

OBSERVATIONS ON THE SPAWNING DISTRIBUTION AND BIOLOGY OF OFFSHORE PACIFIC HAKE (*MERLUCCIUS PRODUCTUS*)

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ABSTRACT

Two cruises were conducted in February 1990 and 1991 to examine the distribution and biology of spawning offshore Pacific hake. The fish spawned during winter, in the southern portion of their range, i.e., south of Cape Mendocino, and offshore of the shelf break over bottom depths exceeding 1,000 m. In 1990, the schools were 110–167 km (60–90 nmi) offshore in midwater depths ranging from 140 to 240 m, over bottom depths of 3,600 and 4,200 m. In 1991 there were six schools containing spawning hake from 35° to 40.5°N, spanning 720 km (390 nmi). There were more males than females in the spawning schools. In 1991 some schools of predominantly post-spawners were encountered; they tended to be inshore of the spawners and were mainly female. The most surprising of the results was the presence of a north-south cline in biological parameters during spawning similar to the one occurring in summer. We discuss the implications of our results for the present migration hypothesis.

INTRODUCTION

The offshore Pacific hake stock ranges from Baja California to southeastern Alaska. It is the most abundant of three stocks of *Merluccius productus* in the north-eastern Pacific Ocean that support international, joint-venture, and domestic fisheries in Canadian and U.S. waters. In total, these fisheries have averaged 190,000 metric tons (t) annually, from 1966 to 1995.

The basic life history was first described by Alverson and Larkins (1969) from year-round observations of Russian and U.S. scientists participating in and assessing the international fishery during the 1960s. They reported that hake migrate annually between spawning grounds (located from central California to Baja California) and summer feeding grounds (located from central Oregon to northern Vancouver Island). During the summer feeding period adult hake are concentrated in large midwater feeding aggregations, centered on the shelf break from central Oregon to northern Vancouver Island (figure 1). There is a latitudinal cline in average age, mean size, and sex ratio; older, larger, and predominantly female fish are found farther north. Spawning, between January and March, centers on the California Bight, seaward of the shelf break as far offshore as 925 km (500

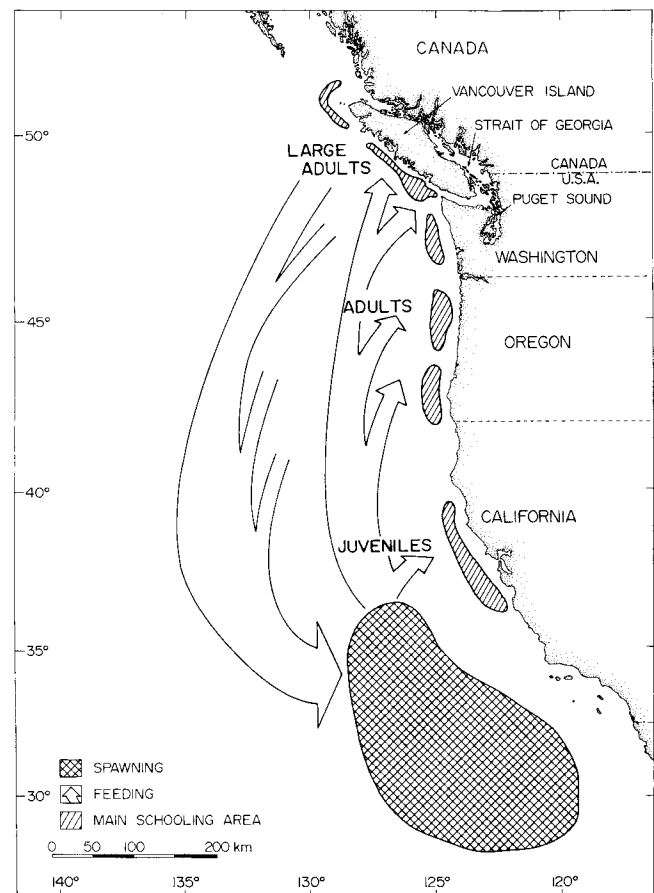


Figure 1. Migration pattern of Pacific hake (modified from Bailey et al. 1982).

nmi; figure 1). Juveniles (<3 years) frequent shelf locations in southern and central California and gradually migrate north and recruit to the main stock.

Alverson and Larkins (1969) synthesized these observations into a migration hypothesis:

1. The adult segment of the population exhibits a large-scale north-south movement: north during spring and summer, and south during late fall and winter.
2. Northward migration of adults is accompanied by movement towards shore and into shallower water.
3. The southward migration is accompanied by movement into deeper water and seaward.

4. Spawning occurs during the winter when hake occupy the southern portion of their geographic range.

The hypothesis was subsequently modified by Francis (1983), who introduced a swimming-speed argument, modified from Ware (1978), to explain the latitudinal cline in age- and size-related parameters. Since then the research has focused on the fishery, and related assessment surveys have been conducted during the summer. In particular, the National Marine Fisheries Service (NMFS) has conducted hydroacoustic surveys triennially since 1977 (Dark et al. 1980; Nelson and Dark 1985; Dark and Wilkins 1994), and the Department of Fisheries and Oceans (DFO) has conducted annual surveys of the Canadian zone since 1990 (e.g., Saunders et al. 1992). Spawning distributions have been inferred from CalCOFI surveys of egg and larval distributions (Bailey 1980, 1981a, 1982; Bailey et al. 1982; Hollowed 1992), and there have been no further direct observations of winter spawning distribution and biology.

Direct observations are desirable for testing the migration hypothesis. Consistent with the hypothesis, the current assessment model assumes that all the hake assessed during the summer return to southern California and contribute equally to spawning success. Harvest strategies have been developed on the basis of maintaining a specific spawner biomass. If the hypothesis is not correct then the basis for conserving the stock may be flawed.

To begin collecting data to test the hypothesis, two cruises were conducted in February 1990 and 1991 to examine the distribution and biology of spawning offshore hake. In this paper we present the results of the cruises, and discuss their implications to the current migration hypothesis.

METHODS

During both surveys a zigzag search pattern was used to locate hake schools in the area bounded on the north by 48°N, on the south by the U.S.–Mexico boundary (approximately 31°N), on the east by the 200-m isobath, and on the west by 130°W. The seaward boundary extended beyond any previous catch of spawning hake. Hull-mounted 38- and 50-kHz Simrad sounders were monitored continuously for midwater echosign. The survey was conducted 24 hours per day, since hake schools exhibit minimal diel behavior during spawning (McFarlane and Beamish 1985). The survey was conducted from the CSS *W. E. Ricker*, a 58-m, 2,500-hp research stern trawler.

When schools were located they were sampled with midwater trawl gear. In 1990, the trawl gear consisted of a Canadian Diamond 5 midwater mesh trawl with a 10-m vertical opening and 3.8-cm cod-end mesh, a pair of 4-m Superkrub midwater trawl doors, and 55-m sweep

wires with 167-kg chain weights. In 1991 we used a Canadian Diamond 7 midwater mesh trawl with 13.5-m vertical opening, 3.8-cm cod-end mesh, a pair of 5-m Superkrub midwater trawl doors, and 80-m sweeps with 300-kg chain weights.

