Migratory Pattern of Argentine Hake *Merluccius hubbsi* and Oceanic Processes in the Southwestern Atlantic Ocean

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Abstract.–The annual migratory cycle of Argentine hake *Merluccius hubbsi* was related to environmental conditions in the Southwestern Atlantic Ocean. In late summer–early fall, hake move northward and offshore towards feeding grounds. A southward and inshore migration towards spawning grounds occurs in early spring. The ends of the migratory circuit are associated with productive ocean fronts. Differences in the migratory pattern between 1978 and 1979 were tied to fluctuations in the latitude of the confluence of the Brazil and Malvinas currents along the shelf break.

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The Argentine hake *Merluccius hubbsi* is the most important species in Argentine fisheries: its landings make up approximately two thirds (in weight) of all Argentine fish catches. Fishery surveys carried out at different times of the year, together with data on the movements of the commercial fishing fleet, have revealed seasonal changes in hake distribution. The inshore spawning migration of adult hake on the Argentine shelf was first described by Hart (1946). Using data from a commercial trawler, Angelescu et al. (1958) showed the change in depth distribution of hake throughout the year. Christiansen and Cousseau (1971) and Bellisio et al. (1978) described the seasonal movements of the Argentine fishing fleet targeting on hake. An extensive research program sponsored by UNDP-FAO between 1968 and 1975 resulted in an improved knowledge of the distribution and migration of Argentine hake (FAO 1975). Otero and Kawai (1981) proposed the existence of two Argentine hake stocks, one migrating approximately between 35°S and 44°S and another moving between 44°S and 50°S. Chung and Tanaka (1985) investigated the displacements of hake using a 1-year series of research cruises. Otero (1986) used several years of commercial fishery data to describe the migration of hake, showing the progressive expansion of effort towards the southern part of the Argentine shelf.

Despite our knowledge of the seasonal distribution of hake, not much is understood about the oceanic conditions which contribute to define the migratory pattern of the species. The objective of this paper, therefore, is to explore the association between the migration of hake and environmental conditions in the southwestern Atlantic Ocean off Argentina and Uruguay. A usual approach is to treat fish distribution as a function of one or a few environmental variables (e.g., water temperature, salinity). Instead, emphasis is placed here on physical features, such as ocean fronts of diverse nature, which are an intrinsic part of the Argentine shelf ecosystem. I will discuss the relevance of these features to the different migratory stages (and, therefore, varying biological requirements) of hake. Historical fishery and hydrographic data are used to establish links between the distribution of hake and oceanic features; any such links may form the basis of specific hypotheses that can be rigorously investigated in the future.

Data and methods

The primary data used to determine the migratory pattern of hake include catch, effort (trawling hours), and area of operations (by 1-degree squares) reported by the Argentine offshore fishing fleet in 1978 and 1979. A detailed description of the fishery data is presented by Podestá

(1987). Data from fishing surveys carried out between April 1978 and April 1979 by German and Japanese research vessels (Ciechomski et al. 1979a, Cousseau et al. 1979) are also incorporated in the discussion.

Monthly maps (not shown) of fishing effort and hake catch-per-unit-effort (CPUE) drawn from the commercial fishery data were used to track the migration of exploited concentrations of hake. The use of commercial fishing statistics to follow fish migration, however, has limitations. The fleet may be targeting on species other than the one being considered. Fleet movements, therefore, may be primarily associated with perceived fluctuations in the abundance of the target species. The Argentine offshore fleet targets mainly on hake; the proportion (in weight) of hake in the catches was >95% during most of the period studied. The proportion of shortfin squid (*Illex argentinus*) in the catches increased during May–July as a result of seasonal overlap in the distributions of both species. Even then, the Argentine fleet did not generally target on squid, which could be considered as bycatch (Juanicó 1982).

The use of fishery data to investigate migration relies on the fishermen's ability to locate the densest aggregations of hake. Several lines of evidence support this assumption. The hake fishery has been taking place for several years and the displacements of fish are well known. Monthly histograms of standardized hake CPUE show a moderately positive skewness (data not shown) that may be partly associated with a widespread knowledge of fish distribution (Quinn 1985). A comparison of alternative formulations for a monthly CPUE index, i.e., an average-of-ratios vs. a ratio-of-averages, confirms that effort was concentrated on areas of higher-than-average hake abundance (Otero 1986). This conclusion is also supported by spatial statistics of fishing effort and CPUE (Rothschild and Yong 1970).

To visualize better the patterns of hake movement, monthly latitudinal and longitudinal weighted averages of fishing effort and hake CPUE were computed according to the procedure described by Rothschild and Yong (1970). In some months, fishing effort was deployed in distinctly separate regions throughout the shelf. This may have reflected true operational differences in the fishing fleet as a consequence of separate centers of fish abundance. To take into account the discontinuity, I grouped all contiguous 1-degree areas, calculated the total fishing effort for each cluster of contiguous areas, and considered only major clusters (those in which effort was >5% of the effort in the most heavily exploited cluster). Most months showed only one valid cluster of areas and, at most, two clusters fulfilled the previous criteria. I computed the spatial statistics of effort for each valid cluster. For the CPUE statistics, the same clusters delimited above were used, but data were included only from areas where five or more trips had been reported, to reduce variability in CPUE values due to low levels of sampling.

