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FEATURED STUDENT RESEARCH PAPER

Family feud: permanent group splitting in a highly philopatric mammal, the killer whale (*Orcinus orca*)

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Abstract

For animals that tend to remain with their natal group rather than individually disperse, group sizes may become too large to benefit individual fitness. In such cases, group splitting (or fission) allows philopatric animals to form more optimal group sizes without sacrificing all familiar social relationships. Although permanent group splitting is observed in many mammals, it occurs relatively infrequently. Here, we use combined generalized modeling and machine learning approaches to provide a comprehensive examination of group splitting in a population of killer whales (*Orcinus orca*) that occurred over three decades. Fission occurred both along and across maternal lines, where animals dispersed in parallel with their closest maternal kin. Group splitting was more common: (1) in larger natal groups, (2) when the common maternal ancestor was no longer alive, and (3) among groups with greater substructuring. The death of a matriarch did not appear to immediately trigger splitting. Our data suggest intragroup competition for food, leadership experience and kinship are important factors that influence group splitting in this population. Our approach provides a foundation for future studies to examine the dynamics and consequences of matrilineal fission in killer whales and other taxa.

Significance statement

Group living among mammals often involves long-term social affiliation, strengthened by kinship and cooperative behaviours. As such, changes in group membership may have significant consequences for individuals' fitness and a population's genetic structure. Permanent group splitting is a complex and relatively rare phenomenon that has yet to be examined in detail in killer whales. In the context of a growing population, in which offspring of both sexes remain with their mothers for life, we provide the first in-depth examination of group splitting in killer whales, where splitting occurs both along and across maternal lines. We also undertake the first comprehensive assessment of how killer whale intragroup cohesion is influenced by both external and internal factors, including group structure, population and group demography, and resource abundance.

Keywords Group splitting · Matrilineal fission · Food competition · Kinship · Philopatry · Killer whale

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Introduction

A matrilineal society is a stable social strategy adopted by many gregarious mammals, revolving around cooperative groups of related females. Most matrilineal societies exhibit sex-biased dispersal; commonly, females are philopatric (remaining in their natal geographic range and/or social group) and males disperse, often around the age of sexual maturity (Greenwood 1980; Johnson 1986; Clutton-Brock and Lukas 2012). Under unfavourable group conditions, often associated with a group's growing size or changing composition, group fission is the primary process by which philopatric females may disperse (e.g. Dittus 1988; Henzi et al. 1997; Holekamp

et al. 1997; Lefebvre et al. 2003; Van Horn et al. 2007). Group fission in matrilineal societies often occurs along lines of maternal relatedness, allowing animals to maintain important, familial relationships while optimizing group size (Chepko-Sade and Olivier 1979; Archie et al. 2006; Widdig et al. 2006; VanderWaal et al. 2009; Sueur et al. 2011). Group splitting, particularly when kin-biased, may have significant influence on individual fitness (Armitage 1987; Dittus 1988; Pollack and Rubenstein 2015) and population genetic structure (Chepko-Sade and Sade 1979; Melnick and Kidd 1983; Widdig et al. 2006).

Although all documented killer whale (*Orcinus orca*) societies are matrilineal, they exhibit varying degrees of natal social philopatry (fidelity to the family group into which they were born). Among social mammals, fish-eating 'resident' killer whales of the eastern North Pacific represent a rare case of extreme bisexual social philopatry, where both sexes remain with their natal group throughout life and individual dispersal is exceedingly rare (Matkin et al. 1999a; Ford et al. 2000). Because of this unusual social strategy, resident killer whales live in highly stable matrilineal groups composed of a female, her offspring and up to five generations of her descendants through maternal lines (Bigg et al. 1990). Because group size is not moderated by individual dispersal, matrilineal splitting provides the only means by which new groups may form in resident killer whale society.

Resident killer whales in coastal waters of the eastern North Pacific occur in three discrete populations that are socially and genetically isolated from one another, despite having overlapping geographic ranges (Bigg et al. 1990; Barrett-Lennard 2000; Ford et al. 2000; Matkin et al. 2007). The genealogy and social organization of these populations are described through several long-term studies that use photo-identification of individually distinct natural markings to conduct annual censuses of individuals (Bigg 1982; Matkin et al. 1999b; Ford et al. 2000; Center for Whale Research 2016; Towers et al. 2020). Our study focuses on the northern resident killer whale (NRKW) population, which has been studied since 1973 and ranges from Washington State to southeastern Alaska (USA). This population has grown steadily since the beginning of its study and was composed of 289 animals in 2014 (Fig. 1a; DFO 2019; Towers et al. 2020).

Early in the study of resident killer whales, it was discovered that individuals lived in highly stable social groups that were termed 'pods'. Although it was initially thought that pods were permanent (Bigg et al. 1976) or long-term breeding units (Bigg 1982), it was soon recognized that pods were composed of one to several 'maternal groups' (Bigg et al. 1987), 'matrilineal groups' (Bigg et al. 1990) or 'matrilines' (Ford et al. 2000; Towers et al. 2020), terminology we use here with revision (Table 1).

During the first decade of study, pods were socially cohesive, and the maternal groups within them associated more regularly with one another than with maternal groups from different pods (Bigg et al. 1990). In the mid-1980s, researchers first observed maternal groups within pods associating less frequently with one another, with some disassociating from one another completely. Of the 16 pods originally identified by Bigg et al. (1990), only half met the definition of a pod by the year 2000 (Ford and Ellis 2002).

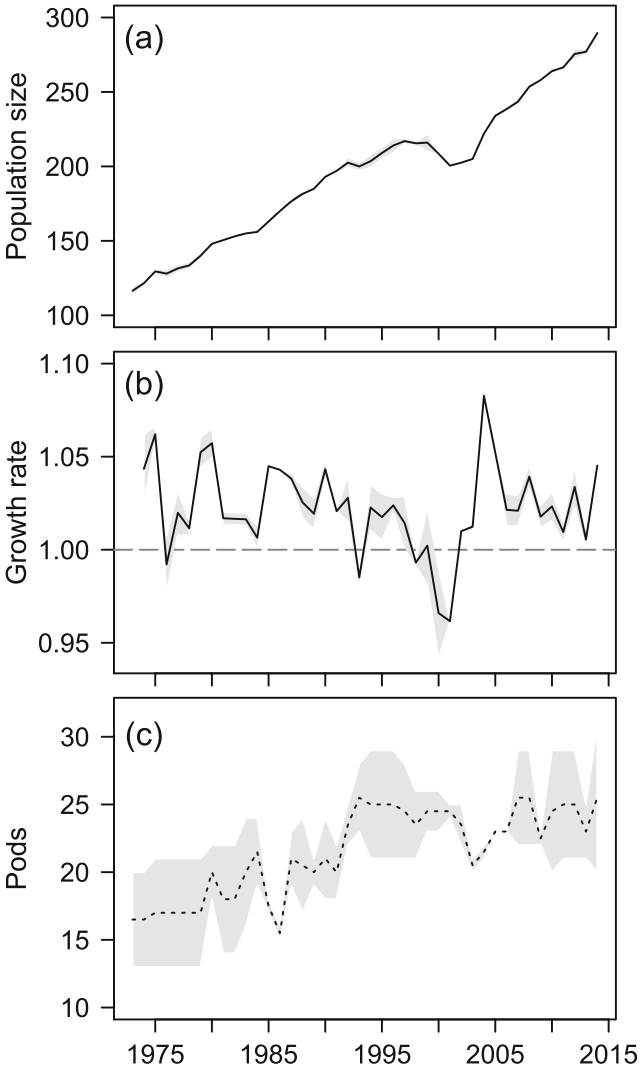

Fig. 1 Northern resident killer whale **a** population size and **b** population annual growth rate, and **c** the estimated number of pods present in the population. Grey shading denotes minimum and maximum values of estimates

Splitting was observed within pods originally composed of both multiple and single maternal groups. In the former case, it was assumed that the various maternal groups originated from a now-deceased, common maternal ancestor (i.e. were of the same matriline; Ford 1989, 1991; Barrett-Lennard 2000; Ford et al. 2000; Deecke et al. 2010). In the latter, the matriarch of the pod was alive at the beginning of the study but, upon her death, her lineage gave rise to several maternal groups that subsequently became socially separated (Fig. 2a). This

Table 1 Resident killer whale social organization terminology. Social grouping terms are hierarchical and have been established over the course of the NRKW study. Group substructures are matrilineal units that we use to describe social group structure (see Supplementary Materials Fig. 1). A *matriline* denotes all individuals descended from a common maternal ancestor. *Direct maternal ancestor(s)* refer to individuals from whom one descends in a direct line through mothers (i.e. mother, maternal grandmother, maternal grandmother's mother, etc.). *Direct maternal descendants* refer to a female's offspring and all offspring of her female descendants (e.g. daughter's offspring, granddaughter's offspring, etc.)

