Evaluating the Mixed Species Feeding Opportunities Provided by Foraging Humpback Whales (*Megaptera novaeangliae*) across Ocean Ecosystems

by
Lindsey Grace Ellett

A THESIS

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Oregon State University

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the requirements for the
degree of

Honors Baccalaureate of Science in Biology
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Abstract approved:____

Ari Friedlaender

Group foraging occurs across many ecosystems and taxa, and benefits some or all individuals in the group by optimizing feeding efficiency. The beater theory describes when individual "beaters" benefit other group members by herding prey into more accessible areas. Humpback whales feed on a variety of small patchy prey, and as large predators could play an integral role in marine group foraging. Using video-tag data I analyzed the frequency humpback whales engaged in group foraging, and the patterns in prey type, foraging techniques, and other predators present. Results showed humpback whales participate in various foraging groups by location. The increased proportion of group bubble net feeding may indicate that humpback whales aid other air-breathing predators in the group by acting as beaters. This study serves as a preliminary investigation into humpback whales' roles in group foraging utilizing subsurface observations. Future research may aim to develop broader spatial and temporal patterns, and compare these patterns to other marine and terrestrial mixed foraging groups.

Key Words: group foraging, *Megaptera novaeangliae*, beater theory, animal-borne tags, behavior

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I understand that my project will become part of the permanent collection of Oregon State University, Honors College. My signature below authorizes release of my project to any reader upon request.

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Evaluating the Mixed Species Feeding Opportunities Provided by Foraging Humpback Whales (*Megaptera novaeangliae*) across Ocean Ecosystems

Lindsey Grace Ellett

Introduction

Mixed species groups may be composed of animals that are either closely or distantly related taxonomically. Groups may congregate for a variety of purposes, lengths of times, and in a wide range of habitats, both terrestrial and marine. Functionally, most mixed species groups aim to increase foraging effectiveness and/or increase predator avoidance per individual (Stensland et al. 2003). In doing this, individuals in mixed species foraging groups are able to compensate for the potential costs of increased competition for resources and increased predator detection of the larger group. Interactions may serve to benefit all individuals, to benefit some while others are neither significantly positively nor negatively affected, or to benefit one or more at the expense of others. Within the group, the amount that each species benefits from the interaction may vary based on specific dynamics, including foraging styles, foraging zonation, prey preferences, and overall group size (Schreffler et al. 2010). Notably, some species, including cetaceans, may congregate due to attraction to the same resources, and not for an explicit benefit from being in close proximity to others (Anderwald et al. 2011). These interactions are often distinguished as mixed species aggregations instead of mixed species groups. Among cetaceans, complex social behaviors that favor group formation and coordination based on relatedness have mostly been observed within the *Odontoceti* suborder (Pomilla and Rosenbaum 2006). 'Resident' orcas (*Orcinus orca*) in the North

Pacific, for example, stay with the pod they were born into their entire lives, and female sperm whales form complex kin-based groups. The creation of these related groups are likely supported by kin selection, wherein coordination with relatives that share a substantial amount of one's own DNA can help increase the chances of that shared DNA being passed on to future generations, overcoming the costs of competition. Cetaceans in the *Mysticeti* suborder, in contrast, appear to lack stable social groups.

Mixed species foraging can have a range and combination of benefits, which ultimately must outweigh negative factors like competition for resources and aggressive interactions to be evolutionarily beneficial behaviors, which include behaviors that increase the likelihood of reproduction. The convoy theory describes how animals may forage in the same areas if they share common predators, as grouping helps to increase predator detection (Diamond 1981). Plains zebras (*Equus quagga*) have been found to decrease vigilance levels to varying extents based on both group size and group composition (Schmitt et al. 2014). When foraging in a single-species group, zebra vigilance declined with increasing numbers. While in mixed-species herds, vigilance levels were lowered to varying extents, compared to when zebras were alone, depending on the type of other species present in the herd rather than the total number of individuals present. Zebras are near-sighted and have acute hearing. They tend to associate with far-sighted species, resulting in their complementary senses better increasing overall detection of predators by the group (Diamond 1981). This strategy is less about resource acquisition and more about increased safety from predators, but it is enabled by similar foraging locations and may help to increase foraging efficiency more indirectly by lowering the energetic costs of high vigilance. In contrast, other foraging theories describe the way in which mixed species foraging leads to more direct increased foraging efficiency. For example, gang theory describes how mixed species foraging may increase resource access when larger groups help to outnumber another territorial species that would otherwise claim the resources entirely (Diamond 1981).

Larger groups may be more efficient at finding patchy food distributions and keeping track of which areas have already been searched than individuals alone. This benefit may be especially relevant in the open ocean. The beater theory describes how individual "beaters" may aid a whole group by herding prey out into more widely accessible foraging areas. This practice can be less beneficial to those that are acting as the beaters, as they incur a greater energetic cost while also increasing potential competition for prey by increasing accessibility. However, within groups of related kin, these costs may be worthwhile if the coordinated feeding increases the survival and reproduction rates of relatives with substantial shared DNA. One species may benefit at the expense of others in the pirate theory, which notes the energetic benefit that some species may gain by taking food from others in the group (Diamond 1981). This typically involves more aggressive interactions than passive scavenging techniques, and thus requires efficient skills for the tradeoff to be beneficial. Schreffler et al. (2010) found that foraging in groups increased capture rate (the number of successful prey captures/time), for some individual seabirds, but not capture efficiency (the number of successful prey captures/number of attempted prey captures) due to species interference, demonstrating one tradeoff made with a group feeding strategy over a solitary one. The energetic balance between more opportunities to catch prey versus a decreased likelihood of each attempt being successful depended on group size and species composition. The feeding efficiency theory clarifies how mixed species groups with similar diets, but which take advantage of different foraging techniques and zones, may experience substantially lower direct competition. Group foraging may also help to reduce an animal's variation in energy intake over time, by providing more opportunities, while reducing energy expenditure, increasing vigilance, and allowing novel foraging technique information to spread (Diamond 1981). Local enhancement involves individuals influencing the learning of others, and this process may help species in a group make food acquisition decisions, such as when and where to forage, what types of prey to focus on and what foraging technique to use, easier (Schreffler et al. 2010).

Feeding roles in groups vary, and can include initiators/producers, which instigate the grouping process and are often nuclear in the congregation; catalysts, which often have more obvious plumage/appearances which serves to alert other individuals and species of the congregation; and joiners, of which some may act as kleptoparasites or suppressors (Anderwald et al. 2011). Kleptoparasites steal food from others in the group, acting as pirates within the pirate theory, while suppressors may decrease group efficiency through utilizing individual foraging techniques that break up the prey concentration. These types of joiners may lead to the foraging group dispersing again if the benefits for others begin to decline substantially. In some mixed species groups only one of the species involved may be benefitting through foraging activities, such as in the oxpecker-ungulate relationship, wherein oxpeckers (*Buphagus africanus* and *Buphagus erythrorhynchus*) feed on ticks on African ungulates (Nunn et al. 2011). While there was some debate over whether the oxpeckers were potentially parasitic in nature, due to their foraging sometimes removing ungulate hide in addition to the ticks, analysis found their relationship was primarily mutualistic. This supports a continued relationship between the two species from both sides, but demonstrates considerations to be made between foraging assemblies and individual benefits and costs.

In the ocean, feeding assemblages may involve seabirds, fish, cetaceans, and pinnipeds in a variety of combinations (Anderwald et al. 2011). Many parrotfishes (*Scaridae*) engage in mixed-species groups as juveniles, often spending more time in a group than alone (Overholtzer and Motta 2000). While each individual's diet composition was similar both when foraging in a group and when foraging alone, group foraging appeared to lower aggressive encounters with other fishes. Being in a group may also enable small individuals to overcome the defenses of territorial herbivores to feed on algal resources that would otherwise be inaccessible. Birds have been observed scavenging from gray whale mud plumes, which may increase foraging efficiency by both concentrating prey and indicating prey locations with significant visual cues (Obst and Hunt 1990). The relative frequency and composition of feeding groups can depend largely on the distance between the group and the breeding colonies of some species. Thus, joiners that exhibit central place foraging, such as pinnipeds and some birds, may be limited by group foraging location, and its distance from land.

Humpback whale (*Megaptera novaeangliae*) foraging patterns involve a range of prey and different foraging strategies depending on location. Differences in local conditions and ecosystems create variations in prey type and availability, resulting in different techniques being the most energetically efficient and thus more frequently used. Humpback whales are within the suborder *Mysticeti*, and thus classified as baleen whales, which feed by filtering small prey from the water through keratin plates (Goldbogen et al.

2013). Prey species may include schooling fish such as capelin, herring, mackerel and sandlance, or euphausiids, which all share grouping behaviors allowing humpbacks to more efficiently feed on dense patches of prey (Clapham 2000). Feeding on masses of very small prey, rather than larger individual prey, may foster group foraging by lowering competition and making scavenging prey more efficient. As generalist predators that can feed on diverse prey types, humpback whales appear to benefit from highly flexible foraging strategies, which allow for high foraging efficiency over broad spatial and temporal scales (Cade et al. 2016). For example, one primary feeding technique used by humpback whales includes lunge feeding, which involves acceleration to high speeds and engulfment of prey-laden waters. The coordination between the timing of lunge feeding engulfment relative to body acceleration has major impacts on the hydrodynamics and energetic efficiency of the lunge feeding techniques used. Humpback whales adapt these phases to be more distinct when targeting krill and more temporally overlapped when targeting agile fish (resorting in more drag). Thus, while humpback whales do not always use the most energetically efficient lunge feeding technique, their flexibility in lunge feeding techniques allows for more dynamic feeding kinematics when targeting evasive fish prey than other lunge feeding whales.

