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Anatomical Specialization in the Gut of Pacific Salmon:
Evidence for Oceanic Limits to Salmon Production?

by

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2 ABSTRACT

4 The stomach (but not intestine) of chum salmon (*Oncorhynchus keta*) is
6 greatly enlarged relative to other species of Pacific salmon. This permits the
8 exploitation of gelatinous zooplankton (jellyfish, ctenophores, and salps) as
10 a major food source, which are an abundant but low energy prey unused by
12 other species of salmon. The unique gut structure of chum therefore allows
14 efficient feeding on a little-exploited branch of the food web and reduces inter-
16 specific trophic competition. The development of this remarkable anatomical
18 specialization suggests that salmon abundances were previously high enough
20 that the resulting trophic competition led to evolutionary selection to reduce
22 trophic competition. As total salmon abundances in the north Pacific are now
24 probably the highest of this century, the carrying capacity of the ocean rather
26 than freshwater could limit overall salmon production if abundances are once
28 again approaching pre-exploitation levels.

20 INTRODUCTION

22 It is widely assumed that the abundance of Pacific salmon (*Oncorhynchus*
24 spp.) is determined as the sum of the carrying capacities of the thousands of
26 streams surrounding the north Pacific. The ocean itself is assumed not to
28 limit overall salmon abundance because of its greater size relative to the total
30 freshwater habitat. As a result, modern theories of salmon management do
32 not consider the possibility that the ocean could impose a density-dependent
34 limit on salmon abundance because these theories explicitly focus on the
36 abundance of single populations in freshwater.

38 Increases since the 1977 regime shift have brought ocean abundances
40 of Pacific salmon back to the high levels of the 1920s (Pearcy 1992; Beamish
42 1993; Hare and Francis 1995). However, the marine growth rates and size at
44 maturity of many salmon populations has decreased at the same time
abundance has increased (Kaeriyama 1989; Ishida et al 1993; Ricker 1995;
Bigler et al 1996). As almost all growth occurs in the ocean, the carrying
capacity of the ocean rather than freshwater could possibly limit overall
production of Pacific salmon (PICES 1996).

38 Salmon are the dominant intermediate level predator in the subarctic
40 Pacific (Pearcy 1992). Although most species are broad generalists in terms
42 of their feeding strategies (Pearcy et al 1988; Brodeur 1990), for much of their
44 life history chum salmon (*O. keta*) have a unique diet that consists of large
amounts of gelatinous zooplankton (review by Arai 1988), an abundant but
low energy prey unused by other species of salmon.

44 Organisms subject to resource limitations frequently show evidence of

46 specialized traits that aid in reducing competition between species by resource
47 partitioning. If productivity of the ocean limited salmon abundance prior to
48 the development of commercial fisheries, when salmon were presumably more
49 abundant, then there should be evidence for this in their evolutionary
50 development. I report here the existence of a morphological adaptation of the
51 gut that is apparently unique amongst vertebrates, and which allows chum
52 salmon to efficiently feed on a branch of the marine food web unused by other
53 salmon species.

54 MATERIALS AND METHODS

56 Adult salmon were collected from commercial salt water fisheries along
57 the British Columbia coast. With the exception of steelhead (*O. mykiss*),
58 samplers were instructed to collect one fish from each of a set of specified
59 weight categories, within a tolerance of ± 100 gms. These sizes were the
60 average weights of each species caught in the B.C. commercial fishery for
61 successive 5 yr periods (1951-56, 1957-61, ...), plus the minimum and
62 maximum annual average size at return observed during the period 1951-92,
63 thus ensuring a wide size range of fish available for the analysis. All fish were
64 frozen whole until analysis. The smallest and largest of each species was
65 analyzed in the present study, plus a sufficient number of intermediate sized
66 fish to ensure that a broad size range of animals for each species were included
67 in the analysis. (Ocean capture ensures that the salmon probably represent
68 a wide range of stocks).

70 Steelhead trout (N=12) were collected from a gillnet test fishery at the
71 mouth of the Skeena River (northern British Columbia). These fish were
72 collected without regard for size, and were probably from Skeena River stocks.

