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Drift, Migration, and Intermingling Of Pacific Halibut Stocks

by

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ABSTRACT

The pending renegotiation of the Halibut Treaty between Canada and the United States and the review of management alternatives for the halibut fishery prompted this reanalysis of data regarding the interrelationships of halibut stocks.

The drift of eggs and larvae, the migration of juvenile halibut, and the movements of adults are discussed in relation to regulatory areas and national boundaries. Contrary to earlier conclusions that stocks in the two major regulatory areas were independent, the results of this study show that these stocks intermingle at all stages of their life history.

Eggs and larvae drift to the north and west away from the spawning grounds and the compensatory movement to maintain the population's geographic position apparently is accomplished mainly by juvenile halibut. The migratory circuit of the major stocks is described.

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INTRODUCTION

The identification of stock units, their degree of intermingling, and the movements of fish across geographic boundaries is information critical to the management of the resource. Not infrequently, this information is needed to resolve biological or political questions associated with the regulation of fisheries. The International Pacific Halibut Commission (IPHC) has conducted tagging experiments, egg and larvae surveys, examined anatomical and biochemical differences, and utilized statistics from the fishery to identify stock components of Pacific halibut (*Hippoglossus stenolepis*). The purposes of this paper are to review past conclusions regarding stock components, migratory behavior and larval drift and, in conjunction with analyses of the distribution of juvenile halibut, to determine the interrelations of the stocks and the extent and character of "transboundary movements" between Canadian and United States waters.

An inherent part of this study was the question: How do stocks maintain their geographic position when ocean currents carry eggs and larvae away from the spawning grounds, particularly when the magnitude of compensatory movement by adults apparently cannot account for the "loss" of these early life history stages? A new thesis is proposed to explain this enigma and a working model is presented to describe the movements of halibut at all life history stages.

This study was prompted by (1) the pending renegotiation of the Halibut Treaty between Canada and the United States and (2) a review of management alternatives for the halibut fishery being conducted by the U.S. North Pacific Fishery Management Council (NPFMC). The United States Fishery Conservation and Management Act of 1976, which created the Regional Management Councils, called for renegotiation of fisheries treaties which are inconsistent with the Act and for withdrawal if a treaty is not renegotiated within a reasonable period of time. On April 1, 1977, the United States Department of State notified Canada that the Halibut Treaty would be terminated if not renegotiated by April 1, 1979; the 2-year notice is specified in the Treaty. The Act also specifies that "To the extent practicable, an individual stock of fish shall be managed as a unit throughout its range, and interrelated stocks of fish shall be managed as a unit or in close coordination". Thus, it is incumbent for the renegotiation of the Treaty as well as the review of management alternatives to consider the interrelations of halibut stocks and the extent of transboundary movements.

Definitions of Movements

Because of conflicting definitions in the literature, it is important to define the terms used in this report to describe the movements of halibut. My selection of definitions borrows heavily from the reviews by Allee et al. (1949) and by Harden Jones (1968).

I use the term "passive" only to describe the movements of eggs. Early stages of larvae also move passively with the currents but, as development progresses, I assume that the postlarvae are capable, to a limited degree, of active, directed movement. In general, the movement of eggs and larvae is denatant (floating or swimming with the current). Movements by juveniles and adults may be either denatant or contranatant (swimming against the current). This definition of contrananant originally was proposed by Meek (1916) and has been adopted by others, for example, Beverton and Holt (1957). Harden Jones (1968) proposed that contranatant specifies a "biological relationship between the migration of the eggs and larvae on the one hand and that of the adults on the other", regardless of whether the adults are swimming with or against the current. I accept his premise but disagree with the use of the term contranatant to define the relationship as it contradicts the original definition.

Local movements or dispersals are distinguished from migrations that generally are long-distance movements that the fish are impelled to make annually (Bowman 1933). Migrations are coordinated with or stimulated by environmental influences, but are under the control of the animal and there is a return to the original locality. The term migration is reserved for reciprocal movements, such as from the feeding grounds to the spawning ground and the return, but is used to describe either leg of the movement.

The term emigration is used for long-distance movements that need not be reciprocal and are not made annually. Compensatory emigration is applied to the movements of juveniles or adults which counteract the drift of eggs and larvae.

Transboundary movements are those that cross either political or regulatory boundaries and may be any of the types described above.

CONCLUSIONS OF PAST STUDIES

The sequence of discussions in this section generally corresponds to the chronology of IPHC studies concerned with the identification of stock components. This approach will enable the reader to follow the past accumulation and interpretation of data pertinent to transboundary movements. In the subsequent section, the reexamination of the data conforms to a biological sequence and proceeds from eggs and larvae to juveniles to adults.

Tagging Experiments

Tagging experiments have been an integral part of the Commission's research program since its inception in 1925. The results of the first tagging studies were reported by Thompson and Herrington (1930), Babcock et al. (1930 and 1931), and Kask (unpublished).[1] Since then, IPHC regularly has included tagging data in its Annual Reports and has published several special papers that emphasized tagging results (Dunlop et al. 1964; Myhre 1966 and 1967; Bell 1967; Peltonen 1969). Other publications have included sections on migration as

[1] "Studies in migration fishing mortality and growth in length of the Pacific Halibut (*Hippoglossus stenolepis*) from marking experiments" by John Laurence Kask, Doctoral Thesis, University of Washington, Seattle, 1935, 145 p.

deduced from tagging studies (Bell and Best 1968; Bell and St-Pierre 1970; Skud 1975; Best 1977).

A major objective of the early tagging work was to identify stock components and to delineate management units. Subsequent analyses of tagging data largely were directed towards estimating mortality and determining the rate of exploitation of particular stock components. Although migrations from particular areas such as the Bering Sea and Shumagin Islands have been discussed in the publications cited above, no comprehensive review of all the experiments has been undertaken to describe migratory behavior, to explain the differences in migratory patterns, or to estimate the degree of intermingling from region to region.

The decision to establish regulatory areas relied extensively on tagging studies in the late 1920's. Thompson and Herrington (1930) and Babcock et al. (1931) concluded that the stocks of adults south of Cape Spencer, Alaska (Area 2) and those north and west of Cape Spencer (Area 3) were basically independent. This conclusion was used to justify the separation of these areas into management units. These regulatory areas and the geographic regions that are mentioned later in the report are shown in Figure 1. Only the first few years of tag recoveries were available when it was decided to establish area boundaries, but differences in age composition and stock abundance also contributed to the decision.

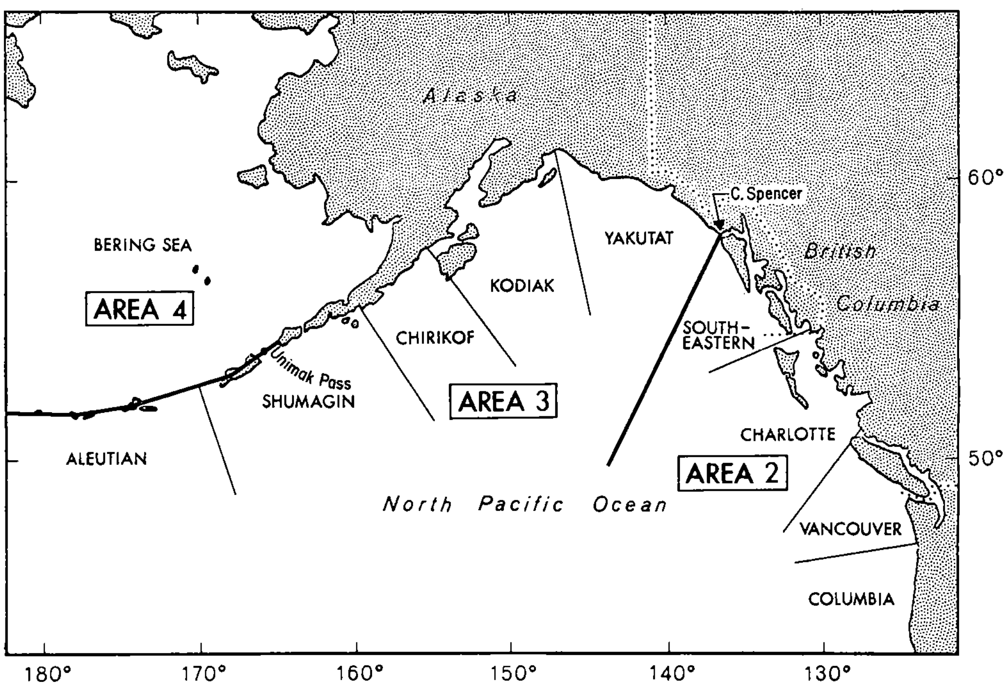

Figure 1. Regulatory Areas 2, 3, and 4 and regional divisions of the coast. Area 1 (Columbia Region and south) was incorporated as part of Area 2 in 1967.

Thompson and Herrington (1930) made the following statement about the migration of halibut in Area 2, "Only 5 and 10 percent were retaken more than 50 miles distant from the tagging localities. The dispersion increases slowly from year to year, as shown by comparisons of seasons, but the bulk of fish remain on home grounds". The authors contrasted these results with those of Area 3 in which migrations were more extensive and interchange occurred "from the eastern side of the Gulf of Alaska as far as Unimak Pass and perhaps beyond . . . five percent only of recoveries from western experiments were retaken south of Cape Spencer, and but one fish from the south was retaken west". They pointed out that halibut tagged in Area 3 predominantly were mature fish and were larger than those in Area 2 and concluded that the two areas separated by Cape Spencer were practically independent. Kask (op. cit.) reached a similar conclusion and stressed the fact that the largest halibut undertook the longest migrations.

The emphasis on the independence of stocks from Area 2 and Area 3 was evident in IPHC's publications through the early 1950's. Van Cleve and Seymour (1953) reviewed the results of tagging experiments that had been interpreted as showing differences between these stocks:

> "Investigation of the nature of the halibut populations of the Pacific Coast have shown that they are separated into two major groups of populations with the boundary between lying approximately at Cape Spencer . . . Tagged mature fish, released in various locations along the entire coast west of Cape Spencer in present regulatory Area 3 were found to move relatively freely between banks in that area. However, off the coast of British Columbia and Southeastern Alaska in present regulatory Area 2 the movements were generally confined to a random distribution within the confines of the small bank on which the fish had been tagged. The number of recoveries of tags which had moved between the two large areas was small in proportion to the chances of recovery expressed in terms of intensity of fishing . . . This contrast in habits of the fish in the two areas was found to be associated with the age and size of fish which predominated in the stocks. To the westward in Area 3 was found a substantial proportion of mature fish and these were found to undertake major migrations between the spawning grounds in the northern and eastern parts of the Gulf of Alaska and the feeding ground farther west. Few mature halibut were found in Area 2 off British Columbia and Southeastern Alaska and the young were primarily non-migratory."

IPHC (1954) summarized results from tagging experiments in 1951-1953 and said the recoveries corroborated "the relative independence of the stocks of fish that were marked on different grounds at the same season".

The emphasis on stock separation and independence changed in later years and IPHC publications began referring to the interrelationship of stocks in the Bering Sea and Areas 2 and 3. During the late 1950's and in subsequent years, the status of the halibut resource in the Bering Sea was a crucial issue. The Convention that created the International North Pacific Fisheries Commission (INPFC) specified that Japan must abstain from fishing halibut in the Bering Sea providing, among other criteria, that the stocks were fully utilized. Discussions in INPFC revolved about estimates of abundance of halibut and the relationship to other halibut stocks. IPHC conducted special tagging experiments in the Bering Sea in 1956 to study this relationship. The first year recoveries "showed a widespread movement into Areas 3A and 2 similar to that observed during the first year of 1930 and 1947 experiments in Bering Sea" (IPHC 1958). Similar references were made in subsequent Annual Reports from 1958 to 1961.

Fukuda (1962) examined the differences in mean weight of halibut from several areas and concluded that the Bering Sea halibut belong to a stock independent from that in Area 3. Dunlop et al. (1964) stated that "in view of the evidence from tagging and the variability in age-weight data, such a conclusion is unwarranted . . . Such emigration indicates that the halibut in the eastern Bering Sea are not biologically separable from those in the eastern Pacific . . . The halibut in southeastern Bering Sea are shown to be a part of the large population west of Cape Spencer and to be related to a lesser degree of that off British Columbia and southeastern Alaska". This same report explained that IPHC's tagging experiments had shown little interchange between the grounds south and west of Cape Spencer and supported the decision to divide the coast into two areas for management purposes, but the report also stated "In contrast, tagging in southeastern Bering Sea has shown a pronounced movement of fish into Area 3 as well as into Area 2". No explanation was provided to account for this incongruity — a pronounced movement from the Bering Sea to Area 2 but little emigration from Area 3 to Area 2.