Total catches were separated by species and weighed to the nearest kilogram. Random samples of hake fork length (cm), sex, maturity, and otoliths (for subsequent ageing) were collected. Otoliths were stored in a 50/50 glycerine/freshwater solution with thymol. Maturity states were visually assessed according to the criteria outlined in Weir et al. 1978. Stomach contents were identified to the lowest possible taxon, and the volume of each item was visually estimated to the nearest 0.5 cc. Hake otolith cross sections were aged with the break and burn method (Chilton and Beamish 1982).

We used the methods outlined in Kabata and Whitaker (1981, 1986) to assess the prevalence of infection with *Kudoa paniformes* and *Kudoa thrypsites*.

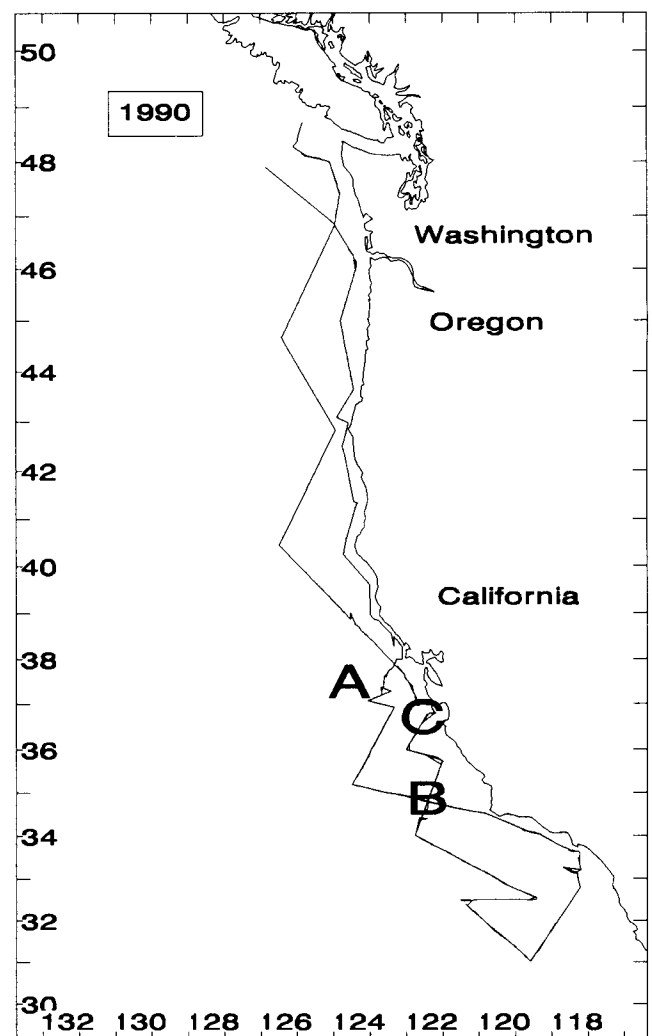


Figure 2. Tracklines sounded and Pacific hake schools (letters) encountered during the February 13–March 4, 1990, survey.

TABLE 1
 Pacific Hake School Descriptions, by Year

School	Location	School dimensions (km)	Date fished	Fishing set	School depth (m)	Capture depth (m) of headrope
1990						
A	93 km SW of Pt. Reyes 37.3°N, 123.7°W Bottom depth ~3,600 m	6 × 9 = 54 km ²	2/17	1	140–180	160
				2	140–180	165
B	200 km W of Pt. Conception 34.9°N, 122.9°W Bottom depth ~4,200 m	11 × 17 = 187 km ²	2/19	6	220–240	220–232
				7	200–230	200–230
				8	190–205	200–220
1991						
A	100 km W of Cape Mendocino 40.8°N, 125.7°W Bottom depth ~2,962 m	4.1 × 4.1 = 16.8 km ²	2/25	12	120–180	190–200
B	165 km W of Pt. Reyes 37.8°N, 124.9°W Bottom depth ~2,225 m	9.1 × 2.2 = 20.0 km ²	2/24	11	180–200	200
C	NW Monterey Bay 37.0°N, 122.6°W Bottom depth 460 m	N/A	2/12	2 & 3	120–140	140–150
D	130 km W of Monterey 36.5°N, 123.5°W Bottom depth ~3,570 m	5.5 × 6.1 = 33.6 km ²	2/21	10	280–300	350–380
E	130 km NW of Pt. Conception 34.9°N, 122.5°W Bottom depth ~4,500 m	2.4 × 9.8 = 23.5 km ²	2/13	4	220–300	240–300
				5	200–280	250–280
F	60 km W of Cape San Martin (NW of Pt. Conception) 35.5°N, 122.0°W Bottom depth ~1,090 m	7.6 × 9.8 = 74.5 km ²	2/20	8	280–350	350
				9	180–310	350
G	150 km SW of Pt. Conception 33.2°N, 121.4°W Bottom depth ~3,800 m	31.6 × 14.8 = 467.7 km ²	2/15	6	380–400	380–450

RESULTS

Cruises were conducted from February 13 to March 4, 1990, and from February 7 to 28, 1991. In 1990, two large schools were encountered 280 km (150 nmi) apart, one at 37°N (school A) and another at 35°N (school B; figure 2). School C contained some spawners but primarily juveniles. The schools were 110–170 km (60–90 nmi) offshore in midwater depths ranging from 140 to 240 m, over bottom depths of 3,600 and 4,200 m (table 1). The thickness of the schools ranged from 10 to 50 m (figure 3).

In 1991 there were six schools containing spawning hake (schools A, B, D, E, F, and G in table 1 and figure 4) from 35° to 40.5°N, spanning 720 km (390 nmi). School C contained only juvenile fish. The depth of the spawners ranged from 120 to 300 m, and the schools were thinner (10–20 m) and less dense than in 1990 (table 1 and figure 5).

Maturity

In both years, the maturity condition of males was predominantly ripe-and-running and spent. The high-

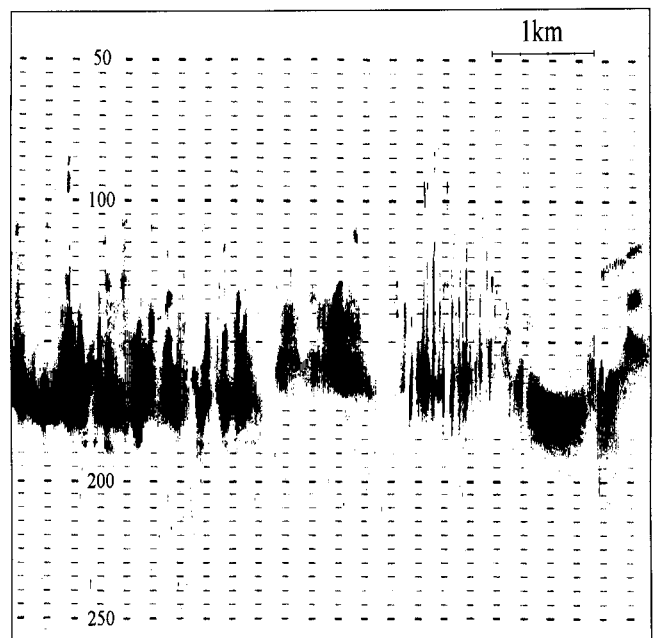


Figure 3. Echogram of spawning Pacific hake, school A, February 17, 1990. Depth in meters.

