Applying the Ideal Free Distribution Theory to two mobile predators on Pacific salmon: Commercial fishers and brown bears

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Abstract

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Many ecological theories have been developed to shed light on the movement patterns of mobile predators foraging on their prey. Apex predators face additional challenges in needing to track mobile prey, both spatially and temporally, unlike herbivores and grazing animals who must only move to match the temporal dynamics of their stationary prey. The Ideal Free Distribution (IFD) was developed to predict the distribution of mobile individuals across heterogenous environments and is commonly used to investigate intraspecific competition of predators while they forage. Most research on the IFD has been done in controlled laboratory settings and has highlighted the need for field or observational studies of highly mobile predators facing complex environments. Bristol Bay, located in southwestern Alaska, hosts two intelligent and mobile apex predators of a large, mobile sockeye salmon population (*Oncorhynchus nerka*)—brown bears

(*Ursus arctos*) and commercial salmon fishers. Bristol Bay's sockeye salmon returns are the subject of a highly valuable commercial salmon fishery and the University of Washington's Alaska Salmon Program (ASP), a long-term monitoring program that has collected data on the salmon, environment, and ecological communities in Bristol Bay since 1947. Through the ASP and in partnership with Alaska's Commercial Fisheries Entry Commission (CFEC), data on both the bears and fishers and their discrete fishing locations was available spanning 20 or more years. This wealth of information, the discrete foraging choices, and the complex environments both predators face make Bristol Bay an excellent study system to test IFD predictions in a non-laboratory setting. In chapter 1, I apply the predictions of two ecological models, the IFD and Holling's Type II functional response, to 25 years of foraging data on brown bears in a series of connected ponds. Using multiple parameterizations of each base ecological model, I determined that pond-specific variability and a year effect, likely influenced by bear abundance, were important in explaining bear foraging patterns. In chapter 2, I apply the predictions of the IFD to the participants of the drift gillnet fleet and their fishing locations from 1980-2019. I found the Bristol Bay drift gillnet fleet underutilized high catch rate areas, even when considering differences in mobility and relative fishing success (two potential IFD assumption violations), indicating that unmeasured safety concerns, travel costs, knowledge of fishing grounds, or other factors affecting movement could be preventing an IFD. In chapter 3, I investigate variation in the drift gillnet fleet movement to determine what causes this variation and potential departure from IFD predictions. I found that across years, average vessel characteristics and information through pre-season forecasted catch and the previous year's catch affected both where captains first fished and how mobile the entire fleet was across a season. I also found that across captains, mobility increased with years of experience and a captain's relative catch and was higher for

nonresident and nonlocal captains than in local ones. Ultimately, my dissertation expands on the applications of the IFD in complex, field environments, by shedding light on how and why brown bears and commercial fishers violate IFD predictions. This work has important management implications because it is necessary to understand the movement of mobile predators in designing effective management strategies, whether ecosystem or fisheries related, to match the ecological, economic, and social needs of the area.

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Dedication

To Carol, Mac, Margie, and Mario for seeing the scientist and feminist in me before I did.

Introduction

The movement of mobile predators, whether animals or humans, has important ecological and practical implications, and is necessary to understand for the management and conservation of ecosystems. Predator movement patterns can shed light on the distribution of resources across an environment, predator-prey dynamics, and potential population regulating factors in a community (Krebs 2014). Some mobile predators, like herbivores and grazing animals, track stationary prey as it changes in abundance over time, while other predators must respond to prey changes in both space and time, as their prey is also mobile. In particular, apex predators commonly target mobile prey (Sergio et al. 2014), and thus are expected to optimize foraging efficiency by maximizing energetic reward per time spent foraging (Emlen 1966, MacArthur and Pianka 1966) across landscapes with temporal (Abrahms et al. 2021) and spatial variation (Quinn et al. 2017). Many ecological models have been developed to investigate how predators select foraging locations (for a general review see Stephens and Krebs 1986), including but not limited to optimal foraging theory (Charnov and Orians 1973, Charnov 1976a; see review in Pyke 1984), central place foraging (e.g., Boyd et al. 2014), evolutionary stable strategies (Maynard Smith 1982), and the Ideal Free Distribution theory (Fretwell and Lucas 1970).

The Ideal Free Distribution Theory (from here on, IFD) was conceptualized by Stephen Fretwell and Henry Lucas in 1970 (Fretwell and Lucas 1970) to investigate the distribution of breeding birds across a landscape, motivated by Lack's (1966) work on the subject (Lack 1966). The IFD theorizes that each habitat, across a distribution of habitats, has a level of "suitability" for breeding, and that "ideal" individuals will move to the habitat most suitable to them and thus maximize their fitness (Fretwell and Lucas 1970). The suitability of a habitat depends on both the resources in the habitat (in the case of the original theory, nest sites) and the number of conspecifics in the habitat. This leads to a “ideal” distribution in which the distribution of individuals matches the distribution of resources (Fretwell and Lucas 1970) because increased competition in high quality habitats decreases their value. The IFD is further developed in Fretwell’s 1972 book and describes that an IFD results in equal success rates across habitats (Fretwell 1972).

The IFD has four main assumptions: 1) individuals are free to move to maximize success; 2) individuals have perfect information about the distribution of resources and conspecifics across habitats; 3) individuals have equal competitive abilities; and 4) habitat suitability decreases with increased conspecific densities (Fretwell and Lucas 1970; Kennedy and Gray 1993). In nature, at least one of these assumptions is violated, commonly the “equal competitive abilities” and “perfect information” assumptions, which has guided the development of the IFD theory through time (Tregenza 1995). The violations of assumptions do not reduce the value of the theory, as the IFD has been applied as a null model to many ecological situations, ranging from breeding to foraging, and the dynamics of individual decisions in birds, flies, fish, and humans, among many other species.

In the context of foraging, the IFD predicts that predator movement is governed by both the distribution of prey and the distribution of competitors. The end result is an IFD with equal per-predator consumption rates, as large patches of prey will host many predators, while small patches of prey will host fewer (Fretwell and Lucas 1970). Most of the early foraging theory work was conducted with fishes in controlled laboratory feeding trials. The controlled laboratory setting allowed researchers to systematically violate the assumptions of the IFD and gave rise to many important findings. By controlling the rate of food availability and measuring individual foraging rates in three-spined stickleback and goldfish, researchers were able to demonstrate violation of the “equal competitive abilities” assumption (Milinski 1984, Sutherland et al. 1988) and observe how an IFD could still be produced. In this case, good competitors distributed according to the patch profitability ratio and then poor competitors distributed according to the same ratio into whatever habitat was left (Milinski 1984), producing an IFD scaled to competitive ability, confirmed with Grand’s work on juvenile coho salmon in an artificial stream environment (Grand 1997). Other laboratory trials investigated the violation of the “perfect information” assumption, by observing how IFD fit increased over time and how individual guppy and cichlid foraging rates were associated with different information gathering strategies (Godin and Keenleyside 1984, Abrahams 1989).

The IFD has not been without criticism, especially due to most of the focus on the theory occurring in simple laboratory environments with few instances of field or observational studies. For ecological models to be useful, they need to be tested in wide variety of settings—experimental, natural, and theoretical. In a review of IFD literature, Kennedy and Gray found systematic underutilization of “good” foraging habitats in comparison to “poor” habitats and concluded that the theory is uninformative because of that departure (Kennedy and Gray 1993). However, many instances of underutilization of “good” habitats can be explained by violations in the IFD assumptions, especially in situations where multiple IFD assumption violations interact (Tregenza 1995). Because controlled laboratory settings have relatively simple choices, between 2 or 3 patch options, field or observational studies can expand more on interacting IFD assumption violations by allowing for more complexity in foraging location choice (Abernethy et al. 2007). While it is rare to find applications of the theory in field environments, they do exist (Walters et al. 2021), and shed light on environments with complex decisions where mobile predators must consider multiple sources of information.

With the IFD focus on foraging behavior, new predator-prey systems began to be tested, including human predators and applications to fisheries, contributing to the need for non-laboratory tests of the IFD. Hilborn called for consideration of fleet dynamics in management to improve management success, explicitly describing the need for studies on individual variation in decisions of where, when, and what to fish (Hilborn 1985). In hopes of shedding light on fleet dynamics and individual variation, the IFD has been applied as a null model to many different fisheries. Hilborn and Ledbetter found uneven catch rates among areas in the British Columbia salmon purse seine fishery, violating the IFD, and Hilborn later attributed this to individual specialization and knowledge of fishing grounds (Hilborn and Ledbetter 1979, Hilborn 1985). In this case, specialization violates the "equal competitive abilities" and "perfect information" assumptions by demonstrating differences in knowledge use. Abrahams and Healey demonstrated that a highly mobile section of the British Columbia salmon troll fleet created equal catch rates in the entire fishery, fulfilling the IFD (Abrahams and Healey 1990). Abernethy applied the IFD to site selection by artisanal shallow-reef fishers and found that lack of knowledge combined with social and economic constraints on movement violated the "perfect information" and "free movement" assumptions of the theory (Abernethy et al. 2007). Additionally, Abernethy draws novel conclusions about motivations in the fishery. Not all fishers were trying to maximize their catch, as some preferred leisure time, indicating that individuals can violate the "maximization of success" assumption, a departure not commonly seen in species other than humans (Abernethy et al. 2007). These combined works demonstrate that fishing systems are excellent case studies of the IFD and that insights gained from departures to the theory can help inform better management policies.

I will use the IFD as a null model to investigate the distribution of two predators in Bristol Bay, Alaska, in response to their sockeye salmon prey. Brown bears and commercial fishers represent two highly mobile predators capable of complex decision-making processes that are each heavily reliant on the salmon they fish. These systems potentially violate IFD assumptions, and I will build on the IFD null model to investigate patterns of movement and competition in the system. In chapter 1, I will apply the IFD and the Type II functional response models to 25 years of data on bear foraging on sockeye salmon in a series of connected ponds in Pedro Bay. I will explicitly consider habitat variation in the model to determine if bears use information on habitat, connecting to the "perfect information" assumption of the IFD. In chapter 2, I will apply the IFD to examine movement in the commercial salmon drift gillnet fleet to see if it fits IFD predictions from 1980-2019. I will consider the violation of the "free to move" assumption of the IFD by looking at mobility across the fleet and the "equal competitive ability" assumption by considering variation in captain-specific relative fishing success. Finally, in chapter 3, I will dive deeper into fisher movement patterns to assess why fleet movement violates IFD assumptions. I will investigate run size, forecasted run size, years of experience, fisher skill, and residency as factors that affect mobility to determine sources of individual variation in movement that could be violating IFD assumptions. The results will inform future fisheries and ecosystem-based management strategies, by shedding light on the decisions of individuals in the commercial fleet and bears competing for the same fish population. Overall, the IFD continues to be a valuable ecological theory that provides insights on individual behavior from breeding to foraging, spatially and temporally, and from seemingly simple dungflies to complex humans. My dissertation adds to the IFD literature, expanding the amount of information known about its application to highly mobile and complex predators in non-laboratory environments.

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Chapter 1: Brown bear (Ursus arctos) foraging on Pacific salmon: Combining habitat variability with Ideal Free Distribution and Functional Response models

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Abstract

The Ideal Free Distribution Theory (IFD) and Type II functional response (FR) model are often used to explain foraging patterns. Here we quantified predation by brown bears (*Ursus arctos*) on adult sockeye salmon (*Oncorhynchus nerka*) in a series of spatially proximate ponds. Salmon abundance varied among years but pond area and depth were fixed, allowing us to examine interactions between prey density and habitat features. We applied versions of the IFD and FR models to 25 years of data on the number and proportion of salmon killed by bears, modifying the IFD model to include habitat features, and FR model to include a year effect, allowing for possible variation in the number of bears foraging. The FR model with a year effect fit the data well, indicating bears could take almost all fish in ponds when fish were scarce, but at high fish numbers, bears were satiated. The IFD and pond effect model also fit well, indicating the fraction of salmon killed by bears was similar across habitats after correcting for pond depth and area that affect foraging success. Overall, bears foraged across all habitats, but killed higher proportions of salmon in smaller and shallower habitats.

Introduction

Apex predators have been extensively studied from diverse scientific perspectives (Sergio et al. 2014), in part because they experience minimal risk while foraging, and are thus much less constrained by risk than animals in lower trophic positions (Lima and Dill 1990). Consequently, they are expected to optimize foraging efficiency, maximizing energetic reward per time spent foraging (Emlen 1966, MacArthur and Pianka 1966) across landscapes with spatial variation in prey abundance and ease of capture (Quinn et al. 2017), and temporal variation as well (Abrahms et al. 2021). The question of how predators select foraging locations with respect to prey abundance and availability has been addressed with various foraging theories (for a general review see Stephens and Krebs 1986) including but not limited to optimal foraging theory (Charnov and Orians 1973, Charnov 1976*a*; see review in Pyke 1984), evolutionary stable strategies (Maynard Smith 1982), and central place foraging (e.g., Boyd et al. 2014). Of particular interest, is how predators balance prey abundance or density with accessibility or ease of capture, on short and longer time scales. Local habitat variation can lead to different foraging patterns (Tollit et al. 1998), particularly across habitat gradients that affect foraging success.

Two models, the Ideal Free Distribution Theory (IFD; Fretwell and Lucas 1969) and Holling's Type II functional response (Holling 1959) have been extensively used to study foraging patterns in freshwater (Murdoch et al. 1975, Power 1983, 1984, Grand 1997), marine (Jeschke et al. 2004, Heithaus and Dill 2006), and terrestrial species (Fretwell 1972, Dale et al. 1994, Walters et al. 2021). The IFD, developed by Fretwell and Lucas (1969) to investigate the distribution of breeding birds across a landscape, has also been applied to questions of how animals select foraging habitats. The IFD theorizes that habitats vary from in profitability for foraging, thus predators move to the optimal habitat, balancing the benefits of prey availability against competition with other predators to maximize foraging success. The IFD has four main assumptions: 1) predators move freely among prey patches; 2) predators have perfect information about the distribution of resources and competitors across habitats; 3) individuals have equal competitive abilities; and 4) patch profitability decreases with increased competition (Fretwell and Lucas 1969, Kennedy and Gray 1993). In nature, at least one of these assumptions is typically violated. Consequently, many studies testing this concept have been conducted in controlled, laboratory situations (Tregenza 1995).

Functional response curves were developed to describe how predators respond to different prey densities (Holling 1959). A Type I functional response is a linear increase in prey consumed with increasing prey density, seen in some copepods (Jeschke et al. 2004). The Type II functional response, wherein as prey density increases, prey consumption increases to an asymptotic point of satiation, handling time constraint, or other limitation, is seen in many species (Taylor 1984, Arditi et al. 1991, Dale et al. 1994, Fryxell et al. 2007). The Type III functional response is sigmoidal; predators are less likely to attack prey at low prey density, as might occur if the predator switched between prey sources, or experienced low initial success until they learn to forage on prey (Murdoch et al. 1975, Murdoch 1977). Overall, a Type II functional response is most common in large predators focusing on a single prey species (Taylor 1984, Van Leeuwen et al. 2007).

For ecological models to be useful, they need to be tested in wide variety of experimental and natural settings. The great majority of studies applying the IFD to foraging decisions have been experimental (Godin and Keenleyside 1984, Milinski 1984, Abrahams 1989, Kennedy and Gray 1993, Grand 1997), though tests in field environments allow for more complexity in foraging location choice (Tregenza 1995). Similarly, most functional response studies have been experiments and mathematical models (Abrams and Ginzburg 2000, Morozov et al. 2008), and applications in natural settings are less common (but see Dale et al. 1994 as an exception). Large terrestrial predators such as brown (*Ursus arctos*) and black bears (*Ursus americanus*) provide good opportunities for such natural tests of these models. Bears consume a very wide range of dietary items (Graber and White 1983, Mowat and Heard 2006, Gunther et al. 2014, Bonin et al. 2020) but when Pacific salmon are available, bears often preferentially feed on them (Berns et al. 1980, Sellers and Aumiller 1994, Reimchen 2000, Van Daele et al. 2013, Adams et al. 2017). The availability of meat and especially salmon is positively associated with body size and reproduction (Hilderbrand et al. 1999*b*, 1999*a*) and density of bears (Miller et al. 1997), thus salmon are especially important as prey for bears in many regions. Salmon spawn annually in discrete sites at highly predictable times of the year, but their abundance varies among years (Stewart et al. 2003, Rogers and Schindler 2008, Quinn et al. 2012). If the discrete breeding groups of salmon are proximate enough, given the mobility of bears, to assess salmon abundance during the breeding season (e.g., Wirsing et al. 2018), the bear – salmon system presents an opportunity to apply the IFD and Type II functional response concepts in a natural setting. Finally, the ability of bears to rapidly consume whole salmon (Quinn 2021) means that the handling and consumption time, which can constrain some foragers (Charnov 1976*b*), does not affect the numbers of salmon killed by bears. While digestive processing time may limit salmon consumption rate, bears preferentially consume the most energetically rewarding parts of salmon when salmon are abundant (Lincoln and Quinn 2019), thus reducing the digestive limit on salmon consumption per unit time.

This paper determined the extent to which bear-salmon foraging patterns followed the predictions of the IFD and Type II functional response models using over two decades of data on predation by brown bears on sockeye salmon in a series of small, discrete ponds in Alaska. We first used the IFD as a null hypothesis: the proportion of salmon killed in all ponds was the same in a given year, and varied among years, being higher when there were fewer salmon. We then tested the hypothesis that salmon are easier for bears to catch in some ponds due to physical features (pond depth and area). Second, we tested the Type II functional response as a null hypothesis: the number of salmon killed by bears in a pond each year would be determined by the number of salmon there, the proportion of salmon killed at low densities, and the maximum number of salmon that could be consumed in each pond. We then modified the null functional response model to capture year to year variation in predation pressure with a multiplicative year effect acting on the asymptotic threshold of maximum salmon consumption. Ultimately, the further parameterizations of both models revealed that bears are effective predators at low prey densities and across a range of habitat sizes, though the lack of bear abundance data constrained our inferences in some respects.

Materials and Methods

Site description

The study was conducted in a series of small spring-fed ponds and interconnecting streams near the village of Pedro Bay (Figure 1; Quinn and Kinnison 1999), in the eastern end of Iliamna Lake, within the Bristol Bay region of southwestern Alaska. The ponds support a modest population complex of sockeye salmon (*Oncorhynchus nerka*), averaging ca. 3100 annually, that are preyed upon by brown bears (Quinn and Kinnison 1999, Lincoln et al. 2020). Sockeye salmon are the only species of Pacific salmon seen spawning in the ponds, and the other fishes (non-anadromous Dolly Varden, *Salvelinus malma*, and slimy sculpins, *Cottus cognatus*) are much smaller and unlikely to be preyed upon by bears. The individual ponds differ in physical attributes, notably depth and area, that might affect ease of salmon capture, but vary little among years. The water is exceptionally clear, owing to their spring sources, and the light granite substrate and lack of overhead cover make the salmon very conspicuous (Table 1; Quinn et al. 2012). The pond complex functions as its own foraging neighborhood, with travel distances as short as 30 m and no more than 560 m among pairs of ponds (Table 1). In contrast, other salmon spawning populations in this area are several km away and have much lower salmon densities, thus increasing the effect of travel distance in tests of the IFD (e.g., Kennedy and Gray 1997). Specifically, aerial surveys by the Alaska Department of Fish and Game over multiple decades (Regnart 1996, and unpublished updates) indicated that the nearest spawning streams and their median sockeye salmon counts were Knutson Creek (2 km away, 1000 salmon), Russian Creek (4 km away, 525 salmon), and Mink Creek (15 km away, 500 salmon). In comparison, the median aerial survey count in the Pedro Bay pond complex was 1800 salmon. Thus, the relative constancy of the habitat, ease of assessing salmon abundance by predators, and distance from alternative salmon populations make the pond complex ideal for investigating bear foraging patterns. No other animal prey are readily available to bears during the salmon spawning season, and examination of scats reveals that they augment the salmon by feeding on berries and other plant material that are spatially dispersed.

The study ponds are connected by small, shallow creeks (average width = 2.1 m, average length = 61.8 m, average depth = 14.6 cm) that collectively average between 2 and 147 sockeye salmon annually. The salmon move up these creeks to access spawning habitat in the ponds where they are available to bear predation for a few weeks before, during, and after spawning until they senesce and die. We excluded the creeks from our analyses because 1) bears presumably forage differently in small, shallow creeks than in larger, deeper ponds, 2) the streams have far fewer salmon that are primarily transiting to ponds where they spawn and die (mean = 15.2 d, Quinn et al. 2012), and in many years no salmon were seen spawning in any of them, and 3) it is difficult to attribute salmon counts to the stream where they are seen because most salmon are moving upstream to spawn in one of the ponds. In contrast, tagging studies indicated that once salmon entered a pond they almost always remained there for the rest of their lives rather than moving to another pond (Quinn et al. 2012).

Survey methods

The Pedro Bay ponds have been surveyed by foot every 3-4 days during the salmon spawning season, mid to late August, from 1995 to 2020, missing only 1997 (Quinn and Kinnison 1999). Counts were conducted by three or more observers from banks and by slowly wading through larger ponds. On each survey the live and dead salmon were counted, and the dead salmon categorized by cause of death (senescence or killed by bears). After each survey, all carcasses were removed to preclude repeat counting on subsequent surveys. Some salmon may be killed by bears and transported too far from the ponds to be counted (Quinn et al. 2009), and some scavenging occurs as well (Lincoln et al. 2021), and that would cause us to overestimate predation. Thus, to some extent these sources of error (transportation and scavenging) are offsetting. However, it is important to note that these were systematic, quantitative surveys but not absolute counts of the numbers of salmon killed. Finally, bears often eat only parts of some carcasses (Lincoln and Quinn 2019), but we did not attempt to adjust the data for this factor (i.e., actual biomass consumed). All field protocols were approved by the University of Washington

Office of Animal Welfare (No. 3142-01) and the Alaska Department of Fish and Game (2020 permit No. SF2020-115).

During the surveys, and sampling conducted prior to this specific study, we have observed brown bears on numerous occasions despite our efforts to make our presence known, but we have never seen a black bear nor a gray wolf (*Canis lupus*). Similarly, motion-activated cameras directed at the ponds detected no predators other than brown bears. These observations, combined with the abundance of paw prints consistent with brown bears and the nature of the bite patterns on carcasses (i.e., vs. those of wolves: Darimont et al. 2003) strongly support our inference that brown bears are the only predators in this system rather than black bears and wolves, though we cannot exclude the possibility that some predation from other species occurs. More broadly, extensive work on these predators indicates that where they occur, brown bears dominate the salmon foraging community (Levi et al. 2020).

The survey coverage varied among ponds and tended to increase over the years. Sampling for Grass Pond, and Ponds 1, 1A, 2, 3, and 4 started in 1995, Trail and Bear Ponds were added in 1996, Berg's Pond was added in 2004, and Big Pond was added in 2011. The number of fish returning to spawn also varied, and all but Bear Pond experienced a year without any salmon. Salmon counts were summarized annually for each pond by adding the cumulative count of dead salmon to the number alive on the last survey date (typically 24 or 25 August; Quinn et al. 2001). We estimated the total number of salmon killed by bears, including those alive on the final survey of the season, using an index with year-specific data following the methods detailed and validated in Quinn et al. 2001. The mutual wariness of bears and humans prevented us from quantifying the number of bears using the pond system and observing their behavior, so data on the salmon were used to infer bear foraging patterns.

Statistical models

To investigate patterns of bear foraging, we used two different approaches based on classic ecological models: the Ideal Free Distribution Theory (Fretwell and Lucas 1969) and the Type II functional response curve (Holling 1959). All models assumed that the observed number of salmon killed by bears was best described by a negative binomial probability distribution. The negative binomial distribution was used because it includes a dispersion parameter that accounts for the addition of heterogeneity in the data greater than that expected by a Poisson distribution (Hilborn and Mangel 1997, Zhang et al. 2012). If data are not overly dispersed, the negative binomial approximates the Poisson distribution, which is commonly used with count data (Hilborn and Mangel 1997). The R function *nlminb* was used to optimize the likelihood function using the maximum likelihood method (R Core Team 2019).

Ideal Free Distribution models

The null IFD model is based on the prediction that the predation pressure in a patch is proportional to the prey resources available (Fretwell and Lucas 1969). Traditionally, work on the IFD in experimental settings has measured the continuous input of prey and the predator density match to that resource renewal rate (Milinski 1984, Oksanen et al. 1995). We were unable to measure bear specific attributes or daily renewal rates of the salmon to each pond, so we summarized the annual total number of fish available and the number killed by bears for each pond. In this case, under the null IFD model the number of salmon killed in a pond would be proportional to the number of fish present.

We assumed the catch rate by bears would be equal in all locations as bears moved between ponds to equalize it. Because we cannot measure catch or effort of individual bears, we relied on the number of salmon killed by bears. We expected that foraging efficiency would decrease at lower salmon density and increase in shallow habitats, based on work elsewhere (Quinn et al. 2017). The total number of salmon was a comparable surrogate for the daily arrival rate because the salmon arrival patterns in the ponds overlap so broadly.

To calculate expected number of salmon killed by bears in pond *p* in year *y* under the null $IFD_{p,y}$, we used Equation 1.

(Equation 1) $$\mathrm{IFD}_{p,y}^{null}=F_{p,y}\ \frac{\Sigma_p K_{p,y}}{\Sigma_p F_{p,y}}$$

Where $F_{p,y}$ is the total number of live and dead salmon seen in pond *p* in year *y* and $K_{p,y}$ is the total number of salmon killed by bears observed in pond *p* in year *y*.

To investigate whether there was variation in the ease of salmon capture by pond, we modified the null IFD model (Equation 1) to include a pond effect that increased or decreased the predicted number of salmon killed in a pond.

(Equation 2) $$\mathrm{IFD}_{p,y}^{pond}=F_{p,y}\ \frac{\Sigma_p K_{p,y}}{\Sigma_p F_{p,y}}\ E_p$$

Where E_p reflects the pond effect or the relative ease of capture of fish in pond *p*, and may be inversely proportional to pond size. We expected that bear foraging would be less efficient in deeper and larger ponds because salmon are harder to catch, based on sampling in streams of varying width and depth (Quinn et al. 2001, 2017). The pond effect captured this variation in ease of capture, so we related the pond effects for each pond to the depth and area of the ponds using a linear regression model.

To directly test the hypotheses that fish are harder for bears to capture in larger and deeper ponds, we fit two additional models estimating the effects of depth and area on the predicted number of bear kills. First, we standardized depth and area across ponds by taking the measurement (either depth or area) of each pond and subtracting from it the mean measurement across all ponds. Positive values indicated that the pond was larger or deeper than the mean and negative values indicated that the pond was smaller or shallower. We ran models using a standardized depth (Equation 3) and area modifier (Equation 4) to investigate the effects of depth and area on predicted number of bear kills.

(Equation 3) $$\mathrm{IFD}_{p,y}^{depth}=F_{p,y}\frac{\sum_p K_{p,y}}{\sum_p F_{p,y}}\,e^{Dd_p}$$

(Equation 4) $$\mathrm{IFD}_{p,y}^{area}=F_{p,y}\frac{\sum_p K_{p,y}}{\sum_p F_{p,y}}\,e^{Aa_p}$$

Where D is the depth coefficient, d_p is the standardized depth (in cm) in pond p, A is the area coefficient, and a_p is the standardized area (in m^2) in pond p. We expected coefficients to be negative, indicating that the predicted number of salmon killed by bears would increase in ponds that are smaller and shallower than the mean, and decrease in ponds that are larger and deeper than the mean.