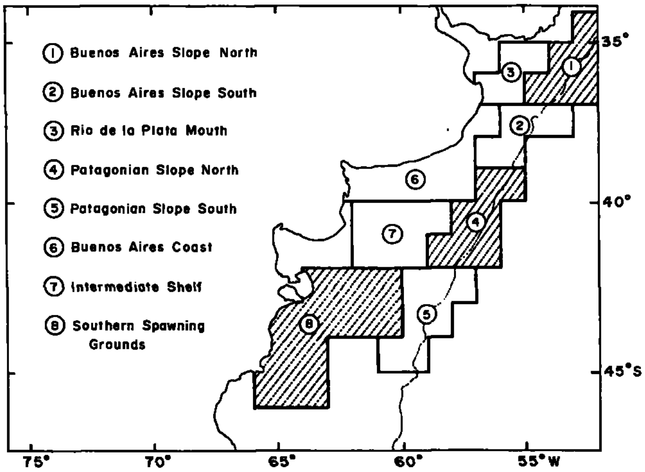

Figure 1

Geographic regions in southwestern Atlantic Ocean used for investigating interannual differences in hake migration. Stippled regions are discussed in the text.

As with most hakes (Jones 1974), tagging Argentine hake has proven so far to be impossible and, consequently, there are no estimates of migratory speed derived from tag returns of individual fish. As an approximation, I estimated hake migration speed by using the spatial statistics of fishing effort calculated above. I calculated the distances between the centers of effort in consecutive months, and then estimated daily migratory speeds by dividing the distances by 30 days (regardless of the specific months involved).

If the migratory pattern of hake is associated with environmental factors, year-to-year differences in their distribution may reflect fluctuations in oceanic conditions. I examined differences in the distributional pattern of hake between 1978 and 1979, and tried to relate those differences to environmental conditions.

A direct comparison of the commercial fishery effort and CPUE data is impossible because (a) there was a change in the format of the fishing tickets (the forms turned in by fishermen upon return to port) between 1978 and 1979, and (b) fishing effort had to be standardized separately for each year because of software limitations (see Podestá 1987).

A new fishing ticket was introduced in 1979 which, due to its design, increased uncertainty on the reported location of effort. To reduce the possibility of error, I grouped the data, originally reported for 1-degree squares, into eight larger geographical regions (Fig. 1).

Because fishing effort had been standardized separately for 1978 and 1979, the cumulative time density approach introduced by Mundy (1982) was used, which

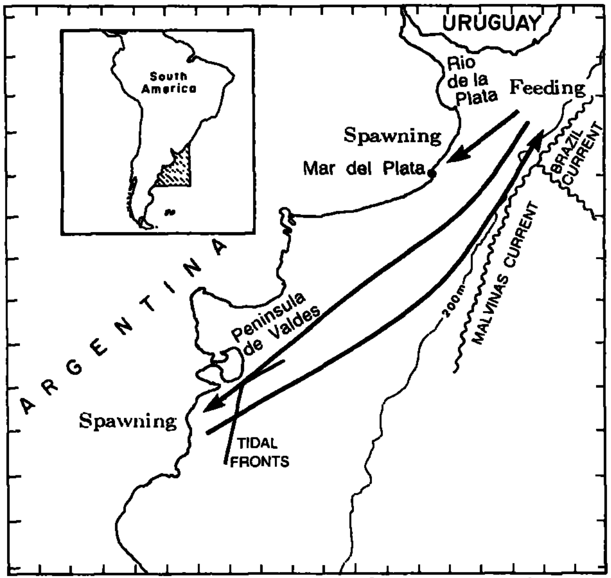

Figure 2
Schematic description of the annual migratory pattern of Argentine hake in southwestern Atlantic Ocean. Approximate locations of some oceanic features mentioned in the text are also shown.

does not require between-year consistency in the measure of effort. The technique is based on the fluctuations in fish abundance as a function of time in a fixed geographic reference frame and originally employed catch or CPUE data (Mundy 1982). However, the regions considered showed no fishing effort during some months and CPUE was undefined; the zero effort value, in contrast, was meaningful. Therefore, I used effort values (hours trawled per month) to construct the cumulative time density series in the manner described by Mundy (1982).

Results

Migratory pattern of hake

Figure 2 shows a schematic description of the migratory pattern of Argentine hake, derived from catch-and-effort statistics of the commercial fleet for 1978 and 1979 and complemented by literature reports. Hake show a cyclic northward-southward migration accompanied, respectively, by offshore-inshore movements.