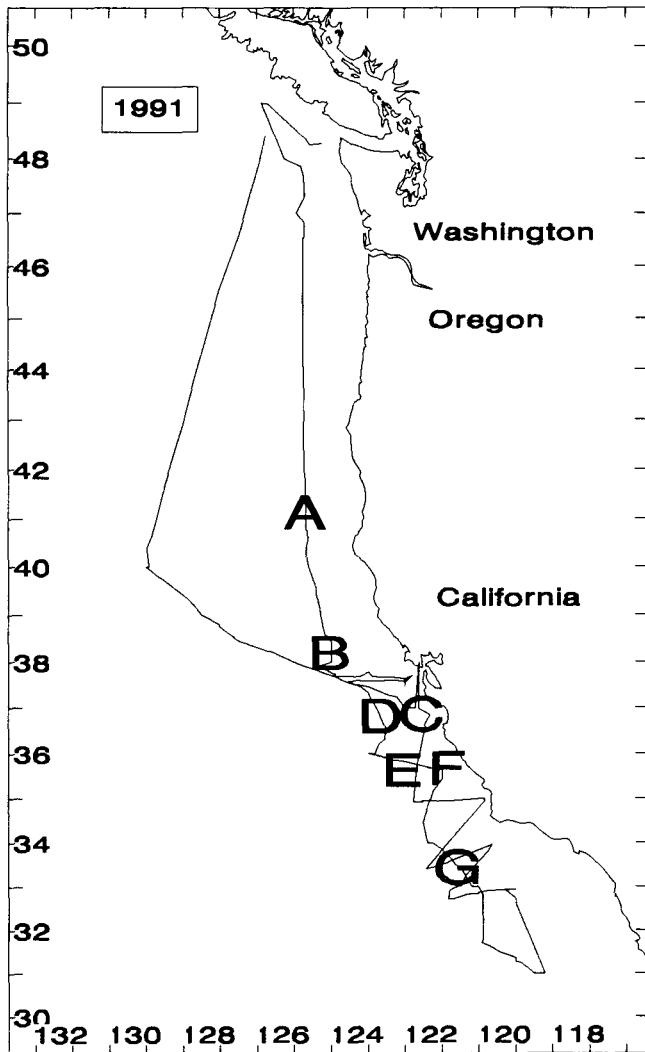


Figure 4. Tracklines sounded and Pacific hake schools (letters) encountered during the February 7–28, 1991, survey.

est proportion of females were either ripe or spent; fewer than 10 percent were actively spawning (ripe-and-running; figures 6, 7).

In 1990, the more northerly school contained a larger proportion of males and females in pre-spawning condition (figure 6), a trend that was less obvious in 1991 (figure 7). In 1991 some schools of predominantly post-spawners were encountered; they tended to be inshore of the spawners except for school G, the southernmost school (figure 7).

Sex Ratio

The sex ratio varied considerably among sets (table 2). Pacific hake from the Strait of Georgia are known to stratify by sex within spawning schools (McFarlane and Beamish 1985), and it is possible that this is a contributing factor. We were, however, unable to demonstrate this for the offshore hake because of their very strong div-

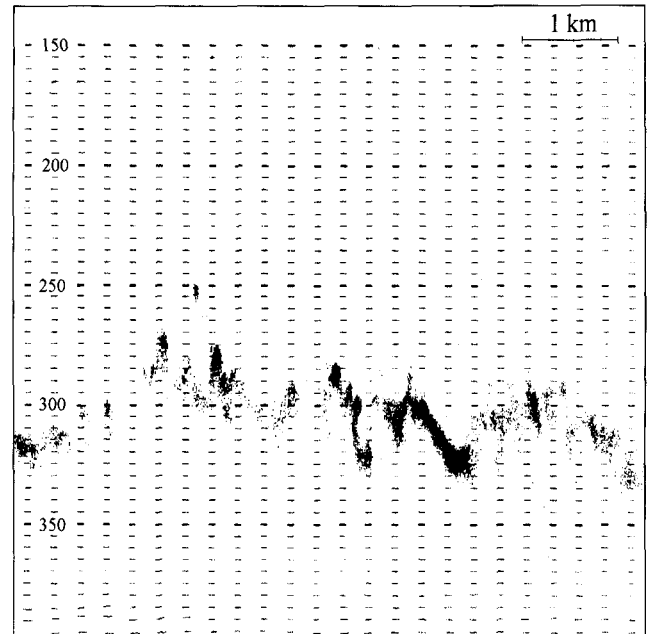


Figure 5. Echogram of spawning Pacific hake, school C, February 12, 1991. Depth in meters.

ing response to the vessel and trawl. This response made discrete depth sampling of the schools difficult.

Nevertheless, there was a clear difference between surveys. In 1990, the sex ratio of the spawning schools ranged from 10% to 28% females; in 1991, the range was much higher: 32%–55%. There is an indication that the proportion of females increases with latitude. At similar latitudes the inshore post-spawning school (F) had a much higher proportion of females than the offshore spawning school (E; table 2).

Age and Growth

The age compositions in both years were dominated by the strong 1980 and 1984 year classes (figure 8). In 1991, the percentage contribution of the older, 1981 year class as age 11's increased with latitude while the percentage of age 4's decreased with latitude.

The mean size of both males and females increased with latitude in 1991 (figure 9). Females increased from 45.4 cm at the southernmost point (school G) to 46.3 cm at the northernmost point (school A). Similarly, males increased from 44.0 cm to 45.5 cm. An ANOVA test of mean length by set found these differences to be significant ($P > .0001$) for both sexes.

Parasite Prevalence

The prevalence of infection with the two species of Kudoan parasites was examined from 50 fish samples collected from schools G, F, D, and A in 1991 (table 3). The proportion infected with *K. paniformes* decreased from south to north. The proportion infected with *K. thryssites*

