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Anne Shaffer, Justin Gross, Morgan Black, Amelia Kalagher, and Francis Juanes

2023

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This article was originally published at:

<https://doi.org/10.1002/aqc.3957>

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Citation for this paper:


Shaffer, A., Gross, J. H., Black, M., Kalagher, A., & Juanes, F. (2023). Dynamics of juvenile salmon and forage fishes in nearshore kelp forests. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 33(8), 822–832.

<https://doi.org/10.1002/aqc.3957>

## RESEARCH ARTICLE

WILEY

# Dynamics of juvenile salmon and forage fishes in nearshore kelp forests

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## Funding information

Patagonia Inc.; Coastal Watershed Institute; University of Victoria

## Abstract

1. North-east Pacific juvenile salmon and forage fishes, including the endangered salmon species Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), chum (*Oncorhynchus keta*), and pink (*Oncorhynchus gorbuscha*), and the forage fishes species of Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), and sand lance (*Ammodytes hexapterus*), utilize kelp environments. Many details of the kelp forest ecosystem function for these fishes are lacking.
2. Kelp forests, salmon, and forage fishes are declining precipitously as the global climate shifts and developments along coastal shorelines expand. It is therefore essential to understand kelp forest function for these species.
3. Analysis of 7 years of snorkelling survey videos indicates that both forage fishes and salmon use kelp forests throughout the outmigration season, and that their interactions occur in small and large groups, primarily along the outer edge of kelp beds. Over the course of outmigration, juvenile Chinook and coho salmon encounter sand lance first, followed by smelt and herring. The majority of interactions are intermingling, in which a subset proceed to predation, primarily on herring.
4. It is important to develop and implement specific fishery and habitat conservation measures to preserve and restore these functions. Long-term research has shown that intact, conserved nearshore habitats function better ecologically than restored habitats, and individual kelp forests can function differently for forage fishes and salmon. Therefore, conservation plans should be developed to conserve wild kelp forests which are documented to provide ecosystem function for salmon and forage fishes, by protecting them from various development impacts, including dredging, filling, and water-quality decline.
5. Coastal restoration is often only successful when ecosystem-limiting factors that result in a loss of habitat are resolved. Kelp forest restoration, therefore, should be prioritized for regions of known high historical kelp forest importance, with restoration actions focused on correcting the limiting factors that caused loss and/or degradation.

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## KEYWORDS

climate change, ecosystem conservation, forage fishes, kelp forests, marine habitats, salmonids

## 1 | INTRODUCTION

Pacific salmon are semelparous, anadromous species with complex life histories that vary depending on species, region, and environmental conditions, with many species dependent on nearshore habitats for juvenile life history stages. A number of populations of salmon species, such as Chinook (*Oncorhynchus tshawytscha*), coho (*Oncorhynchus kisutch*), chum (*Oncorhynchus keta*), and pink (*Oncorhynchus gorbuscha*), are listed as threatened or endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the Endangered Species Act in the USA (Duffy et al., 2010; Chalifour et al., 2019; COSEWIC, 2020; NOAA, 2022).

Forage fishes, including Pacific herring (*Clupea pallasii*), surf smelt (*Hypomesus pretiosus*), and sand lance (*Ammodytes hexapterus*), are designated as priority species by US federal and state agencies and are of growing conservation concern (Federal Register, 2016; WDFW, 2018; Audubon Society, 2020). Forage fishes use the nearshore, including kelp environments, for foraging and as nursery habitat (Miller et al., 1980; Baker et al., 2019; Shaffer et al., 2019; Shaffer, Munsch & Cordell, 2020; Frick et al., 2022). Forage fishes provide a link from primary productivity to higher trophic levels, making them foundational species for coastal systems (Penttila, 2007).

A number of salmon species use nearshore habitats as they outmigrate from natal river systems to marine life history phases. Chinook and coho are predatory fishes that undergo an ontogenetic diet shift from zooplankton to fish as they grow (Juanes, Buckel & Scharf, 2002; Duffy et al., 2010). This transition to piscivory in general leads to an increase in growth rate, and individuals that transition earlier gain a major competitive advantage, as they are larger in size, which is important for their survivorship (Juanes, Buckel & Scharf, 2002; Duffy et al., 2010). Similarly, chum and pink salmon also depend heavily on nearshore zones for their vulnerable life history stages. The numbers of these species have dropped significantly, in part as a result of the construction of in-river dams (Ward et al., 2008). To date, field observations indicate that the kelp forest environments are seasonally important zones for juvenile salmon, and the forage fishes they transition to feeding upon (Shaffer et al., 2019), but the details of complex juvenile salmon and forage fish immigration and emigration, and interaction timing, are not well understood for kelp forests. Gaining an understanding of the seasonal elements of the interactions displayed by juvenile salmon and forage fishes will provide a valuable insight into their developmental timing and diet transition, as well as broader kelp forest ecosystem function (Juanes, Buckel & Scharf, 2002). Such insights will be a useful base on which to build habitat management conservation and restoration priority actions for these important species and habitats.

