TEMPORAL VARIATION IN THE PREY RESOURCE PORTFOLIO OF JUVENILE SALMONIDS DURING FRESHWATER REARING

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OUTLINE

- Chapter 1: Temporal Aspects of Juvenile Salmon Research
- Chapter 2: Asynchronous Prey Resources Create a Year-round Energy Portfolio for Juvenile Salmonids
- Ongoing Work and Future Study
- Take-aways
- Acknowledgements
- References
- Questions

CHAPTER 1: TEMPORAL ASPECTS OF JUVENILE SALMONID RESEARCH

BACKGROUND

- River Continuum Concept (Vannote et al. 1980)
- Spatially continuous "riverscape" ecology (Fausch et al. 2002)
- Short-term datasets fail to capture historical levels of productivity (i.e. the shifting baseline) or reveal coarser scale temporal patterning such as regime shifts (Mejia et al. 2019)
- Recent work on birds, amphibians, reptiles, and mammals found strong seasonal biases in field research (Marra et al. 2015)

RESEARCH OBJECTIVES

Question:

- Is our current knowledge of juvenile salmonid freshwater ecology temporally biased?

Objectives:

- Characterize the temporal aspects of Pacific salmon and trout field research from the last 30 years
- Identify patterns and data gaps in the timing (distribution) and extent (duration) of studies broadly and within sub-topics.

METHODS

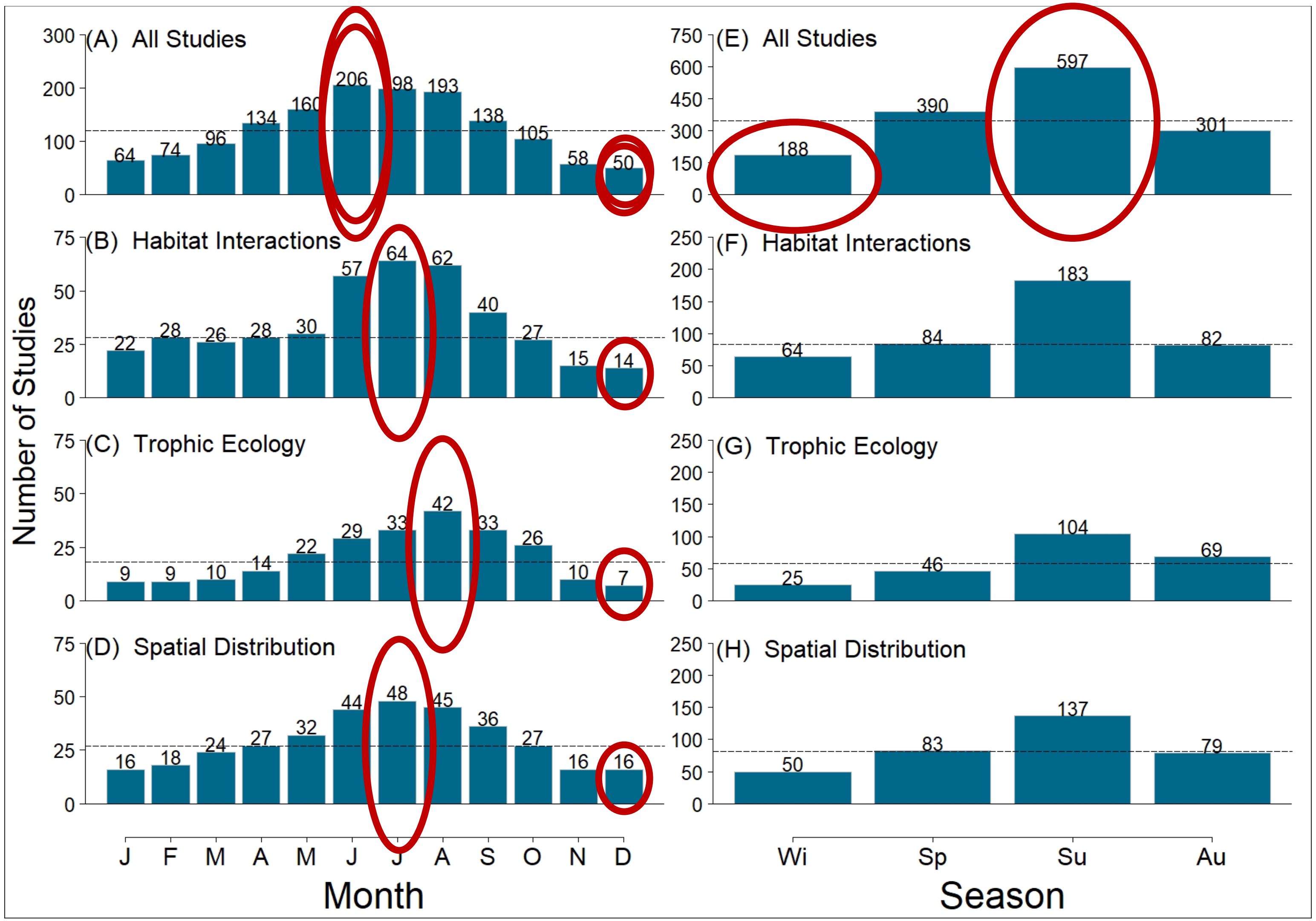
- Literature review
- What months and seasons research occurs in
- The duration of studies
- Whether seasons were studied individually
- Main Focus: 13 journals, *Oncorhynchus* species, 1988-2017, freshwater ecological field research, subtopics of habitat interactions (unit-scale), trophic ecology, spatial distribution (landscape-scale) (n=371)
- Secondary Focus: spatially continuous "riverscape" sampling, *Oncorhynchus* species, 1988-2017 (n=38)

METHODS

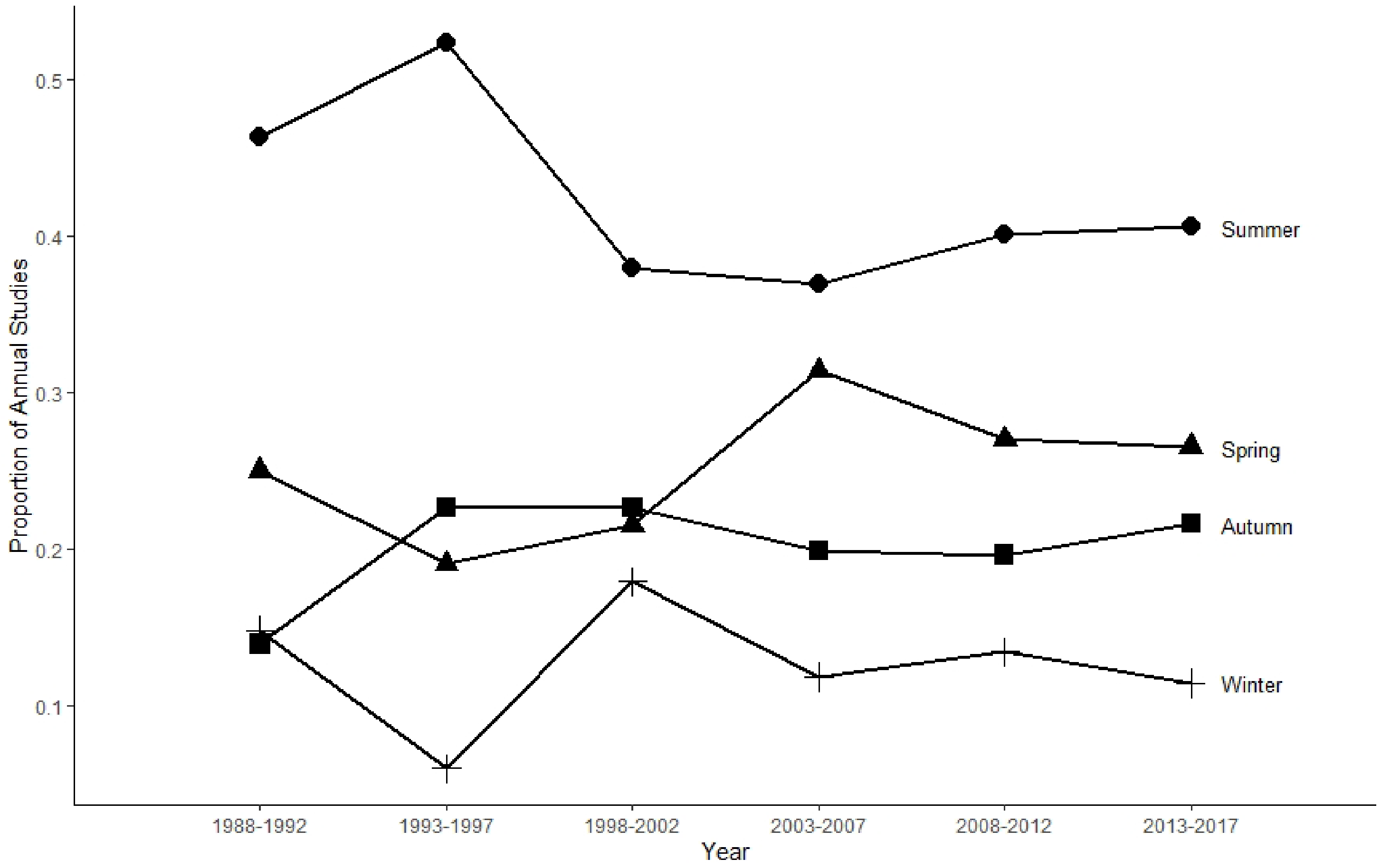
- Presence/absence of data collection during each month of the calendar year
- Seasons defined as Summer (June, July, August), Autumn (September, October, November), Winter (December, January, February), and Spring (March, April, May)
- Pearson X2-tests for temporal biases
- Acknowledge that phenology varies with latitude, elevation, and position in watershed so functional season may vary slightly among locations or context.