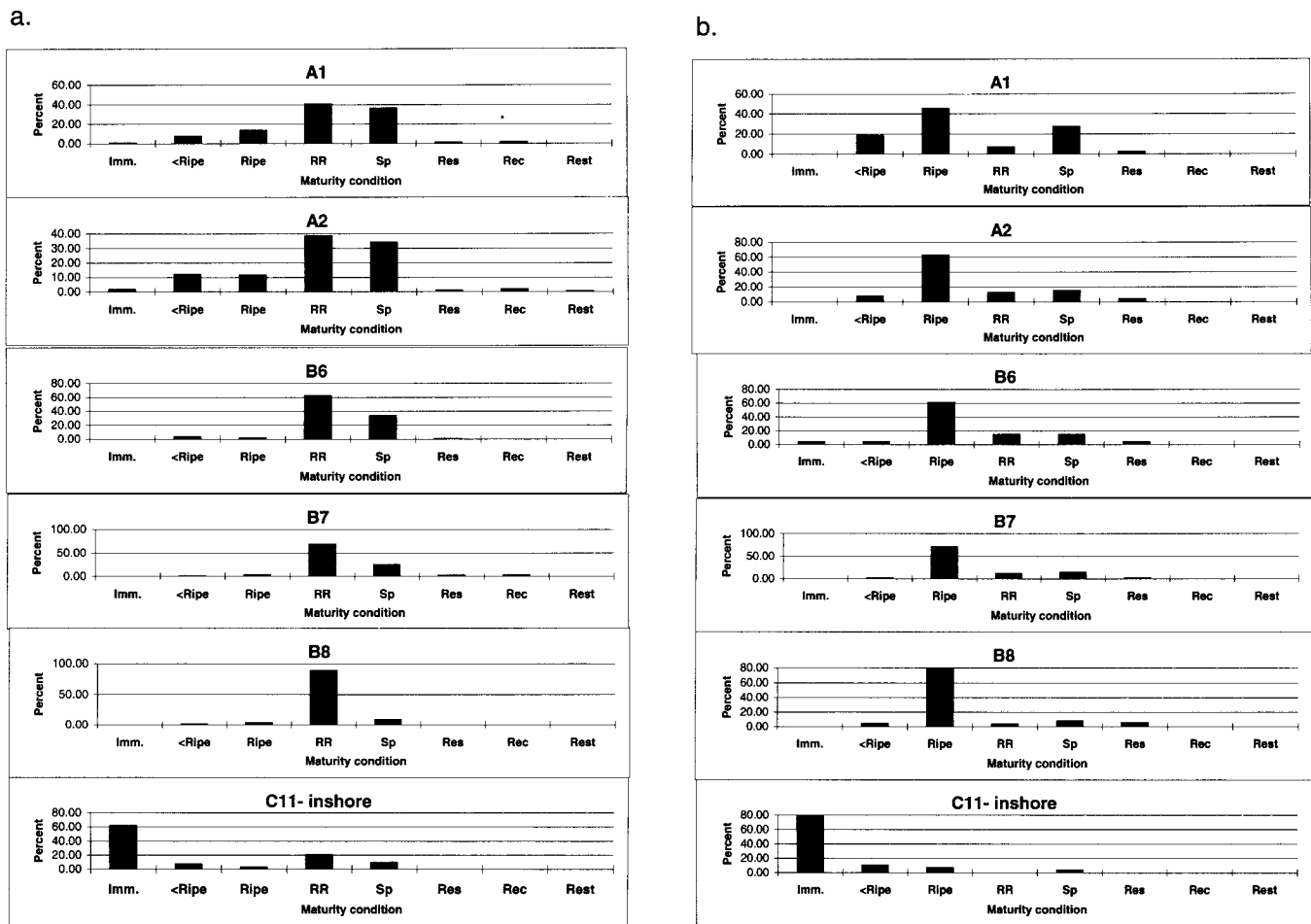


Figure 6. Percent frequency of maturity condition by fishing set, February 1990, for (a) males and (b) females. Maturity conditions as defined by Weir et al. (1978): Imm = immature, RR = ripe and running, Sp = spent, Res = resorbing, Rec = recovering, Rest = resting. Sets are listed by school (letters) and set (numbers).

increased over the three northerly sets but was elevated for the southernmost school.

Feeding

In general, the stomachs of hake captured from the spawning aggregations were empty or everted. In 1990, such stomachs constituted 97%–99% of those sampled. The few food items present consisted of euphasiids, squid, and a sipunculid. In 1991, the percentage of empty and everted stomachs decreased and the diet was more varied (table 4). The change is associated with the samples dominated by post-spawners, suggesting that they had resumed feeding (school G; table 4).

DISCUSSION

Spawning Distribution

These surveys represent the first capture of spawning offshore Pacific hake reported since 1982 (Stepanenko

and Zinovyeva 1982). Our results support the original hypotheses of Alverson and Larkins (1969). Spawning occurred during the winter, in the southern portion of the range, i.e., south of Cape Mendocino, and offshore of the shelf break over bottom depths exceeding 1,000 m (table 1). The offshore locations (60–165 km), depth of the schools (120–400 m), and timing of spawning (February; table 1) were similar to the few direct observations of offshore spawning hake summarized by Bailey et al. (1982).

The presence of fish in spawning condition off Cape Mendocino (40.5°N) extends the northern spawning boundary from that of previous studies which found spawners as far north as 38°N (Anonymous 1969; Ehrlich et al. 1980; Stepanenko 1981). This observation is consistent with larval distributions summarized by Bailey et al. (1982), who inferred that Cape Mendocino was the northern limit of spawning, and by Bailey (1980), who observed that Pacific hake spawning has moved farther

