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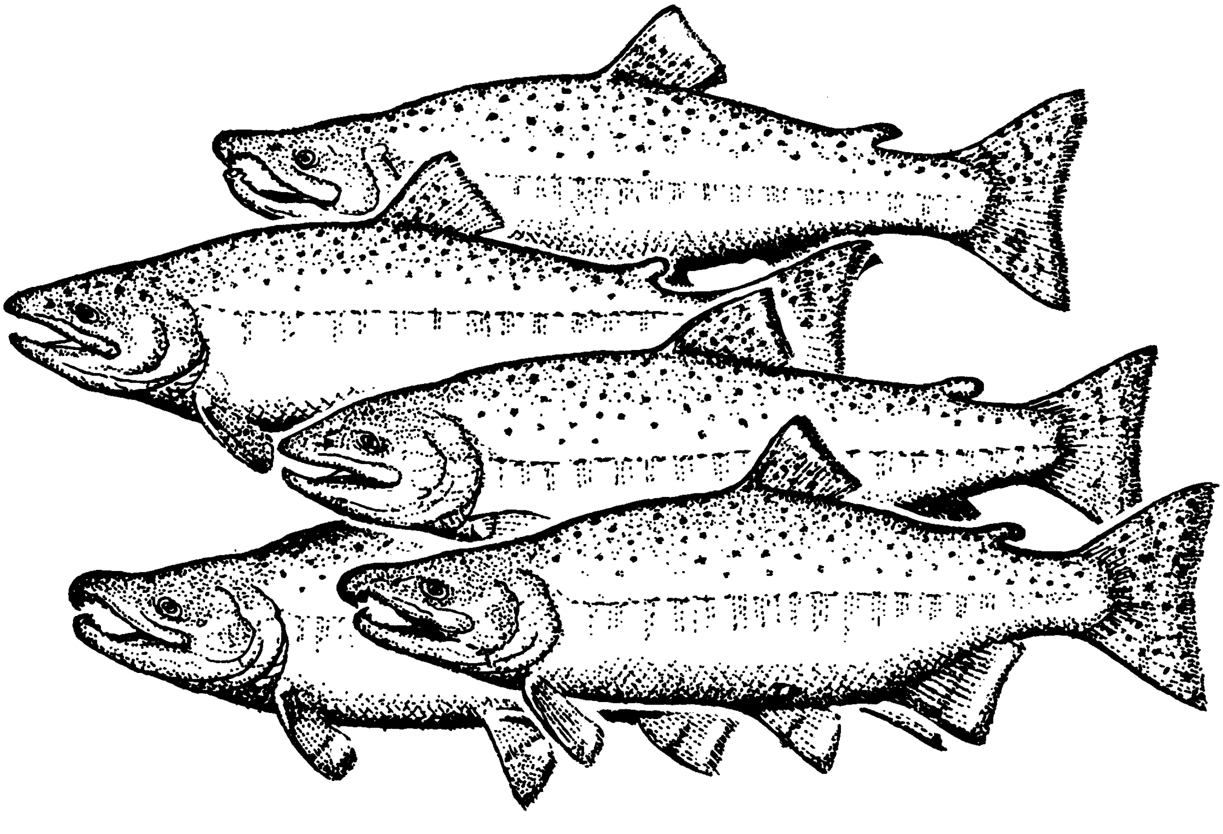
Coho Salmon in North-west Europe

Possible effects on native salmonids



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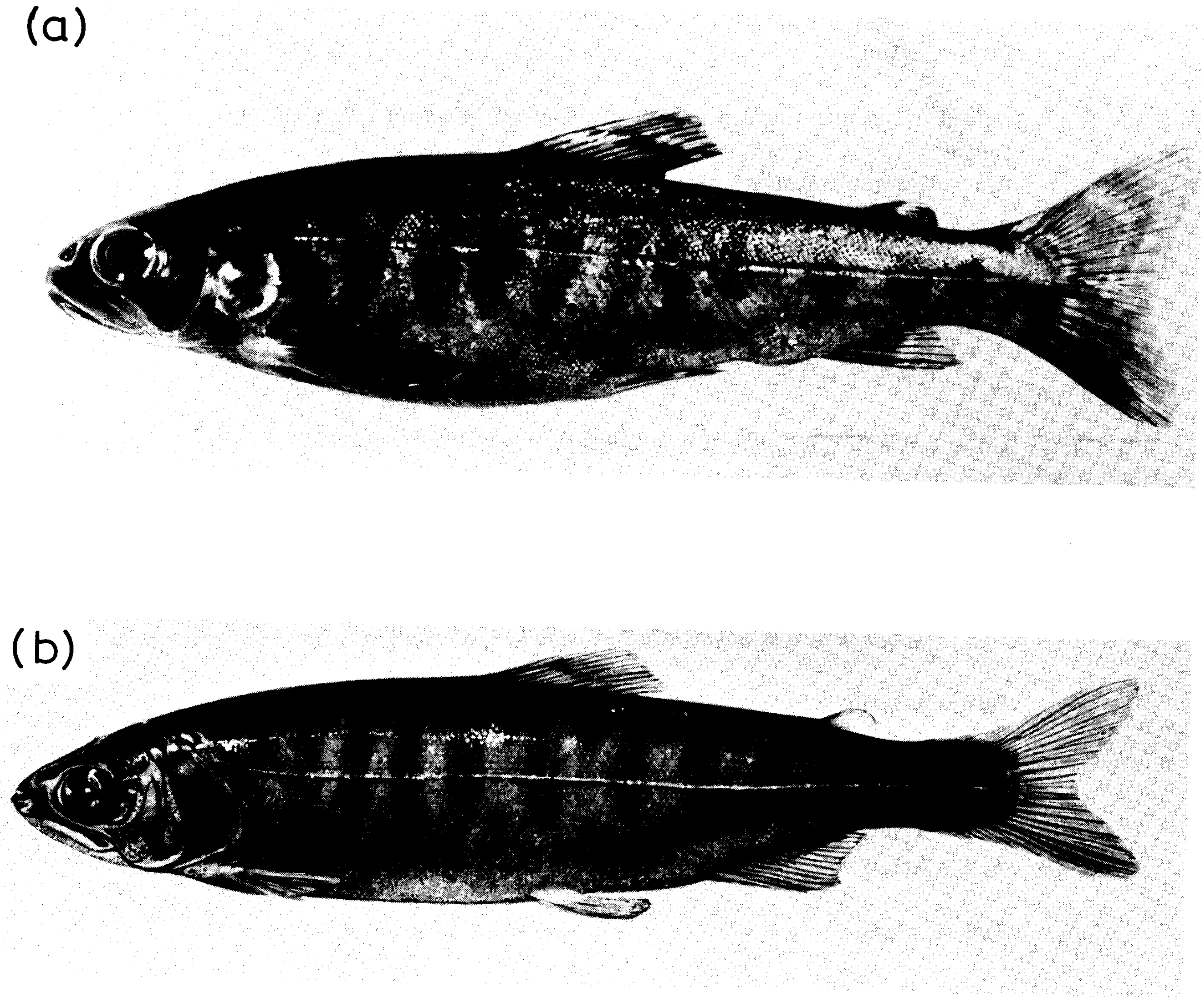

Atlantic salmon parr (a) and coho salmon parr (b). Note the relatively smaller pectoral fins of the coho. A diagnostic feature is the anal fin principal ray count - 8-11 in Atlantic salmon, and 12-17 in coho. Both fish are age 0+, length about 8 cm.

