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35 Cetaceans (whales, porpoises, and dolphins) use only their flukes for propulsion. Flukes
36 are distally located extensions of the tail, and from a biomechanical standpoint, function as a pair
37 of wings (Vogel 1994). Flukes function to produce thrust generated as an anteriorly directed lift
38 force as flukes oscillate vertically (Fish 1998 a,b). Their cross-sections resemble hydrofoils. For
39 a hydrofoil to be effective, a large lift must be produced while drag is minimized; this, in turn,
40 increases the thrust generated (Weihs 1989; Vogel 1994).

41 The hydrodynamic implications of fluke design can be studied by examining the cross-
42 sections (*i.e.*, parasagittal) of the flukes. Cross-section profiles taken along the horizontal axis
43 exhibit what is a typical streamlined hydrofoil profile with a rounded leading edge and a long,
44 tapered trailing edge. This shape is critical for the generation of lift for thrust, while minimizing
45 induced drag (*i.e.*, drag due to lift production; Lighthill 1970; Vogel 1994). The flukes are
46 symmetrical about the chord (Lang 1966; Bose et al. 1990). The cross-sectional profile of the

47 flukes is similar to symmetrical engineered foils (Fish 1998b). The similarity to engineered foils
48 would imply that cetacean flukes would be capable of effectively generating large lift with low
49 drag at higher angles of attack.

50 The typical planform shape of cetacean flukes is characterized as a tapered wing with
51 sweepback (*i.e.*, rearward inclination of the leading edge). Such a wing shape can achieve
52 improved efficiency by reducing induced drag by 8.8% compared to a wing with an elliptical
53 planform (van Dam 1987). Minimal induced drag occurs in swept wings with a triangular
54 planform approximating the design of most cetacean flukes (Chopra and Kambe 1977; Fish
55 1998b). Aspect ratio (*AR*) measures the relationship between the span and planform area of a
56 hydrofoil and is related to the effectiveness of the hydrofoil's design. A low *AR* is characterized
57 as a short, broad wing, whereas a high *AR* wing is long and narrow. A combination of low sweep
58 with high *AR* allows for high-efficiency rapid swimming, whereas high sweep may compensate
59 for the reduced lift production of low-*AR* flukes (Azuma 1983; Liu and Bose 1993). Highly
60 swept, low-*AR* wings produce maximum lift when operating at high angles of attack, when low-
61 sweep, high-*AR* designs would fail (Hurt 1965). This feature aids in the maintenance of high
62 efficiency at slow, sustained speeds (Magnuson 1978), as observed in *Monodon monoceros*, the
63 narwhal. In general, narwhals are regarded as very slow swimmers that seldom exceed speeds of
64 1.7 m s^{-1} (Minasian *et al.* 1984). Although increasing efficiency, the high sweep angle will
65 reduce thrust. Maintenance of thrust would be facilitated by a higher *AR* hydrofoil planform.

66 The external morphology of flukes is generally considered constant among the Cetacea.
67 An acute departure from the typical fluke shape is found in the narwhal. Narwhals are regionally
68 circumscribed cetaceans that inhabit the Arctic Ocean Atlantic sector (Heide-Jørgensen 2009).
69 They are widely distributed in the ice-packed stretches of waters bordering Greenland and the

70 Canadian High Arctic (Laidre *et al.* 2003). The flukes of mature male narwhals have a slightly
71 concave leading edge without sweepback (Fig. 1; Hay and Mansfield 1989). A female narwhal
72 generally has a fluke very similar in shape to that of a dolphin, which is swept back (Fig. 1).
73 Whether or not the differing fluke morphology is an evolved adaptation that coincides with the
74 long, tapering tusk present on most males is unknown (Fish *et al.* 2007).

75 In this study, we compared the fluke geometries of male and female narwhals, which may
76 be associated with hydrodynamic effects. CT (Computerized tomography) scanning was used to
77 obtain data for analyses of the three-dimensional geometry of the flukes.

78 The flukes from four narwhals (two males and two females) were obtained from
79 aboriginal hunters in the vicinity of Broughton Island, Canada. The body lengths of the animals
80 ranged from 2.98-3.60 m (Table 1). Both males had erupted, upper left tusks. Standard body
81 measurements were made including the span of the fluke (*i.e.*, linear distance between fluke
82 tips).

