

A collective navigation hypothesis for homeward migration in anadromous salmonids

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Abstract

Anadromous salmon (genera *Oncorhynchus* and *Salmo*) spend much of their lives feeding in productive northern oceans and then return home to natal sites for reproduction with remarkable accuracy. The mechanisms used for navigation by individuals during migrations are thought to include geomagnetic, celestial and olfactory cues, but rarely are social interactions between individuals considered. Mounting evidence from other taxa indicates that individuals in larger groups can better sense and respond to environmental cues, thus potentially increasing their ability to navigate. Here, we propose that salmon might similarly benefit from collective navigation on their homeward journey. To explore this, we compiled data from multiple studies and found strong evidence that rates of successful homing increase with population abundance, consistent with collective navigation. We then discuss how collective navigation could benefit salmon during each stage of their seaward and homeward migrations, and complement this with a review of salmon sociality. Next, we analyse historic high seas catch records and provide new insight into schooling structure of salmon in the marine environment. We argue that collective navigation likely represents a presently under appreciated

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mechanism enhancing the navigational ability of salmon as well as other migratory species, and outline critical tests of our hypothesis.

Keywords Collective behaviour, density dependent dispersal, homing and straying, meta population dynamics, orientation, schooling

Introduction

The annual return of anadromous (i.e. sea going) Atlantic and Pacific salmon (genera *Oncorhynchus* and *Salmo*, family *Salmonidae*, hereafter 'salmon') to freshwater for reproduction has captured the imagination of scientists, naturalists and native people alike for centuries (NRC 1996). An integral aspect of salmon biology is their remarkable ability to navigate back to natal locations for reproduction after foraging at sea (*Oncorhynchus* reviewed by Quinn 1993; Keefer and Caudill 2013; *Salmo*: Jonsson and Jonsson 2011). Homing (philopatry) and straying (dispersal) are fundamental to salmon ecology, shaping the evolution, and guiding the management of populations (Quinn 2005). The frequency of homing versus straying is thought to exist in a dynamic balance, shaped by site specific selection pressures on the spawning and rearing grounds (Quinn 1984, 1993; Hendry *et al.* 2004).

The proximate mechanisms that facilitate the imprinting and homing processes are increasingly well known [recently reviewed by Ueda (2012) and Keefer and Caudill (2013)]. Briefly, sequential imprinting by downstream migrating juveniles to unique odours of local environments appears to provide a road map during the freshwater phase of the return migration by adults (Scholz *et al.* 1976; Hasler and Scholz 1983; Dittman and Quinn 1996). As freshwater cues are too diluted to be detected at sea, salmon appear to rely on geomagnetic gradients to guide them back to the estuaries of their local rivers (Putman *et al.* 2013), where olfactory cues then predominate (Scholz *et al.* 1976).

Collective behaviour has been shown, both theoretically and experimentally, to increase the ability of individuals in groups to sense and respond to their environments for many taxa, including fishes (Couzin 2009; Berdahl *et al.* 2013). However, at all phases of the life cycle of salmon, migratory orientation has been examined as an individual level process. Although schooling and other forms

of aggregative behaviour are known in salmon, to date a role of collective behaviour in orientation and navigation has not been formally articulated (but see Larkin and Walton (1969) for an early appreciation of the possible role of interindividual interactions).

We present a synthesis of existing datasets, novel analysis, and pertinent empirical and theoretical literature to explore the potential for collective navigation to operate during the adult salmon homing migration. To explore this hypothesis, we first compile published data on homing and straying as functions of abundance and find a significant and consistent trend of declining straying with abundance, in multiple populations and species. Next, we review the literature on collective behaviour and describe how various aspects could improve the navigational ability of salmon at each stage of their homeward breeding migrations by following a hypothetical cohort of migrating salmon from the ocean to their spawning locations. Finally, we analyse data from high seas salmon research and review relevant literature suggesting that salmon migrate in groups or at least at densities high enough to use social information, and they are able to effectively sort into destination specific groups.

Homing and abundance

Quinn and Fresh (1984) reported evidence that straying *decreased* with increasing numbers of returning adults and noted that it was consistent with the findings of Sholes and Hallock (1979). Later, in a review of salmon homing and straying, Hendry *et al.* (2004) found that this trend was indeed widespread, stating that while the mechanism was unclear, the phenomenon presents an 'interesting avenue for future theoretical work' [p. 72]. We hypothesize that navigational ability is enhanced in migrating salmon by acting collectively, providing an explanation for the empirical relationship between abundance and rates of homing or straying by adults.

To explore this idea, we identified seven independent studies reporting both abundance and straying rate (Table 1), estimated by tag recovery programs (e.g. see Regional Mark Processing Center at www.rmpec.org) that quantified the number of fish returning to natal and non natal streams. Figure 1 shows the negative trends between straying rate and run size in all seven studies. In this figure, we divided the data from Jonsson *et al.* (2003) into separate panels for wild and hatchery fish to examine the difference in the trend between these groups, but to be conservative, consider the study of a single independent sample. It is very unlikely that seven negative slopes of seven datasets arose by chance alone (binomial test, $P = 0.008$). Several of the studies included data from multiple populations, and negative trends were observed in 74% of the populations, which again was unlikely to have occurred from chance (binomial test, 25 negative trends of 34 trends, $P < 0.01$). Thus, at the regional (study) and local (population) scale, this consistent trend of decreased straying with increasing abundance was found in Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), steelhead trout (*Oncorhynchus mykiss*), and Atlantic salmon (*Salmo salar*) across various locations and populations (Table 1).

The remarkably swift colonization of large sections of new habitat following point introduction of salmon provides additional, albeit indirect, evidence of a negative relationship between straying and abundance. Non native Chinook salmon introduced into a single river in New Zealand spread in just a few generations to essentially all the rivers where they were ever found (Ayson 1921). This rapid expansion would not be expected based on contemporary straying rates in those populations (Unwin and Quinn 1993).

