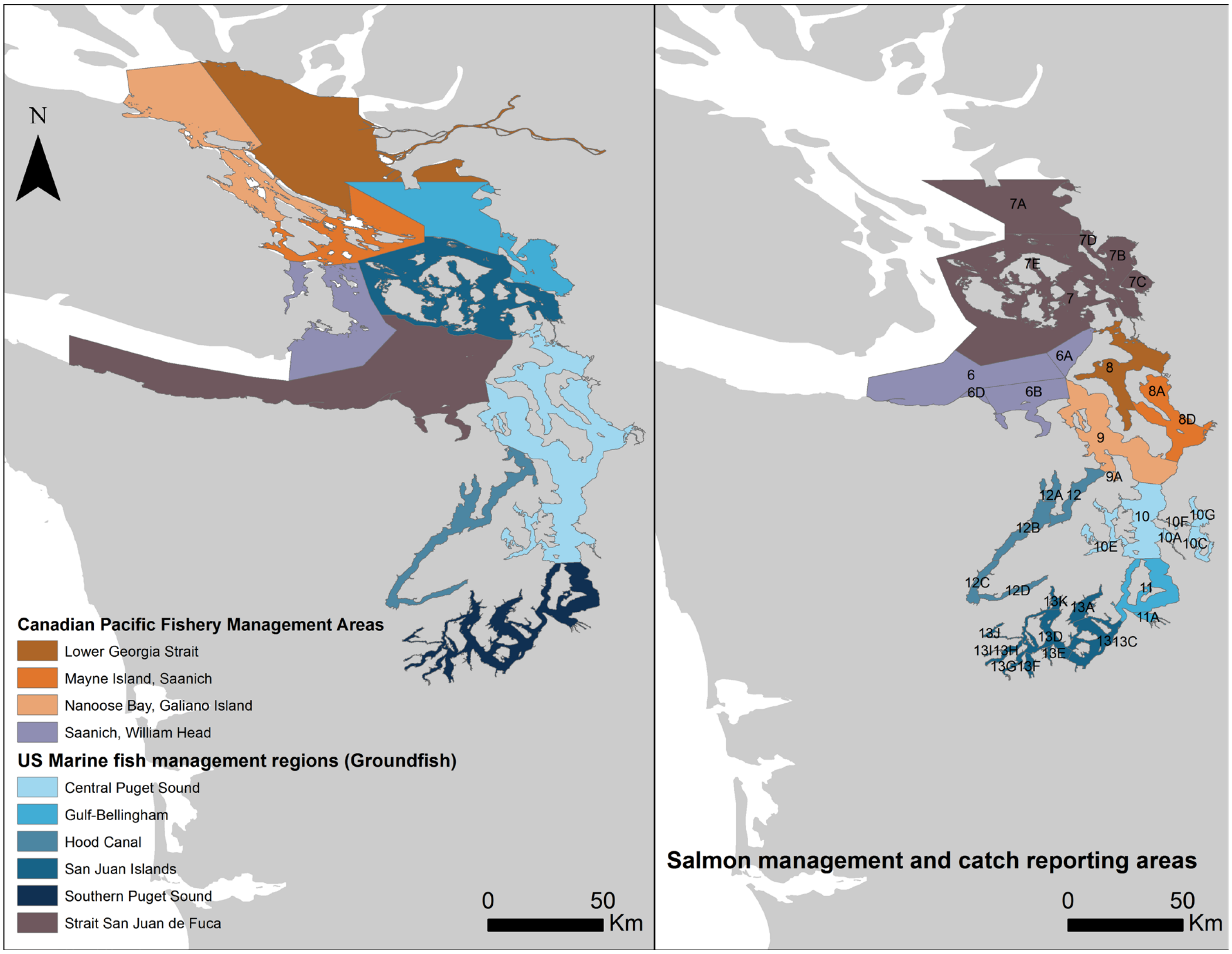

Figure 118. Fisheries management areas in the United States and Canada.

For forward simulations, we estimated a constant fishing mortality rate based on the average catch for all fleets between 2009 and 2018. Thus, we only considered catch for 25 fishing fleets in forward simulations of the model (Figure 119). Average catch of sixgill sharks from 2016 to 2019 was higher than estimated biomass; given that the biomass of sixgill sharks in Puget Sound is extremely patchy, we scaled catch based on the assumption that fishing mortality is 1% of biomass. Spatial distribution of catch in 2011 is shown in Figure 120.

Fishing Restrictions

The current version of the model includes fishing restrictions included in marine protected areas (MPAs). We also applied existing nonspatial fishing restrictions on recreational fishing to the constant fishing mortality vector, as indicated in WDFW's fishing regulations,[26] including:

1. It is prohibited to land yelloweye rockfish into any port in Washington.
2. Closed to fishing for, retention of, or possession of sixgill, sevengill, and thresher sharks.
3. Open only to food fish, forage fish, halibut, bottomfish, common carp, shad, tuna, mackerel, salmon, and sturgeon.

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[26] https://wdfw.wa.gov/fishing/regulations

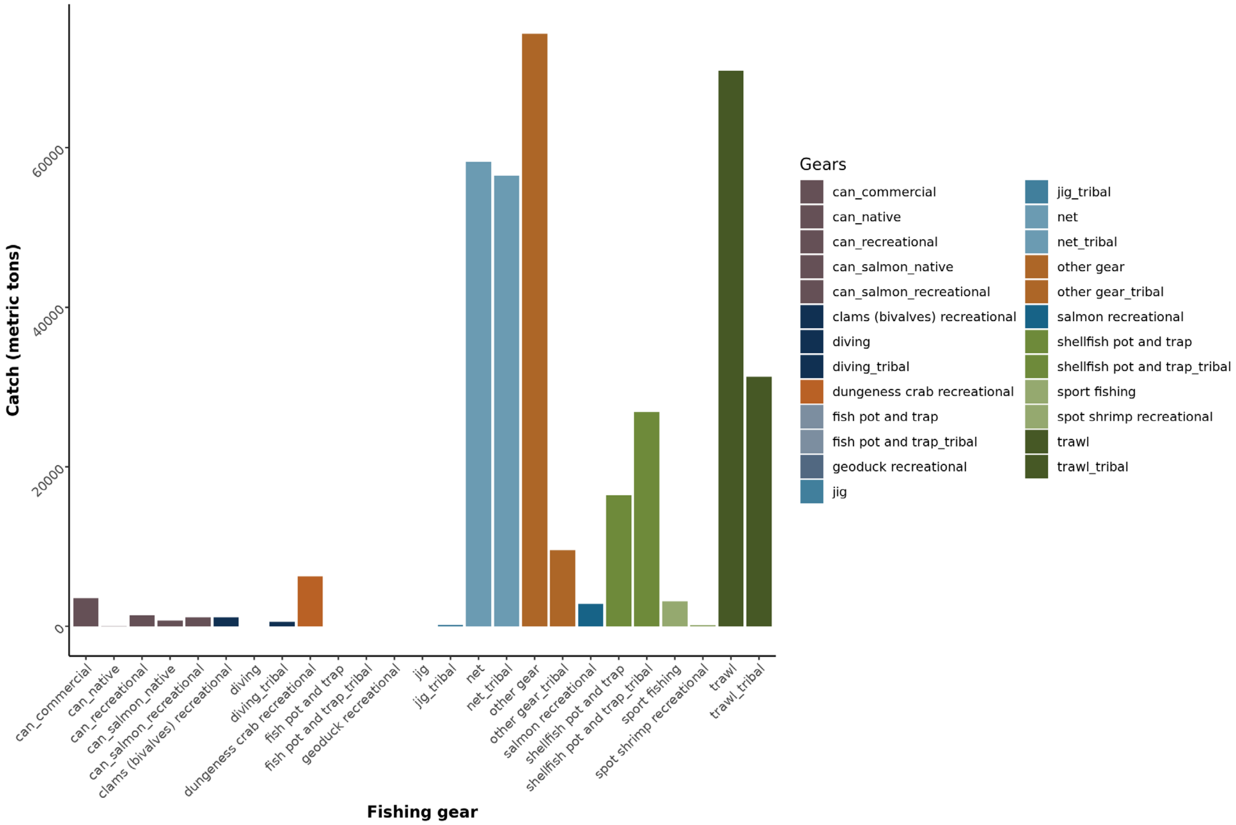

Figure 119. Catch (metric tons) by fishing gear from Puget Sound, 2009–19. Sources in text.

Additional fishing restrictions for Washington, as summarized in the Washington Administrative Code (WAC),[27] and for Canadian waters,[28] will be included in subsequent model refinements.

Marine protected areas in Puget Sound

The fishing effort of the fishing fleets defined in AMPS is limited by the spatial restrictions within marine protected areas in Puget Sound (Figure 121, Table 14). There are 110 officially designated MPAs in Puget Sound, covering 1,483 km^2 and almost 966 km of shoreline (Osterberg et al. 2012). We consider MPAs that overlap with the model domain and where fishing is prohibited or restricted, which includes 44 MPAs declared between 1915 and 2002.

We obtained information on fishing restrictions for each fleet (MCI 2019, WDFW 2019). The MPAs considered include no-fishing areas declared by WDFW to improve fish populations and protect habitat and aquatic reserves (specifically, Smith and Miner Islands and Maury Island Aquatic Reserves, declared by the Washington Department of Natural Resources), to regulate bottomland leasing in critical areas in order to improve marine habitat conditions (Christie et al. 2014). Members of Treaty Tribes are not bound by state or local MPAs or other WDFW fishing regulations, but many MPAs have been included in tribal–state management plans and are closed to harvest by individual tribes as part of conservative management policies (Osterberg et al. 2012, WDFW 2019).

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[27] https://app.leg.wa.gov/WAC/default.aspx?cite=220

[28] http://www.pac.dfo-mpo.gc.ca/fm-gp/maps-cartes/salmon-saumon/index-eng.html

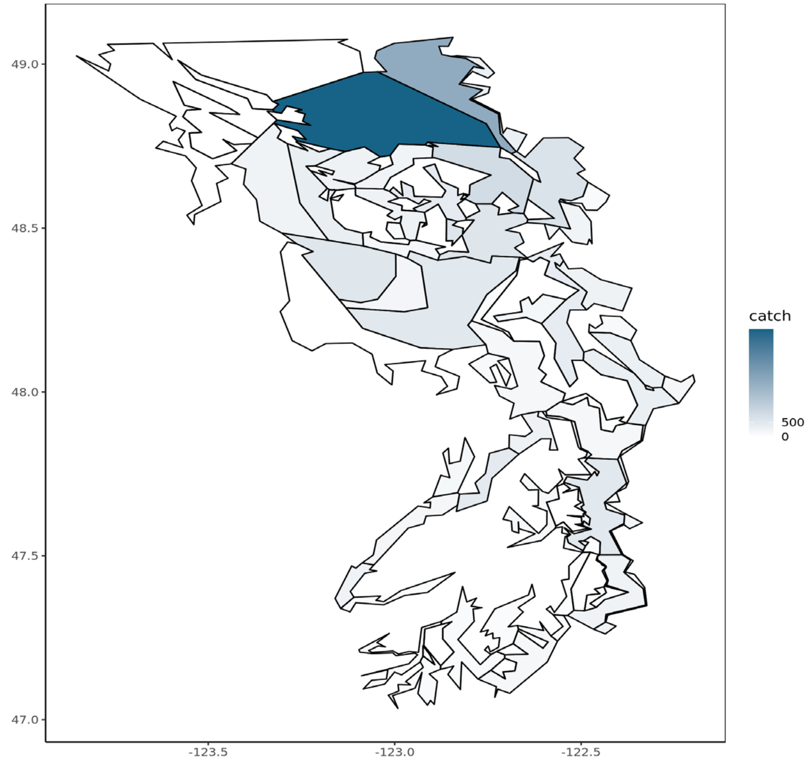

Figure 120. Commercial catch data (metric tons) by Atlantis polygon in 2011.

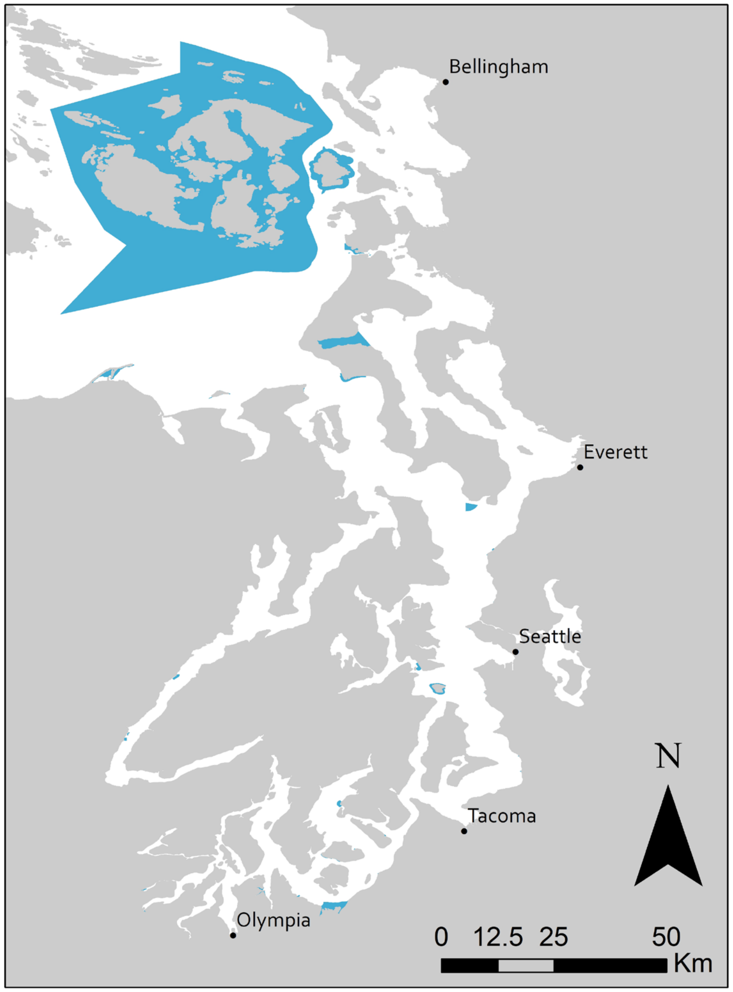

Figure 121. Marine protected areas in Puget Sound, where fishing is prohibited or restricted.

Model Tuning and Diagnostics

We used an iterative process to tune or calibrate the model, adjusting parameters to yield stable ecological dynamics and fit historical observations (Kaplan and Marshall 2016). This approach involved adjusting the most uncertain parameters (e.g., predator–prey interaction rates) to recreate observed patterns (e.g., weight-at-age from observational data). This type of qualitative parameter adjustment is labor-intensive, but gives the modeler a strong understanding of the key parameters and sensitivities in the model. Atlantis does not use automated optimization algorithms to estimate parameters within the model.

We calibrated the dynamic behavior of AMPS in two phases. First, we initialized the model with 2011 estimates of biomass and ran the model forward 30 years without fishing. In the absence of fishing, we assumed that the system should return to a condition similar to its state prior to major commercial exploitation. Our goal in this phase was to produce unfished biomass by functional groups through time and ensure that groups did not go extinct. We aimed for vertebrate structural and reserve *N* (weight-at-age) to be within 0.5 and 1.5 times their initial values. For primary producers and invertebrates, our goal was to keep these groups from extinction; these groups are highly sensitive to changes in parameterization of seemingly unrelated groups. We adjusted recruitment and mortality parameters, including maximum growth rates (*mum*), Beverton–Holt recruitment parameters for fish groups, and quadratic mortality, a density-dependent control. We initially also adjusted recruit weights (parameters *KWRR* and *KWSR* for reserve and structural weight, respectively) to tune vertebrate weights-at-age. We expected that vertebrate densities would maintain an age structure with a general pattern of exponential decline in abundance with age; when this did not occur, we increased the species predation availability and quadratic mortality. We minimized the use of linear mortality, which is density-independent and represents death from disease, senescence, or other mortality sources not explicitly modeled.

In the second calibration phase, we evaluated the model's ability to withstand historical fishing rates based on reconstructed time series (see Catch Reconstruction). During these runs, we initialized the model with 2011 biomass and let it equilibrate for 30 years (spin-up period) to achieve a pseudo-unfished condition that represents the period prior to 1970 (this state is called the "historical model"). We then forced the model using the historical time-series catch data from 1970 to 2011, and compared biomass output to available reconstructed historical biomass data for salmon (Figure 122; Losee et al. 2019) and groundfish (Figure 123; Essington et al. 2021). The salmon historical reconstruction includes adult biomass in Puget Sound to the Strait of Juan de Fuca and only considers Washington State-origin stocks. (Note that Puget Sound pink salmon runs are primarily in odd years, so we do not have biomass estimates for even years.). Once the second calibration phase was completed, the final model parameters were used to test ecological and management hypotheses (this state is the present-day model that will be initialized in 2011).

Finally, we developed catch and biomass equilibrium graphs, a diagnostic tool that can provide information on the production potential of fished stocks and their resilience. We forced the model with varying degrees of fishing pressure, based on a constant mortality rate (parameter *mFC*) on all fished groups, by fishing fleet (as in Figure 118), over a 30-year simulation. We increased fishing mortality stepwise from 0 to 0.95/yr.

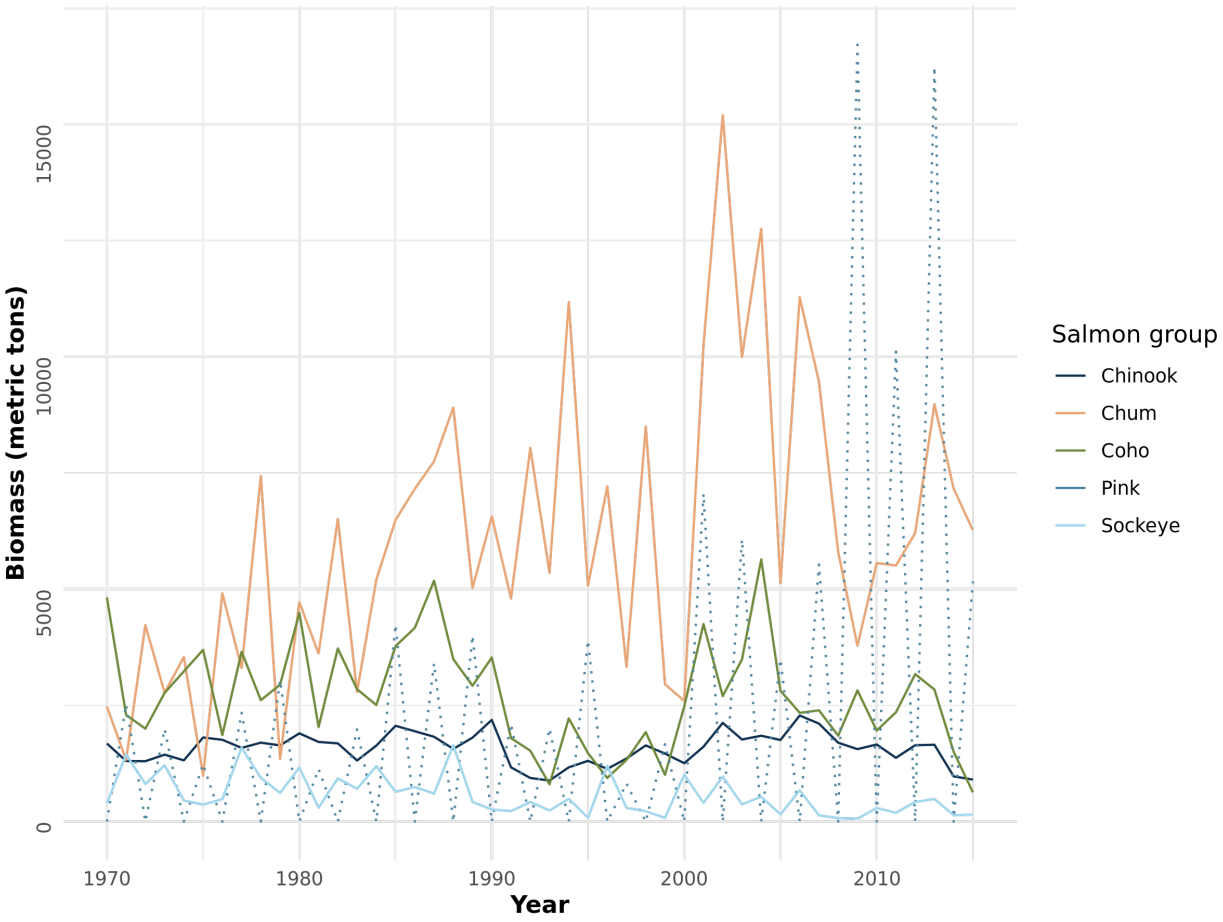

Figure 122. Reconstructed salmon abundance by species, including wild and hatchery fish from Losee et al. (2019). Pink salmon are indicated with a dotted line.

Model Performance

Initial calibration: No fishing

Results from the initial calibration with no fishing are presented in Figures 122 to 126. Note that the first 10 years of the simulation are spin-up years, when many populations increase without fishing. Population age structures and other dynamics stabilize as they evolve from model initial conditions. We, therefore, focus our description mostly on simulation years 10–30. Salmon life histories and dynamics, for instance, tend to illustrate strong spikes in biomass during the first 10 years. Though most salmon group biomasses stabilized after that period, overall, the salmonids were very challenging to parameterize and tune. The complex anadromous life cycle made it more difficult to achieve reasonable recruitment and age-structure behavior. Salmon functional groups in the model are very sensitive to herring population dynamics, reflecting the tight trophic coupling between these groups and underscoring how changes in herring groups in Puget Sound are a key driver of food web dynamics (Essington et al. 2021).

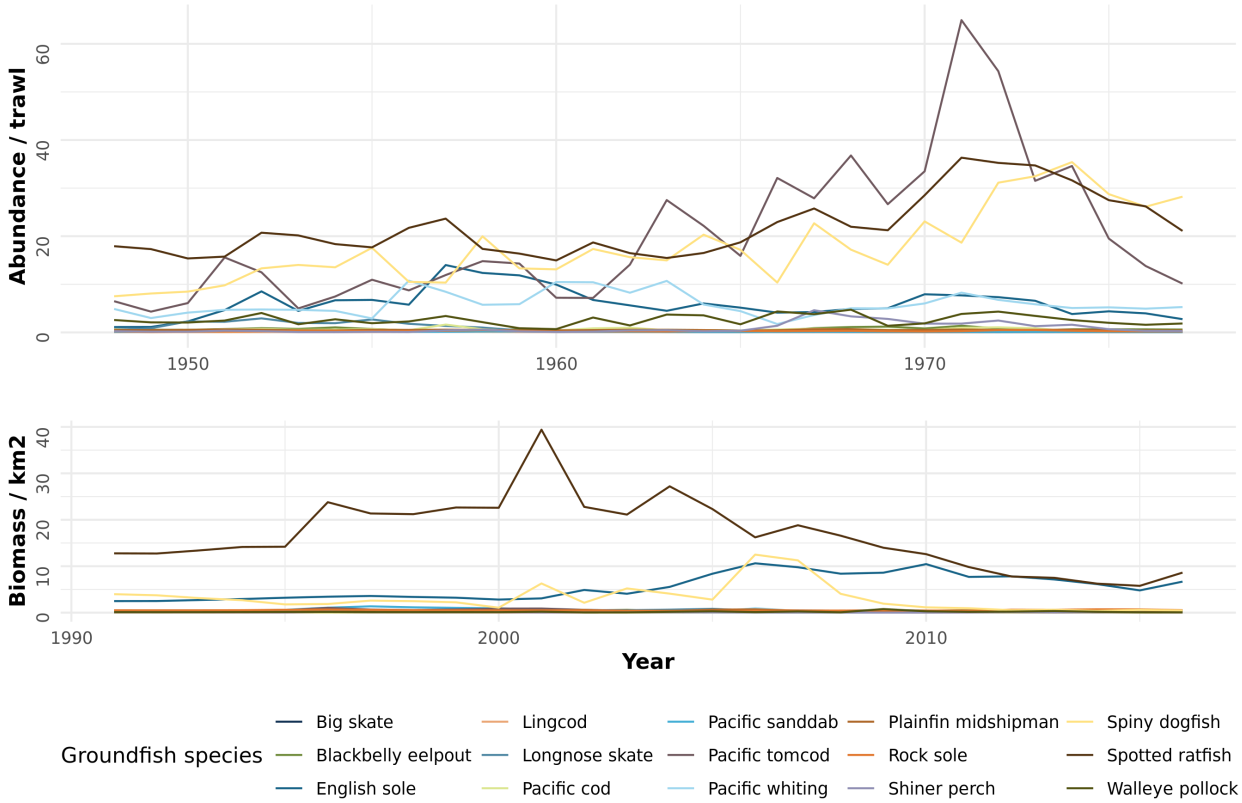

Figure 123. Reconstructed groundfish trajectories, by species (Essington et al. 2021), for (top) historical (1948–77, as abundance/trawl) and (bottom) contemporary (1991–2016, as biomass/km^2).

Our goal for vertebrates in the initial tuning phase was to keep groups from going extinct and to achieve stable biomass through time (Figure 124). Most functional groups show strong yearly and seasonal oscillation, primarily generated by the dynamic of the underlying oceanographic forcing. A few groups—including deep macrozoobenthos, seagrass, and carnivorous infauna—maintain an equilibrium biomass close to their initial values. A few groups decrease over the simulation; for instance, large zooplankton biomass reduces to low levels shortly after the start of the simulation. Carrion detritus degrades quickly into labile and refractory detritus. Piscivorous flatfish go extinct after year 20, despite calibration efforts to prevent this. Most groups showed steady or increasing biomass in response to a release from fishing pressure and trophic interactions.

In this calibration stage, we aimed for an optimal range for structural and reserve nitrogen (components of weight-at-age) to be between 0.8 and 1.2 times initial values. However, a broader range between 0.5 and 1.5 was also acceptable (Figures 125 and 126). A few groups, particularly salmon, show increased reserve nitrogen beyond this range, indicating overconsumption and higher growth. Individual weights-at-age (Figure 127) were generally stable; we did not expect them to be constant, because Atlantis allows differential growth based on time-varying consumption rates. The seabird groups performed poorly, exhibiting counterintuitive patterns in weight-at-age, with decreases as age classes increase. In general, the model did achieve vertebrate densities with a reasonable age structure, where numbers-at-age generally decreased with age class (Figure 128). Salmon functional groups show

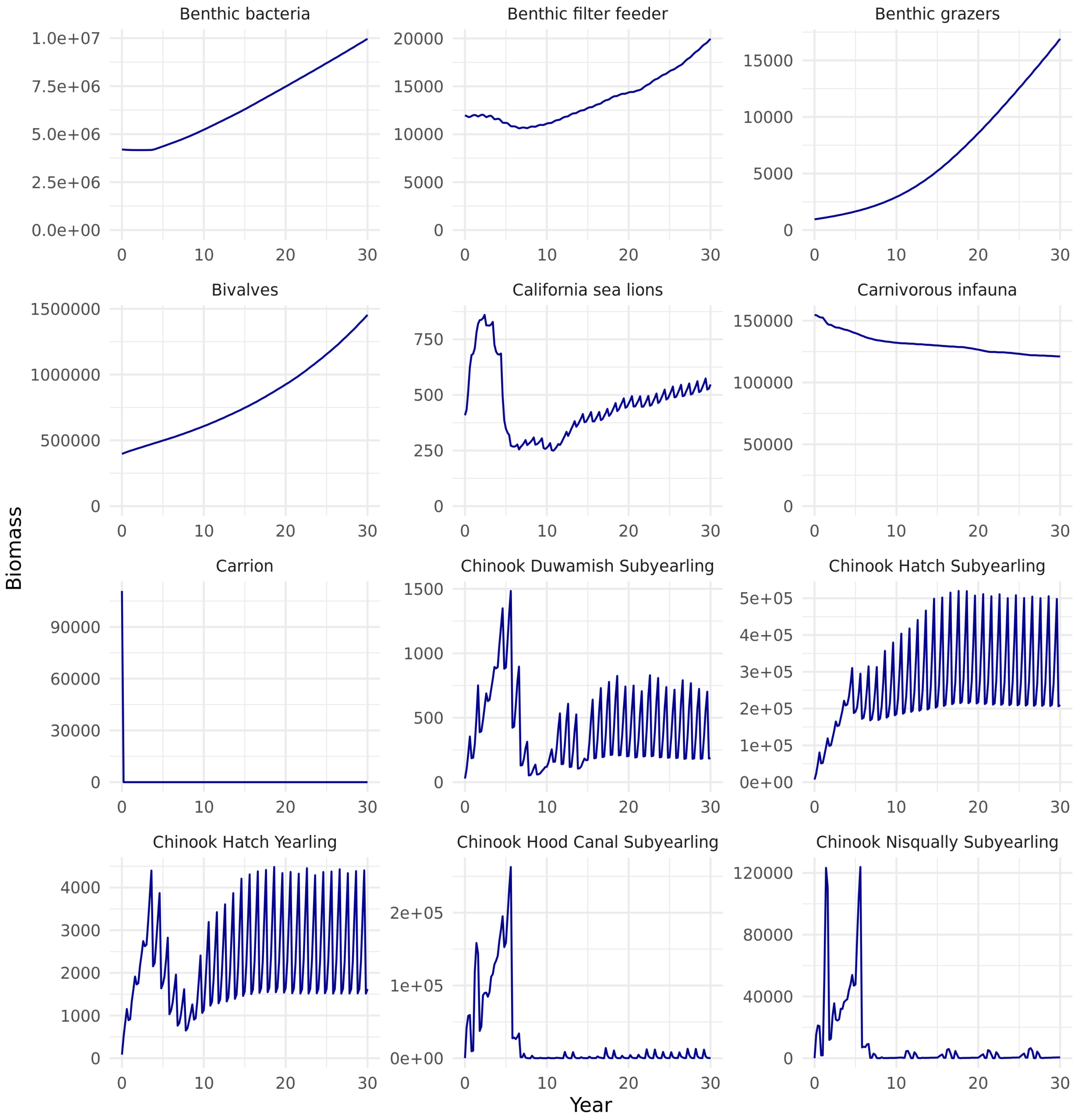

Figure 124. Biomass trajectories (metric tons) for functional groups in AMPS. Results are for 30-year simulations without fishing.

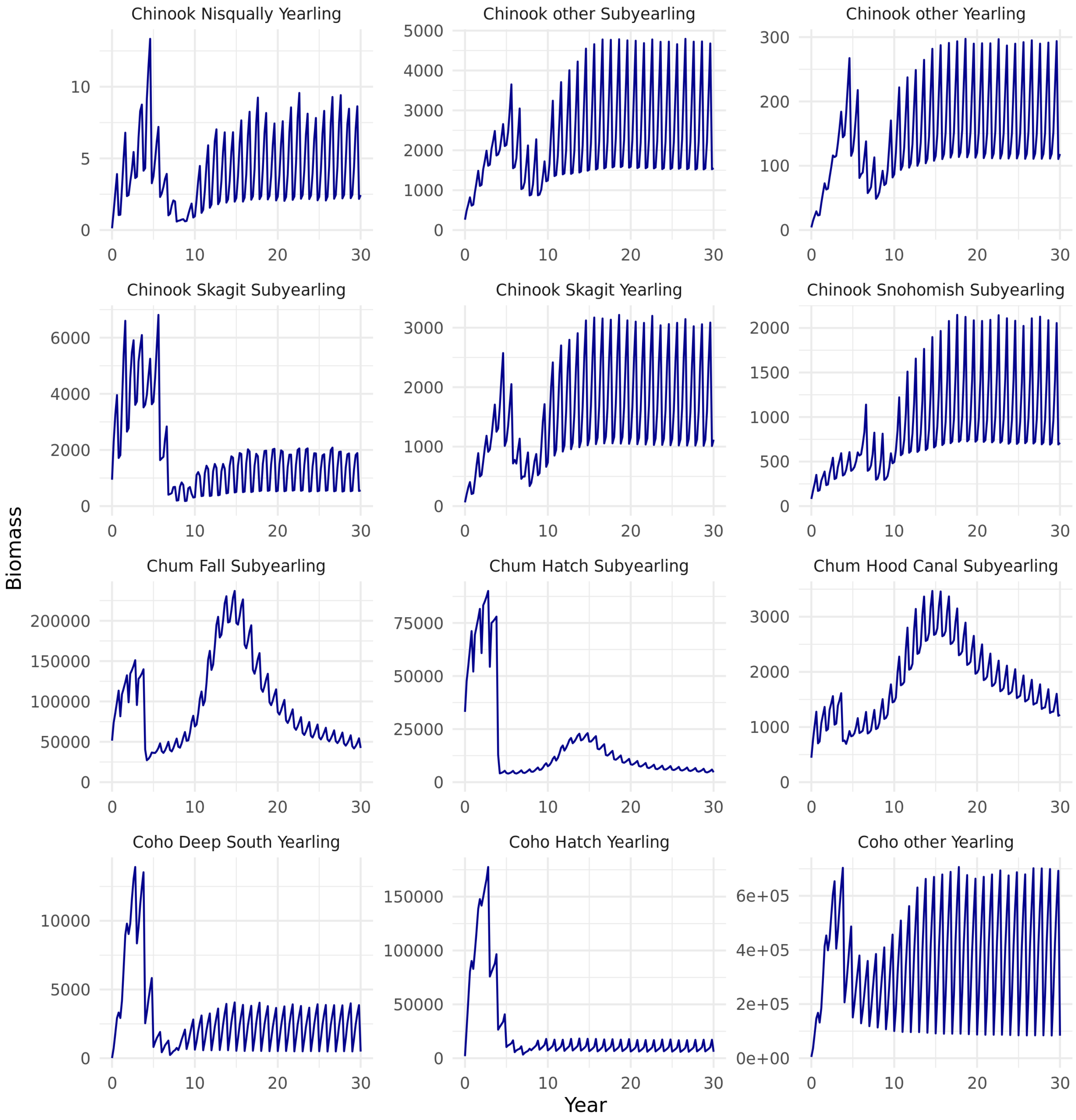

Figure 124 (continued). Biomass trajectories for functional groups in AMPS.