83 The flukes were frozen and shipped to the Canadian Museum of Nature in Ottawa,
84 Canada. The frozen flukes were later transported to the Woods Hole Oceanographic Institution
85 CT imaging facility for scanning. The flukes were placed flat, dorsal side up, on the scanner
86 table, stabilized with plastic wedges and Styrofoam sheets, and scanned tip to tip with span-wise
87 parasagittal cross-sections.

88 CT scans were obtained on a Siemens Volume Zoom CT scanner. Spiral protocols for
89 data acquisition with 0.5- to 1.0-mm detector collimation at 1 mm/sec table feeds were used. All
90 images were reconstructed in both soft tissue and ultra-high resolution kernels with extended
91 attenuation scales to improve discrimination of high density elements. Images were obtained in
92 DICOM formats, and for some data, were reconstructed at 100- μ slice intervals that provide 100

93 μ isotropic voxels needed for finer grain structural analyses. With these parameters, the
94 maximum in-plane resolution was 0.35 mm at 2% of the modulation transfer function. Prior
95 studies suggest 25 μ in-plane pixel resolutions are possible, but a conservative nominal
96 resolution is 50 μ .

97 Because true data base magnifications cannot be obtained from enlargements of
98 processed image files, raw attenuation data were archived onto magneto-optical disks for all
99 scans in order to allow additional post-scan processing as needed. Image files were archived in
100 DICOM format and 512 matrices on CD. The DICOM images of fluke cross-sections were
101 analyzed using OsiriX (OsiriX Foundation, Geneva, Switzerland, version 2.7.5). A total of 2,715
102 fluke cross-sections were examined for all four specimens; this figure excludes the tailstock
103 cross-sections, for which leading and trailing edges of the flukes were not visible.

104 Measurements of the fluke planforms (Fig. 2) included the span (FS ; distance from fluke
105 tip to fluke tip), fluke blade span (BS , distance from root fluke chord; RC , to tip of fluke),
106 planform area (F_a ; total planar area of flukes on the dorsal surface), and sweepback (Λ). RC is
107 the chord at the intersection of the fluke blade and the tailstock. The sweepback was measured as
108 the angle between a line extending from 25% of the fluke chord extending from the cranial end
109 of RC and to the maximum lateral extension of the fluke tip and a line perpendicular to RC (Hurt
110 1965, Fish 1998a, b). The aspect ratio (AR) of each fluke was calculated as FS^2/F_a .

111 Measurements of fluke sections for each CT slice (Fig. 2) were made for the chord length
112 (C), maximum thickness (T), shoulder (S), and leading edge radius (LER) (Fish *et al.* 2006,
113 2007). C was measured as the linear distance from the leading to trailing edge of the fluke. T was
114 the maximum vertical distance between the upper and lower side of the fluke perpendicular to
115 the chord line. S was measured as the distance from the leading edge to the maximum thickness

116 line. For comparison of narwhals of different sizes, C , T , and S measurements were presented as
117 a percentage of BS , starting at 0% at RC to 100% at the fluke tip. Leading edge radius (LER) was
118 the radius of the curvature of the leading edge as determined from the radius of a circle that
119 connects tangential points of the leading edge and the upper and lower surfaces of the cross-
120 section (Hurt 1965). A circle template was used on images taken at 50% of the BS on the two
121 flukes for each individual narwhal to determine radius of the leading edge. LER was presented as
122 a proportion of C (Fish *et al.* 2007).

123 The thickness ratio ($TR = T / C$) and shoulder position ($SP = S / C$) of each cross section
124 were used as indicators of flow structure and the hydrodynamic performance relating to the
125 generation of lift and drag for foils (von Mises 1945; Hoerner 1965).

126 Microsoft Excel 2004 and KaleidaGraph (Synergy Software, version 4.03) were used to
127 statistically and graphically analyze the data collected. Because of differences in fluke sizes of
128 the individual narwhals, comparisons were made using means (\pm one standard deviation). The
129 linear measurements from each CT slice (C , T , S) were averaged for the corresponding slice for
130 each fluke blade for an individual animal. The mean values of each measurement and
131 morphological parameter were calculated for each sex. The small sample size precluded
132 statistical analysis beyond descriptive statistics.

