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The innovation and diffusion of "trap-feeding," a novel humpback whale foraging strategy

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Abstract

The innovation and diffusion of novel foraging strategies within a population can increase the capacity of individuals to respond to shifts in prey abundance and distribution. Since 2011, some humpback whales (*Megaptera novaeangliae*) off northeastern Vancouver Island (NEVI), Canada, have been documented using a new feeding strategy called "trap-feeding." We provide the first description of this foraging innovation and explore the ecological and social variables associated with its diffusion using sightings data, video analysis, and logistic regression modeling. The number of humpback whales confirmed to trap-feed off NEVI increased from two in 2011 to 16 in 2015. Neither the locations of trap-feeding sessions nor prey species consumed differed from those documented during lunge-feeding. However, preliminary results indicate that the schools of fish consumed when individuals trap-fed were smaller and more diffuse than those consumed when whales lunge-fed. Top-ranked models predicting whether an individual would be observed exhibiting trap-feeding behavior included the following parameters: average number of days per year that the individual was seen off NEVI and proportion of the individual's associations that were with other trap-feeders. These results suggest that trap-feeding may be a culturally transmitted foraging innovation that provides an energetically efficient method of feeding on small, diffuse prey patches.

Key words: humpback whale, *Megaptera novaeangliae*, foraging, innovation, cultural transmission, behavior, lunge-feeding, trap-feeding.

The degree to which individuals and populations are able to adapt to ecosystem change can depend on physiology (*e.g.,* Somero 2010), as well as behavioral plasticity (*e.g.,* Wright *et al.* 2010, Sih *et al.* 2011). The innovation and diffusion of novel foraging strategies represent behavioral responses that can allow members of a population to respond

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to shifts in prey abundance, availability, distribution, or behavior (Tuomainen and Candolin 2011). Innovative foraging strategies arise when an individual invents a new feeding behavior or modifies a behavior that is already in use in a population (Reader and Laland 2000). These new strategies can then be transferred to other individuals within the population, a process that can occur through social or asocial learning (*e.g.*, Reader and Laland 2000, Allen *et al.* 2013).

The introduction and diffusion of feeding techniques through groups of individuals or populations has been described for a wide variety of taxa, including mammals (*e.g.*, Kawai 1965, Lefebvre 1995, Allen *et al.* 2013), birds (*e.g.,* Fisher and Hinde 1949, Boogert *et al.* 2008), and fish (*e.g.*, Reader and Laland 2000). Results from these studies suggest that not all individuals within a population are equally likely to adopt new behaviors. Social rank and associations (*e.g.*, Reader and Laland 2001), group size (*e.g.*, Griffin *et al.* 2013), sex (*e.g.*, Reader and Laland 2000, 2001), and hunger level (*e.g.*, Reader and Laland 2000) have been found to affect rates of innovation. However, the social and ecological variables that lead to behavioral innovation remain poorly understood (Reader and Laland 2001, Boogert *et al.* 2008).

Humpback whales (*Megaptera novaeangliae*) as a species are generalist predators that are known to exhibit a wide variety of foraging strategies. These include lunge-feeding (*e.g.*, Jurasz and Jurasz 1979), bubble-net-feeding (*e.g.*, Jurasz and Jurasz 1979, D'Vincent *et al.* 1985, Sharpe 2001), flick-feeding (Jurasz and Jurasz 1979, Ford 2014), bottom-feeding (Hain *et al.* 1995), and lobtail-feeding (Weinrich *et al.* 1992). The diffusion of the lobtail-feeding technique between humpback whales in the Gulf of Maine followed a shift in availability of humpback whale prey in that area. Sand lance (*Ammodytes americanus*) had become the primary prey of humpback whales, following a crash in the local herring stocks (Weinrich *et al.* 1992, Allen *et al.* 2013). In addition to this ecological shift, network-based diffusion analysis indicated that the rapid spread of the behavior throughout this population could most likely be attributed to social transmission (Allen *et al.* 2013).

Humpback whales off British Columbia (BC), Canada, were severely depleted by commercial whaling until 1965 (Gregr *et al.* 2000). Following this exploitation, humpbacks were rarely documented off northeastern Vancouver Island (NEVI), BC, until the mid-2000s. However, the number of individual humpback whales documented through photo-identification annually off NEVI has increased rapidly since this time, from seven individuals in 2003 to 61 individuals in 2015 (McMillan 2014, Nichol *et al.* 2017). Though the majority of the humpback whales that feed in the area each year have been documented off NEVI previously, there are also new, noncalf individuals photographed each year (Fig. S1).

Humpbacks off NEVI feed primarily on juvenile Pacific herring (*Clupea pallasi*), frequently using surface lunge-feeding as a foraging strategy (McMillan 2014). However, since 2011, some individuals in this area have been documented using a novel feeding behavior that we have called trap-feeding. This behavior differs from lunge-feeding in that the whales initiate trap-feeding from a stationary or near-stationary

position, in contrast to accelerating toward their prey while lunge-feeding (Goldbogen *et al.* 2008). Additionally, while trap-feeding, whales hold their mouths open for an extended period of time compared to lunge-feeding.

