The Loop Current and the abundance of larval *Cubiceps pauciradiatus* (Pisces: Nomeidae) in the Gulf of Mexico: evidence for physical and biological interaction

John Lamkin

Southeast Fisheries Science Center
National Marine Fisheries Service, NOAA
75 Virginia Beach Dr., Miami, Florida 33149
E-mail address: John.Lamkin@noaa.gov

Abstract.—By analyzing annual ichthyoplankton survey data from 1983 to 1988, I found a significant positive correlation in distribution and abundance between larval *Cubiceps pauciradiatus* and the Loop Current in the Gulf of Mexico. The data indicate that *C. pauciradiatus* is a species whose adult spawning grounds and larval habitat are tied to sharp temperature gradients. These gradients occur along the edge of the Loop Current in the eastern Gulf of Mexico and along the anticyclonic-cyclonic rings in the western Gulf of Mexico. Transects made across the Loop Current, in 1987 and 1988, show that larval *C. pauciradiatus* is found close to the frontal interface and that peak abundance occurs before peak SST (sea surface temperature).

Variation in the extent of the frontal systems in the Gulf of Mexico would be expected to affect annual recruitment of a species that is tied to a frontal habitat. Annual abundance of *C. pauciradiatus* varied considerably but was similar to that of other pelagic species. This finding suggests that the physical processes in the Gulf of Mexico may affect a wide range of species.

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Bigeye cigarfish, *Cubiceps pauciradiatus,* is a member of the family Nomeidae (suborder Stromateoidei) characterized by Haedrich (1967) as "oceanic fishes of tropical and subtropical waters." Fishes of this family are widely distributed across the Gulf of Mexico, in Caribbean waters, and in the tropical Atlantic, Pacific, and Indian Oceans (Butler, 1979). The family Nomeidae comprises three genera: *Cubiceps*, *Psenes*, and *Nomeus*. *Nomeus* is monotypic, *Cubiceps* has seven species, and *Psenes* six (Haedrich, 1967, 1972; Butler, 1979). *Cubiceps pauciradiatus* Günther is a worldwide tropical species and an important forage fish for porpoises (Perrin et al., 1973) and tuna (Alverson, 1963). Because of their oceanic habitat, cigarfishes are poorly known, and only limited information is available on their distribution. Ahlstrom et al. (1976) described the larval stages of five species of this suborder, including *C. pauciradiatus*. All identifications in this study are based upon their work.

In the central and South Atlantic, Oven et al. (1984) found that *Cubiceps pauciradiatus* was always present in the upper sound-scattering layer. It was also the dominant species in the Gulf of Guinea, accounting for 46–85% of the catch (Salekhov, 1989). Like many fishes, *C. pauciradiatus* migrate to the surface waters at night, concentrating in the upper 70 m. Salekhov (1989) reported that they were abundant and at times the dominant species in night-collected samples where surface-water temperatures were 26.2–28.30°C. Juveniles do not migrate but remain in the 30–90 m stratum. *Cubiceps pauciradiatus* is an intermittent spawner and has a life span of 1 to 2 years. Peak spawning occurs from December to April in tropical waters.

The distribution of this fish in the North Atlantic and Gulf of Mexico is poorly known. In a 1979 study by Houde et al.,[1] *C. pauciradiatus* were the most abundant nomeid in the eastern Gulf. Richards (1984) found this species widely distributed in the eastern Caribbean Sea. In the central and South Atlantic, Salekhov (1989) showed that largest catches of *C. pauciradiatus* occurred in tropical waters along the periphery of cyclonic gyres, the Equatorial Counter Current, and the upwelling region of the Sierra-Leone Ridge. The Gulf of Mexico contains similar frontal areas, such as the Loop

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[1] Houde, E. D., J. C. Leak, C. E. Dowd, S. A. Berkeley, and W. J. Richards. 1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Contract Report to the Bureau of Land Management, rep. AA550-ct7-28, 546 p.

Current in the eastern Gulf and the large warm-core anticyclonic and smaller cold-core cyclonic eddies in the western Gulf. These features form frontal zones across a wide area of the Gulf of Mexico and may be areas in which adult *C. pauciradiatus* are abundant. If *C. pauciradiatus* are abundant around the edges of gyres and upwelling areas, the Gulf of Mexico could be expected to support an extensive population.

This relationship between larval fish and frontal zones has been an area of intense research since Iles and Sinclair (1982) first proposed the existence of larval retention zones caused by oceanographic features. Thermal fronts are defined as a boundary between two water masses that usually have a sharp temperature gradient over short (<10 km) distances (Brandt and Wadley, 1981; Owen, 1989). The biological implications of these features have been recognized by several authors (Brandt and Wadley, 1981; Le Feure, 1986; Richardson et al., 1986, 1989). Thermal fronts are often associated with abrupt changes in salinity, color, turbidity, primary productivity, and phytoplankton species composition and abundance. Fronts may also be considered ecotones and may pose a zoogeographic barrier to both adult and larval fish (Brandt and Wadley, 1981; Richards et al., 1993).

Changes in the distribution and abundance of phytoplankton species across frontal zones have been reported by Seliger et al. (1981), Holligan et al. (1984), Richardson et al. (1985), and Richardson et al. (1986). These authors have reported increased abundance across these features, but the duration and long-term effect of increased phytoplankton abundance on trophic levels have yet to be determined. In a series of papers examining larval herring patches in the Buchan area of Scotland, Richardson et al. (1986) found phytoplankton biomass was highest at a transition zone created by warming waters and tidal mixing. Increased zooplankton abundance across fronts has also been reported (Tranter et al., 1983; Kiørboe and Johansen, 1986; Richards et al., 1989). Trantor et al. (1983) and Kiørboe and Johansen (1986) both reported increased zooplankton biomass concurrent with increased phytoplankton abundance. In a series of transects across the Loop Current, Richards et al. (1989) found increased zooplankton volumes in thermally mixed water close to the outer perimeter of highest surface-current velocity. This occurrence coincided with increases in surface chlorophyll measurements.

The purpose of this paper is to describe the large-scale (Gulf-wide) distribution and abundance of larval *C. pauciradiatus* and their interaction with mesoscale oceanographic features in the Gulf of Mexico. I will show that *C. pauciradiatus* are retained on the cool side of thermal fronts in areas of high productivity. I hypothesize that the temporal persistence of northern excursions of the Loop Current directly affects the abundance and probably the survival of this species. Because this study focuses on larval, rather than adult, *C. pauciradiatus*, the results of this study will help define the role that these oceanographic features play in larval distribution and may help to determine the size of future year classes.

Physical oceanography of the Gulf of Mexico

The Gulf of Mexico is a semi-enclosed body of water, the circulation of which is dominated by the Loop Current. Water enters through the Yucatan Channel and exits through the Straits of Florida. The Loop Current is very dynamic and unstable, pushing as far as 29 degrees north latitude into the Gulf of Mexico and at other times flowing almost directly out through the Straits (Vukovich et al., 1979). These characteristics have caused considerable confusion over the years, and only recently have we begun to understand the dynamics of this system (Leipper, 1970; Behringer et al., 1977; Maul, 1977; Vukovich et al., 1979; Vukovich, 1988; Maul and Vukovich, 1993).

Among the more significant features of the Loop Current are the large (200–300 km at formation) anticyclonic rings generated when the northward intrusion separates from the rest of the Current. These rings are pinched off from the Loop Current and move into the western Gulf shelf where they eventually spin down and break up (Merrell and Vazquez, 1983; Lewis and Kirwan, 1987; Lewis, 1992). The exact mechanism of ring genesis is unclear, but it seems to involve the formation of a narrow intrusion of cold water between the ring and the remainder of the Loop Current (Cochrane, 1972; Vukovich and Maul, 1985; Vukovich, 1986). Hurlburt and Thompson (1980, 1982) used numeric models that showed that inherent instabilities exist within the flow field and eventually result in ring separation. Ring separation occurs every 6–17 months (on average every 11 months [Maul and Vukovich, 1993]).

As these warm-core anticyclonic rings move westward, adjacent mesoscale (20–80 km) cyclonic circulations may develop (Elliot, 1979; Merrell and Morrison, 1981; Merrell and Vazques, 1983; Lewis and Kirwan, 1985). These cyclonic rings may be important biologically; Biggs (1992) found elevated nitrate concentrations just below the mixed layer. Cyclones such as these exist for 6 months or more, during which time they may move tens to hundreds of km (Hamilton, 1992). However, their cold surface expression is limited, and generally these rings can be recognized better by direct sampling from ships or aircraft than from satellites (Hamilton, 1992).