Anthropogenic pressures, including coastal and shoreline development, invasive species, and ocean warming (Filbee-Dexter & Wernberg, 2018; Verdura et al., 2019; Smale, 2020), are causing

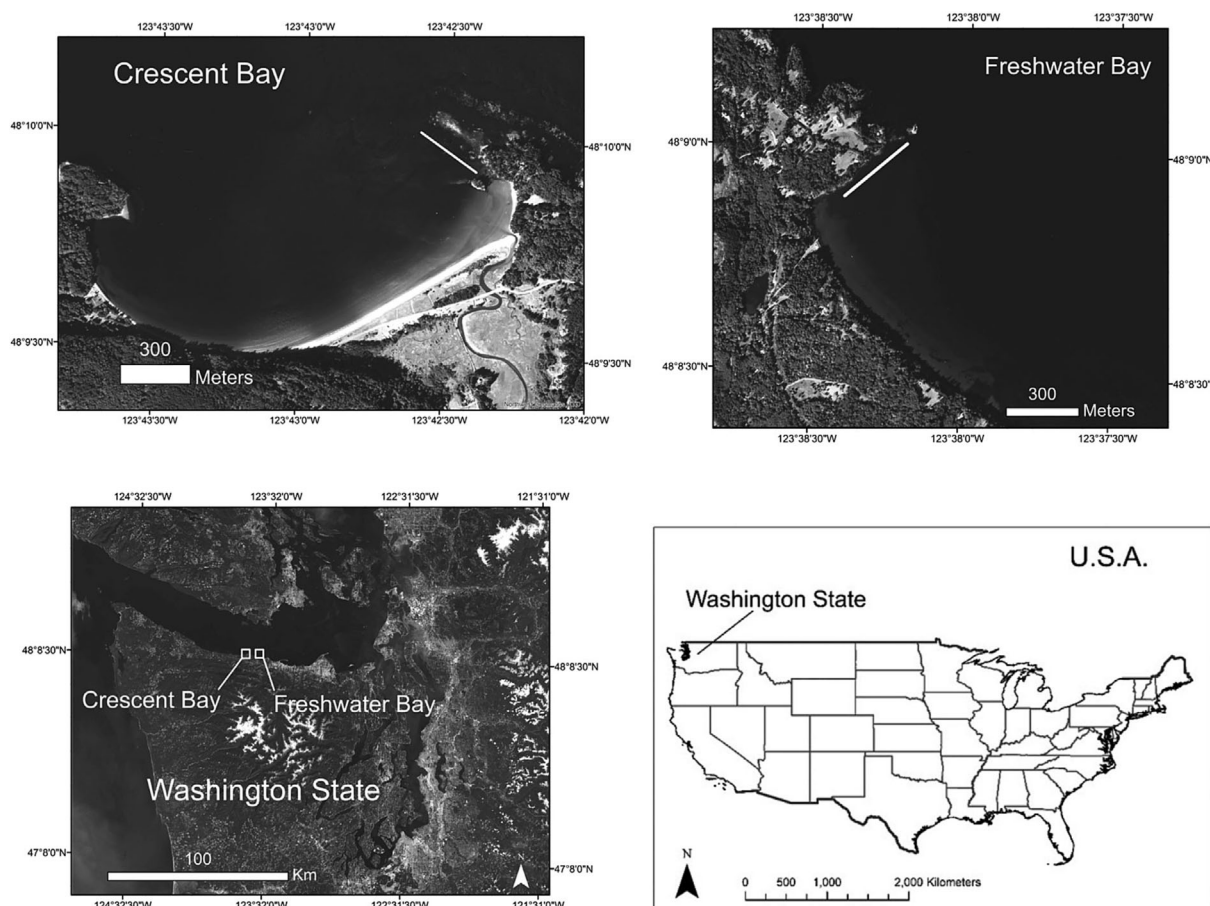
major regional declines in nearshore kelp environments, particularly in the southern Salish Sea and north coastal British Columbia (Krumhansl et al., 2016; Filbee-Dexter & Wernberg, 2018; Pfister, Berry & Mumford, 2018; Verdura et al., 2019; Berry et al., 2021; Starko et al., 2022; Tolimieri et al., 2023). Understanding the dynamics of kelp, salmon, and forage fishes is therefore fundamental to defining the extent to which these stressors affect the coastal ecosystem functions of the nearshore kelp environment. This study defines, for the first time, co-occurrences and interactions between juvenile salmon and forage fishes within the kelp forests of the Salish Sea, including abundance patterns and seasonal shifts that are important to define life history-specific habitat ecosystem functions. Types of interactions and co-occurrences between juvenile salmon and forage fishes were hypothesized to vary temporally, by species, and by habitat type. An increase in predatory behaviour was expected by the salmon across the outmigration season (May–September), and kelp habitat was predicted to play a role in these interactions.

## 2 | METHODS

The project involved analysing video imagery collected during the months of April–October, from 2013 to 2019, taken along snorkelling transects at two locations in the south-central Strait of Juan de Fuca of the Olympic Peninsula of Washington state (Figure 1). Both sites support relatively dense linear nearshore kelp forests and are located within 15 km of the mouth of the Elwha River, the site of a large dam removal restoration project, and so a highly studied, heavily hatchery-managed, and ecologically and culturally important river for fishery and ecosystem restoration (Shaffer et al., 2008; Ward et al., 2008; Peters et al., 2017).

