Literature Review 3

Organization:

The article entries are organized to provide an overview of the behaviour and then focus on key elements starting with the tail-slap and then acoustic characteristics. The articles are then arranged by publication date, while the secondary article is last to provide a broader explanation of the ultimate relationships characterizing this behaviour.

Annotated Bibliographies

Primary:

Simila, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, *71*(8), 1494–1499. https://doi.org/10.1139/z93-210

Summary: This article investigated the feeding behaviour of herring-eating killer whales in northern Norway during the months of high orca abundance (estimated 500) and under good underwater visibility. Simila and Ugarte (1993) aimed to document cooperative feeding in orcas while hunting herring in this observational study. Though this cooperative behaviour was previously described, and thought to increase hunting success, the surface behaviour and prey-catch were unknown. To explore this, orcas were identified utilizing pictures in October-November from 1990-1992 in Vestfjord, Tysfjord, and Ofotfjord. Surface and underwater behaviour observations were written and video-recorded, comprising a total of 419h of observations, including resting, travelling, socializing-playing, and feeding. A behaviour was defined as "feeding" when fish scales, pieces of fish, or stunned fish were observed among active orcas. Carousel behaviour was observed for 20h on the surface and 5h underwater. The carousel method had two phases: herding and feeding. During herding the orcas swam in a uniform direction underneath the herring school gathering the fish closer together in a ball and to the surface. While encircling, orcas were highly vocal with their white undersides towards the fish, performing much lobtailing and porpoising. During feeding, the whales remained highly vocal while their white underside remained towards the fish, emitting large air bubbles adjacent to the school. More orcas were encircling fish than eating and individuals spent more time encircling than feeding. The whales stunned prey by slapping the school with the underside of their flukes, emitting a loud banging sound. They stunned fish one-by-one, unable to capture fish without stunning first. It was unknown whether the loud banging sound from the tail slaps were a by-product or aided in prey stunning. These results were significant as they provided the first underwater analysis of the adapted specialized hunting technique likely evolved for herring abundant waters.

Article Contribution: This article provides a detailed overview of the carousel behaviour, a cooperative feeding method, in killer whales. It further provides the first underwater analysis of this feeding behaviour, clearly defining the social cooperation in manipulating herring and use of their tail slap in stunning prey during predation. This work also provides a series of follow up questions for exploration, on the role of acoustic behaviour, learned (cultural) traditions, and their tail slap including the accompanying sound, in carousel foraging behaviour.

Primary:

Nøttestad, L., & Similä, T. (2001). Killer whales attacking schooling fish: Why force herring from deep water to the surface? *Marine Mammal Science*, *17*(2), 343–352. https://doi.org/10.1111/j.1748-7692.2001.tb01275.x

Summary:

This article investigated the mechanisms of carousel behaviour of the 432 Norwegian herring-eating killer whales (*Orcinus orca)*. Though this feeding behaviour and encircling had previously been characterized in the 25 different groups of orcas in Norway, research did not describe the composition and orientation of herring schools prior to and during predation upon them. Nøttestad and Similä (2001) aimed to investigate the interactions between orcas and herring, and document the antipredator behaviour of herring preceding, during, and following carousel feeding. To do this, modern sonar and echo-sounder technology was employed in northern Norway on November 13th, 1996. Herring school biomass was quantified with an echo-integrator. General behaviour, size, and age/sex composition was recorded from surface observations. Results revealed the herring had an initial biomass of 32 tons (96,000 m^3) which were approached by 10 orcas. All orcas dived in synchrony, working cooperatively to herd the herring school towards the surface, from their initial depth of 160 m. The initially dense school became split by the killer whale's orchestration into three fragments. It is suggested the whales divided herring as smaller schools are much easier to herd and feed upon. Once the whales reached a shallower depth (0-80 m) the feeding phase was initiated. The authors suggest feeding close to the surface allows for visual stimuli usage, while herding from deep, dark waters likely relies exclusively on acoustic signals. Additionally, power and hunting effect decreases significantly in deeper depths compared to shallow. This ecological footnote was significant as it demonstrated carousel foraging may involve herding of deep-water herring to the surface, optimizing their diving-time budget. Furthermore, it demonstrates the maximization of food access close to the surface. Further investigation is required to establish this behaviour in different groups of herring-feeding killer whales.