Materials and methods

Collections in this study were gathered from the NOAA Ship *Oregon II*. Annual surveys were conducted that covered most of the U.S. Exclusive Economic Zone (Richards, 1984). These surveys followed a grid pattern with stations at every 30 minutes of latitude and longitude. Each station consisted of conductivity-temperature-depth (CTD) casts to 200 meters or consisted of an expendable bathythermograph (XBT) drop. Biological samples were collected with 60-cm paired bongo nets of 0.333-mm mesh towed to 200 m or to within 5 m of the bottom at stations <200 m. The nets were towed at a speed of approximately 1.5 kn with a wire angle of 45° and retrieved at a rate of 20 m per minute. A neuston-net tow of 10-min duration (vessel speed approximately 2.5 kn) was also conducted at each station. In 1983 and 1984 only one survey of the northern Gulf of Mexico was completed (Table 1). In the following years, two surveys were completed (1986, 1987, and 1988), each about two weeks apart, although with fewer stations and reduced geographic coverage. There was no survey in 1985. In addition to the normal survey, six transects across the Loop Current were made in 1987. The transect locations were selected on the basis of real-time satellite imagery and frontal analysis and the frontal positions were radioed to the vessel (Richards et al., 1989). Transects 1–6 consisted of stations 2 km apart, and transects 7–8 were 3.6 km apart.

In 1988, a line of stations was sampled along 86°W running from 29.5°N to 27.6°N. All stations except the first two were 8.3 km apart. Biological samples were taken until the 22°C isotherm rose to 100 m. The XBT drops were continued in order to provide a more detailed definition of the water mass. A 1-m Tucker trawl, with three nets and two opening and closing bongo nets, was deployed in addition to the standard gear. Samples were fixed in buffered formalin and transferred to 70% ethanol within 48 hours.

Table 1

NOAA ship *Oregon II* cruise dates covering the period 1983–88.

Cruise	Leg	Date	Year	No. of bongo stations
OT-134		25 April–16 May	1983	99
OT-143		23 April–7 May	1984	98
OT-159	1	22 April–6 May	1986	36
	2	9 May–22 May	1986	37
OT-166	1	15 April –2 May	1987	35
	2	7 May–20 May	1987	35
OT-173	1	15 April –2 May	1988	34
	2	12 May–26 May	1988	35

Bulk zooplankton biomass was estimated from wet displacement volume (dv) (Ahlstrom and Thrailkill, 1960). Samples from the annual surveys were processed at the Plankton Sorting and Identification Center, Szczucin, Poland. The samples from the transects in 1987 and 1988 were processed at the Southeast Fisheries Science Center, Miami, Florida. Fish were identified from the descriptions of Ahlstrom et al. (1976). Catches of larvae were standardized to number under 10 m^2. Bulk plankton standing stocks were standardized to mL of wet displacement volume per 1,000 m^3.

To test the relationship between larval *C. pauciradiatus* and the close proximity (<5 km) of a frontal feature, a chi-square (χ^2) test for one-dimensional count data was performed. Because the sampling grid was held constant, the total number of stations <5 km from a zone of surface-temperature gradient varied in relation to the spatial location and size of the frontal features present in that year. To account for the fact that in some years most of the stations were within 5 km of a frontal zone and in other years few were, the analysis was performed to test whether the percentage of stations with *C. pauciradiatus* <5 km from a frontal feature was greater than the percentage of stations with *C. pauciradiatus* >5 km from a frontal feature. This procedure has the added benefit of accounting for random distribution; i.e. if 90% of the stations are within 5 km of a feature, then expectations are such that 90% of the stations with *C. pauciradiatus* would be within 5 km. Pearson correlation coefficients (r) were also obtained from the relationship between larval *C. pauciradiatus* and plankton volume and between total larvae (number under 10 m^2) and plankton volume from the transects.

The frontal edge of the Loop Current and anticyclonic rings was defined as 22°C at 100 m depth following Leipper, (1970) and Maul and Herman (1985).

Results

Physical oceanography

The circulation patterns preceding and during the 1983–88 April–May ichthyoplankton cruises varied considerably from year to year and within years (cruises) in both the eastern and western Gulf of Mexico. A brief synopsis of the circulation patterns present throughout this study are presented below.

Figure 1 shows the position of the 22° isotherms at 100 meters (Loop Current frontal edge) in the eastern Gulf of Mexico for each of the 5 years covered in this study. In 1983, 1984, and 1988, the Loop Current extended north to 27°N. However, in 1986, the Loop barely penetrated into the sample area, and in 1987, a broad front stretched from 88°W to 84°W, although not as far north as in other years. The positions of the Loop Current and cyclonic-anticyclonic rings are detailed in Figures 2–11.

Although Figure 1 indicates the position of the Loop current at the time of the survey, it does not reflect the dynamics of the system nor the formation of warm-core eddies. The northward penetration and stability of the Loop Current front is directly impacted by formation and separation of warm-core eddies. In 1983, a ring began to form in January but did not separate until March and left the Loop Current extended to the northeast with the northern boundary at 27°N (Fig. 2). It remained in that position throughout most of the spring. In contrast, the Loop Current underwent ring-shedding events in January 1984 and 1986, and the front remained farther south and with a much narrower frontal area (Figs. 3–5). In 1987, and 1988, ring formation had taken place in September–November of the previous year. However, the Loop Current did not push north until the spring of the following year.

The presence or absence of the anticyclonic (warm-core) rings and their companion cyclones (cold-core) also strongly influences the circulation in the western Gulf of Mexico. Anticyclonic rings were present in the western Gulf of Mexico in all years, although their influence on the area sampled varied considerably. In 1983, 1984, and 1986, warm-core rings were present in the western Gulf. In 1987, and 1988, their influence was restricted to the southern part of the survey area, and in 1988, the temperature signature was evident only at 200 m. Cyclones were also present, although the number and position varied considerably from year to year. However, in some years it was not possible to resolve the circulation patterns because of difficulty in obtaining sufficient sample density.

Distribution and abundance

In each year of this study, larval *C. pauciradiatus* were most abundant in temperature gradients: in the Loop Current front between the the 22° and 20° isotherms and in the gradients of 16–20°C associated with cold cyclonic rings. Abundance varied considerably from year to year and between the eastern and western Gulf. Overall, abundance was greatest in 1983 and lowest in 1987. In 1983, *C. pauciradiatus* were present at 41 of 99 stations, with peak catches in the southeast of 162 and 188 individuals under 10 m^2 (Fig. 2). Thirty six of the 41 stations were in the eastern Gulf. In succeeding years, abundance was greatly reduced. In 1984, *C. pauciradiatus* were present at only 9 stations in the eastern Gulf (Fig. 3). This pattern continued through 1988, when *C. pauciradiatus* was found at no more than 9 stations and at as few as 4 (leg 2, 1988). Although *C. pauciradiatus* were present at a few stations inshore, most were found concentrated around the Loop Current, but not in its interior. Peak catches often occurred when a station coincided with a cyclonic meander at the Loop Current or in areas associated with cyclonic rings and cold water intrusions.

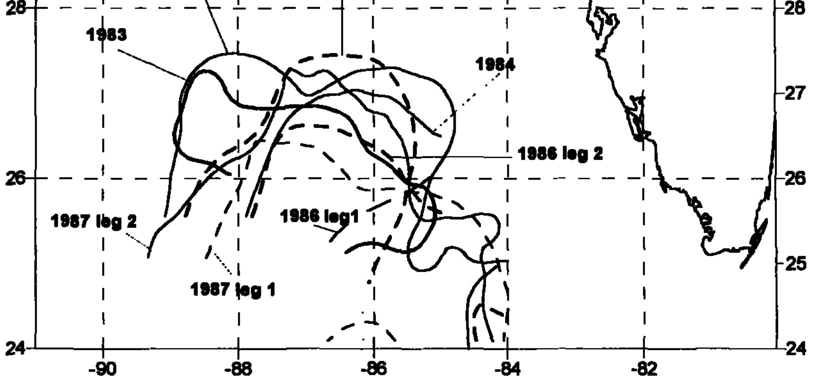

Figure 1

Position of Loop Current (22°C at 100 m) for each year and leg.

Distribution and abundance were considerably different in the western Gulf than in the eastern. Larval *C. pauciradiatus* were found at few stations (except in 1984), and generally in smaller numbers. They tended to be found around the edge of rings (warm and cold) when present. The number of stations occupied in the western Gulf varied considerably from year to year and created difficulties for evaluating the available data and for constructing a meaningful interpretation of the physical oceanography. Both interannual and east–west differences, however, were evident. In 1983, *C. pauciradiatus* was abundant in large numbers at 36 stations in the eastern Gulf of Mexico but were present in only five stations west of 90°W. The following year they were taken at only 9 stations in the eastern Gulf but were found at 17 stations throughout the western Gulf, although in fewer numbers. They were found infrequently in the following years.