Term	Definition
Social groupings	
Population	A community of one or more clans that associate with one another. May be sympatric with but does not mix socially with other populations. (Bigg et al. 1990)
Clan	Maternal groups with vocal dialects that include shared call types[1]. Different clans are acoustically distinct and may represent separate matrilines. (Ford 1991)
Pod	An assemblage of maternal groups that, on average, spend more than 50% of their time together[2] (Bigg et al. 1990). Pods are composed of one or more maternal groups. Maternal groups found in the same pod likely share a common maternal ancestor (i.e. belong to the same matriline)[3]
Maternal group	Individuals[4] descended from a common direct maternal ancestor (matriarch) that always travel together (Bigg et al. 1990). Maternal groups are named after the most recent matriarch of the group and are the core social unit of resident killer whales
Group substructures	
Complete unit (CU)	A living female with no living direct maternal ancestors in the social group, and her direct maternal descendants
Nested unit (NU)	A living female and her direct maternal descendants, nested within a CU (i.e. the female is socially cohesive with at least one direct maternal ancestor). Once socially independent from the rest of its CU, the NU is considered its own CU
Subunit	The largest matrilineal substructure in the group, the most likely subset of the group to socially disperse. For groups without a living matriarch, this refers to the largest CU in the group. For groups with a living matriarch, this refers to the largest NU in the group
Basal unit (BU)	Mother-offspring group composed of a female, her sons, and her daughters without offspring. Any females with offspring of their own are considered a separate BU, excluded from their mother's BU. Unlike CUs and NUs, this unit does not require a living mother

[1] Call repertoires of clans can persist for at least 60 years and likely longer (JKBF 1991, unpubl. data)

[2] Association index selection depends on the bias of a given study's sampling process and therefore one's quantitative delineation of 'pod' may not be equivalent to a simple ratio index (SRI) of > 0.5 (or this study's definition, using HWI > 0.6)

[3] A pod gives rise to further pods when group splitting occurs. For example, a pod is composed of a living matriarch with three daughters, all with descendants of their own. Upon the death of the matriarch, the three daughters and their direct maternal descendants are still considered one pod. When the three daughters become socially independent of one another, three new pods arise—each led by a daughter of the deceased matriarch. Additionally, when a daughter separates from her mother, her nested unit becomes a pod of its own

[4] Maternal groups can include individuals without a living, direct maternal ancestor. These individuals are therefore external to the complete and nested unit terms defined here, as these terms refer to groups requiring a living female and her direct maternal descendants. These individuals are, however, included in a basal unit, which does not require a living mother

process of fission *along* extant maternal lines is the most common form of matrilineal fission and lineage creation (e.g. Furuya 1968, 1969; Nash 1976; Chepko-Sade and Sade 1979; Oi 1988; Ménard and Vallet 1993; Lefebvre et al. 2003; Archie et al. 2006; Widdig et al. 2006).

In the late 1990s, a second form of group splitting was observed in the NRKW population, where a female (along with her direct maternal descendants) would fission with her pod while her mother was still alive (Fig. 2b). This process of fission *across* extant maternal lines was quite unexpected because, until that time, all animals in resident populations were known to stay with their mother for their entire lives. We distinguish these two forms of group fission by the absence and presence of a matriarch, respectively, where the 'matriarch' is considered the oldest extant direct maternal ancestor shared by all individuals in the group.

Whether group splitting in resident killer whales is a mutual or unilateral process and whether it results in locational dispersal is unknown. Therefore here, we use the terms 'social dispersal', 'splitting (from)', or 'separating (from)' broadly, not to suggest directionality within these events, but to simply denote the social partitioning of one's group from the perspective of the given focal animal(s).

Whereas individual social dispersal patterns have been described previously in killer whale populations (e.g. Baird and Whitehead 2000), observations of group splitting have been

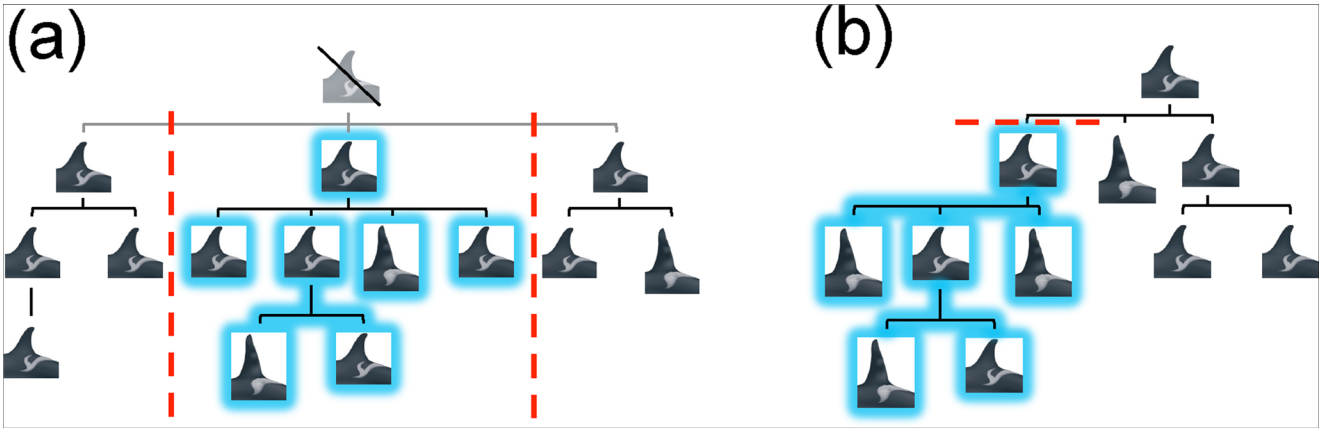

Fig. 2 Matrilineal fission was exhibited in two ways in the northern resident killer whale population. **a** A subunit separates from maternal relatives with which there is no longer a living common maternal ancestor (matriarch). The largest *complete unit (CU)* present in the pod is considered the subunit for this type of splitting. In this example, where a group is composed of more than two CUs, all CUs may simultaneously split apart or the remaining CUs may remain together after separating from the subunit. **b** A subunit separates from a living maternal ancestor and the largest *nested unit (NU)* present in the pod is considered the subunit. Subunits for these theoretical groups are highlighted in blue

noted only anecdotally (e.g. Scheel et al. 2001; Esteban et al. 2015) and not described in detail. Our study provides an in-depth description and quantification of group splitting in the NRKW population, examining the duration of the splitting process, the longevity of splits, the frequency of splitting and whether splitting in the presence or absence of a matriarch differ in those respects. We also relate NRKW population dynamics to splitting and group structure.

In addition to describing matrilineal fission in the NRKW population, we also address concerns that environmental factors could be driving these fission events. Group splitting in the NRKW population was anecdotally observed to coincide with years of low abundance of Chinook salmon (*Oncorhynchus tshawytscha*), their preferred prey (Ford et al. 1998; Ford and Ellis 2006). Thus, there are concerns that salmon abundance, which is impacted by fisheries and other human disturbance, may be affecting the integrity of NRKW social organization.