Functional Response models

We also tested models using a Type II functional response, assuming that at high prey densities the number of prey consumed reaches an asymptote. The form of the Type II functional response is described by two parameters and is conditional on the number of prey (i.e., salmon available in a pond; Holling 1959). First, the slope controls the proportion of total salmon killed by bears at low salmon densities; a slope of 1 would indicate that bears killed all the fish available. The second parameter describes the asymptote that describes the saturation point, or the maximum number of fish that can be consumed at high fish densities. Usually, per capita predation rate of a single predator is measured relative to prey density, but in our test we predict the number of salmon killed by bears in a pond in a year as a function of the number of fish available in a pond (Holling 1959). Equation 5 predicts the number of bear kills $FR_{p,y}$ in pond p in year y using the functional response model:

(Equation 5) $$FR^{null}_{p,y}=\frac{F_{p,y}}{\frac{1}{s_p}+\frac{F_{p,y}}{a_p}}$$

Where $F_{p,y}$ is the total salmon live and dead seen in pond p in year y, s_p is the proportion of salmon killed by bears at low salmon densities in pond p, and a_p is maximum number of salmon killed at high densities.

We hypothesized that the pond-specific saturation point, a_p, would increase with depth and area because larger and deeper ponds could hold more fish (Quinn et al. 2017). To test this against the null hypotheses of no relationship between the habitat feature and saturation, we related the asymptote estimates to the area and depth of each pond using linear regression.

After running the null functional response model, we looked for variability in the estimated slope and asymptote for each pond. The similarity in slope estimates (i.e., high proportion of salmon killed by bears at low salmon densities) caused us to modify the Equation 5 to include a common slope across all ponds.

(Equation 6) $$FR_{p,y}^{\text{common slope}} = \frac{F_{p,y}}{\frac{1}{S} + \frac{F_{p,y}}{a_p}}$$

Where *S* is the proportion of total salmon killed by bears at low fish densities across all ponds.

We assumed that the overall number of salmon killed by bears varied among years, due to likely changes in the number of bears foraging in the vicinity of the pond system or their competitive ability (e.g., age, sex, etc.). Such variability in number and competitive ability of bears should increase variation in predation pressure on the overall system and modify the maximum number of fish killed at high densities, the functional response asymptote, with the asymptote increasing with predation pressure. To account for year to year variability in overall bear predation, we modified Equation 6 to include a multiplicative year effect. This year effect modified the asymptotic point of saturation, adjusting to differences in predation pressure across years.

(Equation 7) $$FR_{p,y}^{\text{year}} = \frac{F_{p,y}}{\frac{1}{S} + \frac{F_{p,y}}{a_p * Y_y}}$$

Where Y_y is the multiplicative year effect in year y.

Model selection and goodness of fit

Model competition was done using Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Akaike 1974, Burnham and Anderson 2002). Models with > 2 AIC$_c$ units from the lowest AIC model were considered to have limited support from the data (Burnham and

Anderson 2002). We inferred the model with the greatest support from the data as the one that had the lowest AIC$_c$ score.

In addition to using AIC$_c$ to compare overall model fit and parsimony, we also calculated two measures of goodness of fit. We calculated the model bias, B_p for pond p, by taking the observed number of salmon killed, subtracting the predicted number of kills, dividing this number by the predicted number killed, then averaging the bias across years (Equation 8). The direction of the model bias estimate indicated whether the model systematically over-predicted (negative value) or under-predicted (positive value) the number of killed in a pond for a specific model. Zero values indicated that the model was equally likely to over-predict or under-predict, depending on the year.

(Equation 8) $$B_p = \frac{1}{N}\sum_y \frac{K_{p,y} - K^*_{p,y}}{K^*_{p,y}}$$

Where $K_{p,y}$ is the observed number of bear kills in pond p in year y, $K^*_{p,y}$ is the predicted number of bear kills in pond p in year y, and N is number of years.

We also calculated the absolute goodness of fit for pond p (G_p), or value of the mean of the absolute value of the ratio between observed and predicted number of bear kills, in the same manner (Equation 9). The absolute goodness of fit represented the percent error in the predictions for a specific model, allowing comparison across models for each pond (G_p) and all ponds as a whole (G).

(Equation 9) $$G_p = \frac{1}{N}\sum_y \left|\frac{K_{p,y} - K^*_{p,y}}{K^*_{p,y}}\right|$$

(Equation 10) $G = \frac{1}{P} \sum_{p} G_p$

Where G_p is the goodness of fit for pond p, G is the goodness of fit across all ponds, and P is the number of ponds in the system. Higher values (error rates) are associated with greater disagreement between model predictions and observations and worse goodness of fit.

Results

Over the 25 years of this study, from 5 – 10,500 sockeye salmon were counted in the pond system per year, and bears killed from 4 to 5,180 of them (Figure 2). The proportion of salmon killed by bears each year varied from 0.4% to 91% and was highest when salmon were scarce. In total, 78,737 salmon (live and dead) were counted across years and 36,874 were salmon killed by bears.

Ideal Free Distribution models

Observed patterns in bear foraging did not perfectly align with predictions under the null IFD model, although the data from some individual ponds were closer to IFD null predictions than others (Figure 3). That is, in some ponds the number of salmon killed by bears was almost proportional to the number available in the pond but in others, the proportion of salmon killed was much greater or smaller than the proportion of total salmon available in that pond. Specifically, in Trail Pond, Grass Pond, and Pond 1, predation levels were closest to IFD null model fit (model error rates of 25%, 30%, and 29%, respectively, for these ponds; Figure 3). Fewer salmon were killed than expected under the null model in two of the largest ponds (Bear and Big), where model bias values indicated that the null model over-predicted the number killed in each pond by 51% and 28%. By contrast, in the smaller Berg's Pond and Ponds 1A, 2, and 3, more salmon were killed than expected from the null model, as evidenced by the positive model bias values for each pond (B_p: 96%, 67%, 64%, 88%).

Across all ponds, the addition of the pond effect reduced error by 21%, from 56% with the null IFD model to 35% when the pond effect was included (Table 3; Figure 4). Most ponds saw improved goodness of fit, with reductions in error ranging from 6-51% by pond. There was no change in the goodness of fit for Bear Pond, although the model bias was reduced from 51% to -6%. The goodness of fit increased for Big Pond and Pond 1 (by 1% and 4% respectively), although the model bias for each pond was lower with the addition of the pond effect ($B_p = 0$ for Big Pond, $B_p = 1\%$ for Pond 1). Overall, the predicted number killed increased in Berg's Pond, Grass Pond, Trail Pond, and Ponds 1A, 2, 3, and 4, as seen in the pond effect magnitudes that are > 1, with 1 representing no change in the predicted number killed from the null model ($E_p = 1.66$, 1.13, 1.18, 1.83, 1.77, 1.96, and 1.39, respectively). Bear Pond, Big Pond, and Pond 1 had pond effects < 1, meaning that the predicted numbers killed decreased with the addition of a pond effect ($E_p = 0.52$, 0.72, and 0.91 respectively). The magnitude of the pond effect was related to habitat, decreasing with increasing depth and area (Figure 5; depth: $p = 0.02$, $R^2 = 0.49$; area: $p = 0.005$, $R^2 = 0.64$), indicating that lower than IFD-expected predation occurred in deeper and larger ponds.

The addition of standardized depth and area to the IFD null model increased the goodness of fit and reduced error, but not to the same magnitude as the addition of the pond effect. Across all ponds, the addition of standardized depth reduced error by 4% and the addition of standardized area reduced error by 7% compared to the IFD null model (Table 3). The negative coefficient estimates for standardized depth and area indicated that fewer salmon were killed relative to the IFD null predictions in larger and deeper ponds (D = -0.03, A = -0.0004). The depth and area models performed similarly when considering model bias by pond. Both models tended to over-predict bear kills at Bear Pond, Grass Pond, and Pond 1, evidenced in their negative model bias values (Depth, B_p: -31%, -5%, -12%; Area, B_p: -34%, -7%, -12%).

Overall, model selection by AIC_c indicated the IFD and pond effect model provided the most parsimonious representation of the data (Table 2). None of the other models tested, the IFD and area, IFD and depth, and IFD null models, were equally well supported by the data (i.e., had $\Delta AIC_c < 2$). The addition of a pond effect that controls for variability in the ease of capture between ponds improved model support over the addition of an area or depth modifier alone.

Functional Response models

Bears did not forage for sockeye salmon in strict accordance with the predictions of the null Type II functional response model (Figure 6). That is, the number of salmon killed was not fully explained by the slope (the proportion of total salmon killed at low salmon densities) and asymptote (the maximum number of salmon consumed at high salmon densities), although there was general agreement between model predictions and observations. The variation in goodness of fit values for each pond showed that in some ponds, bears performed closer to the functional response predictions, but many model predictions were under or over the observed numbers of salmon killed. Specifically, the model error rates less than or equal to 20% in smaller ponds (1A, 2, and 3), indicated predation close to functional response predictions. In Berg's Pond, Grass Pond, Pond 1, Pond 1A, Pond 3, and Trail Pond, the null functional response model on average over-predicted the number of salmon killed by bears by 1-8% as evidence by the negative model bias estimates (B_p = -3%, -1%, -8%, -5%, -3%, -3%). By contrast, in Bear Pond, Big Pond, and

Pond 4, the functional response model on average under-predicted the number of salmon killed by bears (B_p = 1%, 4%, 5%). The model had equal tendencies to over-predict and under-predict the number of killed in Pond 2 (B_p = 0). Additionally, years when few salmon were killed despite their high abundance (2014, 2015, 2016, and 2018; Figure 2; teal dots in Figure 6) fewer salmon were killed than expected system wide. Overall, the model error rate summarized across ponds was 31% (Table 3).

The functional response curves for each pond varied little in slope (Figure 7); the estimated slopes were between 0.998 and 0.999 for all ponds, indicating that at low densities almost all salmon were killed. The exception to this pattern was Bear Pond, where the much lower slope estimate (s_p = 0.383) indicated that bears were unable to kill many fish at low densities (Figure 7, Table 1). The asymptote estimates also varied among ponds. Some ponds clearly reached an asymptote (e.g., Trail and Pond 1), whereas others (e.g., Ponds 2 and 3) approached but did not meet their asymptotes (Figure 7). The asymptote estimates ranged from 293 in Pond 4 to 1,341 in Trail Pond at 1,341, but the asymptote estimates were not related to pond attributes (depth: $p = 0.63$, $R^2 = 0.03$; area: $p = 0.29$, $R^2 = 0.14$).

The modification of the null functional response model to include a common slope estimate across all ponds reduced the number of parameters by 9 and the error rate across ponds by 1% (Table 3). This “common slope” model has a new slope estimate of 0.999, indicating that across all ponds bears killed 99% of the salmon available at low densities. The asymptote estimates remained similar to those predicted by the null functional response model (a_p range = 223 – 1343). The common slope functional response model produced the same bias and goodness of fit estimates across all ponds, except Bear Pond. In Bear Pond, the goodness of fit, or error between the predictions and the observed data, was reduced by 8% and the new bias estimate of -19% (null functional response B_p = 1%) indicated that the model over-predicted the number of salmon killed by bears. Overall, the reduction of parameters in the common slope functional response model improved the fit to the data.

The addition of a year effect to the common slope functional response model improved the overall goodness of fit and reduced error rate across ponds by 8% (Table 3). This model fit the observed number of salmon killed by bears very well; over half of the pond-specific error rates were below 20% (Figure 8). Most ponds in the system had very low model bias estimates (B_p between -5% and 3%), indicating that model predictions were equally likely to over-predict or under-predict the number of salmon killed by bears. The year effect model, like the common slope functional response model, on average over-predicted the number of salmon killed by bears in the deeper Bear Pond (B_p = -18%) but under-predicted the number of salmon killed by bears in the shallower Berg's Pond (B_p = 17%).

The slope estimate across all ponds with the addition of the year effect was 0.928, indicating that roughly 93% of the salmon available at low densities were killed by bears. The addition of the year effect also reduced the asymptote estimates by pond (a_p range = 34 - 806) due to the interaction with the year effect. The overall decrease in asymptote estimates by pond ranged from 40% - 85% with an average of a 65% decrease across ponds. Year effect estimates ranged from a low of 0.004 in 2004 to a high of 111.8 in 2003 and increased with the proportion of the total salmon killed by bears across ponds (p = 0.02, R^2 = 0.21; Figure 9). In years when a low proportion of salmon was killed, the low year effect estimate reduced the pond-specific asymptote to account for the lack of predation in the system. In 2004, for example, only 10 of the 2,739 available salmon were killed by bears, so the year effect model reduced pond-specific asymptotes to between 0.1 and 3.5 fish. In years with a high proportion of fish killed by bears, the high year effect estimate increased the pond-specific asymptote. In 2003, 91% of the salmon were killed by bears so the pond-specific asymptotes were increased to between 3,800 and 90,000 fish. In general, the low year effect estimates were tied to years when < 50% of the salmon were killed (Figure 9). We assume that the year effect largely reflects the number of bears foraging at the ponds and thus the maximum number of salmon consumed. The highest estimate of the adjusted asymptotes indicated that there were enough bears to consume all fish, thus there was no satiation.

Overall, model selection by AIC_c indicated that the functional response model with the common slope and a year effect provided the most parsimonious representation of the data (Table 2). Neither the functional response nor the common slope functional response models received adequate support ($\Delta AIC_c < 2$). The addition of a year effect allowing the asymptotic point of satiation to vary by year significantly improved model fit over the common slope functional response model. The removal of pond-specific slope estimates with the change to a common slope estimated across all ponds also significantly improved model fit over the null functional response model ($\Delta AIC_c = 10.63$).

Comparing the IFD and Functional Response models

The IFD and functional response models described alternative but not mutually exclusive patterns of bear predation. Overall, the model with the most support via AIC_c was the functional response model with a common slope among ponds and a year effect (Table 2). The second most supported model ($\Delta AIC_c = 34.21$) was the IFD and pond effects. The other formulations of the IFD (IFD and area, IFD and depth, and the null IFD), ranked third, fourth, and fifth overall (Table 2). The other functional response formulations, the common slope functional response and the null functional response, ranked sixth and last in terms of ΔAIC_c. Overall, the IFD model formulations had lower AIC_c values than the functional response model formulations, except for the most supported functional response, the common slope and year effect model. Additionally, the functional response models had lower error rates and improved goodness of fit than the IFD models overall (Table 3).

Discussion

We assessed foraging on sockeye salmon by brown bears using different formulations of the Ideal Free Distribution (IFD) and the Type II functional response models (Holling 1959, Fretwell and Lucas 1969). Both theories are widely used in ecology to explain foraging patterns in a wide variety of organisms and ecosystems (Power 1983, 1984, Abrahams and Healey 1990, Dale et al. 1994, Bautista et al. 1995, Jeschke et al. 2004, Abernethy et al. 2007). We found that bear foraging on salmon generally followed the predictions of the simplest IFD and functional response models. In both cases, modifications to the null theory allowed for greater explanatory power to capture bear foraging patterns, although these modifications differed by theory.

Ideal Free Distribution

The IFD predicts that foraging decisions are governed by both resource availability (here, the total number of salmon) and the number of competitors (bears), resulting in equal per-predator consumption rates (Fretwell and Lucas 1969). This result has been supported by experimental manipulations of food patches for guppies and cichlids, as food and competitor density changed, so did the number of foragers using that patch (Godin and Keenleyside 1984, Abrahams 1989), and in field observations of eagles foraging on salmon streams with different prey densities (Walters et al. 2021). We do not know the number of bears using the Pedro Bay pond system, so instead we used the number of salmon killed by bears to infer bear foraging. If bears were foraging in a true IFD and fish were equally vulnerable in all ponds, the number of salmon killed by bears in a pond would be proportional to the number of salmon there. We found that bears did not forage in complete alignment with the null IFD predictions, and some ponds were in closer alignment to the null IFD than others. In Berg's Pond, for example, bears killed a much higher proportion than expected by the null IFD, but in Bear Pond bears killed a smaller proportion than expected (Figure 3). This pattern of over- and under-use of specific ponds was consistent across years, indicating that pond-specific features were driving bear foraging patterns. Bears can assess habitat quality and adjust their foraging patterns as demonstrated in small streams where average predation rates were inversely correlated with stream size (Quinn et al. 2017). Thus, we included a pond effect modifier to the null IFD model to capture pond-specific variability in the ease of salmon capture.

The pond effect improved model fit over the null IFD model, compensating for differences in the ease of salmon capture, and adjusting the predicted number of bear kills in each pond. For example, in Berg's Pond, a relatively small, shallow pond, the predicted number of bear kills increased with the addition of the pond effect, and the predicted number killed decreased in Bear Pond, a larger and deeper pond where foraging efficiency is likely limited (Figure 4). Accounting for habitat variability when foraging, ultimately fulfilling the IFD, was directly tested in Power's (1984) work on armored catfish in Panamanian streams. Catfish density was inversely correlated with the density of the forest canopy which directly affected the growth rates of the periphyton they ate (Power 1984). In both systems, the foragers could assess habitat quality and adjust their behavior to maximize foraging success, two behaviors necessary to fulfill IFD predictions. Although the pond effect coefficient was related to pond area and depth, this adjustment in foraging by pond was not related to the depth or area of the pond alone (Figure 5). The addition of standardized depth and standardized area to the null IFD model did not increase model fit to the same extent as the addition of a pond effect. The pond effect apparently resulted from some interaction between depth and area or other unmeasured factor affecting catchability by pond (Gende et al. 2004).

Overall, the IFD is useful as a starting hypothesis to consider where bears forage when presented with multiple alternatives. By systematically testing the departures from the assumptions of the IFD, the patterns of foraging behavior and the resulting ecological implications can be illuminated (Tregenza 1995). In the case of the bear-salmon system in Pedro Ponds, we could satisfy two of the four IFD assumptions: that bears had perfect information and showed exploitative competition (Fretwell and Lucas 1969, Kennedy and Gray 1993). Central to the IFD is the assumption that individuals have "perfect information" about the distribution of prey resources and competitors, and this is rare in nature. Most work on the IFD has thus been done in laboratory environments in small systems with three or fewer prey patches located very close together (Godin and Keenleyside 1984, Milinski 1984, Sutherland et al. 1988, Abrahams 1989, Kennedy and Gray 1993, Grand 1997). The Pedro Bay pond system provides an ideal non-laboratory test of the IFD because bears can easily assess the abundance of salmon in all ponds by walking short distances (Table 1), the dark red salmon are very conspicuous against the light granite sand of the ponds, and other salmon populations are much less dense and farther away. This may be as close to "perfect information" as one can get in nature, especially because the salmon seldom move among the ponds (Quinn et al. 2012) and the ponds lack the kind of overhead cover that might hide salmon or hinder their capture.

Additionally, our system satisfied the IFD assumption that as conspecific density in a foraging area increases, that habitat's suitability decreases from exploitative competition (Fretwell and Lucas 1969). "Input matching" (e.g., Lessells 1995) can occur in this system because the salmon leave Iliamna Lake, where they are inaccessible as prey for bears, and then enter one or another of the spatially proximate, small ponds that facilitate visual assessment, predation, and rapid consumption (Quinn 2021). Exploitative competition is not necessarily characteristic of bears feeding on salmon, as large, socially dominant bears (typically but not always males) can exclude lower status bears from prime fishing sites on streams (Gende and Quinn 2004, Elfström et al. 2014, Uzal et al. 2022, but see also Gill and Helfield 2012 for a counter-example). This can lead to an Ideal Despotic Distribution (Calsbeek and Sinervo 2002, Church and Grant 2019) if social dominance has a larger effect on energy intake than salmon densities (Gende and Quinn 2004). However, the nature of the ponds and their spatial distribution seems to allow bears sufficient if not similar access, despite differences in social status that might cause interference competition or despotic behavior. The result is effectively exploitative competition with the absence of despotism. Additionally, at high salmon densities bears may still display aggression but bears of low social status still get access to salmon (Stonorov and Stokes 1972, Gende and Quinn 2004) by deferring to the dominant bears and by spending less time at the prime fishing locations. In the Pedro Pond system then, the IFD predictions could be fulfilled even with the variation in competitive ability among individual bears that is likely to occur.

We accounted for two of the four assumptions of the IFD, that bears had "perfect information" and exhibited exploitative competition. We could not directly test the other two IFD assumptions, that bears had equal competitive ability and that they were free to move to maximize foraging success, but we assumed that the assumptions were either satisfied or accounted for. Even if bears varied in competitive ability, this could be captured through an IFD scaled to competitive ability (Grand 1997). We assumed that bears could move freely and that there was no cost to that movement due to the small distances between ponds (Table 1). We found that in this system, habitat variability mattered as bears killed a larger fraction of the available salmon in smaller ponds, but even in large ponds, abundant salmon experienced heavy predation.

Functional Response

The other ecological model we applied to bear foraging was the Type II functional response model that predicts the number of salmon killed by bears by looking at the total number of available salmon, the number of salmon killed over a range of densities. We tested the Type II functional response because bears rely so heavily on salmon during the spawning season, ruling out the possibility of a long period of prey switching (Sellers and Aumiller 1994, Reimchen 2000, Van Daele et al. 2013, Adams et al. 2017). Additionally, bears reach satiation at high prey densities, ruling out the possibility of a Type I functional response (Quinn et al. 2017).

Overall, the number of salmon killed by bears was not perfectly described by the null Type II functional response model. In small, shallow ponds, like Ponds 1A, 2, and 3, bears foraged closest to functional response predictions (Figure 6), indicating that in habitats with high predator efficiency the functional response predictions accurately describe foraging behavior. In larger, deeper ponds, the functional response model under-predicted the number of salmon killed by bears, and in mid-size and mid-depth ponds the bear kills were overestimated (Figure 6). The observation of an effect of habitat on realized functional response model predictions is consistent with findings elsewhere by Quinn et al. 2017, who found that average predation rates were inversely correlated with stream depth and width. Additionally, in years when there was a low percent of total salmon available killed by bears, the functional response model overpredicted the number of bear kills, indicating that in specific years bear predation was lower than expected across ponds (teal dots representing 2014, 2015, 2016, and 2018 in Figure 6). We expected the functional response model would better fit the bear foraging data than the null IFD model, since the slope and asymptote estimates for each pond would take into account variation in the pond-specific habitat and foraging behavior.

We expected the slope estimate, or the number of salmon killed at low prey densities, would be higher in small, shallow ponds that were easier to catch fish in. Contrary to our hypothesis, there was little variation in the slope estimates with all ponds having slopes between 0.998 and 0.999 except Bear Pond (0.383). Bear Pond is a relatively large, deep pond with fewer salmon that other ponds of comparable area (average return = 421). Because the slope estimates did not vary much between ponds, we ran a modified Type II functional response model with a common slope estimate across all ponds. This "common slope" functional response model performed better than the null functional response and had fewer parameters to estimate (Table 2). The new estimated slope for all ponds followed the patterns of the null functional response model, indicating bears killed up to 99% of salmon available at low densities ($S = 0.999$). Bears differ from other predator-prey systems that see a reduction in the proportion of prey consumed at low prey densities (Holling 1959, Taylor 1984, Van Leeuwen et al. 2007). In the Pedro Ponds system, the bears' ability to effectively forage at low prey densities could result from 1) the clear water, enabling the bears to easily see the fish, 2) the combination of shallow water and lack of woody debris or other cover in the ponds, making the fish easy to catch, and 3) short distances between ponds across open tundra and forest, allowing bears to easily assess of salmon abundance across the entire pond system.

We expected to see an asymptote estimate for the maximum number of salmon killed at high prey densities by bears in a year. Some ponds reached a satiation point, like Trail and Grass Ponds, and others that had steep slopes at high prey densities, like Ponds 1A and 3 (Figure 7). The estimated asymptotic satiation point tended to increase with pond depth and area, but the relationship was not significant so other factors must control it. Bears in another area of Bristol Bay showed that asymptotic predation rate did not vary with the width or depth of the streams they were foraging in (Quinn et al. 2017). Overall, the lack of any relationship between asymptote and depth or area was because the whole system showed a linear functional response (Figure 2). When summarized across ponds, the number of bear kills increased linearly with the total number of salmon available, except for a few years with few salmon killed despite high availability (e.g., 2004, 2008, 2014, 2015, 2016, 2018; Figure 2). We speculate these years may have been characterized by few bears foraging in the Pedro Pond system. In high bear kill, high salmon availability years (e.g., 2007, 2010, 2012), asymptotic satiation points were not reached in each pond, likely because there were enough bears to keep foraging even at high prey densities. Alternatively, at high prey densities, bears may satiate quicker, lowering interference competition with decreased foraging times per bear, allowing for multiple bears to exploit the same pond.

Although the common slope functional response model improved the fit to the observed bear predation data, there was still variation across ponds each year. To capture yearly variation in the number and competitive ability of bears in the system, we modified the common slope functional response model to include a multiplicative year effect that modified the asymptotic point of satiation, adjusting this “satiation point” to differences in predation pressure across years. The addition of the year effect drastically improved model fit and was the most supported model overall (Figure 8; Table 2). The common slope estimated for the year effect model was reduced in comparison to the common slope model (*S* = 0.928), concluding that bears foraged effectively at low salmon densities. The asymptote estimates for each pond decreased with the addition of the year effect from their null and common slope functional response model values. Because the year effect interacted with the asymptote estimates for each pond, changes in asymptote estimates resulted from changing predation pressure, in number and competitive ability of bears, among years. This is supported by the increasing relationship between year effect estimates and the proportion of salmon killed by bears across all ponds that year (Figure 9). We hypothesize that the year effect captures variation in the number of bears foraging in the pond, but this change in predation pressure could also be related to the competitive ability of the bears in the pond that year. Adult male bears consume more salmon than females and juvenile bears (Van Daele et al. 2013). Decreases in the proportion of salmon killed by bears in a year could then be explained by the sex and age structure of the bears (e.g., numbers of cubs, sub-adult, and adult bears) foraging in the pond system in a specific year. Ultimately, the year effect, common slope functional response model revealed that year to year variation in predation pressure is important in predicting the number and location of bear kills.

Conclusions

We ran multiple parameterizations of two ecological models. IFD and Type II functional response, to observed bear predation data. Overall, the common slope functional response model with a year effect best fit the data (Table 2). This indicated that year to year variation in the total number and distribution of salmon killed by bears was affected by local salmon density, habitat-specific features, and factors varying among years that we could not measure – likely the number and social status of bears in the area. The importance of accounting for year-to-year variation is supported by the formulation of the IFD null model. The null IFD outperformed the null functional response model because the null IFD directly accounts for variation in the proportion of total salmon killed by bears across ponds each year (Equation 1). Because the IFD models directly account for this year-to-year variability, each parametrization outperforms the functional response models, except for the year effect model (Table 2). The IFD and pond effect model also fit the data well. This model allows us to conclude that habitat variability matters in bear foraging decisions. The functional response models account for variation in habitat quality by altering the asymptote estimates for each pond. Additionally, we observed that the functional response models have lower goodness of fit values than the IFD models (Table 3). Because the functional response models have more parameters to fine tune and estimate predictions, they are better able to fit the observed data and result in decreased goodness of fit estimates.

Through multiple parameterizations of two alternative, but not separate, ecological models, we gained important insights on bear foraging ecology. Bear Pond was the most difficult to forage in, as both null models over-estimated the number of salmon killed there. Bear Pond had both the lowest pond effect and the lowest slope estimate, indicating that bears were not as efficient at foraging in the pond and tended to kill a smaller fraction of the fish. The IFD and functional response models led to important insights on the distribution of salmon killed across ponds. Both types of models indicated that year to year variability in the proportion of total salmon killed by bears is important in determining the number and location of bear killed salmon. This variability is likely attributed to variation in the number and competitive ability of bears, two different measures of predation pressure in the system we were unable to measure. Both models also support that habitat variability across ponds affects the number and location of bear killed salmon. Neither depth nor area alone completely capture habitat variability, thus some interaction between them or another unmeasured variable could affect bear foraging. Ultimately, we discovered that bears were very good at foraging at low salmon densities, and that variation in the number of salmon available and the habitats affected where most salmon predation took place. The spatial ecology predictions of the IFD and the individual behavioral predictions of the functional response, representing two of many ways to investigate foraging ecology, provided insights about the bear-salmon system.

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Figures and Tables

Table 1: Specific attributes of ponds including average depth, area, average number of adult sockeye salmon, and distances (center of pond to center of pond) to the closest and farthest pond in the Pedro Bay Ponds system.