Bell (1967) reviewed results of tagging experiments in the western Gulf of Alaska. He estimated that 21% of the fish tagged near the Shumagin Islands emigrated to eastern grounds, and his data show that less than 10% moved into Area 2 (south of Cape Spencer) and less than 5% to British Columbia. These percentages are not greatly different from those shown by Thompson and Herrington (1930) for emigration from tagging in Area 3. Bell (1967) concluded that the results illustrated "the close relationship between fish in the far western region and on those grounds to the eastward even as distant as the coast of southern British Columbia". He also mentioned the eastward movement of halibut to the spawning grounds in the Gulf of Alaska which "counterbalances the reverse drift of eggs and larvae in the Alaskan current moving in a southwesterly direction along the Alaskan Peninsula and the Aleutian Islands". No geographic reference was included to indicate that this thesis applied to areas south of Cape Spencer.

In reference to stocks south of Willapa Bay, Washington, Bell and Best (1968) concluded:

> "The interrelationship of the halibut south of Willapa Bay, Washington with those to the north off British Columbia and Alaska is evident from the results of tagging and morphometric studies. Numerous halibut tagged throughout the entire range of the fishery and as distant as the Pribilof Islands in the Bering Sea have been recovered from grounds south of Willapa Bay, Washington. Also a reverse movement is demonstrated by the recovery of tags off the coast of British Columbia and Southeastern Alaska that were released off northern California. Furthermore, if there is any halibut spawning south of Willapa Bay, the effects of the prevailing currents upon the eggs and larvae are such as to establish a close relationship between the halibut in Area 1 and those in Area 2 or farther north."

Best (1968) reported on the movements of juvenile halibut (<65 cm) that had been tagged in the Gulf of Alaska. He pointed out that "the predominant direction of movement has been to the east . . . similar to that which has been observed for adults". Although Best showed that juveniles migrated from Area 3 to Area 2, no specific reference was made concerning the interrelationship of stocks in these areas. IPHC (1973) also referred to a movement from Area 3 to Area 2 but did not discuss its significance.

Egg and Larval Studies

Thompson and Van Cleve (1936) described the eggs and larvae of halibut and studied their distribution relative to the ocean currents. The authors discussed the division of the Japanese Current as it approached the North American Coast into the northerly-moving Alaska Current and a southerly California Current. From drift bottle studies, they concluded the division occurred at 50° N (northern Vancouver Island) in August and somewhat further south in the winter. Studies of surface and sub-surface currents (to 1,200 meters) showed a predominant northwesterly and westerly movement at all depths in the Gulf of Alaska and the strongest flow was "just outside the edge of the banks" (McEwen et al. 1930; Thompson and Van Cleve 1936). Drift bottles released in March off British Columbia were recovered in Hecate Strait, southeastern Alaska, near Cape Spencer and Cape St. Elias, in Prince William Sound, Cook Inlet, and near Kodiak Island (Figure 2). Drift bottle releases in other locations also showed a dominant northwesterly movement.

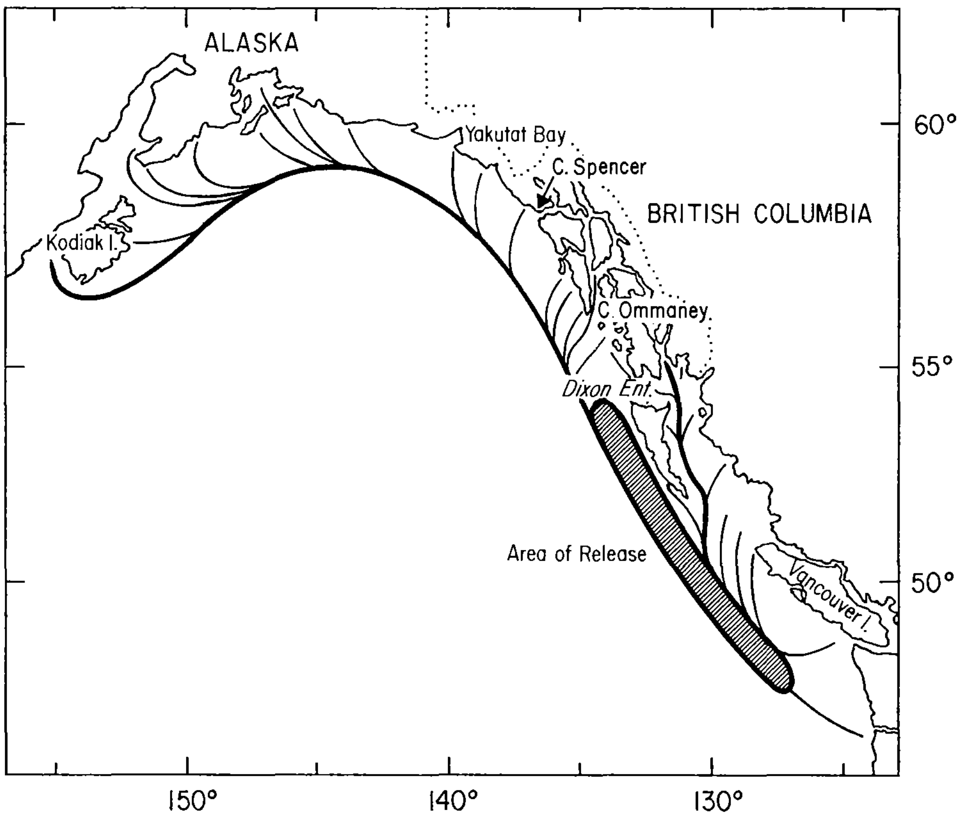

Figure 2. Drift as indicated by the returns from the drift bottles released between March 22 and 25, 1932 (after Thompson and Van Cleve 1936).

Relatively little information on the current system in the Gulf of Alaska was added until the mid-1950's and the state of oceanographic knowledge in the entire North Pacific was considered fragmentary (Fleming 1955). Since then, contributions by many authors have broadened and refined the information on oceanographic features in the Gulf and detailed summaries of these studies have been published by Dodimead, Favorite, and Hirano (1963) and by Favorite, Dodimead, and Nasu (1976). In general, the results of recent studies have confirmed the findings of IPHC's studies on currents and drift. A recent manuscript by Favorite, Laevastu, and Straty (unpublished)[1] related oceanographic conditions and processes in the northeastern Pacific to commercially important fishes, including halibut, and their observations are discussed later in this report.

In conjunction with the hydrographic studies, Thompson and Van Cleve (1936) took plankton samples to study the distribution of halibut eggs and larvae. Sampling stations were not the same each year but included offshore waters in the Gulf of Alaska as well as coastal stations near known spawning grounds in British Columbia and Alaska. The eggs usually were found at depths of 100 to 200 meters near the outer edge of the spawning grounds in January and February. Eggs were occasionally taken as shallow as 40 meters and as deep as 935 meters. No eggs were found in shallow surface waters that were characterized by a relatively low salinity.[2] Newly hatched larvae generally were found in depths below 425 meters outside the edge of the continental slope. As the larvae developed, they rose to the surface and after 3 to 5 months were found at depths of 100 meters or less. Currents carried them inshore where they eventually settled to the bottom in May and June, 6 to 7 months after spawning.

The eggs and stage 1 larvae were taken from northern British Columbia to Kodiak Island (Figure 3). The range of larvae in stages 2 through 4 extended westward beyond Kodiak Island. South of Cape Ommaney, Alaska, only four stage 3 larvae were taken, only one stage 4, and no larvae in stage 5. Thompson and Van Cleve (1936) reported that halibut larvae from the banks west of Cape Spencer were carried westward and offshore in the Gulf Eddy. They found no evidence that larvae were carried south to British Columbia and concluded that "The distribution and drift of the eggs and larvae confirm the result of tagging, racial, and growth investigation of the adults in indicating the separation of the two main stocks of halibut". The authors said that eggs spawned near Cape St. James, British Columbia apparently drifted into deeper waters and were carried northward along the west coast of the Queen Charlotte Islands, but made no mention of movement to Alaskan waters. They concluded that the British Columbia spawning grounds were "dependent upon their own spawning stock for their supply of eggs and young". They stated that because spawning had been so reduced in British Columbia, the number of eggs and young was not sufficient to work out their drift. Their conclusions were reaffirmed by Van Cleve and Seymour (1953):

[1] "Oceanography of the northeastern Pacific Ocean and eastern Bering Sea, and relations to various living marine resources" by Felix Favorite, Taivo Laevastu and Richard R. Straty, U.S. National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Processed Report, June 1977, 280 p.

[2] Forrester and Alderdice (1973) observed the development of halibut eggs in the laboratory and found that the density of each egg increased with time. Their estimates of buoyancy generally correspond with field observations by Thompson and Van Cleve (1936).

"A widespread search for the pelagic eggs and larvae of the halibut produced by the relatively large spawning populations remaining in Area 3 between 1927 and 1930 indicated that few were carried into Area 2, so that in both older and younger stages the two stocks seemed to be practically independent (Thompson and Van Cleve, 1936). The concept of separation of the halibut populations in the two areas during their early life history was supported by an investigation of the ocean currents in the Gulf of Alaska (see Reports 4 and 10, International Fisheries Commission). Since the eggs and young of halibut had been found to be extremely scarce in Area 2 the lack of an outside source of young meant that the halibut stocks in that area must be self supporting and that their rehabilitation would depend upon whatever gains could be made in those stocks alone."

Best (1968) reviewed the results of the early studies on eggs and larvae and presented a diagram of their movements. He showed that the movements in Area 3 (west of Cape Spencer) were independent of Area 2, as previously mentioned; however, he indicated a movement from British Columbia to southeastern Alaska. Bell and St-Pierre (1970) also reviewed the early life history stages of halibut and discussed their movements relative to the ocean currents. They stated that the velocity of these currents at the edge of the continental shelf could be as high as 10 knots and concluded that "the floating eggs, the developing larvae and the postlarvae may be dispersed far from the point where they were produced. Eggs produced on the shelf edge in the eastern Gulf of Alaska and even from more distant grounds to the south could, under some conditions, be the source of the young found in Bering Sea". Neither Best (1968) nor Bell and St-Pierre (1970) mentioned that the movement to Alaska from British Columbia ("distant grounds to the south") differed from the interpretation by Thompson and Van Cleve (1936) nor did they offer an explanation of this difference.

Fishery Statistics and Biological Data

In addition to the migratory behavior of adults and the distribution of eggs and larvae, other information was used to determine whether stock components were independent. Thompson, Dunlop, and Bell (1931) made a detailed analysis of the abundance and yield from Areas 2 and 3. Their paper stressed the validation of statistical parameters and the documentation of changes in abundance within the two areas. Specific reference to the relation of the stocks in the two areas was not emphasized in this paper but was referred to by Thompson and Van Cleve (1936):

"It has already been found (Thompson, Dunlop, and Bell, 1931) from statistics, that the fisheries to the north and west of Cape Spencer have maintained a totally different level of abundance and of yield from the very beginning as compared to those south and east. These levels have reacted differently to the strain of the fishery, indicating virtual independence. When studied from a biological viewpoint, the fish from these sections have shown that type of structural difference which accompanies exposure to differing conditions during growth and which can be perpetuated only by isolation. By marking experiments on fish of marketable size, the extent of this independence and isolation has been determined and measured (Thompson and Herrington, 1930). Hence it is proper to conclude that as far as the marketable sizes are concerned, the fishery cannot draw upon the resources of one section of the coast by fishing in