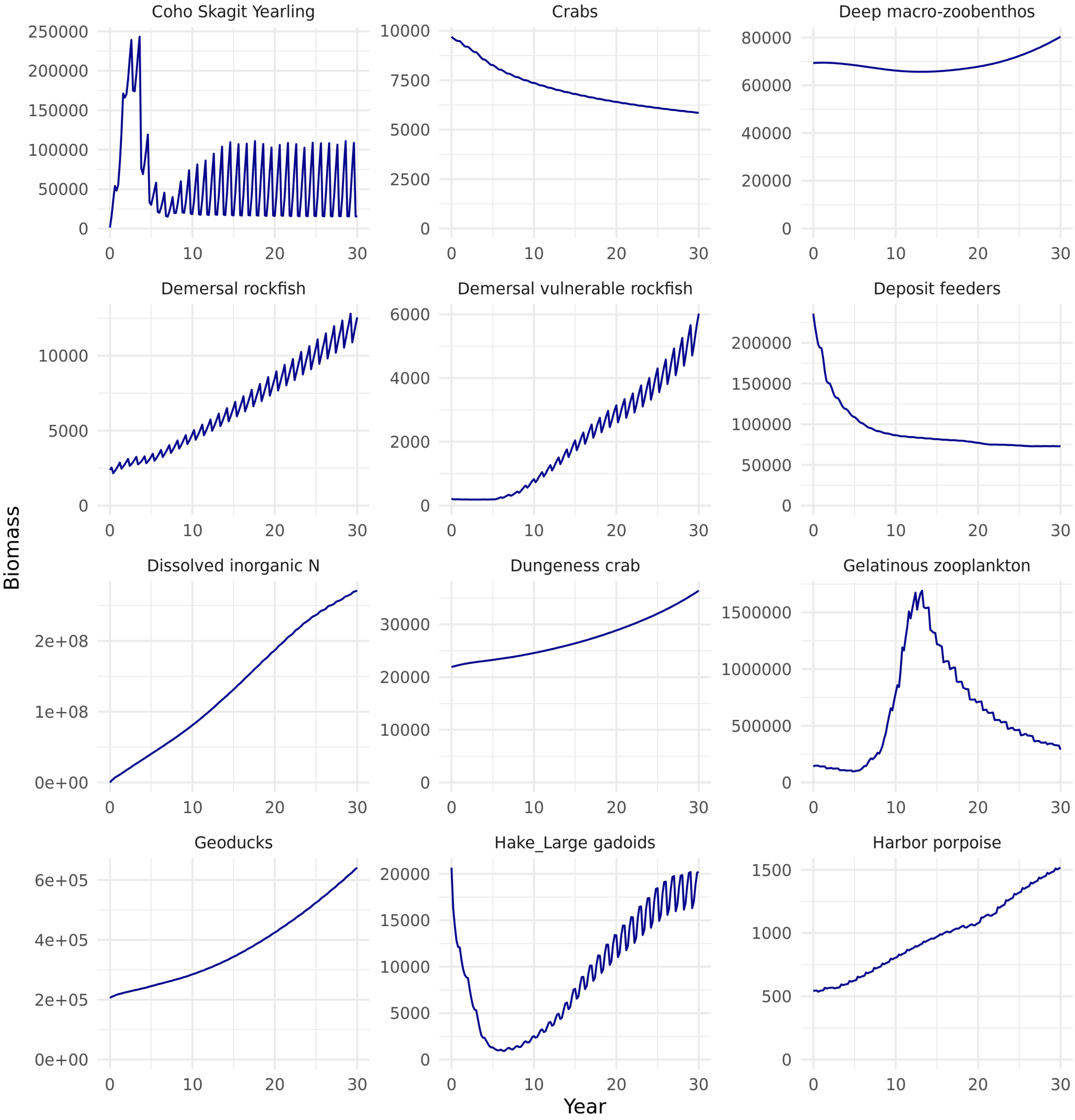

Figure 124 (continued). Biomass trajectories for functional groups in AMPS.

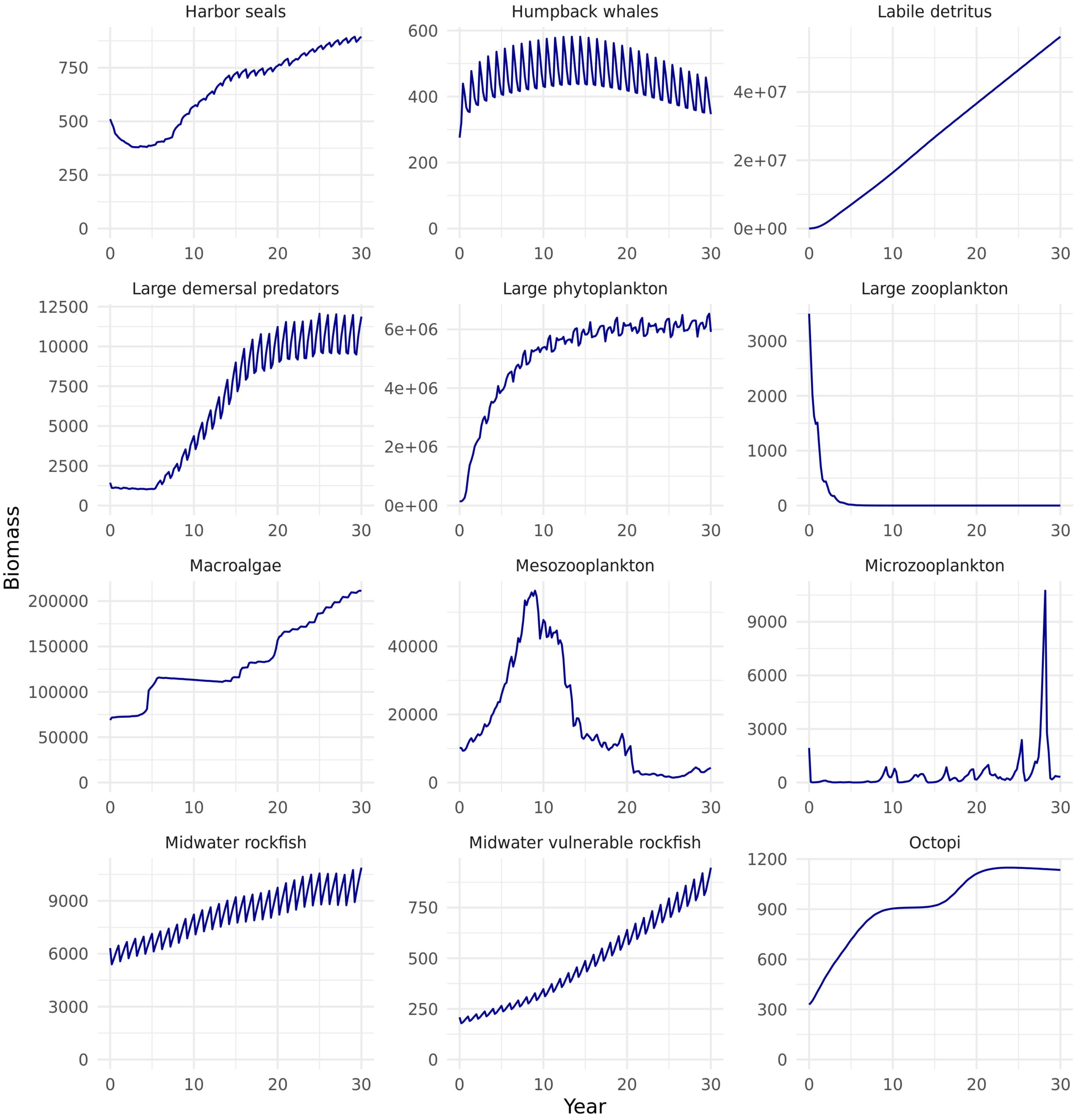

Figure 124 (continued). Biomass trajectories for functional groups in AMPS.

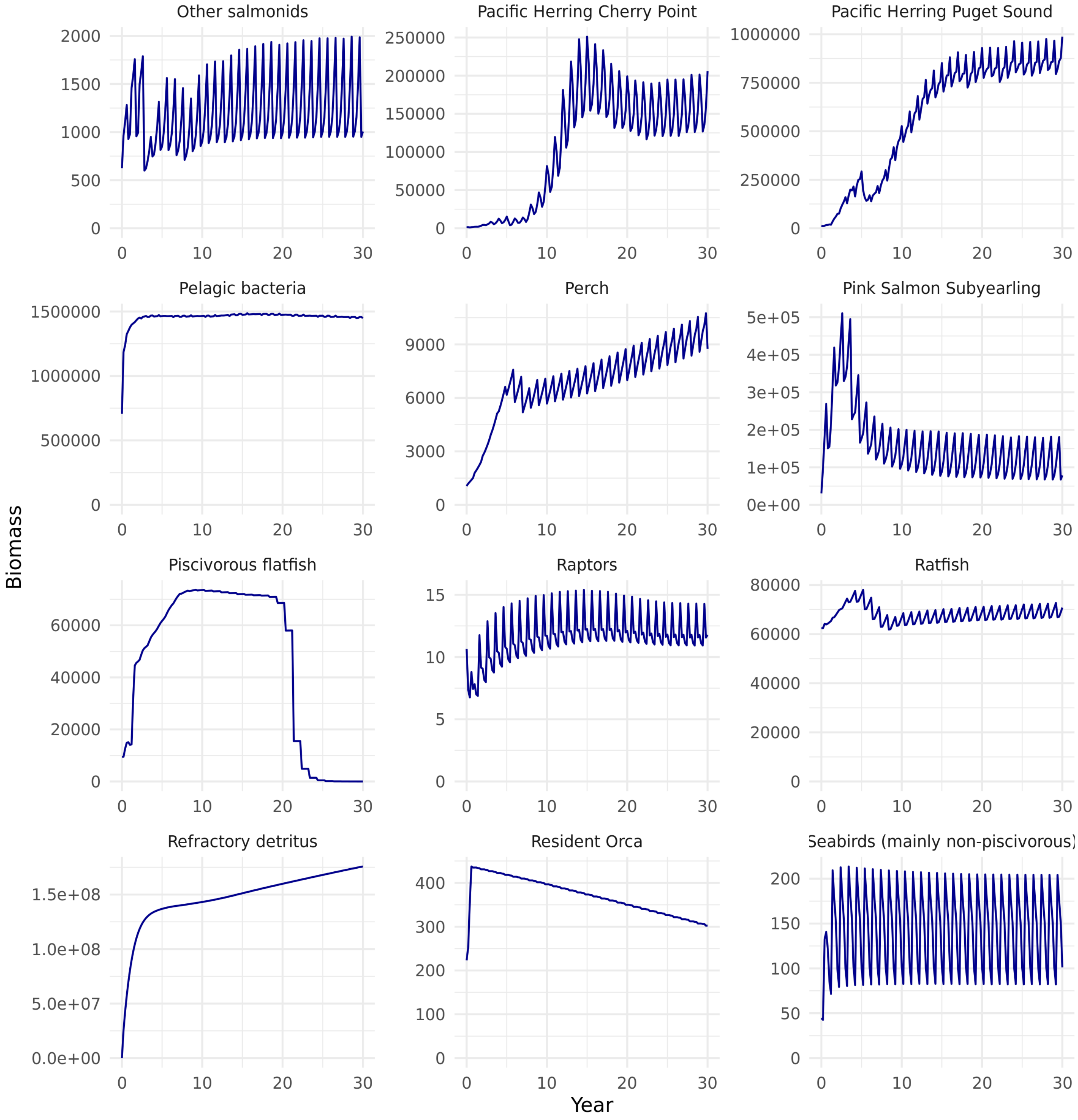

Figure 124 (continued). Biomass trajectories for functional groups in AMPS.

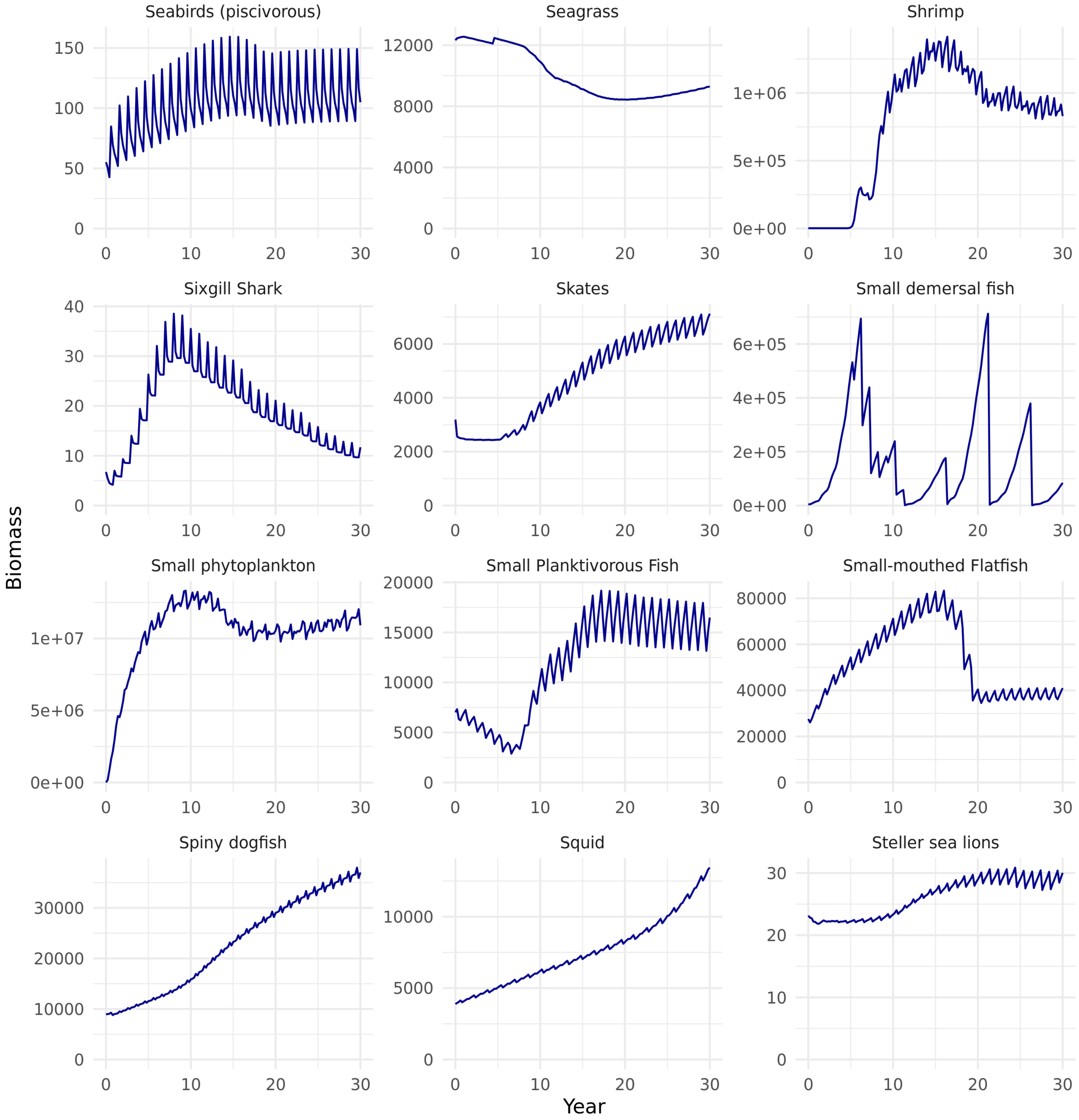

Figure 124 (continued). Biomass trajectories for functional groups in AMPS.

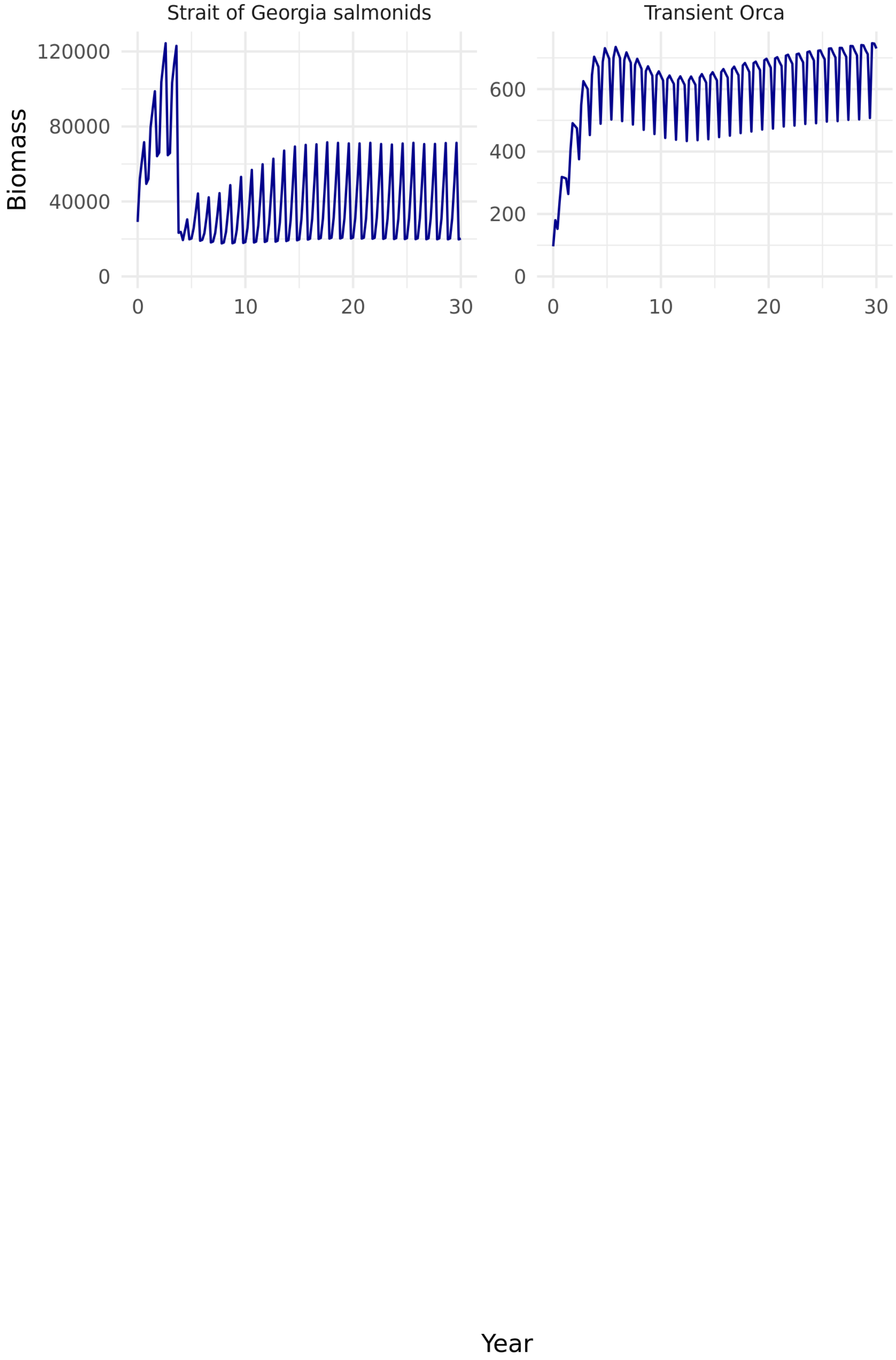

Figure 124 (continued). Biomass trajectories for functional groups in AMPS.

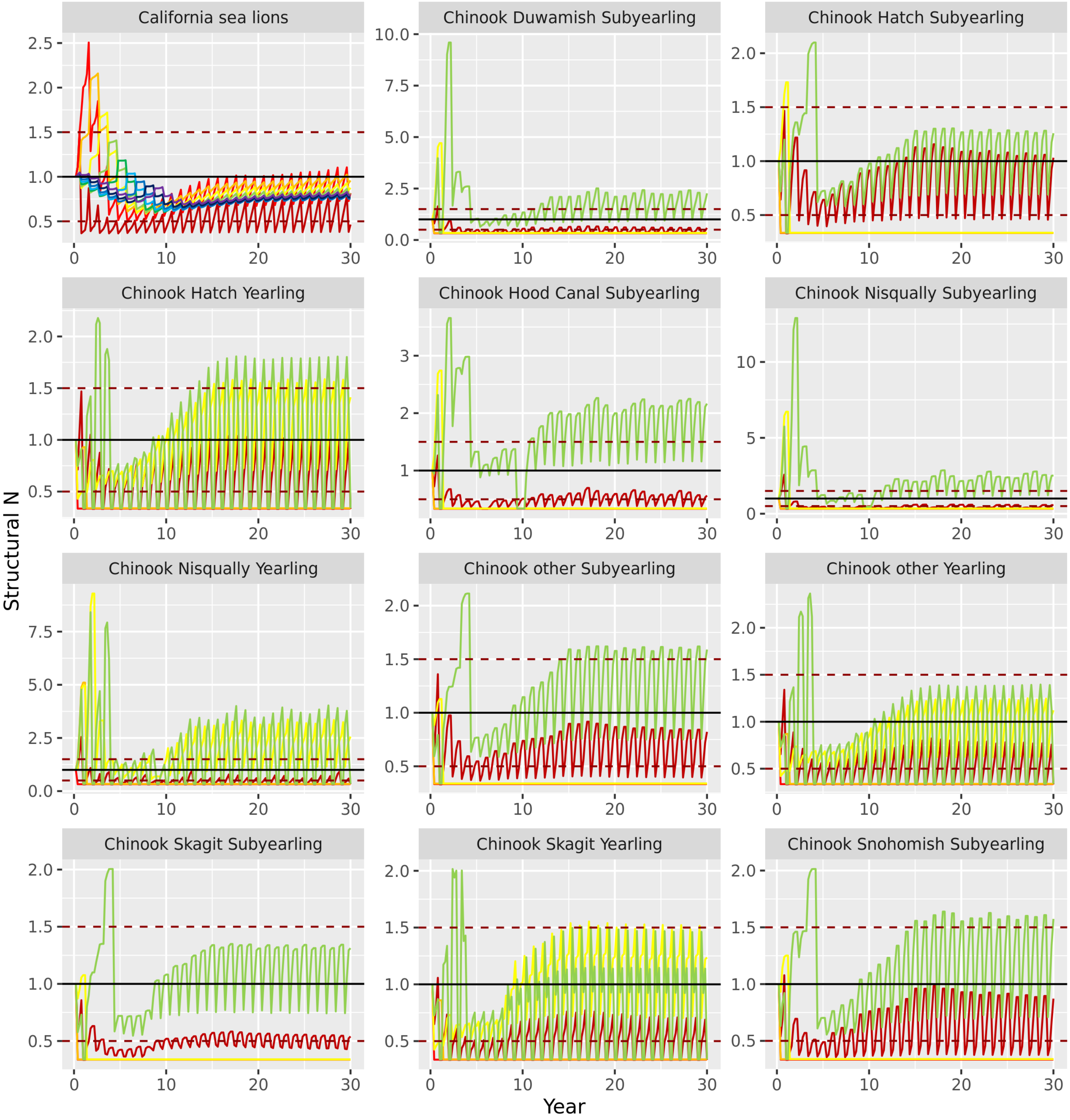

Figure 125. Trajectories for structural nitrogen for age-structured groups in AMPS. Colored lines are age classes. Results are relative to the start of 30-year simulations without fishing.

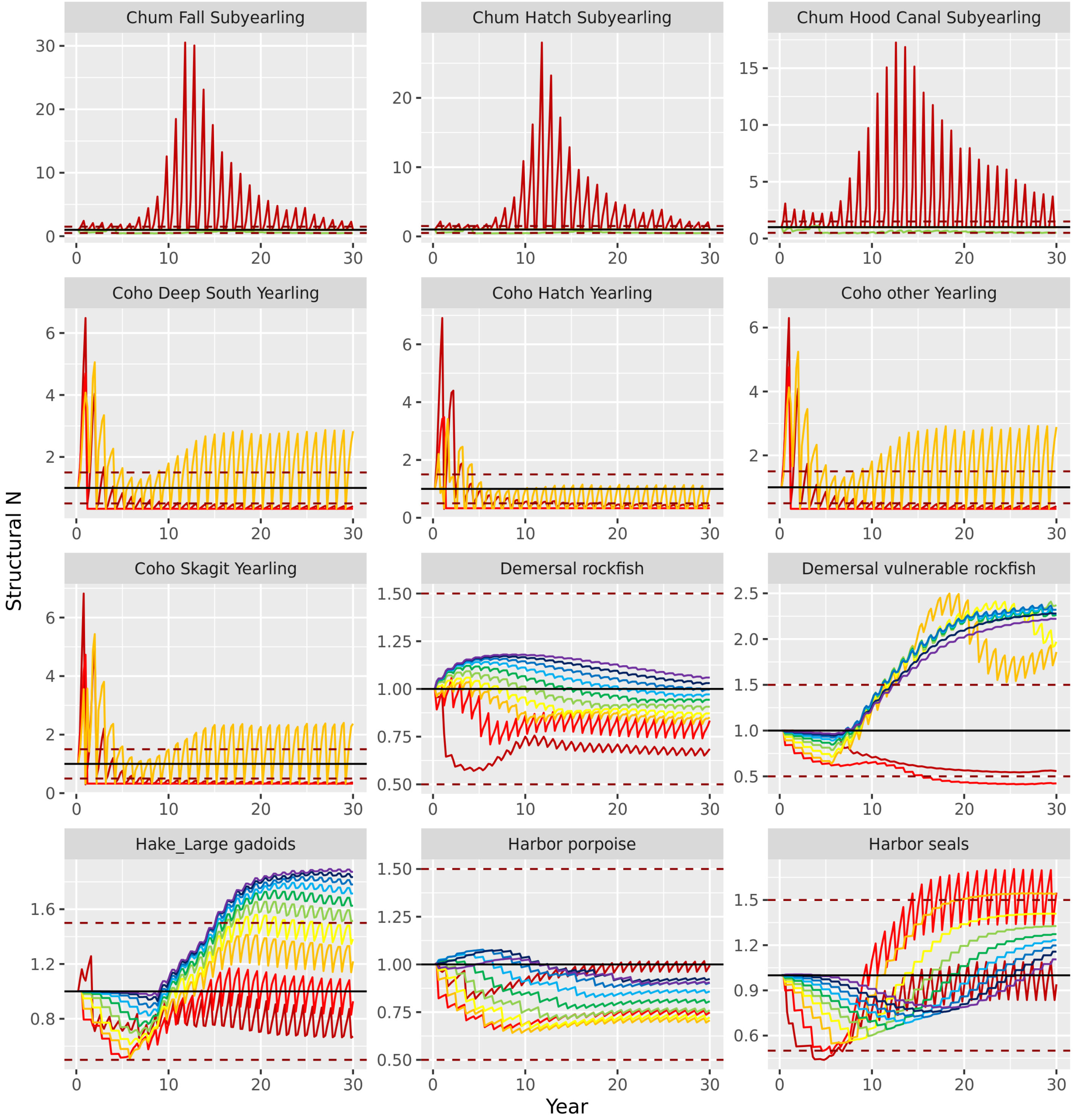

Figure 125 (continued). Trajectories for structural nitrogen for age-structured groups in AMPS.

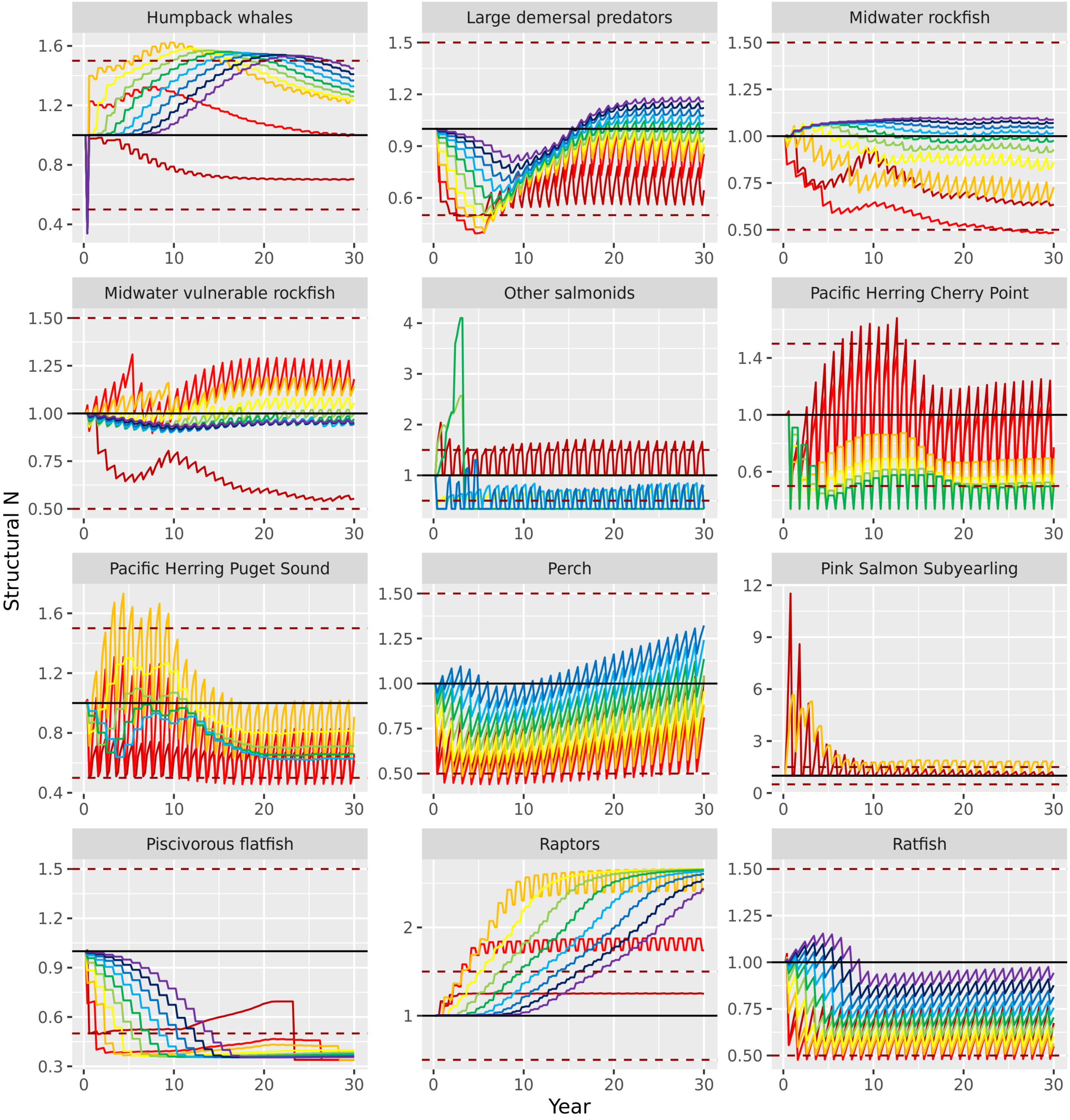

Figure 125 (continued). Trajectories for structural nitrogen for age-structured groups in AMPS.

