

Effects of Rowing on Humeral Strength

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ABSTRACT This study used an aggregate measure of robusticity (based on humeral areal and inertial cross-sectional components) to test the hypothesis that rowing on oceans led to more robust humeri than did rowing on rivers or not rowing at all. Results confirmed the hypothesis that male ocean-rowers had more robust humeri than did male river-rowers or nonrowers. However, although the females from the ocean-rowing populations did not row, they averaged more robust humeri than did females from the non-ocean-rowing populations. Males averaged

greater robusticity than did females. The robusticity of ocean-rowing populations, therefore, does not seem to be due solely to bone remodeling resulting from strenuous rowing. Humeral robusticity is difficult to attribute to specific activities because, in humans, upper limbs are utilized for many activities. Some populations may have more robust humeri because certain environments require greater overall activity levels in order to survive. *Am J Phys Anthropol* 121:293–302, 2003. © 2003 Wiley-Liss, Inc.

Cross-sectional morphology has become an important way to reconstruct the past. Anthropologists have used limb-bone cross sections to examine the effects of division of labor, shifts in subsistence patterns, aging, and physical environments (Bridges et al., 2000; Feik et al., 1996; Ruff, 2000a; Ruff and Hayes, 1983; Stock and Pfeiffer, 2001). Ruff (2000a), for example, compared six Amerind populations (three nonagricultural and three agricultural populations; $N = 268$) occupying three different environments. Two of the populations (one nonagricultural and one agricultural) inhabited a flat region in the South Dakota Plains; two populations (one nonagricultural and one agricultural) lived in a coastal region of Georgia; and two populations (one nonagricultural and one agricultural) occupied mountainous regions in the Northern Great Basin and New Mexico. Ruff (2000a) found that Amerinds who walked on mountainous terrain had more robust femora than those who walked on flat terrain.

In another study, Stock and Pfeiffer (2001) linked differences in upper-limb vs. lower-limb cross-sectional strengths to activity patterns. Stock and Pfeiffer (2001) studied long-bone cross-sections, standardized by size, of 65 Later Stone Age (11000–2000 BP) African individuals and 36 19th century Andaman Islanders in order to determine whether their different subsistence practices led to emphasis of strength in different limbs. The Africans were highly mobile land foragers, whereas the Andaman Islanders, who were not very mobile on land, were highly mobile on water, i.e., swimming and using canoes for hunting and fishing. Stock and Pfeiffer (2001) found that the African population had strong lower limbs and relatively weak upper limbs, whereas the Andaman Islanders had relatively

weak lower limbs and very strong upper limbs, differences that the authors attributed to bone remodeling resulting from activity patterns.

Churchill (1994) examined upper-limb robusticity cross sections and body shape of modern and archaic humans. He concluded that the high upper-limb robusticity in some modern populations, such as the Aleut, likely reflects the strenuous activities engaged in that caused bone remodeling and adaptation to geographical locations overlain atop of a basic *Homo sapiens* upper-body plan. Laughlin et al. (1991) also examined Aleut humeral robusticity, and stated that the demands of hunting marine animals and kayaking on the open ocean were responsible for a high level of robusticity in Aleuts.

The present study attempts to determine whether one can discern the effects of rowing per se on upper-limb bone strength by comparing humeral cross-sections in a number of different population samples, including nonrowers, river rowers, and ocean-rowers. It is clear that terrain should have less effect on upper limbs as opposed to lower limbs, since human upper limbs have been freed from locomotion as a result of bipedalism. However, water is also part of the terrain, and many Amerind populations used their upper limbs to propel water vehicles on oceans, rivers, and lakes. Amerinds invented a va-

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TABLE 1. Sample size

Region	Subsistence	Water	Vehicle	Males	Females	Total
British Columbia	Fishing/hunting/gathering	Ocean/river	Canoe	41	23	64
Alaskan Aleut	Fishing/hunting/gathering	Ocean	Kayak	23	21	44
Georgia	Fishing/hunting/gathering	River/marshes	Tule reed	8	7	15
Georgia	Agricultural	River/marshes	Tule reed	31	30	61
New Mexico	Agricultural	Land	None	48	51	99
Euroamerican prisoners	Industrial	Land	None	25	2	27
Euroamericans	Industrial	Land	None	27	21	48
Total				203	155	358

riety of different boats: canoes, umiaks, kayaks, rafts, bullboats, and tule balsas have all been found in the archaeological record and at the time of European contact (Heizer and Mills, 1953; Miles, 1963). The purpose of this study is to determine whether variation in rowing behavior affects humeral cross sections to the same degree as variation in land terrain appears to affect lower limbs.

To test this hypothesis, I compared humeral cross sections in seven population samples. Ocean-rowers were predicted to have significantly stronger humeral cross sections than river-rowers or nonrowers, because ocean-rowers had to traverse more strenuous systems of water than river-rowers. Rowing on oceans is mainly a male activity pattern (e.g., Halpin and Seguin, 1990; Hrdlicka, 1945; Hudson, 1976), so analyzing the sex differences in arm-bone robusticity will also provide a partial control.

MATERIALS AND METHODS

Samples

A skeletal sample of 358 individuals from seven populations was used in this study (Table 1). All individuals were previously sexed and aged (Churchill, 1994; Cybulski, 1988, 1990, 1992; Ruff and Larsen, 1990). Each population's subsistence pattern, type of water traveled on, and mode of water transportation were determined from the existing literature (Weiss, 2001).

