Utilizing information theory to study the communication system of *Orcinus orca*

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October 26, 2007

Beam Reach Marine Science and Sustainability School
http://beamreach.org/071

INTRODUCTION

Information Theory

Information Theory, originally designed to study the information encoded in human speech, is now applied to animal communication (Beecher 1989; Dingle 1969; McCowan et al. 2002; McCowan et al. 1999; Preston 1978; Steinberd and Conant 1974). Established by Shannon and Weaver (1949), Information Theory is a statistical tool used to determine the structure and organization within communication systems. By analyzing a communication system statistically, Information Theory provides an objective platform on which to compare and contrast the communication systems of species.

McCowan et al. (1999) summarized Shannon and Weaver's paper and explained how Information Theory can be used to evaluate the complexity present within call patterns at many different levels. For example, one could evaluate the complexity of letter patterns, or one could evaluate the higher levels of complexity in word or sentence sequences. The first level of complexity is best evaluated using Zipf's statistic (McCowan et al. 1999; Zipf 1949). Zipf's statistic considers the optimal amount of redundancy and diversity to communicate. A communication system needs a diversity of signals to portray a large amount of information. However, when a repertoire has too much diversity it becomes redundant, with too many signals coding for the same message.

Conversely, noise affects the communication channel. A channel can be defined by the medium through which it is passed, be it the auditory, visual, tactile or olfactory channel, and by the habitat the species lives in. The amount of background noise will vary with the habitat and may interfere with any transmitted signal. In channels with more noise, a signal may need to be repeated to ensure that it is received. This repetition reduces the amount of information transferred. A communication system must possess a balance between diversity and repetition to achieve the optimum transfer of information adapted to the channel of communication (McCowan et al. 1999; Shannon and Weaver 1949).

Zipf's statistic is a graphical representation of a species' optimal balance between diversity and redundancy (McCowan et al. 1999; Zipf 1949). By ranking the signals within a repertoire by frequency and plotting the log of the rank against the log of the frequency, you can compare a species' slope to an optimal information transfer of -1.0 (Fig. 1) (McCowan et al. 1999; Zipf 1949). The optimal balance between diversity and redundancy will shift for different species depending on their differing ecologies. In a habitat where visual cues are easy to use (i.e. open fields), or in a species that is highly solitary, very little information needs to be passed in the auditory channel and little diversity is necessary. The Zipf Statistic for these species will be steeper than -1.0 (less diversity, more redundancy). In species where visual communication is unreliable (i.e. forest or aquatic habitats), or in species that are highly social and require large amounts of information to be passed, the slope will be near -1.0 to optimize the amount of information being transferred. In addition, when comparing age groups within a species, the Zipf statistic will be greater than -1.0 and will shift closer to -1.0 as the individuals mature (McCowen et al. 1999). This phenomenon occurs after birth because young animal's calls are more diverse until they learn the extent of the adult repertoire.

It can be hypothesized that the noisier the channel a species is communicating in, the lower its Zipf statistic (McCowan et al. 1999; Zipf 1949). In a noisier channel, a sender may need to repeat its calls to ensure that the receiver receives the information (McCowan et al. 2002). This would lead to a higher call repetition rate. A higher call repetition rate appears as redundancy on Zipf's slope and would lead to a steeper slope of the regression line (McCowan et al. 2002).

Zipf's relation is a good measure of a repertoire's potential to transfer information (McCowen et al. 1999). But, it does not describe how a communication system is organized. Higher levels of complexity within a communication system are assessed using the Information Theory statistics designed by Shannon and Weaver (1949). The zero-order entropic level (entropy here is defined as the degree of organization) is a measure of the diversity within a repertoire and is calculated with:

$$H_0=\log_2 N$$

where N is number of letters, whistles, or in this case, call types (McCowan et al. 1999; Shannon and Weaver 1949).

First-order entropy is another measure of Zipf's statistic and measures the simple complexity within a repertoire (McCowen et al. 1999). It is calculated using:

$$H_1(A)= -p(A_1)\log_2 p(A_1) -p(A_2)\log_2 p(A_2) \ldots -p(A_N)\log_2 p(A_N)$$

where $p(A_1)$ is the probability or frequency of occurrence of event (i.e call type) A_1 and so on.