Annually, humpback whales migrate from high latitude feeding areas in the spring, summer and autumn seasons, to low latitude breeding regions in the winter months. In the northern hemisphere humpback whales primarily feed on small schooling fish such as herring, capelin, anchovies and sandlance, though Southeast Alaskan populations have more diverse diets that likely reflect regional differences in prey availability (Wright et al. 2016). In contrast, in the southern hemisphere humpback whales have diets that include more euphausiids and fish such as sardines and herring (Stockin and Burgess 2005). Foraging strategies utilized include surface and subsurface lunging, bubble net feeding, and some bottom feeding. There are major differences in the types and prevalence of the specific techniques used between oceans, with these variations likely resulting from individuals aiming to maximize the ratio between their food/energy intake and the energy they have to exert to capture the prey. In order to have a net energy gain, individuals will thus only utilize prey-capture techniques that take more energy when the prey types and amounts will provide more energy than was lost (Clapham 2000). Lunge filter-feeding involves acceleration to high speeds and engulfment of prey-laden waters (Cade et al. 2016). For humpbacks the timing of engulfment typically coincides with body deceleration, though when pursuing agile fish prey more complex skull and body coordination allows for more flexible herding techniques. Surface lunges result from shallow foraging, and in rorqual whale species (which include species like humpbacks that have throat ventral pleats that expand when feeding) these result from opportunistic encounters with surface prey, exploitation of prey by oceanographic fronts, and the use of prey corralling techniques near the surface (Kot et al. 2014). Bubble net feeding involves humpback whales expelling air underwater to create a ring of bubbles around prey to cause them to congregate and allow the following engulfment to be more efficient (Wiley et al. 2011). Bubble nets appear to have a depth limit of about 20 meters, and thus their use is confined to near the surface, likely due to the efficiency of this technique declining at depth with the physics of bubble dispersal. Bottom feeding is a relatively slower feeding technique that involves feeding on the seafloor, and includes diverse strategies such as simple side-rolls, side-roll inversions, and repetitive scooping that occur relatively close to shore (Ware et al. 2013). During bottom feeding many individuals have been noted to have at least one other whale present during the process, and while some appeared to coordinate behavior, others did not.

Humpback whales may feed alone, or engage in coordinated feeding with conspecifics, depending largely on prey type. Humpback whales sometimes form groups, but genetic relatedness estimates have shown no significant association among relatives, with the exception of mother-offspring pairs (Pomilla and Rosenbaum 2006). Coordinated feeding behavior is thought to be most effective when whales encounter fast-moving schooling fish, and less efficient when feeding on slow prey like euphausiids (Clapham 2000). Humpbacks may aid others in their mixed species foraging groups by concentrating prey and flushing them from more inaccessible depths to the surface, especially through the use of bubble net techniques. This concept aligns with the beater theory, and would likely provide a greater benefit to the other species in the group than the humpbacks themselves. Similar roles can be observed in some species of diving birds that help to herd prey closer to the surface, as initiators/producers in their foraging groups (Anderwald et al. 2011). Sperm whales (*Physeter macrocephalus*), Risso's dolphins (*Grampus griseus*) and northern right whale dolphins (*Lissodelphis borealis*) have been observed foraging together such that sperm whales are nuclear to the group (Smultea et al. 2014). However, while Risso's dolphins were aggressively kleptoparasitic to the sperm whales, inducing regurgitation to steal food, the northern right whale dolphins acted as more passive scavengers benefiting from the Risso's dolphins. These findings demonstrate the more intricate effects of group foraging, wherein interactions build upon each other. The northern right whale dolphins would likely not congregate around sperm whales without Risso's dolphins present, due to their less aggressive tactics. Rossi-Santos, Santos-Neto and Baracho (2009) found that dolphins appeared to cause an increase in stress-related behaviors in humpbacks through preying on remoras attached to the whales' bodies, but the difference in proximity required for these interactions and other mixed species foraging groups could lead to different stress consequences. Whether group associations have a net negative effect on the whales would depend on the extent to which competition for prey could decrease their food intake, and whether these groupings caused any stress to the humpback whales.

In some instances humpback whales may be able to benefit from using aerial predators (e.g. birds) as visual cues to prey concentrations (Pierotti 1988). Additionally, in one study, rather than being nuclear to the group, humpbacks acted as joiners to Indo-Pacific bottlenose dolphins' (*Tursiops aduncus*) prey bait balls (Stockin and Burgess 2005). This finding was additionally interesting due to it being a rare example of humpbacks feeding during their migration, rather than fasting, and thus the results cannot serve to describe a known common pattern. These findings may suggest that energy stores and temporal patterns can affect whether humpbacks participate in mixed species foraging, as well as the group role that they fulfill. In this case humpbacks likely benefit in either a one-sided or mutual manner. An example of both species benefitting while group foraging lies in spotted (*Stenella frontalis* and *Stenella attenuata*) and bottlenose dolphins (*Tursiops truncatus*), which have been seen to occasionally coordinate behaviors in a more active foraging relationship (Rossi-Santos et al. 2009).

Prior research has utilized animal-borne tags to track animal movements more thoroughly, assess environmental use, and note animal behaviors (Hays et al. 2016).

Many of the humpback whale feeding techniques described have been much better defined through the use of tags, which can collect a variety of measures, including depth, acceleration and/or video footage information (Cade et al. 2016; Wiley et al. 3011; Ware et al. 2013). The way by which free-ranging predators make foraging decisions with very limited knowledge has also been explored through the use of tag technologies (Sims et al. 2007), results showing that some marine megafauna appear to search probabilistically when they lack prior knowledge of prey distributions. Animal-borne cameras have also been used to assess the foraging tactics and possible coordinated foraging patterns among species such as crabeater seals (*Lobodon carcinophaga*) (Gales et al. 2004). Though multi-sensor tags have been used to understand subsurface phenomena in the past, none have previously incorporated video sensor data to analyze mixed group foraging patterns.

Given the foraging behaviors and broad distribution of humpback whales, the goal of my study is to evaluate the frequency of mixed species group foraging that may be promoted by humpback whales across varying marine ecosystems and prey types. Data was collected and analyzed from multi-sensor animal-borne video recording tags that were deployed on whales in the North Pacific, North and South Atlantic, and Southern Ocean in order to compare the frequency of feeding events that included other predators. Overall humpback mixed species foraging patterns will likely depend on prey types, and their preference being shared among the species present; location, determining which other species are present/abundant in the vicinity; and foraging strategy, as surface and near-surface activity will likely serve as more efficient herding behaviors. Thus, if humpback whales serve as nuclear species in the observed mixed species foraging groups, then more species (birds and pinnipeds) will be present during feeding events when prey are of a type that can be shared, and feeding strategies occur near the surface.

Methodology

Multi-sensor animal-borne video recording tags (Figure 1) were deployed on one humpback whale each in the waters off of Monterey, California; Stellwagen Bank, Massachusetts; Cape Town, South Africa and the Antarctica Peninsula. The CATS-Cam tag can record several hours of footage (up to about a one day duration on humpback whales), is low-light optimized, and has a small footprint (measuring 115 mm by 40 mm) that decreases the chances of the device substantially affecting animal behaviors after the initial attachment (CATS, 2017). The tags can be attached via suction cups, later detaching on their own for easy and noninvasive retrieval. The video tag data analyzed for each region was collected within the feeding season (spring through autumn) for each hemisphere. Data from Monterey was collected in June and October of 2015, Stellwagen data was collected in June of 2015, data from South Africa was collected in November of 2016, and data from Antarctica was collected in January of 2016. Additionally, data analyzed from Monterey, Stellwagen, and South Africa was typically collected from between mid-morning (starting around 0900 hours) through mid-afternoon (around 1500 hours). Antarctica data was collected between approximately 0400 hours and 1200 hours, but sunlight levels for each area offered similar visibility. The data that were analyzed for each location tracked the time, depth, speed, and movements of one whale per feeding region. The tags recorded continuous video for 8-10 hours per deployment, and the cameras were aimed to face forward on the whale so that the mouth was clearly visible in order to determine feeding events. Video footage was analyzed for discreet feeding events based on humpback head motions (visible acceleration and engulfment phases) and visible prey in the images. Surface and subsurface lunges were determined by acceleration forward with head movements pitching upwards quickly as the whales opened their mouths to engulf prey-laden water (Goldbogen et al. 2016) (Figures 2c and 3b). Pressure sensors in the tag produced a continuous depth profile, which was used to determine the whale's feeding event depth and orientation. Utilizing the depth profile in conjunction with video footage, that showed whether the whale broke the surface, allowed lunges to be classified as either surface or subsurface in nature. Bubble nets were also typically observed by head pitches, as the whale accelerated towards the surface, and accompanied by visible streams of bubbles emitted from the individual to help force prey to densely congregate (Wiley et al. 2011) (Figures 2b and 3a). Rare bottom feeding events were determined by a humpback whale rolling to their side at depth, with feeding events visibly disturbing the seafloor such that clouds of sediment would be kicked up (Figure 4c). Examples of the various feeding techniques used within each region can be seen in Figures 2, 3, 4, and 5. For each feeding event, I assessed video from ten seconds before the event to ten seconds after, in order to standardize the length of video analyzed for each event, and noted the presence, number and species of other predators within the visible vicinity. Video clips would be reviewed multiple times to verify the feeding technique used, prey type targeted, and the identity of other animals when present. Identification to the species level was aided by evaluating specific frames of the video, and considering species distribution overlaps and relative abundance within the specific regions of study.

While Monterey, Stellwagen and Antarctica multi-sensor tags had both front and back facing cameras, South Africa had only a front facing camera. The number of other animals visible in group foraging was thus noted per each camera when applicable. Due to the limited field of view the recordings from the tags provided, and variation in cameras facing only forward or both forward and backward depending on region, the presence/absence of other marine predators in the group was evaluated during data analysis instead of their absolute numbers.

