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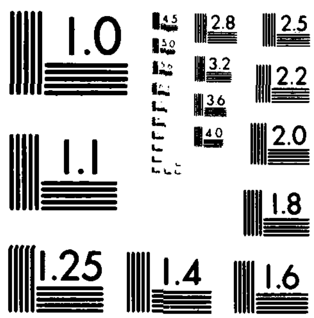

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A SURVEY OF GLUTAMINE SYNTHETASE ACTIVITIES IN TISSUES FROM THREE CLASSES OF FISH

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RESEARCH REPORT

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DEAN OF THE FACULTY
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20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

Enzyme assays using the γ-glutamyl transferase method provided estimates of glutamine synthetase activity in tissues from 18 species of fish. These species included Chinook salmon, Pacific herring, carp, channel catfish, Pacific hagfish, ratfish, spiny dogfish, copper rockfish, Pacific cod, fresh-water and salt-water stingray, and Pacific lamprey. Glutamine synthetase activity in liver and kidney from the classes Chondrichthyes, Cyclostomi and Osteichthyes

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20. ABSTRACT (Continued):

related to each species' need for glutamine. Brain activity was relatively high in all species. Gill and other tissues had very low but detectable glutamine synthetase activity.

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A SURVEY OF GLUTAMINE SYNTHETASE ACTIVITIES IN TISSUES FROM THREE CLASSES OF FISH

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JULY 1980

DEAN OF THE FACULTY

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ACKNOWLEDGEMENTS

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INTRODUCTION

Glutamine is a central compound in the nitrogen metabolism of all species (2, 10). This study of glutamine synthesis in fish is pertinent to aspects of osmoregulation as well. The only known route of glutamine synthesis in all species is activity of glutamine synthetase (EC 6.3.1.2) which catalyzes the following physiologically significant reaction:

$$\text{(1)}\quad \text{L-glutamate} + NH_3 + \text{ATP} \xrightarrow{Me^{++}} \text{L-glutamine} + \text{ADP} + P_i$$

Glutamine synthetase also catalyzes two other reactions which are used to assay activity (7, 12).

$$\text{(2)}\quad \text{L-glutamate} + NH_2OH + \text{ATP} \longrightarrow \gamma\text{-glutamyl hydroxamate} + \text{ADP} + P_i$$

$$\text{(3)}\quad \text{L-glutamine} + NH_2OH \xrightarrow[AsO_4^{3-}]{\text{ADP},\ Mn^{++}} \gamma\text{-glutamyl hydroxamate} + NH_3$$

Assay based on reaction (3) was used in this study due to its greater sensitivity and simplicity (16, 20).

Previous studies of glutamine synthetase in fish were usually limited to one or a few species and thus provide very limited comparative information (5, 6, 8, 15, 18, 19, 21). A previous study, using the same method (16), compared liver and brain activities of three species of teleosts and three species of elasmobranchs. Specific activities were high in brain tissue of all six species, although liver specific activity was high in only elasmobranch species. This large difference between specific activities in liver had not been reported previously and prompted a more comprehensive, comparative study of glutamine synthetase in fish tissues.

This study is a survey of glutamine synthetase activity in liver, kidney and brain tissues from 18 species of fresh-water and marine Cyclostomi, Chondrichthyes, and Osteichthyes. Gill and other tissues of many species were also examined along with liver tissue from a coelacanth (*Latimeria chalumnae*).

MATERIALS AND METHODS

North American (Pacific Northwest) species were kept in aquaria with water adjusted to their normal environmental salinity and temperature. The stingrays were purchased from a local (Seattle, Washington) fish wholesaler. All specimens were sacrificed as soon as practical after acquisition. The sample of coelacanth liver (from *Latimeria chalumnae* #78; 17.2 kg male; frozen for about 18 months prior to use) was obtained from the Society for the Protection Of Old Fishes.

L-glutamine, γ-glutamyl hydroxamate, Na_2ADP, KH_2AsO_4, bovine serum albumin, and imidazole were purchased from Sigma Chemical Company, St. Louis, Missouri. Hydroxylamine-HCl was obtained from Merck & Company, Rahway, New Jersey.