In this study, we provide the first description of trap-feeding as a foraging innovation and explore the ecological factors that may have influenced its innovation and diffusion, as well as the characteristics of the individual humpback whales that have undertaken and continued to use this foraging strategy. To determine whether the diffusion of this strategy may be associated with a change in prey species or availability, we compared the prey species consumed, prey school characteristics, and locations of trap-feeding and lunge-feeding events. Additionally, we compared the age, site fidelity, and social associations of individual humpback whales known to trap-feed, and individuals that have never been documented trap-feeding. Understanding the ecological and social variables that underlie the use of a novel feeding technique provides insight into the abilities of marine mammals to respond to ecosystem change.

Methods

Study Area

NEVI is located between Vancouver Island and the mainland coast of BC, Canada, at 50°38′N, 126°46′W (Fig. 1). This area has been the site of focused whale watching and research effort for over 40 yr; however, this effort was primarily focused on killer whales (*Orcinus orca*) until the mid-2000s, when sightings of humpback whales became more frequent in the area (Fig. S1).

Data Collection

Humpback whale sighting and behavior data were collected as part of a long-term study cataloging the individual humpbacks off NEVI. Data were collected from whale-watch and dedicated research platforms between May and November from 2011 to 2015. Whale-watch data collection was opportunistic and primarily obtained from four vessels that conduct one to three trips daily in the NEVI study area. Dedicated survey effort was conducted from three research vessels that ranged in length from 5.2 m to 7.3 m. The numbers of dedicated survey days were relatively consistent each year, ranging from 41 d in 2013 to 58 d in 2011. Totals of 44, 47, and 45 d of survey effort were conducted in 2012, 2014, and 2015, respectively. Identification photographs were taken using digital SLR cameras with lenses ranging in focal lengths from 70 mm to 400 mm.

Whale data—We identified individual humpback whales based on the pigmentation and trailing edges of their flukes, and/or on the shapes of their dorsal fins (Katona and Whitehead 1981). We determined individual identifications and sighting histories by comparing photographs of these features to humpback whale identification catalogs and sighting

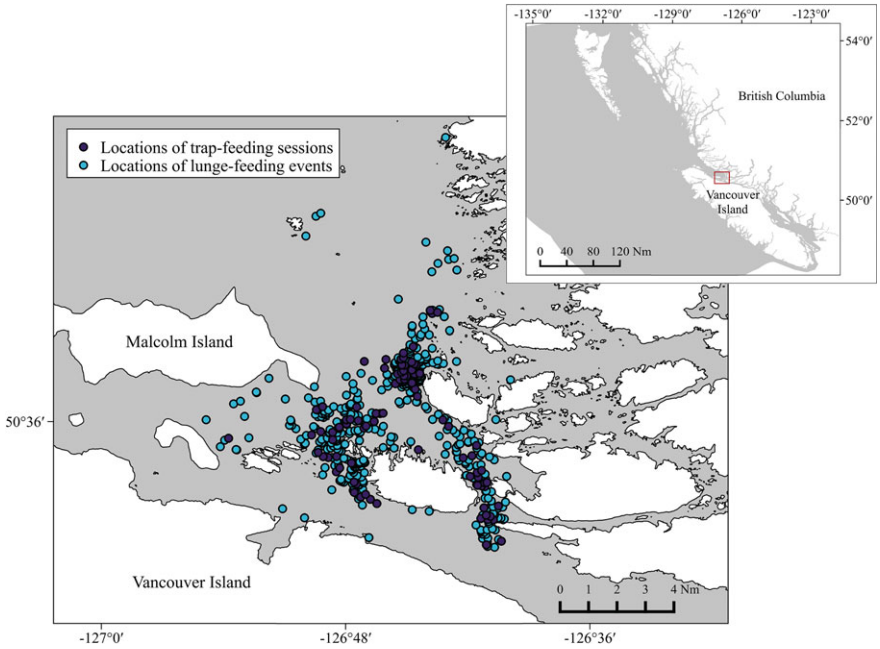

Figure 1. The NEVI study area, located between Vancouver Island and the mainland coast of British Columbia, Canada, and the locations of humpback whale trap-feeding and surface lunge-feeding events documented off NEVI between 2011 and 2015.

databases maintained by the Marine Education and Research Society (MERS) and Fisheries and Oceans Canada (DFO). Sex of individual humpback whales was determined when possible, through photographs of the whales' genital region (Glockner 1983) or through a female's close, consistent association with a calf.

We classified individual humpback whales as "adults," "juveniles," or "unknown age class" based on their known or estimated ages when trap-feeding was first observed off NEVI in 2011. The ages of humpback whales first photographed as calves were known with certainty. For all other individuals, we assigned an age class based on the whale's sighting history, obtained from the MERS and DFO humpback whale catalogs and databases. We considered a whale to be an adult if it was first sighted independently (*i.e.*, not accompanied by its mother) anywhere off the coast of British Columbia four or more years before 2011. Any female humpback whale that was known to have given birth to at least one calf was also considered an adult. Whales known to be <5 yr old in 2011 were considered juveniles, while whales first sighted independently after 2007 were classified as "unknown age class".

