

## Macroscopic intersexuality in salmonid fishes

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**Abstract** The occurrence of individual salmonids with macroscopically identifiable, simultaneous male and female gonads is an uncommon reproductive disorder. Individual specimens have been described, but no larger synthesis of the condition has been made. We first describe two simultaneous intersexual Pacific salmon (*Oncorhynchus* spp.) specimens, encountered during rearing operations in New Zealand and Chile, confirming that the phenomenon occurs beyond the natural range of the genus. A review of these and other isolated specimens within the Salmonidae (*Oncorhynchus*, *Salmo*, *Salvelinus*, *Coregonus*, *Thymallus*) suggests that the disorder takes at least two distinct anatomical patterns, which we call lobular and mosaic. These are consistent with differences in either the degree or onset time of aberrant development from protogynous or neutral

gonadal primordia. The disorder has a low natural incidence (one in several thousand), but the extensive use and study of salmonids makes it likely that natural macroscopic hermaphrodites will be encountered regularly. Isolated specimens have been attributed to environmental contamination, but their widespread occurrence suggests they are primarily a natural phenomenon.

**Keywords** Salmonidae; hermaphrodite; intersexual; gonads

### INTRODUCTION

It is often said that much is learned from exceptions to rules. In salmonids, individuals with visible, simultaneous testicular and ovarian gonadal elements represent occasional exceptions to the rule of gonochoristic sexual development. The general term “intersexual” is used here to distinguish a macroscopic, aberrant phenomenon in a normally gonochoristic species from true hermaphroditism, where the natural sexual condition of the species is for all or most individuals to develop both male and female gonads during their lives (this nomenclature is generally consistent with Lepori 1980). Despite a large number of isolated reports of such individuals (Table 1), there have been few attempts at a wider synthesis of their biology. However, interest in the reproductive development and health of this economically important family of fishes, and recent concerns about the potential for agricultural and industrial environmental contaminants to promote sexual abnormalities such as feminisation of male reproductive organs (e.g., Fraser 1995; Jobling et al. 1998), make a review of the scale and nature of the phenomenon worthwhile.

During a recent study of chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand, and during net pen culture of coho salmon (*O. kisutch*) in Chile, simultaneous intersexuals were observed in maturing condition. This study: (1) describes the New Zealand and Chilean specimens; (2) collates

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information on the occurrence of macroscopically intersexual salmonids (genera *Oncorhynchus*, *Salmo*, *Salvelinus*, *Coregonus*, and *Thymallus*) based on a review of the literature and personal reports known to the authors; and (3) considers the common structural forms of intersexual salmonids, their natural incidence, and their possible relationship to biological contamination.

## RESULTS

### Description of specimens

On 22 May 1997, an age 3 freshwater-reared chinook salmon, with outwardly female characteristics, was identified as intersexual during dissection to remove ova (Fig. 1) at the Glenariffe Hatchery in New Zealand. This 1535 g, 490 mm long individual showed spawning coloration and body shape but had not matured by the end of the 1997 spawning season. When viewed ventrally the left gonad comprised 19.7 g of ova attached to the anterior end of the skein, and 52.2 g of testis attached to the posterior end. The right gonad (81.1 g) consisted entirely of ova. The testicular portion was white and contained thick milt similar to that of normal males approaching ripeness, though the duct to the genital pore was not infused with milt. Ova were of apparently normal size (c. 0.13 g) and number on the remaining gonads, and some eggs were fully mature and loose in the body cavity. The gonadosomatic index (GSI) was 10.0%, compared to mean values of 5.7% for 179 males and 17.7% for 699 females from the same cohort. Use of a sex specific genetic marker (Du et al. 1993) indicated that this salmon was genetically female. This specimen represented the only hermaphrodite out of 2660 fish from the same brood class sampled over 3 years.

