THE EFFECTS OF AGE COMPOSITION AND OCEANOGRAPHIC CONDITIONS ON THE ANNUAL MIGRATION OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*

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ABSTRACT

Adult Pacific whiting (also known as Pacific hake), *Merluccius productus*, migrate each year from spawning grounds off southern California to feeding grounds along the continental shelf break from central California to Vancouver Island. During spring and summer, there are large-scale commercial fisheries for this species in both U.S. and Canadian waters. The stock synthesis model, a flexible, age-structured, maximum-likelihood estimation model, was used to investigate the migratory behavior of Pacific whiting. In this implementation of the stock synthesis model, the U.S. and Canadian zones were defined as separate geographic areas, and the parameters of an age-specific migration function were estimated. Annual coefficients were estimated for the parameter specifying the asymptotic proportion of an age class migrating into the Canadian zone for years with coastwide acoustic surveys (1977, 1980, 1983, 1986, 1989, and 1992). Correlation analysis between these coefficients and a suite of environmental variables revealed that the March–April water temperature anomaly at a depth of 100 m from 30° to 42° N lat. had the highest correlations. High water temperatures were associated with an increased proportion of the Pacific whiting population in the Canadian zone, as occurred during the 1982–83 and 1991–92 El Niño events, whereas in 1989, low water temperatures were associated with a decreased proportion in the Canadian zone. This relationship was used in the stock synthesis model to estimate migration curves for years in which no surveys were made. The results of the stock synthesis models and the correlation analysis suggest that El Niño events promote the northward movement of Pacific whiting via intensified northward currents during the period of active migration. Although estimates of total population abundance are unaffected by modeling the interannual variation in migration, the results provide additional information on the transboundary distribution of the stock, which is important for forecasting how long-term climate change affects the Pacific whiting population.

INTRODUCTION

Marine species in the California Current ecosystem respond in a variety of ways to El Niño conditions. Changes in growth (Dorn 1992), condition (Schoener and Fluharty 1985), and reproductive effort (Ainley and Boekelheide 1990) have commonly been observed. Changes in spatial distribution are perhaps the most obvious response. Two primary mechanisms that change the distribution of marine species are (1) active movement to preferred habitat and (2) transport by altered currents. For planktonic species with limited ability for directed movement, distributional changes are related to transport by altered currents. For example, Bolin and Abbott (1963) found higher abundances of tropical and subtropical phytoplankton off the central California coast during years with elevated water temperatures. For nektonic species, active migration to altered habitat is a more likely mechanism, which apparently accounts for the increased abundance of highly migratory pelagic tunas such as albacore (*Thunnus alalunga*) off British Columbia and Washington during El Niño years (Smith 1985).

This paper describes research on Pacific whiting (*Merluccius productus*), also known as Pacific hake, a gadoid species that is an important component of the California Current ecosystem (Francis 1983). Adult Pacific whiting migrate north in spring to feed in the productive waters along the continental shelf and slope from northern California to Vancouver Island, British Columbia, during summer and fall (figure 1). There are large-scale commercial fisheries for Pacific whiting in both U.S. and Canadian waters during these months. In late autumn, Pacific whiting migrate south to spawning areas from Point Reyes, California, to Baja California (Bailey et al. 1982). Both active migration and transport by currents may change the latitudinal distribution of this species during El Niño years. The annual northward migration could be assisted or hindered by changes in current speed and direction. During El Niño events, upwelling in the California Current ecosystem is inhibited, and transport of subarctic Pacific water is reduced (McLain 1984). Since the thermocline is depressed during El Niño events, when upwelling occurs it brings nutrient-depleted water to the surface, further reducing productivity. The scarcity of food on the usual summer feeding grounds may induce Pacific whiting to forage farther north.