The samples examined consisted of British Columbian Amerinds, Alaskan Aleuts, and Georgia coast nonagricultural and agricultural Amerinds, all of whom were identified in the ethnographic literature as having used their arms for rowing on water so as to hunt, fish, trade, and travel (Hudson, 1976; Miles, 1963; Underhill, 1944). Also examined were cross sections from three nonrowing populations (New Mexico agricultural Amerinds, Euroamerican prisoners of war, and Euroamerican industrialists). The seven groups varied in body size and shape, so these will be compared using standardizations for body size. They employed a variety of subsistence patterns, so these will be controlled with a subanalysis that includes only nonagricultural populations. Although the groups are not homogeneous with regard to geography, subsistence, and material technology, their similarities in age and sex distribution should minimize many sources of variation in skeletal robustness.

For the ocean-rowing group, two populations were used: British Columbian Amerinds and Alaskan Aleuts. The British Columbian sample comes from seven prehistoric archaeological coastal sites located on British Columbia's northwest coast, 50 km south of the Alaska Panhandle, dating from 3500–1500 BP (Cybulski, 1992; MacDonald and Inglis, 1975, 1981). What is known about British Columbian Amerind subsistence behavior is derived from the archaeological record and ethnographic data of similar protohistoric and historic populations (Boas, 1890; Brown, 1977; Cybulski, 1990, 1994). Although the temporal range of skeletal material spans approximately 2,000 years, this time period is characterized by general cultural homogeneity (MacDonald and Inglis, 1975).

The British Columbian Amerinds (mainly males) fished for salmon, trout, pike, sturgeon, and urchins in rivers and the sea (Fradmark et al., 1990). Hunting (also done mainly by males) consisted of individuals using bows and arrows for small marine mammals, such as otters and baby seals, while groups formed to hunt larger marine mammals, such as whales, using several canoes (Drucker, 1955). After a whale was killed, the hunters would tow it back to land where females helped carve it up. The Amerinds of British Columbia also canoed inland up natural channels and rivers to hunt and trap elk, deer, marmot, fox, mink, and many other animals for food and furs. At their home base they either gave the animals to the females to prepare for food or clothing, or took the animals to neighboring communities for trade (Brown, 1977). Female British Columbians also gathered berries, crabapples, tubers, and other starchy roots throughout the year to supplement their diets. Nearly all travel was done by canoes, which were carved, owned, and operated by males. Walking in the bush was not popular because it was difficult and time-consuming, especially during winter (Halpin and Seguin, 1990). Females were comparatively sedentary (Drucker, 1955).

The Aleut skeletal sample is derived from three protohistoric sites on the western Aleutian Islands of Kagamil, Shiprock, and Umnak on the southwestern Alaskan coast dating from 1600 AD and 1800 AD (Churchill, 1994; Hubbard, 1935). Much of what is known about the Aleuts comes from archaeological data and ethnographic accounts (Coxe, 1803; Hrdlicka, 1945; Hubbard, 1935). The Pacific Ocean

off the Alaskan coast is particularly harsh due to contrasting ocean currents and sea ice. Nevertheless, male Aleuts traveled by kayak on the sea to hunt marine mammals, such as walruses, whales, sea lions, harbor seals, and porpoises (Coxe, 1803; Hrdlicka, 1945; Oliver, 1988). Also in abundance were halibut, herring, cod, crab, salmon, and shrimp. In order to hunt, Aleut males used *atlatl*, which were long, narrow boards with one end carved to fit the hand and the other fitted with a small peg to hold the butt of spear shafts (Osborn, 1990). Males also caught birds in flight with *bolos*, which consist of about four 1-m-long strings tied together at one end with small stones attached as weights at the free end (Osborn, 1990). Female Aleuts collected clams and other mollusks (Oliver, 1988). In addition, females gathered kelp and other seaweed, berries, and roots to eat (Osborn, 1990). The females spent much of their time producing materials, such as clothing from furs and basketry from bark (Hrdlicka, 1945).

The river-rowing populations used were Georgia coast Amerinds who derive from archaeological sites spanning over 4,000 years located on the Atlantic coastal plain and the adjoining Gulf coastal plain (Saunders, 2000). The nonagricultural Amerinds, dating between 4000–400 BP, were related to the agricultural Amerinds, dating between 800–400 BP. The differences between the early and later populations appear mainly to be a result of the shift in subsistence pattern from fishing, hunting, and gathering to maize agriculture with fishing and hunting supplements. The changeover to agriculture was related to a decrease in stature and size (Larsen, 1982; Ruff and Larsen, 1990). On the other hand, the agricultural population had less osteoarthritis and lived longer than nonagricultural groups (Larsen, 1982; Ruff and Larsen, 1990). The shift in subsistence pattern affected males more than females (Ruff and Larsen, 1990). For these reasons, subsidiary analyses were conducted, which excluded the agricultural populations.