RESULTS – TEMPORAL DISTRIBUTION OF STUDIES

- Overall, Summer = 40% and Winter = 13%
- Peak = Jun, Low = Dec
- Most frequent month = 3-6x more common than least frequent month

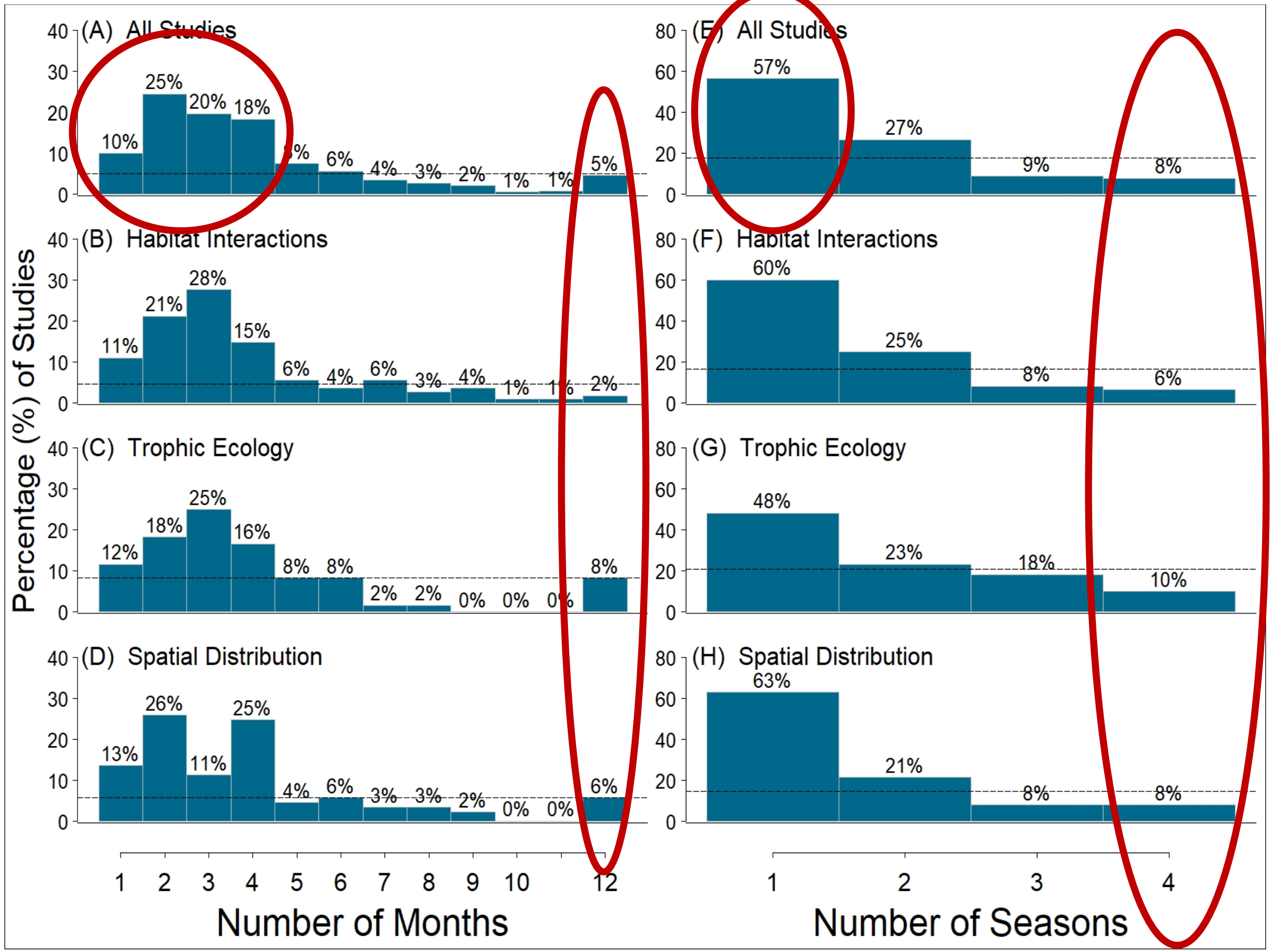


RESULTS – DISTRIBUTION OVER TIME

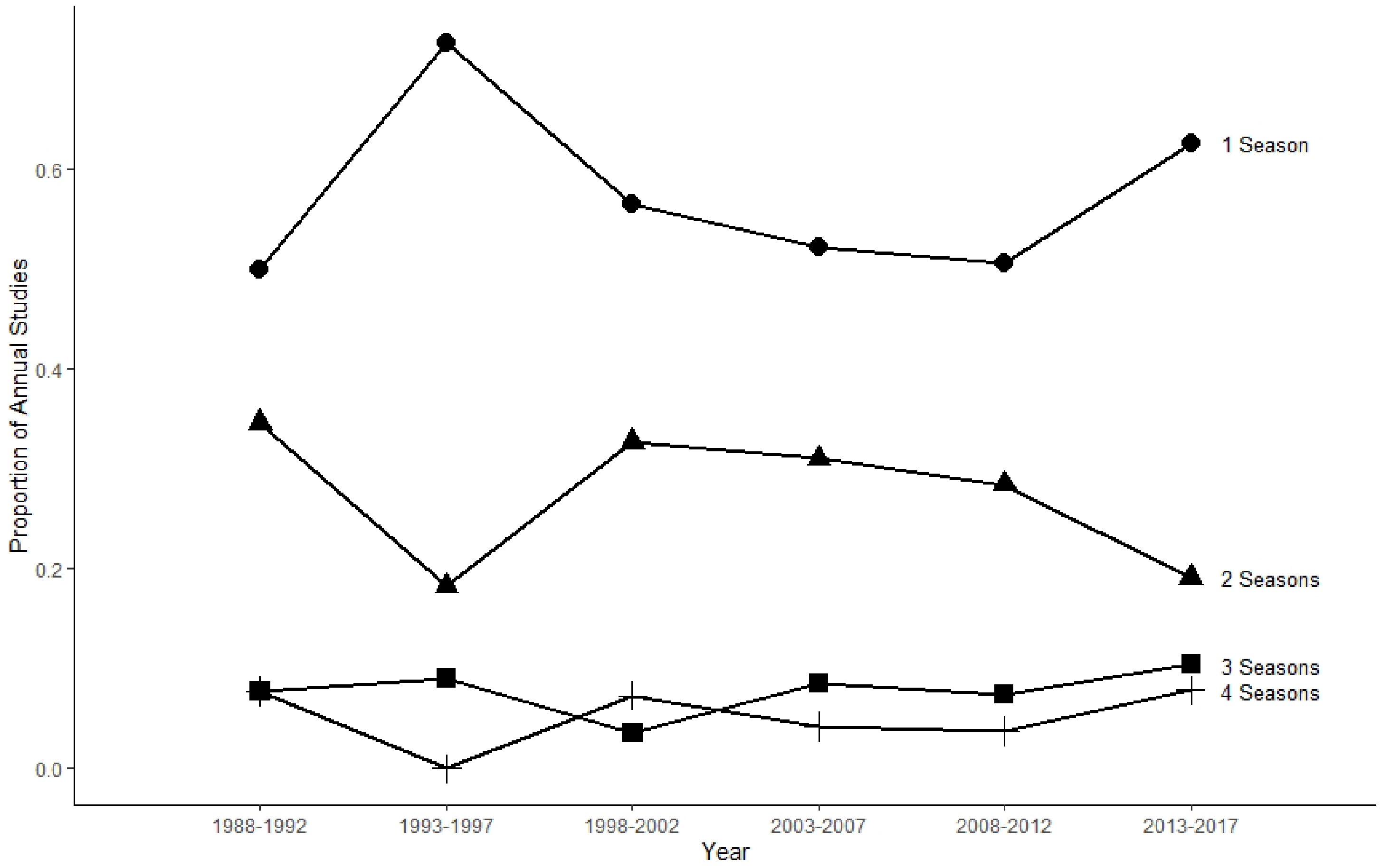


RESULTS – TEMPORAL EXTENT OF STUDIES

- Single Season = 57%
- 4 seasons = 6-10%
- Data from 4 or fewer months = 73%
- Full year = 2-8%