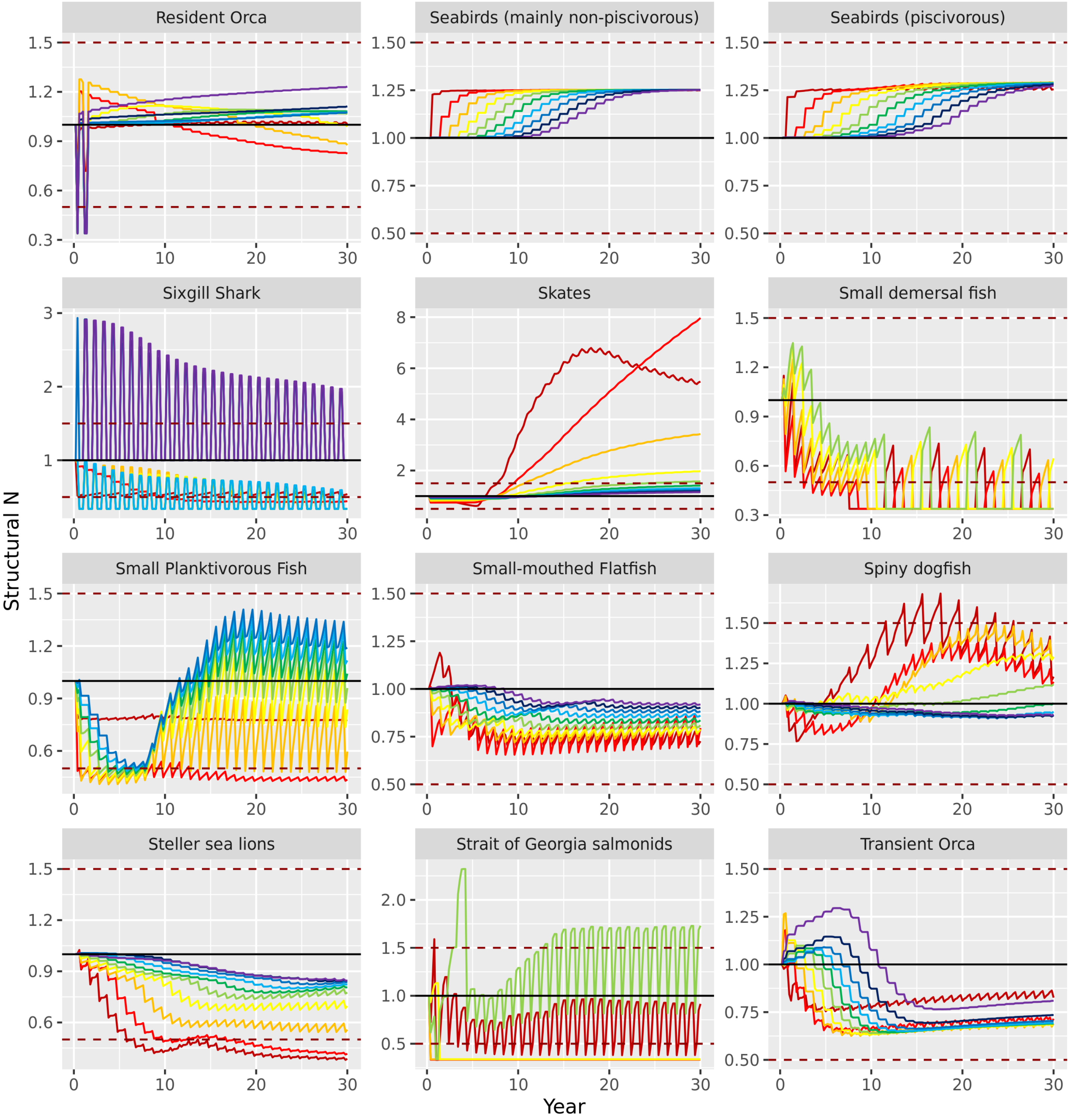

Figure 125 (continued). Trajectories for structural nitrogen for age-structured groups in AMPS.

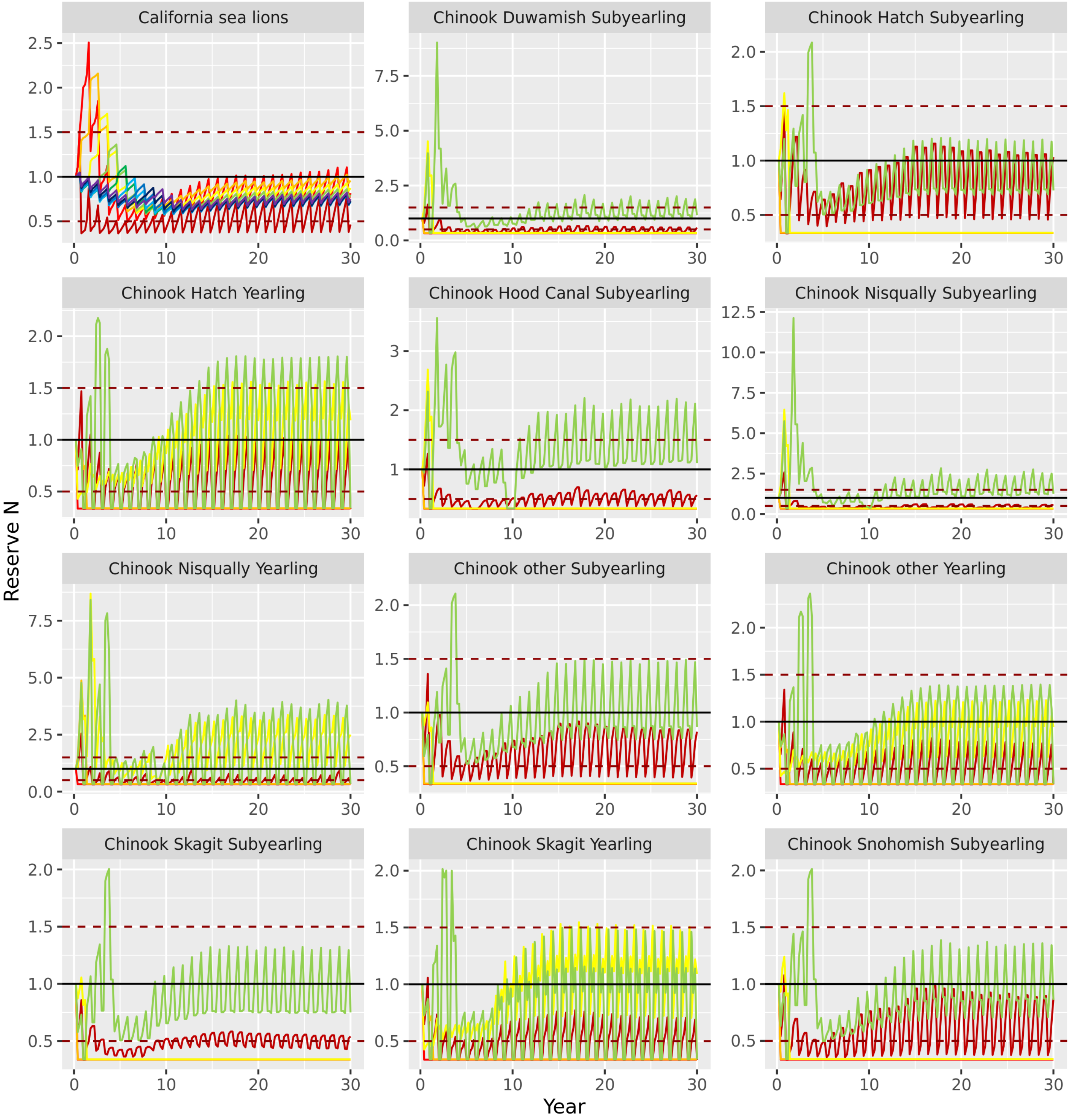

Figure 126. Trajectories for reserve nitrogen for age-structured groups in AMPS. Colored lines are age classes. Results are relative to the start of 30-year simulations without fishing.

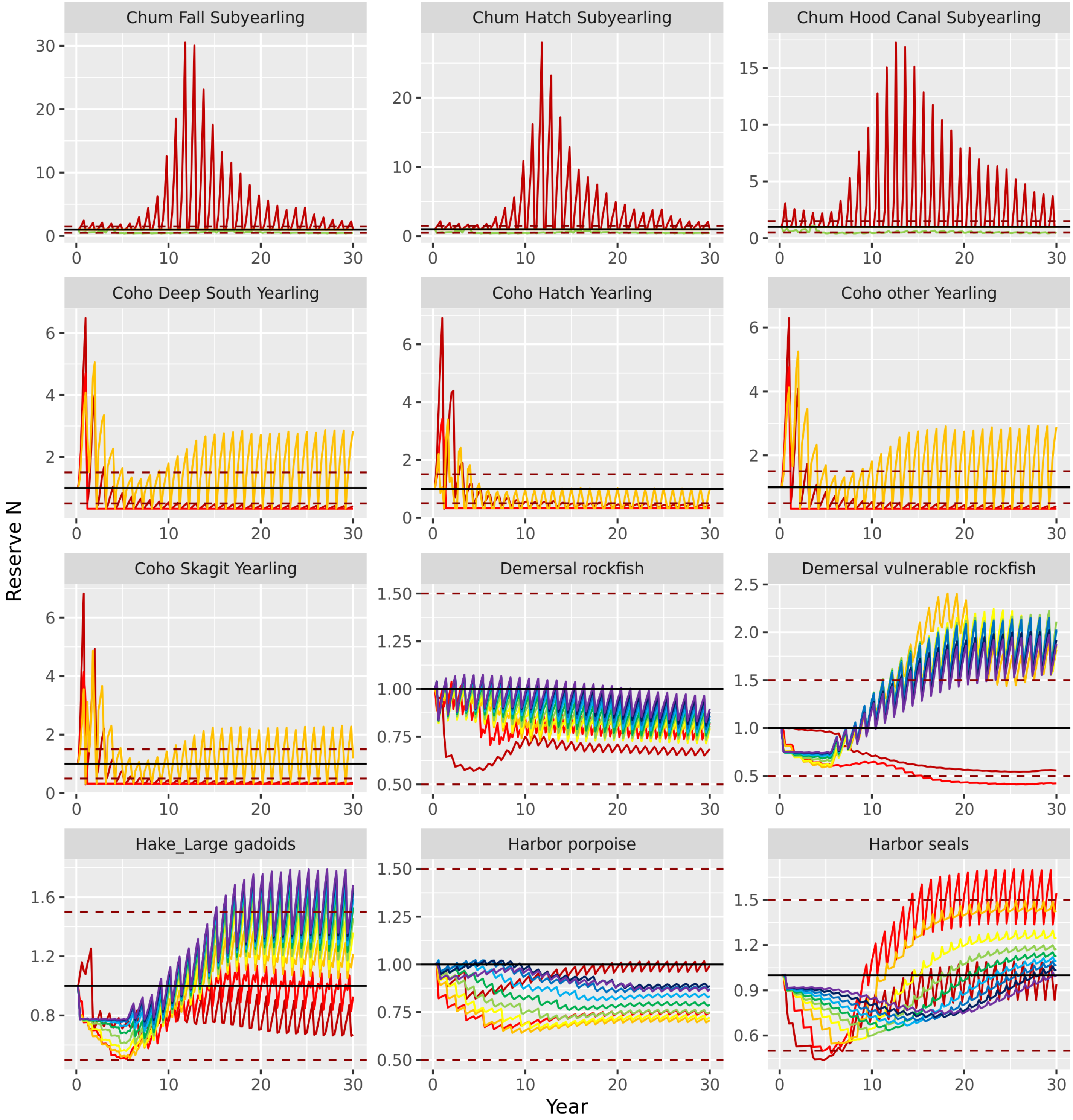

Figure 126 (continued). Trajectories for reserve nitrogen for age-structured groups in AMPS.

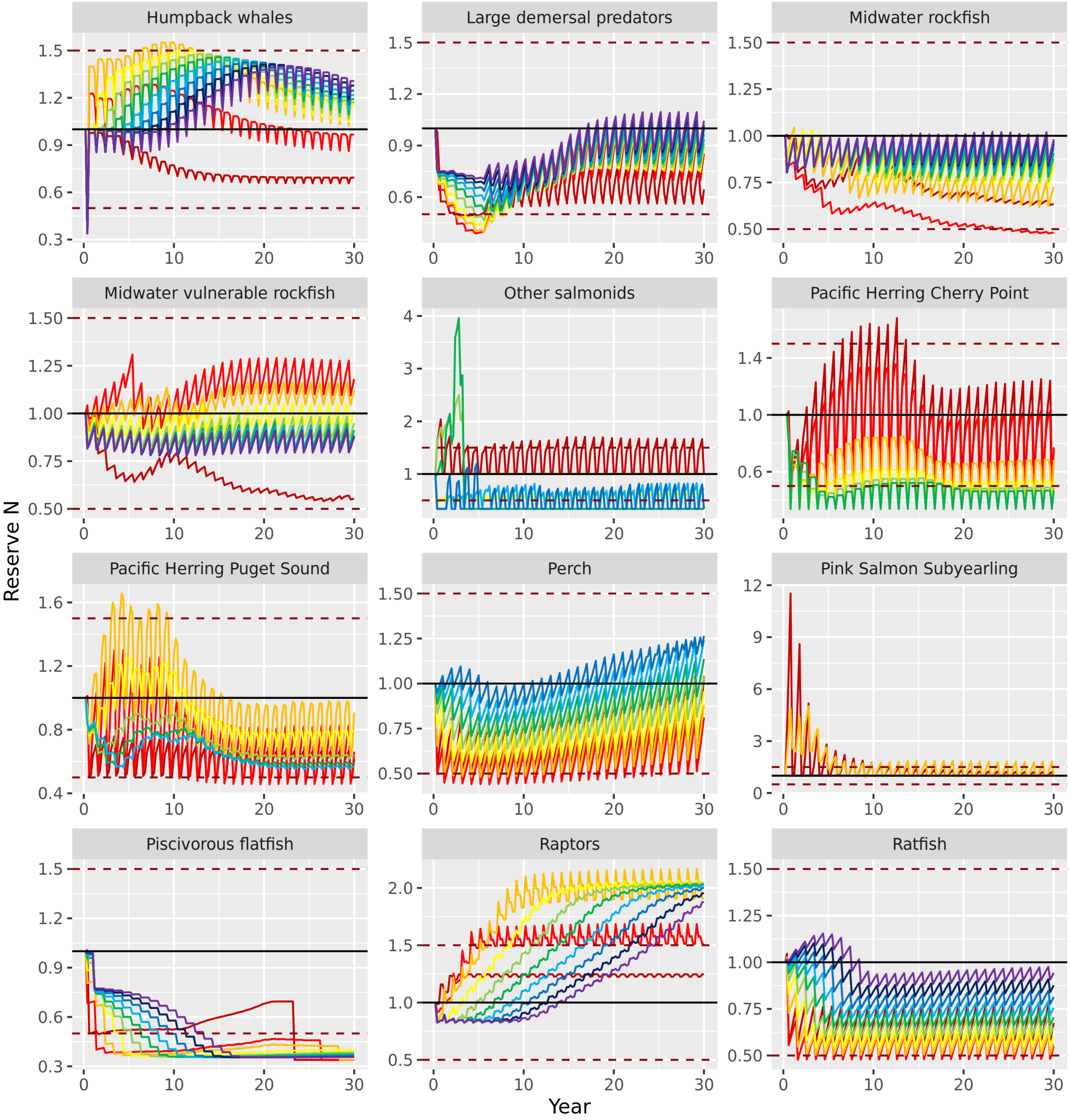

Figure 126 (continued). Trajectories for reserve nitrogen for age-structured groups in AMPS.

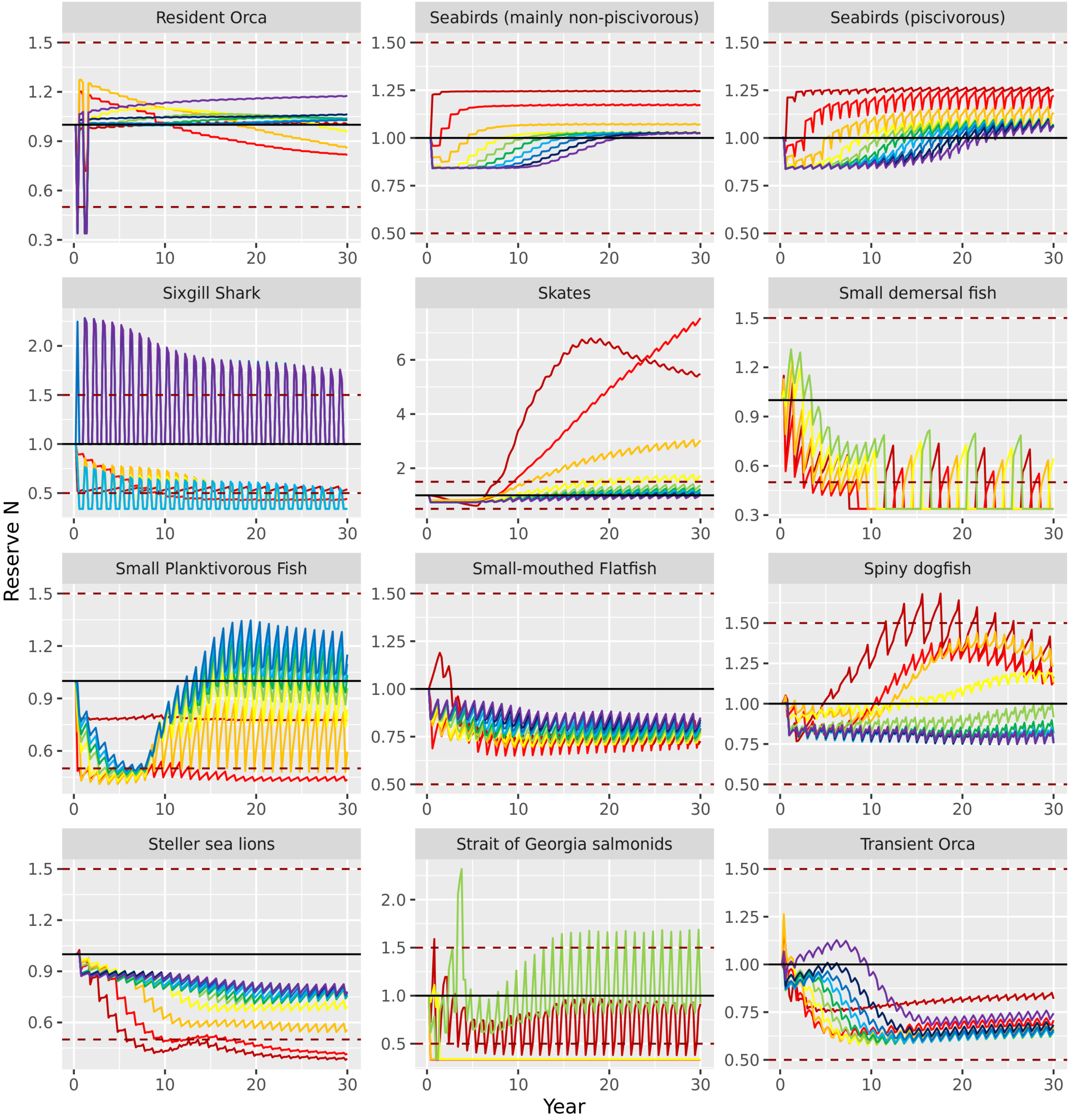

Figure 126 (continued). Trajectories for reserve nitrogen for age-structured groups in AMPS.

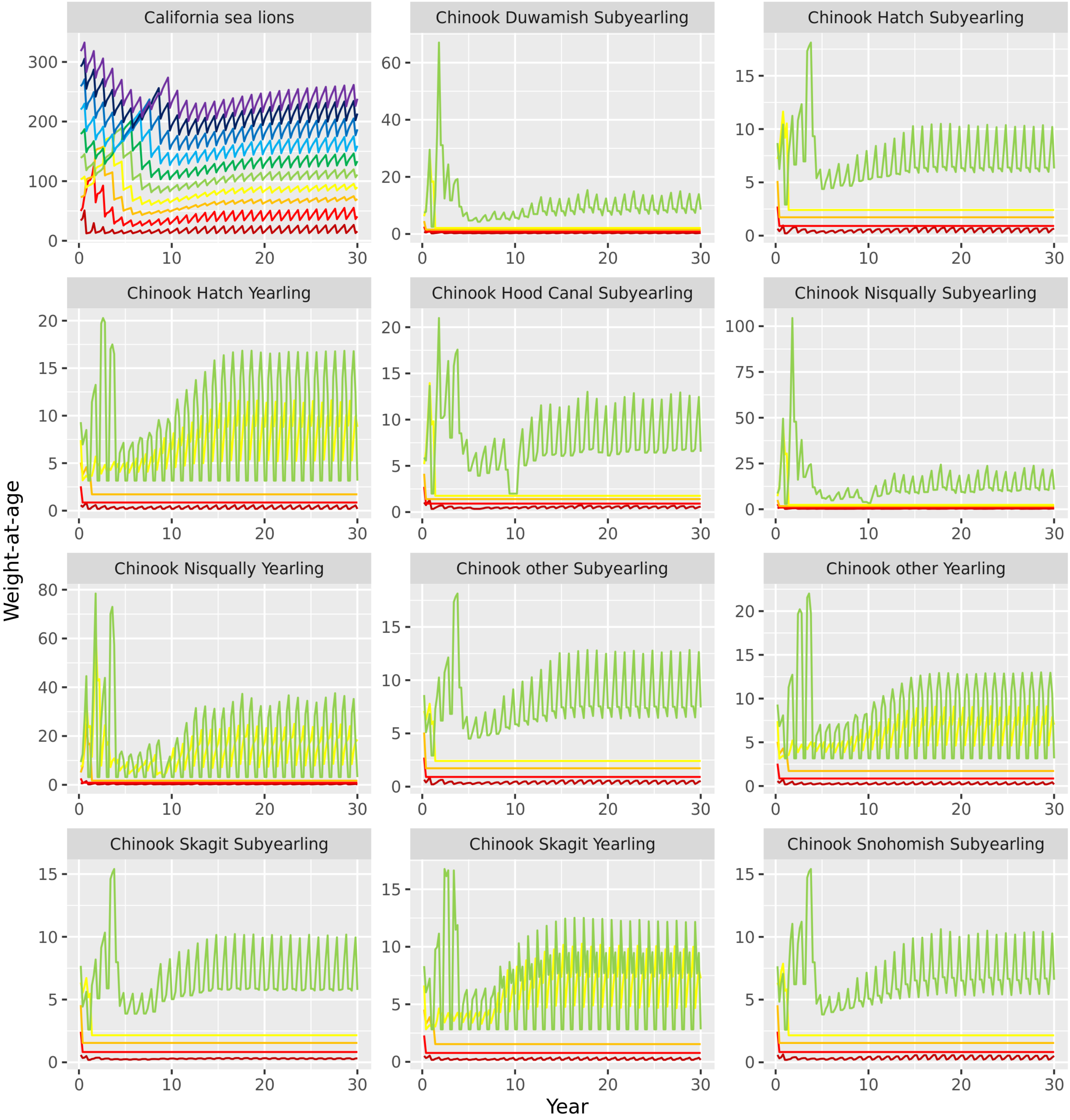

Figure 127. Trajectories for weight-at-age of age-structured groups in AMPS. Results are for 30-year simulations without fishing.

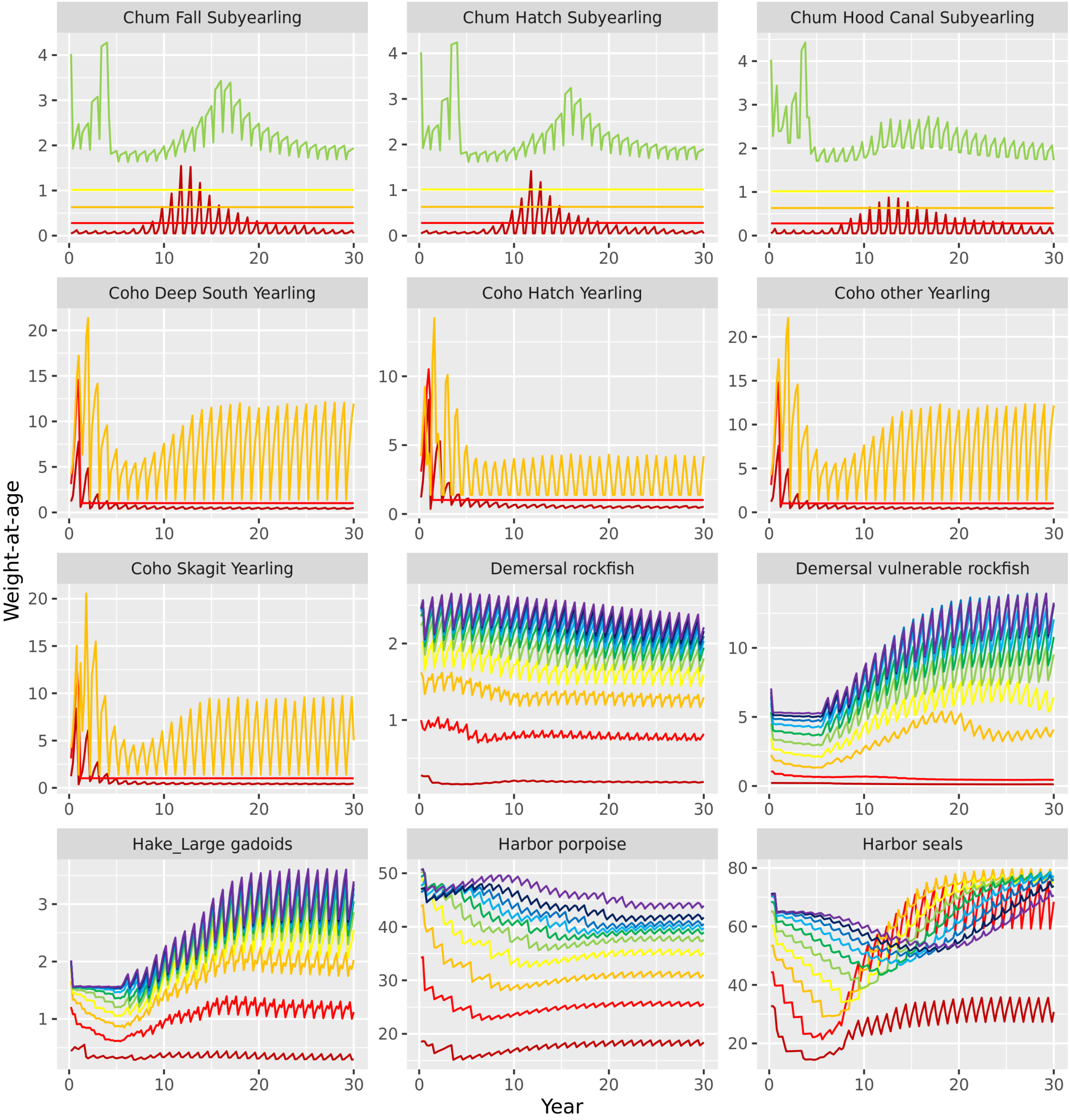

Figure 127 (continued). Trajectories for weight-at-age of age-structured groups in AMPS.

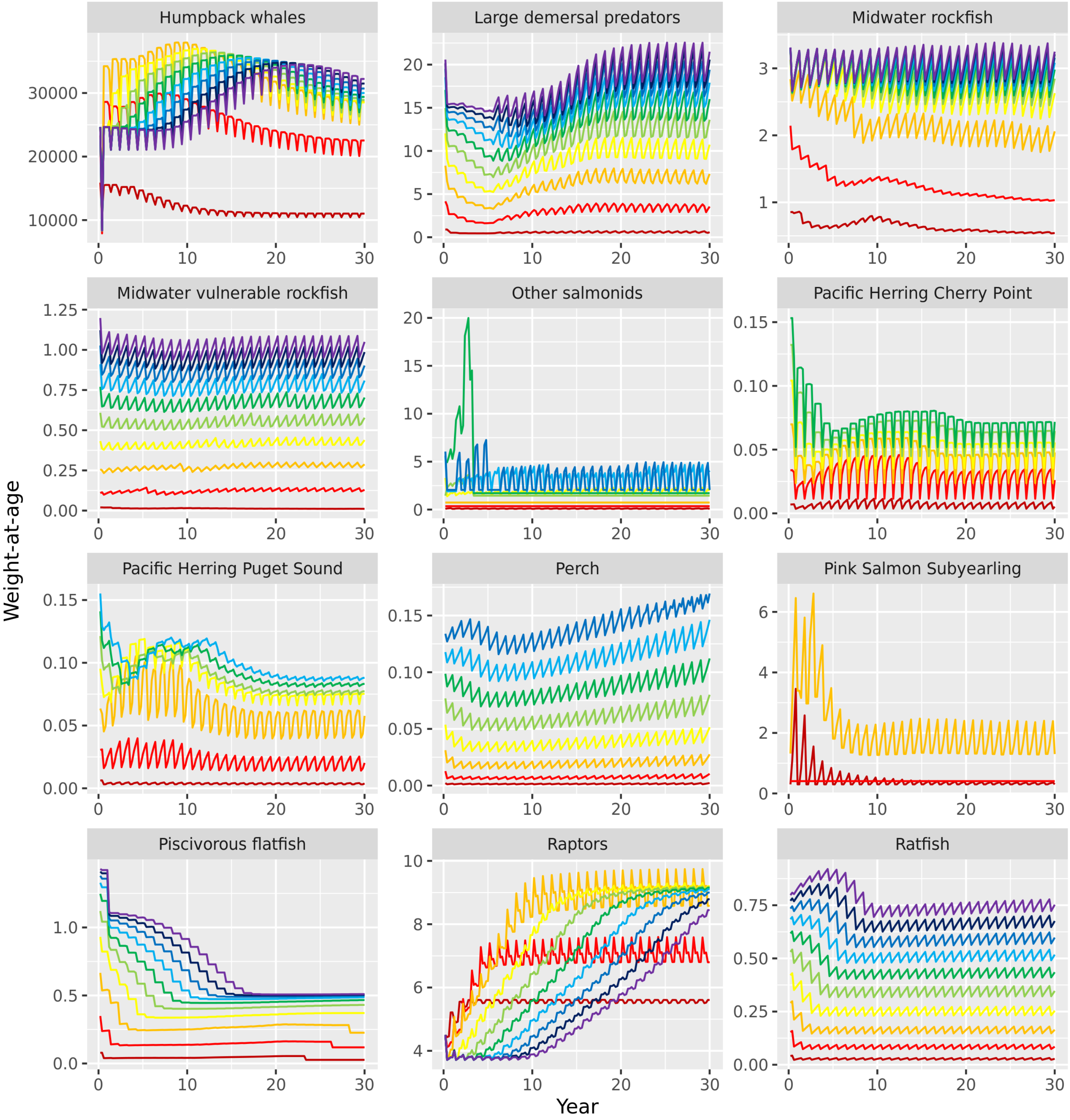

Figure 127 (continued). Trajectories for weight-at-age of age-structured groups in AMPS.

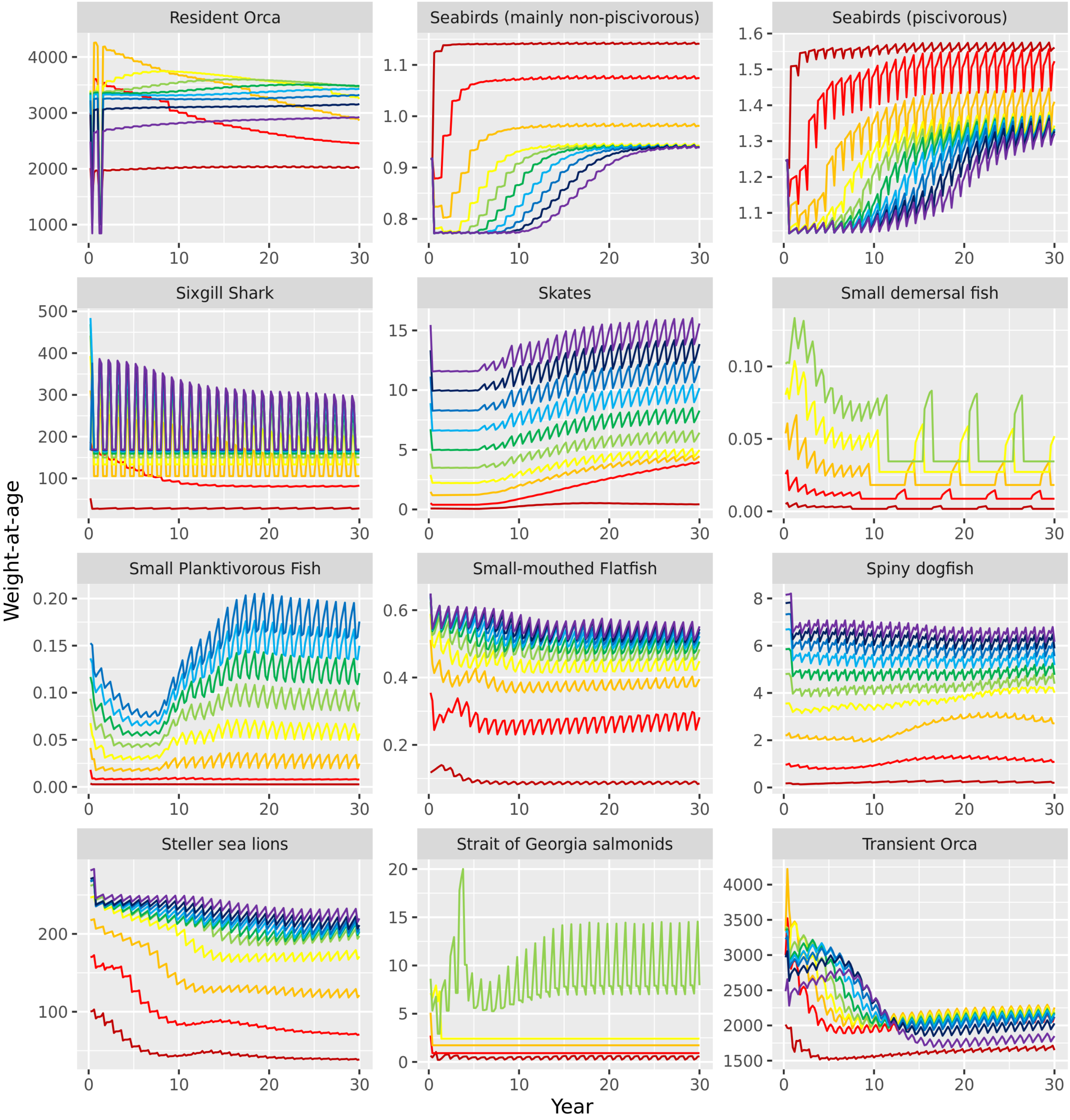

Figure 127 (continued). Trajectories for weight-at-age of age-structured groups in AMPS.