We also documented each time that humpback whales associated with one another, and the individual identifications of each of the associates. Humpback whales were considered "associated" when they were less than one body length apart and were coordinating their behavior. When

two individuals were sighted together more than once on the same day, these sightings were considered as a single association between the two whales.

Behavior and prey data—Observations of trap-feeding and lunge-feeding were collected by MERS researchers, as well as by local whale watching naturalists and captains and fellow researchers, all of whom have been trained to identify individual humpback whales, and to recognize trap-feeding in the field.

Each time that trap-feeding was seen, observers were instructed to document the time at which the behavior began, the individual humpback whale(s) engaging in the behavior, the GPS coordinates and geographical location at which the behavior took place, the species of birds present, whether prey was visible, the time at which the behavior ended, and whether the entire trap-feeding session was witnessed. In addition to these details, observers were instructed to film trap-feeding behavior whenever possible. This allowed for detailed observations of the duration of trap-feeding bouts and sessions and allowed us to examine how individual humpback whales varied in their execution of the behavior. Videos also allowed us to confirm the presence and species of seabirds during trap-feeding sessions and to determine the positioning of the whale relative to its prey.

Several methods were used to determine which prey species were consumed by trap-feeding whales, including photographing or filming prey in the mouths of whales and birds; sampling dead fish following feeding events; and/or filming prey patches underwater using a GoPro camera. Underwater video also allowed us to count the number of fish in the prey schools that were trap-fed on by humpback whales. This was achieved by pausing the videos at times when the entire school was visible. We averaged fish counts over at least three frames for each school, to ensure that the entire school was captured. If the school was disturbed (*i.e.,* a shift in behavior or density of the prey school was observed) before we were able to obtain video, these videos were excluded from analyses. Estimates of the average number of fish in schools that were lunge-fed on in the same area were calculated by McMillan (2014), using underwater video, three-dimensional measurements of fish schools, and length distributions of fish sampled from each school to estimate the volume of the schools and the number of fish they contained.

Statistics

We used a Welch's *t*-test to compare the average number of fish in the schools that were trap-fed on *vs.* lunge-fed on by humpback whales in the same area in 2012 and 2013 (McMillan 2014).

We used generalized linear models (family: binomial, link: logit) to assess which, if any, of the following parameters best predicted whether an individual humpback whale would be observed exhibiting trap-feeding behavior: (1) age class of the individual when trap-feeding was first observed, (2) number of years the individual was seen off NEVI between 2011 and 2015, (3) average number of days per year that the

individual was documented during the years that the individual was present off NEVI, and (4) proportion of the individual's associations that were with other trap-feeders. Individuals were only included in these analyses if they were sighted feeding at the surface off NEVI during the study period (2011–2015). We built a set of models that included each of these parameters, as well as several combinations of these variables, and a null model where the probability of an individual being observed trap-feeding did not depend on any of the above variables (see Table 1 for all models considered). We compared models using the Akaike information criterion (AIC), and by considering the *z*-values and *P*-values associated with model parameters. Models with delta AIC scores of <2 were considered to have equal support.

Behavior Definitions

Lunge-feeding—A feeding strategy in which a whale accelerates toward its prey, then opens its mouth, generating drag that leads to

Table 1. AIC comparisons for models estimating the probability of an individual humpback whale off NEVI trap-feeding, based on the following predictor variables: the average number of days per year that the individual was sighted off NEVI (DaysPerYear), the proportion of the individual's associations that were with other trap-feeders (PropTF), the age class of the individuals when trap-feeding was first documented in 2011 (Status2011), and the number of years that the individual was seen off NEVI since the start of the study (YearsSince2011).

Model	AIC	Δ_{AIC}	Model terms	*z*	*P*
Trap~DaysPerYear+ PropTF+Status2011	46.0	0	Days Per Year	3.12	0.002
			Prop TF	1.50	0.14
			Status2011Juvenile	1.83	0.07
			Status2011Unknown	0.17	0.86
Trap~DaysPerYear+ PropTF	46.3	0.3	Days Per Year	3.42	0.0006
			Prop TF	1.37	0.17
Trap~DaysPerYear	47.2	1.2	Days Per Year	3.64	0.0003
Trap~DaysPerYear+ PropTF+Status2011 +YearsSince2011	47.9	1.9	Days Per Year	2.64	0.008
			Prop TF	1.50	0.13
			Status2011Juvenile	1.83	0.07
			Status2011Unknown	0.13	0.9
			Years Since 2011	−0.19	0.85
Trap~DaysPerYear +YearsSince2011	49.2	3.2	Days Per Year	3.10	0.002
			Years Since 2011	0.19	0.85
Trap~YearsSince2011	64.5	18.5	Years Since 2011	2.40	0.02
Trap~PropTF	65.5	19.5	Prop TF	1.56	0.12
Trap~Status2011	68.9	22.9	Status2011Juvenile	1.95	0.05
			Status2011Unknown	0.14	0.89
Trap~1 (null model)	70.0	24.0			

expansion of the whale's buccal cavity. The whale then closes its mouth around a large volume of water and prey, and expels the water out through its baleen plates (Goldbogen *et al*. 2007). Lunge-feeding can occur at the surface or at depth; however, only surface lunge-feeding events could be observed in this study.

