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HYBRIDIZATION IN SALMONIDS: RESULTS AND PERSPECTIVES

B. CHEVASSUS

Laboratoire de Physiologie des Poissons, I.N.R.A., 78350 Jouy en Josas (France)

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ABSTRACT

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This report presents a critical review of interspecific hybridization in salmonids and discusses the potentiality of hybrids for water management and fish farming.

INTRODUCTION

Since the early work of Green (1881) and Day (1882), a large number of authors have studied in more or less detail the problems of interspecific hybridization in salmonids. The extensive reviews of Schwartz (1972) and Dangel et al. (1973) listed 438 and 611 publications, respectively, on this subject. Recently, Refstie and Gjedrem (1975) and Purdom (1976) emphasized the practical advantage of hybridization in fish to optimize new breeding methods as well as to prevent the disappearance of some natural populations. In this report, we present a critical review of the present data available in the literature and indicate research aspects which we believe should be developed.

BIBLIOGRAPHICAL METHODS

Classification

The concept of species in salmonids, the basis of the notion of interspecific hybridization, gave rise to many studies and still remains an object of controversy. A detailed review of the main problems was published by Behnke (1972) for the genera *Salvelinus* and *Salmo*, and we have used it as a principal reference.

In the genus *Salvelinus* the specific status of *Salvelinus namaycush* and *Salvelinus fontinalis* seems to be well established. On the other hand, the group of Arctic char, spoken of by Behnke, (1972) as “a semantic cloak for

our ignorance", includes a large number of populations of which a neat classification has not been possible. Most hybridization results concern the same taxon *Salvelinus alpinus*. However, some of the important work of Susuki and Fukuda (1971 a, b) concerns *S. pluvius*, considered by Behnke and Shimizu (1962) as a subspecies of *S. malma*. But *S. malma* is sympatric with *S. alpinus* in some zones, thus leading us to consider it as a species distinct from *S. alpinus* (McPhail, 1961). In this report, we thus consider four taxa in the genus *Salvelinus* (Table I): *S. fontinalis*, *S. namaycush*, *S. alpinus* and *S. malma*.

TABLE I

Main taxa in the family Salmonidae

Species	Origin	Vernacular names	
		French	English
<i>Salvelinus alpinus</i>	Linnaeus (1758)	Omble chevalier	Char } Arctic char
<i>Salvelinus malma</i>	Walbaum (1792)	Dolly varden	
<i>Salvelinus fontinalis</i>	Mitchill (1815)	Omble de fontaine	Brook trout
<i>Salvelinus namaycush</i>	Walbaum (1792)	Touladi	Lake trout
		Omble de lac	
<i>Salmo trutta</i>	Linnaeus (1758)	Truite brune	Brown trout
		Truite commune	
<i>Salmo salar</i>	Linnaeus (1758)	Saumon atlantique	Atlantic salmon
<i>Salmo gairdneri</i>	Richardson (1836)	Truite Arc-en-ciel	Rainbow trout
<i>Salmo clarki</i>	Richardson (1836)	Truite fardée	Cutthroat trout
		Truite à gorge coupée	
<i>Oncorhynchus masou</i>	Brevoort	Saumons japonais }	Masu
<i>Oncorhynchus rhodurus</i>	Jordan & McGregor		Biwa salmon
<i>Oncorhynchus tsawytscha</i>	Walbaum (1792)	Saumon royal	Chinook salmon
<i>Oncorhynchus nerka</i>	Walbaum (1792)	Saumon rouge	Sockeye salmon
<i>Oncorhynchus keta</i>	Walbaum (1792)	Saumon keta	Chum salmon
<i>Oncorhynchus gorbuscha</i>	Walbaum (1792)	Saumon rose	Pink salmon
<i>Oncorhynchus kisutch</i>	Walbaum (1792)	Saumon argenté	Coho salmon

In the genus *Salmo*, two main European species are usually distinguished, the Atlantic salmon *Salmo salar* and the brown trout *Salmo trutta*, a polymorphic species including many ecological (*fario*, *trutta*, *lacustris*) or geographical (*ischchan*, *letnica*, *caspicus*) sub-species. The classification of American species, on the other hand, is more complicated. Behnke (1972) indicates that no less than 44 species have been described in this group. However, at present, two series, belonging to two main species *S. gairdneri* and *S. clarki*, may be distinguished, even if some related species (*Salmo chrysogaster*, *Salmo apache*) do not fall into this classification. For this study, we

thus retained only four taxa in the genus *Salmo*: *S. salar*, *S. trutta*, *S. gairdneri* and *S. clarki* (Table I).