Second-order and higher entropies measure how calls are organized and used in conjunction to transmit information (McCowan et al. 1999). To examine information sequencing within the second level of complexity, one must assess the probability that one call follows another:

$$H_2(AB) = -p(A_1B_1)\log_2 p(A_1B_1) - p(A_1B_2)\log_2 p(A_1B_2) \ldots - p(A_1B_N)\log_2 p(A_1B_N)$$

$$-p(A_2B_1)\log_2 p(A_2B_1) - p(A_2B_2)\log_2 p(A_2B_2) \ldots - p(A_2B_N)\log_2 p(A_2B_N)$$

$$\ldots - p(A_NB_N)\log_2 p(A_NB_N)$$

where A_1B_1 is the first event A, which is call type one followed by the second event B, which is also call type one (McCowan et al. 1999). In other words: $p(A_1B_1)$ is how often call type 1 follows call type 1. Similarly, $p(A_1B_2)$ is the probability that call type 2 will follow call type 1. All possible combinations of calls are found and used in the equation and totaled.

When examining the third level of complexity, one must then assess the probability that a certain call will follow two ordered calls and so on giving:

$$H_3(ABC)=H_2\ (AB)+HAB(C)$$

where HAB(C) is the probability that C will occur given that A and B have already occurred (McCowan et al. 1999).

By evaluating the higher orders and plotting the entropic order by the entropic value, one can determine how the information encoded in a communication system is organized (McCowen et al. 1999). A completely random call set gives a slope of zero, while more organized communication systems will yield a successively steeper negative slope (McCowen et al. 1999).

A study by McCowan et al. (2002) investigated and compared organization and development in the communication systems of bottlenose dolphins, squirrel monkeys and humans. By illustrating the utility of Information Theory in comparing these species' communication systems, McCowan et al. (2002) has shown that information theory can be a vital tool for studying animal communication.

<u>Communication in *Orcinus orca*</u>

Orcinus orca is a highly social species with many levels of social organization (Bigg et al. 1990). They congregate in matrilines, which consist of a matriarch, her offspring, and often their successive offspring (Bigg et al. 1990; Ford 1991). A pod is a group of matrilines often found together. Occasionally, two or more pods are found interacting and are called a superpod. At each level of social organization, there is a certain amount of vocal variation. The more closely related the individuals, the more similar their vocal repertoire (Ford et al. 2000; Miller and Bain 2000).

Two *O. orca* communities reside in the waters off the coast of Vancouver Island: the northern and the southern residents. During the summer months, the southern residents inhabit the waters surrounding Vancouver Island, including the Salish Sea, Georgia Strait, Juan de Fuca Strait, and ranging as far south as Puget Sound and as far north as Pender Harbor (Ford et al. 2000). The southern residents were listed under the Endangered Species Act in 2005 (NMSF 2006). They are composed of three pods: J, K, and L (Ford 1991, 1989). The cohesion of these large family units and the successive levels of organization within them require an extraordinary amount of communication to take place between individuals, matrilines, and pods (May-Collado et al. 2007).

Due to the aquatic habitat of *O. orca*, the majority of communication must be conducted vocally. Cloudy waters make visual communication impossible over longer distances, while olfactory cues do not provide the quick response necessary for intricate social interactions (Bradbury and Vehrencamp 1998). This habitat and the complex sociality of *O. orca* have led to complex vocal communication. Ford (1989) described three main types of calls: discrete, variable and aberrant. Discrete calls are stereotypic, have been classified into a set of 29 different call-type categories, each, given an alphanumeric designation (Ford 1987). Many attempts have been made to show clear correlations between discrete call types and behavior, but none have been found (Ford 1991, 1989). This suggests that orcas do not have a one-to-one, call-to-behavior pattern and that their communication system is much more complex (Ford 1989). Variable calls do not seem to have any obvious structure, but are often used along with aberrant calls in highly social and excited states. Aberrant calls are similar to discrete call types that have been sped up and shortened (Ford 1989).

O. orca's social system has evolved to increase fitness. Communication plays a vital role in maintaining any social system. Therefore, *O. orca's* fitness is partly dependent upon communication. It has been suggested that boat traffic is a significant factor affecting the health of the southern resident population (Service 2006). With increased noise in the orca's communication channel, *O. orca* may need to increase the repetition of their calls to ensure that the message is received. Increased vessel traffic could have led to a detectable change in the Zipf Statistic. If so, it would suggest that reduced vessel traffic could increase the amount of information that *O. orca* can share, thereby increasing their fitness.