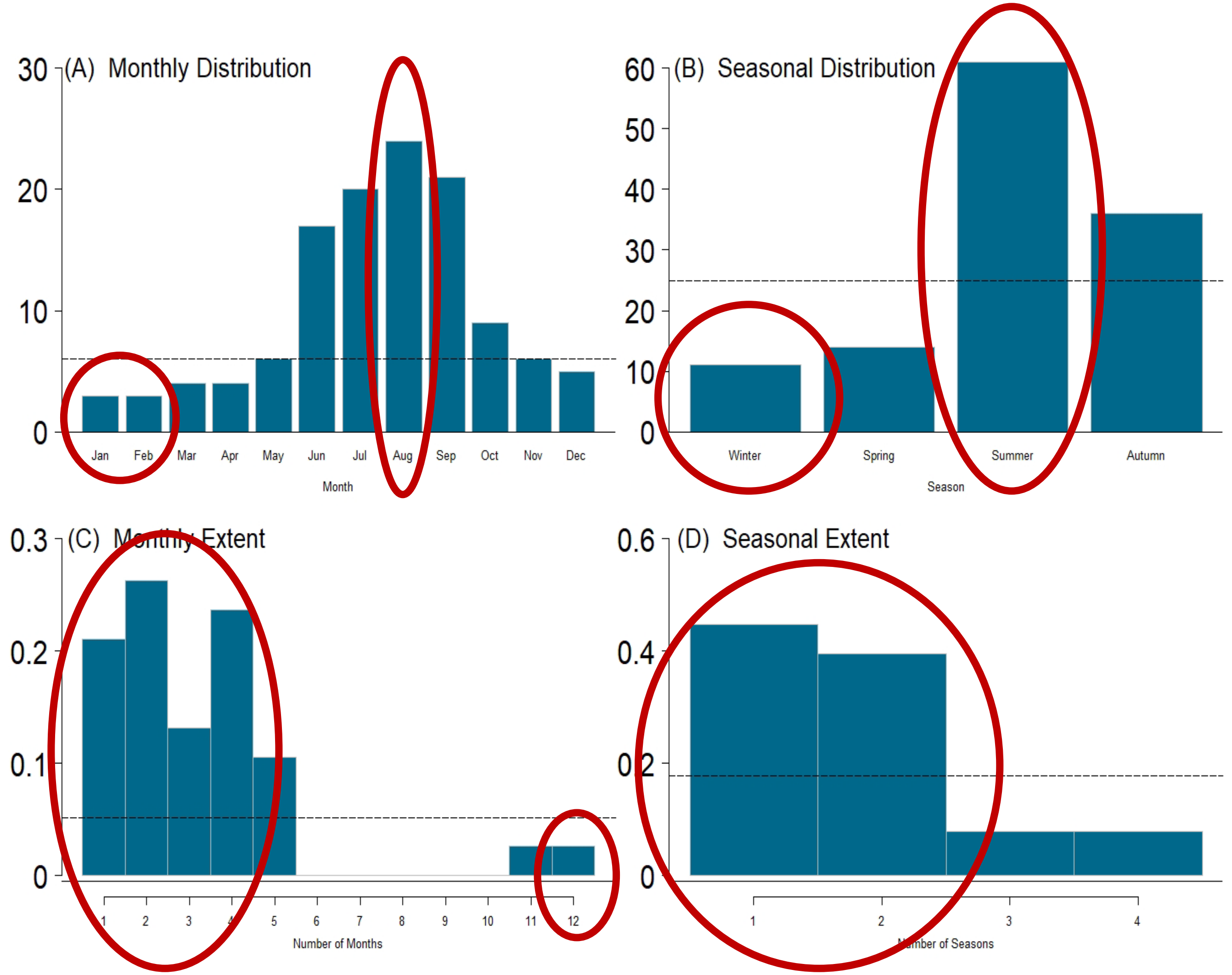


RESULTS – EXTENT OVER TIME



RESULTS – RIVERSCAPE STUDIES

- Summer = 50%
- Winter = 9%
- August is 8x more common than Jan/Feb
- Data from 4 or fewer months = 80%
- Full year = 3%
- Seasonal extent less skewed than ecological studies



SUMMARY

- Recent emphasis on spatially comprehensive sampling (Fausch et al. 2002), but this has come at the cost of time
- Summer overrepresented
- Winter underrepresented
- As much as a 6-fold difference between months for ecological studies and 8-fold difference for riverscape studies
- Short studies much more common than full year

IMPLICATIONS – TEMPORAL DISTRIBUTION

- Winter survival is often a limiting factor to freshwater productivity (Bustard and Narver 1975), and reducing winter mortality is a common objective of restoration efforts (Cederholm et al. 1997)
- Overlooking winter ecology may mean missing out on key ways that we could be improving overwinter survival
- Temporal bias in spatially continuous riverscape sampling hinders our ability to understand temporal changes in fish ecology and use of temporary but vital resources such as habitat and food

IMPLICATIONS – TEMPORAL EXTENT

- Overemphasize ecological phenomena observed in summer
- Potential to temporally extrapolate and draw conclusions based on a subset of the year
- Limit the ability to identify interactions between time periods, carry-over effects, compensatory behavior after/before periods of stress (often caused by environmental conditions such as summer warm temperatures or overwinter survival)
- Fish may not occupy every meter of space available to them, but they do live in every second of time

CHAPTER 2: ASYNCHRONOUS PREY RESOURCES CREATE A YEAR-ROUND ENERGY PORTFOLIO FOR JUVENILE SALMONIDS

BACKGROUND

- Traditional restoration: habitat, hatchery production, hydroelectric dams, and harvest (Naiman and Bilby 1998)
- Maybe we should consider food webs? (Naiman et al. 2012)
- Stream productivity may be more limited by food than physical characteristics (Bellmore et al. 2013; Weber et al. 2014)
- Freshwater rearing (particularly growth) in salmon can have lasting effects on long-term survival (Thompson and Beauchamp 2014; Bond et al. 2008)
- Salmonids may rear in freshwater for a full year (Quinn 2005) and depend on a diverse portfolio of prey resources to support somatic growth, lipid storage, overwinter survival, and smoltification

BACKGROUND CONT.

- Terrestrial subsidies to aquatic systems can account for 50-90% of prey consumption by fishes (Wipfli 1997; Nakano et al. 1999; Kawaguchi and Nakano 2001; Dineen et al. 2007; Li et al. 2016)
- Ephemeral marine subsidies can fuel greater fish growth than benthic or terrestrial invertebrates (Armstrong et al. 2010; Scheuerell et al. 2007; Moore et al. 2008; Bentley et al. 2012)
- Trophic pathways may exhibit temporal variation as pulses (e.g. salmon spawning) or seasonal patterning (e.g. aquatic or terrestrial invertebrate productivity)

BACKGROUND CONT.