Laboratory Leaflet Number 49

COHO SALMON IN NORTH-WEST EUROPE - POSSIBLE EFFECTS ON NATIVE SALMONIDS

by D. J. Solomon

1. INTRODUCTION

Recent importations of coho salmon to Europe for cultivation purposes have been a cause of concern to angling and conservation interests. Most of the concern has been based on the uncertainty of the effect of possible escapes of coho on native populations of Atlantic salmon, sea trout and brown trout. Coho inhabit rivers and streams of the north Pacific coasts of North America and Asia. They spend a year or two in fresh water, and a year or two in the sea before returning to their native streams to spawn. They appear to occupy a similar ecological niche to the native migratory salmonids in the Atlantic area. This report sets out to review the available information on possible ecological interactions during the freshwater phase of the life cycle; it is generally accepted that it is during this stream-dwelling phase, between hatching and migration to the sea as smolts, that most of the natural processes regulating population size in migratory salmonids occur. Interactions during the marine phase and during spawning, the possible introduction and spread of fish diseases, and the possible establishment of 'land-locked' freshwater populations, are not dealt with here. However, these aspects should be borne in mind when considering any policy of introduction of new salmonid species.

There has been a long history of attempts to introduce Pacific salmon (Oncorhynchus spp.) into areas outside their natural range. Most of these have failed, or have been successful only as long as stocks were maintained by continued introductions. Two successful cases, where populations are maintained and have increased entirely by natural spawning, are chinook (O. tshawytscha) in New Zealand (Davidson and Hutchinson, 1938) and pink salmon (O. gorbuscha) in the Great Lakes of North America (Parsons, 1973). Runs of coho (O. kisutch) and chinook in the Great Lakes and of pink and chum (O. keta) in the Kola peninsula of Russia are maintained largely by continued stocking. However, in the latter case, straying pink salmon have apparently colonized rivers in northern Norway, where self-sustaining runs may now be established (Berg, 1977). Other examples of attempts which have succeeded to the extent of achieving returns of adults and some natural spawning (though insufficient to maintain the stock) are pinks in Maine in 1913-27 (Bigelow and Schroeder, 1953) and in Newfoundland in 1958-74 (Lear, 1975).

In recent years there has been a move to cultivate Pacific salmon, particularly coho, in sea cages in North America (Novotny, 1975). Considerable success has been achieved, especially with marketing 'pan sized' fish of around 300 g. In 1971 coho eggs were imported into France for a pilot cage rearing project in Brittany and more have been imported each year since (further details are given in Appendix II). Although the intention has been to contain all the fish in captivity for cage rearing, several escapes have occurred from the sea cages in Brittany and from freshwater farms rearing smolts in Brittany and Normandy. Some of these escapes have been of considerable proportions (see Appendix II) and there are unconfirmed reports of intentional, albeit illegal, releases. Further escapes are likely as long as the cage rearing operation continues, and colonization of nearby rivers, and spread to other areas, is an ever-present possibility. Other small-scale importations of eggs for evaluation of cultivation potential have been made into Norway (Harache, 1976) and the Federal Republic of Germany (Meixner, pers. comm.) but few details are available.

In early 1977, 20 000 coho eggs were imported into Scotland by Unilever Research Ltd. to evaluate the species for rearing in the UK. They have been kept under strict quarantine conditions, with all effluent sterilized, and are confined for life. These conditions were imposed by the Department of Agriculture and Fisheries for Scotland under the Diseases of Fish Act 1937 (Great Britain - Parliament, 1937). Subsequently an Act of Parliament entitled the Import of Live Fish (Scotland) Act 1978 (Great Britain - Parliament, 1978) has become law. Further imports would require licensing under that Act, which has the power to prevent imports on ecological grounds. The 1978 Act may be extended to cover England and Wales, although the Water Authorities already have powers to restrict introductions under the Salmon and Freshwater Fisheries Act 1975 (Great Britain - Parliament, 1975); section 30 requires that permission of the Water Authority must be granted before any fish or their spawn are introduced into an inland water.

It is unlikely that any escapes or intentional introductions will occur in the UK in the near future. Escape and possible introduction of fish in France could lead to the species arriving in the UK by migration, however.

The ecology and behaviour of single-species populations of some native and Pacific salmonids is now reviewed, followed by a description of studies undertaken on interactions between species.

2. ATLANTIC SALMON (Salmo salar) AND BROWN (OR SEA) TROUT (Salmo trutta)

2.1 General ecology and life history

Where they occur independently, these two species have similar behaviour and habitat requirements, so they can be dealt with together. What differences there are will be indicated.

The eggs are laid in gravel in autumn and early winter. They hatch in the early spring, but the young fish spend several weeks in the gravel, subsisting on their yolk sacs. They finally emerge from the gravel in late spring (April-May in the UK), and commence feeding shortly thereafter. Gradually they disperse from the area of hatching, and establish territories which are defended actively. They colonize suitable areas of stream, usually fairly shallow (up to about 30 cm) and with a fair flow of water. The fish occupy particular stations, often on top of or beside a stone, from which they defend their territories and make feeding forays. However, both species are adaptable in their life style, and young fish can successfully colonize a wide range of habitats, including lakes, subject to over-riding water quality considerations. Local genetic adaptation may be involved in the successful colonization of the more extreme habitat types. The fish at this stage are termed parr, and feed mainly on invertebrate drift, within the water and on the surface. Salmon and sea trout (migratory form of brown trout) spend from one year (at southern end of range) to three or more years (north Scotland) in fresh water before becoming smolts and migrating to sea. Brown trout remain in fresh water throughout their lives. Sea trout return to fresh water after a few months to two or more years, and usually return to the sea and spawn subsequently for several years. Salmon return after one to several years, and most die after spawning. A proportion survive to spawn a second or third time.

2.2 Environmental requirements

It is often difficult to determine the preferred habitat of stream species as many individuals of a population may be occupying predominantly sub-optimal areas either as a result of interaction with other species present or by sheer population pressure. Perhaps the best indications can be obtained from natural situations where the species of interest occurs alone or is numerically dominant, and from single-species artificial channel experiments.