An examination of the higher orders of entropy with Information Theory will provide a unique insight into the amount of information that may be encoded within *O. orca* calls and can determine the level of complexity at which the repertoire functions. Information Theory can also provide a statistic that can be used to compare the communication systems of different species. By comparing the levels of organization between species, one can gain insight and compare both social and ecological strategies. By using Information Theory, we can test hypotheses that involve many species and their different communication channels. McCowan et al. (2002) used Zipf's statistic to study vocal learning through development by comparing Zipf's slopes of different age groups. By using Information Theory, one can study the development of the repertoire and determine how important channel noise is during vocal development. Theories on the evolution of vocal development can be tested. Do certain taxa develop faster? When did vocal learning evolve? Information Theory can also be used to compare the information being transferred during interspecies communication and to study the amount of information that is required and used to recognize individuals in a group of conspecifics (Beecher 1989). Information Theory is a powerful tool for studying many aspects of communication.

METHODS

Recordings of *O. orca* were obtained from different locations in the Salish Sea, in Washington state, between 2006 and 2007 (Table 1). Recordings from Lime Kiln Point were taken in 2006, as part of The Whale Museum's Sea Sound project, from a permanent stationary hydrophone located 15 meters from shore at a depth of 8 meters (S. Veirs pers. comm.). Lime Kiln recordings were recorded to a computer using a signal recognition program and then stored to CD.

Recordings were taken in September and October of 2007 in and around Haro Straight and the Straight of Juan de Fuca. These recordings were taken by students participating in the Beam Reach Marine Science and Sustainability Field School, aboard the *Gato Verde* (a 42 foot sailing catamaran). When *O. orca* were located, we lowered a linear towed hydrophone array (Table 1) into the water and followed the orcas as long as their behavior and weather permitted. During recordings, the *Gato Verde* adhered to the whale watch guidelines outlined by Soundwatch (http://www.whale-museum.org/downloads/soundwatch/SWguidelines_02.pdf).

The recordings were taken at a sampling rate of 44100 and 16 bit rate. Recordings were viewed using Xbat (Harold Figueroa) in Matlab 7.4.0 (Mathworks) and Syrinx Version 2.6h (John Burt). Syrinx was used for ease of annotation and Xbat was utilized for ease of viewing.

In Xbat, sound files were viewed at an FFT rate of 1040. The contrast and color of the spectrogram was adjusted as needed to view the call within the background noise. As sound files were viewed, I annotated any call types that could be heard and/or seen on the spectrogram, using Syrinx and an FFT rate of 1024. Syrinx output saved the annotations in a tab-delineated text document.

Call types were identified using Ford's (1987) catalogue of calls produced by *O. orca*. I also used a Call Tutor program developed by Val Veirs to compare the sound of the call. If discrepancies existed between the two, I used Ford (1987) as the ultimate source. Five call types were designated by Ford (1987) as subtypes of two different call types. There is no evidence that *O. orca* regard these calls as subtypes of one call type. I am of the opinion that the subtype's variation from each other is on the same order as calls designated as different call types. Therefore, I designated the subtypes as separate call types. Riesch et al. (2006) identified four different whistle types for the southern residents. But, only 30% of the 152 whistles recorded could be assigned to these four stereotyped whistle groups (Riesch et al. 2006). In order to avoid arbitrarily assigning whistles to a type, I designated all whistles as a single call type (W).

The tab-delineated text files output by Syrinx were imported and saved as a PDF. I used the find function in Acrobat Reader 8.1 (Adobe) to tally the number of occurrences of every call type.

Southern resident pods interact, communicate, and share a repertoire (Ford et al. 2000). Therefore, I used recordings of all resident pods and all combinations of resident pods. The sample size necessary to calculate 3rd order entropic levels with 29 call types was calculated as described in McCowan et al. (1999), using the formula

$$N(r)=n!/r!(n-r)!$$

where r is the entropic order(3) and n is the number of call types(29). The necessary sample size is 3,654.

I used Excel to tally call types, generate graphs, and calculate the Zipf's slope. Zipf's slope for the southern resident's repertoire between the years of 2006 and 2007 was compared to the Zipf's slopes calculated by McCowan et al. (1999, 2002). For comparison, I calculated an additional rough estimation of Zipf's slope from Ford (1991).