Therefore, it appears that straying rates must have been much higher in these initial, sparse, populations. Similar flash expansions due to high straying have been documented in populations introduced at low density in Patagonia (Becker *et al.* 2007; Correa and Gross 2008) and the Great Lakes (Emery 1981; Kwain and Lawrie 1981).

Collective behaviour

Collective behaviour (schooling, flocking, herding, etc.) is ubiquitous among animal taxa (Krause and Ruxton 2002) and is particularly common in fishes (Pitcher and Parrish 1993). A significant benefit for many organisms that live in groups may be collective intelligence (Couzin 2007, 2009), and mounting evidence demonstrates that simple interactions among individuals with relative unsophisticated behaviour may produce complex outcomes that are adaptive at the group level (Bonabeau *et al.* 1999b; Seeley and Buhrman 1999; Franks *et al.* 2002; Camazine 2003; Sumpster 2006; Berdahl *et al.* 2013).

Here, we are interested in a particular facet of collective intelligence: navigational ability. Theoretical work predicts that collective migratory strategies might evolve under a wide range of ecological scenarios (Torney *et al.* 2009, 2010; Guttal and Couzin 2010; Shaw and Couzin 2013), and it may be no coincidence that migrations and other navigational feats are often undertaken by large groups (Beauchamp 2011; Milner Gulland *et al.* 2011). Homing pigeons return more efficiently when released as groups than they do as individuals (Biro *et al.* 2006; Dell'Arciccia *et al.* 2008), and birds with less information can benefit from following others (Flack *et al.* 2012). Theories, like

Table 1 Datasets reporting straying rate as a function of run size.

Study	Species	Number of populations	Location
Sholes and Hallock (1979)	Chinook	1	Feather River, California
Quinn and Fresh (1984)	Chinook	1	Cowlitz River, Washington
Labelle (1992)	Coho	6	Vancouver Island, Canada
Hard and Heard (1999)	Chinook	1	Sashin Creek, Alaska
Schroeder <i>et al.</i> (2001)	Steelhead	3	Oregon, USA
Jonsson <i>et al.</i> (2003)	Atlantic	2	River Imsa, Norway
P.A.H. Westley, T.P Quinn and A. Dittman (Unpublished data)	Chinook	20	Columbia Basin, USA

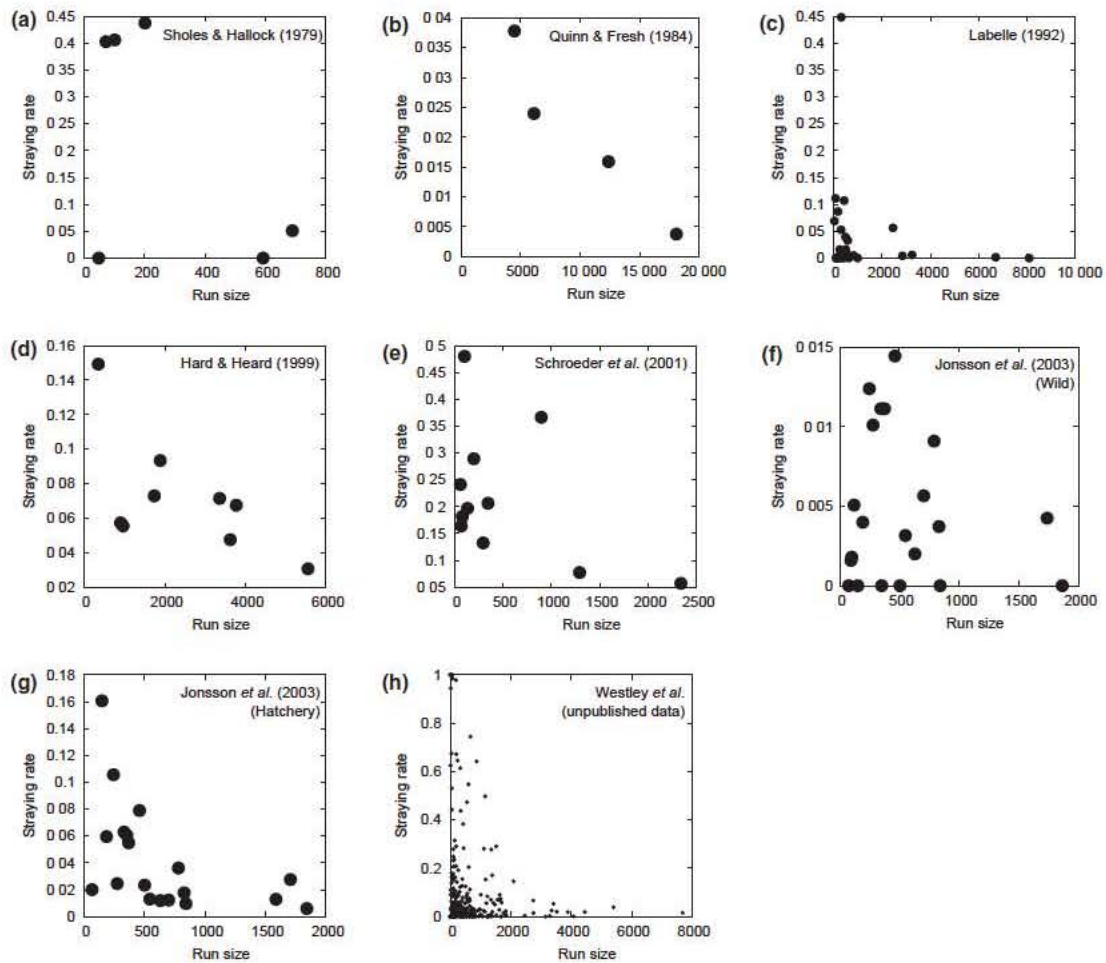


Figure 1 Straying rate as a function of run size. We plot the proportion of salmon straying from their natal river as a function of the total number of salmon from that population returning that year for every study reporting such data. In all the sets, representing four species, there is a negative relationship between the two variables, indicating salmon stray less in years of greater abundance. Naturally, each population has a different range of run sizes and straying rates mediated by the particular environmental conditions that population faces; thus, we do not expect the same quantitative trend in each panel. Note we have partitioned the data of Jonsson *et al.* (2003) into separate panels showing data for wild and hatchery fish.