- If trophic resources vary asynchronously, they create a more stable aggregate available to consumers over time, consistent with the Portfolio Effect (Schindler et al. 2015).
- Many studies have provided insights into components of the full resource portfolio (Ruff et al. 2011; Scheurell e al. 2007) or the importance of allochthonous inputs (Cloe and Garmin 1996; Wipfli 1997); however, virtually none of these encompass the full annual cycle (but see Nakano and Murakami 2001)

RESEARCH QUESTIONS

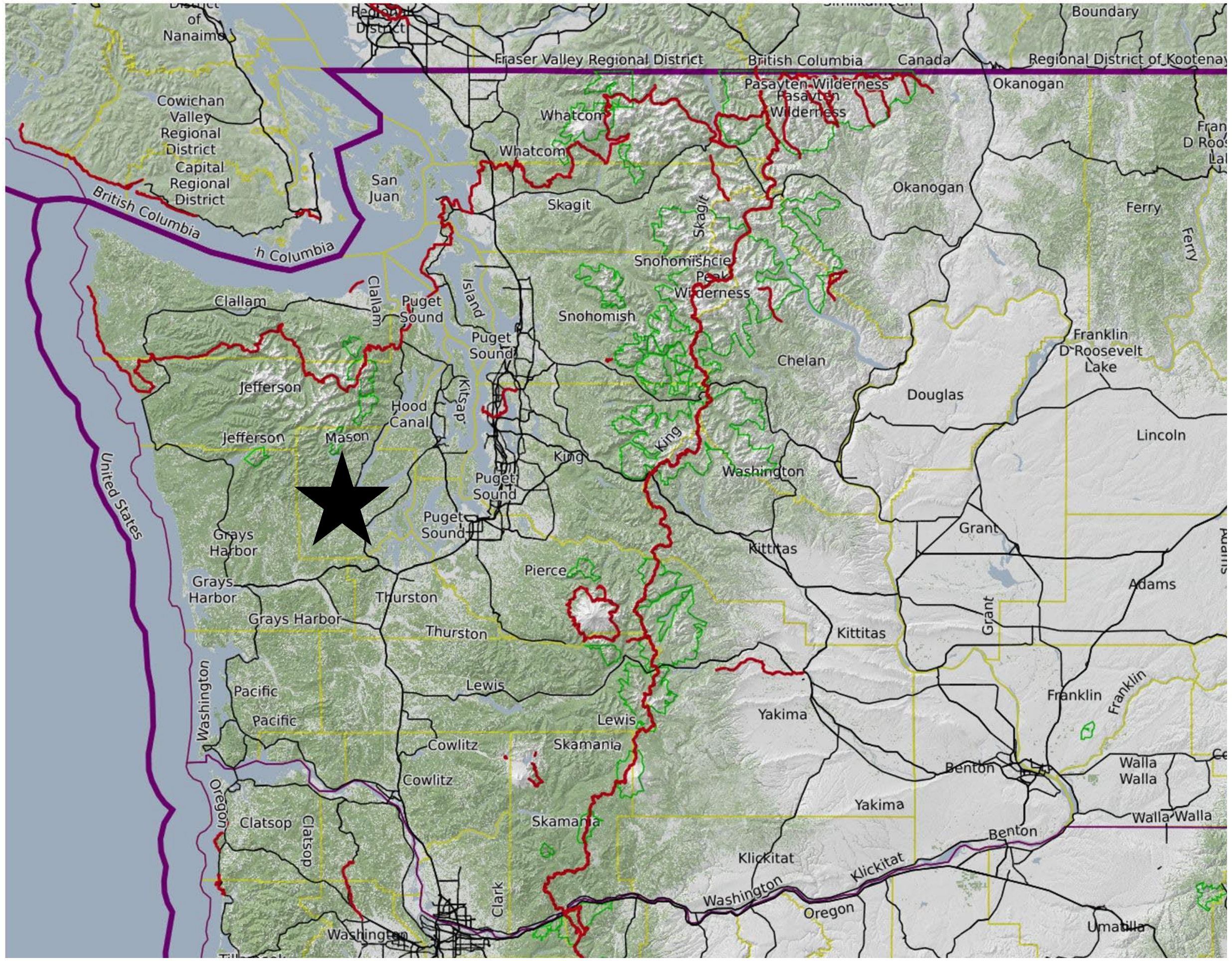
Question:

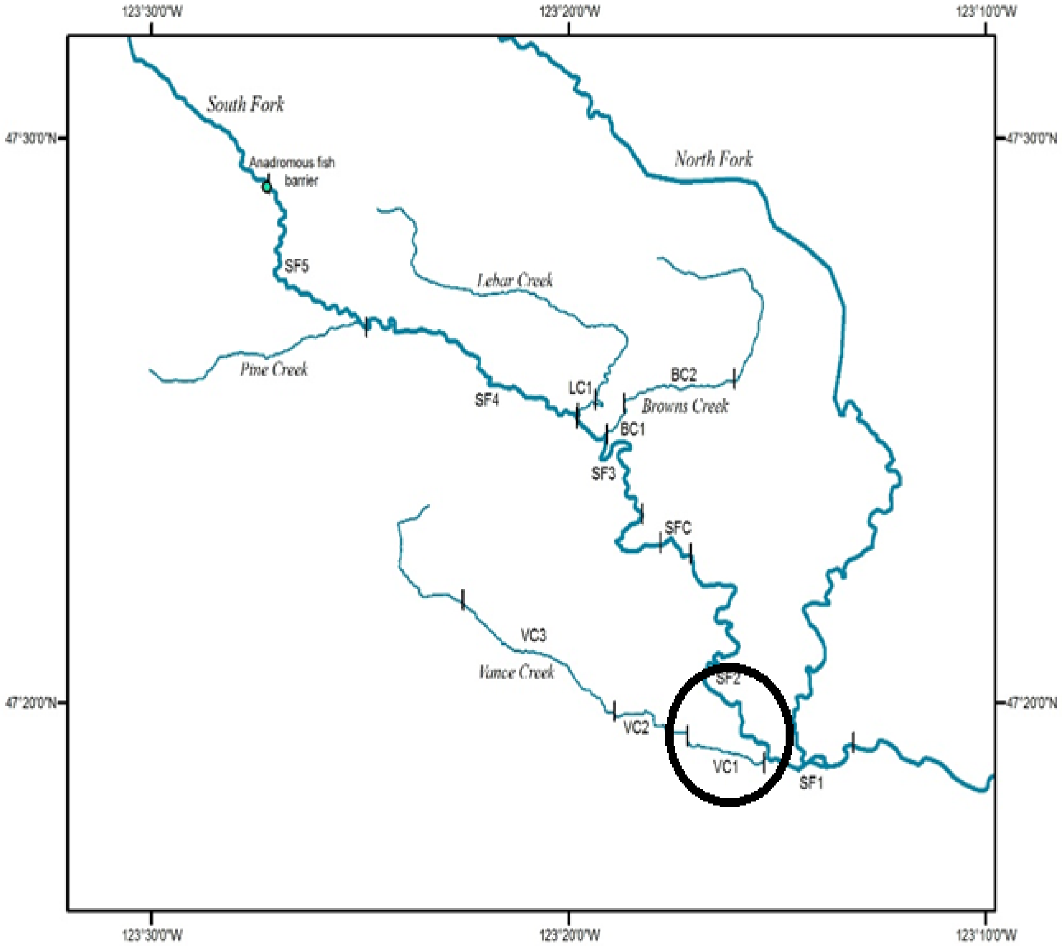
- What do juvenile salmonids eat throughout the full annual cycle?

Objectives:

- Quantify how prey resource composition and biomass vary across time within benthic, drift, and terrestrial sources
- Determine primary sources of diet for juvenile steelhead and coho throughout the annual cycle
- Examine what temporal and taxonomic resolutions reveal key prey items in samples