Trap-feeding—A novel foraging strategy characterized by a humpback whale remaining stationary at or just below the surface with its mouth open for an extended period of time (defined as a minimum of 4 s). The behavior frequently involves the whale spinning in place and/or using its pectoral flippers to push or flick prey into its mouth (Fig. 2, Video S1). Unlike a typical lunge-feeding event, in which the whale accelerates toward the targeted prey (Goldbogen *et al*. 2008), when trap-feeding the whale is stationary or moving slowly prior to opening its mouth.

Trap-feeding bout—A single feeding event that begins when the whale opens its mouth and ends when it subsequently closes its mouth while engaging in trap-feeding.

Trap-feeding session—One or more trap-feeding bouts that begin when a whale initiates trap-feeding (or is first observed doing the behavior) and ends when the whale changes behavior states (*i.e.,* is no longer trap-feeding).

Results

Between 2011 and 2015, a total of 55 individual humpback whales (18 adults, 12 juveniles, and 25 unknown age class whales) off NEVI were observed feeding at the surface. Sixteen of these individuals were confirmed to have trap-fed at least once during the study period.

The ratio of the number of individuals seen trap-feeding to the number of individuals seen surface lunge-feeding but never trap-feeding off NEVI increased annually from 0.07 in 2011 to 0.42 in 2015 (Table 2). All individuals that trap-fed had been documented off NEVI for at least 2 years prior to the first year that they were observed trap-feeding (Table S1), and all had been observed lunge-feeding prior to the first time that they were documented trap-feeding. Four of the individuals that were documented trap-feeding were adults at the beginning of the study, five were juveniles, and the remaining seven were in the unknown age class. The sex of the majority of the trap-feeders was unknown; however, four known females and one known male were documented employing this novel feeding strategy. At least one individual known to trap-feed (BCY0768) is the offspring of a female humpback whale (BCY0177) that has been seen off NEVI every year of this study but has never been documented using this strategy. Trap-feeding locations were consistent with the areas where lunge-feeding events were observed (Fig. 1). In at least five of the trap-feeding sessions that were filmed, the trap-feeding behavior was preceded by an individual humpback whale lunge-feeding on the same school of fish that was subsequently trap-fed on.

In 2013 there were four individual humpback whales (two juveniles and two whales in the unknown age class) that were observed

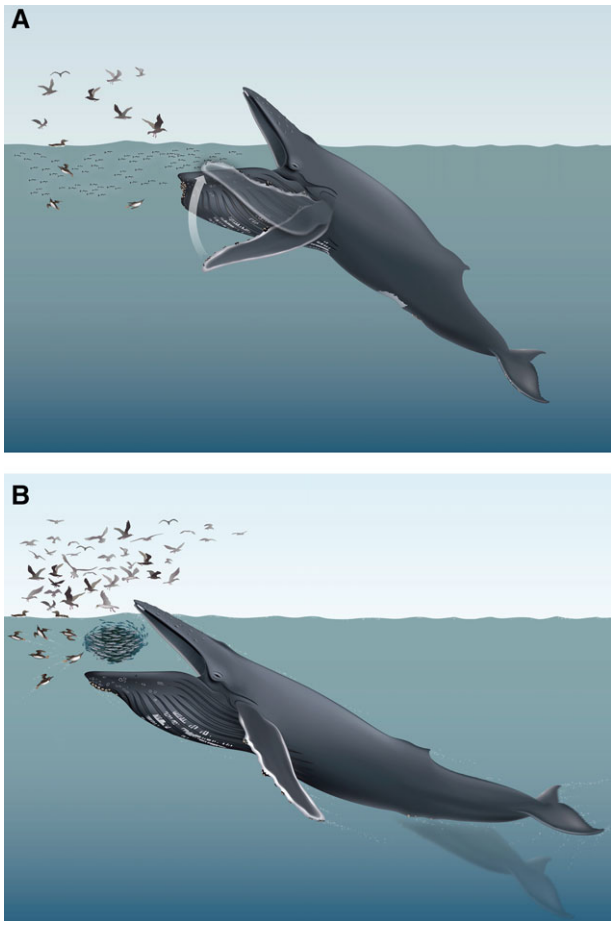

Figure 2. (A) Trap-feeding is characterized by (1) a humpback whale remaining stationary at or just below the surface with its mouth open for a minimum of four seconds and (2) a lack of acceleration prior to the whale opening its mouth. Flippers and/or a spinning motion are often used to direct prey into the whale's mouth. (B) This is in contrast to lunge-feeding, during which a humpback whale accelerates toward its prey. Graphics courtesy of Uko Gorter.

exhibiting an incomplete or rudimentary form of trap-feeding behavior. These individuals fed by opening their mouths from a stationary (or near-stationary) position, but held their mouths open at the surface for fewer than 4 s. Three of these individuals were observed using the complete trap-feeding behavior in a subsequent year (two in 2014 and one in 2015).