133 The FS and F_a were both greater for the male narwhals, due to their larger size. The
134 calculated values for aspect ratio did not show significant differences for male and female
135 narwhals. The main difference was the difference in Λ between the sexes (Table 1; Fig. 1).
136 Females had a mean sweepback angle of 31.4 ± 3.3 degrees and males had mean sweepback
137 angles of 20.5 ± 5.2 degrees.

138 It was noted that male N0004 was slightly immature, judging by its overall smaller body
139 size and tusk and the fluke morphology was slightly swept back. Measurements of the *S* for
140 female N0001 were lower than expected at approximately 15% of span (Figs. 3, 5) because of
141 depressions on the ventral side of the cross-sections.

142 For both sexes, the fluke cross-sections were highly streamlined, having a rounded
143 leading edge and a tapering, trailing edge; fluke sections were also symmetrical about the chord
144 (Fig. 2). Both right and left fluke blades were apparently symmetrical. From the root of the fluke,
145 *C*, *T*, and *S* showed an approximately linear decrease to about 95% of span in which these
146 measurements decreased more rapidly toward the tip (Fig. 3). Differences between male and
147 female narwhals for *C*, *T*, and *S* were only observed near the fluke root. Interestingly, there was
148 no discernable difference in sectional values for *C* between males and females despite the
149 difference in Λ (Fig. 3).

150 *TR* decreased proximally toward the tailstock (Fig. 4). The maximum values of *TR*
151 occurred at the fluke tip. Over the fluke span, males had a mean *TR* of 0.23 ± 0.02 , whereas the
152 females had a mean *TR* of 0.24 ± 0.02 . Differences in *TR* between male and female narwhals
153 were apparent from 20% to 90% of *BS*. Within this range, *TR* for females was 5% greater than
154 for the males.

155 *SP* had a U-shaped distribution along the fluke blade span with the highest values at the
156 tip and root of the flukes and lowest at approximately midspan (Fig. 5). Between 20% and 65%
157 of span, males and females had means for *SP* of 0.28 ± 0.00 and 0.30 ± 0.01 , respectively. Over
158 this range of span the females averaged a 10% greater *SP* than males.

159 No apparent difference of *LER* was found between males and females. Mean *LER* values
160 were 0.05 ± 0.01 and 0.05 ± 0.00 for males and females, respectively.

161 The general morphology of cetacean flukes influences the requirements of energy for
162 swimming. A highly streamlined fluke is characterized by the symmetrical nature of the cross-
163 sections in the sagittal plane. A rounded leading edge and a tapering, trailing edge are
164 characteristics shown in the cross-sections that are fundamental in the generation of lift, while
165 also reducing drag (Webb 1975, Vogel 1994).

166 The parameters *TR* and *SP* influence the pressure distribution of flow over the surface of
167 the flukes. A favorable gradient has pressure decreasing in the downstream direction, which aids
168 in flow over the fluke surface. An unfavorable gradient has pressure increasing in the
169 downstream direction. This ultimately delays the flow over the fluke's surface. The favorable
170 and unfavorable pressure gradients are located upstream and downstream of *SP*, respectively
171 (Fish 2007). An increase in drag results from an unfavorable pressure gradient, because flow will
172 tend to separate from the fluke surface (Webb 1975; Vogel 1994). Thrust increases with lift until
173 a critical point when the fluke stalls due to the separation of flow from the surface. Thus, the
174 displacement of the *SP* further downstream on the fluke section impedes the separation of flow
175 by extending the favorable pressure gradient. However, downstream displacement of *SP* will
176 foster separation, particularly when the section is canted at an angle to the flow. Mean *SP* values
177 ranged from 0.29 to 0.38 for females and male values ranged from 0.27 to 0.36. Female narwhals
178 had a higher *SP* than male narwhals (Fig. 5), indicating that *SP* was placed further downstream
179 on the fluke section.