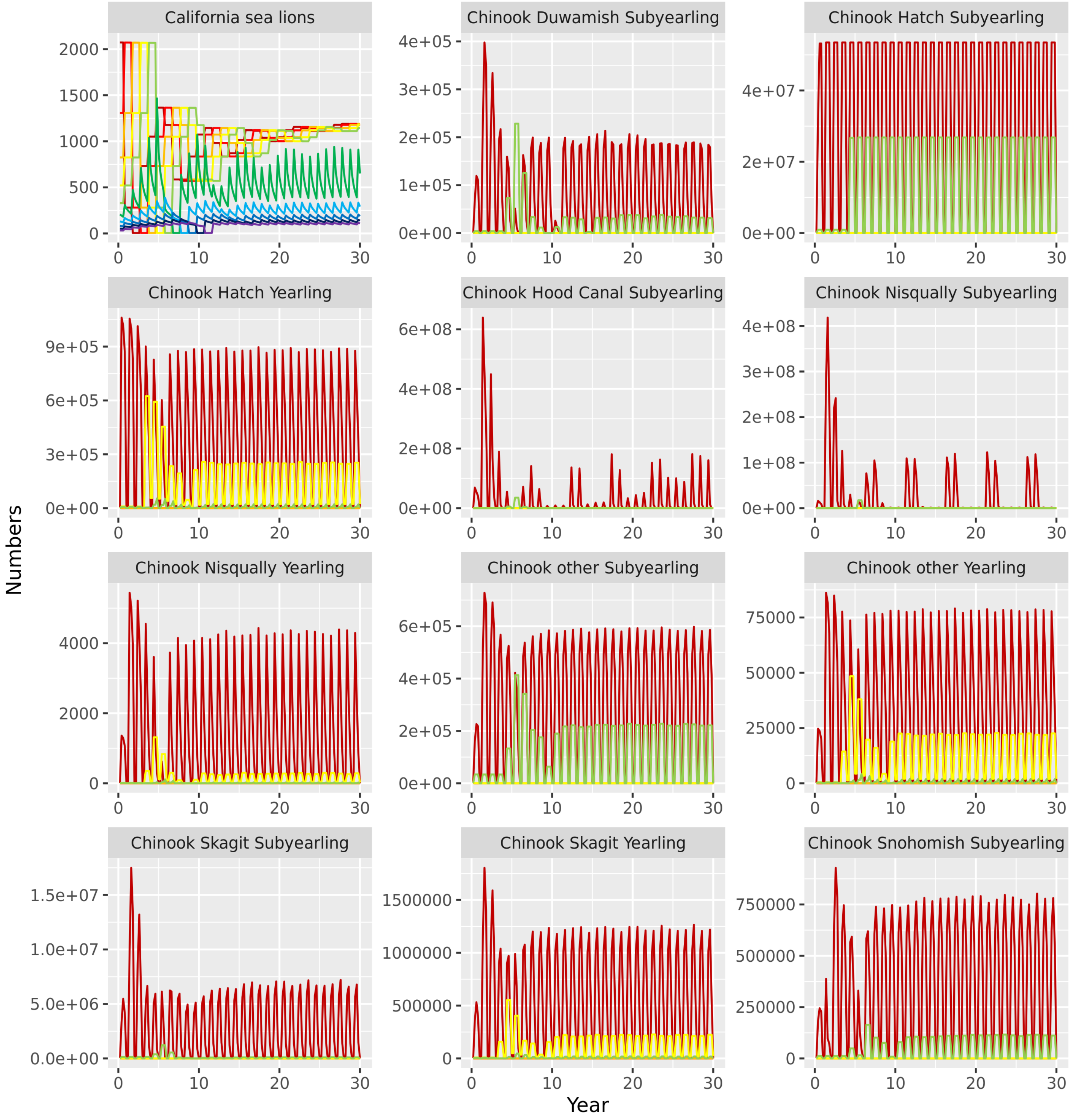

Figure 128. Trajectories for the number of individuals of age-structured groups in AMPS. Results are for 30-year simulations without fishing.

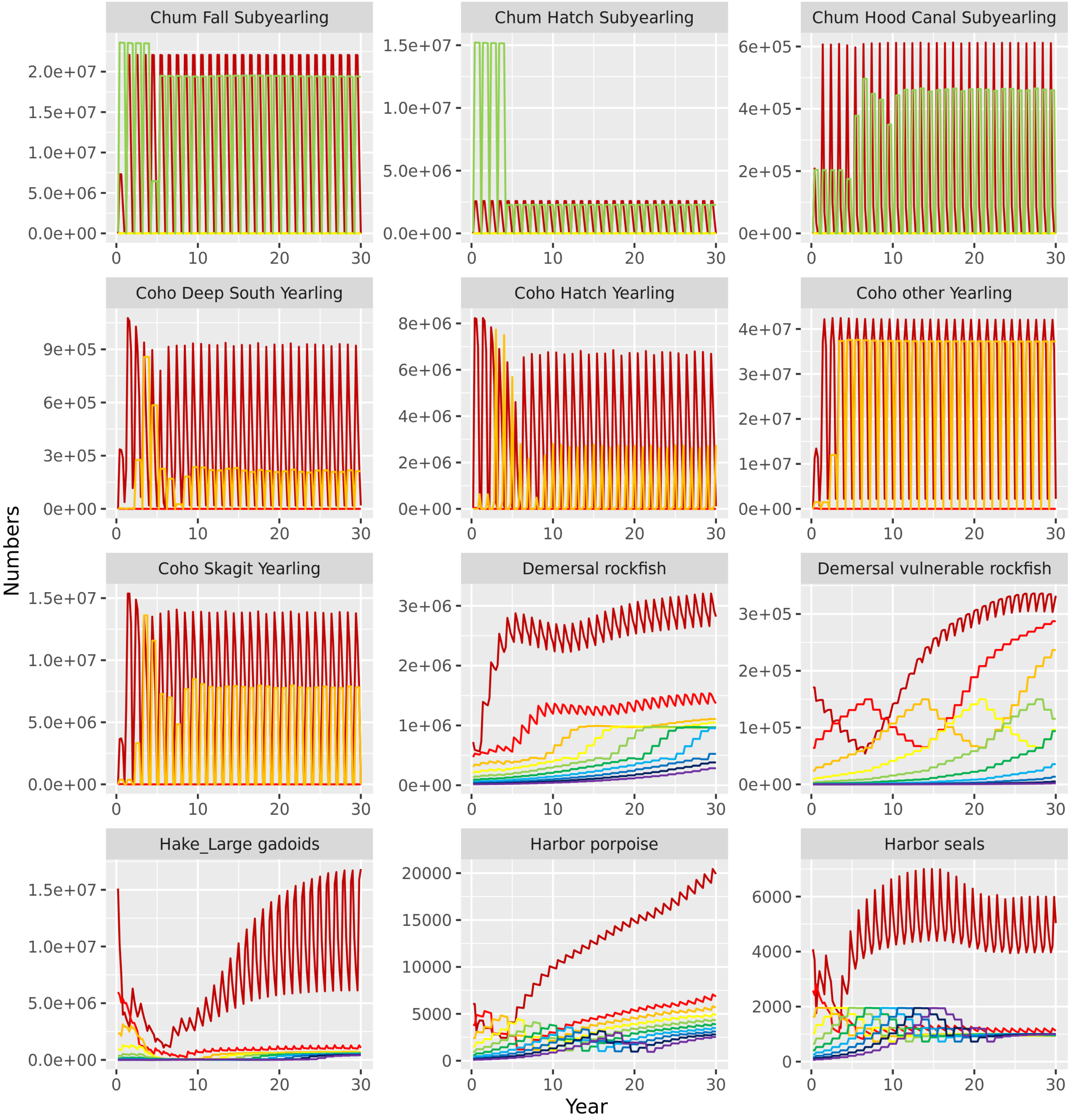

Figure 128 (continued). Trajectories for the number of individuals of age-structured groups in AMPS.

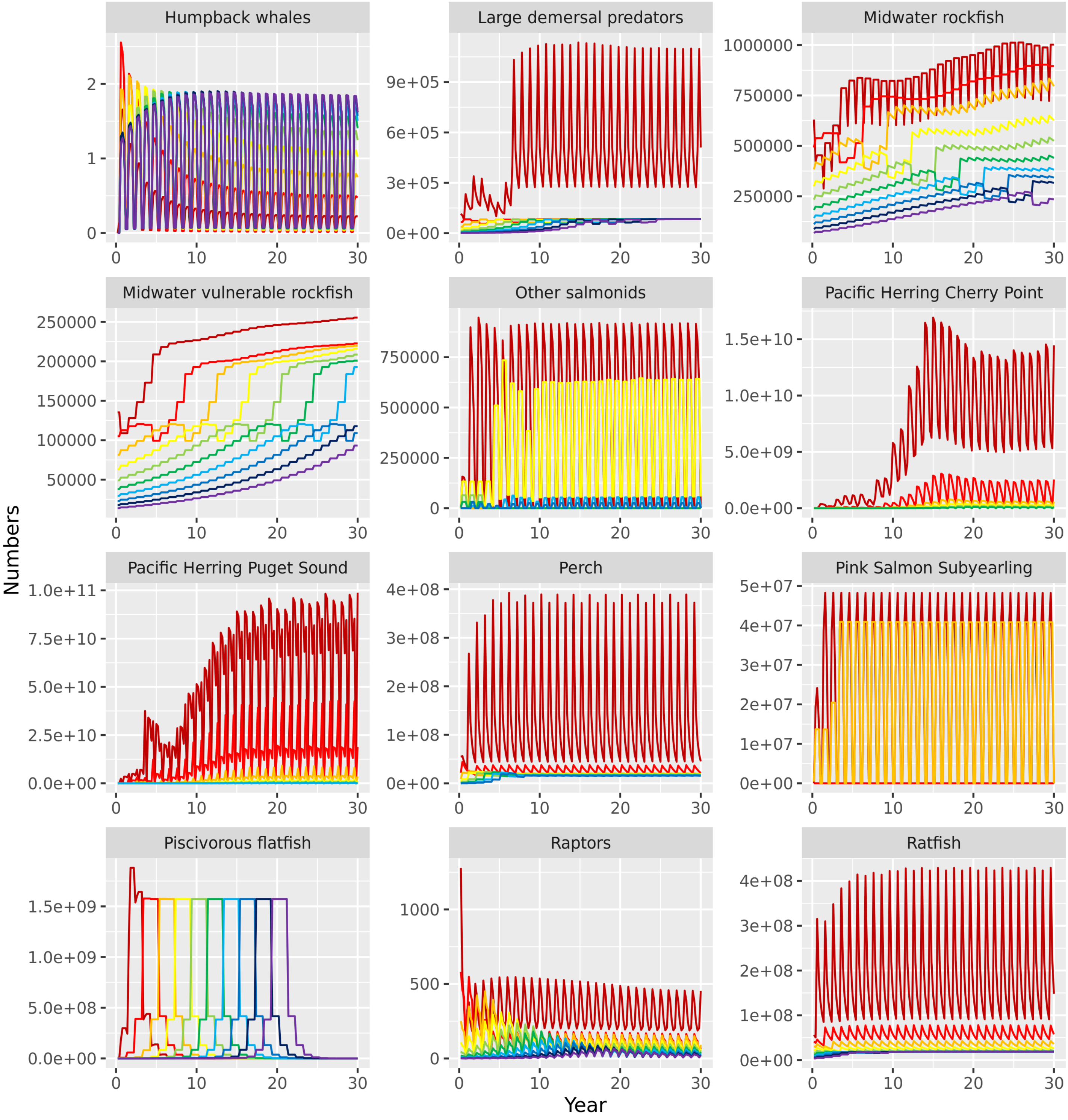

Figure 128 (continued). Trajectories for the number of individuals of age-structured groups in AMPS.

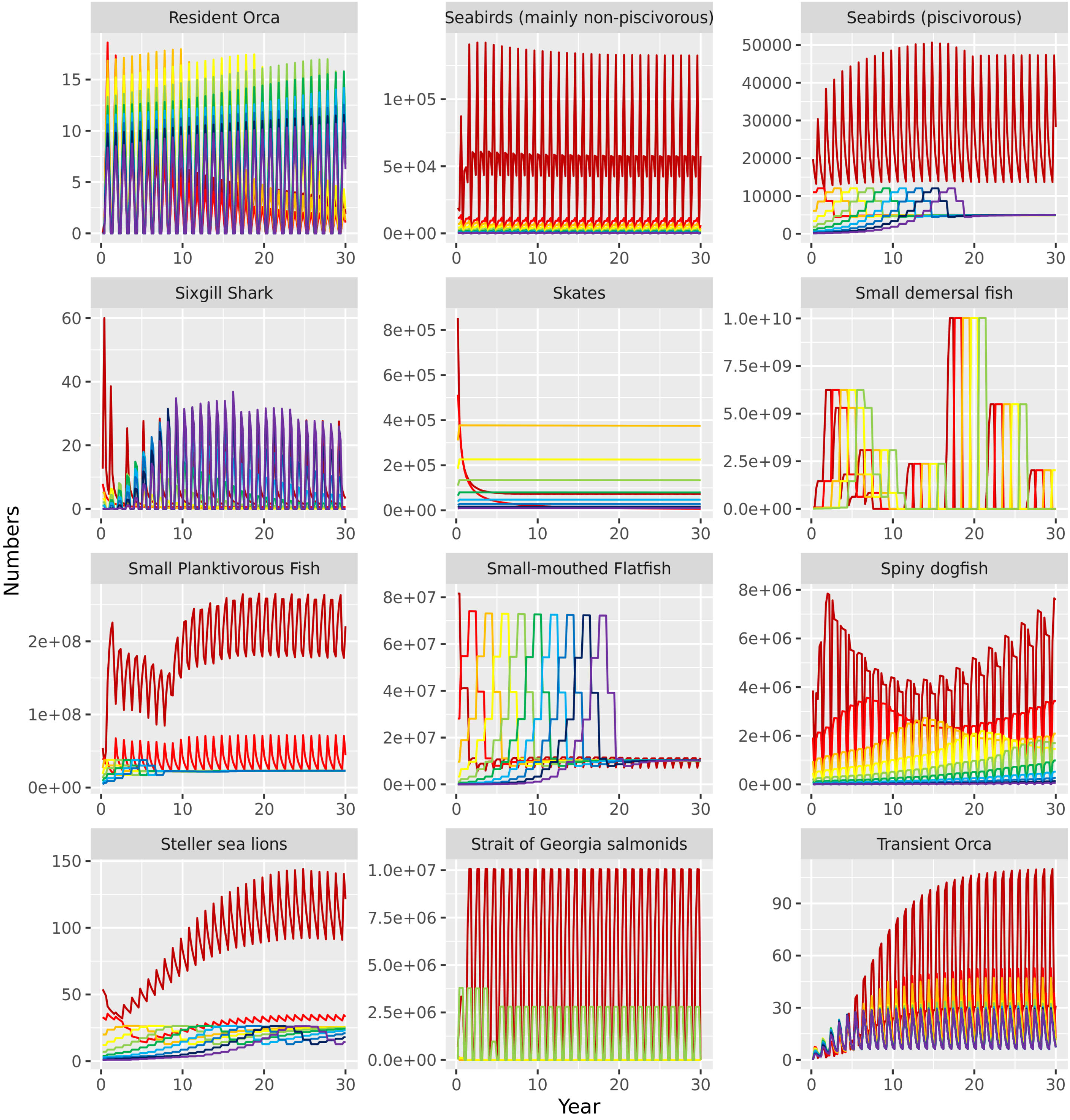

Figure 128 (continued). Trajectories for the number of individuals of age-structured groups in AMPS.

variable recruitment into age class 0, reflecting larval and egg survival. The numbers-at-age of piscivorous flatfish reflect the instability in this group; there is a single recruitment spike at the start of the simulation, reflecting that this group has low weight-at-age and low reserve and structural nitrogen. As a result, the group goes extinct around year 25 in the simulation.

Secondary calibration: Historical catch forcing

We evaluated the model's ability to sustain historical catch forcing and replicate biomass trends under historical fishing pressures after a 30-year spin-up period with no fishing (Figure 129), using the reconstructed fishing time series developed for the model (Figure 117). Most target groups respond reasonably well to fishing pressure, decreasing in biomass due to fishing but persisting through the fishing period (through 2011). Several groups (e.g., bivalves, chum hatchery subyearling, demersal vulnerable rockfish, and both Pacific herring groups), increased their biomass significantly during the 30-year spin-up and had very high biomass when historical fishing pressure starts, with a minimal effect of historical fishery removals. This may indicate inappropriate levels of productivity or growth parameters for these species.

There is a sharp biomass increase in groups, such as coho deep south yearling, coho other yearling, coho Skagit yearling, and squid, driven by a biomass spike in large zooplankton, indicating instability in this zooplankton group. However, other plankton groups perform well, so misrepresentation in this group might not compromise overall model performance. Most groups increased during the spin-up period, except for piscivorous flatfish, which decreased even under no fishing, suggesting the problems may be related to predation and/or productivity. Multiple groups, including chum fall subyearling, spiny dogfish, hake, demersal rockfish, ratfish, other salmonids, and Strait of Georgia salmonids crash after fishing begins, suggesting either: 1) low growth parameters, 2) low population recruitment, or 3) a low overall ecosystem productivity in the model (based on 2011 data). This last point underscores the difficulty of replicating an ecosystem state using contemporary data to represent different historical ecosystem conditions.

Equilibrium scenarios

We developed catch and biomass equilibrium graphs (Figure 130). Equilibrium curves are a diagnostic tool that can be used to assess the resilience of fished stocks. These curves represent the hypothesis that as fishing mortalities increase across a range of simulations, the biomass at equilibrium will decline, with equilibrium catch to peak at some intermediate maximum sustainable fishing rate, *FMSY*. Catch and biomass equilibrium curves were generated by increasing fishing mortality stepwise in 30-year simulations. We tested increasing fixed annual mortality rates from 0 to 0.95, by 0.05 steps. These equilibrium curves are influenced by annual variation in physical conditions and predator–prey dynamics. We applied fishing mortality rates to all groups simultaneously, which greatly reduces the number of simulations necessary. However, simultaneous application of fishing rates to all groups introduces new ecological dynamics; at higher fishing mortality rates, interspecies dynamics become significant (Ainsworth et al. 2011). In Figure 130, each bar corresponds to the end state of a simulation under the specified level of annual fishing

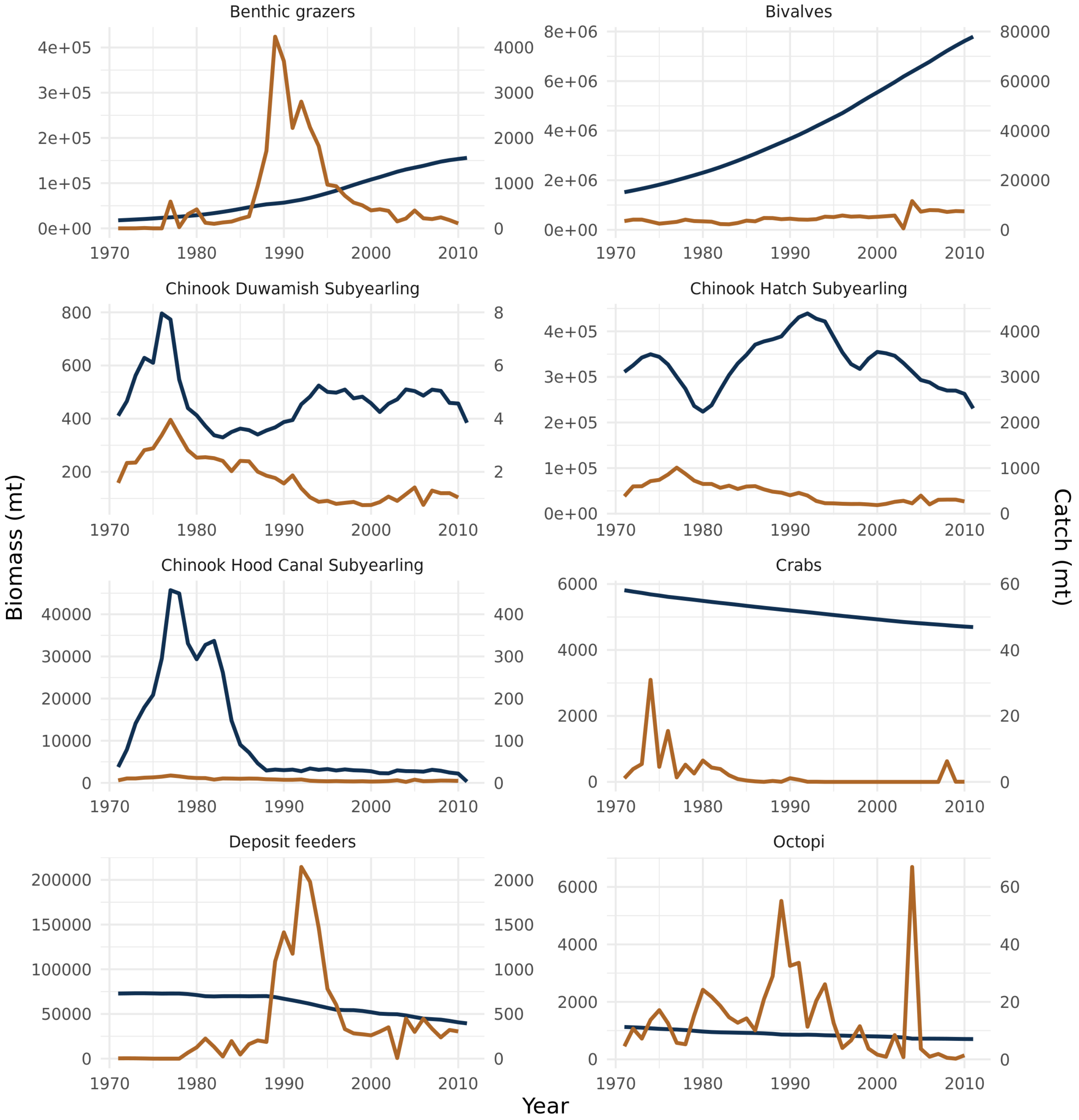

Figure 129. Biomass and catch trajectories (metric tons) for fished groups in AMPS, forced with reconstructed historical catch trends, 1970–2011. Blue line is biomass in the primary *y*-axis, dark orange line is catch in the secondary *y*-axis.

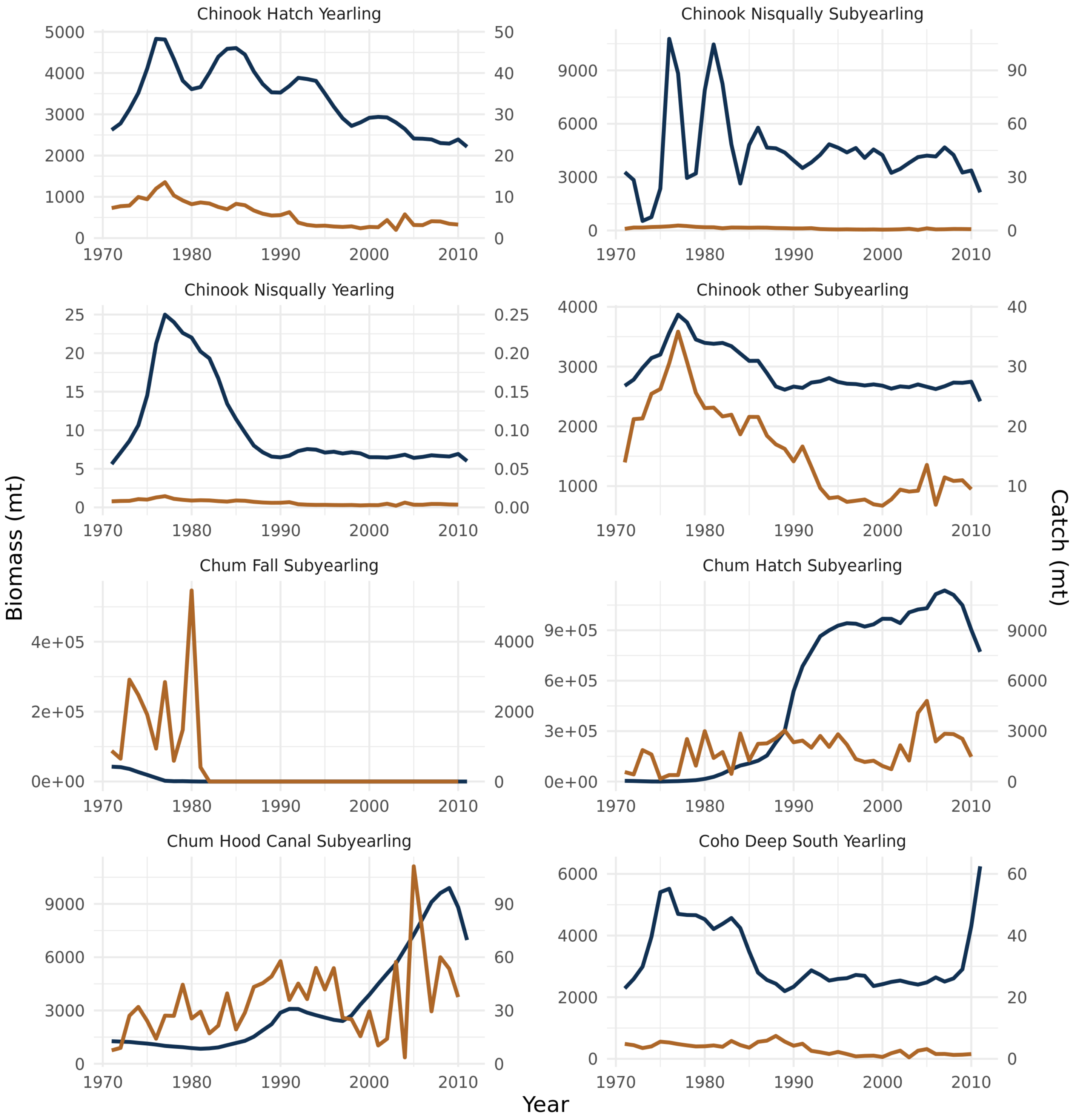

Figure 129 (continued). Biomass and catch trajectories for fished groups in AMPS, forced with reconstructed historical catch trends, 1970–2011.

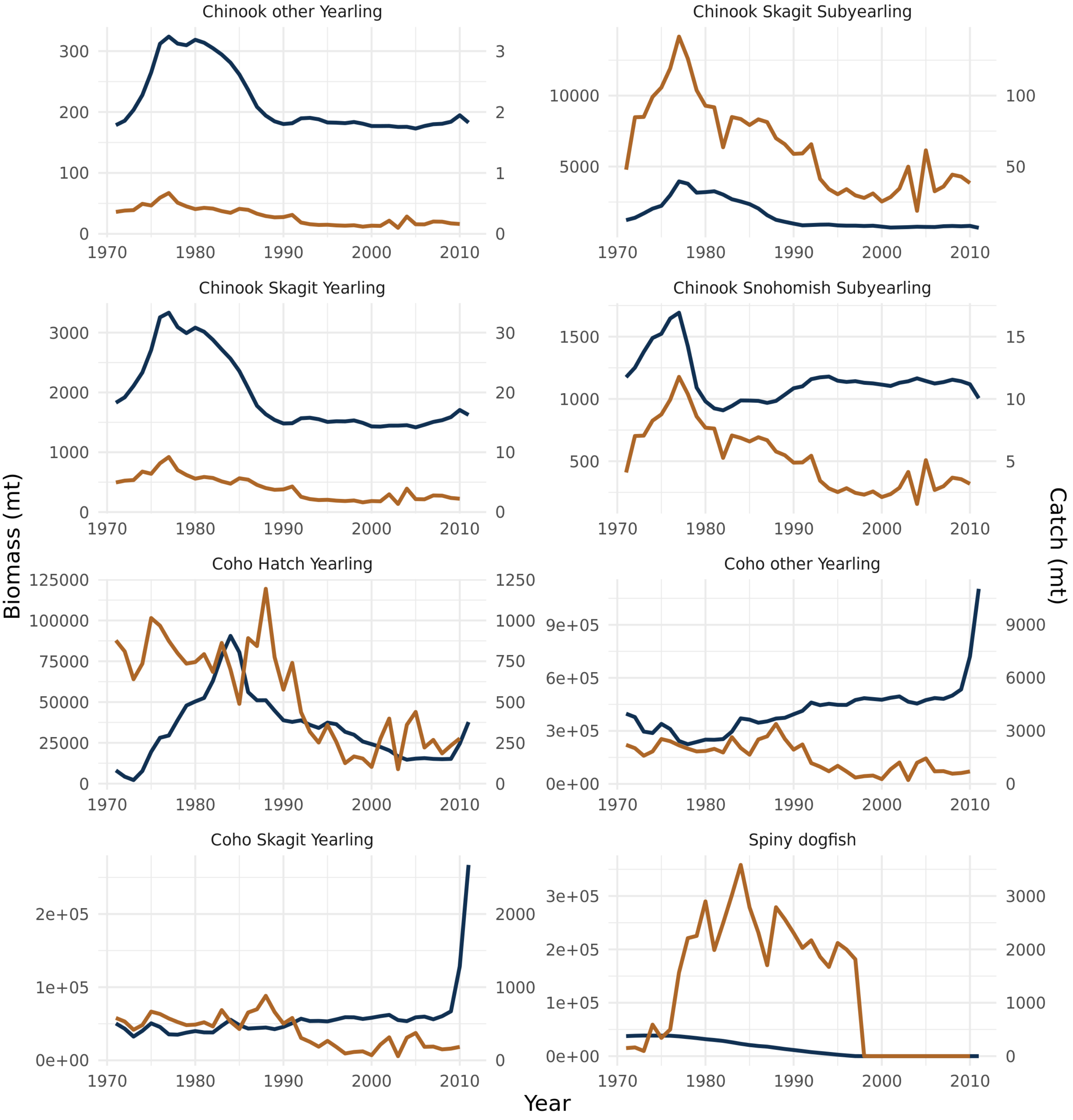

Figure 129 (continued). Biomass and catch trajectories for fished groups in AMPS, forced with reconstructed historical catch trends, 1970–2011.