A 635 mm (3100 g) intersexual coho salmon was discovered during harvesting at a fish farm near Puerto Montt, Chile, on 28 May 1996 (Fig. 2). This fish was 2 years old, of Chilean origin (i.e., from parental stock reared in Chilean waters), and had been reared in a seawater net pen after initial hatching and rearing in fresh water. It was externally coloured as a male, but had female body shape and relatively little snout development. It released mature eggs but upon dissection was found to also possess testes with flowing milt. Gonads were arranged with ova anterior and loose in the body cavity, and testes attached posterior. Total gonad weight was 301 g (ovarian tissue: 270 g, testes: 31 g), giving a GSI of

9.7%. Eggs were 6.8–6.9 mm in diameter and numbered 2355. This fish represented a single individual out of 3000 harvested from its brood.

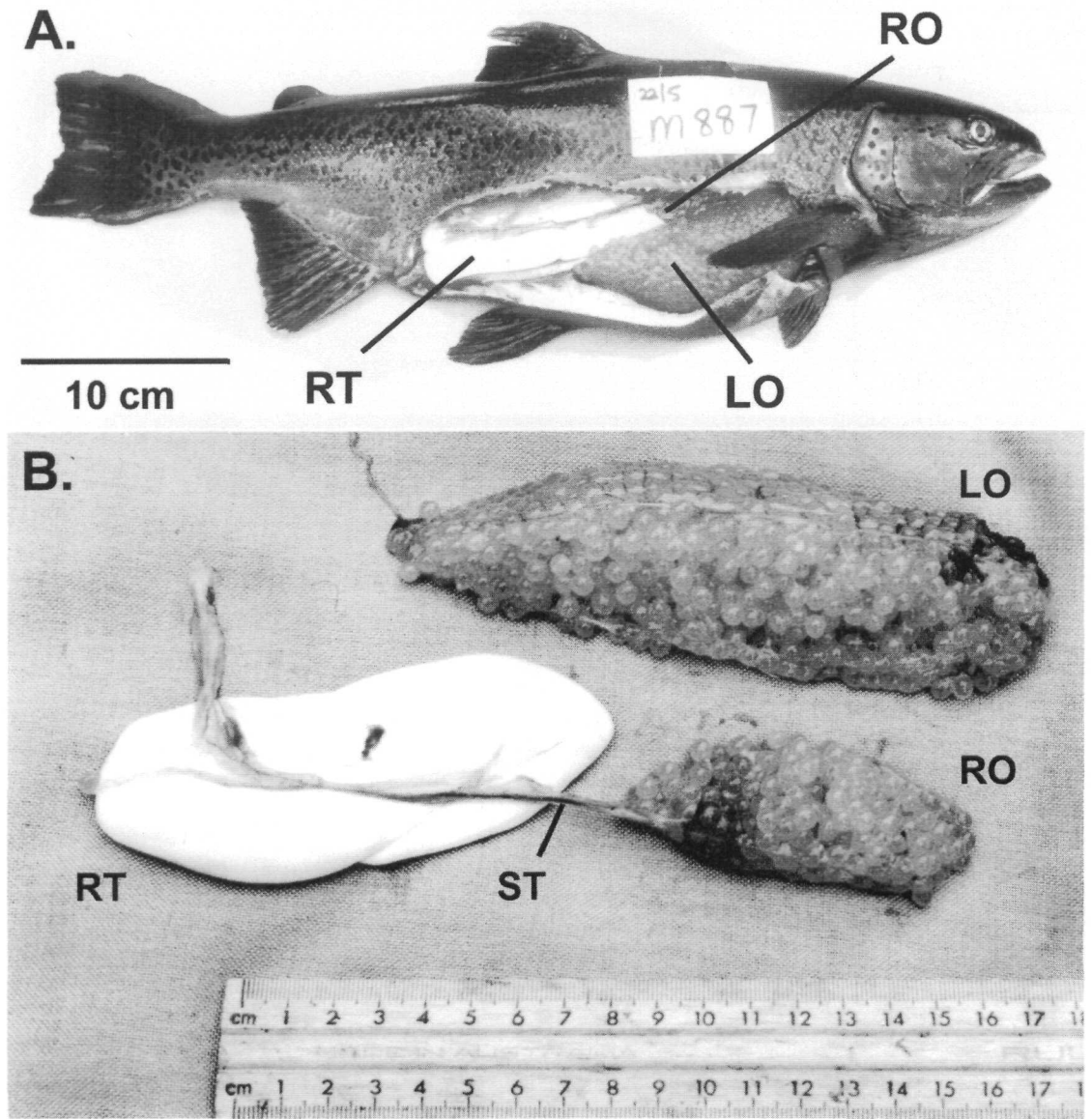
### Other reports

Twenty-nine published and unpublished records of intersexual Salmonidae identified by gross examination are summarised in Table 1. In *Oncorhynchus* records exist for specimens from all species except pink salmon (*O. gorbuscha*) and masu (*O. masou*). In *Salmo* we found examples from both species (*S. salar* and *S. trutta*), and in *Salvelinus* and *Coregonus* we found examples from three species each. In *Thymallus* only a single record was found.

