HOMING AND OLFACTION IN SALMONIDS:
A CRITICAL REVIEW WITH SPECIAL REFERENCE TO
THE ATLANTIC SALMON

By OLE B. STABELL

*Institute of Zoophysiology, University of Oslo, Blindern, Oslo 3, Norway**

CONTENTS

* Present address: Institute of Fisheries, University of Tromsø, P.O. Box 3083 Guleng, N-9001 Tromsø, Norway.

I. INTRODUCTION

Considering the large amount of literature published on salmonid homing, an additional review may seem initially unnecessary. However, some interesting information revealed from the literature, indicates the necessity for an evaluation of the field with special attention paid to the function of olfaction.

Previous reviews in the field of homing (Scheer, 1939; Hara, 1970; Hasler, Scholz & Horral, 1978; Cooper & Hirsch, 1982) and migration (Harden Jones, 1968; Banks, 1969; Leggett, 1977) give useful surveys of the existing literature. All these reviews, however, adhere to established theorems in the field which should not necessarily be accepted as such. The purpose of this article is to reconsider some of these established theorems, and if possible to add some new dimensions, by a re-examination of the basic data.

As a starting point, the 'parent' or 'home-stream' theory will be reviewed. Only data on wild smolt or fingerlings, however, marked and released in their native river or tributary, will be considered. The reason for this lies in genetic considerations, which will be shown to be of great importance in homing. Some basic ecological arguments for isolated river populations will be presented, and data from genetic studies, based on modern biochemical techniques, will be viewed in the light of the 'home-stream' theory. A presentation of currently accepted hypotheses in salmonid homing will then be given, and their validity evaluated on the basis of the natural ecology of the species.

Transplantation experiments in salmonid homing, i.e. the use of non-native eggs, fingerlings and smolt in homing experiments, will subsequently be examined and related to genetic considerations. Further, based on the information revealed, recent studies in fish behaviour, olfactory electrophysiology and analytical chemistry will be evaluated. Conclusions from artificial 'imprinting' experiments will then be re-examined. Finally, homing in salmonids will be discussed in the light of current information in olfaction and salmonid genetics, together with its application to salmonid management.

II. THE 'HOME-STREAM' THEORY

(1) Homing in native fish

The homing of the Atlantic salmon (*Salmo salar* L.) has been considered as one of the most spectacular mysteries in biology. Already in the 16th century, Norwegian

fishermen had their own interpretation of the salmon life-history and navigation. Their remarkable tales were quoted by the priest Peder Clausson Friis in 1599 (Storm, 1881).

In modern history the precise return of the salmon to its native river (i.e homing) has been subjected to extensive scientific observation. Before the Second World War the topic appeared in the literature as the 'home-stream' or the 'parent-stream' theory. In Scotland, marking of wild smolt was started in the River Tay as early as 1903. Through the years, 110 recaptures were made in the Tay, and no recaptures were reported from any other river (Calderwood, 1922, 1940). This record agreed with the view that the Atlantic salmon returns to its natal river.

In the late nineteen-thirties a broad discussion developed on the 'parent-stream' theory. This was initiated by a statement from Huntsman (1937): "I have failed to find a single clear case of salmon returning to its natal river from distant places in the sea, that is, away from the neighborhood of its river mouth." Up until then no fish had been marked as smolt in its native river, registered in the open sea, and then released to be recaptured again in its home river. Rich (1937a, b) connected the concept of 'homing' to the concept of 'local races' in an argument against Huntsman's statement: "There is ample evidence, both observational and statistical, of intraspecific racial segregation in the Pacific salmon. The development and maintenance of such races could not take place if there were much intermingling of the population groups on the spawning grounds."

Calderwood (1937) supported the latter by pointing to a great deal of circumstantial evidence for the existence of separate races of Atlantic salmon in the British Isles. The concepts of 'homing instinct' and 'local races' were also supported by Dahl (1939), and again by Scheer (1939) and Shapovalov (1941). The debate had in fact already been terminated by an article of Huntsman (1939) where he explained that his doubt in the matter had been related only to the return from *distant* places in the sea. Concerning the 'home stream' theory he stated: "I have never expressed a doubt that salmon return on the whole to their native rivers, and indeed I see evidence that such return is, in some cases at least, practically perfect." The evidence on return from the high seas was later reported by Huntsman himself (Huntsman, 1942), and has later been verified in other reports (i.e. Neave, 1964; Carlin, 1969b; Rosseland, 1971).

How accurately does a salmon return to its natal river? This question should be answered carefully. When eggs, parr or smolt are transplanted from one river to another, the river of release is not the native river of the fishes. Transplantation experiments may give useful information on salmon homing and navigation, as will be seen in a later chapter. The correct answers, however, lie in data from natural systems unaltered by man. This implies that only data from experiments on wild fishes can be taken into consideration. The production of artificially propagated fishes of native origin may unintentionally result in a mixing of genetic strains existing within the river. Such mixing may interfere with homing ability, and data resulting from the use of these fish must therefore be considered unreliable. Surprisingly this simple fact seems to have been overlooked by many investigators.

When comparing results from marking experiments, three basic pieces of information are needed: the number of fishes marked, the number of fishes recovered in the river of release, and the number recovered in other streams. The marking systems used naturally put limitations on the recovery data. When fin-clipping is used, the only

reliable data are usually those from the river of release. Tags, on the other hand, give advantages both with respect to data on straying rate and high-sea fishing. Straying rate (SR) here means the ratio:

$$SR = (RR \times 100)/TR,$$

where RR are the number of fishes recovered in streams other than the one of release, and TR represents the total number of fishes recovered in streams. (It should be noted that straying rate equals the percentage of fish recovered in streams other than the one of release from the total stream catch. The expression *percentage* is, however, omitted to avoid confusion with percentages of recovery from those released.)

Table 1 presents data, found in the literature, from 'homing' experiments on native, wild Atlantic salmon. As can be seen, the recovery of fishes in their native stream varies between 1 % and 3·4 % of those released, the only clear exception being experiment no. 7. Very little straying is registrated in the above experiments, the exception again being experiment no. 7. Concerning the straying rate stated in experiment no. 14, Table 1, it should be noted that the cases registered were all within the native watershed. A maximum straying rate of three appears to occur in Canadian and Norwegian rivers. This figure also agrees with data from rivers on the west coast of Sweden where straying rate is less than one (Carlin, 1969a), and with data from Britain and Ireland where straying rate averages 2·7 and 3·0, respectively (Thorpe & Mitchell, 1981).

Data on Baltic salmon (*S. salar* L.) show a straying rate of approximately two (Carlin, 1969a). This figure is, however, regarded as high by Carlin, who proposed that the higher straying of Baltic salmon is influenced by the fact that the tagged fish have nearly all been hatchery smolts, sometimes with a very complicated life history. These data are therefore omitted to avoid confusion.

(2) Ecological confirmation of 'stocks'

From the bulk of literature published on racial segregation in salmonids, a substantial amount indicates that, within a species, reproductively isolated 'stocks' (i.e. sympatric conspecific populations) may be present in a river system. Tributary homing was described for chinook salmon (*Oncorhynchus tshawytscha*) by Rich & Holmes (1928). For the *Oncorhynchus* species in general, a broad review has been given by Ricker (1972).

Reproductive isolation among different populations within the salmonid species was observed many years ago. Concerning the Atlantic salmon, Berg (1934) attributed part of the phenomenon to 'seasonal races'. In northern Russian rivers, two forms of Atlantic salmon were distinguishable, a summer and an autumn form. The *summer* form enters the river in the summer with well-developed sexual products and lays its eggs the same autumn. This form he named a *vernal* race. The *autumn* form return to the river in the autumn with weakly developed sexual products, and lays its eggs in the autumn of the following year. This form he named a *hiemal* race. Berg also pointed out that the fish in the hiemal (autumn) race are of a larger size and usually migrate far up river, while those in the vernal (summer) race are usually small and do not migrate far upstream. Through indirect evidence he rejected the idea that these forms could mingle on the spawning grounds. Atlantic salmon returning to the rivers more than 1 year before spawning have also been reported to occur among the Ungava Bay stocks, in north-eastern Canada, by Power (1981). A general discussion on the origin of seasonal races has been provided by Birman (1981).

Table 1. *Homing experiments with naturally propagated Atlantic salmon, tagged and released within their native river*

Exp. no.	River	Region	Year	Mark used	No. released	Total Recovered No.	%	Recovered in stream of release No.	%	Recovered in other streams No.	%	Straying rate	Reference
1	N.W. Miramichi Dungarvon	New Brunswick	1950–61	Fin-clipped	174509	—	—	2425	1·39	—	—	—	Stasko et al. (1973)
2	S.W. Miramichi Cains	New Brunswick	1950–56	Fin-clipped	78117	—	—	820	1·05	—	—	—	Stasko et al. (1973)
3	S.W. Miramichi	New Brunswick	1958–60	Fin-clipped	17145	—	—	224	1·31	—	—	—	Stasko et al. (1973)
4	N.W. Miramichi	New Brunswick	1960–65	Tag	41614	1005	2·42	840	2·02	0	0	0	Stasko et al. (1973)
5	N.W. Miramichi	New Brunswick	1966–69	Tag	48763	1996	4·09	1648	3·38	0	0	0	Stasko et al. (1973)
6	Miramichi	New Brunswick	1968–69	Tag	12105	275	2·27	147	1·21	0	0	0	Stasko et al. (1973)
7	Magaree	Nova Scotia	1962–69	Tag	5418	42	0·78	9	0·17	1	0·02	10·00	Stasko et al. (1973)
8	West	Nova Scotia	1968–69	Tag	4800	67	1·40	56	1·17	1	0·02	1·75	Stasko et al. (1973)
9	N.W. Miramichi	New Brunswick	1962	Tag	5612	181	3·23	120	2·14	3	0·05	2·44	Saunders (1967)
10	Loneelv	Norway	1956–62	Tag	3929	444	11·30	94	2·39	3	0·08	3·09	Rosseland (1965a)
11	Big Salmon	New Brunswick	1967–71	Carlin-tag	30462	286	0·94	—	0·87	—	—	—	Jessop (1976)
12	Ellidaár	Iceland	1975	Micro-tag	2100	—	—	216	10·29	—	—	—	Ísaksson et al. (1978)
13	Tay	Scotland	1905	Silver wire	5500	—	—	110	2·00	0	0	0	Calderwood (1922)
14	Conon	Scotland	1963–66	Plastic tag	4710	168	3·57	109	2·31	27	0·57	19·85	Mills & Shackley (1971)

Saunders (1967) marked Atlantic salmon smolt on their seaward migration at two counting fences, 33 miles apart, in north-west Miramichi river, New Brunswick. Registration of returns at the same counting fences demonstrated that the adult Atlantic salmon appear to home to that part of the river in which they resided as juveniles. Reports on separate spawning grounds for populations of Atlantic salmon within a river have been given by Jones & King (1946), Went (1949), Berg (1964) and Elson (1973), and for steelhead trout (*Salmo gairdneri*) by Smith (1960, 1969). Precise homing to small tributaries within a watershed has been reported for brown trout (*S. trutta*) by Stuart (1957) and by Tilzey (1977).

As for sockeye salmon (*O. nerka*), temporary obstacles do not hinder it from making attempts to enter the native tributary (Ricker & Robertson, 1935). In fact the tributary-homing tendency in sockeye is very strong, and very few fish chose alternative spawning areas if prevented from entering their native ones. Blocking of the ascent possibilities for the fish may even result in repeated attempts to enter until their eventual death (Hartman & Raleigh, 1964). Pink salmon (*O. gorbuscha*) also demonstrate a predictable pattern of return to specific areas of the stream at specific times (Helle, 1981).

A huge amount of literature could be cited in evidence for 'the stock concept'. Recently, articles summarizing and focusing the topic have been published in the *Proceedings of the Stock Concept International Symposium (STOCS)* convened at Alliston, Ontario 1980 (*Canadian Journal of Fisheries and Aquatic Sciences* 38, no. 12, 1981). Regarding the concept of populations and specific spawning grounds, the papers of Altukov (1981), Altukov & Salmenkova (1981), Helle (1981), Larkin (1981) and Utter (1981) should be especially consulted.

Concerning the Atlantic salmon in particular, the statements by Saunders & Bailey (1978) are relevant: "Each salmon river has its own stock, many medium or large-sized rivers have a number of stocks, one or more in each tributary. There may be separate stocks along the main stem of a long river...The phenomenon of homing in anadromous salmonids coupled with natural selection in response to environmental variation has resulted in the development of numerous stocks which often show obvious differences in physical, physiological and behavioural traits. Homing assures that the majority of a stock returns to its natal stream for spawning thereby maintaining a more or less discrete genetic pool. Genetic differences which develop in a stock through natural selection or genetic drift are thereby maintained and strengthened as a result of relative isolation."

(3) *Biochemical genetics in 'stock' identification*

Modern biochemical techniques have recently been used in studies on racial segregation in salmonids. Gel electrophoresis of tissue or plasma proteins has been used most frequently.

Nyman (1966) found significant differences in the blood serum protein pattern of Atlantic salmon from eastern Canada and Sweden. In neither case, however, could any variation be detected within the sample pools. Nyman (1967) and Nyman & Pippy (1972) later reported differences in serum proteins and liver esterases between Atlantic salmon from Sweden, Norway and Canada. The genetic significance in the variation found was demonstrated in a sample of hybrids between Canadian and Swedish salmon. Also Wilkins (1968) found significant length-correlated variations of anodic haemoglobin components in Atlantic salmon from Scotland, Greenland and Canada.

Møller (1970) found three main patterns of transferrins, made up of two molecular

types, in plasma from hatchery-reared and wild Canadian Atlantic salmon. Using this three-pattern system, similarities in gene frequencies were found in smolt and adult salmon from the same locality. Statistically significant differences that were found between fish from different sample sites gave support to the conclusion that differences between populations existed. In the Miramichi river, significantly more homozygotes than could be predicted from a Hardy-Weinberg distribution were found. This additional result strongly suggested that several genetic populations were present in the river.

Transferrin polymorphism of four proteins, leading to eight phenotype groups, was discovered by Payne, Child & Forrest (1971). Three of the phenotypes were observed in populations of Atlantic salmon sampled in Britain and Ireland. In Canadia samples, one of the 'European' transferrin phenotypes was present, together with four additional ones. Gene exchange between European and North American rivers was therefore concluded to be negligible or non-existent. The authors also found that a sharp transition occurred in Ireland with regard to the gene frequency of one of the alleles. This finding led to the conclusion that, according to the frequency of this particular gene, the salmon of the British Isles are sharply divided into two distinct races, named 'Boreal' and 'Celtic'. The presence of two races of salmon in the British Isles was also supported by Child, Burnell & Wilkins (1976).

A number of biochemical and serological characters in Atlantic salmon were investigated by Wilkins (1971). Differences were found between north American and European samples for at least some of the characters. Seven distinct patterns of non-specific esterases were obtained, each pattern comprising a number of individual bands exhibiting esterase activity. The esterase results indicated that, within the British Isles, the proportions of the different phenotypes may vary between the populations spawning in different watersheds.

On the biochemical genetics of the Atlantic salmon up until the early seventies, reviews were provided by Wilkins (1972a, b). He concluded that the polygenetic variation found in some protein systems studied, together with analyses of phenotype ratios and allele frequencies, indicate that the populations of different river systems are genetically distinct.

Altukov & Salmenkova (1981) reported differentiation in protein phenotype frequencies between river populations of Atlantic salmon in the northern European part of the USSR. In addition, genetic subdivision was displayed in most of their populations during the spawning run. Also sockeye salmon (*O. nerka*) stocks have been identified by use of biochemical genetics, as reported by Grant *et al.* (1980).

Combined studies on several protein systems were carried out on genetic variation in brown trout (*Salmo trutta* L.) by Allendorf *et al.* (1976). Brown trout from four lakes in northern Sweden were examined at ten electrophoretically detected loci, and genetic variation was found at three of them. Absence of heterozygotes at one locus, together with significant correlations to allele frequencies at another, and to body size, provided evidence of two genetically isolated populations in one lake. Large allele frequency differences found between brown trout from different lakes gave additional evidence of a large genetic differentiation in populations within a small geographical area. Allozyme evidence for at least three reproductively isolated sympatric populations of brown trout in Laugh Melvin, Ireland, has been given by Ferguson & Mason (1981).

Ryman & Ståhl (1980) found genetic differences between hatchery stocks of brown

trout and natural populations of corresponding stocks. Highly significant allele frequency changes were found in the hatchery fishes, which indicated considerable lack of intra-stock genetic homogeneity. The result was presumed to be mainly due to the use of too few parents in the founding and perpetuation of the stocks. Their data revealed that hatchery stocks may rapidly lose the genetic variability they were intended to preserve. Results similar to those mentioned have also been obtained within a hatchery stock of cutthroat trout (*S. clarci*) by Allendorf & Phelps (1980).

Using allele frequency distributions at 45 electrophoretically detectable loci, Ståhl (1982) applied the above-mentioned techniques to wild Atlantic salmon from northern Swedish rivers. His data revealed that Atlantic salmon are naturally subdivided into genetically distinct subpopulations, between and within major drainage areas. In addition, the data indicated that to maintain this genetic homogeneity within sub-populations of 2500 to 10000 individuals, the effective migration rate between the populations examined has to be less than one individual per year.

III. HYPOTHESES IN SALMONID HOMING

The phenomenon of homing in fishes is one major link in the chain for maintaining reproductively isolated populations (Behnke, 1972; Saunders & Bailey, 1978). Still, the concept of homing has traditionally been considered in isolation from the field of genetics. Numerous hypotheses have been postulated through the years in attempts to explain the mechanism behind fish navigation. This article will not dwell upon them all, but rather emphasize the basic ones which have been most commonly accepted.

The navigation ability during homing in anadromous salmonids, and the hypotheses related to it, have long been divided into two stages (Huntsman, 1937). A distinction has traditionally been made between navigation in the sea, i.e. in ocean and coastal regions, and navigation adjacent to or within the home river system (Hasler, 1960, 1966; Hasler *et al.*, 1978; Harden Jones, 1968). Division of the navigation ability indeed gives the writer several advantages. This tradition will therefore be followed in the first two sections, breaking with it in the third when navigation ability during homeward migration will be regarded as a single process.

(1) *'Stream' orientation*

(a) *The imprinting hypothesis*

The sense of smell in fishes and their reaction to olfactory stimuli were described by Parker (1910, 1911) and Parker & Sheldon (1913). Before then, questions had been raised about the olfactory sense in migrating species as a factor for detection of their home stream by Buckland (1880), and was raised again by Chidester (1924).

Hasler & Wisby (1951) demonstrated that bluntnose minnows (*Hyborhynchus notatus* Raf.) could be conditioned to respond to water from two Wisconsin creeks. After destruction of the nose tissue, the fish were no longer able to distinguish between the water samples, pointing to olfaction as the sensory basis used in detection. By testing the fish with various fractions of the water separated by distillation, the authors concluded that the active material was some volatile organic substance. A 15-week odour memory was also demonstrated. The condition technique was later applied to coho salmon fry (*O. kisutch*) by Wisby (1952), confirming the odour discriminating ability also in salmonids.

From the above results Hasler & Wisby (1951) introduced a hypothesis of salmonid

migration, later known as *the 'imprinting' hypothesis*. This hypothesis postulates that river and creek water contain some characteristic odours, to which the young salmon become *conditioned* (or imprinted) while in the stream, and which they recognize and orientate to, upon reaching the parent stream as mature migrants. Aquatic plants and soil have been suggested as the origin of these stream odours (see also Hasler, 1954, 1960; Hasler & Larsen, 1955; Hasler *et al.*, 1978).

Wisby & Hasler (1954) demonstrated that the olfactory sense is necessary for salmonids in their fresh water navigation. They captured coho salmon (*O. kisutch*) during their upstream spawning migration in Issaquah Creek and its east fork. The olfactory pits were occluded in one-half of the groups, and all fish were displaced to Issaquah Creek below the junction of the two streams. The control salmon, unlike the anosmic ones, displayed a significant ability to repeat their original choice at the stream junction. The importance of olfaction in the stream phase of homing in fishes has later been confirmed by Gunning (1959), Collins, Trefethen & Groves (1962), Lorz & Northcote (1965), Groves, Collins & Trefethen (1968) and DeLacy, Donaldson & Brannon (1969). See Stasko (1971) for review.

At this point it is worthwhile noting that the previously mentioned 'imprinting' hypothesis (Hasler & Wisby, 1951) is founded on a demonstrated chemical divergence between creek waters and the possibility of conditioning fishes to them, together with a hypothetic use of 'imprinting' by the fish themselves in wild life. The ability for olfactory discrimination in streams, however, as demonstrated by Wisby & Hasler (1954), is not necessarily bound to an imprinting theory, and the link that is commonly suggested in the literature is a purely theoretical one.

Some large-scale experiments, based on 'imprinting' to artificial odours, have been carried out during the last decade in relation to migration in salmonids. With respect to the natural ecology of fishes, these experiments form a special approach, and in order to avoid confusing the reader, the artificial 'imprinting' experiments will be discussed in a separate section (VI. The morpholine approach).

(b) The pheromone hypothesis

White (1934) suggested that the presence of young salmon in a stream is one factor that causes adult salmon to select their spawning stream. His idea was based on experiments in Forbes Creek and Apple river, Nova Scotia. In Forbes Creek he released several hundred Atlantic salmon parr one autumn. The following year he found many of these parr in the region where they were released, and three adult salmon ascended the stream that year. This was the only time during his investigation that adult salmon were found in that area.

In the barren east branch of the Apple river, Atlantic salmon fry were introduced in 1932 (White, 1934). After the introduction of the fry, unmarked adult salmon ascended the east branch in 1932, 1933 and 1934. Spawning of these fish was confirmed by the occurrence of their offspring in the stream the following season.

White proposed that the milt from the precocious male parr was the source of attraction to the adult salmon. Since the male parr mature during the autumn, and salmon enter some of the rivers during spring and early summer, this proposition, together with his first suggestion, have been rejected by several investigators in the field (i.e. Hasler & Wisby, 1951; Stasko *et al.*, 1973; Gardner, 1976).