Classification of the genus *Oncorhynchus* seems relatively well established even if the phylogenetic relationships between species are still debatable. We have used the classification of Vladykov (1962) which distinguishes seven species in the genus *Oncorhynchus* (Table I).

Variability of results

A study of various works dealing with the same hybridization produces very heterogeneous results, thus making a critical review difficult. There are two main reasons for variability.

(1) A lack of strict methodology: when two species are crossed, the only way to advance conclusions is to make a control cross of the same animals with individuals of their own species, and use this control in the same environmental conditions as a basis for comparing the results. Problems concerning the quality of parental gametes, particularly overripe ova, and the quality of the environment are thus partially eliminated. However, in many cases there are either no controls, or if so, they are different from those employed for the crossing. In this report, we will refer only to articles reporting at least one reference to a control kept in the same environmental conditions (Table II).

(2) Intraspecific variability: even when the above criterion is met, there is still some variability which seems at least partly due to intraspecific variability, and especially to the use of different populations. For instance, Alm (1955) and Refstie and Gjedrem (1975) obtained better results by crossing a female *Salmo salar* with migratory male European trout *Salmo trutta trutta* than with the sedentary variety (*Salmo trutta fario*). This variability makes a comparison of growth performance difficult, as the authors state that the same hybrid could be either distinctly inferior or equivalent to one of the parents, or distinctly superior to both parents, as in the case of the hybrid *S. salar* × *S. trutta* (alm, 1955; Piggins, 1965; Refstie and Gjedrem, 1975).

Criteria of hybrid fertility

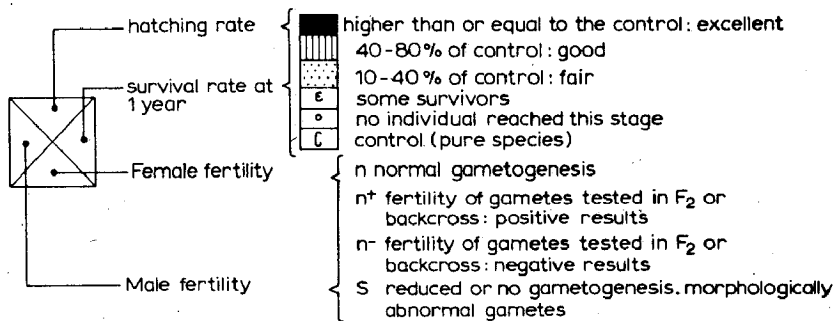
Heterogeneous results present a particularly acute problem in this field. In order to obtain valuable data, a large number of hybrids and controls must be kept until sexual maturity, and this is rarely done. Moreover, the term fertility includes either the idea of egg or milt production or the notion of the viability of these gametes in a new cross (F₂, backcross, triple cross). We have thus used two criteria for fertility in our study (Table III):

- the existence of a gametogenesis, quantitatively reduced or not as compared to the control (comparison of gonadosomatic index);
- the existence of gametes proved viable in a fertilization test; this is usually observed only in hybrids having a gonadosomatic index similar to the control.

TABLE III

Viability and fertility of salmonid interspecific hybrids (From the bibliographic references in Table II)