This paper is the first attempt to go beyond anecdotal reports of range changes of marine species during El Niño events to develop predictive quantitative models for changes in population distribution. Each summer,
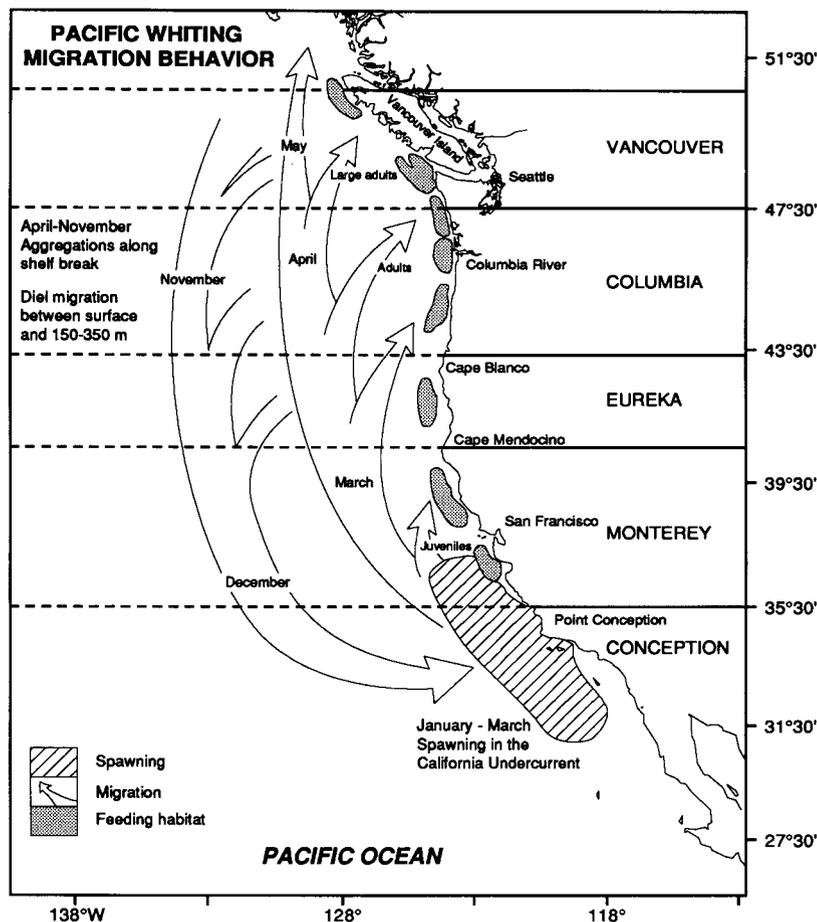
Figure 1. The general pattern of Pacific whiting migratory behavior (modified from Bailey et al. 1982).

some proportion of the Pacific whiting population migrates into Canadian waters. Using the stock synthesis model (Methot 1989), I develop a method for predicting the proportion that migrates. The method takes into account changes in the age structure and abundance of the population, and employs an environmental index that measures the strength of northward transport. I begin by discussing the key features of Pacific whiting natural history, focusing on average migration characteristics and annual migration timing. Next I briefly review El Niño effects on California Current oceanography that could influence Pacific whiting migration. Then I present the stock synthesis model with migration for Pacific whiting. I analyze the results of the model, and discuss the implications of these results in an environment characterized by decadal regime shifts and long-term climate change.

Pacific Whiting Migratory Behavior

Although the general features of Pacific whiting migratory behavior have been known for some time (Alverson and Larkins 1969), new fisheries and expanded surveys have increased our knowledge of Pacific whit-

ing migration and summer distribution patterns. In 1991, a domestic fleet of factory trawlers and mother ships displaced the joint venture fishery for Pacific whiting in U.S. waters. The shore-based fleet, operating primarily out of Newport and Astoria, Oregon, has also expanded rapidly in recent years. These new domestic fisheries have operated outside the seasonal limits of the earlier joint venture and foreign fisheries for Pacific whiting and have provided additional details about the timing of the annual migration. Of course, deriving inferences about the distribution of fish from fisheries data is subject to the caveat that although the presence of fishing indicates the presence of fish, the absence of fishing does not indicate an absence of fish.

Since 1992, the at-sea fishery has opened on 15 April. During the first weeks (15–30 April), the fleet has fished as far north as the U.S.–Canada border (figure 2). This suggests that the population has moved considerably northward by this time. Although the shore-based fishery in Newport and Astoria has not started as early as the at-sea fishery, it has continued until late fall in several years. Earlier conjectures were that the southward

Figure 3. Pacific whiting monthly landings for 1994 in metric tons (MT) at Newport and Astoria, Oregon.
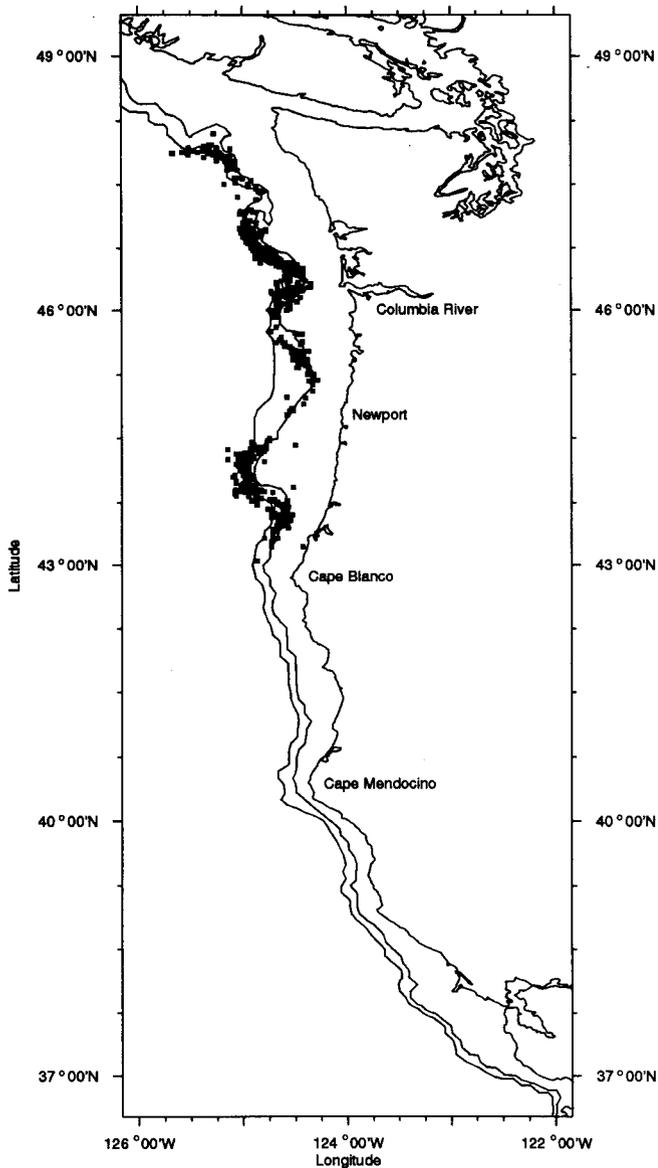