Data was analyzed in order to compare how the presence and composition of group foraging was affected by location, prey type, and humpback whale feeding technique. Given the differences in the amount of data for each region, metrics were calculated as percentages to compare relative proportions of each variable across feeding regions. Feeding events that occurred fewer than ten seconds from the beginning or end of a video were not considered, as a full 20 seconds was not available for monitoring. Additionally, head motions where the head pitched upward but there was no prey present, and it was unclear whether the motion was due to ascending from a dive, instead of foraging, were not counted in order to only record discreet feeding events. During a discreet feeding event humpback whale acceleration was followed by a phase of engulfment, characterized by the head pitching forward, which then resulted in deceleration. Adjustments to mouth orientation that directly followed engulfment were not considered discreet events, as there was not another noticeable acceleration phase before the head pitched upward again.

In order to achieve the goals of this study and compare the relative humpback whale group feeding, prey, and foraging technique patterns across multiple regions, I compared the proportions of feeding events that certain other marine predators (birds, pinnipeds, and/or whales), prey targets, and foraging techniques were observed. Mixed-species groups, which excluded group foraging events where only other humpback whales were present, were similarly compared through the percentage of feeding events that other species were present out of the total number of mixed group events. By comparing group foraging and mixed group foraging patterns to each other, the potential for unique intraspecific motivations for group foraging creating substantial pattern differences would be recognized. Target prey and feeding technique proportions were described in order to find potential correlations between prey and technique type and group foraging tendency. Target prey proportions and foraging technique proportions were compared, not only by location, but between all feeding events, just group feeding events, and just solitary feeding events, in order to determine whether group feeding was more common under certain prey or feeding technique differences. Though only one individual humpback whale was observed within each region the high number of feeding events analyzed for each area helps to estimate important patterns in prey consumption, feeding techniques utilized, and group foraging frequency and composition.

Results

A total of 23 hours, 47 minutes and 15 seconds of video was analyzed (Monterey: 5hr 41min 34sec, Stellwagen: 5hr 18min 50sec, South Africa: 5hr 31min 48sec, and Antarctica: 7hr 15min 03sec) (Table 1). Across the videos analyzed in all four locations, a total of 747 feeding events were measured; 133 in Monterey, 216 in Stellwagen, 169 in South Africa and 228 in Antarctica. Of these feeding events 53.3% involved visible group feeding, in which there was one or more other individual (predators of the same species and/or other species) in camera view within 10 seconds before or after the feeding event. Specifically, humpbacks were found foraging with other animals present in 43.6% of feeding events in Monterey, 38.4% of those in Stellwagen, 76.5% in South Africa and 55.3% in Antarctica (Figure 6).

Humpback whales were found to feed on krill and anchovy species in Monterey, with krill targeted in 54.1% of the feeding events, and anchovy target the other 45.9% (Table 2, Figure 7). Among only group feeding events in Monterey 33.9% involved krill prey and 66.1% involved anchovy prey. In contrast, during solitary Monterey feeding events krill prey were targeted in 70.3% of events, and anchovy in only 29.7%. In Stellwagen, Sandlance were nearly always the prey targeted, composing 99.5% of the feeding event prey, while krill were targeted in only a single group foraging event. In South Africa prey included mostly krill and anchovy, like Monterey, with very rare sandlance feeding events recorded. Krill were prey in 22.9% of all South Africa foraging events, while anchovy were targeted in 74.1%, and sandlance in only 2.9% of the foraging events. In South Africa group foraging events krill were the prey in 21.9% of feeding events, while anchovy were targeted the other 77.3%, and sandlance were targeted only once. Among solitary feeding events krill were the target prey for 26.2% of feeding events in South Africa, anchovy for 64.3%, and sandlance for 9.5%. Lastly, in Antarctica humpbacks were seen to forage 100% on krill. Thus, both their group foraging and solitary foraging events targeted exclusively krill. Across all locations krill were the target prey for 45.5% of feeding events, anchovy for 25.0% of feeding events, and sandlance were the target for 29.5% of all feeding events. When group foraging events occurred, across all locations, krill were prey in 43.8% of the feeding events, anchovy were the prey in 34.8% of the feeding events, and sandlance were the prey in 21.4% of the feeding events. When solitary foraging events occurred, across all locations, krill were the prey targeted in 47.4% of events, anchovy in 14.0% of events, and sandlance in 38.6% of events. Generally, the relative prey composition varied by location, but not between all foraging, group foraging, and solitary. However, in Monterey anchovy composed a greater proportion of prey in group feeding events than solitary events, wherein krill were more common targets.

Whales foraged using bubble nets in three of the four locations; Monterey, Stellwagen, and Antarctica. Surface lunges were noted in Monterey and Stellwagen only, and bottom feeding was present only in South Africa. Subsurface lunges were utilized in all of the surveyed locations (Table 3, Figures 8, 9, and 10). In Monterey 16.5% of all foraging events used bubble nets. In this region 2.8% of solitary feeding events used bubble nets while 34.5% of group foraging events involved bubble nets, demonstrating a 31.7% difference. Subsurface lunge techniques were used in 82.0% of all Monterey foraging events. During solitary feeding in Monterey subsurface lunges were used in 97.2% of the events, compared to 63.8% of group feeding events, a 33.4% difference. In contrast, only 1.5% of all foraging events in Monterey involved surface lunges, which all occurred within group foraging events, resulting in 3.5% of group feeding events in this region involving surface lunges. In Stellwagen bubble nets were used in 63.4% of all foraging events. Group feeding in Stellwagen utilized bubble nets in 81.0% of feeding events, while solitary events involved no bubblenets. Subsurface lunges in Stellwagen were used in 27.8% of foraging. Moreover, 16.7% of group foraging events in Stellwagen used subsurface lunges while 34.8% of solitary events used this technique, a 23.7% difference. Lastly, Surface lunges were utilized in 8.8% of feeding events in Stellwagen. Surface lunges were used in only 2.4% of Stellwagen group foraging events, and in 12.9% of solitary foraging events, demonstrating a 10.5% difference. In South Africa subsurface lunges were used in 97.0% of all feeding events. In this region 99.2% of group feeding events used subsurface lunges, compared to 90% of solitary feeding events, a 9.2% difference. Alternately, bottom feeding composed the other 2.9% of all feeding events in South Africa, contributing to 0.8% of group feeding events and 10.0% of solitary feeding events. Antarctica humpback whales used bubble nets in 54.4% of all feeding events. Antarctica humpback whales utilized bubble nets in 62.7% of group feeding events, and 33.3% of solitary feeding events, a 29.4% difference. Antarctica subsurface lunging occurred among 45.6% of all feeding events. Subsurface lunging contributed to 37.3% of group feeding events and 55.9% of solitary feeding events, exhibiting an 18.6% difference in this region. Overall, bubble net feeding composed a higher percentage of the feeding techniques used among group feeding events compared to solitary feeding events in Monterey, Stellwagen and Antarctica locations, and was not observed in South Africa. In contrast, subsurface lunges composed a lower percentage of the feeding techniques among group events than solitary events in Monterey, Stellwagen and Antarctica. Surface lunges and bottom feeding techniques were not common overall, together utilized in only 3.5% of the total feeding events across all locations.

For all feeding events that used bubble net techniques, the proportion that involved group feeding was higher than the proportion involving solitary feeding by 0.82 in Monterey and by 0.27 in Antarctica (Table 4). In contrast, the proportion of bubble net events that involved group foraging was essentially equal to the proportion that involved solitary foraging in Stellwagen. Bubble nets were not used in South Africa, but group foraging among subsurface lunging was 0.56 higher a proportion in the region, compared to the proportion for solitary feeding. The proportion of subsurface lunging that involved group feeding composed a lower proportion than those for solitary feeding events by 0.32 in Monterey, 0.53 in Stellwagen, and 0.10 in Antarctica. The differences in the proportions of group feeding compared to solitary feeding, among feeding events that used bubble net versus those that used subsurface lunging techniques, can be seen in Figure 11.

Only Monterey and Stellwagen showed humpbacks foraging in the presence of birds. Birds were present in 33.1% of all Monterey feeding events, and in 21.8% of all Stellwagen events (Table 5, Figures 12 and 13). Of the group foraging events in Monterey, 75.9% included birds, while 56.0% of Stellwagen group foraging events had birds present. When only mixed group feeding events were considered birds were present in 70.0% of events in Monterey and 100.0% in Stellwagen. In Stellwagen, bird species included gulls, while in Monterey the birds sighted were mostly shearwaters and some gulls, with cormorants present for two of the events. Pinnipeds (of which all the observed were sea lions) composed mixed species congregations in Monterey and South Africa, but not Stellwagen or Antarctica. They were present in 14.3% of all foraging events in Monterey, and 7.1% all foraging events in South Africa. In Monterey 32.8% of group foraging events contained pinnipeds, while only 9.2% of group foraging events in South Africa included pinnipeds. Additionally, 30.2% of mixed group foraging in Monterey included pinnipeds, while 100.0% of mixed group foraging in South Africa included pinnipeds. Other whales, of which all were other humpbacks, were present in at least some feeding events in all four locations. Additional humpbacks that joined the tagged whale were found in 29.3% of all feeding events in Monterey, 27.3% of all events in Stellwagen, 75.3% in South Africa and 55.3% in Antarctica. In Monterey other humpback whales were present in 67.2% of group foraging events, in Stellwagen they were present among 70.2% of group foraging events, South Africa had humpback whales present for 98.3% of group foraging events, and lastly, Antarctica had at least one humpback present in all 100% of the group foraging events. Whales were the only other individuals that composed foraging groups in Antarctica, where group foraging occurred in 53.4% of all feeding events.

Discussion

The goals of this study were to describe the frequency of mixed species foraging groups that humpback whales may promote across various marine ecosystems, foraging techniques, and prey species. Through video tag analysis I found that humpback whales may play an important role in group foraging patterns with birds, pinnipeds, and other whales. Specifically, they may aid in actively herding prey from greater depths toward the surface, thus making them more easily accessible to many other air-breathing predators.