Article contribution:

This article provided the detailed coordination of killer whales and the behavioural response of orcas to herring situated at deeper depths. Through providing an analysis of overall behaviour, it provided a streamline logical sequence killer whales might follow and sources of adaptation/ variability during “carouselling”. Furthermore, it provided a line of questioning regarding the dependency on the carousel foraging technique on light conditions and the potential need for adapting to low light situations. As an article, it pulled in many of the previously investigated articles, allowing for a greater understanding for this technique.

Primary:

Domenici, P., Batty, R. S., Similä, T., & Ogam, E. (2000). Killer whales (*Orcinus orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps: Kinematic analyses of field observations. *Journal of Experimental Biology*, *203*(2), 283–294. https://doi.org/10.1242/jeb.203.2.283

Summary: This article investigated the role of previously observed underwater tail-slaps in herring-eating killer whales' (*Orcinus orca)* during carousel behaviour as a kinematic analysis had not previously been described. Domenici et al. (1999) aimed to determine the underlying mechanisms of the previously observed tail-slaps through use of a kinematic analysis. To explore this, three pods of orcas (with 10-20 individuals) were observed using underwater video-recordings, to a depth of 15 meters, in a northern Norwegian fjord. Observations determined tail-slaps had separate phases (biphasic) with polar attack angles: negative angles noted as the "preparatory phase" and the "slap phase" with positive angles of attack. During the slap phase, the body of the whale rotates from a concave dorsal contraction (backwards C) to a ventral contraction (forwards C), exhibiting a mean attack angle of 29°. The maximum of 47° was limited by drag forces. Velocity, positively correlated to whale length, increased initially as the attack angle reached 0° (minimal drag allows greater acceleration) and halfway through the slap phase. Maximum force applied by the dorsal-ventral muscular contraction of the tail occurred halfway through the slap phase coinciding with the maximum acceleration of $48 ms^{-2}$ (size-independent). The loud noise was determined to be a by-product of physical contact between the fluke and herring, which caused the debilitation and stuns. Orcas were capable of stunning between 0 (miss) and 16 herring per slap. Lunging aided in rallying, not capture, and occurred at a low speed. This study was significant as it provided a kinematic analysis of the "weapons" utilized to increase efficiency in two ways: 1) tail-slaps are better tactics as they provide fast acceleration allowing high velocity and 2) as tactics against the grouping confusion effect of herring. Further studies are required to establish whether additional herring are stunned by the resulting pressure wave.

Article Contribution:

This article provided a thorough analysis of the tail-slap utilized during the carousel foraging behaviour of killer whales. Additionally, it reinforces the previous understanding of the underwater dynamics during carousel feeding and confirms usage of tail-slap in stunning during the feeding phases. It further established the effective partitioning of a body segment (their tail) to use as a "weapon" to combat difficult manipulation and acceleration of their entire large mass. Finally, it supports previous research's finding that tail slaps are utilized in prey capture over lunging which did yield any successful prey catch.