Table 1. Sound file specifications

Location	Year	Source	Microphone	Recorder
Gato Verde sailing vessel	2007	Beam Reach 2007	LAB core Hydrophone Peak Sensitivity ~ 5000 Hz Down 30 dB at ~200 Hz-10, 500 Hz	Sound Devices 702: Flat from 10 Hz to 40 kHz (+ 0.1, -0.5 dB)
Lime Kiln Point Archived	2006	Whale Museum	Cetacean Research Technology Hydrophone	Desktop computer with built in sound card

RESULTS

I examined 1191calls in about six hours of sound files. I assigned 1090 of those calls to call type. The other 101 calls were either too embedded in background noise to be seen and heard clearly or were variable calls that could not be confidently assigned to call type. 1090 calls was not a sufficient sample size to evaluate the higher levels of entropy. Therefore, I only calculated Zipf's slope (Fig. 2). The calculated Zipf statistic of -1.241 (R^2=0.87, p<.001) is significantly different from the optimal -1 (Standard Error of 0.09).

The rough Zipf's slope derived from Ford (1991) (Fig. 3) was –1.467 (R^2=0.96, p<.001).

Figure 1. Plot of the optimum Zipf's slope of –1.

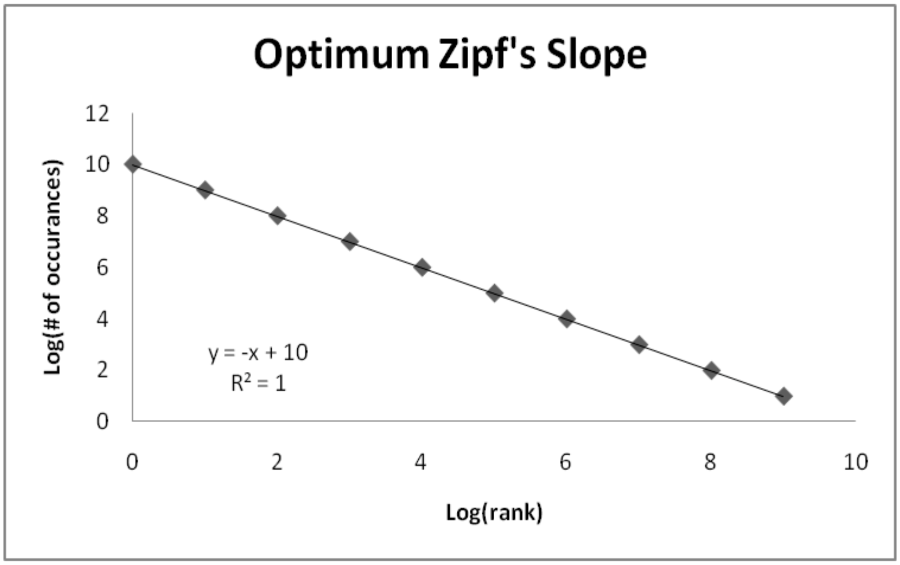


Figure 2. Plot of the $\log_{10}$ of the number of occurrences of a call type vs. the $\log_{10}$ of the rank of that call type; with the regression line used to calculate the Zipf slope.

