W. H. Dieffenbach
October 8, 1963
Fish Distribution

II. Arkansas River:

	Genus	Species	
1. Family Petromyzontidae			
Chestnut lamprey	Ichthyomyzon	castaneus	(Girard)
Southern brook lamprey	I.	gagei	(Hubbs & Trautman)
2. Family Lepisosteidae			
Spotted gar	Lepisosteus	oculatus	(Winchell)
Longnose gar	L.	osseus	(Linnaeus)
Shortnose gar	L.	platostomus	(Rafinesque)
Alligator gar	L.	spatula	(Lacepede)
3. Family Amiidae			
Bowfin	Amia	calva	(Linnaeus)
4. Family Clupeidae			
Skipjack herring	Alosa	chrysochloris	(Rafinesque)
Ohio Shad	A.	ohiensis	(Evermann)
*Gizzard shad	Dorosoma	cepedianum	(LeSueur)
5. Family Salmonidae			
Sockeye salmon (Kokanee)	Oncorhynchus	nerka	(Walbaum)
Cutthroat trout	Salmo	clarki	(Richardson)
⊛ *Rainbow trout	Salmo	gairdneri	(Richardson)
⊗ *Brown trout	S.	trutta	(Linnaeus)
*Brook trout	Salvelinus	fontinalis	(Mitchill)
*Lake trout	S.	namaycush	(Walbaum)
6. Family Hiodontidae			
Goldeye	Hiodon	alosiodes	(Rafinesque)
Mooneye	H.	tergisus	(LeSueur)
7. Family Esocidae			
*Grass pickerel	Esox	americanus vermiculatus	(LeSueur)
Chain "	Esox	niger	(LeSueur)
8. Family Charcidae			
⊗ Banded tetra	Astyanax	fusciatus	(Cuvier)
9. Family Cyprinidae			
Stoneroller	Campostoma	anomalum	(Rafinesque)
⊛ *Goldfish	Carassius	auratus	(Linnaeus)
So. redbelly dace	Chrosomus	erythrogaster	(Rafinesque)
⊛ *Carp	Cyprinus	carpio	(Linnaeus)
Ozark minnow	Dionda	nubila	(Forbes)

II. Arkansas River (continued):

	Genus	Species
Plains minnow	Hybognathus	placita (Girard)
Brassy minnow	Hybognathus	hankinsoni (Hubbs)
Silver minnow	H.	nuchalis (Agassiz)
Speckled chub	Hybopsis	aestivalis (Girard)
Bigeye chub	H.	amblops (Rafinesque)
Hornyhead chub	H.	biguttata (Kirtland)
Flathead chub	H.	gracilis (Richardson)
Silver chub	H.	storeriana (Kirtland)
Gravel chub	H.	x-punctata (Hubbs & Crowe)
*Gold shiner	Notemigonus	crysoleucas (Mitchill)
Pallid shiner	Notropis	amnis (Hubbs & Greene)
Emerald shiner	N.	atherinoides (Rafinesque)
Blackspot shiner	N.	atrocaudalis (Evermann)
Red River shiner	N.	bairdi (Hubbs & Ortenburger)
River shiner	N.	blennius (Girard)
Bigeye shiner	N.	boops (Gilbert)
Ghost shiner	N.	buchanani (Meek)
Bluntface shiner	N.	camurus (Jordan and Meek)
Ironcolor shiner	N.	chalybaeus (Cope)
Common shiner	N.	cornutus (Mitchill)
Bigmouth shiner	N.	dorsalis (Agassiz)
Ribbon shiner	N.	fumeus (Evermann)
Arkansas River shiner	N.	girardi (Hubbs & Ortenburger)
Wedgespot shiner	N.	greenei (Hubbs & Ortenburger)
Silverband shiner	N.	illecebrosus (Girard)
Red shiner	N.	lutrensis (Baird & Girard)
Taillight shiner	N.	maculatus (Hay)
Kiamichi shiner	N.	ortenburgeri (Hubbs)
Plains shiner	N.	percobromus (Cope)
Colorless shiner	N.	perpallidus (Hubbs & Black)
⊘ Chub shiner	N.	potteri (Hubbs & Bonham)
Rosyface shiner	N.	rubellus (Agassiz)
Spotfin shiner	N.	spilopterus (Cope)
Sand shiner	N.	stramineus (Cope)
Topeka shiner	N.	topeka (Gilbert)
Redfin shiner	N.	umbratilis (Girard)
Blacktail shiner	N.	venustus (Girard)
Mimic shiner	N.	volucellus (Cope)
Steelcolor shiner	N.	whipplei (Girard)
Bleeding shiner	N.	zonatus (Agassiz)
Pugnose minnow	Opsopoedus	emiliae (Hay)
Suckermouth minnow	Phenacobius	mirabilis (Girard)
Bluntnose minnow	Pimephales	notatus (Rafinesque)
Fathead minnow	P.	promelas (Rafinesque)
Slim minnow	P.	tenellus (Girard)
Bullhead minnow	P.	vigilax (Baird & Girard)

II. Arkansas River (continued):

	Genus	Species	
Longnose dace	Rhinichthys	cataractae	(Valenciennes)
Speckled dace	R.	osculus	(Girard)
Creek chub	Semotilus	atromaculatus	(Mitchill)
⊗*Tench	Tinca	tinca	(Linnaeus)

10. Family Catostomidae

River carpsucker	Carpiodes	carpio	(Rafinesque)
Plains carpsucker	C.	forbesi	(Hubbs)
Highfin carpsucker	C.	velifer	(Rafinesque)
Longnose sucker	Catostomus	catostomus	(Forbes)
White sucker	C.	commersoni	(Lacepede)
Blue sucker	Cycleptus	elongatus	(LeSueur)
Creek chub	Erimyzon	oblongus	(Mitchill)
No. hog sucker	Hypentelium	nigricans	(LeSueur)
Smallmouth buffalo	Ictiobus	bubalus	(Rafinesque)
Bigmouth buffalo	I.	cyprinellus	(Valenciennes)
Black buffalo	I.	niger	(Rafinesque)
Spotted sucker	Minytrema	melanops	(Rafinesque)
Shorthead redhorse	Moxostoma	breviceps	(Cope)
River redhorse	M.	carinatum	(Cope)
Black redhorse	M.	duquesnei	(Lesueur)
Golden redhorse	M.	erythrurum	(Rafinesque)

11. Family Ictaluridae

*Blue catfish	Ictalurus	furcatus	(LeSueur)
Black bullhead	I.	melas	(Rafinesque)
Yellow bullhead	I.	natalis	(LeSueur)
*Brown bullhead	I.	nebulosus	(LeSueur)
Flat bullhead	I.	platycephalus	(Girard)
*Channel catfish	I.	punctatus	(Rafinesque)
Mountain madtom	Noturus	eleutherus	(Jordan)
Slender madtom	N.	exilis	(Nelson)
Stonecat	N.	flavus	(Rafinesque)
Tadpole madtom	N.	gyrinus	(Mitchill)
Brindled madtom	N.	miurus	(Jordan)
Freckled madtom	N.	nocturnus	(Jordan & Gilbert)

12. Family Anguillidae

American eel	Anguilla	rostrata	(LeSueur)

13. Family Cyprinodontidae

Northern studfish	Fundulus	catenatus	(LeSueur)
Plains killifish	F.	kansae	(Garman)
Blackstripe topminnow	F.	notatus	(Rafinesque)
Starhead topminnow	F.	notti	(Agassiz)
Blackspotted topminnow	F.	olivaceus	(Storer)

II. Arkansas River (continued):

Plains topminnow Fundulus sciadicus (Cope)

14. Family Poeciliidae
Mosquitofish Gambusia affinis (Baird & Girard)

15. Family Amblyopsidae
Southern cavefish Amblyopsis rosae (Eigenmann)

16. Family Gasterosteidae
Brook stickleback Eucalia inconstans (Kirtland)

17. Family Aphredoderidae
Pirate perch Aphredoderus sayanus (Gilbert)

18. Family Serranidae
*White bass Roccus chrysops (Rafinesque)
Yellow bass R. mississippiensis (Jordan & Eigenmann)
⊛ Stripped bass R. saxatilis (Walbaum)

~~18~~ 19. Family Centrarchidae
*Rock bass Ambloplites ruestris (Rafinesque)
Flier Centrarchus macropterus (Lacepede)
*Warmouth Chaenobruttus gulosus (Cuvier)
Banded pygmy sunfish Elassoma zonatum (Jordan)
Redbreast sunfish Lepomis auritus (Linnaeus)
Green sunfish L. cyanellus (Rafinesque)
*Pumpkinseed L. gibbosus (Linnaeus)
Orangespotted sunfish L. humilis (Girard)
*Bluegill L. macrochirus (Rafinesque)
Dollar sunfish L. marginatus (Holbrook)
Longear sunfish L. megalotis (Rafinesque)
Redear sunfish L. microlophus (Gunther)
Spotted sunfish L. punctatus (Valenciennes)
Bantam sunfish L. symmetricus (Forbes)
*Smallmouth bass Micropterus dolomieui (Lacepede)
Spotted bass M. punctulatus (Rafinesque)
*Largemouth bass M. salmoides (Lacepede)
*White crappie Pomoxis annularis (Rafinesque)
*Black crappie P. nigromaculatus (LeSueur)

~~19~~ 20. Family Percidae
Crystal darter Ammacrypta asprella (Jordan)
Scaly sand darter A. vivax (Hay)
Mud darter Etheostoma asprigene (Forbes)
Scalyhead darter E. barratti (Holbrook)
Greenside darter E. blennioides (Rafinesque)
Bluntnose darter E. chlorosomum (Hay)
ENDEMIC Arkansas darter E. cragini (Gilbert)

II. Arkansas River (continued):

	Genus	Species
Fantail darter	Etheostoma	flabellare (Rafinesque)
Swamp darter	E.	gracile (Girard)
Slough darter	E.	grahami (Girard)
Harlequin darter	E.	histrio (Jordan& Gilbert)
Least darter	E.	microperca (Jordan & Gilbert)
Johnny darter	E.	nigrum (Rafinesque)
Goldstripe darter	E.	parvipinne (Gilbert & Swain)
Cypress darter	E.	proeliare (Hay)
Stippled darter	E.	punctulatum (Agassiz)
Orangebelly darter	E.	radiosum (HUbbs & Black)
Orangethroat darter	E.	spectabile (Agassiz)
Redfin darter	E.	whipplei (Girard)
⊛ *Yellow perch	Perca	flavescens (Mitchill)
*Logperch	~~P~~Percina	caprodes (Rafinesque)
Channel darter	P.	copelandi (Jordan)
Blackside darter	P.	maculata (Girard)
Longnose darter	P.	nasula (Bailey)
Leopard darter	P.	pantherina (Moore & Reeves)
Slenderhead darter	P.*	phoxocephala (Nelson)
Dusky darter	P.	sciera (Swain)
River darter	P.	shumardi (Girard)
Stargazing darter	P.	uranidea (Jordan &Gilbert)
⊛ *Sauger	Stizostedion	canadense (Smith)
⊛ *Walleye	S.	vitreum vitreum (Mitchill)

2~~0~~1. Family Sciaenidae
*Freshwater drum Aplodinotus grunniens (Rafinesque)

22 ~~21~~. Family Sparidae
Sheepshead Archosargus probatocephalus (Walbaum)

23 ~~22~~. Family Cottidae
Banded sculpin Cottus carolinae (Gill)

24 ~~23~~. Family Atherinidae
Brook silverside Labidesthes sicculus (Cope)
Mississippi silverside Menidia audens (Hay)

*** 25 ~~24~~. Family Acipenseridae
Shortnose sturgeon Acipenser brevirostrum (LeSueur)

*** This family shouldsbe family number 2.. .

* Denotes species introduced into Colorado (Beckman, 1952).
⊛ " " " " Oklahoma (Moore, 1952).

W. H. Dieffenbach
October 8, 1963
Fish distribution

III. Canadian River System:

		Genus	Species
1.	Family Petromyzontidae		
	Chestnut lamprey	Ichthyomyzon	castaneus (Girard)
	So. Brook lamprey	I.	gagei (Hubbs & Trautman)
2.	Family Acipenseridae		
	Shovelnose sturgeon	Scaphirhynchus	platorynchus (Rafinesque)
3.	Family Polyodontidae		
	Paddlefish	Polyodon	spathula (Walbaum)
4.	Family Lepisosteidae		
	Spotted gar	Lepisosteus	oculatus (Winchell)
	Longnose gar	L.	osseus (Linnaeus)
	Aligator gar	L.	spatula (Lacepede)
5.	Family Amiidae		
	Bowfin	Amia	calva (Linnaeus)
6.	Family Clupeidae		
	Skipjack herring	Alosa	chrysochloris (Rafinesques)
	Ohio shad	A.	ohiensis (Evermann)
	Gizzard shad	Dorosoma	cepedianum (LeSueur)
7.	Family Salmonidae		
	*Rainbow trout	Salmo	gairdneri (Richardson)
	*Brown trout	S.	trutta (Linnaeus)
8.	Family Hiodontidae		
	Goldeye	Hiodon	alosoides (Rafinesque)
9.	Family Esocidae		
	Grass pickerel	Esox	americanus vermiculatus (LeSueur)
10.	Family Cyprinidae		
	Stoneroller	Campostoma	anomalum (Rafinesque)
	*Goldfish	Carassius	auratus (Linnaeus)
	So. redbelly dace	Chrosomus	erythrogaster (Rafinesque)
	*Carp	Cyprinus	carpio (Linnaeus)
	Ozark minniw	Dionda	nubila (Forbes)
	Brassy minnow	Hybognathus	hankinsoni (Hubbs)
	Silvery minnow	H.	nuchalis (Agassiz)
	Bigeye chub	Hybopsis	amblops (Rafinesque)
	Hornyhead chub	H.	biguttata (Kirtland)
	Silver chub	H.	storeriana (Kirtland)
	Gravel chub	H.	x-punctata (Hubbs & Crowe)
	void *Gold shiner	Notemigonus	crysoleucas (Mitchill)

III. Canadian River System (continued):

	Genus	Species	
Pallid shiner	Notropis	amnis	(Hubbs & Greene)
Emerald shiner	N.	atherinoides	(Rafinesque)
River shiner	N.	blennius	(Girard)
Bigeye shiner	N.	boops	(Gilbert)
Bluntface shiner	N.	camurus	(Jordan & Meek)
Bigmouth shiner	N.	dorsalis	(Agassiz)
Ribbon shiner	N.	fumeus	(Evermann)
Wedgespot shiner	N.	greenei	(Hubbs & Ortenburger)
Silverband shiner	N.	illecebrosus	(Girard)
Red shiner	N.	lutrensis	(Baird & Girard)
Kiamichi shiner	N.	ortenburgeri	(Hubbs)
Plains shiner	N.	perpallidus	(Hubbs & Black)
Rosyface shiner	N.	rubellus	(Agassiz)
Sand shiner	N.	stramineus	(Cope)
Topeka shiner	N.	topeka	(Gilbert)
Redfin shiner	N.	umbratilis	(Girard)
Mimic shiner	N.	volucellus	(Cope)
Steelcolor shiner	N.	whipplei	(Girard)
Bleeding shiner	N.	zonatus	(Agassiz)
Pugnose minnow	Opsopoeodus	emiliae	(Hay)
Suckermouth minnow	Phenacobius	mirabilis	(Girard)
Bluntnose minnow	Pimphales	notatus	(Rafinesque)
Fathead minnow	P.	promelas	(Rafinesque)
Slim minnow	P.	tenellus	(Girard)
Bullhead minnow	P.	vigilax	(Gaird & Girard)
Creek chub	Semotilus	atromaculatus	(Mitchill)

11. Family Catostomidae

River carpsucker	Carpiodes	carpio	(Rafinesque)
Highfin carpsucker	C.	velifer	(Rafinesque)
Longnose sucker	Catostomus	catostomus	(Forbes)
White sucker	C.	commersoni	(Lacepede)
Blue sucker	Cycleptes	elongatus	(LeSueur)
Creek chubsucker	Erimyzon	oblongus	(Mitchill)
No. Hogsucker	Hypentelium	nigricans	(LeSueur)
Smallmouth buffalo	Ictiobus	bubalus	(Rafinesque)
Bigmouth buffalo	I.	cyprinellus	(Valenciennes)
Black buffalo	I.	niger	(Rafinesque)
River redhorse	Moxostoma	carinatum	(Cope)
Black redhorse	M.	duquesnei	(LeSueur)
Golden redhorse	M.	erythrurum	(Rafinesque)

12. Family Ictaluridae

Blue catfish	Ictalurus	furcatus	(LeSueur)
Black bullhead	I.	melas	(Rafinesque)
Yellow bullhead	I.	natalis	(LeSueur)
Channel catfish	I.	punctatus	(Rafinesque)

III. Canadian River System (continued):

Mountain madtom *Noturus eleutherus* (Jordan)
Slender madtom *N. exilis* (Nelson)
Stonecat *N. flavus* (Rafinesque)
Tadpole madtom *N. gyrinus* (Mitchill)
Brindles madtom *N. miurus* (Jordan)
Freckled madtom *N. nocturnus* (Jordan and Gilbert)
Flathead catfish *Pylodictis olivaris* (Rafinesque)

13. Family *Anguillidae*
American eel *Anguilla rostrata* (LeSueur)

14. Family *Cyprinodontidae*
No, studfish *Fundulus catenatus* (Storer)
Plains killifish *F. kansae* (Garman)
Blackstripe topminnow *F. notatus* (Rafinesque)
Starhead topminnow *F. notti* (Agassiz)
Blackspotted topminnow *F. olivaceus* (Storer)
Plains topminnow *F. sciadicus* (Cope)

15. Family *Poeciliidae*
Mosquitofish *Gambusia affinis* (Baird & Girard)

16. Family *Amblyopsidae*
Southern cavefish *Typhlichthys subterraneus* (Girard)

17. Family *Centrarchidae*
Rock bass *Ambloplites rupestris* (Rafinesque)
Wormouth *Chaenobryttus gulosus* (Cuvier)
Green sunfish *Lepomis cyanellus* (Rafinesque)
Orangespotted sunfish *L. humilis* (Girard)
Bluegill *L. macrochirus* (Rafinesque)
Longear sunfish *L. megalotis* (Rafinesque)
Redear sunfish *L. microlophus* (Gunther)
Smallmouth bass *Micropterus dolomieui* (Lacepede)
Spotted sunfish *M. punctulatus* (Rafinesque)
Largemouth bass *M. salmoides* (Lacepede)
White crappie *Pomoxis annularis* (Rafinesque)
Black crappie *P. nigromaculatus* (LeSueur)

18. Family *Percidae*
Scaly sand darter *Ammocrypta vivax* (Hay)
Greenside darter *Etheostoma blennioides* (Rafinesque)
Bluntnose darter *E. chlorosomum* (Hay)
Fantail darter *E. flabellare* (Rafinesque)
Swamp darter *E. fusiforme* (Girard)
Harlequin darter *E. histrio* (Jordan & Gilbert)
Least darter *E. microperca* (Jordan & Gilbert)

III. Canadian River System (continued):

Johnny darter *Etheostoma nigrum* (Rafinesque)
Cypress darter *E. proeliare* (Hay)
Orangethroat darter *E. spectabile* (Agassiz)
Redfin darter *E. whipplei* (Girard)
Logperch *Percina caprodes* (Rafinesque)
Channel darter *P. copelandi* (Jordan)
Blackside darter *P. maculata* (Girard)
Longnose darter *P. nasuta* (Bailey)
Slenderhead darter *P. phoxocephala* (Nelson)
Dusky darter *P. sciera* (Swain)
*Sauger *Stizostedion canadense* (Smith)

19. Family *Sciaenedae*
Freshwater drum *Aplodinotus grunniens* (Rafinesque)

20. Family *Cottidae*
Banded sculpin *Cottus carolinae* (Gill)

21. Family *Atherinidae*
Brook silverside *Labidesthes sicculus* (Cope)

I. Platte River System: (continued)

13. FamilyCyorinodontiformes

Banded killifish	Fundulus	diaphanus	(LeSueur)
Plains killifish	F.	kansae	(Garman)
Plains topminnow	F.	sciadicus	(Cope)

14. Famiby Gasterosteidae

Brook stickleback	Eucalia	inconstans	(Kirtland)

15. Family Serriaidae

*White bass	Roccus	chrysops	(Rafinesque)
Yellow bass	R.	mississippiensis	(Jordan and Eigenmann)

16. Family Centrarchidae

*Rock bass	Ambloplites	rupestris	(Rafinesque)
Warmouth	Chaenobryttus	gulosus	(Cuvier)
Green sunfish	Lepomis	cyanellus	(Rafinesque)
*Pumpkinseed	L.	gibbosus	(Linnaeus)
Orangespotted sunfish	L.	humilis	(Girard)
*Bluegill	L.	macrochirus	(Rafinesque)
Redear sunfish	L.	microlophus	(Gunther)
*Smallmouth bass	Micropterus	dolomieui	(Lacepede)
*Largemouth bass	M.	salmoides	(")
*White crappie	Pomoxis	annularis	(Rafinesque)
*Black crappie	P.	nigromaculatus	(LeSueur)

17. Family Percidae

Rainbow darter	Etheostoma	ceruleum	(Storer)
Iowa darter	E.	exile	(Girard)
Johny darter	E.	nigrum	(Rafinesque)
Orangethroat darter	E.	spectabile	(Agassiz)
Striped darter	E.	virgatum	(Jordan)
Banded darter	E.	zonale	(Cope)
*Yellow perch	Perca	flavescens	(MItchill)
*Logperch	Percina	caprodes	(Rafinesque)
Blackside darter	P.	maculata	(Girard)
Sauger	Stizostedion	canadense	(Smith)
*Walleye	S.	vitreum vitreum	(Mitbhill)

18. Family Sciaenidae

*Freshwater drum	Aplodinotus	grunniens	(Rafinesque)

19. Family Percopsidae

Trout- perch	Percopsis	omiscomaycus	(Walbaum)

* Denotes introduced into Colorado Platte River System. (Beckman 1952)

FISH DISTRIBUTION
OF
ARKANSAS, PLATTE, AND CANADIAN RIVER SYSTEMS

BY

William H. Dieffenbach

Submitted as partial fulfilment of
requirements in RW # 290, Fish Zoogeography.

W. H. Dieffenbach
November 5, 1963
Fish Distribution

Arkansas, Platte, and Canadian River Systems.

Endemic Species: (18 species)

Speckled chub	*Hybopsis aestivalis*
Blackspot shiner	*Notropis atrocaudalis*
Ghost Shiner	*Notropis buchanani*
Arkansas River shiner	*Notropis girardi*
? Tail light shiner	*Notropis maculatus*
Colorless shiner	*Notropis perpallidus*
Freckled madtom	*Noturus nocturnus*
Crystal darter	*Ammacrypta asprella*
Mud darter	*Etheostoma asprigena*
Scaly head darter	*Etheostoma barratta*
Arkansas River darter	*Etheostoma cragini*
Slough darter	*Etheostoma grahami*
Harlequin darter	*Etheostoma histrio*
Goldstripe darter	*Etheostoma parvipinne*
Orangebelly darter	*Ethrostoma radiosum*
Leopard darter	*Percina pantherina*
River darter	*Percina shumardi*
Stargazing darter	*Percina uranidae*

	Native	Exotic	Total
Families	25	2	27
Genera	77	6	83
Species	179	12	191

Family	Scientific Name	Classification	
		Water	Area
1. Petromyzontidae			
Chestnut lamprey	Ichthyomyzon castaneus	Ll	S.E.
So. Brook lamprey	" gagei	Lll	S.E.
2. Acipenseridae			
Shortnose sturgeon	Acipenser brevirostrum	I	S.E.
Shovelnose sturgeon	Scaphirhynchus platorynchus	I	S.E.
3. Lepisosteidae			
Spotted gar	Lepisosteus oculatus	Ll	S.E.
Longnose gar	" osseus	L l	S.E.
Shortnose gar	" platostomus	Ll	S.E.
Alligator gar	" spatula	Ll	S.E.
4. Polyodontidae			
Paddlefish	Polyodon spathula	Ll	S.E
5. Amiidae			
Bowfin	Amia calva	Ll	S.E.
6. Clupeidae			
Skipjack herring	Alosa chrysochloris	I	S.E.
Ohio shad	" ohiensis	I	S.E.
Gizzard shad	Dorosoma cepedianum	Ll	S.E.
7. Salmonidae			
Mt. Whitefish	Prosopium williamsoni	S	N.W.
Kokanee	Oncorhynchus nerka	LL	Introduced
Cutthroat trout	Salmo clarki	S	N.W.
Rainbow trout	Salmo gairdneri	S*L	Introduced
Brown trout	S. trutta	S-L	Introduced
Brook trout	Salvelinus fontinalis	S	"
Lake trout	" namaycush	L	~~N.~~". Introduced
American grayling	Thymallus signifer	L	~~N.W.~~ Introduced
8. Hiodontidae			
Goldeye	Hiodon alosiodes	Ll	S.E.
Mooneye	" tergisus	Ll	S.E.
9. Esocidae			
Grass pickeral	Esox americanus	L	S.E.
Chain pickeral	" niger	L	S.E.
No. pike	" lucius	L	S.E.
10. Characidae			
Banded tetra	Astyanax fusciatus	L	~~S.W.~~ {Introduced}

11. Cyprinidae

Stoneroller	*Campostoma*	*anomalum*	I	S.E.
Goldfish	*Carassius*	*auratus*	LL	Introduced
So. Redbelly dace	*Chrosomus*	*erythrogaster*	I	S.E.
No. Redbelly dace	"	*eos*	I	S.E.
Carp	*Cyprinus*	*carpio*	L	Introduced
Ozark minnow	*Dionda*	*nubila*	I	S.E.
Brassy minnow	*Hybognathus*	*hankinsoni*	I	S.E
Silver minnow	"	*nuchalis*	I	S.E.
Plains minnow	"	*placita*	Ll	S.E.
Speckled chub	*Hybopsis*	*aestivalis*	I	Endemic
Bigeye chub	"	*amblops*	Ll	S.E.
Hornyhead chub	"	*biguttata*	Ll	S.E.
Flathead chub	"	*gracilis*	I	S.E. - s.w.
Lake chub	"	*plumbea*	Ll	S.E.
Silver chub	"	*storeriana*	Ll	S.E.
Gravel chub	"	*x-punctata*	I	S.E.
Gold shiner	*Notemigonus*	*crysoleucas*	Ll	S.E.
Pallid shiner	*Notropis*	*amnis*	Ll	S.E.
Emerald shiner	"	*atherinoides*	I	S.E.
Blackspot shiner	"	*atrocaudalis*	I	Endemic
River "	"	*blennius*	I	S.E.
Bigeye "	"	*boops*	Ll	S.E.
Ghost "	"	*buchamani*	Ll	Endemic
Bluntface "	"	*camurus*	Ll	S.E.
Ironcolor "	"	*chalybaeus*	Ll	S.E.
Common "	"	*cornutus*	L	S.E.
Bigmouth "	"	*dorsalis*	Ll	S.E.
Ribbon "	"	*fumeus*	I	S.E.
Arkansas R."	"	*girardi*	I	Endemic
Wedgespot "	"	*greenei*	Ll	S.E.
Silverband "	"	*illicebrosus*	Ll	S.E.
Red "	"	*lutrensis*	I	S.E.
Tailight "	"	*maculatus*	Ll	Endemic?
Kiamiichi "	"	*ortenburgeri*	Ll	S.E.
Colorless "	"	*perpallidus*	Ll	Endemic
Chub "	"	*potteri*	Ll	Endemic
Rosyface "	"	*rubellus*	Ll	S.E.
Spotfin "	"	*spilopterus*	Ll	S.E.
Sand "	"	*stramineus*	I	S.E.
Topeka "	"	*topeka*	I	S.E.
Redfin "	"	*umbratilis*	Ll	S.E.
Blacktail "	"	*venustus*	Ll	S.E.
Mimic shiner	"	*volucellus*	Ll	S.E.
Steelcolor shiner	*Notropis*	*whipplei*	I	S.E.
Bleeding "	"	*zonatus*	Ll	S.E.
Pugnose minnow	*Opsopoedus*	*emiliae*	I	S.E.
Suckermouth minnow	*Phenacobius*	*mirabilis*	I	S.E.
Plains minnow	*Notropis*	*percobromus*	Ll	S.E.
Blacknose shiner	*Notropis*	*heterolepis*	Ll	S.E.
Spottail shiner	*Notropis*	*hudsonius*	Ll	S.E.

11. Cyprinidae (cont)

Bluntnose minnow	Pimephales	notatus	Ll	S.E.
Flathead "	"	promelas	L	S.E.
Slim minnow	"	tenellus	Ll	S.E.
Bullhead minnow	"	vigilax	Ll	S.E.
Blacknose dace	Rhinichthys	atratutus	Ll	S.E.
Longnose "	"	cataractae	I	S.E.
Speckled "	"	osculus	I	S.E.
Creek chub	Semotilus	atromaculatus	I-L	S.E.
Tench	Tinca	tinca	L	Introduced

12. Family Catostomidae

River carpsucker	Carpiodes	carpio	Ll	S.E.
Quillback	"	cyprinus	Ll	S.E.
Plains carpsucker	"	forbesi	Ll	S.E.
Highfin "	"	velifer	Ll	S.E.
Longnose sucker	Catostomus	catostomus	I	S.E.
White sucker	"	commersoni	I	S.E.
Blue sucker	Cycleptus	elongatus	I	S.E.
Creek chub	Erimyzon	oblongus	I-L	S.E.
Hog sucker	Hypentelium	nigricans	Ll	S.E.
Smallmouth buffalo	Ictiobus	bubalus	Ll	S.E.
Bigmouth "	Ictiobus	cyprinellus	Ll	S.E.
Black "	"	niger	Ll	S.E.
Spotted sucker	Minytrema	melanops	I	S.E.
River redhorse	Moxostoma	carinatum	Ll	S.E.
Black "	"	duquesnei	Ll	S.E.
Golden "	"	erythrurum	Ll	S.E.
No. "	"	macrolepidotum	Ll	S.E.
Shorthead redhorse	"	breviceps	Ll	S.E.

13. Family Ictaluridae

Blue catfish	Ictalurus	furcatus	I	S.E.
Black bullhead	"	melas	Ll-L	S.E.
Yellow "	"	natalis	Ll	S.E.
Brown "	"	nebulosus	Ll-L	S.E.
Flat "	"	platycephalus	I-Ll	S.E.
Channel catfish	"	punctatus	I	S.E.
Mountain madtom	Noturus	eleutherus	I-Ll	S.E.
Slender "	"	exilis	Ll	S.E.
Stone catfish	"	flavus	I-Ll	S.E.
Tadpolemadtom	"	gyrinus	Ll	S.E.
Brindled madtom	"	miurus	Ll	S.E.
Freckled "	"	nocturnus	I-Ll	**Endemic?**
Flathead catfish	Pylodictis	olivaris	I-Ll	S.E.

14. Family Anguillidae

American eel	Anguilla	rostrata	I-Ll	S.E.

15. Family Cyprinodontidae

No. studfish	Fundulus catenatus	Ll	S.E.
Banded killifish	Fundulus diaphanus	Ll	S.E.
Plains "	" kansae	Ll	S.E.
Blackstripe topminnow	Fundulus notatus	Ll	S.E.
Starhead "	" notti	Ll	S.E.
Blackspot "	" olivaceus	Ll	S.E.
Plains "	" sciadicus	Ll	S.E.

16. Family Poeciliidae

Mosquito fish	Gambusia affinis	Ll	S.E. (~~Introduced~~)

17. Family Amblopsidae

Southern Cavefish	Typhlichthys subterraneus	L	S.E~~(W.~~)

18. Family Gasterosteidae

Brook stickleback	Eucalia inconstans	I-Ll	S.E.

19. Family Percopsidae

Trout-perch	Percopsis omiscomayus	Ll	S.E.

20. Family Aphredoderidae

Pirate perch	Aphredoderus sayanus	I-Ll	S.E.

21. Family Serranidae

White bass	Roccus chrysops	Ll-L	S.E.
Yellow bass	" mississippiensis	Ll-L	S.E.
Striped bass	" saxatilis	L	~~S~~. (Introduced)

22. Family Centrarchidae

Rock bass	Ambloplites ruestris	Ll-L	S.E.
Flier	Centrarchus macropterus	Ll-L	S.E.
Warmouth	Chaenobruttus gulosus	Ll-L	S.E.
Banded pigmy sunfish	Elassoma zonatum	Ll-L	S.E.
Redbreast sunfish	Lepomis auritus	L	S.E.
Pumpkinseed "	" gibbosus	L	S.E. (~~Introduced~~)
Orangespotted sunfish	" humilis	L	S.E.
Green sunfish	" cyanellus	L	S.E.
Bluegill	" macrochirus	L	S.E.
Dollar sunfish	" marginatus	L	S.E. ~~(Introduced~~)
Longear "	" megalotis	L	S.E.
Redear "	" microlophus	L	S.E.
Spotted "	" punctatus	Ll-L	S.E.
Bantam "	" symmetricus	L	S.E.
Smallmouth bass	Micropterus dolomieui	I-L	S.E.
Spotted bass	" punctulatus	L-Ll	S.E.
Largemouth bass	" salmoides	L	S.E.
White crappie	Pomoxis annularis	Ll-L	S.E.
Black crappie	" nigromaculatus	Ll-L	S.E.

23. Family Percidae

Crystal darter	Ammacrypta asprella	I	Endemic?

23. Family Percidae (con't)

Scaly sand darter	Ammacrypta	vivax	I-Ll	S.E.
Mud darter	Etheostoma	asprigena	Ll	Endemic
Scaly head darter	"	barratta	LL	Endemic
Greenside darter	"	blennioides	Ll	S.E.
Bluntnose "	"	chlorosomum	Ll	S.E.
Arkansas "	"	cragini	Ll	Endemic
Rainbow "	"	caeruleum	Ll	S.E.
Iowa darter	"	exile	Ll	S.E.
Faintail darter	"	flabellare	Ll	S.E.
Swamp darter	"	gracile	Ll	S.E.
Slough "	"	grahami	Ll	Endemic
Harlequin darter	"	histrio	Ll	Endemic
Least darter	"	microperca	I-Ll	S.E.
Johnny "	"	nigrum	I-Ll	S.E.
Goldstripe darter	"	parvipinne	Ll	Endemic
Cypress darter	"	proeliare	Ll	S.E.
Stippled "	"	punctulatum	Ll	S.E.
Orangebelly darter	"	radiosum	Ll	Endemic?
Orangethroat "	"	spectabile	I-Ll	S.E.
Redfin darter	"	whipplei	Ll	S.E.
Banded "	"	zonale	Ll	S.E.
Yellow perch	Perca	flavescens	I-L	S.E.
Logperch	Percina	caprodes	I-Ll	S.E.
Channel darter	"	copelandi	Ll	S.E.
Blackside darter	"	maculata	Ll	S.E.
Longnose "	"	nasula	Ll	S.E.
Leopard "	"	pantherina	Ll	Endemic
Slenderhead darter	Percina	phoxocephala	Ll	S.E.
Dusky darter	Percina	sciera	Ll	S.E.
River "	"	shumardi	Ll	Endemic?
Stargazing darter	"	uranidae	Ll	Endemic
Sauger	Stizostedion	canadense	I-L	S.E.
Walleye	"	vitreum vitreum	I-L	S.E.

