TECHNICAL REPORT 1835
September 2000

# An Integrated Approach to the Creation of a Humpback Whale Hearing Model

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## Acknowledgements

This study was made possible in part thanks to funds from PMS-400DE and the Strategic Environmental Research and Development Program Project CS-1082. The modeling effort reported here was made possible by the estimates of humpback whale basilar membrane resonant frequencies generated by Dr. Darlene Ketten of the Woods Hole Oceanographic Institution, under contract from SERDP Project CS-1082. We thank the Space and Naval Warfare Systems Center High Performing Computer Center for their grant of CPU time on the HP V2500. We also thank Kumar Chellapilla for assistance in structuring the evolutionary programs used for the optimization of the ear models.

# EXECUTIVE SUMMARY

Human activity can generate underwater signals potentially capable of injuring or altering the behavior of mysticetes (baleen whales). Little information exists on mysticete hearing and this information is not likely to be obtained in the near future. In order to provide the Navy with tools helpful in predicting the potential impact of anthropogenic underwater sound on mysticetes, a model of humpback whale (*Megaptera novaeangliae*) hearing was constructed. Anatomical indices of hearing taken from the inner ear of a humpback were used to create a frequency-position function (i.e., predict the range of hearing). Auditory sensitivity and frequency-position functions of the cat and human were then integrated with the humpback frequency-position function to create an audiogram for the humpback. The predicted audiogram was typically mammalian in shape and suggested a maximum acoustic sensitivity between 2 and 6 kHz. A bandpass filter model of humpback hearing, consisting of a series of overlapping pseudo-Gaussian filters, was created and the model design varied via an evolutionary program to optimize model sensitivity. Agreement between model sensitivity and predicted humpback sensitivity always exceeded 90 percent. The computational model of humpback whale auditory sensitivity is used as an auditory weighting function in assessment of sound exposure.

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# INTRODUCTION

Over the last decade the Navy's use of high amplitude acoustic signals in underwater environments has come under criticism for its potential negative impact upon marine mammals (Henderson, 1998; Miller et al., 2000; Rendell and Gordon, 1999; and see MMPA Report 2000). Cetaceans (dolphins and whales) are of particular concern because they rely upon acoustic signals for communication, foraging, and navigation. Furthermore, mysticetes (baleen whales) vocalize at frequencies ranging from 15 to 8000 Hz, which suggests that they are sensitive to frequencies commonly generated by anthropogenic sources (Clark, 1990; Herman and Tavolga, 1980; Richardson and Würsig, 1997). Underwater signals generated by U.S. Navy assets may mask mysticete vocalizations, disturb normal behavior, cause temporary threshold shifts in hearing (TTS), or cause permanent hearing damage (Richardson and Würsig 1997). To date, little is known of the impact of Navy-produced signals on mysticete whales. Assessment has been primarily limited to observations of responses to industrial sound exposure and playback experiments. Unfortunately, high variability within and between studies has made reliable conclusions difficult (Frankel and Clark, 1998; Malme et al., 1985; Malme et al., 1988; Maybaum, 1989; Richardson et al., 1990; Richardson et al., 1985).

Mysticetes are too large to maintain in a controlled environment necessary for traditional audiometric tests, but models of mysticete hearing can contribute to predictions of sensitivity to anthropogenic sounds. Houser et al. (1999, 2000) applied evolutionary programming to a model of the dolphin ear, which consisted of a series of overlapping frequency-domain filters, and were able to match the model's sensitivity to the auditory sensitivity of the dolphin. Given that direct hearing measurements are not likely to be conducted on any baleen whale in the near future, extending these types of computational models to mysticete audition is a logical step towards predicting sensitivity to U.S. Navy generated sounds.

Due to a voluminous middle ear cavity and loosely joined ossicles, it can be argued that mysticetes have a conventional mammalian ear adapted to low frequency reception (Ketten, 1997). Methods for predicting the frequency range of hearing from species-specific auditory anatomy (see Greenwood, 1990 for review) have been advanced and applied to marine mammals by D. Ketten (Woods Hole Institute, manuscript in preparation). If the conventional mammalian ear is assumed, and a frequency-position function can be predicted, psychoacoustic and anatomical measures of hearing from terrestrial mammals with conventional ears can be used to create a predictive mysticete auditory threshold function. A bandpass ear-filter model can then be constructed and output optimized to the predicted threshold as has been performed for the bottlenose dolphin (Houser et al., 1999; Houser et al., 2000; Roitblat et al., 1993).