Working with arctic char in the Salangen river system, northern Norway, Nordeng

(1971) found that individuals of the migratory population returned exclusively to this system. Tagging in the fjord, on the other hand, indicated that the char from both Salangen and other river systems mixed in the sea. He then transported artificially fertilized eggs from the Salangen migratory populations to a hatchery in southern Norway, where they were hatched and reared for 3 years. Individuals of this population were then brought back to the Salangen area, where they were released in the estuaries of Salangen and Løksebotn rivers. The recovery data clearly indicated that the fish preferably return to their parents' stream. The fish in the experiment had never experienced the water from their parents' river. Based on this fact, Nordeng (1971) proposed that the released fish were attracted to the Salangen river system by *attractants* (pheromones) released by their relatives in that system.

The *'pheromone'* hypothesis (Nordeng, 1971) was supported by some casual observations made in the previously mentioned hatchery in southern Norway when rearing the migratory population from the Salangen river system. Immature individuals were tagged and released in a lake below the hatchery. A fortnight later, a great number of these fish were observed under the floor of the hatchery, standing at the outlets from the tanks containing the rest of the population. Individuals from the large population of the local stationary char were not observed.

Solomon (1973) gave support to the 'pheromone' hypothesis with data on Atlantic salmon from rivers of the Bristol Channel area. He suggested that in general the presence of salmon parr in a river renders its estuary attractive to migrating adults, and that a metabolic product of a discrete population secures homing of the fish. Gardner (1976) questioned the possibility that juvenile salmon are essential for successful homing, with the argument that barren streams may become repopulated. Evidently, the 'barren stream' argument can be used to turn down most homing theories, including the one related to 'imprinting'. Since, however, the argument does not discriminate between natural dissemination, possibly due to straying and resulting over time, and the precise homing by the majority of fish within each generation to their native river, it must be classified as invalid. Concerning returns after stocking, I could find no evidence in the literature of transplanted fishes of the genus *Salmo* returning to a stream in which the absence of conspecifics could be proven.

Tilzey (1977) observed a high percentage of homing in brown trout (*S. trutta*) to Swamp Creek, an inlet of Lake Eucumbene, Australia. The homing ability had developed since the species was introduced to the river system in the late 19th century. Just before the 1971 spawning season, nearly all non-migrating, resident brown trout in Swamp Creek were removed by rotenon treatment of the stream, resulting in a steep fall in the 1971 homing percentage. Tilzey suggested that the high degree of homing evident in Eucumbene resulted from genetic isolation within the brown trout population, and that genetics may play a significant role in stream recognition.

(2) *Orientation in ocean and coastal waters*

(a) *The visual sense*

Hasler & Wisby (1958) suggested that fishes are able to orientate by aid of the sun. They displaced white bass (*Roccus chrysops*) up to a distance of 2·4 km from two principal spawning grounds 1·6 km apart in Lake Mendota. Fish released at the spawning ground were recaptured at the same rate as those displaced and released

mid-lake, pointing to a fairly good homing orientation. When floats for tracing were attached, the fish generally moved north from the centre of the lake when released on clear days. On cloudy days, or if the fish were blinded with eyecaps, they moved at random.

A laboratory analysis of the sun-compass mechanism was subsequently made (Hasler *et al.*, 1958). A specimen of *Lepomis macrochirus* was trained at a specific time of the day to find cover in one of sixteen boxes in a circular tank. When trained, the fish entered the training box in a consistent compass direction at any time of the day. Under an overcast sky the choices were completely disorientated. When tested under an artificial sun, the fish responded as though it was the real sun and sought cover in the 'artificial' direction.

Hasler *et al.* (1958) concluded that their field and laboratory experiments strongly suggested that the sun serves as a point of reference, and that the individual fish compensates for its movement by a biological chronometer. Based on the above results the authors also proposed that orientation involving the use of a sun-compass could play a role in homing behaviour of migrating fishes. Braemer (1960) proposed that a quantitative computation of the sun's movement (sun azimuth), affected by the length of the day and the sun's altitude, could be used by the fish in their orientation. His proposition has later been supported by studies of Hasler & Schwassmann (1960) and Schwassmann & Hasler (1964).

The above-mentioned laboratory experiments clearly reveal that fishes have the ability to use the sun as a visual clue. The field experiments performed, however, raise doubts as to the use of the demonstrated orientation ability in natural systems. In the field experiment carried out by Hasler & Wisby (1958), no evaluation was made for the participation of other sense organs than vision in the fish orientation behaviour. In fact, the authors themselves questioned their results by pointing out that differentiation between the two spawning areas apparently took place by mechanisms other than with the aid of the sun. Leggett (1977) also pointed out that conclusive evidence on the use of a sun-compass by the fish in their natural environment has been more difficult to obtain.

Neave (1964) questioned the use of celestial features in salmon navigation. In this respect he had one serious objection. How could a useful compass direction towards a small coastal area be established without some information on the position from which the course is taken? Saila & Shappy (1963) had proposed that homing could be accomplished by random or near-random ocean travel. This was rejected by Neave who pointed out that salmon journeys give the impression of concerted, well timed migrations in a consistent direction, rather than a search for clues by individuals who have 'landed' haphazardly along a vast coastline.

Neave reached the conclusion that throughout the period of ocean life, some awareness of position in relation to the place of origin must be maintained, pointing to the requirement of a bicoordinate system in salmonid navigation. The 'chronometer', proposed by Hasler *et al.* (1958), required for such navigation would have to be capable of telling not only the local time of day but also of comparing local time with 'home' time throughout changing seasons. Neave therefore characterized the suggestions of chronometer navigation as purely speculative. It can be added that a chronometer of the kind proposed would have to be much more accurate than any 'biological clock'

as understood in everyday terminology. Even man had great problems determining longitude in seaward navigation before the invention of the first exact chronometer (Brown, 1956).

As pointed out by Royce, Smith & Hartt (1968), salmon migrate at night as well as during the day and through regions where clouds obscure the sun almost continuously. In addition the salmon migrate along circular as well as straight routes. This circumstantial evidence casts doubts on sun orientation as a primary navigation mechanism.

(b) The olfactory sense

The first step in attempts to explore the role of olfaction in coastal navigation by salmonids was made long ago. Craigie (1926) impaired the olfactory nerves of 259 migrating sockeye salmon (O. nerka), probably on their way to the Fraser river, British Columbia. Together with 254 tagged control sockeye, the fish were released in Deep Water Bay on the east side of Vancouver Island. Three of the control fish and 14 of the operated ones were recaptured in Deep Water Bay. Another 62 controls and 28 operated fish were also recaptured; of these, 59 controls and 23 operated fish were taken in the Fraser river, its tributaries, or near its mouth. Craigie concluded that elimination of the olfactory sensibility appears to interfere to some extent with the migration of sockeye salmon.

Clemens, Foerster & Pritchard (1939) reported results quite similar to that of Craigie (1926). These authors concluded, however, that making due allowance for some physiological disturbance resulting from the operation, the fish evidently were able to make their way to the Fraser river without the use of the olfactory organ.

Bertmar & Toft (1969) impaired the olfactory sense in Baltic salmon (S. salar) captured in River Indalselven, Sweden. The olfactory sense in 191 grilse was eliminated by cutting off the olfactory nerves or cauterizing with a soldering iron. One hundred fish traumatized on the nose and 100 untreated fish served as controls. The fish were then displaced and released in the Sundsvall Bay area 35–40 km north and south of the home river. The traumatized fish orientated towards the home river to the same extent as the untreated controls. Most of the operated fish, however, became disorientated and were caught along the entire coast of the Bothnian Gulf or in the Sundsvall Bay area. Only two neurotomized fish homed together with six cauterized ones. The authors proposed that the burning of the olfactory epithelium in the latter cases might have been inefficient. The results indicated an important role of olfaction in coastal orientation and homing behaviour of Baltic salmon.

The results from the Baltic salmon navigation were confirmed by Toft (1975) in studies on the role of olfaction and vision in spawning migration. In total, 1276 grilse, distributed within five treatment groups, were used in displacement experiments in the Bothnian Gulf area, out of which 451 were recaptured in the spawning season. The data revealed that the tagged controls resumed their spawning migration to the home stream, no matter if released to the north or to the south of its estuary or even in another river. Grilse injured by burning the dorsal side of the rostrum showed the same behaviour after release as the intact ones. Grilse with a destroyed olfactory sense, however, homed at a significantly lower rate than intact fish, when displaced up to a distance of 200 km away from their home river, or even if released in the estuary. Grilse neurotomized on only one side did not deviate significantly from normal behaviour, nor did the grilse

whose visual sense was destroyed and which were then displaced up to a distance of 100 km from their home river.

As for the olfactory-impaired fishes in the experiments of Craigie (1926), Clemens *et al.* (1939) and Bertmar & Toft (1969), the accuracy of their homing was much reduced. Unfortunately, all three experiments were carried out without visually impaired control groups. It is here worth noting that Stasko (1971), reviewing and evaluating sensory impairment experiments in fish orientation, pointed to the possibility that fishes might also be guided by other senses when olfaction is impaired. Schooling, he mentioned, would provide an alternative means of navigation for salmon released on a major migration route.

The data, therefore, seem to indicate that the olfactory sense is mandatory for successful salmonid navigation. It also seems as if earlier scepticism related to olfactory-impairment experiments, resulting from lack of controls for traumatic effects (i.e. Brett & Groot, 1963), can be dismissed when the proper sham-operated controls used by Toft are taken into consideration.

The necessity of olfaction, and the non-requirement of vision for coastal navigation of fishes, has also been supported by experiments performed on chum salmon (*O. nerka*) by Hiyama *et al.* (1967), American shad (*Alosa sapidissima*) by Dodson & Leggett (1974), and anadromous trout (*S trutta*) by Bertmar (1979).

(3) *Homing orientation as a single process?*

(a) Behaviour and water currents

Regarding the high number of operated fish recovered in Deep Water Bay in the experiments of Craigie (1926), he remarked that the fish tended to remain there for some time. This observation seems to be in accordance with the findings of DeLacy *et al.* (1969). The latter examined the importance of olfaction in the homing of chinook salmon (*O. tshawytscha*) in the Lake Washington watershed. Displacement of control fish both up- and downstream from their homing pond revealed that in the absence of the homestream cue, i.e. an upstream displacement, the response of the fish was manifested in a negative rheotaxis. The fish demonstrating such a rheotaxis returned downstream to the location at which the appropriate olfactory stimulation elicited a positive rheotactic behaviour similar to that of fish displaced downstream. As for the fish with olfaction inhibited, the only ones recovered were captured in the salt water gill-net fishery several miles out in Puget Sound. It therefore seemed that the tendency for downstream movement in the absence of olfactory cues was present both for the upstream displaced control fish and for fish denied olfaction by occlusion of the olfactory apparatus.

In a river, the downstream movement of water, together with various degrees of active swimming, will bring fish with a negative rheotaxis downstream. In open sea a negative rheotaxis might contribute to a distribution of the fish within a limited area, depending on the ocean current of that area. Regarded that way, the data from Craigie (1926) may indicate an identical mechanism of orientation in the sea as in rivers, based on a positive rheotaxis to odorant clues.

Support for the assumption that fish follow ocean currents in their migration comes from the studies by Royce *et al.* (1968). Fish do not follow ocean currents only in their migration to and from their feeding areas. During their ocean life they generally travel

'downstream', following the currents associated with ocean gyres in well defined areas. The number of circuits travelled in the gyres depends on the number of winters spent by the salmon at sea. Royce *et al.* (1968) also claimed that responses to all migratory cues must be inherited, not memorized.

Data from Ísaksson (1980) supports the idea that navigation in the sea is dependent on rheotactic behaviour. In 1976, 140 adult Atlantic salmon were transported from Kollafjörður Fish Farm, to a tributary of the Thjorsá river in Southern Iceland to be sportfished. The river was blocked for downstream migration, but a few fish escaped in floods. A month later two of the fish returned to Kollafjörður. The return journey involved a 50-km downstream migration and a 150-km saltwater migration around the Reykjanes peninsula. Ísaksson proclaimed that the smell could only have been important during final stages of return, since a westerly current had to be followed 'downstream' around the south coast until passing Reykjanes. A negative rheotactic response, however, elicited in the absence of proper olfactory cues, and present both in the river and sea, might be the explanation for the total back-track until passing Reykjanes.

(b) Orientation mechanisms

Neave (1964) pointed out that a bicoordinate system must be present in salmonid navigation. It is easy to imagine how positive rheotactic behaviour to odour can be aroused in a stream where the visual sense together with the side line organ can inform the fish of upstream direction. There is a problem, however, as to which type of senses are used in addition to olfaction in open-sea navigation. In the sea the salmon move in the upper water masses (Westerberg, 1979a). Detection of the bottom can for that reason not come into consideration when evaluating additional parameters used in orientation. Since the visual sense has been demonstrated superfluous (Toft, 1975), there is a need to evaluate other parameters in the search for a solution to the problem.

An answer to the question of navigation in the sea may be found in the proposal by Royce *et al.* (1968) that salmon may be capable of detecting the interfaces between moving bodies of water. According to Neave (1964) the view that currents may provide guiding clues fails to explain how orientation to a current can be effected in the absence of fixed reference points. A possible solution to this problem may have been given by Westerberg (1979a) in his proposal of a model for fish orientation. By telemetric studies it was demonstrated that salmon orientation primarily takes place in a *vertical* direction, and that the microstructure formed by the different layers of temperature in the sea is essential for the mechanism of detection. The fish do not demonstrate any long-term temperature preferences, but seem to migrate in temperature layers that are found convenient with regard also to other parameters. Westerberg (1982a, b) linked the mechanism of temperature–microstructure detection to the sense of olfaction, by demonstrating that anosmic fish lose their preference for certain layers, and search at random in the vertical direction. Also the European eel (*Anguilla anguilla*) has been demonstrated to use the temperature–microstructure during its migration in the sea (Westerberg, 1979b).

Information on 'upstream' direction needed for a correct guiding of the fish may therefore be formed by detection of the sliding microstructure layers in the sea, which also possibly produces electromagnetic cues (Royce *et al.*, 1968). These layers are separated by temperature, salinity and density characteristics, and contain odour

information that may be specific to each layer (Larkin, 1975; Westerberg, 1982 a, b). More information on the above will be needed in order to solve the problem. Anyway, it must be considered a breakthrough for the human mind to realize that the sea for the fish is a three-dimensional system, and not a two-dimensional one, as observed from the surface view of man.

(c) *A comprehensive hypothesis*

Based on the natural ecology of salmonid migration, Nordeng (1977) presented a 'pheromone' hypothesis for the total homeward migration in anadromous salmonids. Data from 17 years of investigations of the Salangen river system gave the formal background necessary for this hypothesis (reviewed by Døving, 1979). This hypothesis was based on the migrating schedules of the salmonids in the above river system.

According to Nordeng (1977), the downstream salmon smolt migration in the Salangen river system starts about the 25th of May. The smolt descend almost every evening in batches, migrating with the current in coastal waters. The foremost smolt reach the feeding area at sea in about 10 days, and may induce an inherited response in the maturing salmon, resulting in the start of their homeward migration along the smolt route. About 15 days after the onset of the seaward migration of salmon smolt, the foremost maturing adult salmon reach the mouth of the river. The end of downstream smolt migration from the river, and the lower part of the river system, occurs when the downstream and upstream migration have overlapped through the estuary for about 60 days. Thus, in the course of a migrating period the smolt and corresponding maturing salmon exchange habitats.

From what has been presented in the preceding sub-sections, it appears reasonable to suggest that the navigation outside coastal regions by homing salmon may be dependent on olfaction. In an evaluation of mechanisms behind salmon homeward migration, a genetically related hypothesis seems at this stage also to be the most obvious, when biochemical, sensory and ecological aspects are taken into consideration. This circumstantial evidence may therefore indicate that the homing orientation of salmonids can be regarded as a continous and single process. Several arguments have been presented in the literature, however, against the influence of inheritance in the matter (e.g. Hasler *et al.*, 1978). These arguments will therefore be evaluated by a critical examination of transplantation experiments in the following section.

IV. TRANSPLANTATION EXPERIMENTS

There is a long tradition in the use of non-native fishes for salmonid homing experiments (i.e. transplantations). A series of such experiments with king salmon (*O. tschawytscha*) was started in 1914 by Rich & Holmes (1928) and in 1916 by Snyder (1931). Through the years many transplantation studies have been carried out, based on different species and with a variable approach to the problem, resulting in widely scattered and often confusing conclusions. In the present section some of the most accepted conclusions from the literature will be held up to examination and evaluated. Naturally, only a limited number of transplantation experiments will be taken into consideration, focusing upon the major trends.

(1) *Transplanted* versus *native fish*

(a) *Return of transplanted fish*

Marking of salmon pre-smolt (*Salmo salar* L.) from Lundesokna hatchery, Norway, has been carried out since 1957 (Rosseland, 1965a). The eggs have been of different origins, and the fish have been transplanted and released in a variety of Norwegian rivers. Experiment no. 1 in Table 2 summarizes the marking experiments with Lundesokna fish through the years 1957–62. The data reveal that, out of 22 675 fish marked and released in that period, only 0·09 % has been recovered in the stream of release. Of the fish recovered in rivers, a straying rate of 16 has been recorded. Data from the period 1970–76 on 60 795 fish from the same hatchery, released in a number of rivers, confirm the above trend with 0·16 % returning and a straying rate of 24·8 (Experiment no. 2, Table 2: Rosseland, 1978).

In total, experiments no. 1 and 2 in Table 2 show that a much lower percentage of transplanted fish are recovered in the stream of release compared to native, wild fish as presented in Table 1. In addition, the straying rate is notably higher for transplanted than for wild native fish. These results point to a reduced ability of correct 'homing' orientation in transplanted fish as compared to native, wild fish. Also for chum salmon (*O. keta*), a low rate of return of transplanted fish to the river of release is noted compared to the native river, ranging from only 10 to 20 percent, as reported by Altukov (1981).

The fact that at least some transplanted fish return to the river of release has been used as an argument for 'imprinting', and against an influence of inheritance in salmonid homing orientation (Russel, 1937; Hasler *et al.*, 1978; Scholz *et al.*, 1974, 1975; Rosseland, 1978). Nordeng (1977), however, suggested that return of fish, transplanted into non-native rivers, might depend upon association of the transplants with the migratory systems existing in the rivers of release. The salmonids migrate in schools (e.g. Hartt, 1966). The return to a non-native river might therefore well be explained by the schooling tendency of the transplants. Such an explanation seems also to be in better accordance with data for straying than an explanation founded on an 'imprinting' theory.

Artificially propagated fish of native origin have traditionally been regarded as equivalent to native ones as far as homing ability is concerned. I propose that artificially fertilized and propagated fish, used in homing experiments within their river of origin, must generally be compared with transplanted ones of non-native origin. The reason for this lies in the fact that the parentage of hatchery stocks in many cases are trapped or netted during their upstream spawning migration. Such sampling usually takes place at convenient places, very often sited far down in the watersheds or even in the estuaries. When a river or a tributary contains more than one population of salmon, catching and artificial fertilization may thereby occur at random, and population hybrids may be the result.

As already summarized in this article, olfaction seems vital to the salmonids in their homeward migration. If the production of, and response to, olfactory stimuli in homing is of genetic origin, as postulated by Nordeng (1971, 1977), then a random artificial fertilization could result in a disruption of the orientation ability of the fish. Support for such conclusions is available in the literature as follows.

Artificially raised 'native' Atlantic salmon smolt, originating from the Eira 'stock',

Table 2. *Homing experiments with hatchery raised Atlantic salmon, resulting from artificially fertilized eggs*

Exp. no.	River	Region	Year	Origin of fish	Mark used	Number released	Total recovered		Recovered in stream of release		Recovered in other streams		Straying rate	Reference
							No.	%	No.	%	No.	%		
1	Multiple	Norway	1957–62	Mixed origin	Carlin tag	22675	620	2·73	21	0·09	4	0·02	16·0	Rosseland (1965a)
2	Multiple	Norway	1970–76	Mixed origin	Carlin tag	60795	1094	1·80	97	0·16	32	0·05	24·8	Rosseland (1978)
3	Eira	Norway	1959–62	Eira River	Carlin tag	7795	147	1·89	10	0·13	2	0·03	16·7	Rosseland (1965a)
4	Eira	Norway	1970–76	Eira River	Carlin tag	24860	204	0·82	10	0·04	5	0·02	33·3	Rosseland (1978)
5	Rana	Norway	1970–76	Rana River	Carlin tag	18054	471	2·61	58	0·32	10	0·06	14·7	Rosseland (1978)
6	Miramichi	New Brunswick	1968–69	Unknown	Tags	16600	232	1·40	100	0·60	0	0	0	Stasko et al. (1973)
7	Restigouche	New Brunswick	1969	Unknown	Tags	9990	98	0·98	8	0·08	0	0	0	Stasko et al. (1973)
8	Philip	Nova Scotia	1968–69	Unknown	Tags	9930	164	1·65	47	0·47	0	0	0	Stasko et al. (1973)
9	Margaree	Nova Scotia	1961–70	Unknown	Tags	80805	327	0·40	165	0·20	1	0·001	0·6	Stasko et al. (1973)
10	St John	New Brunswick	1969	Unknown	Tags	17950	81	0·45	62	0·35	0	0	0	Stasko et al. (1973)
11	7 Rivers	New Brunswick	1968–69	Unknown	Tags	174800	—	1·23	—	0·19	—	—	—	Ritter (1975b)
12	4 Rivers	N.B. & N.Sc.	1968–69	Unknown	Tags	34700	—	0·10	—	0·003	—	—	—	Ritter (1975b)
13	Big Salmon	New Brunswick	1963–70	3 Rivers	Carlin tag	85434	267	0·31	—	0·26	—	—	—	Jessop (1976)
14	Kollafjörður	Iceland	1965	Hatchery	Fin-clipped	1000	—	—	82	8·2	—	—	—	Guðjónsson (1967)
15	Kollafjörður	Iceland	1966	Hatchery	Carlin tag	2496	48	1·92	38	1·52	10	0·40	20·8	Guðjónsson (1967)
16	Kollafjörður	Iceland	1971	Hatchery	Tags	3775	176	4·66	166	4·40	8	0·21	4·6	Ísaksson (1976a)
17	Kollafjörður	Iceland	1972	Hatchery	Tags	6612	397	6·00	386	5·84	11	0·17	2·8	Ísaksson (1976a)
18	Kollafjörður	Iceland	1973	Hatchery	Tags	11530	1·186	10·29	1·165	10·10	21	0·18	1·8	Ísaksson (1976b)
19	Ártúnsá	Iceland	1975	Kollafjörður	Micro-tag	2000	13	0·65	7	0·35	5	0·25	41·7	Ísaksson et al. (1978)
20	Ártúnsá	Iceland	1975	Kollafjörður	Micro-tag	4000	96	2·40	65	1·63	26	0·65	28·6	Ísaksson et al. (1978)
21	Ellidaár	Iceland	1975	Kollafjörður	Micro-tag	2000	49	2·45	45	2·25	1	0·05	2·2	Ísaksson et al. (1978)
22	Ellidaár	Iceland	1975	Kollafjörður	Micro-tag	3873	195	5·03	151	3·90	5	0·13	3·2	Ísaksson et al. (1978)
23	Apple River	Nova Scotia	1934	Chaleur Bay	Fin-clipped	3252	98	3·01	92	2·83	6	0·18	6·1	White (1936)

have been released in the river Eira, Norway, for some years. Experiment no. 3 in Table 2 presents data from markings in the Eira river during the period 1959–62 (Rosseland, 1965 a). In total, 7795 smolt were released. Only 0·13 % were recovered in the Eira river. In addition, a straying rate of 16·6 was recorded. In the period 1970–76, 24 860 marked 'native' hatchery fish were released in the Eira river (Experiment no. 4, Table 2: Rosseland, 1978). Only 0·04 % of the fish released were recovered there, and a straying rate of 33 was recorded in other rivers.