The gonads of macroscopic intersexual salmonids generally take one of two structural forms, which we call "lobular" and "mosaic". Lobular gonads are characterised by distinct sections of ovarian and testicular tissue along the supporting structure of one or both gonads, often separated by undifferentiated connective tissue. This form includes the New Zealand chinook and Chilean coho specimens. Mosaic gonads are characterised by more superficial patches of ovarian tissue on the surface of testicular tissue, or scattered and embedded oocytes in the testicular tissue (Gibbs 1956; Blachuta et al. 1991). Mosaic and lobular gonad forms may be combined in some individuals (e.g., Edsall 1970; Porter & Corey 1974). A third form characterised by multiple male and female gonads, may also occur (Crawford 1927; Honma & Chiba 1985), although we found no visual confirmation of this in the published literature and it may be only an artefact of ambiguous specimen description or interpretation.

Although lobular forms were more common than mosaic forms, there were few consistent patterns of testicular or ovarian distribution along the cranial-caudal axis. Segments of both types of tissue were found in various locations and in various amounts along the gonads of different individuals. In individuals for which both gonads were of lobular form, the ordering of testicular and ovarian elements tended to be similar in both gonads (Table 1), suggesting an imperfect, bilaterally-symmetric effect along the cranial-caudal axis. Carcinoma or a cystic tissue body was noted in three specimens. In two of these cases (Maconie 1933; Brown & Scott 1988) one of the structures considered ovarian was cystic, whereas Ross et al. (1963) documented a specimen with advanced hepatocellular carcinoma.

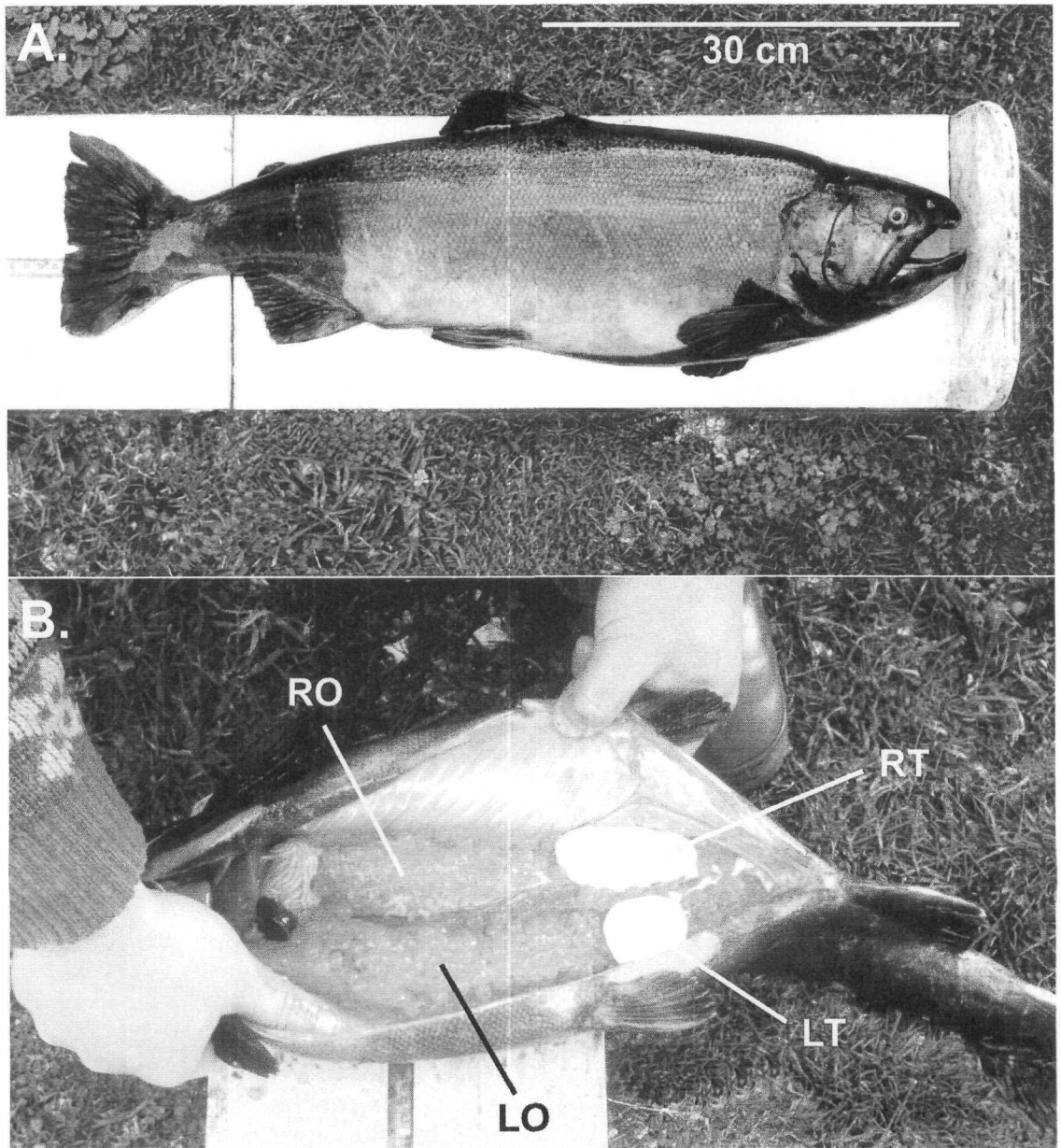
It is difficult to estimate the frequency of macroscopic hermaphroditism from the collected literature because of inconsistencies in reporting the