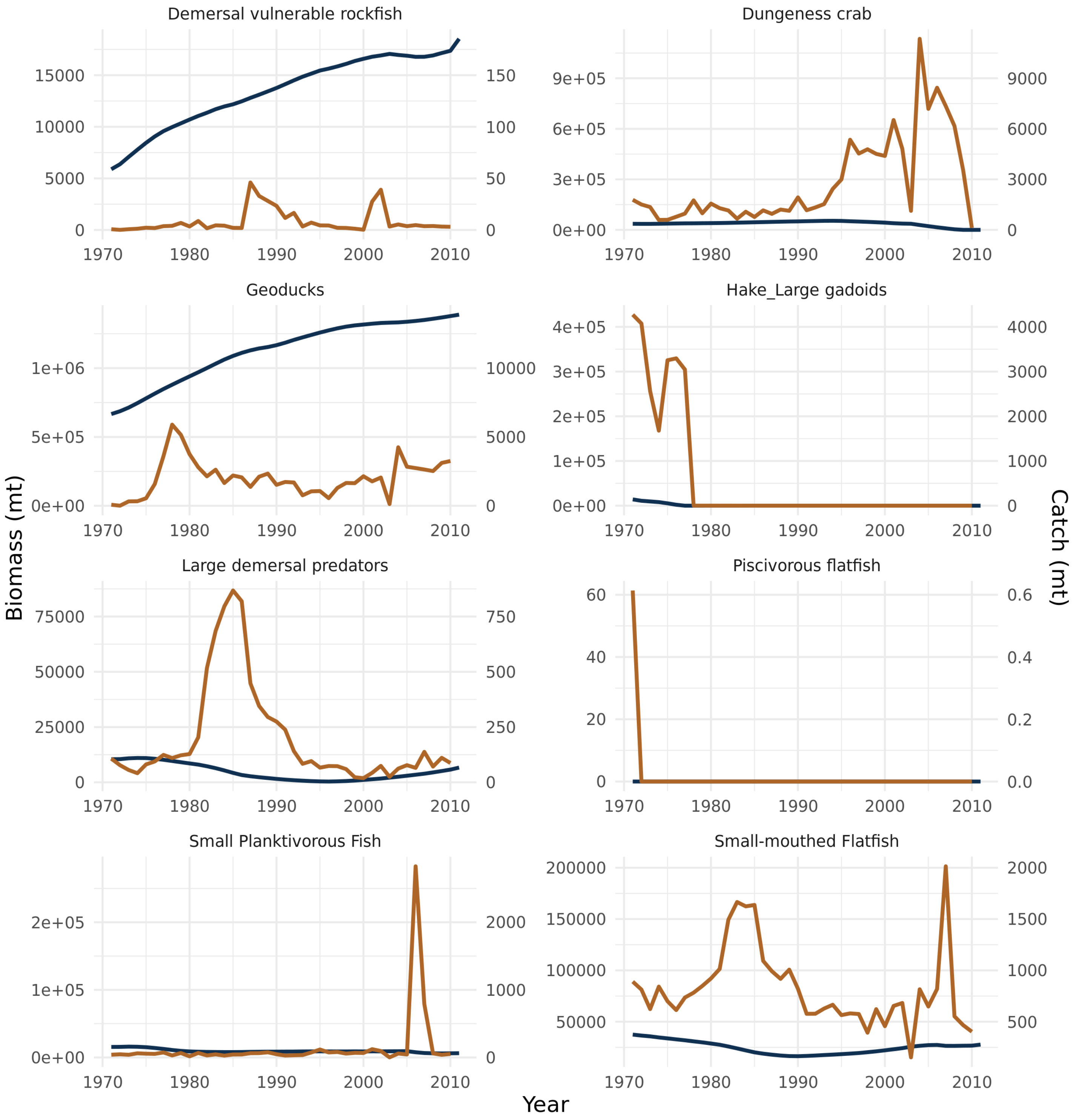

Figure 129 (continued). Biomass and catch trajectories for fished groups in AMPS, forced with reconstructed historical catch trends, 1970–2011.

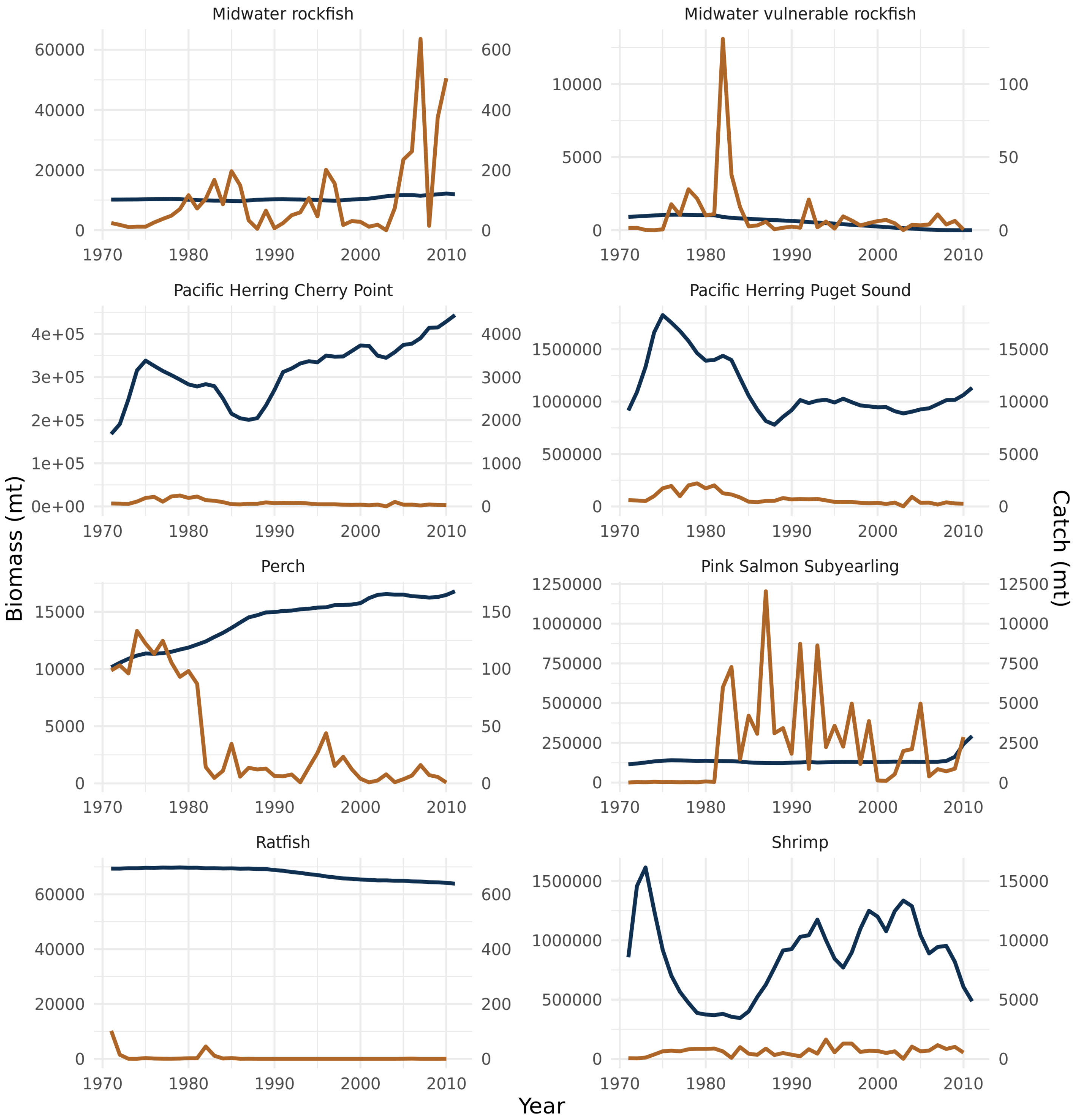

Figure 129 (continued). Biomass and catch trajectories for fished groups in AMPS, forced with reconstructed historical catch trends, 1970–2011.

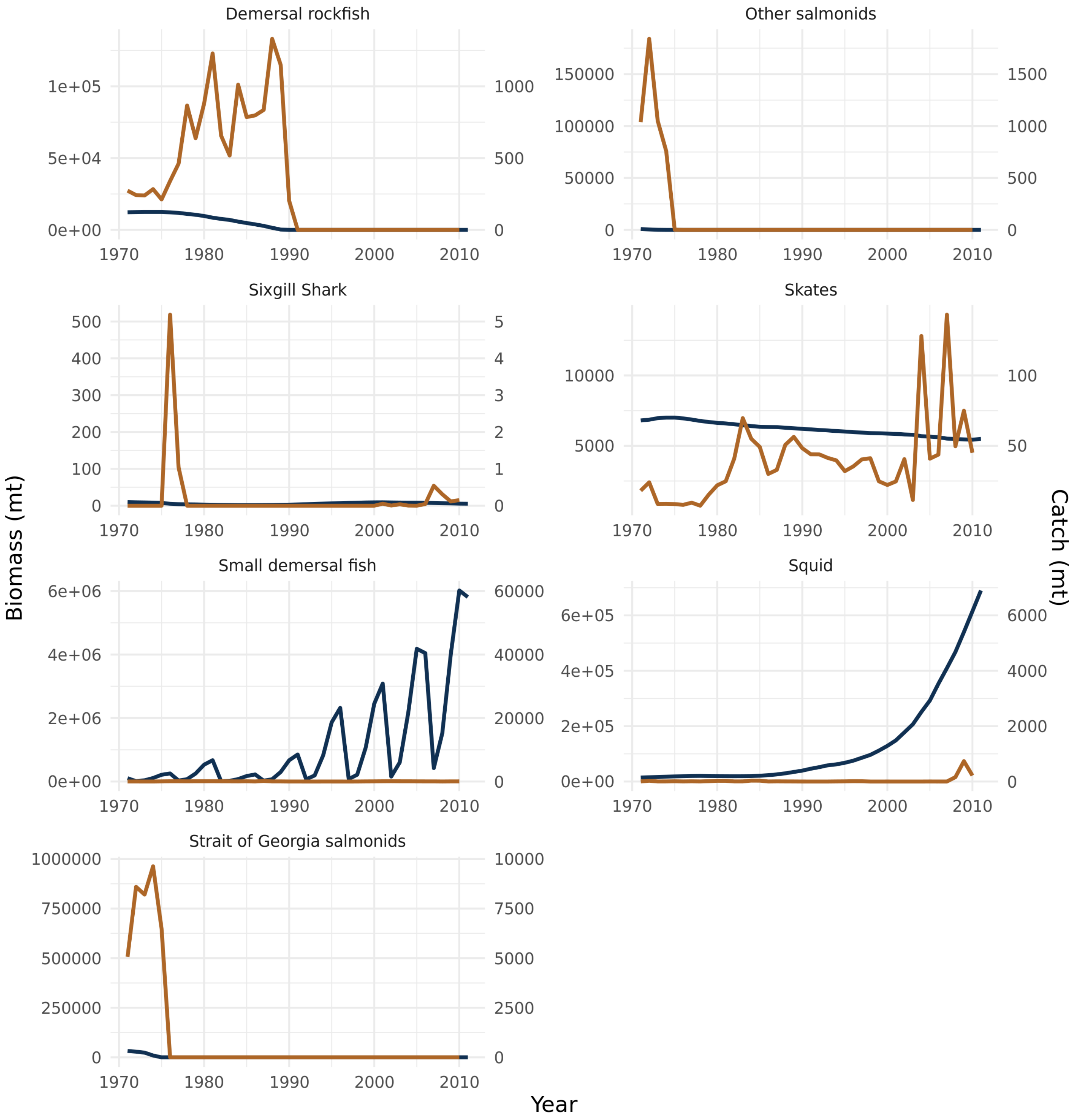

Figure 129 (continued). Biomass and catch trajectories for fished groups in AMPS, forced with reconstructed historical catch trends, 1970–2011.

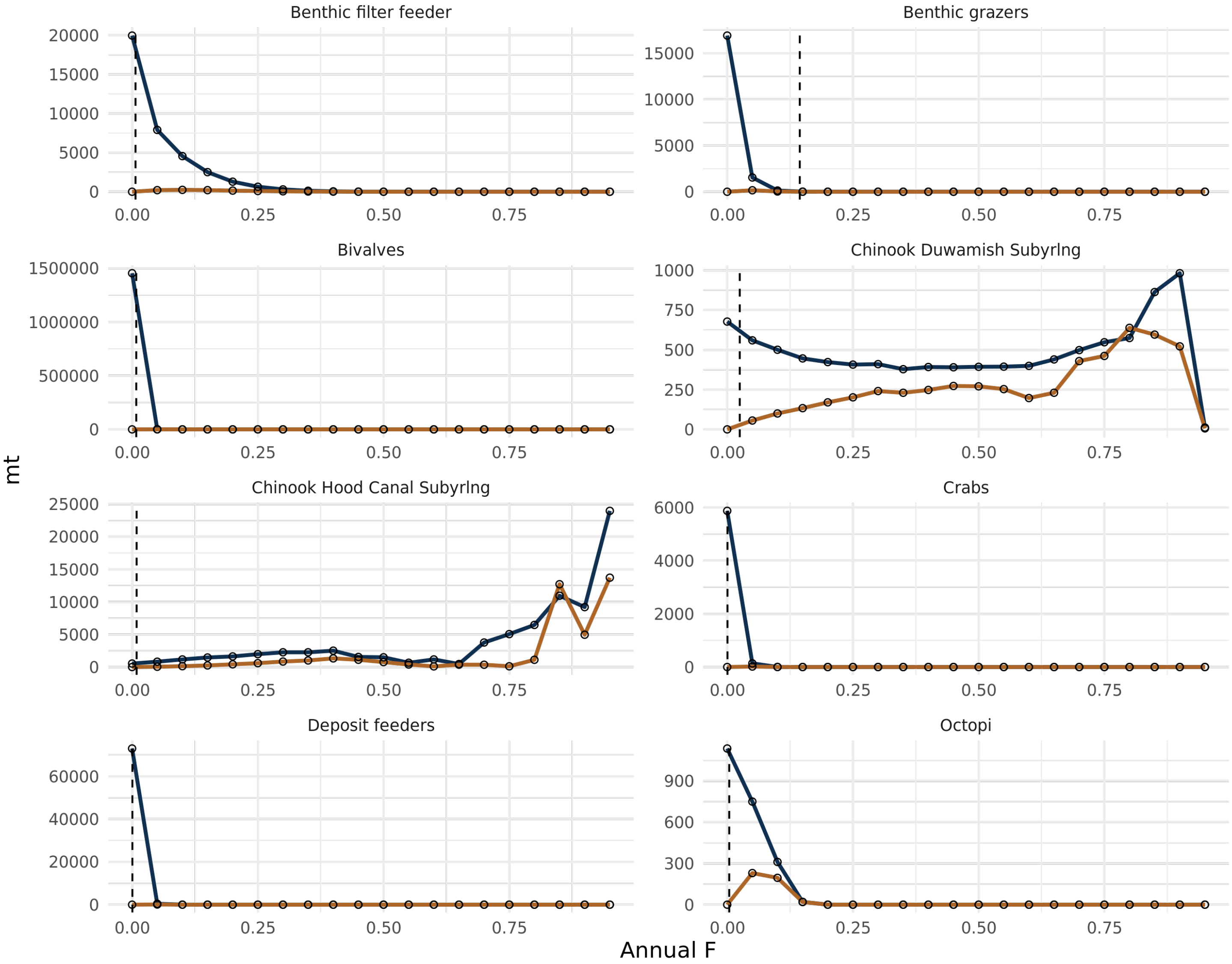

Figure 130. Multispecies biomass (blue line) and catch (dark orange line) equilibrium plots (metric tons) for fished groups in AMPS, forced with increasing fishing mortality and estimated fishing mortality in 2011 (dashed line).

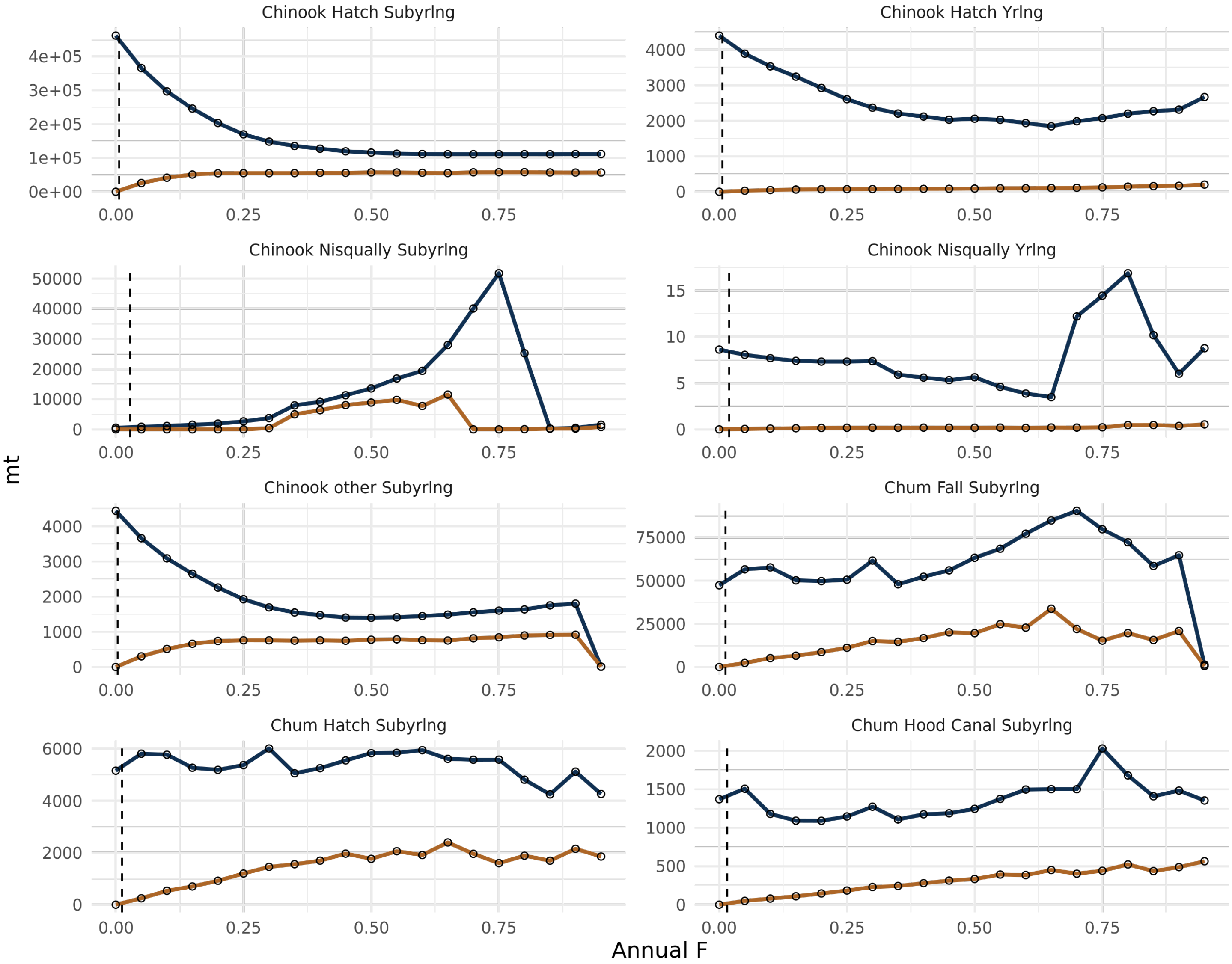

Figure 130 (continued). Multispecies biomass and catch equilibrium plots for fished groups in AMPS, forced with increasing fishing mortality and estimated fishing mortality in 2011.

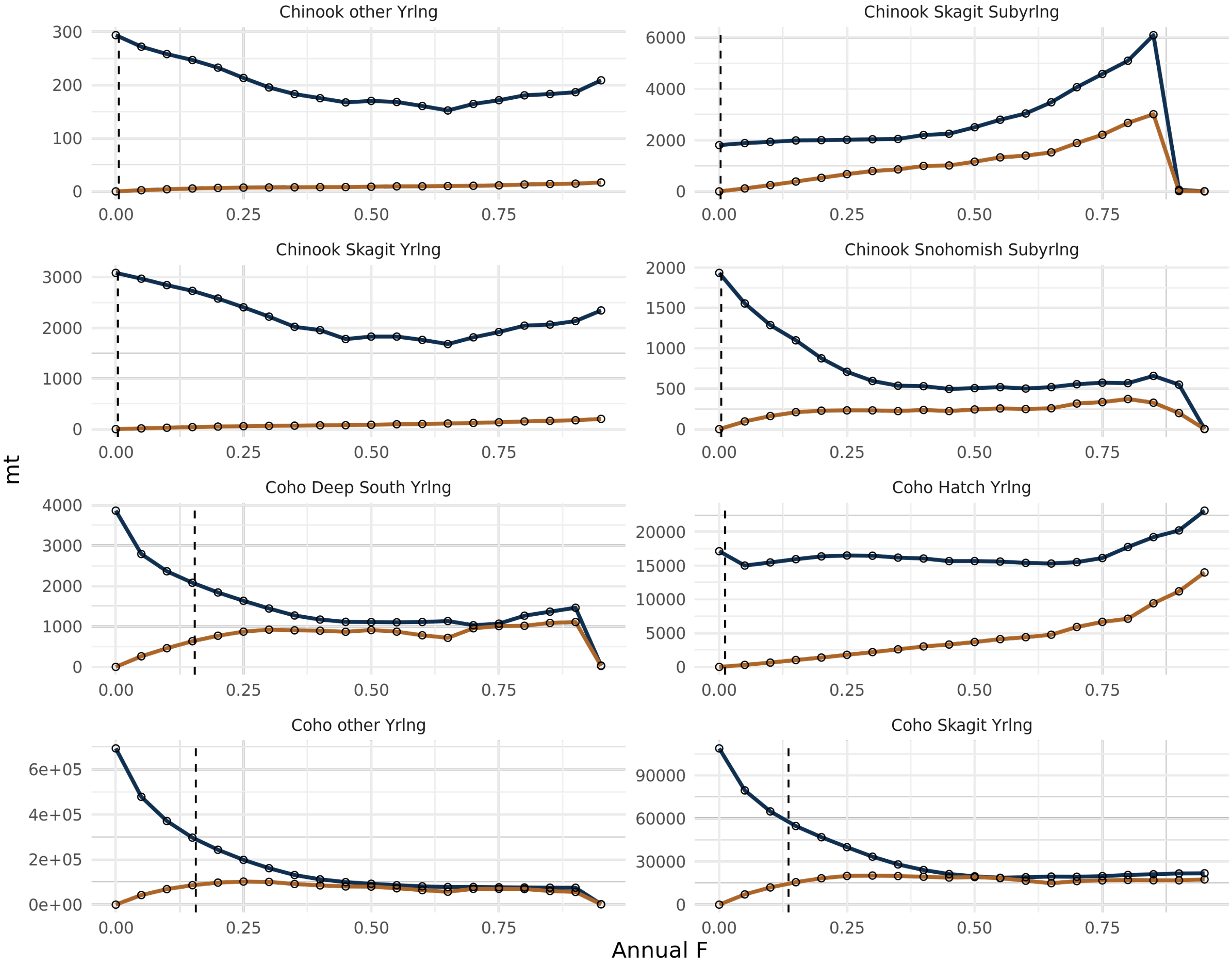

Figure 130 (continued). Multispecies biomass and catch equilibrium plots for fished groups in AMPS, forced with increasing fishing mortality and estimated fishing mortality in 2011.

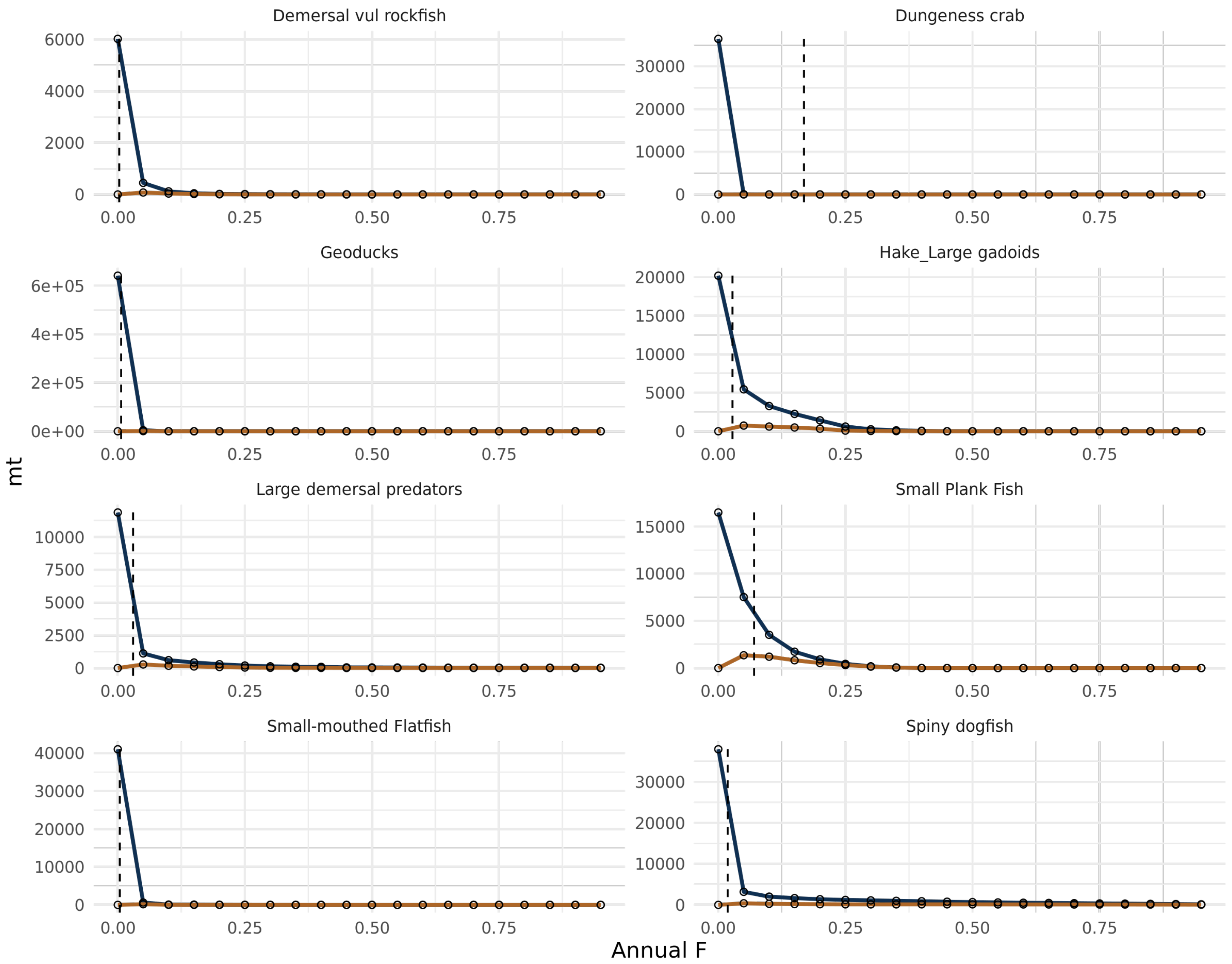

Figure 130 (continued). Multispecies biomass and catch equilibrium plots for fished groups in AMPS, forced with increasing fishing mortality and estimated fishing mortality in 2011.

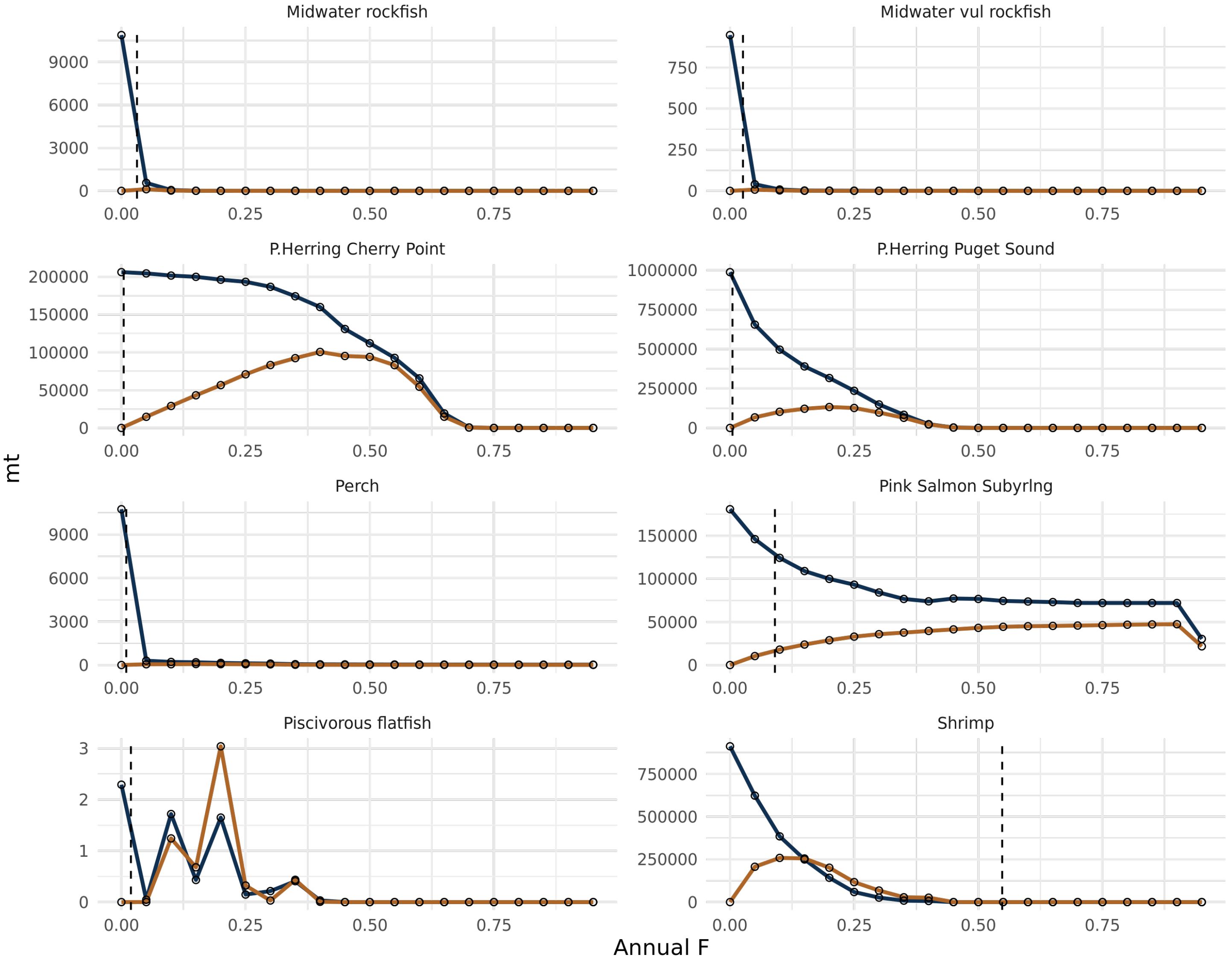

Figure 130 (continued). Multispecies biomass and catch equilibrium plots for fished groups in AMPS, forced with increasing fishing mortality and estimated fishing mortality in 2011.

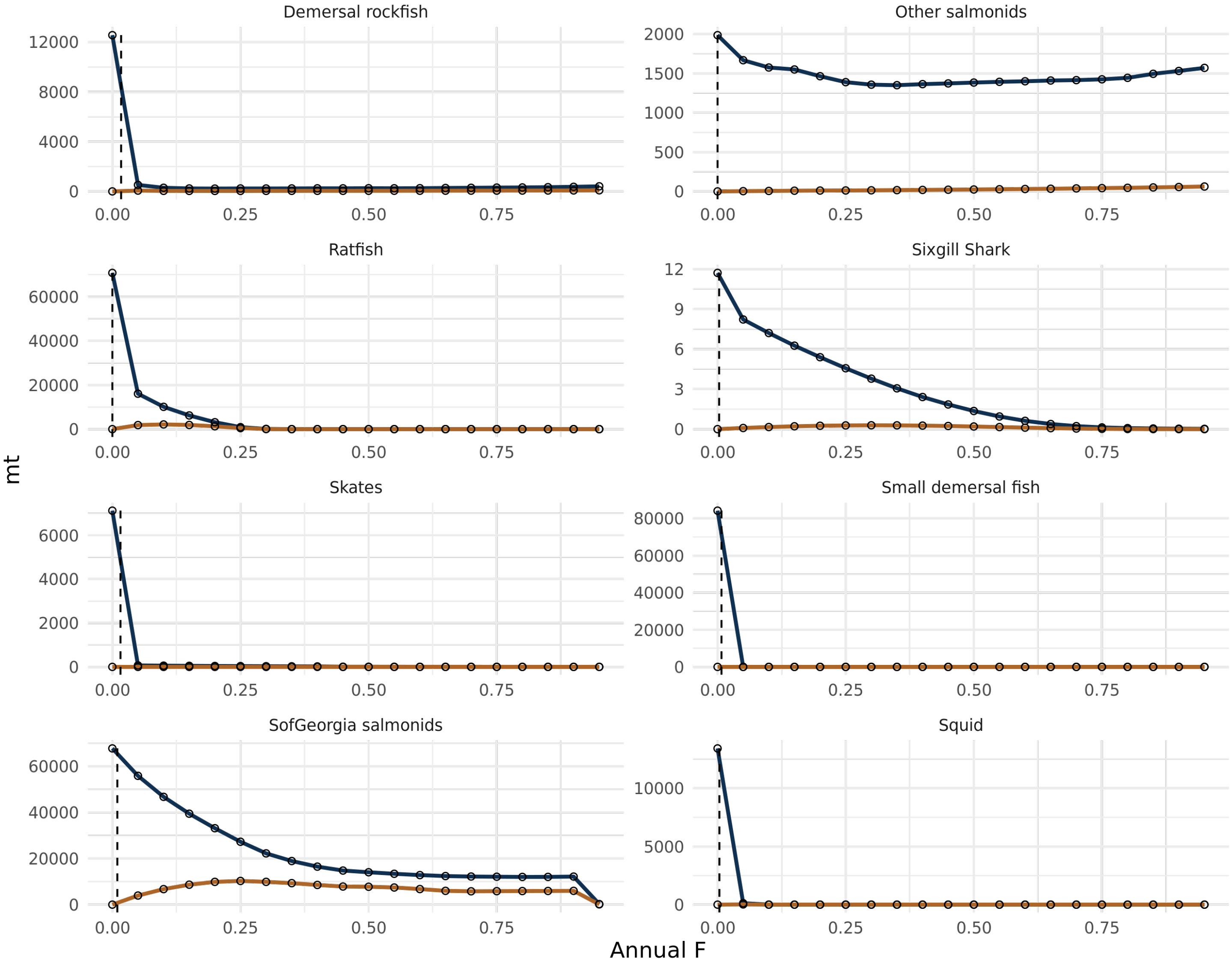

Figure 130 (continued). Multispecies biomass and catch equilibrium plots for fished groups in AMPS, forced with increasing fishing mortality and estimated fishing mortality in 2011.

mortality rates. The left side of the graph represents the biomass level of each group under zero fishing mortality (unexploited biomass), and the maximum height of the catch curve shows maximum sustainable yield and the fishing mortality where it occurs. For many species (e.g., Pacific herring, octopus), we found an expected decrease in biomass with increasing fishing mortality, as well as maximum catches at intermediate fishing mortality rates. Exceptions were for multiple salmon groups, including coho other yearling, other salmonids, and Chinook Skagit yearling. These salmon groups respond less to fishing than to multispecies dynamics (predators being removed simultaneously at high fishing mortality rates). To illustrate this effect, we ran a simulation where fishing mortality rates were only increased for salmon group Coho Skagit yearling (Figure 131), while we applied constant fishing mortality rates (equal to 2011 rates) to all other fished groups. Although biomass does not reach zero under tested annual fishing mortality rates, the shape of the biomass and catch curves approximates the expected response. In this simulation, biomass and catch of Chinook Skagit yearling and coho deep south yearling increase due to the fishing-driven declines in their competitor, coho Skagit yearling. These are examples of salmon's strong trophic effects when varied fishing mortality is applied to all fished groups simultaneously.