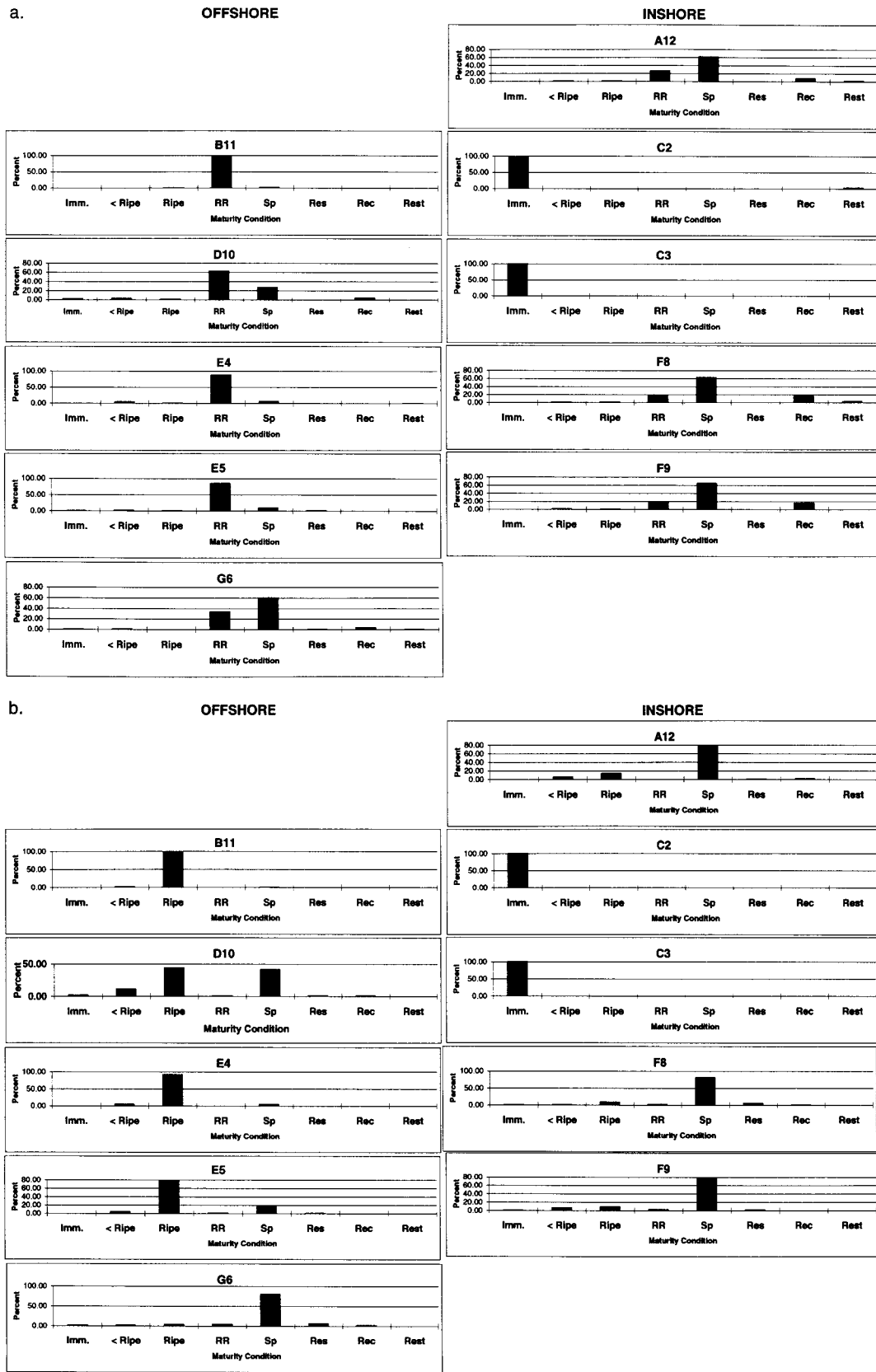


Figure 7. Percent frequency of maturity condition by fishing set, February 1991, for (a) males and (b) females. Maturity conditions as defined by Weir et al. (1978): Imm = immature, RR = ripe and running, Sp = spent, Res = resorbing, Rec = recovering, Rest = resting. Sets are listed by school (letters) and set (numbers) and are presented in latitudinal sequence from north (top) to south (bottom).

TABLE 2
 Percentage of Female Hake by Survey Year,
 Position Offshore, School, and Fishing Set

Offshore				Inshore			
School	Status	Set	Percentage	School	Status	Set	Percentage
1990							
A	Spawning	1	10%	C	Juveniles	9	40%
		2	28%				
B	Spawning	6	17%				
		7	14%				
		8	23%				
1991							
B	Spawning	11	55%	A	Post-spawning	12	57%
D	Spawning & Post-spawning	10	53%				
E	Spawning	4	32%	F	Post-spawning	8	57%
		5	36%			9	54%
G	Post-spawning	6	39%				

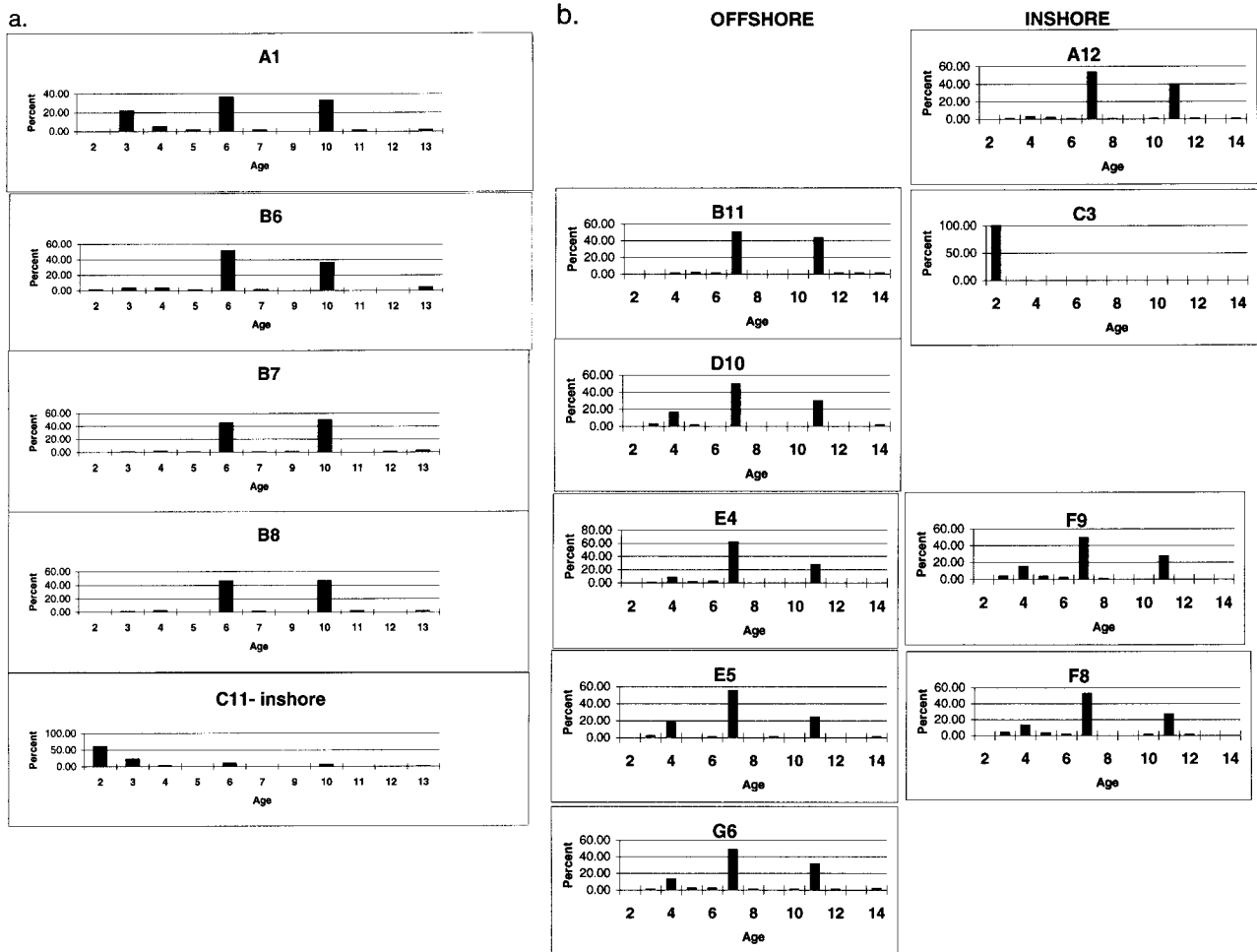


Figure 8. Percent age-frequency compositions of Pacific hake, by set, during February 1990 (a) and 1991 (b). Sets are listed by school (letters) and set (numbers) and are presented in latitudinal sequence from north (top) to south (bottom).

north since the 1950s, when the fish spawned only between Point Conception and southern Baja California.

Although we were unsuccessful in finding hake above Cape Mendocino and below Point Conception, there are several indications that we did not sample the entire

spawning population. CalCOFI surveys conducted during January, February, and April of both 1990 and 1991 found hake larvae throughout the California Bight (Paul Smith, pers. comm.), indicating unsampled spawners south of Point Conception.