**Fig. 1** Intersexual chinook salmon from the Glenariffe Stream Hatchery, New Zealand, showing: **A**, individual with wall of body cavity removed to expose gonads; and **B**, excised gonads. Labels indicate the right ovary (RO); left ovary (LO); right testis (RT); and supporting tissue (ST).

total numbers of normal individuals examined, the few cases in which more than one specimen was found, and no obvious means of estimating how many studies found no intersexuals. However, from our own observations and the data summarised in Table 1 we approximate the incidence in *Oncorhynchus*, *Salmo*, and *Salvelinus* to be c. 1 in

2000–5000. The observed incidence of intersexual specimens in the coregonids appears to be less than in the other salmonid genera (perhaps 1 intersexual in 7000 or more normal specimens with a very wide range in the cases reported). The single reported specimen in *Thymallinae* precludes any estimate of their incidence.



**Fig. 2** Intersexual coho salmon from net pen near Puerto Montt, Chile, showing: **A**, external appearance of specimen, and **B**, interior of body cavity showing male and female gonadal tissue. Labels indicate the right ovary (RO); left ovary (LO); right testis (RT); and left testis (LT).

## DISCUSSION

### Incidence of intersexuals

Our observations of simultaneous intersexual salmonids in both New Zealand and Chile establish

the occurrence of this aberration well outside the natural range of either species, to the extent that the condition can be described as global. Moreover, given the extent to which the disorder has been reported in other salmonids, and the likelihood of

**Table 1** Macroscopic intersexual specimens of the Salmonidae. Gonad structure is described anterior to posterior, right to left respectively for most cases. For lobular forms gonads are detailed on separate lines: R = right gonad, L = left gonad, T = teste, O = ovarian. (FL = fork length (mm), GP = gonad photographs, HP = histological photographs, SP = specimen photograph.)