180 Male narwhals had lower *TR* values when compared to female narwhals. Average *TR*
181 values for male narwhals ranged from 0.195 to 0.285, while female narwhals ranged from 0.207
182 to 0.442. Streamlined foil sections have lower drags with low *TR* values than high *TR* foils
183 (Abbott and von Doenhoff 1959). Low *TR* foils have a small pressure gradient magnitude, which

184 reduces drag (Fish 2007). Conversely, as the TR values increase, as observed in female narwhals,
185 lift is enhanced and stall is delayed. This hydrodynamic performance would be possible because
186 the shape of the cross-section would allow the flow of water to move smoothly over the fluke
187 surface. Similarly, a high SP value leads to delayed stall. Consequently, it would appear that the
188 flukes of male narwhals have a hydrodynamic advantage in reducing drag; however, the cross-
189 sectional design of the flukes of female narwhals would tend to increase lift and delay stall.

190 Other limiting factors of induced drag include the sweep of a fluke (Fish 1998b). Female
191 narwhals have a greater sweepback in fluke planform compared to males. Sweepback of a wing
192 or hydrofoil can reduce the induced drag (*i.e.*, drag due to lift) by as much as 8.8% compared to a
193 wing without sweepback (van Dam 1987). Swept back wings produce maximum lift generation
194 at high angles of attack (Fish 1998b). This would be advantageous particularly at low swimming
195 speeds when the angle of attack of the flukes is high (Fish 1993). However, low sweep angles
196 allow for high-efficiency, rapid swimming (Azuma 1983). Based on this information, it is
197 deduced that females would have increased lift but at low swimming speeds, whereas males
198 would have high efficiency at higher swimming speeds.

199 The hydrodynamic effects produced from differences in the geometries of the flukes,
200 which were stated above, are largely associated with steady flow conditions. The flukes of
201 cetaceans are oscillated incurring the dominance of unsteady flow conditions (Webb 1975; Fish
202 1993, 1998a). Unsteady effects can incur lower lift than for steady motion (Lighthill 1970).
203 Further analysis of narwhal fluke geometry would require examination of unsteady effects,
204 although results based on steady flow conditions can provide an indication of differences in
205 hydrodynamic performance.

206 The differences in fluke design between the sexes of narwhals could have hydrodynamic
207 consequences associated with swimming performance. No differences in swimming speeds
208 between male and female narwhals have been reported, when transiting between locations as
209 during migrations (Dietz *et al.* 1995, Dietz *et al.* 2001, Heide-Jørgensen *et al.* 2002, 2003).
210 However, Laidre *et al.* (2003) found that female narwhals made more dives to deeper depths than
211 males. Deeper destination depths were related to increased swimming speed (Laidre *et al.* 2003),
212 indicating that at least during foraging dives, females could be swimming faster than males. The
213 design of the flukes of females, thus, may be associated with the need to transit to greater depths
214 at fast speed. For males, the increased lift and concomitant thrust production from the low
215 sweepback fluke design may aid in compensating for the increased drag that might accompany
216 the possession of the elongate tusk. Swimming performance by narwhals (i.e., overcoming
217 drag, swimming speed) is associated with the hydrodynamically complex and conflicting
218 relationships of lift and thrust production, reduction in drag, delay in stall, and efficiency,
219 which are dependent on the fluke geometry and kinematics.

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297 Weihs, D. 1989. Design features and mechanics of axial locomotion in fish. *American Zoologist*
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299

300 Table 1. Morphometrics of fluke planforms.

301

SPECIMEN	SEX	BODY LENGTH (m)	FLUKE SPAN (m)	PLANFORM AREA (m ²)	ASPECT RATIO	SWEEPBACK ANGLE (deg)	TUSK LENGTH (m)
N0001	F	3.09	0.71	0.13	3.88	33.7	N.A.
N0002	F	2.98	0.70	0.13	3.63	29.0	N.A.
N0003	M	3.60	0.87	0.19	3.90	16.8	1.00
N0004	M	3.57	0.85	0.19	3.86	24.2	0.44

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306 Figure Legends

307

308 *Figure 1.* CT topograms illustrating the differences between female (N0001, N0002) and male
309 (N0003, N0004) fluke planforms.