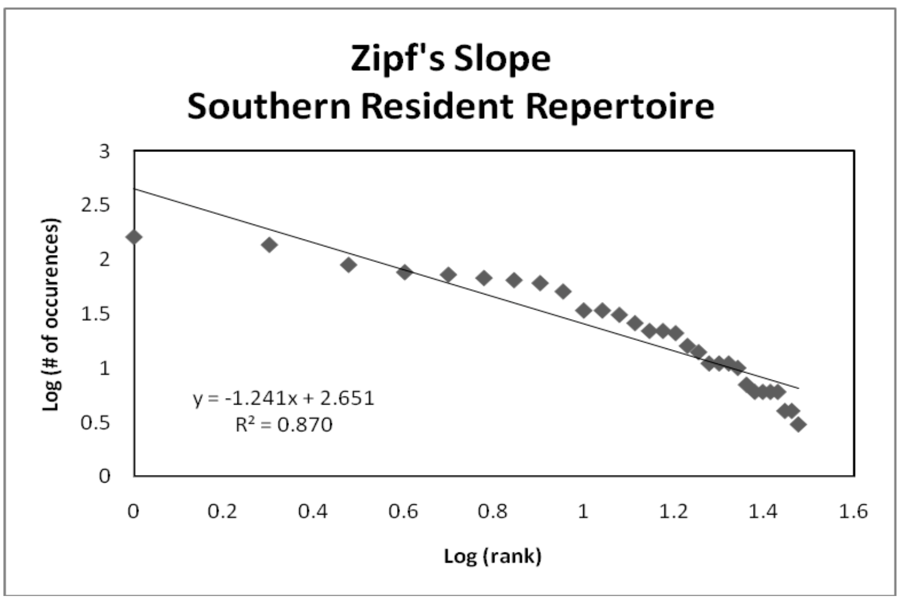
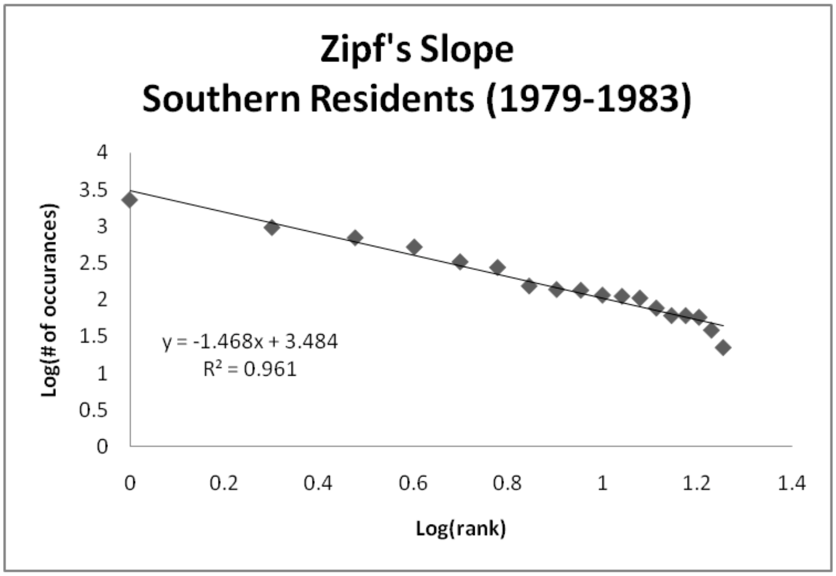


Figure 3. Plot of Zipf's slope calculated from Ford (1991). Calls were recorded from J pod during travelling and foraging.



DISCUSSION

Zipf (1949) and McCowan et al. (1999) argue that communication reaches an optimum rate of information transfer when there is a balance between diversity and redundancy. If a repertoire were diverse to the extreme, there would be a separate word (i.e. call type) for every bit of information and individuals would be unable to communicate. Conversely, if a repertoire is redundant to the extreme, it contains one word (i.e. call type). This one word is insufficient for encoding all the information that individuals need to pass. A Zipf slope of -1 indicates that the optimum balance between diversity and redundancy is present within the repertoire being studied.

The Zipf's slope that I calculated for the southern resident *O. orca* population is significantly steeper than the -1 optimum. This indicates that the southern residents' communication system has less diversity and more redundancy than is optimum. For a population where communication is key in maintaining social bonds and social bonds are key for survival, one would expect the communication system to evolve to be at or extremely near the optimum. Why is the actual Zipf's slope so far from expected?

One explanation may be the level of noise within the channel *O. orca* communicates in. Large levels of background noise decrease reception of a signal. This leads to the sender repeating a signal to insure the receiver hears it. Repetition is akin to redundancy. Less information can be transferred when a signal is repeated, in the same way that a redundant signal transfers less information. Is the background noise level of *O. orca's* acoustic channel inherent or due to anthropogenic activity?

One could hypothesize that, if the inherent background noise levels in the ocean are responsible for the redundancy within *O. orca's* communication system, then a species with a similar evolutionary background should possess a communication system with an equivalent amount of redundancy. McCowan et al (1999) calculated a Zipf's slope for such a species. The value of -0.95 for captive adult *Tursiops truncates* (bottlenose dolphin) suggests that either the inherent background noise of the ocean has not caused the redundancy present within *O. orca's* communication system or captive dolphins have been removed from the noisy background of the open ocean.