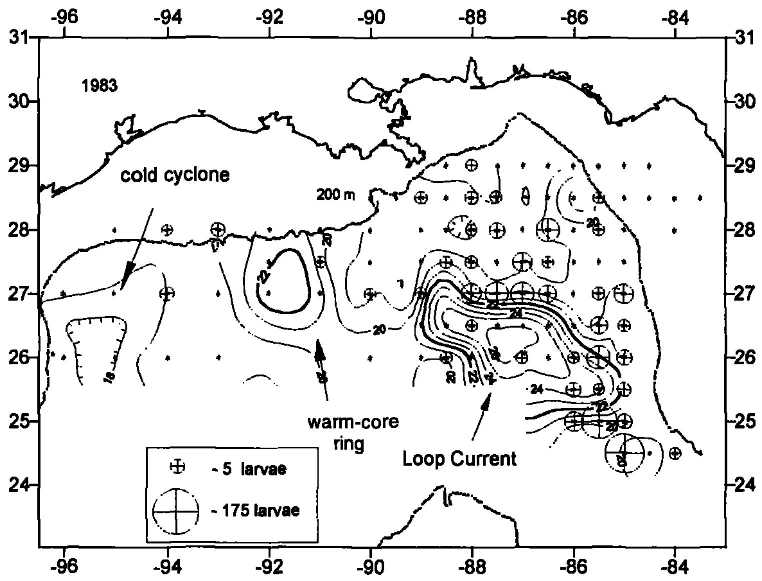

Figure 2

NOAA ship *Oregon II* cruise 134, 25 April–16 May 1983. Temperature (°C) of northern Gulf of Mexico at 100 meters. ⊕ indicates stations where *C. pauciradiatus* was found. Number of larvae under 10 m² ranged from 4 to 188 individuals per station. Asterisk (*) indicates CDT/XBT and bongo or neuston stations.

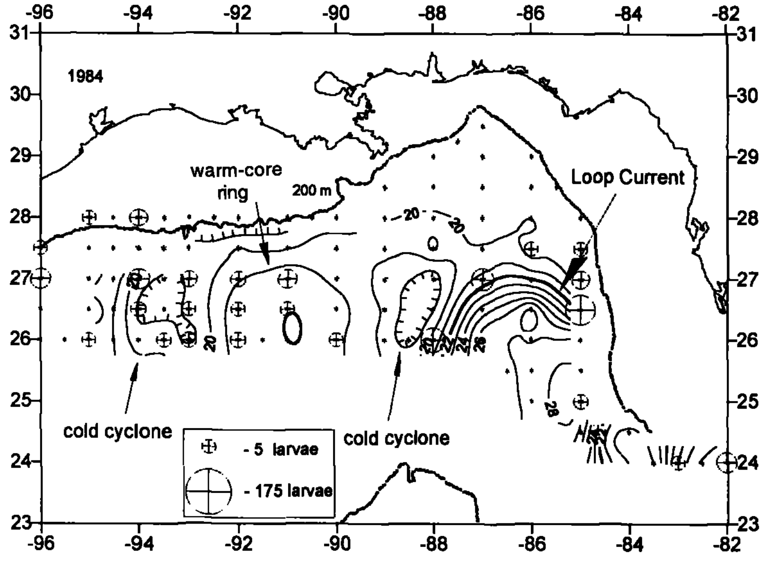

Figure 3

NOAA ship *Oregon II* cruise 143, 23 April–7 May 1984. Symbols as in Figure 2. Number of larvae under 10 m² ranged from 5 to 53 individuals per station.

Total larvae (number under 10 m²) and plankton displacement volumes showed similar trends in abundance. Larval abundance and plankton displacement volumes were generally highest inshore and along the 100-m curve. However, at stations along the edge of the Loop Current and around the cold core rings, numbers of larvae and plankton were often equal to and sometimes exceeded values at the inshore stations.

Transects

Measurements at each station and satellite sea-surface temperatures indicate that in 1987, transects I, II, III, V, VI, and VII crossed surface fronts (Figs. 12 and 13), as did the only transect in 1988 (Fig. 14). Transect I crossed a warm filament extending north from the eastern edge of the Loop. Transect II was south of the origin of the warm filament. Transect III was made in a north–south direction, and transect V was the only transect to cross a cold-core cyclonic ring. Transect VI was on the cool side of the front and is discussed in detail by Richards et al. (1989). Transect VII began on the cool side of the Loop Current along longitude 87°W and crossed south into the northern edge of the Loop. Sea-surface temperatures increased from

25.1°C to a high of 29°C in the middle of the transect. The transect in 1988 (Fig. 14) bisected a northward intrusion of the Loop Current between a cyclonic ring to the west and cooler shelf water to the east.

Figures 15 and 16 show the distribution of *C. pauciradiatus* in relation to SST fronts. Few were found in areas of peak temperatures, and the larvae were generally more abundant on the cool side, although SST was not as important as spatial orientation to the front. Peak abundances occurred at a variety of temperatures (21.5°C–28.7°C) but were always greatest in regions of greatest horizontal temperature gradients. This pattern can best be seen at transect III in 1987 and at the single transect completed in 1988. In transect III, *C. pauciradiatus* were found on both sides of the temperature front but were concentrated around the steepest slope. In 1988, the transect was much longer, and stations were 5 nautical miles apart (Fig. 16). *Cubiceps pauciradiatus* were absent until sea-surface temperatures began to increase significantly and peaked prior to maximum SST temperatures. Few *C. pauciradiatus* were found in the warm Loop Current waters or in the cooler continental shelf waters.

Plankton volumes, total larvae (under 10 m^2), and larvae in the neuston net showed similar patterns (Fig. 17). Perhaps the most important of these is plankton volume because this may show an abundance of the potential prey of larval *C. pauciradiatus*. There was no significant correlation between abundance of larval *C. pauciradiatus* and plankton volume across all transects. However, few larvae were found in the second series of transects (V, VI, VII). When each transect was examined separately, II and III showed high correlations between *C. pauciradiatus* and plankton volume (0.829, P=0.0410, and 0.896, P=0.0002, respectively). In both these transects, larval *C. pauciradiatus* were present in consecutive stations, and the frontal features were well defined. Total larvae (number under 10 m^2) were correlated with plankton volume when examined across all transects (0.236, P=0.0349) but not when compared transect by transect. Within each transect, correlations were highest in III and VII (0.822, P=0.0019, 0.697, P=0.017). The results of the test be-

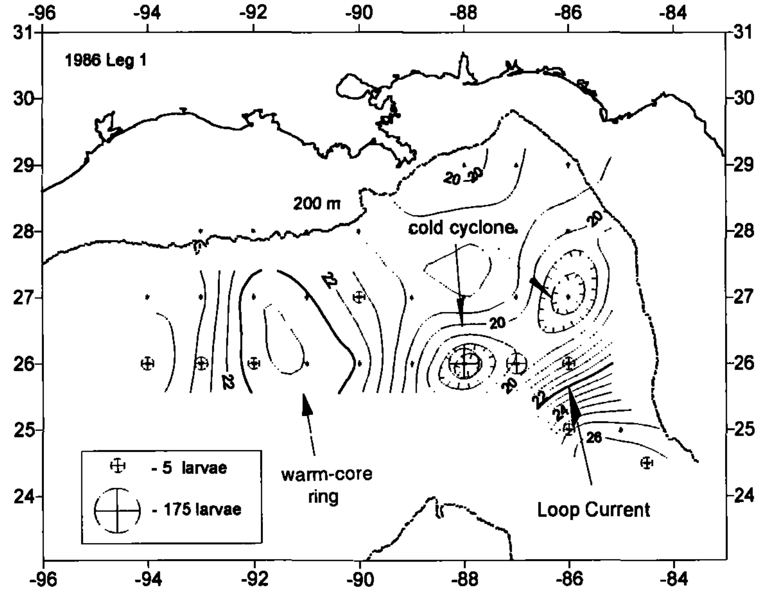

Figure 4

NOAA ship *Oregon II* cruise 159, leg 1, 22 April–6 May 1986. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 6 to 100 individuals per station.