24. Family Sciaenidae

Freshwater drum	Aplodinotus	grunniens	L-Ll	Introduced

25. Family Sparidae

Sheepshead	Archosargus	probatocephalus	L-Ll	S.E.

26. Family Cottidae

Banded sculpin	Cottus	carolinae	I-Ll	S.E ~~N.W.~~ (?)

27. Family Atherinidae

Brook silverside	Labidesthes	sicculus	I-Ll	S.E.
Mississippi silverside	Menidia	audens	I-Ll	S.E.

W. H. Dieffenbach
Fish Distribution
October 15, 1963

The drainages presented in this paper include:

A .... Arkansas River

P .... Platte River

C .... Canadian River

E. or I. denote:

E... Endemic
I... Introduced

x Species present in that river.

O Species not present in that river.

Water classification type:
S Denotes swift type water.
I Denotes Intermediate type water.
L Denotes Lake type water.

Classification of area:

N Northern origin
E Eastern origin
W Western origin
S Southern origin

A total of 191 species were found to be present in these three drainages.

William H. Dieffenbach
Fish distribution
October 15, 1963.

Family	Common Name		Drainage			Classification	
		E. OR I.	A	P	C	Water	Area
1. Petromyzontidae							
	Chestnut lamprey		x	0	x	I	N, E
	So. Brook lamprey		x	0	x	I	N
2. Acipenseridae							
	Shortnose sturgeon		?	x	x	I,S	E
	Shovelnose sturgeon		x	x	x	I	n,E
3. Polyodontidae							
	Paddlefish		x	x	x	I	S
4. Lepisostidae							
	Spotted gar		x	0	x	L	S,[illegible]
	Longnose gar		x	x	x	I	E & SE
	Shortnose gar		x	x	0	I	SE
	Alligator gar		x	0	x	L - I	S
5. Amiidae							
	Bowfin		x	x	x	I	E
6. Clupeidae							
	Skipjack herring		x	0	x	I	SE
	Ohio shad		x	0	x	I	E
	Gizzard shad		x	x	x	L	SE
7. Salmonidae							
	MT. Whitefish		0	x	0	s	W
	Kokanee	I					NWW
	Cutthroat		x	x	0	S,L	NW
	Rainbow trout	I					W
	Brown trout	I					Europe
	Brook trout	I					East
	Lake trout	I					NE
	American grayling		0	?	0	L	N
8. Hiodontidae							
	Goldeye		x	x	x	I	NE
	Mooneye	[illegible].	x	0	0	I	------
9. Esocidae							
	Grasspickeral		x	x	x	L	E
	Chain pickeral	I	x	0	0	L	E
	No. Pike	I	x	x	0	L	E
10. Characidae							
	Banded tetra	I	x	0	0	I	S
11. Cyprinidae							
	Stoneroller		x	x	x	S	E
	Goldfish	I	x	x	x	L	Orient.
	So. Redbelly dace		x	x	x	I	E

11. Cyprinidae (continued)

Common Name	E. or I.	Drainage A	P	C	Classifiaation Water	Area
No. Redbelly dace		0	x0	0	I	NE
Carp	I.	x	x	x	L	Orient.
Ozark minnow		x	0	x	I	E
Brassy minnow		x	x	x	I	S
Silver minnow		x	x	x	I	S
Plains minnow		x	x	?	I	SE
Speckled chub	E..	x	0	0	I	--------
Bigeye chub		x	0	x	I	E
Hornyhead chub		x	x	x	I	S
Flathead chub		x	x	0	I	N & W
Lake chub		0	x	0	L	N
Silver chub		x	x	x	I	N
Gravel chub		x	0	x	?	N,E
Gold shiner		x	x	x	L	N
Pallid shiner		x	0	x	I	SE
Emerald shiner		x	x	x	I	N
Blackspot "	E..	x	0	0	I	----------
River "		x	x	x	S	E
Bigeye "		x	0	x	I	E,N
Ghost "	E..	x	0	0	I	----------
Bluntface "		x	0	x	I	E
Ironcolor "	E..	x	0	0	S	----------
Common "		x	x	0	I,L	E.
Bigmouth "		x	0	x	I	NE
Ribbon "		x	0	x	I	S
Arkansas R. "	E..	x	0	0	I	-----------
Wedgespot "	?	x	0	x	I	?
Silverband "	?	x	0	x	I	?
Red shiner		x	x	x	s,L	E
Taliight "	E?	x	0	0	I	E
Kiamiichi "		x	0	x	I	S
Plains "		x	x	x	I	E
Colorless "	E..	x	0	0	I	----------
Chub "	E..	x	0	x	I	-----------
Rosyface "		x	0	x	I	N, E
Spotfin "		x	x	0	I	NE
Sand shiner		x	x	x	S,I	N
Topeka "		X	x	x	I	?
Redfin "		x	0	x	I	E
Blacktail "	E..	x	0	0	I	----------
Mimmic "		x	0	x	I	NE
Steelcolor shiner		x	0	x	I	E
Bleeding "		x	0	x	S	E
Blacknose "	E..	0	x	0	I	----------
Spottail "	E..	0	x	0	I	(NE)
Pugnose minnow	?	x	0	x	I	E
Suckermouth "		x	x	x	I	E
Bluntnose "		X	X	X	I	E
Flathead "		x	x	x	I	SE
Slim minnow		x	0	x	I	?
Bullhead minnow		x	0	x	I	N & E
Blacknose dace	E..	0	x	0	I	(NE)
Longnose "		x	x	0	I,S	E
Speckled "		x	x	0	I	SW
Creek chub		x	x	x	I	E
,Tench	I..	x	x	x	I,L	Orient.

Family	Common name	E. or I.	Drainage			Classification	
			A	P	C	Water	Area
12. Catostomidae							
	River carpsucker		x	x	x	I,S	N,S
	Quillback		0	x	0	I,L	E
	Plains carpsucker		x	x	0	I	N,S,E.
	Highfin "		x	x	x	I	N,E
	Longnose sucker		x	x	x	I	E
	White sucker		x	x	x	I	E
	Blue sucker		x	x	x	I	N
	Creek chub		x	?	x	I	E
	Hog sucker		x	0	x	I	E
	Smallmouth buffalo		x	0	x	I	S
	Bigmouth "		x	x	x	I	N & S
	Black "		x	x	x	I	N & S
	Spotted sucker	[redacted]. ?	x	0	0	I	N & E
	River redhorse		x	0	x	I	NE
	Black redhorse		x	0	x	I	N & E
	Golden redhorse		x	x	x	I	N & E
	No. Redhorse	[redacted]. ?	0	x	0	I	N & E
	Shorthead redhorse	[redacted]. ?	x	0	0	I	N
13. Ictaluridae							
	Bluecatfish		xx	x	x	I,S	S
	Black bullhead		x	x	x	L	E
	Yellow "		x	x	x	I	S,E,N.
	Brown "		x	?	?	L	E
	Flat "	[redacted]. ?	x	0	0	I	E
	Channel catfish		x	x	x	I,S	SE
	Mountain madtom		x	0	x	S	E
	Slender "		x	x	x	I	N
	Stonecat		x	x	x	I	N
	Tadpole madtom		X	x	x	I	E
	Brindled "		x	0	x	I	S
	Freckled "	E...	x	0	x	I,S	--------
	Flathead catfish		0	x	x	I,S	N
14. Anguillidae							
	American eel		x	x	x	I	N
15. Cyprinodontidae							
	NO. Studfish		x	0	x	I	N
	Banded killifish		0	x	0	I	NE
	Plains killifish		x	x	0	I	E
	Blackstripe topminnow		x	0	x	I	N, E, S
	Starhead "		x	0	x	I	SE
	Blackspot "		x	0	x	I	E
	Plains "		x	x	x	I	N,S,E
16. Poeciliidae							
	MOsquito fish	I...	x	x	x	L	SE

Family	Common Name	E. or I.	Drainage			Classification	
			A	P	C	Water	area
17. Gasterosteidae							
	Brook stickleback		x	x	O	S	NE
18. Amblyopsidae							
	Southern cavefish		x	O	x	L	SE
19. Percopsidae							
	Trout-perch		O	x	O	S,L	?
20. Aphredoderidae							
	Pirate perch	[illegible] ?	x	O	O	I	N & S
21. Serranidae							
	White bass		x	x	O	I	NE
	Yellow bass		x	x	O	L	E
	Striped bass	I.	x	?	x	L	E
22. Centrarchidae							
	Rock bass		x	x	x	L	E
	Flier	[illegible]. ?	X	O	O	L	SE
	Warmouth		X	X	X	L	N, S, E
	Banded pigmy sunfish	[illegible].?	x	O	O	L	S & E
	Redbreast sunfish		x	O	O	L	E
	Pumpkinseed "	I	x	x	O	L	N & E
	Orangespotted "		x	x	x	L	N, E.
	Green sunfish		x	x	x	L	N, S, E.
	Bluegill		x	x	x	L	E.
	Dollar sunfish	I..	x	O	O	L	SE
	Longear "		x	O	O	L	SE
	Redear "		x	x	x	L	SE
	Spotted "		x	O	x	L	SE
	Bantam "	[illegible]..	x	O	O	L	________
	Smallmouth bass		x	x	x	I	N &E
	Spotted bass	[illegible] ?	x	O	O	I	NE
	Largemouth bass		x	x	x	L	N, E, S.
	White crappie		x	x	x	L	N, E.
	Black crappie		X	X	X	L	N, E.
23. Percidae							
	Crystal darter	E. ?	x	O	O	I,S	E
	Scaly sand "		x	O	x	S	NE
	Mud darter	E.	x	O	O	I,S	--------
	Scaly head darter	E...	x	O	O	I,S	--------
	Greenside "	[illegible]. ?	O	O	x	S	(E)
	Bluntnose "		x	O	x	I	NE
	Arkansas "	E...	x	O	O	I	--------
	Rainbow "	[illegible] ?	O	x	O	I	N, E.
	Iowa darter		O	x	O	I	N
	Faintail darter		x	O	x	I	N, E.
	Swamp darter		x	O	x	I	E
	Slough "	E..	x	O	O	I	(SE)
	Harlequin darter	E...	x	O	x	I	(S)
	Least darter		x	O	x	I	NE
	Johnny "		x	x	x	I	N, E, S.
	Goldstripe darter	E..	x	O	O	I	E
	Cypress "		x	O	x	I	SE
	Stippled "		x	x	O	I	SE

Family	Common Name	E. or I.	Drainage			Classification	
			A	P	C	Water	Area
23. Percidae (continued).							
	Orangebelly darter	E ?	x	O	O	S,I	E.
	Orangethroat "		x	x	x	I	SE.
	Redfin darter		x	O	x	I	S.
	Banded "		x	x	O	S, I	N,E.
	Yellow perch		x	x	x	L	E.
	Logperch		x	x	x	I	N
	Channel darter		x	O	x	S-I.	E
	Blackside "		x	x	x	S	E
	Longnose "		x	O	x	S- I	SE
	Leopard "	E..	x	O	O	S-I	----------
	Slenderhead darter		x	O	x	I	E.
	Dusky darter		x	O	x	I	N.
	River "	E ?	x	O	O	I	(NE)
	Stargazing darter	E..	x	O	O	I	-----
	Sauger		x	x	x	I	NE
	Walleye		x	x	x	L	NE
24. Sciaenidae							
	Freshwater drum	I	x	x	x	L	N, S, E.
25. Sparidae							
	Sheepshead		x	O	O	L	S &E
26. Cottidae							
	Banded sculpin		x	O	x	I-S	N
27. Atherinidae							
	Brook silverside		x	O	x	I	N, S, E/
	Mississippi Silverside	[illegible]...	x	O	O	I	----------

Part III

Fishes by Individual Drainage

W. H. Dieffenbach
October 8, 1963
Fish Distribution

I. Platte River System:

		Genus	Species
1.	Family Acipenseridae		
	Shovelnose Sturgeon	Scaphirhynchus	platorynchus (Rafinesque)
2.	" Polyodontidae		
	Paddlefish	Polyodon	spathula (Walbaum)
3.	" Lepisosteidae		
	Longnose gar	Lepisosteus	osseus (Linnaeus)
	Shortnose gar	L. "	platostomus (Rafinesque)
4.	" Amiidae		
	Bowfin	Amia	calva (Linnaeus)
5.	" Clupeidae		
	* Gizzard shad	Dorosoma	cepeianum (LeSueur)
6.	" Salmonidae		
	Mountain whitefish	Prosopium	williamsoni (Girard)
	Cutthroat trout	Salmo	clarki (Richardson)
	*Rainbow trout	S.	gairdneri (Richardson)
	*Brown trout	S.	trutta (Linnaeus)
	*Brook trout	Salvelinus	fontinalis (Mitchill)
	*Lake trout	Salvelinus	namaycush (Walbaum)
	* Kokanee Salmon	Oncorhynchus	nerka (kennerlyi)(Suckley)
	*(?)American grayling	Thymallus	signifer (Richardson)
7.	" Hiodontidae		
	Goldeye	Hiodon	alosoides (Rafinesque)
8.	" Esocidae		
	*Grass pickerel	Esox	americanus vermiculatus (LeSueur)
	*Northern pike	Esox	lucius (Linnaeus)
9.	" Cyprinidae		
	Stoneroller	Campostoma	anomalum (Rafinesque)
	* Goldfish	Carassius	auratus (Linnaeus)
	No. Redbelly Dace	Chrosomus	eos (Cope)
	So. Redbelly Dace	Chrosomus	erythrogaster (Rafinesque)
	* Carp	Cyprinus	carpio (Linnaeus)
	Brassy minnow	Hybognathus	hankinsoni (Hubbs)
	Silver minnow	H.	nuchalis (Agassiz)
	Hornyhead chub	Hybopsis	biguttata (Kirtland)
	Flathead chub	H.	gracilis (Richardson)
	Lake chub	H.	plumbea (Agassiz)
	Silver chub	H.	storeriana Kirtland)
	*Golden shiner	Notemigonus	crysoleucas (Mitchill)

I. Platte River System: (continued)

9. Family Cyprinidae

	Genus	Species
Emerald shiner	Notropis	atherinoides (Rafinesque)
River shiner	N.	blennius (Girard)
Common shiner	N.	cornutus (Mitchill)
Blacknose shiner	N.	heterolepis (Eigenmann)
Spottail shiner	N.	hudsonius (Clinton)
Red shiner	N.	lutrensis (Baird and Girard)
Plains shiner	N.	percobromus (Cope)
Spotfin shiner	N.	spilopterus (Cope)
Sand shiner	N.	stramineus (Cope)
Topeka shiner	N.	topeka (Gilbert)
Suckermouth minnow	Phenacobius	mirabilis (Girard)
Bluntnose minnow	Pimephales	notatus (Rafinesque)
Fathead minnow	P.	prometas (Rafinesque)
Blacknose dace	Rhinichthys	atratutus (Hermann)
Longnose dace	R.	cataractae (Valenciennes)
Speckled dace	R.	osculus (Girard)
Creek chub	Semotilus	atromaculatus (Mitchill)
* Tench	Tinca	tinca (Linnaeus)

10. Family Catostomidae

	Genus	Species
River carpsucker	Carpiodes	carpio (Rafinesque)
Quillback	C.	cyprinus (LeSueur)
Plains carpsucker	C.	forbesi (Hubbs)
Highfin carpsucker	C.	velifer (Rafinesque)
Longnose sucker	Catostomus	catostomus (Forster)
White sucker	C.	commersoni (Lacépède)
Blue sucker	Cycleptus	elongatus (LeSueur)
Bigmouth buffalo	Ictiobus	cyprinellus (Valenciennes)
Black buffalo	I.	niger (Rafinesque~~s~~)
Golden redhorse	Moxostoma	erythrurum (Rafinesque)
Northern redhorse	M.	macrolepidotum (LeSueur)
Mountain sucker	Pantosteus	platyrhynchus (Cope)

11. Family Ictaluridae

	Genus	Species
* Blue catfish	Ictalurus	furcatus (LeSueur)
Black bullhead	I.	melas (Rafinesque)
Yellow bullhead	I.	natalis (LeSueur)
* Brown bullhead	I.	nebulosus (LeSueur)
* Channel catfish	I.	punctatus (Rafinesque)
Slender madtom	Noturus	exilis (Nelson)
Stonecat	N.	flavus (Rafinesque)
Tadpole madtom	N.	gyrinus (Mitchill)
* Flathead catfish	Pylodictis	olivaris (Rafinesque)

12. Family Anguillidae

	Genus	Species
American eel	Anguilla	rostrata (LeSueur)

Distributions of Juvenile Steelhead and Cutthroat Trout (*Salmo gairdneri* and *S. clarki clarki*) Within Streams in Southwestern British Columbia[1]

By G. F. Hartman and C. A. Gill

Fish and Wildlife Branch
Fisheries Research Division, c/o Institute of Fisheries
University of British Columbia, Vancouver, B.C.

ABSTRACT

Trout were collected and identified from 66 streams or stream systems of different size and gradient. Total dissolved solids (T.D.S.) and *p*H were determined on most streams. Size and profile of streams to a large degree determined the species of trout present. Large streams, with drainage area over 130 km^2, were predominantly occupied by steelhead. Small streams, drainage area under 13 km^2, were predominantly occupied by cutthroat. Streams less than 120 km^2 in drainage area with steep gradients, and emptying directly into the sea, usually supported steelhead, as did large rivers. Those which dropped steeply and then levelled and ran through several miles of sloughs usually supported cutthroat. Where both species occurred, cutthroat were most often predominant in the small tributaries and headwaters, and steelhead in the lower reaches of the main stream. Stream *p*H's were usually lower in winter than in summer, but had no obvious effect on trout distribution. Many cutthroat streams had high T.D.S. readings in the lower reaches in summer and low T.D.S. readings in these areas in winter. Otherwise there were no marked differences between steelhead and cutthroat streams in terms of T.D.S.

INTRODUCTION

The distributions of different species of fish within stream systems have been related to a number of physiographic factors, including temperature, *p*H, gradient, and size (Shelford, 1911; Thompson and Hunt, 1930; Trautman, 1942; Burton and Odum, 1945; Starmack, 1956; and Huet, 1959, 1962). Previous studies on distributions of salmonids in southwestern British Columbia (Hartman, 1965) showed that juvenile steelhead trout usually existed in close association with underyearling coho salmon along the lengths of streams. Steelhead and cutthroat trout juveniles, on the other hand, appeared to be segregated into streams of different sizes or into different areas of the same stream system.

In the present study a large number of collections of trout were made in a series of streams of different sizes and gradients in an effort to describe more fully the differences in distribution of young steelhead and cutthroat. The field work for the investigation was carried out between 1960 and 1966. Most of the data were gathered in 1964 and 1965. Stream profiles were determined and measurements of *p*H, total dissolved solids, temperature, and stream

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discharge were taken to determine if any of these factors bore an obvious relationship to the distribution of one species of trout or the other. The work is not intended to describe completely the distributional differences between the two species but is presented rather as a preliminary to a better understanding of their ecological relationships.

STUDY AREA, MATERIALS, AND METHODS

The 66 streams sampled lie in the following regions of southwestern British Columbia: the east coast of Vancouver Island, 16 streams (Fig. 1); the Squamish area, 7 streams; and the lower Fraser Valley, 43 streams (Fig. 2). Names corresponding to stream numbers on Fig. 1 and 2, and approximate drainage areas, are given in Table I. The smaller streams are characterized by high winter and low summer discharge. The larger rivers normally have winter and summer run-off maxima, corresponding with heavy rainfall and snowmelt farther inland respectively.

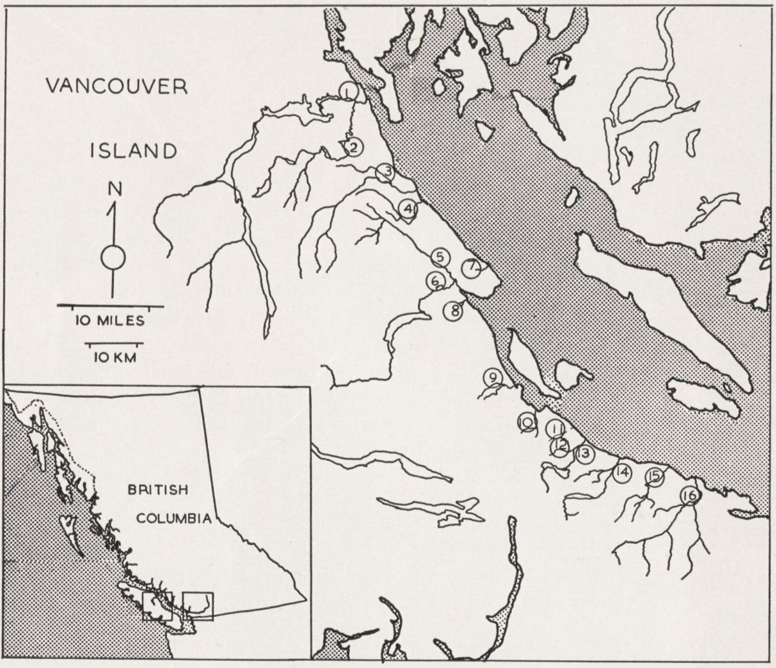

FIG. 1. Locations of streams sampled on the east side of Vancouver Island. Names of streams given in Table I (see text). Inset map shows locations of the two major sampling areas.

Wherever access permitted, collections were made at a series of sites along the full length of each stream. Some inaccessible streams were sampled only at one location.

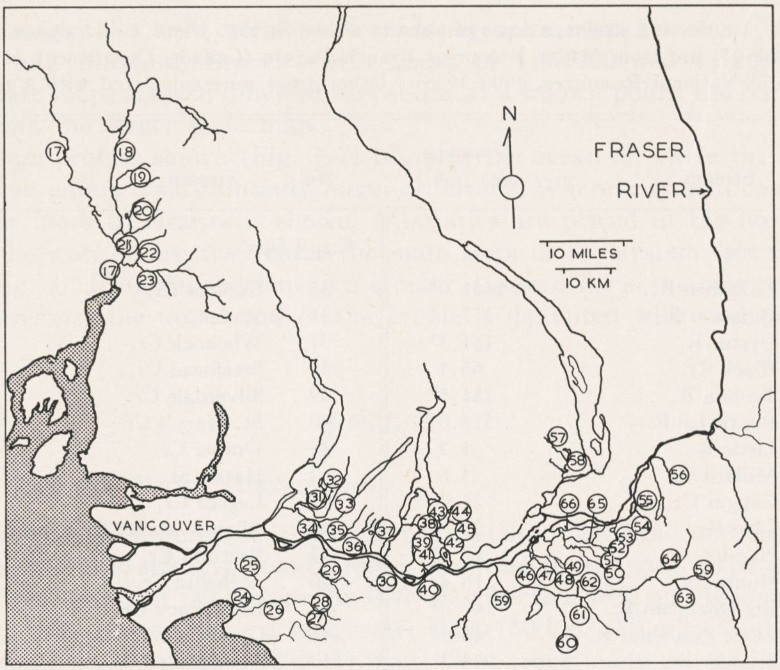

Fig. 2. Locations of streams sampled in the lower Fraser Valley and Squamish area. Names of streams given in Table I (see text).

Most collections were made with 3 × 2 m and 9 × 2 m seines with mesh size approximately 7 mm stretched mesh.

A 440 v, d-c fish shocker, Smith Root Laboratories Type IV, was used to make a limited number of collections. In situations where water depth or bottom topography prevented seining, fish were angled with No. 14 or No. 16 hooks and bait.

In many locations where streams were turbid or very turbulent, explosives were detonated in the water a few meters upstream from a positioned seine net, as described by Hartman (1965).

Measurements of *p*H were taken with a portable *p*H meter, Beckman N or E.I.L., 30C, within 1 min of the time the water sample was drawn from the stream. Total dissolved solids (T.D.S.) of stream water samples were determined in the laboratory with a conductivity bridge, Industrial Instrument R.C.7. Stream discharge data and some drainage areas were obtained from publications of Canada Department of Northern Affairs and National Resources (1960–1963). Stream discharges were estimated at collection sites by visual observations of cross section and velocity, where possible. Data on water chemistry, stream discharge, and drainage area are on file with the Fish and Wildlife Branch.

Trout were identified using six characters which were diagnostic on hatchery-reared fish of known parenthood (Hartman, MS, 1956). The characters were hyoid teeth, hyoid red pigmentation, mid-dorsal parr marks,

TABLE I. Names and drainage areas of streams shown in Fig. 1 and 2. Drainage areas with an asterisk (*) are from Water Resources Branch Papers (Canada Department of Northern Affairs and National Resources, 1960–1963). Other areas were calculated with a planimeter.

No.	Stream	Drainage area (*km*^{2})
Fig. 1		
1	Campbell R.	1461.0*
2	Quinsam R.	277.1*
3	Oyster R.	181.3*
4	Black Cr.	65.1
5	Tsolum R.	251.5*
6	Puntledge R.	518.0*
7	Little R.	4.2
8	Millard Cr.	3.6
9	Cougar Cr.	24.0
10	Chef Cr.	21.0
11	Nile Cr.	17.9*
12	Hunts Cr.	16.4
13	Big Qualicum R.	147.6*
14	Little Qualicum R.	246.1*
15	French Cr.	73.3
16	Englishman R.	287.5*
Fig. 2		
17	Squamish R.	1981.3*
18	Cheakamus R.	813.3*
19	Culliton Cr.	66.7
20	Brohm Cr.	24.5
21	Schoonover Cr.	6.2
22	Mashiter Cr.	46.0
23	Mamquam R.	384.0
24	Serpentine R.	105.0
25	Mahood Cr.	19.7*
26	Nicomekl R.	99.5
27	Anderson Cr.	29.0
28	Murray Cr.	33.0
29	Salmon R.	83.0*
30	Nathan Cr.	35.0
31	Blaney Cr.	18.9
32	Blaney Cr. (east trib.)	2.0
33	S. Alouette R.	205.0*
34	S. Alouette R. trib.	2.0
Fig. 2 (*con't*)		
35	Kanaka Cr.	55.0
36	York Cr.	5.3
37	Whonock Cr.	20.0
38	Steelhead Cr.	14.6
39	Silverdale Cr.	21.2
40	St. Mary's Cr.	2.5
41	Draper Cr.	5.6
42	Hatzic Sl.	55.0
43	Legace Cr.	5.2
44	Allan L. outlet Cr.	9.4
45	Pattison Cr.	7.3
46	Atchelitz Cr.	7.4
47	Luckakuck Cr.	4.8
48	Chilliwack Cr.	15.2
49	Semmihault Cr.	8.3
50	Elk Cr.	16.0
51	Ford Cr.	8.5
52	Nevin and Dunnville cr.	18.0
53	Bridal Falls Cr.	13.0
54	Fraser R. trib. ½ mile west of Jones Cr.	7.0
55	Fraser R. trib. ½ mile east of Jones Cr.	1.1
56	Lorenzetta Cr.	35.0
57	Sakwi Cr.	18.6
58	Weaver Cr.	48.2
59	Chilliwack R.	1250.0*
60	Liumchen Cr.	52.0
61	Chilliwack R. trib. ½ mile west of Tamihi Cr.	6.0
62	Ryder Cr.	7.3
63	Chilliwack R. trib. 5 miles east of Foley Cr.	2.4
64	Foley Cr.	80.0
65	Hope Sl.	85.7
66	Camp Sl.	13.6

maxillary length, and dorsal fin shape and color. Many trout under 1-year old, and some of those 1–2 years old, could not be classified with certainty, even though six characters were used. These fish are included in the results because of the possibility that they represent hybridization in some situations, particularly where both species are known to occur.

Stream profiles were calculated from topographic maps (British Columbia Surveys and Mapping Branch) with scales of 1:50,000 and 1:126,720. In cases where maps showed different elevations at a known point, the data were taken from the larger scale map.

Stream profiles shown (Fig. 3–7) begin at the ocean or where the stream in question enters a substantially larger tributary. Where a system consisting of two or more tributaries is shown, tributaries are placed in the horizontal scale to indicate where they enter the main stem of the system (see Salmon River, Fig. 7). If only a segment of a stream is shown (as is the case with the longer streams) the upper end of the profile is delimited with two diagonal lines.

RESULTS

STREAM SIZE AND TROUT DISTRIBUTION

The principal differences in distribution between steelhead and cutthroat juveniles related to stream size and profile. Steelhead trout appear to be adapted to large rivers or swift tributaries. In 34 of 40 collection sites on the mainstems of 13 large streams, drainage areas greater than 130 km^2 (50 $miles^2$), the identifiable trout were steelhead (Fig. 3). Cutthroat trout made up a minor part of the six other collections.

Cutthroat trout were found in the very small streams or in headwaters. In the 21 small streams with drainage areas up to 13 km^2 (5 $miles^2$), all identifiable fish were cutthroat in 24 out of 33 collections and steelhead in 5 out of 33 collections (Table I, Fig. 4–7). Both species occurred in 3 collections.

Table II, showing the numbers of streams in various drainage area categories in which one species of trout or the other or both occur, indicates that cutthroat trout are predominantly a small stream form. In the four large streams where they occurred, cutthroat made up a minor portion of the trout fauna. Steelhead occurred frequently over the range of stream sizes investigated.

EFFECT OF STREAM PROFILES

If all streams with drainage areas under 120 km^2 (46 $miles^2$) are considered it becomes evident that stream profile as well as size affects the trout species composition. The nine streams of this size in which all the identifiable trout were steelhead drop steeply into a large river or the ocean (Fig. 4). In those streams in which the identifiable trout were cutthroat the gradient is low to moderate (Fig. 5) or is near level and then increases sharply (Fig. 6). Eleven of these streams drain into large slough systems.

Spawning cutthroat trout enter Hope and Camp sloughs but young cutthroats were not obtained in these bodies of water. It is presumed that cutthroat spawners move through the sloughs and spawn in the steep tributaries. Figure 6 shows that cutthroat occur in streams with steep profiles. In all cases except Chef Creek, however, these streams flatten and run through an

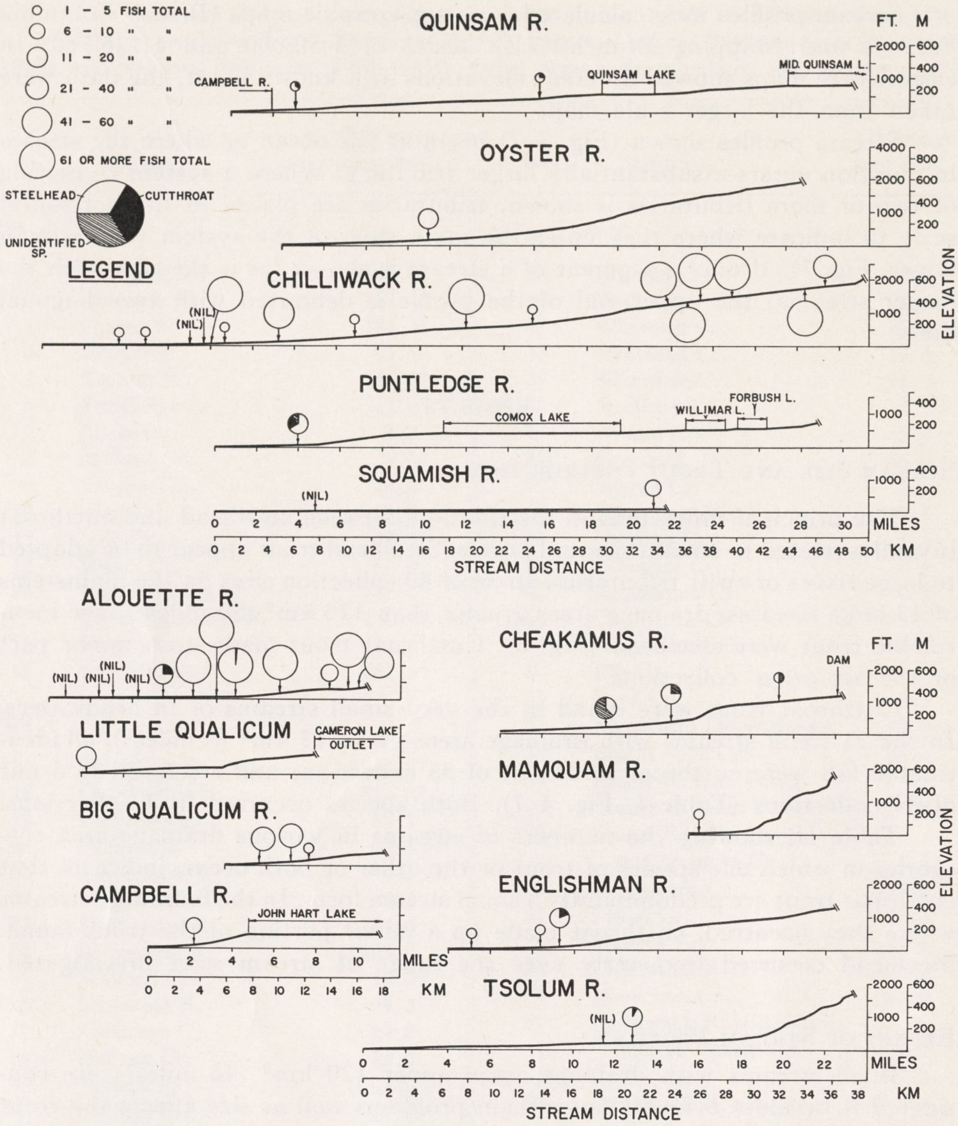

FIG. 3. Profiles of streams with drainage areas greater than 130 km^2, showing locations of sampling stations and sizes and compositions of trout collections. Legend showing sample sizes and composition applies to Fig. 3–7, all of which have the same scale. See text for further explanation of Fig. 3–7.

extensive area of meadowland or slough. The profiles of medium and small streams occupied by cutthroat trout are usually different than those occupied by steelhead trout. However, within either type of stream, cutthroat and steelhead trout were each generally found in riffle-pool complexes or in rocky

TABLE II. Numbers of streams of different drainage areas in which the trout sampled were cutthroat only, cutthroat and steelhead, or steelhead only.