METHODS - STUDY SYSTEM

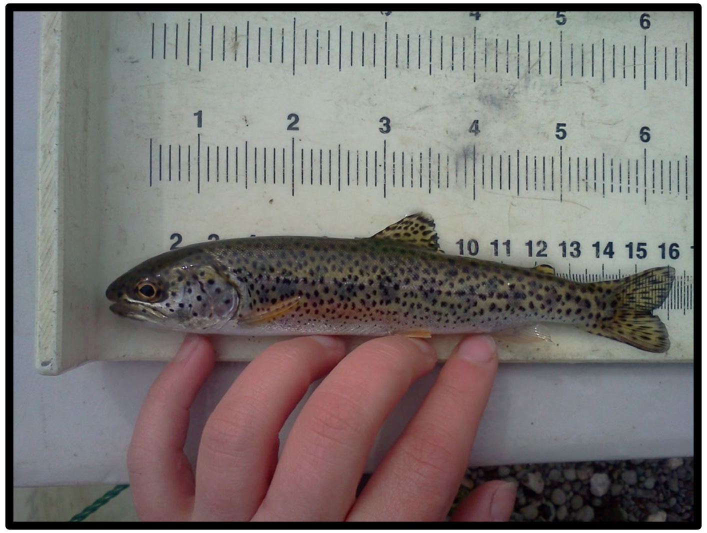




METHODS – DATA COLLECTION

Fish Capture

- Beach Seine
- Minnow Trap
- Screw Trap



Fish Sampling

- 229 Steelhead
- 530 Coho
- Diet, length, fin clip

Environment

- Benthic
- Drift
- Terrestrial

METHODS – DATA ANALYSIS

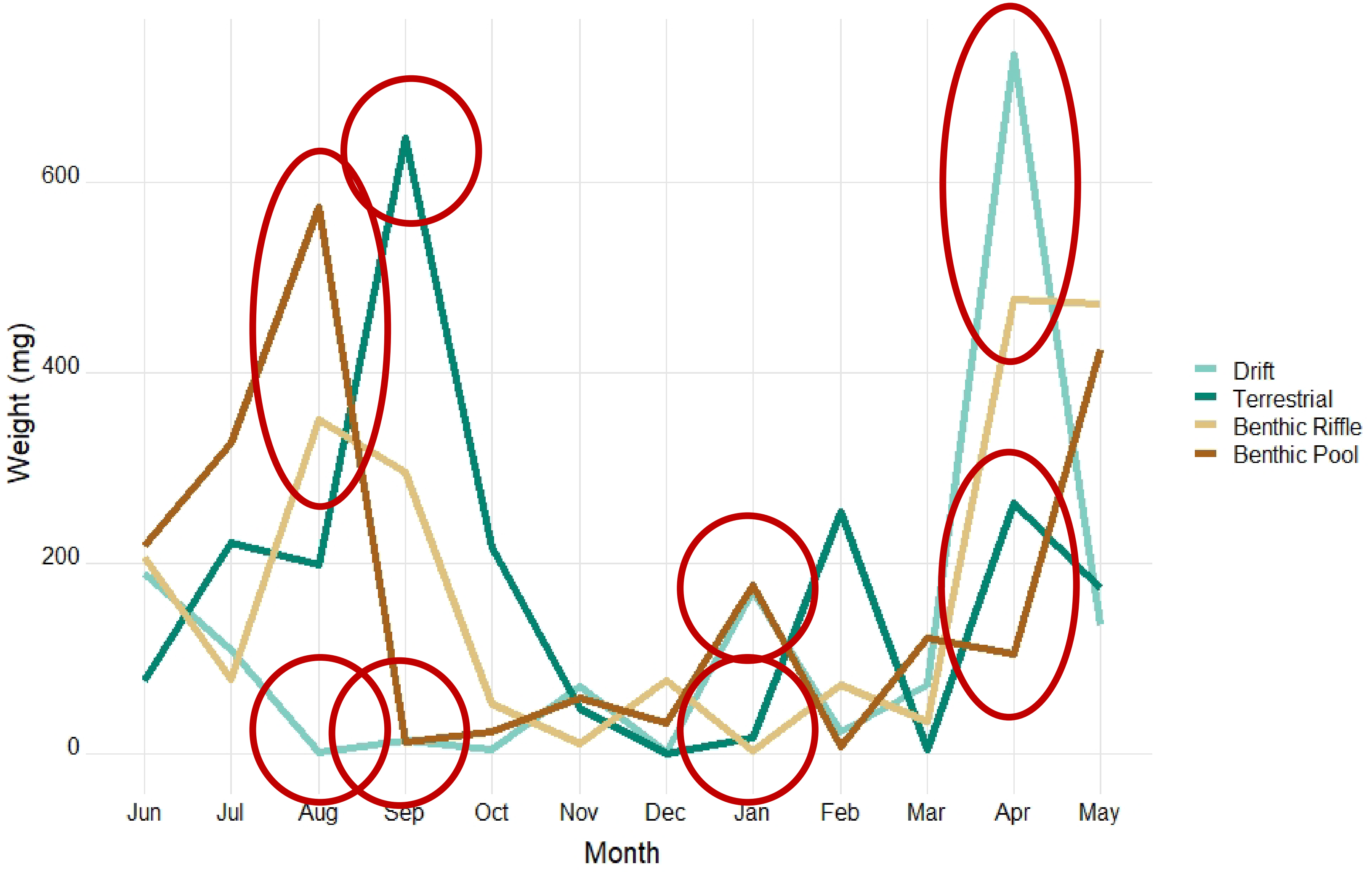
Prey Resources

- ID invertebrates
- Length-weight regressions
- Monthly and seasonal proportions by order and type

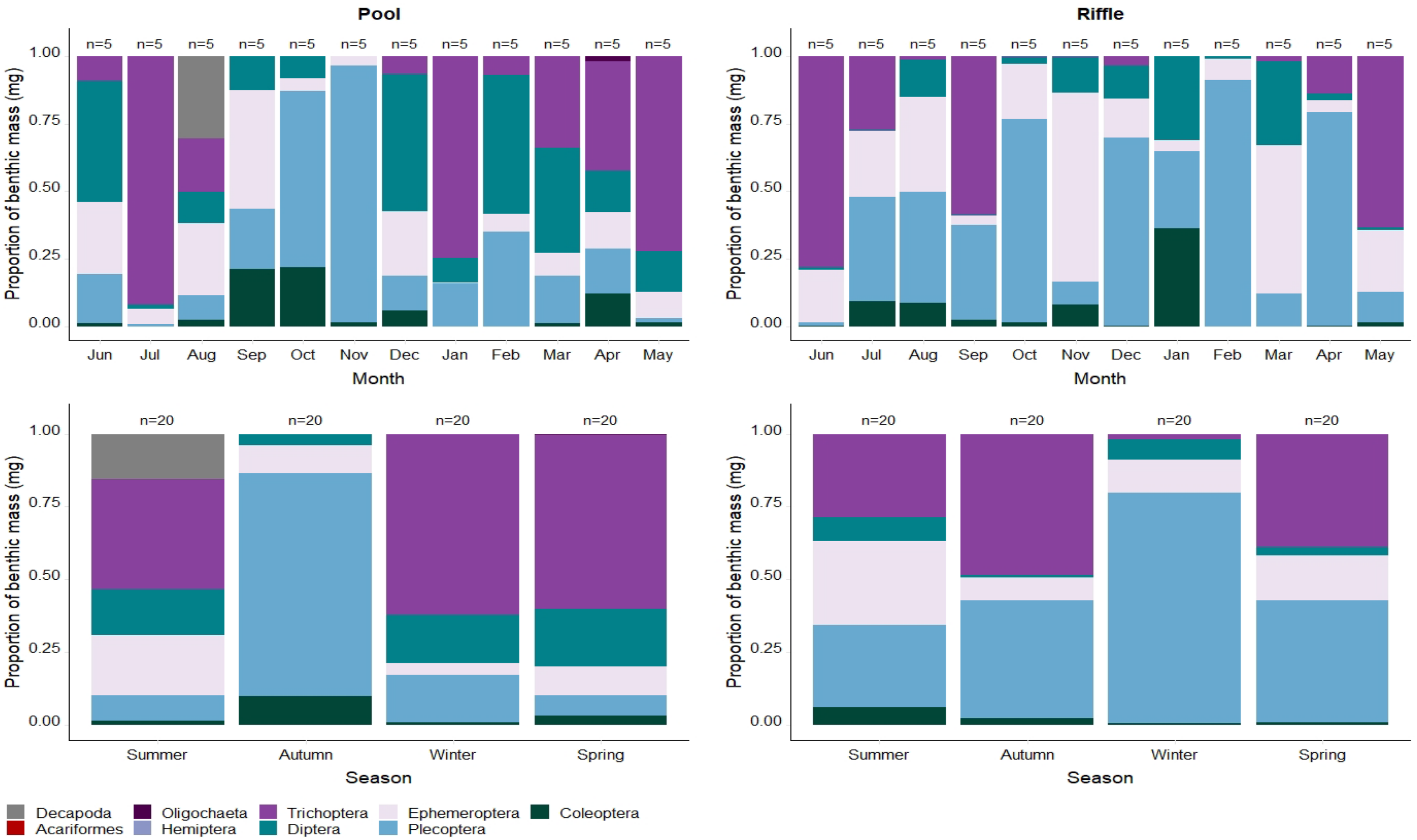
Coho and Steelhead

- Length-weight regressions
- Rations: diet mass (mg)/fish mass (g)
- Feeding selectivity: Vanderploeg and Scavia's (1979) electivity index