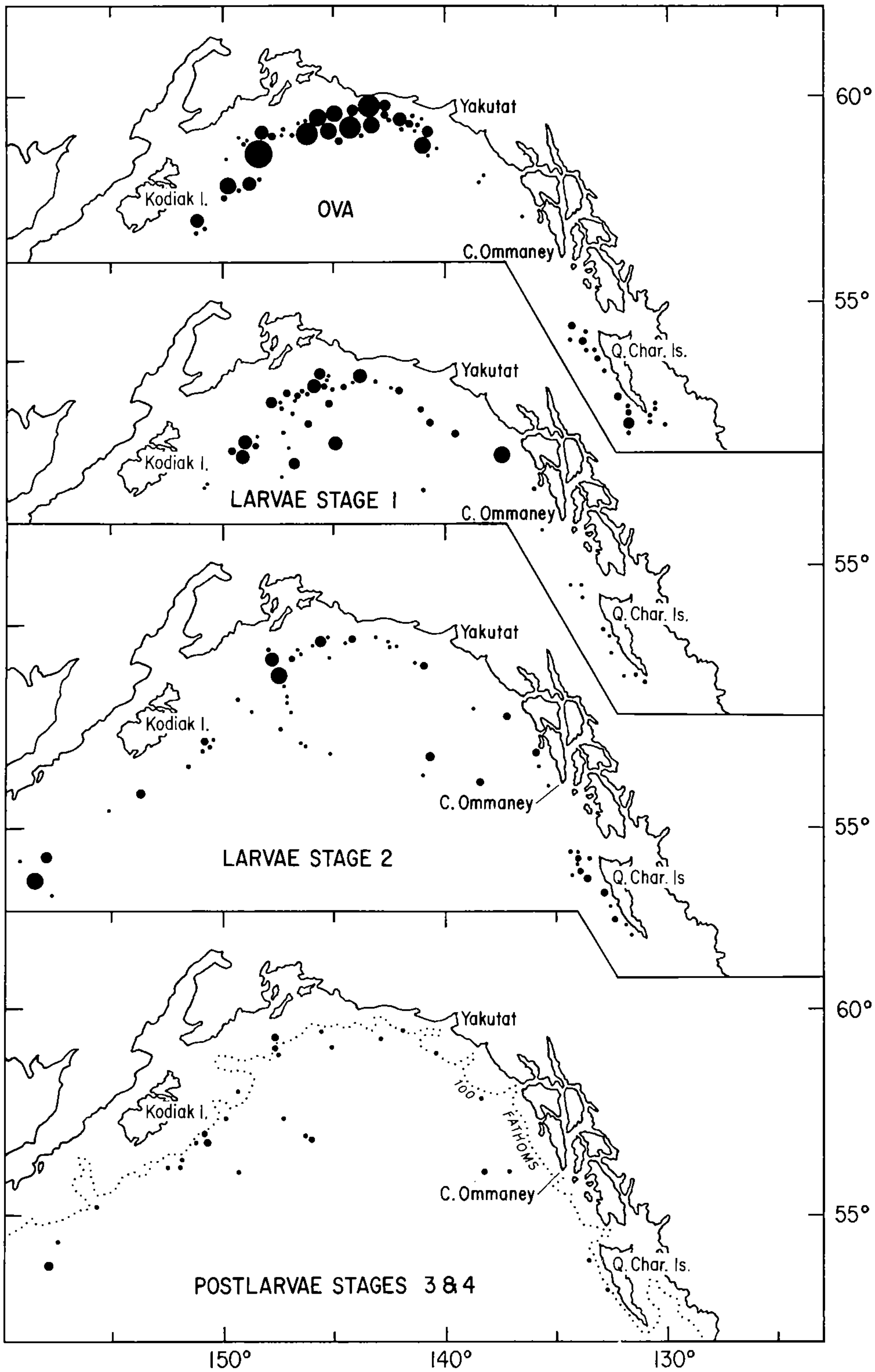

Figure 3. Distribution of halibut eggs and larvae (after Thompson and Van Cleve 1936: "The area of each circle is proportional to the total number of specimens that have been taken in that locality").

another, except within the limits of the individual stocks, and accordingly protection of one stock cannot be regarded as protection of another."

Van Cleve and Seymour (1953) also cited the 1931 publication and referred to the independence of the stocks. Their summary also mentioned factors such as growth and differences in body proportions:

"Additional evidence of the separation of the two stocks of halibut at Cape Spencer was derived from a study of the variations in yield of the fishery during the years prior to 1930 (Thompson, Dunlop and Bell, 1931). The populations in the two areas had declined roughly in proportion to the age and intensity of the fisheries that they had supported. But the decline in Area 2 had begun earlier since the fishery had begun earlier there and the catch per skate had dropped to a lower level than it had in Area 3. On the other hand the catch per skate of fish on the more recently exploited and more remote banks in Area 3 showed plainly that they had been affected by the fishery in other parts of Area 3. The first catches on those banks showed approximately the same catch per skate that was found at the same time in the rest of Area 3 which had already suffered a considerable decline (Figure 22, page 63, Thompson, Dunlop and Bell, 1931). Differences in the growth rates of the fish in the two areas corroborated the results obtained form tagging (Dunlop, Ms.). The separation of the two stocks was further substantiated by differences in body proportions of fish taken in the two areas (Bell, Ms.). The Area 3 fish grow more slowly than do those in Area 2 and the latter have on the average smaller heads than do the western fish."

Studies on juvenile halibut reported differences in size by area and depth but did not relate these findings to movements or to stock components (IPHC 1961 and 1963).

Biochemical Studies

Tsuyuki, Roberts, and Best (1969) analyzed the serum proteins of over 1,000 halibut from British Columbia to the Bering Sea. Four serum transferrin systems were postulated and accounted for eight phenotypes that were observed in the study. The samples were divided into 10 geographic areas and from analyses of the gene frequency, the authors concluded that only one area, southeastern Alaska, was not homogeneous.

Dr. Fred Utter, NMFS, (personal communication) also found genetic uniformity in an enzyme study of flesh samples of halibut collected from British Columbia to the Bering Sea. He did report that a small sample taken from Amchitka (western Aleutian Islands) showed a high frequency of a form of an enzyme that was present only in low frequencies in samples from other sources.

Although these biochemical studies, with one exception, have not demonstrated any differences among the stocks, the results are not conclusive evidence of homogeneity as they only apply to the particular biochemical systems included in the analyses. Studies on the mercury content of halibut showed significant differences between adjacent regions (Hall et al. 1976). This difference could be interpreted as an indication that the stocks are not homogeneous.

REANALYSIS AND ASSIMILATION OF DATA

As previously explained, the sequence of the presentation in this section proceeds from early to late life history stages. Past conclusions regarding stock components are reexamined and the results assimilated with other data that are pertinent to intermingling and transboundary movements. The information presented in this section also was used to formulate a conceptual model of the migratory behavior of halibut which is presented in greater detail later in the paper. The basic premise of this model is that stocks inhabiting Area 2 and Area 3 intermingle at all stages of their life history and that the migrations of juveniles, not adults, compensate for the drift of eggs and larvae and provide the mechanism by which population units maintain their geographic position.

Before proceeding, however, the reader should realize that our knowledge about spawning locations is limited. Spawning takes place along the edge of the continental shelf from November to March and it is assumed that the adults spawn annually. The major spawning sites include Cape St. James, Langara Island (Whaleback), and Frederick Island in British Columbia and Yakutat, "W" grounds, and Portlock Bank in Alaska. Other spawning sites have been reported near Goose Islands, Hecate Strait, and Rose Spit in British Columbia and Cape Ommaney, Cape Spencer, Cape St. Elias, Chirikof, and Trinity "outside" grounds in Alaska. Spawning concentrations also occur in the Bering Sea. Past emphasis on the major spawning areas may have implied that these were the only spawning grounds; in fact, there is reason to conclude that spawning is widespread and occurs in many areas, although not in as dense concentrations as those mentioned above. Evidence to support this conclusion is based on the widespread distribution of mature halibut during the winter months as indicated by research cruises and commercial fishing.

Drift of Eggs and Larvae

The Thompson and Van Cleve (1936) paper contributed greatly to the knowledge of the life history of halibut and provided excellent anatomical descriptions and drawings of halibut eggs and larvae. The paper was one of the earliest in North America to use an interdisciplinary approach, combining hydrographic data with biological information. The authors noted some of the limitations of their study:

> "In making such a comparison it is necessary to point out that we do not know whether there is a difference in the time at which the maximum spawning occurs, so that until this is known for both areas, somewhat different parts of the season may be unwittingly compared. The rapidity with which the eggs are scattered by currents may differ; and the areas covered by the spawning schools have not yet been mapped. In short, the system of sampling the eggs has not been perfected, and the differences shown by a comparison must be large and consistent within the series of samples taken to be acceptable."

Some of these limitations are pertinent to their conclusions regarding the relations of Area 2 and Area 3. Thompson and Van Cleve (1936) used a composite of 9 years of data to show the distribution and abundance of eggs and larvae in the Gulf of Alaska. In part, this approach was dictated by necessity because funds were not great enough to sample the entire coast each year or to sample each area at the same time. This deficiency places severe limitations on quantitative comparisons as well as on conclusions about movements of eggs and larvae. These limitations are apparent in the authors' estimates of the abundance of eggs in Area 2 and Area 3.

Thompson and Van Cleve (1936) reported that the average density of eggs in Area 3 (25.5 eggs per haul) was 10 times the density in Area 2 (2.6 eggs per haul) and credited the low abundance in Area 2 to the "scarcity of spawning adults on those banks". The comparison was based on data collected during January. The only time hauls were taken in January in Area 2 was in 1934; whereas all but one January haul from Area 3 were taken in 1928 and 1929, and the 1928 data accounted for 95% of the eggs. In essence, then, the comparison was made between 1928 for Area 3 and 1934 for Area 2. The reliability of the comparison with a 6-year lag is questionable, particularly so in that the number of eggs per tow in Area 3 was 27.6 in 1928, but less than 5.0 in 1929. Further, the catch per haul in February in this area declined from 12.4 in 1928 to 0.8 in 1934. The difference in abundance between these years *in the same area* was as great as the difference *between areas* (25.5 and 2.6). Another limitation was the varying number of hauls taken within and outside of the area where eggs and larvae were distributed.

As a result of these sampling limitations, the conclusions about abundance and the distribution of eggs and larvae must be qualified accordingly. Without question, however, the authors showed that eggs and larvae were distributed widely and that this distribution was governed by current patterns.

The results of the studies on eggs and larvae were offered as evidence of stock independence (Thompson and Van Cleve 1936):

> "The stock of fish inhabiting Area 3, proved by tagging, growth, and racial work to be distinct from the fish in Area 2, are also distinct during embryonic and larval development due to the currents in the Gulf. None of the young produced on the western banks in Area 3 are carried southward onto the southern banks which are therefore entirely dependent upon their own spawning stock for their supply of young."

In part, their conclusion was based on the distribution of postlarvae in stages 3, 4, and 5, few of which were found south of Cape Ommaney, "in light of the results of the current observations, especially of the drift bottle experiments, it definitely establishes the lack of drift of larvae from the western banks southward to the southern banks". This conclusion addressed the *southerly drift* but the possibility of *northerly drift* from British Columbia to southeastern Alaska or from Area 2 to Area 3, *was not mentioned.* Yet, based on the hydrographic studies and the distribution of larvae shown by Thompson and Van Cleve (1936) in Figure 3, a northerly drift of eggs and larvae from British Columbia to southeastern Alaska and Area 3 is indicated. Because no major spawning ground was known in southeastern Alaska, relatively few samples were taken there in January and February but larvae were present in these samples. During March and April, the proportion of late stage larvae was greater in southeastern Alaska than in British Columbia. Furthermore, Thompson and Van Cleve stated that stations sampled in the Gulf of Alaska showed that eggs and larvae drifted offshore. Conceivably, these eggs and larvae could have been from Area 2 as well as Area 3. Evidence to support the hypothesis of northerly movement from British Columbia is described in the following paragraphs.

Van Cleve and Seymour (1953) reported on the distribution of halibut eggs near the Cape St. James spawning area in British Columbia from 1935 to 1946. The eggs were collected from sampling stations near the Queen Charlotte Islands, 51° to 53° N (Figure 4). The purpose of the study was to estimate the abundance of eggs and to relate the observed changes in abundance to subsequent year class strength.