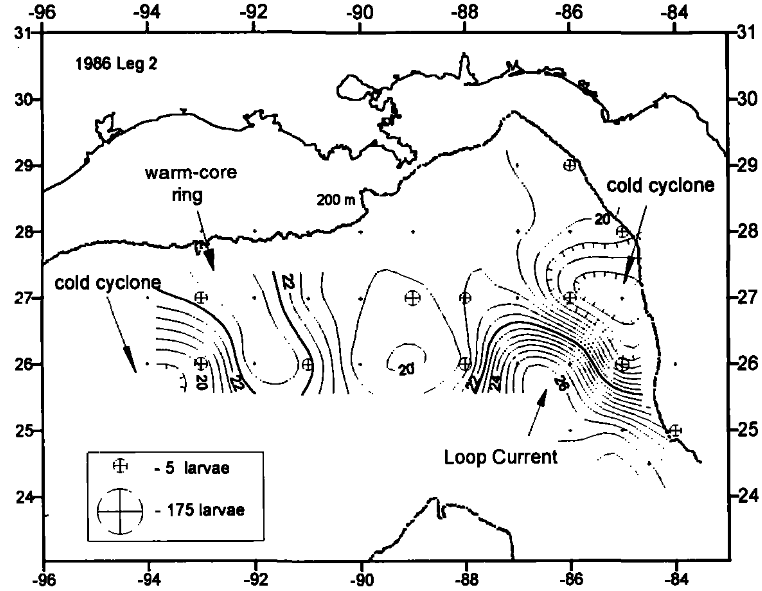

Figure 5

NOAA ship *Oregon II* cruise 159, leg 2, 9 May–22 May 1986. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 6 to 24 individuals per station.

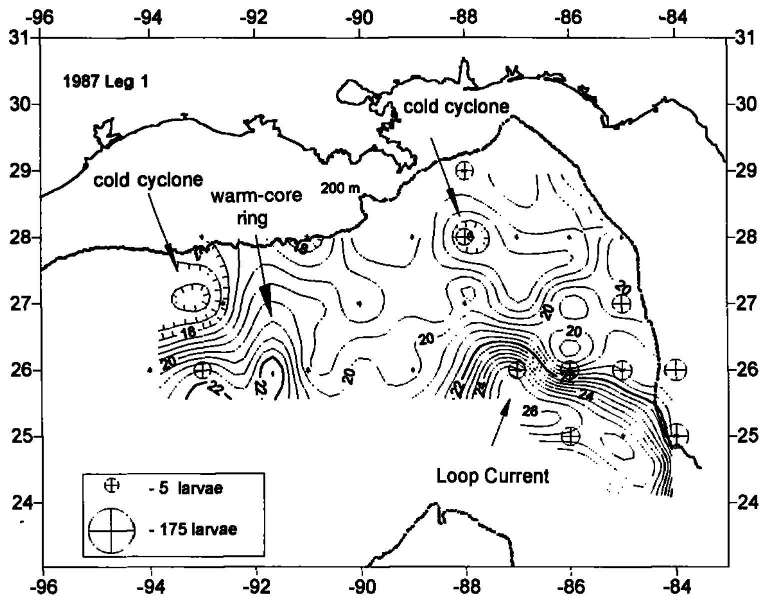

Figure 6

NOAA ship *Oregon II* cruise 166, leg 1, 25 April–16 May 1987. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 7 to 50 individuals per station.

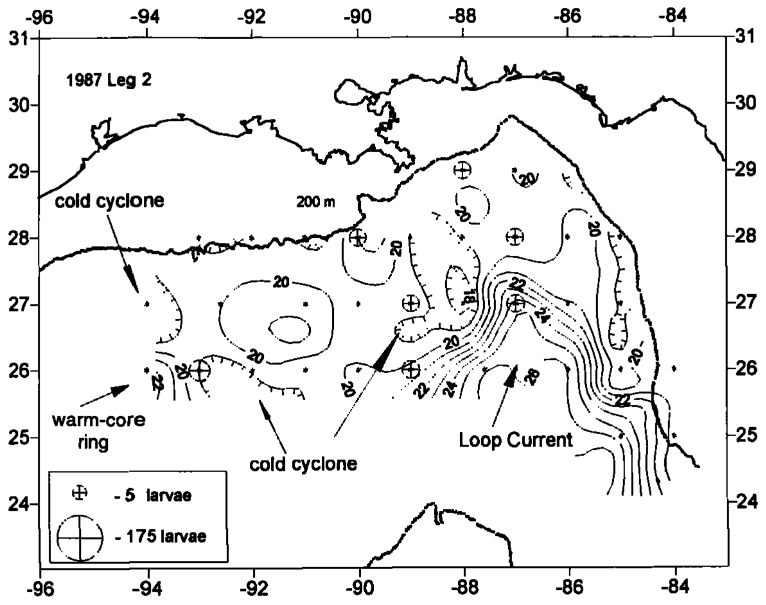

Figure 7

NOAA ship *Oregon II* cruise 166, leg 2, 25 April–16 May 1987. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 7 to 28 individuals per station.

tween larval *C. pauciradiatus* and the close proximity of a temperature front across all cruises yielded a value of 34.128 with a *P*-value of <0.01, indicating a very strong correlation between the presence of *C. pauciradiatus* and frontal zones. Of stations with *C. pauciradiatus*, 84.7% occurred at <5 km, and 15.3% were >5 km from a front. For all stations, the values were 51.8% and 48.2%, respectively.

Such tight spatial correlations with frontal zones are best seen by comparing the abundance of *C. pauciradiatus* in the transects with that in the surveys. In both legs of the 1987 survey a combined mean of 207 (under 10 m^2) larval *C. pauciradiatus* were caught at 14 grid stations. Mean abundance averaged 2–3 fold higher in frontal zones, for 70% of these larvae (160) were taken at nine stations that were on or near a front. Only five stations with 47 larvae (30%) were not associated with an identifiable frontal structure.

In the same 1987 survey, 6 dedicated transects across the Loop Current caught a combined mean of 693 larvae (number under 10 m^2). Larval *C. pauciradiatus* were caught at 22 bongo stations and another 91 were taken in neuston tows. If these numbers are combined, 94.5% were caught along frontal zones.

Results were similar in 1988. During the grid survey, 13 stations contained 343 *C. pauciradiatus*, only one of which was not associated with the front. This station accounted for only 1.7% of the larvae. In the one transect, 330 *C. pauciradiatus* larvae (under 10 m^2) were found at 9 of 16 stations.

Further examination of these transects across the Loop Current and the grid stations shows that *C. pauciradiatus* occur primarily on the cold side of the temperature gradient. When the temperature gradient is well defined and *C. pauciradiatus* are present across the front, abundance is highly correlated with bulk plankton standing stocks (displacement volume maxima). The pattern can be clearly seen in transect III and in the transect completed in 1988 (Figs. 15 and 16). In transect III, *C. pauciradiatus* were not present until sea surface temperature (SST) started to increase, and their abundance peaked just before an SST maximum. Bulk plankton displacement volumes were also at or near maxima at the same stations where *C. pauciradiatus* were abundant. In the 1988 transect, with stations 8 km apart, the patterns of abundance clearly showed that *C. pauciradiatus* prefer the frontal interface between the Gulf common water over the continental margin and the subtropical underwater of the Loop Current. Larvae were not present until the SST began to increase, rose to a peak after the initial temperature increase, then declined sharply in the warmer waters. Bulk plankton displacement volumes did not follow an identical pattern but nonetheless peaked in mid-transect, just before those stations where *C. pauciradiatus* were most abundant. Such patterns may be a spatial consequence of the fact that this transect had stations 8 km apart rather than 3.2 km apart.

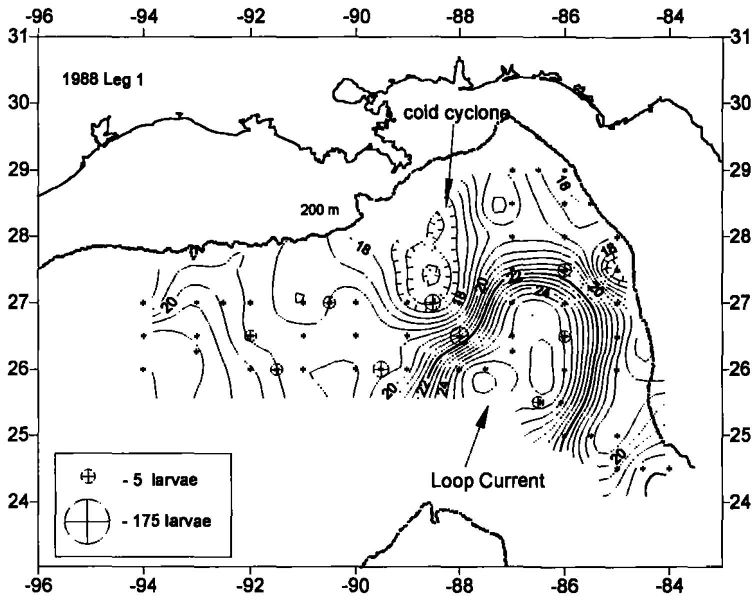

Figure 8

NOAA ship *Oregon II* cruise 173, leg 1, 15 April–2 May 1988. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 6 to 66 individuals per station.

