Missing pieces in the annual cycle of fish ecology: a systematic review of the timing of freshwater fish research focused on juvenile Pacific salmon and trout

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Abstract

In recent decades, fish ecologists have become increasingly aware of the need for spatially comprehensive sampling. However, a corresponding reflection on the temporal aspects of research has been lacking. We quantified the seasonal timing and extent of freshwater fish research reported in the literature. Since reviewing all prior work was not feasible, we considered two different subsets. First, we compiled the last 30 years of ecological research on juvenile Pacific salmon and trout (*Oncorhynchus* spp.) (n = 371 studies). In addition to the aggregate, we compared groups classified by subject matter. Next, to characterize whether riverscape ecology has embraced space at the expense of time, we compiled research across taxa for studies (n=46) that sampled fish in a spatially continuous manner, i.e., those that followed Fausch et al.'s 2002 plea for a 'continuous view of the river…to understand processes interacting among scales.' We found that the temporal distribution of ecological *Oncorhynchus* spp. research effort was biased towards summer (40% occurred during June-August) and the month of June in particular, at the expense of winter work (only 13% occurred during December-February). Riverscape studies were also biased in temporal distribution toward summer (47% of studies) and against winter (11%). It was less common for studies to encompass multiple seasons (43% of ecological *Oncorhynchus* spp. studies and 54% of riverscape studies) and most were shorter than 4 months (73% of ecological *Oncorhynchus* spp. studies and 81% of riverscape studies). These temporal biases may cause researchers to overemphasize ecological phenomena observed during summer and limit our ability to recognize seasonal interactions such as carry-over effects or compensatory responses. Full year and winter studies likely hold valuable insights for conservation and management.

Introduction

A key challenge in conservation is to understand how abiotic and biotic heterogeneity mediate the function of ecosystems and the survival of biota that inhabit these environments. This heterogeneity exists in both space and time, creating a shifting mosaic of physical and biological conditions that has significant ramifications for biota [1]. Phenomena ranging from ontogenetic niche shifts [2] to the stability of fisheries [3] can only be understood by jointly considering interactions between space and time.

However, because resources are limited and characterizing stream heterogeneity is a non-trivial task, it is often not feasible to study multiple dimensions of variation simultaneously. Indeed, many fundamental concepts in stream ecology are either spatially or temporally focused. For example, spatial patterns of biota are often described with minimal reference to time. This applies to early work, such as the longitudinal zonation of fishes [4], but also the River Continuum Concept [5] and the contemporary emphasis on spatially continuous sampling in riverscape ecology [6]. Time is recognized as the “fourth dimension” of the riverscape [7] and the intersections of various temporal and spatial scales has been noted as important [6]. However, in practice, the suffix “scape” often reflects a focus on spatial patterns with less regard for temporal dynamics. Indeed, when Fausch et al. [6] called for stream ecology to embrace a riverscape approach to achieve ‘a continuous view of the river’, the primary emphasis was on closing gaps in space rather than time.

It is often recognized that short-term datasets can be inadequate because they fail to capture historical levels of productivity (i.e. the shifting baseline) or reveal coarser scale temporal patterning such as regime shifts [8]. Likewise, for cyclically patterned temporal variation, interpretations may be misleading if they are based on a limited portion of a cycle. For example, many fish switch between habitat types throughout the diel cycle [9] so only studying animals during daytime may fail to capture important habitats. Similarly, refuge habitat identified in summer may not represent refuge habitat for other seasons and stressors [10]. Riverine systems may exhibit extreme seasonal variation: water temperatures may range by more than 20°C [11], and flows may vary by several orders of magnitude [12]. This variation strongly affects not only fish and other aquatic organisms, but also the feasibility of field sampling. While a temperature logger can effectively collect data every day of the year, the cost and logistical challenges of sampling fish vary tremendously and can strongly govern when biological data are collected. The intra-annual patterns of abiotic variables such as temperature and water quantity are well quantified and describe the "regimes" of freshwater habitat. In contrast, biological variables such as diet, growth, and survival exhibit analogous intra-annual variation, yet their temporal patterning are quantified much less frequently. Extrapolating from data that pertain to specific points in time can lead to misleading interpretations regarding how fish behave, what locations or habitat types are important, and how much biomass ecosystems can produce [13,14]. This extrapolation of temporal data is particularly problematic in the study of mobile organisms that undergo substantial physiological and ecological changes throughout their lifetimes [15]. The objective of this paper is to characterize the temporal attributes of fish ecology research to elucidate potential data gaps that could guide future research.

Recent work on birds, amphibians, reptiles, and mammals found strong seasonal biases in field research [16], but analogous work on fish has been lacking. The assertion that winter fish ecology is an important, yet understudied portion of the research portfolio is not new [17]; however, this hypothesis remains unquantified. It was not feasible for us to screen the research for all fish species during all life phases, so we limited our systematic review to a single genus of fish: *Oncorhynchus*. We focused on juvenile Pacific salmon and trout in freshwater because they are well-studied (providing us the power to detect trends in sampling), they live in highly seasonal environments (which means an incomplete understanding of the annual cycle would be a problem and is thus important to test for), and they are distributed across multiple continents (thus representing a wide-spread species of interest). Here, we characterize the temporal aspects of freshwater fish ecological research within the taxon of Pacific salmon and trout (*Oncorhynchus* spp.) during the last 30 years. We characterized patterns in the seasonal timing and extent of ecological field studies and considered how these patterns varied across three focal topics: fish-habitat interactions, trophic ecology, and spatial distribution. Additionally, we assessed whether spatially comprehensive sampling has come at the expense of time by reviewing the timing of riverscape studies across all fish taxa.

Materials and methods

Data screening

To determine whether and to what extent temporal biases are present in fish field research, we conducted a systematic review of two areas: 1) research within the *Oncorhynchus* species during the juvenile life stage and 2) research across fish species within riverscape studies. We defined riverscape fish studies as those employing spatially continuous (or nearly so) sampling at high extents so that multi-scale patterns could be revealed [6]. These studies are in contrast to the more typical method of using a relatively small number of points to represent large extents. Thus, we did not use spatial extent as a variable in our analysis or a definition of riverscape study, because high extent typically comes through high 'magnification factor' *sensu* Schneider [18] that precludes robust study of spatial heterogeneity [6]. We focused on three temporal aspects of research: 1) what months and seasons research occurs, 2) the duration of studies, and 3) whether research spanned multiple seasons.