Many rivers provided the Georgia Amerindians with fish, such as channel bass, spotted weakfish, trout, and catfish (Larsen, 1982; Jones, 1978). Vast salt marshes and freshwater swamps in the coastal areas also provided a habitat for animal life (Larsen, 1982). Archaeological evidence suggests that both the nonagriculturalists and agriculturalists traveled on water, but the nonagriculturalists did so to a greater extent. The nonagriculturalists traveled daily for food and resources, some of these travels being made throughout the year on water (Hudson, 1976). The agriculturalists moved less frequently, but they did travel the waterways to supplement their diet, and every few years they moved to find fresh soil to farm (Saunders, 2000). The males of both groups of Georgia Amerinds exploited marine resources by fishing and catching shrimp and crabs (Braley et al., 1986; Larsen, 1982). Also, both groups hunted raccoons, birds, and rabbits (Braley et al.,

1986; Saunders, 2000). The nonagricultural Georgia coast females gathered shellfish and vegetation, and prepared the foods (Hudson, 1976; Saunders, 2000). Some of the staple plant food consisted of acorns and hickory nuts, which would be ground to make porridge or bread (Larsen, 1982; Saunders, 2000). Most of the farm work was done by females; this consisted mainly of growing maize (Saunders, 2000).

Three nonrowing populations were used: New Mexican agricultural Amerinds, who mainly traveled on foot; and two Euroamerican samples. The Amerinds were from Pueblo sites in New Mexico and Texas dated between 1250–1600 BP (Churchill, 1994). There are some river-bottom and some upland, nonriver, areas. The Pueblo settlements were permanent, and a village was home to about 300 individuals; however, males, who moved over large resource areas, hunted bison, turkey, and deer (Cordell, 1989). The females provided the majority of the food through maize agriculture and some gathering (Schroeder, 1983). The Pueblo females also raised beans, greens, and squash (Cordell, 1989; Castaño de Sosa, 1965; Schroeder, 1983).

The first of the two Euroamerican samples were English prisoners of war who had died in captivity as prisoners of the French in Quebec, Canada, in the Battle of Quebec during the French Indian Wars (1689–1763). Cybulski (1988) determined that their burials occurred sometime between 1745–1748 AD. The prisoners' early environment (i.e., prior to imprisonment) was probably less harsh than the one they endured in their final years. Most of the men had severe arthritis, disc ruptures, and fractures of their skull, limbs, and back due to hard labor and fights (Cybulski, 1988; Piedalue and Cybulski, 1997). Many of the prisoners had died of fever, consumption, dysentery, and scurvy (Piedalue and Cybulski, 1997). The prison population ate daily rations of bread, beef, peas, and water (Piedalue and Cybulski, 1997).

The other Euroamerican sample was collected from cadavers taken from morgues in the Central Rio Grande region of New Mexico and Missouri. These individuals had lived in urban to semiurban environments from the late 1800s to the mid-1900s (Churchill, 1994). Their occupations ranged from laborers to those who led more sedentary lives, such as academics (Churchill, 1994).

In summary, Alaskan Aleuts and British Columbian Amerinds paddled on the open ocean (Churchill, 1994; Drucker, 1955; Hrdlicka, 1945). Georgia nonagricultural and agricultural Amerinds paddled mainly on rivers (Hudson, 1976). Thus, it was predicted that the British Columbian and Alaskan Aleut populations would have the most robust humeri, the two sets of Georgia Amerind populations would have intermediately robust humeri, and both the New Mexico agricultural population and the two Euroamerican populations would have the weakest humeri. Because upper limbs are used in many human activ-

ities, including food preparation, hunting, and making artifacts, the effect of rowing has to be sufficiently strong to overcome the effects of these other sources of variance.

Cross-sectional measurements

For 2 of the 7 populations (British Columbian Amerinds and Euroamerican prisoners of war), humeri were radiographed at the Canadian Museum of Civilization in Hull, Quebec, to obtain cross-sectional data. Following Ruff and Larsen (1990), humeral lengths were used to mark the 35% of bone length location (in which 100% is the proximal end) where cross-sectional geometries were calculated. Humeri were arranged on the film in anteroposterior orientation (i.e., the anterior side of the bone faces upward and is x-rayed); then, they were arranged on it in mediolateral orientation (i.e., the medial side of the bone faces upward and is x-rayed). Whenever possible, both left and right humeri were radiographed. Magnification errors were removed using the formula:

$$\text{Source to film distance}/(\text{source to film distance} \\ - \text{object center to film distance}).$$

Each radiographed humerus was measured for inner and outer diameters, and the values were used to calculate the derived values: total cross-sectional area (TA), cortical cross-sectional area (CA), moment of inertia about the mediolateral plane (*I_{ml}*), moment of inertia about the anteroposterior plane (*I_{ap}*), and polar moment of inertia (*J*). Total area (TA) was calculated with the formula:

$$\text{TA} = \prod \times (\text{ML outer diameter} \\ \times \text{AP outer diameter}/4)$$

Medullary area (MA) was calculated with the formula:

$$\text{MA} = \prod \times (\text{ML inner diameter} \\ \times \text{AP inner diameter}/4)$$

Then the cortical area (CA) was calculated by subtracting the medullary area from the total area (CA=TA-MA) (Biknevicius and Ruff, 1992).

The formulas used for calculating moment of inertia about the mediolateral plane (*I_{ml}*) and moment of inertia about the anteroposterior plane (*I_{ap}*) were:

$$I_{ml} = \prod/64 \times (T_{ml} \times T_{ap}^3 - M_{ml} \times M_{ap}^3)$$

$$I_{ap} = \prod/64 \times (T_{ap} \times T_{ml}^3 - M_{ap} \times M_{ml}^3)$$

where *T_{ml}* = total mediolateral breadth; *T_{ap}* = total anteroposterior breadth; *M_{ml}* = medullary mediolateral breadth; and *M_{ap}* = medullary anteroposterior breadth (Biknevicius and Ruff, 1992).