The same trend, low percent return and a high straying rate of hatchery-raised 'native' fish compared to wild fish as presented in Table 1, has been found in data from release of artificially raised salmon in the Rana river (Experiment no. 5, Table 2: Rosseland, 1978). An evaluation of data from tagging of salmon smolt, carried out by Atlantic countries from 1963 to 1969, also demonstrates that the return rates of hatchery-reared smolts are lower than those of wild smolts (Vibert & Laurent, 1972).

(b) Survival in the sea

As an explanation for the low percentage return of hatchery-raised fish compared to native, wild ones, it has generally been suggested that survival in the sea for hatchery fishes is lower than for wild fishes. The background argument most commonly used is that lack of natural pressure of selection in hatcheries produces individuals well adapted to hatchery survival and poorly fitted for wild life. Bams (1972), however, demonstrated that in spite of a six-times higher survival of pink salmon (O. gorbuscha) fry in a hatchery, compared to fry from a naturally propagated part of the same stock, the two groups survived sea-life to the mature stage at virtually the same rate.

The suggestion that hatchery-raised fish have a lower survival in sea than wild fish can also be rejected by a closer look at Canadian tagging data on Atlantic salmon. In the period 1961–70, a total of 344 775 hatchery smolts were tagged and released in a selection of Canadian rivers (Experiments no. 6–12, Table 2: Stasko et al., 1973). Out of these, 3092 (0·90 %) were totally recovered, and 722 (0·21 %) were recovered in the stream of release. In the same period (1960–69), 118 312 wild smolts were tagged and released in mainly the same rivers as the hatchery-raised ones (Experiments no. 4–9, Table 1: Stasko et al., 1973; Saunders, 1967). Out of these, 3566 (3·01 %) were totally recovered, and 2820 (2·38 %) were recovered in the stream of release.

Looking at the total percent recovery in the above experiments, 3·3 times as many wild fish as hatchery-raised ones were recovered. At first glance this record gives support to a suggestion of low hatchery-fish survival in the sea. In the stream of release, however, the recovery ratio of wild to hatchery fish was 11·3, based on percentage return. Related to the total recovery data, this record clearly indicates that homing in wild, native fish is much better than in the artificially fertilized ones. Subtracting stream recovery from total recovery, the above data in addition reveal that a ratio of 0·91 for wild fish to hatchery fish exists in sea recovery. In other words, concerning percentage recovery there are virtually more hatchery-raised fish recovered than wild fish in the sea, the only place where comparison of survival can be actually made.

Data from Jessop (1976), for non-native hatchery-raised Atlantic salmon (Experiment no. 13, Table 2), and for wild, native salmon (Experiment no. 11, Table 1), released in Big Salmon river, New Brunswick, also demonstrate that hatchery-raised fish are recovered in the sea as adults at the same rate as wild fish.

The above presented data from Stasko *et al.* (1973) and Jessop (1976) point to the fact that the survival rate in the sea of hatchery-raised Atlantic salmon is equivalent to that of wild fish. Since hatchery fish return to the river of release less frequently than the wild ones, this must reflect on the navigational ability and not on the survival rate. The disturbance of navigational ability must in consequence result from the artificial fertilization of the fish.

A normal survival to adult stage of transplanted hatchery fish was reported for pink salmon (*O. gorbuscha*) by Bams (1976). Most of the transplants in his experiment, however, failed to return to the stream of release. From dozens of within-range pink salmon transplants attempted during the last 6 decades, he found none that had been evaluated for ocean survival prior to fishing mortality. He therefore concluded that a transplanted stock can survive at a normal level until the time of entry into coastal waters.

(2) *Some ambiguous transplantation experiments*

(a) *Commonly cited experiments*

Donaldson & Allen (1957) transplanted hatchery-reared silver (coho) salmon (*O. kisutch*) to two releasing sites in the Lake Washington watershed. The eggs used in the experiment were collected in 1950 from fish ascending Green river, draining into Puget Sound not far from Lake Washington watershed. The progeny was reared for 1 year in a hatchery sited at Green river. The fingerlings were then divided between the ponds of the School of Fisheries, University of Washington, and the State of Washington salmon hatchery on Issaquah Creek, and marked by ventral fin clipping. After another 2 months, the two lots of fish were released from their rearing sites for seaward migration. As adults, the fish returned to the sites of release with only a minimal exchange between the sites. The experiment has as such been used as evidence in favour of 'imprinting' in salmonid migration (Hara, 1970; Scholz *et al.*, 1974, 1975; Hasler *et al.*, 1978).

From the data and arguments presented in sub-section (1) of this section, it should not be expected that the artificially propagated fish released by Donaldson & Allen returned to Green river, since they may well have been hybrids from natural populations. If both releasing sites contained populations of coho salmon during adult return, the return as such by the transplants also seems reasonable, in spite of a low percentage return to the releasing sites (0·34 % and 0·19 %). The *perfect* return to the releasing sites, however, seems remarkable.

Looking at the data on average weight and length of the two groups released, some striking differences are revealed. The fish released in Issaquah Creek had an average fork length of 93·6 mm and an average weight of 10·49 g. The fish released from the School of Fisheries averaged 106·4 mm and 14·82 g. The 2 months of separation at the different rearing stations prior to release could be responsible for these large differences. If, however, the differences between the two lots in length and weight represent separate batches of eggs fertilized, then the absence of a straying between the releasing sites also seems reasonable, according to a genetically based hypothesis.

Coho salmon (*O. kisutch*) were used in a transplantation study reported by Jensen & Duncan (1971), and the results obtained have commonly been used as proof that odour 'imprinting' to the stocking site occurs (Madison *et al.*, 1973; Scholz *et al.*, 1974, 1975; Hasler *et al.*, 1978). During spring 1967, about 650000 coho fingerlings were transported

from the Lawenworth National Fish Hatchery on Icicle Creek, a tributary to the
Wenatchee river, to a fish-handling facility on the north bank of the Snake river, both
rivers in the Columbia river system. The fish were held in spring water 36 to 48 h and
heat-branded before being released. In total 1712 fish were recovered during that
autumn in a trap sited at the outlet of the fish-handling facility. None of the marked
fish was reported to return to the Lawenworth Hatchery. When river water was pumped
through the trap in place of spring water, no fish entered the trap, demonstrating a
striking attraction to the spring water.

Evaluating the above-mentioned report of Jensen & Duncan, it should be stressed
that lack of return of transplanted hatchery fish to their original hatchery should be
regarded as the general rule and not the exception. Nor does an attraction to spring water
provide any definite evidence for 'imprinting', since a nearly continuous holding of fish
throughout ten separate tagging periods during that spring must have given a considerable
opportunity for the fish themselves to mark the substrate of the holding facility (see
section V (1)). Since, in addition, only 286 marked fish (16·7 %) were identified among
those captured in the trap, definite conclusions from the study by Jensen & Duncan
(1971) in favour of any navigation hypothesis should be avoided.

White (1936) transplanted artificially propagated Atlantic salmon fry, progeny of fish
originating from Chaleur Bay, New Brunswick, into the east branch of Apple river,
Nova Scotia, in 1932. Two tributaries flow into Apple river, the east and the west
branch; both originally contained salmon. Some 60 years before the experiment, a dam
was erected at the head of the tide of the east branch, forming a barrier to any spawning
run of salmon. The dam had been out of use for 10 years previous to the experiment,
but the salmon had not become re-established in the stream.

On their seaward migration in 1934, the transplanted smolt were trapped in the east
branch and marked by removal of the adipose fin (Experiment no. 23, Table 2). In 1935,
92 marked grilse entered the east branch, and five 2-year salmon entered in 1936. The
marked fish entering the west branch in these 2 years were six and one, respectively
(White, 1936; White & Huntsman, 1938).

A total of 25000 hatchery fry were placed in the east branch in 1932. After
examination of the river in 1933, the surviving parr were estimated at about 7400. The
number of seaward migrants in 1934 was 3252. It can be assumed that smolts from the
plant left the stream also in 1935. It therefore appears that no contradiction exists
between the Apple river experiment and a genetically based hypothesis for the
navigation of anadromous salmonids.

(b) The pink 'problem'

The pink salmon migrates to sea immediately after hatching, and returns on its
spawning migration the following year. In total a 2-year cycle exists, with spawning
migration of separate populations in even and odd years (Pritchard, 1938; Harden Jones,
1968). The life-cycle of the pink has been used as an argument against 'pheromones'
in salmonid navigation, since rivers perpetuating only even- or odd-year stocks would
contain no fry during migrant return.

Some large-scale transplantations of pink salmon (*O. gorbuscha*) into rivers in the
Atlantic region were started by Soviet biologists in 1956 (Berg, 1961). The fish were
stocked into rivers in the Murmansk and White Sea areas, but apparently the 'homing'

instinct did not work well, and a high number of pink spread into Norwegian waters and ascended many Norwegian rivers. From 1973, spawning of pink in Norwegian rivers was reported, especially in Finnmark county, and fry migrating to sea were observed (Berg, 1977a).

Progeny of pink salmon, caught in Neiden river, Finnmark county, have been propagated to maturity in Norwegian hatcheries (Berg, 1977a). Most of the fish died after maturation, 18–20 months after hatching. It is interesting to note, however, that some females survived spawning, and were still alive a year later. Other females reached 3 years of age without spawning at all. An interesting observation was also that small maturing males have been found in the rivers in Finnmark.

Larkin (1975) proposed that the scent from relatives in fresh water could be the guiding clue for Pacific salmon. Migrating adult sockeye, coho and chinook salmon he mentioned, could follow the year class that is resident for at least a whole year in lakes and rivers. For pinks and chums he stated: "it is only necessary to postulate that the run of the year before (or 2 years before) has left some residual scent. Perhaps this is why pinks have a greater tendency to stray?" Concerning migration in the sea, Nordeng (1977) suggested that homing of pink may be caused by association (i.e. schooling tendency) with other migrating Pacific salmon originating in the same river systems.

Based on the report by Berg (1977a), together with the evidence for genetic control of pink homing given by Bams (1976), and the propositions by Larkin (1975) and Nordeng (1977), it is suggested that even for pink salmon navigation, too rigid conclusions about lack of a 'pheromone' navigation system should be avoided.

(c) *Some additional experiments*

At this stage, one may take a retrospective glance at the data from Rich & Holmes (1928). In the period 1914 to 1924 a series of transplantation experiments with chinook salmon (*O. tshawytscha*) was carried out within the tributaries of the Columbia river system. The eggs were artificially fertilized and hatchery-reared after being taken from their respective tributaries. On the basis of the poor returns recorded after transplantations, the authors tentatively concluded that, in part at least, some element in the complex known as the homing instinct is hereditary. They also found it possible that this could be a determining factor in the establishment or rehabilitation of salmon runs by means of artificial propagation.

Although no tendency was found for transplanted fish to return to the stream from which the eggs were taken, Rich & Holmes reported a striking instance of home-stream return to Spring Creek. This stream was so small that they found it difficult to see how the salmon could find it at all, yet the 'native' fish marked and released here homed better than in any other 'native' stream experiments. Unfortunately, the Spring Creek fish were not used in any transplantation experiments. There is reason to believe, however, that the homing ability was retained due to the size of the stream. That is, if only one population of salmon was present in Spring Creek, as opposed to several populations in other tributaries, population hybrids resulting from random artificial fertilization may here have been avoided.

The only example found in the literature that may disagree with inherited navigational ability in salmonids, is the report by Armstrong (1974). Smolts of the Dolly Varden char (*Salvelinus malma*), transplanted during their oceanward migration, returned to

spawn mainly in the stream of release. The ecology of the Dolly Varden seems, however, complex. Immature migrants showed an extensive straying between the streams, while mature migrants 'homed' specifically. Of the transplanted smolts, some also returned as mature migrants to the native stream. No rigid conclusion should therefore be drawn concerning navigation of this species before a careful investigation has been carried out in relation to inheritance.

(3) *Inheritance and navigation*

(a) *Return to hatcheries*

It should here be noted that in some instances there has been a very good return of hatchery-raised Atlantic salmon to the river of release. Release of hatchery-reared salmon from the Kollafjörður Fish Farm, Iceland, has given remarkably good results of recovery. The fish were released from the fish farm, where they could migrate directly to sea, and recovered as mature salmon in the pond of the farm (Guðjónsson, 1967, 1972).

Releases of fish from Kollafjörður Fish Farm in 1965 and 1966 gave 8·2 % and 1·52 % recovery, respectively, of adult fish in the pond (Experiments no. 14 and 15, Table 2). It is worth noting that external tags were used only in the 1966 experiment, and the straying rate to other rivers was recorded as 20·8. In the period 1967–69, straying rate averaged 17·3 (Guðjónsson, 1970, 1972), while the average return during the years 1966 to 1969 was 2·31 % (Guðjónsson, 1972). Kollafjörður Fish Farm has been self-sustained with milt and eggs since 1963 (Guðjónsson, 1972). It should also be noted that most fish in Iceland data are recovered in rivers, since almost no commercial fishing for salmon takes place in the sea (Ísaksson, 1980).

Tagging experiments during the years 1971–73 gave recovery at Kollafjörður in the range of 4·4 % to 10·1 % of those released (Experiments no. 16–18, Table 2: Ísaksson, 1976a, 1976b). Ísaksson (1976c) claimed that the increase in percentage return was due to the natural photoperiod given to the young fish. This seems, however, not to be the only factor working, since straying rate to other rivers during this period had dropped to 4·6 in the 1971 experiment and further to 1·8 in the 1973 experiment.

As presented in Table 3, the Icelandic tagging data in total demonstrates that percentage return to the fish farm has increased, and straying rate has decreased, from releases in the period 1966 to 1973. Improved hatchery techniques have been claimed to be the background reason for such improvements (e.g. Piggins, 1974). This explanation could well account for the increase in percentage return, but is not sufficient to explain the decrease in straying rate. In addition, the above argument is based on a postulated improvement of survival due to a production of fish more 'fitted' for sea life. Taking into account both percentage return and straying rate, together with the knowledge of equal survival in the sea of hatchery fish compared to wild fish, the above data demonstrate an improvement in *homing ability* for the Kollafjörður fish during the stated period of time.

Tilzey (1977) suggested that if an inherent race-specific character is a major navigational clue, reproductive homing will result in each spawning site becoming increasingly distinctive, which in turn should result in an increasing homing efficiency in successive generations. A pressure of selection, therefore, similar to that suggested by Tilzey and carried out by man, may well have taken place in Kollafjörður Fish Farm.

Table 3. *Results from homing experiments with externally tagged Atlantic salmon at Kollafjörður Fish Farm, Iceland. Data from Guðjónsson (1967) and Ísaksson (1967a, b).*

Year	No. released	Recovered (%)	Straying rate
1966	2·496	1·52	20·8
1971	3·775	4·40	4·4
1972	6·612	5·84	2·8
1973	11·530	10·10	1·8

The 1973 returns in Table 3 are obviously not progeny from the 1972 or the 1971 returns. The data in total, however, demonstrate a general trend that strongly suggests a genetic influence on the salmon navigation ability.

Doubts have been expressed by Piggins (1969) as to whether salmon derived from hatchery-reared smolt could exhibit the same degree of homing instinct as wild salmon. He rejected these thoughts by referring to Irish data which points to well developed homing mechanisms in 'reared' fish. Although he could find no report for 'reared' salmon straying into other river systems in Ireland, he reported an improvement in sea 'survival' resulting in an increase from 0·01 % to 2 % return to the river of release through a 10-year period. Piggins (1974) in fact has suggested that selective breeding is a major factor in the improvement of the recapture rates. As clarified in this review, surivival of hatchery fish in the sea is of the same rate as for wild ones. Hence, there is good reason to believe that also the improvement of 'survival' reported by Piggins merely reflects the homing ability. In other words, the Irish data for hatchery rearing of Atlantic salmon, reported by Piggins (1969), appear to be similar to the Icelandic data in as much as artificial rearing of fish of 'native' origin seems to improve their homing ability over time.

Support to the idea that selective breeding improves the accuracy of homing also comes from the report by Saunders & Bailey (1978). A run of salmon was established in a stream adjacent to the North American Salmon Research Center, New Brunswick. Three stocks were initially used. The stock showing the best performance and apparent adaptability to hatchery and sea-ranching conditions was from a stock that had been hatchery-reared and sea-ranched for three to four generations at another New Brunswick hatchery. The other two stocks were taken from wild spawners.

(b) Return to place of origin

An argument commonly used against the involvement of inheritance in salmonid migration has been that transplanted fish do not return to their river of origin (Donaldson & Allen, 1957; Hara, 1970; Rosseland, 1978). The experiments already mentioned in this article reveal that, if fish resulting from artificially fertilized eggs are used in transplantation experiments, recovery in the 'native' river is not to be expected. This is the case because the navigational ability of hatchery fish in general seems to be impaired. If wild fish, or hatchery fish with stabilized homing ability (i.e. Kollafjörður Fish Farm), are used, homing to the native river should not be expected either. This is indeed the case if the fish do not have a fair chance of detecting olfactory cues from their native river during homing migration; we return therefore to the literature for an evaluation of this case.

In 1962, 170 wild Atlantic salmon smolt were tagged in the River Loneelv and transferred to the outlet of the City Aquarium of Bergen, Norway, a distance of approximately 20 km (Rosseland, 1965 b). On their seaward migration, the opportunity existed for the fish transferred to Bergen to detect olfactory clues of their relatives from the natal river. Two of the smolts were recovered in rivers as adults, one of them in the River Loneelv. The recovery of one fish in its natal river is far from being proof of a genetically based theory in salmon migration. Compared to the arguments commonly used against such a theory, the result seems however, worth noting.

Icelandic transplantation experiments demonstrating return to place of origin have been presented by Ísaksson, Rasch & Poe (1978). In 1975 salmon smolt from Kollafjörður Fish Farm, tagged with microtags, were released in the two rivers Ártúnsá and Ellidaár. The two rivers are located about 10 km on either side of Kollafjörður Fish Farm. The Ellidaár river contains Atlantic salmon of native origin. Recovery of mature migrants, tagged with microtags as wild smolt in 1975, was 10·3 % in the Ellidaár river (Experiment no. 12, Table 1). It should be noted that experiments with microtags give a recovery 1·6 times higher than experiments with Carlin tags (Ísaksson & Bergman, 1978).

Of the marked fish from two separate releases in the Ártúnsá river, 3·63 % were totally recovered (Experiments no. 19 and 20, Table 2). Out of the total number of fish recovered in rivers, a straying rate of 30·1 to other rivers was recorded. Altogether 25·2 % of the total stream recovery returned to Kollafjörður Fish Farm, the place where they had been reared.

In another two release series described by Ísaksson et al. (1978) (Experiments no. 21 and 22, Table 2), the same kind of release as in the Ártúnsá river was carried out in the Ellidaár river. The Kollafjörður fish released in the Ellidaár river were recovered there at a mean of 3·3 %. Straying rate for these release experiments was low, in total only 2·98. However, in all cases of straying registered, the recovery was at Kollafjörður Fish Farm.

In the above experiments, the Ártúnsá river was claimed to be a non-salmon-producing stream. From that, Ísaksson et al. (1978) proposed that: "pheromones may be acting, making the salmon more likely to stray when their home stream does not have a smell of young salmon". In their article Ísaksson and co-workers reveal, however, that planting of smolt had been carried out by the owner of the Ártúnsá river in 1974 at least, and that a considerable amount of untagged salmon were caught in the river in 1976 and 1977.

Kollafjörður fish stray more into the Ellidaár river than into the Ártúnsá river (Ísaksson, 1980), a reasonable result since the contribution from the Ellidaár river was about half the eggs of the original stocking in the fish farm (Guðjónsson, 1972). A well established migration system for the native salmon in the Ellidaár river, and a poorly established migration system in the Ártúnsá river, together with a closer genetic connection of the Kollafjörður fish with navigational clues from fish in the Ellidaár river, seem to give a better explanation in accordance with the data obtained.

(c) Genetic considerations

The significance of genetic influence on homing in salmonids has been demonstrated in the previously mentioned experiment carried out on pink salmon (*O. gorbuscha*) by Bams (1976). Comparison in return from the ocean between an introduced stock and

a hybrid stock (created by crossing females from the introduced stock with males of the local residual stock) revealed that large differences occurred in returns to the river. It was shown that, subsequent to passage through the inshore waters, the relative frequencies of numbers caught shifted greatly in favour of the hybrid fish. At the hatchery stream the expected relative rate of return of the hybrids, based on proportions to size of fry populations released, was 0·53, the observed was 0·91.

Some fish from the introduced stock returned, but the hybrid stock with the addition of the local male genetic complement showed better return to the natal river system. The hybrid fish returned to the river system in a similar proportion to the pure river progeny of two earlier operations. The influence of the male complement alone in the hybrid stock, was however not sufficient to achieve accuracy of return to the natal tributary within the system similar to that of the pure native fish. Bams (1976) therefore concluded that genetic control of homing ability is implicated, not only in locating the home stream, but also the tributary in which the fish were incubated and from which they migrated as fry.