All tissues were excised from freshly sacrificed specimens and homogenized with distilled water in glass, hand homogenizers. The tissue homogenates were assayed for glutamine synthetase according to the method of Webb and Brown (16) under the following conditions: Ten min. incubation at 25°C; pH 6.4 or 6.7 depending upon the optimum of each group (16); 2 ml incubation mixture containing 60 mM L-glutamine, 15 mM hydroxylamine-HCl, 0.4 mM Na_2ADP; 20 mM KH_2AsO_4, 3 mM $MnCl_2$, and 40 mM imidazole. The γ-glutamyl hydroxamate produced by enzyme activity (reaction 3) was complexed with $FeCl_3$ (in HCl) and compared against the γ-glutamyl hydroxamate standard at 500 nm. A unit of glutamine synthetase activity is defined as the production of one μmole of γ-glutamyl hydroxamate per min at 25°C. Protein was determined by the biuret method adapted from Zamenhof (22).

RESULTS AND DISCUSSION

Glutamine synthetase activity in fish tissues was linear with time and enzyme aliquot. Other properties exhibited by glutamine synthetase from Squalus acanthias liver (Table 1) are in accord with properties of the enzyme from other fish (16) and mammals (7, 11). The glutamine synthetase of coelacanth liver homogenate produced less than half maximal activity without ADP and arsenate; about one-fourth maximal activity without either Mn^{++} or glutamine; and about one-eighth maximal activity without hydroxylamine. Boiled enzyme produced no activity.

Body weight ranges are given in Tables 2 and 3 to indicate limitations of sample weight range which affect both organ percentage of body weight and protein content. The body weight ranges are not identical for both tables because organ weights were not routinely determined in the earlier phases of the research. The percentage of body weight of liver was highly variable and was a significant factor in the large differences between the species' hepatic potential for synthesis of glutamine (Figure 1 and Table 4). The protein content of liver was also quite variable and resulted in highly significant differences in specific activity among the species examined here (Tables 3 and 4).

There is a very large difference between specific activity of glutamine synthetase in liver and brain of the species which do not retain urea for osmoregulation. There is a relatively small difference in species which retain urea for osmoregulation. This may help to explain the relationship of liver glutamine synthetase to production of urea in marine Chondrichthyes (17).

The species studied here which retain urea (*Hydrolagus colliei*, *Raja binoculata*, *Squalus acanthias*, and *Taeniura lymma*) (4, 17) have high glutamine synthetase specific activity in liver and kidney. Conversely, the species which do not retain urea (all other species in Table 4) (4, 13, 14) have very low glutamine synthetase specific activity in liver and kidney. The brain activity is relatively high in all species. Other tissues do not contain such high levels of the enzyme (Table 5).

The fresh-water stingray, *Potamotrygon circularis*, is taxonomically distant to the species of Osteichthyes described in Tables 2-5. However, their levels of glutamine synthetase in liver and kidney are closely parallel. This and the relatively high activity in coelacanth liver (3.5 units per g tissue; 0.04 units per mg protein) indicate a direct relationship between liver glutamine synthetase activity and urea retention in the coelacanth (of the class Osteichthyes) (3, 9) and marine Chondrichthyes (4).

These data reiterate that glutamine synthetase is prevalent and very active in brain tissue of all species studied. Further, the enzyme is present at high activity levels in the liver of some fish species; namely, the marine species which coincidentally retain urea for osmoregulation. The function of this activity could be tied to the type and activity of carbamoyl-phosphate synthetase present in liver of urea-retaining species (1, 17). This hypothesis is supported by the relative ability of the liver of each species to synthesize glutamine as shown in Figure 1. The importance of glutamine to the metabolism of some fish is thus greater than proposed in previous reports (6, 21).

SUMMARY

Glutamine synthetase may have a critical function in the nitrogen metabolism and osmoregulation of some fish species. The urea-retaining marine Chondrichthyes had high levels of the enzyme in liver. The non-urea-retaining species had very low specific activity of glutamine synthetase in liver tissue. Glutamine may be a direct precursor of urea in urea-retaining marine Chondrichthyes. Levels of glutamine synthetase in tissues other than liver

and kidney of Chondrichthyes and brain of all 18 species examined here were very low although some activity was detectable in many tissues.

TABLE 1--Requirements for activity and inhibition of *Squalus acanthias* liver glutamine synthetase.