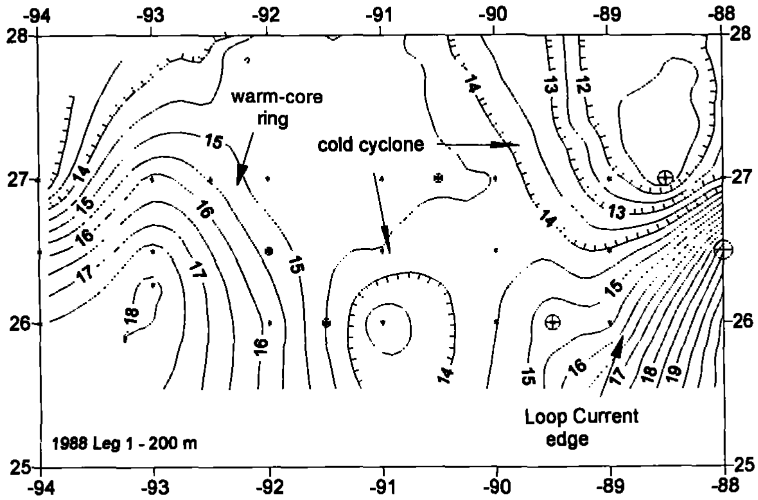

Figure 9

NOAA ship *Oregon II* cruise 173, leg 1, 15 April–2 May 1988. Temperature (°C) of northern Gulf of Mexico at 200 meters. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 6 to 66 individuals per station.

Discussion

In this study, the abundance and distribution of larval *C. pauciradiatus* were examined over five yearly surveys and seven transects. Analyses of survey data and transects depict a species whose adult spawning grounds and larval habitat are tied to sharp temperature gradients associated with the Loop Current in the eastern Gulf and to anticyclonic-cyclonic rings in the western Gulf of Mexico. Larval *C. pauciradiatus* were most abundant near a temperature front. It is apparent from these data and the transects made in 1987 and 1988 that this frontal environment is the preferred habitat and probable spawning area for the adult population of *C. pauciradiatus* in the Gulf of Mexico. Salenkov (1989) found that areas of highest density of juvenile and adult *C. pauciradiatus* in the tropical Atlantic Ocean were situated in zones of high production such as the edge of cyclonic gyres, the equatorial countercurrent, and the upwelling regions of the Sierra Leone Ridge.

In general, fish are often found aggregated at fronts (Brandt and Wadley, 1981; Nero et al., 1990). Currently there are two competing theories to explain this relationship: 1) that fish have thermal requirements and are attracted to temperature gradients, and 2) that fish are attracted to fronts because of the increased concentration of prey (Brandt, 1993). A third explanation may be that spawning in a frontal area may also provide optimal conditions for survival and growth of larvae and that increased concentration of prey may be beneficial for both larvae and adults.

The concentration of biomass at a front may be caused by advection (Olson and Backus, 1985) or by new production. Claustre et al. (1994) found evidence that suggested that the increased biomass found along a frontal region is due to new production. In the Mediterranean they found that frontal stations had phytoplankton biomass levels much higher than those at adjacent zones. These areas of high biomass were dominated by diatoms as opposed to flagellates and cyanobacteria found in typical Atlantic and Mediterranean waters. They concluded that the high biomass levels found at the front are not the result of purely passive accumulation but are the result of physically driven new production.

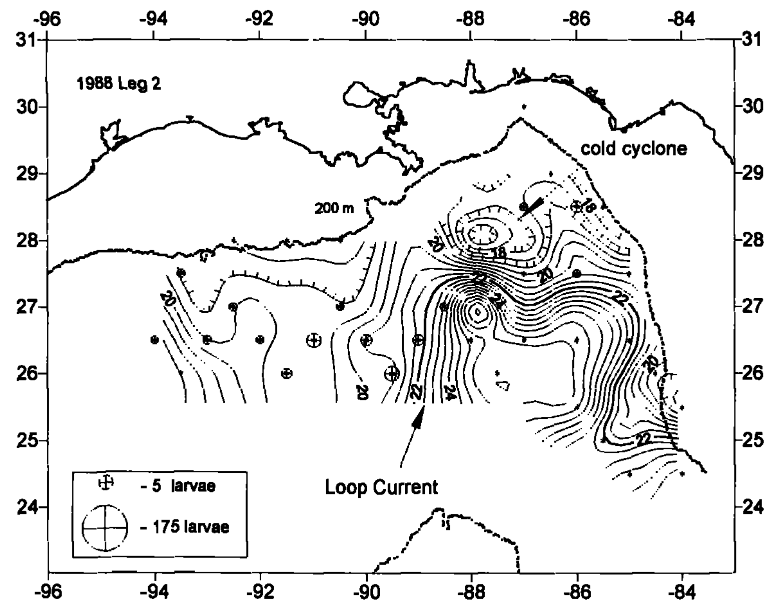

Figure 10

NOAA ship *Oregon II* cruise 173, leg 2, 12 May–26 May 1988. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 5 to 58 individuals per station.

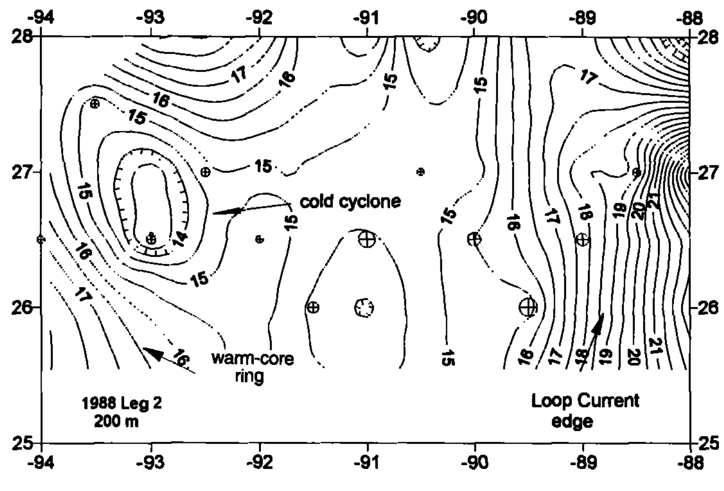

Figure 11

NOAA ship *Oregon II* cruise 173, leg 2, 12 May–26 May 1988. Temperature (°C) of northern Gulf of Mexico at 200 meters. Symbols as in Figure 2. Number of larvae under 10 m^2 ranged from 5 to 58 individuals per station.

The Loop Current and the anticyclonic-cyclonic gyres found in the Gulf of Mexico provide an extensive (and dynamic) frontal habitat, and new production, coupled with coastal production advected off the shelf by ring-ring dipoles (Biggs and Muller-Karger, 1994), may play an important role in maintaining the productivity of these areas. It follows that stability and position of these mesoscale physical features may have a profound impact upon the spawning success of *C. pauciradiatus* and on subsequent recruitment to the stock.

Examination of the survey and transect data indicates considerable within- and among-year variation both in the position, shape, and intensity of the dominant physical oceanographic features as well as in the abundance of larvae and plankton along the front. Variation in the distribution of larvae along the Loop Current is evident and is the result of the interaction of physical and biological processes. As Loop water flows north, it makes an anticyclonic turn to the east and south. The meanders and eddy separations that result can be thought of as forcing mechanisms for ecology and population structure through divergence and upwelling; likewise convergence results in passive accumulation of plankton and larvae and in the formation or dispersion of micro patches of prey.