the ‘many wrongs principle’ (Larkin and Walton 1969; Grünbaum 1998; Simons 2004; Codling *et al.* 2007), predict that such groups may average out errors made by individuals, thereby enhancing the individual navigational strategy (see Box 1). Using an evolutionary model of migrant populations Guttal and Couzin (2010) showed that when interactions among organisms are relatively inconspicuous, such as when migrants do not form coherent groups, they may nevertheless provide vital social cues that aid migration. It has also been shown theoretically

(Torney *et al.* 2009, 2011) and empirically (Berdahl *et al.* 2013) that a group’s ability to climb a gradient can emerge from social rules alone, without any individual level ability to estimate the gradient. In this case, the group does not enhance the individual strategy because no individual taxis exists; navigation would be entirely absent for a lone traveller, but nonetheless emerges at the group level. In general, collective behaviour could simultaneously do both: that is, it can enhance individual strategies as well as lead *de novo* to group level emergent effects.

Box 1. Collective directional estimates

In 1907, Sir Francis Galton was able to estimate the dressed weight of an ox to within a pound by pooling guesses made by many independent observers (Galton 1907). Today, we know this effect as the ‘wisdom of the crowd’ (Surowiecki 2004) or the ‘many wrongs principle’ (Simons 2004) – averaging over many independent estimates tends to suppress outliers. It is thought that this principle applies to animals during their migrations when they are faced with difficult orientation tasks (Larkin and Walton 1969; Simons 2004; Codling *et al.* 2007). Although they may all be intent on the same target, each individual might have some error in its estimation of in which direction that target lies. These errors may be due to noise in whatever cue they are using to orient themselves, noise in their sensing of that cue, or cognitive limitations in processing directional information from the cue. Group movement, such as schooling or flocking, acts to pool the many individual orientation preferences of the group into an average heading, suppressing noise about the mean.

Here, we consider a group of salmon. Each one, using geomagnetic cues, estimates the heading needed to make landfall near the estuary of its natal river system. We define accuracy as the probability of orienting towards a small target of angular size ϕ (for convenience, and without loss of generality, we will say that ϕ is located due north, at $\theta = 0$). As in Larkin and Walton (1969), we assume that the estimates of each individual can be approximated by a circular normal distribution, all centred about the correct direction, $\theta = 0$, that is, there is no bias. Accuracy for a single individual is then given by

$$A(\sigma) = \int_{-\phi/2}^{\phi/2} C(\theta, \sigma) d\theta$$

where $C(\theta, \sigma)$ is the circular normal distribution (probability to orient at angle θ) with variance σ . Due to the sources of noise discussed above, the variance in this distribution might be quite high, so accuracy, A , will be low. If the group orients itself by effectively averaging the heading estimate of each fish, as a consequence of the law of large numbers, the variance in the distribution of group orientations declines as $1/\sqrt{N}$, where N is the number of members in the group (see Larkin and Walton (1969) for details). Thus, for larger group sizes, accuracy is increased nonlinearly.

In Fig. 2, we plot the individual accuracy required to achieve a specific group accuracy for such an orientation task. For a specific group accuracy, the onus on each individual fish to make an accurate directional estimate monotonically decreases as group size increases. Alternatively, by tracing a horizontal line across the plot, one can see that for a set individual accuracy, increasing group size dramatically increases the group accuracy. This demonstrates a simple mechanism by which salmon could use collective behaviour to achieve navigation not possible by an individual, or use collective behaviour to attain the same level of accuracy during migration, but with a reduced cost to each individual.

Collective navigation and salmon migration

Here, we explore the potential role of collective navigation to aid migration of an archetypical cohort of salmon crossing the high seas from their feeding areas to coastal waters, locating the estuary of their home river, and ascending a network of tributaries to their natal site.

Migration from the high seas

Tagging studies indicate that once salmon begin their migration home, they swim at roughly the most energetically efficient speed (ca. 1 body

length per second or ca. 2 km h^{-1}) and exhibit highly oriented travel because they routinely travel $30\text{--}50 \text{ km day}^{-1}$ directly towards their home stream (reviewed by Quinn 2005). A growing body of work reveals that the salmon can detect and use Earth’s magnetic field as a compass (Quinn 1980; Quinn and Brannon 1982) or a map (Bracis and Anderson 2012; Putman *et al.* 2014). Gradients of salinity and temperature are also available to the salmon during this phase, and they may use them to find productive foraging conditions (Leggett 1977), but it is unlikely that they use those cues during their homeward migration (reviewed in Quinn 2005).

Assuming that each fish has some inherent orientation capacity based on geomagnetic or other cues, individuals ostensibly can use schooling to pool their estimates and cancel out the errors and noise in individual directional estimations. This collective pooling of individual abilities into the school would enhance individual level orientation capacity (Larkin and Walton 1969; Grünbaum 1998). Moreover, the group can effectively be led by only a few informed individuals (Couzin *et al.* 2005; Guttal and Couzin 2010; Mueller *et al.* 2013); as group size increases, the fraction required to lead it successfully diminishes (Couzin *et al.* 2005; Guttal and Couzin 2010).