Finally, polar moment of area (*J*) was calculated using the formula:

$$J = I_{ml} + I_{ap}$$

Cortical area value (CA) reflects compressive strength. Total area value (TA) provides information on relative distribution of bone within cross sections. Inertial values (*I_{ml}*, *I_{ap}*, and *J*) reflect bending and torsional strength.

Ruff and Larsen (1990) and Churchill (1994) provided raw data for the remaining five samples. Before the data collected at the Canadian Museum of Civilization could be compared to the other samples, data on unsexed, immature, or pathological individuals were removed, necessary conversions (such as from centimeters to millimeters) were made, and additional values were calculated from raw data (such as polar moment of inertia). The dependent variables (total area, cortical area, moments of inertia about the anteroposterior and mediolateral planes, and polar moment of inertia) were taken on both the right and the left humeri for all but the two Georgia populations, which had already been side-averaged by Ruff and Larsen (1990). Pearson correlations between the various cross-sectional properties for the left and the right arm bones ranged from 0.88–0.97 (mean *r* = 0.93, *P* < 0.01). The remaining data were made comparable to the Georgia populations by side-averaging following the procedure of Ruff and Larsen (1990): 1) Percentage differences between the right and the left sides were calculated using the formula [right – left/right]; 2) humeral properties were adjusted by this factor depending on the direction of asymmetry, and whether the bone was from the left or right side; and 3) sex and population means were substituted for missing data. Then following Ruff et al. (1993), the side-averaged data were standardized for differences in body size by dividing by powers of bone length: areal measures (CA and TA) were standardized by dividing the result by humeral length cubed (HL³), and then multiplying it by 10⁸; moments of inertia and polar moments of inertia (*I* and *J*) were standardized by dividing the result by HL^{5.33} and then multiplying it by 10¹².

An aggregate robusticity variable was constructed by averaging the *z*-scores for log-transformed total area, cortical area, moment of inertia about the anteroposterior axis, moment of inertia about the mediolateral axis, and polar moment of inertia (all of which were taken at 35% of bone length, side-averaged, and standardized by humeral length). An aggregate measure was used because aggregation reduces error variance and increases reliability and predictive validity (Rushton et al., 1983). The sum of a group of multiple measures is a more stable and unbiased estimate than any one measure from the group. Any one measure always has error associated with it. When several measures are combined, errors tend to average out, leading to a more accurate picture of the relationships being tested.

Although the main study data were corrected for body size using humeral length, probable differences in body shape among populations make this method of standardizing less than perfect. For example, it is

well-documented that Aleuts have relatively wide bodies and short limbs (Laughlin, 1951; Churchill, 1994; Ruff, 1994). Using humeral length to standardize for body size leads to underadjustments for populations with relatively shorter limbs, and thus overestimates robusticity in such populations relative to longer-limbed populations (Ruff, 2000b). This problem can be circumvented by estimating actual body masses using skeletal measures that incorporate body shape, e.g., femoral head size or bi-iliac (pelvic) breadth and stature (Ruff et al., 1997). Unfortunately, it was not possible to obtain individually associated measurements of this kind for most of the samples included here. However, to provide some additional information on the possible effects of body shape on the analyses, sex-specific mean body masses for these samples were derived using either mean femoral head breadths or actual body masses obtained from the literature for appropriately matched reference samples, which were then used to standardize mean cross-sectional properties for each property, as described below. No statistical analyses of these data are possible, but results are shown in graphic form for comparison with the main study results.

For the British Columbian sample and the Euroamerican prisoners of war, individual femoral head breadths for the same individuals included in the present study were obtained from Cybulski (2002, personal communication). For the Georgia nonagriculturalists and agriculturalists, sex-specific average femoral head breadths were obtained from the summary data of Larsen (1982) for similar population samples from the Georgia coast. Following Ruff et al. (1991), body mass was calculated using the following formulae:

males: body mass = 2.741

× femoral head breadth – 54.9

females: body mass = 2.426

× femoral head breadth – 35.1

For the Aleut sample, sex-specific mean body masses for western Aleuts were obtained from Laughlin (1951). Using the humeral formulae by Trotter and Gleser (1952) for US whites, average statures for Aleuts in the present study are 160.00 cm (males) and 150.00 cm (females), which are similar to the average heights in the sample from Laughlin (1951) (males = 163.54 cm; females = 152.95 cm). For the Euroamerican sample from New Mexico and Missouri, sex-specific body mass data were obtained from the *Anthropometric Source Book Volume II: A Handbook of Anthropometric Data* (1979). Again using the formulae of Trotter and Gleser (1952) for humeri, the average male height for the New Mexico-Missouri Euroamerican sample used in this study is 172.00 cm; the average female height is 160.00 cm. These compare with average heights of 171.5 cm in males and 160.28 cm in females in the

body mass reference sample. For the New Mexico Amerindian sample, sex-specific average body masses were obtained from Ruff (2000b). Although these body masses were derived for a different Amerindian sample (Pecos Pueblo), both populations came from the southwestern United States, both groups were agricultural, and their average humeral lengths do not differ significantly (for the present sample and the Pecos sample, respectively, males: 303.93 cm and 302.08 cm; females: 286.00 cm and 282.90 cm).