<div>♂</div> <div>♀</div>		SALVELINUS				SALMO				ONCORHYNCHUS						
		ALPINUS	MALMA	FONTINALIS	NAMAYCUSH	TRUTTA	SALAR	GAIRDNERI	CLARKII	MASOU	RHODURUS	TSAWYTSCHA	NERKA	KETA	GORBUSCHA	KISUTCH
SALVELINIUS	ALPINUS (Char)	C	n ⁺	n ⁺	n ⁺	s	s	o								
	MALMA (Dolly Varden)		C	n ⁺	n ⁺	s	s	o		s	s		o			
	FONTINALIS (Brook trout)	n ⁺	n ⁺	C	n ⁺	e	o	o		s	s	s	s			
	NAMAYCUSH (Lake trout)	n ⁺	n ⁺	n ⁺	C	e	o	e		s	s	s	s			
SALMO	TRUTTA (Brown trout)	s	s	s	n ⁺	C	n ⁺	o		s	s		e	o		o
	SALAR (Atlantic salmon)			e	o	n ⁺	C	o					e			o
	GAIRDNERI (Rainbow trout)	o	e	e	e	e	e	C		e	e		e	o		e
	CLARKII (Cutthroat trout)					n ⁺			C							
ONCORHYNCHUS	MASOU (Masou salmon)		o	o		o	o	o		C	n ⁺		e	o		
	RHODURUS (Biwa S.)		s	s	f	e	e	o		n ⁺	C		e	o		
	TSAWYTSCHA (Chinook S.)											C	e	o	n ⁺	n ⁺
	NERKA (Sockeye S.)		o	e	o	o	o	o		o	o	n ⁺	C	n ⁺	e	e
	KETA (Chum S.)											n ⁺	n ⁺	C	n ⁺	
	GORBUSCHA (Pink S.)											n ⁺	n ⁺	n ⁺	C	
	KISUTCH (Coho S.)			o		o	o	o					e	o	e	C



RESULTS

A synthesis of the main results obtained is presented in Table III.

Intrageneric hybridization

Genus Salvelinus

Most of the crosses appear viable in this genus.

Under hatchery conditions, the brook trout (*S. fontinalis*) has a high growth rate, but is also very subject to diseases such as furunculosis. Crosses with Arctic char (*S. alpinus* and *S. malmas*) which has a lower growth rate but is more hardy, give fertile hybrids having a growth rate intermediary between the parents and a survival rate equal to or higher than the Arctic char.

The cross of *S. fontinalis* with the lake trout (*S. namaycush*) gives the 'splake' and the 'brookinaw', hybrids having an intermediary growth rate and satisfactory survival. The splake (*S. fontinalis* ♂ × *S. namaycush* ♀) has been a very successful substitute for the lake trout decimated by the lamprey in the American Great Lakes (Smith, 1970, 1972).

The cross of the lake trout with the Arctic char gives hybrids with a good rate of survival. Gametogenesis in these various crosses is quantitatively normal. In some cases, the F2 or backcross fry are more fragile than the F1 hybrids. However, as in the case of the splake, the hybrids may be re-crossed for several successive generations during which some traits, such as behavioral patterns or growth rate, can be selected (Smith, 1970).

Genus Salmo

This genus is clearly divided into two sub-groups.

(1) A group in western North America (*Salmo clarki*, *Salmo gairdneri*, *Salmo aquabonita*) is considered as interfertile by several authors. This affirmation is based mainly on field data, especially the observation of hybrids after the introduction of one of the species into a zone already occupied by another species. According to Schreck and Behnke (1971): "There is no known genetic incompatibility between any group of western North American *Salmo*". These hybrids have satisfactory growth and survival rates. On the other hand, there are no exact data available on the fertility of these hybrids. Schreck and Behnke (1971) simply indicate: "it is evident from field observations, that *S. aquabonita* readily hybridize with both *S. gairdneri* and *S. clarki* and the hybrid must be relatively fertile".

(2) A group of Atlantic species (*S. salar* and *S. trutta*) also give viable hybrids. These hybrids (*S. salar* × *S. trutta*) have been thoroughly studied and the following main results obtained can be enumerated as follows:

- (i) hatching and survival rates during the first year seem similar to those of the parental controls when the migratory variety *S. trutta trutta* (sea trout) is used. However, results obtained with the sedentary variety (*S. trutta fario*) are poorer;

- (ii) as mentioned above, hybrid growth also seems very variable;
- (iii) hybridization gives better results with the cross *S. trutta* ♀ × *S. salar* ♂;
- (iv) the fertility of these hybrids is the object of controversy: Piggins (1970) apparently obtained viable F₂, F₃ and backcross fish while most other authors (Winge and Ditlevsen, 1948; Alm, 1955; Nygren et al., 1975) found gamete production to be either abnormal or morphologically normal but with very low fertilization and hatching rates. Nyman (1970), carrying out biochemical studies, confirmed the hybrid character of Piggins' animals, while Nygren et al. (1976) obtained a karyotype identical to that of *S. trutta* for some of these animals. Further experimentation is thus necessary in this field.