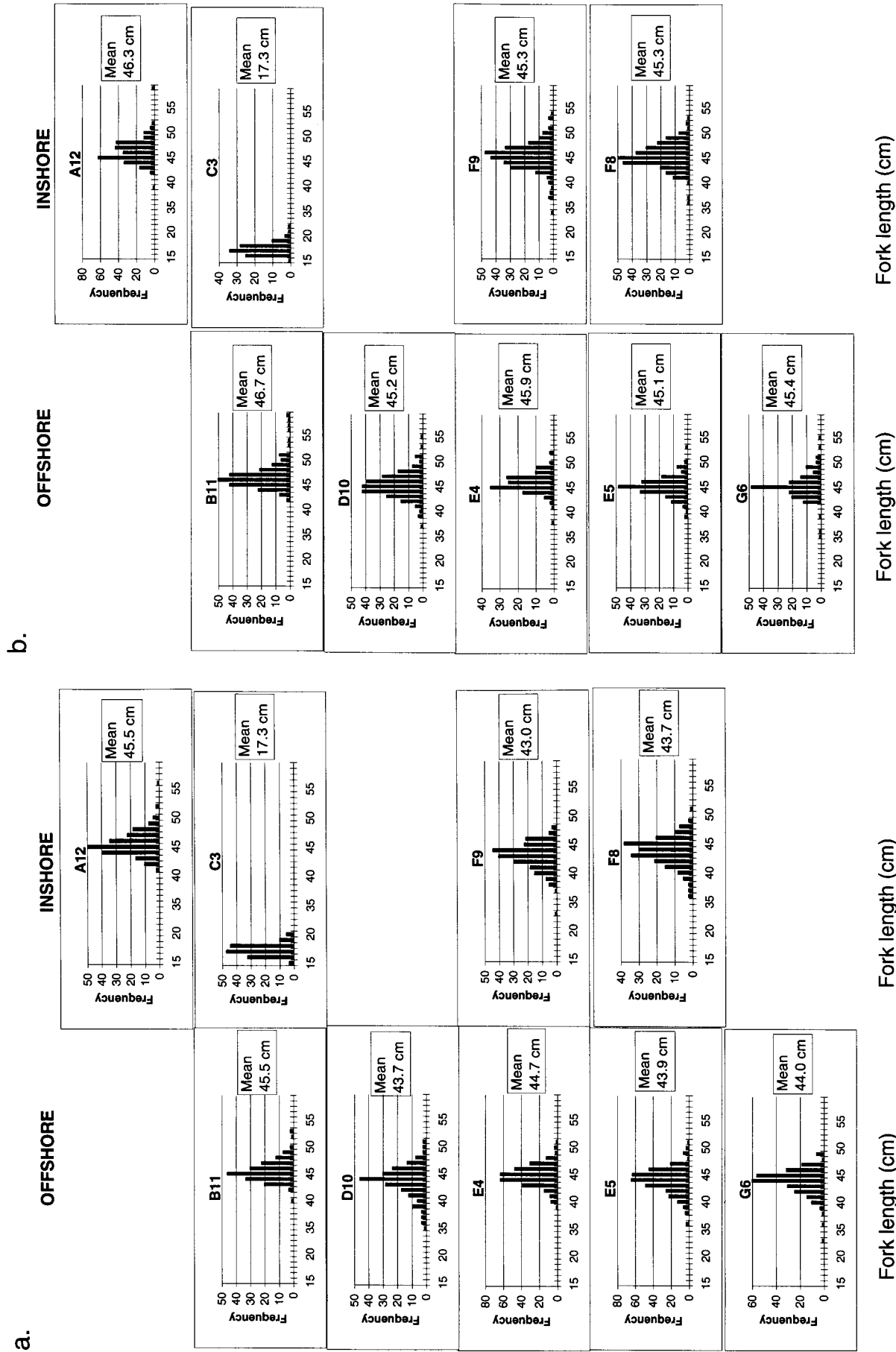


Figure 9. Percent length-frequency compositions of Pacific hake by set, February 1991, for (a) males and (b) females. Sets are listed by school (letters) and set (numbers) and are presented in latitudinal sequence from north (top) to south (bottom).

TABLE 3
Percentage of *Kudoa* Infection in Hake, by Set, 1991

Infection type	Set ^a			
	G6	F8	D10	A12
<i>K. paniformes</i>	44.9	34.0	38.0	25.0
<i>K. thrypsites</i>	22.7	10.0	20.0	17.3
Mixed	14.3	28.0	28.0	28.8
Negative	30.6	28.0	14.0	28.8

^aSet refers to school (letter) and fishing set (number).

In addition, there are aspects of the biological data that indicate we did not survey the older, larger segment of the population that is found in Canadian waters during summer. In the 1991 spawn survey, the mean length of females ranged from 45.4 to 46.3 cm in our sets (figure 9). These fish were comparable in mean size (45.7–46.5 cm) to the females sampled from the South Columbia to Vancouver INPFC areas (M. Dorn, NMFS, unpubl. data; figure 10), during the U.S. 1991 spring fishery. Hake sampled in the 1991 Canadian summer fishery were larger, averaging 48.7 cm (M. Saunders, unpubl. data). Similarly, the prevalence of Kudoan infection during our 1991 survey (table 3) was comparable to prevalence reported by Kabata and Whitaker (1986) for hake found during the summer from Cape Mendocino to northern Oregon. Whether the larger hake were north or south of our sampled distribution is unknown, but the presence of a cline in age- and size-related parameters that is similar in direction to the summer distribution discussed below provides some insight.

Latitudinal Trend in Biological Characteristics

A latitudinal trend in biological characteristics during the summer has been documented in detail (Dark 1975; Francis 1983; Dorn 1995) and explained with an optimal-swimming-speed argument developed by Ware (1978) and adapted for hake by Francis (1983). Briefly, larger fish have higher optimal rates of migration, therefore larger fish reach higher latitudes in summer (Smith 1975; Bailey 1980; Francis 1983; Dorn 1991, 1995).

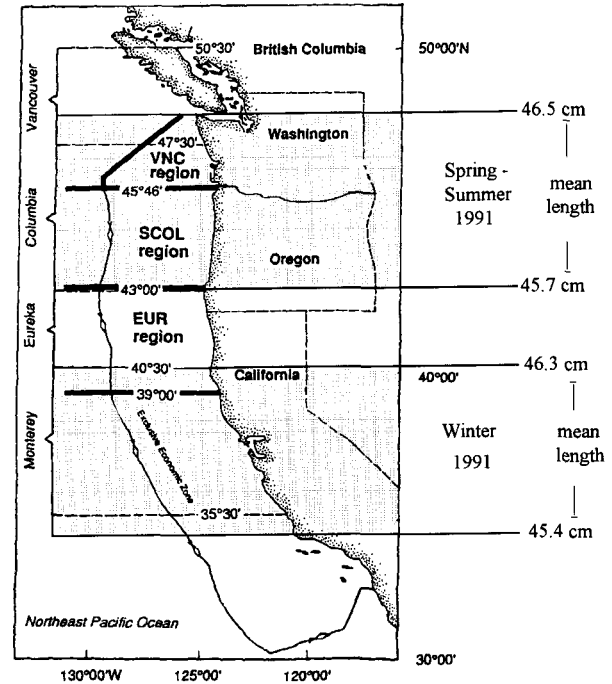


Figure 10. Comparison of the latitudinal range in mean length of spawning females during February 1991 and females of comparable size in the U.S. 1991 fishery. Base map of INPFC regions from Dorn (1991).

In the absence of winter observations, the expected winter latitudinal trends are drawn from conjecture. The current assessments (Saunders and McFarlane, in press; Dorn, in press) and research by Dorn (1995) have assumed that the optimal-swimming-speed argument applies to the southern migration, and that all of the hake return to the point of origin as a mixed stock (Dorn 1995). Smith (1975) hypothesized that the largest fish would migrate from the northern extreme of the feeding migration to the southern extreme of the spawner migration. He and Bailey (1980) suggested that the decline in larvae off Baja California was a result of the developing fishery in the Pacific Northwest, which selectively removed the older fish that would have spawned in the Baja California area.