Results showed that group foraging was common and occurred in all four locations, with an average of 53.6% of all feeding events involving group foraging. Prey composition varied by location, but did not vary notably between group feeding events and solitary feeding events within Stellwagen, South Africa, and Antarctica. This lack of variation in prey composition was due to the humpback whale in Stellwagen feeding only on sandlance, and the humpback whale in Antarctica preying only on krill. However, in Antarctica only other humpback whales were observed group foraging, whereas in Stellwagen a substantial amount of mixed group foraging also occurred with birds. In South Africa anchovy were targeted during a majority of the feeding events, with some krill targeting, and rare sandlance targeting during bottom feeding, both for group foraging and solitary foraging events. Ware et al (2013) found that many humpback whales bottom feed in the presence of at least one other whale, and whale group bottom feeding was noted once within this study. Additionally, most bottom feeding in the prior study occurred at night, when sandlance burrow intot the seabed or form horizontal schools close to the seafloor. Thus, due to the lower visibility for this feeding event, which occurred at greater depths as the whale disturbed clouds of sediment on the seafloor, and the time frame observed including only diurnal behavior, group bottom feeding could be underestimated. In Monterey, humpback whales fed fairly equally on krill and anchovy prey species overall. However, among group foraging events a majority of the feeding events involved anchovy, while among solitary feeding events krill were the more common target. Monterey also had the most variation in group foraging, with birds, pinnipeds and other whales each present during some feeding events. This shift in prey targeting between solitary and group foraging aligns with the past finding that coordinated feeding behavior may be more effective when whales encounter fast-moving, schooling fish like anchovy, and less efficient when feeding on slower krill (Clapham 2000). Knowing the relative abundance and densities of these prey types may help determine whether the humpback whales were feeding preferentially on specific prey in each location or not. Additionally, higher prey abundance and density values could also contribute to the liklihood of group feeding, as larger prey abundances and densities could provide more energetically rich opportunities that can support larger groups.

The proportions of different feeding techniques varied by area, and also exhibited a discrepency within each region when comparing group feeding events to solitary feeding events. The increased proportion of bubble nets used in group feeding compared to its proportion among solitary feeding events may indicate that humpback whales help other individuals in a group by flushing prey from greater depths into more accessible surface waters. This feeding technique may draw in other individuals due to the process creating relatively noticeable visual and auditory cues as the humpbacks blow large amounts of bubbles, which rise to the surface (Wiley et al. 2011). The ability for other marine predators to detect these cues, either from an aerial perspective or from nearby waters, likely limits group composition by affecting which species are made awarene of the feeding opportunity. Circular bubble nets are efficient for coralling prey because many prey, such as herring, are reluctant to swim through a curtain of bubbles even when frightened (Sharpe 2001). In South Africa, no bubble nets or surface lunges were observed, and group foraging included mostly other humpback whales and some pinnipeds. The lack of mixed foraging with birds in this region may, thus, support the idea that mixed group foraging with bird depends on the use of near surface feeding techniques by humpback whales. Humpback whales require a much greater amount of metabolic energy than pinnipeds and birds, and this difference may support the idea that they would be more likely to act as initiators/catalysts versus joiners in the group.When humpback whales congregate large amounts of prey, birds and pinnipeds would likely benefit more from joining, as they would not require as high of a density of food as the whales and could act as scavengers and/or pirates. In contrast, if birds and pinnipeds are more limited in congregating smaller groups of prey due to their size, humpback whales would not benefit as much from joining the group. Prey composition and the proportions of feeding techniques used both varied relative to each other. Knowing the relative abundance and density of prey in each region could be useful in understanding these patterns. More energetically costly feeding techniques, like bubble net feeding, may have been limited in certain regions depending on whether the benefit in the amount of prey that could be consumed would be worth the energy expenditure.

Across all four regions, I found differences in the types of animals that contributed to group foraging patterns with humpback whales. The other species present in the observed foraging groups were all air-breathing animals, which may indicate an energetic efficiency benefit from foraging on prey that has congregated closer to the surface due to humpback whales, which would lower the need to expend energy diving and trying to locate food. Humpback whales that join the feeding group may be driven by different factors than birds and pinnipeds, due to potential intraspecific cultural interactions. While humpback whales do appear to have relatively short social bonds with specific individuals, and relatedness among groups (other than mother-calf pairs) is not significant, they may coordinate to maxinmize food intake fairly often (Valsecchi et al. 2002).

Notably, the pinnipeds observed in the group foraging events were all otariids, rather than phocids. Otariids include fur seals and sea lions, which can be characterized by external ear flaps (pinnae) (Berta et al. 2006). They are generally shallow divers that primarily prey on fast swimming fish. Additionally, otariids rely more heavily on their pectoral flippers for underwater maneuverability, while phocids rely more on full body undulations. Phocids include true seals, which lack external pinnae and are unable to turn their hind flippers forward like otariids are able to, resulting in less adaptable movements, particularly on land. Phocids and otariids have distributions that overlap in Monterey and Antarctica (Monterey Bay Aquarium Foundation 2017, Churchill et al. 2013), whereas only otariids are located in South Africa (Govender, 2015), and only phocids are commonly located in Stellwagen (Center for Coastal Studies, 2017). Thus, the discrepancy in group foraging with humpback whales may be related to the variations in foraging strategies of these taxonomic groups. Though many pinnipeds use generalist feeding strategies, which can be highly flexible depending on the prey type and distribution, niche partitioning is sometimes utilized to lower intraspecific competition (Riedman 1990). Coordinated feeding is utilized most frequently by pinniped species that target large, patchily distributed schools of fish or squid, including many fur seals and sea lions. However, many phocids are more solitary foragers, targeting schooling pelagic fishes and more sessile species (Riedman 1990). Kilian et al. (2015) described how harbor seals (*Phoca vitulina*), a species of phocids, hunted herring prey with observable success only when a small group or single herring was separated from the school. This may have helped the harbor seals avoid the confusion effect schooling provides. Thus, the dense prey congregations that humpback whales create may not be as beneficial for phocids species compared to otariid species.

If humpback whales serve to flush out and herd prey, then they would help serve as initiators/catalysts within the beater theory, which describes the process through which individuals may aid a whole group by ushering prey into more widely accessible foraging areas (Diamond 1981). The beater theory has been observed in birds (Davis and Jackson 2007), mammals (Herremans and Herremans-Tonnoeyr 1997), fish (Baker and Foster 1994), and spiders (Rypstra 1989), and is effective as it reduces the chances of prey escaping. This process, thus, increases prey availability to all of the predators in the group and decreases individual variance in food intake rate over time by providing feeding more opportunities. Herding involves predators more actively restricting prey movement compared to flushing. Bubble nets are an example of herding behavior, as the feeding technique serves to corral prey to increase their population density. In contrast, surface and subsurface lunges may only aid in flushing prey from one area to another, as they are less directive than bubble net feeding. Larger groups may increase efficiency in finding patchy food distributions and in keeping track of searched versus unsearched areas. Local enhancement could additionally help the bird and pinniped species that join the group make food acquisition decisions, concerning which prey to target and the appropriate feeding strategies to use (Schreffler et al. 2010). In some species, such as the little penguin (*Eudyptula minor*), this benefit may be enough to foster group foraging even when catch success is not better, due to positive energetic gains made from an increased probability of detecting prey with conspecifics (Sutton et al. 2015).

Similar group feeding interactions can be seen in the strongly correlated relationship between gray whales and marine birds, wherein the whales' summer foraging in the Bering Sea produces prey-rich mud plumes that provide many birds the opportunity for ephemeral foraging (Obst and Hunt 1990). Nearly 67% of the gray whales in this study engaged in group foraging with birds, whereas birds were present in group foraging within two of the locations I analyzed, and thus birds group foraged with two out of four of the whales I observed. Stomach contents revealed that the whale-associated birds had consumed almost exclusively benthic crustaceans, a major component of gray whale diets, which are not typically present in surface waters. These findings suggest that some whales may not only increase the efficiency with which other predators can capture prey, but create conditions that allow the other predators to expand their diet to include a broader range of prey types as well. Studies of seasonality have shown that group associations can vary annually (Ridoux 1986). For example, marine birds off of the Crozet Archipelago will scavenge near orcas much more often during the summer, when the presence of their penguin and elephant seal (*Mirounga leonine*) prey increases. The discrepancy between birds' winter and summer scavenging patterns is likely due to the summer increase in orca prey also increasing the benefit of the birds scavenging from orca past an energy efficiency threshold. While some scientists note that group foraging may be more opportunistic in nature, the observation that white-chinned petrels (*Procellaria aequinoctialis*) will follow orcas to inshore areas (which the birds do not normally forage in) before the orcas actually begin foraging demonstrates an anticipatory recognition of whales as capable of offering a feeding habitat (Ridoux 1986).

Whereas coordinated feeding between individuals can lead to positive effects for both individuals involved, as is the case of some spotted and bottlenose dolphin group foraging interactions (Rossi-Santos et al. 2009), the beater theory relies on an imbalance of energy expenditure that typically allows some joiner individuals to benefit more than initiators in the group. The extent to which humpback whales are neutrally or negatively affected as beaters in group foraging lies in the level of mixed species competition that arises, and in whether the birds and pinnipeds are just consuming flushed/herded prey, scavenging, or directly engaging in kleptoparasitism. An example of a less competitive beater theory relationship includes the forktailed drongo (*Dicrurus adsimilis*), small insectivorous birds in the Afrotropics that use a wide variety of other larger species as beaters, including giraffes, elephants, buffalos and baboons, even when the disturbances the beaters engage in are not through their own foraging (Herremans and Herremans-Tonnoeyr 1997). Typically, these individuals have little effect on the beaters, who would flush insects whether the drongos were present to benefit or not. Contrastingly, when sperm whales, Risso’s dolphins and northern right whale dolphins sometimes forage as a group, northern right whale dolphins scavenge food more passively, whereas Risso’s dolphins are aggressively kleptoparasitic toward the sperm whales (Smultea et al. 2014).