Symons and Heland (1978) found highest densities of 0+ (fish in their first year) and older salmon at stream velocities of 50-65 cm per sec. Stream tank experiments showed that salmon less than 7 cm in length preferred shallow riffles (10-15 cm deep) with a pebbly substrate (1.6-6.4 cm stone diameter). As they grew larger their preference changed for deeper (more than 30 cm) riffles containing boulders (greater than 25.6 cm diameter). Lindroth (1955) found that both young trout and salmon preferred shallow water (20-30 cm), especially in the margins of the large rivers that he was studying. Salmon have been reported to occupy territories in deeper water; Saunders and Gee (1964) found significant numbers of 1+ (fish in their second year) and 2+ (fish in their third year) occupying pools on a long-term basis. Observations on marked fish showed pool fish and riffle fish retaining their respective habitat choice throughout the period from August to December. The 0+ fish occupied mainly shallow riffles, moving into deeper water during the autumn. The only other salmonids present were brook trout, at a very low density.

Salmon are able to maintain position in fast flows with little effort by using their large paddle-shaped pertoral fins to keep themselves applied firmly to the substrate, e.g. on top of a large stone (Kalleberg, 1958) (Figure 1). In this respect they are better adapted to rapid flows than any of the other salmonids considered here.

2.3 Food and feeding

The food of salmon and trout in fresh water generally represents a sample of the available fauna of suitable size. Benthic organisms such as insect larvae and crustacea, invertebrate organisms of benthic origin drifting within the water column (drift), emerging adult insects of aquatic larvae, small fish and fish eggs, and insects etc. of terrestrial origin are all consumed in variable quantities. There are wide spatial and seasonal variations in diet.

Several workers have compared the stomach contents of stream salmonids with the benthic, drift and terrestrial communities, to attempt to identify any selective feeding behaviour. Atlthough organisms often occur in different proportions in stomach contents and potential prey communities, Egglishaw (1967) suggests that this mainly reflects differences in availability to the feeding fish and the sampling method. Such differences would be influenced by many factors including the behaviour of fish and prey, the physical nature of the microhabitat occupied, time of day of feeding, and vertical distribution of the feeding fish. Egglishaw observed that stomach contents of salmon and trout varied markedly with microhabitat within

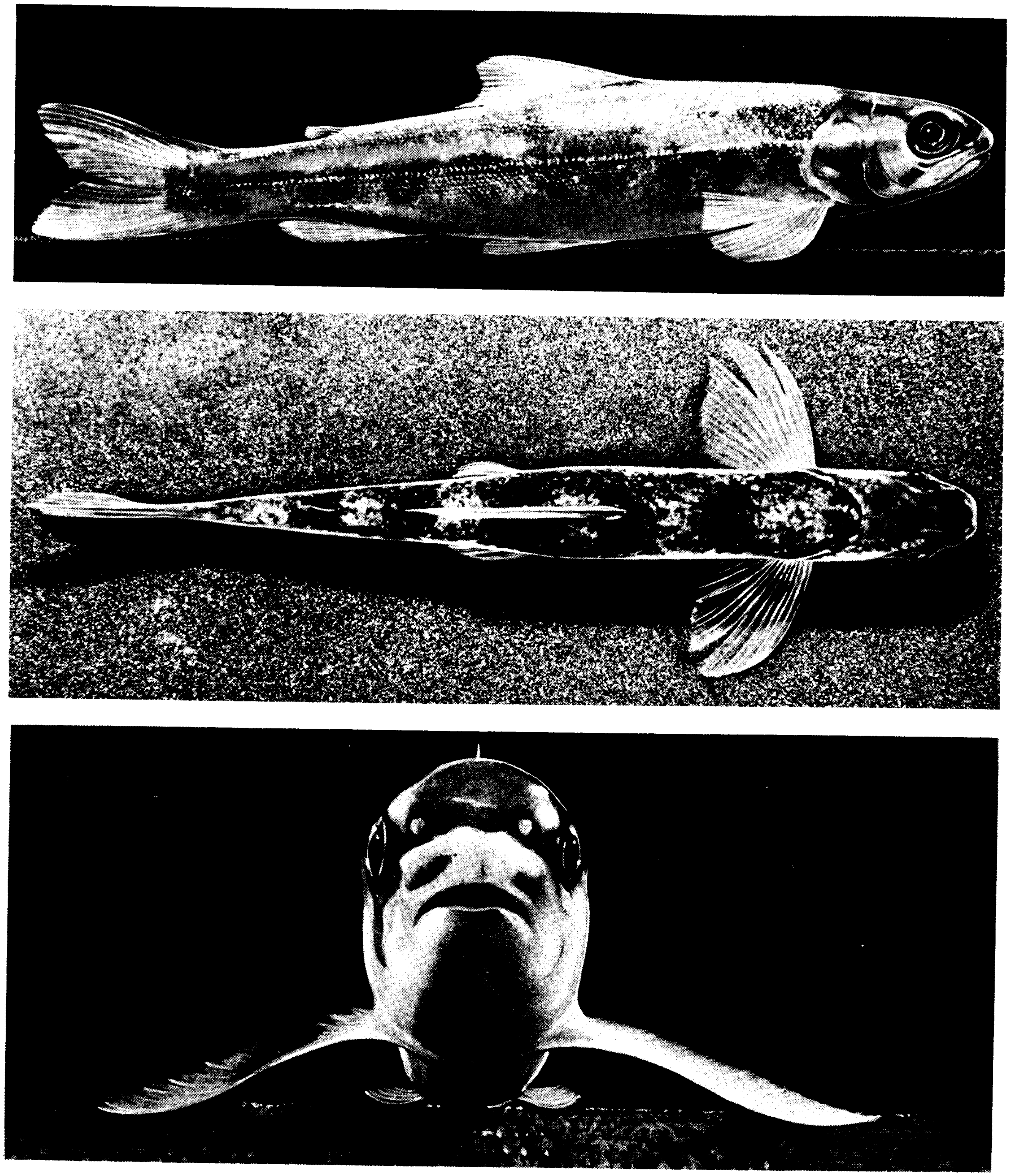

Figure 1 Atlantic salmon parr holding station in a fairly fast flow. Note the use of the large, flexed pectoral fins to keep the fish firmly applied to the substrate. In this way the Atlantic salmon is better adapted to fast flows than the other salmonids considered. (Photographs by G. P. Arnold.)

a short length of stream, such that there were greater differences between salmon in riffles and in pools than between the two species within pools.

2.4 The territory and agonistic behaviour

It is generally accepted that the territory is based on feeding requirements rather than being defined as a particular quantiative area as such (e.g. Chapman, 1966). It basically represents the area defended from the station which the fish occupies most of the time, and its boundaries, as represented by location of encounters with intruders, are somewhat blurred. Kalleberg (1958) refers to a 'centrifugally decreasing gradient of aggressiveness' around the defended station. The territory generally extends further upstream from the station than down, presumably because the fish is sooner aware of intruders approaching from that direction. It extends further along the bed than it does in open water - an intruder can approach much closer without challenge if it is well clear of the bottom. A range of reactions is noted in encounters (Keenleyside and Yamamoto, 1958): charging, nipping and chasing, which result from 'high attack tendencies'; fleeing, which results from 'high escape tendencies'; frontal display and lateral display. These latter two are used where two aggressive fish are contesting dominance; 'frontal display indicates relatively high levels of tendency to attack; lateral displays the tendency to escape'. Agonistic (Greek agon = contest) displays increase while feeding, partly because the fish are more active and confrontations are more likely, and partly because the territory is based on a feeding regime; a feeding intruder is a greater 'threat' than one passing through (Chapman, 1966). There is a slight difference between salmon and trout in the nipping reaction; salmon mainly use a ritual 'threat nip'; trout are more prone to actually nip. All intruders, regardless of species, will usually be chased away from the territory. The more ritual agonistic behaviour is generally used only towards other juvenile salmonids. Salmon and trout, indeed most salmonids, understand each other's behavioural reactions.