Ritter (1975 a) reported a clinical decrease in return rate of hatchery-reared Atlantic salmon with the distance the smolt were transplanted from their native streams. This observation he interpreted as representing a clinal decrease in ocean survival, dependent on the coastal distance between the recipient river and the native stream of the stock. As we have seen, hatchery-reared fishes in general have a low rate of return to their 'home' river, but survive well. Related to a genetic hypothesis in salmonid migration, it may therefore well be that this observation by Ritter (1975 a) reflects the ability of transplanted fishes to respond to migrating clues in the recipient rivers. Regarded that way, the clinal decrease observed by Ritter could also be a 'genetic decrease' in navigational clues due to the dissemination of the species in that area.

In summary, the transplantation experiments referred to appear to reveal that for salmonids inheritance is of utmost importance for the navigational ability. Genetic interference by man due to random artificial propagation, together with transplantations, seems to reduce or even ruin the navigational ability of the fish. Selective breeding over time, however, may improve return of hatchery stocks, similar to that occurring in wild life during natural dissemination. In consequence, the concept of stocks or populations must be taken into consideration when carrying out artificial breeding and management of salmonids.

V. SPECIAL STUDIES RELATED TO SALMONID HOMING

Having evaluated transplantation experiments in relation to salmonid homing, it is worthwhile looking at some additional experiments related to the same subject. Both field and laboratory studies have been carried out in attempts to investigate the mechanisms behind salmon homing, using techniques found in the fields of behaviour, electrophysiology and chemistry. The overlap between the current topics that can be observed in the following presentation results from the fact that some of the studies described have used several techniques.

(1) *Behaviour*

(a) *In relation to odorants in stream water*

A laboratory bio-assay, based on the response of adult migrating sockeye salmon (*O. nerka*) to home-stream water, was suggested by Idler *et al.* (1961). The bio-assay was

based on the response of adult migrating salmon to odour stimulants by dispersal of school or increasing the swimming speed in a tank. The response measured was found to be raised by using home-stream water of the fish tested and also by water from other streams known to support sockeye populations. After a series of physical and chemical treatments of the home-stream water, the substances of interest in the water were thought to be volatile, dialyzable, neutral and heat-labile.

In a later report by Fagerlund *et al.* (1963), the above bio-assay procedures were slightly modified by using dechlorinated water, since unexpected response behaviour had previously been registered occasionally. The response pattern was now graded in a scale from zero to two, and only female fish were utilized, since male fish usually were found to be too active. In the majority of tests carried out the fish responded in a manner that indicated a response to water from their home stream and not to that of other sources. The volatile fraction of the home-stream water was then collected by passing a stream of nitrogen gas through the water, followed by a cooling trap. The results indicated that at least a portion of the stimulatory material was volatile. The fact that recombined volatile and non-volatile fractions induced a stronger response than did the volatile alone, made the authors suggest that also non-volatile material played some part in the stimulation.

By conditioning sockeye salmon smolt to stream water through a 'positive experience' technique (test water prior to food), followed by activity tests similar to those described above, McBride *et al.* (1964) demonstrated an ability also for the smolt to discriminate between creek waters. Positive response patterns were found when fish were stimulated by volatile material from test water, collected by the method of Fagerlund *et al.* (1963).

The expression 'attractant' is used by McBride *et al.* (1964) when describing the active material in their tests. The type of response measured, however, must be questioned. Hand-rinse (i.e. human hands rinsed in water) aroused a response similar to that obtained from home-stream water in the experiments by Idler *et al.* (1961). Since hand rinse was shown to be repellent by Idler, Fagerlund & Mayoh (1956), doubt can be raised as to whether the response measured to the home-stream water in the above reports really was a response to 'attractants' or to other navigational clues.

Additional support to the scepticism in applicability of the above bio-assay is found in the report by McBride *et al.* (1962). Behavioural responses similar to those above were described in juvenile sockeye in response to food extracts. I find it difficult to accept that a behavioural response pattern of such a general character can give any specific information concerning migration.

(b) Rheotactic behaviour

Homing adult fish demonstrate a positive rheotaxis to odorant clues, and a negative rheotaxis in the absence of it, as described for chinook salmon (*O. tshawytscha*) by DeLacy *et al.* (1969). The literature also points out that rheotactic behaviour (Frankel & Gunn, 1961) to olfactory clues in some salmonid species acts as a mechanism to maintain juveniles on the spawning ground. When Atlantic salmon parr were tagged in their stream, recaptures as parr were made in or near places of original capture, pointing to a 'home area' for the individual fish. When parr were moved from their

'home' area, some returned there, whether the displacement was carried out upstream or downstream (Saunders & Gee, 1964).

Results concerning home area and return after displacement similar to those mentioned above, have also been obtained for other stream-living species (Gerking, 1953, 1959; Miller, 1954; Stott, 1967). When the olfactory sense was eliminated, displacement of fishes from their home area resulted in a random distribution within the stream, as demonstrated in the longear sunfish (*Lepomis megalotis megalotis* Raf.) by Gunning (1959), pointing to olfaction as the mandatory sense for maintaining local stability. Innate control of fry migration, probably related to the olfactory sense, has been reported also in sockeye salmon (*O. nerka*) by Brannon (1967, 1972) and in sockeye salmon and rainbow trout (*S. gairdneri*) by Raleigh (1967, 1971).

Positive rheotactic behaviour of male rainbow trout (*Salmo gairdneri*) to ovarian fluid has been described by Emanuel & Dodson (1979). Their study demonstrated that trout can respond unidirectionally to an attractant odour in the water current even when no concentration gradient exists. This mechanism of orientation involves water currents providing the directional cues, and the olfactory stimuli regulating the rheotactic response. Similar mechanisms of orientation by fish to attractive odours, elicited through rheotaxis rather than to cues provided by odour gradients, have also been suggested by Kleerekoper (1967). Concerning behaviour it therefore seems that the best way to accumulate information about, and to detect substances used by, fish in their navigation is to use bio-assays based on rheotactic behaviour. A review of the field has been provided by Arnold (1974).

Atema *et al.* (1973) used a bio-assay based on positive rheotactic behaviour to classify the chemicals that attract alewives (*Alosa pseudoharengus*) to home-stream water. Like salmon, alewives seem to be able to detect and to prefer the chemical odour of their home stream (Thunberg, 1971). A Y-maze system was used, adding the stimulus and the control water into the background flow of the upstream legs. By recording the position of the fish at 15-sec intervals, a preference to home-stream water as opposed to water from other sources was obtained. By physical and chemical treatment of the home-stream water, the attractive substance was classified as of a low molecular weight (Mw less than 1000 Dalton), polar, heat stable, non-volatile and possibly containing acidic and basic centres. The absence of a detectable amount of amino acids in active distillate residue indicated that free amino acids were not involved in the alewife responses to home-stream water.

(c) *In relation to odorants from fish*

Based on the suggestion by White (1934) that presence of fish in a stream influences the entry of other fish, Brett & MacKinnon (1954) tested various fish products by introducing their samples into the path of the salmon moving up a fish ladder. Responses were measured by recording changes in the rate of migration. None of the samples tested produced an increased migration rate. Data from tests with salmon ova and testes indicated that both of these substances might be repellent. The tests were done early in the run when the migration rate was low. This fact, coupled with the fact that the material used was collected from fish of another stream, caused the authors to state that any definite conclusions were unwarranted.

Brett & Groot (1963) pointed out that it remains to be proven whether there is any form of natural species-odour recognition in the Pacific salmon. They reported, however, that some preliminary observations in their laboratory indicated that individual young sockeye react to the apparent presence of others when water from a hidden aquarium containing similar young salmon was introduced.

Høglund & Åstrand (1973) demonstrated a strong preference among juvenile char for water currents containing conspecific odorants to one devoid of it. The experiments were carried out with the Fluviarium Technique described by Høglund (1961). When the olfactory organ was removed the effect disappeared, although the normal preference to water currents seemed unchanged. The results indicated that olfaction plays a dominant role in communication (attraction) between individual young char.

Mature anadromous char (*S. alpinus* L.) were tested for positive rheotaxis to olfactory clues by Selset & Døving (1980). A two-choice system with parallel entrances was used. The fish were attracted to scent from live smolt of their own population, and to intestinal contents from the same group. In a choice between intestinal scent from smolt of their own population and similar scent from another population of sea char smolt, the scent from their own population showed a significantly increased attraction compared to the other. A significant attraction to chemical fractions of intestinal contents from young relatives was also demonstrated. The chemical separation methods used were carried out according to procedures developed by Selset (1980). When bile from the young relatives was tested in the test pen, an attraction, although more obscure, was also demonstrated.

By positive rheotaxis olfactometry, it has recently been demonstrated that also Atlantic salmon parr are able to discriminate between scents from strains of their own species, and that they prefer the scent from their own strain when tested against the scent from another strain. Since salmon parr have an ability for olfactory discrimination between fish odours similar to mature fish, a possible connection between the mechanisms behind 'home area' stability and 'salmon homing' was emphasized (Stabell, 1982*a*).

Quinn, Brannon & Whitman (1983) claimed that adult migrating coho salmon preferred home water without coho odours to an unfamiliar water source (city water), and that water conditioned by juveniles of their own population was not preferred to that conditioned by another strain. Their home water, however, was taken from the Ship Canal in the Lake Washington watershed, which contains natural spawning coho salmon (Donaldson & Allen, 1957). In addition, their competitive experiments with coho odours lacks a satisfactory number of ascents registered, in total only 20. The far-reaching conclusions drawn from the results obtained seem therefore not to be justified by the data presented.

(d) Some special experiments

Foster & Berlin (1980) confirmed the biological significance of fish excretory products in laboratory studies on spawning-site selection by lake trout (*Salvelinus mamaycush*). In one experiment, the fish were provided with a choice of four experimental reefs in a circular pool, together with two kinds of olfactory cues. The odorants presented were: (1) a mixture of freshly stripped milt and ovarian fluid dispersed in the water, and (2) stationary odour sources (egg membranes, sediment and faeces mixed with sloughed mucus) placed on selected reefs.

The milt–ovarian fluid mixture was found slightly repellent to the adult fish. In the stationary-odour-source experiment, 92 % of a total of 6858 eggs were recovered from beneath experimental reefs containing fry faeces and mucus. Also substrate-rubbing ('cleaning') by males, and approaching by females, occurred at the locations containing faeces and mucus but not at other reefs.

In another experiment two pools were used, each with two reefs, one pool with fry faeces and mucus present on one reef and another pool where such odour sources were absent. Although no evidence of spawning was found in either pool, the test odours were found to have an attractant effect as measured by comparing the frequency of specific behaviour at each of the four reefs in the two pools.

Results presented by Sutterlin & Gray (1973) appear to support a pheromone-related hypothesis in salmonid migration. Returns of hatchery-reared and wild Atlantic salmon to a hatchery beside the Saint John River, N.B., were examined. Despite the fact that the hatchery discharge contributed only 1/1000th of the river water flow, 67 % of the returning hatchery fish selected the hatchery and 33 % a hydroelectric dam situated further up the river. Less than 3 % of the wild fish entered the hatchery.

By a two-choice, tank-test system, Sutterlin & Gray measured preference of the hatchery-reared and the wild fish for various water sources. A clear-cut preference by hatchery adults for diluted hatchery effluent versus river water was demonstrated. Wild fish showed no preference for either water. Because hatchery effluent usually contained a 50 % proportion of well water and a 50 % proportion of river water, the effectiveness of the water from the two sources was compared. Both hatchery-reared and wild fish showed a preference for river water, no fish was ever captured in the well water side. The only factor that could change the character of the water, therefore, had to be found inside the hatchery.

The fact that few wild fish entered the hatchery, which had a large source of odour from young fish, made Sutterlin & Gray (1973) question the importance of an attractant effect from young fish. If, however, a race-specific character of the hatchery fish differed from that of the same species in the river, as suggested by Tilzey (1977), then the wild fish could have distinguished between the stocks and orientated accordingly. Circumstantial evidence for multiple stocks in the Saint John River comes from the fact that both spring, summer and autumn runs exist. Evidence for random mixing of genetic strains in the hatchery comes from the information by the authors that homing of hatchery fish to the hatchery during spring and summer runs was considerably less precise than in the autumn runs.

(2) *Electrophysiology*

Hara, Ueda & Gorbman (1965) supported the view that olfaction plays an important role in guidance during the final phases of salmon homeward migration. The study performed was based on infusion of water into the olfactory sacs of chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon, followed by simultaneous electro-encephalographic (EEG) recordings from the olfactory bulbs. When water from natural sources other than the home pond was used, little or no change in the spontaneous EEG pattern was recorded. When water samples from the home pond were used, however, a vigorous response of high amplitude was produced. Also Ueda, Hara & Gorbman (1967) reported an apparent specificity of the EEG response to home water. In their experi-

ment the tested fish consistently responded to their home water, but responded little or not at all to the home water for other spawning groups of fish. From their findings, the authors concluded that each spawning area has its own specific stimulant, or specific combination of stimulants, recognized and responded to in an 'all or none' fashion by the anadromous salmon. (See also review article by Hara (1970).)

The proposition of a selective EEG response pattern to home-stream water versus other water sources was partly rejected by Oshima, Hahn & Gorbman (1969a). Using chinook salmon (O. tshawytscha), they found that the most vigorous response was generally evoked by the home spawning area water, but a situation was found in which non-native water evoked olfactory responses that could not be distinguished from the home-water response. Also Ueda et al. (1971), Dizon, Horrall & Hasler (1973b) and Bodznick (1975) reported that natural non-natal water could elicit EEG responses as large as or larger than those produced by the home water. Oshima et al. (1969b) reported that the responses to water samples from along the fresh-water migrating route were in general equivalent, and therefore did not show any recognizable progression. Accordingly, the homing salmon did not seem to follow the possible olfactory clue of increasing concentration.

New and interesting dimensions in the area of salmon homing came from the observation by Oshima, Hahn & Gorbman (1969a), that presence of fish in the water increased its olfactory stimulating properties. Also Dizon et al. (1973b) found that conditioning of water by conspecifics appeared to increase the EEG response to the home-stream water.

Simultaneously with the growing attention to the role of fish odours in olfactory physiology, Nordeng (1971) proposed that population-specific scent from young conspecifics in the river could be the guiding cue for homing salmonids. Nordeng's pheromone proposition was based on ecological studies.

Døving, Enger & Nordeng (1973) studied some aspects of the pheromone proposal by recording EEGs from the olfactory bulb of Arctic char (S. alpinus L.). Stimulation of the olfactory epithelium with water in which different strains of char had been held elicited conspicuous EEG responses. So did water in which Atlantic salmon had been contained.

Referring to the discrepancy in results from EEG recordings obtained by different authors, Døving et al. (1973) pointed out that in addition to 'fish odour' (i.e. odorants emanating from fish), the olfactory sense in fish also responds to waters of different origin and to various other kinds of olfactory stimuli. The possibility of using EEG recordings as an assay for detection of the odorants used by homing salmonids was therefore precluded. Also Hahn (1976) pointed out that if the EEG proves to be a quantitative rather than a qualitative reflection of brain activity, relating EEG to homing behaviour will prove to be of limited value.

Studying single unit responses released in the olfactory bulb of char (S. alpinus L.) to 'fish odours', Døving, Nordeng & Oakley (1974) demonstrated that odours from different populations of char elicited differential responses. Their results suggest that various strains of fish release different odorants, and that there exists a neural basis for discrimination of these odorants. Bodznick (1978) gave evidence that a similar neural basis also exists for the discrimination between different natural waters. The origin of odorants producing this response was, however, not evaluated.

Oshima *et al.* (1969*a*) observed that fish in a new environmental water, which was initially relatively weakly stimulatory, developed a bulbar EEG to the novel water in 3 days that was not distinguishable from the home-water response. This observation has not been confirmed by other reports. On the contrary, Cooper & Hasler (1974) found no response either to stream or to lake water after holding the fish in such water for 1 week. Also Bodznick (1978), using juvenile sockeyes (*O. nerka*) reared in different natural waters, found that single olfactory bulb units showed no differences in their response properties.

Kaji *et al.* (1975) suggested that the frequency characteristics of the electrical responses (EEG) from olfactory stimulation of homing salmon could be used by man in the discrimination between stream waters. They obtained 'spectral patterns' by computer analysis of induced waves, resulting from nasal infusion of chum salmon (*O. keta*) by various stream waters. Døving & Belghaug (1977), however, demonstrated a linear relationship between the frequency of the induced waves and the temperature of the olfactory bulb. From their results they rejected the frequency of oscillatory waves of the bulb as having implications for the discriminatory ability of poikilotherm animals. They pointed out that if the spectral pattern of the olfactory response reflects the 'neural coding', then the quality of the sensation would change with the temperature of the animal's environment.

Nordeng (1971) and Døving *et al.* (1973) suggested that mucus secreted from the skin of salmonids was the most likely source of fish pheromones. Similar assumptions were also reached by Døving *et al.* (1974). Hara & MacDonald (1976) found the EEG response to mucus substances to be pH dependent, and pointed out that the response pH curve resembled curves obtained with free amino acids. Amino acids had at that time been demonstrated to be potent olfactory stimuli in freshwater catfish (*Ictalurus catus* L.) by Suzuki & Tucker (1971), and in several species of salmonids by Sutterlin & Sutterlin (1971), Hara (1973) and Hara, Law & Hobden (1973). Hara & MacDonald considered it unlikely, however, that amino acids could be involved in recognition of home-stream water.

Thommesen (1978) added valuable information on the function of the olfactory organ in fish. The odour-induced potentials (EEG) in the olfactory bulb of char and trout, resulting from different stimulants, were found to display a differentiated spatial distribution. Water containing fish odour was found to cause the largest responses in the rostral and medial part of the bulb, whereas amino acids elicited the largest responses in the lateral part. The study revealed a new factor with relation to the previously described discrepancy in EEG results, by focusing on the necessity of a critical attitude as to where the recording electrodes should be placed on the olfactory bulb.

Following the discovery by Selset & Døving (1980) that mature anadromous char (*S. alpinus* L.) were attracted to intestinal contents from their own genetic strain, together with the tentative suggestion by Selset (1980) that salmonid pheromones could be of a bile salt nature, Døving, Selset & Thommesen (1980) compared the olfactory potency of bile salts to that of amino acids. The EEG thresholds of the most potent amino acids asparagine and methionine had previously been determined to approximately 10^{-8} M by Belghaug & Døving (1977). The odour threshold for methionine was confirmed by monopolar DC-recordings on the olfactory bulb in char (*S. alpinus* L.) and grayling (*Thymallus thymallus* L.).

The recordings performed were made simultaneously from two positions on the olfactory bulb, according to the spatial specificity reported by Thommesen (1978). The bile salts tested by Døving et al. (1980) demonstrated responses with characteristic spatial differences compared to those of the amino acids. The typical responses to bile salts were located close to the bulbar position, which was found to be the most sensitive position to 'fish odour'. Taurine-conjugated bile salts were found to be up to 1000 times more potent than methionine.

From the results obtained by Døving et al. (1980), it was suggested that two types of olfactory receptors could be acting, one responding to bile salts and the other to amino acids. Odour specificity of receptor sites in salmonids, related to bile salts and amino acids, were later demonstrated by Thommesen (1982), who confirmed a differentiated spatial distribution also for the receptors on the lamellae. Recently, it has been shown that the spatial distribution of the suggested olfactory receptors might be related to the distribution of microvillous and ciliated receptor cells in the olfactory epithelium (Thommesen, 1983).

(3) Chemistry

One aspect of the salmon homing complex that has achieved little attention, compared to the number of papers presented and information gathered, is the chemical composition of the odorants representing the 'home-stream odour'. The minor attention paid to this important field reflects partly the lack of convenient bioassays for testing, as pointed out in the section on behaviour. Since no fish pheromones have yet been chemically identified (Liley, 1982), the absence of attention also reflects a lack of established chemical procedures for the isolation and identification of aquatic odorants.

In their conditioning experiments with bluntnose minnows, Hasler & Wisby (1951) demonstrated the active fraction of creek waters to be some organic volatile material. The fractions tested were obtained by separating the water by distillation. Stream waters must be expected to contain many substances that vary between the streams, and which could originate from many sources. The possibility of conditioning fish to such waters, i.e. producing a response in the animal to some odour in the water by reward or punishment, does not necessarily mean that the substances used in migration have been the active ones. The results of Idler et al. (1961) and Fagerlund et al. (1963), also demonstrating the active material as mainly volatile, dialyzable, neutral and heat-labile, must be carefully evaluated due to the lack of specificity in their bioassay, as mentioned in the section of behaviour (section V (1)).

Based on the suggestion by Nordeng (1971, 1977), and the electrophysiological studies by Døving et al. (1973, 1974), that skin mucus from salmonids could be the source of pheromones, Stabell & Selset (1980) studied skin mucus from fish by chemical means. The study revealed that 'customary' ways of collecting skin mucus could result in contamination by intestinal juice. Presence of free amino acids was demonstrated in 'pure' skin mucus, collected by a 'vacuum cleaning' method, confirming skin mucus as a source of olfactory stimulating substances. It was pointed out, however, that when possible contamination by intestinal juices was taken into consideration, the authors found no evidence of skin mucus acting alone as a source of pheromones in salmonids. The question of skin mucus acting as a source for salmonid pheromones was also raised by Selset & Døving (1980), who could find no attraction in mature migrating char (S. alpinus L.) to 'pure' mucus taken from the skin of juvenile char of the same population.

A chemical procedure for fractionation of salmonid odorants was developed by Selset (1980). The method involves precipitation by acetic acid of high molecular weight material, followed by chromatography with Sephadex G-25 and LH-20 gels. When applied to intestinal content from juvenile arctic char, some fractions from the chemical separation elicited attraction in mature char from the same population (Selset & Døving, 1980). The chemical fractionation methods established by Selset (1980) indicated that the attractive substances could be of steroid nature, and bile salts were presented as a tentative suggestion for salmonid pheromones.

Chemical separation methods, similar to those of Selset (1980), have been applied to excretion products from Atlantic salmon (Stabell, Selset & Sletten, 1982). Examination by thin-layer chromatography of fractionated material from six groups of salmon smolt, originating from three rivers, revealed that eight components varied between the groups. The components demonstrating variation were found in both intestinal contents and skin mucus. The fractions containing the most variable components from intestinal contents also gave the lowest thresholds in electrophysiological measurements carried out by Fisknes & Døving (1982). Since chemical fractions similar to those containing group variations had already been demonstrated as attractants in char by Selset & Døving (1980), Stabell *et al.* (1982) suggested that the examined components were odorants. Although no rigid conclusions were drawn concerning the nature of the examined substances, it was emphasized that if used in chemical communication, they could provide the specific clues needed for a successful return to the home river.