73 At autopsy, fork length, weight, and sex were recorded. The coelomic
74 cavity was opened by cutting through the dorsal musculature at midline down
75 to the spine, and then cutting through the abdominal ribs, exposing the entire
76 coelomic cavity. The transverse septum was left intact, and all organs
77 obstructing view of the digestive tract were removed.

78 After photographing the intact digestive tract the pyloric caeca were
79 dissected from the intestine, blotted dry, and weighed. A second photograph
80 was taken, and the entire digestive tract removed by cutting the esophagus at
81 the connection to the buccal cavity, and cutting the intestine free at the anus.
82 With the exception of one coho (*O. kisutch*) whose stomach and intestine was
83 packed with partially digested fish, the guts contained little food in the
84 remaining animals.

85 The digestive tract was cut into three pieces (esophagus, cardiac plus
86 pyloric stomach, and intestine) and ingested material removed after cutting
87 each section open lengthwise. Each piece of tissue was blotted dry and
88 weighed. The area of each section was measured by laying the material on
1mm² graph paper, tracing the outline of the section, and then counting

90 squares. To prevent stretching of the intestine, the outline was traced on
graph paper before removing the contents. Because the area of the esophagus
92 was small relative to the area of the cardiac stomach and the division line
unclear, the two areas were combined in the measurement of cardiac stomach
94 area. During autopsy, partial records were also kept of the weight of the
pyloric caeca, liver, heart, and spleen.

96 RESULTS

98 Figure 1 provides a photographic comparison of the relative size of the
digestive tract for each North American species of Pacific salmon. The chum
stomach is a strikingly large bag-like structure that nearly fills the coelomic
100 cavity, and is formed of a soft, thin tissue lacking the muscle tone evident in
the other species. In contrast, the stomach of the other species is a thick-
102 walled muscular structure of robust texture. The two most piscivorous species
(Brodeur 1990), chinook (*O. tshawytscha*) and steelhead (*O. mykiss*), have a
104 long, thin, tubular stomach consistent with a diet formed primarily of large
prey items.

106 Scatter plots of stomach area versus body weight show a clear allometric
scaling, with stomach and intestinal area increasing in proportion with
108 $\sqrt{\text{body weight}}$ (Fig. 2). The mean size of the chum stomach is well above the
mean predicted for the other species, while sockeye appear to have slightly
110 smaller than average stomachs for their size. This disparity is also evident
when either the cardiac or pyloric stomach area is compared separately.

112 Comparison of intestinal area with body size indicates that all species
have a similar allometric relationship, so size differences in the digestive tract
114 are limited to the stomach. A more rigorous comparison of these differences
can be made with a box and whisker plot of the ratio
116 $\text{surface area} / \sqrt{\text{body weight}}$ (Fig. 3), which shows that size differences are
indeed confined to the stomach.

118 The weight of the stomach relative to body size was similar for all
species; thus the stomach wall is proportionately thinner in chum despite the
120 two-fold greater surface area. The lining is also unusual, with a soft mucus-
like surface which is easily disrupted mechanically and prominent 1mm high
122 ridges running parallel to the major axis of the stomach. A densely branched
vascular-like network lies on the soft interior surface between the ridges.
124 Visual inspection also revealed the presence of many closely spaced 1-3 mm
long villi on the surface of the longitudinal ridges near the esophagus. These
126 features appear to be unique to the chum in addition to the marked size
difference of the stomach.

128 Comparison of the relative size of the heart, liver, spleen, and pyloric
caeca revealed that the only notable differences were for steelhead, where
130 heart size was significantly smaller than in the other species, and for chum,
where spleen size was smaller (Fig. 4). Given the reputation of the steelhead
132 amongst sports fishermen as a tenacious fighter, a smaller heart was

unexpected.

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DISCUSSION

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In mammals, birds, and fish the primary change accompanying higher nutritional demand is an increase in surface area of the intestine, where food is absorbed, not the stomach (Savory and Gentle 1976; Montgomery 1977; Gross, Wang, and Wunder 1985; Dykstra and Karasov 1992; Vispo and Hume 1995). However, the gross anatomical differences between the digestive tracts of salmon are clearly restricted to the stomach, and intestinal size remains constant.