TABLE 4
Percentage of Prey Occurrence during 1991 Survey

Prey	Set ^a								
	E4	E5	G6	F8	F9	D10	B11	A12	
(Empty stomach)	20.0	70.0	50.7	77.5	52.5	40.0	45.0	67.5	
(Everted stomach)	77.5	20.0	38.0	20.0	40.0	37.5	52.5	30.0	
Euph.	2.5	7.5	0.0	0.0	5.0	10.0	0.0	2.5	
Squid	0.0	0.0	0.0	0.0	0.0	10.0	0.0	0.0	
Myctophid	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	
Fish Rem.	0.0	0.0	0.7	0.0	0.0	2.5	0.0	0.0	
Unid.	0.0	2.5	2.1	0.0	2.5	0.0	0.0	0.0	
Hatchet fish	0.0	0.0	3.5	0.0	0.0	0.0	0.0	0.0	
Unid. crust.	0.0	0.0	1.4	2.5	0.0	0.0	2.5	0.0	
Totals	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	

^aSet refers to school (letter) and fishing set (number).

On this basis, biological characteristics of winter spawning schools were expected to either vary without latitudinal trend, or exhibit trends that were the inverse of the summer distribution. In 1990, we observed only two schools, 280 km (150 nmi) apart, and their biological characteristics were similar. This was not the case during the 1991 survey, when spawning aggregations observed over 720 km (390 nmi), were found to exhibit north-south clines in age composition, sex ratio, mean size, and parasite prevalence that were similar in direction to those during summer. Although based on only one year, our observations do not support the hypothesis that a swimming-speed mechanism alone causes complete mixing or a latitudinal trend in reverse of the summer direction.

We propose that the clines in population biological characteristics are the cumulative effect of four processes affecting individual fish:

One. Adult hake (3+) migrate onshore and northward to summer feeding grounds and offshore and southward to winter spawning grounds (Alverson and Larkins 1969).

Two. Annual displacement of an individual is dependent on body size and the speed of the alongshore components of the prevailing currents.

Given the considerable evidence that the extent of northern migration in summer is related to the strength of poleward-flowing currents (Smith et al. 1990; Dorn 1995), it seems reasonable that there are analogous mechanisms affecting the return migration. There is some support for a relation between oceanographic conditions and spawning distribution. Hollowed (1992) examined larval data and found that although Cape Mendocino appears to be the limit in most years, the boundary may shift north during anomalously warm years.

Specifically, Hollowed (1992) reported that NMFS ichthyoplankton surveys conducted off the coast of Oregon and Washington during the springs of 1980–84, between 40° and 48°N, found hake eggs in 1983 and 1984. Hollowed suggests that this northward shift may have been due to a shift in spawner distribution resulting from the 1982–93 El Niño. Similarly, the presence of young-of-the-year during July 1994, from central Oregon to southern Vancouver Island (M. Saunders, unpubl. data), suggests a northward shift in spawning distribution associated with the warm 1992–93 period. This is consistent with 1992 and 1993 summer observations indicating a northern shift of the stock. In 1992 the triennial acoustic survey found approximately one million t in the Canadian zone—the highest proportion of biomass found there since the inception of the survey in 1977. During 1993, hake were pushed even farther north; there were commercial aggregations in the northern Canadian zone and southeast Alaska (Saunders and McFarlane 1995).

Three. The growth rate of an individual increases with latitude, because of decreased parasite load and/or increased primary and secondary production associated with more northerly waters.

Ware (1992) reports an increasing cline in primary production from southern to northern California which could translate into larger mean size-at-age, assuming that food supply is limiting. MacLellan and Saunders (1995) found that the mean size of the 1980 year class of offshore Pacific hake as age 3's increased with latitude, and hypothesized that the cline resulted from decreasing influence of the 1983 El Niño on productivity with increasing latitude, as reported by Percy and Schoener (1987).

Regarding parasite load, Kabata and Whitaker (1986) developed two competing hypotheses to explain the opposed clines in prevalence and intensity of infection of *K. thryssites* and *K. paniformes*. One hypothesis assumes that California is the site of infection of *K. paniformes* and that a fish is not continuously infected over its life. They postulated that the more heavily infected fish might forgo their migration and cluster near the southern end of their range, as the result of parasite-induced debility.

The alternative hypothesis, based on the assumption that the more prevalent and intensive infection of hake occurs in the southern part of its range, is that part of the hake population fails to migrate. Remaining behind, at, or near the focus of infection, they continue to be exposed to the parasite and thus become more heavily infected. This latter hypothesis is consistent with a persistent north-south cline, with the southern fish remaining in the south and—more important—the largest fish not returning to southern California in most years.

Four. The annual northern displacement of females for a particular cohort is greater than the displacement of males due to sex-specific timing of the post-spawning migration.

If males remain with spawning aggregations longer than females—a behavior noted by McFarlane et al. (1983) for this species in the Strait of Georgia, and for other hake species by Martos and Peralta (1995) and Espino et al. (1995)—then females will have a longer period of northward migration and one which starts earlier. The sex ratios of hake encountered during these surveys provide some support, since spawning aggregations favored males and post-spawning schools favored females. Interestingly, the aggregations of post-spawners tended to be located inshore and were dominated by females. Since the speed of the California Undercurrent intensifies closer to shore, and is strongest during the spawning period (Lynn and Simpson 1987), females could be advected north in larger numbers than males. Bailey (1981b) postulated that hake spawn in the California Undercurrent, noting that bathymetric migrations reported by Ermakov (1974) and Alton (1972) are similar to the dynamics of the California Undercurrent.

Some fundamental aspects of offshore Pacific hake biology remain unresolved; they include the factors, both internal and external, that determine spawning distribution and cause the latitudinal stratification of biological characteristics. Until these aspects of the life history are more fully understood, we must be cautious in applying stock-assessment models which rely on assumptions about the migration that may be incorrect.