This report describes the creation of a bandpass ear model for the humpback whale (*Megaptera novaeangliae*), a medium-size baleen whale with worldwide distribution. Anatomical indices of hearing derived from inner ear histology were used to generate a frequency-position function. Sensitivity-position information is lacking for any mysticete. Thus, the humpback frequency-position data were integrated with the known auditory threshold characteristics of man (*Homo sapiens*) and the domesticated cat (*Felis domesticus*). The result is a predicted audiogram (frequency-sensitivity function) for the humpback whale. Evolutionary programming (EP) techniques were then used to optimize the sensitivity of a bandpass-filter model to the predicted humpback whale audiogram.

## MATERIALS AND METHODS

### Predicting the Humpback Whale Audiogram

An audiometric function predicting the frequency-dependent relative sensitivity of the humpback whale was created on the assumption that the humpback ear could be modeled as a conventional mammalian ear. This was achieved by integrating the auditory threshold function with the frequency-position function of two well-studied mammals with conventional ears, the cat and human, and mapping the resulting sensitivity-position functions onto the frequency-position map of the humpback whale.

Ten measurements of the basilar membrane thickness and width were made along the lengths of basilar membranes obtained from a humpback whale (D. Ketten, pers. comm.). Ratios of thickness to width were determined (Ketten, 1993; Ketten, 1994) as a function of relative position along the basilar membrane. Ratios were normalized against cat thickness to width ratios and frequency-position estimates in order to create a frequency-position map of the humpback basilar membrane (Ketten, pers. comm.). A 3rd order exponential was fit to the frequency distribution in order to generate a continuous cochlear frequency-position function (Figure 1, $r^2 = 0.99$).

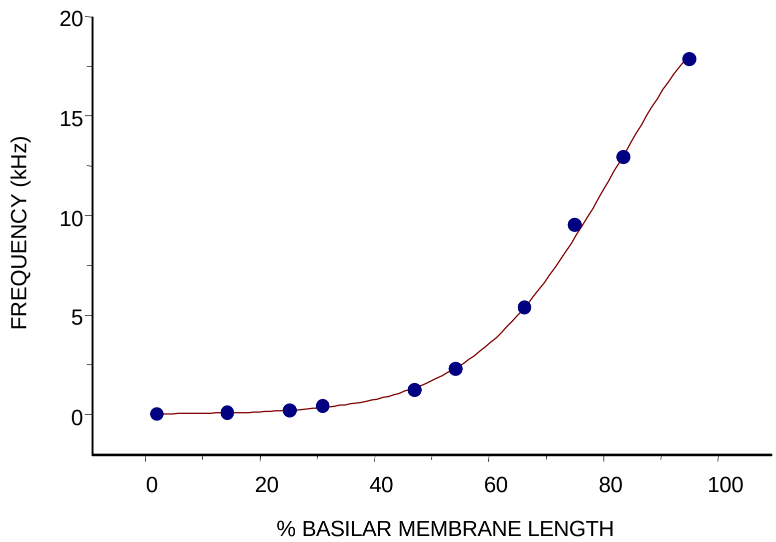


Figure 1. Frequency by relative position along the length of the basilar membrane for the humpback whale. A 3rd order exponential function was fit to the data ($y = 0.08 * \exp(0.15x – (8.74e\text{-}4)x^2 + (1.63e\text{-}6)x^3)$) in order to create the frequency-position function.

Auditory thresholds and cochlear frequency-position functions of the cat and human were integrated with the humpback frequency-position function to create a humpback audiogram. Published cochlear frequency-position functions were obtained for the human (Greenwood, 1990) and cat (Liberman, 1982). For the human

$$f(x) = 165.4(10^{2.1x} - 1)$$

and for the cat

$$f(x) = 456(10^{2.1x} - 0.8)$$

where *f(x)* is frequency and *x* is a proportion of basilar membrane length. For all frequencies at which hearing has been tested in the human and cat (Fay, 1988), the respective relative position on the basilar membrane at which that frequency is predicted to occur was determined. Relative position determinations for the cat were limited to frequencies between 100 Hz and 60 kHz, the frequency range covered by the experimentally determined frequency-position function (Liberman, 1982).