Territories are regularly challenged, and increase in size as the fish grows (see below); however, they may be maintained for a considerable time. In Kalleberg's (1958) stream tank, he observed 0+ salmon retaining territories for a least 23 days, and 2+ parr for at least 49 days. It is likely that in natural conditions considerably longer tenancies exist, though seasonally changing conditions, and growth, may render the initial holding areas unsuitable, so forcing a move.

2.5 Carrying capacity of an area of stream

The carrying capacity of a stream depends on a number of factors:

1. Area of bed suitable for territories. Especially in larger streams and rivers, the areas suitable for young fish may be rather limited. In a wide range of natural streams studied, the area utilized by any one age group of a salmonid species has typically been between 2 and 20% of the total area (Allen, 1969).

2. Age/size of fish. The size of territory increases with the size of fish. Kalleberg (1958) found that about a month after the fish emerged from the gravel salmon territories were about 0.02-0.03 m^2, in a fairly tightly-packed mosaic. Larger parr (up to 15 cm) occupied a square metre or more in open water, and a 23 cm trout commanded about 4 m^2.

3. Visual obstructions. Where fish are unable to see one another, a higher density can be supported. In one of Kalleberg's (1958) stream-tank experiments, mean territory size was reduced from 0.095 to 0.045 m^2 by exchanging gravel for rocks. Turbid water produced the same effect.

4. Current speed. Symons and Heland (1978) found highest densities of salmon parr (1.0 and 0.8 fish per m^2 for 0+ and older fish respectively) under natural conditions in water velocities of 50-65 cm per sec. At sites with lower or higher velocities maximum densities decreased. Kalleberg (1958), using a stream-tank, found that increasing velocity (maximum perhaps less than 65 cm per sec) decreased territory size, and suggested that this might be because the fish were forced to vacate their 'rock top' stations and shelter among the stones, decreasing visual contact. Chapman (1966) suggested that smaller territories at higher water velocities were appropriate as the fish could exploit invertebrate drift in a similar volume of water by commanding a smaller area or width of stream.

   As stream flows are reduced to zero in experimental situations, young salmon and trout will move slowly upstream and form a fairly well-grouped shoal, showing reduced agonistic behaviour. This is discussed in section 2.7.

5. Food availability. As territory defending is believed to be a feeding-motivated behaviour, it is likely that territories will be smaller where food supply is great. As stated above, Chapman (1966) suggests that smaller territories at higher current speeds could be due to the greater supply of drift organisms. Chapman and Bjornn (1969) discuss the evidence for food-linked territory size, but it is inconclusive. Symons (1971) reported results from an experimental stream tank which demonstrated increased aggressive behaviour during periods of food deprivation.

6. Some examples of naturally-occurring population densities of salmon and trout are:

   (a) Shelligan Burn and River Almond, Scotland (Egglishaw, 1967). Time of year - 'end of growth period' (September?)

	Salmon	Trout
0+	1.7-3.7 per m^2 (1.4-3.4 g)	0.7-1.5 per m^2 (1.3-2.8 g)
1+	0.15-0.55 per m^2 (2.2-5 g)	0.05-0.4 per m^2 (0.6-8 g)
Older	< 0.05 per m^2 (1.5 g)	> 0

   (Some of the data have been extracted from histograms and so may not be precise.)

   (b) Tributaries of Lough Erne, Northern Ireland (Vickers, 1969). 1+ salmon, 0.123-0.67 fish per m^2. No data for 0+ fish.

   (c) Welsh Moorland stream (Dee and Clywd River Authority, undated). A 5½ mile stretch was cleared of trout, eels, etc. by electric fishing above impassable falls. Large numbers of salmon fry were stocked in late spring. In June/August 0+ fish were present at an average density of 1.8 per m^2.

(d) Ten streams in England (Le Cren, 1969).
Trout, 0+, 0.2-2.4 per m^2; 1+, 0.1-0.5; older, 0.1-0.3.

(e) Lake District stream (Le Cren, 1961).
Experimental stretches cleared of fish, stop netted and stocked with trout fry in Spring. Above a stocking rate of 12 per m^2 (range about 12-280), the density remaining in September was around 9 per m^2. Note: The whole of the experimental area was apparently suitable for young trout - see section 2.5.

(f) Streams in the Miramichi system, New Brunswick (Elson, 1957).
Increasing the stocking rate of 0+ salmon parr from 55 to 213 per 100 yd^2 led to little increase in the numbers of 1+ parr (16 instead of 15 per 100 yd^2) and 2+ smolts (6 instead of 5). Stocking at 15 per 100 yd^2 gave a proportionate decrease over 55 per 100 yd^2 (4, 1+ parr, 2, 2+ smolts).

2.6 Interaction between year-classes

Symons and Heland (1978) report that 1+ salmon (over 10 cm in length reduced the numbers of the younger year-class (less than 6 cm in length) in deeper water by chasing, and occasionally catching and eating them. Agonistic behaviour, associated with territory defence, was not manifested between the year-classes until the 0+ fish were larger than 6.5 cm, the size at which they start to vacate their territories in shallower water and establish territories 'alongside' the older fish. Kalleberg (1958) found that small parr vacate their 'station' and hide in the gravel nearby when a larger parr approaches - thus it was possible for a small fish to occupy a territory within the much larger territory of a larger fish for 'several days'.

2.7 Overcrowding and shoaling

In most natural salmonid streams, more fry hatch than can establish viable territories in suitable areas. What becomes of these extra fish? In one experiment Kalleberg (1958) intentionally introduced into his stream-tank more fry than there were potential territories. Two fractions of the population occurred, those establishing and defending territories and those failing to do so. The failures were constantly repelled from occupied territories and hid in holes between and under stones which they defended as 'mini territories'. Exchanges between the two fractions did sometimes occur, as a failure successfully challenged a territory-holding fish, but size differences between the two fractions started to appear, putting the deprived fish at an increasing disadvantage. In natural streams, the fish failing to establish territories would presumably emigrate or be passively carried downstream until they found a territory or reached unsuitable areas, where they might suffer heavy predation or die of starvation.