In Box 1, we present a toy model for collective orientation, relevant to salmon making their way from their feeding grounds on the high seas to the mouth of their natal stream, and the results are shown in Fig. 2. The key result is that the navigational onus on the individual decreases as group size increases and that high rates of group accuracy can result through the co migration of relatively poorly orientating individuals. Simulations indicate that directional orientation is needed for salmon to accomplish these migrations, but such models have typically treated salmon as individu-

als, deriving no benefit from group interactions (e.g. Pascual and Quinn 1991; Dat *et al.* 1995; Bracis and Anderson 2012).

Locating and entering the estuary

As salmon approach land, their environment changes dramatically. Variations in salinity and water temperature increase, and the water becomes vertically stratified closer to shore. Currents increase and reverse due to tidal action and interactions with the continental bathymetry. Once in coastal waters, the sea floor comes into sensory range of the migrating fish and they encounter intricate shorelines. Compared to the simplicity of the open ocean, the array of islands, bays, straits and narrows is a veritable maze. Although the precise timing of when geomagnetic or celestial cues give way to olfactory processes is unknown, presumably there is a shift towards the latter during the transition through the estuary (e.g. Hasler 1966).

Experimental evidence reveals that fish in larger groups are better able to sense and respond to complex gradients, like those salmon encounters in estuaries (Lenwood *et al.* 1982; McNicol *et al.* 1996; Berdahl *et al.* 2013). As outlined in Box 1, schooling may allow migrating salmon to pool noisy individual estimates of the appropriate direction to travel (Larkin and Walton 1969; Grünbaum 1998; Codling *et al.* 2007) also see Fig. 2. In addition, larger groups, by virtue of spanning a larger area, might act like a sensory array, sampling for the 'signal' at a spatial scale larger than the 'noise' (Couzin 2007). Furthermore, in gradient tracking and source detection tasks, grouping can lead to a directional response even when no single individual can measure the gradient, and the strength of this response increases for larger groups (Torney *et al.* 2009, 2011; Berdahl *et al.* 2013).

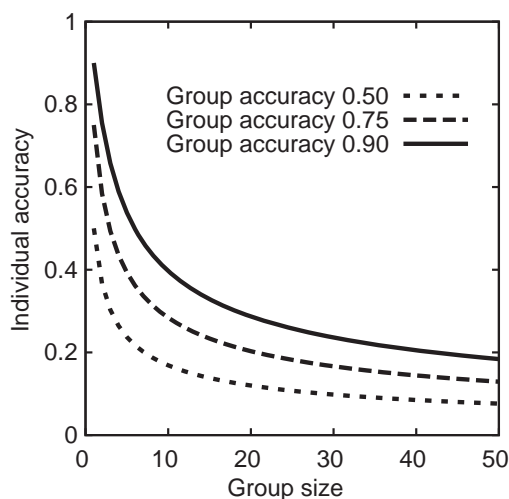


Figure 2 Individual accuracy required to achieve a specific group accuracy for a directional estimation task. Here, accuracy is defined as the probability the directional estimate is within a small, fixed and angular area around the correct direction (see Box 1 for details). For a certain group accuracy, the onus on each individual fish to make an accurate directional estimate monotonically decreases as group size increases. For a given individual accuracy, the group accuracy increases monotonically with increasing group size.

Negotiating the river network

Once migrating salmon enter their natal river system, a positive rheotactic response (i.e. upstream swimming) triggered by detection of an imprinted odour is sufficient to navigate upstream (Johnsen 1982). Fish might search for the most efficient route upstream to minimize energy costs (Hughes 2004; McElroy *et al.* 2012), but for long stretches, navigation is relatively simple upstream.

However, the salmon face a binary decision at each river confluence concerning which branch to ascend.

Locating a small tributary that enters much larger streams may be difficult for migrating salmon. In this case, collective gradient tracking strategies perpendicular to the flow, combined with the rheo-tactic response upstream (Torney *et al.* 2009), would facilitate salmon being on the correct side of the channel in a good position to find these small tributaries. At confluences of similar sized tributaries, salmon presumably could sample the odour cues of both branches by travelling a short distance up both or by simply traversing the river channel at the confluence perpendicular to the direction of flow. Indeed, short term sampling of non natal streams appears to be common in salmon migrating in large rivers (Keefer *et al.* 2009).

The two river branches might have very similar chemical composition, and distinguishing between them could be difficult (Dittman and Quinn 1996). Larger groups of fish are better able to sense odour

cues (Lenwood *et al.* 1982; McNicol *et al.* 1996). Furthermore, empirical (Sumpter *et al.* 2008; Ward *et al.* 2008, 2011; Arganda *et al.* 2012) and theoretical (Condorcet 1785; Ladha 1992; King and Cowlshaw 2007) work on voting and binary decision making shows that larger groups are often able to choose the superior option more often when given two choices. However, this increase in accuracy may be non monotonic and thus maximized at finite group sizes (Kao and Couzin 2014). In Box 2, we present a generic simple model for collective binary decisions based on Condorcet's (1785) jury theorem, analogous to the binary decisions faced by migrating salmon when they confront tributaries. Figure 3 illustrates the shape of the relationship between group accuracy and individual accuracy for groups of varying size. As group size increases, the trend becomes increasingly nonlinear. Thus, for a fixed individual accuracy, the probability the correct branch is chosen increases monotonically with group size.