Figure 2. Haul locations during 15–30 April for the 1993 domestic Pacific whiting at-sea fishery. The 200 m and 500 m isobaths are also shown.

migration began in September (Stauffer 1985), although in the early years of foreign fishing (1967–76), catches in the Canadian zone were regularly reported in November (Beamish and McFarlane 1985). In 1994, the shore-based fishery ceased operations in mid-November (figure 3). Fishermen indicated that they had stopped fishing because of inclement weather and a decline in the availability of Pacific whiting (W. Barss, Ore. Dep. Fish and Wildlife, Marine Science Drive, Building 3, Newport, OR 97365, pers. comm., Dec. 1994). The availability of fish off Oregon in November suggests that the southward migration has not yet begun. From an analysis of early-stage larvae, Hollowed (1992) determined that February was usually the peak spawning
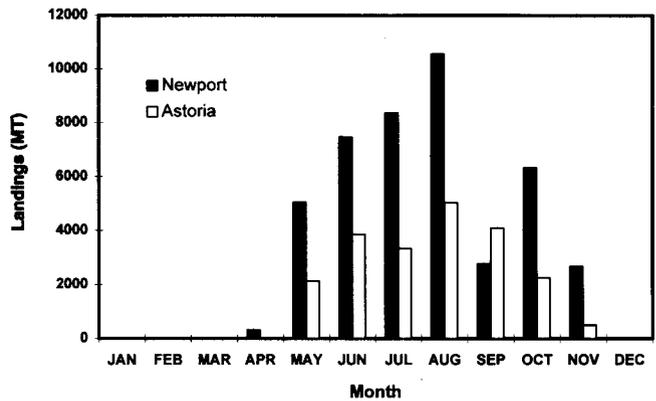
month, with significant spawning also in January and March. This observation, in association with the seasonal pattern of fishing, suggests that the period of maximum northward movement is March and April, and that the southward return migration occurs primarily in November and December.

A coastwide acoustic survey of Pacific whiting was conducted by the National Marine Fisheries Service (NMFS) in summer 1992 (Dorn et al. 1994), and annual series of acoustic surveys of Pacific whiting were conducted by the Canada Department of Fisheries and Oceans (DFO) in 1990–93 (Cooke et al. 1992). These surveys had wider areal coverage than earlier surveys, both offshore of the shelf break and in the north, and produced population estimates considerably higher than those forecast by earlier surveys and models. These surveys reveal that in many years substantial aggregations of whiting are found north of the La Perouse area, where the Canadian fishery occurs. These aggregations extend along the west coast of Vancouver Island and into Queen Charlotte Sound. Pacific whiting density typically increases in a localized area offshore of Brooks Peninsula (50° N). In addition, it is apparent that significant midwater aggregations of Pacific whiting occur as far as 40 km offshore of the shelf break, over water up to 2,000 m deep. In 1992, these off-shelf aggregations were found from northern California to northern Vancouver Island (Dorn et al. 1994).

The migratory behavior of Pacific whiting is strongly age-dependent. It is possible to refine our ideas about the migratory behavior of Pacific whiting by introducing the concept of an annual migratory distance, defined as the distance between the spawning grounds and the northward limit of the annual migration of a particular fish. Figure 4 is a schematic of the age-structured migratory characteristics of Pacific whiting based on the assumption that all spawning occurs off Point Conception, and that the NMFS acoustic surveys in July–August
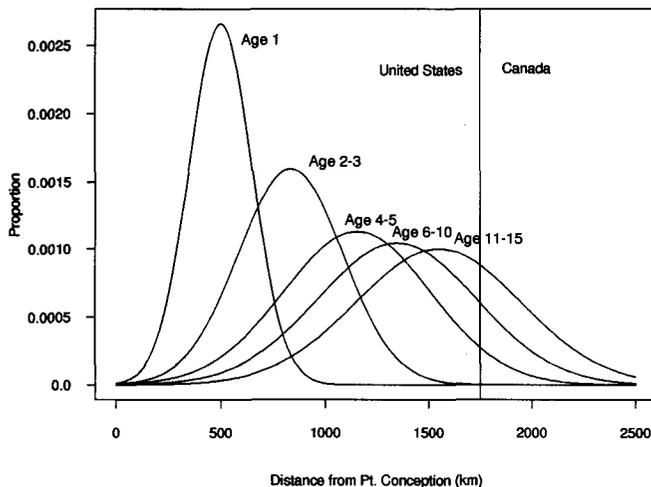
Figure 4. Schematic illustration of the distribution of annual maximum migration distances by age group for Pacific whiting. The *vertical line* at 1,750 km shows the approximate location of the boundary between the United States and Canadian zones.