To examine our first dataset of *Oncorhynchus* research, we reviewed 13 journals that commonly publish research on fisheries ecology as opposed to human consumption of fish. Using the Web of Science database (last searched 4 February 2021), we performed the following search: TS=(salmon OR salmonids OR Oncorhynchus OR salmonine OR Salmonidae) AND SO=(CANADIAN JOURNAL OF FISHERIES "AND" AQUATIC SCIENCES OR Ecology OR Ecology of Freshwater Fish OR Ecosphere OR Ecosystems OR Environmental Biology of Fishes OR Freshwater Biology OR Hydrobiologia OR North American Journal of Fisheries Management OR Oecologia OR PLoS ONE OR Science OR Transactions of the American Fisheries Society) Indexes=SCI-EXPANDED, SSCI, A&HCI, ESCI Timespan=1988-2017. The past 30 years was chosen to characterize the current patterns of research and to make the review more feasible due to limited access to journals during earlier periods of publishing. We screened the articles and selected those that dealt with the ecology of juvenile *Oncorhynchus* species during freshwater residence. The juvenile life stages of fry, parr, and smolt were all included. We included both observational studies and experimental studies conducted in the natural environment. We did not include studies that did not sample fish in the field, laboratory studies, studies occurring in estuarine or marine environments, or studies that collected physical or biological habitat data but did not actually sample fish. Our search terms identified 6,439 articles. After screening for non-eligible articles, 371 were included for analysis in this study (S1 Fig).

For the riverscape review, using the Web of Science database (last searched 23 October 2020), we performed the following search: TS=(riverscape OR spatially continuous OR longitudinal distribution OR Fausch et al. 2002) AND TS=(fish OR fishes OR salmon) AND TS=(stream OR river OR freshwater OR lake) Indexes=SCI-EXPANDED, SSCI, A&HCI, ESCI Timespan=1988-2017. We then examined every article and selected those that dealt with spatially continuous or high spatial extent (at or above segment scale [6]) sampling that included fish data collection. Our search terms identified 411 articles. After screening for non-eligible articles, 46 were included for analysis in this study (S2 Fig).

Data analysis

We classified each publication for both the ecological dataset and the riverscape dataset by the temporal characteristics of data collection to examine the timing and duration of research reported in literature. First, we read the Methods section of each article and screened and recorded the presence/absence of data collection in each month and season. We defined seasons meteorologically as aligned with the calendar months of June 1-August 31 for summer, September 1-November 30 for autumn, December 1-February 28 for winter, and March 1-May 30 for spring. Presence and absence within a single month were used rather than breaking months up by solstice and equinox dates. This was done because the dates of the solstice/equinox change annually, and precise sample dates were often not reported beyond the month and year. Studies may encompass more than one month, therefore the number of data points for these analyses are greater than the number of studies included in the review. Second, we quantified the frequency of the number of meteorological seasons (1-4) that were included in these studies to analyze temporal extent and consideration of inter-seasonal interactions (i.e., carry-over effects).

To explore whether temporal aspects of sampling differed among research areas, we classified each study into three focal areas: 1) fish-habitat interactions and the impact of habitat units and types on juvenile salmonid biology or behavior, 2) trophic ecology including fish diet, foraging, and food web structure, and 3) spatial distribution including movement and landscape-scale distribution. Studies examining fish growth and survival were often presented by researchers as a function of some aspect of one of the three focal areas identified and were classified accordingly. The temporal distribution and extent of sampling effort was then quantified both collectively and by research category. Each study was only classified into one of the three focal areas based on the main objective of the study. Studies that did not fall into one of these four main categories were classified as "Other" and included in overall analysis but not the category-specific analyses.

Statistical methods

We used Pearson x^2-tests in R 4.0.2 to test the null hypothesis that data were randomly distributed across all categories (i.e. sample month, or number of months sampled per year). If no biases were present, we would expect similar distribution across the categories tested. While the test is objective, we acknowledge that the interpretation is subjective due to the assumptions that all months and seasons are equally important and present equal stresses, limitations, or opportunities for growth, fitness, and survival for juvenile salmonids.

Our analyses presented two potential issues: multiple comparisons and non-independence. We used a Bonferroni correction to adjust our threshold for statistical significance (i.e., the alpha value) [19]. We performed 12 tests, so our adjusted alpha was 0.004 (i.e., 0.05/12). To ensure that our interpretation of the Pearson x^2 test was robust to non-independence (from single studies contributing to multiple months or seasons), we used a Monte Carlo approach. Specifically, we performed simulations in which (for the studies with multiple months or seasons) we randomly selected only one month or season to be included in the analysis and then recalculated the x^2 statistic and p-value. We repeated this 10,000 times. This simulation arrived at the same results as the standard Pearson's test (S4 Fig).

We acknowledge that seasonality varies with latitude, elevation, and position in watershed, so the ecological conditions associated with a particular month or season may vary among locations (and thus among the studies in our paper). Thus, the implications of the temporal biases we observed may be somewhat context dependent. Future studies could address this.

Results

Monthly temporal distribution of studies

At a monthly resolution across all ecological topics within juvenile *Oncorhynchus* spp. studies, we found that the most frequently represented month was 3-6 times more common than the least frequently represented month (Fig 1). December was the least represented month across all topics, while the summer months of June, July, and August were most common among topics. The month of June had a significantly higher proportion of studies than the month of December at 14% and 3%, respectively.