Box 2. Collective binary decisions

Much empirical work on binary decision making by animal groups shows that larger groups are often able to choose more accurately the superior option (Sumpter *et al.* 2008; Ward *et al.* 2008, 2011; Arganda *et al.* 2012). Condorcet's (1785) jury theorem is a simplistic model to give us intuition as to why this might occur (see King and Cowlshaw (2007) for a review). In this model, each individual votes for one of the two options and the group, as a whole, adopts the opinion of the majority. Consider a group of salmon heading upstream; paused at a river confluence, each individual salmon in the group estimates which of the two rivers leads to its natal site and chooses the correct branch with probability P , where $P > 0.5$. If the group, through schooling dynamics, moves in the direction of the majority, they will choose the correct branch with probability Q , given by a cumulative binomial distribution:

$$Q(p, N) = \left[\sum_{k > N/2}^N \binom{N}{k} p^k (1-p)^{N-k} \right] + \frac{1}{2} \binom{N}{N/2} p^{N/2} (1-p)^{N/2}$$

(Note that the second term is absent when N is an odd number.) We illustrate this highly nonlinear response in Fig. 3, where we plot group accuracy, Q , against individual accuracy, P , for various group sizes. The larger the group, the more nonlinear the group response are and the more likely the correct branch is chosen. In this simple model, for large group sizes, Q approaches 1 (they vote deterministically for the correct branch) even when P is very close to 0.5; that is, individually, the fish can barely do better than random guessing.

Salmon schooling

For salmon to benefit from collective navigation, they must travel in groups, or at least at densities

sufficient for them to exchange information [such densities need not, however, be particularly high (Guttal and Couzin 2010)]. For most fish species, sight, odour and the lateral line sense are the

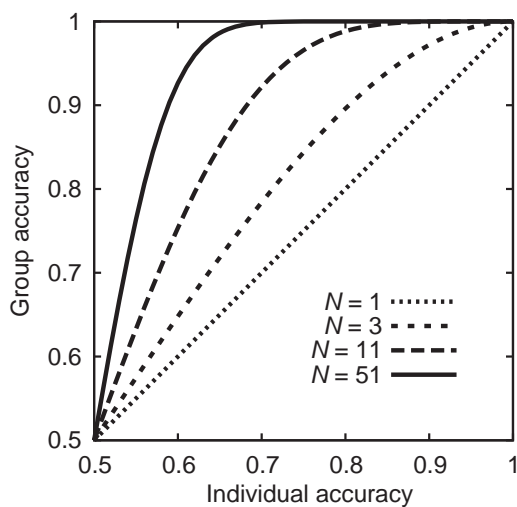


Figure 3 Group accuracy as a function of individual accuracy for various group sizes. In this simple toy model, each individual votes for one of the two options in a binary decision making task and the group collectively chooses the opinion of the majority (see Box 2 for details). Salmon face such binary decisions at river confluences on the river phase of their migration. Fish have been shown to ‘vote’ through schooling dynamics without any explicit signalling (Sumpter *et al.* 2008; Ward *et al.* 2008).

primary sources of social information (Partridge and Pitcher 1980; Faucher *et al.* 2010; Strandburg Peshkin *et al.* 2013). Salmon can detect population specific odours (Courtenay *et al.* 1997) so salmon might be able to travel beyond visual range but nevertheless maintain contact by following pheromone gradients (Couzin and Franks 2003; Detrain and Deneubourg 2006). Such pheromones secreted by adults at a more advanced stage might provide additional cues to guide subsequent migrants. This could be interpreted as a sort of collective intelligence at the population level, but at the individual level due to the signal being asymmetric, it would bestow greater benefit on later migrating individuals.

Salmon likely experiences selective pressure to group for a variety of reasons, including protection from predation (Handegard *et al.* 2012; Marras *et al.* 2012) from larger fish, birds, marine mammals, and sharks, for group hunting (Handegard *et al.* 2012), hydrodynamic benefits (Ross *et al.* 1992; Herskin and Steffensen 1998; Portugal *et al.* 2014), and tracking gradients associated with appropriate living conditions or patchily distributed prey (Couzin 2007; Torney *et al.* 2009, 2011; Berdahl *et al.* 2013). Such coordinated

group living may confer benefits of collective navigation during migrations, even if the grouping originally evolved for other reasons.

Schooling as juveniles

Prior to migrating to sea as juveniles, some species of salmon tend to school (e.g. sockeye salmon (*Oncorhynchus nerka*) in lakes), whereas others tend to be territorial as they feed in streams where food is limited and habitat is defensible (e.g. Atlantic salmon and coho salmon: Quinn 2005; Jonsson and Jonsson 2011). A decrease in territorial behaviour and increase in schooling tendency characterize the transition from a life in freshwater to the marine environment (reviewed by Hoar 1951; Folmar and Dickhoff 1980). Despite clear differences in the patterns and degree of schooling among species (Hoar 1976), there is compelling evidence that juvenile salmon migrate in schools to the sea and that in some species schooling increases their orientation and speed (Hoar 1958a). Extensive observations of sockeye salmon smolts migrating through Babine Lake to the Babine River and downstream to the ocean revealed hundreds of discrete schools of sockeye salmon smolts (Groot 1965, 1972). Babine Lake is about 160 km long and intricate, so well oriented migration is needed to locate the outlet (Johnson and Groot 1963). Indeed, simulations indicated that considerable orientation by fry and smolts was needed to match observed shifts in distribution. However, as with simulations of migration at sea, the potential role of social interactions was not considered (Simms and Larkin 1977).

Schooling in marine waters

Observing fish behaviour in the open ocean is difficult, and accordingly, the social tendencies of salmon are not well understood during the marine stage of their life cycle. To explore the degree to which salmon may be schooling on the high seas, we analysed the catch records (number of salmon of each species caught) in an experimental high seas purse seine fishery in the northern Pacific Ocean from 1956 to 1991 (data provided by K. W. Myers, High Seas Salmon Research Program, School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington). To the extent possible, sampling methods were standardized over years and boats (Hartt 1975). After we removed

records that had anomalies (e.g. the net twisted during the set), the dataset comprised 3520 purse seine hauls, made opportunistically without sonar or fish finding gear to guide the operations.