Pond	Average Depth (cm)	Area (m^2)	Average salmon	Distance to closest pond (m)	Distance to farthest pond (m)
Bear Pond	41.6	1820	421	185	560
Berg's Pond	26.7	185	111	65	560
Big Pond	54.5	3072	1317	70	550
Grass Pond	19.9	1070	676	155	380
Pond 1	26.0	695	502	70	330
Pond 1A	13.5	165	64	60	350
Pond 2	16.5	355	47	60	390
Pond 3	26.6	265	40	50	450
Pond 4	32.9	340	46	50	470
Trail Pond	38.5	1135	881	70	480
Average	29.7	910	411	84	452

Table 2: The candidate model set predicting the number of sockeye salmon killed by bears in each pond divided into the two model types by the double line: the Ideal Free Distribution (IFD) model formulations above the line and the Type II functional response model formulations below the line. The number of parameters, AIC$_c$ values, ΔAIC$_c$ values, and dispersion parameter are reported for each model. A change of >2 units of ΔAIC$_c$ indicates model superiority.

Overall Model Rank	Model name	Number of parameters (*k*)	AIC$_c$	ΔAIC$_c$	Dispersion Parameter
2	IFD + Pond	11	1771.24	*Preferred model*[†]	7.35
3	IFD + Area	2	1834.84	63.6	4.13
4	IFD + Depth	2	1858.45	87.21	3.61
5	Null IFD	1	1898.67	127.43	2.77
1	Functional Response, common slope + Year	37	1737.03	*Preferred model*[*‡]	16.65
6	Functional Response, common slope	12	1992.92	255.89	1.90
7	Functional Response	21	2003.55	266.52	2.02

Note:

† ΔAIC$_c$ values indicate most supported model for the Ideal Free Distribution.

* ΔAIC$_c$ values indicate most supported model for the Functional Response.

‡ ΔAIC$_c$ values indicate most supported model overall.

Table 3: The goodness of fit for each model, summarized across all ponds, for predation by bears on sockeye salmon. This represents the percent error in the predictions across all ponds; lower values represent better goodness of fit.

Model	Goodness of fit, G
IFD + Pond	0.35
IFD + Area	0.49
IFD + Depth	0.52
Null IFD	0.56
Functional Response, common slope + Year	0.22
Functional Response, common slope	0.30
Functional Response	0.31

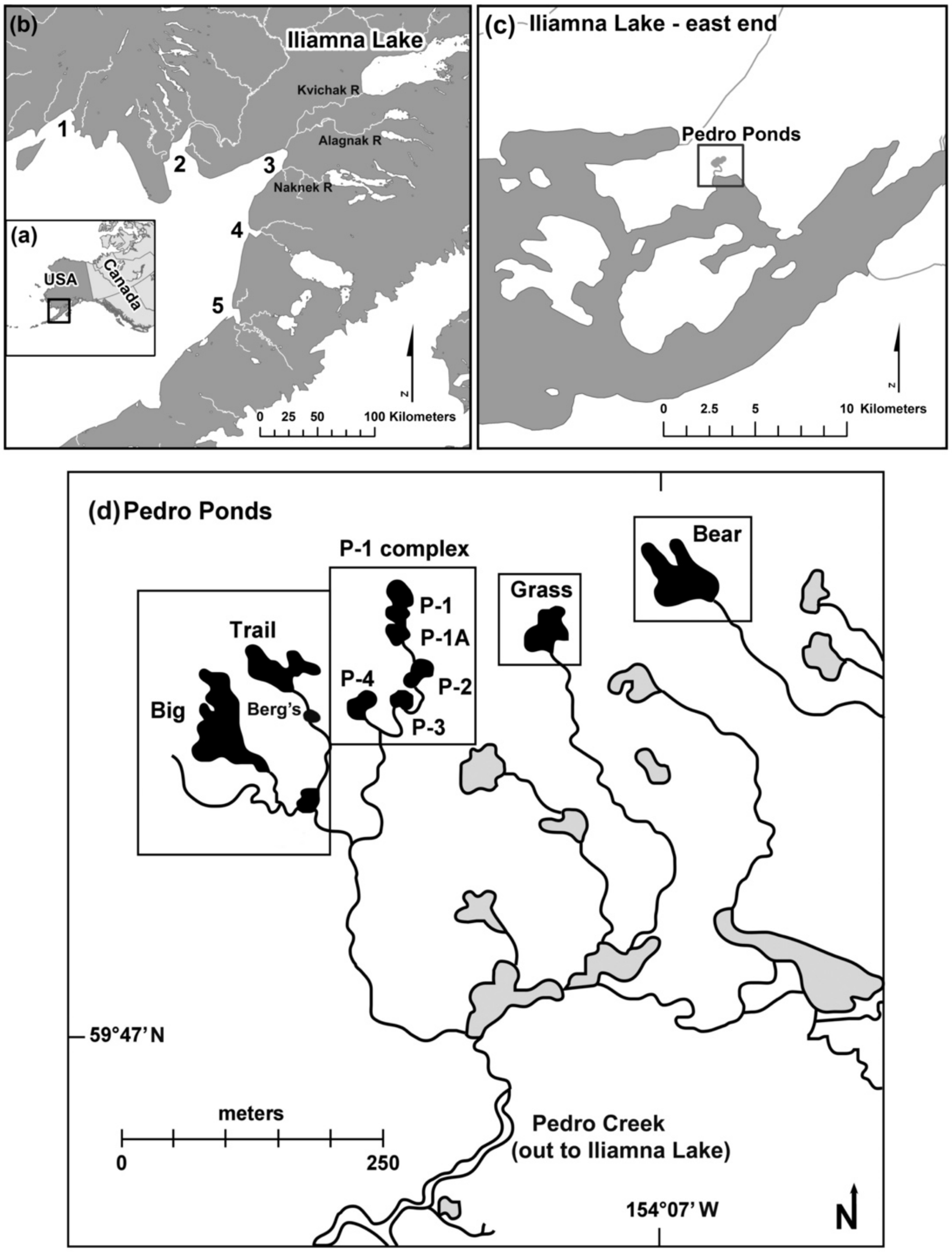

Figure 1: Map of western Alaska, USA (A), showing the location of Iliamna Lake (B), the specific location of the Pedro Pond system on eastern end of the lake (C), and the configuration of the ponds (D). Figure reproduced from Quinn et al. (2012).

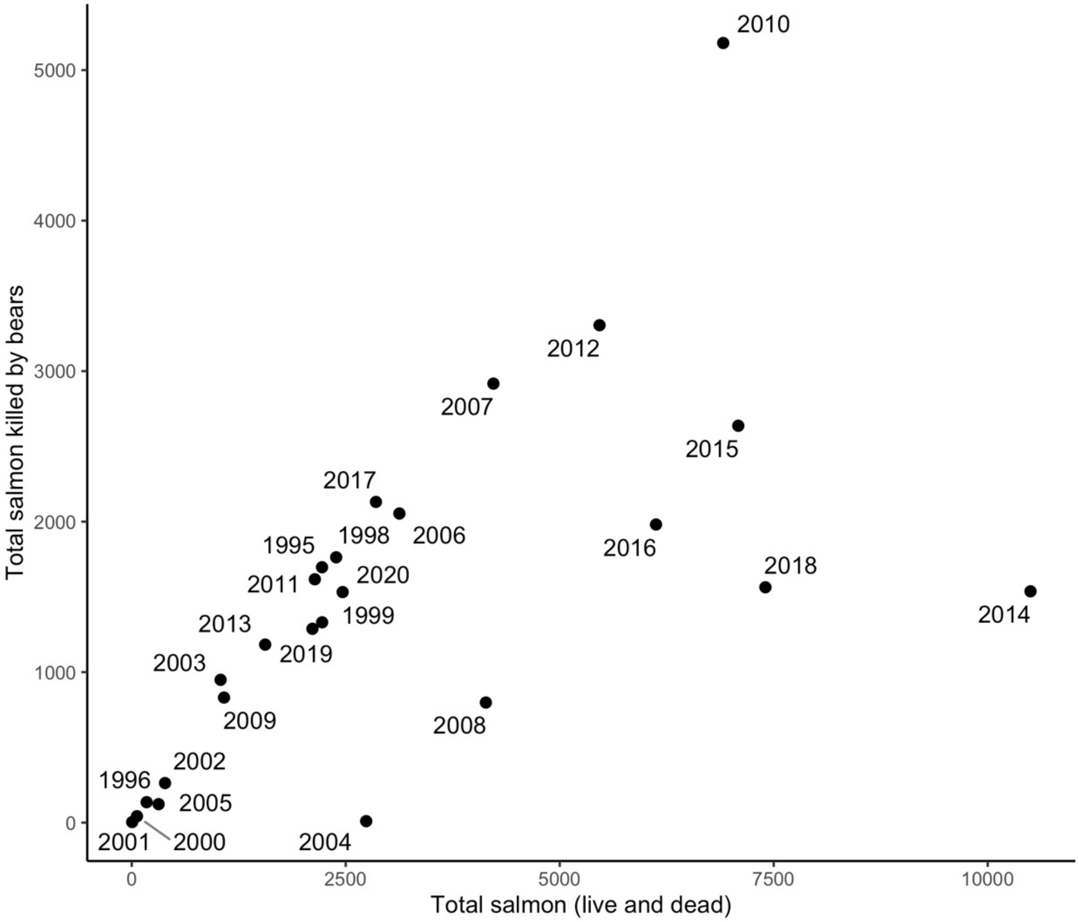

Figure 2: The total number of sockeye salmon available (live and dead) plotted against the total number killed by bears in each year in the Pedro Bay pond complex.

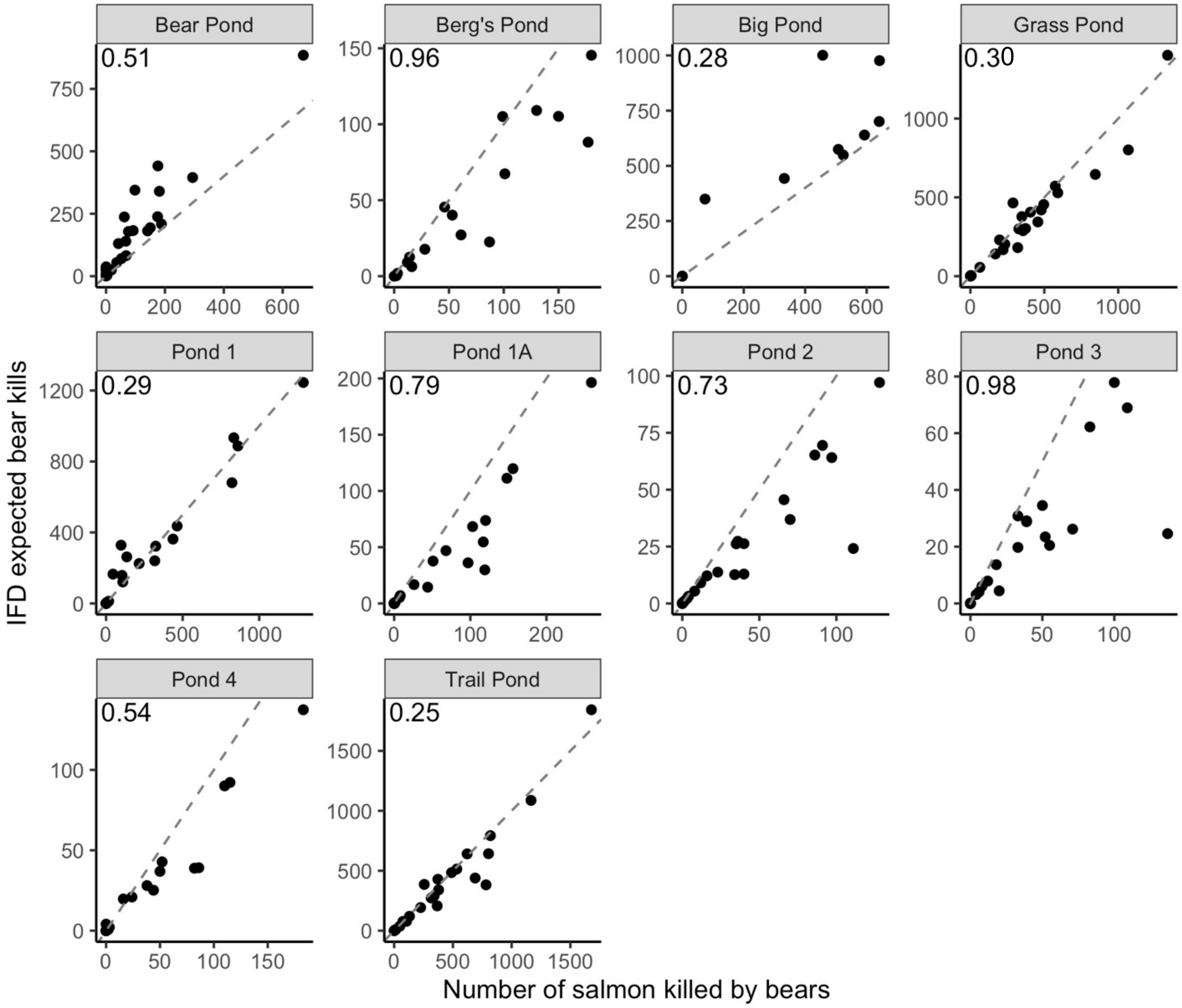

Figure 3: The observed number of sockeye salmon killed by bears annually in each pond plotted against the number predicted from the Ideal Free Distribution. The gray dashed 1:1 line shows the hypothetical perfect model fit. The number in the top-left corner of each panel shows the average error rate between model predictions and observed data for each pond. Lower values represent better fit, G_p.

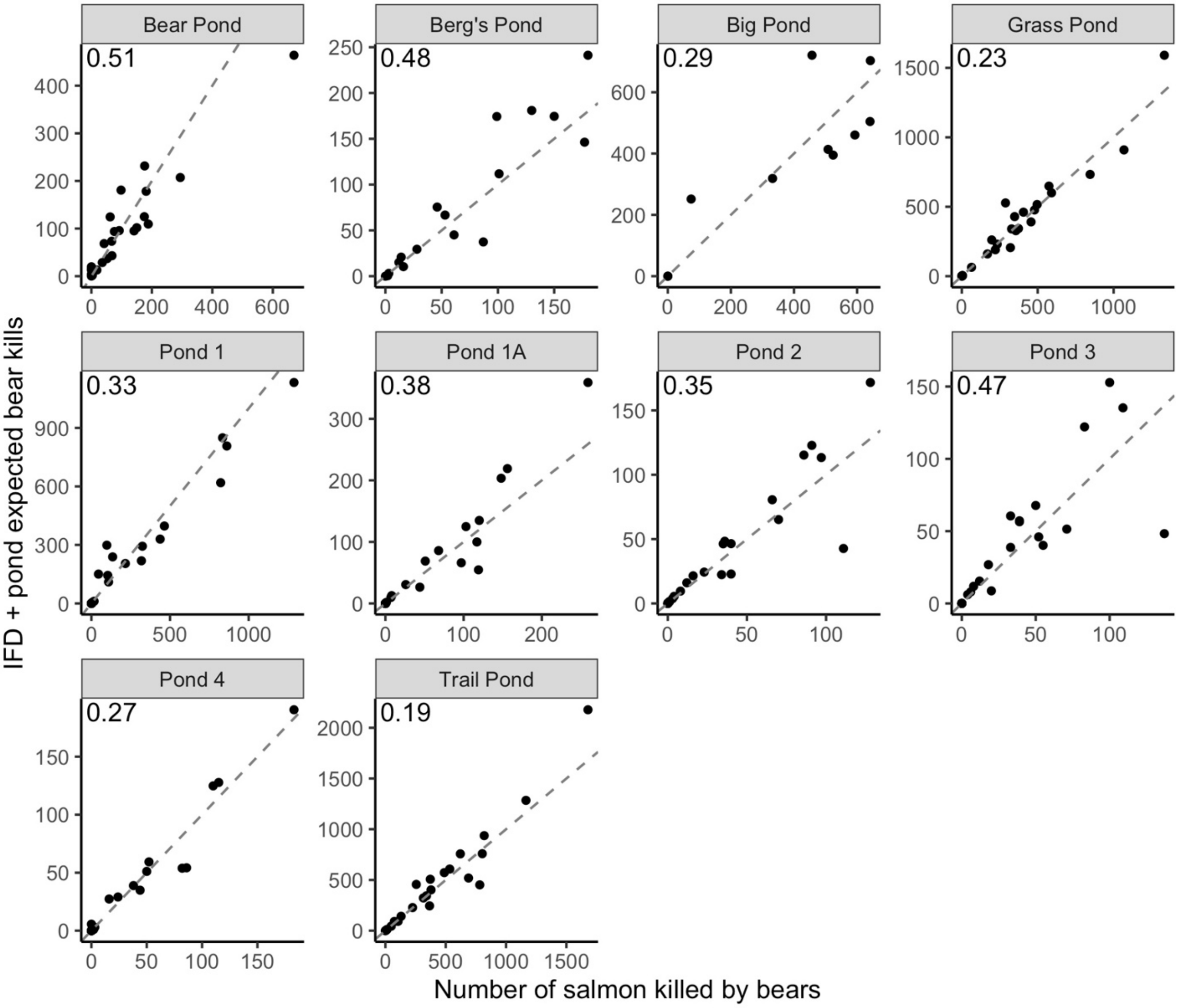

Figure 4: The observed number of sockeye salmon killed by bears annually in each pond plotted against the number killed as predicted by the Ideal Free Distribution, with a pond effect modifier for each pond each year. The gray dashed 1:1 line shows the hypothetical perfect model fit. The number in the top-left corner of each panel shows the average error rate between model predictions and observed data for each pond. Lower values represent better fit, G_p.

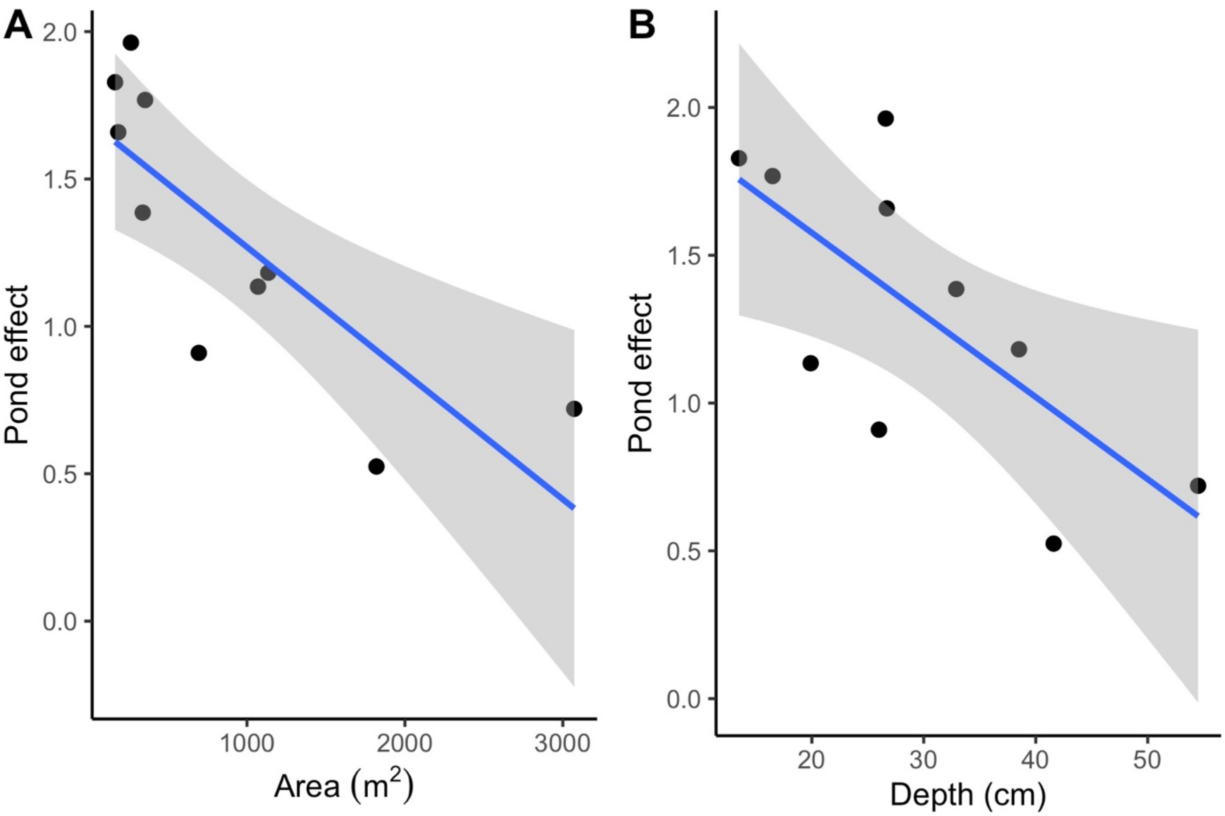

Figure 5: The most supported IFD model included a pond effect, modifying the predicted number of salmon killed by bears based on pond-specific predation patterns. The pond effect estimates are displayed as related to (A) area and (B) depth by linear regression with the estimated relationship in the blue line and 95% confidence intervals in the gray shaded area.

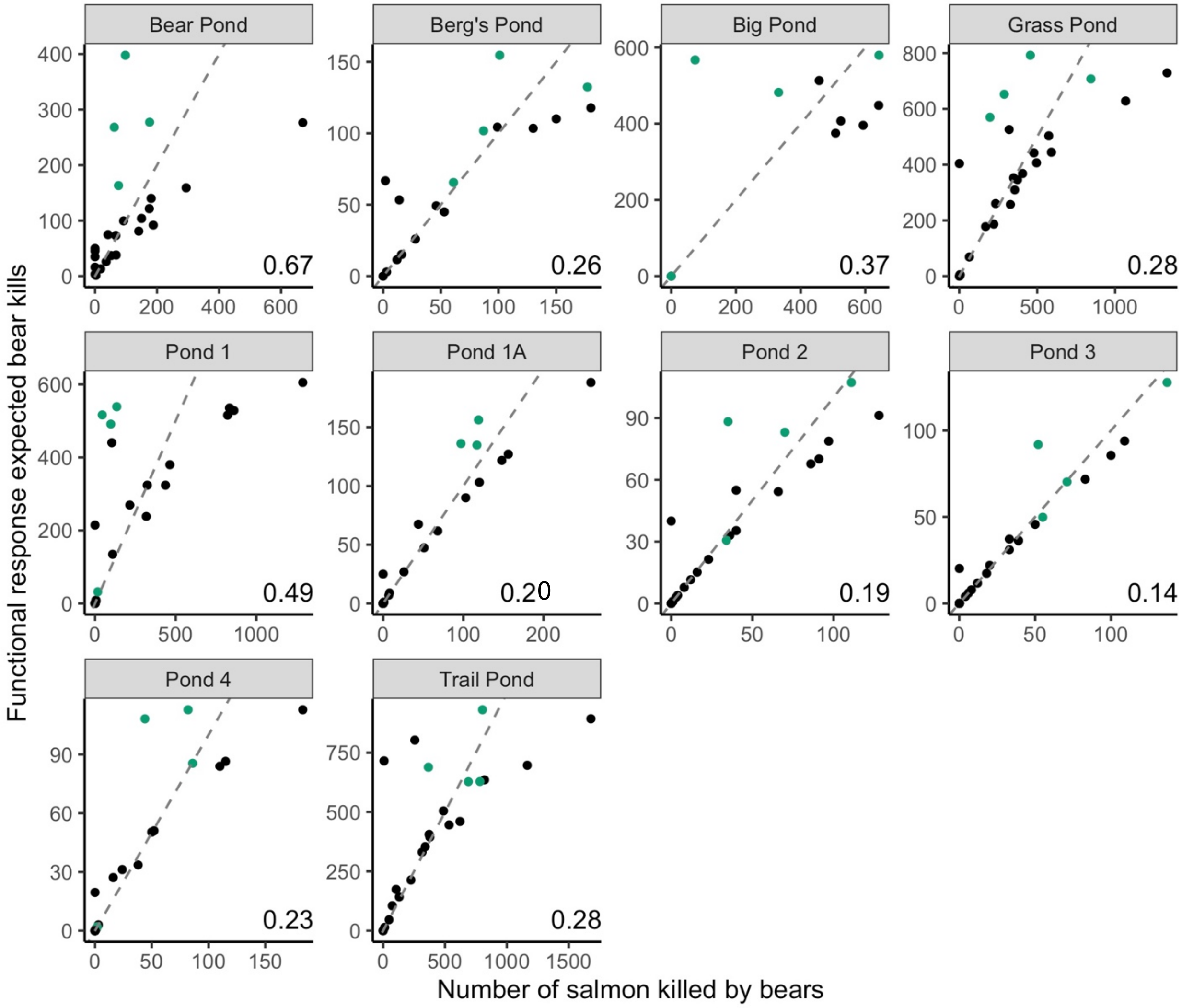

Figure 6: The annual number of sockeye salmon killed by bears in each pond plotted against the number killed as predicted from the Functional Response model. The teal dots represent the years when the percent of total salmon killed by bears was low (2014, 2015, 2016, and 2018). The gray dashed 1:1 line shows the hypothetical perfect model fit. The number in the top-left corner of each panel shows the average error rate between model predictions and observed data for each pond. Lower values represent better fit, G_p.

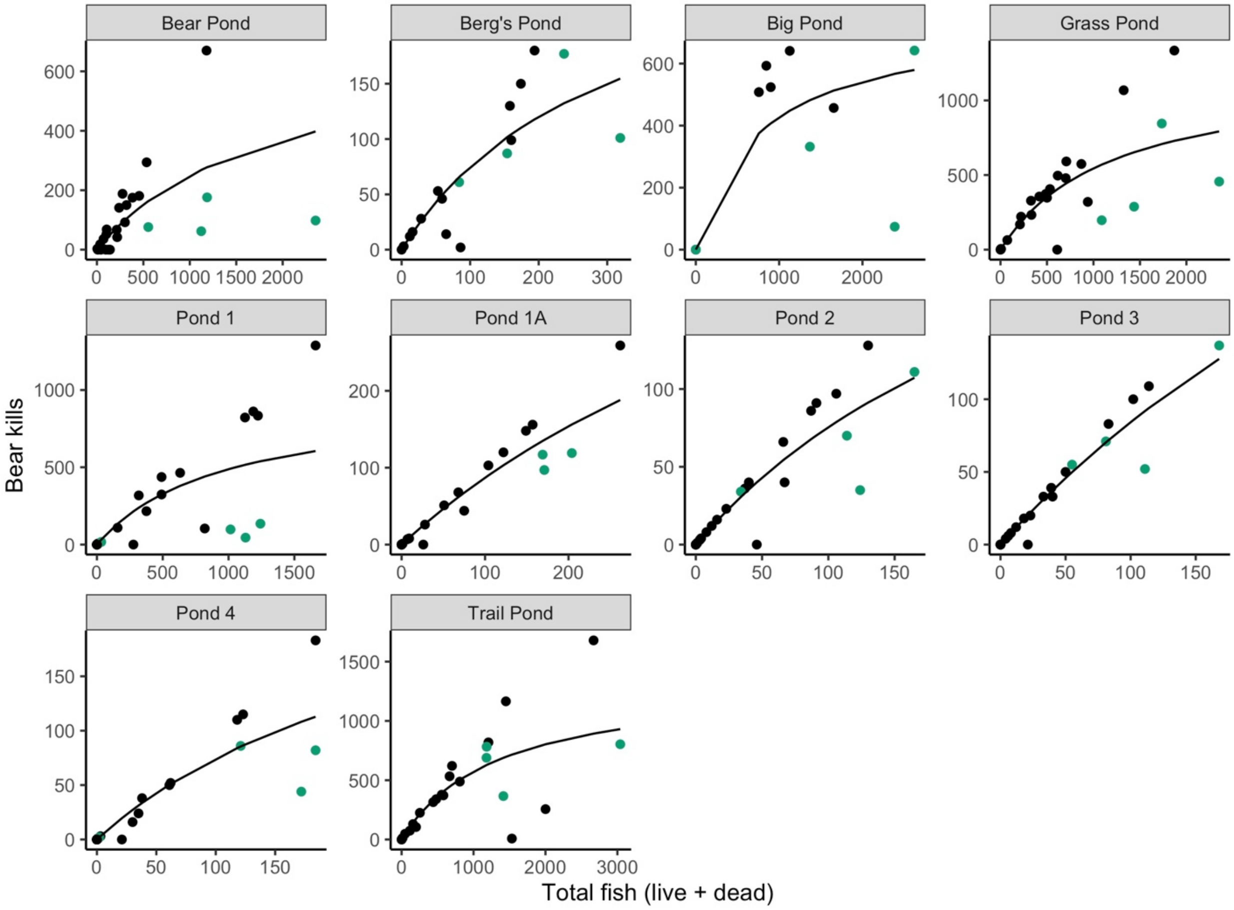

Figure 7: The Type II functional response models for each pond show the total number of sockeye salmon in each pond each year and the total number of salmon killed by bears in that pond each year, with teal dots representing the years when the percent of total salmon killed by bears was low.