We hypothesize that population growth drives group splitting in the NRKW, with groups splitting when they grow to exceed some threshold size. However, of greater ecological interest are the underlying causes of group splitting in NRKWs. Accordingly, we aim to identify factors that make large group sizes unfavourable in this population. We consider four hypotheses to explain the mechanism of NRKW group splitting, recognizing that any number of these processes could be occurring concurrently and are not necessarily independent of one another:

(1) *Food competition:* Reduced per capita prey availability increases intragroup competition for food resources, thus promoting fission to reduce competition. We predict that fission is more likely during years of low salmon abundance than during years of high salmon abundance, and more likely in groups with greater caloric requirements than in those with fewer caloric requirements.

(2) *Kinship:* Relatedness drives kin-directed behaviours that promote philopatry (e.g. food sharing). We predict that fission is promoted when a group's average maternal relatedness decreases, to reduce intragroup competition and optimize potential inclusive fitness benefits of within-group cooperation.

(3) *Reproductive conflict:* Calving synchrony increases intragroup competition for food resources through increased metabolic costs due to lactation. Here, we consider calving synchronous when multiple local females birthed calves within such a time interval that their estimated lactation periods overlapped. We predict that fission is promoted in groups with simultaneously lactating females, to mitigate costs of reproductive conflict.

(4) *Leadership experience*: The capability of a female to lead her group and ensure its survival and reproductive success hinges on her accumulated social and ecological knowledge. We predict that fission is inhibited until a group contains at least two females with sufficient experience to lead their respective groups, where fission is more likely in groups with older non-matriarch females than in groups with younger non-matriarch females.

We use a combined generalized modeling and machine learning approach to explore these hypotheses, giving consideration to extrinsic and intrinsic factors considered likely to affect intragroup cohesion in the NRKW population.

Methods

Assessing intrapod cohesion

Data were derived from a long-term photo-identification study of NRKWs off the coast of British Columbia (BC), Canada, where individuals were identified by dorsal fin features and distinct natural markings on their 'saddle patch', the lightly pigmented area posterior to the dorsal fin (Bigg 1982). Our data consisted of records of boat-based encounters ($n = 4667$) with photographically or visually identified NRKW from 1973 to 2014. An 'encounter' entails documentation of identified individuals exhibiting coordinated group behaviour (e.g. behavioural state, direction of travel) within a geographic area that allows animals to be in acoustic communication with one another. All individuals present within an encounter were considered associated. As this study involved focal animals in the field, blind data recording was not possible. We restricted our analysis to encounters occurring between June and October to reduce potential seasonal influence and ensure comparable survey effort among years.

As individual dispersal in resident killer whale populations is exceptionally rare, we considered male offspring, and female offspring without surviving offspring of their own, representatives of their mother to generate functional units ('basal units', BUs; Table 1, Supplementary Materials Fig. 1) by which to assess intrapod cohesion. We approximated intrapod cohesion using the Half Weight Index association measure (HWI; Cairns and Schwager 1987):

$$HWI = \frac{successes}{N} = \frac{successes}{successes + \frac{1}{2}(failures)} \quad (1)$$

where 'successes' were encounters wherein all basal units of a given pod were present (i.e. at least one member of each basal unit was accounted for). 'Failures' were any encounters in which at least one basal unit within the pod was present and at least one basal unit within the pod was absent. We considered a pod to be socially cohesive if it exhibited strong intragroup association (HWI > 0.6) in the given year. To ensure a minimum threshold of precision, we required that each estimate of intrapod cohesion be derived from a minimum of five unique encounters in the given year to be included in our analyses (Whitehead 2008). On average, groups adequately sampled were encountered 25 times (median = 11, interquartile range, IQR = 22) in a given year (Supplementary Materials Table 1).

Introducing new pods

Fission events (splits) occurred when a previously cohesive pod was not cohesive in the given year, and fusion events (reunions) occurred when a previously split pod was cohesive in the given year (Supplementary Materials Table 1). The membership of new pods was defined according to the association strength among its basal units. This differs from practice in the NRKW study, where the original pod designations as defined by Bigg et al. (1990) continue to be used as fixed delineations of the population. For ease of reference hereafter, we use the term 'legacy pods' to refer to the 16 original pods defined by Bigg et al. (1990).

The number of pods present in the population in each year of the study was estimated taking into account uncertainty in the timing of fission and fusion events due to limitations of sampling. In a given year, inadequately sampled pods that were deemed cohesive in the last year they were adequately sampled (*yls*) and in the next year they were adequately sampled (*yns*) were assumed cohesive. Minimum pod counts were obtained by assuming that all inadequately sampled pods whose state of cohesion was at odds in *yls* and *yns* (i.e. fission or fusion event occurred sometime between *yls* and *yns*), as well as those with no *yls* or *yns* due to the start or end of the study, respectively, were cohesive. Conversely, maximum pod counts were calculated by assuming the aforementioned pods were not cohesive. The number of pods resulting from groups assumed to be incohesive were defined according to the delineation among basal units observed in the incohesive *yls* or *yns*. For pods assumed incohesive without *yls* or *yns*, the number of resultant pods was derived from the number of 'complete units' (CUs) present in the group (Table 1; Supplementary Materials Fig. 1). Our 'best' estimate of pods present in the population was derived from the mean of our minimum and maximum estimates each year.

Population dynamics, pod structure and fission

To investigate potential effects of population dynamics on NRKW social organization, we examined the relationship between NRKW population growth, rates of group fission and fusion, and pod structure (Supplementary Materials Table 1). We examined the effect of population growth using Kruskal-Wallis rank sum testing, comparing net changes in the number of pods and the frequency of matrilineal fission and fusion among three distinct periods of NRKW population growth: (1) 1973–1994, a period of unrestrained growth (λ = 2.75%); (2) 1995–2003, when the population experienced high rates of mortality and no net growth (λ = − 0.04%); and (3) 2004–2014, another period of steady, significant growth (λ = 3.19%) (Fig. 1b, c). We also assessed the relationship between population size and the structure of pods using Pearson correlation tests. Pod characteristics that we examined included the number of pods in the population, the mean number of CUs per pod, the mean number of individuals per CU and the mean number of individuals per pod.

Longevity of fission

To assess the permanence of group fission events, we estimated the probability that a once-cohesive pod would reform following a fission event. We used Kaplan-Meier non-parametric survival analysis (Kaplan and Meier 1958) to estimate the time-sensitive probability of a group remaining apart after fission, using the number of years since a pod had split and whether or not it was a socially cohesive group in the given year. Pods that had not reunited by the end of our time series were considered right-censored. Additionally, we examined the probabilistic timing of reunion events (n = 53) using event-only Kaplan-Meier survival analysis. Survival analysis was conducted using the *survfit* function in the R package 'survival' (Therneau 2014).

Determinants of group fission

Explanatory variables

We selected 12 demographic, genealogical, energetic and environmental measures that were biologically relevant to our four hypotheses to analyse in the context of intrapod cohesion. We assessed these measures at various levels of NRKW social organization, resulting in 21 explanatory variables sampled in each year of our time series.

We assessed seven group demographic measures: counts of individuals and CUs within pods, mean size of CUs within pods, presence of a matriarch, proportions of reproductive females, lactating females and physically mature males within pods, and the age structure within pods (Supplementary Materials Table 2). We derived these measures from annual censuses of the NRKW population, which detail the condition, age and reproductive status of each animal in each year. These data are held in a registry maintained since 1973 by the Cetacean Research Program, Pacific Biological Station (Bigg et al. 1990; Ford et al. 2000; Olesiuk et al. 2005; DFO CRP 2015). We assessed the seven demographic measures at the pod level and some at the level of the subunit and population, resulting in 14 demographic variables. The 'subunit' refers to the largest matrilineal substructure in the pod, considered the most likely subset of the group to socially disperse. As the largest substructure of the pod, the subunit would likely have the greatest caloric needs and the weakest bonds to individuals outside of the subunit (due to lower average relatedness). Also, it would tend to be led by an older (and thereby more experienced) female and have greater leadership capacity in general (due to higher median age). For pods without a living matriarch, this is the largest CU in the group and, for pods with a living matriarch, this is the largest 'nested unit' (NU) in the group (Fig. 2; Table 1; Supplementary Materials Fig. 1). We refer to the matriarch of the subunit as the 'submatriarch'.