	No. of streams with:		
Stream drainage area (km^2)	Cutthroat	Cutthroat & steelhead	Steelhead
0–40	23	11	6
41–80	0	4	4
81–120	0	3	0
121–160	0	0	1
161–200	0	0	1
>200	0	4[a]	7

[a] Cutthroat comprised about 3 and 12% of the trout in two of the four streams and 25 and 29% in the other two.

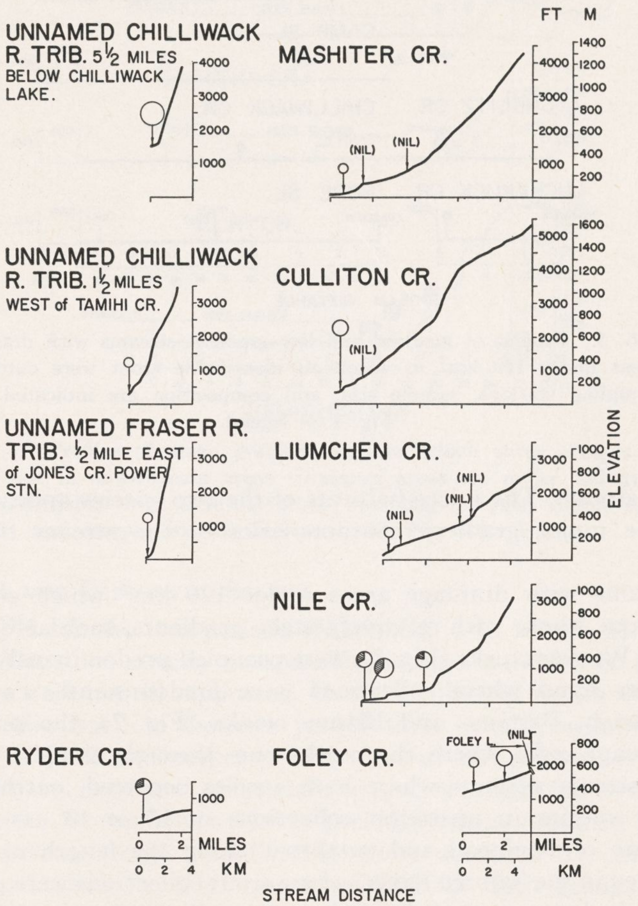

FIG. 4. Profiles of streams with drainage areas under 120 km² in in which all identifiable trout were steelhead. Sampling stations, sample size, and composition are indicated. See Fig. 3 for legend.

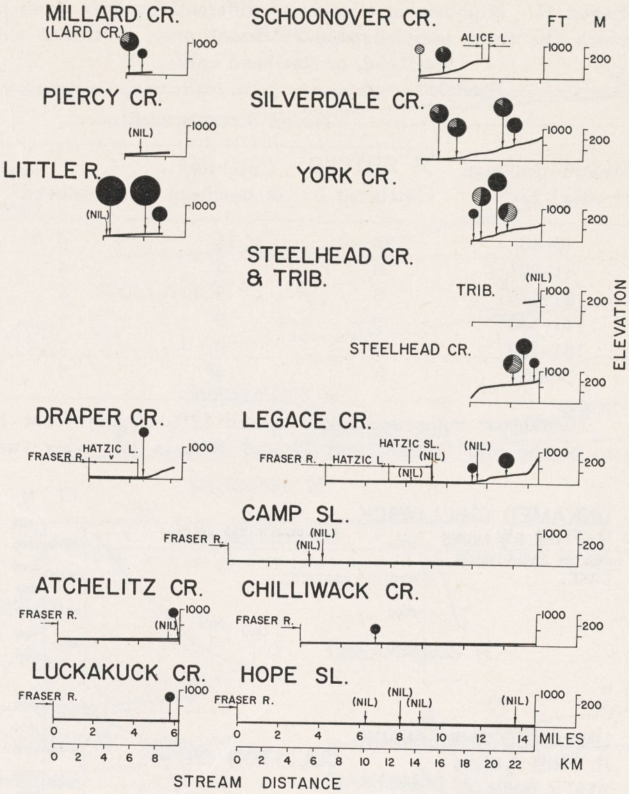

FIG. 5. Profiles of medium and low gradient streams with drainage areas under 120 km² in which all identifiable trout were cutthroat. Sampling stations, sample size, and composition are indicated. See Fig. 3 for legend.

stretches of stream. The micro-habitats of the two species appear to be similar although the major gradient characteristics of the stream they select are different.

In streams with drainage areas under 120 km² which supported both species of trout, those with relatively steep gradients, such as Cougar, Hunts, Brohm, and Weaver creeks (Fig. 7), were occupied predominantly by steelhead. On the other hand where collections were predominantly cutthroat, as in Kanaka, French, Pattison and Blaney creeks (Fig. 7), the profiles level at the downstream ends, where the creeks run through sloughs.

In the stream systems where both species occurred, cutthroat were the predominant species in upstream collections in 10 of 13 cases. Differences in distribution of steelhead and cutthroat along the length of a stream are best illustrated in the Salmon River, where trout collections were predominantly steelhead in the lower part of the main stem of the stream, and predominantly cutthroat in the upper part of the main stem and in the tributaries (Fig. 7).

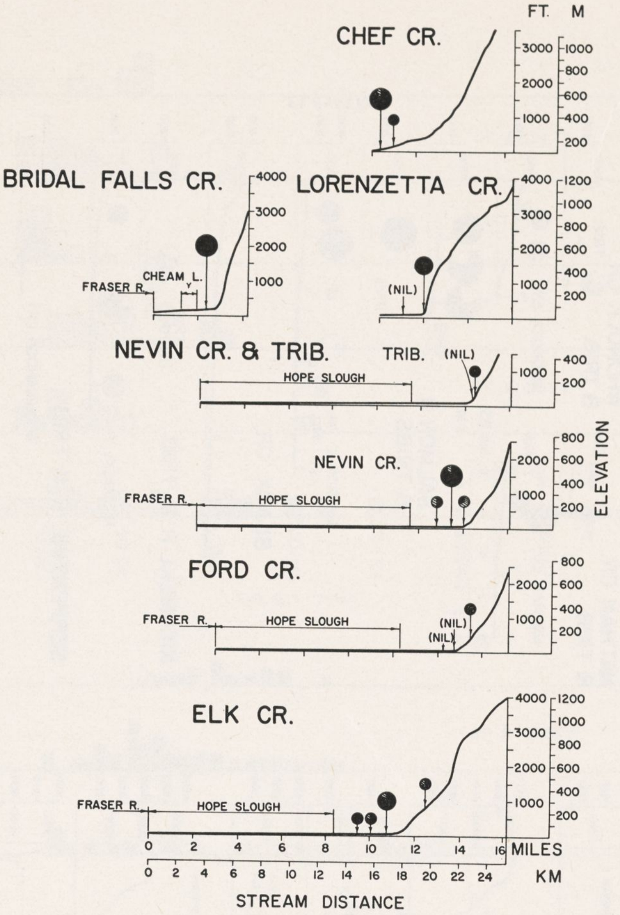

Fig. 6. Profiles of steep gradient streams which enter sloughs or level out in downstream areas. Drainage areas are under 120 km^2. All identifiable trout were cutthroat. Sampling stations, sample size, and composition are indicated. See Fig. 3 for legend.

Effect of *p*H and Dissolved Solids

Data on *p*H for the two periods (November 1 to March 31 and April 1 to October 31) are not strictly comparable because numbers of readings and stations chosen were not all replicated. However, the *p*H values were generally higher during the April to October period than from November to March (Fig. 8). In the April to October period most of the *p*H values for streams with steelhead only, cutthroat only, and the species mixed, fell within the same range. During the November to March period, streams occupied by steelhead only had a narrower range of *p*H's than those occupied by cutthroat only. However, mean values for *p*H were near 7.00 for both groups of streams. The range and mean of *p*H values for streams in which both species occurred were slightly lower than for streams which supported only one species.

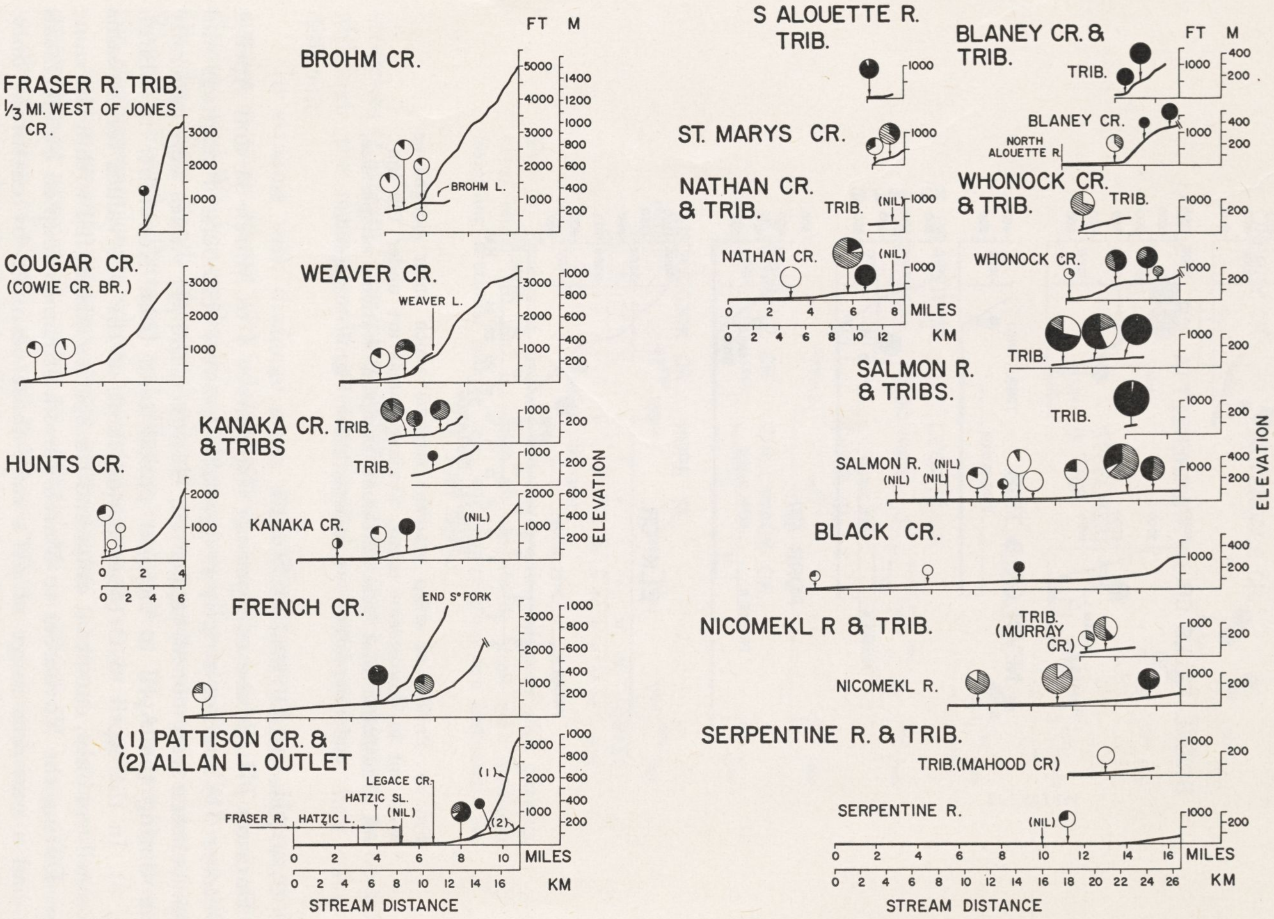

FIG. 7. Profiles of streams with drainage areas under 120 km^2 in which both steelhead and cutthroat occurred. Sampling stations, sample size, and composition are indicated. See Fig. 3 for legend.

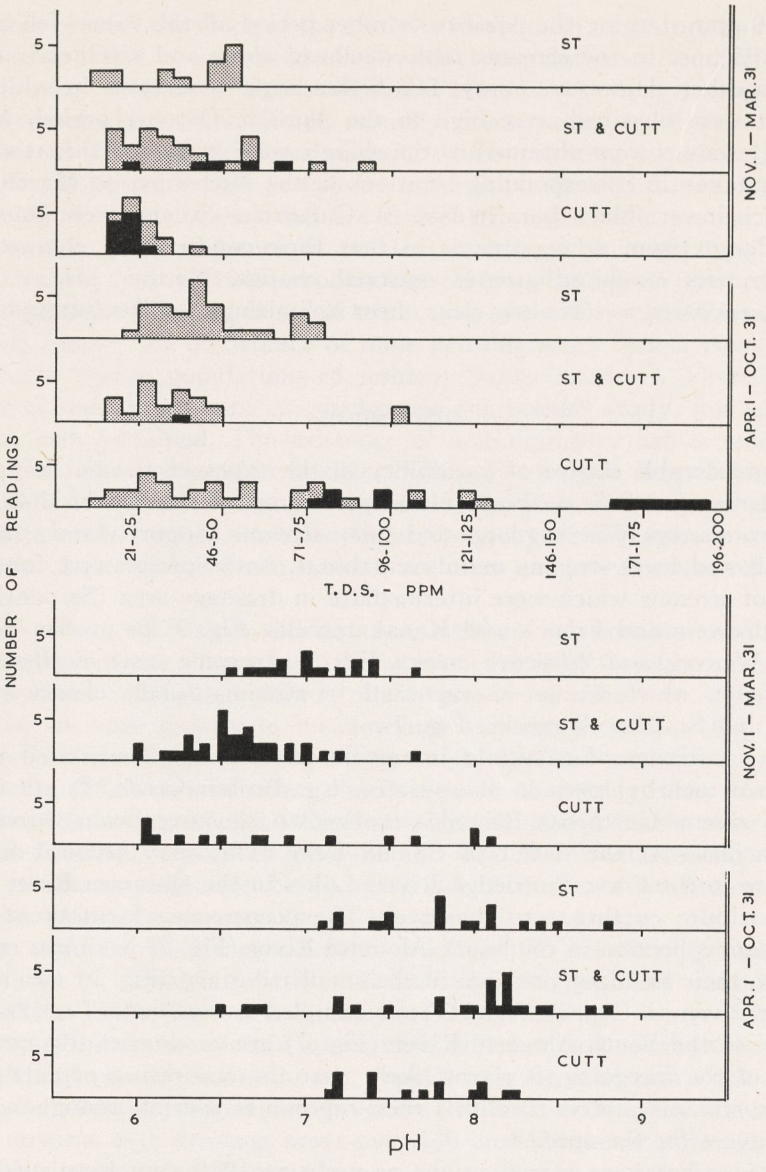

FIG. 8. Total dissolved solids and *p*H in streams with steelhead alone, both cutthroat and steelhead, and cutthroat alone. T.D.S. values indicated by black bars are from slough areas of streams.

Total dissolved solids values in the various streams ranged from 15 to 192 ppm in the April to October period and from 15 to 95 ppm in the November to March period (Fig. 8). During the November to March period virtually all the readings for streams with species both separate and mixed fell between

15 and 80 ppm. During the April to October period all the values fell between 16 and 105 ppm in the streams with steelhead alone and steelhead and cutthroat together. However, many T.D.S. readings in streams in which only cutthroat were obtained were high in the April to October period. Most of these high values were obtained in the slough areas of the cutthroat streams. Readings taken in corresponding locations in the November to March period were much lower (black bars in Fig. 8). Cutthroat streams were thus somewhat different from other streams in that their conductivity characteristics in many cases exhibited greater seasonal change. Neither *p*H or T.D.S., however, appeared to have any clear effect in limiting the distribution of either species.

DISCUSSION

A considerable degree of variability in the types of stream occupied by *Salmo gairdneri* and *S. clarki clarki* leads to some overlap in the distribution of the two species. Whereas large and steep streams support mainly steelhead and small and level streams mainly cutthroat, both species were found in a number of streams which were intermediate in drainage area (Serpentine and Nicomekl rivers and French and Kanaka creeks, Fig. 7) or profile (Kanaka, Cougar, Weaver, and Whonock creeks, Fig. 7). In some cases steelhead enter small streams which are not characteristic of streams usually chosen by them (Blaney and St. Mary's creeks, Fig. 7).

The occurrence of cutthroat in certain streams may be related to their existence in nearby lakes in the system, e.g. Brohm Creek, Puntledge and Quinsam rivers. Cutthroat juveniles are known to move down through fish ladder facilities at the outlet of Comox Lake. This may account for their occurrence in the lower Puntledge River. Lakes in the Quinsam River system may contribute cutthroat to the river. The occurrence of cutthroat in the downstream collection in the South Alouette River (Fig. 3) is almost certainly related to their localized presence in the small tributary (Fig. 7) which enters the main river at that location. Trout sampled a few meters up the small tributary of the South Alouette River (Fig. 7) are predominantly cutthroat. In view of the foregoing, it seems likely that the occurrence of cutthroat in the large streams and in Brohm Creek represents special, though not rare, circumstances for the species.

Previous hatchery introductions as early as 1930 may have altered the distributional relationships of rainbow and cutthroat. Cutthroat were introduced into the Nicomekl, Serpentine, and Salmon rivers and Kanaka Creek in 1933, according to British Columbia Game Department records. Many fish plantings in the past have not been well documented; therefore, it is not clear to what extent past introductions of fish might affect present distributions. However, since introductions to occupied stream habitats are generally not successful, it is unlikely that the distributional characteristics of cutthroat have been seriously confounded by these plantings.

It was beyond the scope of the study to distinguish migratory and resident races of trout. But it was noted that resident populations of cutthroat occur in a tributary of Blaney Creek. Females 111–132 mm long contained eggs which were nearly mature. Small, sexually mature male trout were taken in a number of streams. Steelhead Creek, which contains cutthroat trout in abundance, is not accessible to fish from the Stave River into which it flows. Presumably Steelhead Creek fish are resident in the stream system. Sumner (1952) reports the occurrence of resident cutthroat in migrations in Sand Creek, Oregon. Neave (1949) reports coastal populations of cutthroat trout above impassable falls and in small tributaries in the Cowichan River system, indicating further the occurrence of some non-migratory forms. Neave (1949) also reports coastal populations of resident *Salmo gairdneri*. There was less evidence of residence among *S. gairdneri* in the present study: few small ripe male fish were obtained. The existence of non-migratory fish is pointed out because the role of migration in determining distribution is speculated upon later in this discussion. Although the size and age of most fish sampled suggest that the juvenile coastal trout are largely progeny of migratory forms, some distribution patterns in stream systems are more extensive because of resident forms.

The stream *p*H values did not bear obvious relationship to differences in trout distribution. The data gathered from April to October indicate that stream systems used by cutthroat have greater gradients in T.D.S. (conductivities increase greatly in meadowland and slough areas) (Fig. 8) than those used by steelhead. Although data on *p*H and conductivity do not shed light on the differences in trout distribution in this study, they should not be ruled out as having no effect. Conductivity, *p*H, and probably other features of stream limnology relate to gradient and size. Such features may differ in various stream systems, and hence affect fish, in fashions not indicated by a superficial series of measurements made over all systems.

The existence of ecological zones and specific faunistic groups within streams can be related directly and indirectly to gradient characteristics (Huet, 1959, 1962; Burton and Odum, 1945). Although many British Columbia coastal streams contain zones with different faunas, the distributions of the two species of *Salmo* do not depend only on a stream slope–breadth relation. As already pointed out, juvenile cutthroat occur as a minor species in large streams with drainage areas over 130 km^2 (50 miles^2). Within streams below this size both species occur over a wide range of stream slopes (Fig. 9).

Although the estimations of stream width are extremely rough, the data for British Columbia indicate a high slope–breadth relationship among the smaller streams. The difference between these high values and the curve given by Huet (1959) probably represents a difference between local trout (steelhead and cutthroat) and brown trout as well as a difference in topography.

The micro-habitats in which *Salmo gairdneri* and *S. clarki* are found are very similar; these areas include pools, gravel riffles and runs, rocky turbulent stretches and plunge pools in white water torrent areas. In many streams the

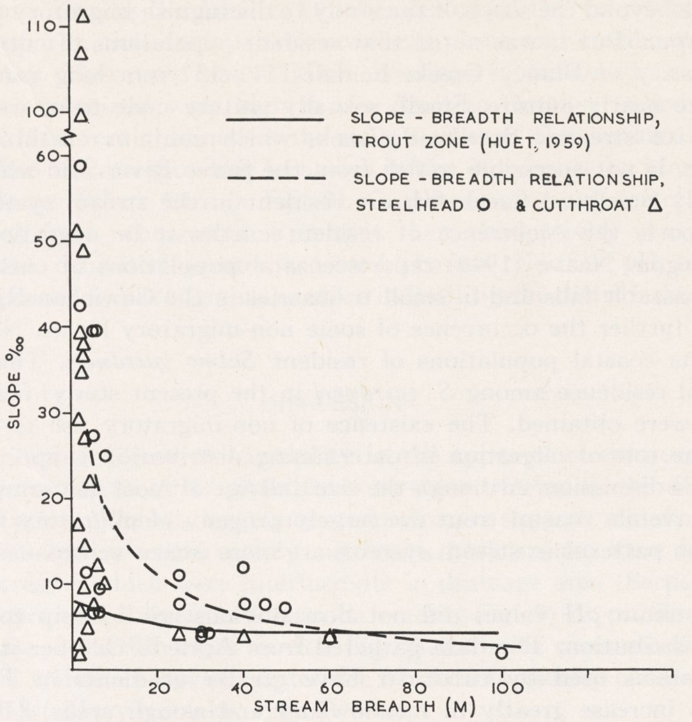

Fig. 9. Approximate relationship between stream gradient and breadth in British Columbia coastal trout streams and in the trout (*Salmo trutta*) zone of western European streams. Data for steelhead and cutthroat are for streams both above and below 130 km^2 in drainage area.

differences in species composition appear to be related to stream conditions below the areas where the fish occur. Such a situation leads to the speculation that differences in juvenile trout distribution may be related directly to differences in the migratory patterns of adults. Adult cutthroat trout presumably enter slough systems, slow-moving streams in meadowland areas, and small tributaries. The much larger adult steelhead, on the other hand, remain in larger streams or enter preferably into fast-flowing tributaries. At present, little comparative information on the migratory responses of the two species is available to support or contradict the idea that differences exist in their migratory behavior or choice of spawning areas.

Although sample sizes were small in some streams and collections were not numerous in others, the evidence that is available strongly indicates that stream size and profile affect trout distribution either directly or indirectly.

The implications of differences in distribution of juvenile steelhead and cutthroat trout in management are significant. In general the small cutthroat streams which run through farmland or sloughs are vulnerable to relocation, straightening, obstruction, and pollution. Fish habitat in the steeper regions of the streams may be destroyed by scouring and debris accumulation as a result of logging activities over a small area of the watershed. Steelhead trout growing in small streams are vulnerable to the same influences as cutthroat. Many steelhead trout, however, dwell in larger rivers, which are less susceptible to local influence or destruction.

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Zoology 223 January 8, 1958 Albert C. Jones

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  - 2. Endemic amphi-American genera: Haemulon (10 Atlantic species, 2 Pacific species), Calamus (8,3), Cynoscion (10,10), Menticirrhus (4,5), Bairdiella (3,2), Iridio (15,4), Citharichthys (7,7), Achirus (4,7), Gobiesox (13,3), Manta (1,1).

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10. Endemic boreal genera of North Atlantic: *Crystallogobius, *Chirolophis, *Zeugopterus, *Scophthalmus, *Raniceps, Cyclopterus, Spinachia. (i* indicates exclusive European distribution)

(9 and 10 are indicators for European North Atlantic)

11. Endemic boreal speics of North Atlantic: *Tautogolabrus adspersus, *Cottus octodecimspinosus, *Hemitripterus americanus, Cyclopterus lumpus, Pholis gunellus, *Zoarces americanus, Hippoglossus hippoglossus, *Liopsetta putnami, Gadus tomcod, Gadus morrhua, Gadus aeglefinus, Gadus virens, Clupea harengus. (* indicates exclusive American distribution)

(11 are indicators for American North Atlantic)

12. Distribution of the arctic and temperate shelf fishes of the northern hemisphere:

	Species	Genera
Total Number	725	335
Characteristic for the North Pacific including the neighboring parts of the Polar Sea	550 (76%)	230 (69%)
Characteristic for the North Atlantic including the neighboring parts of the Polar Sea	150 (20%)	51 (15%)
Common to both regions	25 (3%)	54 (16%)

13. The representation of some genera which are common to both the North Pacific and North Atlantic shelf region:

Genus	Purely North Pacific species	Purely North Atlantic species	Species common to both
Raja	16	8	-
Icelus	7-8	-	1
Artediellus	6	1	-
Careproctus	17	3	-
Pholis	5	1	1
Gadus	5	5	1
Limanda	4	2	-

LAND AND SEA IN THE MIDDLE AND UPPER CRETACEOUS

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FRESHWATER FISH PROVINCES OF
NORTH AMERICA

Modified from Miller, 1958, Fig. 1

John D. Hopkirk
November 22, 1961

"Origin and Affinities of the Freshwater Fish Fauna of Western North America"

Follett, W. I. 1961. The freshwater fishes--their origins and affinities. In: Symposium: The biogeography of Baja California and adjacent seas. Syst. Zool., 1960, 9(3 and 4):212-232.

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"Only about 100 species of strictly freshwater fishes are known west of the Rocky Mountains and north of Mexico -- a depauperate fauna characterized by relicts, monotypic genera, and much regional endemism" (Miller, 1961a). The western fauna has one-half as many families and one-fourth as many species of primary and secondary fishes as the eastern fauna. Twenty of the 100 species mentioned above are locally endangered and may soon vanish because of environmental changes.

The sequence of events responsible for this impoverished fauna began with a trend of increased aridity in the Eocene, an aridity which has been felt more by the western than the eastern portion of North America. Since then our climate, vegetation, and animal life has changed from humid tropical to arid temperate in character (Axelrod, 1952). Species and genera were either gradually extinguished ~~or~~ (*Priscacara*, *Mylocyprinus*) or restricted in range (*Archoplites*, *Mylopharodon*, *Cyprinodon*, etc.).

Complicating this scene was the fluctuating Pacific coastline, which was covered with salt water until the Miocene, whereupon a distinctive freshwater fauna begins to appear. The Coast Range, Sierra, and Rocky Mountains, with their respective drainages, were in their present form by late Pliocene and early Pleistocene times and geographically isolated primary freshwater fishes into provinces (see map). Exchanges of primary fishes between provinces were favored during Pleistocene times of increased runoff from glacial melting.

According to Miller (1959), three families (Umbridae, Cyprinidae, and Catostomidae) of Eurasian origin account for 97 per cent of the primary fish fauna of western North America. Although the differences between the western and eastern fish faunas are recent (post-Miocene), three genera (*Novumbra*, *Columbia*, and *Archoplites*) may be of pre-Miocene age. Only five per cent of the total number of species present overlap, or occur in, both faunas.

- horseradish
- garlic powder
- 'herring

Numbers of families, genera, and species of North American primary freshwater fishes

	Province[1]	Number[2] of families	Number[2] of genera	Number[2] of species
1	Alaskan	5	5	5
2	Columbian	4	12	19
3	Hudsonian	10	27	52
4	Huronian	12	44	112
5	Laurentian	6	17	26
6	Delawarian	9	33	63
7	Floridan	10	38	110
8	Alabaman	9	36	104
9	Mississippian	13	52	260
10	Chihuahuan	6	26	55
11	Coloradan	2	12	23
12	Bonnevillian	2	8	12
13	Lahontan	2	7	8
14	Klamathian	2	5	7
15	Sacramentan	3	11	12
16	Mohavian	2	3	4
17	Santaanian	2	3	3
18	Sanlucan	0	0	0
19	Mexican	6	21	50
20	Guatemalan	5	9	23
21	Panamanian	7	38	70
22	Bahaman	0	0	0

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[1] Province names proposed by J. D. Hopkirk, Nov. 22, 1961

[2] Numbers as given by Miller, 1958, Fig. 1

- most prim. N. Am. cyprinid
- most southerly -
- relationships

ANNOTATED LIST OF FISHES NATIVE TO THE COLORADO RIVER BASIN

Colorado Cooperative Fishery Unit
Colorado State University
Fort Collins, Colorado

INTRODUCTION

The following accounts attempt to concisely summarize the current state of our knowledge of the native fish fauna of the Colorado River basin and to call attention to those forms which are most in need of further study.

The geologic history of the Colorado River basin, indicates the present basin was once a series of independent basins providing areas for fishes to isolate and differentiate in diverse environments. The diversity, high degree of endemism, and marked distinctions of the faunal components of various segments of the basin support such a view.

For this report, the term Colorado basin includes several independent desiccating basins without present connection to the Colorado River system; however, the fishes found in these basins were derived from previous connections with the Colorado system.

It is significant to note that of the 22 fishes listed by the U.S. Department of Interior as rare or endangered in the most recent checklist (1967) - 10 are endemic to the Colorado basin, as construed in this paper.

The following notations are used:

U - Denotes a distribution restricted to the upper basin, above the Grand Canyon, but not including the Little Colorado River.

L - Includes the Little Colorado River, the Grand Canyon and below to the mouth of the Colorado.

V - For the Virgin and White River section of the basin containing a number of small desiccating basins with relict populations derived from previous connections with the Colorado River.

E - Endemic species whose natural distribution is limited to the confines of the basin.

R - Includes the species reported on the most recent rare and endangered species list.

Family Salmonidae: Trouts, Whitefishes, Graylings

Salmo clarkii pleuriticus Cope. Colorado River cutthroat trout - U

The native trout of the Colorado basin closely resembles the Yellowstone subspecies, *S.c. lewisi* which has been widely introduced throughout the basin. Pure populations of the native trout, uncontaminated by hybridization with introduced Yellowstone cutthroat or rainbow trout undoubtedly are rare. Current studies by the Colorado Cooperative Fishery Unit are investigating the systematics of the native subspecies, attempting to discover differentiating characters allowing recognition and separation from hybrid populations and Yellowstone cutthroat. The original downstream distribution of the cutthroat trout included the San Juan River system, but probably not the Little Colorado or the Grand Canyon area.

Salmo gilae Miller. Gila trout - L E R

The native trout of the upper Gila River system is quite distinct from the upper Colorado River cutthroat. The origin and true affinities of this trout are not known. Its range has been drastically reduced, the only pure population identified with any degree of certainty occurs in a tiny headwater section of Diamond Creek, Gila National Forest, New Mexico. Populations of native trout are known from the headwaters of the Black and White rivers, tributaries to the Salt River of the Gila basin in eastern Arizona, and from the headwater tributaries of the Little Colorado River near Mt. Baldy in the same general vicinity. These trout, sometimes referred to as Apache trout, show relationships to *S. gilae* but are differentiated sufficiently to be regarded at least as a subspecies, indicating long separation from the Gila trout of New Mexico. The Apache trout is also included on the rare and endangered species list.

Prosopium williamsoni (Girard). Rocky Mountain Whitefish - U

This species, as the cutthroat trout, is widespread throughout the western United States. The original distribution in the Colorado River system apparently was restricted to the Green River division of the basin. No study has yet compared the Colorado basin whitefish with populations from other basins to indicate the amount of variability and divergence occurring in the whitefish of the Colorado system.

Family Catostomidae: Suckers

Catostomus latipinnis Baird and Girard. Flannelmouth sucker - U L E

Once widespread in all of the larger streams of the basin, it has disappeared from many areas particularly in the lower basin.

Catostomus insignis Baird and Girard. Sonora sucker - L E

The common coarse scaled sucker of the Gila River division of the basin. The complete distribution has not been authoritatively established.

Pantosteus delphinus(Cope). Northern bluehead mountain sucker - U L

A recent publication by Smith (1966) revised the taxonomy of the suckers of the genus Pantosteus. Smith considers Pantosteus as a subgenus of Catostomus, and his research changes many former conclusions concerning correct names, distribution of species, and endemic species. For this report it is not critical if Pantosteus is considered as a genus or subgenus, but Smith's findings on nomenclature, distribution, and relationships are followed in the following accounts of Pantosteus. Smith stated the correct species name for the bluehead sucker should be discobolus Cope and not delphinus. The species discobolus is not endemic to the Colorado basin but occurs in the Bonneville basin and the Snake River. The bluehead sucker is known from the Little Colorado basin but not below the Grand Canyon. Former records of the bluehead sucker from the Virgin River basin and the Bill Williams River of Arizona actually belong to the species P. clarki, according to Smith.

Pantosteus clarki (Baird and Girard). Gila sucker - L E

Formerly considered only from the Gila River division, but the populations previously considered as P. utahensis (Tanner) and P. intermedius (Tanner) from the desiccating White and Virgin basins are in reality P. clarki.

Pantosteus platyrhynchus (Cope). Mountain sucker - U

Smith greatly enlarged the limits of the species platyrhynchus to include the Bonneville, Lahontan, and upper Missouri mountain suckers previously considered as the species virescens, lahontan, and jordani. He found platyrhynchus in the Green River division of the upper Colorado basin, together with the bluehead sucker P. delphinus (= discobolus). This makes a new addition to the native fish fauna of the Colorado basin. It is believed the species name delphinus actually was based on the species platyrhynchus and thus is not available for use as the specific name for the bluehead sucker.

Xyrauchen texanus (Abbott). Humpback sucker - U L E

This highly modified sucker has suffered a great decline in abundance due to the changing environment of the basin. Little is known of its ecology or taxonomy.

Family Cyprinidae: Minnows

Gila robusta-elegans-intermedia complex. Roundtail and bonytail chubs - U L E

This group of chubs, including Gila cypha, comprises one of the most fascinating problems in systematic ichthyology. The extreme variability in morphologies found in the roundtail and bonytail chubs have been described as no less than 12 species. The true situation is not known concerning the actual number of species and subspecies which should be recognized and the pattern of geographical differentiation and intergradation. Do two or more distinct types of Gila occur together without interbreeding? Are there consistant patterns of differentiation associated with geographical divisions? To what degree does environmental modification control the phenotype? The genus Gila of the Colorado basin is attracting well deserved attention as a fruitful field of biological study; however, an immense amount of work will be necessary before this genus is fully understood.

Gila jordani Tanner, described from Pahranagat Valley, Lincoln Co., Nevada, a glacial relict of the disrupted White River, is probably more correctly considered a subspecies of G. robusta.