If the increase in the Zipf's slope of southern residents is not due to inherent ocean noise then it must be due to introduced noise in the environment. Boats are prevalent within the southern residents range and whale watch boats cause significant concern about noise levels around *O. orca* (Baird 2006). Could an increase in vessel noise be contributing to the redundancy of *O. orca's* communication system? A rough calculation of Zipf's slope from Ford (1991) yielded an even steeper slope of –1.4. If the vessel noise theory is to be believed then this would suggest that there was more vessel noise present in the Salish Sea during 1979-1983 than in 2006-2007. If boat noise has remained the same from 1979 to 2007, then it could be hypothesized that the Soundwatch guidelines have reduced the vessel noise around the orcas significantly enough to reduce the repetition in their repertoire.

Ford's (1991) graphs, which I used to extrapolate the Zipf's slope, only illustrated the percentage of call types for 2 behaviors: traveling and foraging. This may suggest that these behaviors require an increase in the repetition of calls. Additionally, these graphs only included recordings when J pod was present, while my recordings included all pods and combinations of pods. The increase in call repetition could be a product inherent of J pod.

Perhaps *O. orca* requires repetition of call types to maintain one particular aspect of their sociality. The repetition of calls may not be repetition by one individual, but repetition by the group as a whole, with one individual calling and the rest repeating the same call to maintain vocal contact.

The -1.241 value may have been reached in human error. The call types I used were classified by Ford. *O. orca* may distinguish between calls in a different manner than Ford classified them. Therefore, it may be that if one could categorize the call types as an orca would recognize them, one would find that *O. orca's* communication system does possess the optimum rate of information transfer with a Zipf's slope of -1.

Zipf's slope is not a measure of the linguistic capabilities of a repertoire. It is an indication of the linguistic potential of a repertoire. A Zipf's slope of -1.241 indicates that *O.*

orca's call types, as classified by Ford (1987) have the potential to encode information with an inefficient redundancy component. You can calculate a Zipf's slope for a system that does not posses a communicative function (McCowan et al. 2005). Zipf developed his statistic to be used with letters, phenomes, or words. Therefore, Zipf's slope should be calculated for a communication system with that system's equivalent of letters, phenomes or words. We are unaware of whether *O. orca* perceive Ford's call types as our equivalent of letters. In order to determine how the information is organized within the communication system, we must evaluate the higher levels of entropy using Shannon and Weaver's (1949) Information Theory. By evaluating the higher orders while viewing Ford's (1987) call types as words, we may find that the higher orders do not contain much information. This would indicate that the call types are not the equivalent of letters and that *O. orca* is using the variation within calls to encode the majority of the information passed during signaling.

There are many possible explanations for the -1.241 Zipf's slope of southern resident *O. orca.* The increase in redundancy may be due to inherently high background noise in the ocean or it may be due to increases in anthropogenic noise. We may have erroneously classified the call types, leading to a miscalculation of Zipf's slope of the communication system. *O. orca* may require the repetition of calls to maintain vocal contact. The decrease in the steepness of the Zipf's slope from 1979-1983 to 2006-2007 could be due to a decrease in vessel noise around the whales or the difference in sampling between the two periods. In the future, studies should be conducted to test these possibilities and determine which is true. It would be vital to understand whether vessel noise has negatively affected the optimum rate of information transfer for *O. orca.* Further studies should utilize Information Theory to discover where the information is encoded and how it is organized within the communication system of *O. orca.* Once we learn

jdwood
Comment: It would be good to flesh this last paragraph out a bit. Use it as a final synopsis of your main conclusions and the next steps needed. Good job.

whether and how we are affecting *O. orca's* ability to communicate, we can learn how to decrease our affect on them.

AKNOWLEDGEMENTS

I would like to thank John Burt for allowing me to use his wonderful program Syrinx; Monica Weiland for handing the Lime Kiln recordings off to me; Scott and Val Veirs for their help and Call Tutor; Captain Mike for being the kind of guy that falls of his dirt bike; Shannon Fowler for her excellent feedback on papers and life; Jason Wood for the brainstorming, corrections, and encouragement; team VaTo for the passing hours on Wednesdays and Sundays; and finally, to my favorite whales: Elise, Liz, Heather, and Wes, for all the good times.

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