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

by

D.W. Welch

Department of Fisheries and Oceans, Biological Sciences Branch  
Pacific Biological Station, Nanaimo, B.C. V9R 5K6  
CANADA

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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  $\pm 100$  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  
1mm<sup>2</sup> 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  
area. During autopsy, partial records were also kept of the weight of the  
94 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  
the chum spleen are substantially smaller than expected relative to  
264 body size. Symbols: Chum (◆); Chinook (●); Coho (▲); Pink (■);  
Sockeye (X); Steelhead (+).

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## REFERENCES

268

Arai, M.N. 1988. Interactions of fish and pelagic coelenterates. *Can. J. Zool.* 66, 1913-1927.

270

Azuma, T. 1992. Diel feeding habits of sockeye and chum salmon in the Bering Sea during summer. *Nippon Suisan Gakkaishi* 58:2019-2025.

272

274

Beamish, R.J. 1993. Climate and exceptional fish production off the west coast of North America. *Can. J. Fish. Aquat. Sci.* 50, 2270-2291.

276

278

Bigler, B.S., D.W. Welch, and J.H. Helle. 1996. A review of size trends among North Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* 53:455-465.

280

282

Brodeur, R.D. 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the north Pacific. INPFC Doc. No. 3557. Available from the Fish. Res. Inst., Univ. of Washington, Seattle, USA., FRI-UW-9016. 38 p.

284

286

Davis, N.D. 1993. Caloric content of oceanic zooplankton and fishes for studies of salmonid food habits and their ecologically related species. *N. Pac. Anad. Fish. Comm. Doc. No.* 15, 10 p.

288

290

Dykstra, C.R., and W.H. Karasov. 1992. Changes in gut structure and function of house wrens (*Troglodytes aedon*) in response to increased energy demands. *Phys. Zool.* 65:422-442.

292

294

Greene, C.W. 1912. Anatomy and histology of the alimentary tract of the king salmon. *Bureau Fish. Bull.* 32:75-101.

296

298

Gregory, W.K., and H.C. Raven. 1934. Notes on the anatomy and relationships of the ocean sunfish (*Mola mola*). *Copeia* 4:145-151.

300

Gross, J.E., Z. Wang, and B.A. Wunder. 1985. Effects of food quality and energy needs: changes in gut morphology and capacity of *Microtus ochrogaster*. *J. Mammal.* 66:661-667.

302

304

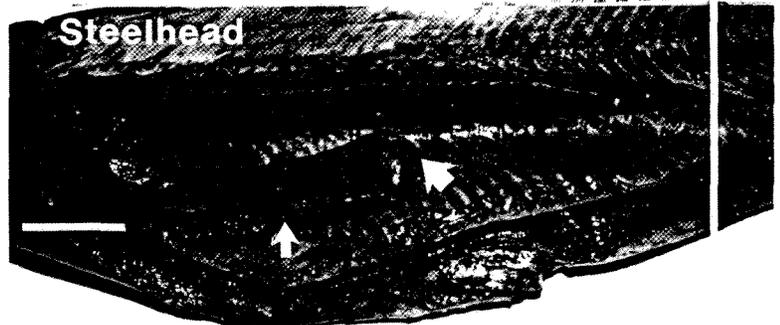
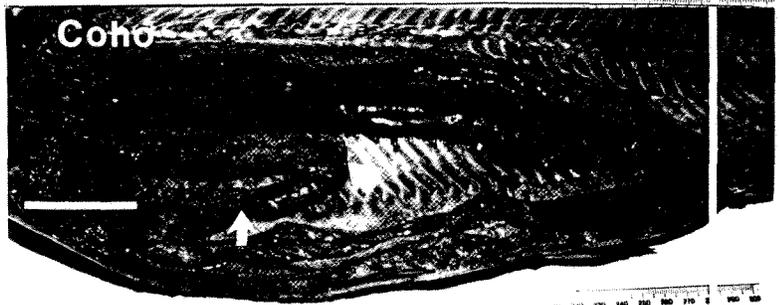
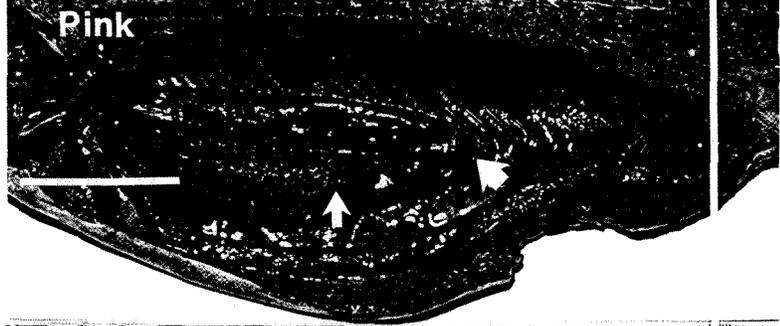
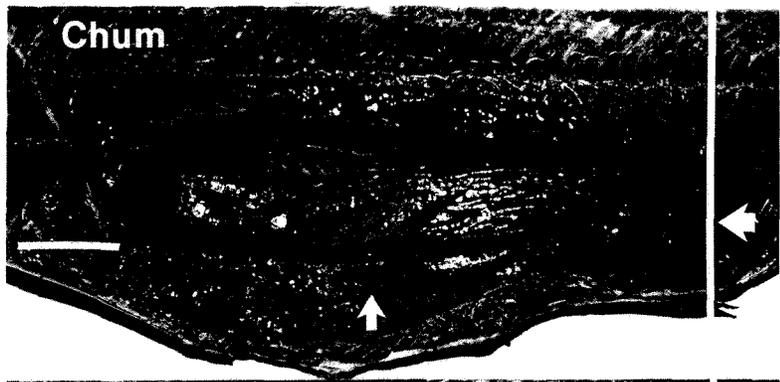
Hare, S.R., and R.C. Francis. 1995. Climate change and salmon production in the northeastern Pacific ocean, p. 357-372. *In* R.J. Beamish [ed.] *Climate Change and Northern Fish Populations.* *Can. Spec. J. Fish. Aquat. Sci.* 121

