



Vocal matching of naval sonar signals by long-finned pilot whales (*Globicephala melas*)

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Manuscripts

1 Concern over the impact of naval sonar on cetaceans has grown dramatically since
2 mass strandings were linked to sonar exercises (Frantzis 1998). Tyack *et al.* (2011)
3 reported that beaked whales stopped echolocating and broke off deep foraging dives
4 when exposed to anthropogenic sounds, avoiding the sound source with a prolonged
5 slow ascent. Avoidance reactions are a common response to anthropogenic sound
6 (Southall *et al.* 2007, Miller *et al.* 2012). By contrast, long-finned pilot whales
7 (*Globicephala melas*) were reported to respond to naval sonar by increasing their rate
8 of vocalization while they were huddling in close ranks, as opposed to swimming
9 away (Rendell and Gordon 1999), which resembles the response seen when long-
10 finned pilot whales were exposed to playbacks of killer whale (*Orcinus orca*) sounds
11 (Curé *et al.* 2012).

12 Little is known of the function of calling in pilot whales. One captive short-
13 finned pilot whale (*Globicephala macrorhynchus*) repeated a stereotyped call made
14 up of two independently modulated tonal frequencies followed by a pulsed
15 component (Caldwell and Caldwell 1969); a similar structure was defined for wild
16 long-finned pilot whales (Nemiroff and Whitehead 2009). Vocal repertoires of groups
17 of long-finned pilot whales recorded in the North Atlantic have been analyzed by
18 extraction of frequency contours (Taruski 1979). Different contours were grouped
19 into seven broad classes with relatively unmodulated calls occurring in low arousal
20 settings and more complex modulation patterns produced in higher arousal states
21 (Weilgart and Whitehead 1990).

22 In order to quantify responses to sonar, behavior, and sound production of
23 long-finned pilot whale groups were recorded before, during and after 30-60 min
24 experimental sonar exposures conducted in Vestfjord, Northern Norway, in 2008 and
25 2009. The recordings revealed calls with similar frequency-modulation patterns as

26 the transmitted sonar signals. Here, we use quantitative comparisons of the contours
27 of calls and sonar signals to test whether or not the pilot whales changed their calls to
28 vocally match the sonar signals used during the experiments. Five whales tagged
29 with DTags (Johnson and Tyack 2003) were followed and tracked visually throughout
30 each experiment. Each experiment consisted of the period from tag on until the tag
31 came off, and included multiple exposures to different sonar signal types (Fig. 1)
32 (Low Frequency Active Sonar - LFAS_{UP}: 1-2 kHz hyperbolic upsweep, LFAS_{DN}: 1-2
33 kHz hyperbolic downsweep, and Medium Frequency Active Sonar - MFAS_{UP}: 6-7
34 kHz hyperbolic upsweep). During each exposure the source vessel approached the
35 tagged whale from a distance of 6-7 km, transmitting sonar pings of 1 s duration with
36 a 20 s interval between pings, starting with a ramp-up procedure in which the source
37 level was increased from 152 dB re 1 μ Pa m to maximum level (214 dB re 1 μ Pa m for
38 LFAS and 199 dB re 1 μ Pa m for MFAS) over a period of 10 min. When the source
39 vessel was 1 km away from the tagged whale, its course was fixed and sonar
40 transmission was stopped 5 min after the whale was passed, marking the end of the
41 exposure. Each exposure had a total duration of approximately 40 min. Details of the
42 experimental procedures are described by Miller et al (2012). The tags recorded sound
43 at a sampling rate of 192 kHz and 16-bit resolution. The sound record was inspected
44 in Adobe Audition (Adobe Systems Incorporated, California, USA) using
45 spectrograms with 4096 FFT points, and those containing calls or series of
46 echolocation clicks were marked. Calls included tonal sounds and pulsed calls that are
47 perceived as tonal due to the high pulse repetition rate. The rate of production of
48 echolocation clicks occasionally increased steadily into a series perceived as a buzz,
49 which were not included in the analysis because they were considered to function in
50 echolocation (Aguilar de Soto *et al.* 2008). Calls were classified into three categories