VI. THE MORPHOLINE APPROACH

(1) *Background experiments*

Starting in 1970, some extensive experiments related to fish migration were conducted for several years in Lake Michigan (Madison *et al.*, 1973; Dizon, Horrall & Hasler, 1973 *a*). The main objective with the experiments carried out was to test the 'imprinting' hypothesis proposed by Hasler & Wisby (1951). The idea behind the experiments was that if salmonid navigation took place by a process of learning ('imprinting') of stream odours during a critical period in the early life of the fish, resulting in the mature individuals' ability to recognize these odours upon migrant return, it should also be possible to 'imprint' fish in the early stages of life to artificial odours, i.e. to synthetic organic compounds not common in Nature.

Three different types of 'imprinting' experiments were carred out, with coho salmon (*O. kisutch*) as experimental animals: (1) census experiments, i.e. marking and release of smolt after exposure to synthetic chemicals followed by registration upon migrant return, (2) electrophysiological recordings, and (3) tracking experiments with floating tracks or ultrasonic equipment.

Morpholine (C_4H_9NO), a heterocyclic amine, was initially chosen as the 'imprinting' chemical, and up until 1973 morpholine alone was used for the experiments reported. Another chemical, phenethyl alcohol (PEA, C_8H_9OH), was also used and from 1973 competitive experiments were conducted exposing groups of fish separately to each of the two chemicals.

Census experiments in relation to artificial 'imprinting' were reported by Cooper *et al.* (1976) and by Scholz *et al.* (1976). Electrophysiological experiments were reported

by Dizon et al. (1973a), and by Cooper & Hasler (1973, 1974, 1976). Ultrasonic tracking experiments were reported by Madison et al. (1973) and by Scholz et al. (1975), while float tracking experiments were reported by Johnsen & Hasler (1980). During the progression of the experimental series, several reviews have been produced (Madison et al., 1973; Scholz et al., 1974, 1975; Hasler & Cooper, 1976; Hasler et al., 1978). In addition, census experiments related to artificial 'imprinting' in steelhead trout (*S. gairdneri*) were reported by Cooper & Scholz (1976) and Scholz et al. (1978a), and in brown trout (*S. trutta*) by Scholz et al. (1978b).

Considering the impressive output of literature published on these artificial 'imprinting' experiments, a detailed description of the experimental series will not be given in the present review. An evaluation of the reports, however, has revealed some striking points that will be discussed in the following sections. Concerning the following assertions made, readers are recommended to consult the original papers for confirmation whenever necessary.

(2) *Odorant properties of morpholine*

Wisby (1952) found that morpholine could be detected by unconditioned coho salmon down to a concentration of 1×10^{-6} mg/l ($1 \cdot 1 \times 10^{-11}$ M). At low concentrations the chemical was found to be weakly repellent. Based on Wisby's findings, the above-mentioned artificial 'imprinting' experiments were performed with a concentration of 1×10^{-5} mg/l ($1 \cdot 1 \times 10^{-10}$ M) morpholine during exposure (Madison et al., 1973; Cooper et al., 1976; Scholz et al., 1976).

Dizon et al. (1973a) exposed $1\frac{1}{2}$-year-old coho salmon smolts to morpholine for 1 month. The fish were held in a Wisconsin hatchery for 10 months together with a control group, and then subjected to EEG tests. When tested with 1 % ($1 \cdot 1 \times 10^{-1}$ M) and 0·01 % ($1 \cdot 1 \times 10^{-3}$ M) morpholine, and the response to these compared with responses to 0·06 N NaCl, a significantly higher EEG activity was found for the morpholine-exposed compared to the control fish. Dizon et al. (1973a) concluded that a long-term olfactory 'memory' existed in coho salmon, resulting from 'imprinting' to morpholine during a critical period. It was stressed, however, that attempts had not been made to determine whether the observed sensitization was exclusively in response to morpholine or also to other stimulatory products.

Scepticism concerning the conclusion in the above-mentioned report was introduced, however, in the report by Cooper & Hasler (1973), who informed that Dizon et al. (1973a) in their experiments had found responses in morpholine 'imprinted' and control fish to 0·1 % ($1 \cdot 1 \times 10^{-2}$ M) morpholine that were *not* statistically different from each other. Tests with 0·1 % morpholine were not reported by Dizon et al. (1973a).

The fish tested by Dizon et al. (1973a) were neither sexually mature, nor had they returned to any releasing site scented with morpholine. Another experiment was therefore performed to test if adult migrating salmon showed a similar response (Cooper & Hasler, 1974). Coho salmon, both morpholine 'imprinted' and control fish, captured in the mouth of Oak Creek upon their returns as adults in 1972 were tested by EEG recordings from the olfactory bulbs. The responses for the two groups of fish were found significantly different when 1 % morpholine was used. No fish responded to concentrations of 0·1 % and 0·01 % morpholine. Cooper & Hasler (1974) concluded that their results demonstrated that olfactory information had been retained for 18 months, the period between smolting and homeward migration.

A pH 7·5 buffer, however, was also found to elicit a significantly different response in the two above-mentioned groups of fish. An alternative conclusion to be reached from Cooper & Hasler's experiment could therefore be that, if exposed to morpholine as a juvenile, a change in olfactory receptivity is produced in the fish that can be detected by using nonspecific stimuli after 18 months. An odour memory as claimed by the authors seems, however, unjustified from the data presented.

Hara (1974) designated morpholine as being olfactory non-stimulatory when tested by electrophysiological means in rainbow trout. When tested at the concentration of 10^{-4} M, morpholine failed to evoke EEG responses. Sutterlin & Sutterlin (1971), using Atlantic salmon, measured multiunit electrical responses from the olfactory mucosa in response to odour stimulation, and also classified morpholine as non-stimulatory.

In accordance with Cooper & Hasler (1974), Hara (1974) and Hara & MacDonald (1975) found that when stimulated by 1 % (1.1×10^{-1} M) morpholine, an initially inhibited EEG response was first recorded, and then slowly replaced by an oscillatory potential which was not terminated by rinsing. The morpholine effect was mainly an off-response, reaching its maximum response level after the stimulus ceased. The magnitude of response to morpholine was in addition found to increase with repeated stimulation, and normal response to amino acids was inhibited after application of 1 % morpholine to the nares. It was pointed out that at 1 % the response to morpholine was 100 million (10^8) times higher than that of the lowest threshold determined electrophysiologically for amino acids. The result obtained caused Hara (1974) and Hara & MacDonald (1975) to suggest that the morpholine solution, instead of acting at specific receptor sites, may have penetrated deep into the olfactory epithelium and caused a nonspecific irritant effect at unspecialized cell surfaces.

Cooper & Hasler (1975) argued against the above criticism by stressing that significant differences in evoked potentials had been detected in response to Oak Creek water scented with morpholine at about 10^{-3} mg/l (1.1×10^{-8} M). Since morpholine responses had not been found at the concentrations of 0·1 % (1.1×10^{-2} M) or 0·01 % (1.1×10^{-3} M), a specific response pattern of the olfactory organ was suggested, working for very low and very high concentrations, similar to that known to exist for magnetic detection. A suggestion of that kind, however, is not in accordance with any current knowledge related to the functional properties of the olfactory organ, and should therefore be considered with care. In addition, no consistent proof has been found demonstrating morpholine as the active stimulus in the applied Oak Creek water mixture.

Cooper & Hasler (1976) reported a significant difference between morpholine-exposed and control fish in only one out of three series with coho salmon for 10^{-3} mg/l (1.1×10^{-8} M) morpholine mixed in Oak Creek water. The data also reveal that L-methionine in the concentration of 10^{-5} M elicited significant response differences in one of the test series. In the same experiment, 1 % (1.1×10^{-1} M) morpholine was found to elicit a significantly different response in all three series of cohos, and also in a parallel experimental series with rainbow trout. It is interesting to note that the EEG response pattern obtained to Oak Creek water scented with morpholine resembles that of L-methionine and not the one commonly obtained from stimulation with morpholine.

Leggett (1977), reviewing the ecology of fish migrations, claimed that the experiments of Cooper & Hasler (1976) effectively dismissed earlier criticisms on the use of morpholine in EEG response experiments. The author of the current review can, however, find no such evidence given in the data provided by Cooper & Hasler (1976).

The procedure of morpholine exposure given by Dizon *et al.* (1973*a*) and Cooper & Hasler (1973, 1976) was adopted for rainbow trout smolt by Hara & Brown (1979), followed by EEG recordings from the olfactory bulb after a period of 12 months. Again the special delayed response pattern of morpholine at 1 % ($1 \cdot 1 \times 10^{-1}$ M) was obtained. At 10^{-2} and 10^{-3} M, the effect of morpholine was primarily found to be a brief inhibition of the spontaneous background activity. No response was recorded with morpholine at 10^{-4} M and lower. In contrast to the previously reported significant differences in response between morpholine-exposed and unexposed groups (Dizon *et al.*, 1973*a*; Cooper & Hasler, 1974, 1976), no such differences were found to morpholine by Hara & Brown (1979). Again it was concluded that the morpholine effect was caused by a mechanism not directly associated with the normal olfactory function. Since no fish failed to respond to morpholine at the concentration of 1 %, it was also suggested that the effects of the chemical were non-specific.

Cooper (1982) rejected the results of Hara & Brown (1979) by pointing out that: (1) 'imprinting' to morpholine had not been demonstrated by behavioural or other experiments, (2) the rainbow trout used in the experiments were a non-migratory group, and (3) the fish in the experiments had not been in spawning condition.

It is worth noting that Cooper (1982) referred to Dizon *et al.* (1973*a*) as support for his arguments. As previously mentioned, Dizon *et al.* (1973*a*) found differences in the EEG responses between morpholine-exposed and unexposed coho salmon that had *not* been used in any behavioural experiments and that were *not* sexually mature when tested (Cooper & Hasler, 1974). It should also be stressed here that *all* salmonid species must be regarded as migratory, whether relating to potamodromous (landlocked) or anadromous strains (Myers, 1949, Harden-Jones, 1968). The behaviour of potamodromous strains of brown trout (*S. trutta*), investigated by Stuart (1957), has in fact been used in arguments for imprinting by Hasler *et al.* (1978) and by Cooper & Hirsch (1982).

Reply to the critique from Cooper (1982) was given by Hara & Brown (1982). Here it was especially stressed that, concerning practical techniques, the use of Pasteur pipettes for adding stimulants to the nose of the fish, as opposed to a continuous flow type of stimulus apparatus, was to be criticized. In total it should therefore be concluded that when the very high concentrations of morpholine necessary to induce EEG responses are taken into consideration, together with the questionable results obtained with that chemical, the odorant properties of morpholine should be questioned.

(3) 'Imprinting' and ecology

(a) The theoretical basis

When discussing 'imprinting' in relation to fish ecology, some fundamental points related to the definition of 'imprinting' should first be considered. When the concept of 'imprinting' was transferred from the visual sense in birds (Lorenz, 1935, 1970, reviewed by Bateson, 1966) to the olfactory sense in fish (Hasler & Wisby, 1951), one out of two important factors necessary to fulfil the criteria for 'imprinting' seems to have been lost, and the other inadequately defined.

Imprinting in birds has mainly been related to moving objects. An immobile source of stimulation can, however, also be detected as such and may be imprinted to. It is important to note, however, that this can only occur if the object is compared to stationary points in the environment. That is, included in the concept of 'imprinting'

lies the fundamental fact that the animal must be capable of perceiving the 'imprinting' stimulus in relation to something (a background), and develop a preference to that stimulus through its relative stimulation. In the transfer of the 'imprinting' theory from vision in birds to olfaction in fish, the principle of relativity has been lost.

How can an animal choose one odour, or a selection of odours, among dozens when the presence and stimulatory properties of these substances remain constant in relation to other odorants present? One approach could be to postulate an innate preference of the fish to certain classes of compounds during a sensitive period. An explanation of that kind does, however, necessarily include a certain influence of genetics. Since influence of inheritance in relation to home-stream detection has been rejected in relation to an 'imprinting' theory (Scholz *et al.*, 1975, Hasler *et al.*, 1978), it appears that when applied to fish, the 'imprinting' hypothesis contains a built-in contradiction.

Imprinting in birds occurs at a time when the young individuals have been subjected to few changes in input. Their capacity to respond selectively to certain aspects of the environment depends on relatively simple preferences which, if learned, were acquired at a stage when the sensory system was poorly developed (Bateson, 1966). Unless a bird has been exposed to a conspicuous object within a short period after hatching, it cannot be imprinted to that object. In contrast, for those salmonid species undergoing smoltification, 'imprinting' has been suggested to occur during smolt stage (Madison *et al.*, 1973; Scholz *et al.*, 1975; Hasler *et al.*, 1978). The sensitive period defined implies that 'imprinting' in fish must occur at a stage where the fish have been subjected to a wide spectrum of input and when the sensory system is already well developed.

The basis for the definition of a sensitive period has been that transplanted fish return to the river of release when released during the smolt stage (Madison *et al.*, 1973; Hasler *et al.*, 1978). Considered from the point of view of natural ecology, it has been shown in this article that alternative explanations can be given for return of transplanted fish. It therefore appears that a sensitive period, which is fundamental to an 'imprinting' theory, must at best be considered as inadequately defined in relation to fish.

(b) Stocking experiments in the Great Lakes

Peck (1970) transferred hatchery-reared Columbia River coho salmon to Lake Superior, where 192400 smolts were released in the Huron River, Michigan, in May 1966. Most smolts left the river within a week and essentially all had entered Lake Superior within a month after planting. Upon maturation and adult return, an extensive straying was recorded over 90 % of the Michigan shoreline of Lake Superior. Of the 120 Michigan streams tributary to Lake Superior, stray coho were reported in 33, and the following year reproduction was confirmed in 16 out of 20 streams surveyed. The return of coho to the Huron River was an estimated 4 % of the number released. That figure is in accordance with those generally obtained from stocking in the Lake Michigan streams, reported from 2 to 8 % (Madison *et al.*, 1973; Scholz *et al.*, 1975; Hasler *et al.*, 1978).

The extensive straying in the above-mentioned coho planting performed in the Huron River, Lake Superior, has been suggested as due to the short time spent by the fish in the stream. In addition, it was suggested that a possible completed 'imprinting' could have occurred in the Cherry Creek hatchery where the fish were held until stocking (Peck, 1970; Hasler *et al.*, 1978).

Planting of coho smolts in the Platte River, a Lake Michigan tributary, gave 19·5 %

return of mature fish to the planting site (Peck, 1970). The coho in the Platte River planting were reared for 12 months prior to release in water supplied by a Platte tributary. Peck suggested that because of the long residence of fish in the Platte tributary water, the fish probably received a good 'imprint'.

The Platte River release, together with the Huron River planting, demonstrate that the survival rate of coho in the Great Lakes is substantial. The Huron River planting gave no exact number for total recaptures, although an extensive straying was recorded. The Platte River planting also failed to give any number for total recovery, but the number of recaptures in the stream of release tells us that survival rate must have been at least that figure.

An indication of substantial straying of coho planted into Lake Michigan streams in general, was given by the number of fish captured in Oak Creek during the period 1970 to 1972 (Madison et al., 1973). In all 3 years the number of unmarked strayers exceeded that of experimental fish.

In the census experiments related to artificial 'imprinting', altogether 0·64 % of the fish exposed to morpholine returned to the scented stream from the planting in 1970 and 2·7 % returned from the planting in 1971 (Madison et al., 1973). From the planting in 1972, 8·4 % of the morpholine-exposed fish returned to the scented stream (Cooper et al., 1976). The release experiments in 1973 and 1974 gave returns of 4·1 % and 4·5 %, respectively, for the morpholine-exposed fish, and returns of 2·7 % and 2·0 % for the phenethyl alcohol-exposed fish. From the above it appears that the 'imprinting' experiments to artificial odours have not given results in percentage return to the stocking site that deviate from results obtained from general stocking procedures in the Great Lakes.

(c) Artificial 'imprinting' experiments

With reference to the previously given explanations on the effects of releasing time and residence period on 'imprinting' (Peck, 1970), results from the artificial 'imprinting' experiments raise doubts with respect to percentage return and straying. Madison et al. (1973) exposed coho salmon smolts to morpholine from April 15th to May 14th in their 1970 release series. The period of morpholine exposure included 1 week after appearance of smolting behaviour. Only 0·64 % of the morpholine-exposed fish returned to the scented stream, and no difference in percentage return was found between the morpholine-exposed group and the unexposed group.

In the 1971 release series, the morpholine exposure was performed from April 13th to May 16th, this time including 2 weeks after the onset of smolting. The return from the 1971 release series gave 2·7 % return of morpholine-exposed fish compared to 0·35 % return of the non-exposed control group. The authors suggested that the difference between the 1970 and the 1971 release series was due to differences in 'imprinting' history, the most important factor being the 1 week longer smolt holding period in 1971.

In the 1972 release series, however, three parallel release sets were performed, with smolt holding periods from April 3rd to May 22nd of 4 days, 1½ weeks and 2 weeks after the onset of smolting (Madison et al., 1973). Upon migrant return, no significant difference was obtained in percent recovery between the three groups of morpholine-exposed fish, being 8·7 %, 7·9 % and 8·8 %, in that order (Cooper et al., 1976). These results demonstrate that differences in percentage return of planted fish cannot be attributed to time of release in connection with smolting.

The total time of exposure to a stream odour does not reflect the percentage return either, as suggested by Peck (1970) in relation to the above-mentioned Platte River planting. In the 1973 release series in Oak Creek, two groups of coho smolts were exposed to morpholine for 44 days, while a third group was morpholine exposed for only 2 days. The number of fish returning to Oak Creek in the autumn of the same year was higher for the 2-day-exposed group than for the 44-day-exposed groups (Cooper *et al.*, 1976; Cooper & Hirsch, 1982). Return of coho from artificial 'imprinting' experiments reveals, therefore, that no apparent consistency can be found between holding (or exposure) time and frequency of migrant returns.

It must be assumed that the coho used in the artificial 'imprinting' experiments have a rate of survival equal to that obtained for other planting experiments performed in the Great Lakes (i.e. at least 19·5 %). Since percentage recapture in the stream of release of artificially 'imprinted' coho ranged from 0·64 to 8·4 (Madison *et al.*, 1973; Cooper *et al.*, 1976; Scholz *et al.*, 1976), a substantial straying must be suggested to have occurred. A moderate straying rate, however, has been recorded for the fish used in the artificial 'imprinting' experiments.

Scholz *et al.* (1976) counted the straying rate of morpholine-exposed fish from their 1973 and 1974 release series as 5·9 in 1974 and 2·4 in 1975. For PEA-exposed fish, straying rate was found to be 9·5 and 7·4 for 1974 and 1975, respectively. As pointed out earlier in this article, fin-clipping does not give reliable data on straying. In the experimental series related to artificial 'imprinting' in Lake Michigan, fin-clipping has always been used for marking. From that, the number of strayers in the artificial 'imprinting' experiment can be assumed higher than those reported.

Looking at the fishing effort conducted in the experimental and the surrounding streams by Scholz *et al.* (1976), further support to the assumption of high straying is given. Taking the Creel census as an example, the data reveal that fishing effort given by number of trips averaged 200·5 for each of the four experimental streams in 1974, whereas 15 other streams in the same area were surveyed with an average fishing effort of only 57·4. Similar data for 1975 give the number of surveying trips as 114·5 and 23·5, respectively. Gill net and electrofishing, the other two fishing methods used, demonstrated the same trend.

The above authors pointed out that the fishing effort reported was not strictly comparable between sites because techniques that worked well at one place were not effective at others. From the total data on fishing effort, however, it must be suggested that the figure for straying rate in the experiments by Scholz *et al.* (1976) seems to be biased because of a higher fishing effort in experimental streams compared to neighbouring streams. Accordingly, a larger straying than recorded may have taken place in the area surveyed.

Altogether, the results from planting and artificial 'imprinting' experiments in the Great Lakes seem to be similar to those obtained from transplantation experiments in general, demonstrating a low percentage return to the stocking site and a high straying rate compared to that expected in natural systems. The data for return and straying indicate, therefore, that 'imprinting' and 'odour memory' may not have been the principal clue for 'home' stream detection, neither in general planting experiments nor in the artificial 'imprinting' experiments with coho salmon performed in the Great Lakes.

(4) *Preference for artificial chemicals*

One striking and crucial point remains in an evaluation of the experiments related to artificial 'imprinting'. Obviously, in the majority of experiments a significantly higher number of fish exposed to artificial odours as smolts preferred the scented streams compared to unexposed fish upon migrant return (Cooper *et al.*, 1976; Scholz *et al.*, 1976). Also the tracking experiments performed indicate that morpholine-exposed fish are able to sense the artificial scent (Madison *et al.*, 1973; Scholz *et al.*, 1975), and apparently demonstrate preference for it when given an alternative choice of non-scented water (Johnsen & Hasler, 1980; Scholz, 1980, 1982). Ultrasonic tracking experiments presented by Scholz *et al.* (1975) demonstrate, however, that morpholine detection may not have been the *principal* clue for 'home-stream' selection in the artificial 'imprinting' experiments.

Fish exposed to morpholine as smolts and stocked in Bear Creek together with controls were recovered in 1974 at Bear Creek as adults (Scholz *et al.*, 1975). The fish were then transported to Manitowoc, where morpholine was added to the Little Manitowoc River that year (Scholz *et al.*, 1976). Equipped with ultrasonic transmitters, the fish were released to the south of the Little Manitowoc River, so that the morpholine-scented stream had to be passed if the fish turned north towards its 'home' stream. Eight 'imprinted' and six control fish were tracked. All of the control fish and one 'imprinted' fish moved past the mouth of the morpholine-scented river. Seven 'imprinted' fish were attracted to the mouth of the Little Manitowoc River and four of them moved for a short distance into the river. After periods of 1–4 h, however, six of the fish continued north while the seventh fish was captured by a fisherman.

Scholz *et al.* (1975) concluded that although 'imprinted' fish appeared to detect morpholine at the Little Manitowoc River, judged from their responses compared to non-imprinted fish, they did not remain in the stream treated with morpholine, but headed north towards the location where they were stocked. It should here be added that if morpholine was the principal clue for 'home' stream detection in the experiments with that chemical, and 'imprinting' had taken place as generally claimed, it would be reasonable to expect that the 'imprinted' fish in the above tracking experiments should have ascended the scented river.