Similarly, willets (*Tringa semipalmata*) are a species of bird that use white ibis (*Eudocimus albus*) as beaters, stealing prey as the ibis probe for polychaetes. This may more negatively impact the ibises as losing prey that they disturb to the willets leads to decreased foraging efficiency (Davis and Jackson 2007). If humpback whales play a substantial role as beaters while group foraging, the scavenging and potential kleptoparasitism that other animals engage in may similarly negatively impact humpback whales, by reducing their available prey intake.

This study is informative due to its use of multi-sensor animal-borne video recording tags, which allowed the observation of a marine predator that has otherwise been difficult to study. While past research has utilized multi-sensor tags to better understand subsurface phenomena, none have previously incorporated video sensor data to analyze mixed group foraging patterns. In exploring marine mixed species foraging patterns, and the role that humpback whales may play in these groups, I provide a foundation to allow for a more thorough comparison between these patterns and those of other known mixed species foraging groups. As a preliminary study, this work serves to estimate the scope of humpback whale mixed group foraging patterns in multiple locations, estimating the impact these whales could have on other species as potential prey providers. While only one individual was observed for each region the high number of feeding events noted for each area has helped to establish valuable estimates of prey patterns, feeding techniques utilized, and group foraging frequencies and compositions.

Advances in mounted technological devices that are able to collect data on environmental conditions, animal movements and physiology have allowed for a more detailed understanding of animal life histories and more holistic comparisons across a wide range of taxa (Hays et al. 2016). Better understanding animal nature can help support more appropriate conservation and management, for example. Gaining understanding of the movements of Adélie penguins (*Pygoscelis adeliae*) during their premolt period helped to justify the creation of the first entirely high seas Antarctic marine protected area (Hays et al. 2016), and tracking the movements of turtles has allowed more descriptive habitat models to be created and used to decrease bycatch (Lewison et al. 2015). Unlike terrestrial animals, marine mammals consistently move horizontally and vertically through their environment as they engage in subsurface behaviors but frequently surface to breathe air, which has made the use of mounted devices particularly useful in their study. Better understanding the short term social interactions of group foraging may help to determine the degree to which other species affect humpback movements or vice versa. Additionally, further study into the magnitude of impact that the role humpback whales play in group foraging has on other marine predators' foraging success and overall metabolic health may encourage more comprehensive conservation plans that focus on the community, and their interactions, rather than individuals alone. If humpback whales commonly congregate to feed with masses of marine birds, then large groups of foraging birds may be used as visual cues to warn marine vessels to be cautious or circumvent an area to avoid whale collisions. Vessel strikes that injure whales are likely underreported, especially in areas like the Gulf of Maine where recreational and commercial vessel activity is common, and when humpback whales utilize foraging strategies that exploit prey in the upper water column they may be at an increased risk for exposure to vessel activity (Hill et al. 2017).

This study was limited technologically and logistically, such that estimates of general trends of humpback whale foraging prey, feeding techniques and groups for each location could be evaluated, but the specificity of broader inferences are limited. The tag mounted cameras used to collect observational data faced only forward and backward, providing a limited view of the potential other individuals that were in the vicinity. Ware et al. (2013) found that humpback whale bottom feeding frequently involves at least one other whale is present, but the murkiness created by sediment being disturbed within our video data could have lead to an underestimation. Similarly, dense bubble nets that obscured camera visibility could have also led to some underestimates of group foraging. Findings are limited statistically due to having a small sample size, with only one whale observed for each region. The observations also occurred over a relatively short time period for each region, and thus may be limited to describing very specific spatial and temporal patterns, that could realistically vary more broadly over longer annual cycles, which may be impacted by long term migrations and behavioral changes. Moreover, the relatively small time frame analyzed for each area did not allow observation of the beginning stages of group formation, which could better show which animals were the inititators/catalysts versus the joiners. The inability to analyze changes in prey abundance and density during the feeding events also limits understanding of whether humpback whales are feeding preferentially, and whether group formation and feeding techniques utilized are influenced by these variables. However, the findings of this study are substantial, and also serve to show that many logistical hurdles to studying group foraging behavior in whales can be overcome with new technological advances.

In future studies greater nuances of humpback group foraging patterns may be assessed in order to better understand spatial and temporal patterns. These broader approaches may also help to further explore whether humpback whales act as beaters in group foraging patterns. If so, further studies could help to determine whether the group foraging that humpback whales foster only supplements other local species' regular foraging, or whether they play a more integral and consistent role in other species being able to obtain adequate amounts of food to fulfill their energy demands. Animals with different life history strategies, such as those that forage a consistent amount throughout the year versus those that engage in concentrated feeding behaviors during certain times of the year, may be impacted differently if they rely heavily on humpback whales as providers of prey access. Some pinniped species, for eample, fast or greatly alter their foraging patterns during their breeding seasons (Coltman et al. 1998). Male harbor seals reduce their food intake while also increasing energy expenditure late in the breeding season. Within the study they appeared to balance energetic costs of reproduction against their small body size constraints by foraging more often earlier in the breeding season, before females arrived in the breeding areas, and by feeding opportunistically. These differences in annual foraging may affect the extent to which they do or do not engage in group foraging. The findings may also show how some long term patterns within an animal's life history may result in extra energy intake being more critical. Researchers may also want to explore how other species of whales, with a variety of locations, prey types, and feeding techniques, compare to humpback whales in their group foraging patterns. The use of a camera with a wider perspective may allow for better estimates of group foraging compositions to be made, and decrease the difficulty of accounting for individuals in the group that may trail the whales or feed off to one side. Cameras with the ability to collect images at greater depths may help to allow observations of a wider range of potential group foraging patterns, especially for deeper subsurface lunging and bottom feeding behaviors. Surface and near surface feeding allows for the observation of humpback whale interactions with mainly other air-breathing animals, whereas at depth there could be a variation in associated mixed foraging composition, including predators that can dive much deeper or predators that are not limited by a dependence on air, such as larger fish. Studies that could compare group foraging trends with prey densities and the relative abundance of other predator species in the region may provide a more thorough understanding of what influences the observed patterns.

Through this study I found that humpback whales participate in a range of foraging groups by location, with varying prey compositions and feeding techniques. Prey composition depended on the location, as did the feeding techniques used. Additionally, group feeding events often involved a greater proportion of bubble net feeding compared to other feeding techniques, which may highlight the way herding prey to more accessible surface waters aid other air-breathing predators in more efficient foraging. This study helps create a foundation for the investigation of humpback whales' roles in group foraging through important subsurface observations, and future research may aim to develop a more broad spatial and temporal understanding of these patterns and how they compare to the group foraging of other marine and terrestrial species.

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Tables and Figures

Table 1. Summary data by location for all feeding events and group feeding events. Sample size n = 1 for each location.

Location	Monterey	Stellwagen	South Africa	Antarctica	For All Locations
Amount of Time Analyzed (Hr:Min:Sec)	5:41:34	5:18:50	5:31:48	7:15:03	23:47:15
Total Number of Feeding Events	133	216	169	228	747
Number of Group Feeding Events	58	84	130	126	398
% of Total with Group Feeding	43.6	38.9	76.5	55.3	53.3

Table 2. Humpback target prey patterns by location for all feeding events, group feeding events, and solitary feeding events.

Location	Monterey	Stellwagen	South Africa	Antarctica	For All Locations
Feeding events with Krill Prey	72	1	39	228	340
Feeding events with Anchovy Prey	61	0	126	0	187
Feeding events with Sandlance Prey	0	215	5	0	220
% Feeding on Krill	54.1	0.5	22.9	100.0	45.5
% Feeding on Anchovy	45.9	0.0	74.1	0.0	25.0
% Feeding on Sandlance	0.0	99.5	2.9	0.0	29.5
Group feeding with Krill Prey	20	0	28	126	174
Group feeding with Anchovy Prey	39	0	99	0	138
Group feeding with Sandlance Prey	0	84	1	0	85
% Group Feeding with Krill	33.9	0.0	21.9	100.0	43.8
% Group Feeding with Anchovy	66.1	0.0	77.3	0.0	34.8
% Group Feeding with Sandlance	0.0	100.0	0.8	0.0	21.4
Solitary Feeding with Krill Prey	52	1	11	102	166
Solitary Feeding with Anchovy Prey	22	0	27	0	49
Solitary Feeding with Sandlance Prey	0	131	4	0	135
% Solitary Feeding with Krill	70.3	0.8	26.2	100.0	47.4
% Solitary Feeding with Anchovy	29.7	0.0	64.3	0.0	14.0
% Solitary Feeding with Sandlance	0.0	99.2	9.5	0.00	38.6

Table 3. Feeding technique patterns by location for all feeding events, group feeding events, and solitary feeding events.