### 2.1 | Video surveys and study site

Video surveys were conducted as a component of a long-term ongoing study documenting juvenile fish use of nearshore ecosystems (Shaffer & Ritchie, 2008; Shaffer, 2019; Shaffer, Munsch & Cordell, 2020). Multiple video surveys per month were conducted year-round in kelp forests of Crescent Bay and Freshwater Bay, Washington (Figure 1; Shaffer et al., 2019). The kelp forests are shallow continuous bands of kelp (in 2–10 m of water) that follow shoreline and/or reef features and consist primarily of bull kelp (*Nereocystis luetkeana*). Videographing snorkellers followed one permanent transect line each along the kelp forest and adjacent non-kelp zones at least 3 m away from the kelp bed at each of the two sites. Wind conditions for snorkelling surveys were always calm (<5 km/h). During each survey, each snorkeller used an underwater GoPro™ set at a minimum of 4 k video resolution at 30 fps, mounted on



**FIGURE 1** Study area (map reprinted with author permission from Shaffer, Munsch & Cordell, 2020).

a 152-cm camera pole, and recorded all salmonids and forage fishes encountered within 3 m of each side of the snorkeller during kelp and non-kelp surveys. All surveys were 60–90 minutes long. Snorkellers began at the start point of the kelp bed and swam the length of the kelp bed, and the observed forage fishes and salmon were videoed. When interactions were observed, the snorkeller paused and videoed the interaction before continuing. Once the end of the transect was reached, the snorkellers moved to the non-kelp zone and swam back to shore while filming. Again, any interaction observed was filmed.

## 2.2 | Video analysis

In the lab, a subset of these videos that had a minimum visibility of at least 3 m for each snorkel survey were selected. Four survey days per month per site were analysed.

For each video, all fish species observed were identified and recorded, abundances were estimated, and binned using a method adapted from Shaffer (2019), as follows: during each video survey the shoal sizes of surf smelt, sand lance, and herring were estimated by visually counting the number of fish in schools, and then binning the counts (Table A1). If more than one shoal was recorded for a species the observations were averaged for the survey by species. Co-occurrences (CO) were recorded only between forage fishes and

salmon when they were in the same video frame. CO types were allocated into the following four categories.

1. Adjacent (AJ), when a single or school of salmon was observed in the same video frame as forage fishes but not intermingling.
2. Intermingling (IM), when a single or school of salmon was observed among forage fishes with no further behaviour actions.
3. Fast approach (FA), when a juvenile salmon made a quick advance towards a forage fish as a possible attempt to feed but no contact was made.
4. Predation (PR), when a forage fish was consumed by a salmon.

Kelp proximity was categorized as present or not. If present, the recording was categorized as on the edge of kelp if two sides or fewer of the fish were bordered by kelp (E), and in kelp (I) if three or four sides of the fish were bordered by kelp.

## 2.3 | Data analysis

Data analysis was conducted using R studio and the ggplot2 package (Wickham, 2011; R Core Team, 2021). Data visualization was used to compare patterns across years, months, group feeding dynamics, species, and interaction types.

Poisson distribution models were used to define interactive relationships between kelp, month, forage fishes, and salmon species to define significant factors for interactions. Pink and chum salmon observations were too few to model. For Chinook and coho, for each model predictor the variables initially considered were: month, juvenile coho abundance, juvenile Chinook abundance, unknown juvenile salmon abundance, abundance of specified forage fish species, and proportions of interactions associated with kelp.

### 3 | RESULTS

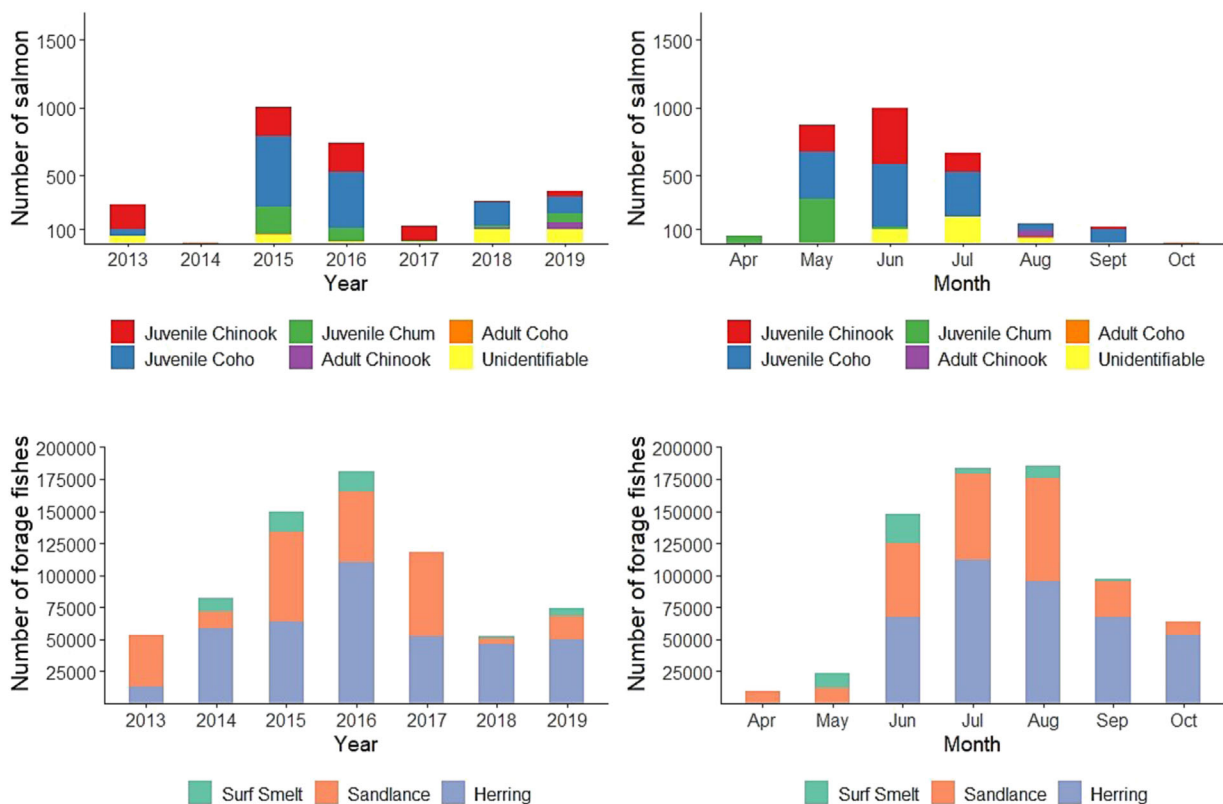
#### 3.1 | Abundances and co-occurrence (CO) types and patterns among salmon and forage fishes