observe the fish at the northern limit of their annual migration. The general characteristics of Pacific whiting migration evident in figure 4 are:

1. The mean migration distance of an age group increases with age.

2. The difference in mean migration distance between the consecutive age groups declines with age. For example, the mean distance migrated by the age-15 and age-14 fish is about the same.

3. Older age groups have a wider distribution than the younger age groups. In other words, the variance of the migratory distance increases with age.

These behavioral patterns are extremely resistant to change. For example, even in years when the population is found farther north, the older age groups are still farther north, on average, than the younger age groups.

The coastal Pacific whiting population is also remarkable for its extreme recruitment variability. The strong year classes (e.g., 1980 and 1984) can be two orders of magnitude larger than weak year classes (e.g., 1981, 1982, 1983, 1985). As a result of this variation in year-class strength, mean age in the population can change substantially as a strong year class passes through the population. For example, between 1983 and 1992, the mean age in the U.S. fishery increased by almost two years as the large 1980 and 1984 year classes became older and were not displaced by equally large incoming year classes. Since the extent of northward migration is related to age, the spatial distribution of the population will be affected by changes in the population age structure independent of any environmental factor.

Potential El Niño Effects on Pacific Whiting Migration

The link between El Niño events in the equatorial Pacific region and changes in oceanographic conditions in the North Pacific Ocean is a subject of active research and some controversy. The linking mechanism that offers the most supporting evidence is an atmospheric teleconnection between an El Niño and an intensification of the Aleutian low (Simpson 1992). The suggested sequence of events that would facilitate increased northward migration of Pacific whiting in the California Current system during El Niño events is the following:

1. Intensification of the Aleutian low through atmospheric teleconnection

2. Enhanced onshore transport of Pacific subarctic water, resulting in elevated sea-surface and subsurface water temperatures, a depressed thermocline, and elevated sea levels along the west coast of the United States and Canada

3. Intensification of poleward transport from the south via strengthened Davidson Current and California Undercurrent flow.

The a priori expectation, therefore, would be that enhanced northward migration of Pacific whiting would be positively correlated with anomalies of surface water temperature, subsurface temperature, and alongshore poleward transport. The potential for El Niño events to provide a boost for northward migrators during late winter and early spring is demonstrated by the path of satellite-tracked drifters. Emery et al. (1985) mapped the path of a satellite-tracked drifter drogued at 30 m during the onset of the 1982–83 El Niño. On 25 Jan. 1983 the drifter was slightly north of San Francisco at 39° N. On 27 Feb. 1983, 33 days later, the drifter was recovered off southern Vancouver Island.

During El Niño years, the normal summer upwelling regime off the West Coast is inhibited, and there is less transport of biomass-rich subarctic Pacific water from the Alaska gyre (Roesler and Chelton 1987). It is apparent, therefore, that northward transport is strong in years when it is advantageous for Pacific whiting to migrate farther north. Such an adaptive migratory pattern would not require complex behavioral adaptations and may indicate why this migratory pattern is so strongly developed in Pacific whiting.

METHODS

Stock Synthesis Modeling of Annual Migration

The stock synthesis model is now widely used to estimate abundance of exploited marine populations. The

strength of the stock synthesis model lies in its flexibility in modeling how fisheries affect populations and how those populations are measured by resource surveys. I use a two-area (United States and Canada) version of the stock synthesis model similar to the model used for the stock assessment (Dorn et al. 1994). The intent here is to use the stock synthesis methodology to study the migratory characteristics of Pacific whiting. The results presented here are intended as a supplement to, not a replacement for, the more detailed annual stock assessments of the Pacific whiting resource (Dorn et al. 1994).

The stock synthesis model is a catch-age analysis that uses survey estimates of biomass and age composition as auxiliary information (Methot 1989). The synthesis model operates by simulating the dynamics of the population. Comparisons are made between the expected value of the observable characteristics of the simulated population and the actual observations of the population from surveys and fishery sampling programs. The goodness of fit to these observations is evaluated in term of log(likelihood). The total log(likelihood) is a weighted sum of the log(likelihood) components for each data type.

The data elements used in the stock synthesis model for Pacific whiting are as follows:

1. A time series of age composition and catch totals from the U.S. and Canadian fisheries for Pacific whiting (1977–93)

2. NMFS acoustic surveys (1977, 1980, 1983, 1986, 1989, 1992)

3. DFO acoustic surveys (Canadian zone only) 1990–93.

The NMFS survey biomass estimates for the Canadian zone were adjusted because of incomplete coverage, as described in Dorn et al. 1994.