In the census experiments performed, morpholine was added to the stream water to an approximate concentration of 10^{-5} mg/l ($1\cdot1 \times 10^{-10}$ M) (Madison *et al.*, 1973; Scholz *et al.*, 1976). The EEG measured threshold (Cooper & Hasler, 1974, 1976) and the behavioural threshold claimed from the census experiments (Cooper *et al.*, 1976; Scholz *et al.*, 1976) therefore differ by a concentration ratio of 10^9 (see also section VI (2)). Comparative studies between electrophysiological thresholds, and behavioural thresholds determined by classical conditioning techniques, have been carried out in relation to amino acids and olfaction in Arctic char (*S. alpinus* L.) by Belghaug & Døving (1977) and Jónsson (1977). The molar behavioural thresholds were found to be 10 to 100 times lower than those obtained by EEG recordings, while the electrophysiological thresholds (10^{-7} to 10^{-8} M) were found to be in accordance with those obtained for other salmonid species by Hara (1973).

Present knowledge on the functional properties of the olfactory sense in fish, together with the inconsistency in results obtained in experiments related to artificial 'imprinting'

therefore seem to support the conclusion by Hara (1974) that the olfactory stimulating properties of morpholine must be questioned. The topic is further complicated through the report by Mazeaud (1981), describing morpholine as a general attractant for salmonids.

How can the general preference obtained in census and tracking experiments by artificially 'imprinted' fish to artificially scented streams be explained? A deeper analysis of the preference phenomenon displayed after artificial chemical exposure seems to be related to fields that go beyond the subject of this review. Nevertheless, the author has attempted to understand the preference phenomenon, and some tentative and alternative suggestions will be presented.

(1) Whatever the sensory system used, the displayed preference could express a positive conditioning to the chemical, resulting from food given during the 'imprinting' period. This explanation, however, appears to be contradictory to the previously mentioned principle of relativity for the applied stimulus in relation to the background odours, since the artificial chemical was given in steady rate concentrations.

(2) The effects of the applied chemicals during exposure could be due to the phenomenon of 'selective degeneration' (Døving & Pinching, 1973; Pinching & Døving, 1974). Long-time exposure to non-natural chemicals, resulting in a suppressed activity of central neurons, could partly explain the preference phenomenon by causing a lack of avoidance response to chemicals acting otherwise as repellants to the intact animals. Again, the explanation appears contradictory to that reported in the literature, since a negative rheotaxis has been demonstrated in both morpholine-exposed and control fish in the absence of morpholine (Johnsen & Hasler, 1980).

(3) A process of learning ('imprinting') of the artificial chemicals may have occurred, established under elevated thyroid hormone levels during smoltification, as proposed by Scholz (1980). It should be noted, however, that this explanation also suffers from the previously mentioned weakness concerning relativity of applied stimulus in relation to the natural chemical background.

Evidently, the explanations given for a functional role of artificial chemicals in 'imprinting' experiments are incomplete. A crucial point still appears to be that even if a process of learning, memorizing and attraction has occurred, no evidence can be found for artificial chemicals working as *olfactory* clues. Since olfaction is demonstrated as mandatory for home-stream detection in salmonids (i.e. Wisby & Hasler, 1954), olfactory 'imprinting' to artificial chemicals in relation to home-stream detection must in consequence also be questioned. The results from studies related to the 'morpholine approach' reveal, therefore, that when looked at from the point of view of natural ecology, the field seems to represent a complex and possibly inconvenient approach to the problem of salmonid homing.

VII. DISCUSSION AND CONCLUSIONS

(1) *Genetic aspects of homing*

In this review, data and arguments have been summarized demonstrating that naturally propagated Atlantic salmon, like wild anadromous salmonids in general, return to their natal river to spawn (i.e. Calderwood, 1940; Dahl, 1939; Berg, 1964). Homing to the natal river appears very precise, since generally little straying has been registered in natural systems (Carlin, 1969a). According to the literature surveyed, the percent

return of wild externally tagged Atlantic salmon to their native river range from 1 %
to 3·4 % of those marked as smolt with a maximum straying rate of 3.

External tags in homing experiments appear to have a negative effect on the fish. The
tagging procedure causes tissue damage which obviously increases mortality, and the
transport burden of the tag may decrease swimming speed and increase visibility to
predators (Saunders, 1968). Comparative studies have also revealed that a substantially
higher mortality must be expected from external tags in relation to internal micro-tags
and fin-clipping (Ísaksson & Bergman, 1978; Berg, 1977b). Reliable records for ocean
captures, river returns and straying of fish in homing experiments must, however, be
available when evaluating data from naturally spawned and artificially raised fish. Thus,
visible and comparable tagging is important and necessary, and only data from
experiments with external tags can be taken into consideration.

Circumstantial evidence has been presented demonstrating that a river system may
perpetuate multiple 'stocks' or populations of Atlantic salmon that can be distinguished
from each other by morphological characteristics (Berg, 1964), stage and age of maturity
(Gardner, 1976), time of entry into the river system (Berg, 1934), and localization of
spawning regions (Went, 1946; Saunders, 1967). As for the presence of sympatric
populations of Atlantic salmon within a river system, evidence has also been provided
through biochemical genetics (Møller, 1970; Ståhl, 1982). Although direct evidence
from tagging experiments for tributary homing in Atlantic salmon is defective, such
evidence is readily available for other salmonid species (i.e. Ricker, 1972; Stuart, 1957;
Tilzey, 1977).

Salmon raised in hatcheries generally demonstrate a far lower percentage return to
the river of release than wild, naturally propagated fish. The difference has been shown
not to result from a low survival rate of hatchery fish in the sea, as commonly suggested,
but is attributed to a decreased navigation ability resulting from human interference
in fish genetics. Since, even in small rivers or tributary systems, salmon may be
subdivided into genetically distinct sympatric populations, the disruption of navigation
ability has been suggested to result from an artificial production of inter-population
hybrid fish. This suggestion would appear to be supported by genetic considerations,
as presented by Dobzhansky (1964) and Helle (1981). Such an interpretation is also
supported by data obtained by Bams (1976), who demonstrated that homing ability in
pink salmon is influenced by inheritance.

The suggestion of decreased navigation ability in artificially raised fish is supported
by the fact that hatchery fish demonstrate a far higher rate of straying than wild fish,
even when released within their natal systems. In many of the experiments reported in
the literature, the return of hatchery-raised salmon has been so negligible that the
biomass gained from returned migrants has been outweighed by that of released smolts.
It appears, therefore, that artificial raising of Atlantic salmon, followed by release in
rivers as smolt, has often been a waste of reproductive capacity which would have been
better utilized by Nature itself.

The literature presented has revealed that several decades of experimental efforts
focused on hatchery techniques and practical methods of smolt release, as reviewed by
Saunders (1977) and Porter (1979), have not produced the desired outcome concerning
return and straying of hatchery fish. To justify the deficiency in the results obtained,
there has been a tendency in salmonid management to reject the 'old' data from salmon

homing experiments, and replace them with so-called 'better' data obtained during the last decade.

Hansen (1983) concluded that straying is common both in reared and wild fish. His data are based on smolt tagging experiments in two Norwegian rivers, demonstrating a straying of 13·8 % and 14·5 % for adult migrants. The rivers that were reported as wild smolt producers, had however been stocked by hatchery fry for several years. The tagging of 'wild' smolt that may originally have been hatchery fry, can result in sources of errors that heavily bias the data obtained. Such data must therefore be rejected as representative for wild or native fish, in the same way as data from hatchery-reared fish in general. It should also be noted here that the conspicuous deviations in percentage return and straying of wild fish presented in experiment no. 7, Table 1, could well result from causal relations similar to those mentioned.

Data available from the literature indicate that the navigation ability of salmonids may display flexibility and adaptability, both during hatchery rearing and natural dissemination after stocking. In natural systems, brown trout have the ability to establish an accurate tributary homing (Tilzey, 1977). In the 'sea-ranching' programmes with Atlantic salmon (i.e. Kollafjörður Fish Farm, Iceland), an equivalent ability appears to be present when direct hatchery releases are combined with self-containment of eggs and milt from returning migrants. The improvement in navigation ability over successive generations must result from the influence of inheritance. Genetic aspects should therefore be strongly considered when the mechanisms behind homing ability in anadromous salmonids are evaluated.

(2) Olfactory aspects of homing

The importance of the olfactory sense in stream orientation by homing fish is well documented. Following the classical work with coho salmon by Wisby & Hasler (1954), several reports were published by other investigators, confirming the original observations. The study by Toft (1975), presented in part in this review, also recognized the importance of the olfactory sense in coastal navigation by homing fish. Olfaction may be essential for the maintainance of navigation ability throughout salmonid homing, and inheritance affects that ability. There therefore appears to be a logical connection between the use of the olfactory sense and the role of genetics in the navigation ability of salmonid fishes.

It has long been known that fishes are able to detect their own species using their sense of smell (Wrede, 1932; Göz, 1941; Frisch, 1941). With regard to chemical communication in general, the existence of species-specific signal substances (pheromones) in fishes is well documented in the literature. As pointed out in the review by Solomon (1977), pheromones play a significant role in fish behaviour and ecology.

Salmonids are attracted to scent from their own species, as reported in char (*S. alpinus*) by Høglund & Åstrand (1973), and olfaction has been demonstrated to be the effective sensory modality. Rainbow trout (*S. gairdneri*) are strongly attracted to water taken downstream from spawning conspecifics and weakly attracted to water taken downstream from mature non-spawning fish (Newcombe & Hartmann, 1973). Ovarian fluid has been shown to be an attractive stimulus to ripe male rainbows (Emanuel & Dodson, 1979), and two basic, ether-soluble substances extracted from post-ovulatory ovaries have been suggested as the pheromones attracting rainbow males (Honda, 1980).

Discrimination ability of scents from genetical strains within their species, and behavioural preference for their own strain's odour, has been demonstrated in mature Arctic char by Selset & Døving (1980). Similar discrimination and preference abilities have also been found in Atlantic salmon parr by Stabell (1982a). In addition, electrophysiological evidence has been provided for char on the ability to discriminate odours of genetically different strains within their species (Døving et al., 1974). A molecular diversity of possible odorants from genetically different strains has also been demonstrated by chemical means in Atlantic salmon (Stabell et al., 1982). The existence of pheromones at both species and sub-species levels would therefore appear to be well documented in salmonids.

Contrary to the commonly accepted 'imprinting' hypothesis in fish migration, which states that fishes can 'imprint' to (or learn) some specific odours originating from soil and plants in their home stream, it has been shown from data in the literature that the fishes themselves may condition the water and 'mark' the substrate in streams and lakes. Evidence for substrate marking has been given by Foster & Berlin (1980), who demonstrated that spawning fish preferred a substrate scented by excretory products from young conspecifics. Data from Miller (1954) also give circumstantial evidence for substrate marking by fish. He found that resident cutthroat trout adopted a new 'home' area when confined to that area of their home stream for more than 30 days. Trout confined for less than that time, however, returned to their original 'home' area, probably guided by smell.

Since it has been proposed that 'imprinting' is a smoltification phenomenon (Scholz, 1980, 1982), Miller's observations would be better explained by a 'washing-out' of the previous marking, followed by a re-marking of the new area. Marking of the substrate by animals in aquatic environments has previously been reported in pulmonate snails by Wells & Buckley (1972) and in salamanders by Jaeger & Gergits (1979). Related to comparative physiology, it is interesting to note that faecal material was also suggested in this latter report to be the source of signal markers.

(3) Pheromones as opposed to 'imprinting'

According to the literature, two hypotheses related to homing and olfaction in salmonids have predominated, an 'imprinting' hypothesis based on learning of stream odours (Hasler & Wisby, 1951), and a pheromone hypothesis based on genetic considerations (Nordeng, 1977). Until recently the most accepted hypothesis has been the one related to 'imprinting'. Arguments in favour of an 'imprinting' hypothesis, however, i.e. that transplanted fishes return to the site of release and not to their native river, have been shown to be invalid in this review because hatchery-raised fish were used in the experiment. Taking into consideration rate of survival, percentage return to site of release and straying rate, the results from transplantation experiments would appear to be better interpreted from the genetical point of view.

The 'imprinting' hypothesis only covers navigation within or close to rivers or streams, and has usually been closely associated with the disputed sun-azimuth hypothesis for ocean and coastal navigation. On the contrary, the genetically related pheromone hypothesis is 'all-in-one', and seems to agree better with ecological and sensory data in all stages of homing navigation in salmonid fishes.

A serious complaint against an 'imprinting' hypothesis also exists because no

evidence has ever been provided as to the nature of the natural substances supposedly used by the fish when 'imprinting'. Only circumstantial and insufficient evidence for 'imprinting' has been provided, using artificial chemicals and indirect approaches. On the other hand, the existence of pheromones is well documented through data obtained within the fields of behaviour and electrophysiology as well as analytical chemistry. With regard to salmonid ecology, it is therefore suggested that the pheromone hypothesis of Nordeng (1977) is the one that should be given future attention.

(4) *Can pheromones be learned?*

In recent years there has been an increased recognition of the role pheromones play in salmonid migration. It seems, however, possibly for historical reasons that many scientists in the field find it difficult to reject a principle of 'imprinting'. As a result, some authors have suggested that 'imprinting' to pheromones may occur (Selset & Døving, 1980; Horral, 1981). Data from several papers has been presented in the current review, relating the navigational ability to inheritance. In addition, two circumstantial points of evidence suggest that the response to olfactory stimuli in salmonid orientation should be related to inheritance and not to learning. Firstly, it is difficult to imagine how the lowermost population in a water-chain could avoid being 'imprinted' also to the odours from other populations. Secondly, the suggested sensitive period for 'imprinting' has been restricted to the period of smolting and seaward migration (Carlin, 1969*a*, *b*; Hasler *et al.*, 1978), and possibly related to elevated thyroid hormone levels during smolting (Scholz, 1980, 1982). Since Atlantic salmon parr are able to discriminate between scents from different genetic strains (Stabell, 1982*a*), the ability to discriminate pheromones obviously exists before the period defined as sensitive for 'imprinting'. Consequently, the 'imprinting' and the pheromone hypotheses in salmonid homing do not appear to be mutually interchangeable.

Bateson (1978), commenting on fruit fly pheromones, pointed out that, even if production of pheromones can be related to a particular genotype, there is no implication that the ability to *detect* a particular pheromone is also related to genotype. He mentioned that a mechanism has not yet been proposed by which the production of a pheromone and the development of a detection mechanism can be genetically linked. Consequently, it is possible that the detection mechanism develops as a result of exposure to the native pheromone.

Taking into account the evidence presented in this review, which suggests that a learning mechanism associated with juvenile life stages in pheromone detection should be rejected, it seems that Bateson's argument can only be accepted if pre-hatching stages of fishes are considered. 'Imprinting' to population-specific pheromones should therefore not be rejected altogether, but the process of learning must occur before hatching, i.e. while the fish is still protected within its egg-membrane. It should be noted that a process of learning at that stage will be purely of neurophysiological interest, since in practical terms artificial management of fishes must be carried out according to the genetic implications of the theory.

(5) *Some problems and misunderstandings*

The expression population specific *pheromone* was used in relation to salmonid migration by Nordeng (1971, 1977). Since pheromones were originally defined at the

species level (Karlson & Lüsher, 1959), the use of the word in connection with population-specific attractants has resulted in confusion. It is not my intention to propose a further subdivision of the pheromone concept. I feel, however, that this is an important point to mention, since considerable misunderstandings occur in the literature. Referring to Nordeng (1971, 1977) and to Solomon (1973), Cooper & Hirsch (1982) state: "These authors do not limit pheromones to substances originating from conspecifics, but simply define pheromones as biological substances used for orientation." No statements, however, can be found in the above papers that give support to such an interpretation.

Geographically close populations of Atlantic salmon have been found to be genetically more similar than those further apart (Ståhl, 1982; Ryman & Ståhl, 1981). The difference in genetical patterns observed between populations may well also be reflected in their pheromones. The odorant spectrum of potential pheromones consists of at least eight different compounds (Stabell et al., 1982). If some compounds represent region-specific odours, and others represent population-specific odours, the total homeward orientation could then be a result of odour choices performed in a stepwise manner, similar to tributary homing in a large water-chain. Data presented by Power (1981), demonstrating region-specificity in salmon behaviour, would appear to agree with the above idea.

In the early stages of the salmonid life cycle, olfaction has been suggested to be important for migration between nursery and feeding areas in sockeye salmon fry (Brannon, 1972), and in relation to 'home area' stability in cutthroat trout (Miller, 1954) and Atlantic salmon parr (Stabell, 1982a). The significance of olfaction during smolt and post-smolt stages in salmonids has, however, yet to be determined. Although the mechanisms underlying navigation ability during seaward migration have been given less attention than the mechanisms controlling spawning migration and homing, localization of oceanic feeding areas appears to be of similar importance for the survival and perpetuation of distinct genetic strains.

(6) Final remarks

The literature covered in this review demonstrates that genetic aspects at the population level are of utmost importance, not only with respect to the fishes' relationship to the physical environment in the home stream, but also to the navigational ability related to homing. Preliminary data focusing on this aspect have been presented previously (Stabell, 1982b). Questions related to salmonid ecology may be better answered if interpreted in the light of population genetics. An example of interpreting a problem in this way has been effectively demonstrated in relation to 'the char problem' by Nordeng (1983).

The ideas exposed imply that genetics at the population level, with special regard to the functional role of olfaction, have management consequences and must therefore be taken into consideration. On the topic of artificial management, it is apparent that if fish genetics at the population level is not considered, then sea-ranching based on harvesting in rivers (Thorpe, 1980a, b), and 'egg banks' for conserving genes (see Saunders, 1981) must be considered to be of limited value.

I will conclude this review by adopting the logical argumentation of Shapovalov (1941). His contribution to the debate on 'homing instinct' can be transferred nearly unaltered to the modern parallel debate by substituting 'pheromone' for 'homing':

"It is true that much of the evidence in favour of the homing 'theory' is, technically speaking, 'circumstantial', in much the same manner that the evidence in favour of the evolution 'theory' and many other biological phenomena is 'circumstantial'. But, when a chain of facts forms a mass of evidence that points in one direction, it seems only reasonable and justifiable to accept the conclusions to which this evidence leads. Far from being pointless to speak of homing instinct unless 'direct' evidence is presented, it seems much more pointless to attack the 'homing theory', and consequently the conservation practices built around it, without a considerable amount of even 'circumstantial' evidence to disprove it".

VIII. SUMMARY

(1) Based on data from the literature, the phenomenon of homing in salmonids is examined with special reference to the Atlantic salmon. Wild, native fish demonstrate an excellent homing ability, judged from percent return to the home river (1–3 %) and straying to non-native watersheds (less than 3 % of returning fish).

(2) The homing ability in wild fish is shown to be closely related to the existence of reproductively isolated populations between and within watersheds, as demonstrated by data from salmonid ecology and biochemical genetics.

(3) Two main hypotheses have dominated the literature on salmonid homing during recent years: (a) An 'imprinting' hypothesis based on a process of learning of stream odours during seaward migration, coupled with sun-orientation for open sea navigation. (b) A 'pheromone' hypothesis related to odours from fish and based on inheritance and the seasonal migrating schedules of discrete populations.

(4) The olfactory sense has been demonstrated as mandatory for salmonids, both in near range and open sea navigation. According to genetic, sensory and ecological aspects of homing, the pheromone hypothesis is therefore concluded to be the most appropriate.

(5) Fish produced from artificially fertilized eggs, released within native systems or transplanted, demonstrate a reduced homing ability. Since hatchery-raised fish demonstrate a survival in sea equivalent to that of wild fish, a genetic disturbance of navigational ability has been suggested, resulting from the production of population hybrids by man.

(6) Studies made in the fields of behaviour, electrophysiology and chemistry strongly suggest that population-specific fish odours are involved in home-stream recognition by salmonids.

(7) An evaluation of 'imprinting' experiments related to artificial organic compounds reveals that: (a) the odorant properties of the applied chemicals must be questioned, (b) imprinting related to olfaction may be based on a weak theoretical foundation, (c) returns obtained in census experiments may be adequately explained through ecological interpretations, and (d) behavioural preferences obtained from exposure to non-natural compounds may be founded on mechanisms not associated with homing.

(8) A logical link between the use of olfaction and the role of genetics in salmonid homing is emphasized, together with its practical implications for salmonid management.

X. REFERENCES

ALLENDORF, F., RYMAN, N., STENNEK, A. & STÅHL, G. (1976). Genetic variation in Scandinavian brown trout (*Salmo trutta* L.): evidence of distinct sympatric populations. *Hereditas* **83**, 73–82.

ALLENDORF, F. W. & PHELPS, S. (1980). Electrophoretic detection of the loss of genetic variation in a hatchery stock of cutthroat trout (*Salmo clarci*). *Transactions of the American Fisheries Society* **109**, 537–543.

ALTUKOV, Y. P. (1981). The stock concept from the viewpoint of population genetics. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1523–1538.

ALTUKOV, Y. P. & SALMENKOVA, E. A. (1981). Application of the stock concept to fish populations in the USSR. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1591–1600.

ARMSTRONG, R. H. (1974). Migration of anadromous Dolly Varden (*Salvelinus malma*) in southeastern Alaska. *Journal of the Fisheries Research Board of Canada* **31**, 435–444.

ARNOLD, G. P. (1974). Rheotropism in fishes. *Biological Reviews* **49**, 515–576.

ATEMA, J., JACOBSON, S., TODD, J. & BOYLAN, D. (1973). The importance of chemical signals in stimulating behaviour of marine organisms, effects of altered environmental chemistry on animal communication. In *Bioassay Techniques and Environmental Chemistry* (ed. G. E. Glass), pp. 177–197. Ann Arbor Science Publ. Michigan.

BAMS, R. A. (1972). A quantitative evaluation of survival to the adult stage and other characteristics of pink salmon (*Oncorhynchus gorbuscha*) produced by a revised hatchery method which stimulates optimal natural conditions. *Journal of the Fisheries Research Board of Canada* **29**, 1151–1167.

BAMS, R. A. (1976). Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). *Journal of the Fisheries Research Board of Canada* **33**, 2716–2725.

BANKS, J. W. (1969). A review of the literature on the upstream migration of adult salmonids. *Journal of Fish Biology* **1**, 85–136.

BATESON, P. (1966). The characteristics and context of imprinting. *Biological Reviews* **41**, 177–220.

BATESON, P. (1978). Early experience and sexual preferences. In *Biological Determinants of Sexual Behaviour* (ed. J. B. Hutchison), pp. 29–59. John Wiley, London.