Gila cypha Miller. Humpback chub - U L E R

This fish parallels the humpback sucker in the development of a peculiar morphology, evidently adapted for bottom living in rapid water. Some specimens indicate a transitional series and perhaps gene flow from the Gila robusta-elegans type to Gila cypha. The specimen on which the name is based came from the Grand Canyon. Further collections from the Grand Canyon should provide significant information on Gila cypha, and how it relates to the robusta-elegans complex. Recent humpback chub specimens from Lake Powell resemble G. cypha, but are fully scaled.

Ptychocheilus lucius Girard. Colorado River squawfish - U L E R

The largest North American species of the minnow family. This species has disappeared through most of its range. Little is known of its life history and ecology.

Rhinichthys osculus (Girard). Speckled dace - U L V

This species has a broad distribution in western North America. Interspecific variability throughout its range is not well known.

Agosia chrysogaster Girard. Longfin dace - L

This genus and species cannot strictly be called endemic to the Colorado system because it is found in the headwaters of the Rio Yaqui. The origin and evolution of *Agosia* most probably occurred in the lower Colorado basin. It is locally abundant in the Gila River system. The variability of *Agosia* and the existence of more than a single species or subspecies has not yet been established.

Tiaroga cobitis Girard. Loach minnow - L E

This genus and species is known only from the Gila River system. It has declined greatly in abundance.

Moapa coriacea Hubbs and Miller. Moapa dace - V E R

This genus and species is endemic to warm springs of the Moapa River, a tributary in the White River system, in Clark Co., Nevada. A relict species now restricted to warmer waters, typically of 87° - 93°F.

Tribe Plagopterini - The Spinedaces.

This group consisting of three genera and six species is found only in the lower Colorado basin and its disrupted tributary, the Virgin River system. They are the only North American cyprinid fishes with spinous fin rays. It is believed they were derived from the genus Gila.

Lepidomeda mollispinis Miller and Hubbs. Middle Colorado spinedace - V E

Miller and Hubbs recognized three subspecies of this species: m. mollispinis of the Virgin River system; m. pratensis, known only from a spring in Lincoln Co., Nevada, now believed to be extinct; and m. albivallis, from the White River segment of the Virgin River basin.

Lepidomeda altivelis Miller and Hubbs. Pahranagat spinedace - V E

This species was known only from two sites in Pahranagat Valley, Nevada. It is now believed extinct due to introductions of carp and mosquitofish.

Lepidomeda vittata Cope. Little Colorado spinedace - L E R

The known range of this species is limited to the upper Little Colorado River system in eastern Arizona. It was once believed extinct, but a few populations have been discovered in recent years.

Meda fulgida Girard. Spikedace. - L E

This genus and species is known only from the Gila River system.

Plagopterus argentissimus Cope. Woundfin - V E

Apparently now restricted to the Virgin River system; once inhabiting the Gila River, but the last specimens known from the Gila basin were collected in 1894.

Family Poeciliidae: Topminnows

Poeciliopsis occidentalis (Baird and Girard). Gila topminnow - L E R

Once widespread in the Gila River system, now found only in a few localities.

Family Cyprinodontidae: Killifishes

Cyprinodon macularius Baird and Girard. Desert pupfish - L

Formerly wide ranging in the lower Colorado basin, this species is rapidly declining. One inimical factor is competition from the introduced mosquitofish, Gambusia affinis.

Perhaps during the Pliocene, connections of streams and lakes of the now desert areas of Death Valley and contiguous basins of California and Nevada, to the lower Colorado system, allowed Cyprinodon access to these basins.

Subsequent isolation has produced an array of species and subspecies. The described forms include: C. salinus Miller, the Salt Creek pupfish of Death Valley; C. radiosus Miller, the Owens Valley pupfish - R; C. nevadensis Eigenmann and Eigenmann, the Amargosa pupfish with six subspecies recognized; and C. diabolis Wales - R, the Devil's Hole pupfish, restricted to a single tiny pool.

Also in the Amargosa desert on the California-Nevada border, the Ash Meadows poolfish, Empetrichthys merriami Gilbert, (now believed extinct) was found. Three subspecies of Empetrichthys latos Miller - R, the only other known species in this genus, occurred in three springs (two springs now destroyed) in Pahrump Valley, Nye Co., Nevada.

The genus Crenichthys has two known species, C. baileyi (Gilbert), the White River springfish found in warm springs along the White River drainage of Nevada, and *C. nevadae* Hubbs, the Railroad Valley springfish from a desiccating basin just west of the White River system, Nye Co., Nevada.

The cyprinodont fishes of the desert areas of the western United States reveal information on past conditions and connections of the Colorado basin and provide insight into the mechanisms and rates of evolution.

Family Cottidae: Sculpins

Cottus bairdi Girard. Mottled sculpin - U L

A widespread species across the northern United States.

Cottus annae Jordan and Starks. Eagle sculpin - U

This sculpin formerly believed endemic to headwater areas in the upper Colorado River basin, is considered identical to *Cottus beldingi* Eigenmann and Eigenmann, of the Lahontan basin, middle and upper Columbia River system and the lower Bear River of the Bonneville basin, by Bailey and Bond (1963).

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Gene Decker

ZOOGEOGRAPHY of Fishes
FW 725

The first few sessions will discuss principles, the distribution of major groups of freshwater fishes and speculate on when and how these distributions came about, the amount of speciation in the various groups, etc.. The remaining meetings will be devoted to student seminars in which we will explore in detail two types of zoogeographical areas. One fully affected by the late Pleistocene glaciation and where the present fish distribution is explained by relatively recent events, perhaps in the last 10,000 years--the other, such as the Colorado River basin, whose origins and isolation extend back to the Miocene or 10 million years or more. Each student will write and present a report, based on a literature survey. This report can emphasize the geological history, explaining the present distribution of fishes, or it can emphasize a particular group (or group of fishes) illustrating the geological and hydrological histories explaining their present distribution and speciation. We will get into some controversial areas such as "local forms or varieties", "dwarf races" and "landlocked races" and "ecotypes". Some actual examples will be explored in depth in an attempt to understand some of the diversity that occurs in nature and its biological significance.

Bob Behnke

POSTGLACIAL REDISPERSAL OF EASTERN NORTH AMERICAN FRESHWATER FISHES

by Carter R. Gilbert   1958

Abstract

Probably no group of eastern North American animals is better suited for the study of zoögeography than the freshwater fishes. Because they are so much more closely confined to their environment than are most other animals, and because the character of the lakes and streams in which they live is a direct result of the effects caused by the advances and retreats of the Pleistocene ice sheets (speaking of course of those living in previously glaciated areas), their present-day distribution throws a great deal of light on the validity of the various hypothesized glacial outlet streams which are thought to have existed in the past.

Since the fossil record in eastern North America is so poor, we have no way of knowing what the distribution of fishes was in the glaciated areas of North America during the first three interglacial periods. We are concerned, then, only with the Wisconsin glaciation and the dispersal which resulted following the retreat of that ice sheet.

This paper is a study of fish distribution within the Great Lakes area. During the Pleistocene this region was entirely covered by ice and, as a result, the fish now present have lived there for a relatively short period of time. It is thought that the various native fishes found refuge during the last glacial advance (and presumably during the other advances as well) in one, or sometimes two, or three areas: Alaska, the Mississippi valley and the Atlantic coast. Following the retreat of the glacier, fishes reentered the Great Lakes by one or more temporary outlets, outlets which existed only for relatively short periods of time. The most important of these outlets were the Mohawk River, which connected glacial Lakes Lundy and Iroquois (forerunners of Lakes Erie and Ontario) with the Hudson River, the Warren River, which drained into the Mississippi valley from glacial Lake Agassiz, and the following four rivers, all of which drained into the Mississippi valley: the Ft. Wayne, which drained the forerunners of Lake Erie (first Lake Maumee and later Lake Lundy); the Illinois, which drained Lake Chicago (predecessor of Lake Michigan); the Fox River, which also drained Lake Chicago; and the St. Croix River, which drained Lake Duluth (forerunner of Lake Superior). Distribution patterns show that all of these outlets probably were used. The fishes which entered the Great Lakes from Alaska are thought to have migrated across Canada by means of the temporary glacial lakes which existed at the foot of the retreating glacier.

In some cases it is difficult to determine the true original distribution patterns of certain fish. This may be the result of either introductions or the presence of man-made canals, such as the Cahicago drainage canal and the canal connecting the Mohawk River with the Great Lakes. Other smaller ~~east~~ canals have also played a part in clouding the natural distribution patterns Because of these one cannot be certain sometimes whether ~~certai~~ a species has entered an area naturally or through these artificial connections.

Finally, this paper shows how some of the fishes which were thought to have existed during the Wisconsin glaciation on the east coast actually made their way across the drainage divide from the Great Lakes following the last retreat of the glacier.

Summary of the Families and Genera of Fishes found in the Great Lakes Region

1. Petromyzontidae - lampreys
   Genera *Petromyzon* (one species), *Ichthyomyzon* (three species), and *Lampetra* (one species)
2. Polyodontidae - paddlefish
   Genus *Polyodon* (one species)
3. Acipenseridae - sturgeons
   Genus *Acipenser* (one species)
4. Lepisosteidae - gars
   Genus *Lepisosteus* (two species)
5. Amiidae - bowfin or dogfish
   Genus *Amia* (one species)
6. Hiodontidae - mooneyes
   Genus *Hiodon* (one species - a second species is discussed)
7. Clupeidae - herrings
   Genera *Alosa* (two species) and *Dorosoma* (one species)
8. Salmonidae (including Coregonidae and Thymallidae) - whitefish, ciscos, grayling and trout
   Genera *Salmo* (one native species), *Salvelinus* (two species), *Coregonus* (thirteen species), and *Thymallus* (one species).
9. Osmeridae - smelts
   Genus *Osmerus* (one species)
10. Catostomidae - suckers
   Genera *Ictiobus* (two species), *Carpiodes* (one species), *Catostomus* (two species), *Hypentelium* (one species), *Erimyzon* (two species), *Minytrema* (one species), *Moxostoma* (seven species), and *Lagochila* (one extinct species)
11. Cyprinidae - minnows (including carp and goldfish)
   Genera *Semotilus* (three species), *Hybopsis* (six species), *Rhinichthys* (two species), *Parexoglossum* (one species), *Exoglossum* (one species), *Chrosomus* (three species), *Clinostomus* (one species), *Opsopoeodus* (one species), *Notemigonus* (one species), *Notropis* (twenty-one species), *Phenacobius* (one species), *Ericymba* (one species), *Hybognathus* (two species), *Pimephales* (two species), and *Campostoma* (one species).
12. Ictaluridae - catfish
   Genera *Ictalurus* (four species), *Pylodictis* (one species), and *Noturus* (five species).
13. Umbridae - mudminnows
   Genus *Umbra* (one species)
14. Esocidae - pikes and muskellunge
   Genus *Esox* (four species)
15. Anguillidae - eels
   Genus *Anguilla* (one species)
16. Cyprinodontidae - killifish
   Genus *Fundulus* (three species)
17. Gadidae - codfish
   Genus *Lota* (one species)
18. Percopsidae - troutperch
   Genus *Percopsis* (one species)
19. Aphredoderidae - pirateperch
   Genus *Aphredoderus* (one species)
20. Serranidae - true basses*
   Genus *Roccus* (one species)

21. Percidae - perches and darters
    Genera *Perca* (one species), *Stizostedion* (two species), *Percina* (six species), *Ammocrypta* (one species), and *Etheostoma* (nine species).
22. Centrarchidae - sunfish, including black bass
    Genera *Micropterus* (two species), *Chaenobryttus* (one species), *Lepomis* (five species), *Ambloplites* (one species), and *Pomoxis* (two species).
23. Atherinidae - silversides
    Genus *Labidesthes* (one species)
24. Sciaenidae - (drums
    Genus *Aplodinotus* (one species)
25. Cottidae - sculpins
    Genera *Cottus* (three species), and *Myoxocephalus* (one species)
26. Gasterosteidae - sticklebacks
    Genera *Eucalia* (one species), *Gasterosteus* (one species), and *Pungitius* (one species)

Summary of the glacial history of the Great Lakes

As the Wisconsin ice sheet began to retreat, the resulting meltwaters formed lakes at the foot of the glacier. Because the glacier acted as a "plug" to any northward flow of water, the rising lakes began to cut outlets to the south. The first and largest of these lakes was called Lake Agassiz. It covered an extensive area and drained into the Mississippi valley by means of the Warren River outlet, which was located in the area of the present southern extremities of the Red River of the North. As the glacier retreated farther, it finally separated, opening a channel to the northeast, the origin of the Nelson River. This drained Lake Agassiz to such an extent that the Mississippi outlet disappeared and the vast lake was succeeded by a series of smaller bodies of water; Lake of the Woods, Lake Winnipeg, and many lesser lakes.

Soon after Lake Agassiz was first formed there appeared farther to the east glacial Lakes Duluth, Chicago and Maumee, the predecessors, respectively, of Lakes Superior, Michigan, and Erie. These lakes, also plugged at their northern extremities, drained into the Mississippi valley by way of the St. Croix (Lake Duluth), the Fox and Chicago (Lake Chicago) and the Ft. Wayne (Lake Maumee) outlets.

As the glaciers receded farther, many changes took place. The lakes changed in shape and form and eventually united into a series of lakes, which finally approached in form, at least to the south, of the present-day Great Lakes. About this time there appeared another outlet, connecting what is now Lake Ontario with the Hudson River, thus uniting temporarily by a freshwater connection the waters of the Atlantic Ocean with those of the Great Lakes.

Finally there was a marine invasion of the St. Lawrence River basin. This body of water, called the Champlain Sea, inundated a large area of southern Canada and the northern United States, and was responsible for the invasion of a number of marine animals which still remain isolated in this area.

Eventually this marine embayment disappeared, and the Great Lakes, as we know them today, were formed.

Discussion

During the last ice age most of northern North America, including all of Ontario, lay beneath the glacier and any living organisms which had populated that area before the ice age began were forced to withdraw into areas not affected by the glaciation or were exterminated. Three regions which were not covered by the ice sheets, in Alaska and the Yukon, in the Mississippi Valley, and in the Atlantic coastal plain, may be considered as possible sources of the present species of fishes occurring in the Great Lakes region by reason of the nature of the retreat of the glacier.

Fishes utilizing the Alaska refugium

As might be expected, those species which remained in Alaska during the glacial advances were all cold-water species. These include all the Salmonids except the brook trout, the nine-spined stickleback (*Pungitius pungitius*), the northern pike (*Esox lucius*), the northern sucker (*Catostomus catostomus*), and the burbot (*Lota lota*). Possibly *Cottus cognatus* should be included in this group also. The northern pike, northern sucker, and the burbot might have had not only a refugium in Alaska, but one in the Mississippi valley as well (see maps 3 and 4; see maps 1 through 4 for all the Alaskan species).

Yes and St Lawrence

The fishes which are thought to have made their way from Alaska postglacially probably followed the retreating glacier very closely. This made it possible for them to successfully pass through the numerous interconnected meltwater lakes which were temporarily connected along the glacier's southern perimeter. The fact that these species could migrate independently of any of the permanent stream systems explains why they now have such a wide range across Canada and Alaska and also why relict populations of such fishes as *Coregonus clupeaformis*, *Coregonus cylindraceus*, *Salvelinus namaycush*, and *Catostomus catostomus* exist in certain isolated areas along the Atlantic coast, the latter species as far south as western Maryland.

Underhill (1957) says that the present distribution of the above fish, as well as others, such as the other species of *Coregonus* found in the Great Lakes, *Cottus ricei*, *Myoxocephalus quadricornis*, and *Pungitius pungitius*, can best be explained by an eastern refugia during the last glacial advance and subsequent dispersal through an eastern outlet of Lake Agassiz (Elson, 1955). I find an east-to-west dispersal for these species hard to believe for several reasons. In the first place, the latter species have never been found in any of the deep lakes of the Adirondacks, areas which provide suitable habitat and which should contain them if they had ever been present. In the second place, the glacier retreated in a northeasterly direction; thus the ice covering the eastern part of North America was the last to leave and the dispersal routes which could permit Atlantic coastal fish to enter the present Great Lakes are were the last to open. By this time it would have been too late for these species, which were now free to migrate to the west, to have reached Alaska since the connected lakes found at the foot of the glacier had long since disappeared. The fact that all of the above species, with the exception of *Cottus ricei* and those species of *Coregonus* which apparently differentiated within the Great Lakes, occur in Alaska means that they must have been present there during glaciation.

Fishes which remained on the Atlantic coast during the Wisconsin glaciation

In the Lake Ontario basin are found six species which obviously have Atlantic coastal affinities. These species, *Exoglossum maxillingua*, *Notropis bifrenatus*, *Notropis procne*, *Notropis analostanus*, *Semotilus corporalis*, and *Esox niger* are widely distributed up and down the coast, and thus certainly remained in this area during the glacial advances. Their ranges are typified by that of the cutlips minnow (*Exoglossum maxillingua*) - map 5. They could have entered the Great Lakes drainage in any one of several ways; entrance could have been into the Finger Lakes region through the Horseheads Outlet (Bailey, 1945), by the Mohawk outlet into glacial Lakes Lundy or Iroquois, or recently by dispersal through the Mohawk-Erie canal and/or other man-made connectives. Unfortunately, the true means of dispersal of these and several other species which are native to the Great Lakes but which have reached some of the Atlantic coastal streams probably will always be clouded because of the canal systems.

Possibly both natural and man-made routes were utilized by some of the above. It is difficult to draw conclusions about *Notropis bifrenatus*, *Notropis procne*, *Notropis analostanus*, or *Exoglossum maxillingua*, since these forms are closely restricted to the Lake Ontario drainage. However, the other two, *Semotilus corporalis* and *Esox niger*, almost certainly reached the Great Lakes in pre-Columbian times, since their present distribution cannot be satisfactorily explained otherwise.

Fishes which utilized both the Mississippi Valley and Atlantic coast refugia

A number of species have been found which definitely spent the last glacial period on both sides of the Allegheny mountains. Those which unquestionably should be included in the list are as follows:

I Species which entered the Great Lakes from both refugia but which apparently did not differentiate into subspecies
  1. *Salvelinus fontinalis*
  2. *Catostomus commersoni*
  3. *Semotilus atromaculatus*
  4. *Notemigonus crysoleucas* (described subspecies are probably clines)
  5. *Rhinichthys cataractae* (subspecies, if any, are not adequately studied)
  6. *Ictalurus nebulosus*
  7. *Ictalurus natalis*
  8. *Noturus gyrinus*
  9. *Stizostedion vitreum*
  10. *Perca flavescens*
  11. *Lepomis gibbosus*

II Species which entered the Great Lakes from both refugia and which apparently did differentiate into subspecies
  1. *Erimyzon oblongus*
  2. *Rhinichthys atratulus*
  3. *Notropis cornutus*
  4. *Notropis hudsonius*
  5. *Esox americanus*
  6. *Fundulus diaphanus*

III Species which reinvaded the Great Lakes from the Atlantic coast only
  1. *Hybognathus nuchalis* (two subspecies)

IV Species which reinvaded the Great Lakes from the Mississippi Valley only
  1. *Amia calva*
  2. *Lepisosteus osseus* (probably two subspecies)
  3. *Aphredoderus sayanus* (possibly two subspecies)
  4. *Notropis chalybaeus*
  5. *Chaenobryttus gulosus*
  6. *Pomoxis nigromaculatus*

As can be seen from the above, some of the species differentiated into subspecies; others did not. *Hybognathus nuchalis* (map 9) is one form in which subspecific differentiation did occur. The range of this species is atypical inasmuch as the Mississippi Valley population failed to reinvade the Great Lakes, while the eastern population did succeed in crossing over into the Lake Ontario drainage. However, if one imagines similar patterns of distribution for the other species, except that the range in the west touches at least one of the four western Great Lakes, a picture of the ranges characteristic of the other species can be formed.

The brook trout (*Salvelinus fontinalis*) and the yellow perch (*Perca flavescens*) are two other species which had glacial refugia on both sides of the mountains (maps 6 and 7). Neither differentiated into subspecies however. The ranges of the two fish to the north are somewhat more extensive than is characteristic of most fishes occupying multiple refugia, but otherwise they are typical. The distribution of *Salvelinus*, it may be noticed, is confined in the east to the highest portions of the Appalachian Mountains. To the west there are only relict populations in certain favorable habitats in the upper part of the Mississippi Valley. Its range, then, is much more extensive now in the reinvaded than in the refugial area. The yellow perch, on the other hand, is found in the lowlands along the east coast, and, being more tolerant of warm waters, is much more tolerant of warm waters, is much more widespread in the Mississippi Valley than is the brook trout.

Fishes which utilized the Mississippi Valley refugium only

By far the largest number of fish now found in the Great Lakes basin came from the Mississippi Valley. Most of them used only this refugium, although some (previously mentioned) were found in the Alaskan or the Atlantic coast areas as well.

In her work on the distribution of the fishes of Ontario, Radforth (1944) considered about a dozen-and-a-half species which are now distributed on both sides of the Appalachians to have utilized both the Mississippi and Atlantic refugia. However, as Bailey (1945) pointed out, their distribution is more likely due to a postglacial redispersal of Mississippi species, probably by way of the Horseheads outlet, from what is now the Finger Lakes region. These species are as follows:

1. *Moxostoma aureolum*
2. *Hypentelium nigricans*
3. *Hybopsis micropogon*
4. *Semotilus margarita*
5. *Campostoma anomalum*
6. *Clinostomus elongatus*
7. *Pimephales notatus*
8. *Pimephales promelas*
9. *Notropis heterodon*
10. *Notropis heterolepis*
11. *Notropis spilopterus*
12. *Notropis rubellus*
13. *Notropis hudsonius* (western subspecies)
14. *Percina caprodes*
15. *Cottus bairdi*
16. *Lota lota*
17. *Eucalia inconstans*

The spotfin shiner (*Notropis spilopterus*) - map 8 - has a range which is typical of the above species. These fish occur in the Mississippi Valley, but they also are found on the Atlantic coast from the Susquehanna drainage as far south as the James. It is significant that they do not occur naturally in the Delaware, Connecticut, or, for the most part, the Roanoke systems.

The best means for determining which forms are recent invaders and which are the older residents of the Atlantic coast is to compare the faunas of the Susquehanna and Delaware drainages. Fishes coming from the Finger Lakes have had access to the former system but not the latter. As a result, there are at least seventeen species which are found naturally in the Susquehanna but not in the Delaware, and these forms should be considered as recent invaders.

At the time of the above faunal invasion the ocean levels still were much lower than they are at present. The shallow bottom of Chesapeake Bay was above water and all streams from the Susquehanna south to the James were connected. As a result, there was much opportunity for faunal interchange among these streams and, as one might expect, the fish fauna of the Susquehanna is, in many respects, more similar to that of the James than to that of the Delaware, even though the latter system is much closer geographically.

There are a number of species found in the Great Lakes and Mississippi Valley which also are found in the Mohawk River drainage. This would seem to indicate a past dispersal through the Mohawk connection with glacial Lakes Lundy or Iroquois. It is fairly certain that interchange actually did occur by this means, but exactly to what extent will never be known, since the construction in the early 1800's of the Mohawk-Erie canal has permitted certain species to cross the drainage divide which would not otherwise have done so. The following is a list of those more western species which are known to occur in the Mohawk-Hudson river systems:

1. *Hypentelium nigricans* (common-possibly entered naturally)
2. *Moxostoma aureolum* (rare)
3. *Pimephales promelas* (rare)
4. *Pimephales notatus* (common)
5. *Semotilus margarita* (rare)
6. *Hybopsis biguttata* (rare)
7. *Notropis atherinoides* (rare)
8. *Notropis heterolepis* (rare)
9. *Notropis rubellus* (locally common)
10. *Notropis spilopterus* (locally common)
11. *Clinostomus elongatus* (rare)
12. *Noturus flavus* (moderately common)
13. *Umbra limi* (rare)
14. *Percopsis omiscomaycus* (moderately common-may have entered naturally)
15. *Percina caprodes* (moderately common)
16. *Etheostoma blennioides* (rare)
17. *Etheostoma flabellare* (moderately common)
18. *Labidesthes sicculus* (rare)

It is, I think, significant, that practically all of the above species are restricted to the upper part of the Mohawk, and most of them also are rather rare. For this reason, it seems that the Mohawk-Erie canal has been a much great factor in the dispersal of most of these fish onto the Atlantic slope. One of the main reasons for believing this is the fact that the Mohawk connective, even during its later stages, was always in rather close proximity to the retreating ice front. It is rather unlikely that the species which are relatively intolerant to colder water conditions would have been able to utilize this outlet during its existence.

Some species, such as *Esox lucius* and *Cottus cognatus*, as well as those existing as relicts in a number of the cold, deep lakes (*Coregonus clupeaformis*, *Coregonus cylindraceus*, *Coregonus artedii*, *Salvelinus namaycush*, *Catostomus catostomus*, and *Hybopsis plumbea*) undoubtedly entered by natural means, either through the Mohawk outlet or (more likely) by movement through the temporary impoundments at the foot of the glacier.

There are a few species, such as *Chrosomus eos*, *Chrosomus neogaeus*, *Hybognathus hankinsoni*, and *Eucalia inconstans* that are restricted to the upper Hudson and/or Atlantic tributary streams which probably entered these drainages by a connection (or crossovers) from the St. Lawrence River. (For further discussion on the distribution of *Chrosomus neogaeus* see a subsequent paragraph). There is a rather low, flat area connecting the upper Hudson with the St. Lawrence, and it is quite possible that these species could have made their way across in this way. It is significant that all of these fish are inhabitants of cold, small, usually boggy bodies of water and thus would have been able to filter into the area without much difficulty.

The distribution of two other species which are found on both sides of the Alleghenies makes little geographic sense. *Ericymba buccata* has been recorded from the Potomac River but from no other streams on the Atlantic coast. For this reason its occurrence in the Potomac probably represents an introduction. *Percopsis omiscomaycus* is known from the Mohawk-Hudson drainage, and Hubbs and Lagler (1947) give its range on the east coast as "from the Hudson River system south to the Potomac." If this is true the species must be quite rare, because Greeley's (1936) report on the survey of the Susquehanna and Delaware River systems in New York failed to mention it. It is possible that *Percopsis* actually does occur in small numbers, at least, in the Susquehanna River in Pennsylvania.

Of those species which have never reached the east coast, there are a number of different combinations of ways in which they entered the Great Lakes and the lakes comprising what was formerly glacial Lake Agassiz. Greene (1935) and Radforth (1944) mentioned five major outlets: the Warren River outlet from glacial Lake Agassiz, the St. Croix River outlet from glacial Lake Duluth, the Fox and Chicago River outlets from glacial Lake Chicago, and the Ft. Wayne or Maumee River outlet from glacial Lake Maumee. The presence of a fish in an area which formerly was drained by one of these glacial outlets has been considered evidence that the species in question used this particular path of entrance. For example, occurrence in both the Mississippi Valley and Lake Erie and its tributaries strongly suggests that the species utilized the Ft. Wayne outlet. In most cases an assumption of this sort is true. However, it is becoming increasingly evident that other factors sometimes may influence distribution. Ecological conditions have changed a great deal since pre-Columbian times, and if we had an adequate picture of the situation as it existed then we would undoubtedly have to revise our ideas concerning the mode of distribution of many species. This is especially true with regard to the northern species which inhabit cold, bog waters. The conditions under which these fish thrive have practically disappeared in the more southern areas; this has been due to both natural and unnatural reasons. In most cases a few relict populations are the only definite clue we have to their former southerly distribution. The lowering of the water table, particularly within the last fifty years, has eliminated the vast majority of the small springs in which such species had been able to survive.

The presence of southern species in the Red River of the North and in the lakes now found within the area of former Lake Agassiz has been considered as indicative of a post-glacial connective between the Mississippi Valley and Lake Agassiz. This is a logical assumption and probably a valid one in most instances, especially when the fish in question is widely distributed to the north. In some cases, however, such as that of *Notropis spilopterus*, *Notropis anogenus*, and *Notropis dorsalis*, this assumption should be made with caution since these species are found only in the southern headwaters of the Red River, in close proximity to the headwaters of both the upper Mississippi and Minnesota Rivers. Present evidence has shown that the barriers connecting both these river systems with the Red River have been broken, at least momentarily, quite recently (Underhill, 1957, pp. 7-8).

It is also possible that some of these species which failed to go very far north in this drainage are limited by the 65° July isotherm (see Radforth, 1944 and Keleher, 1956). To determine, then, which species actually entered by the glacial outlet and which ones came in at a later time is very difficult, since some fish which entered recently could have moved well up the river whereas some of those which entered through the Warren River may have been restricted in their northward dispersal by the temperature factor.

The discovery of a second, eastern outlet from Lake Agassiz (Elson, 1955) means that a number of species whose presence in this area had been attributed solely to entrance through the Warren River outlet may actually have entered through the eastern outlet or may have utilized both outlets. Nor is it impossible that the upper Mississippi may have furnished some sort of a dispersal route into Lake Agassiz, although this was probably of minor importance compared to the other two. In order for one to know with any certainty that the Warren River was the sole outlet utilized by a particular species of fish, several requirements must be met.

First, the species must be fairly widespread throughout the Lake Agassiz region, and second, it must be absent from both the upper Mississippi River and the Lake Superior drainage. Underhill (1957, (considering only minnows and darters) found that three species met these requirements: *Hybopsis storeriana*, *Percina maculata*, and *Percina shumardi*. Probably most, if not all, of the other species, utilized the Warren River, at least in combination with the other outlets, but it is impossible to be absolutely sure of this.

Underhill also believed that the eastern outlet to Lake Agassiz was of major importance in the distribution of at least two species, *Hybopsis plumbea* and *Chrosomus neogaeus*. These two fish are found on the northern Atlantic slope and in a few isolated areas in the upper Mississippi Valley. Although these forms survived the last glacial advance in the latter area, Underhill felt that they did not disperse from that center. As evidence he pointed to the fact that these species are absent both in the St. Croix River system and in the upper Mississippi River above St. Anthony falls. Rather he thought it probable that they had a second refugium on the Atlantic coast and that their present distribution, which extends to the Red River of the North and (for *Hybopsis plumbea*) still farther west, can be accounted for on the basis of a westward migration through the Great Lakes and into glacial Lake Agassiz through the eastern outlet.

This explanation seems to be more convincing for *Chrosomus neogaeus* than for *Hybopsis plumbea*. The latter has a more extensive range than the former, and its presence throughout western Canada and even onto the Pacific slope led Walters (1955, p. 344) to hypothesize a Pacific refugia for this species as well as for *Salvelinus namaycush*, *Catostomus catostomus*, *Rhinichthys cataractae*, and *Lota lota*. The Atlantic coastal distribution of *Hybopsis plumbea* agrees well with that of other species (previously mentioned) which are thought to have arrived there very soon after the retreat of the glacier. The finding in 1954 of a tiny relict population in a small spring creek near Dubuque, Iowa, is definite proof that this species probably had a wide distribution throughout the Mississippi Valley during the Wisconsin, and its present absence from the upper Mississippi and St. Croix rivers may possibly be attributed to ecological factors.

Presence in the Lake Superior and/or the upper St. Croix River has been cited by Greene (1935) as evidence that the species in question penetrated the Great Lakes drainage by means of the St. Croix outlet. As Underhill (1957) pointed out, this is not always a valid criterion. "St. Croix falls," which Greene considered to have formed an impassible barrier to the dispersal of fishes into the upper reaches of this river in recent times are really not falls at all but only a lengthy (about six miles) stretch of rapids in the vicinity of Taylor's Falls, Minnesota. Although it would be difficult at present for a quiet-water form such as *Notemigonus crysoleucas* to traverse this stretch of stream, it would not seen so improbable when considered over a long period of time, especially if it is realized that considerable change could have occurred in this area over the past several thousand years.

Three other species, *Hybopsis biguttata*, *Notropis deliciosus*, and *Notropis dorsalis*, present in the Lake Superior basin, may not have used the St. Croix-Brule connective in their post-glacial dispersal. The bigmouth shiner (*Notropis dorsalis*) is absent from the Lake Superior drainage of Wisconsin, and has a rather local distribution in this same basin in the Upper Peninsula of Michigan (Taylor, 1954). Its absence from the western end of Lake Superior and its abundance in the St. Croix River suggests a post-Lake Duluth migration from the lower Great Lakes.

The hornyhead chub (*Hybopsis biguttata*) and sand shiner (*Notropis deliciosus*) present a more complex problem; both are present, but not common, in the Lake Superior drainage of Wisconsin and Michigan. It is difficult to explain the absence of these minnows from the St. Louis River on ecological grounds, since suitable habitats are present there. That they are absent from the St. Louis River is supported by the fact that Moyle and Kenyon (1947) failed to obtain specimens, although they made 267 collections in this river and its tributaries. The presence of the sand shiner in the Hudson Bay drainage (Radforth, 1944), indicates a tolerance for cold waters and weakens any conclusion based on temperature as a barrier to expansion. The restricted distribution of these species could be explained by their recent migration into the Lake Superior basin from the lower Great Lakes along the south shore of Lake Superior in post-Lake Duluth time, as access to the St. Louis River is barred by impassible falls at Scanlon, Minnesota. Falls near the mouths of the north shore streams and possibly the lack of suitable habitats may explain their absence from the remaining streams of the Lake Superior watershed in Minnesota. Taylor (1954) suggested that the hornyhead chub may have migrated northeastward along the shores of Lake Superior and Lake Michigan. Both species are common in the St. Croix and upper Mississippi rivers and if they used the St. Croix-Brule connective in Lake Duluth time their rareness in the Lake Superior drainage is difficult to explain. While existing evidence is not entirely conclusive, a post-Lake Duluth route of dispersal into the Lake Superior basin is not improbable.

It can be seen from the preceding that a new set of criteria should be used for determining the validity of dispersal into the Great Lakes through the St. Croix outlet: (1) distribution throughout the St. Croix River; (2) distribution in the Lake Superior watershed and showing a center in western Lake Superior; this may be spotty because of the nature of most of the tributary streams bordering Lake Superior; and (3) assuming a suitable habitat therein, presence in the St. Louis River above the falls at Scanlon, Minnesota. In addition, the presence of a species on Isle Royale is excellent evidence that the St. Croix outlet was used, although absence from this area does not necessarily mean that the species in question did not enter in this way (Hubbs and Lagler, 1949)

The distribution of *Hybognathus hankinsoni* does not warrant its inclusion among those fishes using the St. Croix outlet, although Bailey (1954) included this stream as a dispersal route for this species. There are no records for the St. Louis River and the records for the upper St. Croix drainage and western Lake Superior are very spotty. It would seem that this species most likely entered the Great Lakes through the Fox River connective and then worked its way around to the shore of Lake Superior, as did *Hybopsis biguttata*, *Notropis deliciosus*, and *Notropis dorsalis*.