Although the number of individuals that trap-fed increased over the study period, the number of trap-feeding sessions observed and the proportion of trap-feeding sessions to lunge-feeding events varied by year. Once individual humpback whales learned to trap-feed, they continued

Table 2. Summary of the number of humpback whales that trap-fed, the age classes of these individuals, and the ratio of individuals that trap-fed to individuals that lunge-fed but never trap-fed between 2011 and 2015.

Year	Juvenile trap-feeders	Adult trap-feeders	Unknown age class trap-feeders	New trap-feeders	Trap-feeding individuals: lunge feeding individuals
2011	2	0	0	2	0.07
2012	2	2	1	3	0.14
2013	5	2	1	5	0.31
2014	4	3	5	5	0.39
2015	5	4	3	1	0.42

to use this strategy throughout the study period. However, they did not use this technique exclusively, and were instead documented using both lunge-feeding and trap-feeding foraging strategies. The total number of trap-feeding sessions and the proportion of trap-feeding sessions to lunge-feeding events were both highest in 2013 and second highest in 2015. Further, of the five individual humpback whales that have been observed trap-feeding since 2012, all five exhibited the highest number of trap-feeding sessions and the highest proportion of trap-feeding to lunge-feeding in either 2013 or 2015 (Fig. 3).

Video Analysis

A total of 251 bouts in 32 trap-feeding sessions were filmed for further analysis of this foraging strategy. These videos included trap-feeding footage from 11 of the 16 individual humpback whales known to trap-feed. The footage of trap-feeding bouts allowed for analysis of individual variation in the execution of trap-feeding behavior. The average length of trap-feeding bouts across the 32 filmed sessions was 18 s (SD = 14 s). However, there were individuals for whom the average was much shorter (Fig. 4). The average length of a trap-feeding bout for BCY0727, for example, was just 8 s. The longest trap-feeding bout recorded was 82 s, and was performed by BCY0728, the first individual documented trap-feeding off NEVI.

Individual trap-feeders also varied in the use of their pectoral fins to scoop or flick prey into their mouths. Two individuals were not observed using their pectoral fins, while one humpback whale used its pectoral fins in 71.4% of trap-feeding bouts that were filmed. Overall, pectoral fins were used in at least 66 of the 251 trap-feeding bouts. All but one of the individual trap-feeders were also observed to spin while holding their mouths open at the surface. However, individual variation existed in the proportion of trap-feeding bouts that included this spinning behavior. One individual was never filmed spinning, while the individual that used this strategy most often was filmed spinning in 75% of its trap-feeding bouts. Some buccal cavity expansion was observed

during trap-feeding sessions; however, the extent and mechanism of the expansion could not be determined.

Video also allowed for analysis of the orientation of the prey and whales during trap-feeding bouts. When initiating the trap-feeding behavior, humpback whales positioned themselves adjacent to schools of fish that were being fed on from above by gulls and from below by alcids. This led to prey seeking refuge in or next to the whale's open mouth. Both alcids and gulls were foraging on the same prey patches as the humpback whales during every trap-feeding session that was filmed. The gulls most frequently observed were juvenile herring gulls *Larus argentatus* and the alcids most commonly documented were common murres (*Uria aalge*) and rhinoceros auklets (*Cerorhinca monocerata*); however, ancient murrelets (*Synthliboramphus antiquus)* were also seen feeding on the same prey as trap-feeding humpback whales.

Prey consumed by trap-feeding humpback whales was identified in 11 trap-feeding sessions. In all of these sessions, the species being fed on was juvenile (year one) herring; the same prey targeted by humpback whales while surface lunge-feeding in this area (McMillan 2014). We obtained underwater video of the prey schools for three of the trap-feeding sessions. The mean number of herring in the schools that were trap-fed on was 127.0 (SD = 156.0) fish. Though preliminary, this is