I implemented a stock synthesis model with annual migration by assuming that migration occurs at the start of the year (before any fishing takes place) and that the population mixes at the end of the year. I used a three-parameter logistic curve to model the age-specific fraction (m_a, where a is age) of the population migrating into the Canadian zone:

$$m_a = \frac{p_3}{1 + e^{[-p_2(a-p_1)]}},$$

where p_1 is the inflection age, p_2 is the slope, and p_3 is the asymptotic proportion of an age-class migrating into the Canadian zone. Interannual variation in migration is obtained by estimating separate p_3 coefficients for each year. In this way a family of asymptotic curves can be obtained (figure 5). The procedure for incorporating oceanographic indices consisted of several steps. First, a preliminary model estimated the migration coefficients,
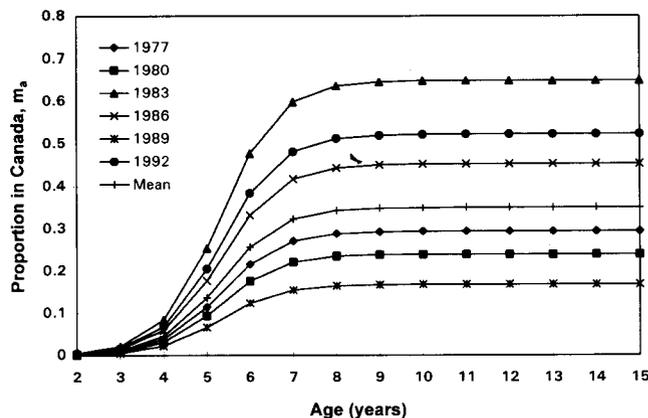

Figure 5. Annual age-specific migration curves estimated with the stock synthesis model. Separate curves are shown for years with a National Marine Fisheries Service acoustic survey (1977, 1980, 1983, 1986, 1989, 1992) and the mean for all years. The curves are the annual age-specific fraction of the population migrating into Canadian waters.

p_{3i}, in NMFS survey years ($i = 1977, 1980, 1983, 1986, 1989,$ and 1992).

Next, I conducted a correlation analysis using these estimated migration coefficients and a suite of oceanographic indices. The oceanographic data consisted of monthly mean temperature at the surface, 100 m, and 200 m for 3-degree-latitude coastal blocks from ships of opportunity. The data were supplied by D. R. McLain (National Ocean Service, Monterey, CA 93942, pers. comm., July 1994). I obtained temperature anomalies for each 3-degree block by subtracting out the long-term mean. I obtained a "north" index by averaging the anomaly for the four blocks extending from 42° N to 54° N, and a "south" index by averaging the anomaly for the four blocks extending from 30° N to 42° N. I used the correlation analysis to select the oceanographic index that correlated best with the estimated migration coefficients during the survey years. I then used linear regression to obtain predicted migration coefficients for years in which no surveys were taken.

Finally, I used the predicted migration coefficients in a final stock synthesis model as part of an environmental likelihood component. This likelihood component had the form

$$l_p = -\sum_i (p_{3i} - \tilde{p}_{3i})^2,$$

where p_{3i} is the model-estimated migration coefficient for year i, and $\tilde{p}_{3i}$ is the predicted migration coefficient from the linear regression from the environmental index for year i. Only the years in which no surveys were made were included in the summation because in years with a coastwide acoustic survey the distribution of biomass is well established by the survey. A large emphasis on this likelihood component would force the model to return the predicted migration coefficients as the estimated

TABLE 1
Likelihood Components for Three Hierarchical Stock Synthesis Models for Pacific Whiting.

Likelihood components	Emphasis	Model 1: No interannual variability	Model 2: Interannual variability in survey years only	Model 3: Interannual variability in all years
U.S. fishery age composition	1.0	−300.4	−311.1	−312.0
Canadian fishery age composition	1.0	−388.6	−385.3	−387.2
NMFS survey, U.S. zone biomass	5.0	3.8	3.9	3.3
NMFS survey, U.S. zone age composition	1.0	−144.8	−143.4	−140.6
NMFS survey, Canada zone biomass	5.0	−2.4	7.2	7.3
NMFS survey, Canada zone age composition	1.0	−148.6	−148.5	−148.3
DFO survey, biomass	5.0	−47.8	−25.6	3.5
DFO survey, age composition	1.0	−141.3	−141.7	−141.5

values; a small emphasis would allow other data to determine their values. For the final model runs, I used an emphasis of 5000 for the environmental component. I selected this emphasis level so that the root mean square error of the fit to the DFO survey observations (0.195) was comparable to the root mean square error of the fit to the NMFS survey observations (0.152), and provided an appropriate trade-off between fitting the DFO survey observations and fitting the predicted migration coefficients.