Fig 1. Temporal distribution of juvenile salmon ecology studies. Left column: monthly distribution (left to right: January to December) of sampling effort for juvenile Pacific salmon and trout studies from 1988-2017 for (A) all studies (X2=289.58, p < 0.0001, n=1476, median=119.5), (B) habitat studies (X2=97.421, p < 0.0001, n=413, median=28), (C) trophic ecology studies (X2=78.131, p < 0.0001, n=244, median=18), (D) spatial distribution studies

(X2=53.67, p < 0.0001, n=439, median=27). Right column: seasonal distribution of sampling effort for juvenile Pacific salmon and trout studies from 1988-2017 for (E) all studies (X2=243.39, p < 0.0001, n=1476, median=345.5), (F) habitat studies (X2=84.482, p < 0.0001, n=413, median=83), (G) trophic ecology studies (X2=56.295, p < 0.0001, n=244, median=57.5), (D) spatial distribution studies (X2=45.258, p < 0.0001, n=349, median=81). The number of studies for each month or season was calculated using presence or absence of research during that time frame. Dashed horizontal lines are data median. Studies may occupy more than one month or season. Seasons were defined meteorologically, but as whole months. Summer is defined as the months June, July, and August; Autumn is defined as the months September, October, and November; Winter is defined as the months December, January, and February; Spring is defined as the months March, April, and May.

Seasonal temporal distribution of studies

Across all ecological topics within juvenile *Oncorhynchus* spp. studies, we found that 39-44% of studies occurred during summer while only 10-15% of studies occurred during winter (Fig 1). There has been little change in the temporal distribution of research efforts with the proportion of winter studies remaining lower than summer studies (Fig 2).

Fig 2. Seasonal study distribution over time. Change in the proportional temporal distribution (seasonal timing) of all studies published from 1988-2017 in 5-year increments.

Monthly temporal extent of studies

At a monthly resolution across all ecological topics within juvenile *Oncorhynchus* spp. studies, we found that most studies had limited temporal extent across the annual cycle, with 71-75% of studies containing data from 4 months or less (Fig 3). Less than 2-8% of studies across all topics encompassed data from all 12 months of the year.

Fig 3. Temporal extent of juvenile salmon ecology studies. Left column: frequency of the number of months per calendar year (1-12) found in juvenile Pacific salmon and trout studies from 1988-2017 for (A) all studies (X2=670.07, $p < 0.0001$, n=371, median=5.1), (B) habitat studies (X2=173.55, $p < 0.0001$, n=108, median=4.6), (C) trophic ecology studies (X2=120.92, $p < 0.0001$, n=60, median=8.3), (D) spatial distribution studies (X2=173.01, $p < 0.0001$, n=89, median=5.1). Right column: frequency of the number of seasons per calendar year (1-4) found in juvenile Pacific salmon and trout studies from 1988-2017 for (E) all studies (X2=230.95, $p < 0.0001$, n=371, median=17.8), (F) habitat studies (X2=80.296, $p < 0.0001$, n=108, median=16.7), (G) trophic ecology studies (X2=19.6, $p < 0.001$, n=60, median=20.8), (H) spatial distribution studies (X2=72.573, $p < 0.0001$, n=89, median=14.6). The extent or duration was calculated by counting the total number of unique months (in a calendar year) that were included in each study and categorizing them by season as defined above. Data median is marked with a dashed horizontal line. Studies were only represented once at their greatest monthly extent and greatest seasonal extent.

Seasonal temporal extent of studies

Across all ecological topics within juvenile *Oncorhynchus* spp. studies, we found that 48-63% of studies occurred during a single season while only 6-10% of studies encompassed field sampling from all four seasons (Fig 3). Only 43% of all studies collected data from multiple seasons and 73% of studies were shorter than 4 months. Again, there has been little change in the temporal extent of research efforts with the proportion of single-season studies remaining significantly higher than multi-season or year-round studies (Fig 4).

Fig 4. Seasonal study extent over time. Change in the proportional temporal extent (number of seasons included) of all studies published from 1988-2017 in 5-year increments.

Riverscape studies

Analysis of riverscape studies across fish species revealed wider biases in temporal distribution at monthly and seasonal scales. The most frequently represented month was 8x more common than the least frequently represented month (Fig 5). January and February were the least represented months, while June, July, August, and September were most common. Summer encompassed 47% of all riverscape studies while only 11% of studies occurred during winter (Fig 5).

Fig 5. Distribution and extent of riverscape studies. (A) Monthly distribution (left to right: January to December) of sampling effort for spatially continuous “riverscape” studies involving all fish species from 1988-2017 (X2=69.089, p < 0.0001, n=158, median=8); (B) seasonal distribution of sampling effort for riverscape studies (X2=54.152, p < 0.0001, n=158, median=33); (C) frequency of the number of months per calendar year (1-12) found in riverscape studies (X2=97.038, p < 0.0001, n=46, median=3.3); (D) frequency of the number of seasons per calendar year (1-4) found in riverscape studies (X2=18.174, p < 0.001, n=46, median=22.83).

The number of studies for each month or season was calculated using presence or absence of research during that time frame. Dashed horizontal lines are data median. Studies may occupy more than one month or season. Seasons were defined meteorologically, but as whole months. Summer is defined as the months June, July, and August; Autumn is defined as the months September, October, and November; Winter is defined as the months December, January, and February; Spring is defined as the months March, April, and May.

Monthly temporal extent was limited within riverscape studies as well. Spatially continuous studies were almost entirely conducted during a limited amount of time: 81% contained data from 4 months or less and only 4% of studies encompassed data from a full 12 months out of the year (Fig 5). Seasonal extent for riverscape studies was the one metric that was more representative than the ecological studies we examined: 46% of riverscape studies occurred during a single season, 35% occurred over two seasons, 9% occurred over three seasons, and 11% occurred during all four seasons (Fig 5).

Discussion

In our review of 371 ecological juvenile *Oncorhynchus* spp. studies and 46 riverscape studies from the last 30 years, we observed strong biases in seasonal timing (distribution) and temporal extent. Within research topics where seasonality is particularly relevant, we observed the same general pattern of temporal bias; the period of summer was overrepresented in the study of fish-habitat interactions, trophic ecology, and spatial distribution. Below we discuss these temporal patterns of data collection and consider their potential causes and consequences.