To assess intrapod maternal relatedness, we estimated the pairwise coefficient of maternal relatedness (assuming a non-inbreeding population) among all individuals within each pod. Matrilineal kinship in NRKWs is inferred by tracing individuals from birth and observing close, long-term associations between females and young animals (Ford et al. 2000; Towers et al. 2020). Our estimates of intrapod maternal relatedness account for known maternal relationships (observed since birth), as well as relationships among animals born before the study whose maternal lineages have been inferred from consistent behavioural observations. These association-based maternal assignments have been genetically validated (Barrett-Lennard 2000). We derived two variables from our genealogically based measure of maternal relatedness. First, we estimated the average pairwise coefficient of maternal relatedness among all individuals within each pod (R*g*). Second, we estimated the average degree of maternal relatedness between the submatriarch and her direct descendants (R*sm*), relative to that between her and the rest of her pod (i.e. her mother and her non-descendant relatives; R*ng*). We refer to this second measure of maternal relatedness as 'relative submatriarch relatedness' (R*xm*; Supplementary Materials Fig. 2). As R*ng* could not always be calculated (i.e. when the most recent common maternal ancestor was unknown), we used R*g* as a proxy for R*ng* in all cases to estimate R*xm*. We deemed R*g* an appropriate substitute for R*ng*, as the two measures were strongly positively correlated in cases where R*ng* was known (Pearson's $r = 0.94$, $p < 0.01$).

To account for a group's nutritional need, we estimated the daily prey energetic requirement (DPER; in kilocalories) at the level of the pod and subunit. Though group size may offer a coarse proxy for a group's nutritional requirements, such requirements vary immensely according to a killer whale's sex, age and reproductive status (Barrett-Lennard et al. 1995; Kriete 1995; Osborne 1999; Williams et al. 2004; Williams and Noren 2009; Noren 2011; Williams et al. 2011). Accordingly, we calculated individuals' DPER values using mass-to-calorie equations described by Noren (2011) and estimated average body masses for age-sex classes noted in Ford et al. (2010a). Because of uncertainty in the energetic costs of growth and lactation, and the effects of those processes on DPER values, we followed a conservative protocol adapted from Noren (2011): all animals' DPERs, except for young juveniles (ages 3–6) and adolescent males (ages 7–12), were calculated using Noren's lower bound equation. To take into account additional energetic costs of rapid growth, DPERs for young juveniles and adolescent males were derived using Noren's upper bound equation.

We accounted for the caloric needs of lactating females by inflating their estimated caloric requirement by 50% (Kriete 1995; Kastelein et al. 2003). We assumed that any animals less than 2 years of age had their caloric requirements satisfied through consumption of their mothers' milk (Kastelein et al.

2003). Any adult-aged animals (12+ years) of unknown sex were presumed to have the same requirements as a female of equivalent age, as we assumed that the sexually dimorphic increase in body size seen in males co-occurs with the onset of sexual maturation, which is physically apparent in the rapid growth of their dorsal fin.

Our final three measures concerned the abundance of food resources available to the NRKW population. We used two measures of Chinook salmon abundance, both aggregate indices that included stocks from Washington State to southeast Alaska (USA): (1) terminal run reconstruction estimates for southeast Alaska, northern BC, central BC, west coast Vancouver Island and Georgia Strait (Vélez-Espino et al. 2014), and (2) ocean abundance estimates for the Fraser River, Puget Sound and the upper Columbia River (Pacific Salmon Commission [PSC] 1987-2015). Terminal run reconstructions, as opposed to actual terminal run sizes, attempt to account for the impact of ocean fisheries, thereby providing a more realistic estimate of fish abundance available to oceanic predators such as killer whales (Kope and Parken 2011). The terminal run reconstruction estimates were stock-specific population indices for individual stocks known to be present in NRKW diet (Ford et al. 2010a; Vélez-Espino et al. 2014), whereas ocean abundance estimates provided approximations of cohort sizes from various stocks vulnerable to oceanic fisheries (PSC 1987-2015). Lastly, our third resource abundance measure was an index of chum salmon abundance that included stocks from Washington State to northern BC and consisted of an annual aggregate from three sources: (1) terminal run estimates from southern and central BC (Vélez-Espino et al. 2013; Fisheries and Oceans Canada 2016), (2) terminal run estimates from northern BC (English et al. 2016) and (3) terminal run estimates for Washington State, including Puget Sound and the outer Washington coast (PSC 1987-2015). The time series of these Chinook and chum measures are summarized in Supplementary Materials Fig. 3.

Statistical analysis

We chose to examine group splitting using two independent and distinct techniques: first, we used machine learning to determine the most powerful singular predictors of intrapod cohesion (HWI); and second, we competed candidate generalized linear mixed-effect models (GLMMs) to determine the most important explanatory model for intrapod cohesion in the NRKW population. We conducted all statistical analyses and figure generation in R (version 3.1.2; R Development Core Team 2015).

We used the same dataset for both techniques: our response variable (HWI) and explanatory variables ($n = 25$) were computed annually for each pod ($n = 56$) in the NRKW population in our time series (Supplementary Materials Table 1). Due to temporal limitations of available salmon terminal run reconstruction data, we restricted the time series used in the machine learning and GLMM analyses to 1980–2010. The working dataset contained 564 pod-year records, comprising 13 pods without, and 43 pods with, a living matriarch. The 13 pods without living matriarchs included seven wherein the CUs were assumed to be related through an unknown common maternal ancestor, and six where the common ancestor was either known or presumed (based on probable and certain maternal relationships; see Ford et al. 2000).

We assessed the relative importance and independent effects of our predictor variables using the random forest (RF) machine learning algorithm (Breiman 2001). The regression RF is an ensemble of independently constructed decision trees, built through the random selection of predictor variables at each node, from which the variable and value that optimizes the split are determined. RF is effectively the mean prediction of the individual trees. Using the R package *randomForest* (Liaw and Wiener 2015), we ran a regression RF with 500 trees and eight variables tried at each split to predict the strength of intrapod cohesion (HWI), with sampling stratified by pod ID. We assessed the relative importance of predictors in two ways: accuracy and node purity. These measures indicate the extent to which mean square error (MSE) and residual sum of squares (RSS), respectively, increase when the given variable is randomly permuted—with large changes indicating important variables.

To explore our four hypotheses of the proximate causes of group fission, we compared a set of GLMMs and selected the top-ranked model(s) using Bayesian information criterion (BIC; Schwarz 1978) score comparisons. We used score differences and model weights for inference: models with score differences less than four (when compared to the score of the top-ranked model) were considered among the top model set, and the top-ranked model of this set was considered the single best model if its weight was greater than 0.9 (Burnham and Anderson 2002).

We fit all candidate models ($n = 42$) with a binomial error distribution (logit link function) using the 'glmer' function in the R package *lme4*, which fits models using maximum likelihood (Laplace approximation) (Bates et al. 2015). We accounted for within-group variation in behaviour and repeated measures by including pod ID as a random effect in the models.

We generated our candidate models using combinations of the explanatory variables to describe each of our four hypotheses. Our candidate model set contained models that considered our hypotheses as independent mechanisms, models that considered biologically relevant combinations of our hypotheses and a null model without any fixed effects (Bolker et al. 2008) (Supplementary Materials Table 3). As we predicted that group splitting in the NRKW population ultimately resulted from population growth, we included group size as a fixed effect in all of our candidate models. This allowed us to

eliminate the effect of group size when comparing models so that we could identify the proximate causes of splitting.