System	Percent of activity
Complete[1]	100
-Glutamine	1
-Hydroxylamine (NH_2OH)	1
-ADP and arsenate (KH_2AsO_4)	2
$-Mn^{++}$ ($MnCl_2$)	1
+ 0.1 mM $MnCl_2$ in place of 3 mM $MnCl_2$	112
Complete[1,2] plus:	
9 mM Methionine sulfoximine	96
9 mM Methionine sulfoximine, 10 mM ATP, 20 mM $MgCl_2$	0
3 mM Methionine sulfoximine, 10 mM ATP, 20 mM $MgCl_2$	0
10 mM ATP, 20 mM $MgCl_2$	24
Complete Alternate Assay[3]	6.3

[1]The complete, reaction (3), system produced 179 units per g liver acetone powder with 60 mM L-glutamine, 15 mM hydroxylamine, 3 mM $MnCl_2$, 0.4 mM ADP, and 20 mM KH_2AsO_4 at 25°C. (pH 6.7).

[2]Methionine sulfoximine and/or ATP and $MgCl_2$ were preincubated with the acetone powder suspension at the concentration shown for 10 min prior to initiation of the reaction by addition of the assay mix. The concentration of the preincubated components during the assay was half that shown above. Controls were preincubated with water.

[3]The complete, reaction (2), alternate assay system produced 11.3 units per g liver acetone powder with 60 mM L-glutamate, 15 mM hydroxylamine, 20 mM $MgCl_2$, and 10 mM ATP at 25°C. (pH 7.2). The reaction (3)/reaction (2) ratio of activities is 16.

TABLE 2--Liver and brain as a percentage of body weight

Species[1]	Organ			
	Liver		Brain	
CLASS OSTEICHTHYES	%BW[2]	BWR[3]	%BW[2]	BWR[3]
Acipenser transmontanus (White sturgeon) Fresh-water	1.1 ± 0.0 (2)	1.02 - 2.05 kg	0.08 ± 0.03 (2)	1.02 - 2.05 kg
Clupea harengus pallasi (Pacific herring) Marine			0.25 ± 0.04 (3)	0.038 - 0.105kg
Cyprinus carpio (Carp) Fresh-water	1.3 ± 0.2 (3)	1.30 - 1.60 kg	0.08 ± 0.02 (3)	1.30 - 1.60 kg
Gadus macrocephalus (Pacific cod) Marine			0.15 ± 0.05 (3)	0.45 - 1.21 kg
Ictalurus punctatus (Channel catfish) Fresh-water	0.9 ± 0.2 (3)	0.093 - 0.116kg	0.24 ± 0.00 (3)	0.093 - 0.116kg
Lepidopsetta bilineata (Rock sole) Marine			0.11 ± 0.05 (6)	0.156 - 0.509kg
Oncorhynchus tshawytscha (Chinook salmon) 2 Fresh-water 2 Marine	0.9 ± 0.1 (4)	0.030 - 0.064kg	0.38 ± 0.09 (4)	0.030 - 0.064kg
Perca flavescens (Yellow perch) Fresh-water	1.3 ± 0.4 (3)	0.138 - 0.240kg	0.09 ± 0.02 (3)	0.138 - 0.240kg
Platichthys stellatus (Starry flounder) Marine	1.0 ± 0.2 (2)	0.318 - 0.320kg	0.08 ± 0.01 (3)	0.318 - 0.520kg
Porichthys notatus (Plainfin midshipman) Marine	2.1 ± 0.2 (2)	0.135 - 0.204kg	0.08 ± 0.02 (3)	0.135 - 0.246kg
Sebastes caurinus (Copper rockfish) Marine	1.1 ± 0.2 (3)	0.145 - 0.423kg	0.14 ± 0.07 (3)	0.145 - 0.423kg
CLASS CYCLOSTOMI				
Eptatretus stouti (Pacific hagfish) Marine	1.9 ± 0.1 (2)	0.215 - 0.240kg	0.03 ± 0.01 (2)	0.215 - 0.240kg
Lampetra tridentatus (Pacific lamprey) Fresh-water	1.2 ± 0.2 (3)	0.475 - 0.740kg	0.02 ± 0.00 (3)	0.475 - 0.740kg