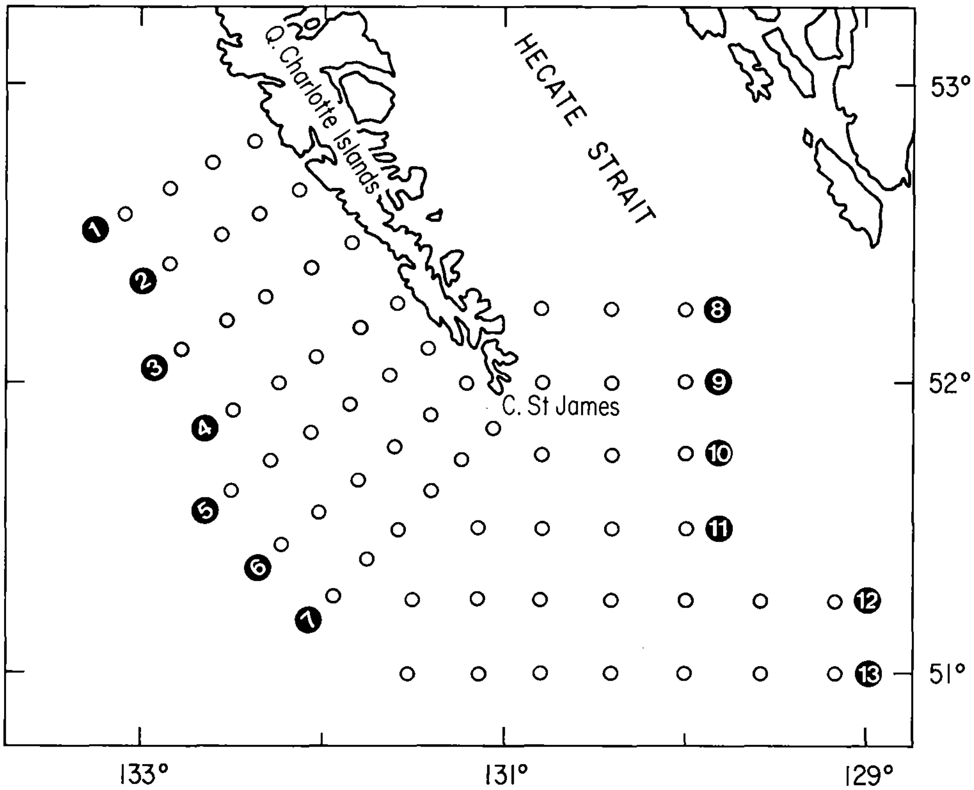

Figure 4. Transects (Nos. 1-13) of sampling stations for halibut eggs (after Van Cleve and Seymour 1953).

The authors drew density contours based on the number of eggs in stage 1 (to closure of the blastopore) at each station each year. Four of these years are depicted in Figure 5. Eggs in stage 2 (from blastopore closure to hatching) were not used in the analysis because their numbers and distribution were "insufficient to enable the drawing of contours". Although the drift of the eggs was not a major emphasis in the paper, the authors concluded that halibut eggs in the area of sampling apparently were "isolated from the eggs produced on other spawning banks and, while the currents may carry some eggs out of the area, the numbers carried into the area are not great enough to be measured by the present sampling technique". The authors did mention an unusually large catch of stage 2 eggs near the northern limit of the sampling grid (52° 45′) in 1942 and said that these eggs may have come from the southeast; and they suggested that eggs well south of Cape St. James could have been from spawning near Vancouver Island.

In my opinion, the orientation of the amoeba-like contours shown in Figure 5 indicate a definitive northerly movement of the eggs that conforms to the general current patterns. This conclusion is based first on the shape (streamlines) of the contours and second on the fact that the highest densities were near known spawning grounds at Cape St. James. There was no indication that extensive spawning occurred in the northern portion of the sampling grid. Not all of the years showed as pronounced a directional movement and, occasionally, southerly protuberances were evident in the contours, but they usually were offset by protuberances to the north which were present every year and predominated for the entire sampling period.

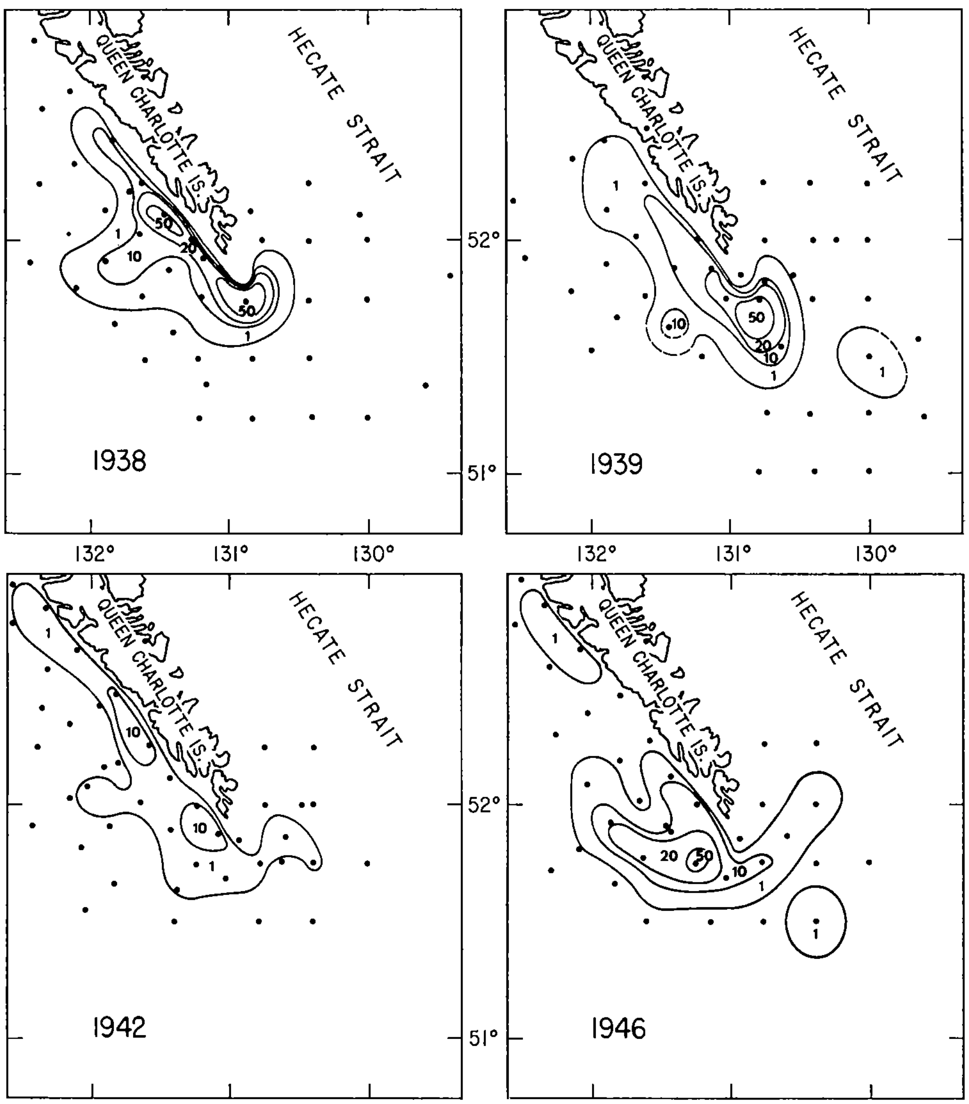

Figure 5. **Density of halibut eggs near Cape St. James, British Columbia. Contours based on number of eggs per standard haul. Dots indicate sampling stations (after Van Cleve and Seymour 1953).**

To test the validity of a northerly movement, I examined unpublished data that Van Cleve and Seymour had tabulated from 1936 to 1943 and I compared the ratio of stage 1 eggs to stage 2 eggs with latitude. Forrester and Alderdice (1973) indicated that stage 2 was reached 6 to 11 days after fertilization, depending on temperature. The seven sampling transects west of the Queen Charlotte Islands were parallel to one another and perpendicular to the coast (Figure 4). I postulated that samples from stations closest to the spawning grounds at Cape St. James should have more eggs in stage 1 than stations to the north, which should be dominated by eggs in the later stage (2) of development. The results are tabulated in Table 1 and show that the ratio of stage 1 eggs to stage 2 eggs was highest at the southerly transects and declined progressively toward the more northern transects (correlation coefficient 0.89). This trend demonstrates that the relative abundance of stage 2 eggs increases with latitude and indicates a northerly drift of eggs.

Table 1. Average catch per station and ratio of stage 1 to stage 2 eggs at each sampling transect, 1935-1943.

Transect	Latitude*	Stage 1 Eggs	Stage 2 Eggs	Stage 1/Stage 2
1	52° 50′	0.62	4.72	0.13
2	52° 40′	0.98	1.72	0.57
3	52° 30′	1.32	2.00	0.66
4	52° 20′	1.06	1.76	0.60
5	52° 10′	3.60	2.47	1.46
6	52° 00′	5.83	2.60	2.24
7	51° 50′	4.13	2.55	1.62

*Approximate latitude of coastal station.

Transects Nos. 8-13 were south and east of Cape St. James and ran parallel to the lines of latitude. Relatively few eggs were taken at these transects, except at No. 10 which was close to the spawning ground at Cape St. James. The ratio of stage 1 to stage 2 eggs declined progressively at transects No. 9 and No. 8, indicating a northerly movement. The average catch at the southern transects (Nos. 11, 12, and 13) were less than 0.5 eggs per station and the ratio showed no trend.

The results of these analyses on the distribution of stage 1 and stage 2 eggs, the shape of the contours showing the distribution of stage 1 eggs, and the current movements provide evidence that eggs from Cape St. James are carried to the northwest. The currents in the Gulf of Alaska indicate that the northwesterly movement would continue to Area 3 and could explain the scarcity of late-stage larvae in Area 2 that was reported by Thompson and Van Cleve (1936). *If one accepts the convincing evidence presented by Thompson and Van Cleve (1936) in developing the thesis of larval drift in Area 3, one cannot, on the same evidence, rule out the existence of transboundary movements of larvae from British Columbia to Alaska nor from Area 2 to Area 3.*

Movements of Juveniles

IPHC began a study in 1955 to estimate the abundance of young halibut and later began to tag juvenile halibut (<65 cm) to obtain information on their distribution and migration. All of these fish were taken with an experimental trawl and most of the halibut tagged were 3-, 4-, and 5-year-olds. (Some juveniles were included in the adult tagging studies, but these were taken mainly on longline gear and usually were 6 years old and older.) Tagging mortality of the young fish is assumed to be high and this, coupled with natural mortality and the incidental capture by foreign and domestic trawls, results in a low recovery rate by the setline fishery.

Best (1968) summarized the early results of the juvenile tagging experiments and presented graphs that showed the more distant movements (Figure 6). He did not attempt to quantify the emigration nor did he discuss the interrelationship of stocks in Area 2 and Area 3. Most of the juveniles were tagged in the summer, and most of the recoveries were near the area of release, but easterly and southerly movements were apparent. Juveniles released in British Columbia showed less extensive movements than juveniles in other regions but, as explained in the next section, juveniles in British Columbia were older than those to the westward and may already have completed their early migration.

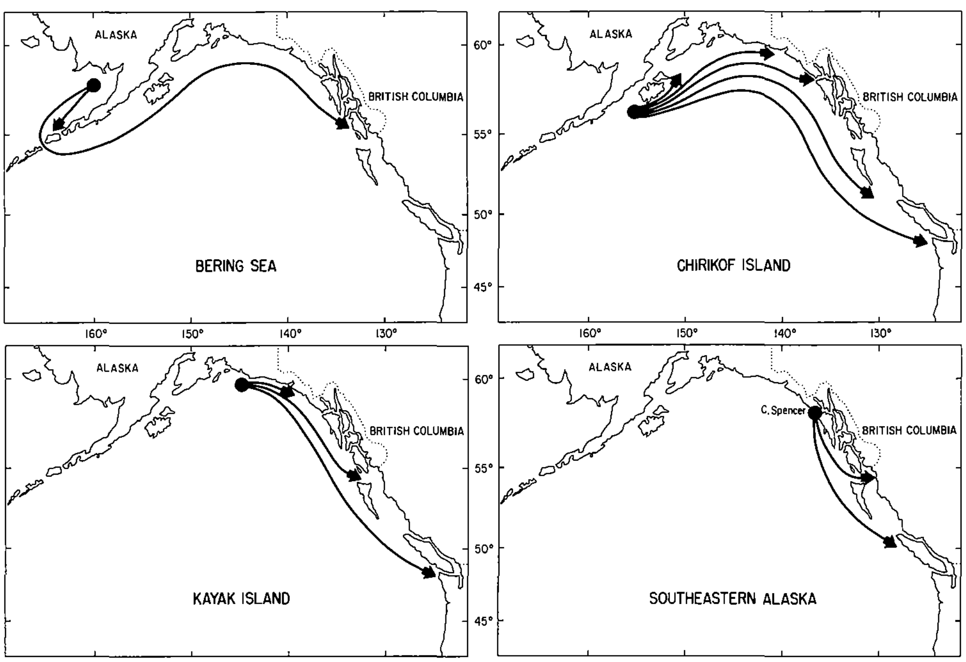

Figure 6. Migratory patterns of juvenile halibut from different tagging sites (after Best 1968).