Forward simulations

We ran 30-year forward simulations using the constant fishing mortality rate estimated based on the average catch for all fleets between 2009 and 2018 (Figure 119). Most target species are able to withstand the constant fishing mortality rates (Figure 132), and catch trajectories reflect biomass trends. Large zooplankton persists at very low biomass levels following the start of the simulation. There is a decrease in the Dungeness crab and hake and gadoids groups, suggesting low productivity in the ecosystem. Piscivorous flatfish crash after 20 years; this is a persistent problem that appears in some but not all simulations, even without changes to biological parameters of this functional group, suggesting an indirect trophic effect that we have not identified. Small demersal fish also crash within ten years of the simulation; this is an intermittent issue due to trophic effects related to trophic interactions with both Pacific herring groups, one that we expect can be corrected in future applications of the model.

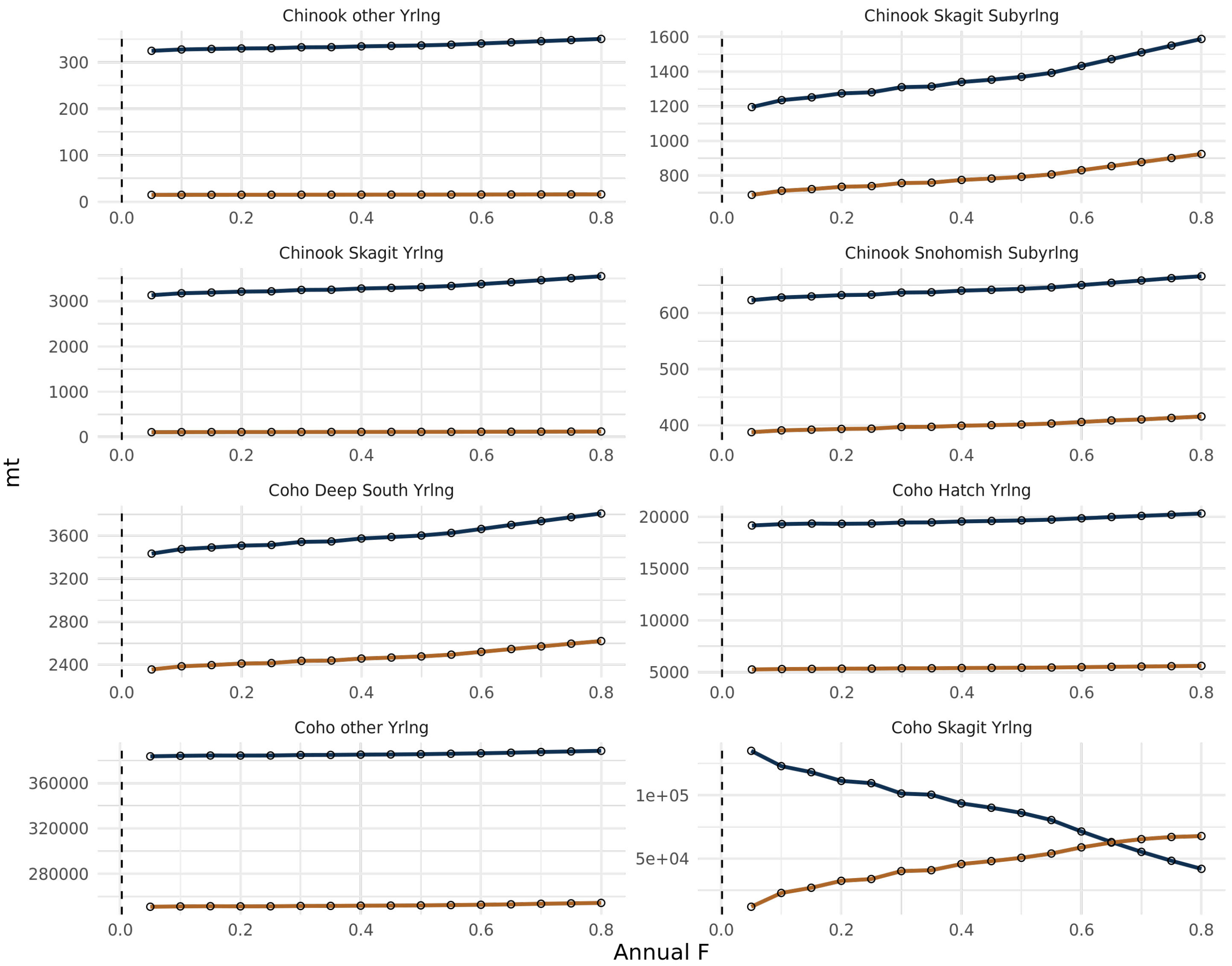

Figure 131. Multispecies biomass (blue line) and catch (dark orange line) equilibrium plots (metric tons) for fished groups in AMPS. Only salmon group coho Skagit yearling was forced with increasing fishing mortality. Dashed line is the estimated fishing mortality.

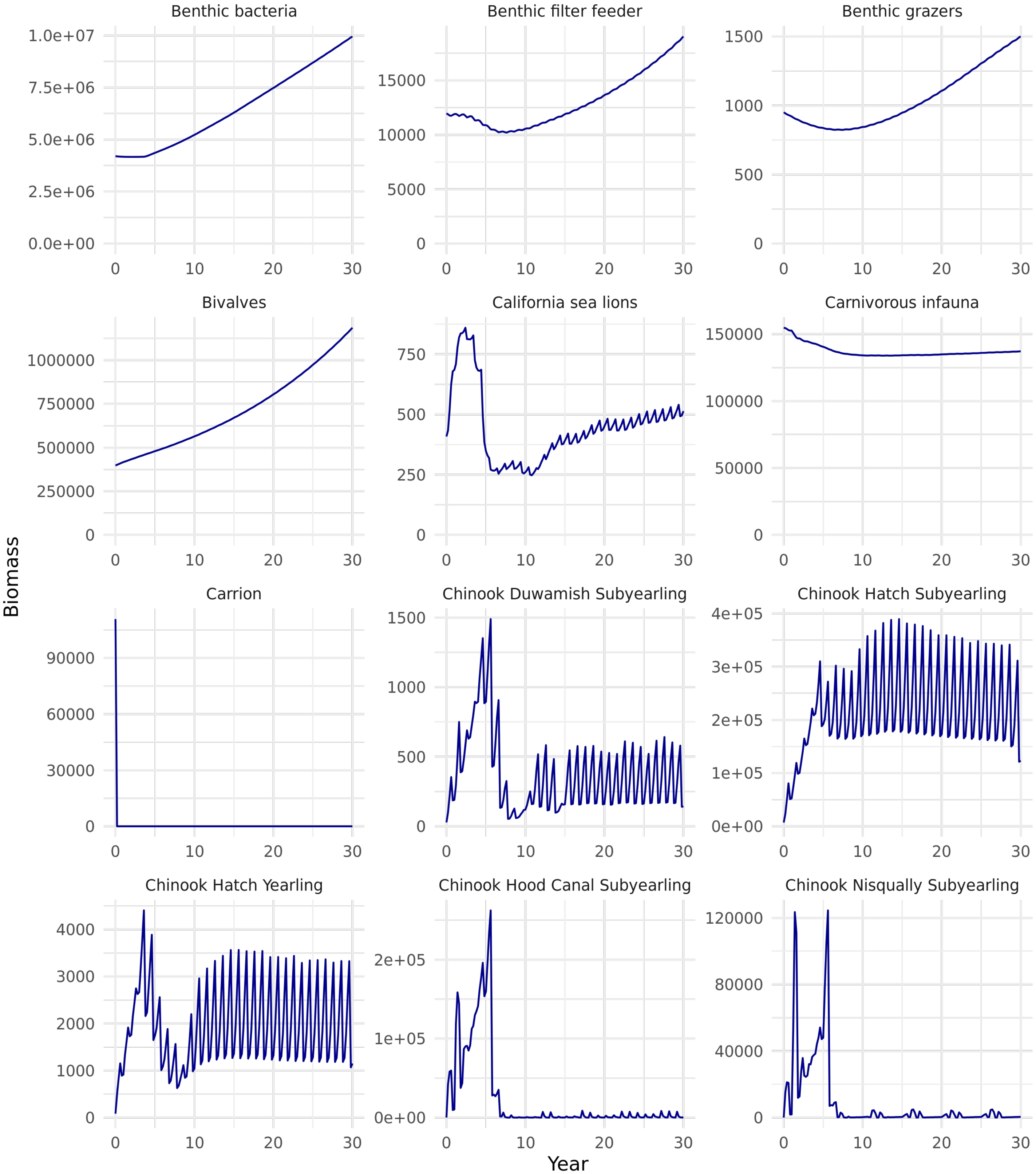

Figure 132. Biomass trajectories (metric tons) for functional groups in AMPS. Scenario forced with constant fishing mortality rates by functional group and fishery, 2011–41.

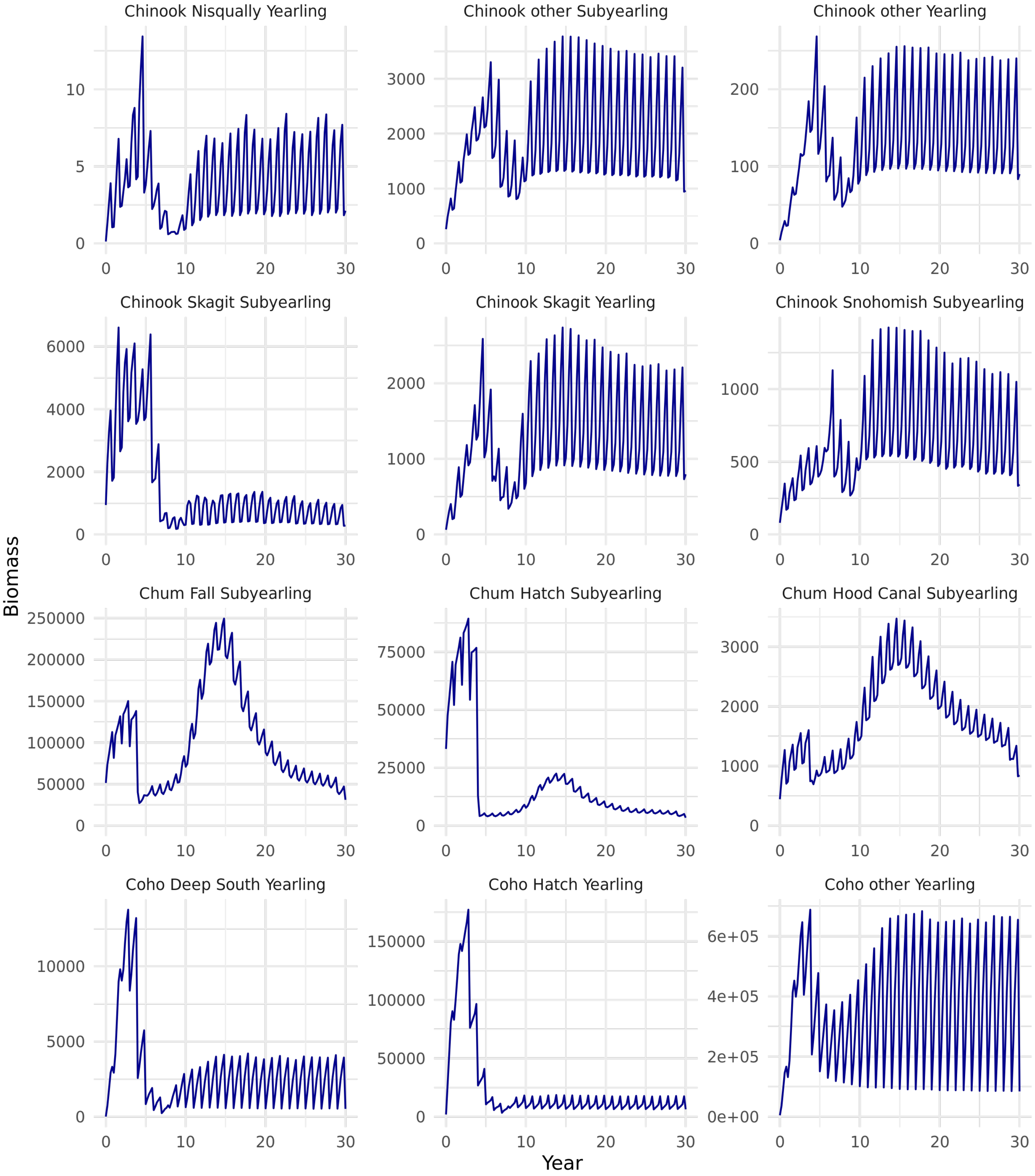

Figure 132 (continued). Biomass trajectories for functional groups in AMPS.

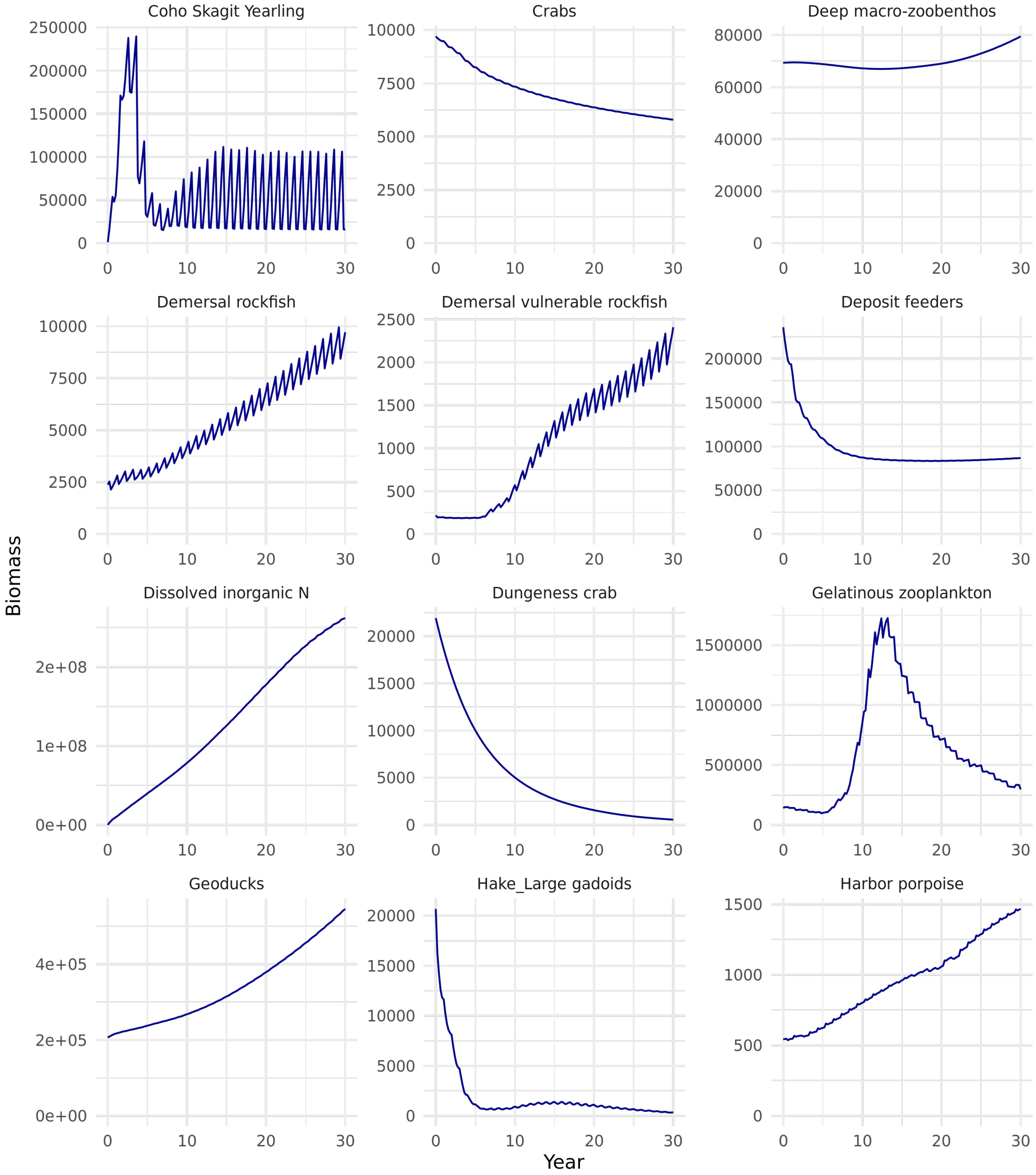

Figure 132 (continued). Biomass trajectories for functional groups in AMPS.

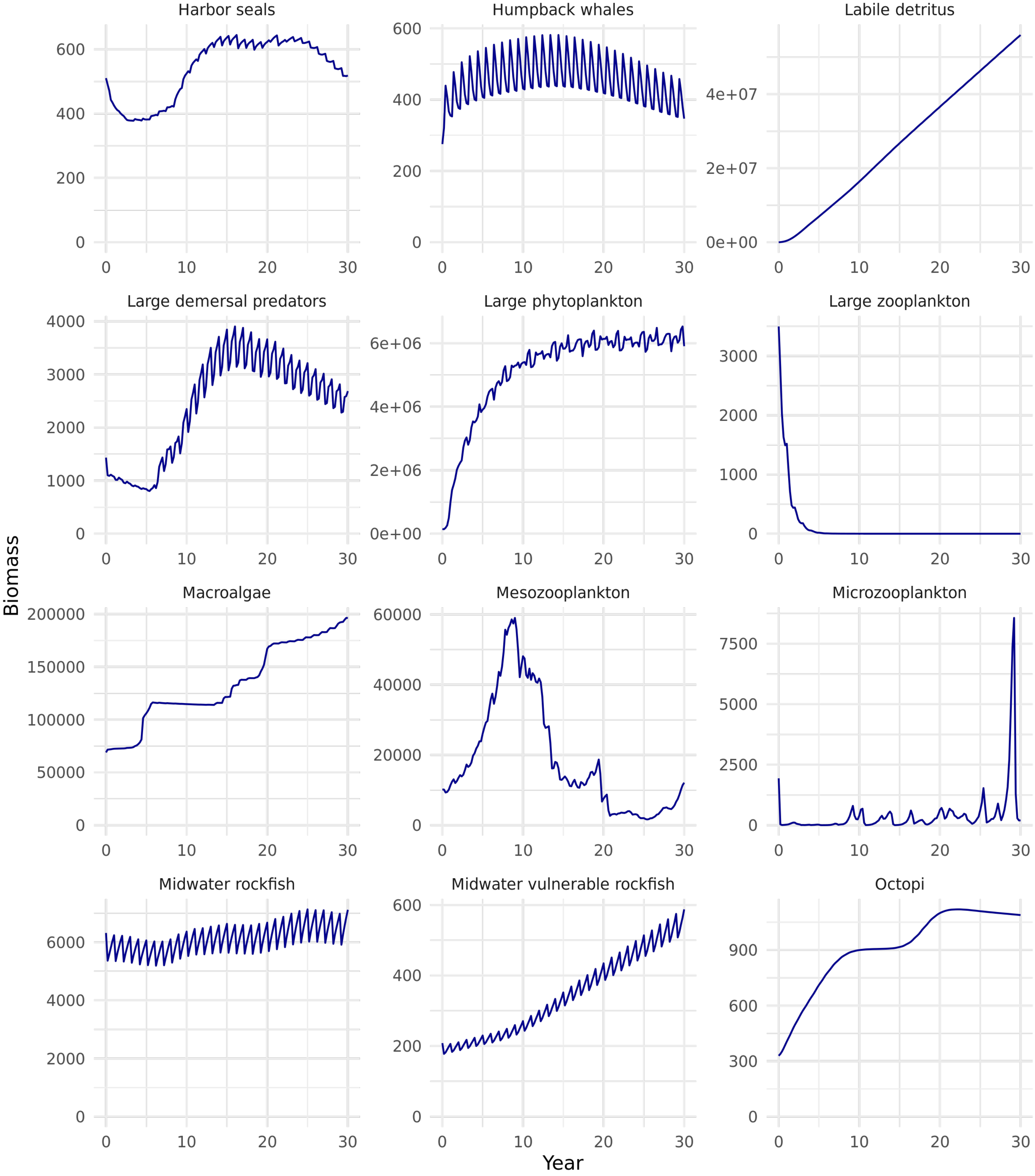

Figure 132 (continued). Biomass trajectories for functional groups in AMPS.

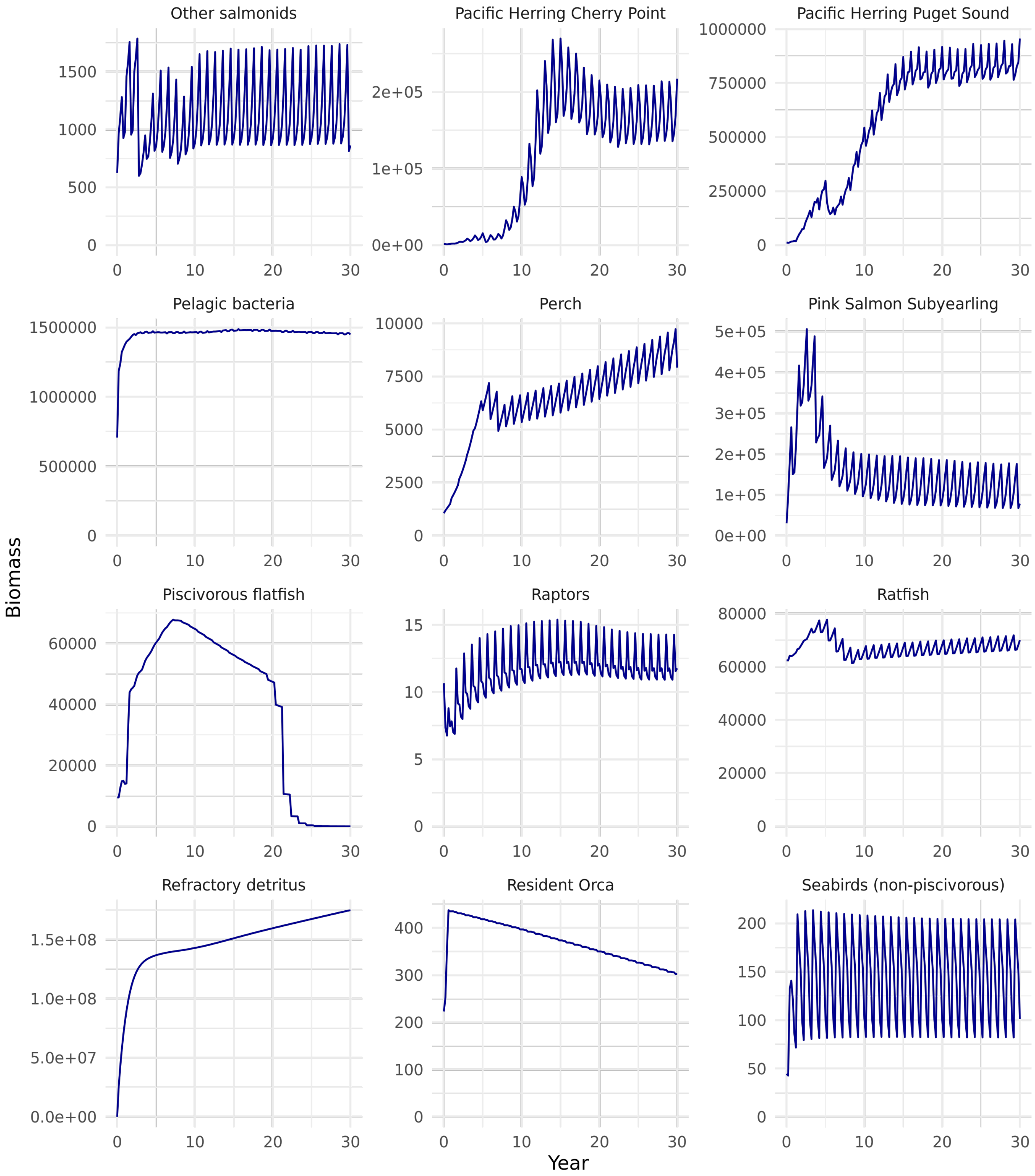

Figure 132 (continued). Biomass trajectories for functional groups in AMPS.

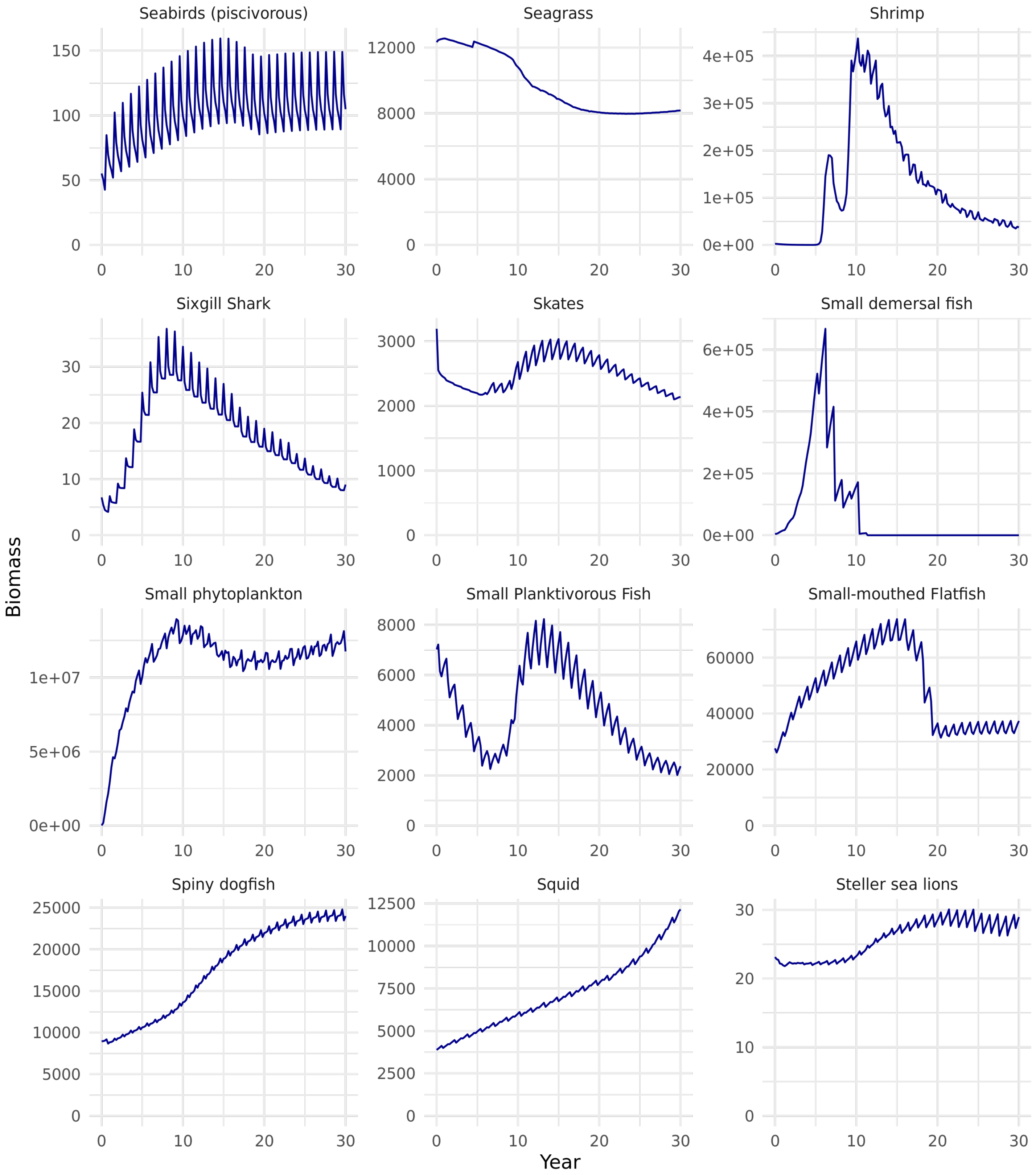

Figure 132 (continued). Biomass trajectories for functional groups in AMPS.

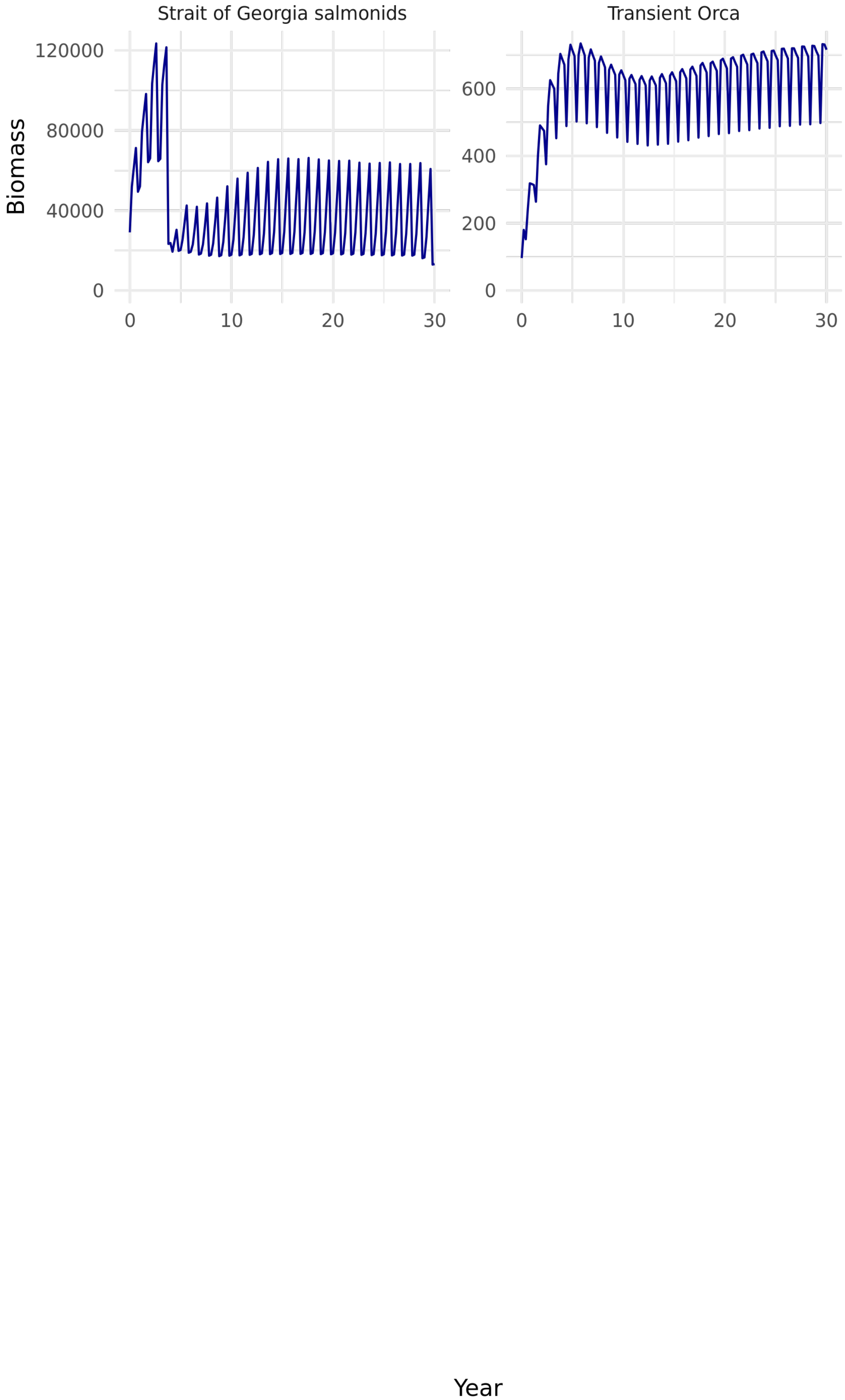

Figure 132 (continued). Biomass trajectories for functional groups in AMPS.