The northernmost area reached by concentrations of hake exploited by the Argentine fleet is off Río de la Plata, between 34°S and 38°S. Hake arrive around May and stay through August, so this area can be considered the wintering grounds. During these months, hake concentrate along the outer shelf and continental slope.

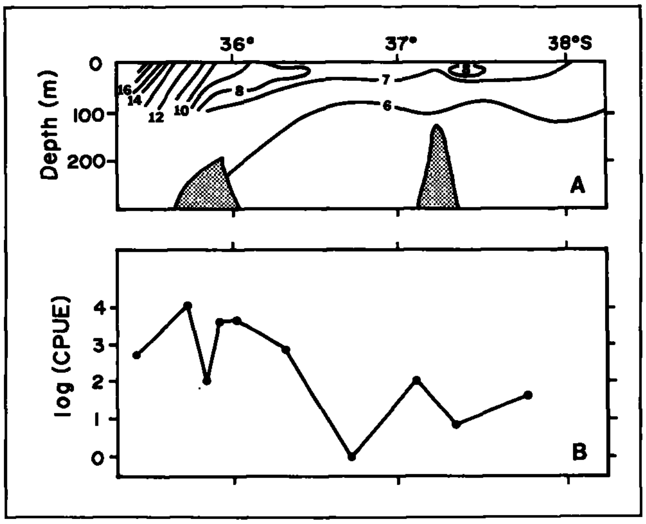

Figure 3
(*A*) Temperature section (°C) along the northern Argentine shelf break, July 1978. (*B*) Log of Argentine hake CPUE at fishing stations occupied at the same latitude as the hydrographic stations, but slightly shoreward. Date from the RV *Walther Herwig*.

Figure 3a shows a temperature section from hydrographic stations occupied along the shelf break, approximately between 35.5°S and 38°S, by the RV *Walther Herwig* in July 1978. The tightening of the isotherms in the northern part of the section (at about 36°S) indicates the confluence of the Malvinas Current, which flows northward carrying nutrient-rich subantarctic waters, and the subtropical waters of the southward-flowing Brazil Current (Olson et al. 1988). Figure 3b shows hake CPUEs in fishing stations occupied at the same latitudes as the hydrographic stations, but slightly shoreward. The highest densities of hake occurred near the Brazil-Malvinas confluence.

By the end of winter (September), a southward movement begins, accompanied by a corresponding inshore migration to shallower waters (Christiansen and Cousseau 1971, Bellisio et al. 1978). During the southward migration, fishing effort is widely scattered and CPUE values are relatively homogeneous throughout the shelf. This suggests a spatial dispersion of hake, which is not observed during the northward leg of the migration (Otero 1986).

The southward migration is associated with a movement towards spawning grounds. Mature female hake can be found year-round (Christiansen and Cousseau 1971), but most of the reproductive activity takes place in spring and summer (Ciechomski et al. 1979b). October and November are months of active spawning for at least some part of the stock(s). Commercial fishery statistics do not allow any conclusions on reproductive status, as only the weight of fish caught is reported.

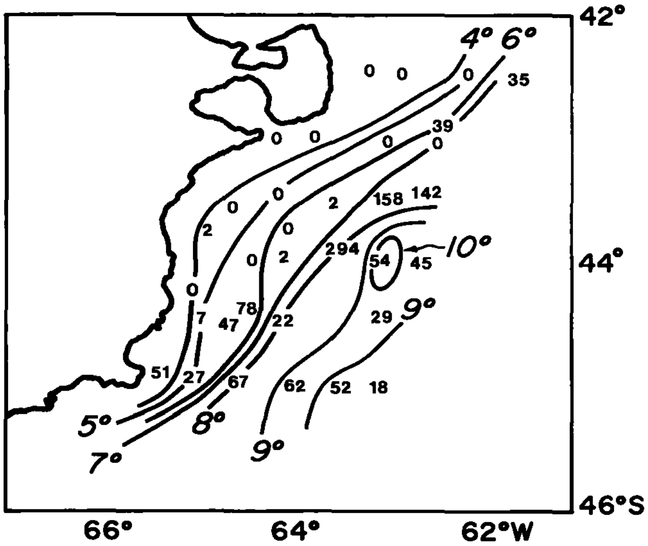

Figure 4

Argentine hake CPUEs (in hundreds of kg/hour) in the southern spawning area, south of Península de Valdés, Argentina, December 1978. Isolines correspond to surface-to-bottom temperature difference (°C), an indicator of water-column stratification; small values indicate well-mixed conditions.

I therefore examined data from egg and larval surveys carried out in early spring and summer of 1978 (Ciechomski et al. 1979b). Ciechomski and Sánchez (1983) established a well-defined relation between egg densities and corresponding adult concentrations.

In early spring (October through mid-November), there are two distinct centers of hake spawning: the northern catch between 36°S and 39°S and the southern between 42°S and 44°S, in waters <100 m deep (Ciechomski et al. 1979b). It is not clear what proportion of the fish spawn in each center, and whether fish that spawned in the northern center continue migrating south or, instead, move directly offshore.