51 of perceived signal-to-noise ratio: 1) for faint, barely detectable calls, 3) for calls that
 52 were loud and clear in the recording and spectrogram, and 2) for sounds that were
 53 intermediate between those two extremes. Only calls in category 3 were analyzed
 54 further as these were most likely to have been produced by either the tagged whale or
 55 by whales in close proximity to the tagged individual. Also the restriction to category
 56 3 calls ensured that frequency contours could be adequately extracted (see below).
 57 The frequency contour of each call was extracted from spectrograms (FFT size 4096,
 58 87% overlap) using a semi-automatic custom program in MATLAB (The
 59 MathWorks, Inc., Massachusetts, USA). Initially we ran an automatic contour
 60 extraction procedure that linked the dominant frequencies of adjacent FFT windows
 61 (Gillespie *et al.* 2013). These contours were checked by an operator who manually
 62 changed them for a better match to the underlying spectrogram. As detailed below, a
 63 dissimilarity metric (m) was calculated between the contour shape of calls and the
 64 three different sonar signals (Figs. 2 and 3).

65 All frequency contours were linearly interpolated to 5 ms temporal resolution.
 66 In each comparison (sonar signal *vs.* call) the contours were shifted past each other
 67 both in frequency and time in 5 ms and 1Hz steps. A matrix of root-mean-squared-
 68 differences (\mathbf{D}) was calculated for each combination of offset values as

$$69 \quad D = d_{\Delta f, \Delta j} = \sqrt{\frac{\sum_{i=j+\Delta j} (s_i - c_{j+\Delta j} + \Delta f)^2}{n_{i=j+\Delta j}}} \quad (1)$$

70 where s is the vector of frequency values (s_i) making up the sonar contour, c is the
 71 vector of frequency values (c_j) of the call, Δf is the frequency offset value and Δj is
 72 the time offset in number of 5 ms steps and $n_{i=j+\Delta j}$ is the number of cases when $i=j+\Delta j$
 73 (*i.e.*, the number of 5 ms bins that overlapped when contours were lagged by Δj). The

74 range of values for Δj was selected so that either sound's duration overlapped by an
75 arbitrary value of at least 75%. The range of values of Δf was selected so that

$$76 \quad \text{MAX}(c)\text{-MIN}(s) < \Delta f < \text{MIN}(c)\text{-MAX}(s) \quad (2)$$

77 The dissimilarity metric for each pair of sonar signal and call being compared was
78 taken as $m = \text{MIN}(\mathbf{D})$. A rotation test (DeRuiter and Solow 2008) randomizing the
79 timing of the exposure period was performed to evaluate the likelihood of calls
80 matching the sonar during each period of sonar exposure by chance alone. The
81 rotation test maintains the call sequence as it was produced and is nonparametric, so
82 autocorrelation in the calling data series does not bias the test statistic. To ensure that
83 when evaluating the effects of one exposure period, the potential effects of other
84 exposures in the same experiment did not confound the analysis, calls recorded during
85 other exposures were removed from the record prior, to running the rotation test. In
86 each iteration of the randomization test, a mock exposure period of the same duration
87 as the exposure was randomly shifted within the non-exposure period (excluding the
88 actual exposure period and any period of tagging attempt on other individuals of the
89 same sub-group). Any part of the mock exposure beyond the end of the recording was
90 wrapped back to the start. The median value of m of all calls, and the median of the
91 5% of sounds most similar to the sonar was recorded within each mock exposure
92 period. The median of all calls was used to evaluate an overall shift in vocal output
93 (i.e. all calls produced became similar to sonar signals). The 5% value is arbitrary, but
94 is effective at limiting the contrast to calls most similar to the sonar, which may
95 include high-quality matches (i.e. evaluates if matching calls were produced in
96 addition to calls within the previous range of similarity). The proportion (P) of the
97 median values obtained by 10,000 iterations of the rotation test lower than the median
98 value observed during each actual exposure was calculated. Since we ran multiple

99 comparison tests we adjusted the critical level of significance α with a Bonferroni
100 correction. We therefore conservatively evaluated the statistical significance for each
101 individual test at a level of 0.004 (α/n ; $\alpha=0.05$, $n=12$ exposure sessions; see below).