Conclusion

Ecosystem models incorporate complex ecosystem interactions, including all major processes such as hydrodynamics, nutrient cycling, food web interactions, and human activities (Bracis et al. 2020). The Atlantis ecosystem modeling framework is recognized as one of the most versatile approaches for ecosystem studies (Audzijonyte et al. 2019). Here, we developed an ecosystem model for Puget Sound, a fjord in Washington State. We carried out extensive data synthesis and analysis to develop data inputs to parameterize the model. The development of the AMPS model emphasizes the need for ongoing field and experimental work in Puget Sound that can support synthesis efforts such as the Salish Sea Marine Survival Project (Pearsall et al. 2021), of which AMPS development was part.

The tuning and calibration shown here demonstrate the operational status of AMPS. This model is generally stable over both no fishing and fishing scenarios and a range of fishing mortalities. In addition, individual weight-at-age diagnostics are well behaved, indicating reasonable values for the diet availability matrix and growth parameters. It is important to note, however, that Puget Sound is part of the Salish Sea, the combined waters of Puget Sound and the Strait of Georgia. Thus, there are ecosystem dynamics that are not considered here. A recently developed model for the Salish Sea (Porobic et al. 2021) contains an aggregated version of AMPS's polygonal structure and functional groups, and integrated its food web. This will allow multimodel comparisons.

We expect AMPS to contribute to efforts to protect and restore the Puget Sound ecosystem and help fill gaps in understanding this marine ecosystem. The increasingly urbanized Puget Sound watershed faces numerous threats, including loss of nearshore habitat, shipping, toxic contaminats, non-point source pollution, and harmful algal blooms (Essington et al. 2021). Forthcoming publications will use AMPS to investigate hypotheses of juvenile salmon survival, the ecosystem impacts of conservation actions directed to Southern Resident killer whales, and the cumulative impacts of ocean warming, pollution, and nutrient inputs.

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Tables

Table 1. Atlantis Model for Puget Sound polygon characteristics, including area, maximum depth, and number of layers. * = boundary box. Polygons 60–88 are islands.

Polygon	Area (km^2)	Depth (m)	Number of layers	Midpoint latitude	Midpoint longitude
0*	1,088.777	–150	5	48.824	–123.469
1	739.309	–150	5	48.842	–123.022
2	341.744	–25	2	48.979	–122.864
3	56.642	–5	1	48.927	–122.747
4	322.559	–50	3	48.644	–123.308
5	191.967	–350	6	48.606	–123.186
6	116.966	–100	4	48.687	–123.132
7	85.117	–150	5	48.698	–123.003
8	230.584	–100	4	48.662	–122.770
9	248.678	–25	2	48.643	–122.584
10	37.256	–5	1	48.587	–122.490
11	67.779	–5	1	48.523	–122.535
12	205.050	–50	3	48.486	–122.764
13	89.459	–50	3	48.566	–122.911
14	82.369	–100	4	48.581	–123.010
15	14.915	–50	3	48.492	–122.997
16	60.972	–100	4	48.431	–122.975
17*	490.843	–100	4	48.153	–123.067
18	287.789	–100	4	48.370	–123.150
19	143.432	–150	5	48.277	–123.031
20	534.884	–100	4	48.270	–122.898
21	44.640	–25	2	48.258	–122.719
22	62.658	–25	2	48.252	–122.637
23	172.975	–50	3	48.171	–122.564
24	102.752	–5	1	48.312	–122.467
25	43.569	–5	1	48.204	–122.415
26	91.786	–100	4	48.119	–122.377
27	33.107	–5	1	48.000	–122.239
28	131.643	–150	5	48.034	–122.366
29	242.838	–100	4	48.092	–122.673
30	42.031	–25	2	48.073	–122.745
31	11.649	–25	2	47.915	–122.538
32	177.710	–150	5	47.876	–122.464
33	33.542	–25	2	47.967	–122.466
34	18.197	–25	2	47.733	–122.382
35	65.690	–50	3	47.889	–122.628
36	76.390	–100	4	47.731	–122.751
37	67.794	–100	4	47.737	–122.842
38	103.128	–150	5	47.610	–122.957
39	43.518	–100	4	47.438	–123.104
40	49.848	–25	2	47.379	–122.992
41	80.121	–25	2	47.716	–122.634
42	48.870	–25	2	47.546	–122.511

Table 1 (continued). Atlantis Model for Puget Sound polygon characteristics.

Polygon	Area (km²)	Depth (m)	Number of layers	Midpoint latitude	Midpoint longitude
43	216.507	–150	5	47.653	–122.462
44	5.049	–25	2	47.640	–122.410
45	9.956	–100	4	47.602	–122.361
46	3.121	–25	2	47.560	–122.405
47	14.489	–100	4	47.534	–122.472
48	48.929	–100	4	47.374	–122.534
49	3.976	–25	2	47.403	–122.416
50	144.196	–150	5	47.412	–122.432
51	12.730	–25	2	47.391	–122.380
52	13.750	–25	2	47.382	–122.462
53	9.243	–100	4	47.279	–122.437
54	14.885	–50	3	47.285	–122.555
55	138.749	–100	4	47.150	–122.670
56	86.507	–50	3	47.289	–122.697
57	142.067	–50	3	47.168	–122.791
58	65.551	–25	2	47.117	–122.947
59	53.070	–25	2	47.151	–122.985
60	58.544	0	0	48.929	–123.446
61	179.880	0	0	48.800	–123.480
62	24.892	0	0	48.848	–123.284
63	30.289	0	0	48.762	–123.247
64	8.380	0	0	48.680	–123.200
65	0.564	0	0	48.641	–123.136
66	12.396	0	0	48.698	–123.038
67	1.485	0	0	48.752	–122.901
68	21.115	0	0	48.697	–122.664
69	149.465	0	0	48.617	–122.886
70	142.907	0	0	48.527	–123.066
71	4.112	0	0	48.600	–123.190
72	16.857	0	0	48.570	–122.960
73	77.799	0	0	48.498	–122.873
74	0.961	0	0	48.595	–122.813
75	15.664	0	0	48.559	–122.802
76	8.230	0	0	48.504	–122.816
77	20.018	0	0	48.572	–122.704
78	21.007	0	0	48.546	–122.613
79	428.587	0	0	48.171	–122.558
80	1.492	0	0	48.012	–122.317
81	72.166	0	0	47.660	–122.536
82	1.637	0	0	47.539	–122.493
83	94.373	0	0	47.416	–122.450
84	10.373	0	0	47.248	–122.629
85	12.758	0	0	47.215	–122.685
86	17.810	0	0	47.165	–122.708
87	49.290	0	0	47.230	–122.882
88	4.970	0	0	47.192	–122.908

Table 2. Atlantis Model for Puget Sound functional group composition, including initial model biomass.

#	Code	Biomass (t)	Group name	Taxa	Common name(s)
1	DC	110,853.97	Carrion		
2	DL	2,626.00	Labile detritus		
3	DR	2,626.46	Refractory detritus		
4	BB	4,203,673.55	Benthic bacteria		
5	PB	706,756.65	Pelagic bacteria		
6	PL	147,529.82	Large phytoplankton	*Skeletonema, Chaetoceros, Thalassiosira, Coscinodiscus, Coccolithophore.*	Diatoms, Coccolithophore.
7	PS	7,764.73	Small phytoplankton	*Gymnodinium, Gonyaulax, Pyramimonas,* and *Dichtyocha.*	Dinoflagellates, phytoflagellates.
8	MA	68,939.95	Macroalgae	Phylum Chlorophyta, Rhodophyta, and Ochrophyta; class Phaeophycea, *Nereocystis luetkeana.*	Green, red, and brown algae, and bull kelp.
9	SG	12,321.35	Seagrass	*Zostera marina*, *Z. japonica*, and *Phyllospadix* spp.	Eelgrass, Japanese eelgrass, and surfgrasses.
10	ZS	1,938.29	Microzooplankton	Ciliates, dinoflagellates including *Noctiluca*, foraminiferans, and radiolarians.	Unicellular heterotrophic protozoans, larval stage of benthic invertebrates, and rotifers.
11	ZM	10,174.04	Mesozooplankton	*Calanus pacificus*; the genera *Acartia, Pseudocalanus, Paracalanus*, and *Eucalanus.*	Copepods.
12	ZL	3,498.52	Large zooplankton	Chaetognaths, pelagic shrimp (e.g., families Sergestidae and Pasiphaeidae), hyperiid amphipods, the pelagic larval stages of benthic macroinvertebrates, and large predatory copepods; euphausiids.	Chaetognaths, pelagic shrimp (e.g., families Sergestidae and Pasiphaeidae), hyperiid amphipods, the pelagic larval stages of benthic macroinvertebrates, and large predatory copepods; euphausiids.
13	ZG	142,197.73	Gelatinous zooplankton	Phylum Cnidaria, Ctenophora, Scyphozoa; phylum chordata, class Appendicularia, Thaliacea; phylum Mollusca; *Aequorea victoria, Aurelia labiata, Cyanea capillata, Phacellophora camtschatica.*	Small hydromedusae, comb jellies, urochordates, larvaceans, pelagic salps, thecosomes, gymnosomes, crystal jelly, moon jelly, lion's mane jelly, fried egg jelly, and siphonophores.
14	SQX	3,885.55	Squid	*Rossia pacifica; Loligo opalescens.*	Stubby squid; opalescent inshore squid.
15	BMD	69,339.77	Deep macrozoobenthos	*Pisaster brevispinus, Luidia foliolata, Leptasterias hexactis, Crossaster papposus, Pycnopodia helianthoides, Solaster dawsoni, Polinices lewisii, Fusitriton oregonensis, Ceratostoma foliatum, Ocinebrellus inornatus, Urosalpinx cinerea*; class Ophiuroidea, *Ctenodiscus crispatus.*	Short-spined pinkstar, flat mud star, six-rayed star, rose star, sunflower sea star, morning sun star, predatory snails and nudibranchs, moon snail, hairy triton, leafy hornmouth, Japanese oyster drill, eastern oyster drill; brittle stars, mud star.

Table 2 (continued). Atlantis Model for Puget Sound functional group composition.

#	Code	Biomass (t)	Group name	Taxa	Common name(s)
16	BD	235,904.42	Deposit feeders	*Parastichopus californicus*; orders Cumacea, Isopoda, Tanaidacea, Amphipoda, suborders Gammaridea and Corophiidea; class Holothuroidea.	California sea cucumber; cumaceans, benthic-oriented copepods, amphipods, isopods, tanaidaceans; sea cucumbers.
17	BG	950.93	Benthic grazers	*Strongylocentrotus droebachiensis, Strongylocentrotus franciscanus; Tonicella lineata, Mopalia* spp., *Cryptochiton stelleri, Katharina tunicata; Brisaster latifrons.*	Green sea urchin, red sea urchin; small gastropods (snails, limpets), chitons, large gumboot chiton, black katy; heart urchin.
18	BMS	328.89	Octopus	*Octopus rubescens*, *Enteroctopus dofleini.*	Red octopus, Pacific giant octopus.
19	DUN	21,915.31	Dungeness crab	*Cancer magister, Metacarcinus magister.*	Dungeness crab.
20	BML	9,703.95	Crabs	*Cancer productus, C. gracilis, C. oregonensis*; family Majidae, superfamily Paguroidea, family Porcellanidae.	Red rock crab, graceful crab, pygmy rock crab; spider crabs, hermit crabs, porcelain crabs.
21	PWN	2,659.18	Shrimp	Genus *Crangon*; genera *Pandalus* and *Pandalopsis*; family Mysidae.	Crangon; pandalid shrimp; mysid.
22	BFF	11,969.17	Benthic filter feeders	*Chthalamus dalli, Balanus glandula, Semibalanus cariosus*; phylum Porifera, Cnidaria (class Hydrozoa, order Pennatulacea), Annelida (class Polychaeta), Phoronida, Bryozoa; *Styela clava, Ciona savignyi, Didemnum* spp.	Barnacles, thatched barnacle; sponges, colonial hydrozoans, sea pens, tube-dwelling worms such as serpulids, horseshoe worms, bryzoans; stalked sea squirt, solitary sea squirt.
23	BIV	397,270.97	Bivalves	*Transennella tantilla, Gemma gemma, Macoma carlottensis, M. balthica, Tresus capax, Saxidomus giganteus, Venerupis philippinarum; Mytilus edulis; Crassostrea gigas, Ostrea conchaphila, Chlamys rubida, C. hastata, Crassadoma gigantea, Patinopecten caurinus* .	Small clams, amethyst gem clam, Charlotte macoma, Baltic macoma, horse clam, butter clam, Manila clam; blue mussel; Pacific oyster, Olympia oyster, reddish scallop, spiny scallop, giant rock scallop, weathervane scallop.
24	GEC	206,257.59	Geoducks	*Panopea abrupta.*	Geoducks.
25	BC	154,708.99	Carnivorous infauna	Annelids (polychaetes), sipunculans, nemerteans, and turbellarians.	Annelids (polychaetes), sipunculans, nemerteans, and turbellarians.
26	HEP	12,844.09	Pacific herring Puget Sound	*Clupea pallasii.*	Pacific herring.
27	HEC	1,477.78	Pacific herring Cherry Point	*Clupea pallasii.*	Pacific herring.
28	FPS	7,021.65	Small planktivorous fish	*Ammodytes hexapterus; Hypomesus pretiosus, Spirinchus thaleichthys, Thaleichthys pacificus; Engraulis mordax; Sardinops sagax.*	Pacific sand lance; surf smelt, longfin smelt, eulachon; northern anchovy; sardine.
29	POP	1,058.33	Surfperch	*Rhacochilus vacca, Cymatogaster aggregata, Embiotoca lateralis, Brachyisticus frenatus.*	Pile perch, shiner perch, striped seaperch, kelp perch.

Table 2 (continued). Atlantis Model for Puget Sound functional group composition.

#	Code	Biomass (t)	Group name	Taxa	Common name(s)
30	CHY	63.90	Chinook hatch yearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
31	CHS	3,550.58	Chinook hatch subyearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
32	CSY	35.76	Chinook Skagit yearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
33	CSS	388.81	Chinook Skagit subyearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
34	CSN	33.35	Chinook Snohomish subyearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
35	CDS	15.87	Chinook Duwamish subyearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
36	CNY	0.09	Chinook Nisqually yearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
37	CNS	9.80	Chinook Nisqually subyearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
38	CHC	56.92	Chinook Hood Canal subyearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
39	CYE	3.18	Chinook other yearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
40	CKS	129.85	Chinook other subyearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
41	COH	1,171.66	Coho hatch yearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
42	COS	728.65	Coho Skagit yearling	*Oncorhynchus tshawytscha.*	Chinook salmon.
43	COD	6.81	Coho deep south yearling	*Oncorhynchus kisutch.*	Coho salmon.
44	COY	2,924.19	Coho other yearling	*Oncorhynchus kisutch.*	Coho salmon.
45	CMS	27,851.91	Chum hatch subyearling	*Oncorhynchus kisutch.*	Coho salmon.
46	CMF	43,219.67	Chum fall subyearling	*Oncorhynchus kisutch.*	Coho salmon.
47	CMH	372.82	Chum Hood Canal summer-run subyearling	*Oncorhynchus keta.*	Chum salmon.
48	PIS	18,428.86	Pink salmon subyearling	*Oncorhynchus gorbuscha.*	Pink salmon.
49	SAL	599.08	Other salmonids	*Oncorhynchus clarkii.*	Cutthroat trout
50	SAF	14,518.03	Strait of Georgia salmonids	*Oncorhynchus tshawytscha, O. nerka.*	Chinook and sockeye salmon.
51	FMM	20,672.26	Hake and large gadoids	*Merluccius productus; Gadus macrocephalus; Theragra chalcogramma.*	Pacific hake; Pacific cod; walleye pollock.

Table 2 (continued). Atlantis Model for Puget Sound functional group composition.

#	Code	Biomass (t)	Group name	Taxa	Common name(s)
52	FVS	1,433.67	Large demersal predators	*Ophiodon elongatus, Scorpaenichthys marmoratus; Anarrhichthys ocellatus.*	Lingcod, cabezon; wolf eel.
53	ROC	2,374.71	Demersal rockfish	*Sebastes caurinus, S. auriculatus, S. proriger, S. maliger, S. elongatus, S. brevispinis, S. empheus, S. diploroa, S. nebulosus, S. nigrocinctus, S. babcocki, S. reedi; Hemilepidotus hemilepidotus, H. spinosus; Myoxocephalus polyacanthocephalus; Sebastolobus alascanus.*	Copper rockfish, brown rockfish, redstripe rockfish, quillback rockfish, greenstriped rockfish, silvergray rockfish, Puget Sound rockfish, splitnose rockfish, China rockfish, tiger rockfish, redbanded rockfish, yellowmouth rockfish; red Irish lord, brown irish lord; great sculpin; shortspine thornyhead.
54	MRO	6,318.84	Midwater rockfish	*Sebastes melanops, S. miniatus, S. flavidus, S. entomelas, S. mystinus.*	Black rockfish, vermillion rockfish, yellowtail rockfish, widow rockfish, blue rockfish.
55	DVR	218.28	Demersal vulnerable rockfish	*Sebastes ruberrimus.*	Yelloweye rockfish.
56	MVR	208.43	Midwater vulnerable rockfish	*Sebastes paucispinis, S. pinniger.*	Bocaccio, canary rockfish.
57	SMD	4,329.99	Small demersal fish	Family of Zoarcidae; Cottidae, Hexagrammidae, Agonidea, Pholidae, Stichaeidae, *Porichthys notatus, Ronquilus jordani, Microgadus proximus, Rhinogobiops nicholsii, Syngnathus leptorhynchus, Aulorhynchus flavidus.*	Eelpouts; sculpins, greenlings, poachers, gunnels, pricklebacks, plainfin midshipmen, northern ronquil, Pacific tomcod, blackeye goby, bay pipefish, tubesnout.
58	FDF	27,590.35	Small-mouthed flatfish	*Microstomus pacificus; Citharichthys sordidus, Psettichthys melanostictus, Parophrys vetulus, Pleuronichthys coenosus, Platichthys stellatus, Citharichthys stigmaeus, Lepidopsetta bilineata, Glyptocephalus zachirus, Hippoglossoides elassodon, Isopsetta isolepis, Lyopsetta exilis.*	Dover sole; Pacific sanddab, sand sole, English sole, C-O sole, starry flounder, speckled sanddab, rock sole, rex sole, flathead sole, butter sole, slender sole.
59	HAP	9,481.36	Piscivorous flatfish	*Hippoglossus stenolepsis.*	Pacific halibut.
60	DOG	7,918.62	Spiny dogfish	*Squalus acanthias.*	Spiny dogfish.
61	SBL	6.75	Sixgill shark	*Hexanchus griseus.*	Sixgill shark.
62	SSK	3,191.75	Skates	*Raja rhina, R. binoculata.*	Longnose skate, big skate.
63	RAT	62,407.77	Ratfish	*Hydrolagus colliei.*	Spotted ratfish.

Table 2 (continued). Atlantis Model for Puget Sound functional group composition.

#	Code	Biomass (t)	Group name	Taxa	Common name(s)
64	SB	55.21	Seabirds (piscivorous)	*Megaceryle alcyon, Chroicocephalus philadelphia, Phalacrocorax penicillatu, Pelecanus occidentalis Larus californicus, Gavia immer, Mergus merganser, Uria aalge, Phalacrocorax auritus, Larus glaucescens, Ardea herodias, Larus argentatus, Lophodytes cucullatus, Oceanodroma leucorhoa, Brachyramphus marmoratus, Larus canus, Fulmarus glacialis, Gavia pacifica, Phalacrocorax pelagicus, Cepphus columba, Mergus serrator, Podiceps grisegena, Gavia stellata, Cerorhinca monocerata, Larus delawarensis, Ardenna grisea, Larus thayeri,* Alcidae, Laridae, Phalacrocoracidae, Gaviidae, Anatidae, Alcidae, Procellariidae, *Aechmophorus occidentalis, Larus occidentalis, L. glaucescens* × *L. occidentalis.*	Belted kingfisher, Bonapartes gull, Brandt's cormorant, brown pelican, California Gull, common loon, common merganser, common murre, double-crested cormorant, glaucous-winged gull, great blue heron, herring gull, hooded merganser, Leach's storm-petrel, marbled murrelet, mew gull, northern fulmar, Pacific loon, pelagic cormorant, pigeon guillemot, red-breasted merganser, red-necked grebe, red-throated loon, rhinoceros auklet, ring-billed gull, sooty shearwater, Thayer's gull, unidentified alcid, unidentified black-wingtip gull, unidentified cormorant, unidentified gull, unidentified large gull, unidentified loon, unidentified merganser, unidentified murre, unidentified murrelet, unidentified seabird, unidentified shearwater, unidentified small alcid, unidentified small gull, unidentified storm-petrel, unidentified tern, western grebe, western gull, western × glaucous winged gull.
65	SP	44.46	Seabirds (mainly nonpiscivorous)	*Fulica americana, Mareca americana, Synthliboramphus antiquus, Bucephala islandica, Branta bernicla nigricans, Haematopus bachmani, Melanitta americana, Arenaria melanocephala, Pluvialis squatarola, Spatula discors, Bucephala albeola, Branta canadensis, Aythya valisineria, Bucephala clangula, Calidris alpina, Mareca strepera, Aythya marila, Tringa melanoleuca, Anas carolinensis, Histrionicus histrionicus, Podiceps auritus, Charadrius vociferus, Anas platyrhynchos, A. acuta, Clangula hyemalis, Podilymbus podiceps, Phalaropus fulicarius, Oxyura jamaicensis, Arenaria interpres, Calidris alba, Charadrius semipalmatus, Chen caerulescens, Melanitta perspicillata, Calidris virgata, Cygnus buccinator, Fratercula cirrhata,* Anatidae, *Limnodromus griseus,* Podicipedidae, Scolopacidae, *Melanitta deglandi.*	American coot, American wigeon, ancient murrelet, Barrow's goldeneye, black brant, black oystercatcher, black scoter, black turnstone, black-bellied plover, blue-winged teal, bufflehead, Canada goose, canvasback, common goldeneye, dunlin, gadwall, greater scaup, greater yellowlegs, green-winged teal, harlequin duck, horned grebe, killdeer, mallard, northern pintail, oldsquaw, pied-billed grebe, red phalarope, ruddy duck, ruddy turnstone, sanderling, semi-palmated plover, snow goose, surf scoter, surfbird, trumpeter swan, tufted puffin, dabbling/pond duck, diving duck, dowitcher, unidentified duck, goldeneye, unidentified grebe, unidentified large grebe, unidentified large shorebirds, unidentified medium shorebirds, unidentified phalarope, unidentified sandpiper, unidentified scaup, unidentified scoter, unidentified small grebe, unidentified small shorebird, unidentified swan, unidentified teal, unidentified turnstone, unidentified yellowlegs, white-winged scoter.

Table 2 (continued). Atlantis Model for Puget Sound functional group composition.

#	Code	Biomass (t)	Group name	Taxa	Common name(s)
66	BE	10.66	Raptors	*Haliaeetus leucocephalus.*	Bald eagle.
67	HSL	510.35	Harbor seals	*Phoca vitulina.*	Harbor seals.
68	CSL	408.55	California sea lions	*Zalophus californianus.*	California sea lions.
69	PIN	23.14	Steller sea lions	*Eumetopias jubatus.*	Steller sea lions.
70	PHR	542.85	Harbor porpoise	*Phocoena phocoena.*	Harbor porpoise.
71	ROR	223.17	Resident orcas	*Orcinus orca.*	Resident killer whale.
72	TOR	96.59	Transient orcas	*Orcinus orca.*	Transient killer whale.
73	HUW	252.11	Humpbacks whale	*Megaptera novaeangliae.*	Humpback whale.

Table 3. Growth rate (*mum*; mg N × d –1 × individual –1) and ingestion rate (clearance; m^3 × mg N –1 × d –1) for invertebrates. Parameters were originally based on an Atlantis model for the California Current (Brand et al. 2007). Post-calibration values are shown.

Functional group		***mum* (g)**	**Clearance (C)**
BB	benthic bacteria	0.79500000000000	n/a
PB	pelagic bacteria	0.75000000000000	n/a
PL	large phytoplankton	0.34528328130000	n/a
PS	small phytoplankton	0.75877500000000	n/a
MA	macroalgae	0.99679165670000	n/a
SG	seagrass	0.19046746940000	n/a
ZS	microzooplankton	0.01990882353000	0.2000
ZM	mesozooplankton	0.00619687500000	0.6000
ZL	large zooplankton	0.04679827680000	0.5000
ZG	gelatinous zooplankton	0.00373964820000	0.2500
SQX	squid	0.00609424840300	0.2500
BMD	deep macrozoobenthos	0.00048575765770	0.4400
BD	deposit feeders	0.00210000000000	0.1400
BG	benthic grazers	0.00505500000000	0.6435
BMS	octopi	0.03138238897000	0.5000
BML	crabs	0.00002400557897	0.6600
PWN	shrimp	0.00005810693185	0.0100
BFF	benthic filter feeder	0.00850000000000	0.1400
BIV	bivalves	0.00066825000000	0.1400
BC	carnivorous infauna	0.00007500000000	0.1400
GEC	geoduck	0.00075000000000	0.0120
DUN	Dungeness crab	0.00839432400000	0.4000

Table 4. Vertebrate life-history parameters. *k* = growth rate, *L inf.* = the asymptotic length at which growth is zero, *a* and *b* = the coefficients of the allometric length–weight relationship, *Recr.* = recruitment. Days are calendar days.

Code	Functional group	Natural mortality	*k*	*L* inf.	Max age	Max length (mm)	*a*	*b*	Age at maturity	Recr. age to fishery (years)	Recr. age (days)[*]	Spawn start (day)[*]	Spawn end (day)[*]	Years per age class	# age classes
HEP	Pacific herring Puget Sound	0.473	0.411	23.206	7.000	457.200	0.010	3.119	3	1	90.000	15	105	1.0	7
HEC	Pacific herring Cherry Point	0.565	0.417	23.767	6.000	457.200	0.010	3.119	2	1	90.000	74	166	1.0	6
FPS	Small planktivorous fish	0.400	0.319	24.400	7.333	300.000	0.017	2.950	2	2	30.000	138	105	0.9	8
POP	Surfperch	1.023	0.302	20.671	7.286	320.625	0.014	3.141	2	2	150.000	172	233	0.9	8
CHY	Chinook hatch yearling	0.940	0.420	101.300	5.000	1,100.000	0.013	3.000	2	4	1.000	60	120	1.0	5
CHS	Chinook hatch subyearling	0.940	0.480	95.200	5.000	1,100.000	0.013	3.000	2	4	1.000	60	180	1.0	5
CSY	Chinook Skagit yearling	0.940	0.420	101.300	5.000	1,100.000	0.013	2.984	2	4	1.000	1	120	1.0	5
CSS	Chinook Skagit subyearling	0.940	0.480	95.200	5.000	1,100.000	0.013	2.984	2	4	1.000	36	196	1.0	5
CSN	Chinook Snohomish subyearling	0.940	0.480	95.200	5.000	1,100.000	0.013	2.978	2	4	1.000	52	166	1.0	5
CDS	Chinook Duwamish subyearling	0.940	0.480	95.200	5.000	1,100.000	0.024	2.838	2	4	1.000	51	181	1.0	5
CNY	Chinook Nisqually yearling	0.940	0.420	101.300	5.000	1,100.000	0.013	3.000	2	4	1.000	121	172	1.0	5
CNS	Chinook Nisqually subyearling	0.940	0.480	95.200	5.000	1,100.000	0.013	3.000	2	4	1.000	33	208	1.0	5
CHC	Chinook Hood Canal subyearling	0.940	0.480	95.200	5.000	1,100.000	0.728	2.017	2	4	1.000	152	181	1.0	5
CYE	Chinook other yearling	0.940	0.420	101.300	5.000	1,100.000	0.013	3.000	2	4	1.000	121	172	1.0	5
CKS	Chinook other subyearling	0.940	0.480	95.200	5.000	1,100.000	0.013	3.000	2	4	1.000	55	160	1.0	5
COH	Coho hatch yearling	1.400	0.980	80.000	3.000	825.000	0.004	3.170	3	2	1.000	91	121	1.0	3
COS	Coho Skagit yearling	1.400	0.980	80.000	3.000	825.000	0.004	3.170	3	2	1.000	60	181	1.0	3
COD	Coho deep south yearling	1.400	0.980	80.000	3.000	825.000	0.004	3.170	3	2	1.000	89	181	1.0	3
COY	Coho other yearling	1.400	0.980	80.000	3.000	825.000	0.004	3.170	3	2	1.000	59	171	1.0	3
CMS	Chum hatch subyearling	1.150	0.350	108.000	5.000	1,080.000	0.002	3.200	3	4	1.000	91	121	1.0	5
CMF	Chum fall subyearling	1.150	0.350	108.000	5.000	1,080.000	0.002	3.200	3	4	1.000	60	120	1.0	5
CMH	Chum Hood Canal summer-run subyearling	1.150	0.350	108.000	5.000	1,080.000	0.002	3.200	3	4	1.000	32	90	1.0	5
PIS	Pink salmon subyearling	1.740	2.300	61.000	3.000	760.000	0.002	3.200	2	2	1.000	91	181	1.0	3
SAL	Other salmonids	0.720	0.374	74.000	8.000	740.000	0.017	3.000	3	7	1.000	115	135	1.0	8
SAF	Strait of Georgia salmonids	0.940	0.480	95.200	5.000	1,100.000	0.013	3.000	2	4	1.000	55	160	1.0	5
FMM	Hake and large gadoids	0.521	0.518	54.602	17.667	631.067	0.010	3.048	2	2	127.500	43	139	1.8	10
FVS	Large demersal predators	0.265	0.211	98.376	20.500	990.000	0.016	3.075	3	2	90.000	46	120	2.1	10
ROC	Demersal rockfish	0.113	0.182	46.736	37.854	463.095	0.014	3.140	5	2	247.500	99	158	3.8	10

[*] Freshwater habitat is not explicitly represented in Atlantis, so for modeling purposes, salmon “recruit” to Atlantis on the day of juvenile outmigration. Recruits are parameterized to appear immediately after (i.e., one day after) a “spawn period” that corresponds with dates of juvenile outmigration.

Table 4 (continued). Vertebrate life-history parameters.

Code	**Functional group**	**Natural mortality**	***k***	***L* inf.**	**Max age**	**Max length (mm)**	***a***	***b***	**Age at maturity**	**Recr. age to fishery (years)**	**Recr. age (days)**[*]	**Spawn start (day)**[*]	**Spawn end (day)**[*]	**Years per age class**	**# age classes**
MRO	Midwater rockfish	0.080	0.319	48.660	31.429	703.333	0.040	2.917	7	2	69.000	1	32	3.1	10
DVR	Demersal vulnerable rockfish	0.134	0.050	74.100	72.500	946.000	0.018	3.006	18	2	60.000	32	243	7.3	10
MVR	Midwater vulnerable rockfish	0.065	0.071	46.000	39.000	835.000	0.013	3.033	6	2	90.000	1	32	3.9	10
SMD	Small demersal fish	0.563	0.433	21.400	5.000	85.000	0.007	3.245	2	2	70.000	32	181	1.0	5
FDF	Small-mouthed flatfish	0.463	0.380	33.939	22.556	419.233	0.009	3.160	2	2	109.333	17	128	2.3	10
HAP	Piscivorous flatfish	0.220	0.219	56.384	22.500	1,783.500	0.004	3.155	8	-	104.000	335	90	2.3	10
DOG	Spiny dogfish	0.094	0.046	121.276	73.500	1,040.000	0.002	3.202	29	2	665.000	275	365	7.4	10
SBL	Sixgill shark	0.058	0.080	425.000	80.000	5,056.667	0.006	3.017	19	2	663.333	32	151	8.0	10
SSK	Skates	0.200	0.057	180.220	25.500	1,489.767	0.004	3.060	7	2	365.000	1	365	2.6	10
RAT	Ratfish	0.215	0.245	45.000	14.100	422.250	0.073	2.465	8	2	270.000	182	243	1.4	10
SB	Seabirds (piscivorous)	0.312	0.000	59.400	18.758	577.746	0.007	3.000	3	-	39.747	111	131	1.9	10
SP	Seabirds (mainly nonpiscivorous)	0.290	0.000	45.000	16.779	430.657	0.010	3.000	2	-	30.000	100	120	1.7	10
BE	Raptors	0.336	0.000	83.000	25.000	830.000	0.008	3.000	4	-	112.000	72	79	2.5	10
HSL	Harbor seals	0.307	0.630	190.000	15.000	1,900.000	0.009	3.000	4	-	300.000	207	338	1.5	10
CSL	California sea lions	0.461	0.352	240.000	10.000	2,070.000	0.011	3.000	5	-	344.000	210	330	1.0	10
PIN	Steller sea lions	0.200	0.392	330.000	25.000	2,630.000	0.005	3.000	6	-	364.000	153	173	2.5	10
PHR	Harbor porpoise	0.192	0.900	183.500	24.000	1,900.000	0.005	3.000	3	-	315.000	182	304	2.4	10
ROR	Resident orca	0.010	0.280	915.000	90.000	9,150.000	0.003	3.000	13	-	485.000	121	274	9.0	10
TOR	Transient orca	0.010	0.280	915.000	90.000	9,150.000	0.003	3.000	13	-	485.000	121	274	9.0	10
HUW	Humpback whale	0.044	0.266	1,814.000	75.000	18,600.000	0.004	3.000	5	-	345.000	1	45	7.5	10

[*] Note: Since freshwater habitat is not explicitly represented in Atlantis, for modeling purposes salmon 'recruit' to Atlantis on the day of juvenile outmigration. Recruits are parameterized to appear immediately after (i.e. one day after) a 'spawn period' that corresponds with dates of juvenile outmigration.

