a poorer food conversion efficiency and survival rate. The lower survival rate (87%) of this group resulted in a total production (final density) only slightly greater than the saltwater group stocked at the same density.

A faster growth rate, better survival, and better food conversion were obtained at the lower stocking density brackish group thus demonstrating the effects stocking density has on these variables. The fact that oxygen was over 7 ppm in all groups throughout this experiment indicates that stocking density and not oxygen stress accounted for this reduction in performance.

Conclusions

The fact that temperature was not constant in all groups precluded a conclusive comparison of the performance of rainbow trout in brackish and fresh water. Nevertheless, the following conclusions can be made from these experimental data:

1. Rainbow trout were converted from fresh to 30‰ salinity in a period of 9 days and were reared to market size at this salinity.
2. Trout fingerlings averaging 60 g each were reared to 266 g in 21°C fresh water with a rapid individual growth rate and an acceptable survival and food conversion rate.
3. Survival and growth rates and food efficiencies were excellent for trout reared in brackish water at an average temperature of 13.5°C.

Literature Cited

ANDREWS, J. W., L. H. KNIGHT, J. W. PAGE, Y. MATSUDA, AND E. E. BROWN.
1971. Interactions of stocking density and water turnover on growth and food conversion of channel catfish reared in intensively stocked tanks. Prog. Fish-Cult. 33:197-203.

AWAKURA, T.
1962. On the tolerance of rainbow trout, *Salmo gairdneri irideus* Gibbons, to salt water. I. [In Japanese.] Sci. Rep. Hokkaido Fish Hatchery 17: 41-48.

AWAKURA, T., H. SHIBATA, AND K. HONMA.
1962. Some observations on the breeding of rainbow trout, *Salmo gairdneri irideus* Gibbons, in salt water. [In Japanese.] Sci. Rep. Hokkaido Fish Hatchery 17:49-57.

DUNCAN, D. B.
1955. Multiple range and multiple *F* tests. Biometrics 11:1-42.

JENSEN, K. W.
1967. Saltwater rearing of rainbow trout and salmon in Norway. Food Agric. Organ. U.N. EIFAC Tech. Pap. 3:43-48.

LEON, K. A.
1970. Some aspects of the comparative biology of an interracial hybrid rainbow trout and the two parental stocks. Ph.D. Thesis, Univ. Washington, Seattle, 125 p.

OSHIMA, Y. (editor).
1968. Suisan yoshoku handbook. Suisan-Sha, Tokyo, 535 p.

SATO, M.
1965. On the culturing of rainbow trout in salt water. Yoshoku/Fish Cult. 2:58-63.

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THE AMOUNT OF SPACE AVAILABLE FOR MARINE AND FRESHWATER FISHES

Cohen (1970) has presented rather careful estimates of the total number of fish species in the world and in each of eight ecological groupings. He found that an "astonishingly high percentage" of bony fishes live in freshwater habitats. According to Cohen's analysis, 41.2% (8,275 species) of all fish species live in fresh water (includes both primary and secondary freshwater fishes). He indicates that this high percentage must reflect the degree of isolation possible in freshwater environments and refers to the great variety of habitats and ecological niches in fresh water and also along tropical shores.

The great number of freshwater fish species becomes even more striking if the volume of fresh water in the world is compared to the volume of the oceans. Indeed, the mode of speciation and the structure of the niche appear highly divergent between the two environments. The oceans account for 97% of all the water in the world whereas the amount of fresh water in lakes and rivers (that which would be available as fish habitat) approaches an almost negligible percentage—only 0.0093% of the world's water (van Hylckama, 1971) (Table 1). In this sense then, 41.2% of all fish species live in less than one one-hundredth of one percent of the available water. Table 2, which is based on Cohen's (1970) data and on the data presented in Table 1, shows the great disparity between freshwater and marine environments in terms of the number of species per unit volume of water. The calculations show that there are about 113,000 km^3 of water per marine species but only about 15 km^3 for each freshwater species, or approximately a 7,500-fold difference. It is, of course, true that a species does not occupy a particular parcel of water to the exclusion of other organisms; nevertheless, it seems conceptually possible and without undue loss of reality to consider that each species has available a certain volume of water which it can occupy. It is known, too, that marine habitats vary greatly from high diversity in tropical shore and coral reef regions to low diversity in open ocean areas (including the deep ocean which constitutes most of the volume of the oceans and in which numbers and biomass greatly decrease with depth). Shore and shelf fishes have about 290 km^3 of water per species compared with about 1,000,000 km^3 for pelagic species (Table 2), or approximately a 3,400-fold difference. If the slope and deep-sea benthic species are added to the pelagic figure, the unit volume of water per species beyond the continental slope is reduced to about 500,000 km^3, which is still a relatively very high figure. The volume of water per species of marine shore and shelf fishes is higher than the freshwater figure by about 20× (290 km^3 vs. 15 km^3). This reflects the similarity in the degree of partitioning in these two regions. Perhaps the number of species per unit volume in the richer tropical reefs exceeds that in a large percentage of freshwater habitats. Also, some marine habitats which are superficially similar to certain freshwater habitats may be expected to have species densities comparable to their freshwater counterparts. Examples might be 1) the deep parts of oceans and lakes (low species density), 2) kelp beds in coastal waters and the vegetated zones of lakes (high species density). It is the open ocean with its broad expanse and great depth that contributes most to the overall very low concentration of species and numbers (discussed below) of marine fishes.