Threshold intensities ($W/cm^2$) of the cat and human were plotted as a function of relative basilar membrane position, converted to dB re: minimum intensity, and fit with a $4^{th}$ order polynomial (figure 2, $r^2$=0.66). This continuous intensity-position function was integrated with the humpback frequency-position function to produce a frequency-dependent threshold function for the humpback. Thresholds were scaled from zero to one in order to produce a frequency-dependent relative sensitivity function.

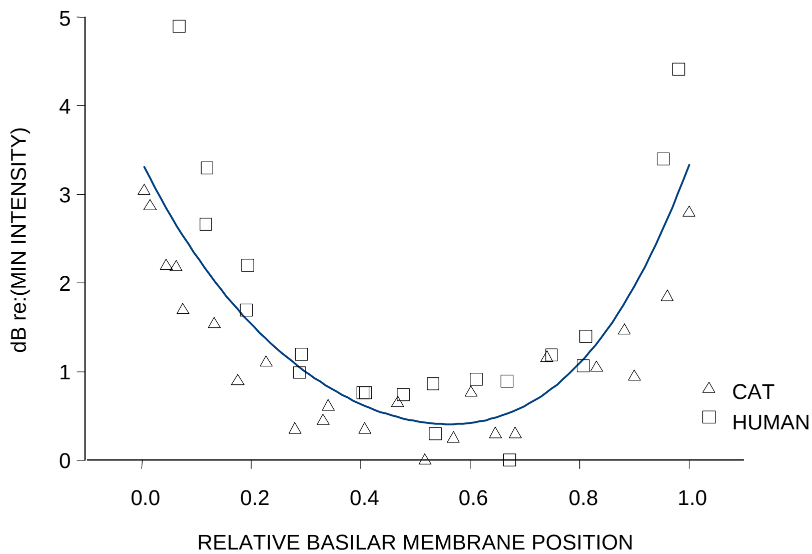


Figure 2. Relative thresholds of the cat and human as a function of relative basilar membrane length. The relationship was determined by integrating experimentally derived frequency-position functions for each species with their respective averaged frequency-dependent thresholds. The fitted function ($y = 3.36 - 12.4*x + 19.72*x^2 - 19.1*x^3 + 11.75*x^4$) provides a predictive sensitivity-position function.

## RESULTS

### Predicted Humpback Whale Audiogram

Frequency by position along the basilar membrane was predicted for ~ 93% of the basilar membrane length (from 2 to 95%, base to apex). Predicted frequency range was approximately 30 Hz to 18 kHz. The predicted humpback whale audiogram, which incorporated an extrapolation of frequency by position to 100% of basilar membrane length, is shown in Figure 3. Threshold is plotted on a relative scale, since we do not have an estimate for absolute sensitivity. The predicted audiogram was U-shaped and typically mammalian with a region of best hearing, defined as relative threshold $\leq$ 0.2, ranging from 700 Hz to 10 kHz. Maximum sensitivity, defined as threshold values

≤ 0.1, ranged from 2 to 6 kHz. Reduction in sensitivity was ~16 dB/octave above 10 kHz and ~ 6 dB/octave below 1 kHz. The most insensitive frequencies occurred at 100 Hz and frequencies ≥ 15 kHz.

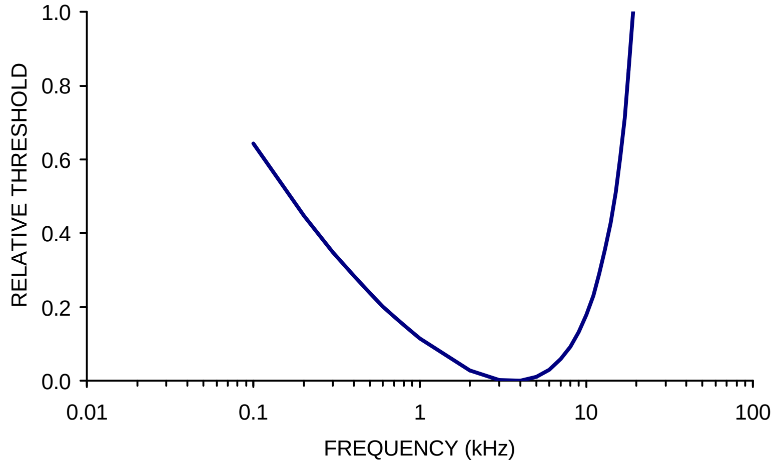


Figure 3. The predicted relative auditory threshold of the humpback whale. The threshold function was determined by integrating the humpback frequency-position function (figure 1) with the sensitivity-position function derived from cat and human audiometric and anatomic data (figure 2).