Later in the season (December–January), several surveys showed that the area 42-47°S becomes the main spawning region. The largest concentrations of hake eggs and larvae in December 1978 were found in shallow waters at 44°S (Ciechomski et al. 1979b). Figure 4 displays the hake CPUEs obtained in the spawning area south of Península de Valdés, during cruise 9 (December 1978) of the *Shinkai Maru.*

In this area, features known as tidal fronts have been described by Carreto et al. (1986) and Glorioso (1987). The fronts separate stably-stratified waters offshore from well-mixed waters inshore. Vertical stratification is generated by surface heating; the well-mixed zone, on the other hand, results from stirring by strong tidal currents and winds (Carreto et al. 1986).

Water column stratification can be described by surface-to-bottom temperature differences, plotted on Figure 4. However, the transition from a well-mixed to a stratified regime and, thus, the location of the tidal front, are not apparent in this figure: temperature differences are >4°C, except in very shallow regions. This may have been due to the development of a shallow thermocline (~10 m) in inshore waters following a few days of calm weather. The location of the front is indicated instead by the transition from a shallow to a deeper (~35 m) thermocline (data not shown) which occurred in the vicinity of water column temperature differences of 7-8°C, as depicted in Figure 4. Highest hake CPUEs were observed near this transition; in contrast, hake CPUEs inshore of the front were very low.

The last portion of the migration, which closes the circuit, is the northward movement. This stage begins in February and lasts through May–June, when hake reach the wintering grounds. Fishing-effort maps suggest that the fish move north and across the shelf up to 40°S during February, and then continue northwards along the shelf break.

Spatial statistics

The spatial statistics are intended to represent "centers of mass" of the distributions of fishing effort or hake relative abundance during each month. Due to the uncertainty in effort location reports in 1979, the centers of fishing effort and hake CPUE are shown only for 1978 (Fig. 5).

The average positions of CPUE and effort showed cyclical north-south and east-west movements during a year. The monthly centers of CPUE and effort were quite similar, implying coincidence in the spatial distributions of fishing effort and apparent hake abundance. This suggests that the fleet was successful in locating dense aggregations of hake and lends confidence to the use of fishing-effort data to follow the commercial densities of migrating hake.

The multiple centers of effort in December, January, and February may be related to the existence of separate spawning groups of hake. On the other hand, the two centroids may merely reflect operational tactics of the fleet; although effort has been standardized to take into account differences in catching power, smaller vessels may lack the endurance or hold capacity required for a trip to the southern spawning grounds. Alternatively, fishermen may perceive that the catch rates in the northern and southern grounds are not so different as to make the longer trip worthwhile.

Speed of hake migration

Distances between monthly centers of effort and estimated speeds of migration are shown in Table 1. There was a bimodality in estimated displacement speeds throughout the year; the two modes corresponded,