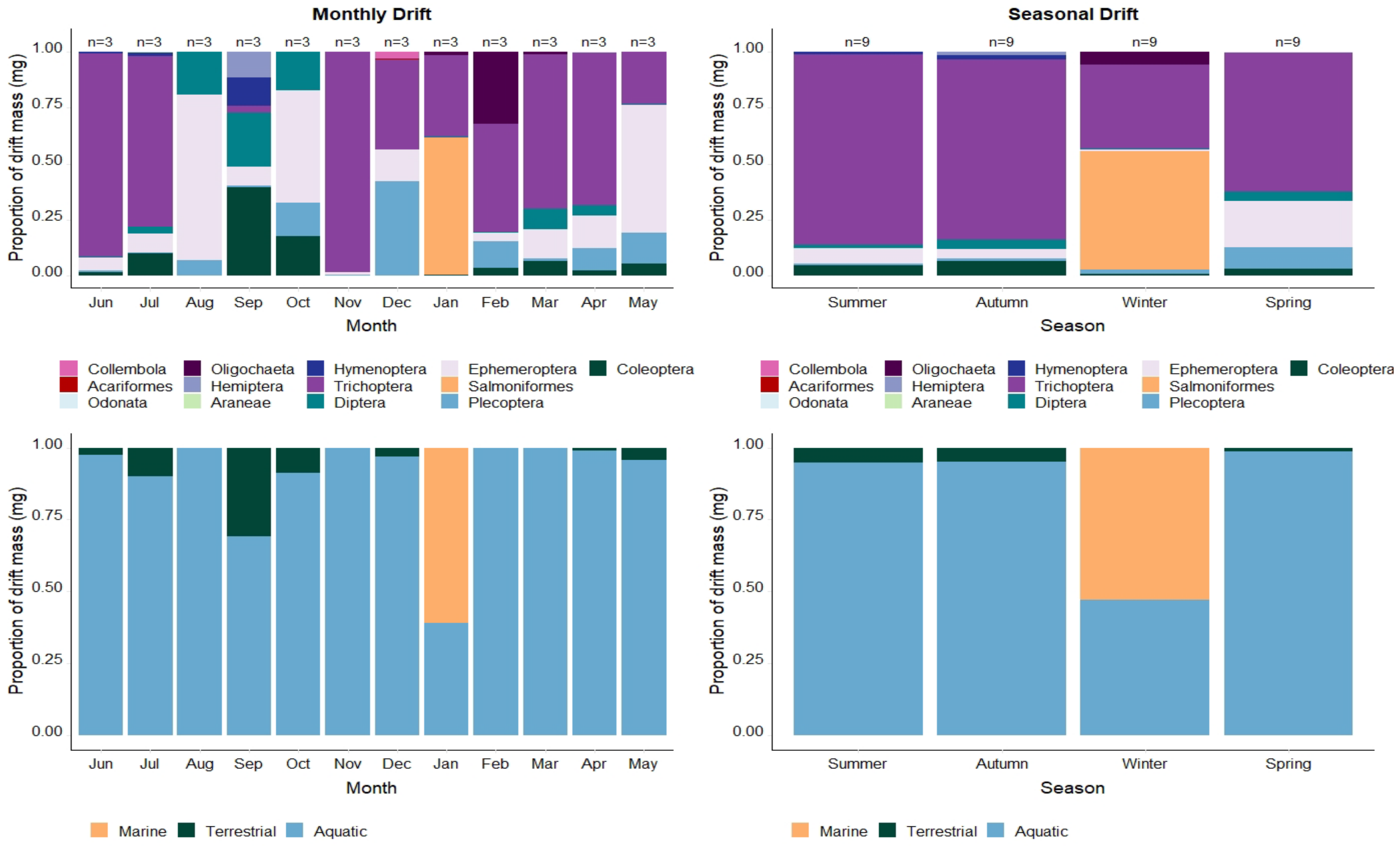
RESULTS – ENVIRONMENTAL PRODUCTIVITY



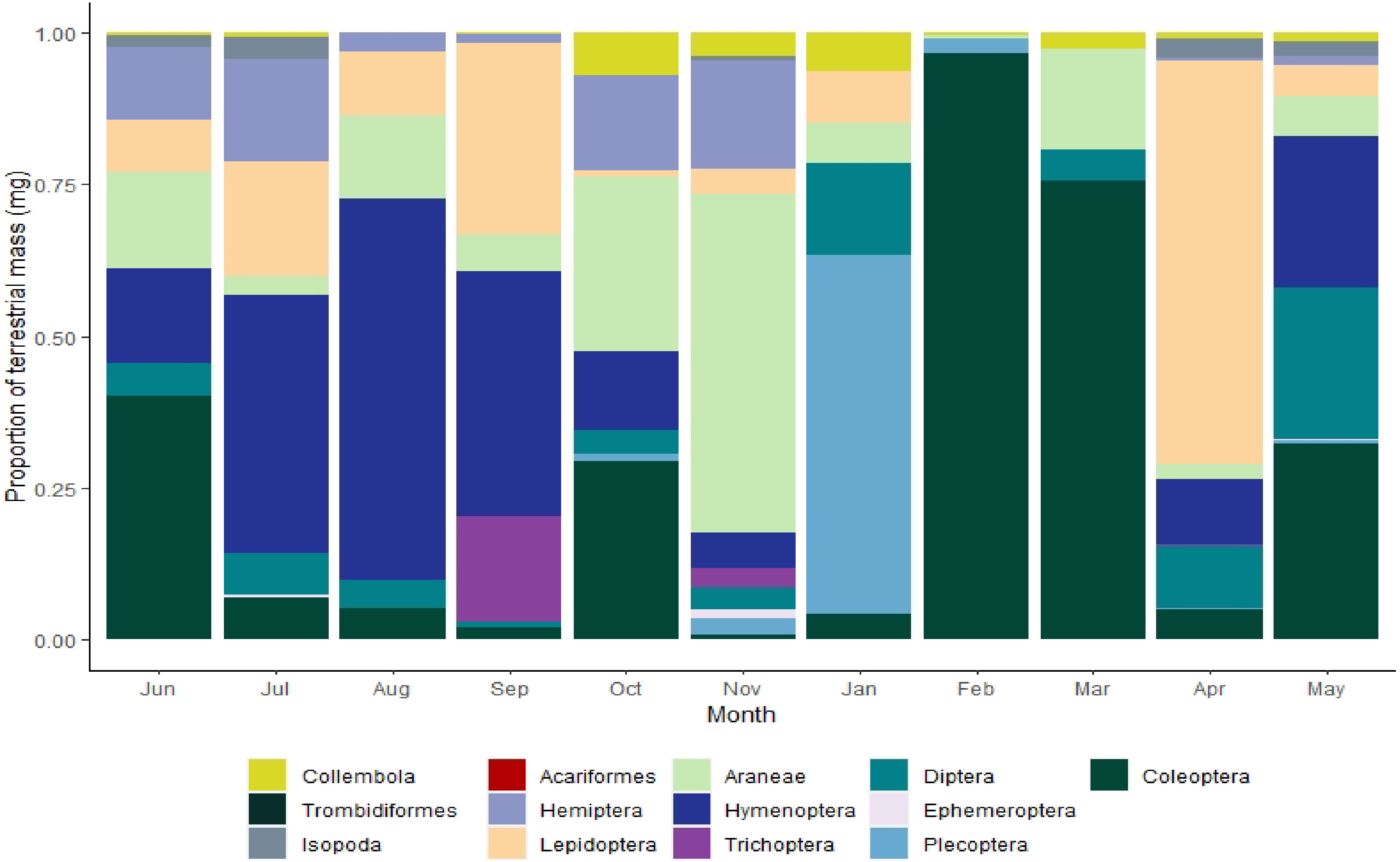
RESULTS – BENTHIC PREY RESOURCES



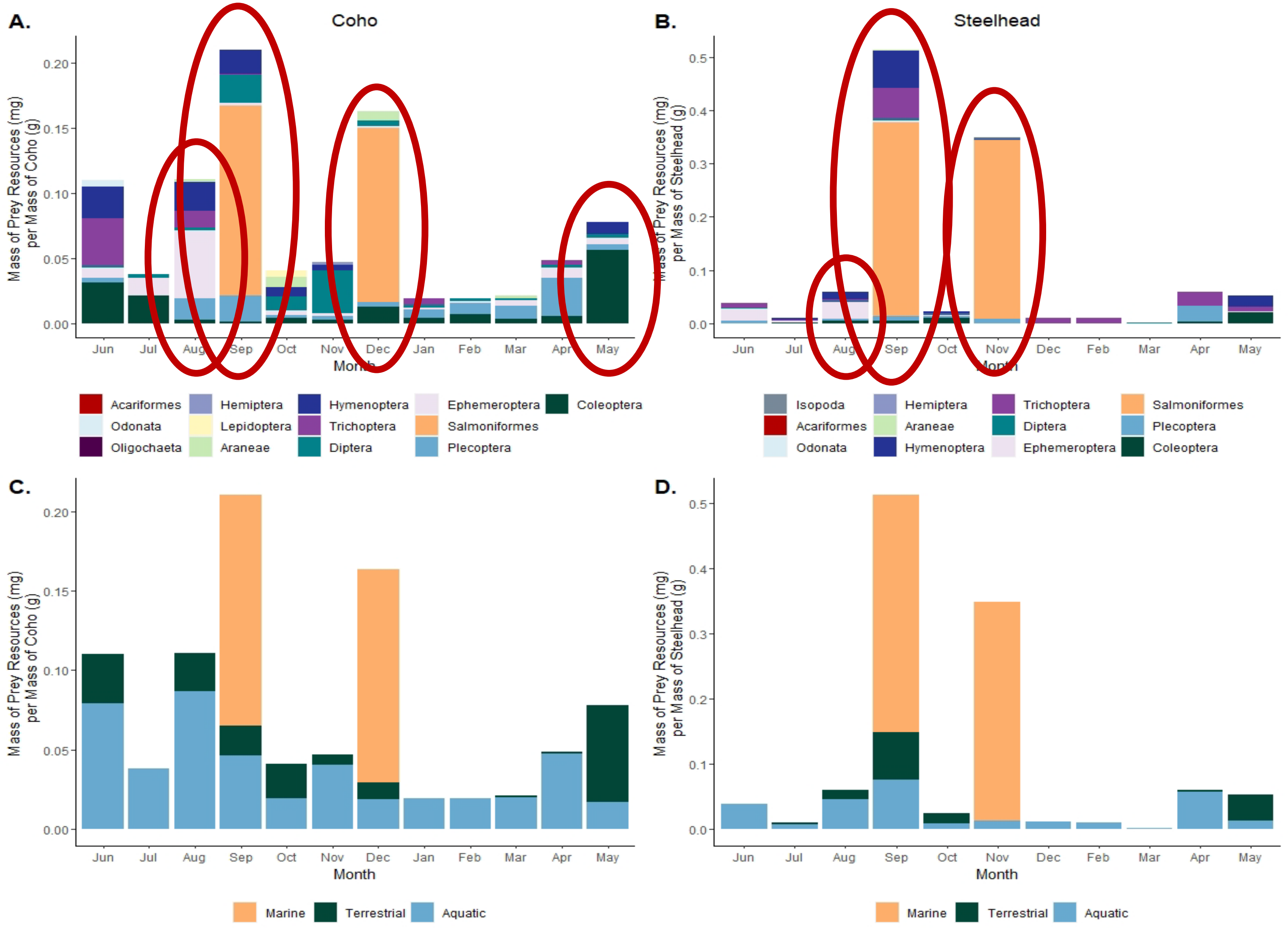
RESULTS – DRIFT PREY RESOURCES



RESULTS – TERRESTRIAL PREY RESOURCES