Figure 4 shows the probability distribution function (PDF) catch size for each species, from the perspective of both the fishers (Fig. 4a) and the fish (Fig. 4b). If salmon were distributed randomly and independent of each other, we might expect catch sizes to follow a Poisson distribution with mean equal to their mean density multiplied by the volume of water the purse seine net strains. However, with the possible exception of steelhead (by far the least numerous species), the observed distributions of catch sizes are not consistent with a Poisson distribution. Instead, the distributions tend to be very broad, spanning several orders of magnitude. The most common catch size was zero (41% of the catches). The rarity of finding any fish, combined with the possibility of finding many when one finds any, suggests that the fish were aggregated in time and space. The three species showing strongest aggregation tendency (pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*) and sockeye) are the most numerous species and also those with the strongest schooling tendencies and least aggressive behaviour as juveniles (Hoar 1958b; Hutchinson and Iwata 1997).

In Fig. 4, catch size is a direct measure of local density of fish, where the spatial scale is a function of the area sampled by the purse seine net. We use catch size as a proxy for group size, but note that this may under sample larger groups if they exceed the size of the net (Makris *et al.* 2006) or if larger groups more easily evade capture. With this in mind, we note that the catch size distribution we observed for salmon is consistent with the broad distributions of group sizes predicted for (Gueron and Levin 1995; Gueron 1998; Niwa 2004; Ma *et al.* 2011), and observed in, fission fusion populations, including those of fish (Bona beau *et al.* 1999a; Makris *et al.* 2006).

As the purse seine data included multiple age classes of fish (i.e. not only those actively migrating home), clustered catches may have arisen if fish were concentrated in areas conducive to feeding. Regardless of their motivation, our analysis shows that fish are patchily distributed on the high seas at densities that would permit the exchange of social information, even if they are not in highly polarized schools (although it does not preclude such schools). Furthermore, the schooling tendency may increase as fish begin their homeward migration. Consistent with this, data from Cooke *et al.* (1987) show that salmon density increases greatly and significantly

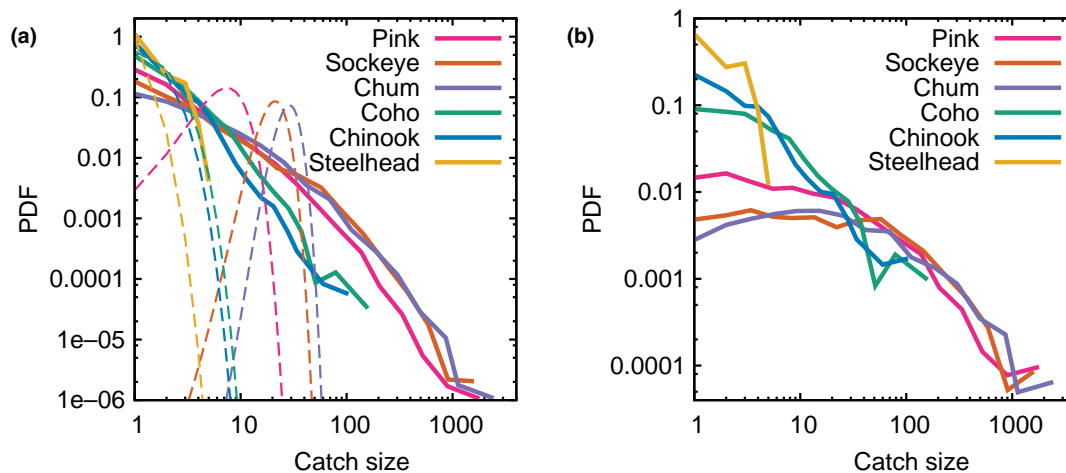


Figure 4 Catch size distributions. (a) The probability distribution function (PDF) of nonzero haul sizes, measured in number of non juvenile salmon, for the experimental purse seine fishery (data provided by K. W. Myers, High Seas Salmon Research Program, School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington). Each colour represents data for a single species. The thinner dashed lines show the corresponding Poisson distributions, assuming the salmon are distributed randomly with the same mean density. The actual distributions (thick solid lines) are broad and non Poissonian, indicating that the fish are aggregated. (b) The PDF of the likelihood of a fish being in a catch of a particular size from the same dataset.

($P = 0.00047$; Wilcoxon signed rank test), as they near shore the (min:median:max) purse seine haul was (0:2:36) offshore and (0:20:2500) onshore. While this may reflect a response to geometric constraints or an increase in their catch ability near shore, it could also indicate an increased sociality in preparation for the mounting difficult navigational tasks ahead.

We note that Mishima *et al.* (1965) documented evidence of salmon grouping at sea based on catches in gillnets. Using acoustic surveys, Nero and Huster (1996) found many small schools (2–4 individuals) of salmon (species unknown) spaced uniformly at small scales (2–200 m) and aggregated at larger scales (400–2000 m). The uniform, rather than random, spacing suggests frequent interactions between the small groups. Thus, the large scale aggregation may exist as a meta group, which would be large enough to span environmental gradients relevant for navigation. Due to the nature of the salmon density distributions (Fig. 4) and their relatively sparse sampling scheme, Nero and Huster (1996) likely missed the very large aggregations in the tail of the distribution, which are numerically rare, yet common from the point of view of an individual, by virtue of those larger groups containing a proportionally larger fraction of the population (see Fig. 4b).