Decreasing stream flows in summer can render holding areas untenable, necessitating migration to deeper areas. As stream flow drops, the water velocity in the fishes' territory will fall as the riffles dry out. The reaction of the fish to decreasing current is to vacate the territory (Kalleberg, 1958). Fish thus become concentrated in what was previously deeper water. As density increases, agonistic behaviour at first increases, then drops as the fish fail to establish maintainable territories. They form a fairly closely-knit, cohesive shoal, a reaction quite different from earlier behaviour. If the 'crowded' flow conditions persist, there is some evidence that aggression does eventually increase again - Kalleberg noted such after only two days.

Intensive fish culture situations represent an extreme in crowding. Under such conditions there is little observable agonistic behaviour. Kalleberg suggests that this could be due to the blocking of normal nervous mechanisms due to continual contact. Chapman (1966) suggests that the broadcast method of feeding used in hatcheries renders territory-holding a dubious advantage. Kalleberg noted that the longer salmon parr had been subjected to the overcrowded 'shoaling' situation, the slower they were to exhibit aggressiveness in the stream-tank. This leads to two conclusions of importance; hatchery-reared fish may be at a distinct competitive disadvantage over wild fish when stocked into streams; and any stream tank studies of interactions based on observations on hatchery-reared fish need very careful interpretation.

3. COHO SALMON (Oncorhynchus kisutch) AND OTHER PACIFIC SALMONIDS

3.1 General coho ecology

Coho salmon have a rather similar biology to Atlantic salmon and sea trout. Typically, the young fish spend a year or two in fresh water before migrating to sea as smolts, and are aggressive and territorial in streams. Their food consists largely of invertebrate drift. However, they differ distinctly from Atlantic salmon in their pattern of microhabitat use. All adults die immediately after spawning.

3.2 Environmental requirements

Coho are generally considered to be pool and margin-dwelling fish, in contrast to Atlantic salmon. Ruggles (1966) conducted experiments with four stream channels, each 200 x 20 ft, divided into two sub-channels. In various experiments depths ranged from 4-12 in (riffles) to 3 ft 9 in (pools). High densities of fry (1 450-1 725 per channel) were stocked, and parr stock and smolt production noted. General conclusions were that holding capacity was determined by availability of low-velocity water. Over twice as many parr remained in channels containing all pool, than in channels containing all riffle. More one-year-old smolts were produced in the pool environment, although most food was produced in the riffle. Highest smolt production was in a riffle and pool combination: it is assumed that the pools provided the fish holding capacity, and that the riffles produced the food. Fish in the riffle situation showed greater agonistic behaviour and territoriality than those in the pools.

Mundie (1969) described coho fry and parr behaviour in natural streams. They showed a preference for shallow margins in relatively slack water. They formed loosely aggregated shoals, with no apparent heirarchical order, and were active in bright sunlight. Their 'territory' appeared to be centred on definite objects; for example, high densitities occurred under log-jams. Feeding forays were frequently made, often into riffle areas. In some natural situations, especially at fairly high densities, fish may set up long-term territories in riffles.

Glova (1978) reported a wide use of a range of habitats at high densities (Table 1).

Table 1 Mean numbers (ranges in brackets) of under-yearling (0+) coho and cutthroat trout per square metre recorded in Holland Stream, Vancouver Island, by Glova (1978). Time of year July-September, temperature 11.5-15.5°C.

Habitat type	Coho		Cutthroat trout	
	1973	1974	1973	1974
Pools (less than 5 cm per sec)	0.86 (0.31-0.92)	1.02 (0.75-1.29)	0.65 (0.10-1.86)	0.35 (0.20-0.55)
Glides (5-20 cm per sec)	0.41 (0.32-0.47)	1.50 (1.18-1.82)	1.00 (0.56-1.69)	0.35 (0.22-0.64)
Riffles (greater than 20 cm per sec)	0.10 (0.07-0.18)	0.38 (0.16-0.60)	1.24 (0.63-1.67)	0.35 (0.05-0.52)

3.3 Coho food and feeding

Coho feed both in the pool and margin situations that they occupy for most of the time, and by making feeding forays into faster water. Like most stream salmonids they are opportunistic predators. They mainly take moving food items, such that invertebrate drift organisms and terrestrial organisms feature to a greater extent in their diet than stationary benthic fauna. Mundie (1969) discusses significant differences observed between the composition of the drift and diet. He suggests that these can be explained by differential diurnal distributions of drift composition and feeding behaviour, and vertical stratification of the drift. The relatively high level of organisms of terrestrial origin in the diet is probably due to the margin-dwelling habit of the fish. Shapovalov and Taft (1954) record yearling coho consuming eggs and fry of salmonids and other fish. Thus as with the Atlantic Salmon and trout (section 2.3), the composition of the diet appears to largely reflect the range of suitable organisms available to the fish within its microhabitat, with relatively little selective behaviour.

3.4 Coho territorial and agonistic behaviour

Generally speaking, coho do not establish individual territories in pools. Rather, the available food and space is partitioned on a dominant heirarchy basis, with the larger fish at the head of pools, and the smaller individuals either downstream or near the bottom. When they do occupy riffles, or when making feeding forays into faster water, they establish aggressively defended territories. The agonistic behaviour is similar to that of Atlantic salmon, with the addition of a 'wig-wag' display (Hartman, 1965) in which the fish accentuate lateral swimming movements, with head either up or down at about 20-30°, and all fins erect. Aggression is more marked at high temperatures, including chasing and nipping - in winter, threat displays predominate.

The pattern of aggression in fast water and shoal-forming at higher densities in slow-flowing water is similar to that of Atlantic salmon. The main difference appears to be the current speed preferred by the two species.

Some naturally-occurring densities have been given in Table 1. Higher densities have been recorded by Hartman (1965) in the vicinity of log jams in a large British Columbia Stream, with up to 7.27 parr per m^2. Overall densities were however very much lower than these figures.

Glova (1978) describes behavioural differences between wild and hatchery-reared coho parr. As has been found with Atlantic salmon (section 2.7), the hatchery fish were significantly less aggressive and showed a greater tendency to remain in pools, than was shown by wild fish.

3.5 Other Pacific salmonids

Brief details of other salmonids are given because they are relevant to studies of interspecific interactions considered in section 4.

The steelhead trout (sea-run form of rainbow trout, *Salmo gairdneri*) is sometimes suggested as being the Pacific salmonid ecologically most similar to the Atlantic salmon. The parr remain in rivers usually for two or three years. The preferred habitat is very similar to that of coho during spring and summer, but in winter trout tend to hide under stones or remain close to the stream bed (Hartman, 1965). The fish are more territorial in nature than coho at low flows. Agonistic behaviour involves relatively more nips and chases, and fewer threat displays,than in coho.

The coastal cutthroat trout (*Salmo clarki*) is another anadromous Pacific salmonid. The 0+ fish occupy a wide range of microhabitats at high densities, particularly riffles and high velocity areas. Age 1+ trout mainly occupy pools. Some naturally-occurring densities are given in Table 1.