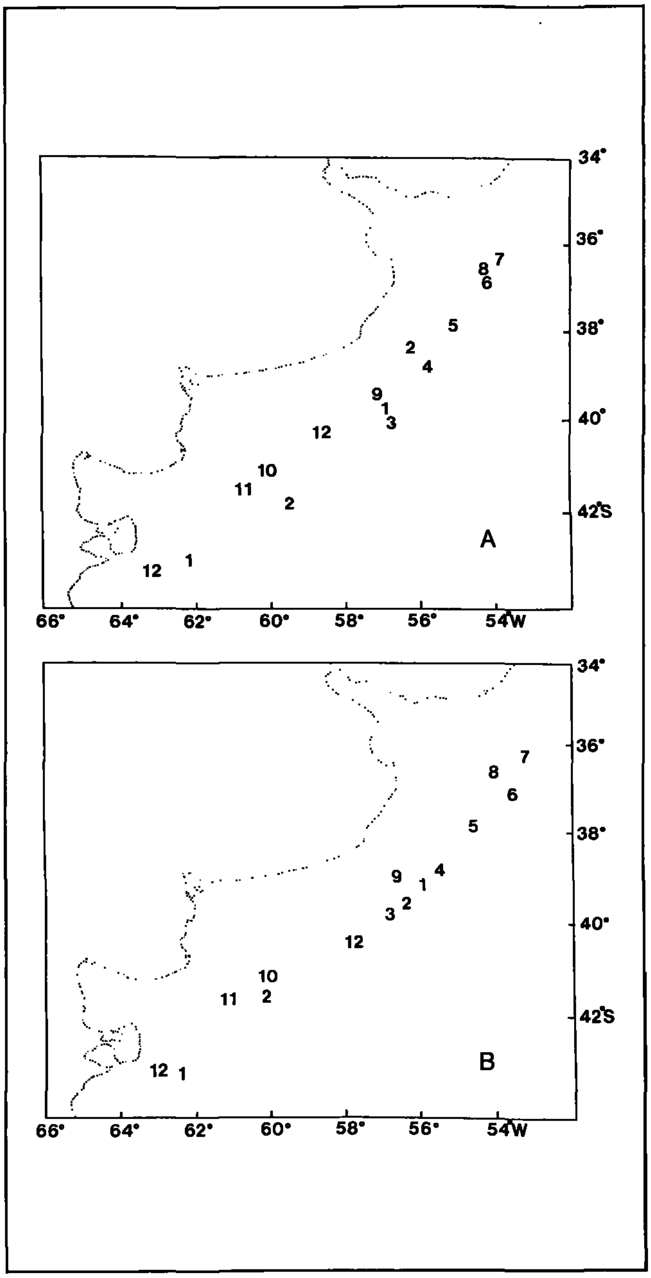

Figure 5

Monthly weighted latitude and longitude means of (a) fishing effort and (b) Argentine hake CPUE in southwestern Atlantic Ocean, computed from 1978 commercial fishery statistics. Numbers indicate months.

Table 1

Distance between consecutive monthly centers of fishing effort in southwestern Atlantic Ocean during 1978 and Argentine hake swimming speeds required to cover those distances in 30 days. When two centers existed in a month, they were indicated as northern (N) and southern (S). Segments marked with an asterisk are considered to be inconsistent with the migratory pattern of hake.

Segment	Distance (km)	Speed required	
		m/sec	km/day
Jan(N)-Feb(N)	128	0.05	4.3
(*) Jan(N)-Feb(S)	297	0.11	9.9
(*) Jan(S)-Feb(N)	636	0.25	21.2
Jan(S)-Feb(S)	244	0.09	8.1
Feb(N)-Mar	144	0.06	4.8
Feb(S)-Mar	276	0.11	9.2
Mar-Apr	131	0.05	4.4
Apr-May	99	0.04	3.3
May-June	122	0.05	4.1
June-July	48	0.02	1.6
July-Aug	37	0.01	1.2
Aug-Sep	351	0.13	11.7
Sep-Oct	285	0.11	9.5
Oct-Nov	49	0.02	1.6
Nov-Dec(N)	188	0.07	6.3
Nov-Dec(S)	264	0.10	8.8

respectively, to speeds of 6–11 km/day and 1–4 km/day (Table 1). Higher speeds, obviously, are associated with periods of active migration.

The estimated speeds of the northward and southward (i.e., feeding and spawning) migrations were similar. Estimated speeds during the most active periods of southward displacement were 11.7 km/day (August–September) and 9.5 km/day (September–October). The latter value was only slightly higher than that computed for the active northward migration, 9.2 km/day (February–March). If a significant difference in southward vs. northward migrating speed exists, it probably cannot be detected using coarse fishery statistics.

The migration speeds estimated above must be considered only as a first approximation, but they generally agree with values reported for a similar species. Francis (1983) estimated swimming speeds for Pacific hake *Merluccius productus* of different ages based on timing of sequential appearance at different latitudes. His estimated speeds for the age classes 4–7, those predominant in Argentine hake catches, range from 9 to 12 km/day. Ermakov (1974; cited in Bailey et al. 1982) concluded from direct observation of a school that the northward migration of Pacific hake is at speeds of 5–11 km/day.

Interannual variability in the migratory pattern of hake

Cumulative time density of fishing effort is shown in Figure 6 for three regions: Buenos Aires slope north (region 1), Patagonian slope north (region 4), and southern spawning grounds (region 8). The values shown in the figures for each month represent the proportion of yearly regional effort accumulated up to the end of that month. Monthly values are joined by line segments in the figures: segments with steep slopes are associated with a relatively large proportion of total regional effort. Conversely, if little or no effort took place within a month, the corresponding segment will be nearly horizontal.

The interpretation of the cumulative time density curves is related to the pattern of hake migration. For example, effort started to accumulate in region 1 (Fig. 6a) around April or May, when fish first arrived in this area on the northward leg of their migration. The S-shaped 1978 curve indicated that there was a single peak in the deployment of effort during winter months (May–August). In contrast, in 1979 most of the effort was deployed between March and June, with a secondary peak in September–October.

In region 4 (Fig. 6b), effort accumulated rapidly during February, March, and April of 1978, as the hake were migrating northwards along the shelf break. Afterwards, effort decreased greatly. In 1979, the initial effort was much like the previous year's, but it tapered off until June, July, and, particularly, August (winter). Effort in winter months was not observed in 1978.

In region 8 (Fig. 6c), the effort patterns were remarkably similar for both years. The curves were flat between March and September, as both the fish and the fleet were absent from the region. During October, November, and December the spawners arrived in the area and fishing effort accumulated rapidly.

Interannual differences between cumulative time density patterns were statistically analyzed using the Kolmogorov-Smirnov (K-S) two-sample test. Because of the large N values (the annual total number of hours trawled in a region), all the K-S tests were significant (see Rugolo 1984), including those for regions not shown. As a consequence, the discussion will focus on regions 1 and 4, where the patterns appeared to differ most between the two years.