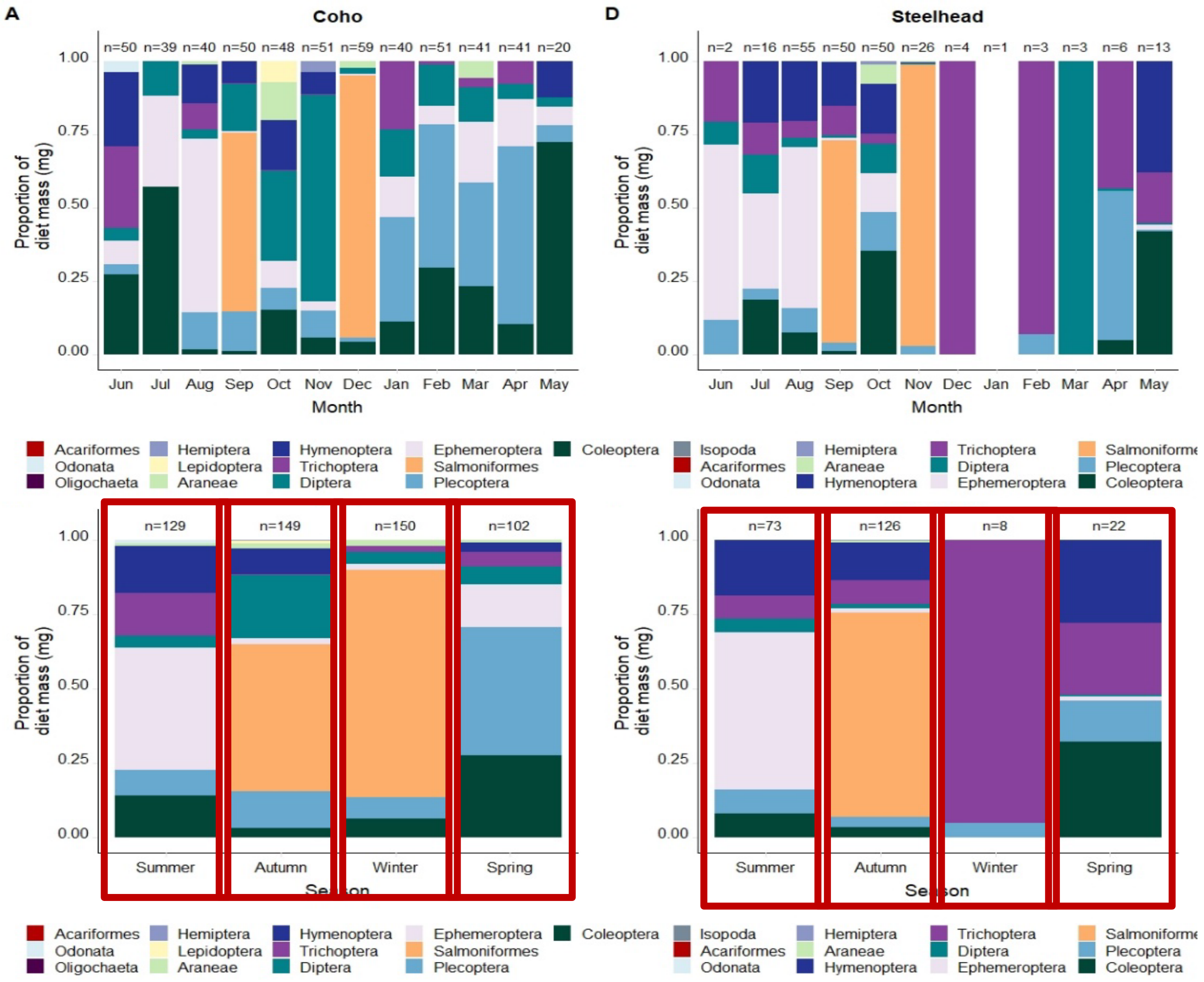


RESULTS – FISH RATIONS



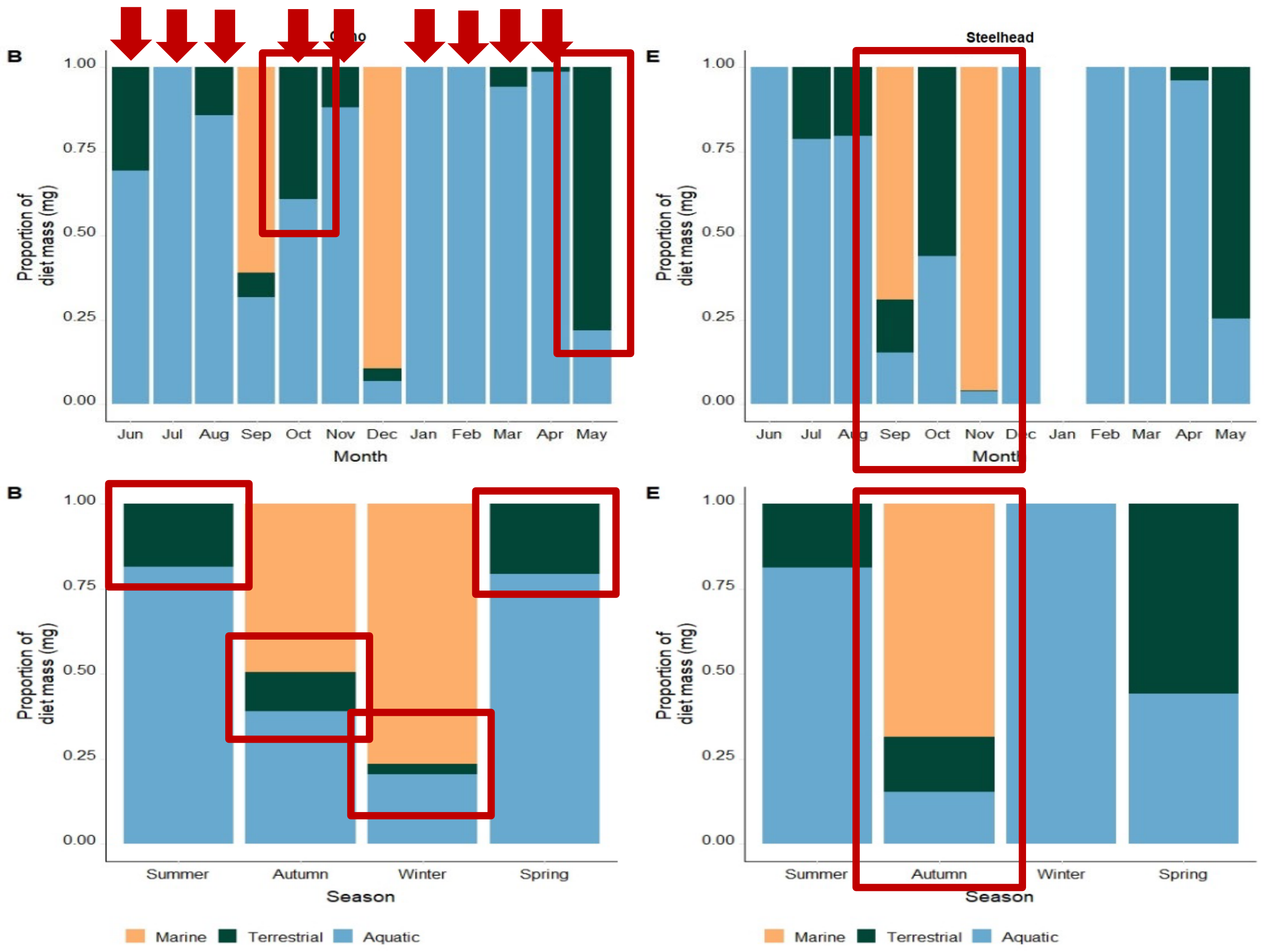
- 66% of May coho diet biomass came from Rove Beetles
- August dominated by Flathead Mayfly nymphs
- Two pulses of salmon eggs (Sep, Nov/Dec)