A total of 105 videos that included 933 observations of forage fishes and salmon, and 177 interactions between forage fishes and salmon

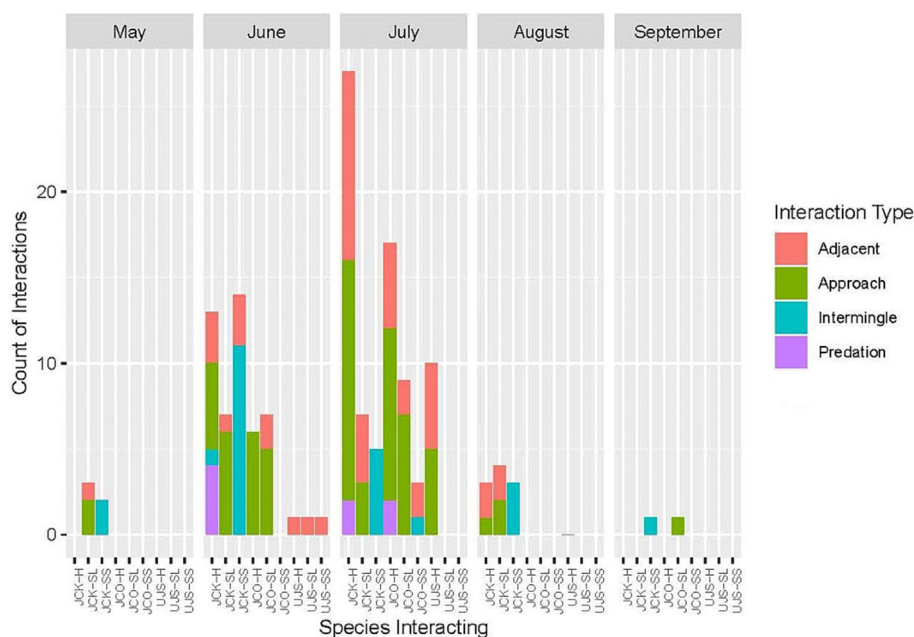
were analysed. Of these, 139 interactions occurred in the kelp forest zone, and 38 interactions occurred in the non-kelp zone. Forage fishes and salmon both first appeared in April (Table 1). All salmon observed were young-of-the-year juveniles (i.e. <100 mm total length, TL) and the majority were Chinook and coho salmon. Juvenile chum salmon were rarely and inconsistently observed. No pink salmon were observed. All salmon and forage fishes were observed from April to October (Figure 2). The majority of herring, surf smelt, and sand lance were juveniles (i.e. <120 mm TL; Shaffer, 2019). Herring and sand lance were the most abundant forage fishes observed for all years and seasons (Figure 2). Seasonal CO types between juvenile salmon and forage fish species show FA and AJ behaviour between Chinook and sand lance beginning as early as May (Figure 3). All CO types between all species increased in June and July and declined in August and September. FA was the most frequent CO type, primarily between Chinook and herring, between coho and herring, between Chinook and sand lance, and between coho and sand lance, in June and July.

**TABLE 1** Summary of interactions of salmon with forage fishes.

Forage fish species	Approaches	Predations	Intermingling	Adjacent	Total
Surf smelt	1	0	24	8	33
Sand lance	27	0	0	11	38
Herring	47	8	3	30	88
Other/unidentified					18
Total	75	8	27	49	177



**FIGURE 2** The maximum number of each species per day recorded from two sites along Strait of Juan de Fuca, 2013–2019.



**FIGURE 3** Number of co-occurrences between species, by type of interaction, during May–September, 2013–2018. Species interactions included juvenile Chinook–herring (JCK–H), juvenile Chinook–sand lance (JCK–SL), juvenile Chinook–surf smelt (JCK–SS), juvenile coho–herring (JCO–H), juvenile coho–sand lance (JCO–SL), juvenile coho–surf smelt (JCO–SS), and unidentifiable juvenile salmon species (US–H, US–SL, and US–SS) for combined sites in the Strait of Juan de Fuca.