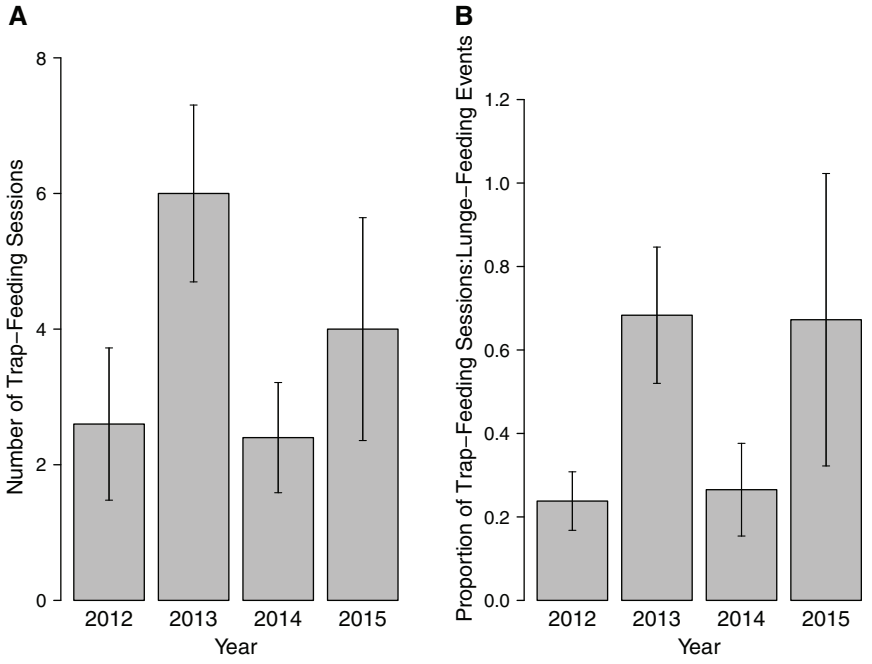

Figure 3. The mean annual (A) number of trap-feeding sessions and (B) proportion of trap-feeding sessions to lunge-feeding events for the five individual humpback whales that have been trap-feeding since 2012. Error bars represent standard error.

significantly smaller than the mean number of herring in schools that were lunge-fed on by humpback whales off NEVI in 2012 and 2013, based on McMillan (2014) (mean = 1,262.8 fish; $t = 3.47$, df = 13.50, $P = 0.004$). Qualitatively, the schools of herring fed on during trap-feeding bouts were consistently less dense than the herring schools that were fed on by lunge-feeding humpback whales (Fig. 5).

Model Results

The probability of observing an individual humpback whale exhibiting trap-feeding behavior was best predicted by: (1) the model that included the average number of days each year that the individual was seen off NEVI, the proportion of associations that were with other trap-feeders, and the age class of the individual when trap-feeding was first observed in 2011; and (2) the model that only included the average number of days per year seen off NEVI and the proportion of associations that were with other trap-feeders (Table 1). Based on both AIC scores and on z and P values, the single variable that best predicted the probability of an individual exhibiting trap-feeding behavior was the average number of days per year that the individual spent off NEVI. Individuals that spent more days per year off NEVI were more likely to be observed trap-feeding than individuals that spent fewer days per year in this area (Fig. 6).

Discussion

Trap-feeding is a foraging innovation that is diffusing rapidly between the humpback whales that feed off NEVI. The spread of a novel foraging strategy has been previously documented for marine mammal populations (*e.g.,* Sargeant *et al.* 2005), including humpback whales (Weinrich *et al.* 1992, Allen *et al.* 2013). However, while some studies have found that individual foraging behaviors are associated with distinct geographical areas (*e.g.,* Hoelzel *et al.* 1989, Sargeant *et al.* 2005) or prey types

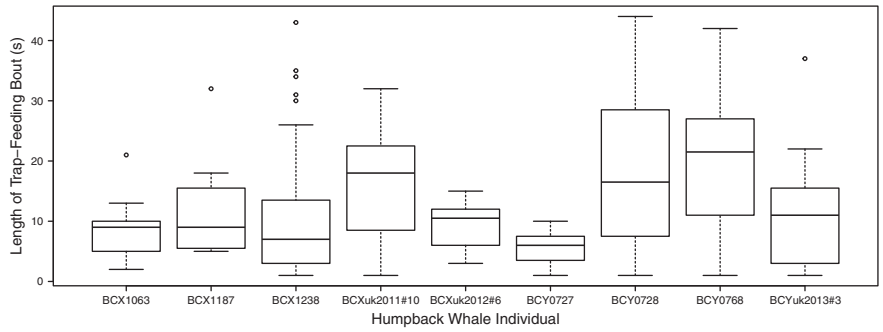

Figure 4. Boxplots showing the individual variation in lengths of trap-feeding bouts for each individual humpback whale that was filmed trap-feeding more than once, where n is the number of trap-feeding bouts that were filmed for each individual.

(*e.g.,* Weinrich *et al.* 1992, Tinker *et al.* 2007, Patterson and Mann 2011), trap-feeding is a feeding innovation that occurs within the same locations and targets the same prey species as the surface lunge-feeding behavior conducted by humpback whales off NEVI. Although individuals are not exclusive in their use of trap-feeding and are inconsistent in the annual frequency of their use of trap-feeding compared to lunge-feeding, once humpback whales began using the trap-feeding technique, they continued to apply this strategy for the duration of the study. This suggests that trap-feeding must confer some energetic benefit to the individuals that learn to use this strategy.