We undertook data exploration of explanatory variables, following protocol described by Zuur et al. (2010). All non-binary predictor variables were centred (mean-subtracted) and scaled (divided by 2 SD) to facilitate the interpretation of effect sizes (Gelman 2008; Schielzeth 2010). We removed highly collinear variables (variance inflation factor, VIF > 3) from models; this occurred either through the removal of the more derived collinear variable or by correcting the collinear variable by its correlated counterpart. The latter correction process entailed fitting the relationship between the correlated variables using LOESS smoothing. The residuals of the resulting model were then used as the values for the 'corrected' variable.

Results

Population dynamics, pod structure and fission

Over the period of our study, NRKW pods and maternal groups grew in size and their average maternal relatedness decreased, creating conditions favourable for group splitting. The process of permanent group fission was prevalent in the 16 legacy pods, with average intrapod cohesion strongly declining over time and only four legacy pods meeting pod association criteria in 2014 (Supplementary Materials Fig. 4). These four legacy pods consisted of three pods composed of a single maternal group, two of which exhibited little-to-no overall growth over the course of the study and one of which exhibited growth (and has since undergone fission; Towers et al. 2020), and one pod composed of multiple maternal groups that exhibited fluctuating cohesion over the course of the study, splitting apart for multiple years no fewer than two times during the study period.

Splitting in the absence of a matriarch occurred at least once in all but two pods capable of undergoing this type of fission and took place within some pods that had resulted from previous fissions, yielding a total of 35 matriarch-absent splitting events among 11 unique pods between 1973 and 2014. Average cohesion among maternal groups in the population showed a moderate, negative correlation to population size (Pearson's $r = -0.53$, $p < 0.01$, $n = 42$). Though observed 38 times during the same period, fission in the presence of a matriarch was less common, occurring in only 50% of pods capable of this type of splitting ($n = 22/44$). Average cohesion within maternal groups exhibited a positive relationship with population size (Pearson's $r = 0.39$, $p = 0.032$, $n = 40$).

Net changes in the number of pods in the population were not significantly associated with population growth (mean change in number of groups per year ± SD = 0.9 ± 2.9 (1973–1994), 1.1 ± 3.9 (2004–2014)) or the period of no net growth (− 0.7 ± 1.8 (1995–2003); K-W $\chi^2 = 3.05$, $p = 0.22$). Rates of fission among the three periods in our time series showed no significant difference from one another (K-W $\chi^2 = 4.36$, $p = 0.11$; mean splits per year ± SD = 1.74 ± 1.42), while rates of fusion were significantly higher during the period of no net growth (K-W $\chi^2 = 7.86$, $p = 0.02$; mean reunions per year ± SD = 2.44 ± 1.94 (1995–2003)) than in the periods of rapid growth (0.77 ± 1.15 (1973–1994), 1.27 ± 1.19 (2004–2014)).

The number of pods present within the population from 1973–2014 was strongly positively associated with population size (Pearson's $r = 0.83$, $p < 0.01$, $n = 42$); on average, for every 17 animals added to the population as a whole, a new pod formed. The size and structure of pods were also closely coupled with population size, with the mean number of CUs per pod decreasing (Pearson's $r = -0.66$, $p < 0.01$, $n = 42$) and the number of individuals per CU increasing as population size increased (Pearson's $r = 0.96$, $p < 0.01$, $n = 42$). Pod sizes observed during our study ranged from 3 to 25 individuals and averaged 8 individuals. The minimum annual average pod size was observed in 1977 (6.3 individuals) and the maximum annual average pod size was seen in 2007 (9.2 individuals). Overall, the mean number of individuals per pod showed a weak positive correlation with population size (Pearson's $r = 0.51$, $p < 0.01$, $n = 42$).

Patterns of fission

Group splitting in NRKWs followed consistent patterns. In all fission events, resulting groups became discrete pods, rather than merging with others. Also, fission was kin-biased; resulting pods were always matrilineal, with individuals remaining with their direct maternal relatives.

In matriarch-present fission events, the split always occurred between the matriarch and her eldest daughter still remaining in the group. In all cases, the eldest daughter was that with the most maternal descendants. Additionally, matriarch-present splitting never occurred in pods composed of more than one CU.

Longevity of fission

According to our Kaplan-Meier analysis, the overall probability that fissioned pods would ultimately reunite was low, at 34% (Fig. 3). However, this probability was markedly different depending on the type of splitting that occurred; pods exhibiting matriarch-absent fission had a 25% probability of reunion, whereas those that underwent matriarch-present fission had a 70% probability of reunion.

Typically, pods that reunited did so within the first 3 years after splitting (mean = 2.5 years; median = 2 years), with a

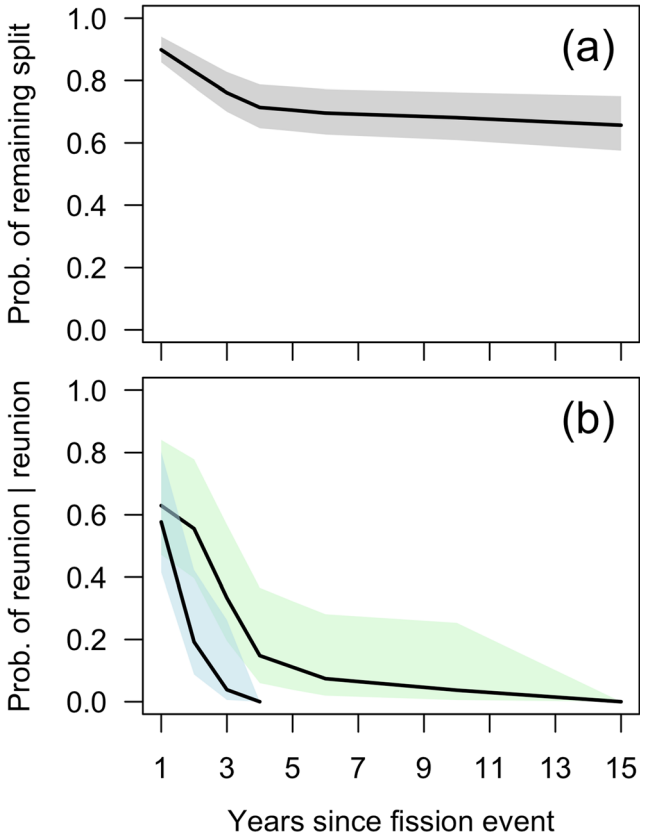

Fig. 3 Longevity of group fission according to **a** the probability that a pod will remain split and **b** the time-sensitive probability of reuniting (given a pod will reunite) according to the type of splitting the pod exhibited (fission in the absence [green] and presence [blue] of a matriarch), as a function of the time elapsed since a fission event

60% probability that the reunion occurred the year following the split. In only 2% of cases (n = 1/53 reunions), fusion occurred more than 10 years after splitting. The longest duration between splitting and reuniting was 15 years (n = 1). In this case, the strong re-association of pod members was temporary, lasting only one sampling period (June–October) before fission occurred again, along the same maternal lines as the original split. All reunions with a matriarch (n = 26) occurred within 4 years of splitting; the probability of reunion occurring more than 2 years after fission was less than 4%. In contrast, the probability of a reunion in the absence of a matriarch (n = 27) occurring more than 2 years after a fission event remained high (cumulative probability of 70%; Fig. 3).

This difference was reflected in the observed durations of the two splitting processes. Permanent splitting in the absence of a matriarch tended to be drawn out; often two decades passed between an apparent weakening of intrapod cohesion and consistent social separation (mean ± SD = 20.2 ± 11.9 years). The process of permanent splitting in the presence of a matriarch tended to occur on a much shorter time scale (mean ± SD = 6.9 ± 5.6 years).