BEHNKE, R. J. (1972). The systematics of salmonid fishes of recently glaciated lakes. *Journal of the Fisheries Research Board of Canada* **29**, 639–671.

BELGHAUG, R. & DØVING, K. B. (1977). Odour thresholds determined by studies of the induced waves in the olfactory bulb of the char (*Salmo alpinus* L.). *Comparative Biochemistry and Physiology* **57** A, 327–330.

BERG, L. S. (1934). Vernal and hiemal races among anadromous fishes. (Translation by W. E. Ricker.) *Journal of The Fisheries Research Board of Canada* **16**, 515–537. (1959).

BERG, M. (1961). Pink salmon (*O. gorbuscha*) in northern Norway in the year 1960. *Acta Borealia, A Scientia, Tromsø* **17**, 1–23.

BERG, M. (1964). *North Norwegian Salmon Rivers*, pp. 245–298. Johan Grundt Tanum Forlag, Oslo. 300 pp. (In Norwegian.) English summary.

BERG, M. (1977a). Pink salmon, *Oncorhynchus gorbuscha* (Walbaum) in Norway. *Institute of Freshwater Research, Drottningholm Report* **56**, 12–17.

BERG, M. (1977b). Tagging of migrating salmon smolts (*Salmo salar* L.) in the Vardnes River, Troms, Northern Norway. *Institute of Freshwater Research, Drottningholm Report* **56**, 5–11.

BERTMAR, G. (1979). Home range, migrations and orientation mechanisms of the River Indalsälven trout, *Salmo trutta* L. *Institute of Freshwater Research, Drottningholm Report* **58**, 5–26.

BERTMAR, G. & TOFT, R. (1969). Sensory mechanism of homing in salmonid fish. I. Introductory experiments on the olfactory sense in grilse of Baltic salmon (*Salmo salar*). *Behaviour* **35**, 235–241.

BIRMAN, I. B. (1981). Ocean migration and origin of seasonal races of anadromous salmon (*Salmonidae*). *Journal of Ichthyology* **21**, 35–47.

BODZNICK, D. (1975). The relationship of the olfactory EEG evoked by naturally-occurring stream waters to the homing behavior of sockeye salmon (*O. nerka*). *Comparative Biochemistry and Physiology* **52** A, 487–495.

BODZNICK, D. (1978). Characterization of olfactory bulb units of sockeye salmon with behaviorally relevant stimuli. *Journal of Comparative Physiology* **127**, 147–155.

BRAEMER, W. (1960). a critical review of the sun-azimuth hypothesis. *Cold Spring Harbor Symposia on Quantitative Biology* **25**, 413–427.

BRANNON, E. L. (1967). Genetic control of migrating behaviour of newly emerged sockeye salmon fry. *International Pacific Salmon Fisheries Commission Progress Report* **16**, 1–31.

BRANNON, E. L. (1972). Mechanisms controlling migration of sockeye salmon fry. *International Pacific Salmon Fisheries Commission Bulletin* **21**, 1–86.

BRETT, J. R. & GROOT, C. (1963). Some aspects of olfactory and visual responses in Pacific salmon. *Journal of the Fisheries Research Board of Canada* **20**, 287–303.

BRETT, J. R. & MACKINNON, D. (1954). Some aspects of olfactory perception in migrating adult coho and spring salmon. *Journal of the Fisheries Research Board of Canada* **11**, 310–318.

BROWN, L. A. (1956). The longitude. In *The World of Mathematics*, vol. II (ed. J. R. Newman), pp. 780–819. Simon & Schuster, Inc. New York.

BUCKLAND, F. (1880). Power of smell in salmon. In *Natural History of British Fishes*, pp. 300–303. Unwin, London, 420 pp.

CALDERWOOD, W. L. (1922). The homing of the salmon. *Scottish Naturalist* **123/124**, 37–43.

CALDERWOOD, W. L. (1937). Homing instinct in salmon. *Salmon and Trout Magazine* **88**, 207–213.

CALDERWOOD, W. L. (1940). Thirty years of salmon marking. *Salmon and Trout Magazine* **100**, 196–207.

CARLIN, B. (1969a). Salmon tagging experiments. *Swedish Salmon Research Institute, Report* **2–4** (3), 8–13.

CARLIN, B. (1969b). The migration of salmon. *Swedish Salmon Research Institute, Report* **2–4** (4), 14–22.

CHIDESTER, F. E. (1924). A critical examination of the evidence for physical and chemical influences on fish migration. *British Journal of Experimental Biology* **2**, 79–118.

CHILD, A. R., BURNELL, A. M. & WILKINS, N. P. (1976). The existence of two races of Atlantic salmon (*Salmo salar* L.) in the British Isles. *Journal of Fish Biology* **8**, 35–43.

CLEMENS W. A., FOERSTER, R. E. & PRITCHARD, A. L. (1939). The migration of Pacific salmon in British Columbia waters. *Publication of the American Association for the Advancement of Science* **8**, 51–59.

COLLINS, G. B., TREFETHEN, P. S. & GROVES, A. B. (1962). Orientation of homing salmon. *American Zoologist* **2**, 399–400.

COOPER, J. C. (1982). Comment on electroencephalographic responses to morpholine and their relationship to homing. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1544–1546.

COOPER, J. C. & HASLER, A. D. (1973). An electrophysiological approach to salmon homing. *Fisheries Research Board of Canada, Technical Report* **415**, 44 pp.

COOPER, J. C. & HASLER, A. D. (1974). Electroencephalographic evidence for retention of olfactory cues in homing coho salmon. *Science, Wash.* **183**, 336–338.

COOPER, J. C. & HASLER, A. D. (1975). Answer to Hara & MacDonald (1975). *Science, Wash.* **187**, 82.

COOPER, J. C. & HASLER, A. D. (1976). Electrophysiological studies of morpholine-imprinted coho salmon (*O. kisutch*) and rainbow trout (*S. gairdneri*). *Journal of the Fisheries Research Board of Canada* **33**, 688–694.

COOPER, J. C. & HIRSCH, P. J. (1982). The role of chemoreception in salmonid homing. In *Chemoreception in Fishes*, pp. 343–362, (ed. T. J. Hara). Elsevier Sci. Publ. Comp., Amsterdam.

COOPER, J. C. & SCHOLZ, A. T. (1976). Homing of artificially imprinted steelhead (Rainbow) trout, *Salmo gairdneri*. *Journal of the Fisheries Research Board of Canada* **33**, 826–829.

COOPER, J. C., SCHOLZ, A. T., HORRAL, R. M., HASLER, A. D. & MADISON, D. M. (1976). Experimental confirmation of the olfactory hypothesis with homing, artificially imprinted coho salmon (*O. kisutch*). *Journal of the Fisheries Research Board of Canada* **33**, 703–710.

CRAIGIE, E. H. (1926). A preliminary experiment upon the relation of the olfactory sense to the migration of the sockeye salmon (*O. nerka*). *Transactions of the Royal Society of Canada* **5**, 215–224.

DAHL, K. (1939). Homing instinct in salmon (*Salmo*). *Salmon and Trout Magazine* **94**, 19–26.

DELACY, A. C., DONALDSON, L. R. & BRANNON, E. L. (1969). Homing behaviour of chinook salmon. *University of Washington, Seattle, Research in Fisheries* **300**, 59–60.

DIZON, A. E., HORRALL, R. M. & HASLER, A. D. (1973a). Long-term olfactory "memory" in coho salmon, *Oncorhynchus kisutch*. *Fishery Bulletin, Washington* **71**, 315–317.

DIZON, A. E., HORRALL, R. M. & HASLER, A. D. (1973b). Olfactory electroencephalographic responses of homing coho salmon, *Oncorhynchus kisutch*, to water conditioned by conspecifics. *Fishery Bulletin, Washington* **71**, 893–896.

DOBZHANSKY, T. (1964). *Genetics and the Origin of Species*, 3rd rev. ed. Columbia Univ. Press, New York, N.Y. 364 pp.

DODSON, J. J. & LEGGETT, W. C. (1974). Role of olfaction and vision in the behaviour of American Shad (*Alosa sapidissima*) homing to the Connecticut River from Long Island Sound. *Journal of the Fisheries Research Board of Canada* **31**, 1607–1619.

Donaldson, L. R. & Allen, G. H. (1957). Return of silver salmon *O. kisutch* to point of release. *Transactions of the American Fisheries Society* **87**, 13–22.

Døving, K. B. (1979). The secret cues for salmon navigation. *Research in Norway*, pp. 45–50. Distributed by The Royal Ministry of Foreign Affairs. (Obtainable in all Norwegian Embassies and Consulates.)

Døving, K. B. & Belghaug, R. (1977). Frequency of induced waves in the olfactory bulb in char (*Salmo alpinus* L.). A temperature dependence. *Comparative Biochemistry and Physiology* **56** A, 577–579.

Døving, K. B. & Pinching, A. J. (1973). Selective degeneration of neurones in the olfactory bulb followed prolonged odour exposure. *Brain Research* **52**, 115–129.

Døving, K. B., Enger, P. S. & Nordeng, H. (1973). Electrophysiological studies on the olfactory sense in char (*Salmo alpinus* L.). *Comparative Biochemistry and Physiology* **45** A, 21–24.

Døving, K. B., Nordeng, H. & Oakley, B. (1974). Single unit discrimination of fish odours released by char (*Salmo alpinus* L.) populations. *Comparative Biochemistry and Physiology* **47** A, 1051–1063.

Døving, K. B., Selset, R. & Thommesen, G. (1980). Olfactory sensitivity to bile acids in salmonid fishes. *Acta physiologica scandinavica* **108**, 123–131.

Elson, P. F. (1973). Genetic polymorphism in Northwest Miramichi salmon, in relation to season of river ascent and age at maturation and its implications for management of stocks. *International Commission for the Northwest Atlantic Fisheries, Research Document* **73/76**, 6 pp.

Emanuel, M. E. & Dodson, J. J. (1979). Modification of the rheotropic behaviour of male Rainbow trout (*Salmo gairdneri*) by ovarian fluid. *Journal of the Fisheries Research Board of Canada* **36**, 63–68.

Fagerlund, U. H. M., McBride, J. R., Smith, M. & Tomlinson, N. (1963). Olfactory perception in migrating salmon. III. Stimulants for adult Sockeye salmon (*O. nerka*) in home stream waters. *Journal of the Fisheries Research Board of Canada* **20**, 1457–1463.

Ferguson, A. & Mason, F. M. (1981). Allozyme evidence for reproductively isolated sympatric populations of brown trout (*Salmo trutta* L.) in Lough Melvin, Ireland. *Journal of Fish Biology* **18**, 629–642.

Fisknes, B. & Døving, K. B. (1982). The olfactory sensitivity to group specific substances in Atlantic salmon (*Salmo salar* L.). *Journal of Chemical Ecology* **8**, 1083–1092.

Foster, N. R. & Berlin, W. H. (1980). Laboratory evidence of pheromone-mediated spawning site selection in lake trout, *Salvelinus namaycush*. In preparation. (Abstract presented at the Am. Soc. of Ichthyol. and Herp. 60th Annual Meeting, Forth Worth, Texas.)

Frankel, G. S. & Gunn, D. L. (1961). *The Orientation of Animals. Kineses, Taxes and Compass Reactions*. Dower Publ. Inc., New York. 376 pp.

Frisch, K. von. (1941). Über einen Schreckstoff der Fischhaut und seine biologische Bedeutung. *Zeitschrift für vergleichende Physiologie* **29**, 46–145.

Gardner, M. L. G. (1976). A review of factors which may influence the sea-age and maturation of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **9**, 289–327.

Gerking, S. D. (1953). Evidence for the concepts of home range and territory in stream fishes. *Ecology* **34**, 347–365.

Gerking, S. D. (1959). The restricted movement of fish populations. *Biological Reviews* **34**, 221–242.

Göz, H. (1941). Über den Art- und Individualgeruch bei Fishen. *Zeitschrift für vergleichende Physiologie* **29**, 1–45.

Grant, W. S., Milner, G. B., Krasnowski, P. & Utter, F. M. (1980). Use of biochemical genetic variants for identification of Sockeye salmon (*O. nerka*) stocks in Cook Inlet, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 1236–1247.

Groves, A. B., Collins, G. B. & Trefethen, P. S. (1968). Roles of olfaction and vision in choice of spawning site of homing adult chinook salmon (*O. tshawytscha*). *Journal of the Fisheries Research Board of Canada* **25**, 867–876.

Gudjónsson, T. (1967). Salmon culture in Iceland. *International Council for the Exploration of the Sea* C.M. 1967/M: 24.

Gudjónsson, T. (1970). The releases and returns of tagged salmon at Kollafjörður, Iceland. *International Council for the Exploration of the Sea*, C.M. 1970/M: 6.

Gudjónsson, T. (1972). Smolt rearing techniques, stocking and tagged adult salmon recaptures in Iceland. *International Atlantic Salmon Foundation, Special Publication Series* **4**, 227–235.

Gunning, G. E. (1959). The sensory basis for homing in the longear sunfish, *Lepomis megalotis megalotis* (Raf.). *Investigations of Indiana Lakes and Streams* **5**, 103–130.

Hahn, W. E. (1976). Electroencephalography of the olfactory bulb in relation to prespawn homing. *Experientia* **32**, 1095–1097.

Hansen, L. P. (1983). Salmon Ranching in Norway. In *Proceedings from the Workshop on Sea Ranching of Atlantic Salmon, Lisbon 1982* (eds. C. Eriksson, M. P. Ferranti and P. O. Larsson), pp. 95–108. Commission of the European Communities, COST 46/4, Brussels 1983.

HARA, T. J. (1970). An electrophysiological basis for olfactory discrimination in homing salmon: A review. *Journal of the Fisheries Research Board of Canada* **27**, 565–586.

HARA, T. J. (1973). Olfactory responses to amino acids in rainbow trout. *Salmo gairdneri. Comparative Biochemistry and Physiology* **44** A, 407–416.

HARA, T. J. (1974). Is morpholine an effective olfactory stimulant in fish? *Journal of the Fisheries Research Board of Canada* **31**, 1547–1550.

HARA, T. J. & BROWN, S. B. (1979). Olfactory bulbar electrical responses of rainbow trout (*Salmo gairdneri*) exposed to morpholine during smoltification. *Journal of the Fisheries Research Board of Canada* **36**, 1186–1190.

HARA, T. J. & BROWN, S. B. (1982). Reply to Cooper (1982). *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1546–1548.

HARA, T. J. & MACDONALD, S. (1975). Morpholine as olfactory stimulus in fish. *Science, Wash.* **187**, 81–82.

HARA, T. J. & MACDONALD, S. (1976). Olfactory responses to skin mucus substances in rainbow trout, *Salmo gairdneri. Comparative Biochemistry and Physiology* **54** A, 41–44.

HARA, T. J., LAW, Y. M. C. & HOBDEN, B. R. (1973). Comparison of the olfactory response to amino acids in rainbow trout, brook trout, and whitefish. *Comparative Biochemistry and Physiology* **45** A, 969–977.

HARA, T. J., UEDA, K. & GORBMAN, A. (1965). Electroencephalographic studies of homing salmon. *Science, Wash.* **149**, 884–885.

HARDEN-JONES, F. R. *Fish migration.* Edward Arnold (Publ.) Ltd., London. 325 pp.

HARTMAN, W. L. & RALEIGH, R. F. (1964). Tributary homing of sockeye salmon at Brooks and Karluk lakes. *Journal of the Fisheries Research Board of Canada* **21**, 485–504.

HARTT, A. C. (1966). Migrations of salmon in the North Pacific Ocean and Bering Sea as determined by seining and tagging, 1959–1960. *International North Pacific Fishery Commission Bulletin* **19**, 1–86.

HASLER, A. D. (1954). Odour perception and orientation in fishes. *Journal of the Fisheries Research Board of Canada* **11**, 107–129.

HASLER, A. D. (1960). Homing orientation in migrating fishes. *Ergebnisse der Biologie* **23**, 94–115.

HASLER, A. D. (1966). *Underwater Guidepost.* Univ. Wisconsin Press. 155 pp.

HASLER, A. D. & COOPER, J. C. (1976). Chemical cues for homing salmon. *Experientia* **32**, 1091–1093.

HASLER, A. D. & LARSEN, J. A. (1955). The homing salmon. *Scientific American* **193**, 72–75.

HASLER, A. D. & SCHWASSMANN, H. O. (1960). Sun orientation of fish at different latitudes. *Cold Spring Harbor Symposia on Quantitative Biology* **25**, 429–441.

HASLER, A. D. & WISBY, W. J. (1951). Discrimination of stream odors by fishes and relation to parent stream behavior. *American Naturalist* **85**, 223–238.

HASLER, A. D. & WISBY, W. J. (1958). The return of displaced large-mouth bass and green sunfish to a "home" area. *Ecology* **39**, 289–293.

HASLER, A. D., HORRAL, R. M., WISBY, W. J. & BRAEMER, W. (1958). Sun-orientation and homing in fishes. *Limnology and Oceanography* **3**, 353–361.

HASLER, A. D., SCHOLZ, A. T. & HORRAL, R. M. (1978). Olfactory imprinting and homing in salmon. *American Scientist* **66**, 347–355.

HELLE, J. H. (1981). Significance of the stock concept in artificial propagation of salmonids in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1665–1671.

HIYAMA, Y., TANIUCHI, T., SAYAMA, K., ISHOKA, K., SATO, R., KAJIHARA, T. & MAIWA, R. (1967). A preliminary experiment on the return of tagged chum salmon to the Otsuchi River, Japan. *Bulletin of the Japanese Society of Scientific Fisheries* **33**, 18–19.

HØGLUND, L. B. (1961). The reactions of fish in concentration gradients. *Institute of Freshwater Research, Drottningholm Report* **43**, 1–147.

HØGLUND, L. B. & ÅSTRAND, M. (1973). Preferences among juvenile char (*Salvelinus alpinus* L.) to intraspecific odours and water current studied with the fluviarium technique. *Institute of Freshwater Research, Drottningholm Report* **53**, 21–30.

HONDA, H. (1980). Female sex pheromone of rainbow trout, *Salmo gairdneri*, involved in courtship behaviour. *Bulletin of the Japanese Society of Scientific Fisheries* **46**, 1109–1112.

HORRAL, R. M. (1981). Behavioral stock-isolating mechanisms in Great Lakes fishes with special reference to homing and site imprinting. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1481–1496.

HUNTSMAN, A. G. (1937). 'Migration' and 'homing' of salmon. *Science, Wash.* **85**, 313–314.

HUNTSMAN, A. G. (1939). Races and homing instinct. *Salmon and Trout Magazine* **96**, 233–237.

HUNTSMAN, A. G. (1942). Return of a marked salmon from a distant place. *Science, Wash.* **95**, 381–382.

IDLER, D. R., FAGERLUND, U. H. M. & MAYOH, H. (1956). Olfactory perception in migrating salmon. I. L-serine, a salmon repellent in mammalian skin. *Journal of General Physiology* **39**, 889–892.

IDLER, D. R., McBRIDE, J. R., JONAS, R. E. E. & TOMLINSON, N. (1961). Olfactory perception in migrating salmon. II. Studies on a laboratory bio-assay for homestream water and mammalian repellant. *Canadian Journal of Biochemistry and Physiology* **39**, 1575–1584.

ÍSAKSSON, Á. (1976a). The results of tagging experiments at the Kollafjörður Experimental Fish Farm from 1970 through 1972. *The Journal of Agricultural Research in Iceland* **8**, 3–13.

ÍSAKSSON, Á. (1976b). Preliminary Results from the 1973 tagging experiments at the Kollafjörður Experimental Fish Farm. *The Journal of Agricultural Research in Iceland* **8**, 14–18.

ÍSAKSSON, Á. (1976c) The improvement of returns of one-year smolts at the Kollafjörður Fish Farm 1971–73. *The Journal of Agricultural Research in Iceland* **8**, 19–26.

ÍSAKSSON, Á. (1980). Salmon ranching in Iceland. In *Salmon Ranching* (ed. J. Thorpe), pp. 131–156. Academic Press.

ÍSAKSSON, Á. & BERGMAN, P. K. (1978). An evaluation of two tagging methods and survival rates of different age and treatment groups of hatchery-reared Atlantic salmon. *The Journal of Agricultural Research in Iceland* **10**, 74–99.

ÍSAKSSON, Á., RASCH, T. J. & POE, P. H. (1978). An evaluation of smolt releases into a salmon and a non-salmon producing stream using two releasing methods. *The Journal of Agricultural Research in Iceland* **10**, 100–113.

JAEGER, R. G. & GERGITS, W. F. (1979). Intra- and interspecific communications in salamanders through chemical signals on the substrate. *Animal Behaviour* **27**, 150–156.

JENSEN, A. & DUNCAN, R. (1971). Homing of transplanted coho salmon. *Progressive Fish Culturist* **33**, 216–218.

JESSOP, B. M. (1976). Distribution and timing of tag recoveries from native and nonnative Alantic salmon (*Salmo salar*) released into Big Salmon River, New Brunswick. *Journal of the Fisheries Research Board of Canada* **33**, 829–833.

JOHNSEN, P. B. & HASLER, A. D. (1980). The use of chemical cues in the upstream migration of coho salmon, *Oncorhynchus kisutch* Walbaum. *Journal of Fish Biology* **17**, 67–73.

JONES, J. W. & KING, G. M. (1946). Winter salmon in the Dee. *Salmon and Trout Magazine* **117**, 154–162.

JÓNSSON, L. (1977). Sensitivity to chemical stimuli in char (*Salmo alpinus* L.) determined by classical conditioning. *Cand. real. Thesis.* Institute of Zoophysiology. University of Oslo. (In Norwegian.)

KAJI, S., SATOU, M., KUDO, Y., UEDA, K. & GORBMAN, A. (1975). Spectral analysis of olfactory responses of adult spawning salmon (*O. keta*) to stream waters. *Comparative Biochemistry and Physiology* **51** A, 711–716.

KARLSON, P. & LÜSCHER, M. (1959). 'Pheromones': a new term for a class of biological active substances. *Nature, Lond.* **183**, 55–56.

KLEEREKOPER, H. (1967). Some aspects of olfaction in fishes with special reference to orientation. *American Zoologist* **7**, 385–395.

LARKIN, P. A. (1975). Some major problems for further study on Pacific salmon. *International North Pacific Fisheries Commission Bulletin* **32**, 3–9.

LARKIN, P. A. (1981). A perspective on population genetics and salmon management. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1469–1475.