## MATERIALS AND METHODS

### Optimized Filter-Bank Ear Model Design

Models of the humpback ear were created as a series of overlapping bandpass filters with a pseudo-Gaussian shape (Houser et al., 1999) that delimited the bandpass region in the spectral power domain. Pseudo-Gaussian filter shapes were generated with peak sensitivity corresponding to the center frequency (µ) of the filter such that

$$\frac{1}{\sqrt{2p}}\exp(-\frac{1}{2}(\frac{x_i - m}{s})^2)$$

where $x_i$ is the $i^{th}$ point on the distribution curve. Each filter was described by a 256 bin vector with each bin corresponding to a 100 Hz binwidth such that the frequency range of the filter was 0.1 to 25.6 kHz.

Filters were distributed from 100 Hz to 18 kHz according to their respective center frequency. Placement of filter center frequency (µ) was calculated as a fractional power of the frequency range emulating the non-uniform spacing of characteristic frequencies on the basilar membrane (Geisler and Cai, 1996). The equation was

$$m = 180^{\frac{f_j}{F_n}}$$

where $F_n$ is defined as the total number of filters used in the model, $f_j$ was the $j^{th}$ filter, and the constant 180 was used to describe the predicted range of hearing (i.e., 180 x 100 Hz binwidth = 18 kHz).

Filter sensitivity was varied through an amplitude-scaling factor ($S$) and filter width controlled by a variable 3–dB bandwidth ($Q_3$) function. These factors have been described previously (Houser et al., 1999; Houser et al., 2000). Substitution of parameters into the pseudo-Gaussian equation produced the final filter form function:

$$\frac{S}{\sqrt{2p}}\exp^{-\frac{1}{2}\left(\left(x_i-(180)^{\frac{f_j}{Fn}}\right)\Big/\left(\frac{180^{\frac{f_j}{Fn}}}{2.351\ Q_3}\right)\right)^2}$$

### ***Evolutionary Programming (EP)***

Parameters determining filter shape and distribution were submitted to an EP scheme with self-adaptive mutation (Fogel, 1995) and a Cauchy mutation operator (Chellapilla and Fogel, 1997). The EP scheme incorporated a (20+20)-EA (evolutionary algorithm) such that populations consisted of 20 “parent” parameter sets with each “parent” producing 1 “offspring” parameter set per generation (Schwefel, 1981).

Parameters of the evolutionary program are given in Table 1 along with the respective initialization boundaries and standard deviation used in calculating mutation step-size. Parameters, including the base value ($y$) of the amplitude scaling factor ($S$) and the equation determining $Q_3$, were mutated via a Cauchy random variable (Chellapilla and Fogel, 1997). The total number of filters ($F_n$) was mutated in a probabilistic manner such that there was an equal probability that $F_n$ would increase by 1 or 2, decrease by 1 or 2, or stay the same, if $20 < F_n < 400$. If $F_n \leq 20$, there was an equal probability that $F_n$ would increment by 1, 2, or stay the same. Conversely, if $F_n \geq 400$, there was an equal probability that $F_n$ would decrement by 1, 2, or remain the same. Thus, minimum and maximum possible values of $F_n$ were 19 and 401, respectively.

Table 1. Model type and associated parameter values with initialization limits, initial standard deviations, and description of parameter function.

| Parameter | Minimum Initialization Limit | Maximum Initialization Limit | Initial Standard Deviation | Definition (a) |
|---|---|---|---|---|
| y | 0 | 10 | 0.5 | base value for filter amplitude scaling (used to calculate S) |
| m | 0 | 10 | 0.5 | slope of the equation determining Q |
| b | 0 | 2 | 0.15 | intercept of the equation determining Q |
| x | 0 | 0.025 | 0.001 | coefficient of the exponent in the equation determining Q |
| Fn | (b) | (b) | (c) | filter number |

(a) See Houser *et al.* (2000) for details on the equations determining *S* and *Q*