TABLE 2--Continued

Species[1]	Organ			
	Liver		Brain	
CLASS CHONDRICHTHYES	%BW[2]	BWR[3]	%BW[2]	BWR[3]
Hydrolagus colliei (Ratfish) Marine	15.2 ± 7.1 (3)	0.100 - 0.580kg	0.31 ± 0.09 (3)	0.100 - 0.580kg
Potamotrygon circularis (Stingray) Fresh-water	4.6 ± 4.8 (2)	0.125 - 0.131kg	1.08 ± 0.18 (2)	0.125 - 0.131kg
Raja binoculata (Big skate) Marine	3.5 ± 1.2 (2)	0.90 - 15.67 kg	0.14 ± 0.10 (3)	0.90 - 15.67 kg
Squalus acanthias (Spiny dogfish) Marine	7.5 ± 1.9 (2)	0.625 - 1.06 kg	0.34 ± 0.10 (2)	0.625 - 1.06 kg
Taeniura lymma (Blue-spotted stingray) Marine	1.4 (1)	0.276kg	1.87 (1)	0.276kg

[1]Scientific name is followed by the common name and habitat.

[2]Organ percentage of body weight, %BW, is listed as the mean ± standard deviation with the number of specimens in parenthesis.

[3]Body weight range of specimens in each species, BWR, is shown in kg.

TABLE 3--Protein content of liver, brain, and kidney

Species[1]		Organ		
		Liver	Brain	Kidney
CLASS OSTEICHTHYES				
Acipenser transmontanus (White sturgeon) Fresh-water	P[2]	125 ± 38 (2)	55 ± 0 (2)	70 ± 20 (2)
	BWR[3]	1.02 - 2.05 kg	1.02 - 2.05 kg	1.02 - 2.05 kg
Clupea harengus pallasi (Pacific herring) Marine	P	140 ± 12 (3)	92 ± 2 (3)	107 ± 17 (3)
	BWR	0.038 - 0.105kg	0.038 - 0.105kg	0.038 - 0.105kg
Cyprinus carpio (Carp) Fresh-water	P	171 ± 7 (3)	82 ± 1 (3)	130 ± 8 (3)
	BWR	1.30 - 1.60 kg	1.30 - 1.60 kg	1.30 - 1.60 kg
Gadus macrocephalus (Pacific cod) Marine	P	136 ± 16 (3)	77 ± 2 (3)	97 ± 4 (3)
	BWR	0.45 - 1.21 kg	0.45 - 1.21 kg	0.45 - 1.21 kg
Ictalurus punctatus (Channel catfish) Fresh-water	P	149 ± 6 (3)	86 ± 3 (3)	112 ± 9 (3)
	BWR	0.093 - 0.116kg	0.093 - 0.116kg	0.093 - 0.116kg
Lepidopsetta bilineata (Rock sole) Marine	P	126 ± 7 (6)	79 ± 7 (6)	117 ± 17 (6)
	BWR	0.156 - 0.509kg	0.156 - 0.509kg	0.156 - 0.509kg
Oncorhynchus tshawytscha (Chinook salmon) 2 Fresh-water 2 Marine	P	151 ± 6 (4)	81 ± 1 (4)	107 ± 8 (4)
	BWR	0.030 - 0.064kg	0.030 - 0.064kg	0.030 - 0.064kg
Perca flavescens (Yellow perch) Fresh-water	P	133 ± 15 (3)	74 ± 2 (3)	75 ± 12 (2)
	BWR	0.138 - 0.240kg	0.138 - 0.240kg	0.138 - 0.240kg
Platichthys stellatus (Starry flounder) Marine	P	122 ± 8 (8)[4]	72 ± 6 (8)[4]	103 ± 8 (3)
	BWR	0.30 - 1.20 kg	0.30 - 1.20 kg	0.318 - 0.520kg
Porichthys notatus (Plainfin midshipman) Marine	P	148 ± 16 (3)	77 ± 11 (3)	103 ± 9 (3)
	BWR	0.135 - 0.246kg	0.135 - 0.246kg	0.135 - 0.246kg
Sebastes caurinus (Copper rockfish) Marine	P	120 ± 22 (3)	75 ± 8 (6)[4]	110 ± 2 (3)
	BWR	0.145 - 0.423kg	0.145 - 0.423kg	0.145 - 0.423kg