306

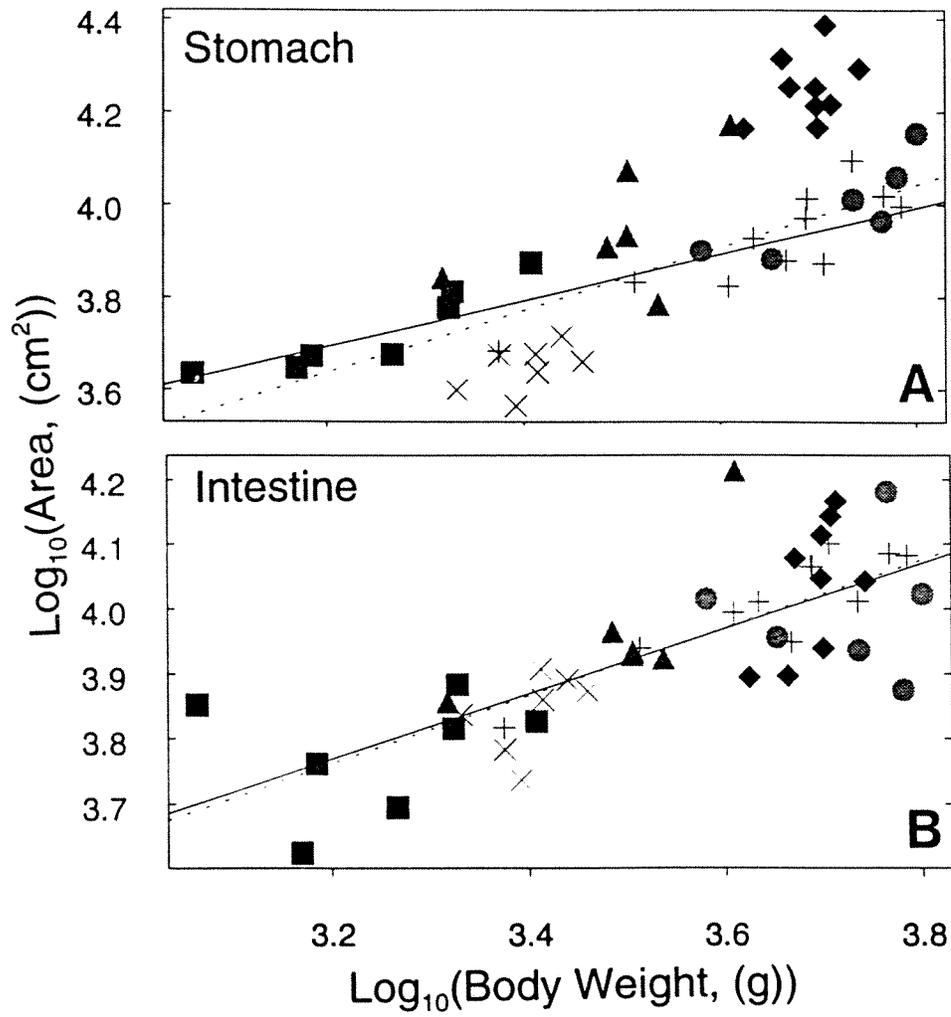
308

- 310 Ishida, Y., N.D. Davis, and K. Tadokoro. 1991. Cooperative Japan-U.S.  
high seas salmonid research in 1991: summary of research aboard the  
312 Japanese research vessel Wakatake Maru, 4 June to 23 July. Int. N.  
Pacific Fisheries Commission Document No. 3669, 35p.
- 314 Ishida, Y., S. Ito, M. Kaeriyama, S. McKinnell, and K. Nagasawa. 1993.  
Recent changes in age and size of chum salmon (*Oncorhynchus keta*) in  
316 the north Pacific Ocean and possible causes. Can. J. Fish. Aquat. Sci.  
50:290-295.
- 318 Jackson, S., D.C. Duffy, and J.F.G. Jenkins. 1987. Gastric digestion in  
320 marine vertebrate predators: in vitro standards. Funct. Ecol. 1:287-  
291.
- 322 Kaeriyama, M. 1989. Aspects of salmon ranching in Japan. Physiol. Ecol.  
324 Japan 1:625-638.
- 326 Larson, R.J., and G.R. Harbison. 1989. Source and fate of lipids in polar  
gelatinous zooplankton. Arctic 42:339-346.
- 328 Montgomery, W.L. 1977. Diet and gut morphology in fishes, with special  
330 reference to the monkeyface prickleback, *Cebidichthys violaceus*  
(Stichaeidae: Blennioidei). Copeia 1977:178-182.
- 332 Nagasawa, K., A. Shiimoto, K. Tadokoro; and Y. Ishida. 1995. Latitudinal  
334 variations in distribution and abundance of plankton and salmonids in  
the northern Pacific ocean and Bering sea in early summer. N. Pac.  
336 Anadr. Fish. Comm. Doc. 139, 16 p.
- 338 Percy, W.G. 1992. Ocean Ecology of North Pacific Salmonids. Univ. of  
Washington Press, Seattle, Wash. 179 p.
- 340 Percy, W.G., R.D. Brodeur, J.M. Shenker, W.W. Smoker, and Y. Endo.  
342 1988. Food habits of Pacific salmon and steelhead trout, midwater  
trawl catches and oceanographic conditions in the Gulf of Alaska,  
344 1980-1985. Bull. Ocean Res. Inst. 26(II), 29-78.
- 346 PICES 1996. Report of the PICES-GLOBEC International Program on  
Climate Change and Carrying Capacity", PICES Sci. Rep. No. 4 N.  
348 Pac. Mar. Sci. Org. Sidney, B.C., Canada.
- 350 Ricker, W.E. 1995. Trends in the average size of Pacific salmon in Canadian  
catches, 593-602. In R.J. Beamish [ed.] Climate Change and Northern  
352 Fish Populations. Can. Spec. J. Fish. Aquat. Sci. 121.