Primary:

Simon, M., Wahlberg, M., Ugarte, F., & Miller, L. A. (2005). Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*). *Journal of Experimental Biology*, *208*(12), 2459–2466. https://doi.org/10.1242/jeb.01619

Summary:

This article investigated additional forces of herring debilitation caused by the killer whale *(Orcinus orca)* tail-slap during carousel feeding. Cavitation, previously described, is the phenomenon where a drastic drop in ambient pressure causes release of dissolved gases, producing a loud distinguishable sound pulse as gas bubbles collapse upon return to typical ambient pressure. Simon et al. (2005) aimed to acoustically analyse tail-slaps, examine possibility of cavitation, and determine additional forces of herring-debilitation. To explore this, orcas were recorded underwater while carousel feeding during October-December in northern Norwegian fjords (n=12-25). Debilitation, defined as a loss of swimming ability and separation from their school, was observed to determine short-term effects. Acoustic recordings then underwent sound analysis. Observations revealed calves swam and performed tail-slaps in synchrony with adults. Tail-slaps only debilitated herring in the immediate vicinity. Contact alone is unlikely the cause of stunning and other factors such as steep pressure gradients, high levels of water acceleration, particle movements, and contact with other fish, likely contribute to sensory overload and loss of buoyancy control. Tail-slaps produced sound signals lasting an average of 318 ms, with multiple bursts of pulses. These pulses had a mean energy content of 169 dB (pp) re. 1uPa at 1m. The tail-slaps' frequencies (beyond 150 kHz), peak frequencies of the tail-slap (below 10 kHz), and average source levels (186 dB (pp) re. 1uPa at 1m), are all consistent with cavitation. Furthermore, tail-slaps were typically performed in the optimal zone for capitation (upper 5 meters). These results are significant as they demonstrate sound pressure alone cannot debilitate herring. Further they provide sound production mechanisms and provide a better understanding of the role of tail-slaps in prey capture. Further studies on the incipient cavitation number (relation between pressure, temperature, velocity, density, and vapour pressure) are required to confirm cavitation in tail-slaps.

Article contribution:

This article expands upon the previous kinematic analysis by providing a detailed acoustic analysis of the tail-slap during carousel foraging. The results and discussion support previous suggestions made where additional herring in the immediate vicinity are stunned by forces outside of direct physical contact. It also provided an additional overview of the carousel behaviour, with videos that aided in understanding the written description. Also, it served to demonstrate cases of learning as the calves practiced by imitating their parents or other adults, reinforcing suggestions of cultural traditions.

Primary:

Van Opzeeland, I. C., Corkeron, P. J., Leyssen, T., Similä, T., & Van Parijs, S. M. (2005). Acoustic behaviour of Norwegian killer whales, (*Orcinus orca*), during carousel and seiner foraging on spring-spawning herring. *Aquatic Mammals*, *31*(1), 110–119. https://doi.org/10.1578/am.31.1.2005.110

Summary:

This article investigated the variation in acoustic signals of killer whales (*Orcinus orca)* between the previously described carousel and seinar foraging. Opzeeland et al. (2005) aimed to determine presence of foraging strategy specific call types and characterize differences (or equivalences) of tail-slap activity, equivalent echolocation, and communication. To explore this, orcas were surveyed and recorded over 18 days in November (2002), and only foraging behaviour was sound-recorded and spectrographically analysed. The number of individuals observed ranged from 6 to 16. Carousel foraging was defined as cooperative hunting where herring are herded close to the surface and eaten one-by-one. Seinar foraging was defined as individual foraging on herring discards from fisheries. Specific communication is required during carousel foraging and accomplished through specific sequences of calls, opposed to the number of isolated calls. Both types of foraging used the same types of calls however there is a higher number of calls per individual during carousel foraging than seinar. This reinforces the importance and necessitation of call communication for coordination in the former. Echolocation clicks increased, in both types of foraging, with the number of individuals foraging. Tail-slaps occurred at a higher rate and had greater relative instances in carousel foraging in comparison to seinar. This article is significant because it outlines behaviour within carousel foraging that is different from other foraging behaviour and the similarities between that may be generalized to all foraging efforts. Further investigation is required to determine whether different groups of herring-eating orcas have specialized on one foraging behaviour. Additionally different pods or groups may utilize distinctive acoustic behaviours, transmitted culturally, which requires additional study.