Lunge-feeding, in contrast to trap-feeding, is a foraging technique that entails a high energetic cost to humpback whales (Goldbogen *et al.* 2008). While lunge-feeding, a whale accelerates toward its prey and then opens its mouth, generating drag that is sufficient to stop the forward momentum of the whale, thus requiring the whale to accelerate from rest for subsequent lunges (Goldbogen *et al.* 2008). Prey patches below some threshold density and size will therefore not provide a net energy benefit to whales using this energetically costly strategy. The lack of acceleration associated with trap-feeding means that this strategy requires much less energy than lunge-feeding; thus, humpback whales can obtain a net energy benefit from smaller and more diffuse prey

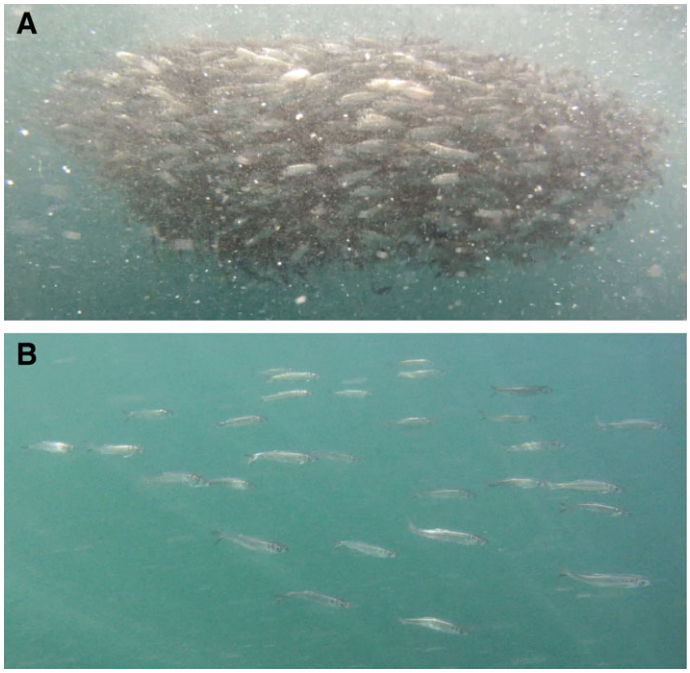

Figure 5. (A) A typical school of herring that was lunge-fed on by humpback whales off NEVI during McMillan's (2014) lunge-feeding study. (B) A school of herring that was subsequently trap-fed on by humpback whale BCX1238 off NEVI in 2013.

patches. Based on the significantly smaller schools of herring targeted during trap-feeding sessions as compared to lunge-feeding, it appears that the trap-feeding behavior may have arisen and spread in response to selective pressure to develop an efficient strategy to feed on small, diffuse prey patches, rather than in response to shifts in available prey species or the need to forage in a new area. It is likely that the annual inconsistencies in the use of trap-feeding are driven by ecological factors; for example, a scarcity of dense herring schools or increased competition for these dense prey patches. Data do not currently exist at the scale required to determine whether the diffusion of trap-feeding off NEVI is associated with a change in herring abundance or density and further research is required to determine the relationship between herring availability and the innovation and spread of trap-feeding.

It appears that birds, specifically alcids and gulls, play a major role in humpback whale trap-feeding behavior off NEVI. Alcids and gulls were present during all filmed trap-feeding sessions, and based on both above-water and underwater video, appeared to be largely responsible for the dynamics and movement of the prey during trap-feeding sessions. "Bird-associated feeding" has been previously documented for cetaceans in the North Pacific Ocean (*e.g.*, Hoelzel *et al.* 1989, McMillan 2014), and although it is typical to consider piscivorous seabirds to be competitors of humpback whales and other cetaceans, humpback whales off NEVI appear to benefit from the birds' abilities to influence prey movement and prey school dynamics. Herring schools provide the opportunity for multispecies feeding aggregations, during which alcids pursue prey from below the water's surface and gulls pursue prey from above; thus serving to concentrate the prey into denser schools (Haynes

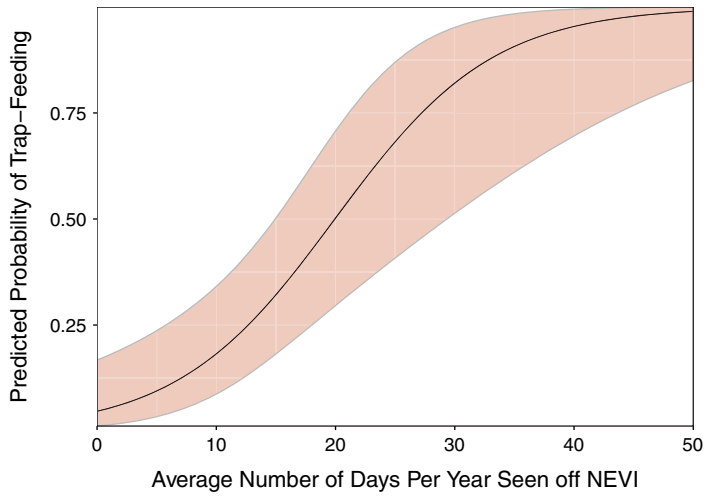

Figure 6. The predicted probability of an individual humpback whale exhibiting trap-feeding behavior as a function of the average number of days per year that the individual was seen off NEVI, based on logistic regression.

et al. 2011). Lunge-feeding humpback whales off NEVI then target these schools, benefitting from the high-density prey aggregations. Trap-feeding humpback whales also appear to benefit from the presence of avian predators. It has long been recognized, by both scientific literature and fishermen, that a wide variety of fish species aggregate under floating or drifting objects or organisms at sea (*e.g.,* Hunter and Mitchell 1968, Castro *et al*. 2002). Among the hypotheses suggested to explain this association between schooling fish and floating objects, the theory that fish are seeking shelter from predators (Gooding and Magnuson 1967) could explain the association between the herring and stationary humpback whales during trap-feeding.