Mean body mass and mean humeral length (for sex- and population-specific data) were then used to standardize the sex-specific and population-specific mean dependent variables. Mean areal measures (TA and CA) were divided by mean body mass; mean inertial measures (*I* and *J*) were raised to the power of 0.73 and divided by mean humeral length times mean body mass (Ruff, 2000b). The values from the 14 sex/sample means were then log-transformed and turned into standard *z*-scores. The *z*-scores from the five dependent variables (TA, CA, *I*_{ap}, *I*_{ml}, and *J*) were added together and divided by 5 to form a mean aggregate robusticity score in the same way the previous aggregate robusticity score was calculated. Finally, rowing and sex differences for the body-mass-standardized data were examined, using the mean aggregate robusticity score in two bar graphs.

Statistical analysis

Data were analyzed using the statistical software program SPSS. The aggregate robusticity measure met all the assumptions required to run parametric tests, and the relationships between the variables were linear. Means and standard deviations were calculated for aggregate robusticity. A two-factor analysis of variance (ANOVA) design was used to analyze the data. The two independent factors were physical environment and sex. The dependent variable was aggregate robusticity. Interactions between factors were also examined. Post-hoc Bonferroni tests were calculated for the ocean-rowing, river-rowing, and nonrowing populations to determine where the differences occurred, such as whether river-rowing and nonrowing populations differed from one another. A subsidiary analysis on subsistence patterns was also carried out. The critical alpha level was set at 0.05.

RESULTS

Table 2 and Figure 1 present the arithmetic means and standard errors for aggregate robusticity variables in *z*-scores for ocean-rowing, river-rowing, and nonrowing groups, separately for both males and females. Figures 2 and 3 display the arithmetic means and standard errors of the aggregate robusticity variable for each population and sex separately.

Ocean-rowing populations average more robust humeri than do river-rowing and nonrowing popu-

TABLE 2. Means and SDs for aggregate robusticity variable (z-scores) of ocean-rowing, river-rowing, and nonrowing populations, separately for males and females

Sex	Ocean-rowing		River-rowing		Nonrowing	
	Mean	SE	Mean	SE	Mean	SE
Males	0.912	0.105	-0.113	0.111	-0.193	0.098
Females	0.375	0.116	-0.767	0.139	-0.554	0.104

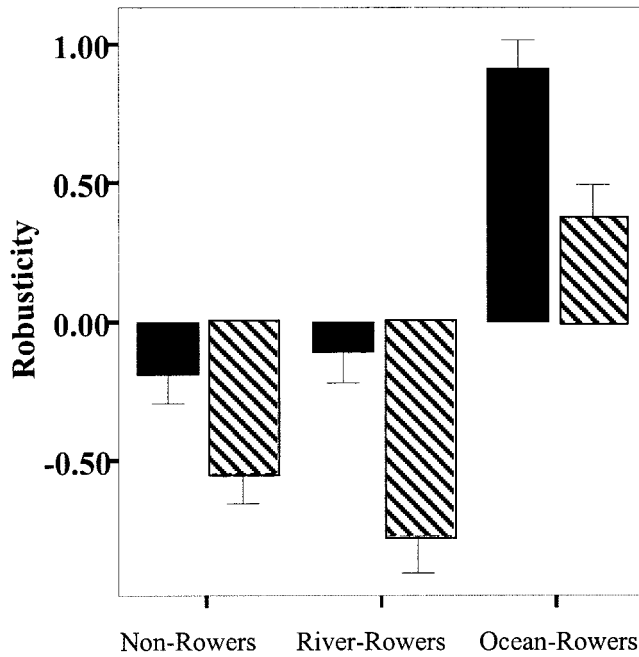


Fig. 1. Differences in aggregate robusticity (z-scores) in non-rowing, river-rowing, and ocean-rowing populations. Data standardized by humeral length. Bars show means + 1 SE. Solid bars, males; striped bars, females.

lations (Tables 3 and 4). Males average more robust humeri than do females (Tables 3 and 5).

Since subsistence pattern has been shown to affect robusticity (e.g., Bridges et al., 2000; Ruff, 1987), it is possible that the high robusticity of ocean-rowing populations could be due to their being nonagriculturalists (fisher-hunter-gatherers), who are generally more robust than agriculturalists or industrialists. A further analysis including only nonagriculturalists, however, shows that ocean-rowers are still more robust than river-rowers (no non-agricultural nonrowing population data were available) (Table 6). Thus, the robusticity of ocean-rowing populations is not due to their general type of subsistence pattern. Nonagricultural males also average more robust humeri than do nonagricultural females (Table 6).