(b) Filter number explicitly set to 40

(c) Probabilistic mutation limited to integer step sizes of $\pm$ 2

Following each generation of the evolutionary program, defined by parameter cloning and mutation, sets of parameter values were inserted into the filter function to create a bank of filters. Each filter bank was evaluated for its sensitivity through a simulated audiometric assessment at {0.1, 0.2, 0.3, …, 0.9} and {1.0, 2.0, 3.0, …, 19.0} kHz, for a total of 28 comparison frequencies (Houser et al., 1999). The filter bank output formed the response curve of the ear model, which was normalized and compared to the predicted humpback whale audiogram. The absolute value of the maximum deviation between the filter bank output curve and the predicted humpback audiogram curve (MaxD) was used as the performance metric for tournament selection (Goldberg and Deb, 1991). Following sensitivity testing of all of the models in a generation, selection of parameter sets for inclusion in the next generation was determined via tournament selection with a tournament size of 10.

EPs were run at the Navy High Performance Computing Center (SSC San Diego) on a Hewlett-Packard V2500 multi-processor system. The V2500 utilized 16 440-MHz 4-way superscalar PA-8500 processors and 16 GB of RAM. Program code was multithreaded according to POSIX standards in order to take advantage of the HPC parallel processing capabilities (Norton and Dipasquale, 1997; see Appendix A). Three EP trials were performed. Trials were terminated if MaxD decreased by less than 0.001 over a series of 100 generations.

## RESULTS

### Ear Model Performance

All ear filter models performed similarly. The best performing ear filter model had a MaxD = 0.09 (Figure 4b), a slightly better performance than the MaxD = 0.10 achieved by the other two models (Figure 4a and 4c). Two of the models converged upon model configurations consisting of 401 filters (Figure 4a and 4b) while the third utilized 263 filters (Figure 4c). Equations for determining filter $Q_3$ and the base value ($y$) of the amplitude scaling factor ($S$) were, respectively:

(Figure 4a)

$Q_3 = 0.76 * \exp((1.4e\text{-}2) * m) + 0.34$, $y = 2.92$

(Figure 4b)

$Q_3 = 0.69 * \exp((1.5e\text{-}2) * m) + 0.23$, $y = 3.51$

(Figure 4c)