Before presenting the results of the juvenile tagging experiments, it is important to emphasize the limitations of the data with regard to quantification of intermingling and transboundary movements. First, no attempt has been made to adjust the rate of recovery to differences in fishing effort. At present, it is not feasible to make such an adjustment because both longline and trawl fisheries are involved and the two types of gear are selective for different sizes of halibut. Further, both domestic and foreign trawl fleets fish in the areas and neither the amount of effort nor the comparative effectiveness is known precisely. Second, the number of recoveries is small and they span several years during which natural mortality is assumed to be high. For these reasons, the percentage of tag recoveries by area cannot be used to estimate the degree of interchange. However, the relative differences in the rate of recovery between areas are informative and demonstrate that transboundary movements by juvenile halibut do exist and suggest that, from certain areas, these movements are extensive.

Results of the juvenile tagging experiments from 1963-1976 are presented in Table 2 and show the total recoveries from tagging at specific locations and the recoveries from British Columbia. The migratory behavior of juveniles tagged at shallow, inshore stations differed from that of juveniles at deeper, offshore stations. This difference apparently was related to age composition which, as shown in the next section, differed between inshore and offshore stations. The lowest percentage (3%) of recoveries in British Columbia was from stations in Icy Strait which are inside the waters of the southeastern Alaska archipelago. The highest percentage was from stations in Shelikof Bay in southeastern Alaska and, although the bay is shallow and classified as an inshore area, it opens directly to offshore waters. All of the stations in the other areas were offshore. Recoveries in British Columbia from Cape Fairweather and Cape St. Elias (Yakutat Region) were 11 and 8%, respectively. The strong eddy known to exist in this region may affect the movement of juveniles or the drift of eggs and larvae and may explain the relatively low rate of movement from these areas. The offshore areas in the western Gulf of Alaska (Cape Chiniak, Chirikof Island, and Unimak Island) showed recoveries in British Columbia of 41%, 17%, and 33%, respectively. The weighted average from these three western areas was 30%, indicating a strong transboundary movement from Kodiak Island and west. These percentages are assumed to be minimal

Table 2. Recoveries of juvenile halibut tagged during 1963-1976.

Area of Release	Region	Total Recoveries	British Columbia Recoveries
Shelikof Bay	Southeastern	56	37 (66%)
Icy Strait	Southeastern	33	1 (3%)
Cape Fairweather	Yakutat	18	2 (11%)
Cape St. Elias	Yakutat	49	4 (8%)
Cape Chiniak	Kodiak	27	11 (41%)
Chirikof Island	Chirikof	24	4 (17%)
Unimak Island	Shumagin	3	1 (33%)

estimates because other migrants presumably were vulnerable to capture in trawl fisheries enroute to British Columbia.

The results of these tagging experiments provide further evidence of the interchange between stocks in Area 3 and Area 2 and show that the movement of juvenile halibut is compensatory to the westerly drift of eggs and larvae.

Age Composition of Juveniles

Age data collected during IPHC surveys of juvenile halibut also provide evidence of transboundary movements. Initially, the surveys were conducted in British Columbia because the commercial catch in this area had the highest proportion of young halibut. However, the catch of juveniles (pre-recruits) was small and IPHC (1958) reported that the abundance of juvenile halibut was greater in the Gulf of Alaska than in British Columbia. IPHC (1966) published information on the number and age of halibut less than 65 cm that were taken in different coastal areas in 1965. The results were presented separately for inshore and offshore stations, and the number of hauls were reported for each location. The samples from the inshore stations were taken with a trawl of 1 1/4-inch mesh and each tow was 15 minutes; a 3 1/3-inch mesh was used offshore and the tows were 1 hour long. The results converted to catch per haul (CPUE) are presented in Table 3.

Table 3. Catch per haul (CPUE) of halibut less than 65 cm by age and locality in 1965 (modal ages underlined).

Area	Age 0	1	2	3	4	5	6+	Total	Mean Age
				CPUE at Inshore Stations					
Kodiak Island	—	<u>49.21</u>	22.79	5.21	1.79	0.43	0.00	79.43	1.5
Cape St. Elias	—	<u>32.17</u>	25.75	11.67	9.75	1.17	1.67	82.17	2.1
Icy Strait	—	—	0.91	1.45	<u>7.55</u>	3.00	0.45	13.36	4.0
Shelikof Bay	0.04	<u>14.50</u>	3.17	2.50	<u>7.25</u>	2.13	0.58	30.17	2.4
Dixon Entrance	—	3.14	1.43	1.86	7.14	<u>8.00</u>	7.14	28.71	4.3
				CPUE at Offshore Stations					
Chirikof Island	—	0.95	6.59	<u>27.18</u>	14.00	6.27	3.85	58.86	3.5
Trinity Islands	—	—	5.50	13.50	<u>18.00</u>	2.50	1.00	40.50	3.5
Kodiak Island	—	—	1.07	9.21	<u>24.04</u>	10.93	2.50	47.75	4.1
Cape St. Elias	—	—	—	0.25	<u>2.50</u>	<u>2.50</u>	1.25	6.50	4.7
Hecate Strait	—	—	—	—	0.42	1.53	<u>2.05</u>	4.00	5.4

The inshore data indicate differences in the abundance of juveniles with age from west to east. The CPUE from Cape St. Elias and Kodiak Island was highest at ages 1 and 2 and declined with increasing age. In contrast, using the same gear, the CPUE in Dixon Entrance was lower for ages 1 through 3 than for ages 4, 5, and 6+. It is particularly noteworthy that the abundance from age 4 and above exceeded that for both Cape St. Elias and Kodiak. Data from Shelikof Bay and Icy Strait did not show a consistent trend, but the abundance of 4-year-olds was greater than the abundance of 2- and 3-year-olds. Further, the abundance of 5-year-olds in these two areas exceeded that of 5-year-olds in Cape St. Elias and Kodiak.

The results from the offshore stations show similar trends, although the peak abundance occurs at a later age than at the inshore stations. After the peak is reached, however, the abundance in the western Gulf of Alaska (Chirikof Island to Kodiak) declines with age as at the inshore stations. Of particular importance is the fact that the modal and mean age is progressively older from west to east (Table 2). The offshore data from Hecate Strait were included in IPHC's (1966) original table but are not entirely comparable because the results are from commercial trawlers. However, the mesh sizes were similar to those of the research trawl that had been used in the area in previous years and also showed the low abundance at the youngest ages. This low abundance of juvenile halibut in British Columbia and southeastern Alaska (except Shelikof Bay) was emphasized in the Commission's Annual Reports.

The scarcity of halibut less than 4 years old at both the inshore and offshore stations in the eastern Gulf, coupled with the relative increase in abundance of older juveniles from west to east, provides evidence of an easterly and southerly movement of juveniles, particularly so because this increase occurs at a life stage when one expects a relatively high mortality.

The CPUE data in Table 3 also suggest that juvenile halibut tend to move offshore with age. However, the mesh size used at the offshore stations was larger than that used inshore and, although both nets were capable of catching 1-year-old fish, the selective properties of the nets differed and must be evaluated before the extent of the offshore movement can be determined.

The west to east shift in abundance with age is apparent in survey data from other years. As an example, the length and age data from the offshore stations in 1971 are presented in Table 4. These data were published by Best (1974) and were not adjusted to the catch per haul. Data collected by observers aboard foreign and domestic trawlers also indicate the difference in the size of juveniles from west to east. The modal size in the Gulf of Alaska was 42 cm (Hoag and French 1976), whereas the modal size in British Columbia was over 62 cm (Hoag 1971). Similar trends were noted in a special trawl survey conducted by IPHC between 1961 and 1963. The mesh size of this net was the same as used in subsequent surveys for juvenile halibut. The average age and length of young halibut (some over 65 cm) increased from Unimak Pass to Cape Spencer and juveniles in deeper, offshore waters generally were older than those inshore.

I also examined the data on juvenile distribution by year class. Evidence of the west to east shift in age was apparent but exceptions, particularly between adjacent areas, were noted. To obtain a composite, I calculated the average age composition by area by year. Unfortunately, not all areas were sampled every year and British Columbia, the most southern area, had the fewest samples. In calculating the average age for each area, I used all the years for which there were data from British Columbia: 1965, 1966, 1971, 1972, 1973, and 1976, except that no data were available from Unimak Island in 1965 and Chiniak Island in 1966 (Figure 7). The 3-year-olds were dominant at Unimak and Chirikof, 4-year-olds at Chiniak, 5-year-olds at St. Elias, and the 5- and 6-year-olds had equal weight in British Columbia. The contrast of declining abundance from ages 3 and 4 in the western Gulf and the increasing

Table 4. Length and age composition of halibut from offshore stations in the Gulf of Alaska, 1971 (from Best 1974).

Length (cm)	Unimak Island	Unimak Island (tagging)	Chirikof Island	Cape Chiniak	Cape St. Elias	Cape Fairweather	Dixon Entrance	Washington Coast
8-10	1	—	—	—	—	—	—	—
11-13	3	—	—	—	—	—	—	—
14-16	6	—	—	—	—	—	—	—
17-19	15	2	2	1	—	—	—	—
20-22	40	51	3	1	—	—	—	—
23-25	37	110	37	5	—	—	—	—
26-28	25	51	197	30	1	—	—	—
29-31	82	231	185	144	2	—	—	—
32-34	78	272	108	232	9	3	—	—
35-37	94	120	79	204	14	8	4	—
38-40	50	76	107	122	22	16	10	—
41-43	27	33	75	79	28	29	17	—
44-46	15	9	95	59	38	20	49	—
47-49	9	4	68	74	30	27	124	—
50-52	15	4	51	62	36	14	274	—
53-55	10	4	43	45	41	16	368	—
56-58	4	1	36	58	32	8	410	2
59-61	5	2	20	46	24	8	405	5
62-64	2	4	29	39	15	4	281	3
65-67	2	—	17	26	16	6	191	4
68-70	1	1	15	25	10	2	100	6
71-73	—	—	13	7	12	3	58	3
74-76	2	—	10	15	8	—	23	3
77-79	—	—	12	4	9	3	12	4
80-82	—	1	9	5	1	—	9	3
83-85	—	—	10	4	2	1	7	—
86-88	—	—	6	4	4	—	3	—
89-91	—	3	8	2	3	1	3	—
92-94	—	—	8	1	3	—	3	—
95-97	—	1	9	2	5	—	1	—
98-100	—	—	10	1	2	—	—	—
>100	1	4	30	9	11	1	—	1
Total	524	984	1,292	1,306	378	170	2,352	34
Age								
1	2	—	—	—	—	—	—	—
2	104	199	48	5	2	—	12	—
3	202	602	592	724	41	25	55	—
4	160	148	303	186	65	50	380	—
5	34	17	103	165	78	42	476	5
6	12	8	63	66	42	16	544	2
7	2	—	23	35	34	10	447	2
8	1	—	3	20	26	8	14	1
9	1	—	—	—	2	1	14	—
10	—	—	—	—	2	1	—	—
Total	518	974	1,135	1,201	292	153	1,942	10
No. Hauls	18	10	32	33	41	7	19	12

abundance to ages 5 and 6 in the eastern Gulf and British Columbia is readily apparent and, as mentioned previously, is evidence of an easterly movement of juveniles.