When body mass is used instead of humeral length to size-standardize variables, the grouped results are generally similar (Fig. 4; compare with Fig. 1), although there is a more even progression from nonrowing to river-rowing to ocean-rowing groups in robusticity, particularly among females. Also, females from the ocean-rowing group are now less robust than male river-rowers and nonrowers, but

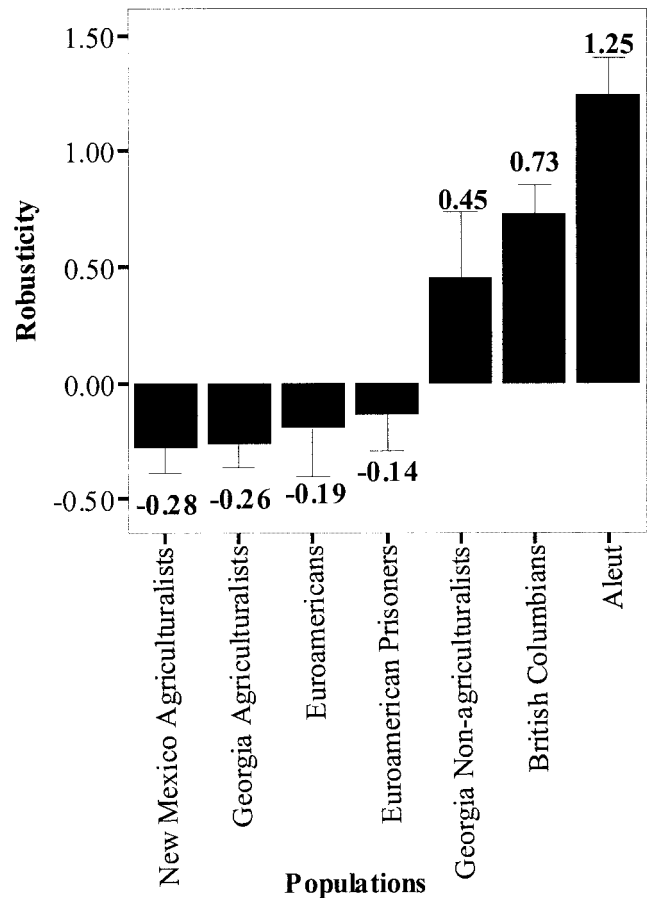


Fig. 2. Differences in aggregate robusticity (z-scores) in males, arranged from lowest to highest by population. Data standardized by humeral length. Bars show means + 1 SE.

they are still the most robust females. However, when examining data for individual populations (Fig. 5), the apparent robustness of females from ocean-rowing populations appears to be the case only for the Aleuts, and not the British Columbian sample. British Columbian females are less robust than the New Mexico agricultural females (who are more robust than their male counterparts) and comparable to the Georgia agricultural females. These differences in results will be discussed in greater detail below.

DISCUSSION

The present study attempted to determine whether one can discern the effects of rowing and type of water rowed upon on upper-limb bone strength by examining humeral cross sections. Although some recent studies questioned the effect of

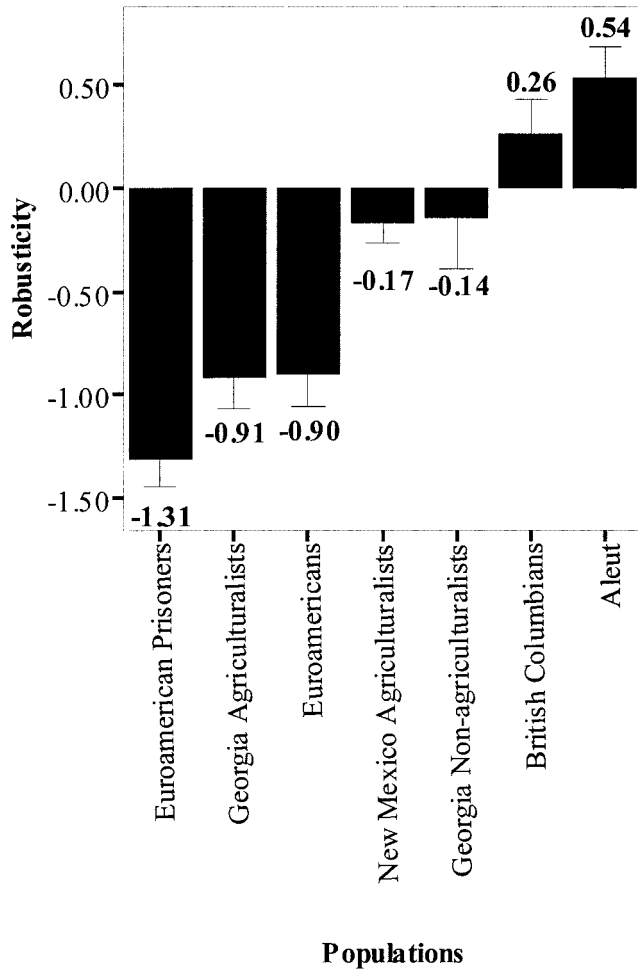


Fig. 3. Differences in aggregate robusticity (z-scores) in females, arranged from lowest to highest by population. Data standardized by humeral length. Bars show means + 1 SE.