Brook trout (*Salvelinus fontinalis*) occur throughout eastern North America, and appear to occupy the same wide ecological niche that *Salmo trutta* does in Europe. There are sea running races as well as strains that remain in fresh water throughout. Gibson (1973) describes the preferred habitat of the juveniles as slow-flowing water (less than 15 cm per sec), about 60 cm deep over boulders. They showed a distinct preference for cover or shade. Brook trout did not occupy the shallower, faster water preferred by Atlantic salmon, though the distribution of the two species overlapped considerably in other microhabitat types. Brook trout have been widely introduced into Europe, including Britain.

4. INTERSPECIFIC INTERACTIONS

4.1 General

The habitats and behaviour of the salmonid species described in sections 2 and 3 vary somewhat, but all overlap considerably. Where species occur together, the differences are often exaggerated, and the species occupy slightly different niches to those that they would occupy if alone. This process is termed interactive segregation (Nilsson, 1967).

4.2 Atlantic salmon and European trout

These two species occur together over most of the range of the salmon - indeed, natural populations of salmon parr without trout are unusual. This has led to a rather confusing situation, where the behaviour and microhabitat use of salmon in the interactive segregated state is often mistakenly assumed to be the same as that which would occur were the salmon present alone. As stressed in section 2.1, the ecology of independent populations of the two species is very similar. Lindroth (1955) found that trout parr occupied the shallow margins of a river, while the salmon were found in somewhat deeper water, (modal depths 5-15 cm for trout, 35-45 cm for salmon). In a similar river without trout, the salmon were found mainly in shallow water. In a stream-tank experiment, Lindroth found that trout and older salmon occupied the deeper water, the 0+ salmon being 'forced' to occupy shallow water. He explained these apparently conflicting results as indicating that the trout were dominant and selected the optimal territories (defined by suitable gravel size) while the salmon were forced to occupy less favourable areas.

Kalleberg (1958) conducted stream-tank experiments with mixed salmon and trout populations. He found that the two species responded to each other's aggressive displays, and that trout generally dominated salmon. The trout were more aggressive (see section 2.4) and were also slightly larger than equivalent year-class salmon. Generally in mixed populations in streams the salmon occupy riffle areas, and the trout occupy slightly deeper water in the margins, pools etc. Backiel and Le Cren (1967) discuss results from a preliminary experiment in a small stream suggesting that the survival of salmon depended on the total number of salmon and trout present, while the survival of trout depended on numbers of trout alone. However, the fact that trout rarely completely oust salmon even in a good spawning year indicates that salmon must have an advantage over trout in the environment to which they are best adapted i.e. riffles. As Nilsson (1967) says 'Slight differences in, for instance, inherent preferences or ability to threaten in different situations maintain segregation where resources are limited'. Thus a balanced, dynamic situation is maintained even where populations of both or either species are high. This important aspect is discussed further in section 4.3.

4.3 Coho salmon, steelhead and cutthroat trout

These species occur naturally together in many Pacific coast streams, for example in British Columbia. Their interactions have been studied in the wild, in stream-tanks and in stream channels by several workers. Hartman (1965) observed interactive segregation between coho and steelhead in summer, with coho in pools and steelhead in riffles. During winter both species occurred together in pools. He noted that where they occurred independently, each species preferred pools throughout the year. The behaviour of the two species was virtually identical in summer, but in winter minor differences existed in their pool-dwelling habits. It was thus in the time of greatest potential competition (summer) that the segregation occurred - presumably competition was much reduced in winter by lowered temperatures and differences in behaviour. From consideration of independent distributions (sections 3.2 and 3.5) it appears that the coho were dominant, and that the steelhead were forced to adopt a modified habit. Complete exclusion was apparently prevented by relatively increased aggression of steelhead in riffles. Hartman reports coho to steelhead aggressive acts at the rate of about 6 per fish per 100 minutes, and steelhead to coho at 0.5 per fish per 100 minutes in pools, whereas in riffles the corresponding figures were about 3.0 and 8.5 acts per fish per 100 minutes. Fraser (1969) used four replicate channels to test the influence of density of mixed populations of coho and steelhead on growth and survival. He found that survival of each species appeared to be largely independent of the density of the other species, with the exception that high densitites of steelhead may have had a slightly depressing effect on coho. In accordance with Hartman's findings, steelhead may have a competitive advantage over coho in riffle situations. Fraser reported differences in feeding behaviour, with coho being more oriented to surface drift, mainly insects of terrestrial origin.

A range of observations on interactions between coho and cutthroat trout populations have been made both in streams and in a stream-tank by Glova (1978). In streams he found that both species exhibited wide habitat utilization at high densities, but at lower densities trout dominated the riffles and coho the pools. Overlap between the species was highest in glides. In streams, competition was further reduced between the species by vertical segregation, with coho feeding predominantly at or near the surface, and trout feeding mainly on the bottom. A decline in trout numbers was coincident with an increase in coho, and the coho occupied a widening range of habitats (Table 1). Cause and effect are not indicated. In the stream-tank, single-species populations occupied similar habitats in summer, with 60-75% of fish in pools, but when the two species were together, coho numerically dominated the pools and trout the riffles. In a 3:1 coho:trout population density, coho overlapped with trout on the riffles to a greater extent than in the 1:1 situation. While feeding, many coho penetrated into riffle areas and either established transient feeding territories superimposed on trout, or displaced some trout into the pools. In winter, at 3°C both species occupied pools both when together and as single-species populations, with little display of aggression. At 5°C some trout occupied riffles, although both species defended riffle territories while feeding.

4.4 Atlantic salmon and brook trout

Gibson (1973) investigated interaction between Atlantic salmon and brook trout in natural populations in the Matamek river, Quebec, and in a stream-tank. In the river, below the falls where the two species occurred together, both occupied rapids in early summer when food was abundant. Later the trout vacated this zone, but above the impassable falls where trout occurred alone they remained near the rapids throughout the summer. It thus appeared that salmon displaced trout in fast water when food was limited. Observations in the stream-tank confirmed this behavioural tendency.

4.5 Atlantic salmon, coho salmon and brook trout

Gibson (1977) studied the interactions of these three species in a stream-tank. The tank was divided into three zones: pool, depth 75 cm, flow 3.8-6 cm per sec; wide channel, depth 45 cm, flow 6-8 cm per sec; narrow channel, depth 45 cm deep, flow 14-17 cm per sec. The total bed area was 13.2 m^2, and numbers of fish used in experiments were six of one species, or six each of two. Experiments were performed at a range of water temperatures from 7°C to 20°C. Salmon parr and brook trout were considerably more aggressive than coho. Brook trout more often displaced coho than did Atlantic salmon, although Gibson's earlier work (section 4.4) indicated that Atlantic salmon were dominant to brook trout. Atlantic salmon and brook trout attacked each other apparently without species discrimination, but among coho intraspecific acts of aggression were more numerous than were interspecific acts. The distribution and behaviour of coho was modified by the presence of the other species, whereas the presence of coho had little effect on the distribution of Atlantic salmon or trout.

There are three important qualifications to these findings:

(i) The coho used were of fish farm origin. Coho from a hatchery have been demonstrated to have a modified behaviour pattern, including reduced aggression (see section 3.4). The Atlantic salmon and trout were from wild stream populations.