Genus Oncorhynchus

The situation seems less clear in this genus because of a lack of crossing experiments. Three groups, however, may be distinguished.

(1) A group of two Japanese species (*O. rhodurus* and *O. masou*) in which reciprocal hybridization gives survival and growth rates equal to or higher than the parental species. However, crosses tried with other species of this genus usually give poor results.

(2) A group of four species (*O. tsawytscha*, *O. nerka*, *O. keta*, *O. gorbuscha*) which may be crossed in numerous ways with varying success. Two hybridizations, *O. keta* × *O. nerka* and *O. gorbuscha* ♀ × *O. keta* ♂, have been extensively studied: in both reciprocal crosses, the first gives fertile hybrids having a satisfactory survival rate and higher growth rate than either of the parents. The second hybridization was carried out on a large scale in the Soviet Union between 1953 and 1958 (Pavlov, 1959); when the hybrids were put into the sea, they attained sexual maturity, the return rates being higher than those of the control, *O. gorbuscha*. However, reciprocal hybridization seemed to produce less interesting results.

(3) It appears necessary to separate *O. kisutch* from the other species since the hybrids obtained are usually not viable. However, these data are taken from old studies (Foerster, 1935), and should be confirmed. The cross *O. kisutch* ♀ × *O. tsawytscha* ♂, which according to Foerster does not reach the eyed stage, gives hybrids having rates of survival and hatching during the first month similar to those of the control *O. kisutch* (Blanc and Chevassus, in press).

Intergeneric hybridization

Genus Salvelinus × *genus Salmo*

Hybridization using *Salmo gairdneri* or *Salvelinus namaycush* as the male or female parent rarely gives high hatching rate; the few fry obtained were not very viable. Thus, we have no data on their fertility.

The two reciprocal crosses *Salmo salar* × *Salvelinus fontinalis* give poor results. However, crosses with *Salvelinus alpinus* do produce interesting

survival and growth rates (Refstie and Gjedrem, 1975; Sutterlin et al., 1977).

The hybrid *Salmo trutta* ♀ × *Salvelinus fontinalis* ♂ (tiger trout) has been thoroughly studied. Its survival and growth rates are intermediary between the parental species and its sterility may be advantageous.

Hybrids between *Salmo trutta* and the chars (*S. alpinus* and *S. malma*) are also sterile, have good survival rates and are characterized by good growth, often higher than that of the parental species (Refstie and Gjedrem, 1975).

Genus Salvelinus × *genus Oncorhynchus*

The data available concern mostly the Japanese *Oncorhynchus* (Suzuki and Fukuda, 1971 a, b, 1973 a, b).

O. masou ♀ was crossed with *S. fontinalis* ♂. Hatching rate was low but later survival rate was much higher than that of *S. fontinalis* control and slightly higher than that of *O. masou* control. On the other hand, growth was low, being about the same as *O. masou*. The adults were sterile, only 5–15% of individuals matured and gave either some tens of abnormal eggs or very little sperm. The gonadosomal index was thus about 2% in these hybrids versus 16–18% in the controls. Reciprocal crosses of *O. masou* × *S. malma* were also done and give about the same results.

O. rhodurus ♀ was also crossed with *Salvelinus fontinalis* ♂. Survival rate was low but both parental species were hard to raise, and therefore comparison was difficult. However, the reciprocal crosses with *S. malma* gave hybrids with equal or higher survival rate than the parents. The fertility of these hybrids was also very low, only 1% for males and 5% for females maturing at 3 years and furnishing a very small number of gametes.

The results on other *Oncorhynchus* are usually negative. Only Uyeno (1972) reports satisfactory survival rate in the cross *O. kisutch* ♀ × *S. fontinalis* ♂. However, the karyotype of these hybrids proved to be identical to that of *O. kisutch*, thus making a real hybridization doubtful. Moreover, Blanc and Chevassus (in press) obtained no hatching with this cross.

Genus Salmo × *genus Oncorhynchus*

Crosses using *S. gairdneri* males usually do not reach the eyed stage. However, *S. gairdneri* ova seem to be fertilizable by the sperm of several species (*O. masou*, *O. rhodurus*, *O. nerka*, *O. kisutch*). Hatching rate is generally good but the hybrids have low survival.