TABLE 3. Two-factor ANOVA results for aggregate robusticity

	Source	Sum of squares	df	F
Main effects	Combined	87.659	3	49.94***
	Rowing	66.122	2	56.51***
	Sex	17.817	1	30.45***
Two-way interaction	Rowing × sex	0.985	2	0.84
Model		91.976	5	31.44***
Residual		160.889	275	
Total		252.866	280	

*** $P < 0.001$.

stresses on bones and the ability for bones to remodel to reduce stresses (e.g., Bertram and Swartz, 1991), many other studies found that stress due to activity does produce bone remodeling (e.g., Jones et al., 1977; Woo et al., 1981; Trinkaus et al., 1994 and references therein). However, the question remains as to whether one can detect the effects of a specific activity, such as rowing, on bone cross sections. The results standardized by body size using humeral length showed that: 1) ocean-rowing populations

TABLE 4. Post hoc Bonferroni results for aggregate robusticity

Source	Mean difference	Standard error
Nonrowing vs. river-rowing	0.0992	0.11990
Nonrowing vs. ocean-rowing	-1.0374***	0.11230
River-rowing vs. ocean-rowing	-1.1366***	0.12319

*** $P < 0.001$.

TABLE 5. ANOVA results for aggregate robusticity on within-population sex differences

	Source	Sum of squares	df	F
Nonrowers	Between sexes	3.363	1	5.87*
	Within sexes	61.294	107	
	Total	64.657	108	
River-rowers	Between sexes	8.136	1	13.62***
	Within sexes	44.224	74	
	Total	52.360	75	
Ocean-rowers	Between sexes	6.571	1	11.16***
	Within sexes	55.371	94	
	Total	61.942	95	

* $P < 0.05$.

*** $P < 0.001$.

TABLE 6. Two-factor ANOVA results for aggregate robusticity, including only preagriculturalists

	Source	Sum of squares	df	F
Main effects	Combined	6.957	2	5.95**
	Rowing	3.051	1	5.22*
	Sex	4.078	1	6.98**
Two-way interaction	Rowing × sex	0.009	1	0.02
Model		11.510	3	6.56***
Residual		62.538	107	
Total		74.047	110	

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

had more robust humeri than river-rowing or non-rowing populations; 2) this pattern occurred regardless of subsistence practices; and 3) these differences occurred in females as well as males. Consequently, although the results confirm that rowing visibly affects limb bone strength, this interpretation is tempered by the fact that females of the ocean-rowing populations also had more robust upper limbs than did the females of nonocean-rowing populations (Fig. 1). Given that females did not row upon the oceans to any great extent (Halpin and Seguin, 1990; Hrdlicka, 1945; MacDonald and Inglis, 1975), the explanation for their increased upper-limb robusticity must be sought in factors other than rowing.

To test whether the ocean-rowing populations' apparent robusticity (male and female) was an artifact of a cold-weather body type, the data were restandardized using body mass rather than humeral length. Allen (1877) noted that in cold climates, distal segments become reduced to decrease the risk of frostbite, and both the Alaskan Aleut and British

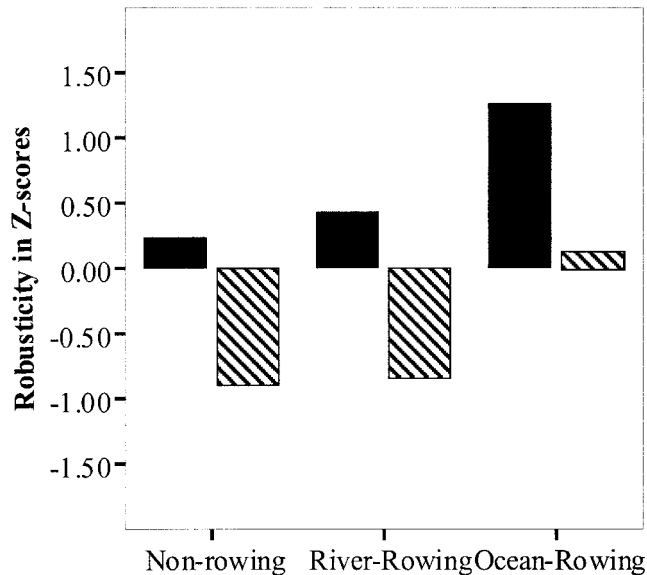


Fig. 4. Differences in mean aggregate robusticity (z-scores) in nonrowing, river-rowing, and ocean-rowing populations. Data standardized by estimated body mass and humeral length. Bars show means. Solid bars, males; striped bars, females.

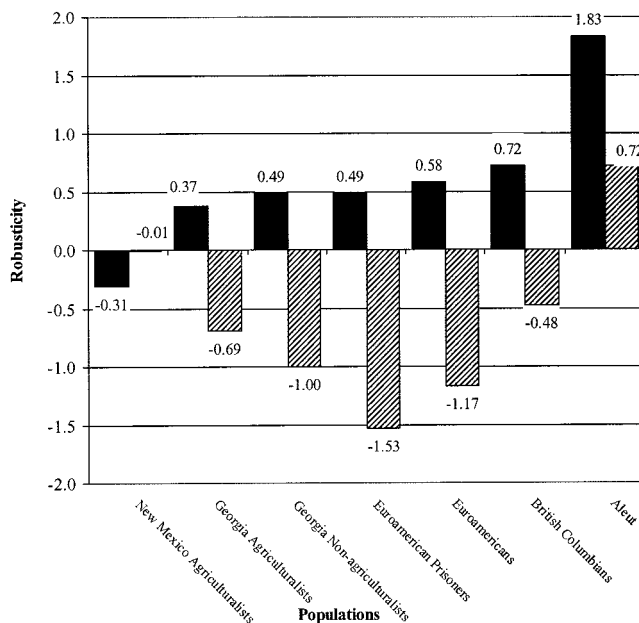


Fig. 5. Differences in mean aggregate robusticity (z-scores) body mass by population. Data standardized by estimated body mass and humeral length. Bars show means. Solid bars, males; striped bars, females.