(ii) The experiments were carried out from November to March, at which time aggression in all species is reduced. Although an artificial temperature regime simulated summer conditions in some experiments, the behaviour cycle may be determined to some extent by endogenous rhythms.

(iii) The current speeds at all points of the tank were lower than the optimum for Atlantic salmon (section 2.2), i.e. the fish may have been forced to occupy areas not of their choice, with consequent truncation of the riffle-pool segregated equilibrium. Further, the shallowest water (45 cm) was deeper than that normally associated with 0+ salmon.

Symons and Martin (1978) found 0+ coho in Frost Fish Creek in New Brunswick while collecting Atlantic salmon parr. They were presumed to be the result of natural spawning by fish which had been released in New Hampshire or had escaped from culture establishments in Maine. Although numbers were small (estimated at 24 fish) there were marked differences in the summer habitat selection of the coho, Atlantic salmon and brook trout. Atlantic salmon occupied the steeper areas of fast flow, while brook trout occupied pools and quieter water. An area of low gradient, choked with alders and surrounded by swamp, contained no Atlantic salmon, but large numbers of brook trout. The coho occupied the pools, and occurred in diminishing numbers in the swampy area. In winter, however, Atlantic salmon were found in the deeper area where they were never seen in summer. Symons and Martin suggested that the habitat requirements of coho are more similar to brook trout than to Atlantic salmon in summer, but that in winter some Atlantic salmon may utilize the brook trout/coho area.

5. CONCLUSIONS

From this review it appears that all the salmonid species considered have rather similar natural histories. They all occupy a range of habitats within the stream and thus exploit a broad, generalized ecological niche. Where two species occur together, the slight interspecific differences in behaviour become exaggerated, and the two species occupy different, narrower (though often overlapping) niches. It is in the aspects of most similar habitat requirements that this interactive segregation takes place most markedly. A dynamic equilibrium is set up, with one species dominant in one series of microhabitats and the second in another. The rather ritualized aggressive behaviour of stream salmonids serves to effect this segregation in a non-wasteful manner. Although the productivity (ultimately number of smolts produced per unit area) of each species is probably reduced by interactive segregation, it is likely that overall stream productivity will be increased, as two or more species, with slightly different ranges of microhabitats that they can occupy will be more efficient at exploiting the whole stream habitat than one alone. It is of course possible that one species would be dominant in all microhabitats, and would completely oust another. This is more likely to happen where two species which have evolved in total isolation, for example Pacific and Atlantic species, interact following an introduction. However, in the case of coho and Atlantic salmon, where observations on interactions have indicated that they seggregate spatially into different microhabitat types, it is unlikely that one species would exclude the other. Indeed, the combination would superficially appear to be an ideal one for maximizing stream production. Atlantic salmon smolt production would probably be reduced somewhat as coho made feeding forays into riffle areas, reducing the food supply available to the Atlantic salmon. While Atlantic salmon might be expected to dominate riffle production, coho exploitation of pools and margins might enhance overall salmon production in the stream. The two species appear to grow at approximately the same rate, though direct comparisons are difficult as growth rates are so dependent on food supply. From the considerations of diet (sections 2. 3 and 3. 3) both species appear to be opportunistic predators feeding largely on drift, and so would be potential competitors for the same food supply. However, it is likely that the agonistic behaviour would cause an interactively segregated partitioning of microhabitat use, such that unsuccessful competitors would be displaced from the arena, rather than remaining in the area to continually compete for the limited food supply.

The habitat preference of coho is more likely to impinge on that of brown trout than on that of Atlantic salmon. However, brown trout appear to be the most aggressive of the salmonids discussed, and are likely to be dominant over coho in at least part of their preferred microhabitat range. From experimental observations, interactions among Atlantic salmon, brook trout, rainbow (or steelhead) trout and brown trout might be expected to be more intense than between coho and Atlantic salmon. However, brook trout and rainbow trout have been widely introduced into Europe including the UK, with no dramatic effect reported on native species so far.

From the rather limited experimental evidence and reported observation available, it is concluded that the accidental or intentional introduction of a spawning stock into the UK is unlikely to have a dramatic effect on native salmonids. Some reduction in populations of Atlantic salmon and trout is likely in colonized streams, but overall salmonid production may be slightly increased. However, it is stressed that the evidence used in arriving at these conclusions is sparse, fragmented, and in some cases weak, circumstantial and annecdotal. It is strongly recommended that before any further action is taken which is likely to result in established spawning stocks of coho in UK streams a more thorough investigation should take place.

Some suggestions are offered as to the type of observations which might provide some of the required information:

(1) Detailed studies on streams in other countries where young Atlantic salmon and coho are found together. It is assumed that the situation in Normandy (see Appendix II) and in New Brunswick (section 4. 5) will be carefully monitored by the appropriate fishery authorities. Any new situations in Europe or North America should also be examined. Although observations in streams of different types may not be strictly applicable to the UK situation, any gross effects would be of great interest.

(2) Controlled stocking experiments, introducing Atlantic salmon and coho into streams from which seaward migration is unlikely to be successful, if such situations could be found. Examples could be clean headwaters of grossly polluted river systems, or streams draining into reservoirs with dams impassable to live smolts.

Another possibility would be a stream within the existing range of the coho, and where introductions of small numbers of Atlantic salmon or brown trout might not be unacceptable. Such areas could include the Great Lakes, North American Pacific coast and the New England States where coho introductions are being made.

(3) Stream-tank observations such as those of Gibson (section 4. 5), using a wide range of environmental conditions, and including interactions of the very early stages immediately after emergence from the gravel.

It is further suggested that consideration is given to the use of either pink (O. gorbuscha) or chum (O. keta) salmon as alternatives to coho for cage culture or ocean ranching. These species migrate to sea as fry, before commencing feeding. The possibility of adverse interaction with native salmonids is thus much reduced. It would of course still be desirable to conduct investigations into any possible risks before such introductions were made.

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APPENDIX I Names and natural distributions of the salmonid fish mentioned in the text

Common names	Latin name	Natural range
Atlantic salmon	*Salmo salar*	Atlantic coasts of Europe (Portugal to Russia) and North America (Connecticut to Hudson Bay). North Atlantic high seas.
Sea trout Brown trout	*Salmo trutta*	Rivers of Europe and West Asia draining to the Atlantic and Mediterranean. Widely introduced, including North America.
Coho salmon Silver salmon	*Oncorhynchus kisutch*	North Pacific coasts of North America (California to Alaska) and Asia. Pacific high seas. Introduced to Great Lakes.
Chinook salmon Spring salmon King salmon Quinnat	*Oncorhynchus tshawytscha*	North Pacific coasts of North America (California to Alaska) and Asia. Pacific high seas. Introduced to Great Lakes and New Zealand.
Chum salmon Dog salmon	*Oncorhynchus keta*	North Pacific coasts of North America (California to North-West Territories) and Asia. Pacific high seas.
Pink salmon Humpback salmon	*Oncorhynchus gorbuscha*	North Pacific coasts of North America (Washington to North-West Territories) and Asia. Pacific high seas.
Steelhead trout Rainbow trout	*Salmo gairdneri*	Coastal streams of Pacific North America (Mexico to Alaska). Widely introduced in North America, Europe (including UK) and elsewhere.
Cutthroat trout	*Salmo clarki*	Coastal streams of North America (California to British Columbia). Inland streams in the Rockies. Inshore Pacific waters.
Brook trout	*Salvelinus fontinalis*	North-east North America from Hudson Bay to Cape Cod, upper Mississippi. Introduced elsewhere in North America and Europe (including UK).