Cold-core submesoscale (~50 km) cyclonic rings that form along the northern edge of the Loop Current would also be expected to affect both the physical and biological component. In the eastern Gulf, these closed cyclonic domes apparently form as a cold perturbation on the northern boundary of the Loop Current and move south along the Florida shelf (Vukovich and Maul, 1985; Vukovich,

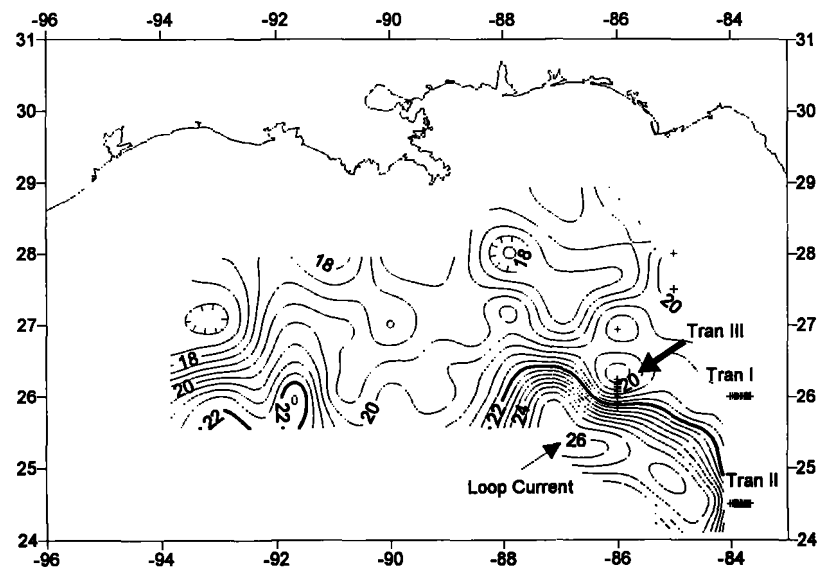

Figure 12
Diagram of transects across the Loop Current (shown as a bold line) in 1987 leg 1.

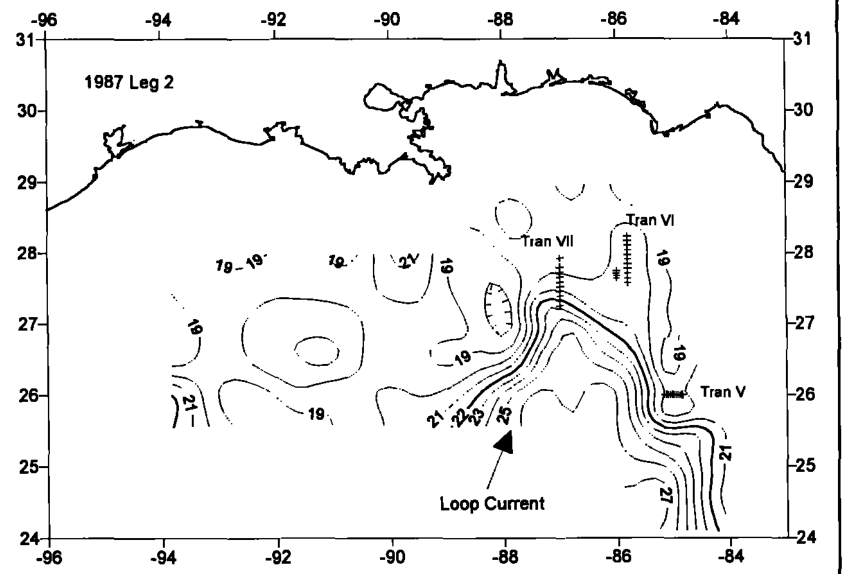

Figure 13
Diagram of transects across the Loop Current in 1987 leg 2.

1986). Large filaments of warm Loop Current water are advected north as much as 300 km in the flow confluence of cold-ring and Loop Current interactions. These cyclonic rings were noted in every survey and the biologically fine structure of one of these was sampled in transect V. Analysis of satellite SST images shows that at least one and often two cold perturbations are generally present along the northern edge of the Loop Current and along the west Florida shelf.

The formation and circulation patterns are not completely understood, but other authors have examined similar features elsewhere. In the western North Atlantic, Pollard and Regier (1990) described the structure and variability of the upper 300-m of fronts. They found that small-scale eddies, tens of kilometers in width, may have vertical velocities as large as tens of meters a day and may approach 50 m/d. Trantor et al. (1983) suggested that in the Tasman Sea, an upwelling-downwelling circulation cell existed at the interface between a cyclonic crescent of cool water and an anticyclonic ring. They reported high concentrations of surface chlorophyll, surface nitrate, and the copepod *Calinoides carcinatus* often associated with upwellings along the edge of a warm core eddy in the cool crescent. Both of these mechanisms act to inject nutrients into the photic zone. However, whether there is a direct effect of these cold-core eddies on larvae and zooplankton of Gulf of Mexico stocks is not clear. Plankton displacement volume and larval abundances are larger, especially in the area between the ring and Loop Current.

Transect V, which apparently bisected a cyclonic ring, had plankton displacement volumes higher than those of any of the other five transects (202 mL/1,000 m). The cold-core rings found to the south are usually associated with increased abundances of both zooplankton and larvae. Maul et al. (1984) found that a cold ring that persisted for several months off the Dry Tortugas was associated with a 3-fold increase in catch per unit of effort of Atlantic bluefin tuna. A cyclonic ring was present in this position in 1983, 1984, and 1988. In fact, in 1983 the highest catches of *C. pauciradiatus* (188 under 10 m^2) were found near this feature along with elevated plankton displacement volume and larval abundance.

Western Gulf of Mexico

The situation in the western Gulf of Mexico is less clear owing to the complexity of the physical regime on mesoscales of 10–100 km, coupled with the fact that fewer ichthyoplankton stations were made in this region. In this region there was no systematic effort to define the features that were present and to sample densely enough in a way that defined coarse scale (<10 km) distributions of larvae. Because surface thermal fronts associated with the warm-core rings are much more diffuse, they were difficult to characterize on the scale of this survey. Several research efforts have been directed to this area in an attempt to understand the complexities of the interaction among large anticyclonic rings generated by the Loop Current, cold dome cyclonic rings, and the continental shelf in the western Gulf of Mexico (Lewis, 1992). Only a few research scientists have dealt with biological components, but they suggest that the cyclonic circulation regions, similar to shelf waters, have a level of primary productivity much greater than that in surrounding oceanic waters (Biggs, 1988). Wormuth (1982) found 1.5–3 times more bulk plankton volume in cyclonic rings than in warm-core rings.

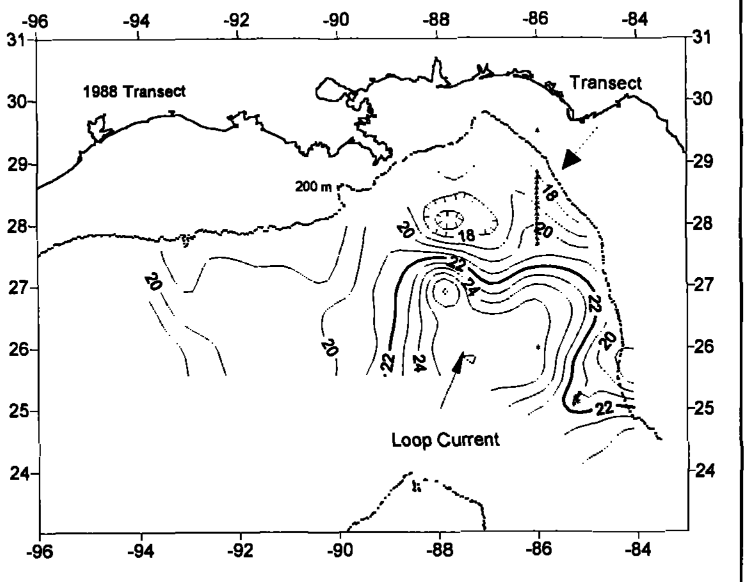

Figure 14

Diagram of transect across the Loop Current in 1988.

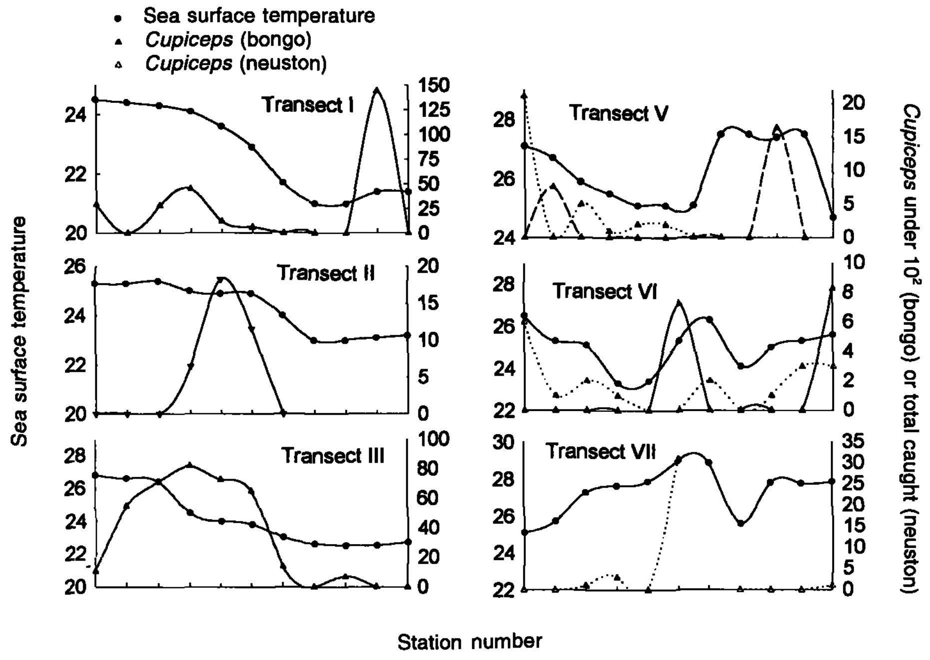

Figure 15

Plots of transects across the Loop Current in 1987. Figure shows SST and number of *C. pauciradiatus* in bongo nets (under 10 m^2) and total number of larvae in the neuston net. Stations were two nautical miles apart.