Bias in temporal distribution of studies

The most conspicuous pattern in the data was the lack of research during winter. For example, the month of December had less than one-quarter as many studies as that of June. Winter studies represented only 10-15% of total ecological research and 11% of riverscape studies. Winter may be tempting to overlook because it is generally a period of low biological activity in freshwater ecosystems. Winter is typically the coldest time of year, limiting the scope for growth and activity in aquatic poikilotherms. Further, winter is the darkest time of year, limiting primary productivity [20] and the foraging opportunity for visual predators [13]. Indeed, many stream-dwelling fishes tend to allocate energy to fat stores in anticipation of winter [21], suggesting it is generally a period of negative energy balance. However, decreased activity does not mean that understanding winter ecology is not important. For example, if fish rely on summer and fall fat stores to survive winter, then any food intake during winter could reduce the risk of depleting energy reserves. Further, in some systems winter growth rates may actually exceed growth rates during other times of the year [22,23]. Recent work has shown juvenile salmonids utilizing different habitats in non-summer seasons [24] and acknowledges that our understanding of non-summer habitat suitability is lacking [25], for a variety of taxa [26]. Identifying winter foraging opportunities, trophic pathways, and habitat use could provide insights into how fish survive during this time of year [27].

In many systems, winter survival is hypothesized to be a limiting factor, or bottleneck, to freshwater population productivity of juvenile Pacific salmon and trout [28]. Therefore, reducing winter mortality is often an objective of largescale restoration efforts [29]. While winter mortality has been widely documented, the mechanisms behind winter mortality remain unidentified or poorly corroborated in many of these fish populations [30]. In one study, increased winter mortality in fish was linked to low late-season growth rates and high depletion of energy reserves accumulated prior to winter [31], emphasizing the need for multi-season research to explain productivity limitations. Further, the validity of winter as a bottleneck for salmonid and non-salmonid species has not been widely supported, partially due to habitat-specific characteristics of each system [17], thus supporting the idea that more research is needed to understand winter fish ecology including habitat use, foraging ecology, winter mortality, and productivity bottlenecks.

While the focus of winter ecology in juvenile salmonids is often on over-winter survival, the impact of winter on freshwater fish populations goes beyond winter mortality. For fish in lakes, daily and seasonal migrations exploit a portfolio of habitats throughout the year [32]. Additionally, the impact of climate change on the length of warm and cold seasons may have unexpected consequences for fish. For example, one study found that shorter winters affected perch populations by altering reproductive timing, egg size, and hatch rate, thus reducing overall reproductive success of females [33]. The shift in season length could also cause a de-coupling of nearshore and pelagic food webs in lakes [34].

The lack of winter research contrasted with an overrepresentation of summer studies. The concern we raise is that relying on summer-biased data could pose problems for conservation and management, specifically when data violate the assumptions for models. For example, species distribution models (SDM) are increasingly used in climate change adaptation and rely on the assumptions that a species occurs in all suitable habitats and that a species only occupies a portion of that suitable habitat due to constraining factors such as competition or predation [35]. Developing such models from temporally biased data would be valid only if the focal species were sedentary and their habitat use did not vary over time. However, it is rarely possible to confirm that a species meets these criteria without having temporally representative data (i.e., you cannot dismiss the possibility of winter habitat shifts without data on winter habitat use). Using data from a limited period of time can cause SDMs to erroneously dismiss critically important habitat [36,15]. For example, one study demonstrated that SDMs based on seasonally biased data failed to identify the habitats needed to support both hibernation and reproduction in bats [37].

Defining climate refugia for fish based on summer-biased data [38] could similarly leave out critical habitats if fish exhibit seasonal movements and require multiple habitat types to complete the annual cycle [39,15]. Recent work focused on coldwater fishes showed how physiological growth potential shifts across river basins through the annual cycle, peaking once during summer in colder tributaries, and twice, during spring and autumn, in warmer downstream areas [15]. Migratory life histories can exploit this spatio-temporal heterogeneity through seasonal movement [34]. However, emerging frameworks for coldwater fish climate adaptation do not place value on downstream growth habitats, because these approaches evaluate habitats based on crowd-sourced data on fish occupancy, which is strongly biased toward summer months [38]. This favors habitats that are optimal during summer at the expense of habitats that function during other seasons. Simulations and empirical studies show that portions of lakes or rivers that are thermally stressful and vacant of fish during summer may be critical for growth during other seasons, fueling migratory life-histories that in turn provision fisheries [34, 15].

Seasonal bias and lack of year-round study may also limit our ability to apply physiological models to fish conservation. For example, bioenergetics models for largemouth bass were found to overestimate winter metabolic costs when the models had been empirically validated using summer conditions [40]. Further, there is increasing evidence that animals can adjust their physiological rates and capacities in response to intra-annual variation such as food availability [41]. This can further introduce error into models that predict metabolism based on data collected during specific times of the year [42,43].

Our current classification system for longitudinal fish zonation is largely based on summer sampling [4]. While recent decades have seen an emphasis on more spatially representative fish sampling [44] and a movement towards multiscale analysis of spatial distributions [45], this work tends to not be temporally representative. For example, spatially continuous “riverscape” sampling has been transformative for our understanding of salmonid spatial distributions [6], yet our results confirm that virtually all of this work is conducted during summer or early autumn [46,47]. Thus, a remaining challenge for riverscape ecology is to achieve a ‘continuous view of the river’ [6] not only in space, but also across the annual cycle.

While longitudinal patterning is inherently relevant to lotic ecosystems (because they are linear networks), fish may also exhibit pronounced spatial patterning in lateral, and vertical dimensions [25]. In temperate regions of the Pacific salmon range, floodplains may only be connected and wetted during winter, so summer-biased sampling may hinder our ability to understand the significance of off-channel habitat use. Where summer and fall are the wet seasons (e.g., much of coastal Alaska), use of off-channel habitats may vary seasonally and require temporally extensive sampling to understand key dynamics. For example, the spatial patterning of juvenile coho salmon on a stream floodplain shifted over time, tracking shifts in water temperature [48] caused by fluctuating water levels. Use of temporary aquatic habitats by fish may be disproportionately important when they are available at the right place and time; however, research is lacking to capture this ephemeral aspect of fish ecology [49].