310

311 *Figure 2.* Planform and sectional fluke dimensions. The upper figure shows a fluke planform.
312 The vertical solid lines show the root chords (*RC*) and the chord (*C*) at 50% of the blade span.
313 The blade span extends horizontally from *RC* to the fluke tip and the span is the horizontal
314 distance between fluke tips. The sweep angle (Λ) is the angle subtended from a line at the 25%
315 of *RC* and the horizontal dashed line. The lower figure shows a CT image of a fluke section. The
316 horizontal line (*C*) illustrates the chord at 50% of blade span, the dashed vertical line is the
317 maximum thickness (*T*), and the distance from the leading edge to the maximum thickness is the
318 shoulder (*S*). The line within the circle indicates the leading edge radius (*LER*), which is
319 determined from the radius of the white circle that connects tangent points of the leading edge
320 with the upper and lower surfaces of the section.

321

322 *Figure 3.* Linear measurements of male and female flukes of the chord (*C*; solid circles),
323 maximum thickness (*T*; open squares) and shoulder (*S*; open triangles) as a percentage of the
324 fluke blade span, where 0% is at the root chord and 100% is at the fluke tip.

325

326 *Figure 4.* Thickness ratio (*TR*) as a function of fluke blade span for male (open circles) and
327 female (solid circles) narwhals.

328

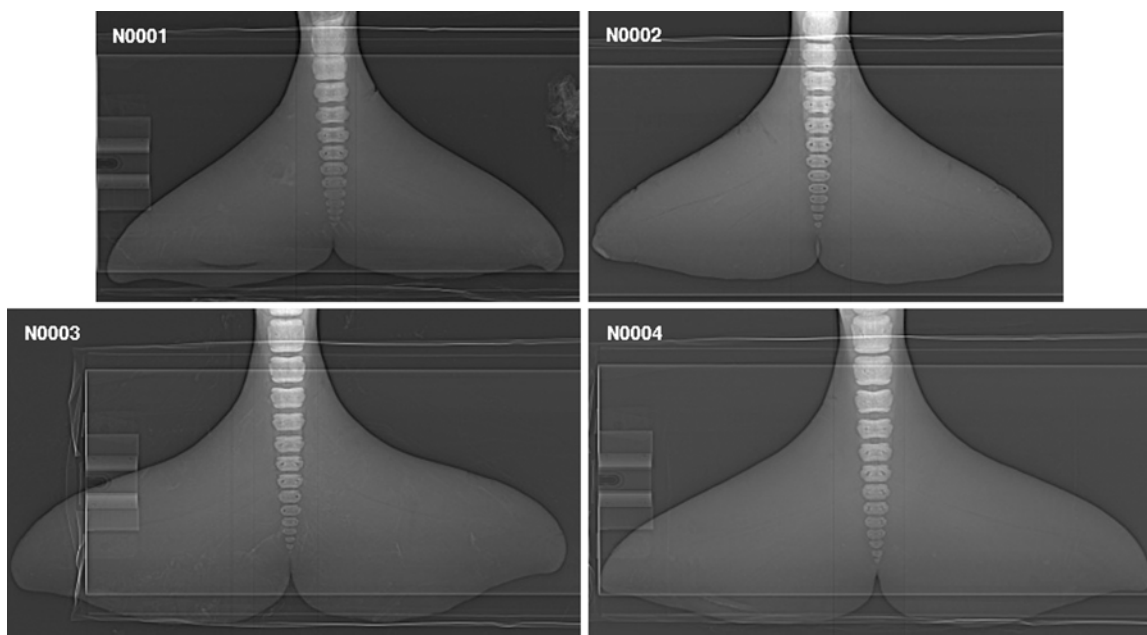
329 *Figure 5.* Shoulder position (*SP*) of male (open circles) and female (solid circles) narwhals as a

330 function of fluke blade span.