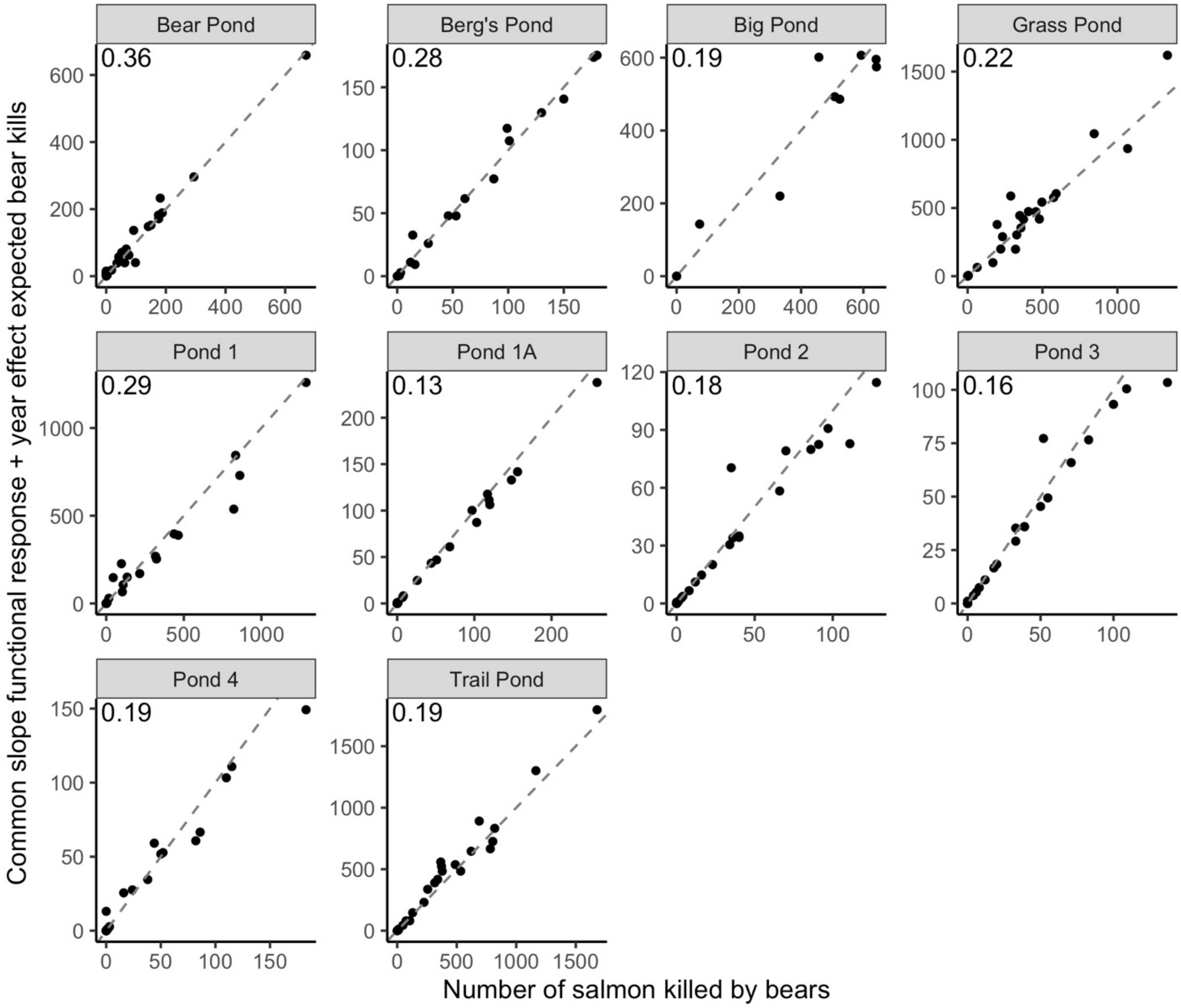

Figure 8: The number of sockeye salmon killed each year by bears in each pond plotted against the common slope functional response and year effect model predicted number of salmon killed. The gray dashed 1:1 line that shows the hypothetical perfect model fit. The number in the top-left corner of each panel shows the average error rate between model predictions and observed data for each pond. Lower values represent better fit, G_p.

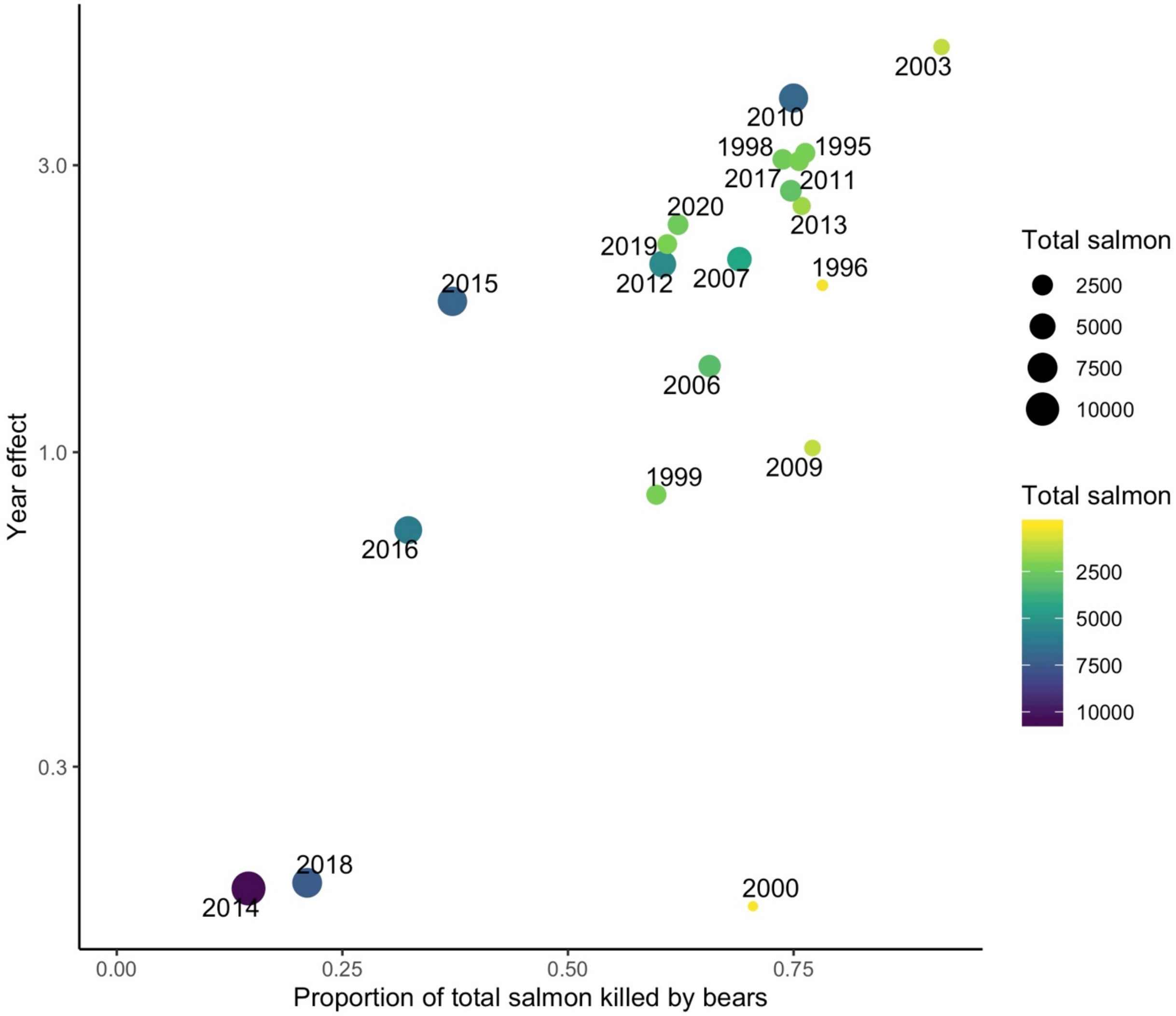

Figure 9: The proportion of sockeye salmon killed by bears across all ponds increases with the year effect estimate from the common slope functional response and year effect model. The size of the point and the color of the point is related to the total number of salmon (live and dead) available across all ponds in that year. The y-axis is on a logarithmic scale.

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Chapter 2: Applying the Ideal Free Distribution to the movement of a highly mobile gillnet fishery for Pacific salmon

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Abstract

Ecological models are used to understand where fishing vessels fish, improving fisheries management success. The Ideal Free Distribution (IFD) predicts equalization of catch across locations in response to distributions of fish and other vessels. We applied the IFD as a null model to investigate the movement and catch per vessel (CPUE) of the sockeye salmon drift gillnet fleet in Bristol Bay, AK, from 1980-2019. The IFD prediction of equal CPUE across areas was not supported, so we explored violations of two assumptions of the theory. We categorized each vessel according to its mobility, highlighting the "free to move" assumption, and found when we removed nonmobile vessels, some districts had fewer vessels than predicted from their high CPUE. We examined the "equal competitive ability" assumption by calculating the average CPUE, relative to success of other vessels. The underutilization of profitable districts persisted. Overall, the fleet underused high CPUE areas when considering differences in mobility and relative fishing success, indicating unmeasured safety concerns, travel costs, knowledge of fishing grounds, or other factors could be preventing an IFD.

Introduction

Fleet behavior, the spatial and temporal patterns of fishing vessel movement and effort, plays a critical role in fisheries management. Understanding fleet behavior allows for identification of areas, stocks, and times that will be exposed to high fishing pressure, aids in understanding economic incentives and limitations in the fishery, and facilitates anticipatory responses to changing management, economic, biological, climatic, and oceanographic conditions (Bucaram et al. 2013, Ono et al. 2018, Fisher et al. 2021). Consequently, the incorporation of fleet behavior is necessary to design management strategies for the unique ecological, economic, social, and cultural aspects of each fishery (Hilborn 1985, Wilen et al. 2002).

Fishing vessels can be viewed as large, mobile predators searching for mobile prey, and ecological models developed to understand spatial and temporal patterns of predator-prey systems can be used to study their behavior. For example, the Optimal Foraging Theory was applied to study Patagonian toothfish (*Dissostichus eleginoides*) longline fishers that experience depredation from odontocete whales, and revealed that differences in tolerance for losses to whales altered the distribution of vessels (Richard et al. 2018). Likewise, game theory predictions applied to small scale gillnetters of African catfish (*Clarias gariepinus*) illustrated that balanced harvesting could emerge without intensive management action when fishers caught large and small fish in proportion to the productivity of the age of the fish (Plank et al. 2017). Ecological models like these can help understand fleet behavior to create informed management strategies.

The Ideal Free Distribution (IFD) theory was developed to investigate spatial and temporal patterns in reproductive habitat use in birds (Fretwell and Lucas 1969), but has also been applied to foraging decisions for many predator-prey systems (for a review see Kennedy and Gray 1993), including not only animals but large and small-scale fisheries (Abrahams and Healey 1990, Gillis et al. 1993, Rijnsdorp et al. 2000, Abernethy et al. 2007). The IFD predicts the distribution of breeding animals or predators in response to the distribution of their nesting sites or competitors and prey, and is useful as a null model to investigate departures from its four main assumptions (Tregenza 1995). The most relevant violations to IFD assumptions for fisheries include the (1) "move to maximize success" and (2) "equal competitive ability" assumptions, as individual fishers have diverse motivations (i.e., maximizing income is not always the primary one) and they also vary in potential catch rates owing to differences in experience, vessel size and condition, and other attributes. Additionally, the theory assumes (3) that fishers have and make use of "perfect information" about the distribution of fish (prey) and competitors. Finally, the IFD assumes (4) that competition exists in the system, and prey resources decrease with increased competitor density (Fretwell and Lucas 1969). This model has been applied to many fisheries to shed light on fishing behavior, illuminating social and economic constraints on movement (Abernethy et al. 2007), individual specialization (Hilborn 1985), and variation in catch rates (Abrahams and Healey 1990).

The drift gillnet fleet in Bristol Bay, Alaska, fishes migrating Pacific salmon (genus *Oncorhynchus*) in spatially discrete fishing districts (Figure 1). The fishery catches several species of salmon but sockeye salmon, *O. nerka*, is by far the most numerous and the primary target. These adult salmon enter five discrete fishing districts as they return to spawn in the rivers associated with the districts, and vessels travel in between these districts to find fish (maximum travel time: 12 hours). There are several notable elements to this fishery. First, collectively it is the largest run of the species, and commercial vessels can catch many hundreds of thousands of dollars' worth of fish in a short time span (Hilborn 2006, Cunningham et al. 2019). Second, the salmon return from the open ocean, and pass through the fishing districts over a very short period. The entire season lasts only about one month and the great majority of the catch in each district occurs within about two weeks (Burgner 1980, Quinn et al. 2007). This combination of high value salmon, geographically delimited areas open to fishing, and compressed timing result in intense competition among the ~1800 vessels in this limited entry fishery. The ecological, economic, and cultural importance of the fishery has motivated the collection of an unusually high quantity and quality of information that is publicly available and relevant to fishers making decisions. Specifically, several months in advance of the fishing season, two different forecasts of the number of fish expected to return to each district are released based on data collected in previous years, one from the Alaska Department of Fish and Game (ADFG) and one from the University of Washington. Then, as the sockeye salmon are approaching the fishing districts, a test fishery operated about 7 days travel time away provides information on catch per unit of effort, body size, and age composition, and in recent years DNA samples are processed within days to indicate the spawning regions that produced the fish, hence where they are returning (Dann et al. 2013). As the salmon encounter the fishery in each district, catches are enumerated and sampled for size and age composition daily, and salmon that escaped the fishery are counted as they migrate upriver, providing daily counts of salmon escapement and catch by district. These data are provided to the managers, commercial salmon processing companies, and the public at large, including vessel captains. This combination of advanced pre-season forecasts, an in-season test fishery, escapement goals, and daily catch and escapement data provides a richness of information on which fishers can base their choice of location that is arguably unique in the world and certainly unique in the realm of salmon management. Thus, it is closer to meeting the assumption of “perfect information” in the IFD than most other fisheries, making this fishery well-suited for testing the IFD.

Using data on the daily catch and location of individual vessels, we applied the IFD as a null model to the distribution of the Bristol Bay drift gillnet fleet from 1980-2019 to assess the extent to which the fishery met IFD predictions. The IFD predicted that vessel movement between spatially discrete fishing districts would adjust to salmon abundance and equalize catches per vessel, producing equal average catch per boat across districts. Alternatively, we investigated the violation of two assumptions that could prevent an IFD from occurring: (1) vessels did not move to “maximize success” and (2) there was a lack of “equal competitive ability” across the fleet. We hypothesized that the mobile component of the drift gillnet fleet is in an IFD but the nonmobile component, the vessels choosing not to move and to fish the same district, prevents an IFD from occurring fleet-wide. We also expected that variation in relative fishing efficiency among vessels would alter IFD predictions, with highly successful vessels fishing in the most productive districts. By investigating patterns of fleet behavior, we can better adapt management rules to highly mobile fisheries with diverse fishers.

Methods

Study system

Bristol Bay, in southwestern Alaska, supports the largest returns of sockeye salmon (*Oncorhynchus nerka*) in the world and other species of salmon in a sustainable fishery (Sands 2006). There are four major fishing districts, each at the mouth of one or more major rivers in the area: Nushagak, Naknek-Kvichak, Egegik, and Ugashik (Figure 1). A fifth, the Togiak district, has fewer salmon, is spatially less proximate than the others, and has unique management restrictions on movement so, for the purposes of this study, it was excluded. Sockeye salmon are caught during their return migration to these rivers in a compressed fishery from mid-June to mid-July (Salomone et al. 2017). The daily in-season pattern of opening and closing the fishery is managed by ADFG biologists, who release daily orders online and by radio to announce openings and closures of the fishing districts (Hilborn 2006). Districts are managed separately to reach escapement goals, set to achieve sustainable yield, for each stock or river system (Erickson et al. 2015, Cunningham et al. 2019). These escapement goals are set in advance of the season, typically do not change from year to year, and are known to all members of the fishing community.

There are two types of commercial salmon fishers in Bristol Bay in addition to an economically valuable recreational fishery and a large and culturally important subsistence fishery (Halas and Neufeld 2018, Panikkar and Tollefson 2018). There are stationary, shore-based set-net fishers and a mobile drift gillnet fleet that is the focus of this study. We categorized the mobile drift gillnet fleet into two groups by fisher behavior, based on knowledge of fishery managers and fishery participants: (1) mobile vessels that switch districts at least once in given a year and (2) nonmobile vessels that fish a single district in a given year. The management of the drift gillnet fleet in Bristol Bay has created specific rules, unique to the area, to control the intense fishing competition resulting from the very numerous salmon, compressed timing of return, and the logistics of processing and shipping salmon to distant markets from these largely road-less areas. With the implementation of the limited entry program in 1975, the number of fishing permits was fixed at ~1800 drift gillnet permits total, and anyone seeking to enter the fishery must acquire the permit from an existing permit holder (Schelle et al. 2004, Hilborn 2006). Additionally, at the beginning of the season each vessel must register to fish a specific district. Captains wanting to move in the middle of the fishing season must notify the ADFG district office and refrain from fishing for 48-h (Sands 2009). This “48-h rule” was implemented in 2003 to allocate more catch to set net fishers and nonmobile drift vessels and is waived when the escapement goals are met in each district.

Drift gillnet fleet vessels are all constrained to be no more than 32 feet in length, but vary in attributes that affect their ability to move and catch fish, including horsepower, hold capacity, the presence of refrigerated seawater systems, and displacement (Gho 2020). Most of these attributes increase over time, due to increases in technology over our study period (Valderrama and Anderson 2010). Additionally, drift gillnet mesh size and net length has been fixed over the season, although the mesh size used has changed in response to decreasing body size in salmon in recent years (Oke et al. 2020, Ohlberger et al. 2023). Information on these vessel attributes was not available due to confidentiality restrictions, although we captured individual vessel variation by looking at the variation in catch per vessel (CPUE) across captains.

Data Sources

The Commercial Fisheries Entry Commission (CFEC) fish ticket database provided information on the movement of individual vessels and their associated landings from 1980-2019. In the drift gillnet fishery, fishers deliver their landings to at-sea fishing tender vessels that deliver the fish to shore-based or floating processing facilities. When fishers deliver their landings, they fill out a ticket that reports the pounds of catch, species, date, associated fishing district, and the identities of the captain, permit, and vessel.

CFEC fish ticket data are confidential so, to protect the identity of fishers, we randomized captain ID to create a non-traceable ID that was unique to each captain. Relevant information was extracted from the CFEC fish ticket database (year, date landed, district, captain ID, whole pounds of sockeye landed, processor), and missing values were coded as NA. Special harvest areas, accessible only under specific management actions, were included in their respective districts. In addition to ensuring that the data was not traceable to individual captains, the CFEC can only report data with groupings (i.e., on a given day in a given district) greater than 4 individual vessels. To further protect confidentiality, those with < 4 were excluded. After filtering to ensure confidentiality, the dataset contained 1,027,040 records of landings by year, date, ID, district, and processor ID.

At the beginning and end of the fishing season, fewer vessels fish compared to the middle of the season, necessitating exclusion of more vessels from our dataset to ensure confidentiality. To account for this factor in a consistent manner, we excluded data from the first 5% and last 3% of the cumulative catch across a season to ensure we had most of the vessels fishing in our data; this defined the core fishing season. We allowed more catch at the end of the season than the beginning to accommodate the later timing of the Ugashik district, as not doing so would have had a biasing effect on data from that district. Additionally, days with no effort, hence no catch, were distinguished from those when there was effort but no catch reported in our dataset due to confidentiality restrictions, and we excluded the latter from analysis and recorded CPUE = 0 for the former.

Analyses

IFD across districts

Under IFD null predictions, if the fishery was in an IFD in a specific year there would be no difference in CPUE across fishing districts. The movement of vessels among districts would equalize CPUE as vessels moved into districts with higher CPUE, thereby reducing competition in the districts they left and elevating CPUE there while increasing competition and reducing CPUE in the area they entered (Figure 2). To determine if districts were in an IFD across the core fishing season, we ran a linear model using the average CPUE across all years as the dependent variable with district as a factor and an interaction between date and year.

For ease of interpretation, we also scaled the CPUE for district (*f*), each day (*d*) and year (*y*), $CPUE_{f,d,y}$ (Equation 1) to the bay-wide CPUE for that day, removing the effect of specific days. We calculated the total bay-wide CPUE, $CPUE_{d,y}$, for that year and date according to Equation 2.

(Equation 1) $$CPUE_{f,d,y} = \frac{C_{f,d,y}}{B_{f,d,y}}$$

(Equation 2) $$\overline{CPUE}_{d,y} = \frac{\Sigma_f C_{f,d,y}}{\Sigma_f B_{f,d,y}}$$

Where $C_{f,d,y}$ is the total catch in pounds in district *f*, on day *d*, in year *y*; $B_{f,d,y}$ is the number of vessels in district *f*, on day *d*, in year *y*; and $CPUE_{d,y}$ is the average bay-wide CPUE for day *d*, in year *y*. Then, we divided the CPUE for each district by the bay-wide CPUE in that day and district to find the scaled CPUE according to Equation 3.

(Equation 3) $$S_{f,d,y} = \frac{CPUE_{f,d,y}}{CPUE_{d,y}}$$

Where $S_{f,d,y}$ is the scaled CPUE in district *f*, on day *d*, in year *y*. If the value for scaled CPUE is greater than 1, the district had higher CPUE than the average bay-wide CPUE on that day and year and if the CPUE was less than 1, the district had lower CPUE than the average bay-wide CPUE on that day and year. We then ran a linear model predicting the daily scaled CPUE, $S_{f,d,y}$, for the core fishing season with district as a factor across all years. A Tukey's honestly significant difference (HSD) post-hoc test was used to look for differences between districts across all years. Additionally, we ran the same model for each year separately. Under IFD predictions, there would be no effect of district on the scaled CPUE.

Categorizing mobile and nonmobile vessels

During the fishing season, each captain decides where to start fishing and whether to move to another district or remain in the same district each day. The proportion of vessels that did not move in a season, here defined as nonmobile, varied across years and districts. We categorized each vessel in each year as mobile (fished 2 or more districts) or nonmobile (fished only 1 district) using the entire fishing season, not trimmed to the core season.

We then tested the hypothesis that the mobile vessels were in an IFD by removing the nonmobile vessels from the core fishing season and running linear regressions on scaled CPUE using district as a factor across all years and for each year. If the mobile vessels were in an IFD there would be no effect of district on scaled CPUE.

Calculating captains' relative success

Across a fishing fleet, there is variation in the success of each captain best described by their catch compared to those of other captains. Relative fishing success is affected by the experience and skill of the captain and crew, movement choices, and vessel characteristics (Gatewood 1983, Hilborn and Ledbetter 1985, Richard et al. 2018). The IFD assumes that all captains have equal competitive abilities, although we know this is often violated in fisheries (Hilborn 1985, Abrahams and Healey 1990). To ask if the violation of the "equal competitive ability" assumption of the IFD, or captain specific differences in daily relative success, affected the number of years the fishery was in an IFD, we calculated the mean relative fishing success for each district, day, and year as described below.

On an individual level, we summarized the daily relative success of each captain fishing in a district on a specific day and year using the full fishing season, not trimmed to the core season. To calculate this, we took the catch, C, of the individual captain *i*, in district *f*, on day *d*, in year *y*, and divided it by the average CPUE ($CPUE_{f,d,y}$; Equation 4). This represented the daily relative success, $\rho_{i,f,d,y}$, of a captain compared to the average across captains *i*, fishing in district *f*, on day *d*, and year *y*.

(Equation 4) $$\rho_{i,f,d,y} = \frac{C_{i,f,d,y}}{CPUE_{f,d,y}}$$

Where a value > 1 shows that captain, *i*, did better than an average vessel and a value < 1 shows that the captain did worse than an average vessel in district *f*, on day *d*, and year *y*.

We then determined an average relative success, ρ_i, for each captain by finding the average of each captain's daily relative success, $\rho_{i,f,d,y}$, across all days they fished according to Equation 5.

(Equation 5) $$\rho_i = \frac{\Sigma_{f,d,y}\,\rho_{i,f,d,y}}{n_d}$$

Where n_d is number of days, *d*, that individual, *i,* fished across all years.

To calculate the relative fishing success of all vessels fishing in a specific district *f*, day *d*, and year *y*, we found the mean of the average relative success of each captain across all captains that made landings in that day district and year, $\overline{\rho_{f,d,y}}$ (Equation 6).

(Equation 6) $$\overline{\rho_{f,d,y}} = \frac{\sum_i \rho_{i,f,d,y}}{n_{f,d,y}}$$

Where $n_{f,d,y}$ is the number of captains that fished in district *f,* on day *d*, in year *y*.

We then divided the scaled CPUE, $S_{f,d,y}$, by the mean relative fishing success, $\overline{\rho_{f,d,y}}$, to find the scaled CPUE standardized by relative fishing success, $\varphi_{f,d,y}$ (Equation 7).

(Equation 7) $$\varphi_{f,d,y} = \frac{S_{f,d,y}}{\overline{\rho_{f,d,y}}}$$

To determine if variation in relative fishing success prevents the IFD from occurring, we ran linear models on the $\varphi_{f,d,y}$ with an effect of district across all years and for each year on the core fishing season. Under IFD predictions, the CPUE measure that considers captain fishing success should be the same across all districts if the districts were in an IFD. We would expect captains with average relative success to be concentrated where CPUE is high, driving down the scaled CPUE standardized by relative fishing success.

Additionally, we restricted our analyses above to mobile vessels and relative fishing success to investigate whether considering variation in fishing success produces an IFD across only the mobile vessels in a year. We ran linear models across all years and for each year that looked at the district effect on scaled CPUE standardized by relative fishing success for only mobile vessels in the core fishing season.

Results

Across 40 years of data, we had 1,027,040 unique observations of vessels' catch in a district, day, and year. Our dataset included 1,041 – 1,728 (mean = 1,472) vessels participating in the fishery each year and 18.2 – 85.4 (mean = 51.6) millions of kg of sockeye salmon caught each year. Our data represented between 66 - 85% (mean = 77%) of the total catch of sockeye salmon caught in Bristol Bay each year and between 82 – 100% (mean = 95%) of the vessels fishing each year.

IFD across districts

We observed that vessels moved into areas with high catches, tracking variability in the timing of the salmon return to different districts (Figure 2). As catch in a district increased, as it did in Naknek-Kvichak district at the end of the season in 2018 (Figure 2E), the number of vessels in that district also increased (Figure 2C), drawing down the overall CPUE there (Figure 2A). Vessel movement decreased the overall variability in CPUE between districts in a season, consistent with IFD predictions, as vessels moved into districts with high CPUE, decreasing CPUE there and increasing CPUE by decreasing competition in the district they left.