The distribution of juvenile salmonids among channel-unit scale habitat types [50] may also vary among months and seasons. For example, one study found that juvenile coho primarily occupied backwater pools in spring, main-channel pools in summer, and alcoves and beaver ponds in winter [51]. Distribution of juvenile salmonids in sub-habitats (e.g. riffles, pools, backchannel ponds) can also impact fish growth and fitness through energetic costs and benefits [52]. While fine-detail studies of fish distribution help identify quality salmonid habitat, our analysis demonstrates that this data implicitly favors summer habitat and devalues winter habitat.

Bias in temporal extent of studies

While a bias against winter studies is seen in temporal distribution, a bias against full annual studies is seen in temporal extent. Ecological *Oncorhynchus* spp. studies examining all four meteorological seasons represented only 6-10% of total research. While it is possible that a small subset of winter studies could encompass the entirety of knowledge needed to fully understand the winter ecology of fish, recent research has demonstrated that this is likely not the case as novel and important insights continue to be found when understudied times of the year are further explored [26]. Research is heavily skewed toward shorter, single season studies: 73% of all studies capturing 4 months or less of data and 57% of studies focused on a single season in isolation. Within riverscape studies, 81% of research occurred during 4 or fewer calendar months. These patterns are similar to patterns observed in the temporal characteristics of mammal, bird, reptile and amphibian research [16]. While there is increasing recognition of the value of long-term study [53], this usually means having multiple years or decades of data collection. Our review shows that there is also a lack of temporal extent in terms of the annual cycle. Lacking extent at this timescale leads to two issues. First, we are likely to temporally extrapolate and draw conclusions based on a subset of the year (as discussed above) and second, we will often lack the ability to identify interactions between different time periods, or carry-over effects [16].

Carry-over effects from one life stage or season can have significant impacts on fitness and survival of individuals and populations in subsequent seasons or life stages [54]. As climate change and increasing water demands make summer more stressful for salmon in regions such as the western United States, there is a strong need to understand how conditions during spring and fall mediate the effects of summer stress on freshwater rearing capacity. The ability of fish to survive negative energy balance during harsh summer conditions should depend on their ability to store energy in spring and rebuild energy stores in fall. For example, over-winter survival of juvenile salmon is often positively associated with larger body size at the onset of autumn [55]. There is evidence that ephemeral food subsidy pulses, such as salmon eggs during the adult spawning season, can positively influence juvenile salmon growth rate and energy density as long as 6 months after this ephemeral resource pulse has disappeared [56]. Whether juvenile salmonids grow large enough to consume eggs depends on their emergence timing and early growth opportunities [57]. Thus, small increases in the growth of fry during spring may determine whether marine subsidies benefit parr during fall, influencing overwinter survival and the size of smolts the following spring, which relates to subsequent marine survival [58].

Sampling during multiple seasons is more likely to capture any carry-over effects that span pre-pulse, pulse, and post-pulse. Food availability, along with temperature, strongly affect fish growth rates with extreme variation in growth between seasons [22,59]. Quantifying fish growth and food resources at multiple points in time are essential to avoid bias in assumptions and to identify ephemeral trophic pathways that could be disproportionately important during that season or in subsequent seasons. Additionally, consequences of increased stress during one season can be observed in subsequent seasons through differences in fish growth, behavior, and survival [60,61]. Compensatory responses, such as growth rate and survival after a period of starvation, may also not be fully realized for many months [62,63]. The lack of full annual cycle research on Pacific salmon has likely hindered our ability to recognize inter-seasonal carry-over effects and compensatory responses, which may become increasingly important in the future.

A core concept in landscape ecology, also applicable to aquatic ecology, is that species often rely on habitat complementation, meaning they utilize different patches of space containing different resources at different times in order to complete their life cycles [64,10]. The use of habitat by juvenile salmonids shifts 1) seasonally as river conditions such as temperature gradually change [51], 2) momentarily as a balance of energetic costs and benefits [65], 3) ontogenetically as resource needs change [2] and 4) ephemerally, such as during discrete events like floods or drought [10]. Without full annual studies, the effects of these stressors on fish (e.g. energetic costs, food availability, competition, predation) are poorly understood. Habitat restoration may be more successful if information is available to allow for targeting of the limiting life stage or limiting habitat in salmonid productivity [66]. It is well-established that the challenges faced by stream-dwelling fishes in winter are vastly different [67]. To best protect the habitat supporting juvenile salmon and trout, more effort is needed to understand the importance of winter ecology.

Considerations

The seasonal bias of research could potentially be a product of two human limitations: environmental challenges and allocation of scarce resources. First, the summer months generally present the least challenging environmental conditions for human access to salmon-bearing habitat, particularly in the Pacific Northwest where a significant amount of fish research takes place: low stream flow, warm temperatures, and minimal precipitation. Sampling fish in the winter months can be particularly challenging, as snow, ice, and high flow events limit safe access for researchers and lead to fish exhibiting behaviors that make them difficult to capture (e.g. winter concealment, nocturnality). Second, academic calendars create a seasonal bias towards summer field work by their very structure, allowing time for field work while classes are on break during summer. Field projects outside of academia also often follow a summer-intensive field season program due to the availability of field technicians who are often college students. Institutional hiring policies can further exaggerate these patterns. For example, at our institution students cannot work > 20 hours per week during non-summer months, and it costs ~30% more to hire seasonal assistants that are not students (due to the need for a temporary hiring agency). This makes non-summer field work considerably more expensive. Thus, a combination of environmental challenges, logistical hurdles, and institutional culture make field work more likely to happen in summer.