LEGGETT, W. C. (1977). The ecology of fish migration. *Annual Review of Ecology and Systematics* **8**, 285–308.

LILEY, N. R. (1982). Chemical communication in fish. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 22–35.

LORENZ, K. (1935). Der Kumpan in der Umvelt des Vögels. *Journal für Ornithologie* **83** (2), 137–213, **83** (3), 289–413.

LORENZ, K. (1970). *Studies in Animal and Human Behaviour* Vol. 1. (Translated by R. Martin.) Methuen, London.

LORZ, H. W. & NORTHCOTE, T. G. (1965). Factors affecting stream location, and timing and intensity of entry by spawning Kokanee (*O. nerka*) into an inlet of Nicola Lake, B.C. *Journal of the Fisheries Research Board of Canada* **23**, 665–687.

McBRIDE, J. R., IDLER, D. R., JONES, R. E. E. & TOMLINSON, N. (1962). Olfactory perception in juvenile salmon. I. Observations on response of juvenile sockeye to extracts of food. *Journal of the Fisheries Research Board of Canada* **19**, 327–334.

McBRIDE, J. R., FAGERLUND, U. H., SMITH, M. & TOMLINSON, N. (1964). Olfactory perception in juvenile salmon. II. Conditioned response of juvenile sockeye salmon (*O. nerka*) to lake waters. *Canadian Journal of Zoology* **42**, 245–248.

MADISON, D. M., SCHOLZ, A. T., COOPER, J. C., HORRAL, R. M., HASLER, A. D. & DIZON, A. E. (1973). Olfactory hypotheses and salmon migration: a synopsis of recent findings. *Fisheries Research Board of Canada Technical Report* **414**, 35 pp.

MAZEAUD, E. (1981). Morpholine, a nonspecific attractant for salmonids. *Aquaculture* **26**, 189–191.

MILLER, R. B. (1954). Movements of cutthroat trout after different periods of retention upstream and downstream from their homes. *Journal of the Fisheries Research Board of Canada* **11**, 550–558.

MILLS, D. & SHACKLEY, P. E. (1971). Salmon smolt transportation experiments on the Cannon River system, Ross-Shire. *Freshwater and Salmon Fisheries Research* 40, 5–8.

MØLLER, D. (1970). Transferrin polymorphism in Atlantic salmon (*Salmo salar*). *Journal of the Fisheries Research Board of Canada* 27, 1617–1625.

MYERS, G. S. (1949). Usage of anadromous, catadromous, and allied terms for migratory fishes. *Copeia* 2, 89–97.

NEAVE, F. (1964). Ocean migration of Pacific salmon. *Journal of the Fisheries Research Board of Canada* 21, 1227–1244.

NEWCOMBE, C. & HARTMAN, G. (1973). Some chemical signals in the spawning behaviour of Rainbow trout (*S. gairdneri*). *Journal of the Fisheries Research Board of Canada* 30, 995–997.

NORDENG, H. (1971). Is the local orientation of anadromous fishes determined by pheromones? *Nature, Lond.* 233, 411–413.

NORDENG, H. (1977). A pheromone hypothesis for homeward migration in anadromous salmonids. *Oikos* 28, 155–159.

NORDENG, H. (1983). Solution to the 'Char problem' based on Arctic char *Salvelinus alpinus* in Norway. *Canadian Journal of Fisheries and Aquatic Sciences* 40, 1372–1387.

NYMAN, O. L. (1966). Geographic variation in Atlantic salmon. *Swedish Salmon Research Institute, Report* 3/1966.

NYMAN, O. L. (1967). Protein variation in various populations of Atlantic salmon. *Swedish Salmon Research Institute, Report* 8/1967.

NYMAN, O. L. & PIPPY, J. H. C. (1972). Differences in Atlantic salmon, *Salmo salar*, from North America and Europe. *Journal of the Fisheries Research Board of Canada* 29, 179–185.

OSHIMA, K., HAHN, W. E. & GORBMAN, A. (1969a). Olfactory discrimination of natural waters by salmon. *Journal of the Fisheries Research Board of Canada* 26, 2111–2121.

OSHIMA, K., HAHN, W. E. & GORBMAN, A. (1969b). Electroencephalographic olfactory responses in adult salmon to waters traversed in the homing migration. *Journal of the Fisheries Research Board of Canada* 26, 2123–2133.

PARKER, G. H. (1910). Olfactory reactions in fishes. *Journal of Experimental Zoology* 8, 535–542.

PARKER, G. H. (1911). The olfactory reactions of the common killifish, *Fundulus heteroclitus* (Linn.). *Journal of Experimental Zoology* 10, 1–5.

PARKER, G. H. & SHELDON, R. E. (1913). The sense of smell in fishes. *Bulletin of the Bureau of Fisheries* 32, 35–46.

PAYNE, R. H., CHILD, A. R. & FORREST, A. (1971). Geographical variation in the Atlantic salmon. *Nature, Lond.* 231, 250–252.

PECK, J. W. (1970). Straying and reproduction of coho salmon (*O. kisutch*), planted in a Lake Superior tributary. *Transactions of the American Fisheries Society* 99, 591–595.

PIGGINS, D. J. (1969). Talking points in salmonid research. *Salmon and Trout Magazine* 185, 51–68.

PIGGINS, D. J. (1974). The results of selective breeding from known grilse and salmon parents. *Annual Report for the Salmon Research Trust Ireland* 18, 35–39.

PINCHING, A. L. & DØVING, K. B. (1974). Selective degeneration in the rat olfactory bulb following exposure to different odours. *Brain Research* 82, 195–204.

PORTER, T. R. (1979). A review of factors affecting the rate of return of tagged Atlantic salmon and effects of tagging. *International Council for the Exploration of the Sea*, C.M. 1979/M, 42 pp.

POWER, G. (1981). Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1601–1611.

PRITCHARD, A. L. (1938). Transplantation of pink salmon (*Oncorhynchus gorbuscha*) into Masset inlet, British Columbia, in the barren years. *Journal of the Fisheries Research Board of Canada* 4, 141–150.

QUINN, T. P., BRANNON, E. L. & WHITMAN, R. P. (1983). Pheromones and the water source preferences of adult coho salmon *Oncorhynchus kisutch* Walbaum. *Journal of Fish Biology* 22, 677–684.

RALEIGH, R. F. (1967). Genetic control in the lakeward migration of sockeye salmon (*Oncorhynchus nerka*) fry. *Journal of the Fisheries Research Board of Canada* 24, 2613–2622.

RALEIGH, R. F. (1971). Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. *Ecology* 52, 291–297.

RICH, W. H. (1937a). 'Homing' of Pacific salmon. *Science, Wash.* 85, 477–478.

RICH, W. H. (1937b). 'Races' and 'homing' of Pacific salmon. *Science, Wash.* 86, 122.

RICH, W. H. & HOLMES, H. B. (1928). Experiments in marking young chinook salmon on the Columbia River, 1916–1927. *Bulletin of the Bureau of Fisheries, Washington* 44, 215–264.

RICKER, W. E. (1972). Hereditary and environmental factors affecting certain salmonid populations. In *The Stock Concept in Pacific Salmon* (eds. R. C. Simon & P. A. Larkin), pp. 19–160. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver. 231 pp.

RICKER, W. E. & ROBERTSON, A. (1935). Observations on the behaviour of adult sockeye salmon during the spawning migration. *The Canadian Field Naturalist* **49**, 132–134.

RITTER, J. A. (1975a). Lower ocean survival rates for hatchery-reared Atlantic salmon (*Salmo salar*) stocks released in rivers other than their native streams. *International Council for the Exploration of the Sea*, C.M. 1975/M: 26, 10 pp.

RITTER, J. A. (1975b). The importance of stock selection to the restoration of Atlantic salmon in New England. *International Atlantic Salmon Foundation, Special Publication Series* **6**, 129–131.

ROSSELAND, L. (1965a). Marking of salmon smolt. 20 pp. (In Norwegian). In *Status of the Year 1965*, from The Royal Norwegian Society of Science, The Museum.

ROSSELAND, L. (1965b). Report on salmon investigations executed. (In Norwegian.) Enclosure to *Report for 1951–1962 from the Inspector of Fisheries*, Department of Agriculture, Oslo.

ROSSELAND, L. (1971). In *Status of the Year 1970 from the Inspector of Fisheries*. (In Norwegian.) Department of Agriculture, Oslo.

ROSSELAND, L. (1978). Experiences from smolt releases in hydrodynamic regulated rivers. In *The Biological Effects of Hydrodynamic Regulation in Reservoirs and Salmon Rivers* (eds. T. B. Gunnerød & P. Mellquist), pp. 243–263. (In Norwegian.) Norges Vassdrags- og Elecktrisitets-vesen/Direktoratet for Vilt og Ferskvannsfisk.

ROYCE, W. F., SMITH, L. S. & HARTT, A. C. (1968). Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. *Fishery Bulletin, Washington* **66**, 443–462.

RUSSEL, E. S. (1937). Fish migrations. *Biological Reviews* **12**, 320–337.

RYMAN, N. & STÅHL, G. (1980). Genetic changes in hatchery stocks of brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 82–87.

RYMAN, N. & STÅHL, G. (1981). Genetic perspectives of the identification and conservation of Scandinavian stocks of fish. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1562–1575.

SAILA, S. B. & SHAPPY, R. A. (1963). Random movement and orientation in salmon migration. *Journal du Conseil international pour L'Exploration de la Mer* **28**, 153–166.

SAUNDERS, R. L. (1967). Seasonal pattern of return of Atlantic salmon in the Northwest Miramichi River, New Brunswick. *Journal of the Fisheries Research Board of Canada* **24**, 21–32.

SAUNDERS, R. L. (1968). An evaluation of two methods of attaching tags to Atlantic salmon smolts. *Progressive Fish Culturist* **30**, 104–109.

SAUNDERS, R. L. (1977). Searanching - a promising way to enhance populations of Atlantic salmon for angling and commercial fisheries. *International Atlantic Salmon Foundation, Special Publication Series* **7**, 17–24.

SAUNDERS, R. L. (1981), Atlantic salmon (*Salmo salar* L.) stocks and management implications in the Canadian Atlantic provinces and New England, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1612–1625.

SAUNDERS, R. L. & BAILEY, J. K. (1978). The role of genetics in Atlantic salmon management. In *Atlantic Salmon : Its Future* (ed. A. E. J. Went), pp. 182–200. Fishing News Books Ltd. Farnham, England.

SAUNDERS, R. L. & GEE, J. H. (1964). Movements of young Atlantic salmon in a small stream. *Journal of the Fisheries Research Board of Canada* **21**, 27–36.

SCHEER, B. T. (1939). Homing instinct in salmon. (*Oncorhynchus*.) *The Quarterly Review of Biology* **14**, 408–430.

SCHOLZ, A. T. (1980). Hormonal regulation of smolt transformation and olfactory imprinting in coho salmon. *Ph.D. Dissertation*. University of Wisconsin, Madison.

SCHOLZ, A. T. (1982). Hormonal regulation of smolt transformation and olfactory imprinting in coho salmon. In *Proceedings of the Salmon and Trout Migratory Behavior Symposium, June 1981* (eds. E. L. Brannon and E. O. Salo), p. 190. University of Washington, Seattle. 309 pp.

SCHOLZ, A. T., COOPER, J. C., MADISON, D. M., HORRAL, R. M., HASLER, A. D., DIZON, A. E. & POFF, R. J. (1974). Olfactory imprinting in coho salmon, behavioural and electrophysiological evidence. *Proceedings of the Conference on Great Lakes Resources 1973* **16**, 143–153.

SCHOLZ, A. T., HORRAL, R. M., COOPER, J. C., HASLER, A. D., MADISON, D. M., POFF, R. J. & DALY, R. (1975). Artificial imprinting of salmon and trout in Lake Michigan. *Wisconsin Department of Natural Resources and Fishery Management Report* **80**, 45 pp.

SCHOLZ, A. T., HORRAL, R. M., COOPER, J. C. & HASLER, A. D. (1976). Imprinting to chemical cues, the basis for home stream selection in salmon. *Science, Wash.* **192**, 1247–1249.

SCHOLZ, A. T., GOSSE, C. K., HORRAL, R. M., HASLER, A. D., DALY, R. & POFF, R. (1978a). Homing of rainbow trout transplanted in Lake Michigan: A comparison of three procedures used for imprinting and stocking. *Transactions of the American Fisheries Society* **107**, 439–444.

SCHOLZ, A. T., HORRAL, R. M., COOPER, J. M. & HASLER, A. D. (1978b). Homing of morpholine-imprinted brown trout, *Salmo trutta*. *Fishery Bulletin, Washington* **76**, 293–295.

SCHWASSMANN, H. O. & HASLER, A. D. (1964). The role of the sun's altitude in orientation of fish. *Physiological Zoology* **37**, 163–178.

SELSET, R. (1980). Chemical methods for fractionation of odorants produced by char smolts and tentative suggestion for pheromone origins. *Acta physiologica scandinavica* **108**, 97–103.

SELSET, R. & DØVING, K. B. (1980). Behaviour of mature anadromous char (*Salmo alpinus* L.) towards odorants produced by smolts of their own population. *Acta physiologica scandinavica* **108**, 113–122.

SHAPOVALOV, L. (1941). The homing instinct in trout and salmon. *Proceedings of the Sixth Pacific Science Congress* **3**, 317–322.

SMITH, S. B. (1960). A note on two stocks of steelhead trout (*Salmo gairdneri*) in Capilano River, British Columbia. *Journal of the Fisheries Research Board of Canada* **17**, 739–742.

SMITH, S. B. (1969). Reproductive isolation in summer and winter races of steelhead trout. In *Symposium on Salmon and Trout in Streams* (eds. M. W. Smith & W. M. Carter), pp. 119–137. H. R. MacMillian Lectures in Fisheries. New York.

SNYDER, J. O. (1931). Salmon of the Klamath River, California. *California Division of Fish and Game, Fishery Bulletin* **34**, 130 pp.

SOLOMON, D. J. (1973). Evidence for pheromone-influenced homing by migrating Atlantic salmon, *Salmo salar*. *Nature, Lond.* **244**, 231–232.

SOLOMON, D. J. (1977). A review of chemical communication in freshwater fish. *Journal of Fish Biology* **11**, 363–376.

STABELL, O. B. (1982a). Detection of natural odorants by Atlantic salmon parr using positive rheotaxis olfactometry. In *Proceedings of the Salmon and Trout Migratory Behavior Symposium, June 1981* (eds. E. L. Brannon & E. O. Salo), pp. 71–78. University of Washington, Seattle. 309 pp.

STABELL, O. B. (1982b). Homing of Atlantic salmon in relation to olfaction and genetics. In *Proceedings of the Salmon and Trout Migratory Behavior Symposium, June 1981* (eds. E. L. Brannon & E. O. Salo), pp. 238–246. University of Washington, Seattle, 309 pp.

STABELL, O. B. & SELSET, R. (1980). Comparison of mucus collecting methods in fish olfaction. *Acta physiologica scandinavica* **108**, 91–96.

STABELL, O. B., SELSET, R. & SLETTEN, K. (1982). A comparative chemical study on population specific odorants from Atlantic salmon. *Journal of Chemical Ecology* **8**, 201–217.

STÅHL, G. (1982). Genetic differentiation among natural populations of Atlantic salmon (*Salmo salar*) in Northern Sweden. *Ecological Bulletin (Stockholm)* **34**, 95–105.

STASKO, A. B. (1971). Review of field studies on fish orientation. *Annals of the New York Academy of Sciences* **188**, 12–29.

STASKO, A. B., SUTTERLIN, A. M., ROMMEL, S. A. & ELSON, P. F. (1973). Migration – orientation of Atlantic salmon (*Salmo salar* L.). In *International Atlantic Salmon Symposium* (eds. M. W. Smith & W. M. Carter), pp. 119–137. The International Atlantic Salmon Foundation. New York and St. Andrews.

STORM, G. (1881). *The Collected Writings by Peder Claussøn Friis*, pp. 111–118. (In Norwegian.) Brögger Forlag, Christiania (Oslo).

STOTT, B. (1967). The movements and population densities of roach (*Rutilus rutilus* L.) and gudgeon (*Gobio gobio* L.) in the river Mole. *Journal of Animal Ecology* **36**, 407–423.

STUART, T. A. (1957). The migrations and homing behaviour of brown trout (*Salmo trutta* L.). *Freshwater and Salmon Fisheries Research* **18**, 27 pp.

SUTTERLIN, A. M. & GRAY, R. (1973). Chemical basis for homing of Atlantic salmon (*Salmo salar*) to a hatchery. *Journal of the Fisheries Research Board of Canada* **30**, 985–989.

SUTTERLIN, A. M. & SUTTERLIN, N. (1971). Electrical responses of the olfactory epithelium of Atlantic salmon (*Salmo salar*). *Journal of the Fisheries Research Board of Canada* **28**, 565–572.

SUZUKI, N. & TUCKER, D. (1971). Amino acids as olfactory stimuli in freshwater catfish, (*Ictalurus catus* L.). *Comparative Biochemistry and Physiology* **40** A, 399–404.

THOMMESEN, G. (1978). The spatial distribution of odour induced potentials in the olfactory bulb of char and trout (*Salmonidae*). *Acta physiologica scandinavica* **102**, 205–217.

THOMMESEN, G. (1982). Specifity and distribution of receptor cells in the olfactory mucosa of char (*S. alpinus* L.). *Acta physiologica scandinavica* **115**, 47–56.

THOMMESEN, G. (1983). Morphology, distribution, and specificity of olfactory receptor cells in salmonid fishes. *Acta physiologica scandinavia* **117**, 241–249.

THORPE, J. E. (1980a). Ocean ranching – general considerations. In *Atlantic Salmon : Its Future* (ed. A. E. J. Went), pp. 152–164. Fishing News Books Ltd. Farnham, England. 253 pp.

THORPE, J. E. (1980b). *Salmon Ranching*. Academic Press. 434 pp.

THORPE, J. E. & MITCHELL, K. A. (1981). Stocks of Atlantic Salmon (*Salmo salar*) in Britain and Ireland. discreteness, and current management. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1576–1590.

THUNBERG, B. E. (1971). Olfaction in parent stream selection by the alewife (*Alosa pseudoharengus*). *Animal Behaviour* **19**, 217–225.

TILZEY, R. D. J. (1977). Repeat homing of brown trout (*Salmo trutta*) in Lake Eucumbene, New South Wales, Australia. *Journal of the Fisheries Research Board of Canada* **34**, 1085–1094.

TOFT, R. (1975). The significance of the olfactory and visual senses in the behaviour of spawning migration in Baltic salmon. (In Swedish.) *Swedish Salmon Research Institute Report* 10/1975.

UEDA, K., HARA, T. J. & GORBMAN, A. (1967). Electroencephalographic studies on olfactory discrimination in adult spawning salmon. *Comparative Biochemistry and Physiology* **21**, 133–143.

UEDA, K., HARA, T. J., SATOU, M. & KAJI, S. (1971). Electrophysiological studies of olfactory discrimination of natural waters by Himé salmon, a land-locked Pacific salmon, *O. nerka*. *Journal of the Faculty of Science, University of Tokyo, Section IV* **12**, 167–182.

UTTER, F. M. (1981). Biological criteria for definition of species and distinct intraspecific populations of anadromous salmonids under the U.S. Endangered Species Act of 1973. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1626–1635.

VIBERT, R. & LAURENT, M. (1972). Return rate of Atlantic salmon and grilse, and distance of their feeding grounds. *International Council for the Exploration of the Sea*, C.M. 1972/12.

WELLS, M. J. & BUCKLEY, S. K. L. (1972). Snails and trails. *Animal Behaviour* **20**, 345–355.

WENT, A. E. J. (1946). Salmon of the river Shannon in 1944 and 1945. *Journal of Animal Ecology* **15**, 155–169.

WENT, A. E. J. (1949). Spring fish. Are there two types of winter salmon? *Salmon and Trout Magazine* **125**, 23–26.

WESTERBERG, H. (1979a). Microstructure and fish behaviour. (In Swedish.) *Oceanografiska Inst/Fiskeristyrelsen*. University of Göteborg. 17 pp.

WESTERBERG, H. (1979b). Counter-current orientation in the migration of the European eel. *Rapports et Procés-verbaux des Réunions du Conseil international pour L'Exploration de la Mer* **174**, 134–143.

WESTERBERG, H. (1982a). Ultrasonic tracking of Atlantic salmon. I. Movements in coastal regions. *Institute of Freshwater Research, Drottningholm Report* **60**, 81–101.

WESTERBERG, H. (1982b). Ultrasonic tracking of Atlantic salmon. II. Swimming depth and temperature stratification. *Institute of Freshwater Research, Drottningholm Report* **60**, 102–120.

WHITE, H. C. (1934). Some facts and theories concerning the Atlantic salmon. *Transactions of the American Fisheries Society* **64**, 360–362.

WHITE, H. C. (1936). The homing of salmon in Apple River, N.S. *Journal of the Biological Board of Canada* **2**, 391–400.

WHITE, H. C. & HUNTSMAN, A. G. (1938). Is the local behaviour in salmon heritable? *Journal of the Fisheries Research Board of Canada* **4**, 1–18.

WILKINS, N. P. (1968). Multiple haemoglobins of the Atlantic salmon (*Salmo salar*). *Journal of the Fisheries Research Board of Canada* **25**, 2651–2663.

WILKINS, N. P. (1971). Biochemical and serological studies on Atlantic salmon (*Salmo salar* L.). *Rapports et Procés-verbaux des Réunions du Conseil international pour L'Exploration de la Mer* **161**, 91–95.

WILKINS, N. P. (1972a). Biochemical genetics of the Atlantic salmon *Salmo salar* L. I. A review of recent studies. *Journal of Fish Biology* **4**, 487–504.

WILKINS, N. P. (1972b). Biochemical genetics of the Atlantic salmon *Salmo salar* L. II. The significance of recent studies and their application in population identification. *Journal of Fish Biology* **4**, 505–517.

WISBY, W. J. (1952). Olfactory responses of fishes as related to parent stream behaviour. Ph.D. Thesis, University of Wisconsin, Madison. 41 pp.

WISBY, W. J. & HASLER, A. D. (1954). Effect of olfactory occlusion on migrating silver salmon (*Oncorhynchus kisutch*). *Journal of the Fisheries Research Board of Canada* **11**, 472–478.

WREDE, W. (1932). Versuche über den Artduft der Elritzen. *Zeitschrift für vergleichende Physiologie* **17**, 510–519.