Across all years (1980-2019), a linear model indicated a significant effect of district and an interaction of date and year on CPUE ($R^2 = 0.135$, $p<0.005$). Specific districts differed in average CPUE across years, violating IFD predictions (Ugashik = 21,192 kg/vessel, $p = 0.112$; Egegik = 21,097 kg/vessel, $p = 0.312$; Naknek-Kvichak = 20,786 kg/vessel, $p < 0.005$;

Nushagak= 20,563 kg/vessel, $p < 0.005$). Not surprisingly, date varied in its effect on CPUE, varying from a positive effect in the peak of the season to negative effects at the beginning and end. Year by itself did not have a significant effect, but specific day and year interactions did, with significant positive effects near the peak of the season. This led us to scale CPUE to the average bay-wide CPUE to control for variation in CPUE by day.

When scaled to remove the day effect, across all years the scaled CPUE differed by district ($R^2 = 0.044$ $p < 0.005$) violating the IFD (Figure 3A). Ugashik had the highest scaled CPUE while Nushagak had the lowest scaled CPUE (Ugashik = 1.10, $p = 0.006$; Egegik = 1.02, $p < 0.005$; Naknek-Kvichak = 0.83, $p < 0.005$; Nushagak = 0.80, $p < 0.005$). A Tukey’s HSD post-hoc test determined that all district pairs differed significantly from each other, except for Nushagak and Naknek-Kvichak ($p = 0.792$). When run for each individual year, the effect of district and the rankings of which district had highest scaled CPUE in each year varied (Table A1). In 28% of the years ($n = 11$) the district had no effect on CPUE ($p > 0.05$), indicating that there was an IFD (Figure 4). These years tended to have shorter than average seasons, less than 48 fishing days.

Mobile and nonmobile vessels

The number of mobile and nonmobile vessels varied across years and by district (Figure 5), averaging 378 to 962 mobile vessels each year (mean = 661) and from 529 to 1,173 that were not mobile (mean = 811). For mobile vessels during the core season, across all years the scaled CPUE differed by district ($R^2 = 0.112$, $p < 0.005$) violating the IFD (Figure 3B). Ugashik had the highest scaled CPUE for mobile vessels while Nushagak had the lowest scaled CPUE (Ugashik = 1.31, $p < 0.005$; Egegik = 1.03, $p < 0.005$; Naknek-Kvichak = 0.90, $p < 0.005$; Nushagak =

0.90, $p < 0.005$). A Tukey's HSD post-hoc test determined that all district pairs differed significantly from each other, except Nushagak and Naknek-Kvichak ($p = 0.999$). Like the entire fleet, mobile vessels showed yearly variation in the effect of district and rankings of districts with the highest scaled CPUE when we ran linear models for each individual year (Table A2). In 18% of the years ($n = 7$) the district did not have a significant effect on CPUE of mobile vessels ($p > 0.05$), indicating that there was an IFD (Figure 4).

Captains' relative success

Across individual captains, the average relative success across all the days they fished varied from 0.003 to 3.931 with an average of 0.922. We found the average relative fishing success in a day, district, and year by taking the average of captains' relative success for all the captains fishing in that day, district, and year. This ranged from 0.55 to 1.65 with an average of 1.00.

For all vessels during the core season, across all years the scaled CPUE standardized by relative fishing success differed by district ($R^2 = 0.180$, $p <0.005$) violating the IFD (Figure 6A). Ugashik had the highest scaled CPUE standardized by relative fishing success while Naknek-Kvichak and Nushagak had the lowest (Ugashik= 1.51, $p < 0.005$; Egegik = 1.06, $p < 0.005$; Nushagak = 0.90, $p< 0.005$; Naknek-Kvichak = 0.89, $p < 0.005$). A Tukey's HSD post-hoc test determined that all district pairs were significantly different from each other, except Nushagak and Naknek-Kvichak ($p = 0.996$). There was yearly variation in the effect of district and rankings of districts with the highest scaled CPUE standardized by relative fishing success when we ran linear models for each individual year (Table A3). In 13% of the years ($n = 5$) the district did not have a significant effect on scaled CPUE standardized by relative fishing success ($p > 0.05$), indicating that there was an IFD (Figure 4).

Captains' relative success and mobile vessels

The average relative success for mobile vessels was slightly greater than that of the entire fleet, ranging from 0.59 to 1.74 with an average of 1.05. For mobile vessels during the core season, across all years the scaled CPUE standardized by relative fishing success differed by district ($R^2 = 0.127$ $p < 0.005$), violating the IFD (Figure 6B). Ugashik had the highest scaled CPUE standardized by relative fishing success for mobile vessels and Naknek-Kvichak had the lowest (Ugashik = 1.31, $p < 0.005$; Egegik = 0.96, $p < 0.005$; Nushagak = 0.85, $p < 0.005$; Naknek-Kvichak = 0.85, $p < 0.005$). All district pairs were significantly different from each other, except for Nushagak and Naknek-Kvichak ($p = 0.998$), using a Tukey's HSD test. Mobile vessels showed yearly variation in the effect of district and rankings of districts with the highest scaled CPUE standardized by relative fishing success when we ran linear models for each individual year (Table A4). In 18% of the years ($n = 7$) the district did not have a significant effect on scaled CPUE standardized by relative fishing success of mobile vessels ($p > 0.05$), indicating that there was an IFD in those years (Figure 4).

Discussion

We used the Ideal Free Distribution (IFD) as a null model to investigate CPUE variation in the Bristol Bay drift gillnet fleet among four fishing districts, building on the literature on fisheries and the IFD (Hilborn 1985, Abrahams and Healey 1990, Rijnsdorp et al. 2000, Abernethy et al. 2007). This is an important "test case" because several key assumptions are fully or largely met – especially with regard to the quality of information available to the fleet, and the quality of data on fleet movement. We assumed an IFD in Bristol Bay would correspond to equal CPUE (in pounds of salmon per vessel each day) among the four fishing districts, as observed in the British Columbia salmon trawl fishery (Gillis et al. 1993). The fleet did not fulfill IFD predictions as a whole or in most years, although in some years, and with modifications to account for IFD assumption violations, the fleet did reach an IFD. We found that the Bristol Bay fleet violated two of the IFD assumptions. First, the presence of "nonmobile" vessels that did not move in a given year violated the "move to maximize success" assumption of the IFD. To account for this, we tested only mobile vessels for the presence of an IFD. Second, Bristol Bay captains varied in their relative success, violating the "equal competitor" assumption of the IFD. We standardized CPUE by relative fishing success, to ask if variation in relative success among captains prevented the IFD.

Vessels in Bristol Bay moved from districts with low CPUE into districts with high CPUE, thus decreasing CPUE in that district and equalizing CPUE across districts, consistent with IFD predictions (Figure 2). We highlighted 2 years, 2018 and 2008, that supported total harvests of 29.4 and 27.6 millions of fish respectively. In both years, the number of vessels fishing in a district tracked the district-specific timing of salmon return, with increases in the number of vessels and catch in a district occurring simultaneously. This vessel movement equalized CPUE across districts, both in a year that ultimately did not support IFD predictions across our 4 models, 2018, and in a year that did follow IFD predictions across our 4 models, 2008 (Figure 2). A similar result was seen in the British Columbia salmon purse seine fleet, where vessels moved into areas with high landed value per boat (Hilborn and Ledbetter 1979). Ugashik, despite having high CPUE, saw fewer vessels overall than the other three districts.

Gillis et al. (1993) theorized that vessels would tolerate lower CPUE if there were safety benefits, after they documented vessel aggregation that lead to increased competition and lower CPUE in the Hecate Strait, British Columbia trawl fishery (Gillis et al. 1993). Ugashik is the most isolated of the fishing districts we examined, requiring the longest travel time to access, and lacks much of the infrastructure that the other three districts have such as at-shore processing plants, grocery stores, boat mechanics, and hospitals. Vessels fishing in Ugashik run a higher risk of having to cease fishing when faced with vessel repairs as they wait for parts to be shipped from elsewhere and captains must tolerate increased safety concerns being isolated from emergency services. Naknek-Kvichak and Nushagak are near Bristol Bay's biggest villages, King Salmon and Dillingham, and host many vessels among them. Vessels may be choosing to avoid fishing in Ugashik, despite the high CPUE, because of safety concerns and a desire to be closer to amenities in Naknek-Kvichak and Nushagak in case of emergency.

We used linear models to ask if the CPUE, scaled to the bay-wide CPUE to remove the day effect, varied across districts for all years combined and for each individual year from 1980 to 2019. Day had an effect on CPUE, which was expected in a highly compressed, competitive fishery where there are fewer fish at the beginning and end of the season to be caught (Hilborn 2006), leading us to create the scaled CPUE measure. Across all years, we found that district had a significant effect on scaled CPUE, violating IFD predictions; Ugashik had the highest scaled CPUE across all years and Nushagak had the lowest (Figure 3A). Ugashik also had the most variability in scaled CPUE across years, due in part to its unique management restrictions. During the first half of the fishing season, Ugashik can be closed by management action to prevent fishers from intercepting fish on their way to the Naknek-Kvichak and Egegik districts. Vessels in Ugashik are more likely to experience no-fishing days, which can reduce CPUE across the entire season and make movement to Ugashik more costly for captains. The Nushagak and Naknek-Kvichak districts had lower scaled CPUE, indicating that more vessels fished there than the IFD would predict. Fishery managers, processing companies, and fishers shared that Nushagak and Naknek-Kvichak host many nonmobile fishers who never switched districts and are also closest to amenities. When we ran linear models for the effect of district on scaled CPUE for each year, we found that for 72% of the years the districts were not in an IFD (Figure 4). A review of IFD studies found the pattern of underutilization of productive sites, in our case Egegik and Ugashik, is common throughout many systems and is due to violations of IFD assumptions (Kennedy and Gray 1993). Abernethy et al. (2007) found that artisanal shallow reef fishers violated the "move to maximize success" assumption, as some members of the fleet preferred to maximize leisure time, and fished in less productive areas closer to home, underutilizing better sites. In the British Columbia purse seine fleet, area specialization caused variation in catch rates and led to underutilization of specific areas by less specialized individuals, violating the "equal competitive abilities" assumption (Hilborn 1985). This led us to consider mobility patterns and relative individual fishing success in investigating departures from IFD predictions.

In Bristol Bay, captains make daily choices on where to fish, leading to different movement patterns across the fleet. For example, some are highly mobile, some fish selected districts, and some seem to never move (i.e., nonmobile fishers; Figure 5). Captains that do not move to districts with higher CPUE violate the "move to maximize success" assumption of the IFD, causing underutilization of good sites. Instead of maximizing catch, captains could instead be maximizing other variables like leisure time (Abernethy et al. 2007) and time at home or with their families, or they could be minimizing operating costs and risks as was documented in a highly uncertain pelagic fishery (Van Oostenbrugge et al. 2001). When only considering mobile vessels, the district effect persisted across all years and for 82% of the individual years, contrary to IFD predictions (Figure 4). There was a decrease in the number of years in an IFD relative to the entire fleet, indicating the pattern of underutilization of good sites was even more prevalent in the mobile fleet or nonmobile vessels were choosing to fish in highly productive districts at the beginning of the season. For mobile vessels, Ugashik had significantly higher scaled CPUE than the other 3 districts (Figure 3B), thus vessels were not moving to that district to take advantage of high catches to the same extent as other districts (Figure 2). There was also a decrease in variability in scaled CPUE for Ugashik's mobile vessels in comparison to the entire fleet (Figure 3), meaning mobile vessels that fished in Ugashik timed their move to avoid district closures in the first half of the season.

Even when including nonmobile vessels, the IFD predicts that the system would eventually come to equal CPUE across districts, since nonmobile vessels should not stay in low CPUE districts. This could occur despite differences in behavior in different sections of the fleet, with mobile vessels considering the number of nonmobile vessels in an area, as we saw with the increased number of years in an IFD when we looked at the entire fleet. Gillis et al. (1993) found that the mobile component of the fleet in the Hecate Strait, B.C. trawl fishery produced an IFD, even when considering stationary vessels. Diversity in fleet behavior, with mobile and nonmobile vessels, has been linked to increased adaptive capacity of the fleet as a whole, as seen in the multispecies Swedish Baltic Sea fisheries (Boonstra and Hentati-Sundberg 2016), allowing fishers to respond to changes in run size and timing of specific species. However, mobile vessels have been linked to better adaptive capacity during climate related shocks, as seen with the response to the marine heatwave and the closure of the Dungeness crab fishery in California

(Fisher et al. 2021). Movement choices thus influence the catch in a specific year and also the variation in catches across all years for individual captains.

Variation in the movement choices by captains led us to consider that average relative success could also vary, leading to the violation of "equal competitive abilities" assumption of the IFD. This violation has been documented in many fisheries from small-scale artisanal reef fishers to highly commercialized pelagic vessels (Rijnsdorp et al. 2000, Abernethy et al. 2007). In the British Columbia salmon troll fleet, the top ranked vessels had catch rates 3.6 times that of the lowest ranked vessels (Abrahams and Healey 1990). Hilborn and Ledbetter (1985) linked one third of the variation in catch rates in the B.C. purse seine fleet to skill of the captain, crew, and nets, and one quarter of the variation to area specialization and knowledge of the fishing grounds. In Bristol Bay, variation in catch rate among vessels is common knowledge with processing plants offering bonuses to their top performing "highliner" vessels. This increased success is associated with their movement decisions relative to other vessels (Gatewood 1983), but also varies with captain knowledge and vessel attributes like horsepower (Wang 2018). Although we were not able to investigate the relationship between relative success and vessel characteristics (size, power, speed, etc.) due to confidentiality limits, we were able to calculate average relative success per captain.

Vessels varied in average relative success with top performing vessels catching up to 3.9 times more than the average vessel. To investigate if differences in relative success and resulting violation of the "equal competitive abilities" assumption caused district specific differences in CPUE, we standardized the scaled CPUE by the mean relative fishing success across captains fishing in that district, day, and year. Despite differences in relative success, in 65% of the one-week trips across 6 years the Dutch beam trawl fleet was in an IFD (Rijnsdorp et al. 2000). This was due to captains with more powerful vessels exploiting the best locations, but can also occur when higher skilled captains exploit more areas (Abrahams and Healey 1990). Contrary to other systems and our predictions, there was a significant effect of district on scaled CPUE standardized by relative fishing success across all years, and in 87% of individual years. The ranking of districts across all years was similar to that of the mobile vessels only, with the highest scaled CPUE standardized by relative fishing success in Ugashik, then Egegik, and finally ending with Naknek-Kvichak and Nushagak, which were not significantly different from each other (Figure 6A). This indicates that individuals with high relative fishing success still fished in lower CPUE districts, potentially out of risk aversion and a desire to be closer to amenities and their fishing partners (Gillis et al. 1993). When we ran the linear models on scaled CPUE standardized to relative fishing success for only mobile vessels, we found similar results in significance of the district across all years and the rankings of each district (Figure 6B), but a decrease in the number of years not in an IFD from 87% to 82%. Captains' relative success and mobility could be linked and how these interact and vary among individuals with different years of experience, and from different areas, deserves further exploration.

Overall, the Bristol Bay drift gillnet fleet was an excellent system to test IFD predictions due to the data on individual vessel catch by day and district available across 40 years, the availability of information to captains, and the diversity of the fishing fleet. We found that the IFD was not fulfilled in Bristol Bay and determined that neither the violation of the "move to maximize success" and "equal competitors" assumptions completely accounted for this departure. There was variability in movement and average relative success across captains in the fleet and persistent underutilization of districts with high CPUE consistent with other systems applying IFD predictions (Abrahams 1986, Houston and McNamara 1988, Inman 1990, Kennedy and Gray 1993). The application of this ecological theory led to insights on movement and fleet behavior in an intensely competitive fishery. The high levels of vessel competition in this productive fishery has led to overcapitalization of vessels with increased investment in hold capacity and refrigerated sea water systems (Valderrama and Anderson 2010). Differences in the capacity to invest in their vessels exists across the fleet, with older and out of state captains being more likely to increase their competitive ability (Gho 2020). Decreased ability to invest in a vessel can lead to decreased catches if captains are unable to move to exploit district variability in catch size and timing, making them sensitive to economic shocks like a low return year for a specific district (Anderson et al. 2017). Ultimately, we found that across a fleet, considering variation in movement, high CPUE fishing districts can be underutilized, indicating that unmeasured factors like risk tolerance, captain and crew characteristics, and vessel characteristics could be preventing movement into those areas. By using ecological theories to explore fleet behavior, and by grounding that science in the social, historical, and cultural context of the area (Bene and Tewfik 2001), we can create management rules that better fit the issues faced by the region.

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Figures

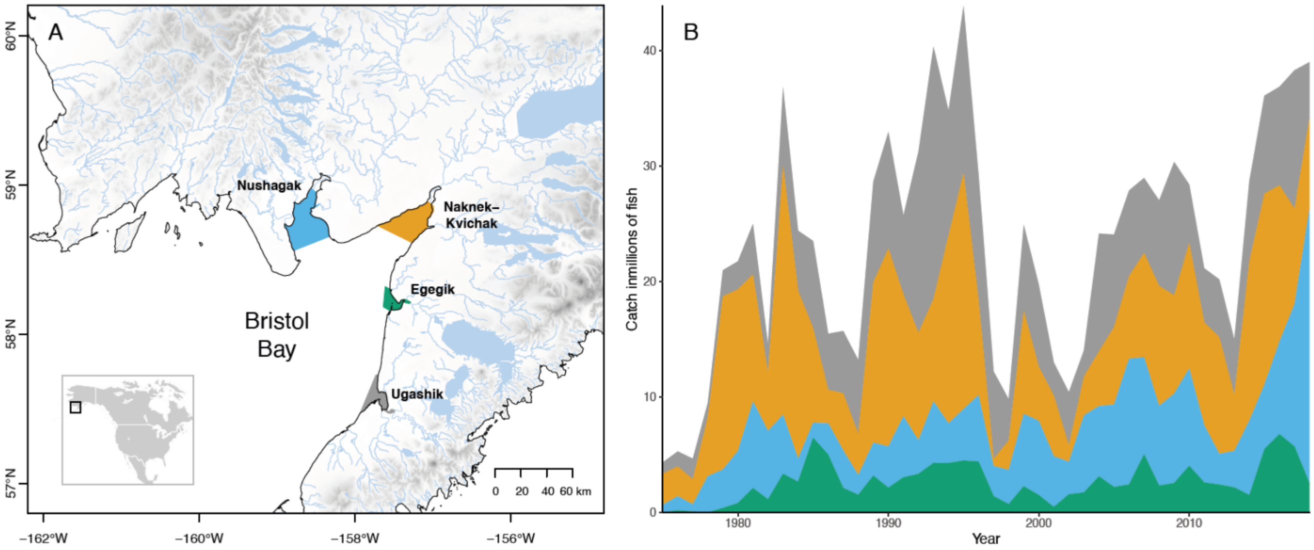
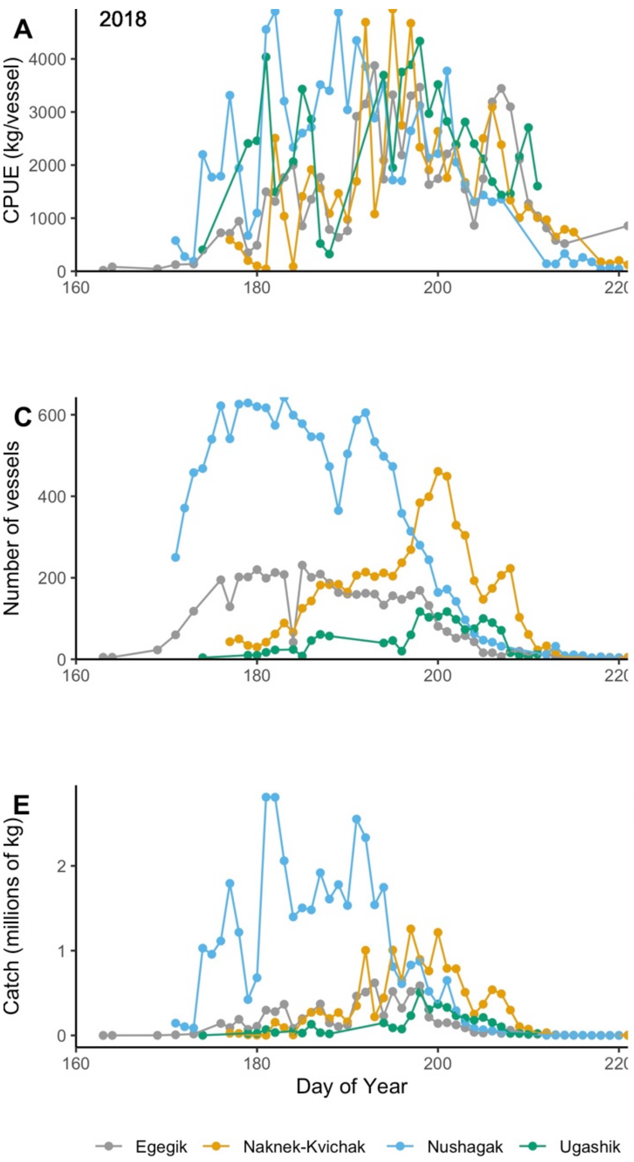


Figure 1: A map of the Bristol Bay fishing districts used in this analysis (A) and the catch in millions of fish from 1975-2019 by district (B). Nushagak is in blue, Naknek-Kvichak in orange, Egegik in gray, and Ugashik in green. The map was modified from Ohlberger et al. 2023. It takes half a day to travel by boat from Ugashik to Nushagak.



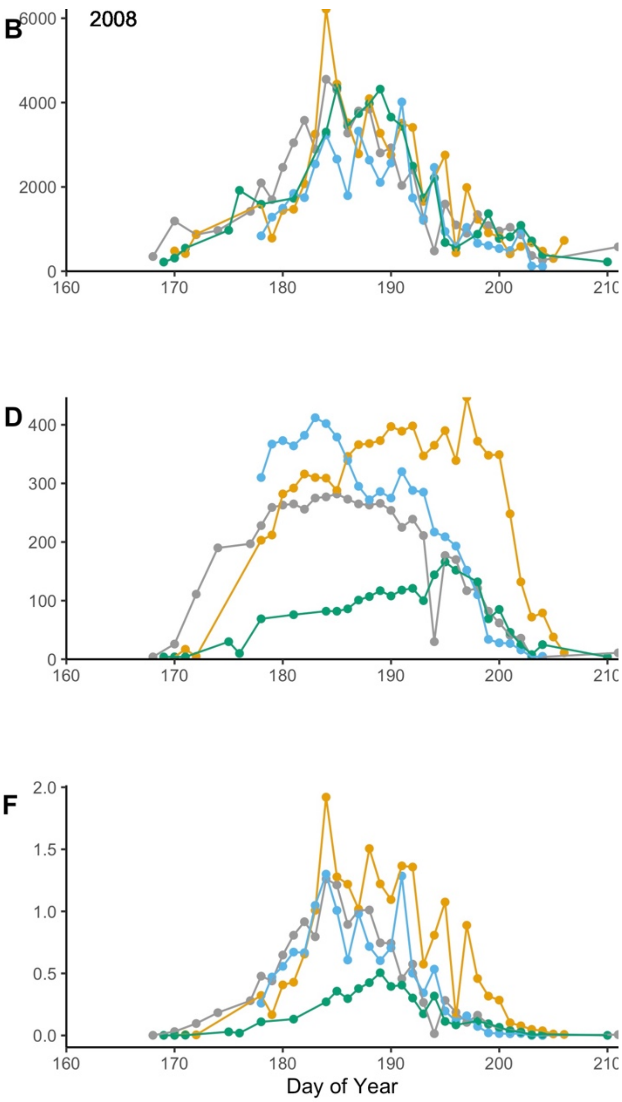


Figure 2: The CPUE in kg/vessel in (A) and (B), the number of vessels in (C) and (D), and the catch in millions of kg of sockeye in (E) and (F) by district across the day of the year in two years, 2018 (left panel) and 2008 (right panel). Egegik is in gray, Naknek-Kvichak in orange, Nushagak in blue, and Ugashik is in green.

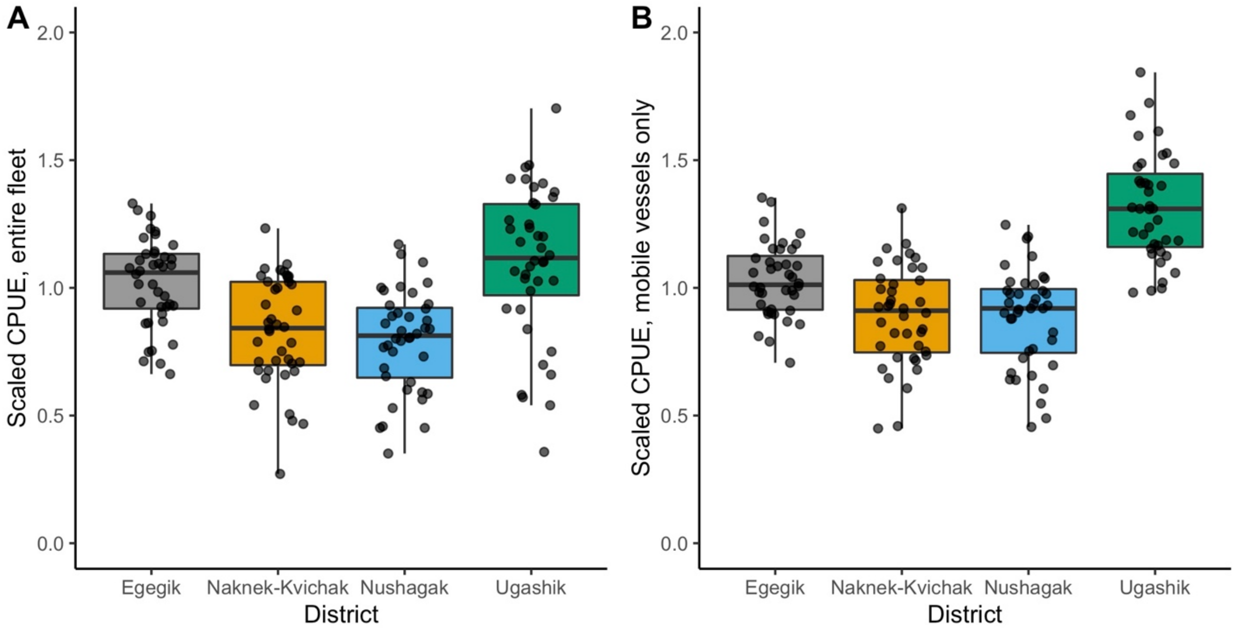


Figure 3: The average scaled CPUE relative to the bay-wide CPUE for each year and district for all vessels (A) and for mobile vessels only (B). The boxplots show the mean as the thick black line and the 25th and 75th percentiles of the data as the upper and lower bounds of the box. A scaled CPUE greater than 1 means that the district was better than the bay-wide average. Egegik is in gray, Naknek-Kvichak in orange, Nushagak in blue, and Ugashik in green.

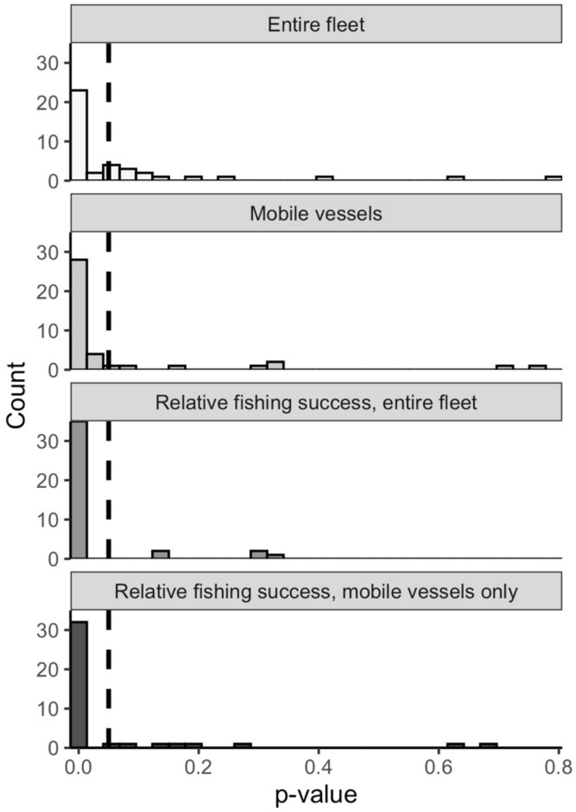


Figure 4: Histogram of the p-values for each year of the linear models looking at the effect of district on scaled CPUE. From top to bottom the models include the district effect on: the scaled CPUE for all vessels, the scaled CPUE for mobile vessels only, the scaled CPUE standardized by relative fishing success for all vessels, and the scaled CPUE standardized relative fishing success for mobile vessels only. The dashed black line represents the p = 0.05 threshold. Values to the left of that line are not in an IFD, while values to the right of the line are in an IFD.