AJ was the second most frequent CO type observed during these months (Figure 3). Successful PR was rare, and all instances were observed in June and July. IM between Chinook and surf smelt and between coho and surf smelt was occasionally observed throughout the study period, with a large increase in June, and with no IM observed in September (Figure 3).

### 3.2 | Group feeding dynamics

Approaches displayed by both juvenile Chinook and juvenile coho, possibly indicating the transition to piscivorous behaviour, rapidly increased in June and July, and then rapidly decreased in August and September (Figure 3).

Twenty-five approaches by juvenile coho were observed, 23 of which were by individuals in a group of between one and 10 salmon. Two of these approaches were by juvenile coho in groups of 11–75 (Figure 4). Thirty-six approaches by juvenile Chinook were observed, 22 of which occurred when they were in a group of between one and 10 salmon. Five approaches occurred when juvenile Chinook were in a group of 76–500 fish, and nine approaches were observed by groups of 11–75 fish. The number of approaches with high numbers of salmon increased between June and July, and then decreased in August and September (Figures 3 and 4).

### 3.3 | Prevalence of interactions related to kelp forest

Of the 177 interactions recorded, 139 (78%) of the interactions, and 100% of the predation events between forage fishes and salmon, were associated with kelp (Figures 4 and 5). Of the observations associated with kelp, 84 occurred along the kelp forest edge and 55 were

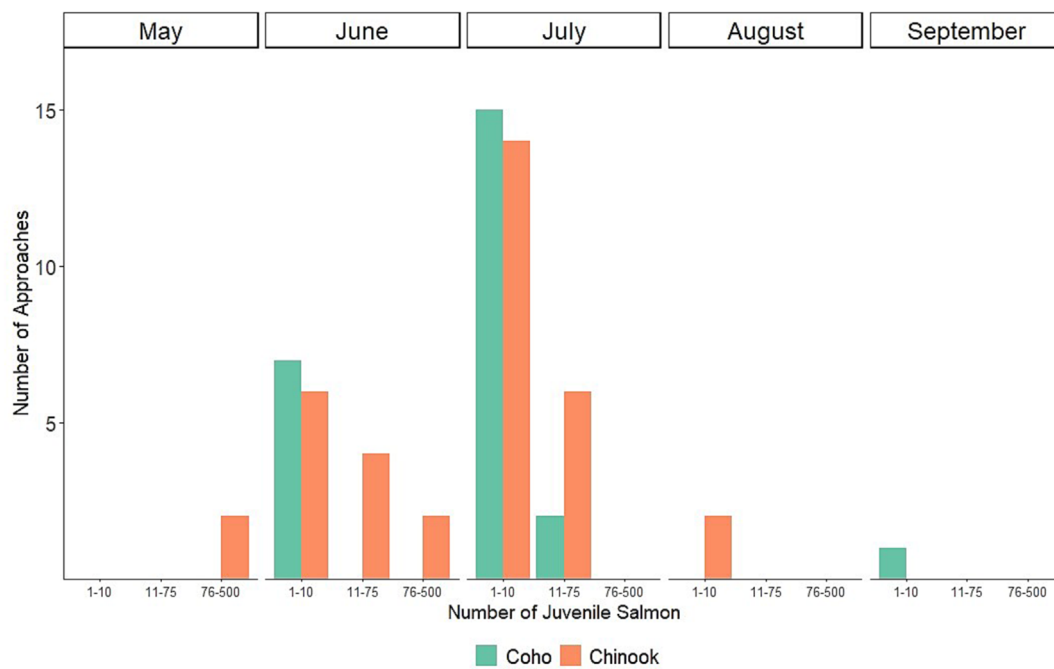
observed deep within the kelp beds. The majority of observations in kelp occurred during July. In August and September, the majority of interactions were not associated with kelp (Figures 4 and 5). Further, the majority of all interactions occurred along the edge of the kelp forest. The relative proportion of COs along the edge versus COs within kelp forests also changed by month, with a greater proportion occurring along the edge during June and July, and then more evenly between the edge and inner kelp forests in August and September.

### 3.4 | Modelling of interactions

For each model, there were seven predictor variables initially considered to define interactions between salmon and each forage species: month, juvenile coho abundance, juvenile Chinook abundance, unknown juvenile salmon abundance, abundance of specific forage fish species, proportions of interactions where kelp was present, and proportions of interactions that happened in kelp. Only four models were found to have significant predictors of interaction. Predictors for IM between surf smelt and juvenile salmon were abundance of coho and Chinook salmon, month, and in-kelp location. For sand lance, FA was the only significant CO, and the significant factors were Chinook salmon and sand lance abundance and in-kelp location. Significant salmon interactions with herring were FA and AJ, and were significantly predicted by Chinook and coho abundance, month, as well as unknown salmon abundance and kelp presence (Table 2).

## 4 | DISCUSSION

Kelp forests are an important contributor to interactions between salmon and forage fishes. Both forage fishes and salmon recruit into the nearshore kelp forests as early as April, when chum salmon and



**FIGURE 4** Number of approaches by juvenile coho and juvenile Chinook towards forage fishes during May–September, 2013–2019. Juvenile salmon group numbers were estimated during the approach behaviour and binned into groups of 1–10, 11–75, and 76–500.