102 Diving depth was measured using the tag's pressure sensor to investigate any
103 relationship between the occurrence of vocal matching and specific behavioral
104 patterns (e.g., foraging during deep dives). A total of 12 exposure sessions were
105 conducted on five tagged long-finned pilot whale (Table 1), yielding 41 h of acoustic
106 recordings. Overlapping calls precluded contour extraction in many cases; therefore
107 of 3,923 calls in the highest category of perceived signal-to-noise ratio only 2,556
108 contours were successfully extracted. Evaluating the median dissimilarity metric of
109 all calls within an exposure period as the test statistic (Table 1), one exposure was
110 significantly different from baseline randomizations: MFAS_{UP} gm08_150c
111 ($P<0.0001$, Figs. 1 and 2). When using the 5% most similar calls (Table 1) two
112 exposures (MFAS_{UP} gm08_150c and LFAS_{DN} gm09_138b (Fig. 3), $P<0.0001$) had
113 calls that were significantly more similar to the sonar than was observed during
114 baseline randomizations. With this analysis we demonstrated that in two of 12
115 exposures pilot whales were significantly more likely to produce calls with frequency
116 modulation similar to the sonar during sonar transmission periods.

117 A pattern of whistles similar to sonar transmissions was found to decrease
118 with increasing time after individual sonar pings in false killer whales, *Pseudorca*
119 *crassidens*, but not in tests of two short-finned pilot whales and a melon headed
120 whale, *Peponocephala electra* (DeRuiter *et al.* 2012). In one of the two exposures
121 where pilot whales matched the sonar in our study, the median difference of
122 frequency modulation between all calls and the sonar, was less than expected based
123 upon call production during periods without sonar transmissions. These results

124 indicate that the whales produced calls that matched the sonar pulses (Table 1 and
125 Fig. 3), and in some cases may have shifted their overall call production to be more
126 similar to the sonar (Fig. 1). This reaction appears either to be a form of vocal
127 matching, which has been described as an individual responding to a stimulus by
128 preferentially producing a similar signal from its repertoire (Stoddard *et al.* 1992) or a
129 form of vocal mimicry, which has been described as an animal copying another
130 species or an environmental noise (Kelley and Healy 2011). Long-finned pilot whales
131 are reported to produce calls with simple up or down modulation patterns similar to
132 the sonar signals used here (Taruski 1979, Weilgart and Whitehead 1990). However,
133 the vocal repertoire of pilot whales remains so poorly defined that it is difficult to
134 demonstrate whether or not a call similar to an artificial model is part of the pre-
135 exposure repertoire.

136 Vocal matching has been reported in birds, frogs, primates, and cetaceans
137 (Dobkin 1979, Sugiura 1998, Gerhardt *et al.* 2000, Janik 2000, Vehrencamp 2001,
138 Kelley *et al.* 2008), and most commonly involves matching a conspecific call. Most
139 studies in vocal matching have focused on songbirds, where a predominant function is
140 to signal aggression (*e.g.*, Vehrencamp 2001). Early work on vocal mimicry also
141 focused on songbirds, where an early review defined vocal mimicry in terms of
142 function as “the use of calls or songs of other species that are predominantly
143 aggressive, predatory, or otherwise noxious.” and argued that vocal mimicry functions
144 in interspecific competition and avoidance of predation (Dobkin 1979). If matching
145 or mimicry among pilot whales functions as described above for songbirds, this might
146 suggest that in two of our exposures, some of the pilot whales might have matched the
147 sonar exposure as an aggressive signal to a potential threat or noxious stimulus.
148 Matching a threat’s acoustic features might also function to communicate about the

149 hazard to other group members. However, other functions have been proposed for
150 vocal matching and vocal mimicry. A recent review of vocal mimicry in songbirds
151 concluded that there is no compelling evidence to support any of the functional
152 hypotheses for vocal mimicry in songbirds, but rather that mimicry may be a by-
153 product of the mechanisms by which birds learn sounds of conspecifics (Kelley *et al.*
154 2008). We have observed apparent cases of vocal matching among animals in our
155 recordings, indication that pilot whales may also have a natural tendency to match
156 conspecific sounds as do some other odontocetes species (Janik 2000, Miller *et al.*
157 2004, Schulz *et al.* 2008). Though we do not currently understand the possible
158 function of vocal matching in pilot whales, one plausible explanation is that matching
159 the sonar represents a by-product of pilot whales' natural tendency to match
160 conspecific sounds. If vocal mimicry is a by-product of vocal matching, then our
161 conclusions of the possible implications of pilot whales matching sonar signals do not
162 greatly depend upon whether the signals were learned or not.