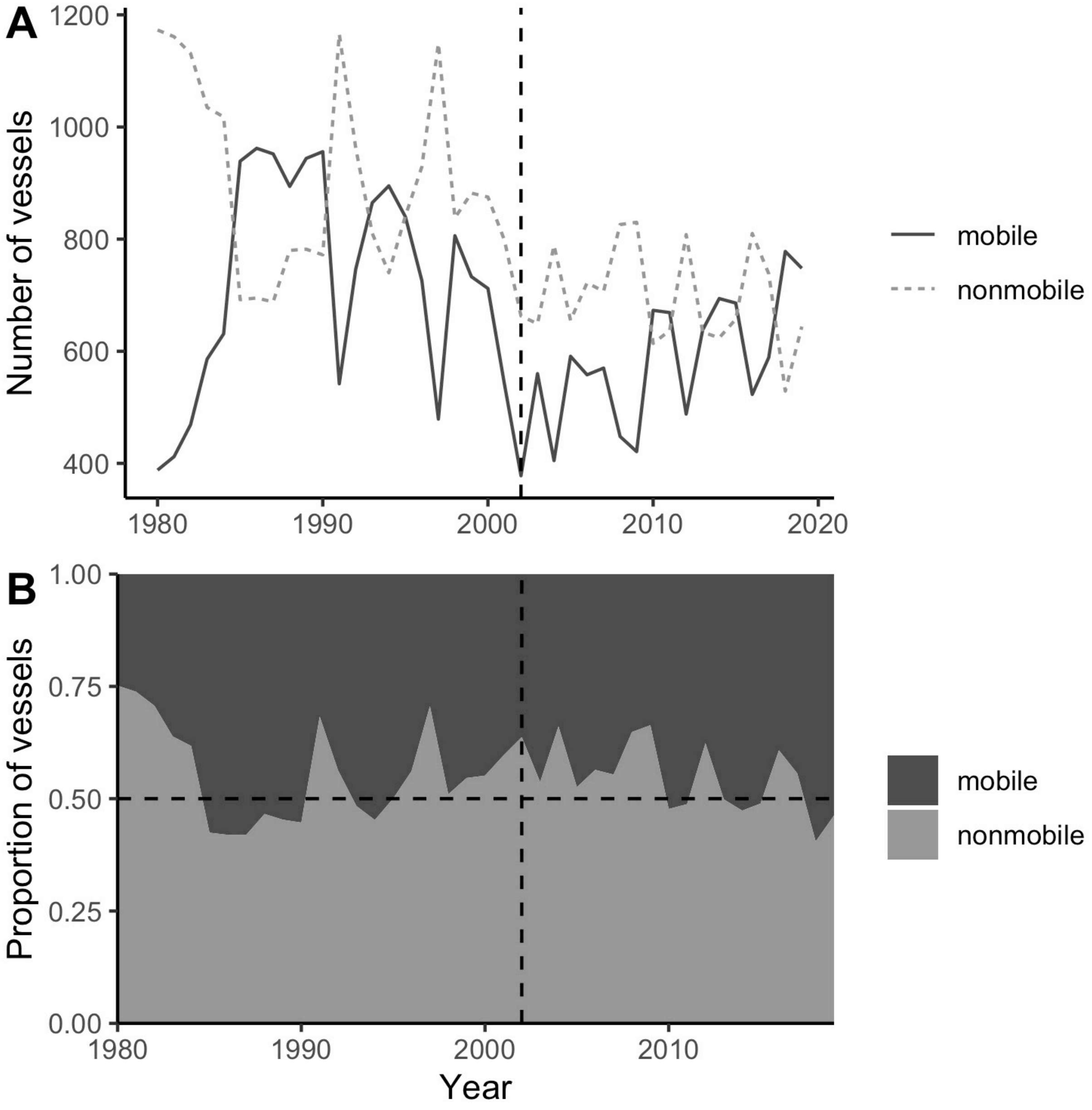


Figure 5: The number (A) and proportion (B) of mobile (dark gray) and nonmobile (light gray) vessels fishing in a season, varies across year. The vertical black dashed lines represent the start of the dual permit program in 2002 where two captains can fish two permits on the same vessel, reducing the number of vessels fishing overall. The horizontal black dashed line in (B) indicates 50% of vessels, demonstrating that pre- and post- dual permit implementation, the proportion of mobile and nonmobile vessels varies similarly.

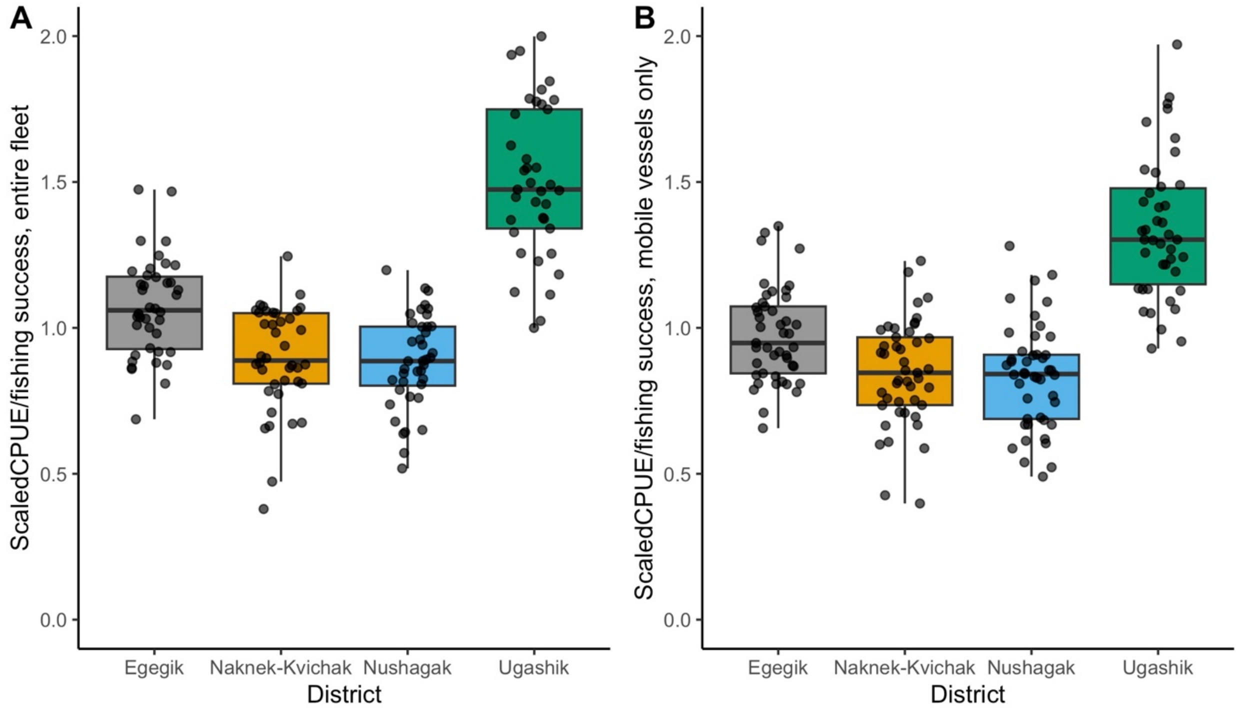


Figure 6: The average scaled CPUE standardized by relative fishing success across years for each district for all vessels (A) and for mobile vessels only (B). The boxplots show the mean as the thick black line and the 25th and 75th percentiles of the data as the upper and lower bounds of the box. Egegik is in gray, Naknek-Kvichak in orange, Nushagak in blue, and Ugashik in green.

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Appendices

Table A1: The linear model results for each year, 1980-2019, for the scaled CPUE model with district as an effect. The coefficient estimates for each district are listed with the p-value that gives the overall effect of district on scaled CPUE that year and the R^2 value.

Year	Egegik	Naknek-Kvichak	Nushagak	Ugashik	p-value	R^2
1980	0.943	0.994	0.902	1.409	0.130	0.110
1981	1.330	0.785	1.005	1.395	<0.001	0.412
1982	0.863	1.000	0.990	1.235	0.102	0.087
1983	1.168	1.013	0.529	1.102	<0.001	0.321
1984	1.095	0.847	0.351	1.128	<0.001	0.231
1985	1.143	0.505	0.451	1.355	<0.001	0.382
1986	1.108	0.720	0.820	1.036	0.172	0.085
1987	1.210	0.715	0.601	0.571	0.025	0.121
1988	0.936	0.480	0.458	1.157	0.036	0.086
1989	1.282	0.709	0.767	1.026	0.031	0.098
1990	0.968	1.040	0.563	0.660	0.004	0.176
1991	0.930	0.935	0.931	1.265	0.059	0.109
1992	1.304	0.659	0.452	0.750	<0.001	0.214
1993	1.078	0.711	0.842	1.201	0.056	0.089
1994	0.898	1.092	0.631	1.180	0.004	0.170
1995	1.083	0.912	0.731	0.915	0.254	0.047
1996	0.860	1.045	0.805	1.106	0.104	0.072
1997	1.231	0.271	0.585	1.101	<0.001	0.226
1998	0.778	0.752	0.654	0.358	0.182	0.064
1999	0.927	0.789	1.100	1.427	0.043	0.105
2000	0.868	0.864	1.001	1.028	0.773	0.016
2001	0.753	1.233	0.792	0.581	0.001	0.198
2002	1.196	0.467	0.685	1.084	0.037	0.123
2003	0.749	0.674	1.170	0.919	0.083	0.084
2004	1.014	0.646	0.981	1.481	0.001	0.201
2005	1.088	1.070	0.831	0.699	0.017	0.121
2006	1.121	0.676	1.020	1.203	0.004	0.131
2007	0.926	1.047	0.775	1.472	<0.001	0.245
2008	1.054	1.049	0.839	0.838	0.059	0.100
2009	1.090	0.877	0.872	1.230	0.003	0.153
2010	0.712	1.024	0.919	1.426	<0.001	0.277

2011	0.662	1.023	0.801	0.988	0.010	0.120
2012	1.135	1.064	0.591	1.332	<0.001	0.405
2013	0.984	0.704	0.860	1.375	0.001	0.203
2014	1.066	1.075	0.750	1.327	0.007	0.166
2015	1.014	0.857	0.804	1.703	<0.001	0.294
2016	1.113	0.830	0.886	1.249	<0.001	0.267
2017	1.133	0.541	0.936	1.052	<0.001	0.203
2018	0.703	0.678	1.132	1.065	<0.001	0.151
2019	1.221	0.838	0.889	0.540	<0.001	0.186

Table A2: The linear model results for each year, 1980-2019, for the scaled CPUE model using only mobile vessels with district as an effect. The coefficient estimates for each district are listed with the p-value that gives the overall effect of district on scaled CPUE that year and the R^2 value.

Year	Egegik	Naknek-Kvichak	Nushagak	Ugashik	p-value	R^2
1980	1.092	0.925	0.826	1.141	0.271	0.077
1981	1.337	0.715	0.989	1.266	<0.001	0.356
1982	0.983	0.945	1.023	1.187	0.138	0.084
1983	1.193	0.995	0.639	1.099	<0.001	0.363
1984	1.353	1.036	0.455	1.154	<0.001	0.372
1985	1.151	0.772	0.547	1.308	<0.001	0.310
1986	1.213	0.727	1.043	1.059	0.100	0.114
1987	1.172	0.929	0.697	1.133	0.088	0.115
1988	1.074	0.751	0.796	2.122	<0.001	0.313
1989	1.175	0.827	0.976	1.419	0.021	0.130
1990	1.042	1.029	0.605	1.125	<0.001	0.364
1991	0.868	0.890	0.904	1.400	<0.001	0.452
1992	1.152	0.683	0.489	1.676	<0.001	0.634
1993	0.989	0.736	0.976	1.724	<0.001	0.398
1994	0.907	1.080	0.656	1.320	<0.001	0.256
1995	1.085	0.902	0.725	1.595	<0.001	0.354
1996	0.857	1.155	0.915	1.310	0.003	0.163
1997	1.086	0.449	0.879	1.844	<0.001	0.419
1998	0.911	1.014	0.902	1.410	0.296	0.075
1999	0.901	0.774	1.247	1.613	<0.001	0.227
2000	0.896	0.937	1.201	1.474	0.011	0.163
2001	0.790	1.312	0.941	1.218	<0.001	0.291
2002	0.991	0.459	0.641	1.528	<0.001	0.382
2003	1.100	0.823	1.193	1.021	0.033	0.130
2004	0.897	0.646	0.988	1.376	<0.001	0.275
2005	0.979	1.108	1.018	0.982	0.762	0.016
2006	1.052	0.679	1.090	1.209	<0.001	0.197
2007	0.916	1.103	0.761	1.521	<0.001	0.275
2008	1.005	0.986	0.937	0.989	0.872	0.010
2009	1.001	0.864	0.920	1.310	<0.001	0.251
2010	0.811	1.079	1.036	1.403	<0.001	0.226

2011	0.935	1.173	0.931	0.998	0.047	0.096
2012	1.116	1.118	0.666	1.237	<0.001	0.281
2013	0.973	0.951	0.880	1.315	0.021	0.142
2014	1.018	1.135	0.752	1.487	<0.001	0.282
2015	1.007	0.838	0.976	1.488	<0.001	0.215
2016	1.059	0.821	1.014	1.166	0.001	0.172
2017	1.259	0.607	0.956	1.171	<0.001	0.351
2018	0.707	0.724	1.124	1.185	<0.001	0.238
2019	1.153	0.919	0.920	1.410	0.001	0.174

Table A3: The linear model results for each year, 1980-2019, for the scaled CPUE model standardized by relative fishing success with district as an effect. The coefficient estimates for each district are listed with the p-value that gives the overall effect of district on scaled CPUE divided by relative fishing success that year and the R^2 value.

Year	Egegik	Naknek-Kvichak	Nushagak	Ugashik	p-value	R^2
1980	1.169	1.023	0.995	1.591	0.073	0.134
1981	1.442	0.818	1.089	1.475	<0.001	0.431
1982	1.123	0.977	1.009	1.488	0.002	0.202
1983	1.205	1.048	0.757	1.318	<0.001	0.319
1984	1.423	1.098	0.515	1.353	<0.001	0.379
1985	1.142	0.844	0.643	1.348	<0.001	0.279
1986	1.233	0.857	1.085	1.115	0.287	0.071
1987	1.234	0.991	0.779	1.231	0.063	0.127
1988	1.160	0.800	0.932	2.490	0.001	0.232
1989	1.320	0.842	1.052	1.703	0.002	0.185
1990	1.068	1.052	0.688	1.277	<0.001	0.293
1991	0.911	0.937	1.018	1.590	<0.001	0.524
1992	1.228	0.803	0.574	2.244	<0.001	0.573
1993	1.033	0.778	1.073	2.040	<0.001	0.483
1994	0.869	1.057	0.747	1.470	<0.001	0.287
1995	1.105	0.893	0.824	1.727	<0.001	0.363
1996	0.854	1.078	0.906	1.321	0.001	0.190
1997	1.131	0.393	0.829	2.006	<0.001	0.507
1998	0.928	1.012	0.856	1.810	0.012	0.205
1999	0.891	0.766	1.187	1.929	<0.001	0.268
2000	0.870	0.887	1.135	1.726	<0.001	0.276
2001	0.803	1.242	0.942	1.471	<0.001	0.294
2002	1.156	0.491	0.669	2.251	<0.001	0.509
2003	1.130	0.678	1.130	1.531	0.003	0.204
2004	0.956	0.662	1.012	1.829	<0.001	0.408
2005	1.039	1.068	0.848	1.004	0.306	0.048
2006	1.040	0.672	0.996	1.557	<0.001	0.280
2007	0.911	1.054	0.793	1.570	<0.001	0.350
2008	1.024	1.028	0.868	1.023	0.198	0.067
2009	1.044	0.876	0.892	1.471	<0.001	0.421
2010	0.857	1.009	0.913	1.531	<0.001	0.300

2011	0.912	1.080	0.821	1.087	0.006	0.146
2012	1.124	1.017	0.651	1.364	<0.001	0.355
2013	1.022	0.890	0.884	1.445	<0.001	0.258
2014	1.047	1.047	0.774	1.675	<0.001	0.340
2015	0.983	0.834	0.849	1.667	<0.001	0.271
2016	1.040	0.808	0.893	1.224	<0.001	0.244
2017	1.191	0.640	0.946	1.195	<0.001	0.301
2018	0.686	0.712	1.059	1.325	<0.001	0.245
2019	1.163	0.851	0.899	1.646	<0.001	0.285

Table A4: The linear model results for each year, 1980-2019, for the scaled CPUE model standardized by relative fishing success using only mobile vessels with district as an effect. The coefficient estimates for each district are listed with the p-value that gives the overall effect of district on scaled CPUE divided by the relative fishing success that year and the R^2 value.

Year	**Egegik**	**Naknek-Kvichak**	**Nushagak**	**Ugashik**	**p-value**	**R^2**
1980	1.134	0.879	0.866	1.316	0.081	0.130
1981	1.300	0.672	0.972	1.241	<0.001	0.350
1982	0.928	0.865	0.962	1.278	0.002	0.215
1983	1.105	0.947	0.664	1.106	<0.001	0.321
1984	1.287	0.983	0.486	1.149	<0.001	0.333
1985	1.043	0.767	0.592	1.248	<0.001	0.268
1986	1.228	0.819	1.152	1.015	0.192	0.088
1987	1.087	0.910	0.733	1.111	0.109	0.107
1988	1.000	0.750	0.851	2.129	0.001	0.241
1989	1.128	0.809	1.121	1.492	0.034	0.117
1990	0.984	0.974	0.652	1.175	<0.001	0.285
1991	0.787	0.843	0.910	1.313	<0.001	0.420
1992	1.051	0.691	0.528	1.746	<0.001	0.530
1993	0.944	0.736	1.024	1.772	<0.001	0.398
1994	0.823	1.022	0.709	1.344	<0.001	0.240
1995	0.985	0.818	0.764	1.575	<0.001	0.333
1996	0.788	1.090	0.895	1.217	0.005	0.155
1997	1.033	0.412	0.855	1.836	<0.001	0.391
1998	0.837	0.942	0.822	1.374	0.179	0.098
1999	0.800	0.702	1.253	1.704	<0.001	0.259
2000	0.813	0.884	1.120	1.459	0.003	0.197
2001	0.711	1.240	0.875	1.307	<0.001	0.325
2002	0.888	0.437	0.583	1.447	<0.001	0.387
2003	1.026	0.717	1.083	1.007	0.009	0.170
2004	0.798	0.602	0.916	1.352	<0.001	0.311
2005	0.901	1.027	0.912	0.958	0.735	0.017
2006	0.915	0.614	0.929	1.298	<0.001	0.258
2007	0.840	0.990	0.698	1.410	<0.001	0.286
2008	0.920	0.921	0.849	0.936	0.706	0.021
2009	0.900	0.781	0.840	1.286	<0.001	0.312
2010	0.790	0.952	0.904	1.425	<0.001	0.278

2011	0.858	1.016	0.838	0.982	0.112	0.073
2012	1.019	0.954	0.618	1.229	<0.001	0.307
2013	0.883	0.789	0.812	1.215	0.005	0.183
2014	0.930	0.984	0.702	1.610	<0.001	0.307
2015	0.871	0.768	0.867	1.436	<0.001	0.258
2016	0.933	0.729	0.873	1.111	<0.001	0.245
2017	1.075	0.583	0.882	1.093	<0.001	0.292
2018	0.646	0.673	0.987	1.155	<0.001	0.241
2019	1.087	0.840	0.863	1.470	<0.001	0.242

Chapter 3: Relative importance of forecasted and realized abundance of salmon and attributes of the captain on vessel movement in the Bristol Bay sockeye salmon fishery

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Abstract

Fishing vessel captains consider many factors when choosing where to fish and whether to move and fish elsewhere, and these decisions affect their catch rate, safety, and other considerations. Catch rates can have cascading social effects on fishery participation, employment, and food security, and affect the ecosystems, thus understanding captain decision processes is important. We investigated such factors using 26 years of data on the mobility of the Bristol Bay Pacific salmon drift gillnet fleet, testing the relative importance of pre-season forecasts and in-season data on salmon abundance available to captains, vessel attributes like horsepower, and captain-specific characteristics like residency and experience. The results indicated that vessels tended to start the season in districts predicted to have more salmon and those where salmon were more abundant in the previous year. During the brief fishing season, vessels tended to move more in years when salmon were more abundant, and with increases in the average horsepower of the fleet, but captain-specific characteristics explained the probability of moving the most. Mobility tended to increase with the captain's years of experience, possession of a dual permit, and relative fishing success. Finally, captains from local (Bristol Bay) communities moved less than nonlocal Alaskans and those from other states; the latter two groups did not differ significantly in tendency to move. These patterns of fishing site choice and mobility in an information-rich,

economically valuable fishery can be compared to the patterns to other fisheries and reveals the use of pre-season and in-season abundance information by individual captains.

Introduction

Given the increasing human demand for fish as food, and the anthropogenic changes that affect aquatic resources, improving fisheries management is essential for maintaining healthy human communities and natural ecosystems. Fisheries management depends on knowledge of vessel distribution and movement, and reflects in large part the choices of the vessel owner or captain (Gatewood 1983, Bucaram et al. 2013). Movement can be projected into the future in response to changing management, as occurred with the closure of the United Kingdom's Exclusive Economic Zone to French fleets in the aftermath of Brexit (Dépalle et al. 2020), and in response to changing climatic conditions as seen with California's Dungeness crab fishery's response to a marine heatwave (Fisher et al. 2021). Fleet movement also affects stock assessments that rely on catch per unit effort (CPUE) data from fisheries, as fleet distribution and movement can bias stock projections (Saul et al. 2020). Overall, research on fleet movement has gained more attention in recent years due to its impacts on the success of management and its connection with the ecological, economic, social, and cultural success of a fishery (Wilen et al. 2002, Boonstra and Hentati-Sundberg 2016, Wijermans et al. 2020).

The movement decisions of a fleet are generally expected to track the likely success of fishing in particular areas based on experience or assessment of prospects. Captains move to maximize their catch by responding to variation in local fish abundance as seen in the French demersal trawl and Australia's northern prawn fisheries (Venables et al. 2009, Marchal et al. 2013). Many aspects of a fishery, including the location, density, and abundance of fished populations, can affect choices of where to fish (Letschert et al. 2023). Captains also respond to the distribution and abundance of competing vessels, as each captain attempts to maximize catch while minimizing costs (Abrahams and Healey 1990, Richard et al. 2018). However, responses to expected catch, even with shared, public information, may vary across individuals, time, and space (Girardin et al. 2017). Other factors like weather and fuel price affect mobility choices, as captains generally reduce travel and remain close to home ports when weather is bad and fuel is expensive (Venables et al. 2009, Letschert et al. 2023). Additionally, vessel attributes like horsepower, hold capacity, and displacement, and captain attributes like experience and fishing success also affect movement choices (Gho 2020). Experience can increase knowledge and specialization in the fishery (Gatewood 1983), but captains may also have different motivations (Abernethy et al. 2007). Captains or crew with additional sources of income may feel less pressure to move to track fish (Sethi et al. 2014, Richerson and Holland 2017). However, datasets that integrate information on captain, vessel, and fishery characteristics are rare, so previous research on movement focused on these factors in isolation (Cutler et al. 2022). Here we fill that gap by investigating movement patterns in a unique dataset that contains data on the CPUE of vessels across time, the biological characteristics of the fishery, and captain characteristics.

The quantity and quality of available data make Bristol Bay ideal for studying fleet movement due to. The commercial drift gillnet fleet catches Pacific salmon (genus *Oncorhynchus*) and especially sockeye salmon, *O. nerka*, in four discrete fishing districts as salmon migrate to their natal rivers to reproduce (Figure 1; Hilborn 2006). Salmon returns vary considerably in magnitude and to a lesser extent in timing across years and districts. The peak fishery operates over a compressed period of less than one month (Burgner 1980, Quinn et al. 2007), thus movement decisions greatly affect fishing success. The fishery is the main income source for the Bristol Bay community, and many local captains have fished there for many years. The fleet also includes nonlocal Alaskan captains and ones that are not Alaska residents, some of whom have participated in the fishery for many years (Gho et al. 2012, Stern et al. 2022). All these captains have access to a wealth of information on which to make movement decisions. Before the season begins, two pre-season forecasts on the magnitude of the salmon return by district are released, one from the Alaska Department of Fish and Game (ADFG) and one from the University of Washington (Cunningham et al. 2019). Just prior to the first fishing opening, and during the season, information on the timing and abundance of the salmon return by district is available through a test fishery operating about 7-days away (based on salmon migration speeds), and the daily catch, escapement, and number of vessels in each district is released (Sands 2009, Dann et al. 2013). Thus, Bristol Bay drift gillnet captains have access to an exceptional and perhaps unprecedented amount of information to make movement decisions affecting their profit and that of their crew.

We used 26 years of information on the movement of the drift gillnet fleet to ask what explains fleet movement in the lucrative Bristol Bay fishery. First, we related the district where each vessel and its captain fished at the beginning of the season to the pre-season forecast and the previous year's catch by district to ask if those sources of information affect where captains begin fishing. Next, we calculated a mobility score for each captain and related this score to captain characteristics like residency, years of experience, and past fishing success relative to other captains. We expected mobility to increase with captain experience and relative fishing success, as more experienced captains would be more confident moving and have higher catches, and to be higher in nonresident and nonlocal fishers who do not have family in the region as compared to Bristol Bay locals. Finally, we investigated how the probability of moving in a year changed over time, and what factors most affected mobility in the whole fleet. Ultimately, we illuminate fleet movement patterns and how they change in different scenarios in a widely studied fishery to help managers create better rules to improve the effectiveness of fisheries management worldwide.

Methods

Study system

In southwestern Alaska, Bristol Bay supports the world's largest returns of sockeye salmon (*O. nerka*) and other salmon species in a sustainable fishery (Sands 2006). The area has four major fishing districts: Nushagak, Naknek-Kvichak, Egegik, and Ugashik; a fifth district, Togiak, is smaller, has unique management restrictions on movement, and is more distant from the other districts and so was excluded from this study (Figure 1). Sockeye salmon are caught in a compressed fishery from mid-June to mid-July during their return migration to their natal rivers (Salomone et al. 2017). ADFG biologists manage the daily openings and closures of the fishery through online and radio orders to achieve sustainable yield through escapement management (Hilborn 2006). Escapement goals are set for each stock or river system before the fishing season and are known to all members of the fishing community (Erickson et al. 2015, Cunningham et al. 2019). The region has valuable recreational and culturally significant subsistence fisheries (Halas and Neufeld 2018, Panikkar and Tollefson 2018), but the great majority of sockeye salmon are taken in two types of commercial fisheries. The stationary shore-based set-net fishers take ca. 10-26% of the catch depending on the district, and the focus of this study is on the mobile drift gillnet fleet that takes ca. 74-90% of the catch depending on the district (Tiernan et al. 2022). We classified the mobile drift gillnet fleet into two groups based on conversations with fishery managers and participants (*pers comm*: Tim Sands and Warner Lew): (1) mobile vessels that switch districts at least once a year, and (2) nonmobile vessels that fish only one district annually.