Greene (1935) discussed the two main problems connected with hypothesizing a dispersal into Lake Michigan through the Fox River connective. First, the Portage canal has permitted some species to enter the Fox River drainage which otherwise would not have done so; these usually can be recognized because of a limited distribution centered around the outlet of the canal (i.e. *Fundulus notatus* and *Etheostoma caeruleum*). Second, the distribution in the Fox River system of some of the big-water species, such as *Roccus chrysops* and *Ictalurus punctatus* is just as readily, if not better, explained by attributing their presence to migration through Lake Michigan and Green Bay.

Thus, fish which definitely can be said to have utilized the Fox River outlet should (1) be smaller-stream species which are not likely to migrate through a large body of water such as Lake Michigan, and (2) have a reasonably wide distribution throughout the Fox River system. *Percina phoxocephala* (map 15) is an example of a fish that has entered the Great Lakes through this outlet alone.

The picture of fish distribution into Lake Michigan by means of the Chicago River outlet has also been clouded by the construction of the Chicago drainage canal. Passage through the canal is believed to be responsible for the occasional records of Mississippi Valley species, such as *Ictiobus bubalus*, *Polyodon spathula*, and Pylodictis olivaris, in the Lake Michigan drainage. This may well be, although the presence of very small populations of the latter two species in Lake Erie is believed to be natural. If so, it would seem logical that their presence in Lake Michigan could be natural as well. (For further discussion of this see a subsequent paragraph). The small-stream inhabiting species, such as Notropis chalybaeus (map 14), which occur in various tributaries of southern Lake Michigan are the best indicators of dispersal through the Chicago River outlet.

Natural passage of fish from the Wabash River into the Maumee is possible today (Miller, 1957); the area around Ft. Wayne, Indiana, is rather low and marshy (at least it was in pre-Columbian times) and it is quite possible that fish could have crossed this barrier during high water conditions. More recently the construction in western Ohio of the reservoir for the Miami-Erie canal, Lake St. Marys, has opened a permanent connection between these two river systems. This body of water connects only headwater areas, thus making it improbable that fishes inhabiting only the main rivers would utilize this connection. However, at least two species, Phenacobius mirabilis and Lepomis humilis, are known to have entered the Great Lakes within the last half century by this means. On the other hand, species such as Ammocrypta pellucida (map 13), Moxostoma carinatum, Hybopsis x-punctata, Hybopsis storeriana, Notropis boops, and Noturus miurus, to name a few, must have entered through the original outlet.

It is known that during much of the existence of the Ft. Wayne outlet Lake Erie was little more than a large, broad river, resembling little the Lake Erie of today. As a result, there was no abrupt constriction of the lake at its confluence with the Maumee River such as now exists. This has been confirmed by van der Schalie (1938 and 1940), who has found that a number of molluscs which usually are confined to big rivers of the Mississippi Valley are known in the Great Lakes region only from streams tributary to the western end of Lake Erie. This is also reflected in some of the species of big-river fish which are known to occur naturally in western Lake Erie and its larger tributaries, such as Hybopsis storeriana, Ictiobus cyprinellus, Pylodictis olivaris, Polyodon spathula, and Moxostoma carinatum. These species are all Mississippi Valley inhabitants which must have entered the Great Lakes through this outlet. It is possible that Pylodictis and Polyodon used the Chicago outlet, but because of the circumstances just discussed, their occurrence in Lake Michigan is not as likely to be natural as it is in Lake Erie.

The possibility that a species such as Lepisosteus productus, which is found both in Lake Erie and in southern Lake Michigan, could have come in originally through only one glacial outlet should be considered. During a warmer climatic period than is not present, this species could have moved around the lower peninsula of Michigan into the other lake; then, when the climate became colder again, the range would have been restricted to the more southerly areas. Since Lepisosteus productus is not found in the Fox River system, this method of dispersal probably did not occur. However, when a species is found in Lake Erie, southern Lake Michigan and in the Fox River system, this possible means of dispersal is not so easily eliminated.

There are a number of species whose distributions are wide longitudinally but rather narrow latitudinally, especially to the east. Bailey's (1954) distribution map of Hybognathus hankinsoni illustrates this point. Other species show the same general pattern, particularly with regards to their range from southeastern Wisconsin to western New York. Fish such as Chrosomus neogaeus, Pfrille Chrosomus eos, Semotilus margarita, Margariscus Notropis anogenus, ort. Notropis heterodon, Q. ort. and Moxostoma valenciennesi are strictly confined to the Great Lakes drainage within the longitudinal zone described above.

The first three species are further characterized by a range which in Michigan extends southward only to about 42° N. latitude, and which fails to include Ohio at all; this can be attributed to a present lack of the cold, bog type of habitat which these fish require. To the east they occur in Nova Scotia (Livingstone, 1953) and to the C. eos and C. margarita ~~westward found~~ in eastern British Columbia (Carl and Clemens, 1953). They also have entered the upper Hudson drainage, probably through a filter connective from the St. Lawrence River. Occurrence in the Mississippi drainage is mostly limited to northern tributaries, with a few relict populations farther south (Hubbs and Lagler, 1947).

The other species show a similar range, but do not extend so far east or west, are not found in the upper Hudson River drainage, occur in Ohio and southern Michigan, and have a slightly more southerly distribution in tributaries of the upper Mississippi.

The most important characteristic of the above ranges is the fact that all species concerned occur in the Mississippi drainage to the west but are absent in the east. Obviously, then, their glacial refugium was only in the western part of the Mississippi Valley. They probably reentered the Great Lakes only through the Fox River and in some cases the St. Croix outlets, then spread eastward into Lake Erie and/or through the Trent River outlet into the St. Lawrence. Their presence in tributaries of Lake Michigan and Lake Erie, then, does not constitute absolute proof that these species reentered the Great Lakes through either the Chicago River or the Ft. Wayne outlets.

Occurrence of the bogwater forms as far west as British Columbia indicates that they may have entered Lake Agassiz and then worked their way westward. If so, their seeming lack of abundance in Manitoba (Keleher and Kooyman, 1956) is rather puzzling. At the same time, the eastern outlet of glacial Agassiz could also have been utilized in their eastward dispersal.

Lastly, the distribution of Hiodon alosoides is interesting inasmuch as this is the only species which is found in the Lake Agassiz area but which has never been recorded from the Great Lakes drainage. Its puzzling absence from the latter area has been thought by some to be due to competition with the closely related Hiodon tergisus. However, the two live together in many other parts of their ranges, so this hypothesis seems to be invalid. It has also been suggested that since Hiodon alosoides is an inhabitant of large, silty waters, the glacial outlets into the Great Lakes were not large enough nor turbid enough for it to enter them. Although this is probably the best hypothesis so far, it still falls far short of a satisfactory explanation of this problem.

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Migratory Tendencies of Lake-run Brown Trout

Marlin L. Hornberger

ABSTRACT

Migratory tendencies of lake-run brown trout (Salmo trutta) in selected Swedish, Scotch, and American lakes are reviewed. Environmental stimuli and effects of adverse environmental conditions on the spawning runs are discussed.

INTRODUCTION

Brown trout (Salmo trutta) are native to Europe. Some brown trout, like many salmonids, migrate to spawn. The purpose of this paper is to describe the migration of spawning brown trout in selected Swedish, Scotch, and American lakes and to discuss environmental stimuli and the effects of adverse environmental conditions on the spawning runs.

DISCUSSION

Shoaling

Before fish which are to spawn enter streams, they collect into shoals off stream mouths. Shoal formation indicates a change in brown trout behavior (Stuart,1953). In a large lake the appearance of trout shoals may be preceeded by a gradual movement of fish toward areas where shoals will form (Pyefinch,1960).

Reasons why trout shoal are not fully known, but maturation of ovaries and testes is probably an important factor. Trout in these shoals, however, vary considerably in their ripeness (Pyefinch,1960).

Spawning

Although dates of shoaling correspond very closely each year, the time that the first fish ascends the stream varies from three to fifteen days. In a typical spawning season in Dunalastair Reservoir, Scotland, the spawning migration is composed of a series of runs which increase numerically from the first small run to a major run during the middle of the spawning period, thereafter decreasing regularly until the first few fish have spawned (Stuart,1957). Generally each year the chief runs are made in a stream rising after a variable period of low water levels or in falling water levels after a flood or freshet. Normally each run is completed within a period of 24 hrs and continued from early morning until late afternoon or from one afternoon until the following morning, depending on the state of the stream level (Stuart, 1957).

Eventhough runs occur uniformily from late summer through early autumn, the timing of the runs varies considerably from one location to the next. Niemuth (1967) reported that migration from Lake Superior into the Brule River, Wisconsin, begins in early July, peaks in August, and is virtually completed by mid-September although there is a small upstream movement through December. He also showed that trout that migrated upstream early (Ausust-September) one year usually moved early the following year and trout moving later (October-November) showed up later. Although trout migrated as early as July, no spawning occurred until October. Gustafson (1951) reported a very similar migratory run in Lake Storsjon, Sweden in which the main migration occurred during July and August with a peak during the early part of August. Brown trout in Lake Rensjon, Sweden, migrate in August and September (Runnstrom, 1957).

Sex ratio and age composition of the run vary from locality to locality. Gustafson (1951) and Munro and Balmain (1956) reported that females were more numerous than males, while Stuart (1957) reported that males were more numerous than females. Gustafson (1951) reported that 90% of the spawning stock were 7 to 10 years old; Runnstrom (1957) reported that spawning fishes were from 4 to 12 years old; Niemuth (1967) reported that the spawning fish were from 4 to 5 years old.

<u>Stimuli initiating spawning runs</u>

In 1938, Carl remarked that the spawning runs up Cowichan River, Vancouver Island were induced by freshet conditions immediately following heavy rainfalls. Stuart (1953) and Munro and Balmain (1956) also determined that increase in water level was a stimulus to upstream migration of spawning brown trout. Niemuth (1967) demonstrated that periods of high turbid water stimulated migration, but this was not the only trigger which induced trout movements because even during July and August, when there was little or no rain and the water was low and clear, migratory brown trout still moved into rivers in significant numbers. Niemuth also found that shallow clear water does reduce the daytime migration of trout and that more trout migrated om dark nights than on bright ~~moonlit~~ moonlight nights.

There is no one consistant rule conserning the role of temperature as a stimulus to migratory runs. Carl (1938) felt that temperature differences were of minor importance. Munro and Balmain (1956) also reported that there seemed to be no relationship between water temperature conditions and the incidence of the runs. In Dunalastair Reservoir, however, shoaling occurred only when the loch temperature fell to about 9°C (Pyefinch, 1960). Pyefinch reported that the main spawning run took place when the temperature of the stream dropped below that of the loch and never when the temperature of the spawning stream was higher than that of the loch. Niemuth (1967) believed that warm waters of the Brule River during spawning runs (in contrast to cold Lake Superior) may be an attraction. He reasoned that the warmer water temperatures may aid or accelerate the development of the reproductive organs.

Effects of floods on migratory runs

According to Gustafson (1951) swiftly rising water levels in a stream have pronounced negative effects on the intensity of migration. Stuart (1957) noted that the pattern of runs was completely altered and the run was extended for a total of 49 days compared with the previous average figure of 36 days when heavy rains and flooding persisted. The major runs were more widely separated than before and were individually composed of a greater number of fish. Fish will neither run, nor, if they have attained the spawning ground, continue their spawning activities at high water levels. Hydraulic barriers to the running fish are formed when the water reaches a certain height in relation to its channel and the activity of spawning fish on the redds is arrested by associated physical phenomena.

Effects of drought on spawning migrations

The most obvious effect of an extended drought is to reduce water levels to a point where trout cannot possibly enter the stream. Pyefinch (1960) reported that shoaling seemed unusually late during a season of extended drought. If the drought lasts long enough, the spawning run may be greatly reduced because of physiological changes of the gonads (Stuart, 1957).

Post-spawning trout dispersal

Brown trout dispersal after spawning is quite variable. According to Stuart (1957), when conditions on the redds are favorable for spawning the majority of female trout spent less than 24 hrs in the stream while the greater proportion of males remained several days. Niemuth (1967) reported the following: (1) brown trout dispersal after spawning is quite erratic; (2) some fish remain in the spawning area while other fish tend to move slowly downstream seeking out deeper pools; (3) at times 25 to 50 or more large trout congregated in a single pool; (4) the downstrean movement starts immediately after spawning and continues into early winter.

O'Donnell and Churchill (1954) reported only limited fish movement after the winter temperature dropped below 40°F. Fallis and Niemuth (1962) also reported little or no fish movement during the cold winter months when water temperatures were in the lower 30's. Niemuth (1967) found that water temperatures in the spring were not an influential factorin trout movements, but downstream movement closely followed ice breakup in late March or early April. Runnstrom reported that no spawners returned to Lake Rensjon (Sweden) until spring and early summer.

Migration of immature trout

Niemuth (1967) observed a spring and fall downstream movement of 3 yr old, 6 to 11 in brown trout which had spent the past two years in the parent stream. Furthermore, he noted that although the number of migrating fish varied from day to day and month to month,the overall downstream movement can best be summarized as a continual trickling of fish from the parent stream into Lake Superior. Stuart (1957) described the downstream migration of juveniles in Lochan an Daim, Scotland as follows: (1) there is a well defined downstream migration chiefly of 1^+ and 2^+ fish each autumnwith a proportion of 0^+ fish migrating at this time; (2) this migration normally occurs before adult spawners enter the stream from the loch, but the two separate movements may coincide; (3) although a small proportion of 1^+ and 2^+ male trout become sexually mature and delay their downstream migration until after the arrival of the adult trout, no female trout have been observed to do so; (4) a similar well defined upstream migration in the spring has also been noted, and this generally takes place around the same date each year; (5) while the seasonal migrarion may be performed by 0^+, 1^+, and 2^+ trout, no fish of either sex above this age have been found to reside in the streams during the summer.

Pyefinch (1960) noted the following in Loch Tummel, Scotland: (1) once fry have dispersed from redds, they become distributed along the stream in which they were hatched but they do not immediately leave this stream to enter the loch; (2) fifty-one per cent of the young fish spent two years in the nursery stream before migrating, 27% spent three years, 15% migrated after one year, and 7% spent four years or longer before migrating; (3) fastest growing fish leave the nursery stream first (i.e. those that migrate when a year old are longer than those that remain and the same seems to be true for two-year-old and older mi migrants); (4) once the young fish has left the nursery stream it does so as a mature fish to spawn. Runnstrom (1957) observed that young trout mainly of age groups I to V (II and III age groups dominate) ascend into the lake around the beginning of June after the ice has broken and after the water has warmed. He also stated that migration terminated in October when the temperature of the water dropped considerably.

SUMMARY

1. Before fish which are to spawn enter streams, they collect into shoals off stream mouths.
2. Although dates of shoaling correspond very closely each year, the time that the first fish ascends the stream varies from three to fifteen days.
3. Eventhough runs occur uniformily from late summer through early autumn, the timimg of the runs varies considerably from one location to the next.

4. Sex ratio and age composition of the run vary from locality to locality.

5. Increasing water levels are a stimulus to upstream migration of spawning brown trout.

6. There is no one consistant rule concerning the role of temperature as a stimulus to migratory runs.

7. Swiftly rising water has a pronounced negative effect on the intensity of migration.

8. The most obvious effect of an extended drought is to reduce water levels to a point where trout cannot possibly enter the stream.

9. Brown trout dispersal after spawning is quite variable.

10. The age of immature fish and the season of migration are highly variable.

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D.W. CHAPMAN and T.C. BJORNN
Idaho Cooperative Fishery Unit
Moscow, Idaho

Distribution of Salmonids in Streams, with Special Reference to Food and Feeding

ABSTRACT

Autecology of fish distributions is treated with particular attention to behavior of young chinook salmon and steelhead trout in Idaho streams. Behaviour of other fish species and races is examined and discussed.

In the warmer months young chinook salmon and steelhead trout are associated with velocities and depths in proportion to body size, shifting to faster and deeper waters as body growth occurs. Interaction for space between species is minimal because of differing times of fry emergence. Distribution close to high-velocity water is food-related and density is socially-controlled with the greatest distributional role of social behavior played among fish of near-equal size. During the day the fish remain in a small home area, then settle at night to the bottom, generally after moving inshore.

Beginning in September many young steelhead and chinook salmon move downstream from tributaries to overwinter in larger streams, often living in the stream substrate. Most fish disappear into the substrate at temperatures below about 5 C, and winter cover is important in holding over-wintering fish.

Distributional behavior of young salmon and steelhead in the warmer months is similar to that of several other salmonid species. Winter hiding behaviour is common in stream salmonids, often preceded by downstream movement in the fall. Return upstream movements in spring often occur. Such behavior in the colder months is probably directly related to water temperature.

INTRODUCTION

For several years we have been trying to understand why young chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Salmo gairdneri*) are found where they are within streams in Idaho. Some components of their distributional behavior have been: obvious diurnal-nocturnal changes in locations occupied: occupancy during summer, and sometimes longer, of specific home areas, downstream exodus of fish in the fall, and winter hiding behavior.

We present evidence in support of the conclusions and speculations listed below about distributional behavior:

1. In the warmer months the young fish are associated with velocities and depths in proportion to body size, shifting to faster, deeper waters as they grow, and in a given

space interaction between juvenile chinooks and steelhead is minimized by differing times of spawning and fry emergence. Distribution close to high velocity water is largely food-related, and density within suitable habitat is socially controlled, the greatest distributional role of social behavior being played among fish of near-equal size. During the day the fish remain in a small home area, and at night settle to the bottom, usually after moving inshore.

2. Generally beginning in September, many young steelhead and chinook salmon move downstream from tributaries, then over winter in larger streams, often living in the stream substrate. This behavior appears to be a function of water temperature, with most fish hiding in the substrate at temperatures below 4.4 - 5.5 C. Winter cover, especially large rocks, is important in holding over-wintering fish.
3. There is much similarity in behavior among several salmonids in streams around the world. Distributional behavior of young salmon and steelhead in the warmer months is similar to that of brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*), eastern brook trout (*Salvelinus fontinalis*), and coho salmon (*Oncorhynchus kisutch*), although there are some differences in cover preferences. In winter, hiding behavior is common among stream salmonids, often preceded by downstream movements in the fall. In species not demonstrating anadromy, return upstream movements in spring often occur. Such movements and behavior in the colder months are probably directly related to water temperature.

In our discussions we will deal largely with the autecology of fish distributions. In the interest of conserving space and time we refer to the excellent treatment of interactive segregation between fish species by Nilsson (1967) and such reports on species interactions as those by Hartman (1965), Kawanabe (1959) and Kalleberg (1958).

DAILY DISTRIBUTION

FOOD-RELATED DIURNAL DISTRIBUTION

In observing the behavior of 0 age chinook salmon in a stream aquarium, we have found distributions of fish to be closely associated with food inlet points (Fig. 1). We fed brine shrimp (*Artemia sp.*) throughout 13-hour days, introducing food at 2, 4, and multiple inlets and found that chinooks distribute themselves both horizontally and vertically to adjust to food supply. One could argue that the fish were conditioned by the food regime, but they certainly adjusted their distribution readily. On January 30, 1966, an upstream shift of the food inlet by about 2 m resulted in a marked upstream shift of chinook distribution within 4 hours (Fig. 1).

Aggression was high downstream from points of food concentration, yet young chinooks concentrated and persisted there when food was abundant. This implies that chinooks, at least, can take advantage of short-term food abundance, subordinating any minimal-space requirement to do so.

Keenleyside and Yamamoto (1962) reported that Atlantic salmon in aquaria will shift distributions in response to food availability, the territories and groupings of fish disintegrating as food enters aquaria. Coho salmon were observed by Mason (1966) to concentrate near the point of drift-food entrance in his experimental stream channel.

Some shifts in salmonid distribution during the day are probably caused by activity rhythms. Confined brown trout have been reported to be active from dawn to dusk, with peaks in activity frequently occurring at dawn (Swift, 1964). These fish were fed supplementally with beef liver. Swift (1962) also reported that confined *S. trutta* feeding on natural foods which entered their cages in Lake Windermere also were inactive at night and active during the day. In most months there was a peak in activity at dawn, according

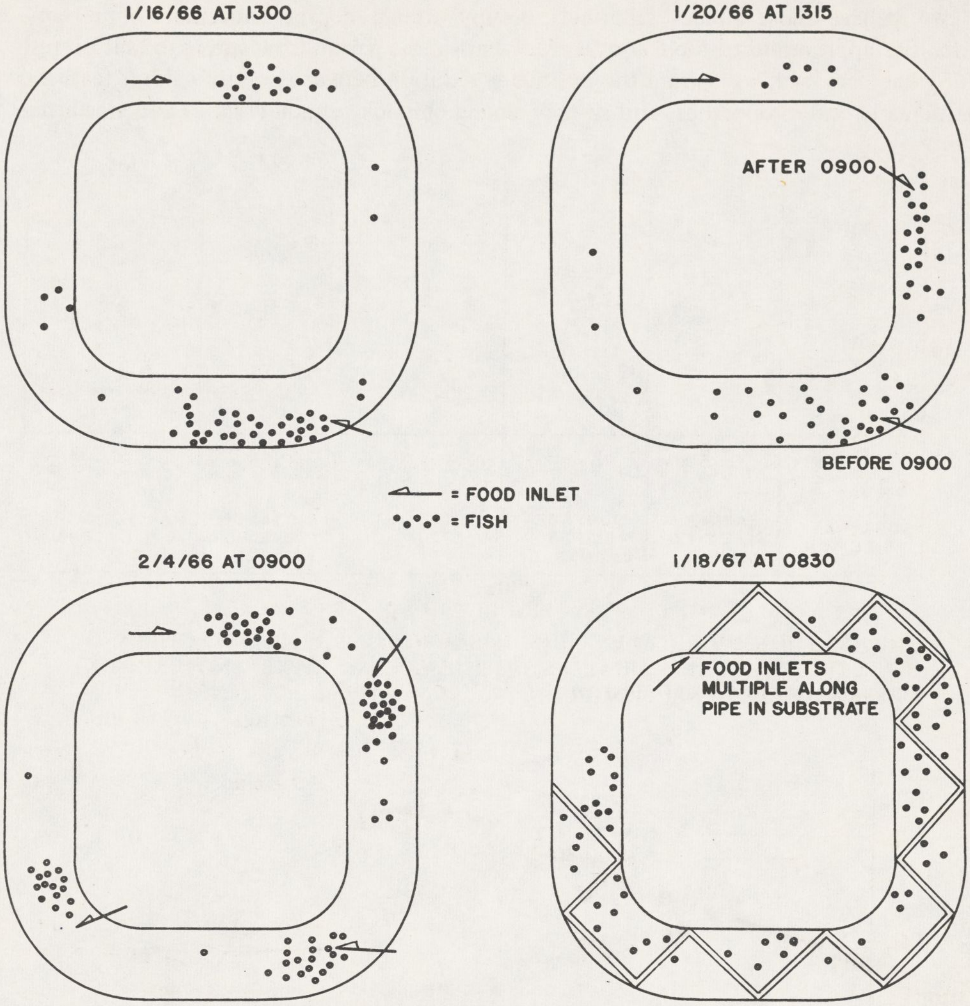

FIGURE 1

DISTRIBUTION OF CHINOOK SALMON FRY IN A STREAM AQUARIUM IN RELATION TO LOCATION OF FOOD INLETS. CURRENT IS CLOCKWISE.

to Swift. Pinsky (1962) has noted that *S. salar* fed intensely at dawn and dusk.

Coho salmon in a stream aquarium moved onto riffles at dusk, often remaining there at night (Mason, 1966), and riffle occupancy was accompanied by increased aggression. Mason noted active feeding by coho at night, especially when moonlight was available. He observed feeding at light levels below 1.076 lumen/m^2, the cone threshold. Mason felt the diel pattern of riffle occupancy by coho was indicative of a feeding rhythm, and that the higher retinal cone sensitivity of coho fry, with threshold to 1.076 lumen/m^2 as compared with 10.8 lumen/m^2 in pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon fry (Ali, 1959), might be of adaptive value in exploitation of the diel organic drift cycle in streams (Waters, 1962). It is time for further research on retinal sensitivity and eye mechanics in several salmonid species.

The activity cycle noted by Swift (1962), with some peaking at dawn, may also be an adaptation to the nocturnal peaking of drift organisms. The diel drift cycle is well-known to aquatic ecologists who fairly consistently have found larger numbers of drifting insects beginning near dusk and ending about dawn.

We believe most stream salmonids occupy stream depths and, more important, velocities appropriate to their body size, at least in the period from spring to fall. Everest (MS) has data which illustrate the positive correlation between certain habitat features, particularly water velocities, and sizes of young chinook salmon (Fig. 2) and steelhead.

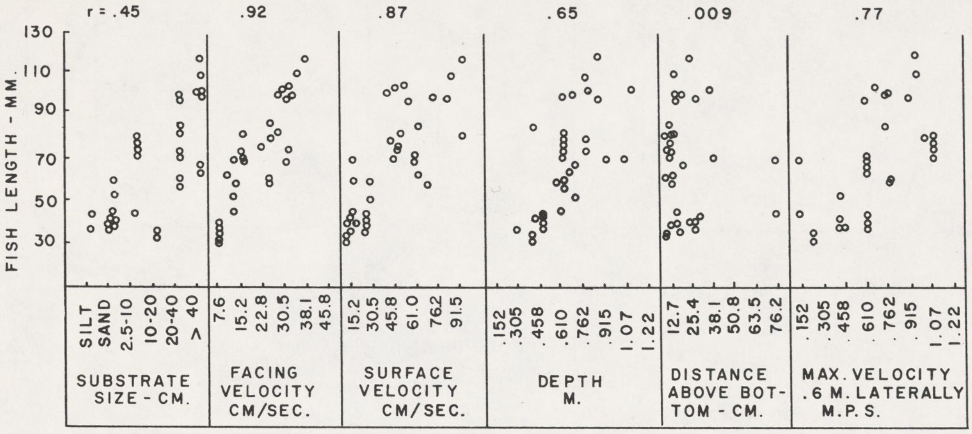

FIGURE 2

THE RELATIONSHIP BETWEEN CHINOOK SALMON OF VARIOUS LENGTHS AND SELECTED PHYSICAL VARIABLES OF THE LOCHSA RIVER AND JOHNSON CREEK (EVEREST, UNPUBLISHED).

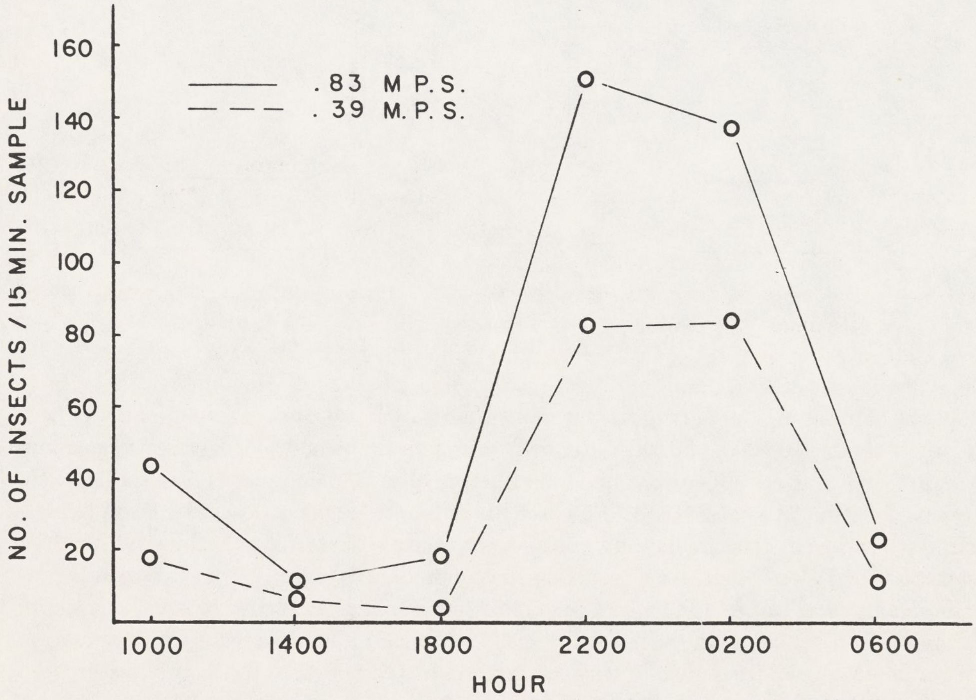

FIGURE 3

NUMBER OF INSECTS CAUGHT PER 15 MINUTE DRIFT-NET SAMPLE AT TWO CURRENT SPEEDS. CROOKED FORK CREEK, 11 JULY 1967 (EVEREST, UNPUBLISHED).

We feel that much of the indirect or underlying reason for positive correlations between fish size and selection of higher-velocity water is food supply. Higher-velocity waters bear a greater stream of food per unit of time. Everest (MS) confirmed this in an Idaho stream (Fig. 3). Everest also briefly examined the proposition that higher velocity waters bear larger organisms than slower waters (Table 1). There was a difference, perhaps not important, between mean sizes of organisms captured in velocities of .39 and .83 mps. This question should be re-examined with the addition of velocities from near zero to .30 mps. Everest did find that organisms drifting at night tended to be larger than those taken in daylight.

TABLE I

MEAN SIZE OF DRIFTING ORGANISMS, IN RELATION TO WATER VELOCITY AND TIME OF DAY, TAKEN IN DRIFT NETS ON 11 JULY, 1967 IN A TRIBUTARY OF THE LOCHSA RIVER, IDAHO. (EVEREST, MS).

Water velocity	*Time*	*Mean size of insects*	*d.f.*	*t value*	*Probability of larger t*
.39 mps	Day	2.75 mm	123	1.04	0.15
.83	Day	2.99			
.39 mps	Night	3.79 mm	448	1.82	0.04
.83	Night	4.30			
Combined data for both velocities	Day	2.92 mm	572	6.67	.0005
	Night	4.12			

We might conclude from the foregoing that fish go where the food is, but we have not been able to assess the relative importance of food supply versus the cover provided by depth and turbulence in causing fish to move toward faster, deeper water as they grow.

The shifts of fish distribution with fish size in large streams in Idaho are similar to shifts of other species in smaller streams. Coho fry in tributaries of coastal rivers occupy very shallow, quiet edge areas and move onto the relatively shallow glides such as those at the tails of pools as they grow. As age I pre-smolts they are found in deeper waters near the heads of pools. Saunders and Smith (1962) reported that brook trout fingerlings occupy riffle areas while larger trout are found in "flat water" near hiding places or in pools. Coastal cutthroat (*Salmo clarki*) often inhabit very shallow, small tributaries of slight velocity as fry, then drop downstream gradually as they grow (Lowry, 1965). The age II and older cutthroat occupy areas of heavy cover such as cutbanks close to the edge of the current in deeper waters. P. Reimers (1968) observed that young fall chinook salmon in an Oregon stream were often in groups organized largely on the basis of size hierarchies, and patchily distributed where food was abundant and positions could be maintained such as eddies where riffles entered pools. Egglishaw (1967) observed that Atlantic salmon shifted distribution as they grew. In river stretches where stones were small and water shallow, large trout or salmon parr were rarely found although fry used such reaches.

In our research on spatial interaction of juvenile steelhead trout and chinook salmon we have developed the hypothesis that differing times of emergence of the two species minimize mutual demands for a given habitat (Fig. 4) at any instant. Newly-emerged fish

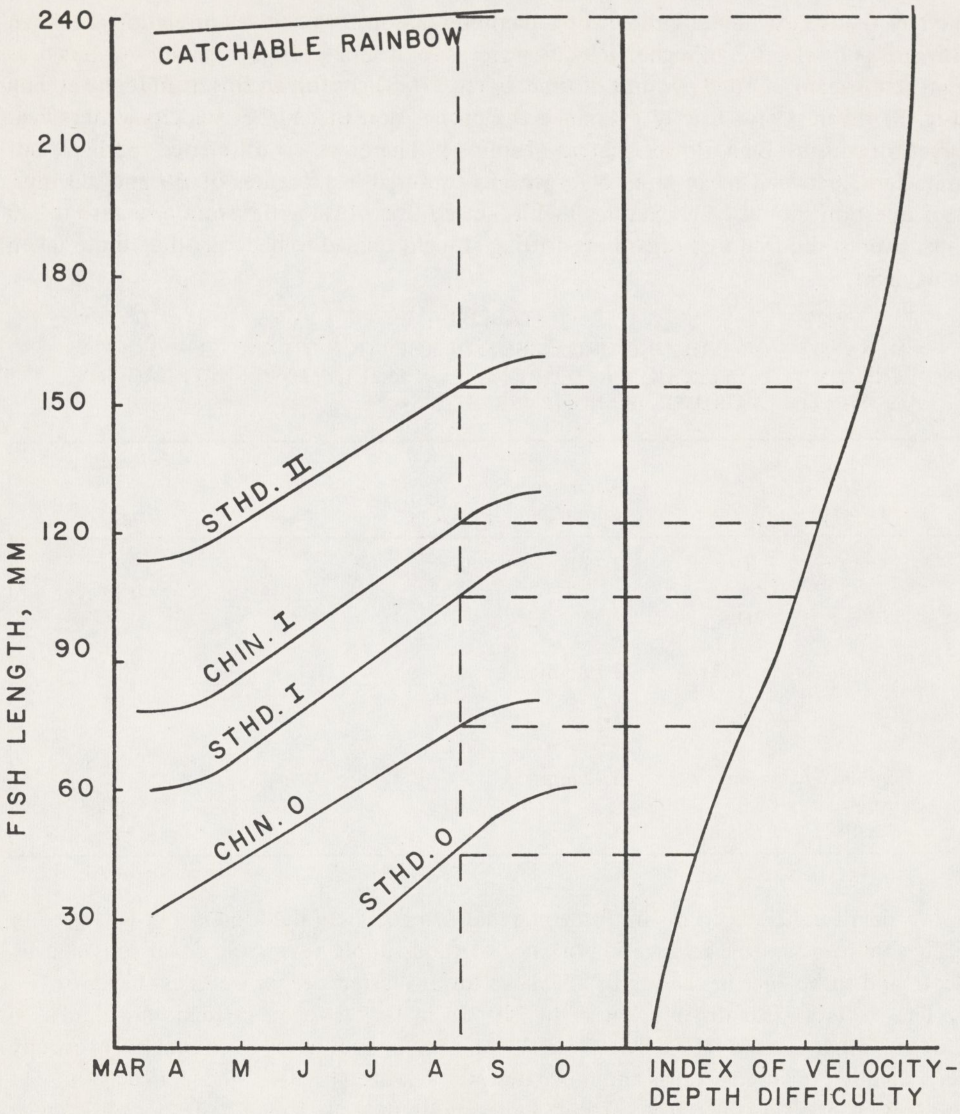

FIGURE 4

GENERALIZED RELATIONSHIP OF FISH SIZE, TIME AND VELOCITY-DEPTH FEATURES USED BY FISH OF VARIOUS SIZES. THE DASHED LINES ARE USED TO INDICATE THAT IN EARLY AUGUST THE DIFFERING SIZES OF FISH OF DISCRETE AGES AND SPECIES LEAD TO SPATIAL SEPARATION IN THE VELOCITY-DEPTH GRADIENT.

prefer or indeed can tolerate only nearly-still water. As growth proceeds the young fish shift toward faster and, to a degree, deeper water. At any one time there are several age and species size groupings which overlap very little, leading to maximal separation on the basis of physical habitat. This shift to deeper, faster waters is probably food-related, although there could be other habitat features contributing to the shift. Cover would be one such feature in larger streams where overhanging objects of mid-day shade are generally absent. Overhead cover provided by turbulence and shelters afforded by large rocks in deeper water tend to be more abundant away from the stream banks in deeper water. As streamflow declines in late summer, velocity becomes less important in controlling use of habitat, and opportunity for interspecific interaction would be maximal.