By comparison, the near surface waters of warm-core rings are oligotrophic and depleted in nutrients; therefore only near the ring edge were there significant concentrations of nitrate at 100 m and elevated primary production in the upper 100 m (Biggs, 1992). Because large anticyclonic rings are oligotrophic, it is unlikely that mobile oceanic predators, such as *C. pauciradiatus* or scombrids, would be found within its interior where prey is presumably scarce.

Despite the paucity of ichthyoplankton stations west of 89° in the Gulf, trends are evident. Foremost of these is that larval *C. pauciradiatus* appear more frequently in collections along the edges of both anticyclonic and cyclonic rings than in tows made inside warm eddies or over the adjacent continental margin. This finding can be seen in 1984 when there were two warm anticyclonic rings separated by a cold cyclonic ring at 26.5°N, 93.5°W (Fig. 3). *Cubiceps pauciradiatus* were distributed primarily around the edge of this cyclone and the leading edge of the incoming warm-core ring to the east.

In 1988 the situation was similar. Most *C. pauciradiatus* larvae were found west of 89°W. Although at 100 m, the Gulf waters west of the Mississippi River seem fairly homogeneous, at 200 m there was considerable structure evident in the water column (Figs. 8 and 10): in leg 1, the edge of a warm-core ring was evident at 26.5°N, 93°W with cooler water to the east (Fig. 9); by leg 2 there was a cold-core ring centered at 26.5°N, 93°W, approximately 83 km in diameter as defined by the 14°C isotherm at 200 m (Fig. 11). These cold-core cyclonic rings may have a life span of 6 months or more, and it is not unusual for there to be a weak temperature signature in the upper 100 m (Hamilton, 1992). In both legs of the 1988 survey west of 89°W, *C. pauciradiatus* were distributed around the edges of the two cold-core rings and in the cooler waters to the east of these features.

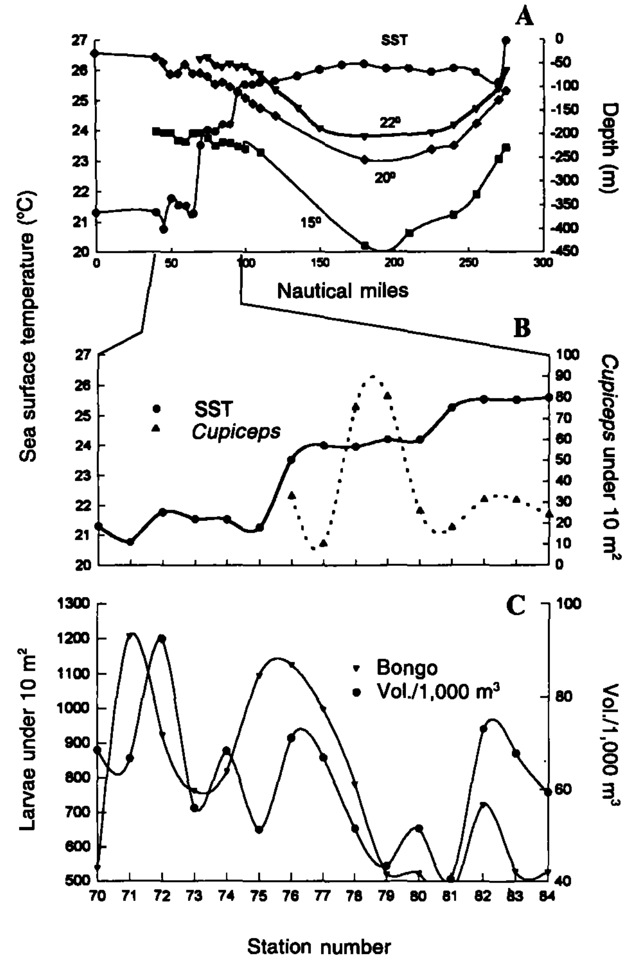

Figure 16

Transect in 1988 south along 86° west, where (A) depicts depth of 15°C, 20°C, and 22°C isotherm and SST, (B) indicates SST and *C. pauciradiatus* at biological stations, and (C) shows total larvae under 10 m² (bongo) and neuston for the same stations as B.

The basic pattern was the same in other years, but oceanographic features could not be as well defined as they were in 1984. First, the large anticyclonic rings often pass south of the survey area and thus are incompletely sampled. Second, after 1984, the number of stations in the western Gulf was reduced, and therefore the physical features could not be as densely sampled as they were the first two years. For a species such as *C. pauciradiatus*, the western Gulf of Mexico may at times provide a variety of frontal habitats, such as those that occurred in 1984. In other years the oceanographic conditions may be less favorable.

Abundance

This year-to-year change in the number and position of mesoscale oceanographic features occurred in both the eastern and western Gulf of Mexico, both within years and between years; the abundance of *C. pauciradiatus* changed similarly. (Fig. 18). *Cubiceps pauciradiatus* larvae were abundant in 1983 but declined thereafter. These changes in abundance are the result of natural mortality because there is no fishery for this species; owing to their pelagic nature, they are taken only occasionally as bycatch by longliners.

Iles and Sinclair (1982) and Sinclair (1988) argued that the existence of a population "depends on the ability of the larvae to remain aggregated during the first few months of life," and that absolute abundance was a function of the physical oceanographic processes of the spawning areas. Population abundance depended on the horizontal size scale of the physical system underlying larval retention. Rothschild et al. (1989) suggested that the physical environment underlies the processes acting on recruitment variability. *Cubiceps pauciradiatus* do not spawn at a specific geographic location as do herring populations, but instead have spawning sites that appear to be tied to dynamic oceanographic features, namely to the Loop Current and its associated rings. Larvae are spawned at the frontal zones regardless of geographic position.

The physical oceanographic processes acting on the spawning sites of *C. pauciradiatus* change im-

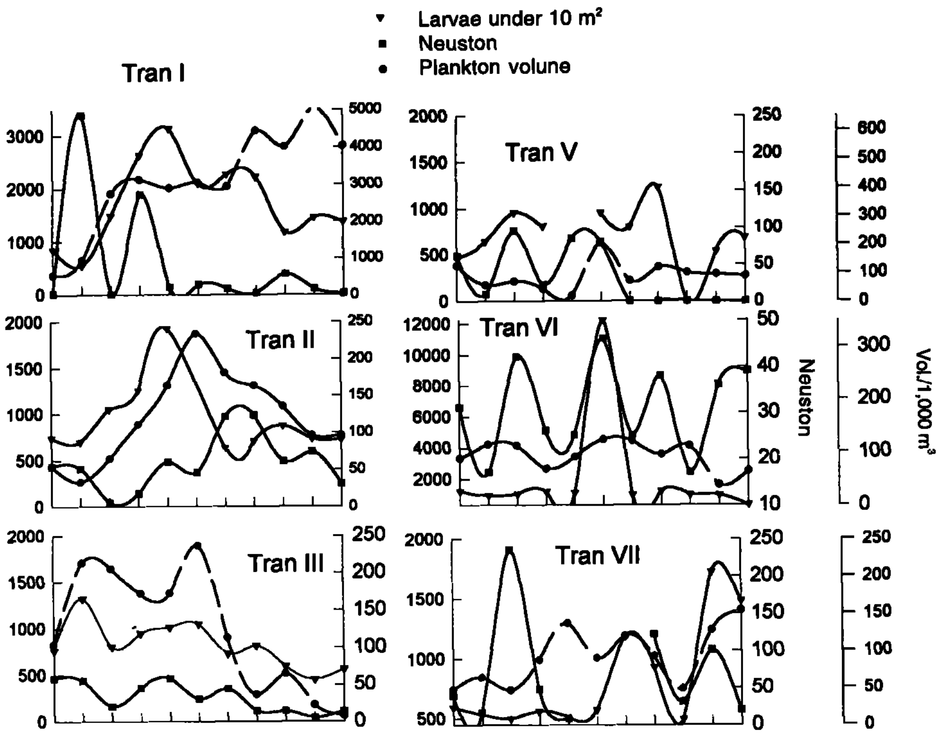

Figure 17

Transects showing (A) SST vs. *C. pauciradiatus*; (B) SST vs.1) fish larvae under 10 m^2 from the bongo net, 2) total fish larvae from the neuston net, and 3) plankton displacement volume from the bongo net.

mensely from year to year and within time scales on the order of weeks. Figure 1 shows the range in variability of the northern perimeter of the Loop Current over the period studied. Not only do the size and north–south position of the front vary, but stability, length, shape, and intensity of the frontal system vary as well.