To control the intense fishing competition resulting from the large harvests of salmon and the compressed timing of their return, the management of the drift gillnet fleet in Bristol Bay has created specific rules that are unique to the area. The limited entry program was implemented in 1975, fixing the number of drift gillnet permits at ~1800 total, thus anyone seeking to enter the fishery must acquire a permit from an existing permit holder (Schelle et al. 2004, Hilborn 2006). At the beginning of the season, captains must register to fish in a specific district, and they must notify the ADFG district offices of any moves throughout the season. Since 2003 captains that switch districts in the middle of the season have to refrain from fishing for 48-h (Sands 2009). In 2004, the Alaska Board of Fisheries passed regulations allowing two permit holders to fish from a single vessel with additional gear, the “dual permit” rule (Gho 2020).

Vessel attributes like engine horsepower, hold capacity, the presence of refrigerated seawater systems, and vessel displacement affect their ability to move and catch fish (Gho 2020). Most of these attributes have increased over time with technological developments but length does not vary much because a 1951 regulation limited motorized vessels to 32 feet (9.75 m) (Gho 2020). Additionally, drift gillnet mesh size and net length has been fixed over each season, although the mesh size used has changed in response to changing body size in harvested salmon (Oke et al. 2020, Ohlberger et al. 2023).

The permit holders in the Bristol Bay drift gillnet fleet represent many communities including Alaskans who live in the Bristol Bay region, those who live elsewhere in the state, and those living outside the state. For analysis of permit allocation among fishers by the state of Alaska’s Commercial Fisheries Entry Commission (CFEC), the fishers are categorized as

Alaskan or nonresident, rural or urban, and local or nonlocal (Gho et al. 2012, Stern et al. 2022). Commonly, these are distilled into three main categories and will be so for the purpose of this project: local Alaskan (from the Bristol Bay borough), nonlocal Alaskan (from outside Bristol Bay), and nonresident or out of state (Apgar-Kurtz 2015, Stern 2020).

Data Sources

The CFEC fish ticket database provided information on the movement of individual vessels and their associated landings from 1994-2019. When captains deliver their landings, they report the pounds of catch, species, date, fishing district, and their identity, permit, and vessel. Because CFEC fish ticket data are confidential, we randomized captain ID to create a non-traceable identifier for each captain. Captain ID remained constant even if they switched vessels over their fishing career. Relevant information was extracted from the CFEC fish ticket database (year, date landed, district, captain ID, whole pounds of sockeye salmon landed, processor, residency of captain, dual permit status), and missing values were coded as NA. In addition to ensuring that the data were not traceable to individual captains, the CFEC can only report data with groupings (i.e., on a given day in each district) greater than 4 individual vessels, thus groupings with < 4 were excluded. After filtering to ensure confidentiality, our main dataset contained 968,621 records of landings by year, date, ID, district, and processor ID. The dataset containing additional information on captain residency and dual permit status contained 895,026 records of landings.

Confidentiality restrictions precluded linking information on vessel attributes and captain to their catches. However, we used publicly available records on permit holder vessel registration from the CFEC to find the average horsepower of active Bristol Bay permit holder’s vessels each year from 1994 to 2019, and ADFG data on catch and escapement by year, day, and district. In addition to these types of in-season information, several months in advance of the fishing season, two different forecasts of the number of fish expected to return to each district are released based on data collected in previous years, one from ADFG and one from the University of Washington Alaska Salmon Program (ASP), and captains were predicted to use the forecasts to choose where to fish at the start of that season.

Movement Measures

We defined four different vessel movement metrics for our analyses. First, because vessels must register to a specific district before fishing begins each season and cease fishing for 48-h if they leave that district, we were interested in where vessels choose to fish first. We determined the first district where each captain landed fish in each year and then summarized, for the entire fleet, the proportion of vessels that first fished in each district by year.

Second, to investigate vessel mobility variation across years (Figure 4A), we determined if a captain was mobile or nonmobile in each year by looking at the number of districts fished. Captains who fished in two or more districts were considered mobile that year whereas those only fishing in one district were considered nonmobile. Third, we investigated each captain's movement over all the years fished (Figure 4B) by calculating the percent, *P*, of each captain's, *i*, total catch, *C*, across all the days, *d*, and years, *y*, they fished that came from each district, *f* (Equation 1).

(Equation 1) $$P_{i,f}=\frac{\Sigma_{d,y} C_{i,f,d,y}}{\Sigma_{f,d,y} C_{i,f,d,y}}$$

We used a threshold value of 95% of the total catch coming from a single district to categorize vessels into mobile (< 95%) and stationary (≥ 95%) across all years they fished (Figure 4B).

The fourth movement metric used the information on percentage of total catch by district, $P_{i,f}$, to determine a mobility score for the districts a captain fished. We found the maximum of a captain's percent of catch coming from one district, $P_{i,f}$, and subtracted this by 1 (Equation 2).

(Equation 2) $M_i = 1\text{-}\max(P_{i,f})$

This mobility score, M_i, varied between 0 and 0.71—a score of 0 was associated with captains that caught 100% of their catch in one district and a high score was associated with captains that distributed their catch evenly across districts.

In addition to our four metrics of mobility, we calculated two captain-specific measures: 1) captain experience (the number of years each captain fished), and 2) a relative fishing success score for each captain using the methods detailed in McElroy et al. 2023 (Chapter 2). For each day a captain fished, we calculated their fishing success relative to other captains fishing that day and district, averaging across all days a captain fished to find their overall relative fishing success.

Analyses

We conducted fleet-wide and captain-specific analyses on movement in the Bristol Bay drift gillnet fleet. Our fleet-wide analyses used our main CFEC dataset, whereas the individual-specific analyses used the dataset with fewer records but two additional variables, captain residency and dual permit status.

Fleet-wide movement

The first choice a captain must make is where to first at the beginning of the season. We hypothesized that captains would use the pre-season information available to them to make this important choice, fishing in districts with the highest forecasted salmon returns. For each district, we related the proportion of vessels first fishing in a district to the proportion of the pre-season forecast coming to that district using a generalized linear model. Additionally, we ran a separate linear model that related the proportion of vessels first fishing a district to the proportion of the previous years' catch that came from that district.

Individual vessel movement

We calculated each captain's mobility score (Equation 2) across all the years they fished. We ran an ANOVA to test for the effect of residency status and used generalized linear models to test separately for an effect of years of experience, relative fishing success, and years fishing a dual permit on captains' mobility scores. We expected mobility to increase with the experience and relative fishing success of a captain, and to be lower in local captains who may want to remain close to home. Then we performed backwards stepwise regression on residency, years of experience, relative fishing success, and the number of years a captain fished a dual permit to determine the model with the most support via AIC_c that predicted the mobility score of a captain (Table 1).

Yearly variation in individual vessel movement

We also determined each captain's mobility each year; captains who fished in more than one district, were considered "mobile" and those that only fished in one district were considered "nonmobile." To investigate what controlled captains' movements in a year, we ran a paneled logit model on the binary movement data, with 0 representing "nonmobile" and 1 representing "mobile." This allowed us to investigate how captain's characteristics influence their probability of movement across years, to see if movement changes as captains become more experienced, successful, and as they change in residency or dual permit status. We also added parameters for the return in a year and forecast in a year, information available to captains, and a term for the average horsepower of vessels fishing in a year, to capture variation in efficiency of vessels increasing over time. We standardized each numeric variable (categorical variables: residency and dual permit status) to allow for direct comparison of the magnitude of each variable's impact on probability of movement.

To assess the predictive ability of the model, we randomly split our data into a model training set (70% of observations) and model testing set (30% of observations). We fit the model above to the training dataset and then we assessed model fit using McFadden's R^2 using the *pscl* package in R, the misclassification rate of the model, and the AUC (area under the curve) value.

Results

Fleet-wide movement

Evidence indicated that captains used pre-season information to decide where to first fish, based on the positive relationship between the proportion of vessels starting in a district and its forecasted salmon return; the Nushagak district had the strongest relationship (Figure 2;

Nushagak: $p < 0.001$, $R^2 = 0.391$; Naknek-Kvichak: $p = 0.002$, $R^2 = 0.328$; Egegik: $p = 0.010$, $R^2 = 0.235$; Ugashik: $p = 0.049$, $R^2 = 0.146$). We also found a significant positive relationship between the proportion of the previous year's catch from each district and the proportion of vessels starting there in the next year (Figure 3; Nushagak: $p = 0.001$, $R^2 = 0.355$; Naknek-Kvichak: $p = 0.003$, $R^2 = 0.308$; Egegik: $p = 0.043$, $R^2 = 0.154$; Ugashik: $p = 0.011$, $R^2 = 0.234$).

These two analyses were conducted separately, instead of in a combined multivariate linear model, due to the positive correlation between the proportion of the previous year's catch by district and the proportion of the forecasted return in a year (Pearson's correlation test: high for Nushagak $r(25) = 0.65$, $p <0.001$, moderate for Egegik $r(25) = 0.49$, $p = 0.010$ and Naknek-Kvichak $r(25) = 0.33$, $p =0.092$, and low for Ugashik $r(25) = 0.16$, $p = 0.423$; see Appendix A1-4).

Individual vessel movement

The mobility score varied among captains from a low of 0.00 (i.e., captains catching 100% of their catch in one district), to a high of 0.71 (mean = 0.19, median = 0.11). Mobility scores varied with the captain's residency status (ANOVA $F= 122.2$, $p < 0.001$), and scores for each residency status differed significantly from the others (Figure 5). Local captains were least mobile, those from outside Alaska were intermediate, and nonlocal Alaskan captains were the most mobile. Overall, there are more nonresident and nonlocal captains as compared to local captains.

More mobile captains tended to be more experienced ($R^2 = 0.042$, $p < 0.001$) and successful ($R^2 = 0.057$, $p < 0.001$). In addition, captains increased in mobility with the number of years they fished dual permits (Figure 6; $F = 29.72$, $p < 0.001$). We ran backwards stepwise regression with the four variables above (dual permit years, years of experience, residence, relative fishing success) as factors predicting a captain's mobility score and found that the most supported model contained all variables (Table 1). The next most supported model did not receive adequate support ($\Delta AIC_c = 48.00$).

Yearly variation in individual vessel movement

The proportion of mobile vessels (i.e., moved at least once in the season) varied from 29% in 1997 to 60% in 2018 (mean = 46%, Figure 4A), but was similar before and after the dual permit rule was implemented in 2003 (before, 1993-2002, mean = 45%; after 2003-2012, mean = 43%). The probability of a captain being mobile in a year increased significantly with relative fishing success, total salmon return, and if the captain was a nonlocal or nonresident (Table 2). The probability of a captain being mobile in a year decreased significantly with years of experience, total forecast that year, and if the captain was a local (Table 2). Local captains had a 19% probability of moving in a year, while nonlocals had a 51% and nonresident had a 48% probability of moving in a year (Table 2). The probability of a captain moving in a year was weakly associated with vessel horsepower increase ($p = 0.059$) and decreased if dual permits were being used ($p = 0.135$, Table 2).

Our analysis of mobility score of captains across all years they fished revealed the opposite effect of years of experience on mobility than the logit model. The proportion of captains that were mobile in a year did not differ for nonlocal and nonresident captains across different years of experience, but there were far more nonmobile local captains across all years of experience (Figure 7). This provides evidence that residency had a far larger effect on the probability of being mobile in a year than years of experience did, explaining the opposite relationships we observed in our two analyses. We trained our model on 70% of our observations and tested its predictive ability on the remaining 30%. The model received moderate support (McFadden's $R^2 = 0.085$), a total misclassification error rate of 35.5% and an AUC value of 0.70.

Discussion

We applied 26 years of information on a well-studied and highly profitable drift gillnet fishery in Bristol Bay to investigate a suite of factors hypothesized to affect variation in movement among captains and years. We combined data on individual captain characteristics (experience, relative success, dual permit status, and residency) with data on average vessel attributes (horsepower) and fishery characteristics (salmon return, previous year's catch, forecasted catch) to illuminate movement among 4 discrete fishing districts (Figure 1). We inferred that captains used available pre-season information on forecasted return by district and the previous year's catch by district to choose their first fishing location. More experienced and successful captains, and those with dual permits, were more mobile, and local captains were less so. Mobility also increased with the total salmon return that year, the average horsepower in a year, and the captain's relative success. Taken together, these results provide novel insights into movement patterns in a fishery, informing future management of Bristol Bay with applications to fisheries worldwide.

Fleet movement patterns vary greatly in many fisheries, as captains respond to many different factors (Gatewood 1983, Letschert et al. 2023). In Bristol Bay, some captains specialized in one district, catching their entire catch in all years there, whereas others fished in two or more districts (Figure 4B). This pattern of area specialization has been linked to specialized knowledge of fishing grounds in British Columbia's salmon purse seine fleet (Hilborn and Ledbetter 1985), and tradition in ITQ-managed New Zealand fisheries, as many captains tended to fish the same area in consecutive years (Marchal et al. 2009). This variation in fleet movement, linked to variability in catch, was also seen in Santa Rosalía's small-scale mixed catch fishery in the Gulf of California (Frawley et al. 2021); vessels that moved and travelled farther away from their home port had higher catches. Because movement can affect catch, understanding movement patterns can shed light on the variation in adaptive capacity across a fleet. In general, more diverse movement patterns increase a fishery's ability to respond to shocks such as low returns, or bad weather conditions (Boonstra and Hentati-Sundberg 2016).

In Bristol Bay, as in many fisheries, captains must register to begin fishing in a specific area prior to the start of the season. Unlike other fisheries, they must cease from fishing for 48-h if they move during the season, thus incurring a high cost in a compressed fishery. We found that the proportion of vessels first fishing in a district each year increased with both the proportion of the forecasted catch returning to that district and the proportion of the previous year's total catch from that same district (Figures 2 and 3). Bristol Bay captains have a unique amount of high-quality information available to them, including two pre-season forecasts, and their use of that information implies that other fisheries might also benefit from improved information. In the US West Coast groundfish trawl fishery, for example, captains avoided areas with no data on recent fishing activity, indicating that spatial forecasts could be beneficial to movement decisions (Kuriyama et al. 2019). Across other fisheries there is low temporal variation in the location and effort choices of captains and high correlation between catch composition and this behavior between time periods (Frawley et al. 2021). This could be due to lack of information, and a tendency to rely on past behavior when fish stock trends are unknown. Additionally, for captains to gather information, they or their fishing partners must fish multiple locations, incurring high costs (Van Oostenbrugge et al. 2001), so instead they may fish close to home ports and accept lower catches. Information on the previous year's catch is also used to guide movements and entry and exit decisions (Mardle et al. 2006). Bristol Bay data, reported here, demonstrate the use of different sources of information in making movement decisions.

The mobility of the Bristol Bay gillnet fleet varied (Figure 4A); in years when salmon were more abundant, captains were more likely to switch districts during the season (Table 2). Movement is costly, and captains may only be willing to incur the cost of movement (both in fuel and lost catch from 48-h waiting period) in years with high potential catches. We predicted that mobility would increase over time with increases in vessel technology but the observed that the increase in horsepower had only a slight, not significant effect, on the probability of movement (Table 2). In other fisheries, like the demersal French trawling fleet, catching efficiency increased 8% each year as older vessels were decommissioned and vessels were upgraded (Marchal et al. 2013). This increase in vessel efficiency has occurred in the limited entry Bristol Bay drift gillnet fleet, resulting in overcapitalization of vessels (Valderrama and Anderson 2010). However, this increase in technology had no apparent effect on the tendency to switch districts, thus other factors seem to limit movement.

The mobility of captains varied with their area of residence; residents were much less mobile than nonresidents and nonlocal Alaskans (Figures 5 and 7). Residents could be responding to different motivations than solely maximizing CPUE like nonresidents and nonlocal Alaskans; they instead could be maximizing time with families or willing to accept lower catches, as seen elsewhere (Abernethy et al. 2007). We hypothesize that high mobility in nonlocal Alaskans is due to the participation of highly competitive captains from within the state who fish multiple fisheries throughout the year and are more confident travelling in a variety of weather conditions (Figure 5). Since the implementation of the limited entry program in 1975, the number of local permits in the fishery has been steadily declining (Gho et al. 2012). This phenomenon has attracted attention, leading to the management actions to maintain catch of local captains (the "48-h" and "dual permit" rules) and community programs to help residents buy permits or upgrade their vessels. Limited entry programs require sufficient capital to purchase a permit or family members willing to transfer their permit. Many fisheries have a history of hosting multiple generations of captains; in Maine and North Carolina, 60% of participants in commercial fisheries have over two generations of their family in the business (Cutler et al. 2022). However, across many US fisheries, the age of captains has been steadily increasing without entry of new members into the fishery, a phenomenon termed "graying of the fleet" (Gho 2020, Cutler et al. 2022). This has been especially drastic in Alaska, with increasing movement away from rural areas to city centers like Anchorage, Juneau, and Fairbanks and participation in non-fishery sectors (Donkersloot et al. 2020). The "dual permit" program was implemented to encourage participation of local captains in the fishery by allowing an extra 50 shackles of net on boats where a second captain fishes with the primary captain, allowing the new captain to gain experience fishing without having to purchase a vessel. Movement increased with years fishing a dual permit (Figure 6), indicating that these teams of captains fished more areas as they became more experienced, and could eventually lead to more local resident mobility.

More experienced and successful captains tended to move more and spread their catch more evenly across districts (Figure 6; Table 2). There has been debate over the perceived "skipper effect" in fisheries; some have hypothesized that this is solely due to crew perception of captains with access to more resources being more successful (Pálsson and Durrenberger 1983), but others argued that better captains catch more fish and have the resources to increase their vessel's efficiency (Gatewood 1984). We found that more successful and experienced captains also moved more, linking the behavior of captains to specific attributes, and reflecting patterns seen in the lobster and conch diving fishery (Bene and Tewfik 2001). However, due to confidentiality restrictions we could not investigate if more mobile captains also had more efficient vessels. This variation in mobility by fishing success is important, because less efficient vessels are more likely to exit fisheries (Mardle et al. 2006). Additionally, less experienced captains may tend to fish closer to home ports and move less (Frawley et al. 2021). Fishing is risky and participants may not have health insurance; 42% of the participants in the Maine and North Carolina fisheries did not have health insurance (Cutler et al. 2022). This risk aversion in new captains could explain the trend we observed as less experienced captains moved less.

Although we investigated the effects of vessel and captain characteristics on mobility, we were unable to look at other important sources of variation like weather and the price of fuel, both of which factors are likely to be important. In German North Sea fishing fleets, weather had a large effect on vessel movement, second only to biological characteristics of the fished stocks and above all other economic, social-cultural, and variables related to regulation (Letschert et al. 2023). In addition, high fuel prices reduced mobility within a season in Australia's northern prawn fishery (Venables et al. 2009). Weather and fuel prices, and other unmeasured economic factors, may influence mobility in Bristol Bay and could be interesting areas of future research.

Mobility in a fishery is important to understand in designing effective management and we found that pre-season information, vessel characteristics, return size, and the residency, experience, and relative fishing success of a captain were important determinants of mobility in

Bristol Bay. The call for considering fisher behavior in fisheries management has been heard (Hilborn 1985), with examples coming from fisheries around the world. In the Galapagos, the implementation of a marine reserve was not successful due to the elastic patterns of lobster vessel movement, and management failing to incorporate that variability (Bucaram et al. 2013). Fishers responded more to the price of lobster than management actions, traveling farther and fishing more when prices were high, impacting the success of different scales of spatial closures. Models projecting fleet behavior are used to anticipate responses to future management, like the closure of fishing grounds (Dépalle et al. 2020) or climate-induced changes (Fisher et al. 2021). The Dungeness Crab fishery in California saw an increased number of small vessels relative to larger vessels temporarily exit the food system in response to a marine heatwave, indicating that managers should concentrate on creating other pathways for fishing for these smaller vessels (Fisher et al. 2021). By increasing our understanding of a highly mobile, well-studied, and information-rich fishery, we can inform on patterns that may emerge in other fisheries. We highlight the need for future studies on captain variability and for an increase in pre-season information available in fisheries. Ultimately, understanding movement patterns in a fishery can lead to increased management success ecologically, economically, socially, and culturally.

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Figures and Tables

Table 1: The candidate model set predicting the mobility score of a captain using backward stepwise regression. The number of parameters, AIC_c values, and ΔAIC_c values are reported for each model. A change of >2 units of ΔAIC_c indicates model superiority.

Model	Number of parameters (*k*)	AIC_c	ΔAIC_c
~ Dual Permit Years + Years of Experience + Residency + Relative Fishing Success	4	-13315	*Preferred*
~ Years of Experience + Residency + Relative Fishing Success	3	-13267	48.00
~ Dual Permit Years + Years of Experience + Residency	3	-13252	63.00
~ Dual Permit Years + Residency + Relative Fishing Success	3	-13234	81.00
~ Dual Permit Years + Years of Experience + Relative Fishing Success	3	-13135	180.00

Table 2: The coefficients, standardized model estimates and standard errors, the transformed model estimates, z-value, and p-values for the binomial logit generalized linear model predicting the mobility of captain, *i*, in year, *y*. For the transformed estimates, a one unit increase in the standardized coefficient is associated with the probability of being mobile listed. This was found by applying an inverse logit transformation to the standardized estimates.

Coefficient	Standardized Estimate	Transformed Estimate	Z value	p-value
$\text{Residency}_{i,y}$: Local	-1.44 ± 0.03	0.19	-41.77	<0.001
$\text{Relative Fishing Success}_{i}$	0.43± 0.01	0.61	34.27	<0.001
$\text{Years of Experience}_{i,y}$	-0.11 ± 0.01	0.47	-8.45	<0.001
Forecast_{y}	-0.14 ± 0.01	0.47	-9.95	<0.001
Return_{y}	0.21 ± 0.06	0.55	13.65	<0.001
Horsepower_{y}	0.03 ± 0.00	0.51	1.89	0.059
$\text{Dual Operation}_{i,y}$: Yes	-0.07 ± 0.05	0.18	-1.50	0.135
$\text{Residency}_{i,y}$: Nonlocal	1.49 ± 0.04	0.51	36.87	<0.001
$\text{Residency}_{i,y}$: Nonresident	1.36 ± 0.04	0.48	35.97	<0.001

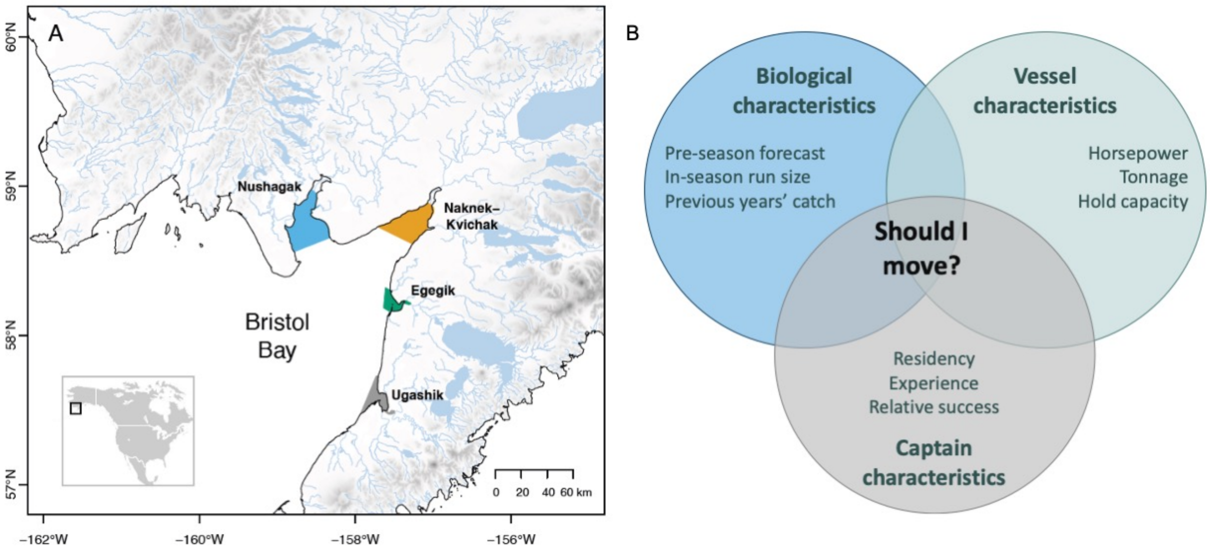

Figure 1: A map of the Bristol Bay fishing districts (A) and a conceptual model illustrating what factors a captain must consider when making movement decisions (B). This map was modified from Ohlberger et al. 2023.

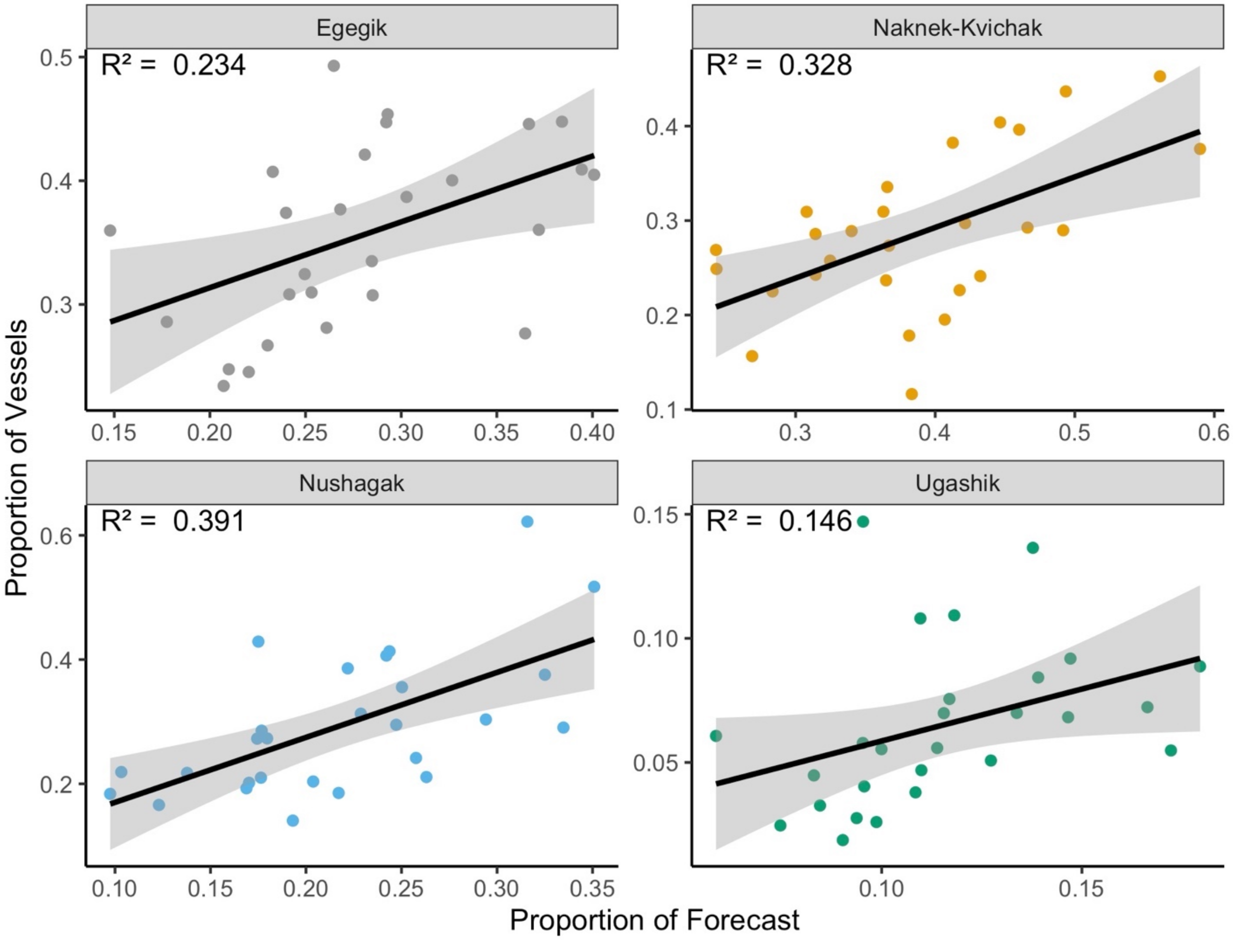

Figure 2: The proportion of vessels that first fish in a specific district each year increases with the proportion of the pre-season forecasted salmon abundance returning to the same district that year. The linear models for each district are represented in the black line with the gray 95% confidence intervals and corresponding R^2 value. Egegik is shown in gray, Naknek-Kvichak in yellow, Nushagak in light blue, and Ugashik in green.