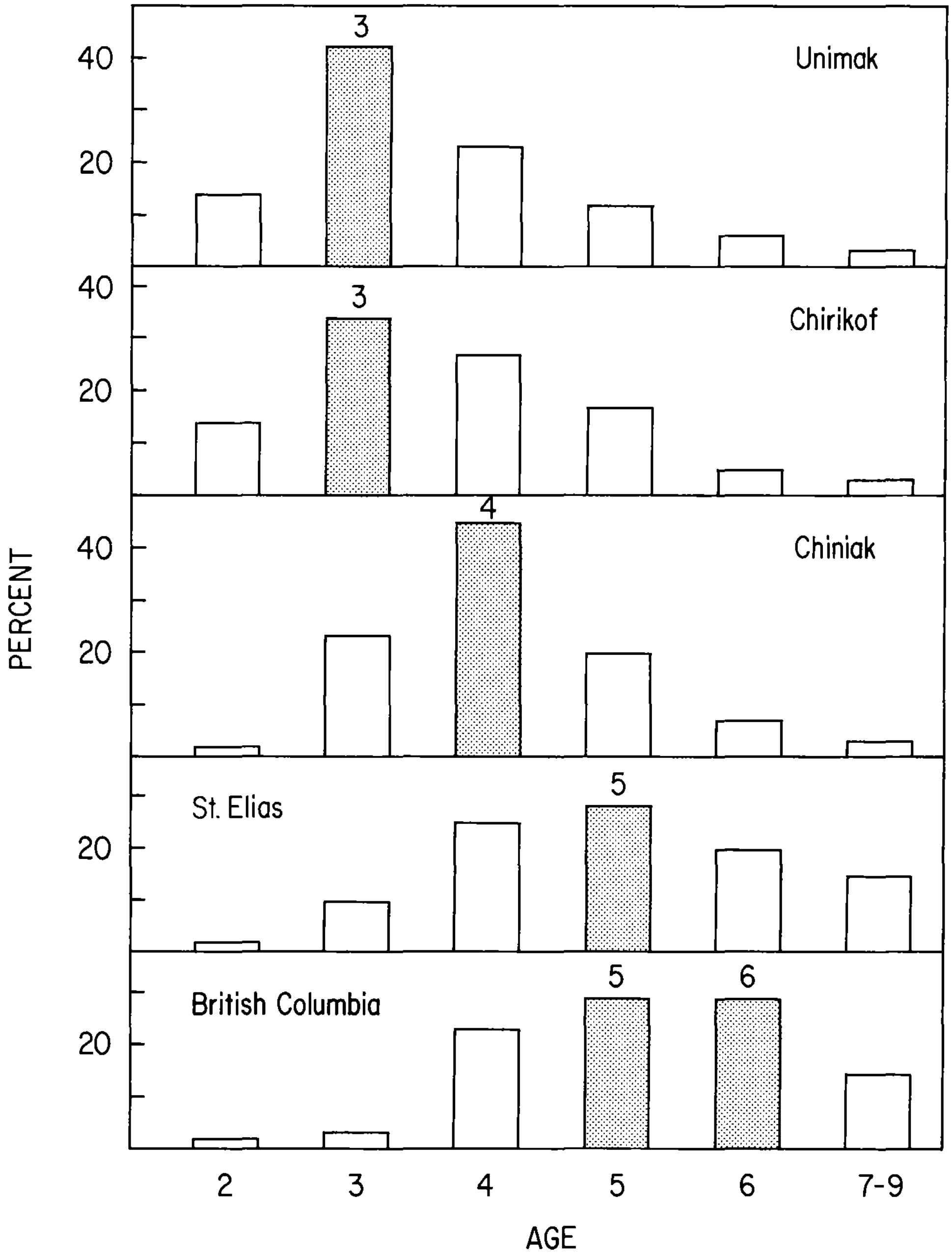

Figure 7. Mean age of juvenile halibut from Unimak to British Columbia.

The age and length composition indicates a movement of juveniles from Area 3 to Area 2. The juvenile movement apparently is a compensatory emigration to the westerly drift of eggs and larvae. Because similar movements are known for many other marine species, the observed movements of juvenile halibut give credence to the thesis that many larvae originating in Area 2 drift to Area 3. Those juveniles returning to Area 2 apparently originated there, whereas juveniles that were spawned in Area 3 apparently remain in Area 3.

Movements of Adults

Neither the design nor the analyses of IPHC's tagging experiments have been directed towards the specific question of transboundary movements between Canadian and United States waters; however, certain experiments do provide information that is pertinent to the question of interchange across national boundaries. The present analysis is based on selected tagging experiments that illustrate the relation of seasonal differences and fish size to migratory behavior. Not all of the available tagging data were analyzed and the objectives of this preliminary examination were to identify factors that affect adult movement and to specify factors to be analyzed in a more comprehensive study. A more thorough analysis will be undertaken when the tagging data and associated information on size and sex of fish and fishing effort are readied for automatic data processing.

Release and recovery locations of halibut tagged between 1925 and 1976 are shown in Table 5; the regional divisions are depicted in Figure 1. Most of these fish were caught with longline gear and relatively few were under 65 cm. Emigration was observed from all regions, but no adult fish tagged in the Gulf of Alaska have been recovered in the Bering Sea. Halibut occasionally travel great distances and six halibut have migrated over 2,000 miles from their point of release. These fish were tagged in the Bering Sea or near the Aleutian Islands and recovered at points from Cape Flattery, Washington south to Cape Mendocino, California. One of the fish was recovered 2 years after being released, the others were recovered 5 or 6 years after their release. The longest movement was from Atka Island to Coos Bay, Oregon, a distance of 2,450 miles. Another halibut released southeast of Cape Navarin, U.S.S.R. during a joint Soviet-IPHC experiment in 1975 was recovered in 1977 near the Shumagin Islands in Alaska, a distance of 1,000 miles.

Although a number of halibut migrated long distances, a high percentage of the fish were recovered in the region in which they were tagged. The percentage of recoveries from halibut tagged in Alaska and recovered in British Columbia (Charlotte Region) generally is less than 5%, suggesting that transboundary movements are limited. However, most of the fish were tagged in the summer and were recovered in the summer (May through September). Recoveries from winter (October through April) releases, which are described in the following paragraphs, show that migrations and transboundary movements vary seasonally.

When halibut were tagged in 1925-1927, commercial fishing was permitted from February through November and recoveries were made throughout this period. Thompson and Herrington (1930) discussed the differences of seasonal movements. In Area 2, the halibut were tagged in the summer and the results showed that the percentage of fish recaptured at distances 50 miles or more

Table 5. **Release and recovery location of tagged adult halibut, 1925-1976.***

Release Region	Number Released	Recoveries by Region								
			Area 3							
		Bering Sea	Shumagin	Chirikof	Kodiak	Yakutat	Southeastern	Charlotte & South	Total	Unknown
Bering Sea	20,435	756	21	69	125	116	83	53	1,223	40
Shumagin	5,992	0	202	104	35	20	24	11	396	10
Chirikof	9,193	0	37	473	91	20	17	10	648	31
Kodiak	16,501	0	17	119	1,294	40	36	25	1,531	31
Yakutat	11,431	0	31	122	428	1,078	62	52	1,773	5
Southeastern	9,729	0	0	0	1	4	1,945	85	2,035	46
Charlotte & South	59,361	0	1	0	7	39	194	17,288	17,529	254
Total	132,642	756	309	887	1,981	1,317	2,361	17,524	25,135	417

*In certain experiments, some juvenile halibut were tagged and are included in this table, but the number is insignificant relative to the number of adults. Most of the juveniles were 5 years old and older.

from the tagging location increased markedly during the winter months. However, most of the halibut were captured during the summer and relatively few of these were taken more than 50 miles from the spawning location. In contrast, the halibut in Area 3 were tagged during the winter and the dispersion was more extensive and was greatest during the summer months, but the recaptures were quite evenly distributed during the fishing season, February to November. Thus, for the most part, the Area 2 experiments were recording summer to summer movements, whereas in Area 3 the movements were from winter grounds. The authors stressed the point that the average size of fish in Area 2 was less than in Area 3 and this may have influenced the differences in the observed movements. Although the experiments between areas were not entirely comparable, the results within each area were informative and showed that movements in Area 3 were more extensive than in Area 2. This general observation was confirmed in more recent experiments even though the fishing season has been much shorter. The seasons in Areas 2 and 3 opened in April from 1938 to 1944 and in May from 1945 to date, except in 1970 (Skud 1977). Since 1970, relatively little fishing has occurred after September. The current season lasts from May to September. As a result, only a few of the more recent tagging experiments provide comparisons of summer and winter movements; however, the results are in general agreement with those of the early experiments. The following comparisons are made from the same tagging area with different times of tagging and the data are from Myhre (1967). For example, I have compared a tagging experiment near Yakutat in August 1954 with one in the same vicinity in November-December 1955. Of the returns from the August tagging, 83% were taken in the area of release and none were taken as far west as Kodiak Island; of the returns from the November-December tagging, only 63% were taken in the area of release and 10% were taken west of Kodiak, the farthest to the Shumagin Islands. Similar results were observed in experiments near Hecate Strait. Returns from a winter release in 1940 showed only 33% being recovered in the area of release and 8% being recovered in areas over 120 miles from the release site. In contrast, in a summer experiment in

1947, 96% of the recoveries were made in the release area and only 2% were made beyond 120 miles. These results indicate that movements differ seasonally and that it is necessary to examine data on a seasonal basis to determine the degree and extent of transboundary movements.

The predominant direction of movement by tagged fish also may differ with the season of release, and this is demonstrated by results of experiments off Yakutat, an important spawning ground (Figure 8). One experiment was conducted in November and December 1926 and the other in August 1951. These experiments were selected to show the variation in recovery patterns as well as the extent of the movements. The 1926 experiment in Area 3 conforms to the generalization that when halibut are tagged in the winter and recovered in the summer, more tags are recovered out of the release area. Most of the recoveries were in the summer and most of the movement was westward. (Later tagging experiments indicate that this westward movement was a return to summer feeding grounds.) A southeasterly movement also is evident, but only 21% of the tagged fish recovered outside of the release area had moved in this direction. In contrast, the 1951 experiment in August showed that the southeasterly movement predominated and, of the tags recovered outside of the tagging area, 67% were in this direction.

These two Yakutat experiments also provide information on the transboundary movements from Area 3 to British Columbia. Based on total recoveries, both experiments showed a transboundary movement of less than 10%. However, in the August experiment, 28% of the recoveries outside the release area were taken in British Columbia or south; whereas in the winter experiment, only 5% of the "outside" recoveries were taken from these southern waters. As might be expected, experiments in southeastern Alaska show a greater percentage of transboundary migrations. During the years prior to 1940, when both winter and summer experiments were conducted, 93% of the tags released in the summer were recovered in Southeastern and only 7% in British Columbia; whereas from winter releases, 63% were recovered in Southeastern and 35% in British Columbia.

Tagging experiments in British Columbia showed similar results. In six selected experiments between 1965 and 1970, a total of 3,812 were tagged in the summer. Most of the recoveries in the summer were from the longline fishery and recoveries in the winter were from foreign and domestic trawlers. Only 1% (8 of 908) of the summer recoveries were taken outside British Columbia, but 52% (13 of 25) of the winter recoveries were outside of British Columbia, indicating greater movement in the winter. The total number of recoveries in winter (25) are less than those in summer (908) because the chances of recovery (fishing effort) are much lower in the winter.

In 46 years (1930-1975), only 67 halibut (including juveniles) that were tagged in British Columbia have been recovered in Area 3, i.e., west of Cape Spencer (Table 6). Most of these recoveries (52) were taken by the setline fishery. These fish were caught from April to October and most were taken between Cape Spencer and Yakutat, but two were taken west of Kodiak Island. The other recoveries (15) were taken by Japanese trawlers between Cape Spencer and Cape St. Elias. All of these trawl recoveries were taken in the winter from December to March during only 6 years (1968-1973). Considering that little or no trawling was conducted in the Yakutat Region before 1967 (Hoag and French 1976), that trawls primarily catch small halibut, and that non-reporting