Egglishaw (1967) suggested that the "alternate spacing" of *S. salar* and *S. trutta* that he observed in stream habitat occurred because of differing sizes of trout and salmon at any one time. He stated trout were generally larger at a given time, possibly because early agonistic encounters between trout and salmon fry were generally won by trout, resulting in occupancy by trout of the most favorable habitat.

Steelhead and chinook salmon actually face velocities at home station or focal point which are lower than those near the home station. For example (Fig. 2), on the average a 70 mm chinook may face a velocity of .23 mps but lie under a velocity of .45 mps and have a maximum velocity .6 m laterally of .6 mps. To a degree facing velocity must dictate usable stations but a fish of given size must perform consistently on feeding darts into food-bearing, higher velocity waters near the feeding station without being swept downstream excessively. Carline (1968) felt that juvenile coho do not take up positions where they must maintain high activity levels.

COVER-RELATED SHIFTS IN DISTRIBUTION

The cover preferences of juvenile chinook salmon and steelhead trout are not clear. Our general impression is that chinooks of a given size are found in deeper water with a smaller substrate particle size than are steelhead trout of the same length. Steelhead are almost invariably associated with rubble particles and are in somewhat shallower water than chinooks. We have noted in laboratory work that chinook fry are easily frightened, darting away on very slight provocation. Steelhead by comparison are almost placid. It could be that steelhead have a "security blanket" resulting from adaptive association with cover provided by rubble, while chinooks must rely on darting flight to escape from predators such as birds. Male (1966) reported that when confronted by overhead stimuli fish of hatchery stock dart wildly about while fish of wild stock tend to move directly to nearby cover feature. Conditioning in wild stocks probably leads to reactions in survivors appropriate for predator avoidance.

There are large differences among salmonid species in their diurnal cover needs during the spring-to-fall period. Brook and rainbow trout often seek overhead cover. Newman (1956) noted that brook and rainbow trout (*Salmo gairdneri*) swam from place to place in a pool in Sagehen Creek in relation to overhead cover, remaining in the edge of shadows. R. Hunt (personal communication) has indicated that brook trout in Lawrence Creek spend much of their time hiding even though considerable quantities of food may be drifting past in more open, unshaded waters. He also noted that wild brown trout remain well-hidden under cover while planted "domestic" brown trout are feeding in the open. The domestic trout may grow faster, according to Hunt, but are more vulnerable to anglers and, presumably, to predators.

Wickham (1967) studied microhabitat of albino brook trout, finding that the fish occupied stations close to cover and spent about 94% of their time in shaded areas. This may partly have been due to the lack of eye pigmentation of albinos. Albino brook trout stations were usually in relatively slow water (mean velocity .1 mps) overlain by swifter water (mean velocity .26 mps). This fast water "overstory" may perform a cover role, but is also likely to provide a food supply.

Saunders and Smith (1962) increased the number of hiding places in a small stream, thereby nearly doubling the brook trout population over age I. Le Cren (pers. comm.) has noted that "lies" or cover are important to older brown trout. He mentions that 0 age trout in the Lake District are distributed in the open, mostly in riffles early in life; that the age I fish are in the open for a while early in the year but otherwise lie under banks, stones, or moss; but that larger fish could rarely be seen.

Lewis (1967) showed that brown trout preferred pools with extensive cover, and that velocity was of lesser significance in correlations of brown trout density with environmental features. For rainbow trout the reverse was true, velocity assuming much more importance than cover. These correlations were undertaken where brown and rainbow trout were sympatric. The results could have been different if allopatric groups were studied.

Brown, brook, and rainbow trout were reported by Butler and Hawthorne (1968) to make use of shade as overhead cover, with browns making the most use, rainbow the least, and brook trout intermediate use of shade. Coho salmon, on the other hand, often use open glide or pool areas in sunlight. Ruggles (1966) reported that pool-like environments of low velocity in experimental channels held twice as many coho as did riffle-like areas when volitional residence was permitted. The addition of shade reduced the initial holding capacity of an experimental channel, and Ruggles suggested coho may avoid areas of dense shade. This conforms to our general impressions of coho and might be adaptation to (1) decreased fall of terrestrial insects in densely-shaded areas as opposed to open areas, or (2) interaction with coastal cutthroat trout, which prefer areas of dense cover. The interaction could be spatial or predator-related.

DIURNAL PERMANENCE OF STATION

Permanence of station of young steelhead during two summers was studied by Edmundson, Everest and Chapman (1968) in Johnson Creek, a Salmon River tributary. Young steelhead (100-175 mm long) were captured, branded, released at the point of capture, then observed with snorkeling and SCUBA for several weeks in the summer of 1965 and 1966. Edmundson *et al.,* found little extensive movement (Fig. 5), 60% of all sequential sightings taking place less than 3 m apart, 85% less than 6 m apart. No difference in distances between sightings was noted in sequential observations in the periods 0830-1000 to 1300-1430 and 1700-1830 each day. In the area studied in Johnson Creek, the stream averaged 20 m wide, 1.2 m deep, and flowed at 4 m^{3}ps during many of the observations.

Because chinook salmon were so small and numerous, Edmundson *et al* (1968) used aquarium observations to examine permanence of station in young chinook salmon. The stream aquarium used was 12.2 m long, 0.6 m wide and about 0.4 m deep. Water flowed in it at an average velocity of 0.15 mps. A downstream trap permitted volitional residence, and fish could be observed through a glass wall in the aquarium. Individual fish were identified by parr-mark configuration. Sixty-seven percent of sequential sightings were less than 0.6 m apart (Fig. 6), and there were no significant differences in distances between sequential sightings from 0830 to 1300, 1300 to 2000, or 0830 to 2000.

Edmundson *et al* observed that yound steelhead and chinook salmon resided in a very restricted home area. These fish were in rather large streams in habitat that could be called “rubbly-glide”. The rubbly-glide habitat was extensive and there were no close-by opportunities for fish to move onto riffles for feeding.

Brook trout (Shetter, 1937), brown trout (Schuck, 1943), cutthroat trout (Miller, 1958), and Atlantic salmon (Saunders and Gee, 1964) all are reported to remain in a limited home area during some or all of their stream life phase. In brown trout and Atlantic slamon (Kalleberg, 1958) and in coho (Mason, 1966) feeding is usually performed from a particular spot. Wickham (1967) reported that the albino brook trout he studied were quite faithful to a limited station or focal point during each daylight period.

Certainly permanence of station confers benefits, familiarity with escape cover and

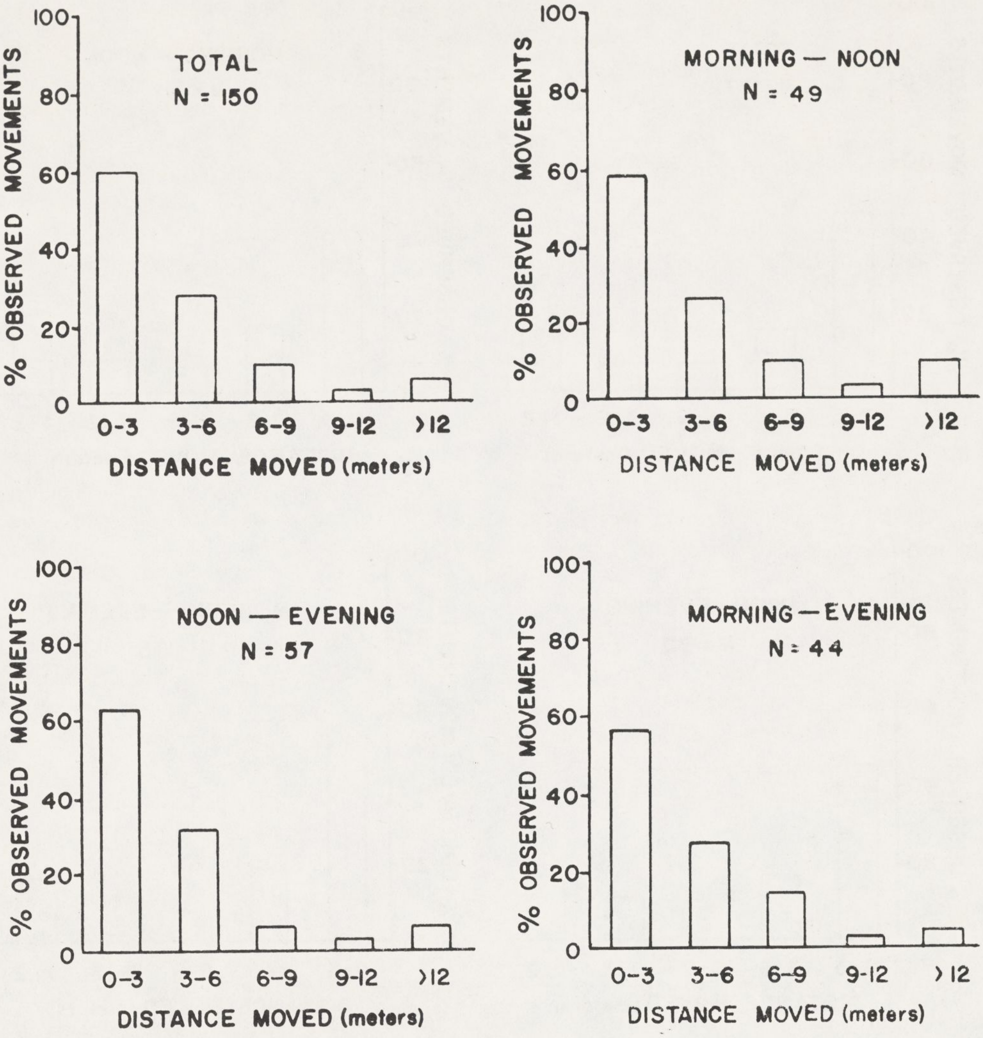

FIGURE 5

THE MOVEMENTS OF BRANDED JUVENILE STEELHEAD IN JOHNSON CREEK DURING THE SUMMERS OF 1965 AND 1966. A MOVEMENT IS DEFINED AS THE DISTANCE BETWEEN SEQUENTIAL SIGHTINGS OF BRANDED FISH ON THE SAME DAY. OBSERVATION DIVES WERE MADE MORNING, NOON, AND LATE AFTERNOON. (EDMUNDSON, ET AL, 1968).

food sources being obvious ones.

DIURNAL-NOCTURNAL SHIFTS IN DISTRIBUTION

Juvenile steelhead trout often occupy positions at night that are quite different from daylight stations. Edmundson *et al* (1968) observed individual branded steelhead trout at night positions in inshore, shallower waters, generally on the bottom, beneath rocks or in crevices in the substrate. Hoar (1953) also reported that juvenile steelhead were inactive at night. The night location of one fish was observed by Edmundson *et al* to be 20 m from the known daytime station and most sequential sightings between day and night were 3 m or more apart. In Figure 7 are plotted some sequential sightings between daylight and darkness, and single sightings of individual branded fish at night. A movement inshore by young steelhead at night was evident. Northcote (1962), reported

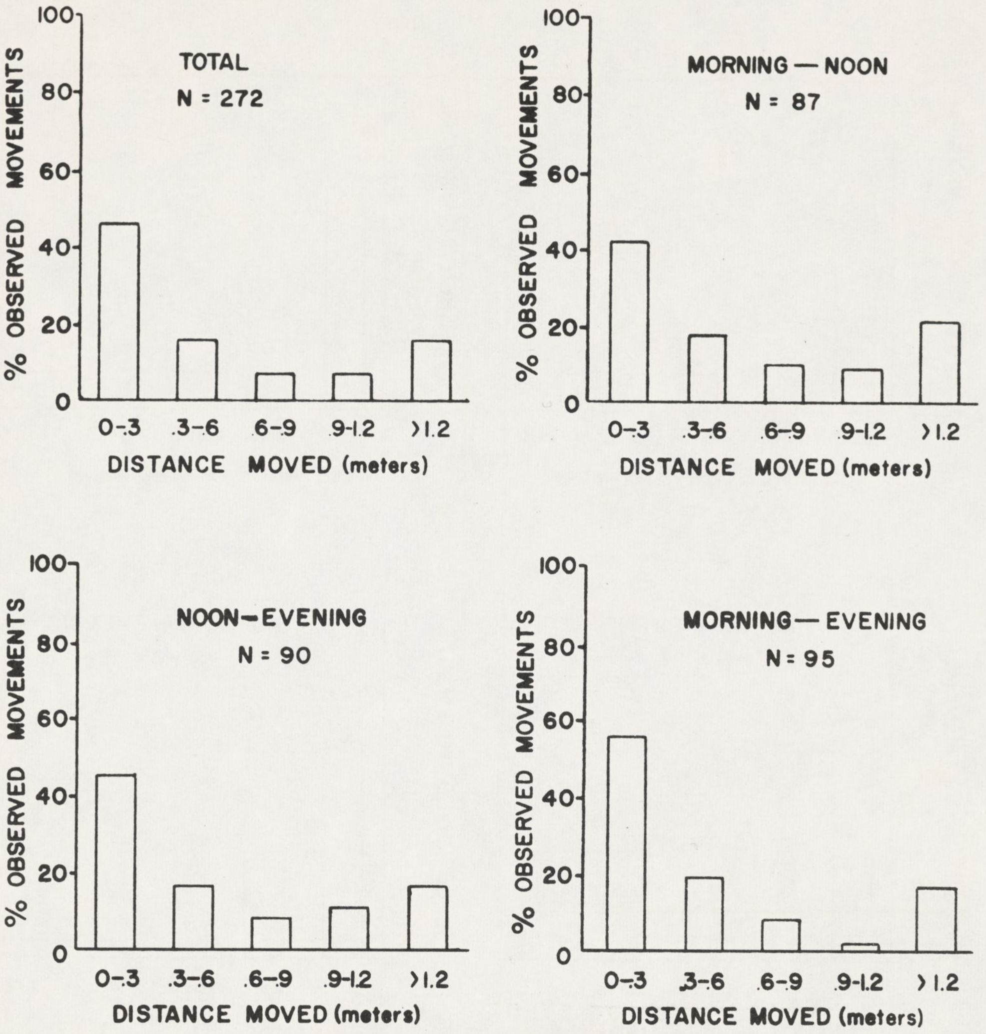

FIGURE 6
THE MOVEMENTS OF JUVENILE CHINOOK SALMON IN A STREAM AQUARIUM AT VARIOUS TIMES OF THE DAY. A MOVEMENT IS THE DISTANCE BETWEEN SEQUENTIAL SIGHTINGS OF INDIVIDUAL CHINOOK ON THE SAME DAY. OBSERVATIONS WERE MADE AT 0830-0900, 1300-1330, AND 2000-2030. (EDMUNDSON ET AL, 1968).

onshore movements of rainbow trout at night, the movement appearing to be positive rather than slow and irregular. Kalleberg (1958), after observing fry of *S. salar* and *S. trutta*, reported that "at least some fry with stations near the glass wall of the aquarium night after night made use of the same sleeping places in fissures between stones, no more than a few centimeters from their daylight stations." Edmundson *et al* noted that chinook salmon were sometimes observed at night on the stream bottom as well as near the surface in quiet shallow waters.

There is evidence that fish of several salmonid species shift positions at dusk and dawn. Newman (1956) noted that brook and rainbow trout in Sagehen Creek, California, moved inshore to shallower waters at night, remaining there until morning, but some fish did not return to daytime feeding stations before mid-day. Mason (1966) reported that coho

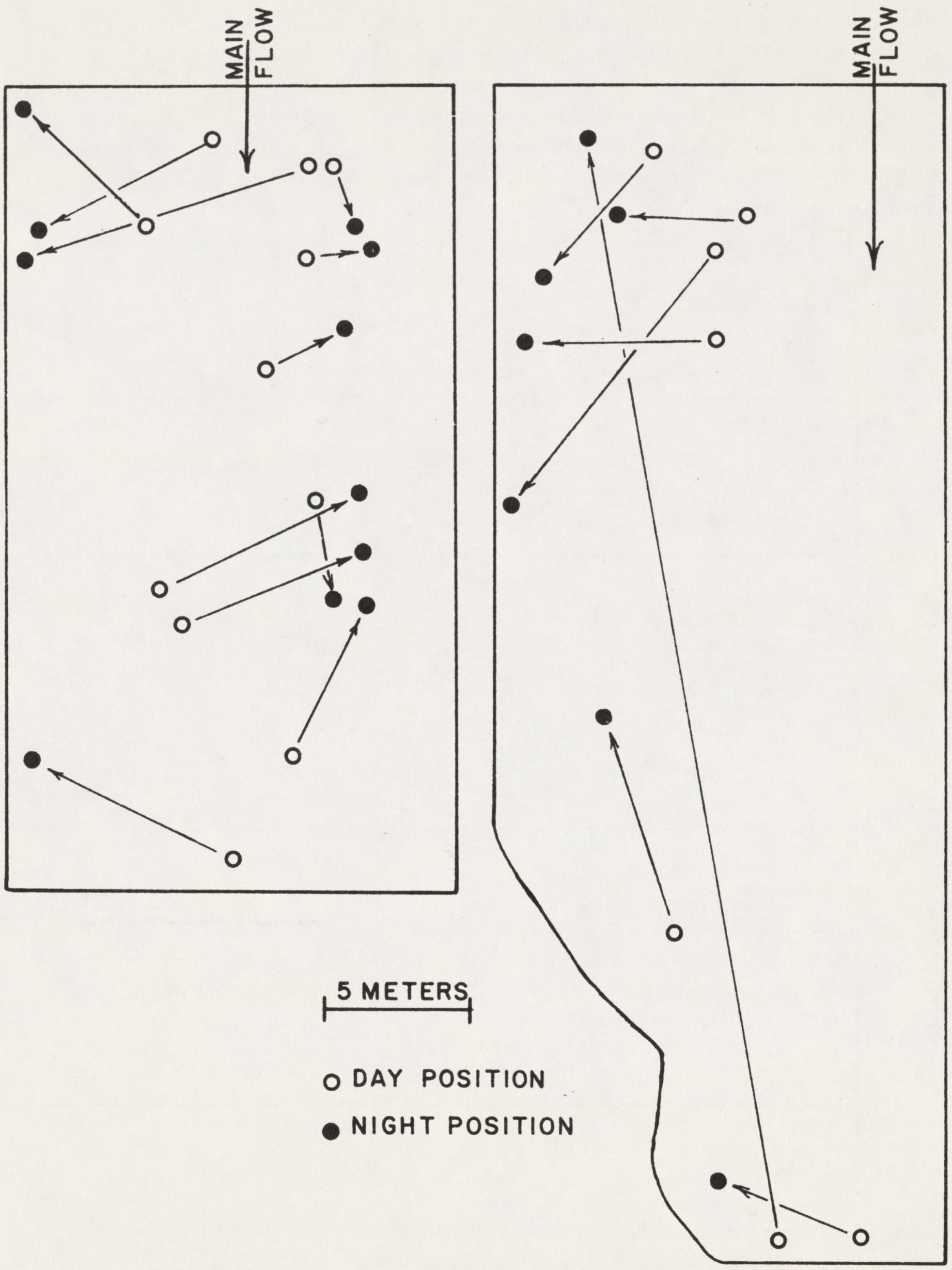

FIGURE 7

THE LOCATION OF DAYLIGHT AND DARK SIGHTINGS IN THE SAME DAY OF BRANDED JUVENILE STEELHEAD IN SUMMER IN THE LOCHSA RIVER (RIGHT DIAGRAM) AND JOHNSON CREEK (LEFT DIAGRAM) (EDMUNDSON, ET AL, 1968).

salmon in stream aquaria used a shallow riffle area at dawn and dusk, dropping downstream into a deeper pool area during the day. Mason also noted increased riffle occupancy at night, with fish moving from an adjacent pool onto the riffle.

Hoar (1953) and Chapman (1962) noted that coho salmon are found on or near the stream bottom in relatively quiet water at night, but the previously-cited data of Mason (1966) were more extensive and routinely obtained and may be more representative. Other reports of inactivity by stream salmonids at night have been made for Atlantic salmon (Hoar, 1953) and brown trout (Lindroth, 1955; Swift, 1962, 1964). Elson (1942) noted that planted *S. salar* fingerlings lie quietly at night in a few cm of quiet water.

The suitability of night-station habitat may be a factor influencing density of fish in stream environments.

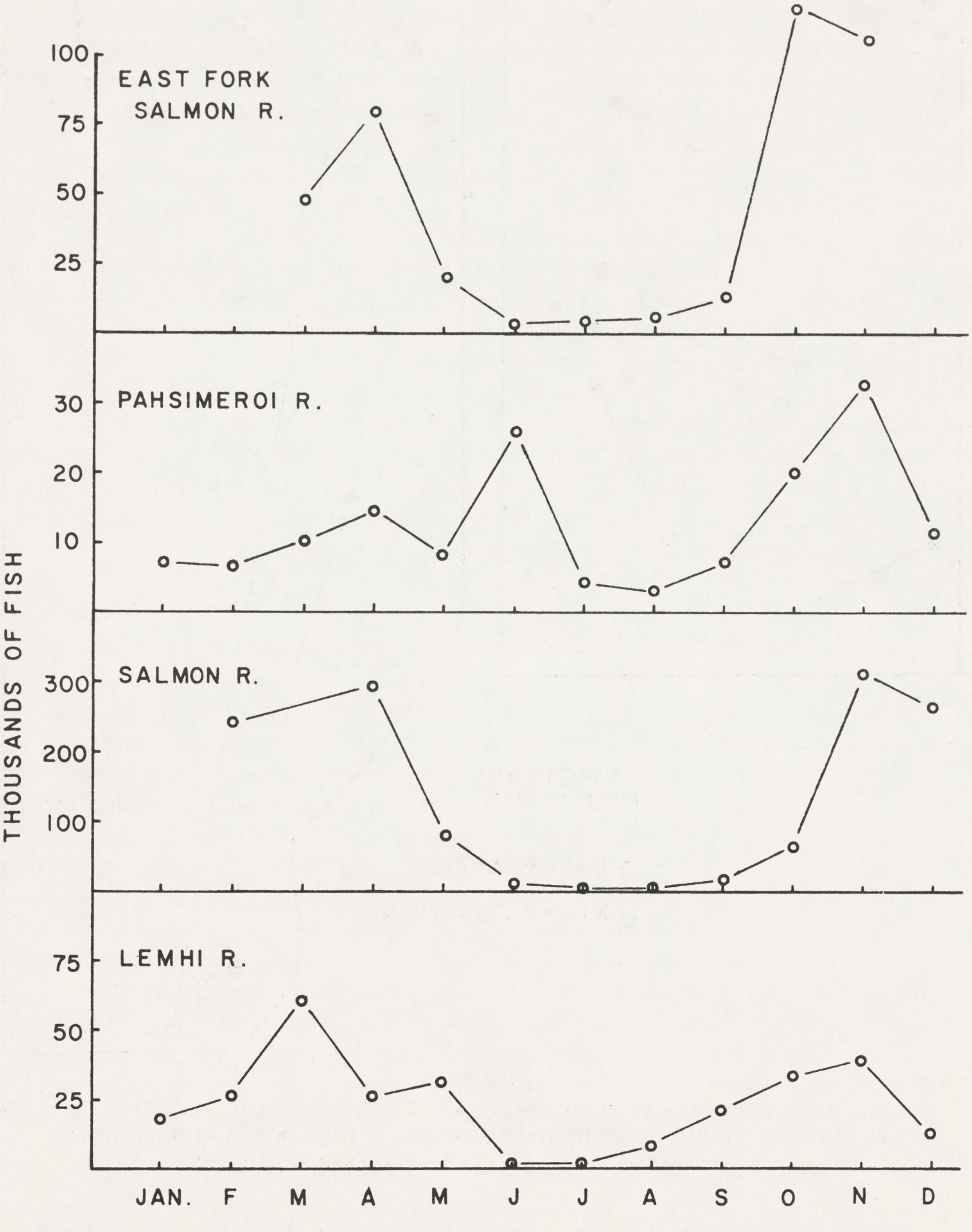

FIGURE 8

THE ESTIMATED NUMBER OF CHINOOK SALMON MIGRATING DOWNSTREAM PAST TRAPPING SITES ON THE SALMON RIVER AND SOME OF ITS TRIBUTARIES.

SEASONAL DISTRIBUTION

EFFECTS OF FOOD SUPPLY ON SEASONAL DISTRIBUTION

In studies at Big Springs Creek, in the Salmon River drainagein Idaho, we have observed juvenile steelhead moving downstream throughout the fall, winter and spring months. Similar fall and winter movements of juvenile chinook salmon and steelhead trout have been observed in other streams of the Salmon River drainage (Fig. 8, Reingold unpublished data).[1]

The fall-winter and in some cases spring movements of fish downstream are not seaward smolt migrations. Mains and Smith (1956) and Raymond[2] (Unpublished data) observed only one major downstream migration of salmon and steelhead in the lower Snake River and that was in the spring months. Fall-winter emigrants from Salmon River tributaries apparently spend the cold months in the Salmon and mid-Snake Rivers. Those salmon and other steelhead which are smolts the subsequent spring resume their downstream migration. The steelhead which have not reached smolt size remain in the streams to rear an additional year or two.

The fall-winter exodus of juvenile salmon and steelhead from most smaller streams in Idaho coincides with decreasing water temperatures. But could the shift be due to reduced food supply? Hartman (1963) and Waters (1962) reported that drift food was less abundant in the winter in the streams they studied.

During 1966 and 1967 we collected samples of drifting aquatic invertebrates and steelhead trout stomachs from Big Springs Creek. Drift insect samples were collected in 5 nets each 30 cm wide, spaced across a uniform riffle at two-hour intervals during a 24-hour period once each month. The calculated daily mean number of insects in drift samples was the mean of 60 samples each collected for 15 minutes. Stomachs were collected from 10 steelhead of the 1966 year class each month beginning in September 1966.

Our data on numbers of drifting insects are in general agreement with the findings of Hartman and Waters, with fewer insects drifting in the winter months (Fig. 9). However, the decline in drift insect abundance did not occur until well after the exodus of steelhead from Big Springs Creek had begun. Many fish started leaving the creek in September while the abundance of drifting insects did not decline until December.

Althouth there were fewer drifting insects in the winter months, the mean number of organisms in fish stomachs increased during the winter. The increase in stomach contents was undoubtedly due at least in part to reduced digestion rates of fish during the winter (Hess and Rainwater, 1939; N. Reimers, 1957). N. Reimers (1957) reported that rainbow trout in Convict Creek required 12 to 16 hours to digest half-gram meals of aquatic organisms at 10 C, but 25 to 44 hours at 1.6 C. The fact that the increase in stomach content of Big Springs Creek steelhead was approximately proportional to the probable decrease in digestion rate suggests to us that perhaps the food supply (drift insects) was adequate even at the lower winter levels.

After extensive studies of trout survival over winter periods, N. Reimers (1957) felt that in streams exposed to severe winter conditions, food is of secondary importance in determining trout survival. The data obtained by Reimers indicated that adverse and exhaustive physical conditions in the stream were the primary cause of fish losses.

Swift (1964) found that the locomotor activity of four brown trout confined in separate cages on the bed of Lake Windermere and artificially-fed was relatively very low when water temperatures were below 5 C. In another experiment with 4 separately-caged

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[1] Melvin Raingold, Idaho Department of Fish and Game, Salmon, Idaho

[2] Howard Raymond, U.S. Bureau of Commercial Fisheries, Seattle, Washington

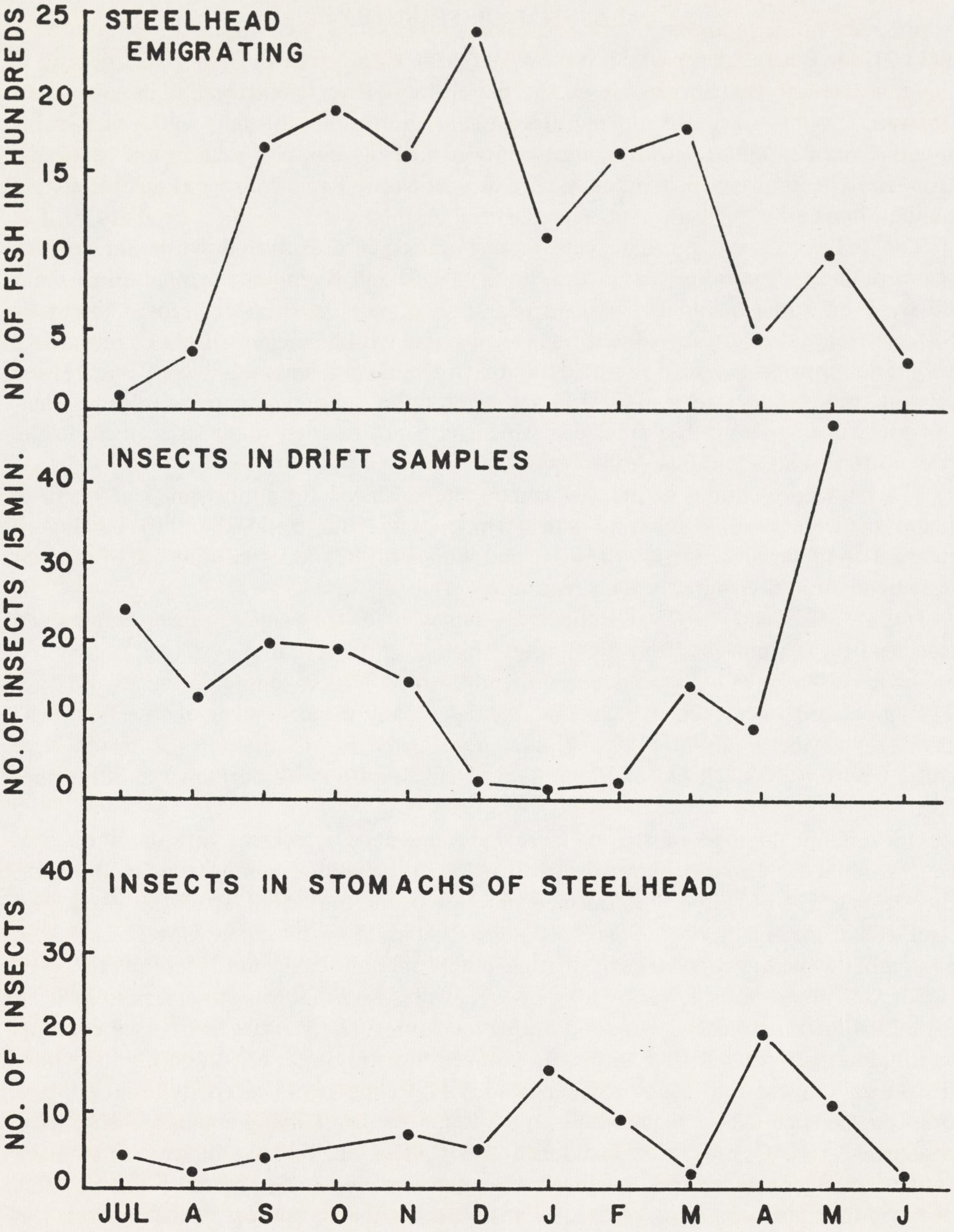

FIGURE 9

THE ESTIMATED NUMBER OF JUVENILE STEELHEAD TROUT LEAVING BIG SPRINGS CREEK, INSECTS COLLECTED IN DRIFT NETS, AND AQUATIC INSECTS IN STEELHEAD TROUT STOMACHS COLLECTED FROM BIG SPRINGS CREEK DURING 1966 AND 1967.

trout feeding on natural foods entering the cages, Swift (1962) learned that locomotor activity was relatively low in winter.

Thomas (1962) found that *S. trutta* and *S. salar* continued to feed in winter, when water temperatures were as low as 5 C. Maitland (1965) also reported that these species fed in winter. McCormack (1962) captured trout which had been feeding in one beck at

3-6 C, and some in another beck had been feeding at 1-2.5 C. Mills (1964) reported *S. salar* fry and parr fed in winter, and that in the River Bran the numerical density of benthic invertebrates was higher in the period November to March than in the warmer months.

Hartman's (1963) observations suggest that at least some *S. trutta* strains in Sweden are relatively inactive in winter. Maciolek and Needham (1952) reported brown and rainbow trout to be active in Convict Creek during winter, feeding regularly. But N. Reimers (pers. comm.) notes that the work was done in a relatively mild winter, and that the evidence for trout feeding in Convict Creek through the winter is inconclusive.

We believe that a decline in abundance of food, either drifting or benthic, is not the primary factor causing the downstream movement of salmon and steelhead juveniles in the fall and winter months. Probably food scarcity also does not cause the shifts in seasonal distribution noted in other stream salmonids.

EFFECTS OF TEMPERATURE AND COVER ON SEASONAL DISTRIBUTION

We have pointed out earlier that the fall-winter downstream movement of juvenile salmon and steelhead in Idaho streams coincided with declines in stream temperatures. In Big Springs Creek the migration also coincided with the loss of aquatic vegetation beds from the stream. Since extensive vegetation beds are not present in the other streams (Fig. 8) where the downstream migration occurs, we believe the loss of vegetation in Big Springs Creek is a secondary (if any) cause of the migration.