Family/species	Source	Location	Operation	Incidence	Age	Arrangement	Fish/testes/ovary size	Comments
<b>Salmoninae</b>								
<i>Oncorhynchus</i>								
<i>O. tshawytscha</i>	Rutter (1902)	Cannery at Black Diamond (Pittsburg), CA, United States, 1901	canning operations	1 fish		T – O T – O – T	1st gonad: 1/4 normal density of ova in ova section 2nd gonad: c. 125 mm of teste and 12 ova described as similar to Black Diamond specimen	Only gonads obtained (GP)
	Rutter (1902)	Battle Cr. Hatchery, Sacramento R. System, CA, United States, 1900	hatchery returns	1 fish		Lobular		Only gonads obtained. Self-fertilisation unsuccessful
	This study	Glenariffe Stream hatchery, Canterbury, New Zealand, 1997	freshwater rearing	1: 2660	3	R: O L: O – T	fish: 1535 g, 490 mm L: 81.1 g ovarian R: 19.7 g ovarian, 52.2 g teste	Outside natural range; genetic sex test performed (GP, SP)
<i>O. kisutch</i>	Crawford (1927)	Chehalis R., WA, United States, 1927	trapped in river	1 fish		Ova loose, testis dorsal	fish: c. 900 mm ovotestis < half of normal gonad space	
	This study	Panitao near Puerto Montt, Chile, 1996	sea pen rearing	1:3000	2	R: O – T L: O – T	fish: 635 mm, 3100 g gonads: ova 270 g, testes 31 g	Outside natural range (GP, SP)
<i>O. keta</i>	Uzmann & Hasselholt (1958)	Chitose R., Hokkaido, Japan, 1956	captured in river	<1: 2000		R: O – T L: O – T	fish: 690 mm FL R: little ovarian tissue L: 1/3 ovarian, 2/3 teste	University of Washington Fish Collection specimen 11404 (GP, SP)
	Hikita & Hashimoto (1978)	Chitose R., Hokkaido, Japan, 1976	captured in river	1 fish	4	R: O – T L: O – T	fish: 701 mm FL, 4.1 kg R: 82 g ovarian, 34 g teste L: 99 g ovarian, 38 g teste plus some ovulated ova	Describes a viable offspring produced by artificial self-fertilisation (GP, SP)
	Hitron & Bonham (1977)	Nisqually R., WA, United States, 1975	captured in river	1 fish		R: O – T L: O – T	fish: 3870 g w/o head R: 2/3 ovarian, 1/3 teste L: 2/3 ovarian, 1/3 teste	University of Washington Fish Collection specimen 20633 (GP)
	Honma & Chiba (1985)	Mouth of Agano R., Niigata City, Japan, 1983	netted near river mouth	1 fish		Ripe teste and unripe ovaries	teste: 160 g R ovarian: 10 g L ovarian: 44 g	Based on extended abstract only
<i>O. nerka</i>	NIWA (unpubl. data)	Glenariffe Stream hatchery, New Zealand, 1980–99	freshwater rearing	A few in 20 years		Lobular		S. P. Hawke, NIWA, Christchurch, New Zealand pers. comm. GP
<i>O. mykiss</i>	Gibbs (1956)	Eel R., CA, United States, 1955	sports fishing	1 fish		Mosaic	R: 2/3 egg patch coverage L < 1/2 egg coverage	
	Ross et al. (1963)	U.S. Fish and Wildlife Service, Western Fish Disease Laboratory, Seattle, WA, United States	freshwater rearing	1 fish	3	R: O – T L: O	fish: 279 mm FL	Hepatocellular carcinoma; interpreted as non-functional (GP, HP)

Table 1 (Continued)