ACKNOWLEDGMENTS

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LITERATURE CITED

- Alton, M. S. 1972. Characteristics of the demersal fish faunas inhabiting the outer continental shelf and slope off the northern Oregon coast. In *The Columbia River estuary and adjacent ocean waters*, A. T. Pruter and D. L. Alverson, eds. Seattle: Univ. Wash. Press, pp. 583–636.
- Alverson, D. L., and H. A. Larkins. 1969. Status of the knowledge of the Pacific hake resource. *Calif. Coop. Oceanic Fish. Invest. Rep.* 13:24–31.
- Anonymous. 1969. Biological characteristics and abundance of Pacific hake and ocean perch off the Pacific coast of North America in 1969. Translated from Russian by E. Maltzeff and P. Macy, NMFS, Seattle, WA.
- Bailey, K. M. 1980. Recent changes in the distribution of hake larvae. *Calif. Coop. Oceanic Fish. Invest. Rep.* 21:167–171.
- . 1981a. Larval transport and recruitment of Pacific hake, *Merluccius productus*. *Mar. Ecol. Prog. Ser.* 6:1–9.
- . 1981b. An analysis of the spawning, early life history and recruitment of the Pacific hake, *Merluccius productus*. Ph.D. diss., Univ. Wash., Seattle.
- . 1982. The early life history of the Pacific hake, *Merluccius productus*. *Fish. Bull.* 80(3):589–598.
- Bailey, K. M., R. C. Francis, and P. R. Stevens. 1982. The life history and fishery of Pacific whiting, *Merluccius productus*. *Calif. Coop. Oceanic Fish. Invest. Rep.* 23:81–98.
- Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. *Can. Spec. Publ. Fish. Aquat. Sci.* 60, 102 pp.
- Dark, T. A. 1975. Age and growth of Pacific hake, *Merluccius productus*. *Fish. Bull.* 73(2):336–354.
- Dark, T. A., and M. E. Wilkins. 1994. Distribution, abundance, and biological characteristics of groundfish off the coast of Washington, Oregon, and California, 1977–1986. NOAA Tech. Rep., NMFS 117, 73 pp.
- Dark, T. A., M. O. Nelson, J. J. Traynor, and E. P. Nunnallee. 1980. The distribution, abundance, and biological characteristics of Pacific whiting, *Merluccius productus*, in the California-British Columbia region during July–September 1977. *Mar. Fish. Rev.* 42(3–4):17–33.
- Dorn, M. W. 1991. Spatial and temporal patterns in the catch of Pacific Whiting in the U. S. management zone during 1978–88. NOAA Tech. Memo. NMFS F/NWC-205, 68 pp.
- . 1995. The effects of age composition and oceanographic conditions on the annual migration of Pacific whiting, *Merluccius productus*. *Calif. Coop. Oceanic Fish. Invest. Rep.* 36:97–105.
- . In press. Status of the coastal Pacific hake resource in 1996. In *Pacific Fishery Management Council, Status of the Pacific coast groundfish fishery through 1996 and recommended acceptable biological catches in 1997*.
- Ehrlich, S., F. Mombeck, and G. Speiser. 1980. Investigations on the Pacific hake stock (*Merluccius productus*) in the northeast Pacific. *Arch. Fishereiwiss* 30:17–38.
- Ermakov, Y. K. 1974. The biology and fishery of Pacific hake, *Merluccius productus*. Ph. D. diss., Pac. Sci. Inst. Mar. Fish. Oceanogr. (TINRO), Vladivostok, USSR (in Russian).
- Espino, M., R. Castillo, and F. Fernandez. 1995. Biology and fisheries of Peruvian hake (*M. gayi peruanus*). In *Hake: fisheries, ecology and markets*, J. Alheit and T. J. Pitcher, eds. London: Chapman and Hall, pp. 339–363.
- Francis, R. C. 1983. Population and trophic dynamics of Pacific hake (*Merluccius productus*). *Can. J. Fish. Aquat. Sci.* 40:1925–1943.
- Hollowed, A. B. 1992. Spatial and temporal distributions of Pacific hake, *Merluccius productus*, larvae and estimates of survival during early life stages. *Calif. Coop. Oceanic Fish. Invest. Rep.* 33:100–123.
- Kabata, Z., and D. J. Whitaker. 1981. Two species of *Kudoa* (Myxosporea: Multivalvulida) parasitic in the flesh of *Merluccius productus* (Ayres 1855) (Pisces: Teleostei) in the Canadian Pacific. *Can. J. Zool.* 59:2085–2091.
- . 1986. Distribution of two species of *Kudoa* (Myxosporea: Multivalvulida) in the offshore population of Pacific hake *Merluccius productus* (Ayres 1855). *Can. J. Zool.* 64:2103–2110.
- Lynn, R. J., and J. J. Simpson. 1987. The California Current system: the seasonal variability of its physical characteristics. *J. Geophys. Res.* 92(C12): 12,947–12,966.
- MacLellan, S. E., and M. W. Saunders. 1995. A natural tag on the otoliths of Pacific hake (*Merluccius productus*) with implications for age validation and migration. In *Recent developments in fish otolith research*, D. H. Secor, J. M. Dean, and S. E. Campana, eds. Columbia, S. C.: Univ. S. Carolina Press, pp. 567–580.
- Martos, A. R., and L. F. Peralta. 1995. Biology and fisheries of northwest African hakes (*M. merluccius*, *M. senegalensis* and *M. polli*). In *Hake: fisheries, ecology and markets*, J. Alheit and T. J. Pitcher, eds. London: Chapman and Hall, pp. 89–124.
- McFarlane, G. A., and R. J. Beamish. 1985. Biology and fishery of Pacific whiting, *Merluccius productus*, in the Strait of Georgia. *Mar. Fish. Rev.* 47(2):23–34.
- McFarlane, G. A., W. Shaw, and R. J. Beamish. 1983. Observations on the biology and distribution of Pacific hake, walleye pollock, and spiny dogfish in the Strait of Georgia, February 20–May 2, and July 3, 1981. *Can. Manuscr. Rep. Fish. Aquat. Sci.* 1722, 109 pp.
- Nelson, M. O., and T. A. Dark. 1985. Results of the coastal Pacific whiting *Merluccius productus*, surveys in 1977 and 1980. *Mar. Fish. Rev.* 47:35–38.
- Pearcy, W. G., and A. Schoener. 1987. Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern subarctic Pacific Ocean. *J. Geophys. Res.* 92(C13):14,417–14,428.
- Saunders, M. W., and G. A. McFarlane. 1995. Pacific hake. In *Groundfish stock assessments for the west coast of Canada in 1994 and recommended yield options for 1995*, J. Fargo and M. Stocker, eds. *Can. Tech. Rep. Fish. Aquat. Sci.* 2069, 440 pp.
- . In press. Pacific hake. In *Groundfish stock assessments for the west coast of Canada in 1996 and recommended yield options for 1997*. *Can. Tech. Rep. Fish. Aquat. Sci.*
- Saunders, M. W., R. Keiser, P. Withler, and W. T. Andrews. 1992. A hydroacoustic survey of Pacific hake on the continental shelf off British Columbia from the Canada/U.S. boundary to Queen Charlotte Sound: August 13–31, 1990. *Can. Manuscr. Rep. Fish. Aquat. Sci.* 2177, 43 pp.
- Smith, B. D., G. A. McFarlane, and M. W. Saunders. 1990. Variation in Pacific hake (*Merluccius productus*) summer length-at-age near southern Vancouver Island and its relationship to fishing and oceanography. *Can. J. Fish. Aquat. Sci.* 47:2195–2211.
- Smith, P. 1975. Pacific hake larval distribution and abundance, 1951–1975. Southwest Fisheries Center Admin. Rep. LJ-75-83, SWFC, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.
- Stepanenko, M. A. 1981. Assessment of stocks and reproduction conditions of Pacific hake and California anchovy in 1981. Pacific Research Institute of Fisheries and Oceanography (TINRO).
- Stepanenko, M. A., and G. V. Zinovyeva. 1982. Assessment of stocks of commercial fishes off the Pacific coast of North America, studies on their qualitative structure and fishery of them in 1981–1982. Interim report. Pacific Research Institute of Fisheries and Oceanography (TINRO).
- Ware, D. M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish. Res. Board Can.* 35:220–228.
- . 1992. Production characteristics of upwelling systems and the trophodynamic role of hake. *S. Afr. J. Mar. Sci.* 12:501–513.
- Weir, K. R., R. J. Beamish, M. S. Smith, and J. R. Scarsbrook. 1978. Hake and pollock study, Strait of Georgia bottom trawl cruise, G.B. REED February 25–March 13, 1975. *Fish Mar. Ser. Data Rep.* 71, 153 pp.

Part III

SCIENTIFIC CONTRIBUTIONS