Conclusion

In recent decades, stream ecology has strongly emphasized the need for more spatially comprehensive sampling of fish [6]; however, temporally comprehensive sampling has not received the same attention. Mapping the entire riverscape can reveal rich, multiscale patterns, but efforts typically fail to reveal how these patterns shift over time. Fish may not occupy every meter of space available to them, but they do live in every second of time. Furthermore, phenomena such as floodplain dynamics [1], seasonal movement [68], portfolio effects [69], resource waves [70], and thermoregulation [71] are driven by the interaction between spatial and temporal variation. While not prescriptive, we propose a short list of research topics that may benefit from year-round research: diet and bioenergetics, terrestrial-aquatic interactions, species distribution and climate change vulnerability, use of ephemeral habitats, portfolio effects and the importance of stable and ephemeral resources, and the impact of carry-over effects on fish survival. We hope that our review encourages researchers to allocate more of their effort to understudied portions of the year, which likely hold valuable insights for conservation.

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Supporting information

S1 Fig. PRISMA 2009 flow diagram for *Oncorhynchus* studies.

(DOCX)

S2 Fig. PRISMA 2009 flow diagram for riverscape studies.

(DOCX)

S3 Fig. PRISMA 2009 checklist.

(DOCX)

S4 Fig. Monte Carlo simulations of the Pearson x^2 test repeated 10,000 times.

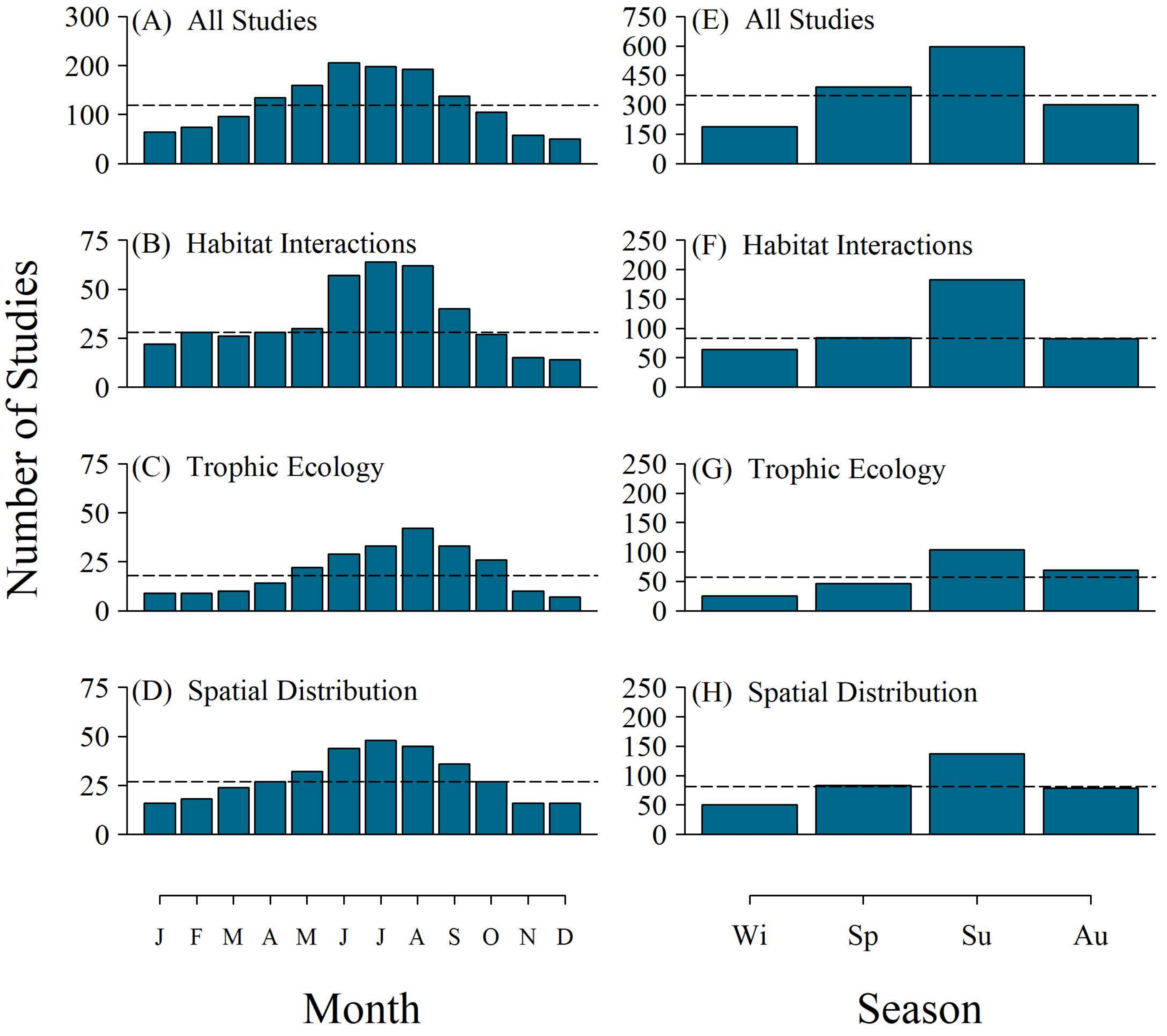
(TIFF)

S1 Table. Articles included in *Oncorhynchus* systematic review.

(CSV)

S2 Table. Articles included in riverscape systematic review.