RESULTS

The stock synthesis migration models were hierarchical, starting with a simple model with no interannual variability in transboundary migration, and progressing to models where the migration differed in each year. During the years of a coastwide NMFS acoustic survey, the spatial distribution of the population is well measured, and there is sufficient information for estimating the migration coefficients independently. In the other years, consistent patterns in the age composition of the U.S. and Canadian fisheries provide some information on the transboundary distribution of Pacific whiting. In trial runs, however, age-composition data alone were insufficient to estimate the migration coefficients. For 1990, 1991, and 1993, when only DFO conducted acoustic surveys of the Canadian zone, the biomass estimates can be matched exactly, since the migration coefficients can move simulated fish across the border without reducing the likelihood to other data sources. Because biomass estimates include statistical error, an exact model fit suggests that the model is overparameterized. Adding an environmental index increases the information in the model, and thus increases the precision of the estimated parameters. Model 1 in table 1 estimates a single migration curve for all years. Model 2 estimates migration coefficients for the years with an NMFS triennial survey, resulting in the set of migration curves shown in figure 5. The largest estimated asymptotic proportion in the Canadian zone was 0.65, which occurred

in 1983 during the 1982–83 El Niño. In 1992, also an El Niño year, the estimated asymptotic proportion in the Canadian zone was 0.52, the second largest value. In 1989, the estimated asymptotic proportion in the Canadian zone was at its lowest value, 0.17.

The correlations between the migration coefficients and the sea-temperature anomalies for survey years were generally positive during the 12-month period prior to the survey (figure 6). Negative correlations occur only
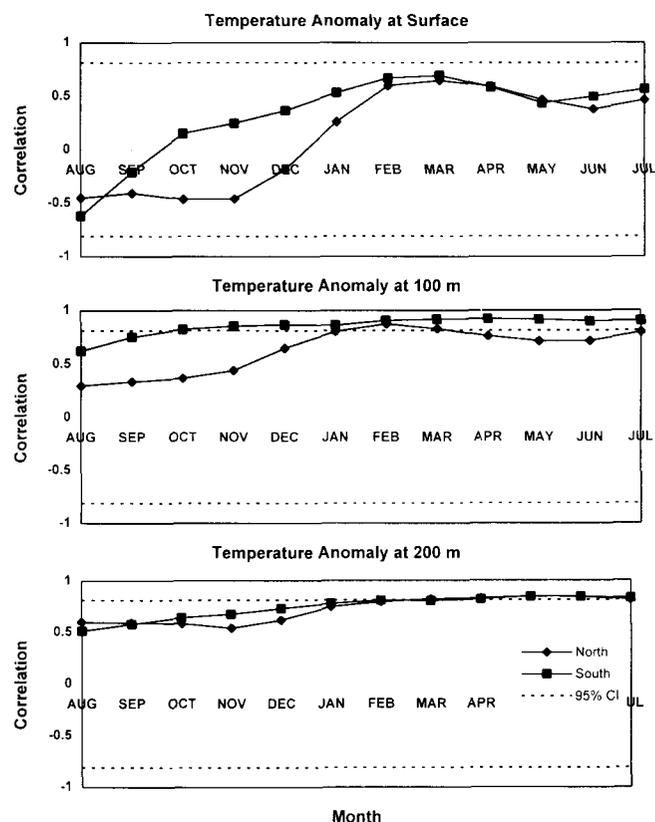

Figure 6. Correlation between estimated migration coefficients for survey years and sea-temperature anomalies (surface, 100 m, 200 m) for 12 months prior to the triennial survey. The "north" index is the mean anomaly for 42° N–54° N; the "south" index is the mean anomaly for 30° N–42° N.

for the surface temperature anomaly in the north. The 95% confidence intervals (Sokal and Rohlf 1981) for the observations under the null hypothesis (no correlation with temperature) show which correlations are the strongest, but should not be used to judge statistical significance, since many correlations were examined. The correlation with temperature anomalies at 100 and 200 m tended to be stronger than the correlation with the surface water temperature anomaly. The "south" index had higher correlations than the "north" index, suggesting that the environmental forcing of migration occurs in the south near the spawning ground rather than in the north on the feeding grounds. Higher correlations occurred during the semester (February–July) immediately before the survey, rather than the preceding semester (August–January). The tendency for high correlations to continue over a sequence of months is not surprising, because the monthly temperature anomalies themselves are highly correlated. Maximum correlations occurred during April–March at 100 m for the "south" index. I used this index in a regression analysis to predict the migration coefficient during the years without a survey.