Our observations in the Salmon and Clearwater Rivers in winter agree with those of Hartman (1965) that young steelhead tended to be under large stones in the winter when water temperatures were below 4 C. We also observed that young chinook during the winter were under large rocks and debris in the substrate. Based on these observations, we theorized that winter cover was required and that winter hiding behavior was triggered by low water temperatures.

We conducted some tests of the response of young steelhead (age I+) to low temperatures in tanks 1.3x1.3x1.3 m deep in early November of 1967, when steelhead in the field were on the verge of entering winter hiding cover. We placed rubble in the tanks and counted the number of steelhead visible above the rubble at various temperature levels. The day length was constant at 13 hours, with light from a 40-watt incandescent bulb gradually brightened and dimmed over one hour at start and end of the day. Fish were fed brine shrimp near the surface, with shrimp being offered in a current produced by an air stone. Steelhead were obtained from Salmon River tributaries in Idaho by electro-fishing and 10 were introduced in each of the tanks within 5 hours of capture. In Figure 10 we depict the numbers of fish visible above the rubble in a tank controlled at 11.6 - 13.9 C and in another in which the temperature was dropped from 12.8 to 1.6 C in 4 days, then gradually raised to 11.6C in several days. The number of experimental fish visible was directly related to temperature in this experiment, and most fish were beneath the rubble at temperatures below 4.5 C.

In each tank at the same time as the tests with steelhead we had placed 10 chinook of the year. In comparing the test and control results we found little evidence of a vertical shift in distribution of chinooks in response to temperature changes. There is the possibility that agonistic behavior in the larger steelhead below the rubble limited the available space in rubble for the smaller chinooks.

In a similar experiment with 20 chinooks (6 weeks old) alone in early spring of 1967 the fish remained above the substrate when temperatures were dropped from 12.2 to 1.1 C. We know that chinooks do often emerge in nature when temperatures are below 4 C. Everest (MS) has observed large numbers of newly-emerged fry in Johnson Creek before

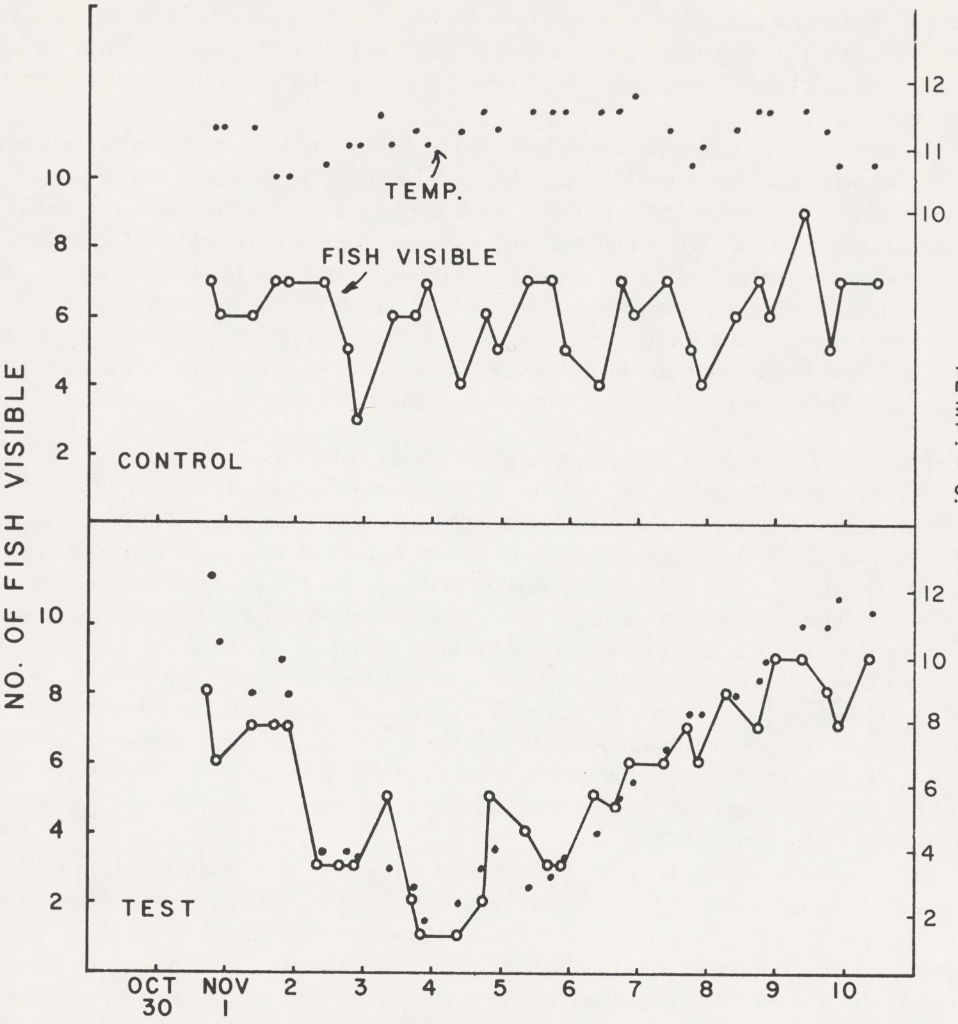

FIGURE 10

THE WATER TEMPERATURE AND NUMBER OF AGE 0 STEELHEAD TROUT VISIBLE ABOVE THE SUBSTRATE IN TEST AND CONTROL VATS.

any steelhead juveniles or yearling chinooks had come out of winter hiding. More testing is needed to establish temperature-related vertical distribution of chinooks.

In December, after young fish in the field had entered the substrate and water temperatures were consistently below 1.6 C, we electrofished in Johnson Creek and held captured fish at 1.6 C until experiments were underway. Ten 0 age steelhead and 10 pre-smolt chinooks (which were larger than the steelhead) were placed in each vat. One vat held the control group, the other held fish exposed to gradually-increasing temperatures. There were no fish above the substrate when water temperature was below 2.8 C (Fig. 11). Numbers of steelhead visible increased gradually until half of the experimental fish were visible at about 5.0 C. At temperatures of 5.5 C or higher, nearly all steelhead were visible and actively feeding. For steelhead in this experiment, temperatures of 5.0 - 5.5 C appeared to mark the boundary between activity and inactivity. Chinook behavior was more erratic (Fig. 11), with about half or more of the fish consistently visible beginning at about 7.2 C.

We also conducted tests in four troughs 1.3 m wide, .6 m deep, and 7.5 m long to

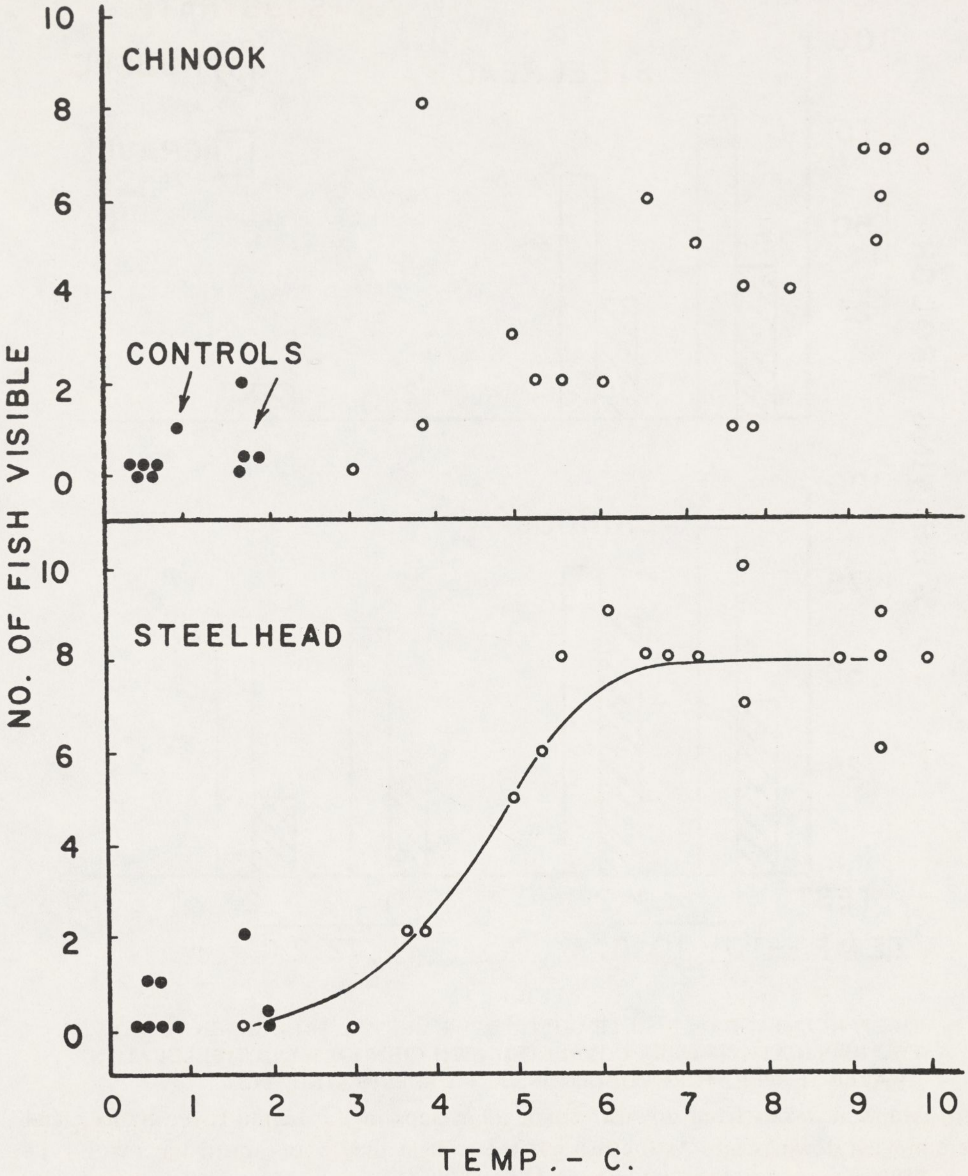

FIGURE 11

THE RELATIONSHIP BETWEEN WATER TEMPERATURE IN THE TEST AND CONTROL VATS AND NUMBER OF FISH VISIBLE ABOVE THE SUBSTRATE.

determine the effect of water temperature and substrate rock size on downstream movements. Spring water (11.1 - 12.2 C) was used in two of the troughs while Hayden Creek water (0 - 10.0 C but generally below 7.2 C) was used in the other two. Of the two troughs with spring water, one had a gravel substrate (1 to 5 cm diameter) and one had a rock substrate (15 to 45 cm diameter). The two troughs on creek water were similarly arranged, one with a gravel substrate and one with a large rock substrate.

Zero-age (7.5 - 12.5 cm) steelhead and chinook were used in the tests. The fish were placed in the troughs and forced with a barrier to remain for a 24-hour acclimation period. The barrier was then removed and the fish allowed to leave as they wished. All

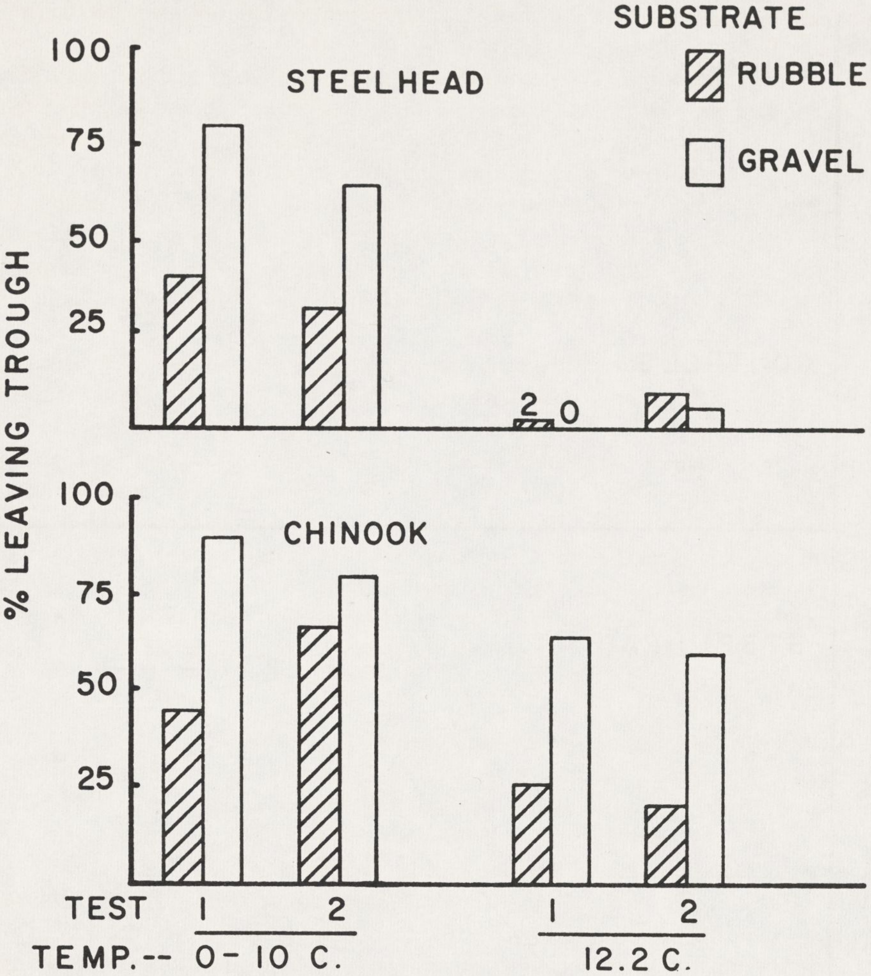

FIGURE 12

THE PERCENTAGE OF FISH LEAVING EXPERIMENTAL TROUGHS IN 10 DAYS. TWO REPLICATIONS WERE COMPLETED WITH CHINOOKS AND STEELHEAD IN 2 WATER TEMPERATURE CONDITIONS AND 2 SUBSTRATE TYPES.

fish used were taken from downstream-migrant traps in the Lemhi River drainage and were moving downstream. As the fish left the troughs they were captured in a Wolf-type trap. The fish were fed dry meal once each day.

Steelhead trout virtually ceased their downstream movement when placed in the troughs with the warmer spring water irrespective of bottom type. The number of steelhead which left the trough with the colder creek water and large rock substrate was about half the number which left the trough with cold water and a gravel substrate (Fig. 12).

In the tests with chinook salmon, about 25% of the fish left the trough with the spring water and large rock (Fig. 12). More than half the fish left the trough with spring water and gravel substrate. Nearly all the fish left the trough with creek water and gravel but fewer left the trough with large rock and creek water.

Our tentative conclusions after these tests are that downstream movement of steelhead is controlled primarily by temperature and modified by the substrate (quality of winter cover). At low water temperatures the reaction of chinook and steelhead to the trough environment was similar. At the higher water temperatures, chinook appeared to find the environment less satisfactory than steelhead.

The extensive fall-winter downstream migrations observed in Idaho streams do not occur in Pacific coastal streams. Chapman (1962) in Oregon, Salo and Bayliff (1958) in Washington, and Shapovalov and Taft (1954) in California found little or no downstream movements of juvenile coho salmon during the fall and winter months. Shapovalov and Taft did observe some downstream movement of juvenile steelhead in Waddell Creek during the fall and winter months but the number was small compared to the number migrating in spring. In many Idaho streams, 50% or more of the juvenile salmon and steelhead which leave the stream (as pre-smolts or smolts) do so during the fall and winter months.

Largely in October a downstream movement of Age 1+, 2+ and some 0+ brown trout occurs in some streams in Scotland (Stuart, 1957), and there is a similar upstream movement in the spring. The downstream movements occur as water temperatures drop or in advance of declines to normal winter levels (less than 4 C). Mallet (1963) found a downstream movement of cutthroat in the fall and an upstream movement in the spring in the Middle Fork of the Salmon River, a stream which becomes very cold in winter. Le Cren (pers. comm.) notes that brown trout seem to live in much the same places in many streams year-round in England, where freezing of streams is rare. Perhaps quite significant is Allen's (1951) report that in much of the Horokiwi stream, in which water temperature rarely was below 7 C, brown trout did not move seasonally, fed all winter, and generally had no winter check on the scales.

COVER-RELATED SHIFTS IN SEASONAL DISTRIBUTION

Lewis (1967) sampled 19 areas in a stream in Montana which contained brown and rainbow trout. In his extensive analyses he found that water velocity and cover accounted for most of the "explained" variation in brown trout numbers, and current velocity was the most significant correlate with rainbow trout abundance.

Elson (1942) stated that young Atlantic salmon prefer swift water but lie behind stones and where strong currents do not strike them directly, and noted that riffles on the water surface seem to satisfy certain cover requirements. In slower water the young fish use cover more and are in deeper water, but still water does not appear to satisfy requirements of the young fish, according to Elson.

Ruggles (1966) suggested that coho may avoid areas of dense shade in experimental channels. At the same time he showed that coho prefer pool habitat to faster, shallower waters. In the deeper water of pools, coho should escape avian predators more easily than would be possible in riffles, and might not require overhead cover. In addition, densely-shaded streams may contain fewer terrestrial and adult aquatic insects than do more open streams.

Dr. Hunt (pers. comm.) has noted that habitat improvement, chiefly increases in pool area and cover, has brought about marked changes in year-round carrying capacity of a section of Lawrence Creek. In-stream current deflectors and bank-covers were installed, increasing average depth of water 60% and pool area by 171%. Permanent year-round cover (15 cm overhead and 30 cm of water depth beneath) was increased by 416%. Movement into the section was about the same before and after the habitat was altered, but movement out of the section was much reduced after the habitat was changed (Table 2). In the period September to April before habitat improvement, 43% of the residents (age 0 and older) moved out of the section, while after alteration only 15% moved out. In April to September, 30% of the residents (and I and older) moved out before alteration, and 11% moved out after improvement. Biomass in the altered section increased over

TABLE II

PROPORTION OF NON-RESIDENT BROOK TROUT IN ALTERED STREAM SECTION IN LAWRENCE CREEK, WISCONSIN IN APRIL AND SEPTEMBER, AND MOVEMENT OF NON-RESIDENT TROUT FROM THE SECTION IN APRIL TO SEPTEMBER AND SEPTEMBER TO APRIL. (R. HUNT – DATA).

		Percent of stock comprised of non-residents in:		
Period	*Number of fish present*	*April (Age I+)*	*Number of fish present*	*Sept. (Age 0+)*
1961-63, before alteration	1695	30% (509 fish)	3536	18% (636 fish)
1965-67, after alteration	2915	29% (845 fish)	3557	17% (605 fish)
		Percent of residents moving out in:		
		Sept.-Apr. (Age 0+)		*Apr.-Sept. (Age I+)*
1961-63		43% (1608 fish)		30% (645 fish)
1965-67		17% (601 fish)		11% (270 fish)

pre-treatment levels. It appears that the altered section of Lawrence Creek is now more attractive to resident trout.

Also of importance are the estimated total population sizes in April and September. After stream alteration, the mean April population size was 172% (2,915 fish) of that in pre-alteration years (1,695 fish). But in September the mean stock sizes before (3,536 fish) and after (3,557 fish) treatment were also identical. To Dr. Hunt and to us this suggests that the principal benefit of habitat improvement in the stream section was in expanded winter holding capacity.

Ruggles (1966) added winter cover in the form of flat "patio" blocks on the bottom of one of his experimental channels. Presumably the coho could find cover beneath the rocks. In comparing a channel with cover and control channel without, Ruggles found that the cover appeared to reduce the channel capacity to hold coho over winter. Hartman (1965) found that coho do not go beneath stones in the winter. They tend to lie near or on pool bottoms in aggregations. Therefore we should expect that if cover in the form of patio blocks has any effect it would be to reduce the substrate suitable for over-wintering coho.

Lewis (1967) reported both brown and rainbow trout tended to move into pools in the winter. In summer fish tended to occupy pools and riffles about equally.

Allen (1941) regarded 7 C as a critical temperature in the life history of young Atlantic salmon. He reported that below 7 C the fish lay quiescent in sheltered places, feeding little and making no growth. In fall when water temperatures dropped below 7 C, the fish disappeared from open water and growth ceased. In spring, as soon as the water temperature rose about 7 C, the fish resumed active life, feeding actively and commencing growth. Allen had information on netting efficiencies in fall, winter and spring which supported the hypothesis of inactivity of *S. salar* below 7 C. He found that fish were much harder to net in winter and concluded they were inactive and under cover.

White (1939) notes that in winter in the Margaree River young salmon are quiescent –

"during winter conditions we have found the salmon parr only beneath stones."

Mason observed behavior of coho (58-94 mm) in February and March in a stream channel. The water temperatures in these months were 5.0 to 7.8 C in February and 5.6 to 8.6 C in March. The fish were quiescent in pools, remaining near the bottom close to each other and rarely displaying aggression. Feeding began in early March, and by late March considerable aggression was noted.

Hartman (1963), working with brown trout in Sweden, found a stronger association of small brown trout with the bottom of an experimental stream in winter. Lower water temperatures tended to cause fish to associate closely with the stream bottom. The brown trout studied tended to remain more in one location in winter than in summer, and agonistic activity was less in winter. Hartman suggests that winter association with cover, shade, and low water velocity could be primarily a mechanism for gaining shelter and remaining in suitable stream areas in winter. He further suggests that summer association with cover, shade and low water velocity in one location may serve largely for efficient feeding. Hartman also notes that the strong tendency of brown trout to hide among stones in the winter and to avoid doing so in the summer, suggests differing seasonal emphases on food and cover. Northcote (1962) has suggested that cold water and short day lengths may facilitate position maintenance by rainbow trout fingerlings from Loon Lake.

The fall downstream movements, the shelter-oriented winter behavior, and absence of fish above the substrate in winter lead us to the conclusion that in relatively cold streams there are advantages in winter behavior which place fish in deeper, quiet waters associated with cover. Such winter behavior could be a means of (1) avoiding unprofitable energy expenditure, (2) predator avoidance, or (3) preventing physical damage by scouring and ice.

SOCIAL BEHAVIOR AS A DIRECT CAUSE OF SHIFTS IN DISTRIBUTION

Animal dispersals caused by social behavior have received considerable attention recently. Wynne-Edwards (1962), Lorenz (1966), and Ardrey (1966) have written on the subject, the latter two workers in semi-popular literature. Dispersal resulting from social behavior is a well-documented phenomenon accepted even by workers who may not agree with some of the attendant hypotheses for regulation of animal numbers.

In stream salmonids, Le Cren (1961) reported general observations of socially-induced downstream emigration in fry of *S. trutta*. Chapman (1962) suggested that downstream drift of coho fry in some Oregon streams was caused by aggressive behavior, the emigrants often being socially unsuccessful. Keenleyside and Yamamoto (1962) note generally the importance of territoriality as a means of insuring individual survival of young *S. salar.*

Incidentally, Keenleyside and Yamamoto (1962) and Owen Fenderson (pers. comm.) have noted that at low densities, increased crowding caused increased aggression. As density increased further, aggression rose to a maximum, then markedly decreased at higher densities. This phenomenon would be an essential prerequisite to successful hatchery operations, or course, but also is of significance in wild stocks. Fenderson (pers. comm.) has noted high densities of brook trout in cold spring areas during warm weather. The normally aggressive trout apparently will tolerate high social loading under some circumstances, although the level of aggression in these circumstances is unknown.

Because of the differing habitat preferences of fish of different sizes it is logical that the greatest distributional role of social behavior is played among fish of near-equal size. Newman (1956) noted the greatest social conflicts between fish of the same size. In a detailed study of the effects of starvation on aggression, Symons (1968) found that the greatest conflicts, in both fed and starved fish, occurred between fish of similar size.

Within the micro-habitat suitable for fish of a given size, social interactions disperse the fish, primarily downstream, until densities are tolerable. This frequently-stated hypothesis (Le Cren, 1965; Chapman, 1966; Kalleberg, 1958; and others) has some interesting components. Some of the questions arising with the hypothesis are: (1) Is aggression increased when food is scarce so that unsuccessful fish emigrate and successful competitors secure enough food to survive and grow (contest) or is the limited available food scrambled away? (2) Is aggression reduced in times of food superabundance so that more fish use a given micro-habitat in times of plenty? (3) If food scarcity brings about increased aggression, what are the upper limits on the amount of aggression or size of territory?

Symons (MS) randomly alternated 3-days of starvation with 3 days of feeding *S. salar* parr, measuring aggression and activity in groups of parr. He found significant increases in aggression during starvation, and suggested that this could lead in nature to expansion of feeding territories in territorial fish. But Symon's studies involved 8 parr (4.5 to 12.5 cm in length) which were confined in 60-liter aquaria and fed twice daily.

Mason's study of coho in stream aquaria with volitional residence and a natural food supply more nearly approximated natural circumstances. One of Mason's aquaria received 37% more volume in potential fish food organisms, as assessed in 7 pairs of drift samples taken over one 24-hour period. Both channels received an initial stocking of 300 advanced sac-fry which were allowed to emerge from simulated redds. After 3.5 months the channel with more drift food entering it held about 57 coho while the channel with less food contained 35 coho. The mean sizes of fish in both channels were about equal.

In the most upstream riffle and pool in the channel with less drift food, densities of coho over 3.5 months were $5.5/m^2$ on the riffle and $27.7/m^2$ in the pool. In the channel with more food, riffle and pool densities were $8.9/m^2$ and $40/m^2$, respectively. The coho were generally territorial in riffles and often in pools, with size governing the outcome of social competition. If the foregoing densities are indices of territory sizes, Mason's results do not contradict those of Symon's, since there was a possible relationship between food abundance and density. This relationship could be reinforced by the fact that fish have more time for aggression when they are less busy with feeding. It does appear probable that food resources are not scrambled away in times of scarcity.

Question (2) above is to some degree answered when we postulate food-linked aggression rates or territory sizes. Another partial answer is that when food is abundant, despotic fish spend more time in feeding and less on aggression (Mason, 1966) which could lead to greater densities of fish in a given habitat. Some workers writing on the influence of abundant food upon aggression have noted increases in aggression after fish were fed to excess (Keenleyside and Yamamoto, 1962; Newman, 1956; Mason, 1966), but the feeding regime in these studies was artificial. Needed are studies of aggression and territoriality under sustained differential levels of food abundance that simulate natural drift patterns. For if salmonids in streams do generally display more aggression with more abundant food supply, the concept of food-linked territoriality cannot be true.

In answering Question (3) one can only postulate that there must be upper limits on aggression and territoriality fixed by piscatorial economics. Expenditures of energy for aggression must be adaptive and energetically efficient, producing more benefit than cost. Carline (1968) notes some of the interesting ramifications of the energetics of food consumption and activity. It is probable that emigration (appetitive behavior?) would be a more efficient means of finding adequate food supplies than would an excessively-enlarged territory.

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ECOLOGY OF PARAPATRIC DISTRIBUTIONS

C. M. Bull

School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia, Australia

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INTRODUCTION

Parapatry describes a distributional pattern in which pairs of taxa have separate but contiguous distributions, abutting along common boundaries. Smith first proposed the word "parapatry" (81, 122) to differentiate situations where the ranges of two taxa are in contact, both from sympatry where ranges overlap, and from allopatry where ranges are separate. The condition of parapatry was known much earlier. For instance, Darwin (38) wrote that the location of a species border was often determined by the border of a related species.

More recently numerous examples of parapatry, from a wide range of taxonomic groups and geographic regions, have been described (53, 61, 64, 71, 82). Parapatry might previously have been more common since continuous patches of habitat where species ranges could have been in contact have now been fragmented by clearance. It may still be more common than is realized, because parapatry is difficult to detect. Detection usually involves taxonomic separation of closely related, morphologically similar taxa, and collection on a fine geographic scale (71). Parapatry has been most frequently reported in birds (40, 46), perhaps because their high visibility makes fine-scale surveys relatively easy. Even among birds, detailed collection may reveal parapatry where sympatry has previously been reported (51).

Initial discussion of parapatry revolved around speciation mechanisms, and

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whether taxa with contiguous distributions actually were in contact and had the potential to interbreed. Smith (123) argued that parapatry was a special case of allopatry where genic interchange was possible without sympatry. All other cases of allopatry, where individuals of two taxa never meet, he defined as dichopatry (a term that has gained little acceptance). Others (14, 26, 70, 80) claimed parapatry to be a special case of sympatry, because contact usually implied some small range overlap.

Parapatry has now become a legitimate separate category of distribution, differentiated from sympatry by the extent of range overlap. For instance Futuyma & Mayer (48) defined two populations as parapatric if they "occupied separate but adjoining areas, such that only a small fraction of individuals in each encounters the other." Key (71) said parapatry involved two populations that "occupied contiguous territories that overlapped only very narrowly in relation to both the length of the overlap zone, and the vagility of the individuals." He suggested the overlap should be no more than a small multiple of the dispersal range of individuals. These definitions recognize some overlap between parapatric taxa. There is no sharp demarcation, but rather a continuum between cases of allopatry, parapatry, and sympatry.

Parapatry is still invoked in discussions of the speciation process. An implicit, though rarely stated, assumption has been that the terms allopatry, sympatry, and (by implication) parapatry refer to closely related species (112), although the parapatric pair are not necessarily the most closely related in the species complex (63, 95). Haffer (52, 53) viewed parapatry as the result of secondary contact of differentiating taxa, reproductively isolated but incompletely speciated because they are not yet ecologically compatible. In this context parapatry differs specifically from sympatry in that parapatric taxa have not previously co-existed and do not currently co-exist. Some mechanism prevents overlap of their ranges. Parapatry does not refer to the state where species have overlapping ranges in which they occupy different, mutually exclusive, habitats. This distributional relationship, allotopy (112), implies a form of ecological compatibility of the species, by use of different niches. Parapatry often results from the first meeting between taxa that have been isolated in geographical refugia and have spread so their ranges now abut. Overlap with habitat segregation may result from that contact, but parapatry is the state (which may be stable for a long time) before there is any overlap.

When two taxa first make contact, parapatry can go through two temporal phases: a non-equilibrium invasion phase in which the range of one expands as it replaces the other, and an equilibrium phase in which a stable boundary is maintained by some balance of the fitness of each taxon. Moving boundaries have been directly observed as one species invades and takes over areas previously occupied by the other (42, 65, 103, 118). This can result in local extinction of the invaded species. Moving boundaries of hybridizing taxa have been inferred from relict mitochondrial DNA in locations where the nuclear genome has been replaced (77).

Whether or not Smith intended parapatry to include hybridizing taxa has been variously interpreted (81, 123). Nevertheless, parapatry is now taken to imply both hybridizing and nonhybridizing contact and, in the evolutionary context, to cover the range of differentiation of taxa from partial to complete reproductive isolation. Key (71) divided parapatry into two categories: hybridization parapatry where the contacting taxa form a narrow hybrid zone; and ecological parapatry, where they may have a narrow overlap zone, but without any hybridization. In fact, parapatric boundaries form a continuum of cases from those with no hybrids to those with many hybrids in the overlap. At the latter end of the continuum a genetic mechanism, negative heterosis, has been proposed as the major factor preventing range overlap of the parental taxa (13, 61). Key (71) defined hybridization parapatry as "parapatry in which the restriction of interpenetration results primarily from the populations mating more or less freely with each other, but either leaving no fertile progeny, or leaving progeny of reduced fertility." Narrow hybrid zones, or tension zones, have been intensively investigated and reviewed (13, 61, 71). Many of 170 cases coincided with environmental ecotones (13, 61), implying a role for ecological factors in preventing overlap. Ecological factors should be more important in those parapatric boundaries where hybridization is more rare. This review concentrates on parapatry where there is little or no hybridization. Haffer (53) called taxa in this relationship paraspecies and saw them as further differentiated in the speciation process than those with hybridization parapatry. They are referred to as species for the rest of this review.

Key (71) defined *ecological parapatry* as "parapatry in which the restriction of interpenetration results primarily from a sharp ecological interface between the habitats of the two populations, sometimes reinforced by competition between them." Haffer (53) further subdivided this relationship into: (*a*) *ecological parapatry,* as defined above, between species not necessarily related, which have distinctly different habitat requirements and occupy widely different ecological zones; and (*b*) *competitive parapatry* where "geographic exclusion in a uniform habitat zone results from competition between populations of two species with nearly identical ecological requirements." The two definitions include hypotheses for how parapatry is maintained. These mechanisms are inferred in many examples of parapatry but are rarely supported either by experimental tests or by adequate data on spatial and temporal dynamics (53).

The study of parapatry has wide implications. For studies of speciation, parapatric taxa may represent a rich source of information about the final stage of differentiation before full species status is achieved (136). For community ecologists, clues to ecological processes permitting coexistence may be derived from parapatry where pairs of species cannot coexist. In biogeography, parapatry provides patterns where the spread of a species could be prevented by another species rather than by physical features. Parapatric boundaries are also an ecological phenomenon in their own right. They are widespread among taxa and geographic regions, and a general theory explaining their structure and maintenance needs to be developed.

MAINTENANCE OF ECOLOGICAL PARAPATRY

The central ecological question about parapatry concerns the mechanisms that prevent range overlap of the contacting species. Five major mechanisms have been suggested. Some are related, and at some boundaries combinations of mechanisms may be involved.

Ecotonal Change

This is the mechanism implicit in Key's (71) original definition of ecological parapatry occurring primarily at a sharp ecological interface. Each species is better adapted for conditions on its own side of the boundary and avoids conditions for which it is less suited across the boundary. An extreme form, in which conditions are intolerable for each species across the boundary, does not require close evolutionary or ecological relationships between the contacting species. Parapatric boundaries also occur on less extreme gradients of elevation (59, 131), climate (74), soil structure (84), water speed (92, 127), and vegetation (126, 127).

Small environmental changes may prevent range expansion of single species. For instance the edge of the range of an established species may coincide with a specific altitude (90, 101) or climatic condition (50, 116, 135), and colonizing species can expand their ranges only into climatically suitable areas (41, 85). The range edge may represent the limit of conditions the species can tolerate physiologically (78, 117) or behaviorally (4), but the relationship between climate and population variables is rarely simple (115). More usually a combination of physical and biological variables influences distribution. A single factor is rarely important (17, 30), except where there is an abrupt distribution edge (17). Where boundaries coincide with climatic changes, other factors correlated with climate may have a more direct influence on an individual's chance of surviving and reproducing (31). Distribution limits can be further complicated by dispersal causing labile boundaries (129).

In relation to parapatry many studies infer that an environmental gradient alone, without any biological interaction, can limit the ranges of both species at the same place. For instance, Ford (45) suggested that cases of parapatry between species of Australian quail thrushes *(Cinclosoma)* at points of sharp habitat change were maintained by adaptations of each species to different habitats. Other studies comment on the coincidence of the parapatric boundary with an environmental change (65, 76, 108) or suggest that parapatry is maintained because each species selects the habitat on its side of the boundary (68, 127).