Article contribution:

This article provided a detailed analysis of acoustic behaviour and a comparative insight. This allowed the structuring of carousel foraging efforts, providing insight to overall orca behaviour with the independence, similarities, and differences between foraging efforts. Further, it allowed the generalization of certain acoustic behaviours, such as call types as it is used in multiple instances and not exclusive. It also served as a good source for identifying other primary research regarding carousel foraging behaviour.

Primary:
Simon, M., Ugarte, F., Wahlberg, M., & Miller, L. A. (2006). Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. *Bioacoustics*, *16*(1), 57–74.
https://doi.org/10.1080/09524622.2006.9753564

Summary:
This article investigated previously observed vocal behaviour of herring-eating killer whales during carousel foraging. Simon et al. 2006 aimed to determine the acoustic characteristics of low-frequency pulsed calls, used by some herring-eating orcas during foraging and immediately prior to tail-slaps. To do this, hydrophones recorded audio during feeding in southern Iceland (n=6-25), and northern Norway (n=2-12) of June-July 2002 and October-December 2000-2001, respectively. "Feeding" was defined, from surface observations, as dives with arched backs, multidirectional surfacing, seabirds retrieving herring at dive sites, and herring observed on the surface. Acoustic signals underwent aural and visual analysis via waveforms and spectrograms. Observations revealed, echolocation clicks, and pulsed calls occurred in all feeding behaviour at a high rate. I36, a unique 3 second, low frequency (peak about 683 Hz) herding call was significantly correlated to tail-slaps, occurring within 1 second prior. This call is a communicative pulse as it does not fall within the optimal frequency for hearing in orcas (2000-80,000 Hz). It does however fall within the sensitive hearing range for herring (100-1000 Hz), classifying it as a herding call which further elicits the anti-predatory response of schooling. As the resonance frequency of the herring's bladder is around 700 Hz, the herding call may cause vibrations of bladder and further inhibit mobility, optimizing and preparing the herring orientation for the orcas' tail-slaps; tail-slap efficiency increases with herring school density. Interestingly, these calls were not observed by Norwegian populations of herring-eating orcas and only those Icelandic, suggesting possible cultural transmission. These results are significant as they demonstrate the possible adaptation of a unique low frequency herding call of Icelandic orcas allowing further manipulation of herring schools prior to tail-slap debilitation. Further investigation is required to determine the effect of varying orca sound signals on herring and the behaviour of orca acoustics.

Article contribution:
This article provided a new element observed in carousel foraging that may be population and group specific. This is important in understanding the variation in this foraging behaviour and how current anthropogenic influences might be adding to the stressors for adaptation in contemporary killer whale populations. This is supported as the article provided possible causes for the adaptation of these calls. It also provided the supporting evidence and understanding to a newer article utilized in this literature review.

Primary:

Samarra, F. I. P. (2015). Variations in killer whale food-associated calls produced during different prey behavioural contexts. ***Behavioural Processes*****,** ***116*****, 33–42. https://doi.org/10.1016/j.beproc.2015.04.013**

Summary:

This article investigated herding calls of orcas *(Orcinus orca)* during carousel foraging, and the potential source of variance when feeding on either spawning (reproduction) or overwintering herring. Herding calls were previously noted to be outside the optimal hearing of orcas but fall inside the sensitive range of frequencies for herring, increasing school density. Additionally previous research had only noted the usage of herding calls in spawning herring and not during the overwintering period. Samarra (2015) aimed to investigate whether herding calls were an additional tactic only used in feeding on less dense schools. To do this, 64 carousel acoustic recordings were collected for the spawning-herring context over four summers in SW Iceland. 354 acoustic recordings were collected for the overwintering-herring context over February and March (2013-2013) in West Iceland fjords. Both sets underwent acoustic analysis, tail-slaps indicated feeding. Observations revealed herding calls occurred in both instances (on spawning and overwintering herring), though were not used in all feeding events. Herding calls reached average peak frequencies of 732±116 Hz and 924±271 Hz during the summer and winter months respectively, statistically higher during winter. Herding call duration was significantly longer when feeding on summer-spawning herring than overwintering herring. Durations were negatively correlated with peak frequencies, likely due to the effort and energy required to make such calls. The call represents a key element of their feeding technique, though it may have developed recently as Sammara suggests possible variance between groups. The calls may also vary to match prey-hearing or their swim bladder resonance. This study is significant as it demonstrates herding calls do not correlate with specific herring contexts, or school density, and is used on summer-spawning herring. Further investigation between pods is required to determine whether herding calls instead be a culturally transmitted behaviour which varies between individuals and groups.