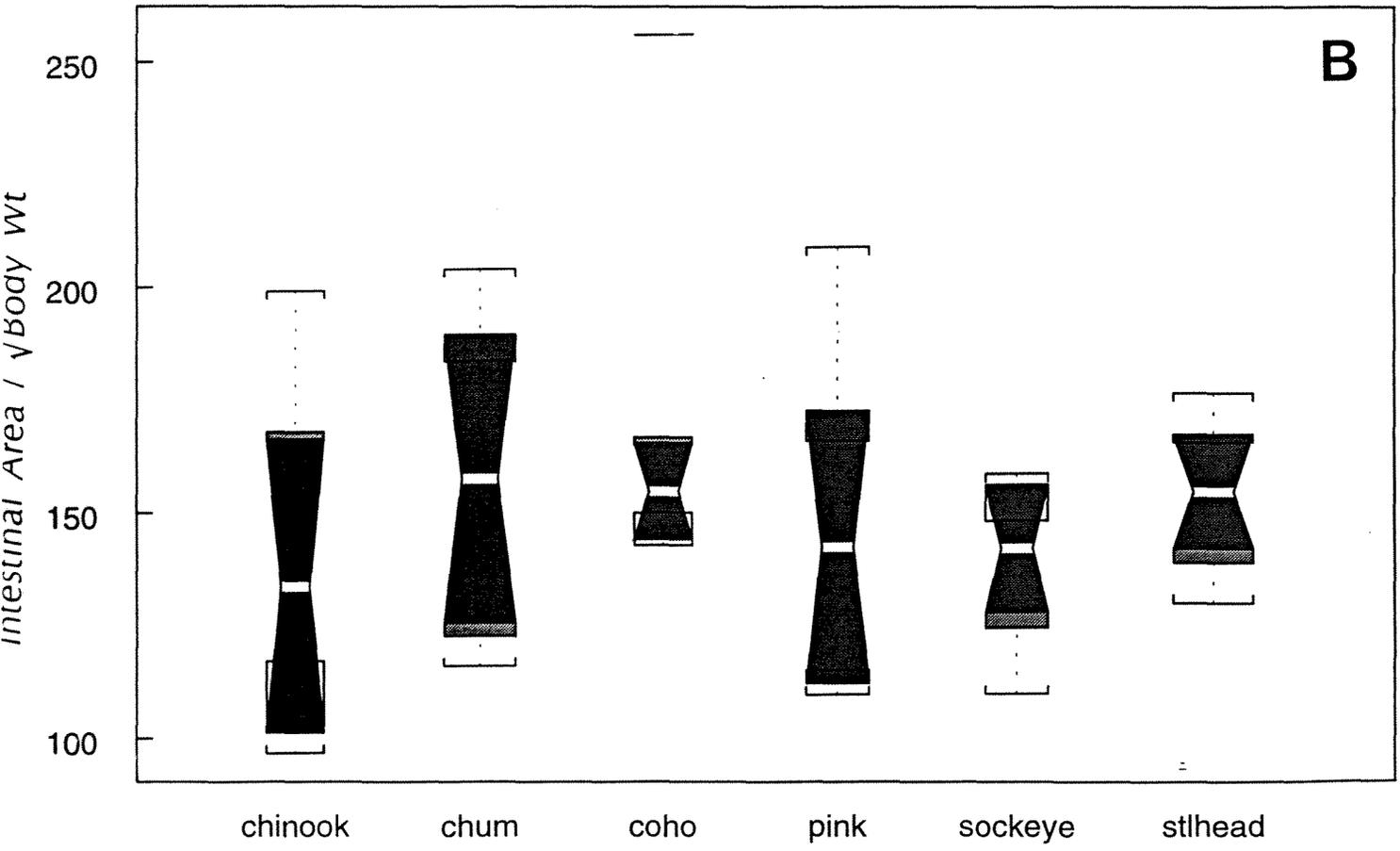
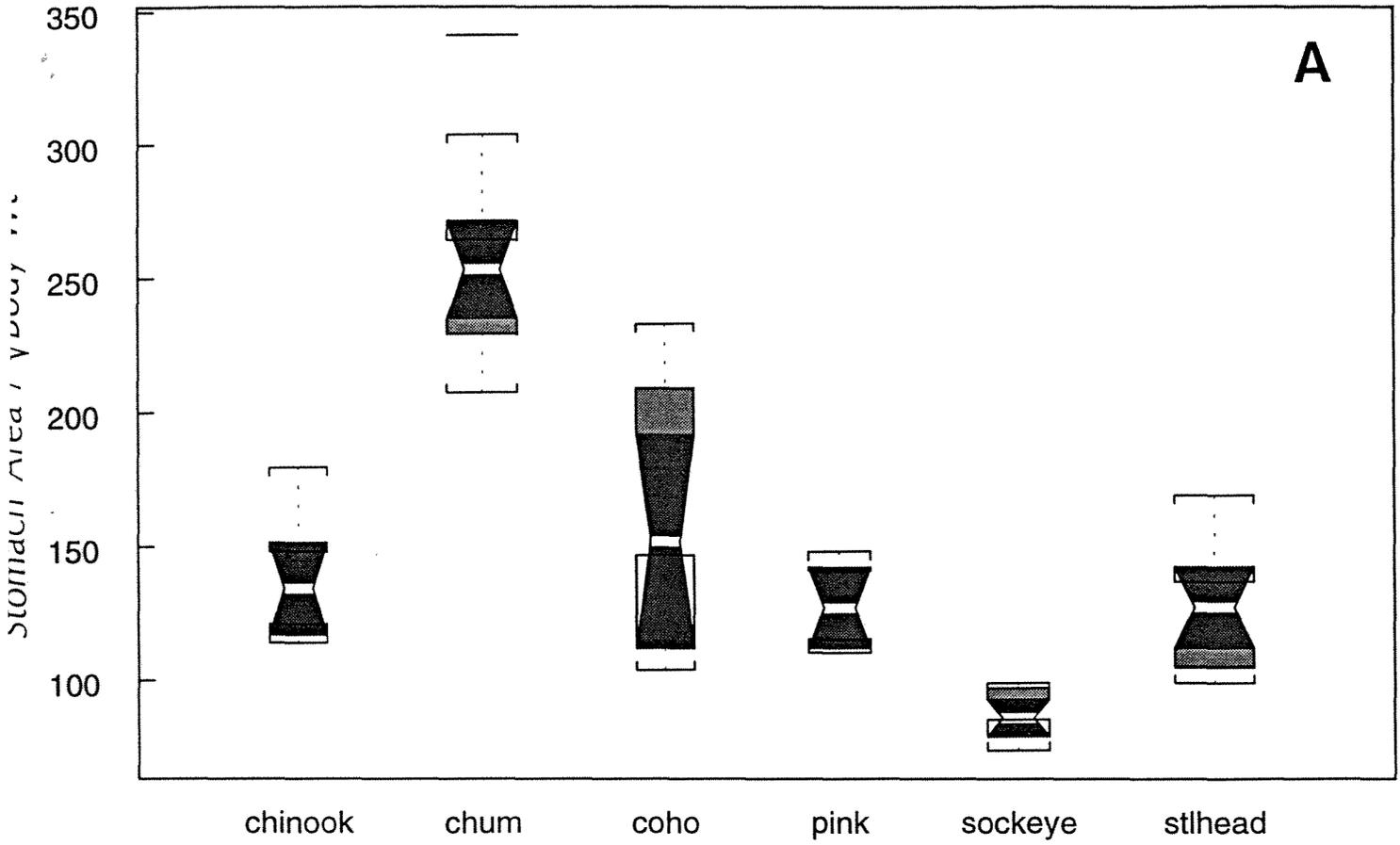
- 354 Savory, C.J., And M.J. Gentle. 1976. Changes in food intake and gut size in  
Japanese quail in response to manipulation of dietary fiber content. Br.  
356 Poult. Sci. 17:571-580.
- 358 Suyehiro, Y. 1942. A study on the digestive system and feeding habits of  
fish. Jap. J. Zool. 10:1-303.
- 360 Vispo, C., and I.D. Hume. 1995. The digestive tract and digestive function  
362 in the North American porcupine and beaver. Can. J. Zool. 73:967-  
974.
- 364 Yasutake, W.T., and J.H. Wales. 1983. Microscopic anatomy of salmonids:  
an atlas. U.S. Fish. Wild. Serv. Res. Pub. 50. 189 p.
- 366 Stearley, R.F., and G.R. Smith. 1993. Phylogeny of the Pacific trouts and  
368 salmon (*Oncorhynchus*) and genera of the family salmonidae. Trans.  
Am. Fish. Soc. 122:1-33.
- 370 Tadokoro, K., Y. Ishida, N.D. Davis, S. Ueyanagi, and T. Sugimoto. 1996.  
372 Change in chum salmon (*Oncorhynchus keta*) stomach contents  
374 associated with fluctuation of pink salmon (*O. gorbusha*) abundance  
in the central subarctic Pacific and Bering Sea. Fisheries Oceanography  
5:89-99.



welch fig. 1



Welch Fig 2



WELCH Fig 3