From the patterns in regions 1 and 4, it appears that the fishing fleet (and, thus, hake) was located further south in 1979 than in 1978. The spatial statistics of fishing effort also reflect a more southerly deployment of effort in 1979. The latitudinal means of fishing effort for July and August 1978 were, respectively, 36.4°S and 36.6°S; the corresponding values for 1979 were 38.2°S and 40.2°S. That is, the "center of mass" of fishing effort in the winter of 1979 was located 2–4 degrees of latitude further south along the shelf break than in 1978. The changes in hake distribution may reflect interannual differences in environmental conditions.

The northernmost extension of the hake feeding migration, reached during June–August, is associated with the Brazil-Malvinas confluence. The confluence is an effective barrier for adult hake of commercial size: aggregations of hake found north of it are mainly formed by juveniles (Rojo and Silvosa 1969). Olson et al. (1988) showed considerable fluctuations in the

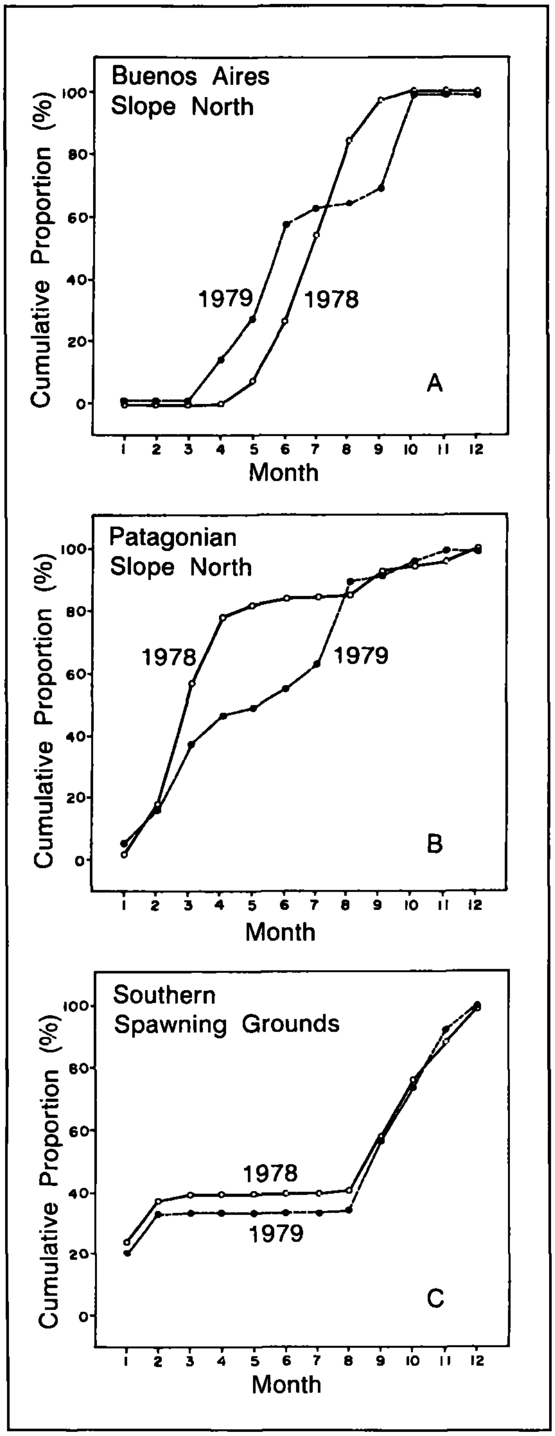

Figure 6
Cumulative time densities for (*A*) Buenos Aires slope north (region 1), (*B*) Patagonian slope north (region 4) and (*C*) southern spawning grounds (region 8). Location of regions is shown in Figure 1.

latitude of the Brazil-Malvinas confluence along the shelf break. Shifts in the position of the confluence plausibly could have been responsible for the differences in hake distribution between 1978 and 1979.

Hydrographic stations occupied by the RV *Walther Herwig* during July 1978 placed the Brazil-Malvinas confluence along the shelf break at about 36°S. In August 1978, the confluence must have been located north of 37°S, as temperatures characteristic of Brazil Current waters were not observed during a cruise carried out by the RV *Shinkai Maru* that reached approximately that latitude (data not shown).

No hydrographic data were available to locate the confluence in July–August 1979. Instead, I used weekly GOSSTCOMP (global ocean sea surface temperature computation) charts for the period 3 July– 28 August 1979. The charts were produced from satellite data by the U.S. National Oceanic and Atmospheric Administration (Brower et al. 1976). The 10°C and 12°C surface isotherms were considered to represent the Brazil-Malvinas confluence at this time of the year. The approximate latitudes at which those isotherms occurred along the shelf break are displayed in Figure 7.

In early July 1979, the confluence was located at about 37°S, only slightly further south than in July 1978. During the last 2 weeks of July 1979, however, it moved to the south, reaching about 42°S by the end of the month. During August 1979, the confluence was generally located around 40°S. The deployment of fishing effort during July–August 1979 coincided roughly with the confluence locations deduced from the GOSSTCOMP charts. This seems to support the hypothesis linking shifts in the position of the Brazil-Malvinas confluence and hake distribution in 1978 and 1979.