TABLE 3--Continued

Species[1]		Organ		
		Liver	Brain	Kidney
CLASS CYCLOSTOMI				
Eptatretus stouti (Pacific hagfish)	P[2]	80 ± 23 (2)	53 ± 15 (2)	30 ± 18 (2)
Marine	BWR[3]	0.215 - 0.240kg	0.215 - 0.240kg	0.215 - 0.240kg
Lampetra tridentatus (Pacific lamprey)	P	87 ± 17 (3)	45 ± 10 (3)	69 ± 2 (3)
Fresh-water	BWR	0.475 - 0.740kg	0.475 - 0.740kg	0.475 - 0.740kg
CLASS CHONDRICHTHYES				
Hydrolagus colliei (Ratfish)	P	25 ± 15 (7)[4]	89 ± 24 (7)[4]	93 ± 21 (5)
Marine	BWR	0.100 - 0.6 kg+	0.100 - 0.6 kg+	0.100 - 0.6 kg+
Potamotrygon circularis (Stingray)	P	89 ± 64 (2)	76 ± 1 (2)	75 ± 3 (2)
Fresh-water	BWR	0.125 - 0.131kg	0.125 - 0.131kg	0.125 - 0.131kg
Raja binoculata (Big skate)	P	95 ± 51 (6)[4]	73 ± 9 (6)[4]	94 ± 18 (3)
Marine	BWR	0.90 - 15.67 kg	0.90 - 15.67 kg	0.90 - 15.67 kg
Squalus acanthias (Spiny dogfish)	P	35 ± 14 (6)[4]	69 ± 7 (6)[4]	90 ± 4 (3)[4]
Marine	BWR	0.625 - 3.0 kg+	0.625 - 3.0 kg+	0.625 - 3.0 kg+
Taeniura lymma (Blue-spotted stingray)	P	199 (1)	105 (1)	117 (1)
Marine	BWR	0.276kg	0.276kg	0.276kg

[1]Scientific name is followed by common name and habitat.

[2]Protein content, P, is listed as mg progein per g tissue (biuret method); mean ± standard deviation. Number of specimens examined is listed in parenthesis.

[3]Body weight range of specimens in each species, BWR, is shown in kg. If weight was not measured, approximate minimum value was derived from length to weight ratios and listed with a +.

[4]Results from a previous study (Webb and Brown, 1976) are included in this value.

TABLE 4--Glutamine synthetase activities: Liver, brain, and kidney

Species[1]		Enzyme activity[2]		
		Liver	Brain	Kidney
CLASS OSTEICHTHYES				
Acipenser transmontanus	TA[3]	0.6 ± 0.8 (2)	6.5 ± 1.1 (2)	0.3 ± 0.0 (2)
(White sturgeon) Fresh-water	SA[4]	0.00 ± 0.00 (2)	0.11 ± 0.02 (2)	0.00 ± 0.00 (2)
Clupea harengus pallasi	TA	2.8 ± 2.0 (3)	73.4 ± 17.3 (3)	1.1 ± 0.3 (3)
(Pacific herring) Marine	SA	0.02 ± 0.02 (3)	0.81 ± 0.21 (3)	0.01 ± 0.01 (3)
Cyprinus carpio	TA	0.7 ± 0.8 (3)	45.4 ± 5.0 (3)	0.7 ± 0.6 (3)
(Carp) Fresh-water	SA	0.00 ± 0.00 (3)	0.55 ± 0.06 (3)	0.01 ± 0.01 (3)
Gadus macrocephalus	TA	1.1 ± 0.3 (3)	58.3 ± 4.8 (3)	4.2 ± 2.2 (3)
(Pacific cod) Marine	SA	0.01 ± 0.00 (3)	0.87 ± 0.06 (3)	0.04 ± 0.02 (3)
Ictalurus punctatus	TA	1.4 ± 0.5 (3)	35.3 ± 6.1 (3)	0.8 ± 0.2 (3)
(Channel catfish) Fresh-water	SA	0.01 ± 0.00 (3)	0.41 ± 0.05 (3)	0.01 ± 0.00 (3)
Lepidopsetta bilineata	TA	1.4 ± 0.3 (6)	77.1 ± 9.7 (6)	3.7 ± 3.7 (6)
(Rock sole) Marine	SA	0.01 ± 0.00 (6)	0.97 ± 0.12 (6)	0.03 ± 0.03 (6)
Oncorhynchus tshawytscha	TA	2.4 ± 0.1 (2)	80.7 ± 7.6 (2)	2.0 ± 0.1 (2)
(Chinook salmon) Marine	SA	0.02 ± 0.00 (2)	1.00 ± 0.09 (2)	0.02 ± 0.00 (2)
Oncorhynchus tshawytscha	TA	0.9 ± 0.1 (2)	75.9 ± 4.7 (2)	1.9 ± 0.1 (2)
(Chinook salmon) Fresh-water	SA	0.01 ± 0.00 (2)	0.94 ± 0.04 (2)	0.02 ± 0.00 (2)
Perca flavescens	TA	0.8 ± 0.5 (3)	82.9 ± 3.1 (3)	0.2 ± 0.2 (3)
(Yellow perch) Fresh-water	SA	0.01 ± 0.00 (3)	1.12 ± 0.02 (3)	0.00 ± 0.00 (3)
Platichthys stellatus	TA	0.5 ± 0.3 (8)[5]	49.7 ± 14.9 (8)[5]	0.5 ± 0.1 (3)
(Starry flounder) Marine	SA	0.00 ± 0.00 (8)[5]	0.68 ± 0.16 (8)[5]	0.00 ± 0.00 (3)
Porichthys notatus	TA	1.0 ± 0.4 (3)	33.2 ± 9.7 (3)	1.0 ± 0.0 (3)
(Plainfin midshipman) Marine	SA	0.01 ± 0.00 (3)	0.43 ± 0.08 (3)	0.01 ± 0.00 (3)
Sebastes caurinus	TA	0.4 ± 0.3 (6)[5]	29.0 ± 9.7 (6)[5]	0.6 ± 0.3 (3)
(Copper rockfish) Marine	SA	0.00 ± 0.00 (3)	0.38 ± 0.12 (6)[5]	0.01 ± 0.00 (3)