The linear regression of the estimated migration coefficients on the temperature anomaly at 100 m was significant, $r^2 = 0.818$, d.f. $= 4$, $p = 0.013$. The temperature anomalies in 1983 (+1.29°C) and in 1989 (−0.42°C) are the largest and smallest temperature anomalies, respectively, and strongly influence the slope of the regression (figure 7). I used the regression equation ($p_3 = 0.28 + 0.30T$, where T is the temperature anomaly at 100 m) to predict the migration coefficients during years when there was no NMFS triennial survey. During 1977–93, none of the temperature anomalies for the years of no surveys were more extreme than the 1983 and 1989 anomalies.
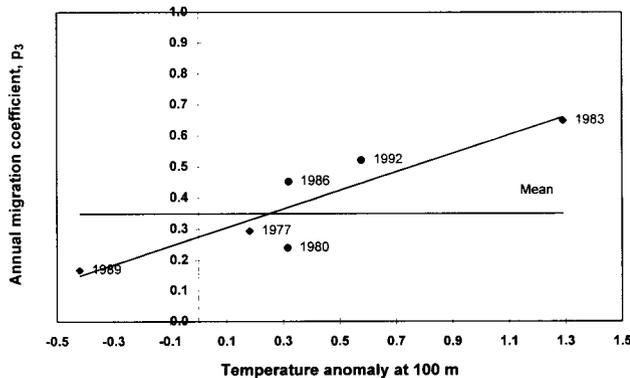

Figure 7. Regression of estimated migration coefficients p_3 for years with a National Marine Fisheries Service acoustic survey (1977, 1980, 1983, 1986, 1989, and 1992) on the March–April temperature anomaly at 100 m. The coefficients p_3 are the asymptotic proportion of the age group migrating into the Canadian zone.

TABLE 2
Estimated Coefficients for a U.S.–Canada Migration Function for Pacific Whiting

Parameter	Prediction based on sea temp. at 100 m	Stock synthesis estimate
p_1	—	5.297
p_2	—	1.478
p_{3i} (i = 1977, . . . , 1993)		
1977	—	0.294
1978	0.367	0.367
1979	0.316	0.314
1980	—	0.240
1981	0.336	0.335
1982	0.304	0.300
1983	—	0.649
1984	0.378	0.381
1985	0.300	0.303
1986	—	0.453
1987	0.371	0.371
1988	0.333	0.332
1989	—	0.169
1990	0.256	0.183
1991	0.202	0.249
1992	—	0.522
1993	0.405	0.397

The parameter p_1 is the inflection point of the logistic curve; p_2, the slope; and p_{3i}, the year-specific asymptotic proportion migrating into the Canadian zone. For years in which no surveys were made, two estimates are shown for p_{3i}: the prediction based on the sea temperature at 100 m, and the final stock synthesis estimate.

In the sequence of models 1–3, most of the improvement in fit—measured by increase in log(likelihood)—for the NMFS acoustic biomass estimate occurs when moving from model 1 to model 2 (table 1). The fit to the DFO surveys improves with each transition between models because the DFO surveys were made in years with an NMFS survey (1992) and also in years without an NMFS survey (1990, 1991, 1993). The substantial improvement in fit also indicates that the environmental index is consistent with the DFO acoustic time series. The model output included estimated coefficients for the migration function (table 2) and the predicted proportion of biomass in the Canadian zone that would have been measured by the NMFS acoustic surveys had they been made in all years (figure 8). This predicted proportion is obtained by filtering the age-specific population biomass through the survey selectivity curve. The mean proportion of biomass in the Canadian zone for all years (22.7%) corresponds reasonably well with the observed mean of the actual surveys (23.8%). Although the temperature anomaly is most positive in 1983, the maximum proportion of biomass in the Canadian zone occurred in 1992. This is due to two factors: a moderately positive temperature anomaly in 1992, and the population's relatively old mean age.
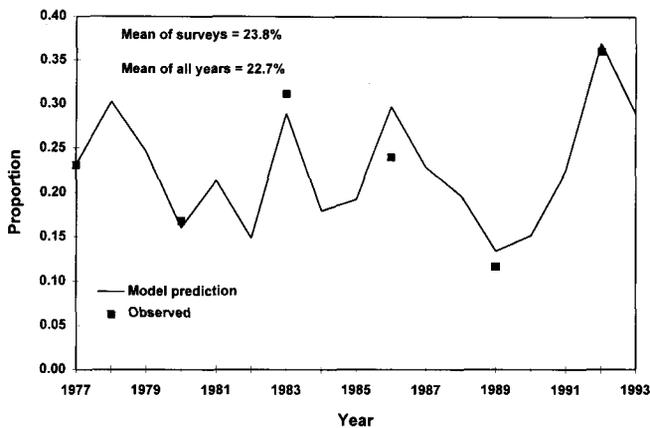
Figure 8. Predicted proportion of Pacific whiting biomass in the Canadian zone during 1977–93, based on a stock synthesis model with an environmental likelihood component. Observed proportion as measured by the National Marine Fisheries Service acoustic surveys in 1977, 1980, 1983, 1986, 1989, and 1992.

Figure 9. March–April temperature anomaly at 100 m, 30° N–42° N, 1944–93.

DISCUSSION

Correlation analysis and stock synthesis models show that the available data on the Pacific whiting population are consistent with a hypothesis that El Niño events promote the northward migration of Pacific whiting via intensified northward currents during the period of active migration. There are two primary benefits from the modeling approach used in this paper. First, a stronger assessment model results from using additional data. For example, the DFO surveys, which cover only the Canadian zone, provide little independent information on overall abundance. But when the environmental index is included in the model, the total population abundance and the value of the migration coefficients jointly determine the expected biomass in the Canadian zone. As a consequence, when a model is fit, the DFO biomass estimates provide additional inference on the total population abundance.