Schooling during upstream migration

On the freshwater stage of their adult spawning migration, salmon often travel together (Banks 1969 and references therein). Schooling behaviour has long been noted by managers tasked with counting the numbers of returning salmon to freshwaters. Writing about the patterns of upstream migration by adult sockeye salmon to the Wood River, Alaska, Mathisen (1962) noted, 'On days of heavy escapement [large numbers of returning fish] they can be observed moving in continuous bands close to both river banks. On days with small escapements the salmon travel in schools of a few to perhaps 100 fish and usually ascend along only one river bank.' [p. 355]. Similarly, pink salmon in southeast Alaska tends to move into freshwater as coherent schools (Davidson *et al.* 1943). Moreover, movement of salmon into streams for spawning can occur in strong 'pulses' of fish entering at once, even in the absence of obvious environmental stimuli to

catalyse the pulses, like increases in flow (e.g. Lorz and Northcote 1965). These group behaviours may be related to predator avoidance, energy conservation through drafting (Hughes 2004) or other effects, but they are also consistent with orientation and consensus decision making, and the various factors are not mutually exclusive.

Stock-specific sorting

Multiple populations of salmon overlap in time and space while at sea; for example, populations of sockeye salmon from throughout their North American distribution were caught and tagged from a single net sample in the Gulf of Alaska (Neave 1964). Thus, if salmon are to form schools for their homeward migration, they must sort into stock or population specific groups. This could be an iterative process, with the necessary homogeneity increasing as the migration progresses. Below, we suggest three ways the salmon might achieve this sorting.

First, substantial evidence indicates that salmon can detect the unique pheromones of their local population and related individuals, and often choose to associate accordingly (Quinn and Bussack 1985; Quinn and Hara 1986; Winberg and Olsén 1992; Courtenay *et al.* 1997; Olsén *et al.* 2004; Fraser *et al.* 2005). Thus, while the pheromone hypothesis proposed originally by Nordeng (1971, 1977) for homing has fallen out of favour as a holistic framework based on a lack of evidence (e.g. Brannon and Quinn 1990), the detection of population specific pheromones may lead to correct group sorting (Ward *et al.* 2007; Griffiths and Ward 2011; and references therein) and would thus be important to the collective navigational process. Moreover, genetic evidence indicates that Pacific salmon populations spontaneously sort by stock in space and time as they near shore (Dann *et al.* 2013). Second, populations within watersheds often differ in the timing of their return to freshwater, which largely reflects differences in thermal regimes on the spawning grounds (Hodgson and Quinn 2002; Doctor *et al.* 2010; Eliason *et al.* 2011). These differences in when individuals begin their upstream migrations may act as a sorting mechanism as population specific run timing likely increases the probability of an individual finding a member of its group. Third, without stock specific recognition, numerical simulations show that groups can spontaneously

partition and split accurately based on slight variations in preferred direction, even when they are not able to distinguish among individuals of differing preferences (Couzin *et al.* 2002, 2005, 2011).

Discussion

We have presented evidence for a collective navigation hypothesis for the homeward migration of anadromous salmon and suggest that the role of social interactions in salmon migrations warrants more detailed examination. We observed a negative relationship between straying rate and abundance in seven independent datasets we reviewed, representing three Pacific species and also Atlantic salmon. To complement these data, we also presented a pair of simple theoretical models that demonstrate how navigational ability could increase with increasing group size at various stages of homeward migration in salmon. Generally speaking, collective navigation effects are predicted to enhance the ability of the individual as well as lead to robust emergent strategies at the group level, not present in any individual. In the following sections, we highlight several outstanding questions and limitations of the collective navigation hypothesis presented here and conclude with avenues for future work.

Group size versus abundance

If salmon complement their individual navigational abilities with collective behaviour, the ability to home will be influenced by the size of the group in which they travel. Both theory (Niwa 2004; Guttal and Couzin 2010) and observation (Hensor *et al.* 2005) in non salmonid species suggest that reduced population density leads to smaller groups in collectively moving populations rather than fewer groups of the same size. Therefore, in years with fewer salmon, individuals may travel in smaller groups, as was observed by (Mathisen 1962). Archived video and sonar recordings maintained by state and federal management agencies used to quantify the numbers of returning salmon might provide an opportunity to explore how group size varies across years of known total run sizes. A quantitative relationship between the expected distribution of group sizes in which salmon travel and their population abundance would provide a more mechanistic

understanding of the potential role of collective navigation during their migration.

Wild versus hatchery salmon

Nearly all the salmon comprised in the datasets on straying rates examined were hatchery produced, and it is unclear whether hatchery salmon are appropriate proxies for wild fish (Quinn 1993; Keefer and Caudill 2013). Both wild and hatchery produced Atlantic salmon exhibited a negative trend between homing and run size, but the strength of the trend between homing and run size was *greater* for the hatchery fish (Jonsson *et al.* 2003). This might indicate that hatchery and escaped aquaculture produced fish exhibit stronger collective effects, possibly because they have been artificially selected for sociality, or this may reflect their prior experience of high densities in the hatchery or farm (Naish *et al.* 2007). Given the paucity of evidence concerning wild fish straying rates, it is unclear whether collective navigation operates differently among wild and hatchery fish.

Patterns among species

One might predict that collective navigation should be most prevalent in more social species (such as sockeye, pink and chum) which have a greater social architecture to support the necessary mechanisms. As discussed above, the increased trend in the more social hatchery fish over the wild fish in Jonsson *et al.* (2003) lends some support to this thinking. An alternative prediction is that collective navigation should be exhibited by populations and species that are more locally adapted and thus under the most intense selection pressures to accurately home (e.g. hypothetically stream type Chinook salmon, sockeye salmon, coho salmon and steelhead). However, if these species spend more time in freshwater, they might have additional opportunity for imprinting and thus might have less need for the collective effect. Also, species that have less opportunity for temporal straying as a means of bet hedging, like pink salmon with their fixed 2 year life cycle, might have increased pressure for spatial straying (The dinga *et al.* 2000; Mortensen *et al.* 2002; Buoro and Carlson 2014) and therefore less incentive to employ collective navigation. Currently, a lack of robust straying estimates and run sizes among

species (however, see Westley *et al.* 2013) impedes the testing of these predictions.