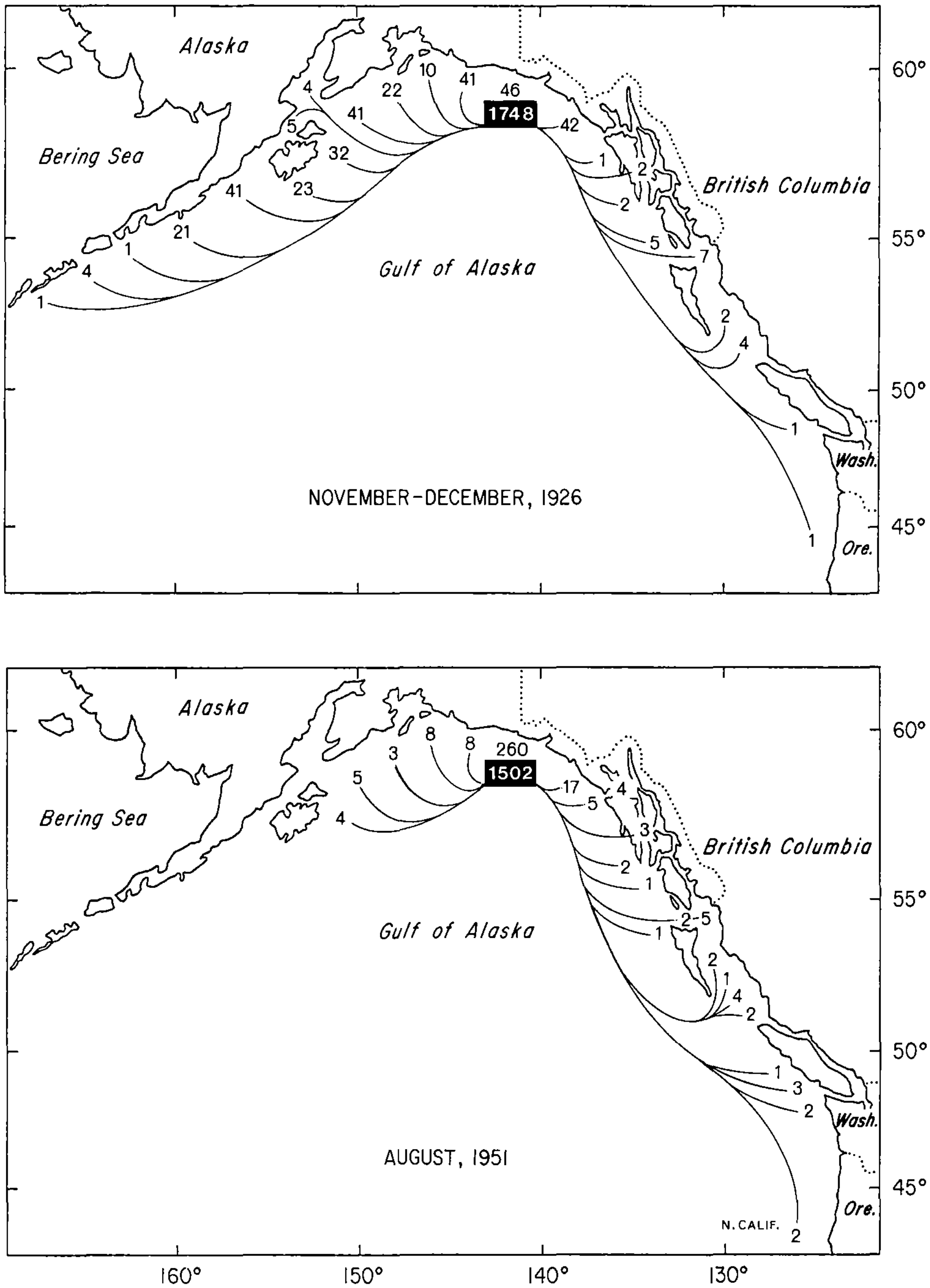

Figure 8. Distribution of recoveries from halibut tagged off Yakutat in November-December 1926 and in August 1951. The number of fish tagged is shown in the black box.

of tags by foreign fishermen probably is much higher than by domestic setline fishermen, many more tags would have been recovered if trawling had been conducted during the winter in the earlier years. Obviously, conclusions reached on the basis of recoveries in the summer do not present a complete picture of migratory behavior, and the winter recoveries indicate that transboundary movement from British Columbia to the Yakutat area is substantially greater than is shown by summer recoveries.

Table 6. Halibut tagged in British Columbia and recovered west of Cape Spencer.*

Region of Recovery	Setline Recoveries	Trawl Recoveries	Total
Yakutat	44	15	59
Kodiak	6	—	6
Shumagin	2	—	2
Total	52	15	67

* The 52 setline recoveries were taken from 1930 to 1975 during the months from April to October; 73% (38 tags) were taken in May, June, and July. All of the trawl recoveries were taken by Japanese vessels from 1968-1973, during December, January, February, and March.

The seasonal difference is not the only factor to consider. For example, the halibut that were recovered by the Japanese trawl fleet (Table 6) had an average length of 78 cm at tagging and 91 cm at recovery. Of the 15 halibut taken by trawls, 11 were recovered between 1968 and 1969 and four were recovered in 1972 and 1973. In contrast, the 8 halibut that were recovered by setline gear, from the same experiments, averaged 86 cm at tagging and 108 cm at recovery. Only 1 was recovered before 1970, whereas 7 were recovered between 1970 and 1974. Although the sample is small, these results suggest that the smaller fish which were recovered by trawls moved to the Yakutat area within the first few years of tagging, whereas the larger fish were not taken in Yakutat by setline gear until several years later, indicating the possible importance of size composition in the interpretation of tagging results. As indicated above, trawl gear is selective for smaller halibut (Myhre 1969).

As discussed earlier in this report, a transboundary movement also is evident between Washington and British Columbia (Figure 9). The results of tagging experiments from this area were presented by Bell and Best (1968) and were updated by Skud (1975). Of 36 tags recovered south of Willapa Bay, Washington, 3 were released near the Aleutian Islands, 8 from the northern Gulf of Alaska, and 25 from the waters of southeastern Alaska and British Columbia. Most of these tags were recovered in the summer. Ten tags released south of Willapa Bay were recovered in British Columbia and southeastern Alaska; 3 were taken during the summer months and 7 in the winter by trawl gear.

The tagging studies indicate that adult halibut generally migrate from summer feeding grounds to winter spawning areas and return to their summer grounds. These migrations are assumed to occur annually. However, some of the adults do not return to the same grounds and make extensive transboundary emigrations that apparently do not occur annually. Data recorded from

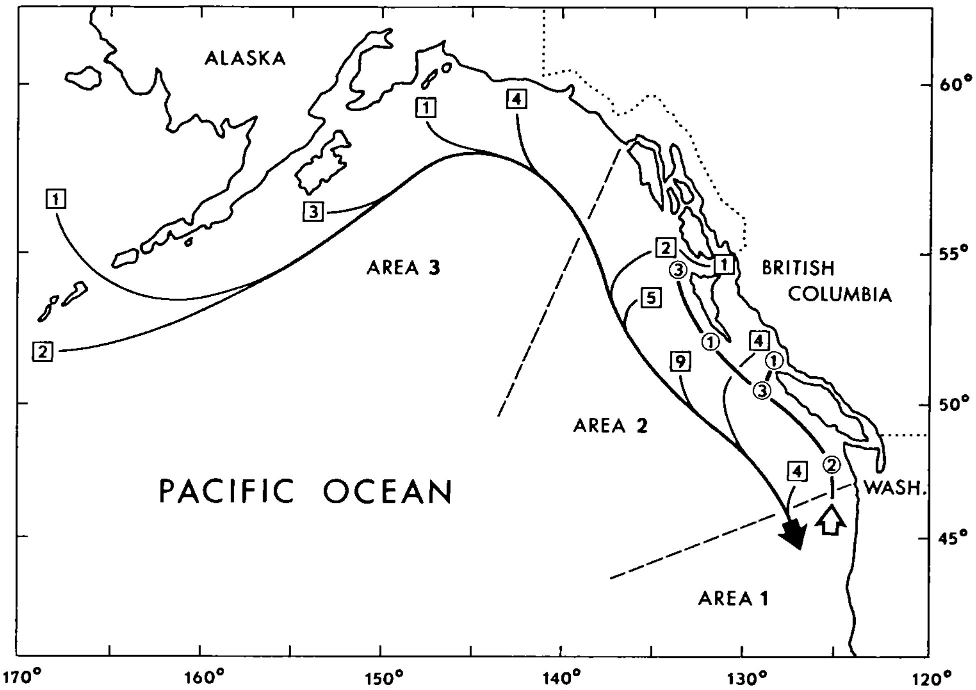

Figure 9. **Transboundary movements across the British Columbia-Washington border. (Boxes show area of release for fish recovered south of Willapa Bay; circles show recoveries of fish that were released south of Willapa Bay.)**

summer to winter and from winter to summer indicate that these movements are more extensive and that patterns of movement may differ from those based on summer to summer tagging experiments. These differences have not been emphasized in past analyses because most of the tags were released and recovered in summer and most of the recoveries were taken in or near the release site. As mentioned previously, further analysis will be made of the adult tagging results when the data are readied for automatic data processing. The experiments discussed in this section were selected to show specific differences, but it should be pointed out that the results from individual experiments in the same area, at the same time of year, may differ from one another.

The separation of juveniles and adults at 65 cm is an arbitrary division consistent with the size limit that was in effect until the early 1970's. Actual size at maturity varies with individuals, from area to area, and has changed as the growth rate has increased. Although the 65 cm size designation generally has been useful in describing differences in migration patterns, the specific determination of maturity stage would be more useful and possibly would explain some of the aberrant migrations, i.e., some of the fish classed as adults may be immature females and some of the juveniles may be mature males. As such, their migratory behavior may differ from those considered in the generalized description of movements.

Compensatory Emigration

Dunlop et al. (1964) were the first to mention that the movements of adult halibut "occur to counteract the drift of the natant eggs and larvae and to maintain the species in its habitat". The statement was made in reference to work by Thompson and Herrington (1930) and Kask (op. cit.) and pertained only to Area 3. Bell (1967) mentioned the close relationship of the halibut stocks and specifically included reference to Area 2, but his emphasis was on the population complex west of Cape Spencer (Area 3) and he concluded that "The eastward movement of the adult fish to fall and winter spawning grounds in the Gulf of Alaska counterbalances the reverse drift of the developing eggs and larvae in the Alaska Current moving in a southwesterly direction along the Alaskan Peninsula and the Aleutian Islands". Best (1977) specifically mentioned that juvenile as well as adult movements counterbalanced the drift of eggs and larvae, in this case, between the Bering Sea and the Gulf of Alaska.

Hence, to date, the specific reference to a compensatory emigration within the Gulf of Alaska has been for adults and has been restricted to the area from Cape Spencer and west. Further, it is based on tagging results, most of which were conducted in the summer, that generally show a relatively low percentage of movement and do not indicate a large scale emigration of mature halibut. The differences in age composition, growth rate, and mercury content between areas also indicate that intermingling among adult stocks is not extensive. Because of these differences and the observed movements and distribution of juveniles, I conclude that *most of the compensatory emigration takes place at the juvenile rather than the adult stage.* Thus, halibut under age 6 that moved from one area to the other would be exposed to the new environment long enough so that the differences in growth rate and mercury content would have time to materialize. Another consideration would be that those juveniles that do migrate have a faster growth rate than those that do not migrate. Evidence to support this thesis was reported in IPHC Annual Reports which showed that the mean size at age increased from west to east. Dunlop et al. (1964) also showed that migrants from the Bering Sea tended to be faster-growing fish than non-migrants.

Favorite, Laevastu, and Straty (op. cit.) also discussed the movements of halibut. They summarized information on currents in the Gulf of Alaska relative to the drift of eggs and concluded that eggs released at the eastern side of the Gulf of Alaska would be advected at speeds of 5 to 10 cm/second to the "head of the Gulf". Eggs released in the western Gulf would be advected at speeds of 50 cm/second and would be carried west of the Alaska Peninsula before rising to surface layers and the larvae could then be carried along three routes: (1) northward into the Bering Sea, (2) westward along the Aleutian Islands in the Alaska Stream, or (3) southward and eastward in the Alaskan Gyre.

The authors said that the northerly movement of eggs away from the spawning grounds and the lack of a consistent southerly movement by adults posed a dilemma insofar as explaining how the stocks were perpetuated in the southern areas. They hypothesized that larvae carried in the Alaskan Gyre would be deposited on the coast from California to southeastern Alaska *the following winter,* suggesting this movement as the mechanism for replenishing the eggs carried out of these areas. Their hypothesis is predicated on the prolonged larval existence of the Greenland turbot (*Reinhardtius hippoglossoides*) which is reported to maintain a pelagic mode up to a length of 70 mm (Hubbs and Wilimovsky 1964).

The information by Favorite et al. on current speeds is most useful and confirms that eggs and larvae from British Columbia can be transported to the western Gulf of Alaska and the Bering Sea during their 6- to 7-month pelagic stage. However, their hypothesis that larvae could be carried in the Alaskan Gyre and not settle to the bottom before the following winter is not consistent with the timing of development documented by Thompson and Van Cleve (1936), who found young halibut (20 to 25 mm) on the bottom in coastal areas during May and June. On this basis, I reject the thesis proposed by Favorite, Laevastu, and Straty. It is my opinion that the compensatory movement of juveniles explains the dilemma posed by these authors. I do not, however, reject the possibility that eggs and larvae may be carried into the Gyre and, as Favorite (personal communication) suggested, this may be a source of extreme losses.

In reference to the movement of larvae in the offshore area, it is of interest to note that three of my reviewers (Fleming, Myhre, and Van Cleve) commented on the distribution of larvae in the central Gulf of Alaska (between 139° and 147°, north of 55° as shown in Figure 3). The reviewers noted that the distribution of larvae in this area formed a circular pattern, suggesting that some of the larvae from the northern Gulf may move south and then east towards southeastern Alaska. Such a movement would correspond to the general location of an eddy described by Thompson and Van Cleve (1936). This eddy was located north and east of the Alaskan Gyre and was a much smaller system. The authors noted that eggs and larvae were carried in the system to offshore waters in the Gulf but did not discuss the ultimate fate of these young stages. The proximity of this eddy to the coast suggests that larvae could be carried to shallow areas in time for metamorphosis in May or June. The high abundance of juveniles found in Shelikof Bay (southeastern Alaska) and the high percentage of recoveries in British Columbia from tags released in Shelikof Bay lends credence to this thesis. Assuming that a portion of the larvae from Area 2 were carried in this eddy and that others were carried to and remained in Area 3, the thesis would be consistent with the observed migrations of juveniles.