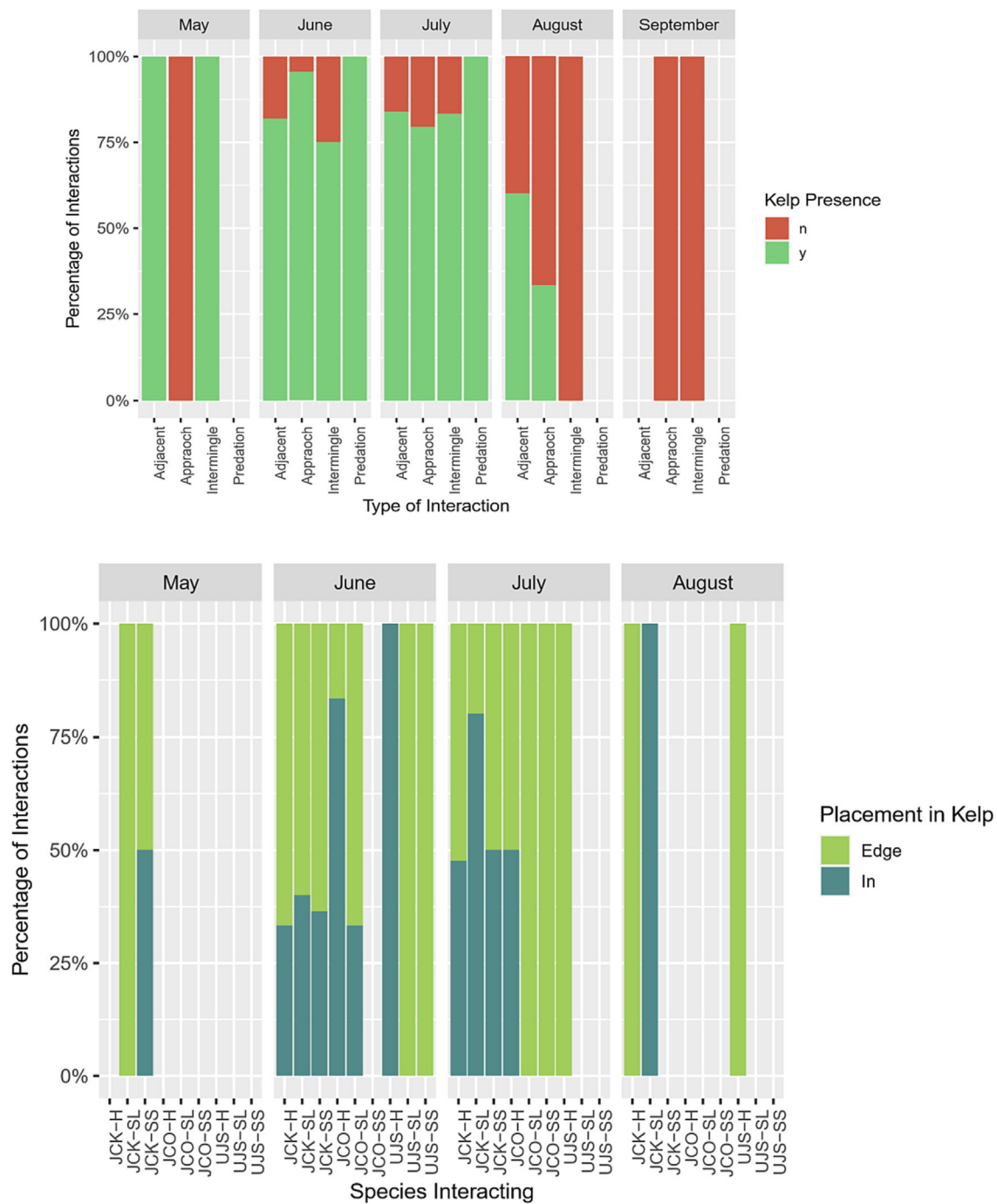
sand lance were briefly observed. King & Beamish (2000) documented diet overlap between juvenile chum and coho salmon, with both sand lance and herring found in the diet of both salmon species in early summer. However, few chum were observed in this study, and no predation on forage fishes by chum salmon was observed.

Interactions were first observed in May between Chinook salmon and both sand lance and surf smelt. Predatory-type behaviour was only observed on sand lance during this month. In June, interactions between juvenile Chinook and coho and juvenile herring and sand lance increased. In contrast, interactions between juvenile Chinook and coho salmon and surf smelt were low throughout the study, and were benign (i.e. not predatory), indicating that herring and sand lance are more important for foraging juvenile salmon, compared with surf smelt, particularly when all three forage species are available. The increase in interactions of both juvenile Chinook and coho with herring and sand lance over May–July is likely to be associated with the increase in abundance of salmon and forage fishes, in particular herring, over the course of the outmigration season. The increased interactions may also signal that salmon are transitioning to depend more on piscivory, and more specifically to hunting juvenile herring and sand lance. This transition to piscivory is consistent with other piscivorous fishes that commonly change diet as they get larger (Juanes, Buckel & Scharf, 2002). The sharp declines in the abundance of both salmon and then forage fishes, as well as interactions between forage fishes and salmon, in August and September, suggest that the fishes are moving out of the nearshore. Similar offshore movements have been documented for juvenile Chinook salmon in Puget Sound, Washington, in September, where they also feed on fishes (Duffy et al., 2010). However, piscivorous behaviours were observed,

including PA and PR by juvenile salmon in the nearshore as early as June, which indicates that the first transition to piscivory occurs up to 4 months sooner than was previously understood. This observation may also indicate that juvenile Chinook salmon in the Strait of Juan de Fuca transition to piscivory earlier than salmon in other regions of the Salish Sea. There was no observed difference in the seasonal transition times to piscivorous behaviour between Chinook and coho, suggesting these two species are developing at similar rates. The low numbers of chum and pink salmon and the lack of juvenile chum/pink salmon–forage fish interactions may be linked to the overall low numbers of juveniles of these species or may indicate that kelp forests function differently for these salmon species.