APPENDIX II Coho salmon in France

Harache and Novotny (1976) describe the history and practice of coho farming in France. Sixty thousand eggs were imported in December 1971 as the first stage in a pilot project by the Centre National pour l'Exploitation des Océans (CNEXO) (Centre Océanologique de Bretagne) in collaboration with the National Marine Fisheries Service from Seattle. Survival to one year of age in fresh water was 50%, but improved in subsequent years, being 85% in 1972 (200 000 eggs) and 96% in 1973 (250 000 eggs). Eggs have been imported each year since 1971. A pilot commercial company was formed in 1973, the Société pour le Developpement de l'Aquaculture en Bretagne (SODAB) with CNEXO as major owner. In 1974 and 1975 fishermen's co-operatives operated other farms. The farms are based on net pens in sea water in the Rade de Brest and in the estuary of the River Jaudy, both in Brittany.

The first attempts to rear the fish in sea water in summer resulted in heavy losses which were related to a combination of high salinity (35‰) and temperature (18°C). This led to the adoption of a winter cycle of sea-water production, with transfer during late summer or early autumn and harvest before the following summer. Smolting survival and growth of fish in salt water pens following this cycle is good, growth at times exceeding 1% per day. The first fish were commercially harvested in 1974 at a weight of 300-800 g, and were marketed in Paris. A total of 6.2 tonnes was marketed by July, and resumed harvesting in December brought the first year total to 7.6 tonnes. Between January and June 1976, 25 tonnes were marketed, mainly by SODAB. The price paid to the farmer averaged £2 per kg. In 1978, 45 tonnes were marketed at an average of £3.75 per kg (Harache 1979a).

Considerable studies of the critical salt water phase have been undertaken by Lasserre et al. (1978), Boeuf et al. (1978a, b), Harache et al. (1978) and Harache et al. (in press). Their results show that time of transfer to sea water must meet the physiological requirements of the species, which depend critically on environmental conditions. Transfer of 0+ smolts in late May, at weight of 18 g, gave excellent results with low mortality and excellent growth. Earlier or later transfer resulted in higher mortalities and slower growth. The 'window' where sea water transfer is feasible thus appears very narrow compared to that which exists in the natural range of the species (Novotny, 1975).

The results are considered very favourable in economic terms by CNEXO, and increases in scale are planned once broodstocks are established. The young fish are reared to smolt size in freshwater farms in Brittany, and in Normandy where excellent groundwater supplies have encouraged the establishment of several fish farms. It is from freshwater farms in Normandy and Brittany, and from the sea pens in the Rade de Brest, that the major escapes have occurred.

Information on the Normandy escapes has been supplied by Euzenat and Fournel of the Conseil Supérieur de la Pêche (CSP), Compiègne region. (pers. comm.). A farm on the River Varenne, a tributary of the Arques which enters the sea at Dieppe, was used to hatch 200 000 eggs in 1973, 300 000 in 1974 and 600 000 in 1975. About 50 000 yearling fish are believed to have escaped to the river in 1974, and about 10 000, 0+ fish in June 1975. The CSP have been carrying out electric fishing surveys for the past ten years, as part of a general survey of salmonid resources. Particular attention was paid to the Varenne after the coho escapes.

Following the first release, about 100 young coho were captured in the river, downstream of the farm, in May 1974. In October 1975, two adults were caught in the Eaulne, another tributary of the Arques. In December that year, 25 adults were caught in a 2 km stretch of the Varenne - scale readings confirmed their ages to be consistent with the 1974 escapes. Mean length was 54 cm (range 42-73) and weight 1 460 g (range 760-3 460). In June 1976, 25 0+ coho were caught in the Varenne; these are thought to have derived from natural spawning, as no coho were held at the fish farm that year. Later that year, a coho 'jack' (a fish having spent only a few months at sea) was caught, presumably derived from the 1975 escape. In March 1977 one yearling fish and, later that year, five adults were caught.

During 1975, two adult coho were caught in the River Bresle, the mouth of which is 25 km north-east of Dieppe, and one in the Canche, 100 km to the north-east. These are likely to have arisen from the Varenne escape.

In view of the number of fish escaping, these figures are indicative of a declining population. This should not be taken to indicate that coho could not establish runs elsewhere, however, as the Varenne supports only a poor run of sea trout and very few Atlantic salmon. Reasons for this include pollution of the lower estuary, poor spawning gravel, and impassable weirs.

Small-scale escapes from sea pens probably occur regularly, but in early 1977 about 6 000 fish escaped in the Rade de Brest (Harache, pers. comm.). These were fish that had been in sea water for about nine months, and weighed about 400 g each. Most of them remained in the vicinity of the cages, and about 4 000 were recaptured. No catches in rivers in the area were reported, and only occasional catches by commercial fishermen and sea anglers have been reported in a limited area in the Rade de Brest.

Another escape occurred from a freshwater farm in southern Brittany (Odet River) when about 10 000 fish (0+, 2 g and 1+, 50-70 g) were accidentally released in March 1976. Electric fishing the day after the release recovered part of the stock. There is no record of adults returning to the river in 1977 or 1978. However, this should not be taken as proof of non-survival of the released stock as there is no trap on the river, and no established net or sport fishery is operating in the area at the expected time of year of returns (October-November).

There have been two reports of illegal intentional introductions by angling clubs (Harache, 1979b). In March 1977, 636 year-old fish (28-35 cm) were released in the Sienne River, south of Cherbourg. At least 100 fish were captured by anglers in the area later in 1977. The second introduction was to the Var River in Southern France, and consisted of 10 000 smolts of 12-15 g released early in 1979.

In August 1977, a coho salmon was caught in the sea in the Channel Islands by an angler. Its age was consistent with the Rade de Brest escape, and with the Sienne introduction.

The present approach of French farmers and CNEXO scientists shows that coho constitutes a viable alternative for salmon farming in the prevailing environmental conditions. The species permits economic production of small fish (pan size - 1 kg) in a short rearing period (12-18 months). This is a quite different product to Atlantic salmon as at present farmed, producing large fish in 2-4 years (Harache, 1979a). However, scientists in CNEXO do consider that if this type of aquaculture is to be developed on the French coast, an investigation of the behavioural interaction with Atlantic salmon might be necessary in the near future (Harache, pers. comm.).

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