TABLE 4--Continued

Species[1]		Enzyme activity[2] Liver	Brain	Kidney
CLASS CYCLOSTOMI				
Eptatretus stouti (Pacific hagfish) Marine	TA[3]	4.4 ± 1.1 (2)	44.4 ± 10.7 (2)	0.4 ± 0.2 (2)
	SA[4]	0.06 ± 0.00 (2)	0.84 ± 0.04 (2)	0.01 ± 0.00 (2)
Lampetra tridentatus (Pacific lamprey) Fresh-water	TA	1.3 ± 0.5 (3)	21.9 ± 9.8 (3)	3.7 ± 0.7 (3)
	SA	0.01 ± 0.00 (3)	0.47 ± 0.11 (3)	0.05 ± 0.01 (3)
CLASS CHONDRICHTHYES				
Hydrolagus colliei (Ratfish) Marine	TA	6.9 ± 2.9 (7)[5]	22.9 ± 2.9 (7)[5]	56.0 ± 9.0 (5)
	SA	0.33 ± 0.14 (7)[5]	0.27 ± 0.06 (7)[5]	0.62 ± 0.11 (5)
Potamotrygon circularis (Stingray) Fresh-water	TA	0.2 ± 0.0 (2)	10.9 ± 0.0 (2)	0.1 ± 0.2 (2)
	SA	0.00 ± 0.00 (2)	0.14 ± 0.00 (2)	0.00 ± 0.00 (2)
Raja binoculata (Big skate) Marine	TA	39.8 ± 20.2 (6)[5]	24.1 ± 4.4 (6)[5]	43.8 ± 5.8 (3)
	SA	0.44 ± 0.12 (6)[5]	0.33 ± 0.05 (6)[5]	0.48 ± 0.12 (3)
Squalus acanthias (Spiny dogfish) Marine	TA	18.4 ± 10.4 (7)[5]	18.0 ± 2.1 (7)[5]	23.3 ± 11.6 (3)[5]
	SA	0.48 ± 0.17 (7)[5]	0.26 ± 0.04 (7)[5]	0.26 ± 0.12 (3)[5]
Taeniura lymma (Blue-spotted stingray) Marine	TA	25.0 (1)	7.4 (1)	45.0 (1)
	SA	0.13 (1)	0.07 (1)	0.38 (1)

[1]Scientific name is followed by common name and habitat.

[2]Standard assay conditions were utilized. Mean of activities is expressed as units ± standard deviation. Number of specimens examined is listed in parenthesis.