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Although the function of the pyloric caeca in fish is not entirely clear, it is generally thought that they aid digestion, possibly through enhancing lipid absorption. It is therefore of some interest that roughly the same amount of tissue is devoted to this organ in chum as the other species. However, as the increased size of stomach is obtained by reducing the stomach wall thickness, it is unclear whether or not the relative surface area of the pyloric caeca is larger in chum. It was not practical to attempt to quantify the surface area of the pyloric caeca.

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Published studies on the anatomy of *Oncorhynchus* date back to nearly the turn of the century (Greene 1912; Suyehiro 1942; Yasutake and Wales 1983). Remarkably, none make mention of the striking difference in the size of the stomach of chum salmon. Only two parenthetical references to the gut structure within the genus appear to have been made, Percy et al. (1988) noting that “[chum] have a different stomach morphology from other salmon with a long muscular stomach with many rugae and furrows in the cardiac portion”, and Azuma (1992) noting “... thick muscles in the esophagus of chum... which are not observed in other salmonids”. However, the similar weight of the stomach despite the greater size clearly indicates that, overall, musculature is reduced.

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If the response to dietary limitation in chum is similar to that in other vertebrates, evolutionary pressure from food limitation should have resulted in a large intestinal surface area to maximize nutrient extraction. Instead, it appears that chum evolved a large stomach to allow rapid consumption of large quantities of gelatinous zooplankton. The strong sphincter at the end of the esophagus noted by Azuma presumably prevents regurgitation when the volume of swallowed material fills the stomach and places it under pressure.

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The development of a huge bag-like stomach and a normal intestine appears to be unique amongst vertebrates. Even the ocean sunfish (*Mola mola*), which can reach massive proportions and has many unusual morphological characteristics, appears to have a rather typical stomach (Gregory and Raven 1934), despite its almost exclusive diet of jellyfish.

Assuming a spherical stomach for convenience and converting the

178 measured surface areas in Fig. 3 to volumetric equivalents, the chum stomach
is capable of holding approximately 3.5 times the volume of other species of
180 equivalent size. Gelatinous zooplankton have a low energy density, so more
must be eaten to provide an equivalent caloric intake. Fish, squid, and
182 crustaceous zooplankton are typically composed of 70-80% water, while
gelatinous zooplankton have a water content near 95% (Davis 1993). The
184 caloric content of non-gelatinous zooplankton is therefore at least 5 times that
of gelatinous zooplankton per unit volume eaten. In fact, because most
186 subarctic jellyfish have low stored lipid levels (Larson and Harbison 1989),
expressed on a dry weight basis the caloric content is often only a third that
of non-gelatinous zooplankton (Davis 1993).

188 A rough calculation is that 15 times the volume of gelatinous
zooplankton must be digested to yield the energy equivalent of non-gelatinous
190 zooplankton. Measured gastric evacuation rates are more rapid for chum than
for pink salmon (Ishida et al 1991), and the pH of the stomach lining is lower
192 in chum than in sockeye (Azuma 1992). In laboratory studies cnidaria are
digested in an acidic pepsin mixture in less than 20 minutes, whereas fish or
194 squid take many hours (Jackson, Duffy, and Jenkins 1987). Digestion is
therefore much more rapid than is possible for non-gelatinous material so, in
196 combination with a large stomach, it may be possible to achieve an energetic
advantage by feeding on gelatinous zooplankton. However, this advantage
198 would appear not to be absolute, because chum are observed to switch from
eating gelatinous zooplankton to a diet more typical of pink salmon in odd-
200 numbered years, when the abundance of pink salmon in the central north
Pacific ocean is low (Tadokoro et al., 1996).

202 CONCLUSIONS

204 The chum gut has evolved in a way that reduces trophic competition
with other species of Pacific salmon. Chum and pink salmon are the most
206 abundant species of Pacific salmon (Pearcy 1992), and the most closely
related (Stearley and Smith 1993). Both species have greatly compressed
208 freshwater life histories, and almost all feeding occurs in the pelagic
environment of the open Pacific. The striking differences in gut morphology
210 therefore suggest that in the past population levels rose to a level high enough
that food was limiting in the ocean. This in turn provided the selective
212 pressure necessary for chum to develop the anatomical adaptations necessary
for exploiting a major branch of the marine food web unused by other salmon
214 species.