TABLE 1.—Supply (km^3) of water in the world available as fish habitat (from data by van Hylckama (1971)).

Item	Volume	Percent of total
Total water in the world	1,360,000,000	100.0
World oceans	1,320,000,000	97.0
Freshwater lakes	125,000	0.0092
Rivers (at any one time)	1,300	0.0001
(remainder of total is ice, groundwater, atmospheric water, etc.)		

TABLE 2.—Volume (km^3) of water available per species in various habitats.

Type of species	Volume/species
Total marine	113,000
Marine shore and continental shelf to 200 m	290*
Marine pelagic beyond continental shelf	1,000,000
Marine pelagic + continental slope and deep sea benthic	500,000
Total fresh water	15

* The volume of water over the continental shelf was calculated by considering that the shelf underlies 7.5% of the ocean surface (Emery, 1969) and that the average depth over the shelf is about 100 m or 2.5% of the ocean's average depth of 4,000 m.

While it is difficult to estimate the number of fish species in an environment, it is much more difficult to even speculate on the number of individuals per species in either marine or freshwater regions. Gadgil[1] arrived at a figure of 4×10^9 as the average number of individuals per fish species based largely on marine data. Certainly, different marine habitats support widely differing numbers of fishes. Pelagic species such as certain anchovies may attain population levels of 10^{12} whereas some rocky shore species may be several orders of magnitude lower in total numbers, perhaps near 10^6 individuals per species. A figure in the middle of the above two estimates would be 10^9, and in this discussion I have considered 10×10^9 to be the average number of individuals per species in the sea. It

[1] Gadgil, M. On numbers of fish. (Unpublished manuscript) Biology Department, Harvard University, Cambridge, Mass. Present address: Maharashtra Association for the Cultivation of Science, Agarkar Road, Poona 4, India.

is fairly certain, I think, that there are fewer individuals per species among freshwater fishes than among marine fishes. The degree of difference in abundance is, however, difficult to estimate or even imagine. There are some very abundant freshwater species such as certain clupeids and cyprinids, but some are quite rare, most notably the desert cyprinodontids of the southwestern United States which may exist only in the thousands or even hundreds per species.

Two values were used for the average number of individuals per freshwater species—a high value (10×10^9), the same as the figure for marine species, and a low value (10×10^6) which I think is a conservative minimum. A range of values conveys more information in comparing the marine and freshwater situations. The calculations in Table 3 show that marine fishes have 10× to 10,000× more space available per individual than freshwater forms, depending upon which freshwater value is chosen. If the lower freshwater figure (10×10^6) is more nearly correct, then the degree of isolation and habitat partitioning in fresh waters becomes even more strikingly apparent. On the basis of total numbers per species, the difference per unit volume between the oceans and fresh water is only 10-fold whereas on the basis of species per unit volume, the difference is approximately 7,500-fold.

TABLE 3.—Volume (km^3) of water available per individual fish in the sea and in fresh water.

Type of species	Number of species	Individuals/ species	Volume/ individual
Marine	11,675	10×10^9	1.1×10^{-5}
Fresh water (1)	8,275	10×10^9	1.5×10^{-9}
Fresh water (2)	8,275	10×10^6	1.5×10^{-6}

The above disparity would seem to be related not only to the degree of isolation but to the relative levels of productivity and biomass in the two environments. Table 4 shows net primary productivity and plant biomass estimates for three major ecosystems: 1) lake and stream, 2) continental shelf, and 3) open ocean. Net primary productivity per unit area in fresh water is about 1.5× to 4× as high as in the sea, and plant biomass per unit area in fresh water is about 2× to 7× as high as in the sea. These figures are perhaps not in great discord with the estimate above that 10× as many fishes occur per unit volume in fresh water as in the sea.

TABLE 4.—Net primary productivity and plant biomass per unit area in three major ecosystems (from data compiled by Whittaker (1970)).

Major ecosystem	Net primary productivity	Biomass
	dry g/m²/year (mean value)	*dry kg/m² (mean value)*
Lake and stream	500	0.02
Continental shelf	350	0.01
Open ocean	125	0.003

These data serve, I believe, to illustrate the quite astounding difference between the amount of space available for freshwater and marine fishes. As Cohen (1970) has emphasized, the calculations also make apparent the need for increased research on freshwater fishes since their habitats are being rapidly modified. In terms of conservation and economic policies, important studies should include those that compare numbers of species and individuals in different local and regional environments in relation to levels of productivity and other factors.

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Literature Cited

COHEN, D. M.
1970. How many recent fishes are there? Proc. Calif. Acad. Sci., Ser. 4, 38:341-345.

EMERY, K. O.
1969. The continental shelves. *In* The ocean, p. 39-52. W. H. Freeman, San Franc.

VAN HYLCKAMA, T. E. A.
1971. Water resources. *In* W. W. Murdoch (editor), Environment, resources, pollution & society, p. 135-155. Sinauer Associates, Stamford, Conn.

WHITTAKER, R. H.
1970. Communities and ecosystems. Macmillan, N.Y., 162 p.

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