Major changes in position may occur within time scales of weeks. In 1986 and 1987, the Loop Current was positioned south of 26°N during the first leg of the survey. In both years the front pushed north before the second leg. In 1987 it moved almost 100 km north in 2 weeks. In other years, 1983, 1984, and 1988, the Loop Current was already at 27°N when the survey began. Over the years studied, the length of the northern perimeter of the Loop Current front ranged from 880 km in 1988 to 182 km in 1986 (as measured along the 22°C isotherm in the area sampled). Length of this front in each year is summarized in Table 2. However, length and position in itself says little about the frontal interface and biological response to hydrodynamic processes.

Larval *C. pauciradiatus* were most numerous in both the eastern and western Gulf of Mexico in 1983. In this year the Loop Current had pushed north in the winter and despite shedding a ring, had been stable for almost 6 months prior to the survey. Plankton displacement volumes were also high, averaging 100 mL/1,000 m^3 in the eastern Gulf and 130 mL/1,000 m^3 in the western Gulf.

Table 2

Length of the Loop Current as measured at the 22° isotherm at 100 m and number of *C. pauciradiatus* larvae caught at grid stations (under 10 m^2).

Date	Leg	Length in kilometers	No. of larvae under 10 m^2
1983		647	1,445
1984		332	258
1986	1	182	179
1986	2	299	124
1987	1	564	170
1987	2	681	44
1988	1	697	219
1988	2	880	307

By remaining in a relatively stable position, the biological components have time to respond to physi-

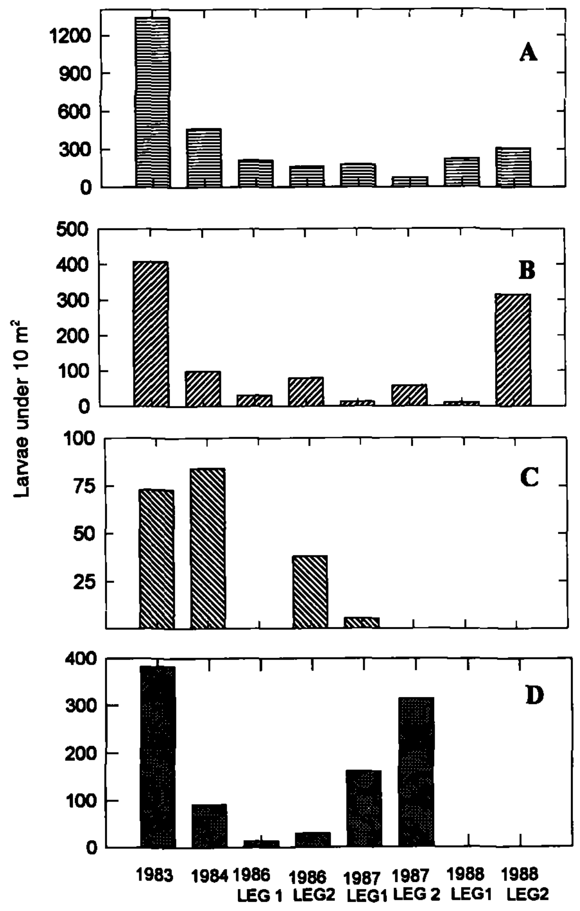

Figure 18

Abundance (number under 10 m^2 bongo) of three species (**A**) *C. pauciradiatus*, (**B**) *Thunnus thynnus*, (**C**), istophorids, and (**D**) *Ariomma melanum* by year and leg.

cal input of upwelling regions, and adults will be concentrated by increased abundances of prey (Atkinson and Targett, 1983). Turbulent mixing is increased at frontal areas; therefore, formation and dissipation of prey patches will also be affected. A recent model by Davis et al. (1991) shows that formation and abundance of microscale patches (<10 m) of prey can change the growth rate of larvae by up to 25%. Frontal regions, with convergent and divergent zones that result in biological gradients such as those found in the transects across the Loop Current, could be expected to lead to patchiness both across and along the front. This model predicts that even small variation in growth rates due to turbulence and patchiness can lead to large fluctuations in recruitment.

In contrast, the years following 1983 were characterized by a less stable Loop Current structure, and fish abundances were considerably reduced. In 1984 the Loop Current did not move north of 27°N until late March, only one month before the survey began (Fig 3). In 1986 the Loop was positioned well to the south, and little frontal habitat was available in the Gulf of Mexico to the spawning population (Figs. 4 and 5). The pattern was similar in 1987 and 1988 (Figs. 6–10). In both years the 22°C isotherm at 100 m began well to the south of 27°N, before pushing north in the spring.

It is not clear what factors are the important ones in driving such variations in abundance. Variance of fish populations is a natural occurrence and the subject of many studies on recruitment. However, the pattern of abundance during these five years was not unique to *C. pauciradiatus*. Aggregation of bluefin tuna (*Thunnus thynnus*), and billfish (Istiophoridae) are also closely tied to the location of thermal fronts (Roffer, et al., 1994). These unrelated pelagic species showed similar trends in larval abundance with peaks in 1983 and with decreases thereafter. *Thunnus thynnus* larval abundance closely paralleled *C. pauciradiatus* abundance, even showing an increase in 1988. *Ariomma melanum*, another stromateoid, showed similar trends in larval abundance (Fig. 18). These fish are benthopelagic over the continental margin, and most adults are taken in bottom trawls at depths of 225–480 m. This certainly indicates that the variation in the Loop Current position and stability may impact the abundance of a wide range of species and not just large pelagic predators such as bluefin and billfish.

Although stability and size of the frontal system are important to frontal species, other physical-biological interactions take place within the system on a variety of scales. The importance of each interaction will vary on time scales ranging from months to days because of the inherent nature of frontal systems. Rothschild et al. (1989) states that it is necessary to consider the "mechanisms of population stabilization at each phase of the life history." Although it has sometimes been possible to tie population fluctuations to a certain physical event (Harris et al., 1992), it is more often the case that we are faced with a much more multidimensional problem.

That large-scale oceanographic processes have a major influence on the abundance of fish stocks has been recognized by a variety of authors. Harris et al. (1988) reported on several species and presented evidence that large-scale changes in the distribution of southern bluefin tuna result from large-scale changes is SST. Koslow (1984) argued that large-scale physical forcing rather than ecological and biological interactions is the dominant factor controlling the recruitment of several northwest Atlantic fisheries. Basin-scale circulation patterns may be the driving influence on the distribution of larval *C. pauciradiatus* and other pelagic species.

In conclusion, this study indicates that larval *C. pauciradiatus* are a frontal species, concentrated at temperature fronts throughout the Gulf of Mexico. This is an important concept that needs to be recognized. Fronts and eddies are fundamental to the world oceans, and they are the only coherent feature in the Gulf of Mexico. The Loop Current itself acts as a zoogeographic barrier separating the oceanic and shelf species (Richards et al., 1993). Although it is not surprising that certain species have evolved to take advantage of this environment, it means that frontal species must be recognized as such in order to sample and manage these stocks effectively.

Spawning-stock biomass estimates are an important consideration in the management of pelagic species. These are inferred from the abundance of larvae taken at fixed stations (CalCofi, SEAMAP). If the target species is tied by life history parameters to a frontal system, then its apparent abundance will be affected by the extent of the frontal system found within the sampled area. For instance, if the frontal system within the area sampled is extensive, higher numbers of larvae are expected. Likewise, if only a small portion of the frontal system is sampled, then numbers are expected to be low, as was the case in 1986. Thus, the lower abundance estimates do not necessarily mean that there were fewer fish spawned that year but, rather, may indicate that they were spawned along the front outside the area sampled.

Accurate abundance estimates are a problem in the Gulf of Mexico because only the northern and eastern Gulf are sampled. The boundaries of the Loop Current pass through the Exclusive Economic Zone of the United States, Mexico, and Cuba, and the large anticyclonic rings often pass south of the area sampled. In addition, there is considerable variation in abundance along a temperature front. It is important to note that the presence of a frontal region in itself does not necessarily constitute a favorable habitat, but favorable spatial and temporal patterns of the front may determine the abundance of the larvae on a basin scale.

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