Determinants of group fission

Machine learning

When scoring variable importance by accuracy (percent increase in mean square error, %incMSE), the RF algorithm ranked the total estimated daily caloric requirement of the pod as the top predictor (%incMSE = 29.0) of intrapod cohesion. The second-ranked predictor, the submatriarch's relative relatedness (Rxm), was significantly less important (%incMSE = 18.1) and was followed closely by the remaining 23 predictors in continuously decreasing importance. The lowest-ranked predictor was Chinook salmon terminal run abundance (%incMSE = 0.3). Variable importance ranked by the increase in node purity (incNP) was very similar to that ranked by accuracy, with DPERg assessed as the top-ranked predictor (incNP = 13.3) and all other 24 predictors following distantly, from the second-ranked predictor, group size (incNP = 6.5), to the lowest-ranked predictor, matriarch presence (incNP = 0.5).

As a singular predictor, the estimated daily caloric requirement of a pod predicts continuously decreasing intrapod cohesion with the increasing nutritional needs of the group, with out-of-bag predictions of HWI explaining 57.9% of the target variance of the training set (MSE = 0.05). The predicted probability of intrapod cohesion drops below 50% as a group's caloric needs reach approximately two million kilocalories per day.

Generalized modelling

According to BIC scoring, a single top-ranked GLMM predicted intrapod cohesion with 100% of the model weight. Of the eleven variables in the top model, seven were statistically significant and associated with each of our hypotheses: group size, relative submatriarch relatedness, proportion of physically mature males, age of submatriarch, proportion of lactating subunit females, chum salmon terminal run abundance and Chinook salmon ocean abundance (Supplementary Materials Fig. 5). Based on post hoc assessment of residuals, this model explained intrapod cohesion of pods with and without living matriarchs with similar success, suggesting that there is no apparent difference in the drivers of the two fission processes.

According to our top-ranked GLMM, group size had the greatest effect on intrapod cohesion, predicting lower cohesion with increasing group size (Supplementary Materials Fig. 5; Fig. 4a). All but two of the food competition variables were statistically significant predictors of intrapod cohesion: higher proportions of physically mature males in the pod predicted weaker intrapod cohesion (Fig. 4b), while increases in Chinook ocean abundance and chum terminal run abundance predicted a slight positive association with intrapod cohesion (Fig. 4d).

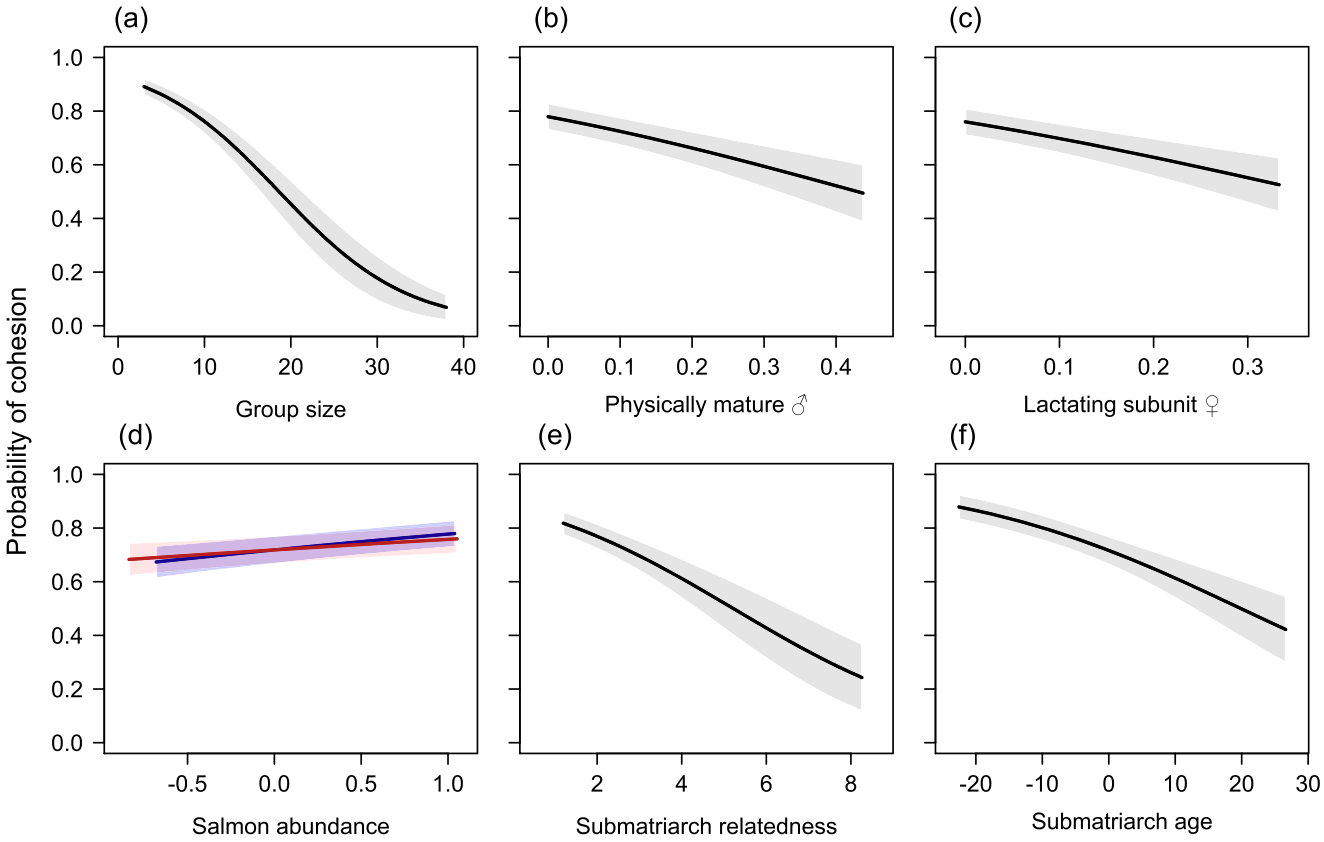

Fig. 4 Probability of intrapod cohesion as predicted by significant predictors of our top GLMM, when setting all other predictor variables to their mean values. **a** Group size (number of individuals in pod). **b** Number of physically mature males (as a proportion of group size). **c** Number of lactating subunit females (as a proportion of group size). **d** Centralized Chinook salmon ocean abundance (blue) and centralized chum salmon terminal run abundance (red). **e** Relative relatedness of the submatriarch (i.e. the submatriarch's average relatedness to her subunit is *x* times greater than her average relatedness to the rest of her pod). **f** Age of the submatriarch (corrected for group size; i.e. *n* years older (+) or younger (-) than the average age of submatriarchs of the same size pod). 95% confidence bands denoted by shading

Reproductive conflict, represented by the proportion of lactating females in the subunit, was a significant predictor of intrapod cohesion, with higher proportions of lactating subunit females predicting weaker cohesion (Fig. 4c). Most splits with a matriarch (85%; $n = 29/34$) during our restricted time series (1980–2010) involved daughters fissioning with a post-reproductive matriarch. Of the five splits involving a matriarch of reproductive age during this period, four (12%; $n = 4/34$) coincided with the matriarch and her daughter having overlapping lactation periods due to synchronous calving. Lactating females were present in both the subunit and the rest of the pod in 25% of all splitting events during this time period ($n = 16/63$), and present only in the subunit in 41% ($n = 26/63$) of these events.

The two remaining significant predictors identified by our top model were associated with our kinship and leadership hypotheses. Relative submatriarch relatedness had a strong effect on intrapod cohesion, predicting weaker cohesion as the submatriarch's relatedness to her direct descendants increased relative to her relatedness to the rest of her pod (Fig. 4e). The age of the submatriarch was also a significant predictor in our top model. When the submatriarch was older than the average submatriarch of a comparably sized pod, weaker intrapod cohesion was observed; whereas if she was younger than the average submatriarch of a comparably sized pod, stronger intrapod cohesion was observed (Fig. 4f).