Location	Monterey	Stellwagen	South Africa	Antarctica	For All Locations
Number Feeding Events Using Bubble nets	22	137	0	124	283
Number Feeding Events Using Surface Lunges	2	19	0	0	21
Number Feeding Events Using Subsurface Lunges	109	60	165	104	438
Number Feeding Events Using Bottom Feeding	0	0	5	0	5
% Feeding Events Using Bubble nets	16.5	63.4	0.0	54.4	37.9
% Feeding Events Using Surface Lunges	1.5	8.8	0.0	0.0	2.8
% Feeding Events Using Subsurface Lunges	82.0	27.8	97.1	45.6	58.6
% Feeding Events Using Bottom Feeding	0.0	0.0	2.9	0.0	0.7
Number Group Feeding Events Using Bubble nets	20	68	0	79	167
Number Group Feeding Events Using Surface Lunges	2	2	0	0	4
Number Group Feeding Events Using Subsurface Lunges	37	14	129	47	227
Number Group Feeding Events Using Bottom Feeding	0	0	1	0	1
% Group Feeding Events Using Bubble nets	34.5	81.0	0.0	62.7	44.5
% Group Feeding Events Using Surface Lunges	3.5	2.4	0.0	0.0	1.5
% Group Feeding Events Using Subsurface Lunges	63.8	16.7	99.2	37.3	54.3
% Group Feeding Events Using Bottom Feeding	0.0	0.0	0.8	0.0	0.2
Number Solitary Feeding Events Using Bubble nets	2	69	0	45	116
Number Solitary Feeding Events Using Surface Lunges	0	17	0	0	17
Number Solitary Feeding Events Using Subsurface Lunges	72	46	36	57	211
Number Solitary Feeding Events Using Bottom Feeding	0	0	4	0	4
% Solitary Feeding Events Using Bubble nets	2.8	52.3	0.0	44.1	33.3
% Solitary Feeding Events Using Surface Lunges	0.0	12.9	0.0	0.0	4.9
% Solitary Feeding Events Using Subsurface Lunges	97.2	34.8	90.0	55.9	60.6
% Solitary Feeding Events Using Bottom Feeding	0.0	0.0	10.0	0.0	1.1

Table 4. The proportion of feeding techniques that were group feeding, the proportion of feeding techniques that were solitary feeding, and the difference between these proportions.

	Location			
	Monterey	**Stellwagen**	**South Africa**	**Antarctica**
Proportion of Group Feeding				
Bubble nets	0.91	0.50	0.00	0.64
Subsurface Lunges	0.34	0.23	0.78	0.45
Proportion of Solitary Feeding				
Bubble nets	0.09	0.50	0.00	0.36
Subsurface Lunges	0.66	0.77	0.22	0.55
Difference in Proportion (Group - Solitary)				
Bubble nets	0.82	0.00	0.00	0.27
Subsurface Lunging	-0.32	-0.53	0.56	-0.10

Table 5. Group feeding prevalence and composition by location, as well as mixed group composition by location. While group feeding includes any additional marine predators in the group, mixed group feeding excludes groups that only included other humpback whales to focus on interspecific patterns.

Location	Monterey	Stellwagen	South Africa	Antarctica	For All Locations
Feeding Events with Birds	44	47	0	0	91
Feeding Events with Pinnipeds	19	0	12	0	31
Feeding Events With Other Whales	39	59	128	126	352
% of Total With Birds	33.1	21.8	0.0	0.0	12.2
% of Total With Pinnipeds	14.3	0.0	7.1	0.0	4.2
% of Total With Other Whales	29.3	27.3	75.3	55.3	47.1
% of Group Feeding with Birds	75.9	56.0	0.0	0.0	22.9
% of Group Feeding with Pinnipeds	32.8	0.0	9.2	0.0	7.8
% of Group Feeding with Other Whales	67.2	70.2	98.5	100.0	88.4
% of Mixed Group Feeding with Birds	70.0	100.0	0.0	0.0	74.6
% of Mixed Group Feeding with Pinnipeds	30.2	0.0	100.0	0.0	25.4

Figure 1. CATS-Cam multi-sensor animal-borne video recording tags.

Figure 2. Monterey A humpback whale (a) foraging with birds after a subsurface lunge for anchovy prey, (b) using a bubble net to capture anchovy prey, (c) exhibiting bird and sea lion group foraging during a subsurface lunge for anchovy prey, and (d) foraging with other whales after a subsurface lunge for anchovy prey.

(a)

(b)

(c)

(d)

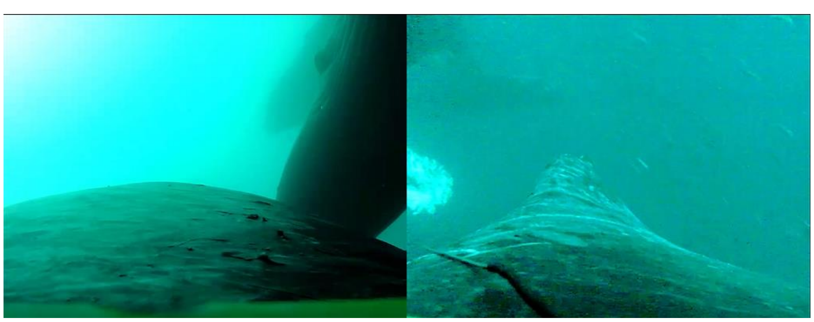
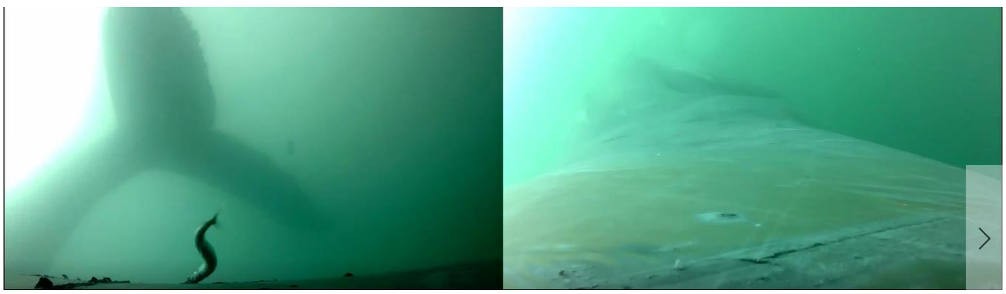


Figure 3. Stellwagen Bank A humpback whale (a) bubble net feeding on sandlance prey, (b) group foraging with another humpback while subsurface lunging for sandlance prey, (c) subsurface lunging for krill prey and (d) group foraging with birds post bubble net feeding for sandlance prey.

(a)

(b)



(c)

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Figure 4. South Africa A humpback whale (a) group foraging with other humpback whales and subsurface lunging for anchovy prey, (b) subsurface lunging for krill prey and (c) bottom feeding on sandlance prey.

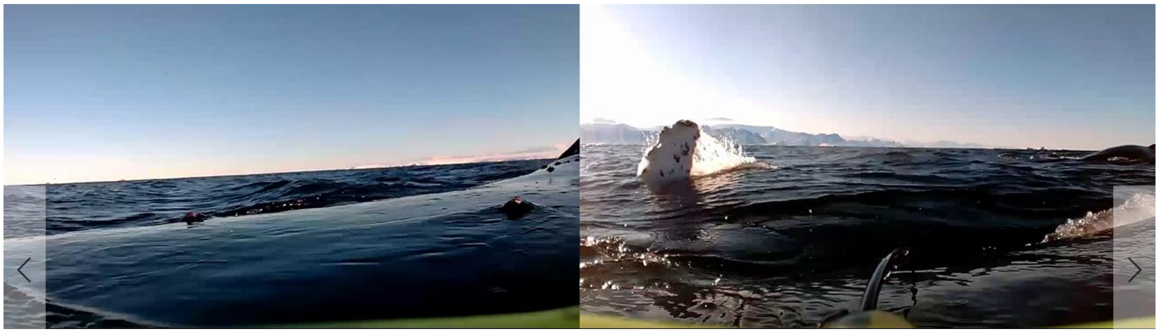
(a)

(b)

(c)

Figure 5. Antarctica A humpback whale (a) group foraging with another humpback whale after bubble net feeding for krill prey and (b) subsurface lunging for krill prey.

(a)



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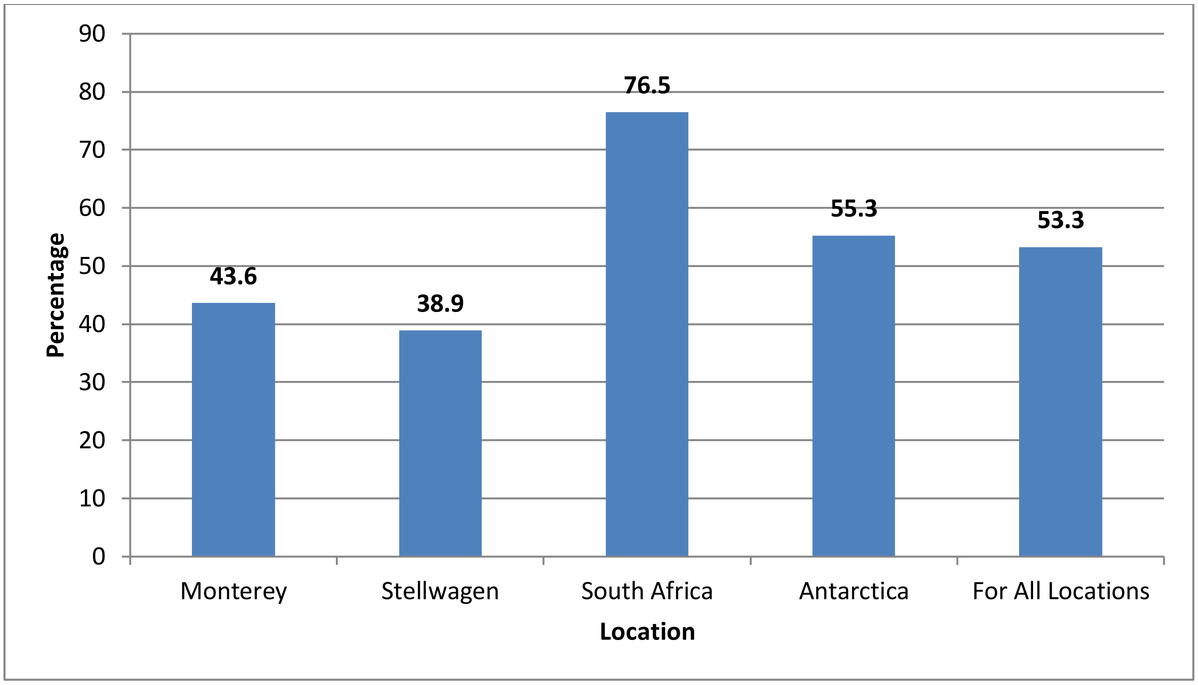

Figure 6. The percentage of feeding events that involved group foraging by humpback whales by region. On average 53.3% of feeding events involved group foraging, with the highest proportion in South Africa.