Intermingling interactions observed among juvenile coho and surf smelt and juvenile Chinook and surf smelt were relatively rare. These COs may suggest a form of mutualism between the species. Juvenile salmon and smelt may both benefit from a reduction in predation risk from other predators (including other predatory fishes such as larger greenling, cabezon, and adult salmon, as well as marine bird predators) through increased schooling numbers, which is another form of anti-predatory behaviour (Magurran, 1990; Feeney et al., 2019). If true, the declining numbers of forage fishes may have additional conservation implications for juvenile salmon, including a shift to other less optimal/more challenging prey and a lower survival rate, linked to reduced food resources.

Kelp is an important component of interactions for these fishes. The high proportion of interactions that occurred in kelp forests, with the highest proportion occurring along the edge of the kelp forest, illustrate that kelp forests play an important role in the interactions among Chinook, coho, and herring. Edge effects are well studied in



**FIGURE 5** Proportion of interactions of salmon and forage fishes associated with kelp forest by month, year, and species, 2015–2019 (see Figure 3 for definitions of species interactions).

**TABLE 2** Significant predictors for specific interactions between forage fishes and salmon.

Species	Interaction	Model	Significant	Variables
Surf smelt	Intermingle	Poisson	Yes	Coho, Chinook, month, in-kelp
Sand lance	Approach	Poisson	Yes	Chinook, sand lance, unknown salmon, in-kelp
Herring	Approach	Poisson	Yes	Chinook, coho, unknown salmon, month, in-kelp
Herring	Adjacent	Poisson	Yes	Chinook, coho, month, kelp presence

vegetated marine environments (Smith et al., 2011; Mahoney et al., 2018), and also appear to be important for salmon and forage fish use of kelp beds.

It appears that group size is also important in determining the nature of interactions. The number of salmon involved in approaches appears to vary, likely reflecting the abundance of fish. At the height of the outmigration season, juvenile Chinook and coho engage in more predation activities when they are in small groups, of between one and 10 fish, and have a larger non-kelp (edge) area to attack from. Together, these two observations illustrate that predating along the edge of kelp in this manner may force herring to shoal up against the kelp, leaving fewer options for herring escape. This function appears to change as the season progresses, with fewer interactions occurring in kelp, and with the interactions that do occur appearing to be more evenly distributed between inner and outer kelp regions, indicating that fish usage of this habitat is both seasonally important and transitory.

Interestingly, chum salmon were observed in very low numbers and only in April, and pink salmon were not observed at all in this study. These two species were once the most abundant salmon in the region (Shaffer et al., 2017). Given the importance of nearshore habitats for these two species, and their planktivorous feeding (Miller et al., 1980; Beacham, 1986), more observations were expected of these two species in kelp forests, which are rich with zooplankton (Shaffer et al., 2019). The absence of outmigrating pink and chum salmon may be linked to large declines in these two species in the Elwha River system, which was constrained by two large-scale dams for over a century (Ward et al., 2008). However, to date, dam removals have not resulted in an increase in chum and pink salmon abundance (McHenry et al., 2020). The lack of juveniles of these species of salmon is a concern for the nearshore of this region.

#### 4.1 | Caveats of this work

Field surveys of this nature are inherently limited by a number of factors. The kelp forests can be challenging to swim through. The specific field conditions needed to acquire useful video imagery, including clear visibility and calm surface conditions, are unpredictable and can be rare during outmigration periods. Snorkellers are recording small, shy, extremely mobile, visually oriented, and predator-averse fishes. The snorkellers are large and resemble seals – notorious fish predators. These fishes are also extremely fast. Interactions between juvenile salmon and forage fishes may last no more than fractions of a second. The data span almost a decade and were acquired by dozens of snorkellers with varying experience in working with juvenile salmon and forage fishes.

Every effort has been made to consistently minimize these variables. All video was acquired using small cameras mounted on 152-cm-long poles that allowed the camera to film well ahead of the snorkeller. The same type of camera and high-resolution setting was used for all videos analysed. The surface/canopy zones of the same stretches of kelp and non-kelp areas were surveyed during each transect. Only trained snorkellers acquired imagery. Physical

conditions were described in the field notes, and only videos with 3-m visibility and calm surface conditions were analysed. Although relative fish abundance was estimated, this analysis did not attempt to estimate fish size (as no calibration for size was available). However, it is clear from the video and companion field notes taken for each set of videos that all salmon were sub-yearling (i.e. <100 mm TL), and that the majority of herring, surf smelt, and sand lance were juveniles (i.e. <120 mm TL; Shaffer, 2019).