(CSV)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100
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(B) Habitat Interactions
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50
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(C) Trophic Ecology
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25
0
(D) Spatial Distribution
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50
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Month
(E) All Studies
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600
450
300
150
0
(F) Habitat Interactions
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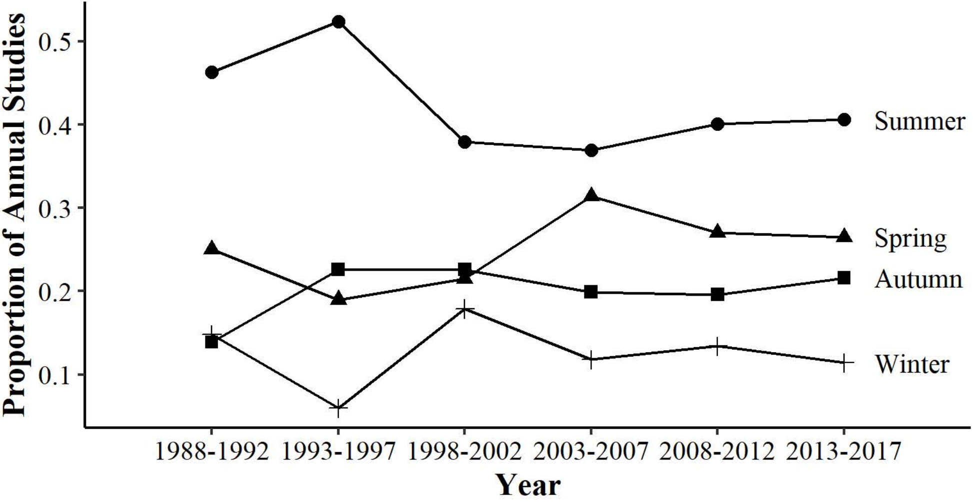
Proportion of Annual Studies
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0.2
0.3
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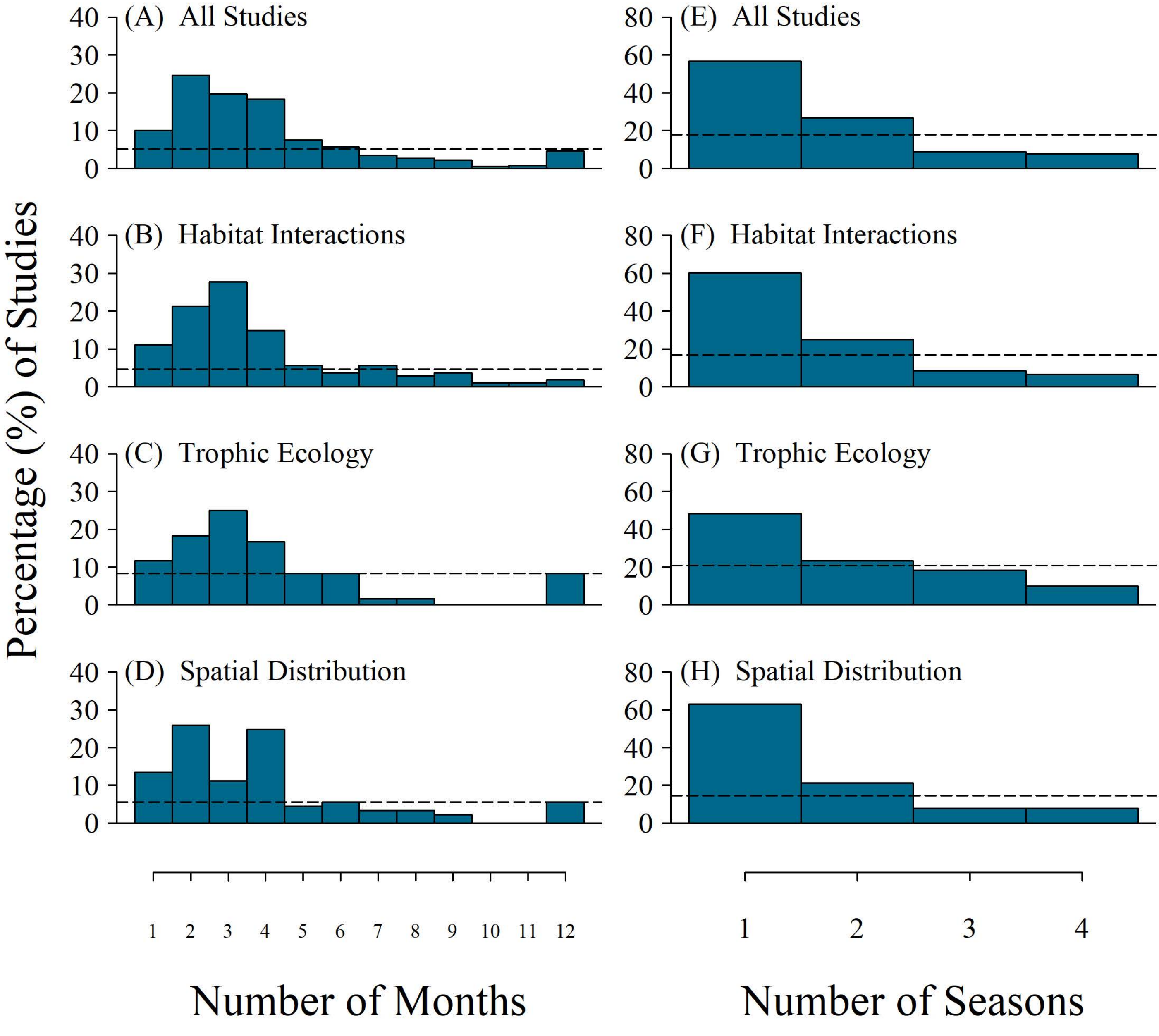
0.5
Summer
Spring
Autumn
Winter
1988-1992
1993-1997
1998-2002
2003-2007
2008-2012
2013-2017
Year