RESULTS – FISH DIET COMPOSITION



- Summer:
  - ➢ Coho= Ephemeroptera (41%)
  - ➢ Steelhead= Ephemeroptera (53%)
- Autumn:
  - ➢ Coho= Salmon Eggs (49%) and Diptera (21%)
  - ➢ Steelhead= Salmon Eggs (68%)
- Winter:
  - ➢ Coho= Salmon Eggs (76%)
  - ➢ Steelhead= Trichoptera (95%)
- Spring:
  - ➢ Coho= Plecoptera (43%) and Coleoptera (27%)
  - ➢ Steelhead= Coleoptera (32%) and Hymenoptera (28%)

RESULTS – TROPHIC PATHWAYS SUPPORTING FISH



- Seasonal: 3-21% of coho diet biomass = terrestrial
- Monthly: 78% of coho diet in May (mostly rove beetles) and 39% in October (mostly spiders) = terrestrial
- Aquatic = over 50% of diet in 9 out of 12 months
- Marine = seasonal may miss multiple pulses

RESULTS – COHO FEEDING SELECTIVITY

Month	Dominant Prey Resources in Coho Diet	%	Electivity Index
June	Northern Case Maker Cadddis Pupa	27%	not found in environmental samples
	Ant	18%	0.54 drift
July	Predaceous Diving Beetle Adult	57%	0.78 drift 0.81 benthic
	Adult Mayfly	24%	0.85 terrestrial
August	Flathead Mayfly nymph	53%	0.79 benthic
	Ant	13%	0.83 terrestrial
September	Salmon Eggs	61%	not found in environmental samples
	Non-Biting Midge Larva	11%	0.52 drift
October	Spider	13%	-0.33 terrestrial
	Predaceous Diving Beetle Adult	12%	not found in environmental samples
November	Non-Biting Midge Pupa	64%	0.12 drift
	Flying Ant	8%	-0.01 terrestrial
December	Salmon Eggs	89%	not found in environmental samples
	Predaceous Diving Beetle Adult	3%	not found in environmental samples
January	Rolled Wing Stonefly nymph	29%	0.60 benthic
	Northern Case Maker Caddis nymph	22%	-0.07 drift -0.92 benthic
February	Rolled Wing Stonefly nymph	36%	0.29 drift 0.66 benthic
	Predaceous Diving Beetle Adult	25%	not found in environmental samples
March	Stripetail Stonefly	25%	0.59 benthic
	Predaceous Diving Beetle Adult	23%	not found in environmental samples
April	Stripetail Stonefly	43%	0.41 drift 0.17 benthic
	Rolled Wing Stonefly nymph	18%	0.41 drift 0.57 benthic
May	Rove Beetle	66%	0.85 terrestrial
	Ant	12%	0.25 terrestrial

RESULTS – STEELHEAD FEEDING SELECTIVITY

Month	Dominant Prey Resources in Steelhead Diet	%	Electivity Index
June	Spiny Crawler Mayfly nymph	35%	0.79 benthic
	Small Minnow Mayfly nymph	25%	0.18 drift -0.14 benthic
July	Small Minnow Mayfly nymph	25%	0.44 drift 0.39 benthic
	Ant	21%	0.85 terrestrial
August	Flathead Mayfly nymph	49%	0.81 benthic
	Ant	12%	0.85 terrestrial
September	Salmon Eggs	69%	not found in environmental samples
	Flying Ant	13%	0.71 drift 0.79 terrestrial
October	Ground Beetle	30%	0.67 drift 0.66 terrestrial
	Small Minnow Mayfly nymph	11%	-0.50 drift 0.48 benthic
November	Salmon Eggs	96%	not found in environmental samples
	Stripetail Stonefly	2%	not found in environmental samples

November	Salmon Eggs	96%	not found in environmental samples
	Stripetail Stonefly	2%	not found in environmental samples
December	Tube Maker Caddis nymph	100%	not found in environmental samples
	n/a	n/a	n/a
January	n/a	n/a	n/a
	n/a	n/a	n/a
February	Tube Maker Caddis nymph	93%	not found in environmental samples
	Rolled Wing Stonefly nymph	7%	0.78 drift 0.78 benthic
March	Non-Biting Midge Larva	100%	0.80 drift 0.82 benthic
	n/a	n/a	n/a
April	Stripetail Stonefly	49%	0.51 drift 0.81 benthic
	Adult Caddisfly	26%	not found in environmental samples
May	Sweat Bee	33%	not found in environmental samples
	Ground Beetle	29%	0.82 drift 0.77 terrestrial

SUMMARY

- Aquatic resources important during summer somatic growth
- Terrestrial subsidies important in May during smoltification and October as fish switch to lipid storage in preparation for overwintering; these subsidies were from different items
- Multiple runs of spawning salmon provided marine subsidies to diet for lipid storage during autumn-early winter, including small population of ESA-listed salmon (contrary to the functional extinction threshold proposed by Moore et al. 2007)
- Ephemeral resources provided largest rations of year
    - Rove beetles in May = 66% of coho diet
    - Salmon eggs in Sep/Nov/Dec = 61-96% of fish diet

IMPLICATIONS

- Potential to miss important prey resources or misinterpret resource contribution depending on timing or frequency of sampling, as evidenced by seasonal and monthly resolution look at fish diet at both order level and trophic pathway level
- Phenological diversity among invertebrate orders and salmon taxa can prolong the availability of prey resources
- Resources with low relative abundance may still be functionally critical when their phenology is unique within the resource portfolio (Armstrong et al. 2020)
- By overlapping seasonal fish foraging with fish rearing phases, food webs could inform targeted fish conservation/recovery efforts

IMPLICATIONS CONT.

- If early marine survival is increased with greater fish size at outmigration (Thompson and Beauchamp 2014??; Bond et al. 2008??), then what resources contribute to early spring fish growth?
- If size at smoltification is related to overwinter survival (??), then what resources increase overwinter survival?
- If overwinter survival increases with greater body size (Bilby et al. 1998; Wipfli et al. 1998; Groot et al. 1995) or greater lipid stores (Berg and Bremset 1998; Cleary et al. 2012??), then what resources increase autumn size and lipid storage?
- If switching from somatic growth to lipid storage requires reaching a size threshold (Biro et al. 2005), then what resources help fish reach that size?

ONGOING WORK AND FUTURE STUDY

- The impact of native and non-native plants on terrestrial subsidies to aquatic systems
  - Terrestrial invertebrate association with plant species
  - Aquatic invertebrate colonization of abscised leaves
  - Links between invertebrates, plant species, and fish diet

- Stable Isotopes
  - Amount of C and N in fish caudal fins compared to standards
  - Non-lethal sampling
  - Longer-term trophic pathways to pair with short-term fish diet sample data, both collected monthly

TAKE-AWAYS

- Chapter 1: Temporal Aspects of Juvenile Salmon Research
  - Field research focusing on juvenile *Oncorhynchus* spp. during freshwater rearing over the past 30 years has been biased toward summer and against winter

- Chapter 2: Asynchronous Prey Resources Create a Year-round Energy Portfolio for Juvenile Salmonids
  - Juvenile salmonids utilize temporally variable ephemeral and stable aquatic, terrestrial, and marine prey resources

- While summer research may be more common, the most exciting results from this field study came from spring and autumn.

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QUESTIONS?