Family/species	Source	Location	Operation	Incidence	Age	Arrangement	Fish/testes/ovary size	Comments
<i>O. clarki lewisi</i>	Benson (1958)	Yellowstone Lake, WY, United States, 1957		1 fish		R: O L: O - T	fish: 320 mm FL; R: 88 mm ovarian; L: 75 mm ovarian, 30 mm teste	Unclear whether testes were separate lobes or part of left ovary
<i>Salmo Unknown</i>	Simpson (1839)	Site unknown c. 1734						Oldest salmonid record known
<i>S. salar</i>	Atz (1964)	c. 1950						Cited by Atz as Fontaine & Vibert (1950)
<i>S. trutta</i>	Stewart (1891)	United Kingdom		1 fish		R: O L: O - T - O	fish: 300 mm; R: 47 mm ovarian; L: 26 mm ovarian, 16 mm testes, 17 mm ovarian	Suggested self-fertilisation (GP)
	De Beer (1924)			1 fish		R: T - O L: T	fish: 60 mm	
	Evensen (1977)	Lake Veslebottvatn, Norway, 1977			7			Not in breeding colour and had probably not spawned
	Maconic (1933)	Waitati Hatchery, Otago, New Zealand, 1933	hatchery propagation	1 fish		Possible multiple form 3 O and 2 T	fish: 514 mm	Outside natural range of <i>Salmo</i> . One ovary possibly a cyst
<i>Salvelinus S. fontinalis</i>	Strand (1958)	New York State Fish Hatchery, NY, United States, 1953	experimental treatment	1 fish		Mosaic		Apparent accelerated maturation due to epinephrine treatment
<i>S. alpinus</i>	Atz (1964)	c. 1938						Cited by Atz as Samal (1938)
	Fraser (1997)	Loch Rannoch, Scotland	field sampling	1:1000	4	R: T L: O - T	fish: 204 mm FL; gonads: 30 oocytes, remainder teste	Author suggests environmental contamination influence (GP)
<i>S. malma</i>	Acara (1968)	Lower Arrow Lake drainage, BC, Canada	sports fishing	1 fish	9	R: T - O L: T - O	fish: 4080 g; equal amounts of testicular and ovarian tissue on both gonads	Interpreted as functional hermaphrodite (GP)
Coregoninae								
<i>Coregonus C. lavaretus</i>	Scott (1975)	Loch Lomond, Scotland	field sampling	1:10000	3-4	mosaic, some ovulated ova	fish: 295 mm FL	Interpreted as functional hermaphrodite. Not all fish examined internally (GP, HP)
	Brown & Scott (1988)	Loch Lomond, 1986	field sampling	1:7500	2-3	R: O - T - O L: degenerate	fish: 197 mm FL, 90 g GSI: 0.24, closer to normal males	Degenerate gonad appeared cystic (GP, HP)
<i>C. clupeaformis</i>	Chen (1969)	Hogan's Pond, Newfoundland, Canada, 1966	field sampling	1:261	4	R: T L: T with O ventral	fish: 286 mm, 225 g ovary: 10 mm of tissue off mesovarium	HP

				1 fish	8	T-O-O variable lobes mosaic portions R: O-T L: T-O-T mosaic portions	fish: 434 mm FL, 1200 g	GP, HP
	Porter & Corey (1974)	South Bay, Lake Huron, Ontario, Canada, 1970	catch sampling					
	Edsall (1970)	Lake Michigan near Frankfort, Michigan, United States, 1955	field sampling	1:50000 over 10 years				Not all fish examined internally (GP)
<i>C. hoyi</i>								
Thymallinae								
<i>T. thymallus</i>								
<i>T. thymallus</i>	Blaichuta et al. (1991)	R. Nysa Klodzka, Barco Slaskie, Poland, 1989	field sampling	<1: 2000	2	mosaic	fish: 280 mm GSI: 0.88, less than normal females or males	Dorsal fin differed from normal males and females (GP)

undocumented cases, the phenomenon probably occurs spontaneously in all salmonid species. Simultaneous intersexuals have also been documented in more distantly related genera of normally gonochoristic fishes, including other freshwater teleosts such as pike (*Esox lucius*; Dominguez et al. 1989), European perch (*Perca fluviatilis*; Jellyman 1976), and *Chondrichthys* (see Atz 1964 for a review).

Given the vast number of salmonids handled, during commercial, scientific, or sporting activities, the widespread occurrence of occasional intersexuals is not unexpected. The natural tendency for investigators to document the exception (i.e., intersexuals) rather than the rule (i.e., normal individuals) will tend to inflate the estimated rate of occurrence, whereas any tendency for anomalous individuals to go unnoticed or unreported will have the reverse effect. The likelihood that reproductive disorders will be noted will also depend on the care with which fish are inspected, and detection of intersexuals may be lower in species with less sexual dimorphism. The apparently lower incidence of intersexual specimens in the Coregonids may reflect such a bias. The incidence of intersexuals in Salmonidae appears consistent with two reports of intersexuals in their phylogenetic relatives, the *Clupeidae*, of 1 in 2276 fish, and 1 in 11290 fish (reviewed in Atz 1964).