Discussion

Feeding migration

The need to find an adequate food supply for maintenance, growth, and reproduction may have contributed to shape the migratory pattern of Argentine hake. Adult hake feed actively after spawning (Hart 1946). The postspawning offshore migration of adults towards the shelf break, then, may correspond to a search for abundant food sources.

The western edge of the Malvinas Current, from about 40°S to its confluence with the Brazil Current, plays an important role in the northward migration of hake, as the fish are closely associated with it for 5–6 months of the year. The boundary between shelf and Malvinas Current waters can be characterized as a shelfbreak front. Shelfbreak fronts elsewhere have been associated with high biological productivity and fishing intensity (Fournier et al. 1979).

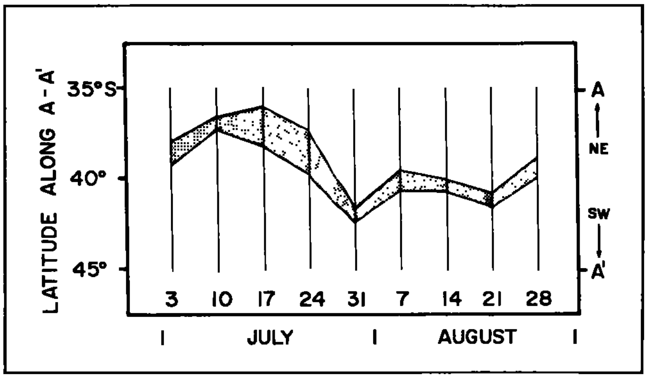

Figure 7
Approximate latitude of the Brazil and Malvinas currents confluence along the shelf break, July–August 1979, derived from GOSTCOMP charts. Each vertical line corresponds to a weekly sea-surface temperature chart. Shaded area represents projection of the 10- and 12°C isotherms along the shelf break, assumed to represent the position of the confluence.

The high productivity of the Malvinas front has been described from ship data (Hubold 1980a,b and references therein). More recently, remote sensing techniques have confirmed this feature: images collected by the Coastal Zone Color Scanner (CZCS) were used to monitor nearsurface concentrations of phytoplankton pigments and, indirectly, phytoplankton biomass. High phytoplankton concentrations occurred along the shelfbreak through spring and summer; in contrast, phytoplankton biomass across most of the shelf decreased rapidly following the late September–early October spring bloom. The shelfbreak, therefore, possibly represents one of the few places where forage is abundant during the summer, following the hake's spawning.

After a second bloom ends on the shelf in the fall (late March–early April), phytoplankton biomass along the shelfbreak remains high into late April. This may in turn support elevated zooplankton concentrations in subsequent winter months (Hubold 1980b), although at that time phytoplankton biomass is low.

The large phytoplankton biomass along the shelf break is probably the result of enhanced supply of nutrient-rich Malvinas Current waters into the euphotic zone, which could happen through a variety of processes. Small-scale eddies along the edge of the Malvinas Current may upwell nutrient-rich waters. This has been shown to occur along the edge of the Gulf Stream, resulting in an increase in phytoplankton and zooplankton biomasses (Paffenhöffer et al. 1984). Dickson et al. (1980) suggested that the interaction between coastally trapped waves propagating along the slope and bottom topography at the shelfbreak could enhance upwelling. The generation of internal tides at the shelfbreak, coupled with episodic wind stress, may increase vertical mixing, again injecting nutrients into the upper layers (Mazé et al. 1986). Additionally, the tilt of the isopycnals or the interleaving of water masses at the front would enhance vertical stability, retaining phytoplankton cells in the euphotic zone (Fournier et al. 1979).

The increased phytoplankton biomass along the shelf break supports large concentrations of zooplankton (Hubold 1980a); species on which pelagic fish feed (e.g., calanoid copepods) are very abundant (Carreto et al. 1981a, b). Species from higher trophic levels also aggregate at the front.

The distribution pattern of anchoita *Engraulis anchoita*, an extremely important prey for hake, is closely associated with the shelfbreak front (Brandhorst et al. 1971). While hake and anchoita coincidentally migrate offshore and then northward along the slope in autumn, the former actively feed on the latter (Ciechomski and Sánchez 1983).

During the northward migration, other components may appear in the hake's diet, such as myctophids associated with the Malvinas Current (e.g., *Gymnoscopelus* spp., *Lampanyctus* spp., and *Myctophum* spp.) and shortfin squid *Illex argentinus* (Cordo 1981). Dense concentrations of shortfin squid occur along the shelfbreak in late fall (Otero et al. 1981). Squid is increasingly found in the stomachs of medium and large hakes between April and July (Angelescu and Cousseau 1969, Cordo 1981). Given their high food assimilation efficiency (Caddy 1983), squid probably play an important ecological role in rapidly transferring energy from lower trophic levels to hake.