[3]Tissue activity, TA, is expressed in units per g tissue. Values below the lower limit of reliable detection, 1.5, are included only to indicate that some activity may be present.

[4]Specific activity, SA, is expressed in units per mg protein.

[5]Results from a previous study (Webb and Brown, 1976) were included in this value.

TABLE 5--Glutamine synthetase activities: Gill and other tissues

Species[1]		Enzyme activity[2]			
		Gill	Muscle	Other[3]	
CLASS OSTEICHTHYES					
Acipenser transmontanus (White sturgeon)	TA[4]	0.8 (2)			
Fresh-water	SA[5]	0.03 (2)			
Clupea harengus pallasi (Pacific herring)	TA	0.0 (1)			0.2 (1)H
Marine	SA	0.00 (1)			---
Cyprinus carpio (Carp)	TA	0.4 (3)			
Fresh-water	SA	0.01 (3)			
Gadus macrocephalus (Pacific cod)	TA	2.2 (1)		0.9 (1)S	
Marine	SA	0.04 (1)		---	
Ictalurus punctatus (Channel catfish)	TA	3.4 (3)			
Fresh-water	SA	0.04 (3)			
Lepidopsetta bilineata (Rock sole)	TA			0.0 (1)M	
Marine	SA			---	
Oncorhynchus tshawytscha (Chinook salmon)	TA	2.4 (2)			
Marine	SA	0.02 (2)			
Oncorhynchus tshawytscha (Chinook salmon)	TA	3.5 (2)			
Fresh-water	SA	0.04 (2)			
Perca flavescens (Yellow perch)	TA	2.1 (3)			
Fresh-water	SA	0.04 (3)			
Platichthys stellatus (Starry flounder)	TA	0.7 (1)	0.0 (1)		
Marine	SA	0.01 (1)	---		
Porichthys notatus (Plainfin midshipman)	TA		0.4 (1)	0.0 (1)R	
Marine	SA		---	---	
CLASS CYCLOSTOMI					
Eptatretus stouti (Pacific hagfish)	TA	2.3 (2)	0.4 (1)	0.0 (1)R	0.5 (1)H
Marine	SA	0.07 (2)	---	---	0.01 (1)H
Lampetra tridentatus (Pacific lamprey)	TA	5.3 (3)		8.4 (1)SC	0.4 (1)H
Fresh-water	SA	0.09 (3)		0.42 (1)SC	0.00 (1)H

TABLE 5--Continued

Species[1]		Enzyme activity[2]			
		Gill	Muscle	Other[3]	
CLASS CHONDRICHTHYES					
<u>Hydrolagus colliei</u>	TA[4]	2.0 (2)		1.4 (1)P	
(Ratfish)					
Marine	SA[5]	0.04 (2)		---	
<u>Potamotrygon circularis</u>	TA	0.2 (1)	0.0 (1)	0.6 (1)M	9.0 (1)SC
(Stingray)					
Fresh-water	SA	0.01 (1)	0.00 (1)	0.01 (1)M	0.11 (1)SC
<u>Raja binoculata</u>	TA	4.0 (1)		1.1 (1)P	1.2 (1)RG
(Big skate)					
Marine	SA	0.09 (1)		0.01 (1)P	0.02 (1)RG
<u>Squalus acanthias</u>	TA	2.4 (1)[6]	1.0 (1)[6]	2.5 (1)S[6]	5.8 (1)RG[6]
(Spiny dogfish)					
Marine	SA	0.04 (1)[6]	0.01 (1)[6]	0.03 (1)S[6]	0.08 (1)RG[6]
<u>Squalus acanthias</u>	TA			1.9 (1)P[6]	9.3 (3)SC[6]
(Spiny dogfish)					
Marine	SA			0.02 (1)P[6]	0.12 (3)SC[6]
<u>Squalus acanthias</u>	TA			2.7 (1)H[6]	
(Spiny dogfish)					
Marine	SA			0.03 (1)H[6]	
<u>Taeniura lymma</u>	TA		1.4 (1)		0.0 (1)RG
(Blue-spotted stingray)					
Marine	SA		0.01 (1)		---

[1]Scientific name is followed by common name and habitat.

[2]Standard assay conditions were utilized. Mean of activities is expressed as units with number of specimens examined in parenthesis.