### Physiological considerations

The physiological processes that induce aberrant gonad development in salmonids are unclear, and are probably several. Reproductive tissue in bony fishes is thought to arise through different embryological processes than in other vertebrates, developing solely from the cortex rather than separately from feminine-cortical (ovarian) and masculine-medullary (testicular) primordia (Adkins-Regan 1987). The relatively high incidence of intersexualism in bony fishes, including normal hermaphroditism in some taxa (e.g., *Serranidae* and *Sparidae*), may reflect this difference (Dodd 1960). Investigators have postulated that the primordial tissue leading to gonadal structures in teleosts has either feminine (Francis 1992) or gender neutral tendencies (D'Ancona 1949). The pattern of sexual arrangement in intersexual specimens of salmonids suggests either partial differentiation from feminine primordia, or mixed development from neutral primordia. In intersexual specimens with cystic bodies or carcinoma, these structures may have either affected the reproductive system directly, or may have been co-symptoms of a more systemic disorder.

The factors responsible for the appearance of at least two broadly distinguishable gonadal forms are also unclear, but may reflect differences in the proportion of masculine and feminine gonadal tissue following their initial differentiation. The mosaic form may arise from a few aberrant cells in an otherwise monosex gonad, whereas the lobular form (in which large gonadal structures of opposite sex appear to become more differentiated as the organism develops toward maturation) may result from a relatively even division between male and female tissues, particularly if there is some physiological antagonism between them. Alternatively, the two forms may reflect differences in the timing of onset of the physiological aberration responsible for the disorder. For example, segments of lobular forms may develop relatively early during gonadogenesis, whereas mosaic forms may reflect later partial re-differentiation of germ cells, a condition that has been artificially induced in salmon and other fishes (e.g., Nakamura 1984; Shibata & Hamaguchi 1988). More use of genetic sex tests on intersexuals (as we performed for the New Zealand chinook specimen), or examination of specimens experimentally induced at different developmental stages, would help to understand their ontogeny.

Environmental contamination has been suggested as a possible cause of intersexualism in salmonids (e.g., Fraser 1997), but we are cautious about this interpretation. First, the disorder has been observed on a near global scale, albeit at low incidence. Although contamination by artificial promoters such as alkylphenol polyethoxylates may be very widespread (Sumpter & Jobling 1995), significant concentrations of these chemicals would be highly unlikely in upper-catchment, glacial systems (such as Glenariffe Stream in New Zealand), or around marine rearing pens in Chile. We would also expect that, if environmental contamination were a significant cause of macroscopic intersexualism, there would be more documented instances of multiple occurrences. We are unaware of any comprehensive studies of salmonids in contaminated versus non-contaminated sites (in contrast to those performed on roach, *Rutilus rutilus* by Jobling et al. 1998), which would help to clarify whether or not isolated intersexual salmonids are a useful indicator of contamination.

Several compounds known to affect sex determination in fishes, such as androgen and estrogen analogues, show a range of effects on gonadal development (often dependent on dose and timing). If applied to salmonids in sufficiently high dosages

(generally much higher than those likely to occur in nature) fully sex-reversed individuals can readily be produced (e.g., Johnstone et al. 1978), although intersexuals are created only rarely (e.g., Nakamura 1984, Piferrer & Donaldson 1989). Even in environments where such compounds might appear as contaminants, therefore, production of macroscopic intersexuals seems unlikely. Exposure to such compounds may contribute to other reproductive abnormalities, such as inhibited structural development of the gonads, increased blood vitelogenin, and histologically apparent intersexualism (Sumpter & Jobling 1995; Jobling et al. 1996; Jobling et al. 1998). However, the incidence of such abnormalities has seldom been documented even in populations where intersexual salmonids have been noted.

The presence of ripe ova and milt in a single individual has been suggested as evidence that functional, simultaneous hermaphroditism (through self-fertilisation) may occur in this evolutionary lineage (Acara 1968), but this conjecture seems unwarranted. The range of gonadal forms reported, dysfunctional features such as incomplete seminal ducts or partly ripe gonads, and the low incidence of the phenomenon, suggest it has little if any evolutionary significance.

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