Ecological and evolutionary implications

A density dependent dispersal rate, in salmon or any migratory species using collective navigation, would have implications for their population dynamics, distribution and patterns of local adaptation. On a local scale, smaller numbers of returning individuals may inhibit their ability to home successfully. Further, copying behaviour, combined with incomplete stock sorting, could lead to net dispersal from small populations to larger ones. Either of these factors might introduce an Allee effect on individual populations, whereby a reduction in population size leads to a reduced rate of returning adults and thus a further decline in the population. While possible, Allee effects in salmon populations are rarely observed (Liermann and Hilborn 1997). At a larger scale, reduced homing at low density should facilitate colonization (Ayson 1921; Emery 1981; Kwain and Lawrie 1981; Becker *et al.* 2007; Correa and Gross 2008), which is profoundly important for salmon because colonization (post glacial, including the present time in Alaska) has been a dominant process in salmon ecology. Across multiple scales, salmonids are locally adapted (Taylor 1991; Fraser *et al.* 2011; Westley *et al.* 2012) and there is much interpopulation genetic heterogeneity. The increase in straying rate due to declining populations could increase gene flow between local populations, thereby altering population genetic patterns. Additionally, increased dispersal tends to favour a generalist strategy, which in turn promotes further dispersal. This positive evolutionary feedback could shift the selection regime and lead to much more homogeneity at the species level (Kisdi 2002; Nurmi and Parvinen 2011). We predict that simulations that link realistic demographic models with density dependent dispersal consistent with collective migration will be especially informative.

Collective behaviour throughout the salmon life cycle

We have focused mainly on the potential role of collective navigation during the adult homing phase, although salmon are social and travel in schools throughout their life cycles, suggesting the

benefits of collective navigation need not be limited to adults during their homeward migration. On their downstream migration, juvenile salmon often migrate through large lakes where the lack of current renders negative rheotaxis useless. This is especially true for schooling sockeye salmon (Groot 1965) that rely on celestial and magnetic cues to migrate through lakes (Quinn 1980; Quinn and Brannon 1982). By travelling in schools, these fish could increase the probability of successfully navigating to sea in a timely manner (Box 1). Indeed, experiments demonstrate that larger schools of juvenile chum and sockeye salmon travel in a more orderly manner and at a faster rate than the smaller groups (Hoar 1958a). Also during this freshwater phase, collective gradient tracking might help juveniles find and remain in water temperatures and other conditions beneficial for feeding and growth. Entering the ocean at an appropriate time is critical for successful foraging and survival (e.g. Scheuerell *et al.* 2009). Synchronization in downstream movement of juveniles could facilitate effective collective temporal decision making (Conradt and Roper 2005) as to the timing of marine entry, possibly even combining independent cues from separate tributaries for more robust decisions. Upon entering the ocean, pooling of genetically coded information about the direction in which to migrate (Putman *et al.* 2014), or behaviours to follow (Burke *et al.* 2014), to reach the feeding grounds might reduce individual error in orientation while *en route* (Box 1). Once on the feeding grounds, collective taxis could improve an individual's ability to track environmental gradients associated with resources and favourable conditions. Finally, as we have discussed throughout, collective navigation may play an important role during the remarkable homeward migration of the adult salmon.

Future directions: testing the collective navigation hypothesis

We suggest several avenues to critically test the collective navigation hypothesis. First, as more dataset becomes available, studies of homing and straying rates as functions of abundance at hierarchical spatial scales (i.e. basin, sub basin, reach, habitat unit) would illuminate the spatial scale and phase of the spawning migration where collective navigation may be most important. Second, salmon moving past obstacles like dams with fish

ladders could provide an interesting opportunistic experimental test bed. Swift passage times correlated with high salmon densities would support the collective navigation hypothesis. Third, experiments where fish are forced to make binary choices between the water flowing in from two separate sources (e.g. y maze designs) could provide a conclusive demonstration. One experimental design could be to allow fish to choose between water with and without an odorant to which they had been imprinted, and our prediction is that larger groups would choose the correct arm at lower concentrations than individuals and small groups. For this and the fish ladder scenario, analysis of individual trajectories might provide insight into specific behavioural mechanisms, as in (Berdahl *et al.* 2013). Additionally, we note that the simple comparison of straying rate and abundance could be extended to other taxa that make long distance migrations in groups to discrete locations and are routinely tagged, like birds, to explore the extent of collective navigation in nature.

Summary and closing thoughts

We have presented a hypothesis that collective navigation during the homeward migration of anadromous salmon improves their capacity to return to natal sites. The evidence suggests that the necessary requirements for collective navigation to be operating in migrating salmon are likely met; salmon form schools for the downstream seaward part of their journey, are aggregated at sea, consistent with schooling behaviour, and continue to school during the freshwater upstream portion of their homeward journey, potentially even increasing their sociality during this phase. Salmon can detect population specific odours and appear to sort into stock specific groups as they approach the home rivers from sea. Taken as a whole, the evidence is consistent with collective navigation acting as complementary mechanism contributing to the remarkable ability of individual salmon homing to natal locations.

We hope this paper will prompt conversation and research to critically test the collective navigation hypothesis presented here and to identify specific mechanisms behind the observed patterns. Although focused here on salmon, the collective navigation hypothesis likely applies to other social taxa that make long distance migrations. Across many taxa, research to date has implicitly

assumed that map, compass and piloting processes are products of the individual alone (see, for example, reviews by Bingman and Cheng 2005; Papi 2006). Broadening the focus from the individual to the collective might unveil fundamental mechanisms underpinning the great mystery of animal migrations.

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