216 Contemporary salmon abundances are the highest recorded this
century, and evidence that open ocean plankton populations are reduced in
218 years and areas of higher salmon abundance is growing (Nagasawa et al 1995;
Tadokoro et al 1996). Current theories of salmon management are based
upon the assumption that the freshwater habitat limits the abundance of
220 individual salmon populations, and do not consider the possibility that the

222 ocean may ultimately cap total abundance. However, on evolutionary time
223 scales the open ocean abundance of salmon was apparently high enough that
224 significant trophic competition did occur, and resulted in an apparently
225 unique anatomical adaptation not seen in other vertebrates.

226 As gelatinous zooplankton are largely unexploited by other salmon,
227 chum have therefore developed a unique trophic niche through anatomical
228 specialization, and exploit a branch of the marine food web unused by other
229 salmon. Because of this specialization, the increasing ocean abundance of
230 both wild and hatchery salmon is likely to continue to reduce growth rates.
231 This in turn suggests that ocean ranching of chum is likely to have the fewest
232 negative effects on wild salmon populations.

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238 FIGURE 1. Gut morphology of the six North American species of
240 *Oncorhynchus*. Individual photographs were enlarged to make the length
242 of the coelomic cavities equal. The vertical bar shows the extent of the
stomach in the chum salmon, and arrows identify the end of the
stomach and the pyloric sphincter. Scale bars are 5 cm long.

244 FIGURE 2. Comparison of surface area for (A) stomach and (B) intestine
246 with body weight. The solid line shows the least squares regression for
248 all species excluding chum; the dashed line shows the same regression
250 holding the slope fixed at 0.5. The fit is virtually identical, showing
that the surface area of the digestive tract scales as the square root of
body weight. Symbols: Chum (◆); Chinook (●); Coho (▲); Pink (■);
Sockeye (X); Steelhead (+).

252 FIGURE 3. Comparison of the ratio of $surface\ area / \sqrt{body\ weight}$ for (A)
254 stomach and (B) intestine. Boxes show the 25th and 75th percentiles
256 of the data for each species, while the whiskers show the range.
Differences in mean size between species are statistically significant at
an approximate 5% level when the notches do not overlap. Data are
plotted without log transformation.

258 FIGURE 4. Comparison of the allometric relationship between the weight
260 of spleen, pyloric caeca, heart, and liver with body weight. The
262 regression lines have been fit to all the data. The steelhead heart and
264 the chum spleen are substantially smaller than expected relative to
body size. Symbols: Chum (◆); Chinook (●); Coho (▲); Pink (■);
Sockeye (X); Steelhead (+).