Such limitations, being a reality of nearshore field study, are likely to play a role in these data. Camera and snorkeller presence may disrupt encounters, resulting in the relatively low number of interaction encounters. Much more information could be gained if snorkelling surveys covered a larger geographic area, and for a longer time. Calibrating the imagery so that fish size could be determined and included as a variable in the analysis would make the work much more informative. New and ever-improving video technology not available when this work began may help with this in the future.

Despite these limitations, the results of carefully curated and interpreted observations reveal, for the first time, how salmon and forage fishes use kelp forests, and provide important insights into ecological processes and specific knowledge that will be valuable for regional shoreline ecosystem management, including the conservation and restoration of kelp forests, salmon, and forage fishes.

#### 4.2 | Implications for conservation

As coastal systems continue to experience anthropogenic pressures, including climate change and environmental degradation, such as water-quality declines and development pressures, understanding, conserving, and restoring kelp forest ecosystem function is rapidly emerging as a coastal management priority. Changes in kelp forests have a strong regional component (Krumhansl et al., 2016). To understand how important these regional changes are to salmon and forage fish resources, it is essential to understand how salmon use coastal systems during vulnerable juvenile life history stages. This study provides important information on the timing and mechanics of kelp forest use by both salmon and forage fishes, and allows managers to begin including salmon and forage fish ecology in considerations for kelp conservation and restoration. This work informs these future management decisions.

The timing of salmon and forage fish recruiting to specific kelp forests, their interactions, and the trophic shifts that occur within the kelp forest ecosystem as the season progresses are all important to consider in prioritizing and implementing shoreline conservation planning. For example, kelp, forage fishes, and salmon are all well documented to be negatively impacted by declines in water quality (Antrim et al., 1995; Welsh, 2015; Francis & Lowry, 2018; Chow et al., 2019). Therefore, preventing oil spills and non-point pollution should be a priority, particularly during April–October, when both juvenile forage fishes and salmon are present in kelp forests. The siting of non-point/stormwater features should consider proximity, conveyance, and impacts to kelp forests, particularly during juvenile

salmon and forage fish migration periods (none of which are currently considered in local, state, or federal shoreline management plans for either the USA or Canada). Further, as not all kelp forests provide the same function for forage fishes and salmon (Shaffer & Ritchie, 2008), areas with functioning, intact kelp forests known to be used by forage fishes and juvenile salmon, should be a priority to conserve. If the function for forage fishes and salmon is not known for a wild kelp zone, it should be defined prior to allowing any damaging shoreline management action, particularly in regions with declining kelp forests. Finally, multiple natural factors, including shifts in water temperature, grazing pressure, and even ecosystem-scale restoration of coastal hydrodynamic processes, can result in the loss of kelp forests (Rubin et al., 2017). Ecosystem restoration of marine vegetated habitats is complex, can take a long time to complete, and is only effective if the limiting factor that resulted in the loss of kelp forest in the first place is corrected (Tan et al., 2020). Therefore, it is important to first identify the underlying reason for the loss of kelp forests. If the loss is caused by anthropogenic forces (e.g. shoreline fill, non-point pollution, or other water-quality issues), addressing the limiting factor disrupting kelp bed formation should be the focus of restoration.

#### AUTHOR CONTRIBUTIONS

**Anne Shaffer:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing—original draft; writing—review and editing. **Justin Gross:** Data curation; formal analysis; writing—original draft. **Morgan Black:** Data curation; formal analysis; investigation; methodology; supervision; validation; writing—original draft. **Amelia Kalagher:** Data curation; formal analysis; investigation; validation; visualization; writing—review and editing. **Francis Juanes:** Formal analysis; funding acquisition; project administration; resources; supervision; writing—original draft.

#### ACKNOWLEDGEMENTS

Dave Parks, Washington State Department of Natural Resources, and dozens of student interns from a broad range of schools, including Peninsula College, Western Washington University, University of Alaska, Eastern Washington University, and University of Ireland, provided hours of snorkelling field assistance. Anna Morgane, Coastal Watershed Institute, generated modelling and kelp interaction results. Kennedy Bolstad assisted with initial data analysis. Funding was provided by Patagonia Inc., the Coastal Watershed Institute, and the University of Victoria. Thank you to all.

#### CONFLICT OF INTEREST STATEMENT

None declared.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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**How to cite this article:** Shaffer, A., Gross, J., Black, M., Kalagher, A. & Juanes, F. (2023). Dynamics of juvenile salmon and forage fishes in nearshore kelp forests. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 33(8), 822–832. <https://doi.org/10.1002/aqc.3957>

## APPENDIX A

**TABLE A1** Method of binning salmon and forage fish abundances, adapted from Shaffer (2019).

Chinook	Coho	Chum	Herring	Sand lance	Surf smelt
0–10	0–10	0–10	0–10	0–10	0–10
11–75	11–75	11–75	11–75	11–75	11–75
76–500	76–500	76–500	76–500	76–500	76–500
501–1,000	501–1,000	501–1,000	501–1,000	501–1,000	501–1,000
1,001–10,000	1,001–10,000	1,001–10,000	1,001–10,000	1,001–10,000	1,001–10,000
>10,000	>10,000	>10,000	>10,000	>10,000	>10,000