163 Recent work on vocal matching and imitation, especially among mammals,
164 emphasizes a diversity of potential functions including affiliative as well as
165 aggressive displays. Many mammals produce contact calls that converge as
166 individuals form social bonds, using matching to maintain social cohesion (Tyack
167 2008). In cetaceans, functions for matching include aggressive or affiliative displays
168 (Janik 2000), reinforcing social bonds (Schulz *et al.* 2008), signaling individual
169 position and coordinating movement trajectories (Miller *et al.* 2004), or signaling
170 alliance membership to third parties (Janik 2000). The diversity of suggested
171 functions limits our ability to infer the function of pilot whales matching sonar
172 signals.

173 We analyzed dive behavior (Table 1), vocal behavior, and group structure

174 during exposure periods in which pilot whales did or did not match the sonar, but no
175 evidence from the sonar exposures supported a particular function for vocal matching
176 of the sonar (Miller *et al.* 2011). Sonar received pressure levels (SPL) were calculated
177 on the tagged whale to verify the audibility of the sonar signals. The only published
178 audiogram for long-finned pilot whales (Pacini *et al.* 2010) reports hearing thresholds
179 between 53.1 to 124.4 dB re 1 μ Pa. These thresholds are all well below the maximum
180 (150-180 dB re 1 μ Pa) received SPL in any of the sonar exposures (Table 1). Although
181 the audiogram does not report hearing thresholds below 4 kHz, assuming that the
182 shape of the audiogram is similar to other odontocetes we expect the sonar received
183 levels to be above the hearing threshold at LFAS frequency. Therefore, it is fair to
184 assume that in all exposures the whales were able to hear the sonar stimulus.

185 Interpretation of the vocal matching reported here is hampered by our limited
186 knowledge of the vocal repertoire of pilot whales, how it develops, the function of
187 these calls or call matching, and whether pilot whales can learn to imitate novel
188 sounds that were not part of their vocal repertoire prior to exposure. If the sonar
189 sounds are similar to a pre-existing sound in the repertoire, which has a particular
190 function, then the response may be modulated by the specific function of the pre-
191 existing sound. On the other hand, we cannot rule out that the pilot whale call
192 contours that were similar to sonar were not part of the pre-exposure repertoire, but
193 rather reflected vocal production learning (Janik and Slater 2000) in which the subject
194 learned to copy the sonar signal.

195 Delphinids such as pilot whales are thought to rely upon social defenses
196 against threats such as predators (Norris and Dohl 1980), which may yield different
197 kinds of responses to anthropogenic stimuli compared to animals more likely to
198 respond with crypsis and/or flight reactions (Morisaka and Connor 2007). If vocal

199 matching (or mimicry) in pilot whales functions against threats, then the matching of
200 the sonar could indicate a more severe reaction to a stressful stimulus than if it were a
201 neutral by-product of vocal matching or vocal learning. We therefore face a situation
202 where our ignorance of basic behavioral ecology, such as the functions of vocal
203 matching, impedes our ability to estimate the impact of this relevant response to
204 anthropogenic sound by wildlife.

205

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215 Committee and the Woods Hole Oceanographic Institution Institutional Animal Care
216 and Use Committee.

217

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Table 1. Dissimilarity metric observed during exposure and median of 10,000 baseline randomizations. The proportion of randomization iterations that produced values below the observed statistic (p) and maximum dive depth and received sound pressure level range for the tagged whale during each exposure is also shown. Cases in which the median score during the exposure was significantly (Bonferroni corrected $\alpha = 0.004$) lower than during baseline randomizations are shown in **bold**.

The number of contours analysed are shown inside brackets.