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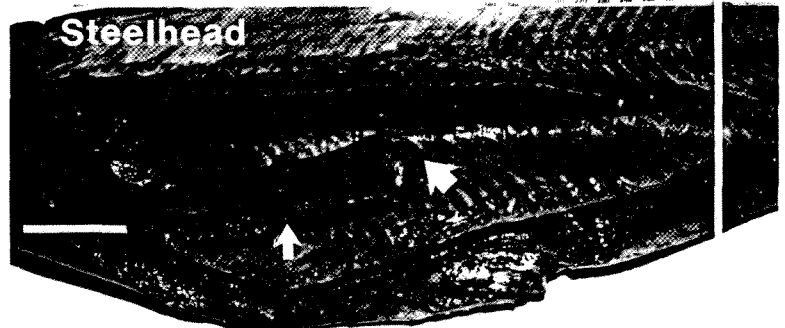
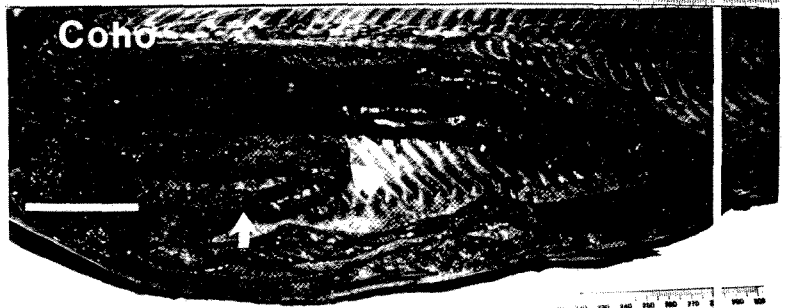
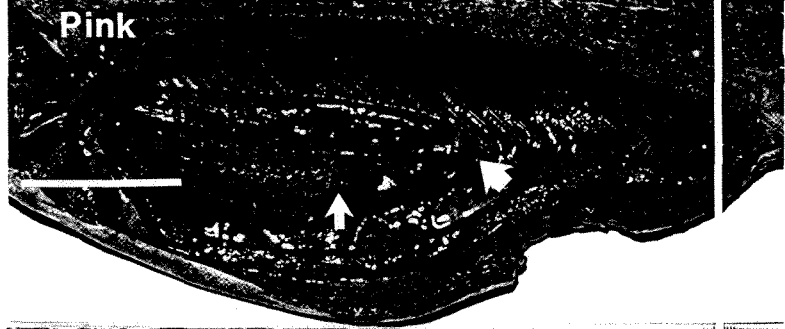