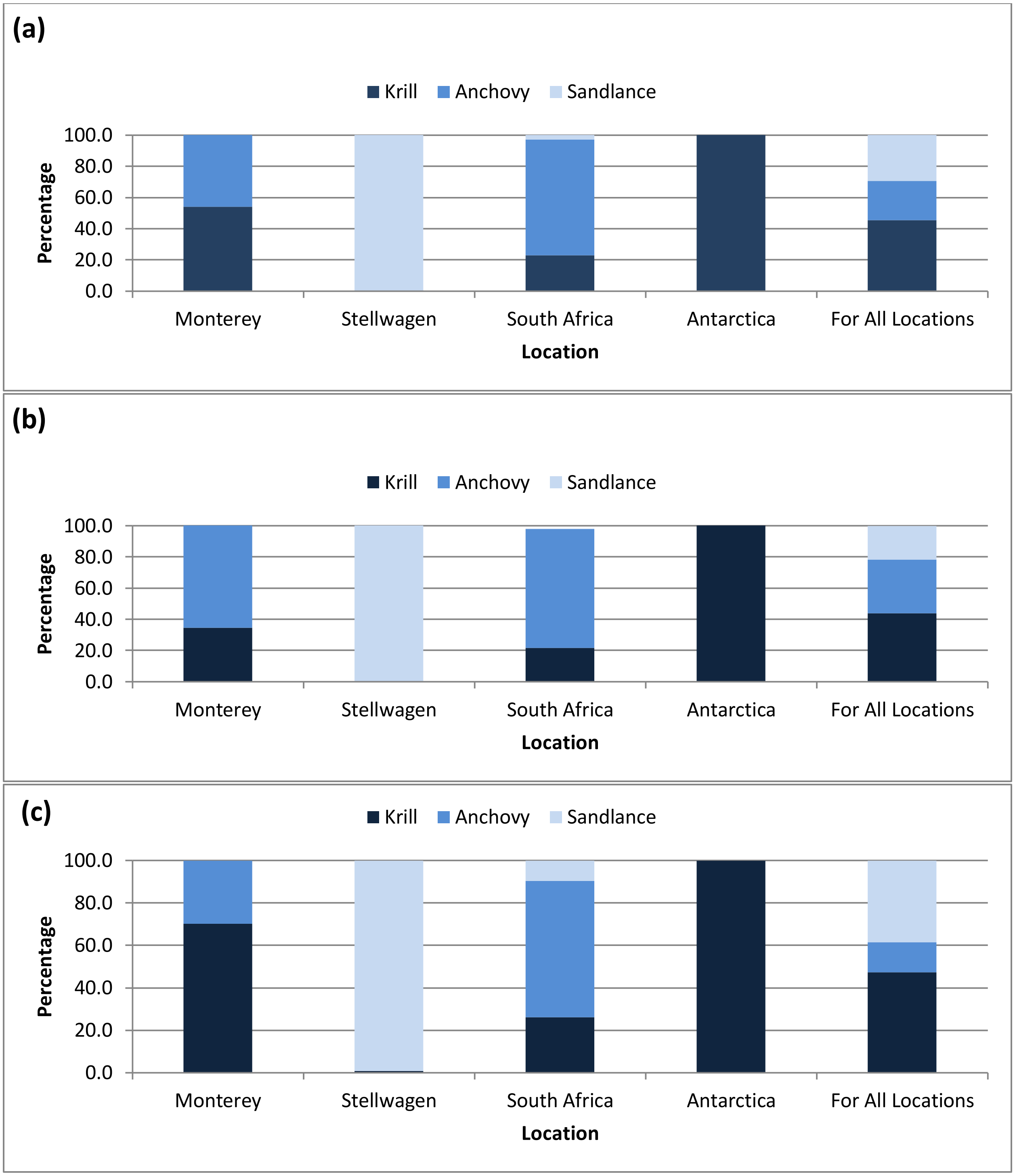

Figure 7. Comparisons of prey composition across feeding regions for both (a) all foraging events, (b) group foraging events, and (c) solitary foraging events.

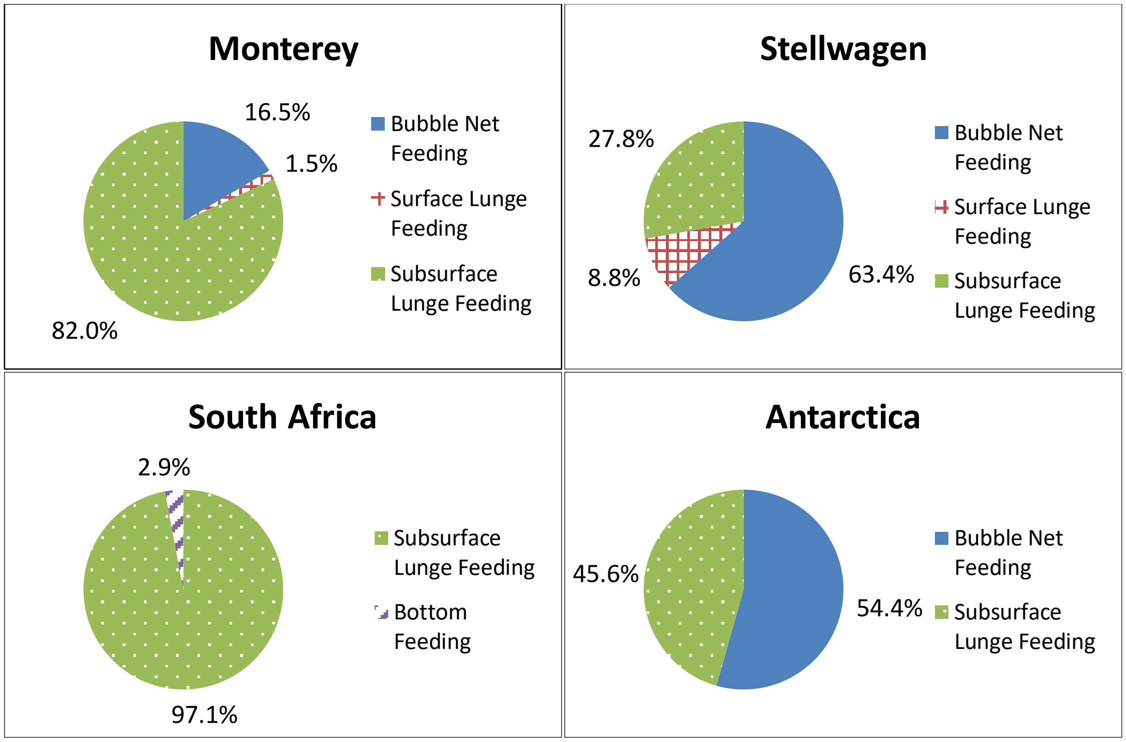

Figure 8. Foraging techniques used by humpback whales for all feeding events while in different feeding regions. Solid blue regions represent the proportion of feeding events involving bubble net feeding, red checkered regions represent the proportion using surface lunge feeding, green dotted regions represent the proportion using subsurface lunge feeding and purple stripes represent the proportion using bottom feeding.

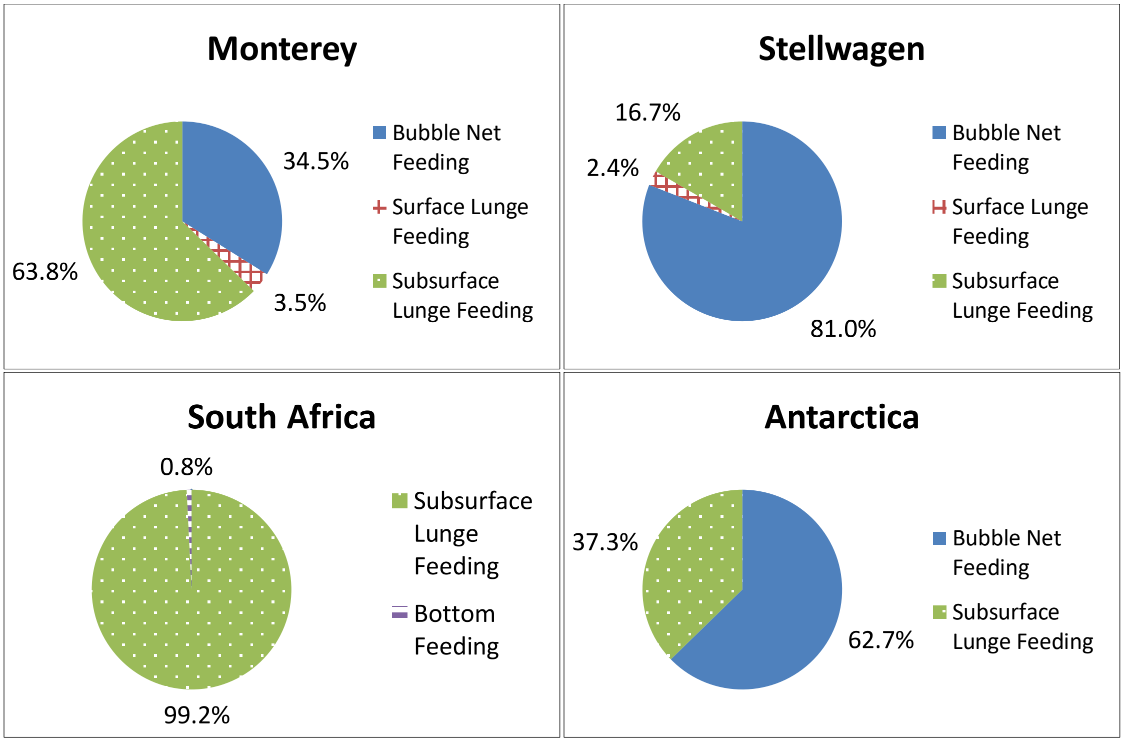

Figure 9. Foraging techniques used by humpback whales while group feeding in different regions. Solid blue regions represent the proportion of feeding events involving bubble net feeding, red checkered regions represent the proportion using surface lunge feeding, green dotted regions represent the proportion using subsurface lunge feeding and purple stripes represent the proportion using bottom feeding.