Discussion

Nearly 50 years after the study of killer whales in the eastern North Pacific began, studies of resident-type killer whales have revealed further complexities of killer whale society. Throughout resident killer whale populations, there is often considerable dynamism in associations observed among pod members over time (Ford and Ellis 2002; Parsons et al. 2009). We now recognize the pod as a social grouping that may only maintain cohesion for a decade or less, presumably due to population growth, demographics or ecological factors. The temporary condition of the pod raises questions about the nomenclature used to describe resident social structure: what do we call pods when they are no longer pods? How do we describe the structure of dynamic social groupings so that they are comparable across years or decades?

Here, we have chosen to retain the term 'pod' for all assemblages of maternal groups that meet the Bigg et al. (1990) criteria at a given time. To distinguish newly formed pods from those originally delineated by Bigg et al. (1990), we use the term 'legacy pod' for pods that have historically existed.

Pods and maternal groups can exhibit varying degrees of maternal relatedness, where a group's common maternal ancestor may be more or less recent, alive or dead, and where female survival may differ, resulting in more or less fragmented groups. As a result of this complexity, we suggest new nomenclature for group structures based on matrilineal units: 'basal units', 'nested units' and 'complete units'. These terms allow social groupings at any level of resident social structure to be described consistently over time and are particularly helpful in light of maternal group splitting, as they provide functional subsets of the maternal group. Complete and nested units must be led by an extant female who is a direct maternal ancestor to all in her unit, which therefore excludes individuals with no living mother and no local offspring (Supplementary Materials Fig. 1). This nomenclature scheme is therefore limited in describing highly fragmented groups and in examining potential fission involving groups of motherless and childless individuals (e.g. orphaned kin separating from grandmother or aunt). This type of group splitting, while not exhibited during the time period of our analysis, has since been observed in the NRKW population (Towers et al. 2020).

Population growth may influence group structure and lead to group splitting, specifically when growth results in a small number of large matrilines per social group and negative or slow growth results in social groups composed of several smaller matrilines (Melnick and Kidd 1983; Lefebvre et al. 2003). Both scenarios may result in group splitting: in the former, groups grow to an unsustainable size, and in the latter, groups are assemblages of small, weakly bonded units. In both cases, splitting is likely due to the decline in inclusive benefits of cooperation resulting from weakened kinship among group members. The NRKW population has steadily increased in size and as of 2014 was 2.5 times larger than it was in 1973, with growth rates nearing and sometimes exceeding the 4% maximum theoretical rate of increase typical of cetaceans (Wade 1998). Given such high population growth and the strong natal social philopatry exhibited by both sexes, new pods were expected to arise in the NRKW population through the process of matrilineal fission (Bigg et al. 1990). Our analysis shows that, though fission does not appear to be directly driven by population growth, the number of pods present within the population is strongly linked to the population's size; roughly, for every 17 animals added to the population as a whole, a new pod formed. Similarly, from a group perspective, our model findings predict that as an NRKW pod grows its probability of remaining a cohesive social unit decreases. An NRKW pod's probability of cohesion drops below 50% when its size reaches 20 individuals (according to our top GLMM) or when its daily caloric need reaches two million kilocalories (equivalent to approximately 122 Chinook salmon averaging 9.8 kg each, Stredulinsky 2016; according to our RF results). These caloric needs are typically found in NRKW groups composed of 10–15 individuals.

Group splitting in the NRKW population occurred in a predictable manner. This was especially notable in the relative frequency of matriarch-absent and matriarch-present fission, with splitting occurring more frequently in the absence of a matriarch, when accounting for the number of pods capable of each type of fission. The differential frequency between the two processes was expected, as it is commonly observed in other species that exhibit matrilineal fission, where groups preferentially split along maternal lines rather than across them, thereby maximizing the maternal relatedness of the resulting groups (Lefebvre et al. 2003; Widdig et al. 2006; Lawson Handley and Perrin 2007).

Splitting in the presence of a matriarch always involved the oldest daughter still remaining in the group splitting from the matriarch with her maternal descendants. Similar patterns of fission in primate populations have been attributed to reverse dominance ranks among sisters (e.g. Chepko-Sade and Sade 1979; Chapais 2004). In rhesus monkeys (*Macaca mulatta*), mature sisters rank in the inverse order of their ages, with the oldest receiving the lowest rank among her sisters (Datta 1988; Holekamp and Smale 1991). In this case, the oldest daughter, being the social subordinate, is 'peripheralized' by her group and disperses (Christian 1970). In NRKW, mothers share prey with their daughters less frequently as a daughter ages, but this correlation is more strongly linked to the existence of the daughter's offspring than her birth rank (Wright et al. 2016). In our study, submatriarchs in matriarch-present fissions were always the leaders of the largest nested unit within their respective pods, and thus we cannot test the effect of relative nested unit size on fission separately from the effect of submatriarch birth rank. Should subunits in these splits continue to be the largest nested units in their pods, regardless of differences in submatriarch birth rank, unit size is likely delineating the subunit. Conversely, should the subunits in these splits continue to be led by the oldest daughter, despite not leading the largest nested unit in her pod, other mechanisms for subunit delineation, such as dominance structures, are likely at play. This would require further investigation, as no dominance interactions have yet been documented among female resident killer whales.

Leadership experience could also explain why the oldest submatriarch was involved in fissioning. The presence of a matriarch promotes intragroup cohesion in many matrifocal mammalian species (e.g. Chepko-Sade and Sade 1979; Wittemyer et al. 2005; Archie et al. 2006; Berry and Bercovitch 2014). Perhaps most importantly, as the oldest member of the group, a matriarch is her group's richest source

of ecological and social knowledge and, through social transmission, can enhance her group's collective knowledge (McComb et al. 2001; McAuliffe and Whitehead 2005). Her leadership undoubtedly affects her group's wellbeing (Foley et al. 2008; McComb et al. 2011; Berry and Bercovitch 2014; Brent et al. 2015) and may influence group members' dispersal decisions. The fitness costs of reduced contact with the matriarch could delay a subunit's social dispersal until the submatriarch has acquired sufficient knowledge from the matriarch (e.g. Lutermann et al. 2006). This may be the case in NRKWs, where our GLMM results suggest that pods with older submatriarchs were more likely to split than were comparably sized pods with younger submatriarchs.

Behaviours that strengthen and maintain social bonds among individuals but are costly to the individual can delineate substructures within groups. Given that animals can be limited as to the number of individuals with which they can conduct interactions, they may be unable to maintain strong bonds with all individuals within their group, beyond a certain group size (e.g. Kudo and Dunbar 2001; Shultz and Dunbar 2007; Pollard and Blumstein 2008; Lehmann and Dunbar 2009; Bergmüller et al. 2010; Dávid-Barrett and Dunbar 2013). Preferential relationships in many social species are dictated by maternal relatedness (Gouzoules 1984; Walters 1987; Wittemyer et al. 2005; Berman et al. 2008), which can also be an indicator of familiarity among individuals (Chapais 2001; Majolo et al. 2008) and is a good predictor of group fission in various species (Chepko-Sade and Olivier 1979; Archie et al. 2006; Widdig et al. 2006; Van Horn et al. 2007; Sueur et al. 2011).

Our results suggest that pod substructuring, delineated by maternal kinship, is an important correlate of group splitting in NRKWs. Although group structure described by the number and mean size of CUs within a pod did not show a strong effect on NRKW intrapod cohesion, a submatriarch's relative relatedness was a significant predictor of cohesion. In populations such as this, with philopatric males and non-local mating, a female's local relatedness increases with age as she produces offspring (Johnstone and Cant 2010; Croft et al. 2017). As a submatriarch's relative relatedness increases, the inclusive fitness benefits resulting from her cooperation with non-lineal relatives may be reduced, particularly compared to those gained from aiding her direct descendants (Frank 2013). This weakened kinship, in turn, may lead to greater substructuring (Lefebvre et al. 2003), where weakening interactions between the subunit and other pod members may result in reduced intrapod cohesion and an increased probability of group fission.