Table 5. Sources of diet data incorporated into the analysis to derive the availability matrix.

#	Source
1	Akmajian, A. M. 2016. Year-round algal toxin exposure in free-ranging Sea lions: Implications of trophic exposure for declining populations. Master's thesis. Western Washington University, Bellingham, Washington.
2	Anderson, E. M., and J.R. Lovvorn. 2012. Seasonal dynamics of prey size mediate complementary functions of mussel beds and seagrass habitats for an avian predator. Marine Ecology Progress Series 467:219–232.
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15	Beaudreau, A. H. and T. E. Essington. 2007. Spatial, Temporal, and Ontogenetic Patterns of Predation on Rockfishes by Lingcod. Trans. Am. Fish. Soc. 136:1438–1452.
16	Bizzarro, J. J., A. B. Carlisle, W. D. Smith, and E. Cortés. 2017. Chapter Four- Diet composition and trophic ecology of Northeast Pacific Ocean sharks. Pages 111–148 in S. E. Larson and D. Lowry, editors. Advances in Marine Biology. Vol. 77. Academic Press.
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Table 5 (continued). Sources of diet data incorporated into the analysis to derive the availability matrix.

#	Source
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26	Cordell, J. R., H. Higgins, C. Tanner, and J. K. Aitkin. 1998. Biological status of fish and invertebrate assemblages in a breached-dike wetland site at Spencer Island, Washington. Technical Report. School of Aquatic and Fishery Science, Fisheries Research Institute, Washington University 9805.
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35	Duffy, E. J., and D. A. Beauchamp. 2008. Seasonal patterns of predation on juvenile Pacific salmon by anadromous cutthroat trout in Puget Sound. Transactions of the American Fisheries Society 137(1):165–181.
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43	Feehan, C. J., B. C. GraumanBoss, R. R. Strathmann, M. N. Dethier, and D. O. Duggins. 2018. Kelp detritus provides high-quality food for sea urchin larvae. Limnology and Oceanography 63(S1):S299-S306.
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Table 5 (continued). Sources of diet data incorporated into the analysis to derive the availability matrix.

#	Source
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47	Ford, J. K., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm, and K. C. Balcomb III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76(8):1456–1471.
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50	Fulmer, J. H., and S. M. Bollens. 2005. Responses of the chaetognath, *Sagitta elegans*, and larval Pacific hake, *Merluccius productus*, to spring diatom and copepod blooms in a temperate fjord (Dabob Bay, Washington). Progress in Oceanography 67(3–4):442–461.
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52	Gordon, C. D. 1965. Aspects of the life-history of *Cymatogaster aggregata Gibbons*. Doctoral dissertation. University of British Columbia, Vancouver, Canada.
53	Gotshall, D. W. 1977. Stomach contents of northern California Dungeness crabs, *Cancer magister*. California Fish and Game 63:43–51.
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59	Howard, S., M. M. Lance, S. J. Jeffries, and A. Acevedo-Gutiérrez. 2013. Fish consumption by harbor seals (*Phoca vitulina*) in the San Juan Islands, Washington. Fishery Bulletin 111(1):27–41.
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Table 5 (continued). Sources of diet data incorporated into the analysis to derive the availability matrix.

#	Source
69	Kennedy, L. A., F. Juanes, and R. El Sabaawi. 2018. Eelgrass as valuable nearshore foraging habitat for juvenile Pacific salmon in the early marine period. Marine and Coastal Fisheries 10(2):190–203.
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71	Lance, M. M., and S. J. Jeffries. 2006. Estimating importance of rockfish, lingcod and other bottomfish in the diet of harbor seals in the San Juan Islands. Contract Report to SeaDoc Society Research Agreement, K004431-22.
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74	Lance, M. M., and S. F. Pearson. 2012. Assembling and assessing seabird diet information in the Salish Sea. Washington Department of Fish and Wildlife. Wildlife Research Division, Olympia, Washington.
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Table 5 (continued). Sources of diet data incorporated into the analysis to derive the availability matrix.

#	Source
94	Navarrete, S. A., and E. A. Wieters. 2000. Variation in barnacle recruitment over small scales: larval predation by adults and maintenance of community pattern. Journal of experimental marine biology and ecology 253(2):131–148.
95	Nelson, B. W., S. F. Pearson, A. J.H., S. Jeffries, A. C. Thomas, A. Acevedo-Gutierrez, I. M. Kemp, M. M. Lance, A. Louden, and M. R. Voelker. 2021. Variation in predator diet and prey size affects perceived impacts to salmon species of high conservation concern. Canadian Journal of Fisheries and Aquatic Sciences. 78(11):1661–1676
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Table 5 (continued). Sources of diet data incorporated into the analysis to derive the availability matrix.

#	Source
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Table 5 (continued). Sources of diet data incorporated into the analysis to derive the availability matrix.

#	Source
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Table 6. Summary of sources for functional group spatial distribution and density.

Functional groups	Data analysis	Data source
Deep macrozoobenthos (BMD), deposit feeders (BD), benthic filter feeder (BFF), bivalves (BIV), crabs (BML), shrimp (PWN).	Geostatistical modeling (VAST).	Washington State Department of Ecology's Puget Sound Assessment and Monitoring Program (PSAMP).
Chinook (CHY–CKS), coho (COH–COY), chum (CMS–CMH), and other salmon functional groups (pink salmon [PIS], other salmonids [SAL], and Strait of Georgia salmonids [SAF]). Spiny dogfish (DOG), small planktivorous fish (FPS), Pacific herring (HEP, HEC), hake and large gadoids (FMM).	Geostatistical modeling (VAST).	Midwater trawl surveys by the RV *Ricker*.

Table 7. Migration parameters for functional groups in AMPS. Salmon data sources are listed in Table 8; data sources for other species are described in the main text. For salmon, two migrations are set. The first is one upstream migration for adults only (with no re-entry into model domain, noted as "n/a"). The second migration is of juveniles migrating out of Puget Sound, returning from the ocean as adults back into Puget Sound. For this second migration, we assume a 45-day window from start to end of the migration: adults are assumed to return to Puget Sound more than 1 day and less than 45 days prior to the first spawner migration upstream. Similarly, juveniles are assumed to migrate out of Puget Sound over a 45-day period, with timing determined by plotting distributions of tagged fish from RV *W. E. Ricker* surveys (see main text).

Code	Functional Group	Start of departure from Puget Sound	Start of return migration to Puget Sound	Migration window (# days)	Percent of population migrating	Years outside model domain
HEC	Pacific herring Cherry Point	182	258	15	100.0%	0
HEP	Pacific herring Puget Sound	182	258	15	100.0%	0
CHY	Chinook hatch yearling (ocean migration)	213	168	45	69.0%	4
CHY	Chinook hatch yearling (spawners)	213	n/a	75	100.0%	0
CHS	Chinook hatch subyearling (ocean migration)	227	168	45	79.0%	4
CHS	Chinook hatch subyearling (spawners)	213	n/a	75	100.0%	0
CSY	Chinook Skagit yearling (ocean migration)	213	165	45	86.0%	4
CSY	Chinook Skagit yearling (spawners)	166	n/a	143	100.0%	0
CSS	Chinook Skagit subyearling (ocean migration)	227	165	45	86.0%	4
CSS	Chinook Skagit subyearling (spawners)	166	n/a	143	100.0%	0
CSN	Chinook Snohomish subyearling (ocean migration)	227	90	45	86.0%	4
CSN	Chinook Snohomish subyearling (spawners)	135	n/a	123	100.0%	0
CDS	Chinook Duwamish subyearling (ocean migration)	227	168	45	74.0%	4
CDS	Chinook Duwamish subyearling (spawners)	213	n/a	60	100.0%	0
CNY	Chinook Nisqually yearling (ocean migration)	213	178	45	73.0%	4
CNY	Chinook Nisqually yearling (spawners)	223	n/a	46	100.0%	0
CNS	Chinook Nisqually subyearling (ocean migration)	227	178	45	73.0%	4
CNS	Chinook Nisqually subyearling (spawners)	223	n/a	46	100.0%	0
CHC	Chinook Hood Canal subyearling (ocean migration)	227	151	45	70.0%	4
CHC	Chinook Hood Canal subyearling (spawners)	196	n/a	47	100.0%	0
CYE	Chinook other yearling (ocean migration)	213	151	45	69.0%	4
CYE	Chinook other yearling (spawners)	196	n/a	62	100.0%	0
CKS	Chinook other subyearling (ocean migration)	227	151	45	79.0%	4

Table 7 (continued). Migration parameters for functional groups in AMPS.

Code	Functional Group	Start of departure from Puget Sound	Start of return migration to Puget Sound	Migration window (# days)	Percent of population migrating	Years outside model domain
CKS	Chinook other subyearling (spawners)	196	n/a	62	100.0%	0
COH	Coho hatch yearling (ocean migration)	213	218	45	94.7%	3
COH	Coho hatch yearling (spawners)	263	n/a	44	100.0%	0
COS	Coho Skagit yearling (ocean migration)	213	126	45	95.7%	3
COS	Coho Skagit yearling (spawners)	171	n/a	173	100.0%	0
COD	Coho deep south yearling (ocean migration)	213	208	45	88.5%	3
COD	Coho deep south (spawners)	253	n/a	30	100.0%	0
COY	Coho other yearling (ocean migration)	213	151	45	94.7%	3
COY	Coho other yearling (spawners)	196	n/a	123	100.0%	0
CMS	Chum hatch subyearling (ocean migration)	196	274	45	100.0%	4
CMS	Chum hatch subyearling (spawners)	319	n/a	44	100.0%	0
CMF	Chum fall subyearling (ocean migration)	196	274	45	100.0%	4
CMF	Chum fall subyearling (spawners)	319	n/a	44	100.0%	0
CMH	Chum Hood Canal summer-run subyearling (ocean migration)	110*	195	45	100.0%	4
CMH	Chum Hood Canal summer-run subyearling (spawners)	240	n/a	60	100.0%	0
PIS	Pink salmon subyearling (ocean migration)	213	215	45	100.0%	2
PIS	Pink salmon subyearling (spawners)	260	n/a	20	100.0%	0
SAL	Other salmonids (ocean migration)	213	127	45	100.0%	3
SAL	Other salmonids (spawners)	172	n/a	26	100.0%	0
SAF	Strait of Georgia salmonids (ocean migration)	227	199	45	79.0%	4
SAF	Strait of Georgia salmonids (spawners)	244	n/a	121	100.0%	0
DOG	Spiny dogfish	1	121	15	90.0%	0
SBL	Sixgill shark (adults)	91	305	30	100.0%	0
PIN	Steller sea lion	32	244	30	65.0%	0
CSL	California sea lion	69	244	30	100.0%	0
BE	Raptors	206	251	7	29.0%	0
BE	Raptors	30	305	60	71.0%	0
SP	Nonpiscivorous seabirds	152	273	30	100.0%	0
ROR	Resident orcas	274	121	45	100.0%	0
TOR	Transient orcas	152	182	15	75.0%	0
TOR	Transient orcas	244	60	60	100.0%	0
HUW	Humpback whales	335	121	30	100.0%	0

*Based on description from Tynan (1997).

Table 8. Salmon life-history parameters. Summary of parameters for salmon groups. Note adult spawn dates are included here, but since freshwater habitat is outside the model domain, for purposes of model parameterization the outmigrant timing to salt water dictates arrival of juveniles into the model. *F* = fry, *P* = parr.

Code	Group name	Adult abundance, 2011	Hatchery releases, 2011	Residency	Adult return to freshwater (day of year)	Adult spawn date (day of year)	Outmigrant timing from streams (day of year)	Out-migrant size (mm)
CHY	Chinook hatch yearling	4,186	Chinook 730,000	31.0%[1]	213–288	258–304[2]	60–120[3]	163[4]
CHS	Chinook hatch subyearling	183,282	Chinook 32,000,000	21.0%[1]	213–288	258–304[2]	60–181[2]	81[4]
CSY	Chinook Skagit yearling	1,059	Chinook	14.0%[5]	166–309	232–319	1–120[6]	120[7]
CSS	Chinook Skagit subyearling	8,152	Chinook	14.0%[1]	166–309	232–319	F 36–126 P 126–196[8]	F 45 P 75[8]
CSN	Chinook Snohomish subyearling	1,420	Chinook	14.0%[1]	135–258[9]	239–328[10]	F 52–166 P 95–157	F 44 P 65[11]
CDS	Chinook Duwamish subyearling	671	Chinook	26.0%[1]	213–273[12]	272–292	F 51–181 P 135–181[13]	F 40 P 75[13]
CNY	Chinook Nisqually yearling	5	Chinook	27.0%[1]	223–269[14]	232–276[14]	121–172[15]	120[15]
CNS	Chinook Nisqually subyearling	536	Chinook	27.0%[1]	223–269[16]	232–276[17]	F 33–54 P 152–208[2]	F 40 P 95[2]
CHC	Chinook Hood Canal subyearling	2,631	Chinook	30.0%[1]	196–243[18]	236–278[18]	152–181[19]	83[19]
CYE	Chinook other yearling	106	Chinook	31.0%[1]	196–258	265–298	121–172[20]	120[21]
CKS	Chinook other subyearling	3,425	Chinook	21.0%[1]	196–258	265–298	F 55–110 P 110–160	F 43 P 63
COH	Coho hatch yearling	78,492	Coho 5,096,000	5.3%[22]	263–304[23]	305–340	91[3]	136 (28 g)[4]
COS	Coho Skagit yearling	41,061	Coho	4.3%	171–344[2]	274–90[2]	60–181[2]	105[24]
COD	Coho deep south yearling	412	Coho	11.5%	253–283[16]	305–327	89–181[25]	105[15]
COY	Coho other yearling	195,888	Coho	5.3%	196–319[26]	298–365[27]	59–171[28]	105[29]
CMS	Chum hatch subyearling	538,000	Chum 46,000,000	0.0%	319–363[30]	344–363	91[3]	45[31]
CMF	Chum fall subyearling	835,000	Chum	0.0%	319–363[30]	344–363	60–120[31]	45[31]
CMH	Chum Hood Canal summer-run subyearling	7,200	Chum	0.0%	240–300[32]	258–300[31]	32–90[32]	39[32]
PIS	Pink salmon subyearling	5,299,000	Pink	0.0%	260–280[33]	260–298[34]	91–181[35]	38[19]
SAL	Other salmonids	70,781	Sockeye	0.0%	172–198[36]	263–295	115–135[37]	135[37]
SAF	Strait of Georgia salmonids	338,178	Chinook	21.0%[1]	244–365[38]	244–365[38]	F 55–100 P 110–160[39]	F 43 P 63[39]

Notes

1. Chinook salmon residency based on hatchery stocks, from Chamberlin et al. (2011).
2. B. Barkdull (personal communication).
3. RMIS database.
4. B. Nelson (personal communication), extraction from RMIS database.
5. Chinook salmon residency based on Nooksack River hatchery stocks, from Chamberlin et al. (2011).
6. Based on outmigrant yearling + subyearling from Skagit River, Jan–Jul (B. Barkdull, personal communication).
7. Very approximate for Skagit River, based on Nisqually River yearling fork length.
8. Skagit River Chinook salmon juvenile outmigrant time and size from Zimmerman et al. (2015).
9. Snohomish River Chinook salmon data from M. Crewson (personal communication), based on 2009–13.
10. Snohomish River Chinook salmon data from M. Crewson (personal communication), based on spawning ground survey data from P. Verhey.
11. Snohomish River delta (J. Chamberlin and M. Pouley, personal communication).
12. Very approximate, based on Chinook salmon in Duwamish River: http://www.govlink.org/watersheds/8/action/salmon-seeson/duwamish.aspx
13. Duwamish fry and parr size and outmigrant timing: Nelson et al. (2004).
14. Assumed same as Nisqually River subyearling.
15. Nisqually River outmigrant timing and size from Klungle et al. (2017).
16. J. Losee (personal communication).
17. J. Moore (personal communication).
18. Hood Canal adult return timing and spawn data from Skokomish Indian Tribe (2017).
19. Based on beach seine data from E. Bishop and H. Daubenberger (personal communication).
20. Very approximate, based on Nisqually River yearling outmigration dates.
21. Very approximate, based on Nisqually River yearling fork length.
22. Coho salmon residency from Rohde et al. (2014).
23. Coho salmon adult return times from Weitkamp et al. (1995).
24. Very approximate; Skagit River coho salmon outmigrant fork length set equal to Nisqually River.
25. S. Steltzner (personal communication) for Cranberry, Skookum, and Goldsborough Creeks.
26. Snohomish River coho salmon data from M. Crewson (personal communication), based on 2009–13.
27. Snohomish River coho salmon estimates of first and last redd dates from M. Crewson (personal communication), based on spawning ground survey data from P. Verhey. Note: spawning duration truncated to end 31 Dec rather than 21 Jan.
28. From Snohomish River coho salmon data from M. Pouley and M. Crewson (personal communication).
29. Very approximate; other coho outmigrant fork length set equal to Nisqually River.
30. Based on Hood Canal chum salmon data from Johnson et al. (1997).
31. Based on values reported in Johnson et al. (1997).
32. Summer-run chum salmon data from Tynan (1997).
33. Pink salmon return times based on Hood Canal values in Hard et al. (1996).
34. Pink salmon spawn dates 244–298 based on Hood Canal values in Hard et al. (1996).
35. Based on beach seine data from E. Bishop and H. Daubenberger (personal communication) and RMIS database.
36. Sockeye salmon adult timing at Ballard Locks from N. Overman (personal communication).
37. Sockeye salmon smolt size and timing from Gustafson et al. (1997).
38. DFO (1999).
39. Assumed same as Chinook other subyearling.

Table 9. Regional Mark Information System (RMIS) domains corresponding to AMPS salmon functional groups. *NPS* = North Puget Sound, *MPS* = Mid-Puget Sound, *SPS* = South Puget Sound, *HOOD* = Hood Canal, *NOWA* = Northern Washington, *SKAG* = Skagit River, *CRGN* = Columbia River, *FRTH* = Fraser River, *UPCR* = Upper Columbia River, *JUAN* = Strait of Juan de Fuca, *LOCR* = Lower Columbia River, *WILP* = Willapa Bay, *GST* = Strait of Georgia, *NWC* = Northern Washington Coast.

AMPS functional group	AMPS code	RMIS domain(s)
Chinook hatch yearling	CHY	All
Chinook hatch subyearling	CHS	All
Chinook Skagit yearling	CSY	SKAG, NOWA
Chinook Skagit subyearling	CSS	SKAG, NOWA
Chinook Snohomish subyearling	CSN	NPS
Chinook Duwamish subyearling	CDS	MPS
Chinook Nisqually yearling	CNY	SPS
Chinook Nisqually subyearling	CNS	SPS
Chinook Hood Canal subyearling	CHC	HOOD
Chinook other yearling	CYE	CRGN, UPCR, JUAN, LOCR, WILP, NWC, MPS, NPS, HOOD
Chinook other subyearling	CKS	CRGN, UPCR, JUAN, LOCR, WILP, NWC
Coho hatch yearling	COH	CRGN, UPCR, JUAN, LOCR, WILP, NWC
Coho Skagit yearling	COS	SKAG, NOWA
Coho deep south yearling	COD	SPS
Coho other yearling	COY	CRGN, UPCR, JUAN, LOCR, WILP, NWC
Strait of Georgia salmonids	SAF	FRTH, GST

Table 10. Chinook adult fork length (FL).

Atlantis group(s)	River	Source or gear	Years	Sample size	Subyearling FL (mm)	Yearling FL (mm)
Nisqually subyearling, Nisqually yearling	Nisqually*	Tribal fishery (driftnet/setnet); hatchery ponds	1993–2004	212	731	723
Skagit subyearling, Skagit yearling	Skagit*	Tribal fishery (drift gillnet/setnet)	1992–96	116	831	793
Duwamish subyearling	Duwamish*	Tribal fishery (drift gillnet/setnet)	1992–2006	382	654	743
All other Chinook subyearling or yearling groups	Growth modeling† for FRAM (Fishery Regulation Assessment Model)		Brood years 2005–08	5,605	702	675

* O'Neill (personal communication).

† McHugh et al. (2015).

Table 11. Adult Chinook and coho salmon parameters for length–weight conversion, based on sampling by S. O'Neill (personal communication). Parameters a and b are for $W = a \times L^b$, where W is wet weight per individual in grams, and L is fork length in mm.

Species	N	a	b	Years
Chinook salmon	1,238	1.32×10^{-05}	3.00000000	1992–2007
Coho salmon	2,926	4.50×10^{-06}	3.16722459	1992–2008

Table 12. Average fish weights (kg) for fish species extracted by recreational fisheries. Based on length–weight data from WDFW port sampling, weight from a bottomfish survey in North Puget Sound (Lauth et al. 1988), or estimated weight from common length using length–weight relationships available in Fishbase (Froese and Pauly 2014).

Species	Average weight
American shad	0.1246
Arrowtooth flounder	1.7917
Big skate	39.3660
Black rockfish	1.2575
Blue rockfish	1.1485
Bocaccio	2.0017
Brown Irish lord	0.9333
Brown rockfish	0.8979
Buffalo sculpin	0.0667
Butter sole	0.2000
C-O sole	0.0550
Cabezon	3.2664
Canary rockfish	1.6286
China rockfish	1.0755
Chinook salmon	4.1047
Chum salmon	3.6169
Cod	2.9788
Coho salmon	4.0086
Copper rockfish	1.0439
Cutthroat trout	18.6000
Dogfish shark	118.9185
Dolly Varden	0.8118
Dover sole	0.4117
English sole	0.1944
Eulachon	0.0320
Flatfish	0.4540
Flathead sole	0.1345
Giant Pacific octopus	30.0000
Great sculpin	9.0000
Greenling	1.1137
Greenstriped rockfish	0.2800
Humboldt squid	20.8636
Kelp greenling	0.8856
Lingcod	4.3266
Longnose skate	0.8273
Market squid	21.6625
Miscellaneous bottomfish	3.9700
Miscellaneous foodfishes	3.0264
Northern anchovy	0.0260
Octopus	30.0000
Pacific cod	2.9788
Pacific hake[*]	0.2500
Pacific halibut	11.1429
Pacific herring	0.5566
Pacific sanddab	0.5830
Pacific sardine	0.1126
Pacific staghorn sculpin	1.0667
Pacific tomcod	0.2600
Pacific whiting[*]	1.3372
Petrale sole	0.7765
Pile perch	0.0178
Pink salmon	0.7973
Plainfin midshipman	0.0564
Puget Sound rockfish	0.0500
Quillback rockfish	1.1084
Ratfish	1.0152
Red Irish lord	0.7354
Redbanded rockfish	4.4400
Redstripe rockfish	1.9123
Rex sole	0.5729
Rock greenling	0.2800
Rock sole	0.6707
Rockfish	1.7542
Sablefish	1.5000
Sand sole	0.7000
Sculpins	0.8000
Sea cucumber	0.1253
Shellfish, general	0.0000
Shiner surfperch	0.0235
Silvergrey rockfish	1.9123
Sixgill shark	364.5000
Skates and rays	0.8273
Slender sole	0.0471
Sockeye salmon	1.9626
Speckled sanddab	0.6989
Spiny dogfish	2.0000
Squid	0.1100
Starry flounder	1.0614
Steelhead	2.4565
Striped seaperch	0.4560
Surf smelt	0.3000
Surfperch	0.7333
Tiger rockfish	1.3854
Unknown salmon	3.9101
Vermillion rockfish	1.6500
Walleye pollock	0.5000
White seaperch	0.1691
Whitespotted greenling	0.3600

[*] Pacific hake and Pacific whiting are the same species (*Merluccius productus*). They are separated here based on the reported catch statistics.

Table 12 (continued). Average fish weights for fish species extracted by recreational fisheries.

Species	Average weight	Species	Average weight
Widow rockfish	1.6000	Yelloweye rockfish	1.2500
Wolf-eel	18.4000	Yellowtail rockfish	1.1325

Table 13. Fleets specified in the model. Table indicates type of fleet: commercial (0) or recreational (1), pelagic (0) or demersal (1), and whether they operate during the night (0), day (1), or both (2).

Name	Commercial or recreational	Pelagic or demersal	Nocturnal or diurnal
Bottom trawl	0	1	1
Bottom trawl, tribal	0	1	1
Canadian indigenous	0	0	1
Clams (bivalves), recreational	1	1	1
Dip net	0	0	1
Dip net, tribal	0	0	1
Diving	0	1	1
Diving, tribal	0	1	1
Dredge	0	1	1
Dredge, tribal	0	1	1
Dungeness crab, recreational	1	1	1
Geoduck, recreational	1	1	1
Gillnet	0	0	1
Gillnet, tribal	0	0	1
Jig	0	0	0
Jig, tribal	0	0	0
Line	0	0	1
Line, tribal	0	0	1
Midwater trawl	0	0	1
Midwater trawl, tribal	1	0	1
Other	0	0	1
Other net	0	0	1
Other net, tribal	0	0	1
Other, recreational	0	0	1
Other, tribal	0	0	1
Pole	0	0	1
Pole, tribal	0	0	1
Pot and trap	0	0	2
Pot and trap, tribal	0	0	2
Salmon, recreational	1	0	1
Seine	0	0	1
Seine, tribal	0	0	1
Set net	0	0	1
Set net, tribal	0	0	1
Shrimp trawl	0	1	1
Sport fishing	1	0	1
Spot shrimp, recreational	1	0	1
Troll	0	0	1
Troll, tribal	0	0	1

Table 14. Marine protected areas (MPAs) in Puget Sound considered in the model. Table includes fishing restrictions, protection level, and year the MPA was established.

Name	Restrictions	Area (ha)	Managing agency	Protection level	Year
Admiralty Head Marine Preserve	Closed to all harvest except recreational sea urchins and sea cucumbers.	35.73	WDFW	Uniform multiple use	2002
Argyle Lagoon San Juan Islands Marine Preserve	Open to recreational and commercial fishing for salmon and trout. Forage fish restricted to only herring. Closed to bottomfish and shellfish. Take of unclassified species by recreational fisheries is allowed.	5.77	University of Washington (UW), WDFW	Uniform multiple use	1990
Brackett's Landing Shoreline Sanctuary Conservation Area	No take.	18.95	UW, WDFW	No take	1970
Carkeek Park	Recreational and commercial fishing for salmon, trout, bottomfish, and forage fish restricted to fin fishing by hook and line. Closed to fishing for shellfish and unclassified species.	9.97	City of Seattle, WDFW	Zoned multiple use with no-take area	2005
City of Des Moines Park Conservation Area	No take.	3.72	City of Des Moines, WDFW	No take	1998
Colvos Passage Marine Preserve	Recreational salmon fishing limited to trolling. Closed to other fisheries.	1.32	WDFW	Uniform multiple use	2000
Dabob Bay Natural Area Preserve	No take.	70.40	WDNR	No access	1987
Discovery Park	Recreational and commercial fishing for salmon, trout, bottomfish, and forage fish restricted to fin fishing by hook and line. Closed to fishing for shellfish and unclassified species.	16.58	City of Seattle, WDFW	Zoned multiple use with no-take area	2005
Dungeness National Wildlife Refuge	Closed to salmon fishing, except 1–31 Oct, when open to recreational fishery for hatchery coho.	577.95	USFWS	Zoned multiple use	1915
Ebey’s Landing National Historical Reserve	Open to recreational fishing, including seaweed harvesting.	7,221.91	Washington Parks and Recreation Commission	Uniform multiple use	1978
Emma Schmitz Marine Preserve	Commercial and recreational fishing for salmon, trout, bottomfish and forage fish restricted to fin fishing by hook and line. Closed to fishing for shellfish and unclassified species.	2.56	City of Seattle, WDFW	Zoned multiple use with no-take area	2005

Table 14 (continued). Marine protected areas in Puget Sound considered in the model.

Name	Restrictions	Area (ha)	Managing agency	Protection level	Year
False Bay San Juan Islands Marine Preserve	Recreational fishing for salmon, trout, and unrestricted species allowed. Closed to fishing for bottomfish and shellfish. Forage fish limited to herring. Commercial fishing for salmon open; closed to bottomfish, trout, and unclassified species. Forage fish limited to herring.	129.37	WDFW	Uniform multiple use	1990
Friday Harbor San Juan Islands Marine Preserve	Recreational fishing for salmon, trout, and unrestricted species allowed. Closed to fishing for bottomfish and shellfish. Forage fish limited to herring. Commercial fishing for salmon open; closed to bottomfish, trout, and unclassified species. Forage fish limited to herring.	172.85	WDFW	Uniform multiple use	1990
Golden Gardens Park	Recreational and commercial fishing for salmon, trout, bottomfish, and forage fish restricted to fin fishing by hook and line. Closed to fishing for shellfish and unclassified species.	5.61	City of Seattle, WDFW	Zoned multiple use with no-take area	2005
Kennedy Creek Natural Area Preserve	No take.	45.23	WDNR	No access	1990
Keystone Conservation Area	No take.	4.61	WDFW	No take	2002
Lincoln Park	Recreational and commercial fishing for salmon, trout, bottomfish, and forage fish restricted to fin fishing by hook and line. Closed to fishing for shellfish and unclassified species.	4.11	City of Seattle, WDFW	Zoned multiple use with no-take area	1922
Nisqually National Wildlife Refuge	No fishing is allowed inside the dike or in the Research Natural Areas. Bank fishing is permitted only in the designated McAllister Creek bank fishing area.	4,632.56	Federal	National Wildlife Refuge System	1974
Octopus Hole Conservation Area	No take.	13.18	WDFW	No take	1998
Orchard Rocks Conservation Area	No take.	41.92	WDFW	No take	1998
Protection Island National Wildlife Refuge	No take.	161.31	Federal	National Wildlife Refuge System	1982
Richey Viewpoint	Recreational and commercial fishing for salmon, trout, bottomfish, and forage fish restricted to fin fishing by hook and line. Closed to fishing for shellfish and unclassified species.	4.68	City of Seattle, WDFW	Zoned multiple use with no-take area	2005

Table 14 (continued). Marine protected areas in Puget Sound considered in the model.

Name	Restrictions	Area (ha)	Managing agency	Protection level	Year
Saltar's Point Beach Conservation Area	No take.	1.81	WDFW	No take	2000
San Juan County/Cypress Island Marine Biological Preserve	Preserve of marine biological materials useful for scientific purposes, except when gathered for human food.	165454.00	UW/Friday Harbor Labs	Uniform multiple use	1923
Shaw Island San Juan Islands Marine Preserve	Recreational fishing for salmon, trout, and unrestricted species allowed. Closed to fishing for bottomfish and shellfish. Forage fish limited to herring. Commercial fishing open to salmon, closed to bottomfish and unclassified species. Shellfish restricted to crabbing, and fishing for forage species is limited to herring.	174.69	UW/WDFW	Uniform multiple use	1990
Skookum Inlet Natural Area Preserve	No take.	43.97	WDNR	No access	1986
South 239th Street Park Conservation Area	No take.	0.08	City of Des Moines, WDFW	No take	1998
South Puget Sound Wildlife Area	No take.	1647.65	WDNR	No access	1988
Sund Rock Conservation Area	No take.	28.79	WDFW	No take	1994
Titlow Beach Marine Preserve	Closed to harvesting of fish and shellfish, except recreational salmon fishing is permitted using lures from shore or nonmotorized craft.	16.85	Metro/Tacoma, WDFW	Uniform multiple use	1994
Waketickeh Creek Conservation Area	No take.	59.18	WDFW	No take	2000
Yellow and Low Islands San Juan Islands Marine Preserve	Recreational fishing for salmon, trout, and unrestricted species allowed. Closed to fishing for bottomfish and shellfish. Forage fish limited to herring. Commercial fishing open to salmon, closed to bottomfish, shellfish and unclassified species. Fishing for forage species is limited to herring.	80.74	TNC/UW, WDFW	Uniform multiple use	1990
Zee's Reef Marine Preserve	Recreational salmon fishing limited to fly fishing. Closed to other fisheries.	22.63	WDFW	Uniform multiple use	2002
Zella M. Schultz/Protection Island Seabird Sanctuary	No take.	12.05	WDFW	No access	1975

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