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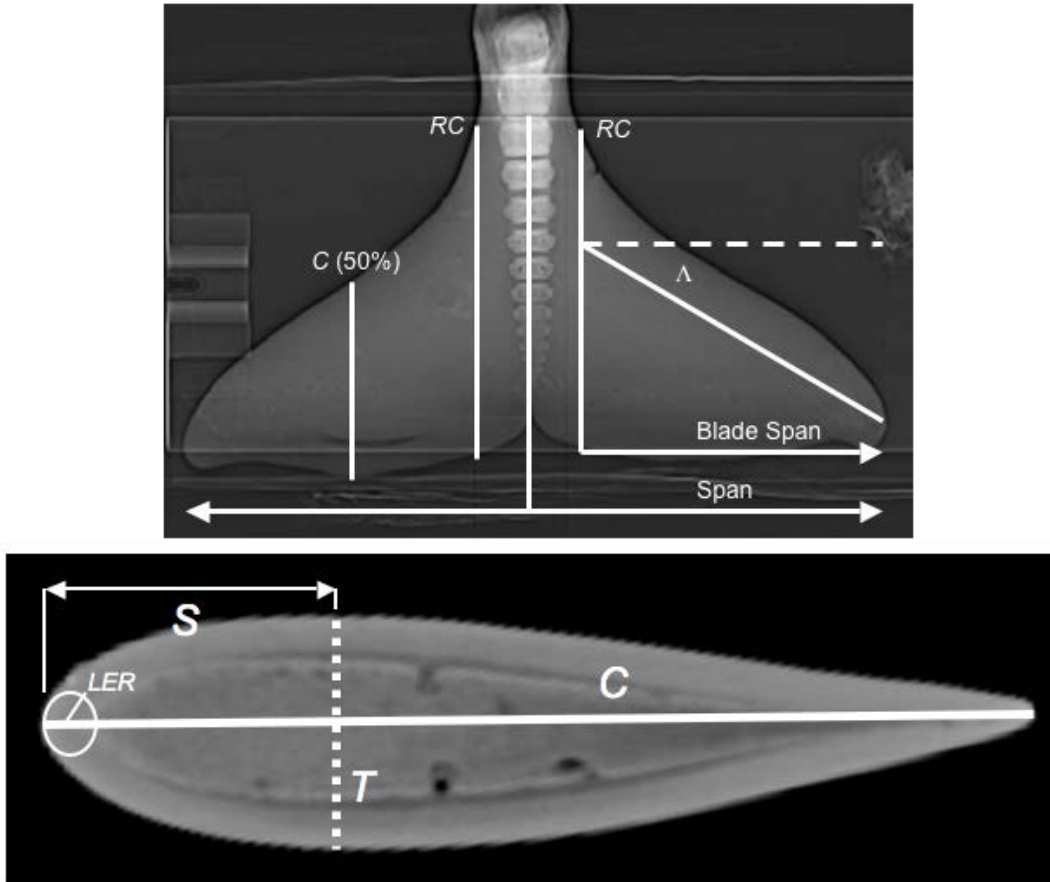
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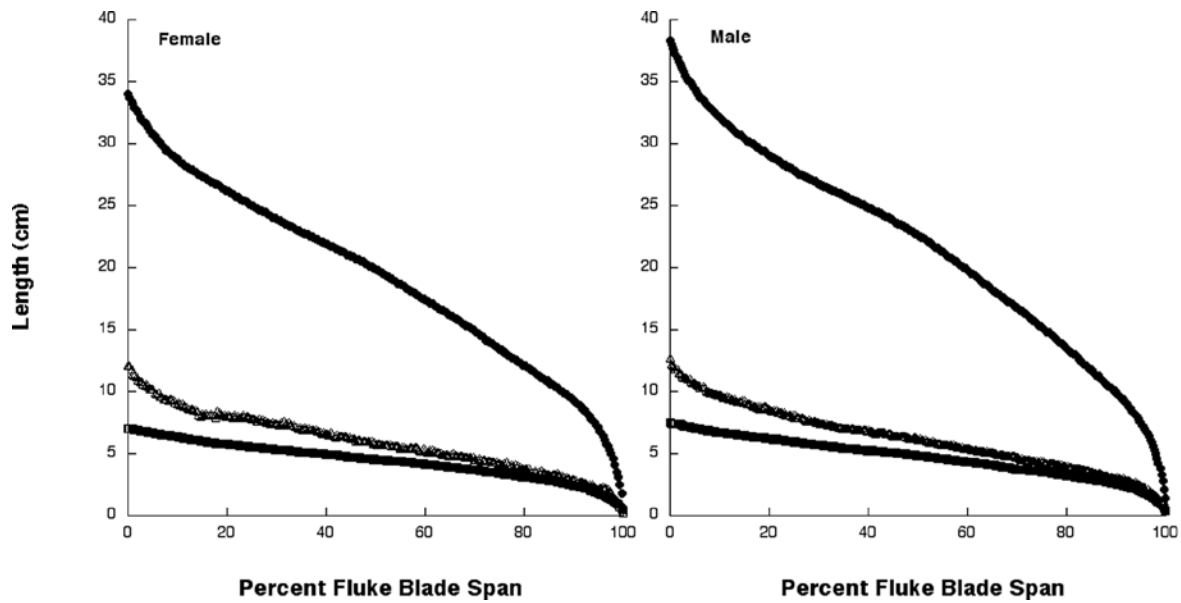
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336 Figure 1.