Article Contribution:

This article provided a greater understanding of herding call usage during carousel feeding and verified its occurrence during both summer and wintering months. This indicates herding calls are not an additional tactic used differently in varying annual-spatial contexts. It also indicated a limitation of their herding calls, indicating energy cost and exertion put into making these calls as higher frequencies are maintained for shorter durations. It also contributed to the main scope of carousel foraging, utilizing the method of determining feeding by tail slaps.

Primary:
Samarra, F. I. P., & Miller, P. J. O. (2015). Prey-induced behavioural plasticity of herring-eating killer whales. ***Marine Biology*****,** ***162*****(4), 809–821.**
https://doi.org/10.1007/s00227-015-2626-8

Summary:
This article investigated carousel foraging of herring-eating orcas *(Orcinus orca)* in all three prey contexts: feeding, spawning, and overwintering (spring, summer, and winter). Foraging during herring-feeding had not previously been described, though the spawning and overwintering life-stages have. Samarra and Miller (2015) aimed to determine whether orcas use the same encircling strategies and calling used in winter during all life-stages of herring. To do this, 16 suction-cup digital archival tags were attached to recording sound, pressure (converted to depth), heading (direction of whale), and location. Acoustic signals underwent spectrogram analysis. Observations revealed all overwintering and spawning feeding events included calls, compared to 74% during the herrings' feeding stage. Calls were not exclusive to feeding, as they occurred during other behaviours. Monophonic calls were found to signal for less specific functions than biphonic calls which likely function in high levels of coordinated directionality changes. Echolocation clicks were produced more often during winter, though necessary in all cases of feeding on spawning herring. Higher echolocation after tail-slaps corresponded with limited terrain visibility and less visual cues. Periods of locomoting were typically quieter. Vocalizations increased during carousel feeding as the school density increased. Carousel behaviour occurred year-round, though more encircling occurred during the spawning life-stage of herring than overwintering. During the feeding and spawning herring life-stage tail-slaps and feeding typically occurred in the top 10m of the water column and under 10 m overwintering. During the latter, herring are not brought to the surface and the seafloor is likely used as a barrier against preventing herring escape, contrary to the former two. This article was significant because they highlighted different adaptations of this feeding behaviour during different life-stages of herring, to decrease energetic investments. Further research is required to investigate the impact of local bathymetry on the carousel feeding strategy of orcas.

Article contribution:
This article provides additional information as to the adaptability of orca carousel behaviour to different herring contexts, including the herrings' feeding stage. They also utilize new techniques that allow a better look into the killer whales' perspective. It also provided an additional source that was included in the review due to the information from it being of high value, contributing to a better understanding of this foraging behaviour.

Primary:

Richard, G., Filatova, O. A., Samarra, F. I. P., Fedutin, I. D., Lammers, M., & Miller, P. J. (2017). Icelandic herring-eating killer whales feed at night. ***Marine Biology*****,** ***164*****(2), 1–13. https://doi.org/10.1007/s00227-016-3059-8**

Summary:

This article investigated acoustic behaviour of herring-eating killer whales *(Orcinus orca)* during night to determine variation and the occurrence of carousel foraging. Previous studies noted usage of the orca's white underside in herding herring close to the surface, prior to tail-slapping debilitation, which would be difficult to use under low light conditions such as at night. Richard et al. (2017) aimed to compare the acoustic behaviour of orcas between night and day to determine whether carousel behaviour occurs at night. To do this, an autonomous acoustic recorder was positioned in an Icelandic fjord for one month during winter and distinguishing between the feeding-specific sounds recording 5-minute intervals every 10 minutes (n=5097). Of the 5 minutes, the first minute was considered. An event was classified as a "feeding event" through the presence of the distinguishable tail-slap sound, made upon contact with herring, and performed in no other instance. Herding calls were categorized as either "linear herding calls", characterized by long durations of high intensities and low frequencies, and "nonlinear herding calls", those with frequency jumps, noise, or subharmonics. Observations of acoustic underwater tail-slaps determined killer whales fed at night though for a shorter duration (50% of time feeding) than day (77% of time feeding). Communicative monophonic calls were produced at a higher frequency at night than day, though both periods had greater monophonic calls than biphonic. Herding calls occurred more frequently at night and were positively correlated with the rate of tail-slaps suggesting greater reliance on sound under low-light conditions. This article was significant as it demonstrated the adaption of carousel foraging, to differing light conditions, optimizing foraging success. Further investigation is required to better understand the functional roles between different sound categories produced during their herding and feeding phases.

Article Contribution:

This article highlights the ability of carousel foraging of killer whales to be used at night and suggests the possible adaptations that allow optimized success of foraging. It further provides a new method to studying killer whales without physical visualization, through analysis of their acoustic signals. This work also provided a series of follow-up questions on vocalization analysis and the role of cultural traditions in establishing this behaviour and tools.

Secondary:

Riesch, R., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B., & Deecke, V. B. (2012). Cultural traditions and the evolution of reproductive isolation: Ecological speciation in killer whales? *Biological Journal of the Linnean Society*, *106*(1), 1–17. https://doi.org/10.1111/j.1095-8312.2012.01872.x

Summary: This article reviews research that describes how cultural traditions and inheritance drives ecotype isolation in orcas proposing that the deterministic mechanism of divergence is culture (non-geographic). Culture, that is population behaviour variation capable of vertical (parent-offspring), oblique (another older individual-younger), and horizontal (intragenerational) transmission through social learning, has been described in *Orcinus orca* comprising the diversity of acoustic communication and social affiliative or hunting behaviour. Dietary specializations on fish often yield greater social reliance in larger groups. Orcas are capable of three types of sounds used in communication and stunning their prey: 1) echolocation, responsible for orientation and prey detection, 2) pulsed calls and 3) whistles. Their communicative sounds vary between spatially separated populations, by their collection of stereotyped pulse calls, sympatric and parapatric populations, as call or whistle types are not shared in populations of different ecotype with overlapping home ranges, and even in social groups within a single population. While members within these clans associate frequently and share stereotype whistles, they do not share call types which are matriline specific in variation (i.e., call-structure within a clan is a learned behaviour from their mother). Cultural characteristics (group behaviour & social structure) may act as a "cultural badge" determining who an individual socializes with. Potential immigrants must adjust behaviourally to the local culture, including hunting strategies, experiencing a drastic decrease in fitness until doing so. The ability to accurately assimilate cultural traditions is potentially age specific, seen by the failure to reintroduce a long-term captive orca. It is not entirely known however whether they have the potential to learn non-natal cultural traits throughout their life or if the imprinting phase is age specific. It is concluded that a combination of the cultural component of behaviour and ecological speciation is the driving force behind orca diversity.

Contribution: This review outlines how orca social hunting behaviour, an aspect of culture, may be a learned behaviour dependent on the ecological factors, independent of geography, which yield variation between different ecotypes of killer whales. It also identifies the impacts on this behaviour, the importance of learning for this behaviour, and the precedence of matriline and group teaching over genetical inheritance. As a review it revealed areas in need of exploration in orca behavioural ecology. It also proved to be a good source for articles pertaining to herring-eating orca hunting behaviour and their tail slap.