Experiment	Exposure	Median dissimilarity of all calls in Hz (number of contours analysed)			Median dissimilarity of 5% most similar calls in Hz (number of contours analysed)			Exposure	
		During exposure	Baseline randomizations	p	During exposure	Baseline randomizations	p	Dive depth max (m)	SPL range (dB μ Pa)
gm08_150c	LFAS _{UP}	403.49 (14)	277.77 (80)	0.56	25.2(1)	29.6(4)	0.13	15	91-170
gm08_150c	MFAS_{UP}	46.63 (9)	298.27 (80)	0	10.51(1)	34.69 (4)	0	24	84-150
gm08_154d	LFAS _{UP}	139.36 (133)	132.78 (778)	0.63	44.59 (7)	53.24 (39)	0.27	65	79-163
gm08_154d	MFAS _{UP}	161.77 (18)	165.37 (778)	0.42	42.76 (1)	63.6 (39)	0.09	9	70-152
gm08_159a	LFAS _{UP}	342.31(8)	208.13 (603)	0.93	199.22 (1)	64.83 (30)	0.9	14	75-175
gm08_159a	MFAS _{UP}	339.29 (45)	197.34 (603)	0.93	95.38(2)	83.29 (30)	0.6	427	74-159
gm09_138b	LFAS_{DN}	86.92 (63)	267.56 (437)	0.05	17.28 (3)	53.48 (22)	0	50	75-175
gm09_138b	LFAS _{UP}	487.69 (25)	300.54 (500)	0.77	121.72 (1)	91.1 (25)	0.45	20	73-167
gm09_138b	MFAS _{UP}	317.36 (60)	330.05 (500)	0.51	167.52(3)	110.6 (25)	0.62	9	76-161
gm09_156b	LFAS _{DN}	254.05 (7)	292.42 (236)	0.34	93.93 (1)	63.47 (12)	0.3	540	91-177
gm09_156b	LFAS _{UP}	207.53 (28)	260.54 (236)	0.35	22.26 (1)	42.31 (12)	0.11	20	68-180
gm09_156b	MFAS _{UP}	556.01(12)	281.48 (236)	0.77	26.85 (1)	43.25 (12)	0.05	550	83-156

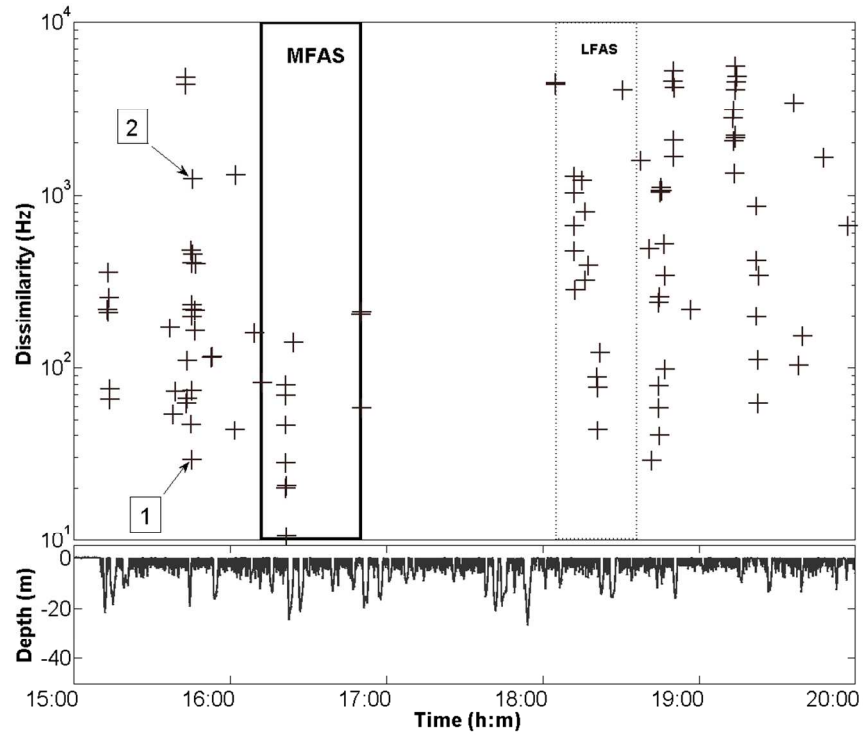


Figure 1. Time series of the dissimilarity metric (m) between contours of whale calls and the MFAS signal (top) and depth (bottom) for the whole tag record for whale gm08_150c (Table 1). Each '+' symbol represents a single call. Full line box indicates the period of MFAS exposure. Calls during LFAS exposure (dotted line box) were not used in the rotation test. No good quality calls were found between the MFAS and LFAS exposures. See figure 2 for description of numbers 1 and 2.
338x250mm (96 x 96 DPI)