337
338 Figure 2.

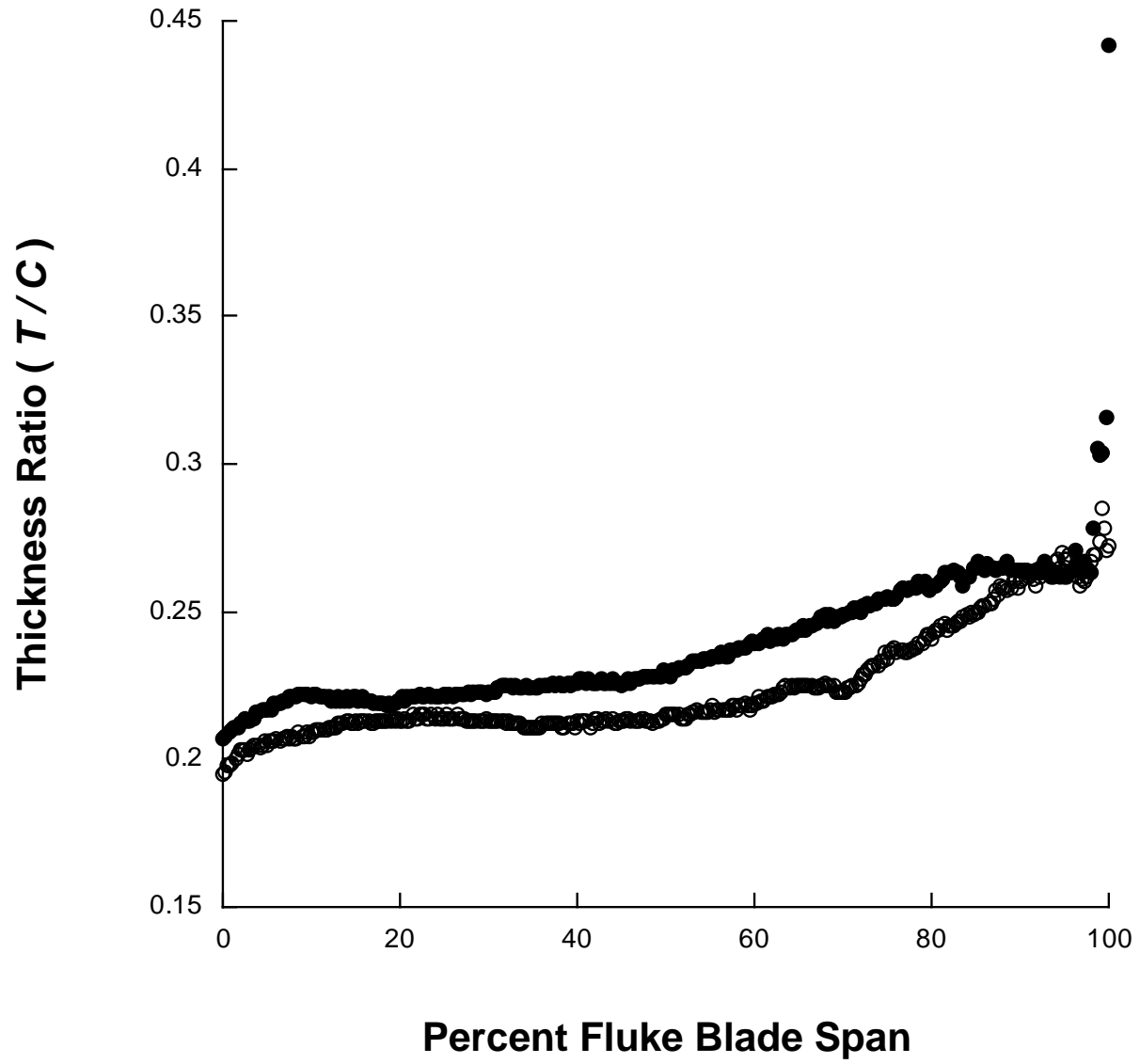
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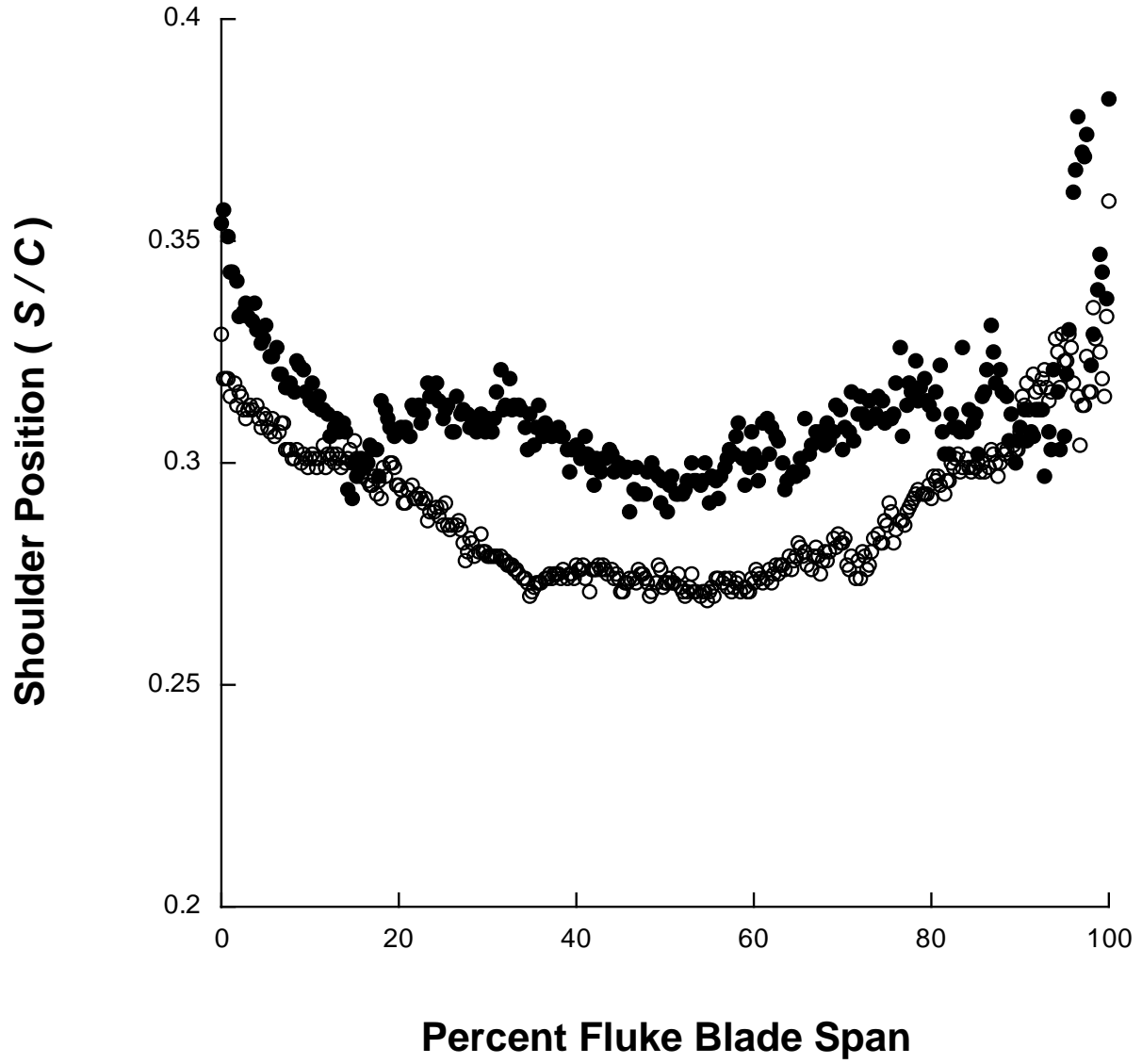
342 Figure 3.



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345 Figure 4.



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348 Figure 5