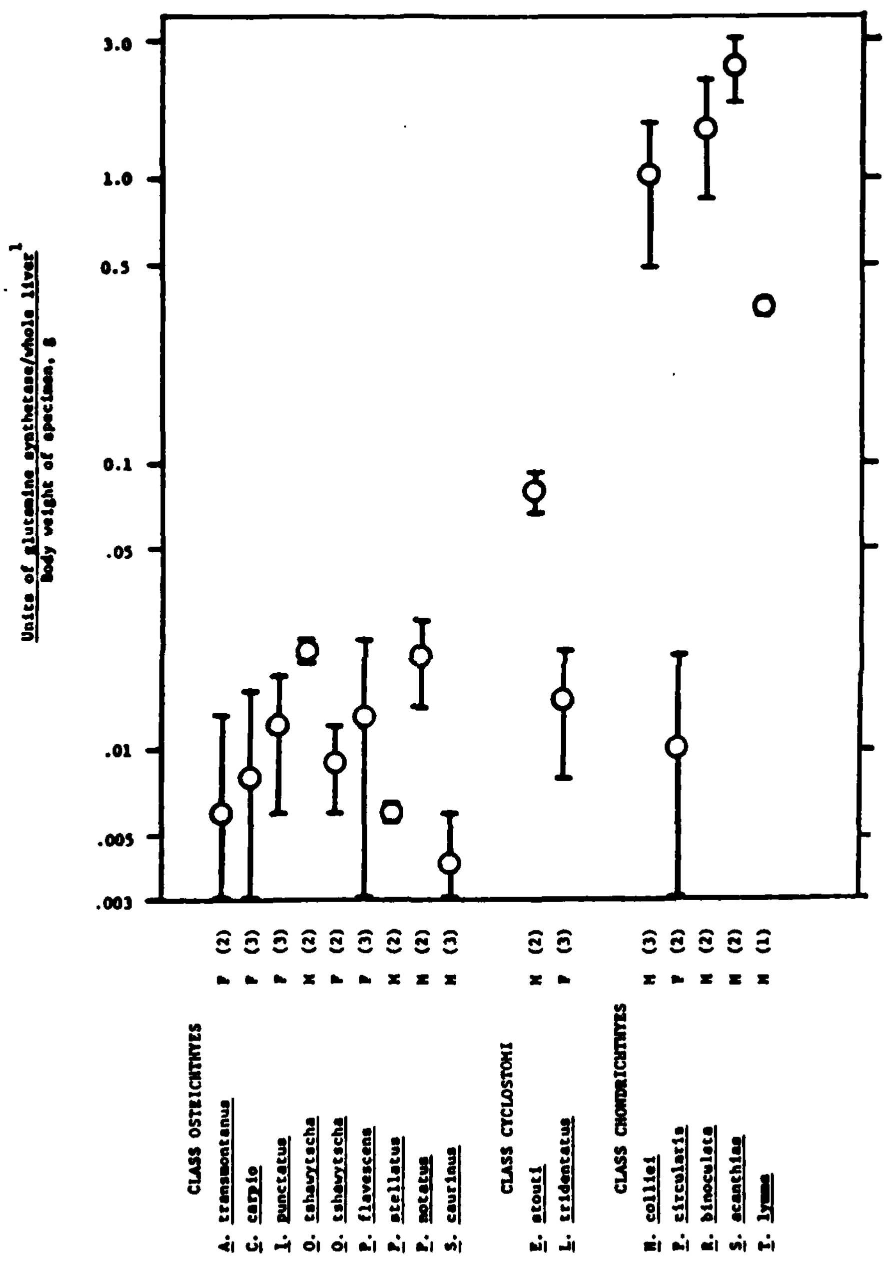
[3]Other tissues are abbreviated as follows: heart, H; milt, M; pancreas, P; roe, R; rectal gland, RG; spleen, S; and spinal cord, SC.

[4]Tissue activity, TA, is expressed in units per g tissue. Values below the lower limit of reliable detection, 1.5, are included only to indicate that some activity may be present.

[5]Specific activity, SA, is expressed in units per mg protein.

[6]Results from a previous study (Webb and Brown, 1976) were included in this value.

FIGURE 1--Hepatic potential for synthesis of glutamine



[1]The mean ± standard deviation is depicted for each species. See Table 4 for full scientific and common names. The number of specimens examined is listed in parenthesis following the habitat of each species. F = fresh-water M = marine

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