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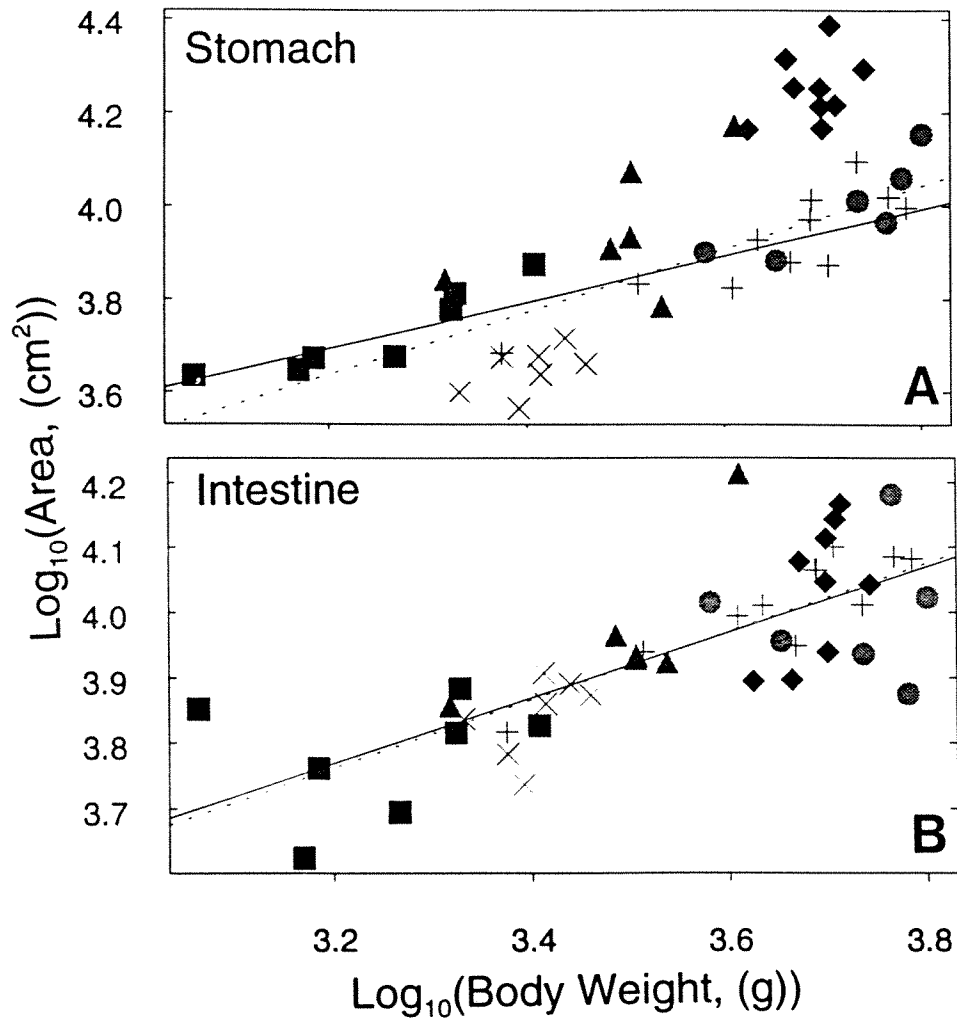
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