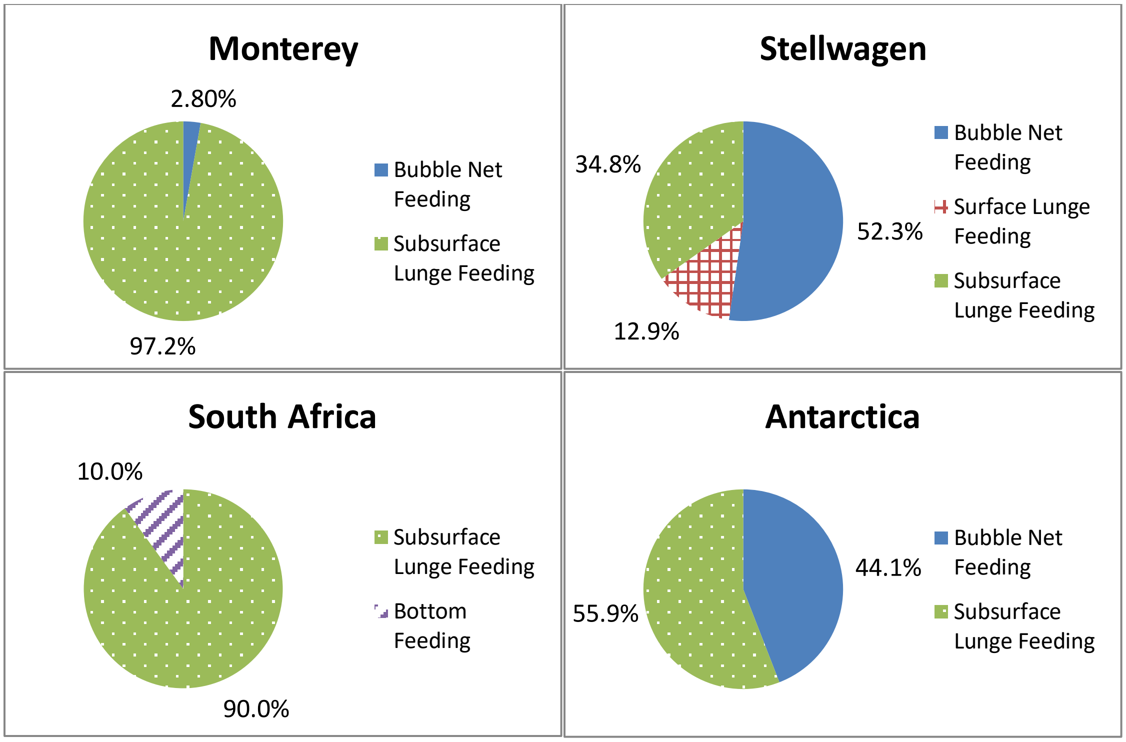

Figure 10. Foraging techniques used by humpback whales while feeding alone in different regions. Solid blue regions represent the proportion of feeding events involving bubble net feeding, red checkered regions represent the proportion using surface lunge feeding, green dotted regions represent the proportion using subsurface lunge feeding and purple stripes represent the proportion using bottom feeding.

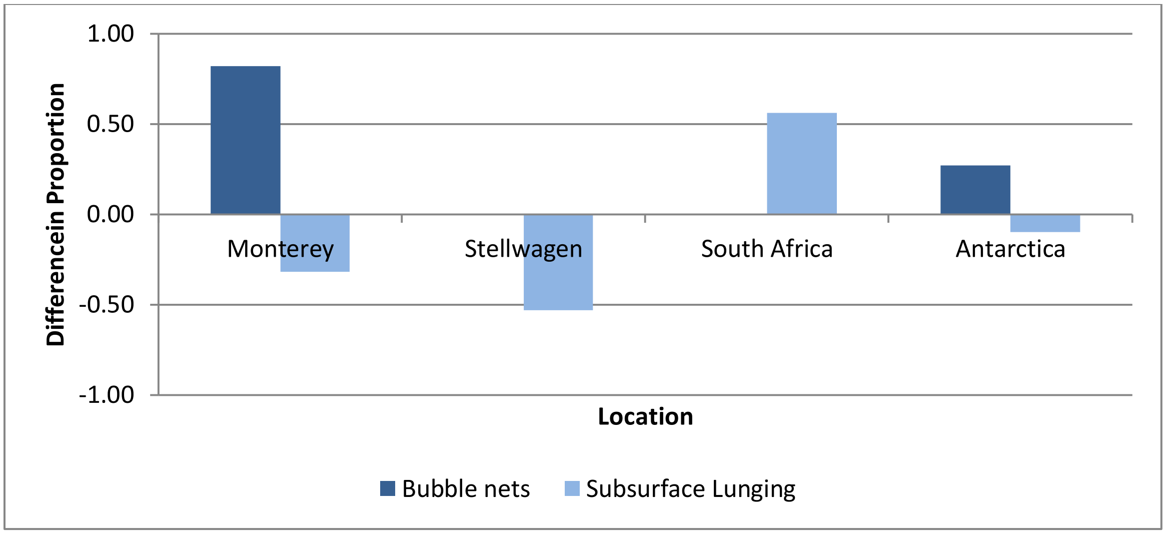

Figure 11. The difference in proportion of feeding techniques that are group foraging events compared to the proportion that are solitary foraging events by location.

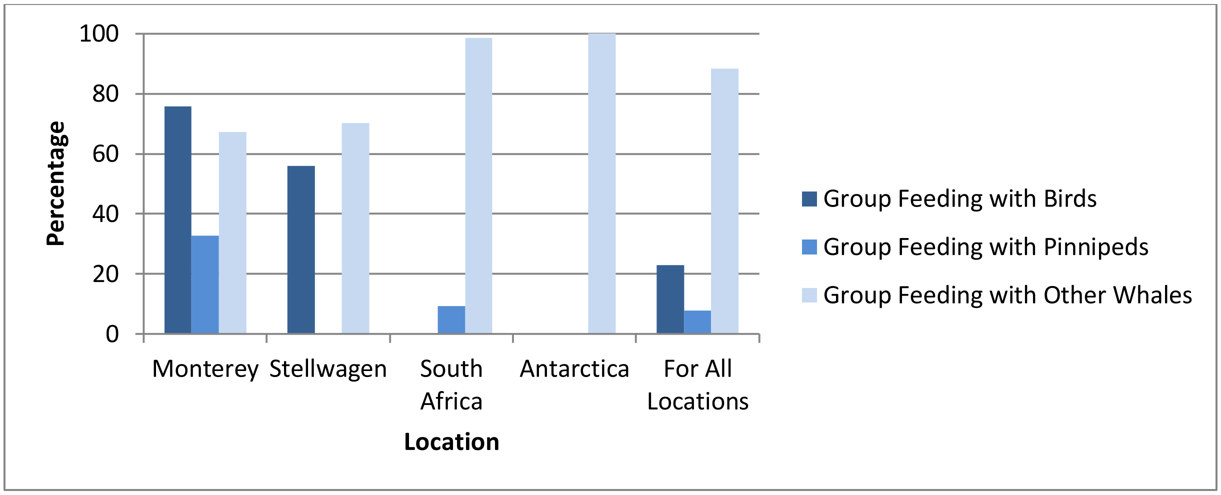

Figure 12. The percentage of foraging events with birds, pinnipeds, and other whales by feeding region for group feeding events. Total percentages for Monterey, Stellwagen and Antarctica add up to over 100% due to some group feeding events having more than one type of marine predator that joined the humpback whale.

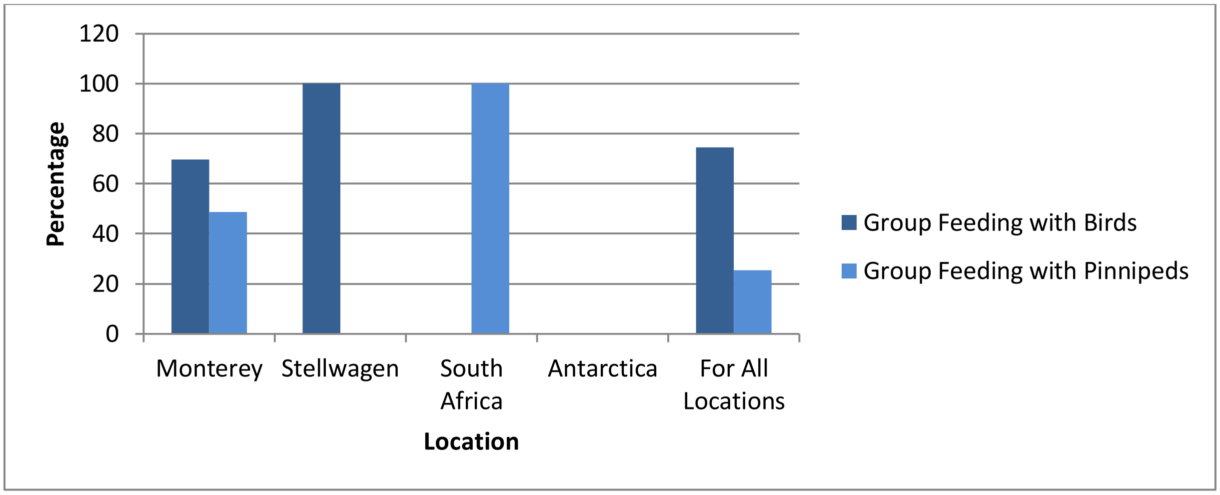

Figure 13. The percentage composition of mixed foraging events, which includes birds and pinnipeds, and disregards other humpback whale interspecies groups. Total percentages for Monterey add up to over 100% due to some group feeding events having more both birds and pinnipeds present.