$Q_3 = 0.74 * \exp((1.2e\text{-}2) * m) + 0.69$, $y = 2.06$

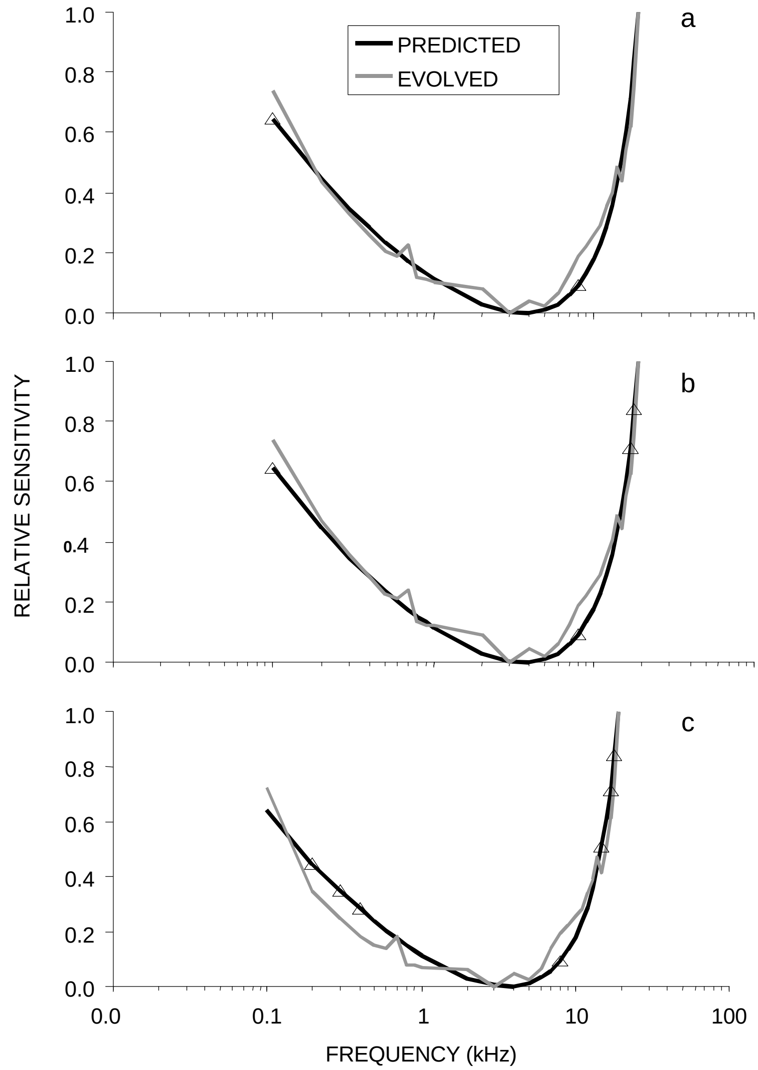


Figure 4. Comparison of the threshold of the three evolved ear models to the predicted threshold of the humpback whale. Triangles indicate frequencies at which maximum deviations between the two sensitivity curves occurred.

Maximum deviations generally occurred above 5 kHz, though the model utilizing a configuration of 263 filters produced 7 such deviations spread across the predicted range of hearing. Nevertheless, reduction in sensitivity above 10 kHz occurred at a rate similar to that predicted by the target sensitivity curve. Frequencies of best sensitivity were at 3 and 5 kHz for all models and there was a consistent sensitivity roll-off below 700 Hz.

## Discussion

Humpback whale basilar membrane morphometry has been combined with conventional land mammal psychoacoustic and anatomic data to produce the first audiometric sensitivity function for the humpback whale. The predicted audiogram spans frequencies at which humpbacks are known to vocalize—humpback songs span frequencies ranging from near infrasonic frequencies to over 8 kHz

(Helweg et al., 1998; Helweg et al., 1990; and Payne, 1983). Presumably these frequencies lie within the range of humpback hearing thus giving ecological validity to the predicted audiogram. Though the audiogram is plausible, its zone of best sensitivity (~ 2 to 6 kHz) is somewhat higher than would be expected from the distribution of frequencies in humpback whale song. Thus, when implementing filter models based upon the predicted audiogram, some degree of caution must be exercised when interpreting the results.

The models created are frequency spectrum filters or auditory weighting functions. They allow a prediction of how the auditory system of the humpback whale attenuates sounds according to the sound’s frequency-specific components. Thus, it can be used to relate the predicted magnitude of a frequency component from a complex signal to that of other constituent components once filtered by the peripheral auditory system. These models only make use of frequency domain information and currently ignore other signal components such as time. However, they serve as the basis for the development of more advanced models capable of incorporating both time and frequency domains.

Methods of determining the impact of anthropogenic noise will likely continue to rely heavily on the use of playback experiments and opportunistic observations of mysticete responses to the exposure of man-made sound. Models of mysticete hearing provided here could be utilized by the Navy to supplement the results of such studies and contextually improve interpretations of behavioral responses to sound exposure. Models will be augmented in the future by inclusion of anatomic information and biomechanical properties from additional auditory structures (e.g., middle ear complex, transfer functions of the oval and round windows). As more information on mysticete hearing becomes available, the effort to increase the biomimetic nature of ear models should continue until such time that absolute auditory thresholds are experimentally determined.

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# APPENDIX A: SOURCE CODE FOR EVOLVING A HUMPBACK WHALE BANDPASS EAR FILTER MODEL

The source code for the evolutionary program created to optimize a series of pseudo-Gaussian designed bandpass filters to the predicted relative auditory threshold of the humpback whale may be found at http://www.spawar.navy.mil/sti/publications/pubs/tr/1835/HumpbackEPcode.doc. The following source code and header files are present:

| | |
|---|---|
| main.C | |
| app.C | app.h |
| member.C | member.h |
| eval.C | eval.h |
| nrutil.C | nrutil.h |
| interp.C | interp.h |
| random.C | random.h |
| objfns.C | objfns.h |

The reader is referred to Houser et al. (1999) for procedures on building the noise (N) and signal + noise (S+N) files used in testing the filter models.

Source code is written in aCC+ and aCC, the proprietary C++ and C language for HP UNIX systems. When porting to other UNIX systems, check the system-specific documentation to resolve cross-platform incompatibilities. Multithreading is achieved through implementation of the pthread libraries for the HP UNIX aCC programming language.

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