Humpback whale pectoral flippers also appear to play an important role in trap-feeding. Pectoral flippers were used in a minimum of 66 of the 251 trap-feeding bouts filmed (27%). Because the vast majority of filming occurred above the water's surface, it is possible that this is a significant underestimate of the use of pectoral flippers; in at least 72 additional filmed bouts (29%), it was not possible to determine whether flippers were used. Humpback flippers measure approximately 4.6 m long (up to one-third the length of a humpback whale's body) and are thought to be adapted for high maneuverability (Fish and Battle 1995). Several additional functions and benefits of humpback whale pectoral flippers have been proposed or described to date. These include: defense against predation (*e.g.,* Ford and Reeves 2008, Pitman *et al*. 2016); intraspecific competition between male humpback whales in their breeding grounds (*e.g.,* Baker and Herman 1984); courtship and mating (*e.g.,* Tyack 1981, Pack *et al*. 2002); and increasing foraging success through manipulating prey behavior (*e.g.,* Sharpe 2001). Our observations of fish being manipulated by flippers during trap-feeding support the "blaze-feeding" hypothesis proposed by Howell (1930) and Brodie (1977) whereby fish may perceive humpback whale flippers as threats and escape into darker gap created by the mouth. Trap-feeding therefore appears to represent another benefit provided by these long appendages, further indicating the association between these long flippers and improved foraging success.

Between 2011 and 2015, the trap-feeding foraging innovation diffused rapidly between the individual humpback whales that feed off NEVI. Foraging techniques and other behaviors can spread through vertical transmission (from parent to offspring; *e.g.,* Krützen *et al*. 2005) and through horizontal transmission (social learning between individuals within a generation; *e.g.,* Noad *et al*. 2000, Allen *et al*. 2013). Several of our top-ranked models included the proportion of the individual's interactions that were with other trap-feeders. This, in addition to the rapid adoption of the trap-feeding behavior among the humpback whales off NEVI and the presence of at least one trap-feeding humpback whale whose mother has never been documented trap-feeding, indicates that this technique is likely spread through horizontal cultural transmission. However, ongoing studies, including genetic analyses of trap-feeding individuals compared to non trap-feeders and network-based diffusion analysis will provide further insight into the spread of this behavior.

All of our top-ranked models included the average number of days per year that an individual humpback whale was seen off NEVI as a significant predictor of whether the individual would be observed trap-feeding. A higher number of sightings per year could make it more likely for these individuals to be documented using this foraging strategy, simply because of the increased opportunity to observe them. However, we sought to minimize this bias by excluding from our analyses any individuals that were not seen feeding at the surface during the study period thus eliminating individuals that were not observed often enough for feeding behavior to be viewed. It is also possible that this result is an indication that site fidelity plays a strong role in the spread of trap-feeding. Behaviors that are transmitted culturally are likely to spread at an increased rate between individuals that spend more time in the same area (Allen *et al.* 2013). Therefore, the more time that individual humpback whales spend off NEVI, the more likely they are to be exposed to other individuals using trap-feeding behavior and to undertake the use of this feeding strategy themselves.

Based on the rapid diffusion of the behavior and the characteristics of the prey consumed using this technique, trap-feeding appears to be an energetically efficient method of foraging on juvenile herring that is culturally transmitted between humpback whales off NEVI. Further research into the dynamics and diffusion of this behavior, and on the prey targeted by trap-feeding humpback whales, will provide further understanding of the social and ecological factors that drive the use of foraging innovations.

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Supporting Information

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Figure S1. The number of individual humpback whales documented off northeastern Vancouver Island (NEVI) each year from 2003 to 2015. "Calves" are first-year calves that are still accompanied by their mothers. "New" are individual humpback whales that had not been documented off NEVI in any prior year. "Resights" are individuals that have been documented off NEVI in at least one previous year.

Video S1. The trap-feeding foraging technique is characterized by (1) a humpback whale remaining stationary at or just below the surface with its mouth open for a minimum of four seconds and (2) a lack of acceleration prior to the whale opening its mouth. Flippers and/or a spinning motion are often used to direct prey into the whale's mouth. Video courtesy of Tavish Campbell.

Table S1. A summary of the age classes, site fidelity, and trap-feeding data for the 16 individual humpback whales known to trap-feed off NEVI between 2011 and 2015. *Note that the number of bouts with flipper use is a minimum estimate, as flippers were often not visible during video analysis of trap-feeding.