Percentage (%) of Studies
(A) All Studies
(B) Habitat Interactions
(C) Trophic Ecology
(D) Spatial Distribution
(E) All Studies
(F) Habitat Interactions
(G) Trophic Ecology
(H) Spatial Distribution
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20
30
40
0
20
40
60
80
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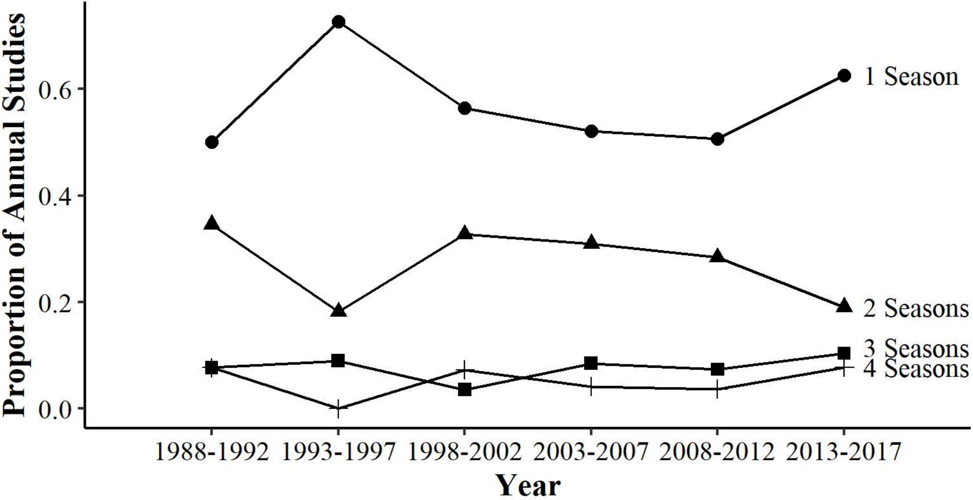
Number of Seasons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3 Seasons
4 Seasons
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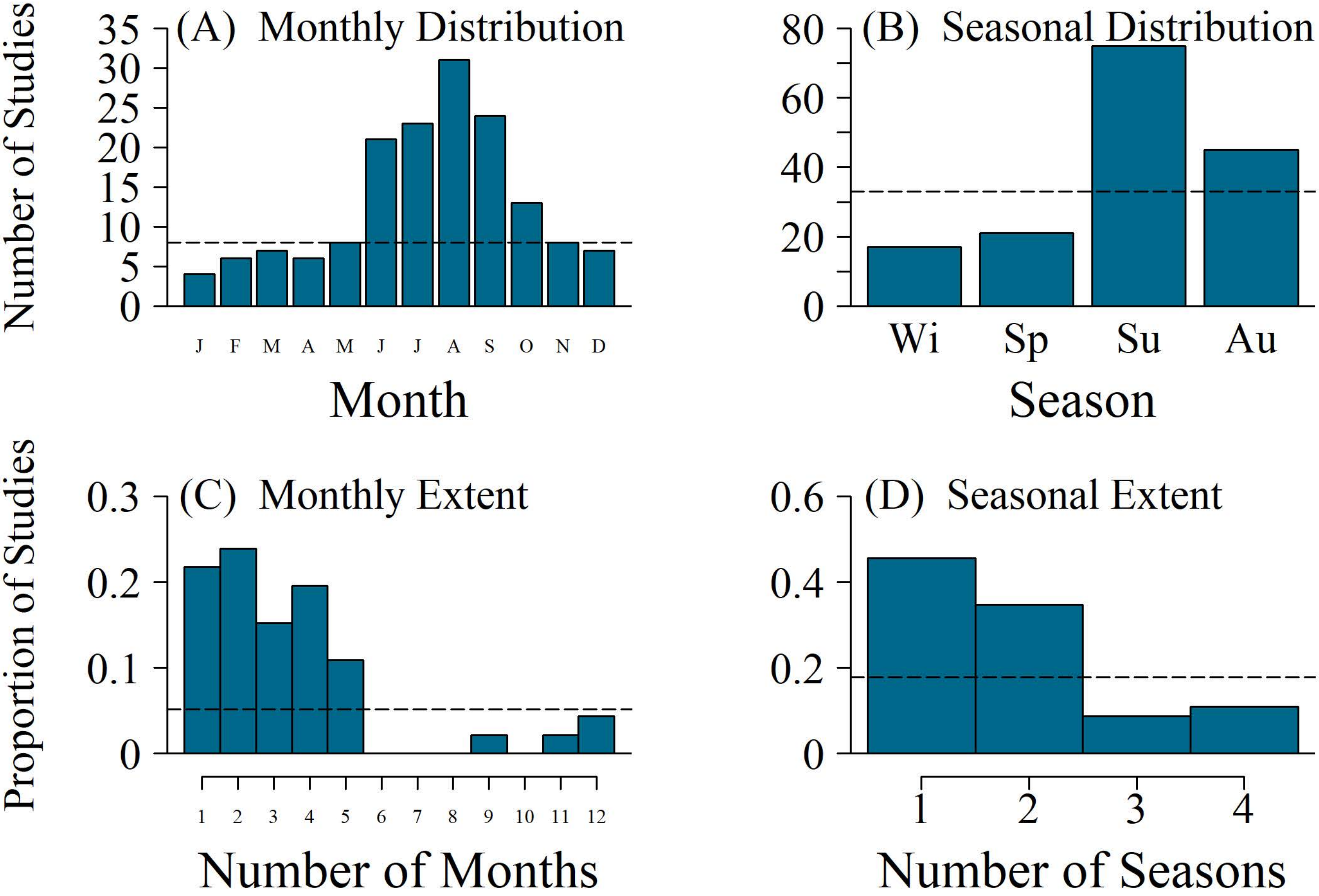
2003-2007
2008-2012
2013-2017
Year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Month
(B) Seasonal Distribution
80
60
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0
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Season
(C) Monthly Extent
Proportion of Studies
0.3
0.2
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3
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5
6
7
8
9
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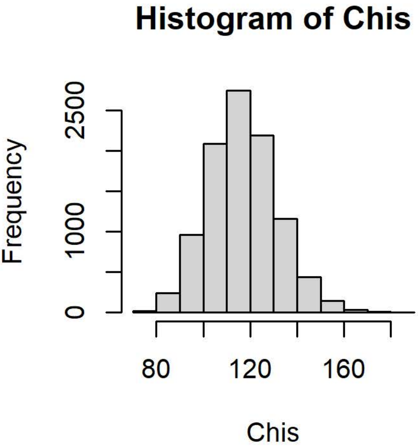
Number of Seasons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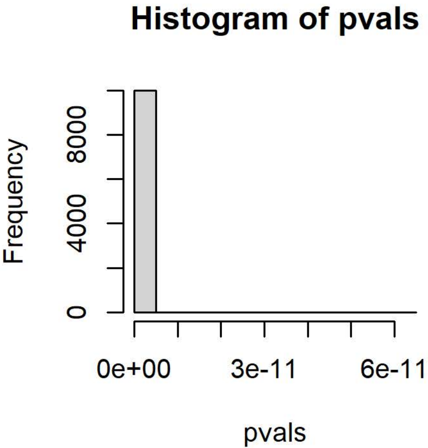
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