When hake reach the northernmost end of their feeding migration in winter, they have access to a large abundance of prey from a variety of closely located environments. In addition to the species found along the shelfbreak, they may feed on anchoita wintering in midshelf waters or on subtropical myctophids from Brazil Current waters. Further south or inshore, in contrast, pelagic fish become rare and the overall abundance of prey decreases rapidly (Angelescu and Cousseau 1969).

Spawning migration

The present migratory pattern of hake may have evolved to maximize chances of reproductive, as well as feeding, success. Starvation is a major source of larval mortality for most fish species. The choice of spawning sites with adequate concentrations and size ranges of larval food may have a great influence on survival. Hake larvae feed almost exclusively on zooplankton, particularly small calanoid copepods (Ciechomski and Weiss 1974).

Regional shifts in hake spawning activity may be related to the seasonal pattern of productivity along the shelf. The phytoplankton spring bloom begins in the north and progresses southward (Carreto et al. 1981a). The spawning activity between 36°S and 38°S in early spring, then, may be tied to increased zooplankton availability resulting from the bloom. However, satellite imagery shows that postbloom phytoplankton biomass here remains low throughout late spring and summer and apparently does not support an extended spawning season. Later in the season, the bulk of the spawning activity takes place between 42°S and 44°S, where production possibly may continue during the summer because of the presence of tidal fronts.

The tidal fronts appear to be associated with enhanced phytoplankton biomass: Carreto et al. (1981a) observed integrated chlorophyll concentrations >200 mg/m^2 at the beginning of October. The increased biomass may be due to enhanced nutrient supply by horizontal mixing from the mixed side or by vertical mixing through the pycnocline. Carreto et al. (1986) found high surface concentrations of nitrates (>6 μm) on the mixed side.

The existence of the tidal fronts has only recently been noticed and, consequently, there is relatively little information on their biological productivity. Nevertheless, high concentrations of zooplankton (expressed in dry weight) have been reported along the fronts (Angelescu and Prenski 1987). There is additional indirect evidence for the relatively high productivity of these features: hake larvae in this area are found to be in an excellent nutritional state, better than elsewhere on the shelf (R. Sánchez, INIDEP, C.C. 175, Playa Grande, Mar del Plata, Argentina, pers. commun., Feb. 1989). Additionally, adult hake find abundant anchoita and squid in the vicinity of the fronts (Angelescu and Prenski 1987).

The tidal fronts occur throughout the summer, for as long as the offshore side of the front remains stratified. Satellite imagery shows that this area, together with the shelfbreak, are the only places where near-surface phytoplankton biomass remains high throughout the summer. The integrated spring–summer production of the tidal fronts area, therefore, may possibly be higher than in most parts of the shelf, although this requires confirmation.

Another factor relevant to the selection of a spawning site is the subsequent transport of eggs and larvae to (or, alternatively, their retention within) areas suitable for further development. Argentine hake show a wide temporal and spatial spawning range: hake eggs are found on the shelf practically year-round. Nevertheless, the gonads do not mature more than once during the main spawning period of spring–summer (Christiansen and Cousseau 1971), suggesting that a number of groups of spawners release eggs throughout a large area and an extended time interval. Argentine hake exhibit a ubiquitous spawning strategy throughout the shelf and, therefore, do not appear to be dependent on larval drift and retention conditions. A possible exception is the shelfbreak area: despite its importance in supporting abundant forage supplies, this area is not a suitable spawning location. Eggs and larvae spawned along the shelfbreak would most likely be carried offshore.

The circulation pattern of the Argentine shelf, as it contributes to larval drift or retention, has not been described in adequate detail. Circulation gyres or topographical features that may contribute to the separation of hake spawning groups on the Argentine shelf are not apparent. If different spawning groups exist, the specificity of their place and time of spawning or, equivalently, the degree of mixing among them, remains unclear.

This work identified apparent differences in the migratory pattern of hake between 1978 and 1979, which were tied to the location of the confluence of the Brazil and Malvinas currents along the shelfbreak. Sosa et al. (1976) mention 60–100 mile changes in Argentine hake distribution associated with wind-induced short-term fluctuations in the position of the confluence. Repeated monitoring of the confluence location through satellite imagery (cf. Olson et al. 1988) would make it possible to further investigate this association.

In summary, the cyclic migration of commercial densities of Argentine hake was roughly described using data from commercial fishing operations. The migratory pattern has evolved to maximize the chances of successful spawning, while ensuring an adequate food supply. During their migratory cycle, hake take advantage of productive ocean features.

A number of issues remain unclear, such as the existence of different spawning groups and the degree of mixing among them. There is little information on the recruitment variability in Argentine hake, so one cannot speculate on the relationship between migratory pattern and recruitment success. The circulation on the Argentine shelf and its influence on larval drift or retention requires much study. Finally, the continued availability of prey for hake larvae throughout the summer in the tidal-fronts environment (which would lead to the bulk of spawning taking place there) needs to be confirmed.

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