However, it is unlikely that a small or gradual environmental cline will alone maintain a parapatric boundary. Key (71) originally proposed that the effect of a sharp ecological interface was sometimes reinforced by competition. Some form of biological interaction is probably required to prevent expansion into the less favorable habitat, except at extreme ecotones. The parapatry between two chipmunk species *(Eutamias)*, at an ecotone, probably resulted from precise habitat choice, which had evolved in each species to avoid habitats where adverse interspecific interactions would occur (127). That is, the boundary is now maintained by the ecotone, although interactions played a role in the past.

An ecotone also represents a resource gradient. Slade & Robertson (121) suggested that along a gradient of increasing resources for one species and diminishing resources for the other, the resources of each may become too sparse in the center, so neither can spread, and a boundary, or even a gap, between the two species is formed. A more likely outcome (35) is that one or both species would switch from specialist to generalist resource use, and if there were no interaction, they would overlap.

Interspecific Competition

Interspecific competition may prevent species from invading each other's ranges across parapatric boundaries (82). Haffer (52, 53) considered that many parapatric species pairs with nearly identical ecological requirements were ecologically incompatible. He thought competition and mutual exclusion should maintain parapatry even in regions of uniform habitat. However, few competition models predict this result without some change in fitness of at least one species across the boundary.

Mayr (80) suggested interspecific competition combined with a gradual climatic cline could maintain parapatric boundaries. Key (71) disagreed because normal climatic fluctuations would allow periodic expansions of the ranges of each species. Then, with a delicate balance of competition, the colonists would only be eliminated slowly, allowing wide overlap rather than sharp separation along gradual clines. For this reason Key (71) considered competition less important than ecotones in maintaining parapatry.

Nevertheless, competition is often inferred to explain parapatry (44, 134). This view is supported by evidence of interspecific territoriality in the contact zone of some parapatric bird species (42, 79). Also, the experimental removal of one species from plots in the parapatric overlap zone led to improved performance, in salamanders (54), or increased range of habitats, in rodents (86), of the other species. Each of two chipmunk species *(Eutamias)* is more successful in interspecific agonistic interactions over food on its own side of a parapatric boundary (16). Similarly, the ant *Wasmannia* recruits to baits more efficiently and aggressively than the species it replaces parapatrically (34).

Theoretical models show that competition along environmental gradients can lead to parapatry. MacArthur (83) modelled one species competitively replacing another along a resource cline. Modifications of this model (121), to include additional resource requirements for the cost of defending territories interspecifically, produced a gap between species on a resource replacement cline. Here neither species could persist, even with adequate resources for a single species. In this model, parapatric contact results from dispersal into the gap. From optimal foraging theory Cody (35) predicted that two potentially competing species along a resource replacement cline would abut parapatrically over areas where either species could exist alone, if they were *K*-selected, but would extensively overlap if *r*-selected.

The included niche model (84) combines a more abrupt environmental change with competition, to predict parapatric boundaries at the physiological limit of the competitively dominant species. The competitively inferior species, with wider physiological tolerance, is restricted to a subset of its potential range where the dominant species cannot persist. This model explains parapatric boundaries, for instance in salamanders (69), gophers (84), and chipmunks (32, 58, 119).

Terborgh (131) compared the relative importance of competition and ecotones as determinants of distributional limits of bird species on altitudinal transects in Peru. Using different slopes, where ecotonal changes occurred at different altitudes, and where congeners were variably present, he deduced that direct or diffuse competition accounted for about two thirds of all distributional limits. The general emphasis on competition and changing competitive fitness along environmental gradients in explaining parapatry may reflect its real importance. Alternatively, it may reflect a bias toward competition among ecologists (55, 105). Other ecological processes, discussed below, may also explain parapatry.

Predation

Predators can limit species distributions. Parapatry could result if a competitively dominant species is more susceptible to predation, and if there is an ecotone or cline where the predator becomes less effective (55, 100). Alternatively, where the combined density of two prey species increases the size of the predator population, the more susceptible prey may be eliminated by the increased pressure. For instance, one species of leafhopper is replacing another parapatrically in California. While less susceptible to an egg parasitoid, its presence enhances the parasitoid population, to the detriment of the other species (118). This "apparent competition" (66) is analogous to an interaction through infectious disease, discussed in the next section.

Parasites and Disease

A parasite and host might coevolve to form a unit, which, through cross-infection, reduces the fitness of naive hosts of another species (10, 47, 105). In Cornell's (37) parasite model for parapatry, each host species has unique parasite and vector species. A vector can transmit its parasite to invading individuals of the other host species, to their detriment if they lack previous experience of, or evolved resistance to, the parasite. The numerical superiority of the resident population and its parasites will prevent invaders becoming established, leading to parapatry without an environmental gradient. Parapatry could also develop if a gradient limits the spread of one host species, when only that species has a parasite-vector system inimical to the other. Parasite-induced advantage has been an explanation for parapatric invasions (104, 105), for instance of the white-tailed deer replacing other cervids (5).

Freeland (47) suggested that species could not coexist without effective barriers to interspecific parasite transmission. He proposed that species related ecologically or phylogenetically would be most susceptible to cross-infection, and hence to interactions via their parasites. Thus, species divergence should reduce parasite-induced interaction, and parasite-induced parapatry. This reflects Haffer's (53) contention that parapatric species are those that have not yet diverged sufficiently for coexistence, although Haffer was contemplating interspecific competition as the mechanism.

In another model, "apparent competition" (66), one of two species that share parasites or infectious diseases can exclude the other because combined host density allows the level of infestation to become higher than on a single host population, and too high for one species to tolerate. That species is then excluded, even when it can persist alone with the disease.

Although these models can explain parapatry, and appear to be important in some cases of invasion parapatry (5, 104, 105), they have not yet been used to explain cases of stable parapatric boundaries.

Reproductive Interference

In narrow hybrid zones, reduced fitness of hybrids diminishes the vigor of colonization attempts across the boundary (11, 61). By analogy, interspecific pairing can reduce reproductive potential of colonizing females and generate parapatry, even where no, or very few, hybrids are produced. Anderson (6) proposed that completely intersterile species may still interbreed where their ranges come in contact, reducing fitness through wastage of reproductive potential. Simulations (6) showed that random pairing alone produced species eplacement clines 62% as steep as those from interspecific competition, nplying comparable potential of the two processes to maintain parapatric oundaries. More reproductive potential was lost by the numerically inferior pecies, so a resident established population would resist low density invasion 6). This model was used to explain the parapatric boundary between two pecies of flycatcher in Europe, and the incursion of one through numerical upremacy onto islands within the range of the other (3).

A similar proposal, the "satyr effect" (110, 111), has males mating in- iscriminately, reducing reproductive potential of heterospecific females hrough the production of sterile eggs, or the blocking of, or physical damage), genitalia. Simulations of a linear series of demes showed satyrization lone could generate stable parapatry if dispersal between demes was low. ncreased interdeme migration led to one species excluding the other (110, 11). The satyr effect was used to explain the parapatric replacement of one ck species by another in Africa (111), and the stable parapatry of two nosquito species in the Bahamas (110, 125).

Another form of reproductive interference is the jamming of reproductive ignals, such that one species cannot transmit as effectively to conspecifics in he presence of the other. Where the effect is symmetrical, a resident species vill resist invasion from a low density colonizer, leading to parapatry, as roposed in acoustically signalling frogs (98), and in chemically signalling icks (8). These examples are discussed in the next section.

WO CASE STUDIES

here are few cases where a parapatric boundary has been closely mapped, nd where alternative hypotheses for its maintenance have been ex- erimentally tested. Two such cases come from South Australia.

One involves two morphologically similar frog species, *Ranidella riparia* nd *R. signifera,* which were once regarded as the same species (133). ubsequent allozyme electrophoresis showed genetic differentiation five imes greater than between other sibling *Ranidella* species (95). *Ranidella iparia,* endemic to the Flinders Ranges of South Australia, has its southern imit at a stable parapatric boundary with the more widespread *R. signifera* 92). No hybrids are found in the narrow overlap zone where *R. riparia* reeds in swift, rocky, west-flowing creeks, and *R. signifera* in slower, more nuddy, east-flowing creeks. Habitat suitable for each species is available eyond the boundary, but neither species extends further into the range of the ther (92).

Laboratory experiments showed that *R. signifera* tadpoles were displaced nore by flowing water (91), and more often chose sheltered habitats, es- ecially in the presence of *R. riparia* (96). In field cages in still creeks, or heltered cages in flowing creeks, tadpoles of both species survived and grew equally well; but *R. signifera* had reduced success when mixed with *R. riparia* in flowing water (93). Even in still water tadpoles of *R. riparia* caused a feeding shift in those of *R. signifera* (97). These results suggest *R. signifera* is prevented from spreading into the swift flowing creeks beyond its range because its tadpoles are adapted to calmer water, and are competitively inferior to *R. riparia*.

Reproductive interference may prevent *R. riparia* from extending into calmer water, a habitat it successfully inhabits outside the range of *R. signifera* (92). Males of *R. riparia* have a relatively complex vocal repertoire (99). Yet their advertisement calls average 24 dB lower than *R. signifera* and may be inaudible to conspecific females in the dense continuous chorus of *R. signifera* (98). Experimentally transplanted *R. riparia* males moved away more rapidly from areas where *R. signifera* males were calling (94). Acoustic jamming may prevent successful colonization by *R. riparia* of creeks where *R. signifera* is established and calling (98).

The second example concerns three tick species that have parapatric distributions in South Australia (124). All infest the same major host, the sleepy lizard *Trachydosaurus rugosus,* whose distribution is continuous across the tick boundaries. The boundary between *Aponomma hydrosauri* and *Amblyomma limbatum* near Mt. Mary has remained stable for over 20 years (C. M. Bull, in preparation). On three transects the boundary center oscillated by less than 800 m over eight years, with no unidirectional trend. The boundary is close to a vegetational ecotone (24, 102, 124). To the north, ground conditions may be too arid for *Ap. hydrosauri,* which is less tolerant of desiccation (25) and seeks less stressful conditions (73, 124). However, transplanted *Am. limbatum* survive as well on either side of the boundary in the litter microhabitats where they wait for hosts (24).

The mechanisms preventing *Am. limbatum* from spreading south across the boundary remain unknown. Interspecific competition appears an unlikely explanation because there are many underused hosts, and because neither species was affected by experimental coinfestation at or above maximum field levels (22). Predators, mainly ants, attack detached ticks, but the ant distributions do not coincide with the tick boundary (23, 33). There is no evidence that lizards from across the boundary are less suitable hosts for attachment and engorgement by ticks (24).

Reproductive interference could be involved in maintaining the boundary. Females initiate mating on the hosts by emitting an excitant pheromone soon after attachment (7). Attached conspecific males will not respond when females of the other species are also attached (8), perhaps because of signal jamming. However, only 13% of lizards close to the boundary carried *Ap. hydrosauri* females, so this would be an ineffectual barrier to colonization by *Am. limbatum* (C. M. Bull, in preparation).

Tick dispersal is slow (20). Over eight years very few *Ap. hydrosauri* colonized north of the boundary, while more *Am. limbatum* colonized south. At least one successful colonization, 1 km south of the boundary, persisted from 1985 to 1988. On the three transects studied, there were consistently low densities of hosts, and low infestation levels per host, in areas immediately adjacent to the boundary (C. M. Bull, in preparation). A role which this population trough may play in maintaining the boundary is explored below.

MODELS OF PARAPATRY

In some cases, such as the reptile ticks, conventional models cannot adequately explain the maintenance of stable parapatry. Other cases of nonhybridizing parapatry have seldom been studied in this detail, so there are few empirical data for generalizations to be developed. Where explanations for parapatry have been sought there was sometimes disagreement (58, 127), often no conclusion (49, 67, 68, 72), and rarely experimental testing of proposed mechanisms. Low dispersal rates, possibly with a population trough, may be key elements in the maintenance of parapatry. Troughs or gaps between parapatric species were often mentioned in early descriptions of parapatry (15, 37, 121) and were detected at the reptile-tick boundary. Low dispersal and the presence of troughs may influence parapatry in two possible ways.

Density Dependent Advantage

The first mechanism is derived by analogy with narrow hybrid zones. Many of these coincide with environmental ecotones (9, 19, 107), but in others, ecological change is gradual relative to the abrupt hybrid zone (128) or undetectable (89). Many hybrid zones are maintained by negative heterosis (61), with a balance of selection against hybrids counteracting dispersal of parental individuals into the zone (11). Low dispersal rate relative to the zone width means that very small, maybe undetectable, levels of selection against hybrids are sufficient to maintain stable zones (12). Thus, in some examples, evidence for reduced hybrid fitness was not found (21). Hybrid zones may be located at density troughs, regions of local decrease of population, with no requirement for an environmental gradient (13, 60, 61). With low dispersal the zone becomes trapped at the trough because neither species can overcome the numerical disadvantage implicit in the negative heterosis mechanism (11). Simulation models show how this may persist for thousands of generations (87). The rarer species always suffer greater proportional losses from interspecific crosses. A hybrid zone in *Podisma* follows such a trough (88).

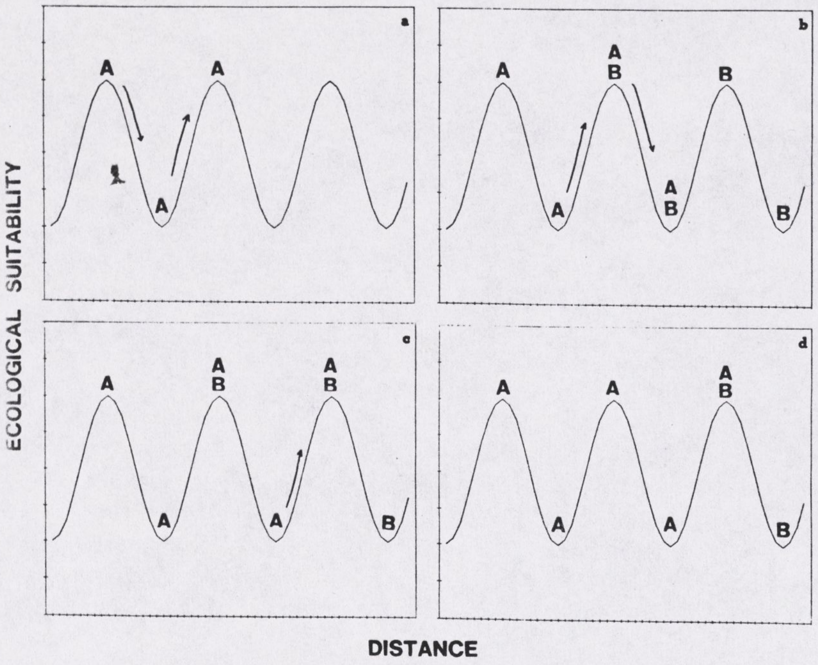
Stable parapatry without hybridization may be maintained in analogous ways. This requires density dependent interactions which depress each species more when it is less numerous. Interactions through reproductive interference, and through parasites and disease, could act in this way as already discussed. With these mechanisms, both a slowly dispersing species and a species colonizing from a population trough will be numerically disadvantaged and less able to penetrate the range of the resident species. The outcome of the species contact will depend upon the strength and symmetry of the interaction and the dispersal rates. Where dispersal is slow, weak interactions will be sufficient to maintain parapatry. Increased dispersal will require stronger interspecific interactions. An asymmetrical advantage to one species may cause the boundary to move and to stabilize only where an environmental cline alters the relative advantages. The greater the asymmetry the further the boundary will move along a cline, in extreme cases leading to the exclusion of one species.

The Deme Model

An alternative model, where interactions do not need to be density dependent, is derived from models of the dynamics of local and regional populations. Migration is a major, but often ignored, component of population dynamics (129, 130). Models in which migration influences the spatial dynamics of populations (43, 56, 57, 113, 114) view regional populations as groups of local populations occupying isolated patches of variably suitable habitat (2). The regional population in these models is only maintained when dispersal from local populations is sufficient to recolonize local extinctions. Empirical evidence supports these models. Local populations on small islands have measurable extinction rates that are higher for smaller or more recently established populations (109, 132); local populations of herbivorous insects frequently establish or go extinct on individual plants (1). Many local populations rely entirely on repeated migratory recruitment for their establishment and maintenance (36), a phenomenon called the rescue effect (18).

A characteristic of the edge of a species range is that there are fewer suitable patches where local populations can establish (17, 138). In peripheral populations of birds, death rates exceed birth rates, and local populations are only sustained by continual migration (137). Carter & Prince (27) developed a model from epidemic dynamics to show that a population could not persist in a region with a high ratio of the rate of patch extinction to the rate of dispersal to reoccupy vacant patches. Their model predicts the abrupt species boundaries on gentle climatic or altitudinal clines that they found for the British prickly lettuce *Lactuca* (28, 29, 106). Small drops in fitness from the presence of another species could have an equivalent effect.

A model for parapatry is illustrated in Figure 1. Assume a species *A* is spreading its range from a source population onto a landscape of "dunes" of ecological suitability such that the distance between adjacent ridges is further than the dispersal range of individuals. Local populations can establish and persist for some time on the ridges. In the troughs there is normally no effective reproduction, and local populations are maintained by migration from the ridges. However, in good years, the trough population can reproduce



igure 1 A model for parapatry with slowly dispersing species in a patchy environment.

fficiently to generate dispersers itself, and the next unoccupied ridge can be ttained. Once established, local populations persist on the ridges as long as ere is occasional interpopulation migration via the troughs. Ephemeral resence in the troughs is maintained by dispersal counteracting extinction, ss effectively if dispersal is lower.

Now suppose there is secondary contact with another species, *B*. Assume ey interact so weakly that local populations of neither are influenced on the dges. In the troughs, however, small interactions may be sufficient to verbalance the equilibrium between dispersal and extinction. The lower the spersal the smaller the interaction needed to exclude one species. Then ther (*a*) the ranges of both species are held at that trough in which contact as first made, because neither can now build up numbers sufficient to lonize and permanently maintain the next ridge; or (*b*) one species, *B*, is ld, but *A* is better adapted, or less affected by interactions, and can expand nto the next ridge. There *A* coexists with *B*, then spreads to the next trough, cludes B from there, so *B* becomes isolated on the previous ridge. That cal population of *B*, now not supported by migration, will eventually go tinct. Meanwhile *A* expands further into the range of *B*, replacing it in this manner, until some environmental change along a gradient reduces its adaptive or competitive advantage in the troughs. The spatial and temporal pattern shown at the reptile tick boundary near Mt. Mary is that predicted by this model (C. M. Bull, in preparation).

CONCLUSION

This view of parapatry emphasizes dispersal as a parameter of prime importance in influencing interspecific interactions. Relatively mobile species will have labile distribution edges and will frequently mix and interact in communities (129). They will be able to colonize and exploit patches within the distribution of other species (120). Only sharp ecotonal changes or strong ecological interactions will lead to parapatry in those species. In contrast, less mobile species like wingless orthopterans (61, 67, 71), amphibians (19, 64, 69, 75, 92), and ants (34, 49, 103) will often form abrupt parapatric boundaries or hybrid zones (62). Even within a taxonomic group, birds tend to disperse less in the tropics (39), and to form more parapatric boundaries there (52, 131) than in temperate forests (90). Parapatry is a phenomenon where interactions with influences beyond the local population may have major implications. Cases of parapatry, previously dismissed as simple examples of competitive exclusion, or of the effect of an ecotone, may prove to be fertile testing ground in a new and richer perspective of past and present processes important in ecological communities.

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MATE CHOICE IN PLANTS: An Anatomical to Population Perspective

Diane L. Marshall and Michael W. Folsom

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131

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INTRODUCTION

Whenever the potential fathers of seeds differ in quality and whenever pollen is available in excess of the amount necessary to sire seeds, plants have both the opportunity and the selective pressure to mate nonrandomly (181). Plant mating may be nonrandom at several genetic, structural, and temporal levels. Genetically, mates may be sorted on the basis of relatedness to the seed parent (121, 137), complementarity of maternal and paternal genotypes (174), and the characters of pollen and pollen donors. Structurally, the physiological decisions that regulate mating may occur among the pollen grains and ovules within individual flowers and fruits (159, 181), among the fruits along branches (103), or across entire plants. Temporally, processes that produce nonrandom mating may occur both before and after pollen arrives on stigmas, during all of the steps from pollen germination through seed maturation, and under varying environmental and physiological conditions across seasons.

Nonrandom mating, which occurs whenever the paternity of seeds is different from that which would result from random use of the pollen available, can occur by mechanisms under the control of pollen donors and pollen tubes, maternal tissues, and embryos (134, 159, 181). All have clear fitness interests in the mating process: Pollen donors and maternal plants can improve fitness by increasing the number and quality of offspring, and embryos must garner sufficient maternal resources to survive to maturity, germinate, and grow to reproductive size. The interests of pollen donors have been relatively

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Zoogeography of North American (North of Mexico) Freshwater Fishes

				Continental Divide			
		no. sp.	Salinity tolerance	E	W	Endemic	Other regions
	Class Agnatha						
	Petromyzontidae	17	2	+	+		1
	Class Osteichthyes						
	Chondrostei						
	Polyodontidae	1	1	+			4
	Acipenseridae	7	2	+	+		1
	Holostei						
	Amiidae	1	1	+		+	
	Lepisosteidae	5	2	+		+	
ORDERS	Teleostei						
Osteoglossiformes	Hiodontidae	2	1	+		+	
Anguilliformes	Anguillidae	1	2	+			1
Clupeiformes	Clupeidae	7	2	+			all
Salmoniformes	Salmonidae	35	2	+	+		1
	Osmeridae	6	2	+	+		1
	Esocidae	4	1	+			1
	Umbridae	4	1	+	+		1
	Ostariophysi						
Cypriniformes	Characidae	1	1	+			2,3
	Cyprinidae	150	1	+	+		1,3,4
	Catostomidae	55	1	+	+		4
Siluriformes	Ictaluridae	40	1	+		+	
Percopsiformes	Percopsidae	2	1	+	+		4
	Aphredoderidae	1	1	+		+	
	Amblyopsidae	6	1	+		+	
Gadiformes	Gadidae	1	2	+			1
Atheriniformes	Cyprinodontidae	30	2	+	+		1,2,3
	Poeciliidae	15	2	+			2
	Atherinidae	3	2	+			211
	Gasterosteidae	4	2	+	+		1
Perciformes	Percichthyidae	4	2	+			1,2,5
	Centrarchidae	32	1	+	+	+	
	Percidae	(3+130)	1	+		(+130)	1
	Sciaenidae	1	2	+			all
	Cichlidae	1	2	+			2,3,4
	Embiotocidae	1	2		+		1 (Japan)
Scorpaeniformes	Cottidae	25	2	+	+		1

Key: Salinity 1, primary freshwater fishes; all or virtually all in family are restricted to freshwater (cannot osmoregulate in seawater); ancestral dispersal assumed to be only by freshwater routes.

Salinity 2, secondary freshwater fishes; most species in family are marine or euryhaline (osmoregulate in both freshwater and seawater); can disperse via ocean. Other species that "sporadically" or "peripherally" occur in freshwater such as gobies, some sharks, flounders, etc., but are not dependent on freshwater (i.e. they freely move back and forth between river and sea) are not included.

Other regions: Other species in family are found in: 1. Palearctic 2. Neotropical 3. Ethiopian 4. Oriental 5. Australian

Endemic (+) means all species in family are endemic to North America.

The superorder Ostariophysi makes up about 90% of all primary freshwater fishes of the world (ca. 6000-6800 sp), but only about 50% of the North American fish fauna.

The (3+130) notation for Percidae denotes three species (yellow perch, walleye, and sauger) and about 130 species of darters.

Note the paucity of families (and species) west of Continental Divide. Considerable extinction of freshwater fishes occurred here and in other parts of the world in the Pliocene.

Topics for Discussion and Speculation

Using fishes as examples, we will attempt to review and synthesize the major principles of classical zoogeography, historical biogeography, and geographical ecology covered to date.

Featured in this all star review will be: extinction, adaptive radiation, convergent evolution, species flocks, competition, predation, competitive exclusion, coevolution and much more.

1. Extinction: Paleozoic fossils in and around Colorado are of marine fishes including some montrous placoderms. Typical freshwater fauna appear in Cenozoic times. Rich deposits of fossils are found in the "Green River Lakes", a series of large lakes of Paleocene and Eocene age (40,000,000-60,000,000 years B.P.) in S.W. Wyoming, N.E. utah, and N.W. Colorado. The fossil fishes represent stingrays (Chondrichthyes, Dasyatidae), paddlefishes (Chondrostei, Polyodontidae), gars (Holostei, genus Lepisosteus), bowfins (Holostei, genus Amia), and following teleost fishes: mooneye (Hiodontidae), bonytongue (Osteoglossidae), herrings (Clupeidae) "African sandfish" (Gonoryhnchidae), suckers (Catostomidae), catfishes (Ictaluridae), trout perches (Percopsidae), perches (Percidae), and species of two extinct families, Asineopidae and Priscacaridae.

   Comparisons with present fish fauna reveals major extinctions, replacements and a few surviving phylogenetic relicts. Chondrichthyes now have no freshwater species in Nearctic or Palearclic regions. A few species of Chondrostei and Holostei -- paddlefish, sturgeons, gars and bowfin -- have persisted to present. Note genera Lepisosteus and Amia occurring 50,000,000 years ago. Also species of families Gonorhynchidae and Osteoglossidae indicate radiation of primitive teleosts from Gondwanaland to Laurasia and into North America. Osteoglossidae is presently represented by one species in Africa, one species in Australia, and two species in South America. A few species of Gonorhynchidae persist in Africa. Both families are primary freshwater fishes.

The mooneyes (Hiodontidae) have persisted to the present with two existing species.

The Ostariophysi are represented by species of suckers (Catostomidae) and catfishes (Ictaluridae), but no minnows (Cyprinidae), the most speciose of all vertebrate families (2000 sp.).

The order Percopsiformes (represented by family Percopsidae) is the most primitive of the advanced teleost fishes. They exhibit characters intermediate between primitive teleosts and advanced teleosts. They were widespread in the Cretaceous but now persist as only a few species in three families, endemic (but probably not autochthonous) to North America. Most species are highly specialized cave fishes. Note similarities with holostei (gars and bowfin).

Percidae is ancient family of "advanced" teleosts. They persist in Holarctic as a few, stable species of yellow perch, walleyes, and European "ruffes", except for a great splurge of speciation of darters in North America, evidently evolved to fill the "substrate" niche, similar to ostariophysean family Cobitidae ("loaches"), which never made it to North America.

Speculate on explanations for persistence of phylogenetic relicts.

What similarities of historical distribution patterns are exhibited by Polyodontidae and Catostomidae?

Catfish (Ictalurus) occurred in western U.S. (Columbia River basin) into the Pliocene. What could have caused their extinction? Centrarchidae were common fishes of Miocene-Pliocene in western U.S. Its present indigenous western distribution is limited to one species in Sacramento River.

Note the similar primitive distribution pattern, and persistence of relicts, in both Percopsidae and Umbridae.

What is similarity among Gadidae, Sciaenidae and Embiotocidae? Why is this phenomenon so much more prevalent in Australia (two species of primary freshwater fishes) and New Zealand (no species of primary freshwater fishes)?

Why are all of the endemic families "primary freshwater" (minor exception with gars)?

What routes of dispersal were used by primary freshwater fishes to become established in North America (Palearctic-Laurasia or Neotropical-Gondwanaland)?

What is basis to recognize provinces (subregions) for freshwater fishes (remember degree of endemism)?

Understand problems of endangered species in terms of rapidly changing environments (changing more rapidly than adaptive evolutionary changes are possible) and sudden exposure to massive invasion of new species -- coevolution has been disrupted.

What is a species flock? How do they "bend the rules" of speciation and taxonomy? North America has, at most, mini species flocks -- a few species of ciscoes (Coregonus) in Great Lakes, perhaps the tui chub of Lahontan basin, and whitefishes (Prosopium) of Bear Lake, which has 4 endemic species -- only three other species of this genus occur in Nearctic and Palearctic (a "relict genus"). Lake Malawi, Africa has more than 300 endemic species of cichlids. Lake Baical has species flock of sculpins, Lake Titicaca of topminnows, and Lake Llanao (Phillipines) of true minnows.

How are past climatic and geological histories interpreted by zoogeographic evidence of primary freshwater fishes. Hint: fish live in water and water runs downhill.

Freshwater fishes make up about 40% of the world's fish fauna (ca. 8000 of 20,000 species) but freshwaters make up less than 1% of the volume of water on earth. With such comparative habitat volumes, it appears that freshwater fishes must speciate more rapidly and more profusely than marine fishes. Why?

Not all regions of the world are equally endowed with all major evolutionary lines (orders and families) and certain types of specializations may be lacking in species of various regions or provinces (ex. feeding on macrophyte vegetation). South America (Neotropical) has about 10 times more freshwater fish species than North America (Nearctic).

Trout

Trout are the aristocrats of inland waters. Their beauty and the charm of the waters in which they live make the trout the most highly prized of the world's game fishes. The traditions, ethics, and refinements of angling are developed to a very high degree for the pursuit of trout. All dwell in boreal waters in hill or mountain streams or in the northerly latitudes of the ocean if they are migratory forms that run to the sea.

The term 'trout' is loosely applied to a number of similar species. The 'true trouts' belong to a group of fishes in the family Salmonidae. This family is divided into three subfamilies: the whitefishes, Coregoninae, the graylings, Thymallinae, and the trouts, salmons and charrs, Salmoninae. These are relatively primitive forms lacking spines in their fins, or any armor or other specialized structures often seen in the higher fishes, such as bass or perch. There is not much agreement in the use of the names trout, salmon and charr. In Europe the name trout is given to the brown or sea trout, _Salmo trutta_, and charr is used for the various forms of the arctic charr, _Salvelinus alpinus._ The Atlantic salmon, although called a salmon, is more closely related to our rainbow trout than it is to the Pacific salmon in the genus _Oncorhynchus_. In North America we have four groups of native charrs which are often called trout. These are the eastern brook trout, *Salvelinus fontinalis*, the lake trout, *S. namaycush*, the Dolly Varden, *S. malma*, and the Arctic charr, *S. alpinus*. These are more closely related to the European and Arctic charrs than they are to the true trouts.

q We have three native trouts in North America. These are the rainbow or steelhead, *Salmo gairdnerii*, the Atlantic salmon, *Salmo salar*, and the black-spotted or cutthroat trout, *Salmo clarkii*. The latter is so called because of the crimson, slash-like markings on each side of the throat. It was found originally from northern California to southern Alaska in coastal waters, and was the only native trout in the interior drainages of the upper Missouri, Colorado, Rio Grande and in the Great Basin in Nevada and Utah. A number of subspecies of cutthroat have been named. Among these are the coastal cutthroat, *S. clarkii clarkii*, the black-spotted trout of Yellowstone Lake and the head of the Missouri River, *S. clarkii lewisi*, and the Lahontan or Nevada cutthroat, *S. clarkii henshawi*. The record trout ever taken by angling weighed over 41 pounds and was a *henshawi* and came from Pyramid Lake, Nevada.

The golden trout of California is a unique fish and is considered a distinct species, *Salmo aguabonita* by some ichthyologists, but only as a subspecies of the rainbow by others. It lives in high, cold streams and lakes, usually above 8,000 feet elevation. Its native habitat was the South Fork of the Kern River in California. Spawning in streams in late June, it will readily hybridize with rainbow trout, producing fertile hybrids. Recently, other forms of golden trout, much like the California type, have been discovered in Mexico and Arizona.

In the genus Salmo, besides the species already mentioned, we have S. ischchan of Lake Sevan and S. mykiss of Kamchatka, both in USSR, and S. letnica of Lake Ohrid, Yugoslavia. There are three other genera of troutlike fishes that are closely related to Salmo. These are Hucho, Brachymystax, and Salmothymus. The genus Hucho has three species. One in the Danube River, one in Siberia, and one in northern Japan. The genus Brachymystax consists of a single species found in Asia. Salmothymus contains a few, little known species in tributaries of the Adriatic Sea in Yugoslavia and Albania.

In the streams tributary to the Pacific Ocean, six species of Pacific salmon, Oncorhynchus, spawn. Five of these species live in North America and a sixth occurs only in northeastern Asia. Like the Atlantic salmon, the Pacific salmon spawns in freshwater but spends most of its life in the sea, returning to freshwater to breed. But unlike the trouts, all Pacific salmon die after spawning. One species of Pacific salmon, the sockeye, Oncorhynchus nerka, may live its whole life in freshwater, never going to sea. This form is known as the kokanee, silver trout, or little redfish.

The whole family Salmonidae was originally restricted to the colder waters of the Northern Hemisphere. Trouts, especially rainbow and brown trout, have been widely introduced into suitable waters in Africa, India, South America, Australia and New Zealand where they have produced fabulous angling. The main requirement for successful trout habitat is clear, cold, well oxygenated waters with suitable gravel for nest building during spawning. Fertilization of the eggs occurs externally as they drop into shallow pockets made by the female in the gravel, after which the female carefully covers them with several inches of gravel. Incubation occurs in the gravel where they are protected from predators. Survival through hatching is often over 90 percent. Length of the incubation period depends upon water temperatures. At 55°F rainbow eggs will hatch in 23 days. At 43°F the incubation period may require as much as 130 days.

The brown trout, Salmo trutta, was originally distributed from North Africa, throughout Europe and in Asia to the Aral Sea and its tributaries. In the Caspian Sea this species has been reported by Russians to reach a weight of 100 pounds. In the northern part of its range, the brown trout has populations which go to sea to grow and mature, returning to freshwater to spawn. A few sea-run brown trout have been reported recently from the Columbia River in Oregon. In this respect they parallel the behavior of Atlantic salmon. The brown trout has been successfully introduced into many American waters. It is the most wary of trout and more difficult to catch than our native American species.

The rainbow, or steelhead, trout was native only to the Pacific coastal streams of North America, from northern Mexico into Alaska. It is a superb game fish, making spectacular leaps when hooked. Rainbows have been known to attain a weight of more than 35 pounds. Temperature-wise, rainbows are the most adaptable of the trouts and can stand water temperatures of 83°F if the oxygen remains high. They are the principal trout propagated in fish hatcheries.

Most salmonids are carnivorous and predatory. When young they eat the microscopic life in water, later turning largely to insects and crustaceans. When very large they are usually piscivorous. A great variety of artificial lures used by anglers are imitations of their aquatic foods. Dry fly fishing for trout is considered the highest form of the angler's art.

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