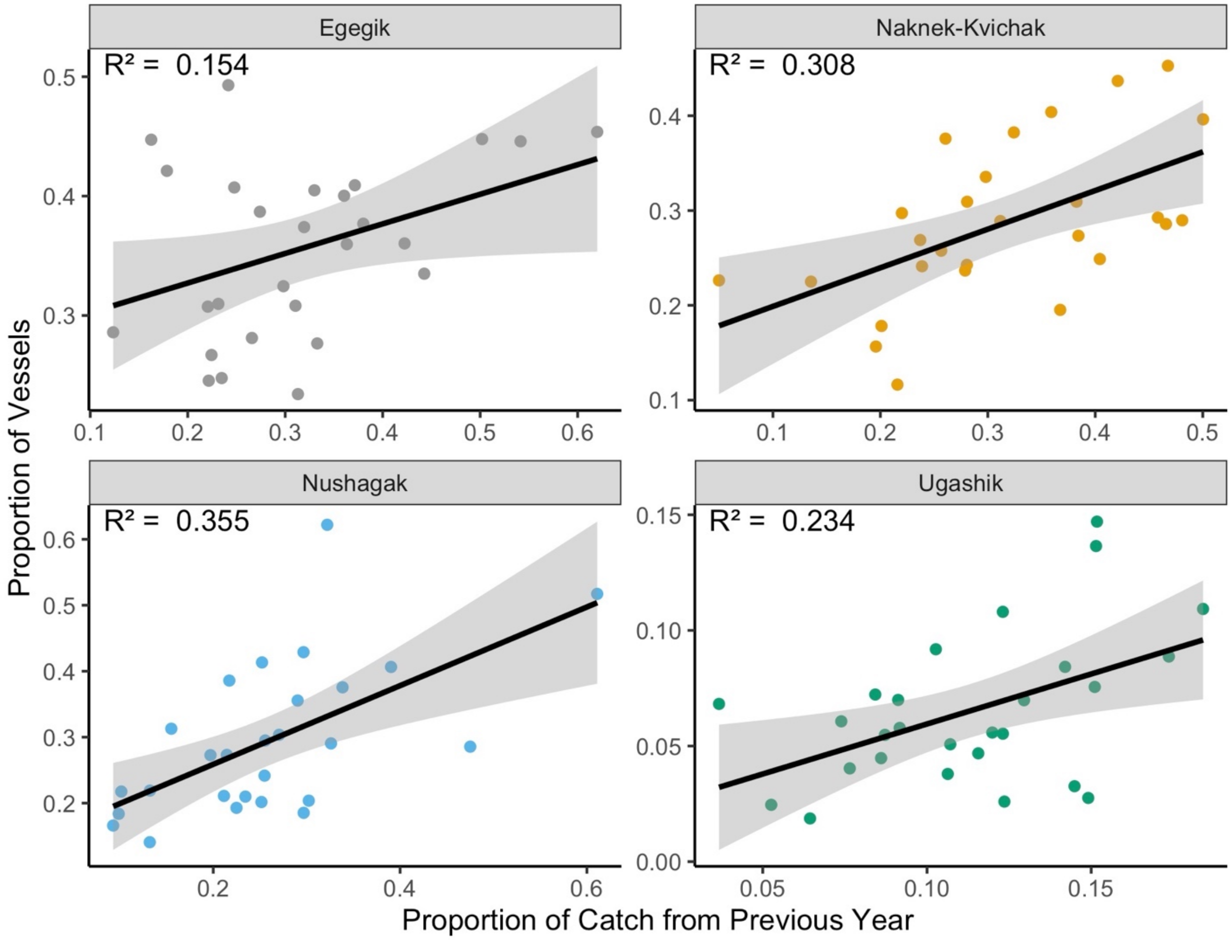

Figure 3: The proportion of vessels that first fish in a specific district each year increases with the proportion of the previous year's harvest coming from that same district that year. The linear models for each district are represented in the black line with the gray 95% confidence intervals and corresponding R^2 value.

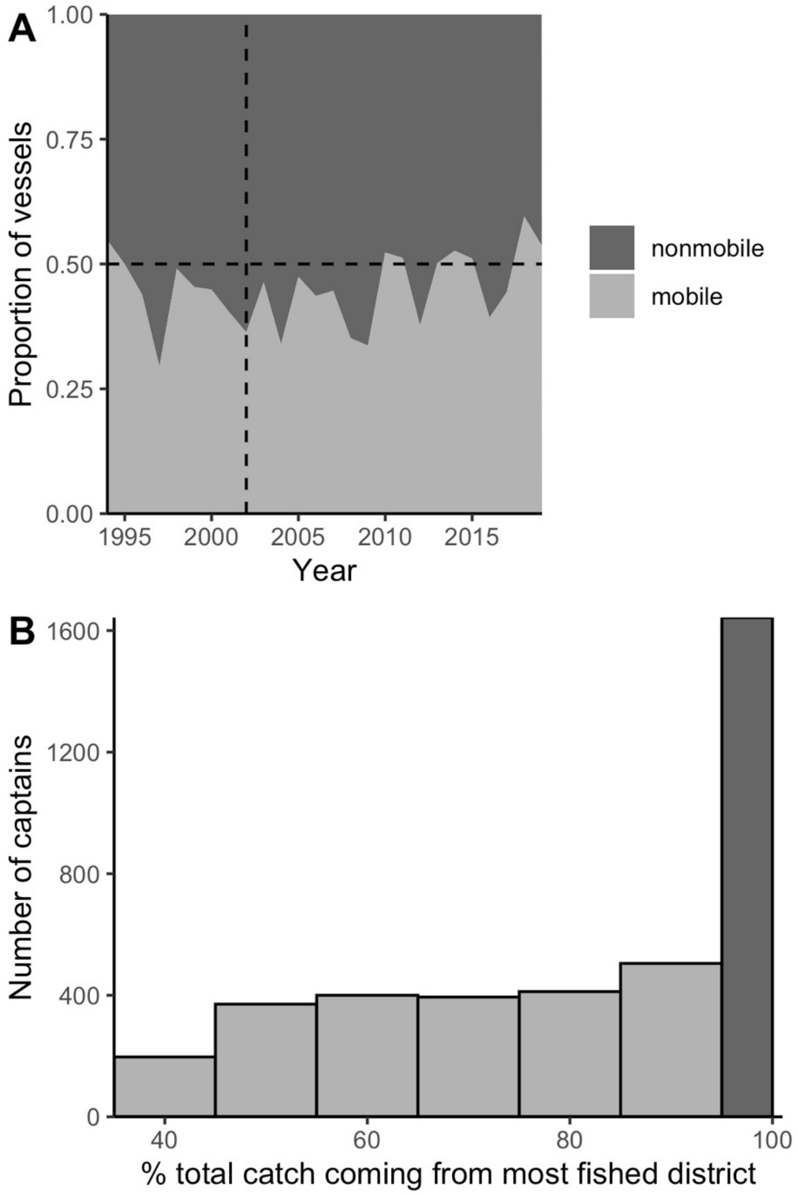

Figure 4: We categorized captains into mobile (light gray) and nonmobile (dark gray) in a single year (A) and across all years they fished (B). In (A) the proportion of mobile and nonmobile vessels are shown across our study period (1994-2019) with the black dashed horizontal line showing the 50% line and the vertical black dashed line showing the implementation of dual permits in 2003. In (B) a histogram shows the percent of a captains' total catch, across all years they fished, coming from their most fished district is against the number of captains in that category.

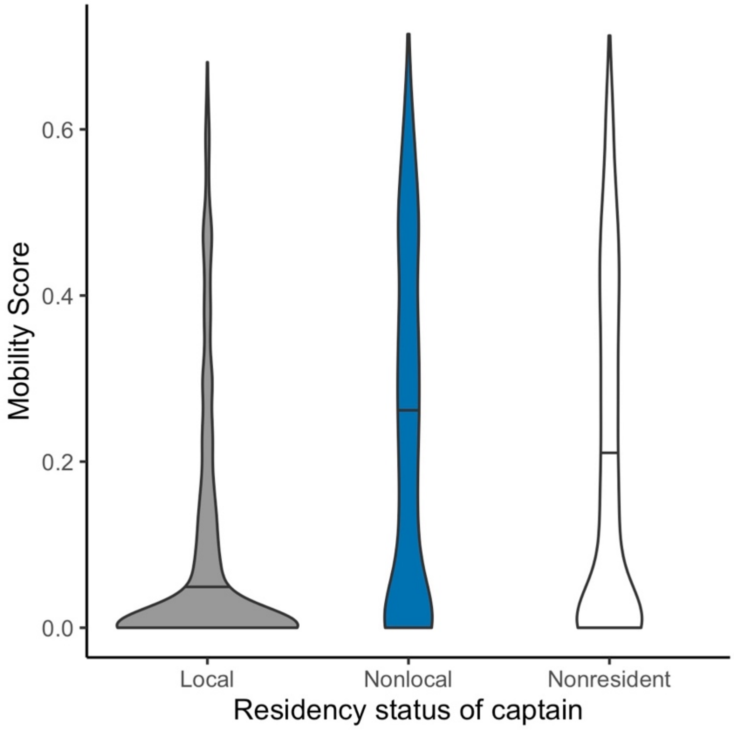

Figure 5: The residency of a captain was related to their mobility score, with local residents being the most stationary and nonlocal and nonresident captains receiving higher mobility scores. The width of the violin plot shows the number of individual captains with that mobility score and the black line shows the mean across that residency category.

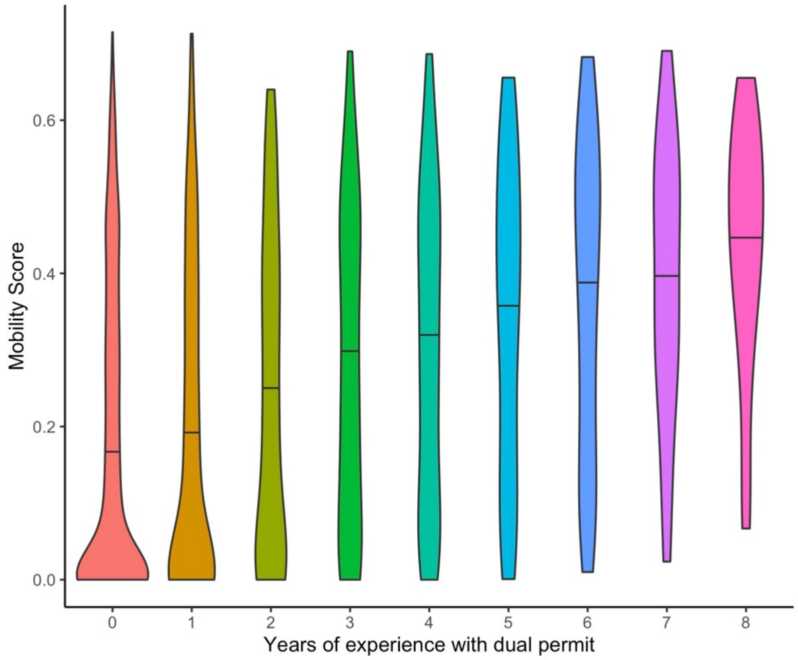

Figure 6: The number of years a captain fished a dual permit was related to an increase in their mobility score. The width of the violin plot shows the number of individual captains with that mobility score and the black line shows the mean across the captains with different years of experience fishing dual permits.

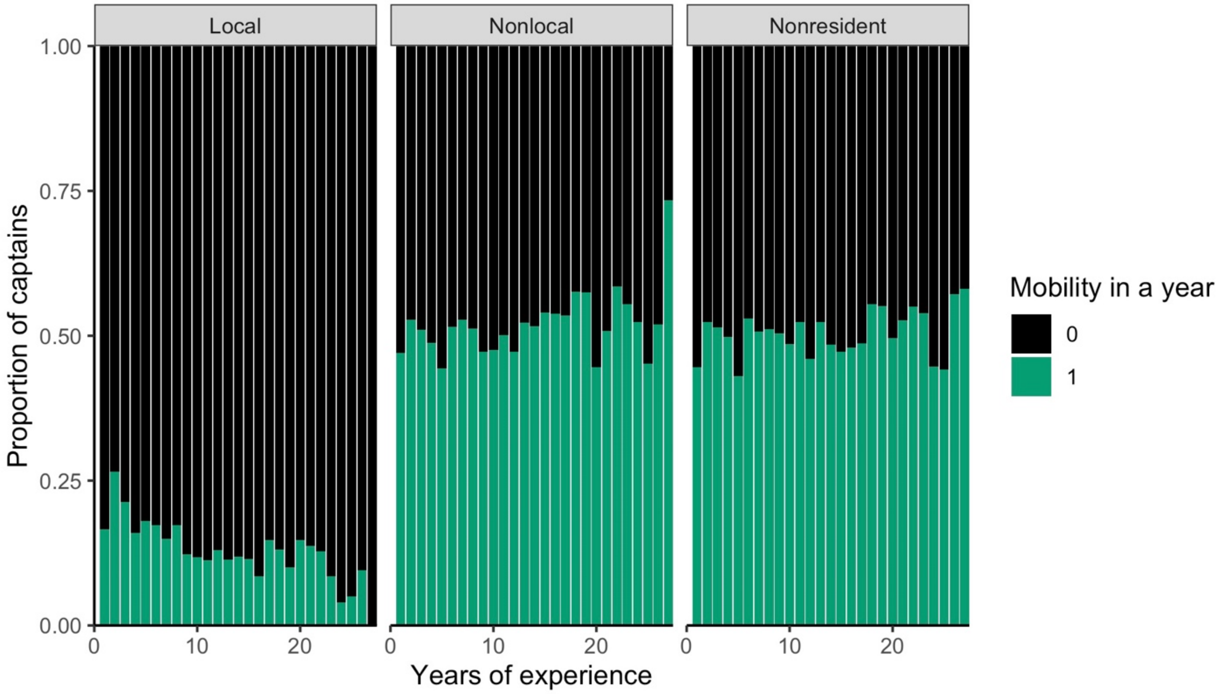

Figure 7: The bar plot shows the proportion of captains that moved in a year (black = did not move, green = did move) as a function of their residence type and years of experience.

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Appendices

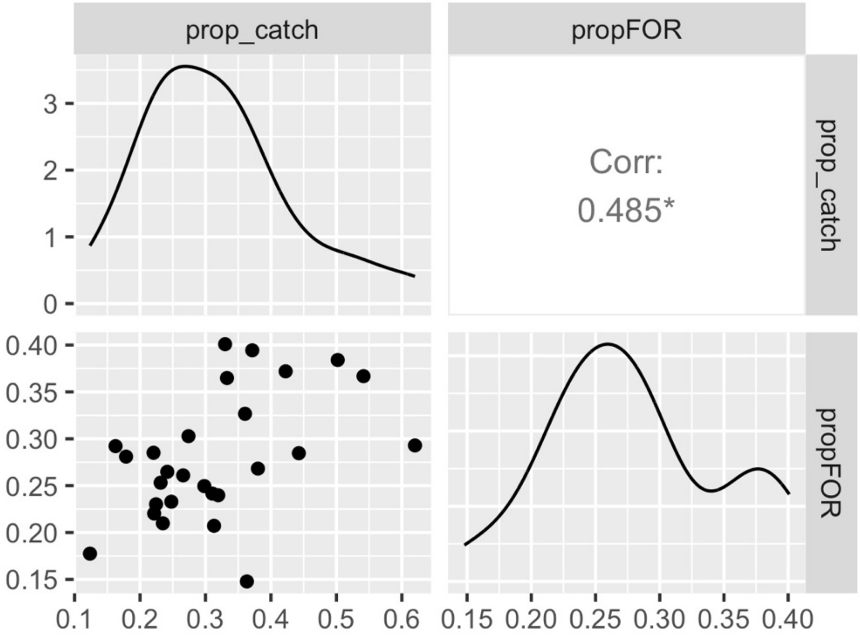

Figure A1: The proportion of the previous year's catch coming from Egegik (prop_catch) and the proportion of the forecasted return from Egegik (propFOR) in a year are moderately positively correlated.

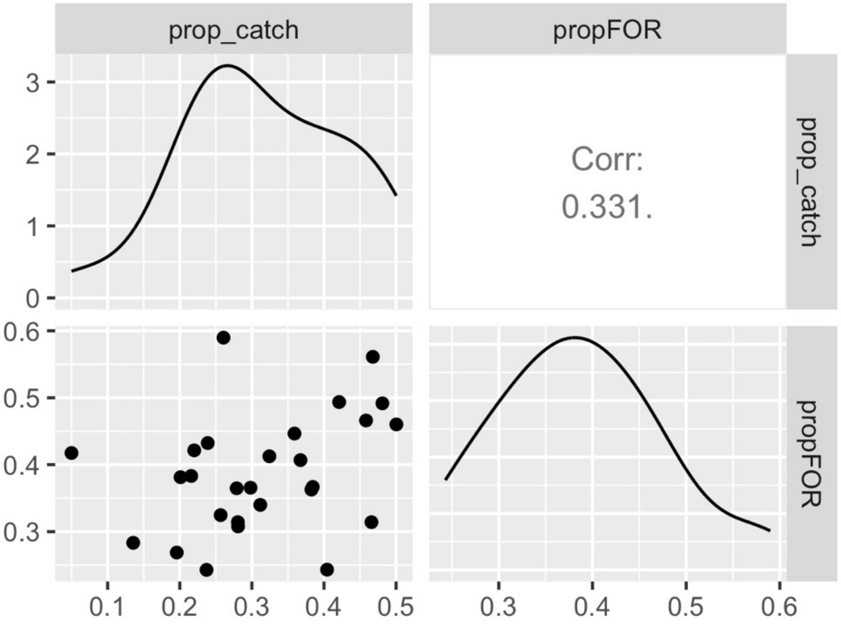

Figure A2: The proportion of the previous year's catch coming from Naknek-Kvichak (prop_catch) and the proportion of the forecasted return from Naknek-Kvichak (propFOR) in a year are moderately positively correlated.

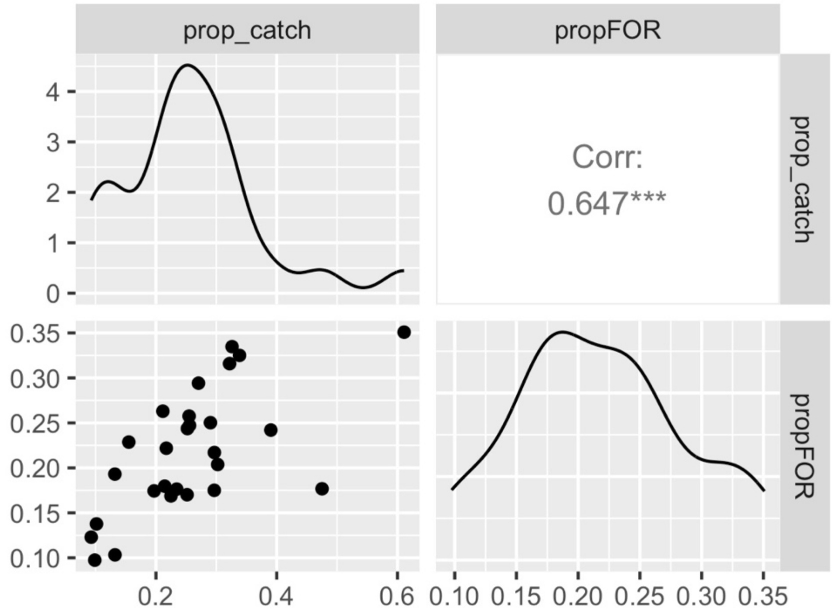

Figure A3: The proportion of the previous year's catch coming from Nushagak (prop_catch) and the proportion of the forecasted return from Nushagak (propFOR) in a year are highly positively correlated.

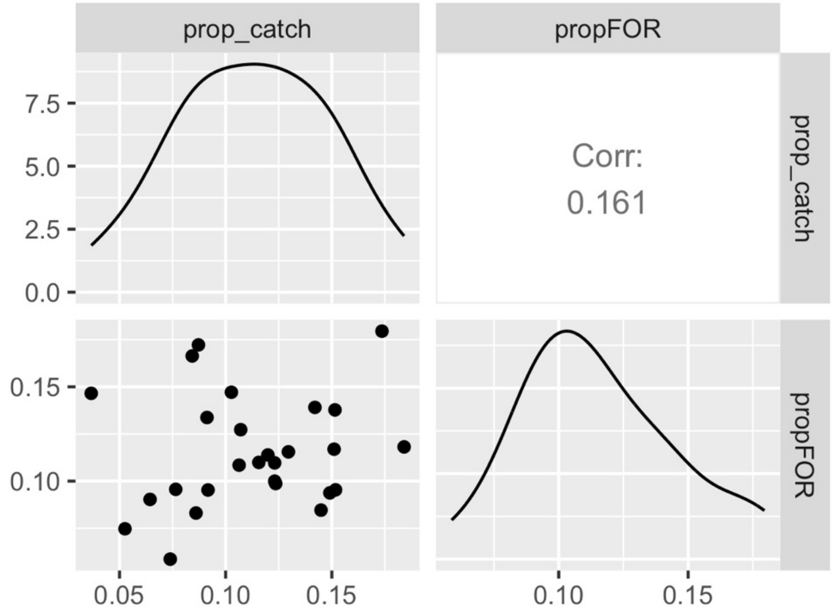

Figure A4: The proportion of the previous year’s catch coming from Ugashik (prop_catch) and the proportion of the forecasted return from Ugashik (propFOR) in a year are weakly positively correlated.

Conclusion

In this dissertation, I applied multiple parametrizations of a classic ecological model that predicts predator distributions in response to their mobile prey, the Ideal Free Distribution theory (IFD), to two apex predators in Bristol Bay, Alaska (Fretwell and Lucas 1969). Brown bears and commercial fishers track salmon abundance through time and across discrete spatial locations to maximize their catches while minimizing foraging costs (Hilborn 1985, Sergio et al. 2014, Quinn et al. 2017). Both predators must respond to variability in the number of salmon and number of competitors across these discrete areas, using multiple types of information to choose their fishing locations. Most work done on the IFD has been theoretical in nature or implemented in simplified, controlled laboratory environments (Kennedy and Gray 1993, Tregenza 1995). My three chapters add to the much-needed work on predator ecological models in complex field environments, illuminating foraging patterns in large, mobile apex predators on their mobile prey.

In chapter 1, I used the IFD and the Type II functional response models to fit 25 years of bear foraging data in a series of connected ponds in Pedro Bay, AK (Holling 1959, Fretwell and Lucas 1969). I found that bears adjusted their foraging in response to prey abundance and habitat variation, the area and depth of ponds, that affected the ease of capture of their salmon prey. This was consistent with IFD predictions, indicating that bears use multiple sources of information when foraging. I also applied the predictions of the Type II functional response model to these foraging data and found the model with an added year effect, accounting for variation in competitive ability of bears across years, best fit the observed patterns in bear foraging. In chapter 2, I applied multiple parameterizations of the IFD model to data on the catch and fishing locations of Bristol Bay drift gillnet fishers across 40 years to investigate IFD assumption violations. Overall, I found that some years fit IFD predictions and had equal catch per vessel (CPUE) across a season in the 4 fishing districts, while other years had districts with significantly higher CPUE than others. When accounting for the violation of the “free to move” assumption of the IFD due to stationary vessels and variability in competitive ability of captains, the districts with higher CPUE still persisted in most years, indicating the fleet was operating contrary to IFD predictions overall. In chapter 3, I used information on captain characteristics, vessel attributes, and run size and forecast variability in a year to investigate what determines the mobility of a vessel to illuminate reasons why the fleet is in violation of the IFD. I found support for information use across the fleet, with increases in the proportion of vessels first fishing a specific district as the forecasted catch in that district and the previous’ years catch in that district increased. Run size influenced fleet-wide mobility, with increases in the number of vessels fishing more than 2 districts in larger return years. Additionally, mobility of individual captains was higher in more experienced and more successful captains, and lower in local captains. This indicates that captain specific characteristics and variation in expected catch could be driving departures from IFD predictions.

The complexity of the Bristol Bay foraging environment, and the high reliance of both predators on their single sockeye salmon prey species, allowed for a robust test of IFD predictions. I was able to investigate multiple interacting assumption violations of the IFD, building off similar work in other fishery systems (Hilborn 1985, Hilborn and Ledbetter 1985, Abrahams and Healey 1990, Abernethy et al. 2007). Interacting assumption violations are likely common in nature, but are limited in IFD literature due to the difficulty of constructing experimental settings where this is possible to test (Kennedy and Gray 1993, Tregenza 1995). Brown bears and the distribution of their foraging across variable ponds demonstrated that they satisfied the “perfect information” assumption of the IFD in this small system with little to no travel costs, a finding rare in nature (Tregenza 1995). Additionally, although bears have been known to demonstrate despotic behavior when foraging (Gende and Quinn 2004), in the ponds system we found no evidence for despotic behavior although there was evidence of “variation in competitive ability” with the high variability of our year effect in the functional response model that we hypothesized was related to the number and competitive ability of foraging bears in a year. A next step in expanding this research on bear foraging could include collecting information on the individual bears foraging in the system and measuring their “competitive ability” as done in Gende and Quinn (2004), allowing us to look for an IFD scaled to competitive ability or identify despotic behavior. Additionally, future work could integrate existing knowledge on bear’s partial consumption of salmon (Lincoln and Quinn 2019) and their preferred salmon body types (Gende et al. 2001) to look for evidence of an IFD that considers variation in calories or freshness of fish across ponds, instead of the total number of salmon.

In the Bristol Bay fishery, we accounted for violations of the “free to move” and “equal competitive abilities” assumptions of the IFD, when we considered variation in mobility and relative fishing success across captains. Despite accounting for these two assumptions, we found the fleet did fit IFD predictions overall, indicating that something else restricts movement decisions and could prevent an IFD from occurring. This was found in other fleet IFD literature, including in small-scale reef fishers who demonstrated alternative motivations that violated the “move to maximize success” assumption and in the British Columbia salmon purse seine fleet where specialized knowledge of some fishers led to increased catches (Hilborn 1985, Abernethy et al. 2007). When investigating patterns of mobility in chapter 3, we determined that residency and years of experience could be driving departures from IFD conditions. A natural expansion of this work could include fisher interviews to investigate how their use of different sources of information plays into their decisions of where to fish and what factors restrict their movement choices—travel costs, radio group communication, weather, the experience of the crew, and other factors.

Predator movement patterns are necessary to understand because predators can restrict the abundance and distribution of prey, help structure ecological communities, and act as a major selective force on prey species (Krebs 2014, Sergio et al. 2014). Because of this, movement patterns in predators must be considered when designing management and conservation policies. In ecosystem-based management, multiple predators can utilize the same prey species, like bears and commercial fisheries in Bristol Bay (Lincoln et al. 2020). By understanding where each predator concentrates their foraging effort and how that changes over time and in response to variation in prey population size, managers can ensure they allow enough fish for both bears and humans while maintaining a stable population of salmon. In fisheries, fleet movement patterns can identify stocks, areas, and times that will be exposed to high fishing pressure, aid in understanding economic limitations and incentives, and anticipate responses to changing economic, biological, management, climatic, and oceanographic conditions (Bucaram et al. 2013, Ono et al. 2018, Fisher et al. 2021). Thus, to create management policies that fit the unique ecological, social, cultural, and economic conditions of fisheries, we must incorporate fleet behavior (Hilborn 1985, Bene and Tewfik 2001, Wilen et al. 2002). Terrestrial, aquatic, and marine ecosystems will face changing environmental conditions in the future due to climate change and its various ecological impacts. Understanding predator movement under various conditions can help predict the effects of our changing world on these populations and help design management to ensure humans, other predators, and valuable fisheries resources can persist together.

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