A CONCEPTUAL MODEL OF HALIBUT MOVEMENTS

The question raised in the Introduction, "How do stocks maintain their geographic position when ocean currents carry eggs and larvae away from the spawning grounds?", has been a concern of fishery scientists for many marine species. Bowman (1933) worked on plaice (*Pleuronectes platessa*) and concluded that "it is obvious that the older fish must undertake at some time active and compensatory movements in the direction opposite to that in which the pelagic stages are carried passively from the spawning grounds by the prevailing currents". This positive posture contrasts significantly with other authors who, lacking documentation of a compensatory movement, expressed concern that eggs and larvae may not be available to replenish the local stocks. For example, Colton and Temple (1961) referred to the spawning on Georges

Bank as an enigma; they concluded that, under average conditions, eggs and larvae of haddock (*Melanogrammus aeglefinus*) and of herring (*Clupea harengus*) were carried away from Georges Bank and lost to the fishery.

Harden Jones (1968) compiled an excellent review of fish migration and provided generalized models of the movements throughout the life cycle, i.e., movements from the spawning ground to nursery area, from nursery to feeding ground, and from feeding back to spawning grounds. As mentioned earlier, he specified that the adult movements compensated for the egg and larval drift. He also presented diagrams of these migrations in relation to oceanic circulation. Cushing (1976) emphasized the seasonal regularity of the migratory pattern and used the term "migratory circuit" to describe the models. He considered this circuit as the base of the system by which a stock maintained itself and its geographic position, i.e., "isolation of the reproductive mechanisms". With a fixed spawning ground from year to year and a regular current system, Cushing credited the larval drift as the geographical base of the stock. Harden Jones (1968) discussed residual as well as tidal currents and emphasized the need for synchronization of spawning time and location with the currents to insure the transport and survival of larvae. He suggested that "the advantage might not lie so much in the choice of a spawning area in its own right, but for its position in relation to a favourable nursery area to which the young are carried passively by the prevailing current". This is a subtle but important distinction and differs from the explanation that compensatory movements to spawning grounds are to maintain the adult population in that specific area.

Other than the supposition that the compensatory movement is executed primarily by juveniles, the observations on halibut conform to these basic concepts and, as a working hypothesis, I propose the following migratory circuit for the halibut stocks in the several geographic regions. In British Columbia and southeastern Alaska (Area 2), spawning occurs during the winter in deep water and the eggs and larvae are carried north and west. Enroute, the postlarvae settle to the bottom at different coastal locations, depending on the speed and direction of the currents as well as the rate of development and the time of metamorphosis. Most of these larvae would settle in the northern Gulf of Alaska, but a few are carried as far west as the Bering Sea. Some of the larvae may be carried to the eddy in the central Gulf and move eastward to southeastern Alaska. From these various points, the juveniles move east and south, eventually returning to nursery areas or feeding grounds such as Dixon Entrance and Hecate Strait. On reaching maturity, the adults initiate their annual migration to spawning grounds, such as Cape St. James, from which they originated. After spawning, the fish move to deep wintering areas until the spring when they move to summer feeding grounds. The occasional summer recoveries in the northern Gulf are assumed to be strays, the winter recoveries in Yakutat of fish tagged in British Columbia may be associated with spawning migrations.

The movement of juveniles from Area 3 to Area 2 as far south as British Columbia is particularly noteworthy in consideration of the effects of the foreign trawl fisheries. As Hoag (1976) indicated, the trawls are selective for halibut under 65 cm and the effort by the foreign fleet in the Gulf of Alaska has been most heavily concentrated in Area 3. Therefore, many of the juvenile halibut taken as an incidental catch in these trawls probably were fish destined to migrate to Area 2. Thus, the loss in yield affects both areas and helps to explain the exceptionally low abundance in Area 2.

In the northern Gulf (Area 3), eggs and larvae from spawning grounds, such as the Yakutat and "W" grounds, are carried westward, generally beyond Kodiak Island, along the Alaska Peninsula, into the Bering Sea and along the Aleutian Island Chain. The larvae metamorphose at different times and settle to the bottom at different locations along this drift pattern. The juveniles migrate eastward toward the spawning grounds but, apparently, many establish "residency" on or near feeding grounds (such as Portlock Bank) that are long distances from spawning areas such as Yakutat. On reaching maturity, the fish then begin their annual easterly migration to the spawning grounds and return to the same general feeding area the following summer. This sequence supports Harden Jones' thesis regarding the selection of the spawning area and its importance to the distribution of eggs and larvae.

The possibility that eggs and larvae from Area 2 and Area 3 can be carried into the Alaska Gyre or other current systems that might prevent them from reaching coastal areas at metamorphosis may be an important factor in governing the strength of each year class. The current patterns do change annually and unfavorable distributions of eggs and larvae could be a factor in the long-term reduction of recruitment that has been observed.

Although the stocks in the Bering Sea have not been discussed in detail in this paper, I have included mention of them here to document the similarities and apparent differences in the migratory circuit from those in Area 2 and Area 3. The wide continental shelf is the most notable feature in the eastern Bering Sea, particularly in contrast to the narrow shelf in the Gulf of Alaska, and the patterns of halibut movements in the Bering Sea apparently are adapted to the local physiography. Climatic conditions are more severe than in the Gulf of Alaska and may be another factor accounting for behavioral differences. The spawning grounds in the Bering Sea are located at the edge of the continental shelf, but both juveniles and adults concentrate along the edge during the winter. Best (1977) summarized early life history studies in the Bering Sea by IPHC, Japan, United States, and U.S.S.R. The circulation patterns indicate that the eggs and larvae spawned at the edge of the continental shelf will remain in the Bering Sea but will drift in a northwesterly direction and conceivably could be carried to the Asiatic side.

During the spring warming in June, the juveniles in the eastern Bering Sea move northeast onto the continental shelf. The oldest juveniles are located in areas farthest east (towards Bristol Bay) and farthest north (to St. Matthews Island). The extent of this movement depends on temperature and is more extensive in the warmer years. The younger juveniles are located closer to the Alaska Peninsula and do not move as far east or north as the older juveniles. This summer movement to shallower depths occurs in the Gulf of Alaska as well but is less pronounced because of the narrower shelf. Tagging experiments in the Bering Sea show that adults also migrate onto the shelf in summer. Based on the size and distribution of juvenile and adult halibut, Best (1977) postulated that there were eastern and western stocks that intermingled in the central Bering Sea. On the other hand, Hardman (1969), based on size and age composition, concluded that there was little intermingling of stocks in the eastern Bering Sea.

Although the size composition and distribution of juveniles indicate that a resident population is involved, eggs and larvae originating in the Gulf of Alaska apparently contribute to the juvenile population in the Bering Sea. Tagging experiments show that most of the juveniles and adults remain in the Bering Sea. A few halibut tagged in the western Bering Sea near Kamchatka, U.S.S.R. have migrated across to Alaskan waters, but no reverse movement has been reported. Tagging experiments also show that some juveniles and adults leave the Bering Sea and migrate to the Gulf of Alaska. Presumably, most halibut that leave the Bering Sea have their origins in Area 3 and Area 2 spawning grounds.

The long distance movements (emigrations) from the Bering Sea and from Area 3 apparently are unrelated to spawning and do not occur annually. No information is available to explain specifically why some adult halibut make this emigration and others do not or what activates the movement. Judging from the experience in areas at the fringes of the range, such as grounds south of Vancouver Island that have failed to recover former abundance after years of reduced effort, I suspect that population density may be one of the agents that stimulates these emigrations. Another explanation may be that the apparent "homing" observed among juveniles is delayed for some individuals until adulthood. Some of the halibut making long-distance moves, particularly those from the Bering Sea, may be strays. If fish moved fortuitously from the Bering Sea into the Gulf of Alaska, the westerly currents could stimulate a contranatant movement and lure the fish eastward beyond the Aleutian Passes and along the Alaska Peninsula. A continued contranatant search for the passes would only lead the fish further astray to the eastern part of the Gulf.

It will be obvious to the reader that the above descriptions of migratory circuits are not specific. Much is yet to be learned and many questions are left unanswered. My intent has been to present a generalized concept or working hypothesis that can be revised and refined as new information becomes available.

SUMMARY AND CONCLUSIONS

IPHC's early publications (1930's to 1950's) stressed the thesis that the stocks in regulatory Area 2 and Area 3 were separate and independent. This conclusion initially was based on the results of tagging experiments and catch statistics but later was supported by interpretations of data on egg and larval drift, anatomical differences, and growth rate. By the late 1950's, IPHC regularly reported on tagging studies that showed a "close relationship" among stocks in the several regulatory areas; however, the rate of exchange between Area 2 and Area 3 was not greatly different from that shown in the early tagging experiments. No explanation was offered to account for the change in the interpretation of stock relationships.

Reexamination of the data on the distribution of eggs and early stages of larvae reaffirmed the original conclusion that there is little or no drift of these stages from Area 3 to Area 2; but contrary to the conclusion that stocks in Area 2 and Area 3 were separate and independent, evidence was presented to show that eggs and larvae from British Columbia drift northward and could be carried to Cape Spencer and beyond. The distribution and abundance of larvae in southeastern Alaska and the lack of late stage larvae south of Cape Ommaney also supported this conclusion. There is the possibility that an eddy in the northern Gulf of Alaska could carry postlarvae to southeastern Alaska.

Tagging of juvenile halibut taken in experimental trawls showed extensive movements from Area 3 to Area 2 and 30% of all recoveries from juveniles released in the western Gulf of Alaska were taken in British Columbia. The abundance of juveniles 2 to 4 years old was highest in the northern and western areas of the Gulf of Alaska, but their abundance declined with age; whereas in southern areas of southeastern Alaska and British Columbia, the peak abundance of juveniles generally occurred at an older age and often increased from ages 4 to 6, indicating extensive movements of juvenile halibut from Area 3 to Area 2.

Results of tagging experiments with adult halibut indicated that interpretations of the extent of interchange between regulatory areas and between countries must consider the season of release and of recovery as well as the size of the fish. The movements of halibut tagged in the summer and recovered in the winter or vice versa generally are more extensive than those from summer to summer and the predominant direction of movement changes seasonally.

The major conclusions reached from this study are (1) that the stocks from Area 2 and Area 3 intermingle at all stages of their life history and (2) that juvenile halibut account for most of the compensatory movement, i.e., counterbalancing the drift of eggs and larvae. Based on the findings of this study, a conceptual model was formulated, describing the migratory circuits of the several stocks. Some of the adult movements do not conform to this general description and at least a part of the compensatory emigration apparently is executed by adult halibut rather than juveniles. Whether these adult movements are related to spawning activities or are size or sex specific is not known. Thus, winter tagging experiments indicate that most of the halibut that spawn near Yakutat are fish that have summer feeding areas in the northern Gulf of Alaska. However, some halibut are from summer feeding grounds to the south. Summer taggings in Yakutat show a pronounced southerly movement but, until an adjustment can be made for fishing effort, the significance of this movement cannot be evaluated.

Although a precise quantification of the interchange between stocks is not feasible at present, collectively these findings indicate that transboundary movements of stock are substantial and extensive. Regarding the mandate of the U.S. Conservation Act that specifies "*To the extent practicable, an individual stock of fish shall be managed as a unit throughout its range . . .*", the biological evidence clearly shows that the movements and range of halibut stocks overlap during all life stages and, in conformance with the Act, this interrelationship necessitates that the stocks be managed as a unit or in close coordination.

At present, the longline fishery only operates during the summer and the gear is selective for adult halibut which, as shown by tagging studies, generally return to the same grounds each summer. Providing that the fishery continues to operate in the summer, it is not unreasonable to assume that the exploitation of the adult stocks in Area 2 and Area 3 can be managed separately because intermingling is not extensive at that time. Further, because different vessels fish in each area, maintenance of separate regulatory areas for the longline fishery still may be the most practical approach for the optimum use of the resource. However, if a longline fishery were instituted during the winter migrations, exploitation could involve a greater mixture of the stocks and the effects of fishing would be similar to those of the trawl fisheries. Although the trawl fisheries target on species other than halibut, they are conducted year-round and are selective for juvenile halibut, many of which will migrate to other areas, so that exploitation involves a mixture of stocks and the effects of fishing in one area cannot be considered independent of effects on the other.

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