Crosses using *S. trutta* ♀ appear more advantageous concerning future survival. Crosses with *O. masou* ♂ and *O. rhodurus* ♂ lead to 50–70% survival rates between the beginning of feeding and 18 months of age. Hybrid fertility is low, the genital products being scarce and abnormal. However, crosses with *O. nerka* ♂ lead to negative results, as well as those with *S. trutta* ♂.

There are very few data on *S. salar*; the only ones available indicate mortality before hatching of the two reciprocal hybrids with *O. kisutch*.

DISCUSSION AND CONCLUSIONS

The problem of natural hybrids

Most studies on hybridization used artificial insemination, thus eliminating the factors of ecological or ethological isolation between species, in order to test only a possible gametic incompatibility or viability of the hybrid genome when karyogamy occurs. However, some authors refer to natural hybridization between the species studied. If these species follow the biological definition of Mayr, such hybridization is bound to be rare. In cases where hybridization rate has been measured, it has been shown to be low. Payne et al. (1972) reported a hybridization rate of 0.4% between *S. trutta* and *S. salar* in English rivers. Moreover, hybrid identification, based on numerical or morphological traits (Ivankov, 1973; Honma, 1974), is not always confirmed by the more exact techniques of karyology or biochemistry (Uyeno, 1972; Nygren et al., 1975).

However, the frequency of natural hybrids may increase considerably in some cases. Thus, *S. gairdneri* and *Salmo clarki*, which are found in sympatry in the zone where their geographical territories overlap, frequently hybridize when one species is transplanted into a zone where only the other existed before (Behnke, 1968). Thus, it may be that when there is gametic compatibility, such hybridization does occur between totally allopatric species artificially grouped in the same environment. This should lead to great prudence in introducing an allopatric species into an environment already populated with salmonids.

Hybridization and classification

The success of hybridization has often been considered as an indication of the evolutionary relationship between two species (Hester, 1970). In that case, there should be some classification relationship involved in successful hybridization. This seems to be true since a major difference separates intra- and intergeneric hybrids. In 43 hybridizations between species of the same genus, 18 can be classed as equivalent to the control concerning hatching rate, while this is the case for only three of the 46 hybridizations cited between different genera. Moreover, interspecific hybrids lead to a qualitatively normal gametogenesis, even if the gametes obtained are not very viable. On the other hand, intergeneric hybrid fertility is extremely low, the few gametes obtained always being inviable (Suzuki and Fukuda, 1973 b). These conclusions, however, are not definitive because, out of 66 interspecific hybridizations, only 43 (55%) were studied, while only 50 out of 144 (34%) intergeneric hybridizations were observed.

Moreover, some observed cleavage between species of the same genera are in agreement with suspected phylogenetic separation. This is the case in the genus *Salmo* in which Atlantic (*S. salar*, *S. trutta*) and Pacific (*S. gairdneri*,

S. clarki) species are clearly separated by hybridization data and are often considered as two subgenera, *Salmo* for Atlantic species and *Parasalmo* for Pacific species.

Hybridization and karyotype

A comparative study of karyotypes has often also been considered as an indication of phylogenetic relationship between species (Simon, 1963). There is a very large diversity of diploid number in salmonids, going from $2n = 84$ in *S. fontinalis* and *S. namaycush* to $2n = 52$ in *O. gorbuscha* (Table IV). However, successful hybridization does not appear to depend on similar chromosome number since besides viable hybrids between species having the same diploid number, as the splake, equally viable hybrids are also found between species with very different karyotypes (*O. keta* ♂ × *O. gorbuscha* ♀). In all cases, the hybrid has a karyotype representing the sum of the haploid stocks of both species (Lieder, 1956; Rees, 1967; Sasaki et al., 1968; Capanna et al., 1973; Gjedrem et al., 1977).

Other authors also believe that karyotype similarity is necessary for the process of meiosis and the production of viable gametes. Nygren et al. (1975) blamed difficulties in chromosome pairing for the low viability of gametes for the hybrid *S. salar* × *S. trutta*, the diversity of the karyotypes of some survivors of the backcross on *S. salar* supporting this hypothesis. However, this is not always a problem because viable second-generation hybrids are reported in species different karyotypes (Alm, 1955; Terao et al., 1965). A karyological study of these F₂ hybrids would thus be very profitable.