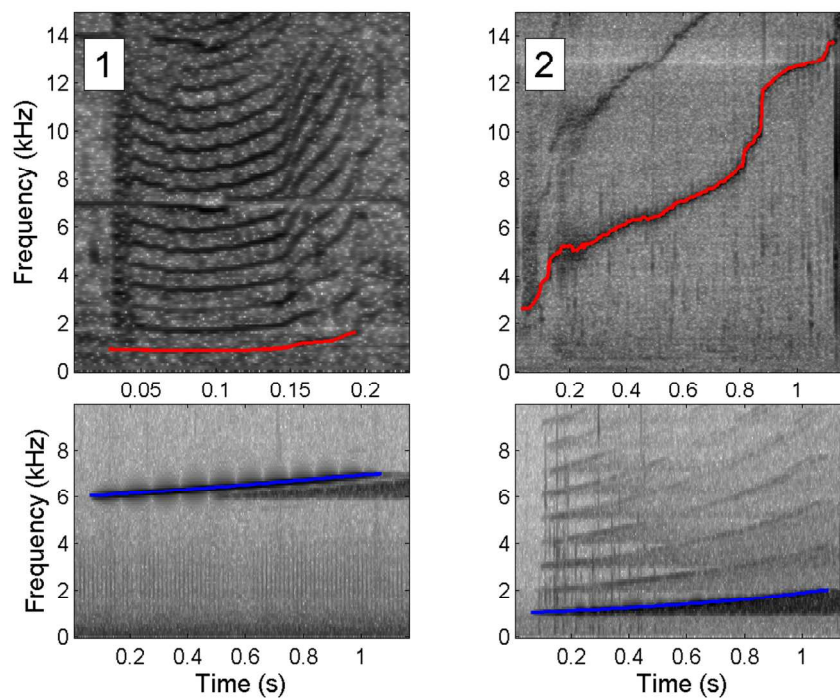


Figure 2. Spectrogram of whale and naval sonar sounds. Top two panels show calls marked on figure 1. Example 1 (top left) is a call with a low dissimilarity value ($m = 29$ Hz) and example 2 (top right) is a call with a high dissimilarity value ($m = 1240$ Hz). Both calls were produced before any sonar exposure. Bottom panels show examples of MFASUP (bottom left) and LFASUP (bottom right) sonar signals as recorded on the Dtag. Color lines represent the extracted contours for each of the examples.
203x152mm (150 x 150 DPI)

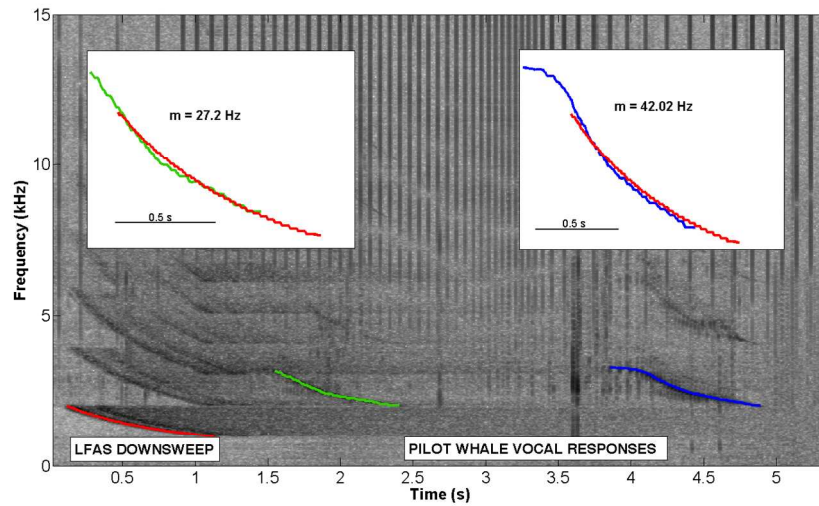


Figure 3. Example spectrogram from deployment gm09_138b during transmission of LFAS downswEEP sonar signals. Red colour represents the extracted sonar contour while green and blue colours represent extracted contours of calls produced by pilot whales. White insets show the offset position of each of the calls contour in relation to the sonar contour corresponding to the minimum dissimilarity metric value.
442x245mm (96 x 96 DPI)