Columbian Amerinds had body shapes that conformed to this rule (Cybulski, 1990; Hrdlicka, 1945). As mentioned previously, using humeral length to standardize for body size leads to underadjustments of robusticity for populations with relatively shorter limbs (Ruff, 2000b).

When examining rowing and sex differences using data standardized by body mass, ocean-rowing populations were still the most robust, but the differences between ocean-rowing and nonocean-rowing

populations were decreased. The three-way pattern of change in robusticity from ocean-rowers to river-rowers to nonrowers was still present in both sexes, suggesting that the differences between groups are not entirely due to rowing, which is mainly a male activity, but rather to factors that affect both sexes. One such factor could be overall higher levels of activity in the ocean-rowing group. The environment that ocean-rowers occupied required individuals to carve whales for meat, scrape hides for clothing, and build longhouses, all without advanced technology (Collier, 1993; MacDonald and Inglis, 1975; Osborn, 1990). These arduous activities and others that ocean-rowing populations engaged in may have increased bone remodeling and created more robust bones, but the effect of any specific activity, such as rowing, could not be isolated.

The greater robusticity of the ocean-rowing populations (both male and female) could also be due in part to the rule of Bergmann (1848), which states that in more northern latitudes, animals are larger for thermodynamic reasons. Larger individuals may have relatively more muscle mass, and this could lead to more robust cross-sections. This same logic also can help to explain the sex difference in robusticity found here.

Greater male than female robusticity was pronounced in all groups (when using either method of standardization). These sex differences are often interpreted as due to sexual division of labor (e.g., Bridges et al., 2000; Ruff, 1987), but many physical sex differences are due to natural and sexual selection. Relatively greater male upper-body strength is universal among human populations. This biological factor may also affect bone remodeling, i.e., the larger muscles produce higher loadings on the upper limb bones, creating more bone remodeling.

When looking at the individual sample means in Figure 5, a somewhat more complex picture emerges. In particular, the British Columbian females are less robust than the New Mexico agricultural females and almost comparable to the Georgia agricultural females. Thus, the data for the British Columbians (males and females) do support the hypothesis that rowing per se affects humeral strength (since only males rowed). However, the very robust Aleut females still deviate from the hypothesis' predictions. Also, the male British Columbians are much less robust than the Aleut males, which puts a wrinkle in the support for the hypothesis. There are several possible explanations for these divergences. The Aleuts perhaps rowed more or rowed on harsher waters than the British Columbians, or it could be that the Aleut lifestyle in general was much more rigorous than any of the other lifestyles, and this would explain the Aleut male and female results. That is, by adding a very rigorous lifestyle (increasing overall bone strength in both sexes) to rowing (in males), the Aleut pattern could be derived from the British Columbian pattern. Another explanation may be that the Aleuts occupied a much harsher

environment that would select against more gracile individuals. Or finally, using the rule of Bergmann (1848), the further north one travels, the larger individuals become, thereby increasing relative muscle mass and increasing bone remodeling.

Another interesting pattern using the body mass-standardized data is that the New Mexico Amerind females have more robust humeri than do their male counterparts. This finding could be due to the arduous lifestyle of the New Mexico Amerind females. They prepared fields, carried water, and ground corn (Castaño de Sosa, 1965; Schroeder, 1983; Stevenson, 1901–1902). However, this reversal in sex differences may also be an artifact of using mean body masses derived from a different population sample (see above).

Another observation is that the male Euroamerican prisoners of war were less robust than the other male Euroamericans, although they were performing a lot of heavy labor (Cybulski, 1988). This lack of robusticity among the Euroamerican prisoners may be due to a poor diet that impeded bone remodeling. Many of the prisoners' skeletal remains showed signs of scurvy, and the diaries associated with the site suggest a diet lacking essential vitamins (Cybulski, 1988).

One implication of these findings is that when using cross-sectional morphology to test hypotheses, the geographical origin of populations needs to be considered. Geographic populations differ in body shape due at least in part to preexisting selection. When standardizing cross-sections for body size, the direction of the effect can depend on which size "control" procedure is used. Using humeral length to standardize for body size creates an underadjustment for shorter-limbed populations, resulting in an overestimation of these populations' robusticity, but this method is useful when no other method for standardization is available. When the data used here were standardized for body size using humeral length, ocean-rowers (who had the shortest limbs) had the most robust humeri; females from ocean-rowing populations had more robust humeri than males from nonocean-rowing populations. Other methods for body size standardization, such as calculating body mass using femoral head breadth, are better for controlling for body shape differences. Unfortunately, such data were not available for the individuals in all of the populations used in this study.

The results reported here also imply that populations differ in upper bone morphology for many reasons. Human behavior, especially that involving the upper-limb bones, is complex, and one component of the behavioral repertoire, such as rowing, does not necessarily drown out effects from other activities. Because lower limbs are used almost exclusively for walking, the environmental factors that shape their cross sections are clearer, whereas bipedality has freed upper limbs of humans from travel, so upper limbs can be used in many more activities.

CONCLUSIONS

In conclusion, both males and females of ocean-rowing populations, especially Aleuts, have greater robusticity than do river-rowing and nonrowing populations. Males are more robust than females. The greater robusticity found in ocean-rowing populations is unlikely to be due solely to the activity of rowing, since females are not thought to engage in ocean-rowing to any discernible extent. The mechanical environment acting on the skeleton is complex, especially for the upper limb.

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