In resident killer whales, maternal relatedness drives differential prey sharing (Wright et al. 2016), a behaviour that, in other species, may allow parental control of dispersal (Ekman and Rosander 1992). Notably, maternal provisioning of offspring in NRKWs declines as offspring mature, particularly for daughters as they reach reproductive maturity and produce their first offspring (Wright et al. 2016). If kin-directed prey sharing reinforces social bonds among resident killer whale individuals, the behaviour may delineate group substructures, where social bonds among individuals of different basal units may be weaker.

Having established group size as the ultimate cause of pod splitting in NRKWs, we then considered why large group sizes in this population might be so costly. Intragroup competition for food was the most strongly supported hypothesis in both our GLMM and RF findings. Group splitting among social animals can optimize feeding opportunities and alleviate competition for food among group members (e.g. Dittus 1988; Whitehead and Weilgart 2000; Ren et al. 2012; Schaffner et al. 2012). A group's nutritional requirement is determined by the number of animals in the group and the proportion of animals that require more food due to metabolic processes such as growth and lactation. We predicted that increased group metabolic requirements would adversely affect intrapod cohesion, because (a) time spent socializing would be sacrificed in favour of foraging to satisfy nutritional needs, thus weakening social bonds within the group, and/or; (b) competition for food among pod members would increase, thus promoting group splitting to improve per capita prey availability.

Our GLMM results indicate that NRKW pods with higher proportions of physically mature males and lactating subunit females had lower intragroup cohesion and a higher probability of fission. A similar negative correlation between males and their group's cohesion has been observed in resident-type killer whales in the western North Pacific (Ivkovich et al. 2010; Filatova et al. 2017). Physically mature males and lactating females have a disproportionate impact on their group's nutritional needs (Noren 2011). Mature males, in particular, have high caloric requirements but contribute little to intragroup prey sharing (Wright et al. 2016). A fully grown male may require 13–16 Chinook salmon (averaging 9.8 kg each) per day, 2–3 times the calories required by a young animal (Stredulinsky 2016). Likewise, a lactating female may be required to catch roughly five more fish each day than her non-lactating counterparts (Stredulinsky 2016), increasing her food intake by 1.5–2 times, especially in the first few months of producing milk (Kriete 1995; Kastelein et al. 2003; Noren 2011).

According to our GLMM results, synchronous lactation within a pod increased the probability that the pod would undergo fission, which suggests that group splitting may be a way to avoid reproductive conflict. In long-lived socially philopatric species such as resident killer whales, the probability of an older female breeding at the same time as younger, closely related females in the same group is high. Younger females have the selective advantage in this inter-generational reproductive conflict, with older females having significantly

less reproductive success than their co-breeding daughters, and thus this reproductive conflict is suggested to have contributed to the evolution of menopause in resident killer whales (Croft et al. 2017). However, the inter-generational (mother-daughter) conflict central to reproductive conflict theory may have only played a small role in the group fission we observed in this population; the great majority of matriarch-present splits involved a post-reproductive matriarch and few splits coincided with a reproductive matriarch and her daughter in direct reproductive conflict. Additionally, there is limited evidence that splitting alleviated broader reproductive conflict between females in the subunit and those in the remainder of the pod; lactating females were present in both groups in only 25% of splitting events. Further, as the proportion of lactating subunit females out-competed lactating females from the whole pod at predicting intrapod cohesion, splitting was likely influenced by insufficient prey availability to females (e.g. Isbell and van Vuren 1996) rather than by avoidance of reproductive conflict between the subunit and other pod members.

Although we expected that higher median group age would predict lower intrapod cohesion because of the increased food requirements of mature individuals, median group age was not a significant predictor of intrapod cohesion in our top-ranked GLMM. From an energetic standpoint, a pod's caloric needs increase as it contains more mature individuals, which in turn might promote fission to alleviate food competition among pod members. Alternatively, mature individuals (especially females) typically contribute the most to caretaking, foraging and prey sharing, behaviours that likely promote social cohesion (Waite 1988; Wright et al. 2016). These competing consequences of age may explain the lack of significance of our age predictor variable. Further, this absence of significant statistical association may be the reason for the disparity between our RF and GLMM results, wherein DPER was found to be an important predictor in the former but not the latter. DPER was the best singular predictor of intrapod cohesion selected by our RF analysis. Our best GLMM model, however, did not include DPER but rather incorporated all individual components from which DPER is derived: number, age and reproductive status of individuals in the group. With the capacity to assess the additive effects of several predictors, our GLMM results showed all components of DPER except age to be strongly relevant to group splitting.

If groups split at a relatively predictable group size, intrinsic—rather than environmental—factors are thought to be primarily responsible for fission (Thierry et al. 2004; Sueur and Maire 2014). However, extrinsic pressures can have a direct impact on the population dynamics and characteristics of a group (Sueur et al. 2011) and may affect the favourability of a group's demographic conditions (e.g. Ekman and Rosander 1992), and therefore may still be important auxiliary factors in group fission. While our findings indicated demographic effects have a greater influence on NRKW intrapod cohesion than environmental factors, two of our salmon abundance predictors remained important explanatory variables in our top-ranked GLMM. Higher abundances of both Chinook and chum salmon (particularly ocean abundance and terminal run abundance, respectively) predicted higher intrapod cohesion. Chinook salmon, which dominates resident killer whale diet from June to September (Ford and Ellis 2006; Ford et al. 2010a; Hanson et al. 2010), is a significant correlate of resident killer whale survival and fecundity (Ward et al. 2009; Ford et al. 2010b; Vélez-Espino et al. 2014) and has also previously been identified as a correlate of social behaviours in resident killer whales, with years of low Chinook abundance associated with smaller group sizes and weaker social network connectivity (Lusseau et al. 2004; Foster et al. 2012). Chum salmon (*Oncorhynchus keta*) is an important component of NRKW diet, surpassing Chinook salmon frequency in NRKW diet in early fall (September–October) (Ford and Ellis 2006; Ford et al. 2010a). Chum salmon abundance is a useful predictor of resident killer whale vital rates (Vélez-Espino et al. 2013), but has not been examined as a predictor of resident killer whale social behaviour prior to this study. Our findings support the growing body of evidence suggesting changes in the quantity and quality of these important prey species affect not only the survival and fecundity of resident killer whale populations but have significant influence on their social dynamics as well.

Conclusion

We demonstrate that large group size drives group splitting in NRKWs and that population growth does not appear to influence the rate at which group fission occurs. Intrinsic group characteristics associated with food competition within large pods provide strong correlates of group splitting in this population, particularly those dictating groups' nutritional requirements (e.g. lactation) and the distribution of food competition within groups (due to substructuring delineated by maternal kinship, likely mediated by kin-directed behaviours like prey sharing). Though food competition within groups is a strong predictor of group splitting, prey abundance has only a marginal effect on intrapod cohesion. Splitting also appears to be inhibited in the absence of adequate leadership; pods require a submatriarch of sufficient experience before group splitting can occur.

Matrilineal fission may have profound effects on an individual's fitness, a population's genetic structure, and processes involving the vertical transmission of knowledge (such as acoustic dialect evolution). We encourage future studies to examine the consequences of matrilineal fission in resident killer whales, for which this work provides a foundation. Our findings further underscore the importance of

incorporating social dynamics into the management of threatened populations of killer whales.

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Data availability The datasets derived and analysed during the current study are available in Electronic Supplementary Materials and in the Open Government repository: https://open.canada.ca/data/en/dataset/8c773994-1031-411b-a1ad-933928daa4ac.

Declarations

Ethics approval and consent to participate All applicable international, national and institutional guidelines for the care and use of animals were followed. Data used in this study were collected under Fisheries and Oceans Canada Marine Mammal Research License no. MML-001. All field procedures were approved by the Pacific Region Animal Care Committee of Fisheries and Oceans Canada (Pacific Biological Station), and complied with the standards of animal care set by the Canadian Council on Animal Care.

Consent for publication Not applicable

Conflict of interest The authors declare that they have no conflict of interest.

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