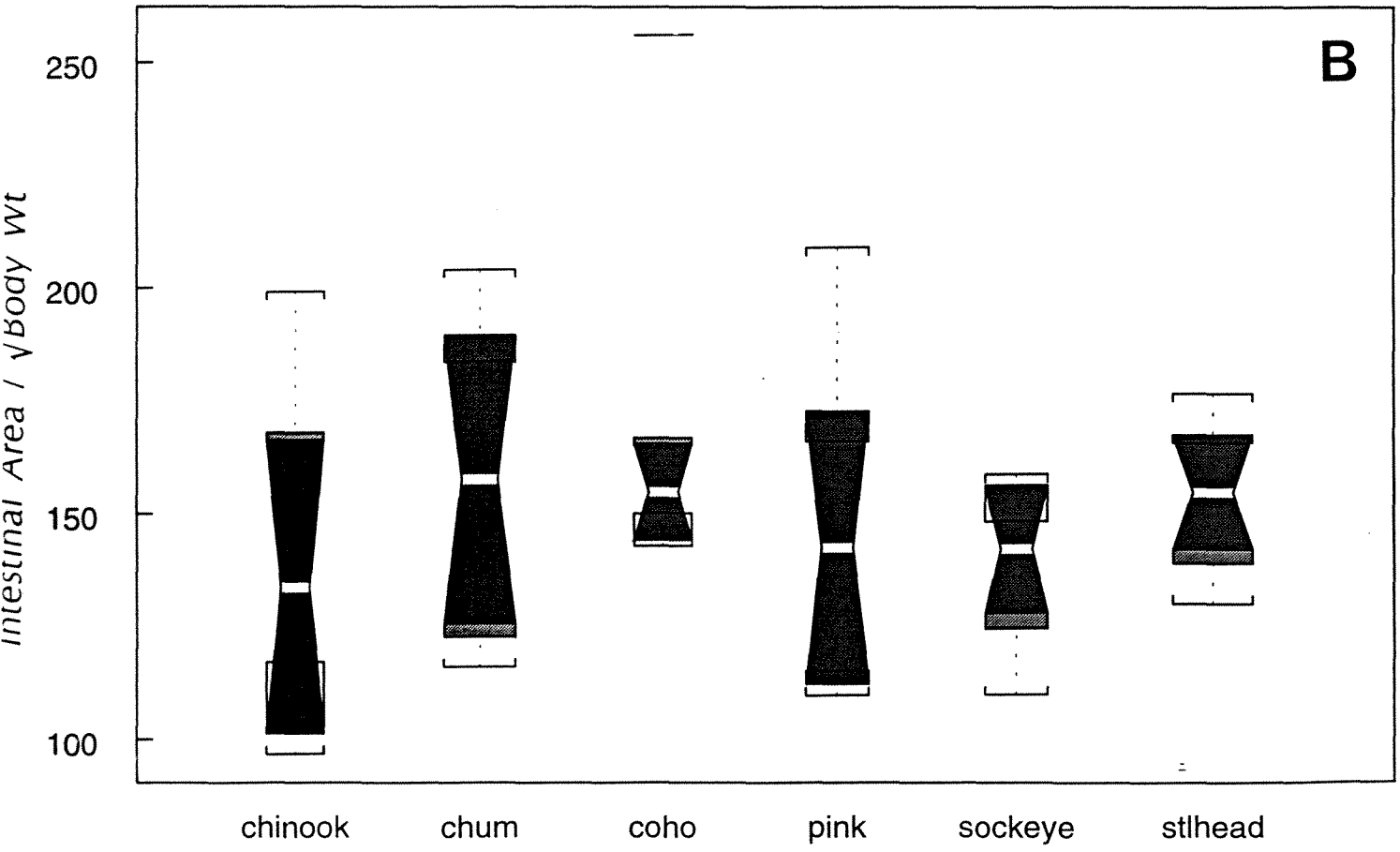
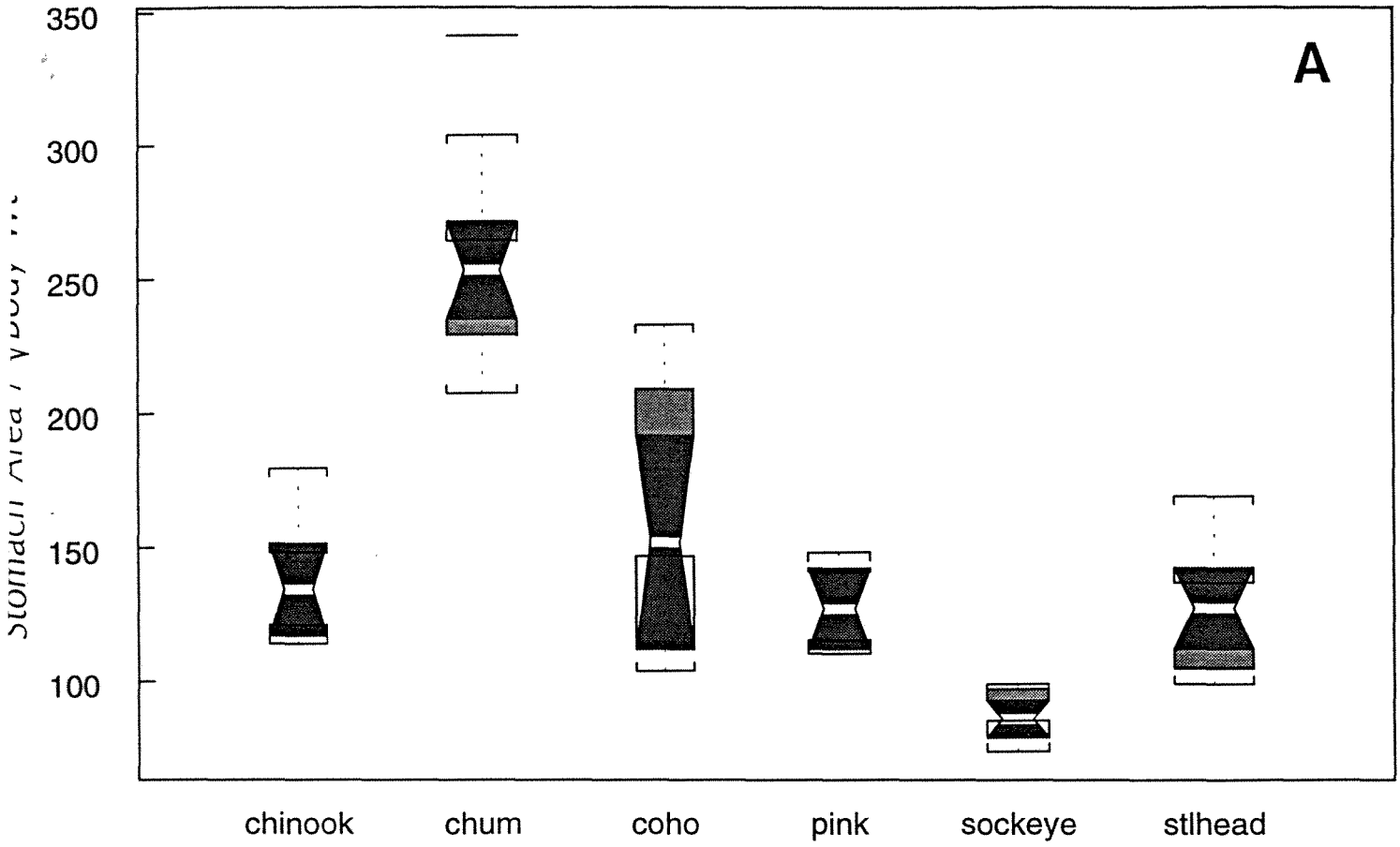
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welch fig. 1



Welch Fig 2



WELCH Fig 3