TABLE IV

Diploid number and arm number (BN) in Salmonidae

Species	$2n$	BN	Reference
<i>Salvelinus alpinus</i>	80	100	Nygren et al. (1971)
<i>Salvelinus fontinalis</i>	84	100	Uyeno (1972)
<i>Salvelinus namaycush</i>	84	100	Wahl (1960)
<i>Salmo trutta</i>	80	100	Nygren et al. (1971)
<i>Salmo salar</i>	58	74	Nygren et al. (1972)
<i>Salmo salar</i>	54–57	72	Roberts (1968, 1970)
<i>Salmo gairdneri</i>	60	104	Simon and Dollar (1963)
<i>Salmo clarki lewisi</i>	64	106	Simon and Dollar (1963)
<i>Salmo clarki clarki</i>	70	106	Simon (1964)
<i>Oncorhynchus masou</i>	66	*	Chernenko and Viktorovskiy (1971)
<i>Oncorhynchus tshawytscha</i>	68	104	Simon (1963)
<i>Oncorhynchus nerka</i>	56	102	Simon (1963)
<i>Oncorhynchus nerka</i>	58	104	Sasaki et al. (1968)
<i>Oncorhynchus keta</i>	74	102	Simon (1963)
<i>Oncorhynchus gorbuscha</i>	52	104	Simon (1963)
<i>Oncorhynchus kisutch</i>	60	112	Simon (1963)

*Not recorded.

Similarity of diploid number does not appear to be a prerequisite for successful hybridization. This observation agrees with the conclusions of Simon, (1963), Rees (1964) and Pegington and Rees (1967). Basing their findings on the relative consistency of the arms number (NF) and of the DNA content of nuclei, these authors believed that karyologic diversity in salmonids consisted of secondary changes (centric fusion, pericentric inversion) and not of alterations in the overall amount of genetic material, as initially hypothesized by Svårdson in 1945.

Hybridization and fish-farming

The first studies on hybridization often produced spectacular results, especially as concerned growth. According to Skinner (1938), the hybrid *S. salar* ♀ × *S. trutta* ♂ reached 5 lb (approx. 2.3 kg) in its fourth year, the control *S. salar* reaching at best 1.5 lb (approx 0.7 kg).

However, later studies have not generally confirmed these observations, and at present it seems that in most cases the hybrids raised in the same conditions as the parental species shows intermediary or, at best, equal growth to that of the better of the parents. Better results have been found for survival rate, the hybrid often being similar, or even superior, to the most hardy species. The result is that, while it is never superior to the parental species for a given criterion, the hybrid does represent an interesting compromise, as for example between fragile, rapid-growing species and more hardy slow-growing species. This is the case in the hybrid *S. fontinalis* ♀ × *S. malma* ♂, uniting a more rapid growth than *S. malma* with a better survival than *S. fontinalis*; the result is higher productivity than either of the parental species (Table V).

Moreover, this advantage may be expressed only in certain breeding conditions. From this viewpoint, it should be advisable to test hybrid aptitudes in a large range of environmental conditions and breeding methods.

With respect to the control of reproduction, the almost total sterility of intergeneric hybrids has already been mentioned. This property may be ad-

TABLE V

Hybrid traits of *Salvelinus fontinalis* × *Salvelinus malma* (from Suzuki and Fukuda, 1971b)

Cross	Survival rate (%) from 3 months to 3 years	Mean weight at 3 years (g)	Ponderal production at 3 years for 1000 3-month-old fry (kg)
<i>S. fontinalis</i> (control)	2	850	17
<i>S. fontinalis</i> ♀ × <i>S. malma</i> ♂	58	150	261
<i>S. malma</i> ♀ × <i>S. fontinalis</i> ♂	43	370	159
<i>S. malma</i> (control)	55	300	165

vantageous, providing that the hybrid has favorable traits otherwise. Particularly important are the problems involved in the sexual maturation of individuals raised in the sea (delayed growth, fragility, loss of quality), and they could perhaps be solved in this manner. Therefore, with this in mind, a very thorough investigation of the intergeneric hybridization is needed as many crosses still remain to be studied.

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