A second benefit of this approach is in predicting population response to climatic variation. During the NMFS acoustic survey years of 1977–92, the March–April 100 m temperature anomaly varied over most of the range of the anomaly for the past 50 years (figure 9). For temperature anomalies within this range, the potential response of Pacific whiting migration to climate change can be predicted. This 50-year period can be roughly divided into three parts: a "cold" period from 1944 to 1957, a "moderate" period from 1958 to 1976 initiated by the 1957–58 El Niño, and a "warm" period from 1977 to the present, punctuated by the spectacular 1982–83 El Niño and several years of negative anomalies in the late 1980s (figure 9). The NMFS acoustic surveys were all made during this warm period (only 1989 has a negative temperature anomaly). Although the mean distribution of biomass estimated from these sur-
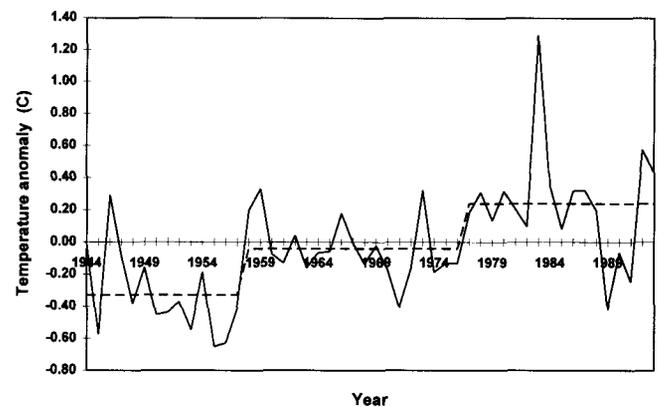
veys is probably close to the true mean for this warm period, it may significantly underestimate the long-term average proportion of biomass in the Canadian zone. A return to cooler conditions would be expected to reduce the biomass in the Canadian zone.

The stock synthesis model used in this paper is based on the assumption that spawning occurs in the same place each year. Maps of Pacific whiting larvae distributions (in Hollowed 1992) show clear interannual differences. In warm years, larval distribution usually shifts northward. The most extreme northward shifts in larval distribution usually occur a year or more after the onset of an El Niño, as in 1984 and 1994. It is unknown whether these changes are due to egg and larval transport or to changes in the location of spawning, or both. The spawning grounds of Pacific whiting are not known with any certainty. A model for Pacific whiting migration that includes changes in spawning location would be useful to develop, but the data are not available for estimating the parameters of such a model.

Ware and McFarlane (1995) show a correlation between a water-temperature time series from Amphitrite Point, a coastal station near La Perouse Bank, and a midwater trawl, volume-swept biomass estimate of Pacific whiting in the La Perouse region. Ware and McFarlane derive a regression equation to predict the biomass of Pacific whiting in the La Perouse region in August as a function of water temperature in the preceding June–July. Although the correlation is strong, it is useful to consider how Ware and McFarlane's relationship differs from that obtained in this paper. First, their correlation does not take into account the age structure of the population. Second, it does not take into account changes in the total biomass of Pacific whiting. Although the results in this paper are also based on patterns of correlation, they suggest that the significant oceanographic events affecting Pacific whiting migration into the Canadian zone occur earlier in the year, more than 500

km south of the La Perouse region. Of course, the Amphitrite Point temperature time series will be correlated with temperatures farther south, so the Ware-McFarlane correlation does not conflict with our results. However, to use a correlation between temperature and Pacific whiting biomass in an ecosystem model of the La Perouse region could potentially lead to incorrect conclusions regarding the trophic role of Pacific whiting. This is because any other ecological process in the model that was a function of water temperature would also be correlated with Pacific whiting biomass.

The primary management implications of this research concern the binational allocation of the Pacific whiting resource. No formal agreement has been reached on how to allocate Pacific whiting yields between U.S. and Canadian fisheries. Discussions have focused on an allocation based on the distribution of biomass between the two zones. However, agreement has not been reached, and since 1993 the United States has set its quota at 80% of the total available yield, and Canada has set its quota at a level that would be 30% of the combined quotas. From the perspective of this research, reaching an agreement that will be appropriate for the indefinite future may be difficult. An agreement based on current climatic conditions could be inappropriate in future conditions. The U.S. and Canadian fisheries have largely developed during a warm period, from 1966 to the present. Under some scenarios for climate change, global warming might result in persistent El Niño–like conditions on the west coast of North America, which could lead to high migration rates to the Canadian zone. Alternatively, a regime shift to cooler conditions is also possible in the near future, leading to decreased migration rates to Canada. The long-term performance of the Canadian fishery for Pacific whiting depends somewhat on climatic conditions. The U.S. fishery is less vulnerable, since it can fish over a much wider latitudinal range within the migration limits of the resource.

ACKNOWLEDGMENTS

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